

Mandible of the giant panda (*Ailuropoda melanoleuca*) compared with other Chinese carnivores: functional adaptation

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The aim of this study was to understand the mandible of the giant panda in morphometric terms to explore differences between the giant panda and other carnivores distributed in China, in terms of functional adaptation. Twelve mandibular variables were studied using bivariate (allometry) and multivariate (principal components analysis, PCA, and discriminant functional analysis, DFA) tools. When deviations were produced from allometric baselines consisting of all the species studied, the giant panda displayed a much more developed mandibular structure than the bear, leopard, and tiger. This may be related to its specific dietary preference for bamboo, which has very strong fibers. Results also indicate that the mandibular structure among carnivores mainly reflects the differences in their dietary preferences and functional adaptation. Three groups were found referring to dispersal profiles expressed by the first two axes of PCA and DFA: (1) the two panda species – the herbivorous carnivores; (2) the black bear – the omnivorous carnivore; and (3) the tiger and leopard – the hypercarnivores. Nevertheless, a significant separation between the two panda species was also found with the profiles displayed by the first and third axes of DFA. In addition to no close evolutionary relationship and phylogenetic development, a noticeable separation between the two panda species found in DFA analysis may be associated with their variation in consuming different parts of the bamboo plant: the giant panda feeds on stems and the red panda feeds on leaves. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 449–456.

ADDITIONAL KEYWORDS: black bear – leopard – mandibular morphology – red panda – tiger.

INTRODUCTION

The giant panda (*Ailuropoda melanoleuca*), a specialized bamboo feeder in the order Canivora, is endemic to China. It differs from most carnivores in being a bamboo eater. This specialization might have occurred in the early Pleistocene, associated with the large bamboo resources that appeared in southern

China at that time (Wang, 1974); more than 60 bamboo species have been tabulated as food for this panda in the five mountainous regions it inhabits (Hu & Wei, 2004).

There have been a number of morphological and functional anatomical studies on the giant panda, focusing on different features, including its general overall comparative anatomy (Davis, 1964; Beijing Zoo *et al.*, 1986), cranial and masticatory apparatuses (Sicher, 1944; Davis, 1964), morphological variation in skulls of extant bears (Sacco & Van Valkenburgh,

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Table 1. Allometric analysis between mandibular dimensions and cranial length in Chinese carnivores

Dependent variable	<i>a</i>	<i>b</i>	<i>r</i>	<i>P</i>
1. CONDYLL Maximum anterior-posterior length of the mandibular condyle	-3.761	1.153	0.81	0.000
2. CONDYLLW Maximum mediolateral dimension of the condyle	-2.774	1.202	0.80	0.000
3. CONM1 Distance from the back of the condyle to the mesial border of the M ₁	-1.786	1.168	0.94	0.000
4. LBCB Bicanine breadth between the labial (buccal) surfaces of the permanent lower canines	-1.784	0.987	0.94	0.000
5. LBMB Bimolar breadth from the buccal surface junction of the waists of the right and left M ₂	-0.631	0.876	0.86	0.000
6. LIAW Incisor alveolar width at the distal margins of the lateral incisor alveoli	-1.721	0.877	0.91	0.000
7. MAM1 Moment arm of the masseter muscle: vertical distance from the top of the condyle to the inferior-most border of the angle	-1.998	1.123	0.96	0.000
8. MAM2 Moment arm of the masseter muscle: direct distance from the top of the condyle to the inferior-most border of the angle	-1.804	1.037	0.63	0.000
9. MANCORW Width of the mandibular corpus at the M ₁ locus	-3.192	1.097	0.79	0.000
10. MANDH Height of the mandible between the M ₁ and M ₂	-2.426	1.094	0.95	0.000
11. MANDSYM Midline length of the symphysis between the inferior margin and the infradentale	-5.416	1.684	0.90	0.000
12. MAT Moment arm of the temporal muscles, from the mid-curvature (point) of the condyle to the apex of the coronoid process	-0.854	0.864	0.84	0.000

Abbreviations: *a*, constant; *b*, exponent; *r*, correlation coefficient.

2004), the special functional anatomy of the radial sesamoid bone, and understanding the manipulating mechanism used for feeding (Pocock, 1939; Endo *et al.*, 1999a, b, 2001).

In order to further explore the functional adaptation of the giant panda to its bamboo diet, three groups of carnivores with different dietary preferences (herbivorous carnivores, the giant pandas, *A. melanoleuca*, and the red pandas, *Ailurus fulgens*; an omnivorous carnivore, the black bear, *Ursus thibetanus*; and hypercarnivores, the tiger, *Panthera tigris*, and the leopard, *Panthera pardus*) were analysed. This was carried out in order to determine whether, and to what degree, the morphology of the masticatory apparatus of the giant panda differs from that observed in carnivores with different diets. Such findings might help elucidate the degree to which differences in morphology among the animals can be directly associated with functional adaptations.

MATERIAL AND METHODS

A total of 151 samples from five species of the Chinese carnivores were used in this study, including 48 samples for giant panda, 16 for red panda, 29 for black bear, 42 for leopard and 16 for tiger. They were all adults, as judged by the full eruption of permanent M₁ (the tiger and leopard)\M₂ (the red panda)\M₃ (the giant panda and black bear) teeth. The left side of the mandible was used to take measurements. The other side was utilized only if the left side was damaged or missing. Twelve raw mandibular variables were analysed in order to obtain profiles reflecting the differences in morphology (Table 1 and Fig. 1).

Because there is a great range in body size between the species, from about 5 kg (the red panda) to 300 kg (tiger) (Gao, 1987), it seemed highly likely that mandibular differences among species might be largely size related. As is common in most biological systems, associated effects of size usually outweigh those of

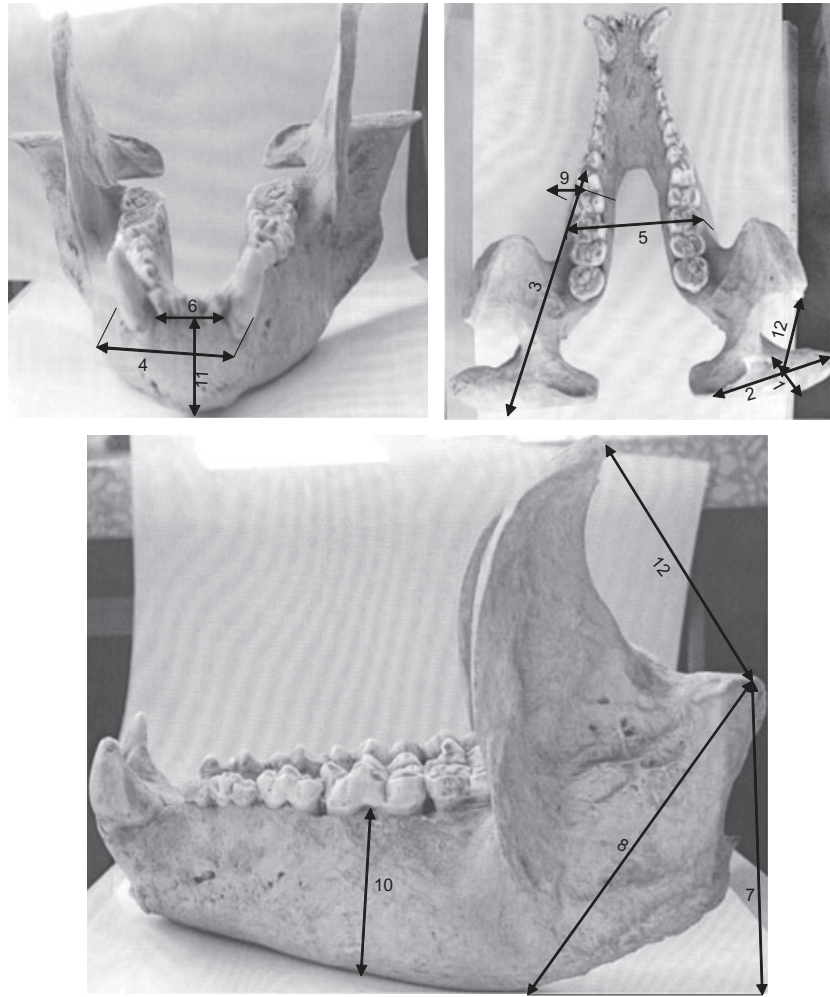


Figure 1. Photographs showing three views of a mandible. The double arrowheaded lines indicate the mandibular variables measured in this study: 1, CONDYLL; 2, CONDYLW; 3, CONM1; 4, LBCB; 5, LBMB; 6, LIAW; 7, MAM1; 8, MAM2; 9, MANCORW; 10, MANDH; 11, MANDSYM; 12, MAT.

shape. This is especially the case when raw measurements are used (De Winter, 1997). Thus, deviations of the data from an allometric baseline (see below) were analysed. This allowed some exploration of variation after the size element had been greatly reduced (Smith, 1981).

The allometric formula, $Y = aX^b$ or $\log Y = \log a + b \log X$, was used in this study. Y , the dependent variable, is, in turn, each mandibular measurement; X , the independent variable, is the cranial length (frequently used as a surrogate for body size when body size is not available; Pan & Oxnard, 2001). Deviations of each mandibular variable from the allometric baseline were estimated by the differentiation between the original and predicted values. According to Smith (1981), this can be formulated as follows:

$$D(\text{deviation}) = \text{antilog}[\log(\text{original value}) - \log(\text{predicted value})].$$

The data were analysed by both principal components analysis (PCA) and discriminant functional analysis (DFA).

RESULTS

The allometric formulae for each of the mandibular variables against cranial length are listed in Table 1. Each of the variables shows a significant relationship with cranial length. There are, however, great variations in these allometric relationships among the variables. Five variables, namely CONDYLL, CONDYLW, CONM1, MAM1, and MANDSYM, all scale positively to cranial length. They thus contrast with LBCB, LBMB, LIAW, and MAT, which scale negatively. The remaining variables are close to isometry.

Deviations from 12 allometric baselines are illustrated in Figure 2. For the giant panda, all variables,

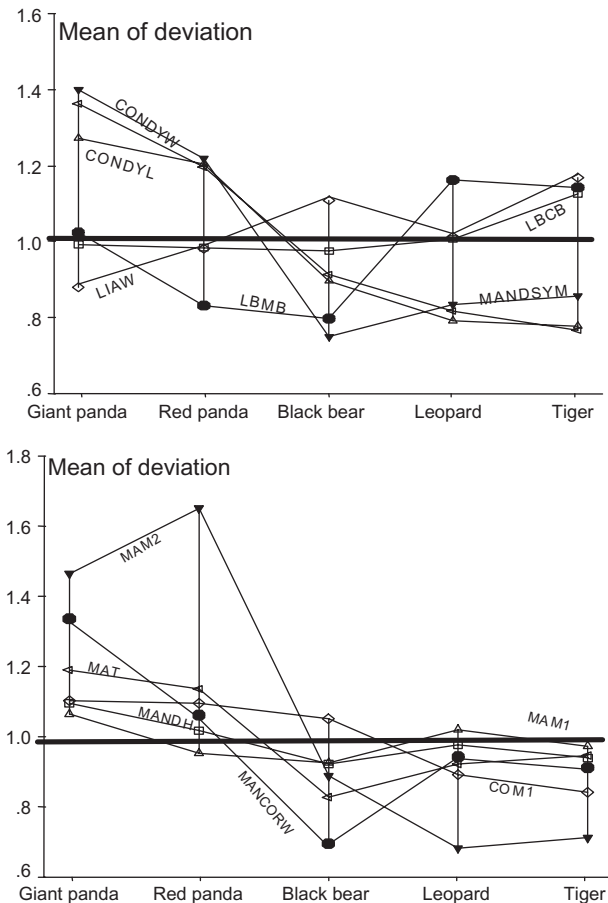


Figure 2. Mandibular deviation comparison between the giant panda and the other Chinese carnivores.

except for LBCB and LIAW, show values that are larger than expected. The variable LBCB is at the expected value, and LIAW displays smaller values than expected. The profile for the red panda is very similar to that of the giant panda, except that the LIAW variable shows a value close to expected, and LBMB and MAM1 display smaller values than expected.

The other carnivores differ from the above, in that most have smaller values than expected. Thus, the black bear has only two variables, LIAW and CONM1, which show larger values than expected. The leopard also has only two variables, LBMB and MAM1, which are larger than expected. Of the remaining variables, LIAW, LBMB, MANDH, and MANCORW have values close to expected, and the rest of the variables have values that are less than expected. The tiger also has values that are less than expected, but LIAW, LBMB, and LBCB are larger than expected, and MAM1, MAT, and MANDH are close to expected.

The results provided by PCA and DFA applied to the deviation-based data are shown in Table 2. The

first two axes of PCA account for 73.22% of the total variations, in which 55.11% and 18.10% are explained by the first and second axes, respectively. The contributions to the first axis of principal component analysis (PC1) from variables are relatively stable, except for LBCB and LBMB that show very low eigenvectors (close to zero), and LIAW that, in contrast to the other variables, displays a negative eigenvector. Four variables, LBCB and LBMB, and CONM1 and MAM2, contrast with each other by showing the largest positive and negative eigenvectors in PC2.

The dispersion of the specimens along the first two axes of the PCA is illustrated in Figure 3. With regard to the first axis, the specimens of the two panda species are located on the right side, whereas the other three species are clustered on the left. The black bear and the red panda are noticeably divided from the other three species along the second axis. The giant panda also shows a clear separation from the other species along this second axis. Three groups of specimens are evident in these first two axes: giant and red pandas, black bears, and leopards and tigers.

The first two functions of DFA account for 98.4% of the total variance. The first axis of discriminant functional analysis (DF1) and DF2 explain 65.8% and 32.6%, respectively. Three variables, CONM1, MAM2, and MANCORW, display the largest coefficients in the first function, which is in contrast with LBMB that shows the largest negative value. Two variables, LBMB and MACORW, which show the largest positive values in the second function, contrast with CONM1 that displays the largest negative coefficient.

The separations of the species along the first two axes of DFA are illustrated in Figure 4. The two pandas form a group significantly separated from the other species on the right-hand side of the first axis. Another two groups are also evident: one consisting of the black bear alone, and the other consisting of the leopard and tiger combined. The second axis separates the black bear and the red panda species, each separately, from the other species. Individuals of the leopard, tiger, and giant panda species overlap extensively along the same function. Thus, the first two axes together separate three clusters: the two panda species, the black bear, and the leopard and the tiger.

DISCUSSION

Our results indicated a clear separation between the mandibles of the giant panda and other Chinese carnivores, and also clearly showed three groups of dispersal profiles from multivariate, PCA, and DFA analysis: (1) the two panda species, the herbivorous carnivores; (2) the black bear, the omnivorous carnivore; and (3) the tiger and leopard, the hypercarnivores (Figs 3, 4). The separation of these species

Table 2. Eigenvalues and eigenvectors of the first two axes in principal components analysis (PCA) and discriminant functional analysis (DFA)

	PC1	PC2	DF1	DF2
Eigenvalues	6.61	2.17	52.70	26.12
Percentage	55.11	18.10	65.80	32.60
Cumulative Percentage	55.11	73.22	65.80	98.40
Eigenvector and Canonical coefficient				
CONDYLL	0.971	-0.313	0.218	0.253
CONDYLW	0.963	0.006	0.565	0.444
CONM1	0.720	-0.407	0.614	-0.742
LBCB	0.002	0.640	-0.251	-0.187
LBMB	0.001	0.893	-0.627	0.895
LIAW	-0.661	0.003	-0.450	-0.358
MAM1	0.626	0.543	-0.027	0.095
MAM2	0.802	-0.420	0.663	-0.330
MANCORW	0.874	0.310	0.667	0.585
MANDH	0.769	0.339	-0.321	-0.139
MANDSYM	0.894	-0.009	0.265	-0.275
MAT	0.883	0.008	-0.362	0.051

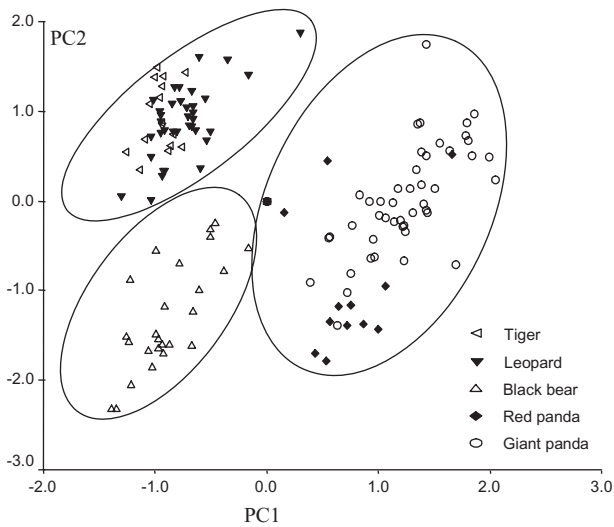


Figure 3. Separations of individuals of the giant panda and the other Chinese carnivores along the first two axes of principal components analysis (PCA) based on deviations.

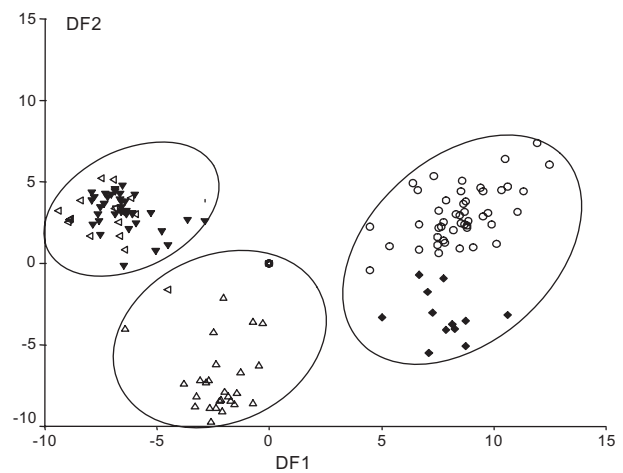


Figure 4. Separations of species of giant panda and the other Chinese carnivores along the first two axes of discriminant functional analysis (DFA) based on deviations with individual specimens plotted. See Figure 3 for the symbols key.

results from dietary preferences and functional adaptation, and not from phylogeny, because the giant pandas and red pandas group together, as these are in different families (Bininda-Emonds, 2004), and so do the tiger and leopards, but the black bears do not group with the giant pandas as these are both ursids.

Thus, the close morphometric relationship, between giant and red pandas, may relate to functional convergences based upon a degree of dietary similarity. Both are less efficient bamboo feeders with low digest-

ibility of dry matter (17–30%) and nutrients (Schaller *et al.*, 1985; Wei *et al.*, 1999b), and show very similar mandibular structures.

Similarities between the two panda species, however, cannot negate their differences. Although both display larger mandibular dimensions than expected, giant pandas show a more strongly developed mandible than red pandas (Fig. 2), and these differences are evident in profiles illustrated by the first and third axes of DFA (Fig. 5). Field studies indicated that the two species have different dietary

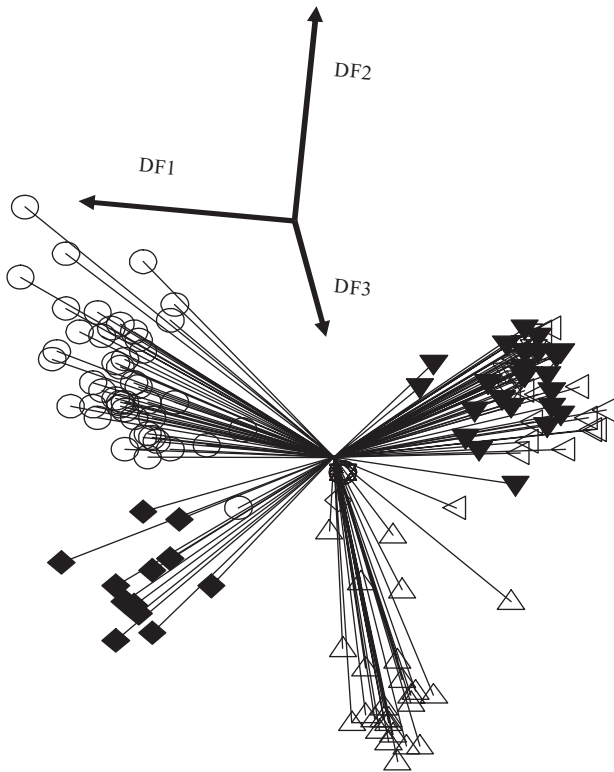


Figure 5. Individual dispersion of the giant panda and the other Chinese carnivores based on deviations radiating from the central point of the first three axes of discriminant functional analysis (DFA). See Figure 3 for the symbols key.

preferences, feeding behaviour, and habitat utilization, although they forage mainly on bamboo and coexist in the same regions (Wei *et al.*, 1999a). The giant pandas mainly feed on bamboo stems, leaves, branches, and shoots (Schaller *et al.*, 1985; Wei *et al.*, 1999a), whereas red pandas only feed on bamboo leaves all year round, shoots in spring, and fruits in summer and autumn (Johnson, Schaller & Hu, 1988; Wei *et al.*, 1999a).

In order to be more certain about the functional adaptation convergence, contributions of variables to similarities and differences among these species should make sense in terms of appropriate biomechanics.

Firstly, when all five species were analysed in the allometric analysis, some variables were either positively or negatively scaled, or were even very close to being isometric (Table 1). Thus, variable contributions such as the strongly developed condyle, both in width and length (CONDYLL and CONDYLW), may indicate that biomechanically the temporomandibular joint bears heavy compression caused by forces formed from different loading arms at different parts of the mandible. This may be especially so for the

longest measure at the symphysis (MANDSYM), which showed the largest positive scale. The greatly enhanced mandibular symphysis and condyle are also strongly related to two other components: the moment arm from the condyle to M_1 (CONM1), an indication of the effective biting force; and the distance from the condyle to the mandibular angle (MAM1), an indication of the long, strong masseter attachment. These may be associated with strong compressive strain deformations at the joint. Strong emphasis on the front and rear parts of the mandible may be associated with specific requirements in the carnivores studied as a whole. Thus, although there some differences exist between species, see below, functional adaptations may relate to specific feeding behaviours, such as use of the front teeth in carnivores for biting, tearing, and compressing prey muscles, and of molar regions in bamboo eaters for breaking down strong fibers in bamboo or other plants.

Secondly, when deviations, mirrored from the baseline formed by all species, were compared, further differences emerge (Fig. 2). The giant panda was uniquely different from the other species, because of its larger mandibular variables (except for incisor length, LIAW), correlated with its dietary preference for bamboo stems (Schaller *et al.*, 1985). Such specific feeding behaviour may have shaped the mandibular structures of giant pandas in order to cope with the specific demands of feeding. For example, the giant panda showed a more developed condyle that could counter loading forces formed in the mandibular corpus (MANDH and MANCORW) and sustain a strong burden from breaking down bamboo stems and chewing hard fibers. The strong compressive forces from such a burden on either side of the mandibular corpus may result in heavy twisting and shearing strains along the front-post axis of the mandibular body. A robust symphysis may help prevent the two sides of the mandible body from separating. The profile of variable contributions for the red panda is very similar to the giant panda, except for the less developed bimolar width (LBMB). This resemblance may relate to similarities in feeding behaviour on bamboo (Schaller *et al.*, 1985; Wei *et al.*, 1999a).

Thirdly, the relationships of other species to pandas may also be important for considerations of function. The black bear differs from the two pandas, and the tiger and leopard, respectively (Fig. 2). Only two variables in the black bear, LIAW and CONM1, display larger values than expected, implying that it has a less developed masticatory apparatus, especially when compared with those of the two pandas. This could be associated with its specific dietary preference. Some field studies indicated that the black bear is an omnivorous carnivore, feeding on leaves, stalks, buds, fruits, acorns, and nuts, and meat from

mammals, birds, and fish (Reid *et al.*, 1991). Fibers taken from these normal plants and the meat from small animals are not as tough as the fibers of bamboo, eaten by pandas, or the muscles of larger animals, eaten by tigers and leopards.

The tiger and leopard are hypercarnivores, preying on animals with a great spectrum of size (Johnson *et al.*, 1993; Biswas & Sankar, 2002; Sankar & Johnsingh, 2002), and also show a quite different mandibular structure (Figs 2–4). The tiger displays larger LIAW, LBCB, and LBMB variables. A much more developed LIAW may be associated with specific incisor usage, from biting and tearing prey muscles, and from the strong stress caused by compressing the upper and lower jaws at the front teeth. Larger LBCB and LBMB imply that the animal has a wider mandible and, correspondingly, a wider masticatory apparatus. This feature may be related to the specific demand of the masticatory apparatus in carnivores. The variables in the leopard are generally similar to those of the tiger, except for LBCB and LIAW, which showed values close to those expected (Fig. 2). With regard to most of the mandibular variables, both displayed less developed mandibles related to their adaptation to carnivorous diets.

In summary, mandibular structures among Chinese carnivores reflect mainly functional adaptation to dietary preferences. Thus, the herbivorous carnivores display more developed mandibles for feeding hard fibers, such as those in bamboo; the omnivorous carnivores show a moderate developed mandibular structure resulting from their omnivorous dietary preference; and the hypercarnivores possess a wider mandible and more developed front teeth, which are supposed to be associated with hunting large-sized prey and the soft fibers of the meat.

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