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甘肃临夏盆地晚中新世鬣狗类群头骨的几何形态测量学及生态形态学分析1)

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在晚新生代大型食肉目动物中，鬣狗科动物地史分布广、种类和数量多，在中国出现于中中新世至更新世晚期的地层中。形态功能学家将鬣狗科的60多个化石种分为似豺、似狼和似灵猫等生态类群，这些生态类群和现生仅存的3个食骨和1个食虫类群形成鲜明的对比。生态形态学是基于生物形态与生态环境的密切关系研究不同物种形态所代表的生态位的一种方法；研究者依靠化石鬣狗类与现生种类牙齿和头骨整体形态的相似度进行了生态形态（ecomorphology）的分类，但尚未对这些已定的生态形态进行过多变量的头骨形状分析。本文拟采用平面几何形态测量学的方法对晚中新世临夏盆地的鬣狗类进行研究，并探讨以头骨形状划分其生态形态类型的可行性。

几何形态测量法是以生物形态的轮廓作为数据的计算方法，虽然目前尚未被国内古生物研究者广泛采用，但自20世纪30年代多变量统计学的理论成熟以来，这一方法的理论基础和软件算法在国外得到迅速发展，至今已成为近代生物学（neontology）和古生物学形态研究领域的一个常用工具。三维几何形态测量分析也因为三维激光扫描仪的普及而变得更简单和直观。然而，化石标本由于埋藏和保存的关系通常会出现变形或残缺不全，使目前几何形态测量方法在古生物学的应用仍主要以平面数据分析为主。平面数据采集的第一步是从与标本某一平面相垂直的角度拍摄数码照片；虽然拍摄平面的选择通常由研究者自定，但一般会选择待研究类群形状变异最具代表性的一面（如，鱼类一般选取侧视）。第二步是形态的数字化，即使用某一种形态测量软件来标出地标点（landmarks；或称界标点、标志点、标点）。地标点的选择对于分析的结果有直接而且重要的影响，一般会选择Bookstein分类中的I型或II型作为地标点的标准。这两种地标点的共同点是可以从解剖学特征上准确地在每一个标本上找到，而无不明确或复现困难的可能性。

数字化后的数据在软件中用数学算法叠加起来（superimposition，或称叠合，重叠），以去除原始图片数据中标本位置、角度及其他与几何形态无关的冗余信息。所有的数字化数据叠加起来后，利用软件计算所有标本之间的几何距离。现在常用的软件中都会以平均

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几何形状作为中心，而且利用类似主成分分析（principal components analysis）的多变量计算来呈现相对扭曲（或称相对反卷）轴（relative warp axis），后者即是可以用来把形态差异视觉化的多变量数据。这些数据可以用平面坐标图来看不同形态的空间分布，也可以用所谓的薄板样条曲线图（thin-plate spline grid）来表示相对形态上的变化。相对扭曲轴所代表的形状数据还经常被拿来与代表几何物体大小的距心值（或称重心距离，centroid size）做回归曲线分析，以便发现种群中某些形态的异速生长模式（allometry）。

本文采用几何形态测量的方法对产自和政地区的鬣狗科 *Hyaenictitherium*, *Ictitherium*, *Adcrocuta* 和旁鬣狗科 *Dinocrocuta* 的材料进行研究，分析了这 4 个属保存完好的头骨标本的侧面形态。与东非大草原现生食肉动物的头骨整体形态分布的比较和分析表明，和政的鼬鬣狗（*Ictitherium*）和鬣型鼬鬣狗（*Hyaenictitherium*）的头骨形状分布介于现生斑鬣狗（*Crocuta crocuta*）、犬科猎狗（*Lycaon pictus*）和金豺（*Canis aureus*）之间，为二者似豺生态形态的解释提供了几何形态测量证据。再者，上述两属化石鬣狗的形状分布与现生斑鬣狗的幼年个体形状重叠，表明现生斑鬣狗头骨的发育机制可能是在鼬鬣狗祖先类型的异速生长规律基础上的持续发育，进而演化出现有的粗壮形态。此外，巨鬣狗（*Dinocrocuta*）和副鬣狗（*Adcrocuta*）的头骨形状与现生的斑鬣狗在几何形态测量空间内有普遍重叠的现象，指示了这些异时出现的种类具有相似的生态形态，因而可能占据相近的生态位。结果还显示巨鬣狗和斑鬣狗的幼年个体形状相近，以及两者从幼年到成年发育的形状变化过程也具有相似的规律。因而，巨鬣狗和斑鬣狗之间的趋同演化不仅表现在成年头骨的粗壮程度上，而且在幼年发育模式中也存在平行演化现象。现生发育学与行为生态学已经证实，相对其他大型食肉动物，现生斑鬣狗发育粗壮头骨形态的机制不是以增速生长，而是以延长发育期来实现的。由此推断，巨鬣狗的发育期有可能和现生鬣狗相当（35 个月），也可能由于具有相对粗壮和巨大的头骨形态，其发育期会延长些。当然，这个新解释仍需要更多的化石数据和发育研究来证实。

关键词：甘肃和政，临夏盆地，晚中新世，鬣狗科，巨鬣狗，生态形态学，几何形态测量学

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GEOMETRIC MORPHOMETRICS ANALYSIS OF CRANIAL SHAPE AMONG LATE MIOCENE HYAENID ECOMORPHOLOGIES IN THE LINXIA BASIN, GANSU, CHINA

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Abstract The carnivoran family Hyaenidae has an evolutionary history stretching ~20 Ma, with high generic diversity in the fossil record and a paucity of living species. Their ecological diversity peaked during the late Miocene, when multiple sympatric species made up a major component of the carnivoran guild in many fossil faunas. Here one group of late Miocene hyaenids and their sister family Percrocutidae, from the Linxia Basin of northwestern China, was studied using geometric morphometrics analysis of cranial shape. The morphology of *Ictitherium* and *Hyaenictitherium* was shown to be intermediate between those of living spotted hyena *Crocuta* and canids *Canis* and *Lycaon*. The larger *Dinocrocuta* and *Adcrocuta* overlap extensively in morphology with extant *Crocuta*. Juvenile *Dinocrocuta* and *Crocuta* are more similar to each other in cranial morphology than either is to adult individuals of their species. Furthermore, adult *Hyaenictitherium* and *Ictitherium* fall within the range of variation of extant juvenile *Crocuta*. These findings indicate that *Crocuta* and *Dinocrocuta* not only converge on robust adult cranial morphology, but may also share similar ontogenetic trajectories; the prolonged period of ontogeny in *Crocuta* required for developing the robust morphology may also be true for *Dinocrocuta*. The ictithere-like morphology of juvenile *Crocuta* suggests that adult cranial shape of the extant hyaenid is obtained *via* continued allometric growth from, and beyond, the ictithere bauplan.

Key words Hezheng, Gansu, Linxia Basin, late Miocene, Hyaenidae, *Dinocrocuta*, ecomorphology, geometric morphometrics

1 Introduction

The Neogene was a time of high taxonomic and ecological diversity for the Hyaenidae, a family of carnivorans that is almost exclusively Old World in their evolutionary history (Werdelin and Solounias, 1991; Turner et al., 2008). Neogene hyaenids are the Eurasian counterparts of the North American canids, having evolved civet-, jackal-, and wolf-like species in absence of competition from the latter during much of the Miocene (Werdelin, 1989, 1996; Wang et al., 1999, 2008). In the late Miocene the diverse ecological morphologies (ecomorphologies) represented by fossil hyaenids resulted in many sympatric species found in mammal faunas across Eurasia. In the late Miocene deposits of China, the hyaenids *Hyaenictitherium wongi*, *H. hyaenoides*, *Ictitherium* spp., and *Adcrocuta* were once all members of the same guild (Deng, 2004; Andersson and Werdelin, 2005). Furthermore, the percrocutid *Dinocrocuta gigantea* filled the role of top predator in earlier late Miocene faunas (Deng and Tseng, 2009). These medium to large carnivorans presumably occupied at least partially distinct ecological niches, in order to have coexisted in those faunas throughout Eurasia.

To test the idea that late Miocene hyaenids and percrocutids occupied at least partially unique parts of a morphological space, the paper analyzes the cranial morphology of relatively complete fossil hyaenid and percrocutid skulls from the late Miocene faunas of Linxia Basin. The Hezheng area of Linxia Basin produces the most abundant fossil faunas anywhere in China, and probably of all Eurasia (Deng, 2005). The mammal faunas stretch from the late Oligocene to the early Pleistocene, and represent multiple fluctuations in climatic and environmental conditions (Deng, 2009). Specimens of *Hyaenictitherium*, *Ictitherium*, *Adcrocuta*, and *Dinocrocuta* from the late Miocene deposits of the Hezheng area were used in this study.

Cranium specimens were analyzed using geometric morphometrics analysis (Rohlf and Marcus, 1993). The technique is a multivariate analysis of shapes, and has been applied in studies of evolutionary trends (Slater and Van Valkenburgh, 2008) and ontogenetic patterns (Tanner et al., 2010) of carnivorans. Complete and undistorted fossil carnivoran skulls are rare in general, and even in the highly fossiliferous Linxia Basin samples are not sufficiently large for stand-alone analysis. Thus, skulls from the modern east African carnivore guild are used to create a morphological space which forms the basis for the analysis and comparison of the fossil specimens.

2 Materials and methods

The basis for cranial shape comparisons of the fossil hyaenids is a morphological space created using cranial shapes of major carnivoran species present in modern east African savannah and woodland communities. A total of 143 individuals of extant carnivorans were used. Thirteen undeformed fossil skulls representing hyaenid taxa found in the late Miocene faunas of the Linxia

Basin (Guonigou, Dashengou, and Yangjiashan faunas of Deng, 2009) were used. No attempt was made to distinguish the sex of the extant specimens, as species were binned into dietary ecomorphological groups and intraspecific variation was not a concern.

Geometric morphometrics analysis is a well-established method of comparing shape differences in organisms using multivariate variables instead of univariate measurements or ratios (Zelditch et al., 2004). A restriction in studies of fossil organisms is the requirement for undistorted and relatively complete specimens. Fossil hyaenid crania are among the most numerous carnivoran cranial material currently known in major collections across the globe; however, complete crania are relatively rare, and for any single fauna not all hyaenid taxa are known by cranial material. The late Miocene deposits of Linxia Basin in northwestern China have produced some of the most spectacular hyaenid and percrocutid fossils in all of Eurasia (Qiu et al., 1988). More importantly, complete skulls are known for all of the late Miocene taxa (*Ictitherium*, *Hyaenictitherium*, *Adcrocuta*, *Dinocrocuta*). Thus, the Linxia material is highly suitable for morphometrics analyses such as the one conducted in this study.

All specimens used were photographed with a Nikon CoolPix 4500 digital camera or an Olympus μ720sw; the skulls were positioned using modeling clay so that their lateral view is parallel to the lens of the camera. Where possible, a grid was placed behind the cranium view so any distortion at the edge of the photos could be detected. Crania placed within the central 30% of the viewing area of the cameras used displayed no distortion around the edge of the specimens, thus cranial morphology was faithfully reproduced by the photos. A scale bar was placed inside the frame of each photo; because carnivore skulls are three-dimensional, the scale was positioned in the mid-sagittal plane of the specimen to approximate the plane at half the total lateral depth of the skull. Twelve anatomical landmarks were used to represent the craniodental shapes, and most of them ($n=8$) are relatively close to the mid-sagittal plane where the scale is placed (Fig. 1). Only Types I and II landmarks were used; these types of landmarks represent joints, sutures, or features of local maxima that could be unambiguously identified across the taxonomic sampling chosen in the study (Bookstein, 1991).

Landmarks were digitized from photographs using TPSDig2.05 (Rohlf, 2006a), which converted points marked on the photographs into Cartesian x,y coordinates. In addition to the twelve anatomical landmarks, two additional landmarks were digitized on the scale bar in each photo representing a distance of 10 mm. The coordinates were then standardized into Procrustes distances using CoordGen6 in the Integrated Morphometrics Package (IMP) (Sheets, 2004), where specimens were aligned on their landmarks, their differences calculated, and absolute size was removed. This operation allowed comparison of the shapes in isolation of their relative sizes, which may independently affect shape via allometry. Furthermore, CoordGen6 also removed the two landmarks on the scale bar after size was calculated, so the remaining data represent only anatomical landmarks. This step is important because regardless of whether the scale bar is in the same position in every photo, digitized landmarks for the purpose of size scaling need to be removed so that only anatomical data remain. Adjusting for scale in this manner has the advantage over resizing and standardizing the photos themselves, because differently-sized specimens all need to be placed within the central 30% of the picture frame to avoid distortion in this particular case, and having a scale bar in the identical position in each photo can be useful for univariate measurements without further resizing the photographs. After scaling and alignment of the digitized landmarks, a relative warp analysis (RWA) was then performed on the set of specimen landmarks in TPSrelw (Rohlf, 2006b). Morphological variation as summarized by RWA can be visualized by plotting the relative warp axes akin to a principal components analysis, and relative differences plotted as thin-plate spline deformation grids (Zelditch et al., 2004). Dietary groups were defined by binning specimens using their known major food item (Nowak, 1999). A list of specimens used is included in the appendix.

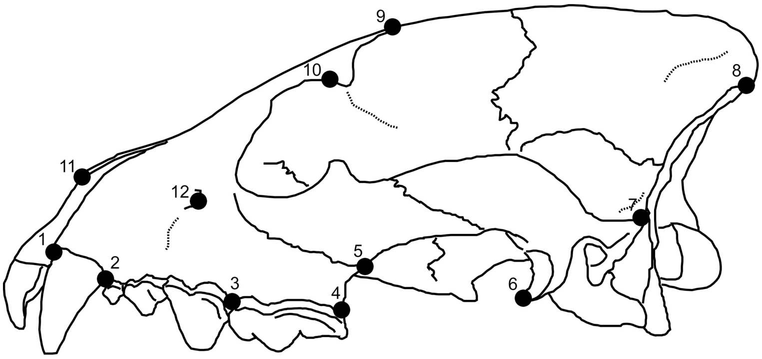

Fig. 1　Anatomical landmarks used in creating a shape morphospace shown in Fig. 2 using geometric morphometrics analysis

1. premaxillary/maxillary/canine junction; 2. maxillary/canine junction on the caudal face of the canine; 3. maxillary/P3/P4 junction; 4. maxillary/P4 junction on the caudal face of the P4; 5. maxillary/jugal junction on the ventral side; 6. ventral tip of post-glenoid process; 7. inflection point of the caudal and ventral faces of the temporal fossa; 8. inflection point of the sagittal/occipital crests; 9. junction between frontal crest and dorsal edge of the cranium; 10. dorsal point of the long axis of the orbit; 11. rostral junction of the nasal/premaxillary; 12. the mid-point of the infraorbital foramen

3　Results

The first three relative warp axes accounted for 75.64% of the total variation (RW1, 33.86%; RW2, 23.62%; RW3, 18.16%). Percentage variance explained dropped to 6.42% on RW4, and all subsequence axes were below 4% of the variance explained. The smaller omnivores (herpestids, viverrids, mustelids) formed a distinct morphological group on the morphospace summarized by RW1 and 2 (Fig. 2); the cranial shape of omnivores is characterized by relatively elongate parietal region, short rostrum region, and dorsoventral compression. Felids and canids also occupy distinct morphological spaces. All felids examined share a similar region of the morphospace, with moderate dorsoventrally deep crania and moderate rostrum length. Among canids, the insectivorous canid *Otocyon* is distinct from other canids, by dorsoventrally compressed braincase and rostrum. The extant bone-cracking *Crocuta* occupies a unique morphospace with caudally set carnassial teeth (premolar 4), and dorsoventrally deep faces and braincase. These *Crocuta* features are shared with *Hyaena*, but the latter develop them to a lesser extent. The insectivorous hyaenid *Proteles* is distinct from the extant bone-cracking hyaenids by having shorter braincase and relatively longer rostrum; these features make *Proteles* morphologically closer to canids and felids.

Within *Crocuta*, specimens are further grouped into two distinct morphospaces, one occupied by immature (with deciduous dentition) and the other by mature individuals. Skull shape, as represented by Relative Warp axis 1 (RW1) scores, is significantly correlated with log centroid size (i.e. geometric size) in the ontogenetic regression of *Crocuta* as calculated by an ANOVA ($r^2 = 0.46$, $F_{1,44} = 37.24$, $p < 0.001$). This significance indicates a large amount of shape variation along RW1 is predicted by the size (i.e. age) of individuals. No such significant trend could be observed for *Dinocrocuta* ($r^2 = 0.04$, $F_{1,6} = 0.18$, $p = 0.69$). However, when all Hezheng hyaenids and percrocutids are analyzed as a group, the regression returned significant correlation between shape variation (RW1) and log centroid size ($r^2 = 0.50$, $F_{1,13} = 12.00$, $p = 0.005$). Among the other taxonomic groups, only canids showed a significant correlation (Table 1). ANOVA of regression analysis of the entire dataset, including both extant and fossil carnivores in the dataset, also returned significant correlation between RW1 skull

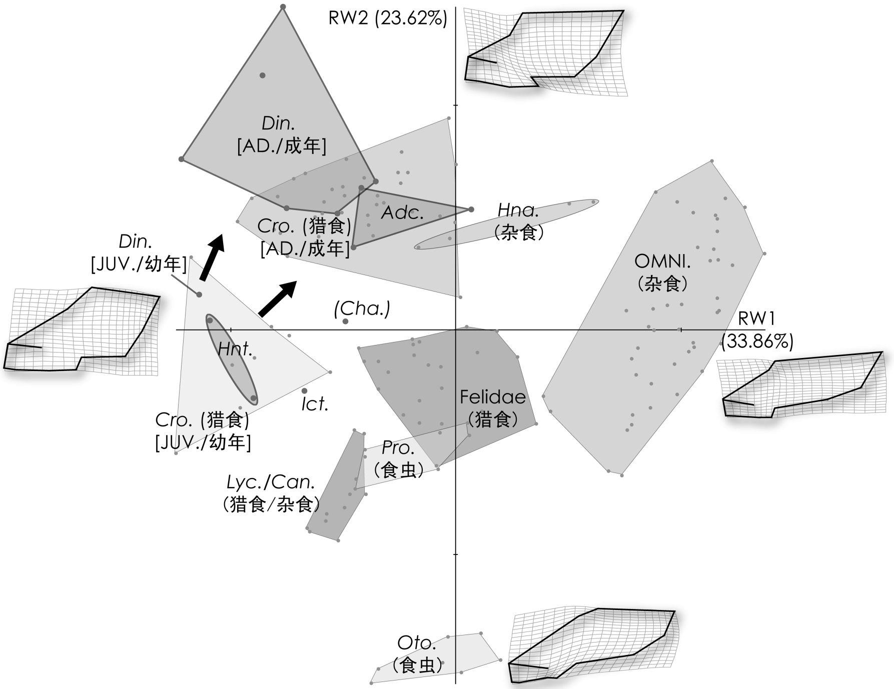

Fig. 2 Morphospace of late Miocene hyaenids and percrocutids of Linxia Basin and modern east African carnivoran guild

X-axis represents relative warp axis 1, and Y relative warp axis 2; thin-plate spline deformation grids show cranial shapes at the extremes of the axes; black arrows indicate general direction of ontogenetic growth of *Dinocrocuta* (left) and *Crocuta* (right) juveniles

Abbreviations: AD. adult; *Adc. Adcrocuta*; *Can. Canis aureus*; *Cha. Chasmaporthetes lunensis*; *Cro. Crocuta crocuta*; *Din. Dinocrocuta gigantea*; *Hna. Hyaena hyaena* and *H. brunnea*; *Hnt. Hyaenictitherium* spp.; *Ict. Ictitherium*; JUV. juvenile; *Lyc. Lycaon pictus*; OMNI. omnivores; *Oto. Otocyon megalotis*; *Pro. Proteles cristatus*

shape and size ($r^2 = 0.50$, $F_{1,155} = 157.34$, $p < 0.001$).

The fossil hyaenids and percrocutids are all "hyena-like" in that they fall within the morphospace of *Crocuta*. *Adcrocuta* fall essentially within the adult *Crocuta* space, whereas *Dinocrocuta* overlaps with *Crocuta* in their cranial shape in both the adult and juvenile/sub-adult specimens. *Hyaenictitherium* fall within the morphospace of juvenile and sub-adult *Crocuta*, with *Ictitherium* close to that distribution as well. The Pliocene *Chasmaporthetes*, long recognized as the most cursorial hyaenid and the only genus to cross Beringia into the New World, is of special interest and thus was included in the analysis. The lone *Chasmaporthetes* specimen falls morphologically somewhere between juvenile and adult *Crocuta*, and close to felids.

Table 1 Analysis of variance of linear regression between RW1 skull shape axis and logarithmic centroid size

Group	n	r^2	F	p
Crocuta only	45	0.46	37.24	<0.001 *
Dinocrocuta only	7	0.04	0.18	0.69
Hezheng specimens	14	0.50	12.00	0.005 *
Small omnivores	45	0.03	1.44	0.24
Felidae	26	0.09	2.37	0.14
Canidae	19	0.29	6.87	0.02 *
Entire dataset	157	0.50	157.34	<0.001 *

* Statistically significant at $p < 0.05$.

4 Discussion

In studying the morphological evolution of carnivorans, phylogeny can play a central role in cranial shape and morphological disparity by limiting potentials for specialization (Werdelin, 1989). Not surprisingly, the small-bodied generalists of the modern east African carnivoran guild are morphologically consistent as an ecomorphology, regardless of their taxonomy. The larger generalists and specialists, however, show clustering within the morphospace by both phylogeny and ecological specialization. All living felids are obligate meat specialists, and their cranial morphology is highly consistent along both phylogenetic origin and ecological specialization. Canids and hyaenids, however, have insectivorous species that group separately from the main morphological types of their respective families. Furthermore, omnivore and meat specialist canids are distinctive in their own morphology, but in the context of the entire carnivoran guild they are rather close to each other. The potential interplay between phylogeny and allometry will be further discussed below.

In terms of the living bone crackers, the availability of both adult and juvenile specimens of *Crocuta* allowed a rough assessment of ontogenetic shape changes, which has been discussed in more depth by Tanner et al. (2010). In the study by Tanner et al. (2010), lateral skull shape in *Crocuta* exhibited significant changes through ontogeny, including lengthening of the zygomatic arches anteroposteriorly and flattening of the postero-dorsal cranium. Furthermore, the mandible appeared to exhibit additional morphological changes even after the cranium had ceased in doing so (Tanner et al., 2010). What was unexpected in this study was the grouping of the sub-adult and adult *Dinocrocuta* with their corresponding age groups in *Crocuta*. However, this result is not surprising by any means; biomechanical convergence between the two genera has been shown by Tseng (2009), and functional analysis of the mandible of *Dinocrocuta* also pointed to the possibility of relatively delayed mandibular growth, as in *Crocuta* (Tseng and Binder, 2010). The general direction of ontogenetic shape changes in the two species is also very similar (Fig. 3); both exhibit a rostrally rotated and deepened braincase, caudal movement of the carnassial tooth, and dorsoventrally deepening rostrum through ontogeny. The parallel shape changes between *Dinocrocuta* and *Crocuta*, and the more pronounced shape change in *Dinocrocuta*, both indicate that *Dinocrocuta* developed the robust bone-cracking morphology along the same trajectory as living *Crocuta*, but simply developed further beyond the degree seen in the modern bone cracker. Furthermore, the development of the robust craniodental morphology in *Crocuta* is not a product of accelerated ontogenetic rates, but instead is manifested in longer developmental periods compared to other carnivorans (Tanner et al., 2010). If *Dinocrocuta* grew in a similar fashion, it would mean that the more pronounced craniodental features necessitated a longer period of growth than living *Crocuta*, or longer than 35 months for skull shape to attain full adult status.

Ictitherium and *Hyaenictitherium* are morphologically closest to canids in the morphospace, whereas the genus *Chasmaporthetes* is closer to felids (Fig. 2). The proximity of these hyaenids to modern carnivorans may speak to the interpretation of the ecomorphology of the former as jackal- and wolf-like, with relatively long and dorsoventrally shallow cranium, and a rostral position of the carnassial tooth relative to more derived hyaenids. However, *Chasmaporthetes* is also intermediate in lateral skull shape between modern *Crocuta* and fossil ictitheres, so its position might only indicate that skull shape alone cannot align this genus with any modern ecomorphological analogs. This is consistent with previous interpretation of *Chasmaporthetes* as a more hypercarnivorous (but still capable of bone-cracking), cursorial hunter than *Crocuta*, a combination of traits not seen in modern carnivores, based on assessment of the post-cranial skeleton (Berta, 1981).

Even though the small sample sizes of fossil hyaenid species prevent an assessment of the

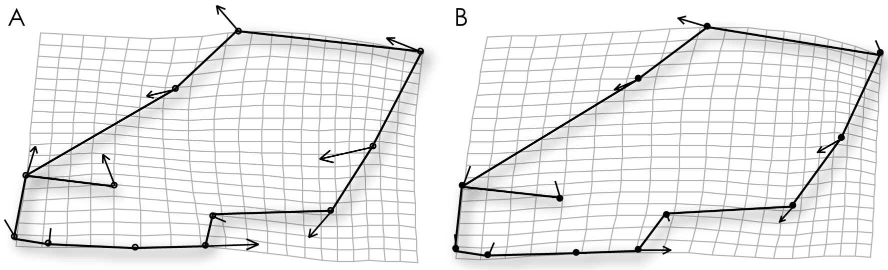

Fig. 3 Thin-plate spline deformation grids of ontogenetic cranial shape changes in *Dinocrocuta* (A) and *Crocuta* (B)
Note essentially identical but more pronounced growth patterns in *Dinocrocuta* as compared to *Crocuta*

variation ranges of cranial shape, their relative positions on the morphospace serve to reveal potential pathways of macroevlutionary changes in skull shape. The shape changes from *Ictitherium* to *Hyaenictitherium*, for example, involve little or no changes in the relative sizes or positions of the carnassial (and, by association, no changes in the anterior premolars); the major change was the elevation of the forehead and the shortening of the caudal braincase (Fig. 4A). The same changes occurred from *Hyaenictitherium* to *Chasmaporthetes*; the lack of pronounced changes between the two genera indicates that increases in absolute size and post-cranial adaptations may instead show differentiating features between them (Fig. 4B). From *Hyaenictitherium* to *Adcrocuta/Crocuta* there was dorsoventral deepening of the rostrum, caudal shift of the carnassial as well as increase in absolute size of the tooth, pronounced deepening of the braincase, and rostral doming of the forehead (Fig. 4C). These shape changes are consistent with the features of the modern bone cracker, and the same pattern of changes is also observed in the ontogeny of *Crocuta*. The ontogeny of the cranium in *Crocuta* may thus be an allometric extension of the evolutionary changes that occurred from the non-specialized *Ictitherium* and *Hyaenictitherium* to the specialized hyaenines *Crocuta* and *Adcrocuta*. It is thus possible that underlying mechanism of the evolution of cranial robusticity involved simply continued growth; more fossil specimens and ontogenetic sequences are needed to further test this hypothesis.

Significant correlation between skull shape along RW1 and skull size is not restricted only to the *Crocuta* ontogenetic series and its corresponding pattern in successive fossil hyaenid genera, but is also true for the canids and the dataset as a whole. Admittedly, the dataset is heavily biased towards a large sample of *Crocuta* specimens, so the significance could be attributed to that species alone (Table 1). Otherwise, an allometric signal among the different African carnivores and the fossil hyaenids and percrocutids at Hezheng, along with the separation of ecomorphologies as taxonomic groups in the morphospace, both indicate a potential influence of phylogeny on ecomorphology (Fig. 2). The smaller carnivores in the generalist category tend to overlap more extensively across different carnivoran families, indicating convergences in cranial shape among unrelated species (Fig. 2; Appendix 1). However, the larger carnivores (felids, canids, hyaenids, and percrocutids) are rather distinct and consistent in their cranial shape, with the exception of insectivorous forms in the Hyaenidae (*Proteles*) and Canidae (*Otocyon*). This observation agrees with previous findings that demonstrate a reduction in morphological disparity in specialized carnivoran clades, which also tend to exhibit larger body sizes (Holliday and Steppan, 2004; Van Valkenburgh et al., 2004). The availability of evolutionary pathways for morphological innovation may be reduced in those specialized clades, and this could be a contributing factor to similar evolutionary and ontogenetic morphological changes observed between *Crocuta* ontogeny and hyaenid evolution from ictitheres to hyaenines.

Based on the skull shape changes summarized by the analysis, more general criteria for diag-

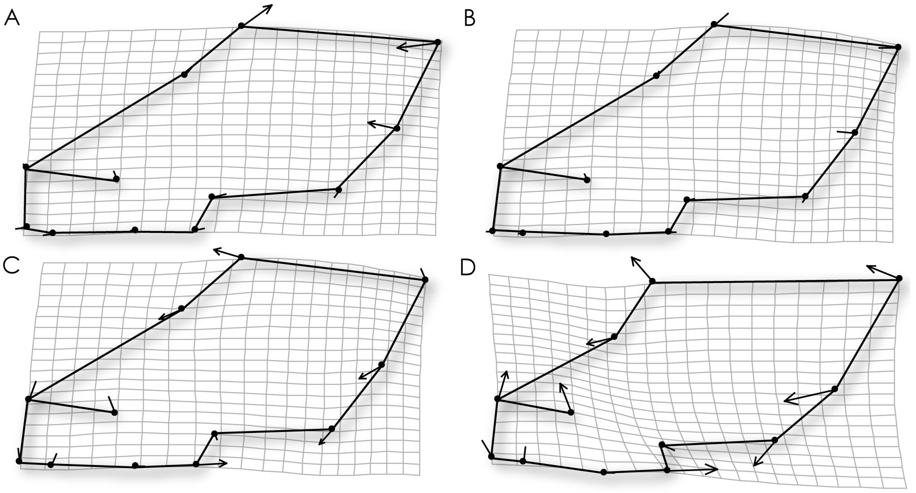

Fig. 4　Thin-plate spline grids showing cranial shape changes in the evolutionary sequence of fossil hyaenids and percrocutids

A. *Ictitherium* to *Hyaenictitherium*; B. *Hyaenictitherium* to *Chasmaporthetes*; C. *Hyaenictitherium* to *Adcrocuta/Crocuta*; D. cranial shape differences between the convergent *Crocuta* and *Dinocrocuta*

nostic differences among genera may be derived from analysis of additional hyaenid specimens. For example, the cranial region in *Hyaenictitherium* tends to be deeper at the frontal and shorter caudally than *Ictitherium*; however, the former shows little shape difference compared to *Chasmaporthetes* (Fig. 4A–B). Taken that many earlier occurrences of *Chasmaporthetes* overlap with the largest of the *Hyaenictitherium* in absolute size, taxonomic differences in the skull may instead be concentrated in dental morphology, the development of more slender premolars, and reduction of posterior molars in *Chasmaporthetes*. The lineage leading from *Hyaenictitherium* to *Adcrocuta*, however, showed pronounced deepening of the entire skull, the posterior position of the carnassial relative to the face, and the rostral thickening of the frontal; these characteristics, along with the increasing robustness of the teeth in the hyaenine lineage (e. g. *Palinhyaena*; Qiu et al., 1979) are quite diagnostic of species in the different genera. These different patterns of change suggest that the major evolutionary stages in hyaenid evolution may be modular in nature, with certain components of the skull evolving at times, and of the dentition in others (Goswami, 2006). Again, a more comprehensive analysis of hyaenid representatives in Eurasia will demonstrate the usefulness of these characters in distinguishing major lineages in the family.

The evolutionary history of percrocutids is poorly known compared to hyaenids. Uncertainties regarding the interrelationships of various percrocutid species in Eurasia and Africa prevent an assessment of the extent to which cranial shape and growth trajectories are symplesiomorphic for the two families, which may be closely related (Werdelin and Solounias, 1991). The occurrence of isolated teeth attributed to *Percrocuta* from the Linxia Basin indicates that percrocutids may have been more diverse during the Miocene than can be appreciated from the current analysis of *Dinocrocuta* only. Percrocutid species appeared to have attained larger and more robust craniodental morphology earlier in geologic time compared to true hyaenids, and the contemporaneous and sympatric occurrences of fossil species from the two families is curious from the standpoint of the skull morphospace; hyaenids became highly abundant and diverse at the end of the Miocene, at a time when percrocutids already occupied a bone-cracker ecomorphological role in the carnivoran guild. Unlike the more straight-forward *in situ* evolution of bone-cracking canids in North America, the interactions between sympatric bone-cracking ecomorphologies in the Old World, and assessment of whether the replacement of percrocutids by hyaenids was passive or active, must await both more detailed records of occurrences as well as more comprehensive studies of percrocutid taxonomy.

Lastly, the large size of *Dinocrocuta* and its cranial robusticity appear to involve continued growth from the morphology represented by *Crocuta* (Fig. 4D). The parallel ontogenetic trajectories between *Dinocrocuta* and *Crocuta* support this interpretation. If so, evolution of the bone-cracking ecomorphology in hyaenids and percrocutids is not only convergent on the final adult morphology, but is parallel in their developmental shape changes as well. As discussed above, this interpretation begs further research into the potential availability (or lack thereof) of different evolutionary and ontogenetic pathways to evolving a specialized ecomorphology such as the bone-cracking carnivoran. Recent studies on the skull biomechanics of the transitional fossil hyaenine *Ikelohyaena abronia* from South Africa using three-dimensional finite element analysis show that whereas skull stress distribution in the stem hyaenine already attained a modern state characteristic of extant hyaenines, bite force and overall functionality of the skull have yet to become highly specialized as in *Crocuta* (Z. J. Tseng and D. Stynder, in preparation). Thus, for the case of hyaenids, cranial shape changes may have preceded increase in body size and skull robustness. Whereas shape changes in localized regions of the cranium (e. g. frontal dome) may require differential growth among the skull bones, the increase in overall skull size and robustness could have proceeded by simply extending the general growth period as demonstrated by modern *Crocuta*. Studies on other convergent lineages such as the borophagine canids of North America could provide more evidence in this regard (Wang et al., 1999).

5 Conclusion

Fossil hyaenids and percrocutids from the late Miocene mammal faunas of the Linxia Basin in northwestern China were analyzed using geometric morphometrics. Comparison of fossil hyaenid and percrocutid cranial shapes within the modern east African carnivoran guild morphospace revealed that the various hyaenid/percrocutid ecomorphologies do not converge upon their modern canid and felid analogs in cranial shape, but instead was clustered within a hyaenid shape space. Evolutionary shape changes across a sequence of hyaenid genera showed a consistent progression of deepening of the braincase and doming of the forehead. The evolutionary cranial shape changes matched ontogenetic shape changes in *Crocuta*, and may indicate a prolonged growth period along the same trajectories as a mechanism in evolving the modern bone-cracking ecomorphology. Furthermore, *Dinocrocuta* and *Crocuta* exhibit parallel ontogenetic shape changes, and indicate that a similar growth pattern of the skull underlies the convergently evolved cranial robusticity in both genera. Additional studies of other bone-cracking lineages such as borophagine canids will provide additional testing for the ideas proposed here.

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Appendix 1 List of specimens used in the geometric morphometrics analysis, with dietary designations in parentheses

LACM. Natural History Museum of Los Angeles County, California; MVZ. Museum of Vertebrate Zoology, University of California

Canidae
Canis aureus (generalist):
LACM14479,52230,56747,56748,70167,70168,70169,70170
Lycaon pictus (meat specialist):
LACM30587,30588,51145,72188
Otocyon megalotis (insectivore):
LACM41790,41792,41793,59645,60618,62843,62844

Felidae (meat specialist)
Acinonyx jubatus: LACM30788,51559
Caracal caracal: LACM42383
Felis silvestris:
LACM14478,14480,41785,41786,41787,41788,45759
Panthera leo:
LACM30786,31182,51294,51296,51297,51553,51567,54393,M567
Panthera pardus:
LACM438,648,30787,31068,51283,51560,54508

Herpestidae (generalist)
Atilax paludinosus:
LACM45746,53750,53751,53753,53754
Bdeogale crassicauda:
LACM42940,42941,42942,56749,56750
Herpestes sanguineus:
LACM36687,40134,45752,45753,53748,53749,56752,56753
Ichneumia albicauda: LACM40136,40137

Hyaenidae
Crocuta crocuta (meat/bone specialist):
LACM30655, MVZ124188, 124259, 165159, 165160, 165161, 165162, 165163, 165165, 165167, 165168, 165169, 165170, 165171, 165172, 165173, 165174, 165175, 165176, 165177, 165179, 165180, 165181, 165182, 173733, 173734, 173736, 173737, 173738, 173739, 173740, 173743, 173751, 175759, 175762, 173763, 173764, 173768, 173771, 173772, 173773, 175801,184088,184089
Hyaena hyaena: LACM31264
Hyaena brunnea: MVZ117842
Proteles cristatus (insectivore): MVZ117841,118478,118479

Mustelidae (generalist)
Ictonyx sp.: LACM42376,56703,56705
Mellivora capensis: LACM30135

Nandiniidae (generalist)
Nandinia binotata: LACM53741,53742,53743,53744,53745

Viverridae (generalist)
Civettictis civetta: LACM42943,53733,53734,71360
Genetta maculata: LACM36692,36695,42935,42936,42937,42938,42939
Genetta rubiginosa: LACM36693,36694,40153,40154,45750

Appendix 2 List of fossil specimens used in the study

HMV. Hezheng Paleozoology Museum, Gansu, China; IVPP. Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MNCN. Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain

Adcrocuta eximia: HMV–1435, 1772, 1773
Chasmaporthetes lunensis: MNCN-67100
Dinocrocuta gigantea: IVPP V 15649, HMV-1279, 1280, 1281, 1282, 1770, 1771
Hyaenictitherium spp.: HMV-0169, 0550
Ictitherium sp.: HMV-0163