Cranial and mandibular morphology of Middle Pleistocene cave bears (Ursus deningeri): implications for diet and evolution

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ABSTRACT

Deninger’s bears (Ursus deningeri) have been studied less frequently than Ursus spelaeus s.l. Our objective is to present, for the first time, an analysis of the skull shape of U. deningeri.

Bear crania and mandibles were digitised with a Microscribe or CT-scanned and the surface models subsequently landmarked. The landmarks were chosen based on a compromise between functional morphology and sample size.

Results show that U. deningeri and U. spelaeus mandibles display very similar morphologies and allometric trajectories, both to each other and to Ailuropoda melanoleuca. It is inferred that masticatory adaptations to a herbivorous diet were already present in the Middle Pleistocene. U. deningeri displays a cranial morphology that is similar to that of U. spelaeus when comparing all species, but U. deningeri has a relatively narrower and dorsoventrally lower zygomatic arch than U. spelaeus, although the masticatory signal is less strong in the skull.

We observe intraspecific differences between different populations of U. deningeri, which could parallel the genetic diversity found in U. spelaeus. The intraspecific differences found within U. deningeri may be temporal and/or geographical in nature and could be related to the evolution of the Late Pleistocene cave bear, but this hypothesis remains to be tested.

Introduction

Middle Pleistocene cave bears, also known as Deninger’s bears (Ursus deningeri), evolved from Ursus etruscus, possibly via Ursus dolinensis (García and Arsuaga 2001), although the taxonomic status of U. dolinensis is highly debated (see Medin et al. 2017 for a review). The fossil remains of the Middle Pleistocene cave bear have been found mostly in Europe (Raia et al. 2009), but some are also found in Asia (Münzel and Aten 2009). Their fossil record is scarcer and thus they are not as well studied as classic cave bears (i.e., Late Pleistocene cave bears; Ursus spelaeus s.l.). In fact, the study of U. deningeri has been done mostly in comparison with the later species. For example, endocranial morphology has been compared between the two species (García et al. 2006, 2007).

U. deningeri is generally regarded as the ancestor of U. spelaeus s.l. (e.g., Andrews and Turner 1992; García et al. 1997, 2006) and the transition between these two species took place around the Middle-Late Pleistocene boundary. However, many intermediate forms between U. deningeri and U. spelaeus s.l. have been described (e.g., Andrews and Turner 1992; García et al. 1997, 2006). U. deningeri and U. spelaeus s.l. are two chronospecies, possibly with U. s. deningeroides as a transitional form between them. They are phylogenetically closely related (Valdiosera et al. 2006) and almost always placed in the same evolutionary lineage (Kurtén 1955; Groiss 1994; Hänni et al. 1994; Galli et al. 2005; García et al. 2006, 2007). Chronospecies are arbitrary divisions of a single evolutionary lineage and the two former species have, indeed, previously been considered to belong to one species (Vila Taboada and Grandal d’Anglade 2001; Baryshnikov 2006).

The first instances of U. deningeri (or U. dolinensis) are from the late Early Pleistocene. Fossils have been found in France, Germany and Spain (Supplementary Information 1) and one specimen of U. ex.gr. deningeri was found in Mongolia (Eisenmann and Kuznetsova 2004). The fact that ex grege is generally intended to indicate affinity, but in the weakest sense of the word (Sigovini et al. 2016), it is likely that rather than U. deningeri per se a similar looking bear was present there. Alternatively, similar to extant U. arctos, U. deningeri had a very extensive distribution. The latter should be tested in the future. U. deningeri is most abundant in the Middle Pleistocene. It is found from the United Kingdom in the west to Russia in the east and from Germany in the north to Italy in the south (Supplementary
Information 1). Two subspecies, *U. deningeri praekudarensis* and *U. deningeri kudarensis* have been found at Kudaro in Georgia (Baryshnikov 2002), although this subspecies might actually be more closely related to *U. spelaeus* s.l. (see below).

A recent molecular analysis reveals a complex phylogeographic pattern with the presence of three Late Pleistocene lineages within cave bears: *U. spelaeus*, *U. ingressus* and *U. deningeri kudarensis* (Knapp et al. 2009). In fact, the latter species seem to have diverged early, likely during the Middle Pleistocene, from the other two (Knapp et al. 2009), but was referred to *U. deningeri* because of morphological similarities. *U. spelaeus* and *U. ingressus* went extinct 25.6 ka and 24.8 ka respectively (Baca et al. 2016; Mackiewicz et al. 2017), but not much is known about when *U. deningeri kudarensis* went extinct.

Middle Pleistocene cave bears are generally smaller than classic Late Pleistocene cave bears (Torres et al. 2001; Garcia 2003) although both have a broad, domed, steep forehead resulting in a midsagittal skull profile interrupted at the orbital region creating a ‘step’, which is more marked in *U. spelaeus* s.l. (Santos et al. 2017). The palate of Middle Pleistocene cave bears is more curved, the metapodials and canines are less robust than those of classic Late Pleistocene cave bears (Witham 2001; Garcia 2003). Males attained roughly twice the body mass of females (Stiner et al. 1998; Stiner 1999). The dental formula of *U. deningeri* (i 3/3, c 1/1, p 1–3/1–3, m 2/3) is more primitive than that of *U. spelaeus* s.l., with variation in the presence of certain premolars while *U. spelaeus* s.l. shows a more derived dental pattern with a reduced number of postcanine teeth and larger occlusal surfaces.

The tooth wear patterns of *U. deningeri* argue for a diet of tough, abrasive materials, such as nuts, tubers, and associated grit (Stiner et al. 1998). Isotope results, however, suggest that *U. deningeri* was highly omnivorous (comparable to *Ursus arctos*) and obtained nearly all of its food from terrestrial and fresh-water habitats (Stiner et al. 1998; Stiner 1999). Postcranial morphology, on the other hand, indicates that food acquisition required digging and prying (Stiner et al. 1998). Additionally, extensive mastication sometimes led to complete obliteration of the cheek tooth crowns in old individuals (Stiner et al. 1998). Both aspects suggest a large herbivorous component in the diet of Deninger’s bear. Even the adult sex ratios found in dens point to a largely herbivorous diet (Stiner 1999). Females always needed to den in order to take care of their offspring, whereas males only hibernated when necessary due to a lack of food, and the longer the males hibernated, the more likely they were to die in their den (Stiner 1999). The more even the sex ratio, the more the animals were dependent on seasonal foods, which likely excluded large game.

The hibernation undergone by some bear species is not a true hibernation, because, due to their size, their body temperature only drops by 4–5°C (Folk et al. 1976, 1977; Watts et al. 1981; Hissa et al. 1994). Bears that ‘hibernate’ do so for three to seven months and they do not eat, drink, urinate or defecate during this time (Folk et al. 1976, 1977; Nelson et al. 1983). Female bears give birth to their cubs and nurse them while ‘hibernating’ or denning (Grandal-d’Anglade et al. 2018). The ‘hibernation’ physiology of Middle Pleistocene and Late Pleistocene cave bears, based on δ13C of tooth enamel, is very similar (Bocherens et al. 1994). Females gave birth in a cave and also sought shelter there with yearling cubs the following winter, based on dental wear stages (Andrews and Turner 1992).

The objective of this paper is to present an analysis of the cranial and mandibular shape of *U. deningeri* compared to other bear species. As this has not been done before, this paper will significantly increase knowledge on the palaeobiology of Deninger’s bear. Furthermore, it will provide information on the earliest adaptations of the cave bear lineage in the Middle Pleistocene. Additionally, this paper aims to interpret the results in terms of dietary adaptations of the masticatory system and assess what this potentially means for the evolution of the Late Pleistocene cave bear from the Middle Pleistocene cave bear. As similar studies have already been performed for the cave bear (Van Heteren et al. 2009, 2014, 2016), the results are directly comparable.

**Materials**

In this study mandibles and crania of Middle Pleistocene cave bears (*U. deningeri*, Figure 1A, C and D) from four different geographical locations (see below) were used (Figure 1, Figure 2). Additionally, as comparative material, 100 adult individuals of eight extant bear species and 13 specimens of the extinct *U. spelaeus* s.l. (Figure 1B) were included.

**Ursus deningeri from the British Isles**

The British *U. deningeri* specimens (Figure 1C and D) in the present study (n = 11) come from Bacton (B) and Pakfield (PK) with most specimens coming from Bacton (n = 10). The open-air site of Bacton in the United Kingdom is of Middle Pleistocene age (Lister 1993, 1996). The sediments at this locality are part of the Cromer Forest-bed Formation, which underlies the Anglian glacial deposits of MIS 12 (ca. 450 ka) age (Lewis et al. 2004). The Cromer Forest-bed Formation was deposited at the western margin of the southern North Sea basin (Lewis et al. 2004). The Cromer Forest-bed (including the deposits at Bacton) includes faunas of various ages, from the Early Pleistocene (ca. 1.8 Ma) up to approximately 500 ka. The bears probably come from sediments closer to the upper end, but for this material, collected before the advent of modern excavation techniques, it is difficult to determine the exact stratigraphic position (Lister, pers. comm.).

There is a single specimen from Pakfield in the dataset. Summer temperatures at Pakfield were significantly warmer than those of the present and precipitation was more seasonal (Candy et al. 2006). The other faunal elements at Pakfield include temperate taxa, such as *Hippopotamus, Palaeoloxodon antiquus* and *Megaloceros dawkinsi*. Pakfield is also part of the Cromer Forest-bed Formation and probably represents a temperate stage during the late Early and early Middle Pleistocene (MIS 20–12), which would be younger than the West Runton Freshwater-bed, but older than Boxgrove (Lee et al. 2006).

**Ursus deningeri from France**

In this study, all the studied materials from France come from unit J, within the ‘Ensemble II’ of the Middle Complex of the cave site of Caune de l’Arago (Tautavel, France). Arago has a long stratigraphical sequence ranging from MIS 17 to MIS 5...
alternating cool and temperate climates (Moigne et al. 2006). The bears studied here, from unit J, are ascribed to MIS 13 (c. 480 ka), which is considered to represent temperate humid conditions (De Lumley and Barsky 2004; Moigne et al. 2006; De Lumley 2015). The ‘Ensemble II’ has yielded four dental hominin remains (De Lumley 2015). However, this complex is dominated by herbivores such as red deer (Cervus elaphus) and fallow deer (Dama clactoniana), and to a lesser extent mouflon (Ovis ammon antiqua), rhinoceros (Stephanorhinus hemitoechus), reindeer (Rangifer tarandus) and horse (Equus ferus mosbachensis), among others. Carnivores are also represented by felids (e.g., Lynx spelaea, Panthera leo spelaea) and canids (e.g., Cuon priscus, Canis mosbachensis) together with U. deningeri (De Lumley and Barsky 2004). Hominins used the cave as a temporary seasonal shelter (De Lumley and Barsky 2004), leaving the cave available for bears during the denning season.

**Ursus deningeri from the Iberian Peninsula**

Two crania and three mandibles of *U. deningeri* studied here come from two different sites in the north of the Iberian peninsula: Sima de los Huesos (SH; Sierra de Atapuerca, Burgos) (García et al. 1997; García 2003; Garcia and Arsuaga 2011) and the ‘Bear sector’ of the cave site of Santa Isabel de Ranero (SIR; Karrantza, Biscay) (Torres et al. 2001). The macro-fossil remains

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**Figure 1.** A) a subadult male cranium of *Ursus deningeri* MEH SH99T/JU 13/14–68 (Sima de los Huesos, Spain) in different views compared to B) an adult male cranium of *Ursus spelaeus*. *Ursus deningeri* mandibles: C) lateral view of BM(NH) M17906 and D) internal view of BM(NH) M17912 from Bacton (United Kingdom). Most mandibles only preserve the corpus (as BM(NH) M17912) and thus it was necessary to repeat the analysis with a more limited set of landmarks.

**Figure 2.** Geographical map encompassing most of the range of *U. deningeri*. The localities of specimens used in the analyses presented here are indicated. A = Caune d’Arago; B = Bacton; P = Petralona; PK = Pakefield; SH = Sima de los Huesos; SIR = Santa Isabel de Ranero.
of the ‘Bear sector’ of SIR are restricted to Deninger’s bears and a
lion (Panthera spelaea; Gómez-Olivencia et al., manuscript in
preparation) which have been dated around 300 ka (Torres
et al. 2014). From SIR, we study a complete cranium (figured in
Gómez-Olivencia 2018) and three virtually complete mandibles
(Gómez-Olivencia et al., manuscript in preparation). The SIR
fossils are housed at three different institutions: Arkeologi
Museoa (Bilbao), the Museu de Ciencies Naturals de Barcelona
(MCNB; Barcelona) and the Institut Català de Paleontologia
Miquel Crusafont (Sabadell). The fossils studied here are housed
at the Arkeologi Museoa (the cranium and two mandibles) and
at the MCNB (one mandible). From Sima de los Huesos (SH; Sierra
de Atapuerca, Burgos), a complete cranium is also included here
(Santos et al. 2017). The SH site has yielded more than six
thousand human remains together with thousands of carnivore
bones, mainly U. deningeri (Figure 1A) (Arsuaga et al. 2014;

**Ursus deningeri from Greece**

A complete cranium of *U. deningeri* covered by carbonate crust
(Santos et al. 2014) from the lower branch of the Petralona site (P;
Chalkidiki, Greece) is also included in this study. This specimen is
housed at the Geology-Paleontology Museum of the School of
Geology of the Aristotle University of Thessaloniki (AUTH).

There are many studies on the chronology of Petralona, and
there are many different hypotheses about the chronology and
faunal assemblages from this site. Petralona has a long stratigra-
phical sequence ranging from pre-Cromerian to an ‘Inter-Mindel’
(pre-Holsteinian) age (Kurtén and Poulianos 1977). In Petralona,
there are two branches into the cave connected by an excavated
trench (Section B): the upper branch (with Section A), which
includes the complete stratigraphic sequence, and the lower
branch, in which only the Cromerian faunas have been recovered.
The lower branch is covered by a stalagmitic layer, which may be
followed from Section B into the lower branch and covers the
human skull and the *U. deningeri* remains (Kurtén and Poulianos
1977). Studies on small vertebrates suggested a ‘middle Middle
Pleistocene’ age (Kretzoi 1977). More recently two different bios-
stratigraphic faunal assemblages were found together on the floor
of Petralona cave (Tsoukala 1989; Crégut-Bonnoure and
Tsoukala 2005). The first one corresponds to the early Middle
Pleistocene (with Pliocrocuta perrieri, *U. deningeri*,
*Praemegaceros, Pliothragus macedonicus*), and the second one to
the late Middle-Late Pleistocene period (with Crocuta crocuta
spelaea, *U. spelaeus* s.l., Capra ibex macedonica). The presence of
the *Pliothragus* and the ibex in the assemblage supports their
 attribution to the late Cromerian complex (ca. MIS 14) and the
Holstienian complex (MIS 6–8) (Crégut-Bonnoure and Tsoukala
based on the study of the carnivore remains of the old collection
concluded that the collection seems to contain three biorstrati-
graphic species-groups. The earliest group includes *Canis arnen-
sis*, *Lycaon lycaonoides*, *Vulpes praegalialis*, *Pliocrocuta perrieri*,
and *Pachycrocuta brevirostris*. It belongs to the early Middle
Pleistocene. The second group consists of the late Middle
Pleistocene species: *U. deningeri, Crocuta crocuta*, and, possibly,
Panthera leo spelaea and *Felis silvestris*. The third, Late Pleistocene
group is formed by *U. spelaeus* s.l. and *U. arctos*.

**Methods**

We used geometric morphometric analyses to quantify shape
differences between species in the skull and the mandible. Due
to missing landmarks on the Deninger’s bears, different subsets of
landmarks were chosen for different analyses. Supplementary
Information 2 details which specimens are included in which
analyses. The potential influence of size on shape was also ana-
lysed. Prior to performing principal component analysis (PCA)
and regression analysis, we performed a generalised Procrustes
superimposition (Zelditch et al. 2004) on the raw coordinates to
remove size, position and orientation. All geometric morpho-
metric analyses were performed in MorphoJ software
(Klingenberg 2011).

**Masseter analyses (mandible)**

There were three *U. deningeri* specimens in the analysis focusing
on the masseter: one from the Iberian Peninsula (SIR), one from
Arago (A) and one from Bacton (B). The landmarks used are
those from Van Heteren et al. (2012), which correspond to the red
landmarks in Figure 3. To remove the effects of allometry, a
pooled regression analysis of the Procrustes coordinates within
species onto the natural logarithm of centroid size (LCS) was
performed (Bookstein 1991; Mitteroecker et al. 2005; Van
Heteren et al. 2016). A permutation test for the null hypothesis
of independence of shape from size was performed with 10,000
permutations (Mielke and Berry 2007). *U. deningeri* specimens
were then compared to the full range of Ursidae in a PCA based
on the regression residuals. Additionally, *U. deningeri* specimens
were compared to a dataset consisting of brown and Late
Pleistocene cave bears.

**Mandibular corpus analyses**

The analyses on the mandibular corpus, in combination with the
condyle, incorporate two Deninger’s bears, both from SIR
(Iberian Peninsula). The landmarks cover the mandibular corpus,
but not the ascending ramus, because this part of the mandible is
often broken. They are a subset of those in Van Heteren et al.
(2016) and correspond to the green landmarks in Figure 3.
Definitions of the landmarks are given in Table 1. The data are
corrected for allometry by using the regression residuals of the
pooled regression analysis of shape onto the LCS (see above).

Additional analyses on the mandibular corpus excluding the
condyle allow for the inclusion of more fossil specimens in the
analysis. The dataset contains 11 Deninger’s bears from the
British Isles (B and PK), primarily from Bacton (B), two from
France (A) and three from the Iberian Peninsula (SIR). The
landmarks are defined in Table 1 and shown in Figure 3.
Analyses on all bears follow the above pattern, but for the PCA
on Deninger’s bears only, no allometric correction was per-
formed, but a regression was nonetheless performed to assess
static allometry. To assess size differences between Deninger’s
bears from different geographic regions an analysis of variance
(ANOVA) and Dunn’s post-hoc test was applied to centroid size
in the software Past (Hammer et al. 2001).
Cranial analyses

The cranial analyses focussed on three Deninger’s bear crania, two from the Iberian Peninsula: one from SH and one from SIR, and one from Greece (P). The landmarks cover the most complete half of each cranium and correspond to those in Van Heteren et al. (2014), except for landmark 2, which is missing in the Sima de los Huesos (SH) specimen. The data were corrected for allometry by using the regression residuals of the pooled regression analysis of shape onto LCS. Initial analyses use all members of the genus Ursus, the giant panda (Ailuropoda melanoleuca) and the spectacled bear (Tremarctos ornatus) as a reference dataset. To further determine the difference between Deninger’s bear (U. deningeri) and its closest relatives, all species except Late Pleistocene cave bears (U. spelaeus s.l.) and brown bears (U. arctos) were subsequently removed from the dataset.

Results

Masseter analyses

A regression of species means onto LCS, shows that 11.8% of shape variance is predicted by size. Nevertheless, the regression is not significant ($p = 0.378$). The pooled regression analysis shows that size explains 9.1% of the shape variance and that the regression is highly significant ($p > 0.0001$).

In Figure 4, U. deningeri is compared to all extant bear species. Middle Pleistocene cave bears cluster together well, occupying an intermediate position in morphospace between U. spelaeus s.l. and U. arctos, though slightly more similar to the Late Pleistocene cave bear. The faunivorous bears (Ursus maritimus, Helarctos malayanus and Melursus ursinus) have relatively low PC1 scores, whereas the herbivorous bears A. melanoleuca and arguably the Late Pleistocene cave bear (Van Heteren et al. 2009, 2014, 2016) and the spectacled bear have relatively high PC1 scores. High PC1 scores are associated with a relative elongation of the grinding basin of the tooth row. Additionally, the condyle is relatively close to the tooth row. Furthermore, the masseteric fossa is relatively closer to the condyle, but the angular process is positioned further away.

In Figure 5, only U. spelaeus s.l., U. deningeri and U. arctos are plotted in a new PCA. U. arctos shows lower PC1 scores than U. spelaeus s.l.. All three U. deningeri specimens (from France and the Iberian Peninsula) plot within the morphospace of U. spelaeus s.l., but with PC1 scores lower than the U. spelaeus s.l. mean. The U. deningeri from SIR, however, plots rather far away from the other two due to its lower PC2 scores. High PC1 scores are associated with a longer tooth row, particularly in the molar area. Additionally, the distance between the tooth row and the condyle is relatively short, and the distance between the angular process and the condyle relatively large.
Table 1. Landmarks used for describing mandibular shape. The last column indicates which landmarks are displayed in which figures. Landmark types determined according to Bookstein (1991).

<table>
<thead>
<tr>
<th>Landmark</th>
<th>Type</th>
<th>Description</th>
<th>Reflects</th>
<th>Figures</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>2</td>
<td>Most rostroventral point of the symphyseal region, between the first incisors</td>
<td>Position and size of symphyseal region</td>
<td>4,5,6,7</td>
</tr>
<tr>
<td>2.</td>
<td>2</td>
<td>Most caudoventral point of the symphyseal region</td>
<td>Position and size of symphyseal region</td>
<td>6,7,8,9,10</td>
</tr>
<tr>
<td>3.</td>
<td>2</td>
<td>Most caudoventral point of the symphyseal region</td>
<td>Position and size of symphyseal region</td>
<td>6,7,8,9,10</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>Most rostroventral point of the masseteric fossa</td>
<td>Insertion, moment arm and size of the deep masseter</td>
<td>4,5,6,7,8,9,10</td>
</tr>
<tr>
<td>5.</td>
<td>3</td>
<td>Most caudal point on the angular process</td>
<td>Insertion, moment arm and size of the pterygoideus and superficial masseter</td>
<td>4,5,6,7,8,9,10</td>
</tr>
<tr>
<td>6.</td>
<td>3</td>
<td>Most dorsal point on the mandibular condyle</td>
<td>Position of the fulcrum of the mandible</td>
<td>4,5,6,7,8,9,10</td>
</tr>
<tr>
<td>7.</td>
<td>2</td>
<td>Most caudal point of the alveola of M₃</td>
<td>Size and caudal extent of tooth row</td>
<td>4,5,6,7,8,9,10</td>
</tr>
<tr>
<td>8.</td>
<td>2</td>
<td>Midpoint on the lateral rim between the alveolae of M₂ and M₃</td>
<td>Relative sizes and positions of the grinding dental elements</td>
<td>4,5,6,7,8,9,10</td>
</tr>
<tr>
<td>9.</td>
<td>3</td>
<td>Most ventral point on the mandibular corpus opposite landmark 9, perpendicular to the curvature of the mandibular corpus</td>
<td>Shape of mandibular corpus</td>
<td>6,7,8,9,10,</td>
</tr>
<tr>
<td>10.</td>
<td>2</td>
<td>Midpoint on the lateral rim between the alveolae of M₂ and M₁</td>
<td>Relative sizes and positions of the grinding dental elements</td>
<td>6,7,8,9,10,</td>
</tr>
<tr>
<td>11.</td>
<td>2</td>
<td>Most dorsal point on the labial border of the alveolus of M₁ between the two cavities for the roots</td>
<td>Size and extent of the grinding and slicing areas of the tooth row, muscle force available at the carnassials</td>
<td>4,5,6,7,8,9,10</td>
</tr>
<tr>
<td>12.</td>
<td>3</td>
<td>Most ventral point on the mandibular corpus opposite landmark 12, perpendicular to the curvature of the mandibular corpus</td>
<td>Shape of mandibular corpus</td>
<td>6,7,8,9,10</td>
</tr>
<tr>
<td>13.</td>
<td>2</td>
<td>Midpoint on the lateral rim between the alveolae of M₁ and P₄</td>
<td>Relative sizes and positions of the slicing dental elements</td>
<td>6,7,8,9,10,</td>
</tr>
<tr>
<td>14.</td>
<td>2</td>
<td>Most caudal point of the canine alveola on the dorsal rim of the mandibular corpus in line with the tooth row</td>
<td>Position of the canine</td>
<td>4,5,6,7,8,9,10</td>
</tr>
</tbody>
</table>

Table 2. Landmarks used for describing cranial shape (Van Heteren et al. 2014). Landmark types determined according to Bookstein (1991).

<table>
<thead>
<tr>
<th>Landmark</th>
<th>Type</th>
<th>Description</th>
<th>Reflects</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>2</td>
<td>opisthion: posterior edge of foramen magnum in the middle of the rim</td>
<td>Position and size of foramen magnum</td>
</tr>
<tr>
<td>2.</td>
<td>1</td>
<td>ventral end temporzygomatic suture: most posterior point on the ventral surface of the jugal</td>
<td>Attachment area of masseter</td>
</tr>
<tr>
<td>3.</td>
<td>1</td>
<td>ventral end zygomaticomaxillary suture: most anterior point on ventral surface of the jugal</td>
<td>Attachment area of the masster</td>
</tr>
<tr>
<td>4.</td>
<td>2</td>
<td>caudal edge of the canine socket on the palatal-facial border</td>
<td>Position of the canine</td>
</tr>
<tr>
<td>5.</td>
<td>2</td>
<td>dorsal point on the facial border of the infraorbital canal</td>
<td>General shape of cranium and face and size of infraorbital canal</td>
</tr>
<tr>
<td>6.</td>
<td>1</td>
<td>supraorbital process</td>
<td>Size of temporal and size and shape of eyes</td>
</tr>
<tr>
<td>7.</td>
<td>2</td>
<td>maxillofrontale: maxilla-frontal suture on the bony margin of the orbit</td>
<td>Size and shape of eyes</td>
</tr>
<tr>
<td>8.</td>
<td>2</td>
<td>dorsal end temporzygomatic suture: most anterior point on dorsal surface of the jugal</td>
<td>Attachment area of the masster</td>
</tr>
<tr>
<td>9.</td>
<td>1</td>
<td>external occipital protuberance</td>
<td>Extent of temporal and digastrics attachments areas</td>
</tr>
<tr>
<td>10.</td>
<td>1</td>
<td>premaxilla-maxilla suture, on the palate</td>
<td>Shape oral cavity</td>
</tr>
<tr>
<td>11.</td>
<td>1</td>
<td>maxilla-palatine suture</td>
<td>Shape oral cavity</td>
</tr>
</tbody>
</table>

**Mandibular corpus analyses**

In the analyses of the mandibular corpus including the condyle, evolutionary allometry is not significant ($p = 0.628$), although 8.6% of the shape variance is predicted by size. When assessing static allometry, size explains 7.9% of the shape variance and the regression is highly significant ($p < 0.0001$).

In the PCA of the mandibular corpus including the condyle, separation between the species is not as clear as in the PCA of the masseter. *A. melanoleuca* no longer occupies its own position in morphospace but overlaps strongly with *U. spelaeus s.l.* and *U. arctos*. In the PCA, the two Deninger’s bears plot on either side of the cave bear cloud (Figure 6) in terms of PC2 scores. Their PC1 scores, however, are very similar to Late Pleistocene cave bears and do not overlap with those of brown bears.

In a PCA including only Late Pleistocene cave bears and brown bears (Figure 7), Deninger’s bears are different from both. They have much higher PC2 scores, which locate them well outside the ranges of both brown and Late Pleistocene cave bears. PC1 is primarily determined by the position of the condyle (Figure 7). In Late Pleistocene cave bears, the condyle is positioned much more posteriorly relative to the other landmarks and the mandible is slightly less deep dorsoventrally. PC2 is primarily determined by the shape of the mandibular symphysis, more positive values indicating a more vertical symphysis relative to the mandibular corpus (Figure 7). In *U. deningeri*, the symphysis is positioned much more anteriorly relative to the other landmarks and is also relatively smaller.

In order to be able to include more Deninger’s bears, a second analysis was performed with the number of landmarks reduced to 9, excluding missing parts such as the mandibular condyle. In this analysis, evolutionary allometry is also non-significant ($p = 0.815$) and only 5.3% of the shape variance is explained by size. Static allometry, however, is significant ($p < 0.0001$) and 6.6% of the shape variance is predicted by size. A PCA on the regression residuals (Figure 8) shows quite similar results to those shown
in Figure 7. All members of the genus Ursus cluster together with the giant panda. In contrast to Figure 7, Figure 8 does not show any empty morphospace between the polar bear and its congener. Additionally, there is complete overlap between the PC scores of the brown bear and both cave bears.

Bears from the British Isles display a much larger size variation than the bears from the Iberian Peninsula, which are relatively large (Figure 9). The bears from France are on average the largest. Although the ANOVA does not display significant results \((p = 0.061)\), Dunn’s post-hoc test does show a significant size difference \((p = 0.036)\) between the bears from France and the British Isles. All Deninger’s bears follow the same static allometric pattern.

There is a clear separation between the Iberian Deninger’s bears on the one side and the French and British bears on the other side on PCs 1 and 2 (Figure 10). The Iberian bears have relatively high PC1 scores and lower PC2 scores than most of the other Deninger’s bears, representing a dorsoventrally deeper mandibular symphysis and a more rostrally placed masseteric fossa (Figure 10). While there is no overlap in the distributions of the species in morphospace, there would be some slight overlap between the 90% confidence intervals (not figured). In the plot of PC2 versus PC3 (not figured), the separation between the bears from Bacton and those from SIR is much clearer, but the bears from Tautavel occupy an intermediate position.
Cranial analyses

The regression of species mean coordinates onto LCS indicates that 35.5% of shape variance can be explained by size ($p = 0.057$). Smaller species tend to have rounder foreheads, whereas larger species have more sloping foreheads (Figure 11). Larger species also have narrower and more anteroposteriorly elongated skulls, including an elongated muzzle. Smaller species on the other hand have relatively wider and shorter skulls with a short muzzle.
Figure 8. Scatter diagram based on the principal component analysis (PCA): PCs 1 and 2 of the residuals of all bear species after a regression analysis of the Procrustes coordinates onto LCS for the mandibular corpus without the condyle. The colours indicate the species. PC1 explains 36.0% of the variance and PC2 23.0%. The shape change associated with each of the axes is represented.

Figure 9. Regression analysis of the Procrustes coordinates of Deninger’s bears (U. deningeri) onto LCS for the mandibular corpus without the condyle. Of the total variance, 14.8% is predicted by LCS ($p = 0.033$).
In the pooled regression analysis, size explains 6.3% of the shape variance and the regression is highly significant ($p = 0.003$). The PCA based on the regression residuals (Figure 12) shows clear separation between most of the species, although Middle Pleistocene and Late Pleistocene cave bears plot rather close together. Members of the genus Ursus (except the Late Pleistocene cave bear) have rather high PC2 scores, whereas the giant panda has much lower PC2 scores. T. ornatus is intermediate in this respect and similar to the Late Pleistocene cave bear. On PC1, there seems to be a phylogenetic signal. Both

Figure 10. Scatter diagram based on the principal component analysis (PCA): PCs 1 and 2 of Deninger’s bears (U. deningeri) for the mandibular corpus without the condyle. PC1 explains 39.4% of the variance and PC2 21.2%. The shape change associated with each of the axes is represented.

Figure 11. Regression analysis of the species’ mean Procrustes coordinates of all members of the genus Ursus and the giant panda and spectacled bear onto LCS for the skull. Of the total variance, 35.5% is predicted by LCS ($p = 0.057$).
cave bears cluster together and have very low PC1 scores. Brown bears have slightly higher scores, followed by both black bears (Ursus americanus and Ursus thibetanus). The most distantly related spectacled bears have the highest PC1 scores. Low PC1 scores, such as those of the cave bears represent a relatively longer muzzle and shorter, but broader, cranial vault (Figure 12). Additionally, the jugal arch is relatively narrow.

In the PCA between both cave bears and brown bears, there is a clear distinction on PC1 between them (Figure 13). Brown bears have a relatively shorter muzzle, a relatively
wider zygomatic arch and a relatively more protruding external occipital protuberance than both cave bear species (Figure 13). The two cave bear species can be distinguished on PC2. Deninger’s bears have a relatively narrower and doroventrally lower zygomatic arch than Late Pleistocene cave bears (Figure 13).

Discussion

The aim of the present paper is to assess the paleoecology of the Middle Pleistocene cave bear based on cranial and mandibular morphology. This allows for an assessment of the morphological starting point of the cave bear lineage and how the Middle Pleistocene cave bear evolved into the Late Pleistocene cave bear.

Our analysis shows that *U. deningeri* is morphologically closer to *U. spelaeus s.l.* than to *U. arctos* although in some features it is in the overlapping morphospace between Late Pleistocene cave bears and brown bears. This is consistent with previous phylogenetic analysis which place the Middle Pleistocene Deninger’s bears as ancestral to Late Pleistocene cave bears sensu lato (García 2003; Baryshnikov 2006).

Evolutionary allometry

All the analyses of evolutionary allometry on the mandible are not significant. It, therefore, appears that there is no effect of size on shape on an interspecific level. In the skull, however, evolutionary allometry is very close to being statistically significant, suggesting that with a slightly larger sample size they might have been significant. Additionally, α = 0.05 should not be seen as a hard cut-off point, but rather as a suggestion of at which likelihood we are no longer willing to accept the null hypothesis. In this case, it seems that the evolutionary allometric pattern in the skull is genuine and can be interpreted biologically.

Although no ontogenetic allometry analysis have been performed in this study, evolutionary allometry in bear skulls appears to follow the general ontogenetic allometric pattern, in that the smaller bears show typical paedomorphic features, such as rounded skulls and short snouts. Figure 11 shows that Deninger’s bear is smaller than the Late Pleistocene cave bear, but has a skull, which is equally elongated, suggesting that a change in shape, possibly as a dietary adaptation, preceded an increase in size in the cave bear lineage.

Diet of *Ursus deningeri*

Of all the PCAs performed on the mandible in the present study, the analyses of the masseter would logically most strongly relate to diet, since the landmarks used were specifically chosen to assess muscle functionality. The other mandibular analyses, such as on the mandibular corpus, provide information on general morphology, such as robusticity, but provide little information on the functionality of the masticatory muscles.

In all mandibular PCAs, Deninger’s bears plot close to Late Pleistocene cave bears. This may be an indication of both a close phylogenetic relationship as well as a similar diet. For example, Figure 4 clearly shows that Deninger’s bears have rather high PC1 scores, like the other herbivorous bears, such as the giant panda and the Late Pleistocene Cave bear, and in contrast to the faunivorous bears. *T. ornatus* also has relatively low PC1 scores, but this is caused by the presence of the premasseteric fossa (Van Heteren et al. 2016). It is noteworthy that despite the close genetic relationship between *U. arctos* and *U. maritimus*, the latter being a descendant from the former, there are clear morphological differences in the mandible (Figure 6), which could be related to the ecological (and dietary) shift that occurred in the polar bears. Although brown and Late Pleistocene cave bears have very similar relative tooth row lengths, brown bears have a relatively smaller moment arm of the superficial masseter than Late Pleistocene cave bears, which is related to a decrease in masticatory efficiency. *U. deningeri* and the other herbivorous bears have a relatively large grinding basin, suitable for masticating tough materials (Mattson 1998). Additionally, the moment arm of the superficial masseter is relatively large and, consequently, this muscle is more efficient than in carnivorous bears. Furthermore, the moment arm of the food items is smaller, also facilitating mastication. Overall, it can be deduced that *U. deningeri* was similarly adapted to a plant-based diet as *U. spelaeus s.l.*.

In the present study, the association between the shape of the cranium and diet and between the allometric trajectories and diet is not as strong as in the mandible. Nogueira et al. (2009) similarly found that the correlation between shape and diet was slightly weaker in the skull (r = 0.96) than in the mandible (r = 0.99) in bats, but no such observation has previously made for Carnivora, to our knowledge. This is probably because the cranium also protects the brain and has other functions, such as olfaction and vision, apart from mastication that also influence the morphology, whereas the shape of the mandible is mainly influenced by masticatory needs. Additionally, the shape of the cranium appears to be strongly influenced by phylogeny (Figure 11). This is possibly because the cranium consists of many bones, which are integrated and generally change together, leaving not much opportunity for specific parts, such as the muzzle, to evolve independently as a response to selection pressures.

Intraspecific variability

In the analysis with only nine landmarks on the mandibular corpus, diet is no longer reflected in morphospace (Figure 7). Even the giant panda, which has the most herbivorous diet of all extant bears plots with the primarily omnivorous members of the genus *Ursus*. When comparing Deninger’s bears from various regions with each other, however, an interesting pattern emerges (Figure 8), which evidently is unrelated to diet. The bears from the British Isles and from France overlap in morphospace, but the bears from the Iberian Peninsula have relatively high PC1 and PC2 scores compared to the others. The main difference in terms of morphology is that the Iberian bears had a relatively larger and, therefore, more stable mandibular symphysis, and a relatively longer moment arm of the masseter. These may be indications of a tougher diet than that of the other European bears. Due to the low
number of fossils studied and the fact that the Iberian bears are also chronologically the youngest, there seems to be a mixed signal of chronology and geography and several hypotheses can be postulated.

A first hypothesis might be that the bears from Santa Isabel de Ranero (SIR) have a different morphology because they are more recent than the other Middle Pleistocene cave bears. If this were the case, one might expect the Iberian bears to more closely resemble Late Pleistocene cave bears. This does not seem to be the case, however.

A second hypothesis could be that the difference between the Iberian and the other Middle Pleistocene cave bears is caused by a geographical barrier. Presently, the British Isles are separated from mainland Europe by the sea. At some moments in the Middle Pleistocene (e.g. MIS 6 and 12), however, sea level was much lower and there was land where the North Sea is now, although there were extensive deltas in the Channel area (Bridgland and D’Olier 1995; Lee et al. 2006). The shared morphology of the French and the British bears suggests that this delta was not much of a barrier for them and they could be considered a single population despite the large geographic distance. In this case, the bears from the Iberian Peninsula could have been relatively isolated from the other European bears by the Pyrenees for a significant amount of time; long enough to develop a distinct morphology.

A third hypothesis, related to the second, postulates that there might have been different cave bear lineages during the Middle Pleistocene, but only one of them led to the Late Pleistocene western cave bears. Such a scenario with multiple lineages is also seen in the Late Pleistocene with at least three Pleistocene western cave bears. Such a scenario with multiple lineages is also seen in the Late Pleistocene with at least three lineages of cave bears: U. spelaeus, U. ingressus and U. deningeri kudarensis (Knapp et al. 2009).

A fourth hypothesis also postulates that there might have been different cave bear lineages during the Middle Pleistocene, each evolving into their own Late Pleistocene lineage. This could be feasible, since a deep split for in the Middle Pleistocene has been shown for these taxa (Knapp et al. 2009).

**Palaeoecology of the cave bear lineage in the Middle Pleistocene**

Detailed dietary analyses presented herein indicated that the Middle Pleistocene cave bear was equally adapted to a plant based diet as the Late Pleistocene cave bear. This suggests that a dietary shift must have taken place before the Middle Pleistocene, possibly during the late Early Pleistocene. The oldest specimen in the sample presented herein is the skull from Sima de los Huesos, which is indeed the smallest and most similar in morphology to brown bears (Figure 13). A previous geometric morphometric study has also suggested a sharp change in the type of dietary adaptations in the mandible towards more foliage on the boundary between U. eterus and the cave bear lineage (Van Heteren et al. 2016).

In Eurasia, at the end of the Early Pleistocene, a faunal turn-over, caused by the evolution and migration of species, took place called the end-Villafranchian event (Van Kolfschoten and Markova 2005; Brugal and Croitor 2007; Palombo et al. 2008). The faunal turnover during the end of the Early Pleistocene and during the middle Pleistocene (Villafranchian to Galerian) maybe opened the opportunity for bears to occupy new ecological niches, as their prey disappeared or more capable competitors entered their environment. Additionally, the change in periodicity of the ice ages from 41,000 to 100,000 years (Raymo and Nisancioglu 2003), which took place around the same time and caused longer and more severe ice ages, could have also influence the diet of the cave bear lineage.

**Conclusions**

The analyses of the Middle Pleistocene Deninger’s bear remains help us to understand the evolution of the cave bear lineage. The morphology of Middle Pleistocene cave bears is very similar to that of Late Pleistocene cave bears, suggesting that the dietary preferences of the Late Pleistocene cave bear were already established in the Middle Pleistocene. Furthermore, there seems to be a clear morphological distinction between the Middle Pleistocene cave bear from SIR and from Bacton. There are four possible scenarios: 1) their chronological age is different, 2) there was a geographical barrier, 3) there were multiple lineages, only one of them leading to the Late Pleistocene cave bear, or 4) there were multiple lineages, and each led to a different Late Pleistocene lineage. At the moment, however, it is unclear what the exact cause was and larger sample sizes and better chronologies will be sought in the future to answer this question.

The analyses of the mandibles and crania show that morphological differences are expressed differently in different anatomical regions. In the cranium, there is a much weaker relationship of shape and allometry with diet than in the mandible. Additionally, the shape of the cranium appears to be more strongly influenced by phylogeny than the mandible. This is possibly due to the fact that the mandible is primarily dedicated to mastication, whereas the cranium serves other functions as well and it is a highly integrated structure.

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