

Chapter 2

The Role of the Central Balkans in the Peopling of Europe: Paleoanthropological Evidence

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Abstract The paucity of fossil human remains from the Central Balkans represents a very serious lacuna in our understanding of human evolution in the Pleistocene of Europe, which is—as a result—strongly influenced by the material from the better researched parts of the continent further to the west of the Balkans. The scant fossil record from the Central Balkans suffers from a lack of archaeological/geological context, and with the exception of the Balanica hominin (BH-1) has no associated chronological data. In this chapter, I present all of the *purported* Pleistocene specimens currently known from the area and discuss their possible affinities.

Keywords Human evolution • *Homo* • Pleistocene • Balkan Peninsula

Introduction

The last three decades have brought about important insights into human evolution in Europe. Dominated over the past 160 years by relatively abundant Upper Pleistocene fossil remains from more westerly parts of Europe and the explanatory models they engendered, the field is rapidly changing with the opening of new geographic areas to intensive research. The discovery of Dmanisi (Gabunia and Vekua 1995) demonstrated a human population outside of Africa by 1.8 Ma, and a recent publication on the Dmanisi cranium D4500 (Lordkipanidze et al. 2013) indicated greater variation among early hominins from a single locality than previously suspected. At the other end of the continent, well-dated

Early Pleistocene sites and contexts emerged in Spain with the oldest hominin find in Europe dated to *ca.* 1.4 Ma at Orce (Toro-Moyano et al. 2013; but see Muttoni et al. 2013; also Spassov 2016 and references therein). Well-documented Early Pleistocene archaeological sites are also known from Italy, although no human remains have been recovered there so far (Manzi et al. 2011). Further to the east, a proposed, though contentious, date of 1.4 Ma at Kozarnika cave in Bulgaria (Ivanova 2016; Spassov 2016) would be contemporaneous with Ubeidiya in Israel (Belmaker et al. 2002). The opening of these new geographic foci to systematic survey and excavation resulted in possibly the greatest advances in human evolutionary studies in Europe over the last two decades. However, we are still far from fully understanding who the first inhabitants of the continent were; what was their relationship to fossil hominins in Asia, Africa, and later European fossil populations; how many migrations into and out of Europe occurred in the Pleistocene; where the migrants came from; and what route they took. The paleoanthropological record of the Central Balkans—currently consisting for the most part of fortuitous finds, or finds gathered from excavations that leave much to be desired—could represent a crucial piece in this puzzle.

The Central Balkans area is at the crossroads of the south-to-north and east-to-west migratory routes that run through the Balkan Peninsula (see also, e.g., Aytsek and Harvati 2016; Doboş and Iovita 2016; Harvati 2016; Spassov 2016; Strait et al. 2016). At the gates to the continent, the Balkan Peninsula is the most logical route of migration from the Levant into Europe—already identified as the confirmed route of animal migrations during the colder phases of the Early Pleistocene (Belmaker et al. 2002). The Central Balkans, defined by the Morava and Vardar rivers and their tributaries, covers most of what is today Serbia (without Vojvodina, which belongs to the Pannonian basin and therefore Central Europe), Eastern Bosnia and Northern Macedonia. More than just a migratory route, this region was also an integral part of the Balkan refugium (Hewitt 2011; Griffiths et al. 2004) for temperate decid-

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uous forests and associated biota (Eastwood 2004; Tzedakis 2004). The potential benefits of a more vigorous research program into the Pleistocene of the Central Balkan Peninsula cannot be overstated: the area could have played an important role in the initial peopling of the continent, in the repopulation of more northerly areas during interglacials, as well as in the demise of the Neanderthals and the advancement of modern humans. Whatever speculative role we can ascribe to the Central Balkans, the region is conspicuous by its absence in most discussions of migration(s) into and out of Europe (see, for example, a recent review by Bar-Yosef and Belfer-Cohen 2013).

Despite its likely importance and the strong tradition of archaeological research in the region, the Central Balkans Paleolithic record is scant (similar to the situation in many neighboring countries; see e.g., Aytsek and Harvati 2016; Harvati 2016; Strait et al. 2016). A strong initial interest in Pleistocene-fauna and tool-bearing caves in the late 1800s–early 1900s (Cvijić 1903, 1918; Žujović 1893; Jovanović 1892) coincided with the discovery of Krapina in adjoining Croatia (Gorjanović-Kramberger 1906; Janković et al. 2016). However, with the exception of some sporadic forays in the 1950s (Gavela 1951), this particular area of archaeology was all but forgotten until the very end of the twentieth century (Mihailović 2008; Mihailović and Bogićević 2016). Against this background, it is not surprising that the hominin fossil record is limited. Most of the purported Pleistocene specimens were uncovered in the late nineteenth and early twentieth century and subsequently lost during the First and the Second World Wars. In a recent AMS ^{14}C dating of six purported Pleistocene specimens from the Natural History Museum in Belgrade and the National Museum in Kraljevo, all were demonstrated to be of Holocene age (Roksandic et al. 2014), stressing the need for great caution in interpreting finds from old excavations.

The total tally of putative fossil hominins currently known from the Central Balkans (Fig. 2.1) includes: (1) a calotte from Bajloni's building discovered and described in 1892 (Jovanović 1892); (2) a mandible from the "loess in the vicinity of Belgrade" found in 1920 and published in 2001 (Roksandic and Dimitrijević 2001); (3) a tooth from Jerinina cave found in 1951, not described (Gavela 1951); (4) a skull fragment from the Kolubara gravel pit found in 1952, not described (Roksandic and Dimitrijević 2001); (5) a mandible found in Mala Balanica cave in 2006 (Roksandic et al. 2011). I will include in this review two additional cranial fragments: (6) a calotte from Bački Petrovac found in 1952 and published in 1966; and (7) a frontal from Žitište found in 1960 and described in 1966 (Živanović 1966; Radović et al. 2014). Both of these were found just north of the Central Balkans in the Pannonian plain of Central Europe. Popular lore mentions several more finds of which there is no mention in the published record. In addition to the specimen from "Bajloni's

building" (Jovanović 1892) discussed later, there is mention of an "antediluvian man" uncovered from unspecified excavations in Cetinjska street. Since "Bajloni's building" refers to the brewery between Skadarska and Cetinjska streets in downtown Belgrade, this "antediluvian man" could potentially refer to the same specimen as the one from the Bajloni's building. A "Neanderthal" from Banovo brdo could be the one described as a "brachycephalic skull" (Žujović 1893, p. 21) uncovered from a loess deposit while excavating pylons for the bridge over the Sava river in Belgrade. Another "Neanderthal skull" from "Palata Albanija" was presumably found together with mammoth bones in 1938. The latter two specimens were recently located in the Natural History Museum in Belgrade. With the generous help of Sanja Paunović and Dr. Zoran Marković, I obtained permission to examine them and take samples for dating. Both skulls are clearly brachycephalic and therefore of post-Pleistocene age and will not be discussed in this chapter.

With the exception of the mandible from Mala Balanica, none of these specimens is associated with an archaeological context. Although unspecified stone tools were reportedly found with the Bački Petrovac specimen (Živanović 1966), given the accidental nature of the discovery, as well as the fact that the tools were neither described nor preserved, such an association cannot be confirmed. A very vague geological context reported as "*with bones of Elephas antiquus*" (Jovanović 1892, p. 30) in "*quaternary layers*" (Jovanović 1892, p. 31) has been reported for "Bajloni's building"; the Belgrade mandible was designated on its museum label as "*from the upper loess*" by its discoverer Professor Laskarev (Roksandic and Dimitrijević 2001, p. 28). The "*brachycephalic skull*" uncovered during the excavations for the Sava bridge—even according to the author—is not of Pleistocene age, although it was found in the loess deposit (Žujović 1893, p. 21): "*Under the third pylon, closer to the Austrian bank, plain river shells were unearthed as low as 12 m below the river bottom, while at the 14th meter, there was a human skull of a brachycephalous man.*" Noting other non-Pleistocene fauna in the river deposits in the area, Žujović (1893, p. 21) quite convincingly describes the taphonomic process that he considered responsible for the mixing: "*The river Sava still, within our memory, raises the plane; it still brings us deposits in which, mixed with river shells and snails, one finds fragments of horse, cattle, pig and sometimes mammoth skeletons that it unearthed from its original layers.*"

In this chapter, I will review what we know about each of the finds recorded in the scientific literature, and what we can learn about them by reexamining the very scant published measurements and descriptions. I will then offer some preliminary suggestions about the place of the Central Balkans in human evolution based on this rather limited evidence.



Fig. 2.1 Map of sites discussed in the chapter: Beograd (Belgrade) stands for both Bajloni's building calotte (BAJ in further text) and the "mandible from the loess in the vicinity of Belgrade" (RGF94/1) specimens. Inset

shows the Balkan Peninsula and its relationship with the Black sea and adjoining regions; location of Belgrade and Balanica anchors the larger map in relation to well-known sites of Krapina (in Croatia) and Dmanisi (Georgia)

Materials and Methods

Before proceeding to describe the specimens in question, a note on the choice of measurements and morphological traits, as well as specimens and taxonomic groups included in the comparative sample, should be made. All the measurements were gathered from the reported original descriptions (for the more recently published material) and from large sets of data on originals by Rightmire (2008) for earlier discoveries (see Table 2.1 for the list of sources). Morphological traits of the mandible were taken from Mounier et al.'s (2009) comprehensive scoring of mandibular specimens. The choice of measurements and morphological traits was guided by the preserved morphology that could be measured or scored, or by the information available in the literature. This has of course resulted in limited comparative samples, which comprise only specimens that preserve the same measurements. In order to maximize the comparative sample, in some cases it was necessary to reduce the number of measurements used (notably for Bački Petrovac), as the alternative—i.e., to compute missing values—could introduce unknown biases.

When discussing hominin populations in the Pleistocene, the notion of "Paleo-deme" or "p-deme" (Howell 1996, 1999), which allows us to distinguish between geographically and chronologically restricted populations and discuss their possible phyletic relationships without implying or rejecting species status is the most appropriate. *Homo heidelbergensis* is a case in point, as it is differently interpreted to include European Middle Pleistocene specimens (*Homo heidelbergensis sensu stricto*), or European and African Middle Pleistocene specimens, (*Homo heidelbergensis sensu lato*), or even to extend to Asian samples (Rightmire 1998; Mounier et al. 2009; Harvati et al. 2010; Stringer 2012; Manzi 2012), or dismissed altogether (Mounier and Caparros 2015). The term Middle Pleistocene European *Homo* (MPEH) will be used here to denote European Middle Pleistocene humans with affinities to Neanderthals. Whenever possible, the comparative sample is grouped into the following categories: (1) *Homo habilis/rudolfensis*, (2) African *Homo erectus/ergaster*, (3) Early Pleistocene Eurasian *Homo*, (4) Asian *Homo erectus*, (5) Middle Pleistocene Asian *Homo*, (6) Middle Pleistocene African *Homo* (MPAfH), (7) Middle Pleistocene

Table 2.1 Linear measurements and angles used in the analysis^a

Group/Specimen	Abbrev.	Measurements used (Martin's number) ^b							References
		M1	M8	M29	M26	M32(5)	M10	M9	
Early Pleistocene Euroasian <i>Homo</i>									
Dmanisi 2700	Dm2700	155	126	89	95	150	85	67	Lordkipanidze et al. (2006)
Dmanisi 2280	Dm2280	177	136	101	108	149	105	65	Lordkipanidze et al. (2006)
Dmanisi 3444	Dm3444	163	132	80	90	148	91	67.5	Lordkipanidze et al. (2006)
African <i>Homo erectus/ergaster</i>									
Daka	Dk	180	133	101	116	141	105	89	Asfaw et al. (2008)
KNM-ER3733	ER3733	182	142	104	119	139	110	83	Lordkipanidze et al. (2006) and Rightmire (1990)
KNM-ER3883	ER3883	182	140	101	118	140	105	80	Lordkipanidze et al. (2006) and Rightmire (1990)
Asian <i>Homo erectus</i>									
Sangiran 17	San17	207	161	118	–	–	–	–	Lordkipanidze et al. (2006)
Bukuran	Bk	194	149	110	–	–	–	–	Grimaud-Herve et al. (2012)
Sinanthropus III	Sin3	188	144	102	–	–	–	–	Weidenreich (1943)
Sinanthropus X	Sin10	190	150	115	–	–	–	–	Weidenreich (1943)
Sinanthropus XI	Sin11	192	145	106	–	–	–	–	Weidenreich (1943)
Sinanthropus XII	Sin12	195.5	147	113	–	–	–	–	Weidenreich (1943)
Ngandong 1	Ng1	198	153	114	128	141	120	106	Kaifu et al. (2008) and Rightmire (1990)
Ngandong 7	Ng2	192	147	116	125	140	116	103	Kaifu et al. (2008) and Rightmire (1990)
Ngandong 11	Ng11	203	160	120	130	138	122	112	Kaifu et al. (2008) and Rightmire (1990)
Ngandong 12	Ng12	201	151	113	121	146	114	103	Kaifu et al. (2008) and Rightmire (1990)
Middle Pleistocene African <i>Homo</i>									
Kabwe	Kb	209	149	120	139	140	118	98	Rightmire (2008) and Murrill (1981)
Elandsfontein	El	202	138	116	–	–	–	–	Rightmire (2008)
Bodo	Bd	–	–	125	144	139	119	105	Rightmire (1996, 2008)
Middle Pleistocene Asian <i>Homo</i>									
Dali	DI	206.5	149.5	114	135	128	119	104	Wu and Athreya (2013)
Jinniushan	Jn	199	140	113	–	–	–	–	Coppens et al. (2008)
Middle Pleistocene European <i>Homo</i>									
Sima de los Huesos 4	SH4	201	164	115	126	140	126	117	Rightmire (2008)
Sima de los Huesos 5	SH5	185	146	106	114	145	118	105.7	Rightmire (2008)
Petralona	Pt	208	165	109	128	140	120	110	Rightmire (2008)
Ceprano	Cep	198	151	106	118	138	118	106	Ascenzi et al. (2000)
Upper Pleistocene <i>Homo sapiens</i>									
Skhul IV	Sk4	206	148	118	132	129.7	121	106	Vandermeersch (1981), Murrill (1981) and Cartmill and Smith (2009)
Skhul V	Sk5	193	146	106	118	130.7	114	99	Murrill (1981), Howells (1989) and Cartmill and Smith (2009)
Skhul IX	Sk9	213	145	114	130	131.6	120	96	Cartmill and Smith (2009)
Djebel Qafzeh 6	Q6	195	144	114	133	126.6	125	109.5	Vandermeersch (1981) and Howells (1989)
Djebel Qafzeh 9	Q9	–	–	115	130	133.8	117	103	Vandermeersch (1981) and Simmons et al. (1991)
Jebel Irhoud 1	JIr1	198	152	108	–	–	–	–	Howells (1989)
Upper Paleolithic <i>Homo sapiens</i>									
Predmosti 3	Pr3	202	143.4	120	137	135	128	104	Lubsen and Corruccini (2011) and Howells (1989)
Predmosti 4	Pr4	192	144	114	133	130	122	98	Lubsen and Corruccini (2011) and Howells 1989
Chancelade	Chan	–	–	111	130	128	127	101	Vandermeersch (1981) and Howells (1989)
Cro-Magnon 1	CrM1	206	153	125	147	125	126	102.5	Howells (1989) and Lubsen and Corruccini 2011
Mladeč 5	MI5	205.6	156	116	–	–	–	–	Frayet et al. (2006)
Mladeč 6	MI6	200.5	166.5	120.5	–	–	–	–	Frayet et al. (2006)
Mladeč 1	MI1	198.5	141.5	114	133	123	126.5	103.5	Wolpoff et al. (2006)
Obercassel 1	Ob1	195	144	118.9	–	–	–	–	Vandermeersch (1981)
Obercassel 2	Ob2	183	134	106.4	–	–	–	–	Vandermeersch (1981)
Khvalynsk	Khv	–	–	115.9	130	136.1	115	94.2	Stansfield and Gunz (2011)
Podkumok	Pod	–	–	108.6	125.4	129.8	115	94.1	Stansfield and Gunz (2011)
Satanay	Sat	–	–	111.4	123	141.9	105	91.5	Stansfield and Gunz (2011)
Skhodnya	Skho	–	–	122.5	140.7	134.9	114	98.9	Stansfield and Gunz (2011)

(continued)

Table 2.1 (continued)

Group/Specimen	Abbrev.	Measurements used (Martin's number) ^b							References
		M1	M8	M29	M26	M32(5)	M10	M9	
Neanderthals									
La Chapelle	LCh	209	157	107	121	137	122	109	Murrill (1981) and Howells (1989)
La Ferrassie I	LF1	208	159	116	135	145	121	109	Murrill (1981) and Howells (1989)
Šal'a	Sal	–	–	110	121	138	127	105	Sládek et al. (2002)
La Quina 5	LQ5	201	139	109	–	–	–	–	Weidenreich (1943) and Cartmill and Smith (2009)
Neanderthal 1	Neand	201	147	116	–	–	–	–	Murrill (1981) and Cartmill and Smith (2009)
Shanidar 1	Sh1	207	154	111.3	119	144	128	110	Trinkaus (1983) and Howells (1989)
Shanidar 5	Sh5	–	–	118	129	147	128	103.5	Trinkaus (1983) and Simmons et al. (1991)
Tabun C1	TbC1	183	141	96	107	130.7	121.5	98	Simmons et al. (1988), Weidenreich (1943) and Cartmill and Smith (2009)
Amud	Am	215	154	120	135	138.5	124	115	Vandermeersch (1981) and Cartmill and Smith (2009)
Specimens from the Central Balkans									
Bajloni's building	BAJ	188	138	104	–	–	–	–	Jovanović (1892)
Bački Petrovac	BP	–	–	118	137	139	117	95	Živanović, (1966)

^aAll measurements are in given millimeters, except M 32 (5), which is given in degrees

^bM numbers follow Martin and Saller (1957): Maximum cranial length (M1); Maximum cranial breadth (M8); Minimum frontal breadth (M9); Maximum frontal breadth (M10); Frontal sagittal arc (M26); Frontal sagittal chord (M29); Frontal angle (M32(5))

European *Homo* (MPEH), (8) Upper Pleistocene *Homo sapiens* from Africa/Near East, (9) Neanderthals, (10) Upper Paleolithic *Homo sapiens*.

Descriptions

"Bajloni's Building" Calotte

This specimen (hereafter BAJ) was found during the excavations of the foundations for the Bajloni's brewery building in the Old Town district of Belgrade in the late nineteenth century. The brewery opened in 1880 and the calotte must have been excavated shortly before that. It was subsequently lost in one of the many bombings of Belgrade in the early twentieth century. Professor Djordje Jovanović (1892) states that it was found two and a half meters below the current street level, on the low ledge that runs from Vidin gate to the Danube River, which he concludes was likely a Pleistocene river terrace. If we accept his claim that the specimen was found in the proximity of several teeth of *Elephas antiquus* (Falconer and Cautley 1847), a species found in Europe between 736 ka (in Italy) and 37 ka (in Netherlands) (Mol et al. 2007), the calotte could be of Pleistocene age.

According to Jovanović's (1892) description "*the skull is not complete. One can see the frontal, parietals, occipital and one temporal bone. Even fragmentary as it is, this skull is quite characteristic. On the frontal which is 104 mm long, one can observe well developed supraorbital arches (or tori). The right arch is more developed than the left. Above the*

right frontal arch there is a rough depression 2 cm by 3 cm. Frontal bossae are almost invisible and in the middle there is a rather well developed sagittal ridge. The forehead is so small and receding that one of our sculptors remarked—on having seen it for the first time—that the skull almost doesn't have any forehead" (Jovanović 1892, p. 33). Further on, he notes that the "*parietal bones are asymmetrical. The right one is more convex than the left. Obelion is very large. On the temporal bone one can see the origin of a strong and well developed temporal muscle and well developed mastoid process. The circumference of the skull was 50.4 cm. The length 18.8 cm and breadth 13.8 cm and accordingly, the cranial index is 72 and the skull is dolichocephalic*" (Jovanović 1892, p. 34). Jovanović promised a more detailed analysis should there be more finds—which he did not doubt—and concluded that "*with its receding forehead, well developed supraorbital arches and well developed temporal bone the skull belonged to a far more primitive man than any so far found in Belgrade*" (Jovanović 1892, p. 34). Unfortunately, no drawings or photographs accompanied this report.

The three measurements are far from sufficient to give us a reasonable picture of the taxonomic position of the specimen. Given the lack of standardization of measurements in the late nineteenth century, to evaluate whether or not the measurements are reliable, row-standardized values were compared with averages for the specified groups (following Harvati et al. 2011). Although limited in scope, the measurements seem to be reliable (Table 2.2). Given the paucity of measurements, a principal components analysis (PCA) run on both raw data and size-adjusted data was not informative. BAJ plotted in the middle of the graph (not shown) between the

Table 2.2 Row-standardized measurements with the means for all groups and BAJ

Group	M1	M8	M29
Early Pleistocene Euroasian <i>Homo</i>	2.22	2.12	1.95
African <i>Homo erectus/ergaster</i>	2.26	2.14	2.01
Asian <i>Homo erectus</i>	2.29	2.18	2.05
Middle Pleistocene African <i>Homo</i>	2.31	2.16	2.07
Middle Pleistocene Asian <i>Homo</i>	2.31	2.16	2.05
Middle Pleistocene European <i>Homo</i>	2.30	2.19	2.04
Early <i>Homo sapiens</i> Africa/Near East	2.30	2.17	2.05
Upper Paleolithic <i>Homo sapiens</i>	2.30	2.17	2.07
Neanderthals	2.31	2.18	2.04
BAJ	2.27	2.14	2.02

Early Pleistocene and the Middle and Upper Pleistocene material, but close to Tabun C1 (a Neanderthal) and Oberkassel 2 (a modern human), both of which are very small females (Bar-Yosef and Callander 1999; Bruzek 2006, respectively).

Frontal bone morphology can be a good indicator of a specimen's general affinities (Athreya 2012). However, only one measurement, the frontal chord, is available for BAJ. Based on values in Table 2.1, at 104 mm, the frontal chord value is just below the range of values for modern humans (106–125), MPEH (106–115), MPaFH (120–125), and MPaSH (113–114) and in the lower range of values for Neanderthals (96–120) and the Asian *Homo erectus* (102–120). While it cannot be taken at face value, this observation gives some support to the description provided by Jovanović (1892) that the forehead is very low, and strengthens the suggestion that it could have been of Pleistocene age. Although descriptions are not detailed enough, frontal keeling and a well-developed mastoid process would be inconsistent with Neanderthals and could point to *Homo erectus* s.l. or robust modern humans. Given its low forehead, existence of sagittal keeling, strong attachment for the temporal muscle, and a pronounced mastoid process, we could very tentatively attribute this specimen to the plesiomorphic end of the spectrum of Middle and Upper Pleistocene variation, consistent with erectus-like and modern-human-like morphology and not consistent with Neanderthal morphology. However, the recorded measurements and the description provided are not sufficient to exclude the possibility that it is a modern human of Pleistocene or even post-Pleistocene age.

Bački Petrovac and Žitište

The other two partial calottes come from the area north of Belgrade in the Pannonian plain: Bački Petrovac and Žitište. The current whereabouts of these two specimens are not known and I could not examine them directly. According to Živanović (1966), only one fragment of a skull was found in

Žitište (Fig. 2.2) comprising the squama and a small part of the horizontal portion of the frontal bone. “*Supraorbital tori are broken; however, based on what remains of them, and given the size of the frontal sinuses, they were well-developed. Frontal eminences were not clearly marked.... The maximum width of the bone is 8 mm and the minimum 1 mm. The bone is fossilized, although it is more compact and less fragile than the other one (Bački Petrovac). Prof Škerlj maintains that this fragment belongs to the skull of a recent human*” (Živanović 1966, p. 190). Not much can be learned from this very short description. The photographs of the specimen (Fig. 2.2) do not show any indication that the frontal fragment deviates from modern human morphology, particularly as there is a clear supraorbital notch. Other than the assertion that it is fossilized (although this cannot be taken for granted given the assessment by Dr. Škerlj reported above), there is no indication that it is not a recent, post-Pleistocene human.

The calotte from Bački Petrovac (Fig. 2.3) was uncovered during the excavation of a brickyard pit in the vicinity of the village of the same name in the 1950s. The fossilized calotte came into the possession of a local schoolteacher and an amateur collector who handed it to Serbian archaeologist Miodrag Grbić. According to Grbić (as reported by Živanović 1966), it was associated with Paleolithic stone tools, which were not described or specified. The calotte consisted of an almost complete frontal, fragmentary parietals (the right one was better preserved), and a small fragment of the ethmoid bone. Živanović presented the specimen in 1960 at an unspecified meeting of Yugoslav anthropologists and published measurements and a description of the fossil in 1966 in *Starinar*, the main archaeological journal in the country—the same one in which the Bajloni's calotte was published in 1892. Subsequently, Živanović published another report likening this specimen to his Proto-Dinarid group of the Padina type (Živanović 1975; Radović et al. 2014). The author notes “*more pronounced superciliary arches than modern ones and a very low forehead. The skull is very long and the volume is low. Morphologically notable are much larger dimensions of the frontal bone than of parietal bones. Regardless of the very pronounced frontal dimensions, the orbits are small*” (Živanović 1966, p. 190).

It is difficult to evaluate Živanović's description on the basis of the published figures alone. Notably, a larger frontal and short parietals are inconsistent with the description of the skull as very long, with low volume. The impression that the skull is low and long could be partially due to the lack of elements that would allow for proper orientation of the skull in *norma lateralis*, demonstrated by the difference between the left and the right profile in Živanović's (1966) original figures. In addition to describing the morphology, Živanović (1966, p. 189) provided a number of measurements, most of them on the frontal bone. As previously noted, the frontal bone has been found to be a good indicator of species status

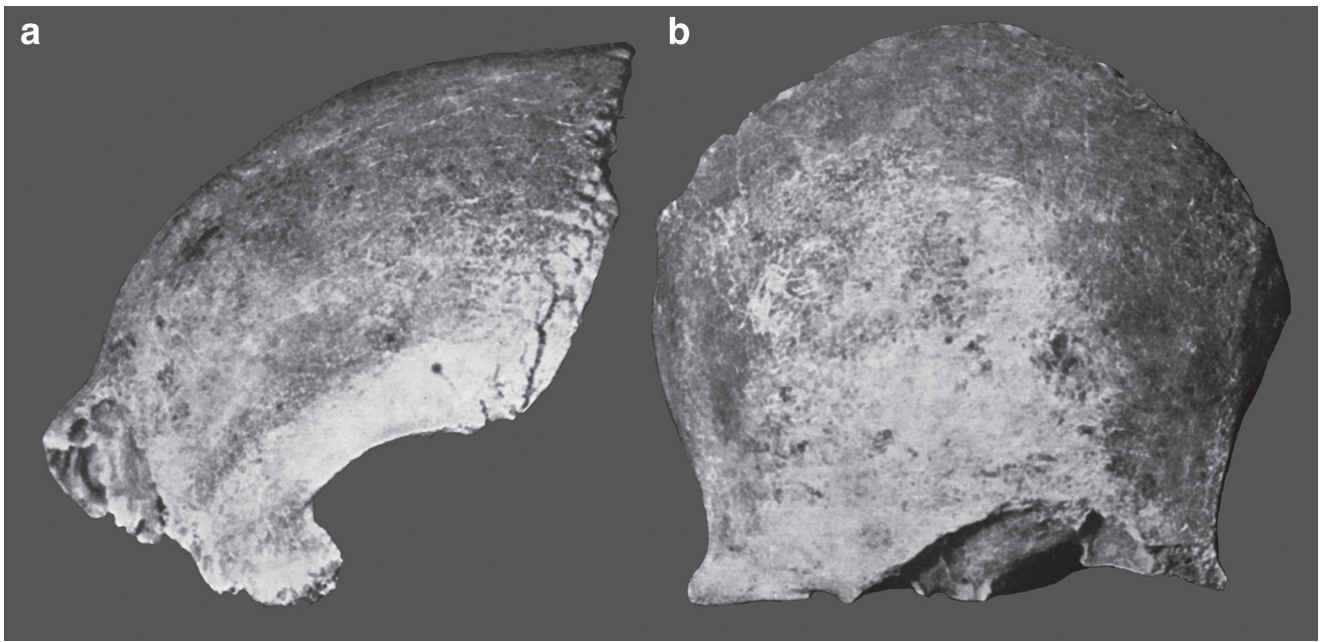


Fig. 2.2 Frontal from Žitište in (a) *norma frontalis* and (b) *norma lateralis*. Adapted from Živanović (1966)

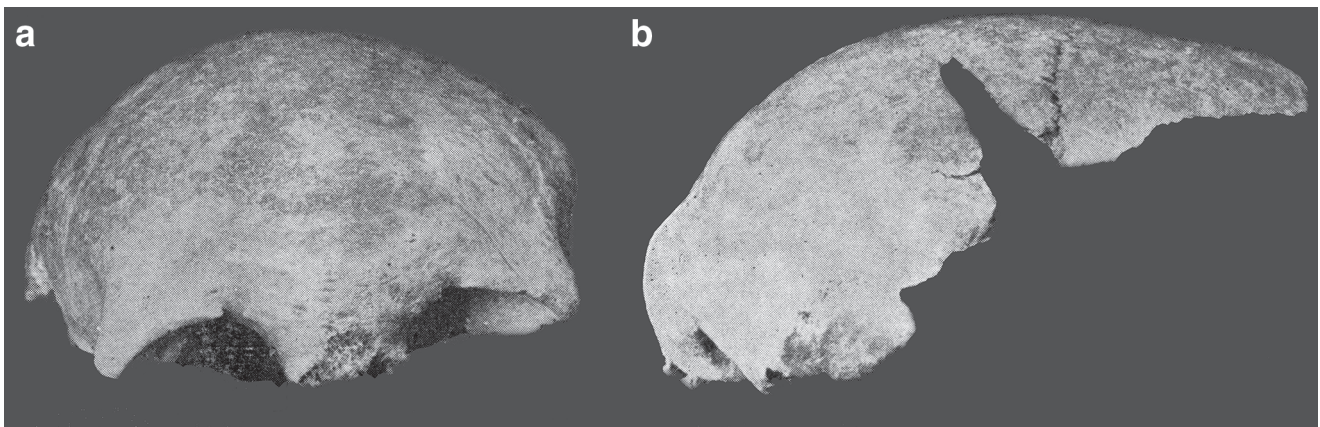


Fig. 2.3 Bački Petrovac calotte in (a) *norma frontalis* and (b) *norma lateralis*. Adapted from Živanović (1966)

in human evolution (Athreya 2012). A detailed reanalysis of these measurements is provided in a recent paper (Radović et al. 2014) and briefly summarized here.

A PCA (Fig. 2.4, Table 2.3) was performed on a variance–covariance matrix of five of the 17 measurements provided by Živanović (1966) for Bački Petrovac. Size-adjusted values were obtained by subtracting the log geometric mean of each variable for each individual from each log-transformed measurement (following Harvati et al. 2011). In order to maximize the comparative sample and strike a balance between the number of measurements and the number of specimens, measurements that are most commonly reported in the literature were selected (see Table 2.1). The optimal

point at which most specimens have the greatest number of measurements was reached at five measurements, present in 33 specimens of the Middle and Upper Pleistocene ages.

The first principal component suggests that 48.4% of total variance is due to size differences even when using size-standardized values. All variables were loading positively, with the exception of the frontal angle (Table 2.3): the low values of the eigenvector for frontal angle indicate that this variable does not have a strong influence on PC1; it is also negative as it is inversely proportional to size, since reducing the angle increases the curvature and therefore the size of the bone. Given the observed overlap between groups, size is not relevant for between-group differentiation. PC 2

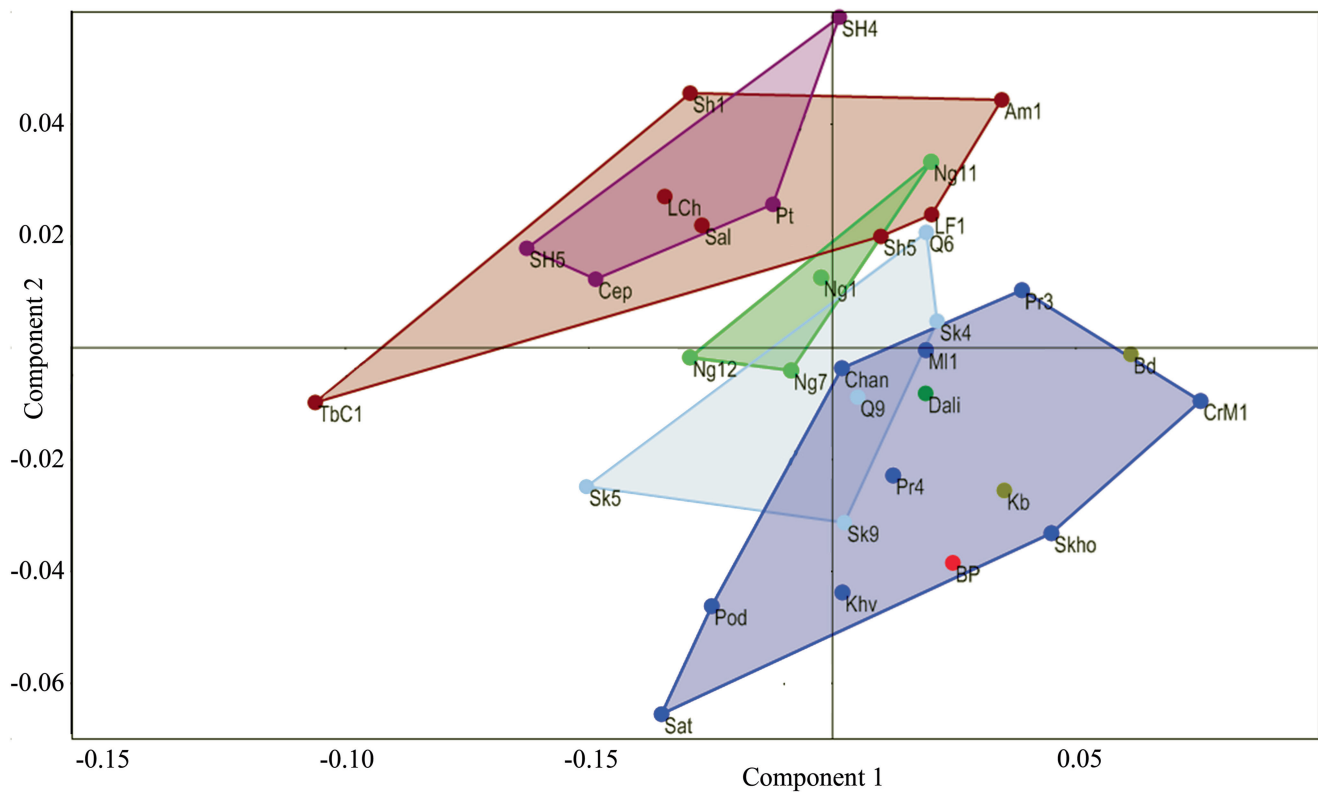


Fig. 2.4 Principal components analysis (PCA) of size-adjusted values for five frontal measurements of Bački Petrovac (BP) and a comparative sample. *Blue*: Upper Paleolithic *H. sapiens*; *Light blue*: Upper Pleistocene *H. sapiens*; *Green*: MPAsH and MPAfH; *Tan*: Neanderthals; *Purple*: MPEH

Table 2.3 Eigenvalues for size-adjusted data and loadings of variables on each axis

PC	Eigenvalue	% variance	M29_frontal chord	M26_frontal arc	Frontal angle (M-32(5))	M10_MFB	M9_min frontal
1	0.00139355	48.421	0.5975	0.779	-0.1103	0.1279	0.08746
2	0.000834579	28.999	-0.002527	-0.1397	0.2089	0.4607	0.8512
3	0.000473695	16.459	0.2754	-0.02104	0.8559	-0.4366	0.02363
4	0.000138295	4.8053	0.05955	-0.05874	0.3824	0.7621	-0.5157
5	3.79E-05	1.3155	-0.7507	0.6081	0.2558	0.0005135	0.0345

(29.0% of the total variance) shows a contrast between breadth and length variables: the strongest positive influence is exerted by both the minimum (M9) and maximum (M10) frontal breadth and the strongest negative influence by the frontal arc. Neanderthals group together with MPEH with wider and shorter frontals and smaller difference between minimum and maximum frontal breadth, while Upper Paleolithic *H. sapiens* and African Middle Pleistocene specimens (especially Kabwe) group together on the opposite end with a larger difference between the two breadths. *H. erectus* and early modern humans are in the middle. PC3 (16.5% of variation; not shown) represents a contrast between the fron-

tal angle and remaining variables, with Bački Petrovac falling within the range of variation of Upper Paleolithic *H. sapiens*, close to Bodo and Kabwe, with a wider frontal angle and longer frontal chord. Since post-Pleistocene modern human variation completely overlaps with Pleistocene modern humans, until the actual remains are located and dated directly, it is not possible to say anything more definitive about the specimen, or ascertain Pleistocene affinities. A new project that aims to recover more materials from this location and the surrounding area is underway and we are still looking for the actual calotte in hope of obtaining a direct date.

Belgrade Mandible RGF94/1

A mandible unearthed in the 1920s from loess deposits in the vicinity of Belgrade is currently housed at the Faculty of Mining and Geology at the University of Belgrade (RGF 94/1). It was rediscovered in the storage drawers of the Geological collection and a description of the specimen was published by Roksandic and Dimitrijević (2001). While (glaciogenic) loess deposits in Serbia are unequivocally associated with the Pleistocene (Marković et al. 2008), new research shows that aridity in the Pannonian basin during the Holocene could produce significant eolian nonglaciogenic loess-like deposits (Sherwood et al. 2013). Given the geographic position of Belgrade on the Southern edge of the Pannonian plane, this is important to keep in mind. The evidence of fossilization has been obscured by the impregnation of the mandible with paraffin, which was performed for conservation purposes. Recently, a ^{14}C date indicating Holocene age has been obtained (Dimitrijević, pers. comm. 28/05/2013). However, at this point, it is not clear to what extent the carbon from the paraffin could have influenced the obtained date. The post-Pleistocene date would be consistent with the attribution of the specimen to an anatomically modern human (Roksandic and Dimitrijević 2001).

Even though this right semimandible is broken off at the symphysis—generally considered to be one of the most unambiguous anatomical area that separates modern human mandibles from more plesiomorphic forms (Schwartz and Tattersall 2000)—it is still possible to see the beginning of a slight exomandibular curvature at the breakage point that could indicate the existence of a bony chin (Fig. 2.5, upper right panel). There are other indicators that the mandible belongs to an anatomically modern human: there is no evidence of a retromolar space, the mental foramen is situated under the P_3/P_4 and is equidistant from the alveolar and basal margins. In addition, the P_3 is bicuspid, and tall and narrow in buccal view. It shows remarkable symmetry in the occlusal view, with a prominent lingual cusp, well-developed marginal ridges, and a clear mesiolingual groove. The central developmental groove is not present, a relatively common variant in modern humans. The mandibular P_3 has been noted for exhibiting the highest variability after the M_3 in modern humans (Cleghorn et al. 2007), but its overall symmetry is often associated with the modern human condition, while pronounced asymmetry is a plesiomorphic trait observed in 40–50 % of *H. erectus*, Neanderthals, and Middle Pleistocene *H. sapiens* (Bailey 2002). The P_4 is tricuspid with the buccal cusp the most prominent; it exhibits a

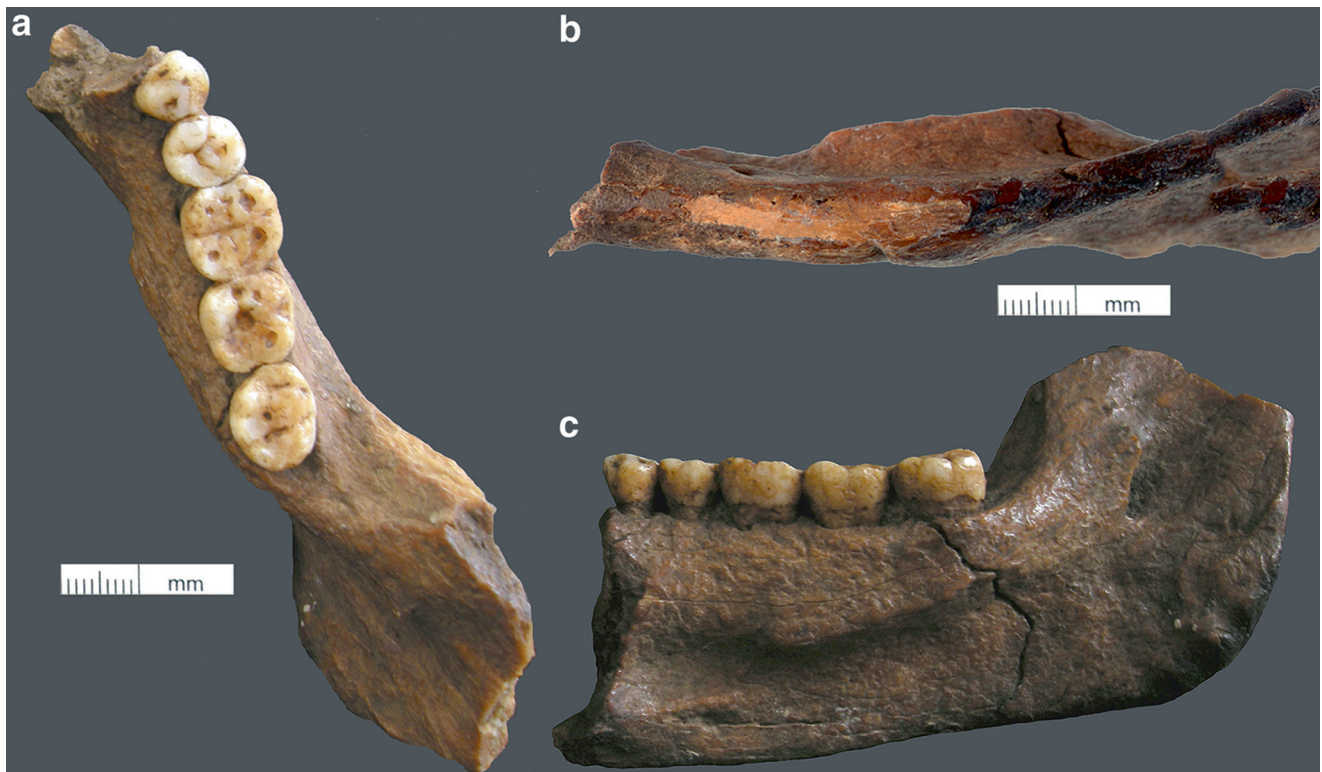


Fig. 2.5 Belgrade mandible RGF94/1. (a) Occlusal view, (b) basal view, and (c) endomanibular view of the specimen from the vicinity of Belgrade

pronounced mesiolingual cusp, without a mesial crest. The tooth shows no marked asymmetry. Asymmetry is predominant in Neanderthals (90%), very rare in modern humans (6%) but occurs in both *H. erectus* and archaic *H. sapiens* at 36% and 33%, respectively (as reported by Bailey 2002, although note small sample sizes). Together with the asymmetry, a mesially placed metaconid and a mesial crest are deemed distinctively Neanderthal features (Bailey and Lynch 2005). This specimen has no mesial crest, and a mesially placed metaconid on its own can be found in modern humans, albeit at somewhat lower and more variable frequencies than in Neanderthals (Bailey 2002: Table 5.6). The M_1 has four cusps, a square outline, an anterior marginal ridge without midtrigonid crest, and a “+4” pattern. The M_2 has a square outline, an anterior fovea and no midtrigonid crest, a “Y4” pattern, and a mesial and central occlusal pit. The M_3 has a six-cusp pattern with an irregular outline and a shallow anterior fovea (Hillson 1996). The teeth are tightly packed and intermolar wear facets are present. One notable feature of this mandible is the extreme development of the mylohyoid line. As can be seen in Fig. 2.5, the mylohyoid line is very strong and begins below the M_1 , forming an abrupt angle in continuation of the sublingual fossa, which is deep and oval in aspect. While not uncommon in modern humans (or Neanderthals), an exaggerated mylohyoid line is rarely mentioned in the literature and needs to be more systematically examined. Kennedy (2000) notes it for the Upper Paleolithic mandible from Bhimbetka, and Mirazón Lahr and Haydenblit (1995) for a Natufian mandible from the cave of Et-Tin. The sublingual fossa is considered as a very variable feature in modern human populations (Uchida et al. 2012).

Table 2.4 shows character states for the mandibular specimens included in the Principal Coordinate Analysis (PCO). These nonmetric traits are taken from Mounier et al. (2009) as relevant for differentiating between MPEH, Neanderthals, and modern humans in Pleistocene Europe. Mounier et al. (2009) used a larger battery of traits and therefore obtained more robust results and a better separation than observed here. This is because RGF 94/1 lacks all of the diagnostic traits of the symphyseal region and the vertical ramus (see also results for the Balanica mandible, below). Nevertheless, the PCO (Fig. 2.6) shows a separation between Neanderthals / MPEH on one hand and modern humans and *H. erectus* on the other hand. RGF94/1 falls in the modern human range of the graph overlapping with *H. erectus* and far from Neanderthal or MPEH morphology.

The Balanica Mandible

Among these fortuitous finds, the Balanica mandible (BH-1) stands out as the only specimen unearthed during controlled archaeological excavations (Roksandic et al. 2011). The

mandible has recently been dated by electron spin resonance (ESR) combined with uranium series isotopic analysis (U-series), and infrared/postinfrared luminescence (IRSL) dating, to older than 392–525 ka (Rink et al. 2013). As such, it represents the oldest radiometrically dated human fossil from Eastern Europe and the Balkans. The mandible was excavated from Mala Balanica cave (N43°20.211', E22°05.115'), part of a two-cave system located in the Sićevo gorge. The cave is situated some 332 m above sea level and currently about 100 m above the Nišava River, with the opening facing SSW across the valley, 7 m away from the entrance to the larger Velika Balanica cave. The gorge is cut through by the Nišava River, which provides an important communication route between two adjoining river valleys. BH-1 originates from layer 3b, three arbitrary 5 cm spits below the base of a pit dug in by “gold diggers” in this area between the field campaigns of the 2005 and 2006 seasons. Below the clandestine pit there are 2 m of compact, water-borne silts and clays. These fine-grained sediments are *in situ*, in their primary position relating to water pooling in this area of the cave (Morley, pers. comm. 4/15/2013). The lowest recorded artifacts were found in layers 1.5 m above the mandible. The animal teeth used for dating originate from the layer directly above the mandible and were recorded *in situ*. The concordance of all three dating techniques—ESR, U-series, and IRSL (Rink et al. 2013)—indicates that the obtained minimum date is reliable; the fact that the mandible was recovered from a layer below the obtained date suggests that the mandible could be slightly older, although probably not substantially.

The BH-1 specimen is a left hemi-mandible (Fig. 2.7), preserved from the posterior margin of the canine alveolus to the mesial aspect of the ascending ramus, with all three molars present in their sockets. The mesial portion of the mandible shows an old breakage filled with sediment, whereas all of the breaks on the distal end are fresh: the lower half of the mesolingual root of the M_3 is missing and the remaining roots are exposed due to the destruction of the adjacent endomandibular lamina. The alveoli of the P_3 and P_4 are complete and are for the most part filled with sediment. The posterior portion of the mandible seems to have been subject to water infiltration resulting in substantial fragility. Complete eruption and closure of the root apex of the M_3 indicates an adult individual, while minimal wear on the M_3 and slight to moderate wear on the M_1 and M_2 each suggest a relatively young adult. Sex could not be determined.

The highly relevant symphyseal region is missing and so is the basal margin mesially from below the mental foramen. The anterior marginal tubercle could not be observed in this specimen as the relevant area is missing. In lateral view, the basal and alveolar margins are almost parallel: the corpus measures 34.2 mm in height at the mental foramen and recedes slightly toward the M_3 , where it measures 31.2 mm. The exomandibular relief is faint: a poorly defined superior

Table 2.4 Character states used in PCO analysis

Group/specimen	Abbreviations	I ^a	J	K	L	N	O	P	Q	R	S	T	U	OO	PP	UU
Early Pleistocene Euroasian <i>Homo</i>																
Dmanisi 211	Dm211	3	2	1	1	2	1	2	2	1	2	3	2	1	2	1
Dmanisi 2600	Dm2600	1	2	1	1	3	2	2	2	2	2	2	2	2	1	1
ATD6-96	ATD6-96	3	2	1	2	2	1	1	2	1	2	2	2	2	1	1
African <i>Homo erectus/ergaster</i>																
KNM-ER992	ER992	3	1	1	3	2	2	1	3	1	2	2	2	1	1	1
Asian <i>Homo erectus</i>																
Sangiran1b	San1b	3	2	1	2	2	2	1	2	1	2	2	2	2	2	1
Sinanthropus H1	SinH1	3	2	2	2	3	2	2	2	2	3	2	1	2	2	1
Middle Pleistocene African <i>Homo</i>																
Tighenif1	Tig1	3	2	1	1	2	1	2	3	1	2	1	2	1	1	1
Tighenif2	Tig2	3	1	1	2	2	1	2	2	2	2	2	2	2	1	1
Tighenif3	Tig3	3	2	2	2	3	2	2	3	2	2	1	3	1	1	1
Middle Pleistocene European <i>Homo</i>																
Mauer	Ma	2	2	2	2	3	2	2	3	3	2	1	3	1	1	1
AT-888	AT-888	3	1	3	1	2	1	2	2	3	3	1	2	3	1	1
AT-950	AT-950	3	2	2	1	3	2	2	3	3	3	1	2	1	1	2
Arago II	Ar2	3	1	3	1	2	2	1	3	3	2	1	3	1	2	2
Arago XIII	Ar13	3	2	2	1	2	1	2	3	2	2	1	2	1	1	2
Montmaurin	Mont	3	2	2	2	2	2	1	2	2	2	1	2	2	1	2
Ehringsdorf F	EhF	3	2	3	2	2	1	2	1	3	3	1	1	1	2	2
Neanderthals																
Krapina J	KrJ	3	2	3	1	3	2	2	2	3	3	1	1	3	1	1
Krapina G	KrG	3	2	3	2	3	2	2	1	3	3	1	1	3	3	2
Spy 1	Spy1	2	1	3	2	1	1	1	2	3	3	1	2	3	2	2
Regourdou	Reg	3	2	3	1	2	1	2	1	3	3	1	2	3	1	1
Bañolas	Ban	3	1	2	3	3	2	2	3	2	3	2	1	2	1	2
La Ferrassie 1	LF1	3	2	3	2	2	2	1	2	3	3	1	1	3	3	2
La Quina H5	LQH5	3	1	2	1	2	1	2	1	3	3	1	2	3	3	2
Shanidar I	Sh1	2	1	2	1	3	2	2	2	3	3	1	2	3	1	2
Amud1	Am1	3	1	3	1	2	1	2	1	3	3	1	2	3	1	1
Zafarraya	Zaf	3	2	3	1	3	2	2	1	2	3	1	1	3	2	1
Early <i>Homo sapiens</i> Upper Pleistocene																
Qafzeh 9	Q9	1	1	1	1	2	1	2	3	2	2	2	2	1	3	1
Skhul V	Sk5	2	1	1	2	1	1	1	2	2	3	1	2	2	1	1
Upper Paleolithic <i>Homo sapiens</i>																
Cro-Magnon 1	CrM1	2	1	1	2	2	1	2	2	1	2	3	2	1	2	2
Ohalo II	Oh2	3	1	1	2	2	1	2	2	1	2	2	2	2	2	2
Abri Pataud 1	AP1	3	1	1	1	1	1	1	2	1	1	2	1	2	3	1
Specimens from the Central Balkans																
Balanica 1	BH-1	3	1	1	2	2	1	1	2	1	2	2	3	2	2	1
RGF94/1	RGF94/1	3	1	1	2	1	2	1	2	2	1	2	2	2	2	2

^aAfter Mounier et al. (2009): except for Balanica 1 and the RGF94/1 which were scored by the author. (**I**) Alveolar margin orientation toward inferior margin: (1) Steep (2) Slowly inclined (3) Parallel; (**J**) *Foramen mentale* number: (1) Single (2) Multiple; (**K**) *Foramen mentale* position toward the tooth row: (1) P3-P4, P4 (2) P4-M1 (3) M1; (**L**) *Foramen mentale* superoinferior position on the corpus: (1) Inferior (2) Midline (3) Superior; (**N**) *Sulcus intertoralis* definition of the hollowed area posterior to the foramen mentale surrounded by the marginal tori: (1) Flat surface (2) Weak: mainly defined by one torus (3) Well: defined by the two tori; (**O**) *Torus marginalis superius* relief: (1) Weak/absent (2) Swelling clearly visible; (**P**) *Torus marginalis inferius* relief: (1) Weak/absent (2) Swelling clearly visible; (**Q**) *Prominentia lateralis* relief: (1) Flat surface (2) Weak swelling (<7 mm) (3) Strong swelling (>7 mm); (**R**) *Prominentia lateralis* position along the tooth row: (1) M1 and M2 (2) M2-M3 (3) M3; (**S**) Retromolar space relationship between the anterior ramus rim and M3 in norma lateralis (1) Covered (2) Partially covered (3) Uncovered; (**T**) Retromolar area inclination (1) Horizontal (2) Inclined (3) Vertical; (**U**) *Extramolar sulcus*: Width of the gutter (1) Absence (2) Narrow gutter (3) Large gutter; (**OO**) Mylohyoid line orientation: (1) Parallel (2) Inclined (3) Diagonal; (**PP**) Mylohyoid line position at the M3 level (1) Low (2) Intermediate (3) High; (**UU**) *Submandibular fossa* depth beneath the alveolar region: (1) Shallow (2) Deep

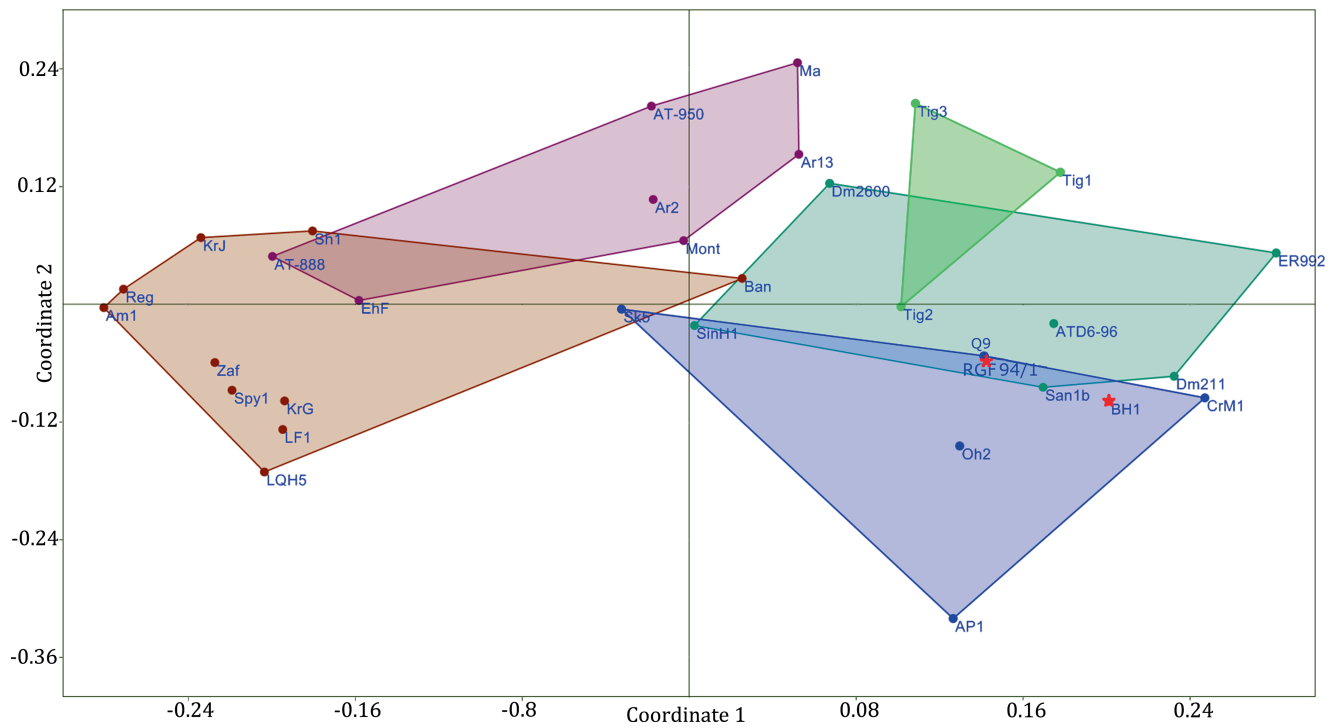


Fig. 2.6 Principal Coordinate analysis (PCO) of character states for all of the traits preserved in BH-1, RGF94/1, and comparative specimens. Blue: Pleistocene *H. sapiens*; Light green: MPAfH; Dark green: Early Pleistocene Eurasian Homo; Tan: Neanderthals; Purple: MPEH

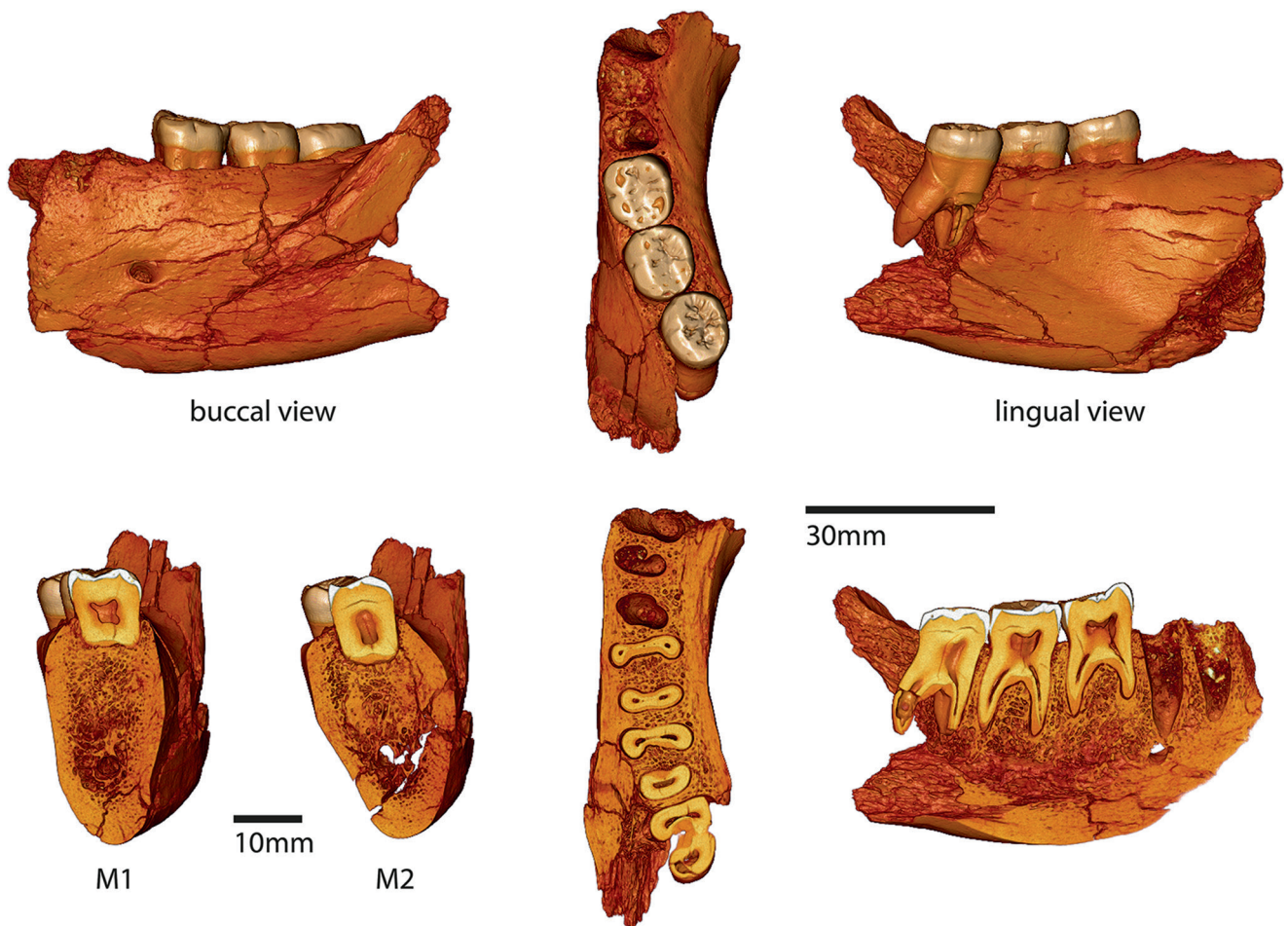


Fig. 2.7 The BH-1 specimen visualized as a volume rendering using the microtomographic images: external morphology of the mandible and internal structures visualized using sections. Reproduced with permission from Skinner et al. (2016): Fig. 1 top two rows

marginal torus represented by a slight change in the orientation of the lamina to the axes of the horizontal branch above and below the mental foramen, transitions smoothly into the lateral prominence. The latter is located at the level of M_1/M_2 , equidistant from the alveolar and basal margins. The ascent of the oblique line begins just above the posterior marginal tubercle, 18.5 mm below the alveolar border at the level of M_1/M_2 vertically, and the mental foramen horizontally. The lateral prominence is more anterior than in Neanderthal and MEPH samples, where it is commonly located under the M_3 (Rosas 2001). The fragment of the exomandibular lamina of the vertical branch shows very slight relief at the masseteric fossa, with no pronounced rugosities. The reconstructed root of the vertical branch does not indicate the presence of a retro-molar space. The mental foramen is oval in shape, situated below the P_4 alveolus, almost equidistant from alveolar and basal margins. While the bone is robust, the relief of the internal surface is not marked. The alveolar border shows thickening on the lingual side from P_3 to M_2 (and possibly beyond), forming a mandibular torus just below the alveolar process, with the width decreasing mesially. The width of the subalveolar plane increases toward the middle portion of the mandible, forming a shelf-like area (oblique rather than subvertical *planum alveolare*) that extends from below the P_3 toward the canines and the symphysis. The subalveolar plane (sublingual fossa) is flat rather than concave. The submandibular fossa is moderately concave, and the expression of the mylohyoid line is moderate, presenting a change in orientation between the subalveolar plane and the submandibular fossa rather than a sharply delineated line. The level at which it begins cannot be ascertained, as the lower portion of the endomandibular face is destroyed in that area. However, it seems to extend toward the P_3 . Its ascent is not steep and it is still present at the level of the mesial alveolar margin of the M_3 beyond which it can no longer be observed due to the breakage (Roksandic et al. 2011).

The mandible is thick in the bucco-lingual dimension. The width of the mandible varies from 19.1 mm at the canine alveolus, becoming more restricted toward the mental foramen (17.8 mm) and M_1 (17.5 mm) and increasing toward the M_2 (18.4 mm) and the M_3 (23.8 mm). The occlusal view shows that the mandibular torus decreases in width from the M_3 to P_3 , while the shelf-like thickening of the alveolar plane increases in width from the M_1 toward the symphysis. The extramolar sulcus is very wide, accentuated by a low and nonsteep oblique line. The substantial width of the extramolar sulcus is further accentuated by a pronounced curvature of the distal portion of dental arcade toward the sagittal plane (Roksandic et al. 2011).

Only the three left molars are present in the BH-1 specimen. Their occlusal outline is subrectangular and elongated mesiodistally. The molars have all five main cusps (protoconid, metaconid, hypoconid, entoconid, and hypoconulid), but

the occlusal surface is not complex, and there are no extra fissures or crests. The hypoconulid is large and buccally aligned on all three teeth. There is an easily observed, wedge-shaped “cusp 7” (*tuberculum intermedium*) (Scott and Turner 1997) in all three molars. The mesial marginal ridge exhibits as a proper ridge in M_1 with no anterior fovea. This feature is continuous and depressed (very low) in M_2 and accompanied by an anterior fovea that is relatively poorly defined; it is represented by a wide depression rather than a deep triangular depression, as described by Scott and Turner (1997). The mesial marginal ridge shows a tubercle on the M_3 and a possible but unclear anterior fovea (Hillson 1996). The M_2 and M_3 present a distal trigonid crest that can be assessed by a short transverse fissure, slightly oblique to the buccolingual fissure. None of the teeth show a continuous midtrigonid crest—considered to be an indicator of Neanderthal affinity as it occurs in 96 % of Neanderthals (Bailey 2002). While the M_1 and M_2 have the same buccolingual width (10.9 mm) and mesiodistal length (11.5 mm), the M_3 is longer mesiodistally (12.1 mm) and narrower buccolingually (10.5 mm) (Roksandic et al. 2011).

A well-developed anterior fovea is common in Neanderthals (87 % according to Bailey 2002) and variable in modern humans (with an 83 % frequency in a sample of modern Croats reported by Gauthier et al. 2010). The presence of “cusp 7” is nondiagnostic, although it is much more common in *H. erectus* (40 %) than in Neanderthals (18.8 %), and variable in modern human populations (3–61 %) (Bailey 2002), with the highest frequencies recorded in Africa (Scott and Turner 1997). The expression of the distal trigonid crest is highly variable (Scott and Turner 1997) and according to Martínón-Torres and colleagues (2008, 2102, 2014) often underscored. It is, however, expressed in higher frequencies in the Dmanisi and Sangiran populations (Martínón-Torres et al. 2008; Martínez de Pinillos et al. 2014). The mental foramen is located under the M_1 in up to 80 % of Neanderthal specimens and 54 % of the Middle Pleistocene samples from Sima de los Huesos (Rosas 2001). This position is often interpreted to be a reflection of the development of marked midfacial prognathism (Quam and Smith 1998). The more anterior position of the mental foramen, its equidistant position in relation to the alveolar and basal margins, and the absence of a retromolar space—all plesiomorphic traits observable in *H. erectus*—reinforce the dental evidence and indicate that the mandible lacks autapomorphies of Neanderthals and their Middle Pleistocene precursors.

The results of the PCO (Table 2.5, Fig. 2.6) reveal that BH-1 plots close to Dmanisi 211, Sangiran 1B, and Upper Paleolithic modern humans. This should not be surprising, given its plesiomorphic character states and complete lack of Neanderthal morphology. Figure 2.6 shows a separation between Neanderthal / MEPH morphology on one hand and modern humans and *H. ergaster/erectus* on the other hand.

In this context, it is interesting to note the position of the Bañolas mandible, whose ambiguous morphology is well illustrated by its position on this graph close to the modern human /*H. erectus* overlap. The Bañolas mandible has been variably treated as a pre-Neanderthal, *H. heidelbergensis*, or Neanderthal, and recently as showing more modern traits (Alcázar de Velasco et al. 2011). The Atapuerca specimen ATD6-96 is placed on the *H. erectus*/modern human part of the graph, while the Sima de los Huesos specimens fall close to the Neanderthals and other MPEH specimens. The Tighenif mandibles overlap with Early Pleistocene Eurasian

specimens close to the *H. erectus*/modern human convex hull, while MPEH show substantial overlap with Neanderthals. On the basis of preserved morphology, BH-1 differs significantly from the MPEH specimens generally grouped under *H. heidelbergensis* (Roksandic et al. 2011). It exhibits plesiomorphic features such as a prominent *planum alveolare*, thick mandibular corpus, wide exomolar sulcus, flat rather than concave sublingual fossa, and poorly defined relief of the submandibular fossa. There is a complete lack of derived Neanderthal features: the mental foramen is below the P₄ alveolus, equidistant from the alveolar and the basal margins, and there is no retromolar space. Dental traits are equally plesiomorphic: mesotaurodontic roots, two mesial and two distal diverticles on the M₁, “Y” fissure pattern, five main cusps, and a well-developed “cusp 7.” Given the size of the mandibular body, the dentition is relatively small, and its size fits well with that of Middle Pleistocene specimens.

A recent examination of the internal structure of the mandibular molars using microcomputed tomography (Fig. 2.8; Skinner et al. 2016) confirmed that the absence of Neanderthal traits in the mandibular morphology of BH-1 should not be regarded as a result of its partial preservation. Skinner et al. (2016) quantitatively assessed the enamel–dentine junction (EDJ) morphology using geometric morphometrics, molar enamel thickness, and the expression of discrete dental traits in comparison to *Homo erectus sensu lato*, *Homo neanderthalensis*, Pleistocene *Homo sapiens*, and recent *Homo sapiens*. The results of the study indicate a primitive dental morphology for BH-1 molars and confirm a lack of Neanderthal affinity.

Table 2.5 Principal coordinates analysis matrix (using chord distance)

Axis	Eigenvalue	Percent
1	72.233	34.111
2	32.475	15.336
3	19.302	9.1151
4	16.591	7.8349
5	15.041	7.1027
6	13.098	6.1854
7	9.4069	4.4423
8	7.6781	3.6259
9	6.725	3.1758
10	5.1328	2.4239
11	3.4586	1.6333
12	2.6406	1.247
13	2.4238	1.1446 ^a

^aOther values explain less than 1 % of variation

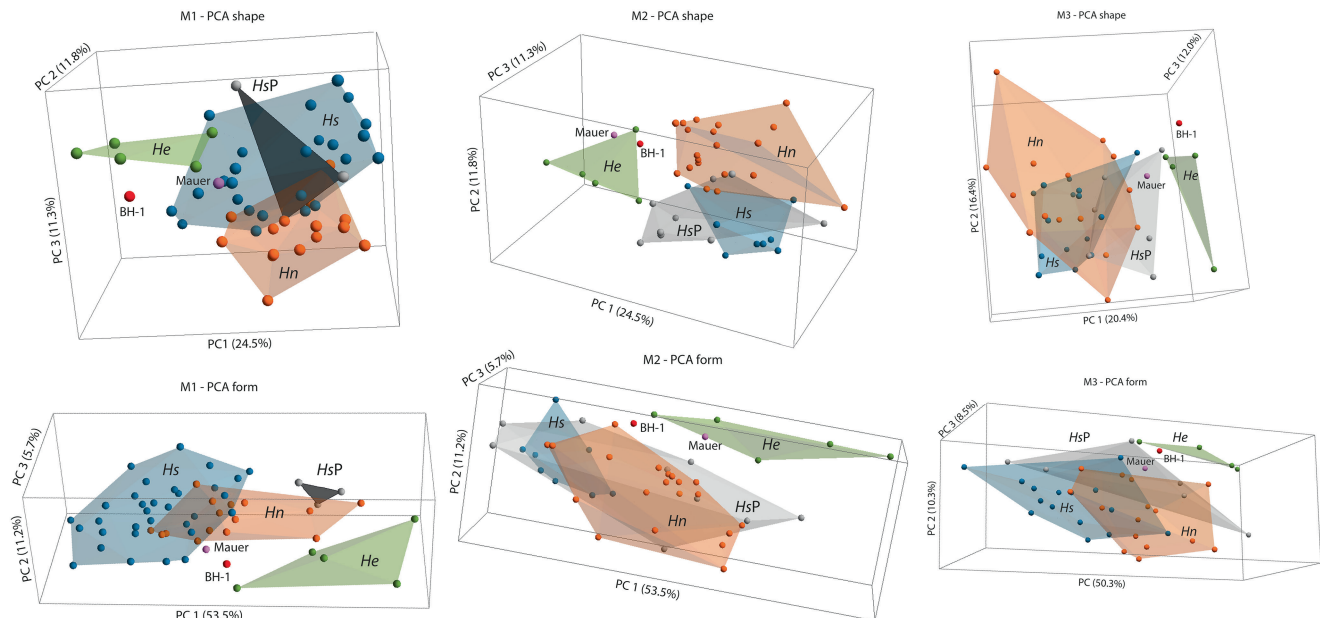


Fig. 2.8 Principal components analyses (PCA) of enamel–dentine junction (EDJ) morphology of the first, second and third molar sample in shape (top) and form (bottom) space. Red sphere—Balanica,

He—*Homo erectus sensu lato*, Hn—*Homo neanderthalensis*, HsP—Pleistocene *Homo sapiens*, Hs—recent *Homo sapiens*. Adapted from Skinner et al. (2016)

Discussion

We have already suggested that the BH-1 mandible could play an important role in our understanding of the evolution of Middle Pleistocene hominins in Europe (Rink et al. 2013). The absence of Neanderthal traits in the BH-1 mandibular morphology could be interpreted as a result of individual variation, as mandibles are generally highly variable. Moreover, the specimen is fragmentary. However, the mandibular morphology, the dental and EDJ morphology, enamel volume, and root morphology all lack Neanderthal features, suggesting that this is not due to the fragmentary nature of the specimen. At the age range earlier than 397–525 ka, the primitive character of the mandible is not entirely unexpected. In the context of an accretion model of Neanderthal evolution (Dean et al. 1998; Hublin 2013), the traits would appear in a mosaic fashion allowing the individual within a population to exhibit Neanderthal morphology in one area of the skull while retaining plesiomorphies in other areas. A recent reevaluation of the Sima de los Huesos cranial remains (Arsuaga et al. 2014)—including seven previously unpublished skulls—confirmed the existence of Neanderthal-derived morphology in these specimens in both mandibular and cranial morphology, as well as on the EDJ. The Sima de los Huesos material is now dated to circa 430 ka by a combination of different methods (Arnold et al. 2014; Arsuaga et al. 2014). According to Arsuaga et al. (2014), changes in the facial skeleton preceded the changes in the braincase and conform to the expectations of the accretion model (Dean et al. 1998). The authors noted the difference between the Sima material and Ceprano and Arago which do not exhibit the same suite of Neanderthal features in the cranial skeleton and postulated several paleodemes within the EMPH.

The Balanica (BH-1) individual could be interpreted as belonging to one of these paleodemes, as we already suggested (Rink et al. 2013). Alternatively, given that the age of BH-1 hominin is only a minimum age, this individual could have belonged to an undifferentiated population, ancestral to both Neanderthal and non-Neanderthal lineages. The lack of Neanderthal traits in both the dentition and the mandible of the Mauer specimen dated to 609 ± 40 ka (Wagner et al. 2010) is consistent with this interpretation, even as it plots closer to Western European specimens in Fig. 2.6.

If an ancestral Neanderthal population continued to develop in relative isolation over the cold periods in the west (as the evidence seems to indicate), the plesiomorphic character of the Visogliano mandible dated to 350–500 ka (Falguères et al. 2008) and the ambiguous morphology of the Ceprano calvaria dated to 353 ± 4 ka (Nomade et al. 2011), might be explained by their geographic distance from such western populations.

When the Middle Pleistocene variability in Europe is examined in the context of geographically and chronologically defined p-demes (Howell 1996), and if we accept several successive migrations into Europe on the basis of lithic (Lycett 2009; Bar-Yosef and Belfer-Cohen 2013) and paleoecological evidence (Carrión et al. 2011), one could postulate a core demographic area (Dennell et al. 2011) from which human populations were reseeded after glaciations. In this population model, which is based on demographic “sources” and “sinks,” a small number of core “sources” in the south of the continent would have repopulated more northern parts during interglacials, with northern groups representing demographic “sinks.” With western source populations as bearers of derived Neanderthal morphology as early as 430 ka in Sima material (Arnold et al. 2014), the observed attenuation of Neanderthal traits in the more easterly or later populations (Visogliano, Ceprano, maybe even Petralona) could be explained by admixture with a group from outside of the isolated glacial refugium, i.e., a population from Southwest Asia.

The Balkan Peninsula (and consecutively the Central Balkans)—which remained in contact with Southwest Asia during glacial times—could be perceived as belonging to this core demographic area. Alternating routes of migration within Eastern Mediterranean were open throughout the Pleistocene: the one, over the coastal areas of the Black Sea, was available during warmer phases; while the other, over the Bosphorus, the Aegean and Ionian shelf was open during glaciations (see Tourloukis 2010, Fig. 6.18). Koufos et al. (2005, p. 181) consider the Eastern Mediterranean—comprised of the Balkan Peninsula, the Aegean Sea, Asia Minor, and the Middle East “as an important domain for mammal exchanges between Asia, Europe and Africa during the Neogene/Quaternary,” where “migration pathways between the three continents crossed” (see also Koufos and Kostopoulos, 2016). While their analysis, similar to that of Spassov (2016), is concerned with early human migrations, there is strong evidence of contact between Eastern European and Asian micromammal fauna in the Middle Pleistocene and beyond (Van Kolfschoten and Markova 2005).

Considering these areas as a single geographic entity places emphasis on the current fossil record of Southeast Europe, which, while comparatively scant, becomes critical for understanding continent-wide processes. While isolation represented the major mechanism of evolutionary change in the west of the continent (Rightmire 1998), causing a bottleneck and fixation of derived traits, the Balkan Peninsula need not have experienced the effects of this isolation. Accordingly, the population that inhabited it and maintained contact with Southwest Asia throughout glaciations would be expected to retain a number of plesiomorphic (i.e., non-Neanderthal)

traits, without precluding morphological changes associated with encephalization and tooth reduction observed in Middle Pleistocene populations on all three continents.

Conclusion

The unambiguous presence of Neanderthals in neighboring Croatia and Greece (see overviews in Janković et al. 2016; Harvati et al. 2009, 2011, 2013; Harvati 2016) leaves little doubt that Neanderthals were also present in the Central Balkans. However, we need to be alert to the possibility that the picture is more complex, and that future Balkan finds might redefine the current understanding of human evolution in Europe, still largely based on the evidence from the west of the continent. Considering the Balkans as part of the larger area open to communication throughout the Pleistocene is not only warranted, but necessary. It will, however, require a shift in our communal perception of the geography of the region. We might need to do away with the perception of the Aegean and the Black seas as barriers for movement of populations and view them as a geographic center of the Eastern Mediterranean Area (Roksandic 2015) which would encompass Southeast Europe and Southwest Asia, and which could have maintained population contact and gene exchange throughout human evolution. This hypothesis needs to be tested within a wider systematic examination and correlation of changes in micro and macro-fauna of the whole Eastern Mediterranean area throughout the Pleistocene.

With more vigorous surveys and small-scale excavations over the course of the last decade, we are slowly starting to understand the relationship of Central Balkan Paleolithic assemblages to the ones in the east and the west (Mihailović and Bogićević 2016). Whether the same chronological sequence of changes can be extended to human groups is up for discussion, and will not be possible to ascertain without further well-contextualized finds and a better understanding of the environment, faunal assemblages, and the chronology in the region. While the specimens—other than the mandible from Mala Balanica—cannot be ascertained as Pleistocene without direct dating, they demonstrate the potential of this area for discoveries from a range of time periods. Obtaining a more substantive body of evidence on human presence and the environment in the Central Balkans will be relevant for fleshing out the process of human evolution in the region and will contribute to our understanding of continent wide processes.

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References

- Alcázar de Velasco, A., Arsuaga Ferreras, J. L., Martínez, I., & Bonmatí, A. (2011). Revisión de la mandíbula humana de Bañolas, Gerona, España. *Boletín de la Real Sociedad Española de Historia Natural. Sección geológica*, 105(1–4), 99–108.
- Arnold, L. J., Demuro, M., Parés, J. M., Arsuaga, J. L., Aranburu, A., Bermúdez de Castro, J. M., et al. (2014). Luminescence dating and palaeomagnetic age constraint on hominins from Sima de los Huesos, Atapuerca, Spain. *Journal of Human Evolution*, 67, 85–107.
- Arsuaga, J. L., Martínez, I., Arnold, L. J., Aranburu, A., Gracia-Téllez, A., Sharp, W. D., et al. (2014). Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science*, 344, 1358–1363.
- Ascenzi, A., Mallegni, F., Manzi, G., Segre, A. G., & Naldini, E. S. (2000). A re-appraisal of Ceprano calvaria affinities with *Homo erectus*, after the new reconstruction. *Journal of Human Evolution*, 39(4), 443–450.
- Asfaw, B., Gilbert, W. H., & Richards, G. D. (2008). *Homo erectus* cranial anatomy. In W. H. Gilbert & B. Asfaw (Eds.), *Homo erectus: Pleistocene evidence from the Middle Awash, Ethiopia* (pp. 265–328). Berkeley, CA: University of California Press.
- Athreya, S. (2012). The frontal bone in the genus *Homo*: A survey of functional and phylogenetic sources of variation. *Journal of Anthropological Sciences*, 90, 59–80.
- Aytek, I. A., & Harvati, K. (2016). The human fossil record from Turkey. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 79–91). Dordrecht: Springer.
- Bailey, S. E. (2002). *Neandertal dental morphology: Implications for modern human origins*. Unpublished PhD, Arizona State University, Phoenix, AZ.
- Bailey, S. E., & Lynch, J. M. (2005). Diagnostic differences in mandibular P4 shape between Neandertals and anatomically modern humans. *American Journal of Physical Anthropology*, 126(3), 268–277.
- Bar-Yosef, O., & Belfer-Cohen, A. (2013). Following Pleistocene road signs of human dispersals across Europe. *Quaternary International*, 285, 30–40.
- Bar-Yosef, O., & Callander, J. (1999). The woman from Tabun: Garrod's doubts in historical perspective. *Journal of Human Evolution*, 37(6), 879–885.
- Belmaker, M., Tchernov, E., Condemi, S., & Bar-Yosef, O. (2002). New evidence for hominid presence in the Lower Pleistocene of the Southern Levant. *Journal of Human Evolution*, 43(1), 43–56.
- Bruzek, J. (2006). The assessment of sex. In E. Trinkaus & J. R. Svoboda (Eds.), *Early modern human evolution in Central Europe: The people of Dolní Věstonice and Pavlov*. New York: Oxford University Press.
- Carrión, J. S., Rose, J., & Stringer, C. (2011). Early human evolution in the Western Palearctic: Ecological scenarios. *Quaternary Science Reviews*, 30(11–12), 1281–1295.
- Cartmill, M., & Smith, F. H. (2009). *The human lineage*. Hoboken, NJ: Wiley-Blackwell.
- Cleghorn, B. M., Christie, W. H., & Dong, C. C. (2007). The root and root canal morphology of the human mandibular second premolar: A literature review. *Journal of Endodontics*, 33(9), 1031–1037.
- Coppens, Y., Tseveendorj, D., Demeter, F., Turbat, T., & Giscard, P. H. (2008). Discovery of an archaic *Homo sapiens* skullcap in Northeast Mongolia. *Comptes Rendus Palevol*, 7, 51–60.
- Cvijić, J. (1903). *Novi rezultati o glacialnoj eposi Balkanskoga poluostrva*. Beograd: Srpska kraljevska akademija.
- Cvijić, J. (1918). *La Péninsule Balkanique: Géographie Humaine*. Paris: Colin.
- Dean, D., Hublin, J.-J., Holloway, R., & Ziegler, R. (1998). On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. *Journal of Human Evolution*, 34(5), 485–508.

- Dennell, R. W., Martínón-Torres, M., & Bermúdez de Castro, J. M. (2011). Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quaternary Science Reviews*, 30(11–12), 1511–1524.
- Doboş, A., & Iovita, R. (2016). The Lower Paleolithic of Romania revisited: New evidence from the site of Dealul Guran. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 171–186). Dordrecht: Springer.
- Eastwood, W. J. (2004). East Mediterranean vegetation and climate change. In H. I. Griffiths, B. Krystufek, & J. M. Reed (Eds.), *Balkan biodiversity: Pattern and process in the European hotspot* (pp. 25–48). Dordrecht: Kluwer Academic.
- Falconer, H., & Cautley, P. T. S. (1847). *Fauna Antiqua Sivalensis: Proboscidea*. London: Smith Elder.
- Falguères, C., Bahain, J.-J., Tozzi, C., Boschian, G., Dolo, J.-M., Mercier, N., et al. (2008). ESR/U-series chronology of the Lower Palaeolithic palaeoanthropological site of Visogliano, Trieste, Italy. *Quaternary Geochronology*, 3(4), 390–398.
- Freyer, D. W., Jelínek, J., Oliva, M., & Wolpoff, M. H. (2006). Aurignacian male crania, jaws and teeth from the Mladeč Caves, Moravia, Czech Republic. In M. Teschler-Nicola (Ed.), *Early modern humans at the Moravian Gate: The Mladeč Caves and their remains* (pp. 185–272). Vienna: Springer.
- Gabunia, L., & Vekua, A. (1995). A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. *Nature*, 373, 509–512.
- Gauta, I., Vazdar, M. A., & Vodanović, M. (2010). Human molar crown traits in Croatian medieval and contemporary populations. *Acta Stomatologica Croatica*, 44, 3e16.
- Gavela, B. (1951). Iskopavanja na paleolitskom lokalitetu Pečina pod Jerininim brdom u Gracu kod Kragujevca. *Glasnik SANU*, III(2).
- Gorjanović-Kramberger, D. (1906). *Der Diluviale Mensch von Krapina in Kroatien*. Wiesbaden: C. W. Kreidel's Verlag.
- Griffiths, H. I., Krystufek, B., & Reed, J. M. (Eds.). (2004). *Balkan biodiversity: Pattern and process in the European hotspot*. Dordrecht: Kluwer.
- Grimaud-Herve, D., Widianto, H., Detroit, F., & Semah, F. (2012). Comparative morphological and morphometric description of the hominin calvaria from Bukuran (Sangiran, Central Java, Indonesia). *Journal of Human Evolution*, 63(5), 637–652.
- Harvati, K. (2016). Paleoanthropology in Greece: Recent finds and implications. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 3–14). Dordrecht: Springer.
- Harvati, K., Darlas, A., Bailey, S. E., Rein, T. R., El Zaatari, S., Fiorenza, L., et al. (2013). New Neanderthal remains from Mani peninsula, Southern Greece: The Kalamakia Middle Paleolithic cave site. *Journal of Human Evolution*, 64(6), 486–499.
- Harvati, K., Stringer, C., & Karkanis, P. (2011). Multivariate analysis and classification of the Apidima 2 cranium from Mani, Southern Greece. *Journal of Human Evolution*, 60(2), 246–250.
- Harvati, K., Hublin, J.-J., & Gunz, P. (2010). Evolution of middle-late Pleistocene human cranio-facial form: A 3-D approach. *Journal of Human Evolution*, 59(5), 445–464.
- Harvati, K., Panagopoulou, E., & Runnels, C. (2009). The paleoanthropology of Greece. *Evolutionary Anthropology: Issues, News, and Reviews*, 18(4), 131–143.
- Hewitt, G. M. (2011). Mediterranean peninsulas: The evolution of hotspots. In F. E. Zachos & J. C. Habel (Eds.), *Biodiversity hotspots distribution and protection of conservation priority areas* (pp. 123–147). Berlin: Springer.
- Hillson, S. (1996). *Dental anthropology*. Cambridge: Cambridge University Press.
- Howell, F. (1996). Thoughts on the study and interpretation of the human fossil record. In W. Meikle, F. Howell, & N. Jablonski (Eds.), *Contemporary issues in human evolution* (Vol. Mem 21, pp. 1–46). San Francisco: California Academy of Sciences.
- Howell, F. (1999). Paleo-demes, species clades, and extinctions in the Pleistocene hominin record. *Journal of Anthropological Research*, 55, 191–243.
- Howells, W. W. (1989). *Skull shapes and the map. Craniometric analyses in the dispersion of modern homo* (Vol. 79). Cambridge, MA: Peabody Museum.
- Hublin, J.-J. (2013). The Middle Pleistocene record. On the origin of Neandertals, modern humans and others. In D. Begun (Ed.), *A companion to paleoanthropology* (pp. 517–537). Hoboken, NJ: Wiley-Blackwell.
- Ivanova, S. (2016). A route through the Balkans and implications for the earliest settlement of Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 187–211). Dordrecht: Springer.
- Janković, I., Ahern, J. C. M., Karavanić, I., & Smith, F. H. (2016). The importance of Croatian Pleistocene hominin finds in the study of human evolution. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 35–50). Dordrecht: Springer.
- Jovanović, D. P. (1892). Prilozi za Paleontologiju srpskih zemalja. *Starinar*, IX, 24–33.
- Kennedy, K. A. R. (2000). *God apes and fossil men: Paleoanthropology of South Asia*. Ann Arbor: University of Michigan Press.
- Koufos, G. D., & D. S. Kostopoulos (2016). The Plio-Pleistocene Large Mammal Record of Greece: Implications for Early Human Dispersals into Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.
- Koufos, G. D., Kostopoulos, D. S., & Vlachou, T. D. (2005). Neogene/Quaternary mammalian migrations in Eastern Mediterranean. *Belgian Journal of Zoology*, 135(2), 181–190.
- Lordkipanidze, D., Ponce de León, M. S., Margvelashvili, A., Rak, Y., Rightmire, G. P., Vekua, A., et al. (2013). A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. *Science*, 342(6156), 326–331.
- Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, R. G., Zollikofer, C. P. E., Ponce de León, M. S., et al. (2006). A Fourth hominin skull from Dmanisi, Georgia. *The Anatomical Record*, 288, 1146–1157.
- Lubsen, K. D., & Corruccini, R. S. (2011). Morphometric analysis of the Herto cranium (BOU-VP-16/1): Where does it fit? *Journal of Contemporary Anthropology*, 2, 1–16.
- Lycett, S. J. (2009). Understanding ancient hominin dispersals using artefactual data: A phylogeographic analysis of Acheulean handaxes. *PLoS One*, 4(10), e7404.
- Manzi, G. (2012). On the trail of the genus *Homo* between archaic and derived morphologies. *Journal of Anthropological Science*, 90, 99–116.
- Manzi, G., Magri, D., & Palombo, M. R. (2011). Early-Middle Pleistocene environmental changes and human evolution in the Italian peninsula. *Quaternary Science Reviews*, 30, 1420–1438.
- Marković, S. B., Bokhorst, M. P., Vandenberghe, J., McCoy, W. D., Oches, E. A., Hambach, U., et al. (2008). Late Pleistocene loess-palaeosol sequences in the Vojvodina region, north Serbia. *Journal of Quaternary Science*, 23(1), 73–84.
- Martin, R., & Saller, K. (1957). *Lehrbuch der Anthropologie* (Vol. 1). Stuttgart: Gustav Fischer.
- Martínez de Pinillos, M., Martínón-Torres, M., Skinner, M. M., Arsuaga, J. L., Gracia-Tellez, A., Martínez, I., et al. (2014). Trigonid crest expression in Atapuerca-Sima de los Huesos lower molars: Internal and external morphological expression and evolutionary inferences. *Comptes Rendus Palevol*, 13(3), 205–221.
- Martínón-Torres, M., Bermúdez de Castro, J. M., Gómez-Robles, A., Prado-Simon, L., & Arsuaga, J. L. (2012). Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *Journal of Human Evolution*, 62(1), 7–58.
- Martínón-Torres, M., de Castro, J. M. B., Gómez-Robles, A., Margvelashvili, A., Prado, L., Lordkipanidze, D., et al. (2008).

- Dental remains from Dmanisi (Republic of Georgia): Morphological analysis and comparative study. *Journal of Human Evolution*, 55(2), 249–273.
- Martinón-Torres, M., Martine de Pinillos, M., Skinner, M. M., Martin-Frances, L., Gracia-Tellez, A., Martínez, I., et al. (2014). Talonid crest expression at the enamel-dentine junction of hominin lower permanent and deciduous molars. *Comptes Rendus Palevol*, 13(3), 223–234.
- Mihailović, D. (2008). New data about the Middle Palaeolithic of Serbia. In A. Darlas & D. Mihailović (Eds.), *The Palaeolithic of the Balkans* (British Archaeological Reports, International Series 1819) (pp. 93–100). Oxford: Archaeopress.
- Mihailović, D., & Bogičević, K. (2016). Technological changes and population movements in the late Lower and early Middle Palaeolithic of the Central Balkans. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 139–151). Dordrecht: Springer.
- Mirazón Lahr, M., & Haydenblit, R. (1995). The human remains from the site of Et-Tin, Israel. *Paléorient*, 21, 97–111.
- Mol, D., de Vos, J., & van der Plicht, J. (2007). The presence and extinction of *Elephas antiquus* Falconer and Cautley, 1847, in Europe. *Quaternary International*, 169–170, 149–153.
- Mounier, A., & Caparros, M. (2015). The phylogenetic status of *Homo heidelbergensis*—A cladistic study of Middle Pleistocene hominins. *Bulletins et Mémoires de la Société d'anthropologie de Paris*. Published on-line August 2015. doi:10.1007/s13219-015-0127-4.
- Mounier, A., Marchal, F., & Condemi, S. (2009). Is *Homo heidelbergensis* a distinct species? New insight on the Mauer mandible. *Journal of Human Evolution*, 56(3), 219–246.
- Murrill, R. I. (1981). *Petralona man: A descriptive and comparative study, with new important information on Rhodesian man*. Springfield, IL: Charles C. Thomas.
- Muttoni, G., Scardia, G., & Kent, D. V. (2013). A critique of evidence for human occupation of Europe older than the Jaramillo subchron (~1 Ma): Comment on Toro-Moyano et al. (2013). *Journal of Human Evolution*, 65, 746–749.
- Nomade, S., Muttoni, G., Guillou, H., Robin, E., & Scardia, G. (2011). First 40Ar/39Ar age of the Ceprano man (central Italy). *Quaternary Geochronology*, 6(5), 453–457.
- Quam, R., & Smith, F. H. (1998). A reassessment of the Tabun C2 mandible. In T. Akazawa, K. Aoki, & O. Bar-Yosef (Eds.), *Neandertals and modern humans in Western Asia* (pp. 405–421). New York: Kluwer Academic.
- Radović, P., Lindal, J., & Roksandic, M. (2014). A re-examination of the human fossil specimen from Bački Petrovac (Serbia). *HOMO Journal of Comparative Human Biology*, 65(4), 281–295.
- Rightmire, G. P. (1990). *The evolution of Homo erectus. Comparative anatomical studies of an extinct human species*. Cambridge: Cambridge University Press.
- Rightmire, G. P. (1996). The human cranium from Bodo, Ethiopia: Evidence for speciation in the Middle Pleistocene. *Journal of Human Evolution*, 31(1), 21–39.
- Rightmire, G. P. (1998). Human evolution in the Middle Pleistocene: The role of *Homo heidelbergensis*. *Evolutionary Anthropology*, 6(6), 218–227.
- Rightmire, G. P. (2008). *Homo* in the Middle Pleistocene: Hypodigms, variation, and species recognition. *Evolutionary Anthropology*, 17, 8–21.
- Rink, W. J., Mercier, N., Mihailović, D., Morley, M. W., Thompson, J. W., & Roksandic, M. (2013). New radiometric ages for the BH-1 hominin from Balanica (Serbia): Implications for understanding the role of the Balkans in Middle Pleistocene human evolution. *PLoS One*, 8(2), e54608.
- Roksandic, M. (2015). The role of Balkans in the peopling of Europe: New evidence from Serbia. In A. R. Sankhyan, (Ed.), *Proceedings of the BH13 Panel: "Exploring Human Origins" 17th IUAES Congress Manchester 2013* (pp. 63–68). Oxford: Archaeopress.
- Roksandic, M., & Dimitrijević, V. (2001). A human mandible from the loess in the vicinity of Belgrade (Yugoslavia). *Human Evolution*, 16(1), 27–36.
- Roksandic, M., Mihailović, D., Mercier, N., Dimitrijević, V., Morley, M. W., Rakočević, Z., et al. (2011). A human mandible (BH-1) from the Pleistocene deposits of Mala Balanica cave (Sicevo Gorge, Nis, Serbia). *Journal of Human Evolution*, 61(2), 186–196.
- Roksandic, M., Radović, P., Alex, B. A., Pavić, S., Paunović, M., & Marković, Z. (2014). Looking for hominins in Museum drawers—possible Upper Pleistocene specimens from Serbia: morphological descriptions and radiocarbon dating. In D. Mihailović (Ed.), *Palaeolithic and mesolithic research in the Central Balkans* (pp. 7–20). Belgrade: Serbian Archaeological Society.
- Rosas, A. (2001). Occurrence of Neanderthal features in mandibles from the Atapuerca-SH site. *American Journal of Physical Anthropology*, 114(1), 74–91.
- Schwartz, J. H., & Tattersall, I. (2000). The human chin revisited: What is it and who has it? *Journal of Human Evolution*, 38(3), 367–409.
- Scott, G. R., & Turner, C. G. I. (1997). *The anthropology of modern human teeth: Dental morphology and its variation in recent human populations*. Cambridge: Cambridge University Press.
- Sherwood, S. C., Windingstad, J. D., Barker, A. W., O'Shea, J. M., & Sherwood, W. C. (2013). Evidence for Holocene aeolian activity at the close of the Middle Bronze Age in the Eastern Carpathian Basin: Geoarchaeological results from the Mureș River Valley, Romania. *Geoarchaeology*, 28(2), 131–146.
- Simmons, T., Falsetti, A. B., & Smith, F. H. (1991). Frontal bone morphometrics of southwest Asian Pleistocene hominids. *Journal of Human Evolution*, 20(3), 249–269.
- Skinner, M. M., De Vries, D., Gunz, P., Hublin, J.-J., Kupczik, K., Klassen, R. P., & Roksandic, M. (2016). Morphological affinity of the Balanica mandible (BH-1): Molar enamel-dentine junction morphology, discrete dental traits, and enamel thickness. *Journal of Human Evolution*, 93, 63–81.
- Sládek, V., Trinkaus, E., Sefčáková, A., Halouzka, R. (2002). Morphological affinities of the Sal'a 1 frontal bone. *Journal of Human Evolution*, 43(6):787–815.
- Spassov, N. (2016). Southeastern Europe as a route for the earliest dispersal of *Homo* towards Europe: Ecological conditions and the timing of the first human occupation of Europe. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context* (pp. 281–290). Dordrecht: Springer.
- Stansfield, E., & Gunz, P. (2011). Skhodnya, Khvalynsk, Satanay, and Podkumokcalvaria: Possible Upper Palaeolithic hominins from European Russia. *Journal of Human Evolution*, 60(2), 129–144.
- Straat, D. S., Orr, C. M., Hodgkins, J., Spassov, N., Gurova, M., Miller, C., et al. (2016). The human fossil record of Bulgaria, and the formulation of biogeographic hypotheses. In K. Harvati & M. Roksandic (Eds.), *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*. Dordrecht: Springer.
- Stringer, C. (2012). The status of *Homo heidelbergensis* (Schoetensack 1908). *Evolutionary Anthropology*, 21(3), 101–107.
- Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J. M., Martinón-Torres, M., et al. (2013). The oldest human fossil in Europe dated to ca. 1.4Ma at Orce (Spain). *Journal of Human Evolution*, 65(1), 1–9.
- Tourloukis, V. (2010). *The Early and Middle Pleistocene archaeological record of Greece: Current status and future prospects*. Leiden: Leiden University Press.
- Trinkaus, E. (1983). *The Shanidar Neanderthals*. New York: Academic.
- Tzedakis, P. C. (2004). The Balkan as prime glacial refugial territory of European temperate trees. In H. I. Griffiths, B. Krystufek, & J. M. Reed (Eds.), *Balkan biodiversity: Pattern and process in the European hotspot* (pp. 49–69). Dordrecht: Kluwer Academic.
- Uchida, Y., Goto, M., Danjo, A., Yamashita, Y., & Kuraoka, A. (2012). Anatomic measurement of the depth and location of the sublingual

- fossa. *International Journal of Oral and Maxillofacial Surgery*, 12, 1571–1576.
- Van Kolfschoten, T., & Markova, A. K. (2005). Response of the European mammalian fauna to the mid Pleistocene transition. In M. J. Head & P. L. Gibbard (Eds.), *Early-Middle Pleistocene transitions: The land-ocean evidence* (pp. 251–262). London: Geological Society, Special Publications, 247.
- Vandermeersch, B. (1981). *L'Homme fossile de Qafzeh*. Paris: C.N.R.S.
- Wagner, G. A., Krbetschek, M., Degering, D., Bahain, J. J., Shao, Q., Falguères, C., et al. (2010). Radiometric dating of the type-site for *Homo heidelbergensis* at Mauer, Germany. *Proceeding of the National Academy of Sciences USA*, 107(46), 19726–19730.
- Weidenreich, F. (1943). *The skull of Sinanthropus pekinensis: A comparative study on a primitive hominid skull* (Vol. 10). Pehpei, Chungking: Geological Survey of China.
- Wu, X., & Athreya, S. (2013). A description of the geological context, discrete traits, and linear morphometrics of the Middle Pleistocene hominin from Dali, Shaanxi Province, China. *American Journal of Physical Anthropology*, 150, 141–157.
- Živanović, S. (1966). Prethodno saopštenje o nalazu dva ostatka lobanja praistorijskog čoveka iz Vojvodine. *Starinar*, XV-XVI, 187–190.
- Živanović, S. (1975). Lobanja iz Bačkog Petrovca. *Starinar*, XXIV-XXV, 155–156.
- Žujović, J. (1893). *Geologija Srbije* (Vol. 1). Beograd.

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