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Pliocene to early Middle Pleistocene ursine bears in Europe: a taxonomic overview

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Abstract. The Pliocene to early Middle Pleistocene bear fauna in Europe can be divided into four main morphophyletic groups. All the known Pliocene bears belong to *Ursus* ex gr. *minimus-thibetanus*. They represent at least two migration events (MN 14–MN 15a and MN 15b–MN 16b). Representatives of this group were recorded also in the late MN 17 and in the Lower to Middle Toringian. *Ursus* ex gr. *etruscus* are present since the early MN 17 and they survived until the Early Biharian. The Early Biharian *U. etruscus* most likely represents a blind lineage in Europe. The oldest representatives of *Ursus* ex gr. *arctos* are known from the late Early Biharian localities, about 1.1 Ma ago (their possible earlier presence – e.g. DA2C$_1$ or Ceyssaguet – require confirmation). The first occurrence of *U. deningeri*, the oldest taxon in *U.* ex gr. *deningeri-spelaeus*, was recorded approximately at the same time.
Keywords. *Ursus*, taxonomy, Pliocene, Pleistocene, Europe

INTRODUCTION

The process of formation of the modern European theriofauna started in the Early Pliocene. Since this period we recognize in Europe not only the representatives of modern mammalian genera, but complete mammalian assemblages that display modern character. Bears became integral part of these faunas. Except agriotheriine bears that persisted from the Miocene, we meet modern ursine bears of the genus *Ursus* Linnaeus, 1758. The direct ancestor of genus *Ursus* is supposed to be among the representatives of Miocene genus *Ursavus* Schlosser, 1899a, but exact time or place of its origin remain unknown. Members of the genus *Ursus* spread all over the Northern Hemisphere during the Pliocene and Pleistocene and produced considerable number of species, from which four survived to the present. Record of ursine bears exists in Europe continuously since the Early Pliocene. Although it is only sporadic in some periods, bears have become one of dominant group of mammals from the Middle to Late Pleistocene.

The main goal of this paper is to present a general overview of the taxonomy of ursine bears in Europe (incl. the Caucasus region). I critically reviewed literature, especially that from the past 20 years, and complemented it by results of my own research.

MATERIAL AND METHODS

I use the term "ursine bear" for members of the subfamily Ursinae in the following sense. I accept the subdivision of family Ursidae Fischer, 1814 into five subfamilies: Ursinae Fischer, 1814, Arctotheriinae F. Ameghino, 1903 (= Tremarctinae Merriam & Stock, 1925), Ailuropodinae Grevé, 1892 (non 1894 as used in McKenna & Bell 1997), Agriotheriinae Kretzoi, 1929, and Ursavinae Kretzoi, 1945. I follow Baryšnikov (2007) in recognizing three genera in the subfamily Ursinae: *Ursus* Linnaeus, 1758, *Helarctos* Horsfield, 1825, and *Melursus* Meyer, 1793. I assign all the European representatives of this subfamily to the genus *Ursus*.

The taxonomic overview given bellow is arranged according to main morphophyletic groups of Eurasian bears sensu Mazza & Rustioni (1994): gr. *minimus-thibetanus*, gr. *etruscus*, gr. *arctos*, and gr. *deningeri-spelaeus* (gr. *maritimus* is not discussed here). In the section about *Ursus* ex gr. *minimus-thibetanus* I discuss all European ursine bears from the Early Pliocene, although e.g. *U. boeckhi* was not explicitly included in this group by Mazza & Rustioni (1994).

The definition and subdivisions of Quaternary period follow Gibbard & Cohen (2008) and Gibbard & Head (2009a,b). The definition and subdivisions of Mammal Ages (Ruscinian, Villányian, Biharian, and Toringian) and their correlation with chronostratigraphical scale as well as the MN-zones follows Fejfar & Heinrich (1983, 1990) and Fejfar et al. (1998). The Italian Faunal Units schema and correlation was adopted from Gliozzi et al. (1997). Biochronological position of several Pleistocene localities was adopted from Maul et al. (2007) and Maul (2007).

All nomenclatural acts presented here conform to the 4th edition of the International Code of Zoological Nomenclature (ICZN 1999; hereafter the *Code*).

Capital and lowercase letters, P/p (premolars), and M/m (molars), refer to upper and lower cheek-teeth, respectively.

RESULTS AND DISCUSSION

Ursus ex. gr. *minimus-thibetanus*

Probably the earliest representative of genus *Ursus* in Europe was recorded from the Early Pliocene (early MN 14) locality Montpellier, France. It is represented especially by two upper second molars (M2) that still bear several *Ursavus*-like characters (Wagner 2006). I believe that also an isolated third lower molar (m3) described and figured by Gervais (1848-1852: 107, pl. 8, fig. 1, 1a) as a new species *Ursus minutus* Gervais, 1852, belongs to an ursine bear (the name was used for the first time by Gervais 1851: 152, but as a nomen nudum). Contrary to Morlo (in Morlo & Kundrát 2001) and Baryšnikov (2007) I do not include it in *Agriotherium* [A. Wagner], 1837. Based on the figure in

Gervais (I have not studied the original specimen) and its comparison with published m3s of *Agriotherium* bears (Lydekker 1884, Hendey 1980, Dalquest 1986, Qiu et al. 1991) I think that m3 in *Agriotherium* is more rounded in outline, with a more closed crown and with rather conical root compared to the figured specimen from Montpellier. In any case, the taxonomic status of this bear remains unresolved.

Undoubted ursine bears were recorded from some, probably slightly younger, Early Pliocene (MN 14) localities in Europe: Kuchurganian beds, Ukraine (Korotkevich 1967), Baraolt-Căpeni (= Barót-Köpecz), Romania (Maier von Mayerfels 1929), Alcoy, Spain (Montoya et al. 2006), and Dorkovo, Bulgaria (Delson et al. 2005). Based on the study of material from Kuchurgan and Baraolt (e.g. the morphology of m1) I suppose that these bears compose a separate migration event and probably also a separate species for which name *Ursus boeckhi* Schlosser, 1899a is available. This name was based on the material from Baraolt-Căpeni by Schlosser (1899a,b,c). Exact relationships of these bears to the previous one as well as the later forms are unclear. At the present state of knowledge it is not possible to exclude their conspecificity with the bear from Montpellier as well as with bears from MN 15a (see below). On the other hand, I reject its conspecificity with *U. minimus* suggested by Morlo (in Morlo et Kundrát 2001) and Baryšnikov (2007).

Bears from MN 15a were found only in the surroundings of Perpignan, France. The material is relatively heterogeneous (in both size and morphology) and its taxonomic position has been subject of controversy during the last 100 years (cf. e.g. Depéret 1890, 1892, Thenius 1947, Viret 1954, Morlo & Kundrát 2001, Baryšnikov 2007). My study of the material in the collection of Muséum de Lyon and Université de Lyon 1 showed that these bears were more similar to the bears of MN 14 than to typical *U. minimus*, but due to the scarcity of material and large variability of bear teeth no precise taxonomic conclusions were reached. But I cannot agree with Mazza & Rustioni (1994) that part of this material represents *Ursus thibetanus*. The similarities mentioned in their paper seem to me to be based on plesiomorphic characters. Moreover, the presence of small cusp(s) distal behind the protoconid of p4 and p3 or relatively broad talon of M2 characterize an earlier evolutionary stage in the bear phylogeny than that represented in Recent *U. thibetanus*. Depéret (1890, 1892) described these specimens under the names "*Helarctos arvernensis* race (mut. asc.) *ruscinensis*" (1890: 34) and "*Helarctos arvernensis* race (mut. asc.) *pyrenaicus*" (1892: 118). Although these names (*ruscinensis* and *pyrenaicus*) were subsequently broadly used (on both specific and subspecific level), I conclude that both were published as infrasubspecific names, and that they are therefore unavailable from above mentioned Depéret's papers (Art. 10.2. and 45.5. of the Code).

Since MN 15b the black bears have become relatively frequent, though not abundant, representatives of European faunal assemblages. They were recorded from the localities from Caucasus to France and from Northern Mediterranean to England (for the last one see Newton 1891 and pers. obs.). The localities with most important finds include Kvabebi (MN 16, Georgia; Vekua 1972), Catacombs of Odessa (MN 15/16, Ukraine; Rošin 1956), Osztramos 7 (MN 16b, Hungary; Jánossy 1978), Węże 2 (MN 15b, Poland; Ryziewicz 1969), Gaville (MN 16, Italy; Berzi 1966), Layna (MN 15b, Spain; Soria &

Morales 1976) and Les Etouaires (MN 16a, France; Mazza & Rustioni 1994). I suppose that these bears represent a new (at least a second) migration wave of the black bears into Europe. They seem to be a little more advanced in the tooth morphology than their earlier relatives, as shown e.g. by the presence of the pre-metaconid elements in the trigonid of m1 (but see the specimen from Včeláre 2 in Sabol et al. 2008). They were recorded from MN 15b to MN 16b and crossed the Ruscinian/Villányian boundary without changing. On the other hand there is no undoubted record from MN 17 (see below). Bears of this type can be called *Ursus minimus* Devèze et Bouillet, 1827 (incl. *U. arvernensis* Croizet et Jobert, 1828 and *U. wenzensis* Stach, 1953). Kretzoi (1954) created for the European bears of *minimus*- and *thibetanus*-type a new (sub)genus *Ursulus*. But because he did not accompany this name by a description or diagnosis, it is only a nomen nudum. Nevertheless, I agree with him that these bears are taxonomically distinct from the bears of the *boeckhi*-type, for which he used the generic name *Protarctos* Kretzoi, 1945 (type species *U. boeckhi*; see Kretzoi, 1945). I also agree with Kretzoi (1954) and Baryšnikov (2007), among others, that none of the European Pliocene black bears are closely related with the genus *Helarctos* (contra e.g. Ryziewiecz 1969).

It seems that since the beginning of MN 17 the black bears were replaced in Europe by *Ursus etruscus*, a newcomer, probably of Asiatic origin (Rustioni & Mazza 1993b). Under these circumstances, the occurrence of *Ursus* ex gr. *minimus-thibetanus* in the latest MN 17 (before *deucalion*-horizon) is very interesting. They were recorded from the Italian locality Poggio Rosso (Mazza et al. 2005) and the Hungarian localities Villány 3 (Kormos 1937; pers. observation) and probably also Kisláng (Kretzoi 1954; pers. observation). The dental material from Villány 3 represents a typical black bear with affinity to both *U. minimus* and *U. thibetanus*. The exact taxonomic status of these interesting finds remains unclear for now. There are two possible explanations: (1) they belong to the latest representatives of an autochthonous lineage of European *U. minimus*; or (2) they represent a new migration event of black bears from Asia, and therefore the first short occurrence of *U. thibetanus* in Europe.

There is no unambiguous record of black bears from the Biharian. Even the taxonomic status of specimens from Chlum IV, Czech Republic, assigned to the black bear by Wagner (2004) is now under doubts and the determination as *Ursus* sp. seems to be more correct. Although I cannot exclude a possible presence of black bears in the European Latest Biharian, their doubtless occurrence starts in the Early Toringian (e.g. Heller 1949) and continues at least to the Saalian glaciation (e.g. Rustioni & Mazza 1993a). Throughout this period they were recorded from the Urals (Baryšnikov 2002a) and the Caucasus region (Baryšnikov 2010) across Central (von Reichenau 1906, Sieber 1949, Nagel & Rabeder 2000, Turner 2000, Musil 2005-2006) and southern Europe (Thenius 1958, Kurtén & Poulianos 1977) to Spain (Torres 1988) and France (Crégut-Bonnoure 1996), but not from Great Britain. These bears represent the last migration event of black bears into Europe and belong to *Ursus thibetanus* Cuvier, 1823 (e.g. Argant 1991, Baryšnikov 1992, Fistani & Crégut-Bonnoure 1993). Several names were used for these bears: *U. mediterraneus* Major, 1873 (Grotta di Reale, Italy), *Plionarctos* (?) *stehlini* Kretzoi, 1941 (Mauer,

Germany), *U. schertzi* Dehm, 1943 (Achenheim, France), *U.* (*Plionarctos*) *telonensis* Bonifay, 1971 (Cimay, France), *U.* (*Selenarctos*) *karabach* Vereŝagin et Tihonov, 1994 (Azyh cave, Azerbaijan), *U. t. kurteni* Crégut-Bonnoure, 1997 (Cèdres cave, France), *U. t. vireti* Crégut-Bonnoure, 1997 (Bruges, France), and *U. t. permjak* Baryšnikov, 2002 (Mohnevskaâ cave, Russia). According to the last revision (Baryšnikov 2007, 2010) only two subspecies are valid in Europe: *U. t. permjak* in the Urals and *U. t. mediterraneus* in the rest of the range in Caucasus and Europe; I agree with this opinion. The genus *Plionarctos* Frick, 1926 comprises early members of tremarctine bears (see Tedford & Martin 2001 for a revision). This name was wrongly applied by Kretzoi (1938) to all Eurasian Pliocene and Pleistocene black bears and this mistake was accepted by several subsequent authors who used this name on generic or subgeneric level for representatives of the Middle Pleistocene *Ursus thibetanus* in Europe.

Ursus* ex. gr. *etruscus

Since the early MN 17 (Early Pleistocene) we meet in Europe representatives of a new ursine evolutionary lineage of, perhaps, Asiatic origin (Rustioni & Mazza 1993b). The most famous localities in Europe yielding remains of these bears are Saint-Vallier (France; Viret 1954, Argant 2004) and La Puebla de Valverde (Spain; Kurtén & Crusafon-Pairó 1977). Bears of this evolutionary niveau were called by Mazza & Rustioni (1992) *Ursus* aff. *etruscus* and described as a separate subspecies by Baryšnikov (2007): *U. etruscus saintvallierensis* Baryšnikov, 2007. Approximately contemporary and morphologically similar bears are known from Middle Asia (Tadzhikistan; e.g. Šarapov 1986, Sotnikova 1989; by Baryšnikov 2007 assigned to the subspecies *U. e. verescagini* Šarapov, 1986) and North Africa (Ahl al Oughlam, Morocco; described by Geraads 1997 as *Ursus* cf. *etruscus*).

Ursus etruscus Cuvier, 1823 (with *U. cultridens* Cuvier, 1824 as its objective synonym; see Art. 72.7. of the Code) was described from the Early Pleistocene locality Figline (Upper Valdarno, Italy; lectotype designated by Berzi 1966). According to the revisions of this species by Mazza & Rustioni (1992) and Baryšnikov (2007), a typical *U. etruscus* occurred in the late MN 17 (Olivola F. U.) and it is proposed by them to be an autochthonous descendent of the former form. In Europe it survived till the Early Pleistocene (Early Biharian). The last certain records are from the faunas equivalent to Farneta F. U. in the Italian biostratigraphical scale – e.g. Pietrafitta (Italy; Rustioni & Mazza 1993c) or Venta Micena (Spain; Torres 1992a). The species was listed (sometime conditionally) also in younger faunas: e.g. Pirro Nord (Italy; Petrucci & Sardela 2009), Monte Peglia (Italy; Basilici et al. 1991), Marjan (Croatia; Malez 1961), Colle Curti (Italy; Mazza & Rustioni 1992), Ceyssaguet (France; Tsoukala 2004), but the taxonomic identity of these specimens is a subject of controversy and some of them can represent early arctoid forms. The species is known from the most of Europe (especially its southern half), but only a few localities (mostly in Italy) yielded abundant material.

Vekua (1996) described from Dmanisi (Georgia; late MN 17) two bear forms as *Ursus etruscus* and *Ursus* sp. Based on the restudy of their figures (Vekua 1996, pl. 14-17)

I agree with Baryšnikov (2007) that both of them represent the same taxon, *U. etruscus vekuai* Baryšnikov, 2007 (they have similar teeth morphology, especially of m1).

Mazza & Rustioni (1992) suggested that *U. etruscus* s. str. was a rather highly specialized form without descendents. In general I agree with this idea, although it was not broadly accepted (e.g. Baryšnikov 2007, Argant 2009, Rabeder et al. 2010). However, Mazza & Rustioni (1992) based their opinion almost exclusively on the Italian material. Therefore the possibility cannot be excluded that the tendency described by them applies only to the Italian population (as a result of (sub)insular effect – cf. Loy et al. 2008 for differences between the skulls of Recent brown bears from Abruzzo and other South European regions) and not the species as a whole.

Ursus* ex. gr. *arctos

Rustioni & Mazza (1993b) were the first in modern times who suggested that brown bears (*Ursus* ex gr. *arctos*) occur in the European late Early Pleistocene (Early Biharian), in particular in Vallonet, France, and with some doubts even in Pirro Nord, Italy. Although bears from Vallonet were later re-determined as *U. deningeri* (Baryšnikov 2007) and those from Pirro Nord, based on additional material, as *U. etruscus* (Petrucci & Sardela 2009), it was an important break into the concepts of European bears taxonomy and phylogeny. Recently, this idea was supported by Rabeder et al. (2010), who revised in their excellent monograph bears from Deutsch-Altenburg, Austria, in particular from the localities DA2C$_1$, DA49, and DA4B (most of the material originated from DA4B, the age of which was estimated at 1.1–1.0 Ma; both others are little older). They concluded (especially on the basis of metapodial bones) that these bears were early representatives of brown bears. They also included in this form a little younger bear from Untermaßfeld, Germany, and, conditionally, also a little older finds from Ceyssaguet, France. Musil (2001) mentioned arctoid affinities of the bear from Untermaßfeld describing it as a new species *Ursus rodei* Musil, 2001. Olive (2006) and Rabeder & Withalm (2006) sugegsted that *U. rodei* is a junior synonym of *U. arctos* Linnaeus, 1758. On the other hand, Argant (2009) and Baryšnikov (2007) considered these bears as one of the oldest representatives of *U. deningeri* (see below). The taxonomic status of *U. rodei* requires further revision. Rosa et al. (2006) listed from pre-Jaramillo layers (TE12 and TE14) of Atapuerca – Sima del Elephante, Spain, a bear species as *U. dolinensis*, but gave no figures or description; therefore the exact taxonomical identity remains unclear.

The Spanish locality Atapuerca – Trinchera Dolina 4 (TD4) that belongs to the terminal Early Pleistocene (Biharian faunas after Jaramillo event and before Matuyama/Brunhes boundary) is probably somewhat younger than Untermaßfeld (see discussion in Kahlke 2006). García & Arsuaga (2001) described from it a new bear species as *U. dolinensis* García et Arsuaga, 2001, suggesting that it represents an early spelaeoid bear. Instead I agree with the broadly accepted view that *U. dolinensis* represents an arctoid form (e.g. Torres 1992b under somewhat ambiguous name *U. prearctos* Boule, 1919; Olive 2006, Baryšnikov 2007, Argant 2009, Rabeder et al. 2010). Two others localities from the terminal Early Pleistocene deserve mentioning: Sackdillinger-Höhle, Germany,

and Žírany, Slovakia. Heller (1956) described an isolated M2 from Sackdillinger-Höhle as *U. sackdillingensis* Heller, 1956 and sugegsted that it is related to early spelaeoid bears. Baryšnikov (2007) synonymized this form with *U. arctos*, while Torres (1992b) and Hilpert (in Ambros et al. 2005) suggested that it is conspecific with *U. thibetanus*. It is necessary to note that it is very problematic to assess taxonomic identity of bear species based on an isolated M2. The locality Žírany yielded a few teeth of a small bear that, according to me, belongs also to arctoid bears (cf. Wagner & Sabol 2007). Due to the scarcity of material the taxonomic status of bears from TD6 (Spain; García & Arsuaga 1999) remains unresolved. The stratigraphical position of the locality Rosia (Italy; Fondi 1972), from which *Ursus* gr. *etruscus-arctos* was listed, is not clear. Its fauna includes both Galerian and Villafranchian elements of large mammals and among micromammals *Mimomys savini* (Azzaroli et al. 1986).

In the earliest Middle Pleistocene (Late Biharian faunas after M/B), some problematic specimens that could also belong to arctoid bears were found. The most interesting seems to be the taxonomic status of *Ursus suessenbornensis* Soergel, 1926 from Süßenborn, Germany. For a long time, this bear was considered as a member of early spelaeoid bears and mostly treated as a subspecies of *U. deningeri* (e.g. Soergel 1926, Kurtén 1969, Baryšnikov 2007). On the other hand, Mazza & Rustioni (1994) synonymized this form with *U. arctos*; Rabeder et al. (2010) agreed, but recognized also *U. deningeri* from this locality. The taxonomic status of Süßenborn bear thus requires further revision. Rabeder et al. (2010) mentioned the presence of brown bears in the newly excavated material from West Runton, Great Britain. I also expect that at least some Late Biharian finds determined as *U. mediterraneus* belong to *U. arctos* s. l., not to *U. thibetanus* (e.g. Kövesvárad, Hungary, Jánossy 1963; Chlum IV, Czech Republic, Wagner 2004).

Brown bears were recorded also from the whole Toringian, more frequently from its second half. Till now, the Early Toringian localities yielded only a few specimens identified as arctoid bears. They include La Romieu (France; Prat & Thibault 1976 and Torres 1992b), Vergranne (France; Chagneau & Prat 1983), Arago (France; Moigne et al. 2006); Château, Br. 4 (France; Argant & Argant 2002, Argant 2009), Hundsheim (Austria; Withalm 2001) and Cueva Mayor (Spain; Rabeder et al. 2010).

Rabeder et al. (2010) were the first in modern times who discussed in detail the taxonomy of Early Pleistocene brown bears. On the basis of a precise description of the material from Deutsch-Altenburg and its comparison with the majority of relevant bear specimens they suggested that European brown bears from the late Early to early Middle Pleistocene (late Early Biharian to Early Toringian) compose a rather uniform group that can be called *Ursus suessenbornensis* Soergel, 1926 (leaving it open whether this taxon will be treated as a species or a subspecies of *U. arctos*). It is important to stress that in several cases the (re-)identification of brown bears (especially from Süßenborn, West Runton, Cueva Mayor and Hundsheim) was based mainly on metapodial bones. Their taxonomical value was suggested by Withalm (2001), who found that metapodial bones of spelaeoid bears are significantly plumper that those of arctoid. His results were based on a huge number of specimens that mostly originated from localities of the Late or late Middle Pleistocene

age. I would like to point out that the following two problems occur by application of this discriminative character by Rabeder et al. (2010): (1) They did not use metapodial bones of Biharian *U. deningeri* in their analysis and gave no evidence that morphological characteristics of the Toringian *U. deningeri* apply also to the Biharian one. Therefore it remains open, whether the observed relative similarity of studied Biharian bears with Recent *U. arctos* (and relative difference to Toringian *U. deningeri*) results from the presence of an arctoid apomorphic character in studied Biharian sample or whether it is based on the presence of a plesiomorphic character (i.e. that the putative arctoid character was present also in early *U. deningeri*). (2) The robustness of this character was supported by phylogenetic analysis. It was shown that *U. etruscus*, the ancestor of both *U. arctos* and *U. deningeri*, had metapodial bones plumper that early brown bears but slender than Toringian *U. deningeri*. Based on this assumption, it could be concluded that this character is apomorphic for arctoid bears and therefore that it was not present in early *U. deningeri*. However, I do not think that there any unambiguous proof exists that *U. etruscus* was a common ancestor for these lineages or that its morphology can be accepted as plesiomorphic in relation to *U. arctos* and *U. deningeri*. Irrespective to this I agree with Pacher (in verb., 2006) that early arctoid bears (sensu Rabeder et al. 2010) show more spelaeoid affinities than the modern *U. arctos*. A possibility cannot be excluded that they represented a separate lineage that was later replaced by modern *U. arctos*. This event could have taken place either on the Biharian/Toringian boundary (which I would be prefer) or in the Middle Toringian between the *suessenbornensis* and *priscus* groups of arctoid bears sensu Rabeder et al. (2010).

Ursus* ex. gr. *deningeri-spelaeus

The earliest representatives of spelaeoid bears occur in Europe approximately in the same time as the arctoid ones. The most important locality seems to be the Vallonet cave, France. I agree with Moullé (1992), Baryšnikov (2007) and Argant (2009) that these bears represent early *U. deningeri*, not with García (2003), who suggested they belong in *U. dolinensis*. The taxonomic status of *U. rodei* remains controversial. According to Baryšnikov (2007) and Argant (2009) this form represents the earliest *U. deningeri* (Baryšnikov 2007 treated it as a subspecies *U. d. rodei*), but other authors assign it to the arctoid lineage (see above). I think that published data indicate that it is more related to the bears from Vallonet than to *U. dolinensis* and I disagree with conspecificity of *U. rodei* and *U. dolinensis* in sense of García (2004). Nevertheless, I cannot exclude its conspecificity with *Ursus arctos* in the sense of Rabeder et al. (2010). Early *U. deningeri* was described also from the locality Cal Guardiola (Spain; Madurell-Malapeira et al. 2009) and Honce (Slovakia; Wagner & Sabol 2007). *Ursus* cf. *deningeri* was mentioned from the contemporary locality Les Valerots, France, by Cordier in Erbaeva et al. (2001) without comment. Von Koenigswald & Tobien (1987) mentioned *U. deningeri* from Mosbach 1, Germany. However, I am not aware of any *Ursus* specimen that doubtlessly originated from Mosbach 1 and I thus consider the presence of *U. deningeri* in this locality unproven.

The record of *U. deningeri* during the terminal Early Pleistocene is very sporadic. Franzen (1999) mentioned *U. deningeri* from Dorn-Dürkheim 3, Germany. Storch et al. (1973) described a damaged D4 sin. from the Hohensülzen bei Worms, Germany, as *Ursus* sp. Mäuser (1987) mentioned *U. deningeri* from the locality Würzburg-Schalksberg, Germany, but the exact age of this locality is unknown. Bajguševa et al. (2001) mentioned *Ursus* sp. from Port-Katon, Russia, belonging to Taman faunal complex, for which the age from 1.2 to 0.8 Ma is proposed. According to Baryšnikov (2007) the bears from Akhalkalaki (Georgia; Vekua 1986) belong to *U. deningeri.*

The exact status of bears from Gombasek 1 (= Gombaszög), Slovakia, seems to be unclear. Kretzoi (1938) described them as *Ursus etruscus gombaszogensis* Kretzoi, 1938 (spelling *gombaszogensis* is a justified emendation of the incorrect original spelling *gombaszögensis*; Art.. 32.5.2.1. of the Code) as the most evolved form of *U. etruscus*. I agree with later authors (e.g. Torres 1992b, Baryšnikov 2007), who included this form to *U. deningeri*. The locality is traditionally placed in the Late Biharian close to the localities such as cave C 718, Czech Republic, or Voigstedt, Germany (Fejfar 1976, Fejfar & Heinrich 1983; but see Horáček & Ložek 1988). According to my preliminary results, based especially on the teeth morphology, I assume that these bears are less evolved than typical *U. deningeri* from the earliest Middle Pleistocene and that they belong to the terminal Early Pleistocene faunas. Further detailed comparisons will be necessary. Both stratigraphical and taxonomical positions of *U. eberbachensis* Heller, 1939 are unclear.

Since the Middle Pleistocene *U. deningeri* became common and abundant in most of Europe and the bears from the spelaeoid lineage became dominant ursids untill the end of the Pleistocene. Localities with *U. deningeri* from the earliest Middle Pleistocene (Late Biharian after B/M) include among others: cave C718, Koněprusy caves, Chlum I and IV (all Czech Republic; Wagner 2004, 2005), Kozi Grzbiet (Poland; Wiszniowska 1989), Kövesvárad (Hungary; Jánossy 1963), Slivia (Italy; Ambrosetti et al. 1979), and probably Tiraspol (Moldova; David 1982). According to Baryšnikov (2007), also bears from Jagsthausen (Germany; Koby 1952), which were described as *U. deningeri suevicus* Koby, 1952, are more similar to the bears from this niveau than to the nominotypical *U. d. deningeri* from the Early Toringian. Based on my preliminary comparisons, I consider the bears from Jagsthausen slightly more evolved than those from the Czech Late Biharian localities, but it is not possible to exclude that observed differences are due to geographical rather than temporal/phyletic variability.

Andrews (1922) described *U. savini* Andrews, 1922 from several, probably mostly Late Biharian localities in England (type locality: Bacon Forest Bed) and assigned it to the spelaeoid lineage. This opinion is broadly accepted and *U. savini* is either considered synonymous with *U. deningeri* (sometimes treated as its subspecies) or is given status of a full species, mostly understood as ancestral of the typical *U. deningeri* (cf. Mazza & Rustioni 1994, Grandal d'Anglade & Vidal Romaní 1997, Baryšnikov 1998, Baryšnikov & Foronova 2001, García & Arsuaga 2001). I agree that this bear belongs to the *deningeri*-group, but I think that it represents an endemic local race (of a small size) that has no direct Toringian descendents. I disagree with Baryšnikov (2007), who synonymized this

form with *U. rossicus* Borisâk, 1930 (= *U. borissiaki* (Kretzoi, 1947)) and *U. uralensis* Vereŝagin, 1973.

The Early Toringian is a stratum typicum for *U. deningeri*. The nominotypical subspecies *U. deningeri deningeri* was described from the locality Mosbach 2, Germany, by von Reichenau (1904). Some other subspecies were described from Early Toringian localities of Europe: *U. d. hundsheimensis* Zapfe, 1948 (Hundsheim, Austria), *U. d. erpfingensis* Heller, 1975 (Erpfingen 4, Germany), *U. d. romeviensis* Prat et Thibault, 1976 (La Romieu, France), – but their taxonomic status is doubtful. *U. deningeri* is well represented in many localities in Western and Central Europe, including Cueva Mayor (Spain; García 2003), Château (France; Argant & Argant 2002), Westbury (Great Britain; Bishop 1982), Mauer (Germany; von Reichenau 1906), Isernia la Pineta (Italy; Azzaroli et al. 1986), Tarkő (Hungary; Jánossy 1976), and Petralona (Greece; Kurtén & Poulianos 1981, Tsoukala 1991). The lineage of *U. deningeri* continued uninterrupted to the Middle Toringian and was characterized by the increase of body size and cheek-teeth complexity. Several new taxa were described from this niveau, but mostly with uncertain validity. The presence of *U. rossicus* Borisâk, 1930, a smaller-sized representative of a peculiar lineage of spelaeoid bears, in the later Middle Pleistocene of East Europe is notable.

Baryšnikov (1994) described specimens of *U. deningeri* from the locality Treugol'naâ Cave, Russia, layers 6, 7a, and 7b, which belong to the Urup Faunal Unit, which is equivalent to the Early Toringian (see Baryšnikov 2002b). Since that time, *U. deningeri* continuously inhabited this region throughout the middle Middle (*U. d. praekudarensis* (Baryšnikov, 1998)) till the Late Pleistocene (*U. d. kudarensis* Baryšnikov in Lûbin et al. 1985). Knapp et al. (2009), who studied the mtDNA of *U. d. kudarensis*, observed that this lineage is genetically very distinct from other members of the *U. spelaeus* clade, which suggests that it could represent an independent species. This view was accepted by Rabeder et al. (2010), who elevated this taxon to *U. kudarensis* and suggested that it splitted from other spelaeoid bears before 1.4 Ma, but I see this date rather overestimated.

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