

Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics

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Abstract

Relative warp analyses of landmarks describing cranial and mandibular shape are used for investigating patterns of morphological variation among extant bears (Mammalia, Carnivora, Ursidae) indicative of diet and feeding behavior. These patterns are used for deriving inferences about the autecology of two extinct species previously assumed to have had different dietary preferences, the North American giant, short-faced bear *Arctodus simus* and the Eurasian cave bear *Ursus spelaeus*. Results reveal a set of shared craniodental traits among the herbivorous bears, including short and vaulted skulls with well-developed zygomatic arches, lateralized orbits and small canines, concave jaws with a highly positioned condyle, large moment arms for the temporalis and masseter muscles, and long cheek teeth. In contrast, those bears that consume animal resources have long skulls with small zygomatic arches, frontalized orbits and well-developed canines, and long jaws with a deep mandibular symphysis, low muscle leverages, a condyle situated at the level of the tooth row and reduced cheek teeth. The craniodental morphology of omnivorous bears is intermediate between those of faunivores and herbivores. This is also the case of the short-faced bear and the cave bear, which suggests that previous reconstructions of the feeding ecology of these extinct species (highly carnivorous for *A. simus* and herbivorous for *U. spelaeus*) should be revised.

Introduction

With eight species distributed among five genera (Fig. 1), the family Ursidae comprises a set of large and powerful mammals that inhabit Eurasia and the Americas. In spite of their low taxonomic diversity, bears show a varied feeding ecology, ranging from the almost entirely carnivorous polar bear *Ursus maritimus* or the insectivorous sloth bear *Melursus ursinus* to the mostly herbivorous Andean spectacled bear *Tremarctos ornatus* and, particularly, the giant panda *Ailuropoda melanoleuca*, which feeds almost entirely on bamboo. The other four ursid species, the North American and Asian black bears *Ursus americanus* and *Ursus thibetanus*, respectively, the Malayan sun bear *Helarctos malayanus* and the brown bear *Ursus arctos*, are in the middle of this trophic range, because they all have an omnivorous diet that includes variable proportions of animal and vegetable resources according to their availability (Table 1). For this reason, the living bears are a fascinating group for analyzing feeding adaptations in an evolutionary and ecological context (Stirling & Derocher, 1990).

Previous ecomorphological studies have reported a strong correlation between the dietary preferences and the craniodental anatomy of ursids, showing a number of

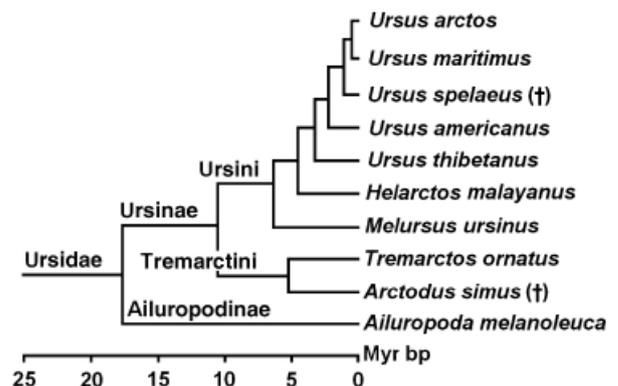


Figure 1 Phylogenetic tree of the family Ursidae, based on nuclear and mitochondrial DNA sequences (Goldman *et al.*, 1989; Talbot & Shields, 1996; Waits *et al.*, 1999; Loreille *et al.*, 2001; Yu *et al.*, 2004; Pagès *et al.*, 2008). In the case of extinct bears (†), the divergence time between the short-faced bear *Arctodus simus* and the spectacled bear *Tremarctos ornatus* is based on the fossil record (McLellan & Reiner, 1994; Soibelzon, Tonni & Bond, 2005), while the divergence time between the cave bear and brown bear *Ursus arctos* lineages is estimated on sequence analysis of ancient mtDNA and cytochrome b gene (Loreille *et al.*, 2001).

Table 1 Sample sizes (crania/mandibles) of bear species and dietary groupings used in the morphometric analyses

Species	Common name	<i>n</i>	Dietary group	References
<i>Ailuropoda melanoleuca</i>	Giant panda	16/16	Herbivore	Schaller <i>et al.</i> (1989)
<i>Tremarctos ornatus</i>	Andean spectacled bear	9/7	Herbivore/omnivore	Peyton (1980)
<i>Melursus ursinus</i>	Sloth bear	24/22	Insect feeder/frugivore	Joshi <i>et al.</i> (1997)
<i>Ursus arctos</i>	Brown bear	28/33	Omnivore	Pasitschniak-Arts (1993)
<i>Ursus americanus</i>	North American black bear	10/10	Omnivore	Pelton (1993)
<i>Ursus maritimus</i>	Polar bear	21/21	Meat feeder	DeMaster & Stirling (1981)
<i>Helarctos malayanus</i>	Malayan sun bear	18/20	Omnivore	Fitzgerald & Krausman (2002)
<i>Ursus thibetanus</i>	Asian black bear	17/21	Omnivore	Reid (1993)
<i>Ursus spelaeus</i> ^a	Cave bear	8/4	Herbivore?	Kurtén (1976)
<i>Arctodus simus</i> ^a	Short-faced bear	6/3	Meat/carrion feeder?	Kurtén (1967); Matheus (1995)

For a review on the average body masses, feeding ecology and dietary preferences of these species, see also Christiansen (2007: table 1).

^aExtinct.

feeding adaptations exclusive of this family among the order Carnivora (Mattson, 1998; Sacco & Van Valkenburgh, 2004; Christiansen, 2007). The skeletal morphology of bears, however, seems to be less constrained than in other terrestrial carnivorans, which may result from (or be the cause of) their broader ecological tolerance and greater opportunism (Van Valkenburgh, 1989; Sacco & Van Valkenburgh, 2004). In this paper, we analyze those morphological patterns of the craniodental skeleton of the living bears that reflect their dietary habits and use this information to make autecological inferences about the feeding ecology of two recently extinct species, the North American short-faced bear *Arctodus simus* and the Eurasian cave bear *Ursus spelaeus*. The reason for selecting these species is that previous ecomorphological and biogeochemical studies have indicated a quite different diet for them, highly carnivorous in the short-faced bear (Kurtén, 1976; Kurtén & Anderson, 1980; Bocherens *et al.*, 1995; Matheus, 1995) and more vegetarian than in other species of the genus *Ursus* in the case of the cave bear (Kurtén, 1976; Bocherens, Fizer & Mariotti, 1990; Bocherens, Fizer & Mariotti, 1994; Stiner *et al.*, 1998; Bocherens *et al.*, 2005, 2006). Thus, the main goals of this paper are (1) to define an empirical morphospace for describing the patterns of variation in the craniodental anatomy of extant bears using landmark-based morphometrics and grid deformations; (2) to compare these morphological patterns with those of other families of the order Carnivora; (3) to interpret the craniodental anatomy of two extinct bears and its ecomorphological implications.

Materials and methods

Skulls of 157 individuals of all the living ursid species were analyzed as well as a number of fossil specimens of *A. simus* and *U. spelaeus* (Table 1). Only adult specimens with the permanent dentition fully erupted were measured. Captive animals were avoided except in eight cases, although it is worth noting that these specimens do not differ morphologically from the wild ones. A similar number of males and females were sampled for extant species and efforts were made to cover the whole geographic range of each species.

The cranial dataset for the living bears was collected in the American Museum of Natural History (New York, USA), the Los Angeles County Museum (Los Angeles, CA, USA), the Natural History Museum (London, UK) and the Museum für Naturkunde (Berlin, Germany). The *A. simus* materials included in the analyses comprise two skulls [FM-25531 (Hay Springs, NE, USA), PM-24880 (Fulton County, IN, USA)], four crania [LACMHC92 and LACMHC134 (Rancho La Brea, CA, USA), FM-99209 and FM-30492 (Ester Creek, AK, USA)] and one mandible [UC-3001 (Rancho La Brea, CA, USA) associated to an incomplete cranium]. The *U. spelaeus* materials analyzed are eight crania (MB.Ma.5020, MB.Ma.1998, MB.Ma.5017, MB.Ma.377, MB.Ma.3022, MB.Ma.2029 and two unnumbered specimens) and four mandibles (MB.Ma.2680, MB.Ma.49357, MB.Ma.1994 and MB.Ma.2007) collected from different localities of Central Europe housed at the Museum für Naturkunde.

Geometric morphometrics allows the multivariate analysis of shape change using configurations of landmarks located in a coordinate system (Bookstein, 1991). Ten landmarks of the lateral view of the mandible and 18 of the cranium were used for defining the craniodental shape space of ursids (Fig. 2). These landmarks were digitized from high-resolution digital images into two-dimensional Cartesian coordinates (x, y) using the software tpsDigv2.05 (Stony Brook State University, New York, NY, USA; available at <http://life.bio.sunysb.edu/morph/>) (Rohlf, 2006a). Jaw landmarks were chosen for measuring the functional moments arms of masseter and temporalis muscles, the position of the jaw condyle relative to the tooth row, the outlever moment arms of the carnassial and the canine, the bending strength of the horizontal ramus, and the lengths of the grinding and slicing dentition. For the cranium, special attention was paid to selecting landmarks that describe its overall shape (e.g. domed or flatted cranial vault), the proportions between the neurocranium and the splanchnocranium, the development of the zygomatic arches, the orientation of the orbits, the relative size of the functional regions of the upper post-canine dentition (i.e. grinding vs. slicing), and the development and position of the canines. For the anatomical definition of these landmarks, see the legend of Fig. 2.

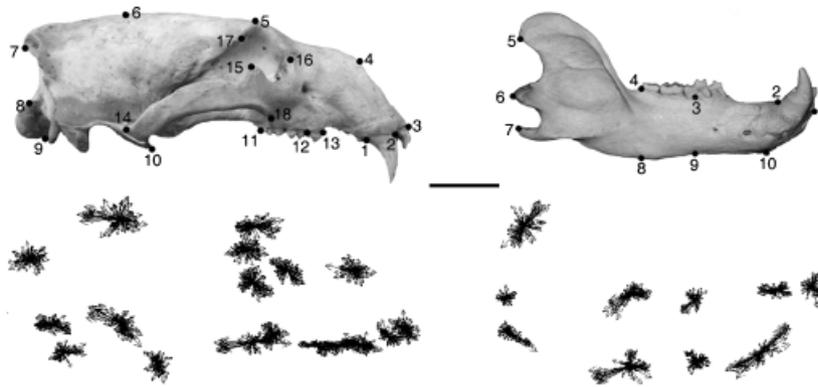


Figure 2 Landmarks used for describing cranial and mandibular shape. Cranium: (1) most postero-dorsal border of the canine alveolus, (2) most antero-dorsal border of the canine alveolus, (3) most antero-dorsal border of the I3, (4) most anterior edge of the nasal bones, (5) dorsal outline directly superior to post-orbital process, (6) dorsal outline directly superior to the end of the zygomatic arch, (7) most postero-ventral point of the occipital crest, (8) intersection between the occipital condyle and the occiput, (9) intersection between the occipital condyle and the paraoccipital process, (10) ventral tip of postglenoid process, (11) posterior edge of the upper tooth row, (12) point between the upper carnassial and the first upper molar, (13) anterior edge of the upper tooth row, (14) postero-dorsal border of the zygomatic arch, (15) dorsal tip of the frontal process of the zygomatic arch, (16) orbit midheight, (17) ventral tip of the post-orbital process, (18) ventral intersection between the zygomatic arch and the maxilla. Mandible: (1) antero-dorsal border of the incisive alveolus, (2) postero-dorsal border of the canine alveolus, (3) intersection between the trigonid/talonid notch of the lower carnassial and the dorsal border of the alveolus of this tooth, (4) posterior edge of the lower tooth row, (5) posterior edge of the coronoid process, (6) most posterior edge of the articular surface condyle, (7) tip of angular process, (8) ventral outline below the mesial end of the tooth row, (9) ventral outline below the trigonid/talonid notch of the lower carnassial, (10) most ventral point of the symphyseal region. Scale bar equals 5 cm. Deviations of the specimens analyzed from the consensus configuration of landmarks are shown.

The overall sample was split in two subsamples, mandibles and crania, and separate morphometric analyses for each were performed in order to include those fossils preserved as isolated crania or jaws. The specimens of both the subsamples were aligned using Procrustes superimposition with the software *tpsRelw* v.1.44 (Stony Brook State University, New York, NY, USA; available at <http://life.bio.sunysb.edu/morph/>) (Rohlf, 2006b), which provided the consensus configurations or mean shapes. Thin-plate spline (TPS) functions were interpolated for deriving the uniform and non-uniform components of shape change. Partial warp scores were calculated for describing the differences between each specimen and the consensus configuration ($\alpha = 0$). Separate relative warp analyses (RWAs), which are in essence principal components analyses of partial warps, were computed with the software *tpsRelw* v.1.44 (Rohlf, 2006b). The relative warps (RWs) summarize the original variance of both the subsamples and describe the major trends in shape change (Rohlf, 1993; Zelditch *et al.*, 2004).

One of the advantages of geometric morphometrics over more traditional methods (e.g. linear measurements and multivariate statistics) is the possibility of depicting graphically the variance explained by the RWs using TPS diagrams for visualizing landmark displacements along the warps as grid deformations and vectors of shape change. These graphs, based on the warp scores of the analyzed specimens, provide an empirical morphospace for bears, which is heuristically useful for evaluating the role of phylogenetic legacy and ecological adaptations as major sources of variation in the morphological traits.

The eight species were distributed among three broad dietary categories for facilitating the ecomorphological comparisons: (1) herbivores, feeding mainly on vegetable resources (*A. melanoleuca* and *T. ornatus*); (2) omnivores, with a diet that includes variable proportions of animal and vegetable resources (*U. americanus*, *U. arctos*, *H. malayanus* and *U. thibetanus*); (3) faunivores, feeding predominantly on animal resources (*U. maritimus* and *M. ursinus*). We admit that these feeding groups are not homogeneous, although the low diversity of the living ursids precludes the use of more specific ecological categories. For example, the first feeding category joins together with the mostly vegetarian spectacled bear and the giant panda, a strict herbivore; similarly, the faunivore category could seem *a priori* less reasonable than the two others, as the texture and material properties of meat and insects, as well as the foraging techniques used by the polar bear and the sloth bear for obtaining them, are quite different. However, we do not use an approach that requires specifying distinct groups for the comparisons, as in the discriminant analyses performed by Sacco & Van Valkenburgh (2004). Instead, we use a methodology based on principal components analysis for exploring the craniodental morphospace of ursids and only use the ecological categories for interpreting the results. In spite of this, our results show a close correlation between the craniodental patterns and the broad dietary groups established *a priori* following the literature: for example, although the two faunivore species feed on quite different resources, they show a number of shared morphological traits that evidence a convergent adaptation to consuming animal matter.

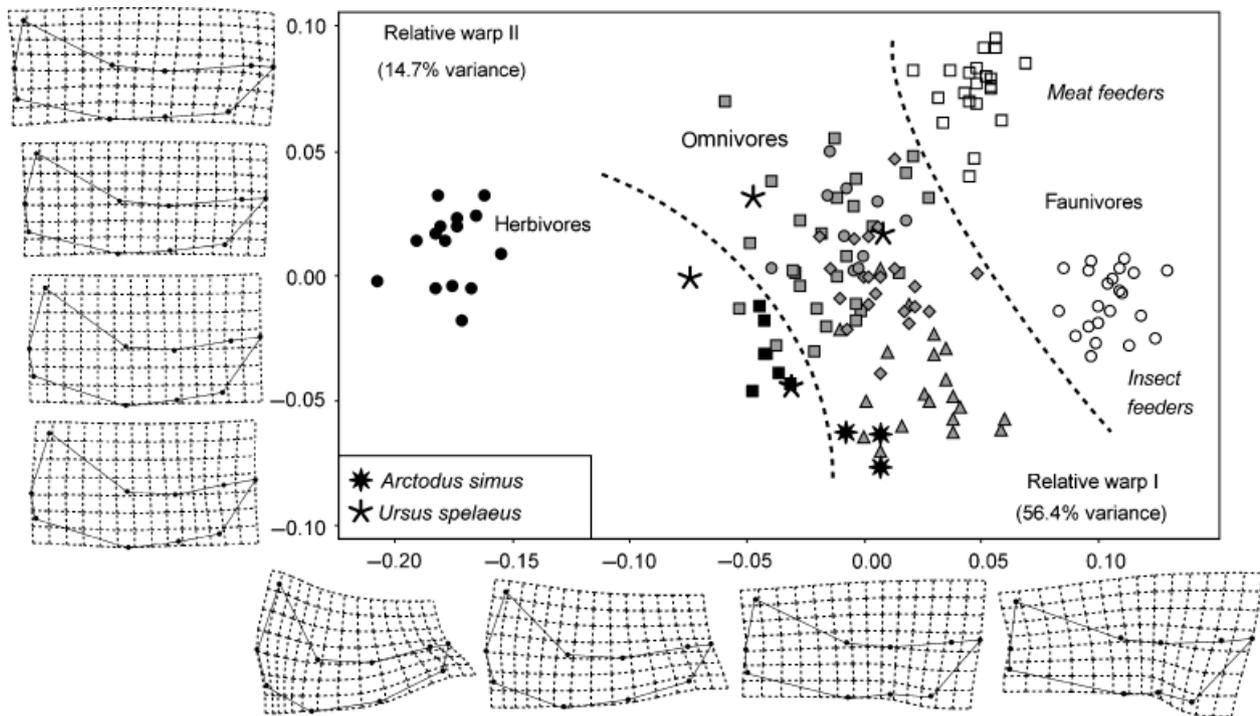


Figure 3 Bivariate plot with the scores of 157 bear mandibles on the morphospace depicted by the first two relative warps. Thin-plate spline diagrams illustrate patterns of landmark displacements along each warp. Black symbols: herbivores (circles, giant panda *Ailuropoda melanoleuca*; squares, spectacled bear *Tremarctos ornatus*). Gray symbols: omnivores (circles, American black bear *Ursus americanus*; triangles, sun bear *Helarctos malayanus*; diamonds, Asian black bear *Ursus thibetanus*; squares, brown bear *Ursus arctos*). White symbols: faunivores (squares, polar bear *Ursus maritimus*; circles, sloth bear *Melursus ursinus*).

Results

Mandibular morphology

The RWA of the W matrix for the 10 landmarks describing jaw shape yielded 16 RWs. The first four have significant eigenvalues (Supporting Information Table S1), but we only show the results for the first two RWs, which jointly account for >70% of the total variance, because the rest mainly highlighted few taxa.

Figure 3 shows the scores for extant and extinct bears on the morphospace defined by the first two RWs. The absence of significant correlations between centroid size and the scores on these warps indicates that the patterns of shape variation among bears described by the RWs do not result from allometric effects. After visual inspection of these results and comparing them with the molecular-based phylogeny of Fig. 1, based on Goldman, Giri & O'Brien (1989), Talbot & Shields (1996), Waits *et al.* (1999), Loreille *et al.* (2001), Yu *et al.* (2004) and Pagès *et al.* (2008), we can conclude that the first axis distributes the species mainly according to their feeding ecology and only secondarily as a result of their phylogenetic affinities (Fig. 3, *x*-axis). For example, all the specimens of the two living ursids that feed on vegetable matter (i.e. the giant panda and, to a lesser degree, the spectacled bear) score negatively on the first RW, as do three of the four cave bears. Figure 3 also includes TPS

diagrams that show the patterns of landmark displacements along this warp, which reveal that the mandibles that take negative scores are comparatively concave and short, have large moment arms for the temporalis and masseter muscles, and show well-developed cheek teeth. In addition, they have a high and posteriorly positioned condyle, placed well above the level of the tooth row, and a horizontal ramus of variable depth, shallow at the level of the canine and deep below the third molar. In contrast, those species that predominantly consume animal resources (i.e. the distantly related polar bear and sloth bear; Fig. 1) take positive scores on the first RW. The TPS diagrams show a distinct jaw anatomy for these species, as their mandibles are larger and more convex, showing smaller moment arms for the temporalis and masseter muscles. In addition, they have a condyle situated at the same level as the tooth row (i.e. the primitive carnivoran condition), a deeper mandibular symphysis and reduced cheek teeth (Fig. 3, *x*-axis). These results are in agreement with those obtained by Sacco & Van Valkenburgh (2004) for the morphological adaptations towards carnivory exclusive of the family Ursidae, which reverse those of non-ursid caniforms. For example, the hypercarnivorous, pack-hunting canids have a shorter rostrum, larger carnassials blades, larger moment arms for the temporalis and masseter muscles, and shorter jaws than the omnivorous canids. However, among ursids, these traits are found in the giant panda and the spectacled bear, species

which both have herbivorous diet. It is worth noting, however, that the hypercarnivorous canids do not show a concave ramus or a jaw condyle placed above the tooth row, features that in the herbivorous bears reflect a functional convergence with ungulates.

According to the scores on the first warp, jaw morphology is an intermediate in the living omnivorous bears between those of species that specialize in consuming animal resources and vegetal matter (Fig. 3, *x*-axis). This intermediate morphology is also the case of all short-faced bears and two out of four cave bears. However, jaw shape in the other two specimens of *U. spelaeus* resembles more the one shown by the herbivorous bears, especially in the case of the spectacled bear, although several brown bears also take similar scores on this warp.

Within the animal matter consumption category, the second RW (Fig. 3, *y*-axis) separates the polar bear, which predominantly consumes flesh, from the sloth bear, which feeds exclusively on termites and ants (Joshi, Garshelis & Smith, 1997). Also, the sun bear and the short-faced bear have the lowest scores on this warp. According to the TPS diagrams that describe landmark displacements on this axis, the latter two species show a comparatively short jaw with a deep horizontal ramus, features which give them a stoutly built appearance. A large moment arm for the temporalis muscle and well-developed canines are also evident in these bears, especially in the case of sloth bear. In contrast, the jaw of the polar bear, the species with the highest scores on this warp, is longer and shallower than in other bears, which gives it a more slender appearance. Compared with the rest of ursids, the polar bear shows a smaller moment arm for the temporalis muscle, reflected in a shorter coronoid process, and well-developed canines. TPS diagrams reveal that the main differences between insect feeders and flesh consumers are the short tooth row and well-developed symphyseal region in the sloth bear compared with the polar bear. Also, the sloth bear shows the coronoid and angular processes more posteriorly placed than in other bears. Finally, there is an empty region in the morphospace between the polar bear and the sloth bear. The absence of an intermediate shape between these species could be tentatively interpreted as reflecting, which no living ursid displays the adaptations for exploiting an ecological niche that involves the regular consumption of vertebrate flesh and insects, as do some small living canids such as foxes.

Cranial morphology

The RWA analysis of the *W* matrix plus the uniform components for the 18 landmarks describing cranial shape yielded 32 RWs (Supporting Information Table S1). We only present here the results obtained for the first three warps, which jointly account for more than 70% of the original variance, because the others reflect minor morphological differences between the taxa. As in the preceding case, the non-significant correlation between centroid size and the scores on these warps reveals the absence of allometric effects.

Figure 4 shows the scores for extant and extinct bears on the morphospace defined by the first three RWs. As in the case of jaw analysis, the first RW describes a morphological pattern, which is mainly correlated with feeding ecology (Fig. 4, *x*-axis). According to the TPS diagrams, the crania of those bears that feed on vegetable matter are short and deep, with a high vault, straight and well-developed zygomatic arches, low, big and lateralized orbits, small canines and well-developed tooth rows. In contrast, the crania of those bears that consume animal matter are larger and shallower, with medially vaulted calvaria, smaller zygomatic arches that are posteriorly downward oriented, small, elevated and frontalized orbits, well-developed canines, and reduced post-canine dentitions. The cranial morphology of omnivores is again an intermediate between those of species that consume exclusively animal or vegetal resources, describing an ecomorphological gradient. Although according to previous studies, *A. simus* and *U. spelaeus* presumably had different feeding ecologies, the specimens analyzed of both the species lie in the region of the morphospace occupied by the living omnivorous bears. However, genealogy could be constraining cave bears to a position in the morphospace close to the brown bears, which are their closest living relatives (Kurtén, 1976). This could hide the possible convergences between *U. spelaeus*, on the one hand, and the living herbivorous bears, *A. melanoleuca* and *T. ornatus*, on the other, as the latter are phylogenetically more distantly related to the cave bear. Similarly, the specimens of *A. simus* score on this warp close to the spectacled bears, which may reflect the common ancestry of both the species as tremarctine bears (Fig. 1).

The second RW (Fig. 4, upper *y*-axis) clearly separates sun bears, which take the highest positive projections, from brown bears, which score on this warp more negatively than the other bear species. As a result, this axis is mainly explained by the cranial morphology of *H. malayanus*, which according to the TPS diagrams is characterized by a medially vaulted calvarium, a short rostrum, small zygomatic arches, a reduced premolar tooth row, well-developed canines and low-positioned orbits. This result agrees with the suggestion of Christiansen (2007) about the 'peculiar-looking' nature of the sun bear cranium (see Supporting Information Figure S1). In contrast, brown bears show larger crania with a more developed rostrum, broader zygomatic arches, more elevated and frontalized orbits and well-developed tooth rows.

The third RW (Fig. 4, lower *y*-axis) separates among faunivores, the carnivorous polar bear from the insectivorous sloth bear. The TPS diagrams confirm that the polar bear has a deeper rostrum, more upwardly positioned orbits and zygomatic arches that are more downward oriented posteriorly. In contrast, the sloth bear shows a flattened rostrum, more outward directed canines, a medially vaulted calvarium, lower orbits and flattened zygomatic arches. It is interesting that the short-faced bear specimens plot on this warp with the highest positive values among omnivores. According to the TPS diagrams, this indicates that the rostrum of *A. simus* is deeper than in other omnivorous

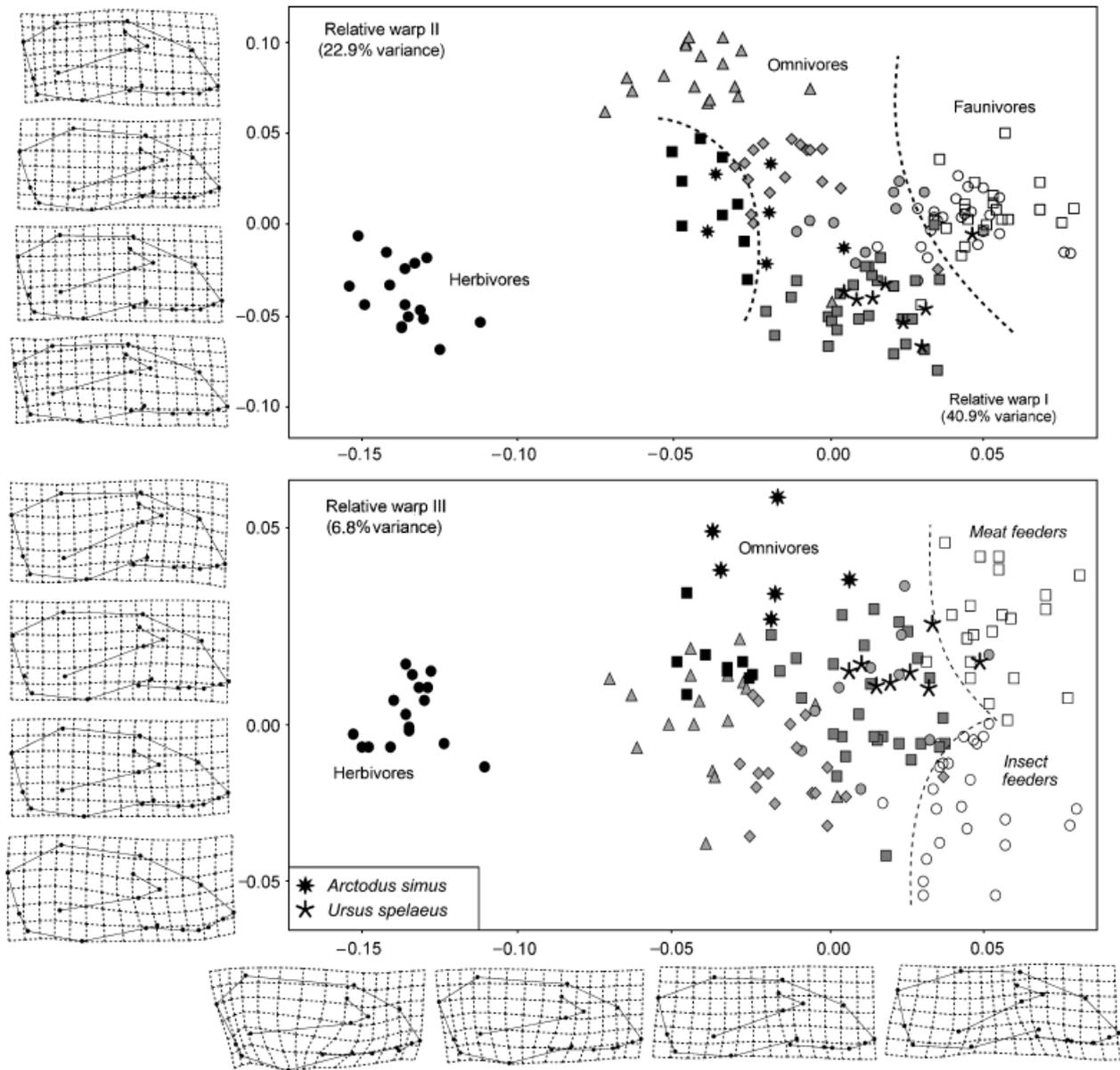


Figure 4 Bivariate plots with the scores of 157 bear crania on the morphospaces depicted by the first three relative warps (RW) (upper graph: RW II on RW I; lower graph: RW III on RW I). Thin-plate spline diagrams describe patterns of landmark displacements along each warp. Symbols are as in Fig. 3.

bears. Finally, in contrast to the results obtained in the morphometric analysis of jaw shape (Fig. 3), the plot with the scores of bears on the first and third RWs (Fig. 4, lower graph) shows that there is no empty space in the cranial morphospace between meat and insect feeders. This suggests the greater evolutionary plasticity of the mandible (Barone, 1986), the morphology of which relates to food acquisition and processing, compared with the cranium, the overall anatomy of which is the result of a compromise among different functions (e.g. feeding, olfactory sense, vision and brain processing). Thus, our results suggest a higher degree of morphological integration and evolutionary conserva-

tism for the cranium compared with the mandible, an issue that will be evaluated in future studies.

Discussion

Overall morphology

Many features of the craniodental morphology of bears are primarily related to their feeding behavior and secondarily to their phylogenetic affinities. For example, the insectivorous sloth bear shares with the carnivorous polar bear a number of convergent craniodental traits that may be

interpreted as adaptations to feed on animal matter, including a flattened and large cranium with frontalized orbits and downward directed zygomatic arches, a comparatively slender jaw with small moment arms for the temporalis and masseter muscles, and poorly developed upper and lower tooth rows. However, there are also some differences between the polar bear and the sloth bear, because the former has smaller moment arms for the masticatory muscles, a deeper rostrum and longer diastemas between the canines and the cheek teeth in the upper and lower dentition. In contrast, the insectivorous sloth bear has a more developed symphyseal region, more outwardly directed canines and post-carnassial molars that are comparatively reduced.

There are also convergent craniodental traits in the two species that specialize on vegetable resources, *A. melanoleuca* and *T. ornatus*, features that are the opposite to some extent of those shown by faunivore bears. However, this set of characters is not as evident as in the preceding case, due to the highly derived morphology of the giant panda compared with the spectacled bear, which has a much wider dietary regime and, consequently, a less specialized craniodental anatomy (Christiansen, 2007). In spite of these differences, our study reveals several traits that could be interpreted as convergent adaptations to herbivory in bears, including a short jaw with large moment arms for the temporalis and masseter muscles, a horizontal ramus which is deep at the level of the third molar and shallow below the canines, well-developed upper and lower cheek teeth, relatively small canines, well-developed zygomatic arches and orbits that are to some extent lateralized. However, the craniodental traits shared by *A. melanoleuca* and *T. ornatus* could be primitive rather than resulting from a functional convergence, as both species are basal in the phylogeny. Under that interpretation, the bear phylogeny of Fig. 1 would show an increasing degree of carnivory from bottom to top. However, this possibility must be discarded on the basis of the fossil record of early bears and their presumed paleoecology; the scarce evidence available suggests that the specialized giant panda evolved from a generalized omnivore, while the ancestor of the Andean bear filled an almost exclusively herbivorous niche (see review in McLellan & Reiner, 1994).

Intermediate characters between those of carnivores and herbivores are indicative of the non-specialized craniodental morphology and thus may be interpreted as adaptations to general omnivory. However, there is one omnivorous species, the sun bear, which displays peculiar craniodental morphology, including a very domed and heavy cranium with wide zygomatic arches, very developed canines and a deep jaw with large moment arms for the masseter and temporalis muscles. These features give *H. malayanus* a stoutly built appearance (Christiansen, 2007). The sun bear also has a mechanical advantage of the temporalis and masseter muscles in excess of that required for an omnivorous diet that includes insects, especially termites and ants, and fruits when available (Joshi *et al.*, 1997). Such bite force is not seen in other insectivorous mammals like the bat-eared fox *Otocyon megalotis*, the falanouc *Eupleres goudoti* or the aardwolf *Proteles cristata*. This unexpected trait

could be related to its dietary habits, as the sun bear frequently tears into trees and termite mounds with both claws and teeth during foraging (Wong, Servheen & Ambu, 2002). Nevertheless, there is always the possibility that this feeding strategy has been adopted recently and the craniodental morphology of the sun bear is still adapted for a more omnivorous diet. However, the lack of fossil record of this species (Fitzgerald & Krausman, 2002) precludes elucidating this issue.

Ecomorphological patterns

The ecomorphological trends for feeding behavior in bears and other large carnivores are somewhat different, as previously indicated by Sacco & Van Valkenburgh (2004). For example, pack-hunting canids show large moment arms for the masseter and temporalis muscles and a comparatively short snout, features that reflect the high biting forces required for seizing and killing large ungulate prey (Van Valkenburgh & Koepfli, 1993). However, the pattern towards hypercarnivory of canids is in part reversed among ursids, because herbivorous and, to a lesser degree, omnivorous bears benefit from having a great mechanical advantage of the jaw-closing muscles combined with a shortened snout. As a result, carnivorous and insectivorous bears have comparatively smaller bite forces than omnivores and herbivores (Sacco & Van Valkenburgh, 2004; Christiansen, 2007). This is not counter-intuitive for an entomophage such as the sloth bear, and probably neither for a carnivore adapted to feed on pinnipeds such as the polar bear, which relies more on shear size than on great bite forces.

The non-specialized morphology of omnivorous bears may be interpreted as an 'adaptation' to feeding on different resources according to their availability. In contrast, the peculiar craniodental anatomy of herbivorous bears seems related to their low digestive efficiency, because *A. melanoleuca* retains the short and relatively simple gastrointestinal tract typical of a carnivore, with a symbiotic microbial community that differs markedly from that of herbivores (Wei *et al.*, 2007). This results in a low digestibility coefficient for cellulose and other complex carbohydrates (Senshu *et al.*, 2007), which constrains the giant panda to consuming huge quantities of bamboo (Schaller *et al.*, 1989). In addition, the fixed craniomandibular joint found in all the members of the order Carnivora (Ewer, 1973) limits jaw movements in herbivorous bears to a vertical plane. This prevents the teeth from being occluded simultaneously for grinding tough foods, as in ungulates, thus forcing the development of high muscle leverages in the giant panda. There are craniodental features of hypercarnivorous canids, including the well-developed carnassial tooth or the crowded premolars, which are also evident in the highly derived morphology of the giant panda and may be interpreted as adaptations to feed on bamboo, which has an extremely tough texture (Sacco & Van Valkenburgh, 2004).

Compared with herbivores, those bears that feed exclusively on animal resources have smaller mechanical advantages of the masseter and temporalis muscles, which allows a

wider gape at the expense of reducing the bite force, a reduced post-canine dentition, smaller carnassial teeth and overall craniodental morphology of slender appearance. These characters are expected in the insectivorous sloth bear, a species adapted to rapidly ingesting prey via suction, a task that does not require large bite forces and well-developed teeth (Sacco & Van Valkenburgh, 2004). The sloth bear shares a number of features with *O. megalotis*, *E. goudoti* and *P. cristata*, including a well-developed symphyseal region, highly reduced cheek teeth and a vaulted palate. It is worth noting that although the cheek teeth of the sloth bear are reduced, this reduction does not reach the extreme degree of the aardwolf. However, these features are not the ones that should be expected in *U. maritimus*. The low muscle leverage of polar bears could indicate that they usually take prey much smaller than themselves (Sacco & Van Valkenburgh, 2004), including juvenile ringed seals *Phoca hispida* and bearded seals *Erignathus barbatus*, although they occasionally prey upon beluga whales *Delphinapterus leuca* (DeMaster & Stirling, 1981). Compared with other ursids, the polar bear has also small carnassials, as in omnivorous canids (Sacco & Van Valkenburgh, 2004). However, given that it feeds primarily on blubber, the carnassial shearing blades are perhaps less necessary than in other carnivores (Sorkin, 2006). The retention of the post-carnassial molars in the polar bear is probably useful for scavenging whale, walrus and seal carcasses, as well as for consuming fruits, small mammals, eggs and vegetation when other foods are not available (DeMaster & Stirling, 1981). However, there is another explanation for the weak carnivorous adaptations of *U. maritimus*. Polar bears evolved recently from brown bears (Kurtén, 1964; Loreille *et al.*, 2001), becoming carnivorous from an omnivorous ancestor and reaching body masses in excess of 500 kg in adult males (DeMaster & Stirling, 1981). Given its huge size, it is plausible to conceive an evolutionary trend towards carnivory involved in acquiring a more slender condition, as evidenced by the RWs. Thus, the polar bear may simply be so large and powerful that it does not require large moment arms for the masseter and temporalis muscles, a deep jaw or a more developed slicing dentition than in brown bears. However, given its predatory habits and the need to cover long distances in the search of prey, the polar bear probably needs a lightened skeleton compared with the more omnivorous brown bear, as suggested by the low limb-bone density of the former, typical of a semiaquatic mammal (Fish & Stein, 1991).

Feeding ecology of extinct taxa

Traditionally, it has been thought that the cave bear was the most herbivorous species of the genus *Ursus*, a conclusion based on its craniodental morphology (Kurtén, 1976; Mattson, 1998; Grandal & López, 2005). This was corroborated by isotopic analyses of fossil cave bear specimens, which provided similar or even lower $\delta^{15}\text{N}$ values than those of sympatric ungulates, indicative of an herbivorous diet based on C3-plants (Bocherens *et al.*, 1990, 1994, 2005, 2006).

However, in species such as bears with a broad dietary spectrum, the inferences based on isotopic studies of single populations may be confusing if we assume that they represent the uniform condition for the entire species (Hilderbrand *et al.*, 1996; Stiner *et al.*, 1998). For example, Hilderbrand *et al.* (1996) and Richards *et al.* (2008) have suggested that the great variation of $\delta^{15}\text{N}$ values in *U. spelaeus* could reflect the fact that cave bears were able to shift to a more omnivorous diet depending on resource availability or even to behave as carnivores. This ecological plasticity is in agreement with the results obtained in our morphometric analyses, which reveal that the craniodental morphology of *U. spelaeus* is characterized by large muscle leverages, well-developed cheek teeth with large carnassial blades, broad zygomatic arches and a stoutly built jaw. Among bears, all these features indicate a non-specialized anatomy and may be interpreted as adaptations to general omnivory, as in brown bears, the closest living relatives of cave bears. In fact, the cave bear specimens included in our analyses plot within the regions of the morphospace occupied by the omnivorous and, to a lesser degree, herbivorous bears (Figs 3 and 4). This may reflect the ability of the cave bear to behave like an omnivore (Richards *et al.*, 2008), as the morphometric study indicates what this extinct species had the potential to eating, even if in many cases they actually had an herbivorous diet, as suggested by the biogeochemistry (Bocherens *et al.*, 1990, 1994, 2005, 2006). Under such interpretation, the lack of specific adaptations towards herbivory would be the result of the short evolutionary history of this species.

With the large males weighing 700–800 kg, an estimate obtained using regression equations adjusted between limb bone dimensions and body mass in extant carnivores (Christiansen, 1999), the short-faced bear *A. simus* exceeded the size of any living ursid and was the largest member of the carnivore guild in the Pleistocene of North America. Kurtén (1967) and Kurtén & Anderson (1980) reconstructed this enigmatic bear as largely carnivorous. This assumption was based on a set of morphological characters that were, in their opinion, convergent with the living felids. These features include a short and broad rostrum, large carnassial blades, a comparatively short body, and long limbs and a more digitigrade stance, features that suggest a more carnivorous diet and a faster locomotion than in the extant plantigrade ursids (Kurtén, 1967; Kurtén & Anderson, 1980). Later, Bocherens *et al.* (1995) and Matheus (1995) confirmed this ecomorphological inference with comparative analyses of the relative abundance of carbon and nitrogen isotopes in samples of bone collagen of *A. simus* and *U. arctos*. These studies revealed a range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in *A. simus* indicative of a diet largely based on terrestrial vertebrates, although it is worth noting that Matheus (1995) concluded that the short-faced bears probably behaved more as scavengers than as active predators. However, the isotopic analyses are not conclusive, because the ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values do not always allow discrimination between highly carnivorous species and other more omnivorous species that include large quantities of

flesh in their diet (Sorkin, 2006). In addition, the isotopic estimates obtained from the single specimens should be extrapolated with caution for the entire species (Hilderbrand *et al.*, 1996), although this also applies to the ecomorphological inferences derived from isolated fossils. In general, we should bear in mind the fact that anatomy points to the range of things that may be done by the members of a species (i.e. their adaptations) and there are things that are not possible to infer from their morphology (e.g. some exaptations). In contrast, pin-pointed studies such as isotopic analyses tell us what individual animals did within that overall repertoire over a certain period of time (in the case of bone collagen isotopes, during the last few years of the animal's life), and we should not confuse the two.

In any case, the craniodental morphology of the short-faced bear, according to our analyses, does not agree with a highly specialized carnivorous diet: the large muscle leverages, the very deep jaw at the level of the third molar, the well-developed zygomatic arches and the long cheek teeth are all characters which, among extant bears, indicate the high biting forces typical of a herbivorous or omnivorous species. Also, the stoutly built appearance of the craniodental skeleton of *A. simus* follows the trend of the living omnivorous ursids rather than reflecting an adaptation to hypercarnivory. Thus, the comparatively short snout of *A. simus* would not be a valid argument for concluding that this bear had a more felid-like feeding ecology, because the extant carnivorous ursids are characterized by long snouts rather than short ones. However, it is worth noting that this does not imply that an extinct bear should follow such pattern, because the polar bear, the only hypercarnivorous species among the living ursids, has a rather peculiar and specialized diet compared with other flesh-eating carnivorans.

Based on its non-specialized craniodental traits, we propose that the different populations of *A. simus* could have fed on different resources according to their availability, as in the case of the living brown bear or the American black bear. In fact, the feeding ecology of the latter two species ranges from almost completely vegetarian to one incorporating a substantial percentage of vertebrate meat, depending on the availability of ungulate prey (Richards *et al.*, 2008). Therefore, although it is obvious that the short-faced bear could have preyed upon the Pleistocene megafauna and probably scavenged the carcasses of ungulates hunted by saber-tooth cats *Smilodon fatalis*, North American lions *Panthera atrox* or dire wolves *Canis dirus*, as evidenced by isotopic analyses, in our opinion, it was not a specialized scavenger or a hypercarnivore. However, we should remember here that there is no modern analog for *A. simus*, because the only hypercarnivorous ursid, the polar bear, preys on marine mammals and usually takes prey on small relative to its body size. For this reason, it requires smaller bite forces than a terrestrial species adapted to consuming large ungulates, which is the dietary niche proposed for the short-faced bear based on isotopic analyses (Bocherens *et al.*, 1995; Matheus, 1995). Thus, the fact that *A. simus* does not

cluster with the polar bear in the craniodental morphospace of ursids should not be considered as a conclusive argument for rejecting the hypothesis that this extinct bear was a specialized meat eater. Instead, it is the presence of features of the craniodental morphology shared with the living omnivorous ursids (e.g. the large moment arms for the chewing muscles, the stoutly built mandible, the well-developed zygomatic arches and the long cheek teeth) which provides the stronger evidence for inferring that this extinct bear had an omnivorous diet (or, at least, that it evolved very recently from an omnivorous ancestor, as suggested by the fossil record).

Conclusions

This study has shown that the craniodental morphology of bears is primarily related to their trophic adaptations and secondarily to their phylogenetic affinities, because it has revealed some remarkable morphological convergences among different feeding groups. Four ursid species, the polar bear, the sloth bear, the Andean bear and the giant panda, have specialized morphologies resulting from their unique feeding ecologies. In contrast, the American and Asian black bears, the brown bear and the Malayan sun bear have a generalized morphology that may be interpreted as indicating their omnivory. The ecomorphological trends resulting from the dietary adaptations of bears are different from those of other large carnivores, particularly canids, as previously indicated by Sacco & Van Valkenburgh (2004) and Christiansen (2007). These 'opposite' trends, which reflect the different evolutionary history of both the families, must be taken into account for predicting the diet of ancient ursids. For example, the shortened rostrum and long carnassial teeth of *A. simus* are not valid arguments for inferring a largely carnivorous diet for this extinct species, because such traits are found among the living omnivorous ursids. In addition, many aspects of the craniodental morphology of *A. simus* are not specialized, which probably indicates a more omnivorous diet than previously thought. Our results suggest that it is necessary to undergo for a more in depth ecomorphological study of the giant, short-faced bear, including the members of other carnivore families (e.g. the pack-hunting canids and the bone-cracking hyenas). In the case of the Eurasian cave bear, although there is compelling isotopic evidence for an herbivorous diet, the generalized craniodental morphology of this extinct bear, typical of the living omnivorous ursids, is in agreement with an ability to change its dietary habits toward omnivory or even carnivory according to resource availability (Richards *et al.*, 2008). Following our results, the most parsimonious interpretation is to consider that these New and Old World bears had an essentially omnivorous behavior. This inference is in agreement with the climatic cycles of the Pleistocene, an epoch in which resource availability (and selection pressure) was frequently changing, especially in the highly seasonal temperate zone inhabited by *A. simus* and *U. spelaeus* (and most living bears). In addition, given the length of the climatic cycles (~100 ka), probably it was not possible for

evolution to track them, which led to the evolution of generalist, omnivorous forms relatively independent of these cycles.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Crania and mandibles of selected specimens of each bear species analyzed in this study. Specimens of *A. simus* taken from Richards & Turnbull (1995). Scale bar lengths are 10 cm for crania and 5 cm for mandibles.

Table S1. Eigenvalues and percentages of variance explained by the relative warps (RW) derived from the analysis of mandibular shape in bears.

Table S2. Eigenvalues and percentages of variance explained by the relative warps (RW) derived from the analysis of cranial shape in bears.

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