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# Functional morphology of Pleistocene and Holocene brown bears (*Ursus arctos* Linnaeus, 1758): a 3D geometric morphometric approach to masseter biomechanics and evolutionary ecology

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# Functional morphology of Pleistocene and Holocene brown bears (*Ursus arctos* Linnaeus, 1758): a 3D geometric morphometric approach to masseter biomechanics and evolutionary ecology

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## ABSTRACT

Little is known about the European Pleistocene brown bear *Ursus arctos* Linnaeus, 1758. To assess its ecological adaptations, the mandibular morphology of fossil *U. arctos* was analysed using 3D geometric morphometrics and compared to that of closely related Ursini. Landmarks for 3D digitisation of the mandible were chosen to reflect functional morphology relating to the *musculus masseter*. Extant and extinct Pleistocene Ursini of the species *U. deningeri* Reichenau, 1904, *U. spelaeus* Rosenmüller, 1794, *U. arctos* and *U. maritimus* Phipps, 1774 were digitised or surface scanned. Generalised Procrustes superimposition was performed on the coordinates and allometry corrected for using a regression analysis pooled by species. Principal component analysis (PCA), canonical variate analysis (CVA), and a multivariate analysis of variance (MANOVA) were performed. PCA and CVA differentiate between species and subspecies in extant Ursini. Fossil *U. arctos* is similar to the extant Eurasian brown bear (*U. a. arctos*). The mandibular morphology of fossil brown bears from cold periods displays similarities to extant bears living in high latitude and high altitude environments, whereas the mandibular morphology of fossil brown bears from warm periods is significantly different to those from cold periods regardless of geological age. The masticatory differences between warm and cold adapted fossil brown bears, found in the present study, indicate that evolutionary flexibility may have played an important role in the survival of brown bears into the Holocene.

KEY WORDS
*Ursus arctos*,
Ursidae,
ursids,
Pleistocene,
geometric morphometrics,
palaeobiology,
palaeontology.

**RÉSUMÉ**

*Morphologie fonctionnelle des ours bruns (*Ursus arctos *Linnaeus, 1758) du Pléistocène et Holocène : une approche de morphométrie géométrique 3D sur la biomécanique des masséters et écologie évolutive.*

Peu de choses sont connues sur l'ours brun européen du Pléistocène, *Ursus arctos* Linnaeus, 1758. Pour évaluer ses adaptations écologiques, la morphologie mandibulaire des fossiles d'*U. arctos* a été analysée à l'aide de la morphométrie géométrique 3D et comparée à celle des Ursini étroitement liés. Les points de repère pour la numérisation 3D de la mandibule ont été choisis afin de refléter la morphologie fonctionnelle en lien avec le *musculus masseter*. Les Ursini actuels et éteints du Pléistocène des espèces *U. deningeri* Reichenau, 1904, *U. spelaeus* Rosenmüller, 1794, *U. arctos* et *U. maritimus* Phipps, 1774 ont été numérisés avec un Microscribe G2 ou scannés en surface. Une superposition de Procrustes généralisée a été effectuée sur les coordonnées, et l'allométrie a été corrigée à l'aide d'une analyse de régression regroupée par espèce. Une analyse en composantes principales (ACP) et une analyse canonique des variétés (ACV) ont été réalisées, et une analyse multivariée de la variance (MANOVA) a été effectuée. L'ACP et l'ACV permettent de différencier les espèces et sous-espèces chez les Ursini actuels. Le fossile *U. arctos* est similaire à l'ours brun eurasiatique actuel (*U. a. arctos*). La morphologie mandibulaire des ours bruns fossiles des périodes froides présente des similarités avec celle des ours actuels vivant dans des environnements de haute latitude et de haute altitude, tandis que la morphologie mandibulaire des ours bruns fossiles des périodes chaudes est significativement différente de celle des ours des périodes froides, quel que soit l'âge géologique. Les différences masticatoires entre les ours bruns fossiles adaptés aux climats chauds et froids, mises en évidence dans la présente étude, indiquent que la flexibilité évolutive a pu jouer un rôle important dans la survie des ours bruns jusqu'à l'Holocène.

**MOTS CLÉS**
*Ursus arctos*,
Ursidae,
ursidés,
Pléistocène,
morphométrie géométrique,
paléobiologie,
paléontologie.

## INTRODUCTION

There are eight currently recognised extant species of Ursidae Batsch, 1788 in five genera (*Ursus* Linnaeus, 1758, *Helarctos* Horsfield, 1825, *Tremarctos* Gervais, 1855, *Ailuropoda* A.Milne-Edwards, 1870 and *Melursus* Meyer, 1793), with diets ranging from folivory to carnivory (Table 1). In the Late Pleistocene of Europe, the now extinct cave bears (*U. spelaeus* Rosenmüller, 1794) were present alongside brown bears (*U. arctos* Linnaeus, 1758). Fossils of brown bears from the Pleistocene are much less abundant than fossils from cave bears in terms of the number of sites and remains (Villaluenga 2011). Most European brown bear fossils date to the Late Pleistocene, but some older brown bears have been identified in the fossil record (e.g., Moigne *et al.* 2006; Sardella *et al.* 2006; Villalba de Alvarado *et al.* 2022; and references therein). Genetic analyses have indicated that the last common ancestor of extant European brown bears lived in the late Middle Pleistocene (Saarma *et al.* 2007; Davison *et al.* 2011). Brown bear fossils have been the subject of detailed phylogenetic analyses based on DNA studies to reconstruct biogeography, population ranges and migration patterns (Davison *et al.* 2011; and references therein) and fossils have been found from North America to North Africa (Barnes *et al.* 2002) and even on islands (e.g., Segawa *et al.* 2021). Thus far, however, only a few studies have focused on the diet of European Pleistocene brown bears (Bocherens *et al.* 2004; García-Vázquez & Grandal d'Anglade 2010; García-Vázquez *et al.* 2018) and all were based on isotopes. To date, there has been no study that has aimed to assess the palaeodiet of European Pleistocene brown bears from a larger geographical area, nor using morphology.

Due to its abundance, most work on fossil bears has concentrated on the cave bear. *Ursus spelaeus* is hypothesised by most authors to have been primarily herbivorous (Bocherens *et al.* 1994; Bocherens *et al.* 1997; Stiner *et al.* 1998; Christiansen 2007; van Heteren *et al.* 2009, 2012, 2014, 2016), based on the morphology of its masticatory apparatus, and isotope analyses, although this interpretation is not supported universally (Richards *et al.* 2008; Figueirido *et al.* 2009).

There are several subspecies of extant *U. arctos*. The Kamchatka bear (*U. a. beringianus*) lives in East Asia (Kurt 1990). Europe is the home of the Eurasian brown bear (*U. a. arctos*) (Pasitschniak-Arts 1993) and the Marsican brown bear (*U. a. marsicanus*) (Ciucci & Boitani 2008). The light coloured Old World forms include the Isabel brown bear (*U. a. isabellinus*) and the blue bear (*U. a. pruinosus*) from the Himalayas (Sowerby 1920), and the Syrian brown bear (*U. a. syriacus*) from Syria and surroundings (Kurt 1990). The North American brown bear (*U. a. horribilis*) shows a variety of colourations (Hall 1984; Kurt 1990).

Extant brown bears are opportunistic omnivores and their diet depends largely on the food items available, including anthropogenic foods (e.g., Frackowiak & Gula 1992; Mattson 1998; Hilderbrand *et al.* 1999; Klinka & Reimchen 2002). Many small-scale studies have analysed the diets of individual populations. For example, in Siberia, the diet of extant *U. arctos* varies throughout the year (Kistchinski 1972). On emerging from their dens, the bears feed on berries, grasses and pinecones.

Vegetative parts of plants serve as their main food at the beginning of summer. In addition, they eat ants, other insects, birds' eggs and small mammals. At the end of summer, when this option is available, great numbers of bears gather near the spawning rivers and streams to feed on salmon. In August and September, bears feed on pine nuts, cones and berries (Kistchinski 1972). Such a list of seasonal food items will vary per subspecies, population and even per individual bear depending on availability. Recent research has shown that spatial variation in brown bear diet is primarily the result of environmental, and particularly climatic, factors (Bojarska & Selva 2012).

Brown bears possess great ecological plasticity and their diet is very diverse, and at times varies from one region to another, from a more vegetarian diet of *U. a. isabellinus* from the Tibetan Plateau, *U. a. horribilis* from Yukon and the brown bears from southern Europe (Clevenger *et al.* 1992; Nawaz *et al.* 2019), to more consumption of animal matter by the bears from China, Norway and Russia (Dahle *et al.* 1998). Carbon and nitrogen isotopes also reflect differences in the diet of brown bears. Grizzly bears from different regions of North America have different diets depending on sex and the access to fish and meat (Mowat & Heard 2011). Bears from the Cantabrian fringe and Apennines consume more vegetative matter than the brown bears that inhabit high altitudes in the Pyrenees and the Alps (García-Vázquez *et al.* 2023) and there are important differences between the sexes (Careddu *et al.* 2021). Even brown bears from different regions within a small continent, such as Europe, have different diets (García-Vázquez *et al.* 2024). The diet of brown bears also varies with the seasons (De Cuyper *et al.* 2023) and winter severity plays a role in brown bear foraging strategies (Bojarska & Selva 2012). Not only does the environment have an effect on brown bear diet, but social learning and maternal effects are also very important (Hertel *et al.* 2024). Additionally, human activities have caused changes in the diet of brown bears (Matsubayashi *et al.* 2015). This ecological flexibility enables brown bears to occupy diverse biomes and highlights their resilience. Moreover, the dietary variability observed in extant brown bear populations can provide important insights into the ecological roles and adaptive strategies of their fossil counterparts.

Fossil carnivores can undergo dietary shifts as a response to environmental change (Flower & Schreve 2014; Baumann *et al.* 2025; van Heteren 2026). This has also been observed in brown bears during the Pleistocene to Holocene transition on the basis of stable isotopes (Rey-Iglesia *et al.* 2019; Krylovich *et al.* 2020), though this does not seem universal (García-Vázquez *et al.* 2018). Previous morphological and morphometric studies have shown a strong correlation between feeding ecology and mandible morphology for Ursidae (Sacco & Van Valkenburgh 2004; Meloro *et al.* 2017; van Heteren & Luft 2026) and other taxa (Pérez-Barbería & Gordon 1999; Nogueira *et al.* 2009; Ross *et al.* 2012). For instance, herbivorous bears like the giant panda (*Ailuropoda melanoleuca* (David, 1869)) exhibit a high coronoid process, which increases the moment arm of the temporalis muscle to deliver more effective force for crushing tough vegetation like bamboo (Sacco & Van Valkenburgh 2004; Christiansen 2008; van Heteren *et al.* 2009, 2016). Conversely, carnivorous ursids like the polar bear (*U. maritimus* Phipps, 1774) possess a lower moment arm, a straighter mandibular corpus and rounded upper canines that are better suited to resist the multidirectional bending stresses generated by struggling prey (Sasaki *et al.* 2000; Christiansen 2008; van Heteren *et al.* 2016). Furthermore, tooth-root morphology serves as a proxy for bite force and the material properties of food (Pérez-Ramos *et al.* 2020). Faunivorous bears, for example, are characterized by enlarged canine roots but reduced post-canine roots, whereas fossil brown bears are intermediate, suggesting they might have been opportunistic omnivores (Pérez-Ramos *et al.* 2020). Other research indicates that Pleistocene brown bears sometimes possessed molar crown dimensions similar to faunivorous species (van Heteren & Luft 2026).

Mandible shape holds substantial information about diet, which may respond to climatic change, implying that there could be a correlation between mandible shape and climate. In addition, recent and fossil mandibles are generally relatively well represented in museum collections. Here, we examine the diet of fossil *U. arctos* throughout the Pleistocene and Holocene by analysing its masticatory morphology and comparing it to that of a range of extant bears to infer dietetary changes in response to climate.

TABLE 1. — Numbers of mandibulae (**n**) used for the analyses.

| **Linnean name** | **Subspecies and fossils** | **n** |
|---|---|---|
| *Ursus arctos* Linnaeus, 1758 | | 94 |
| | *U. a. arctos* | 37 |
| | *U. a. beringianus* | 4 |
| | *U. a. horribilis* | 3 |
| | *U. a. isabellinus* | 8 |
| | *U. a. marsicanus* | 2 |
| | *U. a. pruinosus* | 1 |
| | *U. a. syriacus* | 18 |
| | fossil *U. arctos* | 21 |
| *Ursus deningeri* Reichenau, 1904 | | 2 |
| *Ursus maritimus* Phipps, 1774 | | 13 |
| *Ursus spelaeus* Rosenmüller, 1794 | | 89 |

## MATERIAL AND METHODS

For the analyses, 86 extant specimens and 112 fossil specimens, from a variety of species, including 21 fossil *U. arctos* were used. The institutions where they are stored can be found in the Supplementary Information. Fossil *U. arctos* were identified by the authors, where appropriate assisted by previous species identifications from the literature (Koby 1944; Kurtén 1959; Altuna *et al.* 1982; Ballesio 1983; Torres Pérez-Hidalgo 1988a, b; Delpech 1996; Mussi 2002; Villalba de Alvarado *et al.* 2022) regardless of the species name on label, which was often wrong in the case of older labels. Fossil *U. arctos* were represented from a warm period where they were dated to an interglacial or interstadial, and from a cold period where they were dated to a glacial or stadial. Numbers of specimens per species are given in Table 1.

TABLE 2. — Landmarks used for describing mandibular shape. Landmark types determined according to Bookstein (1991).

| Landmark | Type | Description | Reflects |
|---|---|---|---|
| 1 | 2 | Most rostrodorsal point of the symphyseal region, between the first incisors | Position and size of symphyseal region |
| 2 | 2 | Most rostroventral point of the masseteric fossa | Insertion, moment arm and size of the deep masseter |
| 3 | 3 | Most ventral point on the angular process | Insertion, moment arm and size of the pterygoideus and superficial masseter |
| 4 | 3 | Most dorsal point on the mandibular condyle | Position of the fulcrum of the mandible |
| 5 | 2 | Most caudal point of the alveolus of $M_3$ | Size and caudal extent of tooth row |
| 6 | 2 | Most dorsal point on the labial border of the alveolus of $M_1$ between the two cavities for the roots | Size and extent of the grinding and slicing areas of the tooth row, muscle force available at the carnassials |
| 7 | 2 | Most caudal point of the canine alveolus on the dorsal rim of the mandibular corpus in line with the tooth row | Position of the canine |

Adult specimens of extant and extinct bears were digitised with a Microscribe G2 desktop digitising system (Immersion Corporation, San Jose, CA) or surface scanned with a Go Scan 20 Creaform. When both hemimandibles were present, the more complete was chosen for digitisation. Landmarks were chosen to reflect functional aspects of the mandibular corpus (Fig. 1; Table 2), specifically masseter functional morphology (van Heteren *et al.* 2012, 2019), including information on the tooth row (e.g., landmarks 5 and 6 represent the length of the grinding basin, Table 2).

Using MorphoJ version 1.08.02 (Klingenberg 2010c), raw 3D coordinates were scaled, rotated and translated by Procrustes superimposition. MorphoJ uses a full Procrustes fit and projects the data onto the tangent space by orthogonal projection (Klingenberg 2010b). Reflection was added here to adjust for left and right specimens. Specimens were aligned by principal axes, although the choice of alignment does not influence the statistical results (Klingenberg 2010b). Two separate Procrustes impositions have been performed, one for all the bear species together and one just for the fossil and extant brown bears.

Shape associated with size (i.e., allometry) is still present in the data at this point. To correct for the effects of allometry, a pooled regression analysis within species of the Procrustes coordinates onto log centroid size (Klingenberg 2010a) for all bears was performed. This type of regression, used previously in both traditional and geometric morphometrics (Pierce *et al.* 1994; Bruner & Costantini 2009; Mutsvangwa *et al.* 2010) assumes that the allometry of the different species has the same allometric exponent (slope), but different allometric coefficients (intercepts). Because the brown bears consist of a single species, a normal regression analysis of the Procrustes coordinates onto log centroid size was performed.

Twenty-one fossil *U. arctos*, two *U. deningeri*, 89 *U. spelaeus* and 86 extant specimens (Table 1) were subjected to principal component analyses (PCA). The number of PCs to be retained was determined based on the cumulative percentage of explained variance being over 50%.

Canonical variate analysis (CVA) was performed on the regression residuals of the *U. arctos* regression in MorphoJ version 1.08.02 (Klingenberg 2010c) to investigate shape variation among the *U. arctos* subspecies. Statistical significance was determined using Pillai's trace. Mahalanobis distances were calculated to quantify morphological differences between groups in the CVA morphospace. Permutation tests were performed to assess the statistical significance of these distances, evaluating all pairwise comparisons.

Homogeneity of variances of the CV scores was determined using Levene's test; normality of the data was assessed by the Shapiro-Wilk (S-W) test. A multivariate analysis of variance (MANOVA) was performed on the CV scores to determine the significance of environmental effects along both variates. These statistics were performed in Past 5.1 (Hammer *et al.* 2001).

## RESULTS

### FOSSIL BROWN BEARS COMPARED TO CLOSELY RELATED URSINI

The result of the regression analysis of the Procrustes coordinates of *U. deningeri*, *U. spelaeus*, *U. arctos* and *U. maritimus* onto log centroid size is shown in Figure 2A. The total sum of squares is 0.4407, of which 0.0351 (8.0%) is predicted and 0.4056 is residual. A permutation test against independence gives $p<0.0001$, which is highly significant. It is clear from Figure 2A that the polar bears have a different mandibular shape from the brown bears even though they have similar sizes. The polar bears seem to lie on a different allometric trajectory with higher regression scores. The fossil brown bears are larger than most of the other brown bear subspecies and tend to have lower regression scores at the same size (Fig. 2B). The fossil brown bears from warmer periods are similar in size to the fossil brown bears from colder periods, with the exception of one cold period specimen that is much smaller, and have similar regression scores (Fig. 2C). The regression score primarily correlates with the moment arm of the deep masseter and the grinding basin of the tooth row, as can been deduced from the wireframes.

A PCA was performed on the regression residuals for *U. deningeri*, *U. spelaeus*, *U. arctos* and *U. maritimus* (Fig. 3A). PC1 explains 44.0% of the variance and shows a dietary gradient from the herbivorous cave bear with low PC1 scores to the carnivorous polar bear with high PC1 scores and the omnivorous brown bear between them. PC1 primarily describes the positions of the angular process and masseteric fossa, which correlate with the relative moment arms of the superficial and the deep masseters, respectively. There is a lot

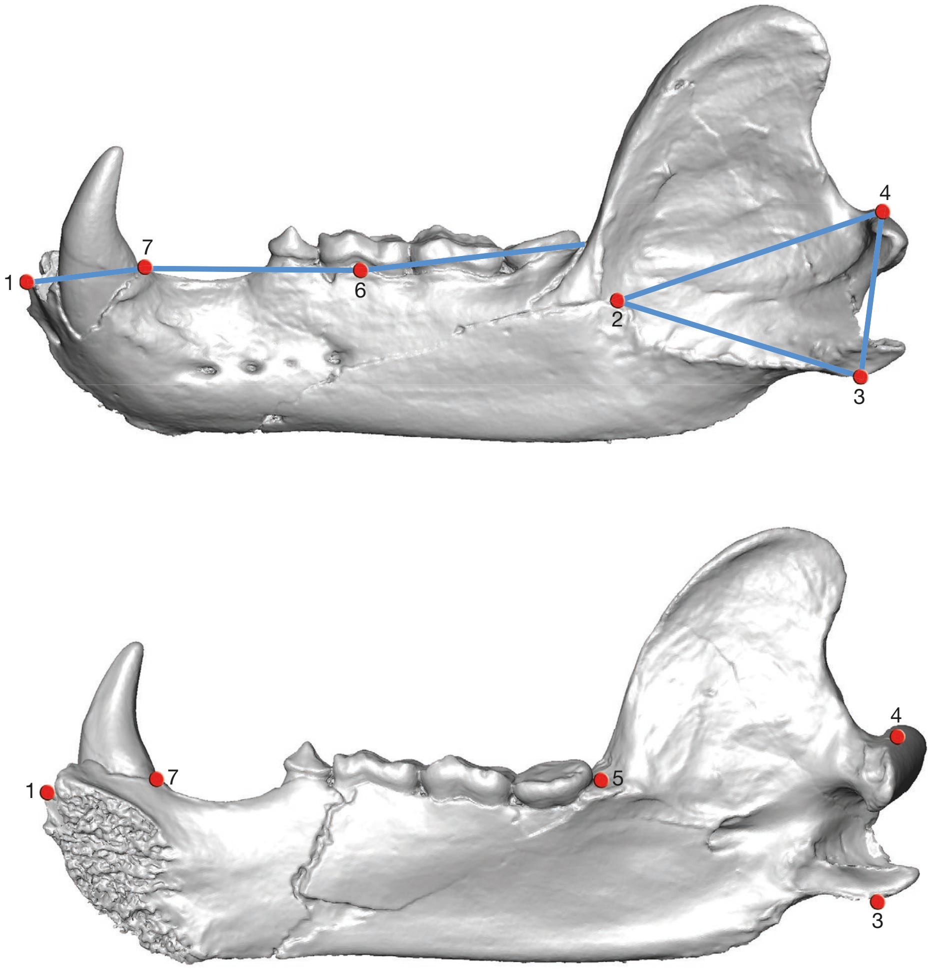

FIG. 1. — Positions of the landmarks on a mandible of *Ursus arctos* Linnaeus, 1758. Landmarks (see details in Table 2): **1**, most rostrodorsal point of the symphyseal region, between the first incisors; **2**, most rostroventral point of the masseteric fossa; **3**, most ventral point on the angular process; **4**, most dorsal point on the mandibular condyle; **5**, most caudal point of the alveolus of M3; **6**, most dorsal point on the labial border of the alveolus of M1 between the two cavities for the roots; **7**, most caudal point of the canine alveolus on the dorsal rim of the mandibular corpus in line with the tooth row.Credits: Anneke H. van Heteren and Mónica Villalba de Alvarado.

of overlap between the brown bear subspecies, but fossil brown bears tend to have relatively low PC1 scores compared to the extant subspecies (Fig. 3B). There is also overlap between the fossil brown bears from warm, ambiguous and cold periods (Fig. 3C). PC2 explains 10.9% of the total variance, which, together with PC1, is 54.9% cumulatively. PC2 primarily correlates with changes in the moment arms of both the deep and the superficial masseters and the length of the postcanine toothrow, particularly the grinding basin.

### Fossil brown bears compared to extant brown bears

The result of the regression analysis of the Procrustes coordinates of the fossil and extant brown bears onto log centroid size is shown in Figure 4A. The total sum of squares is 0.2385, of which 0.0188 (7.9%) is predicted and 0.2196 is residual. A permutation test against independence gives $p<0.0001$, which is highly significant. It is clear from Figure 4A that the fossil brown bears are larger than most extant brown bears, but they seem to lie on the same allometric trajectory. The fossil brown bears from warmer periods and colder periods are similar in size, with the exception of one substantially smaller cold period specimen. They are all on the same allometric trajectory (Fig. 4B).

PCA was performed on the regression residuals of the regression described above (Figs 5; 6). The first three PCs are interpreted, together they explain 52.9% of the variation in the dataset. PC1 explains 22.5% of the total variance, PC2 explains 17.8% and PC3 12.6%. The fossil brown bears overlap with all other subspecies on the first three PCs (Figs 5; 6). The subspecies *U. a. horribilis* and *U. a. isabellinus* show negative values on PC2, whereas the subspecies *U. a. beringinianus* and *U. a. mariscanus* show mostly positive values on PC2. Their distribution of PC scores is very similar to that of *U. a. arctos*. The fossil brown bears from warmer and colder periods overlap when looking at the morphospace through the lens of PCs 1 and 2 (Fig. 5B). However, when looking at PCs 2 and 3 (Fig. 6B), it becomes apparent that the bears from warmer periods are separated from the bears from colder periods and tend to have lower PC3 scores. This corresponds to a more rostroventral position of the angular process and a more caudal position of the masseteric fossa.

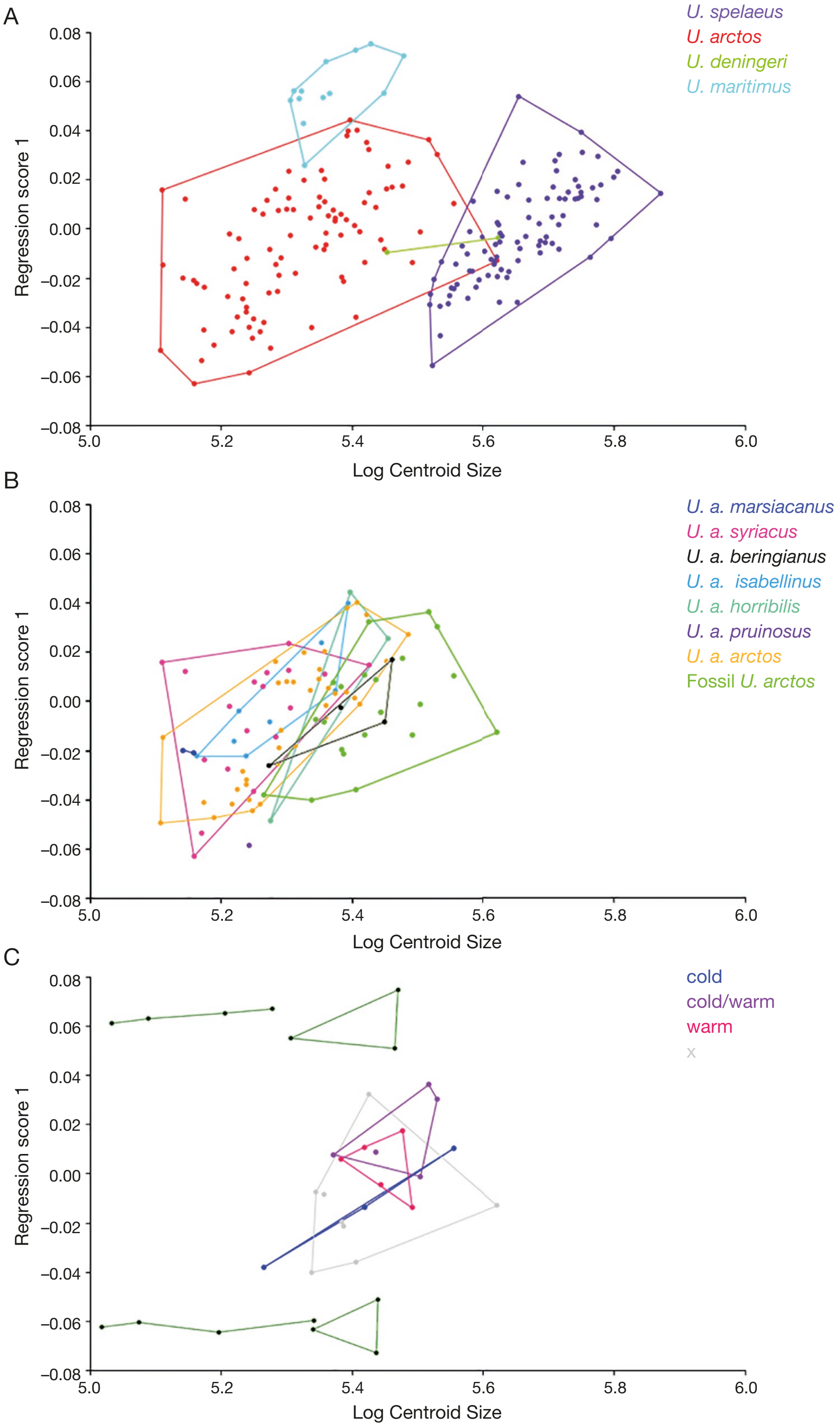

FIG. 2. — Scatterplots of the regression analysis of the Procrustes coordinates of *Ursus arctos* Linnaeus, 1758, *U. deningeri* Reichenau, 1904, *U. maritimus* Phipps, 1774 and *U. spelaeus* Rosenmüller, 1794 onto log centroid size. **A**, **B** and **C** are all in the same morphospace: **A**, all species are represented; **B**, subspecies and fossils of *U. arctos* represented; **C**, attribution of fossil *U. arctos* to warm and cold climatic conditions, "cold/warm" indicates the specimen was dated to a period that could be either and "x" indicates the specimen was not dated, with wireframes representing the shape changes associated with the regression score. Credits: Anneke H. van Heteren and Mónica Villalba de Alvarado.

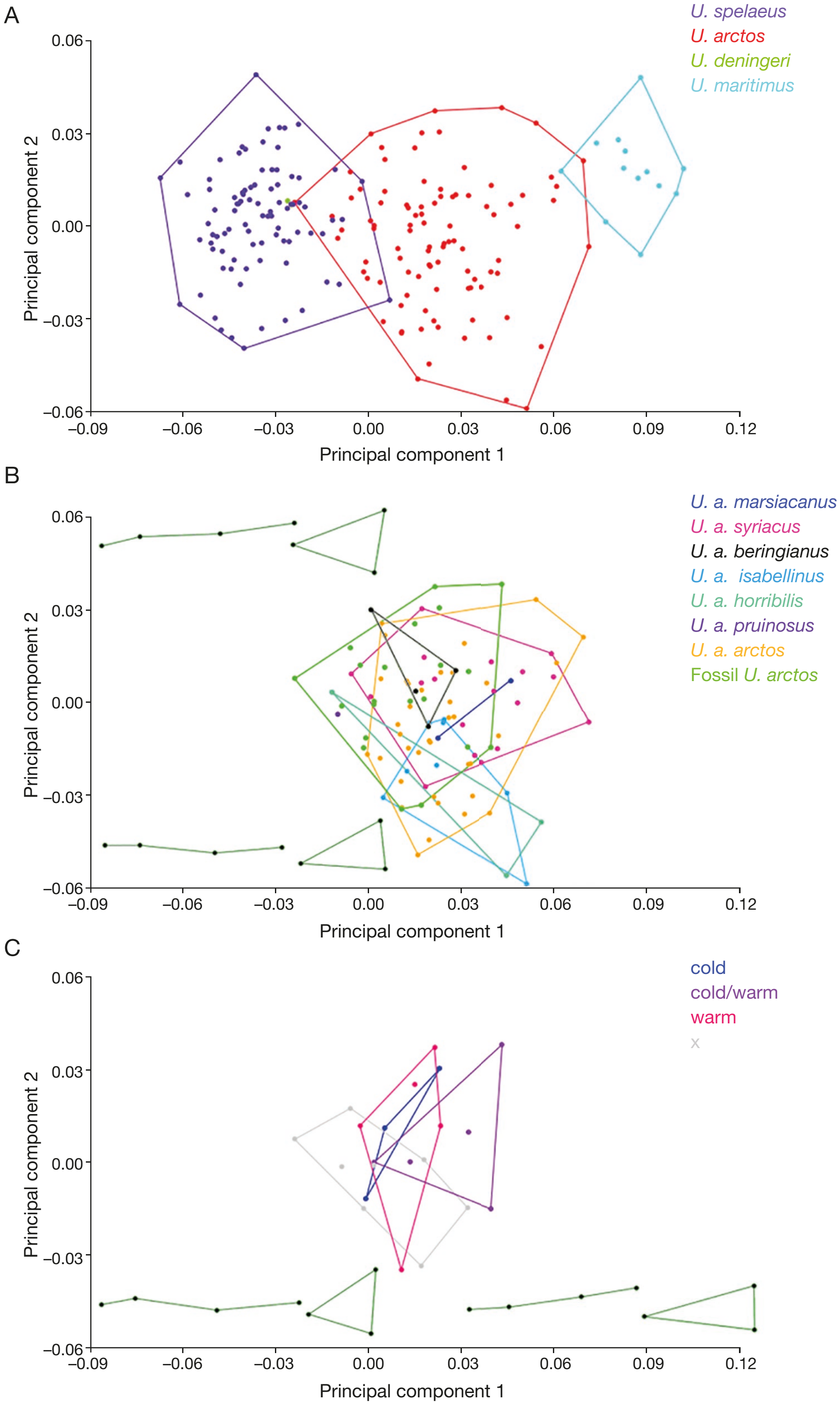

Fig. 3. — Principal components (PC) 1 and 2 of the PC analysis on the regression residuals of *Ursus arctos* Linnaeus, 1758, *U. deningeri* Reichenau, 1904, *U. maritimus* Phipps, 1774 and *U. spelaeus* Rosenmüller, 1794, derived from a regression of Procrustes coordinates onto log centroid size pooled per species. **A**, **B** and **C** are all in the same morphospace: **A**, all species; **B**, subspecies and fossils of *U. arctos* with wireframes representing the shape changes associated with PC2; **C**, attribution of fossil *U. arctos* to warm and cold climatic conditions, "cold/warm" indicates the specimen was dated to a period that could be either and "x" indicates the specimen was not dated, with wireframes representing the shape changes associated with PC1. Credits: Anneke H. van Heteren and Mónica Villalba de Alvarado.

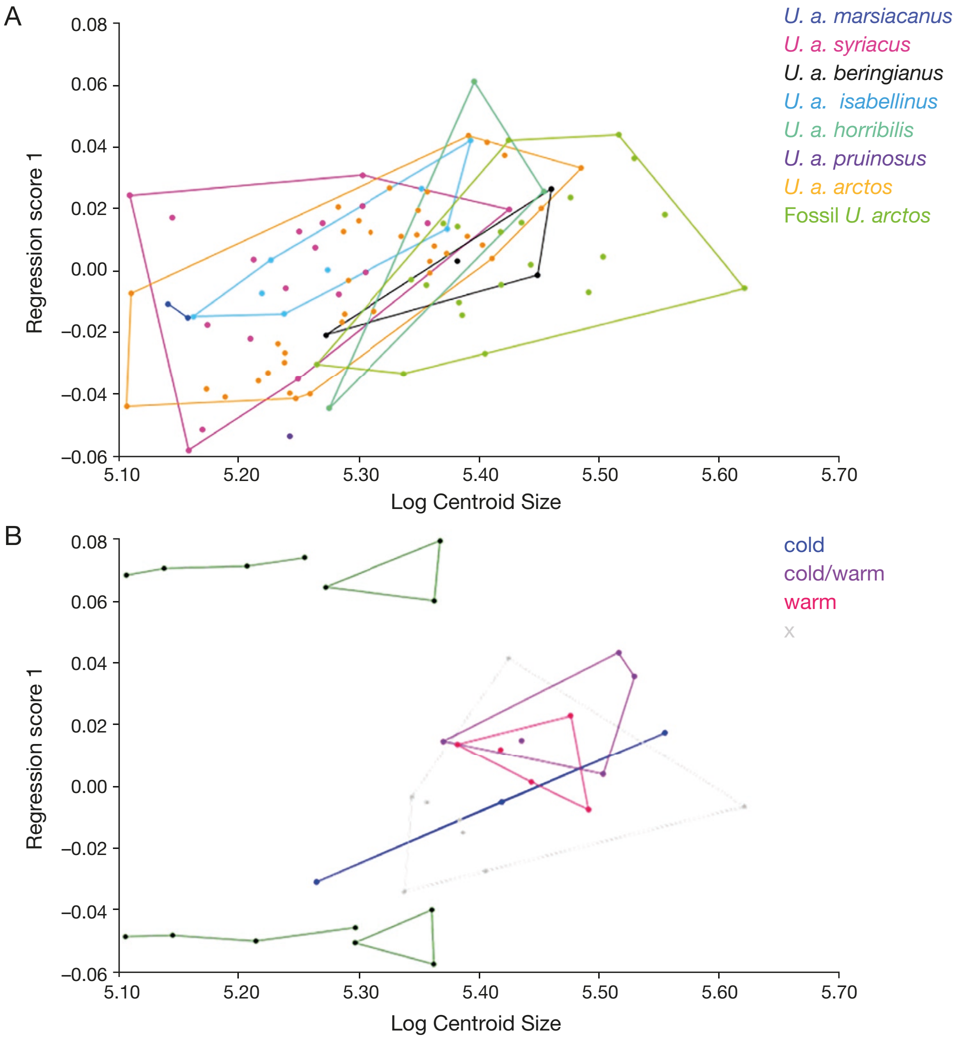

Fig. 4. — Scatterplot of the regression analysis of the Procrustes coordinates of *Ursus arctos* Linnaeus, 1758 onto log centroid size. **A** and **B** are both in the same morphospace: **A**, subspecies and fossils of *U. arctos*; **B**, attribution of fossil *U. arctos* to warm and cold climatic conditions, “cold/warm” indicates the specimen was dated to a period that could be either and “x” indicates the specimen was not dated, with wireframes representing the shape changes associated with the regression score. Credits: Anneke H. van Heteren and Mónica Villalba de Alvarado.

A CVA was performed on the regression residuals for *U. arctos* (Fig. 7A), which showed significant differences between subspecies (Pillai’s trace =1.7519, $p = 0.0015$). CV1 explains 35.2% of the variance and CV2 explains 18.2% of the variance, which is 53.4% cumulatively. CV1 separates *U. a. horribilis* and *U. a. pruinosus* with low scores from *U. a. arctos*, *U. a. beringianus*, *U. a. marsicanus*, *U. a. syriacus* and fossil *U. arctos* with high scores, whereas *U. a. isabellinus* is intermediate between the two sets and overlaps with both. CV1 primarily correlates with the length of the tooth row, the length of the masseter moment arm and the anteroposterior position of the angular process. There is a lot of overlap between the high CV1 brown bear subspecies. Still, *U. a. arctos* is significantly different from almost all other subspecies, except for *U. a. pruinosus* and *U. a. marsicanus*. The fossil brown bears appear most similar to *U. a. arctos* and *U. a. syriacus* in the CVA morphospace. Nevertheless, fossil *U. arctos* is highly significantly different from extant *U. a. arctos* ($p = 0.0051$), but only by a small distance (Table 3). Fossil *U. arctos* is also significantly different from extant *U. a. isabellinus* ($p = 0.0205$) by an intermediate distance (Table 3). On CV2, *U. a. beringianus* has higher CV2 scores than all other extant brown bear subspecies except for four individuals, one each from *U. a. horribilis*, *U. a. isabellinus*, *U. a. pruinosus* and *U. a. arctos*. CV2 primarily correlates with the length of the grinding basin, the moment arm of the superficial masseter and the straightness of the tooth row.

There is no overlap between the fossil brown bears from warm and cold periods, and the fossil brown bears from warm periods have higher CV1 scores and range into the lower CV2 scores (Fig. 7B). Shapiro-Wilk tests indicate that the data for fossil brown bears from cold and warm periods are distributed normally (cold: $n = 3$, CV1 $p = 0.1740$, CV2 $p = 0.4423$; warm: $n = 5$, CV1 $p = 0.8382$, CV2 $p = 0.2410$). A Levene’s test for homogeneity of variance of the two groups indicates that variance is not significantly heterogenous on

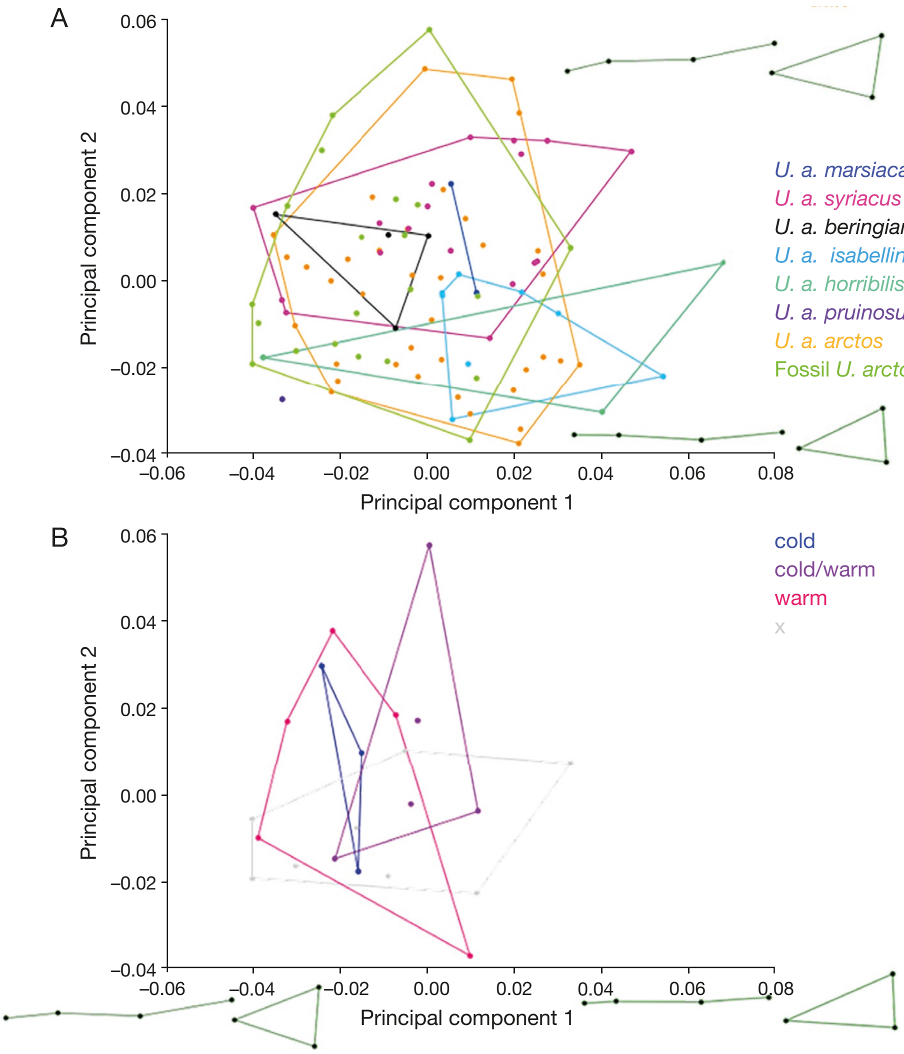

Fig. 5. — Principal components (PC) 1 and 2 of the PC Analysis on the regression residuals of *Ursus arctos* Linnaeus, 1758, derived from a regression of Procrustes coordinates onto log centroid size. **A** and **B** are both in the same morphospace: **A**, subspecies and fossils of *U. arctos* with wireframes representing the shape changes associated with PC2; **B**, attribution of fossil *U. arctos* to warm and cold climatic conditions, "cold/warm" indicates the specimen was dated to a period that could be either and "x" indicates the specimen was not dated, with wireframes representing the shape changes associated with PC1. Credits: Anneke H. van Heteren and Mónica Villalba de Alvarado.

Table 3. — Results of the canonical variate analysis (CVA). Mahalanobis distances are displayed below the diagonal, only for significant results ($p<0.05$). Highly significant values ($p<0.01$) are followed by an asterisk. Relatively large significant distances (>4.0000) are indicated in **bold** and relatively small highly significant distances (<2.000) are indicated in *italics*. *Ursus a. marsicanus* is not significantly different from any of the other subspecies or fossils and is therefore not displayed here.

| | *arctos* | *beringianus* | *fossilis* | *horribilis* | *isabellinus* | *pruinosus* | *syriacus* |
|---|---|---|---|---|---|---|---|
| ***arctos*** | | 0.0163 | *0.0051** | **0.0196** | 0.0005* | | *0.0001** |
| ***beringianus*** | 2.9002 | | | | | | |
| ***fossilis*** | *1.6033** | | | | 0.0205 | | |
| ***horribilis*** | **4.3941** | | | | | | |
| ***isabellinus*** | 2.7329* | | 2.8075 | | | | 0.0105 |
| ***pruinosus*** | | | | | | | **0.0147** |
| ***syriacus*** | *1.5995** | | | | 2.9107 | **5.7233** | |

CV1 ($p = 0.3678$) and CV2 ($p = 0.4174$). To assess potential differences between fossil *U. arctos* from cold and warm periods, a MANOVA was conducted on the first two CVs with warm vs cold as a fixed factor and the CV scores as dependent variables. The difference between fossil brown bears from cold and warm periods is significant ($F(2,5) = 11.96$, $p = 0.01244$). The individuals from cold periods show negative values of CV1 related to a more rostral position of the

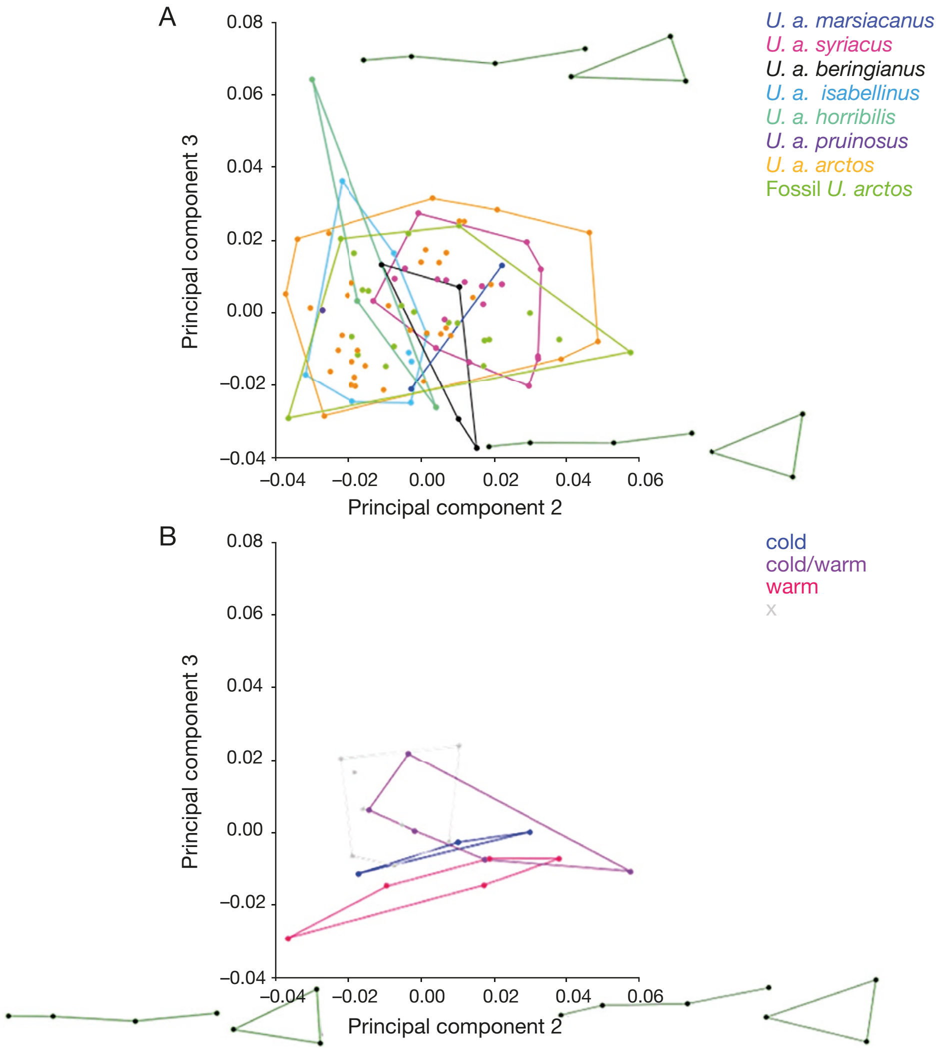

Fig. 6. — Principal components (PC) 2 and 3 of the PC Analysis on the regression residuals of *Ursus arctos* Linnaeus, 1758, derived from a regression of Procrustes coordinates onto log centroid size. **A** and **B** are both in the same morphospace: **A**, subspecies and fossils of *U. arctos* with wireframes representing the shape changes associated with PC3; **B**, attribution of fossil *U. arctos* to warm and cold climatic conditions, "cold/warm" indicates the specimen was dated to a period that could be either and "x" indicates the specimen was not dated, with wireframes representing the shape changes associated with PC1. Credits: Anneke H. van Heteren and Mónica Villalba de Alvarado.

mandibular condyle and the bears from warm periods show positive values of CV1 related to a more caudal position of the mandibular condyle.

## DISCUSSION

It is often implicitly assumed that species that survived the Pleistocene to Holocene transition retained the same morphology and adaptations. Just because they bear the same name, however, does not necessarily mean that they were adapted to the same circumstances. In fact, selection during the Pleistocene/Holocene transition was extremely intense, not only in terms of climate, but also in terms of community structure and consequently food availability, predation pressure and competition (Guthrie 1995; Peyron *et al.* 1998; Johnson 2009). Indeed, dietary differences between Pleistocene and Holocene populations of the same species have been observed in several taxa in other areas of the world (Rivals *et al.* 2007; Fox-Dobbs *et al.* 2008), for example bison in North America (Kohn & McKay 2012) or caprines in Thailand (Suraprasit *et al.* 2020).

Brown bears originally evolved in Asia, from an ancestor called *Ursus etruscus* (McLellan & Reiner 1994). The fossil evidence indicates that there were brown bear like animals in Europe in the Early Pleistocene (Rabeder *et al.* 2010), but there is disagreement on whether these represent early brown bears or whether they were ancestral or related species (Baryshnikov 2007; Palombo *et al.* 2008). Genetic evidence suggests that all extant European brown bears have their last common ancestor in the late Middle Pleistocene and that brown bear evolution in Europe has been continuous at least since this period, coming from six different clades (Saarma *et al.* 2007; Davison *et al.* 2011).

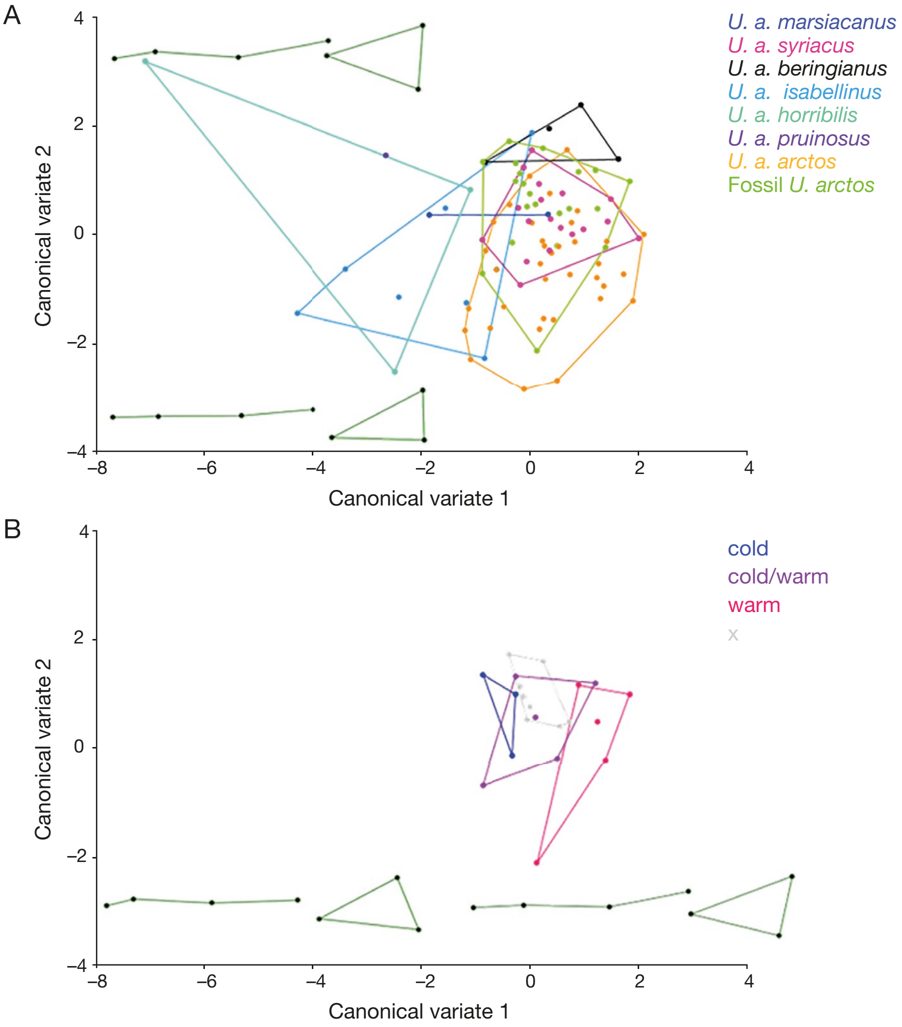

FIG. 7. — Canonical variates (CV) 1 and 2 of the CV Analysis on the regression residuals of *Ursus arctos* Linnaeus, 1758, derived from a regression of Procrustes coordinates onto log centroid size. **A** and **B** are both in the same morphospace: **A**, subspecies and fossils of *U. arctos* with wireframes representing the shape changes associated with CV2; **B**, attribution of fossil *U. arctos* to warm and cold climatic conditions, "cold/warm" indicates the specimen was dated to a period that could be either and "x" indicates the specimen was not dated, with wireframes representing the shape changes associated with CV1. Credits: Anneke H. van Heteren and Mónica Villalba de Alvarado.

The present study assesses the masticatory adaptations of fossil and extant bears, focusing on *U. arctos*, which inhabited Europe during the Late Pleistocene together with *U. spelaeus* (McLellan & Reiner 1994; Davison *et al.* 2011; Viranta & Grandal d'Anglade 2012). The masticatory functional morphology of European Pleistocene *U. arctos* has not previously been analysed quantitatively in reference to its extant conspecifics. The present study contributes to the current knowledge on the diet of fossil *U. arctos* by analysing the relationship between form and function of the masticatory apparatus of closely related Ursini.

The PCAs (Figs 3A; 5A; 6A) represent the morphospaces of *U. arctos*, *U. deningeri*, *U. spelaeus* and *U. maritimus*. The morphology of the bear species involved in the analysis can be interpreted based on their position in morphospace. PC1 primarily correlates with the relative moment arms of the superficial and deep masseters. The deep masseter is most effective when the gape angle is intermediate. This muscle is very strong compared to the superficial masseter for *U. maritimus*, due to a relatively long moment arm of the deep compared to the superficial masseter. For *U. spelaeus* the deep and superficial masseters have almost equal moment arms, mostly because the masseteric fossa is located relatively caudally. This is an indication of rather little strength in the jaw when the jaw is fully opened and the gape is wide, but a more effective masseter muscle when the jaw is more closed compared to the other species. This can be interpreted as an adaptation to grinding, since *U. spelaeus* is thought to have been primarily herbivorous (e.g., van Heteren *et al.* 2012, 2014, 2016; Naito *et al.* 2016; van Heteren & Figueirido 2019). PC2 is mostly determined by the moment arms of both the deep and the superficial masseters and the length of the postcanine toothrow, particularly the grinding basin, with higher PC2 scores indicating an increased mechanical advantage and a longer toothrow. Subspecies of *U. arctos* with high PC2 scores, such as *U. a. arctos*, have a longer tooth row than subspecies with low PC2 scores, such as *U. a. isabellinus*, which is most pronounced distally of the carnassial, resulting in a relatively large grinding basin. The masseteric fossa of species with high PC2 scores is located more rostrally than that of species with low PC2 scores, both relative to the tooth row and the fulcrum. This results in a relatively stronger deep masseter. The strength of the masseter is negatively correlated to the amount of animal-based food in the diet of water-rats (Fabre *et al.* 2017), but it is unclear whether the same holds true for the unrelated *U. arctos*. In musteloids, hard food diets consistently had temporalis and masseter muscles with higher mechanical advantage (Hartstone-Rose *et al.* 2019). The angular process of the mandible is located more ventrally in *U. arctos* subspecies with high PC2 scores than in subspecies with low PC2 scores. This increases the distance between the attachment area of the superficial masseter and the fulcrum, giving this muscle more leverage in subspecies with high PC2 scores.

The results of the present study show that the position in PCA morphospace occupied by fossil brown bears, when all closely related Ursini are considered, generally falls within the range of extant brown bears (Fig. 3). Based on these data, the fossil specimens belong to the same species as the extant brown bears. The fossil *U. arctos* overlap mostly with recent *U. arctos arctos* (Figs 3B; 5A; 6A). The fossil *U. arctos* from cold periods appear to have slightly higher PC1 and PC2 scores than the specimens from warm periods (Figs 3C; 5B), but there is much overlap. On average, however, the mechanical advantage of the masseter, particularly the deep masseter, would have been greater for fossil *U. arctos* from cold periods than from warm periods.

The CVA in this study was designed to emphasize the morphological differences between the various *U. arctos* subspecies. *Ursus a. arctos* has the largest sample size of all subspecies ($n = 37$), giving it the most statistical power (Table 1). It is significantly different from all other subspecies, except for *U. a. pruinosus* ($n = 1$) and *U. a. marsicanus* ($n = 2$) (Table 3), which is possibly due to their small sample sizes rather than true biological similarity. This indicates that the CVA was successful at distinguishing between dissimilar subspecies at a statistically significant level, as long as sample sizes are large enough. *Ursus a. syriacus* also has a large sample size ($n = 18$) (Table 1) and is, additionally, significantly different from *U. a. isabellinus* and *U. a. pruinosus* (Table 3), two subspecies that live at high altitudes (see below for discussion of the implications). Fossil *U. arctos* likewise has a large sample size ($n = 21$). In addition to the significant differences mentioned above, they are also significantly different from *U. a. isabellinus* with an intermediate Mahalanobis distance. Overall, there is a pattern, that subspecies with small sample sizes ($n<5$) are unlikely to be statistically different from the other subspecies with only three exceptions, as mentioned above. This pattern is caused by the fact that the likelihood of a type II error (i.e., accepting the null hypothesis of no difference, when a biological difference, in fact, exists) increases with decreasing sample size (Bezeau & Graves 2001; Algina & Olejnik 2003). As such, in regard to subspecies with small sample sizes, any insignificant difference should be interpreted with caution, but any significant difference could be biologically accurate.

*Ursus a. horribilis, U. a. pruinosus* and *U. a. isabellinus* have relatively low CV1 scores compared to the other subspecies (Fig. 7A). Even though *U. a. pruinosus* has a more carnivorous diet than the other two (Nawaz *et al.* 2019), all *U. a. horribilis* in the present sample come from Yukon or Alaska, so from a high latitude (>60° N). *Ursus a. pruinosus* comes from the Tibetan Plateau and *U. a. isabellinus* comes from the Himalayas, which are both at a very high altitude (*c.* 4000 m and *c.* 6000 m above sea level, respectively). Both high latitudes and high altitudes are associated with colder temperatures. It is noteworthy that *U. a. beringianus*, which also lives at high latitudes (*c.* 57° N), does not cluster with *U. a. horribilis*, *U. a. isabellinus* and *U. a. pruinosus*, but rather displays high CV2 scores. This may be caused by the sea climate on the Kamchatka peninsula with the sea tempering extreme temperatures. Generally, it may be deduced that low CV1 scores are associated with extant brown bear subspecies that are adapted to colder conditions. In addition to climate, the altitude may also be related to the diet, *U. arctos* from high altitudes with higher precipitations, such as bears from the Pyrenees and Alps, show differences in isotopic signatures compared to brown bears from lower altitudes from the Cantabrian and Apennines, with the latter having more frequent consumption of vegetables and fruits (García-Vázquez *et al.* 2023).

There is a clear separation between fossil *U. arctos* that were exposed to colder conditions and those that lived in warmer conditions, with the animals from colder conditions having lower CV1 scores than those from warm conditions. This implies that the fossils from colder periods had similar adaptations to brown bears that currently live in colder conditions. Because the climate was colder and drier in the Late Pleistocene, the climatic conditions currently prevailing at high altitudes and latitudes were then present at lower altitudes. CV1 primarily correlates with the length of the tooth row, the length of the masseter moment arm and the anteroposterior position of the angular process. So, cold adapted brown bears, both fossil and recent, have a longer tooth row and a more efficient deep masseter. In the cold adapted fossil brown bears, a diet approaching that of *U. spelaeus* may have evolved in response to the cold climate. Nevertheless, sympatric brown bears and cave bears from the late Pleistocene still display distinct mandibular shapes, suggesting niche partitioning (van Heteren & Germonpré 2023).

The fossil brown bears in this study display mandibular shapes that are similar to extant European brown bears. As biogeographic reconstructions show that European brown bear presence in Europe has been continuous since the Middle Pleistocene (Saarma *et al.* 2007; Davison *et al.* 2011), this implies that the shape of the mandible of European brown bears has remained relatively stable during the Pleistocene/Holocene transition. However, the fact that warm adapted and cold adapted fossil brown bears are clearly morphologically separated, regardless of their geological age (Fig. 7B), means that they have transformed back and forth several times between two separate morphologies over the last hundreds of thousands of years, whether through genetic evolution, epigenetic inheritance or phenotypic plasticity. Genetic evolution works on geological time-scales typically spanning thousands or millions of biological generations (Rando & Verstrepen 2007). During the Pleistocene, climate would rarely, if at all, have been stable for such a long period of time. Epigenetic inheritance can regulate the phenotype within one generation (Rando & Verstrepen 2007). Epigenetic inheritance, especially prion-based inheritance, is generally considered reversible (Sen & Barnes 2021), and is likely involved in adaptations to highly variable environments (Tyedmers *et al.* 2008; Chakravarty & Jarosz 2018), such as during the Pleistocene. Phenotypic plasticity is also a possibility and could be tested by studying mandibular morphology of captive bears that are kept outside of their normal climatic environment, which is outside the scope of this study. It is probable that both epigenetic inheritance and phenotypic plasticity played a role in the results of our study.

During the Pleistocene and Holocene, the mandible of European *U. arctos* has changed back and forth from a shape that is similar to those in mountainous and arctic brown bear populations to a morphology that is more typical for warm adapted brown bears, including the present morphology of European brown bears. For the warm adapted bears, this includes a decrease in tooth row length. Additionally, the moment arm for the deep masseter has evolved to become shorter. The necessity for an efficient deep masseter, as well as a large tooth row for extensive mastication, was apparently no longer there, when the climate became warmer. This may partly explain why brown bears survived the Late Pleistocene megafaunal extinction and cave bears did not. Cave bears might have been too specialized to reverse their adaptations to herbivory, possibly because their adaptation was partly influenced by irreversible genetic evolution, whereas brown bears were able to adapt through epigenetic inheritance when the climate changed.

The undated and ambiguously dated fossil *U. arctos* cluster with the cold climate fossil *U. arctos*, suggesting that they were also exposed to colder climate conditions during their lifetime. This means that only 1/7 of the fossil *U. arctos* specimens come from warmer climatic conditions. There are several possible, not mutually exclusive, explanations for this skewed distribution. Firstly, the Pleistocene consisted primarily of relatively long cold periods and shorter warm periods. Secondly, there might be a behavioural component at play; *U. arctos* might have sought the protection of caves more often during harsher winters than during milder winters. Thirdly, this might be a taphonomic bias; perhaps warmer conditions were less conducive to fossilization. Fourthly, *U. arctos* population size might have been smaller in warmer periods than in colder periods. The fourth explanation seems unlikely, since *U. spelaeus* was well adapted to colder climatic conditions and would have been more likely to outcompete *U. arctos* during colder periods rather than during warmer periods. The first three explanations seem more plausible.

Given that the difference between the cold climate and warm climate fossil *U. arctos* is approximately similar in magnitude and direction to the difference between *U. a. horribilis* and *U. a. arctos*, it is worth considering that fossil *U. arctos* might actually consist of several chrono subspecies. If so, this could have important implications for our understanding of brown bear evolution and how brown bears adapt to climate change, providing a parallel to contemporary climate change. This also might have ramifications for brown bear conservation efforts.

## CONCLUSION

The results presented here suggest that bear mandibular morphology reflects diet and climate when using analyses based on 3D geometric morphometrics with allometric correction. The results presented here show that the European Pleistocene brown bear did not have a noticeably different masticatory morphology from the average extant brown bear, implying relative morphological and functional stability across the Pleistocene to Holocene transition. Nevertheless, the present analyses show that fossil brown bears occupy distinct positions in CVA morphospace (Fig. 7) depending on the environment they were exposed to. In the Pleistocene, the mandibular morphology of brown bears has evolved between two morphotypes associated with warmer and colder climatic conditions. The masticatory differences between warm and cold adapted fossil brown bears, found in the present study, indicate that, in addition to migration, evolutionary flexibility may have played an important role in the survival of brown bears into the Holocene.

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