UNIVERSITY OF BELGRADE

FACULTY OF PHILOSOPHY

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Ecology and Ethology of human populations living in the Danube Gorges ca. 9500 – 5500 BC.

Bioarchaeological perspectives on dietary behaviors and adaptive strategies during the Mesolithic and Neolithic Transformations

Doctoral Dissertation

Belgrade, 2020

УНИВЕРЗИТЕТ У БЕОГРАДУ

ФИЛОЗОФСКИ ФАКУЛТЕТ

Camille A. de Becdelièvre

Екологија и етологија популација у Ђердапу око 9500-5500 пре н.е.

Биоархеолошке перспективе навика у исхрани и стратегија прилагођавања током мезолитско-неолитских трансформација

докторска дисертација

Београд, 2020

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Date of defense:

"I was born by the river in a little tent
Oh and just like the river I've been running ev'r since
It's been a long time, a long time coming
But I know a change gonna come, oh yes it will"

Sam Cooke, *A Change is Gonna Come*, 1963

Ranging between natural sciences and humanities, Bioarchaeology does suffer – and also significantly benefit – from the subjectivity of the researcher. This work hence reports one leg of a personal journey, started years ago along the Danube river in the attempt to study the behavioral and morphological adaptations of Danube Gorges inhabitants during the Mesolithic-Neolithic Transformations. Many paths followed are only mentioned in this dissertation, which I hope to be the departure for further narratives, new ways of researches and collaborations on this thought-stimulating topic. The trip would not have been possible without the help, advices, trust and support from many – colleagues, friends and family.

I would first like to thank to my supervisor, Pr. Sofija Stefanović for introducing me with this research area, for providing me the opportunity to work on the Danube Gorges osteo-anthropological material, for her guidance and for all her ideas about the Neolithic Demographic Transition, birth conditions and motherhood during prehistory, without which this work would not have been possible. She offered me a doctoral position within the frame of the EU-funded BEAN project (FP 7 BEAN - Bridging the European and Anatolian Neolithic, Grant Agreement N°289966), which provided the financial support to all analyses performed in this thesis, helped my colleague Jelena Jovanović and I with writing the Prefert project (Prehistoric Fertility, length of lactation during the Mesolithic and Neolithic of South-Eastern Europe. Bilateral project CNRS, France and Ministry of Science, Serbia), which established the collaboration that allows for performing biochemical analyses, and she supported me in getting the findings that enabled me to pursue researches during the last years (Premières sociétés agricoles, pratiques alimentaires et stratégies de sevrage des enfants ca 10000-5000 av. n.è.: conséquences biologiques, sanitaires et morphologiques; Fondation Nestlé France, Bourse 2017).

I also want to express my sincere gratitude to Dr Gwenaëlle Goude whose help, training, and scientific advices have been of crucial importance for developing my skills in stable isotope analyses and in the field of Paleodiet. Her critical eye and insightful comments have significantly improved the quality of this dissertation. I am particularly grateful to her for not letting me give up, for her constant encouragements, and for sharing so much of her enthusiasm and energy in science. Un grand merci Gwenaëlle. My heartfelt thanks also go to Dr Jelena Jovanović with whom I shared this scientific journey from the very beginning; she has been helping me in all aspects of my research, has always been a great friend and support in all circumstances. Well beyond scientific data, we collected together valuable memories throughout all Europe. Hvala lepo Jelena.

I am also deeply indebted to Marko Porčić, who taught me theories and methods in Paleodemography and (tried to) introduced me with statistical analyses applied to Archaeology. His view on Evolutionary Archaeology has been an important source of inspiration and I am particularly grateful for all the time he spent to help me in analyzing and interpreting the bioarchaeological information we collected. I am very glad that he accepted to be part of this dissertation committee. I am also grateful to Pr. Vesna Dimitrijević and Dr Ivana Živaljević for the useful discussions about the archaeozoological record from the Danube Gorges and for letting me sample some faunal remains. My grateful thanks go to all my colleagues from the Laboratory for Bioarchaeology at the University of Belgrade, with whom I have shared office during years. The assistance of Marija Marin and Maja Miljević with the work on the osteoanthropological sample was particularly helpful and very appreciated. A special thanks to Mina and Jelena Amzirkov for their tremendous help on bibliography. I also wish to thank Dr Andrej Starović, from the National Museum in Belgrade, for letting me examine and sample human remains from the Early Neolithic site of Ajmana.

I wish to acknowledge all the members of the BEAN team and more particularly Pr. Joachim Burger for his coordination of the project, as well as Pr Stephen Shennan and Pr Jean-Pierre Bocquet-Appel for the influence that their works on the Neolithic Transition had on my research. My presence in the BEAN project has been made possible, in part, by Jean-Pierre; I wish he could have read this thesis. I am grateful to Pr. Barbara Horejs and Dr Christina Papageorgopoulou for accepting to read and to evaluate my research. Thank you to my colleague and friend Dr Zuzana Hofmanová, for our productive exchanges of genetic, isotopic and contextual information concerning Central Balkans Mesolithic and Neolithic sites.

Je suis également reconnaissant envers le Pr Jean-Pierre Bracco ainsi qu'envers le Dr Estelle Herrscher pour m'avoir laissé accéder à la plateforme de biochimie et à la bibliothèque spécialisée du laboratoire LAMPEA (UMR 7269) à la Maison Méditerranéenne des Sciences de l'Homme à Aix-en-Provence dans le cadre de la collaboration permise par le projet Prefert. Je remercie particulièrement Estelle Herrscher, pour ses conseils concernant l'approche isotopique des pratiques d'allaitement et de sevrage en contexte archéologique, ainsi que le Dr Leïa Mion pour toutes les discussions que nous avons pu avoir concernant l'interprétation des données isotopiques. J'exprime également ma gratitude au Dr Pierre Magniez pour m'avoir permis d'intervenir, avec Leïa, dans plusieurs séminaires destinés aux étudiants du master d'Archéologie.

De même, je souhaite remercier les membres du laboratoire ADES (UMR 7268), et particulièrement le Dr Michel Signoli pour leur accueil dans les locaux de l'université d'Aix-Marseille. Un très chaleureux merci aux Dr Aurore Schmitt et Dr François Marchal. Aurore, merci de m'avoir régulièrement redonné du courage et soutenu, François, merci pour tes leçons sur la géologie du quaternaire dans les Ardennes. Merci également à Aurore et au Dr Yann Ardagna de m'avoir permis d'intervenir auprès des étudiants du master d'Anthropologie Biologique. Je suis aussi reconnaissant envers Bérangère Saliba Serre pour avoir toujours répondu à mes questions – souvent chronophages – concernant le traitement statistique des données. Les doctorantes et jeunes chercheuses du laboratoire – Célia Kamel, Frédérique Lagacé, Alexia Lattard, Avril Meffray, Emeline Sperandio, Emeline Verna – m'ont rendu bien plus agréable la rédaction de ce travail.

Je tiens également à remercier le Dr Stéphane Rottier pour son appui lors de mon entrée dans le projet BEAN et son aide dans le cadre du projet collaboratif Prefert, et le Dr Mélie Le Roy pour son aide sur la Bioarchéologie des jeunes enfants et pour tous nos échanges qui, j'espère, dureront encore longtemps.

Ce travail fut enfin rendu possible par le soutien constant et l'aide considérable de mes amies Marie Perin et Charlotte Parent, qui m'ont permis de tenir la fin, la fin-fin, la fin-fin-fin et aussi la toute fin. J'ai également une pensée pour mes amis, ceux de longues dates, ou, ceux, que j'ai connu au cours de cette thèse, de Cherbourg (Chloë, Margaux, Audrey), Tours (Fanny), Bordeaux (Anne, Florence, Raphaëlle, Eva, Jéhan, Mélissa), Belgrade (Jelena Bulatović, Mladen Jovičić, Tanja-Maïa-and-Jelena), Aix et Marseille (Anaïs, Laudine, Christian, David, Vincent, Roxane, Audrey, Mégane) ou d'ailleurs (Marilou, Ysa, Gaëlle).

Pour finir, un immense merci à toute ma famille et particulièrement à mes parents, Olivier et Chantal, pour m'avoir soutenu et supporté pendant ces nombreuses années en tant que doctorant (et les autres aussi) ; merci Cécile, Florent, Yohan, Carole, Marc, Colette, Patrick, Betty, Coline, Lise, Laure et Clément d'avoir été là.

A mon cousin Vincent.

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Abstract

During the Epipaleolithic-Mesolithic periods, groups of foragers reduced their residential mobility and modified their subsistence strategies which gradually led to the farming system at the onset of the Neolithic. The archaeological complex of the Danube Gorges provides a valuable context to examine Mesolithic-Neolithic behavioral adaptations because of its continuous occupation and unique bioarcheological record. This thesis reconstructs dietary strategies by conducting new multi-isotopic analyses on human tissues in order to better apprehend: the relationships between foragers' subsistence adaptations and socio-environmental changes, the ways of diffusion of new dietary behaviors and their bio-demographic consequences. Stable isotope ratios are compared chrono-geographically and interpreted in the light of archaeological and biological contextual information.

Results point to the increasing importance of anadromous fish in the subsistence from 7000 BC in a context of intensified occupation along the riverbanks. After 6200 BC, the local foragers were in direct contacts with Early Neolithic communities settled downstream, who favored the consumption of terrestrial resources probably from domestic species. Some first-generation migrants display stable isotope values characteristic of a terrestrial diet, while their descendants likely adapted to the local means of subsistence oriented toward fishing. Hence, the Neolithization of the Gorges encompasses complex behavioral interactions and gradual socio-cultural changes within a frame of subsistence continuity. Important differences distinguish the children feeding practices of the foragers of the Inner Gorges and of Early Neolithic individuals buried downstream. These different parenting strategies may have influenced the demography of Early Neolithic communities and could be amongst the explanations for the Neolithic Demographic Transition.

Keywords: Bioarchaeology, Mesolithic, Neolithic, Danube Gorges, diet, breastfeeding and weaning, stable isotopes, sulfur

Scientific field: Archaeology

Scientific subfield: Physical Anthropology

UDC number: 574.3(497.11 Đerdap)"633/634"(043.3)
903.28(497.11 Đerdap)"633/634"(043.3)

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Сажетак

Током епипалеолита и мезолита групе ловаца-сакупљача смањују мобилност и почињу да мењају своје прехрамбене навике, што постепено доводи до развоја пољопривреде почетком неолита. Археолошки локалитети у Ђердапу пружају драгоцен контекст за истраживање адаптација људи током мезолита и неолита, будући да су овде обале Дунава биле континуирано насељене, као и због јединственог биоархеолошког материјала. Ова теза бави се реконструкцијом стратегија исхране применом анализа стабилних изотопа узоркованих из људског ткива у циљу бољег разумевања: везе између адаптације исхране ловаца-сакупљача и промена у природном и социјалном окружењу, путева ширења нових образаца прехране и њихових биодемографских последица. Добијене вредности стабилних изотопа људи поређене су хронолошки и географски и интерпретиране у светлу археолошких и биолошких података.

Резултати указују да око 7000 г. п.н.е долази до промене у обрасцима исхране локалног становништва која се огледа у повећаној употреби анадромних врста рибе, што се поклапа са интензивним насељавањем уз обале Дунава у Ђердапу. Након 6200 г. п.н.е ловци-сакупљачи у Ђердапу долазе у директни контакт са ранонеолитским заједницама које су живеле низводно, претежно у области Кључа, чија исхрана се базирала углавном на копненим изворима хране, углавном доместикованих биљака и животиња. Неки од миграната прве генерације имају вредности стабилних изотопа које указују на конзумирање копнених извора хране, док су њихови потомци усвојили локални начин прехране, где је риба имала важну улогу. Дакле, неолитизација Ђердапа обухвата комплексне, постепене интеракције и социо-културне промене у контексту континуитета у исхрани. Резултати показују и да су постојале различите стратегије прехране деце ловаца-сакупљача у унутрашњости Ђердапа у односу на исхрану деце ранонеолитских заједница које су живеле низводно, у области Кључа. Ове различите стратегије родитељства могле су утицати на демографију ранонеолитских заједница и бити једно од објашњења неолитске демографске транзиције.

Кључне речи: биоархеологија, мезолит, неолит, Ђердап, исхрана, дојење, дохрана, стабилни изотопи, сумпор.

Научна област: Археологија

Ужа научна област: Физичка антропологија

УДК број: 574.3(497.11 Đerdap)”633/634”(043.3)
903.28(497.11 Đerdap)”633/634”(043.3)

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1. Introduction: Human Adaptive Strategies during the Foraging-to-Farming Transition.

> The great events of world history are, at bottom, profoundly unimportant. In the last analysis, the essential thing is the life of individual. This alone makes history, here alone do the great transformations take place, and the whole future, the whole history of the world, ultimately spring as a gigantic summation from these hidden sources in individuals".
>
> CG Jung, The Meaning of Psychology for Modern Man, 1934

Despite a high genetic unity, humans feature a considerable phenotypic diversity, expressed through several levels of plasticity: morphological, physiological, and behavioral. Behavioral flexibility – the set of organized actions by which we directly affect our relationship to the environment – is probably the fastest way we adapt (Smith and Winterhalder 1992; Krebs and Davies 1997; Smith 2000; Alcock 2003; Levitis et al. 2009). Although conditioned by different aspects of our biology (genetic, morphology and physiology), these behavioral adaptations can be socially shared and culturally reproduced, at a transmission rate which is quite unique in comparison with most other animal species. During our history as Hominin, we increasingly colonized different ecological niches, adapting our habitual behaviors to the environmental constraints, but also utilizing these behavioral adaptations to shape the environmental conditions according to our morphological and physiological requirements, always seeking for the best adaptive trade-off (Laland et al. 2001; Laland and Brown 2006; Wells and Stock 2007). Our capacity to accommodate new habitats and to enter new ecological niches notably favored dietary flexibility, decreasing in turn physiological specialization, and, through positive feedbacks, contributing to promote the selection of traits that further predispose for continuous niche-probing (Diamond 1997; Wells and Stock 2007; Leonard 2002, 2010; Gross 2017). It has been considered that, from one niche to another, these series of behavioral adaptations and processes of evolution collectively contributed to "make" us Humans (Klein 2009).

Within Anthropology, the field of Eco-Ethology (Human Behavioral Ecology) of past populations seeks to explain the bio-cultural diversity by reconstructing habitual behaviors (Ethology) in the past from the contextual analyses of available cultural, biological and environmental evidence, and by inferring the adaptive strategies developed in relation to the social or natural environments (Ecology) (Broughton and O'Connell 1999; Shennan 2002; Kenett and Winterhalder 2006; Bird and O'Connell 2006; Gremillon and Piperno 2009; Cannon and Broughton 2009). To analyse human adaptations, evolutionary ecologists usually assume that individuals mostly relate to their environment in ways that would enhance their fitness (i.e. their reproductive success), taking advantage both of socio-ecological opportunities and of culturally transmitted information (Smith and Winterhalder 1992; Smith 2000; Winterhalder and Smith 2000; Mulder and Shacht 2012). The study of dietary flexibility and subsistence adaptations – a driving force for our evolution (e.g. Leonard 2002, 2010) – is central to this perspective. Diet is indeed at the direct interface between our biological requirements (the physiology of nutrition), environmental possibilities (resources availabilities), social options (sharing and norms), and cultural transmissions (learning of subsistence activities). For the anthropologist Counihan, Food can be seen as "a many-splendored thing. Essential to biological survival, it takes on myriad meaninds and roles in the ongoing constitution of society and culture. As humans construct their relationship to nature through their foodways, they simultaneously define themselves and their social world" (Counihan 1999:23). The now-famous sentence "dis-moi ce que tu manges, je te dirais ce que tu es" [Tell me what you eat and I will tell you what you are], (Brillat-Savarin 1826), can hence be extended to the bio-cultural study of human societies and populations. Reconstructing ancient dietary behaviors within past social and natural environments provides thus a way to infer essential adaptations related to human-environment relationships (e.g. diet breadth and prey choices; procurement techniques and seasonality), to social organization (e.g. resources distribution; children feeding practices; food taboos and rituals), and to patterns of cultural transmissions (e.g. cooking cultural habits). Ultimately, it represents a means to document some evolutionary mechanisms behind these adaptations, their biological costs and benefits (e.g. dietary adaptations and selective pressures).

The development of the sedentary and agro-pastoral niche during the Early-Middle Holocene (the current geological period, with warmer climate) and its subsequent spread to most anthropized environments represents such a series of behavioral adaptations, where the evolution of subsistence activities deeply affected our natural and social environments, and where cultural innovations influenced several aspects of our own Biology (e.g. Rindos 1984; Wilson 1992; Leach 2003; Smith 2007; Zeder 2009; Stock and Pinhasi 2011; Rowley Conwy and Layton 2011). As Humans, we spent more than 95% of our History being mobile hunter-gatherers (Lee and DeVore 1968). From the end of the Late Pleistocene (after the last glaciation, ca 12.500 BC) and the beginning of the Holocene (ca 9700 BC), some groups of foragers increasingly reduced their residential mobility and modified various aspects of their subsistence strategies, which gradually led, in several regions of the world, to an increased control over the (re-)production of plants and animal species (e.g. Wilson 1992; Price and Gebauer 1995; Byrd 2005; Kennett and Winterhalder 2006; Cohen 2009; Zeder 2009; Rowley-Cowny and Layton 2011). The transition(s) toward the sedentary and agro-pastoral way(s) of life – so-called "the Neolithic Transition" – induced major changes in the structure of human societies and paved the way for a runaway technological development during the Holocene period (Diamonds 1997; Scott 2018). Everywhere in the world, the development of agro-pastoral activities has been associated with a major population growth due to an increased female fertility, perhaps related to metabolic adaptations, to changes in parenting strategies and children feeding practices (Bocquet-Appel and Bar-Yosef 2008, Bocquet-Appel 2011). This population growth likely stimulated the expansion of the agro-pastoral way of subsistence to a broad range of environments, involving the migrations of farmers into regions where hunter-gatherers had constructed their own niche and resulting in local adaptations of the farming niche (e.g. Bellwood 2005, 2008, Bocquet-Appel and Bar-Yosef 2008; Fort 2012, 2015). While enhancing human fitness, the farming transition had a counter-cost: an overall decline in health status which primarily affected children (Cohen and Armelagos 1984; Larsen 2003; Cohen 2008; Lambert 2009). Besides, these series of behavioral adaptations variously impacted our morphology and physiology and exerted new selective pressures on our genome (e.g. Larsen 1995; Leach 2003; Pinhasi et al. 2008; Burger et al. 2007).

Therefore, by reconstructing dietary behaviors in contexts associated with the development of the sedentary and agro-pastoral niche, one shall contribute not only to clarify the chronology of the transition(s), but also to explore the causal relationships between dietary adaptations and other changes in the natural and social environments (e.g. climate fluctuations, sedentism, social structure), to clarify the horizontal and vertical patterns of transmission of subsistence innovations (e.g. migration or cultural diffusion, feeding practices and inter-generational adaptations) and to document, on the long term, the bio-demographic costs and benefits of the shift toward the farming subsistence (e.g. increased fertility, consequences on health and physiology). The contextual study of human organic remains with methods from Bioarchaeological sciences, and particularly the analysis of biomolecular markers such as stable isotopes ratios now provides a direct means to reconstruct dietary behaviors at the population and at the (intra-)individual levels (e.g. Ambrose and Katzenberg 2002; Lee-Thorp 2008; Stock and Pinhasi 2011; Zvelebil and Weber 2013; Beaumont et al. 2015; Katzenberg and Waters-Rist 2018; Larsen 2018). When cross-linked with other bioarchaeological indicators or contextual information, the interpretation of stable isotope ratios allows for examining broad changes and differences in terms of subsistence, and for considering the dietary specifies which could be related to the biological and/or social identities of the deceased. The development of intra-individual methods of analyses now makes also possible a thorough examination of children feeding practices, nutritional health, and dietary transitions experienced over a lifetime, enabling thereby bioarchaeologists to better appreciate the relationships between individual dietary choices and the ways of subsistence of a population or bio-demographic adaptations.

The Mesolithic and Neolithic sites of the region of the Danube Gorges in the Central Balkans, mainly occupied between the 10th-6th millennium BC, document the gradual behavioral adaptations of a group of foragers who built more permanent settlements along the riverbanks, practiced hunting, fishing and dogs' breeding, constructed elaborated architectural achievements, created unique forms of artistic and symbolic expressions, and eventually started to produce pottery and to practice animal husbandry; at the earliest Neolithic in the region, some migrants, mostly descended from Near East Neolithic communities, were buried with the local inhabitants of the Gorges (e.g. Srejović 1969, 1972; Jovanović 1969; Radovanović 1996a; Voytek and Tringham 1989; Roksandić 1999; Boroneanţ 2000; Boroneanţ and Dinu 2006; Borić and Dimitrijević 2007; Bonsall et al. 2008; Borić 2011; Borić and Price 2013; Hofmanová 2017; Mathieson et al. 2018). With a deep temporal sequence of occupation, a substantial human osteo-archaeological assemblage, and high-resolution contextual information concerning subsistence, settlements, symbolic behaviors and Human Biology, these sites now provides the opportunity to go beyond the diachronic reconstructions of ways of subsistence, and to explore, with bioarcheological methods, how the Mesolithic foragers adapted their dietary strategies and shaped their niche, how children feeding practices and maternal nutritional choices were adjusted to changing natural and social environments, or how locals and migrants responded to the new ecological and nutritional possibilities and transmitted their choices.

This first chapter introduces the broad context of the Foraging-to-Farming Transition and the general bioarchaeological approach of this study, details Epipaleolithic-Mesolithic Transformations in Western Eurasia, the development of the agro-pastoral way-of-life and its spreads to South-Eastern Europe, and finally presents the specific aims and the structure of this thesis.

1.1. The Sedentary and Agro-pastoral Transition(s): definitions and approach

1.1.1. Hunters in Transition: towards sedentism and food production

The "Neolithic Revolution"

The "Agricultural Transition", or "Neolithic Revolution", occurred independently in several regions of the world upon a time span of several thousands of years. The term "Neolithic" – literally the New Stone Age – was coined by J. Lubbock (1865) in opposition to the "Paleolithic", and in reference to the changes in terms of technology associated with this period and usually related to agro-pastoral practices (e.g. polished stones, ceramics). The transition to the Neolithic was further designated as a "Revolution" (e.g. E. Desor quoted in Howart 1875) and spread by Gorden Childe (1936) in order to emphasize the importance of the economic and socio-cultural shift induced by the new subsistence system; according to G. Childe (1951:34-35) " when the tools [...] are considered [...] in their totality, they may reveal much more. They disclose not only the level of technical skill [...] but also their economy [...]. The archaeologists's ages correspond roughly to economic stages. Each new "age" is ushered in by an economic revolution [...]". The earliest evidence for grouped and permanent settlements associated with an increased plant selection and stockage are related to the Near East during the climate oscillations of the end of the Pleistocene (ca 12.500-9500 BC; Bar-Yosef and Belfer Cohen 1989; Moore and Hillman 1992; Bar-Yosef 1998; Byrd 2005). At the beginning of the Holocene in these regions of the Levant (Pre-Pottery / Aceramic Neolithic, ca 10.000-7000 BC), the systematic selection, stockage and inter-breeding of some plant and also animal species resulted in their morphological adaptations: it is the case of some species of cereals (einkorn, emmer, bread wheat, naked barley, hulled barley), of pulses (pea, lentil, faba bean, bitter and common vetch, flax and poppy), and of ungulates (cattle, pig, sheep and goat) (e.g. Kuijt and Coring-Morris 2002; Vigne et al. 2005; Zeder 2008; Belfer-Cohen and Goring-Morris 2011; Vigne 2011; Willcox 2014). Other primary centers of domestication appear during the better climate conditions of the Early-Middle Holocene and are also associated with the independent domestication of a range of different taxa (e.g. ca 9500-6000 BC in China, 7000-5000 BC in New-Guinea, 5000-3000 BC in South and Meso-America, after 3000 BC in Sub-Saharian regions; e.g. Bellwood 2005; Demoule 2008). The rise of food production and storage of surpluses has been considered as the trigger for major changes in social organization, the emergence of property ownership, social hierarchy, task specialization, encouraged social division like gender inequalities and accelerated the pace of technological innovations (e.g. Diamond 1997). Concerning the Near East region at least, the Neolithic transition has also been associated with a modification of different aspects of the symbolic repertoire perhaps reflecting major changes in social organization, a conceptual shift in the representation and organization of the world which may have preceded and favored the shift to domestication (e.g. Cauvin 1994; Hodder 2001).

The Neolithic Revolution before the Neolithic Revolution

Considered as the oldest core area for the Neolithic transition, the Near Eastern primary center of domestication is yet not the first time that humans culturally exerted a selective pressure on other species; for instance dogs were domesticated from a wolf ancestor during the Upper Paleolithic (at least before 15.000 BC in Eurasia) independently from the domestication of other animal species (e.g. Dimitrijević and Vuković 2015; Freedman et al. 2016 and 2017). Besides, while sedentism accompanies the development of farming and stockbreeding in the Near East, different regions yielded evidence for a substantial reduction in residential mobility, independently from the adoption of the food production system (e.g. Price and Brown 1985; Voytek and Trigham 1989; Nespoulous 2009; Jordan and Zvelebil 2011). Similarly, although some important technological innovations – such as ceramics or ground stones – have originally been associated with the development of the new means of subsistence and to the intrinsic definition of the "Neolithic" period[1], it is today accepted that they also appeared independently from the shift to food production at different parts of the world, which may have enabled some communities of Late Pleistocene - Early Holocene hunter-gatherers to intensify the exploitation of certain resources (e.g. Barnett and Hoopes 1995; Derevianko et al. 2004; Nepoulos 2009; Huyscom et al. 2009; Wu et al. 2012). Hunter-gatherers did also develop active processes of niche constructions – such as concentration of wild plants into useful stands, small-scale cultivation, burning of vegetation to encourage useful plants, or various forms of specialized hunting – which have been collectively termed "low-level food production" (Rowley-Conwy and Layton 2011). In this perspective, the farming way of life can be seen as one amongst many responses to particular environmental possibilities and social conditions in the process of niche construction, and one may then wonder what truly defines the shift to the farming system. In fact, it can be considered that only the culturally-induced morphological adaptations of a range of species–due to their particular behavioral and genetic characteristics–during the Holocene, has led to a series of inter-related modifications of the natural and social environments, which may characterize the agro-pastoral niche.

1.1.2. The Agricultural Demographic Transition and the expansion of the farming niche

A Demographic Boom

This series of transformations occurred together with a major event of population increase, the so-called "Neolithic Demographic Transition" (Bocquet-Appel 2008, 2011; Cohen 2009; Downey et al. 2014). In a few thousand years, the world population took off under a significant increase in females' fertility, evidenced at different independent centers of domestication by a

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[1] "Neolithic", etymologically the "New stone age"

substantial increase in the number of children in comparison with the number of adults within cemeteries (Bocquet-Appel 2008, 2011). Whether the demographic expansion has stimulated the subsistence shift or was a primary consequence of agro-pastoral innovations, has long been debated (e.g. Malthus 1973 [1803]; Boserup 1965; Cohen 1977, 2009; Bocquet-Appel and Bar-Yosef 2008; Gignoux et al. 2011). It is possible that demography may have been both an effect (limited carrying capacity of the foraging system; population pressure and increased competition for resources) and a consequence of the Neolithic transition (the agro-pastoral dietary and socio-cultural innovations stimulating the population boom; Bocquet-Appel 2008, 2011). Within the frame of globally favorable climate conditions, the trajectories towards the agro-pastoral mode of subsistence may have been oriented by a combination of local innovations, mainly motivated by the need to ensure a secure resource-base to the broader and growing group of people who began to live together on a more permanent basis (Zeder and Smith 2009). This set of innovations could have been gradually selected and further spread because of its positive feedback effect on reproduction, a central element of adaptive success (Lambert 2009). Models seeking to explain the origin and the expansion of farming are yet still debated, and an important emphasis is today placed upon the considerable range of time involved, the regional specificities and the social complexities of the foraging and early farming communities who transformed their niches (e.g. Cohen 2009; Zeder and Smith 2009; Denham 2009; Stock and Pinhasi 2011).

To explain the positive effect of the agro-pastoral lifestyle on females' fertility, it has been suggested that changes in mobility and work-load patterns (sedentism), associated with the consumption of a carbohydrate-rich diet (cereals), a reduction in the duration of lactation (shorter breastfeeding) and different children caring practices (allo-parenting) may have collectively contributed to affect females' energy balance, to increase birth stacking and fertility rates (Bocquet-Appel 2008). A reduction in females' energy expenditure with sedentary lifestyle and an increased consumption of carbohydrates may have affected some aspects of maternal metabolism, stimulating reproductive rates (ibidem). Village life may have also favored a more collective care of children by members of the enlarged communities, and the availability of animal milk and cereals may have provided mothers with a new substitute – similar in appearance – for their own milk, allowing them to shorten the time their offspring rely on maternal milk, and thereby releasing them from the energetic burden of lactation (e.g. Binford 1968; Buikstra 1984; Bocquet-Appel 2008). Besides, changes in the intensity and the frequency of suckling are also known to directly influence the duration of the inter-birth interval and thus the number of children per females (e.g. Vitzthum 1994; Wood 1994; Ellison 1995; Stuart-Macadam and Dettwyler 1995). The evolution of maternal dietary choices and infant feeding strategies may hence have played a role in the demographic increase. Yet, these assumptions are mostly based upon ethnographic comparisons (Binford 1968; Buikstra 1986; Bocquet-Appel 2008), not necessarily confirmed by cross-cultural reviews (Sellen and Smay 2001), and there is a need to gather contextualized bio-archaeological information about parenting strategies and demographic fluctuations during the foraging-to-farming transition (Schurr and Powell 2005; Waters-Rist et al. 2011; Howcroft et al. 2012; Tsutaya and Yoneda 2013).

Agro-pastoral expansions and migrations

This demographic expansion may have been one of the driving forces for the geographic expansion of the farming system (e.g. Bellwood 2005, 2008; Bocquet-Appel 2008; Demoule 2008; Fort 2012, 2015). The farming niche has indeed the advantage that it can be exported outside of the original heartland, modified to cope with the new environments, and hence considerably extended (Rowley-Conwy and Layton 2011). In different regions, linguistic and genetic evidence have indicated that agro-pastoral innovations were related to human migrations, although the extent and the speed of these migrations should have been regionally specific (e.g. Bellwood 2005, 2008; Fort 2012). In many instances, the agro-pastoral niche has extended in the same environment as the foraging one, and agro-pastoralists entered in contacts with some communities of hunter-gatherers who were sometimes already sedentary and who may have also developed various low-scale food production strategies (e.g. Price and Brown 1985; Zvelebil 1986; Price and Gebauer 1995). Whether small groups of farmers infiltrated foragers environments, whether whole populations colonized the foraging niche, or whether foragers decided to adopt or to adapt some aspects of the agro-pastoral innovations, may have differently contributed to shape the local characteristics of the farming niche. The respective choices of migrants and of foragers, the extent of their bio-cultural interactions and mutual influences, and the decision to adapt certain species and cultural innovations more than others into new natural and social environments represent key issues to understand the development of the agro-pastoral way of life.

1.1.3. Consequences on Human Health and Biology

The cost of the transition

There is a substantial record based on the analysis of human remains from archaeological contexts to show that the agro-pastoral transition caused a general increase in morbidity and compromised health in the core centers of domestication but also in areas of geographic expansion (e.g. Cohen and Armelagos 1984; Cohen 1989, 2008; Larsen 1995, 2003; Cohen and Crane-Kramer, 2007; Wittwer-Backofen and Tomo 2008; Pinhasi and Stock 2011). The cost of the agro-pastoral transition has been repeatedly evidenced by the observation of a general decline in oral health (increase prevalence of caries), an increase in non-specific indicators of physiological stress and metabolic disturbances (enamel hypoplasia, cribra orbitalia, porotic hyperostosis), and growth disruptions. In several regions, stable isotope analyses have documented a sudden dietary shift toward the consumption of lower trophic level terrestrial food resources with the development of agro-pastoral practices (e.g. concerning Europe: Tauber 1981; Richards et al. 2003a, 2008; Schulting 2011; Ash et al. 2016; Jovanović et al. 2018). Thus, it has been suggested that hunter-gatherers had a broader spectrum of food resources than early farmers did, and the shift toward a more monotonous diet based on carbohydrates and less rich in proteins and in essential micronutrients has been deemed responsible for the overall health decline, favoring caries, nutritional deficiencies and anemia. In addition, the increased sedentary life associated with a growing number of people and a greater proximity with domesticated animals may have favored the development of zoonotic and infectious diseases (Armelagos and Harpper 2005). Children were probably amongst the first victims of these adverse effects of the farming-way-of life, as suggested by their increasing numbers in agriculturalists cemeteries, by the high occurrence of hypoplasia (defects in enamel formation during the growth of a tooth due to physiological stress), and of growth disruptions (e.g. Bocquet-Appel 2008). The availability of animal milk as a substitute to the maternal milk – yet, with considerable differences in terms of nutrients' composition (Howcroft et al. 2012) – and of carbohydrate-rich foods for the weaning preparations, their earlier introduction and/or a shorter reliance on maternal breastmilk, may have contributed to increase the occurrence of physiological stress during childhood and should have provided suboptimal conditions for growth. Besides, the use of non-sterilized tools, such as ceramics or spoons and their possible contamination by pathogens may have also led to tragic diarrhea (ibidem). It seems thus that the construction of the farming niche may have dramatically favored the populational fitness (reproductive success) in the trade-off with individual fitness (life-expectancy and well-being; Lambert 2009).

New selective pressures

The behavioral, ecological and socio-cultural co-adaptations associated with the sedentary and farming way of life also exerted new selective pressures on human populations, driving continuous human evolution during the Holocene (e.g. Rindos 1984; Leach 2003; Stock 2008, 2012; Zeder 2009; Pinhasi and Stock 2011). Different aspects in the construction of the new niche – starting by the construction of permanent houses – can be interpreted as a "domestication of our own species" (Wilson 1992; Scott 2017), which lead us to underwent similar physiological, morphological and genetic changes as other domesticated species (e.g. Leach 2003; Stock 2008;

Pinhasi and Stock 2011). Sedentism, changes in activity patterns and workload have affected our skeletal health (e.g. development of osteoarthrosis and back pain) but also resulted in a general decrease in skeletal robusticity, an increased circularity of long bones, a decrease in overall body stature or in dental and mandibular size (e.g. Larsen1995; Pinhasi et al. 2008; Larsen and Ruff 2011; Lieverse et al. 2011; Stock et al. 2011; MacIntosh et al. 2016). The analyses of ancient DNA have yielded evidences for direct genetic response to new dietary stress during the Neolithic period: for instance in amylase gene copy variation which aid starch hydrolysis (Perry et al. 2007), and in genes related to lactase persistence – the faculty to digest animal milk after the weaning period – amongst some populations who were substantially practicing dairying (Burger et al. 2007; Itan et al. 2009; Gerbault et al. 2013). The sedentary and agro-pastoral niche provided hence a new platform for biocultural adaptations, which contributed to significantly accelerate the pace of our evolution (Hawk 2007; Stock 2008, 2012; Laland et al. 2010).

1.1.4. Bioarchaeological perspectives on the Foraging to Farming Transition, the frame of the study

A paleodietary approach of the Transition

Counihan's anthropological definition of diet hence makes whole sense when considered in the context of the sedentary and agro-pastoral transition(s), when "humans construct[ed] their [new] relationship through their foodways" and "simultaneously define[d] themselves and their social world" (Counihan 1999:23). **Therefore, by reconstructing dietary adaptations through careful analyses of archaeological remains from contexts spanning the end of the Pleistocene and the first half of the Holocene, one may contribute: (1.) to clarify the chronology of the shift in subsistence and to better understand the causal relationships between dietary adaptations and other changes in the natural and social environments, such as climate oscillations, sedentism, social structure, or symbolic practices; (2.) to examine the mode, the tempo and the extent of the diffusion of agriculture; (3.) and to document some bio-demographic and evolutionary mechanisms behind the adoption of the sedentary and agro-pastoral lifestyle(s)**. Particularly, some emphasis should now be placed upon studying the evolution of subsistence strategies amongst complex communities of Early and Middle Holocene hunter-gatherers prior to the development of farming, how they constructed their ecological niche(s) on the long term, and the relationships between subsistence choices and mobility patterns. In order to clarify how the agro-pastoral way of life spread, it is also essential to examine migrants' dietary preferences, their adaptations to local conditions, their bio-cultural interactions with communities of hunter-gatherers and the impact of these interactions on farmers' and foragers' socio-cultural identities. Besides, the relationships between changes in dietary strategies, demographic behaviors and population dynamics need particular investigations in view of better understanding the bio-cultural causes and consequences of the Agricultural Demographic Transition; the analysis of children feeding practices and parenting strategies amongst hunter-gatherers and farmers, or during periods of contacts between the two niches, shall represent a central issue in this prospect.

Perspectives from Human Bioarchaeology: from individual lives to population history

The contextual study of human organic remains provides a direct means to collect essential data for documenting such mechanisms of human adaptability in relation to events of niche construction and colonization. Bioarchaeological sciences offer a set of methods for studying human organic remains through their dynamic relationships with the environment[2], from external

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[2] Bioarchaeology was originally applied by J.G.D Clark to the study of animal remains from the Mesolithic site of Starr in Britain (Clark 1972), and later refer in Britain to the study of biological remains (human, faunal, botanic) from archaeological context. We hence use here the term "Human Bioarchaeology" to refer to the methods specifically applied to the contextual analysis of human organic remains from archaeological sites intended to address issues related to our understanding of human bio-cultural diversity, in the line with J. Buikstra and C. Larsen definitions of Bioarchaeology as a "form of regionally-based, interdisciplinary research in mortuary site archaeology and human osteology" (Buikstra 1977), and as the bioliogical

osteological observations to virtual, microscopical or biomolecular analyses (e.g. Larsen 2002; Buikstra and Beck 2006; Weiss 2009; Knüsel 2010; Larsen 2018).Gaining notably from technical advances made during the last couple of decades in Forensic identifications and in Biomolecular Archaeology, the study of individual identities and life histories now allows Bioarchaeologists to interpret human remains not only as biological entities or as the decaying results of mortuary practices but as real persons, constructed through biological, psychological and social trajectories, and embodied into a natural, economic, social and cultural contexts (e.g. Sofaer 2012; Zvelebil and Weber 2013). This individual-oriented perspective is made possible by cross-linking various biological and behavioral characteristics such as sex, age at death, health status, ancestry, diet or provenance, with available information about the natural and social contexts considered at several levels, from the grave to the site and the region, from the individual to the population, from the lifetime of an individual to the long-term perspective. This approach has also been favored by the recent progress made in reconstructing whole segments of individual lives from longitudinal biochemical analyses of tissues formed during different periods between birth and death, enabling for example researchers to examine dietary transitions such as the weaning process. Moving between the individual and the population levels, one can now document the ways an individual relates to broader social groups or to the population as a biological entity. It allows researchers for reconstructing the behavioral choices, the needs and preferences of an individual and to examine his biological specificities, or in other words, to consider at the bottom the fundamental variations and patterns of transmissions which makes the evolution of a population possible (Zvelebil and Weber 2011). **Hence, by performing thorough bio-archaeological analyses of human remains dated to the beginning of the Holocene, one can provide valuable information on the bio-cultural mechanisms behind the sedentary and farming transition(s), and on the relationships between human cultural and biological adaptations (Stock 2011; Stock and Pinhasi 2011).**

In particular, stable isotope ratios – biochemical signatures directly related to the digested food (e.g. isotopes of carbon, $\delta^{13}C$, of nitrogen, $\delta^{15}N$, and of sulfur, $\delta^{34}S$) – now represent the most direct and reliable source of bioarchaeological information about diet and nutrition and can also inform about migrations and mobility (e.g. Ambrose and Katzenberg 2002; Lee Thorp 2008; Katzenberg and Water-Rist 2018). When interpreted at the (inter-)population level together with ecological (e.g. zooarchaeological and archaeobotanical data) and chronological (e.g. radiocarbon dates) information, stable isotope ratios may provide broad insights into subsistence and into differences or changes in diet. When interpreted at both population and (intra-)individual levels, and cross-linked with other osteo-biographical (e.g. age, sex, migration, ancestry, health) and cultural (e.g. funerary practices) information, stable isotope signatures may shed further light on patterns of distribution of food resources, on individual adaptations to new environmental conditions, on children feeding practices, and on some aspects of physiological health which long remained silent in the archaeological interpretations of human skeletal remains[3].

Addressing questions and hypotheses about the sedentary and agro-pastoral transition(s) through stable isotope analyses requires to analyse comprehensive skeletal series, with long temporal duration and substantive contextual documentation, in order to reconstruct the subsistence adaptations on the long term, and to appreciate the local biocultural and ecological subtleties which contributed to shape the farming niche (e.g. Larsen 2011; Stock and Pinhasi 2011; Knüsel et al. 2015). Yet, there are only few locations in Western Eurasia where deep temporal sequences of Epipaleolithic to Neolithic occupation associated with vast burial grounds were discovered; the archaeological complex of the Danube Gorges in the Central Balkans represents such context, with

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"study of human remains recovered from archaeological contexts" (Larsen 2002; cf also Buikstra and Beck 2006), in view of "reconstructing the lives and lifestyles of people" (Larsen 2001) and of "interpreting behavior" (Larsen 2015; cf also Knüsel 2010 and Larsen 2018).

[3] As observed by Sofaer in 2006, "once sex and age has been determined, the body no longer seems of interest to the archaeologist. The physiological aspects of the body, which form the foundation of osteological assessments are often silent in the process of interpretation as, in the search for meaning, the emphasis shifts from the body to the objects surrounding it".

evidence for a reduced residential mobility during the Mesolithic, the adoption of animal husbandry, and interactions with migrants descended from Near Eastern Neolithic communities.

1.2. The Farming Transition from the Near East to the Central Balkans

1.2.1. Epipaleolithic and Mesolithic societies of Western Eurasia

Defining the Epipaleolithic and the Mesolithic

At the end of the Late Pleistocene, after the Late Glacial Maximum (ending roughly ca 17.500 BC), foraging communities of the Paleolithic enter periods of overall warmer climate around 12.700 BC, associated with a retreat of glaciers, a rise in sea levels, and important changes in vegetation at many places of the world. Warmer climate oscillations (e.g. Bølling-Allerød oscillations, ca 12.700-10.900 BC) were punctuated by colder events (e.g. Younger Dryas ca 10.900-9700 BC), the last of which just preceding the beginning of the abrupt Early Holocene warming around 9700 BC. In Western Eurasia, the microlithization and geometrization of the stone industry illustrate the behavioral and cultural adaptations to changing environments. Some prehistorians have early emphasized a "gap" in Lubbock's age-system classification concerning this period (de Mortillet, quoted in Piette 1895); the term "Mesolithic" was thus suggested by Hodder M. Westropp (1866, 1872) to characterize the period ranging from the Paleolithic "reindeer period cave" until the introduction of the agriculture, and independently by M. Reboux (1869) to describe the intermediate industries between Paleolithic flakes producers and Neolithic polished axes producers. The definition of the term was further discussed, dividing the proponents of a chronological definition and the proponents of a typological definition, for whom the industries of this period without microliths should not be characterized as "Mesolithic" (as resumed by Orliac 1988). While the term started to spread (e.g. de Morgan in 1909, quoted by Orliac 1988), some researchers rather preferred to use "Epipaleolithic" in view of emphasizing the continuity with the previous Paleolithic period (Stjerna 1910; Obermaier 1924), although both words have sometime been used quite interchangeably (e.g. Childe 1951[4]). The "Epipaleolithic" has then been identified to the cultural groups for which the climate adaptations of the end of Pleistocene-Holocene does not produce any changes in way of life and lithic technology, in opposition with the "Mesolithic" groups, rather found in zones leading to food production (e.g. Clark 1980, Kozłowski and Kozłowski 1986). Yet, such definition of the Mesolithic excludes the regions which display substantial behavioral, ecology or material culture changes but which did not lead to the introduction of agriculture. Hence, by usage in Europe, the "Epipaleolithic" now rather characterizes the industries which occur after the Late Glacial Maximum - mostly associated with evidence for technological adaptations - and which appears to merge technologically into the "Mesolithic" at the beginning of the Holocene (Bahn 2002)[5].

Sedentary Hunter-Gatherers

During the warm oscillations of the Late Pleistocene (Bølling-Allerød oscillations) and at the beginning of the Holocene, forests developed in Europe and in some regions of the Near East[6]and large mammals of the Ice Age were gradually replaced by temperate forests' wild games. (Barbaza 1999; Walker et al. 2009, 2011; Blockley et al. 2012, Crombé and Robinson 2014). The

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[4] G. Childe identified the Mesolithic as "a mere continuance of the Old Stone Age mode of life" until the start of the Neolithic Revolution (Childe 1951)

[5] Therefore, no "Epipaleolithic" development has been identified in regions of Northern Europe such as Scandinavia, mostly re-populated after the 11th millennium BC at the very beginning of the Holocene. In contrast, the term "Mesolithic" is not used to characterize the cultures of the foragers of regions of the Near East, where some essential aspects of the Neolithic – such as the intensified collection, stockage and processing of cereals, use of ground stone tools, construction of grouped and permanent dwellings – have been evidenced in contexts dated to the end of Pleistocene – very beginning of the Holocene. In the Levant some degree of cultural continuity notably in the use of microlithic tools has been observed from the end of the Late Glacial Maximum and the beginning of the Holocene; hence the groups of the "Kebarian" (ca 16000- 10500 BC) and "Natufian" (ca 12000 – 9500 BC) are both characterized as Epipaleolithic, preceding there the Pre Pottery Neolithic (ca 9000-7000 BC) (e.g. Maher et al. 2012).

[6] Boreal forests and grassland before the Holocene, and then more temperate forests in most continental Europe, and more Mediterranean forests, woodlands and grasslands in Southern Europe and regions of the Near East.

retreat of the Glaciers favored the occupation of new environments, for instance in highland and in coastal regions of Northern Europe; more open-air sites, including grouped settlements and evidence for year-round stay, have been identified in Epipaleothic/Mesolithic contexts, mostly close to the sea, rivers or inland bodies of waters (e.g. Clark 1980; Price 1983; Barbaza 1999; Bailey and Spikins 2009; Crombé and Robinson 2014). Archaeological models and genetic data now indicate that Europe should have been repopulated after ca 13.000 BC from refugia notably centered on a Franco-Cantabrian region, on the North-East European Plains and perhaps on South-Eastern Mediterranean Europe (Dolukhanov 1993, 1996; Gamble 1996; Gamble et al. 2005, 2006; Pala et al. 2012; Haak et al. 2015; Fu et al. 2016; Posth et al. 2016; Perreira et al. 2017; Lazaridis 2018). A recent paleogenomic study has notably evidenced that the Early Holocene Hunter-Gatherers discovered in the region of the Danube Gorges in the central Balkans show a strong genetic affinity with Late Pleistocene Hunter-Gatherers discovered in the Anatolian plateau, suggesting that their ancestors should have maintained gene flows (Feldman et al. 2019[7]). Genetically, the inhabitants of post-glacial Late Pleistocene and Early Holocene Western Eurasia can be divided into broad clusters of "Western Hunter-Gatherers" (discovered in most regions of western, central and Mediterranean Europe) and "Eastern Hunter-gatherers" (discovered in regions of the Eastern Plains), between which range the populations discovered in Iberia, Scandinavia, the Baltic and the Dniepr which show affinity to both clusters; the "Caucasian Hunter-Gatherers" and the hunter-gatherers discovered in Anatolia and the Southern Levant are genetically more distant from these clusters and from each other (Haak et al. 2015; Mathieson et al. 208; Feldmann et al. 2019; Vallalba Mouco et al. 2019).

The process of microlithization and geometrization of chipped stone artifacts has also been related to major technological innovations, such as archery, and to a modification in the ways spears and harpoons were made, many examples of adaptations to changing environmental conditions (e.g. Clark 1980; Price 1983; Barbaza 1999; Baileys and Spikins 2009; Crombé and Robinson 2014). Boats, harpoons, fishing nets and traps have been discovered at several sites, suggesting that fishing played an essential role in subsistence activities. Wild games (aurochs, deer and wild boar) were often hunted as well as small mammals, aquatic mammals (e.g. seals), waterfowls, birds and reptiles; snails and mollusks were also collected, discovered in considerable amount at some places, and probably a wild range of plant species as well (ibidem). This availability in abundant and stable resources that can be exploited in the relative vicinity of residential areas has thus been linked to the intensified exploitation of a broader spectrum food resources, on more limited territories than during preceding periods (a process called the "Broad Spectrum Revolution" concerning regions of the Near East; Flannery 1969). The appearance of formal disposal areas for the dead - the first "cemeteries" - can be interpreted as the result of important social and symbolic changes related to the increased territoriality of greater sized communities (Radovanović 1996a). For a long time, these communities were considered as insignificant or even as regressive, because of their apparent lack of art, their microlithic industry and the low-level preys they hunted (Clark 1980). However, major Epipaleolithic-Mesolithic sites with ritual significance have been excavated, and archaeologists have evidenced a variety of architectural achievements (e.g. trapezoidal buildings at Lepenski Vir, round houses of the Natufians, or Megalithic "temple" at Göbekli Tepe; Srejović 1974; Schmidt 1998), artistic expressions (e.g. sculpted boulders, engraved and painted pebbles, rock art with anthropo-zoo-morphic figures or geometric shapes; e.g. Srejović 1972; Schmidt 2000; Lødøen 2003; Radovanović 1997), and of funerary practices (including inhumation and cremation, primary or secondary deposits, skull removals and body disarticulations, diverse grave goods, pigments and parts of animal bodies; e.g. Clark and Neeley 1987; Radovanović 1996c; Stutz 2003).

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[7] Indeed, it can be emphasized that the Balkan peninsula provided during the last glacial period refuge for numerous taxa which then spread in Europe after the deglaciation (e.g. Alexandri et al. 2012) and that the region present some cultural continuity, for instance in lithic industry, between the Late Pleistocene (Epipaleolithic occupation in the Gorges ca 13000 BC) and the Early Holocene (Early Mesolithic from ca 9700/9500 BC; e.g. Boroneanţ 2000; Voytek and Tringham 1989; Radovanović 1996; Mihalović 2008).

1.2.2. The development of the farming niche in the Near East and its spread to Europe

The Natufian and the Pre-Pottery Neolithic: the gradual development of the "Neolithic package"

This series of behavioral and ecological co-adaptations resulted in the gradual domestication of animal and vegetal species by some groups of Epipaleolithic hunter-gatherers in the Near East, and the construction of a niche which will spread to the whole Europe (Bar-Yosef 1998; Rowley-Conwy and Layton 2011; Maher et al. 2012). The elaboration of more permanent hamlets, with houses on dry-stones foundations, by the Natufians foragers of the Southern Levant (ca 12.000-9500 BC), and the intense exploitation of a wild range of animal and vegetal resources in the Mediterranean park forest[8], may have been the trigger for further modifications of the natural and social environments, a "threshold in the development of agriculture" (Bar-Yosef 1998). Wild cereals were harvested, stored and proceeded to sustain a relatively larger semi-sedentary population and it has been hypothesized that the development of dryland scrubs during the cooler event of the Younger Dryas could have pressed the population, perhaps more mobile than during earlier phases, to artificially clearing the scrubs and to re-plant seeds obtained from elsewhere (Younger Dryas Model reviewed in Balter 2010). During the Early Holocene (after 10.000-9500 BC), some populations genetically related to the Natufians of the Southern Levant, as well as other groups of hunter-gatherers in regions of the Taurus mountains and the Upper Tigris-Euphrate valleys, started to build larger settlements, including houses with mudbrick walls and, in a later phase, limestone plastered floors (PPNA, ca 10.000-8800 BC; PPNB, ca 8800-6500 BC; Kuijt 2000; Kuijt and Goring-Morris 2002; Wright 2014; Feldman et al. 2019). Some structures were identified as communal buildings, and cereals were stored in granaries (e.g. Willcox 2014; Kuijt and Finlayson 2009). This deliberate, extended period of storage can be related to the first morphological adaptations of species of crops and pulses during the 10th and 9th millennium BC, notably emmer wheat, einkorn wheat, barley, peas, lentils, bitter vetch, flax and chickpeas (Figure 1; Willcox 2014). Pigs, sheep, cattle and goats were probably domesticated at different places between the Southern Levant, Taurus-Zagros mountains and the Upper Tigris-Euphrate valleys during the 9th millennium BC (Vigne et al. 2004; Vigne 2011). It has been speculated that the intense reliance on a broad spectrum of resources during the Epipaleolithic may have contributed to the selection of some animal and plant species which were rather disregarded during colder periods of the Ice Age, and to their easier transformations due to their particular behavioral, morphological and genetic characteristics (Flannery 1969; Byrd 1989; Stiner 2001; Rowley-Conwy and Layton 2011).

There are now archaeological and genetic evidence that the sedentary foragers which occupied the Central Anatolian plateau, and who developed the village way of life with their own architectural traditions, adopted domestic plants and animals during the 9th – 8th millennium BC (Figure 1; Baird 2011; Ozdoğan et al. 2015; Feldman et al. 2019). This introduction of domesticates to Central Anatolia can be seen as an early phase of adaptations of the farming innovations to different environmental conditions which would later allow agriculture to spread to wetter and more temperate regions of Eurasia. Ceramic started to be made during the 7th millennium BC in southern regions of the Levant and was rapidly imported to Central Anatolia (Baird 2012). In addition to the village life and the adoption of domesticated animals, these Neolithic communities thus shared various cultural similarities, which have been grouped under the term "Neolithic package" (e.g. Çilingiroğlu 2005; Ozdoğan 2008) including notably: ceramics, osseous artefacts (e.g. bone spoons, awls or needles), ground-stone artefacts (e.g. grinding stones, polished axes and adzes), ornaments (e.g. stone bracelets), symbolic representations (e.g. figurines, house models or altars), funerary behaviors (e.g. skull cults, burials in crouched position below the house floors), and architectural

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[8] An extensive exploitation of plant resources by groups of foragers who occupied the region during the previous millennia has also been evidenced (e.g. Weiss et al. 2004) and some scholars emphasize the long timing of the process of behavioral adaptation that eventually enabled the domestication (e.g. Maher et al. 2012), abruptly accelerated around 10.2 ky BP (Weninger 2017).

achievements (e.g. painted plastered lime-stone house floors). While maintaining network of exchanges, Neolithic communities of the Levant also developed regionally specific landscape exploitation strategies, strongly defined household identities, locally specialized craftmen, and practiced diverse ritual practices (Baird 2012).

First spread of the Neolithic to Western Anatolia and the Southern Balkans

After stabilizing during several millennia in the Central Anatolian Plateau, the Neolithic way of life – materialized by this fully developed cultural "package" – was quite suddenly dispersed into Europe, through Western Anatolia and the Balkans Peninsula during the second half of the 7th millennium BC (Figure 1; e.g. Guilaine 2007; Brami and Zanotti 2015; Krauss et al. 2018). The strong material cultural relatedness observed between these regions has been synthesized through the broad designation "Balkano-Anatolian cultural complex" (Garašanin 1997). The probability distributions and the spatial analyses of substantial sets of radiocarbon dates have indicated that the expansion was rather "arrhythmic": gradual advances in Western Anatolia and Southern Balkans around 6700/6200 BC and a rapid spread through Central-Northern Balkans to the Wallachian and Pannonian Plains around 6100-6000 cal BC, where it stabilizes for a longer time until 5500 cal BC (Whittle et al. 2002; Guilaine 2007; Brami and Zanotti 2015; Fort 2015; Blagojević et al. 2017; Krauss 2011, 2016; Krauss et al. 2018). It is now considered that this process involved separate waves of Neolithization, each with its own mode, pace, and trajectories. Between Central Anatolia and the Balkans, at least three different chrono-geographic cultural horizons of Neolithic diffusion, characterized by differences in the disseminated "Neolithic packages" and including a marine trajectory running exclusively along the coasts of the Mediterranean and Aegean, have been identified so far (Brami and Heyd 2011; Ozdoğan 2011a; Reingruber 2011; Horejs et al. 2015; Horejs 2019a and b; Milić 2019). While the inland route took it all the way to Central-Western Europe, the sea-based route further brought the Neolithic cultural and biological components to the West of Mediterranean coasts. The two major chrono-geographical steps of diffusion, around 6600 cal BC for the circum-Aegean dispersal, and ca 6050 cal BC for the Northern Balkans and Pannonian Plain, have also been related to the onset and the end of the Rapid Climate Change, cooling conditions which culminated around 6200 cal BC (the 8.2 cooling event); during the Neolithic expansion, climate may hence have been a "major factor underlying social changes" (Weninger 2009:551; Weninger et al. 2014).

There has been a long standing controversy concerning the ways the farming innovations spread into Europe, dividing the proponents of a demic diffusion (spread of people) and of a cultural diffusion (spread of ideas) (e.g. Childe 1925; Edmonson 1961; Ammerman and Cavalli Sforza 1971; Fort 2012). The westward expansion of the Neolithic outside of its core area has been associated with widespread shifts in settlements occupation and modifications in material cultural assemblages in the Northern Levant which could indicate that some important social and/or demographic changes may have occurred there during the first half of the 7th millennium BC (Ozdoğan 2008). Genetic data and spatial analyses of radiocarbon probability distributions have indicated that demic diffusion was the primary mechanisms in the Balkans, in Central and Western Europe (e.g. Haak et al. 2010; Fort 2015; Omrak et al. 2016; Hofmanová et al. 2016; Mathieson et al. 2018); yet mathematical models also suggest that cultural diffusion may have played some role, and there are evidence for admixture between descendants from European Mesolithic foragers and from Near Eastern Neolithic communities (e.g. Fort 2012; Hofmanová et al. 2017; Mathieson et al. 2018). Between the "exchange of ideas" (no migration) and the "folk migration" (massive migration and population replacement), a series of possible alternate and complementary scenarios have been suggested to explain the mechanisms of expansion, leading to various manners of contacts between the Neolithic farmers and European Mesolithic hunter-gatherers (Zvelebil 2001); these notably include: the "frontier mobility" (small scale movements, slow spread of genes and fast spread of ideas along farmers/foragers borders), the "wave of advance" (farmers' enclaves that grow and serve as local core zone for further spread), and the "infiltration" of a few farmers in foragers' environments, possibly as a "leapfrog" movement (i.e. a selective colonization by small groups of farmers of areas occupied by hunter-gatherers).

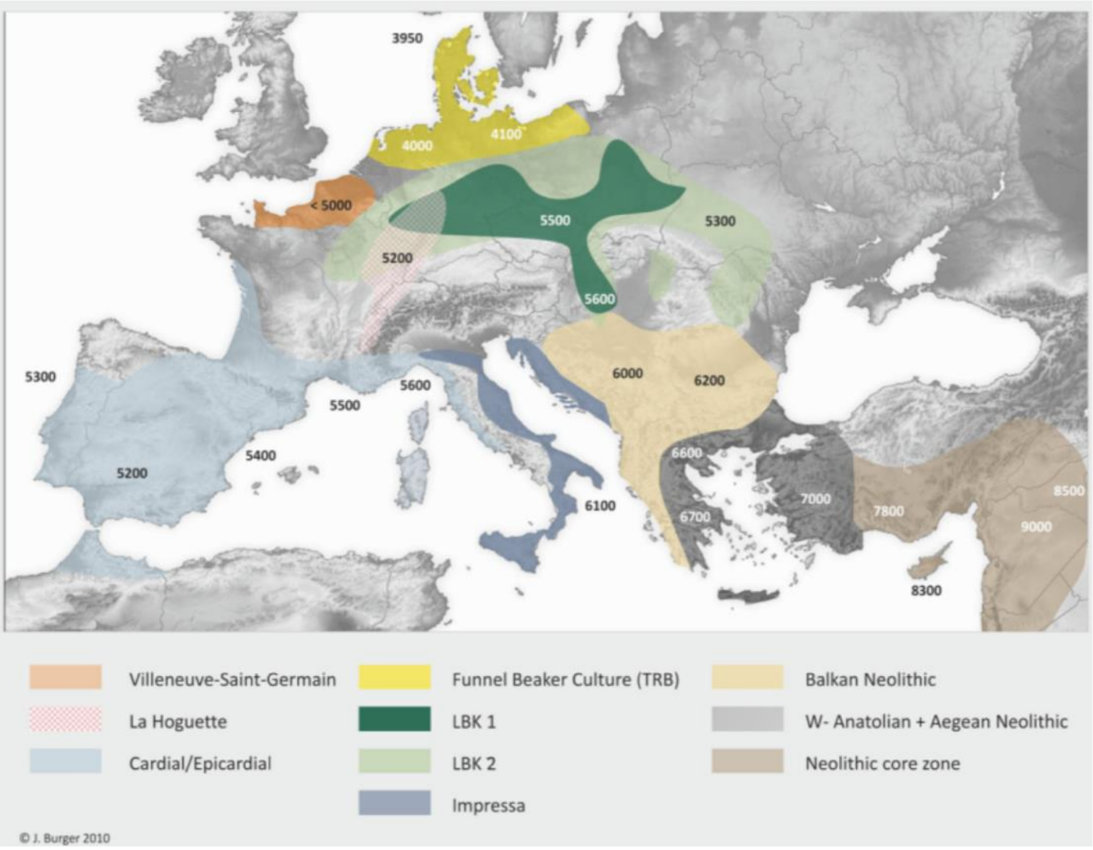

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Figure 1: Map of the chronological spread of the Neolithic, number approximates earliest dates of the appearance of the Neolithic (in years cal BC), associated cultures. Adapted from Burger and Thomas 2011.

Standing between areas of primary and secondary Neolithization, Western Anatolia and the Balkans provide the opportunity to examine not only the reception, but also the adaptation and the transmission of the Neolithic way of life to Central and Western Europe (e.g. Brami and Heyd 2011; Ozdoğan 2011a and b). The Neolithic package appeared quite simultaneously in circum-Aegean regions (ca 6700/6500 – 6200 cal BC), where Neolithic sites displayed strong cultural similarities in terms of artefacts (monochrome ceramic, stone pendants and beads, terracotta figurines, stamps and model houses), architecture (quadrangular houses built and re-built on tell settlements), or subsistence (the dominance of ovi-caprines amongst domesticated animals). Despite these similarities, there are also some local adaptations, for instance in chosen architectural materials or in the level Early Neolithic communities relied on domesticate, fishing and hunting (e.g. Reingruber 2011; Ozdoğan 2011a and b). Although the Mesolithic presence in these regions is quite elusive in comparison with the Central-Northern Balkans, it is also possible that the expansion of the Neolithic may have partly relied on pre-existing networks of exchanges with hunter-gatherers and/or implied exchanges of knowledge, as evidenced notably by obsidian tools (e.g. Gastov and Ozdoğan 1994; Gastov and Schwarzeber 2006; Perles 2003, 2005; Reingruber 2011; Horejs 2016). The strong connectivity between Neolithic settlements of the core areas, new Neolithic settlements, frontier zones and foragers' settlements probably played an important role in the diffusion of farming into Western Anatolia and the Southern Balkans.

1.2.3. Early Neolithic in the Central-Northern Balkans

The Starčevo cultural group

The distribution of Early Neolithic sites in the Central Balkans, the Southern Carpathians and the Wallachian-Pannonian Plains (broad region referred here as "Central-Northern Balkans") suggests that the Vardar and the Danube rivers and its tributaries[9] played a significant role in the rapid expansion of the Neolithic to these new and contrasted landscapes around 6200/6000 BC (Figure 1; e.g. Whittle et al. 2002; Porčić et al. 2016; Blagojević et al. 2017; Krauss et al. 2018). The Early Neolithic sites in this region are related to the Starčevo-Körös-Criş cultural complex (referred here as "the Starčevo culture"), defined on the basis of a broadly uniform range of pottery forms, decoration and manufacturing technology, although there are indications of localized styles across this wide geographic area (Garašanin 1982; Gimbutas 1991; Tasić 1997; Trigham 2000; Whittle et al. 2002; Krauss 2011, 2016; Horejs et al. 2019). The cultural components of Starčevo sites display similarities with the Neolithic of the Southern Balkans and the Anatolian sphere (e.g. monochrome pottery, bone spoons and spatulae, ground stone tools, stone beads, terracotta figurines and altars, burials in flexed position), but also includes elements of local adaptations (e.g. long stone blades in Yellow-Spotted "Balkans flint"; Mesolithic influences in microlithic tools or in osseous industries; e.g. Vitezović 2010, Šarić 2014). The Mesolithic presence is much more documented in the Central Balkans than in South-Eastern regions, notably in the area of the Danube Gorges, where cultural elements of the Starčevo appear ca 6200 cal BC (e.g. pottery), in a general context of continuity with previous Mesolithic traditions (the "Lepenski-Vir" culture; e.g. Radovanović 1996a; Bonsall 2008; Borić 2011). Concerning settlements, there are important differences with the Southern Balkans where tell dominates with quadrangular houses often rebuilt one on top of each other. In contrast, Starčevo settlements are largely "flat", including mostly "pit houses" (Borić 2008). There are also differences in terms of subsistence strategies both between the sites of the Southern Balkans and of the Central-Northern Balkans, and within the area of Starčevo extension. Although domesticated animals mostly dominate the Starčevo zooarchaeological assemblages, at many sites the presence of wild terrestrial animals is more important than in Southern Balkans Early Neolithic contexts (e.g. College et al. 2013; Manning et al. 2013); in the region of the Danube Gorges, the remains of dogs and of wild animals are even over-represented in comparison with the Neolithic domesticates (e.g. Borić and Dimitrijević 2005; Dimitrijević and Borić 2007). Besides, cattle sometimes dominate over ovi-caprines in Starčevo contexts, which differs from Southern Balkans Early Neolithic contexts (Colledge et al. 2013; Manning et al. 2013). The documentation is more scarce concerning crops: the three founder species – einkorn wheat, emmer wheat and barley – have been recovered at Early Neolithic sites of the region, barley being found in smaller proportions though (Colledge et al. 2005; Colledge and Connelly 2007; Filipović and Obradović 2013). The cultivation of pulses is reduced to peas and lentils at several sites, as in Central European Early Neolithic contexts (ibidem). The stable isotope analyses of human remains from Central Balkans Early Neolithic contexts has also indicated a diversity in terms of subsistence: a greater reliance on the consumption of high trophic level resources, including aquatic proteins, for many individuals buried in the Danube Gorges, a more mixed diet or a greater emphasis on the consumption of lower trophic level terrestrial resources for individuals buried in South Pannonia (Whittle et al. 2002; Jovanović 2017). A recent study of skeletal markers of health status also indicates that the Early Neolithic individuals buried in these regions had a greater number of dental caries, indicative of a carbohydrate rich diet than the Mesolithic-Neolithic individuals buried in the Danube Gorges; they also exhibit higher levels of cribra orbitalia, notably related to anemia and micronutrients deficiencies, and of dental enamel hypoplasia, related to childhood physiological stress than the Mesolithic-Neolithic individuals discovered in the gorges, looking – in terms of health status – quite similar as the other central European (LBK) Early Neolithic individuals for which such data are available (Jovanović 2017).

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[9] The Morava, Sava, Drava, Tisa, Drina, Moriš and Tamiš rivers.

Different paleogenomic studies have demonstrated the Near Eastern Neolithic ancestry of analyzed human individuals from most Starčevo contexts (e.g. Gamba et al 2014; Hofmanová 2017; Mathiesen et al. 2018). While admixture between the descendants from European Mesolithic foragers and the descendants from Near Eastern Neolithic communities seems to have been limited (Lipson et al. 2017; Hofmanová 2017), a few sites at several locations along the Danube – notably in the region of the Gorges – and Tisza rivers yet display evidence for a greater degree of admixture (Gonzales Fortes et al. 2017), indicate that one individual with an entire European Mesolithic-like ancestry has been inhumated in some Starčevo-Körös-Criş contexts (Gamba et al. 2014), and also show that some individuals who had an entire European Mesolithic-like ancestry were inhumated at the same burial site as individuals who had an entire Near Eastern Neolithic-like ancestry and as individuals who had both ancestry (Hofmanová 2017). Hence, the local cultural and economic specificities noticed within different regions of the broad Starčevo-Körös-Criş cultural complex might reflect not only the adaptations of subsistence and mobility patterns to different landscape conditions, but also the varying degree of interactions with a larger local Mesolithic population. These adaptations, interactions and possible mutualistic relationships could in part explain the longer standstill of the Neolithic expansion in the region until ca 5500 cal BC, when the farming niche spread to other temperate environments of Central Europe (e.g. Gkiasta et al. 2003; Fort 2015). The number of sites occupied between 6200 and 5500 cal BC suggest an important population growth, followed by a decline, perhaps in relation with a further population spread Northward (Porčić et al. 2016; Blagojević et al. 2017).

A Broader diffusion to Europe

At a broader European level, genetic and cultural data, radiocarbon dates and mathematical models indicate that the farming expansion was rather demic in Central-Western Europe but rather cultural in Northern Europe, the Black and Baltic seas and along the Dniepr (e.g. Fort 2012; Skoglund et al. 2014; Fort 2015; Jones et al. 2017). There is also some genetic evidence for varying proportions of admixture between the descendants from Near Eastern Neolithic groups and from European Mesolithic hunter-gatherers (e.g. Lipson et al. 2017), who coexisted in some regions for centuries, or even millennia (e.g. in Central and Northern Europe; Bollongino et al 2013; Skoglund et al. 2014). Paleodietary studies have also indicated that the transition was associated in many regions of South-Eastern, Central and Western Europe with a shift toward the consumption of more terrestrial resources, probably primarily agricultural products, despite local variabilities; in contrast, some communities who lived in Northern and Eastern Europe, descended from European Mesolithic Hunter-Gatherers, adopted some aspects of the Neolithic way of life, notably pottery, but relied longer on fishing and hunting (Liden et al. 2004; Lillie and Budd 2011; Jones et al. 2017; Terberger et al. 2018). In most regions of Central, Northern and Western Europe, the adoption of agro-pastoral activities was followed by a rapid increase in number of settlements, suggesting a rapid population growth (Shennan et al. 2013), also independently demonstrated by skeletal demography (Bocquet-Appel 2008). The multifarious nature of the Neolithic expansion in Western Eurasia, which followed different paces, entered a variety of natural and social environments, and sometimes involved the long-term coexistence between communities of foragers and farmers, suggests that human behavioral adaptations should be reconstructed with an increased temporal and spatial resolution; the high level of contextualization of the Epipaleolithic/Mesolithic to Neolithic osteo-anthropological assemblages discovered the region of the Danube Gorges offers this possibility.

1.2.4. The Epipaleolithic/Mesolithic to Neolithic occupation in the Danube Gorges, the context of the study

The Epipaleolithic/Mesolithic and Neolithic sites of the archaeological complex of the Danube Gorges (ca 13.000-5500 cal BC) are located in the central part of the northern Balkans, where the Danube cuts its way through the Balkans and the Carpathians mountains, defining there a succession of narrow gorges and small terraces (Figure 2, Figure 3). The region offered privileged conditions for the formation of prehistoric settlements: the diversified geology and the local micro-climate have favored the presence of a broad range of edible plants, of oak forests which covered – at least after glacial times – the riverbanks and the surrounding areas of the hinterland and ensured a constant resource in wild games (Mišić et al. 1969; Radovanović 1996a; 2008; Popa 2003; Filipović et al. 2010); geological formations also created numerous good fishing spots, notably to catch species of anadromous fish migrating from the Black Sea (e.g. Borić 2002a; Bartosiewicz et al. 2008; Živaljević 2017). The archaeological complex of the region is usually considered in reference to two distinct landscape settings (Bonsall 2008): the Danube Gorges stricto sensu (referred in this thesis as "the Inner Gorges"), where the Danube has defined a series of steep-sided canyons, starts after the river leave the Pannonian plain, and the area located further downstream as the Danube exit the Gorges to enter the Wallachian plain in a more hilly environment (referred in this thesis as "the Downstream Area").

The Epipaleolithic and Mesolithic foragers of the Gorges

Some cave shelters (e.g. Cuina Turcului, Climente I and II) were occupied from the end of the Pleistocene (Epipaleolithic period, ca 13.000-9700/9500 BC, Borić 2011), probably as hunting halts, part of broader logistic network of settlements (Figure 4, Figure 5; e.g. Boroneanţ 2000; Mihailović 2008). The Early Holocene human presence at open-air sites (e.g. Padina, Lepenski Vir, Vlasac) is documented from the 10th millennium BC (Early/Middle Mesolithic period, 9700/9500-7400 BC, Borić 2011),and associated with scattered stone structures, rectangular hearths and large burial grounds (e.g. Padina; e.g. Radovanović 1996a; Borić and Miracle 2004; Jovanović 2008; Borić 2011). The Gorges were more intensely occupied from the end of the 8th millennium (Late Mesolithic period, 7400 BC, Borić 2011), whenlocal foragers started to build structures of trapezoidal shape, sometimes with limestone floors; stone-lined rectangular hearths as well as numerous burials were found at several sites (e.g. Vlasac, Schela Cladovei, Hajdučka Vodenica; e.g. Srejović and Latica 1978; Radovanović 1996a; Boroneanţ et al. 1999; Borić and Miracle 2004; Jovanović 2008; Borić 2011; Bonsall et al. 2013; Borić et al. 2014). The appearance of some specific funerary practices (ochre pigments covering some parts of females bodies and of numerous perinates), as well as the red-plastered floors, suggest that there may have been some long-distance connections between the local foragers and the Anatolian Neolithic communities of the Pre Pottery Neolithic (Borić 2011).The foragers of the Gorges hence likely adopted a (at least semi-)sedentary way of life prior to and independently from the adoption of animal and plant husbandry. Dogs are the only recorded domesticates for this period and appear to have been domesticated locally throughout the course of the Mesolithic (Dimitrijević and Vuković 2015). Numerous archaeozoological studies as well as stable isotope analyses (mainly $\delta^{13}C$ and$\delta^{15}N$), indicate that the local population substantially consumed fish, notably anadromous species, as well as wild games, and possibly dogs (Bonsall et al. 1999; 2000; 2004; Borić 2001, 2002a; Grupe et al. 2003; Borić et al. 2004; Borić and Dimitrijević 2005; Živaljević 2017); a pilot study of $\delta^{34}S$ suggested that there might have been some differences either in the consumption of terrestrial and freshwater fish and/or of fish species between some sites and/or period of occupation (Nehlich et al. 2009; Nehlich and Borić 2015; Bonsall et al. 2015b and c).

Interactions – Innovations and Adaptations at the Early Neolithic

From the end of the 7th millennium BC to the beginning of the 6th millennium BC (Transformation / Early Neolithic period, 6200-6000/5900 BC, Borić 2011; Figure 4, Figure 3), period of important climate oscillations (8.2 ky BP cooling event), the inhabitants of the Gorges built more sophisticated stone-lined trapezoidal structures with red-plastered floors and central hearth, and created unique forms of artistic and symbolic expressions: some sculpted anthropo-zoomorphic boulders notably featuring mixed human-fish characteristics (e.g. Srejović 1966, 1972; Radovanović 1996a; Borić 2002a). All these features were present on the eponym site of Lepenski

Vir, where numerous burials have also been uncovered (e.g. Srejović 1966; Radovanović 1996a; Roksandić 1999). During this period the first agro-pastoralists communities of the Early Neolithic *Starčevo culture* settled in the neighboring regions of the Central Balkans (e.g. Whittle et al. 2002; Porčić et al. 2016). New technology (ceramics and new type of ground stones), raw material (the Balkan flint) and body adornments (limestone, spondylus and nephrite beads), characteristic of the Early Neolithic cultures, were then introduced in the local material cultural repertoire (e.g. Radovanović 1996a; Bonsall et al. 2008; Borić 2011). The remains of more than 40 perinates and infants have also been uncovered below the red floors of Lepenski Vir dwellings, a practice which recalls the Anatolian and Southern Balkans Neolithic cultural sphere (Borić and Stefanović 2004; Stefanović and Borić 2008). The presence of these babies below the house-floors might reflect some modification of demographic behavior, parenting strategies and/or children mortality. As D. Borić noted, the sites of the Gorges present then "a fascinating example of cultural hybridity of forager-farmer interactions (...) that lasted probably not longer than two centuries. This cultural hybridization was expressed in all aspects of life, from body decoration, to the appearance of artistic depictions and elaboration of architectural symbolism" (Borić 2011:157).

Although archeozoological data and the study of lipids residues from ceramics suggest a continuity in terms of fish consumption (e.g. Bökönyi 1970; Borić 2001, 2002a; Borić and Dimitrijević 2005; Živaljević 2017; Cramp et al. 2019), the stable isotope analyses conducted on human remains indicate a trend toward more variability, some individual highly consuming aquatic resources, while others favoring terrestrial resources (e.g. Bonsall et al. 1999; 2000; 2004; Grupe et al. 2003; Borić et al. 2004; Nehlich et al. 2009). Recent archaeobotanical studies also indicate that some starch grains recovered from the dental calculus of individuals dated to the Transformation/Early Neolithic and Early/Middle Neolithic phases could have derived from domesticated cereals (Cristiani et al. 2016, Jovanović 2017; reviewed in Filipović et al. 2017). Morphological observations, metric and non-metric osteological biodistance studies carried out on human remains also indicated that the development of the Neolithic in the Gorges was associated with a greater biological heterogeneity than during previous periods of occupation (e.g. Menk and Nemeskéri 1989; Živanović 1986; Roksandić 1999, 2011; de Becdelièvre et al. 2015, oral presentation[10]). A study of strontium radiogenic signal from dental enamel, biochemical signature related to the natural environment where one grew up, has identified the presence of non-local individuals (Borić and Price 2013). Besides, ancient DNA analyses also show that some individuals were descended from European Mesolithic foragers, while others descended from the Near Eastern Neolithic communities, and there is also some evidence of admixture between individuals of different ancestries (Hofmanová 2017; Mathieson et al. 2018).

In the Downstream Area, some Early Neolithic sites display particular cultural affinities with the Starčevo groups, for instance some burials were placed in flexed/crouched position in a multiple grave dated ca 6000 BC at Ajmana, a practice common amongst Early Neolithic communities of the broader Balkan region but unknown in the inner part Gorges before the first centuries of 6th millennium BC (Stalio 1986). After 6000 BC, further important socio-cultural changes occurred in the Gorges (Early/Middle Neolithic period, ca. 5950-5500 cal BC, Borić 2011) as documented by the abandonment of the trapezoidal buildings at Lepenski Vir and the appearance or generalization of some Neolithic tools (e.g. bone spoons, hooks and awls; Borić 2011; Borić et al. 2018). The Neolithic social, aesthetic and symbolic transformations of the 6th millennium cal BC are also attested by the changes in the burial practices and body adornments (e.g. Bonsall et al. 2008; Stefanović and Borić 2008; Borić 2011; Borić et al. 2018). The Neolithic suite of domesticated animals (Bos taurus, Sus domesticus, Capra hircus, Ovis aries) also appeared in the Gorges during this phase but their consumption likely remained subsidiary in comparison with fish and wild game (Borić and Dimitrijević 2007; Dimitrijević 2008; Živaljević 2017). Stable isotope data yet suggest

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[10] de Becdelièvre, C., Porčić, M., Goude, G., Le Guen M.A, Jovanović, J., Stefanović, S. From individual mobility to population dynamics during the Mesolithic and Neolithic transformations in the Danube Gorges (Balkans, ca. 9500–5500 BC): Adaptations and interactions. Research presented at MESO 2015, The Ninth International Conference on the Mesolithic in Europe. (14.-18.09.2015. Belgrade, Serbia).

that a greater number of individuals buried at Lepenski Vir during this phase consumed, on a daily basis, fewer aquatic proteins than during the previous Transformation-Early Neolithic phase (e.g. Bonsall et al. 2000, 2004). strontium radiogenic data identified a greater number of non-local individuals and paleo-genomic analyses more individuals related to Near Eastern Neolithic communities (Borić and Price 2013; Hofmanová 2017). Archaeozoological and archaeobotanical studies, stable isotope analyses of human bones as well as the analyses of organic residues of pottery from remains discovered at Starčevo sites located in surrounding regions of the Central Balkans suggest that the Early communities settled there consumed fewer aquatic resources than in the Gorges and likely relied on animal husbandry and probably on crop cultivation on a greater extent (e.g. Colledge et al. 2013; Manning et al. 2013; Filipović and Obranović 2013; Jovanović 2017; Etbier et al. 2017; Filipović et al. 2017). Besides, while the overall health status of the population of the Gorges remains quite good over the whole Mesolithic-Neolithic sequence, some Transformational-Early/Middle Neolithic females and children – notably those buried at the downstream site of Ajmana – had dental caries and their skeletal remains exhibit higher frequency/degrees of non-specific indicators of physiological stress, as also observed amongst individuals buried on neighboring Starčevo sites (Jovanović 2017).

As emphasized by D. Borić "the nature of adaptations and transformations that can be examined on the basis of abundant archaeological evidence from this region is exemplary for the character of foraging societies that might have existed in the Balkans and other areas of Eurasia during the Early Holocene" (Borić 2011: 157).

1.3. Subsistence adaptations and feeding practices in the Danube Gorges: issues, methods and structure of the study

Issues, sampling strategy and targeted bioarchaeological markers

More than fifty years of researches conducted on the Epipaleolithic-Mesolithic and Neolithic sites from the Danube Gorges have provided a context that is exceptionally well-documented, allowing for examining hunter-gatherer's behavioral complexity prior to the development of agro-pastoral practices and for analyzing their local experience of Neolithization. This thesis thus synthesizes available bioarchaeological information and conducts further stable isotope analyses on human and animal remains, with a particular emphasis on the different socio-biological categories of the community (e.g. males-females, children-young adults-old adults, migrants-locals), in order to examine in which extent the reduction of the residential mobility during the Mesolithic, the increased climate oscillations at the Early-to-Middle Holocene transition, and the Early Neolithic human migrations might have been associated with changes in dietary strategies and social organization. By cross-linking various biochemical signals (strontium radiogenic signal and stable isotopes) with information about ancestry (genetic lineages) and about the mortuary context, this study also explores some patterns of cultural transmission between migrants and locals and some mechanisms of subsistence adaptations upon successive generations. Considering landscape, cultural and biological differences noticed between the Inner Gorges and the Downstream Area, an area rather overlooked by previous biochemical paleodietary studies, a special attention has been paid on sampling Early Neolithic individuals buried downstream, in a particular attempt to examine the behavioral and ecological differences between the different parts of the Gorges and to consider possible spatial differences in the spread of the Neolithic way of subsistence. Finally, perinates, infants and children discovered in different Mesolithic and Neolithic mortuary contexts were analyzed in order to reconstruct maternal nutritional choices, breastfeeding, weaning and post-weaning feeding practices, and to examine thereby the relationships between changes in terms of feeding strategies, sedentism, the adoption of agropastoral practices, and demographic behaviors during the foraging-to-farming transition.

For this purpose, the analysis of $\delta^{34}S$ ratios - only tested as a pilot study in the Gorges - has been systematized on human and animal remains in view of obtaining further information about the origin of the proteins consumed (terrestrial versus different aquatic species; protein from a different environment). $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were analyzed from bone and teeth collagen of children at an intra-individual level in order to obtain information about maternal dietary choices and children feeding strategies. This thesis thus presents the first intra-individual systematic stable isotope analysis of prehistoric remains from the Danube Gorges prehistoric sites and is the first, to our knowledge, to present intra-individual $\delta^{34}S$ values associated with the period of breastfeeding and weaning. $\delta^{13}C$enamel was also extracted, as a pilot study, from teeth enamel formed during teenage in order to reconstruct the energy part (lipids and carbohydrates) of the diet, and to examine, when compared with bone collagen formed later on during life, possible shift in diet between teenage and adulthood. Published stable isotope ratios ($\delta^{13}C$collagen, $\delta^{15}N$, $\delta^{34}S$) have been audited for collagen preservation and chronologically re-assessed in the light of the extensive radiocarbon database made available over the last decades. These biochemical data are interpreted in the light of other available bioarcheological information, notably from the fields of archaeozoology, archaeobotany, paleogenetic, physical anthropology, and paleodemography.

Structure of the thesis

The next chapter (**chapter 2**) details the cultural and biological context of the Mesolithic and Neolithic Transformations in the Danube Gorges, with a special emphasis on available information concerning subsistence, migrations, health and demographic fluctuations. Then, the third chapter of this thesis presents the material and methods of this study (**chapter 3**), and particularly the principles of biochemical paleodietary reconstructions, sampling strategies and protocols of collagen extraction and stable isotope analyses. The two following chapters detail the results of the study: firstly, concerning adults' dietary strategies, then concerning maternal nutritional choices and children feeding practices and finally between teenage and adulthood. The stable isotope values from the adults' bone collagen (**chapter 4**) are examined per period, areas, according to sex, age at death, origins and genetic lineages. Changes and differences in terms of protein intake are discussed in the context of sedentism, subsistence intensification, social organization, migrations, and European Neolithization. Results concerning maternal nutritional choices and children feeding practices are presented in two parts (**chapter 5**): the results of perinates' bone collagen analysis are firstly described to reconstruct mothers' protein intake during pregnancy; the results of the collagen of different tissues formed during childhood are then presented to examine the diet of lactating mothers, breastfeeding and weaning strategies. A particular attention is paid on the physiological and metabolic effects which may have influenced stable isotope values during pregnancy, lactation, weaning and over the growth of a child. These results are finally discussed in the light of other studies of children feeding practices at the foraging-to-farming transition. The sixth chapter reports the first results of a pilot study of $\delta^{13}C$enamel (**chapter 6**) analyzed on tissues formed during teenage to assess changes in the energy part of the diet (lipids and carbohydrates). These results open some prospect to examine possible shifts in diet between teenage and adulthood, and thus to further consider subsistence transitions experienced at the individual level. The final and concluding chapter (**chapter 7**) summarizes the main results of this thesis, emphasizing, on one hand, the contributions of this study to our understanding of dietary adaptations during the first part of the Holocene in the Danube Gorges, and on the other hand the methodological contributions and concerns in the use of stable isotope analyses and opens prospects of research on the Ecology and Ethology of the Danube Gorges Mesolithic-Neolithic population.

2. The context of the Mesolithic and Neolithic Transformations in the Danube Gorges.

The Danube river is an important route way throughout Europe, and hence played an important role in the diffusion of the agro-pastoral way of life into Europe (Figure 2). The topography of the Gorges offered many shelter places attractive for prehistoric human occupations and provided a natural corridor between Southeastern and Central Europe for the spread of human populations, the exchange of goods and ideas. More than 25 prehistoric sites have been discovered in the region of the Danube Gorges and related to the local Epipaleolithic "Clisurean" culture, the Mesolithic-Neolithic "Schela Cladovei - Lepenski Vir" culture, or the Neolithic "Starčevo - Cris" culture (Boroneanţ 2000). These sites document the gradual behavioral transformations of mobiles groups of Epipaleolithic foragers (ca 13.000-9500 cal BC), to sedentary fisher-hunter-gatherers of the Mesolithic period (ca. 9500-6200 cal BC) and early pottery users who practiced animal husbandry during the Neolithic period (ca. 6200-5500 cal BC).

Figure 2: Map of the Danube Gorges showing principal Epipalaeolithic, Mesolithic and Neolithic sites. From Borić 2011.

2.1. Geographical settings and history of research

2.1.1. The region of the Gorges: location and landscape

The region of the Danube Gorges forms an approximately 130 km stretch of the Danube River, as the Danube leaves the Pannonian plain, separating the Carpathian Mountains from the North-Western foothills of the Balkans Mountains, to enter the Wallachian plain downstream (Figure 3). The Danube Gorges is one of the longest (more than 100km in total) and largest (each gorge being ca 150-200m wide) gorges in Europe and a particularly rich geological formation, consisting of sedimentary, metamorphic and magmatic rocks of different ages and structures (Popa 2003). The upper section of the Inner Gorges (referred in this thesis as "the **Upper Gorges**") consists of the Golubačka and the Gospođin Vir Gorges. Most of the Mesolithic-Neolithic sites in this section have been discovered in the Gospođin Vir Gorges in small terraces at proximity of whirlpools and rapids caused by the particular local geology[11] (e.g. sites of Padina, Lepenski Vir and Vlasac on the right bank of the river). A further downstream, the lower section of the Gorges (referred in this thesis as "the **Lower Gorges**") consists of the Kazan and the Sipska klisura gorges. The Kazan gorges (divided in great and small Kazan) are narrow with an irregular riverbed, high cliff walls and many rapids. Rock-shelters have been discovered there, including notably Epipaleolithic horizons of occupation (Climente I and II, Cuina Turcului on the left bank of the Danube) as well as Mesolithic-Neolithic open area sites (e.g. Icoana, Razvrăta, Veterani on the left bank and Hajdučka Vodenica on the right bank). In Sipskak lisura, the fourth gorge, strata are also often protruded from the water creating dangerous rapids. Mesolithic-Neolithic settlements have been found at the very exit of this Gorge (e.g. Ostrovul Banului and Schela Cladovei). The relief became much more moderate when entering the Downstream Area. The river is there flanked by a broad alluvial plain, comprising a series of terraces where other prehistoric settlements have been discovered (e.g. Ajmana, Velesnica, Kula, Knjepište and Ušće Kameničlog potoka in the right bank and Ostrovul Corbului and Ostrovul Mare in the left bank). Between the Lower Gorges and the Downstream Area, the Danube forms a large loop; the localities of the right bank of the Upper Gorges (e.g. Padina, Vlasac, Lepenski Vir) may hence have been connected to the most downstream localities (e.g. Velesnica) via a shorter way in the hinterland across the Miroč plateau (Radovanović 1996a).

Figure 3: Views of the different parts of the Gorges. Top left: the gorge from Lepenski Vir in the Gospođin Vir, looking towards Vlasac (©Ivana Radovanović 2008, from Bonsall et al. 2008). Top right: view of Kazan Gorge, where are located the cave sites of Climente II, Cuina Turcului and Veterani terrace (from Wikimedia Commons Contributors 2018[12]). Bottom: the confluence of the Zamna river in the Downstream Area, between the sites of Velesnica and Kula (© Ivana Radovanović, 2008, from Bonsall et al. 2008).

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[11] Cutting through greenish slate, Jurassic sandstones, and quartz porphyries, erosion caused the deepening of whirlpools, creating a number of large caldrons in the riverbed up to 30 m deep. Large protruding rocks has meant that this section of the river was notoriously difficult to navigate, clues of which are in the Gorge's name, 'Lady's vortex' (Borić 2002a)

[12] Danube near Iron Gate 2006.JPG. (2018, February 6). *Wikimedia Commons, the free media repository*. Retrieved 09:51, March 03, 2020 from https://commons.wikimedia.org/w/index.php?title=File:Danube_near_Iron_Gate_2006.JPG&oldid=285615200.

Due to the specific geomorphology, the arena of the Gorges provided a privileged environment for the formation of prehistoric settlements. Today, the climate in the Gorges is warmer in winter and cooler in summer with 20% less rainfall than surrounding areas (Radovanović 1996a). The flora of the Danube Gorges is incredibly rich and diverse, both in terms of taxonomy and ecology, due to the variability on soil formations. Several phyto-regions overlap at this location which is also a refugium for various tertiary relic plant species (Mišić et al. 1969; Mišić 1981). The presence of rapids and whirlpools, created by irregularities in the riverbed resulting from the differential erosion of the underlying rocks of various natures, provides one of the best places in the region for fishing large species of migratory sturgeons, which has been extensively documented ethnographically (Acipenseridae; e.g. Borić 2002a; Bartosiewicz et al. 2008; Živaljević 2017). It has been suggested that sites with Mesolithic-Neolithic sequences are located exactly at those best places for practicing whirlpool fishing (ibidem). During prehistory the riverbanks were probably covered by oaks forests (Filipović et al. 2010), likely occupied by numerous species of wild game (Bökönyi 1972, 1978; Dimitrijević 2000, 2008). All these aspects of the local ecology should have significantly contributed to the development of the long-lasting occupation of the Gorges and to the adaptation to a rather sedentary way of life.

2.1.2. Discovery of the prehistoric sites

Most sites of the Gorges have been discovered during the 1960's and the early 1970's in the course of the construction of the first hydroelectric plant Đerdap (Iron Gate) I (Figure 3). The archaeological rescue excavations have been undertaken at the following Paleolithic to Neolithic sites (Borić 2011): Alibeg (1971), Vodneac (1970), Padina (1968-1970), Stubica (1970), Ilishova (1970). Izlaz (1970), Lepenski Vir (1965-1970), Vlasac (1970-1971), Cuina Turcului (1961-1964-1969), Climente I (1964-1965, 1968-1969). Climente II (1961, 1968-1969), Veterani Cave (1964-1966), Veterani terrace (1968-1969), Hajdučka Vodenica (1966-1969), Răzvrata (1967-1968), Icoana (1967-1969), Ostrovul Banului (1966), Schela Cladovei (1965, 1967-1968) et Donje Butorke (1964). A second phase of excavations then begin in the late 1970's and early 80's with the creation of the second dam (Iron Gate II), a further downstream (Borić 2011): Ajmana (1981–1982 and 1984) Knjepite (1982-1983), Kula (1980-1984), Ostrovul Corbului (1972 - 1976, 1977-1980), Ostrovul Mare km 873 and 875 (1978), Ušće Kameničlog potoka (1981), and Velesnica (1981-1982).These archaeological sites were subsequently submerged due to the creation of an artificial lake, raising the water level from 13 up to 30 m above the previous river level. Further excavations have been possible only at two sites which were not entirely submerged: Schela Cladovei(excavated more or less continuously between 1981 and 2007; Boroneanț 1990, 2000; Bonsall et al. 1997; Boroneanț et al. 1999; Boroneanț and Dinu 2006; Boroneanț 2012) and Vlasac (re-excavated between 2006 and 2009; Borić 2006; 2007c; Borić 2008; Borić et al. 2008). Finally, in 2005-2006 the site of Aria Babi was also discovered on a hill facing the Danube above the Upper Gorges; it is the only occupation of the right bank located more in the hinterland (Borić and Starović 2008).

2.1.3. The chronological debate

Local Mesolithic pottery makers

During the past 40 years of works on these sites, a long-lasting and though-stimulating debate focused on the interpretation of the chronological sequence, required condition to further understand the mechanisms of foragers' adaptations and the origin of farming in the region. One of the key disagreements concerned the interpretation of structures observed at some sites but undocumented elsewhere in Europe: the red-plastered trapezoidal buildings with central hearths and statuaries, discovered in contexts associating typically Mesolithic-like cultural features, but also aspects characteristics of the first Neolithic societies. The main excavators of two adjacent sites on the right bank of the Upper Gorges - Lepenski Vir (D. Srejović) and Padina (B. Jovanović) - had differing interpretations of these trapezoidal structures: B. Jovanović considered that most buildings should be associated with the development of the Early Neolithic in the region because of the presence of ceramics on the floors of Padina (Jovanović 1969), while D. Srejović claimed that these structures at Lepenski Vir should be understood as a local Mesolithic achievement and explained the presence of ceramics by incursions from later Starčevo (Neolithic) occupational layers (Srejović 1969). According to D. Srejović the "culture of Lepenski Vir"[13] was an authentic local phenomenon, formed independently of similar phenomena in the Middle East (Srejović 2001a). In the next decades, several scholars, such as B. Voytek, R. Tringham, J. Chapman and I. Radovanović, tended to consider that the appearance of settlements with specific forms of architectures, sculptures and numerous burials, should be linked to "complex" Mesolithic foraging communities, but also assumed that this degree of social complexity should have been triggered by the exchanges of goods with the first farming communities of the region (Voytek and Tringham 1989; Radovanović and Voytek 1997; Tringham 2000) or by the need to preserve territories and to maintain identities (Chapman 1989; 1993; border or frontier model). D. Borić further emphasized the limits of associating such fixed "Mesolithic" and "Neolithic" labels with the "foraging" and the "farming" ways of subsistence when coming to characterize socio-cultural identities, considering that their dichotomization would inevitably result in the identification of patterns of acculturation or of resistance (Borić 1999; 2005b; 2005c).

It is the publication of photos showing in situ pottery on the trapezoidal house floors which finally threw D. Srejović's periodization into doubts, advocating for the need to a reconsider the chronological correlations between the final centuries of the Mesolithic in the Danube Gorges and the spread of the early Neolithic communities in the region (Garašanin and Radovanović 2001). Important radiocarbon dating programs undertaken from the end of the 90's have shed new lights on the chronological sequence, with almost 300 dates being published until today (Figure 4; Bonsall et al. 1997, Boroneanţ 2000; Păunescu 2000; Cook et al. 2001; Whittle et al. 2002; Bonsall et al. 2004; Borić and Miracle 2004; Dinu et al. 2007; Borić and Dimitrijević 2007; Bonsall et al. 2008; Borić and Dimitrijević, 2009: Cook et al. 2009; Borić et 2011; Bonsall et al. 2015; Borić et al. 2018). Concerning the absolute dating, a research effort had to be firstly dedicated to methodological concerns related to the identification of a "freshwater reservoir effect" since the first dates obtained on human remains appeared older than they should be due to the intake of old carbon from the consumption of aquatic resources (e.g. Cook et al. 2002, 2009). Jointly to the re-interpretation of the stratigraphy at Lepenski Vir (Borić 1999; 2002a and b, 2008; Garašanin and Radovanović 2001; Borić et al. 2018), radiocarbon dates provided the confirmation that the red-plastered floor trapezoidal buildings were in used around 6200 - 5900 BC, i.e. at the time of the spread of the earliest Neolithic in the Central Balkans (e.g. Borić 2011; Borić et al. 2018). However, radiometric dates associated with some red-plastered floors vaguely of trapezoidal shape discovered at the site of Vlasac have also shown that the earliest forms of trapezoidal buildings may have appeared as early as the beginning of the 7th millennium BC, but likely faded away in the course of 7th millennium before being revived again at Lepenski Vir (Borić 2008, 2011). Given that the practice of making red-plastered floor has been documented at PPNB (8550 – 6750 BC) and PPNC (c. 6750 – 6300 BC) sites of Anatolia, it has been hypothesized that the identification of such floors associated with Late Mesolithic horizons may indicate a very early phase of contacts with some Near-Eastern Neolithic communities (ibidem). The reappearance of more sophisticated floors at Lepenski Vir may have been triggered by a new series of more intense contacts after 6200 BC (ibid.). It has also been shown that some of these buildings may have been still in use at Padina during the Neolithic (Early Starčevo) phase of occupation of the site (Borić and Miracle 2004; Jovanović 2008). In addition, the new radiocarbon dates have confirmed the very long span of the occupation of the Mesolithic-Neolithic Gorges, the earliest Holocene settlements dating back to the 10th millennium BC and all sites being abandoned in the mid-6th millennium BC, during the development of the full farming Late Neolithic period associated with the Vinča culture (Borić 2011).

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[13] as defined by D. Srejović (1966), later called "the Schela Cladovei - Lepenski Vir " culture by V. Boroneanţ, responsible for the excavations at Schela Cladovei on the left bank of the river (Boroneanţ 1989; 1999).

The chronological frame

This thesis uses the period labeling adopted by Borić and Dimitrijević (2007 and 2009; Borić 2011), which drawn upon these stratigraphic and radiometric chronological reassessments (Figure 4; Figure 5). After an **Epipaleolithic** occupation at some rock-shelter sites (circa 13.000 – 9700/9500 cal BC), the Mesolithic horizons can be divided into two periods: the **Early Mesolithic** (circa 9700/9500 -7400 cal BC), which sees the first open-air sites with hearths, stone structures and numerous ground burials, is followed by the **Late Mesolithic** (circa 7400 - 6200 cal BC), characterized by an important intensity of occupation and network of settlements, the first form of red plastered floors buildings, rectangular stone central hearths and numerous burials. After 6200 cal. BC local foragers likely came into contacts more intensively with the Neolithic communities settled Southern in the Balkans peninsula, and started to create more sophisticated forms of trapezoidal buildings with plastered floors and statuary, and to adopt a part of the Neolithic package (e.g. ceramics, some adornments). The term **Transformation/Early Neolithic** (circa 7400 - 6200 cal BC) has been advocated to label this period as a substitute to "Transitional", rather connoted by the linear and pre-determined conception of a fixed trajectory toward the Neolithic way of life (Borić 2005b and c). Finally, the Early/Middle Neolithic period - also considered as the **Neolithic period** (circa 6000/5900-5500 cal BC) - is featured by further changes in terms of settlements (abandonment of trapezoidal buildings at most sites), material culture (intensified presence of different aspects of the Neolithic cultural repertoire, new ovens, appearance of bone spoons), beliefs (change in funerary practices, symbolism) and subsistence (e.g. adoption of animal husbandry).

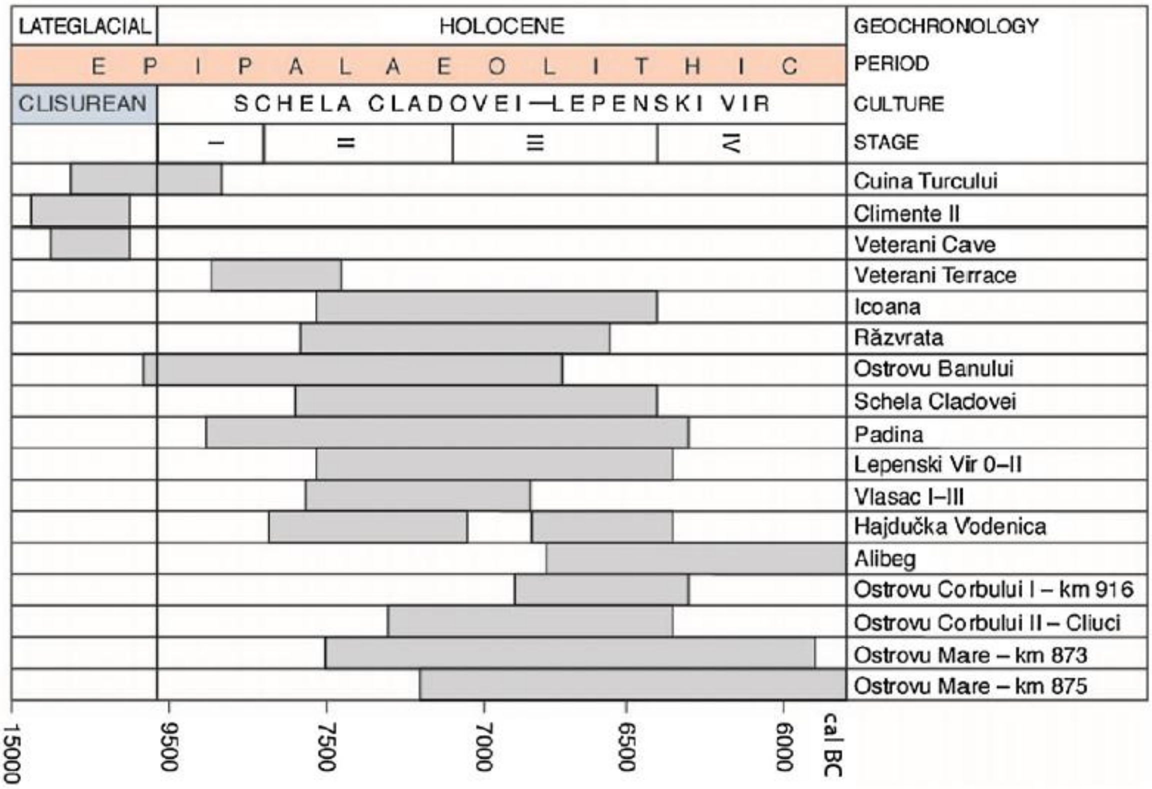

Figure 4: Periodization, chronology and terminology of the later Stone Age in the Iron Gates, according to Boroneant, (2000). From Bonsall 2018.

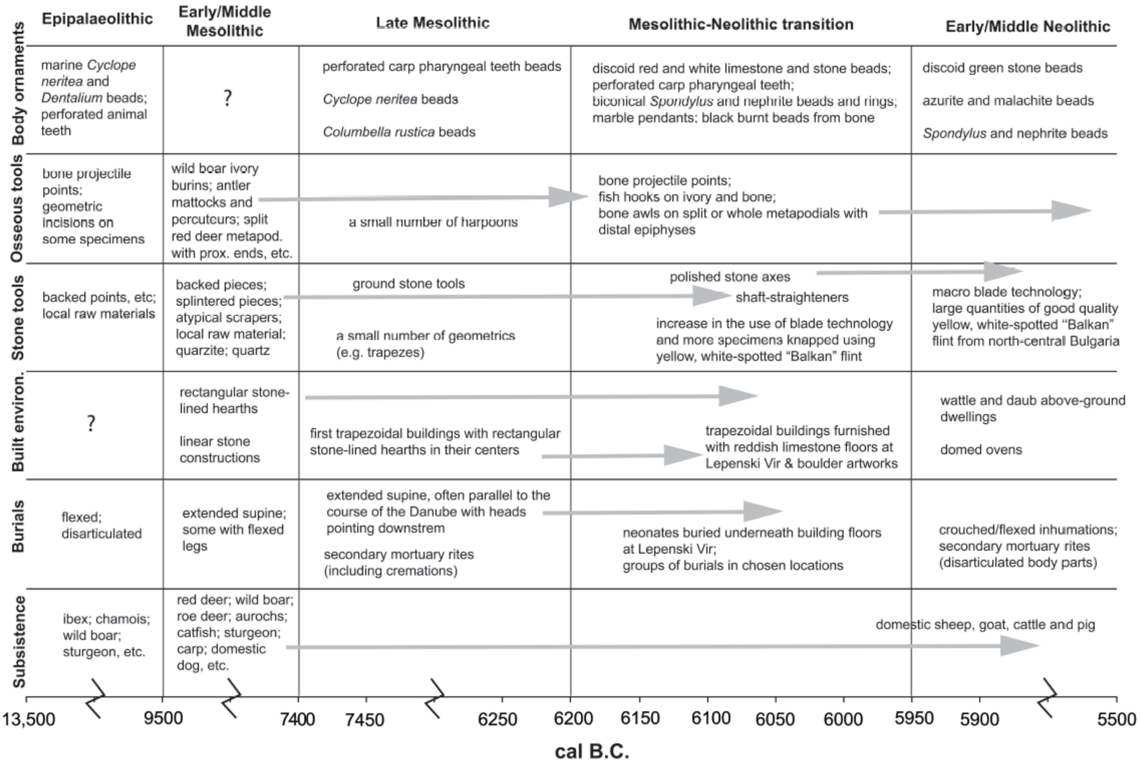

Figure 5: Summury of the Mesolithic-Neolithic developments in the Gorges. From Borić and Price 2013.

Settlements with architectural features, artefacts and patterns in mortuary practices will be presented per chronological periods in the next section "Chrono-cultural overview", while a further section "Bioarchaeological overview" will particularly focus on the current bioarchaeological state of art concerning subsistence, health and population dynamics during the Mesolithic and Neolithic Transformations.

2.2. Chrono-cultural overview: settlements, artefacts, and burials

2.2.1. The Epipaleolithic period

2.2.1.1. Settlements

The earliest radiocarbon date for human presence in the Danube Gorges is associated with the Epipaleolithic period (13.000 – 9700/9500 cal BC) Borić 2011). This period, originally named Clisurean by the Romanian archaeologists after the local name for the Gorges Clisura (Boroneanţ 2000), is featured by the occupation of rock shelters such as Cuina Turcului and Climente II, and a front terrace (Veterani) on the left bank of the Danube. Structured hearths, bordered by stones or perhaps parts of broader dug-in structures, have been reported (Boroneanţ 2000).

2.2.1.2. Stone and bone industries

Lithic tools should have been primarily used for hunting, as part as projectiles tools, or for carving meat, leather working and fur processing, but also for working other raw materials (bone or wood), engraving, drilling or boring objects of diverse materials (Boroneanţ 2000; Mihailović 2008). The local Epipaleolithic chipped stone industry is characterized by the use of microlithic tools. Backed points, scrapers, bladelets, burins and borers, raclettes and splintered flakes were mostly made on-sites with the local grey flint, but also with quartz and quartzite. The pronounced standardization of tools and the high degree of selectivity of the raw material may indicate an important level of specialization in the local Epipaleolithic production of artifacts (Mihailović 2008). The casual presence of some obsidian pieces, material probably originating from the TokAJ Prešov region (modern day Slovakia and Hungary), indicates a substantial degree of mobility and the existence of long-distance connections (Boroneanţ 2000, Păunescu 1970, 2000; Mihailović 2008). At some sites, such as Cuina Turcului, the ratio of faunal remains and the lithic raw material used points to the greater exploitation of resources in the immediate vicinity of the settlement (base camp?); since some elements also point to broader regional mobility (e.g. obsidian), it is possible that these sites may be parts of a broader "logistical system of settlements" (Mihailović 2008:15).

Animal long bones, ribs, tusks or antlers were used as raw material to make awls, fishhooks or projectiles (Boroneanţ 2000; Mihailović 2008). These tools could be used as part of everyday tasks, like fishing, hunting or making clothes. Some bone artifacts were decorated with rectilinear geometric patterns, zigzag and net motifs which bear similarities to decorated osseous objects found at various contemporaneous epigravettian sites across the Apennine Peninsula and other areas of the Balkans (Mărgărit 2010; Borić 2011). The possibility of long distance connections is also supported by the presence of items related to body decoration, such as beads and appliqués, and particularly ornaments made of the marine shell Cyclope neritae (Borić and Cristiani 2016; 2019); dentalium beads, perforated animal teeth and gastropods shell were also used as adornments (ibidem).

2.2.1.3. Burial practices

Human remains were recovered at Cuina Turcului cave, mostly as scattered bones or clusters of disarticulated bones in several different locations within the rock-shelter (minimum 6 individual), although the excavator did not rule out the possibility that they may represent disturbed burials (Păunescu 1978). However, the radiocarbon measurements of two individuals date them back to the later, Early Holocene, occupation of the Gorges circa 9850-9250 cal BC (Bonsall et al. 2015a). One articulated burial has been found at Climente II; the individual was buried in a contracted position within a pit, with red ochre deposited above the body (Boroneanţ 2000). Flint artifacts (a scraper and two crescents) and a bone spear were found accompanying the deceased. Another disarticulated child skull and teeth were also found in the immediate vicinity.

2.2.2. The Early Mesolithic period

2.2.2.1. Settlements and architecture

The beginning of the Early Mesolithic in the Gorges (9700/9500 – 7400 cal BC) coincides with the climatic improvement of the Early Holocene and has been related to a move from caves and rock shelters to open-air sites (Boroneanţ 2000). Indeed, sporadic traces of human presence during this long period has been attested on several river terraces of the right (Padina, Lepenski Vir, Vlasac, possible layers at Hajdučka Vodenica) and the left (Razvrăta, Icoana, possible layers at Ostrovul Banului, Ostrovul Corbului, Schela Cladovei and Veterani terrace) banks of the Danube, likely at attractive fishing places (Radovanović 1996, Borić 2011).

Elements of constructions have been found as partially preserved elongated and circular stone structures and some rectangular stone-lined hearths, yet perhaps dated to a later phase of the Early Mesolithic (first half or mid-8th millennium BC; Borić and Miracle 2004; Jovanović 2008; Bonsall 2008; Bonsall et al. 2015a; Borić and Dimitrijević 2009; Borić 2011). These elements of solid constructions associated with vast burial grounds indicate the increased frequentation of the riverbanks, perhaps associated with decreased residential mobility. It is possible that the intensity of Later Mesolithic and Neolithic occupation may have damaged Early Mesolithic contexts at many locations, undermining thereby our understanding of chronological, cultural and occupational specificities (Borić 2011).

2.2.2.2. Stone and bone industries

Concerning chipped stone tools, the continuity with the Epipaleolithic tradition is marked in the repertoire of tools with the presence of backed pieces, geometric artifacts, and scrapers, suggesting that the sites were particularly oriented towards hunting (Mihailović 2008; Mitrović 2018). However; flakes predominate in the assemblage and a low variability in the type of tools and in the level of tool standardization has been noticed (ibidem); a decrease has also been observed in the level of raw material selectivity (almost always local raw material, grey flint, and also quartzite and quartz; ibid.). The narrowing of the repertoire of artefacts, the increased use of flakes and the low level of selectivity in raw material contrasts with the Epipaleolithic chipped stone record; it could be interpreted as a consequence of modifications in hunting strategies related to the environmental changes of the Early Holocene (increased exploitation of forests' game), of longer stay at habitation sites where different activities were performed (reduced residential mobility), and thus of the disintegration of previous Epipaleolithic system of settlements (logistical network of settlements, nature of occupations and type of activities conducted within the sites).

Amongst bone artifacts, awls and projectiles still prevail, in continuity with previous traditions, while tools made of antlers and tusks of wild boar were encountered in small quantity, for instance wild boar ivory burins or antler mattocks and percuteurs found at Lepenski Vir (Radovanović 1996a, Boroneanţ 2000, Beldiman 2005). The tradition of engraved bone and stone objects continue during this period, with a more limited repertoire of motif decorative though (Mărgărit 2010, Borić and Cristiani 2016, 2019).

2.2.2.3. Burial practices

The Early Mesolithic is featured by the presence of numerous burials discovered at almost all sites, with the greatest number of individuals discovered at the site of Padina where distinct disposal areas have been evidenced (Radovanović 1996, Roksandić 1999, Borić and Miracle 2004, Jovanović 2008). Extended inhumation was the norm and individuals were often placed perpendiculars to the Danube (Radovanović 1996, Roksandić 1999, Wallduck 2013, Bello et al. 2016). At Padina, the remains of at least twelve individuals were found in and below an "elongated stone construction"; large stones had been placed upon individuals burials to form a sort of long cairn, probably used during a long period of time (radiometric dates of two individuals respectively 9250 - 8790 cal BC and 8450 to 7960 cal BC, Borić and Miracle 2004). Amongst the disarticulated burials discovered at the shelter-cave of Cuina Turcului, the two individuals who have been ^{14}C-dated are assigned to the Early Mesolithic period (Bonsall et al. 2015a). A particular burial rite documented at several contemporaneous sites has been associated with the later phase of the Early Mesolithic period, after 8500 BC: seated burial with crossed legs (Borić 2011). One such burial was found at Lepenski Vir and also at Vlasac, while at Padina, two individuals were for sure deposited in this specific position[14] (Figure 6; Radovanović 1996, Roksandić 1999, Jovanović 2008, Borić 2011). It has been hypothesized that this body position may have been reserved for important individuals as a form of special body treatment (e.g. Radovanović 1996a), but it can also reflect a particular and chronologically limited cultural practices, possibly associated with a specific group-clan of foragers.

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[14] the documentation is less clear for four other individuals due to burial disturbances (Jovanović 2008). Other burials with similarly crossed legs are known from the sites of Ostrovul Corbului and Kula, but absolute datation are still required (Borić 2011).

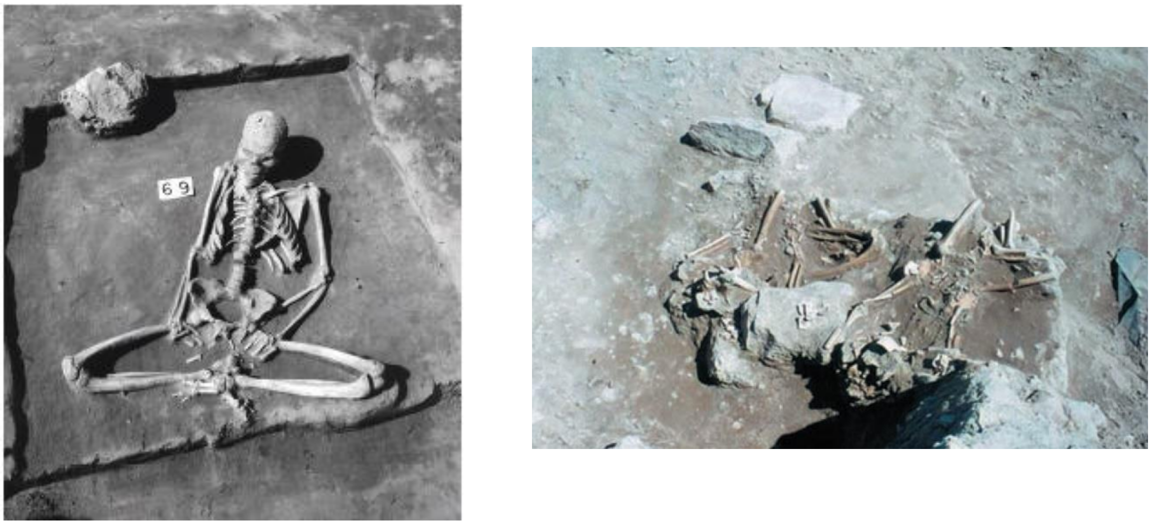

Figure 6: Early Mesolithic seated burials with crossed legs in "lotus position". Left: Burial 69, Lepenski Vir (photo: Srejović 1969). Right: Burial 17, Vlasac (photo: Center for Archaeological Research, Faculty of Philosophy, Belgrade University. Adapted from Figure 6, Borić 2011.

2.2.3. The Late Mesolithic period

2.2.3.1. Settlements

The "iconic period" of the whole Mesolithic development in the Danube Gorges started during the second half of the 8th millennium BC, with the Late Mesolithic period (7400-6200, Borić 2011). This period is characterized by a continuity of earlier Mesolithic ways of existence and occupation of locales, but also by some cultural innovations and by an important network of settlements in the whole area. This phase is particularly well documented at the sites of Vlasac (Upper Gorges, right bank), Hajdučka Vodenica (Lower Gorges, right bank) and Schela Cladovei (exit of the Gorges, left bank), and traces of human presence in this period were also noticed at Padina, Razvrăta, Icoana, Ostrovul Banului, Ostrovul Corbului, Kula and Velesnica (Păunescu 1996; Borić and Miracle 2004; Bonsall 2008; Borić 2011; Bonsall et al. 2015). In the light of the current radicarbon and cultural chronological evidence, Lepenski Vir was not occupied during approximately a thousand of years around 7400 and 6200 BC, which contrasts with the intensity of occupation at Vlasac and Schela Cladovei (Borić 2011).

Several structures with approximately trapezoid shaped-base were discovered at Schela Cladovei, and similar structures including reddish limestone floors were found at Vlasac; rectangular stone-lined hearths were also found at several sites in the Gorges, notably in the center of these buildings (Figure 7; Radovanović 1996a; Boroneanţ 2000; Borić 2011). Considering that red-plastered floors were also made in the Near-East during the PPNB (c 8550-6750 BC) and PPNC (c 6750-6300 BC) periods, it has been suggested that the examples discovered at Vlasac might have been somewhat influenced by the practices of South-western Asia Neolithic communities through long distance connections for instance via the Danube and the Black Sea coast (Borić 2011). In any cases, the use of more durable settlements could indicate a reduction of residential mobility and more durable stays at specific locations.

2.2.3.2. Stone and bone industries

A considerable number of artifacts from knapped stones, bones and horns has been discovered in Late Mesolithic contexts (e.g. Kozłowski and Kozłowski 1982, 1984, Radovanović 1996a; Boroneanţ 2000; Antonović2003; Vitezović 2011; Mitrović 2018). Quartzite-made tools prevail amongst the Late Mesolithic chipped stone artifacts and gray flint is also very frequent; these raw materials were mostly acquired locally, in the vicinity of the settlements (Mitrović 2018). Proportions of the different type of tools and raw materials indicated both "specialization" and "greater mobility", and also an "extended stay" at settlements, which, when considered all together, may suggest that foragers could have been staying longer at some sites, while frequently visiting others (ibidem). In contrast with the previous periods, the Late Mesolithic settlements may have been more oriented toward workshop activities than hunting (ibid.).

Various types of tools were also made exclusively from massive pebbles with a quite unique repertoire for the European Mesolithic, such as mallet-scepters, grindstones, hammer stones, weights, querns, anvil and sling balls. They were produced with minimal interventions and this industry developed entirely autochtonously under sedentary living condition, probably as a response to basic needs such as hunting, fishing or processing grain food (Antonović 2003). Particularly, some of these ground stones, such as mallet-scepters, have been linked to the development of a specific type of fishing big species in whirlpools (e.g. Živaljević2012).

Concerning the bone industry, numerous objects were made of antlers, a dominant raw material in many European Mesolithic cultures (Radovanović 1996). Objects made in ribs and limbs bones of deer and aurochs were also numerously found, and teeth of wild boar, deer, bear and beaver were also utilized for small artifacts (ibidem). These raw materials were used to make awls, points, needles, bores, tranchets, chisels, polishers and scrapers for everyday need; some tools made of antler were specially used for tilling soil and working wood, such as hoes, axes, hammer-axes, picks, pickaxes and plows; finally various projectiles, harpoons, fishhooks, knives and points were used for hunting and fishing (Srejović and Letica 1978; Bačkalov 1979; Radovanović 1992; Vitezović 2011). The appearance of harpoons on Late Mesolithic contexts might be associated with some changes in the local fishing practices. Perceived indirectly through the presence of other stone, bone and antler tools, wood was certainly omnipresent as a raw material in everyday life objects, hunting tools, boats and certainly architectural elements (as documented in numerous other European Mesolithic contexts, in modern days Russia, Scandinavia or British Islands). Evidence for artistic activities associated with the Late Mesolithic is quite meager, restricted to stones decorated with abstracts or figural engraved motifs.

2.2.3.3. Burial practices and body adornments

The important number of Late Mesolithic graves discovered at Vlasac and Schela Cladovei has significantly contributed to expand our understanding of European Mesolithic lifeways and deathways (e.g. Srejović and Latica 1978; Boroneanț et al. 1999; Borić et al. 2014). Individuals were most frequently deposited extended supine, parallel to the Danube, with their head pointing downstream (Figure 7). This position has been interpreted in relation to the anadromous species of fish (the sturgeons for instance) that swim upstream every spring to spawn and return back to the Black Sea in the fall; in foragers' representation of the world, the constant returning of migratory fish might have been associated with cycles of regeneration and with the idea that the "ancestral fish" may have carried down the souls of the dead foragers back to the sea (Radovanović 1996). At some sites, such as Vlasac, Schela Cladovei or Hajdučka Vodenica, burials were clustered around rectangular hearths, which may indicate that members of a clan, family or the like were buried there.

Secondary burials were also documented, whether as burials with missing anatomical parts, or as secondarily interred part of bodies, sometimes pilled or anatomically arranged (Radovanović 1996a,b,c; Roksandić 1999; Borić 2010a and b; Boroneanț and Bonsall 2012; Wallduck 2013; Borić et al. 2014; Wallduck and Bello 2016; Bello et al. 2016). Analyses of the frequency and distribution of cutmarks has suggested that partially skeletonized remains were defleshed, before being re-inhumated (Wallduck and Bello 2016; Bello et al. 2016). Cremated remains have also been discovered, and it has been suggested that the cremation should have been undertaken on dry remains rather than fleshed corpses (Borić et al. 2009). It has been noticed that secondary burials, which commonly involved the internments of skulls, were more often practiced on the remains of older men, and exceptionally of women and children (Radovanović 1996a, b, and c). These practices may have been part of specific rituals, steps in the mourning and funerary process, perhaps related to a depersonalization of the dead that helped to forget his individual identity ("dismembering"), while maintaining collective memory of the social group ("remembering"; Borić 2010b). Stones have been found above some graves, probably as markers or memorials but also inside the graves, deposited above the bodies, perhaps as a symbolic way to maintain the corpse (Boroneanţ and Boroneanţ 2010; Boroneanţ and Bonsall 2012).

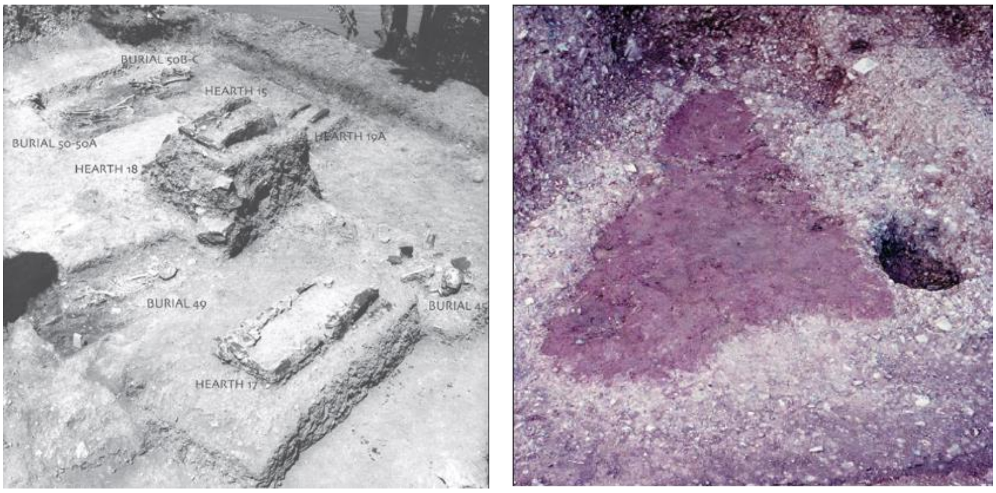

Figure 7: Vlasac, Late Mesolithic, architecture and burials. Left: burials in extended supine position and rectangular hearths. Right: dwelling 1 with reddish flooring. Photographs: Center for Archaeological Research, faculty of Philosophy, Belgrade University. From Borić et al. 2008.

Grave goods notably included red deer antlers, perhaps associated with the idea of "life-cycle", annual fall and rebirth (Radovanović 1996, Borić 2003a and b). Besides, dogs' mandibles have been placed into a few burials at Vlasac[15], and the head of a dog was also found in a pit - similar to human secondarily burials - which leads some authors to question the notion of person-beast dichotomy amongst local Mesolithic foragers (e.g. Radovanović 1999). Some parts of the bodies of some individuals buried at Vlasac and at Schela Cladovei were also covered with ocher. It has been noticed that, in the early phase of Vlasac, ocher was incorporated into burials regardless of age or sex while later the men were excluded from these practices, and the pigment was sprinkled only on the pelvic area of women, and on perinates (Radovanović 1996; Borić and Stefanović 2004). 26 fetus and perinates were uncovered at Vlasac, the majority of them buried in graves with women[16], probably as the consequence of the death of the mothers following complications experienced during pregnancy or during the birth process (Borić and Stefanović 2004). This restriction of ocher use to females' pelvis and to perinates suggests that there should have been a particular concern for the death of pregnant women, a "communal focus on a misfortune in respect to miscarriages" (Stefanović and Borić 2008:158). The association between birth and death hence highlighted by the deposition of red ocher on the dead bodies of babies and mothers also echoes the idea of "life-cycle", which may have been playing a central role in forager's representation of the world (e.g. Radovanović 1996a,b,c, Borić 2003a and b). Interestingly, at some Neolithic sites of Anatolia such as Çatal Höyük (partly contemporaneous of the late Mesolithic occupation of Vlasac), some females and juveniles were also buried with ocher, often in domestic contexts (Stefanović and Borić 2008).

The long-distance connections of Late Mesolithic foragers are also suggested by the presence in the graves of ornaments made of certain species of marine shells (Cyclope neritae and

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[15] As well as one Transformation/Early Neolithic burial at Lepenski Vir (Radovanović 1999)

[16] In most cases the perinate or young infant was found associated with the adult; in the burial 67, a female was found covered with ocher and with the bones of a foetus located in the pelvic area (Srejović and Latica 1971; Borić and Stefanović 2004)

Columbella rustica) in some burials from Vlasac and Schela Cladovei, alongside with appliqués made of carp teeth (Cyprinidae pharyngeal teeth) which are unique to the region. These ornaments were most likely originally sewn onto a garment which adorned dead bodies and also primarily accompanied females as well as children[17] (Borić and Stefanović 2004; Cristiani and Borić 2012; Cristiani et al. 2014; Borić and Cristiani 2016, 2017a and b; 2019).

2.2.4. The period of Transformation/Early Neolithic

2.2.4.1. Settlements

The Transformation/Early Neolithic phase in the Gorges (6200-6000/5900 cal BC) coincides with the emergence of the first cattle-breeding and pottery makers communities in the Central Balkans (Whittle et al. 2002) with whom the local inhabitants developed intensive contacts, as evidenced by the intrusion of some Neolithic technologies in a local cultural repertoire yet also characterized by a continuity with the previous indigenous traditions and unique architectural and artistic achievements (e.g. Srejović, 1972; Borić 2011). This period has been mostly defined based upon the interpretations of the stratigraphy of the eponym site of the Lepenski Vir culture, which fixed the controversy between the proponents of a "Mesolithic/Neolithic" phase (Figure 8; Srejović 1988, Voytek and Tringham 1989), a "Final Mesolithic" phase (Radovanović 1996; Bonsall 2008), an "Early Neolithic" phase (Jovanović 1969) and a "Transformation/Early Neolithic" phase (Borić and Dimitrijević 2007, Borić 2011). We favor here this last term as a better and non-linear reflection of the dynamic nature of socio-cultural changes (Borić 2005b and c).

This period - the shortest of the sequence (only three centuries) - began during the climatic oscillation of the 8.2 cooling event, at a time when many occupations of the river terraces in the Lower Gorges and the Downstream Area were abandoned (Icoana, Ostrovul Banului, Ostrovul Corbului, Schela Cladovei, Velesnica). It is still debated whether the lack of evidence of occupation might be related to the increased precipitations and magnitude of flooding or to the arrival of Early Neolithic communities further downstream (Bonsall et al. 2002b, 2015a versus Borić and Miracle 2004; Borić et al. 2008; and Borić et al. 2016). Indeed, several sites of the Inner Gorges were occupied during this period (Lepenski Vir, Hajdučka Vodenica, Vlasac, Padina, Stubica, Alibeg), while some Early Neolithic settlements, featuring different material cultural aspects characteristic of the Starčevo group, were established in the Downstream Area after 6.1 ky BC (Ajmana, Knjepište or Ušće Kameničkog potoka; radiocarbon measurement only for Ajmana; Borić et al. 2011, Bonsall et al. 2015a). Further ^{14}C dates are requested to determine whether the sites of Velesnica, Kula, Ostrovul Corbului and Ostrovul Mare - amongst the most downstream sites associated with the local Mesolithic/Neolithic settlement network - were continuously occupied between the Late Mesolithic and the period of Transformation. It is hence possible that Schela Cladovei and close-by sites located at the exit of the Danube Gorges, and previously occupied during the Late Mesolithic, may have been temporarily abandoned during the period of initial contacts with new farming groups, perhaps as "a new line was being established" (Borić et al. 2011:181), at a time when the expansion of Early Neolithic communities may have also been slowed down by the climate pejoration.

2.2.4.2. Architecture

Elaborated trapezoidal buildings with reddish limestone floors discovered at the site of Lepenski Vir and of Padina in the Upper Gorges might have been a revival of the practice of plastering floors around hearths, perhaps triggered by the contacts with Early Neolithic

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[17] for instance, the child VL 21 discovered at Vlasac has been buried with 50 perforated Cyclopae meritea shells and covered by cyprinidae teeth (Borić and Stefanović 2004)

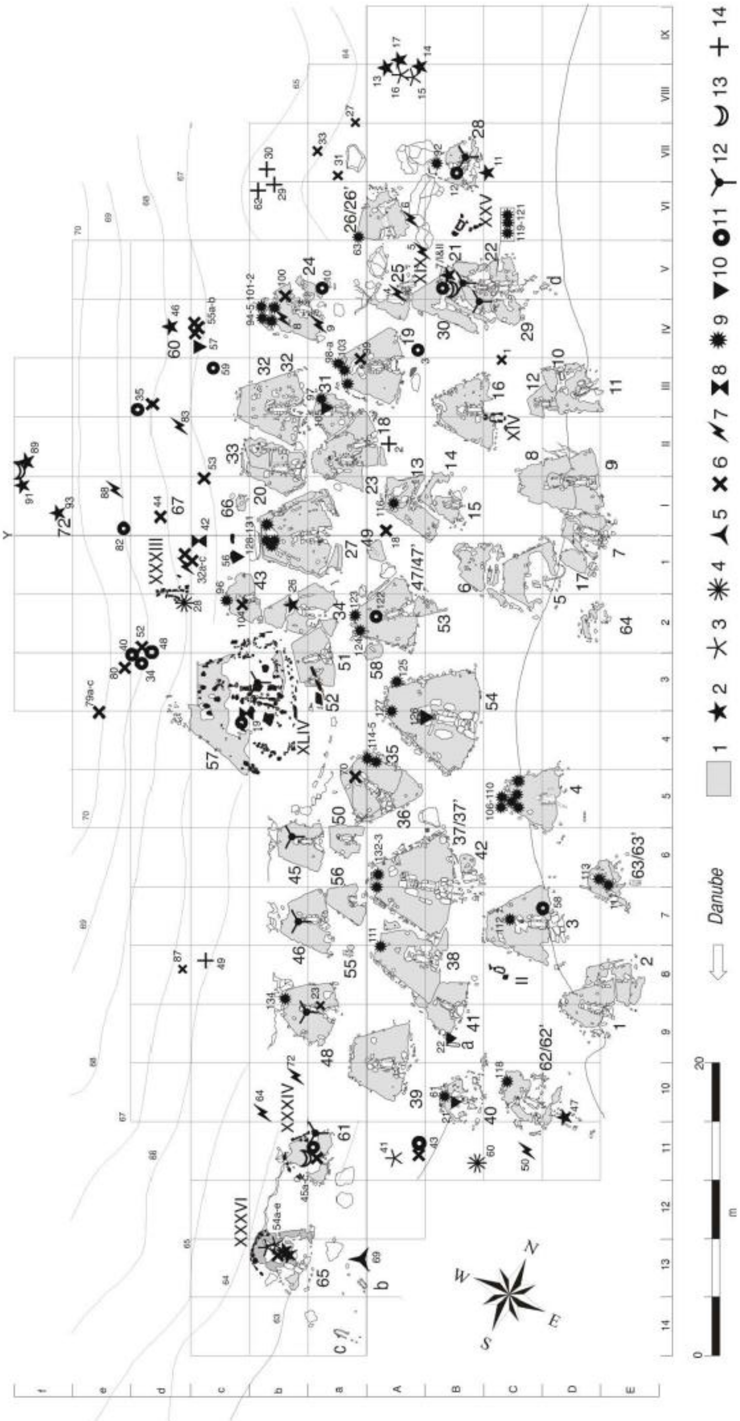
communities (Figure 8; Figure 9). The function of some features of certain trapezoidal buildings, like the A-shaped stone constructions which were surrounding some of the central hearth, remains ill-understood (Radovanović 1996a). While these buildings recall the shape of the Traskavac Mountain, visible directly across the site of Lepenski Vir (Srejović 1969, Radovanović 1996, Borić 2002a), they could also be interpreted as a reflection of the old seated burials of the 8th millennium BC (Borić 2011) and perhaps played a symbolic role in the memory of the ancestors meanwhile celebrating associated elements of the natural environment. These buildings denote the particular mixture between local Mesolithic traditions (e.g. central rectangular hearths, trapezoidal shape, and unique sculptures) and the Neolithic influences of the Southern Balkans and Western Anatolia (concept of the 'home', use of reddish limestone floors; Borić 2007b). At Hajdučka Vodenica, in the Lower Gorge, a floored area made of burned clay has also been discovered around a rectangular stone-made hearth; this structure is yet not associated to the typical buildings of Lepenski Vir and Padina by the excavator (Jovanović 1984, 2008).

At certain sites of the Downstream Area, some architectural features - and associated artefacts - contrast with what is documented in the Inner Gorges; yet, it should be mentioned that the radiocarbon dates currently available for some of these sites – Ajmana and Veslesnica – originate from human remains, and there are some methodological concerns on whether they might appear slightly older than they actually are (e.g. Bonsall et al. 2015a versus Borić 2011). It is hence possible that some should rather be dated to the end of the Transformational period or to the beginning of the next phase. Besides, it is not certain that the burials are strictly contemporaneous from dated burials. At the site of Ajmana, a floor area of "burned clay" and approximately of trapezoid shape was also discovered, including a central hearth, but also with remains of daubs around (Stalio 1986); a domed oven, found at other sites of the Gorges (e.g. Lepenski Vir, Padina and Schela Cladovei) after 6000 cal BC, was also discovered (ibidem). At Velesnica, a circular hearts of packed earth with a substructure of stones is described by the excavators; they also described concentrations of stones, pebbles, daub shells and pottery which may have served as foundation for a floor with a thin layer of mud or daub, perhaps of a rectangular and above-ground building quite typical of the Starčevo cultural group (Vasić 1986, 2008). Finally, at Kula, one of the most downstream sites, several structures have been documented, including the ground plan of a trapezoid house with a floor of packed earth and evidence for a burned beam, and a rectangular hearth with close-by triangle-shaped structures of stones which looks quite similar as the buildings known in the Inner Gorges; yet the chronology of these structures remain to be established and it is possible that some might be associated to an earlier Mesolithic phase (Sladić 1986).

2.2.4.3. Sculptures

The particular nature of the site of Lepenski Vir is also underlined by the presence of a large quantity of objects made of bone, antler, tusk of wild boar, various kind of stones, minerals and rocks decorated with abstract or figural engraved motifs (Figure 9; e.g. Srejović 1972; Rodovanović 1996, 1997). Amongst these decorated objects, sculpted and engraved boulders were embedded within the plastered floors of the habitation, considered thus as elements of stable furnishings in the habitations. They were often found at the rear of the hearth and in the left section of the habitation (ibidem). A few were placed just above the heads of deceased individuals interred in burial pits under the floor. A few such finds could also be found at Hajdučka Vodenica, Padina, the Cuina Turcului rock shelter and Velesnica. While simple depressions were created in some boulders, others were engraved with motifs of meander, angles or concentric circles, and some others clearly depict hybrid human-fish beings (ibid.). This symbolic (totemic?) association between anatomical elements of the anadromous fish and of human beings have been interpreted as further evidence for the fluidity of human and animal relationships in foragers' world (Borić 2005a, 2007a, Živaljević2012). These representations completely differ from the contemporaneous Early Neolithic clay figurines found frequently in Anatolia and the Balkans and also numerously in

Starčevo–Körös–Criş contexts representing human being, mostly females, and/or animal – often cattle. It can be noticed that at the excavations from Velesnica report two larges oval boulders with central depressions (pestles) identified as "altars" as well as a "double horned amulet made of burned clay (Vasić 1986).



Key: 1) limestone floor; 2) extended skeleton parallel to the Danube; 3) headless extended skeleton; 4) extended skeleton; 5) seated skeleton; 6) disarticulated postcranial bones; 7) contracted and flexed skeletons; 8) headless contracted skeleton; 9) skeletons of neonates and children; 10) human mandible; 11) human skull; 12) red deer skull with antlers; 13) aurochs' skull with horn cores; 14) post-Neolithic burials

Figure 8: Trapezoidal buildings and construction stones of Lepenski Vir phase I according to Srejović (after Srejović 1981) and types of burials from all phases. (from Borić and Price 2013).

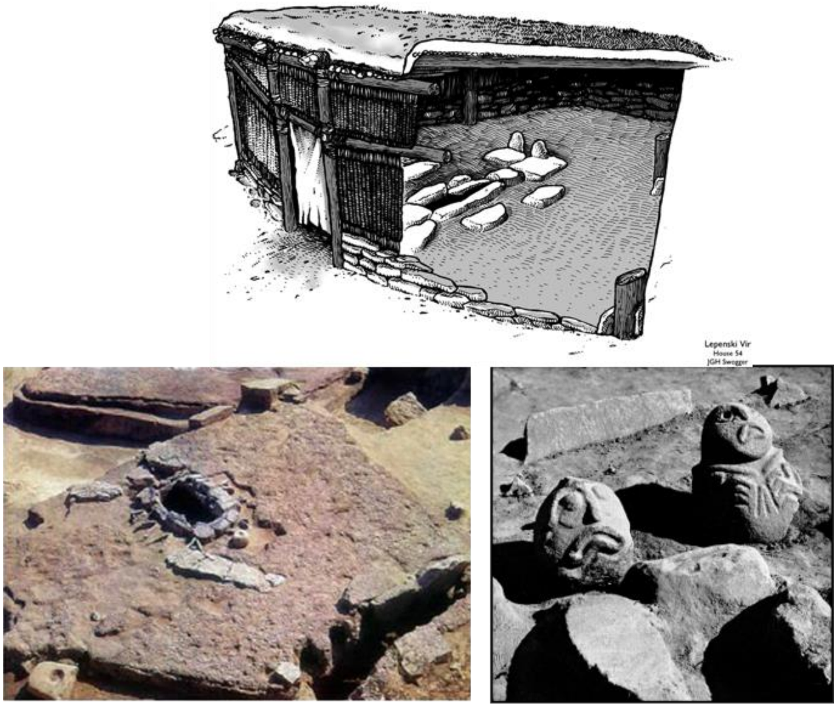


Figure 9: Architectural elements and sculpted boulders from the Transformational phase of Lepenski Vir. Top: reconstruction of Building 54 from Lepenski Vir (drawing J. G. Swogger, from Borić 2011). Bottom left: dwelling 24 with reddish floor, hearth and stone construction (from Srejović 1972). Bottom right: sculpted boulders from dwelling 44 (from Srejović 1972).

2.2.4.4. Neolithic technological novelties

In the material cultural repertoire, besides the continuity with the Mesolithic period, various typically Neolithic items also started to be used (e.g. pottery, ground stone axes, "Balkans" flint and long chipped stone blades, Neolithic-like ornaments). The pottery discovered in Transformational layers is characteristic of the Early Neolithic in the wider area - Starčevo-type fine monochrome (usually red) and white-dotted painted pottery (e.g. Garašanin and Radovanović 2001) - but assemblages of the gorges are characterized by the frequent occurrence of shallow large-size vessels on perforated foots (Perić and Nikolić 2004). These conical bowls with large opening on square perforated foots were originally identified as cult vessel ("ceramic altars") but it is now assumed that they should have been used in every days life, perhaps for cooking fish, judging by traces of use (ibidem). Besides these distinct forms, the pottery at most sites of the gorges is of spherical and hemispherical shapes. All vessels were made of clay with large quantity of organic admixtures and mostly made locally; "straw" is mentioned as an adjunct in the pottery found at Ajmana. Pottery was rarely decorated, most often with nail or nail and finger impression, and given that pottery with ornaments executed by application or painting are quite exceptional, they may have not been used for every day's life (ibid.). Weighs have been discovered at Ajmana and Velesnica and may have been used for looms or for fish nets. A domed oven in clay was also discovered at the site of Ajmana.

Another Neolithic novelty concerns the ground stone tools repertoire; while tools such as mallet-scepters, grindstones, hammer stones, or weights continue to be used during the Transformation/Early Neolithic period, a different type appears at the sites: ground-edge tools, axes, adzes and chizels characterized by a semi semi-circular cross-section and made of specific hard and fine-grained rocks of grey-greenish color (Antonović 2003). This technology, typical of Starčevo culture, was imported in the Gorges and some of the artifacts were imported as well judging by the raw material utilized. These tools were most likely used in building activities for woodworking, and probably represented an addition in the quality of life of the inhabitants of the Gorges (ibidem). A local workshop for ground axes has been evidenced at the downstream site of Velesnica (Sladić 1986).

A new material also became widespread at the end of the 7th millennium BC in chipped stone assemblages: the so-called "Balkans flint", used abundantly in the Balkans during the Early Neolithic (Radovanović 1996; Šarić 2014; Mitrović 2018). Large macro-blades with steep retouch were produced with this yellow white-spotted flint, usually connected to changes in economy towards agricultural productions. On the other hand, persistence in older Mesolithic traditions has also been observed, for instance with the presence of tranchet at Lepenski Vir (Šarić 2014). Proportions and ratios of the different type of tools and raw materials pointed to a shorter stay of communities, who reduced the range of activities that are seasonally conditioned (Mitrović 2018). It has also been noticed that the "presumed prestigious articles in the neolithization of the Iron Gates (pressure technique, Balkan flint and blade making technology) do not occur in special contexts or separate spaces, as presumed in the 'border' model of neolithization [e.g. Radovanović and Voytek 1997]. In this sense, social competition is not expressed (...)" (Mitrović 2018: abstract).

Concerning osseous industry, there is continuity in the previous Mesolithic traditions of antler working and in the particular form of boar tusk points, antler chisels and projectiles points (Vitezović 2010, 2011). New osseous technique also appears during the period for instance fishing hooks made with new mechanical drilling technique or different type of bone awls on split (Borić and Price 2013, Supp. Mat). A bone spoon – or spatula –, typical amongst the Starčevo communities of the Central Balkans, has been discovered at the site of Ajmana (Stalio 1986); a similar example has been described at Schela Cladovei and related to a context dated circa or after 6000 cal BC (Bonsall et al. 2008).

2.2.4.5. Burial practices and body adornments

The Mesolithic mortuary canon was being followed at several sites of the Upper Gorges (Lepenski Vir, Vlasac and Padina) with extended inhumations placed on their back and oriented parallel to the river, the head pointing downstream (Radovanović 1996, Borić and Miracle 2004, Borić et al. 2009, 2014; Stefanović 2016). In contrast, at Hajdučka Vodenica in the Lower Gorges, between 6400-6050 cal. BC, some burials were discovered grouped, individuals being on extended supine but with the head oriented upstream (Radovanović 1996, Borić and Miracle 2004), which could perhaps reflect the particular choice of some social group, or clan. At Lepenski Vir some burials were placed in the trapezoidal buildings, sometimes through the plastered floors, probably upon their abandonment as domestic features (Figure 10); in some cases the sculptures were placed on the floors directly above the heads of the deceased interred through the floor (Radovanović 1996b, 2000). The continuity in mortuary practices also concerns disarticulations and secondarily burials (Figure 10). A preference for the manipulation of skulls has been noticed, whether through the discovery of skull burials or of headless individuals, which could be related to the metonymic importance of this anatomical element, standing for the entire deceased individual, his personality, spirit or mindset (Srejović 1972, Radovanović 1996, Stefanović and Borić 2008). The presence of burials and particularly of disarticulated bones within the houses, often at proximity of the hearth, has been interpreted as a belief in "hearth guardians" (Srejović 1972), the idea that ancestor's bones next to the hearth may have given this area ancestral potency, acting as secondary agents with ‘powerful apotropaic potencies’ (Stefanović and Borić 2008: 165). Disarticulated remains, as well as red deer antlers, may also have been deposited at the point of building abandonment suggesting a possible association between the identity of the dead building users' and the end of the life of the structure itself (Radovanović 2000; Borić 2005a; Stefanović and Borić 2008). The presence of sculpted boulders - usually embedded in the plastered floors - above some burials also emphasizes the mutual relationship between habitations, sculptures and the identity of the deceased (ibidem).

The frequent repetition of such ritual practices which involved "the ancestors" may have played a unifying role of importance for the local communities who were then experiencing contacts with a somewhat different Neolithic ways of life (Borić 2010).

The remains of 40 neonate burials were also found, buried underneath the red-plastered floors of 17 trapezoidal buildings at Lepenski Vir (Figure 10; Borić and Stefanović, 2004; Stefanović 2006; Stefanović and Borić 2008). While the adult burials were located rather close to the hearth, the infant burials were placed in the rears of the houses, which may indicate "embodied social, age and gender boundaries in the use of building space" (Stefanović and Borić 2008: 139). Over the red-plastered floors, pits of different shape distinguish the infants' burials; stone were also used to elaborate and mark the grave. The burial rite thus evolved from a parental concern for the dead of their offspring toward a shared experience of the emotional impact of these deaths, placing the body in the center on the domestic sphere. This shift from individual to collective level may have represented an important change in local mindsets at the onset of the Early Neolithic (Borić and Stefanović 2004), and perhaps a local evolution of parenting strategies (shared responsibilities? more collective child-caring?). The red ocher which covered some parts of the bodies of pregnant women and babies at Vlasac during the previous centuries is now only found on the floors of the buildings at Lepenski Vir, evoking here also a possible association between the house and the ritual. It is possible that the infant may not have been considered as capable being protected on a dangerous journey to the underworld and therefore needed "the protection of the building, ancestral powers and apotropaic potencies anchored in these structures, their hard limestone floors, hearths and sacred heirlooms, such as sculpted boulders" (Stefanović and Borić 2008: 163-164). The practice of burying infants under the floors of buildings also points to oriental and meridional Neolithic influences given that perinates and juveniles have been found buried through house floors or associated with architectural elements or with red ocher amongst at many Neolithic sites across Anatolia and the Southern Balkans (Stefanović and Borić 2008).

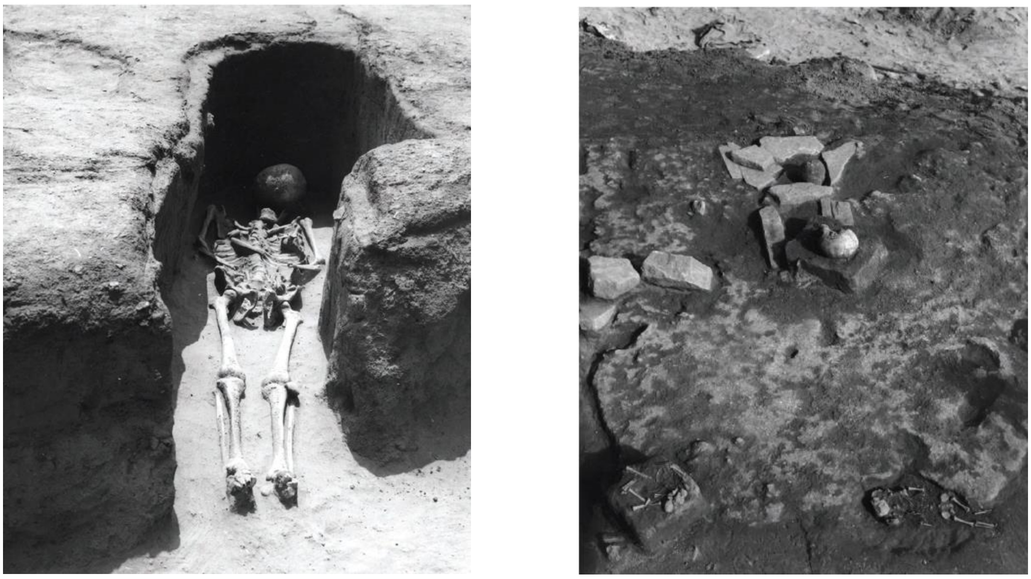


Figure 10: Burials from Lepenski Vir, period of Transformation. Left: burial 26 inserted through the plaster floor of dwelling 34 (Photo: Institute of Archaeology, Belgrade). Right: Disarticulated human cranium 122 above the hearth of dwelling 47 and perinates' burials 123 and 123. Photo: Institute of Archaeology, Belgrade. From Bonsall et al. 2008.

During the period of Transformations, a change in the type of ornaments accompanying the deceased has been identified at both Lepenski Vir and Vlasac in the Upper Gorges. While carp teeth ornaments characteristic of the Late Mesolithic body decoration in the region are retained in some burials, ornaments from Cyclope neritea marine gastropods disappear as a type of "exotic" material and beads made of Spondylus marine shell appears as a new type of long distance material for decorative items, together with reddish and whitish limestone beads and marble pendants ("amulets") (Borić 2011). Although these individuals were buried according to the typical Mesolithic burial rite, the presence of such beads indicates influences in the style of body decoration coming from the expanding network of Early Neolithic groups surrounding this region (ibidem). Particularly, some of these Early Neolithic communities may have been already occupying the Downstream Area circa 6000 BC.

Individuals buried in the Downstream Area after 6100 cal BC may have been bonded to this network: at Velesnica and at Ajmana, apart from the presence of early Starčevo cultural aspects which are undocumented at sites of the Inner Gorges for this period (e.g. use of daub in construction, domed oven; presence of a bone spoon, a fragmented bovine figurine; Stalio 1986, Sladić 1986), the burial practices also clearly sort out of what is known in the Mesolithic of the Inner Gorges. At Ajmana, a group burial contained 17 individuals - mostly juvenile - placed in flexed position upon what has been described as several levels of burial interments (Stalio 1992). At Velesnica two graves contained the remains of single crouched or tightly flexed inhumation and one grave contained the remains of seven individuals (adults and children), comprising five individuals all but one placed in a similar flexed position one above the others, as well as the articulated remains of two additional individuals (Vasić 1986, 2008). Interestingly, at the bottom of the grave one child - ^{14}C dated to the Transformations period (6205-5935 cal. BC, Bonsall 2015) - was buried in a kind of crouched position (legs crossed with foots at the tights), which recall the seated buried of the Early Mesolithic; besides, the disarticulated bones of a neonate dated to the Mesolithic (7530-7185 cal. BC; Bonsall 2015) were found associated with this skeleton. It could be hypothesized that the position of the child at the bottom of the grave may have been chosen by Early Neolithic people after they found some older grave, in reference to "the olders". At the site of Kula, an individual has also been found in seating position, as well as several individuals in supine position (Sladić 1986), but it should be kept in mind that they have not been ^{14}C dated and that these type of inhumation were practiced in the Gorges during the Mesolithic. In contrast "group burial" as documented at Ajmana and Velesnica (exemple of "collective" graves?) has not been described in the region during the previous period and the lateral flexed position is typical for the Early Neolithic period from the Near-East to Central and Western Anatolia.

2.2.5. The Early/Middle Neolithic period

2.2.5.1. Settlements and architecture

During the next period, identified as the Early/Middle Neolithic (6000/5900 to 5500 cal. BC, Borić and Dimitrijevic 2009, Borić 2011), numerous localities are occupied in the Gorges with an intensified presence of Starčevo cultural features, and animal husbandry became practiced (ibidem). Hence, the local inhabitants of the Gorges have fully adopted technological elements of the Neolithic and new aesthetics in body decoration before practicing animal husbandry. In the broader Balkans region, there is mostly continuity between the end of the 7th millennium and the first half of the 6th millennium BC, which sees a consolidation of the Early Neolithic network of settlements (Whittle et al. 2002). Many settlements used during the previous period are still occupied (Vlasac, Padina, Lepenski Vir, Hajdučka Vodenica, Padina, Alibeg, Ajmana, Velesnica) or re-occupied (Schela Cladovei, Icoana, Cuina Turcului, Ostrivul Banului, Climente). The site of Aria Babi is the only occupation discovered on a hill in the Danube Gorges hinterland (ibidem).

The architecture of these settlements is mostly characterized by semi-dug structure of irregular or rectangular bases and circular hearths; remains of daubs and wattle have only been scarcely found. A similar pattern observed at other sites across the Balkans may indicate an intentional destruction of previous above-ground dwellings by the Early Starčevo people (Borić 2008). At Lepenski Vir, most of the trapezoidal buildings must have been abandoned after 6000 cal

BC. In contrast, at Padina, some trapezoidal buildings may have been continuously used for domestic purposes. Several domed ovens, characteristic of the Early Starčevo in the region but not documented in the inner part of the Gorges before 6000 cal. BC, have been found at several sites such as Lepenski Vir, Padina, and Schela Cladovei, contrasting sharply with local traditional Mesolithic rectangular hearths.

After ca. 5500 BC, it appears that almost all previously used sites in the region were abandoned and there was a hiatus of more than one millennium before some have been re-occupied (Borić 2011). The Middle/Late Neolithic groups of the Vinča culture (ca 5400-4500 cal BC) did not reoccupy these sites and only very few sites in the region are dated to the period (sites of Gornea and Ornita-Ljubcova in the Inner Gorges; Ostrovul Golu and Zbradila-Kordovo, in the Downstream Area). From this change in settlement patterns with the start of the Late Neolithic in the Gorges, it has thus been suggested that the "fully developed agricultural ad stock-breeding economy characterizing Vinča groups completely ignored or avoided the riverine resources of the Danube Gorges, and that only a few, newly founded settlements in the region during the Late Neolithic utilized those areas more suitable for agricultural practices (Borić 2011:183)".

2.2.5.2. Ceramics, lithics and bone technology

Concerning ceramics, it has been suggested that the monochrome and white dotted painted pottery might have been exclusively characteristic of an Early phase of the Early Neolithic of the Balkans while linear and curvilinear dark painting may be rather associated with a later phase (Schubert 1999), but there is no real change in the repertoire of shapes between 6200 and 5900 cal BC.

Regarding chipped stones, a reduction in the spectrum of raw materials used over time has been noticed, with an increased used of Balkans flint (Mitrović 2018). A general increase in the use of blade technology has also been observed, while fewer pieces were produced by knapping on anvil; during the latter phase of occupation of Lepenski Vir, knapping was probably less performed at the site and the higher proportion of retouched blade tends to indicate an increased mobility of the Early Neolithic groups (ibidem).

Interestingly a retouched blade of dark grey raw material found in the hinterland site of Aria Babi yielded macroscopical traces of use suggesting its function for harvesting (Gurova, forthcoming, quoted by Borić 2011). The site of Aria Babi is the single occupation founded on the side of hill sloping toward the Danube and it may be assumed that agricultural activities might have been practiced there. Finally, concerning osseous industry, new tool types introduced during the previous period became dominant in the bone tool making repertoire of this period (fishhooks made with drilling technique; flat symmetrical awls on worked metapodial epiphyses; Borić and Price 2013, Supp. Mat). For instance, bone spoons have been discovered at the downstream sites of Schela Cladovei, Velesnica and Ajmana (Stalio 1986; Bonsall 2008).

Four ceramic hoards have been uncovered at Lepenski Vir, containing objects probably considered as prestigious goods: a necklace made from Spondylus green nephrite stone and Columbella rustica beads (hoard 1), ground stone axes (hoard 2) and blanks of "Balkan" flint, originating from present day Bulgaria (hoard 3 and 4). Besides, two beads of copper minerals have also been found (malachite and azurite), most likely originating from the near-by mining site of Rudna Glava which continued to be used in later prehistoric periods (Borić 2011).

2.2.5.3. Burial practices

A shift in terms of burial practices is associated with the 6th millennium BC at Lepenski Vir: the crouched position, typical of the Near-East Neolithic and European Early Neolithic communities (including early Starčevo of the central Balkans), replaces the local Mesolithic canon of extended supine position (Figure 11; Radovanović 1996c; Borić 2011; Stefanović 2016). Such inhumations in crouched position have also been documented in the Downstream Area at the site of Velesnica during the Transformation-Early Neolithic period and at the site of Ajmana circa 6000 BC. There are over 20 such primary burials, mostly in the backfilled areas of the abandoned houses, and a number of secondary or disarticulated burials found across the site can also be assigned to this phase. Apart from Lepenski Vir, a continuity in the deposition of human remains have been documented at some other locales with a few individuals deposited in extended supine position or found disarticulated for instance at Padina (n=1; Borić 2011) and at Hajdučka Vodenica (n=1; Borić 2011) and at Vlasac (n=3; Mathieson 2018). Although there might have been some continuity with the rituals of secondarily burials, one cannot ensure that the values assigned to these body manipulations have not changed. For instance, in the grave 7, the skull of an Early/Middle Neolithic individual, LV 7/IIb[18], was placed on the left shoulder of the Transformation/Early Neolithic individual LV 7/Ia[19] and an aurochs skull was placed on his left shoulder. The presence of aurochs skulls in two burials at Lepenski Vir clearly points to the symbolic repertoire of the Southern Balkans and Anatolian Neolithic communities (Cauvin 2000) and may indicate some deeper changes in the ideology of the communities who buried their dead at this site during the 6th millennium BC.

Figure 11: Crouched inhumations from Lepenski Vir, Early-Middle Neolithic phase. Left: burial 8 (bottom) and burial 9 (top), above dwelling 24. Photo: Institute of Archaeology, Belgrade; from Bonsall et al. 2008.

2.3. Bioarchaeological overview: people and lifestyle in the Danube Gorges.

2.3.1. Archaeozoological and archaeobotanical studies: environment and subsistence

Although limited by issues of representativeness of plant and animal assemblages – remains were not systematically collected during the original excavations at most sites – archaeozoological and archaeobotanical studies still represent the basic source of information about local ecosystems and food webs. Represented species provide a general insight on the exploited environments, the dietary possibilities and broad subsistence behaviors. In the cultural context of adoption of Neolithic technologies at localities which yielded long-lasting Mesolithic (semi-)sedentary occupations, a particular effort has been dedicated to track changes in foraging strategies and to

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[18] 6080-5746 cal BC ; Borić 2011

[19] 6230-5985 cal BC ; Bonsall et al. 2011

date the appearance of first domesticated species (e.g. Borić and Dimitrijević 2005 and 2007; Dinu et al. 2008; Vuković and Dimitrijević 2013; Cristiani et al. 2016; Filipović et al. 2017).

Direct evidence of plant consumption related to Mesolithic-Neolithic occupation is scarce and circumstantial, mostly due to the absence of systematic sediment sampling, sieving and flotation during the original excavations in the 1960's-1980's. Yet, there can be little doubt that a range of edible plants was available in the Gorges and exploited by the local prehistoric inhabitants, at least to obtain essential nutrients for their health. The analysis of modern Djerdap phytocenosis (until the construction of the dam) shows that 44% of the plant species found are usable for human consumption, and 59% of species for game nutrition (Mišić et al. 1969; Mišić 1981).

2.3.1.1. Archaeobotanical data

2.3.1.1.1. Palynology

Pollen grains retrieved in some layers of sediments and from coprolites during the original excavations in the 1960-1980's at Lepenski Vir, Vlasac, Icoana and Cuina Turcului provide useful lines for the reconstruction of past vegetation and landscapes (Grigov 1969; Carciumaru 1973, 1978; Pop et al. 1970). They indicated the presence of a wide array of plant taxa in the nearby areas where forests likely included a rich shrubby vegetation. Numerous species of deciduous and coniferous trees have been identified, comprising oak (Quercus sp.), elm (Elmus sp.), lime tree (Tilia sp.), birch (Betula sp.), hazel (Corylus sp.), alnus (Alder sp.), pine (Pinus sp.), maple (Acer sp.), beech (Fagus sp.), junipers (Juniperus sp.), hemlock (Tsuga sp.), willow (Salix sp.), fir (Abies sp.), spruce (Picea sp.), hornbeam (Carpinus sp.), ash (Fraxinus sp.), and walnut trees (Juglans sp.). Although the representation of these different taxa may have changed according to the climatic oscillations of the Early Holocene, the contextual information for these samples remains very broad and can hardly be associated with a specific climatic sub-phase (Filipović et al. 2017).

Pollens from many herbaceous plants have also been identified as well as ferns, moss and fungal spores (identified families: Asteraceae, Caryophyllales, Cyperaceae, Ephedraceae, Elaeagnaceae, Fabaceae, Geraniaceae, Kanuculaceaea, Lamiaceae, Linaceaea, Lycopodium, Malvaceae, Plantaginaceae, Poaceae, Polygonaceae, Polypodiaceaea, Rhamnaceae, Rosaceaea, Saxifragaceae, Umbeliferare, Urticaceae). Some of these taxa have edible flowers, fruits-nuts, leaves, berries, seeds or roots and may have also been consumed as species, herbal tea or used for medical purposes (Filipović et al. 2015; 2017). Although retrieved from coprolithes, the pollen grains discovered at Vlasac and Icoana cannot strictly be associated with human diet since there is no clear evidence that the coprolithes are of human origins or that the detected pollens are not from intrusive sediments (Filipović et al. 2017). Based on size criteria, Cârciumaru (1973) identified some of these pollen grains as wild grasses (Gramineae) or as cultivated grasses (Cerealia) and interpret the greater presence of bigger-sized grains (Cerealia) in the upper layers of these sites as evidence of plant cultivation. However, the size-criteria cannot be used as sole indicators of domesticated taxa, and the stratigraphic and chronological characterization used by the author remains insecure (Filipović et al. 2017). During the decades following the excavations of the sites of the Gorges, the collection (and even cultivation) of plant foods has also been inferred from the presence of red deer antler artefacts interpreted as digging implements (digging sticks, hoes, and mattocks; e.g. Tringham 1968; Srejović and Letica 1978; Prinz 1987; Boroneanţ 1989).

2.3.1.1.2. Anthracology and carpology

Sieving and flotation have been practiced during the more recent excavations of Schela Cladovei and Vlasac which took place during the 1990-2000's and yielded charcoal remains as well as charred macro-botanical remains (Mason et al. 1996; Filipović et al. 2010; Borić et al. 2014).

Concerning Mesolithic contexts at Schela Cladovei few fragments of possible root/tuber tissue (parenchyma) were found, a couple of seed/fruit remains and some wood charcoal; the post-Mesolithic contexts (Neolithic and Iron Age deposits, combined in the available report) yielded wood charcoal, a small number of seeds (including cereal? grain) and a part of probable sloe/plum-type fruit stone (Mason et al. 1996). Concerning Vlasac, most of the macro-botanical assemblage derived from burials and primarily cremations (Filipović et al. 2010; Borić et al. 2014; Filipović et al. 2017). In Late Mesolithic contexts, the most commonly occurring are the remains of cornelian cherry (Cornus mas) fruit stones, the majority of which derived from cremations; non-burial deposits produced very little plant material, mainly fragments of cornelian cherry fruit stones. Concerning the Transformation-Early Neolithic and Early-Middle Neolithic layers –mostly burial fills – cornelian cherry was also the most commonly found taxon, along with a few remains of common dogwood (Cornus sanguinea), hazelnut (Coryllus avellane), and elder (Sambucus ebulus/nigra) Since most of analyzed deposits from Vlasac originate from cremations and burial fill, the relatively frequent find of cornelian cherry fruit stones – even when Cornus charcoal was not identified (i.e. not used as firewood) – suggests that this fruit could have served as an element of the ritual (ibidem). Its symbolic value perhaps arose from its red color, as ochre pigment was also frequently used in the local mortuary ritual (ibidem). The charcoal assemblage is characterized by a high variability with the same taxa as previously evidenced by palynological analyses (Grigov 1969; Carciumaru 1973, 1978; Pop et al. 1970), with a dominance of Cornus (e.g. dogwoods or cornelian cherry) and Quercus (e.g. oak) and secondarily Cotinus (e.g. smoke-tree), Corylus (e.g. chestnut), Fraxinus (e.g. ash), Prunus (e.g. plum) and Betula (e.g. birch). The specific presence of some species in some funerary contexts – such as Prunus – might reflect a "selection patterns related to the symbolic use of [these] plant species" and a possible "preference in their specific uses" (Filipović et al. 2010:157). It should be emphasized that the general paucity of botanical remains is likely dur to selective preservation issues, since charred remains are mostly preserved (overrepresentation of remains from cremations) and that most plants eaten raw or used for crafts are not preserved. Although cornelian cherry may have been particularly used for symbolic purposes it should be underlined that its fruits are edibles (drupes), widely used as food and valued in medicine due to high vitamin C content (Klimenko 2004). In general, nuts, berries, roots and seeds could have been stored for long periods and possibly consumed year-round; however, evidence for plant stockage has not been documented.

2.3.1.1.3. Starch grain analyses

Finally, analyses of starch grains have recently provided valuable information about the plants which may have been consumed during the Mesolithic and Neolithic periods (Filipović et al. 2015; Cristiani 2016, Jovanović 2017, Filipović et al. 2017). On the surface of a grinding stone found in the Mesolithic layers at Vlasac granules of starch were detected and interpreted as possible parts of tubers and nuts processed to be eaten (Filipović et al. 2015). In different studies of the anthropological sample conducted quite simultaneously, two groups of researchers have successfully retrieved the remains of various herbaceous plants from human dental calculus (Cristiani et al. 2016, Jovanović 2017, Filipović et al. 2017). Due to their location - trapped on calculus formed on the surface of the teeth – one may expect the analyses of grains to reflect more directly the possible absorption/consumption of plants than the botanic analyses previously mentioned. As part of her doctoral research, J. Jovanović detected starch grains in the dental calculus of several Mesolithic (5 grains on the teeth of 4/12 examined individuals) and Neolithic individuals (30 grains on the teeth of 17/41 examined Transformations-Neolithic individuals; Jovanović 2017; Jovanović et al. 2017). It can be noticed that the analyzed dental calculus of some individuals buried at the downstream site of Ajmana yielded a greater number of grains per tooth (>5 for two individuals) than the analyzed individuals buried at the other sites of the Gorges (maximum 2 grains per teeth). Besides, this study also included some Early Neolithic individuals buried at sites located in the nearby region of Vojvodina (Golokut-Vizić and Vinča-Belo-Brdo, South Pannonia) on which the author found a much higher number of grains (131 grains in the dental calculus of 9/11 individuals). The remarkable difference in the number of starches between the Early Neolithic populations that resided in and outside the Danube Gorges may reflect the differential preservation of starch, variations in the diet, and/or beginnings of/increase in the consumption of starch-rich food (domesticated cereal?) in the neighboring regions of the Gorges. The latter is consistent with the earliest evidence of domesticated cereals (such as wheat and barley) and pulses (lentils, peas) in Starčevo-Criş contexts of the wider region, possibly as early as ca 6400 BC (Cârciumaru 1996; Whittle 2002; Bogaard and Walker 2011; Filipović and Obradović 2013; Filipović et al. 2017). This would suggest that the consumption of starch-rich food may have remained subsidiary in the economy of the Gorges during a longer time, perhaps due to the environmental conditions and the presence of abundant protein resources there. Because of the resolution of obtained microscope image (and interpretative cautiousness), the author only attributes most taxa to the broad family of Poaceae. In an adjunct to this study, where she used a different protocol to analyse the calculus of three Early Neolithic individuals, she identified, in one of them (the child LV 61, buried at Lepenski Vir ca 6225-5915 cal. BC[20]), grains with characteristics which are consistent with those seen in Triticae, a tribe of large-seeded grasses to which belong the Near Eastern and European Early Neolithic species (einkorn, emmer and barley; Filipović et al. 2017).

The study of Cristiani et al. (2016) was much more successful in terms of number of recovered grains and level of identification. Hundreds of starch granules were recovered from the teeth of nine individuals buried at Vlasac during the Late Mesolithic and the period of Transformation-Early Neolithic and from three individuals buried at Lepenski Vir during the Early-Middle Neolithic. Starch grains have been attributed to the Triticeae, Paniceae, Aveneae and Fabeae; most of Triticeae starches were surprisingly found in the Mesolithic sample. As suggested by Cristiani et al. there may have been possible exchanges of cereals (as early as 6600 cal. BC) between the Late Mesolithic inhabitants of the Gorges and the Neolithic world of the South of the Balkans peninsula or the region of the Marmara; besides the finding of numerous grinding stone tools at Vlasac is also in agreement with the processing of plant foods during the Late Mesolithic. However, this study has been criticized for “certain methodological problems and uncertainties in this aspect of their work that bring into question the proposed taxonomic determination of starches”, particularly in relation to the criteria used for the exclusion of some wild taxa (Filipović et al. 2017:103). Several types of starch were also related by the authors to wild plant taxa which may have been used and consumed according to them (e.g. Aveneae tribe, Arrhenatherum elatius var bulbosum, Setaria species, Vicia genus). Many of these plants can have been eaten either raw, cooked or drink as herbal tea; they may also have been prepared, for any other medical or symbolic purposed and absorbed/inhaled during the preparation; indeed, there is various possible routes for the inclusion of starch into dental calculus, and Cristiani et al. also suggests that one of them may have been the inhalation during their processing (prior to cooking) that could have included grinding, as suggested by the presence of grinding stones at Vlasac. On-going analyses conducted by both groups of research now include improved identification procedure, further consideration of the taphonomy, the use of a broader sample, as well as complementary techniques of analyses (e.g. proteomic; radiocarbon analyses) in order to better assess – chronologically and geographically – the beginning of, and the increase in, domesticated plant consumption in the Balkans (Jovanović et al. 2018 unpublished podium presentation[21]).

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[20] Bonsall et al. 2015

[21] Jovanović, J., Power, R., Stefanović, S. New insights into subsistence practices at the Mesolithic-Neolithic transition in the Central Balkans: data from dental calculus analysis. Research presented at the 24 EAA annual meeting (05-08.09.2018, Barcelona, Spain).

2.3.1.2. Archaeozoological data

The archeozoological documentation available for several sites of the Upper Gorges (Lepenski Vir, Vlasac, Padina), the Lower Gorges (Cuina Turcului, Răzvrata, Icoana, Hajdučka Vodenica) and the Downstream Area (Schela Cladovei, Ostrovul Corbului, Kula, Velesnica, Knjepište) indicates that the prehistoric inhabitants of the Gorges hunted a number of wild game species present in the dense forests surrounding the bank of the Danube, and of course also fish various aquatic species (Clason 1980; Bökönyi 1969, 1970, 1972, 1978, 1992; Bolomey, 1973; Nalbant 1970; Mikić 1999; Bartosiewicz et al. 1995, 2001, 2008; Dimitijević 2000; Borić 2001; Borić and Dimitijević 2005, 2006, 2007; Dimitrijević 2008; Greenfield 2008; Dinu 2010; Dimitrijević and Vuković 2015; Borić et al. 2014; Dimitrijević et al. 2016; Bălășescu et al. 2017; Živaljević 2017; Živaljević et al. 2017). Unfortunately, the archaeozoological assemblages from most sites might suffer from representativeness biases since animal bones were mostly hand-collected during the original rescues excavations (1960's-1970's) and given that water-sieving has been practiced only at Schela Cladovei (Bartosiewicz et al. 1995, 2001, 2006, 2008) and in the newly excavated layers of Vlasac (Borić et al. 2014). For some assemblages, fish bones are not mentioned or detailed per species (e.g. Icoana; Ostrovul Corbului; Hajdučka Vodenica); others have been studied as a single units (e.g. Vlasac, Hajdučka Vodenica; Ostrovul Corbului) or using a relative chronology nowadays re-assessed (e.g. Lepenski Vir); finally some data still remain to be published concerning some other sites (e.g. Ajmana). Despite these limits, researchers have mostly emphasized the continuity over the Mesolithic-Neolithic sequence as well as geographic similarities throughout the Gorges in terms of species' representation (e.g. Borić 2001; Borić and Dimitijević 2007).

2.3.1.2.1. Represented species

Based on the number of identified specimens, red deer (Cervus elaphus) is the most represented mammal species; its meat probably provided a substantial contribution to the diet, while bones represented an important raw material for tool manufacturing (e.g. Borić and Dimitijević 2005; 2006; 2007; Dimitrijević 2008). Wild boar (Sus scrofa), dog (Canis lupus familiaris), aurochs (Bos primigenius) and roe deer (Capreolus capreolus) were then represented at somewhat higher frequency than other species, found in much lower proportions: mostly chamois (Rupricapra rupricapra), brown bear (Ursus arctos), wolf (Canis lupus), beaver (Castor fiber), red fox (Vulpes vulpes), pine marten (Martes martes), badger (Meles meles), wild cat (felis sylvestris), lynx (Lynx lynx) and hare (Lepus europaeus). If red deer are from far the most commonly hunted animals, dog remains have also been found numerously and clear morphological evidence now suggest that they were locally domesticated throughout the Mesolithic period (Bökönyi 1975, 1978; Dimitrijević and Vuković 2015). In terms of number of identified specimens, dogs were the second most represented mammal taxon at Vlasac (Bökönyi 1978), in the Mesolithic-Transformational layers of Lepenski Vir (Lepenski Vir I/II; Bökönyi 1975) and in the Neolithic layer of Padina III (Clason 1980). Cut marks and traces of burning observed on dog remains suggest that they have been, at least in some cases, slaughtered and/or defleshed by humans (Clason 1980; Dimitrijević 2008). Other domesticated animals - cattle (Bos domesticus), pig (Sus domesticus), sheep (Ovis aries) and goats (Capra hircus) - only appear in the local animal bone record after 6000/5900 BC (Borić and Dimitrijević 2009).

Given their abundance in the archaeozoological assemblages, fish also played an important role in the diet of the Danube Gorges communities. In most horizons the number of identified specimens of fish equals or exceeds those of terrestrial mammals (e.g. Schela Cladovei Mesolithic; Vlasac Mesolithic and Neolithic; Lepenski Vir Mesolithic and Transformations; Padina Neolithic; Clason 1980; Bökönyi 1975; 1978; Bartosiewicz et al. 1995; 2001; Živaljević et al. 2017). The remains of stationary freshwater species of cyprinids - especially carps (Cyprinus carpio) - were frequently found, as well as wels catfish (Siluris glanis), and in much lower frequency pike (Esox lucius), pikeperch (Stizostedion lucio perca) and bream (Abramis brama). Several anadromous species of sturgeons - beluga (Huso huso) and from the Acipenser genus (Danube sturgeon, Acipenser gueldenstaedtii, sterlet, Acipenser ruthenus, stellate sturgeon, Acipenser stellatus), and an anadromous species of cyrpinids, vyrezub (Rutilus Frisii), were also found in high frequency at most sites; these species migrates seasonally from the Black sea (Živaljević 2017; Živaljević et al. 2017). Finally, Huchen, a potamodromous salmon endemic to the Danube basin (living in the estuaries and seasonally migrating upstream), was also frequently found at several sites. Ethnographic evidence suggests that a particular sort of fishing in whirlpools was being practiced in the region until the 20th century (Figure 12; e.g. Borić 2001; Bartosiewicz et al. 2001; Živaljević 2012; 2017). Bone hooks have been discovered at several sites; ground stone scepters have also been interpreted as possible fishing clubs, and some stone weights as parts fishing nets (e.g. Antonović 2008; Živaljević 2012). The large size of certain species (beluga sturgeon and catfish in particular) and the fact that approximately two-thirds of their overall weight represent edible protein (Živaljević 2017) suggest that fish represented a substantial source of nutrients. In addition, large females produce over ten kilograms of roe (nutritious caviar), which could also have been consumed by the Danube Gorges inhabitants. However, given the poor preservation of fish bones in comparison to those of mammals, it is difficult to assess whether hunting or fishing occupied a more important role in the Danube Gorges diet. It has been suggested that wild game and freshwater fish, which were available throughout the year, represented staple food, whereas fishing large sturgeons took place in the early spring and in autumn, coinciding with the annual migrations of sturgeons from the Black Sea (Radovanović 1992; Bartosiewicz et al. 2008; Dimitrijević et al. 2016). The social organization and daily activities of local foragers may thus have been regulated by fishing seasons and animal migrations.

Finally, waterfowl animals[22] (at most sites), molluscs (particularly from the Unio genus - the freshwater mussels, found in quantity at Kula, Schela Cladovei and Vlasac - as well as snails), tortoises and turtles (Tortudo and Tortuga genus mentioned concerning the assemblages of Vlasac, Schela Cladovei and Razvrăta) and frogs (Anura order mentioned concerning the assemblages of Vlasac and Schela Cladovei) complete the spectrum of the meat that should have been locally consumed. Apart from being consumed, some animals were also certainly particularly hunted for clothes and/or adornments, such as the fur-bearing mammals (brown bear, wolf, beaver, badgers and otters) as well as several species of birds targeted for feathers (e.g. raptors), or shells (e.g. Cyclope neritae and Columbella rustica) and fish for beads and appliqués (e.g. Vyerzub teeth found in some burials surrounding the deaths, probably as remaining part of their clothes, coats or cloaks; Cristiani and Borić 2012). Apart from being found in domestic contexts, parts of dogs' and aurochs' skulls, red deer antlers and fish teeth have also been discovered inside several burials. Besides, red deer antlers were found deposited over the abandoned floors of the trapezoidal dwellings at Lepenski Vir. Considering the presence of sculpted boulders with mixed human-animal features at Lepenski Vir, these discoveries have led some researchers to suggest that the local Mesolithic foragers have probably assigned a particular symbolic values to some animal species, probably in a shamanic-type of animal-human relationships (e.g. Radovanović et al. 1996b ; Borić 2005a and 2007a; Živaljević 2012).

2.3.1.2.2. Chronological tendencies

Species representation from the Epipaleolithic to the Mesolithic

Although the sequence is mostly characterized by continuity in terms of represented species, main diachronic tendencies can be emphasized. Available faunal data concerning the Epipaleolithic-Early Mesolithic cave shelter of Cuina Turcului indicated a change between the layer I (ca 13.300 – 11.700 cal. BC; Păunescu, 2000) and the layer II (ca 10.500-9200 cal BC; ibidem) with a greater presence of wild boar in the former layer while Alpine ibex (Capra ibex) and chamois (Rupricapra rupricapra) dominate the assemblage in the second layer (Figure 13; Nalbant 1970; Bolomey 1973).

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[22] The Danube Gorges area is today an important wintering area for many wildfowl species, especially ducks.

The fact that ibex and chamois were more intensively hunted at the end of Epipaleolithic times could be related to climatic oscillations of the Younger Dryas, to changes in the nature of occupation of the sites or to local hunting choices (e.g. Mihailović 2008). While bream is the dominant fish taxon in both layers, it can be mentioned that a broader spectrum of aquatic species has been discovered in the latest layer of Cuina Turcului (Figure 13; Nalbant 1970; Bolomey 1973) including anadromous acipenser, which might indicate the development of new fishing strategies, perhaps related to an increased occupation/frequentation of the river banks (although data from a single site might not be entirely representative of the local foraging strategies; Borić 2011).

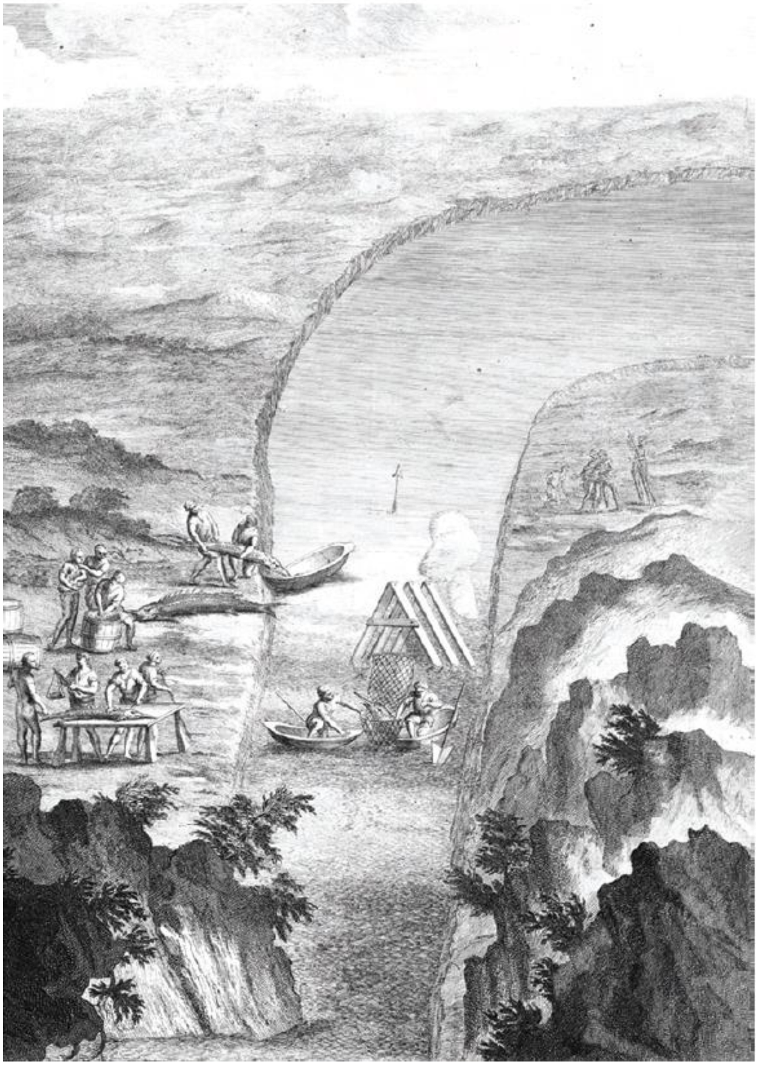

Figure 12: Sturgeon fishing at the exit from the Inner Gorge (from Marsigli 1726).

Following the environmental changes induced by the Holocene climate improvement, red deer and secondarily wild boars, aurochs and roe deer likely became the most commonly hunted mammals (Figure 13 ; Figure 14). Based upon the observation of higher frequency of ungulates' bone remains at Cuina Turcului (Nalbant 1970; Bolomey 1973) and the oldest layers of Padina (Padina I; Clason, 1980), in contrast with later Mesolithic assemblages (Lepenski Vir, Vlasac and Schela Cladovei; Bökönyi 1975, 1978; Bartosiewicz et al. 1995, 2001), it has been suggested that the terrestrial mammals might have represented a staple food during the Epipaleolithic and Early Mesolithic period, and that fishing might have been increasingly important in the course of the Me-

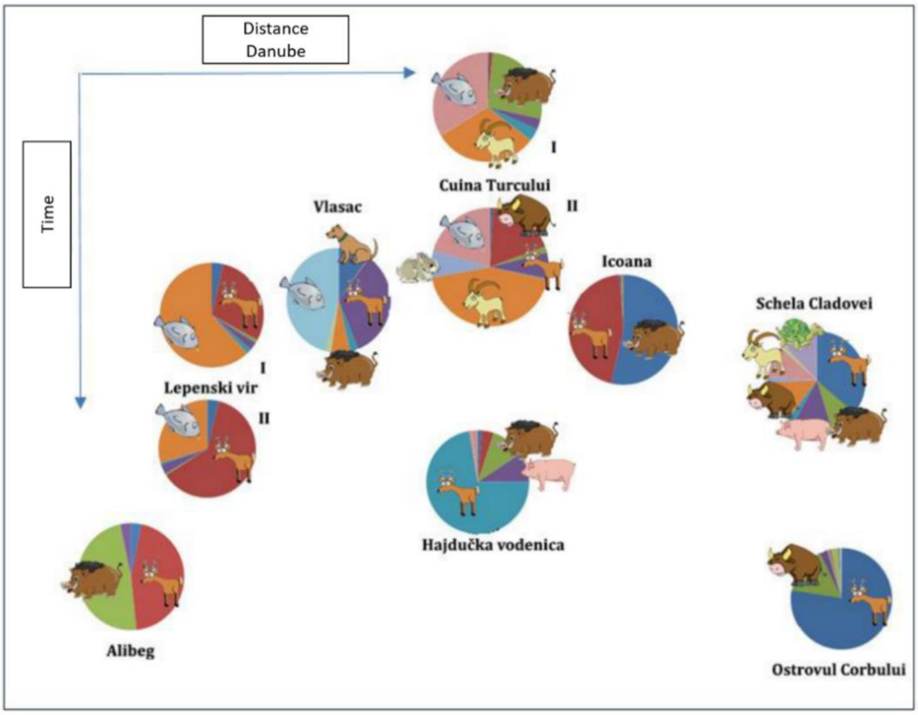

Figure 13: Representation of animal remains per species for different prehistoric sites of the Gorges (number of remains per species; from Mitrović 2018, based on data from Bartosiewicz et al. 2001, Bökönyi 1969, 1978, Bolomey 1973, Borić 2002a, Boroneanț 2011, Clason 1980 and Greenfield 2008).

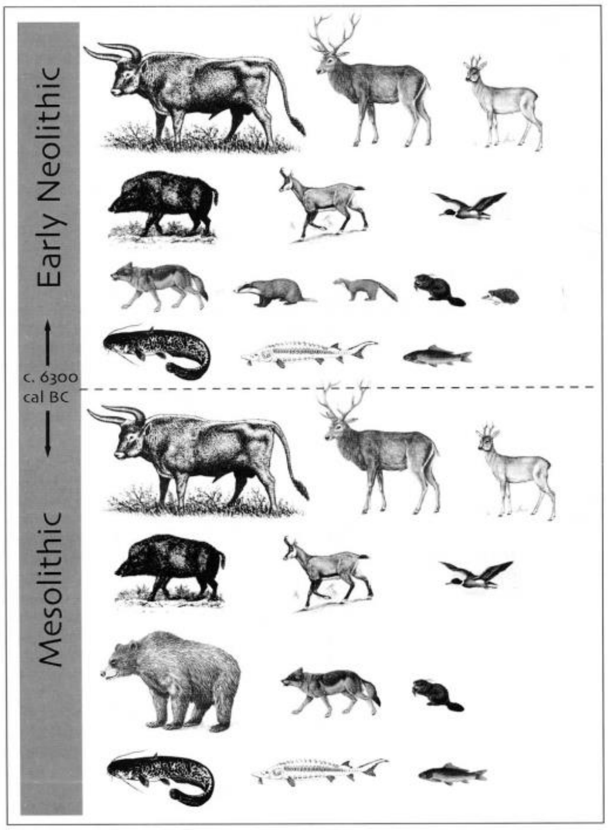

Figure 14: Schematic depiction of diachronic changes in species represented at Lepenski Vir (Borić and Dimitrijević 2006).

solithic (Borić 2001). The results of the morphometric studies conducted by Dimitrijević and Vu and Vuković (2012) indicated that dogs should have been locally domesticated in the course of the Early-Middle Mesolithic (ca 9700/9500 – 7400 cal BC). Results of recent works concerning the seasonality of resources exploitation in the Danube Gorges, interpreted in the context of higher resolution of radiocarbon dates, architectural features and artefact related to the Late Mesolithic occupancy, "signal that by this time these locations were a home to fairly sedentary populations practicing an exclusively hunter-gatherers-fisher lifestyle" (Dimitrijević et al. 2016:115).

Species representation at the Neolithic Transition

During the Mesolithic-Neolithic Transformation period (ca 6300/6200-6000/5900 cal BC), more elaborated and permanent dwellings were built at the time when the first food-producing communities arrived in the region of the Central Balkans. Yet, only certain elements of the Neolithic lifestyle were then incorporated by local foragers (technologies such as ceramics) and subsistence strategy remained mostly based on the consumption of wild game and big fish hunting, at least in the Inner Gorges until 6000 cal BC (Figure 13; Figure 14; e.g. Borić and Dimitijević 2005, 2006, 2007; Dimitrijević 2008). The analyses of bones found under the floors of the houses indicated that various activities related to the preparation and the consumption of food, the use and processing of bone tools and skins of animals took place in the houses (Dimitrijevic 2008). Fish and wild game meat could also have been dried and smoked on large stone hearths and stored for winter.

After ca 6000 cal BC, important changes occur in the Gorges in terms of settlement strategies (e.g. abandonment of trapezoidal houses) and symbolic practices (e.g. new burials in crouched position), and the Neolithic domesticated triad of animals - cattle, pigs, sheep and goats – were imported from the south Balkans and the Near-east (e.g. Borić and Dimitrijević 2007). While animal husbandry and stockbreeding played a major role in the subsistence of the Early Neolithic Starčevo culture communities (6200–5200 cal BC) settled in the surrounding regions of the Central Balkans, wild animals remain prominent in many faunal assemblages of the sites of the Gorges, particularly in the Inner Gorges (e.g. proportion of wild mammals: 74.5% at Lepenski Vir layer III; 84.4% at Hajdučka Vodenica; and 92.64% at Padina, layer B according to Greenfield 2008; and 95,6% in Velesnica according to Mikić 1999, although the only radiocarbon dates obtained from burials suggests an occupation before 6000 BC at this site). It has thus been suggested that "while Neolithic people in Central Serbia were primarily highly mobile semi-nomadic stockbreeders living in large open areas where they established their camps and were mostly engaged in raising cattle and to a smaller extent in farming, hunting and fishing, the inhabitants of Lepenski Vir were confined to small areas where natural factors unsuitable for agriculture had been a favorable activity for intensive fishing" (Borić 2011: 183). Yet, the number of identified wild mammal specimen is more numerous than the number of identified fish specimen in the Neolithic layers of Lepenski Vir (Bökönyi 1975), which may indicate some changes in the local subsistence practices during the Neolithic periods. At Lepenski Vir, the proportion of the different aquatic species also changed between the period of Transformations and the Early/Middle Neolithic (ca 5900-5500 cal BC) with higher proportions of cyprinids and vyrezub during the former period and higher proportions of catfish during the latter period (Živaljević 2017), a pattern yet not observed at other locations such as Schela Cladovei (Bartosiewicz et al. 1995, 2001). Finally, it can be mentioned that some wild species which were absent in Mesolithic assemblages are represented in very small proportions in the Neolithic assemblages: wild donkey and utva (Radovanović 1992).

2.3.1.2.3. Geographical tendencies

While the faunal spectrum is quite homogeneous throughout the Gorges, some local specificities can be pinpointed. Concerning hunted games, deer are prominent at almost all sites, except at Icoana in the Lower Gorges where wild boars represented the first number of identified specimens (Figure 13; Bolomey 1973). Concerning second most commonly found taxa, aurochs have been more frequently found at Lepenski Vir in the Mesolithic horizon and at Schela Cladovei (Mesolithic-Neolithic layers), while wild boars have been more frequently found at Lepenski Vir in the Neolithic horizons, at Vlasac, Padina, Hajdučka Vodenica and Răzvrata(Clason 1980; Bökönyi 1975, 1978; Bartosiewicz et al. 1995, 2001; Greenfield 2008; Živaljević et al. 2017). A possible degree of hunter-gatherers control over wild boars has been suggested to interpret the important frequency of suids remains found at sites of the Lower Gorges and their apparent smaller size (Bolomey 1973; Dinu et al. 2006 and 2008). While the remains of domesticated animals are under-represented in comparison with wild mammals in the Inner gorges, they have been found in much greater proportions at some sites located immediately at the exit of the Gorges and in the Downstream area where they are the dominant taxon (e.g. Schela Cladovei: Figure 13; Bartosiewicz et al. 1995, 2001; Mihajlovac-Knjepište: Bökönyi 1992). In the Neolithic layers of Schela Cladovei, at the exit of the Gorges, the remains of terrestrial mammals are also more represented than fish (Bartosiewicz et al. 1995, 2001).Amongst domesticated animals, the remains of cattle have been most frequently found at Lepenski Vir, Schela Cladovei and Padina (with goat-sheep as second most commonly found domesticated species at Lepenski Vir and Schela Cladovei and pig at Padina). Pigs were most commonly found at Hajdučka Vodenica in the Lower Gorges, perhaps in relation to the wild boar hunting tradition there. Finally, caprines was the dominant taxon at Mihajlovac-Knjepište, which could be associated with the cultural specificities of the sites of the Downstream Area where other cultural aspects rather point to the Starčevo world than to the indigenous traditions (Borić 2011).

The proportions of remains of the different fish species also vary between the sites. In the Epipaleolithic layers of Cuina Turcului, bream is the dominant taxon (Nalbant 1970; Bolomey 1973). For instance, catfish are frequent in the Mesolithic layer of Padina, with vyrezub, and absolutely dominates the ichthyological assemblage of the Transformations-Neolithic layer (Živaljevic 2017). The Mesolithic layers of Lepenski Vir contained a significant amount of huchen and secondarily catfish, vyrezub and cyprinids while Transformational layers contained more vyrezub and cyprinids and secondarily huchen and catfish and the Neolithic layers more catfish (ibidem). The remains of sturgeons have also been frequently identified in all the sequence of Lepenski Vir and in greater quantity than at other sites of the Upper Gorges, Vlasac and Padina (ibid.). At Vlasac in the Upper Gorges, vyrezub, cyprinids and catfish are the most represented fish taxon (Bökönyi 1978; Živaljevic 2017); at Razvrăta in the Lower Gorges, the remains of vyrezub and catfish have been most commonly found (Bălăşescu et al. 2017).At Schela Cladovei, in the exit of the Gorges, cyprinids and acipenser sturgeons were the most identified at both Mesolithic and Neolithic layers (Bartosiewicz et al. 1995, 2001). Finally, in the downstream Mesolithic-Transformation site of Kula the anadromous species of Hucho and Huso have also been identified as dominant (Živaljevic et al. 2017).

Thus, it is possible that environmental changes and the development of new strategies may have led to a first change in fishing strategies between the Epipaleolithic and the Mesolithic period, bream being most represented at Cuina Turcului while catfish, vyrezub, carp, sturgeons and salmons were more represented during the Early Holocene sequence. Long lasting fishing traditions may have been associated with some sites, perhaps in relation to the ecology of some species (e.g. habitats of some stationary freshwater fish), the environmental conditions (presence of whirlpools) and the nature occupation of some sites (fishing camps or permanent residential sites). Catfish are particularly associated with the site of Padina, while cyprinids (vyrezub and carps) have been more frequently found at Vlasac, Lepenski Vir, Razvrăta and Schela Cladovei. At Lepenski Vir, Schela Cladovei and Kula anadromous species (sturgeons, hucho) have been found in higher quantity than at other sites. Particular connections between the locality of the Upper Gorges, where is located Lepenski Vir, and the region of Ključ in the downstream area where is located the site of Kula have been suggested (Radovanović 1996a and b), and may explain, in addition to the local environmental conditions, some similarities in the faunal assemblages (Živaljević et al. 2017). Finally the important occurrence of catfish in the Transformation-Neolithic layers of Padina and the presence of this species in greater frequency in the Neolithic layers of Lepenski Vir might also indicate that some changes may have occurred in the fishing strategies in the Upper Gorges during the Neolithic period; yet, the proportion of catfish remains much lower than carps, cyprinids and acipenser sturgeons in the Neolithic layer of Schela Cladovei, at the downstream exit of the Gorges.

2.3.2. Osteo-anthropological studies: morphology, demography and health

The sites of the Gorges are also unique in Western Eurasia by the discovery of the skeletal remains of more than 500 human individuals, spanning the whole sequence. Other large osteoanthropological assemblages of similar context includes sites from the Baltic area, Scandinavia, and the Dniepr rapids or the Iberian Atlantic coast, but are whether of smaller size or of larger regional distribution (Roksandić 1999). Only on the right bank of the Danube the remains of at least 392 individuals have been discovered at Padina, Vlasac, Lepenski Vir, Ajmana and Velesnica (Roksandić 1999, 2008; Radosavljević and Krunić 1986, Mikić and Sladić 1994[23]) - the central material for this thesis - and more than 200 individuals on the sites of the left bank, Schela Cladovei, Climente, Cuina Turcului and Ostrovul Corbului (Boroneanţ 1970; 1990; Păunescu 1970, 1978, 1990; Mogoşanu 1978; Boroneanţ et al. 1999).

Between the 70's and the 90's, the first publications of contextual data and osteo-archaeological analyses notably provided the basic mortuary and anthropological parameters such as burial description and body position, age, sex, morphological characteristics and pathologies (Nemeskéri 1969; Boroneanţ, 1970; 1990; Păunescu, 1970, 1978, 1990; Srejović and Latica 1978; Zoffmann 1983; Zivanović 1975b and c; 1976b, 1986; Radosavljević and Krunić 1986, Mikić and Sladić 1994; Roksandić 1999). These publications, as well as the new excavations conducted at Schela Cladovei and Vlasac (e.g. Boroneanţ 2000; Borić 2008; Boroneanţ and Boroneanţ 2009) have enabled researchers to further examine patterns in mortuary practices and to explore issues related to physical adaptations, health, diet, population dynamics and migrations (e.g. Nemeskéri and Lengyel 1978; Y'Edynak 1978; Grga 1996; Radovanović 1996a and c, 2000; Boroneanţ, et al. 1999; Bonsall et al. 1997, 2000; 2004; 2015b; Roksandić 1999, 2000, 2008a, 2012; Grupe et al. 2003; Borić et al. 2004; Borić and Stefanović 2004; Jackes et al. 2008; Stefanović and Borić 2008; Nehlich et al. 2009; Borić et al. 2009, 2014; Borić and Price 2013; Boroneanţ and Bonsall 2012; Hofmanová 2017; Mathieson et al. 2018).

2.3.2.1. Morphometric analyses and physical appearance

2.3.2.1.1. First approaches and physical classifications

Like much of anthropology on the continent during the 1970's and 1980's, the first analyses of the Danube Gorges assemblages were particularly focused on normative classifications of physical types. For instance, Živanović described, concerning the remains discovered at Padina, Hajdučka Vodenica and Velesnica, a local homogeneous population which he assumed to have resided in the area since the Upper Paleolithic and to have developed from a native Cro-magnoid race along the Danube (1975a, 1975b, 1975c, 1976b, 1976c, 1979b, 1986, and 1988). Individuals were described as having long skulls with large supraorbital ridges, low vaults and large mandibles, and robust limbs with strongly marked muscle attachments. Živanović, Nemeskéri and Szathmráy also observed a temporal trend toward gracilization at Lepenski Vir, Vlasac, Padina, Hajdučka Vodenica and Velesnica, interpreted as the effect of a local evolution over generations (ibidem, Nemeskéri and Szathmráy 1969; Nemeskéri 1978). Mikić, y'Edinak and Fleish attributed this general

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[23] The minimum number of individuals was calculated by Roksandić (1999)

gracilization, also found on the masticatory apparatus, as a consequence of Neolithization and changes in diet (y'Edinak 1978; y'Edinak and Fleish 1983, Mikić 1980, 1981), while Menk and Nemeskéri later suggested the effect of a progressive replacement in population (Menk and Nemeskéri 1989). It has also been observed that the skulls and long bones of some individuals buried at Velesnica in the Downstream Area display more gracility (Živanović et al. 1986) and some individuals also buried downstream at the locality of Ajmana, were compared to "a mediterranean gracile type", comparable, according to the anthropologists, to the individuals from Lepenski II-III phase (Transformations-Neolithic periods, Radosavljević and Krunić 1986). Paleo-serological examinations have also been carried out by Lengyel (1970, 1978) in order to categorize the population at Lepenski Vir and Vlasac into groups based on blood-type, but the reliability of such analyses have been later questioned (Roksandić 2010). Several authors also found a strong degree of sexual dimorphism amongst the population (Nemeskéri and Szathmráy 1978, Mikić 1981) and it has been suggested, both on the results of blood-types and of metrics, that women were more homogeneous than men at Vlasac (matrilocal groups? Nemeskéri and Lengyel 1978; Nemeskéri and Szathmary 1978).

2.3.2.1.2. Biodistance studies and migrations: foragers and foreigners

Following the observation of a tendency towards more gracility amongst Neolithic individuals, M. Roksandić performed a biodistance study of Mesolithic and Neolithic individuals, based on formalized statistical analyses of metric and non-metric anatomical variation dataset (Roksandić 1999, 2000, 2008a and 2012). Re-examining the samples from Padina, Lepenski Vir, Vlasac and Hajdučka Vodenica (Roksandić 1999), and later from Velesnica (Roksandić 2008b), M. Roksandić calls into doubts the accuracy of previous sexual diagnoses, considering that they were based both on pelvic and on skull features associated with greater robusticity in males than in females, which can be a problem in case Early Neolithic migrations contributed to morphological heterogeneity in the Gorges. She re-estimated the sex of the individuals using a more conservative approach and also noticed the strong degree of sexual dimorphism amongst the population of the Gorges. The results the biodistance analyses of individuals buried at Padina, Lepenski Vir, Vlasac and Hajdučka Vodenica, indicate a "local biological continuity in the region, with a high initial degree of heterogeneity, and the effect gradual temporal ordering as the most likely explanation for the pattern of change [;] a more pronounced difference at the time of contact with Neolithic populations argues for a limited 'seeping in' of a non-local population" (Roksandić 2008a:55). She did not see the effects of important population replacement, but rather suggested that, at the time of contacts, the site of Lepenski Vir should have represented a central place both for a limited resident population and for a much larger non-resident who identified this locality as an ancestral place of ideological significance (supporting hence Radovanović interpretation of this period as a phase of "consolidation" of the Lepenski Vir culture; e.g. Radovanović 1996b, c and d; Radovanović and Voytek 1997). Finally, she also found that females were more homogeneous than males but concerning infra-cranial metric data only. Given that the infra-cranial skeleton is more sensitive to environmental factors (e.g. nutrition, climate, physical activity) than the skull, which thus better reflect biological distance between individuals, she suggested that males may have been more adversely affected by environmental pressures than females (Roksandić 2012).

In the course if our work on the osteo-anthropological sample, we re-analyzed the sample of non-metric anatomical variation scored by M. Roksandić with up-dated chronological assignment[24], increasing the number of individuals from the Downstream Area, and adopting a more conservative approach by selecting only 10 anatomical variations shown to be correlated to

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[24] Numerous individuals from Vlasac assigned to a contact phase by M. Roksandić were rather radiocarbon dated to the Late Mesolithic, and some individuals dated to the transformational phase from Lepenski Vir should rather be assigned to the Early-Middle Mesolithic period

genetic (de Becdelièvre et al. 2015 and 2017a unpublished podium presentations[25]). These data were then compared with analyses of differences in skull morphology, assumed to be less influenced by environmental influences than the infra-cranial morphology. Biodistance analyses for anatomical variations confirmed the gradual effect of time (local adaptation rather than population replacement), with more variability at the Transformations/Early Neolithic period. Concerning skull measurements, the Principal Component Analyses have shown that individuals buried downstream at the site of Ajmana rather range at one margin of the local variability.

2.3.2.1.3. Physical activity and bodily adaptations: bodies in transition

In addition to examining issues related to migrations, the osteo-anthropological sample is also currently being re-analyzed with a specific focus on activity-related adaptations (Villotte et al. 2014; de Becdelièvre et al. 2013, 2017b unpublished poster and podium presentations[26]). The Bioarchaeology of habitual activity relies on bone tissues' properties to remodel over the life when subjected to a repetitive or intense physical activity. In the local context of the Mesolithic-Neolithic transformations, these approaches are particularly important to infer changes in terms of mobility and physical activities associated with sedentism along the riverbanks and with the new Neolithic way-of-life and to explore issues related to the distribution of tasks and modification of social organization.

Villotte and his colleagues have recently analyzed the frequency of External Auditory Exostosis (EAE), a condition shown to be associated with a frequent contact with cold water (Villotte et al. 2014). The results indicate a high frequency of EAE during the Mesolithic in the Gorges and a gradual decline from the Early Mesolithic to the Neolithic period, with a possible threshold at the beginning of the Transformation/Early Neolithic period. This is consistent with the general pattern observed in Europe of lower frequency of EAE during the Neolithic in comparison with the Late Mesolithic, suggesting a change in the activities associated with the river, such as fishing, diving or bathing. However, the observation of such gradual pattern in the Danube Gorges also warns for genetic factors behind the expression of this condition. Interestingly, the Late Mesolithic females buried at the site of Vlasac display more EAE than males (a tendency yet not statistically significant), which is surprising as in many prehistoric groups the males display more EAE than the females.

In order to infer possible changes in patterns of physical activities over the Mesolithic-Neolithic transformations, the aspects of muscles attachments, both pathological damages and robusticity (musculo-skeletal stress markers), have been scored at different sites of the skeleton (de Becdelièvre et al. 2013 unpublished poster presentation[27]). Preliminary results have shown a gradual reduction in the frequency of muscle attachments' pathological damages and in the robusticity of muscle attachments over time, particularly concerning females. Besides, the morphological and geometric characteristics of the upper and lower limbs of long bones (cross-sectional geometric properties) are also currently being analyzed with the new technique of morphological mapping (de

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[25] de Becdelièvre, C., Porčić, M., Goude, G., Le Guen M.A, Jovanović, J., Stefanović, S. From individual mobility to population dynamics during the Mesolithic and Neolithic transformations in the Danube Gorges (Balkans, ca. 9500–5500 BC): Adaptations and interactions. Research presented at MESO 2015, The Ninth International Conference on the Mesolithic in Europe. (14.-18.09.2015. Belgrade, Serbia).

de Becdelièvre, C., Jovanović, J., Hofmanová, Z., Stefanović, S. Who were the earliest farmers? Interactions - innovations - adaptations at Earliest Neolithic of The Central Balkans, Human Bioarchaeological Perspectives. Research presented at the 23rd European Association of Archaeologists Annual Meeting, (30.08.-03.09. 2017. Maastricht, Netherlands).

[26] de Becdelièvre C., Jovanović J., Stefanović S., Porčić M. 2013. Female mobility during the Mesolithic and the Neolithic in the Danube Gorges (Balkans, 9500-5500 BC). Research presented at the Conference on the 150th Anniversary of the discovery of the shellmiddens at Muge. (21.-23.03.2013. Muge,Portugal).

de Becdelièvre, C., Le Guen M.A., Porčić M., Jovanović, J., Stefanović, S. 2017. Behavioral Adaptations - Morphological Adaptations: new contributions from Morphometric Mapping for the understanding of Mesolithic-Neolithic transformations (Balkans; 10 000 - 5000 BC). Research presented at the 7th Annual Meeting of the European Society for the study of Human Evolution (ESHE) (21.09.-23.09.2017. Leiden, the Netherlands).

[27] Cf note supra

Becdelièvre et al. 2015, 2016, 2017a unpublished poster and podium presentations[28]). This study has enabled us to quantify the observed diachronic trend towards more gracility (reduced cortical thickness) as well as the decline in the robusticity of muscles' attachments at specific sites (e.g. linea aspira on femur); it also indicates that the sections of long bones gradually became more circular. This tendency towards long bones' increased gracility and circularity is systemic – affecting both upper and lower limbs - but appears greater on the bones of the lower limbs. These results suggest the long-term adaptation of foragers' bodies to a sedentary way of life in the ecological niche of the Danube Gorges. More research is now conducted to refine whether this new sedentary lifestyle could have involved new patterns of sexual division of tasks and to disentangle possible behavioral and genetic influences of migrations at the Early Neolithic on long bone morphology (e.g. arrival of females with different adaptive histories and patterns of habitual activities).

Changes in habitual activities - or in the way to perform some of these activities - over the Mesolithic and Neolithic periods, have also been inferred from evidence for the use of teeth in non-masticatory ways, i.e. as tools or third hand in everyday tasks (Radović 2013). Notably, specific wear of anterior teeth has been observed at all sites and periods and has been broadly related to tasks involving bone, stone and skin treatment, processing of animal's tendons or fibers for basket (teeth used to hold tool or raw material or directly for tearing, softening and cutting). During the Transformations – Early/Middle Neolithic period, more females buried at Lepenski Vir had chipping and notching than males; besides, some females buried at Lepenski Vir during the Early/Middle Neolithic period exhibit both an intense wear of front teeth as well as interproximal grooving, and other specific notches, which can be associated with changes in terms of "cultural utilization" of the teeth, in the distribution of certain tasks and/or in the way to perform certain activities, such as rope or basket-making, perhaps in relation to the adoption of certain Neolithic behavioral and technological novelties in the Gorges.

2.3.2.2. Paleodemographic reconstructions

The osteo-anthropological sample of the Danube Gorges, with its geographical homogeneity and chronological continuity, has also provided the opportunity to examine changes in the demographic structure of the local Mesolithic-Neolithic population, not only migrations, but also growth, fertility and mortality (Meiklejohn et al. 1997; Bocquet-Appel et al. 2002; Jackes et al. 2008). Indeed, the emergence of the sedentary and agro-pastoral way of subsistence has been associated with a major event of demographic increase and it has long been discussed whether the shift firstly occurred amongst hunter gatherers' societies and then stimulated the development of farming (e.g. Boserup 1965; Cohen 1977 and 2009), or rather occurred as a primarily consequence of farming innovations (following a "Malthusian demographic model"; Bocquet-Appel and Bar-Yosef 2008; Lambert 2009; Gignoux et al. 2011). The model of a Neolithic demic diffusion into Europe also implicitly relies on the assumption of the low growth rates of "indigenous hunter-gatherers" in opposition with the higher fertility of the Neolithic "colonizing groups" (e.g. Fort, 2015). In contrast, the evidence for an intense Early Holocene occupation of the Gorges, as well as the discovery of an increasing number of perinates in Late Mesolithic and Transformations-Early Neolithic contexts (e.g. Borić and Stefanović 2001; Stefanović 2006; Stefanović and Borić 2008), suggest the possibility of a local increase in fertility and/or in infant mortality rates.

2.3.2.2.1. Mortality profile and life expectancy

The first paleodemographic approach in the Danube Gorges was performed by J. Nemeskéri (1978) who reconstructed the mortality profile of the site of Vlasac. His results indicated a quite long life expectation at birth (25-35 years old), shorter for females though; yet, it should be mentioned that this method has been widely criticized as being highly dependent to preservation

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[28] Cf note supra

issues and to the methods of age determination (e.g. Bocquet-Appel and Masset 1982). In any cases, J. Nemeskéri noticed that numerous people, including some who had developed skeletal traces of pathologies, still lived at an old age. He also attempted to reconstruct the number of individuals who may have lived per generation and suggested that a quite few individuals - around 8-15 - may have been living contemporaneously at each occupied locality in the Gorges.

2.3.2.2.2. Growth rates

Applying less biased demographic indicators Meiklejohn et al. (1997) further noticed the proximity between Vlasac sample and the Karelian Mesolithic-Neolithic cemetery of Olenii Ostrov (use of the mean childhood mortality index and the juveniles to adult ratios, which are free from the need for a precise estimation of adult age and which did not include the 0-5 years old age category, usually underrepresented in archaeological contexts due to taphonomic factors and/or differential mortuary practices). For these sites he suggested a rather stable and stationary population with both low fertility and low mortality; in both cases, while archaeological data suggest an apparent increase in the intensity of occupation, this does not seem to be related to demographic processes internal to the population but rather to a change in alternate behavioral characteristics (in the nature of the occupation, residential mobility…). Compiling data from several sites of the Gorges (Padina, Vlasac, Lepenski Vir and Hajdučka Vodenica[29]), Bocquet-Appel (2002) compare the sample with a broad sample of European Mesolithic and Neolithic sites. His results also indicate a stationary population, comparable to other European Mesolithic samples (Skateholm, Vedbaeck in Norther Europe, Moita de Sebastiao in Southwestern Europe), which differs from most European Neolithic sites with higher growth rates. Jackes et al. (2008) further examine these data per sites and chronological periods and include data from two others Early Neolithic sites Velesnica and Ajmana. Their results confirm previous observation for the Mesolithic demography, indicate a possible drop in fertility at Lepenski Vir during the time of the Mesolithic-Neolithic contacts (i.e. Transitional or Transformational period), interpreted in relation to the infiltration of migrants amongst the local population (higher number of adults in comparison with children) and a population growth during the Neolithic.

Considering the number of radiocarbon dates made available these two former decades (e.g. Borić 2011), and important changes in burials' chronological assignments, these paleodemographic results are currently being re-assessed (Porčić et al. 2014 and de Becdelièvre et al. 2019 unpublished posters and podium presentations[30], de Becdelièvre et al. 2020 *in preparation*). We investigated the representativeness of the sample and limited demographic reconstructions to the Late Mesolithic to Neolithic periods, using adequate indicators (growth rate calculated on the p (5-19) index). Up-dated results confirm that the Late Mesolithic population was stationary (Figure 15). The growth rate during the transformational periods at Lepenski Vir appears slightly higher than the Late Mesolithic estimates. Skeletal data for the Early Neolithic sites of Ajmana and Velesnica downstream (ca 6200-5800 cal. BC), also indicate much higher growth rates, similar as for many Neolithic agricultural sites of Europe; yet, it should be borne in mind that these two samples are smaller (respectively 17 and 7 individuals), and thus may be subjected to any depositional (cultural selection?) or post-depositional bias (non-exhaustive sample?). Finally, the growth rate obtained for the Neolithic sample from Lepenski Vir remains low but is still higher than during the transformation period (e.g. Bocquet-Appel 2002). Hence, we rather suggest (*contra* Jackes et al., 2008) that the arrival circa 6000 BC of Neolithic communities settled in the Downstream Area, with different demographic patterns as well as the introduction of animal husbandry, may have positively

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[29] Minimum number of individuals and age estimated by Roksandić 1999

[30] Porčić M., de Becdelièvre, C., LeRoy, M., Jovanović, J., Stefanović, S., Thomas, M., Shennan, S., Timpson, A. Investigating local demographic fluctuations during the Mesolithic and the Neolithic in the Danube Gorges: a review of radiocarbon, skeletal and settlement evidence. Research presented at *the 20th European Association ofa rchaeologists Annual Meeting. (*10-14.09.2014, Istanbul, Turkey).
de Becdelièvre, C., Blagojević, T., Jovanović, J., Porčić, M., Hofmanová, Z., Stefanović, S. Paleodemography of the Danube Gorges Mesolithic and Neolithic Transformations: comparing radiocarbon, skeletal and molecular evidence. Research presented at Jean-Pierre Bocquet-Appel Tribute Conferences. (02-03. 07. 2019. Aix-en-Provence, France). Paper in tribute to J.P. Bocquet-Appel in preparation (de Becdelièvre el. 2020)

influenced the demography of the inhabitants of the inner part of the Gorges. In addition, Porčić and Nikolić (2015) recently estimated growth rate for the period of Transformations/Early Neolithic at the site of Lepenski Vir by combining the archaeological settlement evidence (data on house floor areas and stratigraphic information) and ethnoarchaeological information (floor area-to-household size, house-use life, hunter gatherer group size) with mathematical models of house accumulation and population growth within the Approximate Bayesian Computation framework. Growth rate estimates based on house floor areas suggest a higher growth rates than estimated from the skeletal data, rather coinciding with Neolithic communities. According to the authors the initial population at Lepenski Vir must have been low, within the range of 5-20 people (which is consistent with the estimation of J. Nemeskéri based on the structure of the skeletal sample from Vlasac), while the final population size corresponds to ethnographically documented village size of people dependent on aquatic resources (30-40 people).

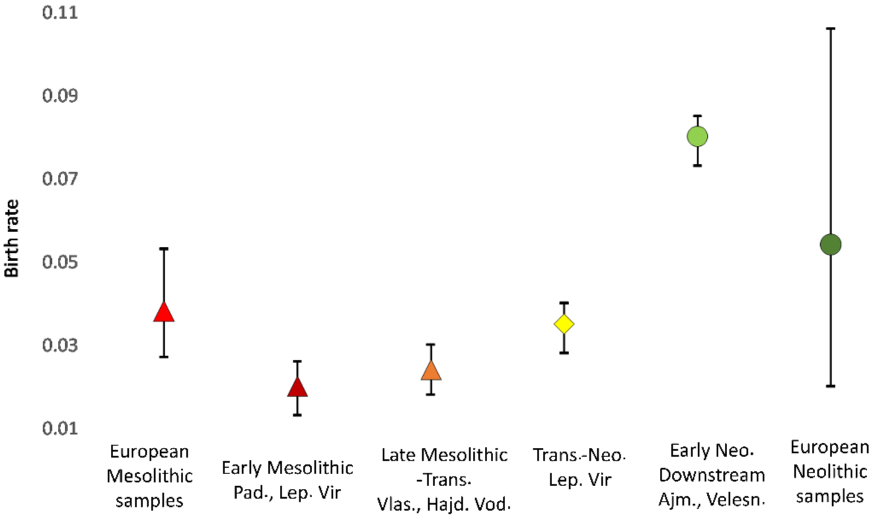

Figure 15: Birth rates and 95% confidence intervals inferred from the juvenility index ($_{15}p_5$) for the Mesolithic-Neolithic sites of the Gorges (reassessment, de Becdelievre et al. forthcoming) and comparison with Mesolithic (n=9) and Neolithic (n=91) european populations (data from Bocquet Appel 2001 and Downey et al. 2014).

2.3.2.2.3. Intensity of occupation

A statistical procedure was also applied to the summed probability distribution (SPD) of 250 radiocarbon dates obtained since the end of the 90's on human, animal and charcoal remains in order to examine fluctuations in the intensity of the occupation of the Gorges ("dates as data", methods developed by Shennan et al. 2013 and Timpson et al. 2014, which now takes into account possible sampling, calibration and taphonomic biases). Radiocarbon data were also spatially interpolated, using a kernel density smoothing function (following Manning and Timpson 2014). The results of the SPD method suggest a statistically significant increased occupation in the Gorges circa 6700-6400 cal BC (Figure 16). When the spatial dimension is added, it appears that the occupation became more intense at all parts of the Gorges around 7400 cal BC, with a statistically significant peak in the intensity of occupation ca 6500 cal BC. This could be interpreted as an effect of the Late Mesolithic sedentism in the region (7400-6400/6200 cal BC). This peak is followed by a decrease in the intensity of occupation around 6450-6250 cal BC, which could be whether interpreted as an effect of the 8.2 cooling event or of a territorial restructuring. A second significant increase in the intensity of occupation occurred between 6250 and 5900 cal BC, at the time when the settlement of Lepenski Vir was flourishing and when the foragers of the Gorges developed contacts with the Early Neolithic communities who settled in the neighboring regions of the Central

Balkans (Figure 16). Finally, the occupation of the Gorges declined after 5800 cal BC and the region seems mostly abandoned to later Neolithic settlements around 5000 cal BC (statistically significant drop in the probability distribution).

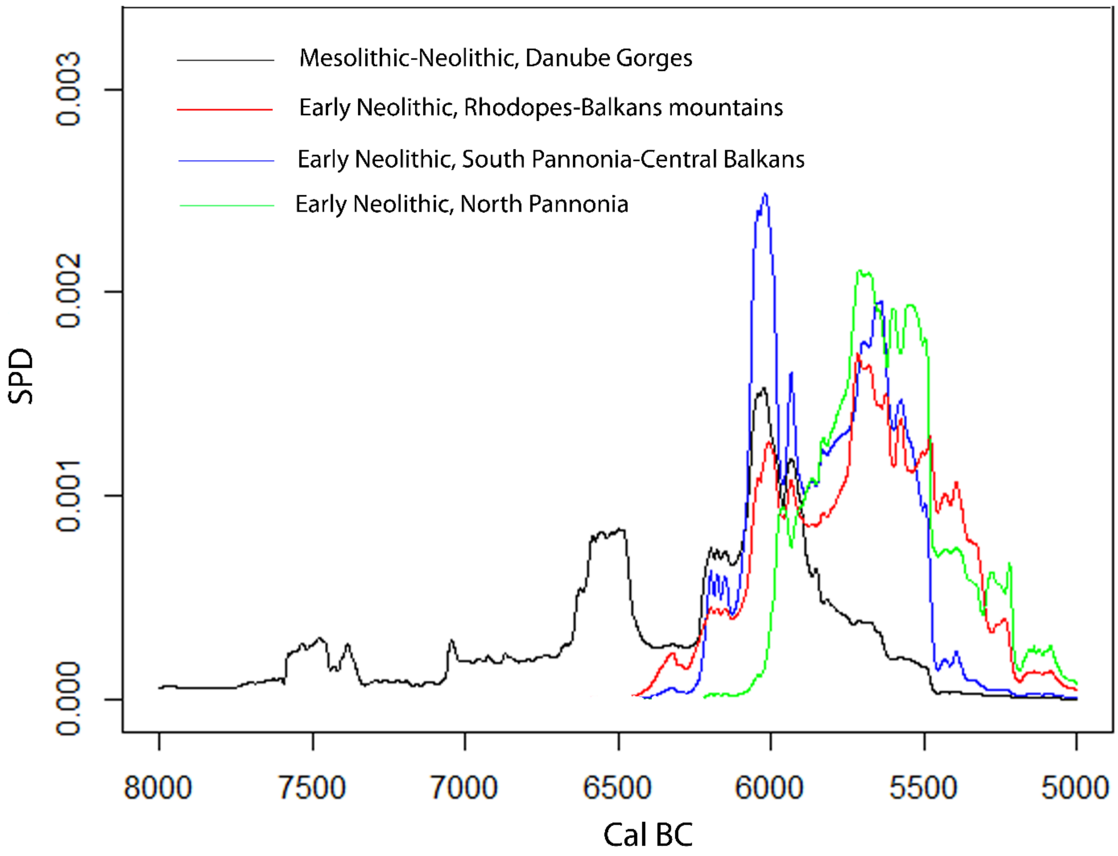

Figure 16: Comparison of the Summed Calibration Probability Distribution (SCPD) of radiocarbon dates from the Danube Gorges (n= 222, data from Borić 2011, Bonsall et al. 2015, Borić 2018 and Pročić et al. forthcoming) with the SCPD of neighboring regions presented in figure 1 (results of Porčić et al. 2016 and Blagojević et al. 2017). From de Becdelièvre et al. forthcoming.

2.3.2.2.4. Demographic fluctuations in the Danube Gorges, synthesis

Taken as a whole, results indicate that the occupation of the Gorges became more intense after ca 7400 cal BC, probably under the effect of the increased sedentism of a stable and stationary population of foragers. Circa 6200-5800 cal BC, some Early Neolithic communities who had demographic patterns similar as other European Neolithic farmers (including high fertility and mortality), settled in the downstream area (sites of Ajmana and Velesnica). At that time, the growth rate of the locality of Lepenski Vir in the Upper Gorges slightly increases, perhaps in relation with the infiltration of Early Neolithic migrants into the local population (assuming that the local population was occupying the site during most time of the year). The representation of age categories in the skeletal assemblage of the Early Neolithic sites settled downstream ca 6000 – which show more cultural similarities with the Starčevo complex – also suggest higher growth rates, similar as for many Neolithic agricultural sites of Europe. The summed probability distribution of radiocarbon dates suggests that after 5800 cal BC the Gorges became less intensely occupied; this decline coincide with a more intense Early Neolithic occupation broader Central Balkans and Southern Pannonian plain ca 5900-5500 BC. It is hence possible that this environment was less suitable for the agropastoral practices of Starčevo people, and that the former foragers' way of living and of being became increasingly forsaken by the appearing Neolithic social ethos. Yet, the Early Neolithic increase of occupation in the Central Balkans and Pannonian plain was also followed by a bust after 5400 cal BC (Figure 14; Blagojević et al. 2017). The application of teeth cementum methods on the Danube Gorges osteo-anthropological sample (e.g. Roksandić et al. 2009; Radović 2012), and researches conducted on the potential to infer some life-history parameters from anomalies in the annual deposition of tooth cementum (e.g. pregnancy events; Kagerer and Grupe, 2001) would now represent important prospects for the understanding of local Mesolithic-Neolithic demographic adaptations (Penezić et al. 2019). Besides, these results also call for further researches on the relationships between changes in reproductive behaviors, subsistence strategies and migrations at the Earliest Neolithic in the region.

2.3.2.3. Health status and pathologies

Skeletal analyses of human remains from pre-agricultural and early agricultural centers throughout the world have shown that the shift to food production significantly affected overall human health, the adverse cost of the agricultural and demographic transition (e.g. Larsen 1995, 2003; Cohen and Crane-Kramer 2007; Lambert 2009). Analyses of population from various chrono-geographic contexts have indicated that the increased consumption of carbo-hydrate rich food resources and the restriction of the diet-breath had contributed to deteriorate the oral health, to increase nutritional deficiencies and the frequency of physiological stress; it is also assumed that new children feeding practices – the use cereal-based weaning preparations and an earlier age at weaning – had an adverse effect on immune defenses, increased the frequency of physiological stress experienced early in life and affected the conditions for somatic growth; increase in females' fertility and changes in children feeding practices may have also affected females' metabolism; finally, the demographic expansion as well as closer contacts with domesticated animals probably contributed to increase the spread of pathogens, infectious diseases and zoonoses. During the last 50 years, several groups of researchers have examined the evidence for pathologies as well as non-specific indicators of stress on the osteo-anthropological samples of several sites of the Danube Gorges, providing now a clear picture of changes in the overall health, and offering some insights on nutritional conditions and on the type of diseases experienced by the Mesolithic and Neolithic populations (e.g. Nemeskéri and Lengyel 1978; Y'Edynak 1978; Grga 1996; Radović and Stefanović 2013; Jovanović 2017).

2.3.2.3.1. Dental analyses and oral health

Dental caries

One of the most constantly reported features from dental analyses of different assemblages of the Gorges is the very low incidence of caries (Figure 17; e.g. Padina, Vlasac, Hajdučka Vodenica, Lepenski Vir and Ajmana: Y'Edinak 1978, Meiklejohn and Zvelebil 1991; Grga 1996; Bonsall et al. 1997; Radović and Stefanović 2013; Jovanović 2017). These low rates of caries have been taken as indicators of a diet rich in proteins and low in carbohydrates. All dental caries have been identified on the teeth of individuals dated to the Transformational-Neolithic periods, mostly females discovered at Lepenski Vir (amongst five individuals buried at Lepenski Vir who display evidence for caries, four were identified as females and one as a male), as well as adult (one female and one undiagnosed) and children discovered at the site of Ajmana (Figure 17; Jovanović 2017). Interpreted in association with the evidence for cultural changes post 6200 cal BC in the Gorges (adoption of some Neolithic technologies) and with the indication for greater biological heterogeneity amongst the Early Neolithic population, the presence of caries could indicate whether the introduction of new dietary practices and/or the arrival of people with a different genetic background (more sensitivity to caries?) and behavioral habits (higher consumption of carbohydrates?). Yet, J. Jovanović has also observed that the rate of caries in the Gorges during the periods of

Transformation and the Neolithic period remain lower than in most other Early Neolithic populations, including the Neolithic communities from close-by regions of South Pannonia (southern part of the Carpathian basin) which tends to suggest that the diet probably remained highly based on the consumption of high protein resources in the Gorges during the Neolithic (Figure 17; Jovanović 2017). Some inter-proximal grooves noticed on the teeth of four Transformational/Early-Middle Neolithic individuals buried at Lepenski Vir and of one Mesolithic individual buried at Vlasac, in some cases associated with traces of gingival inflammation, have been related to possible therapeutic actions (Radović 2013). It is interesting to notice that females were more affected by caries (females buried at the sites of Lepenski Vir and Ajmana), which could be explained whether by a dietary difference between males and females or by the effect of sex-specific migrations at the Early Neolithic in the Gorges (i.e. Neolithic migrant females more sensitive to caries than the local population). It should be mentioned that females are generally more affected by caries than males, which can be due to behavioral factors, but which may also have biological causes (earlier eruption of teeth for girls, hormonal differences e.g. Lukacs 2011). Given that hormonal fluctuations experienced during pregnancies have been shown to reduce the antimicrobial activity by influencing the composition and the flow rate of saliva, it has been speculated that the increased female fertility associated with the agricultural transition, in combination with the carbohydrate-rich diet, may have increased the rates of females' dental caries (Lukacs 2008). Finally, the fact that the Early Neolithic children buried at Ajmana were particularly affected by caries could point to a difference in terms feeding practices, an earlier introduction of carbohydrates-rich food or/and difference in food preparation and consistency (e.g. cooked food which may have formed sticky layers over young children teeth; appearance of porridge or "Neolithic bread"?; Jovanović 2017).

Dental calculus and periodontal disease

A particularly high degree of supragingival dental calculus has been reported at all sites of the Gorges (e.g. Y'Edinak 1989; Borić et al. 2011; Radović and Stefanović 2013; Jovanović 2017), which is in accordance with the low incidence of dental caries, since both supragingival calculus and dental caries are related to the plaque ph and to the consumption of a high protein diet (Hillson 1979). However, as observed for dental caries, other factors may also influence dental calculus formation, either cultural (e.g. food preparation), environmental (e.g. water ph), and/or physiological (e.g. salivary flow rate, level of calcium in blood; Jovanović 2017). Besides, high rates of calculus have also been noticed on Neolithic communities settled in close-by regions of the Balkans and were rather interpreted as an effect of the consumption of high-viscosity cooked carbohydrate-rich food (ibidem). Concerning the periods of Transformations and the Early-Middle Neolithic periods, it has been observed that more females exhibit high degree of calculus and affected teeth than males (Jovanović 2017), which could either indicate a change in terms of social organization (distribution of tasks, access to resources) or be related to sex-specific migrations (e.g. males or females who were originate from a different environment, with different dietary-culinary habits and/or oral hygiene).

Periodontal disease has also been reported as common amongst individuals buried at the sites of Padina and Vlasac (Zivanović 1975; Y'Edynak 1978 and 1989) and periodontal pockets have been observed at Schela Cladovei (Bonsall et al. 1997). The periodontal disease mostly occurs from hosts immune and inflammatory response triggered by infections and the actions of micro-organisms such as bacteria and calculus can be a factor promoting its development. It can be noticed that recent studies suspected the possibility of bacteria oral-to-oral transfer between dogs and their owners (Oh et al. 2015), which is can be of importance in a context of dogs' domestication. Yet, it has been emphasized that identification of this condition in archaeological material is problematic since there is some potential for confusion with normal bone loss associated with ageing and dental attrition (e.g. Clarke et al. 1986).

Enamel hypoplasia

The occurrence of enamel hypoplasia, a defect in teeth in which the amount of enamel is deficient because of physiological stress experienced during childhood (at the time of formation of the crown), has also been examined on the teeth of prehistoric individuals from several sites of the Gorges (Y'Edinak 1978 and 1989, Borić et al. 2011, Radović and Stefanović 2013; Jovanović 2017). On-going research indicate that more individuals had several hypoplasia per teeth during the Early Neolithic than during the previous periods, which suggests that they experienced some episodes of stress more often (Figure 17; Jovanović 2017; de Becdelièvre et al. 2017a unpublished podium presentation[31]). Higher occurrence can be observed at the site of Lepenski Vir (in prevalence) and at the site of Ajmana (in frequency). When considering immature individuals separately, the occurrence of hypoplasia (both frequency and prevalence) is higher amongst children of Ajmana, which indicates that many children buried downstream died when after experiencing episode(s) of physiological stress. Yet, the frequency of hypoplasia is also high amongst those who survived adulthood, indicating that some of them successfully manage to cope with the experienced stress. In contrast, the occurrence of hypoplasia is also high amongst Early Mesolithic children buried at Padina, but very low amongst the adult buried at this site (despite the small sample size, 2/5 children with hypoplasia versus 1/10 adults), suggesting that these Early Mesolithic children did probably not manage to cope with the physiological stress that they experienced. The occurrence of hypoplasia remains lower on the teeth of individuals buried in the Gorges than on the teeth of Early Neolithic individuals buried close-by areas of the Balkans, which suggests that the Mesolithic and Neolithic individuals buried in the Gorges likely grew up in quite favored environmental conditions (Figure 17; Jovanović 2017).

Based on the location of the defects on crowns, one can roughly estimate the age of appearance of the defect: the physiological stress was most frequently experienced ca 2.5-4 years for all periods considered together, with a peak around 3-3.5 years (Jovanović 2017; Jovanović et al. 2015 and de Becdelièvre et al. 2017a unpublished poster and podium presentations[32]). The age at which the physiological stress was the most frequently experienced is slightly different between periods: it occurs on average between 3 and 4 years old during the Late Mesolithic and the Transformation/Early Neolithic periods and a bimodal pattern can be observed for the Early-Middle Neolithic period, with frequent stress experienced around 2-2.5 years and then around 5 years. When observing data for children independently, results suggest that Early-Middle Neolithic children (those who died during childhood after experiencing some physiological stress) also most frequently experienced stress events earlier (ca 2.5-3.5 years old) than Mesolithic children (ca 3.5-4.5 years old). Amongst individuals buried at sites located in the close-by regions of the central Balkans, the bimodal pattern of a frequent stress experienced circa 3-3.5 years old and after 5 is also apparent (Jovanović 2017). These differences might in part be related to the stress of weaning and to possible changes in children feeding practices during the Neolithic period, perhaps a shorter period of breastfeeding, an earlier supplementation with food less rich in proteins and essential micro-nutrients, and increased use of non-sterilized tools (e.g. ceramics, bone spoons). Interestingly, it has also been observed that boys most frequently experienced stress later than girls during the Late Mesolithic period (3.5-4.5 versus 2.5-3.5 years old), which could be due to multiple biological (e.g. earlier eruption of teeth in girls) and cultural factors (e.g. differential parental investment in boys and in girls).

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[31] de Becdelièvre, C., Jovanović, J., Hofmanová, Z., Stefanović, S. Who were the earliest farmers? Interactions - innovations - adaptations at Earliest Neolithic of The Central Balkans, Human Bioarchaeological Perspectives. Research presented at the 23rd European Association of Archaeologists Annual Meeting, (30.08.-03.09. 2017. Maastricht, Netherlands).

[32] Jovanović, J., de Becdelièvre, C., Stefanović, S., Le Roy, M., Herrscher E., Goude, G. 2015. Breastfeeding strategies and children's health status during Mesolithic-Neolithic transition in Serbia. Research presented at the Workshop Paleodiet meets Paleopathology. Using Skeletical Biogeochemistry to link ancient health, food and mobility. (15-16.10.2015. Santiago de Compostela, Spain).
de Becdelièvre, C., Jovanović, J., Hofmanová, Z., Stefanović, S. Who were the earliest farmers? Interactions - innovations - adaptations at Earliest Neolithic of The Central Balkans, Human Bioarchaeological Perspectives. Research presented at the 23rd European Association of Archaeologists Annual Meeting, (30.08.-03.09. 2017. Maastricht, Netherlands).

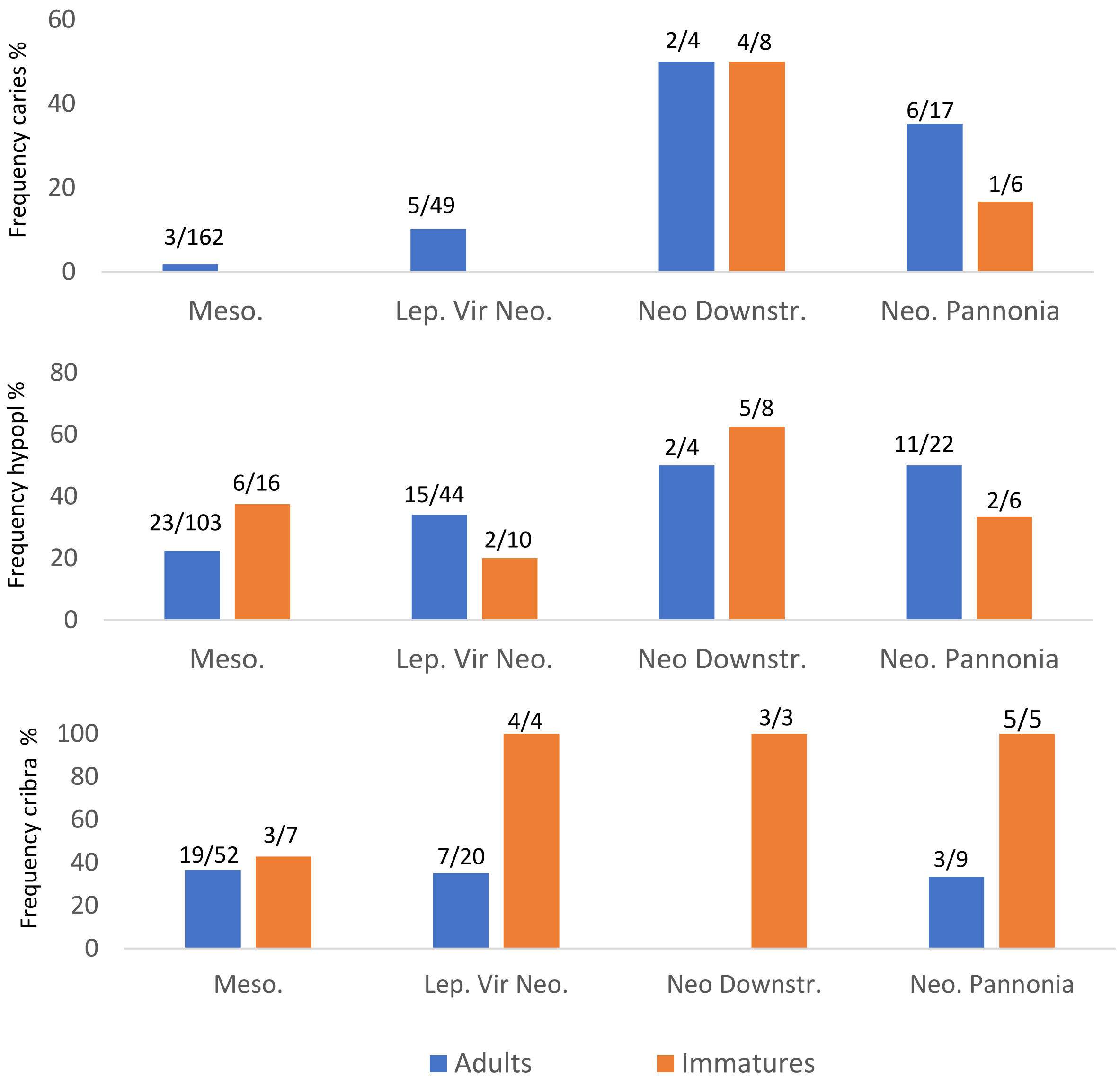

Figure 17: Frequencies of dental caries, linear enamel hypoplasia and cribra orbitalia for the sites of Lepenski Vir, Padina, Vlasac, Hajdučka Vodenica and Ajmana, and Early Neolithic sites from southern Pannonia (data from Jovanović 2017; Jovanović, de Becdelièvre et al. in prep.).

Teeth wear

Finally, anthropologists working on different assemblages also noticed the high degree of tooth wear (e.g. Padina, Vlasac, Lepenski Vir, Hajdučka Vodenica, and Schela Cladovei: Zivanović 1975; Y'Edinak 1978; Grga 1998; Bonsall et al. 1997; Borić et al. 2011; Radović 2013; Jovanović 2017). For instance, Đ. Grga (1998) reported that slightly more than half of total number of teeth he examined was exposed to some level of abrasion (55%). High degree of tooth wear, particularly concerning posterior teeth, could be related to the crushing of hard substance, such as bones, nuts or dried fish or meat for instance, but also of small gravels within consumed fish (Zivanović 1975; Y'Edinak 1978; Bonsall et al. 1997; Radović 2013). Yet, although important tooth wear has been observed on molars, heavier anterior tooth wear has been noticed for individuals from most sites and all period (e.g. y'Edinak 1978; Bonsall et al. 1997; Grga 1998; Radović 2013), which could also be related to the use of teeth in a non-masticatory way (Radović 2013).

2.3.2.3.2. Skeletal evidence for metabolic disease, malnutrition and infections

Cribra orbitalia and porotic hyperostosis

Skull lesions – cribra orbitalia and porotic hyperostosis – have also been observed on individuals buried at several sites (Angel 1984; Borić et al. 2011; Jovanović 2017; de Becdelièvre et al. 2017a[33] unpublished podium presentation). These lesions are usually associated with anemia and micronutrient deficiency (iron and vitamin C deficiency concerning cribra orbitalia, depletion in vitamin B12 reserves concerning porotic hyperostosis) but can also be caused by various diseases, parasites and inflammatory processes (in the case of hyperostosis porous). In the Danube Gorges, the frequency of cribra orbitalia remains quite similar over time and comparable with other Mesolithic populations (Figure 17; Jovanović 2017). Mesolithic adults display more healed than active lesions suggesting that they managed to cope with the biological stress experienced, while Neolithic adult display slightly more active lesions than Late Mesolithic individuals. It has also been noticed that Early Neolithic children were more affected than adults, particularly concerning those buried in the Downstream Area, which suggests that they may have been less successful at coping with the experienced nutritional deficiencies. The frequency of cribra orbitalia is also high amongst Early Neolithic children buried in close-by regions of the Central Balkans, perhaps a consequence of a lower quality diet and greater amount of zoonotic diseases (Jovanović 2017). Porotic hyperostosis has been observed at very frequent rates in the Danube Gorges concerning both Mesolithic and Neolithic periods (Jovanović 2017; de Becdelièvre et al. 2017a unpublished poster presentation[34]); in higher frequency than amongst most other European Early Neolithic populations (Jovanović 2017). The main difference between the Mesolithic and the Neolithic is related to the activity patterns, with more healed lesion during the Mesolithic. Neolithic females had particularly lower rates of healed lesions. Porotic hyperostosis has also been reported amongst other European Mesolithic population ((Meiklejohn and Zvelebil 1991) and its high frequency in the Danube Gorges could be associated to the possible presence of some infectious diseases, which may have contributed to disturb the metabolism of micronutrients (ibidem).

Metabolic diseases

Although the paleopathological examinations of Late Mesolithic individuals discovered at Vlasac performed by Nemeskéri and Lengyel (1978) support a rather good health status, the authors additionally reported evidence for metabolic disease and malnutrition. They mentioned rickets (11 children; 44%), osteomalacia (11 adults) – the adult equivalent of rickets – and scurvy (3 children and 2 adults). Rickets and osteomalacia are manifestations of vitamin D deficiency, most often due to a combination of poor exposure to sunlight and dietary deficiency or, less frequently, a result of abnormal loss of calcium from the body due to disease. Scurvy occurs when the diet is deficient in vitamin C. Bonsall et al. (1997) yet emphasized the fact that rickets, osteomalacia and scurvy have not been observed on the other samples from the Gorges and that the diagnosis of these conditions by Nemeskéri and Lengyel seemed to have been entirely based on biochemical analysis of bones - including calcium and vitamin levels - which should be regarded with caution given the possible diagenetic alterations. Drawing on available information concerning the osteo-anthropological sample from Vlasac and other Mesolithic coastal sites (particularly Franchti cave in Greece, as well as Ertebolle contexts in Scandinavia), Meiklejohn and Zvelebil (1991) provided an interesting interpretation to these evidence for possible nutrition-related diseases. They indeed emphasized the fact that vitamin D and/or calcium deficiency – associated with rickets, osteomalacia – would be surprising in populations which may have access to abundant fish resources. Their observation can also be extended to iron and B12 vitamins, associated with cribra orbitala and porotic hyperostosis; besides, cornelian cherry charcoal and fruits stones, whose fruit is particularly rich in vitamin C have

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[33] Cf note supra

[34] Cf note supra

been frequently retrieved on Late Mesolithic context at Vlasac. Meiklejohn and Zvelebil thenceforth suggest the possible implication of parasitic infections, especially Diphyllobotherium tapeworm, endemic to the Danube Basin and to Scandinavia. Significant levels of intestinal parasites amongst the sedentary fisher-hunter-gatherers living in Scandinavia, the Danube Basin and maybe some other coastal regions, may indeed have affected their liver ability to metabolize some micro-nutrients, otherwise abundant in their environment. Increased residential permanence, higher population densities along bodies of waters and high reliance on aquatic resources, features that characterize the Scandinavian, Balkans and Eastern European groups of hunter-gatherers, could have favored the rate of infections. It can be noticed that dogs may be similarly affected by some parasites also hosted by humans, such as Diphyllobotherium, and domestication may have contributed to facilitated mutual infections and impacted on health status.

Inflammatory processes

Nemeskéri and Lengyel (1978) already noticed the presence of inflammatory processes on the bones of Late Mesolithic individuals discovered at Vlasac. S. Stefanović (2012) systematically analyzed traces of infections according to the type and activity of the pathological change and suggested that they might have been caused by a bacterium related to the Treponema genus, responsible for treponemal diseases. The presence of similar traces of infections has also been observed on the long bone of perinates, examined with X-ray, which suggested the possibility for a congenital disease, transmitted from mother to child in utero or during the birth process. The author also interpreted cut-marks observed on some skulls as possible attempts for healing treatment, cutting and scalping to remove soft tissues of infected patients. Yet, other authors also interpreted similar cutmarks as post-mortem body manipulations (e.g. Wallduck and Bello 2014; Bello et al. 2016). If such interventions took place, it is possible that inflammation after cutting might have caused porotic hyperostosis in some cases. She also noticed that more Transformational-Neolithic individuals buried at Lepenski Vir display more advanced stages of infection than Late Mesolithic individuals, perhaps an indication that the intensity of the infection may have increased over time. Generally speaking, it is possible that the population growth and arrival of migrants at the advent of the Neolithic may have increased pathogens in the Danube Gorges population.

2.3.2.3.3. Growth patterns and body proportions

Adults body proportions

Finally, reconstructed body proportions and growth patterns have also been regarded as indicators of unspecific stress and biological distance amongst the local Mesolithic-Neolithic population (Jovanović 2017; de Becdelièvre et al. 2015 and 2017a unpublished podium presentations[35]). Indeed, the skeletal morphology is influenced both by genetic and environmental factors: for instance, stature is under genetic control but can be altered by episodes of retardation during periods of malnutrition, undernourishment or chronic diseases (e.g. Goodman et al. 1984; Kemkes-Grottenthaler 2005). Results indicated differences in terms of body proportions (size, weight and body mass index) between individuals dated to the Mesolithic periods and to the Transformational/Neolithic period. Mesolithic females were taller (average and standard deviation: 166±5cm, n=17 versus 160±4cm, n=15) and heavier (65±4kg, n=17 versus 58.5±6kg, n=13) than Transformational/Neolithic females and were also slightly more fit (body mass index Mesolithic females=22.7±1.5, n=10; Transformational-Neolithic females=21.8±1.8, n=13). Interestingly, the reconstructed body proportions of Early Neolithic females buried in close-by regions of the Central

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[35] de Becdelièvre, C., Porčić, M., Goude, G., Le Guen M.A, Jovanović, J., Stefanović, S. From individual mobility to population dynamics during the Mesolithic and Neolithic transformations in the Danube Gorges (Balkans, ca. 9500–5500 BC): Adaptations and interactions. Research presented at MESO 2015, The Ninth International Conference on the Mesolithic in Europe. (14.-18.09.2015. Belgrade, Serbia).

de Becdelièvre, C., Jovanović, J., Hofmanová, Z., Stefanović, S. Who were the earliest farmers? Interactions - innovations - adaptations at Earliest Neolithic of The Central Balkans, Human Bioarchaeological Perspectives. Research presented at the 23rd European Association of Archaeologists Annual Meeting, (30.08.-03.09. 2017. Maastricht, Netherlands).

Balkans indicated that they were in general smaller than Mesolithic and Neolithic females from the Gorges but not necessarily lighter than the Neolithic females buried in the Gorges (average: 154cm, n=6 and 60kg, n=4), with a higher body mass index (average 24.2kg, although small sample size of 3 females; Jovanović 2017). Mesolithic males were also taller (179±6cm, n=22; versus 171±7cm n=8) than Transformational/Neolithic males but only very slightly heavier in average (72±0.4kg, n=16 versus 71±0.4kg, n=6) and thus slightly more fit (body mass index: 22.9±2, n=15; versus 23.8±2.7, n=5)[36]. In a study conducted in parallel, MacIntosh et al. (2016) compared reconstructed body proportions of individuals from the Danube Gorges in a broader sample of Central European Neolithic individuals. They also observed noticed the reduction in body size and mass for males and females[37].

Children growth patterns

The study of growth trajectories from birth to 15 years old performed by Pinhasi et al. (2011) did not reveal any major differences when comparing the Mesolithic and the Neolithic periods. The authors only insist on the later age of attainment of dimension per age for some Mesolithic-Neolithic children in comparison with modern samples and on some intra-population variability which could both be due to genotypic variations or to environmental difference (e.g. higher Mesolithic tibio-femoral index for Mesolithic newborns and variability in femoral/humeral proportions amongst the Danube Gorges individuals; Pinhasi et al. 2011). More recently, we compared reconstructed body proportions per age for children with modern reference growth curves for stature, weight and body mass index (use of the Denver WHO and CDC "reference" curves; Jovanović et al. 2016 unpublished podium presentation[38]). Results indicated that 1/5 Mesolithic child fall below the 95 percentiles of nowadays reference curve versus 3/10 Transformational-Neolithic concerning body size, 0/2 Mesolithic versus 4/8 Transformational-Neolithic concerning body weight and 0/1 Mesolithic versus 3/7 Neolithic concerning the body mass index.

The observed decrease in body size is consistent with a general pattern documented for Eastern and Central Europe where South-Eastern and Eastern European hunter-gatherers have higher body size than Neolithic farmers (e.g. Holt et al. 2018). These differences may in part be due to decline conditions for somatic growth (nutrition, chronic disease, reduced mobility) with the development of farming practices, as also suggested by our reconstructions of children body proportions per age. Yet, preliminary results also suggest that foragers were slightly taller during the Early Mesolithic than during the Late Mesolithic: the decline in body proportions could have been initiated before the Neolithic transition, and might rather be associated with reduced residential mobility than with the adoption of a agro-pastoralist diet. Besides, considering that significant reduction of the body size in Europe has also been observed during major events of climate changes (Holt et al. 2018), it could be hypothesized that the 8.2 cooling event could also have impacted body size. Interestingly, the decline in size associated with the Mesolithic-Neolithic transition affected both males and females while the decline in weigh affected only females. This could lead to the conclusion that body size may have been more influenced by sedentism and/or by Early Holocene climatic oscillations than weight. In contrast, observed changes in females' weight could be a

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[36] No reconstruction of body proportions could be performed by Jovanović (2017) for Early Neolithic males buried in South Pannonia (Vojvodina and Šumadija) due to the state of preservation of the studied sample.

[37] Body size for Mesolithic-Early Neolithic Males from the Danube Gorges: 171.15±6.82cm, n=23 versus Neolithic Males from Central Europe: 171.15±5.65cm, n=76
Body mass for Mesolithic-Early Neolithic Males from the Danube Gorges: 70±47cm, n=16 versus Neolithic males from Central Europe: 62.11±7.52cm, n=57
Body size for Mesolithic-Early Neolithic Females from the Danube Gorges: 157±6.75cm, n=27 versus Neolithic females from Central Europe: 152±5.5cm, n=50;
Body mass for Mesolithic-Early Neolithic Females from the Danube Gorges: 55.08±3.56cm, n=5 versus Neolithic females from Central Europe: 51.94±4.46cm, n=32

[38] Jovanović, J., de Becdelièvre, C., Goude, G., Herrscher E., Stefanović, S. 2016. Children feeding practices and growth patterns during Mesolithic-Neolithic transition in the Danube Gorges. (28.08.-02.09.2016.8th *World Archaeological congress,* Kyoto, Japan)

consequence of a particular social structuration (differential activity/mobility patterns and access to resources), of a change in females' nutritional health and energetic balance (reduced mobility and/or specific diet), or in the level of physiological stress experienced (increased number of pregnancy, specific diet and/or particular infectious). Finally, it is possible that Early Neolithic migrants may have additionally brought in the Gorges the genetic bases for smaller body proportions; yet, Early Neolithic females buried in the Gorges remained taller than those buried in the close-by regions of the Central Balkans, perhaps because of the nutritional reservoir represented by the Danube river and/or, as an effect of the admixture between local hunter-gatherers and incoming Neolithic farmers.

2.3.2.3.4. The overall health of the Danube Gorges population, synthesis

Skeletal markers of health, physiological and nutritional stress hence indicate that the health of the Mesolithic and Neolithic inhabitants of the Danube Gorges is comparable with other European Mesolithic populations of sedentary hunter-fisher-gatherers who relied on a diet rich in proteins, particularly from aquatic resources. Non-specific markers of physiological stress do not reveal the health decline usually associated with the agricultural transition. However, hyperostosis porous has been observed at very frequent rates over the Mesolithic and the Neolithic in the Gorges, cribra orbitalia was also reported, and traces of inflammatory processes, as well as possible biochemical evidence for metabolic diseases, possibly affected by taphonomic contaminations though. These features might be associated to a disturbed metabolization of micro-nutrients, perhaps caused by some parasites present in the aquatic resources consumed or and/by infectious diseases.

The presence of dental caries has been reported on the teeth of some Transformational and Neolithic females buried at Lepenski Vir and Ajmana and of some Early Neolithic children buried at Ajmana, which suggests that they might have consumed a diet more rich in carbohydrates (introduction of cereal-based food?). The preliminary results of ongoing research also indicate a higher occurrence of enamel hypoplasia at these sites and show that Neolithic children also experienced physiological stress events earlier than during the previous periods. Finally, a decline in body size could have been initiated by the development of a more sedentary lifestyle, and accentuated by climatic oscillations, and/or Early Neolithic migrations and gene flows. A specific decline in females' weight might be related to behavioral and physiological adaptations and/or to sex-specific migrations. Although the sample size is very small, it has been observed that more children dated to the Neolithic period fall below nowadays reference curves for body proportions than Mesolithic children, perhaps because they experienced more physiological stress earlier in life, which might, hypothetically, be related to differences in terms of feeding practices and/or of infectious loads.

2.3.2.3.5. Traumatic injuries and evidence for physical violence

Several authors have observed traumatic lesions on the skeletal remains of individuals buried at the sites of Lepenski Vir, Vlasac and Schela Cladovei (Nemeskéri and Lengyel, 1978; McSweeney et al. 2000[39]; Roksandić 2004; Roksandić et al. 2006). M. Roksandić examined this sample with the hypothesis that violent interactions may have been associated with the spread of the Early Neolithic in the region, notably related to territory claims, population increase and social competition (Roksandić 2004; Roksandić et al. 2006). On sites of the right bank, only a few individuals (6/418 observed by Roksandić) exhibit traces of traumatic injuries (parry fractures, projectile points injuries, depressed fractures and impacts on frontal bones) and some of them likely died of the wounds. In the area III of Schela Cladovei, slightly more individuals (7/28 individuals buried on this sector)

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[39] McSweeney K., Boroneanţ V., Bonsall C. 2000. *Warfare in the Iron Gates Stone Age: The Evidence from Schela Cladovei.* Unpublished paper presented at The Iron Gates in Prehistory: New Perspectives, March 30th to April 2nd 2000, Edinburgh.

showed evidence of projectile wounds, parry or skull fractures (McSweeney et al. 2000). Most of these individuals have been dated or chrono-culturally assigned to the Late Mesolithic period (except one Early Mesolithic and one Early/Middle Neolithic). The author thus concluded that these traumatic lesions probably result from sporadic episodes of interpersonal conflicts – perhaps more intense at Schela Cladovei – rather than endemic warfare in the region and cannot be related to violent opposition between foragers and farmers (Roksandić et al. 2006).

2.3.3. Bio-molecular analyses: diet, mobility and population dynamics

While the quantitative analyses of plant, animal and human remains at a macro- or microscopical level have provided valuable information about the general ways of subsistence and population dynamics over the Mesolithic and Neolithic Transformations, the application of biomolecular methods have notably enabled researchers to perform direct inferences of the nutritional state, the geographical origin and/or the ancestry of numerous individual buried in the Gorges and to substantially increase the resolution of paleodietary and paleodemographic reconstructions (e.g. Bonsall et al. 1997; Borić et al. 2004; Nehlich et al. 2009; Borić and Price 2013; Hofmanová 2017; Mathieson et al. 2018).

2.3.3.1. Stable isotopes analyses: paleodietary reconstructions

During the two last decades, along with the multiplication of radiocarbon dating research, several stable isotopes paleodietary studies have been conducted on the paleo-anthropological and archaeo-zoological samples from the Danube Gorges (Bonsall et al. 1997, 2002; Grupe et al. 2003; Borić et al. 2004; Nehlich et al. 2010; Nehlich and Borić 2015; Bonsall et al. 2015b, c). These studies have collected direct paleodietary information at the individual and population level, have contributed to reconstruct the local food web and to understand the resources exploited by the Mesolithic and the Neolithic populations and have also enabled to reinterpret the results of radio-carbon dating studies and to reassess the local chronology (e.g. Cook et al. 2001, 2009; Borić and Miracle 2004; Borić 2011; Borić et al. 2014; Bonsall et al. 2015a; Borić et al. 2018). They are based on the assumptions that "you are what you eat", and that the isotopes ratios of some chemical elements (i.e. the relative abundance of the different "forms", or isotopes, that can take an atom of the same element) – here carbon, $\delta^{13}C$, nitrogen, $\delta^{15}N$, and sulfur, $\delta^{34}S$ – measured in an organic tissue (e.g. bone, horn or teeth) should reflect the isotopic signature of the ingested food in a given environment (cf part 3.2). Specifically, $\delta^{13}C$ and $\delta^{34}S$ have been used to distinguish between the consumption of aquatic species and of terrestrial animals and $\delta^{15}N$ has proven to be a relevant marker of the trophic position since it increases at each step of the food web; given that the aquatic environment has a longer food chain than the terrestrial one and due to basic difference amongst plants, the fish consumers should also show higher $\delta^{15}N$ values than meat consumers (ibidem). These markers have been analyzed in the collagen from bone tissue and mainly inform on the protein part of the diet.

2.3.3.1.1. First $\delta^{13}C$ and $\delta^{15}N$ analyses: a focus on chronological patterns

The first analysis of the stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ was carried out by C. Bonsall and his group of research (Bonsall et al. 1997) on human individuals buried at the sites of Lepenski Vir (n=33), Vlasac (n=29) and Schela Cladovei (n=8). A limited number of local contextualized animals were included in this first study: only 7 bovids from Schela Cladovei, 3 from Lepenski Vir as well as 3 fish (undetermined species) and 1 otter bone from Lepenski Vir. The stable isotopes values of these animals are compared with the values of food resources available to native north American population (terrestrial, marine and aquatic herbivores, omnivores and carnivores) and to modern day European (sea fish, dairy products, terrestrial mammals and vegetables) in order to locate human values in the food web. The results suggest that Mesolithic foragers had a high protein diet, "in which the bulk of the protein was derived from riverine food sources" (Bonsall et al. 1997:85). They also evidence a shift on dietary patterns at Lepenski Vir, where more burials dated post 7600 BP (i.e. ca 6450 cal BC) exhibit significantly lower $\delta^{15}N$, which suggests that their diet contained higher proportions of terrestrial food. These lower $\delta^{15}N$ values "may reflect the introduction of stock-raising and/or cultivation in the Iron Gates", suggesting that "the transition from Late Mesolithic to Neolithic at Lepenski Vir was not characterized by a wholesale shift in subsistence from foraging to farming [and that…] traditional food sources were not abandoned in favor of agricultural produces" (ibidem). Besides, significant differences have also been evidenced between the isotopic signals of Mesolithic males and females buried at Vlasac and Lepenski Vir, which have been primarily explained by the authors in terms of "movement of individuals between groups, linked to the practice of local group exogamy" (ibidem). Although this research was clearly a landmark study in the field of Mesolithic-Neolithic paleodietary reconstructions, several caveats should be emphasized: individuals with C/N ratios below the limit value of 2.9 – criterium today used to assess the quality of collagen preservation – were included in the study and other criteria nowadays frequently used (i.e. the nitrogen and carbon contents) were not used back then; based upon the general stable isotope trends observed per periods, the value of some individuals were used for the chronological assignment, which can be seen as a circular approach; the criteria used for the sex diagnosis, including skull morphological characteristic as primary criteria, have been criticized (Roksandić 1999; cf part 2.3.2); a limited number of animal remains from local archaeological contexts have been included in the study.

2.3.3.1.2. Evidencing the freshwater reservoir effect

It has been observed that the radiocarbon dates obtained on human remains used in this study were significantly older than the dates obtained on charcoal remains from similar contexts (Cook et al. 2001). From this observation, and the conclusion that Danube Gorges foragers were substantially including riverine resources in their diet, it has been suggested that their bone collagen value may be depleted in ^{14}C as a consequence of the absorption of carbon from a reservoir that differed in ^{14}C specific activity from the contemporary atmosphere – in other words, "older carbon from the river" - resulting in ^{14}C ages that were too old. The paired measurements of radiocarbon from the bone of five individuals discovered at Schela Cladovei, and of seven bone projectiles points made from long bone splinters of ungulates (thus free from the so-called "freshwater reservoir effect") and found in direct association with these five skeletons, have enabled Cook et al. to establish the magnitude of this freshwater reservoir effect, calculated as 540±70 radiocarbon years. Using human $\delta^{15}N$ values as a measure of the proportion of the diet derived from aquatic foods, a correction has been applied to human bone age at all these sites (with respective 100% aquatic and terrestrial diet endpoints fixed at respective $\delta^{15}N$ values of 17‰ and 9 ‰). The authors also refined the date of the change from aquatic to a mixed diet to circa 7100 BP (i.e. ca 6000 cal BC). All subsequent radiocarbon and stable isotopes studies systematically applied a correction factor to the obtained ^{14}C values (e.g. Bonsall et al. 2000; Grupe 2003; Borić et al. 2004; Borić and Miracle 2004; Nehlich et al. 2010; Borić 2011; Borić et al. 2014; Bonsall et al. 2015a, b, c; Hofmanová 2017; Mathieson et al. 2018; Borić et al. 2018).

While they have been establishing the freshwater reservoir correction method, Bonsall and his co-workers also re-interpreted the stable isotopes chronological pattern observed in the original study by integrating $\delta^{13}C$ and $\delta^{15}N$ data collected for an additional 37 skeletons from Lepenski Vir and 9 from Vlasac (Bonsall et al. 2000). They suggested then that the local subsistence should have changed from a high reliance on aquatic resource to an "intermediary" phase, and eventually a "fully agricultural" stage. They also concluded that these changes likely coincided with the period of house building. In this study, the stable isotopes values of 10 children from Lepenski Vir and 7 from Vlasac were also examined in relation to the adult values, and a "nursing effect" (higher $\delta^{15}N$ due to breastfeeding) was suggested for some of them. However, no more conclusion could be performed concerning children feeding practices given that the age of children was not included in the analyses. It should be mentioned that the stable isotope dataset for these additional 46 analyzed individuals is not available in the study.

2.3.3.1.3. Establishing the local food web

Grupe, Borić and their colleagues (Grupe et al. 2003; Borić et al. 2004) analyzed a broader sample of Mesolithic and Neolithic animal specimens (n=41 from 12 species, both terrestrial and aquatic; Vlasac=40; Padina=1) and human individuals (Vlasac, n=51; Lepenski Vir, n=47; including duplicated measurements from some individuals already analyzed by Bonsall et al. though). It can already be emphasized that 10/51 analyzed human, 4/12 dogs, and 5/12 fish from Vlasac and 9/47 analyzed humans from Lepenski Vir does not fulfill one of the criteria nowadays used by stable isotopes researchers to estimate the quality of collagen preservation (C/N ratio, nitrogen and carbon contents). Stable isotopes results for the faunal samples meets physiological expectations: concerning terrestrial mammals, herbivores (red deer and roe deer) display lower $\delta^{13}C$ and $\delta^{15}N$ values than omnivores (wild boars and brown bears), themselves lower than most carnivores (wolves, dogs and pine martes); concerning fish, the piscivorous catfish, beluga and sturgeons appear enriched in $\delta^{15}N$ in comparison with the detritivorous carp. Regarding the aquatic ecosystem, the authors observed that freshwater fish display the broadest range of $\delta^{13}C$ values, with an important variability in the values of carp, interpreted as an effect of their specific feeding behavior and to the wide range of $\delta^{13}C$ value in freshwater ecosystems (Grupe et al. 2003). It has also been observed that the analyzed specimen of beluga sturgeon exhibits the highest $\delta^{13}C$ values, probably due to its migratory behavior (Borić et al. 2004). The authors additionally noticed that modern specimens of zander and catfish caught at Golubac (the entrance to the Danube Gorges upstream) have much lower $\delta^{13}C$ than the archaeological specimens, an effect that they relate to major changes in the riverine ecology over time. Concerning the terrestrial ecosystem, they observed that canids display slightly higher $\delta^{15}N$ values than most other terrestrial mammals, and than most analyzed specimen of fish, and emphasized the fact that wolf and dogs have almost undistinguishable stable isotope signature. They hence suggested that "dogs from Vlasac most probably lived on leftovers of fish and games discarded by humans, while the rather enriched $\delta^{15}N$ values exhibited by wolves require further attention, especially in the context of canid domestication" (Borić et al. 2004:231[40]). By the inclusion of different specimens of animals from various species this study contributes significantly to our understanding of local ecological systems and food webs. However, it should be emphasized that all but one specimen analyzed originate from the site of Vlasac, and, despite the fact that they noticed major differences in the stable isotopes values of modern and archaeological fish, the authors did not examine the faunal stable isotope values chronologically.

In the light of their reconstruction of the local food webs, Grupe, Borić and their colleagues suggested that that the consumption of large-size carnivorous fish – and perhaps of fish roe – as well as meat of terrestrial carnivores, including dogs, should have contributed to elevate humans' nitrogen values (Borić et al. 2004). They hence criticized the endpoint value suggested by Cook et al. (2009) for a 100% aquatic derived diet (17‰), suggesting that this value should rather reflect a mixed diet from several protein rich food sources (i.e. including the meat of carnivorous animals) and not only fish. The observed broadening of the dietary spectrum in terms of nitrogen values concerning the later periods of occupation of Lepenski Vir, has then been related to a change in lifestyles, particularly to a greater consumption of herbivores meat by some individuals (Grupe et al. 2004). Borić et al. particularly call into question Bonsall et al. association between the stable isotope changes observed at Lepenski Vir and the introduction of agricultural practices in the region (Borić et al. 2004). Based on the archeozoological data, they argued that the different stable isotope

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[40] Yet, the absence of difference between wolf and dogs could also be due to the small sample size of analyzed wolves (n=3) in comparison with dogs (n=13), and to the elevated nitrogen values displayed by one of the wolves.

values noticed for some individuals buried at Lepenski Vir may rather reflect their preferences for the consumption of hunted games than an actual shift to agricultural products, that the subsistence change at this site lagged behind the appearance of Neolithic technology 200-500 years old, and that Bonsall et al. may have been too influenced by the situation of Schela Cladovei[41], located in a different environmental settling than the sites of the Inner Gorges. Finally, it can be mentioned that the stable isotopes values of 25 neonates discovered at Vlasac (n=12) and Lepenski Vir (n=13) were also included in their analyses. Concerning these children, Grupe et al. only mentioned that "more neonates who had obviously never been fed mother's milk were encountered at Mesolithic Vlasac than at Neolithic Lepenski Vir" (i.e. higher δ^{15}N values concerning neonates from Lepenski Vir), which could have some "meaning in terms of the ceremonial uses of the sites" or simply be "due to a sampling artefact" (Grupe et al. 2003:204).

2.3.3.1.4. Radiocarbon studies and stable isotope values

Apart from paleodietary studies, δ^{13}C and δ^{15}N values from human and animal bone have also been reported from different radiocarbon dating studies, discussed quite unevenly (Whittle et al. 2002; Borić and Miracle 2004; Bonsall et al. 2004; 2008; 2015a; Borić et al 2008; 2014; 2018; Borić 2011). These data allow for extending the human sample size to other sites such as Padina and Hajdučka Vodenica (Borić and Miracle 2004) in the Inner Gorges and Ajmana and Velesnica in the Downstream Area (Borić 2011; Bonsall et al. 2015a) and to increase the number of analyzed terrestrial mammals from the sites of Lepenski Vir, Vlasac and Padina (Whittle et al. 2002; Borić and Miracle 2004; Borić et al 2008; 2014; 2018; Borić 2011).

Only based on the δ^{13}C and δ^{15}N values of 24 radiocarbon dated individuals from Lepenski Vir, Bonsall et al. further reconsidered the hypothesis of a "transitional diet" and rather insist on the subsistence variability during the Final Mesolithic-Early Neolithic phase due to the presence of some individuals with lower nitrogen values (Bonsall et al. 2004; 2008). They interpreted this pattern in association with "the status of 'sacred site'", that may have been assigned to Lepenski Vir "that is, one with special religious significance for the people who lived within its 'catchment' or zone of influence" (Bonsall et al. 2008: 194, quoting Srejović 1969, 1972; Gimbutas 1991; Bonsall et al. 2002b and Radovanović et al. 2006). They provide a number of possible explanations for the presence of individuals who were less relying on the consumption of aquatic resources, who "could : **1.** be Members of a local population, or even a single co-resident group, with highly variable dietary preferences; **2.** Belong to a phase when farming started to make a significant contribution to the local economy — presumably in the latter part of the 6200–6000 BC time-range; **3.** belong to a time(s) when there was a shift in the Mesolithic subsistence base, toward greater reliance on wild terrestrial resources; **4.** be local Mesolithic foragers who moved away to live with hunter-gatherers (with more terrestrial-based diets) or farmers, but were returned to Lepenski Vir for burial; **5.** be incomers who originated among either, a) hunter-gatherers or b) farmers in the hinterland, and subsequently moved into the Lepenski Vir locality (e.g. on marriage, or as slaves/war captives); **6.** be members of outlying a) hunter-gathering or b) farming communities who had some connection with Lepenski Vir and were brought there for burial." (Bonsall et al. 2008:194).

Based on stable isotope data obtained in these radiocarbon studies, Borić (2008, 2011) noticed that the lower δ^{15}N values observed for some Transformational-Early Neolithic individuals buried at Lepenski Vir could also be found at the downstream site of Ajmana for the only two individuals analyzed from this site (AJ 6 and AJ 7); a later publication of ^{14}C dates by Bonsall et al. (2015a) suggested that some Early Neolithic individuals buried downstream at Velesnica also display similarly low δ^{15}N values. According to C. Bonsall and his colleagues: "these stable isotope data indicate that Early Neolithic people living along the Danube regularly consumed fish, though to a

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[41] C. Bonsall and V. Boroneanţ leading the excavations conducted at Schela Cladovei, located just at the downstream entrance of the Gorges, during the 1990's (e.g. Boroneanţ et al. 1999; Bonsall et al. 2013). Archaezoological data for the Neolithic occupational layer at this site (e.g. Bartosiewicz et al. 1995, 2001) indicates a greater representation of domesticated animals than concerning the Neolithic layer at Lepenski Vir (e.g. Bökönyi 1970)

lesser extent than their Mesolithic predecessor" (Bonsall et al. 2015a:42). However, these values clearly contrast with the few Early Neolithic dated burials from Padina, Hajdučka Vodenica and Vlasac which display much higher δ^{15}N values. Borić emphasized that "such a pattern indicated the heterogenous nature of the process of transformation even within this micro-region" (Borić 2008:34). Further paleodietary research crossing biochemical markers, local archaeofaunal and archaeobotanical data are thus required to clarify the observed δ^{15}N differences between the Downstream Area, Lepenski Vir in the Upper Gorges and the other sites of the Inner Gorges.

In 2009, Cook et al. responded to some comments made by Borić et al. (2004) on their method to estimate the reservoir effect and reconsider the origin of this reservoir effect in the view of the stable isotopes data made available. They discount the theory for the high δ^{15}N values being derived from the consumption of the meat of higher trophic level animal on the simple basis that this would not have generate the very obvious age offsets that exists between human bone ages and those of contemporaneous animal bone and woof charcoal. Besides, in case of a consumption of scavengers such as dogs, they also mention the fact that the inclusion of aquatic-derived proteins (enriched in "old carbon" atoms) can be indirect. According to species representation in the archaeozoological record at several sites of the Gorges (e.g. Nalbant 1970; Clason 1980; Bartosiewicz et al. 1995, 2001; Bartosiewicz and Bonsall 2004; Bartosiewicz et al. 2008; Borić and Dimitrijević 2005) but also on the stable isotopes values of fish remains published by Borić et al. (2004), the authors also consider that the assumed "freshwater reservoir effect" could be, at least in part, due to the consumption of some anadromous species and thus may rather be re-considered as a "marine reservoir effect". The authors also highlight the tendency in Borić et al. (2004) data toward heavier δ^{13}C and δ^{15}N human values as the Final Mesolithic is approaching, which could be due to an increase in the consumption of aquatic resources and/or to a change in the aquatic species targeted. They explained that at the time of the publication of their original paper, the popular view was that a giant freshwater lake had occupied the Black Sea basin until 6700 BP (e.g. ca 5600 cal BC; Ryan et al. 1997) but that subsequent works have suggested that this conversion could have occurred earlier, at around 8400 BP (ca 7500 cal. BC) or even before, or may have result from multiple incursion from the Mediterranean into the Black Sea (Major et al. 2006; Bahr et al. 2006; Martin et al. 2007). This consideration may have some important implication for the calculation of the chronological offset caused by the reservoir effect since the marine reservoir effect could be smaller than the freshwater reservoir effect (Kwiecien et al. 2006). From this study, it appears that further works are needed to better estimate changes in the relative proportion of stationary freshwater fish and migratory species in the local Mesolithic diet over time.

2.3.3.1.5. δ^{34}S analyses: a pilot study

A pilot study was conducted by Nehlich et al. in 2009 to explore the use of sulfur isotopes (δ^{34}S) as an indicator of the consumption of freshwater fish on Mesolithic and Neolithic remains from the Danube Gorges and neighboring region. δ^{34}S, δ^{13}C and δ^{15}N were analyzed on the remains of 19 humans and 8 animals from four Early Mesolithic to Early-Middle Neolithic sites of the Danube Gorges – Vlasac (n human=4, n fish=3), Padina (n human=4, n non-human terrestrial mammal=5), Lepenski Vir (n human=8), and Hajdučka Vodenica (n human=3) – and from five Neolithic humans discovered in an Early Starčevo context at the site of Vinča, along the Danube upstream from the Gorges in Šumadija. Results show a difference in the sulfur isotope values between analyzed fish (high δ^{34}S values; cyprinidae, n =2 and acipenseridae, n=1) and terrestrial animals (low δ^{34}S values: aurochs, n=2, chamois – wild boar – roe deer, n=3). Yet, it can be mentioned that the criteria used for the validity of collagen preservation are not met for the two cyprinids fish. Concerning humans, the authors found that low nitrogen isotope values were associated with low sulfur isotope ratios, reflecting the low sulfur isotopic values of the terrestrial animals. They noticed that the highest human nitrogen isotope values also coincided with higher sulfur isotope ratios, which are related to the higher sulfur isotope values of the freshwater fish, and related intermediate sulfur to a mixed diet of both terrestrial and freshwater resources. They observed important intra-site differences, suggesting that the Mesolithic human buried at Padina did not consumed, or only in little amount, freshwater fish, that the intake of aquatic resources was minor for one individual buried at Hajdučka Vodenica and at Vlasac but more substantial for other Mesolithic individuals buried at these sites and for most Transformational-Early Neolithic buried at Lepenski Vir. The stable isotopes values of one Transformational-Early Neolithic, of the two analyzed Early-Middle Neolithic individual buried at Lepenski Vir and the individuals buried at the Neolithic site of Vinča also suggest a terrestrial diet. Looking through the prism of chronology, the authors thus suggest that the diet encompasses more local variations than assumed by previous biochemical studies during the Mesolithic and Early Neolithic periods (exploitation both of terrestrial and aquatic ecosystems), while later during the Neolithic the diet was more concentrated on terrestrial habitat, and excluded aquatic resources.

Nehlich et al. interpretations of δ^{34}S results have been further discussed in a debate which was particularly focused on the issue of Mesolithic dietary variability (Bonsall et al. 2015b and c, Nehlich and Borić 2015). One of the main criticisms made by Bonsall et al. concerns the suggestion that high δ^{15}N values associated with rather low δ^{34}S values, a pattern mostly observed concerning Mesolithic individuals buried at Padina (and two individuals buried at Hajdučka Vodenica and Vlasac), could be explained by the consumption of meat from suckling mammals (elevated δ^{15}N value due to the nursing effect), which is not justified by the archaeo-zoological record. Rather, they suggested that δ^{34}S data could reveal an underlying chronological trend overlooked by Nehlich et al., where Early Mesolithic individuals (e.g. most individuals buried at Padina) show lower values than Later Mesolithic individuals. They emphasized the need for more radiocarbon dates and the integration of a greater amount of information concerning the food web (more δ^{34}S data for animal remains). Particularly, they suggest that there might have been significant fluctuations in the geochemistry of the river through time (and hence in fish δ^{34}S), and/or in the proportions of anadromous fish (elevated marine sulfur signal) entering the human diet due to differences in local river conditions, environmental fluctuations and changing subsistence patterns. Replying to these comments Nehlich et al. applied Bayesian mixing model for dietary reconstructions, quantifying the proportions of terrestrial mammals, freshwater fish and terrestrial suckling animal intake for five individuals (Nehlich and Borić 2015). However, as further commented by Bonsall et al. (2015c), the output of a model is only as good as its input; the absence of discovery of remains of suckling mammals at sites were water-sieving have been practiced in the Gorges (e.g. Schela Cladovei), the need to increase the sample of animal δ^{34}S values and the necessity to take into account possible environmental effect on stable isotope values particularly undermine attempts to perform precise quantifications of the different putative diet sources.

2.3.3.1.6. Organic residue analyses in pottery: fatty acids' δ^{13}C values

A recent biochemical study analyzed pottery shreds from Early Neolithic contexts of Lepenski Vir, Vlasac, Schela Cladovei, Aria Babi and Velesnica in order to identify the origin of organic residues possibly remaining on the vessels (Cramp et al. 2019). In most cases the most abundant fatty acids from degraded animal fats were detected. The determination of fatty acids δ^{13}C values further indicated that non-ruminant carbon stable isotope signature was dominant in over 50% of residues. The presence of specific aquatic biomarkers suggests that, in most cases, this non-ruminant signature is associated with aquatic product processing, and most likely migrating fish. In fewer cases, residues could be compatible with ruminant adipose tissues. The authors also emphasize that the additional contribution of other terrestrial non-ruminants – notably pigs and dogs – is possible, and that the important amount of fats in some aquatic resources may have contributed to blur, in some cases, the presence of fats from other sources. In any cases, the dominance of aquatic signature greatly contrasts with the evidence from other Balkan Neolithic sites, particularly sites of the Northern Balkans and Carpathian basin where dairies likely represented an important part of the subsistence (Ethier et al. 2017). Possible explanations include that: pottery users in the Gorges had diet drawing heavily on aquatic resources, pottery was used for restricted purposes, that the places where the ceramics were used were not the places where other animal resources were prepared, and that the sites of the gorges were only seasonally occupied for fishing. Whether vessels were being brought by farmers making use of local environmental resources or were incorporated into the existing practices of local foragers, or a combination of the two, in any case, the dominance of fish residues in the pots can be seen to represent a change in how fish was processed, the ceramic technology facilitating new cooking practices such as stews, soups or rendering oils.

2.3.3.2. Strontium radiogenic analyses: first generation migrants

Strontium isotope analyses ($^{87}Sr/^{86}Sr$) have been conducted by Borić and Price (2013) on numerous Mesolithic and Neolithic individuals buried in the Gorges (n=167) in order to detect first-generation migrants at advent of the Neolithic in the region. Indeed, the strontium signal of soil and water varies spatially, and is passed to living organisms over the food web without significant modification. Since tooth enamel forms during childhood, the strontium signature of a tooth should reflect the value of the place where the analyzed individual has grown up (cf part 3.2.4). Thus, local and non-local individuals can be differentiated by comparing teeth radiogenic strontium signal with the local baseline (defined using the local geology and/or faunal remains). The authors firstly notice a relationship in $\delta^{15}N$ and $^{87}Sr/^{86}Sr$ with the chronological age of the samples, a broadening of values appearing after ca 6200 cal. BC (Figure 16). Greatest strontium variation is exhibited by Transformational and Neolithic individuals, particularly with lower nitrogen values (more terrestrial diet associated with the transformational and Neolithic periods). The authors also emphasized that "because there are several isotope ratio sources in the region [i.e. different geological bedrocks: mostly metamorphic, limestone and igneous rocks, clastites, coal, gravels and clays], there is no objective way to define a specific threshold for identifying foreign individuals" (Borić and Price, 2013:4). Yet based upon information about geological variation, strontium measurements in modern and archaeological fauna from several sites in the area, and the human range (mean and standard deviation value: 0.7095±0.0007 radiogenic points), they designated the individuals below ca 0.7085 and above ca 0.7100 as non-locals (Figure 18).

Interestingly, amongst the three Epipaleolithic individuals analyzed for strontium, one has been identified as non-local (i.e. migrant, born outside of the region), while only one of the 30 analyzed Early Mesolithic falls at the limit of the defined local range. Although this may be due to the small size of the Epipaleolithic sample analyzed, it coincides with the archaeological interpretations of reduced residential mobility based upon settlements and lithic evidence. Amongst 99 Early to Late Mesolithic individuals analyzed, only three were identified as non-locals, for a period yet covering more than three thousand years. strontium isotope ratios indicate a dramatic increase in the numbers of non-locals buried in this region at two sites - Lepenski Vir and Ajmana– during the period of Transformation-Early Neolithic and a fortiori concerning during the Early/Middle Neolithic period: amongst 25 analyzed individuals buried in the Inner Gorges during the period of Transformations, 5 have been identified has non-locals and 7/13 for the Early/Middle Neolithic (all buried at Lepenski Vir); 2/12 individuals buried downstream at the Early Neolithic site of Ajmana ca 6000 BC have been identified as non-locals (AJm 7 and AJm 15). While the strontium value of most individuals identified as non-locals exceeds the upper boundary of the defined local strontium range, the value of the two individuals discovered at Ajmana and of one Early-Middle Neolithic individual discovered at Lepenski Vir fall below the lower boundary.

The authors identified all but one non-locals buried at Lepenski Vir as females and suggested that women came to these sites from Neolithic communities as part of "ongoing social exchanges"

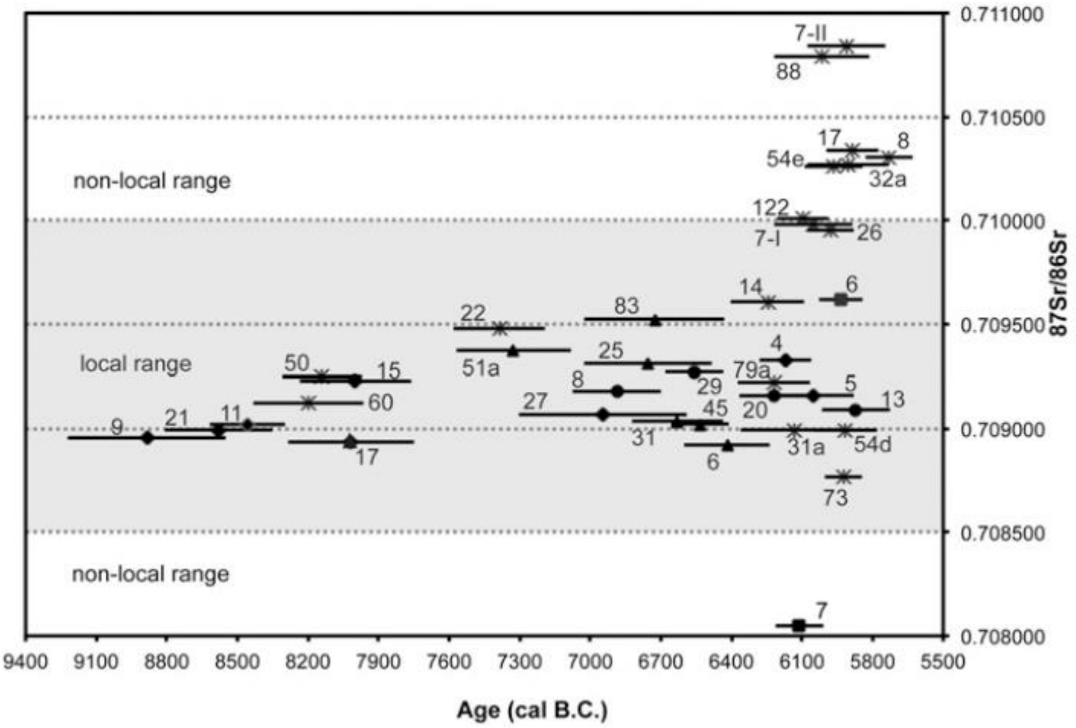

Figure 18: Scatterplot between 87Sr/86Sr and radiometric dates. Lines correspond to calibrated ^{14}C ranges B.C. at 95% confidence, associated with burial numbers from different sites of the Gorges. Ajmana (square); HajdučkaVodenica (circle); Lepenski Vir (star); Padina (diamond); Vlasac (triangle). From Borić and Price 2013.

such as "reciprocal mating network between the Danube Gorges foragers and the earliest farming communities in the surrounding areas" (Borić and Price 2013:5). They also observed that the Early Neolithic individuals buried at Ajmana were discovered placed in several layers on top of each other in crouched/flexed position typical for the Neolithic period in the Balkans and not represented in the mortuary canon of the Inner Gorges before 6000 BC; the 7 non-locals associated with the Early/Middle Neolithic phase of Lepenski Vir were also all primary crouched/flexed burials. Finally, they mentioned that two non-local individuals from Lepenski Vir (32a and 88 had traces of caries and were characterized by largely terrestrial intake, suggesting significantly different dietary intake (typical Neolithic cereal-based diet?). Yet, they underline the fact that some of the non-locals have rather high δ^{15}N values (e.g. LV 7/IIb), indicative of an aquatic diet, while some individuals with a local strontium signature display rather low δ^{15}N values (e.g. LV 26). The strontium evidence thus identified migrants, who "originated in several geologically distinct areas", and chronological information indicate that there were probably "several chronologically separate events during which individuals from likely Neolithic communities interacted with and became incorporated into forager communities in the Danube Gorges in the centuries after ca 6200 cal B.C" (Borić and Price, 2013:5).

Comparing locals and non-locals, first bioarchaeological insights into their behaviors and physics

Further bio-archaeological researches included comparisons of locals and non-locals, further informing on their behavioral and/or biological specificities and possible reciprocal influences (e.g. Radović 2013; Jovanović 2017; Filipović et al. 2017). Skull measurements rather suggest a greater biological between non-locals and locals than in-between the locals, a tendency also confirmed by the analyses of non-metric anatomical variations selected for their genetic etiology, which also show statistically significant differences between the two groups (de Becdelièvre et al. 2017a unpublished podium presentation[42]).

The few Transformational-Early/Middle Neolithic females buried at Lepenski Vir which exhibited evidence of a different cultural use of front teeth have all been identified as non-locals (Radović 2013; cf part 2.3.3). They were perhaps used to perfume some habitual activities, such as rope- or basket-making in a different way as the locals. The Neolithic sample analyzed by Cristiani et al. (2016) for dental calculus trapped starch grains only comprised three non-local females and they all yielded grains: two cases (LV 8 and LV 20) a few grains from the Triticae family, which included European domestic crop species, and one case (LV 32a) grains from another family – Paniceae – but in considerable number (>200). However, another study also shows that 35% of individuals for whom the analysis of calculus yielded starch grains could be identified as locals and a similar proportion as non-locals (Jovanović 2017; Filipović et al. 2017).

Recent researches conducted on health status have also indicated that both locals (n=6) and non-locals (n=5) had dental caries but that several caries were identified only on the teeth of non-locals, some exhibiting 3-5 caries (LV 32a and LV 88; Jovanović 2017). Important rates of calculus - supra-gingival and sub-gingival - have been noticed on the teeth of locals and of non-locals, including individuals with caries and/or for whom rather low $\delta^{15}N$ values have been observed (for instance LV 32a, LV 88, LV 26, or AJ 7). This pattern suggests that the association between strontium radiogenic signal, lower nitrogen values, dental caries and rates of calculus accumulation are not straightforward. Concerning supra-gingival calculus, Jovanović (2017) emphasized the fact that while a link between the formation of plaque and diet rich in protein has been recognized it has also been established that carbohydrate-rich diets with less abrasive components and soft texture can facilitate plaque deposition and mineralization (Lukacs 1989). Besides, higher nitrogen has also been rather related to the consumption of aquatic resources and some of these individuals may have a diet rather focused on meat from games and domesticated. High rates of sub-gingival calculus observed on multiple teeth of one non-local (AJ 7) may rather have a non-dietary aetiology, perhaps related to poor oral hygiene; particularly, it has been suggested that the use of teeth as tool could have facilitated bacterial infection (Jovanović 2017). The frequency of linear enamel hypoplasia (physiological stress events experienced during childhood) is also slightly higher on the teeth of non-local individuals (53% versus 30%).

Finally, humerus and femurs morpho-metric maps and cross-sectional geometric analyses also indicated that the sections of the long bone of non-locals were more symmetrical and some entheseal attachments appear more robust at different sites along the bones (de Becdelièvre et al. 2017[43] unpublished poster and podium presentations). Their long bones thus relate a different history of adaptation and more research is now conducted in order to better understand these differences in terms of patterns of habitual activity and/or of environment frequented.

2.3.3.3. Ancient DNA analyses: migrations and admixture

Several paleo-genomic studies have recently extracted the DNA of Mesolithic and Neolithic humans buried in the Danube Gorges and analyzed these genetic data together with datasets from other Eurasian prehistoric and modern individuals in order to examine the modality of the Neolithic diffusion (cultural exchange, major demic diffusion, infiltration of a few…), to estimate the extent of foragers and farmers admixture, and to clarify chrono-geographic patterns in these events (Hofmanová 2017; González-Fortes et al. 2017, Mathieson et al. 2018). Analyses of ancient DNA (aDNA) conducted during the last decade on other Mesolithic and Neolithic samples from Europe

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[42] de Becdelièvre, C., Jovanović, J., Hofmanová, Z., Stefanović, S. Who were the earliest farmers? Interactions - innovations - adaptations at Earliest Neolithic of The Central Balkans, Human Bioarchaeological Perspectives. Research presented at the 23rd European Association of Archaeologists Annual Meeting, (30.08.-03.09. 2017. Maastricht, Netherlands).

[43] de Becdelièvre, C., Le Guen M.A., Porčić M., Jovanović, J., Stefanović, S. Behavioral Adaptations - Morphological Adaptations: new contributions from Morphometric Mapping for the understanding of Mesolithic-Neolithic transformations (Balkans; 10 000 - 5000 BC). Research presented at the 7th Annual Meeting of the European Society for the study of Human Evolution (ESHE) (21.09.-23.09.2017. Leiden, the Netherlands).

have indicated that the Mesolithic hunter-gatherer-related ancestry can be subdivided into "Eastern" and "Western" hunter-gatherers-related ancestry and that Early Neolithic individuals from Central-Western and South Europe trace their ancestry in large majority from a third source: Anatolian-originated people who migrated into Europe through the Aegean region (e.g. Bramanti et al. 2009, Gamba et al. 2014, Mathieson et al. 2015, Hofmanová et al. 2016). However, different modes of genetic and cultural interactions between hunter-gatherers and farmers have also been observed, involving: long time coexistence and admixture in Southern Scandinavia (e.g. Skoglund et al. 2012), gradual adoption of various Neolithic features by hunter-gathers without admixture with farmers from Anatolian origin in the Baltic and the Dniepr region (e.g. Jones et al. 2017), long time coexistence of communities of farmers with Anatolian ancestry and foragers with a European hunter-gatherers ancestry (Bollongino et al. 2013) and the integration of individuals with a European hunter-gatherers ancestry into Neolithic communities in some regions of Central Europe (Gambe et al. 2014). Finally, genetic admixture has also been observed in later Neolithic stages in Central and Western Europe as "hunter-gatherer resurgence", increase in ancestry typical for hunter-gatherers in Middle and Late Neolithic samples (e.g. Haak et al. 2015). In this context, Hofmanová (2017) analyzed three genomes as well as genome-wide data (nuclear regions and mitogenomes) of 53 Mesolithic and Neolithic individuals buried at sites of the Danube Gorges; González-Fortes et al. (2017) analyzed three genomes, and Mathieson et al. (2018) the genome-wide data of 40 individuals buried in the Gorges.

2.3.3.3.1. Haplogroups: maternal and paternal lineages

These studies have documented the presence of the mitochondrial haplogroups (maternal lineages, mt-haplogroups) U amongst the Danube Gorges Mesolithic foragers, especially the haplogroup U5 a maternal lineage found to be very common amongst Western European pre-Neolithic hunter-gatherers. Interestingly, several Mesolithic individuals were also assigned to the mt-haplogroup U4, frequently documented amongst eastern hunter-gatherers of the Baltic and Dniepr regions (Hofmanová et al. 2017; Mathieson et al. 2018). Other mt-haplogroups, less frequently or not yet evidenced amongst European Mesolithic foragers have also been identified in the Gorges (e.g. K1c and K1f, H13 and H4, I3, X2; ibidem). Mesolithic individuals were all assigned to Y-chromosome haplogroups (paternal lineages, Y-haplgroups) R1b and I2, a paternal lineage also frequent amongst the Eastern and Western European Mesolithic hunter-gatherers (Mathieson et al. 2018). Concerning the period of Transformations-Early Neolithic and the Early-Middle Neolithic period, a mixture of both European Mesolithic-like hunter-gatherer haplogroups (U) and of haplogroups not documented amongst other European Mesolithic foragers but documented amongst the European and Near-East Neolithic (K1a, K1b, N, T, J, H[44]) have been identified. Interestingly, most Transformations-Neolithic non-U haplogroups were identified at the site of Lepenski Vir (and one K1a identified at Padina, Mathieson et al. 2018), while Transformations-Early Neolithic individuals buried at Hajdučka Vodenica and Vlasac were assigned to U maternal lineages. Hofmanová (2017) noticed that the proportion of non-U haplogroups was more important during the Early-Middle Neolithic period at Lepenski Vir than during the previous Transformational-Early Neolithic period (56% of non-U during the period of Transformations versus 75% during the Neolithic in Hofmanová's dataset). Mitochondrial data thus suggest that the proportion of individuals with an ancestry pointing to the Near-East Neolithic ("Agean-like" or "Anatolian"-like ancestry) increase between the period of Transformations-Early Neolithic and the Early-Middle Neolithic at Lepenski Vir, which could have been caused by a continuous incoming of people with this genetic affinity in the community or by a difference in the number of children that individuals with a Near-Eastern Neolithic-like ancestry might have had. A fewer number of

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[44] Before the studies of Hofmanová (2017) and Mathieson et al. (2018), the haplogroup H was not identified amongst Mesolithic western and eastern European hunter-gatherers (only identified on one Caucasian hunter-gatherers from the site of Kotias, Georgia; Jones et al. 2017, Mathieson et al. 2018), and was assumed to be introduced with Neolithic farmers (Pinhasi et al. 2012).

Transformations-Neolithic individuals were assigned to paternal lineage, but it can be mentioned that one transformational and one Early-Middle Neolithic individual were assigned to Y-haplogroups previously undocumented amongst European Mesolithic foragers (G2 and C2; Hofmanová 2017).

2.3.3.3.2. Genetic distance analyses

Genetic distance and relatedness between individuals and groups of individuals were further statistically explored by the authors. Mesolithic individuals from Vlasac (mostly Late Mesolithic) were found to be closer to previously published sequences from Pre-Neolithic European contexts, while samples dated to the Transformations-Early Neolithic period and a fortiori those dated to the Early/Middle Neolithic appeared more related to other groups from Neolithic Europe (Figure 19; Hofmanová 2017).

Mesolithic population structure

The Mesolithic hunter-gatherers buried in the Gorges also show a mixture of Western Hunter-Gatherer- and Eastern Hunter-Gatherers-related ancestry (WHG contributing approximately 85%, and EHG approximately 15%, of ancestry according to Mathieson et al. 2018), in agreement with the presence of U5 and U4 haplogroups. Interestingly, Hofmanová also noticed that the Mesolithic individuals other than Vlasac (from Lepenski Vir, Ostrovul Corbului and Padina) in her sample were relatively close to other samples from the Paleolithic period which could indicate that the Mesolithic samples from the Danube Gorges might be a relict of the hunter-gatherers population that survived the Last Glacial and is different to Holocene populations of Western Europe (Hofmanová 2017). This hypothesis could coincide with the presence of particular mt-haplogroups not documented amongst other European Mesolithic populations (e.g. H haplogroups for 3 individuals from Ostrovul Corbului and one from Lepenski Vir), as also suggested by Mathieson et al. ("Possible scenarios include genetic contact between the ancestors of the Iron Gates population and a northwestern-Anatolian-Neolithic- related population, or that the Iron Gates population is related to the source population from which the Western Hunter-Gatherers split during a re-expansion into Europe from the southeast after the Last Glacial Maximum", Mathieson et al. 2018:3).

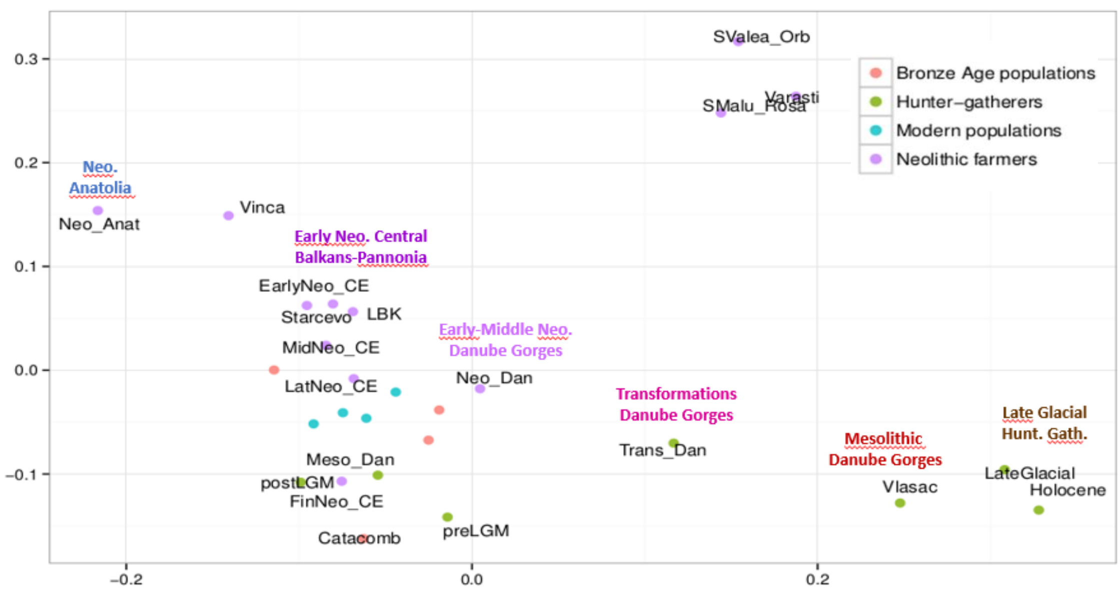

Figure 19: Multidimensional scaling of mitochondrial DNA genetic distance, adapted from Hofmanová 2016.

Neolithic population structure

Concerning the period of Transformations-Neolithic, results also indicate that some individuals buried at Lepenski Vir had an entire Near-Eastern Neolithic-like ancestry (Hofmanová 2017, n=2; Mathieson et al. 2018, n=2), while others had an entire European Mesolithic hunter-gatherer-like ancestry (Hofmanová 2017, n=3). Besides, two individuals buried at Lepenski Vir and one at Padina had a mixed ancestry (Hofmanová 2017, n=1; Mathieson et al. 2018, n=2). Interestingly, it has been noticed that some individuals with non-local strontium radiogenic signals were assigned to European and Near-Eastern Neolithic-like mt-haplogroups (Hofmanová 2017) or had an entire Near-Eastern Neolithic-like ancestry and ate "a primarily terrestrial diet" (Mathieson et al. 2018:3). However, it has also been found that individuals identified as local belong both to U and non-U haplogroups (which would be logical under the assumption that first generation migrants with Near-East Neolithic-Like ancestry may have children born in the Gorges; Hofmanová 2017); in addition, one individual with a U5 haplogroup was also identified as non-local and may hence originate from other hunter-gatherers community (ibidem). Genetic distance analyses also indicated that Transformations-Neolithic non-locals were closer to the cluster of European Neolithic groups than to local individuals from the same periods (ibid.). Most importantly, results of Hofmanová (2017) and of Mathieson et al. (2018) did not confirm that the Near-Eastern Neolithic like ancestry was carried to the Danube Gorges mostly by women, which suggest that the pattern observed by Borić and Price (2013) may either be due to a sample bias or to methodological issues, given that previous sexual diagnoses were partially based on gracility criteria and that genetically more-distant individuals migrated in the Gorges and admixed with the local foragers at the advent of the Neolithic.

Interestingly, while most other Early Neolithic individuals from the Southern and Central Balkans analyzed are shown to be closely related to the Anatolian and Aegean Neolithic (Hofmanová 2017; Mathieson et al. 2017), some individuals buried at the site of Malak Preskavets in Wallachia had significantly more hunter gatherers ancestry (82% of Near-Eastern like ancestry versus 15% of European Mesolithic Hunter-gatherers-like ancestry; Mathieson et al. 2017). Gonzales Fortes et al. (2017) have also evidenced that one Eneolithic genome from a Transylvanian site (Gura Baciului) is genetically predominantly Mesolithic hunter-gatherers like (60%), which could be whether an effect of an admixture during an earlier period of the Neolithic or of a later resurgence. These results also somewhat coincide with the discovery of a Mesolithic-Hunter-gatherer-like genome in an Early Neolithic (Starčevo–Körös*)* context northern in Pannonia (Tiszasz*ől*ős-Domaháza; Gamba et al. 2014).

2.3.3.3.3. Neolithization and complex interactions in the Central Balkans

The results of these studies thus provide support for complex interactions amongst hunter-gatherers and farmers in the Balkans. Individuals with Near-Eastern Neolithic-like ancestry came into contacts with individuals with a European Mesolithic-like ancestry in the Danube Gorges, at least around 6200-6000 BC, and probably contributing to the local adoption of Neolithic innovations. The site of Lepenski Vir may have represented a focal point for cultural and biological exchanges, as indicated by the presence of individuals from diverse ancestry and by the evidence for admixture. During the first centuries of the 6th millennium BC, individuals with Near-Eastern Neolithic-like ancestry increasingly migrated in the Gorges, while they also developed numerous new settlements in the Central Balkans and Pannonian plains. At some places, the level of admixture with the descendants of Mesolithic hunter-gatherers was higher (e.g. Malak Preskavets in Wallachia) and/or some individuals entirely descended from European Mesolithic hunter-gatherers were integrated amongst Early Neolithic communities (e.g. Tiszasz*ől*ős-Domaháza in Pannonia). However, the effects of the observed admixture at Lepenski Vir did not propagate with the same intensity in Central Europe where European Mesolithic-like ancestry was low amongst Early

Neolithic communities, which again contrasts with the situation in Scandinavia, and in some regions of Eastern Europe, perhaps because of differences in the size of hunter-gatherer populations and in how the different environmental conditions were suitable enough to early farming practices.

3. Methods: stable isotope analysis and human osteobiographies.

The substantial effort made during the previous decades to refine the chronology of the Mesolithic-Neolithic transformations in the Danube Gorges, the new information concerning the geographic origin and the ancestry of numerous Mesolithic and Neolithic individuals, new research conducted on archaeobotanical and archaeozoological remains, on population dynamics and health status, now provide a new frame to re-interpret the local stable isotope variability and thereby to further explore Early Holocene subsistence adaptations and the local experience of the Neolithic Transition.

In this study, new stable isotope analyses were conducted and interpreted, at the population and the individual level, alongside collected data previously published (Bonsall et al. 1997; Grupe et al. 2003; Borić et al. 2004; Nehlich et al. 2010; Borić et al. 2011; Borić and Price 2013; Bonsall et al. 2015). These data were analyzed geographically and chronologically and cross-linked with biological information concerning age at death, sex, provenance and ancestry. The age at death and the sex of individuals buried at the site of Padina, Vlasac, Lepenski Vir, Hajdučka Vodenica and Ajmana were estimated for the purpose of this study, and only individuals from these sites were considered for the analyses that involved the age of formation of the tissue considered or sex-determined individuals.

3.1. Chronological assignment and biological characterization

3.1.1. Published information about chronology, provenance and ancestry

All individuals were chronologically assigned using absolute dates (Borić, 2011; Bonsall et al. 2015) and the relative chronological assignment used by Borić et al. (2004), Borić and Price (2013) and Stefanović (2016). Information about origin derived from the interpretation of the strontium radiogenic signal published by Borić and Price (2013; cf part 2.3.3.) and information about ancestry derived from the ancient DNA analyses performed by Hofmanová (2016) and Mathieson et al. (2018; cf part 2.3.3).

3.1.2. Age at death estimation

Given that the skeletal changes associated with growth and development occur rapidly and follow specific milestones, a precise and accurate age at death can be established for immature individuals (considered here as those who died before 20 years old), which is of particular importance for reconstructing children feeding practices. Methods that established the relationships between biological and chronological age are based on reference samples of individuals of known age. Concerning perinates, the age at death was determined using equations based on the length of long bones (Fazekas and Koza 1978). The schedule of teeth formation (Moorrees et al. 1963a, 1963b) – assessed through ct-scan – and of dental eruption (Ubelaker 1978) was used to estimate the age at death of infant and children until the age of 12-13 years (completion of apex of second permanent molar). The age at death of children for whom no teeth were preserved or teenagers was determinates according to the length of long bones and to the observed stage of epiphyseal fusion (epiphyses fused or not to the diaphysis; Stoukal and Hanakova 1978; Scheuer and Black 2000). Fusion of secondary center of ossification were finally used to discriminate adult from immature individuals aged at death ca 15-20 years old (Scheuer and Black 2000; Buikstra and Ubelaker 1994; Veschi and Fachini 2002). When different indicators were observed (e.g. length of different bones), the broadest age interval was selected, except in the case of infants and children with preserved teeth where the estimated dental age – considered as the most reliable indicator (e.g. Scheuer and Black 2000) – has been favored over bone growth and maturation indicators.

Concerning mature individuals, accuracy is favored over precision in the age estimation, given that the process of ageing involved an important inter and intra-population variations, being also dependent to genetic, environmental and behavioral factors. Adult individuals (individuals with bone of adult size) were firstly classified as ⩾ 25 years old, ⩾ 30 or 20-30 years old according to the fusion of the pubic symphysis and of the sternal end of clavicle (Buikstra and Ubelaker 1994; Black and Scheuer 1996; Scheuer and Black 2000). When coxal bones were preserved enough, a probabilistic method of age estimation based on the morphological changes of auricular surface and of the pubic symphysis was applied (Schmitt 2005, 2008). Based on large-size samples of individuals with known age at death and including an important inter-population variability, these methods provide the probabilities that analyzed individual died within different broad age intervals. For purpose of comparison with stable isotope results, adults were then further regrouped into the following broad categories: adult size (>15 years old), middle aged adults (30-49 years old), old adults (>50 years old).

3.1.3. Sex determination

The sex determined by M. Roksandić (1999) for Mesolithic-Neolithic individuals buried at the sites of Padina, Vlasac, Lepenski Vir and Hajdučka Vodenica was reassessed in this study applying formalized probabilistic based methods allowing for optimizing the accuracy of the results (Bruzek 1991, 2002; Murail et al. 1998, 2005). A two-step procedure was followed to minimize the effect of the high inter and intra-population variability in the expression of skeletal skeletal dimorphic traits (following Murail et al. 1998):

- a primary diagnosis using methods established on pelvic bone – which sexualization features only slightly differ at an inter-population level – from substantial reference samples of individuals with known sex, proven to be accurate at a 95% threshold (Bruzek 1991, 2002; Murail et al. 2005); this procedure hence provide an accurate "intra-population reference sample";
- a secondary diagnosis allowing for allocating the sex of individuals indeterminate with the primary diagnosis using their extra-pelvic anthropometric characteristics after testing the discriminating power of each features on previously allocated individuals from the "intra-population reference sample" (Van Vark 1971; Murail et al. 1998).

These analyses consider individuals of adult size >15 years old[45]. Only individuals with preserved infra-cranial remains were examined, excluding dislocated skulls and mandible found in various burials, individuals represented by a few anatomical elements or too fragmented, cremations and the remains of individuals deemed to originate from insecure context due to observed morphological discrepancies (also noticed by Roksandić 1999). The final sample hence encompass 156 individuals.

Primary diagnosis: an "intra-population reference sample" based on the hip bone

Two methods based on pelvic features have been jointly applied: a probabilistic morphometric approach (Murail et al., 2005) and a morphological approach (Bruzek 1991, 2002). Combining these two approaches, we minimize the observer errors (Murail et al., 2005) and maximize the number of sex determinations (Bruzek 1991, 2002)[46]. The latter is based on the observation of sexualization features of five discriminating characters; yet given the poor state of preservation of coxal bones from the Danube Gorges prehistoric sample and the need for a large

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[45] The Iliac crest of two individuals aged at death 15-20 years old was not entirely mature; measurements involving this anatomical part were removed to determinate the sex of these individuals.

[46] The morphometric method developed by Bruzek (2002) is based on the observation of sexualization features of five discriminating characters; yet given the poor state of preservation of coxal bones from the Danube Gorges prehistoric sample and the need for a large enough sub-sample to be able to perform a secondary diagnosis, sex was sometimes allocated after the observation of less than 3 discriminating characters; in these cases, the diagnoses were always in accordance with the allocations made by M. Roksandić.

enough sub-sample to be able to perform a secondary diagnosis, sex was sometimes allocated after the observation of less than 3 discriminating characters; in these case, the diagnoses were always in accordance with the allocations made by previous anthropologists. 45 sex were allocated during the primary diagnosis: 19 males and 26 females. Results from the morphological and the morphometric approaches were always consistent. When only some of the sexualization features ("conditions", in the morphometric methods) of one discriminating character could be observed, a sex "trend" was simply recorded; this "trend" was further compared, when possible, with results from the secondary sexual diagnosis, the following step in our protocol.

Secondary sexual diagnosis: a probabilistic approach

The anthropometric characteristics of individuals from the primary sample of sex-determined individuals was used to compute a set of discriminant functions that achieve maximum separation between sex-categories (following Van Vark 1971). These functions were applied to the skeletal measurements of indeterminate individuals according to their probability of being classified as male or female (following Murail et al. 1998). 49 standard measurements were taken on all individuals from the sample, according to their state of preservation (Martin, quoted by Brauer, 1988); infra-cranial measurements included mainly bone length, epiphysis breath and midshafts perimeters and diameters; 6 mandibular measurements were also considered. A mean of right and left measurements was computed to overcome the possible bias that may imply the strongest use of one limb and to increase the number of individual values[47]. This procedure should be applied to a "biologically homogeneous population", which is limited in the case of the Danube Gorges prehistoric sample by the broad timespan considered and by the presence of non-local individuals. To minimize this bias, individuals were pooled into 2 groups: 14 Mesolithic females and 13 Mesolithic males Vs 12 Transitional/Neolithic females and 6 Transitional/Neolithic males. Given that each functions will consider only a part of these sub-samples (the individuals for which the variables could be recorded given their state of preservation), the size of the Transitional/Neolithic male subsample is too small to be representative of the possible dimorphism of this sub-population.

To prevent from this bias, it was decided to:
- compute functions based on the Mesolithic sample of known sex, then applied on the Mesolithic sample of unknown sex (discriminant functions of group A);
- compute functions excluding Transformational-Neolithic individuals, then applied only on the sample of local individuals of know sex (discriminant functions of group B);
- compute functions based on the whole sample, then applied on the whole sample of unknown sex (discriminant functions of group C);
- reject systematically the functions of the group C which were not in concordance with the functions of the group A and B.

Shapiro-wilks normality tests were performed for each variable. Discriminant functions implies a combination of 2 to 5 measurements and of 1 to 3 bones. The strength and the significance of the discriminating function were tested for each measurement, for combinations of measurements grouped per bones and finally for combinations of measurements grouped per anatomical regions, including:

- series of univariate ANOVAs, variables with a Wilks' Lambda <0,55 and a p<0,05 were always favored;
- the equality of covariance matrices; when possible by the sample size, the equality of covariance matrices was tested through Box's M. tests. Values for the tested variables were always non-significant (p>0,001);
- a Wilk's Lambda <0,55; all functions with a Wilks' Lambda >0,55 were rejected. All functions with p >0,05 for chi-square test were rejected;

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[47] Given that this secondary diagnosis relies on metric variables, i.e on measures of size and robusticity, it can only be applied on individuals of adult size. Thus, the 2 adolescents were removed from our primary sample to develop the discriminant functions.

- a systematic adequacy of classification and the use of posterior probabilities; all the functions of group A and B that doesn't correctly classify 100% of the individuals of known sex were rejected. Considering that the group C was larger than the groups A and B, all functions from the group C that doesn't correctly classify 100% of the individuals of known sex, with a Jacknife procedure, were rejected. Finally, all functions that doesn't *a priori* allocate the sex of the individuals at a threshold level of 0,95% probability of belonging to the accurate group were rejected.

Eleven functions were selected for the group A, 7 for the group B and 5 for the group C. Considering that discriminant functions may provide contradictory results, the final diagnosis was based on the principle of majority (Murail et al. 1998): a majority of significant probabilities (significant is here defined as being above a threshold level set at 0,90%) to be male or female would indicate the male or female sex accordingly; a minimum of two significant probabilities of belonging to the male or the female group were required to calculate a final diagnosis (M, F or I). A few functions for each group use similar variables. Hence functions were grouped into sets of functions and the score (M, F or I) was firstly calculated per set of functions, further compared to obtain the final sex estimates. Finally, diagnoses for group A, group B and group C were compared for Mesolithic individuals and for individuals of local origin. For Mesolithic and non-local individuals, final diagnoses established using functions from the group A, B and C were always in accordance.

When only one function provides a result with more than 0,90% of belonging to one group, this result was compared with the "sex trend" recorded during the primary sexual diagnosis and it was decided to assign a final sex if the results of the function was in accordance with the observed “sex trend”. In order to increase the sample size of sex-determined individuals, 5 criteria of craniofacial sexualization features (nuchal crest, mastoid process, supra-orbital margin, glabella, mental eminence) were scored on a numerical scale from 1 – 5 following standard protocol (Buikstra and Ubelaker, 1994); an average of the five criteria was computed only when at least 3 criteria were available. Individuals with an average score >2.5 were considered as possible females and individuals with a final score <3 were considered as possible M. This final score was concordant with the results from primary diagnosis for 100 % of the individuals (24/24) and with secondary diagnosis in 94% of the cases (16/17). This parameter was thus additionally used in the cases only the results of one function could be considered, provided that both infra-cranial metric and cranial morphological sex-trends were in accordance.

The morphological and probabilistic morphometric method as well as defined discriminant function were then applied to the adult individuals buried at Ajmana. Finally, the stable isotope values of the perinates buried at Vlasac and Lepenski Vir could be also be analyzed according to the chromosomal sex determination published by Čuljkovic et al. (2008) and Stefanović and Borić (2008).

3.2. Methods of stable isotope analyses in Bioarchaeology

3.2.1. Definitions and applications

Applied in routine for many years, the stable isotope analyses of organic remains from archaeological contexts can provide information about human diet, subsistence strategies, mobility, environment and physiology (e.g. Ambrose and Katzenberg 2001; Lee Thorpe and Sponheimer 2006; Lee-Thorpe 2008; Reitseima 2013; Balasse 2015; Herrsher and Goude 2015; Katzenberg and Water-Rist 2018). Stable isotope studies of organic remains are based on the premise that “you are what you eat”, i.e. that your body should reflect the biogeochemical signature of the food consumed. The results of more than 40 years of research on (paleo-)ecology, controlled experiments and modeling (e.g. Ambrose and Norr 1993; Hobson et al. 1993, Phillips and Koch 2002), now provides Bioarchaeologists with a solid understanding of physiological and environmental causes for the variability in these biochemical signals, allowing them to perform thorough reconstructions of behaviors and ecology in the past.

3.2.1.1. Stable isotope ratios: basic concept

Chemical elements, atoms and stable isotopes

Isotopes are different versions of a chemical element, with different mass but the same chemical properties (Hoefs 1997; Sulzman 2007; Katzenberg 2008). Atoms, basic building blocks of matter, are made up of several elementary particles grouped in the nucleus (protons, with a positive electric charge, and neutrons, with a neutral charge) and distributed around the nucleus (as an electron cloud, negative charge); a chemical element is a species of atom having the same number of protons in their nuclei. For instance, the element carbon regroups all atoms which have 6 protons (atomic number 6); carbon (C), Hydrogen (H), Oxygen (O) and nitrogen (N) are the four most abundant elements in the biosphere, and thus in our body. Atoms of a chemical elements may have different number of neutrons in their nuclei; these atoms of the same species but with a different atomic mass are called isotopes. For instance, ^{12}C, ^{13}C, ^{14}C are different isotopes of carbon, containing respectively 12, 13 and 14 neutrons in the nucleus.

Because of an excess nuclear energy (excess protons or neutrons in the nucleus of the atom), some isotopes are unstable or radioactive and will hence spontaneously decay at a constant rate over time (called half-life), resulting in radioactive emissions and its transformation into another isotope of the same elements or of another chemical elements. Knowledge about the half-life values of some chemical elements have enabled the development of radiometric dating methods (e.g. Libby 1955). On the contrary with radioactive isotopes, the stable isotopes of a chemical element remain constant over time. The abundance of the different isotopes of a chemical element (for instance the abundance of ^{12}C and of ^{13}C) varies in the environment because of various physical and/or physiological processes.

Stable isotope fractionation

Because of their different atomic mass, isotopes have different kinetic properties and participate in physical and physiological reactions at different rates. For instance, during the conversion of atmospheric CO_2 into glucose by plants, the lighter isotope ^{12}C will be preferentially used over the heaver isotope ^{13}C. This isotopic offset - enrichment or depletion of an isotope of the same chemical element versus the other - is called *fractionation*. Atoms constituting the atmosphere, water and soils are partly integrated into the biosphere by plants and subsequently by animals through the food chain. During the process of photosynthesis (plant production – or biosynthesis – of matter using light energy), but also when breathing, drinking and eating, stable isotopes fractionation occurs as biological tissues – such as bone – are being formed and replaced. Hence, for some elements such as carbon, nitrogen, oxygen or sulfur, the stable isotope signatures of an organism may vary according to environmental settings (e.g. the signature of soils and waters and of local plants), to its position in the food chain (e.g. plants, herbivores, omnivores or carnivores) and/or to its physiology (photosynthesis pathways, ruminants or not, catabolic or anabolic state…). After the death of an organism, the quantity of radioactive isotopes will change as they are decaying and not replaced by new tissue synthesis; in contrast, the abundance of stable isotope will remain the same, provided that the tissues remain protected from external contaminants and alteration factors (such as soils bacteria).

Stable isotope ratios (δ)

Isotopic content is calculated as the ratio between the heavier and the lighter isotope, compared to an international standard because the amplitude of natural variation of these ratios is generally very small (Hoefs 1997; Sulzman 2007, Katzenberg 2008). The stable isotope difference in isotopic composition of a sample relative to the composition of the international standard, noted "δ" and expressed in part per mil (‰), is calculated as:

$$\delta_E X\ (‰) = [\ (\ R_{sample}/R_{standard}) - 1)\ ] \times 1000$$

where X refers to the chemical element of interest (in this study carbon, C, nitrogen, N, and sulfur, S), E is the atomic mass of the heavier (and less abundant) (respectively 13, 15 and 34) and R the isotopic ratio of the sample (e.g. $^{13}C/^{12}C$ for carbon; $^{15}N/^{14}N$ for nitrogen; $^{34}S/^{32}S$ for sulfur) compared to the isotopic ratio of the standard. The international standard used for the different isotopes included in this study are the Vienna Pee Dee Belemnite limestone for the isotopic ratio of carbon (V-PDB; Craig 1957), the atmospheric nitrogen for the isotopes of nitrogen (AIR; Mariotti 1983) and the meteoric troilite for the isotopes of sulfur (the Canon Diablo Troilite from Arizona, USA or CDT; Krouse 1980).

The numerical difference between two delta values – or isotopic spacing, for instance the difference between the $\delta^{13}C$ values of a plant and of an herbivore or between the $\delta^{13}C$ values extracted from blood and teeth – is called isotopic spacing or offset and reported as Δ (e.g. $\Delta^{13}C_{herbivore\text{-}plant}$ or $\Delta^{13}C_{blood\text{-}teeth}$).

3.2.1.2. Applications in Bioarchaeology

First researches on carbon and nitrogen to reconstruct past food webs

Carbon was the first element for which it was realized, between the 1960's and the 1980's, that stable isotope variations may have some potential to investigate past diets (reviewed by van der Merwe 1982; Katzenberg and Waters-Rist 2018). Back then, some researchers working on radio-carbon dating noticed some unexpected variations in dates derived from some human skeletal remains and observed differences between maize and charcoal remains from similar contexts (Hall 1967; Bender 1968). At the same time, Smith and Epstein (1971) also found that variations in $^{13}C/^{12}C$ amongst plants could be due to specific photosynthesis process. Some plants, such as maize, fixe carbon by a different pathway, and contains more ^{13}C relative to ^{12}C than most plants from temperate regions; this physiologically induced greater abundance in ^{13}C than the standard used for radio-carbon dating resulted hence in erroneous dates. The timing of these discoveries also coincides with the development of a new technique for collagen (the main protein from bone) extraction from archaeological bones, for purposes of ^{14}C dating by Longin (1971). With such knowledge, the abundance in $^{13}C/^{12}C$ could be used in the first stable isotope paleodietary study which aimed at tracking the consumption of maize among historical American populations (Vogel and Van der Merwe 1977). Thereafter, Tauber demonstrated the usefulness of carbon stable isotopes to distinguish between Mesolithic consumers of marine resources and Neolithic consumers of terrestrial resources, focusing on prehistoric populations living in the coasts of Denmark (Tauber 1981).

Meanwhile, DeNiro and Epstein (1978; 1981) conducted controlled feeding experiments on several species in order to study the relationship between the stable carbon and nitrogen isotope ratios in diet and in animal tissues. The potential of nitrogen isotopes ($^{14}N/^{15}N$) was then further explored during the following decade (Schoeninger and DeNiro 1984; Ambrose and DeNiro 1987). In 1989, a study performed on mothers and children pairs put forward the elevated ^{15}N values of the tissues of the babies during breastfeeding (Fogel et al. 1989), opening an avenue of research on the length of breastfeeding and weaning practices, major biodemographic variables (e.g. Katzenberg et al. 1996; Beaumont et al. 2015), and, when applied on animals, on herd management practices (e.g. Balasse et al. 1997).

New markers, improved techniques and samples, broadening of addressed issues

Although carbon and nitrogen still remain the isotopes the most commonly analyzed in human remains, oxygen ($^{18}O/^{16}O$) and strontium ($^{87}Sr/^{86}Sr$), have also been increasingly analyzed since the 1980's to gain information on residence and mobility (e.g. Erickson 1985; Price et al. 2002; Daux et al. 2005). Nowadays, the stable isotopes of sulfur are currently included in paleodietary studies (e.g. Richards et al. 2001; Nehlich2015) and the potential of other elements is being explored (e.g. Ca, Cu, Fe, Mg, Sr, Zn; Jaouen and Ponce 2017).

Since the 1990's, some efforts have also been done towards analyzing broader samples of human remains in view of revealing possible intra-population variations related to age, sex, or for instance social status (e.g. Ambrose et al. 2003; Herrscher 2003; Prowse et al. 2007; Reitsema and Vercellotti 2012). Besides, the importance to include more systematically different potential food sources from archaeological contexts in order to better assess the causes for human local and regional variability in isotope signatures has also been frequently emphasized (e.g. Herrsher and Goude 2010; Goude and Fontugne 2016).

From the 1980's onward, apart from the collagen protein in bone, other tissues have also been analyzed: bioapatite - the mineral part - extracted from bone (e.g. Sullivan and Krueger 1981; Lee-Throp et al. 1989) or from teeth enamel (e.g. Lee Throp and Merwe 1991; Balasse 2002) but also collagen protein from dentine (e.g. Balasse et al. 1997; Fuller et al. 2003) or keratin protein from hair, nail and horns (e.g. O'Connell et al. 2001; Iacumin et al. 2001).The development of multi-sampling strategies at the end of the 1990's (e.g. Balasse 2002) and more recently micro-sampling methods on human teeth (e.g. Burt and Garvie Lok 2013; Scharlotta et al. 2013), as well as research on compound-specific stable isotope analyses[48] (e.g. Fogel and Tuross 2003; Naito et al. 2013), is now contributing to move the field towards a much higher resolution of analyses. Multi and micro-sampling strategies enables researchers to examine changes in diet or different events of migration experienced over different periods of life of an individual and new marker allows for more thorough reconstruction of the diet. Jointly, the adaptation of statistic models from ecological to archaeological studies (e.g. Kellner and Schoeninger 2007; Tsutaya 2013; Fernandes et al. 2014), and progress in lab-controlled feeding studies (e.g. Webb et al. 2016; 2017a and b), help to manage and to interpret collected biochemical information.

With these markers, improved techniques and sampling strategies, stable isotopes analyses nowadays tackle issues related to local climate fluctuations (e.g. van Klinken 1994; Hedges et al. 2004), animal ecosystems (e.g. Bocherens et al. 1994; Bocherens and Drucker 2003), herding practices (e.g. Balasse et al. 1997; Fremondeau et al. 2012), agricultural practices (e.g. Retseima et al. 2013), migrations (e.g. Erickson 1985; Price et al. 2002), life history, individual mobility, weaning patterns or dietary transitions (e.g. Henderson et al. 2014; Scharlotta et al. 2013, 2018), or even health and physiology (e.g. Katzenberg and Lovell 1999; Beaumont et al. 2015).

3.2.2. From chemical elements to biological tissues, human nutrition

Plants and animals mostly obtain the chemical elements required for the synthesis of tissues from their environments, through the processes of photosynthesis, respiration, and diet. For instance, animals acquired the atoms of oxygen and hydrogen from respiration, from molecules of water or from the ingested food; most other chemical elements – such as carbon, nitrogen, sulfur… - are also acquired from the food. These atoms are then integrated into the biological tissues through two main metabolic processes: (1.) catabolic pathways, where the organism breakdown molecules - made of different chemical elements - into smaller units and produce energy; (2.) anabolic pathways that construct molecules from smaller units (biosynthesis) and require energy.

The catabolism of food begins with digestion; the ingested food is firstly mechanically and chemically broken down into smaller structural units, called macronutrients and micronutrients (e.g. Boland et al. 2004; Stevens and Humes 2004; Fox 2006). In contrast, the ingested water is

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[48] the signature of the different amino acids that make up the collagen protein.

incorporated in the body during the process of digestion without being chemically altered. Macronutrients include proteins, carbohydrates and lipids. Proteins are made up of different type of amino acids (e.g. aspartate, cysteine, glutamate, glutamine, histidine…); carbohydrates include monosaccharides such as fruits and starch sugar and disaccharides such as sucrose and lactose; lipids include fatty acids, glycerol and cholesterol. Micronutrients, needed in smaller amounts, mainly include vitamins and minerals.

Several physiological aspects of digestion differ according to the dietary behavior of the species considered, since some organs of herbivores, omnivores and carnivores specialized in the course of evolution to process food resources of different composition. Concerning humans and vertebrates, after the food has been break down through the digestive tract, nutrients are mainly assimilated in the small intestine and the colon into the blood and/or lymphatic systems.

3.2.2.1. Integration of chemical elements, basic principles of metabolism and digestion

Water

Water, main source of hydrogen and oxygen atoms, is universally required for the maintenance of homeostasis in mammal and composed up to 60% of the human body amongst which 75-90% comes from ingested waters. Water is mostly absorbed in the small intestine and distributed into fluids compartments, within the cells (intracellular fluid compartment), or in the interstitial fluid that is surrounding the cells (extracellular fluid compartment). Incoming and outgoing water flows are regulated to maintain the body water balance (Kavouras and Anastasiou 2010); the isotopic compositions of total body water are therefore closely related to those of water ingested as fluids or via food (Luz et al. 1984; Bryant and Froelich 1995; Kohn 1996).

Proteins

Proteins, the building blocks of the body, are macromolecules that all share a common structural feature which includes: an α-carbon (carbon atom) to which are bonded an amino group (NH_2), a carboxyl group (COOH), and a variable side chain (differing molecules attached to the core structure). All proteins are hence composed of carbon (C), nitrogen (N), hydrogen (H) and oxygen (O) atoms and the different amino acids are distinguished by the composition of the side chain. Amino acids are commonly grouped into essential one, vital and acquired through diet and non-essential one, which can be synthesized. Essential amino acids cannot be synthesized de novo by the body, and thus should be taken entirely from diet; because of their small mass, they only undergo a very small isotopic fractionation process when being assimilated. The stable isotope composition of assimilated essential amino acids is this expected to be rather similar as the composition of the ingested food (Schwarcz 2000). In contrast, non-essential amino acids can be entirely synthesized by the organism, although they can also be taken from the diet.

Amongst mammals, the catabolism of amino acids mostly occurs at the liver site through mechanism of transamination and deamination. Transamination is a chemical reaction that transforms an amino group into ketoacid (specific organic acid mainly used to produce energy) to produce glutamate, a non-essential amino acid. Glutamate can then undergo deamination, a chemical reaction that remove an amino group to convert the amino acid into ammonia (NH_4). The excess ammonia, toxic for our body, is eliminated via the urea cycle; it has been observed that, during this process, lighter isotopes of nitrogen (^{14}N) are preferentially eliminated over the heavier (^{15}N). The remaining part of the transformed amino acid is mostly made up of carbon and hydrogen, and is recycled for the synthesis of other molecules or oxidized for energy. In case of protein caused mal-nutrition, urea nitrogen can be re-cycled and re-utilized for tissue synthesis (Ambrose 1993; Hobson et al. 1993; Fuller et al. 2004).

Carbohydrates

Carbohydrates are considered as the body's main source of energy because it provides energy faster than the other macro-nutrients. Carbohydrates, including sugar and starches, are mostly made up of OH hydroxyl groups (oxygen bonded to hydrogen) and aldehyde (carbon double-bonded to oxygen, and to hydrogen and a side chain) or ketone functional groups bounded with carbon atoms. They are also processed into glucose at the liver site and mostly stored as glycogen (complex carbohydrate that serves for energy storage) in the liver. The isotopic composition of stored glycogen should thus be related to the composition of ingested carbohydrates (Schwarcz 2000).

As liver storage capacity is limited, excess glucose is converted into triglycerides (an ester composed of glycerol – a molecule with three hydroxyl groups – and fatty acids), aggregated with specific proteins before being released into the blood and collected by adipose tissue. According to body energetic requirements, the liver would release glycogen into the blood as glucose, then distributed to cells and used to produce adenosine-5'-triphosphate (ATP), a molecule that provides the energy needed for chemical reactions in the metabolism. This released glucose can also be stored as glycogen in muscle tissue.

Lipids

The body needs lipids – or fats – for growth and energy and to synthesize hormones and other substances needed for its activities. Fats (fatty acids, glycerol and cholesterol) are the slowest source of energy but the most energy-efficient form of food. They are first assimilated into the lymphatic systems before joining the blood system. Fatty acids and glycerol are mainly made up of long chain of carboxylic acids and composed of carbon, hydrogen and oxygen atoms. They can be found in blood as triglycerides and are either stored in adipose tissue or used for energy as ATP in adipose tissue, skeletal muscle and liver. Cholesterol - of more complex structure than fatty acids and glycerol - is metabolized and partially stored at the liver site. Stored triglycerides can be mobilized when glucose critically decline in blood in order to produce necessary ATP (to provide cells with energy). The isotopic compositions of body fatty acids, glycerol and cholesterol should therefore be related the composition of the ingested fats, which are generally depleted in ^{12}C in comparison with the other macronutrients (DeNiro and Epstein 1977; Jim et al. 2006; Logan et al. 2008).

Vitamins and minerals

Apart from water, carbohydrates, proteins and lipids, vertebrates also need other nutrients in smaller quantity, for proper growth, development and physiology; these are called 'micro-nutrients', which regroup vitamins and minerals.

Vitamin is an heterogeneous group of organic molecules, divided into fat-soluble vitamins (A, D, E and K) and water-soluble vitamins (B-complex and C), needed in small quantities for vital metabolic activities, but that the human body is unable to synthesize in adequate amount (Bhagavan and Ha 2011). They are mostly absorbed in the small intestine (and in ileum or colon for vitamins B12 and C) through different mechanisms, can be transported into plasma and processed at most tissue sites or by some specific organ sites (liver and kidney for D vitamin).

In addition to the four major structural elements (oxygen, hydrogen, carbon and nitrogen), other elements existing in natural environment are also used in smaller amount by vertebrate bodies; these elements – called 'minerals' - can be required to perform vital metabolic activities but cannot be synthesized and the excess intake of some can be toxic to vertebrates. They can be divided into major elements (> 1 mg/kg) and trace elements (< 1 mg/kg), further classified according to their benefits to the organism: the deficiency in major elements (such as sodium, potassium, chloride, calcium, phosphorus, magnesium and sulfur) and in essential trace elements (such as copper, iron, zinc, iodine…) can be detrimental to the body, while the essential nature of other trace elements remains unclear (e.g. strontium, lithium, nickel), and it has been shown that some trace elements could be toxic in excess (e.g. gold, mercury and lead) (Berdanier et al. 2007). Minerals are mostly absorbed in the small intestine through different mechanisms and stocked in the liver and the bones. The isotopic compositions of micro-nutrients which cannot be bio-synthesized should be directly related to the composition of ingested food and fluids (e.g. Capo et al. 1998; Balter 2001).

3.2.2.2. Chemical composition, storage and utilization of the main nutrients

Stable isotopes can be analyzed from all biological tissues, most usually bone and tooth in archaeological applications but also hair, horn, or nail (e.g. Lee-Thorp et al. 1989; Sharp and Ceiling 1998; O'Connell et al. 2001; Iacumin et al. 2001; Lamb 2015). Each tissue, with its own dynamic of formation, is recording a specific stable isotope signal. Both bone and teeth tissues, the most commonly preserved tissues in archaeological contexts, have been analyzed in this thesis.

3.2.3. The basic bioarchaeological material for stable isotope analyses

3.2.3.1. Bone tissue

Bone composition

Bone is made up of six different tissues including: (1.) periosteum, a fibrous membrane that covers the outer surface of bones; (2.) compact bone, made up of osteons which are cylindric units composed of lamellae organized concentrically around a central canal which house nerves and blood vessels; (3.) cancellous bone, more porous like a sponge, made up of a network of trabeculae also composed of lamellae; (4) hyaline cartilage on joint surface; (5) red marrow, in the cavities of cancellous bone, which produce red and white blood cells and (6) yellow marrow, the fat tissue in the center of long bone (Williams et al. 1995). In archaeological contexts, compact and cancellous bones are usually the best-preserved and the most commonly found bone tissues. Externally, bones can be classified based on their shape: long, short, flat, irregular bones (ibidem). The diaphysis (the tubular part) of long bone (e.g. limb bones) is made up of compact bone filled with red marrow (for immature individuals) and yellow marrow (for mature individuals). The epiphyses (extremities) of long bones are made of cancellous bone filled with red marrows and covered with cartilaginous tissues. Short bones (for instance small bones of hands or feet) are made up of a mass of compact bone covering cancellous bone. Flat bones (e.g. parts of skull, ribs or coxae) are made up of two compact bone plates surrounding a plate of cancellous bone. Finally, irregular bones (e.g. vertebrae) combine these different structures.

Both compact and cancellous bone are dense connective tissues composed of an organic matrix of the structural protein, collagen, studded with inorganic minerals. Dry bone is ca 70% inorganic and ca 30% organic by weigh and water. Most of the organic portion (ca 85-90%) is collagen, the remainder including non-collagenous proteins, proteoglycans and lipids (Mays 1998; White and Folkens 2005; Katzenberg and Waters-Rist 2018). The mineral component consists mostly of calcium phosphate (hydroxyapatite), containing carbonate ions. The composition of the bone tissue can slightly vary according to the anatomical part, age of the individual, its health and genetic factors (Williams et al. 1995).

Bone formation and remodeling

Bone started to be formed in utero by specialized connective tissue cells called osteoblasts, clustered in ossification centers (Sheuer and Black 2002). Concerning compact bone, osteoblasts secrete the matrix of collagen – osteoid – and mineralized bone tissue which gradually replace a primitive cartilage model (endochondral ossification). Long bones first grow from primary ossification centers located in the diaphysis and then from secondary ossification centers located in the epiphysis until both parts are fused. Irregular bones also have several ossification centers while short bones have only one. The ossification of flat bones of the skull is slightly different, starting from a fibrous membrane where osteoblasts secrete the osteoid to form trabeculae (intermembranous ossification). Both endochondral and intermembranous ossification produce immature bone, which undergoes a process of bone deposition (by osteoblast cells) and resorption (by osteoclast cells), called bone remodeling or bone turnover, to produce mature bone.

Over the life, the joint action of osteoblasts and osteoclasts produce a constant bone remodeling, necessary for renewing bone in order to maintain strength and mineral homeostasis (Robling et al. 2006). With growth, the rate of bone turnover is much faster for neonate, infants and children and decline with age. During the first year of life, bone is completely remodeled on average three times; at ten years a complete turnover need ca. 3 years; after 15-20 years old, more than a decade is generally necessary to renew the organic pool (Valentin 2003; Hedges et al. 2007). The rate of this process is faster concerning trabecular bone than compact bone (and thus for flat bones such as ribs than long bones). The rate of bone turnover also varies with many factors, age at the first place, but also intensity of physical activity, diet, sex, body mass, health status, growth, hormones, anatomical parts, ethnicity, menopausal status (e.g. Han et al. 1997; Valentin 2003; Hedges et al. 2007; Seibel 2005). This differential rate of bone remodeling is thus an important parameter to take into consideration in paleodietary studies (e.g. Parkington 1991; Hedges et al. 2007). For adults, it is generally considered that bone tissues broadly reflect the last 10-15 years of an individual life (Hedges et al. 2007), while this period may be very variable according to the age of analyzed children (Valentin 2003). Some anatomical elements, like long bone diaphyses, may average a dietary signal over a longer of time than others, like ribs, which may reflect dietary intake during a shorter period before the death of the analyzed individual. In case the individual studied died of some injuries or of a pathology which may have caused bone remodeling (e.g. osteomalacia), the most recently remodeled part of the bone should, in theory, reflect the nutritional status of the individual during the very last period of his life (e.g. Katzenberg and Lovell 1999).

3.2.3.2. Dental tissues

Teeth composition

A tooth can be divided into two main parts: (1) the crown, emerging from the alveolar process, which shape depend on its masticatory function; (2) the root, fixing the tooth into the maxillar or the mandibular bone, which contains the root canal enabling the passage of nerves and blood vessels in the tooth (Hillson 2005). The distal extremity of the tooth, where the nerves and blood vessels enter the root canal, is called the apex; the root canal then leads to the center of the tooth, the pulp chamber, approximately located at the junction between root and crown (the neck of the tooth). Teeth are made up of four tissues: three hard tissues – enamel, dentine and cementum – and one soft tissue, the pulp.

Enamel is located only in the crown and is made up at more than 95% of minerals, primarily hydroxyapatite; this mineral is organized in much longer crystals of calcium phosphate than in bone tissues. The remaining organic part contains proteins of amelogenins and enamelins. Dentin, located just below the crown enamel and main tissue of the root, has a similar composition as bone, with ca 70% of minerals (mostly hydroxyapatite) and ca 30% of organic content by weigh, mostly collagen molecules. Cementum is the thin surface layer of the tooth root, covering the dentin; it is slightly softer than dentin and consists of ca 50% inorganic material (hydroxyapatite) by weight and ca 50% of organic matter (collagen and proteoglycans) and water. Finally, pulp in the center of the tooth is a soft tissue (no mineral part) mostly including nerves, blood vessels and odontoblasts cells which are responsible for the production of dentine tissue. The biochemical analyses of teeth found in archaeological contexts are mostly conducted on the two main tissues: enamel and dentine.

Teeth formation

Humans, like most mammals, have several dentitions, one gradually replacing the other, distributed on the maxillar (upper teeth) and on mandibular bones (lower teeth): (1) the deciduous teeth of juveniles (concerning human children: 20 teeth including 8 incisives, 4 canines and 8 molars), and (2) permanent teeth (concerning human adults: 32 teeth 8 incisives, 4 canines, 8 premolars and 12 molars). The rate of teeth development, mineralization and eruption is well known for most species (e.g. concerning humans: Moorees 1963a and b; Ubelaker 1978; Sheueur and Black 2002). With the development and the emergence of a permanent tooth, the root of the deciduous tooth will gradually be resorbed until the tooth fall. Concerning humans, deciduous teeth started to be formed in utero, mostly erupt (i.e. stated being visible in mouth) between ca 6 months and ca 2 years old; all roots are completed around 3-4 years and started to fall around 5-6 years until 10-12 years (ibidem). Permanent teeth started to develop during the first years of life and mostly erupt between 6 years (first permanent molar) and 12 years (second permanent molar; the age at eruption of the third permanent molar being highly variable; ibid.). Hence, after ca 10-12 years, only permanent teeth are present in the mouth.

Teeth are formed from tooth germs which are organized into three parts - the enamel organ, the dental papilla and the follicle - and occurred as a complex process encompassing different stages (bud, cap, bell, crown; Hillson 2005). The cells of the enamel organ give rise to ameloblasts, which produce enamel, and will also determinate the root shape of a teeth. Dental papilla contains cells that develop into odontoblasts, dentin-forming cells. The junction between the enamel organ and the dental papilla also determines the crown shape of a tooth. Mesenchymal cells contained within dental papilla are responsible for the formation of tooth pulp. Finally, the dental sac of follicle gives rise to cementoblasts, osteoblasts and fibroblasts which respectively forms cementum, the alveolar bone around the roots of teeth, and the periodontal ligament which connect teeth to the alveolar bone.

Contrary to bone, enamel and dentine are not remodeling after being formed and mineralized; thus, their chemical composition should remain the same, apart from possible diagenetic alterations (Hillson 2005). Only cementum has the potential to remodel over time, becoming thicker around the root apex. Secondary dentine is being laid down very slowly over life by the odontoblasts on the wall of the pulp chamber in permanent teeth, and only after the tooth is fully developed. Finally, tertiary dentine can be produced at specific sites on the pulpal wall in response to damage on the dentine surface such as wear or caries. Since the timing of the mineralization of the different tissues is well-known, and considering that enamel and dentine do not remodel over time and that secondarily deposed tissues can be easily located, teeth represent a tissue of choice for who wants to assess dietary or environmental variables related to different periods of infancy and childhood (e.g. Balasse et al. 2002; Fuller 2003; Erickson and Liden 2012; Scharlotta et al. 2014; Beaumont et al. 2015).

3.2.3.3. Tissues' composition: collagen and bioapatite

Organic part - Collagen

In human and animal bio-archaeological studies, stable isotopes are now routinely analyzed in the collagen protein of bone and teeth (e.g. Ambrose and Katzenberg 2001; Lee-Thorpe 2008; Balasse 2015; Herrsher and Goude 2015; Katzenberg and Water-Rist 2018). Elongated fibrils of collagen are the major organic component of mammals' skin, tendons, cartilage, blood vessels, bone and teeth. There are 28 different types of collagen, according to their amino-acids composition and which hence have different functions (Campbell 1995; Campbell and Smith 2002). Yet, they all share the same structure: a bunch of fibers made up of three polypeptide chains (amino-acids chain with peptide bonds), coiled together in a form of triple helix (ibidem). More than 95% of bone collagen is type I, completed with type III and V (Melkko et al. 1990; Niyibizi and Eyre 1994). Polypeptide chains are particularly rich in glycine, proline, alanine, hydroxyproline and glutamic amino acids, which contribute mainly to the collagen carbon and nitrogen pool (Bolboacă and Jäntschi 2007). The stable isotopes of carbon, nitrogen and sulfur, have been most usually analyzed on bulk collagen (general collagen stable isotope signal); however, they can also be directly analyzed in the amino acids that form the collagen proteins and provide further information to further estimate the quality and/or the quantity of the different resources consumed (e.g. Fogel and Tuross 2003; Naito et al. 2013). Because of its structural relationship with crystals of hydroxyapatite, collagen can be preserved up to hundreds of thousands of years (e.g. Richards and Trinkaus 2009), but certain burial conditions are not likely to favor this preservation; hence, researchers have established means to estimate preservation (cf part 3.3.2), and have also sought for other sources of carbon that could be related to the dietary intake (e.g. bioapatite).

Mineral part - Hydroxyapatite

The mineral part of bone, enamel and dentine is mostly made up of hydroxyapatite, organized in larger crystals in enamel than in bone tissue (Mays 1998). Hydroxyapatite is a calcium phosphate ($Ca_{10}(PO_4)_6(OH)_2$; atoms of calcium, phosphorus, oxygen and hydrogen), also containing carbonate ions (CO_3^{2-} ; electrically charged atoms of oxygen, bounded to an atom of carbon). The relatively small size and large surface areas of the crystals makes possible vacancies and ions substitutions, critical to normal bone function (Kuhn 2001; Boskey 2013). Hence, Ca^{2+} ions (calcium) can be for instance substituted by Sr^{2+} (strontium) for instance. On archaeological material, isotopes - most frequently of carbon, oxygen and strontium - can thus be measured on phosphate, carbonates or substituted ions from bone and from teeth in order to reconstruct ancient diet, environment or mobility (e.g. Sullivan and Krueger 1982; Lee-Thorp et al. 1989; Kohn 1996; Price et al. 2002; Lee-Thorp and Sponheimer 2003, 2006a; Daux et al 2005; Bentley 2006).

The analysis of carbon from bone mineral was originally proposed to circumvent issues of bad collagen preservation (Sullivan and Krueger 1981). Yet, it has further been considered that carbonate could be altered in the postmortem environment by exchanges between constituents of buried none and carbonates from the sediments (Schoeninger and DeNiro 1984). Due to the its different structure, it has been argued that teeth tissues, and especially enamel, should be much more resistant to diagenetic alteration (Lee-Thorp et al. 1989; Lee-Thorp and van der Merwe 1991; Sponheimer and Lee-Thorp 1999; Lee-Thorp and Sponheimer 2003, 2006b). However, it should be kept in mind that the dietary information contained in teeth may be different than in bones, because of the differential timing of teeth and bone tissue formation (contrary to bone, teeth enamel does not remodel over life and thus reflect a childhood signal). Methods to identify diagenetic alteration of bone minerals have also been developed (e.g. Wight and Schwarcz 1996; Katzenberg et al. 2009). Besides, it has also been suggested – and experimentally validated – that carbon in the carbonate of bones and teeth comes from different dietary components than the carbon in collagen (e.g. Krueger and Sullivan 1984; Ambrose and Norr 1993; Tieszen and Fagre 1989). Indeed, collagen is formed from carbon contained in amino acids synthesized by the body or from ingested proteins and thus primarily reflects the protein part of diet. While carbon from carbonates in bone and teeth originate from dissolved bicarbonate in the blood, which comes from carbohydrate, lipids and proteins. Hence, joint analyses of carbon from apatite and carbonate may provide a more complete reconstruction of the diet (e.g. Ambrose et al. 2003; Kellner and Schoeninger 2007; Froehle et al. 1010, 2012). Oxygen and strontium used in isotope studies of paleoclimate and residence studies are also analyzed in the mineral part of bone (e.g. Erickson 1985; D'angela and Longinelli 1993; Kohn 1996; Price et al. 2002; Balasse et al. 2002; Daux et al 2005; Bentley 2006). While the stable isotopes of oxygen can be extracted from carbonate (CO_3^{2-}), the signature is more likely to be altered by diagenetic process than when analyzed from phosphate (PO_4) (Garvie-Lok et al. 2004).

3.2.4. The different element analyzed for the study of past behaviors and ecology

3.2.4.1. Carbon ($\delta^{13}C$)

The stable isotopes of carbon were the first to be used for paleodietary reconstructions due to the familiarity of archaeologists with radiocarbon dating (as reviewed by van der Merwe 1982; Katzenberg and Waters-Rist 2018). The two stable isotopes of carbon are ^{12}C and ^{13}C, respectively distributed in the proportion of 98,9% versus 1,1 % on earth (O'Leary 1988; Farquhar et al. 1989).

Variations in $\delta^{13}C$ amongst plants

Carbon is assimilated by animals in their diet; therefore, plants stable isotopic signature condition the different isotopic ratios found throughout the food chain. Plants extract the carbon they need for their development from carbon dioxide (CO_2); in this process, the lighter isotope - ^{12}C - is integrated faster than the heavier ^{13}C. Because of this fractionation, terrestrial plant tissues are enriched in ^{12}C in comparison with atmospheric carbon dioxide (Marshall et al. 2007, Katzenberg 2008). Plants' content in $\delta^{13}C$ ($^{12}C/^{13}C$) then vary according to environmental parameters and photosynthetic pathways (O'Leary 1981, 1988; Farquhar et al. 1989; Marshall et al. 2007). The C_3 photosynthetic pathway, involving the production of a molecule composed of three carbon atoms during a first stage of photosynthesis, is common amongst most aquatic plants and terrestrial plants which can be found in temperate and cold climate (i.e. trees and most eatable plant of the European continent before the industrial and globalized period; Smith et Epstein 1971; DeNiro et Epstein 1978). The $\delta^{13}C$ values of C_3 plants range ca -27,0 ‰ (from ca -36 to -22 ‰; Smith et Epstein 1971; Deines 1980; O'Leary 1981). The C_4 photosynthetic pathway (production of a 4 carbon atoms-made molecule), is followed by herbaceous plants from warm and dry tropical and sub-tropical environments. In Europe, before the arrival and democratization of American or African plants such as corn, sugar cane or sorghum, the only C_4 plant consumed was millet (Panicum miliaceum and Setaria italica). These plants discriminate less against the heavier isotope - ^{13}C - than do temperate plant species and their $\delta^{13}C$ values range ca -12,5 ‰ (from ca -19.0 to -6.0‰; ibidem). Following this discovery, $\delta^{13}C$ has been used to document the consumption of C4 plants, such as maize, amongst human population (Figure 20; e.g. Vogel and van der Merwe 1977; van der Merwe and Vogel 1978) or domesticate (Katzenberg 1989). Finally, plants following the CAM photosynthetic pathway (Crassulacean Acid Metabolism) alternate between the two previous pathways over days and night, and thus their $\delta^{13}C$ overlap those of C_3 and C_4 plants (Smith et Epstein 1971; Deines 1980; O'Leary 1981). Plants of this type are quite rare - mostly desert succulent plants - and none were found in Europe before industrial time.

Various environmental factors may also influence plants' isotopic ratios. Terrestrial plants use atmospheric CO_2, which $\delta^{13}C$ values in preindustrial time was circa -6.5‰, while aquatic plants use dissolved carbonate with $\delta^{13}C$ values approximating 0‰ (Smith et Epstein 1971; DeNiro 1987; Farquhar et al. 1989; Bocherens 1999; Katzenberg 2008). It follows that C_3 aquatic plants, mainly marine plants, have higher $\delta^{13}C$ values than C_3 terrestrial plants (Figure 20). In contrast, plants from freshwater environments also use organic carbon, originating from waste and decomposition products from plants and animals, which result in lower $\delta^{13}C$ values (DeNiro 1985; Farquhar et al.1989; Zohary et al 1994; Dufour et al. 1999; Katzenberg and Weber 1999). Therefore, humans who consume freshwater resources, such as fish, should display lower $\delta^{13}C$ values than marine resources consumers, which may exhibit particularly high $\delta^{13}C$ values. Fish migratory behavior and habitat may also influence the values of consumers: for instance the consumption of anadromous fish, who migrates seasonally from the sea to spawn in the rivers, may result in high $\delta^{13}C$ values, similar as the signal of marine resources consumers (e.g. Grupe et al. 2003; Fuller et al. 2012). It has also been shown that fish $\delta^{13}C$ values may vary according to their habitat, for instance in deeper or shallow waters of lakes (e.g. Dufour et al. 1999; Katzenberg et al. 2012). In brackish and estuarine environments, the mix of fresh and marine waters results in lower $\delta^{13}C$ values than in marine ones but higher $\delta^{13}C$ than in terrestrial ones (Grupe et al. 2009; Eerkens et al. 2013; Salazar-García et al. 2014).

In forests, the decay of organic remains also result in lower CO_2 atmospheric $\delta^{13}C$ values; in addition to lower temperatures and light, this "canopy effect" may lower forests plants' $\delta^{13}C$ values from 2 to 5‰ in comparison with plants from more open environments (van der Merwe 1982; Farquhar et al. 1989; Heaton 1999). Temperatures, light, aridity, CO2 concentration, soil salinity, and physiological stress may also influence plants $\delta^{13}C$ values (Farquhar et al. 1989; Ambrose 1991; Tieszen 1991). Knowledge about such environmental variability in $\delta^{13}C$ values has been used for instance to infer some agro-pastoral practices and/or to reconstruct local landscapes (e.g. Balasse et al. 2002; Bocherens et al. 2005; Ervynck et al. 2007; Britton et al. 2008).

Variations in $\delta^{13}C$ amongst vertebrates

Amongst vertebrates, the molecule of collagen (the main protein, or organic part of bone and teeth), but also the ions of phosphates and carbonates from bioapatite (the mineral part of bone and teeth), are made of carbon. Therefore, it has been suggested that carbon in bone and particularly in teeth carbonate could be used in case collagen was too badly degraded (e.g. Sullivan and Krueger 1981; Lee-Thorp et al. 1989). Due to the high mineralization of teeth tissue, teeth carbonate may be particularly resistant to taphonomic alteration (such as post-depositional exchanges between sediments and bone carbonates; e.g. Lee-Thorp and van der Merwe 1991; Sponheimer and Lee-Thorp 1999; Lee-Thorp and Sponheimer 2003, 2006b; Lee-Thorp 2008; Zazzo 2014). It has yet been evidenced that collagen and bioapatite record slightly different dietary information (Krueger and Sullivan 1984; Ambrose and Norr 1993; Tieszen and Fagre 1993; Howland et al 2003; Drucker and Bocherens 2004; Jim et al. 2004, 2006; Koch 2007; Froehle et al. 2010; Fernandes et al. 2014). Indeed, collagen is composed of amino acids, which partially originate from ingested proteins, while carbonates in bone are formed from dissolved bicarbonate in the blood and this comes from all macronutrients (carbohydrate, lipid and proteins). Thus, while carbon in collagen is predominantly routed from dietary protein (and subsidiary from other dietary sources), in contrast, carbon in bioapatite reflects whole diet (mainly energy - fats and carbohydrates - and the remaining part of protein not expressed in collagen).

From plants to herbivores, and at each trophic level of the food chain, a small fractionation occurs as carbon is used for the synthesis of new tissues, resulting in higher $\delta^{13}C$ values for consumers in comparison with their diet (Figure 20; DeNiro et Epstein 1978, van der Merwe 1982). In collagen (organic part of bone and teeth), the isotopic offset (fractionation) is ca 5‰ between the diet and the consumer, and ca 0-1‰ between two trophic levels (prey-predator) (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981; Bocherens and Drucker, 2003). Therefore, although broad differences in $\delta^{13}C$ values should primarily allow for distinguishing between the consumption of C3/C4 plants and resources from terrestrial/freshwater/marine environments, it can also provide information on its position in the food webs. Concerning bioapatite, the isotopic offset ranges ca 9-14.5‰ between the whole diet and the consumer - depending on species' diet, metabolism and on the tissue analyzed[49] (estimation from Salesse 2015; data from Passey et al. 2005; Howland et al. 2003; Warinner and Tuross 2009). As for collagen, the stable isotope enrichment between two trophic level for bioapatite has been estimated around 0-1‰ (Cerling and Harris 1999; Passey et al. 2005; Lee-Thorp 2008). A recent animal feeding experiment has shown that carbon tissue to whole diet spacings for different tissues (bone collagen, muscle liver, blood, plasma, faeces) may substantially vary when even a small proportion of marine resources is included in the diet, which may be caused by an preferential routing of non-essential amino-acids rich in heavy carbon when consuming marine resources (Webb et al. 2017a).

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[49] ca 10.7±1.4‰ concerning bone apatite and ca 13.4±1‰ concerning enamel; estimation from Salesse 2015; data from Passey et al. 2005; Howland et al. 2003 and Warinner and Tuross 2009

Variations in $\Delta^{13}C_{carbonates\text{-}to\text{-}collagen}$ according to dietary sources

Lipids have been shown to be $\delta^{13}C$-depletedin comparison with the other macro-nutrients (DeNiro and Epstein 1977; Ambrose and Norr 1993; Jim et al. 2006; Post et al. 2007; Logan et al. 2008). Therefore, given that a minor part of carbon constituting collagen is routed from the non-protein part of the diet, and since the carbon constituting bioapatite is formed from all macro-nutrients, the $\delta^{13}C$ diet to consumer spacing value is expected to vary according to the quantity of proteins and lipids in the diet (Ambrose and Norr 1993, Kellner and Schoeninger 2007; Froehle et al. 2010; Eerkens et al. 2013 ; Fernandes et al. 2014). The difference between the $\delta^{13}C$ apatite and $\delta^{13}C$ collagen ($\Delta^{13}C_{carbonates\text{-}to\text{-}collagen}$spacing) has also been correlated to the food web, which may be partially due to the fact that animals contain more fat than plants (Grupe et al. 2009); hence, it has been evidenced that the $\Delta^{13}C_{carbonates\text{-}to\text{-}collagen}$ spacing is smaller in carnivorous than herbivorous animals (e.g. Lee-Thorp et al. 1989; Kellner and Schoeninger 2007; Grupe et al. 2009; Shin and Hedges 2012; O'Connell and Hedges 2017; Codron et al. 2018). Reference data for free-ranging animals (Lee-Thorp et al. 1989; Kellner and Schoeninger 2007; Codron et al. 2018), animals from archaeological contexts (Grupe et al. 2009; Shin and Hedges 2012) and experimental diet data (O'Connell and Hedges 2017) suggest that the $\Delta^{13}C_{carbonates\text{-}to\text{-}collagen}$ should range above 5.5‰ for herbivores, circa 4-7.5‰ for omnivores animals, circa 2-6.5‰ for carnivores animals and broadly circa 0-8‰ for marine animals (Appendix A.V.3).

When macronutrients all originate from the same food sources, for instance protein and energy (carbohydrates and lipids) deriving from the meat of C3 grazing herbivores, the diet is called "monoisotopic". In case of monoisotopic diet, $\delta^{13}C$ apatite value is enriched of ca 9.3 to 14.4‰ in comparison with the $\delta^{13}C$ value of the diet, and $\delta^{13}C$ collagen is enriched of ca 5‰ in comparison with the diet. Thus, it can be estimated that the $\Delta^{13}C_{carbonates\text{-}to\text{-}collagen}$ offset for a monoisotopic diet should range around 4.3-9.4‰[50], which notably coincides with obtained values for free ranging herbivores animals (Appendix A.V.3). In contrast, in case of the consumption of proteins and energy from different C3/C4/marine resources, the $\Delta^{13}C_{carbonates\text{-}to\text{-}collagen}$ offset appears either: (1.) larger in case of a mixed C3 derived proteins and C4 energy (>ca 7‰ for bone apatite), (2.) smaller in case of a mixed C4 or marine derived proteins and C3 energy (ca <2‰ for bone apatite), (3.) intermediary in case of 100% marine derived proteins and C4 energy, or in case of mixed proportions of proteins and energy from different food sources (Kellner and Schoeninger 2007; Warinner and Tuross 2009; Froehle et al. 2010). Based on the results of these animal feeding experimental data for bone carbonate and bone collagen stable isotope values, models have been developed enabling to estimate the environment from which originate the different macro-nutrients (C3/C4/marine) and to quantify proteins and energy (Kellner and Schoeninger 2007; Froehle et al. 2010; 2012; Eerkens et al. 2013). Comparing the $\delta^{13}C$ from collagen and from bioapatite may thus provide a more complete picture of the diet.

Macronutrient scrambling and nutritional stress

When dietary protein is insufficient for tissue building, it has been suggested that amino acids might come "scrambled" from other dietary macronutrients such as carbohydrates or lipids for tissue synthesis (e.g. Keenleyside et al. 2006; Prowse et al. 2004, 2005). In situations of fasting, malnutrition, starvation, some researchers have documented various responses of $\delta^{13}C$ values (rise of decline) in the different tissues analyzed (whole body, muscles, livers, blood, dentine, or hair) of different animal and human individuals, which has been particularly associated to the body depletion in $\delta^{13}C$-depleted carbon from lipids in relation with its utilization for the synthesis of new tissue (e.g. Doucett et al. 1999; Cherel et al. 2005; Mekota et al. 2006; Gaye-Siessegger et al. 2007; Graves et al. 2012; Lehn et al. 2011; Neuberger et al. 2013; Beaumont and Montgomery 2016). In some situations of energy restriction or infectious disease, the observation of higher $\delta^{13}C$ values have also been interpreted as a modification of carbohydrate metabolism in favor of pathways that preserve and recycle bodily carbon (Deshner et al. 2012; Oslen et al. 2014).

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[50] 4.3-7.1‰ for bone apatite, 7.4-9.4‰ for teeth enamel

3.2.4.2. Nitrogen (δ^{15}N)

Shortly after carbon, researchers started to explore the potential of the stable isotopes of nitrogen – ^{14}N and ^{15}N – for paleodietary reconstructions (DeNiro and Epstein; 1978, 1981; Schoeninger and DeNiro 1984). ^{14}N is the most abundant isotope of nitrogen, providing ca 99,636 % of nitrogen on earth, versus 0,364 % for ^{15}N (De Laeter et al. 2003; Sulzman 2007).

Variations in δ^{15}N amongst plants

As mentioned in the case of carbon, animals are also mostly assimilating nitrogen through food; thus, plants similarly condition the different isotopic ratios found throughout the food chain. Although various environmental factors may explain a part of δ^{15}N variability amongst plants (Heaton et al. 1986; van Klinken et al. 2000), the greatest differences observed amongst vertebrates are rather related to existence of an important trophic effect at each level of the food chain (DeNiro and Epstein 1981; Minagawa and Wada 1984; Bocherens and Drucker 2003; O'Connell et al. 2012).

Atmospheric nitrogen (N2) is the primary standard with a value of 0‰; the assimilation of nitrogen by plants result in a small fractionation effect favoring ^{14}N (Finlay and Kendall 2007) and differential patterns of nitrogen fixation amongst plants are responsible for an important part of their variation in δ^{15}N. nitrogen-fixing plants (leguminous, Fabaceae), which acquire the nitrogen they need from atmosphere thanks to a symbiotic bacteria, have isotopic nitrogen values around 1‰ (Schoeninger and DeNiro 1984). Similarly, cyanobacteria, the aquatic equivalent for leguminous plants, use dissolved nitrogen and also have stable isotope values approximating 0‰ (ibidem). Non nitrogen-fixing plants get nitrogen from decomposed organic matter, which breaks down ammonia and nitrate; there δ^{15}N values is around 3‰ on average, but soils δ^{15}N values mostly depend of local environmental conditions and soils chemistry (Schoeninger and DeNiro 1984; Bocherens and Mariotti 2002; Finlay and Kendall 2007; Koch 2007). Aridity, soil salinity and some agricultural practices (manuring) may increase plants δ^{15}N values and thus may influence local animals and human stable isotope signal as well (Ambrose 1991, Heaton et al. 1986; Sealy et al. 1987; Bogaard et al. 2007, 2013; Koch 2007; Britton et al. 2008; Reistema et al. 2013). Therefore, it has been suggested that species from different ecosystem should not be directly compared without considering the isotope composition of the local food web (Ambrose 1991). Non nitrogen-fixing marine plants tends to have δ^{15}N values around 7‰ (Schoeninger and DeNiro 1984; Bocherens and Mariotti 2002), which is likely due to the higher isotope values of nitrates dissolved in sea waters (DeNiro 1987; Ambrose 1993).

Variations in δ^{15}N amongst vertebrates and fractionation along the food web

On the contrary to carbon, nitrogen amongst vertebrate is only found in the amino acids that makes up proteins, and not in lipids or carbohydrates (Schoeller 1999). An important isotope enrichment has been noticed at each level of the food web, estimated around 3-5‰ (Figure 20; DeNiro and Epstein 1981; Minagawa and Wada 1984; Schoeninger and DeNiro 1984). However, this offset may vary from 1 to 7‰, notably according to the species or to the tissues analyzed and to the quality and quantity of the protein consumed protein (e.g. Koch et al. 1991, Bocherens and Mariotti 2002; Bocherens and Drucker 2003; Vanderklift and Ponsard 2003; Robbins et al. 2005; O'Connell et al. 2012). The exact cause of this enrichment is still not entirely understood, but it could be explained, in part, by the preferential excretion of ^{14}N-enriched urea, leaving more ^{15}N to be utilized for tissue synthesis (DeNiro Epstein 1981; Ambrose 2000). Different environmental conditions such as aridity or manuring practices will directly influence terrestrial herbivores δ^{15}N ratios, and then further affect the values of terrestrial omnivores and carnivores (e.g. Sealy et al. 1987; Ambrose 1991; Bocherens and Mariotti 2002; Britton et al. 2008; Reitsema et al. 2013). Therefore, a range of potential food sources from the same context should ideally be analyzed in order to interpret sample of interests in the light of the stable isotope variability of other organisms from the same environment. The metabolism of species may also influence nitrogen isotope signal:

for instance, ruminants have, on average, higher δ^{15}N values than non-ruminants (Sponheimer et al. 2003). In addition to the higher isotopic signal of aquatic primary producers (plants) in comparison with their terrestrial counterparts, food chain is also longer in aquatic than in terrestrial ecosystems, therefore, fish consumers usually have higher δ^{15}N ratios than terrestrial meat consumers (e.g. Walker and DeNiro 1986; Dufour et al. 1999; Grupe et al. 2003, 2009; Katzenberg et al. 2012). In a lab-controlled pig feeding experiment, a strong linear relationship has been evidenced between tissues δ^{15}N values and the amount of marine protein consumed, but δ^{15}N values do not became consistently elevated until at least 25% of the dietary protein source became marine derived (Webb et al. 2017b); this could be due to the differential incorporation of amino-acids from terrestrial and marine dietary protein.

Since both δ^{15}N values and $\Delta^{13}C_{apatite\text{-}collagen}$ are substantially varying according to the trophic level, a correlation is expected between these variables; some researchers have proposed models to use these different markers in order to quantify the intake of different dietary sources and/or to better distinguish the relative proportion of different macro-nutrients from varying sources (e.g. Froehle et al. 2012; Fernandes et al. 2014).

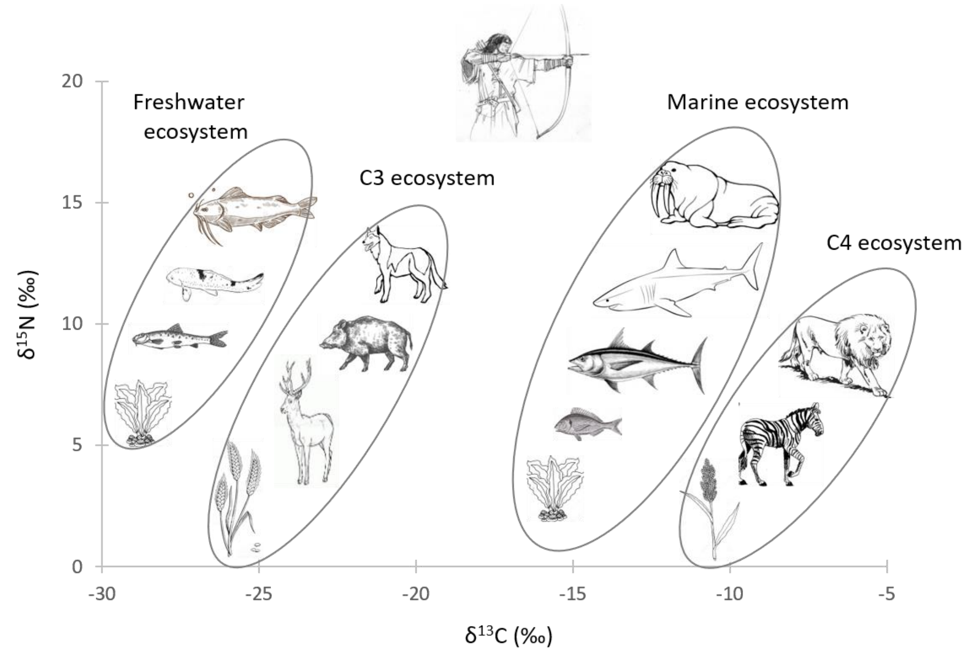

Figure 20: Theoretical δ^{13}C and δ^{15}N values for animals from trophic webs of different ecosystems.

Disturbed nitrogen balance and δ^{15}N values

When the ingested amount of nitrogen equals the amount of excreted nitrogen, the body is considered in nitrogen balance (Katzenberg and Waters-Rist 2018). Under different physiological conditions or situations of biological stress, the nitrogen balance can be disturbed, which may impact the δ^{15}N values.

During events of biological stress such as mal-nutrition, under-nutrition, starvation or infectious disease, the body is mainly in catabolic state (i.e. when more molecules are break down than built up) and in negative nitrogen balance (as not enough nitrogen from dietary protein is ingested and used by the body for molecule building). Such conditions have been associated with elevated δ^{15}N values (e.g. Hobson and Clark 1992; Hobson et al. 1993; Katzenberg and Lovell 1999; Cherel et al. 2005; Fuller et al. 2005; Mekota et al. 2006; Neuberger et al. 2013; Robertson et al. 2014; Olsen et al. 2014; Hertz et al 2015; Doi et al. 2017). It has been assumed that when less nitrogen (proteins) is ingested than required for protein maintenance and synthesis, the body catabolizes its own tissues, which causes an additional fractionation of nitrogen stable isotopes. Both the quantity and the quality of ingested protein may thus influence δ^{15}N values (Adam and

Sterner 2000; Focken 2001; Robbins et al. 2005; McCutchan et al. 2003; Water-Rist and Katzenberg 2009). In case of water stress, it has also been suggested that more urea – enriched in ^{14}N - may be excreted relative to the total volume of urine, resulting in a retention in ^{15}N available for tissue synthesis and thus higher δ^{15}N values (Ambrose and DeNiro 1986; Ambrose 1991; White and Armelagos 1997).

In contrast, during period of growth, the body is mainly in anabolic state (i.e. mainly building up new molecules), and in positive nitrogen balance (as more nitrogen from protein is ingested for molecules building than excreted). Although stable isotope ecologists and physiologists have not reach a consensus on this issue, it is possible that the speed of growth may have an effect on δ^{15}N values as the body has less time to select the lighter isotopes in case of faster accretion rates, resulting on a reduced trophic spacing (Sick et al. 1997; Gaye-Siessegger et al. 2003, 2004; Fuller et al. 2004, 2005; Trueman et al. 2005; Williams et al. 2007; Water-Rist and Katzenberg 2009; Reitsema 2013; Reitsema and Muir 2015; Reynard and Tuross 2015; Webb et al. 2017). It has also been suggested, particularly in case of fast tissues accretion associated with the state of pregnancy, that δ^{15}N values may decrease as a result of an increase salvage of isotopically lighter nitrogen from urea to respond to the high nitrogen demand of the rapidly increasing body (e.g. Fuller et al. 2004). It has also been suggested that rapidly growing tissues may results in a differential incorporation of amino acids from different food sources (e.g. terrestrial and marine; Webb et al. 2017b). These effects of pathology and growth on δ^{15}N must hence be carefully taken into consideration when interpreting stable isotopes variability, particularly for when discussing the values of outsiders (e.g. elevated δ^{15}N values: a particular social rank related to high protein consumption or a sick individual?) or intra-individual variations (e.g. lower δ^{15}N values: period of protein restriction or physiological effect of growth?). These newer areas of inquiries now contribute to broaden the field of stable isotope research to questions related to issues related to the nutritional and physiological health of past populations (Reitsema 2013).

3.2.4.3. Sulfur (δ^{34}S)

Stable sulfur isotopes have recently also become a common aspect of paleodietary research (e.g. Richards et al. 2001; Privat et al. 2007; Nehlich et al. 2009, 2010; Nehlich 2015). sulfur is an essential part of all living cells, playing an important role in protein structures. The four stable isotopes of sulfur are ^{32}S (95.02% of all available sulfur on earth), ^{34}S (4.21%), ^{33}S (0.75%), and ^{36}S (0.02%) (Faure 1986). The ratio between the lighter isotope ^{32}S and the heavier isotope ^{34}S is commonly analyzed in archaeology (Nehlich 2015). Inorganic sulfur is incorporated into biomolecules at the base of food-webs mainly from soil and atmosphere and from water sulfate in freshwater and marine environments. Sulfate from soils and freshwater environments mainly originate from rains, ground waters and additionally from the weathering of different rock-type and sulfur bearing minerals with different δ^{34}S values (Krouse 1989; Nehlich 2015). Terrestrial influenced rain may vary around -5‰ and +10‰ and freshwater sulfate between -15‰ and +20‰ while ocean seawater sulfate shows less variation and range around 20‰ (Figure 21; Nehlich 2015). Coastal environments tend to have higher sulfur signal due to the sea spray effect and to oceanic influenced rain (ibid.).

Plants transform inorganic sulfur into the amino acids of cysteine further synthesized into methionine, which are then passed along the food webs within proteins (Krouse et al. 1996; Noji and Saito 2003). Plants δ^{34}S value are 0 to 4‰ lower than the value of assimilated sulfur from the environment. As for carbon and nitrogen, some researchers have demonstrated the existence of differences in the δ^{34}S values of consumers and of food resources, but the magnitude of this difference may be highly variable according to species and the different tissues considered (average difference of +0.5±2.4‰ estimated by Nehlich 2015 for data on different taxa and tissues collected by Peterson et al. 1985; Katzenberg and Krouse 1989; Hesslein et al. 1993; Richards et al. 2001; McCutchan et al. 2003; Barnes and Jennings 2007; Tanz and Schmidt 2010). sulfur is abundant in hair (keratin protein) but there is very little sulfur in bone collagen (0.16%). The $\delta^{34}S$ value of keratine reflect both the value of methionine, which is not fully synthesized in vivo in vertebrates and therefore must be provided by diet, and of cysteine which can be both taken up from diet and catabolized from the internal cycling of methionine (Finkelstein et al. 1988). In contrast, of these two amino-acids, only methionine residues are found in mammalian type I collagen, the major organic constitutes of bone (Eastoe 1955). Therefore, it is assumed that $\delta^{34}S$ value of bone collagen should therefore directly reflect he methionine that has been incorporated from the dietary protein (Nehlich 2015). In marine environments the $\delta^{34}S$ values should be higher (close to + 20‰) than in terrestrial (ca. −15‰ to +15‰) and freshwater ecosystems (ca. −22‰ to +20‰; Figure 21). Therefore, combined with other elements, sulfur stable isotope ratio analysis has been used to distinguish the consumption of marine, terrestrial and freshwater resources (e.g. Leach et al. 1996; Richards et al. 2001; Craig et al. 2006; Privat et al. 2007; Hu et al. 2009; Nehlich et al. 2010, 2011) or as a tool to discuss migration patterns of past humans and animals (Vika 2009).

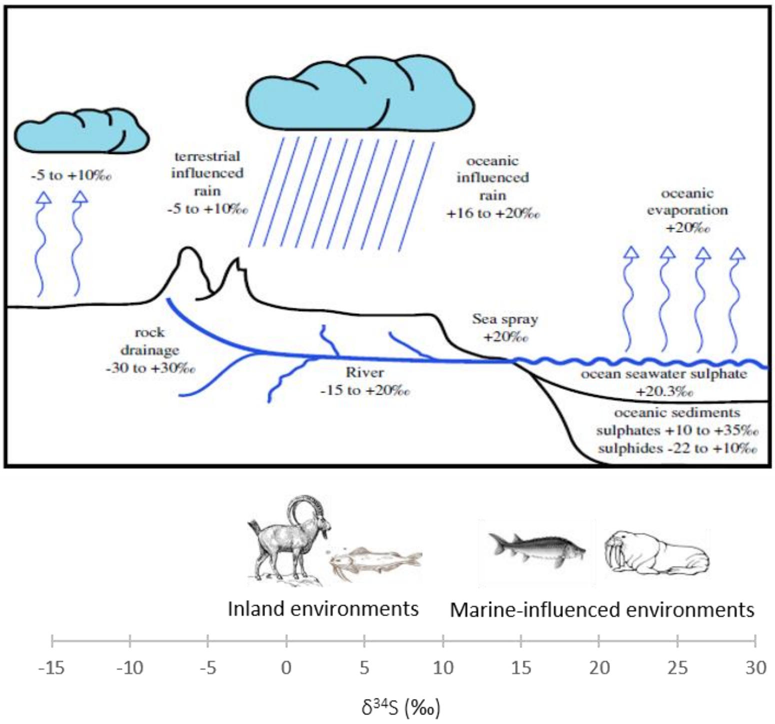

Figure 21: Schematic overview of the cycling of sulfur and its expected sulfur isotope values within the environment. Adapted from Nehlich 2015.

When using $\delta^{34}S$ ratios as a paleodietary marker, it should be kept in mind that fish, and particularly marine fish, has higher amount of methionine in its proteins than terrestrial animals (e.g. Eastoe and Leach 1958), which means that, theoretically, even a small consumption of fish may influence consumers' $\delta^{34}S$ values. Besides, it can be mentioned that Webb et al. (2017b) have recently evidenced a small fractionation effect of -1.5±0.8‰ on the bone collagen of pigs fed on a lab controlled diet (n=35), confirming hence some observations made by Barnes and Jennings (2007) and Tanz and Schmitt (2010). Interestingly, this offset increases with the increasing consumption of marine resources (from ca -0.5‰ to -2.5‰; Webb et al. 2017b). These results advocate for further methodological research in order to clarify the physiological processes beyond metabolism of dietary sulfur.

3.2.4.4. Summary: the joint use of δ^{13}C, δ^{15}N and δ^{34}S values in paleodietary studies

The combination of these three markers now becomes usual in human bioarchaeological studies. δ^{13}C and δ^{15}N vary among plants according to environmental and physiological factors and increase at each level of the food chain, allowing identifying herbivores and carnivores (Figure 20; e.g. De Niro and Epstein, 1978, 1981; Bocherens and Drucker, 2003). Fish also exhibit higher δ^{15}N values than terrestrial animals, and marine species display higher δ^{13}C values than freshwater fish and terrestrial animals (e.g. Richards 2002; Grupe et al. 2009). δ^{13}C also helps to distinguish the type of plants consumed (C3 and C4 photosynthetic plants) (e.g. Schoeninger and DeNiro 1984; Schwarcz and Schoeninger 1991). The comparison of δ^{13}C extracted from collagen and from apatite enables researchers to discuss the departure from a mono-isotopic, i.e. the consumption of macro-nutrients (proteins and energy) from different origins (e.g. Kellner and Schoeninger, 2007; Froehle et al. 2010, 2012; Eerkens et al. 2013). Concerning δ^{34}S, plants and animals vary depending upon environmental factors, and may thus inform on migration or on the consumption of resources originating from different environments; while the marine ecosystem displays the highest values, the terrestrial ecosystem exhibits lower values (Figure 21; Nehlich 2015).

Analyzed tissues should be carefully selected considering the timing/rate of formation and other anthropological parameters (such as age, sex or pathology) should also be taken into account when interpreting individual variations since physiological conditions may particularly influence δ^{13}C and δ^{15}N values (e.g. Reistema 2013). Other environmental factors may also affect the stable isotope values (e.g. canopy effect, soil salinity, manuring practices…), and thus human stable isotope values should be analyzed with presumed food sources originating from the same context (e.g. Van Klinken 1994; Hedges et al. 2004; Goude and Fontugne 2016). However, considering issues related to the preservation of plant remains from archaeological sites, particularly for old excavations when water-sieving was not always practiced, the stable isotope values of herbivores (including the broadest number of species possible) may be used as a baseline proxy for a 100% plant-based diet.

3.2.4.5. Other isotopic markers (δ^{18}O, ^{87}Sr/^{86}Sr, compound specific analyses…)

Strontium radiogenic signal (^{87}Sr/^{86}Sr) is now often used to examine the provenance of human and animal in archaeological assemblages. It is called “radiogenic” since ^{87}Sr originate from the decay of an isotopes from rubidium element (^{87}Rb). The strontium signal of soil and water vary spatially, and it is passed to living organisms over the food web without significant modification (e.g. Ericson 1985; Price et al. 2002; Wright 2005; Bentley 2006). Since tooth enamel forms during childhood, the strontium signature of a tooth should reflect the value of the place where an individual grew up. Thus, local and non-local individuals can be differentiated by comparing teeth radiogenic strontium signal with the local baseline (defined using the local geology and/or faunal remains). In the Danube Gorges, an increasing number of non-locals have hence been identified amongst the sample during the period of Transformations-Early Neolithic and the Early-Middle Neolithic, mainly buried in the typical Neolithic crouched position at the site of Lepenski Vir (Borić and Price 2013). Because of the strontium isotope difference between marine and terrestrial foods, they can also be used in paleodiet studies (Sealy et al. 1991). With the development of micro-sampling strategies and high-resolution analyses, multiple samples are now performed to examine individual mobility patterns during childhood-teenage (e.g. Scharlotta and Weber 2014; Scharlotta et al. 2018).

δ^{18}O is also used for paleo-environmental reconstruction and to examine diet and mobility but will just be mentioned here since this marker has not been included in this research. δ^{18}O mostly decrease with increasing latitude, increasing altitude and distance from coasts, mainly because more of the heavy isotope ^{18}O falls in precipitations (Dansgaard 1964). The δ^{18}O values of an organism is strongly with the $\delta^{18}O$ values of local meteoric waters and can thus be used to trace climatic fluctuations (e.g. Longinelli 1984; Luz et al. 1984; D'Angela Longinelli 1990; Daux et al. 2005, 2008). As for strontium radiogenic signal, the comparison of tissues formed during different period of life may inform on geographic origin, migration or individual mobility patterns (e.g. Sealy et al. 1995; White et al. 1998; 2004; Balasse et al. 2002).

Jointly from the development of stable isotopes, the measurement of trace elements – elements in small proportions in our body such as calcium, magnesium, strontium – have also shown useful for paleodietary reconstruction (e.g. Sillen and Smith, 1984; Balter 2004; Sponheimer and Lee Thorpe 2006). Nowadays the potential of the isotopes of other elements (e.g. Ca, Cu, Fe, Mg, Zn...) is being explored to further distinguish between food resources, or geographical origins but also to examine metabolic disturbances or even for purposes of sex determination (e.g. Jaouen and Pons 2017). Besides moving to another scale of analyses, measuring the signature of different amino acids that makes up the collagen protein may also help understanding the causes for stable isotopes variability (e.g. Fogel and Tuross 2003; Naito et al.2016).

3.2.5. Isotopes and children feeding research

Maternal nutritional choices from pregnancy to the completion of the weaning process, but also during older childhood, may have a direct on the demography of a group by influencing children morbidity and mortality, as well as fertility rates (e.g. Binford 1968; Hassan 1981; Buikstra et al. 1986; Dettwyler 1995; Katzenberg 1996; Sellen and Smay 2001). Indeed, despite the universal biological determinant of lactation, there is a substantial plasticity in the modalities of the weaning process (in terms frequency of suckles, introduction of solid food, total length of lactation, nature of the weaning food), related to socio-cultural factors, environmental variables or individuals choices. Therefore, with the development of stable isotopes techniques, past parenting dietary strategies and children feeding practices have rapidly represented major issues of interest for bioarcheologists, notably in context of subsistence transition, urbanization and industrialization or migrations - niche colonization, food shortage and starvation (e.g. Fogel et al. 1989; Katzenberg 1996; Richards et al. 2002; Eerkens et al. 2011; Howcroft et al. 2012; Tsutaya and Yoneda 2013, 2014; Humphrey 2014; Reynard and Tuross 2015; Beaumont et al. 2015; Fulminante 2015; Tsutaya et al. 2017).

Stable isotopes, breastmilk and supplementary food

Given that a breastfed child is only fed on maternal milk nutrients during the period of exclusive suckling and that $\delta^{15}N$ increase at each trophic level, it has been shown, as expected, that his tissues are elevated in $\delta^{15}N$ values in comparison with the tissues of his nursing mother (Fogel et al. 1989). Ecological studies and nutritional experiments on mother-child pairs have enabled to quantify the offset between maternal tissues, the milk and the offspring tissues (e.g. $\Delta^{15}N_{\text{child keratin-maternal keratin}}$ estimated ca 1.7-2.8‰; Fogel et al. 1989, Fuller et al. 2006; Reynard and Tuross 2015; Herrscher et al. 2017). A slight offset has also been evidenced between the $\delta^{13}C$ values of maternal tissues and the values of the tissues of the breastfed offspring (e.g. $\Delta^{13}C_{\text{child keratin - maternal keratin}}$ estimated ca 0-1‰; Fuller et al. 2006; Herrscher et al. 2017). Hence, while the tissues formed during pregnancy may be influenced by the maternal nutritional health (e.g. Fuller et al. 2005; Kinaston et al. 2009; Beaumont et al. 2015), after birth, the tissues of an infant should be gradually enriched in ^{15}N and in ^{13}C with breastfeeding, following the rates of protein turnover and the replacement of the previous placental stable isotope signal (e.g. Fogel et al. 1989; Fuller et al. 2006; Tsutaya and Yoneda 2013, 2014; Reynard and Tuross 2015; Herrscher et al. 2017). After the introduction of solid food and the diminution of suckles, the $\delta^{15}N$ signal of the child should decrease, describing a typical breastfeeding-weaning "bell curve" (ibidem e.g. Appendix A.III.17. part. A.). Given the magnitude of variations of carbon isotopic ratios associated with the consumption of different food resources (terrestrial/marine/freshwater; C3/C4 plants), fluctuations in $\delta^{13}C$ values has also been used in archaeological contexts to consider the nature of the weaning food supplemented (e.g. Katzenberg et al. 1993; Dupras et al. 2001; Richards et al. 2002; Howcroft 2012; Water-Rist et al. 2011; Beaumont and Montgomery 2013). In contrast, until now there has only be a very little application of $\delta^{34}S$ ratios to infant weaning to discuss the origin of supplemented proteins (Nehlich et al. 2011).

Population approaches

The first stable isotope studies dedicated to children feeding practices in the past mostly examined $\delta^{15}N$ and $\delta^{13}C$ fluctuations at a population level, by comparing the bone stable isotope values of children who died at different ages with the stable isotope variability of females from the population (the putative mothers; e.g. Fogel et al. 1989; Katzenberg et al. 1993, 1996; Clayton et al. 2006; Tessone et al. 2007; Prowse et al. 2008; Haydock et al. 2013; Bourbou et al. 2013; Tessone et al. 2015). It is considered that a child is entirely weaned when its $\delta^{15}N$ values range within the adult variability; inflexions on trendlines fitted on the $\delta^{15}N$ and $\delta^{13}C$ values of cohorts of children also enabled researchers to estimate the "population" age for introduction of supplementary food. Yet, this population approach is highly dependent on the method of children age estimation, which actually provides a range of estimate and not an exact point (Scheuer and Black 2005); additionally, the bone tissue reflects the stable isotope signal of a child over a period before its death, which varies according to the rate of bone remodeling, itself dependent on growth rate (Valentin 2003). The introduction of Bayesian method to the estimation of age at weaning from bone $\delta^{15}N$ values recently enabled to take into account this limit (Tsutaya and Yoneda 2013). Besides the population approach requires a significant number of individuals who died during the breastfeeding and the weaning period, which is uncommon in archaeological contexts since the age category 1-5 is often the least represented (Bocquet-Appel et al. 2002). It also relies on the basic assumptions that (1.) mothers consumed similar food during pregnancy and breastfeeding as during the rest of their lives; (2.) most children were weaned at similar age and with quite similar food resources (Herrsherr 2013; Reynard and Tuross 2015; Beaumont et al. 2015). Although this approach is useful in broadly estimating averages life-history parameters amongst a population, underlying assumptions cannot be reflective of human behavioral complexities.

Intra-individual approaches

In order to circumvent these limits, intra-individual sampling strategies have been developed by comparing the stable isotope values of tissues formed during different periods of childhood: for instance, different part of fast and slow renewing bone (e.g. Waters-Rist et al. 2011), bone tissues and teeth tissues (e.g. Herrscher 2003; 2013; Kaupova et al. 2014), or different parts of teeth formed at different age (e.g. Wright and Schwartz 1998; Fuller et al. 2003; Eerkens et al. 2011; Howcroft et al. 2012, 2014; Burt and Garvie Lok 2013; Burt 2014; Beaumont et al. 2013, 2015; Henderson et al. 2014; Sandberg et al. 2014 Beaumont and Montgomery 2016; Beaumont et al. 2018; King et al. 2018a and b; Scharlotta et al. 2018). However, another potential problem with using stable isotopes of nitrogen from the tissues of individuals who died during childhood is that their death might be related to the experience of nutritional stress and thus they may not be representative of the studied population (a bias stamped "selective mortality" as part of the osteological paradox; e.g. Katzenberg et al. 1996; Beaumont et al. 2015; Reynard and Turross 2015). Besides, since $\delta^{15}N$ may be elevated in situations of nutritional stress, it may not be possible to separate the trophic effect of breastfeeding from the cause of death in some cases; however, it is still not clear whether this might represent a serious problem (seeReynardandTuross2015).

One way to avoid the problem of individuals who died in infancy or early childhood is to analyzed tissues that were formed early in postnatal development and that can be isolated from older children and adults. A first application of this approach was based on the analysis of stable isotopes of carbon and oxygen from the carbonate of enamel of tooth formed at different age, based on the assumption that breastmilk has a different $\delta^{18}O$ signatures than the drink water and that $\delta^{13}C$ substantially varies according to the nature/origin of food resources (Wright and Schwarcz

1998). This method has then been applied to the $\delta^{15}N$ and $\delta^{13}C$ values from the dentine of teeth formed at different age, including parts of crowns and/or of roots (e.g. Fuller et al. 2003; Howcroft 2013; Howcroft et al. 2012, 2014). Easier to apply to animal teeth – of bigger size than human teeth - in view of inferring herding practices (changes in length of lactation, birth seasonality or herds mobility; e.g. Balasse et al. 2001, Balasse 2002), intra-tooth multiple samples were firstly restricted to a maximum of four samples per human tooth (Fuller 2003). The development of micro-sampling techniques and advances in mass spectrometer that allow for the analysis of much smaller samples has more recently enabled some researchers to increase the number of samples per teeth to 5-15 sections, opening important prospects in the reconstruction of past life-histories (e.g. Eerkens et al. 2011; Burt and Garvie Lok 2013; Burt 2014; Beaumont et al. 2013, 2015; Henderson et al. 2014; Sandberg et al. 2014; Beaumont et al. 2015; Beaumont and Montgomery 2016; Beaumont et al. 2018; King et al. 2018a and b; Scharlotta et al. 2018).

3.3. Sampling, material preparation and stable isotopes measurements

3.3.1. Sampling strategies: tissues selected, and element analyzed

3.3.1.1. Adult bone collagen analyses ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$)

Published stable isotopes data concerning Mesolithic and Neolithic humans discovered in the Danube Gorges were firstly collected in an extended database, integrating available life-history information about age at death, sex, origin, and ancestry (**$\delta^{13}C$and $\delta^{15}N$: n=172; $\delta^{34}S$ n=19**; Bonsall et al. 1997; Grupe et al. 2003; Borić et al. 2004; Nehlich et al. 2010; Borić et al. 2011; Borić and Price 2013; Bonsall et al. 2015a[51]). Published animals' stable isotopes values from numerous species were jointly collected to discuss the local ecological context (**n total= $\delta^{13}C$-$\delta^{15}N$=81, $\delta^{34}S$=8;** including terrestrial herbivores: $\delta^{13}C$-$\delta^{15}N$=33, $\delta^{34}S$=4; terrestrial omnivores: $\delta^{13}C$-$\delta^{15}N$=7, $\delta^{34}S$=1; terrestrial carnivores: $\delta^{13}C$-$\delta^{15}N$=21, $\delta^{34}S$=0; stationary freshwater fish: $\delta^{13}C$-$\delta^{15}N$=10, $\delta^{34}S$=2; anadromous fish $\delta^{13}C$-$\delta^{15}N$=5, $\delta^{34}S$=1; terrestrial wild animals: $\delta^{13}C$-$\delta^{15}N$=46, $\delta^{34}S$=5; Mesolithic domesticated taxon [dogs]: $\delta^{13}C$-$\delta^{15}N$=13, $\delta^{34}S$=0; Neolithic domesticated taxa [cattle and goat]: $\delta^{13}C$-$\delta^{15}N$=2, $\delta^{34}S$=0; ibidem).

Previously published stable isotope studies mainly focused on the $\delta^{13}C$and$\delta^{15}N$ stable isotope ratios and only one publication analyzed $\delta^{34}S$ ratios focusing on a small sample of 19 humans and 8 animals (Nehlich et al. 2009). While $\delta^{34}S$ proved to be a good discriminant criteria to distinguish terrestrial and aquatic ecosystem, the results of this study have been extensively discussed (Bonsall et al. 2015b and c, Borić and Nehlich 2015) as to understand whether diachronic and geographic variations in $\delta^{34}S$ and $\delta^{15}N$ mostly relate to changes in the consumption of aquatic resources versus terrestrial one or to changes in the species of fish consumed (freshwater fish versus anadromous fish migrating seasonally from the Black sea). Considering the importance of this debate in a context of increased sedentism along the riverbanks and of the agricultural transition, new $\delta^{34}S$ analyses were carried out on the bone collagen of a significant sample of Mesolithic-Neolithic adult individuals (**n $\delta^{34}S$=75).**

A special attention was paid to sample radiocarbon dated individuals and individuals discovered at sites located in different parts of the Gorges – including the Downstream Area not included in the study of Nehlich et al. (2009) – in view of examining chronological changes in dietary practices as well as geographic specificities. Besides, emphasis was placed on sampling individuals with determined sex and assigned to a precise age category (re-estimated using probabilistic methods) and with available strontium information in view of reconstructing the diet of the different socio-biological categories of the population (males / females; young / old; locals / migrants). Care

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[51] In case several $\delta^{13}C$and $\delta^{15}N$ values was obtained for the same individuals in these studies, only the most recent data was considered in the following analyses.

was also taken to sample individuals jointly analyzed for ancestry in order to reconstruct the dietary adaptations of individuals born in the Gorges who descended from Mesolithic hunter-gatherers, and of individuals descended from Near-Eastern Neolithic communities (migrants or born in the Gorges).

Amongst selected individuals, those with available $\delta^{13}C$ and $\delta^{15}N$ values from published studies were analyzed only for $\delta^{34}S$ (n=42) and the other were also analyzed for $\delta^{13}C$, $\delta^{15}N$ (n=33). For purposes of preservation ribs were sampled primarily and, when not possible, collagen was extracted from long bones, part of skulls or mandibles.

$\delta^{34}S$ was also analyzed on different animal species, terrestrial and aquatic, local and domesticated (**n total= $\delta^{34}S$=17, $\delta^{13}C$-$\delta^{15}N$=22**; *including* terrestrial herbivores: $\delta^{34}S$-$\delta^{13}C$-$\delta^{15}N$=6, terrestrial omnivores: $\delta^{34}S$-$\delta^{13}C$-$\delta^{15}N$=3; terrestrial carnivores: $\delta^{34}S$-$\delta^{13}C$-$\delta^{15}N$=2; stationary freshwater fish: $\delta^{13}C$-$\delta^{15}N$-$\delta^{34}S$=5; anadromous fish $\delta^{13}C$ - $\delta^{15}N$=4, $\delta^{34}S$=3; terrestrial wild animals: $\delta^{13}C$-$\delta^{15}N$-$\delta^{34}S$=6; Mesolithic domesticated taxon: $\delta^{13}C$-$\delta^{15}N$-$\delta^{34}S$=2; Neolithic domesticated taxa: $\delta^{13}C$-$\delta^{15}N$-$\delta^{34}S$=3). Since specimen from radiocarbon dated contexts were favored, various anatomical elements were sampled, according to the state of preservation.

3.3.1.2. Children bone and dentine collagen analyses *($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$)*

In order to reconstruct feeding practices, published stable isotopes values from the bone collagen of immature individuals were firstly examined according to the age at death, re-estimated using morphological, metric methods and jaws' ct-scans (cf part 3.1.1.). Given the small number of infants and children analyzed in previous published paleodietary studies ($\delta^{13}C$, $\delta^{15}N$ total immature=35; fetuses and perinates n=19; 1 month-5 years, n=4: 5-15 years, n=13; $\delta^{34}S$ total immature=1), collagen protein was additionally extracted from bone and dentine tissues formed at various stages of life - during pregnancy, infancy and childhood – and analyzed for $\delta^{13}C$,$\delta^{15}N$ and $\delta^{34}S$.

In order to explore the maternal diet and nutritional health during pregnancy, collagen was extracted from the cortical bone of 26 additional Mesolithic – Early Neolithic fetuses and perinates and $\delta^{34}S$ was systematically measured when the amount of extracted collagen was sufficient ($\delta^{34}S$, n=19; $\delta^{13}C$, $\delta^{15}N$, n=24). Cortical parts of long bones were mostly sampled since the structure and small size of perinates' ribs made the sample too invasive for the extraction of a sufficient amount of collagen. Fetuses and perinates' stable isotopes values could be examined per sex, using published aDNA sex-determination (Čuljković et al. 2008).

In order to examine the different dietary transitions experienced during childhood, an intra-individual strategy was set, based on the schedule of dental development and the differential growth rate of tissues (Figure 22). Such multi-sampling strategy enables to examine longitudinal stable isotopes fluctuations over different periods of the life of a child, to maximize the extent of paleodietary information for small sample size and to circumvent several of the above-mentioned limits inherent to the population approach of children feeding practices (cf part 3.2.5). As presented in Figure 22, cortical bone and different part of teeth of 27 children aged between 3-6 months and 10-11 years old, including:

a) The crown of a first deciduous molar, which should reflect a dietary signal formed between ca 6 months in utero and ca 11 months (Moorrees et al. 1963a; AlQahtani et al. 2010; Beaumont and Mongtmery 2015). $\delta^{13}C$ and $\delta^{15}N$, n=22; $\delta^{34}S$, n=19.

b) The crown of a first permanent molar, which should reflect a dietary signal formed between ca 2 months and ca 3.5 years old (Moorrees et al. 1963b; AlQahtani et al. 2010; Beaumont et al. 2013). $\delta^{13}C$ and $\delta^{15}N$, n=22; $\delta^{34}S$, n=20;

c) The growing extremity of the root of a tooth (apex in formation), which should reflect a dietary signal formed some time before the death of a child (e.g. Herrsher 2013). The range

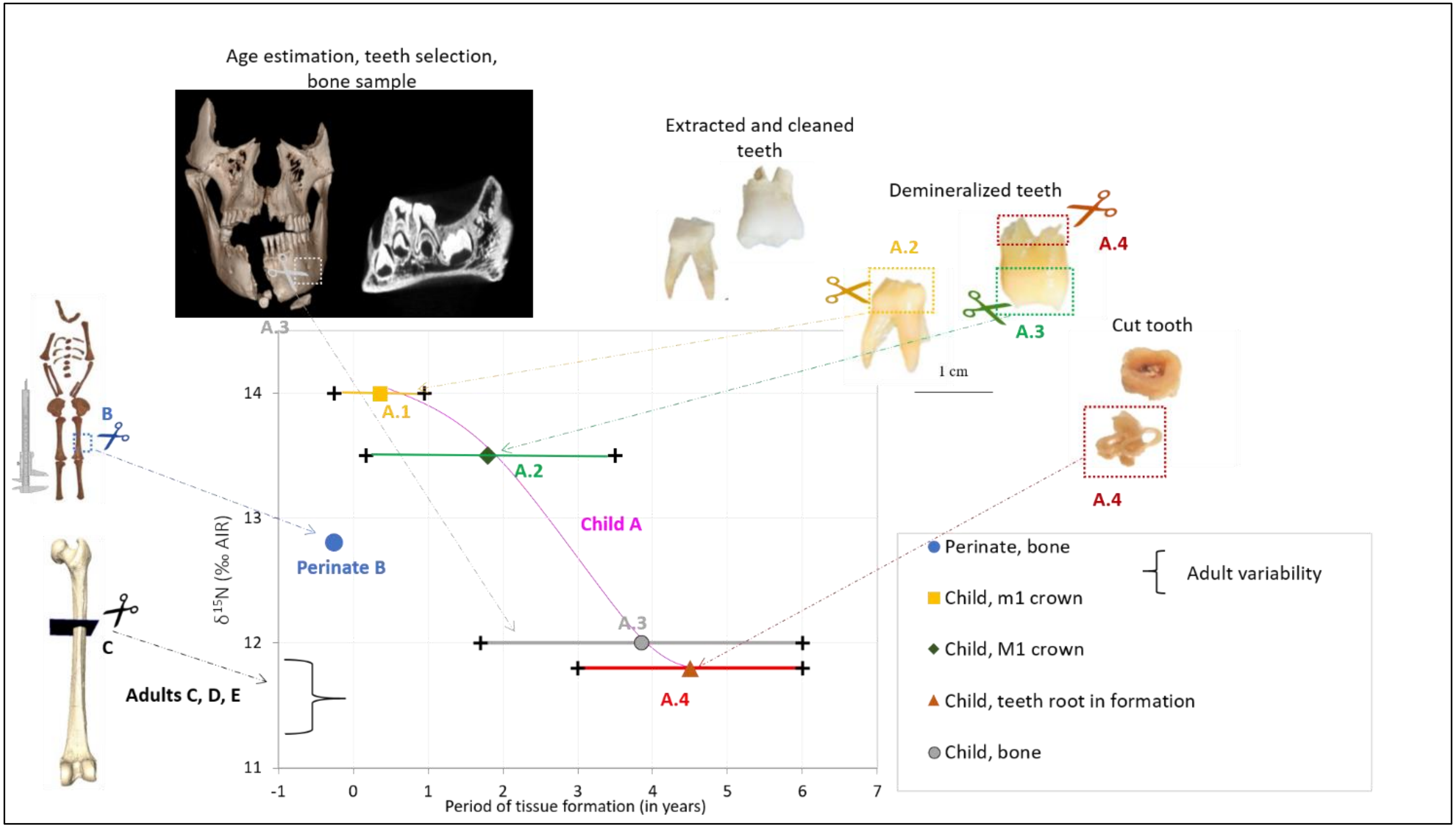

Figure 1: Sampling strategy and protocol applied to reconstruct maternal nutritional choices and feeding practices. Age determination (ct-scan child Ajm 11), tooth selection, extraction and preparation. Comparison of the intra-individual multi-sampling data (A.1, A.3, A.4) gathered for children aged at death ca 1-10 years (e.g. child A) with perinates' and adult bone stable isotope variabilities (e.g. perinate B, adults C, D, E). From de Becdelièvre et al. 2015.

of the estimated age at death of the child was thus used to refer to this signal. Because of the estimated age at death of the child was thus used to refer to this signal. Because of teeth differential growth patterns, it is possible that samples of different teeth located at similar location may not be entirely contemporaneously (Sandberg et al. 2014). Therefore, we tried to sample systematically the root of deciduous and first permanent molars (only in one case, LV 71, the root of a canine was sampled). Children were sampled from birth to 10-11 years old, since after this age the formation of the apex of the root of the first permanent is already completed (Moorrees et al. 1963b; AlQahtani et al. 2010; Beaumont et al. 2013). In three cases, the sampled root was already in beginning of resorption (the first deciduous molars of the children AJm 12, AJm 8, aged at death ca 3-5/6 years old, and the first deciduous canine of the child LV 71, aged at death 4-6 years old). The range from 3/4 of the formation of the root to the completion of the apex was used to refer to these signals (Moorrees et al. 1963a and b; AlQahtani et al. 2010; Beaumont and Mongtmery 2015). Finally, the sampled root of the first permanent molar of one child was already closed (AJm 13), the range for the age of completion of the apex (Moorrees et al. 1963a,b; AlQahtani et al. 2010; Beaumont and Mongtmery 2015) was used to refer to this signal. n children 1 month-5 years: $\delta^{13}C$ and $\delta^{15}N$ = 8; n children 5-10 years: $\delta^{13}C$ and $\delta^{15}N$ = 15. Enough collagen for joint analysis of $\delta^{34}S$ could be extracted only in one case (AJ 16, aged at death 1.5 – 4 years).

d) Cortical part bones which should reflect a dietary signal formed a longer time before the death of the child than the growing root of a teeth (Herrsher 2013), depending to bone turnover velocity at the age at death (mandibular bones associated with the sampled teeth were mostly sampled). Thus, the lower limit of the range of the estimated age at death of a child has been standardized considering the turnover velocity rates at this age (using bone renewing rate provided by Valentin, 2003). The results are here presented using both the estimated age at death and the standardized age at death to refer to this signal (cf Appendix A.III). n children 1 month-5 years: $\delta^{13}C$ and $\delta^{15}N$ = 17, $\delta^{34}S$=12; n children 5-15 years: $\delta^{13}C$ and $\delta^{15}N$ = 14, $\delta^{34}S$=15.

Sampled crowns were not damaged by – or only present a small degree of – abrasion or by caries. Children teeth are also free from secondary dentine, which is deposited at very slow rates over life. In the other way, it should be kept in mind that because of the angular incremental growth of dentine, it is possible that the stable isotope values of the crown of molars of an individual who died for example at 7 years old includes - close to the neck - some dentine formed slightly older than the crown of an individual who died for instance at 3 years old (Beaumont et al. 2013).

3.3.1.3. Adult teeth carbonates analyses (δ^{13}Cenamel)

Additional information about children dietary adaptations over the Mesolithic-Neolithic Transformation has also been collected from the analysis of the carbon stable isotopes ratios measured on teeth enamel carbonates ($\delta^{13}C_{enamel}$). Until now, the biochemical proxies for the study of the prehistoric diet in the Danube Gorges focused on differences in terms of protein consumption since the stable isotopes analyzed in collagen primarily reflect the protein part of the diet (DeNiro and Epstein 1981; Schoeninger and de Niro 1984; Ambrose 1993; Ambrose and Norr 1993; Jim et al. 2004; Katzenberg 2008; Lee-Throp 2008; Froehle et al. 2012; Fernandes et al. 2014; Nehlich 2015). In contrast, apatite carbonates reflect the carbon signal of the whole diet (carbohydrate and fat as well as amino acids not used for protein synthesis; Ambrose and Norr 2013; Jim et al 2004; Froehle et al. 2002; Fernandes et al. 2014). In the context of the agricultural transition, the analysis of $\delta^{13}C$ ratios from apatite may thus provide a useful proxy to detect differences in the energy part of the diet and particularly in the fat component of resources, as lipids have depleted $\delta^{13}C$ ratios compared to proteins and carbohydrates (DeNiro and Epstein 1977; Jim et al. 2006; Logan et al. 2008).

Due to its high mineralization (ca. 96%; Hillson, 2005) and relatively better preservation in comparison with bone tissue (Lee-Thorp and Sealy, 2008; Zazzo, 2014), teeth enamel has been preferentially selected for this preliminary study of $\delta^{13}C$ ratio from the apatite of Danube Gorges inhabitants ($\delta^{13}C_{enamel}$). Crowns of third permanent molars were selected because of the availability of remaining samples of teeth analyzed for paleogenetic analyses (Hofmanová 2016), in order to limit further alterations of the prehistoric sample. This signal, formed between ca 8-15 years old (Moorrees et al. 1963a; AlQahtani et al. 2010; Beaumont and Mongtmery 2015), also enable to document the transitional period of life (between childhood and teenage) for which the less paleodietary information were available, due to smaller sample size of children who died at this age, and to avoid the possible influence of weaning on $\delta^{13}C$ ratio. Therefore, results should mainly inform on broad differences in terms of total energy consumed around 8-15 years by the Mesolithic and Neolithic individuals who survived to adulthood and thus for whom other bio-anthropological parameters were available, such as sex, geographic or genetic origin.

The third molar crowns of 50 Mesolithic-Neolithic individuals were sampled for $\delta^{13}C_{enamel}$ analyses. Concerning one individual (LV 66), the second permanent molar, formed at a younger age (2-8 years; Moorrees et al. 1963b; AlQahtani et al. 2010; Beaumont and Mongtmery 2015) was analyzed. A few individuals died circa 15-19 years old (LV 122, 57, 48 and AJ 3) or as young adult (<30 years old: LV 54E, 66, 37): their bone collagen and third molar apatite signal may have been partially formed contemporaneously.

In this study, a total of **179** samples has been analyzed for $\delta^{13}C_{collagen}$ and $\delta^{15}N$, **212** samples for $\delta^{34}S$ and **50** samples for $\delta^{13}C_{enamel}$.

3.3.2. Material preparation and stable isotope measurements

Collagen and carbonate extraction

Bone and teeth samples were firstly cleaned by $Al2O_3$ abrasion. Collagen was then extracted from bone following the protocol developed by Longin and adapted by Bocherens (Longin 1971; Bocherens 1992; collagen extraction achieved in LAMPEA laboratory[52]).

Bone was crushed (0.710 mm) and powder was demineralized during 20 min with an HCl solution (1M) and then rinsed and filtered. The remaining filtrate was soaked into a NaOH solution (0.125M) for 20h, rinsed and filtered. The filtrate is dissolved into a weak acid solution (HCl, pH2) at 100°C during 17h and filtered with an Ezee Filter®. The solution is then frozen and freeze dried during 48h. Teeth were soaked entirely into an HCl solution (0.5M) in the fridge (5°C). Once completely demineralized (including enamel part), teeth were rinsed and cut at strategic points as presented in Figure 22. The selected piece of teeth collagen was then prepared as for bone. Extraction yield is calculated on freeze dried samples, and only samples over 1% of collagen are analyzed.

Carbonates from teeth enamel were prepared following the protocol developed by Balasse et al. (2002). Whole crowns were crushed in order to sample ca 10 mg of powder. Organic components were removed with a NaOCL (2-3%) solution (0.1 ml per mg) for 24h and then rinsed five times with a H_2O_2 solution. Contaminants were removed with a CH_3COOH (0.1 mole per liter) solution (1 ml per mg) for 4 hours and rinsed five times with a H_2O_2 solution. Samples were finally dried in the oven at 65°C for 18h.

Mass Spectrometer measurements

Collagen and carbonates elemental composition and stable isotope ratios are analyzed by EA-IRMS (Europa Scientific elemental analyser coupled to Europa Scientific 20-20 IRMS; Iso-Analytical Ltd,

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[52] LAMPEA – Laboratoire Européen de Préhistoire Europe Afrique - UMR 7269, CNRS, Aix Marseille Université, Ministère de la Culture ; Aix-en-Provence, France (http://lampea.cnrs.fr/spip.php?article1085)

UK). The reference material used for analysis was laboratory standards calibrated against and traceable to comparison international standards (IAEA); the measurement error is 0.05‰ for $\delta^{13}C_{collagen}$, 0.14‰ for $\delta^{13}C_{apatite}$, 0.2‰ for $\delta^{15}N$ and 0.3‰ for $\delta^{34}S$.

3.3.3. Preservation of bone collagen and bioapatite

Bone collagen

Concerning the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ analyses performed in this study, the quality of the extracted collagen was controlled by selecting only samples with carbon and nitrogen content ≥ 30% and 10% respectively (van Klinken 1999), and samples C:N ratios (atomic ratio) between 2.9 and 3.6 (DeNiro 1985). Concerning $\delta^{34}S$, only the mammals (humans and animals) with a sulfur content of 0.2%, C:S ratio of 600± 300 and N:S ratio of 200±100 were included in the analysis, following the advices provided by Nehlich and Richards (2009). For the sulfur analyses of fish collagen, Nehlich and Richards advocated a sulfur content that approximate 0.4% and a C:S ratio ranging between 125-225 and a N:S ratio ranging between 40-80.

However, for three fish samples (lab codes A.37, A.38 and A.45), enough collagen could only be extracted for one stable isotope measurement, and it has then be decided to favor sulfur over carbon and nitrogen given that $\delta^{34}S$ ratios has only been previously published for three specimens from Vlasac (Nehlich et al. 2010). Therefore, for these fish the atomic ratios could not be used to assess the quality of the collagen (there S% remaining between 0,15 and 0,3). Besides, two other fish samples are also slightly out of the advised range whether for sulfur content or for the C:S or N:S ratios (cf App. B.IV-V; A.34: S=0,4%; C:S=250, N:S=72; A.41: S=0,4%; C:S=278 and N:S=87) while remaining in the advocated range for carbon and nitrogen content as well as C:N ratios (respectively C=37,2%; N=12,5%, C:N=3,5; C:37,6%; N:15,1%; C:N=3,2). Two of the three fish from Vlasacanalyzed by Nehlich et al. (2009) similarly exceeds the criteria defined by Nehlich and Richards (yielding very similar C:S and N:S ratios to A.34 and A.41; specimen IG-F-9: S=0,4%; C:S=241, N:S=72; IG-F-11: S=0,4%; C:S=279, N:S=87, in Nehlich et al. 2009; cf App. B.IV-V. Therefore, considering the difficulty to obtain fish collagen with S%, C:S and N:S criteria within the advocated ranges, it was decide to follow the integrative procedure adopted by Nehlich et al. (2009) and to include the two fish specimens (A.34 and A.41) in this study. It is noteworthy that such difficulties to extract well-preserved collagen for fish remains have been previously noticed by other researchers even for $\delta^{13}C$ and $\delta^{15}N$ stable isotopes (e.g. Fuller et al. 2012).

Some of the studies which previously analyzed stable isotope ratios on prehistoric human and animal remains from the Danube Gorges did not provide the carbon and nitrogen contents and/or the atomic ratios whether because these criteria were not systematically used at the time of the publication (e.g. Bonsall et al. 1997) and/or because these studies were rather performed for purposes of radiocarbon dating rather than for paleodietary reconstructions (and stable isotopes were measured with an AMS device rather than an IRMS device; e.g. Cook et al. 2002; Whittle et al. 2002; Borić and Miracle 2004; Bonsall et al. 2008; Borić et al. 2008; Borić and Dimitrijević 2009; Borić 2011; Borić and Price 2013; Bonsall et al. 2015).

Therefore, concerning human remains, the differences between individuals falling in the advised range of collagen preservation (for C%, N% and C/N) and the individuals for whom some of these criteria were not available was statistically tested per chronological periods (Early Mesolithic, Late Mesolithic, Transformation/Early Neolithic, Neolithic), and for sites per chronological phases (for Padina, Vlasac, Lepenski Vir, Ajmana and Hajdučka Vodenica). The difference reveals significant only for the $\delta^{13}C$ values of the Late Mesolithic individuals discovered at the site of Vlasac (Mann Withney, > 0,05). Indeed, when the criteria concerning the preservation of collagen were provided by the authors (Grupe et al. 2003; Borić et al. 2004, Neihlich et al. 2010), 23% of human samples and 22% of faunal samples related to the Mesolithic occupation of Vlasac fall without the advocated range for the quality of collagen (versus only 9% for the

Transformational-Neolithic site of Lepenski Vir). Therefore, the previously published stable isotope values of the Late Mesolithic individuals from Vlasac were included in this study only when the criteria for collagen preservation were provided by the authors (exclusion of 21 Late Mesolithic individuals) and were within the acceptable range.

Concerning the site of Lepenski Vir, amongst the previously published stable isotope values with associated C%, N% and C:N information, four Transformational-Neolithic individuals (LV 26; LV 7/Ia; LV 7IIb; LV 91) exhibit proper C/N ratios but are below the recommended range for C% and N% (LV 26: C%= 24,5; N%=8,3; C/N= 3,5; LV 7/1a: N%= 7,4; C%= 21,1, C/N= 3,3; LV 7/IIb: N %=9,6; C%=22,7; C/N=3,3; LV 91: N%:8,3 C%:22,2; C/N: 3,1). For three of them δ^{34}S analyses were performed in this study (LV 26; LV 7/Ia and LV 7/IIb) and the S%, C/S and N/S ratios are within the acceptable ranges (LV 26: S%=0,2%, C/S=345; N/S=98; LV 7/1a: S%=0,2; C/S=303; N/S=100; LV 7/IIb: S%= 0,2; C/S= 357 N/S=130). Considering the importance of these individuals in the local context of Neolithizition (as reflected by their context of discovery, widely discussed by Bonsall et al. 2002; 2008 and 2015a, Borić et al. 2004, Borić and Price 2013), and since three of them have been analyzed for their strontium radiogenic signature (LV 26, LV 7/Ia, LV 7/IIb; Borić and Price 2013) and one for ancient DNA (LV 26; Hofmanová 2016), it was decided to include them in this study, taking into account their lower C% and N% in data interpretation.

The δ^{13}C and δ^{15}N values of two Early Mesolithic and two Early Neolithic human discovered at the site of Cuina Turcului, two Early Neolithic human discovered at the site of Icoana and seven Early Neolithic human discovered at the site of Velesnica were published by Bonsall et al. (2015a) with the atomic ratios but without joint C% and N% information. Since they all display C:N values of 3,2 and given that no statistical difference between the individuals with well-preserved collagen and the individual without available criteria was found for these periods, it was decided to include these individuals in this study. Concerning the site of Schela Cladovei, only 8 Late Mesolithic individuals were published by Bonsall et al. (1997), without any of the criteria nowadays used to assess the quality of the collagen; therefore, it was decided to include these individuals only in the analyses per sites (Appendix A.II.14-17), where these individuals could be identified.

Finally, concerning faunal remains, since animal stable isotope values are expected to vary according to their ecology, dietary and migratory behavior, as well as physiology (e.g thermoregulation, hibernation, gut microbiome), differences between specimen with available collagen criteria and those without the available criteria should be assessed per species. However, only deers were sufficiently represented to perform these tests per periods (Mesolithic and Neolithic) and sites (Padina, Vlasac and Lepenski Vir) and no difference were detected for none of the tested elements (Mann Withney, no difference at the 0,5 level). Considering that a statistically significant difference was found for the Late Mesolithic humans from Vlasac, it was yet decided to jointly remove all faunal remains from the Mesolithic phase of Vlasac published without the available criteria for collagen preservation (exclusion of 9 specimens). Apart from Vlasac, Lepenski Vir and Padina, the stable isotopes values of some ungulates species from Schela Cladovei were also published by Cook et al. (2001) without information about the quality of collagen preservation; however given that this broad taxa grouped both omnivores (such as wild boars) and herbivores (such as deer), it was decided not to include the ungulates from Schela Cladovei in this study.

Every analyses presented in the Appendix A.I and A.II (animal and human adults collagen) were duplicated in order to compare the results (a.) integrating all data (all individuals with a valid collagen plus individuals for which collagen criteria were not available) with (b.) only individuals for which the collagen quality criteria were available and respected. Theses duplicated analyses are presented here for data plotted per periods (Appendix A. II. 1-10).

Enamel apatite

Contrary to collagen, there is no consensus regarding methods to assess the preservation of bioapatite (Lee-Thorp and van der Merwe 1991; Zazzo 2001; Koch 2007; Zazzo 2014; Salesse et al. 2014). Due to the high mineralization of teeth tissue, carbonate are more resistant to taphonomic alteration in enamel than in bone hydroxyapatite (e.g. Lee-Thorp and van der Merwe 1991; Sponheimer and Lee-Thorp 1999; Lee-Thorp and Sponheimer 2003, 2006b; Lee-Thorp 2008; Zazzo 2014). It has been advised to use only samples which yielded a volume of CO_2 ca 700 mm^3 (Zazzo 2001); hence only teeth sample with a volume of CO^2 ranging ca 550-950 were used in this study. The expected absence of correlation between δ^{13}Capatite and extracted weight or CO^2 volume was then statistically tested with Spearman coefficient ratios (following Mion et al. 2016). Only a weak statistical correlation was found between CO^2 volume and human samples ($R^2 = 0.379$ for $p=0.016$). Finally, it can be mentioned that analyzed faunal remains from the sites range in the expected values for fish and terrestrial herbivores (Appendix A.V.1 – A.V.3).

3.4. Statistical analyses

The results of individual stable isotope ratios were systematically displayed in bivariate plots (Appendix A.I-A.V.). The significance of observed tendencies between two independent groups were tested with Mann Whitney U test using a threshold level of significance (p) $\leq$ 0,05.

In addition, a principal component analysis (PCA) was also performed to summarize, analyze and graph the dietary information contained within the different stable isotope variables (δ^{13}Ccoll, δ^{15}N, δ^{34}S; Appendix A.IV). Through linear combination of these original variables (based on the diagonalization of variance and covariance matrices), PCA identifies the factors that explain most of their variance, i.e. creates new independent variables - Principal Components - that contains most of the original information. The first component extracts most of the variance between original variables, the second, the variance that has not been expressed by the first one and so on. By reducing data multi-dimensionality, the calculation of Principal Components enables to analyze the correlation between the variables and, once orthogonally projected, to describe the distances between the individuals or groups of individuals studied. A total of 190 human and animal individuals were included in the analysis. The analysis has been restricted to the first two components since they expressed more than 85% of the total variance in all performed PCA. The correlation between the original variables was tested by the Pearson's chi-square test (correlation matrix), KMO and bartlett tests. Although significant correlations were observed in all performed ACP (KMO index > 0.7 and Bartlett test significant at the 0.05 level, correlation matrix and significance provided in table infra), one should point out that the ideal 5:1 cases-to-variables ratio could not be follow, which substantially restricts the significance of Bartlett test. The PCA solution was rotated using an oblique rotation (oblimin) since it provides a more accurate and realistic representation of how the variables are correlated (correlation between the two components = 0.535; Iobucci et al. 2001). PCA scores were further projected as well as the rotated variables to visualize their correlation and their contribution to new axes (the closer to the axis is the variable, the most it contributed to this component; Appendix A.IV.1). Thanks to the oblimin rotation, δ^{34}S contributes the most to the first axis, which hence should mainly reflect the variance related to the terrestrial-inland versus coastal-marine ecosystems while δ^{15}N contributes the most to the second component, which should primarily reflect the trophic position. Both influenced by environmental and trophic effects, δ^{13}Ccoll logically contribute equally to both components. The circle of correlation was also projected to consider the representation of each variables to the PCA (also summarized by communalities; Appendix A.IV and Table 1).

Table 1 : Correlation matrix and extracted communalities for the PCA; the individual scores and the circle of correlation are presented in Appendix A.IV.

	Correlation matrix* δ13Ccoll	 δ15N	 δ34S	Extracted communalities
δ13Ccoll	1	0.553	0.558	0.72
δ15N	0.553	1	0.51	0.937
δ34S	0.558	0.51	1	0.914

*all correlations were significant (on-tailed test p<0.000)

In order to reconstruct maternal dietary practices and children feeding strategies, stable isotope ratios were analyzed and interpreted at the individual level (cf supra intra-individual multisampling strategies) and at the population level. In order to describe, at a population level, the stable isotope fluctuations over childhood, δ^{13}C, δ^{15}N, and δ^{34}S values of bone and teeth tissues formed during different period of childhood were longitudinally smoothed using a loess statistical procedure, and loess curves were further superimposed to the bivariate graphs of age at tissues formation and stable isotope values (cf Appendix A.III.12 – A.III.18 pp. 390-397). The loess procedure (locally estimated scatterplot smoothing) is a non-parametric regression method that combines multiple regression models in a k-nearest-neighbor-based meta-model by fitting simple models to localized subset of the data in order to build a function that describes the deterministic part of the variation, point by point. Defined smoothing parameter – or bandwidth (the fraction of the number of data points used in each local fit, i.e. how much of the data is used to fit each local polynomial) – and the degree of the polynomial (degree 1 or 2), have been empirically defined according to the sample size and temporal distribution of the different groups compared (e.g, the stable isotope values of perinatally-formed bone collagen have a time-span in gestational weeks while the values of teeth segments are formed over years but distributed quite evenly in our samples; greater sample size for δ^{15}N and δ^{13}C than δ^{34}S). Bandwidths ranging between 0.7 – 0.85 and a 2nd degree polynomial were applied to the δ^{13}C and δ^{15}N values of perinatally formed bone and for children teeth (n ranging between 14-22). A bandwidth of 0.75 and a 1st degree polynomial has been applied to the δ^{13}C and δ^{15}N values of children bone (n ranging between 10-12 individuals). Finally, a bandwidth ranging between 0.9 and 1 and a 1st degree polynomial has been applied to δ^{34}S values (n ranging between 5-12). For some analyses (cf Appendix A.III.15-18), the stable isotope fluctuations for the different elements were compared on the same scale by standardizing stable isotope values into Z-scores. The resulting loess curves were discussed, considering sample size and temporal distribution, in the light of intra-individual stable isotope fluctuations.

4. Dietary strategies over the Mesolithic-Neolithic Transformations, tasting the difference.

- Adult bone collagen stable isotope signatures, protein routing -

4.1. A note concerning animal stable isotope variability

Animals' stable isotope values are presented in appendix A.I, B.IV-V. The new $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values broadly confirm the general reconstruction of the local food-web previously performed by Grupe et al. (2003) and Nehlich et al. (2009) and additionally evidence particular inter-specific, inter-site and diachronic variations which should be further taken into consideration when analysing human stable isotope signatures.

Carbon and Nitrogen isotope variability: the local food-web

As expected, fish display higher $\delta^{13}C$ and $\delta^{15}N$ values than terrestrial herbivores; terrestrial herbivores range on average lower in $\delta^{13}C$ and $\delta^{15}N$ than terrestrial omnivores, displaying themselves lower values that terrestrial carnivores (Figure 23; Figure 24).

Amongst fish, the main difference for the isotopes of carbon and nitrogen relates to their migratory behaviour: the averages $\delta^{13}C$ and $\delta^{15}N$ values of anadromous-potamodromous fish ($\delta^{13}C$=-19.1±1.3‰ and $\delta^{15}N$=9.3±1.2‰; n=7[53]) are higher than the average values of the broad group of "freshwater species" ($\delta^{13}C$=-22.3±2.5‰ and $\delta^{15}N$=8±1.5‰ n=11; Figure 23; Appendix A.1.11). Beluga sturgeons (Huso huso) exhibit the highest $\delta^{13}C$ and $\delta^{15}N$ values, which should be related both to its migratory and dietary behaviours (anadromous and piscivorous). We pooled in a large group of "freshwater fish" specimens of common carps (Cyprinus carpio), fish identified as cyprinids (Cyprinidae), and one wels catfish (Siluris glanis) discovered at Lepenski Vir (Figure 23; Figure 24; Figure 26). The analyzed specimen of piscivorous wels catfish (Siluris glanis) exhibits the highest $\delta^{15}N$ values. Grupe et al. (2003) noticed a wide $\delta^{13}C$ variability of carps of fish from the Mesolithic assemblage of Vlasac (Cyrpinus carpio) and explained this wide range of $\delta^{13}C$ values by the omnivorous-detritivorous dietary behaviors of these fish and by the fact that they tend to become increasingly carnivores while growing in size (n=3[54], ranging between -23.3‰ and -20.3‰ concerning $\delta^{13}C$; ranging between 6.4‰ and 7.9‰ concerning $\delta^{15}N$). Two "cyprinidae" discovered at Vlasac analyzed by Nehlich et al. (2009) range in the high part of this $\delta^{13}C$ variability ($\delta^{13}C$=-19.8 – -20.1‰ and $\delta^{15}N$=6.8-7.4‰). Our results concerning common carps[55] from the Mesolithic-Neolithic context of Lepenski Vir and Padina suggest yet significantly lower $\delta^{13}C$ values and slightly higher $\delta^{15}N$ values than these studies (n=5, average $\delta^{13}C$: -24.1±2.4‰ ranging between -26.9‰ and -21.9‰; average $\delta^{15}N$: 7±0.6‰ ranging between 6.4‰ and 7.9‰). Interestingly, Živaljević and her colleagues (Živaljević 2017; Živaljević et al. 2017), recently produced both morphological and aDNA evidence for the presence of an anadromous species – vyrezub (*Rutilusfrisii*) – from the same cyprinidae family as the common carp, previously unidentified in these samples (cyrpinids being either identified as Cyprinus carpio or grouped as "cyprinidae" by Bökönyi 1972; 1978; Clason 1980). Nowadays, vyrezub inhabits large brackish estuaries of the Black, the Azov and the Caspian Sea and often migrates to rivers in autumn and in spring. Živaljević (2017) identified the remains of this fish in important proportion in the Mesolithic layers of Vlasac and the Transformational layers of Lepenski Vir. Therefore, it is possible that the aforementioned $\delta^{13}C$ variability of the cyprinids, and specifically the higher values of some specimen discovered in the Mesolithic layers of Vlasac analyzed by Nehlich (2009), could be due to their long-distance migratory behavior.

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[53] Average and standard deviation values

[54] Only fish specimens from Vlasac which respect the criteria for collagen preservation were included in this thesis

[55] These fish were identified as common carp by our colleague I. Živaljević during her recent reassessment of the ichtyoarchaeological sample from these sites of the Upper Gorges (Živaljević 2017)

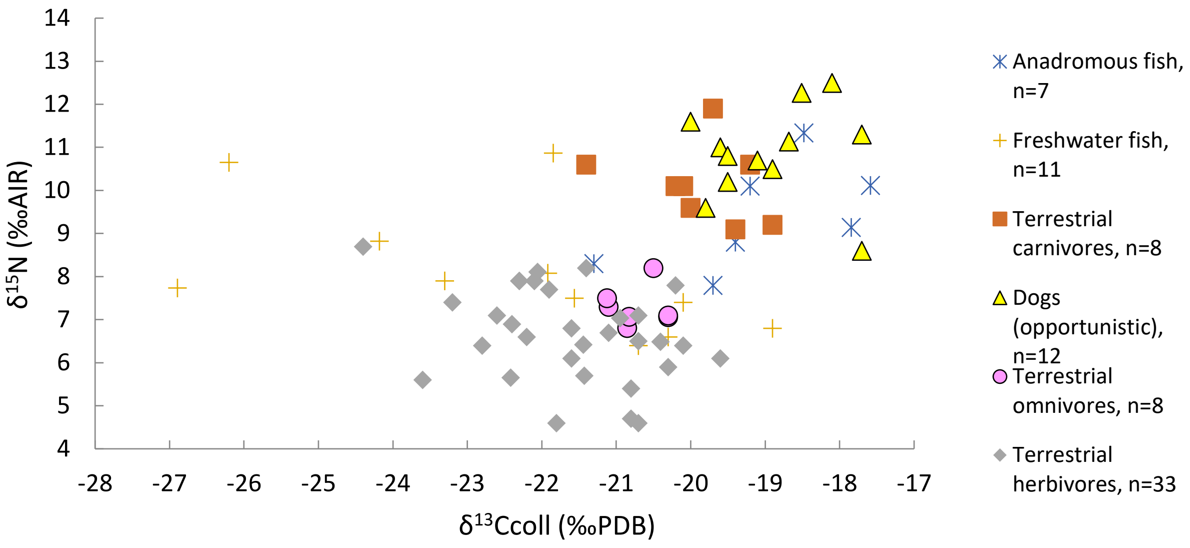

Figure 23: Bivariate plot of δ13C and δ15N for different groups of animals from prehistoric sites of the Gorges

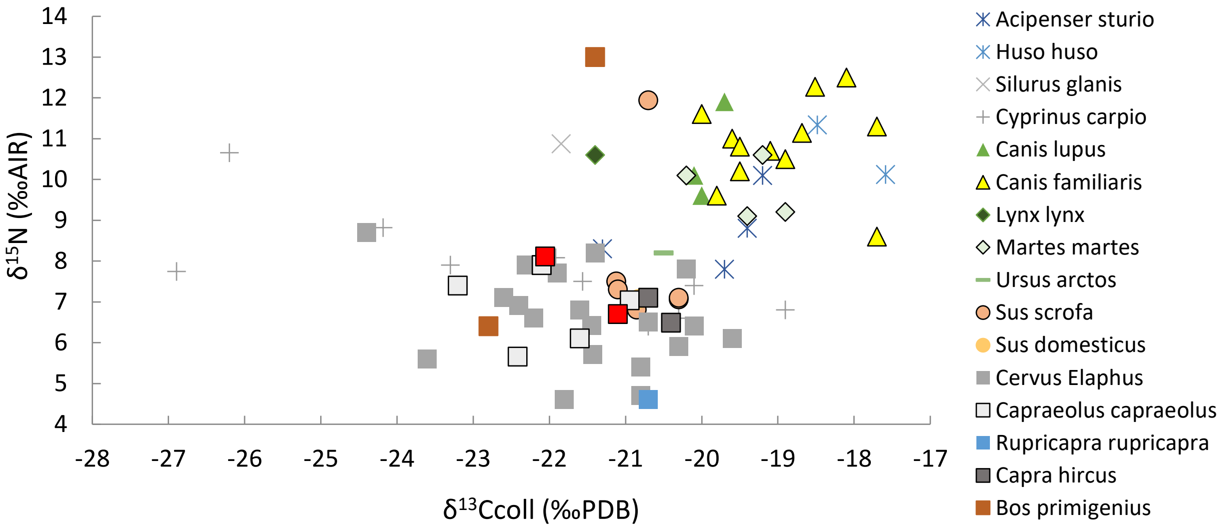

Figure 24: Bivariate plot of δ13C and δ15N for different animal species from prehistoric sites of the Gorges

Concerning terrestrial herbivores, red deer (Cervus elaphus), the most represented specimen in our sample and in the faunal assemblages of the Gorges, exhibits the broadest carbon and nitrogen variability (δ^{13}C=-21.6±1‰ and δ^{15}N=6.6±1‰; n=20; Figure 24). Neolithic domesticated herbivores (Bos domesticus and Rupricapra rupricapra) range in the high part of the δ^{15}N variability of their wild counterparts, which might either be due to the fodders that they consumed, and/or to a kind of "byre" effect, similar to soil manuring (domesticates perhaps stayed closer to their faeces and urines, enriched in δ^{15}N, than wild animals; Appendix A.I.14). It can be noticed that one specimen of wild boar and one specimen of aurochs displays higher δ^{15}N values than the others, likely a suckling signal (individual described as a “juvenilis” boar by Grupe et al. 2003 and “young” aurochs by Nehlich et al. 2009). The analyzed specimen of brown bear (Ursus arcto) also exhibits slightly higher δ^{13}C and δ^{15}N than the other omnivores included in this sample (Sus scrofa) which can be related to the fact that this species may include greater proportions of animal meat in their diet, and particularly may feed on aquatic resources. Only the sample of herbivores was of sufficient size to examine stable isotope values according to radiocarbon dates[56]. One can notice that a few specimens, mostly red deer from the assemblage of Lepenski Vir dated between 6200-5950 cal BC display slightly elevated δ^{15}N values (>7.9‰, n=9) and lower δ^{13}C values (>-21.9 ‰, n=9; Additional figure A.I.A and A.I.B). Although this tendency could be due to the different origin of these specimen (e.g. brought from more distant hunting expeditions?) or to the colder climatic conditions (end of the 8.2 event; physiological effect?), it could also be related to a simple effect of the sample size and to the differential preservation of the collagen[57]. Apart from this tendency, the comparison of faunal values per broad archaeological periods did not reveal significant differences (the variations between analyzed freshwater fish – cyrpinids – discovered in Mesolithic contexts and in Neolithic contexts being possibly related to species differences as previously mentioned; Appendix A.I.9).

Most of the remains of animals included in this study originate from three sites of the Upper Gorges - Padina, Vlasac and Lepenski Vir. The stable isotope values for the remains of seven animals discovered at Schela Cladovei analyzed by Bonsall et al. (2008) were not included in presented graphs because they were only identified as "ungulates" and may thus belong either to species of omnivores or of herbivores (δ^{13}C=-21±0.5‰ and δ^{15}N=6±1.9‰; data presented in App. B.IV-V). They range within the δ^{15}N and δ^{13}C variability of the ungulates discovered in the Upper Gorges, rather close to the δ^{13}C values of analyzed specimens of wild boar (taxon over-represented at Schela Cladovei in comparison with the other sites of the Inner Gorges, Batosciewicz et al. 1995, 2001). Subtle stable isotope differences can be observed amongst the animals discovered at different sites of the Upper Gorges (Appendix A.I. 16-22). The terrestrial herbivores discovered at Lepenski Vir (n=25; Mesolithic-Neolithic) display higher δ^{13}C values than the terrestrial herbivores discovered at Padina (n=4; Mostly Mesolithic), and the terrestrial herbivores discovered at Vlasac (n=11; Mesolithic) range in between (Appendix A.I. 20). However, to relate the δ^{13}C variation to the place where the animal remains were found – only distant a dozen of km within the Gorges – may appear counter-intuitive. These intra-site patterns of stable isotope variation do not seem to be affected by the chronological period considered[58]. One cannot disregard the possibility that these differences could be due to collagen preservation since only 16/36 analyzed specimens displayed well-preserved collagen[59]; despite the smaller sample size, well-preserved individuals from Padina and Lepenski Vir display an average δ^{13}C difference (Lepenski Vir =-21.4±0.7‰, n=6; Vlasac and Padina= -22.1±0.9‰n=10). The possibility that some local diagenetic processes may have influenced stable isotope values, even when the extracted collagen ranges within the advised molecular weight, has been demonstrated by some experimental research (e.g. Grupe et al. 2006); particularly, it has been shown that selective biogenetic collagen break-down by soil microorganisms may result in shift in δ^{13}C towards lighter values and an overall enrichment of δ^{15}N in the range of a trophic level effect (ibidem). Apart from these methodological considerations, these slight differences could also result from the differential origin of hunted animals (differences in hunting strategies amongst humans occupying the different sites over the Mesolithic-Neolithic periods).

Concerning terrestrial carnivores, it has been previously noticed that the analyzed specimen of lynx exhibits much lower δ^{13}C values than the other carnivores, either because this animal preferred densely wooded areas (as suggested by Grupe et al. 2003) and/or because its territory may cover very broad areas (Figure 23). Dogs, the only Mesolithic domesticated species, display slightly

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[56] Since a statistically significant difference (Mann Whitney for p <0,05) has been noticed concerning the δ^{13}C values of individuals discovered in the Late Mesolithic context of Vlasac with available criteria for collagen preservation (cf part 3.3.2) and with the individuals for whom these criteria were not available, the latter were removed from the analyses. Given the smaller size of the remaining sample, amongst faunal remains, only the values of herbivores could be examined according to their radiocarbon values (additional figure A.I.A.-B).

[57] Upon these 24 specimens with associated radiocarbon dates originating from the faunal assemblages of Padina and Lepenski Vir, the criteria for collagen preservation were only available for 6 individuals. Indeed, since a statistically significant difference (Mann Whitney for p <0,05) between individuals with well-preserved collagen and individuals for whom the criteria for collagen preservation were not available has only been noticed concerning the Late Mesolithic site of Vlasac, it has been decided to include in this study the individuals for whom these criteria were not available from all the other contexts in a concern of sample representativeness (cf part 3.3.2).

[58] Indeed, the tendency for higher δ^{15}N values and lower δ^{13}C values noticed amongst herbivores radiocarbon dated to the period of Transformations in comparison with those dated to the Early-Middle Mesolithic mostly concern Mesolithic-Neolithic individuals discovered at Lepenski Vir (n=21, versus 3 from the assemblage of Padina (Appendix additional figure A.I.A.-B).

[59] Cf footnote supra

elevated $\delta^{13}C$ and $\delta^{15}N$ ratios ($\delta^{13}C$=-19±0.8‰ and $\delta^{15}N$=10.8±1‰, n=12) in comparison with all other terrestrial carnivores, notably with wolves ($\delta^{13}C$=-20±0.8‰ and $\delta^{15}N$=10.2±0.9‰, n=8; Appendix A.I.14; Figure 24). It can be explained by the fact that dogs have an opportunistic dietary behavior and should have consumed human food leftovers, notably fish remains (Grupe et al. 2003).Interestingly, while dogs exhibit on average higher $\delta^{13}C$ than the wolves, the pine martes ranges in between, which may be explained by the scavenging behavior of this small carnivore, also probably living close to human settlements (Figure 24). Dogs' stable isotope values reflect a different spatial pattern of variation: the dogs discovered at Padina (n=3; Late Mesolithic) range higher than the dogs discovered at Lepenski Vir on the $\delta^{13}C$ axis (n=2; Early Mesolithic and Transformational contexts) and the canidae from Vlasac display the lowest $\delta^{13}C$ values (n=7; Mesolithic context; Appendix A.I.19).It can be mentioned that the criteria for collagen preservation were not available for the dogs discovered at Padina which display the highest $\delta^{13}C$ values (analyzed by Whittle et al. 2002; average=-17.9±0.85‰ n=3); yet the specimens from Lepenski Vir (analyzed in this study; average=-18.6±0.1‰, n=2) and from Vlasac (analyzed by Grupe et al. 2003; average=-19.8±0.8‰, n=7) fulfilled the required criteria for collagen preservation. Hence, one plausible explanation for the intra-site variations would rely in the differential feeding practices and, in case dogs feed on human leftovers, to differences in the subsistence strategies of human who occupied these sites (cf part 4.2.3).

Sulfur, discriminant between marine and terrestrial-freshwater ecosystems

The new $\delta^{34}S$ results jointly obtained on animal collagen discriminate three groups, reflecting the differences previously noticed in faunal $\delta^{13}C$ values: (1) terrestrial omnivores and herbivores with low $\delta^{34}S$ values (4.5±1.3‰, n=14), (2) the broad group of freshwater fish with $\delta^{34}S$ values widely ranging from very low to high (6.3±7‰, n=6), and finally (3) anadromous and potamodromous fish which display high $\delta^{34}S$ values (14.6±1.3‰, n=3) as well as the two analyzed dogs, which display even higher values (15 and 15.6‰; Figure 25; Figure 26; Appendix A.I.4 ; Appendix A.II.8). These differences are well-reflected by the two first axis of the principal component analysis (Figure 27).

The similarly high $\delta^{34}S$ values of analyzed specimens of sturgeons (n=1) and of huchen (n=2), which contrasts with the broad variability encompassed by the other fish, may be specifically related to their migratory behaviour and to the fact that these fish spent an important part of their lives either in the environment of the Black Sea or in marine-influenced waters from the Danube estuary (anadromous/potamodromous fish: $\delta^{34}S$ average=14,6±1,3‰ n=3; $\delta^{15}N$ average=9±1‰ n=5; $\delta^{13}C$ average=-19,4±1,3‰ n=5). This result is consistent with the general observation of elevated $\delta^{34}S$ values amongst marine ecosystems (Nehlich 2015)[60]. Contrastingly, the specimens pooled as "freshwater fish" encompassed a broad range of $\delta^{34}S$, which overlaps both terrestrial herbivores and anadromous/potamodromous species variabilities and echoes their broad $\delta^{13}C$ variability (Figure 24; Figure 26; Figure 27; Appendix A.I.1-6; 16-18). Two specimens of wels catfish, exhibit low $\delta^{34}S$ values ($\delta^{34}S$ average=3,7±2,5‰ n=2; $\delta^{15}N$=10,9‰ n=1; $\delta^{13}C$=-21,8‰ n=1; Figure 26). Cyprinids samples displays the broadest $\delta^{34}S$ variability ($\delta^{34}S$ average=7,2±7,3‰ n=5; $\delta^{15}N$ average=7,8±1,2‰ n=10; $\delta^{13}C$ average=-22,4±1,7‰ n=10). Amongst cyprinids, three specimens for which we present new $\delta^{34}S$ values have been discovered in Mesolithic and Neolithic contexts at Padina and were estimated as "common carps" by the ichtyioarchaeologist working on the sample (Živaljević 2017); they range in the lower part of cyprinids variability concerning the isotopes of the sulfur and carbon elements ($\delta^{34}S$ =2,8±5,6‰; $\delta^{15}N$ average=9±1,5‰; $\delta^{13}C$=-26±1,5‰). In contrast, two specimens of "cyprinidae" derived from the Mesolithic assemblage of Vlasac and were

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[60] When grouped per dietary behaviors - Appendix A. I. 6 - carnivores and piscivores fish appear lower in $\delta^{34}S$ than the fish which are more insectivores and benthivores. However, this tendency can be simply due to the fact that the $\delta^{34}S$ values of two fish considered as carnivores-piscivores originate from a freshwater catfish while the $\delta^{34}S$ values of the fish considered as benthivores-insectivores originate anadromous sturgeons and on the potamadromous huchen. Given that only a small trophic effect has been related to the isotopes of the Sulphur element (Nehlich 2015; Webb et al. 2017b) and that much larger $\delta^{34}S$ differences have been observed between terrestrial and marine ecosystems (ibid.), the wide variability noticed in the prehistoric fish from the Danube should rather be related to their migratory than dietary behaviours.

identified by Nehlich et al. (2009); they display both higher δ^{34}S and δ^{13}C values than the carps from Padina (δ^{34}S =14±0‰; δ^{15}N average=7,1±0,5‰; δ^{13}C=-19,5±0,9‰; Appendix A.I.16-19).

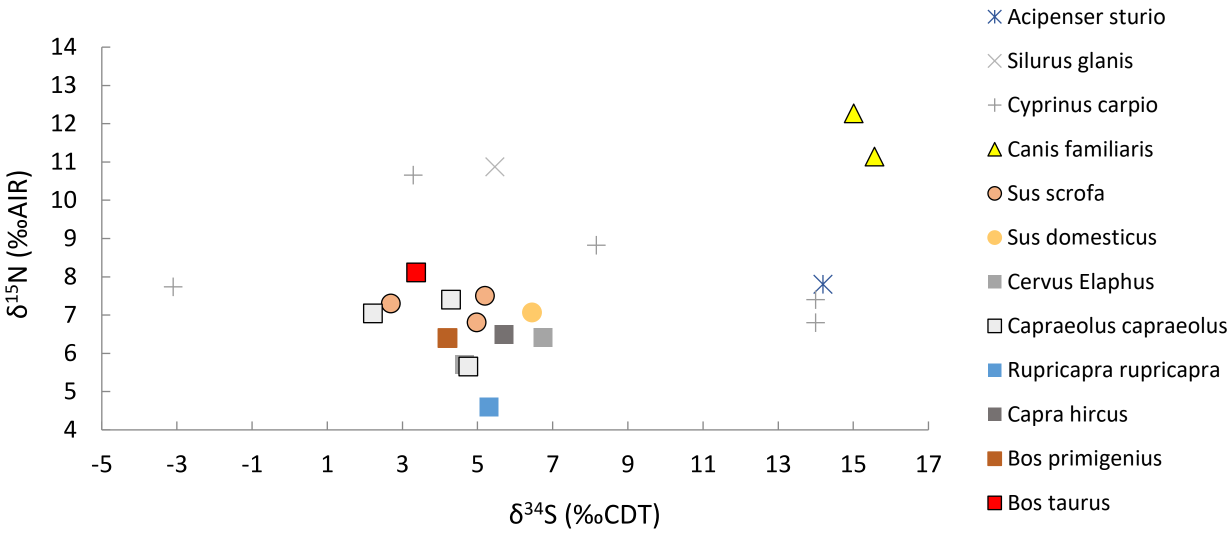

Figure 25: Bivariate plot of δ^{34}S and δ^{15}N for different animal species from the prehistoric sites of the Gorges

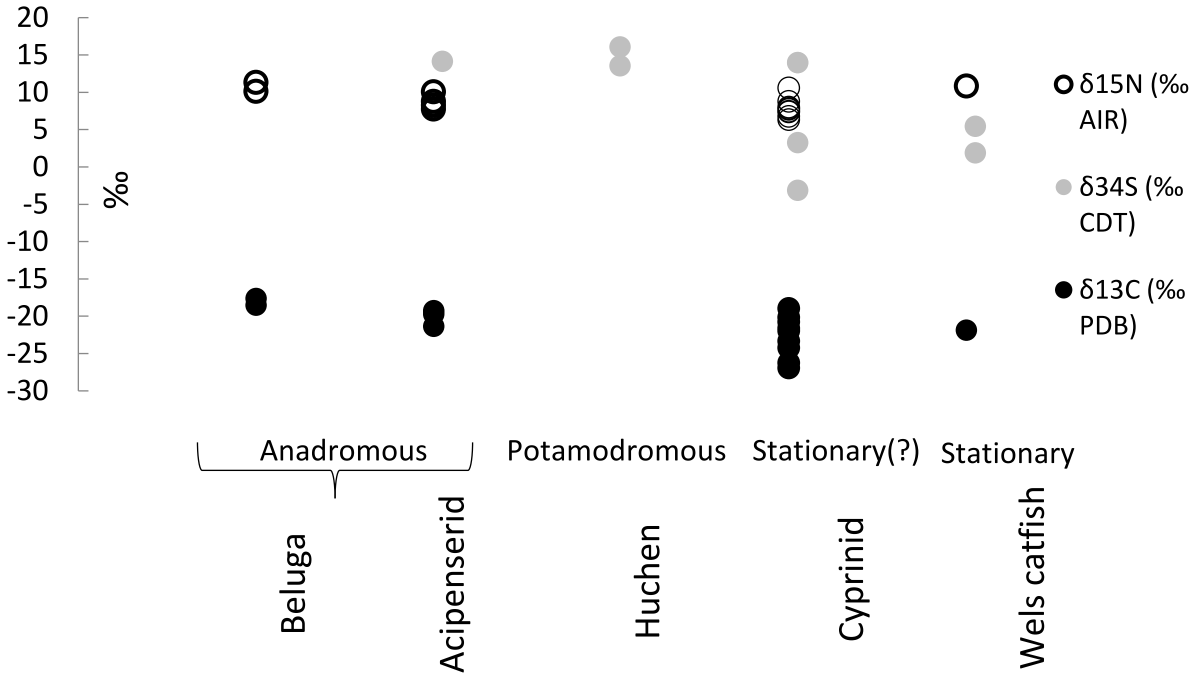

Figure 26: δ^{13}C, δ^{15}N, δ^{34}S for different fish species grouped according to their migratory behavior

Considering that only fish identified as "anadromous and/or patamadromous" as well as "cyprinidae" exhibit high δ^{34}S values (>13.5‰) while the stationary freshwater common caps and wels catfish, the terrestrial herbivores and omnivores display significantly lower values (<8.5‰), it is likely that δ^{34}S can be used as a good marker of the consumption of long distance migrating fish. Dogs range very close to the anadromous fish for δ^{13}C and δ^{34}S, which indicate that they were likely consuming substantial amounts of long-distance migratory fish (Figure 24; Figure 25; Figure 27; Figure 28; Figure 29; Appendix A.IV.2). Such elevated δ^{34}S values for dogs have already been observed at several Neolithic sites in Denmark (Norsminde and Bjornsholm) and were interpreted as an evidence that the dogs feed in large proportions on marine mammals (Craig et al. 2006).

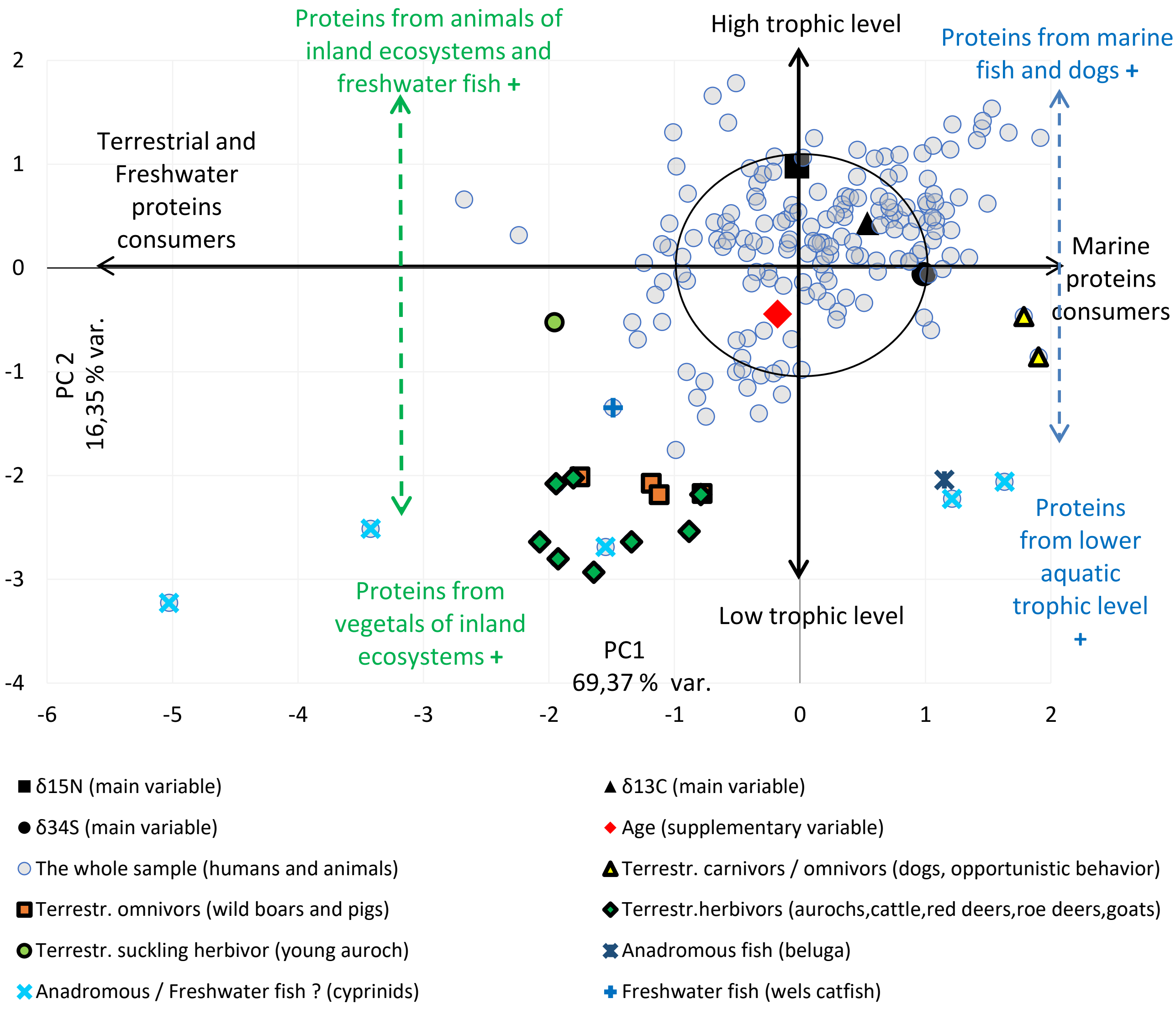

Figure 27: Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals (δ^{13}Ccoll, δ^{15}N, δ^{34}S) extracted from the collagen of prehistoric humans and animals from the Danube Gorges area (whole sample). The variables participating to the PCA are plotted, as well as individual scores for the whole sample; of prehistoric humans and animals from the Danube Gorges area (whole sample). The variables participating to the PCA are plotted, as well as individual scores for the whole sample; individual scores for different groups of animals are here highlighted.

4.2. The Mesolithic subsistence: red deer hunters, fishermen and dogs' breeders

Adult humans' stable isotopes values are presented in Appendix A.II, B.I-II. Early Mesolithic adult human isotopic ratios range from -21.5 ‰ to -18.7‰ (Δ=-19.8‰; n=28) for carbon, 12.1‰ to 16‰ (Δ=14.4‰; n=28) for nitrogen and 4.1‰ to 10.9‰ (Δ=6.6‰; n=23) for sulfur while late Mesolithic adults human isotopic ratios range from -20.4‰ to -17.5‰ (Δ=-19.5‰; n=43) for carbon, 11‰ to 16.5‰ (Δ=14.7‰; n=43) for nitrogen and 4.2‰ to 13.6‰ (Δ=10.9‰; n=18) for sulfur (Appendix A. II).

4.2.1. Temporal trends (1) - the δ^{13}C and δ^{15}N evidence, on the importance of fish in the Mesolithic subsistence

4.2.1.1. Aquatic food resources

As extensively discussed by scholars, Mesolithic human δ^{15}N signal is particularly high in the Danube Gorges, indicative of the consumption of high trophic level resources by local foragers (e.g. Bonsall et al. 1997; Grupe et al. 2003; Bonsall et al. 2002; Borić et al. 2004; Bonsall et al. 2004; Figure 24; Appendix A.I.3; Figure 28). Given the location of the sites along the riverbanks, these elevated δ^{15}N values have been related to the consumption of aquatic resources. Fish bones were indeed over-represented amongst archaeozoological assemblages: 30% of vertebrate identified specimens in the assemblage of Lepenski Vir (Bökönyi 1969, 1972), 43% at Schela Cladovei (Bartosiewicz et al. 2001), and 60% at Vlasac (Bökönyi, 1978) and at Padina (Clason, 1980). This ichtyoarchaeological record suggests that fishermen exploited a wide range of species: **stationary freshwater fish** - carp *Cyprinus carpio* and many other representatives of the Cyprinidae family, Wels catfish *Siluru sglanis*, pike *Esoxlucius*, pikepearch *Sander lucio perca* - but also the **potamodromous huchen** *Hucho hucho*, as well as **anadromous sturgeons** - beluga *Huso huso*, Russian sturgeon *Acipenser gueldenstaedtii*, ship sturgeon *Acipenser nudiventris*, stellate sturgeon *Acipenser stellatus* - which were migrating from the Black Sea each year to spawn in the Danube (Clason 1980; Bartosiewicz et al. 1995; 2001; 2008; Dinu 2010; Živaljević 2017; Živaljević et al. 2017).

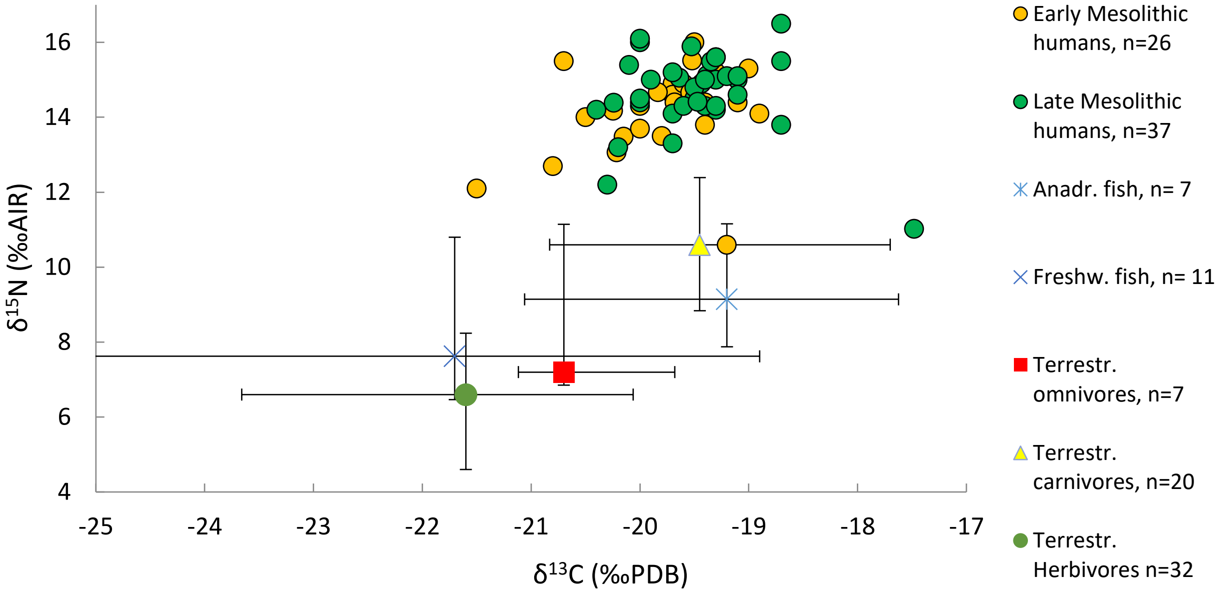

Figure 28: Bivariate plot of δ^{13}C and δ^{15}N for Mesolithic adult humans (>15 yrs) and animals from sites of the Danube Gorges. Bars represent the 97.5/2.5 percentiles.

The δ^{15}N and δ^{13}C values obtained for different species of fish and their comparison with prehistoric human stable isotope values confirm that fish were substantially included in the diet (Figure 24; Figure 28; Appendix A.I.3; 5-6; A.II.3). The fact that Mesolithic humans broadly range in between the δ^{13}C variability of stationary freshwater fish and of anadromous/potamodromous species, suggest that they consumed a broad range of aquatic species. As mentioned by Fischer et al. (2008), regarding the carbon element, a combination of marine and freshwater fish would indeed effectively cancel each other's stable isotope values. It has also been shown, on lab-controlled experiments comparing pigs fed with terrestrial and marine diet, that greater proportions of marine resources in the diet should result in greater δ^{13}C offsets between the tissues of the consumer and the whole diet (Webb et al. 2017a) and that at least 25% of marine-derived proteins in the diet is necessarily for a significant δ^{15}N difference between the values of those who consumed higher proportions of marine resources and the values of those who consumed less marine resources (Webb et al. 2016). Apart from fish flesh, the roe of anadromous fish ("caviar") - which migrates seasonally to spawn upstream - could have also provided a significant amount of nutrients for the local prehistoric fishermen. Related to the riverine ecosystem, the waterfowl species that fed on the fish may also have contributed to elevate the human signature in δ^{15}N; yet, the remains of wildfowl birds have been scarcely recorded on the site of the Gorges (e.g. Bökönyi 1972; 1978). Finally, freshwater mussels (*Unio* species[61]) have been identified to a various extent in faunal assemblages, sometimes with shell breakage patterns indicative of their consumption (Pickard et al. 2017; Živaljević et al. 2017); however, these shellfish could have quite low δ^{15}N values due to their lower trophic position (e.g. Graniero et al. 2016) and may not have participated to the elevated human biochemical signal.

A significant enrichment in δ^{15}N and δ^{13}C values of human bone collagen between the Early and Late Mesolithic has been previously noticed by scholars (Cook et al. 2009). However, after removing the Late Mesolithic individuals from Vlasac whose collagen preservation criteria were not available (cf part 3.3.2), it seems that this Late Mesolithic stable isotope enrichment should be nuanced (Figure 28; Appendix A.II.3; 7; 9). Indeed, the difference between the Late Mesolithic individuals with well-preserved collagen and those without collagen quality criteria was significant on the carbon axis, the Late Mesolithic individuals from Vlasac without quality criteria exhibiting significantly higher δ^{13}C values. Yet, this Early to Late Mesolithic enrichment remains significant for δ^{15}N ratio (Mann Withney test, $p<0,05$) and close to be significant for δ^{13}C (Mann Whitney test, $p=0,057$[62]). When crossed with radiocarbon dates, the results reflect this slight elevation in δ^{15}N ratio for some individuals dated after 7400 cal BC (but not concerning δ^{13}C values; Figure 30; Figure 31). We previously mentioned slightly elevated δ^{15}N values for some herbivores dated to the period of Transformations-Early Neolithic in comparison with the Early-Middle Neolithic, which suggests that the slight enrichment noticed for some humans might be related to changes in the values of consumed faunal remains. However, it can also be noticed that these elevated δ^{15}N values are associated with

Late Mesolithic individuals discovered in the Lower Gorges – Downstream Area at Schela Cladovei and Hajdučka Vodenica, while the two individuals discovered at Padina range within the same values as the Early Mesolithic individuals discovered at this site. Hence the higher stable isotopes values of Late Mesolithic humans might rather be related to inter-site differences than to an actual change in subsistence patterns.

4.2.1.2. The consumption of red deer, wild boars and dogs

Apart from aquatic resources, the stable isotopes values of Mesolithic individuals may also be influenced by the consumption of higher trophic level terrestrial resources, such as terrestrial omnivores and carnivores. Besides, although the frequent inclusion of higher trophic level resources in the diet should have particularly influenced the δ^{15}N values of the local Mesolithic foragers, their δ^{13}C signal is also compatible with the consumption of herbivores' meat (Figure 24; Figure 28; Appendix A.I.3; 7; 12). Indeed, the remains of red deer are also over-represented in the osteo-archaeological assemblages of most sites in the Danube Gorges, deer being the first terrestrial mammal found in terms of vertebrate identified specimens at Lepenski Vir (34%,Bökönyi 1969, 1972), Padina (28%; Clason 1980), and Vlasac (22%; Bökönyi 1972 and 1978). Wild boar is the

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[61] Because animal bones were mostly hand collected during the 60's to 80's campaigns of excavations in the Danube Gorges and since the primary focus of the first archaeozoological publication was dedicated to mammals and fish remains (e.g. Bökönyi 1972; 1978; Clason 1980), it is possible that freshwater mollusks were neglected. In recent reassessments of the archaeozoological assemblages from the Late Mesolithic sites of Kula and Schela Cladovei located on the Downstream Area, a significant number of mollusks belonging to*unio* species were found with specific shell breakage patterns, suggesting their consumption (Pickard et al. 2017; Živaljević et al. 2017).

[62] four Early Mesolithic individuals clearly exhibit lower δ^{13}C values while four Late Mesolithic individuals clearly exhibit higher δ^{13}C values than the common distribution of both groups.

second most represented taxon of ungulates at most sites, and the first at Icoana in the Lower Gorge; its consumption should have contributed to the elevated δ^{15}N values (Bökönyi 1972; 1978; Clason 1980; Dimitrijević 2000; 2008).

The remains of dogs' – the only Mesolithic animal species locally domesticated (Dimitrijević and Vuković, 2013) – have also been frequently found at most sites of the Gorges, and even represent the second most frequent terrestrial taxon identified at the assemblage of Vlasac (beyond wild boars; Bökönyi 1978). Dogs elevated δ^{13}C and δ^{15}N values, notably in comparison with wolves, suggests that they should have been consuming human leftovers, including aquatic resources (Grupe et al. 2003; Figure 24; Figure 28). It has been suggested that dog remains could be used as a proxy for the study of human diet in archaeological contexts, in cases human remains have not been found or could not be sampled (e.g. Noe-Nygaard, 1988; Clutton-Brock and Noe-Nygaard 1990; Eriksson and Zagorska, 2003; Guiry, 2012; Guiry and Grimes, 2013; Guiry, 2013; Goude and Fontugne 2016). For instance, it has been widely discussed whether the contrasting δ^{13}C and δ^{15}N values of canidae from two Mesolithic sites in England (Star Carr and Seamer Carr) could be related to their differing terrestrial / marine diet, hence reflective of the differential patterns of mobility of their "owners" or should rather be associated with environmental differences (Clutton-Brock and Noe-Nygaard 1990; Day 1996; Schulting and Richards 2002; Dark 2003; Schulting and Richards 2009). Yet, the observation of lower dogs' position in the food web (Goude 2007; Herrscher and Le Bras-Goude 2010), or of their broader variability in comparison with the values of associated humans (Eriksson and Zagorska, 2003), suggests that the extent to which dogs can be viewed as reliable proxies of human diets likely depends on archaeological contexts. In the Gorges, contextual data suggest that dogs may have also been consumed by the foragers: their remains were often found disarticulated and fragmented like red deer and wild boars, their long bones and skulls exhibiting similar breakage patterns as wild game species (Bökönyi 1975; Clason 1980; Dimitrijević 2008); carnivorous gnawing marks have also been found on some dogs bones, suggesting that the remains of canidae consumed by human were eventually left to other dogs (Dimitrijević 2008). The consumption of canidae, ethnographically well-documented (e.g. Milliet 1995; Diamonds 1997; Morey 2010), has also been demonstrated on numerous archaeological contexts including European Epipaleolithic, Mesolithic and Neolithic sites (e.g. Wing 1978; Snyder 1991; Benecke 1987; Schwartz 1997; Morey 2006, 2010 ; Horard-Herbin et al. 2014). Dogs, fed of meals that included fish and the meat of other dogs, could have also contributed to a certain extent to the elevated δ^{15}N and δ^{13}C values of some Late Mesolithic individuals buried in the Lower Gorges.

4.2.1.3. ... and plants?

The picture of the diet drawn by the analysis of bone collagen stable isotope ratios should always be considered as biased toward an over-representation of meat compared to plants. Indeed, meat is richer in proteins easily metabolized by the human digestive tract than plants and stable isotope ratios analyzed in the protein of collagen mostly reflects the protein part of the diet (rather than equally proteins, fats and carbohydrates; Ambrose and Norr 1993). Apart from anadromous fish, dog, red deer and wild boar, the Mesolithic foragers of the Danube Gorges surely included various sort of plant in their meals. There is yet no evidence of extensive plant storage in the Danube Gorges, plant remains being only scarcely documented, due to preservation and collection biases (cf part 2.3.1; Filipović et al. 2010; Borić et al. 2014). The analysis of starch grains found trapped in foragers' dental calculus has recently provided additional information about some of the plants that were locally consumed, although a part of these botanic remains may also derived from plants used for non-dietary purposes[63](Filipović et al. 2015, Cristiani et al. 2016, Jovanović 2017, Filipović et al. 2017). Discovered grains have been related to various species of herbaceous plants, including the family of Triticeae, to which belong einkorn, emmer and barley, the Near Eastern and European Early Neolithic species of domestic crops (Cristiani et al. 2016). The presence of some ground

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[63] such as medicinal (healing plants), sanitary (cleaning the teeth), technical (means of eating) or symbolic purposes.

stones in Late Mesolithic contexts (e.g. Vlasac, Antonović, 2008), which have been used to process plants (fibers? starch grains?), also questions the possibility of a Late Mesolithic change in the (dietary?) use of plant. In the light of stable isotope values, one can only say that human elevated δ^{15}N signal indicates an important consumption of animal proteins; yet, it is most likely that some sort of grasses, green leaf wild vegetables, berries, wild fruits, nuts, tubers and roots, flowers, and mushrooms were also locally consumed, especially considering that the Early Holocene environment of the Gorges provided plenty of edible plant resources (e.g. Filipović et al. 2017).

4.2.2. Temporal trends (2) - the δ^{34}S debate, on the specific role of anadromous fish and dogs in the local diet

While we observed an important overlap between the Early and Late Mesolithic δ^{13}C and δ^{15}N ratios, we can notice an actual shift up in the stable isotope of the sulfur element, almost all Late Mesolithic exhibiting higher δ^{34}S values than the Early Mesolithic[64] (moving from a mean of 6.6‰ to 10.9‰; Figure 29). This shift up likely occurred during the first half the 7th millennium BC (Figure 32). The individual scores in the Principal Component Analyses (PCA) clearly discriminate the Early to Late Mesolithic adults on the first principal component, which is mainly influenced by the variance inδ^{34}S but also secondarily by the variance inδ^{13}C stable isotope ratio (Appendix A.IV.2.; 4).

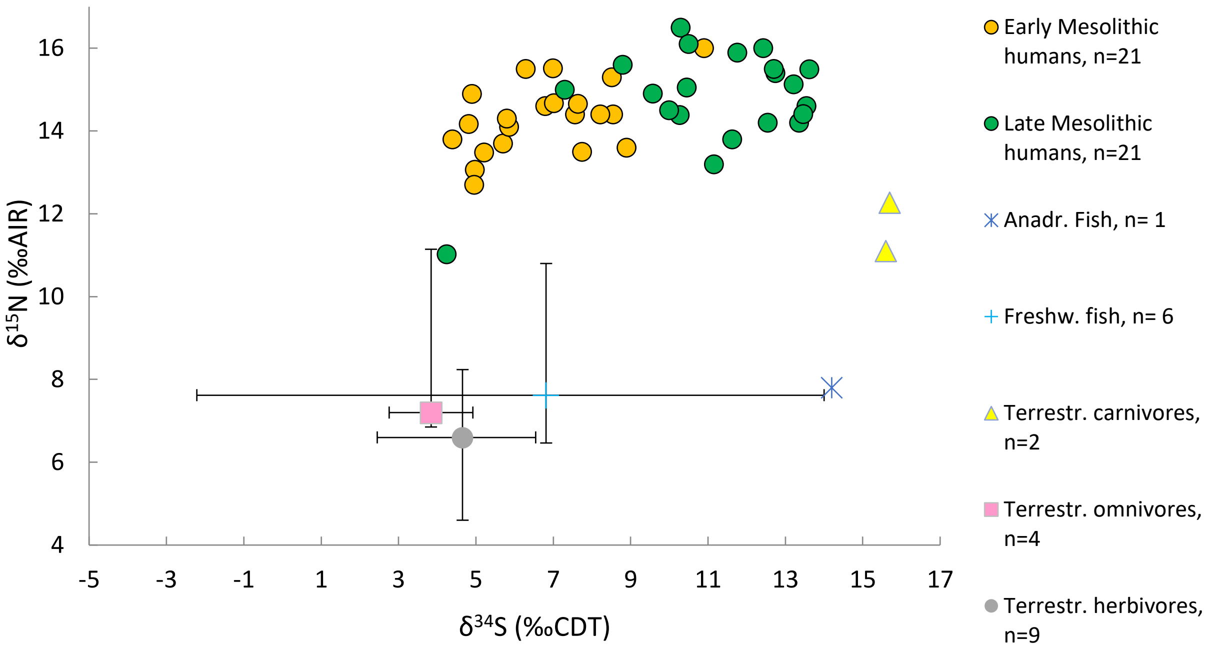

Figure 29: Bivariate plot of δ^{34}S and δ^{15}N for Mesolithic adult humans (>15 yrs) and for animals. Bars represent the 97.5/2.5 percentile

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[64] Only one Early Mesolithic individual - LV 104 - exhibits higher δ^{34}S values (10, 9‰), falling into the Late Mesolithic variability, and two Late Mesolithic individuals - VL 16 and VL 26 - exhibit lower δ^{34}S values (respectively 7,3 and 4,2 ‰), falling into the Early Mesolithic variability (Appendix A.II. 5). Based on the common variance in the isotope of the 3 elements, the individual LV 104 falls in the Late Mesolithic group (δ^{13}C=-19,5‰; δ^{15}N=16‰; δ^{34}S=10,9‰). This teenager was found disarticulated under the floor of the house 43 from Lep. Vir and has not been ^{14}C-dated yet. Therefore, his high δ^{34}S values might simply points to a problem of chronological assignment (Late Mesolithic?). The analysis of the common variance in the stable isotope values of the male VL16 rather ranges him amongst the Early Mesolithic individuals (δ^{13}C=-19,9‰; δ^{15}N=16‰; δ^{34}S=7,3‰). In the monograph of the site of Vlasac (Srejović and Latica, 1978), the authors mentioned "a disarticulated skull" found close to the lower limbs of the individual Vlasac 17 - himself ^{14}C dated to the Early Mesolithic. Given that VL 16 has not been ^{14}C dated, it may rather be assigned to the Early Mesolithic than to the Late Mesolithic. Finally, the male Vlasac 26 has a very different stable isotope signature for the 3 elements (δ^{13}C=-17,5‰; δ^{15}N=11‰ and δ^{34}S=4,2‰), differing from the whole Mesolithic and Neolithic population. His strontium radiogenic signal (0,709558) falls amongst the highest values of the local range; hence, although he has been identified as a local individual, the possibility of his non-local origin cannot be fully disregarded. Alternately, the combination of high δ^{13}C values but low δ^{15}N and δ^{34}S values could also be related to the consumption of C4 plants. If the consumption of C4 plants appears unlikely for the Late Mesolithic period, the individual Vlasac 26 has not been^{14}C dated and it should be recalled that some individuals discovered at the site of Lepenski Vir have been dated to historical periods (Bonsall et al. 2004; Bonsall et al. 2008).

4.2.2.1. The $\delta^{34}S$ debate: inter-site or chronological differences?

The application of $\delta^{34}S$ stable isotope ratio has been validated on archaeological context as a good discriminant between the aquatic and the terrestrial ecosystems - or as a possible marker of mobility - since the $\delta^{34}S$ ratio reveals to be higher in marine environment or in coastal regions than in the hinterland, and given that rivers may encompass different values according to local bedrock geology (Nehlich 2015). Therefore, several factors could explain the Late Mesolithic shift up in $\delta^{34}S$ signatures, including: (1.) environmental factors, whether diachronic changes in the $\delta^{34}S$ values of the local terrestrial ecosystem or in the Danube hydrosphere, affecting thereby the stable isotopes values of the tissues of the anadromous fish further consumed by humans; OR (2.) human behavioral factors, whether an Early to Late Mesolithic shift in the local diet or an important human mobility during the period with a Late Mesolithic local population change. The last hypothesis - human migration - can already be disregarded, given the small number of Mesolithic non-local individuals identified according to the local signal in radiogenic strontium and considering the genetic and phenotypic continuity observed amongst the population.

In the first study of $\delta^{34}S$ stable isotope ratio obtained for 18 prehistoric individuals from the Gorges, Nehlich et al. (2009) already noticed a difference between the Early Mesolithic individuals from Padina and the Late Mesolithic to Neolithic individuals from Vlasac, Hajdučka Vodenica and Lepenski Vir. It has then been discussed whether this difference could reflect some inter-site pattern within the Gorges or should rather be related to a diachronic trend (Nehlich et al. 2009; Bonsall et al., 2015 b and c; Borić and Nehlich 2015). Previous interpretations for this difference in $\delta^{34}S$ values mostly focused on behavioral factors; it has been suggested whether that (A.) aquatic resources played a more important role in the human diet during the Late Mesolithic in Vlasac and during the period of Transformation in Lepenski Vir than during the Early Mesolithic in Padina, where human were rather favoring the consumption of terrestrial resources (Nehlich et al. 2009; Borić and Nehlich 2015); OR that (B.) humans consumed aquatic resources throughout the whole Mesolithic period in all these sites but actually started to favor the consumption of different species of fish from the Late Mesolithic, perhaps in relation with the location of their fishing camp within the Gorges (Bonsall et al. 2015 b and c). The $\delta^{34}S$ values jointly obtained on human and faunal remains in this study shed a new light on this debate.

The new values obtained for the Early Mesolithic individuals from Lepenski Vir and Vlasac and for the Late Mesolithic and Early Neolithic individuals from Padina now show that changes in $\delta^{34}S$ values should rather be related to a generalized increase at the Late Mesolithic rather than to inter-sites differences (Appendix A. II. 2.; 15). Indeed, the $\delta^{34}S$ shift up can be observed between Early Mesolithic, and Late Mesolithic - Transformational individuals buried at Padina, but also between the Early and the Late Mesolithic individuals buried at Vlasac, and between the Early Mesolithic and the Transformational-Neolithic individual buried at Lepenski Vir (Figure 25; Appendix A.I.4; 5; Appendix A.II.8; Appendix A.IV.4.).

4.2.2.2. The $\delta^{34}S$ shift: Late Mesolithic subsistence adaptations?

Based upon the observation of differences in the ratios of terrestrial mammal bones versus fish remains between Late Epipaleolithic - Early Mesolithic faunal assemblages (Cuina Turcului, and Padina I) and later Mesolithic contexts (Vlasac and Schela Cladovei), it has been suggested that fishing might have been increasingly important in the course of the Mesolithic (Borić 2011, data fromNalbant 1970; Bolomey 1973; Bökönyi 1975, 1978; Clason, 1980; Bartosiewicz et al. 1995, 2001). In the light of these archaeozoological results, Borić and Nehlich (2015) have interpreted the combination of low $\delta^{34}S$ and high $\delta^{15}N$ values observed for the analyzed Early Mesolithic human from Padina as the indication of a subsistence rather based on the consumption of terrestrial resources (lower $\delta^{34}S$), but which included higher trophic level resources, such as suckling mammals for instance (higher$\delta^{15}N$); in contrasts Late Mesolithic and Transformational humans from

Hajdučka Vodenica, Vlasac and LepenskiVor may have consumed aquatic resources in a greater extent (higherδ^{15}N and δ^{34}S). However, the bones of immature mammals were not so well represented in the archaeozoological record while one would have expected to find them numerously in the case of an important Early Mesolithic consumption of suckling mammals, especially if we consider that even bones of fish, small rodents and human perinates were preserved despite the fact that the bone assemblages were mostly hand collected (Bonsall et al. 2015)[65]. The fact that our new results associate elevated δ^{34}S values (above 13.5‰) with anadromous and potamodromous fish species (acipenser and beluga sturgeons, and huchen) and low values (below 8.5‰) with stationary freshwater species (carps and catfish) indicates that observed Late Mesolithic shift up in humanδ^{34}S values should be related to the consumption of long distance migratory fish.

It is worth mentioning that sulfur from collagen is only found in the amino acid methionine which is represented in higher quantity in the collagen or in the gelatin of marine fish than in the proteins of cattle, human or freshwater fish species (Beveridge 1947; Eastoe 1955, 1957). Therefore, the consumption of even small amounts of marine fish might, in theory, provide a greater extent of metabolically useable sulfur to the amino acids pool of the consumer than a similar consumption of cattle or freshwater fish. It is thus possible for an equal consumption of marine fish and of cattle to have an unbalanced influence in the tissue sulfur isotopic composition of the consumer, with a greater contribution of sulfur from the fish methionine (Nehlich 2015). Given that the δ^{34}S ratios of anadromous fish appears higher than the δ^{34}S ratios of the terrestrial herbivores and of the freshwater fish on prehistoric remains from the Danube Gorges, an equal consumption of anadromous fish and of freshwater fish and/or terrestrial herbivores might have resulted in elevated δ^{34}S ratios (because of the greater contribution of the sulfur from anadromous fish). This would give some support to the idea that Early Mesolithic humans were not consuming - or to a very limited extent - anadromous fish, while Late Mesolithic included these fish in their diet, not necessarily in very important amount though. Yet, this remains hypothetical since the internal cycle of methionine in the human body is currently not entirely understood (Nehlich 2015; Webb et al. 2017b); in any cases, it supports the hypothesis that the Early to Late Mesolithic difference in δ^{34}S values should be related to the consumption of anadromous species.

Besides, the elevated values of analyzed dogs (n=2; respectively 15‰ and 15.6‰) confirm that they were probably fed on these fish as well; elevated Late Mesolithic humans δ^{34}S values might hence be jointly related to the consumption of dogs' meat, particularly considering the above-mentioned archaeozoological evidence for - at least casual - cynophagia. The fact that the values of these two dogs exceed the maximal values of Humans (Late Mesolithic: 13.2‰; Transformation-Early Neolithic: 14.8‰), suggests that dogs may have consumed marine resources. This could be either due to their consumption of anadromous fish in an even higher extent than human meals (only fish for the dogs?), or to the consumption of their own meat, which could further elevate their δ^{34}S signal[66]. Several experimental studies indeed agree on the existence of a slight tissue-to-diet offset for the stable isotope of the sulfur element, but yet document a broad variation in its magnitude, ranging from ca -5 to +7‰ (Nehlich 2015; Webb et al. 2017b). A recent lab-controlled pig feeding experiment has shown that an entirely marine-based diet (100% marine proteins) may induce specific metabolic pathways that result in negative food-to-consumer δ^{34}S offset (consumer depletion in comparison with diet, circa -2 to -4‰; Webb et al. 2017b). Since only one specimen of anadromous fish provided well-preserved collagen, it is possible that their δ^{34}S variability might extend over the values of the analyzed specimens of dogs (i.e. above 15,5‰). Besides, it is also possible that dog and human bodies metabolize sulfur-containing amino-acids in different ways, and also differently than the pigs or than the animals analyzed in the experimental feeding studies, which could then explain the broad variability obtained by scholars in terms of δ^{34}S diet-to-tissue offset. It can be mentioned that several cases of foraging behavior by gray wolves on salmon streams have been observed by ethologists (Darimont et al. 2003); in the light of the elevated canidae and

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[65] Water sieving was practiced only for the site of Schela Cladovei (Bartozciewics 1995) and for some layers of the site of Vlasac (Borić et al. 2014).

[66] cf supra: carnivores gnawing marks were found on some dogs' long bones, Dimitijević et al. 2008

humans' $\delta^{34}S$ values, one may further question the possible relationships between dogs' local domestication and dogs' foraging capabilities.

4.2.2.3. The "Bosphorus hypothesis": an increased marine incursion in the Black Sea shifting up anadromous $\delta^{34}S$ values?

Animal $\delta^{34}S$ values does not show any real diachronic increase that would relate the Late Mesolithic human shift up to some environmental change, neither concerning the signals of anadromous or potamodromous fish nor concerning the signals of freshwater species or terrestrial mammals (Appendix A.I.8; 10; 13; 11; 15). However, given the difficulties encountered to extract well-preserved collagen on fish remains[67] and thus the small size of the sample of anadromous - potamodromous species analyzed here (n=3), the results should be interpreted with caution. The fact that almost all Late Mesolithic humans exhibit higher $\delta^{34}S$ values and the very small overlap noticed between the Early and the Late Mesolithic human $\delta^{34}S$ ranges could indeed be seen as evidence in support of the diachronic environmental $\delta^{34}S$ change hypothesis, since one would not expect a human behavioural change to be so systematic. Besides, the archaeozoological record do not document any major change in the representation of wild game, freshwater and anadromous species which could support the hypothesis of a dietary shift[68]; only the gradual domestication of canidae through the Mesolithic may be associated with the diachronic shift up in human sulfur values, but it implies anyways that dogs fed on the fish. In our sample, only the two specimens of potamodromous fish have been ^{14}C dated to the period of Transformation; the only anadromous specimens analyzed have just been broadly attributed to a Mesolithic context. Therefore, more data concerning the stable isotopes of the sulfur element should now be specifically collected on specimens of fish ^{14}C-dated to the Early Mesolithic period in order to ascertain whether or not potamodromous/anadromous species were included in the Early Mesolithic diet in a smaller extent than they were during the Late Mesolithic, and also to (un)validate the hypothesis of an environmental diachronic shift up in $\delta^{34}S$ values.

Yet, some support for the hypothesis that the shift in $\delta^{34}S$ values might have been caused by some environmental factors can be found downstream, toward the Black Sea, where anadromous fish spent most of their lives. It has been indeed suggested that important hydrological events may have occurred in the whole Black Sea Basin at the very end of the Pleistocene and during the first part of the Holocene and contributed to change some important aspects of the ecological baseline there (e.g. the "opening of the Bosphorus": Ryan et al. 1997; Major et al. 2006; Bahr et al. 2006; Martin et al. 2007). Following warming climate and melting glaciers, the increasing river flows may have resulted in a rise of sea levels, gradually leading the Black Sea basin to shift from a Lake system toward a marine system during the Early Holocene, either abruptly (Ryan et al. 1997), or more gradually (e.g. Major et al. 2006; Bahr et al. 2006; Martin et al. 2007). This hypothesis has been previously suggested solely based on the observation of the enrichment in $\delta^{13}C$ and $\delta^{15}N$ between the Early and the Late Mesolithic humans in the Danube Gorge (Bonsall et al. 2000; Cook et al. 2009). The authors suggested that the fluctuating salinity of the Black Sea could have influenced the food resources available to the sturgeons, shifting the stable isotope values of their tissues and further of humans who consumed the fish during their seasonal migration in the upper stretches of the Danube. Our new $\delta^{34}S$ results could be interpreted in the light of this hypothesis; indeed, a stable isotope study of pyrite formation in the Black Sea conducted on Pleistocene and Holocene horizons by Calvert and colleagues has evidenced some fluctuations in the $\delta^{34}S$ values of Pyrite (Calvert et al. 1996). Particularly, they relate an increase in

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[67] A similar difficulty in extracting well preserved collagen from fish remains was also seemingly encountered by Nehlich et al. (2009; table 3, individuals IG-F-9 and IG-F-11) for the analysis of the sulfur element and by Fuller (2012; table S1) for the analysis of the carbon and nitrogen elements.

[68] Deer, wild boars, sturgeons, huchen, cyprinids and catfish are represented through the whole chronological sequence of occupation of the Gorges. Only dogs may not be represented in the earliest phase of the Mesolithic, since it may not have been locally domesticated during the 10th millennium yet; however, it worth to notice that well-stratified archaeozoological information is scarce for the Early Mesolithic phase of occupation, e.g. Dimitrijević 2008.

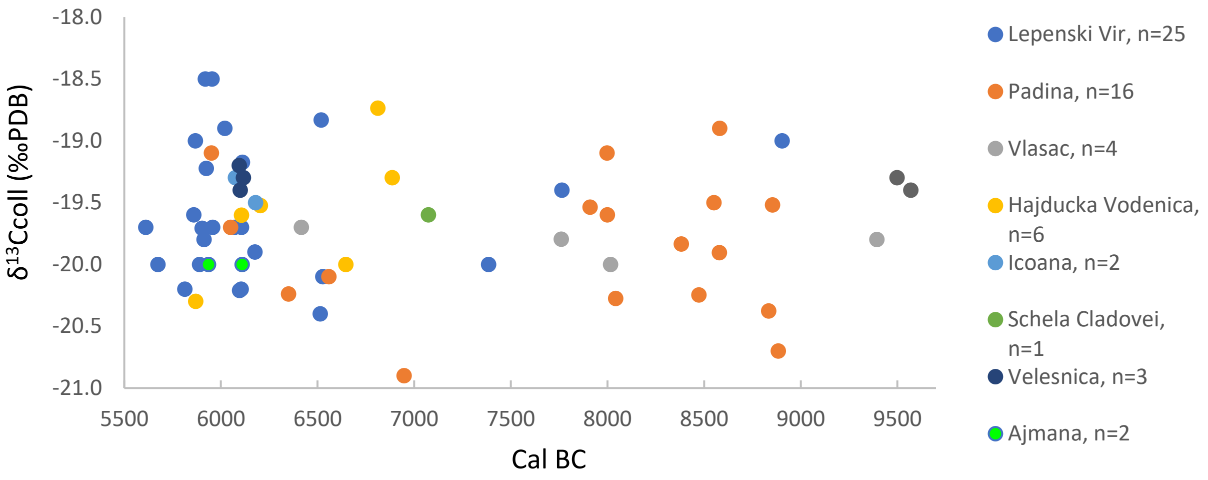

Figure 30: Bivariate plots of δ^{13}Ccoll and radiocarbon dates. Only individuals aged > 10 years old. Calibrated dates and corrected for freshwater reservoir effect (Borić 2011; Bonsall et al. 2015a). Late Mesolithic individuals from Vlasac without criteria for collagen preservation excluded.

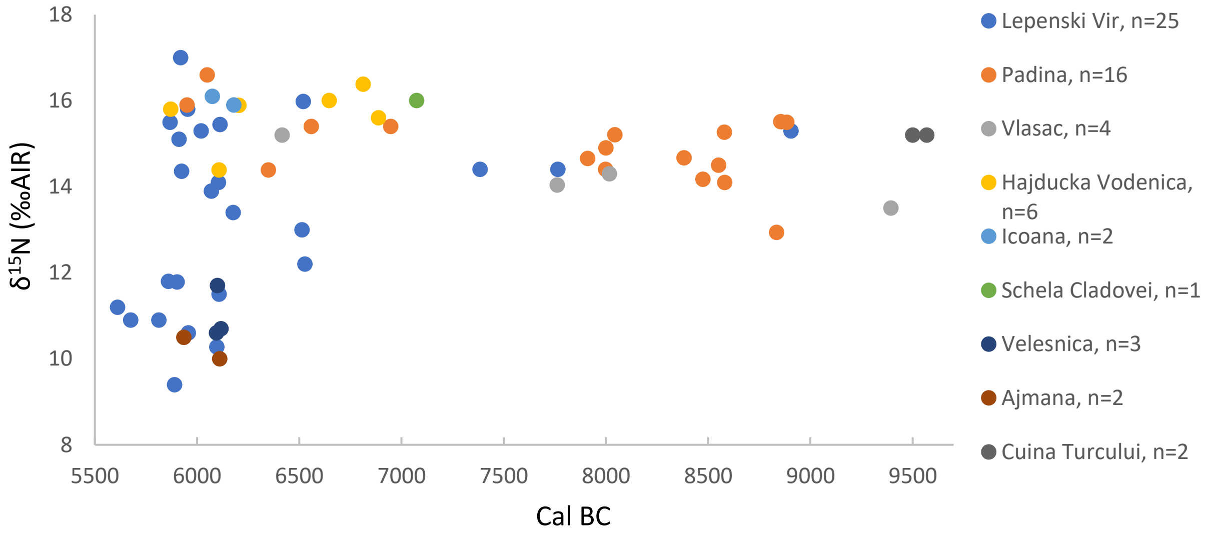

Figure 31: Bivariate plots of δ^{15}N and radiocarbon dates. Only individuals aged > 10 years old.

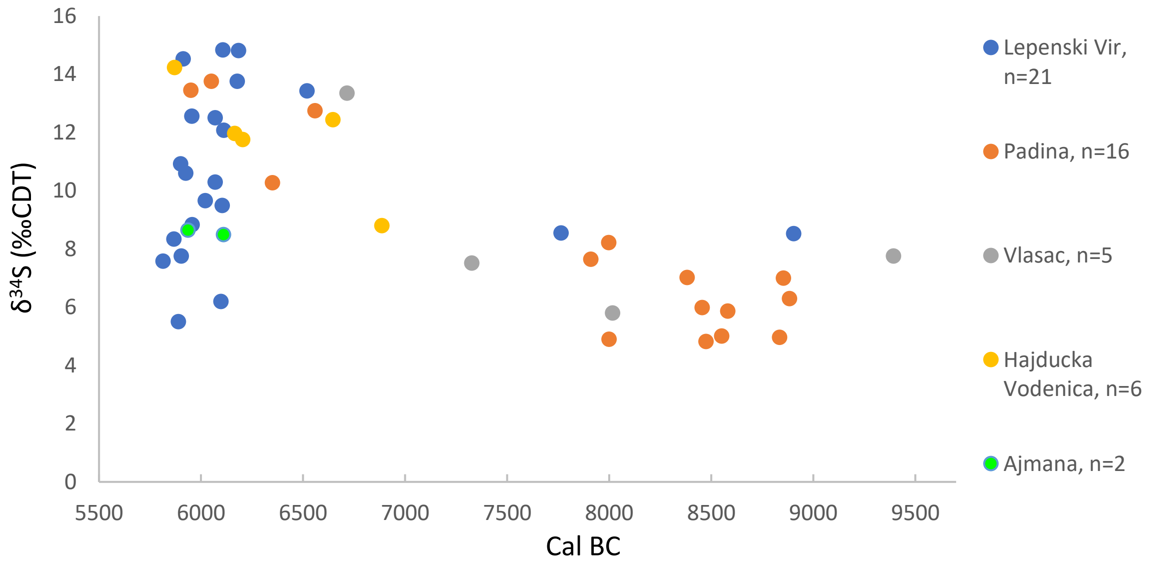

Figure 32: Bivariate plots of δ^{34}S and radiocarbon dates.

$\delta^{34}S$ values to an episode of inclusion of seawater into the Black Sea in relation with its connection to the Mediterranean Sea[69]. More recently, based upon modelling experiments, isotope analyses and micropaleontological reconstructions, the date of the Black Sea reconnection to the global ocean has been recomputed to 7000 cal BC (Soulet et al. 2011; Soulet 2012). Our results coincide with these dates, the shift up in human $\delta^{34}S$ values occurring in the Danube Gorges between 7076 and 6480 cal BC, which is also the time of increased density of Mesolithic occupation (VL 51: 7572-7082 cal BC, $\delta^{34}S$ value: 7.5‰; VL 54: 7024-6399 cal BC, $\delta^{34}S$ value:8.8‰; HV 8 dated 7076-6699 cal BC, $\delta^{34}S$ values: 13.5‰; VL 25 dated 7026-6481 cal BC, $\delta^{34}S$ value:11.4‰[70]). This hypothesis of an environmental shift in the $\delta^{34}S$ values of the Black Sea ecosystem might actually be compatible with changes in the consumption of aquatic resources, and particularly anadromous-potamodromous species, by the Late Mesolithic foragers of the Gorges. Indeed, it has been shown that the increased salinization substantially affected the local biota, a gradual shift from lacustrine to marine ecosystems which occurred over 900 years old (ca 7000-6100 cal BC, Soulet et al. 2011); it might hence be hypothesized that the increased incursion of marine water in the Black Sea may have also affected different aspects fish ecology (type of species represented? Greater presence of anadromous species? Changes in their reproductive or migrative behaviors?), perhaps resulting in the increasing availability of anadromous species in the upper stretches of the Danube river over the 7th millennium cal BC.

4.2.2.4. Summary: subsistence adaptation in the course of the Mesolithic

Interpreted in combination with $\delta^{13}C$ and $\delta^{15}N$ values, the new $\delta^{34}S$ results have provided further insights into subsistence adaptations over the Mesolithic period in the Danube Gorges. Previous paleodietary studies have indicated the major role of fishing in the local ways of subsistence, alongside with the hunt of terrestrial mammals, primarily red deer and wild boars, and the collect of various sort of plants. More specifically, **in this study we observed a shift up in human $\delta^{34}S$ values during the Late Mesolithic period which can be related to the consumption of long-distance migratory fish (anadromous species). It is possible that important environmental events which occurred during the Early Holocene in the Black Sea basin – namely the increased incursion of marine water from the enlarging Bosphorus – may have contributed to modify the $\delta^{34}S$ and $\delta^{13}C$ values of long-distance migratory fish species and, in turn, of the humans who ate the fish in the region of the Gorges**. It can also be assumed that the increased salinity might have affected some aspects of the ecology of the Black Sea basin, perhaps resulting in the increasing availability of anadromous fish in the upper stretches of the Danube river over the 7th millennium cal BC. If confirmed on a greater sample of fish specimens from Early and Late Mesolithic contexts, the exact dating of the shift up in $\delta^{34}S$ values may contribute to our understanding of major ecological changes which occurred in the Black Sea and its tributaries during the first part of the Holocene. The archaeozoological documentation for Epipaleolithic and Mesolithic contexts of the Danube Gorges have indicated the presence of greater proportions of fish remains in the Late Mesolithic contexts of Vlasac and Schela Cladovei than in Late Epipaleolithic – Early Mesolithic faunal assemblages of Cuina Turcului and Padina I, and more specifically, the presence of the anadromous cyprinid vyrezub in important amount in the Late Mesolithic assemblage of Vlasac (Nalbant 1970; Bolomey 1973; Bökönyi 1975, 1978; Clason, 1980;

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[69] In the study from Calvert et al. 1996, measurements were taken successively on three horizons in a core sample: units 1, 2 and 3. In the oldest unit - unit 3 dated to the Pleistocene - two successive measurements display elevated values from 6.42‰ to 14.58‰ and are interpreted as reflecting the possible effect of the first reconnection of the Black Sea to the Mediterranean Sea. However, no ^{14}C dates is associated to the "unit 3" and much more significant changes in the $\delta^{34}S_{pyrite}$ are recorded between the "unit 3" (Pleistocene) and the upper "unit 2" and "unit 1" (Holocene, dated from 7540 BP to modern time) with $\delta^{34}S$ values being depleted from 12‰ in unit 3 to an average of -31‰ in unit 2. So, we may wonder whether the change in Unit 3 recorded by Calvert and colleagues in unit 3 may really be associated with a possible change in the $\delta^{34}S$ values of anadromous fish that may have shift up human values between the Early and the Late Mesolithic period. Besides, we may also wonder to which hydrological/geological event(s) could be related the further changes which are of much higher amplitude and if these changes would be reflected in the collagen values of anadromous fish after ca 6000 BC. It would therefore be important to sample diachronically anadromous fish from the Danube river (or adjacent rivers connected to the Black Sea Basin) in order to check if similar changes are locally reflected in the $\delta^{34}S_{coll.}$ of fish and thereby possibly of humans.

[70] Radiocarbon dates from Borić 2011; 95.4% probability corrected for the freshwater reservoir effect.

Bartosiewicz et al. 1995, 2001, Živaljević 2017). The results of this study confirm that fishing should have played a significant role in the local subsistence throughout the Mesolithic period, likely of increasing importance from the end of the 8th millennium BC, and that long distance migrating species were substantially consumed during the Late Mesolithic period (after 7000 cal BC) which may be due to an adaptation of fishing strategies in the Danube Gorges perhaps in relation with changes in the availability of different aquatic species.

In addition, $\delta^{34}S$ values also indicated that dogs, locally domesticated in the course of the Mesolithic, were substantially consuming marine-derived proteins; the comparisons of humans and dogs stable isotope values, suggest that the Mesolithic foragers may have also consumed the meat of dogs, which is consistent with some archaeozoological contextual information (e.g. Bökönyi 1975; Clason 1980; Dimitrijević 2008).The Late Mesolithic shift up in humans' $\delta^{34}S$ values might thus reflect a particular step in the process of dogs' domestication. It has indeed been suggested that the modalities of dogs’ consumption may vary according to the nature of the domestication process itself, i.e. to the idea about dogs’ integration into the social sphere and to the advantages arising from this new relationship for the community (Milliet 1995). In the Gorges, dogs likely held a particular position in local foragers’ settlement life, being the first and unique domesticated animal (accepted in the “domestic” sphere?), who also consumed similar food as humans (fed on human leftovers? Or because they took parts into some aspects of subsistence practices, including fishing?). Interestingly, some remains of dogs have been found deposited in Late Mesolithic and Transformational funerary contexts at Vlasac, Lepenski Vir and Kula (Srejović and Letica 1978; Radovanović 1999; Živaljević et al. 2017): their mandibles were associated with human bodies[71], perhaps as a personification of the whole animal whose domestication contributed to shorten the jaws and to overcrowd the teeth (Radovanović 1999;Živaljević 2015). Since human skulls and mandibles were often found disarticulated as well, it is possible that a similar or complementary mortuary rite may have jointly involved parts of humans’ and dogs’ bodies[72]. According to Radovanović (1999), dogs may have been perceived as "neither person nor beast" by the prehistoric foragers of the Danube Gorges; indeed, the animal may have accompanied humans in hunting-fishing expeditions, participating actively to subsistence activities, and may have also provided a year round availability in meat, a more passive – albeit essential – contribution to the social group in case of food shortages or harsh winters. Dogs’ mandibles were hence perhaps eventually placed within human burials as a symbolic means to complete a process in which humans and dogs prey together and shared their meals along the riverbanks, and in which dogs may have also represented an essential food resource in some circumstances.

4.2.3. Spatial tendencies: inter-sites stable isotope differences

4.2.3.1. The Early Mesolithic

Subtle inter-site variations can be noticed concerning the Epipaleolithic-Early Mesolithic periods: individuals buried at the site of Lepenski Vir (Early-middle Mesolithic; Upper Gorges) and Cuina Turcului (Late Epipaleolithic-Early Mesolithic; Lower Gorges) exhibit higher carbon, nitrogen and sulfur stable isotope ratios than the two individuals buried at the site of Vlasac (no sulfur values for individuals buried at Cuina Turcului); the individuals from Padina encompass the widest range of $\delta^{13}C$ and $\delta^{15}N$, including the lowest values, and are lower in average than the individuals buried at Lepenski Vir (Figure 33; Figure 34; Appendix A.II.14; A.IV.2; A.IV.4).

We previously mentioned a tendency towards lower $\delta^{13}C$ values for the terrestrial herbivores discovered in Padina and Vlasac than in Lepenski Vir; the fact that Early Mesolithic humans displays a similar pattern of variations may be an additional evidence for their important consumption at

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[71] Except concerning grave 81 at Vlasac where the almost-complete skeleton of dog has been found articulated, headless though (Srejović and Letica 1978).

[72] according to Živaljević 2015, dogs’ mandibles might have occasionally "slipped" into the role occupied by human mandibles.

that time. In contrast, the dogs discovered at Padina display the highest $\delta^{13}C$ values, which might indicate their lesser consumption either at the site of Padina and/or generally during the Early Mesolithic. The higher $\delta^{13}C$ and $\delta^{34}S$ values of the individuals buried at the site of Lepenski Vir during the Early Mesolithic period may also indicate their greater consumption of anadromous and potamodromous species in comparison with the individuals buried at Padina. These interpretations are broadly consistent with the archaeozoological record which documents a higher frequency of ungulates than fish in the earliest Mesolithic phase of occupation of the site of Padina, which contrasts with later phases (Clason 1980), and a greater representation of acipenserids and huchen (anadromous and potamodromous species) on the Early Mesolithic layers of Lepenski Vir than Padina (Živaljević 2017). Inter-site stable isotopes variations may thus indicate slight differences in the subsistence behaviors of the individuals buried at Padina and at Lepenski Vir between the 10th and the 8th millennium BC: a higher consumption of wild game than fish at Padina and/or a preference towards the consumption of stationary freshwater species, and probably a higher consumption of anadromous than stationary freshwater species by the individuals buried at Lepenski Vir than by those buried at Padina. These dietary differences could be related to differences in the availability of fish species at specific spots and/or to changes in subsistence behaviors, some individuals buried at Lepenski Vir and Vlasac being possibly associated to later phase of the Early-Middle Mesolithic period (Borić 2011).

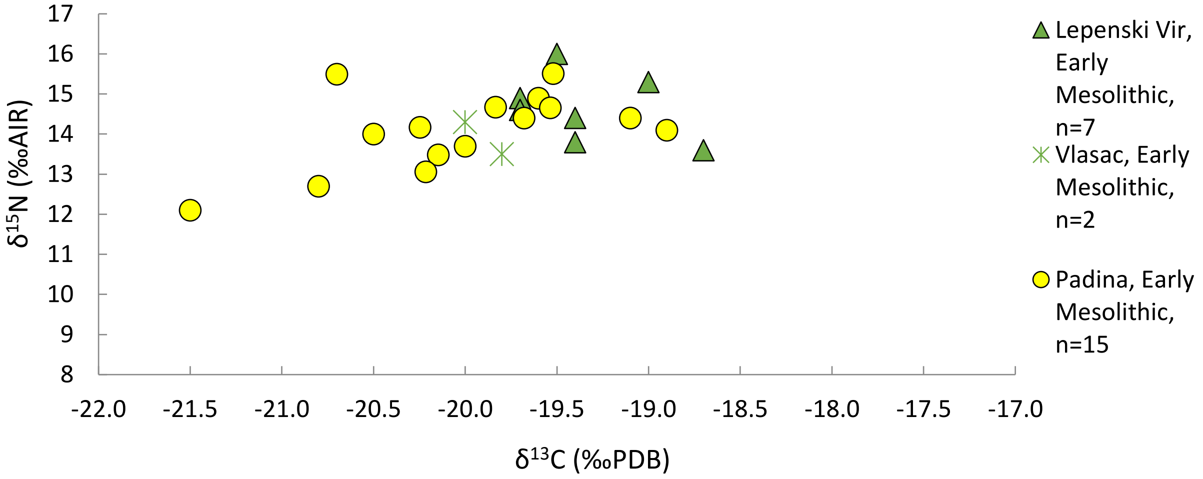

Figure 33: Bivariate plot of $\delta^{13}C$ and $\delta^{15}N$ for Early Mesolithic adult humans (>15 yrs) per sites of the Upper Gorges

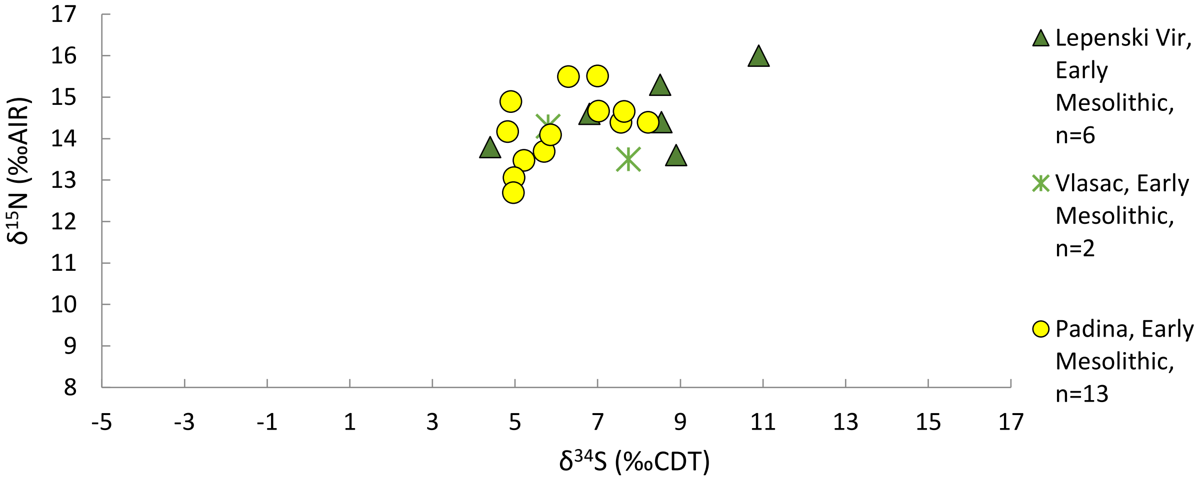

Figure 34: Bivariate plot of $\delta^{34}S$ and $\delta^{15}N$ for Mesolithic adult humans (>15 yrs) per sites of the Upper Gorges

4.2.3.2. The Late Mesolithic in the Upper Gorges

Padina, the catfish spot and Vlasac, the vyrezub spot

Apart from a general shift up in $\delta^{34}S$ values, slight stable isotope differences also discriminate the Late Mesolithic individuals buried at the different sites of the Upper Gorges (Figure 35). The two individuals buried at Padina fall within the lower $\delta^{13}C$ range of the individuals buried at Vlasac, in the continuity of what has been previously observed concerning the Early Mesolithic period (yet, they do not differ for the $\delta^{15}N$ and $\delta^{34}S$ stable isotope; Appendix A.II.12; Figure 37). However, in contrast with the previous period, the only Late Mesolithic individual buried at the site of Lepenski Vir display a $\delta^{13}C$ value lower than the average values obtained for the Late Mesolithic individuals buried at Vlasac[73] (Appendix A.II.12). As noticed concerning the Early Mesolithic period, the inter-site pattern in human $\delta^{13}C$ values is mirrored by the values of freshwater fish: freshwater fish discovered at Padina being lower in $\delta^{13}C$ than those discovered at Vlasac (Appendix A.I.16; 18). Similarly, terrestrial herbivores from Vlasac also exhibit higher $\delta^{13}C$ and $\delta^{15}N$ values than those from Padina (Appendix A.I. 20). Although human and herbivores $\delta^{13}C$ inter-site variations might be related to local differences in the isotopes values of the plants consumed, the fact that a similar pattern of spatial variation can be observed on freshwater fish species confirm that fishing freshwater species remains important during the Late Mesolithic period.

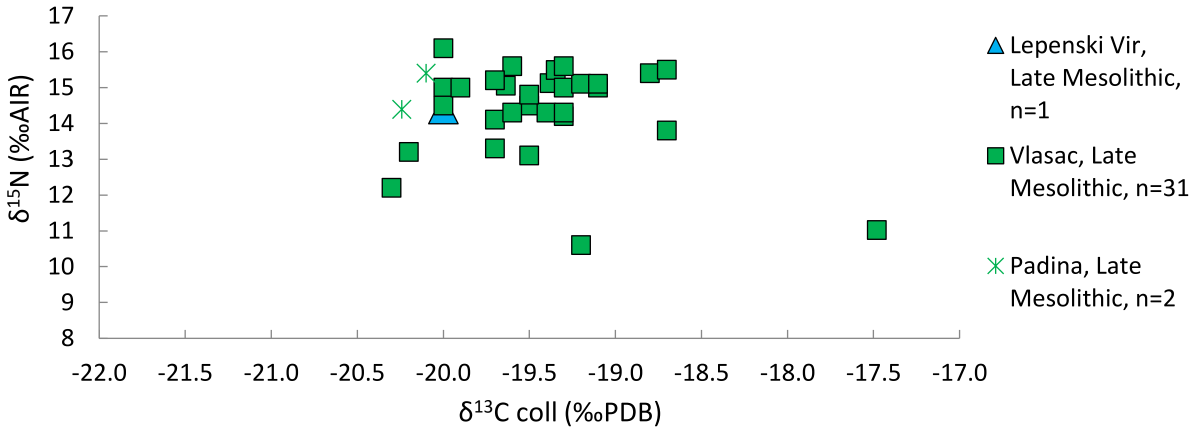

Figure 35: Bivariate plot of $\delta^{13}C$ and $\delta^{15}N$ for Late Mesolithic adult humans (>15 yrs) per sites of the Upper Gorges

Such continuity in fishing freshwater species has been suggested by ichtyoarchaeologist for the locality of Padina where the remains of catfish have been found in quantity (Živaljević 2017). The higher $\delta^{13}C$ stable isotope values for human from Vlasac could also be correlated to a local consumption of vyrezub, the anadromous cyprinid, which is the most represented taxon amongst the ichtyioarchaeological remains from this site (Živaljević 2017). However, for both sites, human signature in $\delta^{34}S$ is high and do not differ, which suggests that anadromous-potamodromous fish were also widely consumed at Padina during the Late Mesolithic (vyrezub, huchen and sturgeons being anyway still represented in the faunal spectrum of Padina, although in a lesser extent than catfish). Besides, the PCA, based on the common variance in the three elements for both humans and animals, does not really discriminate the diets of Late Mesolithic individuals from Vlasac and from Padina (Appendix A.IV.2).

Although most Early Mesolithic humans included in our analyses have been found on the site of Padina and most Late Mesolithic originate from the osteoanthropological assemblage of

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[73] It should be recalled here that the stable isotopes values for this individual have been measured with an AMS device and the authors did not provide the criteria for the quality of collagen preservation (Borić and Price, 2013), while the stable isotope ratios in the study of Grupe et al. (2003) and Nehlich et al. (2009) and in this study were measured with an IRMS device. This Late Mesolithic individual from Lepenski Vir was included in our study considering that we did not observe any statistically significant difference (for Mann Withney test with $p < 0{,}005$) neither between the individuals from Lepenski Vir for whom the criteria of collagen preservation were respected and those for which these criteria were not available, nor between the Late Mesolithic individuals for whom the criteria of collagen preservation were respected and those for whom these criteria were not available.

Vlasac, the Early to Late Mesolithic trend toward elevated δ^{13}C and δ^{15}N values and the shift up in δ^{34}S values cannot be solely explained by the observed inter-site differences in human and animal stable isotope values. Indeed, the Late Mesolithic and Early Neolithic individuals from Padina exhibit higher δ^{15}N values than the Early Mesolithic individuals from this site and much higher δ^{34}S values (from an average of 6,2 ‰ to 12,6 ‰); similarly Late Mesolithic individuals from Vlasac exhibit higher δ^{13}C, δ^{15}N and δ^{34}S values (respective averages of -19,4‰, 14,6‰ and 11,17‰) than the Early Mesolithic individuals from this site (respectively -19,9‰, 13,9‰ and 6,7‰). Thus, although some intra-site differences remain, probably due to the local availability in different species ("good fishing spots"), the consumption of anadromous-potamodromous likely became more important in the Late Mesolithic ways of subsistence.

4.2.3.3. The Late Mesolithic in the Lower Gorges and in the Downstream Area

Higher trophic level resources consumption downstream?

Concerning the Lower Gorges and the Downstream Area, the individuals discovered on the sites of Schela Cladovei and of Hajdučka Vodenica fall in the upper part of the δ^{15}N range of the individuals discovered in the Upper Gorges but do not differ in terms of δ^{13}C and δ^{34}S values (Appendix A.II.12; 14; Figure 36; Figure 37; Figure 38). Given that no associated fauna from the sites of Hajdučka Vodenica and Schela Cladovei could be analyzed for their stable isotope signals[74], one may suggest that the particularly high position of humans from these sites on the δ^{15}N axis could be related to some local slight variations in animal stable isotope values. However, although this explanation cannot be entirely excluded, it should also be borne in mind that the signals in δ^{13}C and δ^{34}S are expected to be more sensitive to environmental differences than the signal in δ^{15}N which would always be more influenced by the trophic position. One should yet recall that the criteria of collagen preservation downstream were not available for these individuals from the site of Schela Cladovei (analyzed by Bonsall et al. 1997), and that they were included in our analyses only for purposes of spatial comparison. Nonetheless this δ^{15}N elevation can also be noticed for the Late Mesolithic individuals from Hajdučka Vodenica which respected the collagen preservation criteria[75]. The existing archaeozoological documentation for the sites located in the Lower Gorges relates an important presence of acipensiridae (for Schela Cladovei, Bartosiewicz et al. 1995; for Kula, Živaljević et al. 2017), salmonidae (Huchen for Kula, Živaljević et al. 2017) and vyrezub (for Kula, Živaljević et al. 2017 and for Răzvrata,Bălăşescu, et al. 2017; broader taxon of cyprinidae for Schela Cladovei, Bartosiewicz et al. 1995). Between Hajdučka Vodenica and Schela Cladovei, rapids once marked the exit of the Danube from the Inner Gorges[76] and created there a bottleneck in the upriver migration of anadromous fish, leading to a seasonal concentration of these fish just below the rapids (Bartosicwicz and Bonsall 2004). However, to assume a greater consumption of these anadromous species at these sites of the Lower Gorges - Downstream Area than upstream, one would rather need to observe higher values in δ^{13}C and δ^{34}S than elevated δ^{15}N, which is not the case. Remains of local carps have also been found numerously in Schela Cladovei (Bartosiewicz et al. 1995), and its consumption may account for local human elevated δ^{15}N signal, but not necessarily more elevated than for the sites located upstream where the species has also been found in quantity (Živaljević 2017).

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[74] One can only interpret the stable isotope differences noticed between the individuals inhumated on the sites of the Upper Gorges, since faunal stable isotope data are derived only from determined taxa discovered on this part of the Gorges. For the sites located downstream, we only the stable isotope values of some "ungulates" from the site of Schela Cladovei were available (Cook et al. 2002); however, the very broad taxonomic information provided by Cook et al. - "ungulate" – (including both herviores and omnivores species) limits possible behavioral interpretations; They range within the δ^{15}N and δ^{13}C variability of the ungulates discovered in the Upper Gorges, rather close to the δ^{13}C values of analyzed specimens of wild boar

[75] besides, we found a statistically significant difference between those whom collagen respected the preservation criteria and those for whom these criteria were not available only on the δ^{13}C isotope concerning the Late Mesolithic individuals buried on the site of Vlasac

[76] These rapids ceased to exist when the river was impounded by the Iron Gates I dam.

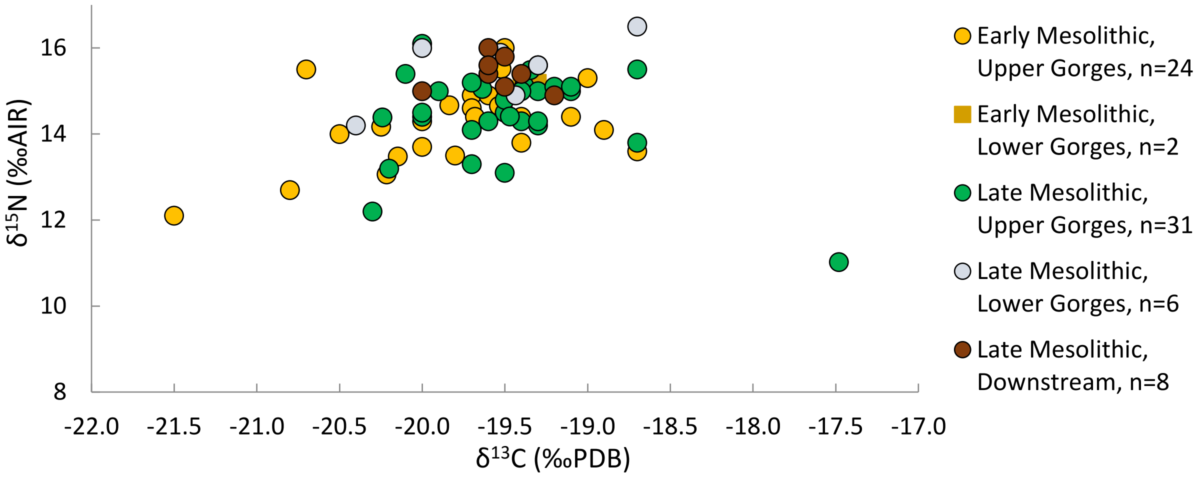

Figure 36: Bivariate plot of $\delta^{13}C$ and $\delta^{15}N$ for Mesolithic adult humans (>15 yrs) per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)

A further downstream, on the sites of Schela Cladovei and Kula, freshwater mussels have been discovered in quantity, with breakage patterns indicative of their consumption (Pickard et al. 2017; Živaljević et al. 2017). Yet, this mollusk has a low trophic position in the aquatic food web and might be of quite low $\delta^{15}N$ signal (Graniero et al. 2016). The importance of wild boars amongst the archaeozoological record of some sites of the Lower Gorges - Downstream Area such as Icoana or Schela Cladovei could provide possible lines of explanation for this elevated $\delta^{15}N$ signal (Boloney 1973; Bartosiewicz et al. 1995; Dinu et al. 2006). Indeed, omnivores are higher in the trophic web than herbivores and therefore display higher $\delta^{15}N$ stable isotope ratio (Figure 24). Remains of tortoises have also been found in number on the site of Schela Cladovei, but they have been determined as the terrestrial (and herbivore) Testudo Graeca by Bartosiewics et al. (1995), so probably of a lower trophic position than the aquatic turtle (Pond Tortoise) found upstream on the site of Vlasac (Bökönyi 1978). It seems therefore that whether higher trophic species of aquatic animals or of water birds, or an important local consumption of fish roe, perhaps together with a more important inclusion of wild boars in the diet, may have contributed to these high $\delta^{15}N$ values.

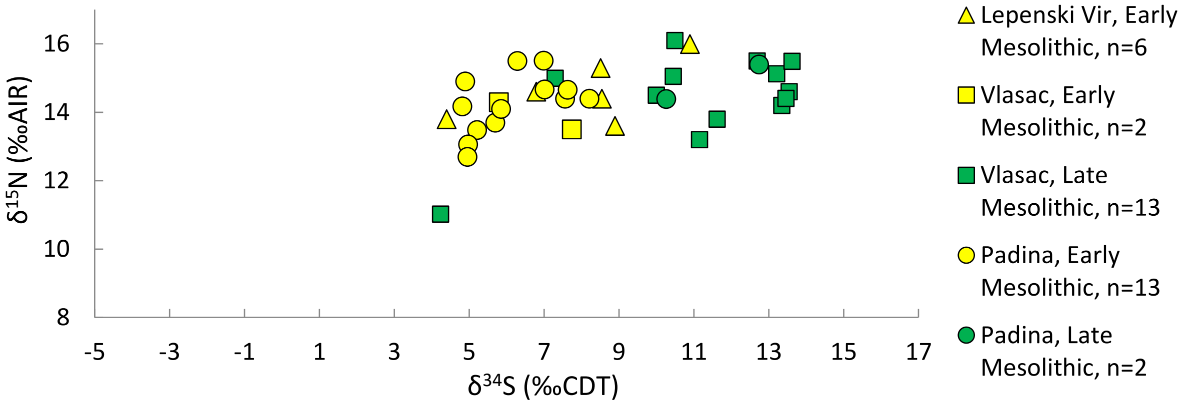

Figure 37: Bivariate plot of $\delta^{34}S$ and $\delta^{15}N$ for Mesolithic adult humans (>15 yrs) per sites of the Upper Gorges

Cooking practices such as fire baking, boiling, smoking or drying meat/fish may also slightly shift up stable isotope ratios, and highest cooking effect has been noticed for fish flesh (median $\Delta^{15}N$: +1.2‰ and maximal $\Delta^{15}N$ of 2.3‰ for boiled fish and up to 3.5‰ for fried fish; Royer et al. 2017). Additionally, other non-behavioral factors may also have contributed to influence the elevated δ^{15}N values, such as diagenetic processes (eg. Grupe et al. 2006), physiological effects (e.g. Reistema 2013) or differences in gut microbes (Reynard and Tuross 2015).

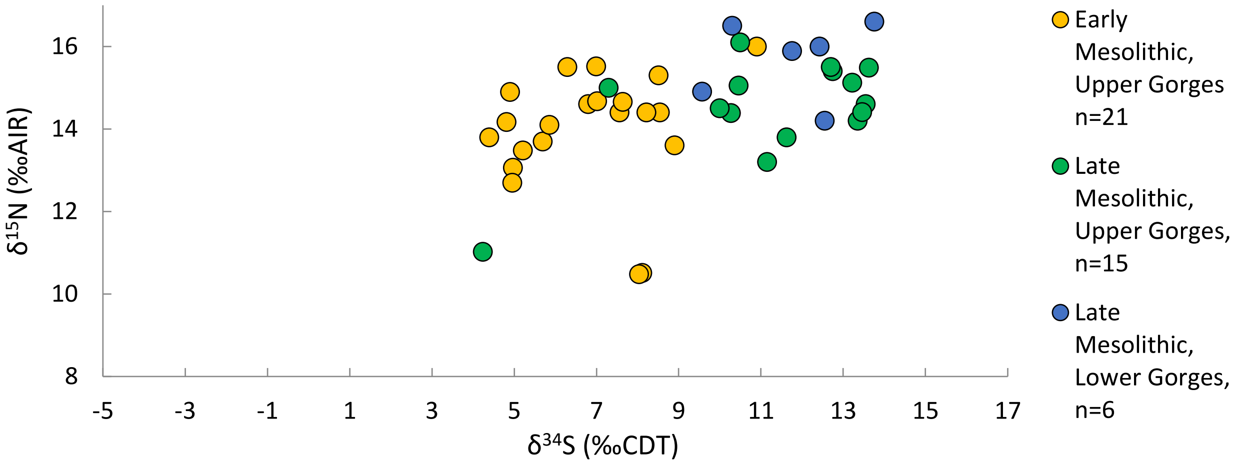

Figure 38: Bivariate plot of δ^{34}S and δ^{15}N for Mesolithic adult humans (>15 yrs) per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)

4.2.3.4. Summary: some centers of specialized subsistence strategies along the Gorges?

To summarize, the observation of subtle inter-site stable isotope differences on human buried at the different sites of the Gorges, suggests that individuals buried at these localities may have consumed very local species and/or may have favored the consumption of slightly different species at each localities, which is in broad concordance with the archaeozoological documentation. Given that some of these sites – Padina, Vlasac and Lepenski Vir – are distant of less than a dozen of km, the assumption that humans may have been eating – at least during the last decade of their lives – animals from the localities where they have actually been buried, would be an indication for rather low patterns of residential mobility.

The stable isotope values of the Early Mesolithic individuals buried in the Upper Gorges at the site of Padina could have been more influenced by the consumption of freshwater fish and terrestrial herbivores than the stable isotope values of the individuals buried at Lepenski Vir who may have been consuming more anadromous sturgeons, perhaps because of species differential availability at various fishing spots. These results are broadly compatible with the representation of the different taxa at different sites (Borić 2001, 2002a; Živaljević 2017). Despite the generalized shift up in δ^{34}S values, subtle stable isotope variations are also noteworthy concerning individuals buried at different sites during the Late Mesolithic. While the signals of Late Mesolithic individuals buried at Vlasac seem more influenced by the consumption of anadromous fish, individuals buried at Padina may have been fishing more stationary freshwater species. This is also consistent with the ichtyoarcaheological record at these sites, which indicates a greater proportion of vyrezub at Vlasac and of catfish at Padina (Živaljević 2017). The Late Mesolithic individuals discovered in the Lower Gorges and in the Downstream Area also range in the very upper part of the δ^{15}N range of the individuals buried upstream at that time. Although we cannot entirely exclude the possibility that this pattern could reflect non-dietary processes (diagenetic processes, culinary practices, physiological effects or difference in gut micribiome), it could be related to the specific consumption of some different species of aquatic animals, fish roe, waterfowl birds, dogs or to a more important practice of wild boar hunting on the sites located downstream than in the Upper Gorges (where red deer hunting was favored?). These stable isotope inter-site differences provide some support to the hypothesis that the sites of the Gorges may have been oriented toward specialized fishing, at a time when the Mesolithic communities were probably living (almost) all year by the river.

4.2.4. Origin, sex and age-related stable isotope differences: insights into the Mesolithic social organization

4.2.4.1. Origin-related stable isotope differences (1): paleodiet and the strontium radiogenic evidence

Concerning the whole Mesolithic period, five individuals have been identified as non-locals based on their strontium radiogenic signal (Borić and Price, 2013; previous demographic part II); three of them were included in this stable isotope study (one Early Mesolithic individual - Pad 30 - and two Late Mesolithic individuals, HV 11and VL 32)[77].

The Early Mesolithic female Padina 30[78] exhibits lower $\delta^{13}C$ and $\delta^{15}N$ values than the local Early Mesolithic individuals (Appendix A.II.21); the Late Mesolithic female Vlasac 32[79] also exhibits lower $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values than the local Late Mesolithic individuals; the Late Mesolithic male Hajdučka Vodenica 11[80] falls within the Late Mesolithic variability for $\delta^{13}C$ and $\delta^{15}N$ values, but also displays lower $\delta^{34}S$ values than most of the local Late Mesolithic individuals[81] (Appendix A.II.21). Yet, it should be specified that the Early Mesolithic individual Pad. 30 was analyzed for $\delta^{13}C$ and $\delta^{15}N$ by Borić and Price (2013) who did not provide the criteria used to assess the quality of collagen preservation. Therefore, it cannot be entirely excluded that her lower stable isotope values might be related to a problem of collagen preservation. Nonetheless, the difference between the Early Mesolithic individuals from Padina which fulfills the criteria for collagen preservation and those for which these criteria were absents was not statistically significant (Mann Whitney, for $p>0,005$; cf part 3.3.2). Besides, the collagen of the Late Mesolithic individual VL 32 fulfills the preservation criteria used here and this individual also exhibits lower $\delta^{13}C$ and $\delta^{15}N$ values than the Late Mesolithic local individuals.

It is thus possible that the individuals Pad 30, VL 32 and HV 11 perpetuated in the Gorges the dietary habits which they had before migrating. The Early Mesolithic individual Pad 30 (lower $\delta^{13}C$, $\delta^{15}N$ than the locals) and the Late Mesolithic individual VL 32 (lower $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ than the locals) were perhaps consuming more terrestrial proteins (from meats and C_3 plants) than the local Mesolithic foragers of the Gorges. In contrast, the individual HV 11 may have been favoring the consumption of aquatic resources and/or higher trophic level resources (high $\delta^{13}C$ and $\delta^{15}N$, similar as the locals), but it is likely that he did not substantially consumed anadromous species nor the meat of dogs (lower $\delta^{34}S$ than the locals). It should be stressed here that these lower stable isotope values could be interpreted in terms of dietary differences only provided that the stable isotope signals of the fauna from the environment(s) where they lived before migrating into the gorges were roughly similar to the stable isotope signals of the fauna from the Danube Gorges region, a parameter which unfortunately cannot be assessed. Finally, it is also possible that these three individuals adopted the local dietary practices after migrating into the Gorges but died shortly after their arrival; indeed, it is accepted that circa 15 years are necessary for a complete turnover of bone proteins (Valentin 2003), and thus for an entire renewal of the stable isotope signature.

One Late Mesolithic individual - Vlasac 26[82] - has been identified as local but displays a very different signature for the isotopes of the three elements ($\delta^{13}C=-17,5‰$; $\delta^{15}N=11‰$ and $\delta^{34}S=4,2‰$; Figure 28; Figure 29; Appendix A.II.1; 3; 5).The combination of a very high $\delta^{13}C$, a low

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[77] Given that a statistically significant difference (Mann Whitney for $p <0,05$) was perceived between the Late Mesolithic individuals from Vlasac for which the criteria ensuring the quality of collagen preservation were documented (%C, %N, %S, C/N - C/S and N/S atomic ratios) and those for which these values were not available, a significant number of individuals previously analyzed by Bonsall et al. 1997 and Borić et al. 2008 have been excluded from this study. One Late Mesolithic non-local individual, Vlasac 49, analyzed for $\delta^{13}C$ and $\delta^{15}N$ was thus not included in this study.

[78] diagnosed as female, aged at death >30 years.

[79] a female aged between 30-39 when she died; $\delta^{13}C= -20,2‰$; $\delta^{15}N=13,2‰$; $\delta^{34}S=11, 5‰$

[80] a male aged at death >30 yrs; $\delta^{13}C= -19,4‰$; $\delta^{15}N=14,9‰$; $\delta^{34}S=9,6‰$

[81] three Late Mesolithic individuals identified as locals according to their strontium radiogenic signature - VL 26, VL 16 and HV 8 - exhibit lower $\delta^{34}S$ values than the non-local individuals VL 32 and HV 11 (Appendix A.II.24). Yet, only the individual HV 8 has been ^{14}C-dated to the Late Mesolithic period (7076-6699 cal. BC, Borić, 2011).

[82] a male aged at death between 30 and 49 years.

δ^{15}N and a very low δ^{34}S differs from the signature of all others Mesolithic and Neolithic individuals of the Gorges. His strontium radiogenic signal falls amongst the highest values of the local range, close to the upper local limit[83]. Hence, although he has been identified as local, the possibility of his non-local origin cannot be entirely disregarded. Alternately, the combination of high δ^{13}C values but low δ^{15}N and δ^{34}S values could also be related to the consumption of C$_4$ plants. Although the consumption of C$_4$ plants appears unlikely for the Late Mesolithic period (the millet do not became widespread in the Caucasus and Europe before the Chalcolithic and the Bronze Age; e.g. Ligthfoot et al. 2013; Herrscher et al. 2018), the individual Vlasac 26 has not been ^{14}C dated and it should be recalled that a few individuals discovered at the site of Lepenski Vir have been ^{14}C dated to the Chalcolithic, to the Roman period and to the Middle-Age (Bonsall et al. 2004; 2008)[84]. The specific signature in δ^{13}C, δ^{15}N and δ^{34}S of the individual VL 26 could thus be whether related to his origin outside of the Gorges, to his particular dietary behavior rather focused on the consumption of δ^{13}C depleted resources and/or to a problem of chronological assignment (individual dated posterior to the Neolithic period and to the spread of millet in Europe?).

4.2.4.2. Origin-related stable isotope differences (2): paleodiet and aDNA

Concerning the Mesolithic period, Ancient DNA analyses identified the mitochondrial[85] clades U4 and U5 in high frequency amongst the foragers of the Gorges (Hofmanová 2016; Mathieson et al. 2018; cf part 2.3.3). These maternal lineages are also common amongst other European Mesolithic populations (e.g. Mathieson et al. 2018). Concerning paternal lineages - information provided by the analysis of the Y-chromosome - all Early and Late Mesolithic individuals with available Y-data have been assigned to the R1b and I2 Y-clades, lineages which are also frequent amongst the Eastern and Western European Mesolithic Hunter-Gatherers (Mathieson et al. 2018). Apart from the U4 and U5 maternal lineages, other mt-clades have been detected on a few Mesolithic individuals of the Gorges - the lineages K1c and K1f[86], U8[87], H13[88], I3[89], X2[90] - which is unique for a Pre-Neolithic[91] European population. Indeed, the K1 mt-clade has been detected only on one Aegean Mesolithic individual[92] and the H haplogroup has been detected only on one Caucasian Epipaleolithic/Mesolithic individual[93]; apart from these two cases, all these clades (K1, U8, H13, I3 and X2) are absent amongst the Eastern-Western European and Scandinavian Pre-Neolithic Hunter-Gatherers, but have been identified on Middle/Near Eastern and European Neolithic or post-Neolithic contexts (e.g. Mathieson et al. 2018). To explain this particular ancestry, Mathieson et al. (2018) suggested "that the Iron Gates population [could be] related to the source population from which the [Western Hunter Gatherers] split during a re-expansion into Europe from the southeast after the Last Glacial Maximum". As an alternate - and simpler - scenario, it is also possible that the Mesolithic population of the Balkans, in contrast with other European Hunter-Gatherers, included genetic contacts with some Middle and Near Eastern Neolithic-related or Pre-Neolithic populations (Hofmanová, 2016; Mathieson et al. 2018).

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[83] ^{87}Sr/^{86}Sr value of 0,709558, falling thus close to the upper limit of 0,709628 (cf part 2.3.3).

[84] These historic individuals also fall in the high part of the local δ^{13}C range and in the low part of the local δ^{15}N range (respective averages of -18,4‰ and 9,5‰; Bonsall et al. 2004 and 2008).

[85] the mitochondrial DNA being transmitted only by mothers, it informs about maternal lineages, in contrast with the Y-chromosome which informs about paternal lineages.

[86] This mt-clade has been identified for 3 Early Mesolithic individuals: Pad. 16a (8265-7820 cal. BC, new ^{14}C date Mathieson et al. 2018); Pad. 18b (9115-8555 cal. BC, new ^{14}C date Mathieson et al. 2018); Velesnica 1G/3 (9755-9275 cal. BC, new ^{14}C date Mathieson et al. 2018);

This mt-clade has been identified for 4 Late Mesolithic individuals: VL 41 (6767-6461 cal. BC, new ^{14}C date Hofmanová 2016); VL 45 (7045-6535 cal. BC, new ^{14}C date Mathieson et al. 2018); Schela Cladovei M50 (7060-6570 cal. BC, new ^{14}C date Mathieson et al. 2018); and VL 45.

[87] Individual VL 51b (7940-7585 cal. BC; new ^{14}C date Mathieson et al. 2018); VL 52: attributed to the Late Mesolithic (?) (Boric and Price 2013)

[88] The H13 clade has been identified on 3 Early Mesolithic individuals from the Romanian site of Ostrovul Corbului (M2, M47a, M57; M2 has been ^{14}C-dated to 7582-7190 cal. BC, new date Mathieson et al. 2018) and on an Early Mesolithic individual discovered at Lepenski Vir, LV 126

[89] non-local female Pad. 30 assigned to the Early Mesolithic period

[90] Individual VL2 assigned to the Late Mesolithic period

[91] Although some of the individuals belonging to these clades might be assigned to later chronological periods (no ^{14}C dates for the Ia3 and X2 individuals; cf notes supra), others have yet been radiocarbon dated to the Mesolithic (^{14}C dates for the K1c, K1f, H13, and U8 individuals; cf notes supra).

[92] Greek Mesolithic site of Theopatra (Hofmanová et al. 2016)

[93] Armenian Epipaleolithic/Mesolithic site of Kotias (Jones et al. 2015)

When one compares genetic lineages and paleo-dietary information, it appears that the two Non-U individuals included in this stable isotope study - Pad.30 and Pad.18b- display lower values than the individuals assigned to the U4 and U5 mt-clades. We previously noticed that the non-local female Pad. 30, assigned to the lineage I3a, displays lower $\delta^{13}C$ and $\delta^{15}N$ than the rest of the Early Mesolithic population ($\delta^{13}C$ =-21,5‰; $\delta^{15}N$=12,1‰; Appendix A.II.22; A.IV.10). Similarly, the local female Pad. 18b[94] who belong to the k1f lineage also exhibits lower values for the isotopes of the three elements ($\delta^{13}C$ =-20,8‰; $\delta^{15}N$=12,7‰ and $\delta^{34}S$=5‰; Appendix A.II.22; A.IV.10). Yet, it should be specified here that the Early Mesolithic individuals Pad. 18b and Pad 30 were both analyzed for $\delta^{13}C$ and $\delta^{15}N$ by Borić and Price (2013) who did not provide the criteria used to assess the quality of collagen preservation. Another non-dietary explanation could be considered to explain these lower stable isotope values: it may be suggested that individuals who belong to different genetic lineages could have slightly different gut microbiota which may, in turn, affect the individuals' stable isotope values; yet, recent research rather suggests that environment, behavior and diet dominates over host genetics in shaping the human gut microbiota (Rothschild et al. 2018). The common variance in the stable isotope of the three elements indicates that Pad. 18b may have been consuming more terrestrial than aquatic resources and perhaps lower trophic level resources than the rest of the local population (probably a greater consumption of herbivores meat and C_3 plants than omnivores meat and fish; Appendix A.IV.10). Since she was born and/or has spent most of her childhood in the Gorges (local strontium radiogenic signal recorded in her teeth), her lower stable isotope values may indicate that she could have been reproducing slightly different dietary practices, perhaps transmitted by her ancestors who came into the Gorges (second generation migrants?). Alternately, it is also possible that this female, born in the Gorges, spent the major part of her life outside the region - maybe amongst a community to whom she was related (k1f lineage) - and eventually returned into the Gorges at the end of her life. The Late Mesolithic Non-U individual included in this stable isotope study - VL 41[95] assigned to the K1f clade - ranges within the stable isotope variability of the individuals assigned to the U4 and U5 mt-clades (Appendix A.II.22; A.IV.10), suggesting that he had similar dietary habits than most of the population, substantially consuming aquatic resources. Concerning paternal lineages, there is no noticeable differences in terms of stable isotope between the two Y-clades represented amongst the local foragers - I2 and R2b - whether for the Early or the Late Mesolithic periods (Appendix A.II.24).

These results indicate that, despite displaying a significant degree of sedentism, the Mesolithic population of the Gorges should not be considered as a closed community. Although most of the Mesolithic individuals analyzed for strontium were identified as locals, a few individuals originate from other regions, probably from some other European Mesolithic communities and perhaps also from some Neolithic-related Near Eastern community (or their Pre-Neolithic ancestors). Some of the first-generation migrants (e.g. Pad. 30, VL 32, or HV 11) perhaps perpetuated in the Gorges their own dietary traditions - or died too early after their migration for their collagen to reflect the dietary shift. One local female who may have been the descendant of a migrant (Pad. 18b) perhaps reproduced in the Gorges some different dietary habits (of her ancestors?) - or moved out of the Gorges after childhood and came back in the region at the end of her life.

4.2.4.3. Sex-related stable isotope differences

In the first $\delta^{13}C$ and $\delta^{15}N$ study carried out on the Danube Gorges osteo-anthropological sample, Bonsall et al. (1997) observed some sex-related dietary differences amongst the Mesolithic

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[94] Pad. 18b: 9115-8555 cal. BC, new ^{14}C date Mathieson et al. 2018

[95] VL 41: 6767-6461 cal. BC, new ^{14}C date Hofmanová 2016

individuals discovered at Lepenski Vir and at Vlasac: lower average δ^{13}C and δ^{15}N values for females from Vlasac than Males and a tendency for females from Lepenski Vir to be associated with higher δ^{13}C values than males. The authors suggested then that the "dietary intake differed between the adult males and females represented at both sites" (Bonsall et al. 1997). However, after two decades of bioarchaeological researches on stable and radiogenic isotopes carried out on the Danube Gorges osteoanthropological sample, it appears that several caveats should be considered regarding this precursor study: (1.) in the absence of absolute dating, the authors assigned the males and females from Lepenski Vir whether to the "Mesolithic period" or to "the Neolithic period" *on the basis of their stable isotope values*; (2.) they did not provide the criteria utilized to assess the quality for collagen preservation; (3.) they also did not specify the method used to determine the sex of the individuals discovered at Lepenski Vir. Therefore, these results were here re-assessed using new δ^{13}C, δ^{15}N and δ^{34}S data, after updating individuals' chronological assignment and applying a homogeneous protocol of sexual diagnosis on the individual discovered at different sites (Lepenski Vir, Hajdučka Vodenica, Padina and Ajmana).

Evidence for a sex-specific pattern

Concerning the Early Mesolithic period, the interpretations are limited by the small size of the male sample (n males=3; n females=12); yet, it is worth mentioning that males range in the high part of females' δ^{13}C and δ^{15}N variability[96] (two of them exhibiting higher δ^{15}N than females and one higher δ^{13}C; Appendix A.II.21). Two Early Mesolithic males have been jointly analyzed for δ^{34}S and display higher values than the cohort of females (Appendix A.II.21; Figure 39). Nonetheless, it should be stressed that the males from this sample have been discovered at the site of Lepenski Vir, while most of the Early Mesolithic females have been discovered at the sites of Padina and Vlasac (Appendix A.II.21). We previously considered the possibility that certain localities along the Gorges may have provided particular spots for specific subsistence strategies, such as catfishing at Padina or sturgeon fishing at Lepenski Vir. Thus, the observed male-female stable isotope difference could rather be due to some inter-site behavioral and/or ecological differences. Interestingly, the only Early Mesolithic female from Lepenski Vir included in this study[97] displays lower δ^{34}S values than the Early Mesolithic males discovered at this site, falling within the range of the females from Padina (Appendix A.II.21). Yet, it should be mentioned that individuals of undetermined sex discovered at the site of Padina ranges within and even slightly lower than females variability for the isotopes of the three elements (Padina females: δ^{13}C=-19,9±0,3‰; δ^{15}N=14,2±0,2‰; δ^{34}S=6,4±1,4‰; Padina individuals of undetermined sex: δ^{13}C=-19,9±0,3‰; δ^{15}N=14,3±1‰; δ^{34}S=5,8±1‰). Therefore, in the current state of research, it remains difficult to favor the sex-related dietary difference hypothesis over the observed intra-site pattern.

Concerning the Late Mesolithic period, the fact that we had to remove from the interpretations an important number of individuals buried at Vlasac which have been analyzed in previous studies due to issues of collagen preservation, has substantially reduced the number of sex-determined individuals considered in this thesis (cf part 3.3.2. Some females are associated with lower δ^{15}N and higher δ^{34}S values than males (Appendix A.II.21), although this tendency is not statistically significant at the 0,05 level (Mann Whitney for δ^{15}N and δ^{34}S yet close to the significance threshold, respectively p=0,075 and p=0,088; Mann Whitney for δ^{13}C p=0,687). This tendency is reflected by the individual scores of the PCA (Figure 17). When considered per sites, it appears that the Late Mesolithic females discovered at Vlasac have a tendency to be associated with higher δ^{34}S values than males, but not with higher δ^{15}N (Mann Whitney for δ^{34}S close to the significance threshold with p=0,063; Mann Whitney for δ^{15}N p=0,4, and for δ^{13}C p=0,9; yet only 4 females and 5 males buried at Vlasac were analyzed for δ^{34}S). Since two males from Hajdučka Vodenica display the highest δ^{15}N values, it is also possible that the observed male-female difference might be rather related to some inter-site behavioral and/or ecological differences. Yet, the only Late Mesolithic fe-

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[96] LV 60 (δ^{13}C= -19‰; δ^{15}N=15,3‰ and δ^{34}S=8,5‰); LV 64 (δ^{13}C= -19,7‰; δ^{15}N=14,9‰); LV 69 (δ^{13}C= -19,4‰; δ^{15}N=14,4‰ and δ^{34}S=8,5‰);

[97] LV 68 (-19,7‰; δ^{15}N=14,6‰ and δ^{34}S=6,8‰);

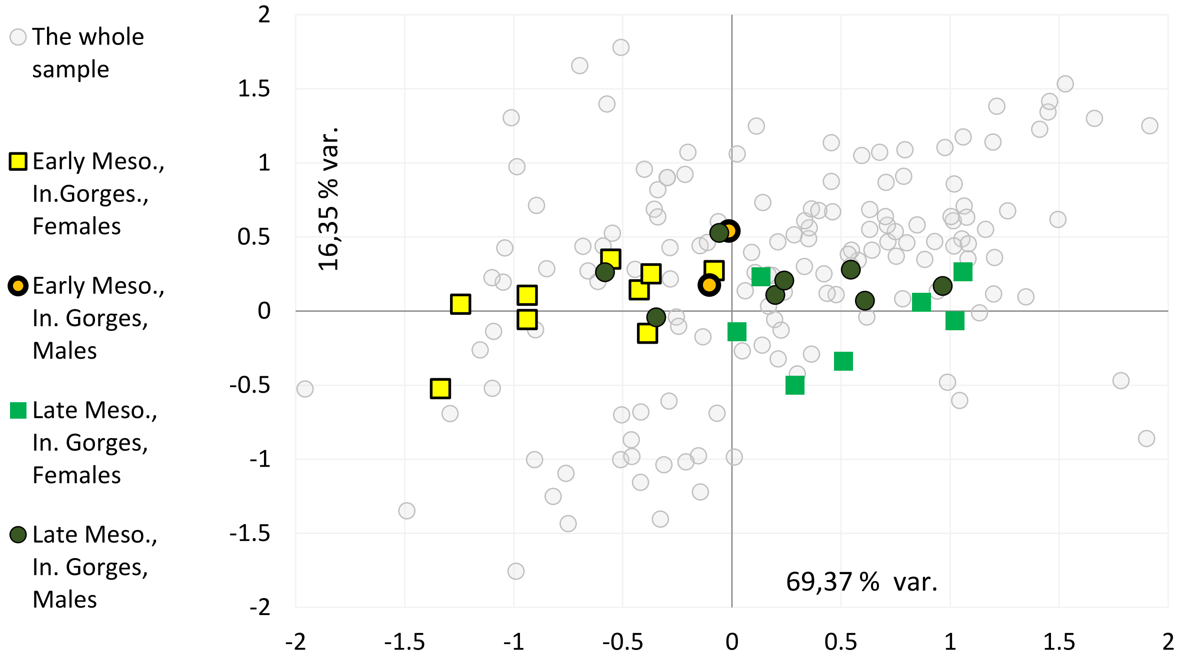

Figure 39: Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Mesolithic adults (>15 yrs) grouped per sex and per archaeological periods are here highlighted.

male from our sample discovered at Hajdučka Vodenica and included in this study also exhibits lower $\delta^{15}N$ than the three males from this site (two of them displaying the highest $\delta^{15}N$ values Appendix A.II.21). Finally, it should be recalled that the two Late Mesolithic males from Vlasac who exhibit the lowest $\delta^{34}S$ values have not been radiocarbon dated yet (individuals VL16 and VL26); the context of their discovery as well as their particular stable isotope signature warn for the accuracy of their chronological assignment[98]. When the Late Mesolithic sample is considered without these two individuals, only the tendency toward lower $\delta^{15}N$ values for females appears to be statistically significant (Mann Withney for $\delta^{15}N$ p=0,032; for $\delta^{34}S$ p=0,234 and for $\delta^{13}C$ p=0,784); besides, no significant difference appears when one considers independently the Late Mesolithic sample from Vlasac without these two individuals (Mann Whitney for $\delta^{15}N$ p=0,236; for $\delta^{34}S$ p=0,229, and for $\delta^{13}C$ p=0,815). Therefore, these results should be considered with caution, and further improvement in the protocols for sex diagnoses will be necessary to (un-)validate the observed tendencies.

Non-dietary explanations: migrations or physiology

In the case where the members of one sex are chosen for marriages in communities geographically distant it is possible that the biochemical signal of males and females will slightly differ in the analyzed population (as suggested by Bonsall et al. 1997). Indeed, given the slow remodeling rate of an adult bone[99], the collagen of incoming males or females can inform about their former dietary habits (before they migrated in the new community); it is also possible that the

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[98] The analysis of the common variance in the stable isotope values of the male VL 16 rather ranges him amongst the Early Mesolithic individuals ($\delta^{13}C$=-19,9‰; $\delta^{15}N$=16‰; $\delta^{34}S$=7,3‰). In the monograph of the site of Vlasac (Srejović and Latica, 1978), the authors mentioned "a disarticulated skull" found close to the lower limbs of the individual Vlasac 17 - himself ^{14}C dated to the Early Mesolithic. Given that VL 16 has not been ^{14}C dated, it may rather be assigned to the Early Mesolithic than to the Late Mesolithic.
The male Vlasac 26 has a very different stable isotope signature for the 3 elements ($\delta^{13}C$=-17,5‰; $\delta^{15}N$=11‰ and $\delta^{34}S$=4,2‰), differing from the whole Mesolithic and Neolithic population. His strontium radiogenic signal (0,709558) falls amongst the highest values of the local range; hence, although he has been identified as a local individual, the possibility of his non-local origin cannot be fully disregarded. Alternately, the combination of high $\delta^{13}C$ values but low $\delta^{15}N$ and $\delta^{34}S$ values could also be related to the consumption of C4 plants. If the consumption of C4 plants appears unlikely for the Late Mesolithic period, the individual Vlasac 26 has not been ^{14}C dated and it should be recalled that some individuals discovered at the site of Lepenski Vir have been dated to historical periods (Bonsall et al. 2004; Bonsall et al. 2008).

[99] 10-15 years are necessary for a complete turnover of adult bone (Valentin 2003)

incomers of one sex continue to perpetuate their former dietary habits in their community of adoption. However, it should be borne in mind that only a very few individuals were identified as non-locals amongst the Mesolithic anthropological assemblage of the Gorges (only three amongst the sample analyzed for stable isotope: one male and two females[100]). Therefore, if exogamy was practiced by the local Mesolithic communities, it should rather be understood as small-scale regional exchanges than as long-distance migrations. Besides, one would expect the practice of exogamy to influence more the isotopes of the carbon and sulfur element (more sensitive to environmental differences) than the isotopes of the nitrogen element and results reveal a possible tendency for Early and Late Mesolithic females to be associated with lower δ^{15}N values. This tendency concerning δ^{15}N ratios could also be related to the physiological effect of pregnancy, when the body enters positive metabolic balance, which leads to a depletion in the heavy isotope of nitrogen (Fuller et al. 2004). Yet, it should be borne in mind that the stable isotopes values analyzed in the bone collagen at an adult age should reflect an average dietary signal over several years[101] and that attempts to find a "pregnancy effect" on modern osteoanthropological assemblages, for which historical records concerning the numbers of childbirth per woman were available, have been unsuccessful (Nitsch et al. 2010).

Resources allocation, dietary taboos and labor organization

Alternately, sex-related stable isotopes differences could also be related to the preferential access to certain food for the members of one sex, or to particular dietary taboos (Bonsall et al. 1997). It has been evidenced amongst many foraging societies, that some food taboo coincides with critical periods of females' reproductive career such as menarche, pregnancies, lactation and, sometimes, menses (Spielmann 1989; Speth, 1990). These taboos are most often related to the consumption of meat and particularly fresh meat. It is thus possible that frequent protein restrictions may have resulted in a subtle lowering of females δ^{15}N values in comparison with males, females rather favoring the consumption of fat-rich and carbohydrate-rich foods during these periods of life. In the Danube Gorges, it would be tempting to relate such a system of food taboos - or of preferential access to some food resources - to the symbolic values that were probably assigned to some animal species (e.g. Borić 2005a, 2007a). Interestingly, it has been noticed that, in the early phase of Vlasac, ocher – which red color, uncommon in the natural environment, may recall the blood – was incorporated into burials regardless of age or sex, while later males were excluded from this practices, and the pigment was exclusively sprinkled on the pelvic area of females and perinates (Radovanović1996; Borić and Stefanović 2004).

A preferential access to some food resources for the members of one sex may also be due to the sexual division of labor; it is indeed ethnographically documented that, amongst foragers, females often specialize in gathering while men often specialize in hunting (e.g. Speth 1990; Bird 1999). The participation in lengthy hunting expeditions may allow males greater access to wild game meat. Some Late Mesolithic males buried at Hajdučka Vodenica and at Vlasac were perhaps more involved in fishing and wild-boar hunting (higher δ^{15}N) than females buried at Vlasac; yet, it remains unclear whether or not they favored the consumption of different fish species (no δ^{13}C difference; higher δ^{34}S for females buried at Vlasac?). Surprisingly, the analyses of External Auditory Exostosis show that the frequency of exostosis was higher in the auditory meatus of Late Mesolithic females (32%) than in the meatus of the Late Mesolithic males (19%) buried at the site of Vlasac, which suggests that females were perhaps more engaged in some activities that involved a frequent contact with cold waters than males (although this difference did not prove to be statistically significant; Villotte et al. 2014). Besides, the preliminary results of on-going analyses of skeletal markers of physical activities have also shown a pattern of gradual reduction in the frequency of muscle attachments' micro-trauma and in the robusticity of muscle attachments over time, which is greater

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[100] the Early Mesolithic female Pad 30 (δ^{13}C=-21,5‰; δ^{15}N=12,2‰; analyzed by Boric and Price 2013, in the absence of available information about collagen preservation this individual not included in the study), the Late Mesolithic female VL 32 (δ^{13}C=-20,2‰; δ^{15}N=13,2‰; δ^{34}S=11,2‰) and the Late Mesolithic male HV 11 (δ^{13}C=-19,4‰; δ^{15}N=14,9‰; δ^{34}S=9,6‰)

[101] 10-15 years are necessary for a complete turnover of adult bone (Valentin 2003)

amongst females (cf part 2.3.2; de Becdelièvre et al. 2013, 2015, 2017, unpublished oral and poster presentations[102]). Similarly, the preliminary results of ongoing analyses of body proportions have also shown that, between the Mesolithic and the Neolithic period, males became on average shorter, but their average weigh remain the same, while females' average size and weigh both decline substantially between these two periods (ibidem); yet, this pattern could be related both to changes females' patterns of subsistence and physical exertion and/or to the arrival of females with different body proportions during the Early Neolithic period, which is also supported by the strontium radiogenic evidence.

These different behavioral, morphological and symbolic line of evidence raises the hypothesis of possible changes in some aspects of social organization, in the status of females' their access to resources and/or their role in the community. To increase the amount biochemical data for accurately sex-determined individuals represents hence now an important prospect of research to better understand the relationship between sedentism and social complexification amongst society of hunter-gatherers prior to the appearance of the agro-pastoral way-of-life, as well as the possible impact of the sedentary lifestyle on our biology.

4.2.4.4. Age-related stable isotope differences

Concerning the age at death, the sulfur axis discriminates middle-aged and old individuals for the Early Mesolithic period (Appendix A.II.29). However, here again the three old individuals originate from the anthropological assemblage of Lepenski Vir, while the others originate from the assemblage of Padina or Vlasac; besides, this difference is not reflected by the PCA (Appendix A.IV.12). For the Late Mesolithic Period, there is a possible difference between middle aged and old adults on the nitrogen axis (Appendix A.II.29), but this is not reflected by the PCA (Appendix A.IV.12) and this tendency could also rather be associated to the observed sex-related dietary differences.

4.2.5. General summary and discussion: sedentism, intensive fishing and structured societies

Subsistence adaptation, local specialization and social organization

Interpreted in combination with δ^{13}C and δ^{15}N values, the new δ^{34}S results presented in this study have provided further insights into subsistence adaptations over the Mesolithic period in the Danube Gorges. Previous paleodietary studies had emphasized the importance of fishing in the local Mesolithic ways of subsistence, alongside with the hunt of terrestrial mammals - particularly red deer and wild boar - and with the collect of a wide range of wild plants (e.g. Srejović and Letica 1978; Radovanović 1996; Bonsall et al. 1997; Bartosiewicz et al. 2001; Borić et al. 2004; Borić and Dimitrijević 2007; Filipović et al. 2017; Živaljević 2017). In this study, we observed a shift up in δ^{34}S signals during the first part of the 7th millennium BC, and jointly elevated δ^{13}C and δ^{15}N values for some individuals. This generalized shift up in δ^{34}S values could be related to an increased consumption of anadromous-potamodromous fish species during the Late Mesolithic and/or to a shift up in the δ^{34}S values of these fish, due to important environmental changes that occurred in the Black Sea during the Early Holocene. There is indeed a body of geomorphological, biochemical,

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[102] de Becdelièvre C., Jovanović J., Stefanović S., Porčić M. 2013. Female mobility during the Mesolithic and the Neolithic in the Danube Gorges (Balkans, 9500-5500BC). Research presented at the Conference on the 150th Anniversary of the discovery of the shell middens at Muge.(21.-23.03.2013. Muge, Portugal).
de Becdelièvre, C., Porčić, M., Goude, G., Le Guen M.A, Jovanović, J., Stefanović, S. 2015. From individual mobility to population dynamics during the Mesolithic and Neolithic transformations in the Danube Gorges (Balkans, ca. 9500–5500 BC): Adaptations and interactions. Research presented at MESO 2015, The Ninth International Conference on the Mesolithic in Europe. (14.-18.09.2015. Belgrade, Serbia).
de Becdelièvre, C., Le Guen M.A., Porčić M., Jovanović, J., Stefanović, S. 2017. Behavioral Adaptations - Morphological Adaptations: new contributions from Morphometric Mapping for the understanding of Mesolithic-Neolithic transformations (Balkans; 10 000 - 5000 BC). Research presented at the 7th Annual Meeting of the European Society for the study of Human Evolution (ESHE) (21.09.-23.09.2017. Leiden, the Netherlands).

and radiocarbon evidence to suggest a reconnection of the Black Sea to the global ocean from 7000 cal BC (e.g. Ryan et al. 1997; Soulet et al. 2011). This increased marine water incursion from the enlarging Bosphorus strait should have affected the δ^{34}S signal of long distant migrating species and further of the Danube Gorges foragers who ate the fish. The hypothesis of an environmental shift in the δ^{34}S values of the Black Sea ecosystem could be compatible with changes in the consumption of aquatic resources by the Late Mesolithic foragers of the Gorges, considering that the increased salinity of the Black Sea should have considerably changed the biota and consequently may have affected different aspects of fish ecology (type of species represented? Greater presence of anadromous species? Changes in their reproductive or migrative behaviors?). This hypothesis remains to be confirmed by conducting δ^{34}S analyses on a broader sample of well-dated fish bones discovered in Early and Late Mesolithic contexts; it may provide some important contribution to the current debate on the modality and the ecological consequences of the salinization of the Black Sea and open some further prospects on its impacts on the subsistence adaptations of the Early Holocene foragers who lived on the surrounding coastal environments or along the tributaries of the Black Sea basin (e.g. Agacli Mesolithic groups, Danube Gorges or Dniepr foragers).

In addition, the δ^{34}S results have confirmed that dogs substantially fed on aquatic resources – notably anadromous fish – either because they consumed human leftovers, in relation with their specific position as the only domesticated species (accepted in the "domestic" sphere?), or perhaps because they accompanied humans during activities related to fishing or to fish-processing. Interpreted in the light of archaeozoological documentation, the stable isotope values have also indicated that humans may have been consuming dogs and, at least occasionally, fed the dogs with their own canine meat. The observed shift up in humans' δ^{34}S values noticed at the beginning of the 7th millennium BC may thus be related humans' consumption of aquatic resources, but also of the meat of dogs' fed on the fish. In the Gorges, the remains of dogs – particularly their mandibles or skulls – were found deposited in Late Mesolithic and Transformational contexts at Vlasac, Lepenski Vir and Kula, in the same ways as red deer antlers (Srejović and Letica 1978; Radovanović 1999; Živaljević et al. 2017). "Neither person, nor beast" (Radovanović, 1999), dogs certainly held a particular position in the daily life and in the symbolic world of local foragers and the choice of placing their mandibles in humans burials during the Late Mesolithic may echo either the effect that had domestication on the jaws and the bark of the animal or the particular relationships that human and dogs share within the local foodways.

Human and animal stable isotope results have also revealed specific inter-site variations which, when interpreted in the light of archaeozoological documentation, confirm that individuals buried at different locations along the Gorges should have been consuming certain resources in different proportions. For instance, it is likely that anadromous fish species should have been more consumed by the individuals buried at Lepenski Vir than by those buried at Padina during the Early-middle Mesolithic. Concerning the Late Mesolithic period, although the global shift up in δ^{34}S values confirms that anadromous/potamodromous species were significantly consumed by the local foragers, we also observed subtle inter-sites differences in the isotopes of the three elements which are consistent with available information from the archaeozoological documentation. Namely, the anadromous vyrezub and/or dogs' meat may have been consumed in greater amount by the Late Mesolithic individuals buried at Vlasac than by those buried at other sites, the individuals buried at Padina may have favored the consumption of catfish, and the individuals buried in the Lower Gorges may also have included a greater amount of some high trophic level resources in their diet (big fish, fish roe or waterfowl birds? wild boars?). This pattern could notably be linked to the presence of favorable conditions for fishing different species and to their differential availabilities at various locations along the river (the presence of "good fishing spots" for catching different species).

Finally, the results have indicated a tendency towards different males and females' stable isotope values concerning the Late Mesolithic period, namely a tendency towards lower δ^{15}N values and higher δ^{34}S values which yet remains difficult to interpret in terms of dietary habits. Food taboos towards the consumption of meat or fish during specific periods of females' reproductive careers have been ethnographically documented amongst many groups of hunter-gatherers across the world (e.g. Spielmann, 1989; Speth, 1990) and might hypothetically result in lower $\delta^{15}N$ values (as previously mentioned by Bonsall et al. 1997). Interestingly, it has been previously noticed that ocher was exclusively sprinkled on the pelvic area of females and on the bodies of neonates during the later Mesolithic phase of occupation of Vlasac (Radovanović1996; Borić and Stefanović 2004). A preferential access to some food resources for the members of one sex may also result from the sexual division of labor. Other morphological lines of evidence have also indicated some differences between males and females, interpreted in terms of a frequent contact with water (Villotte et al. 2014) and of activity-related adaptations to the sedentary way of life (cf part 2.3.2; de Becdelievre et al. 2013 and 2017, unpublished poster presentations[103]). Increasing the amount of biochemical data for accurately sex-determined individuals – notably by using biomolecular methods of sex determination, by achieving additional targeted stable isotope sampling and by analyzing the stable isotope of specific amino-acids, should now enable to further explore some aspects of the social organization of the local Mesolithic communities.

On fishing and sedentism during the Early Holocene

The $\delta^{34}S$ results have thus confirmed the importance of long-distance migratory species in the local ways of subsistence at least from the Late Mesolithic period, which is of particular interest in a context of increased sedentism along the riverbanks during the Early Holocene. Indeed, ever since the discovery of the sites of the Schela Cladovei - Lepenski Vir culture, it has been suggested that fishing played a crucial role in the formation of prehistoric settlements in the Danube Gorges (Jovanović 1969; Srejović 1969, 1972; Bartosiewicz et al. 1995; Radovanović 1996, 1997; Bartosiewicz et al. 2001; Borić 2001; Borić and Dimitrijević 2007; Jovanović 2008; Dinu 2010; Živaljević 2012). The classical view developed between the 1960's and the 1980's of increasingly complex foraging societies suggests that groups of nomads, who hunted terrestrial mammals and lived in caves during the Epipaleolithic / Early Mesolithic periods, reduced their residential mobility to establish semi-permanent settlements on the banks of the Danube during the Late Mesolithic / Transformational periods under an intensified practice of fishing (Radovanović 1996). This view mainly arose from the relatively scarce evidence for the Early Mesolithic human occupation of the Gorges, which sharply contrasts with the Late Mesolithic and Transformational impressive mortuary record, sophisticated architectural features, and substantial amount of animal bone remains and artifacts. It should yet be borne in mind that Early Holocene foragers' mobility patterns should have been manifold and complex, including for instance the permanent stay of only a part of the community, as well as frequent, lengthy and long-distance expeditions, complex networks of settlements of different functions, and multiple variations in patterns of seasonal occupations[104]. Besides, the adoption of a sedentary way of life has certainly not been a straightforward trajectory during the four millennia of the Early Holocene and should have encompassed periodic episodes of return to a more mobile way of life.

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[103] de Becdelièvre C., Jovanović J., Stefanović S., Porčić M. 2013. Female mobility during the Mesolithic and the Neolithic in the Danube Gorges (Balkans, 9500-5500BC). Research presented at the Conference on the 150th Anniversary of the discovery of the shell middens at Muge.(21.-23.03.2013. Muge, Portugal).
de Becdelièvre, C., Le Guen M.A., Porčić M., Jovanović, J., Stefanović, S. 2017. Behavioral Adaptations - Morphological Adaptations: new contributions from Morphometric Mapping for the understanding of Mesolithic-Neolithic transformations (Balkans; 10 000 - 5000 BC). Research presented at the 7th Annual Meeting of the European Society for the study of Human Evolution (ESHE) (21.09.-23.09.2017. Leiden, the Netherlands).

[104] The evidence for a year-round occupation of the settlements in the riverbank should not be interpreted as an indication that the local groups of sedentary foragers were remained enclosed societies. Indeed, occasional excursions and long distance exchanges were most likely practiced as it is suggested by the presence of shells of marine mollusks from the Adriatic and/or the Black sea region found in some Late Mesolithic graves from Vlasac and Schela Cladovei (Srejović and Latica 1978, Boroneanţ et al. 1999). The technique to plaster dwellings' floors, which appears during Late Mesolithic on the site of Vlasac, also recalls the lime plaster pyrotechnology in use in Western Anatolia from the first part of the 7th millennium BC (and earlier in other regions of the Near East), evoking possible long-distance contacts between local Danubian foragers and Western Anatolian farmers (Borić 2011).

Reduced residential mobility and subsistence adaptations in the Early/middle Mesolithic

There is some evidence for a reduction of daily mobility prior to the Late Mesolithic period. For instance, the presence of a vast burial ground associated with solid stone constructions in the Early Mesolithic layers of Padina (e.g. Jovanović 1987; Borić 2011) suggests a more permanent occupation than one would assume in the case of a temporary hunting camp. The fact that most Early Mesolithic humans originate from the Gorges, according to their strontium radiogenic signature, also indicates that the patterns of residential mobility should have been restricted to a broad regional territory (Borić and Price 2013). Observed differences in lithic assemblages between the Epipaleolithic site of Cuina Turcului and the Early Mesolithic layers of Padina have been related to a modification of hunting strategies and to longer stays at this latter settlement (Mihailović 2008). In addition, there is both anthropological and archaeozoological evidence to suggest that Epipaleolithic and Early Mesolithic foragers were consuming fish or that their subsistence activities should have been in part oriented towards the river. Their elevated $\delta^{15}N$ values suggests the consumption of high trophic level resources, fish or substantial amounts of terrestrial omnivores or carnivores' meat. The study of External Auditory Exostosis – a condition shown to be related to the exposition of the ear canal to cold water – has suggested that both Early and Late Mesolithic foragers buried in the Gorges were in very frequent contact with water (Villotte et al. 2014). Besides, major differences have been noticed in the faunal assemblages between layers dated to the Late Pleistocene and layers dated to the Early Holocene, not only concerning the representation of different species of terrestrial mammals, but also of aquatic species, including notably a broadening of represented species[105] (Borić 2011, Živaljević 2017). The environmental changes of the Late Pleistocene-Early Holocene transition might thus be associated with longer stays at sites located along the riverbanks and to an adaptation of subsistence strategies – notably concerning fishing practices – as early as the Early/middle Mesolithic period.

Late Mesolithic sedentary way-of-life, and fish harvesting

Statistical tests of the summed probability distribution of a substantial dataset of radiocarbon dates from Epipaleolithic to Neolithic sites recently performed has confirmed a significant increase in the intensity of occupation of the Gorges during the first half of the 7th millennium BC (cf part 2.3.2; Porčić et al. 2014, de Becdelievre et al. 2019, poster presentations[106]). The oldest forms of dwellings with plastered floors and stone lined rectangular hearths, discovered in Late Mesolithic contexts at the site of Vlasac, have been dated to the first half of the 7th millennium BC (Borić 2011); several structures with approximately trapezoidal shape base and central rectangular hearths were also discovered at the Late Mesolithic site Schela Cladovei (Radovanović 1996; Boroneanț 2001). The analyses of the proportion of different type of chipped stone tools and lithic raw material discovered in Late Mesolithic contexts have also suggested an "extended stay" at some sites, as well as the more frequent visits of others, and indicated that Late Mesolithic settlements were more oriented towards workshop activities than Early Mesolithic assemblages, where hunting activities seemed of greater importance (Mitrović 2018). The representation of different animal species at the two Late Mesolithic assemblages for which water sieving has been practiced – Vlasac and Schela Cladovei – attests that a broad range of animal species was being exploited, including various species of small mammals, birds, reptiles amphibians

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[105] While bream is the dominant fish taxon in both layers Cuina Turcului, a broader number of aquatic species has been discovered in the latest layer (Late Pleistocene – Early Holocene transition; Borić 2011 data from Nalbant 1970; Bolomey 1973); the recent reassessment of ichthyofaunal assemblages from Mesolithic contexts of Padina (Early to Late Mesolithic) and of Lepenski Vir (Early-Middle Mesolithic) has also confirmed the presence of a broad range of species, with a dominance of huchen (at Lepenski Vir), catfish and vyrezub (at both sites; Živaljević 2017). It should yet be kept in mind that the archaeozoological documentation may suffer from representativeness biases, since water-sieving has been practiced only at Schela Cladovei and in the most recently excavated layers of Vlasac, and given that the faunal record for some sites has been studied as a single units and not as separate phases.

[106] Porčić M., de Becdelièvre, C., Le Roy, M., Jovanović, J., Stefanović ,S., Thomas ,M., Shennan ,S, Timpson, A. Investigating local demographic fluctuations during the Mesolithic and the Neolithic in the Danube Gorges :a review of radiocarbon, skeletal and settlement evidence. Research presented at *the 20th European Association of archaeologists Annual Meeting. (*10-14.09.2014, Istanbul, Turkey).
de Becdelièvre, C., Blagojević, T., Jovanović, J., Porčić, M., Hofmanová, Z., Stefanović, S. Paleodemography of the Danube Gorges Mesolithic and Neolithic Transformations: comparing radiocarbon, skeletal and molecular evidence. Research presented at Jean-Pierre Bocquet-Appel Tribute Conferences. (02-03. 07. 2019. Aix-en-Provence, France).

and mollusks (Bartosiewicz et al. 1995, 2001; Borić et al. 2014); the presence of these lower-ranked preys could be related to an intense exploitation of local resources and to the extended stay at the sites. The reexamination of archaeozoological indicators of seasonality of food resource exploitation carried out by Dimitrijević and colleagues (2016) also supported the hypothesis of a year-round occupation of Late Mesolithic-Transformational settlements. Interpreted together, these different archaeological lines of evidence suggest that the local occupation of the Gorges should have been more intense between the end of the 8th millennium and the mid-7th millennium BC under the effect of a further reduction in residential mobility – or a new episode of sedentism – and of an intense exploitation of local resources.

Based upon the observation of differences in the ratios of terrestrial mammal bones versus fish remains between Late Epipaleolithic - Early Mesolithic faunal assemblages (Cuina Turcului, and Padina I) and later Mesolithic contexts (Vlasac and Schela Cladovei), it has been suggested that fishing might have been increasingly important in the course of the Mesolithic (Borić 2011, data fromNalbant 1970; Bolomey 1973; Bökönyi 1975, 1978; Clason, 1980; Bartosiewicz et al. 1995, 2001). A recent reassessment of ichtyoarchaeological data has indicated a substantial increase in the number of catfish bones at Padina between the Mesolithic and the Transformational phase, of the remains of carps and of the anadromous vyrezub at Lepenski Vir between the Early-middle Mesolithic and the Transformational phase, and the strong dominance of vyrezub remains in the Late Mesolithic-Transformational layers of Vlasac (Živaljević 2017). These data are broadly consistent with the observed shift up inδ^{34}S results which confirms the important consumption of anadromous species during the first half of the 7th millennium BC and with the patterns of intra-site stable isotopes variations. There are also other archaeological elements to suggest some adaptations of fishing strategies in the Gorges in the course of the Mesolithic: for instance the remains of a few harpoons, absent in Early-middle Mesolithic contexts, have been discovered in Late Mesolithic contexts; some components of the Late Mesolithic local ground stone industry have also been interpreted, in the light of the local histo-ethnographic documentation, as weights for fishing nets and as "fishing mallets" (Antonović 2003, 2006, 2008; Borić 2002a). Indeed, archives and ethnographic records for the 18th to 20th centuries relates the local utilization of mallets as fish stunners, but also of fences, fishnets, and particular basket traps to catch big fish, notably anadromous species, in the whirlpools created by the specific geomorphology of the Gorges. Since the remains of fishing tools (e.g. fish hooks and harpoons) were only scarcely found it has been suggested that similar techniques of fishing traps, nets and stunners could have been used by the local Late Mesolithic fishermen (e.g. Borić 2002a; Antonović 2008; Bartosiewicz et al. 2008; Dinu 2010; Živaljević 2012). Finally, the essential role played by the Danube river in the lives of Late Mesolithic foragers is also reflected by their burial ritual: the extended position parallel to the river with the head pointing upstream, recall the seasonal migration of sturgeons to go spawning, became the local mortuary canon during that period (Radovanović 1996).

The assumption that the local fishermen occupied sites on a year-round basis, at least from the Late Mesolithic period, has led some authors to consider the possible existence of food storage systems for wintertime (Voytek and Tringham 1989; Bonsall 2008). For instance, the quadrangular stone lined structures, common features of Mesolithic settlements in the Danube Gorges usually considered as hearths, have been alternatively interpreted as storage structures by Voytek and Tringham (1989). Bonsall (2008) mentions that the soil infilling of one such feature excavated at Schela Cladovei contained a large number of fish bones, which were not fire-damaged, and that magnetic susceptibility readings on soils samples failed to identify the pit as hearth. It is also possible that these quadrangular pits may have been used whether to smoke and/or as platforms to sun-dry the fish and/or to stock the food for winter months. In addition, domesticated dogs should have also jointly provided the local Late Mesolithic foragers with a convenient food repository available year-round.

Early Holocene sedentism and subsistence intensification: the seeds of the agro-pastoral transition

When interpreted together these different lines of evidence suggest two possible scenarii: (1.) a more permanent occupation of sites located on the riverbanks during the Early/middle Mesolithic, associated with a gradual intensification in the exploitation of local food resources, which led to the development of specialized fishing strategies at some locations during the Late Mesolithic; (2.) a discontinuous occupation of the Gorges in the course of the Mesolithic which notably involved the more intense and more permanent occupation of some sites after 7400 cal BC, associated with an intense exploitation of local resources and the development of specialized fishing techniques. In any cases, the first centuries of the 7th millennium BC can be linked to the construction of more permanent structures, an increased intensity of occupation and the substantial consumption of anadromous-potamodromous fish species, perhaps more numerous during their seasonal migrations to the upper stretches of the Danube after 7000 cal BC. Various species of stationary freshwater and anadromous fish were caught at different spots along the Gorges probably according to their differential availability, and dogs - also fed with marine-influenced proteins - should have represented an additional food repository. This pattern of reduced residential mobility, intensified exploitation of river resources and increased population-size at some sites may have affected some aspects of local foragers' social organization and of their symbolic world.

Such (semi-)sedentary lifestyle has also been suggested for various populations of Epipaleolithic and Mesolithic foragers in Western Eurasia (Rowley-Cowny 1983, Price and Brown 1985, Zvelebil 1986; Wilson 1992), such as the Natufian in the Levant (Bar-Yosef et al. 1989), the inhabitants of the sites of Star Carr or Oronsay in the British Islands (Conneller et al. 2012; Mithen 2000), of Skateholm in South Scandinavia (Larsson 1990), or of the Muge and Sado shell middens in the Iberian Peninsula (Bicho et al. 2010). In different regions of the Near-East, the Epipaleolithic and PPNA periods have been associated with the construction of more permanent settlements, with an intensified exploitation of resources in restricted environments – such as gazelle or wild herbaceous plants – and with the development of storage capacities (e.g. Flannery 1968; Bar-Yosef et al. 1989; Bar Yosef 1998; Kuijt, and Finlayson 2009; Layton and Conwy 2011; Munro 2009). In Europe, most of the areas with evidence for intense Mesolithic occupation are located along the coasts and close to major bodies of water. Numerous lines of archaeozoological and stable isotope evidence now suggest that many groups of European Mesolithic foragers were substantially consuming aquatic resources, fish, sea or freshwater mammals and mollusks (e.g. Tauber 1981; Price 1983; Zvelebil 1986; Richards and Schulting 2001; Shulting 2011; Lillie and Budd 2011; Dupont and Marchand 2016). For instance, the Early Mesolithic hunters and fishers from the site of Norje-Sunnasund in Southern Scandinavia practiced food-storage and specifically developed some fish fermentation techniques which implied a daily return subsistence strategy (Boethius 2017). The Atlantic inhabitants of the Iberian shell midden also intensively collected fish and mollusks during the 6th millennium BC (Bicho et al. 2010). The same process of reduced residential mobility and subsistence intensification which lead, in regions of the Near-East, to the gradual domestication of animal and plant species could thus be suggested for different regions of Europe during the Early Holocene, such as the Danube Gorges. However, apart from dogs, the behavioral and genetic characteristics of most targeted resources in the abundant environments of Early Holocene temperate Europe did not lead to the similar process of morphological adaptations which characterizes the appearance of agriculture per se. The type of harvested resources and the balance between environmental conditions, subsistence intensification, and population growth rate amongst European Mesolithic foragers likely did not make such behavioral response to Early Holocene ecological changes necessarily, or even possible.

4.3. The Neolithic subsistence: traditions, interactions and adaptations

Adults human values are presented in Appendix A.II, B.I.-II. In the Inner Gorges, for the Transformation/Early Neolithic period human adults' isotopic ratios range from -20.7‰ to -18‰

(Δ=-19.3‰; n=34) for carbon, 10.3‰ to 16.8‰ (Δ=14.5‰; n=34) for nitrogen and 3.9‰ to 14.8‰ (Δ=11.3‰; n=21) for sulfur. Concerning the subsequent Early-Neolithic period in the Inner Gorge, values range from -20.3‰ to-18.3 ‰ (Δ=-19.3‰; n=23) for carbon, 9.4‰ to 17‰ (Δ=13.4‰; n=23) for nitrogen and -3‰ to 14.5‰ (Δ=8.6‰; n=16) for sulfur. The values of Early Neolithic individuals buried in the Downstream Area values of range from -20.3‰ to -19.2‰ (Δ=-19.7‰; n=9) for carbon, from 9.6‰ to 11.7 ‰ (Δ=10.5‰; n=9) for nitrogen and from 8‰ to 8.6‰ (Δ=8.2‰; n=6) for sulfur (Appendix A. II.1-2; 4; 6; 18; 20).

The $\delta^{13}C$ and $\delta^{15}N$ results suggest that a broadening of human dietary spectrum occurred during the period of Transformation and the subsequent Neolithic period in the Danube Gorges. This local variability encompasses both some individuals who favored the consumption of aquatic resources and some who preferred proteins derived from terrestrial foodstuffs (as extensively discussed by Bonsall et al. 1997; Grupe et al. 2003; Borić et al. 2004; Nehlich 2009; Bonsall 2015b; Figure 40; Appendix A.II.4; 6; 18; 20). New data obtained for the stable isotopes of the sulfur element support these observations, and a further integration of geographical and biological variables now shed a new light on the local paths of Neolithization. Rather than a sudden dietary shift, stable isotope results provide the picture of gradual changes within a global pattern of continuity in the local environment of the Gorges.

4.3.1. Temporal trends, subsistence variability at the onset of the Neolithic

4.3.1.1. Subsistence practices during the period of Transformation - Early Neolithic

During the period of Transformation some individuals have slightly higher $\delta^{13}C$ and $\delta^{15}N$ than during the previous Mesolithic period. The new results for $\delta^{34}S$ confirm this trend (Figure 41). However, since we also observe a slight increase from the Mesolithic to the Neolithic in the $\delta^{15}N$ stable isotope ratio of freshwater fish and possibly in the $\delta^{13}C$ stable isotope ratio of anadromous fish (the only anadromous fish dated to an Early Neolithic context exhibit higher $\delta^{13}C$ values, Appendix A.II.9), human higher values may be rather explained by local environmental changes than by the inclusion of more fish in the diet. In any cases it confirms that the diet of some individuals dated to the Transformational-Early Neolithic period was focused on the consumption of fish. In contrast, for this period, a group of individuals have significantly lower values in $\delta^{13}C$ and $\delta^{15}N$ than the rest of the population; they also exhibit lower $\delta^{34}S$ values (Figure 41). Since there are no similar diachronic tendencies in faunal stable isotope ratios (Appendix A.II.7-13), the lower $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values observed for some individuals should rather be related to behavioral differences than to environmental factors. A third group of individuals range in between those with high stable isotopes values and those with low stable isotopes values (with $\delta^{13}C$ values ranging between ca -20‰ and -19.5‰, $\delta^{15}N$ values ca 13-14‰ and δ^{34} values ca 9-11‰). This broad range of stable isotope values is also reflected by the scattered scores of the PCA (Figure 42; Appendix A.IV.5).

4.3.1.1.1. Fish and dogs' consumers

A continuous fish consumption

The highest values observed in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ can be explained by a continuous consumption of anadromous/potamodromous fish and probably jointly of dogs (upper and lower right quadrants of the PCA; Appendix A. IV.3; 5). A similar continuity with pervious Mesolithic traditions is also documented by the archaeozoological record. For instance, for the phase of Transformation and the Neolithic phase of Lepenski Vir, the remains of cyprinids, catfish and huchen have been found

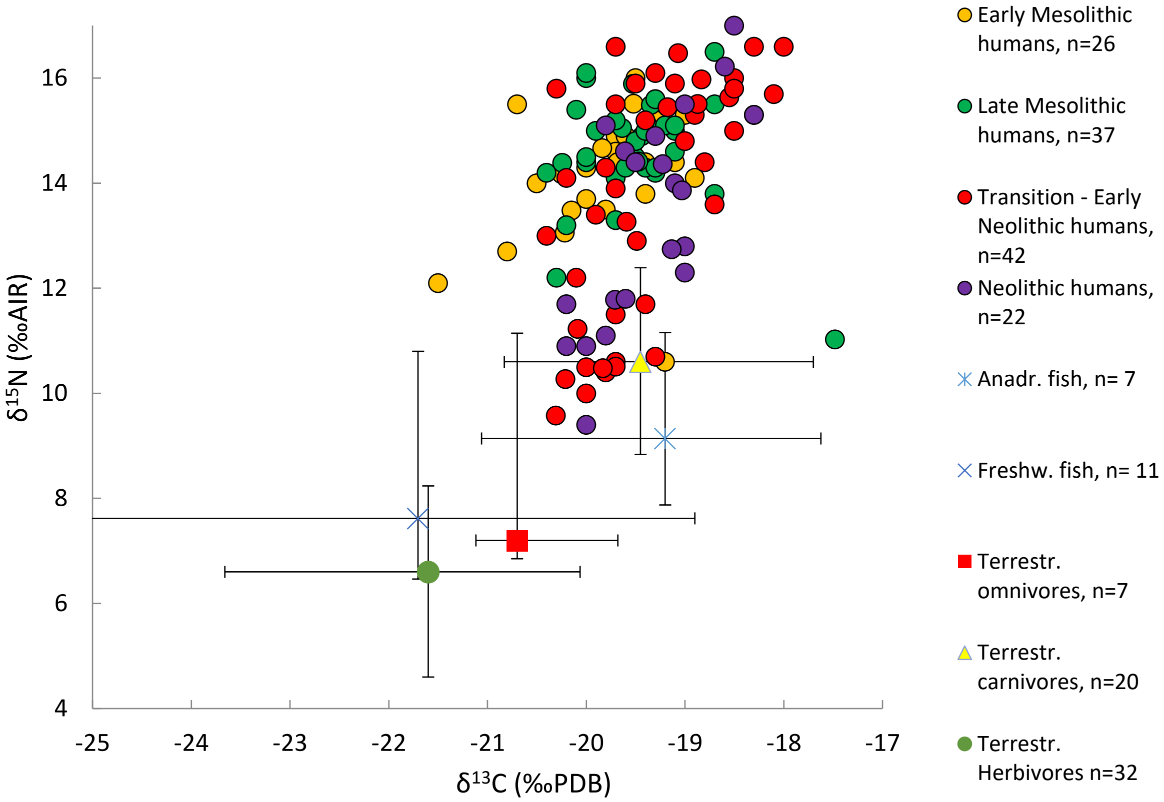

Figure 40: Bivariate plot of δ^{13}C and δ^{15}N for adult humans (>15 yrs) and animals from the prehistoric sites of the Danube Gorges

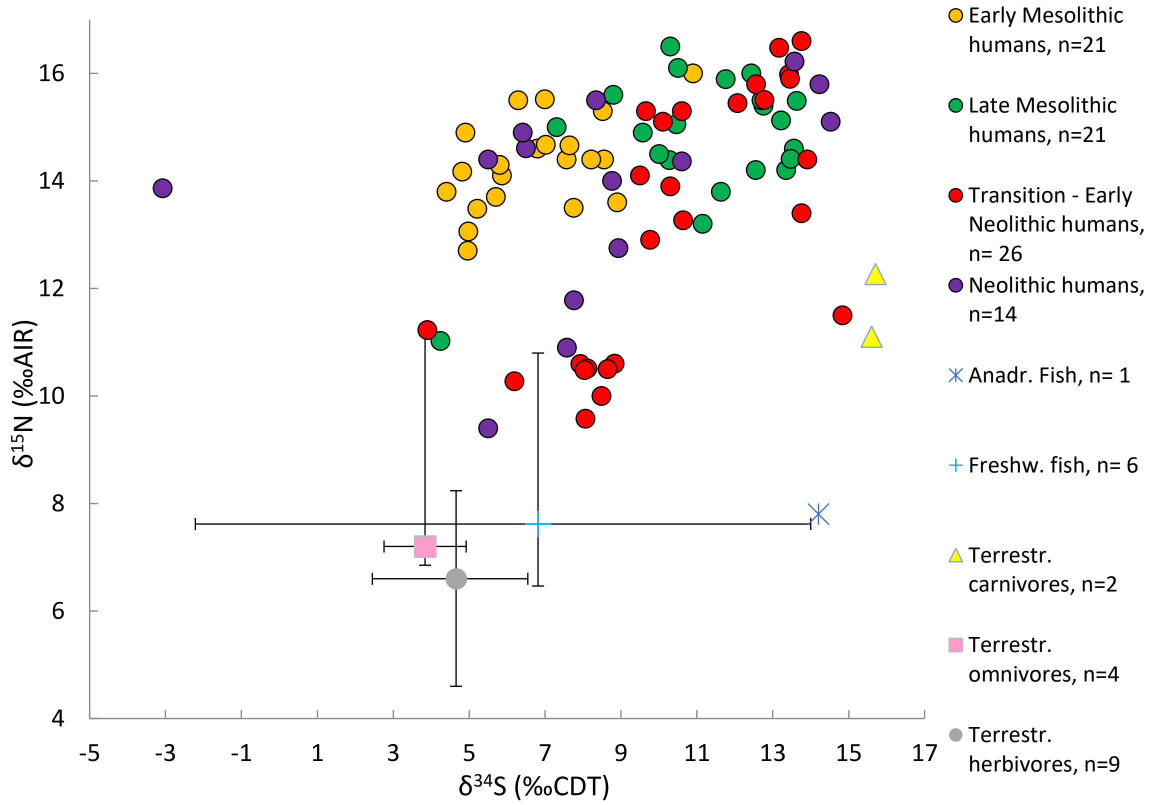

Figure 41: Bivariate plot of δ^{34}S and δ^{15}N for adult humans (>15 yrs) and animals from the prehistoric sites of the Danube Gorges

numerously, together with acipenserids[107] also extensively recorded amongst the Mesolithic and Neolithic fauna at Schela Cladovei (Bartosiewicz et al. 1995; Zivaljević 2017). The remains of dogs were also found numerously in most of the Early Neolithic phases of Lepenski Vir, Schela Cladovei, Hajdučka Vodenica and Padina (e.g. Bökönyi 1969, 1972; Bartosiewicz et al. 1995; Dimitijević 2000, 2008; Borić and Dimitrijević 2006; Dimitrijević and Vuković 2015). These slightly higher averages $\delta^{13}C$ and $\delta^{15}N$ values have been related to the 8.2 ky BP cooling event by some scholars who suggested that more severe winters and increased flooding threats may have urged the local foragers to a greater reliance on the consumption of stored resources and of the meat of dogs, available year-round (Bonsall et al. 2002, 2008; 2014). Indeed, the hearths uncovered at several sites dated to the transformational-Early Neolithic period (e.g. Lepenski Vir; Padina) appear more complex; some are surrounded with particular ∀-shaped stone constructions that may have been used as bases to wedge some sort of wooden scaffold structure perhaps utilized for drying and/or smoking the food (Radovanović 1997). The elaboration of these hearths, placed on the centre of more sophisticated trapezoidal buildings, could thus be related to a greater need for storing dried or smoked foodstuffs which year-round consumption may have contributed, to a certain extent, to elevate humans' stable isotope values. However, it should be considered that Transformational-Neolithic freshwater fish appears slightly elevated in $\delta^{15}N$ values in comparison with Mesolithic fish, and given that the only anadromous fish from our sample dated to the Transformational period also exhibits slightly higher $\delta^{13}C$ than those discovered in a Mesolithic context (Appendix A.I.7; A.I.9; A.I.11), it is possible that the Neolithic individuals with elevated stable isotope values did not consume more fish than the individuals dated from the previous periods, but it for sure confirms that tthese individuals should have included more fish and/or dogs' meat in their diet than their contemporaries who display the lowest stable isotope ratios.

Human, fish and dogs, "fluid boundaries"

Interestingly, during this period the inhabitants of Lepenski Vir sculpted anthropo-zoomorphic boulders, amongst which many present several anatomical features of the human and sturgeon bodies mixed (Srejović 1969). These sculptures have been interpreted as "apotropaïc representations of mythical ancestors" or "fish-gods" (Srejović 1972), maybe created with the idea to protect the sedentary population against the growing threat from flooding of the Danube (Bonsall et al. 2002). Alternatively, these symbolic boulders have also been considered as a means for local foragers of asserting their traditions at a time when the Early Neolithic farming communities were already spreading in the Southern Balkans (Radovanović 1997). Now, the $\delta^{34}S$ and $\delta^{13}C$ stable isotope results have revealed that the individuals buried at the site of Lepenski Vir during the Early Mesolithic period were probably already consuming more sturgeons that their contemporaries buried at Vlasac and Padina, maybe in relation with fishing facilities provided by the local natural conditions[108]. Therefore, one may suggest that the symbolic values assigned to these big fish by the Early Neolithic fishermen could root in the deep-time of the Mesolithic; it is possible that the long-term tradition of fishing sturgeons at Lepenski Vir may have led the local foragers to associate this "sturgeon spot" with a place where the human-sturgeons "totemic relationship" was created. Thereby, the symbolic association between the human body and the body of this fish has been analyzed as an evidence for the "fluidity" of the relationships between humans and animal species in local foragers' mindsets (Borić 2003a and b, Borić 2005a, Živaljević 2012, Živaljević 2015).

These "fluids boundaries" between humans and animals have also been suggested for other species, all of major importance in the local subsistence. Red deer antlers - symbol of seasonality, rebirth, and life cycles - have been found associated with the dead inside several burials of Lepenski Vir or placed on the top of abandoned floors of some houses from Lepenski Vir (Borić 2003). The only species locally domesticated during the Mesolithic, dogs, have also been found deposited in

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[107] acipenserids were more represented on the assemblage of Lepenski Vir than for other sites of the Upper Gorges (Živaljević 2017).

[108] "Lepenski Vir" can be translated from Serbian into "the whirlpool of Lepenski".

funerary contexts at Vlasac, Lepenski Vir or Kula (Srejović and Letica 1978; Radovanović 1999; Živaljević et al. 2017). Dogs probably held a particular position in the daily life of local foragers, remaining closely related to their settlements (accepted in the domestic sphere?) and sharing with them similar meals made of fish. According to Radovanović (1999), dog might have been perceived as "neither person nor beast". Dogs' mandibles were mostly found associated with human bodies[109], perhaps as a personification of the whole animal (Radovanović 1999, Živaljević 2015) whose domestication contributed to shorten the jaws and to overcrowd the teeth (Dimitrijević and Vuković 2015). Placing dogs' mandibles within human burials may also be interpreted as an achievement - or a further step - in this cycle where human shared their meals with the dogs, ate the animal (or "absorbed" it), and also fed it with its own meat[110]. Since human skulls and mandibles were often found disarticulated, it is even possible that some dogs may have been treated in death the same way than human, in a related - similar, joint or complementary - mortuary rite[111]. Finally, hundreds of teeth of the anadromous vyrezub, have also been found within some burials of Vlasac and Schela Cladovei, used as appliqués on clothing that cover large part of the bodies of the dead Cristiani et al. 2012). These different sorts of connexions between the human and the animal bodies indicate that their interactions in the prehistoric Danube Gorges must have gone far beyond the simple prey-predator dietary relationship.

4.3.1.1.2. Meat and plants' consumers

A different dietary behavior

In contrast, the lowest stable isotope values observed for a group of individuals dated to the period of Transformation could clearly be related to a different dietary behavior: a greater consumption of terrestrial proteins than their contemporaries buried in the Gorges. While the consumption of proteins from freshwater fish may also have contributed to the observed $\delta^{13}C$ and $\delta^{34}S$ signals, yet it is unlikely that humans' lowest stable isotope values were only derived from their consumption since the difference between the lowest $\delta^{15}N$ values of humans and the average $\delta^{15}N$ value of freshwater fish here is only 2‰, i.e. below the documented $\delta^{15}N$ prey-predator offset (Appendix A.I.1; A.II.1). These lower values are thus most likely related to the consumption of terrestrial proteins, whether proteins from hunted game, from domestic animals, or from C_3 plants. For now, no bones of pig, cattle or ovi-caprines - the Neolithic triad of domestic animals - have been dated before 6 ky BC in the region of the Gorges (Borić and Dimitrijević 2007). For C_3 plants to influence human stable isotope signatures analyzed in bone collagen, one would expect their consumption in much larger extent than the consumption of animal meat, since stable isotope analyzed in collagen should mostly reflect the protein part of the diet (Ambrose and Norr 1993; Fernandez et al. 2012) and given that animal meat contains proteins easy to metabolize for the human body in a greater extent than C_3 plants. Therefore, it can be assumed that the group of individuals with low $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values consumed C_3 plants in a higher extent than the individuals with high stable isotope ratios and that their diet included more plants than meat; though, it is most likely that they jointly consumed the meat of wild game and perhaps additionally some freshwater fish. Such plants may have belonged to various wild species of gathered berries, roots, green-leaf plants, and tubers (etc...) or to the Early Neolithic species of domestic crops. The evidence that cereals were consumed during the Mesolithic-Neolithic occupation of the Danube Gorges is yet very scarce (Filipović et al. 2017).

These individuals are located in the lower left quadrant of the PCA, which points to their mixed diet (plants, meat of terrestrial mammals and freshwater fish) and confirms that anadromous species and dogs did not represent an important part of their usual meals (Figure 42). Despite the absence of remains from domesticate in the Gorges before 6 ky BC, it remains yet possible that the

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[109] Except concerning grave 81 at Vlasac where the skeleton of dog has been found articulated but headless (Srejović and Letica 1978).

[110] carnivorous gnawing marks being documented on dogs' long bones, Dimitrijević 2008.

[111] according to Živaljević 2015, dogs' mandibles might have occasionally "slipped" into the role occupied by human mandibles.

biochemical signature of these individuals may have been largely influenced by the consumption of cereals and livestock, in case they died within the following years after their arrival in the Gorges (the stable isotope values analyzed in bone collagen would hence not reflect their latest dietary adaptation[112]). In any cases, it is worth mentioning that the broadening of humans' stable isotope range toward lower values echoes the appearance of some Neolithic technologies in the Gorges such as ceramics and bone spoons during this period[113] (Borić 2011). Furthermore, it has been hypothesized that some ground stone artifacts – the so called "mallet-scepters" discovered in the transformational context of Lepenski Vir and made of different raw materials – should have been "imported" from Neolithic communities settled in the Balkans (Antonović 2008). It is possible that these "mallet-scepters", as well as other ground stones and the curved stones "altars" could have been used to process plants. Interpreted in the light of stable isotope results, the presence of such technologies supports the idea that a wind of change started to blow around 6200 BC, introducing some novelties in the local dietary behaviors and cooking habits.

4.3.1.2. Subsistence practices during the Early-Middle Neolithic period

4.3.1.2.1. Neolithic stable isotope variability

Continuity in $\delta^{13}C$ and $\delta^{15}N$ variability

After the period of Transformation/Early Neolithic, the Neolithic period (the "Early-Middle Neolithic") has been defined mostly based upon the arrival of the Neolithic triad of domestic animals and on a change in the nature of the settlements (abandonment of trapezoidal buildings and development of wattle and daube above-ground dwellings; Borić 2011). Similarly, to the previous Early Neolithic period, the range of δ^{15}N and δ^{13}C values encompassed by Neolithic individuals is also broad. Some individual display high δ^{15}N values (above 14‰, Figure 40; Appendix A.II.4) and δ^{13}C values (above -19,6‰ for most of them; ibid.), suggesting a continuity with local Mesolithic dietary traditions. In contrast, other display lower δ^{15}N and δ^{13}C values (respectively below 12 ‰ and below -19.6‰; ibid), falling thereby into the same range than the lowest values previously noticed for some Early Neolithic individuals. Three individuals range in between these two extremes for δ^{15}N (around 13‰) but also have slightly elevated δ^{13}C values (ca 19‰; ibid). Based on δ^{15}N and δ^{13}C values, one may already suggest several different dietary behaviors: one group of individuals who extensively consumed fish and/or the meat of dogs (high δ^{13}C and δ^{15}N), in continuity with local Mesolithic dietary traditions, one group of individuals who may have consumed more proteins derived from terrestrial animals, from plants and perhaps jointly from freshwater fish (lower δ^{15}N and δ^{13}C values) and one group ranging in between (with middle-range δ^{15}N values and rather elevated δ^{13}C values) who perhaps included equally fish and meat or favored the consumption of different species (rather omnivorous than herbivorous mammals? rather freshwater than anadromous fish?).

A shift down in $\delta^{34}S$ values

A specific pattern appears on the δ^{34}S axis: only four Neolithic individuals display δ^{34}S values exceeding 9‰ most Early Neolithic individuals ranges between 9-15‰ (Figure 41; Appendix 20[114]). This Early Neolithic to Neolithic δ^{34}S shift down is significant for the individuals buried at the site of Lepenski Vir (Mann-Whitney for $p < 0,05$). These lower δ^{34}S values could whether be interpreted as: (1.) a dietary shift toward the consumption of terrestrial animals and freshwater fish rather than dogs and anadromous fish; (2.) a shift in the δ^{34}S values of anadromous fish and/or a joint change in the availability of sturgeons in the Danube Basin (as previously suggested for the Late Mesolithic period); (3.) the arrival of migrants with a different δ^{34}S signal and possibly different dietary habits.

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[112] about 10-15 years is required for the entire turnover of an adult bone, and thus for a complete renewal of the stable isotope signal (Valentin 2003).

[113] which may have appeared a bit earlier in the Downstream Area, but only after 6000 BC on the site of the Inner Gorges.

[114] 11 upon 14 individuals analyzed have a δ^{34}S value lower than 9‰, including most of the Neolithic individuals with high δ^{13}C and δ^{15}N signals.

Neolithic anadromous fish analyzed for sulfur do not exhibit any particular stable isotope increase (Appendix A.I. 10-11) which may support the environmental δ^{34}S shift hypothesis. Yet, because of the difficulty that we encountered to extract well-preserved collagen from fish remains[115], the sample of "Neolithic" fish with δ^{34}S values is particularly small –

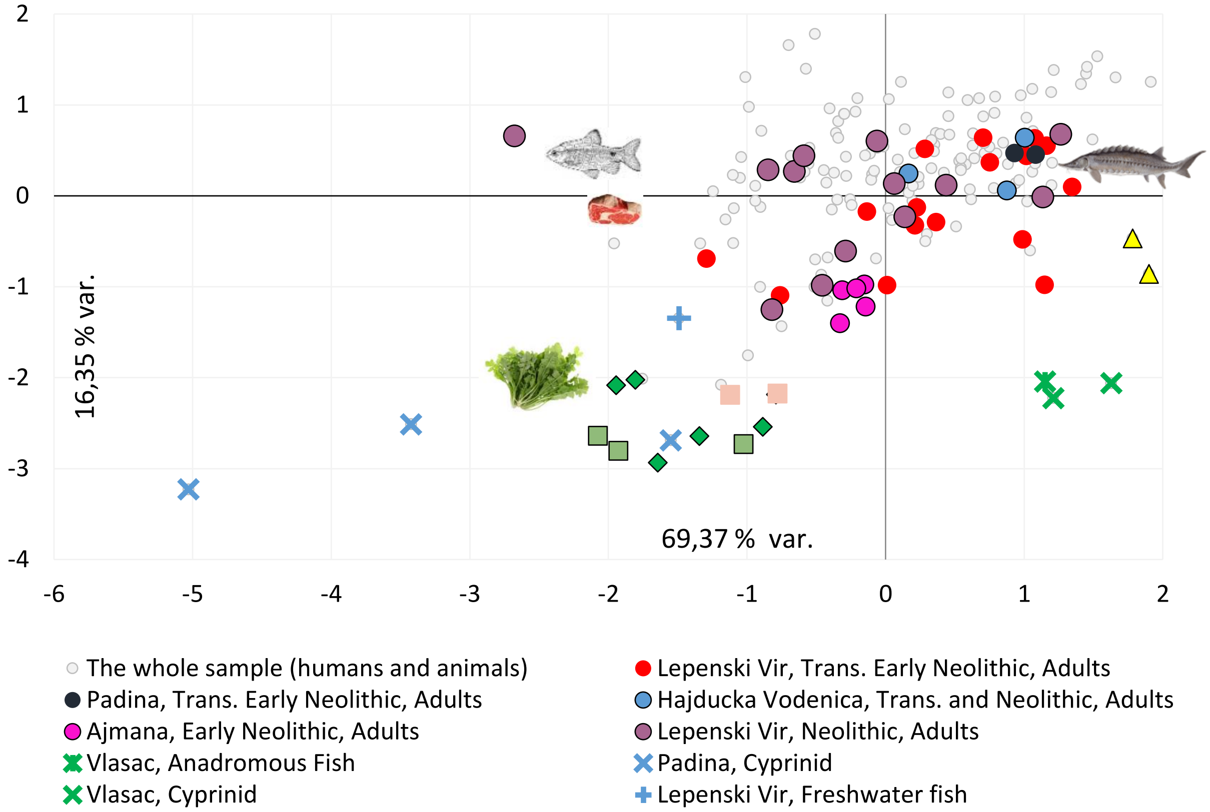

Figure 42: Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from collagen protein. Individual scores for Trans. and Neolithic adults (>15 yrs) grouped per archaeological periods and per sites and for different animal groups per sites are here highlighted.

two anadromous fish and two freshwater fish are dated to the Neolithic period - all being associated to the Transformation/Early Neolithic period[116] (before 6000 BC). It is thus possible that the beginning of the Late Atlantic climate warming during the 6th millennium BC - after the 8.2 ky cooling event - could have affected the whole hydrological system of the Danube, of the Black sea and of their tributaries. On the other hand, the δ^{34}S study by Calvert and colleagues for pyrite from the Black Sea does not show any significant decrease in δ^{34}S values, at least not of similar magnitude than the fast increase noticed on layers related to the Late Pleistocene - Early Holocene periods (Calvert et al. 1996). Furthermore, in case of an environmental effect on δ^{34}S values, one would have expected the signals of all individuals to be lower; yet the δ^{34}S values obtained for three Neolithic individuals range amongst the highest values obtained for the whole prehistoric sample[117] (Appendix A.II.6). Besides it is worth mentioning that only five Neolithic individuals exhibit δ^{15}N values that exceed 15‰ (versus fifteen Early Neolithic individuals; Appendix A.II.4) - three of them jointly display δ^{13}C values that exceed -19‰ (versus twelve Early Neolithic individuals; Appendix A.II.4). The three Neolithic individuals with the highest δ^{34}S values (above 11‰) also exhibit elevated δ^{15}N (>15‰; Appendix A.II.6). Therefore, it is possible that the Early Neolithic to

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[115] A similar difficulty in extracting well preserved collagen from fish remains was also seemingly encountered by Nehlich et al. (2009) for the analysis of the sulfur element and by Fuller (2012) for the analysis of the carbon and nitrogen elements, who included many fish specimens that exceeded the collagen quality criteria.

[116] No successful collagen extraction on ^{14}C dated specimen related to the 6th millennium BC

[117] The very high δ^{34}S ratios cannot be related to an error in chronological assignment since two of these individuals have been ^{14}C dated to the Neolithic period: LV 7/IIb (6080-5746 cal B.C; Borić 2011) and HV 13 (6010-5720 cal BC; Borić 2011).

Neolithic $\delta^{34}S$ shift down could be jointly associated with slightly lower $\delta^{13}C$ and $\delta^{15}N$ values (although not statistically significant at the population level; Mann Withney for $p < 0,05$), which would rather suggest a dietary than environmental explanation. Besides, given that numerous non-locals have been pinpointed amongst Neolithic individuals buried at Lepenski Vir, the Neolithic lower $\delta^{34}S$ values might therefore be rather related to some behavioural differences than to some environmental factors.

Three different dietary tendencies during the Neolithic

The results of the Principal Component Analysis indicate a broader variability for the Neolithic period (Figure 42). Three groups of individuals can thus be distinguished amongst the Neolithic cohort (Figure 42). A first group of individuals (group 1) jointly display lower $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values (located in the lower right quadrant of PCA; Figure 42), indicative of a diet mostly focused on terrestrial proteins (C_3 plants and meat) with a possible input of freshwater fish. These individuals fall within the exact same range of values than the Transformational-Early Neolithic individuals with lower stable isotope signatures. Another group of Neolithic individuals (group 2) display higher $\delta^{15}N$ but rather low $\delta^{13}C$, and much lower $\delta^{34}S$ (in the upper left quadrant of the PCA; Figure 42): the diet of these individuals should have included freshwater fish as well as the meat of terrestrial animals. Their high $\delta^{15}N$ signal shows that their diet was for sure not focused solely on the consumption of C_3 plants. Finally, a last group of individuals (group 3) still fall in the range of anadromous/potamodromous fish and dog's consumers dated back to the previous periods of Transformation or Late Mesolithic[118]. One individual has significantly lower $\delta^{34}S$ values than the rest of Neolithic individuals (and of all prehistoric humans), while remaining in the range of Neolithic human for $\delta^{13}C$ and $\delta^{15}N$ values (individual LV 52[119], located at the extreme right of the PCA; Figure 41; Figure 42). Since $\delta^{34}S$ is related to environmental differences (especially to marine-coastal versus inland environments), it is possible to explain the lowest values noticed for this individual by his possible migration in the Gorges, probably within the last years of his life[120] (no strontium radiogenic signal obtained for this individual in the study of Borić and Price, 2013).

4.3.1.2.2. Neolithic novelties

Since the Neolithic triad of domestic animal appears in the archaeozoological spectrum of the sites of the Inner Gorges during the first half of the 6th millennium BC (Borić and Dimitrijević 2007), the consumption of their meat - and maybe of dairy - could be amongst the possible explanations for the lower stable isotope values of some Neolithic individuals (group 1 and 2, lower in $\delta^{13}C$ and $\delta^{34}S$). Indeed, the wild and the domestic fauna display similarly low stable isotope signals[121] (Appendix A.1.14). However, one should also emphasize that, in every sites of the Inner Gorges, domestic animals only represent a minor part of the fauna. At Lepenski Vir, where Neolithic domesticates are the best-represented, only 25% of identified herbivores and omnivores were of domesticated morphology (Greenfield 2008). The hunt of wild game remains thus most probably important in the local Neolithic way of subsistence. Although the discovery of domestic taxa of plants is still discussed in the prehistoric sites of the Gorges (Filipović et al. 2017), their consumption appears quite probable during the Neolithic period given that the remains of crops have been recovered in several other sites dated to the 6th millennium BC and located close-by in the central Balkan (Filipović and Obradović 2013). A greater consumption of cereal might thus explain, to a certain extent, the lowest stable isotope values obtained for some Neolithic individuals (group 1: lower $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$). It is worth mentioning that bone spoons appear in the cultural

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[118] These elevated scores cannot be related to an error of chronological assignment since three individuals belonging to this group 3, LV 73 and LV 7/Ia and HV 13 have been ^{14}C-dated to the Neolithic period (respectively 6080-5746 cal B.C, 6005-5845 cal BC and 6010-5720 cal BC, Borić 2011).

[119] Individual aged at death more than 15 years old, of undetermined sex, disarticulated skeleton.

[120] before the local $\delta^{34}S$ signal to be recorded in his collagen.

[121] Yet, one can notice that domestic herbivores range in the higher part of wild herbivores $\delta^{15}N$ variability (Appendix A.1.14), which could be whether due to: (1) the inclusion of slightly higher trophic resources in their fodders; (2.) a kind of "byre" effect - similar to soil manuring (domesticates perhaps stayed closer to their faeces and urines, enriched in $\delta^{15}N$, than wild animals).

repertoire of the prehistoric sites of the Inner Gorges after 6 ky BC[122], as well as new kind of "domed oven" (Borić 2011), which suggests that the Neolithic dietary adaptations inferred from the archaeozoological and biochemical data may have coincided with some local changes in cooking practices, means of food elaboration or ways of food absorption.

Interestingly, the results of the study of External Auditory Exostosis performed by Villotte et al. (2013) has indicated a decrease of their frequency through time, with more than 30% of exostoses recorded on the Mesolithic sample, 20% on the individuals dated to the period of Transformation and only 6% on the Neolithic individuals discovered at Lepenski Vir; besides, the study suggests that the individuals with the lowest δ^{15}N values does not display auditory exostoses. Althoug there is probably a genetic component to this condition, it has been related to a frequent contact of the head with cold water, leading the authors to interpret the decrease of their frequency during the Neolithic in the Gorges as "a decrease in the significance of fishing after 6200 cal BC", yet in a regional context of global "continuity in the exploitation of riverine resources".

Beyond documenting some change in dietary preferences, the fact that the δ^{34}S signature of most Neolithic individuals does not seem to be influenced by the signal of dogs and of anadromous fish may also reflect some further changes in the local mindsets. Dogs were perhaps then raised for purposes of hunting or to protect the herds, rather than used as a food repository. The values assigned to the different species may have changed with the adoption of animal husbandry. The "fish gods" were not sculpted anymore during the Neolithic in the Gorges. At this time, the contemporaries Anatolian and Balkans' first farming societies preferred to express the symbolic dimension of bovid, as suggested by the frequent discovery of bucranium in domestic or mortuary contexts dated to the 7th and 6th millennium BC (Cauvin 1994).

4.3.1.3. Summary: stable isotope evidence for foragers and farmers interactions in the Gorges

Carbon, nitrogen and sulfur stable isotope signals indicate **a broader variability in the dietary choices of Transformational/Early Neolithic (ca 6200-5950 BC) and Early/middle Neolithic individuals (ca 5950-5500 BC), in comparison with the previous Mesolithic period (ca 9500-6200 BC**). **The elevated stable isotope signatures of some Early Neolithic individuals indicate that they substantially consumed aquatic resources - and specifically anadromous fish - as well as the meat of dogs, in continuity with the previous Late Mesolithic traditions.** Such continuity is also documented by the archaeozoological record. For a few individuals, the stable isotope signal appears even higher than during the previous period, which might be related to a greater reliance on stored resources (dry/smoked fish and or domesticate canidae which represents a food repository available year round) in the context of climatic deterioration (8.2 ky cooling event). Yet, one cannot disregard the possibility that these higher values might also be related to a diachronic environmental trend toward elevated stable isotope values for fish maybe due to ecological changes occurring downstream in the Black Sea (increasing salinity through the Early-Middle Holocene?). Interestingly, this period is featured by the sculpted anthropo-zoomorphic boulders at Lepenski Vir, amongst which many presents several anatomical features of the humans' and sturgeons' bodies mixed. At a time when early farming communities settled in the Balkans, these original symbolic creations could be interpreted as a means for local foragers to assert their cultural and behavioral traditions, as totemic representations of local ancestors, or as offering to the Danube God. These symbolic association between the human body and the body of the fish may also reflect the fluidity of the relationships between the species, symbolic connections that probably included the dogs - only domesticate species in the Gorges at that time - who were fed on the fish and on the meat of their own species, who were consumed by humans and whom mandible sometimes accompanies humans in the burials.

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[122] Some bone spoons discovered on the site of the Downstream Area could be slightly older, perhaps dated to the decades before 6000 BC, given the ^{14}C dates obtained for humans from these sites (Bonsall et al. 2015a).

In contrast, some Early Neolithic individuals favored the consumption of terrestrial proteins - from C_3 plants and from the meat of herbivores - perhaps with an additional input of freshwater fish. Yet, no remains of the Neolithic triad of domestic animals have been discovered in the Gorges at this period and the evidence for the consumption of cereal prior 6 ky BC is still scarce and debated; it is possible that these individuals may have mostly consumed wild gathered plants and the meat of wild games. Since some Neolithic technologies were adopted (e.g. ceramics, ground stone artifacts...) at the end of the 7th millennium BC in the region, it is also possible that some novelties may have been introduced in the local dietary behavior and perhaps in cooking habits.

While the network of early farming communities is developing in the Central Balkans and the Pannonian plain **during the first half of the 6th millennium BC,** some changes occurred in the Gorges in terms of cultural repertoire (new type of wattle and daube above-ground dwellings; domed ovens...), and of ways of subsistence (Neolithic domesticated species of animals, perhaps of crops). In contrast with the previous period**, less individuals consumed dogs and anadromous fish; some individuals rather favored the consumption of terrestrial proteins from C_3 plants and herbivores (meat and milk from domesticate?) while other included more freshwater fish in their diet.** The development of the "Neolithic" thus most likely occurred gradually within the Gorges, probably through successive interactions with neighboring farming communities. Some members of the neighboring Neolithic communities may have migrated into the Gorges and sustained their mode of subsistence whether based on agro-pastoral traditions or on wild game hunting, freshwater fishing and plant gathering. This last strategy may also have arisen from an adaptation of migrants' traditions to the local mode of subsistence. At the same time, some local foragers may have favored the consumption of meat from hunting games or from domesticate herbivores, and preferred plants or crops over the consumption of anadromous fish and dogs. Considering the archaeozoological record and given the absence of evidence for a significant storage of starch grains in the Gorges, **it seems that agro-pastoral activities remained subsidiaries in the local prehistoric economy, probably because this environment was not suitable for the very early farming practices, because it was a place plenty of wild resources, or because of the strong local foraging traditions.** It should anyway be borne in mind that some Neolithic individuals may have also settled in the Gorges during a late period of their lives, and that their stable isotope may rather inform on their former dietary habits, which then could explain a discrepancy between their biochemical signal and the local archaeozoological and botanical documentation. The rejection of dogs' meat and anadromous fish consumption by many Neolithic individuals may also indicate that they assigned some different values to these species, which could reveal a deeper change in the local mindsets (different symbolic values assigned to domesticate species such as cattle? A different function and place for dogs?). New $\delta^{34}S$ results interpreted together with contextual data thus suggest that, despite some continuity with previous foraging traditions, some important socio-cultural and behavioral changes also featured the 6th millennium BC in the Gorges. A thorough examination of inter-site and intra-site variations, notably examining the diet of the different socio-biological categories of the population and their mortuary context, can shed further lights on the local path of Neolithization.

4.3.2. Spatial tendencies: inter-sites stable isotope differences

4.3.2.1. A wide stable isotope variability at Lepenski Vir

For the period of Transformation and the Neolithic period, some important inter-site differences can be observed in the Inner Gorges. Individuals buried at Lepenski Vir account for the wide range of stable isotope values, including both very high and very low $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ values (Appendix A. II. 13; 15). This biochemical variability could be due to the particular status that was probably attributed to the site at the end of the 7th millennium BC. Indeed, the site of Lepenski Vir is known for the number of sophisticated trapezoidal buildings furnished with reddish limestone floors and the associated sculpted boulders. Some sculptures - mixing humans and sturgeons bodily features - recall the importance played by anadromous fish in the local subsistence, a tradition which may root on the deep time of the Mesolithic. The important mortuary record of Lepenski Vir also features new practices that point to the South-Eastern Neolithic sphere such as burying neonates under the floors, or the presence of new ornaments such as limestone, spondylus and nephrite beads. Many non-locals have been identified in the osteoanthropological assemblage using the strontium radiogenic signal (Borić and Price 2013). Interpreted together, these different features suggest that the site could have represented a central place of particular ideological significance, where the population from neighboring localities gathered for specific social events, symbolic or mortuary ceremonies (Chapman 1989; Bonsall et al. 1997). Apart from the time when these social gathering may have taken place, the site could have been occupied year-round, as suggested by the archaeozoological study carried out on the seasonality of resources exploitation there (Dimitrijević et al. 2017). At the end of the 7th millennium cal BC, Schela Cladovei at the very entrance of the Gorges ceased to be occupied on a regular basis, which has been interpreted as a consequence of the climatic deterioration of the 8.2 ky cooling event, and increased risks of Danube flooding (Bonsall et al. 2002b, Bonsall 2015); to gather and settle on the sites of the Upper Gorges may have represented then for local foragers a practical and/or symbolic means to counter-act the increasing threat of the flooding of the Danube and to celebrate the "Fish God" of Lepenski Vir (Srejović 1972). Alternatively – or in addition - it is also possible that the foraging population of the broader region regrouped on the localities of the Upper Gorges because of the intensified Neolithic presence in the Southern Balkans during this period. The "fluorescence" of Lepenski Vir in the Upper Gorges at the end of the 7th millennium (Bonsall 2008) may have resulted from the contacts with these Early Neolithic communities, foragers perhaps accepting or prompting these interactions and affirming at once their original cultural identity.

During the first half of the 6th millennium BC, further important socio-cultural changes occurred at Lepenski Vir as suggested by the abandonment of the trapezoidal buildings, the end of the boulder artwork, the adoption of the typical Neolithic crouched position, the appearance of new sort of wattle and daub dwellings and of domed ovens, and the introduction of animal husbandry (Borić 2011). It is thus possible that the site evolved toward a different model of occupation, keeping nonetheless its "gathering function", as indicated by the broad range of stable isotope values also encompassed by the individuals dated to the Neolithic. The site of Lepenski Vir was then perhaps occupied by the descendants of the local foragers, but also of the migrants who arrived before 6000 BC and by new generations of migrants who settled there at the beginning of the 6th millennium BC.

4.3.2.2. Places of foraging traditions in the Inner Gorges

The δ^{15}N and δ^{34}S values of the Early Neolithic individuals buried at Padina in the Upper Gorges and at Hajdučka Vodenica and Icoana in the Lower Gorges (δ^{34}S values only for Padina and Hajdučka Vodenica) fall within the upper part of the range of the individuals buried at Lepenski Vir (Appendix A.II. 13-16; 18; 20). Such inter-site difference has already been noticed for the previous Mesolithic period in terms of lower δ^{13}C for the individuals buried at the site of Padina, and higher δ^{15}N for the individuals buried at Hajdučka Vodenica[123]. It may indicate a continuous reliance on

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[123] Although the quality criteria for the collagen preservation of the Early Neolithic individuals buried at Padina were not provided by the authors (Borić and Price 2013) and measured with an AMS device (as well as the stable isotopes of individual discovered at Icoana), no statistically significant difference (for Mann Whitney test at $p < 0,005$) was found neither between the individuals from Padina for whom the criteria of collagen preservation were respected and those for whom these criteria were not available, nor between the Early Neolithic individuals for whom the criteria of preservation were respected and those for whom these criteria were not available. Besides, the only statistical difference observed between these two groups (with and without collagen quality criteria) was found for some Late Mesolithic individuals discovered at Vlasac and concerns the stable isotope of the carbon element and not the nitrogen element. It is also noteworthy that the individuals from Icoana and Padina display the same elevated δ^{15}N values

aquatic resources at these sites as well as the inclusion of long-distance migratory fish species and of the meat of dogs in the local diet. Indeed, apart from the remains of wild game - red deer and wild boars - the bones of dogs have been found numerously in the Early Neolithic layers of Padina, together with a very large number of fish bones, mostly catfish (Clason 1980; Zivaljević 2017)[124]. Regarding the ichtyorchaeological record, the high δ^{34}S values of the two individuals discovered at Padina are thus surprising given that one would expect catfish - of lower δ^{34}S ratio - to be the staple food there. And yet, in the light of stable isotope results, the individuals buried in Padina during the Early Neolithic have probably consumed more anadromous fish than the individuals buried there during the previous Late Mesolithic period, and than most of their contemporaries buried in other sites of the Gorges. All but one adult Neolithic[125] individuals analyzed for stable isotope originate from the osteoanthropological assemblage of the site of Lepenski Vir[126], which restricts possible spatial comparison for this period. Nonetheless, one individual from Hajdučka Vodenica (HV 13) is dated to the Neolithic[127] and also show particularly high δ^{15}N and δ^{34}S ratios (highest δ^{34}S ratios than the individuals from Hajdučka Vodenica related to the period of Transformation but lowest δ^{13}C; Appendix A.II.14; 16; 18; 20).

The diet of the individuals buried at Padina, and Hajdučka Vodenica most likely relied on the consumption of aquatic resources, ever since the Mesolithic period, perhaps because these places were known for being particularly good fishing spots. It is interesting to note that, while Neolithic domesticates represent more than 25% of the Neolithic fauna discovered in Lepenski Vir, they only account for 15% of the faunal remains discovered in Hajdučka Vodenica and only 7% of the faunal remains discovered in Padina (Greenfield 2008). Considering the small numbers of livestock bone and the scarcity of early Neolithic burials uncovered at these localities, it has been suggested that these sites could have rather been used as seasonal fishing camps than as permanent residential places (Bonsall 2008). Given that Hajdučka Vodenica, Icoana and Padina were continuously occupied from the Late Mesolithic to the Neolithic period (Borić and Miracle 2004), these localities may also have represented some places of strong local identity where the foragers perpetuated the local fishing traditions, only accepting some aspects of the Neolithic package.

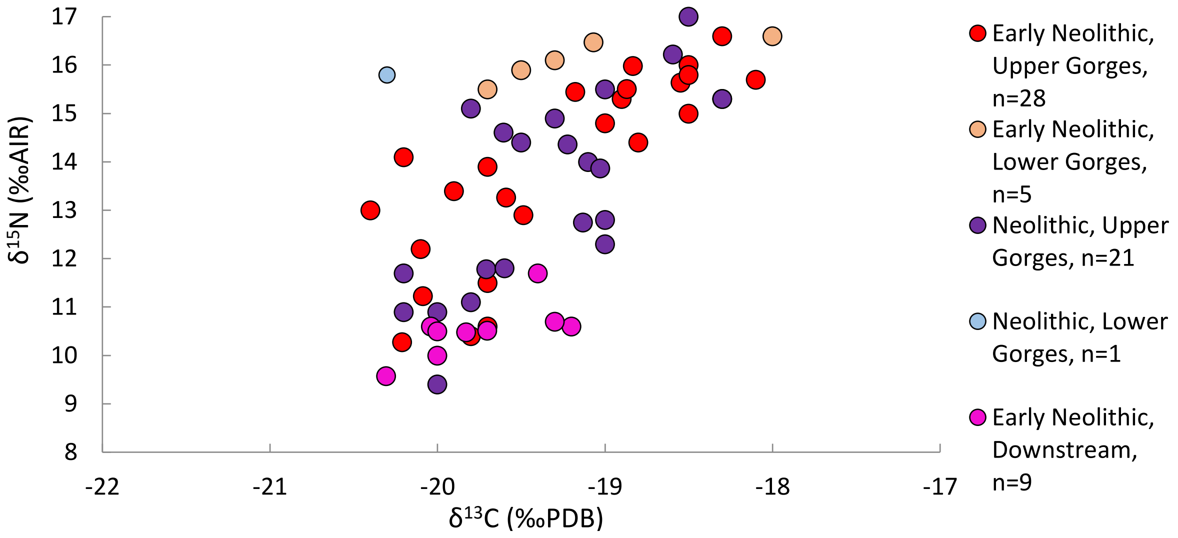

Figure 43: Bivariate plot of δ^{13}C and δ^{15}N for Neolithic adult humans (>15 yrs) per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)

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than the individuals from Hajdučka Vodenica (located just in front of Icoana along the Danube river), for whom the collagen preservation quality criteria were available and respected.

[124] The fauna from Hajdučka Vodenica and Icoana have not been analyzed stratigraphically (Bolomey 1973; Borić 2002a).

[125] Early-Middle Neolithic.

[126] Only a very small number of graves found on other sites of the Gorges have been related to a Neolithic context, i.e. after 6000 BC

[127] Individual HV 13, old adult, male, dated 6016-5726 cal. BC (Borić 2011), with a local biogeochemical signature (Borić and Price 2013).

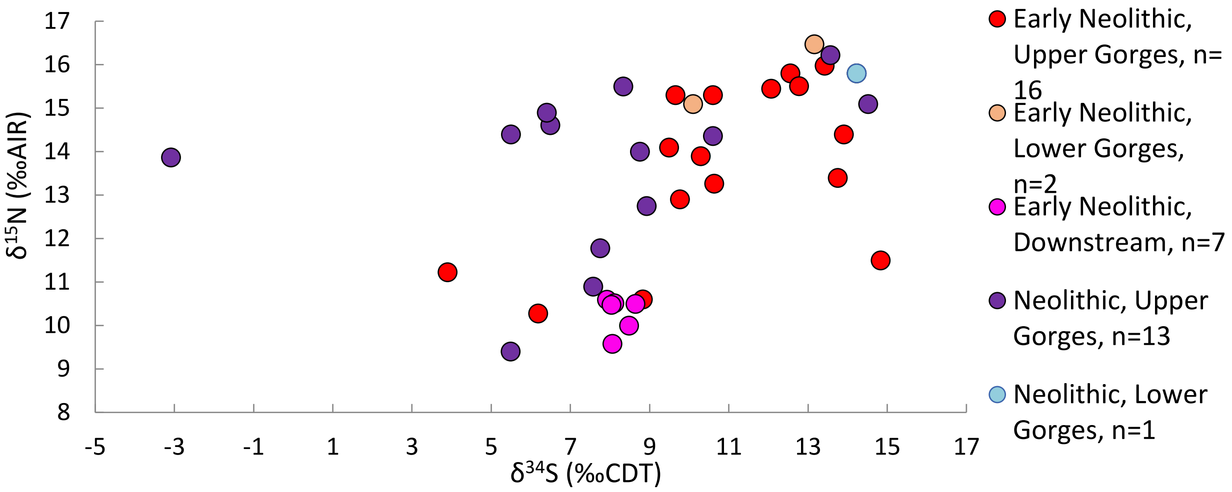

Figure 44: Bivariate plot of $\delta^{34}S$ and $\delta^{15}N$ for Neolithic adult humans (>15 yrs) per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)

4.3.2.3. Different means of subsistence in the Downstream Area: the earliest farming communities?

Downstream, "touch not the fish"

The high stable isotope signatures of the Early Neolithic individuals buried in the Lower Gorges significantly differ from those of their contemporaries buried at the sites of Ajmana and Velesnica, located less than 20km as the crow flies downstream (Appendix A.II.14; 16; 18; 20). Indeed, most Early Neolithic individuals with the lowest $\delta^{15}N$ signals (< 12‰), the lowest $\delta^{34}S$ signals (< 9,5‰) and also quite low $\delta^{13}C$ signals (< -19,8 ‰) have been discovered on the site of Ajmana (Figure 42; Figure 43; Figure 44). The individual buried on the site of Velesnica display very similar $\delta^{13}C$ and $\delta^{15}N$ than those buried at Ajmana, albeit slightly higher[128] (average difference yet < 0,5‰). These low stable isotope signals also fall in the lowest $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ range of the Early Neolithic and Neolithic individuals buried at Lepenski Vir, although being slightly higher in $\delta^{13}C$ and $\delta^{34}S$ and lower in $\delta^{15}N$ values (average difference < to 0,5‰). While the individuals buried on the sites of the Lower and Upper Gorges rather differ in the $\delta^{15}N$ values and are influenced by the consumption of high trophic level resources, the stable isotope values of the individuals buried downstream at Ajmana and Velesnica are more influenced by the consumption of lower trophic resources and differs both in $\delta^{15}N$ and $\delta^{13}C$ values; it suggests that the slight stable isotope differences observed between the individuals buried at Ajmana and the individuals buried at Velesnica might reflect some differences in the selection and in the consumption of C_3 plants (different crops?), while the differences noticed between the individuals inhumated in the site of the Inner Gorges could rather be related to the consumption of different species of aquatic-influenced animal species. Finally, one cannot disregard the possible contribution of other non-dietary factors to these slightly different stable isotope values, for instance individuals' physiological state and/or the effect of the gut microbiome... In contrast with the slight inter-site variations observed downstream, it should be emphasized that the difference in terms of $\delta^{15}N$ between the Early Neolithic individuals buried in the Upper Gorges (Hajdučka Vodenica, Icoana) and the individuals buried in the Downstream Area (Ajmana, Velesnica) approximates 5.5 ‰, i.e. too much to be solely explained in terms of environmental difference for sites located so close. The results of the PCA

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[128] It should be emphasized that, although the individuals from Ajmana and from Velesnica respected the advised molar C/N indicative of a well-preserved collagen, yet the stable isotope ratio for the individuals from Velesnica were measured with an AMS device (Bonsall et al. 2015a), while the stable isotope of four individuals from Ajmana were measured with an IRMS device in this study; yet, the stable isotope of two individuals from AJamana were also measured with an AMS device by Borić (2011), and fall in the exact range than the other measured with IRMS. Since no faunal remains from the sites located downstream could be analyzed for stable isotopes and given that the magnitude of the inter-site differences is very small, one cannot exclude the possibility for these variations to be related to environmental factors.

also reflect these dietary differences (Appendix A. IV. 3). These lower values could be related to a mixed diet including mostly proteins derived from C_3 plants, proteins derived from the meat and/or the milk of terrestrial herbivores, and perhaps additionally from freshwater fish. Given the low $\delta^{15}N$ values it is unlikely that fish were the staple food and it seems that, contrary to the site of the Inner Gorges, anadromous/potamodromous fish, dogs and species related to the aquatic ecosystems (wildfowl birds, otters, turtles) were probably not included in the local diet or only at very small extent[129].

These Early Neolithic individuals have been radiocarbon dated circa 6200 - 5850 BC[130] (Boric 2011; Bonsall 2015a), i.e. to the period of Transformation/Early Neolithic and to the beginning of the Early-Middle Neolithic period. Unfortunately, the faunal remains from Ajmana have not been published yet with associated radiocarbon dates and are currently under analyses. From the faunal remains discovered in Velesnica, Vasić (2008[131]) only mentions the importance of "red deer, aurochs and wild boars" amongst the Mesolithic fauna and that "wild animals dominated over domestics (95,62%)" in the Early Neolithic layers. Interestingly, the Neolithic layers of some sites located in the Downstream Area present significantly more domestic animals than in the Inner Gorges, such as Schela Cladovei (Bartoswievicz 1995, 2001), where the remains of cattle and caprines have been extensively recorded or Mihajlovac-Knjepište where caprines are even the dominant taxon (Bökönyi 1992). In contrast, on the site of Kula, occupied from the Mesolithic to the Neolithic, red deer, huchen, vyrezub, and sturgeon as well as mollusk are the most represented species; apart from dogs, the remains of domestic animals have not been found (Živaljević et al. 2017). However, since the faunal remains do not originate from radiocarbon dated context, it may mostly relate to Mesolithic contexts. It could also be an indication for the parallel existence, downstream, of sites previously occupied during the Mesolithic, which perpetuated a subsistence based on the old fishing, hunting and dogs raising traditions and the newly settled sites which opted for different strategies. The subsistence of the Early Neolithic individuals buried at Ajmana and Velesnica may thus have relied on the hunt of wild game, but perhaps also included the consumption of meat and/or dairies from domesticated species. The discovery of ground stones, interpreted as weights for fishing net (Radosavljević and Krunić 1986; Vasić 2008), suggests that freshwater fish were probably consumed at these localities as well, yet, in a much smaller extent than upstream inside the Upper Gorges (and certainly not anadromous species, in the light of stable isotopes results). In the absence of archaeo-botanical analyses, the important consumption of C_3 plants - and maybe of crops - can only be hypothesized. In any cases, results indicate that circa 6000 BC the individuals buried in the Downstream Area (Ajmana and Velesnica) and the individuals buried in the Upper Gorges (Hajdučka Vodenica and Icoana) opted for very different dietary strategies.

Velesnica and Ajmana were unoccupied before the end of the 7th millennium BC contrary to most sites of the Inner Gorges, already inhabited during the previous Mesolithic times. Both sites are characterized by various Early Starčevo features such as pottery, bone spoons and spatulas, altars, ground stones or even "portable hearths" (Radosavljević and Krunić 1986; Stalio 1992; Vasić 2008). Some of these features, such as bone spoons and spatulas, only appears in the cultural repertoire of the Inner Gorges after 6000 BC In both sites, the skeletons were found in the typical Early Neolithic "crouched position" sometimes within multiple graves, interpreted as collective (Figure 45; Stalio 1992; Radosavljević and Krunić 1986; Živanović 1986). The practice of collective burials, which rather points to the Neolithic world, remains absent during the whole prehistoric occupation of the Inner Gorges and the "crouched position" - frequent in the Early Neolithic of the Near East and of the South Balkans - only appears in the Inner Gorges after 6000 BC (Borić 2011). In this context and considering their low stable isotope signatures, the individuals buried downstream at Velesnica and Ajmana might have represent - or directly descends from - some of

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[129] Even the consumption of the meat of dogs fed without fish should, in theory, result in higher $\delta^{15}N$ ratios.

[130] For Ajmana: 6214 – 6008 cal BC and 6030 – 5842 cal BC (Borić 2011). For Velesnica: 6020-5845 cal BC, 6215-6020 cal. BC, 6080-5920 cal. BC, 6210-5990 cal. BC, 6205-5985 cal. BC, 6205-5935 cal. BC (Bonsall 2015a). One neonate from Velesnica may belong to another archaeological layer since it has been 14C dated to the Mesolithic period 7530-7185 cal. BC (Bonsall 2015a), i.e. one millennium earlier.

[131] Vasić 2008 quoting the unpublished doctoral dissertation of Mikić, 1999.

the earliest groups of Neolithic farmers which were certainly in contacts with the autochthonous foraging population living upstream in the Gorges. The Downstream Area, where the Danube left the Gorges to enters the Wallachian Plain, represents indeed an area much more suitable for early agricultural practices than the Inner Gorges.

Figure 45: Burials 2C-F from the "multiple burial" of Velesnica, Early Neolithic. From Vasić 2008

Mesolithic and Neolithic interactions downstream

Between 6700/6600 to 6200 cal BC, Early Neolithic communities spread into Western Anatolia and into the Southern Balkans; the spread through the Central-Northern Balkans, the Wallachian and the Pannonian plain is quite rapid around 6100-6000 cal BC (Guilaine 2007; Brami and Zanotti 2015; Fort 2015; Blagojević et al. 2017). Scholars have suggested a correlation between the pace of Neolithic diffusion in these regions and the Rapid Climate Change (ca 6600-6050 cal BC, which culminates with the cooling event of 6200 cal BC; Weninger 2009; Weninger et al. 2014). Through the bio-geographic examination of the earliest Neolithic settlements in South-Eastern Europe, Krauss et al. (2018) recently suggested that the earliest Neolithic groups would appear in regions with similar climatic and environmental conditions than those in the Mediterranean and that "moving further to the north along the north-south oriented river systems of the Central Balkans, the Neolithic economy based on agriculture and stockbreeding would first have to be adapted to the relatively harsh winters in the Balkans". They consider that "it would have been possible to apply the new Neolithic lifestyle in the neighboring areas of Thrace, Walachia, Dobrudzha and the Carpathian Basin only after a certain period of adaptation". According to the authors, "available ^{14}C-data show that the adaptation period is identical to the time-span of Rapid Climate Change " (Krauss et al. 2018:24).

The lack of evidence of occupation ca 6200-6000 cal. BC at Schela Cladovei where the Danube quit the Gorges, has led some authors to suggest its abandonment during this period, perhaps as an effect of the increased frequency of Danube floods (8.2 cooling event; e.g. Bonsall 2002b; Bonsall et al. 2014). Yet, ^{14}C dates suggest that the sites of Velesnica and Ajmana were occupied at least circa 6100-6000 cal BC (Borić 2011; Bonsall et al. 2015a) and cultural chronological evidence indicates that the site of Kula, located a further downstream of Ajmana, was also occupied during the Transformations period (ca 6200-5900 cal BC). An inter-relatedness between the micro-regions of the Upper Gorges and of the Downstream Area has been suggested for the Mesolithic - Transformational periods, notably based on similarities observed in subsistence patterns, architectural features, funerary practices and decorative elements at the sites of Lepenski Vir and of Kula, perhaps directly connected via the Miroč plateau land route (Radovanović 1996a, b and c; Živaljević et al. 2017). These cultural similarities thus contrast with the sites of Velesnica and Ajmana, where some cultural elements, funerary practices and human stable isotope values rather points to the Starcevo cultural sphere. Hence, around 6200-6000 cal BC, some localities of the Gorges may have been some foragers' enclaves in the Downstream Area (e.g. Kula at the entrance of the Miroč plateau land route), while others may have rather some enclaves of the Early Neolithic communities (e.g. Velesnica and Ajmana). With other newly established settlements of the Downstream Area, such as Ušće Kameničkog potoka and Mihajlovac-Knjepište (located circa 30km downstream from Ajmana), these sites may have represented the northern fringe of an Early Neolithic network of settlements centered on the valleys of the Struma-Timok-Morava rivers and of the Mesta-Timok-Iskar rivers (as suggested by Krauss et al 2018; Fig. 4). In contrast, some of the previously occupied sites (such as Schela Cladovei) have been abandoned, or less frequented during the period, perhaps because new lines of demarcation between the communities were drawn or because their situation may have been less advantageous regarding the harsher winter times.

It can be hypothesized that the transformational - Early Neolithic individuals with similarly low stable isotope signatures buried at Lepenski Vir in the Upper Gorges, at the other end of the Miroč plateau land route (Figure 42; Figure 43; Figure 44), may have shared a common origin with these individuals buried downstream or may have maintained some closer contacts with them than had the other individuals buried at other sites of the Inner Gorges. They could be some members of these Early Neolithic communities who moved to live upstream in the Gorges and whether died in the years following their arrival in the Gorges (keeping thus the biochemical signal characteristic of their previous mode of subsistence[132]) or perpetuated their mode of subsistence there, probably contributing to influence the local foragers. Or they could have been some local foragers who moved to live with the Neolithic community downstream and on death returned to their ancestral home for burials. Under circumstances of harsher winters, the last centuries of the 7th millennium BC might have hence represented the time necessarily for foragers and farmers mutual adaptations in this environment, enabling then the development of interactions that should have been benefited to both communities. It is possible that the first farming communities may have then not only entered into new a natural environment different from Mediterranean regons, but also into a new social environment, i.e. into regions where foragers' population density was probably much higher than in the Southern Balkans or in Western Anatolia.

4.3.2.4. Summary: places of local identity, places of Neolithic novelties and centers for interactions

Some inter-site stable isotopes differences of important magnitude can be observed in the region of the Danube Gorges during the Early Neolithic and Neolithic periods. **The Individuals buried at the localities of Padina in the Upper Gorges and at Hajdučka Vodenica and Icoana in the Lower Gorges exhibit the highest δ^{15}N and δ^{34}S values, indicating a continuous reliance on aquatic resources there, and pointing to the consumption of anadromous fish and of dogs meat at these sites.** These results are rather consistent with the archaeozoological record, and particularly with the fact that Neolithic domesticates only account for a very small part of the Neolithic fauna discovered at these sites (between 7% and 15% according to Greenfield 2008). Sites at these localities may have been used as seasonal fishing camps rather than as permanent residential places; they may also have represented places of strong local identity where the foragers perpetuated the local fishing traditions, and only accepted some aspects of the Neolithic package (e.g. ceramics).

These high stable isotope signatures significantly differ **from the lower values of the contemporaries Early Neolithic individuals buried at the sites of Ajmana and Velesnica downstream.** It suggests that circa 6000 BC some individuals who decided to be buried at less than 20km as the crow flies opted for very different subsistence strategies. **The lower stable isotope values of the individual buried downstream could be related to a mixed diet that mostly included proteins derived from C_3 plants, from the meat and/or the milk of terrestrial**

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[132] 10-15 years is the time needed for bone turnover, thus for the entire renewal of collagens stable isotope signal (Valentin 2003).

herbivores, and additionally some freshwater fish. The Downstream Area, in the North-West of the Wallachian Plain, represents indeed an area much more suitable for early agricultural practices than the Inner Gorges .Interestingly these sites were amongst the only in the Gorges to be unoccupied before the end of the 7th millennium BC and are characterized by numerous Early Starčevo cultural features (ceramics, ground stones, bone spoons, funerary practices; Figure 45). Therefore, **the individuals buried at Ajmana and Velesnica might have represented - or were directly descended from - some of the earliest groups of Neolithic farmers**.

Finally, the osteoanthropological sample of Lepenski Vir in the Upper Gorges features a wide variability in terms of stable isotope values including both very high and low stable isotope values. This biochemical variability could be due to the particular status that was probably attributed to the site from the end of the 7th millennium BC. Indeed, the importance of the symbolic record and the cultural specificities of this site indicate that **this locality could have represented a central place of particular ideological significance for the prehistoric population of the region, where people from neighboring localities gathered for particular social events, symbolic or mortuary ceremonies**. These events may have been the time for some interactions with migrants and perhaps for the adoption of different technologies (e.g. ceramics, ground stones, Neolithic adornments) and of new practices (farming subsistence? different mode of cooking?). Given the stable isotope proximity that can be observed between the Early Neolithic individuals who exhibit the lowest values at Lepenski Vir and the individuals buried downstream at Ajmana and Velesnica, one can suggest that these individuals perhaps maintained some particular relationship during their lives (same origin? relative? frequent contacts and same dietary habits?). In the Downstream Area, some sites (e.g. Kula) may have represented foragers'enclaves, possibly connected to Lepenski Vir in the Upper Gorges via the Miroč plateau land route, while others (Ajmana, Velesnica) may have represented early agro-pastoralists' enclaves, with rathere fluids and porous lines of demarcations.

The individuals with the lowest stable isotope signal buried at Ajmana, Velesnica and Lepenski Vir sites may have represented the vectors for the outspread of the Neolithic practices in the Gorges. During the first centuries of the 6th millennium BC, while the mode of occupation of the site probably evolved, yet the local biochemical signal still encompasses an important variability, which suggests that the site probably remained an attractive place for the neighboring population. Interestingly, at Lepenski Vir, the Neolithic domesticates accounts for 25% of the Neolithic fauna, i.e. much more than in the other sites of the Inner Gorges. In any cases, farming remained subsidiary in the local mode of subsistence even during the first centuries of the 6th millennium BC, perhaps because of the topographic situation of the Gorges, a region abundant in aquatic resources but maybe less suitable for the early agricultural practices.

4.3.3. Origin-related stable isotope differences (1): paleodiet and the strontium radiogenic evidence, a direct insight into the spread of the Neolithic

4.3.3.1. Comparing the diet of locals and non-locals: Transformation-Early Neolithic period

Evidence for different dietary behaviors

The comparison of locals and non-locals[133] stable isotope signatures can provide direct information on the diffusion of the Neolithic biological and behavioral component within the Gorges. For the period of Transformation - Early Neolithic, the stable isotope signals of the non-locals appear scattered, some falling within the variability of the group of Early Neolithic individuals with high stable isotope values (LV 13, LV 27a, LV 54e) and others falling within the variability of the group of Early Neolithic individuals with low stable isotope values(LV 26, LV 7/Ia, LV 122, AJ

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[133] identified thanks to their strontium radiogenic signal (Borić and Price 2013; cf part 2.3.3).

7, AJ 15, AJ 3[134]) (Appendix A.II. 21; A.IV.8). It is noteworthy that all locals from Lepenski Vir and from the other sites of the Inner Gorges exhibit high stable isotope values, while only the non-locals buried at Lepenski Vir and Ajmana and locals buried Ajmana exhibit low stable isotope values (Appendix A.II. 21; A.IV.8). The individuals buried at the site of Ajmana downstream and the non-local individuals buried at the site of Lepenski Vir in the Upper Gorges are thus responsible for the lowest stable isotope values noticed for the period of Transformation/Early Neolithic in the region.

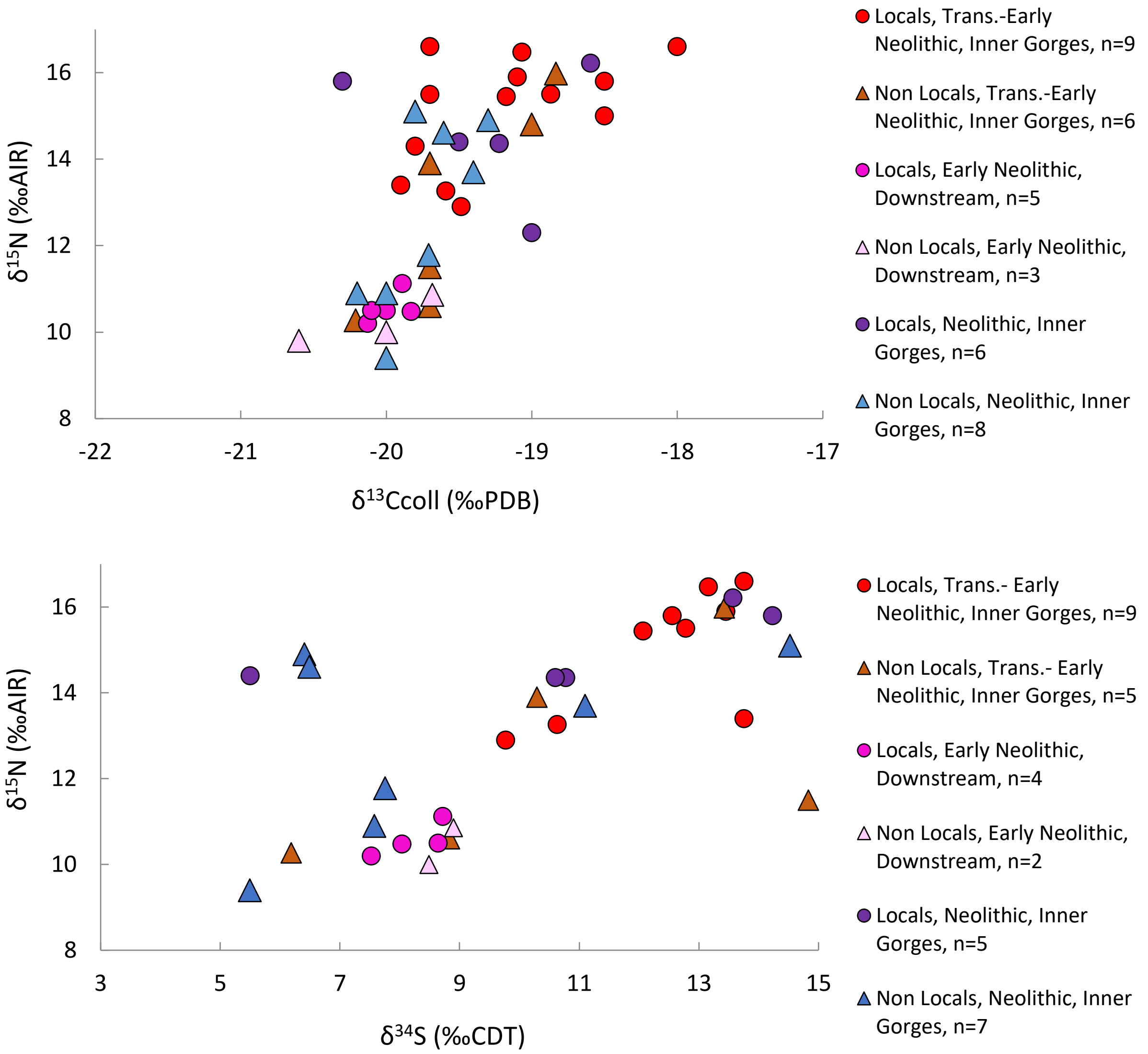

Figure 46: Bivariate plots of $\delta^{13}C$ - $\delta^{15}N$ and $\delta^{34}S$ - $\delta^{15}N$ for Neolithic humans (>5 yrs) grouped chronologically and according to their geographic origin (locals and non-locals discriminated according to their signal in radiogenic strontium, $^{87}Sr/^{86}Sr$ Borić and Price 2013)

According to their very distinct radiogenic strontium signature, some non-locals should have grown up in geologically distinct regions (Borić and Price 2013). Amongst the individuals defined as non-locals from the anthropological assemblage of Ajmana, one can thus distinguish the individuals AJ 7 (aged at death 30-40 years old) and the child AJ 15[135] (4.5-7 years old) from the child AJ 3[136] (aged at death 9.5-14.5 years old) based on their very different strontium signature.

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[134] Apart from LV 26, LV 7/Ia and LV 122, only the individual LV 82 exhibits significantly lower stable isotope values ($\delta^{13}C$=-20,1‰, $\delta^{15}N$=11,2‰ and $\delta^{34}S$=3,9‰; Appendix A.II.4; 6), but was not included in the strontium radiogenic study of Borić and Price 2013.

[135] with $^{87}Sr/^{86}Sr$ values of 0,7080 and 0,7084, they fall below the lower limit of 0,7085 defined by Borić and Price 2013.

[136] his $^{87}Sr/^{86}Sr$ value - 0,7099 - falls above the upper limit of 0,7096 (cf part 2.3.2).

Interestingly, their stable isotope values also reflect this difference. Indeed, theδ^{15}N ratios of AJ 7 and AJ 15 - respectively 10‰ and 9,8‰ - range below the values of locals from Ajmana (average 10,45‰) while AJ 3 falls above with a value of 10,9‰. Similarly, the δ^{13}C ratio of AJ 7 and AJ 15, and of the locals from Ajmana are inferior to -19,8 (AJ 7: -20‰; AJ 15: 20.6‰) while AJ 3 has a δ^{13}C ratio of -19,7‰. AJ 3 also displays the highest bone collagen δ^{34}S value (8.9‰) of all individuals aged more than 5 years discovered at the site (average and standard deviation: 8.2±0.4‰ n=8). Besides, it is worth mentioning that the stable isotope values of AJ 3 are very similar than the stable isotope values of two other non-locals from Lepenski Vir which also have very close ^{87}Sr/^{86}Sr values[137]: LV 26 and LV 7/Ia[138] (with respective values of δ^{13}C=-19,7‰; δ^{15}N=10,6‰; and δ^{13}C=-19,7‰; δ^{15}N=11,5‰). Therefore, the non-locals which explain the lower part of the stable isotope range for the period of Transformation may have originated from different regions but decided whether to be buried at the site of Ajmana downstream and/or at the site of Lepenski Vir in the Upper Gorges. The proximity noticed in terms of ^{87}Sr/^{86}Sr, δ^{13}C and δ^{15}N signals between one non-local individual buried at Ajmana and several non-locals buried at Lepenski Vir suggest that they may have shared a common origin. These results provide thus a further evidence for the interrelatedness between these two micro-regions of the Danube Gorges.

However, since it remains impossible to know the stable isotope values of the fauna and the flora of their "places of origin", the slight stable isotope differences noticed between the non-locals of different strontium radiogenic signature cannot be interpreted in terms of differential dietary habits. In contrast, the magnitude of the differences in δ^{13}C, δ^{15}N and δ^{34}S between the non-locals with low stable isotopes values - who also exhibit similar ratios than the local individuals buried at the sites of Ajmana - and the other individuals buried at the sites of the Inner Gorges may rather be related to their different mode of subsistence. Indeed, one would expect the isotopes of the carbon and of the sulfur elements to be affected by possible local environmental variations and here, the average δ^{15}N difference between the group of non-locals with low stable isotope values and the other individuals buried in the Inner Gorges approximates 4,5‰. Therefore, while the locals and the non-locals (LV 13, LV 27a, LV 54e) who were buried at sites of the Inner Gorges and who exhibit high stable isotope ratios should have consumed fish - particularly anadromous species - and the meat of dogs, the other non-locals from Lepenski Vir and Ajmana should not have included these resources in their usual diet, which was probably mostly based on the consumption of herbivores, C_3 plants and maybe additionally of some freshwater fish (LV 26, LV 7/Ia, LV 122, AJ 7, AJ 15, AJ 3). Interestingly, in the dental calculus of the individual LV 7/Ia, the starch grains of a species from Poaceae family that could belong to Triticeae tribe, to which domestic cereals belong, has been detected (Jovanović 2017).

Several scenarii - non mutually exclusive - can be considered to explain the stable isotope values of non-local individuals. Concerning the non-locals with the highest stable isotope values, it is possible whether that they came in the Gorges with similar dietary habits than the locals or that they adopted the local dietary practices long enough before they died for the stable isotope values analyzed in their collagen to reflect their diet[139]. Concerning the non-locals with the lowest stable isotope values, it is possible that they were in contacts, originated from the same groups or belong to the same broad web of Early Neolithic communities as the individuals buried downstream at

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[137] their ^{87}Sr/^{86}Sr values of 0,7099 - also fall above the upper limit of 0,7096 (cf part 2.3.3).

[138] However, it should be recall that these two individuals are amongst the four individuals for whom the N% and C % published by Borić et al. (2004) fall beyond the advised values for a well-preserved collagen (**LV 26**: N%= 8,2; C%=22; S%=0,18; C/N=3,49; C/S = 345 and N/S=98,7; **LV 7/1a**: N%=7,4; C%=21; S%=0,18; C/N=3,31, C/S=303 and N/S= 98,6). Since the molar C/N, C/S and N/S and the S% are within the acceptable ranges, and given the importance of the stable isotope values of these individuals, already discussed in the local context of Neolithization (Bonsall et al. 2000; Borić et al. 2004; Bonsall et al. 2008; Bonsall et al. 2015a), they were eventually included in this study. The fact that their stable isotope values but also their strontium radiogenic - measured in the mineral part of teeth enamel - are very close and also fall the closest to the other non-local AJ 3, whom collagen quality criteria were all respected (N%: 14,7; C%:40; S%: 0,25; C/N:3,1; C/S:421; N/S: 133), rather suggests that these stable isotope ratios should actually reflect valid palaeodietary signals. Besides, for the site of Lepenski Vir as well as for the Transformational periods and Neolithic periods, we did not find any significant difference in the distribution of individuals for whom the advised criteria for collagen preservation were respected and those for whom these criteria were not available (Mann-Whitney, at the 0,05 level; cf part 3.3.2)

[139] 10-15 years is the time needed for bone turnover, thus for the entire renewal of collagen stable isotope signal (Valentin 2003).

Ajmana, since they had quite similar biochemical signatures. It is also possible that they reproduced their own lifestyle in the Gorges or that they died too early after their arrival in the Gorges for their dietary adaptation to be recorded in their bone collagen (in this case, the analyzed stable isotope signal should inform on their dietary habits before they arrived in the Gorges). In any cases, it is worth mentioning that, while the range of stable isotope values encompassed by the non-locals is broad, in contrast, all individuals determined as locals for the Early Neolithic period exhibit high stable isotope values. These results indicate that, while some non-locals may have adapted to the local diet, in contrast none of the locals adapted to the dietary practices of non-locals. If some non-locals with low stable isotope signal actually originate from Early Farming communities settled downstream and represent some of the first generation of farming migrants who arrived in the Gorges, then it is interesting to notice that the local foragers did not choose to adapt to the dietary habits of the non-locals. During this early phase of foragers-farmers interactions in the region, the local foragers of the Inner Gorges accepted some Neolithic migrants, adopted some of the Neolithic technologies such as ceramics or some ground stones artifacts, but decided to keep their own dietary traditions.

Direct contextual evidence for cultural interactions: the cases of the individuals LV 54D and LV54E

The case of the individuals LV 54D and LV 54E may provide some further insight into the interactions between locals and non-locals. These two females were found at the same location, placed over the abandoned space of the trapezoidal building 65 (Figure 47) and have been respectively ^{14}C dated 6340-6015 cal. BC and 6210-5930 cal. BC (i.e. Period of Transformation - Early Neolithic; Bonsall et al. 2015). LV 54D was found dislocated, probably disturbed by the deposition of LV 54E who lay down extended on her back. LV 54D was determined as local and LV 54E as non-local (Borić and Price 2013). While both females exhibit very close δ^{13}C and δ^{15}N values (LV 54 D: δ^{13}C =-19,9‰; δ^{15}N=13,4‰; LV 54 E: δ^{13}C =-19,7‰; δ^{15}N=13,9‰), the δ^{34}S values of the local female LV 54D appears significantly higher (LV 54 D: δ^{34}S=13,7‰; LV 54 E:

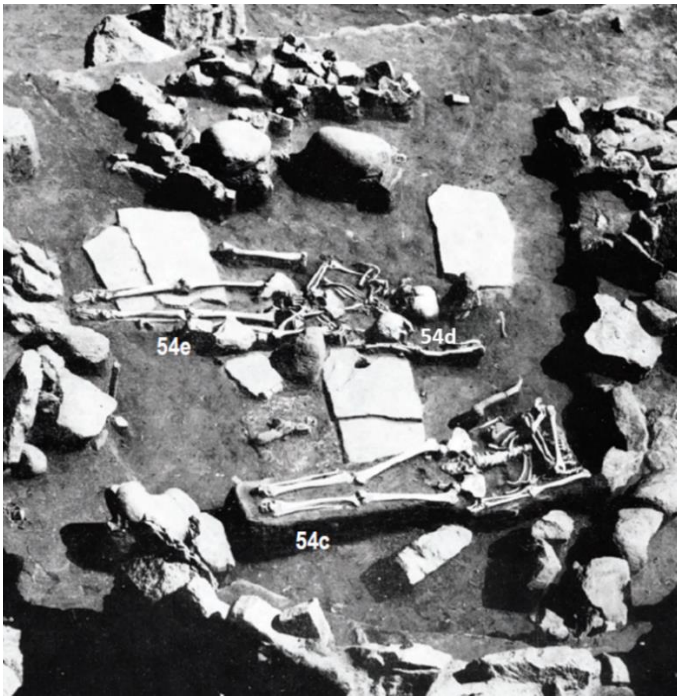

Figure 47: Lepenski Vir dwelling 65, Transformation/Early Neolithic individuals 54E (foreground, extended supine; non-local; non-U maternal lineage) and 54D (foreground, disturbed; local non-U maternal lineage). Photo: Institute of Archaeology, Belgrade. Adapted from Bonsall et al. 2008.

δ^{34}S=10‰). Although they probably both had a rather mixed diet, substantially including aquatic re resources, it is possible that the δ^{34}S values of the non-local female remain slightly lower, perhaps in relation with the environment where she was living before migrating in the Gorges (greater consumption of stationary freshwater fish and terrestrial games than anadromous fish species?).Their very close δ^{13}C and δ^{15}N values and the fact that they buried at the same location within the building 65 suggest that they perhaps share special bonds during their lives. Interestingly, the non-local female LV 54E, probably buried after LV 54D[140], has been found associated with red and white limestone beads of discoid shape, clearly pointing to Balkans' and Anatolian Neolithic cultural traditions, but also with a piece of carved deer antler, which rather recall local Mesolithic traditions. It is worth mentioning that other Early Neolithic individuals discovered buried close-by within the same building 65, but who were not included in the strontium radiogenic study of Borić and Price (2013), also display very similar δ^{13}C but varying δ^{15}N and δ^{34}S values[141].

4.3.3.2. Comparing the diet of locals and non-locals: Early/Middle Neolithic period

Evidence for different dietary behaviors

Amongst analyzed individuals for their strontium radiogenic signal, much more were determined as non-locals during the Neolithic period (after 6 ky B.C) than during the period of Transformation/Early Neolithic (about 55% of Neolithic analyzed individuals were determined as non-locals). Neolithic non-locals appear more scattered than the locals for the stable isotope of the three elements. As noticed concerning the previous Early Neolithic period, individuals of local origin range on the high part of stable isotope variability while only non-locals are responsible for the lowest stable isotope values (Figure 46; A.IV.8). Concerning δ^{34}S ratio, only one local individual - LV 74 - exhibits a lower signal (δ^{13}C=-19,5‰; δ^{15}N=14,4‰; δ^{34}S=5,5‰); therefore the shift toward lower δ^{34}S values after 6 ky BC previously noticed, seems rather due to the presence of non-local individuals in the Gorges than to an environmental changes in the δ^{34}S values of the Danube/Black Sea basin. Most locals still included anadromous fish and/or dogs in their diet, only LV 74 did not include these resources but probably included freshwater fish (low δ^{34}S ratios but high δ^{15}N). Only one non-local consumed anadromous fish and/or dogs (LV 7/IIb, the only one which display high δ^{34}S and high δ^{15}N[142,143], being located in the right part of the PCA, Appendix A.IV.8). Other non-local rather favored freshwater fish (exhibiting low δ^{34}S ratio but high δ^{15}N and thus located in the upper left quadrant of the PCA, it is the case of the non-locals LV 66 and LV 20 who display similar values as the local LV 74). Other, finally, probably favored the consumption of terrestrial proteins, mostly derived from terrestrial herbivores and C_3 plants (LV 8, LV 88, LV 32a, LV 17, lower left quadrant of PCA). Here again, this interpretation can be sustained only provided that the stable isotope values for the fauna and the flora of their "place of origin" were roughly similar to the values of the local fauna and flora in the Danube Gorges region; however, given the magnitude of the difference in terms of δ^{15}N values observed between the group of non-locals with lower values and the individuals with high values, it should rather reflect a different dietary behavior than some local environmental variations. It is noteworthy that starch grains of a

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[140] according to stratigraphy and to the 14C dating, although the ^{14}C probabilities mostly overlap (Bonsall et al. 2007, Bonsall et al. 2015a)

[141] LV 54B: δ^{13}C =-19,8; δ^{15}N=10,4‰; LV 54 C: δ^{13}C =-20,2‰; δ^{15}N=14,1‰; δ^{34}S=9,5‰; LV 54C has also been ^{14}C dated to 6215-5995 cal. BC by Bonsall et al. (2015); the combination of high δ^{15}N=14,1 and low δ^{34}S and δ^{13}C for the individual LV 54C is quite unusual in the Gorges for the period of Transformation and could be related to a high consumption of aquatic resources but not marine-influenced (only stationary freshwater fish), which could indicate the non-local origin of this individual.

[142] LV 7/IIb: δ^{15}N= 15,1‰ and δ^{34}S = 14,5‰; However, it should be recall that this individual is amongst the four individuals for whom the N% and C % published by Borić et al. (2004) fall beyond the advised values for a well-preserved collagen (N%=9,59; C%=22; S%= 0,16; C/N=3,26, C/S=357 and N/S=129). Since the molar C/N, C/S and N/S and the S% are within acceptable ranges, the stable isotope values of LV 7/IIb were eventually included in this study.

[143] the non-local child LV 56, aged at death 6-9 years old, also displays slightly higher δ^{15}N (13,7‰) and δ^{34}S values (11,1 ‰) than the other non-locals, although these values remain lower than the adult LV 7/IIB (δ^{15}N=15,1‰ δ^{34}S=14,5‰). Besides, since this individual died at a young age, and during a period of growth spurt, one cannot exclude that these elevated stable isotope values could be affected by non-dietary physiological factors.

species from Poaceae family have also been found on the dental calculus of the non-local individuals LV 8, LV 20 and LV 32a (Cristiani et al. 2016).

It is thus possible that these new generations of migrants came from different regions and/or already had different dietary traditions when they arrived in the Gorges. Some (those with high stable isotope values) may have originated from other foraging societies while others (those with low stable isotope values) may have originated from Neolithic communities who already relied on an agricultural mode of subsistence. In any cases, most of them (apart from LV 7/IIb) did not included anadromous fish and/or the meat of dogs in their diet. It is possible that they reproduced their own dietary habits within the Gorges, or that they died in the years following their arrival there (too early for the stable isotope signal of their new diet to be recorded in their collagen). In continuity with the previous Early Neolithic period, most locals keep perpetuating the old Late Mesolithic foraging traditions. Although several generations of non-locals arrived in the Gorges and are responsible for the lowest stable isotope values, although these migrations were contemporary with the adoption of some aspects of the Neolithic package, most locals choose to keep their own mode of subsistence, reproducing their tradition for several centuries.

Neolithic migrants' life histories: the cases of LV 7/Ia and LV 7/IIb

For the period of Transformation/Early Neolithic, locals (exhibiting high stable isotope values) and non-locals (exhibiting both high and low stable isotope values) were found whether in extended supine position or disarticulated, and no specific funerary customs could be related to the non-locals. During the Neolithic period, a change in terms of funerary practices is noteworthy: crouched position, characteristic of the Balkans and Anatolians' Neolithic cultures, mostly replaces the Mesolithic traditional extended supine position. Interestingly, all Neolithic individuals exhibiting low δ^{34}S values as well as all those who display low δ^{13}C and δ^{15}N values were found in crouched position, including almost all non-locals and a few locals (Figure 48). In contrast, the individuals who display high stable isotope values were found either in crouched position or disarticulated. The disarticulated skull LV 7II/b (Figure 49) belong to the only non-local individual who displays significantly higher δ^{15}N and δ^{34}S ratios (δ^{15}N=15,1‰; δ^{34}S=14,5‰; δ^{13}C =19,8‰)[144,145]. It is worth mentioning that the only disarticulated skull analyzed for radiogenic strontium and dated to the previous period of Transformation - LV 122 - was also non-local (one of the non-locals displaying low stable isotope values; undetermined sex, died at teenage)[146], probably in relation with the particular value which was assigned to this anatomical element, as echoed by the presence of red deer antlers, aurochs skull, or dogs' mandibles within some burials.

While this skull of the individual LV 7/IIb has been ^{14}C dated to the Neolithic period[147], it has been found in the grave of LV 7/Ia, a male buried extended supine through the floor of the building 21 and dated to the Transformational period[148] (Figure 49). Interestingly, the individual LV 7/Ia was also estimated as non-local according to its strontium radiogenic signal[149]. Both individuals also exhibit very close δ^{13}C and δ^{34}S ratios (LV 7/Ia: δ^{13}C =-19,7‰; δ^{34}S=14,8‰; LV 7/IIb: δ^{13}C =-19,8‰; δ^{34}S=14,5‰), but differs on the δ^{15}N values (LV 7/Ia: δ^{15}N=15,1‰; LV 7/IIb: δ^{15}N=11,5‰). Through different paleodietary and ancient dating projects, several δ^{13}C and

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[144] Apart from the disarticulated mandible of the non-local child LV 56 which also yield higher δ^{15}N (13,7‰), and δ^{34}S values (11,1 ‰) than the rest of the group, although lower than the values of the adult LV 7/IIb.

[145] LV 7/IIb: δ^{15}N= 15,1‰ and δ^{34}S= 14,5‰; However, it should be recall that this individual is amongst the four individuals for whom the N% and C % published by Borić et al. (2004) fall beyond the advised values for a well-preserved collagen (N%=9,59; C%=22; S%= 0,16; C/N=3,26, C/S=357 and N/S=129). Since the molar C/N, C/S and N/S and the S% are within acceptable ranges, the stable isotope values of LV 7/IIb were eventually included in this study.

[146] Some disarticulated mandibles were identified as part of the bodies of local individuals, LV 126 (Early Mesolithic), LV 32 (Late Mesolithic), LV 37 and LV 39 (Neolithic), as well as one non-local child, LV 56. Amongst them all those analyzed for stable isotope display high values. Yet, only the calvaria and the facial skulls of LV 122 and LV 7/IIb (found without mandibles) were estimated as non-locals. Amongst individuals analyzed for strontium radiogenic signals, these two non-locals are thus the only individuals which were discovered as disarticulated calvaria and facial skulls (without mandibles).

[147] 6080-5746 cal. BC (Borić 2011)

[148] 6225-5907 cal. BC, 6243-5917 cal. BC (Bonsall et al. 2008); 6216-5884 cal. BC (Borić 2011); 6230-5985 cal. BC (Bonsall et al. 2015a)

[149] This individual - with a strontium value of 0,79980 - falls for strontium radiogenic signal just on the limit of 0,710 defined by Borić and Price (2013) and above the upper limit value of 0.796 below which range most of the individuals of the Gorges.

δ^{15}Nvalues have been measured on the collagen of the extended supine Early Neolithic individual LV 7/Ia during the last 15 years: by Bonsall et al. in 2001 (δ^{15}N=15,8); Borić et al. in 2004 (δ^{13}C =-19,7‰; δ^{15}N=11,5‰), by Bonsall et al. in 2008 (δ^{13}C=-17,5‰ and -18,1 ‰; δ^{15}N=16,6‰ and 16,2‰), by Borić 2011 (δ^{13}C =-18,9‰; δ^{15}N=11,5‰) and by Bonsall et al. 2015a (δ^{13}C =-18,3‰ and -18,1 ‰; δ^{15}N=16,1‰ and 16,1‰)[150]. From these studies, we can see that the δ^{13}C values of LV 7/Ia ranges from -17,5‰ to -19,7‰ and that the δ^{15}N values ranges from 11,5‰ to 16,6‰. These differences were first interpreted as a possible error of labeling (Borić 2004), but, after further measurements, it has been suggested that they may be rather due to the different anatomical element on which the collagen was extracted (Bonsall et al. 2015a). Indeed, the lowest δ^{15}N and δ^{13}C values (11,5‰; -19,7‰ and -18,9‰) were measured on collagen extracted from a rib (Borić 2011), while the highest values (16,1‰ to 16,6‰ and -18,3‰ to -17,5‰) were measured on collagen extracted from a femur (Bonsall 2008; 2015a). Since ribs are supposed to remodel faster than long bones (e.g. Tsutaya and Yoneda 2013), it has been suggested that these varying values may reflect a dietary change from an aquatic based diet toward a more terrestrial diet; hence, this result might mirror the adoption of the new Neolithic way-of-life within the time of the individual life history (Bonsall et al. 2015a). This hypothesis would indicate that this non-local adopted a terrestrial diet after migrating within the Gorges, perhaps pointing then to its origin in other foraging communities and suggesting that he may have been influenced by other non-locals after his arrival in the Gorges. Yet, the elevated δ^{34}S values that we measured on collagen also extracted from a rib (δ^{34}S= 14,8‰, this study), very close to the value measured on the skull of the individual LV 7/IIb (δ^{34}S= 14,5‰, this study), rather indicate that this individual included anadromous fish and/or dogs meat during the last years of his life. It should be recalled that both individuals LV 7/a and LV 7/IIb are amongst the four individuals for whom the N% and C % published by Borić et al. (2004) fall beyond the advised values for a well-preserved collagen (**LV 7/1a**: N%=7,4; C%=21; S%=0,18; C/N=3,31, C/S=303 and N/S= 98,6; **LV 7/IIb**: N%=9,59; C%=22; S%= 0,16; C/N=3,26, C/S=357 and N/S=129). Since the molar C/N, C/S and N/S and the S% are within acceptable ranges and given the importance of the stable isotope values of these individuals in the local context of Neolithization, their stable isotope values were eventually included in this study[151].

The fact that LV 7/Ia and LV 7/IIb are both non-locals and that one was placed within the grave of the other is quite consistent with their similar δ^{13}C and δ^{34}S values (and maybe δ^{15}N as well, given the values obtained by Bonsall et al. 2000; 2008; 2015a). As previously hypothesized for LV 54D and LV 54E, these results also suggest that the non-locals LV 7/Ia and LV 7/IIb may have shared particular bonds during their lives. Although the ^{14}C dates suggest that the skull LV 7/IIb was younger than the extended supine individual LV7/Ia, and was probably added a posteriori in the grave, radiocarbon dates also show an overlap between 6080 and 5907 BC suggesting that these individuals may also have been contemporary during a part of their lives. While the skull of the individual LV 7/IIb was found relying on left shoulder of the individual LV 7/Ia, the skull of an aurochs with horns was found on his right shoulder. The skull of a red deer with antlers has also been found on the left side of LV 7/Ia and has been ^{14}C dated to the Neolithic[152], although it remains unclear whether this skull was associated to the burial or deposited in a related pit. The presence of these skulls anatomically associated with the body of the dead (surrounding his head on his right and left shoulder) are further evidence in favor of the fluidity of the relationship between human and animal species in the prehistoric Danube Gorges. Red deer antlers - symbols of rebirth and seasonality often found placed on the abandoned floors of the dwellings at Lepenski Vir (Borić 2003, 2005a) - are known to be utilized for symbolic purposes by European Mesolithic foragers (e.g.

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[150] In this study we used the δ^{13}C and δ^{15}N values provided by Borić et al. 2004, since they used an IRMS (while the other samples were measured with an AMS dating device), given that they provide the criteria for collagen preservation (C%, N% and the atomic ratio C:N; while only Bonsall et al. 2015 provide the associated atomic ratio).

[151] Although, one cannot disregard the possibility that the stable isotope values of these two individuals could be affected by diagenetic effects, we did not find significant difference in the distribution of the individuals for whom the advised criteria for collagen preservation were respected and those for whom these criteria were not available neither for the individuals discovered on the site of Lepenski Vir, nor for the individuals dated to the Transformational periods and Neolithic periods (Mann-Whitney, at the 0,05 level).

[152] 5888-5728 cal. BC (Borić 2011)

at Starr Carr in the British Islands; Little et al. 2016). In contrast, bovid bucranium rather point to the symbolism of Balkans, Anatolian and Near Eastern Neolithic communities (e.g. at Çatal Höyükin Anatolia; Mellaart 1967).

Figure 48: Lepenski Vir, grave 32a, Early/middle Neolithic. Individual in the typical Neolithic crouched position (non-local individual, assigned to a non-U maternal lineage and with low stable isotope values, indicative of a terrestrial diet). Photo: Center for Archaeological Research, Faculty of Philosophy, University of Belgrade; from Borić and Price 2013.

Figure 49: Transformation/Early Neolithic individual 7/Ia (extended supine; non-local) and Early/Middle Neolithic individual 7/IIb (dislocated skull; non-local) from Lepenski Vir. Photo: Center for Archaeological Research, Faculty of Philosophy, University of Belgrade; Bonsall et al. 2008

The man LV 7I/a migrates in the Gorges around 6 ky BC, at a turning point for the development of the Neolithic in the region. The observation of differences in the $\delta^{13}C$ and $\delta^{15}N$ values of different anatomical elements analyzed during successive paleodietary studies suggest that this individual may have consumed a greater extent of lower trophic level resources and a lesser extent of aquatic resources at the end of his life. After his death, he was buried through the floor of a dwelling in the typical Late Mesolithic - Transformational extended supine position. His burial was probably re-opened[153] for the deposition of the skull of another non-local - LV 7/IIb - of an aurochs bucranium and maybe of red-deer antlers. The close stable isotope values (in particular $\delta^{34}S$) exhibited by the disarticulated skull of the individual LV 7/IIb values and the extended supine individual LV 7/1a also suggests that these two individuals probably had quite similar dietary habits during a period of their lives. Given that the disarticulation of a skull (calvaria and facial skull) is documented for another non-local at Lepenski Vir (no cases of local disarticulated skulls at the site) and considering the symbolic value assigned to this anatomical element in many societies, one can imagine that this specific treatment may have somehow been related to the status of these non-local individuals. The human and the animal skulls were symbolically deposited on the shoulders of LV 7/Ia, in a particular anatomical arrangement which might recall the fluidity of the relationships between species in the Prehistoric Danube Gorges (Borić 2005a; Živaljević 2015). Although this association between the animal and the human bodies and the symbolic values that were assigned to some species by the local foragers certainly root in the deep Mesolithic time, the choice to introduce an aurochs skull in the grave rather reflect the Neolithic novelties that seep into the symbolic record at that time. Thus, just like the two females LV 54D and LV 54E, who were buried a few decades earlier on the floor of another dwelling at Lepenski Vir, the case of the two non-locals LV 7/Ia and LV 7/IIb further illustrates the mosaic of cultural interactions that occurred within the Gorges at the transition between the 7th and the 6th millennium BC. These interactions

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[153] as suggested by the slightly younger ^{14}C dates of LV7/Ia

put the local foragers in touch with individuals that certainly originated from different regions, and probably from societies with different means of subsistence, some foragers and some early farmers who brought in the Gorges their own traditions and contributed there to a unique cultural syncretism. And yet, most locals perpetuated their own foraging traditions through the first centuries of the 6th millennium BC, probably accepting some of the Neolithic novelties but choosing to keep their dietary habits. When interpreted together, biochemical and contextual data available for some local and non-local individuals indicate that the development of the Neolithic in the region should not be understood as a straightforward process of acculturation.

A particular rite for a non-local individual? The case of LV 52

Similarly, the Early-middle Neolithic individual with the lowest δ^{34}S value (non-local origin? δ^{34}S: -3.1‰, value from a rib), has been discovered disarticulated in the grave 52, which containsthe remains of at least two other individuals and of a domestic goat; it is also the only occurrence at the site of a burial within a typical Neolithic domed oven (Stefanović 2016; Wallduck, and Bello 2016). A radius was found in this grave (of the same individual?) with cut marks and traces of incisions suggesting that it has been removed from a fleshy corpse, cleaned and engraved with a set of notches, similar as those observed on other bone, antler and elongated ground stone artifacts and interpreted as possible counts of past events (Wallduck and Bello 2016). In the light of the very low δ^{34}S value noticed on a rib, it may also be hypothesized that the act of engraving may have whether be done in relation with a specific status assigned to the non-local individual or that what has been interpreted has "counted events" may in fact have to do with the presence or the arrival of non-locals in the Gorges and/or that the engraved radius may have been purposely placed within a grave containing the remains of a non-local. This practice might have been associated with an appropriation of the remains of a non-local, the utilization of the remains of an individual from a different origin and history, perhaps during rites of passage or to mark out time or cycling events.

4.3.3.3. Summary: the local experience of Neolithization

During the period of Transformation/Early Neolithic, some of the non-locals had similar dietary patterns as the locals, relying on the consumption of aquatic resources, including in their diet anadromous fish and the meat of dogs. Others, in contrast, had a diet mostly based on the consumption of herbivores, C_3 plants and maybe additionally of some freshwater fish. These non-local individuals are responsible for the lower stable isotope variability noticed at Lepenski Vir. Interestingly, they display close stable isotope values to the individuals buried downstream at the site of Ajmana. Besides, some non-locals from Lepenski Vir and some non-locals from Ajmana exhibit very close ^{87}Sr/^{86}Sr, δ^{13}C, δ^{15}N and δ^{34}S signals while other non-locals - with different ^{87}Sr/^{86}Sr- also exhibit different stable isotope values. It suggests that some non-locals buried at Lepenski Vir and at Ajmana may have shared a common origin, which further strengthens the hypothesis of a particular interrelatedness between these two micro-regions and also confirms the importance played by the Neolithic communities settled in the Downstream Area for the Neolithization of the Inner Gorges.

The non-locals dated to the subsequent Neolithic are actually responsible for the observed Neolithic shift down in δ^{34}S values. They were whether favoring the consumption of terrestrial resources (protein from meat and C_3 plants) or of freshwater resources. Interestingly, the remains of starch grains which might belong to some domestic species of cereal have been identified on some of the teeth of several Early Neolithic and Neolithic non-local individuals (albeit also discovered on Late Mesolithic individuals from the site of Vlasac and on other individuals from Lepenski Vir and from Ajmana; Cristiani et al. 2016, Jovanović 2017).

Migrants thus probably originate from different regions, maybe from some other foraging societies, and/or from some communities of early farmers and/or groups that maintained close contacts with the early farming communities settled downstream and in the south-eastern Balkans.

A few of them may have adapted their diet to the local mode of subsistence after their migration in the Gorges. **While the range of stable isotope values encompassed by non-locals is broad, in contrast, all individuals determined as locals exhibit higher stable isotope values. It indicates that most of the locals keep perpetuating the old Late Mesolithic foraging traditions**. Although several generations of non-locals successively arrived in the Gorges with different dietary habits, although these migrations were contemporary with the adoption of some aspects of the Neolithic package, most locals choose to keep their own mode of subsistence, reproducing their tradition for several centuries.

The specific cases of the individuals LV 54D - LV 54E and LV7/Ia - LV 7/IIb provide a closer insight into these interactions (Figure 47; Figure 49). The Early Neolithic non-local female LV 54D was found at the same location as the local female LV 54D, on the floor of the building 65 at Lepenski Vir. Since these two females were buried together and exhibit similar stable isotope values, it is possible that they shared particular bonds during their lives. After she died, LV 54E was buried close to LV 54D, with artifacts which were perhaps associated both to her former life out of the Gorges (typical Neolithic beads) and to the time she spent there (red-deer antlers). Similarly, the skull of the Neolithic non-local individual LV 7/IIb was placed into the grave of the Early Neolithic non-local individual LV 7/Ia buried in extended supine position through the floor of the building 21 at Lepenski Vir. It has been debated whether some differences obtained in the measurements of δ^{13}C and δ^{15}N from different anatomical elements of LV 7/Ia in previous paleodietary studies (Bonsall et al. 2000, 2008, 2015a; Borić et al. 2004, Borić 2011), should be related to some mislabeling or to possible problem of collagen preservation, or to the differential rate of bone renewal perhaps indicating then a shift at the very end of his life toward the consumption of more terrestrial food (evidence for the dietary transition at the individual level? Bonsall et al. 2015a). It can also be noticed that these two individuals exhibit very close δ^{34}S values, which could whether related to their non-local origin or to the fact that they adopted a similar diet after migrating in the Gorges. Interestingly, some aspects of the burial ritual recall here the Mesolithic traditions (extended supine position, presence of a red deer antlers), but other rather point to the Neolithic practices (presence of an aurochs skull in the grave, burial through the house floor) or to both (skull removals; while mandibles were often found disarticulated in the Mesolithic graves, the practice to remove calvaria and facial skulls points to the Neolithic world). These piecewise elements of prehistoric life histories get a glimpse of the complex cultural syncretism that occurred in the Danube Gorges at the advent of the Neolithic. Biochemical analyses indicate that the local development of the Neolithic should not be considered as sudden population replacement nor as a straightforward process of acculturation.

4.3.4. Origin-related stable isotope differences (2.): paleodiet and paleogenetic, an insight into the process of dietary adaptations over generations

Mitochondrial and Y-chromosome haplogroups

Concerning the period of Transformation/Early Neolithic and the Neolithic period in the Danube Gorges ancient DNA analyses (Hofmanová 2016; Mathieson et al. 2018) identified some maternal lineages - the mitochondrial[154] clades (mt-lineages) H3, J1 and J2, K1a and K1b, N1a, T1a and T2e - which have also been found amongst Near Eastern and European individuals but which are unknown amongst the European Pre-Neolithic foragers (Figure 50). These clades are notably absent amongst the Mesolithic foragers of the Gorges and only arrived in the region after 6.2 ky BC In contrast, some Early Neolithic and Neolithic individuals are related to the mt-lineage U5[155],

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[154] the mitochondrial DNA being transmitted only by mothers, it informs about maternal lineages, in contrast with the Y-chromosome which informs about paternal lineages.

[155] Genetic clade particularly found amongst individuals dated to the Mesolithic Europe and absent from the Early Neolithic population from the Near East; this mt-haplogroup is particularly frequent amongst the Mesolithic foragers of the Danube Gorges (dated before 6.2 ky BC; Hofmanová 2016; Mathieson et al. 2018).

typical amongst the European Pre-Neolithic foragers and absent amongst Near Eastern Early Neolithic individuals. This U5 clade is particularly frequent amongst the Mesolithic foragers of the Gorges (pre 6.2 ky B.C). Therefore, the analysis of mt-haplogroups[156] show that a mixture of "rather Pre-Neolithic-like maternal lineage" (U5, pointing to a European Mesolithic ancestry) and "rather Neolithic-like maternal lineages" (Non-U, pointing to a Non-European Neolithic ancestry) features the advent of the Neolithic in the Danube Gorges.

Data concerning paternal lineages - provided by the Y-chromosome - are less informative since they suffer from a more limited number of comparable studies (Pinhasi et al. 2012) and from the poor number of haplogroups (Y-lineages) which have successfully been assigned to Neolithic individuals on the osteo-anthropological assemblage of the Danube Gorges[157] (Hofmanová 2016 and Mathieson et al. 2018). Yet, results enable to assign five Early Neolithic individuals to the I2 Y-lineage (individuals HV 19-20(1), LV 27D and LV 91) and R1 Y-lineage (individuals Pad. 4 and LV 61), frequent amongst the local Mesolithic foragers; three of them were associated to the typical "European Pre-Neolithic-like" U5 mt-lineage (HV 19-20(1), LV 27D and LV 91) which means that both their maternal and paternal lineages can be traced back to the European Pre-Neolithic Hunter-Gatherers. One of the R1 individuals were associated with a K1a mt-lineage (Pad 4) and with a H40 mt-lineage (LV 61), suggesting that their maternal ancestry can be found amongst Neolithic communities living out of the Gorges and their paternal ancestry amongst some European Mesolithic communities. Two individuals, LV 73 and LV 82, have been respectively assigned to G2 and C2 Y-clades and were associated to the H3 and T2 mt-clades, maternal and paternal lineages previously identified on some European and Near Eastern Neolithic individuals[158]; both the maternal and paternal lineages could be found amongst Neolithic communities living outside of the Danube Gorges.

Genetic datasets were also analyzed by Hofmanová (2016) and Mathieson et al. (2018) with ADMIXTURE, a model based maximum likelihood method of estimating individual ancestry using nucleotide polymorphism (Alexander et al. 2009). The results support the information provided by genetic lineages and indicate that some Transformation - and Neolithic individuals (LV 27, LV 27D, LV 91, Pad. 5 and HV 19-20/1) are only related to the European hunter-gatherers, that some others (Pad 4, LV 61 and LV 93) have a mixed ancestry, while some individuals (LV 54E, LV 73 and LV 82) are only related to the Near Eastern and European Neolithic.

The analyses of ancestry thus indicate that some migrations from other Neolithic communities likely occurred in the region after 6.2 ky BC ("infiltration of individuals of Aegean origin" according to Hofmanová 2016) and included both females and males (maternal and paternal lineages). Some (early-)Neolithic individuals are only descended from Neolithic migrants, others are only descended from the local Mesolithic foragers - indicating some degree of genetic continuity amongst the inhabitants of the Gorges - and there is also evidence for admixture between Mesolithic lineages and newly arrived Neolithic lineages.

4.3.4.1. Stable isotope values and ancestry

Haplogroups and stable isotopes signatures

When one compares the stable isotope values of (Early-)Neolithic individuals grouped according to their lineages (Figure 51; Appendix A.II.22; A.IV.10), an important overlap appears between the individuals with U5 mt-clade ("rather Mesolithic-like lineage") and the individuals with Non-U mt-haplogroup ("rather Neolithic-like lineages"). Despite this overlap, it is worth noticing

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[156] clades or lineages

[157] Y-haplogroups available for only seven Neolithic individuals when grouping the studies of Hofmanová 2016 and Mathieson et al. 2018

[158] While the Y-haplogroup C2 is unknown amongst the European prehistoric population, the clade C1 has recently been identified on other individual related to European Early Neolithic contexts (Mathieson, 2018). However, Z. Hofmanová emphasized that it has been identified on a "position [...] very likely placed in an unstable part of the Y-chromosome because it appears in many sections of the Y chromosomal tree and the haplogroup assignment for LV 82 can be thus considered highly uncertain" (Hofmanová 2016).

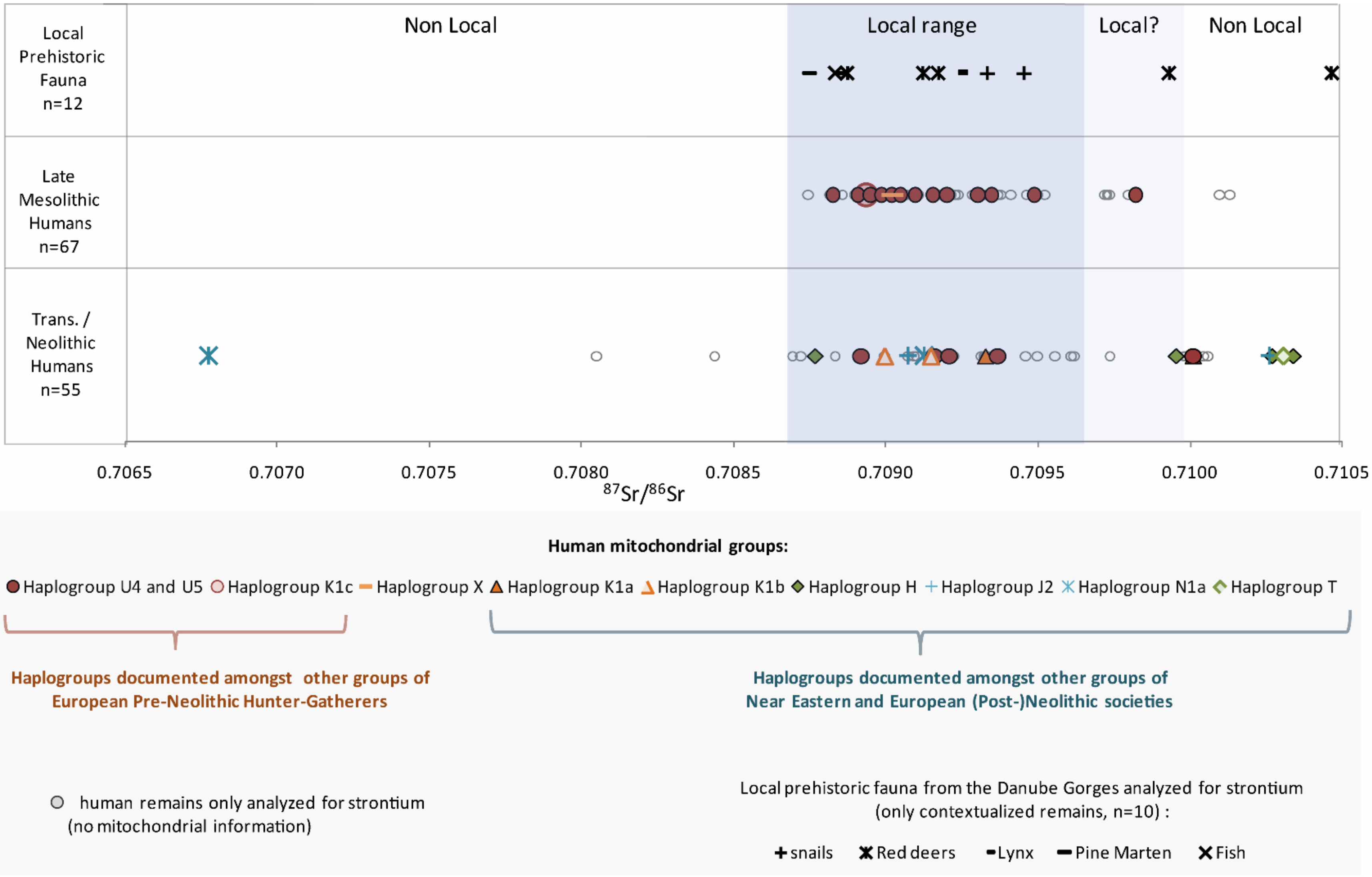

Figure 2: Strontium radiogenic signals of Mesolithic and Neolithic individuals discovered in the Danube Gorges (data from Borić and Price 2013) and associated mitochondrial DNA haplogroups (data from Hofmanová 2017 and Mathieson et al. 2018). From de Becdelièvre et al. 2020.

that some individuals who belong to the U5 mt-clade display the highest δ^{15}N ratios (above 16,5‰16,5[159]) and that all adult individuals assigned to the U5 mt-clade also display δ^{15}N values that exceed 13‰[160]. In contrast, some individuals who belong to non-U mt-haplogroups ("rather Neolithic-like lineages" H, T; K1a) are responsible for the lowest δ^{15}N values (<12‰[161]; Figure 51; Appendix A.II.22; A.IV.10). Amongst the different maternal lineages, three dietary groups can be distinguished (ibidem):

- **(1)** most individuals with the T and H mt-haplogroups ("rather Neolithic-like lineage"). They exhibit the lowest stable isotope values and thus probably had a terrestrial diet, favoring the consumption of terrestrial herbivores/omnivores and of C_3 plants. Since the individuals who belong to the H[162] haplogroup display slightly higher stable isotope values (for the three elements) than the individuals with the T[163] haplogroup, they perhaps included more fish in their diet. Two individuals with the H and T lineages[164] have an entire ancestry pointing to the Near Eastern and European Neolithic (no evidence for admixture with "European Pre-Neolithic foragers", associated with the C2 and G2 Y-clade, "rather Neolithic-like lineages") and the ADMIXTURE analysis also additionally indicates a mixed ancestry for one individual[165] assigned to the H lineage.

- **(2.)** the individuals with the J and N mt-haplogroups ("rather Neolithic-like lineage"). They display higher stable isotope values than the individuals with T and H mt-haplogroups for the three elements. Their stable isotope values appear quite central within the stable isotope distribution of Danube Gorges prehistoric inhabitants (respectively circa -19,5‰ and 9‰). Thus, they likely had a mixed terrestrial and aquatic diet and consumed more aquatic resources - whether freshwater[166] or anadromous[167] - than the individuals with T and H haplogroups. The individual with the J haplogroup[168] also has an ancestry only pointing to the Near Eastern and European Neolithic (no evidence for admixture with "European Pre-Neolithic foragers").

- **(3)** the individuals with the U ("rather Mesolithic-like lineage") and K ("rather Neolithic-like lineage") mt-haplogroups. They mostly display high δ^{15}N (above 13‰[169]) but scattered δ^{13}C, and δ^{34}S values. Some individuals assigned to these clades display the highest stable isotope values for the 3 elements[170;171]: they were probably favoring the consumption of anadromous fish species (and/or the meat of dogs fed with these fish). Others, who exhibit high δ^{15}N but low δ^{34}S[172;173], were probably favoring the consumption of freshwater fish species over anadromous species; they were perhaps also secondarily favoring the meat of terrestrial omnivores who exhibit slightly higher δ^{15}N

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[159] cases of the individuals HV 17-20(1) (δ^{15}N=16,6‰; δ^{13}C=-18‰);,Padina 4 (δ^{15}N=15,9‰; δ^{13}C=-19,1‰, and δ^{34}S=13,4‰) and LV 89a (δ^{15}N=17‰ and δ^{13}C=-18,5‰).

[160] Only the child LV 57, who died above 12 yrs old, display δ^{15}N values of 12,7‰ (δ^{13}C=-19,1‰, and δ^{34}S=8,9‰)?

[161] cases of the individuals LV 26 (δ^{15}N=10,6‰; δ^{13}C=-19,7 ‰, and δ^{34}S=8,8‰) ; LV 8 (δ^{15}N=9,4‰; δ^{13}C=-20‰, and δ^{34}S=5,5‰); LV 82 (δ^{15}N=11,2‰; δ^{13}C=-20,1‰, and δ^{34}S=3,9‰); LV 32a (δ^{15}N=11,8‰; δ^{13}C=-19,7‰, and δ^{34}S=7,8‰); LV 122 (δ^{15}N=10,3‰; δ^{13}C=-20,2‰, and δ^{34}S=6,2‰).

[162] cases of the individuals LV 26 (δ^{15}N=10,6‰; δ^{13}C=-19,7‰, and δ^{34}S=8,8‰); LV 93 (δ^{15}N=12,2‰; δ^{13}C=-20,1‰); LV 35 (δ^{15}N=11,2‰; δ^{13}C=-19,7‰); LV 32a (δ^{15}N=11,8‰; δ^{13}C=-19,7‰, and δ^{34}S=7,8‰) who belong to the haplogroup H. Only the adult individual LV 73 belong to the haplogroup H and has higher δ^{15}N ratio but averageδ^{34}S ratio (δ^{13}C=-19,2‰, δ^{15}N=14,4‰, and δ^{34}S=10,6‰), suggesting that his diet probably substantially included aquatic resources, both freshwater and marine-influenced fish species. Similarly, the child LV 61 was also assigned to the H mt-haplogroup and exhibit higher stable isotope values (δ^{13}C=-19,1‰, δ^{15}N=16,2‰, and δ^{34}S=12,5‰); yet, since he was aged at death 4-7 years old, these values could reflect the lactation signal and therefore, this child was excluded from the figures in appendix A.II.25 and A.IV.10.

[163] cases of the individuals LV 8 (δ^{15}N=9,4‰; δ^{13}C=-20‰, and δ^{34}S=5,5‰) and LV 82 (δ^{15}N=11,2‰; δ^{13}C=-20,1‰, and δ^{34}S=3,9‰) who belong to the haplogroup T

[164] LV 82 (T2 mt-clade associated with the C2 Y-clade) and LV 73 (H3 associated with the G2a Y-clade)

[165] LV 93 (no Y information available)

[166] case of the individual LV 66 (δ^{15}N=14,9‰; δ^{13}C=-19,3‰, and δ^{34}S=6,4‰)

[167] cases of the individuals LV54E (δ^{15}N=13,9‰; δ^{13}C=-19,7‰, and δ^{34}S=10,3‰) and LV 27b (δ^{15}N=13,3‰; δ^{13}C=-19,6‰, and δ^{34}S=10,6‰)

[168] LV 54E (no Y chromosome information)

[169] Amongst the individuals who belong to the K1a lineage, only the individual LV 122 had a lower δ^{15}N value (δ^{13}C=-20,2‰, δ^{15}N=10,2‰, and δ^{34}S=6,1‰), indicative of his rather terrestrial diet.

[170] cases of the individuals Pad. 5 (δ^{15}N=16,6‰; δ^{13}C=-19,7‰, and δ^{34}S=13,8‰), LV 87(1) (δ^{15}N=15,5‰; δ^{13}C=-18,9‰, and δ^{34}S=12,8‰); HV17-20(1) (δ^{15}N=16,6‰; δ^{13}C=-18‰;) and LV 89a (δ^{15}N=17‰; δ^{13}C=-18,5‰) who belong to the U haplogroup

[171] cases of the individuals Pad. 4 (δ^{15}N=15,9‰; δ^{13}C=-19,1‰, and δ^{34}S=13,5‰) and LV 11 (δ^{15}N=15,8‰; δ^{13}C=-18,6‰, and δ^{34}S=10,8‰) who belong to the K haplogroup

[172] cases of the individuals LV 74 (δ^{15}N=14,4‰; δ^{13}C=-19,5‰, and δ^{34}S=5,5‰), LV 20 (δ^{15}N=14,6‰; δ^{13}C=-19,6‰, and δ^{34}S=6,5‰) and probably LV 91 (δ^{15}N=13‰; δ^{13}C=-20,4‰) who belong to the U haplogroup

[173] case of the individual LV 19 (δ^{15}N=15,5‰; δ^{13}C=-19‰, and δ^{34}S=8,3‰) who belong to the K haplogroup

than terrestrial herbivores. Some individuals assigned to the U and K haplogroups display quite medium stable isotope values for the three elements[174;175] (similarly to the individuals who belong to the J and N haplogroups); they probably opted for a mixed diet which included both marine-influenced and terrestrial proteins. Only the individual LV 122, who belong to the K haplogroup, displays lower stable isotope values for the three elements and likely had a more terrestrial diet. Three individuals assigned to the U haplogroup have an ancestry only pointing to the European Pre-Neolithic foragers, and had a diet that includes anadromous fish and/or dogs' meat[176], or a mixed aquatic and terrestrial diet[177]; one individual with the K1 clade had a mixed ancestry and likely had a diet which included anadromous fish and/or dogs' meat[178].

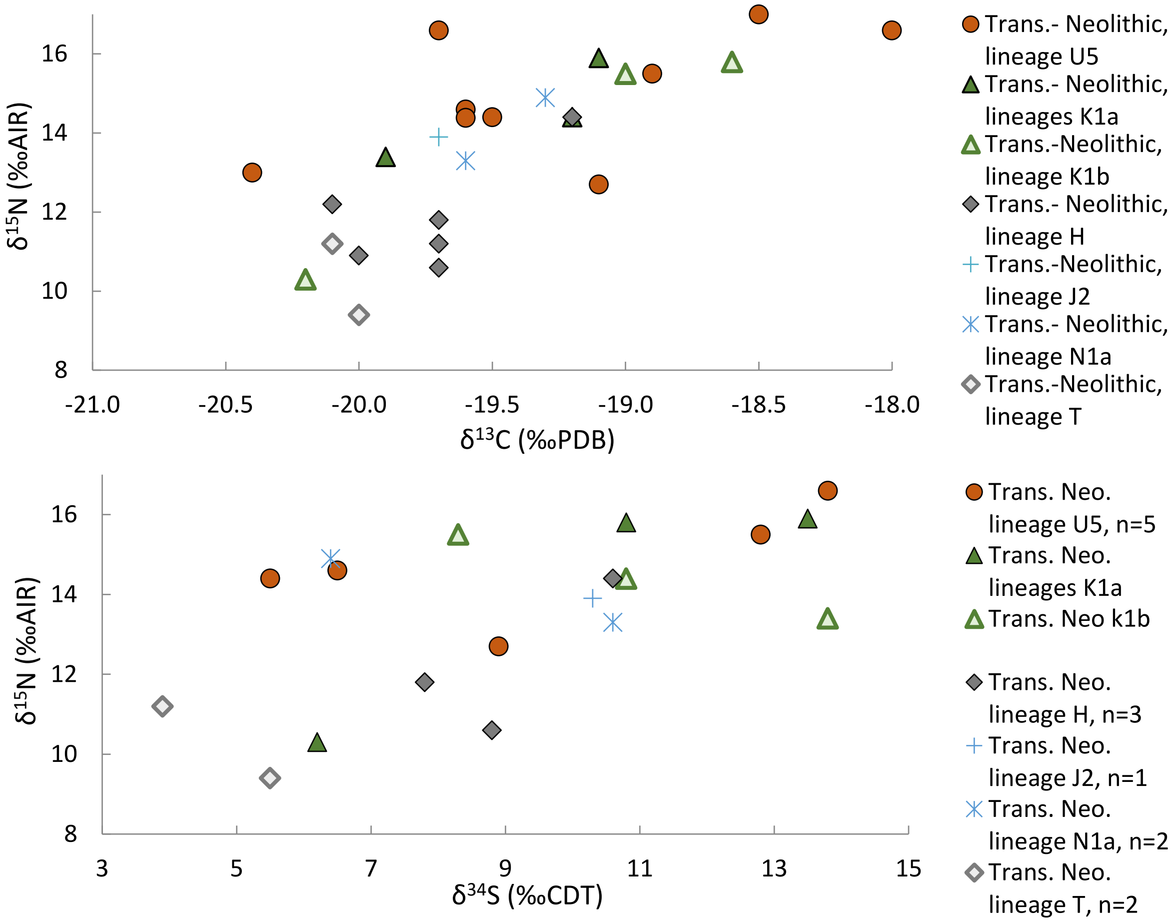

Figure 51: Bivariate plots of $\delta^{13}C$ - $\delta^{15}N$ and $\delta^{34}S$ - $\delta^{15}N$ for Mesolithic and Transformational - Neolithic humans (>5yrs) grouped chronologically and per maternal genetic lineages (mitochondrial DNA: Hofmanová 2016; Mathieson et al. 2018)

The subsistence of individuals assigned to Mesolithic-like lineages and to Near-East Neolithic-like lineages

These results show that some individuals assigned to the same haplogroups also had similar dietary habits (e.g. groups T and H who were eating at a lower trophic level, group N and J who had a more mixed diet, including some aquatic resources), which makes possible to hypothesize that they were perhaps more closely related (from similar communities? family groups?) than they were to the individuals assigned to the other haplogroups (e.g. K and U who encompasses a broader

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[174] case of the individual LV 57 ($\delta^{15}N$=12,7‰; $\delta^{13}C$=-19,1‰, and $\delta^{34}S$=8,9‰) who belong to the U haplogroup

[175] cases of the individuals LV 43 ($\delta^{13}C$=-19,2‰, $\delta^{15}N$=14,4‰, and $\delta^{34}S$=10,8‰); LV 54D ($\delta^{13}C$=-19,9‰, $\delta^{15}N$=13,4‰, and $\delta^{34}S$=13,8‰) who belong to the K haplogroup

[176] case of the individual Pad. 5 ($\delta^{15}N$=16,6‰; $\delta^{13}C$=-19,7‰, and $\delta^{34}S$=13,8‰), HV 19/20-1 ($\delta^{15}N$=16,6‰; $\delta^{13}C$=-18‰)

[177] probable case of LV 91 ($\delta^{15}N$=13‰; $\delta^{13}C$=-20,4‰)

[178] case of Pad 4 ($\delta^{15}N$=15,9‰; $\delta^{13}C$=-19,1‰, and $\delta^{34}S$=13,5‰; K1 mt-clade and R1 Y-clade)

range of stable isotope, including lower and higher values). This possibility is currently being tested by further genetic distance analysis performed at a genome-wide level, notably by the comparison of groups based upon individuals' stable isotopes values (in collaboration with Z. Hofmanová). Since most individuals who belong to the most frequent clade amongst the Mesolithic inhabitant of the Gorges - the mt-lineage U5 - also favored the consumption of aquatic resources (elevated δ^{15}N ratios), it can be assumed that they represent the direct descendants of the local Late Mesolithic fishermen and that they perpetuated the subsistence tradition of their ancestors. Given that the group of individuals typed K had a similarly broad stable isotopes distribution as the group of individuals typed U (Figure 51; Figure 52; Appendix A.II.22; A.IV.10), it can be hypothesized that this group may encompass people from quite different origin, for example some individuals which originate from Neolithic communities which relied on a similar mode of subsistence as the local Mesolithic foragers (with the U5 lineage) and/or also some individuals who descended from groups of Neolithic migrants and who adopted the means of subsistence perpetuated by the descendants of the Mesolithic foragers (with the U5 lineage), perhaps in relation with the particular environmental conditions of the Gorges.

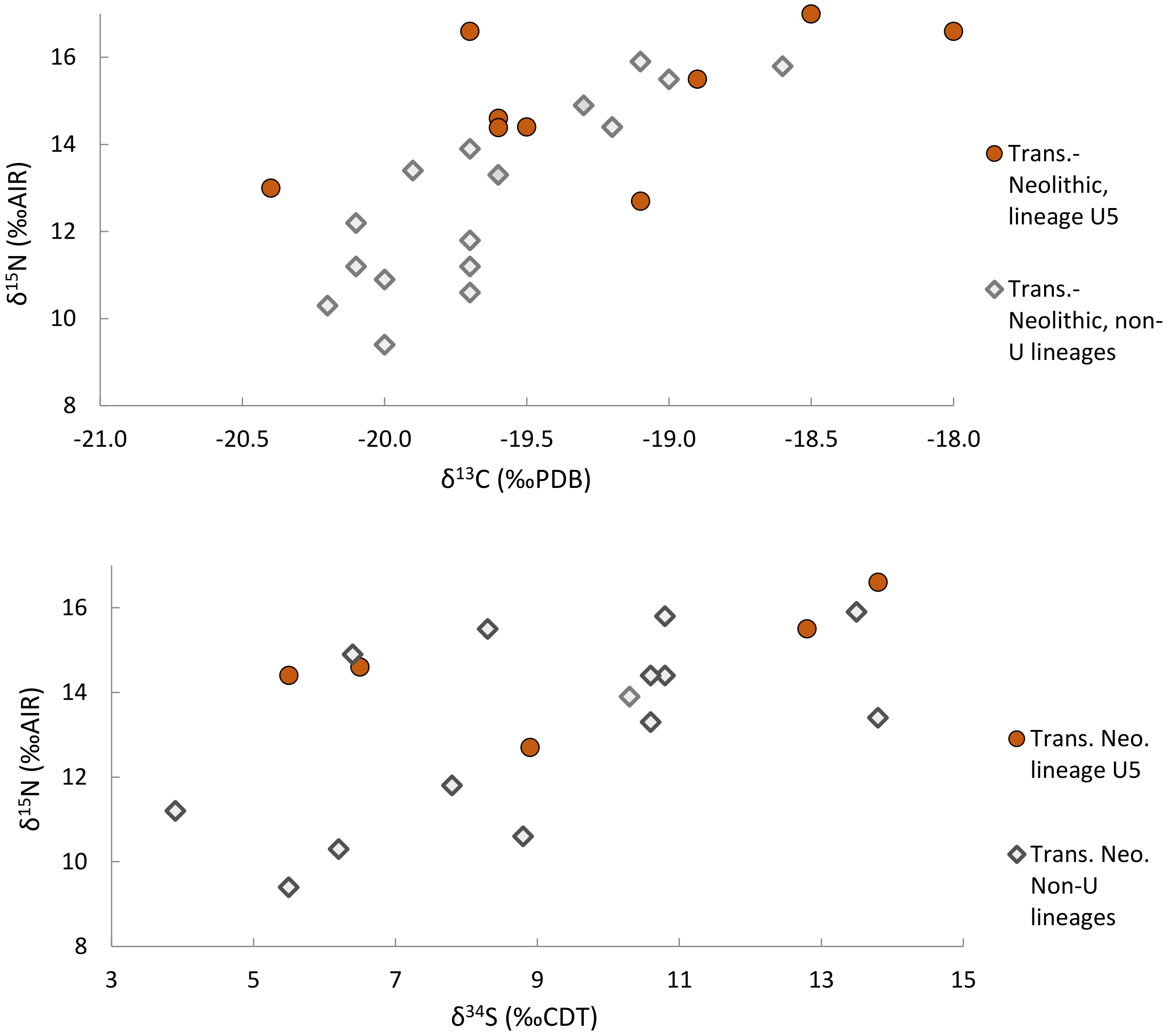

Figure 52: Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Transformational – Neolithic humans (>5 yrs) grouped per maternal genetic lineages (mitochondrial DNA; Hofmanová 2016; Mathieson et al. 2018).

It can be observed that the K-typed individuals who likely consumed anadromous fish (and/or the meat of dogs) have all been assigned to the period of Transformation/Early Neolithic[179] (before 6 ky B.C). On the contrary, the Transformational Early Neolithic individuals who belong to the others "Neolithic-like lineages", whether had a mixed terrestrial and marine-influenced diet[180] (N and J haplogroups) or favored the consumption of terrestrial proteins[181] (H and T haplogroups) (Figure 51; Figure 52; Appendix A.II.25; A.IV.10). It is thus possible that some individuals assigned to the K haplogroups may have been the first descendants from Early Neolithic communities to be in contacts with the local fishermen during the period of Transformation/Early Neolithic and to adopt the local subsistence practices. Some probably mixed with groups of foragers, as suggested by the mixed paternal and maternal ancestries of the individual Pad 4 (with a K1a "rather Neolithic" maternal lineage and the R1b "rather Mesolithic-like" paternal lineage; also indicated by the ADMIXTURE analysis, Mathieson et al. 2018). Unlike the Early Neolithic individuals assigned to the K haplogroup, most Early Neolithic and Neolithic individuals who belong to the haplogroups T and H ("rather Neolithic-like lineage") perpetuated a terrestrial diet; two of them have been both maternally and paternally assigned to "rather Neolithic-like" lineages[182] and one of them probably had a mixed ancestry, according to the ADMIXTURE analysis[183]. It is hence possible that some of these individuals assigned to the haplogroups T and H may represent the first-generation migrants from farming communities. By comparing these results with the strontium radiogenic evidence one can now glean direct information about: 1. the diet of first generation migrants from Neolithic communities (non-locals with a "rather Neolithic-like" mt-haplogroup), 2. the diet of their descendants (locals with a "rather Neolithic-like mt haplogroup") and 3. the diet of the descendants of the local foragers (locals with a "rather Mesolithic-like mt haplogroup), allowing to explore the mechanisms of dietary adaptation upon successive generations at the Neolithic transition.

4.3.4.2. Comparing aDNA information, strontium radiogenic evidence and stable isotopes values.

The comparison of strontium radiogenic signal for the different mt-haplogroups indicates that local and non-local individuals do not belong to a specific maternal lineage (they have been assigned both to U and Non-U lineages; Figure 50). Having a local isotopic signature does not necessarily signify to descend from a "Mesolithic-like maternal lineage"; nor a non-local signal means to be related to a "Neolithic-like maternal lineage". Concerning paternal lineages, the strontium radiogenic signal is only available for three individuals: two locals with "rather Mesolithic-like" Y-clade (Y1 and R1) and one local with a rather "Neolithic-like" Y-clade (G2). Therefore, it appears that some individuals grew up in the Gorges and have ancestry amongst the Mesolithic foraging communities[184] (locals with U haplogroups), others grew up in the Gorges but are descended from Neolithic migrants (locals with Non-U haplogroups)[185], or had a mixed ancestry[186]; one individual migrates in the Gorges and has ancestry amongst Mesolithic foragers[187] (non-local with U haplogroup); and finally some individuals migrated in the Gorges and have ancestry amongst some Neolithic communities (non-local with non-U haplogroups[188]). These results suggest that both

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[179] Pad 4 (δ^{15}N=15,9‰; δ^{13}C=-19,1‰, and δ^{34}S=13,5‰); LV 11(δ^{15}N=15,8‰; δ^{13}C=-18,6‰, and δ^{34}S=10,8‰); and perhaps LV 54D (δ^{13}C=-19,9‰, δ^{15}N=13,4‰, and δ^{34}S=13,8‰), whose elevated δ^{34}S values indicate the consumption of anadromous fish, but the slightly lower δ^{13}C and δ^{15}N may also indicate the inclusion of terrestrial proteins in his diet.

[180] LV 27b (δ^{15}N=13,3‰; δ^{13}C=-19,6‰, and δ^{34}S=10,6‰)
and LV 54E (δ^{15}N=13,9‰; δ^{13}C=-19,7‰, and δ^{34}S=10,3‰)

[181] LV 26 (δ^{15}N=10,6‰; δ^{13}C=-19,7‰, and δ^{34}S=8,8‰)

[182] LV 82 (T2 mt-clade associated with the C2 Y-clade) and LV 73 (H3 associated with the G2a Y-clade) and entire ancestry pointing to the Near East Neolithic according to the ADMIXTURE analysis (Hofmanová 2016)

[183] LV 93 (no Y information available)

[184] at least a maternal ancestry for Pad.5; LV 87(1); LV 74; both maternal and paternal ancestry for sure in case of HV 17-20/1 (U5 mt-clade and I2 Y-clade); probable case of LV 93 as well, according to ADMIXTURE analyses

[185] at least maternally LV 27b, Pad. 4; LV 43; both maternally and paternally for sure in case of LV 73; and probably of LV 54E, according to ADMIXTURE analyses

[186] identified case of Pad. 4

[187] at least maternally for LV 20

[188] at least maternally for LV 26; LV 32a; LV 54E; LV 122; LV 66; LV 8.

locals and non-locals probably had descendants who stayed and lived in the region. All non-locals discovered in the Inner Gorges have been identified in the osteo-anthropological sample of Lepenski Vir; the fact that they belong to various lineages, including the U5 "rather Mesolithic-like" clade, supports the idea that Lepenski Vir should have been, at that time, an attractive place for people originating from different horizons and probably with different means of subsistence.

The diet of locals, assigned to a European Mesolithic-like haplogroup

The comparison between stable isotope values and individuals' geological and genetic origins (Figure 14; Appendix A.II.23; A.IV.9), shows that the locals, whether they have been assigned to the U5 clade (four of them) or to Non-U haplogroups (three K, one N, and one H), exhibit high stable isotope signals (δ^{15}N above 13‰; δ^{13}C above -20 ‰ and δ^{34}S above 12 ‰). In contrast, the non-locals assigned to Non-U haplogroups, display lower stable isotope values (δ^{15}N below 15‰; δ^{13}C below -19‰ and δ^{34}S below 12 ‰). Although δ^{34}S discriminates well locals (from every haplogroups) and non-locals (from "rather Neolithic mt-lineages"), there is some overlap between the two groups concerning δ^{13}C and δ^{15}N (Appendix A.II.23; A.IV.9).

All locals who have been assigned to the "rather Mesolithic-like" U5 mt-clade had a diet oriented toward the consumption of aquatic resources (high δ^{15}N; Appendix A.II.23; A.IV.9), including anadromous species[189] (high δ^{15}N and high δ^{34}S) or - in one case - favoring freshwater species and some terrestrial resources such as the meat of omnivores[190] (high δ^{15}N and low δ^{34}S). Interestingly, within the same grave 79 at Lepenski Vir, the Early Neolithic individuals LV 79b and 79c who both belong to the U5 mt-haplogroup[191] have been found disarticulated and associated with the local individual 79a who exhibits elevated stable isotope values[192]. Their association in death, their elevated stable isotope values, their "Mesolithic-like" maternal lineages and their local strontium signal suggest that they were perhaps some relatives who were descended from local Mesolithic foragers, who perpetuated the local mode of subsistence and who eventually decided to be buried together respecting the local Mesolithic funerary customs.

The diet of the locals, assigned to a Near-Eastern Neolithic-like haplogroup

Most locals with a "rather Neolithic-like mt-lineage" display close stable isotope values to the locals with the "rather Mesolithic-like U5-clade" (Figure 53; Appendix A.II.23; A.IV.9); they were whether favoring the consumption of anadromous fish[193] (K haplogroup) or had a mix marine-influenced and terrestrial diet[194] (medium / less elevated δ^{15}N, δ^{13}C and δ^{34}S values; K, N and H haplogroups). Thus, it can be assumed that the locals with "rather Neolithic-like mt-lineage" (three K, one N and one H) may have descended from Neolithic migrants who whether originated from Neolithic communities with similar dietary habits than the locals foragers or who adopted the local mode of subsistence based on fishing.

The diet of non-locals assigned to a Near Eastern-like haplogroup

In contrast, non-locals with rather "Neolithic-like mt-haplogroups" display lower stable isotope values. Four of them exhibit lower values for the isotopes of the three elements, indicative of a terrestrial diet[195] (Figure 53; Appendix A.II.23; A.IV.9). Since they are non-locals, belong to clades which appear in Europe during the Neolithic period, and perpetuated a terrestrial diet, one

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[189] cases of the Early Neolithic individuals Pad 5 (δ^{13}C=-19,7‰, δ^{15}N=16,6‰, and δ^{34}S=13,8‰); HV 17-20(1) (δ^{13}C=-18‰, δ^{15}N=16,6‰); LV 87(1) (δ^{13}C=-18,9‰, δ^{15}N=15,5‰, and δ^{34}S=12,8‰).

[190] case of the Neolithic individual LV 74 (δ^{13}C=-19,5‰, δ^{15}N=14,4‰, and δ^{34}S=5,5‰).

[191] no Y-chromosome information available for them.

[192] LV 79a δ^{13}C=-18,5‰, δ^{15}N=15,8‰, and δ^{34}S=12,5‰; no aDNA information available for this individual

[193] cases of the Early Neolithic individuals Pad. 4 (δ^{13}C=-19,1‰, δ^{15}N=15,9‰, and δ^{34}S=13,5‰; K mt-haplogroup) and maybe LV 54D (δ^{13}C=-19,9‰, δ^{15}N=13,4‰, δ^{34}S=13,8‰; K mt-haplogroup); The elevated δ^{34}S values for the female LV 54D indicate the consumption of anadromous fish but his slightly lower δ^{13}C and δ^{15}N may also point to the inclusion of terrestrial proteins in her diet.

[194] case of the Early Neolithic individuals LV 27b (δ^{13}C=-19,6‰, δ^{15}N=13,3‰, and δ^{34}S=10,6‰; haplogroup N) and of the Neolithic individuals LV 43 (δ^{13}C=-19,2‰, δ^{15}N=14,4‰, and δ^{34}S=10,8‰ K mt-haplogroup); and LV 73 (δ^{13}C=-19,2‰, δ^{15}N=14,4‰, and δ^{34}S=10,6‰; H mt-haplogroup).

[195] case of the Early Neolithic individual LV 26 (δ^{13}C=-19,7‰, δ^{15}N=10,6‰, and δ^{34}S=8,8‰;haplogroup H); and LV 122 (δ^{13}C=-20,2‰, δ^{15}N=10,3‰, and δ^{34}S=6,2‰; haplogroup K); and of the Neolithic individuals LV 32a (δ^{13}C=-19,7‰, δ^{15}N=11,8‰, and δ^{34}S=7,8‰; haplogroup H) and LV 8 (δ^{13}C=-20‰, δ^{15}N=9,4‰, and δ^{34}S=5,5‰; haplogroup T)

may assume that they probably originated from Early Farming communities. In the current state of research, it cannot be established whether these non-locals reproduced in the Gorges the mode of subsistence of their ancestors or opted for the dietary practices of the local foragers but died too early after their migration for the signal of their new diet to be reflected in the collagen of their bone[196]. In contrast, their putative descendants likely adopted the local fishing means of subsistence since the locals with "Neolithic-Like mt-haplogroups" exhibit higher δ^{15}N. The three locals assigned to the K1a and b clades display significantly higher stable isotope values[197] than the only non-local assigned to the K haplogroup[198]; similarly, the only Neolithic local individual assigned to the H haplogroup[199]display higher stable isotope values than the two non-locals assigned[200] to this haplogroup; the local individual assigned to the N haplogroup also exhibit higher δ^{13}C and δ^{34}S values[201] than the non-local assigned to this haplogroup[202] (but yet he had slightly lower δ^{15}N ratio than the non-local). While first generation migrants may not have adapted to the subsistence of the Gorges, or perhaps died within the years following their migration, it seems that their descendants mostly adopted the local practices.

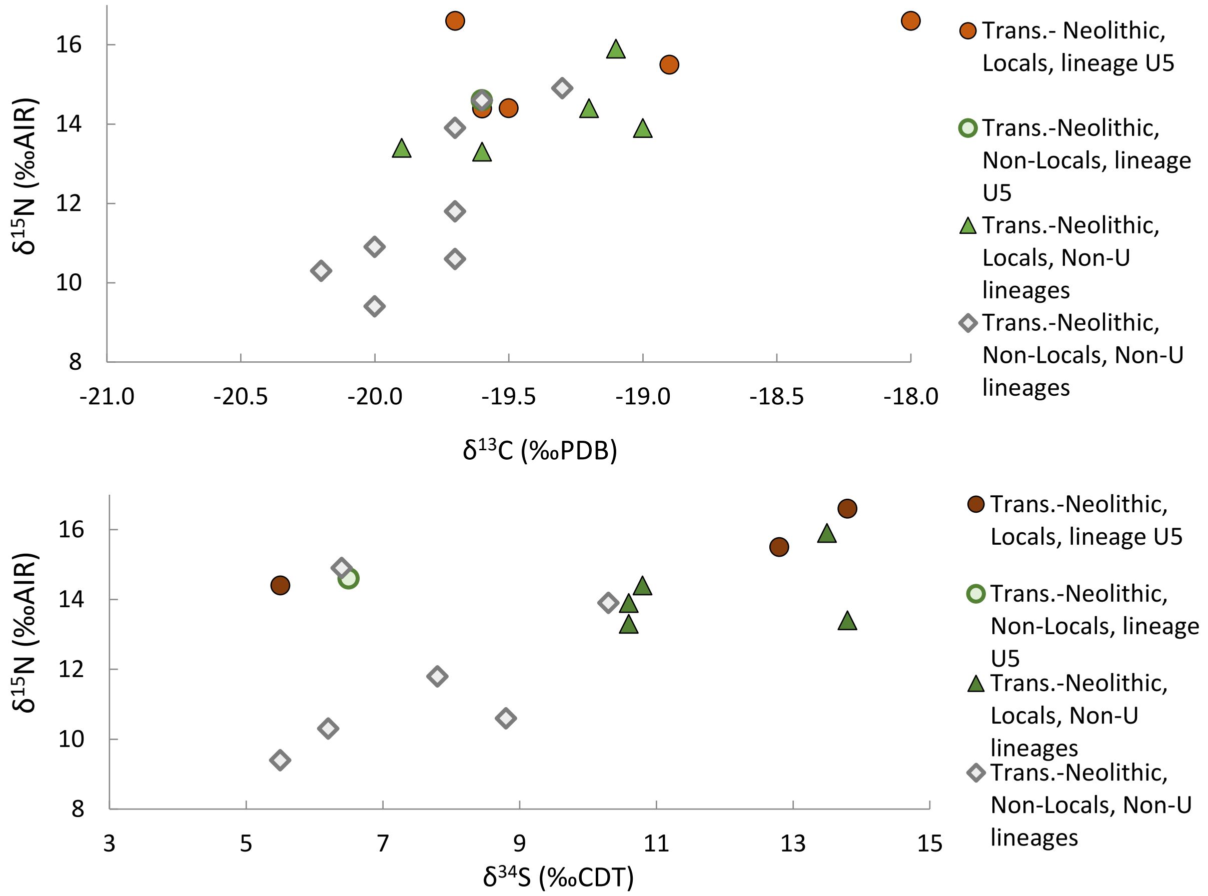

Figure 53: Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Transformational - Neolithic humans (>5 yrs) grouped per maternal genetic lineages (mitochondrial DNA; Hofmanová 2016; Mathieson et al. 2018) and according to their geographic origin (locals and non-locals discriminated according to their signal in radiogenic strontium, ^{87}Sr/^{86}Sr Borić and Price 2013)

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[196] circa 10-15 years is necessarily for a complete bone turnover (Valentin, 2003)

[197] The locals Pad. 4 (δ^{13}C=-19,1‰, δ^{15}N=15,9‰, and δ^{34}S=13,5‰), LV 43 (δ^{13}C=-19,2‰, δ^{15}N=14,4‰, and δ^{34}S=10,8‰) and LV 54D (δ^{13}C=-19,9‰, δ^{15}N=13,4‰, and δ^{34}S=13,8‰)

[198] the non-local individual LV 122 (δ^{13}C=-20,2‰, δ^{15}N=10,3‰, and δ^{34}S=6,2‰)

[199] the local LV 73 (δ^{13}C=-19,2‰, δ^{15}N=14,4‰, and δ^{34}S=10,6‰)

[200] non-locals LV 26 (δ^{13}C=-19,7‰, δ^{15}N=10,6‰, and δ^{34}S=8,8‰) and LV 32a (δ^{15}N=11,8‰; δ^{13}C=-19,7‰, and δ^{34}S=7,8‰)

[201] the local LV 27b (δ^{13}C=-19,6‰, δ^{15}N=13,3‰, and δ^{34}S=10,6‰)

[202] the non-local LV 66 (δ^{13}C=-19,3‰, δ^{15}N=14,9‰ and δ^{34}S=6,4‰)

However, it should be specified that two non-local individuals with "rather Neolithic like mt-lineage" and the only non-local with the rather "Mesolithic-like" U5 mt-haplogroup display higher $\delta^{15}N$ stable isotope values than the other non-locals (>13‰; Appendix A.II.23), pointing to a diet which substantially includes aquatic resources. The Early Neolithic non-local female LV 54E (J mt-lineage[203]) exhibits medium $\delta^{15}N$ and $\delta^{34}S$[204], indicative of a mixed terrestrial and marine-influenced diet and the Neolithic non-locals LV 66[205] (N haplogroup) and LV 20[206] (U haplogroup) exhibit elevated $\delta^{15}N$ ratios but lower $\delta^{34}S$ ratios, indicative of their consumption of freshwater fish (and perhaps jointly of some terrestrial food of slightly higher trophic level such as the meat of wild boars). Therefore, the theoretical opposition between local fishermen with rather Mesolithic-like lineage and non-local farmers with rather Neolithic-like lineage should be nuanced. The advent of the Neolithic in the Danube Gorges was likely associated with the interactions of some people who probably originated from manifold geographic horizons, who had various genetic ancestries and who likely perpetuated different ways of subsistence.

Interestingly, the two females - non-local LV 54E and local LV 54D - buried at the same location within the building 65 and who display very similar $\delta^{13}C$ and $\delta^{15}N$ values[207] (Figure 47; *cf* part 4.3.3*)* belong to two different Non-U haplogroups (J for the non-local and K for the local female). One - LV 54D - may have been descended from a migrant but was born in the Gorges while the other - LV 54E - grew up outside of the Gorge and perhaps adapted to the local ways of subsistence. The non-local female was probably buried after the local female, with artifacts recalling both Balkans' Neolithic cultural tradition (discoid limestone beads) and the Mesolithic symbolic record (carved deer antler). Within the grave 27 were discovered the remains of the local individual LV 27b who belong to the N1a mt-haplogroup, of the individual LV 27d who belong to the U5 mt-haplogroup[208], of the non-local individual LV 27a and of the child LV 27c who both exhibit high and very close $\delta^{13}C$ and $\delta^{15}N$ values[209] (Figure 54). The facts that some of them were identified as locals and others as non-locals, that they belong to very different maternal lineages (rather "Mesolithic"-like and "Neolithic"-like), that they had a diet mostly favoring the consumption of aquatic resources or mixed terrestrial and aquatic, and that they were all gathered in death, are further evidence pointing to the behavioral and cultural interactions that occurred circa 6 ky BC in the Danube Gorges between some individuals originating from different horizons.

Figure 54: Lepenski Vir, grave 27, Transformation/Early Neolithic. At least five individuals were discovered, mostly dislocated. Amongst them, one individual was determined as local and assigned to a Non-U maternal lineage (27b), one as local (LV 27a) and one assigned to the U5 maternal lineage (LV 27D; appearing skull). Photo. from Stefanović 2016.

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[203] No evidence of mixed ancestry for this individual (only a "Neolithic"-like ancestry according to ADMIXTURE analyses)

[204] LV 54E ($\delta^{13}C$=-19,7‰, $\delta^{15}N$=13,9‰ and $\delta^{34}S$=10,3‰)

[205] LV 66 ($\delta^{13}C$=-19,3‰, $\delta^{15}N$=14,9‰ and $\delta^{34}S$=6,4‰)

[206] LV 20 ($\delta^{13}C$=-19,6‰, $\delta^{15}N$=14,6‰ and $\delta^{34}S$=6,5‰)

[207] LV 54E ($\delta^{13}C$=-19,7‰, $\delta^{15}N$=13,9‰ and $\delta^{34}S$=10,3‰); LV 54D ($\delta^{13}C$=-19,9‰, $\delta^{15}N$=13,4‰ and $\delta^{34}S$=13,7‰)

[208] no available stable isotope values; individual with an entire "European Pre-Neolithic"-like ancestry according to ADMIXTURE analyses

[209] LV 27a: $\delta^{13}C$=-18,8‰, $\delta^{15}N$=15,9‰, and $\delta^{34}S$=13,4‰; no aDNA data available; LV 27c: $\delta^{13}C$=-18,5‰, $\delta^{15}N$=15,6‰, no strontium Radiogenic signal available and no aDNA data available for this children; children LV 27c aged at death 10-12 years old.

4.3.4.3. Adding the temporal dimension: the influence of successive generations of migrants

While some Early Neolithic individuals with the U5 and K1 mt-lineages display elevated δ^{34}S values (>13‰[210]), all Neolithic individuals analyzed for aDNA exhibit lower δ^{34}S values, whatever haplogroup they have been assigned to. Apart from LV 122, who likely had a terrestrial diet[211], all U5 and K1 Early Neolithic individuals had a diet which included anadromous fish and dog's meat[212] (high δ^{34}S and δ^{15}N ratios) or a mixed terrestrial and marine-influenced diet[213] (medium δ^{15}N and δ^{34}S values). All of those who were also analyzed for strontium have been identified as locals. Other Early Neolithic individuals - mostly identified as non-locals - had a mixed diet (mt-haplogroups N and J) or display lower stable isotope values for the three elements, indicative of a terrestrial diet (mt-haplogroups H and T). In contrast, for the Neolithic period, U5 and K individuals (locals and non-locals) whether favored freshwater fish over anadromous species[214] or had a mixed terrestrial and aquatic diet[215], perhaps including the meat of some terrestrial omnivores such as wild boars (higher δ^{15}N and lower δ^{34}S values). Other Neolithic individuals (mostly non-locals) whether favored freshwater fish (and perhaps some higher trophic terrestrial food resources; haplogroup N) or had a rather terrestrial diet (haplogroup H and T).

These results suggest that the descendants of Mesolithic foragers (locals, U5) and of the migrants who adopted the local pattern of subsistence during the period of Transformation (locals, mostly K1a and K1b) rather favored freshwater fish and/or the consumption of terrestrial resources over anadromous species (and dogs meat) during the Neolithic period. Considering that the Early Neolithic individuals assigned to the U5 and K1 lineages have been discovered at the sites of Padina, Hajdučka Vodenica[216] and Lepenski Vir and that all Neolithic individuals assigned to these lineages have been discovered at the site of Lepenski Vir, the perceived stable isotope difference between Early Neolithic and Neolithic U5 and K1 individuals may be partially related to the inter-site dietary differences that we previously noticed between these localities[217]. It is thus possible that the behavioral syncretism which could have resulted from the arrival of migrants at Lepenski Vir circa 6 ky may have gradually led most descendants of the foragers to abandon the consumption of dogs and anadromous fish. This dietary diversification could be whether related to the introduction of husbandry and cereal consumption (more mixed terrestrial/aquatic diet), or to a local change in fishing strategies at this spot (catching more freshwater species), or to a change in dogs' raising practices (dogs raised for other purposes than dietary?). Yet, it should also be borne in mind that the lineages which are associated with a substantial consumption of anadromous fish during the Early Neolithic period in the Gorges (U and K) are also those which are rather associated to freshwater fishing (U and N) or to a mixed terrestrial-aquatic diet (U and K) during the Neolithic period. It is therefore also possible that the individuals who belong to these lineages may have mostly continued to perpetuate the local fishing traditions through the Early Neolithic and the Neolithic periods and that the perceived Neolithic δ^{34}S shift down could be alternatively due to

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[210] cases of Pad. 5 (δ^{13}C=-19,7‰, δ^{15}N=16,6‰, and δ^{34}S=13,8‰; U haplogroup), LV 87(1) (δ^{13}C=-18,9‰, δ^{15}N=15,5‰, and δ^{34}S=12,8‰; U haplogroup); Pad. 4 (δ^{13}C=-19,1‰, δ^{15}N=15,9‰, and δ^{34}S13,5‰; K haplogroup) and LV 54 D (δ^{13}C=-19,9‰, δ^{15}N=13,4‰, and δ^{34}S=13,8‰; K haplogroup)

[211] LV 122 (δ^{13}C=-20,2‰, δ^{15}N=10,3‰, and δ^{34}S=6,2‰; U5)

[212] cases of HV 17-20/1 (δ^{13}C=-18‰, δ^{15}N=16,6‰; U5), Pad. 5 (δ^{13}C=-19,7‰, δ^{15}N=16,6‰, and δ^{34}S=13,8‰; U5), LV 87(1) (δ^{13}C=-18,9‰, δ^{15}N=15,5‰, and δ^{34}S=12,8‰; U5), Pad. 4 (δ^{13}C=‰, δ^{15}N=‰, and δ^{34}S‰; K1), and LV 11 (δ^{13}C=-18,6‰, δ^{15}N=15,8‰, and δ^{34}S=10,8‰; K1)

[213]cases of LV 91: δ^{13}C=-20,4‰, δ^{15}N=13‰; LV 54D: δ^{13}C=-19,9‰, δ^{15}N=13,4‰, and δ^{34}S=13,8‰;

[214] LV 74 (δ^{15}N=14,4‰; δ^{13}C=-19,5‰, and δ^{34}S=5,5‰; U5); (LV 20: δ^{15}N=14,6‰; δ^{13}C=-19,6‰, and δ^{34}S=6,5‰; U5); LV 19 (δ^{15}N=15,5‰; δ^{13}C=-19‰, and δ^{34}S=8,3‰; K1)

[215] LV 57 (δ^{15}N=12,7‰; δ^{13}C=-19,1‰, and δ^{34}S=8,9‰; U5); LV 91 (δ^{15}N=13‰; δ^{13}C=-20,4‰,; U5) and LV 43 (δ^{15}N=14,4‰; δ^{13}C=-19,2‰, and δ^{34}S=10,6‰; K1)

[216] Pad. 4, Pad. 5 and HV 17-20(1)

[217] Padina and Hajdučka Vodenica as places were the fishing traditions throughout the Mesolithic and Neolithic periods, contrasting with the Neolithic broadening of the dietary spectrum noticed at Lepenski Vir.

non-behavioral factors such as a shift in fish δ^{34}S values or an ecological change in the availability of the different species after 6 ky B.C[218].

4.3.4.4. Summary: adaptations and continuity over successive generations of migrations

Concerning the period of Transformation-Neolithic, ancient DNA analyses identified a mixture of lineages which have been documented amongst local foragers of the Gorges during the previous Mesolithic period (e.g. U mt-haplogroup) and of lineages which are known amongst some other Neolithic population of Europe and of the Near East but which have not been documented amongst European Pre-Neolithic populations (e.g. H, I, J, N, T mt-lineages; Hofmanová 2016; Mathieson et al. 2018). **As a general pattern, the individuals who belong to the "rather Mesolithic-like lineages" had a diet oriented toward the consumption of aquatic resources while some individuals who belong to "rather Neolithic-like lineages" had a more terrestrial diet, although there is some overlap between both groups.** The K1a and b lineages ("rather Neolithic-like maternal lineage"[219]) display the same stable isotope distribution than the individuals with U5 lineage (rather "Mesolithic-like"[220]); the members of this lineage perhaps arrived earlier in the Gorges and adopted the local practices. In contrast, the stable isotope values of the individuals who belong to the haplogroups T and H ("rather Neolithic-like maternal lineage"; also associated with the "rather Neolithic-like C and G paternal lineages") are indicative of a more terrestrial diet, which suggest that they did not adopted the local means of subsistence based on fishing.

By comparing aDNA information with the strontium radiogenic evidence and stable isotope values, one can explore the process of dietary adaptations upon successive generations. **As a general trend, locals, whether they have been assigned to "rather Mesolithic-like lineages", or to "rather Neolithic-like lineages", exhibit medium-to-high stable isotope signals, indicative of their aquatic-based means of subsistence. Most of them likely consumed anadromous fish (and/or the meat of dogs) or had a mixed terrestrial and marine-influenced diet. In contrast, most non-locals with a "rather Neolithic-like lineage"[221] exhibit lower stable isotope values for the three elements, suggesting that they probably favored the consumption of terrestrial proteins. These non-local individuals may thus have originated from farming communities. Therefore, it seems that numerous first-generation migrants did not adapt to the means of subsistence perpetuated by the local foragers or perhaps died within the years following their migration. In contrast, their descendants mostly adapted to the local ecological conditions.**

Finally, it is noteworthy that, amongst the sample of individuals analyzed for aDNA and stable isotopes, some individuals who have been assigned to the period of Transformation/Early Neolithic and to the U5 and K1 mt-lineages display elevated δ^{34}S values, while all the individuals who have been assigned to the Neolithic period exhibit lower δ^{34}S values, whatever haplogroup they belong to. It suggests that the descendants of the Mesolithic foragers of the Gorges rather favored freshwater fish over anadromous species (and dog's meat) during the Neolithic period, or had a more mixed terrestrial and aquatic diet. It is thus possible that the behavioral syncretism which may have resulted from the arrival of migrants at Lepenski Vir circa 6 kyr gradually led the descendants of the foragers to reduce the consumption of marine-influenced proteins, whether because of the competing availability of livestock and crops resources, or because of a local change in fishing strategies and/or in dog's raising practices.

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[218] As previously mentioned, we consider that a shift down in the δ^{34}S values of anadromous fish after 6 ky BC is less likely to explain Neolithic human lower δ^{34}S values than a change in diet since some ^{14}C dated Neolithic individual still display high δ^{34}S values (e.g. HV 13 and LV 7II/b; no associated aDNA data).

[219] one individual, Pad 4 related to the K1a lineage have a mixed ancestry, with the "Mesolithic-like" R1 paternal lineage (mixed ancestry also confirmed by the ADMIXTURE analyses)

[220] no evidence of admixture for individuals belonging to this lineage

[221] H, K and T haplogroups; some of them also having a paternal ancestry pointing to migrant Neolithic communities

At the end of the 7th millennium BC some migrants who belong to new Neolithic lineages arrived in the Danube Gorges; they had a rather terrestrial diet or a mixed terrestrial and marine-influenced diet. Some of these Neolithic migrants who favored the consumption of terrestrial resources may have originated from early farming communities settled south-eastern in the Balkans. Although these migrants perhaps brought in the Gorges some of the Neolithic technologies which appeared in the archaeological sequence then (ceramics, ground stones, some ornaments...), their interactions with the locals did not result in a sudden change in the local ways of subsistence: the local descendants of Mesolithic foragers continued to perpetuate the traditional mode of subsistence, particularly consuming higher trophic food resources, such as anadromous fish species or dogs' meat. Interestingly, the descendants of these first-generation migrants were also consuming fish; they likely adopted and/or adapted the local means of subsistence.

During the first centuries of the 6th millennium BC, other generations of migrants arrived in the Gorges. They whether had a more terrestrial diet or favored the consumption of freshwater fish and of terrestrial herbivores-omnivores over anadromous fish species and over the meat of dogs. They probably brought in the Gorges the domestic species of cattle, sheep, goat and pigs and perhaps also domesticated crops. At that time, the descendants of the local foragers still consumed aquatic resources, but whether favored freshwater species, or opted for a mixed terrestrial and aquatic diet. These subsequent generations of migrants may thus be responsible for deeper behavioral and cultural adaptations in the Danube Gorges, in terms of subsistence (lesser focus on the consumption of anadromous fish and dogs), of site occupation (abandonment of the trapezoidal buildings, new kind of buildings and domed ovens) or even in the symbolic record (changes in mortuary practices with the generalization of the crouched position). The comparison of ancient DNA and stable or radiogenic isotopes thus strengthens the idea that the pattern of Neolithization of the Gorges should be understood neither as a rough replacement of population nor as a straightforward process of acculturation or a sudden behavioral shift but rather as a mosaic of interactions between people originating from different horizons which resulted in mutual and gradual adaptations over centuries.

4.3.5. Sex and age-related stable isotope differences

Sex-related stable isotope differences

The groups of males and of females assigned to the period of Transformation-Neolithic both encompass wider stable isotopes distributions than the groups of Mesolithic males and females (Appendix A.II.26.). Although a specific diet cannot be associated to the members of one sex, it is worth mentioning that some females buried at Lepenski Vir during the period of Transformation and the Neolithic period as well as some Early Neolithic females buried at Ajmana yet exhibit lower δ^{13}C ratios (<-19,8‰) than the other males and females buried in the region of the Gorges; they are associated with low to medium δ^{15}N values (<-14,6‰). Besides, some Neolithic females buried at Lepenski Vir as well as the Early Neolithic females buried at Ajmana also exhibit lower δ^{34}S (<8,5‰) than the other males and females buried in the region of the Gorges (Appendix A.II.26-27).

Transformational males' and females' stable isotopes differences

Concerning the period of Transformation/Early Neolithic in the Inner Gorges, four females discovered at Lepenski Vir display medium to low δ^{13}C ratios (<-19,7‰), associated with medium to high δ^{15}N values (ca 12-14‰) and δ^{34}S values (ca 9,5-14‰) and thus likely had a mixed terrestrial and aquatic diet, including the consumption of anadromous fish and/or dogs meat (Appendix A.II.26-27). One of them has been identified as a local and one as a non-local (Appendix A.II.28). Two other females discovered at Lepenski Vir and identified as locals exhibit high stable isotope values (δ^{13}C=-19,2‰ and -18,5‰; δ^{15}N=15,4‰ and 15‰; δ^{34}S= 12,1‰) (Appendix

A.II.26-28). They likely favored the consumption of aquatic resources and particularly consumed anadromous fish and/or the meat of dogs. One local female discovered at Padina also exhibit medium δ^{13}C (-19,7‰), high δ^{15}N (16,6‰) and δ^{34}S values (13,8‰), which suggests that she had a similarly marine-influenced diet.

Two non-local males discovered at Lepenski Vir, exhibit lower δ^{13}C (-19,7‰ and -19,7) and δ^{15}N (10,6‰ and 11,5‰) values, ranging close to the group of females with lower stable isotope values. One also displays lower δ^{34}S value (8,8‰) indicative of his rather terrestrial diet, while the other exhibits higher δ^{34}S ratios (14,8‰), suggesting that he had a mixed terrestrial and marine-influenced diet and/or that this particular signature (low δ^{15}N and high δ^{34}S) could be related to his environment of origin. Finally, the three other males discovered at Lepenski Vir, Hajdučka Vodenica and Padina (two identified as locals), display high stable isotope values for the three elements (δ^{13}C >-19,1; δ^{15}N>15,9 and δ^{34}S=13,5, n δ^{34}S=1); two local males thus display the highest δ^{13}C and δ^{15}N values obtained for sex-diagnosed Early Neolithic individuals (Appendix A.II.26-28).

Concerning the Early Neolithic period downstream, the Early Neolithic females discovered at the site of Ajmana display rather low δ^{13}C (ca -19,7‰), δ^{15}N values (ca 10,5‰) and δ^{34}S values (ca 8‰) values (Appendix A.II.26-27); they likely favored the consumption of terrestrial proteins (the meat of terrestrial herbivores and C_3 plants) and perhaps secondarily consumed some freshwater fish.

When males' and females' stable isotopes results are considered as a whole for the period of Transformation/Early Neolithic, the sex-related dietary tendencies observed amongst Mesolithic individuals does not seem sustained. It should be related to the presence in the region some Early Neolithic communities who likely had a more terrestrial diet, and to the presence in the Inner Gorges of non-local individuals with a different biochemical signature. Indeed, two non-local males buried at Lepenski Vir and the females buried at Ajmana rather favored the consumption of terrestrial proteins. Concerning local individuals buried in the Inner Gorges, both males and females were likely consuming anadromous fish and dogs or had a mixed aquatic-terrestrial diet. Since the end of the IV^th^ millennium BC was a period of climate change associated with harder winters and probably increased floods of the Danube, it is possible that both sex relied more on stored resources (e.g dried fish and meat) and on the food repository that represented domestic dogs. Besides, the increasing contacts with farming communities may also have impacted some aspects of the local social organization. Nonetheless, it may be stressed that two local males, buried at Lepenski Vir and Hajdučka Vodenica, still exhibit the highest δ^{13}C and δ^{15}N ratios while some females - locals and non-locals, buried at Lepenski Vir - exhibit the lowest δ^{13}C ratios. Therefore, amongst local individuals, although both males and females likely had access to high protein resources and aquatic food, it is possible that some males somewhat consumed more marine-influenced proteins, perhaps an effect of the social organization of labor.

Neolithic males and females' stable isotopes differences

Concerning the Neolithic period, females encompass a broad range of δ^{13}Cand δ^{15}N values but exhibit lower δ^{34}S than the two males buried at Lepenski Vir and Hajdučka Vodenica (females δ^{34}S <8,5‰; males δ^{34}S values=10,6‰ and 14,2‰; Appendix A.II.27). These females thus rather favored the consumption of terrestrial resources (C_3 plants and the meat of terrestrial herbivores) and of freshwater fish, while the two males whether had a mixed terrestrial and marine-influenced diet or substantially consumed anadromous fish and the meat of dogs. This difference is reflected by their individual scores in the PCA, most Neolithic females falling in the left quadrants together with the Early Neolithic females from Ajmana, while most females dated to the period of Transformations, as well as Early Neolithic and Neolithic males, rather fall in the right quadrants (Appendix A.IV.7). All Neolithic females with a lower δ^{34}S signal who have been analyzed for strontium radiogenic isotopes were identified as non-locals while the two Neolithic males with a higher δ^{34}S signal were identified as locals (Appendix A.II.28).

$\delta^{34}S$ results indicate a difference between the non-local Neolithic females discovered at Lepenski Vir, who favored the consumption of terrestrial resources and/or freshwater fish and two local males - from Lepenski Vir and Hajdučka Vodenica, who likely included more marine-influenced resources in their diet. Although these different stable isotope values could be due to an effect to the small sample size (n males=2), or to the differential origins of males and females (non-local females and local males), it may also be related to a Neolithic social system where the members of one sex had a preferential access to certain food resources or to the existence of some food taboos, as suggested for the previous period of occupation. It could also be related to the Neolithic organization of labor, with males practicing fishing and females being more dedicated to some farming activities or to wild plant gathering. Eventually, considering the possibility of a local Neolithic exogamic system where several generations of females from neighboring farming communities may have migrated in the Gorges after 6 ky BC, it can be hypothesized that descendants from local foragers may have perpetuated the fishing traditions while the non-local females perhaps reproduced the subsistence traditions of their communities of origins and/or of their maternal lineages or simply died before that their collagen may be influenced by the signal of their new diet.

Age-related dietary differences

Finally, when the isotopic ratios of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ are cross-compared with the age categories, no significant differences can be observed in the diet between young, middle-aged and older neither for the period of Transformation, nor for the Neolithic period (Appendix A.II.29; A.IV.13), just as for the whole previous Mesolithic period.

4.3.6. General summary and discussion: neolithized foragers and mezolithized farmers?

Different subsistence patterns at the Earliest Neolithic

Stable isotope data concerning the period of Transformation and the Neolithic period reflects a broadening of the dietary spectrum on a population level with a stronger emphasis, for some individuals, toward the consumption of proteins derived from terrestrial resources and for others toward the consumption of freshwater fish. Rather than a sudden dietary shift, stable isotope results provide the picture of gradual changes within a global pattern of continuity in the local environment of the Gorges. While humans buried at some localities in the Inner Gorges, such as Padina or Hajdučka Vodenica, substantially consumed aquatic resources (particularly anadromous fish) and/or dogs' meat, some individuals buried in the Downstream Area, at sites – Ajmana, Velesnica – which feature various cultural elements pointing to the Starčevo (Early Neolithic) cultural sphere, rather favoured terrestrial resources (*e.g.* terrestrial herbivores and carnivore's meat, plants) or consumed fewer aquatic resources on a daily basis. The situation is mixed concerning the individual buried at Lepenski Vir in the Upper Gorges, some displaying high stable isotope values indicative of a continuity with former local dietary traditions, and other a more terrestrial dietary pattern.

Evidence for behavioral adaptations upon generations

The investigation of the diet of locals (those who grew up in the Gorges) and non-locals (the first generation migrants), through the comparison of stable and radiogenic isotope values (C, N, S and Sr), indicates that, in the inner part of the Danube Gorges, locals substantially consumed aquatic resources and/or dogs' meat, while some of the non-locals, discovered at the site of Lepenski Vir, mostly relied on the consumption of terrestrial resources. The stable isotope values of these non-locals suggest that they whether died within the years following their arrival on these sites or kept their former dietary habits after migrating in the Gorges. Downstream, at the site of Ajmana, both locals and non-locals had a more terrestrial diet. Some non-locals, from the assemblage of Lepenski Vir had a similar diet as locals, suggesting that they may originate from communities with similar subsistence strategies or that they may have adapted to the local practices after their migration in the Gorges. The presence of locals and of non-locals with different dietary behaviors makes difficult the observation of sex-oriented patterns in subsistence; and yet, it can be noticed that local males had the highest stable isotope values and that non-local males and females display the lowest stable isotope values. It is hence possible that the arrival of non-locals may have affected some aspects of the local social organization; increasing the sample of stable isotope values for accurately sex-determined individuals will represent an important perspective to explore this issue.

The comparison of stable and radiogenic isotopes with the aDNA indicates that most of the non-locals (the first generation migrants) discovered at Lepenski Vir were related to “Near Eastern Neolithic lineages” and that locals were whether assigned to typical "European Mesolithic-like lineages" (the putative descendants of local foragers) or to "Near Eastern Neolithic lineages" (the putative descendants of migrants). While those who grew up in the Gorges and who belong to "European Mesolithic-like lineages" were substantially consuming aquatic resources, in contrast some non-locals from "Near Eastern Neolithic-like lineages" favored the consumption of terrestrial proteins. Interestingly, all of their putative descendants (locals with “Near Eastern Neolithic lineages”) exhibit stable isotopes values similar as the local descendants of European Mesolithic foragers (locals with “European Mesolithic lineages”). These results provide hence a direct evidence for the adaptations of the descendants of Early Neolithic farmers to the local subsistence strategies and environmental conditions.

The Neolithization of the Gorges step by step

***At the end of the seventh millennium BC* (circa 6200-5900 cal BC),** when some aspects of the Neolithic package appear in the Gorges (e.g. ceramics, typically Neolithic polished axes-adzes, and beads), a few non-local individuals related to "Near Eastern Neolithic-like" lineages were buried into the Gorges at Lepenski Vir. The interactions of the descendants of local Mesolithic foragers with these migrants suggest the adoption of a part of the "Neolithic package" in the Gorges during this period. Some people had a diet oriented toward the consumption of terrestrial resources and their skeletal remains may thus represent the earliest organic remains of Early Farmers in the region. In contrast, the descendants of local foragers (individuals born in the Gorges with a rather "European Mesolithic-like lineage") perpetuated a way of subsistence that substantially included the consumption of aquatic resources, and particularly anadromous fish species. Some other non-locals from "Near Eastern Neolithic lineages" were also consuming aquatic resources, which suggests that that they came from communities with a similar mean of subsistence as the foragers of the Gorges or that they adapted to the local practices. At that time, Lepenski Vir almost certainly was a central place of high ideological significance (boulder artworks, numerous burials) encouraging interactions between people originating from different horizons. Interpreted within the funerary context, these bioarchaeological markers indicate that some locals and some non-locals, assigned to "European Mesolithic-like" and to "Near Eastern Neolithic-like" lineages, have been gathered in a multiple grave (*e.g.* burial LV 27), rooting thereby after death the relationships that they may have maintained during their lives. Some of the migrants, and some of their putative descendants (born in the Gorges with "Near Eastern Neolithic-like" lineages), who display similar paleo-dietary signatures, have been found buried together (*e.g.* burials LV 54D-E). In some cases (*e.g.* burials LV 7 and 54D-E; Figure 47; Figure 49), some artifacts can be related to the local traditions (e.g. red deer antlers), while others rather point to the Anatolian and Southern Balkans Neolithic sphere (*e.g.* Neolithic-like beads, auroch skull), symbolizing simultaneously their integration in the local community and their will to keep aspects of their original culture.

Around 6000 BC some individuals, both local and non-local, were buried in the downstream area at the sites of Ajmana and Velesnica in the typical Neolithic crouched position, not documented in the inner part of the Gorges before the sixth millennium BC (Figure 45). They favored the consumption of terrestrial resources. Considering that numerous cultural features at these sites points to the Balkans' early Neolithic sphere and given the stable isotope similarity between some people buried at Ajmana and at Lepenski Vir, it can be assumed that the communities who buried their dead downstream at that time should have played a significant role in the Neolithization of the Gorges. They may represent some of the earliest groups of Neolithic farmers which were certainly in contacts with the autochthonous foraging population living upstream in the Gorges (Figure 55).

During the first half of the sixth millennium BC (circa 5900-5500 cal BC), the Neolithic domestic animals appeared in the Danube Gorges, and some aspects of the Neolithic package became more intensively used (e.g. ceramics, Neolithic-like osseous tools) which might indicate some adaptations in culinary practices. Most descendants of the local foragers (the locals from rather "European Mesolithic-like lineages") were still including aquatic protein in their diet, perpetuating the local traditions, although a few of them may have opted for a mixed terrestrial and aquatic diet or favored the consumption of different fish species. At that time, further generations of migrants from "Near-Eastern Neolithic-like lineages", more numerous, arrived in the Gorges. As documented in the preceding period, some of these non-locals had a terrestrial diet while others were consuming aquatic resources. They were mostly buried in the typical Neolithic crouched position and could be responsible for the intensified presence of various aspects of the Neolithic cultural repertoire in the Gorges, both in terms of technology and of symbolism (Figure 48). As suggested by their high δ^{13}C and δ^{15}N values, the descendants of migrants - the locals (born in the Gorges) from "Near Eastern Neolithic-like" lineages - were substantially consuming aquatic resources. Although the influence of local traditions cannot be disregarded - some sort of local process of Mesolithisation - these dietary adaptations could be mostly related to the environmental conditions, the Gorges providing excellent fishing spots. However, most non-locals and their descendants display lower δ^{34}S values, unlikely related to some environmental fluctuations in anadromous fish δ^{34}S values since a few contemporaneous individuals with a local strontium radiogenic signal exhibit rather elevated δ^{34}S values. This difference could be due to their lesser consumption of anadromous fish – perhaps associated with a change in the population of these migratory species and/or with the practice of different fishing strategies (appearance of new type of bone hook) – or may eventually be related to a change in dogs' breeding practices, perhaps to different social values assigned to the dogs. Hence, from a bioarchaeological perspective, the Neolithization of the Danube Gorges should not be understood as a straightforward process of acculturation or a sudden behavioral shift. On the contrary, results reflect the mosaic picture of complex behavioral interactions and gradual socio-cultural changes within the framework of local economic continuity. The sixth millennium in the Gorges thus features the arrival of a number of migrants with different dietary habits who have probably been responsible for important socio-cultural changes and who also adapted, over successive generations, to the local way of subsistence.

The Danube Gorges in the broader context of European Neolithization

Concerning various regions of Europe, scholars have suggested a sudden shift from the consumption of marine and riverine proteins during the Mesolithic towards the consumption of terrestrial and carbohydrates during the Neolithic (e.g. Tauber 1981; Richards et al. 2003a; Shulting 2011). It includes mostly the coastal regions of Denmark, Britain and Ireland, Brittany, northern Spain, Central Portugal and the Mediterranean, with some individual exceptions though (Shulting 2011). It has been suggested that this pattern may be related to different symbolic and social values between European Mesolithic foragers and the early Neolithic farming communities, with a possible taboo toward the consumption of fish, perhaps considered as the wild resources favored by the "undomesticated" hunters, amongst early agro-pastoralists ("touch not the fish"; Thomas 2003); however, this idea has been further discussed on the light of the remains of aquatic species (such as shells) in quantities on certain Neolithic sites from some of these regions (Milner et al. 2004 versus

Richards and Shulting 2006). Other studies rather document the presence of highly terrestrial Mesolithic diets in the Meuse basin and Aquitania (Bocherens et al. 2007; Schulting et al. 2008) or more gradual changes and/or continuity in fishing traditions during the Neolithic, for instance in some regions of Central-Northern Germany, Netherlands, Scandinavia, Dniepr and the Baltic (Lidén et al. 2004; Lubke et al. 2007; Smits and Van der Plitch 2009; Lillie and Budd 2011). It should be emphasized that the shift towards terrestrial stable isotope values at the onset of the Neolithic does not necessarily mean a shift towards the consumption of farming resources but can also be related to various hunting and gathering strategies. The differences in which communities relied on the farming productive economy during the Early Neolithic may relate to the ecological circumstances, including the environmental landscape and the importance of Mesolithic foraging populations and their cultural traditions, the extent of interactions between groups of farmers and of foragers, and considerations related to the relative potential for productive mixed farming system, versus the productivity of wild resources.

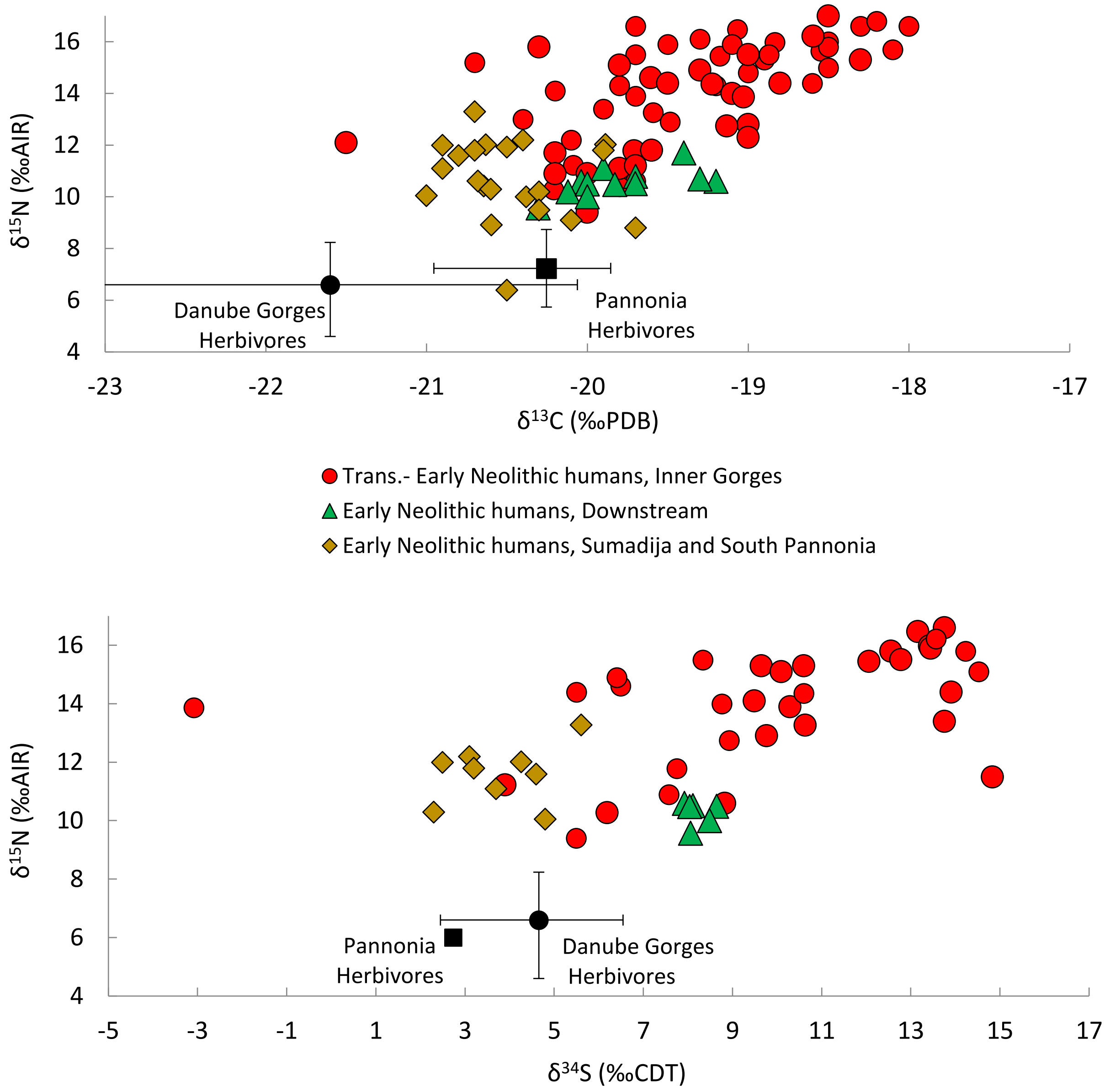

Figure 55: Bivariate plots of δ13C - δ15N and δ34S - δ15N for Early Neolithic individuals from the Central Balkans

Stable isotope studies dedicated to sites located between Central Anatolia and South-Eastern Europe rather indicated that Neolithic communities were consuming proteins derived from terrestrial resources, mainly from domesticated species – cereal, pulses, sheep and goats – according to the zooarchaeological and archaeobotanical documentation (Richards et al. 2003b; Lösch et al. 2006; Papathanasiou 2003). A similar situation is observed for other Mediterranean communities which were colonized by Neolithic farmers (ca. 5500–3400 BC) from the Aegean (e.g. Lightfoot et al. 2011; Le Bras-Goude et al. 2006; Goude 2007), although new data suggest that marine protein could have contributed, in a smaller degree than protein, to the diet of some Neolithic individuals in Southern France (Naito et al. 2013; Goude et al. 2017; Salazar-Garcia et al. 2018). Inland, the situation seems more variable. In the Central Balkans, the comparison of the diet of individuals buried in the Danube Gorges with individual buried in the neighboring regions of South Pannonia (Figure 55), indicates that at some sites, individuals consumed quite similar proportions of aquatic and terrestrial proteins as those buried at the site of Ajmana or of the individuals buried in the Inner Gorges with the lowest stable isotope values; at other sites they clearly favored the consumption of terrestrial resources, or on the contrary, consumed slightly higher proportions of aquatic resources than at Ajmana, but still in lower proportions than most Transformational-Neolithic individuals buried in the Inner Gorges (Jovanović, de Becdelièvre et al. 2018). Further North in the Pannonian Neolithic diet was mainly composed of terrestrial plants and animals (Whittle et al. 2002; Pearson and Hedges 2007; Giblin 2011), despite some exceptions (e.g. Gamarra et al. 2018). In central Europe, the subsistence of Early and Middle Neolithic communities is quite variable, from a small input of freshwater fish to a strong dependence on aquatic resources (e.g. Durrwachter et al. 2006; Smits et al. 2010).

Studies that allow for direct comparison between dietary strategies and ancestry at the Early Neolithic in Southeastern and Central Europe are very few. From the data of Mathieson *et al.* (2018; supp. mat.), it can be noticed that amongst nine Early Neolithic individuals with Near Eastern ancestry, radiocarbon dated to the end of the seventh or to sixth millennium BC and discovered at sites located downstream of the Gorges, between the Balkans and the Wallachian, and upstream in the south of Pannonian plain, only one individual displays high δ^{15}N values indicative of the substantial consumption of aquatic resources[222]. It would for instance now be important to collect paleodietary data on the Early Neolithic individuals buried at the site of Malak Preslavets, located further downstream closer to the Black Sea, who show significantly more hunter-gatherer ancestry than the other Early Neolithic individuals from this region (currently no available stable isotope values; see Mathieson *et al.* 2018, supp. mat.). Early Neolithic individuals discovered at the site of Vinča in the southern part of the Pannonian Plain, display slightly higher δ^{15}N values than the individuals buried at Ajmana, but lower than most Transformational-Early Neolithic individuals buried in the Danube Gorges and have Near-Eastern Neolithic-like maternal lineages (Hofmanová 2016; Jovanović, de Becdelièvre et al. 2018). Two Early Neolithic individuals discovered at the site of Tiszaszlos (Körös context) in the Northern part of the Pannonian Plain, display significantly lower δ^{13}Cand higher δ^{15}N values (important consumption of freshwater fish) than the other Early Neolithic individuals discovered at neighboring sites, and interestingly the genomic analyses performed for one of them indicate an ancestry entirely consistent with European Hunter-Gatherers (Gamba *et al.* 2014; Gamarra *et al.* 2018).

In the light of these scarce data, it seems that in the Balkans (apart from the region of the Danube Gorges), Wallachia and Pannonia, the descendants of Mesolithic hunter-gatherers were mostly perpetuating their foraging way of subsistence, despite the presence of farmers-herders descended from Near Eastern Neolithic communities who mostly had a terrestrially-oriented diet, although sometimes including the consumption of aquatic resources. Concerning some parts of

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[222] This individual, discovered in a Starčevo-Criş context at the site of Măgura Buduiasca (circa 250 km downstream of the Gorges), has been radiocarbon dated to 6061-5985 cal. BC. He displays δ^{15}N values of 13.27‰ and δ^{13}C values of -18.88‰ and has been assigned to the K1 lineage (documented amongst Mesolithic foragers in the Gorges and amongst Near east European Early Neolithic communities).

Central Europe, it has been suggested that the coexistence of such parallel societies may have lasted for a long time (see Bollongino *et al.* 2013). In other regions, for instance along the Baltic Sea or in the Dniepr Rapids region, technological aspects of the Neolithic package have been adopted as early as the sixth millennium BC by populations who had an entire European hunter-gatherers-like ancestry (no evidence of admixture with descendants from Near Eastern Neolithic communities; Jones *et al.* 2017; Mathieson *et al.* 2018) and who kept relying on hunting and fishing until at least the mid fifth millennium BC (Lillie and Budd 2011; Mathieson *et al.* 2018, stable isotopes values in Supp. Mat.). Between Northern Central Europe and Scandinavia, populations of fisher-hunter-gatherers of the fourth and third millennium BC (pottery users; Pitted Ware Culture) have co-existed for a long period with the first farmers (TRB culture) of the region (*e.g.* Liden *et al.* 2004; Terberger *et al.* 2018); while the genomic data of these fisher-hunter-gatherers display no evidence for genetic introgression from farmers, in contrast, farmers' DNA suggest that they should have been partially incorporated into expanding farming groups (Skoglund *et al.* 2014).

When crossing bioarchaeological line of evidence, it appears that a single model of Neolithization cannot explain the diverse dynamics of foragers and farmers interactions in Europe. The original connections between populations relying on these two different means of subsistence should have involved various vertical and horizontal patterns of cultural transmission. In Southeast, Central and Western Europe, the farming way of subsistence brought by the descendants of Near Eastern Neolithic communities ultimately prevailed after a variable period of co-existence with foragers, but it only involved a small degree of admixture. In Northern Europe, the incorporation of foragers into early farming groups may have been greater. In contrast, in some regions of Eastern Europe most aspects of the Neolithic package were gradually adopted by the local descendants of Mesolithic foragers without significant admixture with the descendants of Near Eastern Neolithic communities. In the Danube Gorges, the adaptation of the descendants of the first farmers to the local fishing traditions, as well as the degree of admixture in this micro-region, seems to have been quite unique for Southeast and Central Europe. Performing high resolution biogeochemical analyses is required to provide further insights into mobility patterns and dietary adaptations of the first farmers and the last hunters of the Balkans. This chapter therefore demonstrates the perspectives that are made available by the direct comparison of data about diet, migration and ancestry to our understanding of Neolithization and, beyond, of the dynamics of subsistence transitions.

5. Maternal nutritional choices from pregnancy to the post-weaning period.

- Immature bone and dentine stable isotope signatures, protein routing –

An adequate nutritional intake during the early stages of life, from pregnancy to infancy and childhood, is of primary importance for the future growth, the long-term health and the survival of a child. Parents' dietary strategies thereby have a direct influence on children mortality and in turn on the overall health of a population. Maternal nutritional health during pregnancy can influence the body proportions of a neonate and his future susceptibility to diseases; during lactation, the quality and quantity of breast-milk is also of paramount importance to protect the infant from growth delays, growth stunting, anemia and general health (Kennaugh and Hay 1987; Spielmann 1989; WHO and UNICEF 2003, Black et al. 2008). Then, the transition from the breast milk to solid food is a critical passage during early childhood when the toddler is increasingly exposed to new environmental pathogens and to nutritional stress (Knodel and Kinter 1977; Katzenberg et al. 1996; WHO and UNICEF 2003, Black et al. 2008; Quilan 2007). Mother dietary choices from pregnancy to the completion of children weaning not only define the future health and survival of the offspring, but also impact the maternal metabolism. Indeed, breastfeeding is known to disturb mothers' ability to breed during a period of time[223], the lactational amenorrhea, hence affecting the fertility rates of a population (Bongaarts 1978, 1982; Vitzhum 1994; Wood 1994; Ellison 1995; Stuart-Macadam and Dettwyler 1995, Valeggia and Ellison 2009). **By impacting both females' fertility and children health, parents' dietary strategies significantly contribute to define the fitness of past populations; one historic event when it is assumed that changes in terms of parenting behaviors should have particularly affected human demography is the Neolithic Transition (Bocquet-Appel 2008).**

On archaeo-anthropological assemblages, recent methodological improvements in the resolution of the stable isotope signals and in the choice of the analyzed tissues now enable not only thorough reconstructions of weaning patterns but also the joint exploration of issues related to children nutritional health and to the diet and the physiology of expectant and lactating mothers (e.g. Herscherr 2003; Fuller et al. 2006; Eerkens et al. 2011; Eerkens and Bartelink 2013; Kinaston et al. 2009; Nitsch et al. 2010, 2011; Howcroft et al. 2012, 2013, 2014; Beaumont, 2013; Beaumont et al. 2015; Burt and Garvie-Lok 2013; Burt 2015; Hendersen et al. 2014; Sandberg et al. 2014; Reynard and Tuross 2015; Tsutaya et al. 2015a and b, 2017; Beaumont et al. 2018). Amongst the Danube Gorges archaeoanthropological sample, the remains of numerous foetus, perinates, and infants provide direct organic evidence related to the conditions of pregnancy, birth and early childhood during the Mesolithic and the Neolithic (Borić and Stefanović 2004; Stefanović 2006; Stefanović and Borić 2008). **By comparing perinates' stable isotope values with signals gathered on bone and teeth tissues of older children this study reconstructs the dietary strategies of Mesolithic and Neolithic parents and examine changes in several biodemographic variables: (I) the nutrition of expectant mothers; (II) infant, toddlers and young children breastfeeding and weaning strategies; (III) childhood diet.**

5.1. Perinatal bone collagen stable isotope signature: maternal and foetal nutritional health

The foetus, "feeding on the mother", is dependent on maternal nutrient supply; via the placenta, the fetal metabolism proceeds with some nutritive regulations to sustain its own requirement of rapid intra-uterine growth and development (Munro et al. 1983; Kennaugh and Hay 1987). Newborn and infant protein turnover are known to exceed by 15 folds the protein intake (Reynard and Tuross 2015) and the rate of neonatal bone renewing has been estimated to average

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[223] The contraceptive effect of post-partum or lactational amenorrhea is particularly significant during the first 6 months, for children exclusively breastfed and when children are fed "around the clock" (Wood 1994; WHO 1999, Valeggia and Ellison 2009).

300% per years (Valentin 2003). Pregnancy is also a state of faster protein turnover and bone remodelling for the mother (Thompson 1992; Hellmeyer et al. 2006). Therefore, perinatal bone stable isotope signal should be primarily influenced by the maternal pregnancy diet, a variable which cannot usually be inferred in archaeological contexts given the slow rate of adult bone remodeling under usual metabolic situation (10-15 for an entire renewal; Valentin 2003). Maternal nutritional health plays a role on the mortality and fertility of a population by exposing the offspring to some toxins which may be detrimental for his health, by influencing neonatal weigh and fat reserves and the future growth trajectories of the offspring, and by affecting the quality and quantity of breast-milk (Kennaugh and Hay 1987; Spielmann 1989; Barker 1998; Roseboom et al. 2012). In some ethnographically documented population of hunter-gatherers, the diet of expectant and lactating females differs from the diet of the group, for health and/or symbolic reasons (Kennaugh and Hay 1987; Speth 1991; eHRAF 2010; Meyer-Rochow 2009). Although it is assumed that changes in females' diet may have affected human demography at the transition to agriculture (Bocquet-Appel 2008), the particular issue of Mesolithic-Neolithic pregnancy-specific diets has not been explored yet on osteoarchaeological samples.

If children fast rates of bone renewal, as well as expectant mother faster protein turnover, suggest that foetus and perinates should be primarily influenced by the maternal diet in the course of pregnancy, it is yet unknown to which extent the maternal stable isotope signature before pregnancy may affect the biochemical values of an offspring tissues. Besides, in the weeks - first month following a childbirth, the stable isotope values of the newborn baby should shift with the consumption of breastmilk (Fogel 1989; Miller 2000; Fuller et al. 2006), of different nutritive composition than the placental intake (Kennaugh and Hay 1987). Since the average age at death of perinates included in this study has been estimated to 35-41 gestational weeks[224] (Figure 56), it can yet be assumed that most of them were stillborn or died within the first weeks following the birth and hence that their stable isotope values should not be influenced by breast-milk.

Perinates from the site of Lepenski Vir dated to the period of Transformation/Early Neolithic are in average higher for the isotopes of the three elements ($\delta^{13}C$=-19,1‰, n=21; $\delta^{15}N$=16,8‰, n=22; $\delta^{34}S$=13‰, n=11) than the Late Mesolithic foetus/perinates from Vlasac ($\delta^{13}C$=-20‰, n=16; $\delta^{15}N$=15,5‰, n=16; $\delta^{34}S$=10,4‰, n=9; Figure 56; Figure 57). This difference is also reflected by the common variance of the three elements by the PCA (Appendix A.IV.16) and is significant for all isotope ratios (Mann Whitney for $p<0.05$). In contrast, when we only compare adult females, there are no statistical differences between both sites for any of these elements (Mann Whitney, $p<0.05$). Nonetheless, one should here emphasize that only a small number of adult individuals with associated stable isotope values within the acceptable range of collagen preservation[225] were accurately diagnosed as females: for the Late Mesolithic site of Vlasac - 8 females for $\delta^{13}C$ and $\delta^{15}N$ and 4 for $\delta^{34}S$ - and for the Transformation/Early Neolithic phase of the site of Lepenski Vir - 6 females for $\delta^{13}C$ and $\delta^{15}N$ and 4 for $\delta^{34}S$. The difference is not significant neither when Neolithic females buried at Lepenski Vir are added to the sample neither when Early-Neolithic and Neolithic individuals without available information for collagen preservation were added to the sample[226].

Statistical comparisons between perinates and females for each site also indicate significant differences (Mann Whitney, $p<0.05$). Concerning the Late Mesolithic site of Vlasac, significant differences between the perinates and the females can be noticed for the isotopes of the nitrogen element (perinates being higher than females) and for the isotopes of the carbon element (perinates being lower than females). The stable isotope signatures of perinates-females pairs discovered

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[224] birth time estimated circa 37-41 gestational weeks, based on modern standards; only one perinate - LV 83b, the only one related to the Neolithic period, has an estimated age at death circa 44,5-47,5 gestational weeks, falling thus between the perinatal period (one month after birth) and the beginning of infancy.

[225] Only adults with criteria for collagen preservation and within the acceptable range were including as purposes of comparison with the children.

[226] for the Late Mesolithic site of Vlasac, the individuals without available criteria for collagen preservation were never included in the analyses since we find a statistically significant difference between the individuals within respecting the standards for collagen preservation and the individuals for whom the information was not published in previous paleodietary studies (cf part 3.3.2).

buried together on the Late Mesolithic site of Vlasac (putative mothers and perinates; Borić and Stefanović 2004), reflect these $\delta^{15}N$ and $\delta^{13}C$ offsets (Appendix A.III.4). For the Transformation/Early Neolithic phase site of Lepenski Vir (Transformation/Early Neolithic) only the difference in the isotopes of the nitrogen element between perinates and females is significant (perinates being higher than females; Mann-Whitney, $p>0,05$). When adding Neolithic females, the difference become also significant the sulfur element (perinates being higher than females); yet, this is likely due to the presence in the sample of Neolithic non-local females with lower $\delta^{34}S$ values, probably not representative of the stable isotope values of Early Neolithic females. The results of Mann-Whitney exact tests carried out on the pooled sample - all perinates compared to all females - indicate a significant difference between all perinates and all females only for the $\delta^{15}N$ ratios (for $p <0,05$).

Finally, one can notice the lower $\delta^{15}N$ signal of the only perinate dated to the Neolithic phase of Lepenski Vir in comparison with the other perinates (LV 83b: $\delta^{13}C=-19,2$; $\delta^{15}N=14,6‰$; Figure 56; Figure 57). His $\delta^{15}N$ and $\delta^{13}C$ values yet fall in the variability of Neolithic females from this site (Neolithic females, n=6: average $\delta^{15}N=12,9 \pm 2,5‰$; average $\delta^{13}C=-19,5 \pm 0,7‰$). He is also the oldest perinate of the sample, aged at death 46,25±2,5 gestational week (first weeks of "infancy").

5.1.1. Perinates' $\delta^{15}N$ values (1): the biological stress hypothesis

At both sites, perinates $\delta^{15}N$ values appear significantly elevated in comparison with the cohort of females (Figure 56). Longitudinal stable isotope analyses carried out on modern mothers and breastfed infant pairs indicate that a diet-to-consumer trophic effect is associated with breastfeeding, resulting in elevated $\delta^{15}N$ values for the suckling infant (Fogel 1989; Fuller 2006). Yet, it is unlikely that all perinates $\delta^{15}N$ elevation could be related to maternal milk consumption, since two foetus from Vlasac also range in the high part of female $\delta^{15}N$ variability[227] and given that all perinates from Lepenski Vir aged at death between 36 and 39 gestational weeks also exhibit elevated $\delta^{15}N$ values. This females-to-perinates offset could thus be explained by an important consumption of protein-rich resources, and particularly aquatic food, by mothers at both sites. Since perinates from Vlasac are also associated with lower $\delta^{13}C$ values than the females buried at this site, these elevated $\delta^{15}N$ ratios could be related to a higher consumption of freshwater fish and maybe jointly of herbivores meat by expectant females in comparison with their usual diet (provided that the analyzed females are representative of the sample of Late Mesolithic females who lived in the region). In contrast, at Lepenski Vir, perinates elevated $\delta^{15}N$ values are not associated with a significant elevation in $\delta^{13}C$ and/or $\delta^{34}S$ which could point to the consumption of specific aquatic resources (marine-influenced and/or freshwater); it may thus suggest a particular consumption of meat from omnivorous or carnivorous animal by expectant females in comparison with their usual diet (but not the meat of dogs which should result in elevated $\delta^{34}S$ values, Appendix A.1.2).

Alternately, these elevated $\delta^{15}N$ values could also be related to maternal and/or neonatal metabolic adaptations. Indeed, stable isotope studies carried out on a variety of animal species indicate that situations of biological stress - fasting, starving, illness - result in elevated $\delta^{15}N$ values (e.g. Hobson and Clark 1992; Hobson et al. 1993; White and Armelagos, 1997;Doucett et al. 1999; Katzenberg and Lovell 1999;Polischuk et al. 2001; Fuller et al. 2005; Kempster 2007; Mekota et al. 2006; Williams 2007; Deschner et al. 2012; Olsen et al. 2014; D'ortenzio et al. 2015; Hertz et al 2015; Doi et al. 2017). In normal conditions, when proteins are utilized for tissue building, isotope fractionation occurs during transamination (synthesizing non-essential amino acids) and deamination (breaking down the excess proteins not used for tissue building) . Following this fractionation, the body tissues are enriched in $\delta^{15}N$ while body wastes (urea) are enriched in ^{14}N re-

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[227] (VL 84(1) aged at death 30-35 gestational weeks; $\delta^{15}N$ = 15,5‰; VL 66b, aged at death 31-35 gestational weeks; $\delta^{15}N$ = 15,5‰)

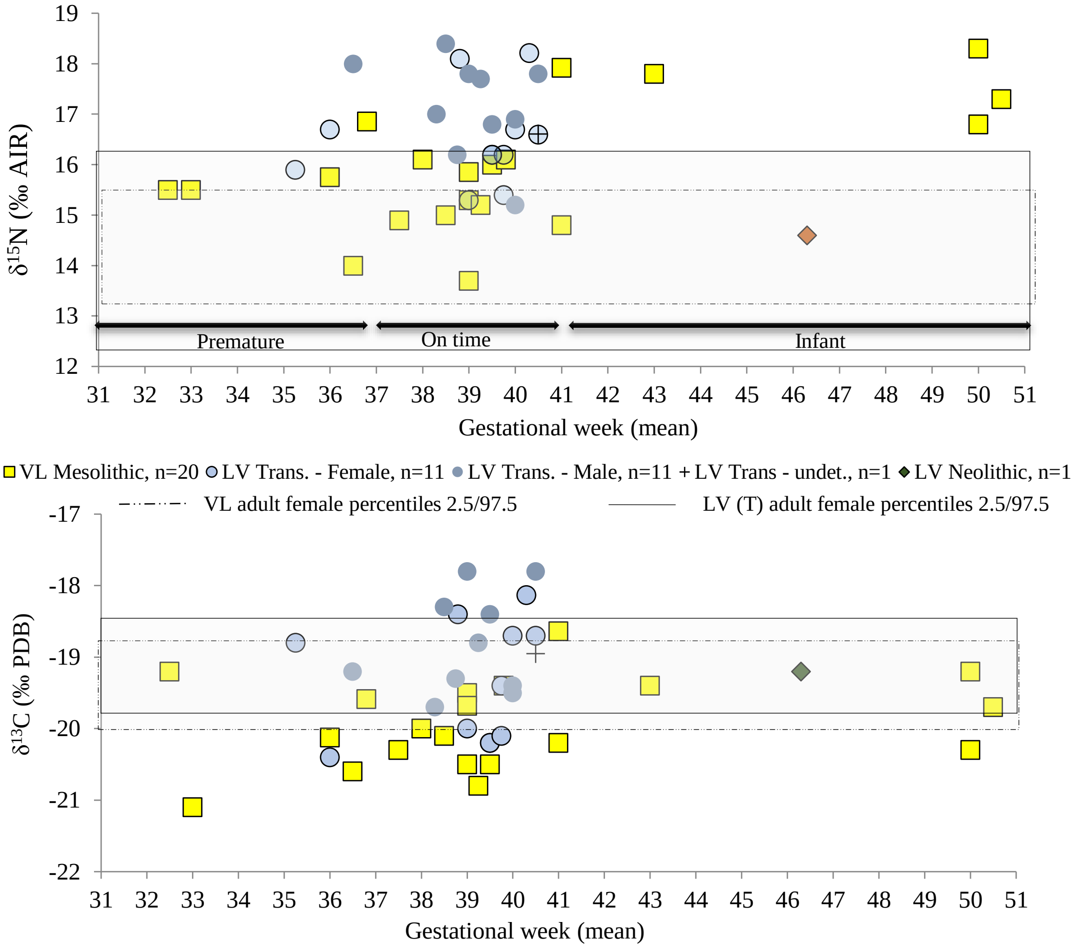

Figure 56: Bivariate plots of δ15N (top) and δ13C (bottom) and the age at death of perinatal individuals (gestational weeks) from the site of Vlasac (Late Mesolithic) and the site of Lepenski Vir (Trans.-Neolithic).

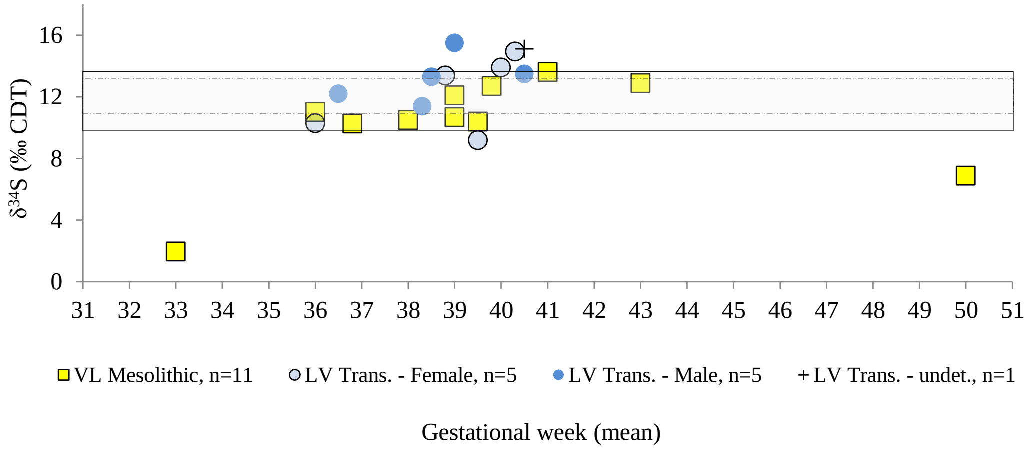

Figure 57: Bivariate plot of δ34S and the age at death of perinatal individuals (gest. weeks) from the site of Vlasac (Late Mesolithic) and the site of Lepenski Vir (Trans.-Neolithic) (cf caption symbols in Fig. 56)

lative to the ^{15}N values of the diet (Schoeninger and DeNiro 1984; Schoeninger 1985). When an individual does not ingest enough proteins - and therefore ingest less nitrogen than it requires for basic physiological processes and tissue maintenance - its body enters catabolism and negative nitrogen balance, metabolizing then its own resources. Repeating the process of transamination and deamination hence enrich the tissues in ^{15}N. Joint modification of δ^{13}C values in situation of biological stress has not been systematically observed and may depend of the tissues analyzed and/or of the nature of the experienced biological stress (Hertz et al. 2015; Doi et al. 2017). The response of $\delta^{34}S$ under specific metabolic adaptations has not been documented yet; although the fractionation mechanisms associated with the isotopes of sulfur remain ill-understood, they remain of smaller magnitude than for the isotopes of nitrogen (Nehlich 2015; Webb et al 2017).

In the light of these studies, elevated $\delta^{15}N$ values observed on perinatal formed tissues from archaeological samples have been interpreted as a response of the body to starvation, infectious or metabolic diseases which could have led to the early termination of pregnancies and to premature births (Kinaston et al. 2009; Pearson et al. 2010; Beaumont et al. 2015; Beaumont et al. 2018). The hypothesis that specific biological stress may have been responsible for the elevated $\delta^{15}N$ values noticed for the perinates from the Danube Gorges assemblage should thus be taken into consideration, especially since these data are directly derived from the tissues of individuals who died during the perinatal period and not from targeted sampling performed on some perinatal-formed tissues of individuals who have survived older childhood or adulthood. One could thus consider that maternal metabolic stress, perhaps caused by starvation or pathological conditions, might be amongst the possible factors responsible for these elevated $\delta^{15}N$ ratios and hence for the early death of these Mesolithic and Neolithic babies. However, by comparing our data with published studies, especially with the analyses of perinatal formed tissues of some individuals who survived older childhood and adulthood, it seems that other physiological effects - specific of the state of pregnancy - should also be jointly considered to interpret these elevated $\delta^{15}N$ signatures.

5.1.2. Perinates' $\delta^{15}N$ values (2): the pregnancy effect

During the last 15 years of anthropological research dedicated to fetal, neonatal, infant and maternal stable isotope signatures, it has often been observed that perinates encompass a wider than expected range of $\delta^{15}N$ values. This pattern has been noticed, whether: **(1)** in the comparison of stable isotope ratios analyzed in the bone collagen of perinates and of adult individuals from osteo-archaeological assemblages (Katzeenberg et al. 1993; Jay et al. 2008; Kinaston et al. 2009; Pearson et al. 2010; Nitsch et al. 2011; Burt 2013; Tsutaya et al. 2013; Reynard and Tuross 2015); **(2)** in the comparison of stable isotope ratios analyzed in layers of dentine formed before or after the birth, on teeth of modern individuals (Burt and Garvie-Lok 2013) or from osteo-archaeological assemblages (Burt 2014; Beaumont et al. 2018); **(3)** in the comparison of stable isotope ratios analyzed in the hair keratin of modern mother and newborn pairs (De Luca et al. 2012). All these studies, performed on individuals who died at birth but also on individuals who survived older childhood or adulthood, are reporting a wider range of $\delta^{15}N$ values for the tissues formed during the perinatal period than for the tissues formed at an older age. Hence, it seems that the perinatal $\delta^{15}N$ signals are most probably altered by some alternate physiological processes which are not necessarily related to nutritional deficiencies, pathologies or complicated pregnancies. In a transverse stable isotope study of the hair keratin from a modern cohort of mothers and newborns, De Luca et al. (2012) observed that the stable isotope signals of the newborns were consistently higher than the signals of their mothers. By performing some longitudinal stable isotope monitoring of pregnant mothers' hair keratin, Fuller et al. (2004, 2005) and of D'ortenzio et al. (2015) have documented a gradual depletion in mothers' $\delta^{15}N$ values in the course of pregnancy. The authors of these reference studies all agree on the existence of a perinate-to-mother "offset", where perinates $\delta^{15}N$ values are elevated in comparison with the mothers' signals. They suggest that this offset could be simultaneously related: **(1.)** to the high rates of protein turnover of the growing foetus/neonates, and **(2.)** to the shift in the metabolic balance of expectant mothers.

We previously mentioned that events of starvation or of nutritional stress may cause a negative metabolic and nitrogen balances, which should result in elevated $\delta^{15}N$ values[228]. In contrast, during period of growth and pregnancy, it is assumed that the body enters positive metabolic and

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[228] catabolic state where the body catabolizes its own tissues to obtain the needed nitrogen not anymore provided by the dietary intake, thereby repeating transamination-deamination and elevating the $\delta^{15}N$ values.

nitrogen balances where more nitrogen is ingested for new tissue synthesis than expelled, which may result in lower δ^{15}N values (Katzenberg and Lovell, 1999; Fuller et al. 2004, 2005; Waters-Rist and Katzenberg, 2010; de Luca et al. 2012; D'ortenzio et al. 2015; Hertz et al. 2015; Doi et al. 2017). More specifically, the gradual depletion in the δ^{15}N signals of expectant females observed by Fuller (2004, 2005), de Luca et al. (2012) and D'ortenzio et al. (2015) has been explained by two different pathways: **firstly**, the maternal body preferentially route more dietary amino acids toward deposition and synthesis, without undergoing the processes of transamination and deamination and thus without undergoing the isotopic fractionation stage(s) that enrich the body in δ^{15}N; **secondly**, the maternal body decrease urea excretion -probably because of an increase urea salvage by the micro-flora of the colon- which could cause a return of isotopically light nitrogen from the urea to her metabolic pool, hence lowering her δ^{15}N values (Fuller et al. 2004, 2005; de Luca et al. 2012; D'ortenzio et al. 2015). Notably, it has been evidenced that early in gestation there is a significant decrease in urea synthesis in association with a decrease in the rate of transamination of leucine (nitrogen containing essential amino acid; Kalhan and Parimi 2006). It has also been evidenced that foetus and young infants are experiencing very high rates of protein turnover, exceeding protein intake by 10-15 folds (Jackson 1994), and it is assumed that increasing deamination and transamination rates probably result in elevating the offspring δ^{15}N values (de Luca et al. 2012; D'ortenzio et al. 2015). The combination of these mechanisms of amino-acids routing by the maternal metabolism, together with the high rate of fetal protein turnover, could therefore explain the δ^{15}N offset observed between perinates and females.

Because of this pregnancy characteristic δ^{15}N depletion, it has been suggested that observing particularly low δ^{15}N values in females' bone collagen from osteoarchaeological context might indicate their death during pregnancy or childbirth (Fuller et al. 2006). This hypothesis could be amongst the explanations for the lower δ^{15}N values observed for some of the Neolithic non-local females discovered at the site Lepenski Vir (cf part 4.3.4). Yet, this pregnancy-effect has been tested by Nitsch et al. (2010) in an osteoarchaeological assemblage with documented parity status and the results show that women who never gave birth had δ^{15}N and δ^{13}C values that were indistinguishable from women who had given birth to a large number of children. This is most probably because the rate of adult bone turnover is too slow for a stable isotope change occurring in such a small period of time as pregnancy to be recorded in the collagen protein. Besides, since lower values in δ^{13}C and δ^{34}S have also been observed for these Neolithic non-local females, we consider that their lower δ^{15}N values should rather be interpreted as an effect of behavior (dietary and/or mobility) than as a biological effect of pregnancy. Performing some longitudinal stable isotope micro-sampling in the dentine of the third molars[229] of some females could now represent an avenue to detect some potential events of pregnancies in archaeological context, especially by comparing the dentine δ^{15}N values with tooth cementum "crisis lines" which can also be related to events of pregnancy (Kagerer and Grupe 2001).

5.1.3. Perinates' δ^{13}C and δ^{34}S values: insights on the maternal diet

In the light of stable isotope studies conducted on modern mothers and newborn pairs and on archaeological foetus-perinates and adult females, the δ^{15}N difference noticed between the perinates and the females buried at both sites may be interpreted as a physiological effect of pregnancy. Yet, it can be noticed that the average δ^{15}N offset is greater between Early Neolithic females and perinates from Lepenski Vir than between Late Mesolithic females and perinates from Vlasac (+1,47‰ for perinates buried at Vlasac; +3,3‰ for perinates buried at Lepenski Vir; Figure 56). This greater offset could be related to an additional physiological response of expectant females buried at Lepenski Vir to some complications that could have occurred during their pregnancies. It

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[229] Since there is no renewing in layers of dentine formed during the growth of a tooth; and given that the 3rd model is usually erupting after around the menarche.

is also possible that the δ^{15}N ratios of some perinates from Lepenski Vir were already elevated by the consumption of breastmilk (the consumption of breastmilk being associated with an enrichment in ^{15}N; Fogel et al. 1989; Fuller et al. 2006). Finally, this higher δ^{15}N offset could also be due to the consumption of resources enriched in ^{15}N such as meat of omnivores and carnivores' animals or aquatic food.

Interestingly, the δ^{15}N, δ^{13}C and δ^{34}S values of the Early Neolithic perinates buried at Lepenski Vir are significantly higher than the values of the Late Mesolithic perinates buried at Vlasac, which is also reflected in the PCA (Appendix A.IV.16). These results support the hypothesis that expectant females from Lepenski Vir were probably consuming more marine-influenced protein (anadromous fish and/or dogs' meat) than the expectant females from Vlasac. Since this difference is not reflected by the adult females, it may point to particular pregnancy diet for Late Mesolithic females (favored terrestrial herbivores meat and/or C_3 plants?) or for Early Neolithic females from Lepenski Vir (more aquatic resources? marine-influenced proteins?). Apart from δ^{15}N, only the difference in δ^{13}C was statistically significant between the females and the perinates from Vlasac (lower values for perinates, despite some overlap; Figure 56; Figure 57). Yet, it has to borne in mind that only 4 females were analyzed for δ^{34}S (with available collagen preservation criteria) and that a group of 5 perinates exhibit lower δ^{34}S values than these adult females (<11‰; Figure 57). This suggests that the expectant mothers of some perinates buried at Vlasac may have favored the consumption of terrestrial and freshwater resources over marine-influenced proteins, usually included in the Late Mesolithic diet. No difference in terms of δ^{13}C and δ^{34}S distinguish the females and the perinates buried at Lepenski Vir; here again, only 4 Early Neolithic females were analyzed for δ^{34}S, and a group of 4 perinate display higher δ^{34}S values than the analyzed females (>13,7‰; Figure 57) important consumption of marine-influenced proteins for the expectant mothers of these children).

These results suggest that: **(1.)** the diet of analyzed females from Late Mesolithic and Early Neolithic females was not significantly different; **(2.)** some Late Mesolithic expectant females may have been consuming more resources depleted in ^{13}C - such as C_3 plants, herbivores meat or freshwater fish - than the other females; since we also previously noticed slightly lower δ^{15}N values for Mesolithic females in comparison with Late Mesolithic males (although not significant; Mann Whitney p=0,075), these lower perinatal δ^{13}C values could particularly indicate a higher consumption of C_3 plants by expectant females, but it can also simply points to an absence of consumption of marine-influenced proteins (anadromous fish and/or dogs meat); **(3.)** Early Neolithic expectant females were likely consuming more marine-influenced proteins than the Late Mesolithic expectant females but not than the Early Neolithic females buried at the site (no statistical differences between Early Neolithic females and perinates, although some perinates display higher δ^{34}S values than the females). Finally, the lower δ^{15}N value of the only Neolithic perinate from the sample indicate that his mother was likely consuming fewer aquatic resources than the Early Neolithic mothers. He falls in the high part of females δ^{15}N variability and within Neolithic females δ^{13}C variability, which suggest that the diet of his mother should not have differed from the diet of other Neolithic females buried at Lepenski Vir.

In an attempt to better disentangle the differential effects of diet, physiology and health on the stable isotope values of perinates from Vlasac and Lepenski Vir, the fluctuations in the values of each elements were compared from 36 gestational weeks to the beginning of infancy by the means of a data longitudinal smoothing procedure (Z-score standardization and Loess statistic smoothing; Figure 58 part A; Figure 59 part B).

5.1.4. Stable isotope fluctuations from fetal stage to lactation

A broader stable isotope variability at birth

To further explore the possible effect of maternal physiology and nutritional health on the stable isotope values of Mesolithic and Neolithic perinates and to clarify possible fluctuations of stable isotope values at birth, perinates stable isotope values between 36 and 41 gestational weeks were longitudinally smoothed (loess statistical procedure: Figure 58 part A; Figure 59 part B). The resulting curves indicate a dip in the stable isotope values of the three elements between 38 and 39,5 gestational weeks at both sites and suggest a greater magnitude of stable isotope variation between 38 and 39,5 gestational weeks at Lepenski Vir then at Vlasac. Between 39,5 and 41 gestational weeks, the stable isotope curves are increasing at both sites. (Figure 58 part A; Figure 59 part B)[230].

An important magnitude of variation in foetal and perinatal bone collagen stable isotope values has been noticed on several osteoarchaeological samples from various contexts, including elevated and/or depleted δ^{15}N and δ^{13}C values in comparison with adult females' values (Katzenberg et al. 1993; Fogel et al. 1997; Dupras et. al. 2001; Richards et al. 2002; Jay et al. 2008; Nitsch et al. 2011; Burt 2013; Haydock et al. 2013; Tsutaya et al. 2013; Reynard and Tuross 2015; Pearspn et al. 2015). Only a few osteoarchaeological studies provides an estimation of the age at-death of foetuses and perinates, enabling to examine the possible fluctuations in children bone collagen stable isotope values during the course of pregnancy, at delivery and during the first weeks post-partum (Richards et al. 2002; Jay et al. 2008; Pearson et al. 2010; Redfern et al. 2012; Burt 2013). Although foetuses and perinates from the medieval cemetery of Wharram Percy (n=10 aged 28-48 gestational weeks; Richards et al. 2002) fall within the adult female range, it can be observed that, amongst five perinates aged 33-42 gestational weeks, four display lower δ^{15}N and lower δ^{13}C values than the youngest foetuses and the older perinates; the only individual aged 39 gestational week - the excepted time for a "normal" delivery - exhibit the lowest δ^{15}N value. Most foetuses and perinates from the Iron Age site of Wetwang Slack (n=10 aged 18-45 gestational weeks; Jay et al. 2008) exhibit δ^{15}N and δ^{13}C values above the adult females' range; the highest δ^{15}N and δ^{13}C values are displayed by the perinates aged 37-41 gestational weeks. Concerning the site of Teouma (Lapita Culture), perinates (n=7, aged 20-40 gestational weeks; Kinaston et al. 2009) are higher in δ^{15}N and lower in δ^{13}C than the females of the group, which has been interpreted as the result of in-utero stress related to chronic maternal ill-health. Only six perinates from Toumea have been aged-at-death between 35,5 and 40 gestational weeks and only one after 38,2 gestational weeks, which also limits the comparison with our sample. Yet, it can be noticed that perinates are rather elevated in δ^{15}N and δ^{13}C around 38 gestational weeks and that the only individual aged at death 39 gestational weeks exhibit the lowest δ^{13}C values and also falls in the low part of the range of δ^{15}N values. Two "foetuses" from the Neolithic site of Aşikili Höyük exhibit higher δ^{15}N values than the "perinates" and the adult females (Pearson et al. 2010). Redfern et al. (2012) report the stable isotope values of four perinates from Late Iron Age burials from Dorset (aged 37-42 gestational weeks), who fall within the adult females δ^{13}C range, but above adult females δ^{15}N values; it can be noticed that one individual aged 40 gestational weeks display lower δ^{13}C values (-1‰) than one individual aged 38 gestational weeks (but similar δ^{15}N[231]). Finally, concerning the medieval site of Fishergate house, Burt (2013) reports the stable isotope values of four foetus (aged 2-3 months in utero) and one perinate (at birth) who also fall within the adult females δ^{13}C range, but above adult females δ^{15}N values; the perinate exhibit lower δ^{15}N and δ^{13}C than three of the foetuses (the foetuses and the perinate being above the adult female δ^{15}N standard deviation but ranging within the adult female δ^{13}C deviation). Most studies dedicated to intra-teeth stable isotope analyses does not allow for enough precision to provide a detailed picture of intra-individual stable isotope fluctuations in the weeks preceding and immediately following birth (Burt and Garvie Lok 2013; Burt 2014; Beaumont et al. 2015; King et al. 2018a and b); yet, some scholars noticed important δ^{15}N fluctuations around birth (Burt and Garvie Lok 2013; Burt 2014) as well as a broader-than-expected range of δ^{15}N and δ^{13}C values at birth (Beaumont et al. 2015). Recently, Beaumont et al. (2018) improved the resolution of the incremental dentine sampling, providing four δ^{13}C and δ^{15}N values for a perinate tooth from the Anglo-Saxon Raunds Furnells site, spanning thereby for this individual the last 3-4

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[230] Although the possibility of a sample-size effect cannot be excluded, weeks are represented by several perinates for each site; the loess procedure takes into account the values of each point to build a function that best fits segments of the data (Figure 58 part A).

[231] the two other perinates aged 37-42 and 38-40 gestational weeks can hardly be compared with the two perinates aged 38 and 40 gestational weeks given the overlap in their age estimation

months of pregnancy. Contrasting with the wide variability of perinatal bone collagen stable isotope values noticed at the population level, dentine stable isotope profile of this perinate appears quite stable, albeit slightly increasing during the last trimester of pregnancy ($\delta^{15}N$ =+0,3‰; $\delta^{13}C$=+0,5‰); more stable isotope data acquired with high resolution dentine micro-sampling on broader samples of perinates and infant teeth should in the future enable to clarify whether the pattern of variations noticed around birth at a population level is actually due to individual longitudinal fluctuations.

Possible hormonal explanations

Longitudinal and cross-sectional stable isotope studies conducted on the tissues of modern expectant females and newborn babies, interpreted in the light of physiological adaptations during pregnancy, might provide some clues to explain these $\delta^{15}N$ and $\delta^{13}C$ variations noticed around birth (Figure 58):

1. During the first part of the pregnancy, some women who are experiencing morning sickness caused by endocrine adaptations[232] are enriched in ^{15}N as an effect of Negative nitrogen balance (Fuller et al. 2004[233] and 2005[234]; Figure 58 part B and C).

2. During the second half of the pregnancy, most pregnant women are gradually depleted in $\delta^{15}N$ (Fuller et al. 2004, 2005; de Luca et al. 2012; D'ortenzio et al. 2015; Figure 58 part B). This maternal gradual $\delta^{15}N$ depletion may be related to a specific routing of amino acids toward deposition and synthesis but also to an increase retention and reuse of urea nitrogen, likely driven by important hormonal fluctuations[235] (Fuller et al 2004; Figure 58 part C). The foetus, feeding off the mother and experiencing fast rate of protein turnover, is inversely enriched in $\delta^{15}N$ (de Luca et al. 2012; D'ortenzio et al. 2015).

3. At the end of pregnancy, important hormonal fluctuations occur as an interaction between the placenta and the maternal endocrine system, particularly an increase in prolactin, oxytocin and glucocorticoids[236] (Austin and Short, 1984; Figure 58 part C). It has been shown that nutritional stress increase the levels of glucocorticoid and glucocorticoids have profound effects on metabolic processes including protein metabolism (Leakey et al. 1994; Tomiyama et al. 2010; Deschner et al. 2012; Robertson et al. 2014); glucocorticoids have also been found to be associated with enriched $\delta^{15}N$ (Deschner et al. 2012) and whether enriched (Deschner et al. 2012) or declining (Robertson et al. 2014) $\delta^{13}C$ values during period of nutritional stress. It is known that pre-term infants, subjected to important stress, may produce an even higher level of insulin-counter-regulatory hormones - cortisol, glucagon and adrenalin- which may interfere with glucose production and use (Kennaugh and hay 1987). It is thus possible that natural endocrine fluctuations and birth stress could affect the fetal-neonatal stable isotope signal at the end of pregnancy. On the stable isotope analysis of newborn and young infant fingernails, Fuller et al. (2006) noticed that, during the first 12-14 weeks, 7 of 8 infants from the analyzed sample have fetal $\delta^{13}C$ values that decrease toward the time of birth (fingernails formed in utero). The authors speculate that this pattern may be associated to "a small (≤ 0,5‰) change in carbon metabolism in either the mother or foetus, or a variation in the placental uptake and/or transport of carbon" (Fuller et al. 2006: 285). It is also possible that $\delta^{13}C$ values of the foetus (and maybe of the mother) decrease at the end of pregnancy as an effect of the increase

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[232] Increasing rates of Human Chorionic Gonadotropin can cause morning sickness (Hyperemesis Gravidarum) during the first trimester of pregnancy (Niebyl 2010; Figure 58 part B and C)

[233] Longitudinal stable isotope analyses of the hair of 10 expectant females. In Figure 58 (part B), loess curves (smoothing trend-lines) have been fitted on the $\delta^{15}N$ and $\delta^{13}C$ data provided by Fuller et al. for a sub-sample of 4 women (data available only for 4 women) after standardizing data into Z-scores.

[234] Longitudinal stable isotope analysis of the hair of 8 pregnant women who experienced morning sickness (Hyperemesis Gravidarum). In Figure 58 (part B) a loess curve (smoothing trend-line) has been fitted on the $\delta^{15}N$ data converted into z-scores ($\delta^{13}C$ values not provided by the authors). The authors found statistically significant differences between conception, the time when women experienced nutritional stress (morning sickness) and childbirth for $\delta^{15}N$ but not for $\delta^{13}C$.

[235] a rise in progesterone and estrogens and by the state of resistance to insulin (Roberge et al. 1967; Kahlan et al. 1998; Mojtahedi et al. 2002; Kalhan and Parimi 2006)

[236] a rapid decline in progesterone and estrogens is followed by a gradual increase in prolactin and by a sudden surge in oxytocin and glucocorticoids, triggering the maternal contractions and the future mechanisms of lactation (Austin and Short, 1984; Figure 58 part C).

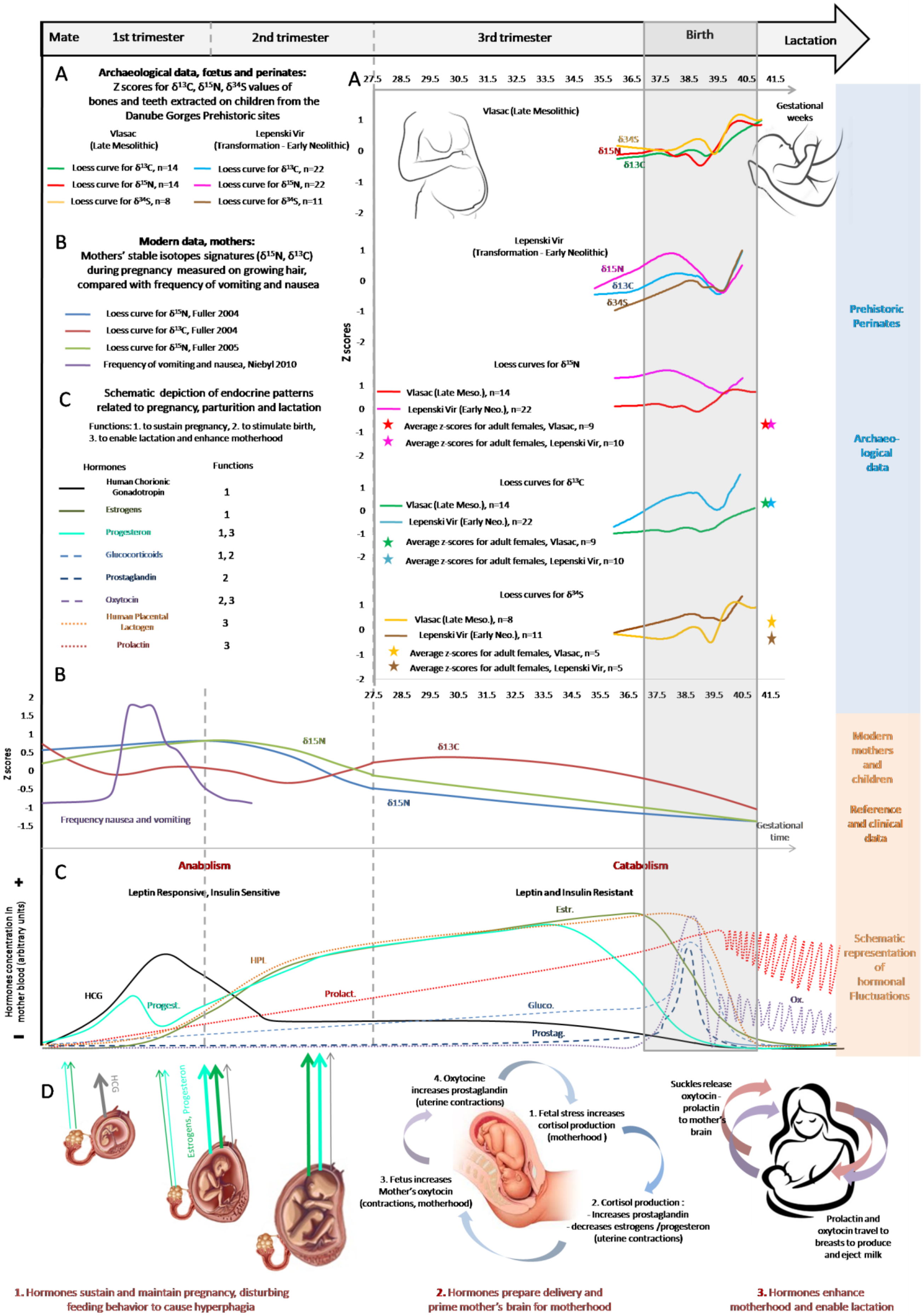

Figure 58: Comparison of perinates' stable isotopes loess curves with clinical data (caption details: Appendix A.III)

use of fat stores built up by the mother during the first semesters to be increasingly available for the foetus during the last trimester (Butte et al. 2000).

4. At birth a fall in neonatal respiratory quotient indicates a switch to fat metabolism, interpreted as a rapid post-natal adaptation to the new nutritive composition of breast milk (Kennaugh and Hay 1987). In the course of the first post-partum months the infant $\delta^{15}N$ and $\delta^{13}C$ values should be gradually and continuously enriched in the heavy isotopes as an effect of maternal milk consumption (Fogel et al. 1989; Millard 2000; Fuller et al. 2006; Figure 59).

Elevated maternal stress at the end of pregnancy?

The magnitude of stable isotope variations between 37 and 41 gestational weeks observed for perinates from Vlasac and Lepenski Vir may thus be related to an interaction between maternal nutritional health and pregnancy-induced physiological adaptations and/or to the effect of birth stress and/or to the nutritional transition between the placental nutrition and the introduction of breast-milk. The greater variability in the stable isotope values of the Early Neolithic perinates around 37 and 40 gestational weeks in comparison with the values of the Late Mesolithic perinates might hence indicate increased maternal stress at the advent of the Neolithic. If a surge in glucocorticoids is normal in late pregnancy, too elevated level in cortisol is dangerous for the outcome of the pregnancy, with a risk of miscarriage or premature birth (Whadwa et al. 2011). However, it should be here emphasized that we are interpreting the resulting picture from a statistical smoothing procedure applied on a small sample (Vlasac perinates, n= 21, for Lepenski Vir perinates, n= 19). As an alternate hypothesis, it is possible that the variations noticed in the stable isotope values of Early Neolithic perinates may simply reflect the adult variations observed at the site of Lepenski Vir, in a context where some migrants with lower stable isotope values have been identified amongst a population who favored the consumption of higher trophic level resources. It would thus be possible that the mothers of some perinates consumed more aquatic resources than the mothers of the perinates who died around 39-40 gestational weeks and who display lower $\delta^{13}C$ and $\delta^{15}N$ values (one perinate also exhibit lower $\delta^{34}S$ value at 39,5 gestational week). Yet, these perinates from Lepenski Vir exhibit higher $\delta^{15}N$ values than those from Vlasac, whereas the Early Neolithic adults with lower stable isotope values buried at Lepenski Vir exhibit significantly lower $\delta^{15}N$ values than the Late Mesolithic adults buried at Vlasac (Appendix A.II.3-4; 21).

The fact that the broad range of perinates $\delta^{15}N$ values observed at the end of pregnancy and at birth are also reflected by $\delta^{13}C$ could be an indication in favor of the dietary hypothesis (some Early Neolithic mothers from Lepenski Vir consuming higher trophic level resources than others), but could also be related to the complex mechanisms of carbon fractionation under certain metabolic states and associated with certain tissues (e.g. Hobson and Clark 1992; Doucett et al. 1999; Polischuk et al. 2000; Kempster et al. 2007; Williams et al. 2007; Deschner et al. 2012; Hertz et al. 2015; Herrscher et al. 2017). In contrast, the fact that these variations are also mirrored by the $\delta^{34}S$ isotope would rather support the dietary hypothesis, given that the stable isotope ratio of sulfur analyzed in human bone collagen is expected to reflect directly the values of the ingested food (Nehlich 2015[237]). Yet, it can be recalled that a small $\delta^{34}S$ fractionation between two trophic levels of the food web has been evidenced in several studies, although encompasses a large standard deviation (+0.5‰ ± 2.4‰ estimated by Nehlich et al. 2015[238]). In a recent study, Webb et al. found a systematic depletion between the $\delta^{34}S$ value of the food and the consumer bone collagen values (average -1,5±0,8‰, Webb et al. 2017b); this offset was of higher magnitude when the protein part

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[237] In bone collagen sulfur is actually found in methionine, an amino acid which is not biosynthesized by the body but directly routed from the ingested food. In contrast, cystein, the other sulfur-containing amino-acid present in human and animal tissues (e.g. muscles, hairs, horns) can be internally synthesized from methionine.

[238] data from Peterson et al. 1985, 1986; Gonzales-Martin et al. 2001; McCutchan et al. 2003; Richards et al. 2001; Barnes and Jennings 2007; Tanz and Schmidt 2010.
Offset calculated on both methionine- and cystein-containing tissues. On tissues containing cystein some variations in the $\delta^{34}S$ values have been interpreted as a possible consequence of internal metabolic process (McCutchan et al. 2003; Richards et al. 2001; Tanz and Schmidt 2010).

of the food was 100% marine-derived (circa -3‰). An offset of -0,5±0,4‰ has also been recorded between piglets collagen and saw milk (Webb et al. 2017b) and an offset varying between +0,7‰ and -1,7‰ between the collagen of a kid and maternal goat milk (Tanz and Schmidt 2010; for one couple goat and kid[239]). It remains thus possible that the internal cycle of methionine could result in small δ^{34}S fractionation, for instance via transsulfuration and methylation pathways (e.g. the conversion of homocystein back to methionine, Finkelstein et al. 1988), although there is no available isotopic information available concerning these metabolic pathways (Nehlich 2015). The δ^{34}S values of some of the oldest perinates from Lepenski Vir and from Vlasac (>39,5 gestational weeks, Lepenski Vir n= 4 and Vlasac n= 4; Figure 57), might thus be slightly elevated as an effect of breastfeeding (joint δ^{15}N and δ^{13}C elevation), although this could also be an effect to the small sample size. Interestingly, amongst the perinates from the Danube Gorges analyzed for δ^{34}S, the only foetus displays much lower values than older perinates (Figure 57: individual VL 66b, δ^{34}S=2‰; δ^{34}S median of perinates from Vlasac=10,7‰). While his δ^{15}N signal remains within the range of other perinates, his δ^{13}C signal also appears slightly lower than most of the babies (δ^{15}N=15,5‰; δ^{13}C=-21,1‰). This lower fetal δ^{34}S value could thus be whether interpreted as an effect of a change in the metabolism of methionine during the course of pregnancy or could be related to the behavior of his mother (lower δ^{34}S and δ^{13}C values: a particular diet? a non-local female?).

5.1.5. General summary and discussion: maternal diet, health and physiology during pregnancy

Evidence for a maternal pregnancy-specific diet during the Late Mesolithic

In theory, perinates tissues are formed from the nutrients ingested by the mother and their stable isotope values should therefore be primarily influenced by the maternal diet. **In the sample of the Danube Gorges, both Late Mesolithic perinates from Vlasac and Early Neolithic perinates from Lepenski Vir display significantly elevated δ^{15}N values in comparison with the females buried at these sites**. In the light of reference stable isotope studies conducted on mothers and newborn pairs as well as osteoarchaeological studies conducted on foetus-perinates and adult females tissues, **this δ^{15}N offset may be interpreted as a physiological effect of pregnancy due to the high rates of protein turnover of the growing foetus/neonates, and to the shift in the metabolic balance of expectant mothers. The δ^{15}N offset is on average greater between the Early Neolithic females and perinates from the assemblage of Lepenski Vir (+3,3‰) than between the Late Mesolithic females and perinates from the assemblage of Vlasac (+1,47‰); this difference could be interpreted as an additional physiological response of expectant females buried at Lepenski Vir to some pregnancy complications, and/or as the beginning of breast-milk consumption by some perinates from Lepenski Vir and/or as an effect of difference in maternal dietary practices between the Late Mesolithic and the Early Neolithic.** The diet of adult females remains equally based on the consumption of aquatic resources from the Late Mesolithic to the Early Neolithic, but Late Mesolithic and Early Neolithic perinates exhibit significant difference for the three isotopes, suggesting some differences in the diet of expectant females. **Concerning the assemblage of Vlasac, lower perinatal δ^{13}C ratios in comparison with the values of adult female tissues (and lower δ^{34}S values at least for some perinates) indicates that some Late Mesolithic expectant females may have been consuming more terrestrial proteins (C_3 plants - herbivores meat) and/or freshwater fish than the non-expectant females buried at this site.** Since we previously noticed a tendency for Late Mesolithic females to be associated with lower δ^{15}N values than males and given that the observed δ^{15}N offset is smaller for the assemblage of Vlasac than for the assemblage of Lepenski Vir, it is possible that some Late Mesolithic expectant females particularly consumed less animal

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[239] an offset of +0,7‰ has been recorded on bone collagen and an offset of -1,7‰ has been recorded on cartilage collagen; sulfur from both bone and cartilage only derived from methionine amino acid.

resources (aquatic resources and meat) and more plant food during pregnancy. **In contrast, it seems that the diet of expectant females from Lepenski Vir was similar as the local daily diet, substantially including aquatic food and particularly marine-influenced resources, as well as the meat of terrestrial omnivores and carnivores** (higher δ^{34}S values even noticed for some perinates, although not significant at the population level). However, interpretations are here limited by the small size of analyzed females for δ^{34}S for whom the standard criteria for collagen preservation were available (Late Mesolithic females from Vlasac analyzed for δ^{34}S n=4; Early Neolithic females analyzed for δ^{34}S n=4). **The only baby analyzed for the Neolithic phase of the site of Lepenski Vir displays lower δ^{15}N values than the other perinates dated to the period of Transformation/Early Neolithic, but he falls in the δ^{13}C variability of perinates dated to the period of Transformation/Early Neolithic. It is possible that his Neolithic mother included fewer aquatic resources than the Early Neolithic mothers.** Since he falls within the stable isotope variability of local Neolithic females, his lower δ^{15}N resource may rather reflect the Neolithic shift toward the consumption of more terrestrial resources than a Neolithic pregnancy-specific diet. Yet, this child is also older than the other perinates (aged at death 46,25±2,5 gestational week) and his particular stable isotope values may reflect some further nutritional and/or physiological event.

This Late Mesolithic pregnancy-specific diet might be related to a local system of social or sexual division of labor where expectant females may not have taken a daily part to the tasks which were usually assigned to the females. It is also possible that the symbolic values that were probably attributed to certain species by the foragers of the Gorges induced some particular food restrictions or ascriptions when comes to expectant females. For instance, some taboos perhaps forbad the consumption of some species during the time of the pregnancy such as anadromous fish or the meat of dogs. On the contrary, some particular food may have been favored and cooked in order to relieve some of the discomforts of pregnancy. It is also possible that the foetus themselves bear some particular social or symbolic status, constraining in turn the maternal diet. A widespread taboo toward the consumption of meat - and particularly fresh meat - by pregnant females has been documented amongst many traditional societies, especially foraging communities (Spielmann 1989, Meyer-Rochow 2009, eHRAF 2018). Some groups whose subsistence highly relied on fishing, such as the Nunaviak or the Nuutka, forbid the consumption of fish or marine mammals during the time of pregnancy and lactation (Spielmann 1989). **Such taboos can magnify the effects of nutritional deficiencies already experienced by some females hunter-gatherers, with a possible negative impact on the health of the offspring (e.g. Akerman 1975; Ugwa 2016); in contrast, these norms are sometimes based on the specific nutritional requirements of expectant females and may, for instance, limit the negative consequences of some food toxins on the development of the foetus (Spielmann 1989, Meyer-Rochow 2009).** In any cases, although the females-perinates difference in δ^{13}C ratios appears statistically significant, yet an important overlap appears between the two groups and only some of the expectant females likely had a different diet, which questions the taboo-hypothesis (rather an individual choice of some mothers, in relation with what was perceived as healthy to eat during pregnancy?). Finally, it has also been hypothesized on a prehistoric archaeoanthropological assemblage **that noticed different in perinates' stable isotope values could be related to the seasonality of birth and to available resources during periods of pregnancies** (Pearson et al. 2015). This possibility may open important prospects of research in reproductive ecology and socio-biology on mating strategies or the conception time amongst prehistoric societies.

An aquatic-oriented pregnancy diet during the period of Transformation

Concerning the period of Transformation/Early Neolithic, the diet of the mothers of the perinates buried at Lepenski Vir did not significantly differ from the diet of other females and males buried at this site, including substantial proportion of anadromous fish and/or dogs' meat. It is possible that some norms and customs – such as the symbolic value assigned to some animal species or periods considered as optimal for pregnancy and birth –changed at the end of the 7th millennium BC. It is also possible that the climate deterioration which occurred after 6.2 ky BC may have led to an increased reliance on dried food (meat and fish) and on dogs meat (available yearlong) for the whole population, and particularly for pregnant females who were probably the most "nutritionally vulnerable" members of the group (Speth 1990). A female requirement in protein increases during pregnancy (Kennaugh and Hay 1987), but an excess of protein in comparison with energy (fats and carbohydrates) can be detrimental to the health of the offspring, resulting in low birth weight (Matsueda and Niiyama 1982; Spielmann 1987). De Luca et al. (2012) found that mothers who had the highest δ^{15}N values (associated with a high protein diet) gave birth to babies with smaller head circumferences. Yet, some of the fish consumed in the Gorges are particularly rich in fatty acids (e.g. sturgeons, salmons, catfish), and fat is the body's most concentrated source of energy. Besides, the elevated δ^{15}N, δ^{13}C and δ^{34}S values of the perinates buried at Lepenski Vir suggest that their mothers were likely consuming marine-influenced proteins, but it does not mean that carbohydrates-rich foods were neglected by these Early Neolithic mothers. The comparison of long bone measurements for Late Mesolithic and Early Neolithic perinates from Vlasac and Lepenski Vir did not indicate significant differences (Pinhasi et al. 2011). The authors just stress the fact that the Danube Gorges prehistoric perinates display more variability – particularly for femoral/humeral proportions – than the other archaeological and modern sample analyzed, which they rather interpreted as an intra-population variation in heritability of genotypic traits that control limb growth than as an effect of environment and behavior (Pinhasi et al. 2011). Although fish food is enhanced in some micro-nutrients which are essential for the proper course of pregnancy – such as A and B vitamins, iodin, Zinc, or n-3 fatty acids (Black et al. 2008) – it also includes important amount of the sulfur-containing amino-acid Methionine (particularly marine fish) whose excess may adversely affect maternal short-term reproductive function and the long-term physiology of the offspring (Matsueda and Niiyama 1982; Rees et al. 2006). Particularly, it has been suggested that high level of methionine may cause a deficiency in glycine amino-acid, in DNA and protein methylation, affect the birth weight and the growth trajectory of the offspring, or disturb maternal endocrine parameters during pregnancy, especially the level of glucocorticoid and progesterone (ibidem).

We perceived some differences in stable isotope values around birth which may, hypothetically, be related to maternal and fetal endocrine fluctuations and to the metabolic adaptations that follow the end of placental nutrition. Just as we observed a greater females-to-perinates δ^{15}N offset for the Early Neolithic assemblage of Lepenski Vir, we also noticed that the perinates buried at this site exhibit more variable stable isotope values at birth. Since all these Mesolithic and Neolithic babies died at the end of pregnancy or shortly after birth, it is likely that the level of maternal and perinatal stress was particularly elevated; yet, the important variability of stable isotope values at birth noticed for the Early Neolithic perinates buried at Lepenski Vir suggests that some Early Neolithic mothers may have experienced particular birth-stress and hormonal disturbances. Causes for such biological stress could be multiple, ranging from infectious contaminations to food-borne pathogens. The new interactions with external Neolithic communities, involving possible expositions to new pathogens, could be amongst the explanations; the effect of a diet enriched in aquatic proteins and fatty acids on the maternal physiology should also be taken into consideration, particularly since excess methionine during pregnancy may affect the endocrine parameters (Reese et al. 2006). **It should nonetheless be emphasized that these interpretations are not based on data gathered at an intra-individual level; therefore, the variations observed in stable isotope values at birth could also be due to some differences in the diet of the Early Neolithic mothers. For instance, the Early Neolithic mothers of some children who died at birth may have been consuming more terrestrial proteins than the Early Neolithic mothers of those who died before, resulting in the lower stable isotope values observed for some perinates at birth. It is thus alternately possible that some of the non-local adults discovered at Lepenski Vir, who exhibit lower δ^{15}N, δ^{13}C and δ^{34}S values**

than the others, may be the mothers of the perinates who exhibit the lowest stable isotope values. **Differences in birth seasonality may also account for this stable isotope variability.** Yet, these perinates still display higher values than several Late Mesolithic perinates buried at Vlasac.

Interestingly, the funerary practices related to perinates changed between the Late Mesolithic and the Early Neolithic period: while Late Mesolithic perinates were found associated with adults in burials at Vlasac, the Early Neolithic perinates were buried under the plastered floors of the dwellings on the site of Lepenski Vir (Borić and Stefanović 2004; Stefanović 2006; Stefanović and Borić 2008). This practice of burying perinates separately underneath the floors of the buildings was common amongst many Neolithic communities across Anatolia and the South Balkans (Bachvarov 2008) and may further reflect the biological and cultural interactions of the local inhabitants of the Gorges with this Balkano-Anatolian Neolithic cultural sphere (Borić 2011). It is possible that the parents of some perinates come from an outer Neolithic community and that they have reproduced this practice in the Gorges after the death of their children. This practice may also reflect a deeper shift in the way this society was managing the emotional impact of newborn deaths, placing now the bodies of the babies in the center of the domestic sphere, which could perhaps be related to some changes in birth-condition and pregnancy-stress during the Early Neolithic period.

Maternal nutrition and children health

Since a foetus is capable to proceed with an autonomous nutrient regulation via placental mechanisms (Munro et al. 1983; Kennaugh and Hay 1987), the unbalanced diet of an expectant female should actually rather affect the long-term health of the child than the short-term survival of the perinate (Spielmann 1989; Black et al. 2008). Under- or mal-nutrition during pregnancy may indeed lead to thinner babies, with lower fat reserves, who may experience growth issues and be at higher risks of chronic diseases in relation with endocrine disturbances in utero and during childhood (Spielmann 1989; Barker 1998; Roseboom et al. 2001; Black et al. 2008). An unbalanced consumption of carbohydrates, fats or proteins may also adversely affect the immunological quality of colostrum and breast milk and increase the future child susceptibility to disease (Spielmann 1989; Black et al 2008). It is hence possible that the high incidences of childhood biological stress frequently recorded amongst Early farming communities (e.g. Goodman and Armelagos 1989) may be partially due to maternal nutritional deficiencies, particularly to a focus on the consumption of carbohydrates-rich food at the expense of protein- and fat-rich resources. However, in the Danube Gorges, the diet of the Early Neolithic mothers of those who died during the perinatal period was rich in marine-influenced proteins and in fats from aquatic resources, but not necessarily depleted in carbohydrates. The diet of the mother of the only Neolithic perinate analyzed here may have included less marine-influenced resources. Yet, this Neolithic perinate falls in the nitrogen variability of Mesolithic perinates and in the carbon variability of Transformational/Early Neolithic perinates, which suggests that his mother was likely consuming proteins from terrestrial and aquatic animals. The comparison of children long bone measurements from birth to 15 years old did not reveal significant differences in terms of growth patterns between the Late Mesolithic and the Early Neolithic and Neolithic periods, most children falling below the curve of a modern reference population until the age of 7-9 years old (Pinhasi et al. 2011). Recent reconstructions of body mass indicate that one Early Neolithic and one Neolithic children buried at Lepenski Vir as well as two Early Neolithic children buried at Ajmana aged at death between 5 and 12 years old fall below the modern standard curves for body mass, in contrast with two Late Mesolithic children aged-at-death 6-7 years old who fall within the modern curve (Jovanović et al. 2016, unpublished podium presentation[240]). Since the stable isotope results for the adults from Ajmana indicate a more terrestrial diet, like for the Neolithic period of Lepenski Vir, it is possible that an emphasis on carbohydrates (at the expense of other nutrients?) by the Neolithic mothers of some Neolithic children buried at Lepenski Vi rans at Ajmana during pregnancy and

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[240] Jovanović, J., de Becdelièvre, C., Goude, G., Herrscher E., Stefanović, S. 2016. Children feeding practices and growth patterns during Mesolithic-Neolithic transition in the Danube Gorges. (28.08.-02.09.2016. *8th World Archaeological congress,* Kyoto, Japan)

lactation may have affected the future growth of these children. For now, the results for the only Neolithic perinate from Lepenski Vir just indicates that his mother was consuming less marine-influenced proteins than the Early Neolithic mothers. **It should yet be kept in mind that perinate stable isotope values inform about the *diet of the mothers of children who died at birth* and thus may not be entirely representative of the diet of the mothers of children who survived older childhood. By analyzing stable isotopes at an intra-individual level on the tissues formed at different period of the life of older children, we gathered complementary information about the diet of the mothers of children who survived later childhood, on the influence that the maternal diet may have on lactation, and on breastfeeding and weaning practices.**

The stable isotope values obtain on perinates from archaeological contexts do not solely reflect what the mothers eat but also jointly inform on maternal nutritional and physiological health, of importance for the future growth and health of the offspring. Although more research is needed to unravel the intricacies of the metabolic processes behind perinates stable isotope signature - particularly $\delta^{13}C$ and $\delta^{34}S$ values, still ill-understood - the possibility to examine jointly maternal nutritional and physiological status during prehistory opens important prospects in the fields of paleo-neonatalogy, past patho-physiology and ontogenetic studies.

5.2. Children bone collagen and dentine stable isotope signatures: breastfeeding and weaning practices.

After birth, the important physiological adaptations initiated by the maternal metabolism in the course of pregnancy (Figure 58 part C) continue to play a major role in the survival of the offspring: they trigger and further maintain the process of lactation[241]. Perinatal nutrient delivery indeed changes from a placental continuous intravenous supply to intermittent intestinal feedings. Thenceforth, it is through the practice of breastfeeding that the maternal nutritional choices directly influence the future development and the health of the offspring. Breastfeeding should be understood as a whole dietary process (Dettwyler 1995) which includes several important transitions: (1) a stage of exclusive suckling; (2) a stage of declining milk consumption in conjunction with the introduction of supplementary food; (3) and the complete cessation of suckles - the "age at weaning"- actual beginning of the childhood diet[242]. The average age for the introduction of solid food amongst traditional and modern societies broadly falls around 0,5 - 1 year; for the end of weaning it falls around 2,5 years[243] (according to ethno-historical surveys, Dettwyler 1995; Sellen 2001; Sellen and Smays 2001). Nonetheless, these general tendencies also encompass a mosaic of different practices which rely on children developmental milestones (e.g. the eruption of the first deciduous teeth), on socio-cultural constructs (e.g. religious beliefs and discourses of hygienists, construction of identities), on environmental factors (e.g. local availability in appropriate weaning food, pathogen loads) and of course on the mothers individual choices. It is assumed that this variability in children feeding practices may significantly influence human demographic fluctuations.

In fact, it is considered that breastfeeding and weaning practices may influence females' fertility by reducing or by prolonging the period of postpartum or “lactational” amenorrhea[244] (Vitzhum 1994; Wood 1994; WHO 1998; Valeggia and Ellison 2009). It may also affect the children morbidity and mortality rates since inappropriate weaning preparations can cause dietary deficiencies or expose the infant to dangerous pathogens. Therefore, it has been suggested that major changes in terms of infant feeding practices may have played a role in the agricultural demographic shift (Binford 1968; Hassan 1981, Buikstra et al. 1986; Sellen and Smay 2001; Bocquet-

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[241] cycle of oxytocin and prolactin stimulations of lactogenesis

[242] "Weaning" should therefore be understood as a whole process and not as a single event (Dettwyller, 1995).

[243] all subsistence systems being considered together.

[244] the period of post-partum amenorrhea is indeed influenced by the energetic burden of lactogenesis - maintained by suckling frequencies through hormonal cycles - and by the burden of carrying and caring the infant (Vitzhum 1994; Wood 1994; WHO 1998; Valeggia and Ellison 2009)

Appel 2008). This relationship between weaning practices and demographic fluctuations has been explored through the stable isotope analyses of archaeological populations from different subsistence systems: by documenting children feeding practices amongst prehistoric foragers (e.g. Clayton et al. 2006; Waters-Rist et al. 2011; Howcroft 2013; Eerkens and Bartelink 2013; Howcroft et al. 2014; Tessone et al 2015; Tsutaya et al. 2013, 2015b, 2016), amongst early farmers (e.g. Pearson et al. 2010; Howcroft et al 2013), or amongst historical societies that span from the Neolithic to the industrial period (e.g. Mays et al. 2002; Richards et al. 2002; Fuller et al. 2003; Prowse et al. 2008; Haydock et al. 2013; Bourbou et al. 2013; Burt 2013; Tsutaya et al. 2013, 2014; Sandberg et al. 2014; Hendersen et al. 2014; Beaumont et al. 2015; Beaumont et al. 2018; King et al. 2018; Scharlotta et al. 2018a and b). Weaning behaviors amongst some pre-agricultural societies have also been directly compared with farmers practices (e.g. Fogel, 1989; Katzenberg 1993, 1996; Schurr 1998; Schurr and Powell 2005; Howcroft, 2013; King et al. 2018b); yet, most of these studies suffer from large temporal or geographical gaps between compared populations.

Therefore, stable isotope ratios have been here analyzed on teeth and bones of Mesolithic and Neolithic children from the Danube Gorges region in order to reconstruct children feeding practices within the local ecological and bio-cultural context and to examine the evolution of weaning behavior over the sedentary and farming transitions. Combining both life-history and population approaches, stable isotope data collected at an intra-individual level are compared with trend lines computed for the cohort of children. Thereby, changes in the prehistoric feeding behavior are here examined over several dietary transitions: (1.) from the placental nutrition to breastfeeding; (2.) during solid food supplementation; (3.) from the completion of weaning to the adoption of the childhood diet and/or of the adult subsistence.

5.2.1. How to interpret infant and young children longitudinal stable isotopes fluctuations

δ^{15}N fluctuations: the timing of food supplementation and the frequency of suckles

δ^{15}N has proved to be a relevant marker of the trophic level, with a prey-predator isotopic enrichment estimated to 3-6‰ (Bocherens et al. 2003; O'Connell et al. 2012). Therefore, given that a breastfed child is only fed on the maternal milk nutrients during the period of exclusive suckling, the tissues of the infant are expected to be elevated in ^{15}N in comparison with the signals of the maternal food, of the maternal milk and of the maternal tissues. Nutritional experiments on breastfed and non-breastfed mother-child pairs showed a gradual enrichment of -1.7 to -2.8‰ in the tissues (infant fingernail keratin and maternal hair keratin) of breastfed children in relation to their mothers (Fogel et al. 1989; Fuller et al. 2006). A fractionation has also between demonstrated between maternal tissues and the milk, showing that the trophic difference between the child and the milk values is of even greater magnitude than between the maternal and the offspring tissues (Reynard and Tuross 2015; Herrscher et al. 2017). The differences in ^{15}N between the maternal tissue value and the value of her milk has been estimated circa -0.5 to -2.5‰ based on available data from animal (circa -0.5 to -2.3‰: Jenkins et al. 2001; estimated milk to collagen offset by Reynard and Tuross 2015; Howland 2003), the comparison of means value of maternal hair and of milk on human cohort samples (circa -2.5‰; de Luca et al. 2012; Romek et al. 2013) and the longitudinal study of the δ^{15}N fluctuation in the milk and nail tissues of a women (Herrscher et al. 2017). On this longitudinal study, Herrscher et al. (2017) also estimated that the δ^{15}N difference between the milk values and the values of a breastfed child average +3.7‰ before food diversification and +4.5‰ at the onset of food diversification. Hence, after birth, the tissues of an infant are gradually enriched in ^{15}N with breastfeeding, following the rates of protein turnover and the replacement of the previous placental δ^{15}N signal; some time after the introduction of solid food and the diminution of suckles, the δ^{15}N signal of the child should decrease, describing a typical breastfeeding-weaning "bell curve" (Figure 59 part A). Therefore, the tissues of a breastfed child formed during the first post-partum month should, in theory, reflect the δ^{15}N values of the placental period, plus the beginning of the ^{15}N breastfeeding enrichment; further, a tissue formed when the child was exclusively or mostly relying on breastmilk should display higher ^{15}N values; eventually, a tissue formed when the child was increasingly relying on supplementary should display depleted δ^{15}N values in comparison with the exclusive breastfeeding period. **The pattern of δ^{15}N values can thus be used to examine the duration of the period of exclusive suckling and the reduction in the frequency/duration of suckles.** When applying this method, it should be kept in mind that the stable isotopes differences between analyzed tissues will depends on the timing and the rate of tissues' synthesis.

Beyond reflecting the timing of the weaning process, the δ^{15}N values of tissues formed during the exclusive suckling period should also - in theory - be influenced by the maternal diet. For instance, the tissues of a breastfed child whom mother had a diet rich in animal proteins should display higher δ^{15}N values than the tissues of a breastfed child whom mother eat at a lower trophic level (Herrscher et al. 2013; Reynard and Tuross 2015; Beaumont et al. 2015). It can also be hypothesized that the composition of the maternal diet might affect the magnitude of the breastfeeding trophic effect, although some control-feeding research should be conducted to explore this possibility[245]. Besides, the exact magnitude of the stable isotope offset between maternal diets and childhood stable isotope values have also not been documented yet on reference samples. Similarly, the magnitude of the δ^{15}N depletion in later-formed tissues should also be influenced by the nature of the weaning protein introduced to the child. For instance, the tissues formed during the exclusive breastfeeding period of a child whom mother consumed lower trophic level resources would be expected to exhibit lower δ^{15}N values than the similar tissues of a breastfed child whom mother rather favored the consumption of meat and/or aquatic resources. The introduction of C_3 plants in the weaning food should also cause greater δ^{15}N depletion than a supplementation with higher trophic level resources such as fish. Finally, it should be borne in mind that alternate physiological effects may also additionally influence the maternal and child δ^{15}N values, such as tissues' catabolism during periods of biological stress (Fuller et al. 2005; Beaumont et al. 2015).**Therefore, in addition to the timing of food supplementation, one may use δ^{15}N values to discuss the nature of the maternal diet and of the supplemented proteins, provided that care is taken to consider longitudinal δ^{15}N fluctuations and to examine jointly other proxies such as δ^{13}C and δ^{34}S.**

δ^{13}C fluctuations: the timing of food supplementation and the type of protein supplemented

A small δ^{13}C fractionation effect between two different levels of the food web has also been estimated to 0 to 1‰ (collagen to collagen prey-predator fractionation; DeNiro and Epstein 1981; Bocherens and Drucker 2003) and an offset averaging 5‰ has been calculated between the value of the whole diet and the collagen value of the consumer (Ambrose and Norr 1993). Based on the study of human and animals' mothers and offspring pairs, a δ^{13}C offset of 0-1‰ has been estimated between the tissues of a breastfed child and of the mother (Jenkins et al. 2001; Fuller et al. 2006; de Luca et al. 2011; Herrscher 2017[246]). The difference between maternal tissues and milk values has

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[245] In a controlled feeding experiment, Webb et al. (2016) analyzed the influence of varying proportions of terrestrial and marine proteins on the δ^{15}N values of pigs, sows and piglets grouped in 5 dietary groups, ranging from 0 to 100 % of marine-derived proteins. The information about sow - piglet pairs were not provided by the authors and the piglets were already fed with solid food when slaughtered; yet, the piglet fed each group also consumed sow milk of the same dietary groups. We computed the average sow to piglet femur collagen offsets for each dietary group. No trophic effect difference can be observed between the groups of saws and of piglets fed from 0 to 50% marine proteins (sow to piglet average difference ranging from -0.2 to 0.2‰ according to the dietary groups), which is likely due to the fact that piglet were already fed with solid food when slaughtered. However, it is interesting to notice that the difference between sows and piglets fed 100% marine is 0.7‰, even though piglets were already supplemented when slaughtered. While the authors evidence a linear relationship between the amount of marine protein consumed and theδ^{15}N diet to tissue offset for pigs and piglets, speculatively attributed to differential incorporation of amino-acids from terrestrial and marine dietary proteins, it also seems that the maternal-to-offspring offset increases in the case when lactating mothers and babies consumed more marine proteins. Since piglets were both breastfed and supplemented, this could also be due to a different utilization of the amino acids associated with their metabolic state of fast growth. The hypothesis that the composition of the maternal diet may influence the magnitude of the breastfeeding trophic effect should be further explored, particularly on human samples.

[246] The results of the experimental study of Webb et al (2017a) also reveal a difference of +3‰ between the δ^{13}C collagen values of a group of sows and of a group of piglets, but no information about maternal to offspring pair in this study and the piglets were already fed with solid food when

been estimated to circa +2.1±0.9‰ based on animal data (Jenkins et al. 2001; Webb et al. 2017a[247]) and up to 4.8 ‰ for humans (Herrscher et al. 2017; one human mother-infant pair), which for humans should coincide with the expected difference between the stable isotope value of the diet and of tissues. The stable isotopes difference between the offspring tissues and the milk has thus been documented to +1.9±0.8‰ based on animal data (Jenkins et al. 2001[248]) and circa +5‰ for human (Herrscher et al. 2017). Herrscher et al. (2017) have also detected changes in maternal milk $\delta^{13}C$ values, up to +2.5‰, in the course of breastfeeding and weaning - perhaps' related to physiological problem linked to lactation or maternal stress - and it is unknown to which extent these effect may influence the tissues of a child. Therefore after birth the tissues of an infant should be slightly enriched in ^{13}C with breastfeeding in comparison with the value of the maternal tissues (Figure 59 part A); further fluctuations in $\delta^{13}C$ values be related to changes in the carbon source of dietary protein consumed by the mother or supplemented to the child, or to particular physiological effect during lactation.

In the absence of C_4 plant consumption and in a homogeneous environmental context such as the Danube Gorges, human carbon isotope ratios should mostly differ in accordance with the proportion of terrestrial and freshwater resources versus marine resources in the diet (e.g. Dufour et al. 1999; Richards et al. 2003a; Richards and Schulting 2006; Fuller et al. 2012; Webb et al. 2017). While nitrogen is only found in protein, carbon is found in all dietary fractions (proteins, carbohydrates and fats); thus, although preferentially routed from protein (Ambrose and Norr 1993; Jim et al. 2006; Fernandes et al. 2014), the $\delta^{13}C$ signal from bone collagen may be somewhat sensitive to changes in carbohydrate and lipid intake. Thus, the $\delta^{13}C$ values of a child weaned with C_3 plants (rather enriched in carbohydrates in comparison with fats/proteins) would be expected to drop between the end of the exclusive breastfeeding period and the end of the weaning process (as evidenced by Fuller 2006[249]). In contrast, the $\delta^{13}C$ values of a child weaned with animal protein should be less depleted than in the case of a weaning with C_3 plants (e.g. Fuller 2006[250]). In the case when marine fish are substantially included in the weaning diet, one may expect the $\delta^{13}C$ weaning effect to be cancelled (no drop in $\delta^{13}C$) given that marine resources have higher $\delta^{13}C$ signatures than terrestrial resources and that a significant consumption of marine protein rather increases the diet-to-tissues carbon offset (Webb et al. 2017a). Since European freshwater fish broadly exhibit similar or lower $\delta^{13}C$ values than terrestrial herbivores (e.g. Dufour et al. 1999; Fuller et al. 2012), the introduction of freshwater fish to a breastfed child should rather result in the depletion of his carbon isotope ratios. Besides, differences between the maternal diet and the food supplemented to the child may also influence the $\delta^{13}C$ response of the child tissues. For instance, the results of the cohort study of Webb et al. (2017; pig cohort) suggest that the increasing proportions of marine-derived proteins in the maternal diet may result in greater diet-to-maternal tissues, diet-to maternal milk, maternal tissue-to-maternal milk and maternal milk-to-children tissues offsets[251]. If the maternal diet substantially includes marine resources, the $\delta^{13}C$ increase in the tissues of a child weaned with marine food might be slighter than if the maternal diet was solely terrestrially oriented. Theoretically, the greatest cases of $\delta^{13}C$ depletion should be noticed when a breastfeeding mother significantly consumed marine resources but that the offspring was only supplemented with plant foods. Differences between the maternal and the offspring diet as well as possible changes in the type of

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slaughtered (piglets consumed the milk of sows from the same dietary groups as them). We computed the average sow to piglet femur collagen offsets for each dietary group.

[247] The results of the experimental study of Webb et al (2017a) also reveal a difference of ca +2.1±0.5‰ between the means $\delta^{13}C$ value of sows and the means $\delta^{13}C$ of piglets.

[248] The results of the experimental study of Webb et al (2017a) also reveal a difference of ca +3±0.4‰ between the means $\delta^{13}C$ value of sows and the means $\delta^{13}C$ of piglets.

[249] In the reference study of Fuller et al. (2006), the pattern of children $\delta^{13}C$ curve drop when cereals, fruits and vegetables were introduced.

[250] This is also reflected by the study of Fuller et al. (2006): at the time when meat was introduced to most children, $\delta^{13}C$ values tend to increase

[251] Yet, no information about maternal to offspring pair in this study and the piglets were already fed with solid food when slaughtered (piglets consumed the milk of sows from the same dietary groups as them).

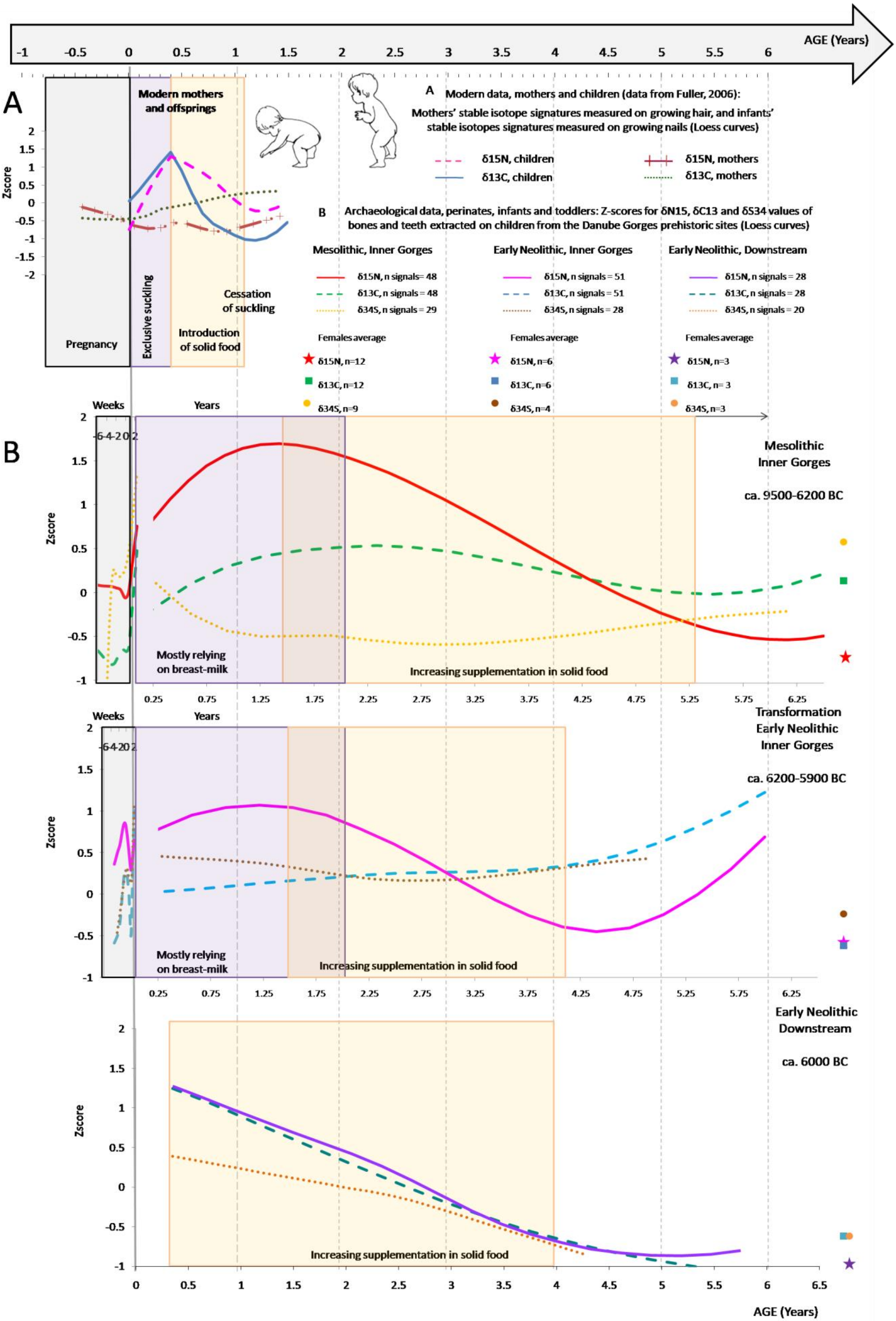

Figure 59: Comparison of prehistoric children stable isotope loess curves with reference data (caption details: Appendix A.III)

proteins consumed by the mother during lactation and/or supplemented to the toddler should thus be taken into consideration when interpreting the $\delta^{13}C$ fluctuations in the tissues of a child. **In intra-individual approaches, the pattern of $\delta^{13}C$ values can thus be used in addition to $\delta^{15}N$ to evaluate the timing of solid food introduction, and to examine the diet of breastfeeding mothers and of weaned children (marine versus terrestrial resources; protein-rich/energy depleted foodstuffs versus energy-rich/protein depleted foodstuffs) and to consider possible physiological disturbances linked to biological stress (Beaumont et al. 2015, 2018; Beaumont and Montgomery 2016).**

$\delta^{34}S$ fluctuations: differences between maternal diet and children weaning proteins

Since higher $\delta^{34}S$ ratios are associated with marine ecosystems in comparison with terrestrial/freshwater ecosystems, the isotopes of sulfur can be used, in combination with $\delta^{13}C$, to disentangle between terrestrial and marine resources contribution to the maternal diet and to the weaning preparations and/or to consider issues of mothers and children mobility (Nehlich and Richards 2009).In human bone collagen, $\delta^{34}S$ is found in Methionine, directly routed from the ingested food, and thus is not expected to fractionate between two trophic levels. However, a small fractionation effect has been evidenced in some studies, but has not been well-constrained yet (+0.5‰±2.4‰, Nehlich 2015[252]; -1.4±0.8, Webb et al. 2017b) and some researchers have suggested an association between the protein quantity in the diet and the diet-to-tissue offset (greater offsets in case of higher protein diet: McCutchan et al. 2003; Richards et al. 2001). In a controlled feeding study of pigs' tissues $\delta^{34}S$ values, Webb et al. (2017) observed greater offset when the protein part of the food was 100% marine derived. Concerning lactation, breastfeeding and weaning, their data also reveal that the maternal milk is rather depleted in comparison with the maternal diet (-0.8±1‰) particularly when marine resources are consumed (-1.45±0.3‰ in case of 100% marine food included in the diet)[253]. Besides, the average $\delta^{34}S$ values of piglets' femur collagen appears slightly depleted in comparison with the average values of sows' milk (on average -0.6‰, ranging from 0 to -1.1‰ according to the dietary group considered by the authors[254]). In contrast, Tanz and Schmidt report variable results for the $\delta^{34}S$ difference between the milk of a goat and the collagen of her kid, varying from +0.7‰ (for milk to bone collagen difference) to -1.7‰ (for milk to cartilage collagen difference).

In theory, a toddler supplementation with weaning preparations that include similar proportions of marine and terrestrial proteins as in the mother diet should not significantly affect the $\delta^{34}S$ ratios of the tissues formed during the breastfeeding and weaning period. Yet, given that negative offsets of greater magnitude have been documented between the $\delta^{34}S$ values of the maternal food and the values of her milk in case of greater consumption of marine proteins, it can be hypothesized that the $\delta^{34}S$ response of the tissues of a child formed during the period of breastfeeding might slightly differ according to the proportion of marine food consumed by her mother. Similarly, since greater diet-to-tissues $\delta^{34}S$ offsets have been documented in case of higher protein diet, it can be hypothesized the $\delta^{34}S$ response of a child tissues might vary according to the proportion of proteins included in his weaning diet. In any cases, when both mother and child consume marine resources, one would expect the $\delta^{34}S$ signals of a child tissue to be higher than when both mother and child favored the consumption of terrestrial resources. In contrast, if a child

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[252] Calculated using data from Peterson et al. 1985, 1986; Gonzales-Martin et al. 2001; Richards et al. 2001; McCutchan et al. 2003; Barnes and Jennings 2007; Tanz and Schmidt 2010; Human and non-human animal's samples.

[253] $\Delta^{34}S$ maternal diet to milk: +0.45±0.2‰ when no marine food has been included in the diet; of -1±0.9‰ in the case when 15-50% marine food has been included in the diet and of -1.45±0.3‰ in case of 100% marine food included in the diet (Webb et al. 2017b).

[254] No information about mother and offspring pairs was provided by the authors; therefore, we calculated the $\delta^{34}S$ difference between the average values of sows' milk and the average values of piglets' collagen per dietary groups (defined by the authors according to the proportion of marine resources consumed). The comparison between sows and piglets' femur collagen did not reveal systematic positive or negative differences depending on the type of diet (on average .02‰, ranging between -0.5‰ to +0.7‰ according to the dietary group considered). It should yet be mentioned that piglets were already fed with solid food when slaughtered. Finally, the maternal bone collagen to milk $\delta^{34}S$ offset (on average -0.6 ±0.9‰) does not appear stronger with the increasing proportion of marine food consumed by the saws.

is fed with more marine resources than included in the maternal diet, one should expect its $\delta^{34}S$ signals to rise; on the other hand, if a child is only fed less marine resources than included in the maternal diet, one would expect its $\delta^{34}S$ signals to drop. One would also expect changes in the maternal and the offspring diet to influence the $\delta^{34}S$ values of the tissues of the toddler. $\delta^{34}S$ fluctuations could be associated with maternal and child mobility, for instance a decline in $\delta^{34}S$ values in the tissues of a child could indicate a migration from seacoasts to an inland environment or to river systems with quite different $\delta^{34}S$ geological baseline. However, in the Danube Gorges, it has been demonstrated that the consumption anadromous fish and perhaps also of dog's meat (themselves fed with aquatic resources) should influence local human $\delta^{34}S$ value. Hence, only based upon fluctuations in $\delta^{34}S$ value, one cannot discriminate between possible maternal and child migrations and/or changes/differences in the consumption of aquatic resources locally available. Besides, the possibility of a diachronic fluctuation in $\delta^{34}S$ values between the Early and the Late Mesolithic, perhaps due to environmental changes in the Danube-Black Sea complex should be kept in mind (cf part 4.2.2.).

Summary: the expected breastfeeding and weaning curve

To summarize: (1.) the longitudinal fluctuations in the $\delta^{15}N$ and $\delta^{13}C$ values of tissues formed at the end of pregnancy, during infancy and early childhood should reflect **the shift from placental nutrition to breastfeeding** (increasing $\delta^{15}N$ and $\delta^{13}C$ values), **the decline in suckling frequency/duration related to the increasing reliance on solid food nutrient** (decline in $\delta^{15}N$) **and finally the cessation of suckles** (stabilization of $\delta^{15}N$ values to the later childhood); **(2.)** the magnitude of inter-individual differences in the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values of tissues formed during the first year of life can also be used to infer **broad differences in the diet of mothers**, provided that the tissues compared were formed at the same age and keeping in mind that $\delta^{15}N$ and $\delta^{13}C$ signals should be enriched by breastfeeding and/or may already be influenced by an early introduction of solid food; high/low $\delta^{15}N$ values should indicate the consumption of high versus low trophic level resources; high/low $\delta^{13}C$ may indicate the consumption of high versus low trophic level resources, of terrestrial-freshwater versus marine resources but may also be influenced by the proportion of lipids ($\delta^{13}C$ depleted); high/low $\delta^{34}S$ values should depend upon the consumption of marine versus terrestrial resources; **(3.)** the longitudinal fluctuations in $\delta^{13}C$ and $\delta^{34}S$ of tissues should jointly inform on **the type of food supplemented to the toddler, changes in maternal diet and possibly on the mobility of the mother and the child**; greater $\delta^{13}C$ depletion could be observed with the consumption of proteins from lower trophic level resources, from some stationary freshwater fish species or of resources enriched in fats; contrastingly slighter $\delta^{13}C$ depletion or increasing $\delta^{13}C$ values might be associated with the consumption of proteins from higher trophic level resources, particularly marine resources; decline/increase in $\delta^{34}S$ could be noticed in case in case of changes in the proportions of terrestrial-freshwater and of marine proteins consumed or if the weaning preparations included different proportions of these resources than the maternal diet. Finally it should be borne in mind that physiological effects such as nutritional stress experienced by the mother or the child during breastfeeding or during the weaning process might also influence the $\delta^{13}C$ and $\delta^{15}N$ values of the offspring tissues (e.g. Beaumont et al. 2015; Beaumont and Montgomery 2016; Beaumont et al. 2018).

On the Danube Gorges sample, the $\delta^{13}C$ and $\delta^{15}N$ trend-lines of children tissues reflect the expected pattern associated with breastfeeding and weaning (Figure 59; A.III.18.). We previously observed elevated $\delta^{15}N$ values of the bone collagen of most Mesolithic and Early Neolithic perinates analyzed in comparison with the bone collagen value of adult females, perhaps as a physiological effect of pregnancy (cf part 5.1.2*)* and noticed that he $\delta^{15}N$ and $\delta^{13}C$ values of the bone tissues of the oldest perinates were enriched in comparison with the values of perinates who died at a younger amenorrhea age (Figure 58; A.III.17). The comparison between perinates and older children smoothed stable isotope trend-lines reveal that the collagen of the children who died during the first month post-partum may have already been enriched in ^{15}N and ^{13}C as an effect of breastfeeding, the breastfeeding-induced trophic effect being of greater magnitude than the observed pregnancy effect (Figure 59 part B). The δ^{15}N and δ^{13}C bone collagen values of the three infants from Vlasac who died between 2 and 3 months post-partum range within the variability of the first deciduous molar crowns (Figure 56; Figure 60; Mesolithic Inner Gorges) which are indeed expected to average a dietary signal spanning between 6 months in utero and 1 year (AlQahtani et al. 2010). This rapid bone collagen postpartum enrichment has been noticed on the remains of children from other archaeological contexts (e.g. Richards et al. 2002; Reynard and Tuross 2015) and can be explained by the fast rates of protein turnover and of bone remodeling at that age (Jackson 1994; Valentin, 2003). As expected by the breastfeeding-weaning stable isotope model, the post-partum ^{15}N enrichment appears greater than the enrichment in ^{13}C (lower trophic effect for δ^{13}C; Figure 59; Appendix A.III.18).

Given that tissues analyzed are formed over quite long periods of time (e.g. crown of first permanent molars, formed between 3 months and 4 years, AlQahtani et al. 2010), and considering the overlap between the signals analyzed (e.g. the formation of the crowns of first permanent and deciduous molars overlap during the first year of life), in this study the observation of relative differences in terms of breastfeeding and weaning patterns takes precedence over the estimation of absolute age at weaning[255]. Fluctuations in stable isotope values are thus here firstly examined to infer broad changes in the proportion of solid food and of breast milk consumed ('predominantly breastfed' versus 'predominantly supplemented') rather than inferring a precise age for solid food introduction and for the cessation of suckles.

5.2.2. Weaning results (1) – the timing of solid food supplementation

5.2.2.1. 'Predominantly breastfed' versus 'predominantly supplemented': the Mesolithic toddlers

δ^{15}N and δ^{13}C fluctuations in the signals formed during the first years of life can be used complementarily to infer the reduction in suckling frequency/duration associated with the introduction of supplementary food. **Concerning the Mesolithic, the teeth δ^{15}N population trend line suggests that the frequency/duration of suckles was significantly reduced <u>after</u> most of the time of the formation of the crown of the first permanent molar** (i.e. 2 months-4 years; midpoint for the crown formation at 2,08 years; Figure 60; Figure 62). The bone δ^{15}N trend line also shifts during or at the end of the second year of life[256](Appendix A.III. 15; Figure 59[257]). δ^{13}C trend lines also display a shift after this age, but remain elevated for a slightly longer time, which can be explained by the possible use of high trophic level resources, and particularly marine-influenced proteins, to supplement children (Appendix A.III. 15; 17). It should be borne in mind that beyond the age of 6 months, breast-milk cannot fully meet the energetic and nutritional requirement of the infant (WHO 1998; Dewey 2013), thus these results indicate that "predominant suckling" was probably practiced during the first year and at least during a part of the second year of the life of most Mesolithic children analyzed. Although supplementary food may have been

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[255] The absolute ages for the crowns of the first permanent and deciduous molars (the mid points 0,35 and 2,08 years old used in the graphs in Figure 60, Figure 61, Figure 62, Figure 63, are only provided here as a matter of convenience to ease diachronic and spatial comparisons.

[256] On Figure 60, the Mesolithic δ^{15}N bone curve appears depleted from birth, which can be explained by the small number of bone signals available between birth and 4 years and a half (n=4). In contrast, in Figure 62 , the δ^{15}N curves were computed including the bone signals of the perinates.

[257] In Figure 60, Figure 61, Figure 62, Figure 63 (Appendix A.III 12-16), bone stable isotope loess curves were computed using the mid-point of the estimated range of the age at death for each child. In contrast, in Appendix A.III.17-18, stable isotope loess curves (including both bone and teeth signals) were computed using the mid-point of teeth tissues formation range and the mid-point of standardized bone values taking into account the rate of bone renewal. Indeed, given the rate of bone renewing, bone collagen should - in theory - record the dietary signal *for some time before* the death of a child. Hence, in order to better reflect the age of the dietary signal possibly reflected by stable isotopes values, the lower limit of the age at death estimation of each child was placed earlier by taking into account the rate of bone renewal estimated by Valentin, 2003. In Appendix 17-18, loess curves were calculated using the mid-point values of these "broader time span" which should be understood as the "broader period *possibly* reflected by the bone collagen of a child". This remains yet a rough approximate, considering the limits of age determination and given that the rates of bone renewal are not constant (growth being more saltatory, with periods of stasis and spurts, and also depending on the health of the child; Lampl 2012).

introduced much earlier, the shift toward a greater consumption of solid food and the reduction of suckling frequency/duration did not occur - on average - before the second year of life.

A closer look at intra-individual data (Figure 60; Figure 61; Appendix A.III.19-20) suggests that the weaning choices of Mesolithic mothers were quite variable. Indeed, the δ^{15}N signals of the crowns of the first permanent molars are either enriched in the heavy isotope in comparison with the stable isotope signal of the crowns of their first deciduous molars (cases of the Early Mesolithic child Pad 11 and of the Late Mesolithic child VL 53, respective enrichments of +0.6‰ and 1.4‰), remain stable (case of the Late Mesolithic child VL 51) or, in contrast, are already depleted (slight depletion in the case of the Early Mesolithic child Pad 23, -0,5‰, and greater depletion in case of the Late Mesolithic child VL 18c, -1‰). The case of a δ^{15}N enrichment between the two crowns (e.g. Pad 11, VL 53) suggests a continuous reliance on breast milk as a major source of protein during most of the time of the formation of the crown of the first permanent molar[258] (predominantly breastfed). In contrast, the case of a δ^{15}N depletion between the two teeth signals (VL 18c; Pad 11) suggests that these children already substantially reduced the frequency/duration of suckles during most of the time of the formation of the crown of their first permanent molars (predominantly supplemented). The slighter δ^{15}N depletion for the child Pad 11 may indicate a later shift toward the reliance on supplementary food than the child VL 18c.

The δ^{13}C values of the crowns of the children VL 53 and Pad 11 follow a similar increase as their δ^{15}N values (respective first deciduous to first permanent crowns Δ^{13}C: +0.7‰ and +0.3‰), which should be due to the later reduction in suckling frequency/duration for these children. Concerning VL 18c, although the crown of the first deciduous molar is depleted in δ^{15}N in comparison with the crown of the first permanent molars, δ^{13}C rather increases (Δ^{13}C: +0.3‰, associated with a δ^{15}N depletion of -1 ‰), which could be related to the introduction of a food of higher trophic level than the maternal diet. Concerning Pad 23, the smaller δ^{15}N depletion of his first permanent molar (Δ^{15}N: -0.5‰) is associated with quite stable δ^{13}C values (Δ^{13}C: -0.1‰), which either indicates that this child have been supplemented with solid food of high trophic level or that he was predominantly breastfed for a longer time than VL 18c. This pattern might also be due to the fact that the stable isotope values of the milk of the mother of Pad 23 were likely more elevated (first deciduous molar δ^{15}N value: 19.8‰; first deciduous molar δ^{13}C value: -18.6‰) than the values of the milk of the mother of the child VL 18c (first deciduous molar δ^{15}N value: -18.4‰; first deciduous molar δ^{13}C value: -20.7‰). Indeed, it is possible to assume that higher stable isotope values of the maternal milk related to the consumption of higher trophic level resources by the mother may "cancel out" the lowering effect of weaning food supplementation during the transitional period of mixed breast-milk and solid food consumption.

Finally, the longitudinal teeth δ^{13}C and δ^{15}N values of the child VL 51, aged at death 7.5-10 years old, do not display the expected breastfeeding effect: the teeth crowns and growing root remain stable. This pattern could be explained by a cessation of suckles before most of the time of the formation of the crown of the first deciduous molar (i.e.: before 3-6 months?). However, it cannot be excluded neither that this child may have been predominantly relying on breast milk during most of the time of the formation of the crown of his first permanent molar, could have been jointly supplemented with some lower trophic level resources than the maternal diet ("cancelling out" the breastfeeding offset) and may have then started to consume higher trophic level resources between the time of the formation of the crown of his first permanent molar and the time of the formation of the analyzed tooth root, shifting thus his stable isotope signal up to the signal of the maternal milk.

It seems that the breastfeeding strategies of Mesolithic mothers were somewhat variable, some opting for a later reduction of the frequency/duration of suckles (e.g. Pad 11, VL 53) than others (e.g. VL 18c - in between situation for Pad 23 - possible case of a very early cessation of suckles for VL 51?). Yet, concerning Mesolithic children, we particularly lack

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[258] Formation of the crown of the first deciduous molar: between 6 months in utero and 1 year; midpoint at 0,35 year old; formation of the crown of the first permanent molar: between 2 months and 4 years; midpoint at 2,08 year old (Beaumont et al. 2013).

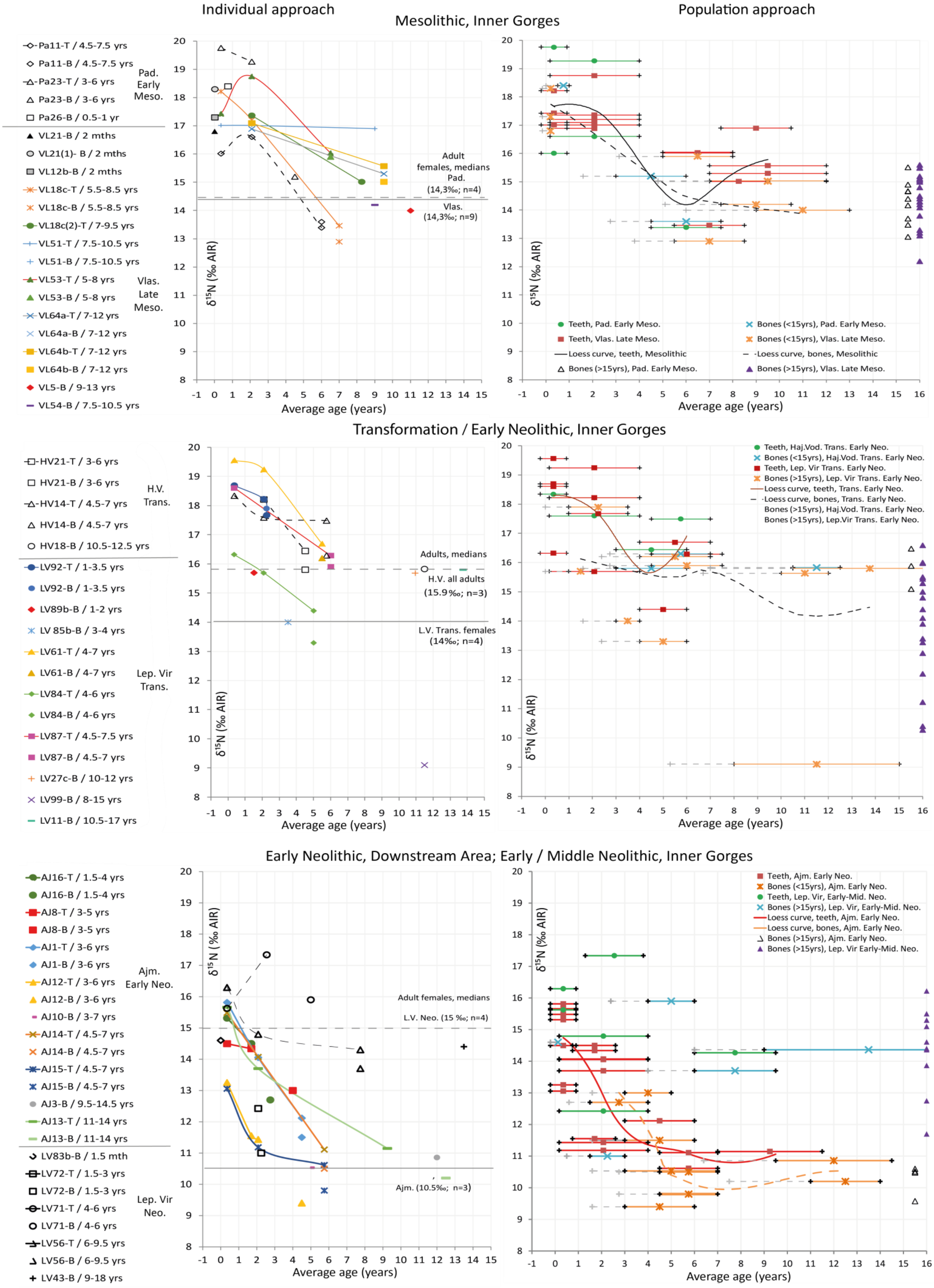

Figure 60: Intra-individual and population approaches for children δ15N signals
(caption details: Appendix A.III)

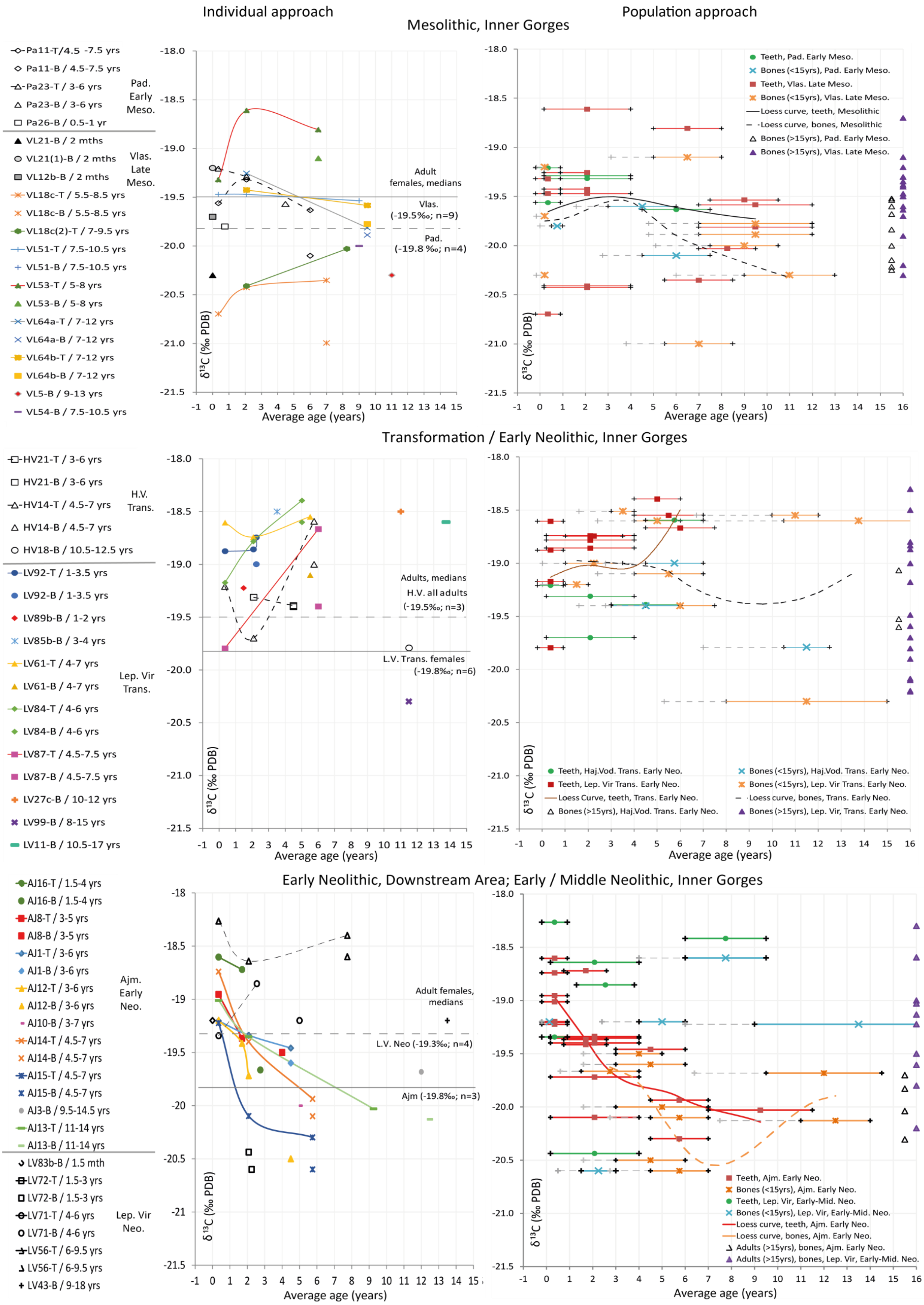

Figure 61: Intra-individual and population approaches for children δ^{13}C signals (caption details: appendix A.III)

the signals related to the early period of toddlerhood (ca 3/5 years). Therefore, the patterns of breastfeeding could be examined only for 5 children spanning a whole period of three thousands of years, which may explain the variability noticed in mothers choices: differences perhaps related to broad environmental (e.g. different resources availability over the Mesolithic), behavioral (more sedentary Late Mesolithic mothers?) or socio-cultural factors (individual choices or different norms over the communities burying their death at Padina and Vlasac?). As a future prospect of research, analyzing the stable isotope signals of the crowns of adult first permanent molars could enable to add valuable paleodietary data concerning this important stage of life, between birth and 3/5 years old.

5.2.2.2. 'Predominantly breastfed' versus 'predominantly supplemented': Early Neolithic toddlers buried in the Inner Gorges

The period of Transformation / Early Neolithic

Concerning the period of Transformation/Early Neolithic in the Inner Gorges, the teeth and bone $\delta^{15}N$ population trend line suggests that the reduction in suckling frequency/duration may have occurred slightly earlier than suggested by the Mesolithic children $\delta^{15}N$ trend lines (Appendix A.III. 15-17). $\delta^{13}C$ population trend lines tends to increase between birth and 5-6, which should be due to the nature of weaning proteins introduced (Appendix A.III. 15; 17).

According to their depletion in $\delta^{15}N$, the children LV 61, LV 92, HV 14, LV 84 likely started to reduce the frequency/duration of their suckles *before* most of the time of the formation of their first permanent molar crown (respectively $\Delta^{15}N$: -0.3‰, -0.5‰, -0.7‰ and -0.6‰; Appendix A.III. 12-13; 19-20).). It can be noticed that the smaller first permanent molar crown $\delta^{15}N$ depletion of the children LV 61 and LV 92 (-0.3‰ and -0.5‰) are associated with almost no changes in terms of $\delta^{13}C$ (LV 62: $\Delta^{13}C$ difference of -0.1‰; LV 92: similar $\delta^{13}C$ values). In contrast, the children LV 84 and HV 14 display both slightly greater first molar crown $\delta^{15}N$ depletion (-0.6‰ and -0.7‰) and greater $\delta^{13}C$ offsets (LV 84: +0.4‰; HV 14: -0.6‰). It is therefore possible that the children LV 61 and LV 92 relied for a longer time of the consumption of breast milk than the children LV 84 and HV 14. However, it should be considered that the child LV 92 died during the formation of his first permanent molar crown; hence the stable isotope signal of the crown of his teeth may indicate diet at a slightly younger age than the signal of the crown of the other children. In contrast, the strong $\delta^{15}N$ depletion of the root of the analyzed tooth of LV 62 (first permanent molar to tooth root $\Delta^{15}N$: -2.5‰) confirms that this child reduced more significantly the frequency/duration of his suckles after most of the time of the formation of the crown of his first permanent molar.

The pattern of depleted $\delta^{15}N$ values associated with elevated $\delta^{13}C$ values displayed by the teeth of the child LV 84 suggest that he may have relied at an earlier age on the consumption of solid food of higher trophic level (more marine-influenced proteins?) than his mother diet (molar crowns $\Delta^{15}N$: -0.6‰, $\Delta^{13}C$ +0.4‰). The child HV 14 may also have been supplemented earlier than the child LV 61, but likely with proteins of similar nature or of lower trophic level than his mother diet (molar crowns $\Delta^{15}N$: -0.7‰, $\Delta^{13}C$ -0.6‰). Alternately, the smaller first deciduous to first permanent molar crown $\delta^{15}N$ and $\delta^{13}C$ offsets noticed for LV 92 and LV 61 in comparison with the offsets noticed concerning the children LV 84 and HV 14 could also be due to the higher values of the milk of their mothers (first deciduous molar $\delta^{15}N$ value: respectively 19.6‰ and 18.6‰; first deciduous molar $\delta^{13}C$ value: -18.6‰ and -18.9‰) in comparison with the milk of the mothers of the children LV 84 and HV 14 (first deciduous molar $\delta^{15}N$ value: 18.3‰ and 16.3‰ ; first deciduous molar $\delta^{13}C$ value: -19.2‰ and -19.2‰).

The Early-Middle Neolithic period

Concerning the Early-Middle Neolithic period, longitudinal stable isotope values (including the signal of the first deciduous molar) could be analyzed only on the dentine of

two children: LV 56 and LV 71 (Appendix A.III. 12-13; A.III. 19-20). δ^{15}N and δ^{13}C results indicate that the child LV 56 started to reduce the frequency/duration of suckles before most of the time of the formation of the crown of the first permanent molar (first deciduous to first permanent molar crown Δ^{15}N: -1.5‰; Δ^{13}C: -0.3‰). The magnitude of the nitrogen offset is here greater than for all other Transformation and Early/Middle Neolithic children from the sample, which may indicate either an earlier reduction of suckling frequency or a supplementation with resources of lower trophic level than the maternal diet. Given the small magnitude of the carbon offset, the hypothesis of an earlier diminution in the frequency/duration can be favored. Concerning the child LV 71, collagen could not be extracted from the crown of his first permanent molar but was obtained for the apex his first deciduous canine which should theoretically reflect the diet between 1.3 and 3.8 years old (midpoint falling at 2.55 year)[259], so partly contemporaneously to the time span reflected by the crown of the first permanent molar. The increasing δ^{15}N and δ^{13}C values between the crown of the first deciduous molar crown and the canine apex (Δ^{15}N: -1.7‰; Δ^{13}C: -0.4‰) could be either related to a continuous reliance on breast milk as the major source of proteins during the three first years of life and/or to a supplementation with higher trophic level resources during this period.

Finally, concerning the child LV 72, who died between 1.5 and 3 years old, although no collagen signal could be obtained for the crown of his first deciduous molar, yet his bone collagen should have averaged a dietary signal formed contemporaneously or slightly older than the crown of his first permanent molar. Since his δ^{15}N and δ^{13}C bone signals are already slightly lower than the signal of his first permanent molar (Δ^{15}N: -1.4‰; Δ^{13}C: -0.2‰), it can be assumed that this child was already consuming some weaning food before his death; yet, this interpretation remains here speculative given the uncertainty related to the exact age at death of the toddler.

During the period of Transformation/Early Neolithic in the Danube Gorges children were likely predominantly relying on breast milk during an important part of the time of the formation of the crown of their first permanent molar; yet some children (LV 84, HV 14) may have relied earlier on supplementary food and/or reduced the frequency/duration of their suckles earlier than others (LV 61, LV 92). During the Early-Middle Neolithic period the longitudinal teeth data acquired for two children exhibit different patterns either related to the type of food supplemented or to the timing of the weaning process; one of them (LV 56) was probably weaned earlier than all others Transformational-Early/Middle Neolithic toddlers.

5.2.2.3. 'Predominantly breastfed' versus 'predominantly supplemented': The early Neolithic toddlers buried downstream

The pattern of δ^{15}N and δ^{13}C population trend lines for the Early Neolithic children buried downstream suggests that the suckling frequency/duration started to be reduced and that solid food was already significantly consumed <u>**before**</u> most of the time of the formation of the crown of the first permanent molar (Figure 62; Appendix A.III.15-17; 19-20). Indeed, the crowns of the first permanent molars of most children appear depleted in ^{15}N in comparison with the crown of their first deciduous molars (Δ^{15}N: AJ 1=-1.8‰; AJ 12=-1.8‰; AJ 13=-2‰; AJ 14=-1.4‰; AJ 15=-1.9‰; Figure 60; Appendix 19-20). The first permanent molar of almost all of them also display depleted δ^{13}C values, although the magnitude of this offset varies (Δ^{13}C: AJ 1=-0.5‰; AJ 12=-0.2‰; AJ 13=-0.4‰; AJ 14=-0.7‰; AJ 15=-0.9‰; Figure 61; Appendix 19-20).

Concerning the individuals AJ 16 and AJ 8, collagen could not be extracted from the crown of their first permanent molar but was obtained for the apex their first deciduous molar which should theoretically reflect the diet between 0.75 and 2.6 years old (midpoint falling at 1.7 year)[260],

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[259] Collagen extracted from the extremity of the root of this tooth (apex closed); time span used for the dietary signal: between 3/4 of root formation and the time of apex closure (Moorrees et al. 1965a).

[260] collagen extracted from the extremity of the root of this tooth (apex closed); time span used for the dietary signal: between 3/4 of root formation and the time of apex closure (Moorrees et al. 1965a).

so partly contemporaneously to the time span reflected by the crown of the first permanent molar (0.25 to 4 years, midpoint at 2.08). For both children, the depletions in ^{15}N and ^{13}C between these two signals is smaller than the first deciduous to first permanent molar crowns depletion noticed for other children (AJ 16: $\Delta^{15}N$= -0,7‰, $\Delta^{13}C$= -0.3‰; AJ 8: $\Delta^{15}N$= -0,3‰, $\Delta^{13}C$= -0.4‰). This should be due to the fact that the stable isotope signals of the crowns of the first permanent molars of the other children encompass tissues formed between 0.25 and 4 years and which thus may have already been more influenced by solid food and by the reduction in suckling frequency. The teeth roots of AJ 16 and AJ 8 should "average" the stable isotope signal of their diet upon a smaller amount of time (0.75-2.6 years) and thus more accurately reflect the diet of the toddler around 2 and 3 years old. Yet, it should be noticed that AJ 16 also exhibits the highest first deciduous molar crown $\delta^{13}C$ signal amongst children buried at Ajmana (-18.6‰); as suggested for the children Pad 23, LV 92 and LV 61, in case the maternal diet included higher trophic level resources (e.g. marine-influenced resources), it is possible that the toddlers stable isotope values remain elevated for a longer time during the period of transitional diet (mixed solid food and breast milk). The same explanations could be provided for the first deciduous molar crown to root stable isotopes depletion of the child AJ 8 (first deciduous molar crown $\delta^{13}C$ signal: -18.9‰); yet, concerning this child, it should be noticed that his root appears more depleted in carbon than in nitrogen ($\Delta^{15}N$= -0.3‰, $\Delta^{13}C$= -0.4‰). This pattern could be caused by the additional physiological effect of some biological stress experienced during the weaning process (Reitseima et al. 2013; Beaumont et al. 2015; King et al. 2018b).

Therefore, it seems that the choices of the mothers of the Early Neolithic children buried downstream in terms of weaning were quite homogeneous, most children having already substantially reduced the frequency/duration of their suckles before most of the time of the formation of the crown of their first permanent molar.

The difference between the $\delta^{15}N$ molar crown offset of the Mesolithic children buried in the Inner Gorges (-0.1±0.9‰[261], n=5; Appendix A.III.19-20) and the $\delta^{15}N$ molar crown offset of the Early Neolithic children buried downstream (-1.6±0.4‰, n=5) is statistically significant (Mann-Whitney, $p<0.05$) but not the difference between the $\delta^{15}N$ molar crown offset of Early Neolithic children buried in the Inner Gorges (-0.9±1.1‰, n=5) and $\delta^{15}N$ molar crown offset of the Early Neolithic children buried downstream, nor the difference between the $\delta^{15}N$ molar crown offset of the Mesolithic children and the $\delta^{15}N$ molar crown offset of the Early Neolithic children buried in the Inner Gorges (Mann Whitney, $p>0.05$).

The difference between the $\delta^{13}C$ molar crown offset of the Mesolithic children buried in the Inner Gorges (on average -0.2±0.3‰, n=5) and the $\delta^{13}C$ molar crown offset of the Early Neolithic children buried downstream (on average -0.5±0.3‰, n=5) is statistically significant as well as the difference between the $\delta^{13}C$ molar crown offset of the Early Neolithic children buried in the Inner Gorges (-0.07±0.3‰, n=5) and the $\delta^{13}C$ molar crown offset of the Early Neolithic children buried downstream (Mann-Whitney, $p<0.05$) but not between the $\delta^{13}C$ molar crown offset of the Mesolithic children and the $\delta^{13}C$ molar crown offset of the Early Neolithic children buried in the Inner Gorges (Mann-Whitney, $p>0.05$). These differences are also reflected by the results of the PCA, when the individual scores are examined per age categories (Figure 68).

These results indicate that, on average, the Early Neolithic children buried downstream at Ajmana may have been relying earlier on supplementary food than the Mesolithic children inhumated in the Gorges and were probably weaned with quite different resources (greater $\delta^{15}N$ and $\delta^{13}C$ offsets, both statistically significant). The smaller standard deviation associated with the average $\delta^{15}N$ depletion of the first permanent molar crown of the Early Neolithic children buried downstream (±0.4‰ versus ±1‰ for Mesolithic and Neolithic children buried in the Inner Gorges) suggest that **the breastfeeding practices of the**

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[261] average and standard deviation values

Early Neolithic mothers of the children buried downstream were more homogeneous than the choices of the mothers of the children buried in the Inner Gorges.

5.2.3. Weaning results (2) – the length of lactation

5.2.3.1. The cessation of suckles, Mesolithic children

Dropping with the diminution in the frequency of suckles, the stabilization of $\delta^{15}N$ values during toddlerhood and childhood should inform about the end of the weaning process and thus about the total length of lactation. Concerning the Mesolithic period inside the Danube Gorges, the $\delta^{15}N$ population bone and teeth trend lines reach the adult females variability around the age of 4 years and stabilize to later childhood values around the age of 5-6 years old (5 years for teeth curves, 6.5 years for bone curves and 5.5 years for the curves computed including both teeth and bone signals; Figure 60; Appendix 15; 17). However, it should be emphasized that dietary signals are lacking between the ages of 3-5 years old (no teeth root values and only one bone value at this age).

A closer look at intra-individual data and at first permanent molar crowns to teeth root nitrogen offsets suggests that most children may have been weaned earlier than the age of 5 years (Appendix A.III. 12; 19; 23). It has been noticed that the $\delta^{15}N$ and $\delta^{13}C$ values of the different tissues analyzed for the child VL 51 remain stable from his first year of life (first deciduous molar crown) to his death (tooth root value), which suggests that he may have stopped suckling before the main time of the formation of the crown of the first deciduous molar (before ca 3 months of age). The individuals Pad 11, VL 53, and VL 18c (respectively aged at death 4.5-7.5, 5-8 and 5.5-8.5 years old) exhibit great first permanent molar crown to growing root depletions ($\Delta^{15}N$: Pad 11=-3,2‰; VL 53=-2,8‰; VL 18c=-3.6‰). Their bone also display very similar $\delta^{15}N$ values as their growing roots ($\Delta^{15}N$ bone to growing root: Pad 11=+0,2‰; VL 53=-0,1‰; VL 18c=-0.6‰), suggesting that they probably reach this $\delta^{15}N$ signal a longer time before their death. For instance, the stable isotope signal of the bone collagen of the individual Pad 11 may have averaged some values formed between 3 and 4 years old in case this child died at 4.5, the lower possible limit of his age at death according to our estimation. Only the $\delta^{15}N$ values of the tissues of the child VL 53, aged at death 5-8 years old, remain slightly above female variability but this could be due to the fact that this child has probably been supplemented with some marine, given the elevated $\delta^{13}C$ and $\delta^{34}S$ values of the growing edge of the root of his tooth (respectively -18.8‰ and 13.1‰). These results hence suggest that Pad. 11, VL 53 and VL 18c were likely already entirely weaned before the period spanning between 4.5-8.5 years old.

Concerning the child VL 18c, it can be noticed that the drop in $\delta^{15}N$ starts from birth and appears greater than the 2-3‰ documented weaning effect (first deciduous molar crown to growing tooth root $\delta^{15}N$ offset=-4,8‰). Given that $\delta^{13}C$ values are contrastingly slightly elevated (first deciduous molar crown to growing tooth root $\delta^{13}C$ offset=-+0,3‰), this drop cannot be interpreted as the effect of an early supplementation with a food of lower trophic level than the maternal diet. Such continuous drop in $\delta^{15}N$ starting from birth has been interpreted as the possible result of a complicated pregnancy and the experience of elevated in utero stress (Beaumont et al. 2015) or as a "classical weaning trajectory with slight interactions with stress or physiological difference in the mother-infant pairs causing slightly larger than normal drop in ^{15}N values"(king et al. 2018b).

The children VL 64a and 64b (no first deciduous molar crown signals), who died older than the other Mesolithic children analyzed (between 7-12 years old), were probably still suckling after most of the time of the formation of the crown of their first permanent molar given the magnitude of the nitrogen depletion between this signal and the growing root of the analyzed tooth (for both of them -1.5‰), unless this depletion indicates a later shift toward the consumption of lower trophic level resources (joint depletion in $\delta^{13}C$ respectively -0.6‰ and -0.2‰). Finally, no collagen could be extracted from the growing edge of a root of the child Pad 23 who died between 3-6 years old, but the magnitude of $\delta^{15}N$ depletion of his bone collagen signal in comparison with his first permanent molar ($\Delta^{15}N$: -4‰; bone collagen value within Early Mesolithic females variability), suggests that he was probably already weaned before his death.

Hence, although the population trend line suggests that the end of weaning may have occurred between 4 and 5, given the lack of signals reflecting diet around the age of 3-5 years old, one can just say that the children who died between 3-6 (Pad 23) and 4.5-8.5 (Pad 11; VL 53 and VL 18c) were probably entirely weaned some time before their death. The average cessation of suckling may thus have occurred after most of the time of the formation of the crown of the first permanent molar (so probably after 2 years old, midpoint for the formation of that tooth) and 4-5 years old.

5.2.3.2. The cessation of suckles: Early Neolithic children buried in the Inner Gorges

The period of Transformation / Early Neolithic

Concerning the period of Transformation / Early Neolithic, the $\delta^{15}N$ population trend lines reach the adult females' variability around the age of 3 years and stabilizes to later childhood values around the age of 4 years old (Figure 60; Appendix 15; 17). However, it should be emphasized that dietary signals are lacking around the age of 3-4 years old (only one bone value between 3 and 4). If we exclude the individual LV 84, which range in the adult variability from the signal of the crown of his first deciduous molar, the teeth roots and bone signals of the other individuals who died between 3 and 7.5 (HV 21, HV 14, LV 87 and LV 61 and respectively aged at death 3-6, 4.5-7.5; 4.5-7.5; 4-7) range within the adult female stable isotopes variability. Given the magnitude of the first permanent molar crown to teeth root $\delta^{15}N$ depletion of the children HV 21, LV 61 and LV 84 ($\Delta^{15}N$, respectively HV 21=1.8‰; LV 61=-2.5‰; LV 84=-1.3‰), it can be assumed that these individuals were already entirely weaned before their death (aged at death: HV 21: 3-6 years old; LV 61 4-7; LV 84: 4-6 years old). The nitrogen value of the tooth root of the individual HV 14 (aged at death 4.5-7 years old), is similar as the signal of the crown of his first permanent molar (only small first deciduous to permanent molar crown nitrogen depletion of -0.5‰), which suggests that he may have stopped suckling before most of the time of the formation of the crown of his first permanent molar and was probably weaned with food including high trophic level resources. The longitudinal $\delta^{15}N$ data gathered for LV 92, aged at death between 1 and 3.5, are also only slightly declining (between the first permanent molar crown and tooth root=-0,5‰). Considering the age at death of this child, this small depletion may indicate that he died during the process of weaning, before 3 years old.

The Early-Middle Neolithic period

Concerning the Early-Middle Neolithic period, longitudinal teeth data could be gathered only for two Neolithic children (LV 71 and LV 56; Appendix 19; 23; Figure 60), for whom first deciduous molar crowns already appear within females variability, indicating that their mothers perhaps had a more terrestrial diet than some of the females of the group. The child LV 56, dead between 6-9.5 years old, experienced a greater depletion in $\delta^{15}N$ between the time of the formation of his first deciduous molar crown and the time of the formation of his first permanent molar crown (-1.5‰) than between the time of the formation his first permanent molar crown and of the analyzed part of the tooth root (-0.5‰). This pattern suggests that he probably mainly reduced the frequency/duration of his suckles before most of the time of the formation of the crown of his first permanent molar (similarly as the Transformational child HV 14). Concerning the child LV 71 (no first permanent molar crown stable isotope signal), the pattern of increasing $\delta^{15}N$ and $\delta^{13}C$ values between the crown of his first deciduous molar and his canine apex ($\Delta^{15}N$: -1.7‰; $\Delta^{13}C$: -0.4‰) followed by depleted $\delta^{15}N$ and $\delta^{13}C$ values bone collagen at death (canine root to bone offsets: $\Delta^{15}N$: -1.4‰; $\Delta^{13}C$: -0.3‰) may either indicate a late reduction of suckling frequency/duration (after

1.3-3.8 years old but before his death 4-6 years old) or a dietary event posterior to the weaning process.

Intra-individual data thus indicate that some Transformational / Early Neolithic children (HV 21, LV 61, LV 84, LV 87) likely stopped suckling after most of the time of the formation of the crown of their first permanent molar (probably after 2 years) before their death between 3 and 7.5 years old. This is consistent with the population trend line suggesting that suckling was over after 3-4 years old. One Transformational-Early Neolithic child, HV 14, and one Early-Middle Neolithic child, LV 56, may have been weaned before or during most of the time of the formation of the crown of their first permanent molar (before or during the second year of life). Finally, the Transformational-Early Neolithic toddler LV 92 likely died during the weaning process, between 1.5 and 3 years old.

5.2.3.3. The cessation of suckles: Early Neolithic children buried downstream

The δ^{15}N trend lines for the Early Neolithic children buried downstream at the site of Ajmana reach the adult females variability and older childhood values around the age of 4-5 years but the δ^{15}N curve of teeth signals already appears less steep from 3 years old (Figure 60; Appendix 15; 17).

The magnitude of the δ^{15}N depletion between the crowns of the first permanent molars and the growing roots of the teeth of several children (AJ 1, 14, 13, respectively aged at death 3-6, 4.5-7 and 11-14 years old) indicates that they were still consuming maternal milk after most of the time of the formation of their first permanent molar, although they were probably already increasingly relying on the consumption of supplementary food during this period (respective Δ^{15}N: -2‰, -3‰, -2.6‰; Figure 60; Appendix A.III.19; 23). The children AJ 1 and AJ 14, who respectively died between 3-6 and 4.5-7 years old, also exhibit small teeth root-to-bone δ^{15}N offset (-0.6‰ for both children), which suggests that they probably stop consuming maternal milk some time before their death.

Concerning the child AJ 12, the extremity of the growing root of the analyzed tooth (first deciduous molar) was already closed, reflecting a signal formed contemporaneously to the crown of his first permanent molar; indeed, the δ^{15}N and δ^{13}C values of these two signals appears quite similar (no nitrogen offset, carbon offset of 0.3‰). In contrast, the magnitude of the δ^{15}N depletion between the signal of his first permanent molar crown and of his bone suggests that this child was probably already weaned some time before his death (Δ^{15}N= -2‰, died around 3-6 years old). The child AJ 15 experienced a greater depletion in δ^{15}N between the time of the formation of his first deciduous molar crown and the time of the formation of his first permanent molar crown (-2‰) than between the time of the formation his first permanent molar crown and of the analyzed part of the tooth root (-0.6‰); this could indicate a cessation of suckling before or during most of the time of the formation of the first permanent molar crown (similar case as noticed for HV 14 and LV 56).

Finally, concerning AJ 8 and AJ 16 (aged at death between 1.5-4 years and 3-5 years), the δ^{15}N depletion between the signal of the apex of their first deciduous molar (signal around 0.75 and 2.6 years, no first permanent crown value) and of their bone (signals some time before their death) suggest that they likely already reduced the frequency/duration of suckles before their death (Δ^{15}N respectively: 1.1‰ and 1.4‰); given that the magnitude of the depletion noticed for the contemporaneously formed tissues of the other children is greater (e.g. AJ 1, 14, 13, 12), it is possible that they died before the completion of the weaning. Alternately, they may have been supplemented with some higher trophic level resources than the other children.

Therefore intra-individual data suggests that most children (AJ 1, 14, 13, 12) probably stopped suckling between the time of the formation of the crown of their first permanent molar (midpoint at 2 years old) and their death (between 3-7 years old for AJ 1, 12, 13, 14) while one of them probably stopped consuming maternal milk earlier (AJ 15). Finally, 2 children AJ 16 and AJ 8

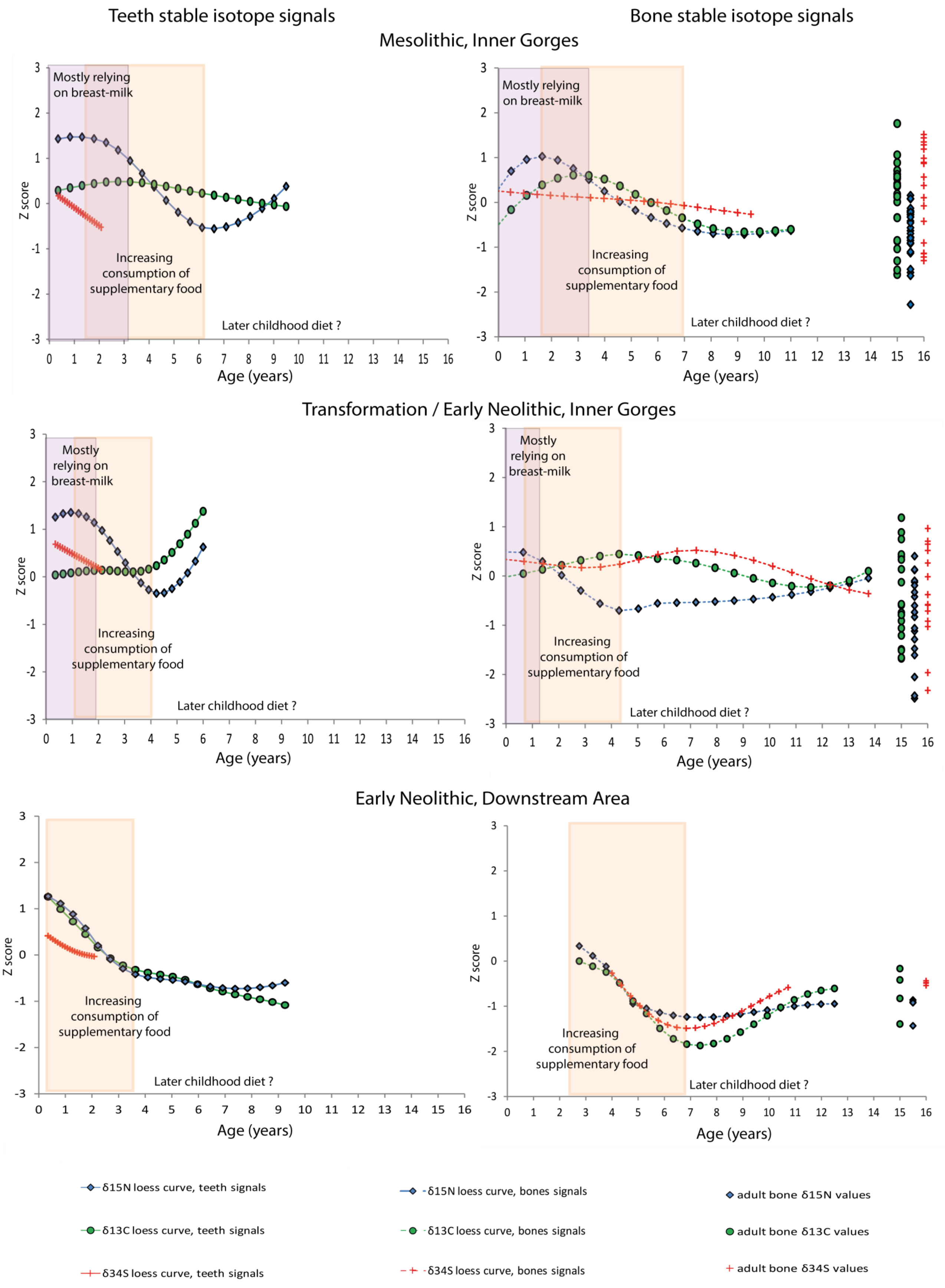

Figure 62: Comparison of $\delta^{15}N$ -$\delta^{13}C$ - $\delta^{34}S$ loess curves computed on children tissues
(caption details: appendix A.III)

may have died during the weaning process (respectively between 1.5-4 and 3-5 years old). **This is broadly consistent with an average completion of the weaning process after the age of 2 but before 3-5 years as suggested by the broad population trend line** (e.g. Figure 59).

5.2.3.4. Summary: the timing of the weaning process, introduction of solid food and length of lactation

To summarize, it has been observed that: (1.) on average, Mesolithic and Transformational/Early Neolithic children may have relied on breast-milk as the primary source of nutrients for a longer time - and were probably weaned with quite different resources **-** than the Early Neolithic children buried downstream and than one of the Neolithic child buried at Lepenski Vir after 6000 BC; besides, the children buried in the Downstream Area should have been supplemented with different proteins than the children buried in the Gorges; (2.) on average, children stopped suckling after most of the time of the formation of the crown of their first permanent molar but before the age of 4-5 years, although some children from each chrono-cultural context may have been entirely weaned earlier; (3.) breastfeeding and weaning practices were more variables during the Mesolithic and the Neolithic in the Inner Gorges than during the Early Neolithic period in the Downstream Area. This variability could be related to the wide chrono-cultural context analyzed for the Mesolithic period and hence perhaps to differences in terms of resources availability or degree of mobility over the Mesolithic but also to the presence of migrants during the Transformational-Early Neolithic period at Lepenski Vir. The Early Neolithic mothers of the children buried in the "multiple grave" of Ajmana opted for a different strategy to feed their children (same family group?) than the mothers of the children buried upstream, which could be related to essential differences in the socio-cultural norms of these communities.

5.2.4. Weaning results (3) – maternal nutritional choices and weaning food

On the earliest post-partum formed tissues, $\delta^{13}C$ and $\delta^{34}S$ values can be used - together with inter-individual differences in $\delta^{15}N$ - to examine the diet of breastfeeding mothers. Yet, it should be kept in mind that the $\delta^{13}C$ and $\delta^{34}S$ signals of the first deciduous molars of some children may reflect only the signal of the infant diet, in case of very early cessation of suckling (possible case of VL 51 for instance). Later-formed tissues should -in theory- respond in $\delta^{13}C$ and $\delta^{34}S$ according to the nature of the weaning proteins introduced to the child, particularly if these proteins differ from the mother diet. Individual scores of the PCA synthesizes this paleodietary information (individual scores of the PCA examined per age categories in Appendix A.IV.14-16).

In the analyzed sample, while $\delta^{15}N$ trend lines are systematically depleted with the reduction in the frequency of suckles, in contrast patterns of $\delta^{13}C$ trend lines vary between individuals and according to the chrono-cultural group considered which is likely due to the differential nature of the weaning proteins supplemented to the children (Figure 62; Appendix A.III.15-17). **Yet, $\delta^{34}S$ teeth trend lines reveal a particular pattern: the signal of the crown of the first permanent molar is quasi systematically depleted in comparison with the signal of the first deciduous molar, independently of the chrono-cultural considered (**Figure 62; Figure 63). When loess curves are computed including perinataly-formed bone collagen, a slight depletion can also be observed between birth and circa 2 years old (Figure 62; Appendix 17-18). A closer examination of intra-individual data reveals that the first permanent molar crowns of 11 children amongst 14 for which longitudinal teeth $\delta^{34}S$ values were obtained are depleted in comparison with the values of their first deciduous molars crowns (Figure 63; Appendix A.III.20). Two children exhibit similar first deciduous to first permanent molar crowns $\delta^{34}S$ values (VL 51 and AJ 15) and only one child displays increasing $\delta^{34}S$ crowns values (LV 84). The $\delta^{34}S$ values of the first permanent molars are, on average, lower by -0.5±0.6‰ in comparison with the values of the first deciduous molars when considering the crowns of the 14 children of the sample and by -0.7±0.5‰ when considering only the 11 children exhibiting that depletion. Concerning one individual - AJ 16 - the stable isotope values of the first permanent molar crown could not be measured but the closed apex of the teeth root (midpoint of the signal at 1.7 years old) also yielded depleted δ^{34}S values (first deciduous molar crown to root δ^{34}S offset = -2‰).

5.2.4.1. δ^{34}S fluctuations during infancy: maternal diet, weaning food or a trophic effect of lactation?

First deciduous to first permanent molar crown δ^{34}S offset: an effect of maternal nutritional choices?

Possible dietary interpretations for this tendency toward δ^{34}S depleted permanent molar crowns could be that:

- 1) most lactating mothers shifted their diet towards the consumption of lower δ^{34}S resources in comparison with their pregnancy diet,
- 2) most children were supplemented with some food depleted in δ^{34}S in comparison with the diet of their mother, for instance some terrestrial resources such as meat and C_3 plants.

Since the children Pad. 11, LV 92, and LV 61 were probably still mostly relying on breast-milk during an important part of the formation of the crowns of their first permanent molar (no or only slight Δ^{15}N), it is possible that their lactating mothers may have consumed higher amount of δ^{34}S depleted food resources while breastfeeding (successive depletions of -0.2‰, -0.6‰ and -1.6‰). Concerning these children, the δ^{34}S depletion is not systematically associated with a joint depletion in δ^{13}C (successive Δ^{13}C offsets: +0.6‰; 0‰; -0.3‰), as it might be expected in case the mothers started to consume more terrestrial proteins or freshwater resources; yet the absence of joint first permanent molar crown δ^{13}C depletion could be explained, in theory, by the slight breastfeeding trophic effect associated with the isotopes of carbon.

Similarly, the children Pad 23, VL 18c and AJ 16, who exhibit already δ^{15}N depleted first permanent molar crowns (or depleted apex of the first deciduous molar root in case of AJ 16), may have been supplemented with a food lower in δ^{34}S than the material diet (successive depletions of -0.7‰, -0.5‰ and -2‰), but not systematically associated with a joint depletion in δ^{13}C (successive Δ^{13}C offsets: -0.1‰; +0.3‰; -0.1‰). Although these children were already substantially consuming solid food during most of the time of the formation of the crown of their first permanent molar (depleted in δ^{15}N), it is also possible that a joint shift in maternal diet could also be responsible for the δ^{34}S depletion.

The first permanent molar crowns of the Transformational/Early Neolithic and Early-Middle Neolithic children HV 14, LV 56, AJ 1, AJ 14, AJ 13 display depletions in the isotopes of the 3 elements (on average Δ^{15}N: -1.5±0.5‰; Δ^{13}C: -0.4±0.2‰ ; Δ^{34}S: -0.8±0.5‰), suggesting a supplementation with terrestrial protein of lower trophic level than the maternal diet.

In contrast, LV 84, AJ 15 and VL 51 display either positive or an absence of first permanent to first deciduous crown δ^{34}S offset; it can be noticed that the first deciduous molar crown of these three children also display the lowest δ^{34}S values for the group of Late Mesolithic (VL 51: 8.2‰) of Transformation/Early Neolithic (LV 84: 10.7‰) and of Early Neolithic analyzed children (AJ 15: 7.5‰). The first permanent molar crown of the child LV 84 appears depleted in δ^{15}N values (-0.6‰) but elevated in δ^{13}C and in δ^{34}S, which suggests that this child was already consuming a solid food enriched in marine-influenced proteins in comparison with the maternal diet at the time of the formation of this tooth. The stable isotope values of the child VL 51 remain constant from the signal of his first deciduous molar crown to his death, which could indicate an early cessation of suckles and a stable diet. The first permanent molar crown of the child AJ 15 is not depleted in δ^{34}S but strongly depleted in δ^{13}C and δ^{15}N (Δ^{15}N: -1.9‰; Δ^{13}C: -0.9‰, Δ^{34}S:0‰), which could be explained by a reduction in suckling frequency before most of the time of the formation of this crown (depletion in δ^{15}N), and the consumption of a food probably of lower trophic level (depletion in δ^{15}N and in

δ^{13}C) but of similar origin as the maternal diet (both maternal and child diet being more terrestrial oriented, inducing a low δ^{34}S and no first deciduous to first permanent molar crown δ^{34}S offset).

Finally, preserved collagen could not be extracted from the crown of the first deciduous molar of the child LV 72 (aged at death 1.5-3 years old), but the crown of his first permanent molar displays lower δ^{13}C and δ^{34}S values than the teeth crowns of other Transformation, Early Neolithic and Early-Middle Neolithic children analyzed, indicating that his mother likely had a more terrestrial diet; interestingly, his bone collagen is elevated in δ^{34}S (+0.8‰) but contrastingly depleted in δ^{15}N (-1.4‰) and δ^{13}C (-0.2‰) in comparison with the signal of his first permanent molar. This child may have already significantly reduced the frequency/duration of his suckles around 1-3 years (lower bone δ^{15}N) and was probably jointly supplemented with preparations including more (anadromous) fish and/or dog's meat than the maternal diet (only small bone δ^{13}C depletion associated with elevated bone δ^{34}S).

It should be borne in mind that the mothers of analyzed children likely had heterogeneous diets (broad range of δ^{15}N, δ^{13}C and δ^{34}S values for perinates bone collagen, for the crown of the first deciduous molars, and for adult mothers), some including marine-influenced resources (e.g. Lepenski Vir, period of Transformation), others favoring terrestrial resources (e.g. Ajmana) or having a mixed diet (e.g. Padina and Vlasac). It may thus appear counter-intuitive to assume that almost all the mothers of analyzed children introduced δ^{34}S-depleted solid food in comparison with their diet despite the broad variety of their own dietary choices. Particularly, in the case of the children Pad 23, VL 18c and AJm 16 (who already reduced the frequency/duration of their suckles before most of the time of the formation of the crown of the first permanent molar according to their depleted δ^{15}N value), it appears difficult to define which food resources, lower in δ^{34}S than the maternal diet (in theory, more terrestrial proteins or freshwater fish than consumed by the mother) but not in δ^{13}C, may have been supplemented. This variation might be explained by the broad range of δ^{13}C values encompassed by local freshwater fish species. Alternately, the possibility that δ^{34}S values may be responsive to the particular physiological states of pregnancy and lactation or to breastfeeding should be considered jointly to the differential origin of the weaning food supplemented to the toddler.

A possible physiological offset: hypothesis of first deciduous molar δ^{34}S *enrichment with breastfeeding*

Since it has been suggested that consumers tend to have slightly higher δ^{34}S values in their tissues in comparison with their diet, on average +0.5±2.4‰ (estimated by Nehlich et al. 2015), and given that a value of +0.7‰ has also been recorded between the bone collagen of a kid and maternal goat milk (Tanz and Schmidt 2010), it could also be hypothesized that the crowns of the first deciduous molars could have been enriched in δ^{34}S under a trophic effect of breastfeeding. In this case, observing δ^{34}S depleted values for the crowns of first permanent molars would indicate that solid food - not necessarily depleted in δ^{34}S in comparison with the maternal diet - was introduced before most of the time of the formation of that tooth. It is worth mentioning that the oldest perinates from Vlasac and Lepenski Vir, aged at death between 40 and 42 gestational weeks (n=5), are rather elevated in δ^{34}S in comparison with most of the perinates who died before 40 gestational weeks (n=15; Figure 57; Figure 58; Figure 59). At both sites, the δ^{34}S value of these older perinates (circa 14-15‰) range in the high part of the δ^{34}S range of the crowns of the first deciduous molars analyzed (circa 8-15‰). This tendency has also been noticed for the isotopes of the carbon and the nitrogen elements (Figure 56; Figure 58; Figure 59). Despite the small number of older perinates included in sulfur analyses (n δ^{34}S values for perinates aged 40-42 gestational weeks=5; a sample size effect?), these elevated perinatal δ^{34}S values could reflect the influence of maternal diet on the composition of breastmilk.

However, we noticed that the crowns of the first permanent molar of some children (e.g. Pad 11, LV 61 and LV 92) remains elevated in δ^{15}N and δ^{13}C, likely as an effect of continuous reliance on breast-milk as the major source of proteins, but are already depleted in δ^{34}S. Yet, the δ^{15}N and δ^{13}C breastfeeding offsets might be greater (respectively 2-3‰ and 0-1‰) than this hypothetical δ^{34}S trophic elevation, and given the broad time span averaged by the analyzed signals, these offsets would

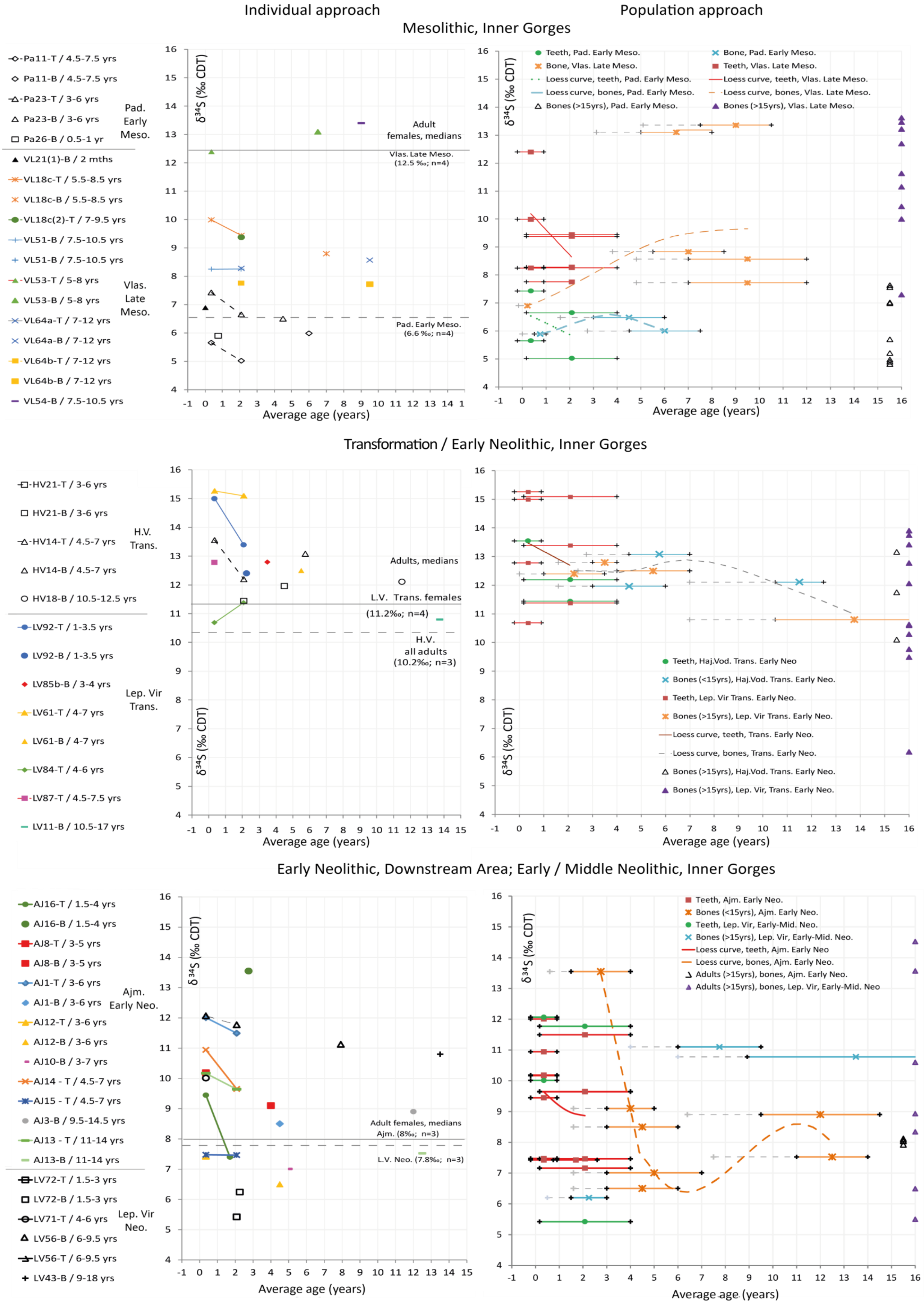

Figure 63: Intra-individual and population approaches for children δ34S signals (caption details: appendix A.III)

also depend upon the proportions of breastmilk versus of supplementary food consumed by the toddler as well as upon the nature of this food. It is indeed possible that nitrogen, carbon and sulfur containing amino-acids could be unevenly routed and metabolized according to food sources (as suggested by Webb et al. 2016, 2017a and b), which could hypothetically result in $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ responses at different rates into rapidly growing tissues (as recently suggested for $\delta^{13}C$ and $\delta^{15}N$ by Beaumont et al. 2018).

If we consider the possibility of a slight $\delta^{34}S$ trophic elevation under the effect of breastfeeding, then the cases of the three children who does not exhibit such elevation (VL 51, LV 84 and AJ 15) may still be explained by a greater reliance on solid food during or before most of the time of the formation of the crown of their first deciduous molar, which is still consistent with the pattern of their $\delta^{13}C$ and $\delta^{15}N$ values. Their weaning food may have been similar to the maternal diet (case of AJ 15; of VL 51?) or may have included more marine-influenced resources than their mother diet (case of LV 84). Some children, HV 14, LV 92, AJ 14 and AJ 16 exhibit greater $\delta^{34}S$ offsets (circa -1 to -2 ‰), indicative of the introduction of $\delta^{34}S$ depleted protein, which is in accordance with the joint decline observed in $\delta^{13}C$ and $\delta^{15}N$ (suggestive of the introduction of lower trophic level terrestrial resources) for HV 14 and AJ 14, but which is more surprising in the case of AJ 16 and LV 92 who display much smaller $\delta^{13}C$ and $\delta^{15}N$ offsets perhaps as an effect of the introduction of aquatic proteins from $\delta^{34}S$ depleted freshwater species and/or of a longer reliance on breast milk as the main source of proteins.

A possible physiological offset: hypothesis of first deciduous molar $\delta^{34}S$ *depletion with breastfeeding*

Alternately, some authors have rather documented negative $\delta^{34}S$ offsets between food sources and consumers' tissues, varying from -0.5‰ to -1.5‰ (e.g. Paterson et al. 1986; Barnes and Jennings 2007; Webb et al. 2017b). Recent results from the control feeding study of a cohort of pigs, saws and breastfed piglets (Webb et al. 2017b) did not indicate significant differences between the $\delta^{34}S$ values of offspring (piglet consuming both saw and pelleted food) and of mothers collagen (on average 0.02±0.4‰)[262], but they show $\delta^{34}S$ negative offset between the value of the offspring collagen and of the maternal milk (-0.5±0.4‰, lower piglet collagen value)[263], and between the values of the sow's collagen and her milk (-0.6±0.9‰; lower saw collagen value). Similarly, while Tanz and Schmidt (2010) recorded an offset of +0.7‰ between the kid bone collagen value and maternal goat milk, they also observed an offset of -1.7‰ between the kid cartilage collagen value[264] and the maternal milk. Considering the possibility of negative mother milk-to-offspring offsets, the observed $\delta^{34}S$ depletion of the crown of the first permanent molars of most analyzed children may be interpreted as an effect of milk consumption rather than as the consequence of weaning food introduction. In this case breastfeeding would result in increasing the $\delta^{15}N$ and $\delta^{13}C$ values but contrastingly decrease the $\delta^{34}S$ values. Indeed, examined at a population level the tendency of declining postpartum $\delta^{34}S$ values seems to be broadly concordant with increasing or elevated $\delta^{15}N$ and $\delta^{13}C$ signals (Figure 62; Appendix A.III.18[265]; Figure 59).

It has been suggested that the $\delta^{34}S$ offset may not only vary according to the tissue analyzed (e.g. Tanz and Schmidt 2010), but also according to the protein quantity in the diet (McCutchan et al. 2003; Richards et al. 2001; Nehlich et al. 2009; Nehlich 2015); negative offsets have thus been noticed in case of low protein diet (average offset of -0.5±0.56‰ for low protein diet; McCutchan et al. 2003). It is therefore possible that changes in terms of nutrient composition of the diet that occurred at birth (Kennaugh and Hay 1987) may affect the nature of the maternal-to-child tissue $\delta^{34}S$ offset. Indeed, although carbohydrates are the main fuels for the growth of the foetus, amino acids are also found in high concentration in placenta and in foetus plasma for the protein synthesis

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[262] average and standard deviation estimated from Webb et al. 2017 using the average values of saws and of piglets for 5 different dietary groups ranging from terrestrial to marine (data for pairs mothers and offspring not available).

[263] cf note supra.

[264] both bone and cartilage tissues only comprise the sulfur-containing amino-acid methionine

[265] The $\delta^{34}S$ depletion during the first years of life is yet less clear on the population trendline computed on bone values, but this may be due to the small number of bone signals with associated $\delta^{34}S$ values for the age of 1-4 years old (n=3 for the whole sample).

(Munroe 1983, Cetin 2001). In comparison with the placental nutrition, breast-milk represents a significant source of lipids for the infant (circa 4% of total milk composition); it also provides much more energy (carbohydrates represent circa 7% of total milk composition) than proteins (<1% of total milk composition) to the sucker. Besides, it is known that the abundance of sulfur varies in the different food sources according to their concentration in methionine and cystein, resulting in their unbalanced influence on the $\delta^{34}S$ signature of the consumer (Nehlich 2015). As for other human tissues, methionine is found in small quantity in breast milk in comparison with the other essential amino acids (Csapo and Salamon 2009; Zhang et al. 2013). Concerning the placental nutrition, animal experiment studies have shown that methionine is amongst the amino-acids that are transported most rapidly from the placenta into the fetal circulation (Paolini et al. 2001) and it has been observed that the uteroplacental tissues are producing methionine during late stages of pregnancy, likely from maternal homocysteine (Chang et al. 1998; Regnault et al. 2002). Furthermore, specific adaptive changes in methionine metabolism have also been evidenced during pregnancy, involving particular rates of transsulfuration and transmethylation (Dasarathy et al. 2009). Hence, it can be hypothesized that a transition to a milk diet, potentially lower in amino-acids/proteins than the placental diet, or perhaps simply containing lower concentrations of methionine and cystein and/or depleted in ^{34}S, could be amongst the explanations for the decrease in sulfur values observed between the crowns of the first deciduous and permanent molars. This hypothesis yet remains speculative in the absence of $\delta^{34}S$ reference studies dedicated to maternal, placental and fetal tissues and to exclusively breastfed infants.

Although the hypothesis of a negative $\delta^{34}S$ offset associated with breastfeeding is less consistent with the observed $\delta^{34}S$ enrichment of the bone collagen of older perinates (>40 gestational weeks; an effect of sample size? Figure 57; Figure 58), it remains relevant when considering the low $\delta^{34}S$ values observed on the bone collagen a young infant from Vlasac aged at birth 2,5 months (VL 21(1) $\delta^{34}S$=6,9‰; Figure 57; Figure 63). Indeed, since the $\delta^{15}N$ and $\delta^{13}C$ values of this child are elevated in comparison with the adults from this site, ranging in the variability of the crowns of the first deciduous molars ($\delta^{15}N$=18,3‰ and $\delta^{13}C$=-19,2‰; Appendix A.III. 12-13), it is quite unlikely that this child was already entirely weaned at that age. It is therefore possible, whether that the mother of this child had a very terrestrial diet, that she came from another region (different $\delta^{34}S$ signature) or that his bone collagen became depleted in ^{34}S under some physiological effects of lactation-breastfeeding which would remain to be further explored on reference samples of breastfeeding mother and infant pairs. The hypothesis of a negative $\delta^{34}S$ breastfeeding offset is also compatible with the possibility of an earlier cessation of suckles for the children LV 84, AJ 15 and VL 51 whose teeth crowns do not exhibit such $\delta^{34}S$ depletion.

A greater $\delta^{34}S$ *breastfeeding offset in case of maternal marine protein consumption?*

While Webb et al. (2017b) indicated a systematic $\delta^{34}S$ depletion between the diet and the collagen of pigs under a controlled diet (−1.5 ± 0.8‰, n=), their results also show that the magnitude of this offset is greater when including marine proteins in the diet and significantly greater when the diet included more than 50% of marine-derived protein (average $\Delta^{34}S$ for 0% of marine protein intake: -0.7± 0.6‰ ;for 50% of marine protein intake: -1.2± 0.6‰, for 100% of marine protein intake: -2,7±0,6‰). Under the assumption of a negative breastfeeding offset, these results might indicate that the more the mother consumes marine-influenced resources, the greater could be the offset. In other words, it is possible that, when the mother eats more marine-influenced proteins, the tissues of the child may be comparatively more $\delta^{34}S$-depleted.

This last possibility would lead thus to a different interpretation of the values of some Early Neolithic children: namely, that HV 14, LV 92, AJ 14,and AJ 16 may exhibit greater $\delta^{34}S$ offsets (circa -1 to -2 ‰) because the diet of their mothers significantly included aquatic protein, and particularly anadromous fish (or dogs meat, themselves fed of fish). Indeed, it has been noticed that many Early Neolithic adults buried at the site of Hajdučka Vodenica and Lepenski Vir exhibit stable isotope values indicative of their consumption of aquatic resources (and/or dogs' meat, elevated in $\delta^{34}S$). The analyses of perinatal bone collagen indicated that expectant females were likely including marine-influenced proteins in their diet, and probably to a greater extent than the Late Mesolithic expectant females from Vlasac. This interpretation is also consistent with the elevated $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ of the crown of the first permanent molars of these for children (Appendix A.III. 12-14). Interestingly AJ 14 and AJ 16 display the highest $\delta^{13}C$ crown molar values amongst children from this site, also ranging within the highest value of the children discovered at Lepenski Vir and above the values documented for Mesolithic children. However, this association between marine-influenced protein and greater post-natal $\delta^{34}S$ depletion is not systematic: some children (such as LV 61, LV 56, AJ 1 Figure 63), exhibit higher first deciduous molar crown $\delta^{34}S$ values and yet display a smaller first permanent depletion $\delta^{34}S$ (respectively 0,2‰ and -0,5‰). This could be due related to the type of food provided to the toddler which may "cancel out" the magnitude of the trophic offset due to the maternal diet. In contrast, the children who does not show $\delta^{34}S$ first permanent molar crown depletion also exhibit the lowest $\delta^{34}S$ first deciduous molar crown values for the site of Lepenski Vir (LV 84: 10.7‰) of Vlasac (VL 51: 8.2‰) and Ajmana (AJ 15: 7.5‰) and range in the lower part of adult variability for each site, suggesting that their mothers rather had a more terrestrial (or including lower amount of marine-influenced proteins) diet than the other females of the groups.

Summary: early post-natal fluctuations in $\delta^{34}S$

To summarize, a **first deciduous to first permanent molar crown $\delta^{34}S$ depletion has been observed on the teeth of 11 children upon 14 individuals analyzed, originating from every chrono-cultural context considered** (average depletion: -0.7±0,5‰; Figure 62; Figure 63; 23). This depletion could be related to:

-1) a change in maternal dietary choices during lactation,

-2) differences in the origin of the proteins consumed by the mothers and supplied to the children (marine versus freshwater or terrestrial proteins),

-3) a physiological offset possibly caused by pregnancy or lactation and breastfeeding (as suggested in Tanz and Schmidt 2010; Webb et al. 2017b).

Indeed, several animal controlled-feeding experiments have documented small consumer-to-diet $\delta^{34}S$ offsets (on average +0.5±2.4‰, as reviewed by Nehlich et al. 2015). Besides, it has also been suggested that the diet-to-consumer $\delta^{34}S$ offset may vary according to the quality of the diet (Mc Cutchan et al. 2003; Richards et al. 2001), and to the amount of methionine consumed (Nehlich et al. 2015). Since the shift from the placental nutrition to post-birth diet should coincide with an important nutritive adaptation for the offspring and given that placental nutrients, breast-milk and supplementary food likely had different concentration in methionine, **it is possible that these dietary transitions - from pregnancy to weaning - may have influenced differently the $\delta^{34}S$ values of the crowns of the first deciduous (partially formed in utero and during breastfeeding) and first permanent molars (partially formed during breastfeeding and over the weaning process).** It is thus possible that the crowns of the first deciduous molars were rather $\delta^{34}S$ enriched during breastfeeding, implying that the crowns of the first permanent molars would have further been $\delta^{34}S$ depleted as an effect of solid food supplementation. Alternately, it is also possible that the crowns of the first deciduous molars were rather $\delta^{34}S$ enriched at the end of pregnancy or that the crowns of the first permanent molars were rather $\delta^{34}S$ depleted under the effect of breastfeeding. These different possibilities have interpretative implications when comparing the duration of the period of "predominantly breastfed" versus "predominant suckling". Yet, it should also be borne in mind that we are comparing signals that average broad time spans (e.g. the crown of the first permanent molar formed between two months post-partum and four years) and that nitrogen, carbon and sulfur containing amino-acids could be unevenly routed and metabolized according to food sources (as suggested by Webb et al. 2016, 2017a and b), which could hypothetically result in $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ responses at different rates into rapidly growing tissues (as recently suggested for $\delta^{13}C$ and $\delta^{15}N$ by Beaumont et al. 2018). Finally, it is possible that the differential consumption of terrestrial, freshwater or marine-influenced proteins by the lactating mothers and by the supplemented child may have influenced the magnitude of the $\delta^{34}S$ offset (as suggested by Webb et al. 2017b).

Only 3 children do not exhibit first deciduous to first permanent molar crown $\delta^{34}S$ depletion: AJ 15, VL 51 and LV 84 (Vlasac, Lepenski Vir and Ajmana; Late Mesolithic and Early Neolithic) and it has been noticed that the $\delta^{34}S$ signal of their first deciduous molar is always lower than the $\delta^{34}S$ signal of other children of the group. It is thus possible that the mothers of these children relied less on marine-influenced proteins than the mothers of other children and/or that these children reduced the frequency/duration of suckles earlier than the others (both possibilities being compatible with their $\delta^{13}C$ and $\delta^{15}N$ values). The child LV 84 exhibit enriched $\delta^{34}S$ values, which suggests that he was supplied with some solid food enriched in marine-influenced proteins in comparison with the maternal diet before most of the time of the formation of the crown of his first permanent molar. In contrast, some Early Neolithic children exhibit greater $\delta^{34}S$ depletion (LV 92, HV 14, AJ 14; AJ 16; Lepenski Vir, Hajdučka Vodenica and Ajmana) whether because the diet of their mother substantially includes the consumption of anadromous species or as an effect of the introduction of $\delta^{34}S$-depleted proteins in comparison with the maternal diet before most of the time of the formation of the crowns of their first permanent molars (both possibilities being compatible with their $\delta^{13}C$ and $\delta^{15}N$ values). The observation of changes in $\delta^{34}S$ values between tissues formed in utero and during the first years of life thus demonstrate the need to take into account the complex interactions between physiology and maternal and child dietary change when interpreting stable isotope values. Trying to unravel these intricacies with a multi-element approach now allows for more nuanced reconstructions of maternal dietary choices.

5.2.4.2. Maternal diet and weaning food during the Mesolithic period.

Maternal dietary variability

Concerning the Early Mesolithic period, the $\delta^{13}C$ and $\delta^{34}S$ stable isotope signals of the first deciduous molars of the children buried at Padina and of the bone of the young infant Pad 26 ranges in the adult variability[266]. It suggests that **the diet of pregnant and lactating females was probably quite similar as the diet of the other females of the group, likely a high trophic level diet, based on the consumption of meat and fish (notably stationary freshwater fish)** (Appendix A.III. 12-14; 19; A.IV.14-15). Yet, it can be observed that the $\delta^{15}N$ values of the first deciduous molar of the child Pad. 23 (19.7‰) and of the bone collagen of Pad 26 (18,4‰) is much higher than the tooth value of the child Pad 11 (16‰) suggesting probable differences in the amount of animal proteins - and particularly aquatic proteins - consumed by their mothers.

Concerning the Late Mesolithic period, the broad range of $\delta^{13}C$ and $\delta^{34}S$ stable isotope values of the tissues formed between the end of the pregnancy and the first months post-partum (first deciduous molars, young infants bone tissue) indicate some variability in maternal dietary choices (Figure 61**;** Figure 63; PCA. A.IV.14)**.** Indeed, the first deciduous molar crown of the child VL 18c and the bone tissue of the young infant VL 21(1) display low $\delta^{13}C$ (<-20‰) and $\delta^{34}S$ values (<8‰) ranging out -or in the lower part- of the adult variability (Figure 61; Figure 63). Their mothers probably included less marine-influenced proteins (anadromous and/or dogs' meat) than more adults of the group, exhibiting values closer to the Early Mesolithic variability (Appendix A.IV.14-15). The first deciduous molar crown of VL 51 also displays rather low $\delta^{34}S$ values (8.2‰) but associated with higher $\delta^{13}C$ (-19.4‰) perhaps in relation with the consumption of specific freshwater species. Yet, it has been previously suggested that the stable isotope values of the first deciduous molar of this child may be more influenced by solid food than the first deciduous molar of the other children and may thus no more be influenced by the signal

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[266] in the interpretations of children stable isotopes values, only the adults with available information about collagen preservation were included, as a purpose of comparison.

of the maternal diet. In contrast, the first deciduous molar crown of the child VL 53[267] exhibits higher $\delta^{13}C$ (>-19.5‰) and $\delta^{34}S$ values (>10‰), indicating the consumption of marine-influenced proteins (Figure 61; Figure 63). This child also exhibits the greatest breastfeeding offsets (first deciduous to permanent molar crowns $\delta^{15}N$ offset: +1.4‰; $\delta^{13}C$ offset: +0.7‰), which could be explained by a maternal consumption of aquatic resources. Indeed, the experimental study of Webb et al. (2016 and 2017a) evidenced greater $\delta^{15}N$ and $\delta^{13}C$ maternal diet to tissue, tissue to milk and milk to diet offsets in case of a diet based 100% of marine proteins.

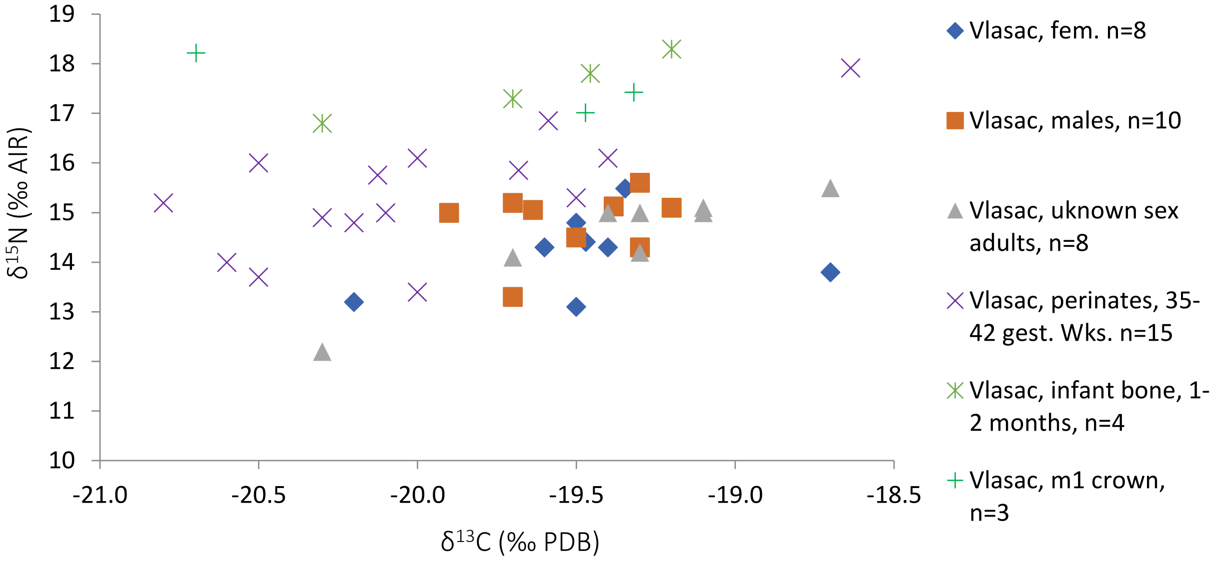

Figure 64: Bivariate plot of $\delta^{15}N$ and $\delta^{13}C$ for tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from Vlasac, Late Mesolithic.

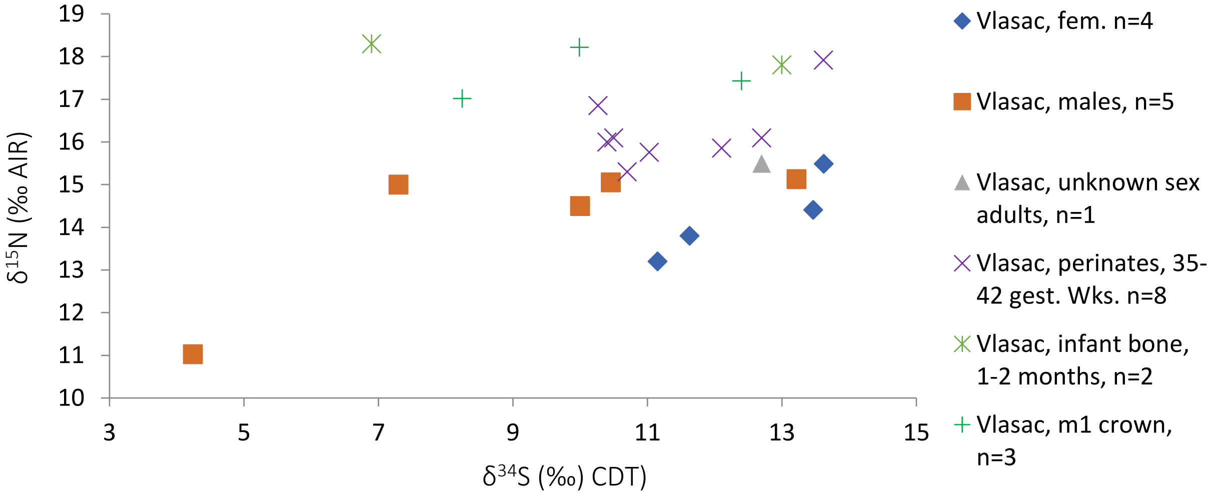

Figure 65: Bivariate plot of $\delta^{34}S$ and $\delta^{15}N$ for tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from Vlasac, Late Mesolithic.

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[267] This individual has not been radiocarbon dated and his stable isotope values range within the variability of Transformation/Early Neolithic children. Considering that the most recent excavations at Vlasac have evidenced the continuity in the occupation of the site during the Transformation and Early-Middle Neolithic phase with associated burials (Borić et al. 2008, 2014), the possibility that this child might rather be assigned to the later phase cannot be disregarded.

We previously noticed that the $\delta^{13}C$ values of perinate bone collagen (formed in utero) are significantly lower than the values of adult female bone collagen, which could be interpreted as the indication that some Late Mesolithic expectant females may have been consuming $\delta^{13}C$-depleted resources in comparison with non-expectant females. The observation of lower $\delta^{13}C$ values for the bone of the infant VL 21 and for the molar crowns of the children VL 18c and VL 18c(2) and of lower $\delta^{34}S$ values for the molar crowns of most children (VL 21, 18c, 18c(2) and 64b) in comparison with adult values also suggests that some Late Mesolithic mothers were favoring the consumption of depleted $\delta^{13}C$ and $\delta^{34}S$ resources, at least during the time of their pregnancy and lactation Figure 64; Figure 65; Appendix A.IV.13-14; A.IV.16). Although it cannot be excluded that analyzed adults might not be representative of the local variability (Late Mesolithic adults n $\delta^{13}C$ = 15; n $\delta^{34}S$=9), it is possible that some females consumed less marine-influenced proteins, either in relation with what they perceived as healthy to eat while they were pregnant and lactating or because of some specific socio-cultural norms. The taboos toward the consumption of protein and fat rich resources during pregnancy, widespread amongst many hunter-gatherers societies, also often applied to the period of lactation and can be related to the symbolic values assigned to the maternal milk and/or to considerations about its nutritional and health characteristics (Spielmann 1989, Meyer-Rochow 2009, eHRAF 2010). These dietary specificities could also result from the particular position of pregnant females and mothers in the Late Mesolithic society, perhaps because of a particular system of labor division.

Weaning food: mixed terrestrial and aquatic resources

Concerning the type of weaning proteins supplemented to the Mesolithic children, it can be noticed that bone and teeth $\delta^{13}C$ population trend lines broadly follow the pattern of the $\delta^{15}N$ trend line, but remain elevated longer and display less variation, which may indicate the use of high trophic level resources (Figure 61; Figure 62; Appendix AIII.17).

Concerning the Early Mesolithic period, the $\delta^{13}C$ value of the growing root of the analyzed teeth of Pad 23 is similar as the $\delta^{13}C$ value of the crown of his first deciduous molars; the bone value of Pad 11 (no collagen from the growing edge of a root) appears just slightly $\delta^{13}C$ depleted in comparison with his first permanent molar crown (-0.3‰); this pattern **suggests that they were probably supplemented with proteins quite similar as in the diet of their mothers, likely of high trophic level**. Since their $\delta^{34}S$ values remain quite low, it is possible that these children were mostly supplemented with proteins from meat or from freshwater fish, probably jointly with C_3 plants (Appendix A.IV.14-15). Yet, as previously suggested (cf part 4.2.2), it is possible that the $\delta^{34}S$ values of anadromous fish may have been lower during the Early Mesolithic period than during the Late Mesolithic period; in this case, one cannot disregard the possible inclusion of marine-influenced proteins in the weaning mush of Early Mesolithic children. Indeed, the bone value of the child Pad 11 (aged at death 4.5-7 years old) appears slightly elevated in ^{34}S in comparison with the value of his first permanent molar crown (+1.1‰ in comparison with his first permanent molar crown and +0.3‰ in comparison with his first deciduous molar crown), which might indicate that he was perhaps consuming some food slightly higher in $\delta^{34}S$ than his mother.

Concerning the Late Mesolithic period, the longitudinal $\delta^{13}C$ and $\delta^{34}S$ values indicate that most children were probably consuming mixed terrestrial and aquatic resources, either with a similar signal as the resources consumed by their mothers (e.g. VL 64b, VL 51?), or slightly depleted in $\delta^{13}C$ (VL 64a) or in $\delta^{34}S$ (VL 18c) (Figure 61; Figure 63; Appendix A.III.19; A.III. 23; PCA A.IV.14-15). The growing root of the analyzed tooth of VL 18c(2) is slightly enriched in ^{13}C in comparison with the crown of his first permanent molar which displays quite low $\delta^{13}C$ (similar as VL 18c), suggesting that he was consuming either higher trophic level resources or more marine-influenced proteins than his mother. Despite these slight differences, it can be noticed that the $\delta^{34}S$ values of all these children range in the lower part of the adult variability. Hence, as suggested for their mothers, these children were mostly consuming less marine-influenced proteins than analyzed adults, which could be related to their strategy for food acquisition, caring mothers and children being certainly, with the oldest, the most sedentary members of the group. Only the teeth and bone $\delta^{13}C$ and $\delta^{34}S$ values of one child, VL 53, contrastingly range in the high part of the adult variability. This child, as well as his mother, was consuming more marine-influenced proteins than the other analyzed children and their mothers, which could relate to a particular status, an origin amongst a different foraging community or at a different geographical location; it is also possible that they may have not been contemporaries with the other Late Mesolithic children analyzed.

5.2.4.3. Maternal diet and weaning food: children buried in the Inner Gorges during the Transformation and Neolithic period

Maternal diet, an emphasis on aquatic resources

The stable isotope values of the crowns of the first deciduous molars of the children buried at Lepenski Vir and at Hajdučka Vodenica during the period of Transformation/Early Neolithic indicate that some lactating females substantially consumed aquatic proteins (LV 92, LV 61, HV 14; LV 87: $\delta^{15}N$ values >18‰, $\delta^{13}C$ >-19.8‰ and $\delta^{34}S$>12.5‰; Figure 60; Figure 61; Appendix A.III.12-15; A.III.19). These results confirm the stable isotope difference noticed between the perinatal bone collagen of Late Mesolithic and Transformational-Early Neolithic children in terms of $\delta^{13}C$ and $\delta^{34}S$ values (Figure 64; Figure 65; Figure 66; Figure 67), suggesting that the Early Neolithic mothers of the children buried at Lepenski Vir were consuming more species of anadromous fish (and/or dogs meat) than the Late Mesolithic females. Although their $\delta^{13}C$ values remain within the variability of adult bone collagen, the $\delta^{34}S$ values of crowns of the first deciduous teeth of LV 92, LV 61, HV 14 exceed the adult $\delta^{34}S$ variability (respective values of 15‰, 15.3‰ and 13.3‰), suggesting that the mothers of these children may even have consumed more marine-influenced proteins than the other females of the group (a specific pregnancy-breastfeeding diet?). Likewise, we previously hypothesized that greater first permanent molar $\delta^{34}S$ depletion could be associated with a maternal consumption of anadromous fish and it has been noticed that two of the three individuals who exhibit the greatest depletions have been discovered on the sites Lepenski Vir and Hajdučka Vodenica ($\delta^{34}S$ depletion >1‰ between deciduous and permanent molars of the children LV 92, HV 14). The mothers of some of these children may have been consuming less aquatic resources, or different freshwater species considering the lower $\delta^{15}N$ and $\delta^{34}S$ values of the first deciduous molar crown of the child LV 84 (respectively 16.3‰ and 10.7‰; more terrestrial resources?) and $\delta^{13}C$ value of the child LV 87 (-19.8‰; different freshwater species?).

Concerning the Early-Middle Neolithic period (post 6 ky BC),the stable isotope values of the first deciduous molar crowns of LV 56 and LV 71 as well as the bone value of the infant LV 83b (aged at death 1-2 months) range in the $\delta^{13}C$ variability of the tissues of analyzed Transformational-Early Neolithic children but are slightly lower in $\delta^{15}N$ and $\delta^{34}S$ ($\delta^{13}C$ range: -19.3- -18.3‰; $\delta^{15}N$ range: 14.6-16.2‰; $\delta^{34}S$: 10-12‰; Figure 60; Figure 61; Figure 63). Given that the Transformational-Early Neolithic child LV 84 also displays similarly slightly lower $\delta^{15}N$ and $\delta^{34}S$ values and considering that these children have not been ^{14}C-dated but assigned according to contextual information, it is possible that they might all be contemporaries and perhaps all dated to the Early-Middle Neolithic period. Indeed, the lower $\delta^{34}S$ values of Early-Middle Neolithic individuals in comparison with the individuals dated to the period of Transformation was also noticed for most adults buried at Lepenski Vir and should be interpreted cautiously since they might be rather related to some ecological factors (lowering of the $\delta^{34}S$ values of the Black Sea - Danube basin?) than to behavioral differences. Yet, their lower $\delta^{15}N$ signals suggest that they may have been consuming slightly fewer aquatic resources than the mothers of LV 92 and LV 61, or perhaps included different aquatic species in their diet (high first deciduous molar crown $\delta^{13}C$ value of LV 56: -18.3‰). As previously noticed, the crown of the first permanent molar of LV 84 is enriched in $\delta^{13}C$ (+0.4‰) and in δ^{34}S (+0.7‰) in comparison with the crown of his first deciduous molar, suggesting either that his mother started to favor the consumption of marine-influenced proteins during lactation or that this child was supplemented with marine-influenced proteins before most of the time of the formation of the crown of his first permanent molar.

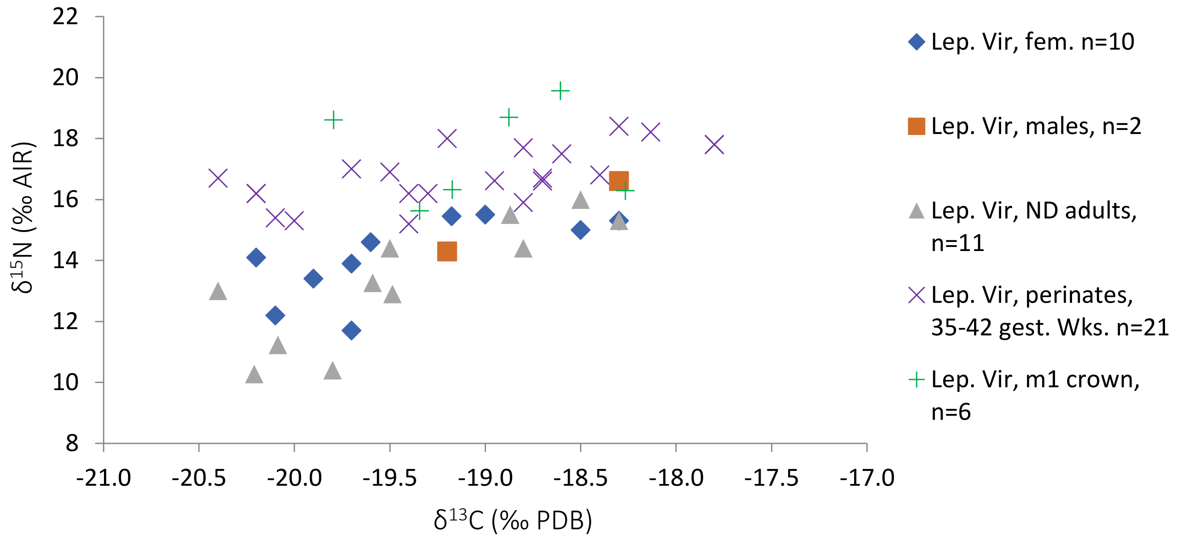

Figure 66: Bivariate plot of δ^{15}N and δ^{13}C for tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from Lep. Vir, Transform. and Neolithic.

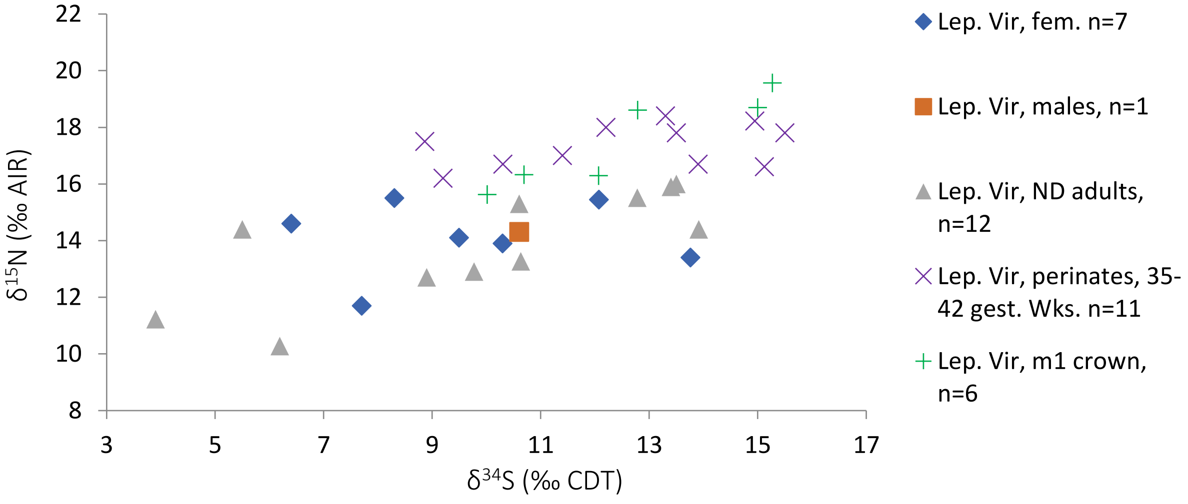

Figure 67: Bivariate plot of δ^{34}Sand δ^{15}Nfor tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from Lep. Vir, Transform. and Neolithic.

Weaning food: the use of marine-influenced proteins in weaning preparations

Concerning Transformational/Early Neolithic children, the δ^{13}C population teeth and bone trend lines appear increasing after the period when breastfeeding was the predominant source of nutrients, indicating the use of marine-influenced proteins in children weaning preparations (Figure 61; Figure 62; Appendix AIII.17). The individual scores in the PCA indicate that the children of the Early Neolithic mothers who included substantial amount of aquatic resources in their diet were also supplemented with high trophic level resources, and likely some marine-influenced proteins (Appendix A.IV. 14-15). While children feeding practices were more variable during the Late Mesolithic period, the Early Neolithic children analyzed were almost all fed with some preparations that included marine-influenced proteins. After the age of 3 years old, the $\delta^{13}C$ values of most children range in the high part of the adult variability, which indicates that they may have been consuming even higher amount of marine-influenced proteins than most adults of the groups (Appendix A.III. 13).

Intra-individual data have been collected for two children buried at the site of Hajdučka Vodenica, HV 14 and HV 21 (Figure 61; Figure 63; Appendix A.III. 19; A.III.23). The first permanent molar crown of HV 14 is $\delta^{13}C$ depleted (-0.5‰) in comparison with the signal of his first deciduous molar and this child exhibits a greater $\delta^{34}S$ depletion than most other children (-1‰). These offsets suggest that he may have firstly been supplemented with some preparations which either included more terrestrial resources than his mother's diet (e.g. C_3 plants and terrestrial mammals' meat and fats) or different aquatic resources (e.g. freshwater species). After most of the time of the formation of the crown of his first permanent molar, the $\delta^{13}C$ and $\delta^{34}S$ values of his tissues increase, probably because of an increased consumption of marine-influenced proteins. HV 21 (no first deciduous molar signal) is the only child dated to the period of Transformation who does not display increasing growing root $\delta^{13}C$ values (-0.1‰). Yet, his bone value appears slightly enriched in $\delta^{34}S$ in comparison with the crown of his first permanent molar (+0.6‰), suggesting that he may have been consuming $\delta^{34}S$-enriched food in comparison with his weaning preparation.

Concerning the Transformational-Early Neolithic phase of the site of Lepenski Vir, the children LV 92 and LV 61 exhibit the highest $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$, associated with stable $\delta^{13}C$ values from birth to death (no first deciduous molar to teeth root $\Delta^{13}C$ offsets). While the $\delta^{34}S$ signal of the first permanent molar crown of LV 61 remains stable, the $\delta^{34}S$ signal of the first permanent molar crown of LV 92 is depleted in comparison with the signal of the crown of his first deciduous molar (-1.6‰). It is hence possible that LV 92 may have been consuming similar amount of marine-influenced proteins as his mother and that LV 61 was perhaps still significantly relying on the consumption of breast-milk when he died (between 1-3.5 years old), and/or that he may have been jointly supplemented with some $\delta^{34}S$-depleted resources in comparison with the diet of his mother (terrestrial meat? stationary freshwater fish?). The crown of the first deciduous molar of the child LV 87 (no first permanent molar crown signal) displays lower $\delta^{13}C$ values than the crowns of other children, but the growing root of the analyzed tooth appears significantly enriched (+1.1‰). Although his mother may have been consuming different aquatic species or perhaps had a more terrestrial-aquatic mixed diet (elevated $\delta^{15}N$ values, 18.7‰), the weaning preparation of this child likely included more marine-influenced resources.

A group of children - LV 84, LV 85b and LV 89b - display lower $\delta^{15}N$ values than the others, associated with elevated $\delta^{13}C$ values. The longitudinal teeth data obtained for LV 84 (constant lowering of $\delta^{15}N$ values, associated with a constant increasing $\delta^{13}C$ and increasing first deciduous to first permanent molar crowns $\delta^{34}S$ values) suggest that he should have been supplemented before most of the time of the formation of the crown of his first permanent molar with some marine-influenced proteins. This pattern of declining $\delta^{15}N$ values and contrastingly increasing $\delta^{13}C$ values has also been associated with periods of recovery from biological stress and weigh gain (Mekota et al. 2006; Cherel et al 2006; Beaumont et al. 2016). It is hence possible that this child may have experienced a period of biological stress either in utero or during his first year of life, and that his mother tried to "mitigate" this stress by supplementing him with some weaning preparations containing nutrient dense aquatic resources (possible case also of the child LV 87?).

It is worth mentioning that these children - LV 84, LV 85b, and LV 89b - have been found buried quite close, in the western part of the site, and that all of them were found dislocated or as isolated skulls and/or mandibles. Within the same grave LV 89 were found the remains of the skull of the child LV 89b, of an adult buried in extended supine position (LV 89a) and parts of an aurochs skull (Stefanović 2016). As mentioned for the grave 7, the presence of the bucrane rather points to the Early Neolithic cultures of Western Anatolia and of the Southern Balkans than to the local

Mesolithic symbolic record. It could be hypothesized that some of these children with lower δ^{15}N signal might have been related to Early Neolithic migrants who adapted to the local feeding practice (increasing δ^{13}C values in the tissues of LV 84). Yet, the adult found in the grave LV 89 (individual LV 89a) displays elevated δ^{15}N and δ^{13}C values (δ^{15}N: 17‰; δ^{13}C: -18.5‰) and has been assigned to the haplogroup U5, typical amongst European Pre-Neolithic foragers (Hofmanová 2016). In contrast, the child LV 61, who has been discovered in the typical local Mesolithic extended supine position, parallel to the Danube, has been assigned to the maternal lineage H40 and to the paternal lineage R1, indicating a mixed ancestry (also confirmed by admixture models applied by Mathieson et al. 2018). The case of this child, who was predominantly breastfed during an important part of the time of the formation of the crown of his first permanent molar and who has been supplemented with some preparations which included marine-influenced proteins, illustrates the adaptation of some of the descendants of Early Neolithic locals to the local resource base and behavioral habits. Finally, one of the Transformational-Early Neolithic children who died older, circa 10-15 years old, exhibits significantly lower δ^{13}C and δ^{15}N than the other children of that age (LV 99; δ^{13}C:-20.3 and δ^{15}N=9.1), ranging within the variability of non-local individuals: he could be one of the first generation migrants who arrived in the Gorges circa 6ka BC (no strontium radiogenic signal available).

Concerning children assigned to the Early-Middle phase of Lepenski Vir, longitudinal data also indicate that supplementary food included marine-influenced proteins (cases of LV 56 and LV 71, perhaps associated with prolonged breastfeeding in the case of LV 71). The child LV 56 (aged at death 6-9.5 years old) has been identified as non-local according to the strontium radiogenic values of the crown of his first permanent incisive (Borić and Price, 2013) which formed quite at the same time as the crown of the first permanent molar (6 months-4 years; AlQahtani et al. 2010; AlQahtani et al. 2010). Interestingly, we previously observed that the crown of the first permanent molar of this individual is the most depleted in ^{15}N amongst all analyzed Mesolithic-Neolithic children buried in the Inner Gorges and also displays an important depletion in ^{13}C (respectively -1.5‰ and -0.4‰): he was likely predominantly weaned before most of the time of the formation of the crown of his first permanent molar and probably before arriving in the region of the Gorges. Although this pattern contrasts with most of the other children buried inside the Gorges, and looks rather similar as the weaning trend displayed by most Early Neolithic children buried in the Downstream Area, yet his stable isotope values also indicate that he and his mother were consuming marine-influenced resources, which suggests that he perhaps grew up somewhere close to the Danube river. In contrast, one child - LV 72 - displays significantly lower first permanent molar crown and bone collagen values for the isotopes of the three elements than all the other Early Neolithic children analyzed, ranging below the adult variability (no first deciduous molar crown and growing root signal; crown signal, δ^{13}C: -20.2‰, δ^{15}N: 12.4‰, δ^{34}S: 6.4‰). These lower stable isotopes values suggest the terrestrial nature of his mother diet and/or of his supplementary food. Since this child died between 1.5-3 years old, the dentine collagen of the crown of his first permanent molar (i.e. formed between 2 months and hypothetically 3 years old), may have averaged a paleo-dietary signal over a slightly younger age than the time span averaged by his bone collagen. His bone collagen appears rather δ^{13}C and δ^{15}N depleted in comparison with the signal of the crown (respectively -0.2‰ and -1.4‰), but rather enriched in δ^{34}S (+0.6‰) which could indicate that, although the mother of this child likely favored the consumption of terrestrial and lower trophic level resources than the mothers of all other Early Neolithic children analyzed, her child may have been supplemented with some resources enriched in δ^{34}S in comparison with her diet. Therefore, **it seems that, at the time of the intensification of the Neolithic way-of-life in the Gorges, some mothers still opted for aquatic proteins to feed their children in the Gorges (e.g. LV 56 and LV 71), while others may have favored terrestrial resources (LV 72?).**

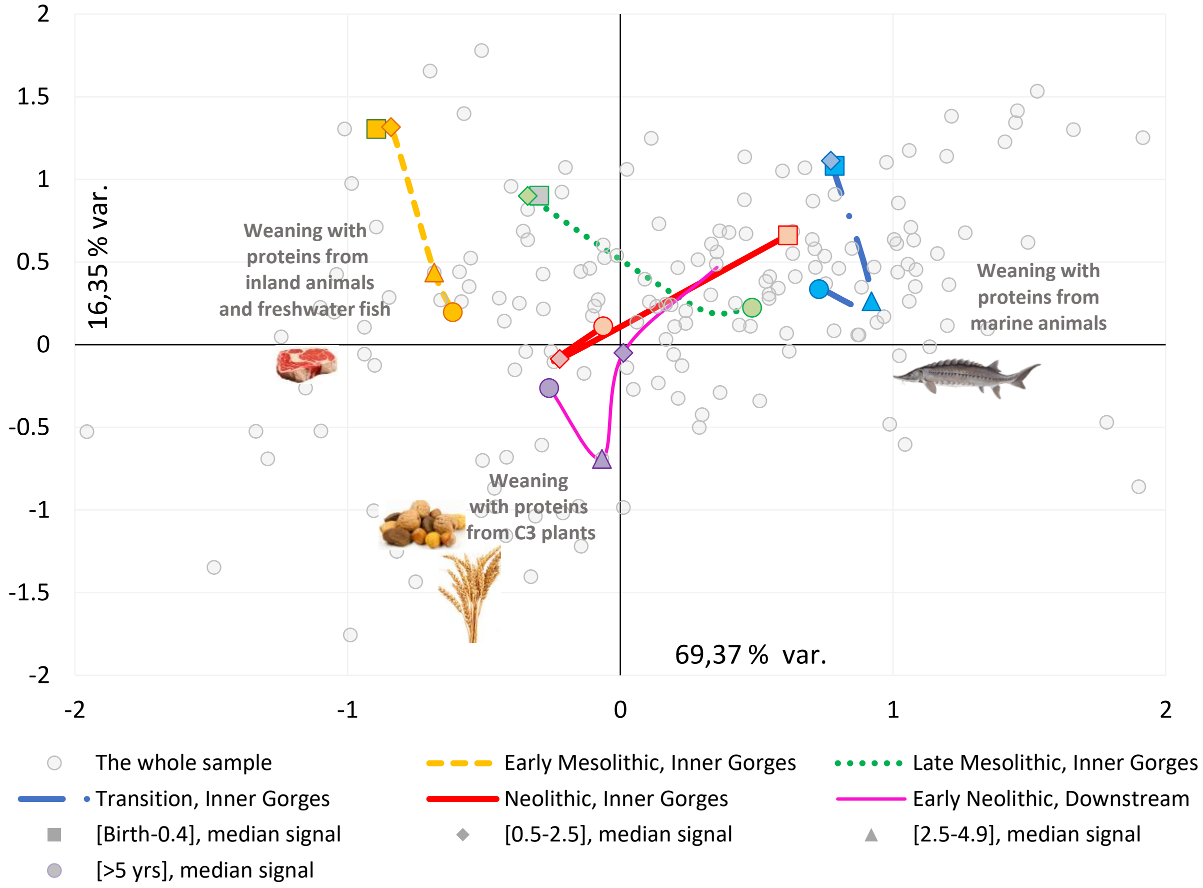

Figure 68: Bivariate plot for the two first axes of Principal Component Analysis of stable isotope signals extracted from the collagen protein. Median ages of individual scores for the stable isotope signals from the different tissues sampled are here highlighted

5.2.4.4. Maternal diet and weaning food: Early Neolithic children buried downstream

Maternal diet: a mixed terrestrial and aquatic diet

The crowns of the first deciduous molars of the children discovered at Ajmana display quite elevated δ^{15}N ratios (between 13‰ and 16‰; Figure 60; Appendix A.III.19). Although less elevated than the early-formed tissues of most Mesolithic and Early Neolithic children buried upstream, they range within the variability of the Early-Middle Neolithic children buried at Lepenski Vir (after 6 ky BC; LV 83b, LV 56, LV 71). These δ^{15}N ratios are associated with elevated δ^{13}C ratios (between -19.2‰ and -18.5‰), ranging within the variability of the Transformational and Early-Middle Neolithic children buried upstream, and with low to medium δ^{14}Sratios (between 7.5‰ and 12‰; Appendix A.III. 13-14; 19; PCA A.IV. 14-15). It can be noticed that the first deciduous molar crowns of two children, AJ 12 and AJ 15 exhibit lower δ^{15}N and δ^{34}S values (δ^{15}N= respectively 13.1‰ and 13.3‰; δ^{13}C=-19.2‰ and δ^{34}S: 7.5‰) than the first deciduous molar crowns of the children AJ 1, 8, 13,14,16 (average δ^{15}N=14.4±0.5‰; δ^{13}C=-18.9±0.2‰; and δ^{34}S: 10.5±1‰). **It is hence possible that the mothers of the children AJ 1, 8, 13, 14, 16 had a diet quite similar as the mothers of some of the Transformational-Early/Middle Neolithic individuals buried in the gorges (LV 83b, LV 71, LV 56, LV 84), i.e. a mixed terrestrial and aquatic diet, probably including less marine-influenced proteins than the mothers of the other Transformational Early Neolithic children LV 92, LV 61 and HV 14). The mothers of AJ 12 and AJ 15 may**

have been consuming more terrestrial and lower trophic level resources or less aquatic proteins (Appendix A.III. 12-14; 19; PCA A.IV.14-15).

Weaning food: supplementation with exclusively terrestrial and lower trophic level resources

Further signals are gradually and strongly depleted in the heavy isotope of the three elements, as reflected by the population trend-lines (first deciduous molar crown: δ^{13}C=-18,9±0,2‰ δ^{15}N=14,7±1,15‰; δ^{14}S=10±1,5‰; first permanent molar crown: δ^{13}C=-19,7±0,5‰; δ^{15}N=12,5±1,6‰; δ^{34}S=9±1,8‰; growing edge of teeth root: δ^{13}C=-19,8±0,4‰ δ^{15}N=11,3±0,6‰; adult bone collagen: δ^{13}C=-20±0,3‰; δ^{15}N=10,2±0,4‰; δ^{34}S=8±0,1‰ Figure 62; Appendix A.III.15-17; A.IV.5). The teeth of some children display greater δ^{15}N and δ^{13}C depletions than expected according to the model of a 2-3‰ δ^{15}N breastfeeding offset (first deciduous molar crown to analyzed root Δ^{15}N offset: AJ 13= -4.6‰; AJ 14= -4.4‰). Although these drops in δ^{15}N could hypothetically be related to physiological differences in the maternal-offspring pair or to the recovery from complicated pregnancies, the fact that they are associated with depletions in δ^{13}C and δ^{34}S rather support the possibility of a stable isotope difference between the food consumed by the mothers and the food supplemented to the children. It is indeed possible that the mothers of some children buried at the site of Ajmana (for instance the mothers of AJ 13 and AJ 14) may have consumed resources of higher trophic level than the food they used to wean their children. It can also be hypothesized that that the mothers of these children changed their diet during lactation toward the consumption of lower trophic level resources, which may have contributed to shift down the stable isotope values of their breastmilk and thus of the tissues of the sucker. In contrast, we previously noticed that the child AJ 15, whose first deciduous molar crown stable isotope values are lower than the values of the crown of the children AJ 1, 8, 13, 14, 16 also displays similar molar crowns δ^{34}S values (no deciduous to permanent molar crown offset), which can be due to the fact that his mother, who had a more terrestrial-oriented diet, may have supplemented him with a food quite similar as her own diet.

After 3-4 years old, children stable isotopes values range within the variability of the adults discovered at the site (Figure 60; Figure 61; Appendix A.III.12-15). Given the magnitude of the stable isotope offset between the crowns of the first deciduous molars of AJ 8, AJ 1, AJ 13 and AJ 14 AJ 16, and the highest stable isotope obtained for the adult buried at Ajmana (on average Δ^{15}N=-4.3‰; Δ^{13}C=-0.8‰; Δ^{34}S=-2‰), it can be assumed that the mothers of these children may have included slightly higher trophic level resources in their diet (more aquatic proteins?) than the females buried there. However, it should be pointed out that stable isotope values are only available for 6 adults buried at Ajmana[268] who therefore may not be representative of all adults of the community who buried their dead at Ajmana. Indeed, it can be recalled that 3 Early Neolithic adults discovered at the site of Velesnica, located about 20 km downstream, display slightly higher δ^{13}C (-19.3±0.1‰; Bonsall et al. 2015), one of them being associated with higher δ^{15}N values (on average 11±0.6‰; the individual 2A/2E displaying a δ^{15}N value of 11.7‰; Bonsall et al. 2015; Appendix A.II.14). Three children discovered at this site - aged at death between 3-11 years old - exhibit slightly lower δ^{15}N values than the adults (δ^{15}N= 10±0.1‰; δ^{13}C=-19.4±0.3‰) which could also either be due to the fact that they were weaned with lower trophic level supplementary food than the adult diet and/or to a specific interaction between physiology and the maternal and infant diet.

Particular cases: higher trophic level supplemented proteins, longer breastfeeding, physiological stress

Amongst the children buried at Ajmana, the important magnitude of the first permanent molar crowns δ^{15}N and δ^{13}C depletion of AJ 12, 14 and 15 (average Δ^{15}N:-1.7±0.3‰; Δ^{13}C:-0.7±0.2‰) suggests that these children have been supplemented before most of the time of the formation of that crown and probably with low trophic level and terrestrial resources.

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[268] This study, plus 2 additional adults analyzed by Borić (2011) for δ^{13}C and δ^{15}N and by Jovanović et al. (2018) for δ^{34}S, but for whom carbon and nitrogen atomic ratios were not available and thus who have not been included in this study. These two individuals, AJ 6 (δ^{13}C=-20‰, δ^{15}N=10.5‰, δ^{34}S=8.6‰) and AJ 7 (δ^{13}C= -20‰, δ^{15}N=10‰, δ^{34}S=8.5‰), range within the δ^{13}C and δ^{15}N variability of the 4 individuals included in this study but exhibit slightly higher δ^{34}S ratios (+0.7‰ and +0.8‰ in comparison with the average of the 4 individuals included here).

In contrast, the first permanent molar crown of the individual AJ 1 is less depleted in δ^{13}C (Δ^{13}C:-0.1‰; Δ^{15}N:-1.6‰), indicating that he may have been supplemented with some resources of higher trophic level than the other children. Yet, given that the first deciduous molar crown of this child also displays the highest δ^{15}N and δ^{14}S values (respectively 15.9‰ and 12‰), it is possible that the consumption of aquatic resources by his lactating mother may have contributed to maintained δ^{13}C elevated values in his tissues for a longer time.

The same case can be noticed for AJ 16 (no first permanent molar signal, but tooth root apex value formed between 0.75-2.6 years; Δ^{13}C:-0.8‰; Δ^{15}N:-0.1‰), who also display the highest first deciduous molar crown δ^{13}C signal (-18.4‰). We previously observed that his first deciduous molar crown to apex δ^{34}S depletion (-2‰) is greater than the first deciduous to first permanent molar crown δ^{34}S depletion of all other analyzed children, which could be due to the difference between the aquatic-oriented diet of his mother and the terrestrial origin of his supplementary food. Yet, it can be noticed that the δ^{34}S signal of his bone collagen is much higher than the δ^{34}S signal of the apex of his first deciduous molar and than the tissues of all other children buried downstream (bone δ^{34}S=13.5‰; bone to apex Δ^{34}S=+6.1‰); in contrast, it appears lower in δ^{13}C (bone δ^{13}C:-19.7‰; bone to apex Δ^{13}C =-1‰) and in δ^{15}N (bone δ^{15}N=12.7‰; bone to apex Δ^{15}N =-1.4‰). This is surprising considering the fact that this individual has been aged at death 1.5-4 years old and thus that his bone collagen signal should average a dietary signal formed over a time span in part similar to the analyzed apex of his first deciduous molar (formed circa 0.75-2.6 years old). In case the individual died older than 3 years, then it is possible that he may have consumed more marine-influenced food just before his death than during the time of the formation of the apex of his first deciduous molar. Considering the young age at death of this individual, it is possible that his mother may have decided to supply him with more aquatic proteins, perhaps as an important source of nutrients during a period of biological stress. δ^{13}C and δ^{15}N bone depleted values could then be explained by the fact that different nutrients and amino-acids may not be utilized and routed by the body at the same pace according to the type of food consumed, to particular metabolic situations and to the tissues analyzed (e.g. Beaumont et al. 2015; Beaumont and Montgomery 2016; Beaumont et al. 2018; King et al 2018b).

Finally, the child AJ 8 (no first permanent molar signal, but tooth root apex value formed between 0.75-2.6 years) displays δ^{13}C first deciduous molar crown to apex depletion (Δ^{13}C: -0.4‰), but no offset in δ^{15}N (-0.1‰). This pattern may either be explained by a slight interaction of breastfeeding with the physiological effect of a biological stress (starvation of pathology may increase δ^{15}N values; e.g. Reitsema, 2013) or by the consumption of different food resources with a lower δ^{13}C signal.

Different children feeding strategies concerning the Early Neolithic communities buried at Ajmana

Hence, the mothers of most children buried at Ajmana (AJ 1, 8, 13, 14, 16) probably had a mixed diet but some of them chose to supplement their children with some preparations which included substantially lower trophic level terrestrial resources (C_3-based gruels or mush, maybe with cereals? A.IV.14-15). The possibility that animal milk or dairies may have been used in these preparations cannot be disregarded. Indeed, although $\delta^{13}C_{coll}$ mostly reflects the protein part of the diet, it may be somewhat sensitive to energy as well (Ambrose and Norr 1993, Fernandez et al. 2014); considering that lipids are depleted in δ^{13}C in comparison with other macronutrients (Ambrose and Norr 1993), and that dairies are rich in lipids, it is possible that the introduction of some dairies may result in depleted δ^{13}C. Besides stable isotopes values of two suckling animals discovered in the Gorges, a wild boar and a young auroch range ca 11-13 ‰ for δ^{15}N and ca -20.5--21.5‰ for δ^{13}C, which is compatible with the stable isotope values of children from Ajmana. Yet, although the analysis of organic residues on pottery shreds from Early Neolithic sites of the Northern Balkans revealed that dairies were consumed in the region around 6 ky BC (Ethier et al. 2017), recent analyses of Early Neolithic vessels from sites of the Inner Gorges(Vlasac and Lepenski

Vir) and of the Downstream Area (Velesnica and Schela Cladovei) rather indicate that they were used to process fish (Cramp et al. 2018).

While the Early Neolithic children buried in the Inner Gorges were likely already consuming marine-influenced proteins before the age of 5 years (probably in a greater amount than most of the adults of the group), the Early Neolithic children buried at Ajmana were supplemented with lower trophic weaning food. It is possible that the mothers of some children buried at Ajmana perhaps chose to consume higher trophic level resources during their pregnancy, maybe to sustain the requirements in nutrients of their metabolic state. It can also be hypothesized that some of them spent more time in the Inner Gorges and/or at spots where fishing was favored. Indeed, based on the closeness observed in the biochemical signals of carbon, nitrogen, sulfur and strontium, we previously hypothesized some relatedness between some non-local individuals buried at Lepenski Vir and at Ajmana. Considering that these sites are only distant about 50 km and are both located along the Danube, the noticed differences concerning children breastfeeding and weaning practices may rather be interpreted in terms of socio-cultural habits than of resource availability. Interestingly, the AJ 15 has been identified as non-local based upon the strontium signal of the crown of his first deciduous incisive (formed before 6 months; AlQahtani et al. 2010; other children AJ 3, 12, 13, 14, 16 identified as locals by Borić and Price 2013); his tissues also displays the lowest stable isotopes values for the three elements. It could thus be hypothesized that a small number of individuals, perhaps originating from some Early Neolithic farming communities (e.g. the mother of AJ 15, the adult non-local AJ 7), may have influenced the dietary choices of some local females who were used to consume more aquatic resources, or perhaps took the responsibilities for raising their children (different allo-parenting model?).

5.2.4.5. Summary: maternal dietary choices and prehistoric weaning recipes

A particular diet for mothers and children during the Late Mesolithic?

In addition to assessing breastfeeding parameters, our effort to reconcile longitudinal and cross-sectional approach to children dietary transitions offers insight into the nature of the maternal and offspring diet, into changes and differences in the resources consumed by mothers and supplemented to the toddlers. Thereby, it has been noticed **that some of the Late Mesolithic mothers favored the consumption of δ^{13}C depleted resources** (for instance the mothers of VL 21(1), VL 18c) **and of δ^{34}S depleted resources** (for instance the mothers of VL 21(1), VL 18c and VL 51), which supports the hypothesis of a possible maternal-specific diet previously suggested by the analysis of perinatal-formed bone collagen (perhaps related to the early termination of some pregnancies or to some infants' death). However, it should be mentioned that not all mothers opted for the consumption of particular resources; some others were likely consuming substantial amount of marine-influenced proteins (for instance the mothers of VL 53).

Similarly, while the few Early Mesolithic children analyzed (Pad 11 and 23) should have been supplemented with resources quite similar as consumed by their mothers and by the other members of the groups, in contrast, **most of the analyzed Late Mesolithic children were supplemented with less marine-influenced proteins (or more mixed terrestrial-aquatic resources) than included the diet of most adults** (e.g. VL 18c, VL 51, VL 64a and 64b). Only one child (VL 53) was supplemented with some weaning preparations which included substantially more marine-influenced proteins, ranging in the high part of adult stable isotope variability for the three elements (particular position in the society? native from a different location or belonging to a different social group? issue of synchronicity of the sample?). In any cases, the particular diet inferred for Late Mesolithic mothers and children could be due to the existence of some food taboos, perhaps in relation with what was then perceived as healthy for the growth of the offspring, or with the nutritional, health or symbolic values that were assigned to the maternal milk. These dietary specificities could also result from the status of expectant females, mothers and children in the Late

Mesolithic society, perhaps because of the local system of distribution of tasks and of strategies for food acquisition.

A great emphasis on marine-influenced proteins for Transformational/Early Neolithic mothers and children

The longitudinal stable isotope values of the children buried at Lepenski Vir and at Hajdučka Vodenica during the period of Transformation/Early Neolithic indicate that most lactating females were substantially consuming marine-influenced proteins, sometimes in even greater amount than most non-expectant females (e.g. LV 61 and 92), **and were also supplementing their children with marine-influenced proteins, sometimes in even greater amount than in their own diet** (e.g. LV 84, 87, HV 14). This pattern contrasts with the infant feeding practices inferred for the Mesolithic period, and seems in accordance with the role of marine-influenced proteins in the diet of Early Neolithic individuals buried in the Inner Gorges. It might reflect some deeper change concerning the organization of foragers' society and the place of "vulnerable" members of the group, perhaps related to the differential availability of some species (greater availability of some long-distance migratory fish? development of new stocking/cooking techniques) and to the values assigned to these animals.

A group of children, found dislocated, display slightly lower δ^{15}N values (LV 84, 85b, 89b); one of them was discovered in a grave which also included parts of an aurochs skull (LV 89), rather pointing to the Southern Balkans and Anatolian Neolithic symbolic record than to the local Late Mesolithic practices. Hence, it may be hypothesized that these children could be the descendants of migrants who adapted to the local practices. The only child of the sample analyzed for aDNA (LV 61) had a mixed ancestry (H mt-haplogroup, and R1 Y-haplogroup, greater contribution of "Neolithic-like" genetic contribution according to the ADMIXTURE Analysis, Mathieson et al. 2018), and displays elevated longitudinal stable isotopes values, suggesting that his mother favored the consumption and the use of aquatic resource for his supplementation. In contrast, the bone value of a child who died older (LV 99 aged at death circa 8-15 years old) exhibits significantly lower stable isotope values than all children analyzed, perhaps indicative of his non-local origin.

The stable isotope values collected on the teeth of some children assigned to the Early-Middle Neolithic phase of occupation of the site of Lepenski Vir (post 6 ky BC) indicate **a certain variability in the breastfeeding and weaning choices of Neolithic parents, probable consequence of the interactions between the descendants of local fishermen and successive generations of migrants** who arrived in the region with different feeding habits. The child LV 56, identified as non-local, was predominantly weaned before most of the time of the formation of the crown of his first permanent molar. His stable and radiogenic isotope signals also indicate that he - and his mother - were consuming marine-influenced resources before he arrived in the region of the Gorges which suggests that he perhaps grew up somewhere close to the Danube river. The stable isotope values of other analyzed children either indicate their supplementation with marine-influenced proteins, perhaps associated with a longer reliance on breastmilk (e.g. LV 71), or, in contrast, with terrestrial resources (e.g. LV 72).

Farmer-like mushes for the Early Neolithic children buried downstream?

While most of the Transformational-Early Neolithic children buried in the Inner Gorges (6.2-5.9 ky BC) were already consuming marine-influenced proteins before the age 5 years, the Early Neolithic children buried downstream at the site of Ajmana (circa 6 ky BC) were mostly supplemented with terrestrial resources, sometimes of lower trophic level than the diet of their mothers. Based upon the stable isotope values of the crowns of their first deciduous molars, it is indeed possible to suggest that the mothers of some of the children recovered in the "multiple burial" of Ajmana (AJ 1, 8, 13, 14, 16) had a diet quite similar as the diet of the mothers of some of the Transformational/Early-Middle Neolithic children buried in the Inner Gorges (LV 83b, LV 71, LV 56, LV 84; mixed terrestrial and aquatic diet). In contrast, the teeth of two other children discovered in the same context (AJ 12 and AJ 15) display lower values for the three elements, suggesting that their mothers had a more terrestrial diet or favored the consumption of lower trophic level resources. In view of the low stable isotope values of the adults discovered in the grave, it is possible that they may not be entirely representative of the diet of all members of the community who used the grave. It can also be hypothesized that some mothers perhaps chose to include more aquatic resources in their diet during their pregnancy, maybe to sustain the requirements in nutrients of their metabolic state in a context where most members of the community were favoring the consumption of lower trophic level resources.

Although the weaning preparations of some children (e.g. AJ 1; AJ 16) may have included more aquatic resources than concerning the other toddlers (e.g. AJ 15), most of them were probably supplemented with proteins from terrestrial herbivores and C_3 plants (cereals?; milk? e.g. AJ 12; 13; 14; 15). Interestingly, the tissues of AJ 15, the only child from the assemblage of Ajmana which has been identified as non-local[269], also display the lowest stable isotopes values which might reflect the behavioral influence of some migrants on feeding and parenting practices of the other users of this grave.

5.3. Post-weaning stable isotope fluctuations, physiological effects.

5.3.1. A systematic bone-to-teeth stable isotope offset

A post-weaning pattern: lower bone $\delta^{13}C$ and $\delta^{15}N$ values in comparison with coterminous dentine

Concerning post-breastfeeding stable isotope values, it has been observed that the $\delta^{13}C$ and $\delta^{34}S$ longitudinal teeth values of most Late Mesolithic children range in the lower part of adult variability, which could be related to the strategies of food acquisition of caring mothers and young children. The $\delta^{34}S$ bone values of the children who died around 6-10 years old also indicate that they may have consumed less marine-influenced proteins than the rest of the group (VL 18c, VL 51, VL 64b; Appendix A.III.14). Although this pattern could be related to the sample size (10 adults and 8 children analyzed for $\delta^{34}S$), it is also possible that childhood was considered as a particular social stage in the Late Mesolithic society. During the periods of Transformation - Early/Middle Neolithic, the $\delta^{15}N$ and $\delta^{13}C$ bone values of three children who died between 9 and 17 years old (LV 27c, LV11 and LV 43; Appendix A.III.12 and 13) also range in the higher part of the adult variability, indicating that they have been consuming particularly high trophic level resources; in contrast, one Transformational individual -LV 99- aged at death 8-15 years old, display lower $\delta^{15}N$ and $\delta^{13}C$ values than the adults, which might be associated with the lower stable isotope values of non-locals who arrived in the Gorges during this period. Concerning the Early Neolithic children discovered on the site of Ajmana, downstream, bone stable isotope values of two teenagers range within the adult variability (AJ 13 and AJ 3; ibidem). Interestingly, when one finally compares children bone stable isotope values with latest-formed dentine signal analyzed (tooth root signal), a particular trend appears: **for children who died between 3 and 10 years old, bone collagen $\delta^{13}C$ and $\delta^{15}N$ values are almost always than dentine collagen values[270], regardless of the chrono-cultural context considered** (Figure 69).

In the whole sample, the $\delta^{15}N$ bone values of 17/20 children and the $\delta^{13}C$ bone values of 15/20 children appear depleted in the heavy isotope in comparison with the apex of the analyzed tooth ($\Delta^{15}N$ and $\Delta^{13}C \geqslant 0.2‰$); the $\delta^{15}N$ bone value is slightly higher than the tooth value only in two cases (in both cases $\Delta^{15}N=2‰$), while the bone $\delta^{13}C$ value is never higher than the tooth value (Figure 69; Appendix A.III.18-19; 22). In fact, the stable isotope values of the growing edge of a tooth root should reflect the nutritional status of a child during the last months of his life and the stable isotope signals of bone collagen, partially formed contemporaneously with the tooth growing

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[269] strontium signal of the crown of the first deciduous incisive, formed before 6 months (AlQahtani et al. 2010)

[270] $\delta^{34}S$ has not be analyzed on growing edge of teeth since minimum amount of collagen was extracted in order to obtain a dietary signal the closest possible to the death of a child; therefore, the amount of collagen extracted only allowed for one mass spectrometer measurement and the isotopes of carbon and nitrogen were always favored.

root, should average stable isotope signal formed upon a longer time before his death during childhood. When considering all cases of co-forming bone and teeth tissues, an average difference of -0.3±0.2‰ can be noticed concerning δ^{13}C, and of -0.6±0.4‰ concerning δ^{15}N (n=16; average and standard deviation values). According to our previous interpretations of longitudinally formed stable isotope dentine values, apart from LV 92 and LV 72 (aged-at-death around 1-3.5 years old), all children were already mostly consuming solid food during the time of the formation of the analyzed growing roots.

Although the average δ^{13}C bone-to-tooth root offsets are quite similar for the different chrono-cultural context compared, Mesolithic children display smaller δ^{15}N bone-to-tooth root offsets (Δ^{15}N=-0.3±0.3‰; Δ^{13}C=-0.3±0.2‰; n=5) than the Transformational-Neolithic children buried in the Inner Gorges (Δ^{15}N=-0.7±0.5‰; Δ^{13}C=-0.3±0.2‰; n=8) and than the Early Neolithic children buried downstream (Δ^{15}N=-0.7±0.1‰; Δ^{13}C=-0.2±0.1‰; n=3). It can also be noticed that the bone-to-teeth offsets of the children buried in the Inner Gorges during the Transformational-Neolithic periods are the most variable. The children who display the greatest δ^{15}N offsets (⩾0.8‰) can be identified as AJ 15 (Early Neo.), HV 14 and LV 84 (Trans.) and LV 72 (Early-Middle Neo.); we previously inferred for these children supplementation whether with terrestrial protein (AJ 15; LV 72) or marine-influenced proteins (HV 14 and LV 84) before most of the time of formation of the crown of their first permanent molar. The children who display the greatest δ^{13}C offsets (⩾0.5‰) can be identified as LV 61 and LV 87 (Trans.), Pad. 11 and VL 18c (Meso.); we previously inferred for these children whether a long reliance on breast milk during most of the time of the formation of the first permanent molar crown and/or a supplementation with aquatic proteins (LV 61, Pad 11, LV 87?), or an earlier supplementation with more mixed terrestrial/aquatic resources (VL 18c). The individuals who likely relied during a longer time on the consumption of breast-milk protein exhibit a smaller δ^{15}N offset (Δ^{15}N=-0.1±0.3‰; Δ^{13}C=-0.4±0.1‰; n=4), than those who have been supplemented earlier with solid food (Δ^{15}N=-0.8±0.3‰; Δ^{13}C=-0.3±0.2‰; n=7). Concerning sulfur, data collected for the co-formed tissues of two children indicate a contrasting pattern: the first permanent molar crown of the child LV 72 is lower in δ^{34}S than his bone value (-0.8‰), while the first permanent molar crown of the child LV 92 is higher in δ^{34}S than his bone value (+1‰).

A pattern which can be observed on multiple studies, regardless of the chrono-cultural context

Apart from the Danube Gorges prehistoric sample, this bone-to-teeth stable isotope offset can been observed on many other osteo-archaeological assemblages that included contemporaneously formed bone and teeth tissues (Richards et al. 2002; Fuller et al. 2003; Herrscher 2003, 2013, Kaupová et al. 2014; Beaumont et al. 2015; 2018; King et al. 2018b)[271]. Before 4-5 years, stable isotopes difference between bone and teeth might, in theory, be associated with the different timing of formation of the tissues and thus with the differential proportion of proteins from breast-milk utilized for the synthesis of the tissue (Herrscher 2003, 2013), yet, several cases this offset has been noticed on δ^{15}N and sometimes δ^{13}C values of children aged 4-5 to 10 years (e.g. Richards et al. 2002; Fuller et al. 2003; Herrscher 2003). It can be noticed that, for several aforementioned samples, the use of plant-based weaning preparation has been suggested (Richards et al. 2002; Fuller et al. 2003; Beaumont et al. 2015, 2018; King et al. 2018b). Besides, in some cases,

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[271] Almost three-quarters of analyzed children from the cemetery of Saint Laurent de Grenoble (Middle-Age to Modern time, France), indicate higher growing tooth root δ^{15}N values in comparison with the bone (for Δ^{15}N ⩾0.2‰), including children who died between 4-5 and 10 years old (Herrscher 2003, 2013). Similarly, more than two-thirds of the children analyzed by Kaupová et al. (2014) from Early Medieval Central European rural and urban sites display higher δ^{15}N teeth root values in comparison with bone (Δ^{15}N ⩾0.2‰), including a few children who died around 4/6 years old. The data from Richards et al. (2002) and Fuller et al. (2003) for the Middle Age site of Wharram Percy (England) also indicate systematically higher dentine values in comparison with bone. The dentine δ^{15}N value appears higher than the bone value for 9/10 children (aged above 3 years old) for whom these tissues were formed contemporaneously and 10/10 children jointly exhibit higher dentine δ^{13}C values; it can also be observed that the greatest bone-to-teeth depletions were experienced between 5 and 7.5 years old. Concerning the XIXth century cemeteries of Lukin Street (London) and of Kilkeny Union Workhouse (Ireland), Beaumont et al. (2015) reported that 15/19 individuals exhibit higher dentine δ^{15}N values than bone and 11/19 display higher dentine δ^{13}C values than bone; most children being aged at death under 3.5 years. 16/16 children discovered at the Anglo-Saxon site of Round Furnels exhibit higher dentine δ^{15}N values in comparison with bone while 6/16 display higher dentine δ^{13}C values (Beaumont et al. 2018). This offset is also documented in the data from King et al. (2018) concerning the δ^{15}N and δ^{13}C values of the co-forming bone and dentine tissues of 4/5 analyzed children from the Atacama desert (Agricultural to Inca period; children aged at death below 3.5 years old; King et al. 2018).

it has been suggested that some analyzed children should have been subjected to an elevated level of nutritional stress whether associated with starvation (great Irish Famine; Beaumont et al. 2015) or harsh environmental conditions (Atacama desert; King et al. 2018). In contrast, only some of the individuals analyzed by Howcroft et al. (2012), from prehistoric samples of Scandinavia (Early Middle Neolithic and Iron Age necropolis), exhibit higher dentine δ^{15}N and δ^{13}C values and it has been suggested that the subsistence of these populations were substantially oriented towards the hunt of marine mammals. Similarly, the datasets from late Medieval Fishergate House site (UK) also reported more cases of lower than higher dentine to bone δ^{15}N and δ^{13}C values for children whose weaning diet may have included higher trophic resources, such as fish and pork meat[272] (Burt et al. 2015). **Noticing the same pattern on the tissues of post-weaned children from such a variety of historical and geographical backgrounds, suggests that the bone-dentine offset must be caused by physiological effects, perhaps in interaction with diet (type of protein consumed?).**

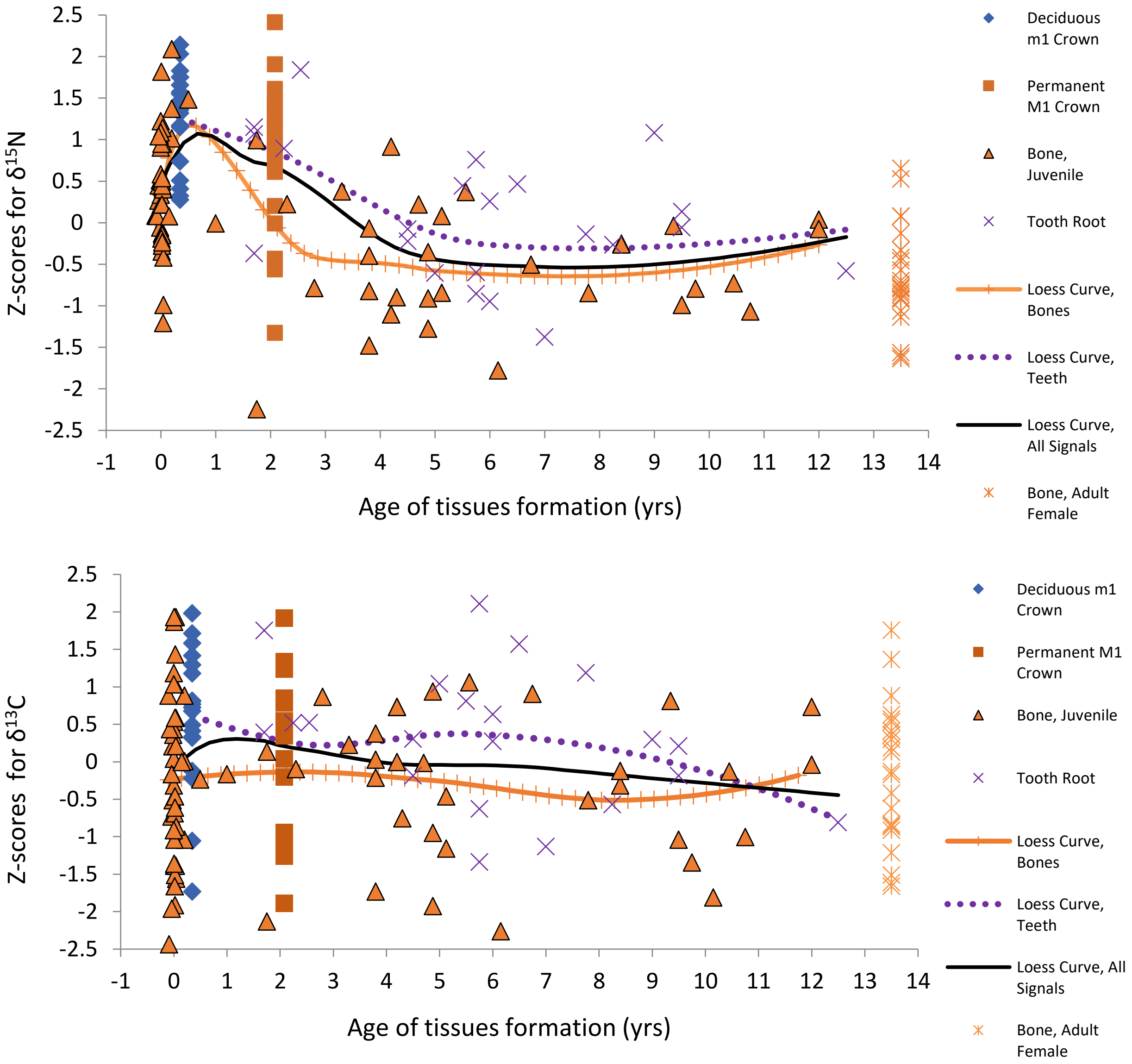

Figure 69: Bivariate plots of δ^{15}N - δ^{13}C signals and the estimated age at formation of all analyzed tissues from birth to 13 years old (cf. caption details: Appendix A.III)

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[272] However, in the dataset of Burt et al., it can be noticed that all individuals who exhibit higher bone δ^{15}N values in comparison with teeth dentine were rejected "has not reliable" for δ^{13}C because of insufficient weigh "to generate dependable carbon results" (Burt et al. 2015: 279 and 281).

5.3.2. Explaining the offset: physiological effects of stress and growth

Bone – dentine collagen type differences?

As indicated by Beaumont et al. (2018:536), "there is no evidence to suggest that there is any difference in the proteins in type 1 collagen between dentine and bone and so these values must be reflecting the δ^{13}C and δ^{15}N in new tissue laid down by dentinoblasts or osteoblasts". In terms of laboratory treatment, Beaumont et al. (2018) mentioned the possible effect on the stable isotope values of filtration of the bone collagen but not the dentine; yet, both bone and dentine samples were filtrated in the collagen extraction protocols used in this study, which only differ in the demineralization stage (bone demineralized during 20 min with a HCl solution (1 M); teeth soaked entirely into a HCl solution (0.5 M) during several days at 5°C); similarly, Fuller et al. (2003) only mentioned a longer time of demineralization for teeth than bone because of the enamel caps. In fact, **a possible explanation to the dentine-bone collagen offset could be related to the differential pattern of bone and teeth growth (Beaumont et al. 2015, 2018).** Indeed, it has been suggested that bone formation may be arrested or slowed down in situations of high nutritional stress while teeth would continue to grow at the same rate regardless of nutritional status (Ambrose 1993; Hatch 2012; Elamin and Liversidge 2013; Beaumont et al. 2015, 2018). Human growth is saltatory, encompassing episodes of growth saltation and periods of stasis mediated by environmental and genetic factors; growth delay caused by nutritional stress can later be caught-up by episodes of growth spurts (Lampl 2012). **Hence, teeth stable isotope values might be more influenced by the metabolism of nutrients during situations of high nutritional stress than bone, which could, hypothetically, be more influenced by the metabolism of nutrients during periods of growth spurts.**

δ^{13}C and δ^{15}N response to particular metabolic situations – catabolism and anabolism states

Events of biological stress (catabolic state, negative nitrogen/protein balance), such as mal-nutrition, under-nutrition, starvation or infectious diseases, have been associated with elevated δ^{15}N values (e.g. Hobson and Clark 1992; Hobson et al. 1993; White and Armelagos, 1997; Doucett et al. 1999; Katzenberg and Lovell 1999; Cherel et al. 2005; Haubert et al. 2005; Fuller et al. 2005; Mekota et al. 2006; Gay-Siesseger et al. 2007; Deschner et al. 2012; Neuberger et al. 2013; Robertson et al. 2014; Olsen et al. 2014; D'ortenzio et al. 2015; Hertz et al 2015; Lehn et al. 2015; Doi et al. 2017). When less nitrogen (proteins) is ingested than required for tissues maintenance and synthesis, it is assumed that the body catabolizes its own tissues, causing an additional fractionation of nitrogen stable isotopes. The nature and the duration of the experienced nutritional stress should influence the magnitude of this δ^{15}N fractionation (e.g. Polishuk et al. 2001; Fuller et al. 2004; Kempster et al. 2007; Roberston et al. 2014; Olsen et al. 2014; Hertz et al. 2015; Doi et al. 2017). In contrast, concerning nitrogen fractionation mechanisms during growth (anabolic state, positive nitrogen/protein balance), stable isotope ecologists and physiologists have not reached a consensus[273] (e.g. Ponsard and Averbuch 1999; Fuller et al. 2004; Truman et al 2005; Gay Siessegger et al. 2004; MacAvoy et al. 2005; Waters-Rist and Katzenberg 2010; Reitsema and Muir 2015). **It has been suggested that the body may route directly from dietary proteins the non-essential amino-acids increasingly required for the high rates of protein building associated with periods of growth spurts, bypassing transamination and deamination mechanisms, and thus lowering δ^{15}N values** (Sick et al. 1997; Gaye-Siessegger et al. 2003, 2004; Fuller et al. 2004 and 2005; Trueman et al. 2005; Williams et al. 2007; Water-Rist and Katzenberg 2009; Reitsema 2013; Reitsema and Muir 2015; Reynard and Tuross 2015). It is

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[273] *Lower δ^{15}N diet-to-tissue offset during period of growth or of rapid increase in body mass*: Fantle et al. 1999; Oelbermann and Scheu 2002; Gaye-Siessegger et al. 2003, 2004; Fuller et al. 2004 and 2005; Trueman et al. 2005; Williams et al. 2007; Reitsema and Muir 2015

Higher δ^{15}N diet-to-tissue offset during period of growth or of rapid increase in body mass: Minagawa et al. 1984; Hobson and Clark 1992; Gorokhova and Hanssen 1999; Roth and Hobson 2000; MacAvoy et al. 2005; Haubert et al. 2005. Hertz et al. 2015

No δ^{15}N growth effect: Kempster et al. 2007 also possible that the salvage of isotopically lighter nitrogen thanks to the gut microbiome may decrease the δ^{15}N values of organisms who experienced a rapid increase in body mass (e.g. Fuller et al. 2004). Besides, chronically malnourished children may have a microbiome that lags behind their age in terms of development (Gorden 2012), which may further result in developmentally related differences in amino-acids and nitrogen metabolism (Reynard and Tuross 2015). Feeding experiments exploring the effect of nutritional stress experienced during periods of growth obtained somewhat diverging results, perhaps because of the competing influence of growth and nutritional deprivation, of the level of nutritional stress experienced and of the period of life considered (Ponsard and Averbuch 1999; Williams et al. 2007; Kempster et al. 2007; Waters-Rist and Katzenberg 2009).

Concerning the fractionation of the stable isotopes of carbon in situations of stress or growth, animal experimental feeding studies and observations conducted on modern samples also reached differing conclusions[274] (e.g. Hobson and Clark 1992; Cherel et al. 2005; Williams et al. 2007; Truman et al. 2007; Deshner et al. 2012, Robertson et al. 2014; Hertz et al. 2015; Doi et al. 2017). The first stages of food restriction are associated with the metabolism of carbohydrates and lipids (e.g. Lusk 1928; Wang 2006; McCue 2012), and it has been shown that lipids are lower in ^{13}C than the bulk δ^{13}C (De Niro and Epstein 1977; Ambrose and Norr 1993; Post et al. 2007). Some researchers have hence explained the enrichment in whole-body, muscles, livers, blood, and lipids δ^{13}C values observed in situations of nutritional stress by the increased utilization of ^{12}C from lipids, leaving proportionally more ^{13}C in these tissues (Doucett et al. 1999; Gaye-Siessegger et al. 2007; Graves et al. 2012). However, a meta-analysis of fasting animal feeding experiments has also found that, when tissues are treated with lipids extraction, the δ^{13}C offset of starving animals is smaller (Doi et al. 2017). It is thus possible that tissues δ^{13}C response to nutritional stress may differ according to tissues content in lipids and to the pace of tissues nutrient allocation and utilization. Research performed on the hair and the nail keratin of humans who experienced nutritional stress has reported joint patterns of increasing δ^{15}N and declining δ^{13}C values (Neuberger et al. 2013; Lehn et al. 2011); similarly, Beaumont and Montgomery (2016) observed a trend of increasing δ^{15}N and decreasing δ^{13}C values on the dentine collagen of humans who lived during the Great Irish Famine. The nature and the length of the experienced nutritional stress may also influence tissues response in δ^{13}C; for instance, it is possible that the use of lipids during the first stages of nutritional deprivation and the use of proteins in more critical situations may differently influence tissues δ^{13}C values. In case of protein-induced malnutrition, the body may catabolize amino-acids from its own resources in muscles, but also from other exogenous macronutrients - carbohydrates and lipids - to replace the insufficient intake in proteins, a sort of "macro-nutrient scrambling" mechanism (Prowse et al. 2005, Williams et al. 2007, Reitsema et al. 2013). In situations of energy restriction or in case of disease or infection, higher δ^{13}C values have been interpreted as a modification of carbohydrate metabolism in favor of pathways that preserve and recycle bodily carbon (Deshner et al. 2012; Oslen et al. 2014).

Bone post-weaning dips around between 1 and 7 years old

Several stable isotope studies of past children feeding practices have documented lower δ^{15}N and/or δ^{13}C bone values around the age of 1-7 years in comparison with later childhood or adulthood values (e.g. Tuross and Fogel 1994; Richards et al. 2002; Turner et al. 2007; Jay et al. 2008; Nitsch et al. 2011; Water-Rist et al. 2001; Sandberg et al 2014; Reynard and Tuross 2015; Reitsema et al. 2016). These "post-weaning dips" may be associated with lower trophic

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[274] *No effect of stress or growth on the δ^{13}C diet-to-tissue offset:* Hobson and Clark 1992; Hobson et al. 1993; White and Armelagos 1997; Gorokhova and Hanssen 1999; Katzenberg and Lovell 1999; Fantle 1999; Roth and Hobson 2000; Fuller et al. 2004; McCue 2008; Kempster et al. 2007; Truman et al. 2007; Reitsema and Muir 2013; Robertson et al. 2014; Hertz et al 2015; D'ortenzio et al. 2015; Doi et al. 2017.

Higher δ^{13}C diet-to-tissue offset found in situations of nutritional stress and/ or of growth: Hobson and Clark 1992; Hatch et al. 1995; Doucett et al 1999; Polishuk et al. 2001; Gay-Siessegger et al. 2007; Deshner et al. 2012, Graves et al. 2012; Olsen et al 2014.

Lower δ^{13}C diet-to-tissue offset found in situations of nutritional stress and/or of growth: Polishuk et al. 2001; Oelbermann and Scheu 2002; Cherel et al. 2005; Haubert et al. 2005; Mekota et al. 2006; Williams et al. 2007; Lehn et al. 2011; Neuberger et al. 2013; Hertz et al. 2015.

weaning preparations that substantially included plant food, sometimes mixed with animal milk (e.g. Tuross and Fogel 1994; Richards et al. 2002; Fuller et al 2005; Turner et al. 2007; Jays et al. 2008; Sandberg et al. 2014; Reistema et al. 2016). In contrast, in many cases where it has been suggested that weaning preparations probably included higher trophic level resources, δ^{15}N did not reveal such depleted pattern (e.g. Dupras et al. 2001; Howcroft et al. 2012 and 2013; Burt 2013; Haydock et al. 2013; Tsutaya et al. 2014; Burt et al. 2014), although this tendency is not systematic (e.g. Water-Rist et al. 2011; Pearson et al. 2010[275]). In the Danube Gorges sample, lower bone stable isotope values in comparison with the adult range can be noticed concerning the carbon element for children buried at the Early Neolithic site of Ajmana for whom we reconstructed a weaning diet made of lower trophic level resources (Appendix A.III.15); however, this trend may also simply be related to the lower stable isotope values of the mothers of the two children - AJ 12 and 15 - who display lower values than the rest of the group for the isotopes of the three elements. In a meta-analysis of childhood post-weaning nitrogen and carbon stable isotope ratios, which included 29 non-hunter-gatherers and 7 hunter-gatherers populations from archaeological contexts, Tsutaya et al. (2017) found that post-weaned children tend to be lower in δ^{13}C and δ^{15}N than the mean values of adults; these differences appear statistically significant only for non-hunter-gatherers populations. Besides, amongst these non-hunter-gatherers populations, they found a negative correlation between the δ^{13}C values of post-weaned children and the values of adults, indicating that the higher the adults δ^{13}C values, the lower the children δ^{13}C values. It is thus plausible that amongst non-hunter-gatherers populations, children post-weaning diet may have included higher proportions of lower trophic levels resources than adults, particularly terrestrial C_3 plants. However, this explanation does not exclude the possibility that stable isotope may be jointly responsive to the particular metabolic state of children who are experiencing fast rates of protein accretion with growth.

In fact, the observed bone-to-teeth stable isotope offset and bone post-weaning dips could be related to the same metabolic effect of growth which lower down a child bone stable isotopes values after the reduction of suckles (after the removal of breast-milk δ^{15}N signal). Between 1 and 6 years old, a child should grow faster in size than in weigh (international standard BMI curve: e.g. WHO 2006; Figure 70). Interestingly, the shape of the body mass index curve between birth and 7 can be superimposed with the δ^{15}N weaning and post-weaning stable isotope curve (ibidem), which also coincides with the period of greatest bone-to-teeth offset (e.g. Appendix A.III. 18). It can thus be hypothesized that between 1 and 6 years old, the fast rate of bone growth in comparison with body weigh intake requires a rapid mobilization of dietary amino-acids, a more direct routing toward sites of tissues synthesis and perhaps a greater re-utilization of lighter stable isotopes by the gut microbiome. This growth effect could be emphasized in case of lower protein dietary intake and/or if the nutrient intake does not fulfill the higher metabolic requirements of the growing body, when less heavy nitrogen is available for protein synthesis or when the body may have to utilize δ^{13}C from other exogeneous or endogeneous macro-nutrients. The negative correlation that Tsutaya et al. (2017) found between non-hunter-gatherers children and adults δ^{13}C values (the higher the δ^{13}C values of the adults, the lower the δ^{13}C values of the children) might hence be interpreted as an effect of "macro-nutrient scrambling", carbon being normally synthesized by the adult metabolism while the growing organism of children perhaps utilized carbon from different macro-nutrients found in lower trophic level resources. Finally, one may recall that some longitudinal fluctuations of maternal milk δ^{13}C values has been evidenced during breastfeeding (Herrscher et al. 2017), perhaps also be related to gradual changes in lactating females δ^{13}C signal (Reitsema and Muir 2015; Fuller et al. 2006, Appendix A.III.17), which could also be an alternate (or additional?) explanation to lower post-weaned children δ^{13}C bone values.

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[275] δ^{15}N post weaning dip documented at an intra-bone level by Water Rist et al. (2010) for children fed with freshwater fish and mammals or, in contrast not documented by Pearson et al. (2010) for children rather fed with C3 plant food.

It should be mentioned that post-weaning dips have also been documented on the intra-individual teeth profiles of some individuals mostly fed with C_3 pants gruels (Eerkens et al. 2001; Eerkens and Bartelink 2013; Sandberg et al. 2014), this pattern not being systematically observed though (only a few dips dentine stable isotopes dips documented in Beaumont et al. 2013; 2015; Beaumont and Montgomery 2016 and 2018; King et al. 2018). Interestingly, most cases of dentine post weaning dips in the data from Beaumont et al. (2015; XIXth century and Neolithic sites, UK) concerns individuals who died before root completion, contrasting with individuals who survived after root completion. The results of Sandberg et al. (2014) also reveal such ^{15}N dips on the teeth profiles of some individuals who survived early adulthood but who experienced stress events associated with the weaning process (as evidenced by the timing of hypoplasia). Besides, this study shows that while the bone $\delta^{15}N$ values of the individuals who died remain lower between 5 and 10 years old, the teeth $\delta^{15}N$ values of some of the individuals who survived adulthood tend to increase after 5/6 years old. In the Danube Gorges sample, $\delta^{15}N$ teeth population trend-lines (teeth loess curves) suggest a possible dip around 4-6 years for Mesolithic and Transformational children, although it could be related to the structure of the analyzed sample (Appendix A.III. 12; 15); higher resolution teeth samples would be required to clarify the pattern.

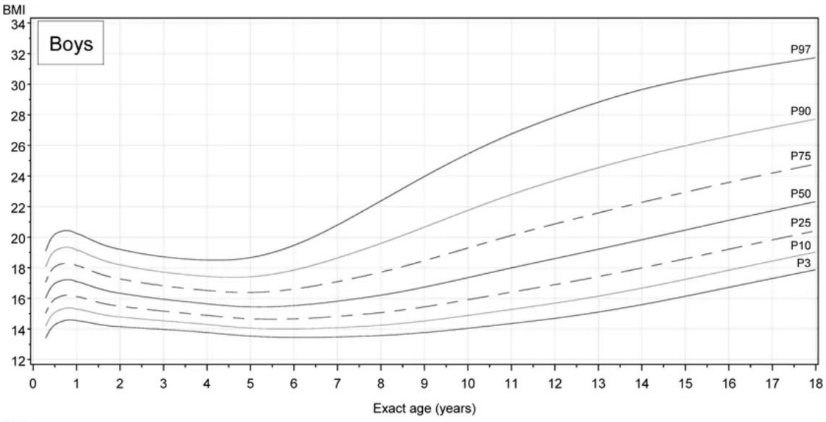

Figure 70: Body mass index percentiles for children and adolescents in Germany, reference curve from a national sample (from Shaffrath Rasorio et al. 2010)

Concerning other tissues, the longitudinal reference study from Fuller et al. (2006) reports slight $\delta^{13}C$ post-weaning dips on the nail keratine of 4/5 children and joint $\delta^{15}N$ dips on the keratin of 2/5 children[276] (Appendix A.III.17. part A). Reitsema and Muir (2015) also documented lower $\delta^{15}N$ and $\delta^{13}C$ values in the blood serum of several juvenile monkeys in comparison with the adult variability or with their isotope values at older age; the authors directly tested the relationship between post-weaning dips and several anthropometric measurements related to size, weight and girth but failed to find correlations. As argued by the authors, it remains yet possible that the observed dips in blood serum could be associated with growth in other bodily systems than skeletal growth. Similarly, Waters-Rist and Katzenberg (2010) specifically tested the lowering effect of growth on the $\delta^{15}N$ bones values of sub-adult individuals old discovered in a protohistoric ossuary from Ontario. On the remains of juveniles aged 7-19, the authors compared different parts of bones growing at various speed rates, and concluded for no significant differences; they interpreted the absence of growth-effect as a consequence of the slower rates of bone renewal during late childhood and teenage in comparison with late-infancy/early childhood (Valentin 2003). The observation of post-weaning dips on some teeth profiles or on keratine or blood tissues does not necessarily invalidate the possibility that the observed bone-teeth offset could be partially due to a lowering effect of bone growth: it remains possible that growth in other bodily systems (teeth,

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[276] data for exclusively breastfed and not fed with formula.

digestive, brain, nervous; Reitsema et al. 2015) may also influence the stable isotopes values of other tissues, and perhaps to a lesser extent than the bone tissue.

Lower bone stable isotope values around 1-7 years old: a joint effect of growth and nutritional stress?

In the light of animal feeding experiments, of reference studies conducted on modern samples and of observations performed on archaeological samples, **it is possible to suggest that the observed bone-to-teeth stable isotope offset could be related to two mechanisms associated with the differential pattern of bone and teeth growth.** Firstly, in case of nutritional stress, the growing dentine of a tooth may record higher $\delta^{15}N$ values while the bone may delay its growth, reducing the production of new collagen, and thus being less influenced by the elevated stable isotope values; it is also possible that the teeth $\delta^{13}C$ values might be particularly elevated in case of energy restricted diet. On the other hand, during periods of growth spurts - and perhaps particularly between 1 and 6 years old, when children experience faster growth rates in size than in weigh - bone $\delta^{15}N$ values may be lowered down. In case of lower trophic level food consumption, of supplementation with plant-based food or of a moderately low intake of proteins, it is possible that the growing bone could be particularly depleted in ^{13}C. It should be borne in mind that other tissues, including dentine, keratine or blood, may also putatively be influenced by the lowering effect of growth in specific bodily systems, perhaps yet in a different magnitude than bone cells. **In short, amino acids might be unevenly routed to tissues, particularly in specific metabolic situations of growth and/or stress.** Although speculative, these two physiological mechanisms might explain why the bone-to-teeth offset appears greater during the biological stage of early childhood, after the child tissues ceased to be influenced by maternal milk protein, and before 7 years old, at the time when body mass started to increase significantly**.** It has been reported that the offset tends to disappear from the end of the tooth formation (Beaumont et al. 2018), but it is possible that elevated level of nutritional stress associated with growth delay may maintain greater bone-to-teeth offset after that age. Beaumont et al. (2018) also suggested a possible correlation between peak dentine $\delta^{15}N$ values and growth delays, although this study is limited by the facts that peak nitrogen dentine values should theoretically be associated with breastfeeding and that the observed correlation coefficient remain weak ($R^2<0.2$). Similarly, Herrscher (2003) observed bone-teeth offsets for children aged up to 10 years old in archaeological context and mentioned that a phase of slowdown in growth was observed in the studied sample before 5 years, further caught up between 5 and 9 years old.

5.3.3. Bone-to-teeth stable isotope offset: a possible marker of nutritional stress during period of growth?

Comparing bone-to-teeth stable isotope offset and children growth trajectories

In the Danube Gorges prehistoric osteo-anthropological sample, Transformational-Neolithic children buried in the Inner Gorges and Early Neolithic children buried in the Downstream Area exhibit higher $\Delta^{15}N$ than the Mesolithic children. Based upon the longitudinal fluctuations in dentine $\delta^{15}N$ and $\delta^{13}C$ values, we also previously suggested that the stable isotope values of some Transformational - Early Neolithic children may have been influenced by some events of biological stress experienced in utero or during the breastfeeding-weaning process (earlier/greater first permanent molar drop in $\delta^{13}C$ than in $\delta^{15}N$ for LV 61 and AJ 8; contrasting pattern of declining $\delta^{15}N$ values and increasing $\delta^{13}C$ values for LV 84 and LV 87). Interestingly, Pinhasi et al. (2011) suggested a trend of catch-up growth for the femoral length of Danube Gorges' Mesolithic children, not observed for Neolithic children, who remain below nowadays reference growth curve (Denver Growth curves). Yet, it should be mentioned that the sample size is here very small, only two Mesolithic children being aged between 1 and 8 years old and two Neolithic children between 1 and 12 years old; within the limits of the cross-sectional approach to growth trajectories in the past, it cannot be ascertained that the child who survived did experience growth delay at an earlier age. Concerning humeral and tibial length, the authors also noticed that two Neolithic children aged at death above 12 ranges below the reference curve.

On-going research on body proportions (body size, mass and body mass index) also indicated that several children related to the Transformational / Early-Middle Neolithic phase in the Inner Gorges and the Early Neolithic phase downstream range below nowadays reference growth curves (Jovanović et al. 2016; de Becdelièvre et al. 2017, unpublished podium presentation[277]; use of the Denver WHO and CDC "reference" curves). The stable isotopes values of co-forming bone and teeth tissues have been collected for five children for whom body proportions were reconstructed (LV 92, HV 14, VL 53 and VL 18c). The child LV 92, who died around 1.5-3 years old while still significantly consuming breast-milk, ranges slightly below the nowadays reference curve for Body Mass Index; he exhibits quite similar bone and teeth growing root δ^{15}N values associated with slightly lower bone δ^{13}C values (Δ^{15}N: +0.2‰; Δ^{13}C:-0.3‰), probably related to the fact that both tissues were influenced by the breast-milk values at his death and that he was jointly supplemented with marine-influenced proteins. Concerning children who died after 3 years old, the Transformational child HV 14 (aged at death 4.5-7) ranges below the body size reference curve, and also displays one of the greatest bone-to-teeth Δ^{15}N offset (Δ^{15}N =-1.2‰), greater than the Late Mesolithic child VL 53 (aged at death 5-8), who ranges within the 5-95% limit of the current reference curves (Δ^{15}N =0.3‰). In contrast, these two children exhibit similar bone-to-teeth Δ^{13}C (HV 14=-0.4‰; VL 53=-0.5‰). Concerning body mass, the Early Neolithic child AJ 14 (aged at death 4.5-7), who ranges below the reference curves, displays quite similar offsets than the children VL 53 and VL 18c (aged at death 5.5-8.5), who ranges within the curve (AJ 14: Δ^{13}C=0.2‰, Δ^{15}N=0.6‰; VL 53: Δ^{13}C=0.5‰, Δ^{15}N=0.3‰; VL 18c: Δ^{13}C=0.6‰, Δ^{15}N=0.6‰). Additionally, bone and teeth stable isotope values were also collected for the Early Neolithic child AJ 13, aged at death older (11-13 years old), who displays lower body size, body mass and body mass index than the reference comparison samples. Although the bone tissues of this older child was likely formed after his root dentine tissue (apex already at the beginning of resorption; dentine value formed circa 7-11.5 years old), it can be noticed that he also displays a Δ^{15}N offset of -0.9‰ (associated with a bone-to-teeth Δ^{13}C=-0.1‰), which can whether be interpreted as a continuous body depletion in ^{15}N under the consumption of lower trophic during later childhood, or as an effect of elevated level of biological stress which may have impacted the child growth. In any cases, it should be borne in mind that growth trajectories should also be driven by a strong genetic component; therefore, differences in terms of body proportions noticed between the Mesolithic and the Transformation-Neolithic period could also somewhat be related to the presence in the Gorges of different genetic lineages after 6200 cal BC and growth patterns in the past might have been quite different than nowadays (limit of the "reference" samples used for long bone and body proportions growth rates).

Higher nutritional stress for Transformational, Early Neolithic and Neolithic children?

Thus, it has been noticed that: **1.** Transformational/ Early Neolithic and Neolithic children exhibit higher average co-forming bone-to-teeth δ^{15}N offset than Mesolithic children (but not higher Δ^{13}C); **2.** some Mesolithic individuals might have caught-up long bones growth delays after 8 years old, on the contrary to some Transformational-Neolithic individuals (Pinhasi et al. 2011), and a few children dated to the Transformational-Early Neolithic period deviate from nowadays reference growth curves (although the sample size of analyzed children in this study is very limited; Jovanović et al. 2016; de Becdelièvre et al. 2017, unpublished podium presentations[278]); **3.** some Transformational - Early Neolithic individuals who display the highest Δ^{15}N bone-to-teeth offset

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[277] Jovanović, J., de Becdelievre, C., Goude, G., Herrscher E., Stefanović, S. 2016. Children feeding practices and growth patterns during Mesolithic-Neolithic transition in the Danube Gorges. *8th World Archaeological congress,* (28.08.-02.09.2016. Kyoto, Japan).

de Becdelièvre, C., Le Guen M.A., Porčić M., Jovanović, J., Stefanović, S. 2017. Behavioral Adaptations - Morphological Adaptations: new contributions from Morphometric Mapping for the understanding of Mesolithic-Neolithic transformations (Balkans; 10 000 - 5000 BC). Research presented at the 7th Annual Meeting of the European Society for the study of Human Evolution (ESHE) (21.09.-23.09.2017. Leiden, the Netherlands).

[278] Cf note supra

also display differences in terms of body size and/or in body mass index (HV 14, AJ 13), although this tendency is not systematic (e.g. AJ 14). **It is therefore possible that some Transformational-Early Neolithic children may have experienced some episode of biological stress, influencing the growth of their bone and resulting in greater $\Delta^{15}N$ bone-to-teeth offset. Concerning Transformational-Early Neolithic contexts in the Inner Gorges, where we also noticed higher neonatal stable isotope variability, it could be hypothesized that some mothers may have chosen to supplement their children with higher trophic level resources (fish, dogs meat) in order to mitigate a stress experienced by their offspring at birth, during infancy and early childhood and which perhaps had some longer term consequences on their health and growth. Concerning the site of Ajmana, the greater $\Delta^{15}N$ bone-to-teeth offset might be associated with the consumption of lower trophic level resources,** as documented in other contexts (e.g. Fuller et al. 2003; Beaumont et al. 2015, 2018; King et al. 2018).

Indeed, it has been suggested that prolonged breastfeeding, associated with nutrients from animal origin (fats, proteins, vitamin B 12, folates, iron, zinc, iodin...), is implicated into positive outcomes for a child health, growth and ability to survive adulthood (Black et al. 2005; de Luca 2012; Reitsema and Vercelatti 2012; Sandberg et al. 2016; Beaumont and Montgomery 2016). We also observed that, on average, the children who substantially relied on the consumption of breast-milk during most of the time of the formation of their first permanent molar crown exhibit a smaller $\Delta^{15}N$ offset than the children who reduced the frequency of their suckles earlier (although it concerns only four children). The infant feeding practices of some Mesolithic mothers (longer breastfeeding, mixed diet) may thus explain the smaller $\Delta^{15}N$ offset displayed by the bone and dentine tissues of their offspring.

Factors that may have influenced the magnitude of the $\Delta^{13}C$ offset remain yet quite unclear. Animal feeding experiments suggested that the joint effect of growth and nutritional effect could have influenced the offset; however, we have not perceived any particular difference between the chrono-cultural groups considered, nor when integrating available information about body proportions. In some cases, this offset may be caused (or emphasized?) by the increasing consumption of marine-influenced proteins (the growing edge of a root recording a signal more influenced by higher trophic level resources than bone; e.g. LV 87, LV 84, LV 56, HV 14; Appendix A.III. 14); a physiological difference in the routing of carbon-containing amino-acids between bone and dentine sites is also possible (systematically higher dentine $\delta^{13}C$ values also in the datasets Fuller et al. 2003).

5.3.4. Summary: growth, nutrition and physiology during childhood

When one compares children bone stable isotope values with the latest-formed dentine signal analyzed (tooth root signal), a particular trend can be observed: for children who died between 3 and 10 years old, bone is almost systematically lower in $\delta^{15}N$ and $\delta^{13}C$ than partially co-forming dentine collagen tissues. In fact, the stable isotope values of the growing edge of a tooth root should reflect the diet of a child during the last months of his life and the stable isotope signals of bone collagen, formed partially contemporaneously with the tooth growing root, should average a dietary signal over a longer time before his death. Therefore, one would expect different bone and growing tooth dentine stable isotope values to reflect a dietary change experienced just before the death of a child. According to this model, results should indicate that almost all children aged at death between 3 and 10 years old switched their diet towards the consumption of higher trophic level resources just before their death, which could be interpreted as a late return to breastfeeding for sick and dying children or as a late supplementation with animal proteins. However, observing such pattern regardless of the chrono-cultural context seems quite counter-intuitive considering that we reconstructed the use of isotopically very different weaning resources between the Inner Gorges (use of aquatic resources) and the Downstream Area (rather terrestrial and C_3 plant-based preparations). Besides, similar bone-dentine offsets have been noticed on the co-forming tissues of children aged 3 to 10 years from a variety of historical and geographical backgrounds, often concerning children fed with rather terrestrial resources and plant based weaning preparations, which suggests the possible effect of alternate biological factors or an interaction between diet and physiology during childhood (e.g. Richards et al. 2002; Herrscher et al. 2013, Kaupová et al. 2014; Beaumont et al. 2015; 2018; King et al. 2018b).

In the light of animal feeding experiments and observations on modern samples, it can actually be suggested that the dentine-bone collagen stable isotopes offset could be related to two mechanisms associated with the differential pattern of bone and teeth growth: **1.** firstly, it has been suggested that bone formation may be arrested in situations of biological stress - delays which can be later "caught up" by episodes of growth spurts during better time - while teeth would continue to grow at the same rate regardless of nutritional status (Ambrose 1993; Elamin and Liversidge 2013; Beaumont et al. 2015, 2018). In situations of nutritional stress, the growing dentine of a tooth may thus record elevated $\delta^{15}N$ values (Hatch et al. 2012; Reitsema et al. 2013; Beaumont et al. 2015, 2018), while bone, reducing the production of new collagen, would contrastingly be less influenced by the elevated stable isotope values. It is also possible that the teeth $\delta^{13}C$ values might be particularly elevated in case of energy restricted diet (e.g. Deshner et al. 2012; Olsen et al. 2014). **2.** On the other hand, during periods of growth spurts, $\delta^{15}N$ values may be lowered down (Waters-Rist and Katzenberg, 2009; Reitsema 2013; Reitsema and Muir 2015). In case of lower trophic level food consumption, of supplementation with plant-based food or of a moderately low intake of proteins, it is also possible that the growing bone could be particularly depleted in ^{13}C, under a sort of "macro-nutrient scrambling" mechanism (e.g. Prowse et al. 2005; Williams et al. 2007; Reitsema 2013; Beaumont and Montgomery 2016). Lower bone post-weaning values around the age of 1-7 years old ("post-weaning dips") have been documented on several archaeological populations, often associated with the consumption of lower trophic level resources (e.g. Tuross and Fogel 1994; Richards et al. 2002; Turner et al. 2007; Jay et al. 2008; Nitsch et al. 2011; Sandberg et al 2014; Reynard and Tuross 2015; Reitsema et al. 2016; Tsutaya et al. 2017). These "post-weaning dips", as well as the bone-to-teeth offsets, may actually coincide with the age of 1-6 years old when children experience faster growth rates in size than in weigh, suggesting a possible physiological mass balance effect on stable isotopes values (Figure 70). Experiencing nutritional stress or a lower protein intake during this period of high protein accretion might emphasize the lowering of bone stable isotope values and the magnitude of bone-to-teeth offset. In other words, during periods of growth in body size, amino acids could be unevenly routed to bone and teeth tissues, particularly when the nutrient intake does not satisfy the requirements of the growing organism.

In the Danube Gorges osteo-anthropological sample, it has been noticed that Transformational-Neolithic children exhibit higher average co-forming bone-to-teeth $\delta^{15}N$ offset than Mesolithic children (but not higher $\Delta^{13}C$). Besides, the children who substantially relied on the consumption of breastmilk during most of the time of the formation of their first permanent molar crown also exhibit a smaller $\Delta^{15}N$ average offset than the children who reduced suckles' frequency at a younger age. Interestingly, on-going research on growth rates now indicates that a few children dated to the Transformational-Early Neolithic period also deviate from reference growth curves, which could be due to the presence of new genetic lineages in the Gorges after 6.2 cal BC and/or to childhood environmental conditions (Pinhasi et al. 2011; Jovanović et al. 2016; de Becdelièvre et al. 2017, unpublished podium presentation[279]). A few Transformational - Early Neolithic individuals who display the highest $\Delta^{15}N$ bone-to-teeth offset also exhibit differences in terms of body size and/or in body mass index, although this tendency is not systematic, and the sample size remains very limited. It is thus possible that some Transformational-Early Neolithic children may have experienced some episodes of biological stress which influenced the growth of their bones and result in greater $\Delta^{15}N$ bone-to-teeth offset. Concerning Transformational-Early Neolithic

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[279] Cf note supra

contexts in the Inner Gorges, where we also observed large neonatal stable isotope variability, it could be hypothesized that some mothers may have chosen to supplement their children with higher trophic level resources in order to mitigate a stress experienced by their offspring at birth and during infancy. Concerning children from the Early Neolithic site of Ajmana, the greater $\Delta^{15}N$ bone-to-teeth offset might be associated with an earlier reliance on lower trophic level resources and a rough transition to plant-based weaning preparations, while prolonged breastfeeding and the use of mixed resources by some Mesolithic mothers may have buffered a child health against the weaning stress. To circumvent the limits of the "selective mortality" - data originating from children who died, who should anyways have experienced some level of biological stress and who may not be representative of the individuals who survived - future prospects will be to compare the bone and dentine data with longitudinal molars stable isotopes profiles of Mesolithic and Neolithic individuals who survived adulthood and with the exact timing of enamel hypoplasia appearance at an individual level (e.g. Sandberg et al. 2014).

The observation of bone and teeth stable isotope offset suggests that both bone and teeth tissues could carry information of different nature concerning health, nutrition and physiology and question some interpretations of past children feeding practices and survivorship based upon the direct comparison of bone and teeth values. Further research would be needed to precise whether the observed $\Delta^{13}C$ bone-teeth offset reveals related to diet and/or to a different routing of amino-acids in specific metabolic states and to establish the potential of using children stable isotopes bone-teeth offsets as possible markers of nutritional stress markers, of particular interest in contexts of subsistence transition.

5.4. General discussion: infant feeding strategies and the foraging to farming transition, bio-cultural implications

5.4.1. The model of the Agricultural Demographic Transition

The assumptions for the causes of the Neolithic Demographic Transition include several important changes in maternal nutritional and reproductive behaviors that may have positively influenced fertility: notably better food predictability and storage (relaxation of birth control and fertility constraints), change in maternal nutritional status (increased consumption of carbohydrates influencing overall energetics), children caring practices (different village life, workload patterns and allo-parenting strategies), and breastfeeding strategies (earlier weaning e.g. Buikstra et al. 1986; Armelagos 1991; Bentley et al. 2001; Bocquet-Appel 2008; Page et al. 2016). Because there is a well-established correlation between the breastfeeding activity and the post-partum subfecundity (e.g Konner and Worthman 1980; Van Ginneken 1978; Howie et al. 1981; Howie and McNeilly 1982; Worthman et al. 1993; Vitzthum 1994), **researchers have associated demographic differences observed between mobile hunter-gatherers and sedentary agriculturalists with differences in the length of breastfeeding, either in relation to the burden of carrying offspring for mobile foragers (longer length of lactation to avoid several dependent offspring), to difference in social organization (village life allowing for a allo-parental care), or to the availability of new weaning food (cereals and animal milk) and technologies (e.g. ceramics for cooking soups and porridges) more suitable for an earlier introduction of supplementary food** (e.g. Binford 1968; Birdell 1968, Binford and Chasko 1976; Lee 1979; Blurton Jones 1986; Buikstra et al. 1986; Armelagos et al. 1991; Bocquet-Appel 2001; Bentley et al. 2001).

Ethnographic surveys

In the ethnographic literature, there are manifold examples of differences in the attitudes towards infant and children feeding practices amongst groups of hunter-gatherers and farmers, even for populations sharing the same environments (Vitzthum 1994; Macadam and Dettwyller

1995; Sellen and Smay 2001; Hewlett and Lamb 2005; Lancy 2015; eHRAF 2018). For instance, the majority of Bofi foragers (central Africa) are practicing demand breast-feeding often until mothers' next pregnancy, believing that a forced weaning may be detrimental to the health of a child (Fouts 2004; Fouts et al. 2005). In contrast, the Bofi farmers coerce their children to stop suckling around the age of 18-24 months; at the time a child is considered as "being weaned", special meals forbidden to older siblings - such as sweetened rice - are prepared for the toddler, symbolizing the social transition from infancy to childhood (ibidem). Differences in children post-weaned diet have also been often reported: amongst many groups of foragers the offspring are not considered dependent to a specific diet and sometimes practice "independent foraging", while amongst many communities of herders and crop farmers, "food provisioning" may vary for socio-cultural reasons, children may participate to subsistence activities such as field works and sometimes the best food is reserved for some adults (Hewlett and Lamb 2005; Lancy 2015).

The hypothesis that farmers weaned children earlier because of the availability of a new type of starchy weaning food has been statistically tested on a broad sample of populations with various subsistence systems ranging from agriculturalists and herders to foragers (Sellen and Smay, 2001, Sellen 2009). The authors found no qualitative evidence to suggest that hunter-gatherers lacked all kind of appropriate weaning food. Contrary to the predictions, they found that foragers presented the earliest age for the introduction of solid food (ca 4.8±0.8 months versus 5.5±0.8 months for farmers), and that hunter-gatherers tends to breastfeed longer that population less dependent upon hunting (27±1.5 months versus ca 21±1 months). It should yet be emphasized that the sample size of foragers considered by the authors for the age at introduction of supplementary food is very small (n extractive groups for liquid food=6, for liquid=1)[280]. Apart from subsistence economy, breastfeeding patterns may also depend to how close from home subsistence activities can be performed, and how childcare can be shared with other members of the communities (e.g. Sellen and Smay 2001; Hewlett and Lamb 2005; Bogin 2016). In several societies of foragers and of farmers, it is the role of the elderly – for instance the grandmother – or of the older siblings to take care to the older siblings in the absence of the mother (e.g. Hadza hunter-Gatherers in Tanzania or Bofi farmers in Central Africa; Kelly 1995; Fouts et al. 1995). Hence, the degree of reliance on food production and extraction, of subsistence specialization, of daily mobility, the resource proximity, the size of the community, as well as the support of wet-nurses or not, are numerous variables that may influence differently the length of lactation, feeding strategies and females fertility patterns. Finally, environmental conditions, such as resources availability, aridity, climatic fluctuations and pathogen loads may also play an important role in maternal decision to wean their offspring and in their feeding choices (McDade and Worthman, 1998; Sellen, 2007; Cantrelle and Leridon, 1971; Lindstrom and Berhanu, 2000).

Despite sample size limitation, the results from the ethnographic meta-analysis conducted by Sellen and Smay demonstrated that hunter-gatherers did not lack appropriate weaning food and that weaning and breastfeeding strategies amongst traditional societies include a broad range of practices, but they show a broad pattern of longer average breastfeeding amongst foragers, and they did not denied the existing relationship between breastfeeding and weaning and fertility, nor that the shift towards agriculture may have modified some aspects of the structure of breastfeeding. The author suggested that other elements may have differently influenced foragers and famers breastfeeding practices such as differences in the organization of work or pathogen loads. In any cases, it should be kept in mind that before the Neolithic period, no parent would have been able to use animal milk or domesticated cereals in weaning preparations. Besides, while there has been a considerable emphasis on timing parameters and the length of lactation, there is evidence to suggest that hormonal mechanisms and female metabolism may have been more sensitive to

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[280] Only 6 groups of foragers could be included in the analysis of this solid food supplementation; besides it can be emphasized that farmers and herders presented an early age for introduction of liquids (ca 3.5±1 months for farmers and 4.7±2.6 months for herders) while only one group of forager is included for this parameter.

changes in terms of frequency and duration of suckles, rather than to the introduction of weaning food and the total duration of breastfeeding (e.g. Howie et al. 1981; Howie and McNeilly 1982; Worthman et al. 1993; Fink et al. 1992; Vitzthum 1994).

Archaeological testing

In archaeological contexts, stable isotope studies of infant feeding practices amongst populations with different means of subsistence across the world have been reviewed by R. Howcroft (2013) and by T. Tsutaya and his colleagues (2013). Although the mean age for introduction of supplementary food detected by Tsutaya et al. is slightly earlier amongst hunter gatherers (0.93±0.3 year), than some non-hunter-gatherers populations (1.11±0.85 year), it can be mentioned that the range of variation includes both earlier and later values for this last group. The data collected by R. Howcroft also revealed that proportionally more hunter-gatherers introduce supplementary food after 6 months than population relying on an agro-pastoral means of subsistence (71.5% of the sample versus 55.5% of the sample). Besides, both studies reported a slightly later completion of weaning amongst hunter-gatherers than non-hunter-gatherers (3.01±1.25 years versus 2.74±1.35 years for non-hunter-gatherers; Tsutaya et al. 2013). This tendency of gradual and lengthy weaning observed for hunter-gatherers is in concordance with the results from ethnographic observations (Sellen and Smay 2001). Further comparative paleodietary studies also indicated greater variability in the isotopic values of children from extractive subsistence economy (Chinique de Armas and Pestle 2018, for Caribbean populations), as well as a tendency for lower $\delta^{13}C$ and $\delta^{15}N$ values and of greater adult-to-children stable isotope offset amongst non-hunter-gatherers children (Tsutaya et al. 2013; 2017; meta-analysis), which can be associated with the more homogeneous use of plant-based weaning preparations amongst sedentary agriculturalists groups. Only a few studies of population from the North-American continent directly compare the results of stable isotope analyses and paleodemographic proxies population before and after the agricultural and sedentary transition, and noticed no association between subsistence and mobility patterns, breast-feeding strategies and changes in reproductive behaviors (Schurr 1997; Schurr and Powell 2005; Pfeiffer et al. 2017; Schurr 2018). The variability of children feeding practices evidenced by these studies of populations from different chrono-cultural contexts demonstrate the complexity of human reproductive ecology and the diversity of maternal responses to different environmental conditions.

5.4.2. Children feeding practices at the Neolithic Transition in Eurasia

Concerning the agro-pastoral transition in Western Eurasia, in spite of the quantity of studies dedicated to the Neolithic Demographic Transition and to the spread of agro-pastoral practices, the analyses of Mesolithic and Neolithic children feeding practices have been quite neglected and most available information derived from paleodietary studies of (too) small sample size (e.g. Bocherens 2007; Ogrinc and Budja 2007; Pearson et al. 2010; Cienkosz-Stepanczak *et al.* 2017). Considered together, bone stable isotope studies of Neolithic communities from Anatolia (dated 9th – 7th millennium BC) suggest that supplementation broadly started between 6 month and 1 years and that breastfeeding was practiced until 2-3 years old (Richards et al. 2002; Pearson et al. 2010, 2015 ; Özdemir et al. 2019). While data for the site of Izkirtepe (Northern Anatolia) indicate the earliest onset of the weaning (around/before 6 months?), bone values of children from the easternmost site Cayonu suggest a continuous reliance on breastmilk as the main source of protein at least until 1-2 years old and a subsequent (abrupt?) cessation of breastfeeding ca 2.5-3.5 years old (Pearson et al. 2010; Özdemir et al. 2019). These differences could be in part due to environmental factors (aridity and/or pathogen loads) and to subsistence choices (the weaning food), the means of subsistence of individuals buried at Cayonu being rather oriented towards the consumption of pulses and meat from suidae, while analyzed individuals from Central and Western Anatolia likely relied more on the consumption of cereals and dairies (Pearson et al. 2010). These results are broadly in concordance with the idea that with the availability of dairies (raw milk?) and of high carbohydrate products (such as cereals), mothers may have been more likely to start and/or end breastfeeding earlier.

Although the detailed age estimation is not provided, bone stable isotopes analyses of individuals from Early Neolithic LBK sites of Central Europe (Central Germany, 6th millennium BC) suggest that children were weaned around 3 years old and were fed with cereals, animal meat from livestock and perhaps dairies (Oelze et al. 2012). Permanent teeth longitudinal profiles (n=7) and children bone stable isotope values of individuals from a Late Neolithic collective burial from Spain (Alto de la Huesera; 3500-2900 cal BC), indicate varying weaning patterns: some individuals, mainly males, likely relied on breastmilk as a main source of nutrients for a shorter time (<1 year) than others (Fernandez-Crespo et al. 2018). The authors reconstructed a protracted breastfeeding period (until 3-4 years old), interpreted as an individualized response to cope with harsher periods of food shortage. They suggested that children were firstly fed with cereal-based preparations and further consumed a diet similar as the adults, including dairy product and domestic animal milk. Interestingly, the lowest stable isotope bone values are found for children aged around 4-8 years old in both studies (concerning nitrogen for the LBK contexts and concerning carbon for Alto de la Huesera), which coincides with the general pattern observed by Tsutaya et al. (2017) for non-hunter-gatherer children (a physiological mass balance effect in relation with the introduction of lower trophic level and protein-depleted weaning food?).

Bone and dentine stable isotope values for foragers of the pitted ware culture (pottery user foragers from South Scandinavia-Baltic; 3rd millennium BC), in contact with the Neolithic groups of the Funnel Beaker and of the Corded Ware ceramic culture, also indicate an average introduction of solid food before 6 months and a cessation of breastfeeding between 2 and 3 years old, despite some important variations (Howcroft 2013; Erickson and Liden 2013). Infant feeding preparations likely include marine proteins, although practices were adapted to the different ecological conditions. Concerning individual buried at the Pitted Ware site of Västerbjers, Erickson and Liden also reported significantly higher stable isotope values for dentine formed during teenage in comparison with dentine formed during later childhood and adult bone values, interpreted as an effect of a particular rite of passage that involved an intense seal-hunting. Yet, this pattern may also be explained by the general physiological offset that we also noticed between bone and dentine and could thus be disconnected from behavioral causes (cf part 5.3.). Dentine data for 3rd millennium farming communities from a number of sites in Poland (and a small number of individuals per sites) reflect - in spite of an excepted variability - a sharper drop in breastmilk intake during the first year of life than observed concerning roughly contemporaneous foragers of the Pitted Ware culture (Howcroft 2013). On average, the cessation of suckles occurred around 3 years old (Howcroft 2013; Cienkosz-Stepanczak *et al.* 2017). While some individuals display a more gradual weaning pattern, a few may have already been weaned at the age of 6 months (Howcroft 2013). The type of food varies according to chrono-cultural contexts, but cereals and domesticated animal products should have often been included in weaning preparations (Cienkosz-Stepanczak *et al.* 2017).

Taken as a whole, available information concerning Mesolithic and Neolithic children feeding strategy in Europe hence broadly fit with the general pattern of a supplementation that starts around 6 months and with a cessation of breastfeeding between 2-3 years observed amongst non-industrialized societies (Sellen and Smay 2001). Hunter-Gatherers (pitted ware culture) tend to practice a more gradual weaning, and to use higher trophic level resources. Besides the development of farming generally entailed a more uniform diet throughout life, in relation with the mobility of foragers and with the use of cereal and domesticated animal products (Erickson and Liden 2013; Howcroft 2013). However, there is a lack of information concerning children feeding practices amongst foragers or during contacts periods. Besides, while the European Neolithic covers a broad time span of four millennia and very different environments, the age at weaning remains an ecologically contingent variable, which may vary according to multiple factors independent from the broad mean of subsistence, including the degree of reliance to agropastoral products, resources availability, pathogen loads as well as socio-cultural reasons. In this context, our results concerning the prehistoric complex of the Danube Gorges contribute to fill a gap concerning breastfeeding practices amongst European foragers and the Neolithic "Infant Feeding Transition", by clarifying the adjustments of maternal nutritional choices over changing Mesolithic-Neolithic natural and socio-cultural environments, and by considering their possible influence on the local demographic patterns.

5.4.3. Population dynamics, children feeding strategies in the Danube Gorges

Demographic fluctuations

Ongoing analyses of the radiocarbon dataset used as a proxy for population fluctuations indicate two main episodes of increased intensity of occupation in the region of the Gorges: during the Late Mesolithic (ca 6700-6400 cal BC), and during the period of Transformations (ca 6200-5900 cal BC; cf part 2.3.2; Porčić et al. 2014 and de Becdelièvre et al. 2019 unpublished posters and podium presentations[281], de Becdelièvre et al. 2020 *in preparation*). Birth rates inferred from the skeletal sample of the Inner Gorges suggest that the Mesolithic-Neolithic population buried in the Inner Gorges was stationary, ranging in the lower part of European Mesolithic variability (ibidem). A more permanent occupation at several locations along the Gorges, probably associated with the Late Mesolithic fishing intensification, might hence explained the noticed increased intensity of occupation before 6400 cal BC (an effect of change in residential mobility rather than increased fertility). The second episode of increased intensity of occupation (ca 6200-5900 cal BC), may be associated with the arrival of Early Neolithic communities in the Central Balkans, the presence of migrants in the Gorges originating from these communities, the adoption of a part of the Neolithic package (ceramics) and the attractiveness of the central site of Lepenski Vir. Although still in the range of European foragers, inferred birth rates appear slightly higher during the period of Transformation and a fortiori during the Neolithic period, which could be in part related to the interactions with migrants and the introduction of cultural novelties in the Gorges. In contrast, the higher proportion of immatures individuals buried downstream ca 6000 cal BC, at the Early Neolithic multiple burials of Velesnica and Ajmana, suggests much higher birth rates, typical for farming communities. In the broad region of the Central Balkans, the period ca 6000-5500 cal BC is associated with the demographic expansion of Early Neolithic communities, while the intensity of occupation gradually declines in the Danube Gorges.

The stable isotope analyses conducted on tissues formed in utero, during lactation and later childhood, have indicated major differences in terms of weaning times (structure of breastfeeding) between the Mesolithic and Neolithic children buried at sites located in the Inner Gorges and the Early Neolithic children buried at Ajmana downstream. These results have also shown important differences in terms of maternal dietary choices (supplemented proteins) between the Mesolithic, the Transformational period and the Early Neolithic children buried in the Inner Gorges and in the Downstream Area.

Maternal nutritional choices and feeding practices in the Inner Gorges: the importance of aquatic resources

Although data include some variability, average trendlines suggest that analyzed Mesolithic children mostly relied on breastmilk as the major source of protein until 1-2 years old and were likely breastfed for more than 3 years. These results are in keeping with ethnographic accounts and

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[281] Porčić M., de Becdelièvre, C., Le Roy, M., Jovanović, J., Stefanović, S., Thomas, M., Shennan, S, Timpson, A. Investigating local demographic fluctuations during the Mesolithic and the Neolithic in the Danube Gorges: a review of radiocarbon, skeletal and settlement evidence. Research presented at *the 20th European Association of archaeologists Annual Meeting. (*10-14.09.2014, Istanbul, Turkey).
de Becdelièvre, C., Blagojević, T., Jovanović, J., Porčić, M., Hofmanová, Z., Stefanović, S. Paleodemography of the Danube Gorges Mesolithic and Neolithic Transformations: comparing radiocarbon, skeletal and molecular evidence. Research presented at Jean-Pierre Bocquet-Appel Tribute Conferences. (02-03. 07. 2019. Aix-en-Provence, France). Paper in tribute to J.P. Bocquet-Appel in preparation (de Becdelièvre el. 2020)

paleodietary studies which document the practice of prolonged breastfeeding and gradual weaning amongst groups of foragers from different latitudes (e.g. Weber et al. 2002; Clayton et al. 2006; Waters-Rists et al 2011, Garner et al. 2011, Eerkens et al. 2011; Eerkens and Bartelink 2013, Tsutaya et al. 2013b; Tessone et al. 2015; Greenwald et al. 2016; Chinique de Armas et al. 2017, Scharlotta et al. 2018; Gardner et al. 2018; eHRAF 2018). A part of Late Mesolithic mothers should have consumed lesser marine-influenced proteins than the rest of the population during pregnancy and lactation and included in weaning preparations similar resources as in their own diet. This variability can be related to the broad time span covered by the analyzed samples (issue of synchronicity of the sample), to the seasonality of birth (concerning tissues formed in utero), to social organization and division of labor, food taboos and symbolism, or to what was perceived as healthy for the development and the growth of the offspring. Since there is no noticeable stable isotope shift between the weaning and the post-weaning period which might suggest an independent child foraging, children carbon and sulfur variability should rather be related to the continuity of parental individual feeding choices throughout later childhood.

The results for analyzed Transformational and Neolithic children buried in the Inner Gorges suggest that their mothers choose, on average, to reduce the intensity of suckles slightly earlier than concerning the previous period of occupations, i.e. during the second year, although this difference did not appear statistically significant and encompass variations. Average trendlines also indicate a continuous breastfeeding until at least 3 years old. In contrast with the previous periods of occupation, pregnant and lactating females substantially consumed marine-influenced proteins and choose to include in weaning preparations even higher amount of aquatic resources than in their own. The tissues of a few Transformational and Neolithic children formed at various age exhibit lower stable isotope values, which could be indicative of their non-local origin. The use of aquatic proteins to wean children has also been ethnographically documented: for instance, amongst groups of Northern Hemisphere foragers and fishermen, fats from terrestrial mammals, fish and seals were introduced quite early in infancy, and premastication of tougher food items was a common method of making fish, meat and venison, and fibrous roots and vegetal items, easily digestible for infants (e.g. amongst the Ainu, the Koryat and Yakuts, the Yupik and Inupiak, as quoted by Waters-Rist et al. 2010 and Tsutaya et al. 2015b; eHRAF 2018). Other paleodietary studies of foragers from different latitudes also reach similar conclusions, including European foragers (e.g. Waters-Rists et al. 2010; Howcroft 2013; Tustaya et al. 2015b; Smith et al. 2017; King et al. 2018; Gardner et al 2018).

Birth, death, life cycle and fish migrations: representation of time and conception of childhood

The observed changes in maternal nutritional choices noticed between the Late Mesolithic and the period of Transformation also chronologically coincide with a change in children funerary practices (Figure 71; Figure 72). While perinates and infant of were often found associated with adults in burials during the Late Mesolithic, the bodies of babies enter the domestic sphere during the period of Transformations, being buried in the rear of trapezoidal buildings, below the red lime plastered floor (Figure 72). The practice of burying perinates below (red plastered) house floors was common amongst the Near-Eastern-Balkan Neolithic sphere and could have been brought in the Gorges by migrants may reflect a modification of parenting strategy and/or of the management of the emotional impact of the death of newborn (Borić and Stefanović 2004; Stefanović 2006; Stefanović and Borić 2008). While the consumption of anadromous fish represented a substantial contribution to the diet of mothers and of young children, several sculpted boulders deposited just above the house floor depicted mixed human-like and sturgeon-like features. Associated with practices that involved the manipulation of parts of adult bodies, notably reburial of skulls, these sculpted boulders have been interpreted in relation to rituals involving apotropaic functions of the houses, where ancestors and totemic animals protect the becoming of the deceased children within the architectural space (Borić 2003 and 2005a; Stefanović and Borić 2008) Thereby, Near-Eastern Neolithic practices may have been adapted to local symbolic representations and means of expression. The ochre, color easily associated with blood (birth-death, female menstruation?), symbolically shifted from deposition above females' pelvic areas and the body of neonates toward the whole floor of the house, new receptacle for neonates' bodies during the period of Transformations. The particular nutritional choices of Transformational mothers may thus have to do with the increasing economic and symbolic importance of anadromous fish in foragers' society

Figure 3: Burial H297 from Vlasac with carp and Cyclope neritea ornaments (left). Reconstruction of cloak-type embroidered garment worn by a Late Mesolithic mother and her child on the basis of ornaments' distributions in Burials H2 and H 297 (right, drawing Mauro Cutrona). Adapted from Cristiani and Borić 2012

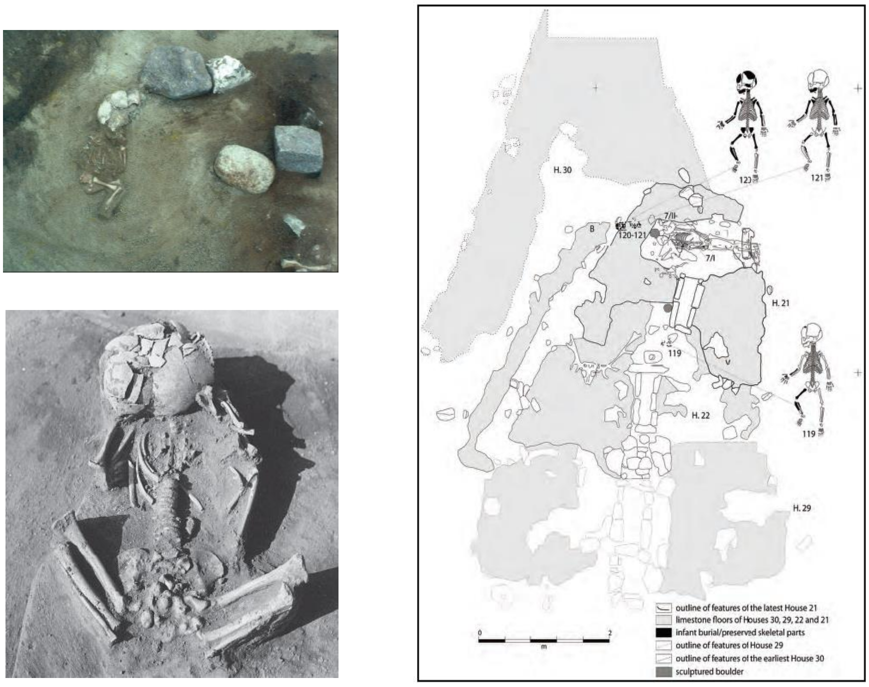

Figure 4: Burials from Lepenski Vir, period of Transformation. Perinate burial 98 from dwelling 19 (left, top), child burial 97 (left, bottom) and drawing of the dwellings 21, 22 and 29 with perinates burials 119, 120 and 121 and adult burial 7 (right). From Stefanović and Borić 2008.

after 6500-6200 cal BC. An easy association comes into mind when considering these contextual relationships between dead babies, anadromous fish and the house floors: a concern toward the expression of permanence and of cyclical aspects of time, perhaps as a mean to face the ultimate anxiety of a baby dramatic death. While house could indeed materialize the continuity of a family group (lato sensu), plastered floors were cyclically rebuilt one upon the other, and red-deer antler – falling and re-growing every year – were deposited upon the floors of abandoned houses. It is possible that the wide variability of Late Mesolithic and Transformational neonatal bone stable isotope values might reflect changes in birth seasonality, which could have coincide after 6200 BC associated with the time of the cyclical return of sturgeons-fish to spawn upstream in the river. Such relationships between the houses, age-related burial practices, symbolic artefacts, and subsistence practices that echoes the marking of time has also been suggested for Anatolian Neolithic (Pearson et al. 2015).

At Lepenski Vir there was a difference in the way individuals of different age groups were buried (Stefanović and Borić 2008). Amongst children, only neonates and three older children were buried below the house-floors: LV 61, LV 92, LV 97[282], respectively aged 4-7, 1.5-3.5 years old and determined as "juvenilis" (Stefanović 2016). Above the burial 92, two sculpted burials were found, one with "visible but 'closed' eyes" (carved horizontal lines – Stefanović and Borić 2008; Figure 74), and above the burial LV 61, a boulder representing a "face with eyes 'opened up' as engraved circles, as on all other representational boulders" (Figure 73; Stefanović and Borić 2008:164). While the LV 61 could have been entirely weaned at his death, the elevated values of the latest formed tissues of LV 92 clearly suggest that this child was still suckling. These differences in burial practices and in boulders' representations might relate to the differential social stage ascribed to the child at the time of his passing (ibidem): neonates without formed social persona may have remained associated to the house where they were born; a close-eye boulder could have been associated to the suckler who spent most of his time with his nursing mother while an open-eye boulder may have been deposited above the burial of the child who started to involve into different social activities. Weaning indeed represents an important stage in the social transition from being an infant to be a child, with a shift in the amount of time spent with the mother and with the other members of the community. Amongst analyzed children, these two also display the most elevated carbon, nitrogen and sulfur and LV 61 is the only analyzed children with available aDNA information, which indicate that he had a mixed European Mesolithic-like and Anatolian Neolithic-like ancestry (Hofmanová 2017). The presence of sculpted boulders might hence advertise the specific status of these children who also perhaps underwent a process of "nutritional socialization", that may have involved the consumption of aquatic resources from the youngest age. Similarly, the tissues of the Neolithic child LV 56 (Early-Middle Neolithic period, aged at death 6-10 years old), the only non-local child from the analyzed sample, also display elevated stable isotope values, indicative of his substantial consumption of marine-influenced proteins. Apart from remains of neonates, of the children LV 61, LV 92 and LV 97, only two burials of adults were dug through the building floor (LV 7, including LV 7/1a and 7/IIb and LV 26), placed in a different positions than the children (extended positions on their backs oriented with the heads pointing downstream - LV 7/1a and LV 26 - or disarticulated - skull LV 7/IIb, Figure 72 right; Borić and Stefanović 2008). As previously developed, the strontium values of these individual indicate their non-local origin (Borić and Price 2013) and the available mitochondrial aDNA information for LV 26 (haplogroup H5; Hofmanová 2017) also rather points to his Near-Eastern Neolithic ancestry (cf supra part 4.3.2 – 4.3.3). The fact that only the bodies of individuals whom presence in the community was relatively recent – neonates, young children, notably from mixed origin, or some non-local adults – were buried through the plastered-floor, points to the "multi-faceted" social role of the dwellings (Borić 2007b and 2008), where should have been practiced different "rites of passage" (perhaps involving nutritional transitions)

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[282] LV 97 is stored at the Lepenski Vir museum and was not examined in the frame of this PhD research; only available information assigned it to the "Juvenilis" category (Stefanović 2016).

that probably contributed to define and ascribe the levels of social-integration of the different components of foragers' community.

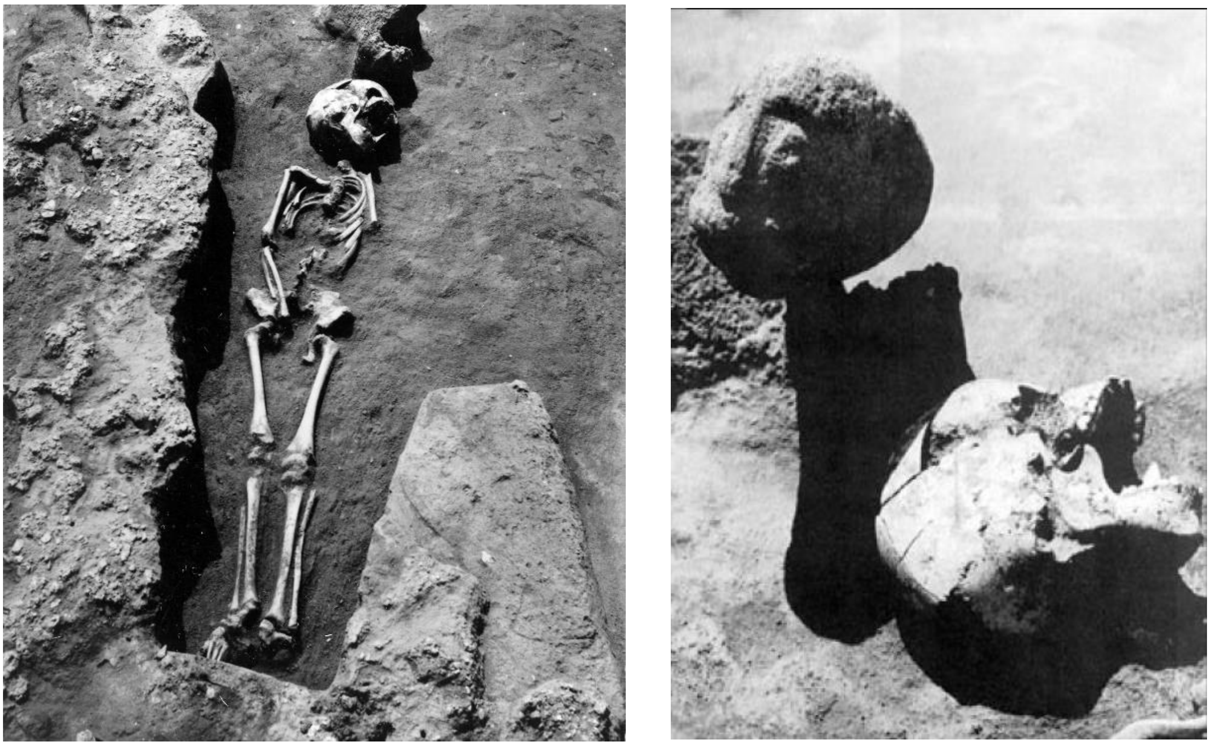

Figure 5: Child burial 61 in dwelling 40 (left, from Stefanović 2016), and "mermaid" boulder found above (right, from Srejović and Babović 1983). Lepenski Vir, period of Transformation.

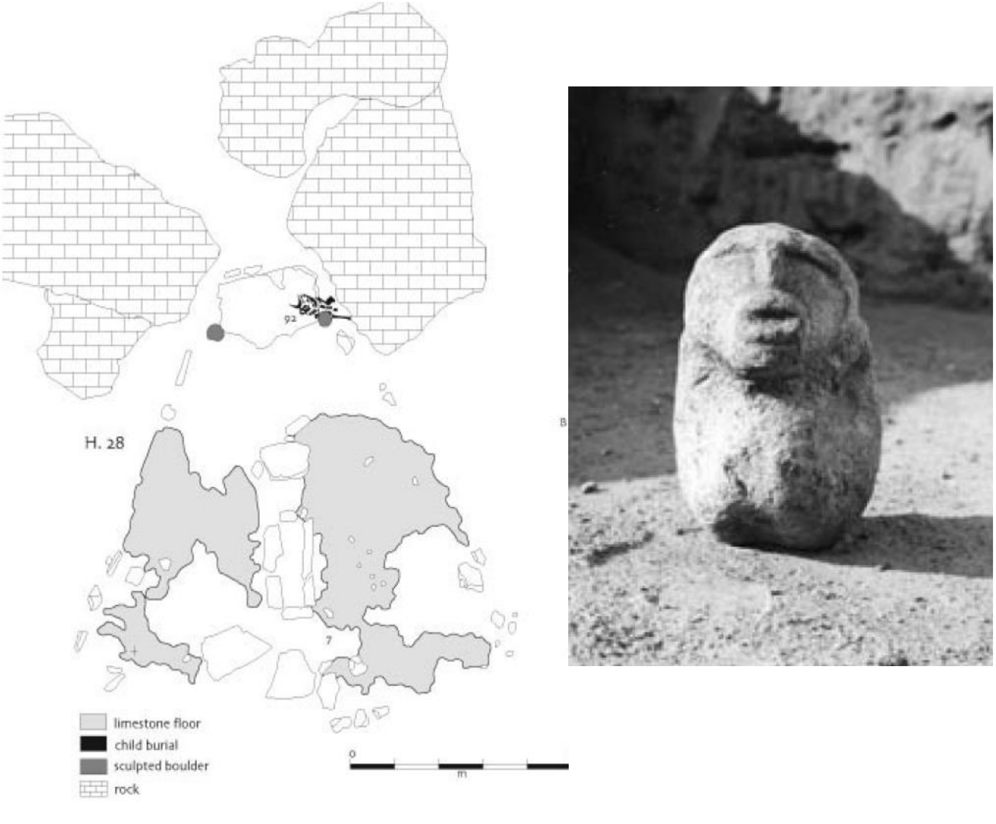

Figure 6: Dwelling 28 and child burial 92 (left) with associated Boulder 'Adam' (right, photo: Srejović and Babović 1983) from Lepenski Vir, period of Transformation Adapted from Borić 2005a.

Different weaning norms amongst the Early Neolithic of the Downstream Area

The breastfeeding and weaning practices of the Early Neolithic children buried downstream significantly differ with the practices of Mesolithic and Neolithic children buried in the Inner Gorges. They relied earlier (during the first year) on preparations mostly based on terrestrial lower trophic level resources and were probably breastfed until ca 3 years, which is consistent with the data available for Anatolian and Central European Early Neolithic communities (e.g. Oelze et al. 2012; Özdemir et al. 2019). Cereal and milk, perhaps with masticated meat and fats from terrestrial may have been the main component of these new weaning food (probably gruel-like preparations, bread or semi-liquid type of porridges). Domesticated cereals were present in the Early Neolithic sites of the Central Balkans and finds of querns and grinding stones at several sites suggest the preparation of cereal grain foods (Antonović 2003). While the analysis of lipids from ceramics indicated that pots mainly used to process fish in the region of the Gorges (Cramp et al. 2019), they contained residues of terrestrial mammal fats and dairies at most Early Neolithic of the region (Ethier et al. 2017); ceramic residues of dairies were more commonly found in early Neolithic context from the Central Balkans, where cattle remains were also more frequent than in Southern regions (ibidem). Milk and ground cereals would have been a good choice for gruel–they are easy to prepare and would have probably been available year-round. Hence, this study gives new insights into the potential importance of new domesticated products as weaning food at the earliest Neolithic, now ascertained for later period of European prehistory (e.g. Bronze Age, Donne et al. 2019). Genetic evidence indicate that children were also the only individuals able to digest raw animal milk during the 7th and 6th millennium BC. This new substitute – similar in appearance – to the maternal milk, may have increased the survival probability of children whom mother died giving birth and may have provided mothers an opportunity to be released earlier from the burden of lactation. These results are in line with ethnographic and paleodietary studies which suggest that the children who grew up in agro-pastoralist communities are more likely to be weaned and with animal milk and crop-derived food rich in carbohydrates, than sub-adults in hunter-gatherers populations (Sellen and Smay 2005; Hewlett and Lamb 2005; Lancy 2015; Tsutaya and Yoneda 2013; Tsutaya 2017; Chinique de Armas and Pestle 2018). Apart from the availability of milk cereal and ceramics, bone spoon characteristics of the Near-Eastern and Balkan Neolithic package may have also contributed to differences in the ways weaning food were prepared and served. Recent microscopic analyses of traces of uses on bone spoons from Starčevo contexts outside of the Danube Gorges have shown that they should have been used by babies, for mouthing activities and-or in relation with the development of new feeding practices (Stefanović et al. 2019). These kind of Neolithic bone spoons have been discovered only at Lepenski Vir in the Inner Gorges, Schela Cladovei at the exit of the Gorges and Ajmana and Velesnica downstream (Stalio 1986; Bonsall 2008; Vithezović 2017; Stefanović et al. 2019). As suggested by Stefanović and colleagues (2019), this different "maternal Neolithic package" may reflect deep differences in social organization related to baby care between European foragers and the first Neolithic agro-pastoralists.

Concerning some children buried at Ajmana, the results revealed a stable isotope offset of particularly important magnitude between dentine tissues formed during pregnancy-lactation and dentine tissues formed after supplementation, suggesting that maternal diet may have been richer in aquatic proteins than weaning preparations (e.g. AJ 1, 14, 13). Since analyzed adults display similar stable isotope values as weanlings, it is possible that they may not be entirely representative of the Early Neolithic individuals who buried their dead in the Downstream Area, or that some mothers chose to include more aquatic resources in their pregnancy diet to sustain the requirements in nutrients of their metabolic state. Interestingly, the child with the lowest stable isotope values (AJ 15) – who also displays a gross tooth decay (Jovanović 2017; Jovanović et al. 2015, de Becdelièvre et al. 2017, unpublished poster and podium presentations[283]) – has been identified as non-local.

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[283] de Becdelièvre, C., Jovanović, J., Hofmanová, Z., Stefanović, S. Who were the earliest farmers? Interactions - innovations - adaptations at Earliest Neolithic of The Central Balkans, Human Bioarchaeological Perspectives. Research presented at the 23rd European Association of Archaeologists Annual Meeting, (30.08.-03.09. 2017. Maastricht, Netherlands).

Interpreted together, these results question the possible influence of some migrants on the feeding practices of the other users of the grave, which would indicate a very different model of "nutritional socialization" than previously suggested for the Inner part of the Gorges and which may question the role of mothers in the transmission of the "agro-pastoral taste". While we noticed some variability in breastfeeding and weaning patterns amongst the different chrono-cultural groups analyzed, the feeding practices seem to have been more variable concerning the Mesolithic-Neolithic children buried in the Inner Gorges than concerning the Early Neolithic children buried in the Downstream Area. Considering that analyzed children from the Downstream Area were discovered grouped in a "multiple burial", the homogeneous weaning pattern might be explained by kinship ties. Besides, **the (practical and symbolic) values assigned by early agro-pastoralists to weaning foodstuffs may have been quite different from what Mesolithic foragers considered as appropriate. Agro-pastoral groups probably contributed to spread into Europe a very different conception of household, motherhood and of childhood than had the Mesolithic foragers, that may have included different "weaning norms". Such different parenting strategies may have differentially influenced Mesolithic foragers and Neolithic farmers demographic regimes.**

5.4.4. Maternal nutritional choices and health status: optimal feeding strategies and differential parental investments

Apart from females' fertility, these different ideas about childhood and children feeding practices may have also differently affected children morbidity and mortality rates. The model of the Neolithic Demographic Transition, as posited by J.P. Bocquet-Appel, indeed assumes that increased mortality rates should have followed and balanced the elevated fertility, and it has been suggested that children should have been the first victims of the agricultural shift (Bocquet-Appel 2001, 2008, 2011; Cohen 2008; Downey et al. 2014; Page 2016). The examination of bone and teeth markers of health status on skeletal assemblages from various foraging and farming contexts has also indicated an overall – although not systematic – pattern of health deterioration, including markers of metabolic disease and stress experienced during childhood (Armelagos et al. 1991; Bocquet-Appel and Bar-Yosef 2008; Cohen 2008; Pinhasi and Stock 2011). Changes in infant feeding practices, poorer nutritional conditions and an increase in pathogen loads due to the proximity with life-stock and to increased number of people living together have been deemed responsible for this increase morbidity and – assumed – mortality rates. Several studies noticed a relationship between weaning age and survivorship in various populations, from prehistory to nowadays (Katzenberg et al. 1996; Black et al. 2008; Pearson et al. 2010; Tenfeld et al. 2012; Sandberg et al. 2014; Beaumont et al. 2015; Beaumont and Montgomery 2016). Introducing supplementary food too early may be risky for children (unprepared gastrointestinal track and immunological system, loss of breastmilk nutrients), as well as a long reliance on low quality gruels (risks of iron-deficiency anemia, micronutrients deficiencies) or a belated supplementation (poor development of the immunological system, and inadequacy between breastmilk nutrients supply and new requirements for a child growth; e.g. Rawland et al. 1978; Armelagos et al. 1991; Macadam and Dettwyler 1995; WHO 2002; Black et al. 2005; Sellen 2007). The maternal decision to weigh the relative risks of initiating and delaying the introduction of supplementary food according to local ecological conditions has hence been stamped the "weaning dilemma" (Rawland et al. 1978).

It should be emphasized that all individual studied here – Mesolithic and Neolithic – did not survive to adulthood, which questions their representativeness: they may all have been at higher susceptibility of dying because of suboptimal feeding practices and/or may have experienced physiological stress for any reasons (inadequate diet or pathology) which could have also interfered with their stable isotope values

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Jovanović, J., de Becdelièvre, C., Stefanović, S., Le Roy, M., Herrscher E., Goude, G. 2015. Breastfeeding strategies and children's health status during Mesolithic-Neolithic transition in Serbia. Research presented at the Workshop Paleodiet meets Paleopathology. Using Skeletical Biogeochemistry to link ancient health, food and mobility. (15-16.10.2015. Santiago de Compostela, Spain).

(Katzenberg et al. 1996; Reynard and Tuross 2015). On this last point, the examination of longitudinal patterns of δ^{15}N and δ^{13}C covariation yet help to disentangle behavioral from physiological influences (Beaumont et al. 2015; Beaumont and Montgomery 2016). Keeping in mind that the skeletal evidence for physiological stress may point to individuals who were resistant enough to survive these stresses at least until their expression on bones or teeth ("the osteological paradox", Wood et al. 1992), the joint consideration of available indicators of health status, age at death and stable isotope fluctuations may provide further life history information about the relationships between experienced stress and nutrition amongst analyzed Mesolithic and Neolithic children (e.g. Prowse et al 2008; Hendersen et al. 2014; Sandberg 2014).

Dental pathologies

The general pattern of "health decline" often associated with the onset of the farming system has not been documented in the region of the Danube Gorges (cf part 2.3.2; Borić et al. 2011; Jovanović 2017; Jovanović et al. 2015, de Becdelièvre et al. 2017, unpublished poster and podium presentations[284]). Only a few Transformational-Early-Middle Neolithic individuals display evidence for dental caries, mostly absent amongst Mesolithic foragers. Those were discovered at the sites of Lepenski Vir (adults, mostly females, both non-locals and locals) and of Ajmana (adults and most children, including one adult female and two individuals of non-local origins), which coincides with the information from stable isotope analyses. The observation of a few dental caries mostly on the teeth of females interestingly follows the broad expectations of the NDT model, which features a dramatic increase in the occurrence of dental caries amongst females (Lukacs 2008). Observed amongst numerous populations spanning from the Neolithic to nowadays, this greater occurrence of caries in females' teeth have been explained by the influence of hormonal fluctuations during pregnancy on the composition and the flow rate of saliva (ibidem). With the shift towards carbohydrate-rich food consumption and a greater number of pregnancies, the Neolithic females were at higher chance of developing caries than their Paleolithic and Mesolithic ancestors. These results appear in line with the evidence for an increased number of non-local individuals – mostly females who ate at a lower trophic level – buried in the Inner Gorges from 6200 cal BC, but also with the higher growth rates inferred for the Early Neolithic period, notably concerning Early Neolithic communities of the Downstream Area. The fact that only Early Neolithic children buried Downstream at Ajmana, were affected by caries is consistent with the inferred differences in terms of infant feeding strategies between the Mesolithic-Transformational children buried in the Gorges and the children buried in the Downstream Area. These children (AJ 12-13-14-15) exhibit the lowest δ^{13}C and δ^{15}N values at death (from 3-6 years old to 11-14 years old) and the only non-local child AJ 12 exhibits the more developed tooth decay and the lowest stable isotope values from the group.

Skull lesions and metabolic diseases

Porotic hyperostosis, a skull lesion which can be the consequence of various pathological conditions, including parasites and inflammatory processes, has been observed at very frequent rates throughout the whole Mesolithic-Neolithic sequence (Angel 1984; Meiklejohn and Zvelebil 1991; Borić et al. 2011; Jovanović 2017). Currently ongoing researches indicate that Transformational and Neolithic individuals buried in the Inner Gorges (adults and children) exhibit proportionally less healed lesion than the Mesolithic individuals; the frequency of active lesion is also higher amongst children buried at Ajmana (Jovanović et al. 2015, de Becdelièvre et al. 2017, unpublished poster and podium presentations[285]). Several children analyzed for stable isotope values were associated with porotic hyperostosis (VL 64a, VL 51, VL 53, VL 5, HV 18, LV 61, LV 71, LV 43, AJ 1, AJ 3, AJ 8, and AJ 13), including high degree (VL 51, VL53, AJ 1) and active lesion (AJ 1, AJ 13, and LV 61). Amongst them, some children buried in the Gorges exhibit either particularly elevated δ^{15}N values associated with the breastfeeding period (exaggerated breastfeeding bell-curve) and elevated δ^{13}C values (VL 53), or slightly longer δ^{15}N than δ^{13}C

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[284] Cf note supra.

[285] Cf note supra

breastfeeding elevation and subsequent increasing δ^{13}C values during childhood (LV 61). Concerning the two children buried in the Downstream Area with active and/or high porotic (AJ 1 and AJ 13), they display slightly higher δ^{15}N and δ^{13}C values during early childhood than the others.

Cases of cribra orbitalia, lesions caused by metabolic disturbances, anemia and micronutrient deficiencies, have also been reported in the Mesolithic-Neolithic sequence of the Gorges (Borić et al. 2011; Jovanović 2017). Concerning the adults, the frequency of cribra orbitalia remains similar throughout the sequence (ca 30% for adults), although slightly more active lesions has been noticed on Transformational-Neolithic adults and no adults buried at Ajmana display evidence of lesion. Notewithstanding the fact that the sample of children with traces of cribra orbitalia is too small for comparisons to be significant (less than 5 individuals per geo-chronological groups), the dentine stable isotope values of several children exhibiting lesions can be considered (VL 53, HV 14, LV 71; active lesion concerning LV 71 and HV 14). They exhibit either particularly elevated δ^{15}N values associated with the breastfeeding period (exaggerated breastfeeding bell-curve) and elevated δ^{13}C values (cases of VL 53 and LV 71) or just a slight δ^{15}N weaning decline associated with a sudden elevation in δ^{13}C values (case of HV 14). Amongst the two analyzed children buried at Ajmana with traces of cribra orbitalia, one child (AJ 1), who also exhibit porotic hyperostosis displays slightly higher stable isotope values than the other children discovered in the burial, while the other (AJ 15) displays the lowest values. Interestingly, cribra orbitalia has also been observed on the skull remains of one neonate from Lepenski Vir, burial 120 (aged at death 36-41 gestational weeks; Stefanović and Borić 2008). This child displays one of the highest δ^{15}N values for this age group, also associated with high δ^{13}C and δ^{34}S values (δ^{15}N = 18.6 ‰, δ^{13}C : -18.3‰; δ^{34}S=13.3‰), which strengthens the assumption that the particularly elevated stable isotope values observed concerning neonates buried at Lepenski Vir should be related to a complex interaction between maternal physiology, physiological stress and aquatic resources consumption.

Enamel hypoplasia and physiological stress

Although the occurrence of enamel hypoplasia, caused by events of physiological stress experienced during childhood, remains low in the Gorges throughout the Mesolithic-Neolithic sequence in comparison with other archaeological populations (Jovanović 2017), greater frequencies of affected individuals have been noticed concerning the Early Neolithic individuals buried at Ajmana after 6000 cal BC, both adults and children. Interestingly, effort to determinate the age at which these stresses occurred indicate that most individuals experienced around 2.5-4.5 years old during the Mesolithic, and between 2.5-3.5 years old concerning Transformational and Neolithic children buried in the Inner Gorges and Downstream (Jovanović 2017; Jovanović et al. 2015, de Becdelièvre et al. 2017, unpublished poster and podium presentations[286]). This result coincides with the general isotope trendline which suggests overall later cessation of breastfeeding concerning the Mesolithic period. The comparison of the age at appearance of stress with longitudinal teeth stable isotope profiles also indicates that several children – mostly Transformational to Neolithic – experienced some episodes of elevated physiological stress during the weaning process (VL53, HV 14, LV 71, LV 87, and AJ 3, 13, 14, 15), ca 2-3.5 years old, while a few Late Mesolithic children may have experienced these stress at the end or after the end of the weaning process (after 3.5-4.5 years old; P11; VL 18c and VL 64a and 64). Only three Early Mesolithic children had well-preserved jaws allowing for considering hypoplasia P11, P23, P26a): two of them exhibit episodes for stress and were also included in the stable isotope analyses (P11 and P23). Given that dental hypoplasia were not frequently observed on the teeth of Early Mesolithic adults, it is possible that these children may have been less successful at surviving stress. The early Mesolithic parents of these children may have practiced protracted breastfeeding to provide a longer source of nutrients and buffer against/delay the consequences of these stress (age at stress ca 5 years for P11). Concerning Late Mesolithic and Transformational-Neolithic children buried in the Inner Gorges, the age at stress either coincide with elevated δ^{15}N values during the breastfeeding period (exaggerated breastfeeding bell-curve) associated with quite elevated δ^{13}C values (VL 53; case of LV 71?) or with an increase in δ^{13}C values

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[286] Cf note supra.

during the weaning process (decline in δ^{15}N values (HV 14; LV 87). Some of these children display higher degree of porotic hyperostosis (VL 53) and cribra orbitalia (HV 14, LV 71, AJ 1 and AJ 15). Finally, concerning our ongoing research on children body proportions, it can be mentioned amongst the children that appear below today's reference curves (body size: LV 71, AJ 3 ad AJ 13; body weight: LV 71, LV 27c, AJ 13 and AJ 14), on display elevated longitudinal stable isotope values (LV 71), while the other, rather depleted values (AJ 3, 13, 14). Similarly, we did not find correlation between children bone-to-teeth important offset and enamel hypoplasia.

The etiology of skeletal expressions of physiological stress are likely diverse; in the Gorges, it has been notably suggested that parasitic infections, for instance tapeworm fish, may have affected foragers' ability to metabolize some essential micronutrients (e.g. Meiklejohn and Zvelebil 1991). Increased rates of inflammatory processes on skulls and long bones have also been interpreted as the evidence for infectious diseases and perhaps increased infectious rates with the increased interactions with people from diverse horizons during the period of Transformations (Stefanović 2012). In the Gorges, some association between the timing of hypoplasia, the presence of cribra orbitalia and of porotic hyperostosis and stable isotopes fluctuations suggests that mothers may have developed individualistic feeding strategies adapted to environmental stressors. For instance, a protracted breastfeeding and gradual breastfeeding has been suggested for the Early Mesolithic child P11, who later exhibit some physiological stress. The particularly elevated δ^{15}N ratios observed during the breastfeeding period of the Late Mesolithic child VL 53 – who also display porotic hyperostosis and cribra orbitalia – could be associated with the appearance of an hypoplasia and may be explained by the interaction between breastfeeding, physiological stress and perhaps a supplementation with aquatic resources, as suggested by its jointly high δ^{13}C and δ^{34}S values. During the period of Transformations-Neolithic, several children display hypoplasia during the weaning, associated with an increased consumption of aquatic resources (e.g. HV 14, LV 87, LV 71), and may also display protic hyperostosis or cribra orbitalia (e.g. HV 14; LV 71). It is possible that the mothers of these children opted for aquatic resources as an accurate source of proteins and micro-nutrients to buffer against the physiological or metabolic stress experienced by the offspring. In contrast, despite the higher occurrence of stress experienced during the weaning process, the children buried at Ajmana were fed with similar plant-based preparations and perhaps with milk. Only one child – AJ 1 – has cribra orbitalia and high degree of active porotic hyperostosis and may have been feed with food of slightly higher δ^{13}C values (more aquatic resources? or suides meat?). A greater number of children buried at Ajmana exhibit active porous hyperostosis and cribra orbitalia and the occurrence of dental hypoplasia is more frequent amongst adults and children discovered at Ajmana than amongst Mesolithic-Neolithic individuals buried in the Inner Gorges. An earlier introduction of weaning food of lower protein-content might have been detrimental to the health of children, notably because of the invasion of new pathogens, the decrease of the positive effect of passive immunity with breastmilk; the use of non-sterilized equipment, such as ceramics and bone spoons, may have increased children contaminations; reliance on a low quality gruel for an extended period of time after weaning may also increase the risk of iron-deficiency anemia, nutritional deficiency and infections (Rheinhold 1982; Sandberg et al. 2014). Besides animal milk does not contain the same nutritional content than maternal milk, used too early – in replacement of maternal milk – or without adequate additional supply in nutrient, it may have caused gastrointestinal infections and micro-nutrient deficiencies, notably iron-deficiency anemia (Howcroft et al. 2012; Dunne et al. 2019).

5.4.5. Some possible bio-demographic mechanisms beyond the Neolithic Demographic Transition

The results hence suggest intrinsic differences between Mesolithic foragers' and Early Neolithic agro-pastoralists' parental strategies. **While mothers of the children buried in the Inner Gorges may have opted for individualistic feeding strategies, probably in concordance with the value assigned to aquatic resources by the local foragers, in contrast "weaning norms" were so strong**

that Early Neolithic communities disregarded the use of aquatic resources at the detriment of a child health. Fertility may have benefited from higher childhood mortality, because the later would have reduced the time with a dependent offspring (Knodel 1968; Preston 1978; Armelagos and Maes 2006). Perhaps not the primary impetus that triggered population growth in core areas of agricultural development, children mortality per itself may have paradoxically contributed to stimulate females' fertility when changing ecological conditions, through mechanisms of quality-quantity trade-off (Page et al. 2016). It has been hypothesized that where the cost of having fewer survival offspring than the optimal number is greater than the cost of ending up with too many, fertility rates will increase above that needed to compensate for the mortality rate (Leslie and Winterhalder 2002, Winterhalder and Leslie 2002; Page et al. 2016). This scenario might be particularly relevant for secondary areas of Neolithization, such as the Central Balkans, where the farming niche spread particularly rapidly into new environmental conditions. **Mediated by different cultural conceptions of household, maternity and childhood than those which prevailed amongst groups of European Mesolithic foragers, the spread of the Neolithic into various environments may have been accompanied by a different response to the "weaning dilemma", whereby mothers may have invested more in offspring quantity rather than quality and thereby increased their reproductive fitness. Such intricacies between fertility and mortality might hence have contributed to the fast spread of the Neolithic in some regions of Western Eurasia (Pérez-Losada and Fort 2010), such as the Central Balkans**. Coupled with paleodemographic proxies, further life-history analyses conducted on Early Neolithic individuals from Western Anatolia to Central Europe may allow for further exploring these hypotheses in contexts of mobile early Neolithic groups, migrations, population growth and elevated level of physiological stress (e.g. Bocquet-Appel and Bar-Yosef 2008; Hershkovitz and Gopher 2008; Porčić et al. 2016; Ash et al. 2016; Blagojević et al. 2017; Jovanović 201). The development of serial dental sampling strategy may also allow for comparing the nutritional and health profiles of those who died during childhood with those who survived adulthood and hence to further explore the influence of differential feeding strategy on later health outcome and survivorship.

In various respects it can be assumed that the influences of maternal nutritional strategies and children feeding practices on females' fertility among pre-industrial societies might have been more complex than assumed by the hypothesis of a breastfeeding-induced hormonal control on ovulation; attempts to understand these influences should involve a multivariate approach (Roth 1981; Ellison 1994; Vitzthum 1994). Valleggia and Ellison have suggested that the resumption of post-partum fertility may not depend on the intensity of nursing per se but rather on maternal metabolic budget (Valleggia and Ellison 2006, 2009). Ovulatory cycling has been found to resume when a woman has experienced a sustained period of positive energy balance and the considerable energetic cost of lactation to maternal metabolic budget should most likely influence the timing of this transition towards positive energy balance and return to fertility (ibidem). Drawing upon this "metabolic load model", it has also been hypothesized that changes in nutrition with the shift towards high carbohydrate food consumption (higher energy intake), earlier weaning (lower energy expenditure), in conjunction with changes in activity patterns related to the sedentary lifestyle, village life, social and workload organization (lower energy expenditure) may have jointly contributed to affect maternal energetics and to influence females' fertility patterns (Bocquet-Appel 2008). With a different conception of household and childhood, older children may have also contributed to underwriting the energetic cost of caring for the toddlers, releasing maternal energetic budget for reproduction (Kramer and Boon 2002). **The differential amount of aquatic proteins and carbohydrates food consumed by the mothers of the Mesolithic-Neolithic children buried in the Inner Gorges and of the Early Neolithic children buried in the Downstream Area or in the broader Central Balkans, as well as the differential parental investment in each offspring and perhaps different allo-parenting practices may hence have jointly contributed to locally influence the fertility rates**.

Some studies have suggested that adiposity, lean body mass and body mass index (BMI) correlates with females' fertility rates, because of the total energetic cost of pregnancy and lactation (Tracer 1991;

Page 2016). While a generalized reduction in body height is associated with the Neolithic Transition in Europe (e.g. Holt 2018), preliminary results for the Central Balkans also suggest that Early Neolithic females – particularly those buried in the Southern Pannonia plain – had higher BMI than the Mesolithic females buried in the region of the Gorges (e.g. Jovanović 2017; de Becdelièvre et al. 2017, unpublished podium presentation[287]). This higher BMI may have provided females with a greater reserve to deal with successive pregnancies. Besides, fertility is not only defined by changes in post-partum interval duration but may also be significantly influenced by the total duration of the reproductive period, of which utilization may be socially prescribed (Frische 1978; Roth 1981). It has been suggested that the age at menarche should be very sensitive to the accumulation of fat in a woman's body (Frische 1978). A diet enriched in carbohydrate and greater adipose storage – perhaps reflected by the inferred differences in BMI – may have hence contributed to an earlier attainment of menarche by Early Neolithic females. R. Howcroft emphasized that "the determinants of female fertility do not […] only act in adulthood, rather there is an increasing body of evidence to suggests that conditions experienced in early life can shape a women's reproductive potential" (Howcroft 2013: 66). The conditions experienced in utero may indeed influence the age at menarche and the overall body proportions: girls who had lower birth rates reached menarche earlier and had smaller adult size than those with higher birth rates (Cooper et al. 1996; Ibáñez et al. 2000; Dos Santos 2002) and children born during harsher periods had a greater number of offspring (Huber and Fieder 2009). Childhood environment may also further influence the onset of menstruation and adult ovarian function (Cooper et al. 1996; Dos Santos 2002; Núñez-de la Mora et al. 2007). **It is hence possible that the differential conditions experienced from fetal stage to childhood may have differently impacted Mesolithic and Early Neolithic females' developmental trajectories.** As overall shorter size is documented amongst European Neolithic females, it is possible that the new nutritional conditions experienced in utero and during childhood, as well as the different pathogen loads or environmental stressors, may have resulted in a physiological adaptation where reproduction has been prioritized over growth and development. **As hypothesized by R. Howcroft, our results suggest that differences in children feeding strategies at the advent could have affected maternal fertility level, by influencing not only the duration of the post-partum interval, but also different aspect of the reproductive development of the child**. Assuming that children feeding strategies may have affected females' reproductive development, and notably favored fertility, it is also possible that the intake of animal milk and of cereal during essential phases of ontogenesis may have also played a role in the gradual selection of alleles that facilitated the digestion of lactose and carbohydrate during later childhood and adulthood between the Neolithic and later periods of Bronze age (Burger et al. 2007; Perry et al. 2007; Itan et al. 2009; Gerbault et al. 2011; Mathiesen et al. 2015).

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[287] Cf note supra

6. δ^{13}Cenamel: a pilot study on childhood to adulthood dietary transitions.

- Third permanent molars stable isotopes signatures, carbohydrates-lipids-proteins routing -

6.1. δ^{13}Cenamel, methodological considerations

Additional information about dietary adaptations over the Mesolithic-Neolithic Transformation have been collected from the analysis of the carbon stable isotopes ratios measured, as a pilot study, on third molar enamel carbonates (δ^{13}C$_{enamel}$) – a tissue formed during teenage – on the remaining samples of teeth analyzed for paleogenetic analyses (cf part 3.3.). In the context of the agricultural transition, the analysis of δ^{13}C ratios from apatite may provide a useful proxy to detect differences in the energy part of the diet and particularly in the fat component of resources, as lipids have depleted δ^{13}C ratios compared to proteins and carbohydrates (DeNiro and Epstein 1977; Jim et al. 2006; Logan et al. 2008).

6.1.1. Establishing the local stable isotope baseline

Carbon enamel values jointly obtained on the teeth of C$_3$ terrestrial herbivores (mean herbivores values: -14.3‰; Appendix A.V.1.) and freshwater fish (mean fish values: -5.8‰; Figure 75) range in the excepted values for these ecosystems (Lee Throp et al. 1989, Kellner and Schoeninger, 2007; Grupe et al. 2009, Shin and Hedge 2012; Codron et al. 2019). Although the sample size is small, both Mesolithic terrestrial herbivores analyzed (n=2) range within the variability of Neolithic terrestrial herbivores (n=5), which suggests that the local environmental conditions did not dramatically change through time. Concerning humans, results show different ratios according to the time period and to the site considered (Figure 75). Early and Late Mesolithic humans display lower δ^{13}Cenamel values ranging from -16‰ to -14‰ (mean±1SD: -14.9±0.4‰, n=22). The δ^{13}Cenamel range of Transformation and Neolithic individuals buried in the Inner Gorges is broader, from -15.7‰ to -12.4‰, including higher values (mean±1SD: -13.7±0.9‰, n=22). Individuals buried downstream, at the site of Ajmana, display higher δ^{13}Cenamel values. These results suggest a difference in the energy part of the diet of Mesolithic children-teenagers in comparison with the childhood-teenage diet of some of the Transformational-Neolithic buried in the Inner Gorges and with the childhood-teenage diet of individuals inhumated downstream: particularly the diet of Mesolithic individuals may have included more fats, δ^{13}C depleted, likely from the consumption of meat or fish, than the Neolithic one which may have included greater proportions of carbohydrates and fat-depleted resources perhaps from plant-based resources (cereals?).

6.1.2. Establishing the Δ^{13}Cenamel-to-collagen spacing

The difference between the δ^{13}C apatite and δ^{13}C collagen values has been correlated to the food web, since herbivores, omnivores and carnivores exhibit different Δ^{13}C carbonates-to-collagen spacings in relation with the fact that animals contain more lipids than plants, the offset being smaller in carnivorous than in herbivorous animals (e.g. Lee-Throp et al. 1989; Kellner and Schoeninger 2007, Grupe et al. 2009, Shin and Hedges 2012, O'Connel and Hedges 2017; Codron et al. 2019). Besides, the Δ^{13}C carbonates-to-collagen offset could also inform upon the departure from a mono-isotopic diet, i.e. whether macro-nutrients consumed originated from a single or differing ecosystem(s) (e.g. C$_3$, C$_4$, terrestrial, marine or freshwater; e.g. Kellner Schoeninger 2007, Froehle et al. 2010, Froehle et al. 2012). Considering that δ^{13}C bone apatite value is enriched of ca 10.7±1.4‰ in comparison with the δ^{13}C value of the diet (estimation from Salesse 2015; data from Howland et al. 2003 and Warinner and Tuross 2009), that δ^{13}C enamel value is enriched of ca

13.4±1‰ in comparison with the δ^{13}C value of the diet (estimation from Salesse 2015; data from Passey al. 2005 and Warinner and Tuross 2009), and given that δ^{13}C collagen is enriched of ca 5‰ in comparison with the diet (Ambrose and Norr, 1993), it can be estimated that the Δ^{13}C carbonates-to-collagen offset for a mono-isotopic diet should range around 6-8‰, varying according to the tissue analyzed (bone apatite or teeth enamel). For prehistoric herbivores of the Danube Gorges, the Δ^{13}C enamel-to-collagen has been calculated using the average deer collagen values: animals range between 6 and 9‰, which also coincides with the reference Δ^{13}C bone apatite-to-collagen values for free ranging herbivores (Figure 76). Hence, it can be assumed that an individual with Δ^{13}C apatite-to-collagen values close to 6‰ and Δ^{13}C enamel-to-values close to 8‰ should have a mono-isotopic diet based on the consumption of C_3 plants (both energy and proteins mainly derived from C3 plant) while lower Δ^{13}C offsets may indicate the departure from a mono-isotopic diet, for instance the consumption of proteins from a marine environment and of energy from C_3 terrestrial environment (such as plants).

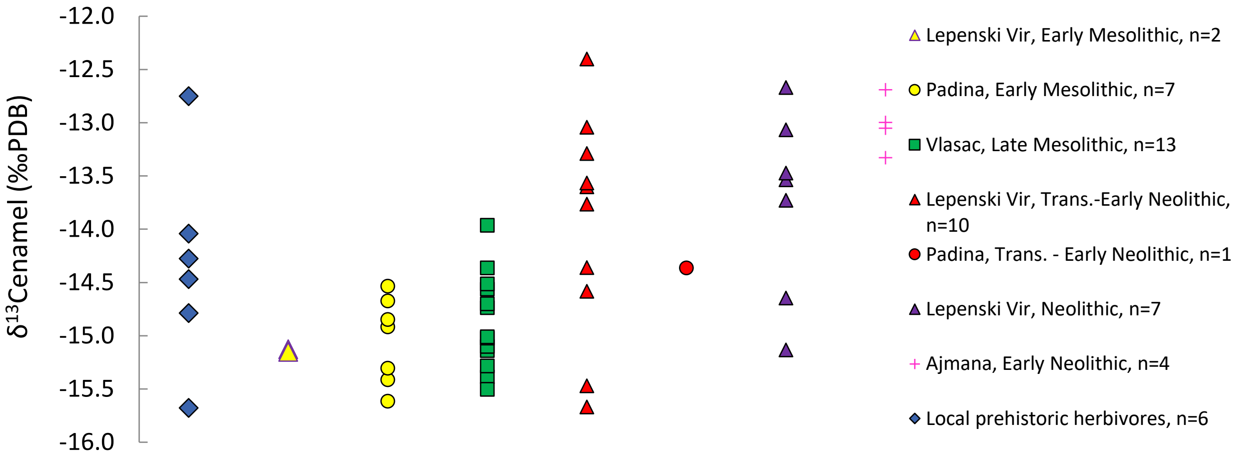

Figure 75 : $\delta^{13}C_{enamel}$ of Mesolithic and Neolithic humans grouped chronologically and per sites

One can stress that the trophic level between dietary δ^{13}C values and δ^{13}Cenamel is greater than between dietary δ^{13}C values and δ^{13}C bone apatite values, which can be due to an additional fractionation occurring during tooth enamel formation related to the release of bicarbonate ions by ameloblasts (Webb et al. 2014). Several archaeological studies[288] compared this Δ^{13}C enamel and Δ^{13}C apatite for the same individuals, estimating offsets of +0.6±1.5‰ (Loftus and Sealy 2012; n=33), +1.7±2.5‰ (France and Owsley 2012; n=16), +1.7±0.8‰ (Salesse et al. 2015; n=109), +1.74±1.19‰ (Zhu and Sealy 2018; n=51); +1.8±2.3‰ (Santana-Sagredo et al. 2015; n=19). Therefore, since the reference Δ^{13}C carbonate-to-collagen for animal was computed using bone carbonate (Figure 76, right part), we considered more accurate to compare the Δ^{13}Cenamel-to-collagen of prehistoric human (Figure 76, left part) and of animals with a Δ^{13}Cenamel-to-collagen *corrected for enamel to apatite spacing of +1.8‰* (Figure 76, right part). It should be emphasized that this approach only provides a broad indication for the possible range of values encompassed by Danube Gorges human Δ^{13}C apatite-to-collagen values, and it must be born in mind that: (1.) the relationship between δ^{13}C enamel and δ^{13}C bone apatite is not linear (Zhu and Sealy 2018) and (2.) in most cases, the δ^{13}C bone collagen signal was formed later on during the life of the individual (at death) than the δ^{13}C enamel signal (between 8-15 years). Considering these limitations, further models developed to quantify the proportions of energy and proteins from C_3, C_4 or marine ecosystems (Kellner and

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[288] These studies mostly compared adult bone values with the values of second premolars, second and third permanent molars, all formed above 3 years. The study of Webb et al. (2014) indicates a greater offset (+4.3±1.2‰; n=10), but focused on the bone of children who died between 4 and 10 and included first permanent molars and may thus be influenced by particular weaning and growth effects (cf part 5.3*).* Other studies whom sample may be affected by the weaning/growth effect or which did not specify which teeth were analyzed and/or the individual age at death are not mentioned here (e.g. Serreno et al. 2008; Zazzo et al. 2013).

Schoeninger 2007; Froehle et al. 2012; Eerkens et al. 2013) were not applied in this study given that they have been based upon δ^{13}C apatite values *from bones* of animals fed with monitored diet.

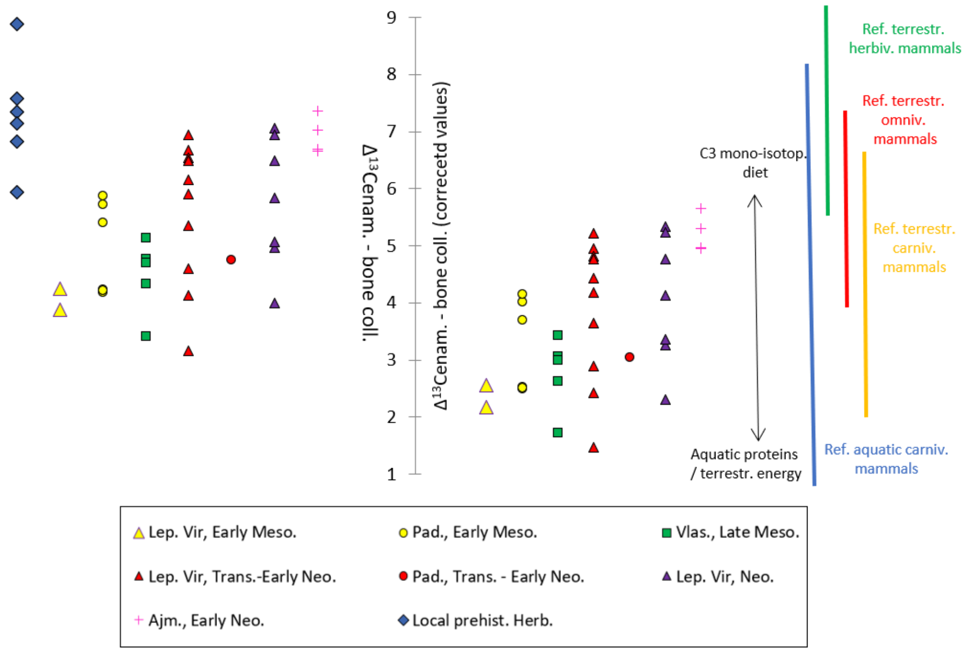

Figure 76 : $\delta^{13}C_{\text{enamel - bone collagen}}$ of Mesolithic and Neolithic humans grouped chronologically and per sites (cf caption details: Appendix A.V.)

6.2. Changes in the energy component of the diet

6.2.1. Mesolithic teenagers' diet

Early and Late Mesolithic human δ^{13}C enamel values range in the lower part of the local prehistoric human variability, suggesting that the diet of children-teenagers was likely more influenced by the consumption of fats from meat and fish than the diet of Transformational and Neolithic children-teenagers (Appendix A.V. 2). Yet, it can be mentioned that the two Early Mesolithic individuals buried at Lepenski Vir as well as some of the individuals buried at Padina exhibit higher δ^{13}C collagen values and thus lower δ^{13}Cenamel-to-collagen values than the other individuals buried at Padina (Appendix A.V. 3-4). This could be explained by a difference in the consumption of fish species, at least at the adult age (different collagen value). It is possible indeed that the higher Δ^{13}Cenamel-to-collagen values of the Early Mesolithic individual buried at Lepenski Vir and of some of the individuals buried at Padina may be related to a greater departure from the mono-isotopic diet and to the dietary combination of isotopically enriched marine-influenced protein and isotopically depleted fuel (fats from fish and meat and C_3 carbohydrates). The comparison of Δ^{13}C enamel-to-collagen values with the isotopes of Nitrogen and Sulfur also support this interpretation (Appendix A.V.4): two individuals buried at Padina with lower δ^{13}C collagen values and higher Δ^{13}C enamel-to-collagen values also display high δ^{15}N values but lower δ^{34}S values than the others, suggesting that they were probably including less marine-influenced resources (anadromous fish) than the other in their diet. One individual also exhibits lower δ^{13}C collagen values and higher Δ^{13}C enamel-to-collagen associated with lower δ^{34}S and δ^{15}N values (Pad. 18b: δ^{15}N=12.7‰), suggesting that he may have consumed fewer aquatic resources than the others.

Concerning the collagen stable isotope values of the children-teenagers who did not survive to adulthood, it has been suggested that the few Early Mesolithic children analyzed buried at Padina had a diet similar as most adults: probably a mixed diet including an important consumption of meat from terrestrial game and freshwater fish (Appendix A.III. 9; 12-14). However, it can also be noticed that two that two individuals buried at Lepenski Vir aged at death circa 15-19 years old exhibit higher $\delta^{15}N$ and $\delta^{13}C$ or $\delta^{13}C$ and $\delta^{34}S$ values than Early Mesolithic adults (Appendix A.III.9). Therefore, considered jointly these results indicate that: (1.) most Early Mesolithic individuals had a diet enriched in the consumption of proteins and lipids from animal meat and fish from childhood; (2.) the Early Mesolithic individuals buried at Lepenski Vir and probably some of the individuals buried at Padina were consuming marine-influenced fish species already during teenage; in contrast, the stable isotope values of children and of some adults buried at Padina have rather been influenced by the consumption of stationary freshwater and terrestrial games; (3.) the comparison of the collagen values of those who died during childhood-teenage with the collagen values of those who survived adulthood, and with the apatite signal around 8-15 years old of those who survived adulthood, does not suggest important differences in terms of dietary habits between childhood, teenage and adulthood during the Early Mesolithic period; the analyzed children from Padina who died during childhood probably had a mixed diet, including stationary freshwater resources and terrestrial games while some of the individuals buried at Lepenski Vir who survived to late teenage or adulthood likely consumed more marine-influenced species. (4.) since the comparison of $\delta^{13}C$ enamel values with $\delta^{13}C$ collagen values suggests that some Early Mesolithic were consuming marine-influenced species, the $\delta^{34}S$ shift perceived between the Early and the Late Mesolithic cannot be solely explained by a sudden dietary change but should rather be understood as a combination of environmental and behavioral factors (i.e. a shift toward higher values perhaps under the increased salinity of the Black Sea and of the Danube estuary and a greater consumption of anadromous species by most members of the Late Mesolithic community).

The values of $\delta^{13}C$ enamel of those who survived to adulthood (no teenagers or young adults in the Late Mesolithic sample analyzed for $\delta^{13}C$ enamel) are similar as the values obtained for the Early Mesolithic period (Early Mesolithic: 15.1±0.3‰; Late Mesolithic: 15±0.4‰; Figure 75). The $\Delta^{13}C$ enamel-to-collagen values also indicate a rather carnivorous diet, probably with the combination of isotopically enriched proteins (marine-influenced) and depleted fats and C_3 carbohydrates (Figure 76). Yet, regarding collagen stable isotope values, we noticed that the analyzed children who died before or around 10 years old range for $\delta^{13}C$ in the lower part of adult variability and exhibit lower $\delta^{34}S$ than analyzed adults (Appendix A.III.9). It is thus possible that late childhood and teenage represented a transitional period when Late Mesolithic individuals increase the consumption of anadromous fish and/or dogs' meat. It can also be hypothesized that the diet of the children analyzed for collagen stable isotopes - the children who died - may not have been representative of the diet of the diet of those who survived, who perhaps included higher amounts of fats and of proteins from marine-influenced fish in their diet (fishes from the salmonidae and acipenseridae family having rather high fat contents), sources of nutrients which may have contributed to buffer against biological stress. Results also indicate a possible difference in males and females values, albeit limited by the size of the sample, Late Mesolithic males from Vlasac (n=3; average: -14.8±0.3‰) ranging in the low variability of females from the site (n=5; average: -15.2±0.4‰; Appendix A.V.6). It can thus be hypothesized that some position or role within the Late Mesolithic community may have been socially defined during late childhood and/or teenage. This possibility may open insights on important periods of "passage" during the lives of prehistoric individuals and would have implications for our understanding of the symbolic and socio-cultural organization of the Mesolithic society.

6.2.2. Transformation-Neolithic teenagers’ diet

Concerning the period of Transformation/Early Neolithic and the Early-Middle Neolithic, one can notice a broadening of $\delta^{13}C$ enamel signal toward lower values (<-14‰), which suggests that some individuals probably consumed, around 8-15 years old, resources with a lower fat-content than the resources consumed by Mesolithic children-teenagers, likely more plant resources and less meat/fish (Figure 75). The Δ^{13}Cenamel-collagen offset of these individuals is also closer to the C_3 mono-isotopic diet and to the values of terrestrial herbivores mammals (Appendix A.V.3). Several Transformational-Neolithic individuals from the assemblage of Lepenski Vir who exhibit higher δ^{13}Cenamel, as well as one Early Neolithic individual from Ajmana, died during teenage or as young adults, and it can thus be assumed that their collagen reflect a stable isotope signal partially formed contemporaneously to the analyzed enamel signal (individuals AJ 3, LV 122, LV 48, LV 54E, LV 66; δ^{13}Cenamel: 13-13.6‰; Appendix A.V.5). Four of them have a Δ^{13}C which coincides with the reference values of omnivorous animal. All individuals buried at the site of Ajmana exhibit higher δ^{13}C enamel signal (<-13.3‰) which confirms the observations performed on the analyses of children and adult bone collagen (Figure 75): these individual likely consumed less marine-influenced fish and had a rather fat-depleted diet, probably including greater amount of carbohydrates in their diet (cereals?).

In the Inner Gorges, we previously noticed that the δ^{13}C collagen values of those who died before 8-10 years old range in the high part of adult variability, suggesting that they were consuming marine-influenced resources during childhood; most individuals who died between 10-19 years also display elevated collagen values and only two teenagers range in the low part of adult variability (Appendix A.III. 10; 12-14). This broadening of the δ^{13}C enamel signal toward higher values could thus indicate whether that the children analyzed for collagen (the children who died) may not be representative of the diet of all children or that some children shifted their diet toward a lower consumption of fats and proteins from animals and a greater consumption of carbohydrates from plants after 8-10 years old. Alternately, this broadening may also be due to the presence of non-local individuals and of individuals with a different genetic ancestry as the local Mesolithic foragers (non-U maternal lineages, rather pointing to the Near East Neolithic), who perhaps had a different δ^{13}C signal before migrating in the Gorges.

When the δ^{13}C enamel signal of locals and non-locals discovered in the Inner Gorges are compared, one can notice some overlap (Appendix A.V.7, upper graph). Most non-locals exhibit rather low δ^{13}C enamel values (<-14‰ in 6/9 cases) but three of them range in the variability of Mesolithic locals (>-14‰: LV 27a, 7Ia and 20) and four Transformational/Neolithic locals display higher values (<-14‰: LV 54D, 48, 37 and 87/1). Concerning genetic ancestry, seven individuals with the rather "Near Eastern and European Neolithic like" maternal lineages J, T, K, H, N exhibit higher δ^{13}C enamel values (LV 66, 8, 82, 32a, 54e, 122, 54D) and one Neolithic individual with the rather "European Pre-Neolithic like" U5 lineage exhibits lower δ^{13}C enamel values (LV20), similar as the values of Mesolithic individuals typed U5 (Appendix A.V.7, middle graph). In contrast, one individual assigned to the rather "Near Eastern and European Neolithic like" N (LV 27b) displays lower δ^{13}C enamel values and one U-typed individual (LV 87/1) has high δ^{13}C enamel values. When both strontium and ancestry are cross-compared with δ^{13}C enamel (Appendix A.V.7, lower graph), it appears that all non-locals assigned to Non-U maternal lineages (J, H, N, T, K lineages) exhibit higher δ^{13}C signal (<13.5‰): these individuals probably arrived in the Gorges after the formation of the crown of their third permanent molar. Their putative descendants, the locals assigned to Non-U maternal lineages (K and N lineages), exhibit lower values (between 13.8 and 15.5‰), which suggests that some of them consumed fat-enriched resources between 8-15 years old, perpetuating the local subsistence practices. Yet, one local individual assigned to the U5 lineage (LV 87/1) has the highest δ^{13}C enamel signal (-12.4‰), suggesting that his diet may have included less fat and proteins from meat/fish and more C_3 carbohydrates.

Therefore, a part of the Transformational-Neolithic broadening in δ^{13}C enamel signal can be related to the childhood/teenage diet of the non-local individuals with Non-U haplogroups probably before they migrated in the Gorges. The δ^{13}C enamel signal of some of their descendants rather indicates that they substantially consumed fats from meat/fish around 8-15 years old, similarly as local Mesolithic individuals. In contrast, some of the Transformational-Neolithic locals, including an individual U-typed (rather European Pre-Neolithic like), also consumed lower amounts of fats from fish-meat when they were 8-15 years old. When interpreted in the light of the results obtained on the longitudinal collagen sampling of the children who died, these results also suggest whether that some of the local children shifted their diet around 8-10 years old toward a lower consumption of fish and meat or that the collagen stable isotopes values of the sample of children who died might not be entirely representative of the diet all Early Neolithic children (some children were perhaps particularly fed with marine-influenced resources to buffer against specific biological stress experienced early in their life?).

6.3. Gathering life-history information, childhood-to-adulthood shift in diet

At a life-history level, further clues about changes in diet between childhood and adulthood can be collected by looking for possible mismatch between the δ^{13}C enamel signal at 8-15 years old and the dietary information obtained from the joint analysis of stable isotopes collagen signals at death (δ^{13}C, δ^{15}N and δ^{34}S). For instance, it can be noticed that some Transformational - Neolithic individuals buried at Lepenski Vir exhibit quite elevated δ^{13}C enamel - collagen spacings, indicative of a rather C_3 monoisotopic diet but also display elevated δ^{15}N and δ^{34}S values, rather indicative of the consumption of marine-influenced proteins (Appendix A.V.4). Hence, based upon their δ^{13}C collagen, δ^{15}N and δ^{34}S values, individuals have been assigned to four broad diet groups[289], informing about their diet at the time of their death: "marine-influenced proteins consumers", "aquatic and/or higher trophic level resources consumers", "mixed aquatic and terrestrial diet", "terrestrial or lower trophic level resources consumers"; the δ^{13}C enamel was then examined per dietary groups in order to identify possible mismatch between the dietary information around 8-15 years old and the information at death (Figure 77; Figure 78). It can be first noticed that all but one Mesolithic individuals display lower δ^{13}C enamel values (<14.4‰) and range, as expected, in the marine-influenced stable isotope values and aquatic or higher trophic level resources consumers; besides, all Early Neolithic individuals buried at Ajmana display higher δ^{13}C enamel values (>13.3‰) and range in the group of terrestrial and lower trophic level resources consumers (Figure 77; Figure 78), confirming that their diet at teenage and at the adult age should have been quite similar. In contrast, individuals from the period of Transformation - Neolithic discovered in the Inner Gorges range in all defined dietary groups; in several cases the δ^{13}C enamel appears lower or higher than one would expect from the examination of collagen results.

6.3.1. From terrestrially oriented diet to an increased consumption of aquatic resources

Two Transformational-Neolithic individuals stands out from the "marine-influenced" group with a higher δ^{13}C enamel signal than the others (Figure 78; Figure 79): LV 87/1 (aged at death >15; Transformation/Early Neolithic, local, U5 maternal haplogroup; δ^{13}C enamel: -12.4‰, δ^{13}C collagen: -18.9‰, δ^{15}N: 15.5‰, δ^{34}S: 12.8‰) and LV 37 (aged at death 17-20; Early-middle Neolithic, local, δ^{13}C enamel: -13.6‰, δ^{13}C collagen:-18.6‰, δ^{15}N: 16.2‰, δ^{34}S: 13.6‰). They may have increased their consumption of fats and proteins from anadromous fish between 8-15 years old and the years before their death. Yet, it should be mentioned that one of them - LV 37 - died around 17-

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[289] Dietary groups were defined as following, taking into account the local ecological baseline and individuals' position in the PCA:
- Group 1, "marine-influenced proteins consumers": δ^{15}N > 14‰; δ^{13}C > -19.4‰; δ^{34}S> 11.5‰.
- Group 2, "aquatic and/or higher trophic level resources consumers": δ^{15}N > 14‰; δ^{13}C > -19 ‰; δ^{34}S> 9‰.
- Group 3, "mixed aquatic and terrestrial diet": δ^{15}N = >12‰ - < 14‰; δ^{13}C >-19 - <-19.7‰; δ^{34}S<10.6‰.
- Group 4, "terrestrial or lower trophic level resources consumers": δ^{15}N = < 12‰; δ^{13}C<-19.7‰ δ^{34}S<9‰.

Two individuals, LV 7Ia and LV 54D, discussed previously, were not assigned to these dietary groups and defined as "outsiders" because of their particular stable isotope signature in comparison with the cohort. LV 7Ia exhibit unusually elevated δ^{34}S signal, indicative of a marine-influenced diet (14.8‰) in comparison with his δ^{13}C and δ^{15}N values (respectively -19.7‰ and 11.5‰) rather indicative of a more mixed or lower trophic level diet. The individual LV 54D also ranges out with an elevated δ^{34}S signal (13.4‰) and medium δ^{15}N values (13.4‰) associated with rather low δ^{13}C values (-19.9‰).

20 years old, hence his stable isotopes values could whether be interpreted as a rapid increase in aquatic resources consumption or as the indication of a particular departure from the mono-isotopic diet with most energy (lipids and carbohydrates) originating from the consumption of C_3 terrestrial resources and, in contrast, most amino-acids routed from the consumption of marine-influenced proteins; it should be further explored whether particular metabolic conditions may result in a different stable isotope discrimination at sites such as enamel apatite crystals and bone organic content.

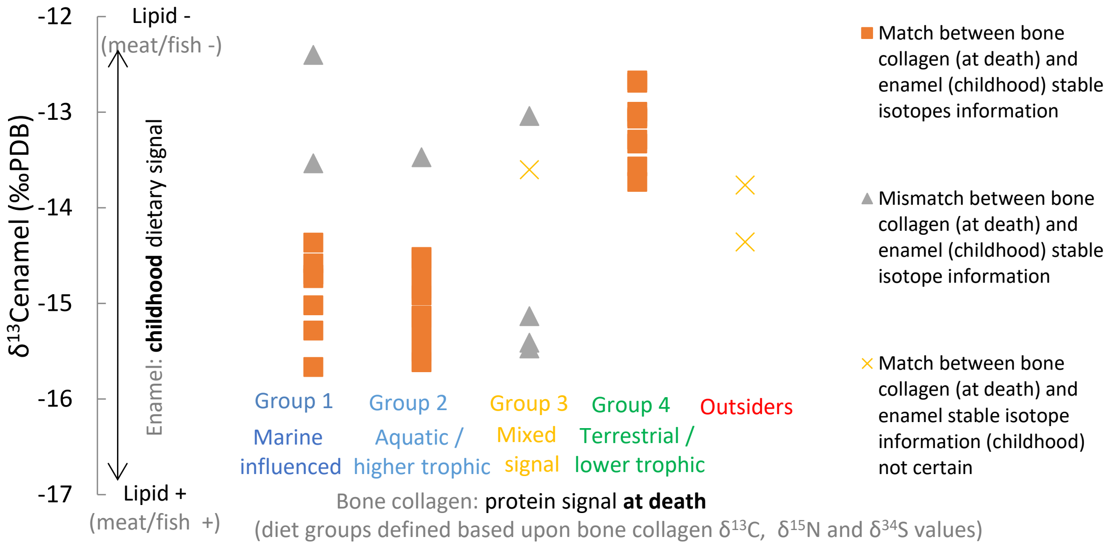

Figure 77 : $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values (signal at death) (caption details: Appendix A.V.)

One Neolithic individual stands out from the group of "aquatic resources and higher trophic level resources consumers" with a higher $\delta^{13}C$ enamel signal than the others (Figure 78; Figure 79): LV 66 (Early-middle Neolithic, Non- local, $\delta^{13}C$ enamel: -13.5‰, $\delta^{13}C$ collagen:-19.3‰, $\delta^{15}N$: 14.9‰, $\delta^{34}S$: 6.4‰). This individual died around 25-30 years old, but it should be recalled that $\delta^{13}C$ enamel was analyzed in the crown of his second permanent molar, formed at a younger age than the third permanent molar (2-8 years; AlQahtani et al. 2010), and which thus may inform about his childhood diet before or close to the time when he arrived in the Danube Gorges (teeth analyzed for strontium: first permanent incisive, formed between birth-4.5 years). Hence, his $\delta^{13}C$ enamel signature may reflect a post-weaning dietary shift, perhaps the adaptation to a diet including greater amounts of freshwater resources.

6.3.2. From a mixed diet to an increased consumption of terrestrial resources

Several individuals also exhibit rather intermediate collagen stable isotope values ($\delta^{15}N$:12.5-14‰; $\delta^{13}C$ collagen: -19- -19.7‰; $\delta^{34}S$: 9-10.6‰) but are associated with rather low or rather high $\delta^{13}C$ enamel values (LV 27b, LV 57, LV 54E; Appendix A.V.9-11). The stable isotope signature of the individuals LV 27b and LV 57 may be either influenced by a subsequent consumption of terrestrial mammals or may indicate a reduction in the consumption of marine-influenced resource (LV 27b: aged at death >15; Transformation - Early Neolithic, local, N mt-haplogroup, $\delta^{13}C$ enamel: -15.5‰, $\delta^{13}C$ collagen:-19.6‰, $\delta^{15}N$: 13.3‰, $\delta^{34}S$: 10.6‰; LV 57: died at teenage; Early-middle Neolithic, $\delta^{13}C$ enamel: -15.1‰, $\delta^{13}C$ collagen:-19.1‰, $\delta^{15}N$: 12.7‰, $\delta^{34}S$: 8.9‰). This last possibility appears less convincing concerning the teenager LV 57 since his bone collagen and teeth enamel signal should have been formed partially contemporaneously. Interestingly, the individual LV 27b is descended from the "Near Eastern Neolithic-like" mt-haplogroup N, absent in the Gorges before 6.2 cal B.C, and was born in the region (local strontium signature). It may be hypothesized that this individual was fed with aquatic resources during childhood and further reduced the consumption of marine-influenced proteins at an adult age, perhaps under the influence of the arrival of new generations of non-local individuals. Within the grave 27, he was discovered with other individuals, including the individual LV 27d (belonging to the U5 mt-haplogroup, and entire "European Mesolithic-like" ancestry according to ADMIXTURE analyses) and the non-local individual LV 27a. The non-local individual LV 27a (aged at death >30), exhibits a very low δ^{13}C enamel signal (-15.7‰) and collagen values indicative of the consumption of marine-influenced proteins (δ^{13}Ccollagen=-18.8‰, δ^{15}N=15.9‰, and δ^{34}S=13.4‰). It can thus be hypothesized that this individual whether migrated in the Gorges before teenage (strontium signal analyzed on the second permanent premolar formed circa 2-6 years old; AlQahtani et al. 2010) or came from a community which relied on a similar means of subsistence as in the Danube Gorges.

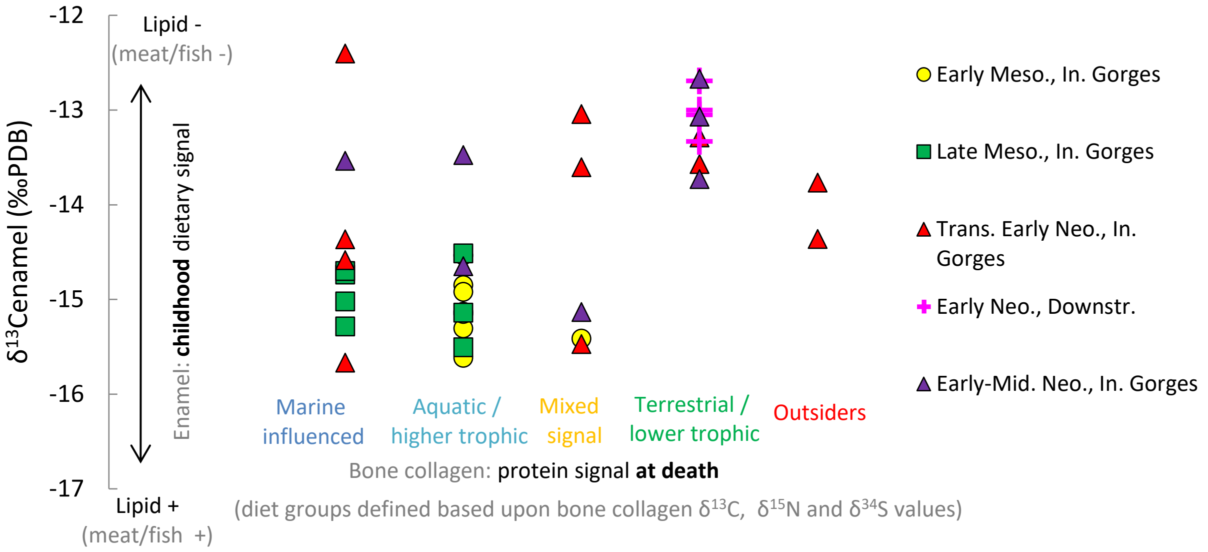

Figure 78 : $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen stable isotope values (cf caption Appendix A.V.8.) and per chronological periods.

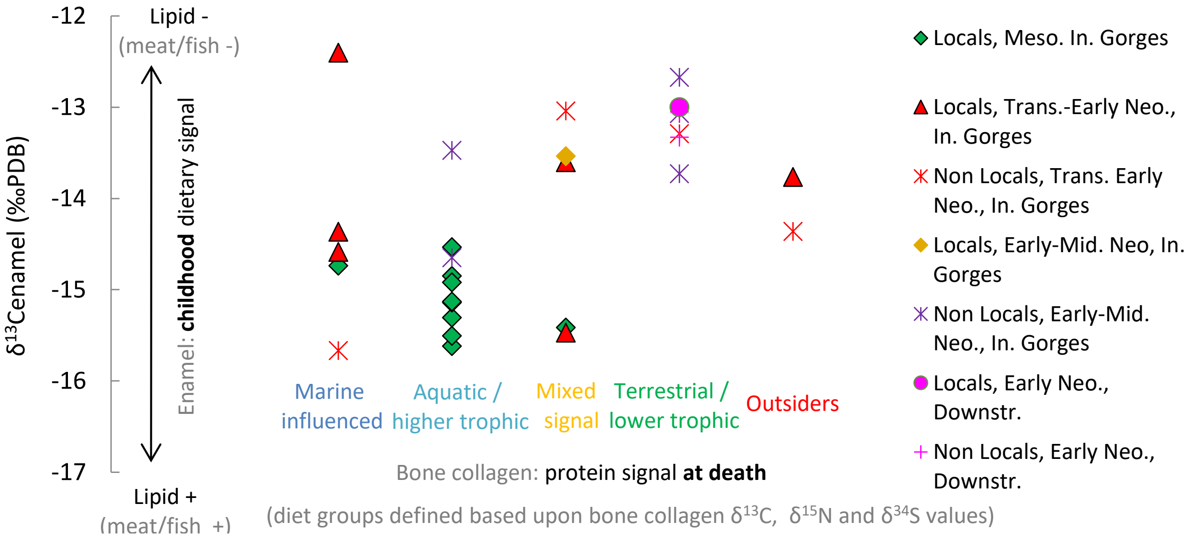

Figure 79 : $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen stable isotope values(cf caption Appendix A.V.8.) and according to their provenance (strontium radiogenic signal, Borić and Price 2013).

6.3.3. From a mixed diet to an increased consumption of aquatic resources

Finally, the young female LV 54E (aged at death 20-25 years old; Transformation - Early Neolithic, Non local, J mt-haplogroup, δ^{13}C enamel: -13‰, δ^{13}C collagen:-19.7‰, δ^{15}N: 13.9‰, δ^{34}S: 10.3‰) also displays low δ^{13}C enamel values, associated with collagen stable isotopes values rather indicative of a mixed diet, quite aquatic influenced. It is possible that the δ^{13}C enamel values of this non-local female reflects the value of the place where she grew up, which would suggest that she migrated in the Gorges after the age of 15 years old, and that her collagen values gradually record the shift toward a higher consumption of aquatic resources between her arrival in the region and her death around 20-25 years old. This female was buried within the building 65 at the same location as the female LV 54D (aged at death > 40; Transformation/Early Neolithic, local, K1b haplogroup; δ^{13}C enamel: -13.8‰, δ^{13}C collagen:-19.9‰, δ^{15}N: 13.4‰, δ^{34}S: 13.7‰), which we classified as outsider given its higher δ^{34}S signal but rather low δ^{13}C collagen and intermediate δ^{15}N values (Figure 78; Figure 79). It can be mentioned that her δ^{34}S signal was analyzed in this study from the collagen of a rib, which is a faster remodeling bone, while Borić et al. (2004) did not provide information concerning the anatomical element sampled for δ^{13}C collagen and δ^{15}N analyses. It is hence possible that her stable isotopes values indicate the increased consumption of aquatic and marine-influenced proteins in the course of her life. A similar trajectory could also be proposed for the non-local female LV 54E, buried at the same location with artifacts pointing both to the Anatolian and southern Balkans Neolithic sphere (limestone beads) and to the local Mesolithic traditions (red deer antlers).

6.4. Various scenarii of life history dietary adaptations and prospects in the use of δ^{13}Cenamel values

Considered jointly, results concerning possible individual dietary changes between childhood and adulthood at the Neolithic transition enable to distinguish different cases: (1.) the locals who perpetuated an aquatic or a mixed diet from late childhood to adulthood (e.g. Transformational-Early Neolithic individuals LV 14, LV 48, Pad. 4; Pad. 4 being assigned to the K1a mt-haplogroup); (2.) the locals who may have reduced their consumption of marine-influenced resources after childhood/teenage (e.g. Transformational-Early Neolithic individual LV 27b, N mt-haplogroup); (3.) the locals who rather increased their consumption of aquatic resources after childhood or teenage (e.g. Transformational-Early Neolithic individual LV 87/1, U5 mt-haplogroup; possible case of LV 54D of K1b mt-haplogroup); (4.) the non-locals assigned to non-U haplogroups (migrants descended from Near East Neolithic maternal lineages), whom enamel stable isotope signal and adult bone collagen values both indicate the continuous consumption of lower trophic level, fat-depleted, terrestrial resources (the Transformational-Early Neolithic individual LV 122, and the Early-middle Neolithic individuals 8, 32a, 88, assigned to the K1a, T, and H mt haplogroups); (5.) the non-locals assigned to non-U haplogroups, who may have increased their consumption of aquatic resources between childhood and adulthood (the Transformational-Early Neolithic individual LV 54E and possible case of the Neolithic individual LV 66?); (6.) the non-locals, whom enamel's and bone collagen signals both suggest the consumption of aquatic proteins and/or of fat-enriched resources (the transformational-Early Neolithic individual LV 27a and the Early-Middle Neolithic female LV 20 assigned to the U5 haplogroup); it can be hypothesized that they may have migrated in the Gorges quite early (before 8-15 years old?) or have originated from a community relying on a similar means of subsistence as in the region of the Gorges.

Hence, circa 6 ky BC, while most non-locals individuals assigned to non-U haplogroups (migrants descended from Near East Neolithic lineages) keep perpetuating their means of subsistence, or died shortly after their migration (e.g. LV 122, 8, 32a and 88), some may have increase their consumption of aquatic resources, perhaps adapting to the local practices (LV 54E, LV 66?). The information concerning their putative descendants, the locals assigned to Non-U haplogroups, indicates that they relied on the consumption of aquatic resources from teenage (Pad. 4), or that they may have increased or reduced the consumption of aquatic resources after teenage (LV 27b; 54D). Surprisingly, the only Early Neolithic local individual assigned to the U5 haplogroup included in the analysis of $\delta^{13}C$ enamel (possible descendant of the local; LV 87/1), may have increased his consumption of aquatic resources after teenage.

Finally, concerning the downstream site of Ajmana, locals and non-locals display quite similar $\delta^{13}C$ enamel values, which suggests that the rather fat-depleted, terrestrial C_3 mono-isotopic diet, may have been brought by non-locals who locally reproduced the habits from their community of origin (similar teenage and adult stable isotope signals for the non-locals as for those who grew up locally). These results thus further inform about the life-history of the descendants of local Mesolithic foragers and of Early Neolithic migrants at the earliest development of the Neolithic in the region and enable to examine, at an individual level, the adaptations of locals to the arrival of people with different practices, but also the adaptations of non-locals after their migration into the Gorges. In most cases non-locals kept their dietary traditions or died too early after migrating for their bone collagen to record the dietary shift; however, situations of possible dietary changes are also documented, for some non-locals and some locals, either towards an increased or a reduction in the consumption of aquatic resources. This variability indicates that the behavioral interactions and mutual influences should not be over-simplified to straight patterns of acculturation, and that individuals may have experienced several important dietary transitions over a lifetime.

This preliminary study of $\delta^{13}C$enamel values brings complementary information on the non-protein part of the diet of local prehistoric children-teenagers. It confirms the diversity of the resources exploited by the Early Mesolithic foragers, indicates that the diet of analyzed Late Mesolithic children who died during childhood may have been specific, validates the dietary differences perceived between locals and non-locals in the Inner Gorges and the different strategies of the individual buried downstream at the site of Ajmana who rather favored the consumption of plant-based resources. Informing about the energy part of the diet, it appears a relevant marker to explore issues related to the spread of agriculture in Europe. The comparison of the enamel values with stable isotope values finally indicates that more dietary variability was experienced over the lives of some Early Neolithic individuals. This approach should thus in the future be complemented by the analysis of stable isotope values from bone apatite values (energy part of the diet during adulthood) and from dentine collagen (protein part of the diet during childhood) in order to perform more direct comparison of the diet of those who died during childhood and of those who survived adulthood but also to further document individual dietary transitions at the time of foragers and farmers interactions.

7. Conclusions: hunters and farmers in transitions, life-history perspectives

By examining the long-term subsistence adaptations of Danube Gorges' foragers in the Central Balkans and their experience of the farming expansion, this thesis has gained insights into some adaptive mechanisms underlying the sedentary and agricultural transition(s). The prehistoric complex of the Danube Gorges has indeed provided a valuable archaeological context to examine human behavioral adaptations during the first part of the Holocene – prior to and during the spread of the Neolithic – because of the temporal depth of the sequence and the continuous Mesolithic and Neolithic occupation (ca 9700-5500 cal BC), because of its location between Mediterranean and Temperate Europe, and because of the large number of highly contextualized Mesolithic and Neolithic burials associated with layers of occupations. These sites document notably: an increased sedentism along the river banks independently from the apparition of farming (Mesolithic period, ca 9700-6200 cal BC); the development of unique cultural traditions, the adoption of Neolithic technologies and the presence of migrants at the time when the first Neolithic communities settled in the Central Balkans (period of Transformation-Early Neolithic, ca 6200-5950 cal BC); the subsequent adoption of animal husbandry, associated with important cultural changes and an increased number of migrants in the local mortuary record (Early-Middle Neolithic, ca 5950-5500 cal BC).

In this thesis, a life-history approach of dietary strategies was adopted by conducting new multi-isotopic analyses (δ^{13}Ccollagen, δ^{15}N, δ^{34}S, δ^{13}Capatite) on human remains at the (intra-)individual and the population level, allowing for examining individual dietary variations, as well as changes in the ways of subsistence of the population (multiple samples per individuals; total Mesolithic and Neolithic individuals with stable isotope information, n=264). **At the population level**, stable isotope data were interpreted diachronically and spatially together with new analyses jointly performed on animal remains and in the light of available contextual information concerning subsistence, climate, patterns of occupation, material cultural novelties, or demographic fluctuations. **At the individual level**, biochemical data were cross-linked with other osteo-biographical information such as age at death, sex, origin and ancestry, health status, or the mortuary context. Since the Neolithic expansion in the Central Balkans has been associated with the migration of individuals descended from Near east Neolithic communities, a special attention has been paid to stable isotope variations according to individual provenance (strontium radiogenic signal) and ancestry (ancient DNA). To further explore the influence of dietary behaviors on the mechanisms of the demographic transitions, we also examined the evolution of maternal nutritional choices and children feeding strategies. Stable isotope values were thus also analyzed **at the intra-individual level**, on different tissues formed during pregnancy, infancy and throughout childhood, and results were interpreted in the light of information about population dynamics and health status. **Hence, we were able to better apprehend the relationships between subsistence adaptations and changes in the natural or social environments, the ways of transmission of dietary behaviors, of diffusion and adaptations of agro-pastoral practices, and some biodemographic consequences of the farming transition.**

The results from previous stable isotope studies conducted on remains from the region were collected and carefully audited for collagen preservation criteria; the analysis of δ^{34}S ratios, only previously tested on the small sample of individual the Danube Gorges, has been systematized on human remains and on a range of different animal species as a relevant marker to discriminate the consumption of different terrestrial and aquatic resources. While previous stable isotopes studies focused on the protein intake, through the analyses of δ^{13}C and δ^{15}N values in bone collagen, δ^{13}C was here also analyzed in enamel apatite in order to further examine the changes in the energy part of diet (lipids and carbohydrate) over the Mesolithic and Neolithic transformations. Multiple isotope analyses of Early Neolithic individuals buried immediately downstream, in an area under-considered in previous paleodietary studies (previous study n individuals =8), were also performed (additional analyses of 13 individuals, including intra-individual multi-sample). The resolution of cross-linked biomolecular information (e.g. stable isotopes, radiocarbon, radiogenic strontium, aDNA) is unique for a prehistoric population. Finally, it is the first intra-individual paleodietary approach developed on human bioarchaeological remains from the Central Balkans, the first systematic study of δ^{34}S values in dentine, and the largest study of pregnancy nutritional choices, breastfeeding and weaning practices conducted on a Western Eurasian Mesolithic-Neolithic sample.

By examining the adaptations of subsistence strategies and dietary behaviors in the environment of the Danube Gorges prior to and during the Neolithic Transition, this thesis has mainly contributed to our understanding of: (1.) the relationships between subsistence intensification and sedentism; (2.) the local chrono-geographical pattern of the Neolithic diffusion, and the mutual influences between migrants and locals; (3.) the role of children feeding strategies on the Neolithic Demographic Transition.

7.1. Subsistence specialization and sedentism: Late Mesolithic fish harvesters

Previous paleodietary studies have emphasized the importance of fishing in the Mesolithic ways of subsistence, alongside with the hunt of terrestrial mammals - particularly red deer and wild boar. **In this study, we observed a shift up in δ^{34}S signals during the first part of the 7th millennium BC. i.e. at the time of the increased of intensity of occupation in the Gorges and of the construction of the first form of trapezoidal buildings.** This result could be related to an increased consumption of anadromous-potamodromous fish species during the Late Mesolithic and/or to a change in the δ^{34}S signal of some food resources. There is indeed a body of geomorphological, biochemical, and radiocarbon evidence to suggest that the reconnection of the Black Sea to the global ocean through the enlarging Bosphorus may have shifted up the δ^{34}S values of the Black sea ecosystem after ca 7000 cal BC. The consumption of long-distance migrating fish (e.g. anadromous sturgeons, beluga and vyrezub, and potamadromous salmons migrating from the estuary) by the Late Mesolithic fishermen of the Danube Gorges may have thus contributed to shift up their δ^{34}S signatures. Besides, it is also possible that the gradual incursion of marine water in the Black sea may have affected some aspects of the ecology of anadromous fish (reproductive and/or migratory behaviors), resulting in their greater availability in the upstream stretches of the Danube during the first half of the 7th millennium BC. **Hence, the increased intensity of occupation along the riverbank observed ca 7000-6500 cal BC could be associated with the increased importance of long-distance migrating fish species in the local way of subsistence, also reflected in the symbolic repertoire, perhaps due to some ecological changes in the Black Sea basin**. This hypothesis should be confirmed on a greater sample of anadromous fish and could have some important implications for our understanding of the Natural History of the Black Sea, and of the ways of life of the prehistoric populations who lived on the surrounding coastal environments or along its tributaries (e.g. Agacli Mesolithic groups, Danube Gorges or Dniepr foragers).

In addition, the δ^{34}S results have also confirmed that dogs substantially consumed aquatic resources, perhaps from human leftovers. **Interpreted in the light of archaeozoological documentation, the stable isotope values have also indicated that humans may have been consuming dogs and, at least occasionally, fed the dogs with their own canine meat.** The observed shift up in humans' δ^{34}S values noticed at the beginning of the 7th millennium BC may thus be related humans' consumption of aquatic resources, but also of the meat of dogs' fed on the fish. Although a specific status may have been assigned to the dogs, being the only domesticated animal at that time and whom particular body parts where placed in the burials, they may have also represented a convenient food repository available year-long for humans, especially during times of food shortages or during the greater climate oscillations of the Great Climate Change (ca 6600-6000 cal BC).

Humans' and animals' stable isotope results are also consistent with the results from the studies of faunal remains representation, and suggest that **the individuals buried at different sites**

along the Gorges throughout the Mesolithic were consuming different resources. The analyses of δ^{13}C in enamel tissue have confirmed that Mesolithic individuals substantially consumed fats from fish and higher trophic level terrestrial animals (omnivores and carnivores) throughout the whole period. In addition, the comparison of this signal with bone collagen stable isotope values has also confirmed that Early Mesolithic individuals had variable dietary behaviors; some individuals buried at Padina (the "catfish spot") were notably consuming less aquatic resources – particularly anadromous fish species – than the others. Concerning the Late Mesolithic period, we also observed more subtle stable isotope inter-sites differences which suggests differences in the amount of marine-influenced proteins (anadromous fish) included in the diet. This pattern could notably be linked to the presence of favorable conditions for fishing different species at certain locations, and to their differential availabilities along the river ("good fishing spots"), and to the development of specialized fishing strategies.

The results have also shown a tendency towards different stable isotope values between Mesolithic males and females, which, if confirmed by increasing the sample of stable isotopes values for sex-determined individuals, could be interpreted in the light of other lines of bioarchaeological evidence as related to the distribution of tasks and/or to their differential status in community. The analyses of tissues formed in utero, during lactation and childhood, also suggest that a part of the Late Mesolithic mothers consumed substantially less marine-derived proteins during the period pregnancy and lactation and that some children were fed with preparations including different resources, depleted in δ^{13}C (terrestrial resources, stationary freshwater fish). However, it should be emphasized that these results do not concern the tissues of all analyzed children and may also be affected by issues of size and/or of synchronicity of the sample. Such dietary behaviors could be the result of a local system of social or sexual division of labor where expectant and lactating females may not have taken a daily part to the tasks which were usually assigned to the females. It may also have to do with what was then perceived as healthy during pregnancy, for the development and the growth of the offspring, or it could have been associated with the nutritional, health or symbolic values assigned to the maternal milk. In particular, considering the specific mortuary patterns that were associated with perinates' and females' bodies (deposits of ochre on perinates' bodies and females' hips), it can be suggested that the observation of such stable isotope variability might be related to the symbolic values that may have been assigned to different food resources and to particular restrictions or ascriptions for their consumption by pregnant-lactating females or young children.

These results hence further document the relationships between sedentism and subsistence specialization amongst a community of European foragers during the Early Holocene. In the Danube Gorges, the first half of the 7th millennium BC is associated with the construction of more permanent structures, an increased intensity of occupation and the substantial consumption of anadromous-potamodromous fish species, perhaps more numerous during their seasonal migrations to the upper stretches of the Danube after 7000 cal BC. It can either be suggested that a gradual decline in residential mobility may have led to an intensified exploitation of resources from the surrounding environments and to the development of more specialized fishing strategies, or that a new episode of sedentism may have been fostered by favorable climatic conditions, changes in fish species availability and/or by the development of new fishing practices. This pattern of reduced residential mobility, intensified exploitation of river resources and increased population-size at some sites may have affected some aspects of local foragers' social organization (e.g. increased sex division of labour or greater social tenses as evidenced by skeletal evidence for inter-personal violences). Similar examples of intensified exploitation of resources in limited territory have been reported for other populations of Epipaleolithic-Mesolithic foragers from Western Eurasia, such as the Natufian, the Atlantic shell collectors or the Atlantic coast, or the Scandinavian Mesolithic fishermen. However, while this process may have led in regions of the Near-East to the development of the farming system, the type of resources harvested by the

Mesolithic foragers and the balance between environmental conditions, subsistence intensification, and population growth rate did not make such adaptive strategy necessary or even possible in Europe.

7.2. Patterns of Neolithization, migrations and subsistence adaptations

Concerning the period of Transformation-Early Neolithic and the subsequent Early-Middle Neolithic period, previous paleodietary studies have indicated a broadening of the stable isotope variability, notably towards lower values indicative of the consumption of lower trophic level terrestrial food resources. Particularly, **our results have shown that a part of this broadening can be related to individuals buried in "multiple burials" around 6100-5800 cal BC in the Downstream Area, at newly founded settlements (the sites of Ajmana and Velesnica) which display greater cultural similarities with the Starčevo Early Neolithic cultural sphere than the sites located in the Inner Gorges**.

In contrast, most individuals buried contemporaneously at close-by sites of the Inner Gorges clearly favored the consumption of aquatic resources (notably individuals buried at Vlasac, Padina, Hajdučka Vodenica, Icoana). These sites were previously occupied during the Mesolithic and the archaeological context rather indicates a cultural continuity with previous Mesolithic traditions. **Only stable isotope results for the central site of Lepenski Vir, in the Inner Gorge, display a high variability, indicating that some individuals substantially consumed aquatic resources, while other rather favored terrestrial lower trophic level foodstuffs.** The results of δ^{13}Cenamel pilot study have also confirmed the major differences observed with collagen analyses between Mesolithic individuals, and Early Neolithic individuals buried in the Downstream Area. While the δ^{13}Cenamel values of Mesolithic individuals were influenced by the substantial consumption of lipids from aquatic animals, the results for individuals buried downstream suggest a lower consumption of animal fats and a greater consumption of plants, and individuals buried at Lepenski Vir exhibit a broad range of values. Despite the very low incidence of dental caries in the Danube Gorges, their occurrence was noticed on a greater number of Transformational-Neolithic individuals, mostly adult females buried at Lepenski Vir and Ajmana as well as children buried at Ajmana, pointing to their greater consumption of carbohydrate-rich resources. Finally, although δ^{15}N values indicate a continuity in the consumption of aquatic resources concerning many individuals buried after 6000-5900 cal BC at Lepenski Vir, we also noticed a shift down in δ^{34}S values which could be either related to some environmental changes (for instance in the availability of anadromous fish species), or more likely, to changes in terms of fishing strategies and/or dogs' breeding practices, and/or to the greater presence of migrants in the osteo-anthropological assemblage.

A previous strontium radiogenic study has demonstrated that an increasing number of non-local individuals, mostly females, has been buried at Lepenski Vir in the Inner Gorges during the period of Transformations, and a fortiori during the Early-Middle Neolithic period, and has also identified their presence in the Downstream Area ca 6000 cal BC. Recent paleogenetic analyses of individuals buried at sites of the Inner Gorges have indicated the presence of individuals with a European Mesolithic-like ancestry, of individuals with a Near-Eastern Neolithic-like ancestry, and of individuals with both ancestries (evidence for admixture). The comparison of δ^{13}Cenamel analyzed on teeth formed during teenage with bone collagen stable isotope signal (formed during the years before the death of the individual) has also indicated a greater number of "discrepancies" between the enamel and the collagen values of Transformational-Early/middle Neolithic individuals. These discrepancies can be due to the different signal of the non-locals and-or to the fact that a greater number of Transformational-Neolithic individuals shifted their dietary habits between teenage and adulthood than during the previous periods of occupation.

By comparing directly stable isotope data with information about migration (strontium radiogenic) and about ancestry (genetic), we have been able to clarify the responses of the local foragers, of the Neolithic migrants and of their descendants to the new ecological and dietary possibilities that they encountered. **Results indicated that the non-locals buried at Lepenski Vir (mostly of Near-Eastern Neolithic-like ancestry) display a broad range of stable isotope values and confirmed that some of them are responsible for the lower stable isotope values noticed at this site. Most importantly, this study has also revealed that the descendants of migrants (the individuals with a local strontium radiogenic signature and a Near-Eastern-like Neolithic ancestry) were substantially consuming aquatic resources. This result is a direct evidence for the adaptations of the descendants of Neolithic migrants to the local ecological conditions**. The interpretation of these bioarchaeological markers within the mortuary context also lends support for the integration of non-local individuals arrived before 6000 cal BC, which contributed to the development of a unique cultural syncretism in the region, and suggested that subsequent migrations (post 5950 cal BC) should have brought further behavioral and cultural novelties into the Gorges (greater number of migrants and of Neolithic Anatolian-like ancestry, lower overall δ^{34}S values, generalization of flexed position, appearance of animal husbandry and change in patterns of occupation).

This thesis has thus confirmed the important role of the Downstream Area and of agro-pastoral migrants in the Neolithization of the Danube Gorges. With greater climate oscillations, the period around 6300-6100 cal BC may have been a time of mutual adaptations for the foragers of the Gorges and for the first Neolithic communities settled in the Central Balkans between Wallachia and the south of Pannonia, before their demographic expansion and spread to the broader Pannonian plain around 6000 cal BC. These Early Neolithic communities not only entered then different biotopes and landscapes, but also encountered there a new social environment, local foragers' population density being certainly much higher in the Northern-Central Balkans than in Southern regions. Around 6000 cal BC, newly occupied settlements in the Downstream Area may have represented some "Early Neolithic enclaves" in the region. These first Neolithic communities likely developed contacts with the local foragers of the Inner Gorges, and notably with the individuals buried at the central site of Lepenski Vir in the Inner Gorges, where the cultural syncretism contributed to the development of an original material and symbolic repertoire. Migrants certainly played an important role in the diffusion of a part of the Neolithic package in the Inner Gorges before 6000 cal BC (ceramics, Neolithic-like ground stones and adornments), and some of them adopted the local ways of subsistence. The comparison of different biomolecular lines of evidence also indicates that, from 6200 cal BC onwards, the descendants of the migrants in the Danube Gorges substantially consumed aquatic resources. The development of mutualistic relationships – through the exchange of goods and blood – should have provided some advantages for farmers to adapt the agro-pastoral niche to the new biomes of temperate Europe, allowing for a faster spread of Neolithic practices. After 5900 cal BC, further generations of migrants brought new components of the Neolithic in the Gorges, such as animal husbandry or new mortuary practices, and may have adapted some aspects of the local subsistence practices (change in fishing strategies?). Despite the introduction of herding practices this last period is associated with a gradual decline in the intensity of the occupation of the Gorges while the Neolithic presence intensified in the neighboring regions of the Central Balkans. The environment of the Gorges may not have been suitable (rugged topography) and/or attractive (new Neolithic social ethos) enough for the demographically expanding Starčevo groups and their agro-pastoral practices, resulting in shifting places of influences towards fertile plains.

Hence, from a bioarchaeological perspective, the Neolithization of the Danube Gorges should not be understood as a straightforward process of acculturation or a sudden behavioral shift. On the contrary, results reflect a mosaic picture of complex behavioral interactions and gradual socio-cultural changes within a frame of subsistence continuity at the end of the 7th millennium BC. These interactions include both the introduction of cultural material novelties, the integration of migrants and their adaptations to the local ways of subsistence.

During the first centuries of the 6th millennium BC, while more numerous migrants brought further cultural changes, agropastoral activities remain subsidiary. The very scarce published data that allow for comparing ancestry and dietary behaviors for individuals buried in other regions of the Central Balkans, Wallachia and Pannonia rather suggest that the descendants of Mesolithic hunter-gatherers were mostly perpetuating their foraging way of subsistence, despite the presence of farmers-herders descended from Near Eastern Neolithic communities. Available aDNA and stable isotope information concerning other regions of Europe indicate different scenarii: in Southeast, Central and Western Europe, the farming way of subsistence brought by the descendants of Near Eastern Neolithic communities ultimately prevailed after a variable period of co-existence with foragers, but it only involved a small degree of admixture; in Northern Europe, the incorporation of foragers into early farming groups may have been greater after a long period of co-existence; in some regions of Eastern Europe most aspects of the Neolithic package were gradually adopted by the local descendants of Mesolithic foragers without significant admixture with the descendants of Near Eastern Neolithic communities. Hence, when crossing various line of bioarchaeological evidence, it appears that a single model of Neolithization cannot explain the diverse dynamics of foragers and farmers interactions in Europe. These different "patterns of Neolithization", due to the diversity in encountered social and natural environmental conditions, and to the different modes of horizontal and vertical patterns of cultural transmission, probably contributed to shape the Neolithic niche in Western Eurasia.

7.3. Children feeding practices and the Neolithic Demographic Transition

By comparing the stable isotope values of different tissues formed intra-utero, at birth, during infancy and childhood, we have gained new insights into the adaptations of maternal nutritional choices over the Mesolithic and Neolithic transformations: the times of the breastfeeding and weaning process, maternal diet during pregnancy and lactation, and the type of food supplemented to toddlers.

Regarding the times of the weaning and breastfeeding process, it has been noticed that Mesolithic and Transformational/Early Neolithic children buried in the Inner Gorges may have relied, on average, on breast-milk as a primary and main source of nutrients for a longer time than the Early Neolithic children buried downstream. The Early Neolithic children buried downstream at Ajmana likely experienced a more abrupt dietary transition than the Mesolithic-Transformational children buried in the Gorges. Although there is some variability in breastfeeding and weaning patterns amongst all examined chrono-cultural groups, the feeding practices seem to have been more variable concerning the Mesolithic-Neolithic children buried in the Inner Gorges than concerning the Early Neolithic children buried in the Downstream Area. This variability could in part be related to the temporal depth of the Mesolithic period, but also to the presence of migrants during the Transformational-Early Neolithic period at Lepenski Vir, who may have come in the Gorges with different feeding habits. In contrast, **the results rather point to the behavioral homogeneity of the group of analyzed Early Neolithic individuals buried in the multiple burial of Ajmana downstream**, which either suggests that most of these children may have originated from the same family group, or which could point to the strong socio-cultural component of children feeding strategies amongst early agro-pastoralists, the "weaning norm".

The analyses of tissues formed in utero, during lactation and childhood have indicated that **a part of Late Mesolithic mothers may have favored the consumption of lower trophic level terrestrial proteins or freshwater-fish derived proteins over marine-influenced proteins (anadromous fish and/or dog meat). In contrast, the stable isotope values of the tissues of Transformation-Early Neolithic individuals have indicated that the Early Neolithic mothers of the children buried in the Gorges were substantially consuming marine-influenced proteins during pregnancy and lactation. Children weaning preparations also**

contained aquatic resources, in even higher amounts than the diet of their mothers or of the other adults of the groups in most cases. The use of aquatic resources to wean children has also been suggested for other populations of foragers from archaeological contexts of the Northern hemisphere and have been ethnographically documented. The period of Transformation is featured by a change in funerary practices, the bodies of perinates and infant being buried under the floors of Lepenki Vir dwellings, according to a custom which was common amongst Neolithic communities of the Balkano-Anatolian sphere and which could have been brought into the Gorges by migrants. The deposition of these babies below the house floors might reflect some modification of reproductive behavior, parenting strategies and/or young children mortality rates, which took place at the time of the first contacts with the Early Neolithic communities. **In this context, the importance of fish in maternal nutritional choices could either be related to the symbolic values that may have been assigned to these animals by the local foragers. It can also have to do with a will to buffer some physiological stress perhaps associated with climate oscillations, with migrations, or with changes in pathogen loads.** Only a few Transformational-Neolithic children display substantially lower stable isotope values than the others, suggesting that they were fed lower trophic level diet: perhaps because of their non-local origin or of non-local's influences. When cross-linked with the few available biological and cultural information related to the origin of buried children, the results rather indicated the adaptation to the local ecological conditions. For instance, the only child from our stable isotope sample with available aDNA information had a mixed ancestry; he displays the highest stable isotope values and was buried under a sculpted boulder displaying unique features, advertising his special status. These results confirm thus the observed vertical pattern of migrants' adaptations to the local subsistence strategies and-or ecological conditions.

The stable isotope values longitudinally collected on the teeth Early Neolithic children buried downstream at Ajmana, have suggested an earlier reduction in suckling frequency and an earlier reliance on preparations mostly based on terrestrial lower trophic food resources, which strongly contrasts with the high protein–based preparations provided to the Mesolithic and Transformational children buried in the Inner Gorges. These children were probably amongst the first in the region to be fed with some kinds of "Neolithic breads", or porridges that may have included cereals and milk as well; until later phases of the Neolithic children were indeed the only individuals to be able to digest raw animal milk. The availability of animal milk – similar in appearance to maternal milk – and of new cereal-made mushes, could have allowed the Neolithic mothers for an earlier reduction in suckling frequency. The role of children feeding practices, and specifically of an early and continuous supply with preparations made of animal milk and cereal mushes during essential phases of children ontogenesis, on the gradual selection of alleles favoring the digestion of milk at an adult age or starch hydrolysis over the Neolithic would now require further investigations. A stable isotope offset of particularly important magnitude has been noticed between dentine tissues formed during pregnancy-lactation and dentine tissues formed after supplementation for some individuals, suggesting that the diet of some mothers may have been richer in animal proteins than children diet. It is thus possible that the values of adults discovered in the multiple burial may not be entirely representative of the diet of all members of the community who used the grave, or that some mothers chose to include more aquatic resources in their pregnancy diet to sustain the requirements in nutrients of their metabolic state. **In any cases, the observation of an opposite pattern of stable isotope fluctuations between Transformational-Early Neolithic children buried in the Inner Gorges and the Early Neolithic children buried downstream suggests that Early European agro-pastoralists had quite different ideas about children feeding practices than foragers did.** This difference has been often discussed in the ethnographic literature related to various contexts and has been associated with differential level of parental investment and-or to contrasting conceptions of children status or role in the community. Dental caries have been identified on the teeth of four children uncovered at Ajmana, either died ca 5-15 years old or who display the lowest carbon and nitrogen stable isotope values; the child with the lowest vales, who also exhibits a gross tooth decay, has been identified as non-local. Interpreted in the light of the greater stable isotope offset noticed between tissues formed during pregnancy-lactation and tissues formed during supplementation, this pattern might reflect the influence of some migrants on the feeding practices of the other users of this grave.

These new data hence contribute to fill a gap in the current state of knowledge about Mesolithic and Neolithic children feeding practices in Europe related to the scarcity of data for Mesolithic foragers and transitional contexts, to the small sample size of analyzed individuals or to the diversity of applied methodologies. **Interpreted in the light of researches on population dynamics and health status, these results provide a direct support to some assumptions for the mechanisms of the Neolithic Demographic Transition.** While some ethnographic surveys and meta-analyses of archaeological data have either indicated broad differences in the total length of lactation or in the type of weaning food provided to hunters' and farmers' toddlers, **this study is the first to document directly strong differences in terms of times of breastfeeding and of weaning recipes between Mesolithic and contact-period foragers and Early Neolithic agro-pastoralists.** Ongoing works on paleodemographic reconstructions indeed suggest that the Mesolithic-Neolithic population buried in the Inner Gorges was rather stationary, with an increased density of occupation during the period of Transformation-Neolithic probably due to the presence of migrants buried at Lepenski Vir. In contrast, the higher proportion of immatures individuals (aged 1-19 years old) buried at the Early Neolithic multiple burials of Velesnica and Ajmana downstream ca 6000 cal BC suggests higher growth rates, typical for farming communities. The Early Neolithic network of agropastoral settlements in the neighboring regions of the Central Balkans also substantially intensified during the first half of the 6th millennium BC. If confirmed on a broader sample of Central Balkans Early Neolithic individuals**, it is possible that the earlier reduction in suckling frequency may have released mothers from the energetic burden of lactation and contributed to their higher fertility rates.**

The general pattern of "health decline" often associated with the onset of the farming system has not been documented in the region of the Danube Gorges. Yet, researches conducted on health status have reported more dental caries and evidence for higher level of childhood physiological stress concerning individuals buried at Ajmana and at Lepenski Vir after 6000 cal BC. The skeletal examination of individuals buried in the neighboring regions of the Central Balkans – where humans' stable isotope variability coincides with the values of the individuals buried in the Downstream Area – has also indicated significantly higher proportions of non-specific skeletal indicators of physiological stress, metabolic diseases, dental caries as well as lower average body size than in the Gorges. **While the consumption of resources rich in proteins and micronutrients during childhood may have acted as a buffer against physiological stress for Mesolithic and Transformational children buried in the Inner Gorges, a more abrupt weaning transition, with carbohydrate-rich but animal protein-depleted resources, and a childhood diet rather low in animal proteins, could have been detrimental to the health and the growth of Early Neolithic children buried downstream or in other regions of the Central Balkans.** Apart from the availability of cereals and animal milk, the Neolithic technologies, such as ceramic and new type of bone spoons should have played an important role in feeding practices; this "infant feeding Neolithic package", including non-sterilized tools, may have also contributed to higher infection rates. Besides, it is possible that the environmental conditions experienced from fetal stage to childhood may have specifically impacted Early Neolithic females' developmental trajectories, and that their metabolism adapted quite early in conditions of higher nutritional stress to prioritize reproductive development over growth. **In the trade-off with individual fitness (life-expectancy and well-being), the demographic expansion of the farming niche and changes in children feeding practices, probably dramatically contributed to favor the populational fitness (reproductive success).**

7.4. Methodological contributions

Regarding the reliability of paleodietary reconstructions, we firstly wish to emphasize the need for great care in the use of stable isotope ratios from some early publications where information concerning the analyzed anatomical elements or concerning the criteria for the validity of collagen were not always provided. Significant stable isotope differences have thus been evidenced in this study between individuals with well-preserved collagen and individuals from the same biocultural contexts for which previous studies did not provided molar ratios, urging to caution when using these data. Multiplying stable isotopes analyses of different elements (here carbon, nitrogen, strontium and sulfur), from different tissues (here bone, dentine and enamel), compared with adapted Bayesian or multivariate statistic methods (here principal component analyses), had enabled us to increase the precision and the accuracy of behavioral inferences.

By comparing at the individual level different bio-archaeological sources of information, from different markers and biological tissues, the life history approach has allowed for exploring some mechanisms of cultural transmission and subsistence adaptations. While there is nowadays an increasing number of paleodietary and paleogenetic studies dedicated to the Mesolithic and Neolithic periods, only a few actually compared aDNA and stable isotope data**; by cross-linking these data at the individual level and by adding the strontium radiogenic information, this thesis has examined for the first time on a substantial prehistoric sample the diet of locals, of migrants and also of their putative descendants, shedding some lights on mechanisms of dietary adaptations over successive generations at the earliest Neolithic**.

The analysis of sulfur isotope ratios conducted on a broader sample of human and animal remains has allowed for better understanding the causes for local variations in δ^{34}S values, confirming its benefits not only to distinguish between terrestrial and aquatic diet but also to specify the consumption of different aquatic resources (namely, stationary freshwater versus anadromous-potamodromous fish**). We have highlighted the possibility that the local humans' δ^{34}S signals could be widely influenced by changes in the sulfur values of the Black Sea, which demonstrates the importance of jointly analyzing a broad range of species – notably aquatic – from associated geographical and chronological contexts to unravel the environmental and behavioral influences on the local δ^{34}S variability.** The δ^{34}S analyses of human and fish remains from archaeological contexts in some riverine, brackish or coastal environments may thus provide insights on local ecological modifications, related for instance to changes in sulphate sources, salinity fluctuations, or species' behavioral adaptations, of importance for understanding long term human subsistence adaptations or ecosystems sustainability.

At the intra-individual level, we found a quasi-systematic δ^{34}S difference between first deciduous molar crowns and first permanent molar crowns, the latter being almost always depleted (average depletion: -0.7±0,5‰, n=11). Interpreted the light of other fluctuations in δ^{13}C and δ^{15}N values and of the results from animal feeding experiments**, these results might be related to a fractionation that occur between maternal nutrient supply and the tissues of the child at the end of pregnancy or during the period of exclusive breastfeeding**. It can also be suggested that the consumption of proteins from different origins (e.g. marine versus terrestrial proteins) by the lactating mother and by the supplemented child may have influenced the magnitude of this offset. This research is the first, to our knowledge, to analyze dentine δ^{34}S ratios in an intra-individual paleodietary study of breastfeeding and weaning practices. The results hence support at an intra-individual level the presence of a small δ^{34}S trophic effect, and confirm the benefits of analyzing Sulfur isotope ratios jointly with other elements in order to examine differences between maternal diet and weaning preparations in contexts of aquatic resources consumption or of human migrations.

Beyond informing on breastfeeding and weaning practices, the comparison of multiple stable isotope signals from different biological tissues has also revealed some patterns which could be related to nutritional health during pregnancy, lactation, and growth. The stable isotope analyses of perinatally-formed bone collagen have indicated higher average neonates' $\delta^{15}N$ values in comparison with females' variability, a tendency noticed on other archaeological populations which can be associated with the metabolism of pregnant females and with the high rates of protein accretion during the growth of the offspring. Yet, the observation of a greater females-to-perinates $\delta^{15}N$ offset for the Early Neolithic assemblage of Lepenski Vir than for the Late Mesolithic assemblage of Vlasac, and of more variable $\delta^{13}C$ and $\delta^{15}N$ values around birth, could be either due to higher level of physiological stress and perhaps endocrine disturbances experienced by mothers at Lepenski Vir, or to an effect of marine-derived consumption during pregnancy, or to the presence of migrants' expectant females and their offspring in the sample.

A systematic $\delta^{13}C$ and $\delta^{15}N$ offset in the values of children coterminous bone and teeth tissues, has also been evidenced in this thesis (on average: -0.3±0.2‰ for $\Delta^{13}C$ and -0.6±0.4‰ for $\Delta^{15}N$, n=16). **This offset could be related to two mechanisms associated with the differential pattern of bone and teeth growth**: (1) arrested bone formation and elevated teeth $\delta^{15}N$ values in situation of nutritional stress; (2) lower bone $\delta^{15}N$ values during periods of growth spurts and lower bone $\delta^{13}C$ values in case of a moderately low intake of proteins. When examining data from other archaeological populations, it appears that lower bone post-weaning values is frequent around the age of 1-7 years old, particularly in case of lower trophic level resources consumption. These "post-weaning dips" coincide with the time when children experience faster growth rates in size than in weigh, suggesting a possible physiological mass balance effect on stable isotopes values. In the Danube Gorges osteo-anthropological sample, it has been noticed that Transformational-Neolithic children and children who reduced the frequency of suckles earlier exhibit higher average co-forming bone-to-teeth $\delta^{15}N$ offset. These results warn for the direct comparison of stable isotope values from different tissues, even when formed contemporaneously, and urge to caution when using results from children feeding studies which compare such tissues. Further research is needed on reference samples with more ample information about pregnancy, breastfeeding and weaning strategies and experienced nutritional stress, but the possibility to examine issues related to maternal and childhood physiological health and growth disruptions opens new prospects to further understand the bio-demographic cost of the Agricultural Transition.

Finally, this thesis has also confirmed the usefulness of using $\delta^{13}C$enamel as a relevant paleodietary marker of changes in terms of carbohydrates and lipids consumption at the Neolithic Transition. $\delta^{13}C$enamel has indicated significant differences between Mesolithic animal fat-rich food consumers and Early Neolithic carbohydrate-rich food consumers which were not detectable in $\delta^{13}C$collagen. When interpreted with collagen stable isotope values, $\delta^{13}C$enamel results have confirmed the variability of subsistence behaviors during the Early Mesolithic and indicated that a greater number of Early Neolithic individuals may have shifted their dietary habits between teenage and deaths. By analyzing $\delta^{13}C$ from coterminous dentine and enamel tissues, and from bone apatite, one may now clarify the causes for these variations and perhaps further document some trajectories of migrants' or locals' dietary adaptations at the onset the Neolithic.

7.5. Perspectives

Considering these results, analyzing stable isotope ratios in a range of plant remains from Mesolithic and Neolithic contexts and applying other markers such as non-traditional isotope (e.g. zinc) or amino acids (e.g. $\delta^{15}N$ of glutamic acid and phenylalanine), would now allow for broadening our understanding of the local stable isotope variability and of the resources consumed. Particularly, these applications could allow for further specifying Early to Late Mesolithic subsistence adaptations in the context of Early Holocene environmental adaptations and increased sedentism, notably concerning the amount of terrestrial versus aquatic resources consumed, and changes in the type of species fished. It could also help discriminating which plants were consumed by Late Mesolithic foragers and by the Early Neolithic individuals settled in the Downstream Area, a key question considering the nutritional importance of plant resources for foragers, and their contrasting invisibility in the (bio-)archaeological record, and of course the chronology of crop cultivation in the region. The results from current ongoing researches on starch grains trapped in dental calculus shall soon contribute to shed some lights on these issues. Besides, performing proteomic analyses in dental calculus from the teeth of Early Neolithic individuals could provide valuable information on the earliest consumption of dairies and on its possible importance in Early Neolithic children feeding practices.

Most importantly, the application of high-resolution intra-individual biogeochemical analyses on Mesolithic and Early Neolithic individuals from across the Central Balkans would now provide essential data regarding the individual experience of Neolithization. By micro-sampling permanent teeth dentine, one could document dietary transitions and nutritional health from pregnancy and fetal stage to early adulthood. The results concerning those who died during childhood, analyzed in this thesis, could then be directly compared with the values of those who survived until adulthood in order to further explore the possible influence of dietary behaviors on mortality, health and life expectancy. The direct comparison of teeth stable isotope profiles with the age for the onset of linear enamel hypoplasia (physiological stress experienced during childhood), crisis lines assessed from methods of cementum annulation (physiological stress experienced during adulthood), and with paleodemographic proxies, shall provide interpretative keys to unravel the causes for stable isotope complexities and to examine the physiological costs of the farming transition. In complement, the application of non-traditional stable isotope analyses (e.g. copper, iron, calcium) on permanent teeth could also allow for examining changes in females' reproductive career milestones such as the age of menarche or of the first pregnancy and to further understand some bio-demographic mechanisms beyond the Agricultural Demographic Transition. Finally, by conducting high resolution stable and radiogenic isotope on adult permanent teeth, one may also refine patterns of mobility (numbers of migrations from birth to teenage) and processes of subsistence adaptations to local environmental conditions. Such analyses would be particularly relevant for regions of the Central Balkans and of Pannonia, where the first Neolithic farmers are assumed to have been highly mobile agro-pastoralists, who had to adapt the farming niche to the temperate environmental conditions characteristic of the whole continental Europe.

Applied to other regions and periods, the Life History approach may enable Bioarcheologists to test and to reassess the models of the farming expansion, and beyond, may contribute to deepen our understanding of the dynamics of subsistence transitions. The possibility to compare directly various level of bioarcheological information related to behavioral adaptations, demographic and genetic selection, or physiological and morphological flexibility, now opens up new avenues of research to consider the causes for todays' remarkable human phenotypic diversity, to examine the mechanisms underlying demographic cycles in world of billions, and, ultimately, to contemplate possible paths for our biocultural evolution at the advent of the Anthropocene.

List of figures and tables

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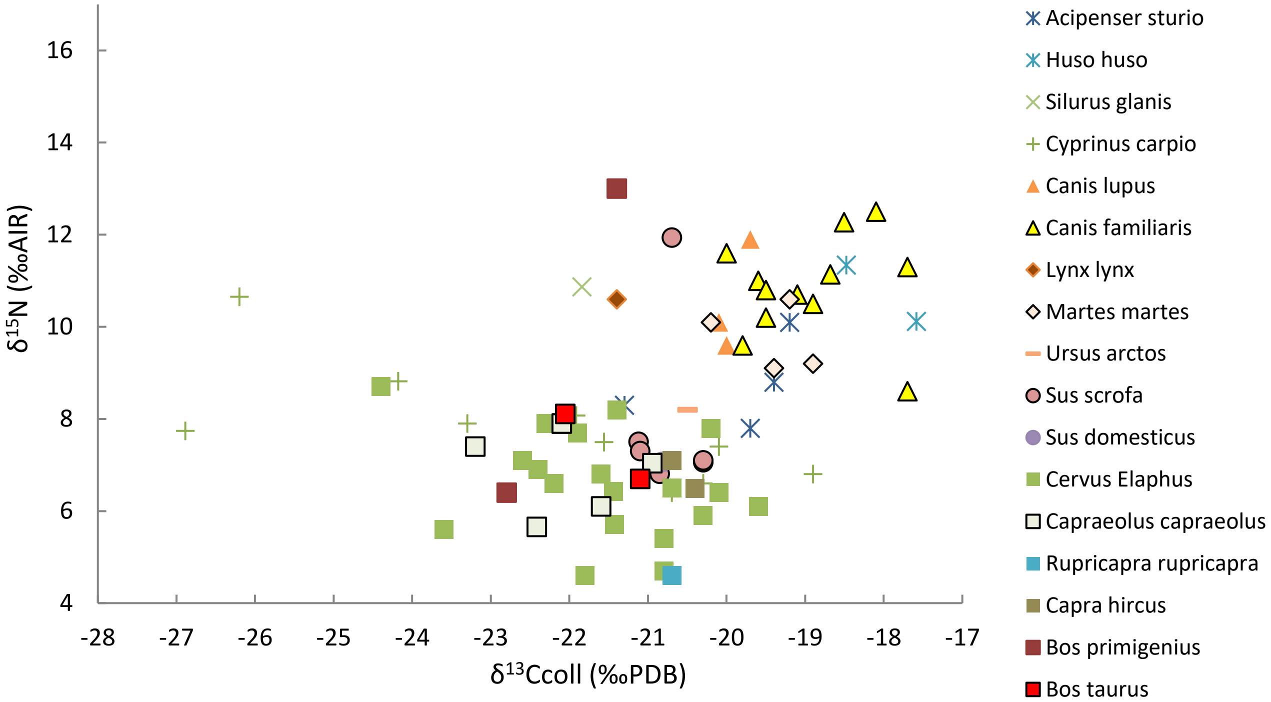
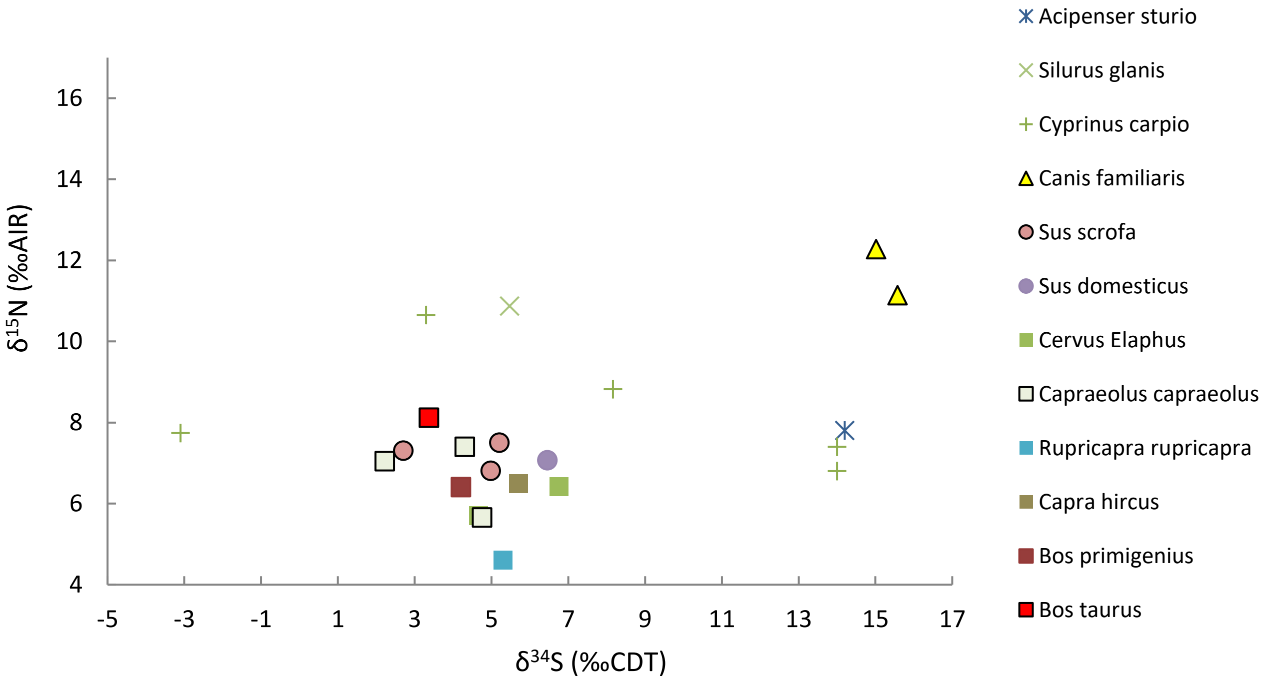
APPENDIX A.I. Animal ecology: environmental baseline for stable isotopes extracted from the collagen protein (δ^{13}Ccoll, δ^{15}N, δ^{34}S) of prehistoric individuals from the Danube Gorges

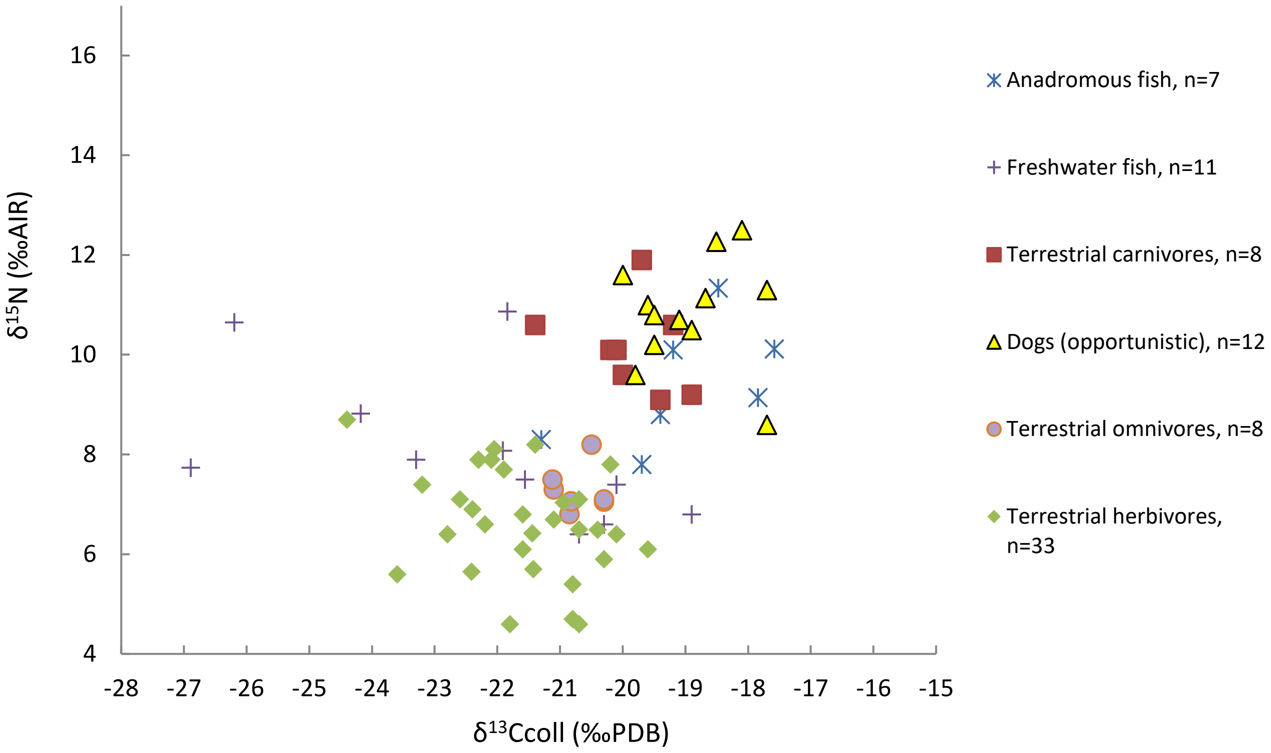
Analyses per species, behaviors and ecological niches



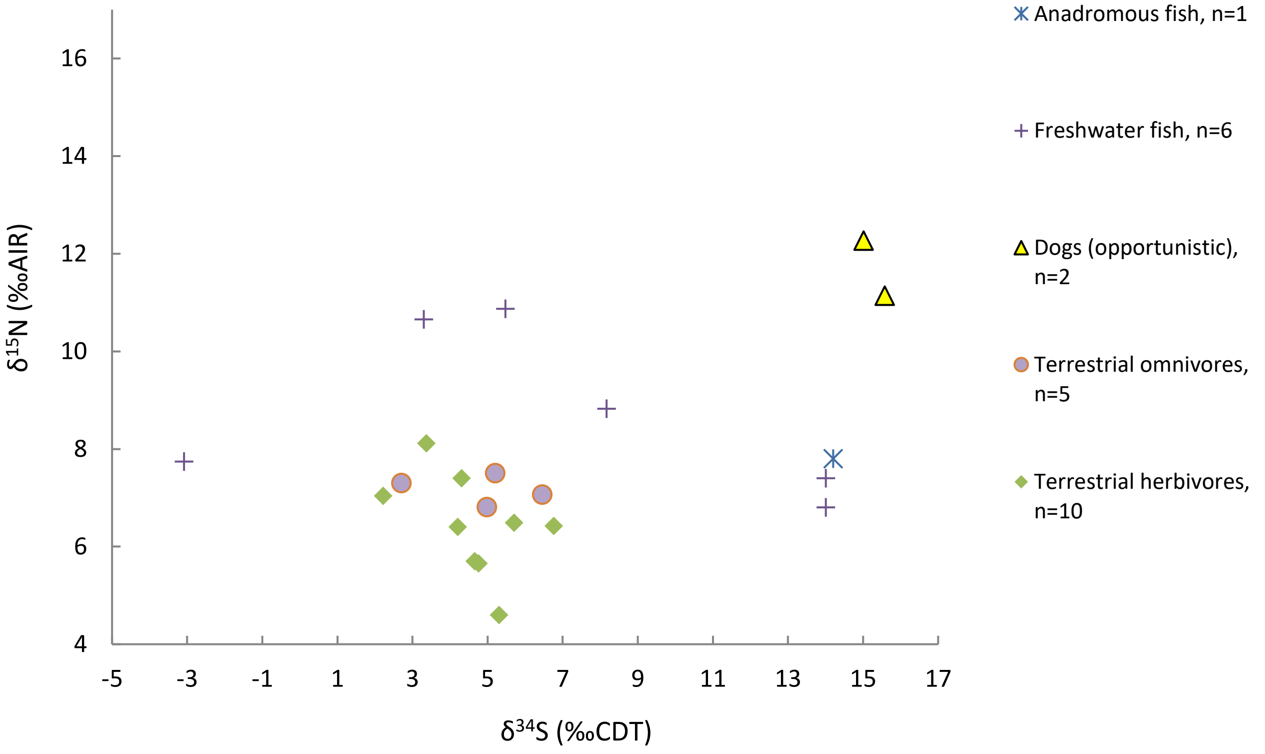
A.I.1. Bivariate plot of δ^{13}C and δ^{15}N for different animal species from the prehistoric sites of the Danube Gorges



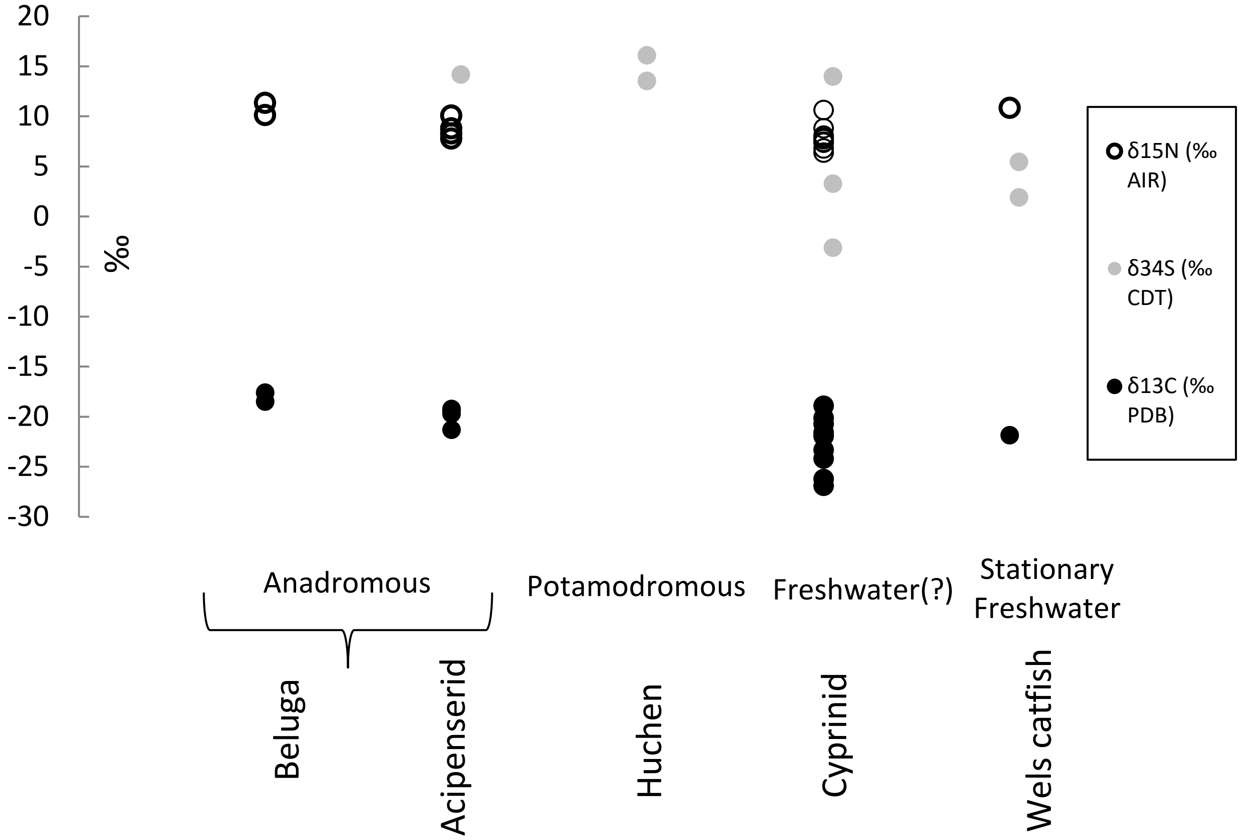
A.I.2. Bivariate plot of δ^{34}S and δ^{15}N for different animal species from the prehistoric sites of the Danube Gorges



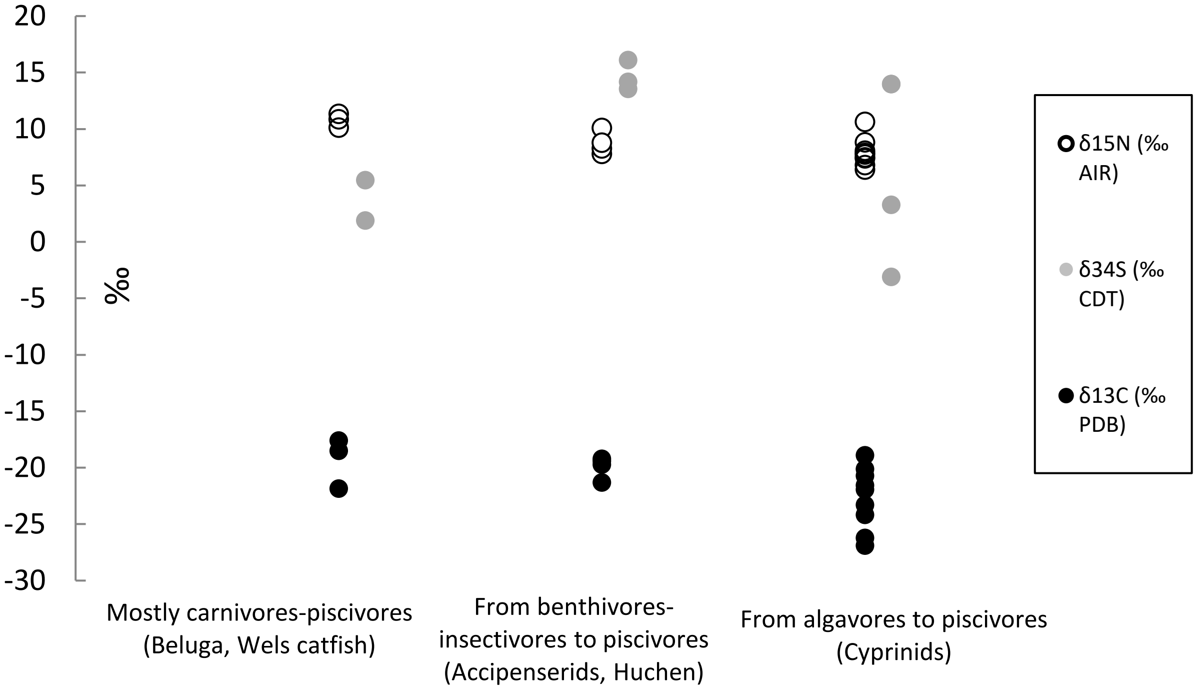
A.I.3. Bivariate plot of δ^{13}C and δ^{15}N for different species grouped according to their behavior



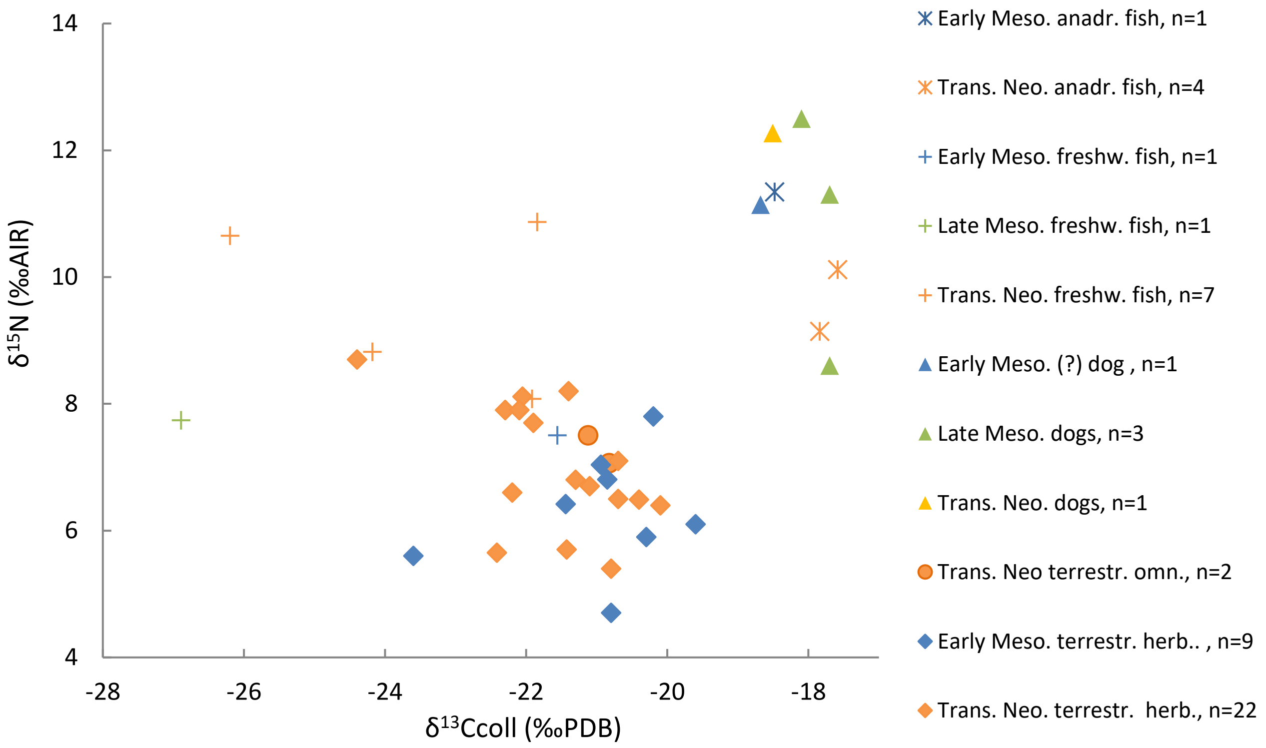
A.I.4. Bivariate plot of δ^{34}S and δ^{15}N for different species grouped according to their behavior



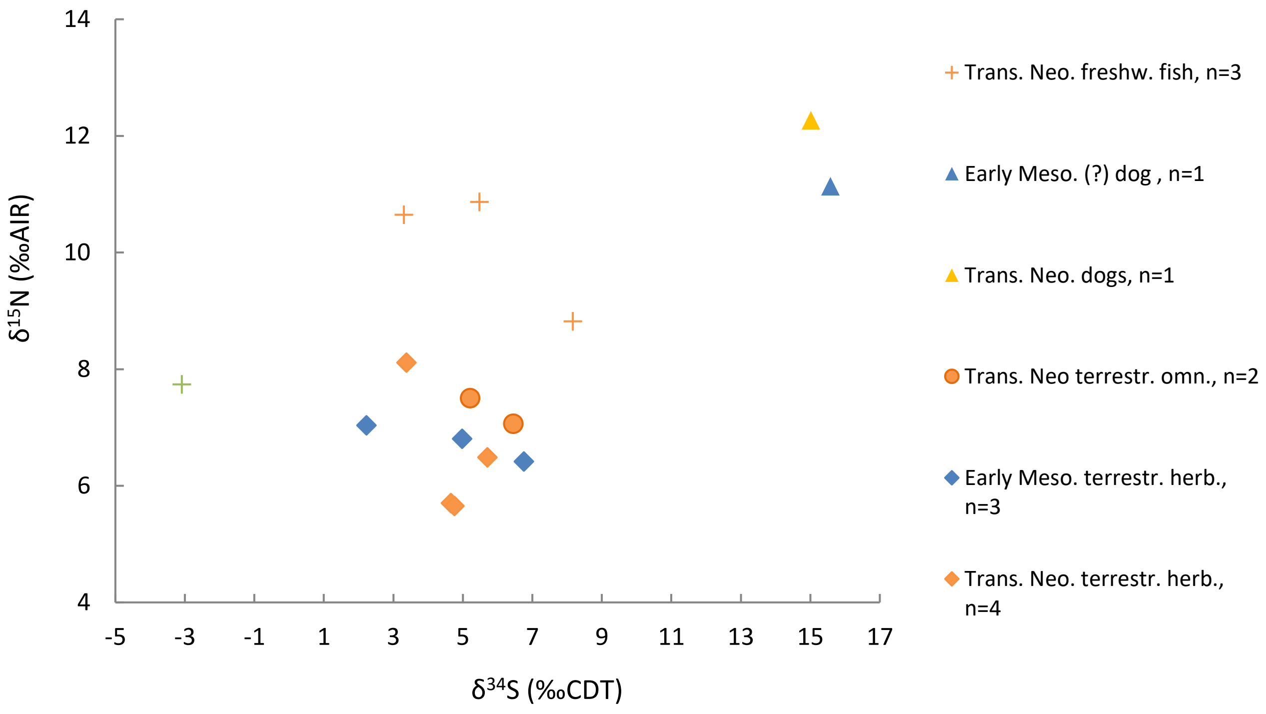
A.I.5. δ^{13}C, δ^{15}N, δ^{34}S for different fish species grouped according to their migratory behavior



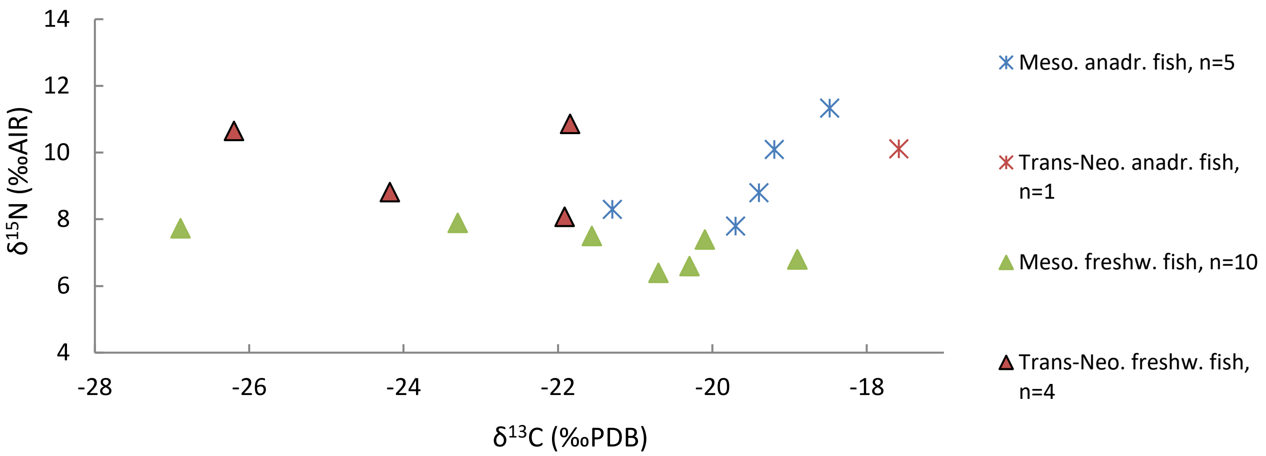
A.I.6. δ^{13}C, δ^{15}N, δ^{34}S for different fish species grouped according to their dietary behavior



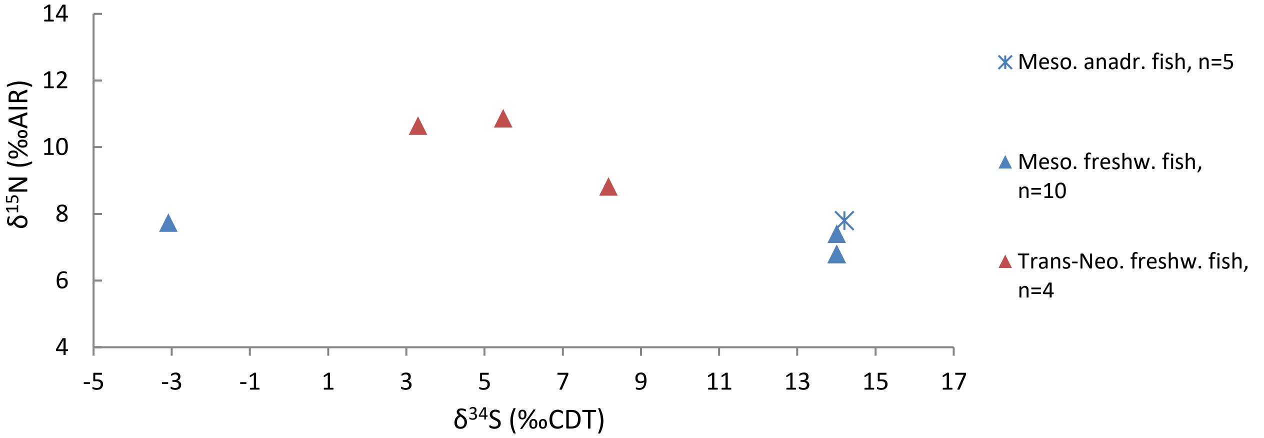
A.I.7. Bivariate plot of δ^{13}C and δ^{15}N for different species, grouped according to their behavior and archaeological periods. Only radiocarbon dated individuals.



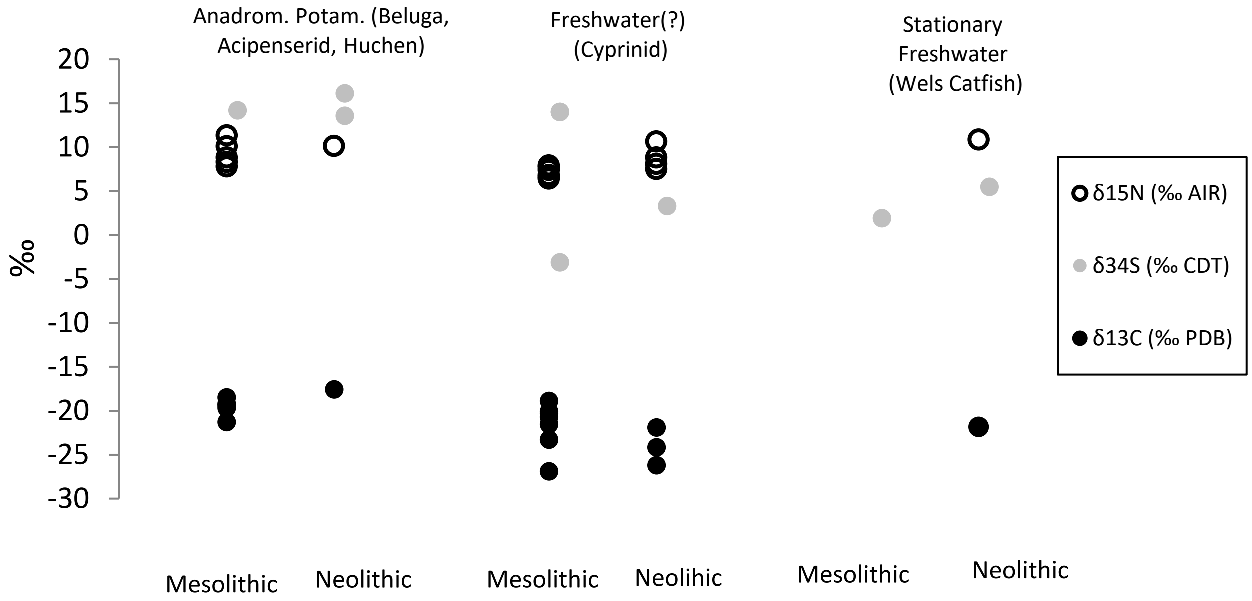
A.I.8. Bivariate plot of δ^{34}S and δ^{15}N for different species, grouped according to their behavior and archaeological periods. Only radiocarbon dated individuals.



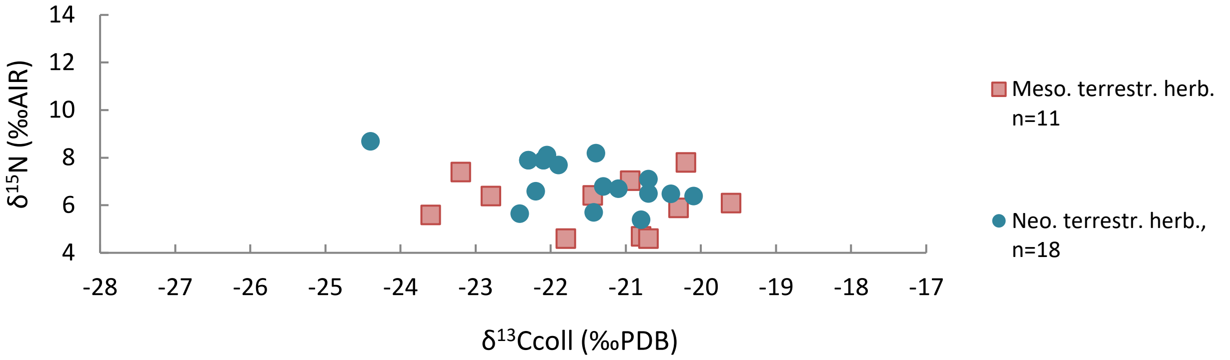
A.I.9. Bivariate plot of δ^{13}C and δ^{15}N for fish grouped according to their migratory behavior and archaeological periods



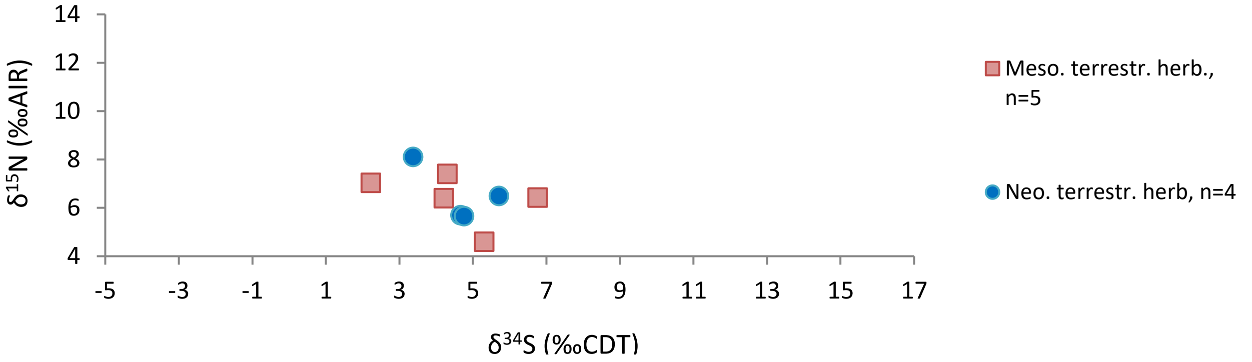
A.I.10. Bivariate plot of δ^{34}S and δ^{15}N for fish grouped according to their migratory behavior and archaeological periods



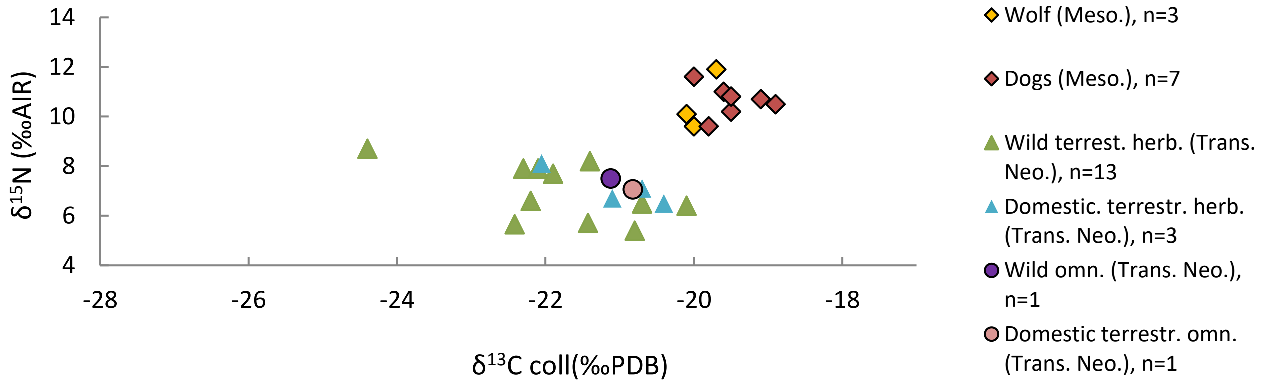
A.I.11. δ^{13}C, δ^{15}N, δ^{34}S for different fish species grouped according to their migratory behavior



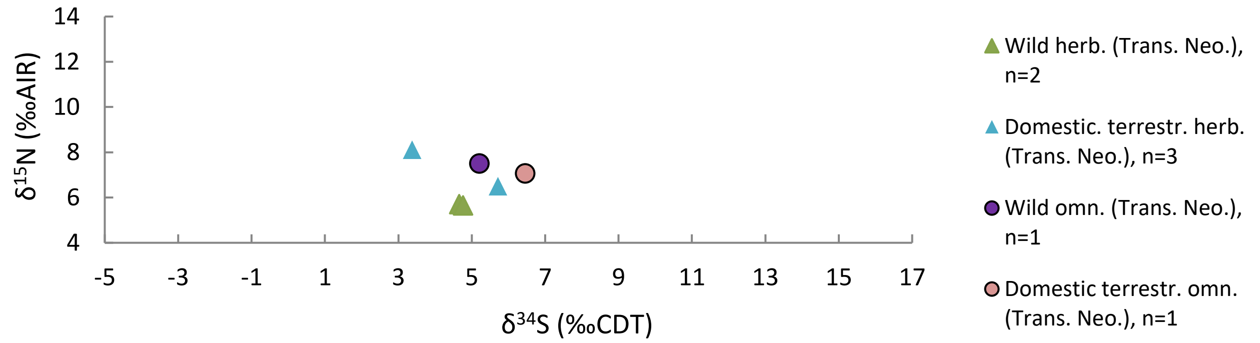
A.I.12. Bivariate plot of δ13C and δ15N for terrestrial herbivores grouped according to archaeological periods



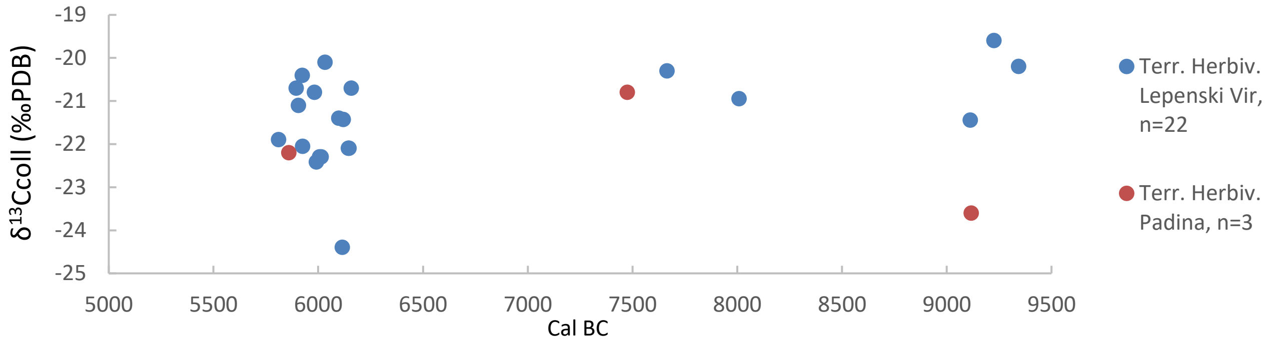
A.I.13. Bivariate plot of δ34S and δ15N for terrestrial herbivores grouped according to archaeological periods



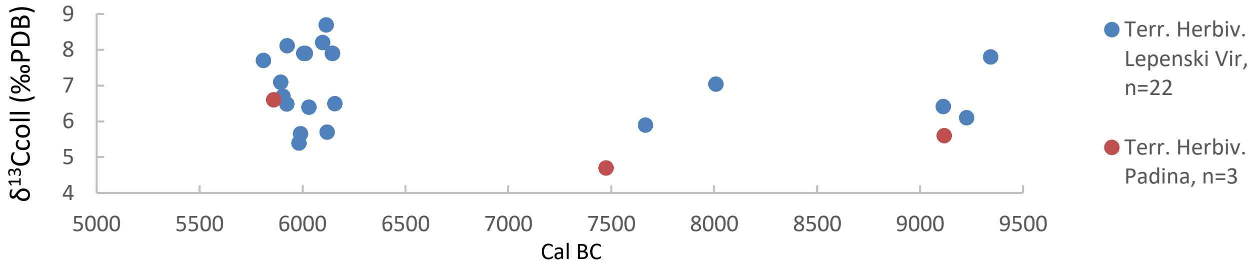
A.I.14. Bivariate plot of δ13C and δ15N for terrestrial herbivores grouped according to their wild/domesticated state



A.I.15. Bivariate plot of δ34S and δ15N for terrestrial herbivores grouped according to their wild/domesticated state

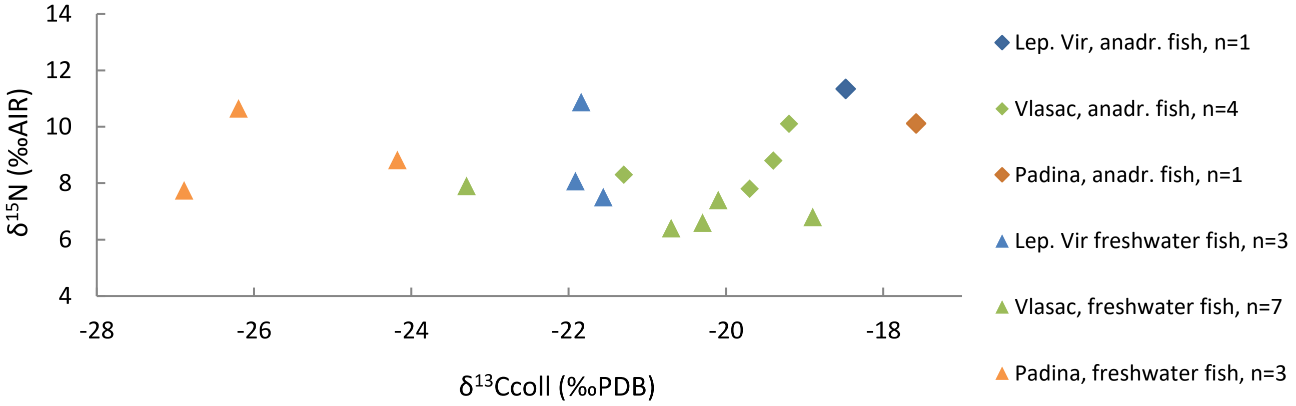


A.I.A. Bivariate plots of δ^{13}Ccoll and radiocarbon date. Calibrated dates and corrected for freshwater reservoir effect (Borić 2011a). Late Mesolithic individuals from Vlasac without criteria for collagen preservation excluded.

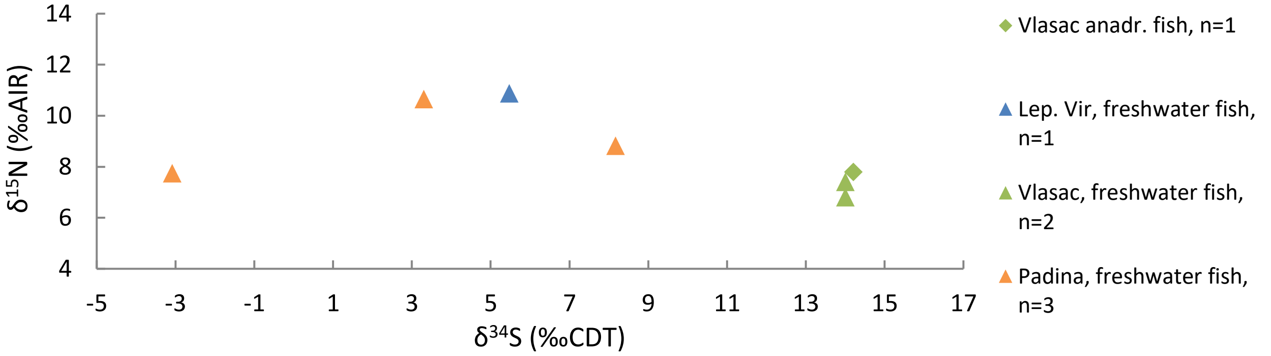


A.I.B. Bivariate plots of δ^{15}Nand radiocarbon date. Calibrated dates and corrected for freshwater reservoir effect (Borić 2011). Late Mesolithic individuals from Vlasac without criteria for collagen preservation excluded.

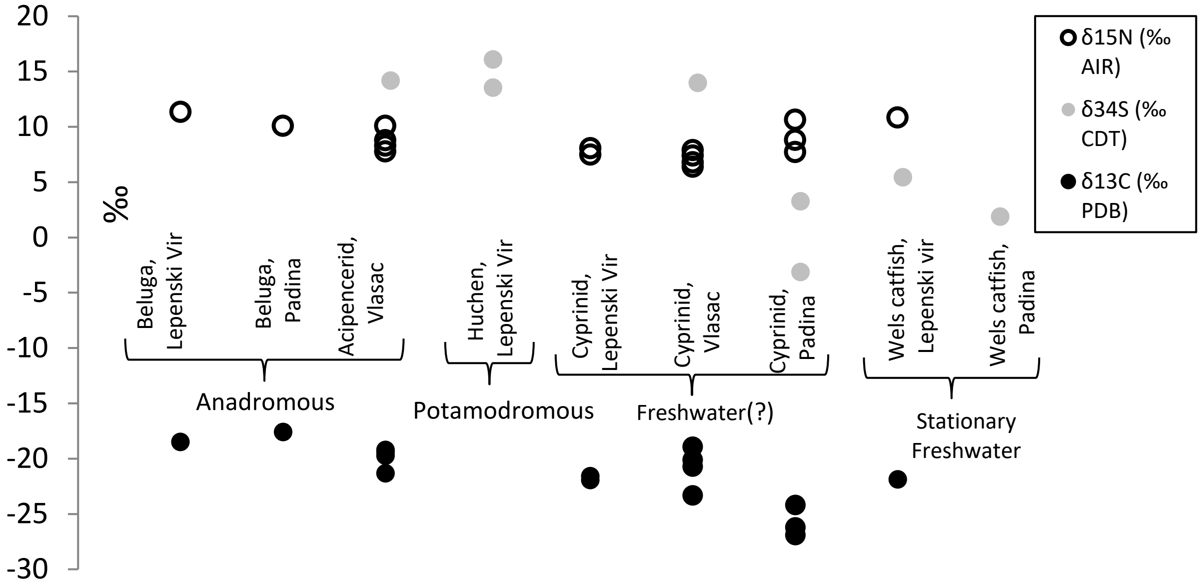
Geographical analyses



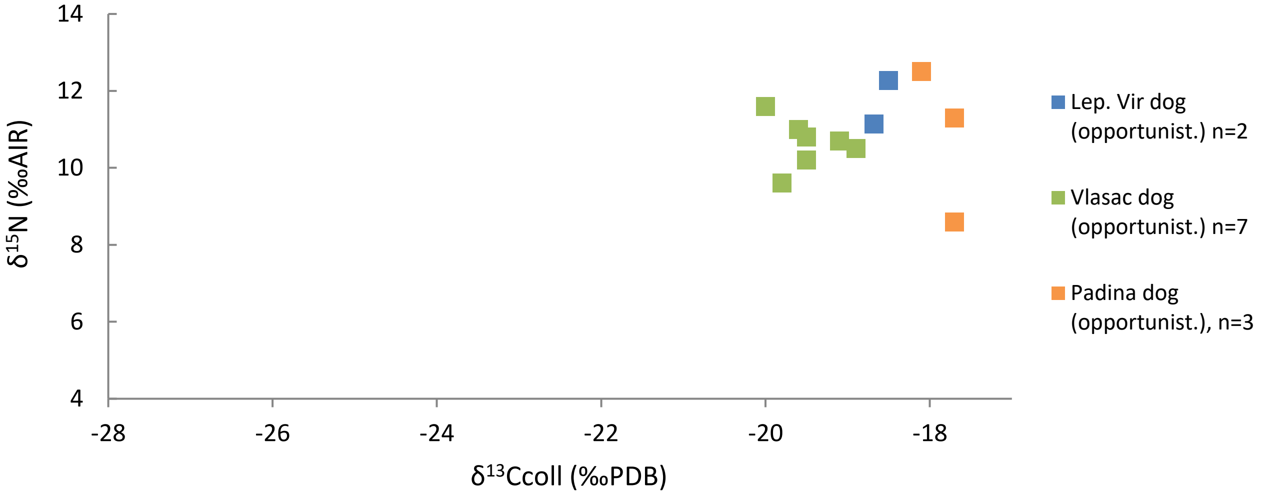
A.I.16. Bivariate plot of δ^{13}C and δ^{15}N for fish grouped according to their migratory behavior and site of discovery



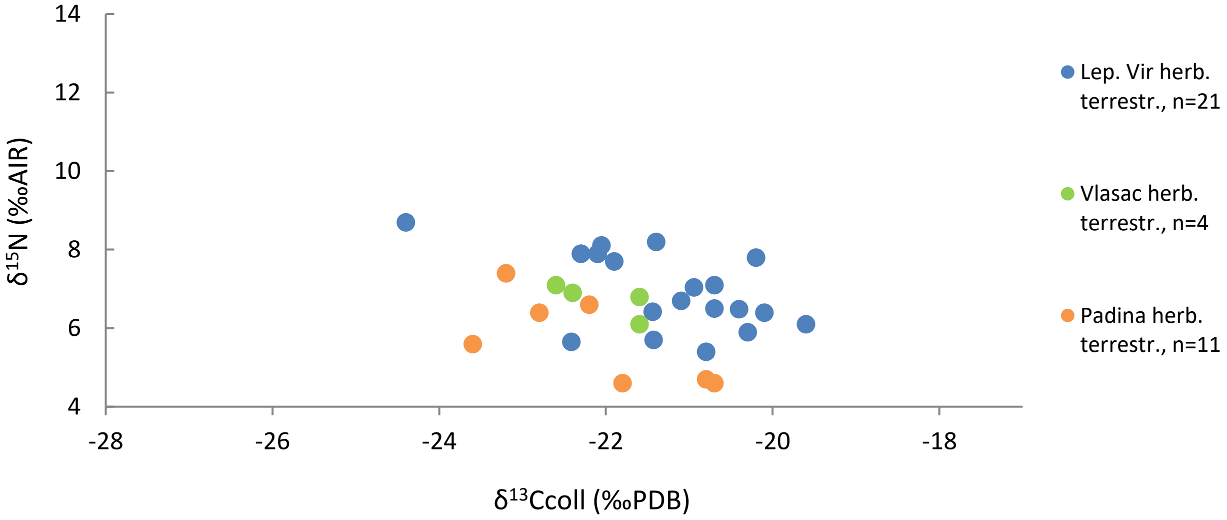
A.I.17. Bivariate plot of δ^{13}C andδ^{15}N for fish grouped according to their migratory behavior and site of discovery



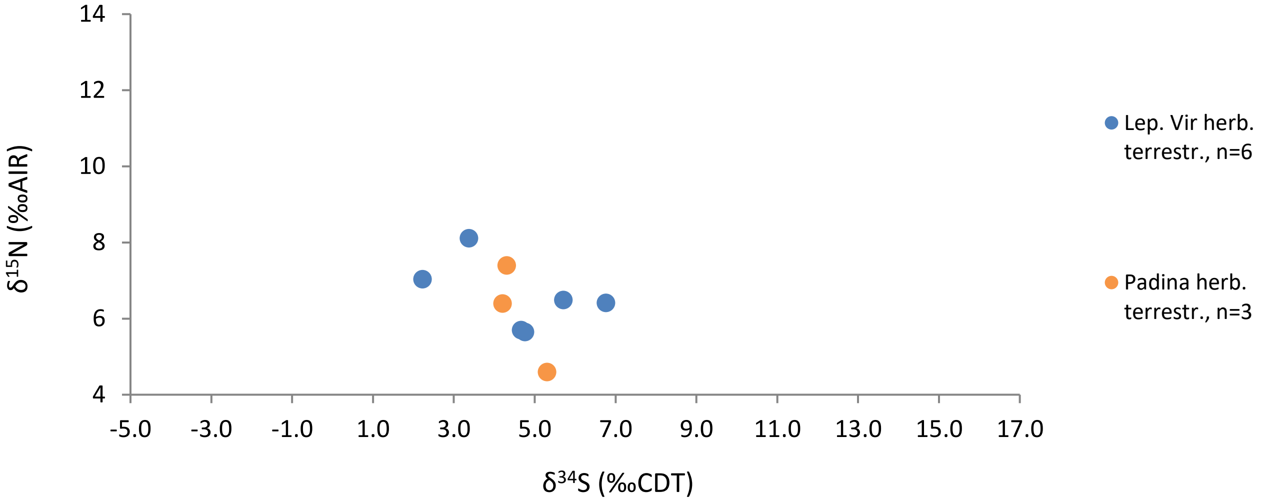
A.I.18. Plot of δ^{13}C, δ^{15}N and δ^{34}S for fish grouped according to the migratory behavior and site of discovery



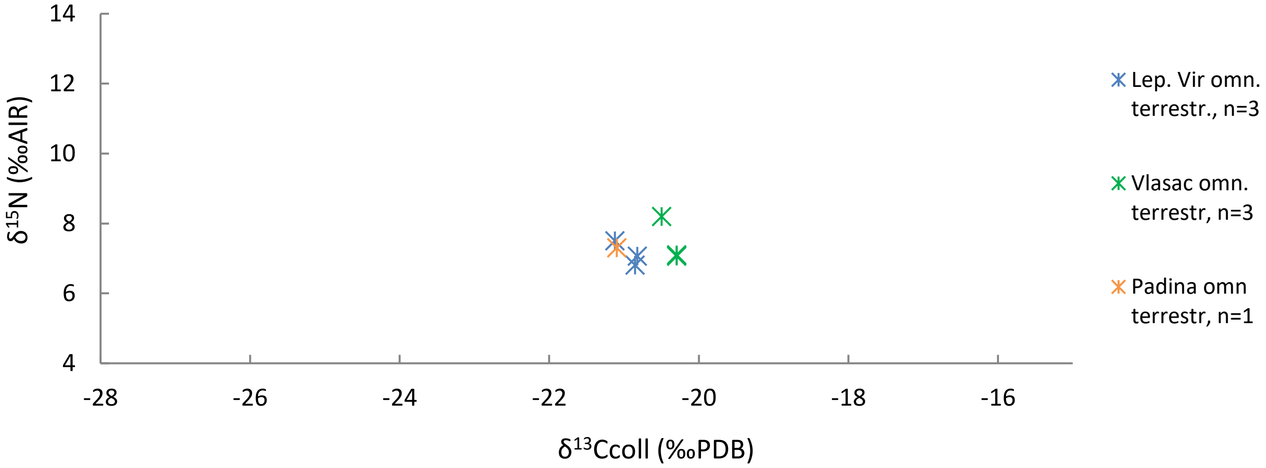
A.I.19. Bivariate plot of δ^{13}C and δ^{15}N for dogs grouped according to the site of discovery



A.I.20. Bivariate plot of δ^{13}C and δ^{15}N for terrestrial herbivores grouped according to the site of discovery



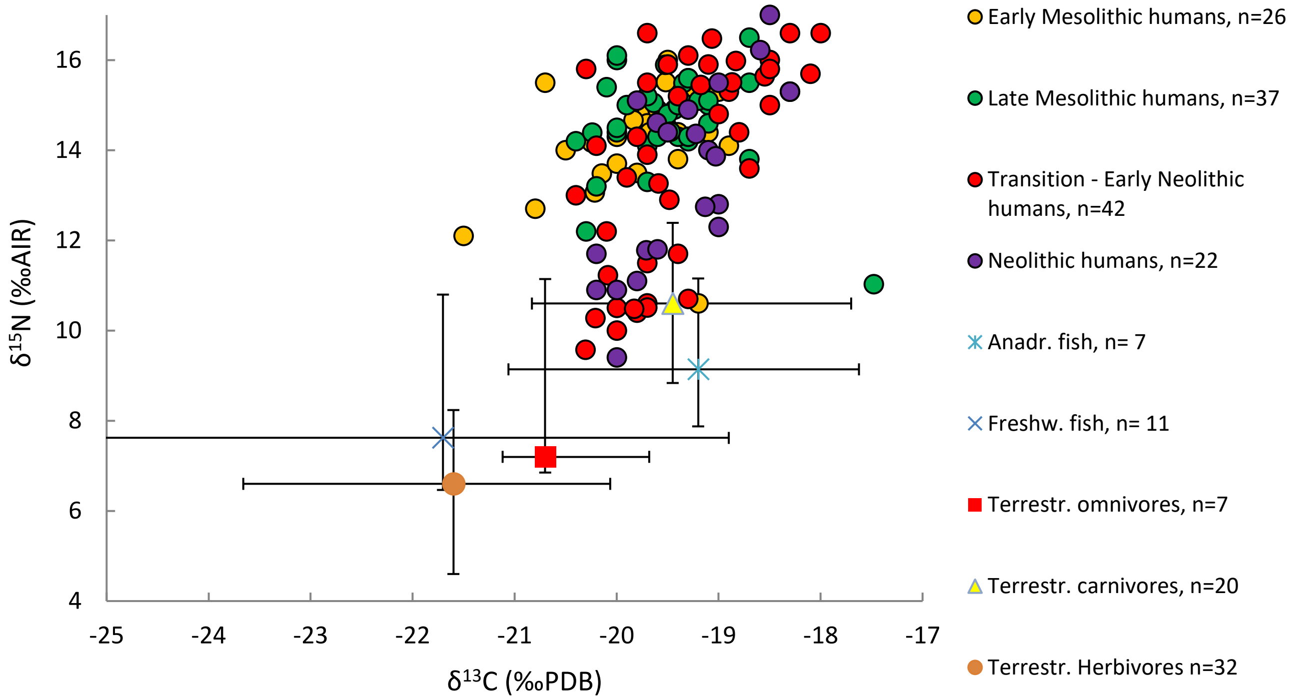
A.I.21. Bivariate plot of δ13C and δ34S for terrestrial herbivores grouped according to the site of discovery



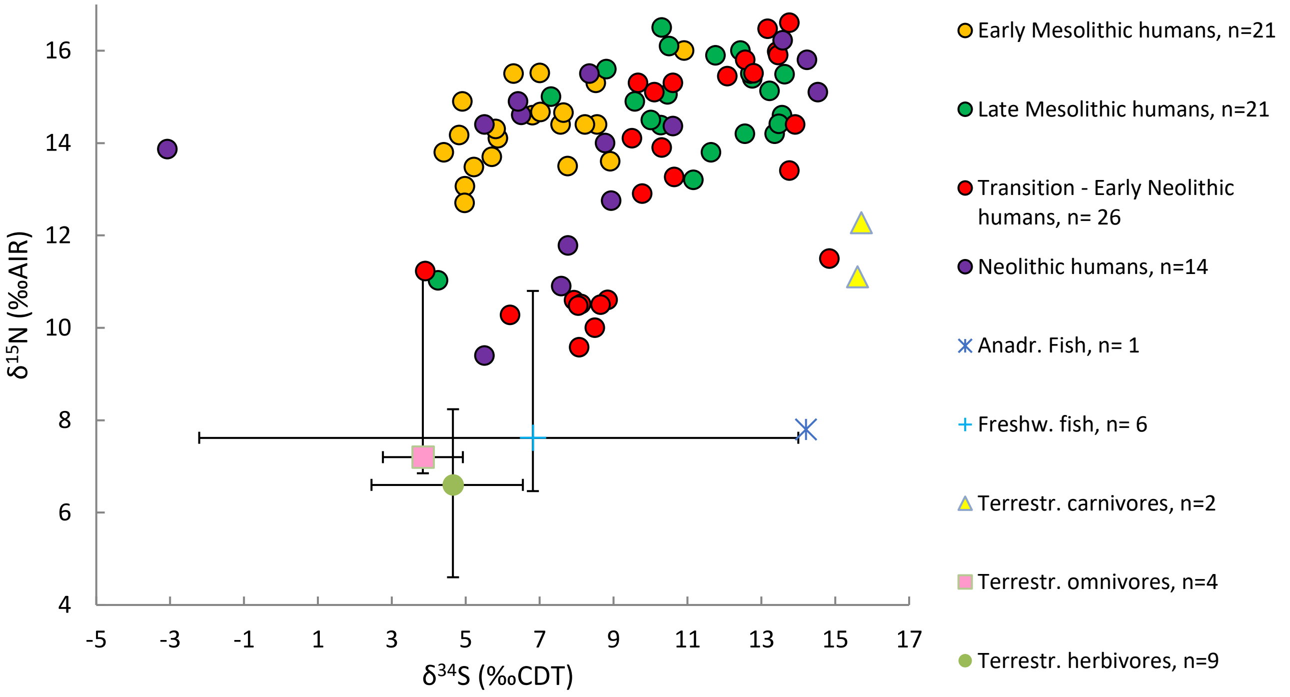
A.I.22. Bivariate plot ofδ13C and δ34S for terrestrial omnivores grouped according to the site of discovery

APPENDIX A.II. Human diet: multiple stable isotope extracted from the collagen protein (δ^{13}Ccoll, δ^{15}N, δ^{34}S) of adult prehistoric individuals from the Danube Gorges

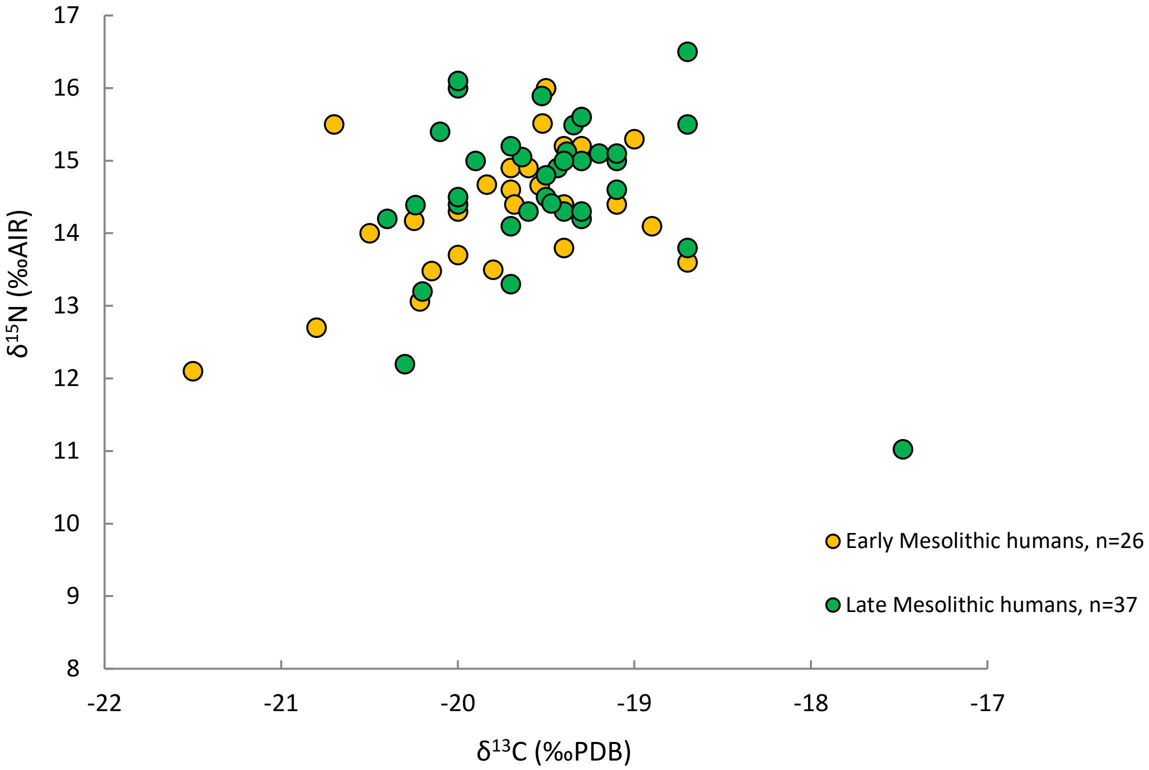
Chronological analyses



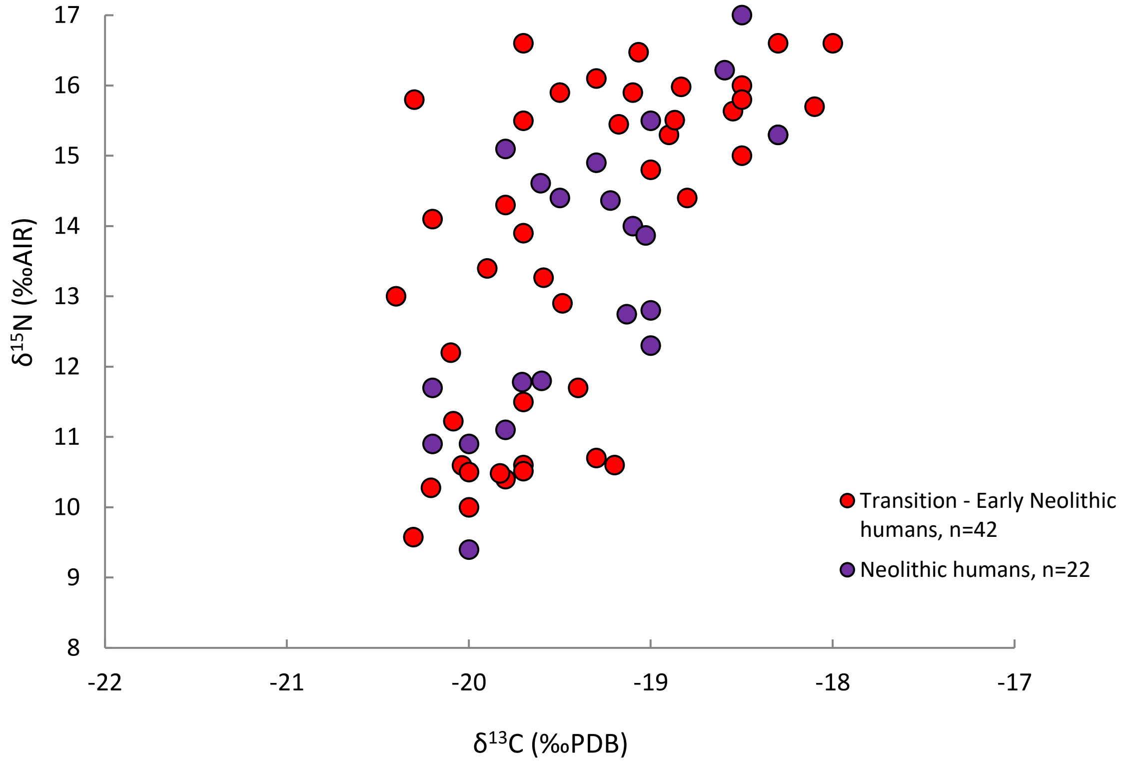
A.II.1. Bivariate plot of δ^{15}C and δ^{15}N for adult humans (>15 yrs) and animals from the prehistoric sites of the Danube Gorges. Bars represent the 97.5/2.5 quartiles.



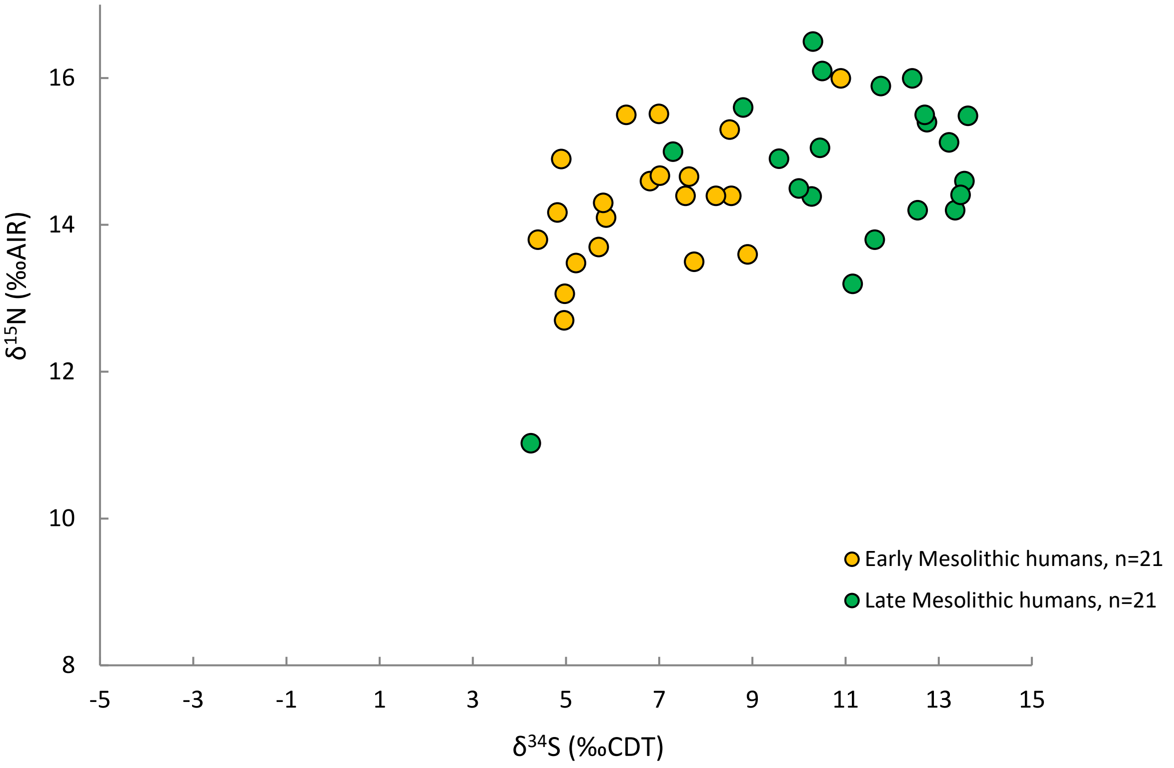
A.II.2. Bivariate plot of δ^{34}S and δ^{15}N for adult humans (>15 yrs) and animals from the prehistoric sites of the Danube Gorges. Bars represent the 97.5/2.5 quartiles.



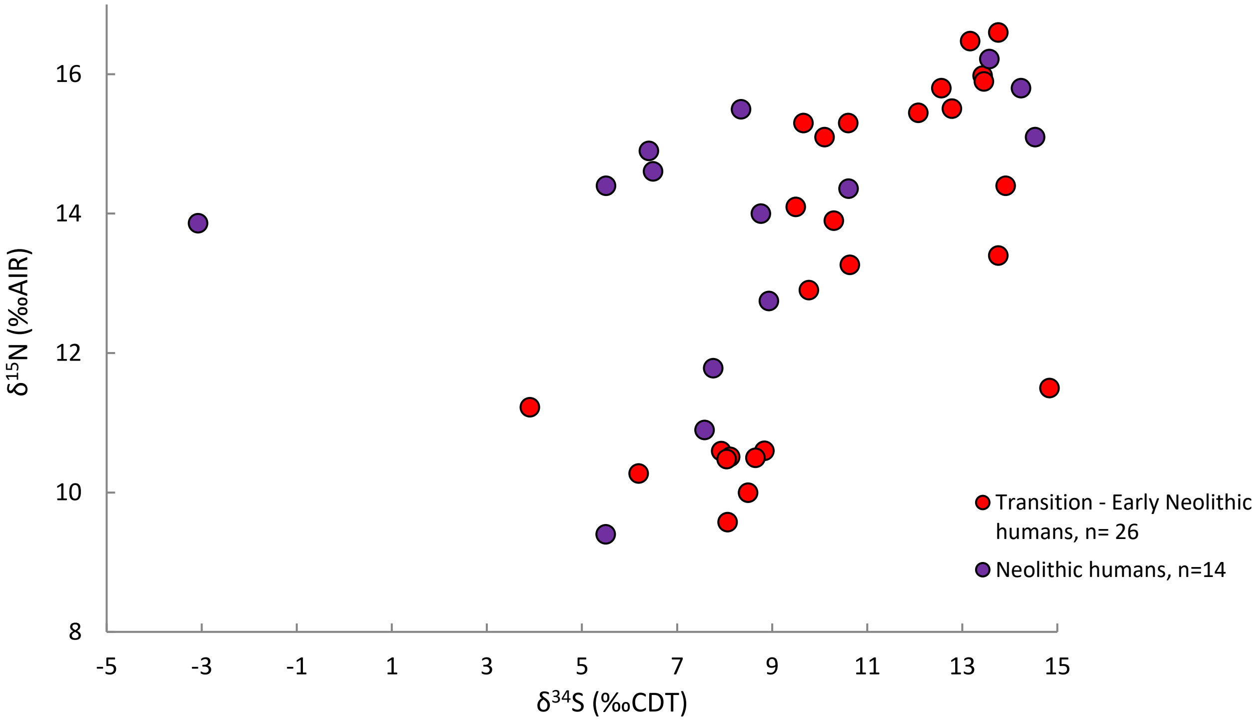
A.II.3. Bivariate plot of δ13C and δ15N for Mesolithic adult humans (>15 yrs) from the Danube Gorges



A.II.4. Bivariate plot of δ13C and δ15N for Neolithic adult humans (>15 yrs) from the Danube Gorges

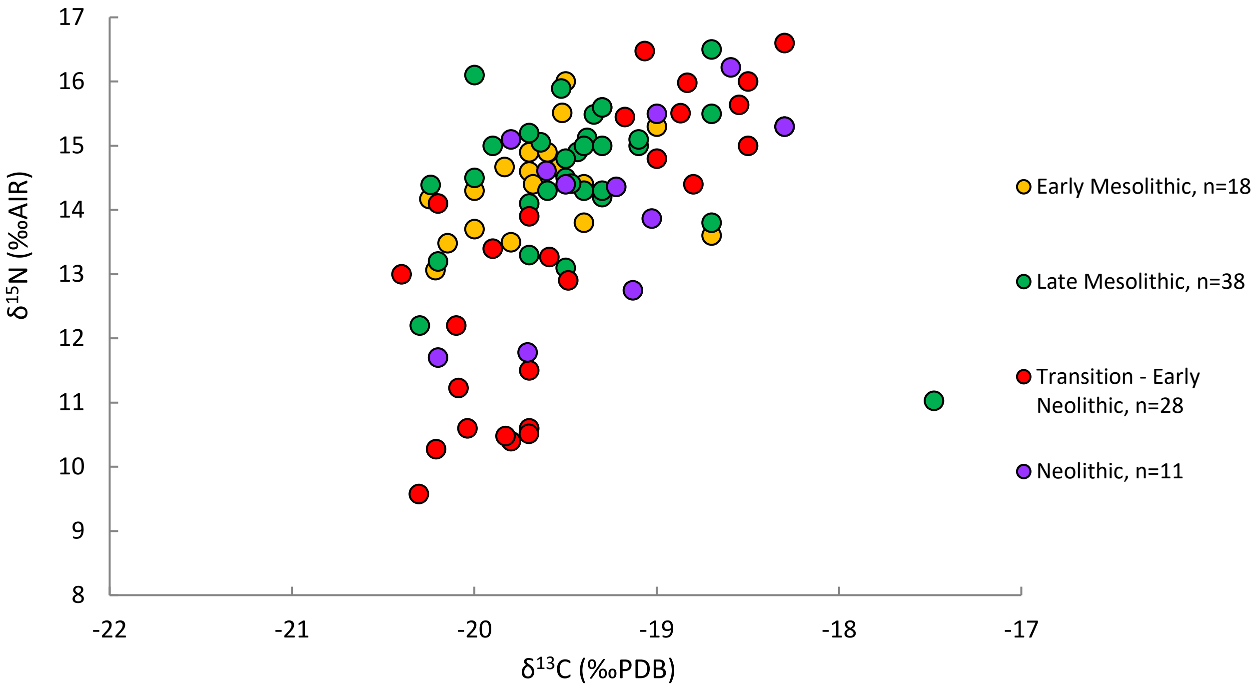


A.II.5. Bivariate plot of $\delta^{34}S$ and $\delta^{15}N$ for Mesolithic adult humans (>15 yrs) from the Danube Gorges

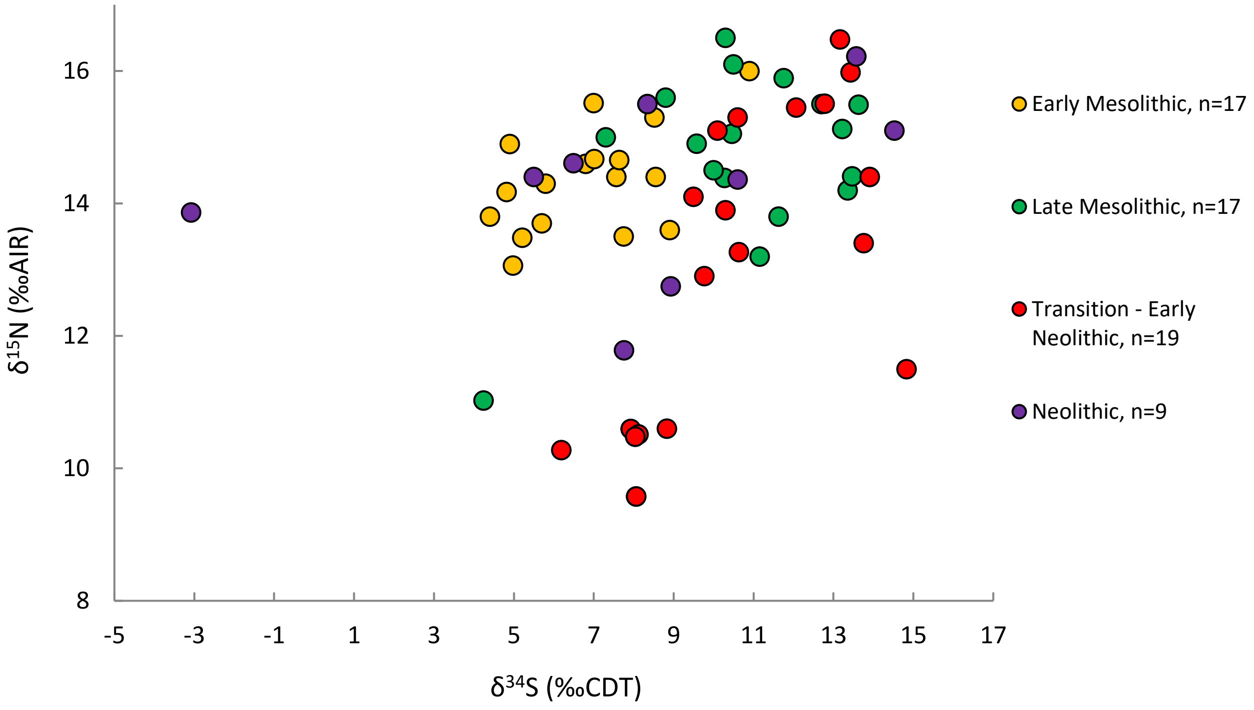


A.II.6. Bivariate plot of$\delta^{34}S$ and $\delta^{15}N$ for Neolithic adult humans (>15 yrs) from the Danube Gorges

Bivariate plots solely with humans for which the criteria for collagen quality were available

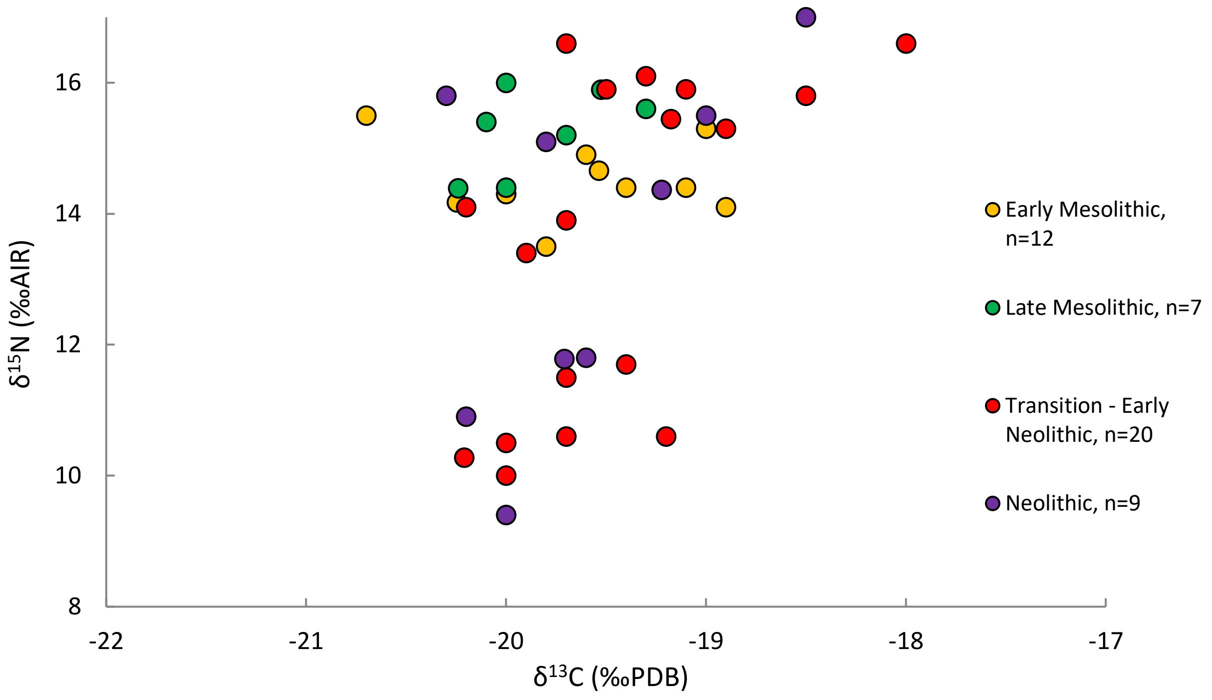


A.II.7. Bivariate plot ofδ^{13}C and δ^{15}N for prehistoric adult humans (>15 yrs) from the Danube Gorges, only individuals for which collagen quality criteria were available and respected

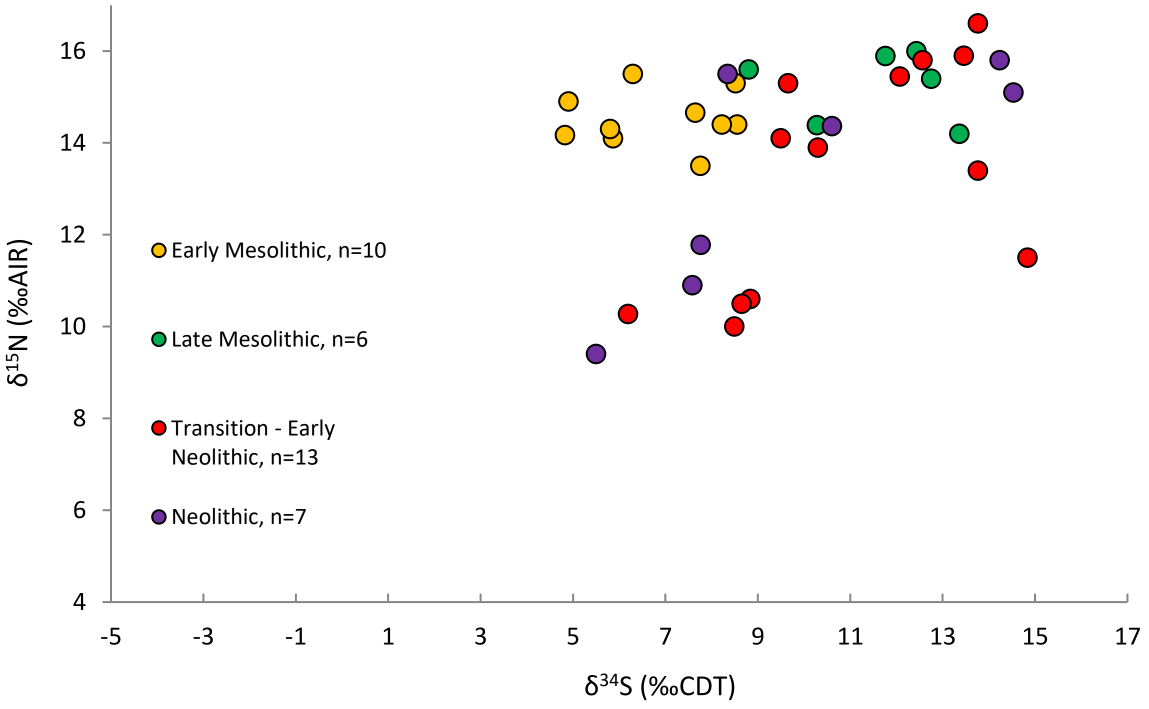


A.II.8. Bivariate plot of δ^{34}S and δ^{15}N for prehistoric adult humans (>15 yrs) from the Danube Gorges, only individuals for which collagen quality criteria were available and respected

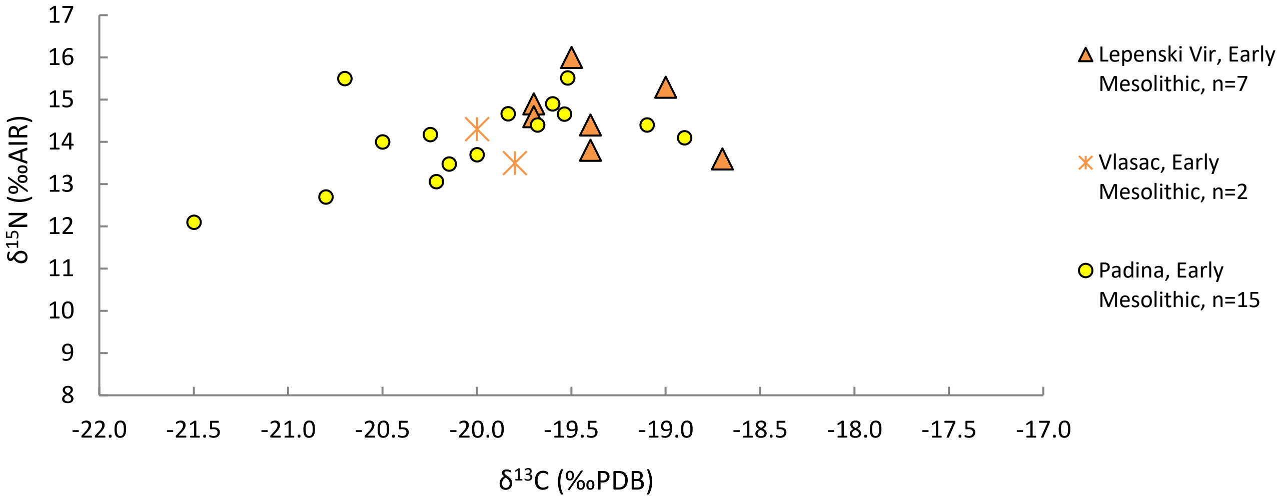
Bivariate plots solely with humans ^{14}C dated



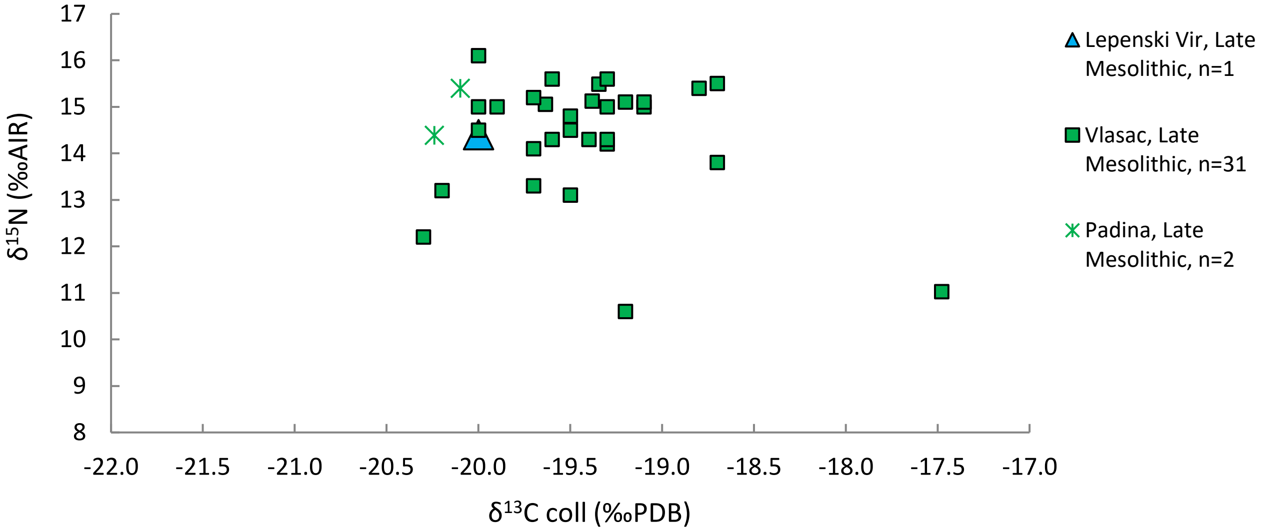
A.II.9. Bivariate plot ofδ^{13}C and δ^{15}N for prehistoric adult humans (>15 yrs) from the Danube Gorges, only radiocarbon dated individuals



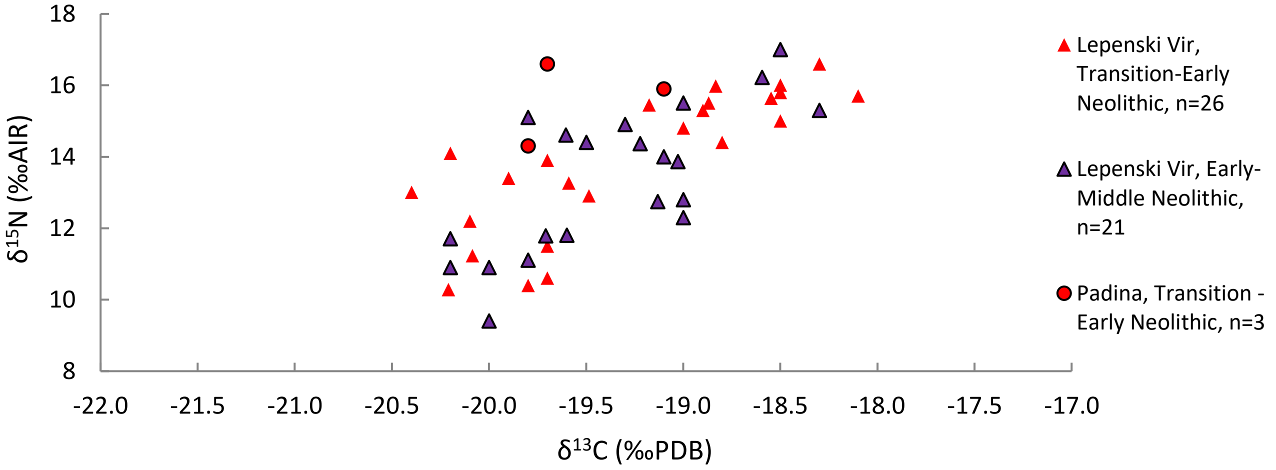
A.II.10. Bivariate plot of δ^{34}S and δ^{15}N for prehistoric adult humans (>15 yrs) from the Danube Gorges, only radiocarbon dated individuals



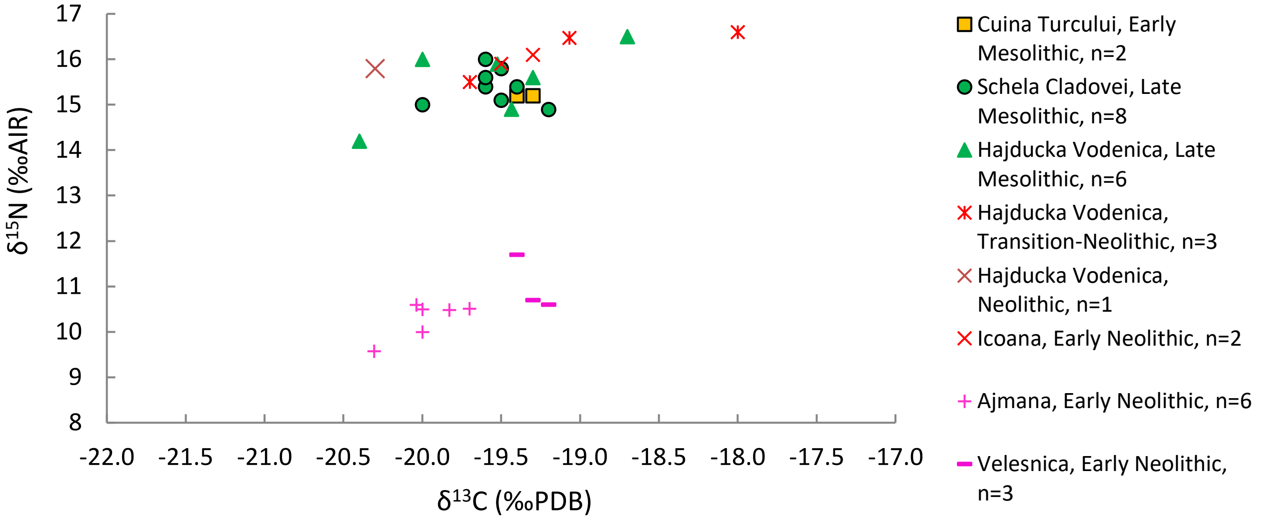
A.II.11. Bivariate plot of δ^{13}C and δ^{15}N for Early Mesolithic adult humans (>15 yrs) per sites of the Upper Gorges



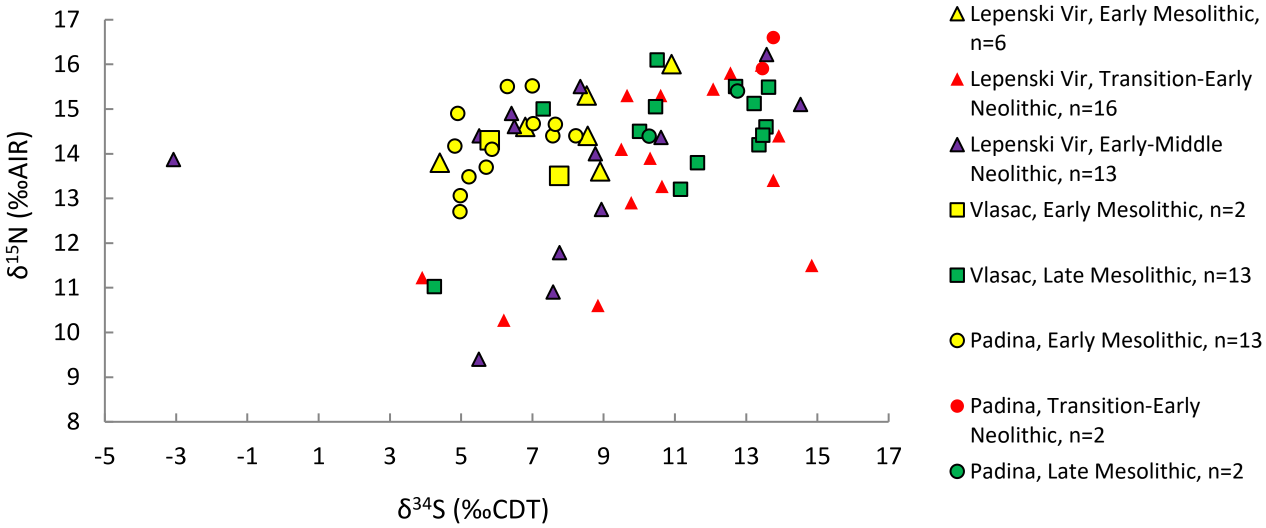
A.II.12. Bivariate plot ofδ^{13}C and δ^{15}N for Late Mesolithic adult humans (>15 yrs) per sites of the Upper Gorges



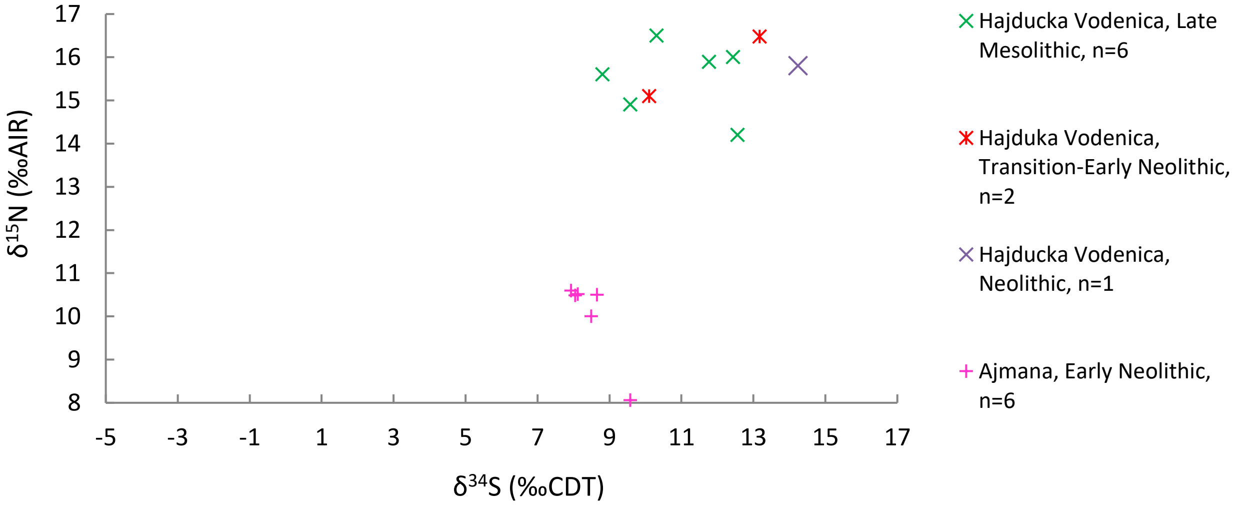
A.II.13. Bivariate plot of δ^{13}C and δ^{15}N for Neolithic adult humans (>15 yrs) per sites of the Upper Gorge



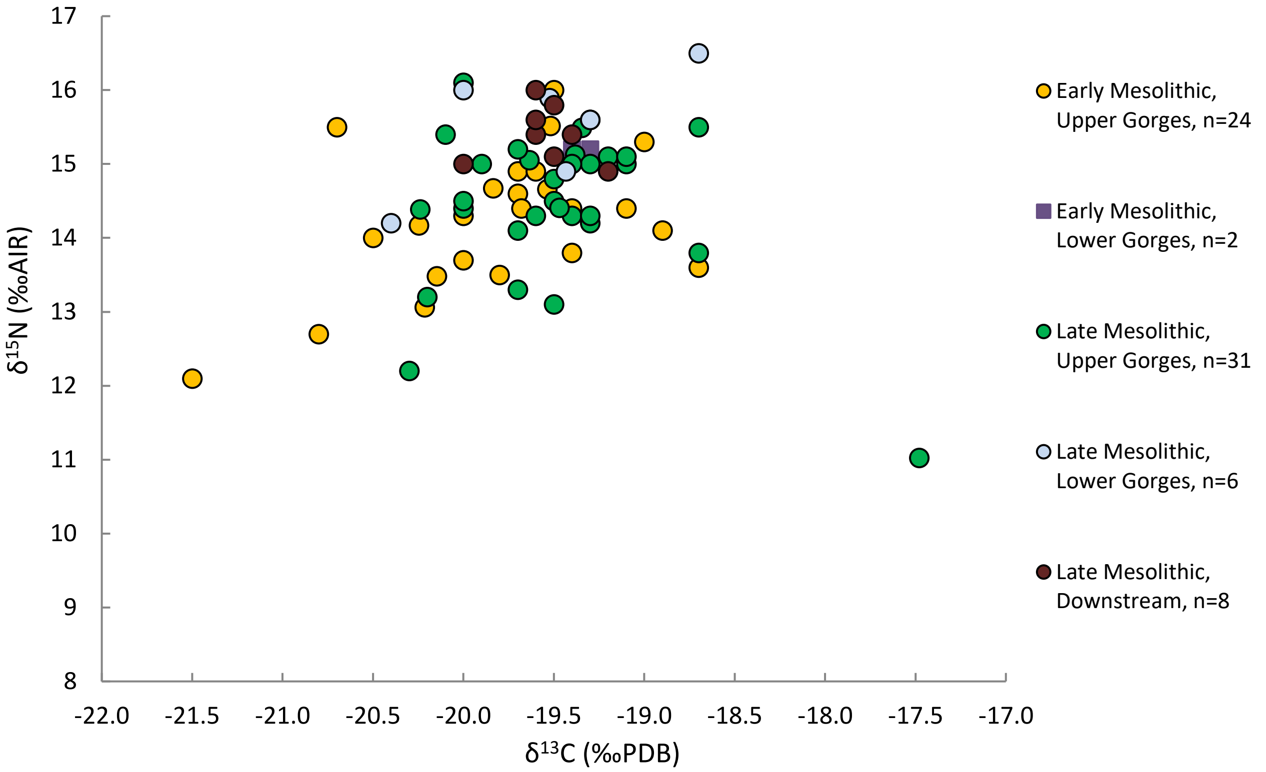
A.II.14. Bivariate plot of δ^{13}C and δ^{15}N for Mesolithic and Neolithic adult humans (>15 yrs) per sites of the Lower Gorges and located downstream



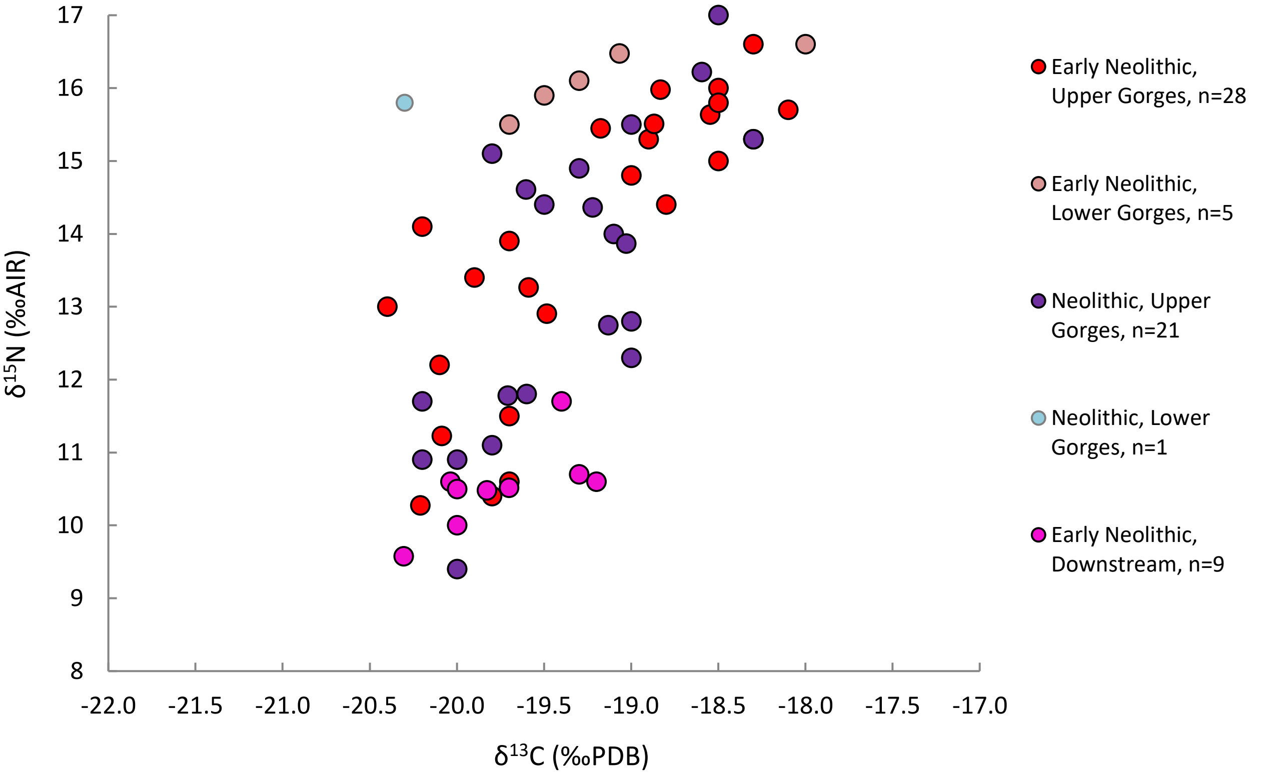
A.II.15. Bivariate plot of δ^{34}S and δ^{15}N for Mesolithic and Neolithic adult humans (>15 yrs) per sites of the Upper Gorges



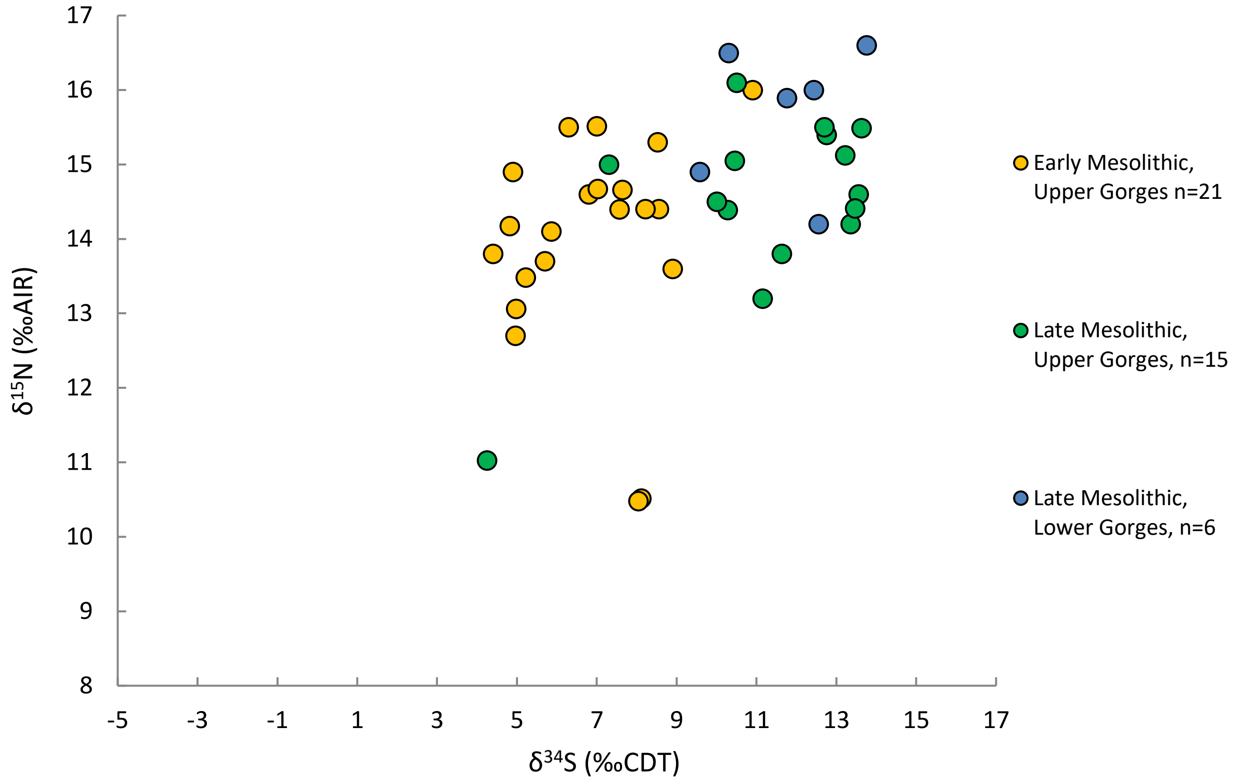
A.II.16. Bivariate plot ofδ^{34}S and δ^{15}N for Mesolithic and Neolithic adult humans (>15 yrs) per sites of the Lower Gorges and located downstream



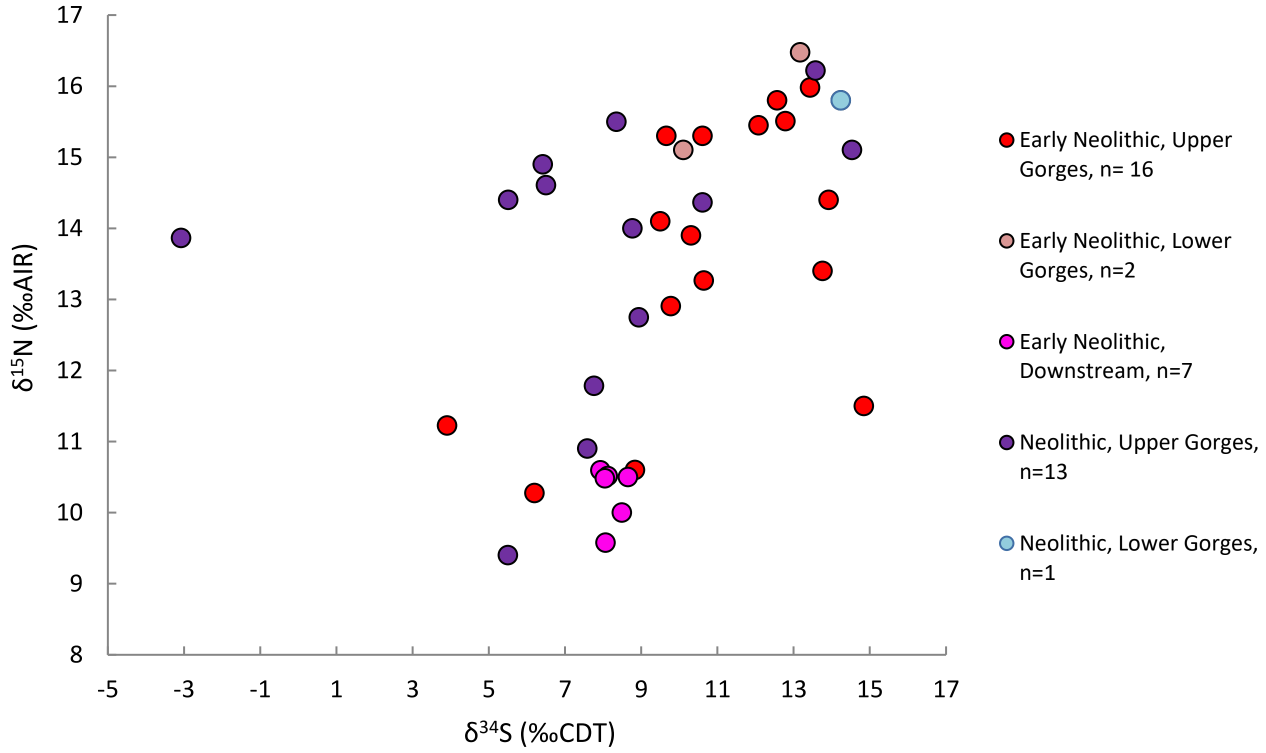
A.II.17. Bivariate plot ofδ^{13}C and δ^{15}N for Mesolithic adult humans (>15 yrs) per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)



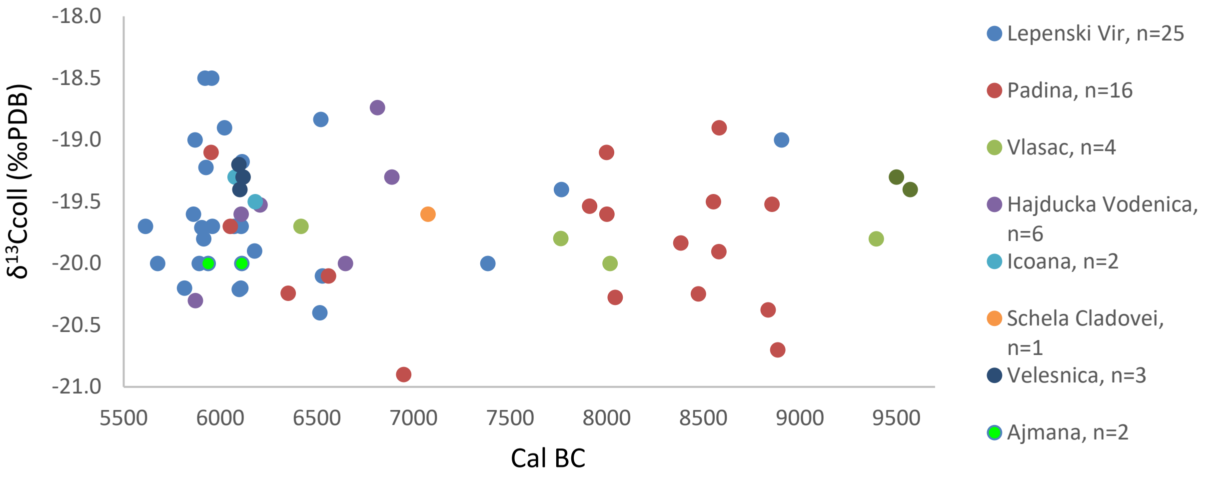
A.II.18. Bivariate plot of δ^{13}C and δ^{15}N for Neolithic adult humans (>15 yrs) per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)



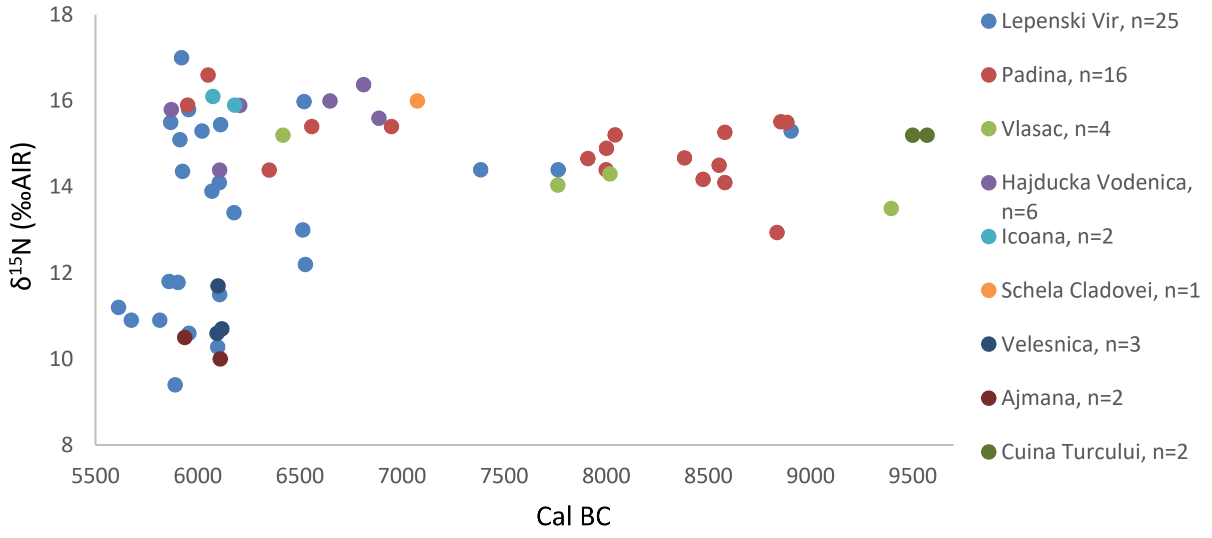
A.II.19. Bivariate plot ofδ^{34}S and δ^{15}N for Mesolithic adult humans (>15 yrs)
per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)



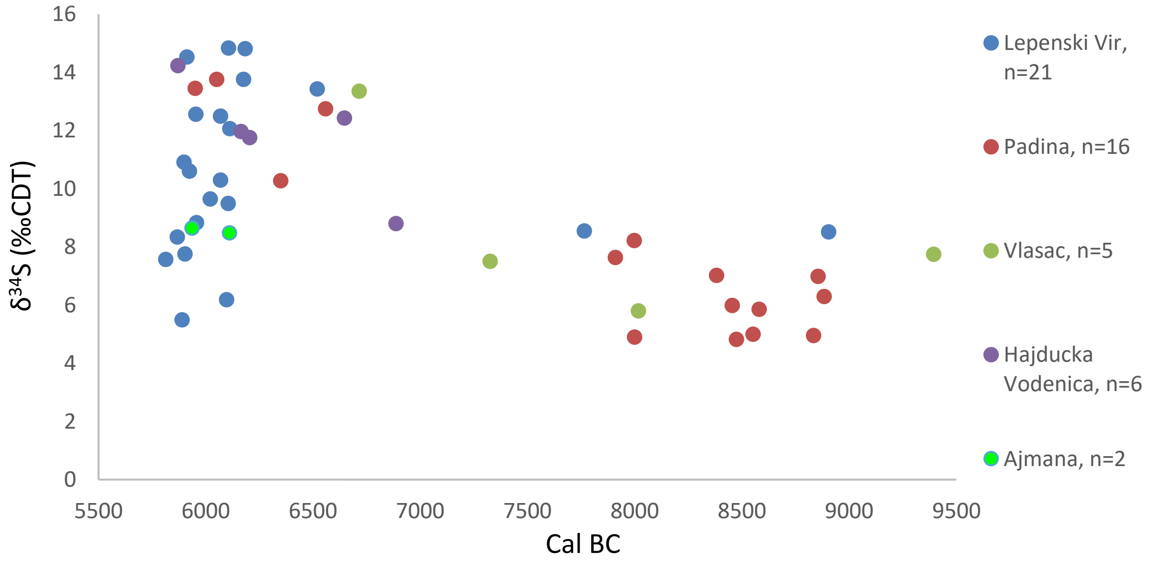
A.II.20. Bivariate plot ofδ^{34}S and δ^{15}N for Mesolithic adult humans (>15 yrs)
per geographical areas of discovery (Upper Gorges, Lower Gorges, Downstream Area)



A.II.A. Bivariate plots of δ¹³Ccoll and radiocarbon dates. Only individuals aged > 10 years old. Calibrated dates and corrected for freshwater reservoir effect (Borić 2011; Bonsall et al. 2015a). Late Mesolithic individuals from Vlasac without criteria for collagen preservation excluded.

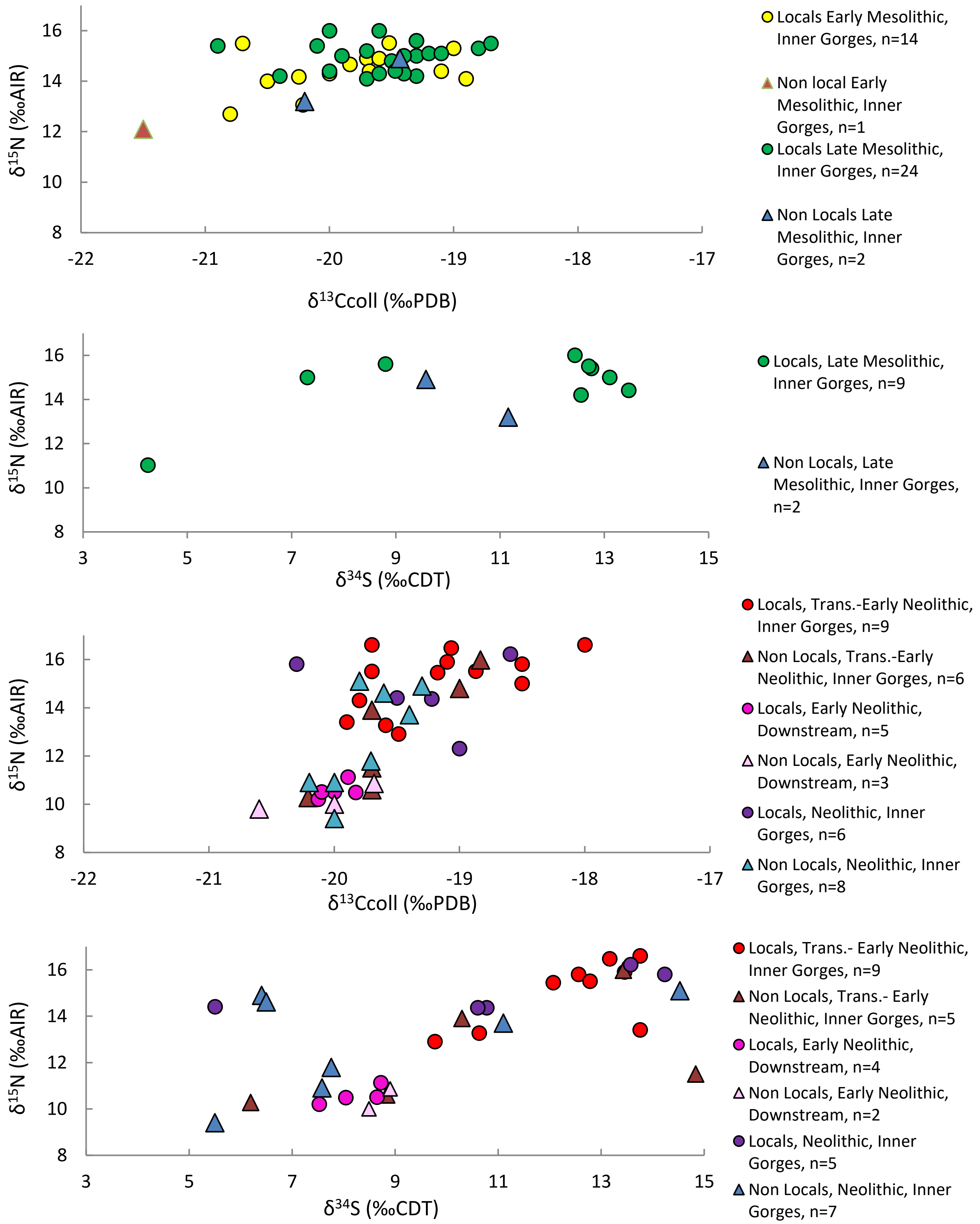


A.II.B. Bivariate plots of δ¹⁵N and radiocarbon dates. Only individuals aged > 10 years old.

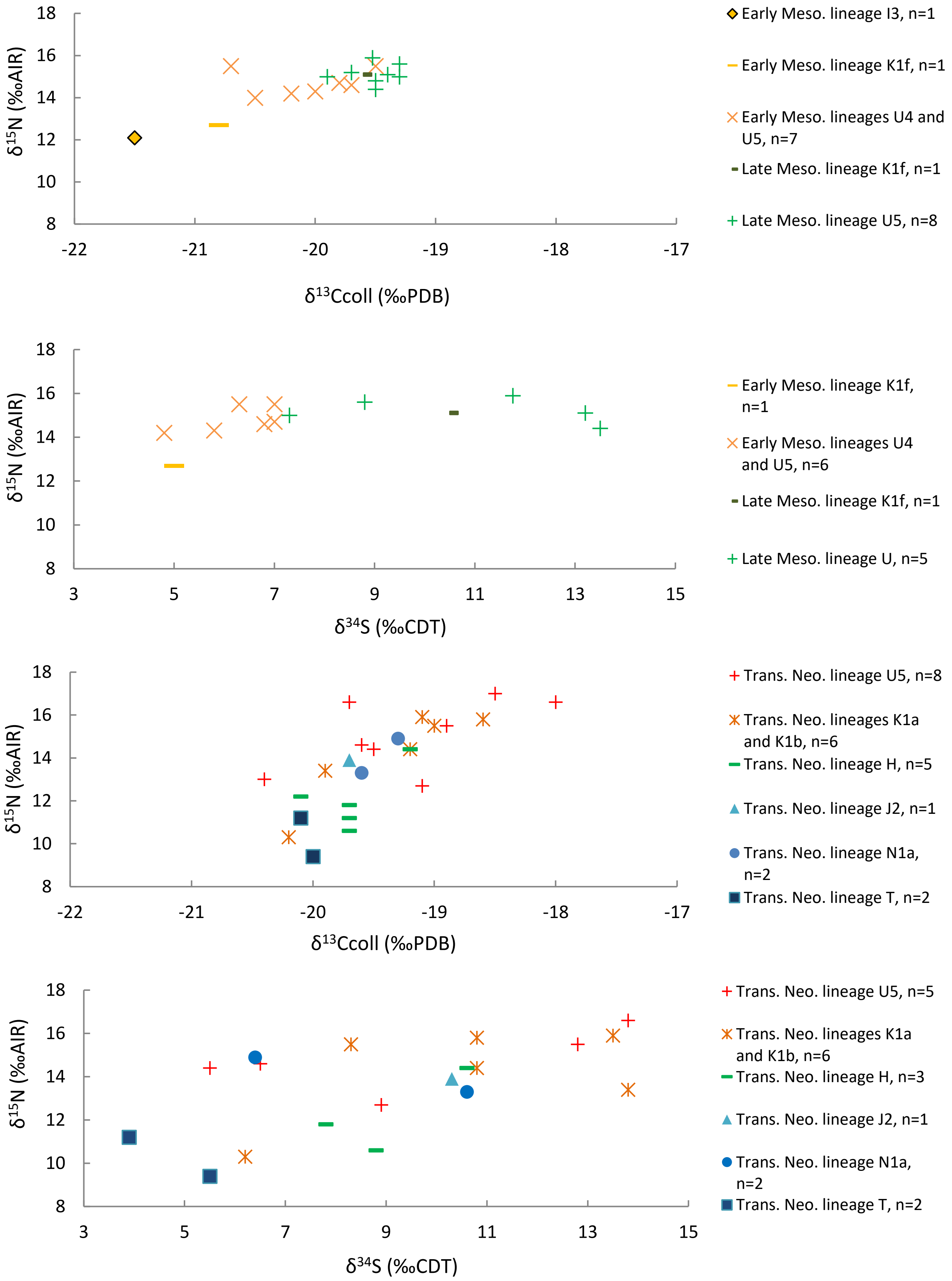


A.II.C Bivariate plots of δ³⁴S and radiocarbon dates.

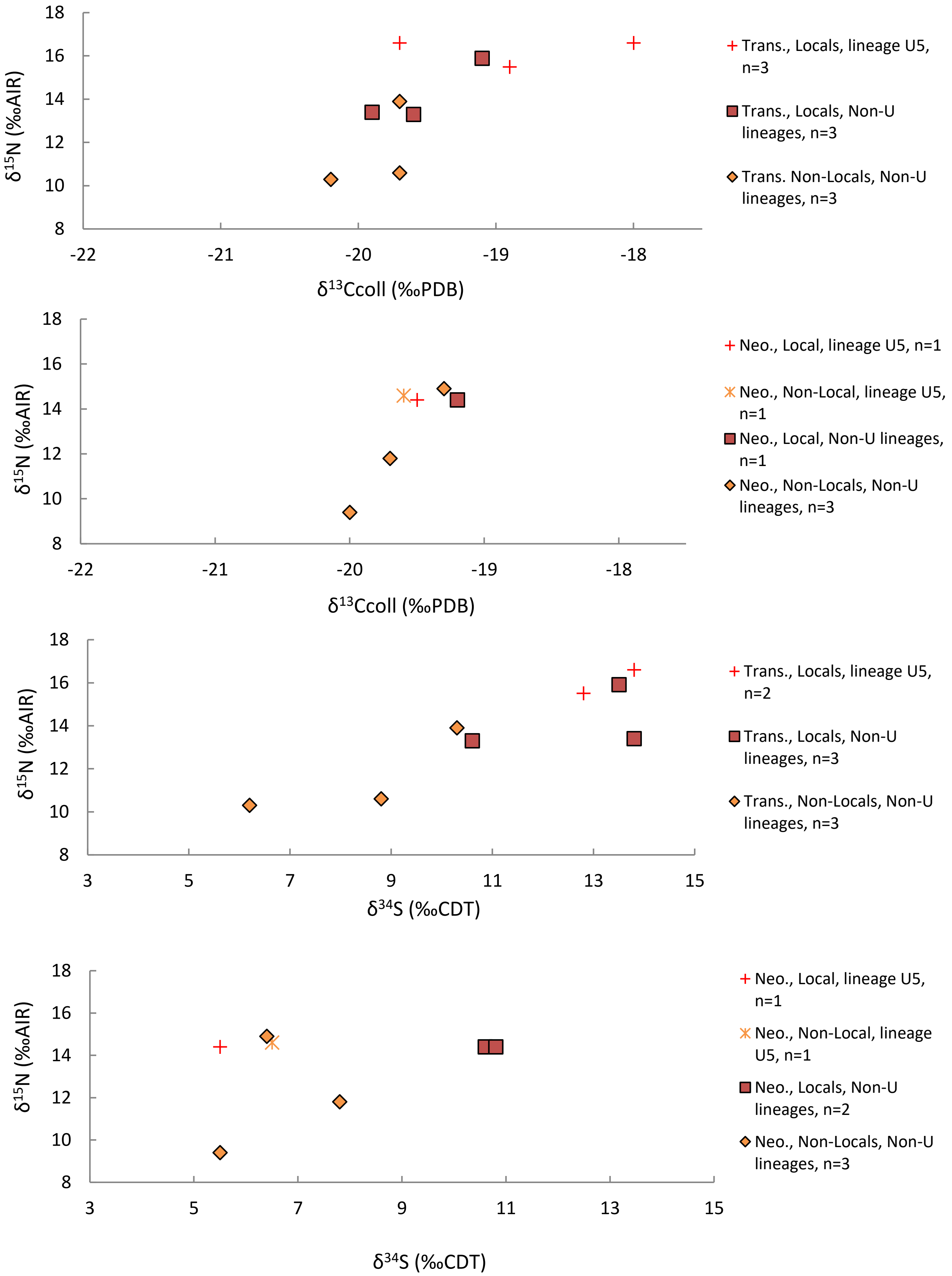
Analyses per geological area of origin and genetic lineages



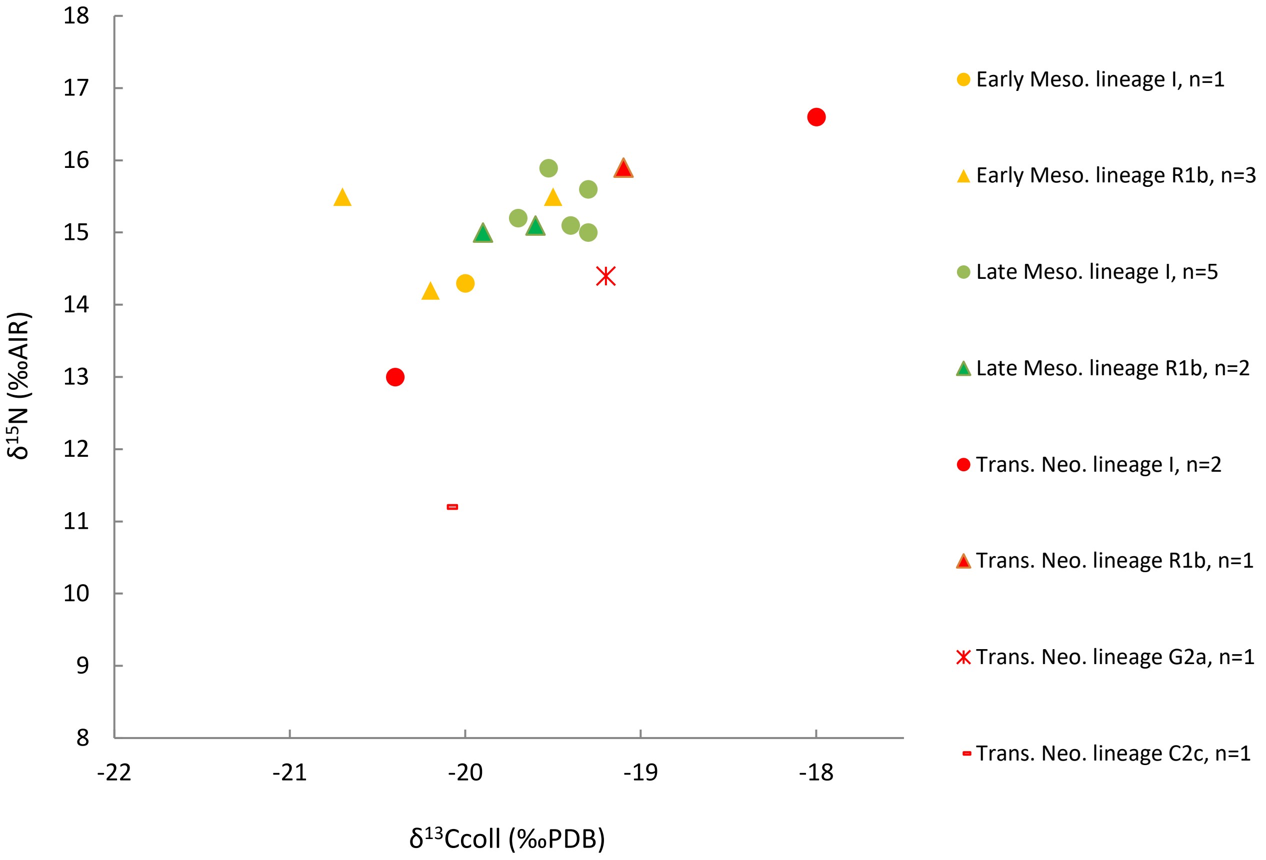
A.II.21. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Mesolithic and Neolithic humans (>5 yrs) grouped chronologically and according to their geographic origin (Locals and Non-Locals discriminated according to their signal in radiogenic strontium, ^{87}Sr/^{86}Sr Borić and Price 2013)

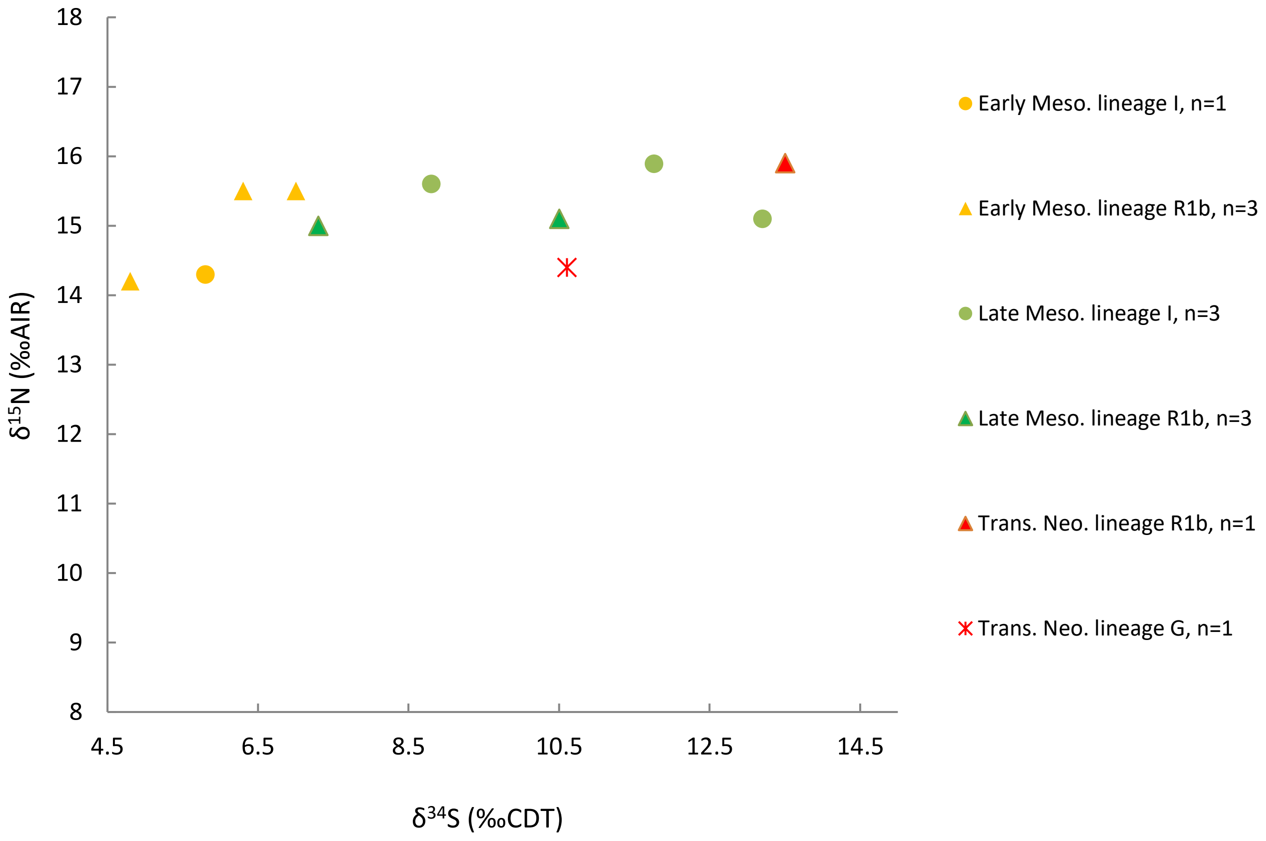


A.II.22. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Mesolithic and Trans.-Neolithic humans (>5 yrs) grouped chronologically and per maternal genetic lineages (mitochondrial DNA; Hofmanová 2016; Mathieson et al. 2018)



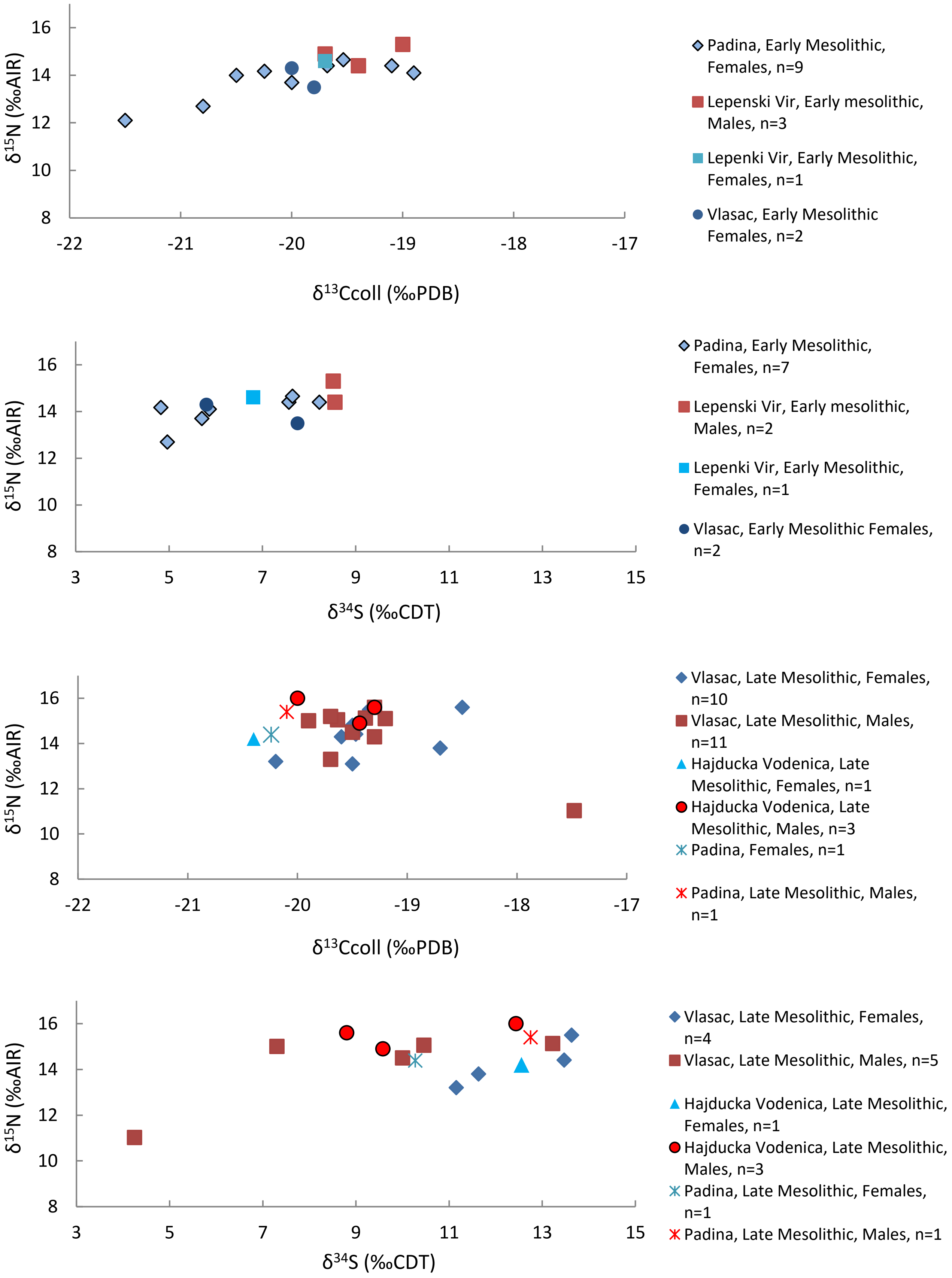
A.II.23. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Trans.- Early Neolithic and Neolithic humans (>5 yrs) grouped per maternal genetic lineages (mitochondrial DNA; Hofmanová 2016; Mathieson et al. 2018) and according to their geographic origin (Locals and Non-Locals discriminated according to their signal in radiogenic strontium (^{87}Sr/^{86}Sr Borić and Price 2013)



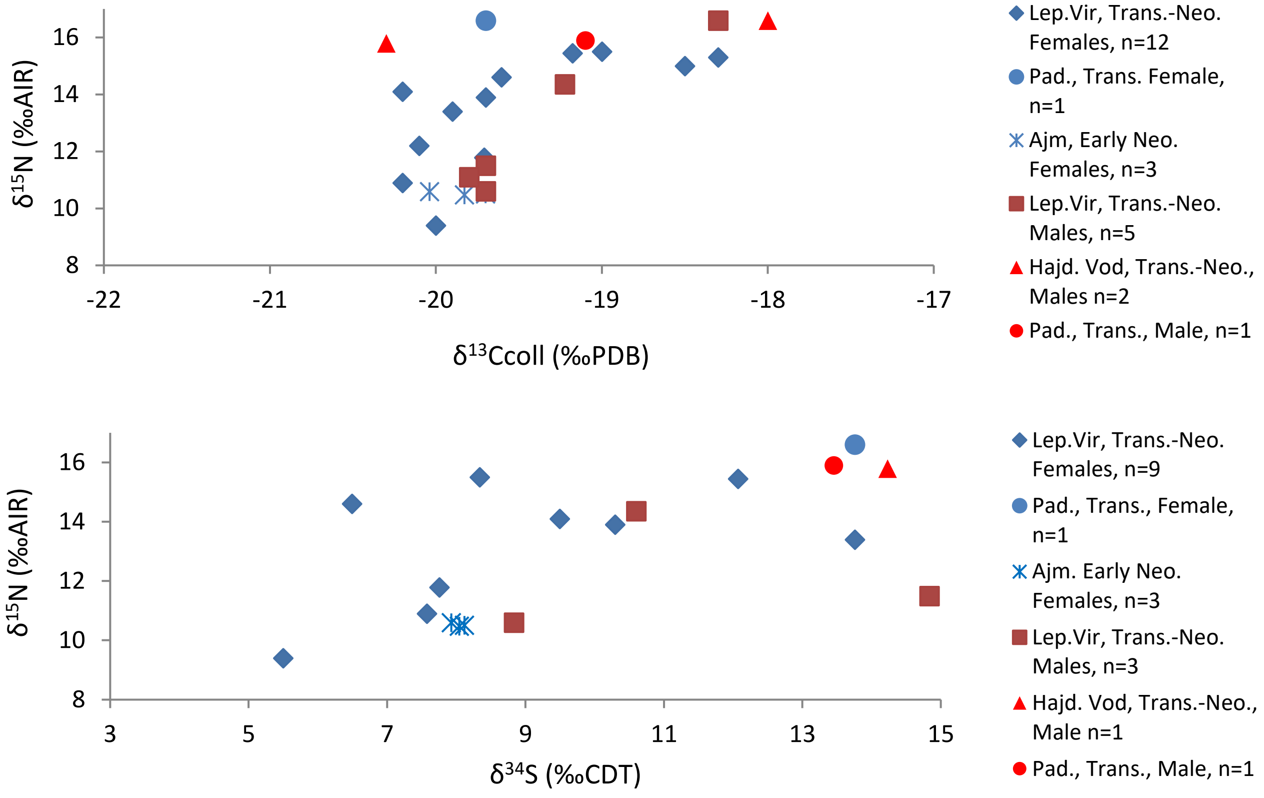


A.II.24. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ15N for Mesolithic and Neolithic humans (>5 yrs) grouped chronologically and per paternal genetic lineage (Hofmanová 2016; Mathieson et al. 2018)

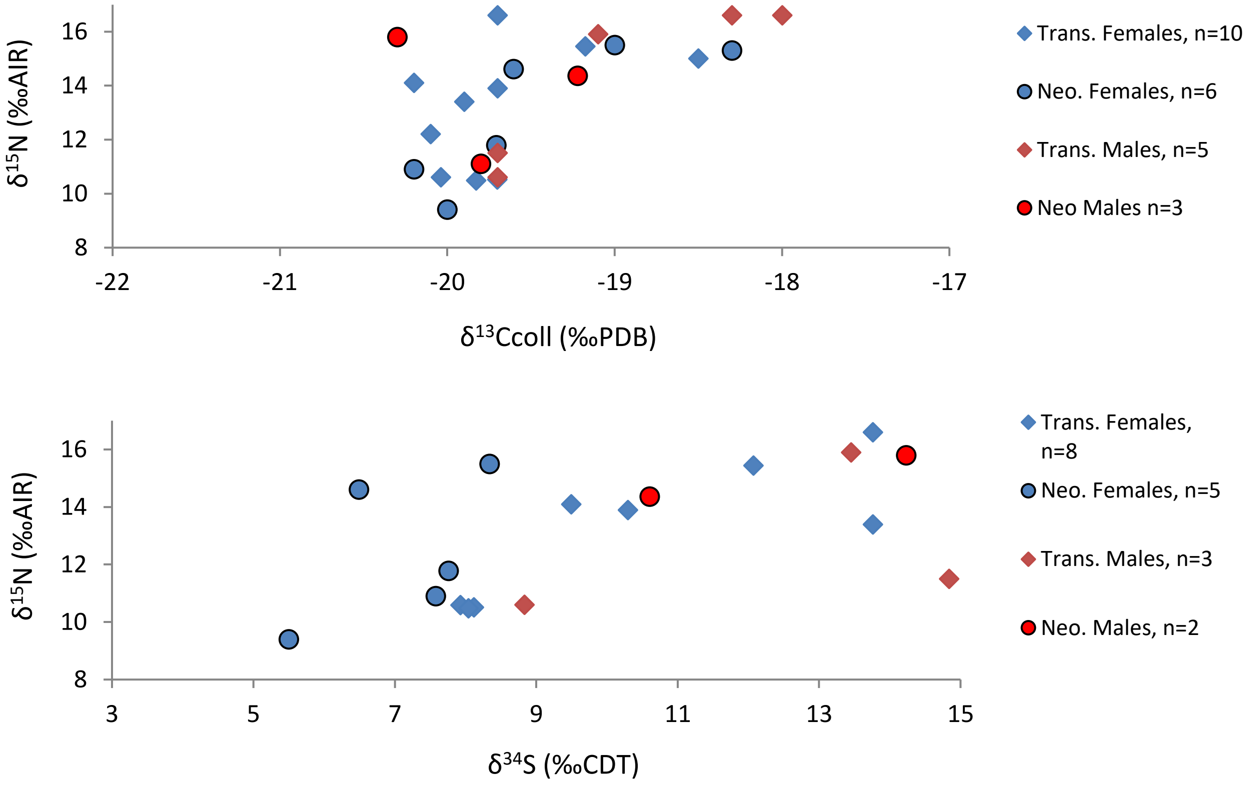
Analyses per sex and per age



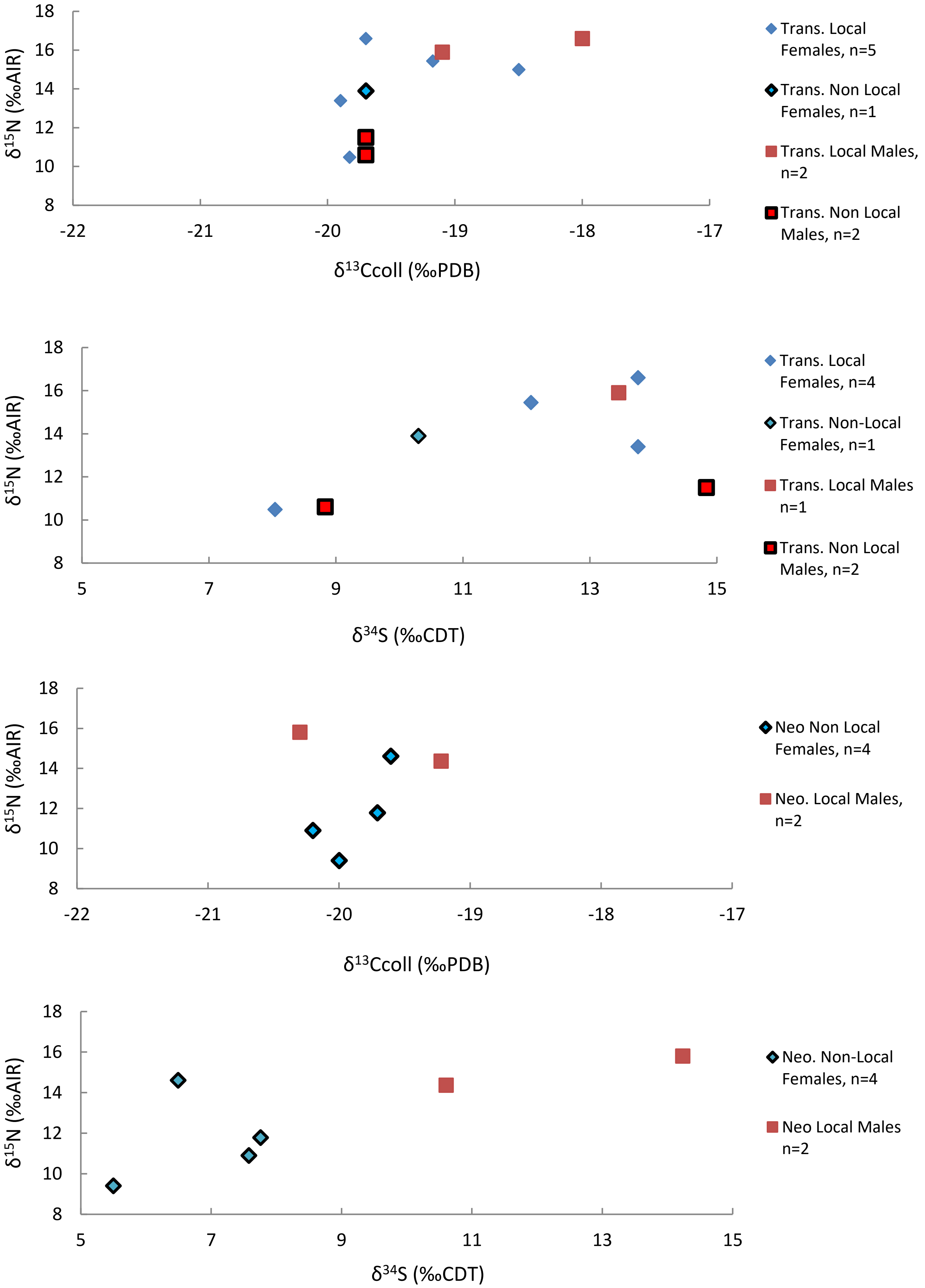
A.II.25. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ15N for Mesolithic adult humans (>15 yrs) grouped chronologically, per sites of discovery and per sex



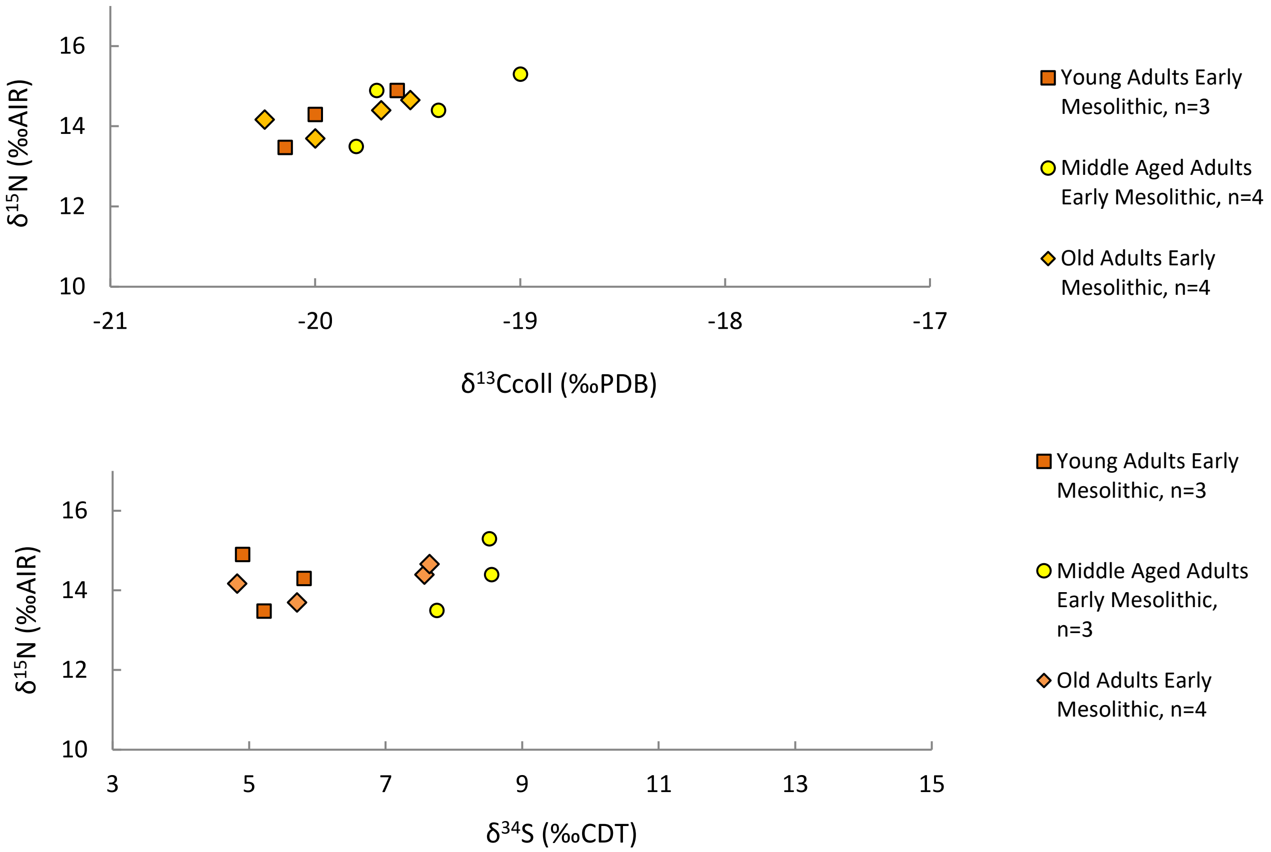
A.II.26. Bivariate plots of δ13C - δ15N and δ34S - δ15N for Neolithic adult humans (>15 yrs) grouped per sites of discovery and per sex



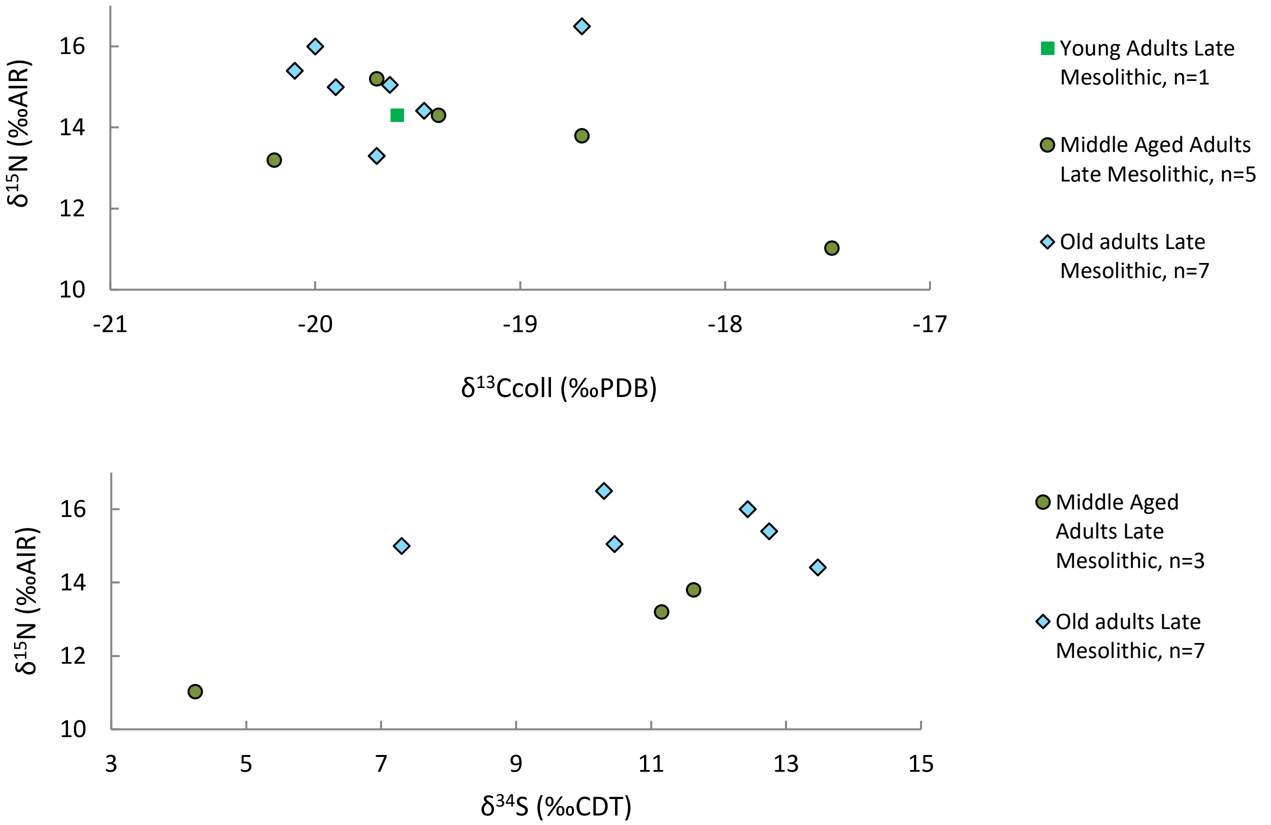
A.II.27. Bivariate plots of δ13C - δ15N and δ34S - δ15N for Neolithic adult humans (>15 yrs) grouped chronologically, and per sex



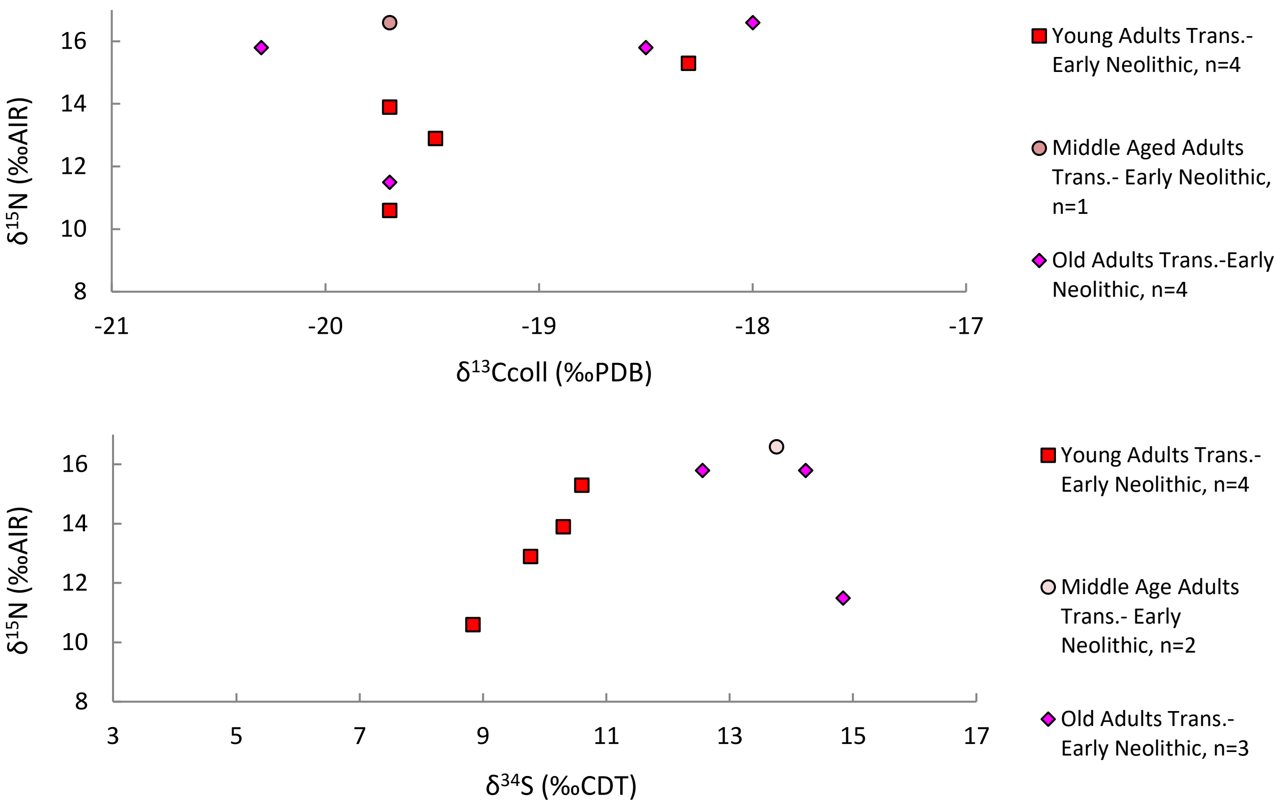
A.II.28. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Neolithic adult humans (>15 yrs) grouped chronologically and according to their geographical origin (Locals and Non-Locals discriminated according to their signal in radiogenic strontium, ^{87}Sr/^{86}Sr Borić and Price 2013)



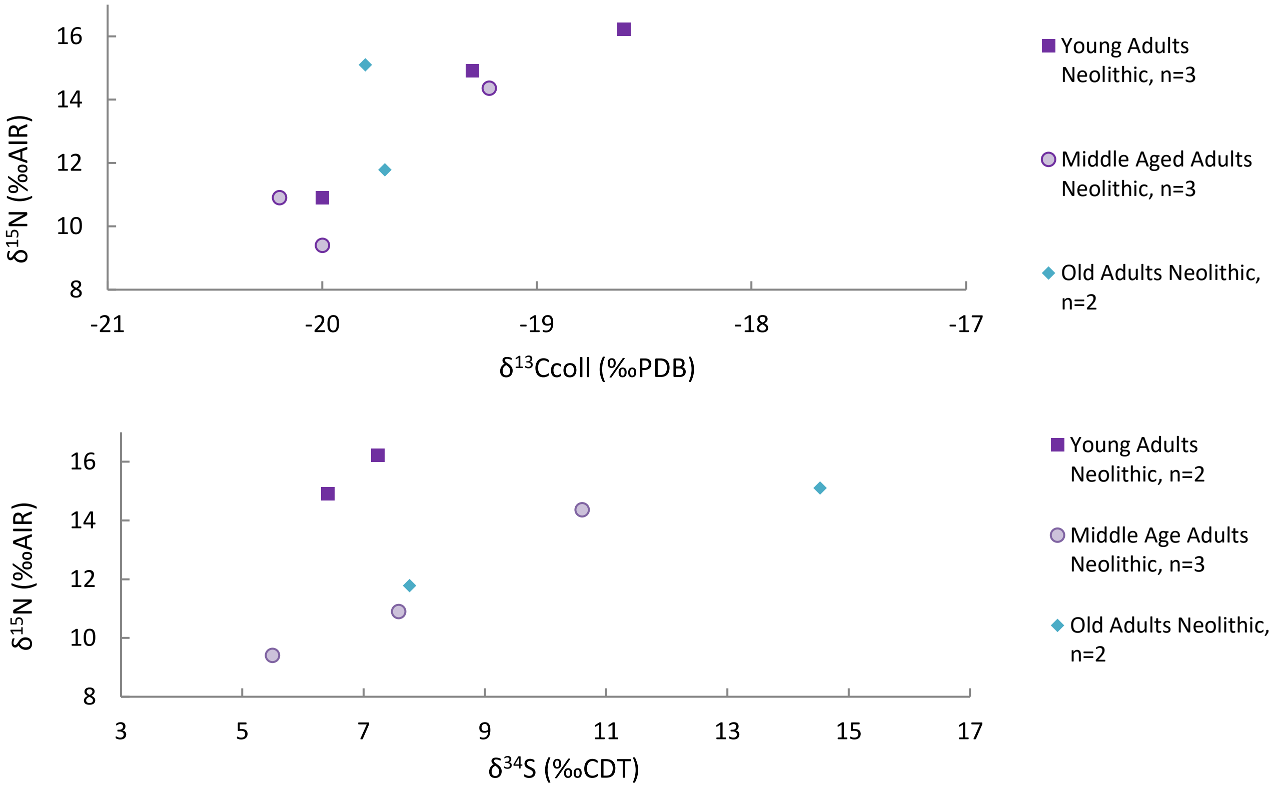
A.II.29. Bivariate plots of δ13C - δ15N and δ34S - δ15N for Early Mesolithic adult humans (>15 yrs) grouped chronologically and per age at death



A.II.30. Bivariate plots of δ13C - δ15N and δ34S - δ15N for Late Mesolithic adult humans (>15 yrs) grouped chronologically and per age at death

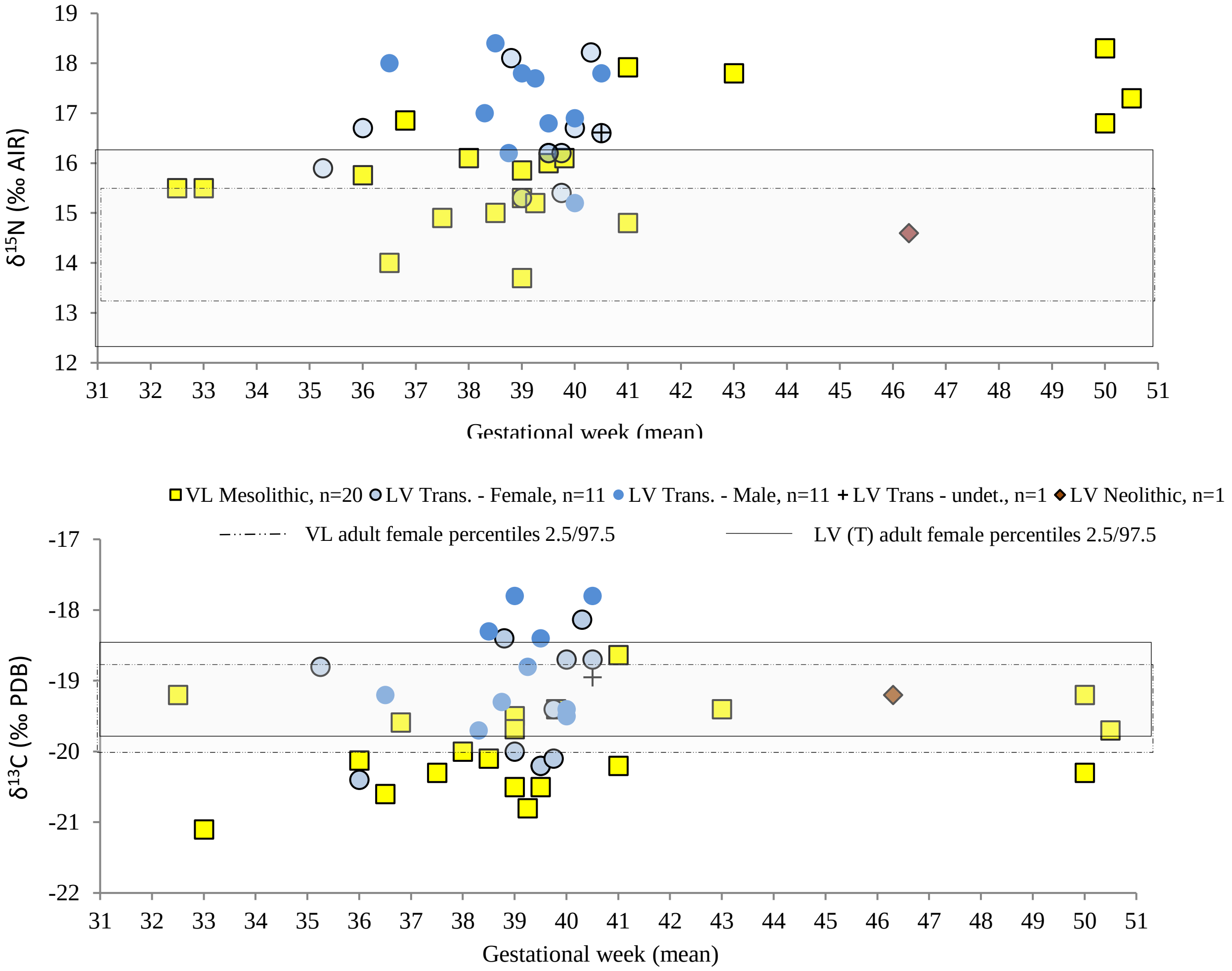


A.II.31. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Transformations - Early Neolithic adult humans (>15 yrs) grouped chronologically and per age at death

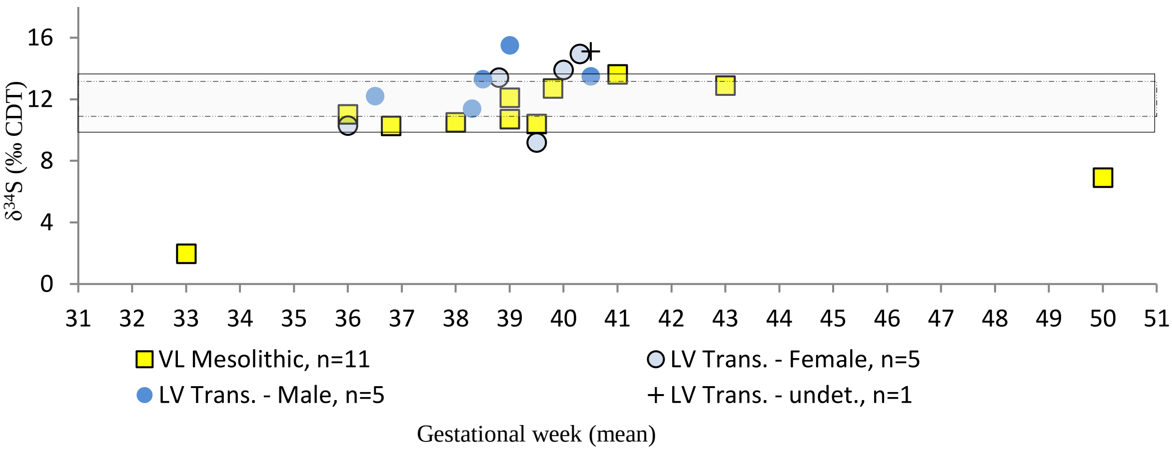


A.II.32. Bivariate plots of δ^{13}C - δ^{15}N and δ^{34}S - δ^{15}N for Early-Middle Neolithic adult humans (>15yrs) grouped chronologically and per age at death

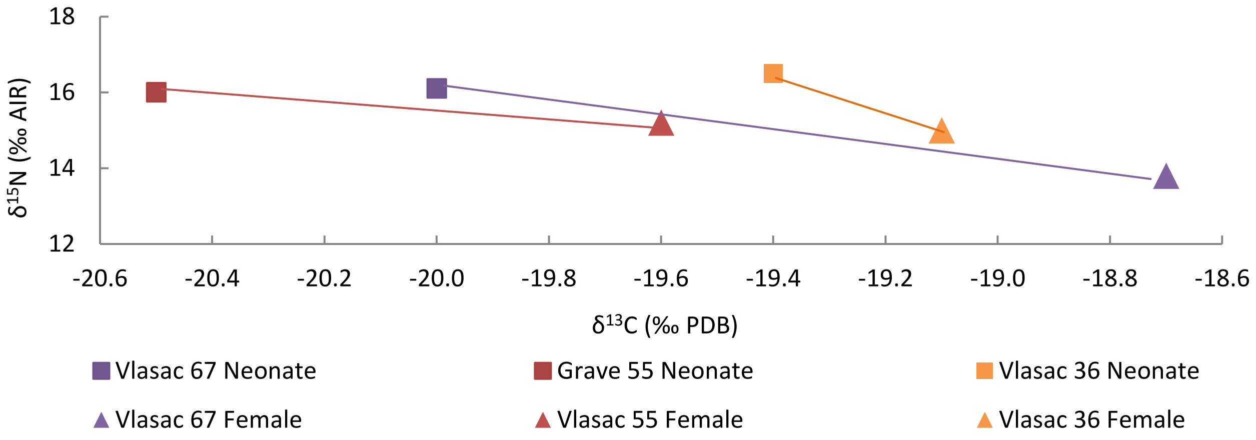
APPENDIX A.III. Children feeding practices: intra-individual multi-sampling strategy - δ^{13}Ccoll, δ^{15}N, δ^{34}S extracted from the collagen protein of prehistoric children from the Danube Gorges



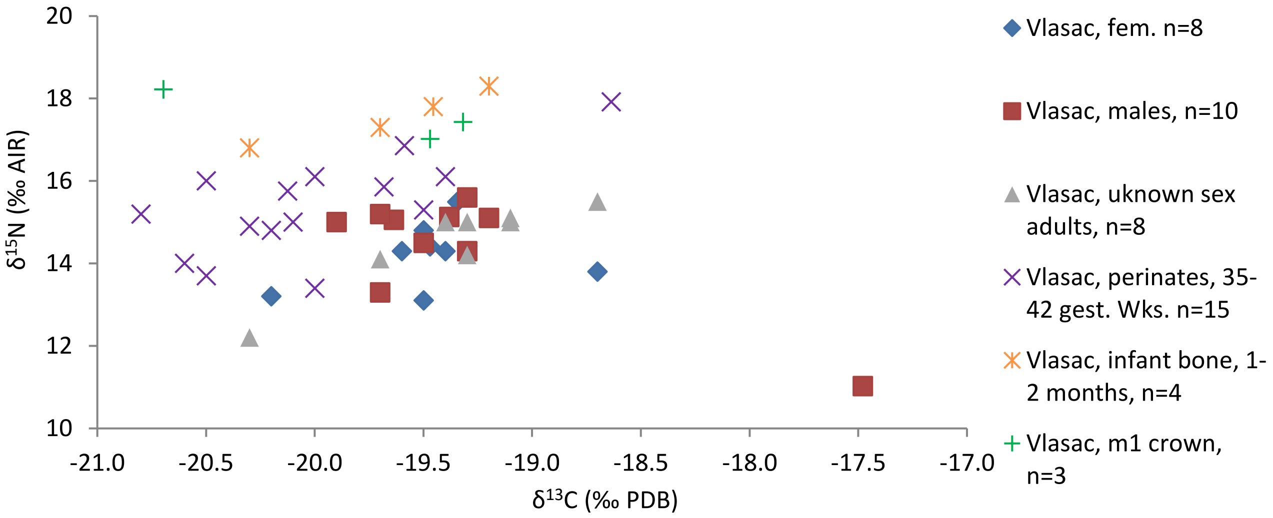
A.III.1 and 2: Bivariate plots of δ^{15}N (top) and δ^{13}C (bottom) and the age at death of perinatal individuals (gestational weeks) from the site of Vlasac (Late Mesolithic) and the site of Lepenski Vir (Trans.-Neolithic).



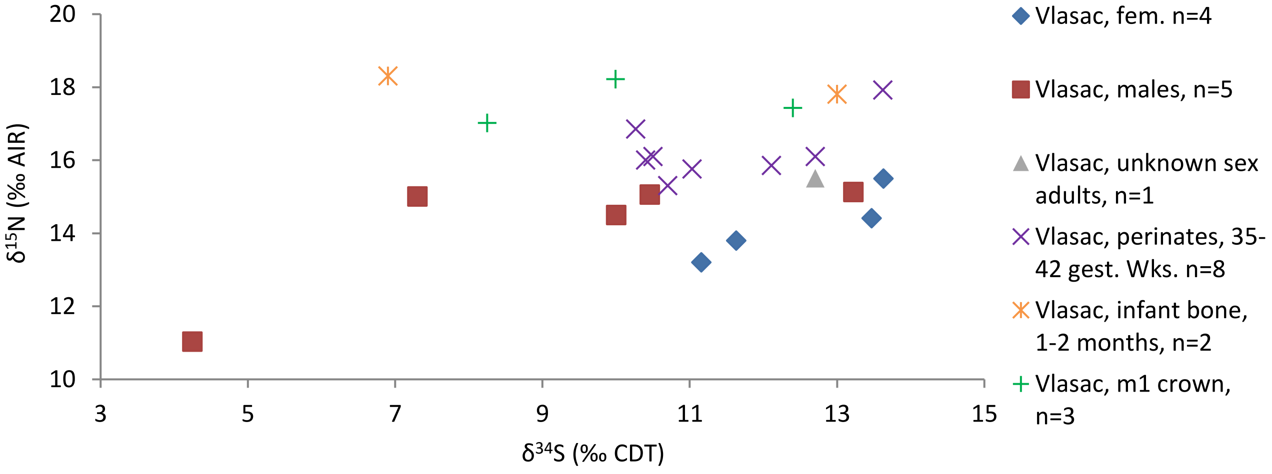
A.III.3: Bivariate plot of δ^{34}S and the age at death of perinatal individuals (gestational weeks) from the site of Vlasac (Late Mesolithic) and the site of Lepenski Vir (Trans.-Neolithic).



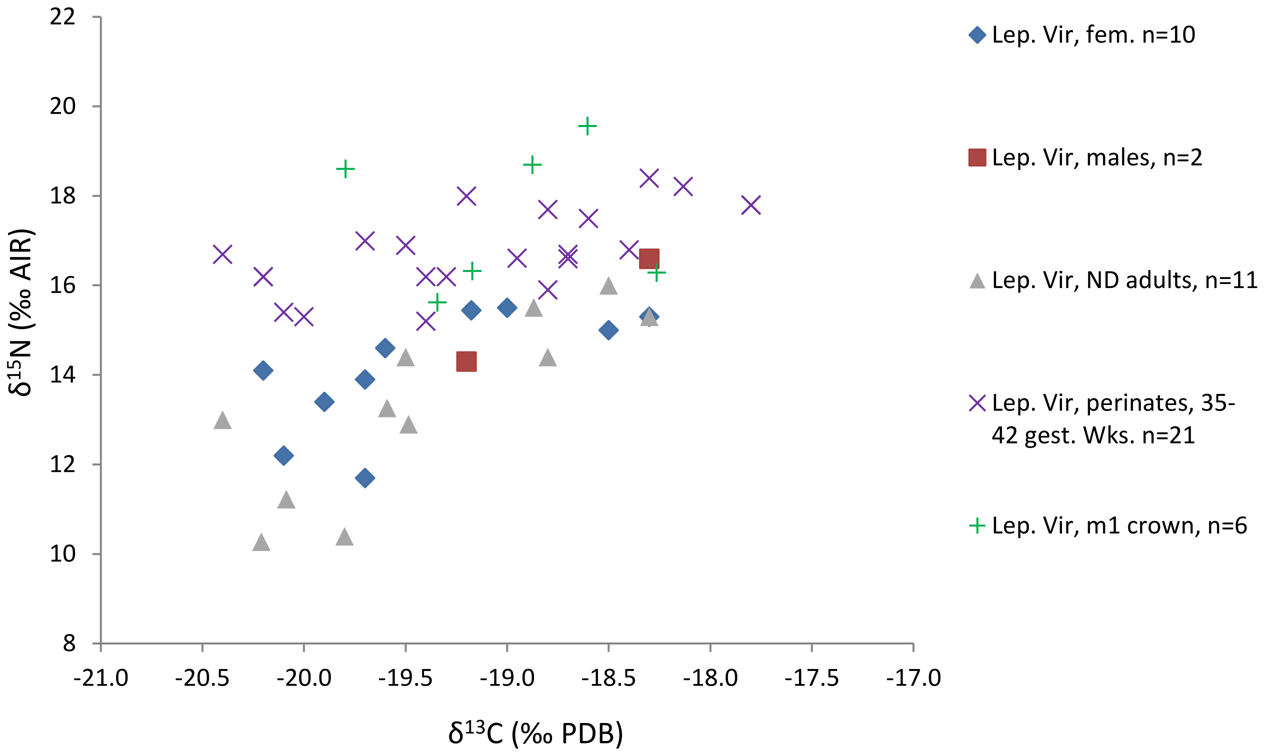
A.III.4. Bivariate plot ofδ^{15}N and δ^{13}C of perinatal individuals (gestational weeks) from the site of Vlasac (Late Mesolithic) and the site of Lepenski Vir (Trans.-Neolithic).



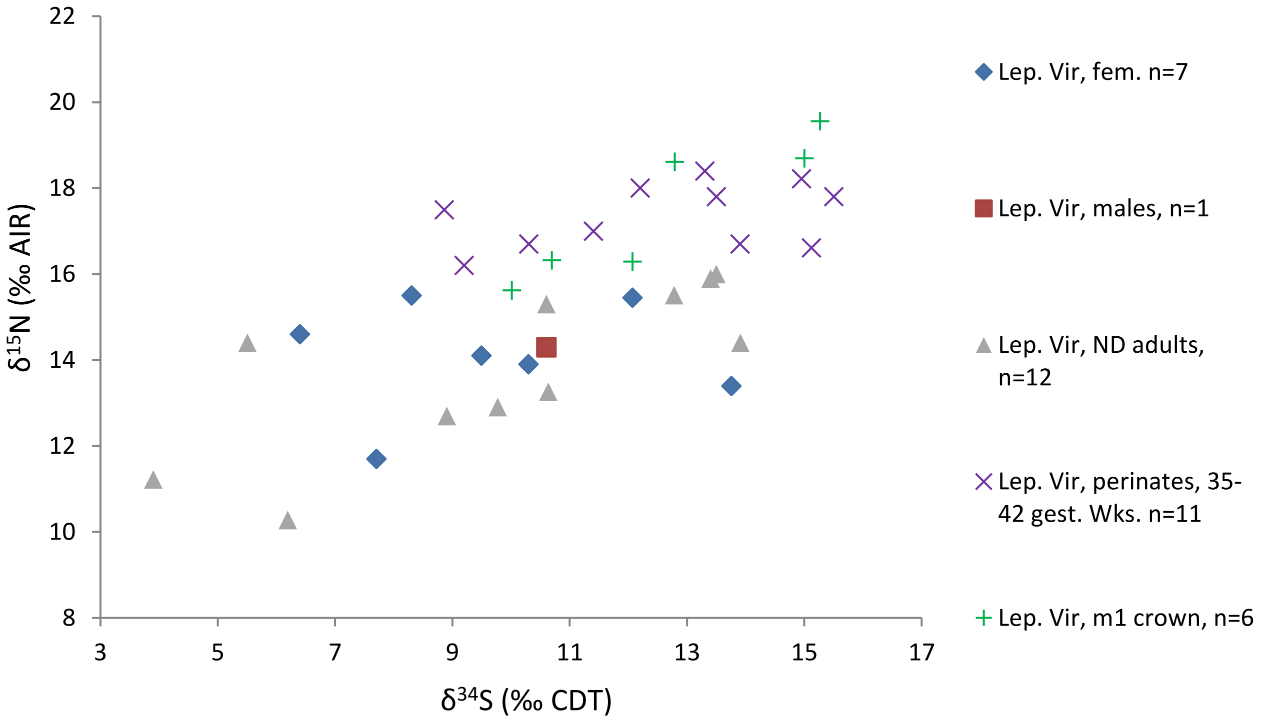
A.III.5. Bivariate plot of δ^{15}N and δ^{13}C for tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from Vlasac, Late Mesolithic.



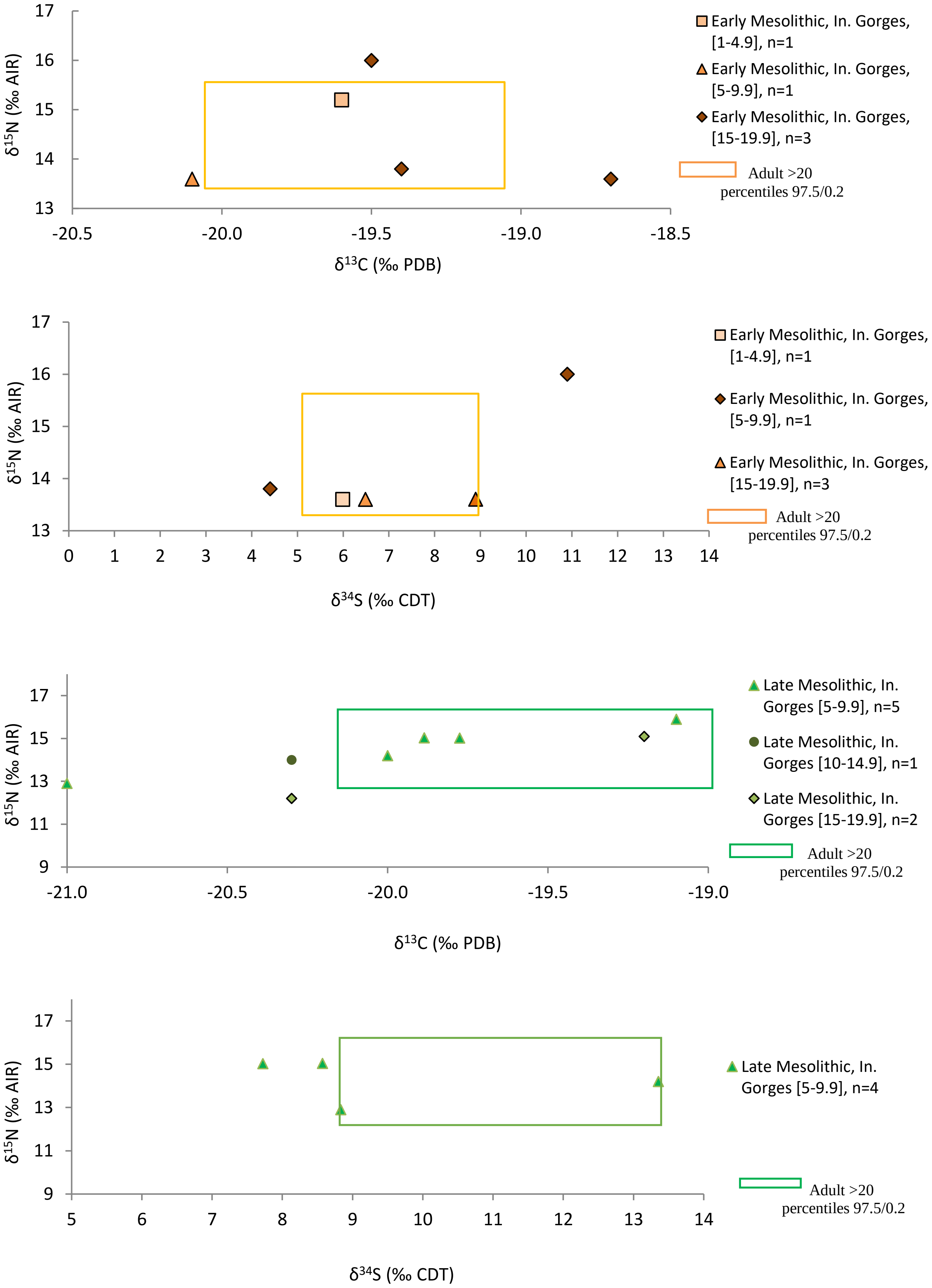
A.III.6. Bivariate plot of δ^{34}Sand δ^{15}Nfor tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from Vlasac, Late Mesolithic.



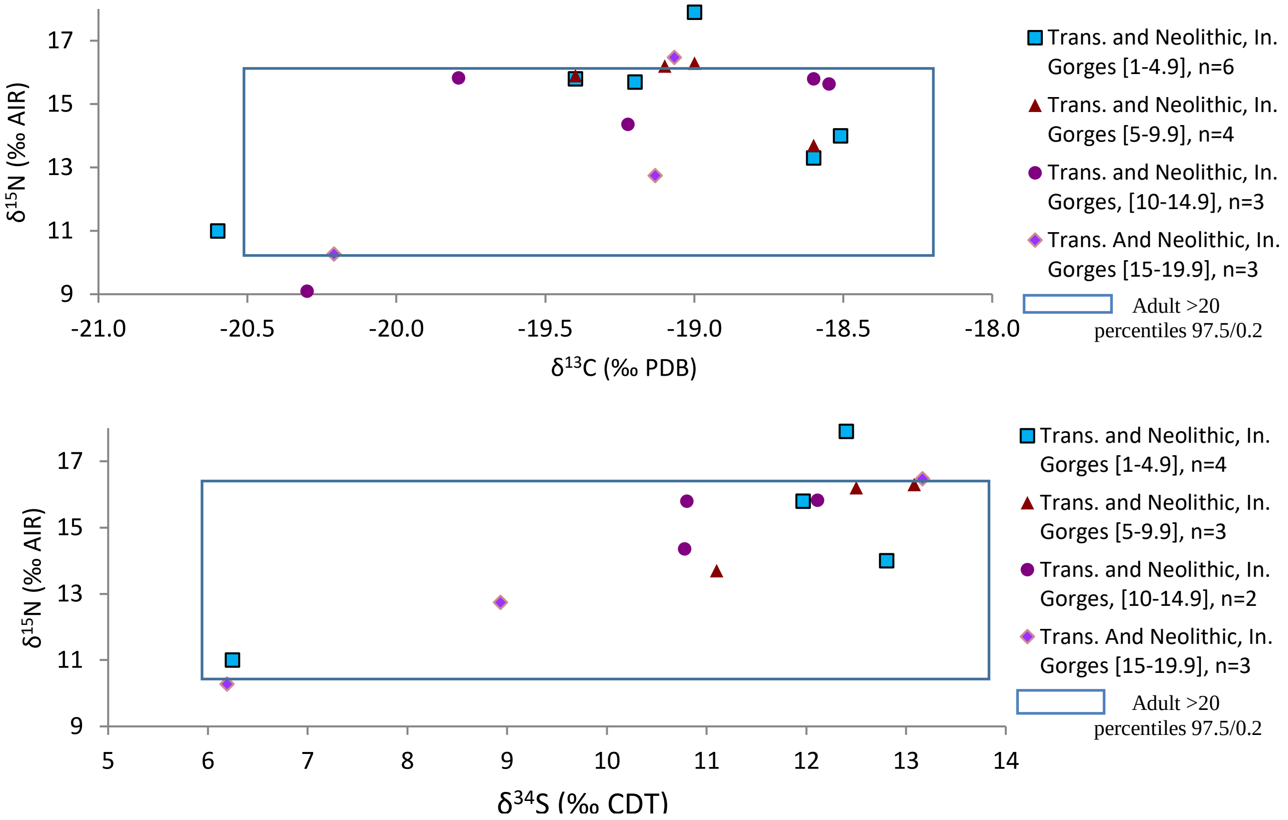
A.III.7. Bivariate plot of δ15N and δ13C for tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from Lep. Vir, Transform. and Neolithic.



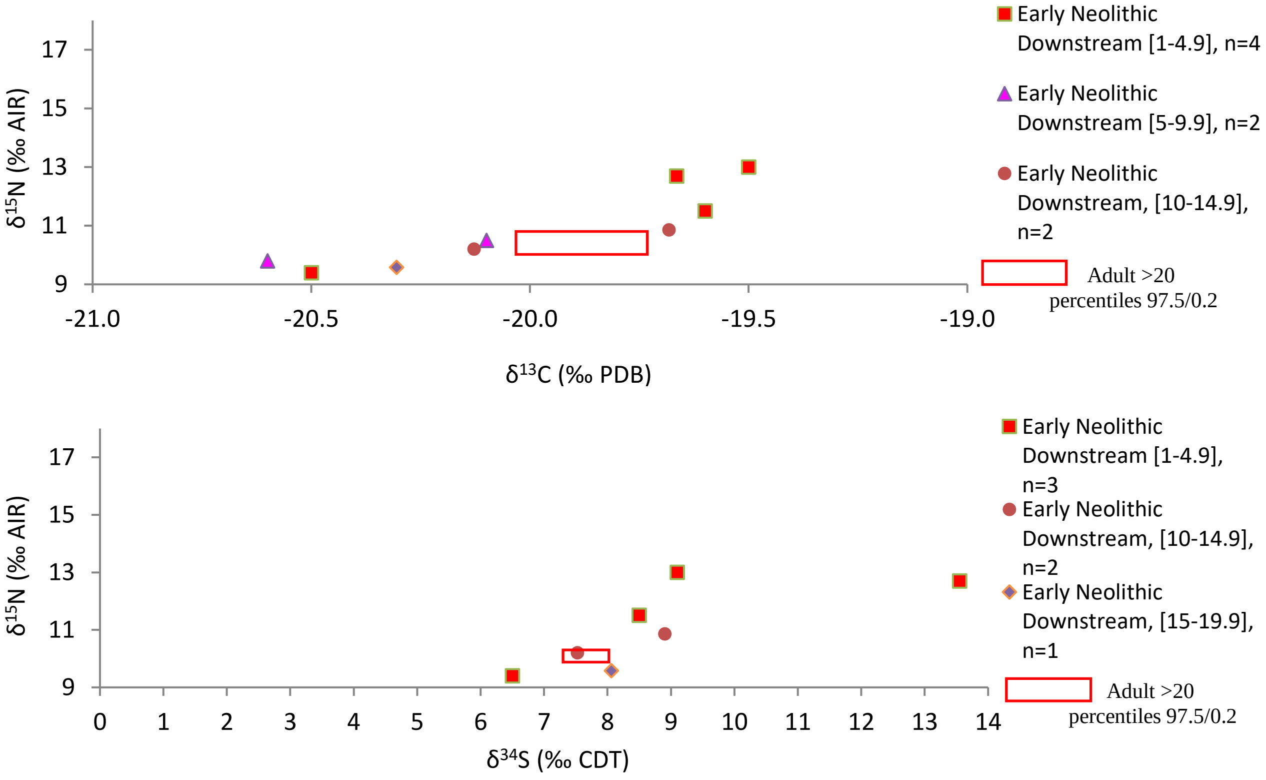
A.III.8. Bivariate plot of δ34Sand δ15Nfor tissues formed in utero and during the first months of life compared with the values of adult bone collagen. Samples from LepVir, Transform. and Neolithic.



A.III.9. Bivariate plots of $\delta^{15}N$ - $\delta^{13}C$ and of $\delta^{15}N$ - $\delta^{34}S$ of Mesolithic immature individuals from the Inner Gorges per age categories.



A.III.10. Bivariate plots of δ^{15}N - δ^{13}C and of δ^{15}N - δ^{34}S of Neolithic immature individuals from the Inner Gorges per age categories.



A.III.11. Bivariate plots of δ^{15}N - δ^{13}C and of δ^{15}N - δ^{34}S of Neolithic immature individuals from the Downstream Area per age categories.

Titles details for the figures pages 391-396

A.III.12. (P.391). Bivariate plots of children [birth-10 yrs] δ^{15}N signals and the estimated age for the formation of the analyzed tissues. For the dentine crown signal, we used the average age of formation of the crown; for the growing root of a teeth and the bone signal, we used the average age at death (midpoint of the estimated interval); concerning the bone values, the broader time span possibly reflected by the isotope signal given the rate of bone renewal was indicated by dashes placed after the lower limit of age estimate (calculated using bone Valentin 2003); the sample was divided per chronological / geographical areas of interest. **A.**(Left) Intra-individual approach, each line represents one child, each symbol one sample; in caption= T: teeth signal; B: Bone signal **B.** (Right) Population approach, each symbol represents one sample, with the minimum and maximum limits of the age estimate for the formation of the analyzed tissues(black cross)as well as the longer time span possibly reflected by bone signal (light grey cross and dashes); loess curves (computed independently for bone and teeth signals) are superimposed to the stable isotope values.

A.III.13. (P.392). Idem. Bivariate plots of children [birth-10 yrs] δ^{13}C signals and the estimated age for the formation of the analyzed tissues; details in title for figure A.III.12.

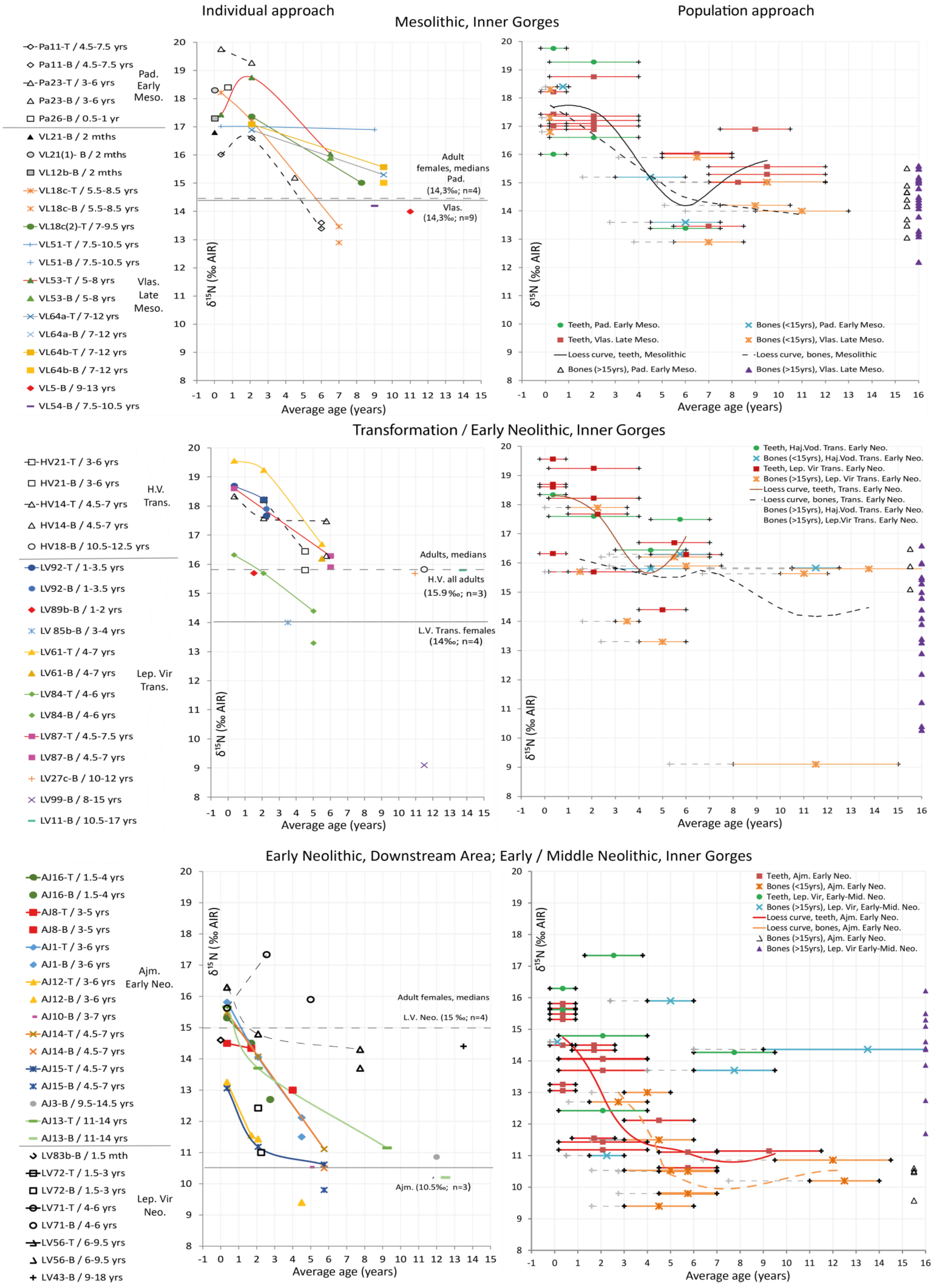
A.III.14. (P.393). Idem. Bivariate plots of children [birth-10 yrs] δ^{34}S signals and the estimated age for the formation of the analyzed tissues; details in title for figure A.III.12.

A.III.15. (P.384). δ^{13}C δ^{15}Nand δ^{34}S fluctuations from the period in utero to 6 years. Analyses were performed per chronological/geographical groups of interest. For each group compared (e.g. Mesolithic, Early Neolithic Inner Gorges, Early Neolithic Downstream), tissues δ^{13}C, δ^{15}N and δ^{34}S values were standardized into z-scores (independently for bone and teeth) and loess curves were then computed using standardized data (for the age used for each signal cf supra A.III.12)

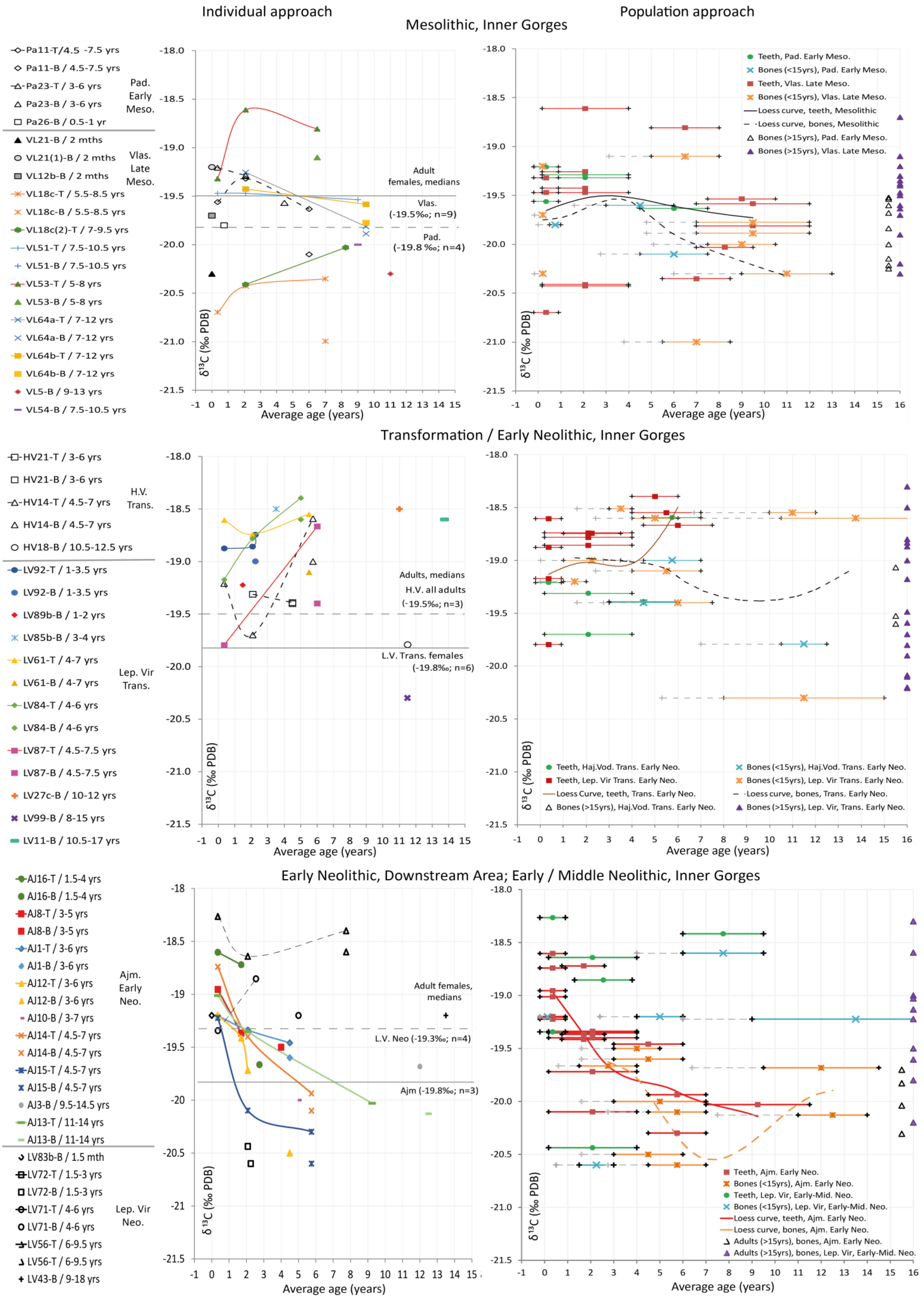
A.III.16. (P.395). δ^{34}S, δ^{13}C and δ^{15}Nfluctuations from 35.5 to 41 gestational weeks in the prehistoric sample compared with reference data and schematic models for the fluctuation of hormones during pregnancy. All data are fitted on a timeline from conception to birth. **A.** Archaeological data; for each site (Vlasac, Late Mesolithic and Lepenski Vir, Early Neolithic), δ^{13}C, δ^{15}N and δ^{34}S were standardized into Z-score and loess curves were computed using standardized data and the average age-at-death (midpoint of the estimated interval). **B.** Reference data concerning the fluctuations of stable isotopes values in maternal tissues during pregnancy (Fuller 2004 and 2005) and comparison with clinical data concerning the frequency of nausea amongst expectant females (Niebyl 2010).**C.** Schematic models for endocrine fluctuations during pregnancy (adapted from Austin and Short 1984).

A.III.17. (P.396). Comparison of fluctuations in δ^{34}S, δ^{13}C and δ^{15}N from the period in utero to 6 years in the prehistoric sample with reference data. **A.** Reference data from fuller (2006). **B.** Archaeological data; the sample was divided according to chronological/geographical groups of interest. δ^{13}C, δ^{15}N and δ^{34}S bone and teeth were standardized into Z-score and loess curves were then computed using standardized data for both bone and teeth tissues (bone and teeth signals grouped). The average age of the bone signal was placed slightly younger than the midpoint of the age at death estimated range, in order to include the greatest time *possibly* averaged by the analyzed bone collagen according to the rate of bone renewal. Therefore, the lower limit of the age at death estimation of each child was placed earlier by taking into account the rate of bone renewal estimated by Valentin (2003); loess curves were then calculated using the mid-point values of these "broader time span".

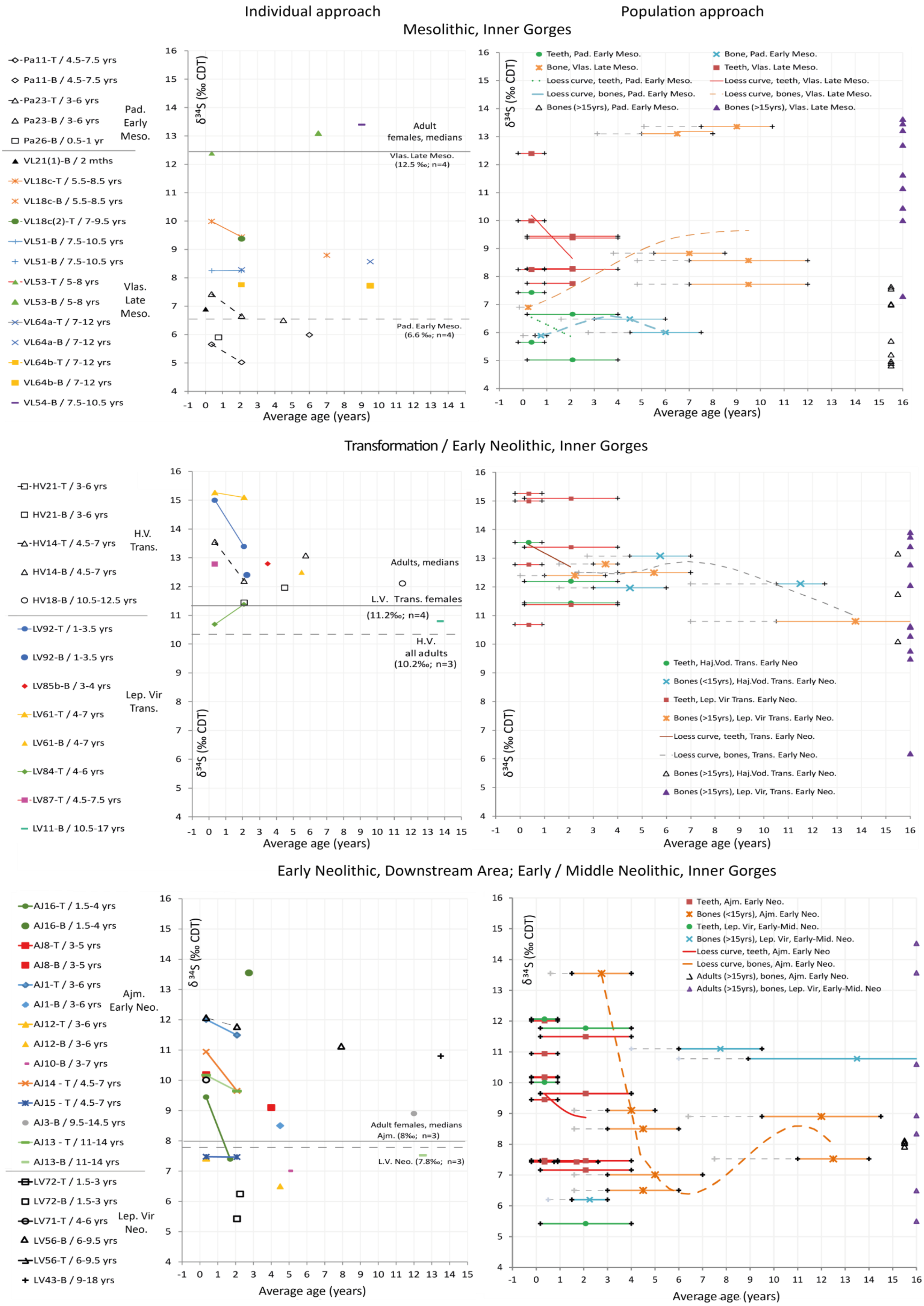
In the following graphs (A.III. 12-17), only adults within the acceptable range of the standard criteria used to estimate the quality of collagen (C%, N%, S% and the atomic ratios) were included as purposes of comparison with the children.



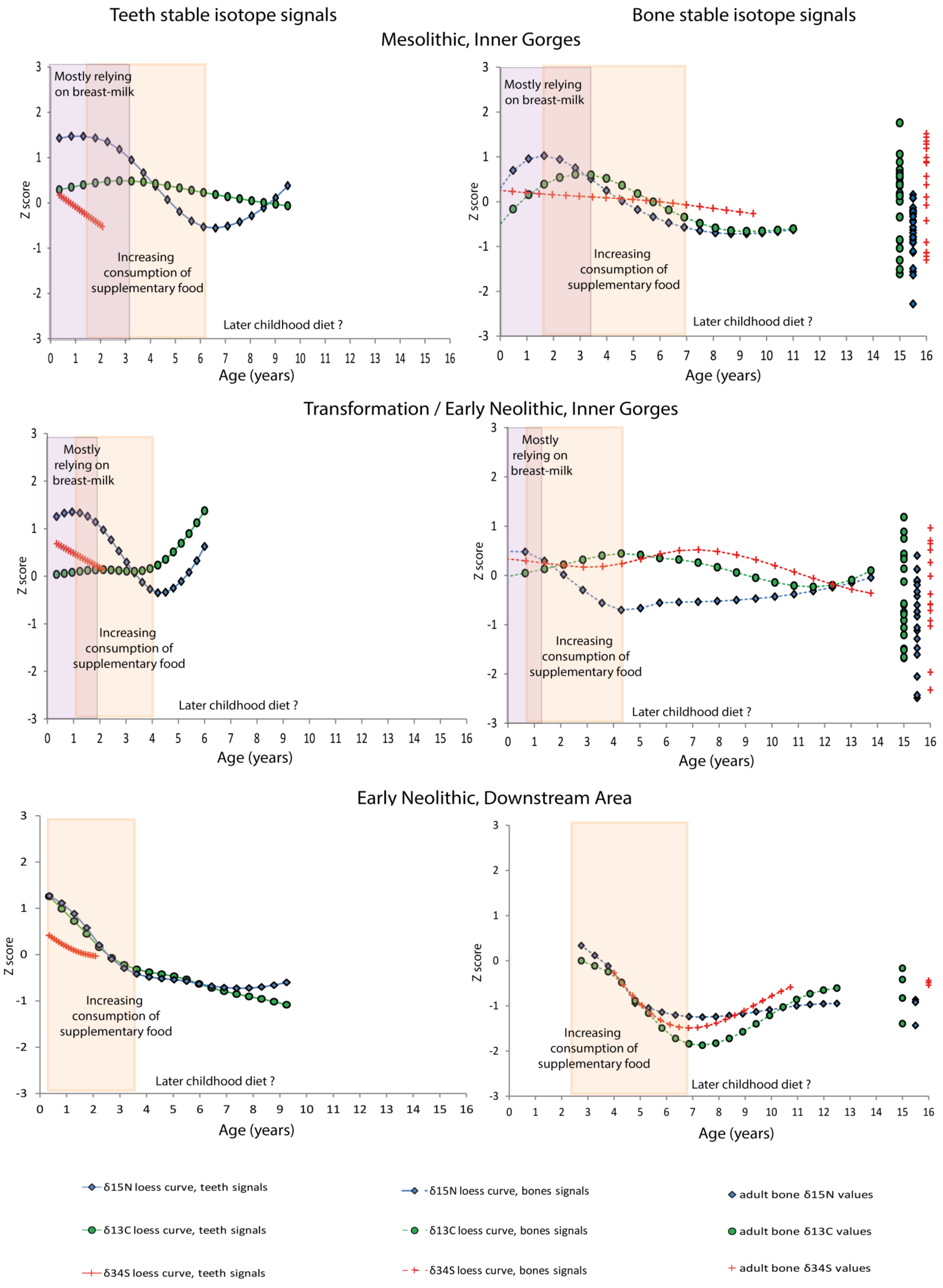
A.III.12. Intra-individual and population approaches for children δ15N signals (title details p. 390)



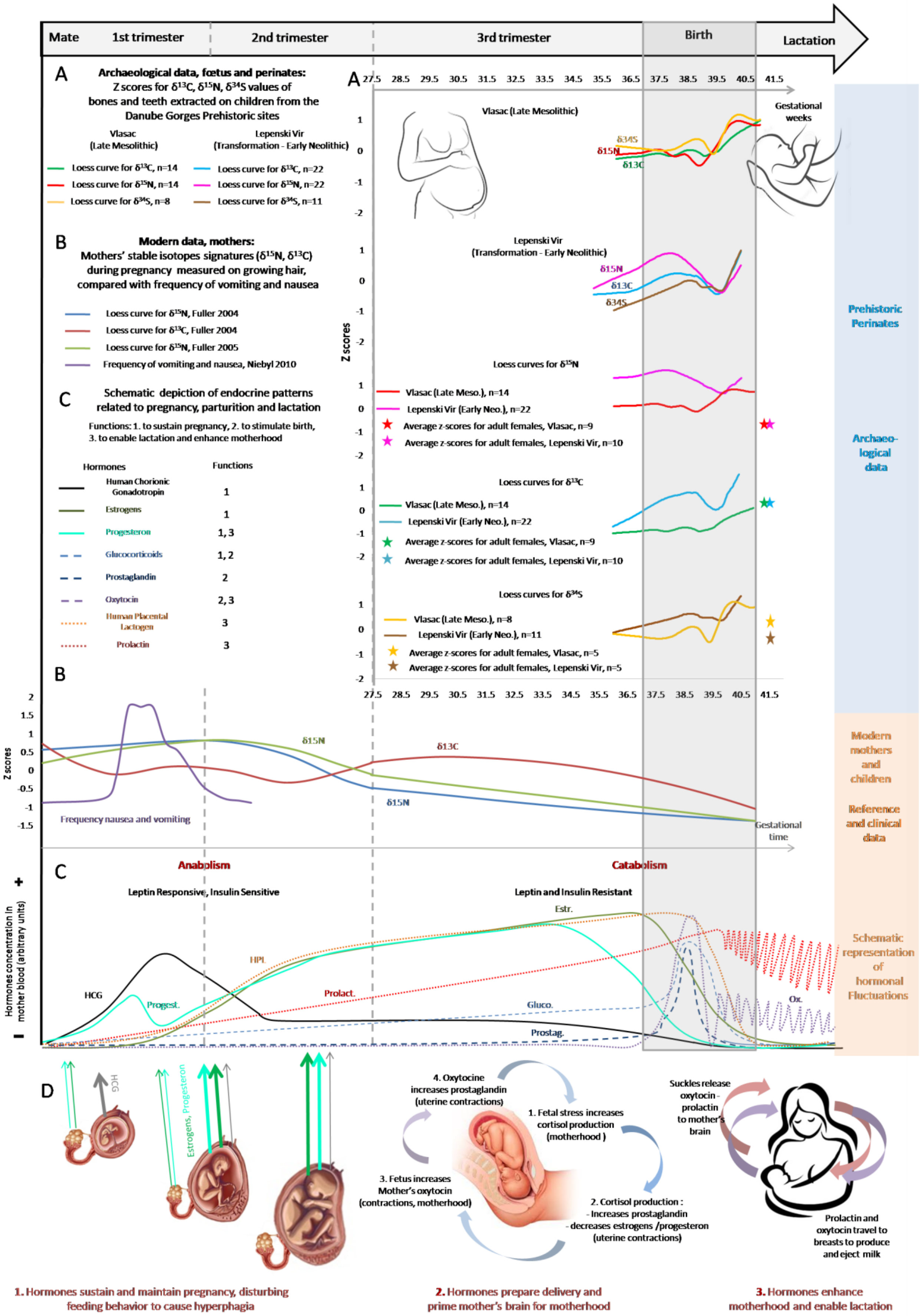
A.III.13. Intra-individual and population approaches for children δ13C signals (title details p. 390)



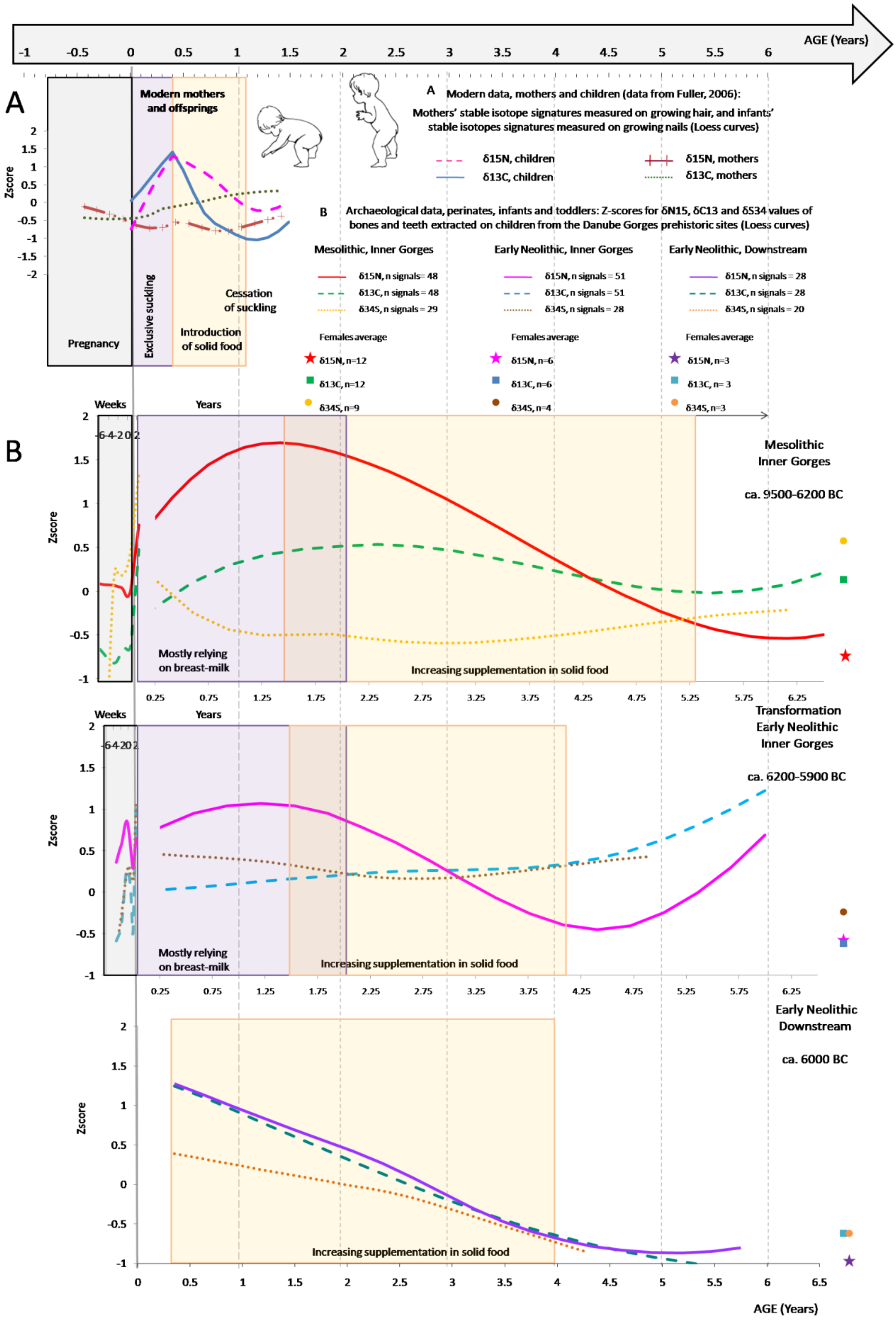
A.III.14. Intra-individual and population approach for children δ34S signals (title details p. 390)



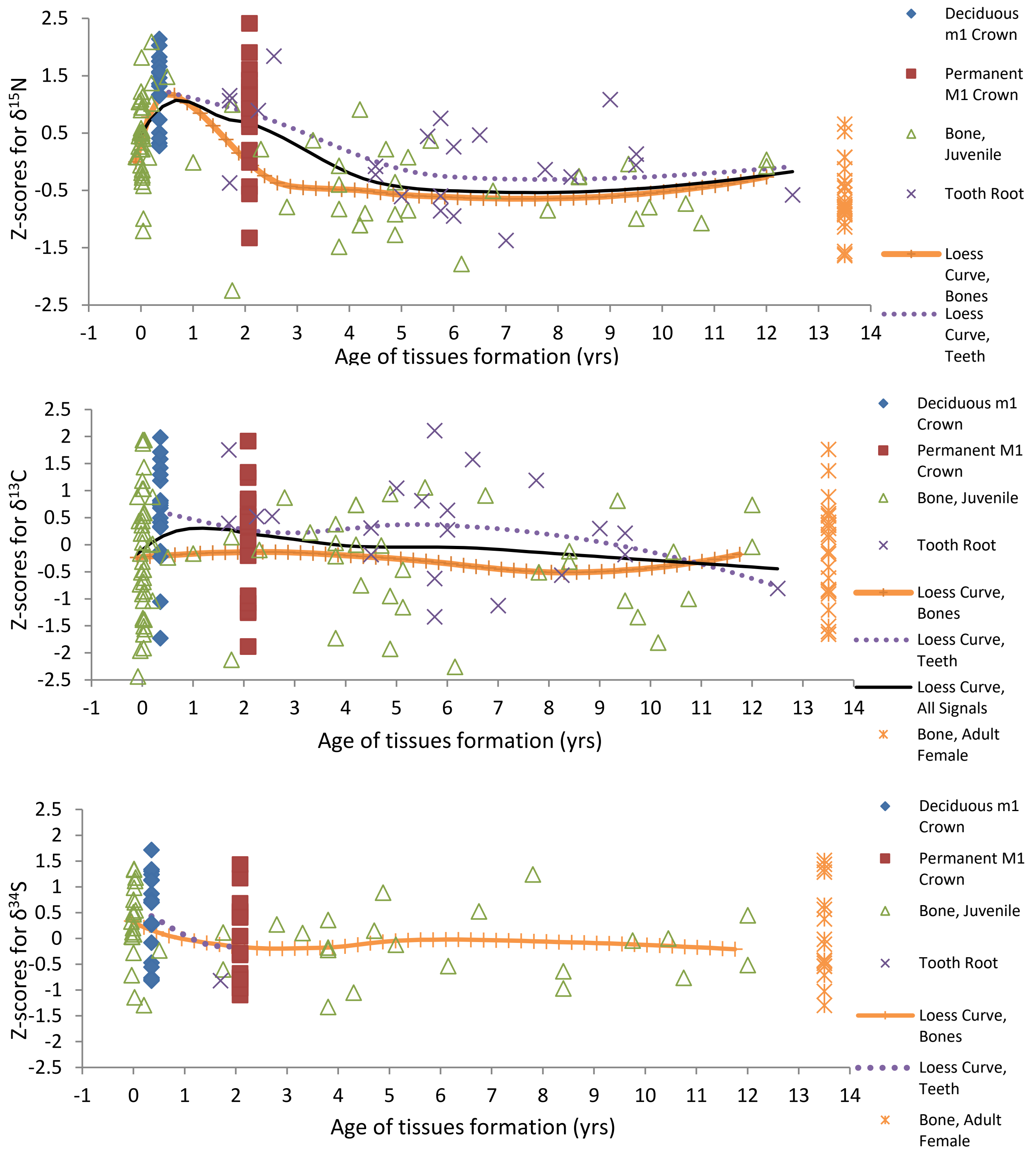
A.III.15. Comparison of $\delta^{15}N$ - $\delta^{13}C$ - $\delta^{34}S$ loess curves computed on children tissues (title details p. 390)



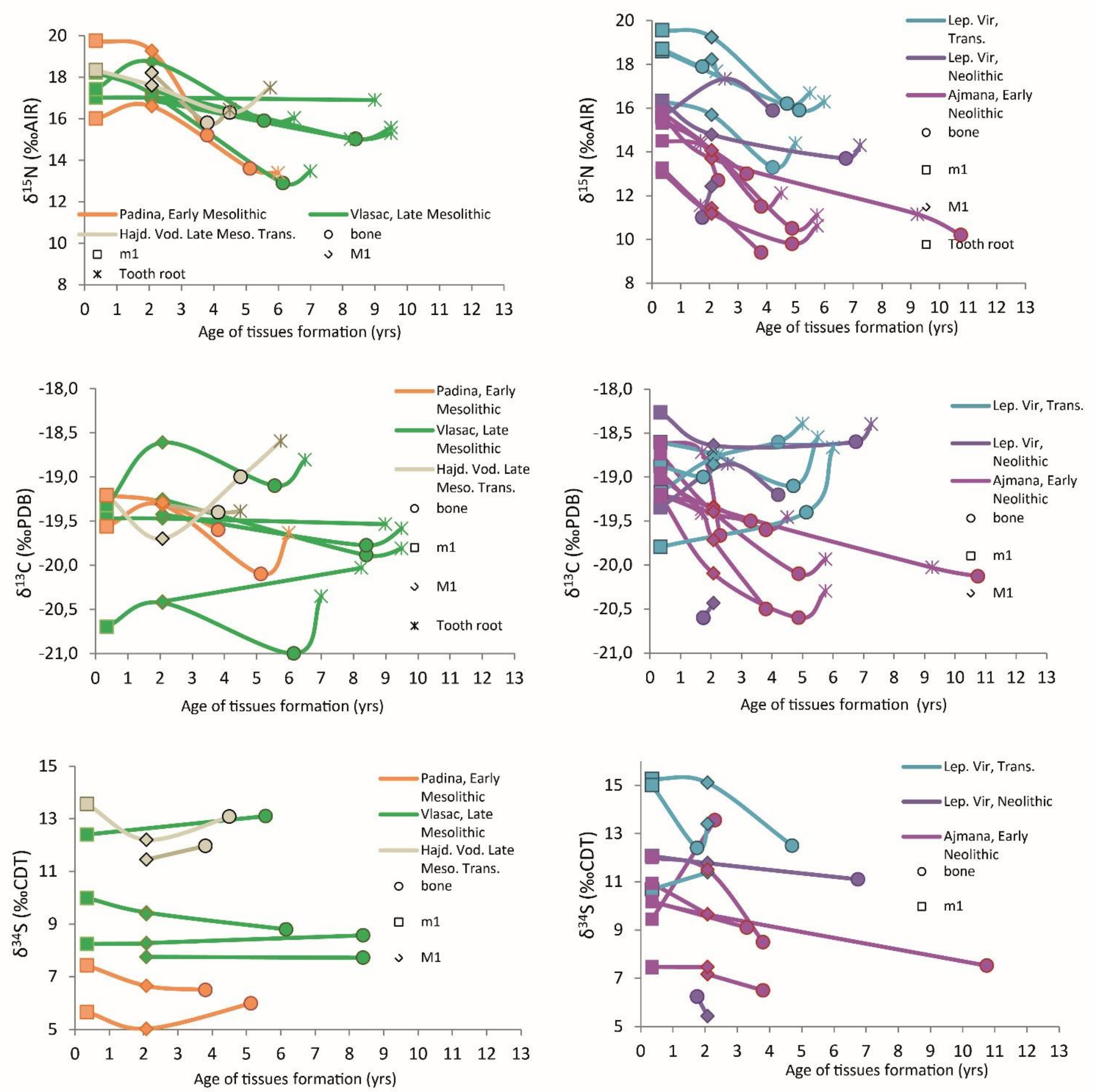
A.III.16. Comparison of perinates stable isotopes loess curves with clinical data (title details p. 290)



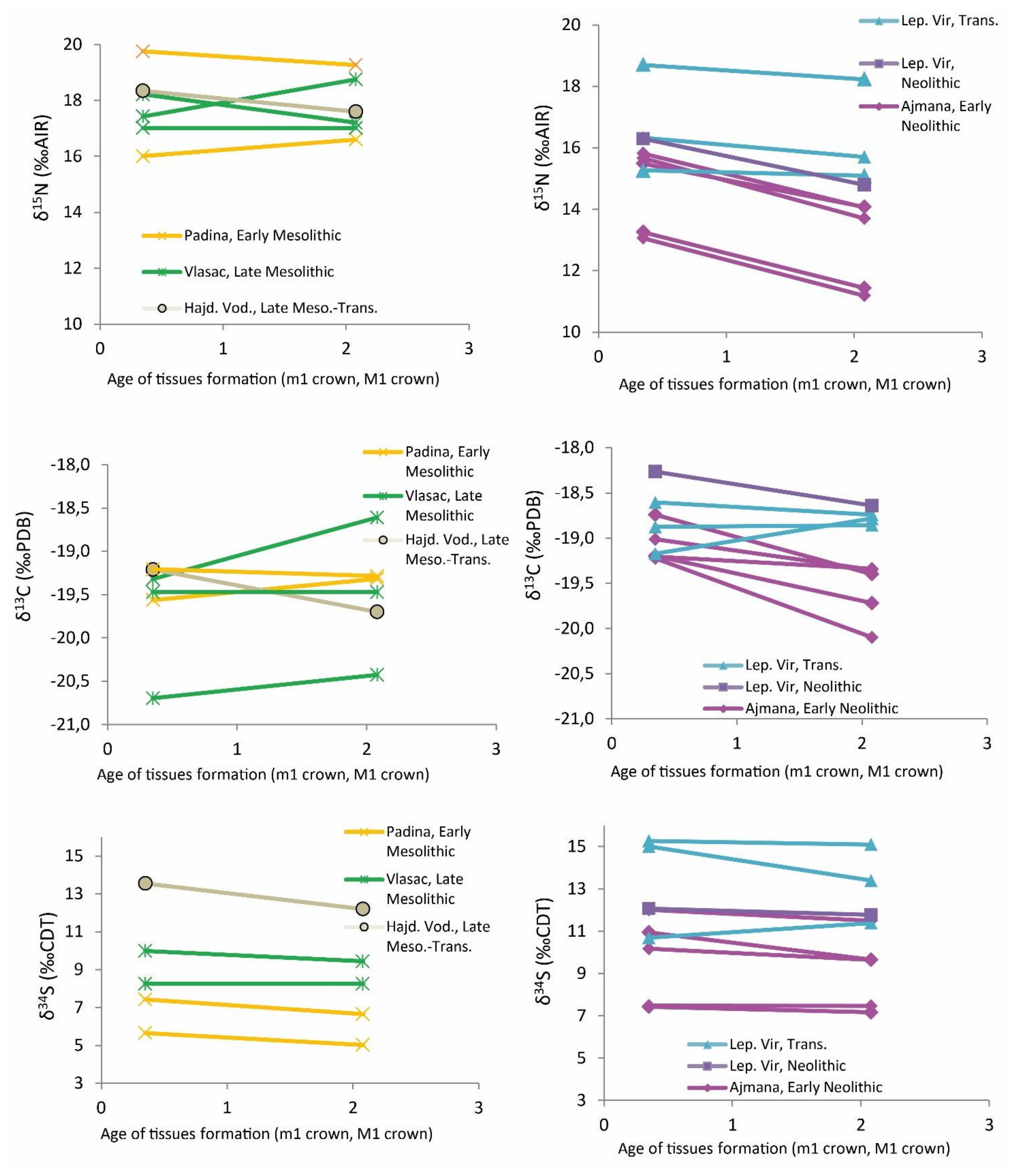
A.III.17. Comparison of prehistoric children stable isotope loess curves with reference data (title details p. 390)



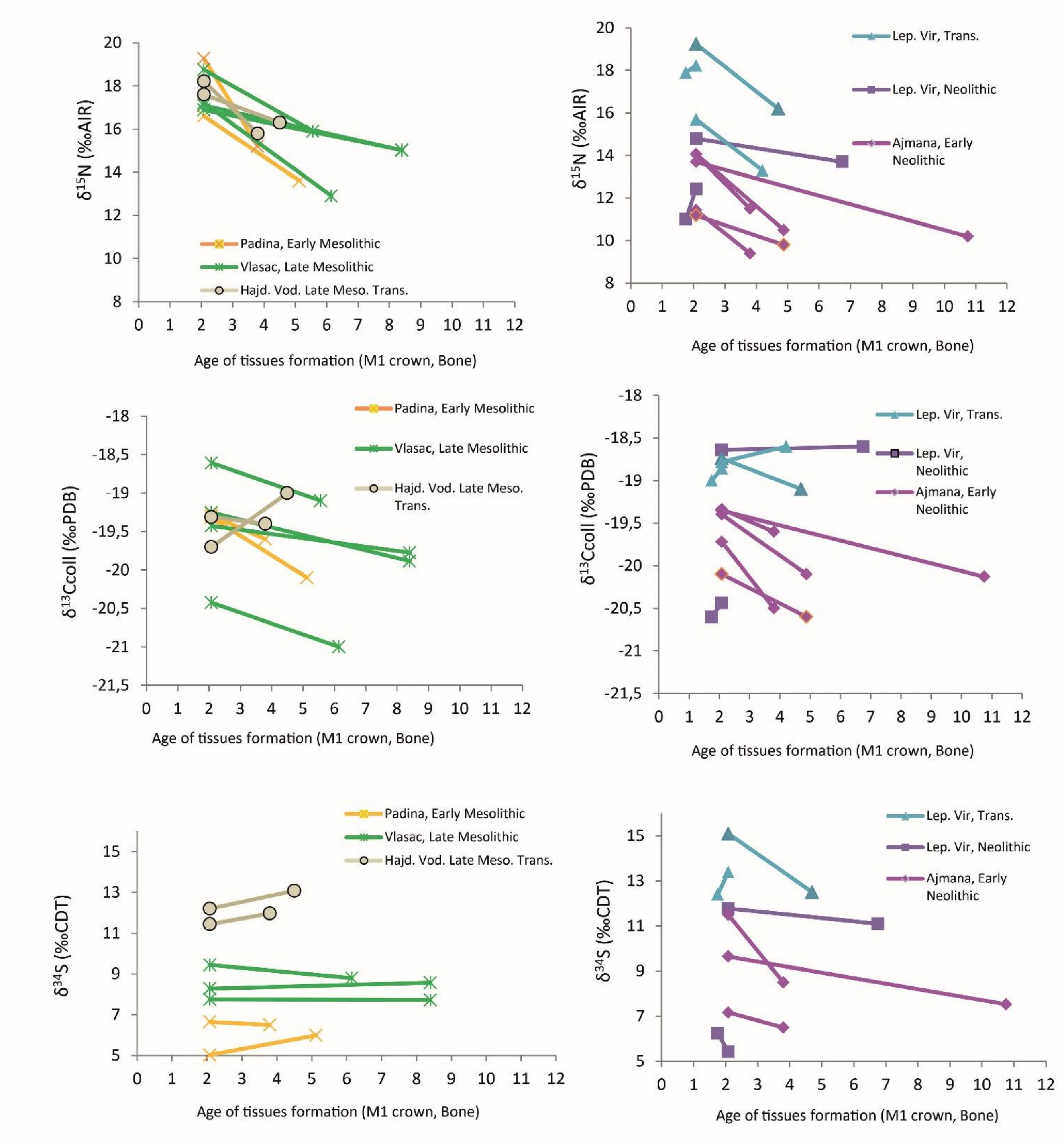
A.III.18. Bivariate plots of δ^{15}N, δ^{13}C and δ^{34}S signals and the estimated age at formation of the analyzed tissues (cf. details for the estimated age used here in the title of the appendix A.III.12, p. 390). Loess curves were superimposed on bone and teeth roots signals. Comparison with the stable isotope variability of adult female bone collagen. The δ^{15}N, δ^{13}C and δ^{34}S values were firstly standardized for each chrono-cultural group (turned into Z-scores) in order to remove the stable isotope variation related to the context and to compare tissues stable isotope variations at the level of the entire Mesolithic-Neolithic population. For Z-score standardization, groups were defined as: Early Meso. individuals from Padina; Late Meso. individuals from Vlasac; Meso.-Transf. individuals from Hajd. Vod.; Transf.-Early Neo. individuals from Lep. Vir; Early Neo. individuals from Ajmana; Neol. individuals from Lep. Vir. For the dentine crown signal, we used the average age of formation of the crown; for the growing root of a teeth and the bone signal, we used the average age at death (midpoint of the estimated interval). The average age of the bone signal was placed slightly younger than the midpoint of the age at death estimated range, in order to include the greatest time *possibly* averaged by the analyzed bone collagen according to the rate of bone renewal. The lower limit of the age at death estimation of each child was placed earlier by taking into account the rate of bone renewal estimated by Valentin (2003) and loess curves were then calculated using the mid-point values of these "broader time span".



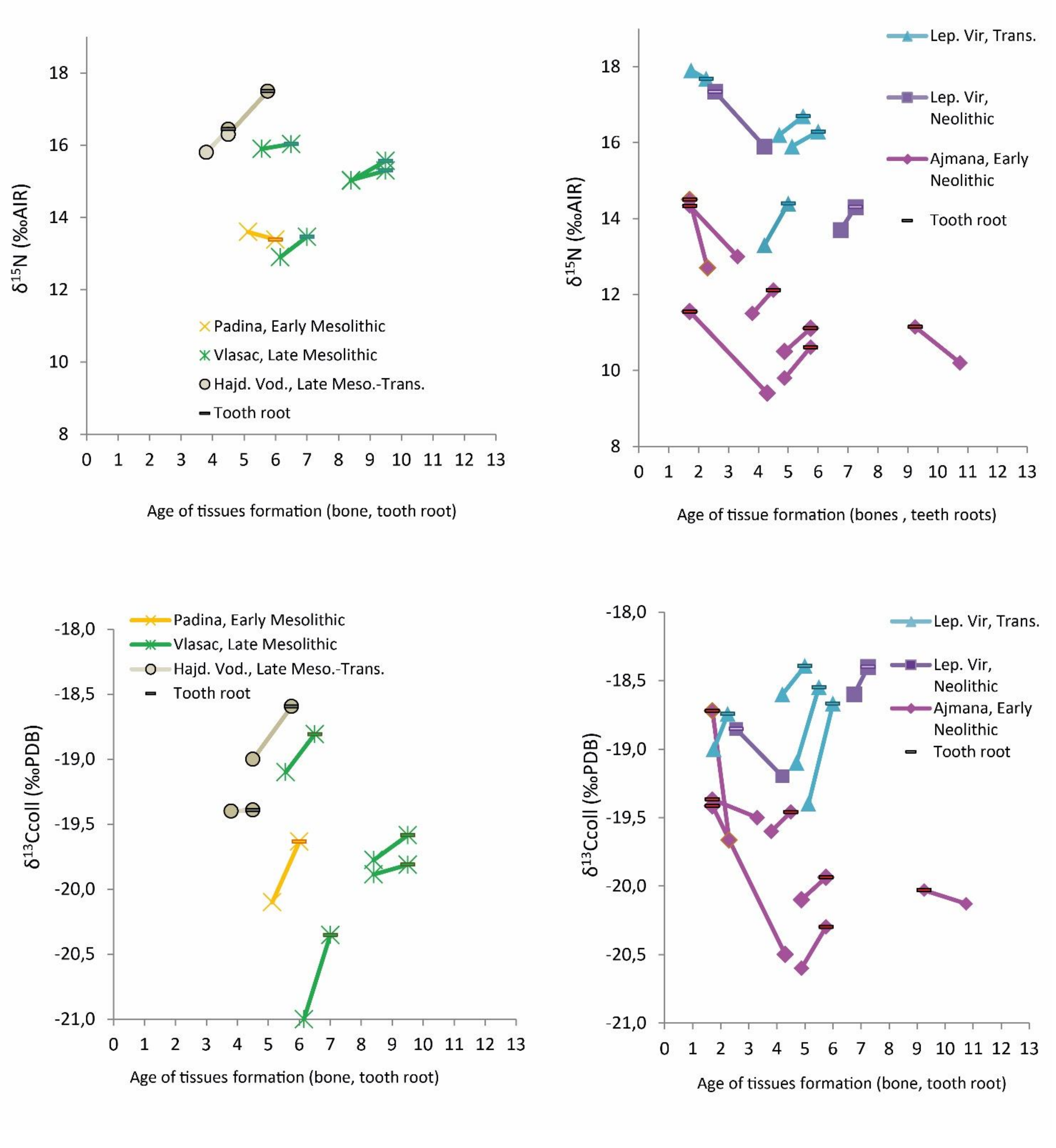
A.III.19. Bivariate plots of δ15N, δ13C and δ34S signals and the estimated age at formation of analyzed tissues (cf details for the estimated age used here in the title of the appendix A.III.12. p. 390); intra-individual approach, each line represents a child, each symbol a tissue analyzed; sample divided per periods and per sites. **These plots reveal the lower δ15N and δ13C values of bone collagen in comparison with the dentine signals.**



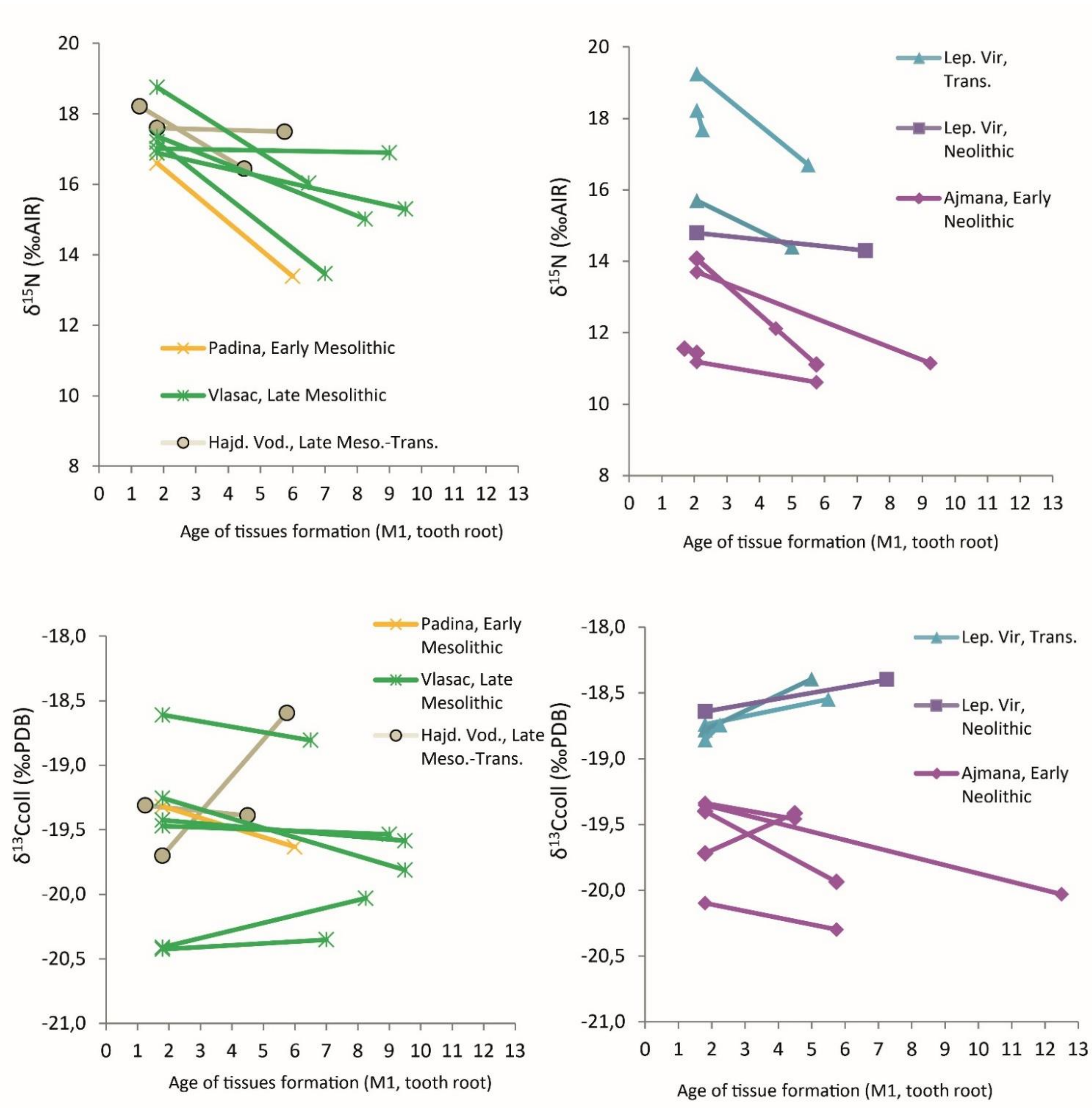
A.III.20. Bivariate plots of $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ signals and the estimated age at formation of the analyzed crowns of the first deciduous and permanent molars (cf details for the estimated age used here in the title of the appendix A.III.12. p. 390); intra-individual approach, offset between m1 crown and M1 crown; children grouped per periods and per sites.



A.III.21. Bivariate plots of δ^{15}N, δ^{13}C and δ^{34}S signals and the estimated age at formation of the analyzed crowns of the first permanent molars and bone samples; (cf details for the estimated age used here in the title of the appendix A.III.12. p. 390); intra-individual approach, offsets between M1 crown and bone; children grouped per periods and per sites.

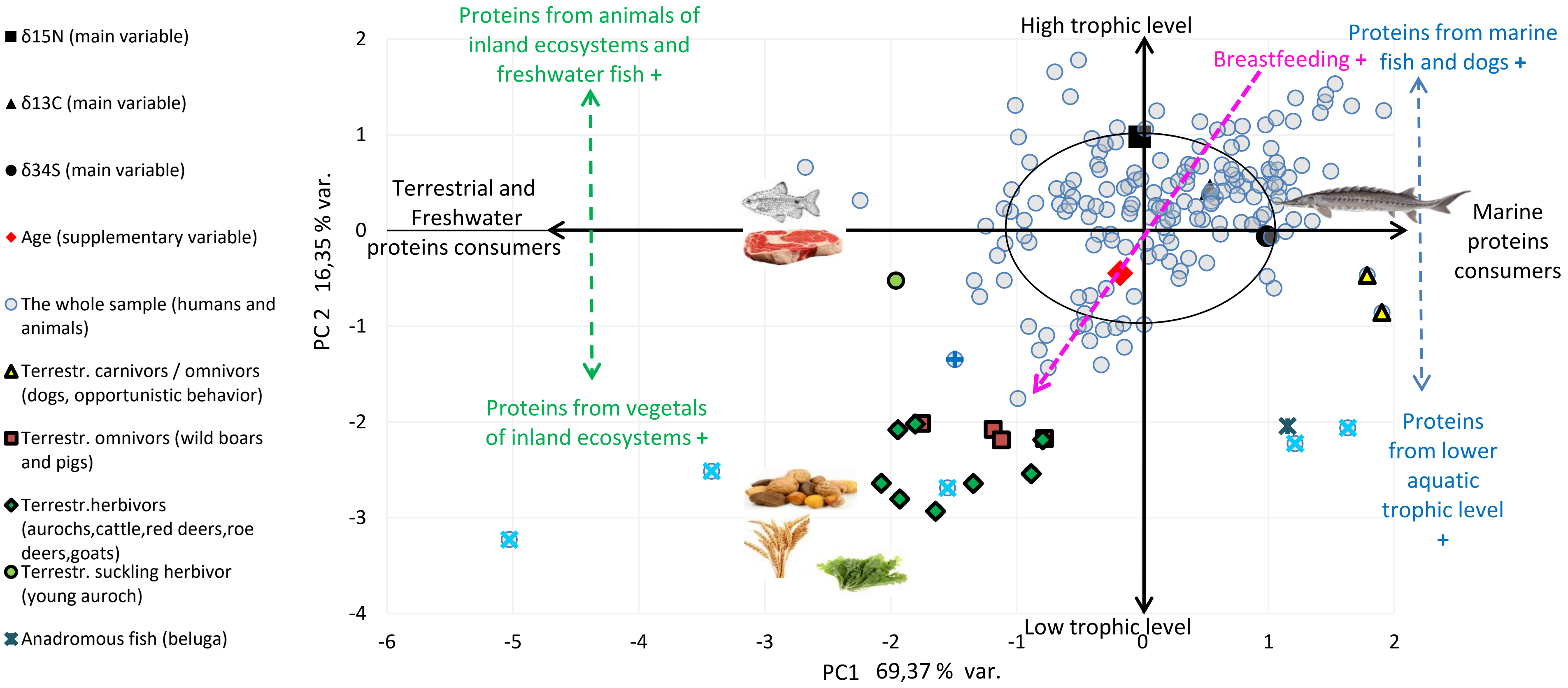


A.III.22. Bivariate plots of δ15N or δ13C signals and the estimated age at formation of the analyzed bone samples and teeth growing roots; (cf details for the estimated age used here in the title of the appendix A.III.12. p. 390); intra-individual approach, offsets between bone and tooth growing root; tooth root value differentiated from bone value by a dash; children grouped per periods and per sites.

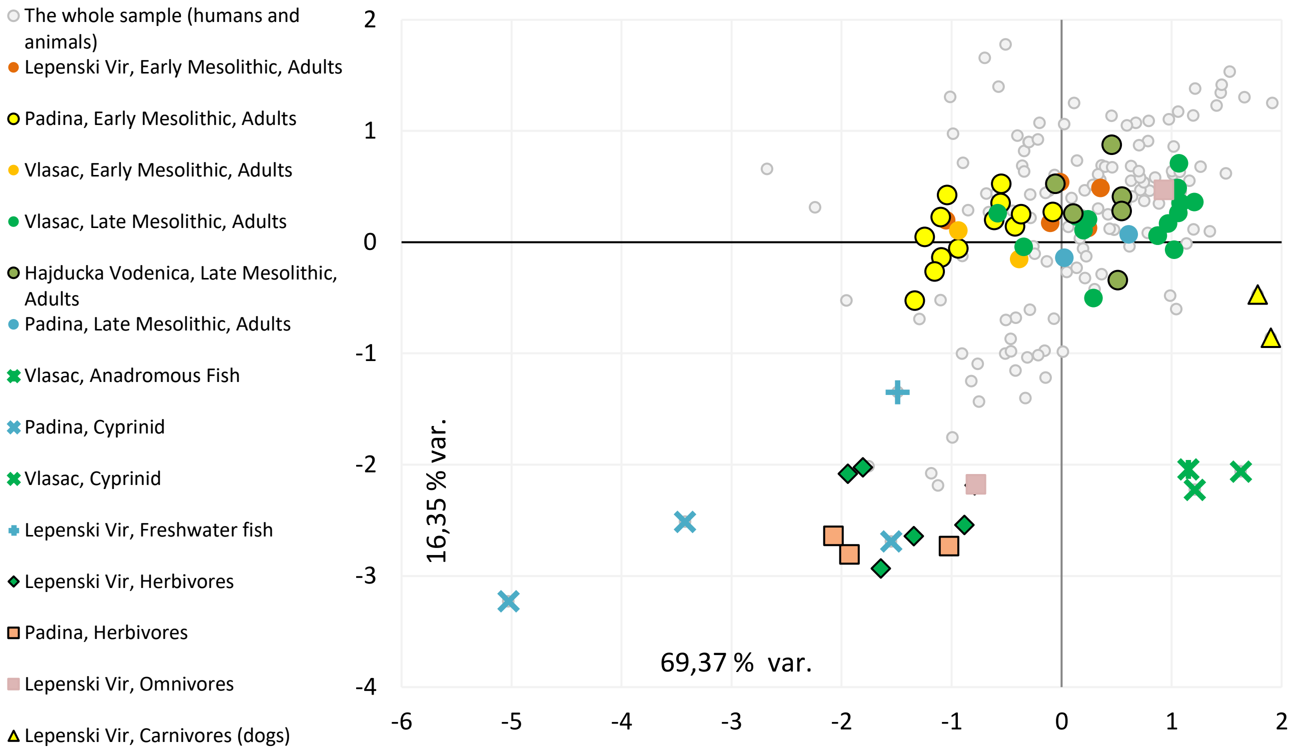


A.III.23. Bivariate plots of $\delta^{15}N$ or $\delta^{13}C$ signals and the estimated age at formation of the analyzed crowns of the first permanent molars and teeth growing roots;(cf details for the estimated age used here in the title of the appendix A.III.12. p. 390); intra-individual approach, offsets between M1 crown and tooth growing root; children grouped per periods and per sites.

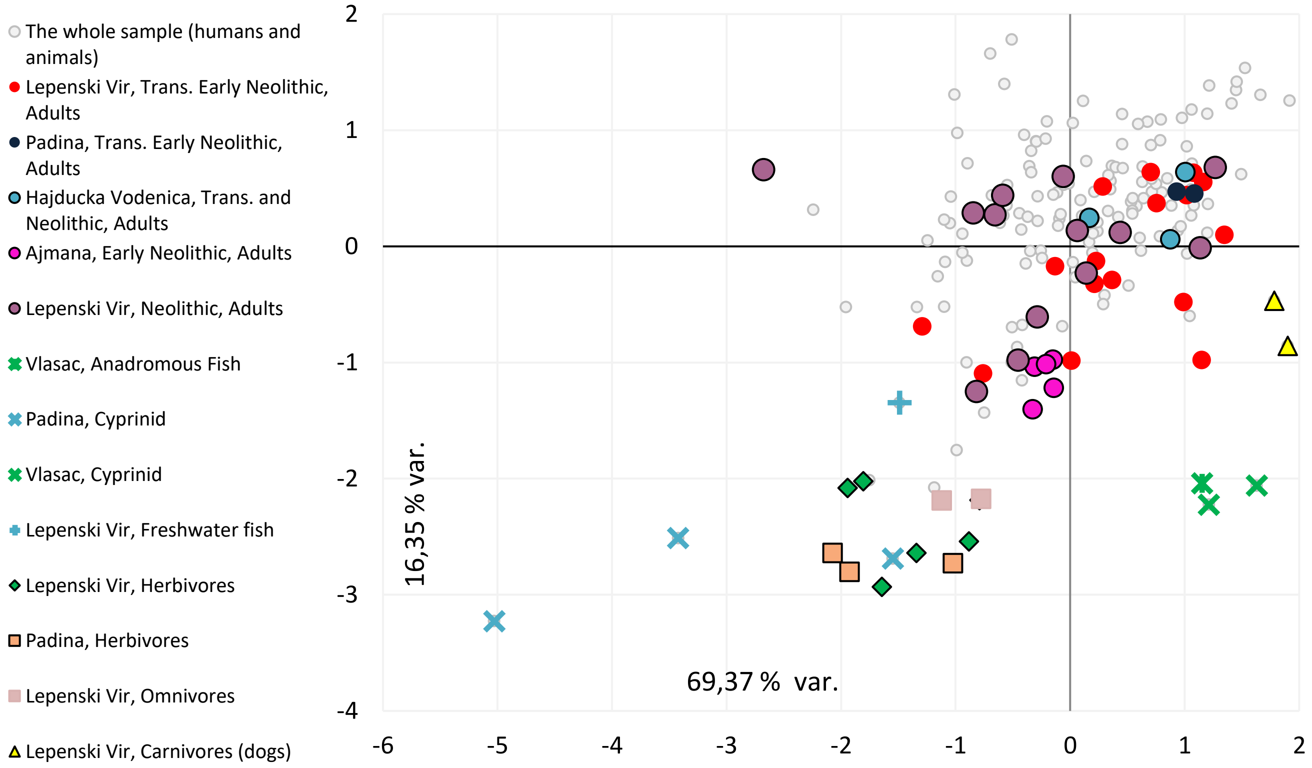
APPENDIX A.IV. Principal Component Analysis of isotope signals extracted from the collagen protein (δ^{13}Ccoll, δ^{15}N, δ^{34}S



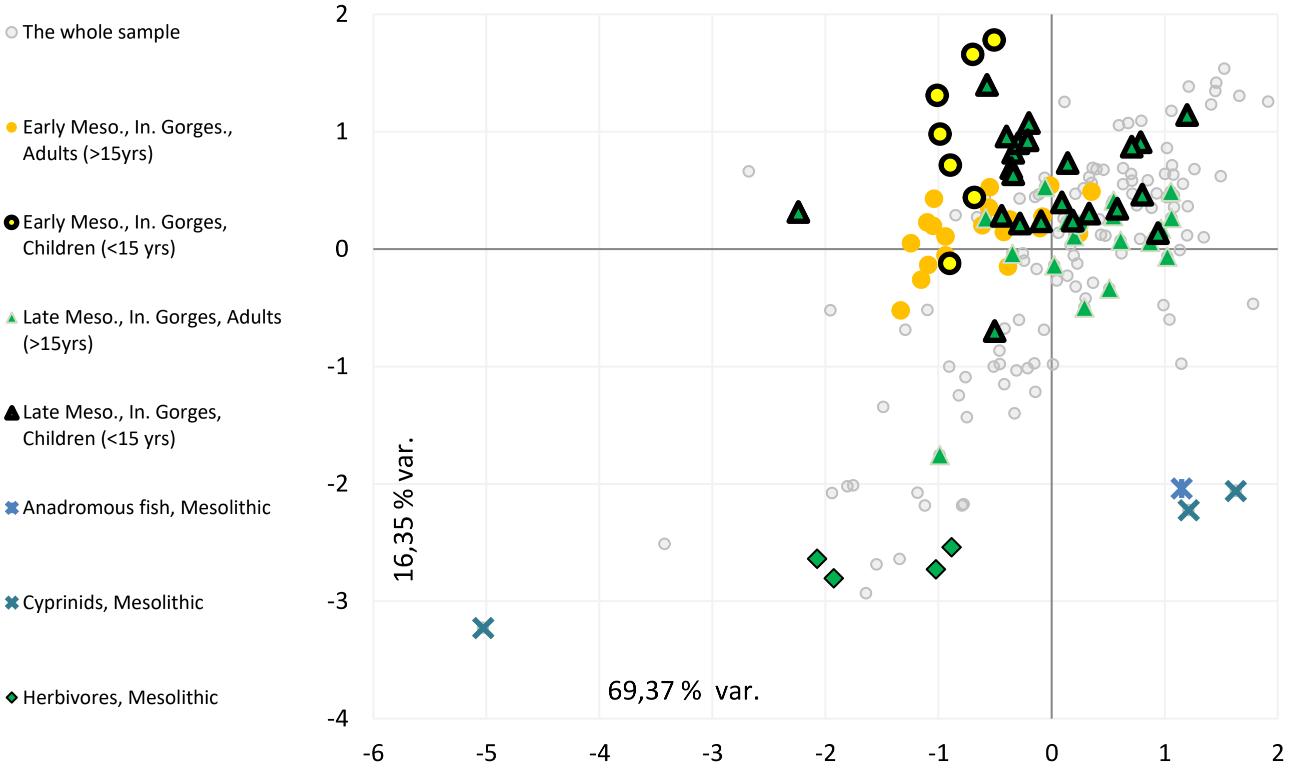
A.IV.1. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals (δ^{13}Ccoll, δ^{15}N, δ^{34}S) extracted from the collagen of prehistoric humans and animals from the Danube Gorges area (whole sample). The variables participating to the PCA are plotted, as well as individual scores for the whole sample; individual scores for different groups of animals are here highlighted.



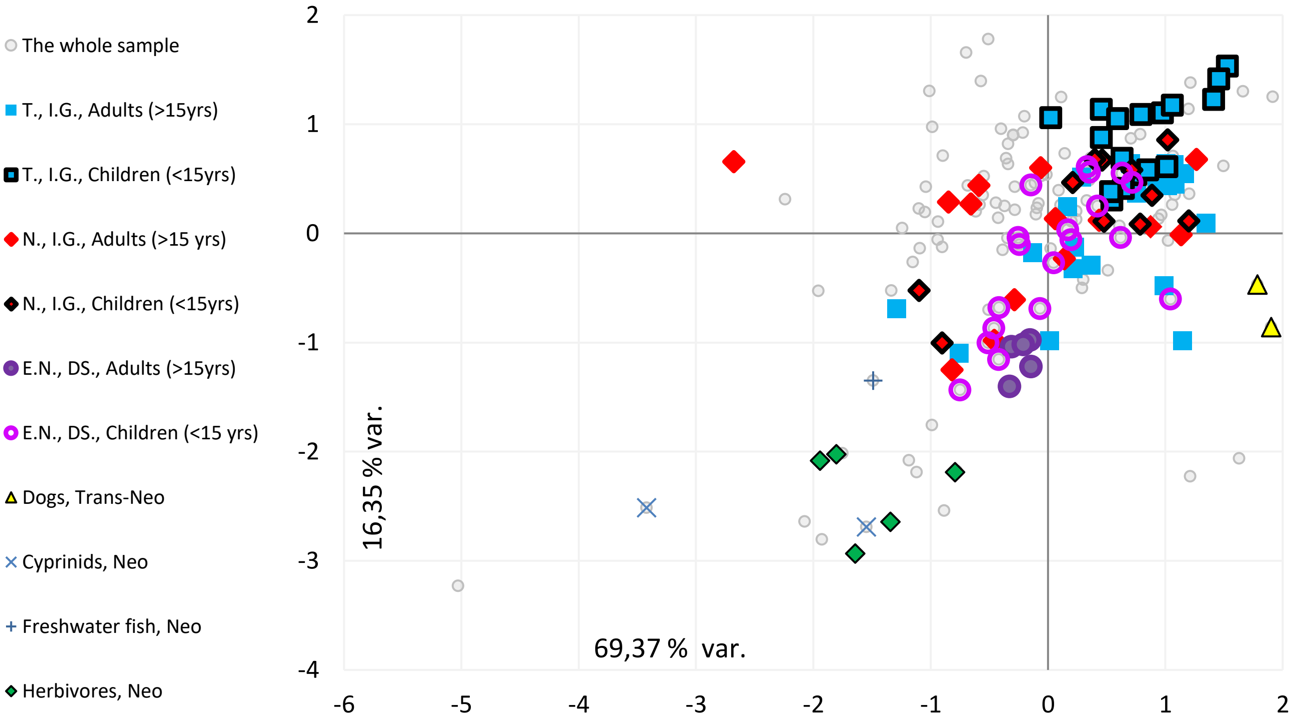
A.IV.2. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from collagen protein. Individual scores for Mesolithic adults (>15 yrs) grouped per archaeological periods and per sites and for different animal groups per sites are here highlighted.



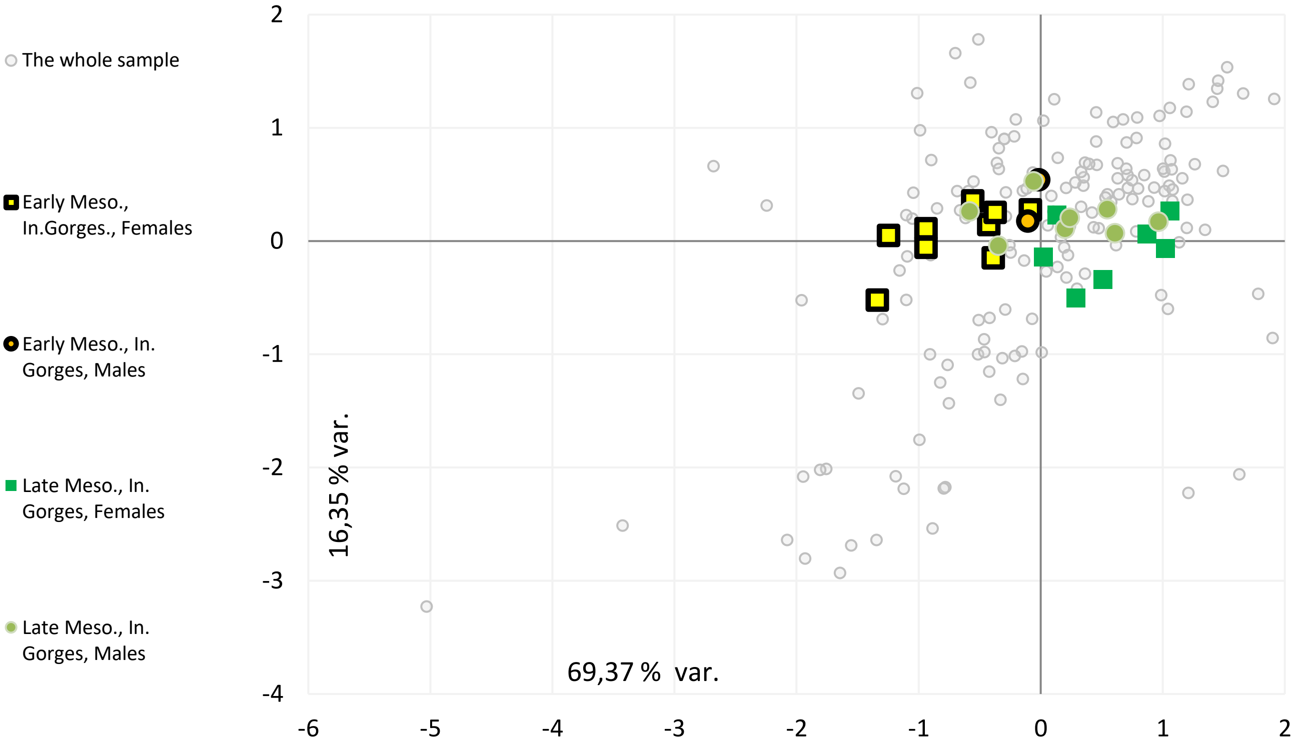
A.IV.3. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from collagen protein. Individual scores for Trans. and Neolithic adults (>15 yrs) grouped per archaeological periods and per sites and for different animal groups per sites are here highlighted.



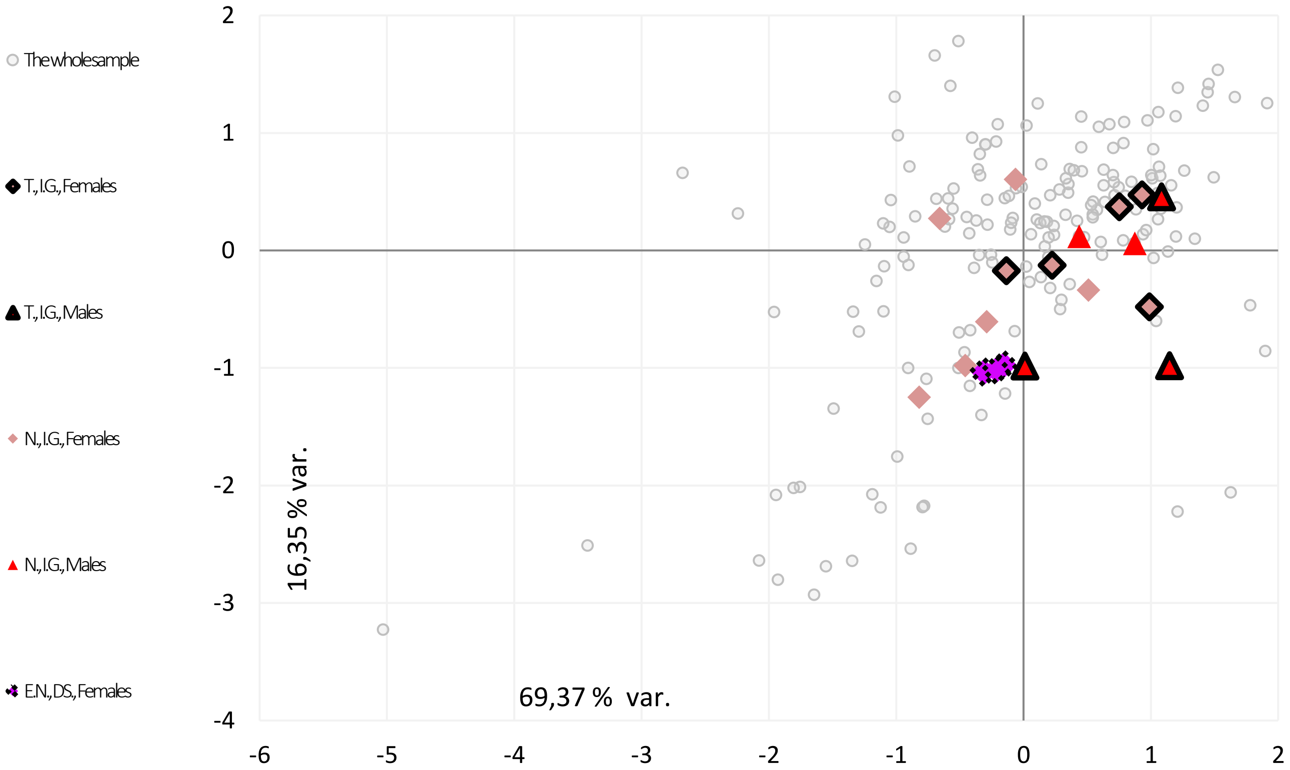
A.IV.4. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from collagen protein. Individual scores for Mesolithic humans grouped per archaeological periods and per age categories and for different animal groups are here highlighted.



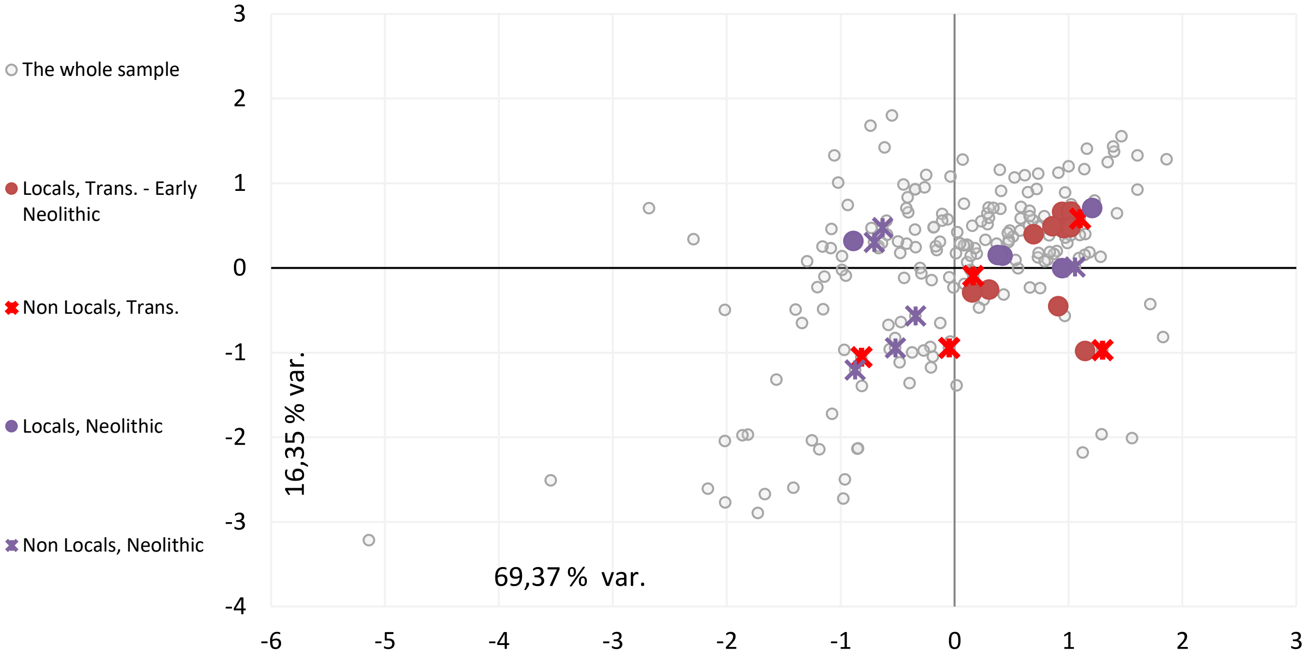
A.IV.5. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from collagen protein. Individual scores for Trans. and Neolithic humans grouped per archaeological periods and per age categories and for different animal groups are here highlighted.



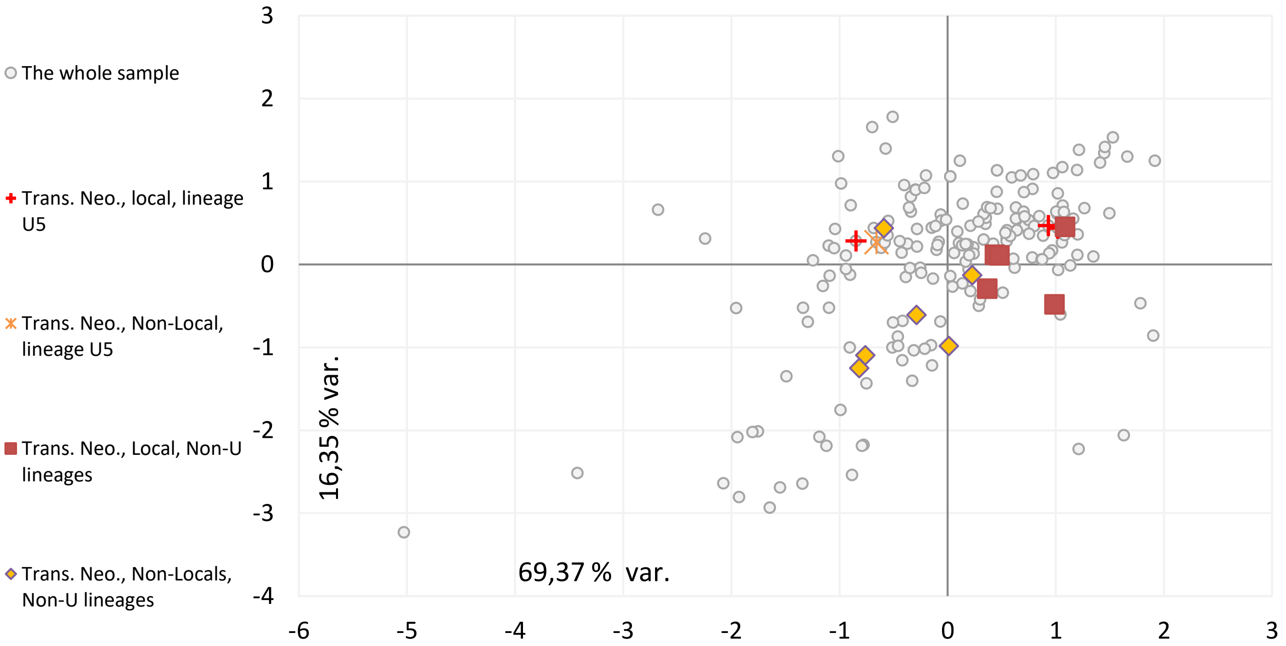
A.IV.6. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Mesolithic adults (>15 yrs) grouped per sex and per archaeological periods are here highlighted.



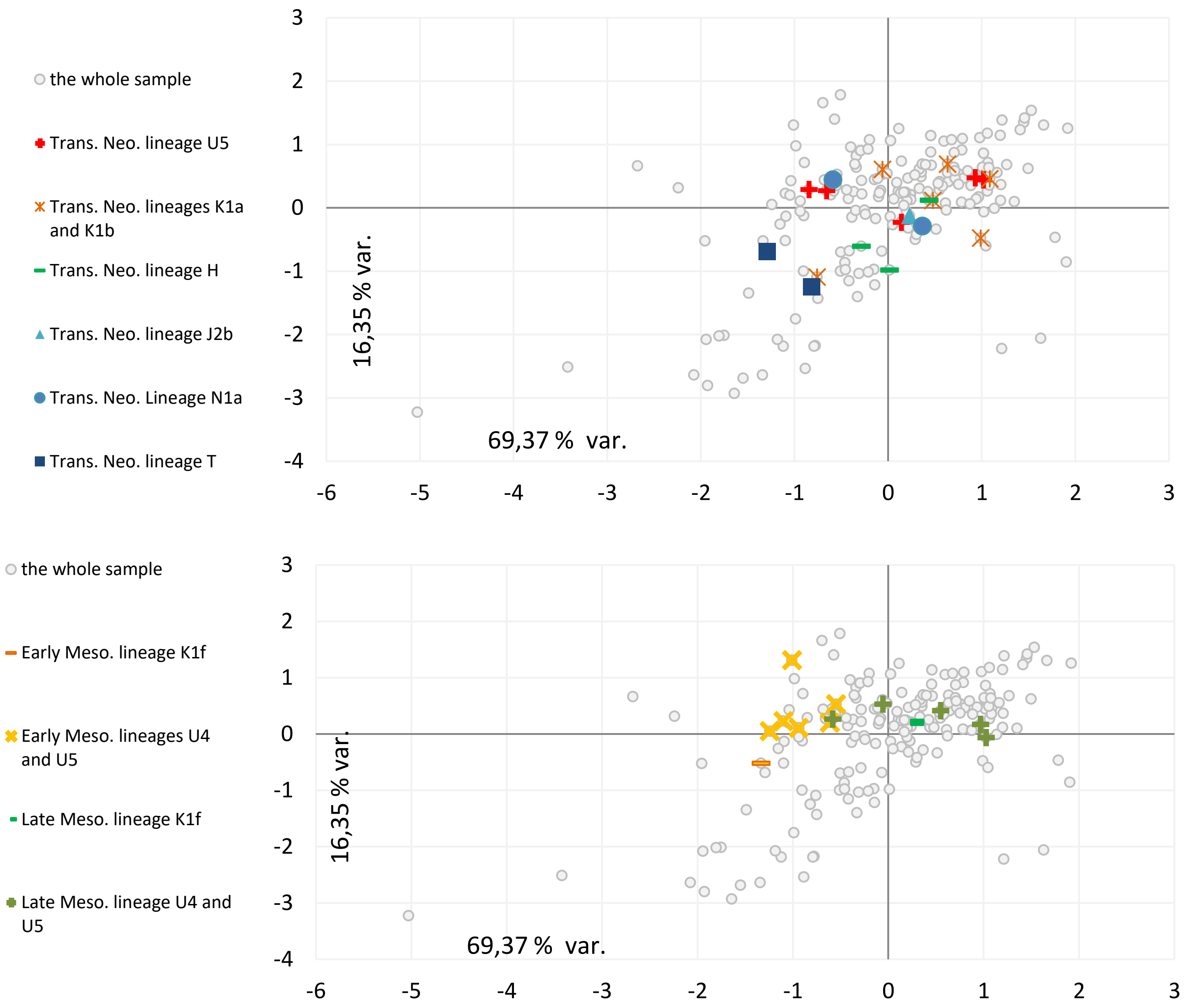
A.IV.7. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Trans. and Neolithic adults (>15 yrs) grouped per sex and per archaeological periods are here highlighted.



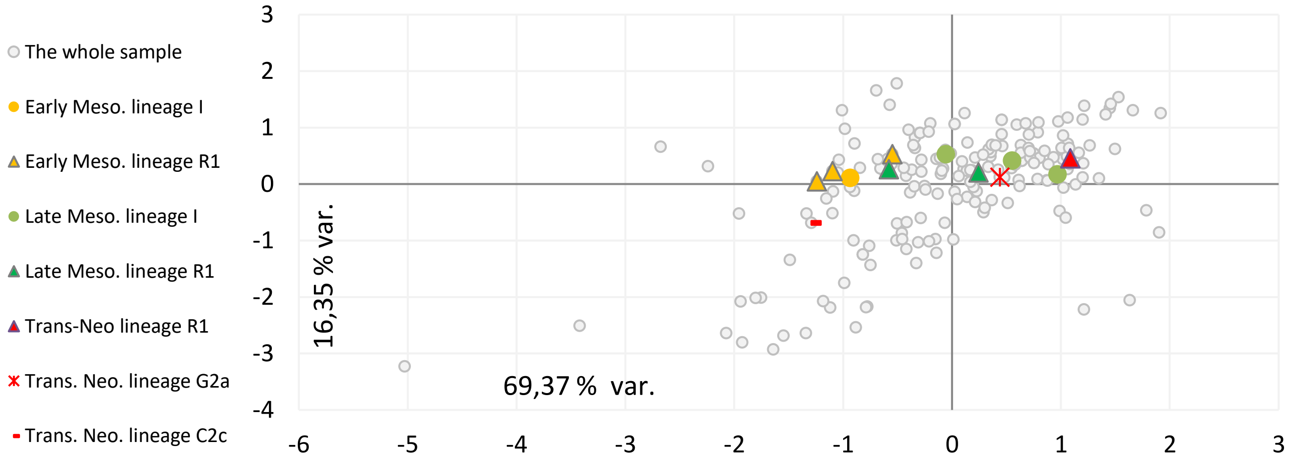
A.IV.8. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Trans. and Neolithic adults (>15 yrs) grouped per geological origins (Locals and Non-Locals discriminated according to their signal in radiogenic strontium, Borić and Price, 2013) are here highlighted.



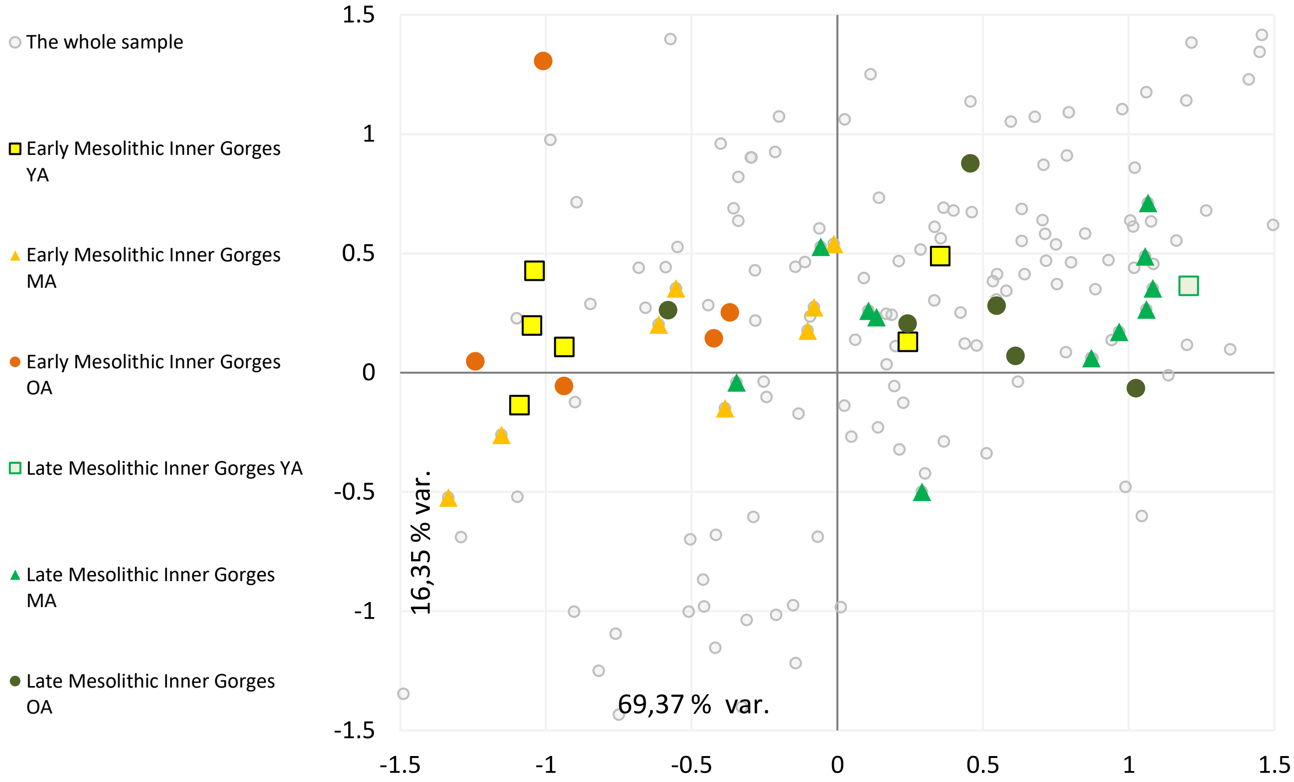
A.IV.9. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Trans. - Neolithic adults (>15 yrs) grouped per maternal genetic lineages (mitochondrial DNA; Hofmanová 2016; Mathieson et al. 2018) and geological origins (Locals and Non-Locals discriminated according to their signal in radiogenic strontium, Borić and Price 2013) are here highlighted.



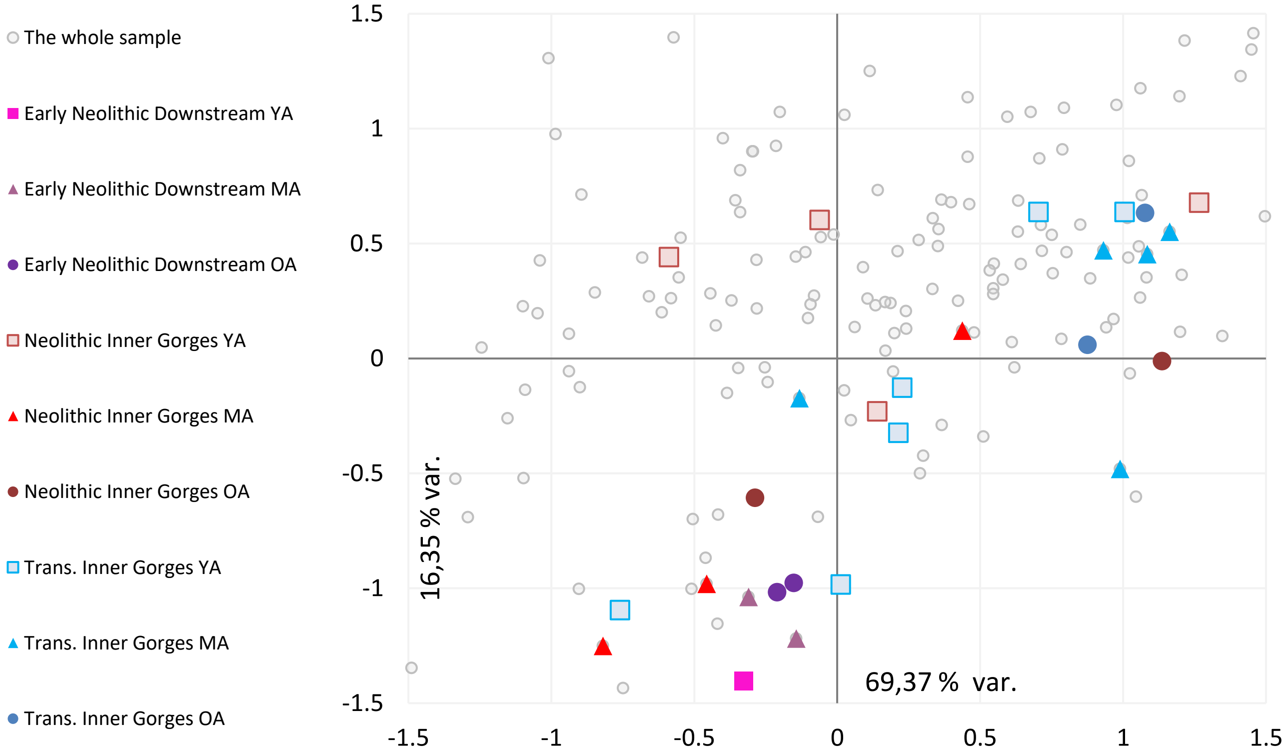
A.IV.10. Bivariate plots of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Mesolithic and Trans. - Neolithic adults (>15 yrs) grouped per maternal genetic lineages (mitochondrial DNA; Hofmanová 2016; Mathieson et al. 2018) are here highlighted.



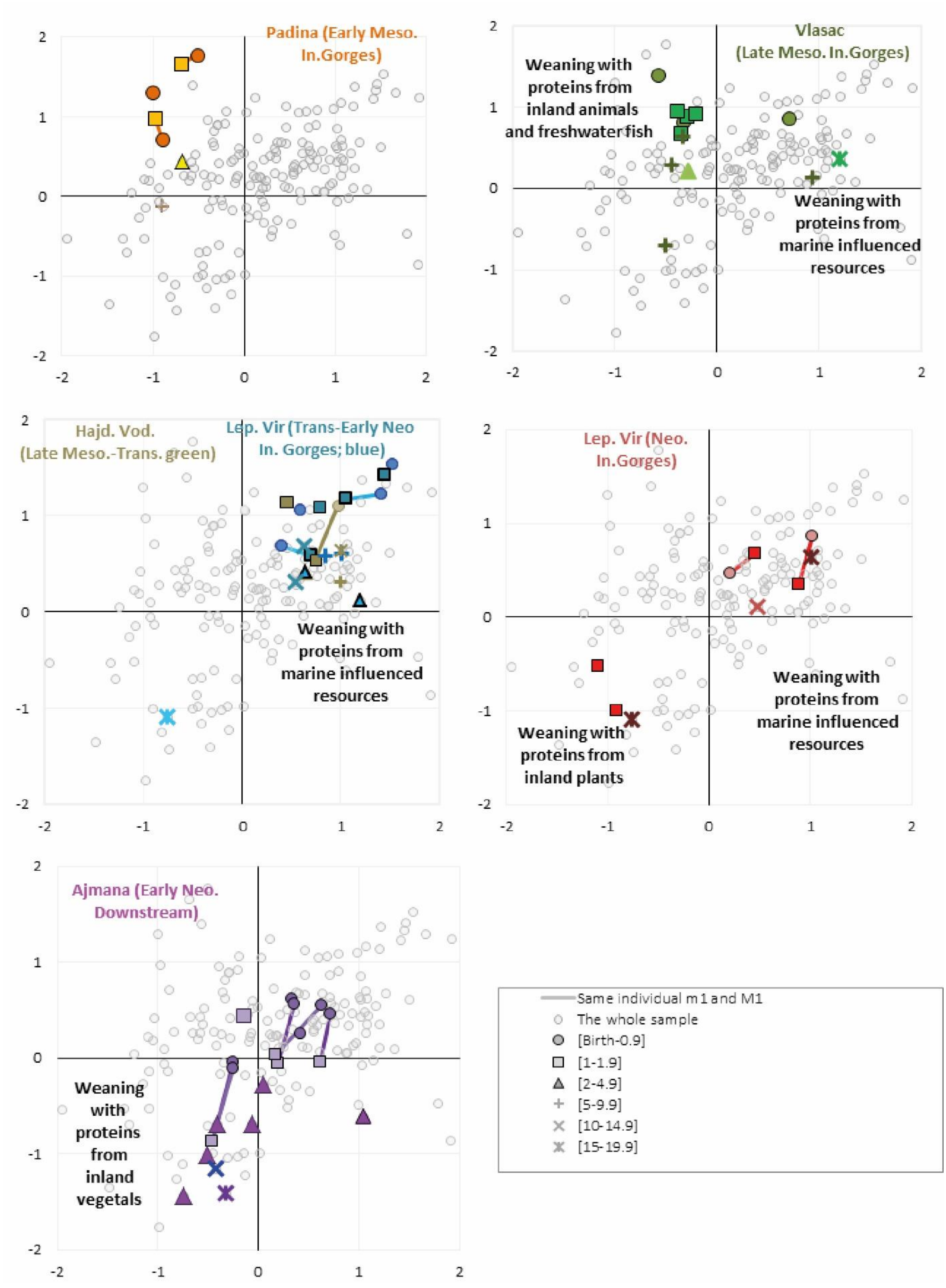
A.IV.11. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Trans. - Neolithic adults (>15 yrs) grouped per paternal genetic lineages (Y-chromosome; Hofmanová 2016; Mathieson et al. 2018) are here highlighted.



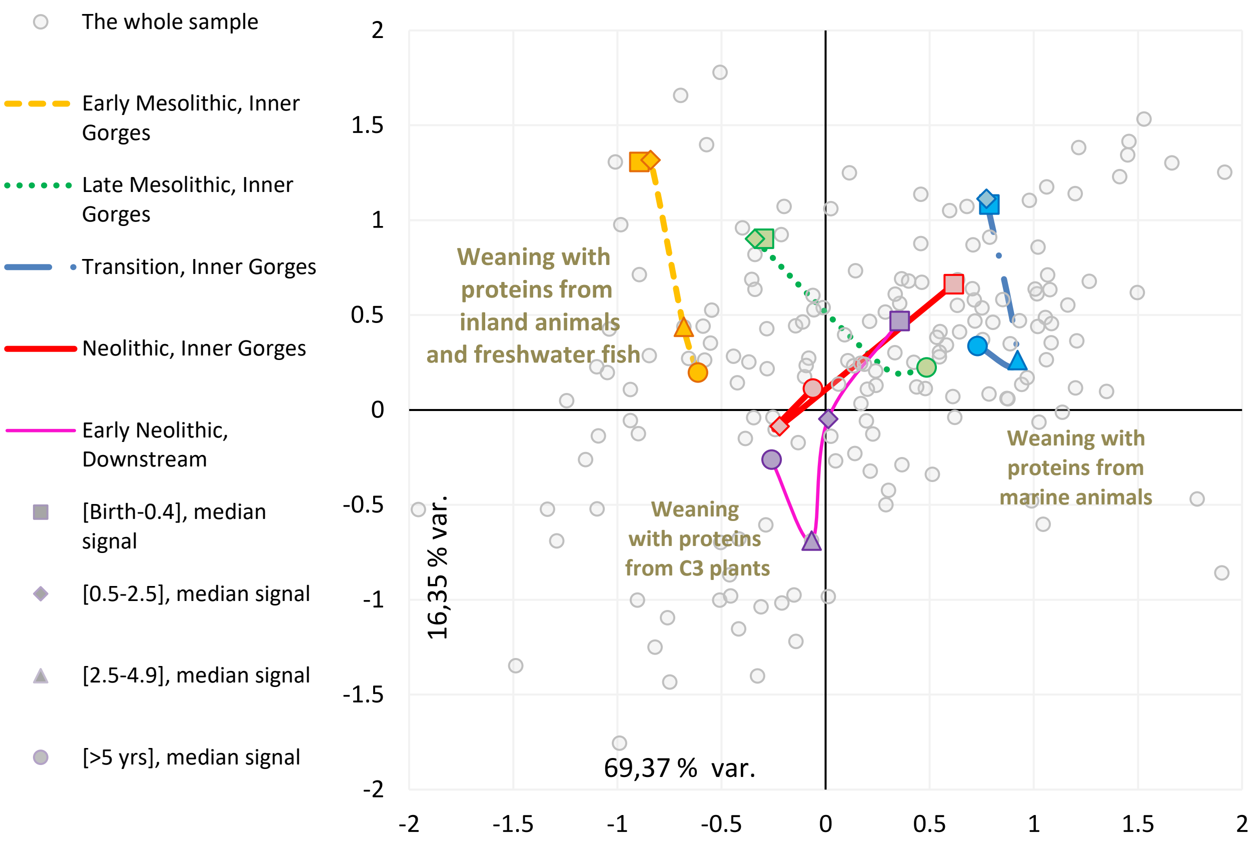
A.IV.12. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for Mesolithic adults (>15 yrs) grouped per archaeological periods and per age at death (Young Adult, Middle aged Adult and Old Adult) are here highlighted.



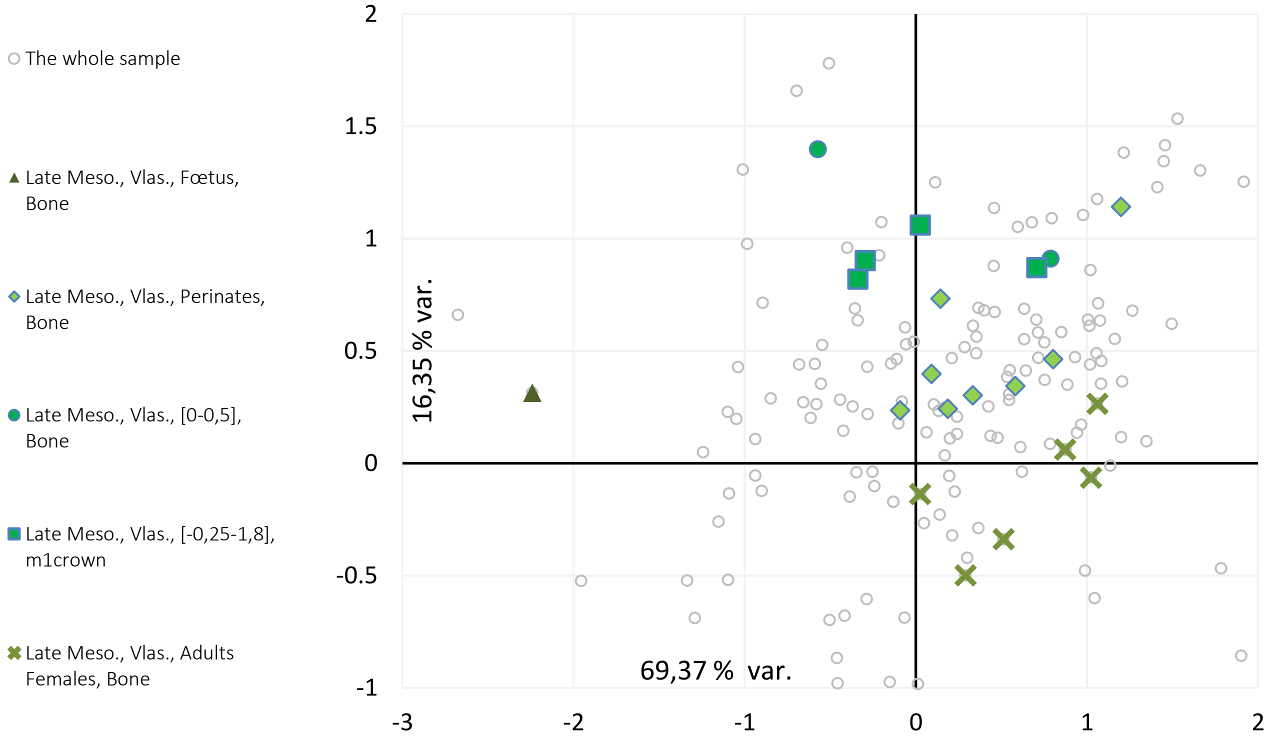
A.IV.13. Bivariate plot of the two first axes of the Principal Component Analysis of all stable isotope signals extracted from the collagen protein. Individual scores for Neolithic adults (>20 yrs) grouped per archaeological periods and per age at death (Young Adult, Middle aged Adult and Old Adult) are here highlighted.



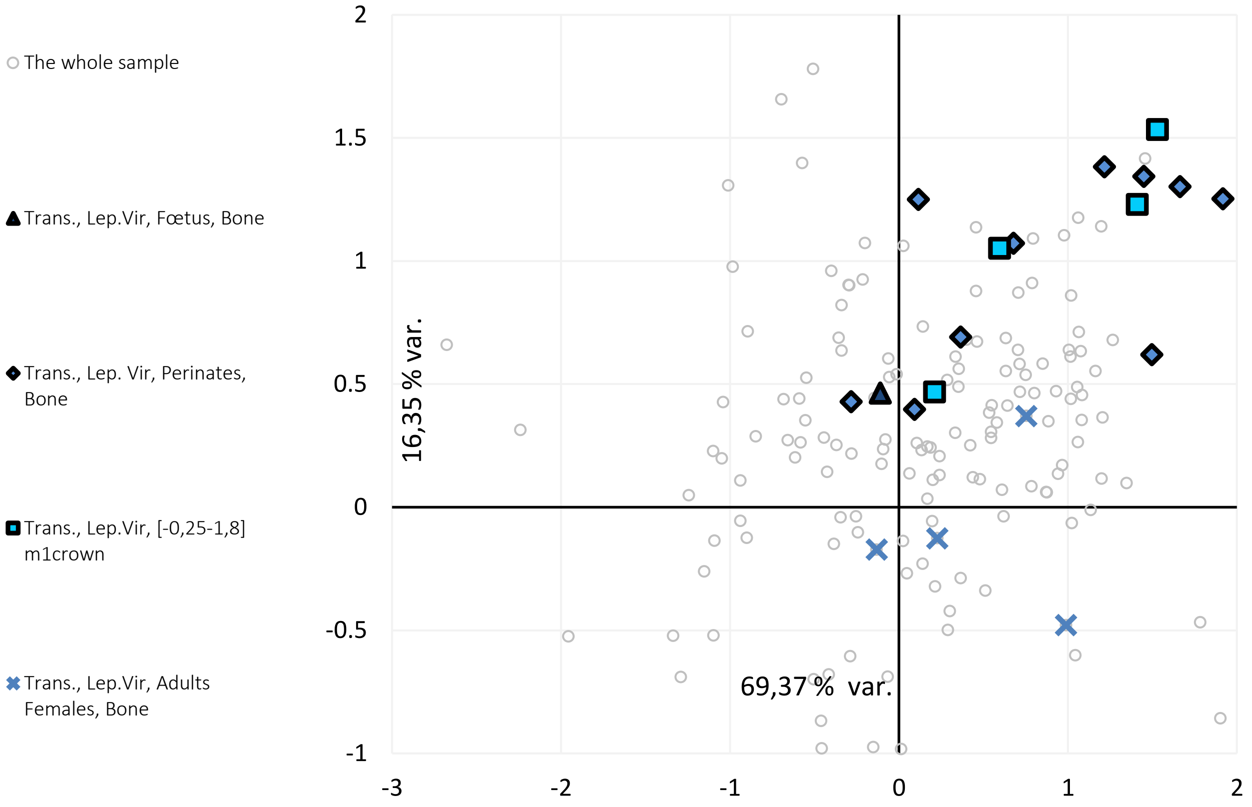
A.IV.14. Bivariate plot of the two first axes of the Principal Component Analysis of stable isotope signals from collagen. Individual scores for the different tissues sampled are here highlighted per chronological periods.



A.IV.15. Bivariate plot for the two first axes of Principal Component Analysis of stable isotope signals extracted from the collagen protein. Median ages of individual scores for the stable isotope signals from the different tissues sampled are here highlighted.



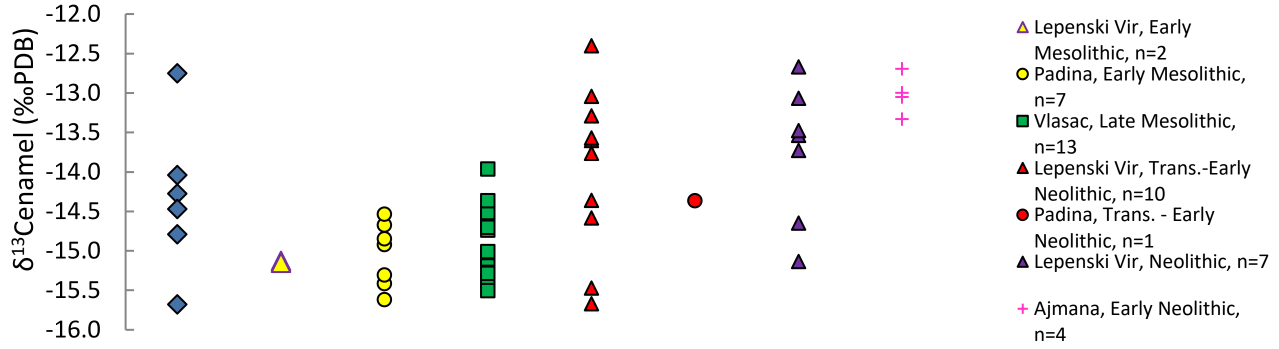
A. IV. 16. Bivariate plot for the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for perinatal individuals and for adult females (putative mothers >15 yrs) from the site of Vlasac (Late Mesolithic) are here highlighted.



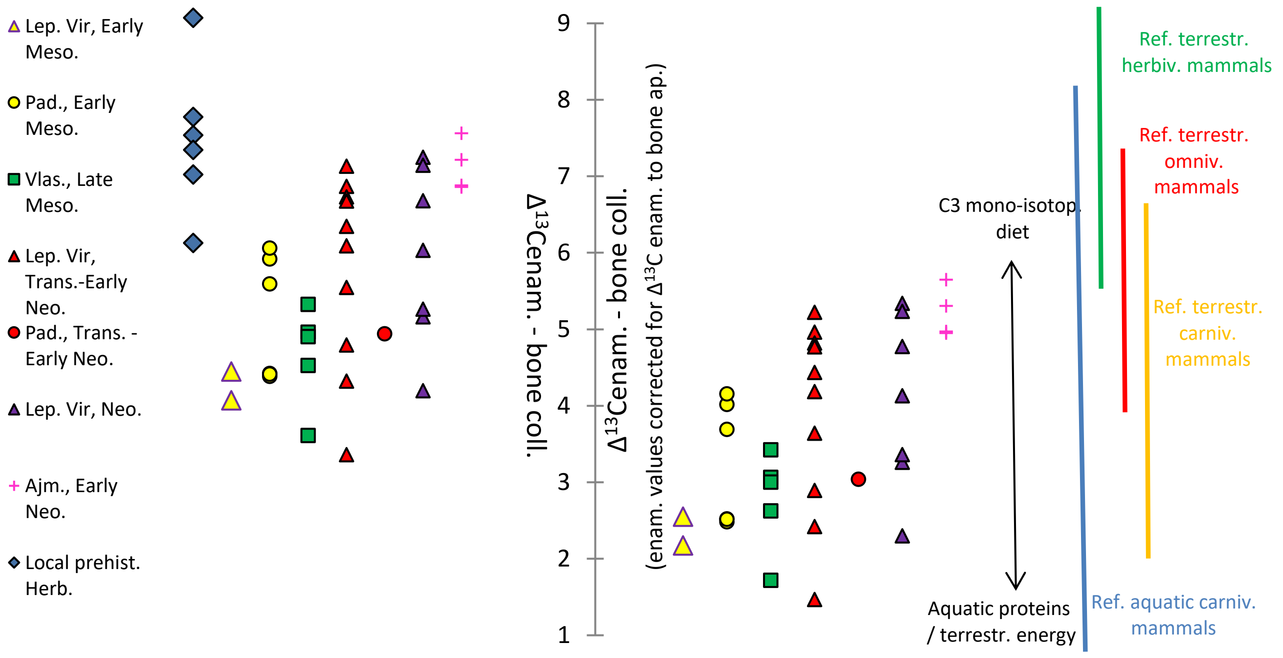
A. IV. 17. Bivariate plot for the two first axes of the Principal Component Analysis of stable isotope signals extracted from the collagen protein. Individual scores for perinatal individuals and for adult females (putative mothers >15 yrs) from the site of Lep. Vir (Trans. Early Neolithic) are here highlighted.

APPENDIX A.V.δ^{13}C analyzed in third permanent molars carbonate

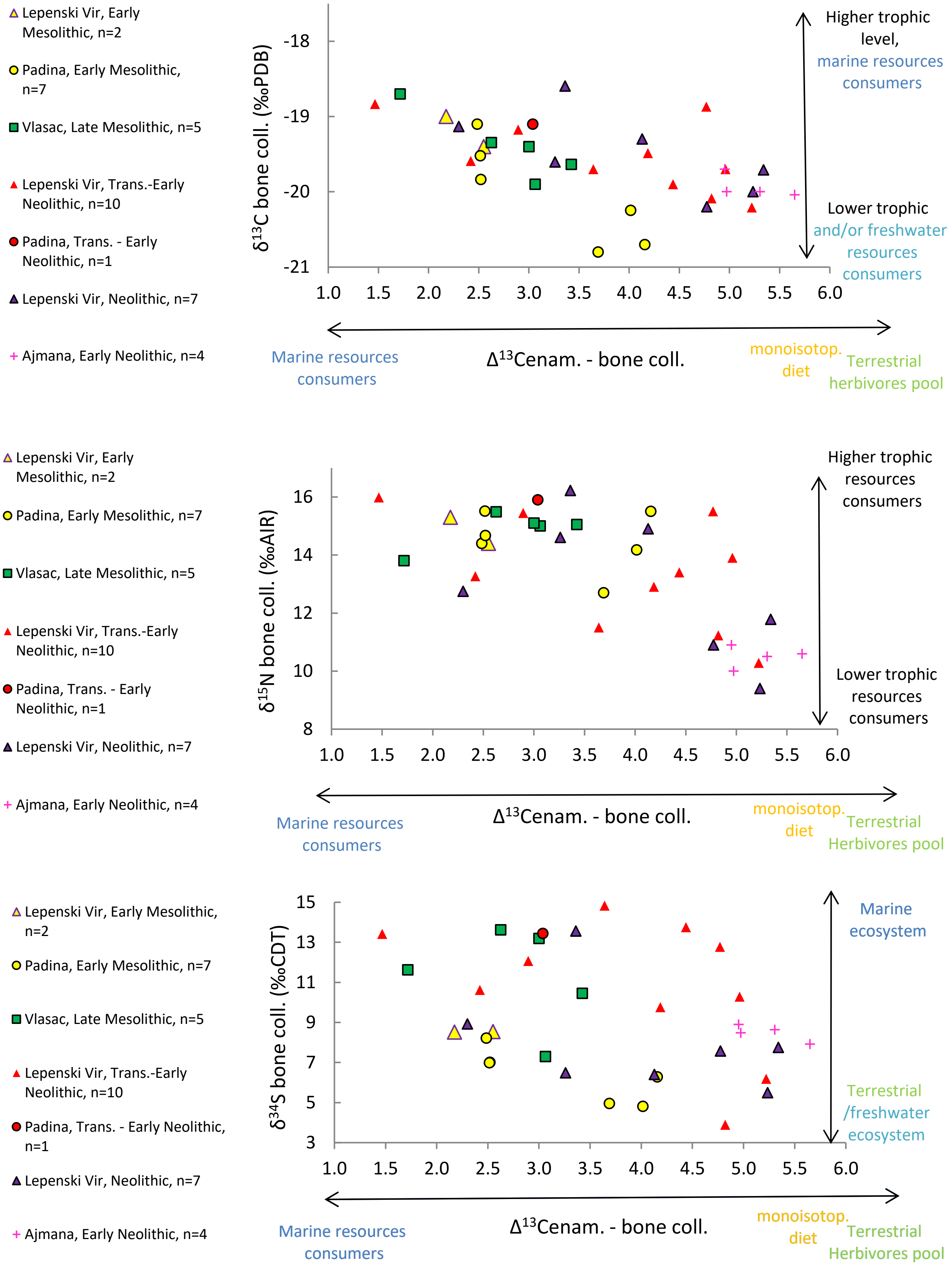
A.V.1. δ^{13}C$_{enamel}$ of different animal species and grouped chronologically



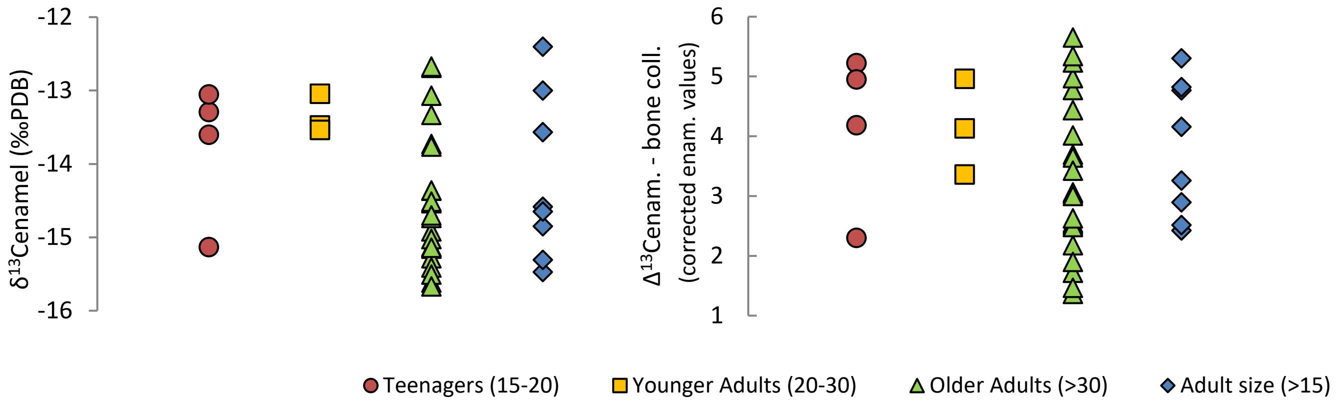
A.V.2. δ^{13}C$_{enamel}$ of Mesolithic and Neolithic humans grouped chronologically and per sites



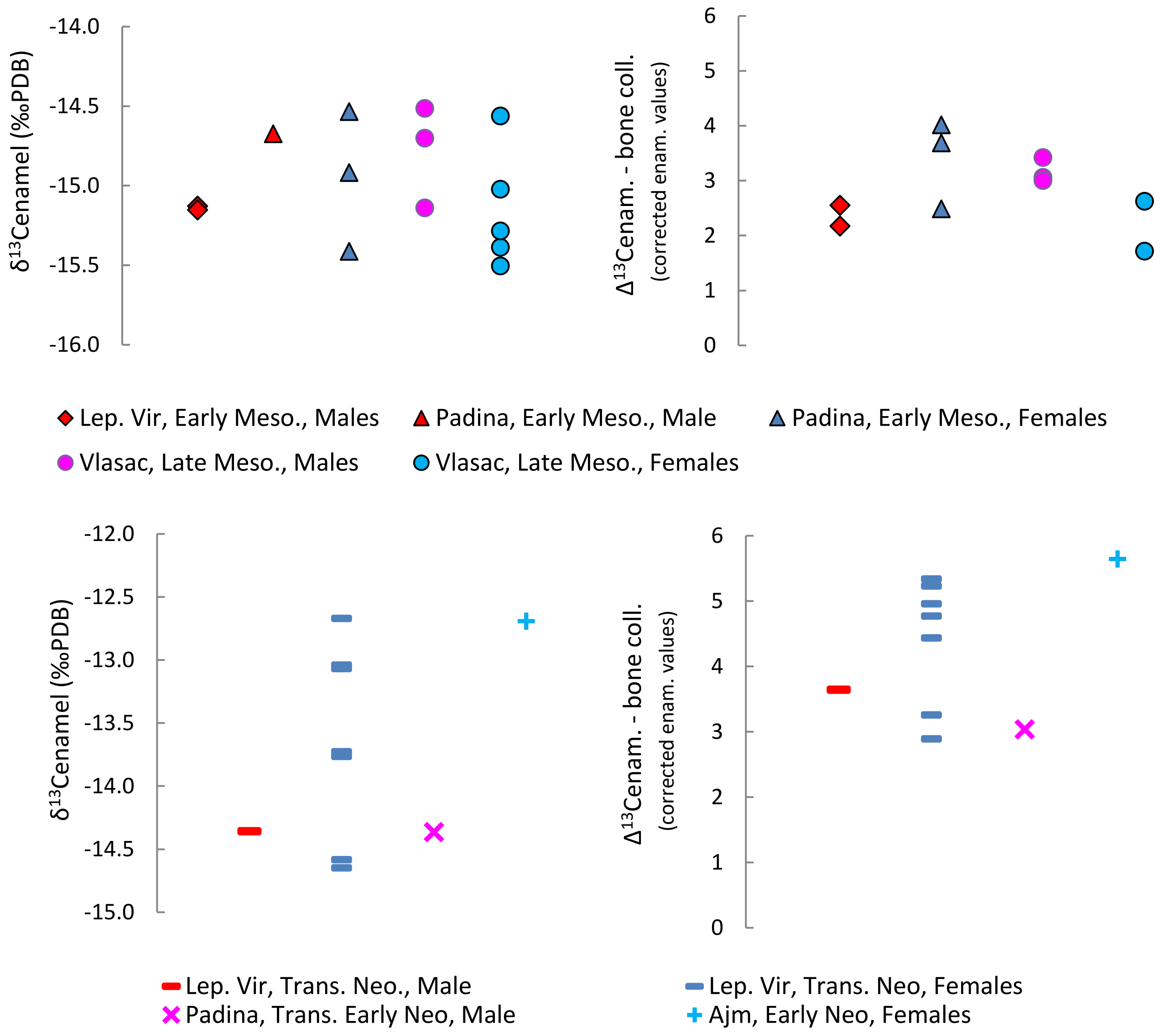
A.V.3. δ^{13}C$_{enamel\ -\ bone\ collagen}$ of Mesolithic and Neolithic humans grouped chronologically and per sites. Herbivores δ^{13}C$_{bonecollagen}$was calculated with the average δ^{13}C$_{bonecollagen}$of local prehistoric herbivores. In the right part, δ^{13}C$_{enamel}$has been corrected for a Δ^{13}C$_{enamel\text{-}bone\ apatite}$ offset of +1.8‰ based upon the data from France and Owsley (2012), Santana-Sagredo et al. (2015), Salesse et al. (2015), Zhu and Sealy. (2018). Reference data for free-ranging animals in Lee-Thorp et al. (1989), Kellner and Schoeninger (2007), Codron et al. (2019), from archaeological contexts in Grupe et al. (2009; for marine mammals) and Shin and Hedges (2012, for terrestrial herbivores), and experimental diet data of O'Connell and Hedges (2017). Experimental diet values for the deviation from a mono-isotopic diet in Kellner and Schoeninger (2007), Warriner and Tuross (2009), Froehle et al. (2010).



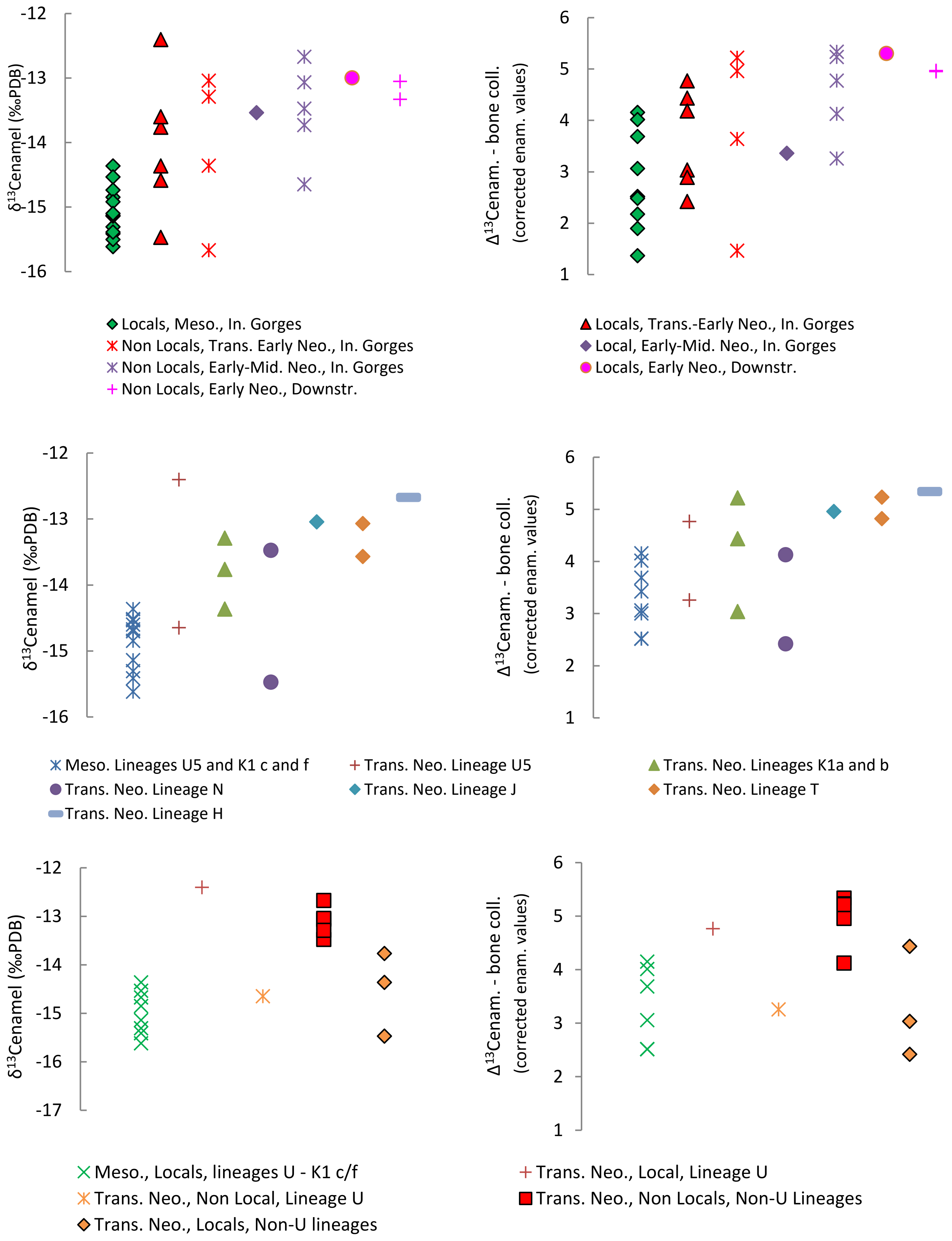
A.V.4. $\delta^{13}C_{\text{enamel – bone coll.}}$ And $\delta^{13}C_{\text{bone coll.}}$ (top), $\delta^{15}N_{\text{bone coll.}}$ (middle), $\delta^{34}S_{\text{bone coll.}}$ (bottom) of Mesolithic and Neolithic humans grouped chronologically and per sites. $\delta^{13}C_{\text{enamel}}$ has been corrected for a $\Delta^{13}C_{\text{enamel-bone apatite}}$ offset of +1.8‰ (cf caption figure A.V.3.)



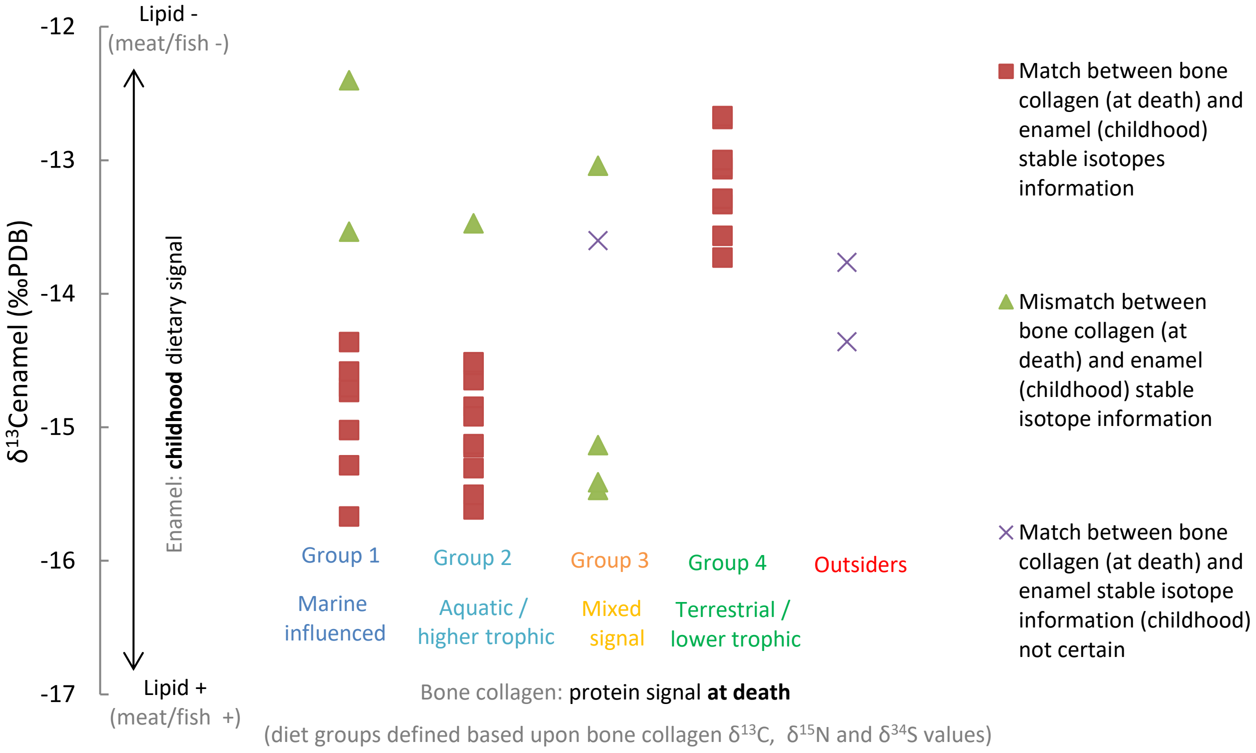
A.V.5. $\delta^{13}C_{enamel}$ (left) and $\delta^{13}C_{enamel – bone\ coll.}$ (right), of Mesolithic and Neolithic humans grouped per age categories. $\delta^{13}C_{enamel}$ has been corrected for a $\Delta^{13}C_{enamel\text{-}bone\ apatite}$ offset of +1.7‰ (cf caption figure A.V.3.)



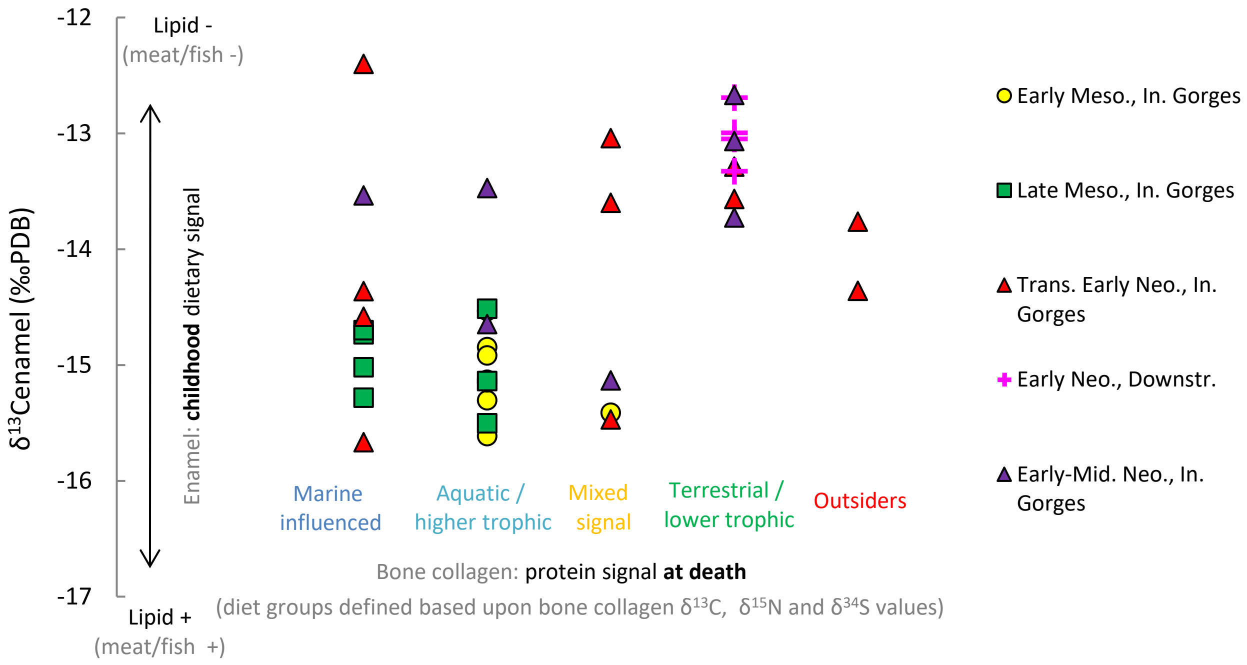
A.V.6. $\delta^{13}C_{enamel}$ (left) and $\delta^{13}C_{enamel – bone\ coll.}$ (right), of Mesolithic and Neolithic humans grouped according to sex. $\delta^{13}C_{enamel}$ has been corrected for a $\Delta^{13}C_{enamel\text{-}bone\ apatite}$ offset of +1.7‰ (cf caption figure A.V.3.)



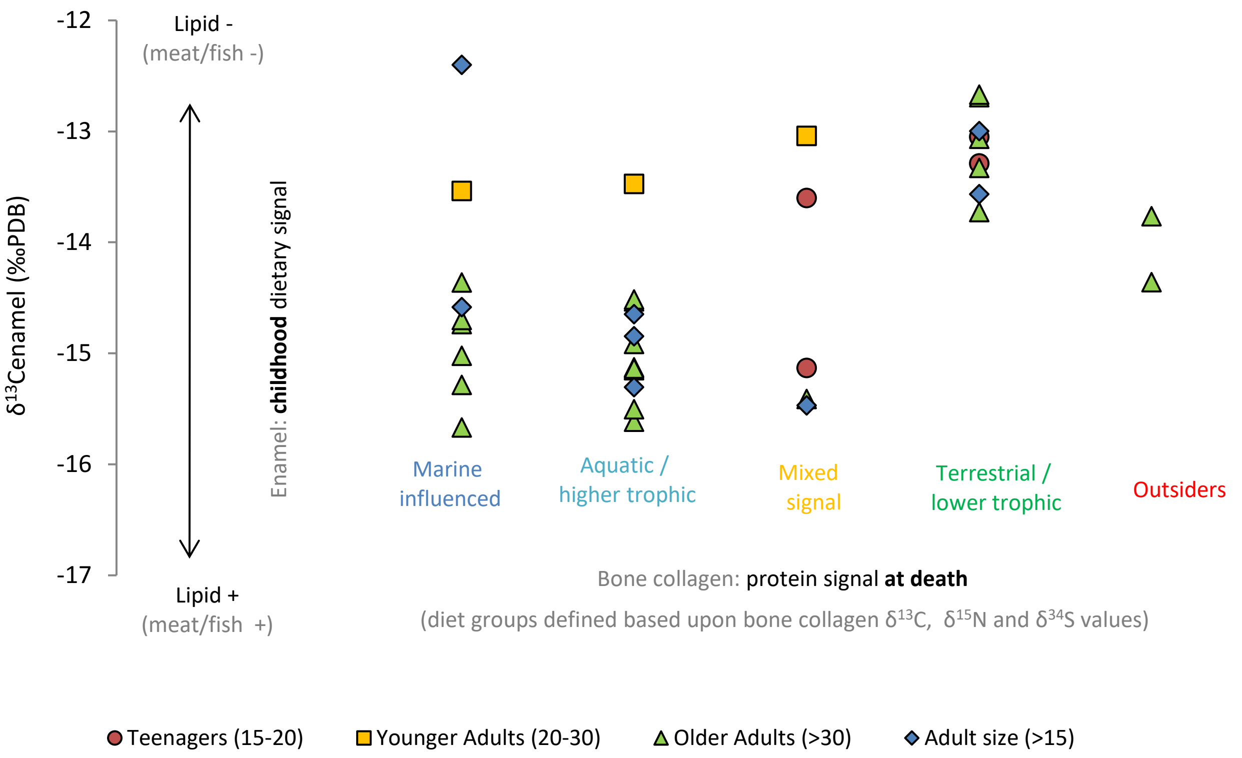
A.V.7. $\delta^{13}C_{enamel}$ (left) and $\delta^{13}C_{enamel - bone\ coll.}$ (right), of Mesolithic and Neolithic humans grouped according to their geological origin (top; Strontium radiogenic signal, Borić and Price 2013), according to their maternal genetic lineages (middle; mt-haplogroups, Hofmanová 2016) and according to provenance and genetic information cross-compared (bottom).



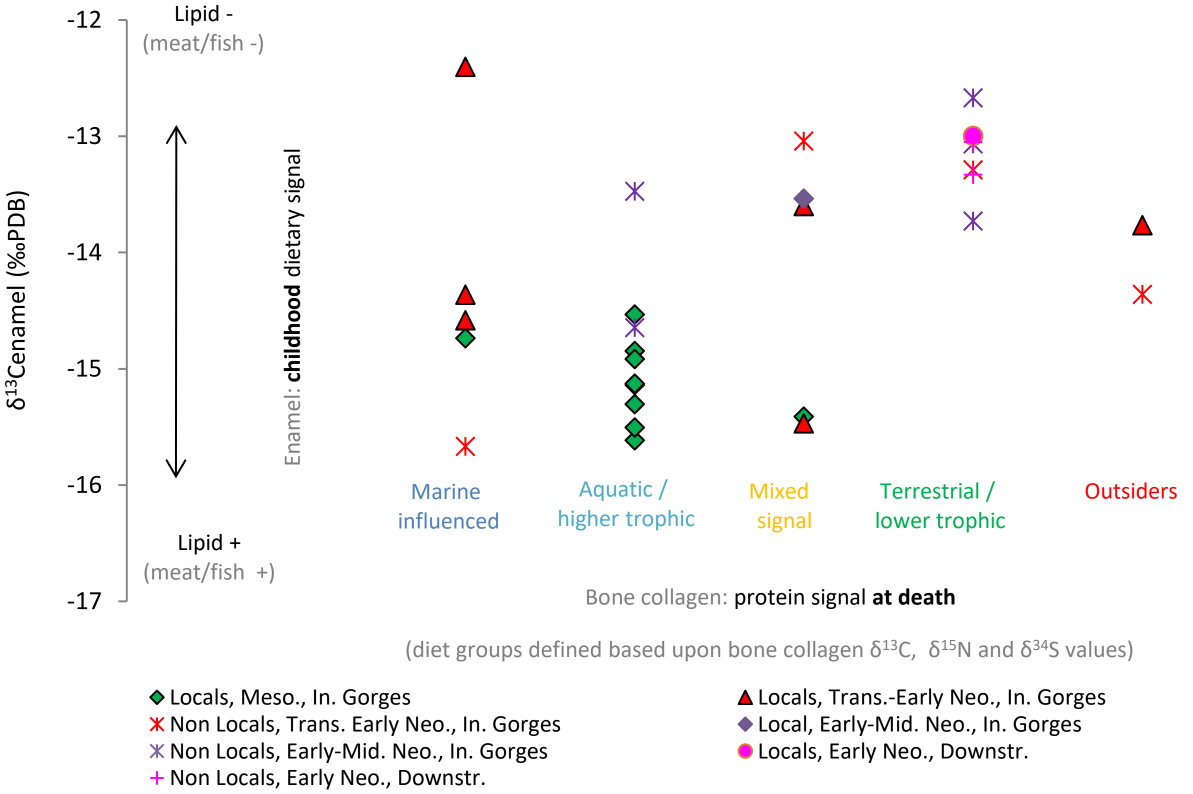
A.V.8. $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values (signal at death). Dietary groups were defined as following: Group 1, "marine-influenced proteins consumers"($\delta^{15}N >$ 14‰; $\delta^{13}C >$ -19.4‰; $\delta^{34}S >$ 11.5‰); Group 2, "aquatic and/or higher trophic level resources consumers" ($\delta^{15}N >$ 14‰; $\delta^{13}C >$ -19 ‰; $\delta^{34}S >$ 9‰); Group 3, "mixed aquatic and terrestrial diet"($\delta^{15}N$ = >12‰ - < 14‰; $\delta^{13}C$ >-19 - <-19.7‰; $\delta^{34}S$<10.6‰); Group 4, "terrestrial or lower trophic level resources consumers" ($\delta^{15}N$ = < 12‰; $\delta^{13}C$<-19.7‰ $\delta^{34}S$<9‰).Two individuals, LV 7Ia and LV 54D, were not assigned to these dietary groups and defined as "outsiders" because of their particular stable isotope signature in comparison with the cohort.



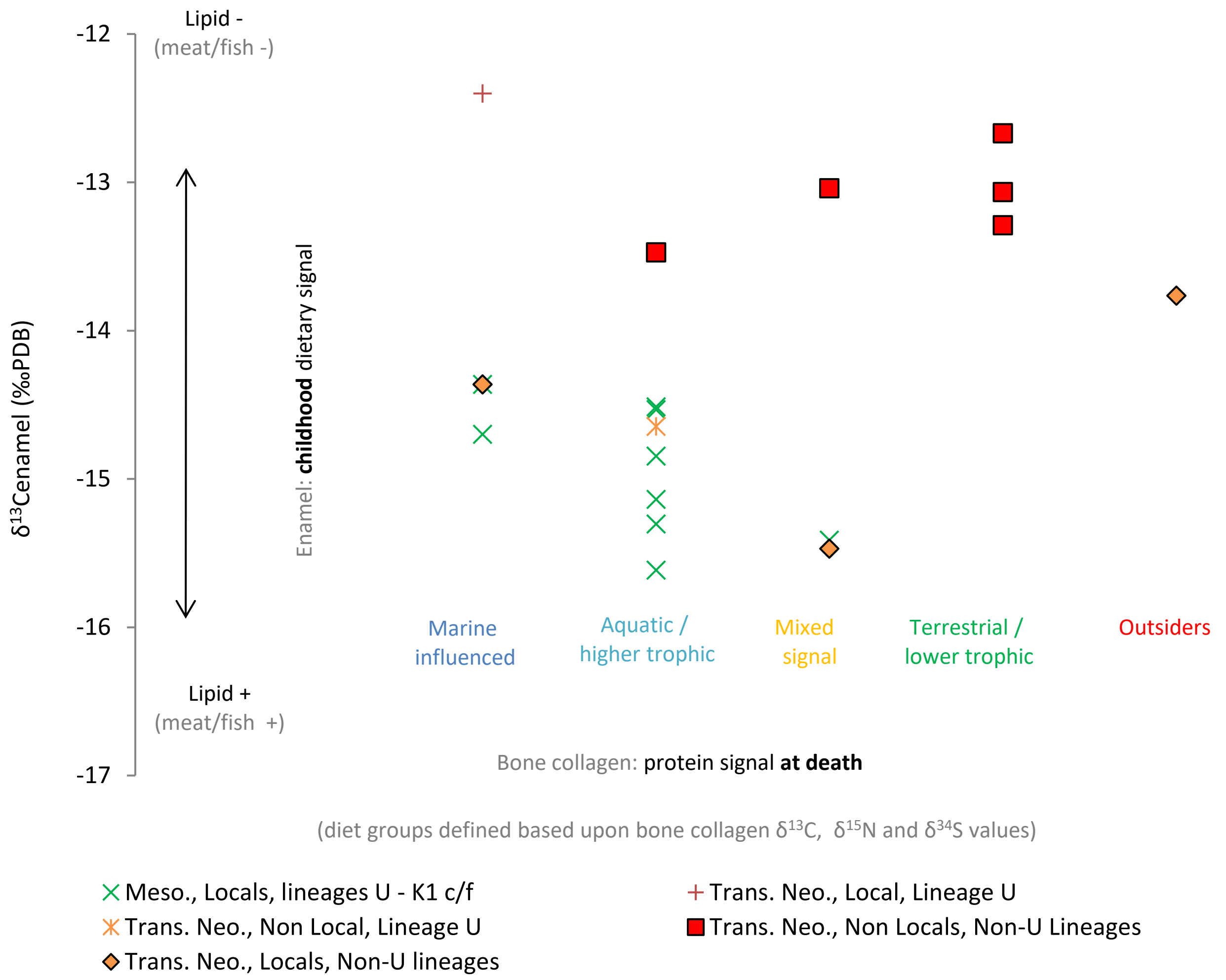
A.V.9. $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen (cf caption figure A.V.8.) and per chronological periods.



A.V.10. $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen (cf caption figure A.V.8.) and per age categories.



A.V.11. $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen (cf caption figure A.V.8.) and according to their geological origin (Strontium radiogenic signal, Borić and Price 2013).



A.V.12. $\delta^{13}C_{enamel}$ (signal between 8-15 years old) for prehistoric individuals grouped according to their diet inferred from their bone collagen (cf caption figure A.V.8.) and according to their geological and genetic origin (Strontium radiogenic signal, Borić and Price 2013; mt-haplogroups, Hofmanová 2016).

APPENDIX B.I. Chronological and biological information associated with human individuals included in this study[1]

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
A	AJ 1	Early Neo				3-6 yr						
A	AJ 10	Early Neo				3-7 yr						
A	AJ 11	Early Neo			F	Middle-aged or old adult						
A	AJ 12	Early Neo				3-6 yr	i	0,708834	L			
A	AJ 13	Early Neo				11-14 yr	i	0,709497	L			
A	AJ 14	Early Neo				4.5-7 yr	i	0,709336	L			
A	AJ 15	Early Neo				4.5-7 yr	i	0,708437	NL			
A	AJ 16	Early Neo				1.5-4 yr	33	0,709323	L			
A	Aj 3	Early Neo				9.5-14.5 yr	44/45	0,709985	NL			
A	AJ 5	Early Neo				15-20 yr						
A	AJ 6	Early Neo	6030-5842	Boric 2011	M?	Young adult	17	0,709618	L			
A	AJ 7	Early Neo	6214-6008	Boric 2011		Middle-aged adult	48	0,708048	NL			
A	AJ 8	Early Neo				[1-4]						
A	AJ 8a	Early Neo			F	Old adult						
A	AJ 9	Early Neo			F	Old adult	15	0,708720	L			
CC		Epipaleo?				Adult Size (>15-?)	M	0,708972	L			
CT		Epipaleo?			F?	Adult Size (>15-?)	36/46	0,708635	L			
CT		Epipaleo?			F?	Adult Size (>15-?)	36/46	0,710380	NL			
CT	CT 1	Epipaleo - Early Meso	9845-9295	Bonsall et al. 2015	F	Adult Size (>15-?)						
CT	CT 2	Epipaleo - Early Meso	9745-9255	Bonsall et al. 2015	M?	Adult Size (>15-?)						
CT	CT 3	Trans. - Early Neo	6205-5780	Bonsall et al. 2015		Perinate?						
CT	CT 4	Early-Middle Neo	5985-5735	Bonsall et al. 2015		Child						
HV	HV 11	Late Meso-Trans.			M	Middle-aged or old adult	48	0,711917	NL			
HV	HV 13	Early-Middle Neo	6016-5726	Boric 2011	M	Old adult	17/27	0,709091	L			
HV	HV 14	Late Meso-Trans.				4.5-7 yr						
HV	HV 15 S.G.	Late Meso-Trans.				Adult Size (>15-?)				U5	I2	Mathieson et al. 2018
HV	HV 15/1	Trans.-Early Neo	6361-6050	Boric 2011		Adult Size (>15-?)				U5a	I2	Mathieson et al. 2018
HV	HV 16	Trans.-Early Neo				14-18 yr	36	0,70932	L			
HV	HV 17-20(1)	Trans.-Early Neo	6368-6068	Boric 2011	M	Old adult	46	0,70916	L	U5	I2	Mathieson et al. 2018
HV	HV 17-20(4)	Trans.-Early Neo				Middle-aged or old adult	37	0,70921	L			
HV	HV 18	Late Meso-Trans.				10.5-12.5 yr						
HV	HV 21	Late Meso-Trans.				3-6 yr				U5	I2	Mathieson et al. 2018
HV	HV 22	Late Meso-Trans.			M?	Old adult						
HV	HV 23-25	Trans.-Early Neo				Adult Size (>15-?)						
HV	HV 26-28(3)	Trans.-Early Neo				7.5-11 yr	44	0,70933	L			
HV	HV 29	Late Meso-Trans.	6860-6434	Boric 2011	M	Old adult	48	0,70927	L			
HV	HV 30	Late Meso-Trans.			F	Adult Size (>15-?)	26	0,70930	L			
HV	HV 31	Late Meso	7035-6590	Mathieson et al. 2018		Adult Size (>15-?)				U5b	R1b	Mathieson et al. 2018
HV	HV 33	Late Meso-Trans.			F	Adult Size (>15-?)	17	0,70892	L	U5		Mathieson et al. 2018
HV	HV 33(1)	Late Meso-Trans.				Adult Size (>15-?)	48	0,70914	L			
HV	HV 8	Late Meso-Trans.	7076-6699	Boric 2011	M	Middle-aged or old adult	48	0,70918	L	U5	I2	Mathieson et al. 2018
HV		Late Meso - Trans.			?	?	27	0,70937	L			
I		Late Meso			F	Adult Size (>15-?)	M1	0,70958	L			
I	M1	Early Neo	6230-5920	Bonsall et al. 2015		Adult Size (>15-?)						
I	M2	Early Neo	6355-6005	Bonsall et al. 2015		Adult Size (>15-?)						
LV	LV 1	Early-Middle Neo			M	Middle-aged or old adult						
LV	LV 100	Early Meso				14-18 yr						
LV	LV 101	Trans.-Early Neo				37-44 wk						
LV	LV 102	Transition-Early Neo			F	32-40 wk						
LV	LV 103	Transition-Early Neo			M	36.5-42 wk						
LV	LV 104	Early Meso				15-20 yr						
LV	LV 105	Early Meso?				Adult Size (>15-?)				U5		Hofmanova 2017
LV	LV 106	Trans.-Early Neo			M	38-43 wk						
LV	LV 107	Trans.-Early Neo			M	37-42 wk						
LV	LV 108	Trans.-Early Neo				38-42 wk						
LV	LV 109a	Trans.-Early Neo			F	37.5-42 wk						
LV	LV 11	Trans.-Early Neo				10.5-17 yr				K1a		Hofmanova 2017
LV	LV 110	Trans.-Early Neo			F	37-42 wk						
LV	LV 111	Trans.-Early Neo			F	36.5-43 wk						
LV	LV 113	Trans.-Early Neo			F	36-42 wk						
LV	LV 116	Trans.-Early Neo			F	Perinate						
LV	LV 118	Trans.-Early Neo			F	32.5-38 wk						
LV	LV 120	Trans.-Early Neo			M	36-41 wk						
LV	LV 121	Trans.-Early Neo			M	35.5-41 wk						
LV	LV 122	Trans.-Early Neo	6208-5987	Boric 2011		15-18 yr	26	0,71001	NL	K1a		Hofmanova 2017
LV	LV 125	Trans.-Early Neo			M	36-41.5 wk						

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
LV	LV 126	Early Meso			F?	Adult Size (>15-?)	I	0,70962	L	H13		Hofmanova 2017
LV	LV 127	Trans.-Early Neo			F	38-43 wk						
LV	LV 128	Trans.-Early Neo			F	36-43 wk						
LV	LV 129	Trans.-Early Neo			M	36-42 wk						
LV	LV 13	Trans.-Early Neo			M?	Adult Size (>15-?)	33	0,71004	NL			
LV	LV 13(1)	Trans.-Early Neo				Adult Size (>15-?)	44	0,70931	L			
LV	LV 14	Trans.-Early Neo	6235-5990	Bonsall et al. 2015	F	Adult Size (>15-?)	13	0,70961	L			
LV	LV 16	Trans.-Early Neo			F?	Adult Size (>15-?)	43	0,70910	L			
LV	LV 17	Early-Middle Neo	5836-5632	Mathieson et al. 2018		15-30 yr		0.710338	NL	HV		
LV	LV 19	Early-Middle Neo	5984-5752	Boric 2011	F	Young or middle-aged adult				K1b		Hofmanova 2017
LV	LV 20	Early-Middle Neo			F	Adult Size (>15-?)	31	0,71001	NL	U5		Hofmanova 2017
LV	LV 21	Early Meso				Adult Size (>15-?)	47	0,70950	L	X2		Hofmanova 2017
LV	LV 22	Late Meso	7580-7190	Boric 2011	M?	Adult Size (>15-?)	37	0,70948	L			
LV	LV 23	Trans.-Early Neo				Adult Size (>15-?)						
LV	LV 26	Trans.-Early Neo	6025-5890	Bonsall et al. 2015	M	Young adult	22	0,70995	NL	H		Hofmanova 2017
LV	LV 27	Trans.-Early Neo								U5		Hofmanova 2017
LV	LV 27a	Trans.-Early Neo			F?	Middle-aged or old adult	15	0,71094	NL			
LV	LV 27b	Trans.-Early Neo				Adult Size (>15-?)	32	0,70912	L	N1		Hofmanova 2017
LV	LV 27c	Trans.-Early Neo				10-12 yr						
LV	LV 27d	Trans.-Early Neo				Old Adult				U5		Hofmanova 2017
LV	LV 28	Trans.-Early Neo			M	Adult Size (>15-?)	43	0,70946	L			
LV	LV 31a	Trans.-Early Neo	6361-5902	Boric 2011		Adult Size (>15-?)	35	0,70899	L			
LV	LV 32a	Early-Middle Neo	6076-5731	Boric 2011	F	Old adult	35	0,71027	NL	H+1		Hofmanova 2017
LV	LV 32b	Early-Middle Neo	6080-5720	Boric 2011	F?	Middle-aged or old adult						
LV	LV 32c	Early-Middle Neo				Adult Size (>15-?)						
LV	LV 35	Early-Middle Neo	5748-5475	Boric 2011	M?	8-13 yr				H3v		Hofmanova 2017
LV	LV 37	Early-Middle Neo				Young adult	I	0,70918	L			
LV	LV 39	Early-Middle Neo			F?	Adult Size (>15-?)	33	0,70907	L	J2		Hofmanova 2017
LV	LV 41	Trans.-Early Neo				Adult Size (>15-?)						
LV	LV 42a	Early-Middle Neo			M?	Adult Size (>15-?)						
LV	LV 42b	Early-Middle Neo			F	Young or middle-aged adult						
LV	LV 43	Early-Middle Neo				9-18 yr	25	0,70915	L	K1b		Hofmanova 2017
LV	LV 44	Trans.-Early Neo	6232-5810	Boric 2011		Adult Size (>15-?)						

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86* *	Local/Non Local	Mt Haplo	Y Haplo	Reference
LV	LV 45a	Trans.-Early Neo				Young adult						
LV	LV 45b	Trans.-Early Neo	6355-6015	Bonsall et al. 2015	M	Middle-aged or old adult						
LV	LV 47	Trans.-Early Neo			F	Adult Size (>15-?)	43	0,70907	L			
LV	LV 48	Trans.-Early Neo				Young adult	37	0,70956	L			
LV	LV 50	Early Meso			M	Middle-aged or old adult	33	0,70925	L			
LV	LV 51	Early-Middle Neo				Adult Size (>15-?)						
LV	LV 52	Early-Middle Neo				Adult Size (>15-?)						
LV	LV 54b	Trans.-Early Neo				Adult Size (>15-?)						
LV	LV 54c	Trans.-Early Neo	6215-5995	Bonsall et al. 2015	F	Middle-aged or old adult						
LV	LV 54d	Trans.-Early Neo	6340-6015	Bonsall et al. 2015	F	Middle-aged or old adult	32	0,70899	L	K1b		Hofmanova 2017
LV	LV 54e	Trans.-Early Neo	6210-5930	Bonsall et al. 2015	F	Young adult	45?	0,71026	NL	J2		Hofmanova 2017
LV	LV 55a	Early-Middle Neo				Adult Size (>15-?)						
LV	LV 56	Early-Middle Neo				6-9.5 yr						
LV	LV 57	Early-Middle Neo				>12 yr				U5		Hofmanova 2017
LV	LV 6	Early-Middle Neo				15-18 yr				N		Hofmanova 2017
LV	LV 60	Early Meso	9175-8635	Bonsall et al. 2015	M	Middle-aged adult	21	0,70912	L			
LV	LV 61	Trans.-Early Neo	6225-5915	Bonsall et al. 2015		4-7 yr				H40		
LV	LV 63	Trans.-Early Neo			F	37-43 wk						
LV	LV 64	Early Meso			M	Middle-aged adult	11	0,70926	L			
LV	LV 66	Early-Middle Neo				Young adult	21	0,70677	NL	N1		Hofmanova 2017
LV	LV 67	Early Meso				14-18 yr						
LV	LV 68	Early Meso			F	Middle-aged or old adult				U4		Hofmanova 2017
LV	LV 69	Early Meso	7940-7590	Bonsall et al. 2015	M	Middle-aged adult						
LV	LV 7/Ia	Trans.-Early Neo	6230-5985	Bonsall et al. 2015	M	Old adult	36	0,70998	NL			
LV	LV 7/II-b	Early-Middle Neo	6080-5746	Boric 2011		Old adult	26	0,71084	NL			
LV	LV 70	Trans.-Early Neo				Adult Size (>15-?)						
LV	LV 71	Early-Middle Neo				4-6 yr						
LV	LV 72	Early-Middle Neo				1.5-3 yr						
LV	LV 73	Early-Middle Neo	6005-5845	Boric 2011	M	Middle-aged adult	34	0,70877	L	H3v	G2	Hofmanova 2017
LV	LV 73(1)	Early-Middle Neo				Adult Size (>15-?)	C	0,70974	L			
LV	LV 74	Early-Middle Neo			M?	Adult Size (>15-?)	33	0,70921	L	U5		Hofmanova 2017
LV	LV 75	Trans.-Early Neo			F?	Old adult	23	0,70915	L			
LV	LV 79a	Trans.-Early Neo	6020-5890	Bonsall et al. 2015	M?	Old adult	33	0,70922	L			

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
LV	LV 79b	Trans.-Early Neo				Young Adult				U5		Hofmanova 2017
LV	LV 79c	Trans.-Early Neo				Adult Size (>15-?)				U5		Hofmanova 2017
LV	LV 8	Early-Middle Neo	5990-5790	Bonsall et al. 2015	F	Middle-aged adult	43	0,71031	NL	T1		Hofmanova 2017
LV	LV 82	Trans.-Early Neo				Adult Size (>15-?)				T2	C2	Hofmanova 2017
LV	LV 83a	Early-Middle Neo				Adult Size (>15-?)	44	0,70869	L			
LV	LV 83b	Early-Middle Neo				44-48.5 wk						
LV	LV 84	Trans.-Early Neo				4-6 yr						
LV	LV 85b	Trans.-Early Neo				3-4 yr						
LV	LV 86	Trans.-Early Neo				Adult size				J		Hofmanova 2017
LV	LV 87	Trans.-Early Neo				4.5-7.5 yr						
LV	LV 87(1)	Trans.-Early Neo				Adult Size (>15-?)	45	0,70937	L	U5		Hofmanova 2017
LV	LV 88	Early-Middle Neo	5984-5644	Boric 2011	F	Middle-aged adult	22	0,71079	NL			
LV	LV 89a	Early-Middle Neo	6060-5780	Bonsall et al. 2015		Adult Size (>15-?)				U5		Hofmanova 2017
LV	LV 89b	Trans.-Early Neo				1-2 yr						
LV	LV 9	Early-Middle Neo	5980-5740	Bonsall et al. 2015		Adult Size (>15-?)						
LV	LV 90	Trans.-Early Neo			M	Adult Size (>15-?)						
LV	LV 91	Trans.-Early Neo				Adult Size (>15-?)				U5	I2	Hofmanova 2017
LV	LV 92	Trans.-Early Neo				1-3.5 yr						
LV	LV 93	Trans.-Early Neo			F	Middle-aged or old adult				H		Hofmanova 2017
LV	LV 94	Trans.-Early Neo	6068-5811	Boric 2011	M	37-43 wk						
LV	LV 95	Trans.-Early Neo			F	37.5-43 wk						
LV	LV 96	Trans.-Early Neo			M	37-43 wk						
LV	LV 98a	Trans.-Early Neo			M	34-39 wk						
LV	LV 99	Trans.-Early Neo				8-15 yr						
OC	OC 1	Late Meso	7580-7190	Mathieson et al. 2018		Adult Size (>15-?)				H13	R1	Mathieson et al. 2018
OC	OC 24	Late Meso				Adult Size (>15-?)				K1c	R1	Mathieson et al. 2018
OC	OC 32	Late Meso	7021-6473	Mathieson et al. 2018		Adult Size (>15-?)				K1		Mathieson et al. 2018
OC	OC 2	Meso				Adult Size (>15-?)				H13		Hofmanova 2017
OC	OC 47a	Meso				Adult Size (>15-?)				H13		Hofmanova 2017
OC	OC 57	Meso				Adult Size (>15-?)				H4a		Hofmanova 2017
OC	OC 58	Meso				Adult Size (>15-?)				U3b		Hofmanova 2017
P	P 1	Late Meso				Adult Size (>15-?)	47	0,70977	L			
P	P 11	Early Meso	8616-8296	Boric 2011		4.5-7.5 yr						

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
P	P 12	Early Meso	8753-8351	Boric 2011	M	Young adult	17	0,70907	L	U5	I2	Mathieson et al. 2018
P	P 13	Early Meso			F?	Young adult						
P	P 14	Early Meso	8703-8246	Boric 2011	F	Old adult	P?	0,70907	L	U5	R1	Mathieson et al. 2018
P	P 15	Early Meso	8237-7761	Boric 2011	F	Middle-aged or old adult	28	0,70923	L			
P	P 16	Early Meso	8200-7800	Boric 2011	F?	Young adult	34	0,70917	L			
P	P 16a	Early Meso			F	Old adult	16	0,70873	L	K1c		Mathieson et al. 2018
P	P 17	Early Meso			F?	Middle-aged or old adult	47	0,70914	L	U5		Mathieson et al. 2018
P	P 17(1)	Early Meso				Adult Size (>15-?)	P?	0,70896	L			
P	P 18	Early Meso			F?	Middle-aged or old adult	48	0,70896	L			
P	P 18b	Early Meso			F	Middle-aged or old adult	48	0,70900	L	K1f		Mathieson et al. 2018
P	P 19a	Early Meso			F	Old adult						
P	P 1a	Late Meso	6470-6230	Boric 2011	F	Adult Size (>15-?)						
P	P 2	Late Meso	6648-6470	Boric 2011	M	Old adult	36	0,70910	L			
P	P 20	Early Meso			F	Adult Size (>15-?)	17	0,70902	L			
P	P 21	Early Meso	8810-8352	Boric 2011	F	Middle-aged or old adult	36	0,70899	L			
P	P 22	Early Meso	9140-8570	Mathieson et al. 2018		Adult Size (>15-?)	26	0,70905	L	U5	R1	Mathieson et al. 2018
P	P 23	Early Meso				3-6 yr						
P	P 23(1)	Early Meso				Adult Size (>15-?)	26	0,70896	L			
P	P 24	Early Meso	9297-9194	Mathieson et al. 2018	F	Middle-aged or old adult	36	0,70885	L			
P	P 25	Early Meso			F	Adult Size (>15-?)	38	0,70903	L	U5		Mathieson et al. 2018
P	P 25(1)	Early Meso				Adult Size (>15-?)	16/26	0,70899	L			
P	P 26a	Early Meso	8805-8355	Mathieson et al. 2018	F	0.5-1 yr						
P	P 27	Late Meso	7306-6590	Boric 2011		9.5-14.5 yr	M	0,70906	L			
P	P 28	Early Meso				Adult Size (>15-?)	48	0,70896	L			
P	P 30	Early Meso			F	Middle-aged or old adult	47	0,70999	NL	I3		Mathieson et al. 2018
P	P 4	Trans.-Early Neo	6061-5841	Boric 2011	M	Middle-aged or old adult	48	0,70933	L	K1a	R1	Mathieson et al. 2018
P	P 5	Trans.-Early Neo	6224-5878	Boric 2011	F	Middle-aged adult	M?	0,70916	L	U5		Mathieson et al. 2018
P	P 5a	Trans.-Early Neo				Adult Size (>15-?)	16	0,70921	L			
P	P 6	Early Meso			F	Adult Size (>15-?)	M?	0,70949	L	U4		Mathieson et al. 2018
P	P 6a	Early Meso			F	Old adult	38	0,70899	L			
P	P 7	Early Meso	8208-7613	Boric 2011	F	Old adult						
P	P 9	Early Meso	9221-8548	Boric 2011		Adult Size (>15-?)	46	0,70895	L	U5	R1	Mathieson et al. 2018
P	P26	Early Meso				Old Adult	M	0,70909	L	U5		Hofmanova 2017

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
P		Early Meso				Adult Size (>15-?)						
SC	M12	Late Meso				Adult Size (>15-?)	M	0,70928	L	U5	R1	Mathieson et al. 2018
SC	M26	Late Meso				Adult Size (>15-?)	M	0,70978	L			
SC	M35	Late Meso				Adult Size (>15-?)	36/46	0,70944	L			
SC	M39	Late Meso				Adult Size (>15-?)	M	0,70907	L			
SC	M42	Late Meso				Adult Size (>15-?)						
SC	M43	Late Meso	7451-6698	Boric 2011		Adult Size (>15-?)	M	0,70944	L	U5		Mathieson et al. 2018
SC	M46	Late Meso	7340-6640	Mathieson et al. 2018		Adult Size (>15-?)						
SC	M46/1	Late Meso	7340-6640	Mathieson et al. 2018		Adult Size (>15-?)				U5	I2	Mathieson et al. 2018
SC	M47	Late Meso				Adult Size (>15-?)						
SC	M48	Late Meso				Adult Size (>15-?)						
SC	M49	Late Meso				Adult Size (>15-?)						
SC	M50	Late Meso	7060-6570	Mathieson et al. 2018		Adult Size (>15-?)				K1	R	Mathieson et al. 2018
SC	M50	Late Meso	7060-6570	Mathieson et al. 2018		Adult Size (>15-?)				K1		Mathieson et al. 2018
SC	M55	Late Meso				Adult Size (>15-?)						
SC	NN1	Late Meso				Adult Size (>15-?)	26/27	0,70915	L			
SC	NN2	Late Meso				Adult Size (>15-?)	M	0,70978	L			
SC	NN3	Late Meso				Adult Size (>15-?)	M	0,70923	L	U5		Mathieson et al. 2018
SC	NN4	Late Meso				Adult Size (>15-?)	M	0,70915	L			
Vel	Veles 1	Early Neo	6020-5845	Bonsall et al. 2015		Child						
Vel	Veles 2A/2E	Early Neo	6210-5990	Bonsall et al. 2015	F?	Adult Size (>15-?)						
Vel	Veles 2B/2F	Early Neo	6215-6020	Bonsall et al. 2015	F?	Adult Size (>15-?)						
Vel	Veles 2C	Early Neo	6080-5920	Bonsall et al. 2015		Child						
Vel	Veles 2D	Early Neo	6205-5985	Bonsall et al. 2015	F?	Adult Size (>15-?)						
Vel	Veles 2G	Early Neo	6205-5935	Bonsall et al. 2015		Child						
Vel	Veles 2G-1	Late Meso	7530-7185	Bonsall et al. 2015		Perinate?						
Vel	Veles 1G/3	Early Meso	9755-9275	Mathieson et al. 2018		Adult Size (>15-?)				K1c		Mathieson et al. 2018
Vla	H232	Late Meso	6636-6476	Mathieson et al. 2018		Adult Size (>15-?)				U5		Mathieson et al. 2018
Vla	H267	Late Meso	6615-6400	Mathieson et al. 2018		Adult Size (>15-?)				U5		Mathieson et al. 2018
Vla	H317	Late Meso	6635-6375	Mathieson et al. 2018		Adult Size (>15-?)				U5		Mathieson et al. 2018
Vla	H327	Late Meso	6645-6465	Mathieson et al. 2018		Adult Size (>15-?)				U5		
Vla	H53	Early-Middle Neo	6006-5838	Mathieson et al. 2018		Adult Size (>15-?)				U5		Mathieson et al. 2018
Vla	U21	Early-Middle Neo	5995-5710	Mathieson et al. 2018		Child				U4	I2	Mathieson et al. 2018

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
Vla	U297	Late Meso?				1-2 yr						
Vla	U62	Early-Middle Neo	6000-5725	Mathieson et al. 2018		perinate				U4	I2	Mathieson et al. 2018
Vla	U64	Late Meso	6570-6255	Mathieson et al. 2018		Adult Size (>15-?)				U4	I2	Mathieson et al. 2018
Vla	VL 10	Late Meso				35-40 wk						
Vla	VL 11a	Late Meso			M	Adult Size (>15-?)						
Vla	VL 12a	Late Meso				>33 wk						
Vla	VL 12b	Late Meso				48-53 wk						
Vla	VL 13	Late Meso				Adult Size (>15-?)	28	0,70910	L	U5		Hofmanova 2017
Vla	VL 14	Late Meso			F	Old adult	16	0,70910	L			
Vla	VL 15	Late Meso			F	Middle-aged or old adult						
Vla	VL 16	Late Meso			M	Old adult	28	0,70937	L	U5	R1	Hofmanova 2017
Vla	VL 17	Early Meso	8286-7749	Boric 2011	F	Young adult	37	0,70893	L	U4	I	Mathieson et al. 2018
Vla	VL 18a	Late Meso			M	Middle-aged or old adult				U5	IJK	Hofmanova 2017
Vla	VL 18c	Late Meso				5.5-8.5 yr						
Vla	VL 18c	Late Meso				5.5-8.5 yr						
Vla	VL 18c(2)	Late Meso				7-9.5 yr						
Vla	VL 19	Late Meso				34.5-39 wk						
Vla	VL 19a	Late Meso				Adult Size (>15-?)	15?	0,70902	L			
Vla	VL 2	Late Meso				Middle-aged or old adult	14?	0,70911	L	X2		Hofmanova 2017
Vla	VL 21	Late Meso				48-52 wk						
Vla	VL 21(1)	Late Meso				48-52 wk						
Vla	VL 22	Late Meso				Adult Size (>15-?)						
Vla	VL 23	Late Meso				Middle-aged or old adult	43	0,70891	L			
Vla	VL 24	Late Meso	6647-6625	Boric 2011	F	Young adult				K1f	R-R1	Hofmanova 2017
Vla	VL 25	Late Meso	7026-6481	Boric 2011		Middle-aged or old adult	34	0,70931	L			
Vla	VL 26	Late Meso			M	Middle-aged adult	2,0	0,70956	L			
Vla	VL 27	Late Meso			F	Middle-aged adult	38	0,70914	L			
Vla	VL 28	Late Meso				Middle-aged adult	42	0,70909	L			
Vla	VL 29	Late Meso			F	Young adult	32	0,70895	L			
Vla	VL 30	Late Meso				Adult Size (>15-?)	35	0,70987	NL	U5		Hofmanova 2017
Vla	VL 31	Late Meso	6823-6436	Boric 2011	M	18-20 yr	26	0,70904	L	U5		Hofmanova 2017
Vla	VL 32	Late Meso			F	Middle-aged adult	17	0,71013	NL			
Vla	VL 34	Late Meso				Adult Size (>15-?)	48	0,70927	L			

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
Vla	VL 35a	Late Meso				35-42 wk						
Vla	VL 36	Late Meso			F?	Young or middle-aged adult						
Vla	VL 36(1)	Late Meso				35-47 wk						
Vla	VL 37	Late Meso				Middle-aged or old adult						
Vla	VL 38	Late Meso			F	Middle-aged adult	13	0,70910	L			
Vla	VL 40	Late Meso			F	Middle-aged or old adult	33	0,70917	L			
Vla	VL 41	Late Meso			M	Old adult				K1f	R1	Hofmanova 2017
Vla	VL 42(1)	Late Meso				37.5-42 wk						
Vla	VL 43	Late Meso			M	Old adult	42	0,70911	L			
Vla	VL 44	Late Meso			M	Old adult						
Vla	VL 45	Late Meso	6654-6411	Boric 2011	F?	Middle-aged or old adult	38	0,70902	L	K1c	I2	Mathieson et al. 2018
Vla	VL 46	Late Meso			F	Middle-aged or old adult						
Vla	VL 47	Late Meso				Adult Size (>15-?)	42	0,70942	L	U5	IJ-I2	Hofmanova 2017
Vla	VL 48	Late Meso	7024-6430	Boric 2011	F	Old adult	16	0,70936	L			
Vla	VL 49	Late Meso			F?	Adult Size (>15-?)	33	0,71016	NL			
Vla	VL 49(1)	Late Meso				Middle-aged or old adult				U5		Hofmanova 2017
Vla	VL 4a	Late Meso			M	15-18 yr	38	0,70907	L			
Vla	VL 4b	Late Meso				Adult Size (>15-?)	I?	0,70929	L			
Vla	VL 4b(1)	Late Meso				41-45 wk						
Vla	VL 5	Late Meso				9-13 yr						
Vla	VL 50	Late Meso			M?	Middle-aged or old adult						
Vla	VL 50(1)	Late Meso				34-38 wk						
Vla	VL 50a	Late Meso				Middle-aged or old adult						
Vla	VL 50a(1)	Late Meso				36.5-42 wk						
Vla	VL 50b	Late Meso			M	Old adult						
Vla	VL 51	Late Meso	7572-7082	Boric 2011		7.5-10.5 yr	43	0,70937	L			
Vla	VL 51a	Late Meso	7572-7082	Boric 2011	F	Middle-aged or old adult	43	0,70937	L			
Vla	VL 51b	Late Meso				7.5-11.5 yr				U8		Hofmanova 2017
Vla	VL 52	Late Meso			F	Middle-aged or old adult				U8		Hofmanova 2017
Vla	VL 53	Late Meso?				5-8 yr						
Vla	VL 54	Late Meso	7032-6401	Boric 2011	M	7.5-10.5 yr						
Vla	VL 55	Late Meso			F	Middle-aged or old adult	33	0,70940	L			
Vla	VL 55(2)	Late Meso				37-42 wk						

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
Vla	VL 58	Late Meso				13-16 yr						
Vla	VL 58b	Late Meso				37-41 wk						
Vla	VL 59	Late Meso				33-40 wk						
Vla	VL 6	Late Meso	6600-6235	Boric 2011	M	Middle-aged adult	36	0,70892	L	U5	I	Mathieson et al. 2018
Vla	VL 60	Late Meso			M	Old adult	33	0,70899	L			
Vla	VL 60(1)	Late Meso				37-41 wk						
Vla	VL 61	Late Meso				38-44 wk						
Vla	VL 62	Late Meso				36-42 wk						
Vla	VL 63	Late Meso			M	Middle-aged or old adult						
Vla	VL 64a	Late Meso				7-12 yr						
Vla	VL 64b	Late Meso				7-12 yr						
Vla	VL 65a	Late Meso			M?	Adult Size (>15-?)	23	0,70904	L			
Vla	VL 66b	Late Meso				31-35 wk						
Vla	VL 67	Late Meso			F	Middle-aged adult						
Vla	VL 67(1)	Late Meso				36-40 wk						
Vla	VL 69	Late Meso				Middle-aged or old adult	27	0,70925	L			
Vla	VL 69a	Late Meso			M	Adult size (>15-?)	41	0.709068	L	U5		Hofmanova 2017
Vla	VL 6a	Late Meso	6600-6235	Boric 2011		36-40 wk						
Vla	VL 7	Late Meso				14-18 yr						
Vla	VL 70	Late Meso				Middle-aged or old adult	17	0,70914	L			
Vla	VL 71	Late Meso			F	Young adult	43	0,70925	L			
Vla	VL 72	Early Meso	9946-8843	Boric 2011	F	Middle-aged adult						
Vla	VL 74	Late Meso				Old adult	28	0,70913	L	U5		Hofmanova 2017
Vla	VL 78	Late Meso			M	Middle-aged or old adult	34	0,70919	L			
Vla	VL 78a	Late Meso			M	Middle-aged or old adult	14	0,70907	L	U4		Hofmanova 2017
Vla	VL 79	Late Meso			F	Old adult	16	0,70891	L			
Vla	VL 80	Late Meso			F	Adult Size (>15-?)						
Vla	VL 80a	Late Meso			F	Young or middle-aged adult	26	0,70900	L	U5		Mathieson et al. 2018
Vla	VL 81	Late Meso			F	Adult Size (>15-?)						
Vla	VL 82(1)	Late Meso				Middle-aged or old adult	34	0,70923	L			
Vla	VL 82(2)	Late Meso			F	Adult Size (>15-?)	35	0,70903	L			
Vla	VL 82(3)	Late Meso				Adult Size (>15-?)	42	0,70905	L			
Vla	VL 83	Late Meso	7024-6430	Boric 2011	F	Old adult	34	0,70952	L			

							Strontium analyses			DNA Anlyses		
Site	Curated n°	Period	Datation* (cal. BC)	Reference	Sex	Age	Anatomical part	Sr87/Sr86 **	Local/Non Local	Mt Haplo	Y Haplo	Reference
Vla	VL 84(1)	Late Meso				30-35 wk						
Vla	VL 9	Late Meso			F	Old adult	36	0,70955	L	U5		Hofmanova 2017
Vla	U 69	Trans.-Early Neo		Mathieson et al. 2018		Perinate				U4	I2	

A: Ajmana; CT: Cuina Turcului; HV: Hajdučka Vodenica; I: Icoana; LV: Lepenski Vir; P: Padina; SC: Schela Cladovei; Vel: Velesnica; Vla: Vlasac.

* AMS ^{14}C ages corrected for freshwater reservoir effect and calibrated (95.4% probability), from Borić 2011, Bonsall et al. 2015 and Mathieson et al. 2018 (method for freshwater reservoir effect correction in the respective references)

** Reference for radiogenic strontium analyses (^{87}Sr/^{86}Sr): Borić and Price 2013

[1.] Individuals with strontium radiogenic information but no other stable isotope values were also included in this table

APPENDIX B.II. Stable isotope values for adult human individuals included in this study*

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Curated n°	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extracted weight	Volume CO2
A	AJ 6	Cranium	-20,0	10,5				Boric 2011	Cranium	8,6	0,3			This study	48	-13,0	624	592
A	AJ 7	Cranium	-20,0	10,0				Boric 2011	Cranium	8,5	0,2			This study	48	-13,3	612	545
A	AJ 11	Rib	-20,0	10,6	39,0	14,1	3,2	This study	Rib	7,9	0,2	564,6	175,0	This study	48	-12,7	631	572
A	AJ 5	Rib	-20,3	9,6	31,8	11,5	3,2	This study	Rib	8,1	0,2	448,1	138,4	This study				
A	AJ 8a	Rib	-19,7	10,5	36,1	13,1	3,2	This study	Rib	8,1	0,2	535,8	165,9	This study				
A	AJ 9	Rib	-19,8	10,5	39,1	14,4	3,1	This study	Rib	8,0	0,2	429,3	135,9	This study	48	-12,6	677	357
A	AJ 3														Molar	-13,0	597	633
CT	1	Bone	-19,4	15,2			3,3	Bonsall et al. 2015										
CT	2	Bone	-19,3	15,2			3,3	Bonsall et al. 2015										
HV	HV 22	Bone	-18,7	16,5	40,3	14,6	3,2	Nehlich et al. 2010	Bone	10,3	0,2	536,0	166,4	Nehlich et al. 2010				
HV	HV 23-25	Bone	-19,6	15,1	39,5	13,8	3,3	Nehlich et al. 2010	Bone	10,1	0,2	525,4	157,3	Nehlich et al. 2010				
HV	HV 8	Bone	-19,3	15,6	45,0	15,8	3,3	Nehlich et al. 2010		8,8	0,2	598,5	180,1	Nehlich et al. 2010				
HV	HV 13	Cranium	-20,3	15,8				Boric and Price 2013	Cranium	14,2	0,2			This study	38	-14,7	609	418
HV	HV 29	Bone	-20,0	16,0				Boric and Price 2013	Rib	12,4	0,2			This study	38	-14,2	567	457
HV	HV 30	Bone	-20,4	14,2				Boric and Price 2013	Rib	12,6	0,2			This study				
HV	HV 11	Long Bone	-19,4	14,9	38,5	14,0	3,2	This study	Long Bone	9,6	0,2	473,6	147,1	This study				
HV	HV 15 S.G.	Rib	-19,5	15,9	38,9	14,1	3,2	This study	Rib	11,8	0,2	562,8	175,4	This study				
HV	HV 16	Long Bone	-19,1	16,5	36,3	13,0	3,2	This study	Long Bone	13,2	0,2	531,3	163,5	This study				
HV	HV 17-20(1)	Bone	-18,0	16,6				Boric and Price 2013										
HV	?	Bone	-19,7	15,5				Boric and Price 2013										
I	M1	Bone	-19,3	16,1			3,2	Bonsall 2015										
I	M2	Bone	-19,5	15,9			3,5	Bonsall 2015										
LV	LV 100	Bone	-18,7	13,6	46,0	15,6	3,4	Nehlich et al. 2010	Bone	8,9	0,2	611,8	177,8	Nehlich et al. 2010				
LV	LV 104	Bone	-19,5	16,0	45,5	16,4	3,2	Nehlich et al. 2010	Bone	10,9	0,2	605,2	187,0	Nehlich et al. 2010				
LV	LV 13	Bone	-19,0	14,8	40,2	14,5	3,2	Nehlich et al. 2010	Bone		0,2	534,7	165,3	Nehlich et al. 2010				
LV	LV 45a	Bone	-18,3	15,3	35,7	12,9	3,2	Nehlich et al. 2010	Bone	10,6	0,2	474,8	147,1	Nehlich et al. 2010				
LV	LV 67	Bone	-19,4	13,8	47,6	16,4	3,4	Nehlich et al. 2010	Bone	4,4	0,2	633,1	187,0	Nehlich et al. 2010				
LV	LV 68	Bone	-19,7	14,6	45,0	15,6	3,4	Nehlich et al. 2010		6,8	0,3	399,0	118,6	Nehlich et al. 2010				
LV	LV 74	Bone	-19,5	14,4	45,2	15,7	3,4	Nehlich et al. 2010	Bone	5,5	0,2	601,2	179,0	Nehlich et al. 2010				
LV	LV 44	Bone	-18,9	15,3				Bonsall et al. 1997	Metatarsal	9,7	0,2			This study				
LV	LV 51	Bone	-19,1	14,0				Bonsall et al. 1997	Phalanx	8,8	0,2			This study				
LV	LV 66	Bone	-19,3	14,9				Bonsall et al. 1997	Rib	6,4	0,2			This study	27	-13,5	583	824
LV	LV 8	Bone	-20,0	9,4				Bonsall et al. 1997	Metacarpal	5,5	0,2			This study	18	-13,1	648	892
LV	LV 88	Bone	-20,2	10,9				Bonsall et al. 1997	Rib	7,6	0,2			This study	38	-13,7	644	631
LV	LV 79a	Scapula	-18,5	15,8				Boric and Price 2013	Cranium	12,6	0,2			This study				
LV	LV 19	Bone	-19,0	15,5	42,5	17,0	2,9	Boric et al. 2004	Rib	8,3	0,2	667,1	227,9	This study				

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Curated n°	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extracted weight	Volume CO2
LV	LV 26	Bone	-19,7	10,6	24,6	8,2	3,5	Boric et al. 2004	Rib	8,8	0,2	345,0	98,8	This study				
LV	LV 32b	Bone	-18,8	12,6	35,4	14,4	2,9	Boric et al. 2004	Rib	10,9	0,2	566,2	198,1	This study				
LV	LV 41	Bone	-18,8	14,4	45,9	18,0	3,0	Boric et al. 2004	Long Bone	13,9	0,2	747,6	250,6	This study				
LV	LV 45b	Bone	-18,2	16,8	37,6	11,6	3,8	Boric et al. 2004	Rib	14,8	0,2	614,1	162,4	This study				
LV	LV 54c	Bone	-20,2	14,1	43,2	14,6	3,4	Boric et al. 2004	Rib	9,5	0,2	619,2	179,9	This study				
LV	LV 54d	Bone	-19,9	13,4	29,2	10,8	3,2	Boric et al. 2004	Rib	13,8	0,2	415,2	130,8	This study	18	-13,8	633	933
LV	LV 54e	Bone	-19,7	13,9	43,1	13,8	3,4	Boric et al. 2004	Rib	10,3	0,2	628,5	172,4	This study	48	-13,0	634	831
LV	LV 60	Bone	-19,0	15,3	29,7	9,6	3,6	Boric et al. 2004	Rib	8,5	0,2	378,2	104,5	This study	28	-15,1	600	921
LV	LV 69	Bone	-19,4	14,4	32,4	11,8	3,2	Boric et al. 2004	Rib	8,5	0,2	455,3	141,5	This study	28	-15,1	613	970
LV	LV 7/Ia	Bone	-19,7	11,5	21,1	7,4	3,3	Boric et al. 2004	Rib	14,8	0,2	303,5	99,6	This study	28	-14,3	625	948
LV	LV 7/II-b	Bone	-19,8	15,1	22,8	9,6	3,3	Boric et al. 2004	Cranium	14,5	0,2	357,2	129,0	This study				
LV	LV 122	Cranium	-20,2	10,3	41,5	15,3	3,1	This study	Cranium	6,2	0,2	572,5	181,4	This study	18	-13,3	612	743
LV	LV 14	Long Bone	-19,2	15,4	36,9	13,4	3,2	This study	Long Bone	12,1	0,2	536,1	166,5	This study	48	-14,6	593	819
LV	LV 20	Rib	-19,6	14,6	38,0	13,8	3,2	This study	Rib	6,5	0,2	526,0	164,1	This study	48	-14,6	593	865
LV	LV 27a	Rib	-18,8	16,0	37,8	13,8	3,2	This study	Rib	13,4	0,2	522,8	164,1	This study	18	-15,7	628	924
LV	LV 27b	Femur	-19,6	13,3	38,4	13,7	3,2	This study	Femur	10,6	0,2	502,3	154,2	This study	38	-15,5	619	938
LV	LV 32a	Rib	-19,7	11,8	34,9	12,4	3,3	This study	Rib	7,8	0,2	443,3	134,7	This study	48	-12,7	641	924
LV	LV 37	Mandible	-18,6	16,2	40,3	14,6	3,2	This study	Mandible	13,6	0,2	551,6	171,2	This study	28	-13,5	626	904
LV	LV 48	Temporal	-19,5	12,9	39,9	14,4	3,2	This study	Temporal	9,8	0,2	536,0	166,2	This study	48	-13,6	594	919
LV	LV 52	Rib	-19,0	13,9	38,3	14,0	3,2	This study	Rib	-3,1	0,2	629,3	197,4	This study				
LV	LV 57	Mandible	-19,1	12,7	40,9	15,0	3,2	This study	Mandible	8,9	0,2	566,7	178,4	This study	38	-15,1	623	916
LV	LV 73	Rib	-19,2	14,4	39,3	14,5	3,2	This study	Rib	10,6	0,2	621,1	195,5	This study				
LV	LV 87(1)	Rib	-18,9	15,5	40,5	14,9	3,2	This study	Rib	12,8	0,2	560,8	176,5	This study	48	-12,4	645	911
LV	LV 32c	Bone							Ulna	12,3	0,1			This study				
LV	LV 1	Bone	-19,8	11,1				Bonsall et al. 1997										
LV	LV 23	Bone	-18,1	15,7				Bonsall et al. 1997										
LV	LV 55a	Bone	-19,0	12,8				Bonsall et al. 1997										
LV	LV 83a	Bone	-19,0	12,3				Bonsall et al. 1997										
LV	LV 89a	Bone	-18,5	17,0				Bonsall et al. 1997										
LV	LV 9	Bone	-19,6	11,8				Bonsall et al. 1997										
LV	LV 17	Bone	-20,0	10,9				Boric and Price 2013										
LV	LV 22	Bone	-20,0	14,4				Boric and Price 2013										
LV	LV 28	Bone	-20,7	15,2	21,9	8,1	3,7	Boric et al. 2004										
LV	LV 31a	Bone	-18,6	16,2	32,3	11,2	3,9	Boric et al. 2004										
LV	LV 42a	Bone	-20,2	11,7	44,3	15,4	3,4	Boric et al. 2004										
LV	LV 42b	Bone	-18,3	15,3	41,9	16,4	3,0	Boric et al. 2004										

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Curated n°	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extracted weight	Volume CO2
LV	LV 47	Bone	-18,5	15,0	42,1	16,2	3,0	Boric et al. 2004										
LV	LV 50	Bone	-19,5	14,2	35,7	10,9	3,8	Boric et al. 2004										
LV	LV 54b	Bone	-19,8	10,4	37,6	14,7	3,0	Boric et al. 2004										
LV	LV 64	Bone	-19,7	14,9	42,3	16,0	3,1	Boric et al. 2004										
LV	LV 70	Bone	-18,5	16,0	44,8	16,2	3,2	Boric et al. 2004										
LV	LV 90	Bone	-18,3	16,6	41,3	16,0	3,0	Boric et al. 2004										
LV	LV 91	Bone	-20,4	13,0	22,2	8,3	3,1	Boric et al. 2004										
LV	LV 93	Bone	-20,1	12,2	34,2	12,1	3,3	Boric et al. 2004										
LV	LV 82	Rib	-20,1	11,2	39,8	14,5	3,2	This study	Rib	3,9	0,2	529,6	165,8		18	-13,6	598	894
P	?	Bone	-19,7	15,6	42,3	15,0	3,3	Nehlich et al. 2010	Bone	4,1	0,2	589,0	179,0	Nehlich et al. 2010				
P	P 12	Bone	-19,5	14,5	37,3	13,3	3,3	Nehlich et al. 2010	Bone	5,0	0,2	488,0	149,0	Nehlich et al. 2010	18	-14,7	599	938
P	P 16	Bone	-19,6	14,9	45,9	16,4	3,3	Nehlich et al. 2010	Bone	4,9	0,2	610,5	187,0	Nehlich et al. 2010				
P	P 19a	Bone	-20,0	13,7	44,9	15,6	3,4	Nehlich et al. 2010	Bone	5,7	0,2	597,2	177,8	Nehlich et al. 2010				
P	P 15	Hand bone	-19,1	14,4				Boric and Price 2013	Rib	8,2	0,2			This study	18	-14,9	642	741
P	P 18b	Bone	-20,8	12,7				Boric and Price 2013	Mandible	5,0	0,2			This study	Molar	-15,4	577	875
P	P 2	Bone	-20,1	15,4				Boric and Price 2013	Rib	12,7	0,2			This study				
P	P 21	Bone	-18,9	14,1				Boric and Price 2013	Rib	5,9	0,2			This study				
P	P 4	Cranium	-19,1	15,9				Boric and Price 2013	Metacarpal	13,5	0,2			This study	38	-14,3	636	689
P	P 5	Cranium	-19,7	16,6				Boric and Price 2013	Rib	13,8	0,2			This study				
P	P 9	Cranium	-20,7	15,5				Boric and Price 2013	Cranium	6,3	0,2			This study	48	-14,8	604	909
P	P 13	Rib	-20,1	13,5	42,1	15,4	3,2	This study	Rib	5,2	0,2	630,6	197,4	This study				
P	P 14	Long Bone	-20,2	14,2	36,3	11,9	3,5	This study	Long Bone	4,8	0,2	449,6	126,6	This study	18	-14,5	617	763
P	P 17	Rib	-19,8	14,7	40,5	14,8	3,2	This study	Rib	7,0	0,2	601,2	188,0	This study	48	-15,6	629	897
P	P 18	Rib	-20,2	13,1	39,3	14,5	3,2	This study	Rib	5,0	0,2	610,3	192,1	This study				
P	P 1a	Fibula	-20,2	14,4	40,4	14,7	3,2	This study	Fibula	10,3	0,2	579,4	180,7	This study				
P	P 22	Cranium	-19,5	15,5	35,7	12,9	3,2	This study	Cranium	7,0	0,2	565,2	175,6	This study		-15,3	627	946
P	P 6a	Rib	-19,7	14,4	42,5	15,5	3,2	This study	Rib	7,6	0,2	610,8	191,2	This study				
P	P 7	Rib	-19,5	14,7	40,8	14,8	3,2	This study	Rib	7,6	0,2	587,2	182,5	This study				
P	P 30	Bone	-21,5	12,1				Boric and Price 2013										
P	P 5a	Bone	-19,8	14,3				Boric and Price 2013										
P	P 6	Bone	-20,5	14,0				Boric and Price 2013										
SC	M42	Bone	-19,4	15,4				Bonsall et al. 1997										
SC	M43	Bone	-19,6	16,0				Bonsall et al. 1997										
SC	M46	Bone	-19,2	14,9				Bonsall et al. 1997										
SC	M47	Bone	-19,5	15,1				Bonsall et al. 1997										
SC	M48	Bone	-19,5	15,8				Bonsall et al. 1997										

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Curated n°	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extracted weight	Volume CO2
SC	M49	Bone	-19,6	15,4				Bonsall et al. 1997										
SC	M50	Bone	-19,6	15,6				Bonsall et al. 1997										
SC	M55	Bone	-20,0	15,0				Bonsall et al. 1997										
Vel	2A/2E	Bone	-19,4	11,7			3,2	Bonsall et al. 2015										
Vel	2B/2F	Bone	-19,3	10,7			3,2	Bonsall et al. 2015										
Vel	2D	Bone	-19,2	10,6			3,2	Bonsall et al. 2015										
Vla	VL 11a	Bone	-19,5	14,5	45,5	16,7	3,2	Nehlich et al. 2010	Bone	10,0	0,2	605,2	190,4	Nehlich et al. 2010				
Vla	VL 16	Bone	-19,9	15,0	44,5	15,5	3,4	Nehlich et al. 2010	Bone	7,3	0,2	591,9	176,7	Nehlich et al. 2010	48	-15,1	595	733
Vla	VL 17	Bone	-20,0	14,3	44,6	15,8	3,3	Nehlich et al. 2010	Bone	5,8	0,2	593,2	180,1	Nehlich et al. 2010				
Vla	VL 70	Bone	-18,7	15,5	44,3	15,9	3,3	Nehlich et al. 2010	Bone	12,7	0,2	589,2	181,3	Nehlich et al. 2010				
Vla	VL 25	Bone	-17,8	15,2				Bonsall et al. 1997	Rib	11,4	0,2			This study	28	-14,7	595	694
Vla	VL 31	Bone	-18,5	14,9				Bonsall et al. 1997	Rib	13,0	0,2			This study				
Vla	VL 45	Bone	-19,1	15,4				Bonsall et al. 1997	Rib	13,2	0,3			This study	48	-14,3	608	921
Vla	VL 49	Bone	-19,2	14,8				Bonsall et al. 1997	Rib	12,6	0,3			This study	38	-15,0	650	907
Vla	VL 50	Bone	-19,0	15,4				Bonsall et al. 1997	Rib	13,2	0,2			This study	38	-13,9	590	894
Vla	VL 51a	Bone	-19,1	14,4				Bonsall et al. 1997	Rib	9,1	0,2			This study	48	-15,5	637	926
Vla	VL 83	Bone	-19,1	14,6				Bonsall et al. 1997	Rib	13,6	0,3			This study				
Vla	VL 24	Bone	-18,7	14,4	42,9	17,8	2,8	Grupe et al. 2003	Rib	13,3	0,2	709,2	252,2	This study	38	-14,6	628	897
Vla	VL 32	Bone	-20,2	13,2	45,9	15,9	3,4	Grupe et al. 2003	Rib	11,2	0,2	674,8	200,9	This study	27	-16,0	589	462
Vla	VL 48	Bone	-18,4	14,7	37,6	15,6	2,8	Grupe et al. 2003	Rib	12,6	0,2	542,5	193,2	This study	28	-15,4	634	892
Vla	VL 55	Bone	-19,6	15,2	58,7	17,7	3,9	Grupe et al. 2003	Rib	12,9	0,2	911,2	235,8	This study				
Vla	VL 67	Bone	-18,7	13,8	45,8	18,1	3,0	Grupe et al. 2003	Rib	11,6	0,2	735,3	249,6	This study	28	-15,3	626	911
Vla	VL 72	Bone	-19,8	13,5	49,7	16,7	3,5	Grupe et al. 2003	Rib	7,7	0,2	581,8	167,6	This study				
Vla	VL 18a	Rib	-19,4	15,1	37,7	14,0	3,1	This study	Rib	13,2	0,2	588,1	186,7	This study	48	-14,7	644	806
Vla	VL 26	Rib	-17,5	11,0	39,8	14,7	3,1	This study	Rib	4,2	0,2	565,4	178,8	This study	18	-9,2	599	855
Vla	VL 41	Temporal	-19,6	15,1	38,7	13,9	3,2	This study	Temporal	10,5	0,2	577,4	178,1	This study	38	-14,5	594	692
Vla	VL 46	Rib	-19,3	15,5	39,2	14,3	3,2	This study	Rib	13,6	0,2	617,9	193,6	This study	38	-15,0	38	860
Vla	VL 9	Rib	-19,5	14,4	38,4	14,1	3,2	This study	Rib	13,5	0,2	599,1	188,9	This study	18	-15,6	118	299
Vla	VL 14	Bone	-19,4	15,9				Bonsall et al. 1997										
Vla	VL 15	Bone	-18,6	15,9				Bonsall et al. 1997										
Vla	VL 2	Bone	-18,9	13,9				Bonsall et al. 1997										
Vla	VL 22	Bone	-18,6	14,8				Bonsall et al. 1997										
Vla	VL 28	Bone	-19,0	13,8				Bonsall et al. 1997										
Vla	VL 29	Bone	-18,8	15,4				Bonsall et al. 1997										
Vla	VL 37	Bone	-19,1	14,4				Bonsall et al. 1997										
Vla	VL 40	Bone	-19,5	14,8				Bonsall et al. 1997										

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Curated n°	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extracted weight	Volume CO2
Vla	VL 50a	Bone	-19,4	14,8				Bonsall et al. 1997										
Vla	VL 50b	Bone	-19,0	14,6				Bonsall et al. 1997										
Vla	VL 52	Bone	-19,1	14,9				Bonsall et al. 1997										
Vla	VL 56	Bone	-18,5	15,6				Bonsall et al. 1997										
Vla	VL 57	Bone	-19,3	13,9				Bonsall et al. 1997										
Vla	VL 60	Bone	-18,8	15,3				Bonsall et al. 1997										
Vla	VL 23	Bone	-19,3	14,2	48,7	16,7	3,4	Grupe et al. 2003										
Vla	VL 27	Bone	-19,4	14,3	51,6	17,5	3,4	Grupe et al. 2003										
Vla	VL 36	Bone	-19,1	15,0	39,8	13,5	3,4	Grupe et al. 2003										
Vla	VL 38	Bone	-18,8	15,3	36,8	14,9	2,9	Grupe et al. 2003										
Vla	VL 44	Bone	-19,7	13,3	49,0	16,4	3,5	Grupe et al. 2003										
Vla	VL 47	Bone	-19,3	15,0	45,0	15,0	3,5	Grupe et al. 2003										
Vla	VL 4a	Bone	-19,2	15,1	46,6	15,5	3,5	Grupe et al. 2003										
Vla	VL 4b	Bone	-19,1	15,1	48,6	16,3	3,5	Grupe et al. 2003										
Vla	VL 6	Bone	-19,7	15,2	41,1	16,5	2,9	Grupe et al. 2003										
Vla	VL 63	Bone	-19,3	14,3	44,8	17,6	3,0	Grupe et al. 2003										
Vla	VL 65a	Bone	-19,7	14,1	41,2	16,6	2,9	Grupe et al. 2003										
Vla	VL 69	Bone	-19,4	14,4	37,6	15,8	2,8	Grupe et al. 2003										
Vla	VL 7	Bone	-20,3	12,2	40,2	13,9	3,4	Grupe et al. 2003										
Vla	VL 71	Bone	-19,6	14,3	37,2	12,0	3,6	Grupe et al. 2003										
Vla	VL 74	Bone	-19,4	13,1	28,7	16,6	2,0	Grupe et al. 2003										
Vla	VL 78	Bone	-19,3	15,6	45,3	14,8	3,6	Grupe et al. 2003										
Vla	VL 78a	Bone	-18,9	14,5	35,5	14,6	2,6	Grupe et al. 2003										
Vla	VL 79	Bone	-18,6	14,8	36,3	16,0	2,8	Grupe et al. 2003										
Vla	VL 80	Bone	-19,5	13,1	38,6	15,5	2,9	Grupe et al. 2003										
Vla	VL 80a	Bone	-19,5	14,8	36,5	12,0	3,5	Grupe et al. 2003										
Vla	VL 81	Bone	-19,0	13,7	30,1	13,2	2,5	Grupe et al. 2003										
Vla	VL 84	Bone	-19,4	15,0	44,0	16,2	3,2	Grupe et al. 2003										
Vla	VL 19a	Bone													48	-15,1	586	889

A: Ajmana; CT: Cuina Turcului; HV: Hajdučka Vodenica; I: Icoana; LV: Lepenski Vir; P: Padina; SC: Schela Cladovei; Vel: Velesnica; Vla: Vlasac

* The $\delta^{13}C_{enamel}$ value of the child AJ 3 (aged at death ca 9.5-14.5 years old) – the only immature human individual analyzed for this marker – was also included in this table.

APPENDIX B.III. Stable isotope values for immature human individuals included in this study

Site	Curated n°	Age	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical Part	δ34S	S%	C/S	N/S
A	AJ 1	3-6 yr	Mandible	-19,6	11,5	39,4	14,1	3,2	This study	Mandible	8,5	0,2	582,2	178,6
A	AJ 1	3-6 yr	M.1.root	-19,5	12,1	39,8	14,5	3,2	This study					
A	AJ 1	3-6 yr	M.1.crown	-19,3	14,1	40,1	14,8	3,1	This study	M.1.crown	11,5	0,2	525,6	166,1
A	AJ 1	3-6 yr	m1.crown	-19,2	15,8	40,9	15,0	3,2	This study	m1.crown	12,0	0,2	526,1	165,8
A	AJ 10	3-7 yr	Femur	-20,0	10,5	41,6	15,1	3,2	This study	Femur	7,0	0,2	560,6	174,9
A	AJ 12	3-6 yr	Mandible	-20,5	9,4	41,9	15,3	3,2	This study	Mandible	6,5	0,2	655,6	205,2
A	AJ 12	3-6 yr	M.1.crown	-20,7	10,7	35,2	11,8	3,5	This study					
A	Aj 12	3-6 yr	M.1.crown	-19,7	11,4	39,8	14,4	3,2	This study	M.1.crown	7,2	0,2	553,1	171,3
A	Aj 12	3-6 yr	m1.root	-19,4	11,6	38,3	13,8	3,2	This study					
A	AJ 12	3-6 yr	m1.crown	-19,2	13,3	38,9	14,1	3,2	This study	m1.crown	7,4	0,2	483,6	150,4
A	AJ 13	11-14 yr	Rib	-20,1	10,2	40,6	14,9	3,2	This study	Rib	7,5	0,2	560,2	176,8
A	Aj 13	11-14 yr	M.1.root	-20,0	11,1	39,0	14,3	3,2	This study					
A	Aj 13	11-14 yr	M.1.crown	-19,4	13,7	39,8	14,8	3,1	This study	M.1.crown	9,6	0,2	529,7	168,6
A	AJ 13	11-14 yr	m1.crown	-19,0	15,7	39,5	14,6	3,2	This study	m1.crown	10,2	0,2	487,9	153,9
A	AJ 14	4,5-7 yr	Mandible	-20,1	10,5	33,2	11,3	3,4	This study					
A	AJ 14	4,5-7 yr	M.1.root	-19,9	11,1	39,5	14,4	3,2	This study					
A	AJ 14	4,5-7 yr	M.1.crown	-19,4	14,1	40,0	14,7	3,2	This study	M.1.crown	9,7	0,2	553,5	174,4
A	AJ 14	4,5-7 yr	m1.crown	-18,7	15,5	39,6	14,5	3,2	This study	m1.crown	10,9	0,2	501,8	157,3
A	AJ 15	4,5-7 yr	Mandible	-20,6	9,8	38,0	13,3	3,3	This study					
A	AJ 15	4,5-7 yr	M.1.root	-20,3	10,6	41,8	15,4	3,1	This study					
A	AJ 15	4,5-7 yr	M.1.crown	-20,1	11,2	40,8	14,9	3,2	This study	M.1.crown	7,5	0,2	558,1	174,3
A	AJ 15	4,5-7 yr	m1.crown	-19,2	13,1	40,0	14,7	3,2	This study	m1.crown	7,5	0,2	526,4	165,5
A	AJ 16	1,5-4 yr	Femur	-19,7	12,7	30,7	12,1	2,9	This study	Femur	13,5	0,2	463,6	156,9
A	AJ 16	1,5-4 yr	m1.root	-18,7	14,5	39,5	14,2	3,2	This study	m1.root	7,4	0,2	491,6	151,3
A	AJ 16	1,5-4 yr	m1.crown	-18,6	15,3	39,6	14,4	3,2	This study	m1.crown	9,4	0,2	491,8	152,8
A	Aj 3	9,5-14,5 yr	Rib	-19,7	10,9	39,8	14,7	3,1	This study	Rib	8,9	0,3	421,1	133,6
A	AJ 8	3-5 yr	Mandible	-19,5	13,0	35,9	13,0	3,2	This study	Mandible	9,1	0,2	530,5	164,7
A	Aj 8	3-5 yr	m1.root	-19,4	14,3	39,0	14,1	3,2	This study					
A	AJ 8	3-5 yr	m1.crown	-19,0	14,5	40,4	14,7	3,2	This study	m1.crown	10,2	0,2	535,5	167,2
CT	3	Perinate (?)	Bone	-19,1	17,1			3,3	Bonsall et al. 2015					
CT	4	<10 (?)	Bone	-19,4	13,9			3,1	Bonsall et al. 2015					
HV	HV 14	4,5-7 yr	M.1.crown	-19,3	16,2	39,1	14,1	3,2	This study	M.1.crown	12,3	0,2	507,2	156,7
HV	HV 14	4,5-7 yr	Mandible	-19,0	16,3	41,9	14,9	3,3	This study	Ulna	13,1	0,2	592,3	180,5
HV	HV 14	4,5-7 yr	M.1.root	-18,6	17,5	42,3	15,3	3,2	This study					
HV	HV 14	4,5-7 yr	m1.crown	-19,2	18,3	40,0	14,8	3,1	This study	m1.crown	13,6	0,2	443,0	140,4
HV	HV 18	10,5-12,5 yr	Mandible	-19,8	15,8	36,3	13,3	3,2	This study	Mandible	12,1	0,2	501,2	157,6
HV	HV 21	3-6 yr	Mandible	-19,4	15,8	32,2	11,7	3,2	This study	Rib	12,0	0,2	454,9	141,7
HV	HV 21	3-6 yr	M.1.root	-19,4	16,4	36,7	13,4	3,2	This study					
HV	HV 21	3-6 yr	M.1.crown	-19,3	18,2	38,3	14,1	3,2	This study	M.1.crown	11,4	0,2	500,6	157,5
HV	HV 21	3-6 yr	m1.crown	-19,8	18,2	18,0	6,2	3,4	This study	m1.crown	10,3	0,1	386,8	113,7
HV	HV 26-28(3)	7.5-11 yr												
LV	LV 101	37-44 wk	Humerus	-19,0	16,6	30,5	10,8	3,3	This study	Humerus	15,1	0,2	410,5	124,9
LV	LV 102	32-40 wk	Humerus	-20,4	16,7	40,8	14,8	3,2	This study	Humerus	10,3	0,2	602,9	187,5
LV	LV 103	36.5-42 wk	Bone	-18,8	17,7	57,1	90,2	3,4	Boric et al, 2004					
LV	LV 106	38-43 wk	Humerus	-17,8	17,8	38,8	13,9	3,2	This study	Humerus	13,5	0,2	469,1	144,1
LV	LV 107	37-42 wk	Bone	-18,4	16,8	49,1	17,1	3,3	Boric et al, 2004					
LV	LV 108	38-42 wk	Femur	-18,6	17,5	38,5	13,7	3,3	This study	Femur	8,9	0,2	424,1	129,3
LV	LV 109a	37.5-42 wk	Bone	-19,4	16,2	44,3	15,4	3,4	Boric et al, 2004					
LV	LV 11	10,5-17 yr	Bone	-18,6	15,8	45,5	15,8	3,4	Nehlich et al. 2010	Bone	10,8	0,2	605,2	180,1
LV	LV 110	37-42 wk	Bone	-20,2	16,2	45,3	16,0	3,3	Boric et al, 2004					
LV	LV 111	36.5-43 wk	Bone	-20,1	15,4	48,3	16,5	3,4	Boric et al, 2004					
LV	LV 113	36-42 wk	Rib	-20,0	15,3	33,4	12,0	3,2	This study					
LV	LV 116	Perinate	Bone	-19,5	15,3	43,4	15,3	3,3	Boric et al. 2004					
LV	LV 118	32.5-38 wk	Bone	-18,8	15,9	40,8	14,8	3,2	Boric et al, 2004					
LV	LV 120	36-41 wk	Humerus	-18,3	18,4	40,6	14,5	3,2	This study	Humerus	13,3	0,2	490,9	150,3
LV	LV 121	35.5-41 wk	Humerus	-19,7	17,0	35,9	12,9	3,2	This study	Humerus	11,4	0,2	502,6	154,8
LV	LV 125	36-41.5 wk	Bone	-19,3	16,2	61,7	21,6	3,3	Boric et al, 2004					
LV	LV 127	38-43 wk	Bone	-18,7	16,6	33,5	12,3	3,2	Boric et al, 2004					
LV	LV 128	36-43 wk	Humerus	-20,2	16,2	35,1	12,5	3,3	This study	Humerus	9,2	0,2	444,6	135,7
LV	LV 129	36-42 wk	Fibula	-17,8	17,8	36,3	12,9	3,3	This study	Fibula	15,5	0,2	419,8	127,9
LV	LV 27c	10-12 yr	Femur	-18,5	15,6	39,9	14,3	3,2	This study					
LV	LV 35	8-13 yr	Bone	-19,7	11,2				Bonsall et al. 1997					
LV	LV 43	9-18 yr	Rib	-19,2	14,4	39,3	14,5	3,2	This study	Rib	10,8	0,2	591,3	186,2
LV	LV 56	6-9,5 yr	Mandible	-18,6	13,7	43,7	15,8	3,2	This study	Mandible	11,1	0,2	645,8	200,1

Site	Curated n°	Age	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical Part	δ34S	S%	C/S	N/S
LV	LV 56	6-9,5 yr	M.1.root	-18,4	14,3	39,2	14,1	3,2	This study					
LV	LV 56	6-9,5 yr	M.1.crown	-18,6	14,8	40,0	14,5	3,2	This study	M.1.crown	11,8	0,2	535,8	166,0
LV	LV 56	6-9,5 yr	m1.crown	-18,3	16,3	39,4	14,3	3,2	This study	m1.crown	12,1	0,2	441,7	137,3
LV	LV 61	4-7 yr	Mandible	-19,1	16,2	40,2	14,4	3,2	This study	Mandible	12,5	0,2	629,0	193,1
LV	LV 61	4-7 yr	M.1.root	-18,5	16,7	37,5	13,8	3,2	This study					
LV	LV 61	4-7 yr	M.1.crown	-18,7	19,2	36,1	13,2	3,2	This study	M.1.crown	15,1	0,2	521,9	163,9
LV	LV 61	4-7 yr	m1.crown	-18,6	19,6	38,5	14,1	3,2	This study	m1.crown	15,3	0,2	467,2	146,7
LV	LV 63	37-43 wk	Ulna	-18,7	16,7	40,6	14,1	3,3	This study	Ulna	13,9	0,2	490,9	146,1
LV	LV 71	4-6 yr	m1.crown	-19,3	15,6	35,6	12,9	3,2	This study	m1.crown	10,0	0,2	506,8	158,0
LV	LV 71	4-6 yr	Mandible	-19,2	15,9	40,6	14,8	3,2	This study					
LV	LV 71	4-6 yr	M.1.crown	-19,3	16,5	27,9	9,9	3,3	This study	M.1.crown	11,2	0,2	360,3	109,9
LV	LV 71	4-6 yr	canine.root	-18,9	17,3	37,2	13,2	3,3	This study					
LV	LV 72	1,5-3 yr	Mandible	-20,6	11,0	39,0	14,0	3,2	This study	Mandible	6,2	0,2	494,9	152,3
LV	LV 72	1,5-3 yr	M.1.crown	-20,4	12,4	38,5	13,6	3,3	This study	M.1.crown	5,4	0,2	468,1	141,9
LV	LV 83b	44-48.5 wk	Humerus	-19,2	14,6	38,4	13,8	3,2	This study					
LV	LV 84	4-6 yr	Mandible	-18,6	13,3	38,6	14,0	3,2	This study					
LV	LV 84	4-6 yr	M.1.root	-18,4	14,4	39,3	14,0	3,3	This study					
LV	LV 84	4-6 yr	M.1.crown	-18,8	15,7	40,0	14,5	3,2	This study	M.1.crown	11,4	0,2	562,7	174,6
LV	LV 84	4-6 yr	m1.crown	-19,2	16,3	33,7	11,9	3,3	This study	m1.crown	10,7	0,2	433,4	130,9
LV	LV 85b	3-4 yr	Radius	-18,5	14,0	44,2	15,9	3,2	This study	Radius	12,8	0,2	679,9	209,2
LV	LV 87	4,5-7,5 yr	M.1.crown	-19,6	15,8	29,1	9,4	3,2	This study	M.1.crown	11,8	0,2	464,4	128,3
LV	LV 87	4,5-7,5 yr	Mandible	-19,4	15,9	42,6	15,1	3,3	This study					
LV	LV 87	4,5-7,5 yr	M.1.root	-18,7	16,3	43,6	15,7	3,2	This study					
LV	LV 87	4,5-7,5 yr	m1.crown	-19,8	18,6	39,3	14,1	3,2	This study	m1.crown	12,8	0,2	474,7	145,7
LV	LV 89b	1-2 yr	Mandible	-19,2	15,7	37,0	12,7	3,4	This study					
LV	LV 89b	1-2 yr	m1.crown	-20,5	15,7	10,1	3,2	3,7	This study					
LV	LV 92	1-3,5 yr	m1.root	-18,7	17,7	39,0	14,5	3,1	This study					
LV	LV 92	1-3,5 yr	Mandible	-19,0	17,9	41,1	14,8	3,2	This study	Mandible	12,4	0,2	607,4	187,5
LV	LV 92	1-3,5 yr	M.1.crown	-18,9	18,2	36,7	13,5	3,1	This study	M.1.crown	13,4	0,2	518,4	163,9
LV	LV 92	1-3,5 yr	m1.crown	-18,9	18,7	37,8	14,0	3,1	This study	m1.crown	15,0	0,2	507,9	161,3
LV	LV 94	37-43 wk	Bone	-19,4	15,2	34,8	13,0	3,1	Boric et al, 2004					
LV	LV 95	37.5-43 wk	Femur	-18,1	18,2	37,2	13,4	3,2	This study	Femur	14,9	0,2	506,4	157,0
LV	LV 96	37-43 wk	Humerus	-19,5	16,9	33,4	11,0	3,5	This study					
LV	LV 98a	34-39 wk	Humerus	-19,2	18,0	37,3	13,4	3,2	This study	Humerus	12,2	0,2	496,1	152,8
LV	LV 99	8-15 yr	Bone	-20,3	9,1	37,9	13,7	3,2	Boric et al. 2004					
P	P 11	4,5-7,5 yr	M.1.root	-19,6	13,4	38,3	13,6	3,3	This study					
P	P 11	4,5-7,5 yr	Mandible	-20,1	13,6	38,9	13,4	3,4	This study	Cranium	6,0	0,2	510,9	150,9
P	P 11	4,5-7,5 yr	m1.crown	-19,6	16,0	38,4	13,3	3,3	This study	m1.crown	5,7	0,2	530,8	157,7
P	P 11	4,5-7,5 yr	M.1.crown	-19,3	16,6	38,4	14,1	3,2	This study	M.1.crown	5,0	0,2	570,9	179,2
P	P 23	3-6 yr	Bone	-19,6	15,2				Boric and Price 2013	Cranium	6,5	0,2		
P	P 23	3-6 yr	M.1.crown	-19,3	19,3	36,8	13,4	3,2	This study	M.1.crown	6,7	0,2	522,8	163,0
P	P 23	3-6 yr	m1.crown	-19,2	19,8	29,3	10,2	3,3	This study	m1.crown	7,4	0,2	418,9	124,6
P	P 26a	0,5-1	Mandible	-19,8	18,4	35,8	12,7	3,3	This study	Mandible	5,9	0,2	469,1	142,7
P	P 27	9,5-14,5 yr	Bone	-20,9	15,4				Boric and Price 2013					
Vel	1	3-7 yr (?)	Bone	-19,8	9,9			3,2	Bonsall et al. 2015					
Vel	2C	7-11 yr (?)	Bone	-19,2	9,9			3,2	Bonsall et al. 2015					
Vel	2G	5-9 yr (?)	Bone	-19,3	10,1			3,2	Bonsall et al. 2015					
Vel	2G-1	Perinate (?)	Bone	-19,3	14,7			3,2	Bonsall et al. 2015					
Vla	U297	1-2 yr	Mandible	-19,3	17,5	35,4	12,7	3,2	This study	Mandible	8,5	0,2	523,1	160,9
Vla	VL 10	35-40 wk	Bone	-20,3	14,9	43,5	15,3	3,3	Grupe et al, 2003					
Vla	VL 12a	>33 wk	Bone	-20,0	13,4	39,6	14,7	3,1	Grupe et al. 2003					
Vla	VL 12b	48-53 wk	Bone	-19,7	17,3	43,2	14,9	3,4	Grupe et al, 2003					
Vla	VL 18c	5,5-8,5 yr	Bone	-21,0	12,9	33,9	11,5	3,4	Grupe et al. 2003	Mandible	8,8	0,2	498,8	144,8
Vla	VL 18c	5,5-8,5 yr	M.1.root	-20,4	13,5	38,4	14,4	3,1	This study					
Vla	VL 18c	5,5-8,5 yr	M.1.crown	-20,4	17,2	39,8	14,9	3,1	This study	M.1.crown	9,4	0,2	512,3	164,0
Vla	VL 18c	5,5-8,5 yr	m1.crown	-20,7	18,2	40,1	14,9	3,1	This study	m1.crown	10,0	0,2	557,2	177,5
Vla	VL 18c(2)	7-9,5 yr	M.1.root	-20,0	15,0	38,6	14,7	3,0	This study					
Vla	VL 18c(2)	7-9,5 yr	M.1.crown	-20,4	17,4	39,6	14,5	3,2	This study	M.1.crown	9,4	0,2	565,9	178,1
Vla	VL 19	34.5-39 wk	Femur	-19,6	16,9	42,1	15,4	3,2	This study	Femur	10,3	0,2	580,8	181,7
Vla	VL 21	48-52 wk	Bone	-20,3	16,8	28,9	9,8	3,4	Grupe et al, 2003					
Vla	VL 21(1)	48-52 wk	Radius	-19,2	18,3	39,2	14,0	3,2	This study	Radius	6,9	0,2	579,3	177,3
Vla	VL 35a	35-42 wk	Bone	-20,1	15,0	41,9	14,1	3,5	Grupe et al, 2003					
Vla	VL 36(1)	35-47 wk	Femur	-18,6	17,9	38,6	14,0	3,2	This study	Femur	13,6	0,2	481,4	149,6
Vla	VL 42(1)	37.5-42 wk	Humerus	-19,4	16,1	39,7	14,3	3,2	This study	Humerus	12,7	0,2	555,8	171,6

Site	Curated n°	Age	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical Part	δ34S	S%	C/S	N/S
Vla	VL 4b(1)	41-45 wk	Humerus	-19,5	17,8	28,9	10,3	3,3	This study	Humerus	13,0	0,2	457,8	139,0
Vla	VL 5	9-13 yr	Bone	-20,3	14,0	47,4	15,2	3,6	Grupe et al. 2003					
Vla	VL 50(1)	34-38 wk	Femur	-20,1	15,8	38,1	13,9	3,2	This study	Femur	11,0	0,2	518,8	162,6
Vla	VL 50a(1)	36,5-42 wk	Bone	-20,8	15,2	42,7	14,8	3,4	Grupe et al, 2003					
Vla	VL 51	7,5-10,5 yr	Bone	-21,9	9,8	28,5	9,2	3,6	Grupe et al. 2003	Fibula	7,5	0,2	372,0	102,3
Vla	VL 51	7,5-10,5 yr	M.1.root	-19,5	16,9	40,3	14,7	3,2	This study					
Vla	VL 51	7,5-10,5 yr	M.1.crown	-19,5	17,0	40,1	14,8	3,1	This study	M.1.crown	8,3	0,2	528,3	167,0
Vla	VL 51	7,5-10,5 yr	m1.crown	-19,5	17,0	40,1	14,8	3,1	This study	m1.crown	8,2	0,2	495,2	156,5
Vla	VL 53	5-8 yr	Mandible	-19,1	15,9	41,4	14,9	3,2	This study	Rib	13,1	0,2	625,6	193,0
Vla	VL 53	5-8 yr	M.1.root	-18,8	16,0	38,7	14,1	3,2	This study					
Vla	VL 53	5-8 yr	m1.crown	-19,3	17,4	39,1	14,4	3,1	This study	m1.crown	12,4	0,2	543,0	171,7
Vla	VL 53	5-8 yr	M.1.crown	-18,6	18,8	40,2	14,4	3,2	This study					
Vla	VL 54	7,5-10,5 yr	Bone	-20,0	14,2	31,5	12,3	3,0	Grupe et al. 2003	Long Bone	13,4	0,3	329,2	110,3
Vla	VL 55(2)	37-42 wk	Humerus	-20,5	16,0	36,6	12,8	3,3	This study	Humerus	10,4	0,2	486,8	145,9
Vla	VL 58	13-16 yr								Metacarpal	8,3	0,2		
Vla	VL 58b	37-41 wk	Bone	-20,5	13,7	39,8	13,0	3,6	Grupe et al, 2003					
Vla	VL 59	33-40 wk	Bone	-20,6	14,0	42,8	15,0	3,4	Grupe et al, 2003					
Vla	VL 60(1)	37-41 wk	Humerus	-19,5	15,3	37,0	13,3	3,2	This study	Humerus	10,7	0,2	492,1	151,6
Vla	VL 61	38-44 wk	Bone	-20,2	14,8	42,3	14,0	3,5	Grupe et al, 2003					
Vla	VL 62	36-42 wk	Tibia	-19,7	15,9	38,9	13,8	3,3	This study	Tibia	12,1	0,2	518,5	157,6
Vla	VL 64a	7-12 yr	Mandible	-19,9	15,0	37,1	13,5	3,2	This study	Mandible	8,6	0,2	519,7	161,5
Vla	VL 64a	7-12 yr	M.2.root	-19,8	15,3	40,6	14,4	3,3	This study					
Vla	VL 64a	7-12 yr	M.1.crown	-19,3	16,9	38,3	13,8	3,2	This study	M.1.crown	8,3	0,2	605,1	186,9
Vla	VL 64b	7-12 yr	Cranium	-19,8	15,0	36,4	13,0	3,2	This study	Cranium	7,7	0,2	514,6	157,8
Vla	VL 64b	7-12 yr	M.1.root	-19,6	15,6	37,6	13,3	3,3	This study					
Vla	VL 64b	7-12 yr	M.1.crown	-19,4	17,1	38,2	13,9	3,2	This study	M.1.crown	7,8	0,2	502,7	157,0
Vla	VL 66b	31-35 wk	Humerus	-21,1	15,5	40,1	14,1	3,3	This study	Humerus	2,0	0,2	627,4	189,1
Vla	VL 67(1)	36-40 wk	Humerus	-20,0	16,1	38,7	13,5	3,3	This study	Humerus	10,5	0,2	541,8	162,0
Vla	VL 6a	36-40 wk	Bone	-19,6	16,8	3,3	12,0	2,7	Grupe et al. 2003					
Vla	VL 84(1)	30-35 wk	Humerus	-19,2	15,5	37,7	13,6	3,2	This study					

A: Ajmana; CT: Cuina Turcului; HV: Hajdučka Vodenica; I: Icoana; LV: Lepenski Vir; P: Padina; SC: Schela Cladovei; Vel: Velesnica; Vla: Vlasac

APPENDIX B.IV. Chronological and biological information associated with non-human animal individuals included in this study[1]

Site	Curated n°	Lab code	Period	Datation (cal. BC)	Reference	Taxa	Anatomical element	Sr87/Sr86	Reference
A		F2311	Early-Middle Neolithic?			Snail Helix sp.		0,709403	Boric and Price 2013
HV		F2121	Modern			Snail Helix sp.		0,708712	Boric and Price 2013
HV		F2120	Modern			Snail Helix sp.		0,708897	Boric and Price 2013
HV		F2119	Modern			Snail Helix sp.		0,709360	Boric and Price 2013
I		F3270				Snail Helix sp.		0,708977	Boric and Price 2013
I		F3269				Snail Helix sp.		0,709166	Boric and Price 2013
I		F3267				Sus scrofa	Tooth	0,709056	Boric and Price 2013
I		F3272				Sus scrofa	Tooth	0,709567	Boric and Price 2013
I		F3266				Sus scrofa	Tooth	0,711242	Boric and Price 2013
LV		OxA-16211	Early-Middle Neolithic	5996-5811	Boric 2011	Bos taurus			
LV	LV 905a-01/1	A.24	Early-Middle Neolithic	6002-5845	Boric 2011	*Bos taurus*			
LV	LV bb-33/5	A.20	Early Mesolithic			*Canis familiaris*			
LV	LV 1082/3	A.23	Transition-Early Neolithic			*Canis familiaris*			
LV	LV 831a/1	A.25	Early-Middle Neolithic	6000-5845	Boric 2011	*Capra hircus*			
LV		OxA-16253	Early-Middle Neolithic	5988-5798	Boric 2011	Capra hircus			
LV	LV 558/1	A.14	Transition-Early Neolithic	6068-5913	Boric 2011	*Capreolus capreolus*			
LV	LV bb-33/12	A.11	Early Mesolithic			*Capreolus capreolus*			
LV		OxA-15998	Transition-Early Neolithic	6231-6056	Boric 2011	Capreolus capreolus			
LV		OxA-2176-18	Transition-Early Neolithic	6231-6060	Boric 2011	Capreolus capreolus			
LV	LV 1301a/2	A.9	Mesolithic			*Capreolus capreolus*			
LV	LV 1196/3	A.13	Transition-Early Neolithic			*Capreolus capreolus*			
LV	LV 558/1	A.12	Transition-Early Neolithic	6068-5913	Boric 2011	*Capreolus capreolus*			
LV		OxA-15999	Transition-Early Neolithic	6061-5902	Boric 2011	Cervus Elaphus			
LV	LV 1302/2	A.7	Transition-Early Neolithic			*Cervus elaphus*			
LV		OxA-11703	Early Mesolithic	7740-7587	Boric 2011	Cervus Elaphus			
LV		OxA-16002	Transition-Early Neolithic	6058-6004	Boric 2011	Cervus Elaphus			
LV	LV 1314a/1	A.3	Early Mesolithic	9295-8926	Boric 2011	*Cervus elaphus*			
LV		OxA-X-2176-19	Transition-Early Neolithic	6240-6070	Boric 2011	Cervus Elaphus			
LV		OxA-16537	Early-Middle Neolithic	5888-5728	Boric 2011	Cervus Elaphus			
LV		OxA-16072	Early Mesolithic	9441-9241	Boric 2011	Cervus Elaphus			
LV		OxA-16009	Transition-Early Neolithic	6100-5925	Boric 2011	Cervus Elaphus			
LV		OxA-16075	Transition-Early Neolithic	6084-5926	Boric 2011	Cervus Elaphus			
LV		OxA-16078	Transition-Early Neolithic	6206-5989	Boric 2011	Cervus Elaphus			
LV		OxA-16077	Transition-Early Neolithic	6212-6016	Boric 2011	Cervus Elaphus			
LV	LV 1315a/8	A.1	Early Mesolithic	9441-9241	Boric 2011	*Cervus elaphus*			
LV	LV 1090/2	A.6	Transition-Early Neolithic			*Cervus elaphus*			
LV	LV 1300a/1	A.5	Transition-Early Neolithic	6231-6060	Boric 2011	*Cervus elaphus*			
LV		OxA-16076	Early Mesolithic	9298-9150	Boric 2011	Cervus Elaphus			
LV	LV bb-33/3	A2	Mesolithic			*Cervus elaphus*			
LV		F2187	Transition-Early Neolithic			Cyprinidae sp.	Pharingeal Teeth	0,708964	Boric and Price 2013
LV		F2188	Transition-Early Neolithic			Cyprinidae sp.	Pharingeal Teeth	0,709203	Boric and Price 2013

Site	Curated n°	Lab code	Period	Datation (cal. BC)	Reference	Taxa	Anatomical element	Sr87/Sr86	Reference
A		F2311	Early-Middle Neolithic?			Snail Helix sp.		0,709403	Boric and Price 2013
HV		F2121	Modern			Snail Helix sp.		0,708712	Boric and Price 2013
HV		F2120	Modern			Snail Helix sp.		0,708897	Boric and Price 2013
HV		F2119	Modern			Snail Helix sp.		0,709360	Boric and Price 2013
I		F3270				Snail Helix sp.		0,708977	Boric and Price 2013
I		F3269				Snail Helix sp.		0,709166	Boric and Price 2013
I		F3267				Sus scrofa	Tooth	0,709056	Boric and Price 2013
I		F3272				Sus scrofa	Tooth	0,709567	Boric and Price 2013
I		F3266				Sus scrofa	Tooth	0,711242	Boric and Price 2013
LV		OxA-16211	Early-Middle Neolithic	5996-5811	Boric 2011	Bos taurus			
LV	LV 905a-01/1	A.24	Early-Middle Neolithic	6002-5845	Boric 2011	*Bos taurus*			
LV	LV bb-33/5	A.20	Early Mesolithic			*Canis familiaris*			
LV	LV 1082/3	A.23	Transition-Early Neolithic			*Canis familiaris*			
LV	LV 831a/1	A.25	Early-Middle Neolithic	6000-5845	Boric 2011	*Capra hircus*			
LV		OxA-16253	Early-Middle Neolithic	5988-5798	Boric 2011	Capra hircus			
LV	LV 558/1	A.14	Transition-Early Neolithic	6068-5913	Boric 2011	*Capreolus capreolus*			
LV	LV bb-33/12	A.11	Early Mesolithic			*Capreolus capreolus*			
LV		OxA-15998	Transition-Early Neolithic	6231-6056	Boric 2011	Capreolus capreolus			
LV		OxA-2176-18	Transition-Early Neolithic	6231-6060	Boric 2011	Capreolus capreolus			
LV	LV 1301a/2	A.9	Mesolithic			*Capreolus capreolus*			
LV	LV 1196/3	A.13	Transition-Early Neolithic			*Capreolus capreolus*			
LV	LV 558/1	A.12	Transition-Early Neolithic	6068-5913	Boric 2011	*Capreolus capreolus*			
LV		OxA-15999	Transition-Early Neolithic	6061-5902	Boric 2011	Cervus Elaphus			
LV	LV 1302/2	A.7	Transition-Early Neolithic			*Cervus elaphus*			
LV		OxA-11703	Early Mesolithic	7740-7587	Boric 2011	Cervus Elaphus			
LV		OxA-16002	Transition-Early Neolithic	6058-6004	Boric 2011	Cervus Elaphus			
LV	LV 1314a/1	A.3	Early Mesolithic	9295-8926	Boric 2011	*Cervus elaphus*			
LV		OxA-X-2176-19	Transition-Early Neolithic	6240-6070	Boric 2011	Cervus Elaphus			
LV		OxA-16537	Early-Middle Neolithic	5888-5728	Boric 2011	Cervus Elaphus			
LV		OxA-16072	Early Mesolithic	9441-9241	Boric 2011	Cervus Elaphus			
LV		OxA-16009	Transition-Early Neolithic	6100-5925	Boric 2011	Cervus Elaphus			
LV		OxA-16075	Transition-Early Neolithic	6084-5926	Boric 2011	Cervus Elaphus			
LV		OxA-16078	Transition-Early Neolithic	6206-5989	Boric 2011	Cervus Elaphus			
LV		OxA-16077	Transition-Early Neolithic	6212-6016	Boric 2011	Cervus Elaphus			
LV	LV 1315a/8	A.1	Early Mesolithic	9441-9241	Boric 2011	*Cervus elaphus*			
LV	LV 1090/2	A.6	Transition-Early Neolithic			*Cervus elaphus*			
LV	LV 1300a/1	A.5	Transition-Early Neolithic	6231-6060	Boric 2011	*Cervus elaphus*			
LV		OxA-16076	Early Mesolithic	9298-9150	Boric 2011	Cervus Elaphus			
LV	LV bb-33/3	A2	Mesolithic			*Cervus elaphus*			
LV		F2187	Transition-Early Neolithic			Cyprinidae sp.	Pharingeal Teeth	0,708964	Boric and Price 2013
LV		F2188	Transition-Early Neolithic			Cyprinidae sp.	Pharingeal Teeth	0,709203	Boric and Price 2013

Site	Curated n°	Lab code	Period	Datation (cal. BC)	Reference	Taxa	Anatomical element	Sr87/Sr86	Reference
P		IGF4	Mesolithic			Rupricapra rupricapra			
P	*Rutilus frisii*	Pad_F1	Mesolithic			Rutilus frisii			
P	PA 10.70/69/2	Pad_F2	Mesolithic			Rutilus frisii			
P		A.45	Mesolithic			*Silurus glanis*			
P		IGF7	Mesolithic			Sus scrofa			
P		OxA-16940	Late Mesolithic	6633-6464	Boric 2011	Ungulate			
SC		F3262				Sus scrofa	Tooth	0,710570	Boric and Price 2013
SC		F3263				Sus scrofa	Tooth	0,711645	Boric and Price 2013
SC		F3265				Sus scrofa	Tooth	0,712214	Boric and Price 2013
SC		F3621				Sus scrofa	Tooth	0,713849	Boric and Price 2013
SC		OxA-8585	Late Mesolithic	6908-6454	Boric 2011	Ungulate			
SC		OxA-8550	Late Mesolithic	7002-6468	Boric 2011	Ungulate			
SC		OxA-8584	Late Mesolithic	7036-6648	Boric 2011	Ungulate			
SC		OxA-8579	Late Mesolithic	7028-6452	Boric 2011	Ungulate			
SC		OxA-8580	Late Mesolithic	7332-6111	Boric 2011	Ungulate			
SC		OxA-8549	Late Mesolithic	7032-6644	Boric 2011	Ungulate			
SC		OxA-8582	Late Mesolithic	7520-6232	Boric 2011	Ungulate			
Vla		P10	Mesolithic			Acipenser sturio			
Vla		P2	Mesolithic			Acipenser sturio			
Vla		P11	Mesolithic			Acipenser sturio			
Vla		IGF12	Mesolithic			Acipenseridae			
Vla		OxA-16543	Late Mesolithic	7034-6693	Boric 2011	Bos primigenius			
Vla		1 (9)	Mesolithic			Canis familiaris			
Vla		7 (43a)	Mesolithic			Canis familiaris			
Vla		Comga B(canis f1)	Mesolithic			Canis familiaris			
Vla		Comga B(canis f2)	Mesolithic			Canis familiaris			
Vla		Comga B(canis f3)	Mesolithic			Canis familiaris			
Vla		6 (m28-36)	Mesolithic			Canis familiaris			
Vla		Comga A(canis f4)	Mesolithic			Canis familiaris			
Vla		4 (8a)	Mesolithic			Canis familiaris			
Vla		8 (50a)	Mesolithic			Canis familiaris			
Vla		5 (35a)	Mesolithic			Canis familiaris			
Vla		Comga B(canis l1)	Mesolithic			Canis lupus			
Vla		Comga B(canis l2)	Mesolithic			Canis lupus			
Vla		OxA-16216	Late Mesolithic	7047-6699	Boric 2011	Capreolus capreolus			
Vla		12 (1200)	Mesolithic			Capreolus capreolus			
Vla		OxA-16218	Late Mesolithic	7028-6651	Boric 2011	Cervus Elaphus			
Vla		OxA-16217	Late Mesolithic	6900-6593	Boric 2011	Cervus Elaphus			
Vla		OxA-16080	Late Mesolithic	6638-6479	Boric 2011	Cervus Elaphus			
Vla		OxA-16544	Late Mesolithic	6006-5838	Boric 2011	Cervus Elaphus			
Vla		14 (1808)	Mesolithic			Cervus elaphus			
Vla		16 (45a)	Mesolithic			Cervus elaphus			
Vla		13 (2026)	Mesolithic			Cervus elaphus			
Vla		IGF9	Mesolithic			Cyprinidae sp.			
Vla		IGF11	Mesolithic			Cyprinidae sp.			
Vla		P12	Mesolithic			Cyprinus carpio			
Vla		27 (P28)	Mesolithic			Cyprinus carpio			
Vla		P11	Mesolithic			Cyprinus carpio			
Vla		P10	Mesolithic			Cyprinus carpio			
Vla		18 (P17)	Mesolithic			Cyprinus carpio			
Vla		P25	Mesolithic			Cyprinus carpio			
Vla		21 (54a)	Mesolithic			Huso huso			
Vla		OxA-16539	Late Mesolithic	6393-6229	Boric 2011	Large mammal			
Vla		Comga A	Mesolithic			Lynx Lynx			
Vla		F2194	Mesolithic			Lynx lynx	M3 inf.	0,709316	Boric and Price 2013
Vla		m1	Mesolithic			Martes martes			
Vla		m7-12	Mesolithic			Martes martes			
Vla		m9	Mesolithic			Martes martes			
Vla		m8	Mesolithic			Martes martes			
Vla		F2195	Mesolithic			Martes martes	Mandibule	0,708849	Boric and Price 2013
Vla		F2196	Mesolithic			Martes martes	Mandibule	0,708942	Boric and Price 2013
Vla		20 (P23)	Mesolithic			Silurus glanis			
Vla		25 (P33)	Mesolithic			Silurus glanis			
Vla		OxA-16221	Late Mesolithic	7022-6698	Boric 2011	Sus scrofa			
Vla		Comga A(sus s1)	Mesolithic			Sus scrofa			
Vla		Comga A(sus s2)	Mesolithic			Sus scrofa			
Vla		Comga A(sus s3)	Mesolithic			Sus scrofa Juvenil			
Vla		OxA-16214	Late Mesolithic	7163-6818	Boric 2011	Ursus arctos			
Vla		m18	Mesolithic			Ursus arctos			

A: Ajmana; CT: Cuina Turcului; HV: Hajdučka Vodenica; I: Icoana; LV: Lepenski Vir; P: Padina; SC: Schela Cladovei; Vel: Velesnica; Vla: Vlasac

AMS ^{14}C ages corrected for freshwater reservoir effect and calibrated (95.4% probability), from Borić 2011

[1.] Individuals with strontium radiogenic information but no other stable isotope values were also included in this table

APPENDIX B.V. Stable isotope values for non-human animal individuals included in this study

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Code	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical Part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extr. weight	Vol. CO2
LV	OxA-16211	Horncore	-21,1	6,7				Boric and Dimitrijevic 2009										
LV	A.24	MTT	-22,1	8,1	40,3	14,7	3,2	This study	MTT dext.	0,2	3,4	587,8	184,0	This study				
LV	A.20	Ulna	-18,7	11,1	40,8	14,9	3,2	This study	Ulna sin.	0,2	15,6	601,4	188,9	This study				
LV	A.23	Ulna	-18,5	12,3	37,0	13,7	3,1	This study	Ulna dext.	0,2	15,0	534,1	169,8	This study				
LV	A.25	MTC	-20,4	6,5	41,0	15,0	3,2	This study	MTC dext.	0,2	5,7	649,3	203,5	This study				
LV	OxA-16253	Mandible	-20,7	7,1				Boric and Dimitrijevic 2009										
LV	A.14	Mandible	-22,4	5,7	34,1	12,2	3,2	This study	Mandible dext.	0,2	4,8	498,2	152,6	This study				
LV	A.11	Vert.	-20,9	7,0	40,4	15,0	3,1	This study	Intermed. dext.	0,2	2,2	611,9	194,6	This study				
LV	OxA-15998	MTC	-22,1	7,9				Boric and Dimitrijevic 2009										
LV	OxA-2176-18	Molar	-22,1	7,9				Boric and Dimitrijevic 2009										
LV	A.9														P4	-14,4	617	880
LV	A.13														M1 /3	-14,02	589	897
LV	A.12														M2	-15,66	588	875
LV	OxA-15999	MTT	-20,8	5,4				Boric and Dimitrijevic 2009										
LV	A.7	Vert.	-21,4	5,7	43,1	15,7	3,2	This study	Vert. thoracal	0,2	4,7	687,0	213,9	This study				
LV	OxA-11703	Antler	-20,3	5,9				Boric and Dimitrijevic 2009										
LV	OxA-16002	Vert.	-20,1	6,4				Boric and Dimitrijevic 2009										
LV	A.3	MTT	-21,4	6,4	27,9	9,2	3,5	This study	MTT	0,2	6,8	453,3	128,8	This study				
LV	OxA-X-2176-19	MTC	-20,7	6,5				Boric and Dimitrijevic 2009										
LV	OxA-16537	Skull	-21,9	7,7				Boric and Dimitrijevic 2009										
LV	OxA-16072	Molar	-20,2	7,8				Boric and Dimitrijevic 2009										
LV	OxA-16009	Mandible	-22,3	7,9				Boric and Dimitrijevic 2009										
LV	OxA-16075	Antler	-22,3	7,9				Boric and Dimitrijevic 2009										
LV	OxA-16078	Skull	-21,4	8,2				Whittle et al. 2002										
LV	OxA-16077		-24,4	8,7				Whittle et al. 2002										
LV	A.1														M2	-12,7	581	872
LV	A.6														I2	-14,2	270	811
LV	A.5														M1/2	-14,7	581	753
LV	OxA-16076	Antler	-19,6	6,1				Boric and Dimitrijevic 2009										
LV	A2														P4 sup.	-12,3	270	394
LV	A.28	Vert.	-21,6	7,5	28,3	9,1	3,6	This study										
LV	A.30	Rib	-21,9	8,1	30,7	10,7	3,3	This study	Costae									
LV	OxA-8725	Vert.	-16,9	9,7				Whittle et al. 2002										
LV	A.35	Vert.	-18,2	9,2	22,2	6,9	3,7	This study										
LV	A.38								Vert.	0,1	16,1			This study				
LV	A.37								Vert.	0,2	13,6			This study				

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Lab code	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical Part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extr. weight	Vol. CO2
LV	A.39	Dentale	-18,5	11,3	39,2	14,3	3,2	This study	Dentale dext.	0,3	8,5	396,4	124,1	This study				
LV	LV _F1														Dentes	-6,3	604	797
LV	LV _F2														Dentes	-6,9	598	946
LV	A.34	Vert.	-21,8	10,9	37,2	12,5	3,5	This study	Vert.	0,4	5,5	249,6	71,8	This study				
LV	A.32	Vert.	-21,2	10,9	19,9	4,8	4,8	This study	Abdominal Vert.	0,2	11,4	247,5	51,4	This study				
LV	A.26	Scapula	-20,8	7,1	38,9	14,0	3,2	This study	Scapula dext.	0,2	6,5	602,6	186,0	This study				
LV	A.17	MTC	-20,9	6,8	41,9	15,3	3,2	This study	MTC IV dext.	0,2	5,0	618,8	194,0	This study				
LV	A.18	Phalanx	-21,1	7,5	38,6	14,1	3,2	This study	Phalanx III	0,2	5,2	549,6	171,8	This study				
LV	OxA-8618	Long Bone	-21,2	3,9				Whittle et al. 2002										
LV	OxA-8610	Long Bone	-21,6	4,7				Whittle et al. 2002										
P	IG-F2		-22,8	6,4	45,9	16,1	3,3	Nehlich et al. 2010		0,2	4,2	610,5	183,5	Nehlich et al. 2010				
P	OxA-9034	Tibia	-17,7	8,6				Whittle et al. 2002										
P	OxA-9053	Ulna	-17,7	11,3				Whittle et al. 2002										
P	OxA-9056	Tibia	-18,1	12.5				Whittle et al. 2002										
P	IGF8		-23,2	7,4	42,8	15,2	3,3	Nehlich et al. 2010		0,2	4,3	569,2	173,3	Nehlich et al. 2010				
P	Padina 17	Mandible	-21,8	4,6	40,55	14,67	3,22	Boric et al. 2004										
P	OxA-9055	Mandible	-20,8	4,7				Whittle et al. 2002										
P	OxA-17144	Foot bone	-23,6	5,6				Borić and Miracle 2004										
P	OxA-9052	Antler	-22,2	6,6				Whittle et al. 2002										
P	A.41	Cranium	-26,9	7,7	37,6	13,6	3,2	This study	Cranial	0,4	-3,1	277,7	86,4	This study				
P	A.42	Cranium	-24,2	8,8	30,8	10,8	3,3	This study	Cranial	0,4	8,2	219,2	65,8	This study				
P	A.43	Pterygiophore	-26,2	10,7	33,8	12,0	3,3	This study	Pterygiophore	0,4	3,3	223,5	68,2	This study				
P	A.51	Vert.	-17,8	9,1	20,5	7,0	3,4	This study										
P	A.54	Dentale	-17,6	10,1	27,6	10,2	3,1	This study										
P	OxA-9054		-21,5	5,7				Whittle et al. 2002										
P	OxA-16937		-22,8	8				Borić and Miracle 2004										
P	IGF4		-20,7	4,6	45,1	14,5	3,6	Nehlich et al. 2010		0,3	5,3	399,9	110,2	Nehlich et al. 2010				
P	Pad_F1														Dentes	-5,133	593	916
P	Pad_F2														Dentes	-4,6	598	924
P	A.45								Vert.	0,3	1,9			This study				
P	IGF7		-21,1	7,3	45,8	15,5	3,4	Nehlich et al. 2010		0,2	2,7	609,1	176,7	Nehlich et al. 2010				
P	OxA-16940	Antler	-21,1	6,7				Borić and Miracle 2004										
SC	OxA-8585		-20,9	4,5				Cook et al. 2002										
SC	OxA-8550		-21,2	4,7				Cook et al. 2002										
SC	OxA-8584		-21,5	4,7				Cook et al. 2002										
SC	OxA-8579		-20,6	5				Cook et al. 2002										
SC	OxA-8580		-20,8	6,1				Cook et al. 2002										

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Lab code	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical Part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extr. weight	Vol. CO2
LV	A.39	Dentale	-18,5	11,3	39,2	14,3	3,2	This study	Dentale dext.	0,3	8,5	396,4	124,1	This study				
LV	LV _F1														Dentes	-6,3	604	797
LV	LV _F2														Dentes	-6,9	598	946
LV	A.34	Vert.	-21,8	10,9	37,2	12,5	3,5	This study	Vert.	0,4	5,5	249,6	71,8	This study				
LV	A.32	Vert.	-21,2	10,9	19,9	4,8	4,8	This study	Abdominal Vert.	0,2	11,4	247,5	51,4	This study				
LV	A.26	Scapula	-20,8	7,1	38,9	14,0	3,2	This study	Scapula dext.	0,2	6,5	602,6	186,0	This study				
LV	A.17	MTC	-20,9	6,8	41,9	15,3	3,2	This study	MTC IV dext.	0,2	5,0	618,8	194,0	This study				
LV	A.18	Phalanx	-21,1	7,5	38,6	14,1	3,2	This study	Phalanx III	0,2	5,2	549,6	171,8	This study				
LV	OxA-8618	Long Bone	-21,2	3,9				Whittle et al. 2002										
LV	OxA-8610	Long Bone	-21,6	4,7				Whittle et al. 2002										
P	IG-F2		-22,8	6,4	45,9	16,1	3,3	Nehlich et al. 2010		0,2	4,2	610,5	183,5	Nehlich et al. 2010				
P	OxA-9034	Tibia	-17,7	8,6				Whittle et al. 2002										
P	OxA-9053	Ulna	-17,7	11,3				Whittle et al. 2002										
P	OxA-9056	Tibia	-18,1	12.5				Whittle et al. 2002										
P	IGF8		-23,2	7,4	42,8	15,2	3,3	Nehlich et al. 2010		0,2	4,3	569,2	173,3	Nehlich et al. 2010				
P	Padina 17	Mandible	-21,8	4,6	40,55	14,67	3,22	Boric et al. 2004										
P	OxA-9055	Mandible	-20,8	4,7				Whittle et al. 2002										
P	OxA-17144	Foot bone	-23,6	5,6				Borić and Miracle 2004										
P	OxA-9052	Antler	-22,2	6,6				Whittle et al. 2002										
P	A.41	Cranium	-26,9	7,7	37,6	13,6	3,2	This study	Cranial	0,4	-3,1	277,7	86,4	This study				
P	A.42	Cranium	-24,2	8,8	30,8	10,8	3,3	This study	Cranial	0,4	8,2	219,2	65,8	This study				
P	A.43	Pterygiophore	-26,2	10,7	33,8	12,0	3,3	This study	Pterygiophore	0,4	3,3	223,5	68,2	This study				
P	A.51	Vert.	-17,8	9,1	20,5	7,0	3,4	This study										
P	A.54	Dentale	-17,6	10,1	27,6	10,2	3,1	This study										
P	OxA-9054		-21,5	5,7				Whittle et al. 2002										
P	OxA-16937		-22,8	8				Borić and Miracle 2004										
P	IGF4		-20,7	4,6	45,1	14,5	3,6	Nehlich et al. 2010		0,3	5,3	399,9	110,2	Nehlich et al. 2010				
P	Pad_F1														Dentes	-5,133	593	916
P	Pad_F2														Dentes	-4,6	598	924
P	A.45								Vert.	0,3	1,9			This study				
P	IGF7		-21,1	7,3	45,8	15,5	3,4	Nehlich et al. 2010		0,2	2,7	609,1	176,7	Nehlich et al. 2010				
P	OxA-16940	Antler	-21,1	6,7				Borić and Miracle 2004										
SC	OxA-8585		-20,9	4,5				Cook et al. 2002										
SC	OxA-8550		-21,2	4,7				Cook et al. 2002										
SC	OxA-8584		-21,5	4,7				Cook et al. 2002										
SC	OxA-8579		-20,6	5				Cook et al. 2002										
SC	OxA-8580		-20,8	6,1				Cook et al. 2002										
SC	OxA-8549		-20,4	7,7				Cook et al. 2002										
SC	OxA-8582		-22	9,4				Cook et al. 2002										
Vla	P10		-21,3	8,3	36,28	12,75	3,32	Grupe et al. 2003										
Vla	P2		-19,4	8,8	42,01	14,31	3,42	Grupe et al. 2003										
Vla	P11		-19,2	10,1	44,35	15,82	3,27	Grupe et al. 2003										
Vla	IGF12		-19,7	7,8	41,8	15,1	3,2	Nehlich et al. 2010		0,5	14,2	222,4	68,9	Nehlich et al. 2010				
Vla	OxA-16543	Metapodal	-21,9	7,2				Boric et al. 2008										
Vla	1 (9)	Humerus	-23,1	9,4	20,1	9,28	2,53	Boric et al. 2004										
Vla	7 (43a)	Tibia	-19,8	9,6	31,78	10,68	3,47	Boric et al. 2004										
Vla	Comga B(canis f1)	Humerus	-19,5	10,2	43,36	15,06	3,36	Grupe et al. 2003										
Vla	Comga B(canis f2)	Mandible	-18,9	10,5	28,78	10,82	3,21	Grupe et al. 2003										
Vla	Comga B(canis f3)	Tibia	-19,1	10,7	35,57	14,22	2,92	Grupe et al. 2003										
Vla	6 (m28-36)	Humerus	-19,5	10,8	39,67	12,65	3,66	Boric et al. 2004										
Vla	Comga A(canis f4)	Radius	-19,6	11,0	29,87	10,55	3,3	Grupe et al. 2003										
Vla	4 (8a)	Mandible	-18,5	11,0	45,51	13,3	3,73	Boric et al. 2004										
Vla	8 (50a)	Pelvis	-20,3	11,0	31,33	12,92	2,83	Boric et al. 2004										
Vla	5 (35a)	Mandible	-20,0	11,6	45,58	14,12	3,6	Boric et al. 2004										
Vla	Comga B(canis l1)	MTC	-20,0	9,6	44,18	15,41	3,34	Grupe et al. 2003										
Vla	Comga B(canis l2)	Foot bone	-20,1	10,1	51,17	17,67	3,38	Grupe et al. 2003										
Vla	OxA-16216	Skull	-22,1	5,8				Boric et al. 2008										
Vla	12 (1200)	MTT	-21,6	6,1	39,62	13,19	3,51	Boric et al. 2004										
Vla	OxA-16218	Antler	-22,5	5,9				Boric et al. 2008										
Vla	OxA-16217	Antler	-22,4	6,5				Boric et al. 2008										
Vla	OxA-16080	Antler	-20,6	6,6				Boric et al. 2008										
Vla	OxA-16544	Skull	-21,3	6,8				Boric et al. 2008										
Vla	14 (1808)	Antler	-21,6	6,8	68,59	22,03	3,63	Boric et al. 2004										
Vla	16 (45a)	Mandible	-22,4	6,9	34,57	12,76	3,16	Boric et al. 2004										
Vla	13 (2026)	Antler	-22,6	7,1	43,63	15,2	3,5	Boric et al. 2004										
Vla	IG F9		-18,9	6,8	36,3	12,7	3,4	Nehlich et al. 2010		0,4	14,0	241,4	72,4	Nehlich et al. 2010				
Vla	IG F11		-20,1	7,4	41,9	15,3	3,2	Nehlich et al. 2010		0,4	14,0	278,6	87,2	Nehlich et al. 2010				
Vla	P12		-21,2	6,3	29,08	12,74	2,66	Grupe et al. 2003										
Vla	27 (P28)	Mandible	-20,7	6,4	29,47	9,91	3,47	Boric et al. 2004										
Vla	P11	Vert.	-20,3	6,6	47,12	16,36	3,34	Grupe et al. 2003										
Vla	P10		-20,8	7,1	20,01	7,02	3,32	Grupe et al. 2003										
Vla	18 (P17)	Mandible	-23,3	7,9	41,29	13,24	3,64	Boric et al. 2004										
Vla	P25	Mandible	-23,7	9,8	23,67	8,49	3,26	Grupe et al. 2003										
Vla	21 (54a)	Dentale	-17,7	11,1	34,44	10,18	3,95	Boric et al. 2004										

		Carbon and nitrogen analysed in collagen							Sulfur analysed in collagen						Carbon analysed in bioapatite			
Site	Lab code	Anatomical part	δ13C	δ15N	C%	N%	C/N	Reference	Anatomical Part	δ34S	S%	C/S	N/S	Reference	Selected tooth	δ13C	Extr. weight	Vol. CO2
Vla	OxA-16539		-21,7	6,8				Boric et al. 2008										
Vla	Comga B(lynx)	Ulna	-21,4	10,6	45,3	15,08	3,51	Grupe et al. 2003										
Vla	m1	Mandible	-19,4	9,1	35,51	12,39	3,32	Grupe et al. 2003										
Vla	m7-12	Pelvis	-18,9	9,2	46,65	15,98	3,39	Grupe et al. 2003										
Vla	m9	Mandible	-20,2	10,1	34,89	11,63	3,5	Grupe et al. 2003										
Vla	m8	Mandible	-19,2	10,6	39,77	13,66	3,39	Grupe et al. 2003										
Vla	20 (P23)	Vert.	-20,2	9,3	23,28	6,75	4,02	Boric et al. 2004										
Vla	25 (P33)	Vert.	-20,9	10,6	24,84	7,81	3,71	Boric et al. 2004										
Vla	OxA-16221	Tusk	-20,7	7				Boric et al. 2008										
Vla	Comga A(sus s1)	Tibia	-20,3	7,1	43,75	15,17	3,27	Grupe et al. 2003										
Vla	Comga A (sus s2)	Tibia	-20,3	7,1	43,75	15,17	3,27	Boric et al. 2004										
Vla	Comga A (sus s3)	Scapula	-20,7	11,9	46,83	16,75	3,26	Grupe et al. 2003										
Vla	OxA-16214	Canine	19,5	8,4				Boric et al. 2008										
Vla	m18		-20,5	8,2	30,97	10,84	3,34	Grupe et al. 2003										

A: Ajmana; CT: Cuina Turcului; HV: Hajdučka Vodenica; I: Icoana; LV: Lepenski Vir; P: Padina; SC: Schela Cladovei; Vel: Velesnica; Vla: Vlasac

BIOGRAPHY

Camille de Becdelièvre is a Bioarchaeologist specialized in the analyses of human organic remains from archaeological contexts. He applies methods from Human Osteology, Molecular and Mortuary Archaeology to address issues related to behavioral and biocultural adaptations. His area of interest particularly focuses on the (trans)formation of human ecological niches and its relationships with the modification of human life history strategies. His researches notably include the context of the Mesolithic and Neolithic transformations in the Central Balkans, a framework to explore the behavioral mechanisms beyond the sedentary and farming transitions.

He received an interdisciplinary academic education, being graduated in History and in Archaeology in 2008-2009 (University of Tours) and completing a master degree in Biological Anthropology in 2011 (University of Bordeaux). In 2013, he started doctoral studies in the department of Archaeology of Belgrade University under the mentorship of Prof. Dr. S. Stefanović. Apart from this theoretical training, he participated between 2005-2011 to numerous field works as excavation assistant. Between 2012-2016, he has been employed as researcher within the EU-funded BEAN project, to analyze the mechanisms of the Neolithic demographic transition. In the period 2013-2015, he was also involved in the bilateral French-serbian co-funded PREFERT project, focused on the evolution of children feeding practices during the Mesolithic-Neolithic transition, and between 2017-2018 he was granted by Nestlé France Fondation to conduct researches on nutritional adaptations at the beginning of agriculture in the Balkans.

During this period, he collaborated with partners from numerous European institutions, published 10 scientific papers in peer-reviewed journals and monographs, and participated to 35 presentations in international conferences. He also gave lectures to master students in Archaeology and Biological Anthropology from Aix-Marseille university, and participated to several events of scientific outspread.

образац изјаве о ауторству

Изјава о ауторству

Име и презиме аутора Camille de Becdelièvre

Број индекса 7A13-7

Изјављујем

да је докторска дисертација под насловом

Екологија и етологија популација у Ђердапу око 9500-5500 пре н.е. Биоархеолошке перспективе навика у исхрани и стратегија прилагођавања током мезолитско-неолитских трансформација

- резултат сопственог истраживачког рада;
- да дисертација у целини ни у деловима није била предложена за стицање друге дипломе према студијским програмима других високошколских установа;
- да су резултати коректно наведени и
- да нисам кршио/ла ауторска права и користио/ла интелектуалну својину других лица.

У Београду, 29.06.2020

Потпис аутора

Изјава о истоветности штампане и електронске верзије докторског рада

Име и презиме аутора Camille de Becdelièvre

Број индекса 7A13-7

Студијски програм Doktorske studije arheologije

Наслов рада:

Екологија и етологија популација у Ђердапу око 9500-5500 пре н.е. Биоархеолошке перспективе навика у исхрани и стратегија прилагођавања током мезолитско-неолитских трансформација

Ментор Pr. Dr. Sofija Stefanović

Изјављујем да је штампана верзија мог докторског рада истоветна електронској верзији коју сам предао/ла ради похрањивања у **Дигиталном репозиторијуму Универзитета у Београду.**

Дозвољавам да се објаве моји лични подаци везани за добијање академског назива доктора наука, као што су име и презиме, година и место рођења и датум одбране рада.

Ови лични подаци могу се објавити на мрежним страницама дигиталне библиотеке, у електронском каталогу и у публикацијама Универзитета у Београду.

У Београду, 29.06.2020

Потпис аутора

образац изјаве о коришћењу

Изјава о коришћењу

Овлашћујем Универзитетску библиотеку „Светозар Марковић“ да у Дигитални репозиторијум Универзитета у Београду унесе моју докторску дисертацију под насловом:

Екологија и етологија популација у Ђердапу око 9500-5500 пре н.е. Биоархеолошке перспективе навика у исхрани и стратегија прилагођавања током мезолитско-неолитских трансформација

која је моје ауторско дело.

Дисертацију са свим прилозима предао/ла сам у електронском формату погодном за трајно архивирање.

Моју докторску дисертацију похрањену у Дигиталном репозиторијуму Универзитета у Београду и доступну у отвореном приступу могу да користе сви који поштују одредбе садржане у одабраном типу лиценце Креативне заједнице (Creative Commons) за коју сам се одлучио/ла.

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У Београду, 29.06.2020

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6. **Ауторство – делити под истим условима**. Дозвољавате умножавање, дистрибуцију и јавно саопштавање дела, и прераде, ако се наведе име аутора на начин одређен од стране аутора или даваоца лиценце и ако се прерада дистрибуира под истом или сличном лиценцом. Ова лиценца дозвољава комерцијалну употребу дела и прерада. Слична је софтверским лиценцама, односно лиценцама отвореног кода.