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Biśnik Cave and its biostratigraphical position based on equid remains

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Abstract. Excavations in Biśnik Cave have revealed a more or less complete depositional sequence covering the period of MIS 8 to the Holocene. Nearly all layers have produced faunal remains, contributing important information on a fauna of a period which is under-represented in Eastern European Pleistocene collections. Since this region acted as a hinge between the steppe environments of Russia and Central Asia and the oceanic regions of Western Europe, as well as providing refugium areas, research on the site presents an important advance in our knowledge of the late Middle Pleistocene and early Late Pleistocene in this area. Caballoid horse remains present an important source of information on the biostratigraphical position of sites dating from this period, as well as furnishing information on climatic conditions and biogeography based on morphological characteristics. Horse remains from Biśnik Cave are here analysed against a background of other late Middle and Late Pleistocene samples. Remains from all layers in the cave can be attributed to *Equus ferus*. A gradual morphological change is documented in the sedimentary sequence. Large, robust and somewhat primitive specimens were recovered from the interglacial and interstadial lower deposits, indicating a highly productive but relatively open environment. Their morphology could indicate links with Central Asian populations. The upper sedimentary layers witness a size decrease, while the horses remained robust in the glacial and increasingly marginal environments of the Last Glacial.

Key words: Middle Pleistocene, Late Pleistocene, Biśnik Cave, Equidae, biostratigraphy, ecomorphology, biogeography.

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I. INTRODUCTION

Biśnik Cave is situated on the western slope of the dry valley Dolina Wodąca near Pilica, within the Smoleńsko-Niegowonicki range in Poland (CYREK et al. 2010). The cave is a part of a large cave system with two main northwest-facing entrances about 7 m above the valley bottom. The cave is 73 m long with a rock shelter of 5 x 8 m and three chambers, each about 12 m^2 in size (MIROSŁAW-GRABOWSKA 2002; Fig. 1). Since 1991, when Neolithic and Palaeolithic tools were found, excavations have been undertaken by the Silesian Jurassic Landscape Parks Complex (1992-1996), the State Committee for Scientific Research Projects (1997-2000), the Institute of Archaeology and Ethnography of the University of Nicolaus Copernicus in Toruń, the Institute of Geological Sciences of the Polish Academy of Sciences and the Department of Palaeozoology of the University of Wrocław (2000-present), so far covering an area of 260 m^2.

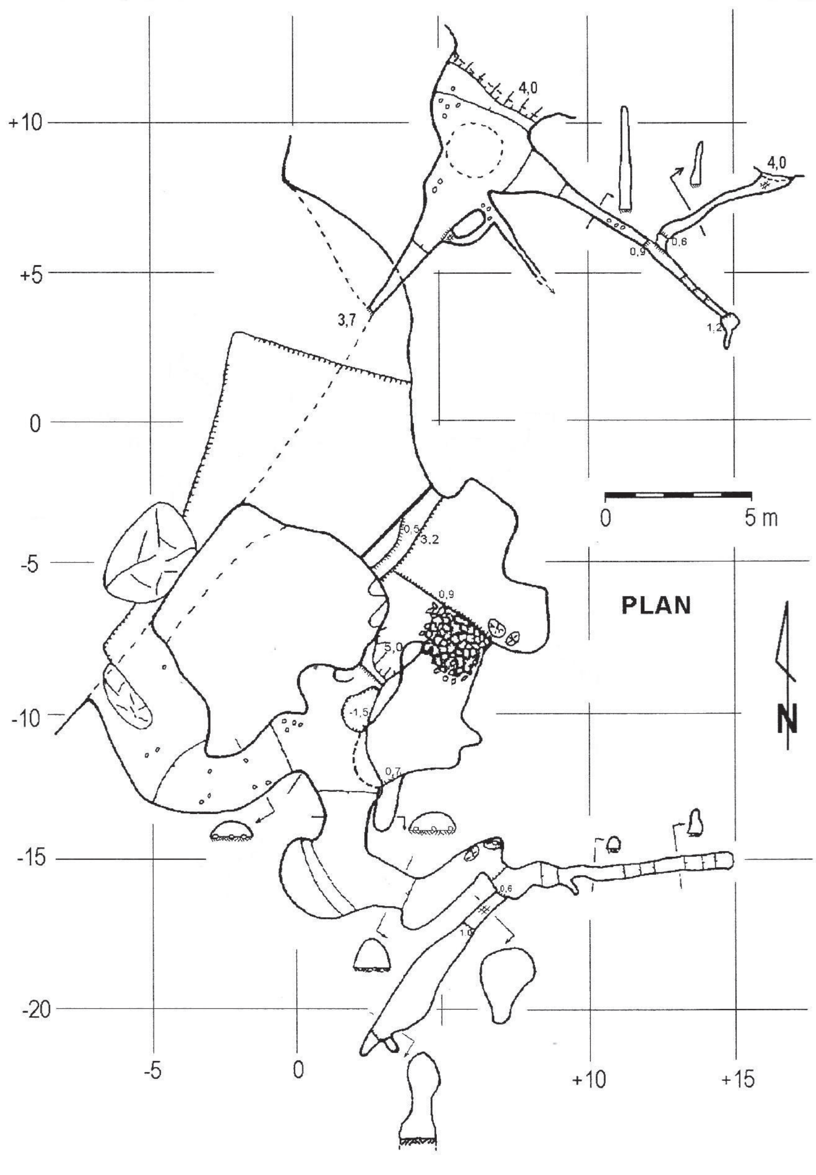

Fig. 1. Plan of Biśnik Cave (after CYREK et al. 2009)

The 7 m thick sedimentary sequence of the cave can be subdivided into three main series, deposited on Pliocene *terra rossa* (Fig. 2). Correlation of the sediments with the Polish Quaternary sequence is based on absolute dating (Table I), sediment characteristics and the morphology of limestone inclusions originating from the disintegration of the walls and ceiling of the cave (MIROSŁAW-GRABOWSKA 2002).

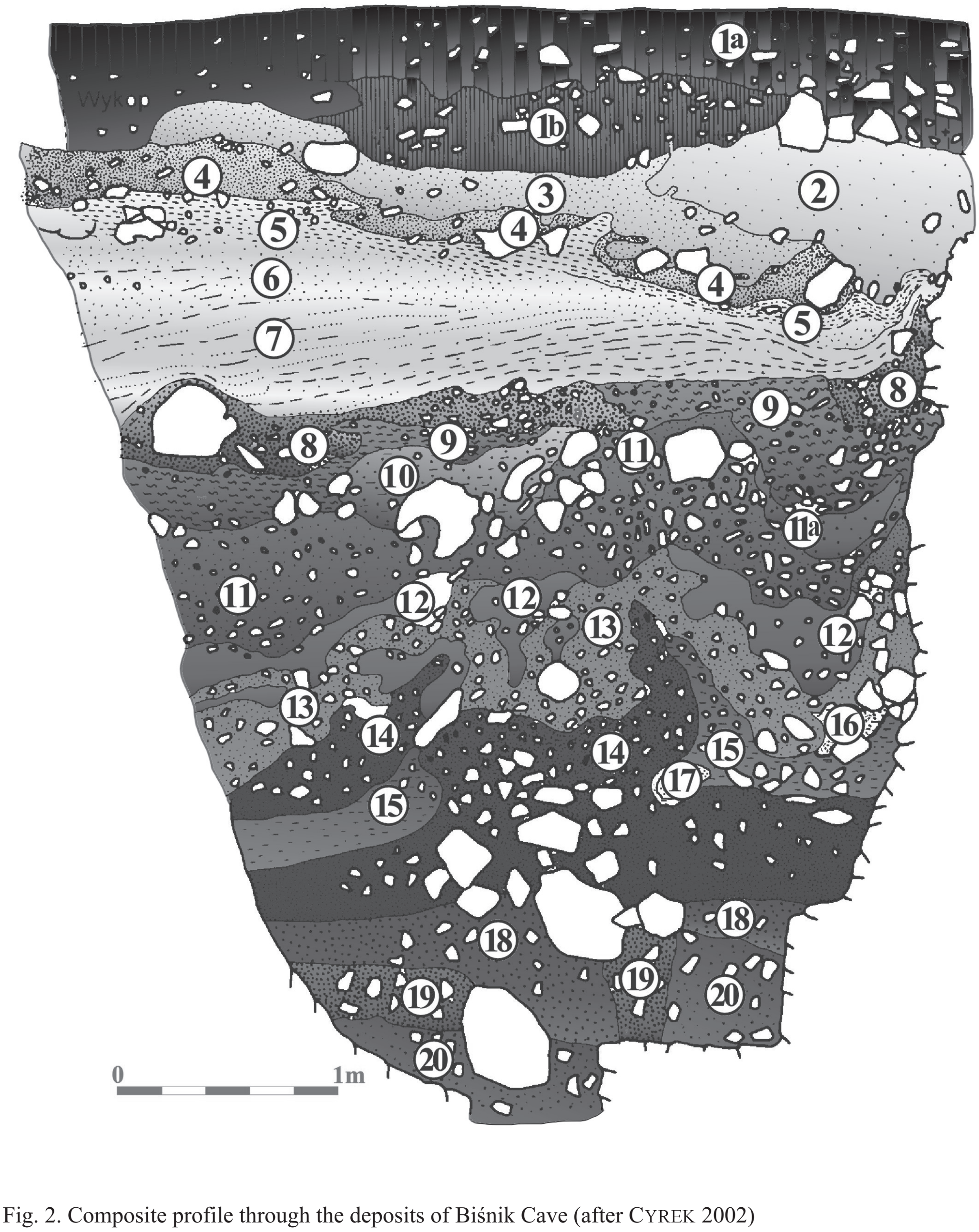

Fig. 2. Composite profile through the deposits of Biśnik Cave (after CYREK 2002)

Table I

Results of absolute dating methods for various layers of Biśnik Cave (CYREK et al. 2010)

Layer	Method	Date (ka BP)
2	U-series on bone	37-93 (EUmin-LUmax)[1]
	TL on sediment	25 ± 3
		26 ± 3
		29 ± 4
3/4	U-series on bone	32-79 (EUmin-LUmax)
	TL on flint	54 ± 10
		58 ± 11
5/6	TL on sediment	67 ± 15
7	U-series on bone	94-96 (EUmin-LUmax)
8	U-series on bone	106-270 (EUmin-LUmax)
	TL on sediment	120 ± 22
9	U-series on bone	11-30 (EUmin-LUmax)
	TL on sediment	96 ± 27
		127 ± 24
	TL on flint	81 ± 17
		86 ± 14
		94 ± 17
10	U-series on bone	48-106 (EUmin-LUmax)
	TL on sediment	101 ± 27
	TL on flint	97 ± 17
11	U-series on bone	60-153 (EUmin-LUmax)
	TL on flint	108 ± 21
12	U-series on bone	31-66 (EUmin-LUmax)
	TL on sediment	142 ± 27
	TL on flint	122 ± 22
		135 ± 23
13	U-series on bone	63-143 (EUmin-LUmax)
	TL on flint	126 ± 25
14	U-series on bone	56-126 (EUmin-LUmax)
	TL on flint	81 ± 17
		139 ± 33
		195 ± 35
		224 ± 49
15	U-series on bone	216-930 (EUmin-LUmax)
	TL on flint	195 ± 35
18	U-series on bone	116-346 (EUmin-LUmax)
	TL on sediment	230 ± 60
	TL on flint	230 ± 51
		279 ± 97
19	U-series on bone	125-346 (EUmin-LUmax)
	TL on sediment	569 ± 182
	TL on flint	568 ± 131

[1] EU=Early Uptake model; LU=Linear Uptake model (PIKE & HEDGES 2001)

Series I (layers 19-8), deposited on top of a basal erosional layer (layer 20), represents a dry cave environment. The lowermost part of this series (layers 19-16) was deposited during the Odranian Glacial (MIS 8) in an open environment with taiga and deciduous forest, although the lower parts of layer 19 represent an interstadial temperate, forested environment (CYREK et al. 2009). The cold-stage sediments are followed by temperate forest-steppe deposits (layer 15) dating from the Lubawa Interglacial (MIS 7, MIROSŁAW-GRABOWSKA 2002). A return to open environments with taiga is evidenced in layer 14, which is correlated with the Warthanian Glaciation (MIS 6). The strongly weathered limestone particles and the forest-adapted fauna in layers 13 and 12 are indicative of a warm period, correlated with the Eemian (MIROSŁAW-GRABOWSKA 2002). The upper part of Series I (layers 11-8) indicates renewed cold conditions during the early Vistulian and the Toruń Stadial (MIS 5d-c). The series was terminated by a partial collapse of the cave's ceiling, after which only a rockshelter remained.

Series II (layers 7-5) was accumulated by flowing water in a cold environment with some tree cover during the Gniew Interstadial (MIS 5b-4; MIROSŁAW-GRABOWSKA 2002). The aeolian deposits of Series III were deposited during the Grudziądz Interstadial (layers 4 and 3, MIS 4-3) and the Last Glacial Maximum (layer 2, MIS 2). The sequence is capped by Holocene loams (layer 1).

Thirteen phases of hominin occupation were discovered in the first main chamber (CYREK et al. 2009). So far a total of over 200,000 vertebrate remains and 3,000 stone and bone artefacts have been recovered from the site (CYREK et al. 2007). The artefacts belong to the Acheulean, Micoquian and Mousterian traditions, with Levallois artefacts present from the oldest layers (layer 19). This makes Biśnik Cave the oldest cave locality in Poland with traces of hominin use, and one of the oldest locations in Europe with evidence for the use of the Levallois technique (CYREK et al. 2009). In layer 5, a possible shelter or windscreen structure, consisting of a ring of rubble enclosing a concentration of bones and flint artefacts, was found in the entrance of the cave (MIROSŁAW-GRABOWSKA 2002). The Eemian layers contained hearths (CYREK et al. 2007). Upper Palaeolithic, Neolithic and Bronze Age artefacts have been recovered from the upper layers.

Bird bones of 81 species have been found, stemming from wetland, coniferous and deciduous forests and ecotones (CYREK et al. 2007; STEFANIAK et al. 2009b). Of the 80 species of small and large mammals identified, animals adapted to forest environments are found in both warm- and cold-period sediments, possibly indicating a refugial role for the south Polish uplands during both the Saalian and Weichselian (Vistulian) glaciation (SOCHA 2009; STEFANIAK et al. 2009b; SOCHA et al. 2010). Evidence of repeated immigration episodes of both tundra and steppe fauna was found in the cold period sediments. The large mammal fauna is dominated by carnivore remains (STEFANIAK & MARCISZAK 2009). The results of palaeontological, palaeoecological and palaeoclimatological investigations indicate that during deposition of the sediments in Biśnik Cave the climate was close to temperate, characteristic of the deciduous-coniferous forest zone of the Northern Hemisphere (SOCHA et al. 2010).

Horse remains from Polish Pleistocene sites date mainly from the Last (Vistulian) Glaciation (STEFANIAK & MARCISZAK 2009), with the exception of a small assemblage from Nietoperzowa Cave (WOJTAL 2007) and a single Early Pleistocene specimen from Żabia Cave (STEFANIAK et al. 2009a). Although horse fossils form only a small part of the mammalian assemblage from Biśnik Cave, they have been found in most layers of the sedimentary sequence. These remains therefore (apart from the specimen from Żabia Cave) are the oldest horse remains from Poland, and the only Middle Pleistocene assemblage. The horse lineage is also one of the few Pleistocene large mammal lineages for which clear biostratigraphical and ecomorphological patterns have been documented (EISENMANN 1991a,b; VAN ASPEREN 2009a, 2010). The relatively large continuity of deposition in the cave from MIS 8 to the Holocene thus enables an investigation into the late Middle and Late Pleistocene occupation history and palaeoecology of horses in this part of Europe. Furthermore, they are an important source of information for biostratigraphic purposes (VAN ASPEREN in prep.), since they form the easternmost finds of the Middle Pleistocene equid lineages known so far, with good evidence for their age from absolute dating methods (Table I). Here, we present and analyse the Biśnik Cave horse remains in order to establish their biostratigraphical, ecomorphological and biogeographical significance.

II. MATERIAL AND METHODS

Material from Biśnik Cave

To date, the sediments of Biśnik Cave have yielded a total number of 257 equid fossils. Equid remains occur in most sedimentary units, but they are more abundant in the interglacial (layers 15 and 13-12, n = 39) and interstadial (layers 7-3, n = 46) units than in the glacial (layers 20-16, 14 and 2, n = 20) and stadial (layers 11-8, n = 32) units (Table II). The dentition, cranial and postcranial skeleton are all represented (Table III), but the fragmentation rate is high. The more compact bones such as metapodials, phalanges, carpals and tarsals, as well as longbone epiphyses, are relatively well-preserved, but complete longbones are rare. Although a full taphonomic study of fragmentation patterns has not yet been undertaken, several specimens bear clear evidence of hominin and carnivore use,

Table II

Numbers of horse remains from the different layers in Biśnik Cave

Layer	n	Layer	n	Layer	n	Layer	n
1	3	5/7	2	10	5	15	13
1a/1b	2	6/7	20	10/10a	2	15/16	1
1/2	2	7	11	11	9	18	3
2	7	7e	1	12	8	19	5
2/4	25	7/8	6	12/13	4	Cultural layer 2	3
2/5	20	7e/8	4	13	13	Second chamber	1
2/6	2	8	5	13/13a	1	Unprovenanced	45
4	3	8a	2	13/16	1		
5	4	8/10	1	14	5		
5/6	4	9	8	14/15	5	**Total**	**257**

Table III

Representation of different parts of the horse skeleton in Biśnik Cave

Dentition		Other skeletal remains	
Upper dentition	n	Element	n
I1	10	Cranium	4
I2	3	Mandibula	3
I3	8	Vertebrae	1
DP2	3	Pelvis	3
DP3/4	7	Scapula	2
P2	4	Humerus	1
P3/4	6	Radius	3
M1/2	16	Carpalia	6
M3	8	Metacarpus	6
Lower dentition	n	Anterior first phalanx	2
di2	1	Tibia	4
di3	1	Astragalus	4
i1	10	Calcaneus	5
i2	8	Tarsalia	5
i3	3	Metatarsus	8
dp2	1	Metapodium 2/4	3
dp3/4	4	First phalanx	2
p2	11	Second phalanx	2
p3/4	15	Third phalanx	1
m1/2	26	Sesamoideum	1
m3	6	Dental fragments	38
canine	2	**Total**	**257**

which indicates that the deposition of these remains is related to the frequent occupation of the cave by hominins and carnivores.

Late Middle and Late Pleistocene equids

We compare the Biśnik Cave remains with fossils from various late Middle and Late Pleistocene sites from northwest Europe to examine relationships and adaptive features of the Biśnik Cave equids. In the late Middle Pleistocene a single caballoid horse lineage inhabited northwest Europe (VAN ASPEREN in press). This lineage, which occurs throughout both cold and warm stages, is represented by several ecotypes (VAN ASPEREN 2010). These animals are here all regarded as a Middle Pleistocene form of *Equus ferus* (ICZN 2002; VAN ASPEREN in press). Remains from the Lower Travertine of the MIS 7 site Weimar-Ehringsdorf, the MIS 6 sites Wannen (faunal assemblages 1-3 cf. TURNER 1990) and Schweinskopf (indicated as DE MIS 6 in the figures), and the Eemian sites Taubach and Weimar (indicated as DE MIS 5e in the figures) are used as a comparative dataset (VAN ASPEREN 2009a). In addition, two samples from MIS 7 and MIS 6 sites in the British Isles are included (VAN ASPEREN 2009b).

During the Late Pleistocene, several caballoid horse lineages can be distinguished, all of smaller size than the Middle Pleistocene forms (EISENMANN 2004). The early Weichselian form, known as *Equus germanicus*, is thought to have given rise to *Equus gallicus* in Western Europe (EISENMANN 1991b). In Eastern Europe, another ecotype in the same species complex is known as *Equus latipes* (KUZMINA 1997; EISENMANN 2004). These ecotypes are variously described as separate species, or as subspecies of *E. caballus* (CARDOSO & EISENMANN 1989) or *E. ferus*. The latest Pleistocene sees the appearance of *Equus arcelini*, a small caballoid with different morphological features from the earlier lineage (EISENMANN 1991b). Here, these are all regarded as subspecies of *E. ferus*. Horse remains from Wallertheim layer F (Germany, late MIS 5), and Zwoleń (Poland, late MIS 5 - MIS 3) have been included in *Equus ferus germanicus* (VAN ASPEREN unpublished data; CONARD et al. 1995; GAUTIER 2005). The sample for *Equus ferus gallicus* is from the French MIS 3 site Jaurens (CARDOSO & EISENMANN 1989; EISENMANN online data 2007, 2008). For *Equus ferus latipes*, a sample from the Upper Palaeolithic (MIS 3-2) site Kostenki 4, Russia is examined (KUZMINA 1997) and *Equus ferus arcelini* is represented in the Magdalenian levels of the French site Solutré (GUADELLI 1987).

Equus hydruntinus, a stenonid equid, occurs throughout this period (ORLANDO et al. 2006) and is sometimes found alongside a caballoid species, for example at the sites Swanscombe (UK; VAN ASPEREN unpublished data), Wallertheim (Germany; GAUDZINSKI 1995) and Emine-Bair-Khosar (Crimea, Ukraine; VAN ASPEREN et al. in prep.). The species, also known as the European wild ass, occurs mainly in assemblages dominated by steppic species typical of dry but relatively temperate environments (EISENMANN & BARYSHNIKOV 1994; STEWART 2007; MARKOVA et al. 2010). Because of its stenonid morphology and small size, its remains are readily distinguishable from caballoid equid fossils (EISENMANN 1979, 1984; KUZMINA 1997).

Methods

All skeletal elements were measured with vernier callipers, and measurements were recorded to 0.1 mm. For the dental material, mesiodistal length and buccolingual width, and on the upper premolars and molars the length of the protocone, were measured on the occlusal surface without cement, and tooth height was measured on the buccal aspect from the division of the roots to the occlusal surface (EISENMANN 1980, 1981). Since it is very difficult to distinguish between the third and fourth premolar and between the first and second molar when isolated teeth are examined, these were analysed together, as third/fourth premolar and first/second molar respectively. Measurements of the postcranial bones were taken according to EISENMANN (1979, metapodials), EISENMANN et al. (1988, humeri, radii, femora, tibiae and third phalanges), DIVE & EISENMANN (1991, first phalanges) and VON DEN DRIESCH (1976, all other elements). In the following sections, the maxillary dentition is indicated as P2-4 and M1-3 and the mandibular dentition as p2-4 and m1-3. Measurements on the cranial and postcranial bones are abbreviated with 'V', e.g. V1 = measurement 1. A data file listing all specimens and measurements is available from the authors upon request.

Size and morphological features vary between the various equid lineages, and significant variation occurs between different ecotypes within the caballoid lineage (EISENMANN 1979, 1980; DIVE & EISENMANN 1991; VAN ASPEREN 2009a, 2010). Such variation can be visualised in log ratio diagrams, in which the logarithms of the measurements are plotted against a standard (SIMPSON 1941; SIMPSON et al. 1960). Size differences are reflected in the vertical distance between specimens on the same measurements, while shape differences are apparent when the relative proportions of several measurements vary between specimens. The standard chosen as the base line or reference line of the diagram is usually a closely related species. For Pleistocene equids, the species most commonly used as a standard is *Equus hemionus* (e.g. EISENMANN 1979; DIVE & EISENMANN 1991), and this convention is followed here. The order in which the measurements appear in the diagrams is chosen according to the differential survival of different parts of the bone, such that measurements that often cannot be taken on incomplete specimens are at both ends of the axis, while measurements that show characteristic proportions in particular equid groups are placed next to each other (EISENMANN 1979).

III. SYSTEMATIC PALAEONTOLOGY

All dental remains show a caballoid morphology, indicating all remains belong to species in the caballoid lineage. The dental remains from Biśnik Cave form a homogeneous sample (not shown). As in the dental remains, all postcranial remains that are complete enough to preserve diagnostic features have a caballoid size and shape. The single tibia specimen, from layer 2, is small and falls outside the variation in length for *Equus ferus gallicus* from Jaurens and *E. f. latipes* from Kostenki (Table IV, Fig. 3a). It falls within the

Table IV

Measurements on the tibia from Biśnik Cave and various samples of Pleistocene caballoid horses (UK MIS 7, DE MIS 6: VAN ASPEREN 2009a; Wallertheim F: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997; Solutré: GUADELLI 1987); GL = greatest length, Bd = breadth of the distal epiphysis, Dd = depth of the distal epiphysis

Sample	n max	GL			Bd			Dd		
		mean	min	max	mean	min	max	mean	min	max
Biśnik Cave	1	365.1	–	–	83.5	–	–	50.6	–	–
UK MIS 7	12	370.5	354.0	390.0	–	–	–	–	–	–
DE MIS 6	10	368.3	356.0	390.0	85.0	73.0	91.1	51.7	46.2	54.7
Wallertheim F	1	374.5	–	–	–	–	–	–	–	–
Jaurens	3	382.7	375.0	394.0	78.3	72.0	83.5	49.6	45.5	53.5
Kostenki	38	378.6	366.0	395.5	–	–	–	–	–	–

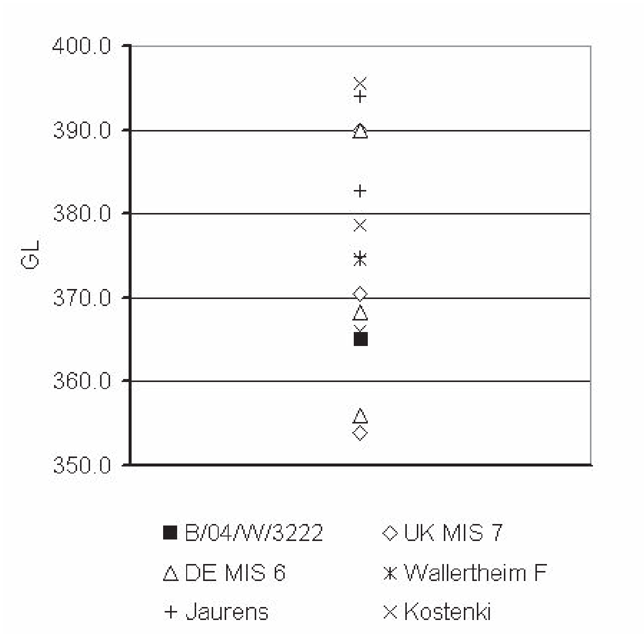

Fig. 3a. Scatterplot of tibia length for the specimen from Biśnik Cave and various samples of Pleistocene caballoid horses (UK MIS 7, DE MIS 6: VAN ASPEREN 2009a; Wallertheim F: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997).

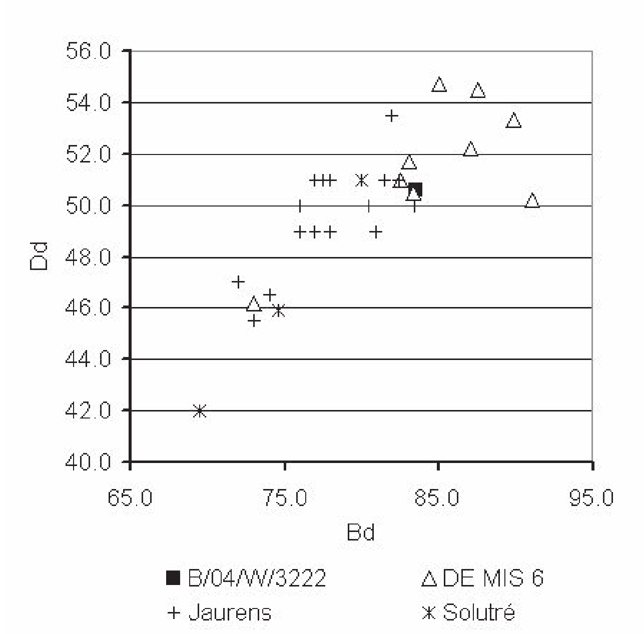

Fig. 3b. Scatterplot of measurements on the distal epiphysis of the tibia for the specimen from Biśnik Cave and various samples of Pleistocene caballoid horses (DE MIS 6: VAN ASPEREN 2009a; Jaurens: EISENMANN online data; Solutré: GUADELLI 1987).

Table V

Measurements on the astragali from Biśnik Cave and various samples of Pleistocene caballoid horses (UK MIS 7, DE MIS 6: VAN ASPEREN 2009a; Wallertheim F: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997; Solutré: GUADELLI 1987); BFd = breadth of the distal articular facet, GH = greatest height

Specimen / sample	n max	BFd			GH		
		mean	min	max	mean	min	max
1771	–	58.3	–	–	68.2	–	–
1726	–	61.4	–	–	67.6	–	–
B/03/W/2775	–	57.4	–	–	65.1	–	–
B/04/W-3299	–	58.4	–	–	67.9	–	–
Weimar-Ehringsdorf	10	61.8	57.8	63.6	70.3	64.7	74.8
DE MIS 6	3	57.0	52.9	62.1	65.3	61.0	71.0
Jaurens	19	62.4	58.0	66.0	55.1	51.0	60.0
Kostenki	129	64.1	58.5	71.0	60.8	55.5	68.2
Solutré	80	52.9	48.0	57.3	59.7	54.5	64.0

variation observed for glacial horses from Wannen and British horses from the MIS 7 interglacial. However, when measurements on the distal epiphysis are plotted, the Biśnik Cave specimen plots at the lower end of the variation for MIS 6 horses from Germany and at the upper end of the variation for *E. f. gallicus* and *E. f. arcelini* (Fig. 3b). This reveals the high robusticity of the Biśnik Cave specimen relative to the other Late Pleistocene samples. Three astragali from layers 7 and 7e (nos. 1771, 1726 and B/03/W/2775) and one from layer 15 (no. B/04/W-3299) all fall within the variation for astragali from German MIS 7 and MIS 6 sites (Table V, Fig. 4), but there is no overlap with later Late Pleistocene material from Jaurens, Kostenki and Solutré.

Horse metapodials and first phalanges vary in morphological characteristics over time and between different environments (EISENMANN 1979; DIVE & EISENMANN 1991; VAN ASPEREN 2010). They therefore give clues to the biostratigraphical position and environmental conditions of the layers in which they were found. Of the metacarpals (Table VIa), three specimens could be included in a log ratio diagram (Fig. 5). The metacarpals from layer 15 (no. B35/98/9) and layer 9 (no. B/05/4563) are closest in absolute size to metacarpals dated to MIS 7 and MIS 6 remains from Germany. However, both metacarpals have more strongly developed distal epiphyses (V12-14) than the comparative samples. The third metacarpal (no. B/05/W/4986), from layer 8, is somewhat smaller in absolute size, with some measurements being closer to those of Late Pleistocene species. It has a robust diaphysis (V3).

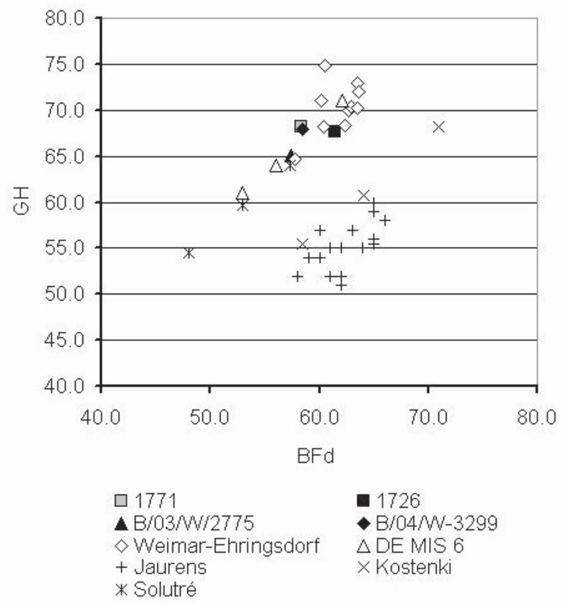

Fig. 4. Scatterplot of measurements on the astragali from Biśnik Cave and various samples of Pleistocene caballoid horses (Weimar-Ehringsdorf, DE MIS 6: VAN ASPEREN 2009a; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997; Solutré: GUADELLI 1987).

Table VIa

Measurements on the metacarpals from Biśnik Cave, *Equus hemionus* (EISENMANN 1979) and various samples of Pleistocene caballoid horses (UK MIS 7, UK MIS 6, Weimar-Ehringsdorf, DE MIS 6, DE MIS 5e: VAN ASPEREN 2009a; Wallertheim F: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Solutré: GUADELLI 1987; Zwoleń: GAUTIER 2005)

Specimen / sample	n max	V3	V10	V11	V12	V13	V14
Biśnik Cave no. B35/98/9	–	–	56.3	58.2	44.7	34.7	37.9
Biśnik Cave no. B/05/4563	–	–	57.4	56.8	44.5	34.7	34.2
Biśnik Cave no. B/05/W/4986	–	44.3	51.2	–	40.0	32.3	–
Equus hemionus	22	25.7	38.9	38.7	29.3	24.3	26.1
UK MIS 7	40	40.3	53.8	55.0	41.1	32.3	34.0
Weimar-Ehringsdorf	11	41.3	55.5	55.6	41.9	32.8	34.4
UK MIS 6	5	35.8	45.7	47.1	34.7	27.5	28.0
DE MIS 6	15	41.8	54.6	55.1	38.9	30.7	33.2
DE MIS 5e	4	42.5	55.3	55.1	41.4	32.3	34.6
Wallertheim F	5	37.4	52.5	51.0	39.6	31.2	33.1
Jaurens	25	36.9	50.3	51.7	37.9	29.3	31.1
Solutré	44	34.6	48.2	49.9	36.6	28.5	30.4
Zwoleń	4	36.9	52.1	53.7	–	–	–

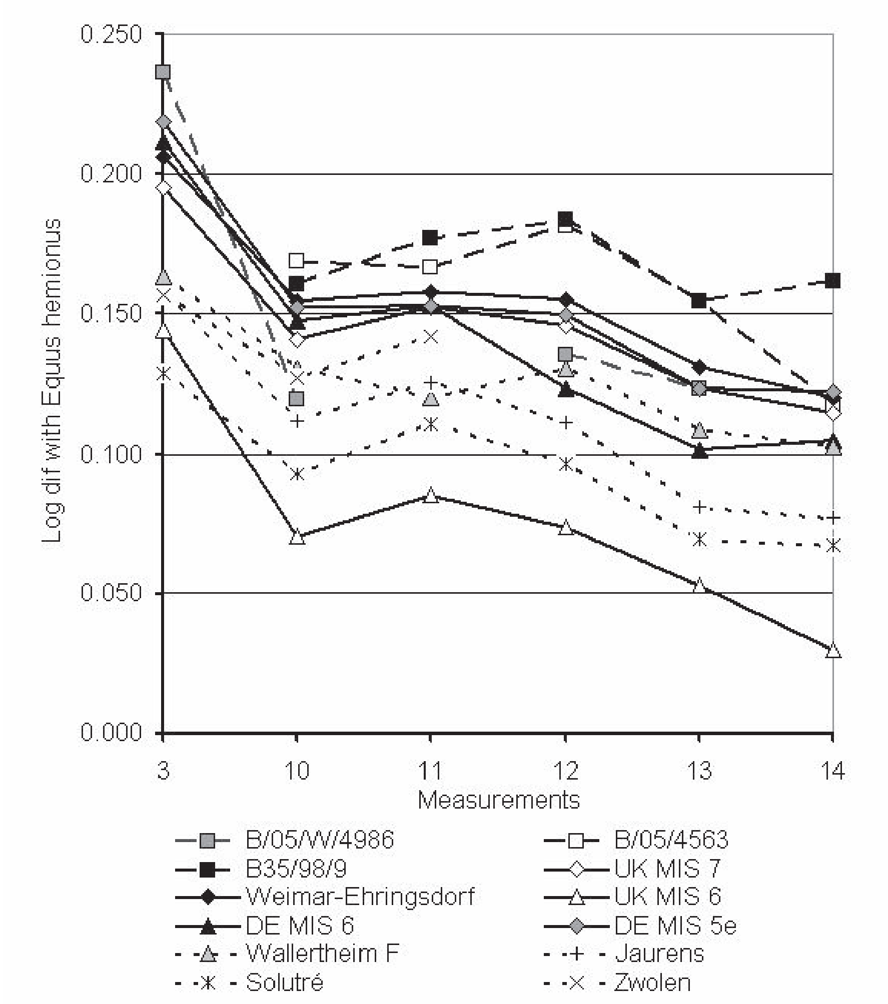

Fig. 5. Log ratio diagram of measurements on the metacarpals from Biśnik Cave and various samples of Pleistocene caballoid horses (UK MIS 7, UK MIS 6, Weimar-Ehringsdorf, DE MIS 6, DE MIS 5e: VAN ASPEREN 2009a; Wallertheim F: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Solutré: GUADELLI 1987; Zwoleń: GAUTIER 2005); reference sample: *Equus hemionus* (EISENMANN 1979).

Seven metatarsals (Table VIb) were complete enough to include in a log ratio diagram (Fig. 6). The metatarsal from layer 5 (no. W-8811) is very similar in size and morphology to those of *Equus ferus gallicus*. The metatarsal from the boundary between layers 7 and 5 (no. B17/98/12), the specimen from layer 7 (no. 1725) and a metatarsal from unknown provenance (no. B96/1059) are of somewhat larger size, with a robust diaphysis (V3) and much relief on the distal epiphysis (V12-14). These metatarsals furthermore have deep diaphyses (V4) and broad proximal epiphyses (V5, V7). The metatarsals from the interglacial layers (nos. B5/06/W5224, layer 13, and B35/98/10, layer 15) as well as the specimen

Table VIb

Measurements on the metatarsals from Biśnik Cave, *Equus hemionus* (EISENMANN 1979) and various samples of Pleistocene caballoid horses (UK MIS 7, UK MIS 6, Weimar-Ehringsdorf, DE MIS 6, DE MIS 5e: VAN ASPEREN 2009a; Wallertheim: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997; Solutré: GUADELLI 1987; Zwoleń: GAUTIER 2005)

Specimen / sample	n max	V1	V3	V4	V5	V6	V10
Biśnik Cave no. W-8811	–	273.1	35.8	34.8	55.4	43.7	52.5
Biśnik Cave no. B17/98/12	–	–	42.3	–	–	–	56.2
Biśnik Cave no. 1725	–	–	38.8	37.0	60.2	46.4	–
Biśnik Cave no. B130/97/7	–	–	–	–	–	–	59.7
Biśnik Cave no. B5/06/W5224	–	–	47.2	34.4	–	–	62.3
Biśnik Cave no. B35/98/10	–	–	44.3	–	–	–	58.9
Biśnik Cave no. B96/1059	–	–	36.5	–	60.8	45.7	–
Equus hemionus	22	250.6	25.2	25.3	40.5	35.1	38.0
UK MIS 7	54	282.1	39.2	36.0	58.2	47.8	57.2
Weimar-Ehringsdorf	7	283.5	39.2	37.9	56.5	47.4	55.7
UK MIS 6	10	245.8	32.7	29.0	50.2	40.1	47.0
DE MIS 6	19	278.4	38.5	36.2	57.7	47.1	55.8
DE MIS 5e	1	–	39.4	36.4	–	50.7	–
Wallertheim F	5	286.7	38.1	36.2	57.0	48.6	54.6
Jaurens	17	267.6	36.1	34.3	54.2	42.2	52.3
Kostenki	60	281.2	36.2	–	56.5	–	–
Solutré	32	261.4	33.6	32.0	50.5	–	48.9
Zwoleń	4	275.5	–	37.4	56.9	–	53.4

Specimen / sample	n max	V11	V12	V13	V14	V7	V8
Biśnik Cave no. W-8811	–	54.4	39.6	28.7	29.6	50.2	10.4
Biśnik Cave no. B17/98/12	–	53.8	44.1	32.8	36.0	–	–
Biśnik Cave no. 1725	–	–	–	–	–	54.5	10.1
Biśnik Cave no. B130/97/7	–	59.3	–	32.5	33.3	–	–
Biśnik Cave no. B5/06/W5224	–	60.9	47.2	35.1	39.4	–	–
Biśnik Cave no. B35/98/10	–	57.3	44.5	33.8	37.3	–	–
Biśnik Cave no. B96/1059	–	–	–	–	–	54.0	–
Equus hemionus	22	37.5	30.0	23.9	26.5	35.9	9.0
UK MIS 7	54	55.9	42.4	32.4	35.4	51.5	13.0
Weimar-Ehringsdorf	7	54.4	41.8	31.7	35.2	51.8	11.7
UK MIS 6	10	47.5	36.1	27.6	28.8	44.3	11.2
DE MIS 6	19	55.0	41.7	30.1	34.0	52.0	12.8
DE MIS 5e	1	–	–	–	–	53.7	–
Wallertheim F	5	53.8	41.8	31.2	35.4	50.1	14.6
Jaurens	17	53.6	39.9	29.6	33.2	47.9	13.7
Kostenki	60	56.0	–	–	–	–	–
Solutré	32	50.7	38.3	28.2	31.6	45.5	10.9
Zwoleń	4	54.4	–	–	–	–	–

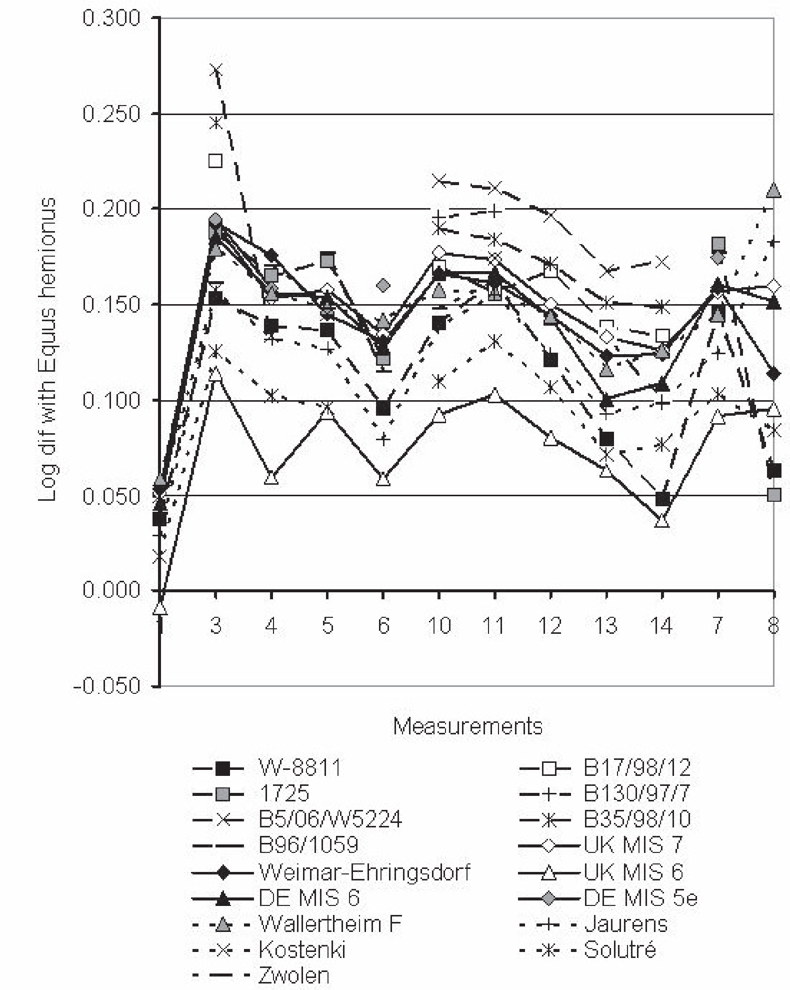

Fig. 6. Log ratio diagram of measurements on the metatarsals from Biśnik Cave and various samples of Pleistocene caballoid horses (UK MIS 7, UK MIS 6, Weimar-Ehringsdorf, DE MIS 6, DE MIS 5e: VAN ASPEREN 2009a; Wallertheim F: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997; Solutré: GUADELLI 1987; Zwoleń: GAUTIER 2005); reference sample: *Equus hemionus* (EISENMANN 1979).

from layer 11 (no. B130/97/7) are all large compared to the cold-climate metatarsals. They are larger than the average for MIS 5e horses from Germany and MIS 7 horses from Germany and the British Isles.

The anterior first phalanx recovered from layer 15 (no. B65/98/13) is similar in size and morphology to other late Middle Pleistocene samples (Table VII, Fig. 7). The specimen has a short supra-tuberosital length (V10) relative to the infra-tuberosital length (V11).

Overall, the horse remains from Biśnik Cave are similar in size and morphology to caballoid horse remains from the late Middle and Late Pleistocene of northwest and central

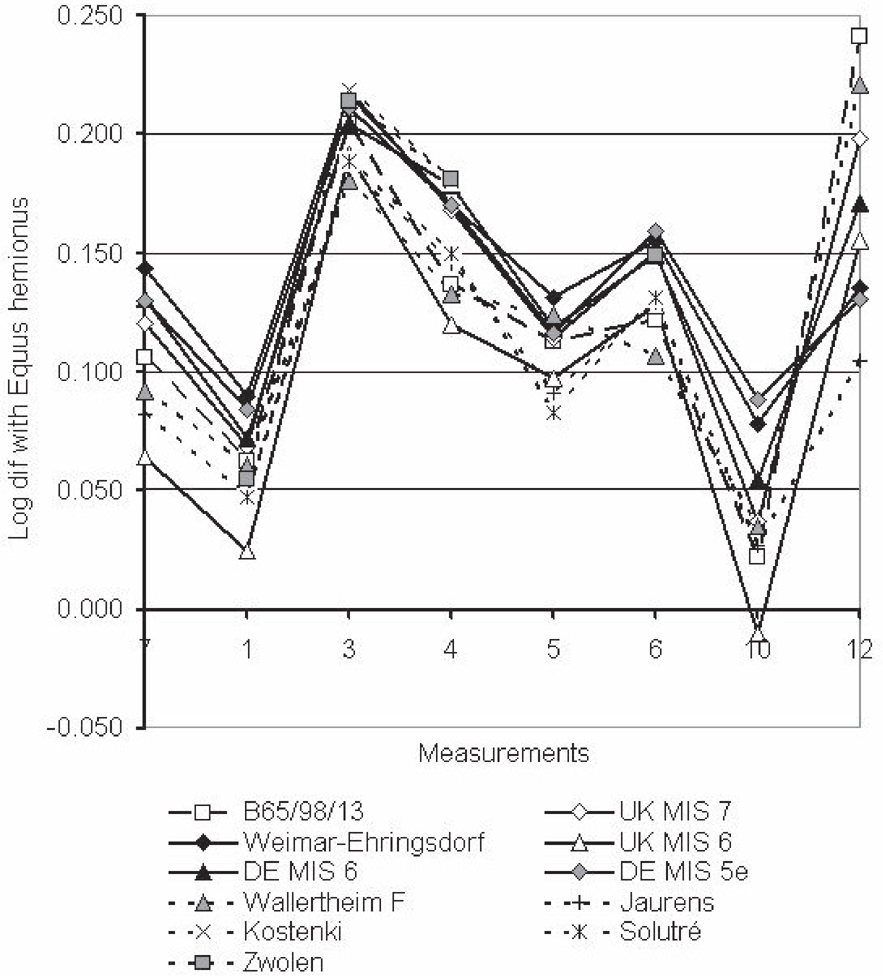

Fig. 7. Log ratio diagram of measurements on the anterior first phalanx from Biśnik Cave and various samples of Pleistocene caballoid horses (UK MIS 7, UK MIS 6, Weimar-Ehringsdorf, DE MIS 6, DE MIS 5e: VAN ASPEREN 2009a; Wallertheim F: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997; Solutré: GUADELLI 1987; Zwoleń: GAUTIER 2005); reference sample: *Equus hemionus* (DIVE & EISENMANN 1991).

Europe. It has been proposed to refer all caballoid horses from this time period to a single species, *Equus ferus* (ICZN 2003; VAN ASPEREN in press), with possible subspecific status for the smaller Late Pleistocene forms. However, limited evolutionary change occurred within this lineage over time, and various ecotypes can be recognised with adaptive features which enabled these populations to survive in the climatic extremes of Pleistocene Europe (VAN ASPEREN 2010). The specific and adaptive affinities of the Biśnik Cave horses are discussed below.

Table VII

Measurements on the anterior first phalanges from Biśnik Cave, *Equus hemionus* (DIVE & EISENMANN 1991) and various samples of Pleistocene caballoid horses (UK MIS 7, UK MIS 6, Weimar-Ehringsdorf, DE MIS 6, DE MIS 5e: VAN ASPEREN 2009a; Wallertheim: VAN ASPEREN unpublished data; Jaurens: EISENMANN online data; Kostenki: KUZMINA 1997; Solutré: GUADELLI 1987; Zwoleń: GAUTIER 2005)

Specimen / sample	n max	V7	V1	V3	V4
Biśnik Cave no. B65/98/13	–	61.4	88.4	39.3	56.3
Equus hemionus	15	48.1	76.5	24.6	41.1
UK MIS 7	36	63.5	89.6	40.6	60.6
Weimar-Ehringsdorf	8	66.9	94.2	40.4	60.8
UK MIS 6	3	55.7	81.0	38.2	54.2
DE MIS 6	8	64.9	90.3	39.3	62.0
DE MIS 5e	2	64.9	93.0	39.9	60.8
Wallertheim F	4	59.4	88.0	37.2	55.9
Jaurens	29	58.1	85.4	37.6	57.5
Kostenki	95	–	–	40.6	62.3
Solutré	85	–	85.3	37.9	58.0
Zwoleń	2	–	86.9	40.2	62.4
Specimen / sample	n max	V5	V6	V10	V12
Biśnik Cave no. B65/98/13	–	40.0	48.5	61.6	18.0
Equus hemionus	15	30.8	36.7	58.5	10.3
UK MIS 7	36	40.1	51.8	63.6	16.3
Weimar-Ehringsdorf	8	41.7	52.4	70.1	14.1
UK MIS 6	3	38.6	49.2	57.1	14.8
DE MIS 6	8	40.5	51.7	66.2	15.3
DE MIS 5e	2	40.3	52.9	71.7	14.0
Wallertheim F	4	41.0	46.9	63.3	17.2
Jaurens	29	38.0	49.4	62.2	13.1
Kostenki	95	–	–	–	–
Solutré	85	37.4	49.6	–	–
Zwoleń	2	–	51.6	–	–

IV. BIOSTRATIGRAPHY

Little size and shape variation occurs in caballoid dental elements over the course of the late Middle and Late Pleistocene (VAN ASPEREN 2009a), and this is reflected in the dental elements from Biśnik Cave, which show essentially no size or shape differences between the earlier and later material, or between cold-climate and temperate-climate samples. In contrast, the postcranial elements give clear clues to the age and affinities of the material, although the small sample size prevents more definitive conclusions. Over the late Middle Pleistocene, the supra-tuberosital length (V10) of the first phalanges increases relative to the infra-tuberosital length (V12; DIVE & EISENMANN 1991; VAN ASPEREN 2009a). The phalanx from Biśnik Cave, which dates in MIS 7, shows the primitive condition. The astragali from all layers up to layer 7 are similar in size and morphology to those from late Middle Pleistocene sites. There is a clear morphological contrast with astragali of the later Late Pleistocene forms *Equus ferus gallicus* and *E. f. latipes*. A slight size decrease can be observed between layers 15-9, with very large specimens, and layers 8-7, with metapodials that are similar in size and shape to late Middle Pleistocene samples and early Late Pleistocene fossils. The single metatarsal dating from MIS 4 (layer 5) is clearly smaller. This metatarsal is also the only specimen in which the supra-articular distal breadth (V10) is clearly smaller than the articular distal breadth, an advanced evolutionary feature (EISENMANN 1979; VAN ASPEREN 2009a).

The uniquely complete stratigraphical sequence in Biśnik Cave, with horse remains found in nearly all layers, provides a way to study the equid biostratigraphy of this part of Europe. Material from layers 15-9 is most similar to eastern European remains dating from MIS 7 to MIS 5, and thus extends the time span of this lineage into early MIS 4. During MIS 4, a size decrease occurred, and the limited evidence suggests that by the end of MIS 4 horse body size decreased to the level of that observed in the ecotype *Equus ferus gallicus*.

V. ECOMORPHOLOGY

The European caballoid lineage is characterised by phenotypic variation that can be interpreted as fluctuating adaptation to glacial and interglacial conditions over the climatic cycles of the Pleistocene (VAN ASPEREN 2010). During glacial periods, these equids were robust, and decreased in body size towards the most severe glacial episodes. In interglacial conditions, these animals were large and robust in dry, continental environments, and more slender and of smaller body size in oceanic climates. Several features of the Biśnik Cave fossils can be interpreted against this background.

Remains from the MIS 7 and MIS 5e interglacials are large and fairly robust. These features are in accordance with the relatively dry and continental but temperate climate postulated for MIS 7 in Eastern Europe (RUDDIMAN & MCINTYRE 1982). MIS 5e, in contrast, was characterised by dense forest over large areas of Europe (CHEDDADI et al. 1998; KUKLA et al. 2002; VELICHKO et al. 2005). However, horse remains from Eemian sites in Germany are equally large and robust as the Biśnik Cave remains (VAN ASPEREN 2010). Horse populations seem to have been small during this period (VAN ASPEREN 2009a), so that pressure on resources was low enough to enable the horses to grow to large size. This morphotype continues through MIS 5d-c, when conditions were still relatively mild in comparison to the later Vistulian. This is especially clear for layer 9, which contained abundant remains of forest-adapted species (CYREK et al. 2009).

An increase in robusticity and a decrease in size characterises horse fossils from layers dated to MIS 5b-2. Remains from this period have robust, deep diaphyses and a broad proximal epiphysis, traits also found in horses from German MIS 6 sites. The tibia found in layer 2 (MIS 2) is rather short and robust, and falls just outside the variation for *Equus ferus* *gallicus* and *E. f. latipes*. In length, it is close to the average for German MIS 7 and MIS 6 sites, although in robusticity it falls at the lower end of the variation for these comparative samples. Although inferences based on a single specimen are far from conclusive, it can be hypothesised that the severe glacial conditions of MIS 2 induced small body size and high robusticity in the caballoid horse lineage, similar to the pattern documented for MIS 6 horses in the British Isles, which lived in a marginal environment with limited resources (VAN ASPEREN 2009b, 2010, 2011). The climatic conditions in Poland during MIS 2 were markedly less favourable for horses than the interstadial conditions at Jaurens (MIS 3) and Kostenki (MIS 3-2), which are located in the more oceanic western Europe and the refugium area of Crimea (MARKOVA 2011), respectively. A similar argument could be made for the morphological traits of *Equus ferus arcelini*.

VI. BIOGEOGRAPHY

Caballoid horses live in a wide range of environments, but are best adapted to mosaic steppe environments (LINKLATER 2000). The core areas of their natural range in Eurasia are located in the steppic regions of Central Asia. It is therefore expected that horse populations would contract to these regions when climatic conditions were unfavourable in Europe, such as during oceanic interglacials and at glacial maxima, followed by range expansion when suitable habitats became available again. Such patterns of repeated immigration from Asia have been documented for mammoths (LISTER & SHER 2001; LISTER et al. 2005). Due to a lack of excavated Middle Pleistocene sites with horse remains in the source area of these populations, similar patterns can as yet not be demonstrated for caballoid horses. However, there are some indications in the Biśnik Cave material that such range contractions and expansions did take place. The first phalanx from the layer dated to MIS 7 is more primitive than its contemporaries in Germany. An influx of steppe species has been postulated for MIS 7 (SCHREVE 2001; KAHLKE et al. 2002), and less advanced horse populations may have migrated into eastern Europe along with a suite of other steppe-adapted animals. The marginal environments of the MIS 6 glacial maximum may have led to the local extinction of horse populations in Europe, followed by renewed immigration from refugium areas. The morphological data for this period certainly imply that the MIS 6 horses lived in very unfavourable climatic conditions. The low abundance of horses in MIS 5e may indicate that populations whose range mainly comprised Central Asia only occasionally ventured into Europe. However, more data on Eastern European and Central Asian faunas is needed to test these hypotheses. Horse abundance increases during later MIS 5 and MIS 4, and by MIS 4 it seems a single lineage, known as *Equus ferus gallicus*, became established throughout Europe, as evidenced by the morphological similarities between the Jaurens and Biśnik Cave layer 5 specimens.

VII. CONCLUSIONS

The sediments of Biśnik Cave are unique for Poland in providing a more or less continuous sequence of deposits dating from MIS 8 through to the Holocene. The cave is one of the very few sites in Poland to produce Middle Pleistocene horse remains, and the only site so far to yield material covering the entire period from MIS 7 to the late Vistulian.

All horse remains can be attributed to the caballoid species *Equus ferus*. Morphologically, the fossils from Series I are similar to other late Middle and early Late Pleistocene samples. These animals seem to have thrived in the steppic environment of MIS 7 and MIS 5d-c, while the somewhat primitive first phalanx may indicate repeated waves of immigration from the steppic areas of Central Asia, where selection pressures can be postulated to have been lower than in the more forested areas of Europe. A gradual size decrease characterises the remains from Series II and III, with a morphotype similar to the western European *Equus ferus gallicus* being found in the MIS 4 deposits. These glacial horses were also rather robust. The size decrease culminates in the small-sized, robust remains from MIS 2, representing a population living in marginal periglacial environments. However, due to the limited number of remains these conclusions must be regarded as preliminary.

Although our knowledge of the Last Glacial fauna of Europe is well-developed, there are still many questions about faunas of the earlier Pleistocene. Since the Middle Pleistocene is the period when hominin groups became established in Europe, important advances in our understanding of this process could be made by studying the fauna and vegetation of this period. At present, our knowledge of eastern and south-eastern European fauna and flora of the Middle Pleistocene is limited. Data for more eastern regions of Russia and Central Asia is virtually nonexistent. Given the importance of these regions as source areas for faunal migrations and refugia for many species, and given the impact that faunal dynamics will have had on hominin populations, research into fossil remains from these areas will greatly aid in developing models of the hominin colonisation of Europe.

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