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Author(s): Zhijie Jack Tseng , Qiang Li , and Xiaoming Wang

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A NEW CURSORIAL HYENA FROM TIBET, AND ANALYSIS OF BIOSTRATIGRAPHY, PALEOZOOGEOGRAPHY, AND DENTAL MORPHOLOGY OF *CHASMAPORTHETES* (MAMMALIA, CARNIVORA)

ZHIJIE JACK TSENG,^{*,1,2,†} QIANG LI,³ and XIAOMING WANG^{1,2,3}

¹Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A., jtseng@amnh.org;

²Integrative and Evolutionary Biology Program, Department of Biological Sciences, University of Southern California, Los Angeles, California 90089, U.S.A.;

³Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

ABSTRACT—Recent field work in the late Cenozoic Zanda Basin in southwestern Tibetan Plateau has provided new fossil evidence of vertebrate faunas spanning the late Miocene to Pleistocene, which represents new occurrences hitherto unknown in that region of Asia. In this paper we describe a new species of the cursorial hyaenid *Chasmaporthetes*, *C. gangsriensis*, sp. nov., from the Zanda Basin. *Chasmaporthetes gangsriensis* is smaller than other Plio-Pleistocene Eurasian records of the genus, and retains relatively wide premolars that are underdifferentiated in size. The m1 talonid has a trenchant hypoconid typical of *Chasmaporthetes*, but with a trigonid length-to-width ratio lower than all specimens referred to the genus. Metatarsal and phalangeal elements referred to *C. gangsriensis* are long and gracile, indicating cursorial abilities typical of *Chasmaporthetes*. With an age of early Pliocene (4.89–4.08 Ma), *C. gangsriensis* is morphologically the most basal Pliocene *Chasmaporthetes* in China, and is consistent with the ‘out of Tibet’ hypothesis for some Pleistocene megafauna. An analysis of nasal bone morphology revealed large intraspecific variation in extant spotted hyenas, showing that it is not a reliable criterion for species diagnosis in *Chasmaporthetes*. An evaluation of the biostratigraphic relationships among Asian and North American occurrences of *Chasmaporthetes* indicates that the genus first dispersed into the New World during the early Blancan North American land mammal age (NALMA) with likely ancestry close to the heterogeneous sample of *C. lunensis* in Eurasia. The possibility of a second dispersal is indicated by a mixed sample of specimens with significantly smaller p4/m1 length ratio than other *Chasmaporthetes*.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Neogene fossil mammal localities are relatively abundant in Eurasia, and offer valuable insights into the paleozoogeography of both extant and extinct genera (NOW database, 2010). Dispersal patterns among European and Asian Neogene mammals appear to be associated to a certain degree with Tibetan Plateau uplift (Fortelius et al., 2003; Qiu and Li, 2004), and the extensive area occupied by the plateau itself offers the potential to further test environmental associations of mammal evolution (Wang et al., 2007). Furthermore, dispersals of Eurasian carnivoran genera to the New World have occurred via repetitive filter-bridge-type events, making the understanding of East Asian mammal paleozoogeography important for interpreting selective dispersal (Qiu, 2003). Here we describe the first occurrence of the cursorial hyena *Chasmaporthetes* on the Tibetan Plateau, partially filling in a gap in the paleozoogeographic distribution of this most widespread genus of Hyaenidae. In addition, we summarize available biostratigraphic and morphometric information regarding Eurasian species of *Chasmaporthetes*, in order to gain a better understanding of their character evolution during the late Neogene.

Geologic Setting

The new fossil materials were discovered in Zanda Basin in Tibet Autonomous Region, China. Zanda Basin is a late Cenozoic (late Miocene through Pleistocene) sedimentary basin located just north of the Himalaya Range in western Tibet (Fig. 1). The basin is bound by the South Tibetan Detachment System to the southwest and the Indus Suture to the northeast (Saylor, 2008; Wang et al., 2008). The axis of the basin is parallel to the general arc of the Himalaya Range. There is a ~800 m sequence of fluvial, lacustrine, eolian, and alluvial fan deposits in the Zanda Basin. The lowest 200 m of the sequence is composed of cross-bedded sands and conglomerates. The middle 250 m is composed of upward coarsening lacustrine progradational parasequences. Upward coarsening continues in the top 350 m, with the profundal lacustrine (lake center) facies replaced by deltaic or lake margin deposits (Saylor et al., 2010a, 2010b; Deng et al., 2011). The middle section of the Zanda sequence is the most fossiliferous in mammal remains.

Fossil Mammals

A partial palate of *Palaeotragus microdon*, a fossil giraffid, was recovered in the Xiangze (Chinese Pinyin: Xiangzi) Farm area of the Zanda Basin during a Chinese Academy of Sciences expedition in 1976 (Zhang et al., 1981). Subsequently, a nearly complete skull of a hipparionine horse, *Hipparion zandaense*, was collected near the Daba village in the southeastern part of the basin (Li and

*Corresponding author. †Current address: Division of Paleontology, American Museum of Natural History, 200 Central Park West at 79th Street, New York, New York 10024, U.S.A.

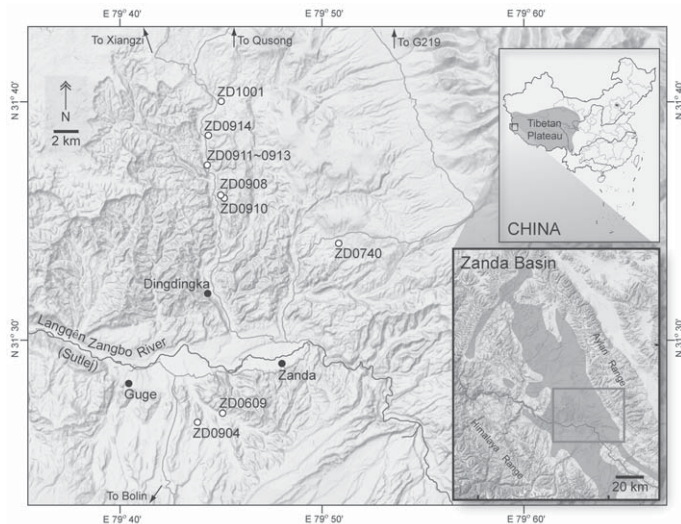


FIGURE 1. Locality map showing key vertebrate fossil localities in Zanda Basin, Ngari Prefecture, Tibetan Autonomous Region, China. Gray lines represent dirt roads. Black circles represent villages and towns.

Li, 1990). Aside from these reports, there were no further significant finds or systematic effort in collecting fossil vertebrates prior to our field trips starting in 2006.

Our collection of fossil mammals in five field seasons (2006–2007, 2009–2010, 2012) allows the establishment of a faunal sequence in the basin for the first time (Wang et al., 2013). These include small-mammal assemblages from IVPP locality ZD0609 and ZD0904 with *Mimomys*, *Apodemus*, *Trischizolagus*, and *Ochotona*; *Aepyosciurus*, *Nannocricetus*, and *Prosiphneus* from IVPP locality ZD1001; the raccoon dog *Nyctereutes* (IVPP locality ZD0624, near Xiangze); *Vulpes*, *Meles*, *Mustela*, and a cougar-sized felid (all from IVPP locality ZD1001); a new woolly rhino (Deng et al., 2011); and a skeleton of *Hipparion zandaense* (Deng et al., 2012). Most localities are within the middle unit in the Zanda sequence. Overall, the fossiliferous middle Zanda sequence yields faunas that are of Pliocene age, although the upper alluvial conglomerates and lower fluvial sandstones range into Pleistocene and Miocene, respectively.

During the 2009 field season, a team led by one of us (Q.L.) discovered skull fragments of a fossil hyaenid while prospecting along the northern trail of Zandagou. Among the materials collected were partial lower jaws, maxillae, and toe bones. Those materials form the basis of this study.

Institutional Abbreviations—**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **PPM**, Panhandle-Plains Historical Museum, Canyon, Texas, U.S.A.; **SAM**, Iziko South African Museum, Cape Town, South Africa.

Anatomical Abbreviations—**l**, length; **m1**, lower first molar; **mtP4**, metastyle of upper P4; **P1–P4**, upper first premolar to fourth premolar, respectively; **p2–p4**, lower second premolar to fourth premolar, respectively; **paP4**, parastyle of upper P4; **trml**, trigonid of m1; **w**, width.

METHODS

Anatomical terms follow those in Miller (1979) and Werdelin and Solounias (1991). Log-ratio diagrams of metric comparisons

were constructed following the method outlined by Simpson (1941). Most of the specimens examined firsthand were North American and Chinese specimens; all other occurrences were studied by photographs or casts, and measurements for those specimens were taken from the relevant published values (see Supplementary Data). All measurements, except for those taken from literature, were made using a Mitutoyo vernier caliper to the nearest 0.2 mm.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

Family HYAENIDAE Gray, 1869

CHASMAPORTHETES Hay, 1921

CHASMAPORTHETES GANGSRIENSIS, sp. nov.

(Figs. 2–4, 9; Table 1)

Emended Generic Diagnosis—Medium- to large-sized hyaenids; P4 metastyle equal to or longer than paracone, as in hyaenines; p1 and m2 absent, unlike *Hyaenictis* in which m2 is present; cusps on premolars aligned along the long axis of each tooth, anterior accessory cusp not lingually deflected as in derived hyaenines; occlusal outlines of lower premolars oval and slender, not laterally bulbous as in robust hyaenines, and not as narrow as in *Lycyaena*; p4 accessory cusps equal in size and symmetrical, more so than in hyaenines; p4 posterolingual cingulum reduced to a short ridge, as in hyaenines; m1 metaconid absent, unlike *Lycyaena* and less derived hyaenid genera; m1 talonid has a trenchant hypoconid with reduction of other cusps, unlike *Hyaenictitherium*, which has two to three well-developed talonid cusps; metatarsal and phalanges elongate and gracile, distinct from all ictitheres and hyaenines.

Species Diagnosis—Size of p2 relative to p3 larger than all other *Chasmaporthetes*; m1 with trenchant trigonid wider for its length than any other *Chasmaporthetes*; m1 talonid two-cusped, with a central trenchant hypoconid and a greatly reduced entoconid, not three-cusped as in *Lycyaena* and *Hyaenictitherium*, or unicuspid as in more derived *Chasmaporthetes lunensis* and *C. ossifragus*; ventral outline of the posterior ramus ascends sharply towards condyloid process, not with strong ventral deflection as in more derived *C. lunensis* and *C. ossifragus*; lower premolars (p2–p4) are least size-differentiated among all *Chasmaporthetes*.

Etymology—Hay (1921) did not give an etymological origin for his naming of *Chasmaporthetes*, the first hyaenid described in North America; however, based on his original description of the locality from which fossil materials containing *Chasmaporthetes ossifragus* were collected, we interpret the etymology for the genus name to as follows: ‘chasma’, Latin for fissure, chasm, or a hole in the Earth; ‘por’, Spanish for by or for; ‘thētes’, Greek term for the lowest economic class, i.e., workers, in ancient Athens. “The fossils were discovered in a fissure in a Carboniferous limestone. This fissure was entered in the making of some prospect holes by the workmen of the copper company” (Hay, 1921:617). ‘Gangs’, Tibetan for snow; ‘ri’, Tibetan for mountain. Species designation refers to the snow-capped Himalaya and Aylari ranges surrounding the type locality in Zanda Basin.

Locality—IVPP ZD0908, eastside of the Zandagou trail, approximately 14 km northwest of the Zanda County seat (Fig. 1). All materials described herein were collected in a gully off the Zandagou trail, from a terrace above the east face of a steep hill; the disarticulated teeth, cranial, and foot bones were discovered on a weathered surface, scattered within a 2 m by 2 m area. Additional enamel fragments of the same individual were found further down the hill. No other fossils were found in the vicinity.

Material—IVPP V18566.1, left maxillary fragment, preserving LC1 alveolus, broken LP1–3, partial LP4, and partial M1 alveolus; IVPP V18566.2, right maxillary fragments preserving the

rostral opening of the infraorbital foramen and posterior root of LP3, and fragment with broken LP2; IVPP V18566.3, partial left dentary with Lc1–Lp4, broken Lm1, and piece of the left condyloid process; IVPP V18566.4, partial right dentary with Ri1–c1 alveoli, Lp2, broken Lp3, and partial Lp4–m1, with broken coronoid process; IVPP V18567.1, partial right metatarsal II, missing proximal articulation; IVPP V18567.2, proximal phalanx II; IVPP V18567.3, distal phalanx II of the foot.

Age—Lower part of the middle Zanda sequence, early Pliocene; 4.89–4.08 Ma based on paleomagnetic and biostratigraphic correlations in Deng et al. (2011, 2012) and Wang et al. (2013).

Description—The upper and lower jaw materials are assigned to the same individual, based on proximity of discovery (a single location on the outcrop), characters of preservation, and similarity in size and wear stages of the teeth. The two right maxillary fragments are too broken to exhibit any significant amount of morphology, but demonstrate the position of the posterior P3 root immediately below the rostral opening of the infraorbital foramen. The single root was identified as posterior P3 root because the two roots of the upper premolars are distinguished by a large groove that extends along the length of the rostral face of the posterior root and the caudal face of the anterior root, respectively. The other right maxillary fragment preserves only the roots of RP2 and the bone surrounding them; the tooth crown is broken at the base, but a distinct posterior accessory cusp (PAC) is still visible behind the main cusp. The maximum dimensions of RP2 at the crown-root boundary are 17.5 mm (l) × 8.6 mm (w). The left maxillary fragment is more complete, preserved rostrally to the posterior wall of the canine alveolus, caudally to the edge of the maxilla and the base of the jugal part of the zygomatic arch (Fig. 2A). Dorsally, the fragment preserves the infraorbital foramen and the ventral base of the orbit. The suture between the zygomatic bone and the maxilla is oriented vertically at the dorsal border of the orbit, and turns caudally at a sharp angle (~95°) at the position between the orbit border and the infraorbital foramen; the suture then continues diagonally towards the ventrocaudal direction, ending ventral to the base of the zygomatic arch where the fragment ends. On the maxillary bone at the position of the P4 roots, there is a distinct depression or fossa referred to by Qiu et al. (2004) as a ‘thumbprint fossa’ in *Chasmaporthetes*. The medial border between the maxilla

and the zygomatic at the infraorbital margin is parallel with the lateral edge of the zygomatic bone; the rostral region close to the caudal opening of the infraorbital foramen being narrower, with the zygomatic expanding wider caudally past the position of the P4 posterior root.

On the ventral surface, the sulcus for the anterior palatine foramen extends rostrally to the position medial to P1. The RP1 is broken at the root, which is circular in the exposed cross-section. RP2 is broken as well, but what is left of the base of the crown shows an elongate tooth with a distinct, slightly worn PAC, and a weak posterior cingulum extending lingually (but not labially). The anterior half of RP3 is missing entirely, but the posterior half of the tooth is very similar in morphology to RP2, differing only in the larger size of the former. The edges of the posterior P3 are oval, with no lingual protrusion visible. The parastyle and paracone of RP4 are preserved, the metastyle blade is incomplete, and the protocone is broken off. The P4 parastyle is the lowest crowned of the labial cusps, and a small preparastyle is present; the paracone is the highest-crowned cusp, and exhibits slight apical as well as lingual wear at the tip. The metastyle, although broken labially, is complete on the lingual side and is slightly longer than the paracone. There is a strong basal cingulum extending from the posterior edge of the tooth along the lingual face, with the whole occlusal outline of the tooth widening lingually at the position of the paracone, forming a large lingual shelf for the protocone. The anterior border of the shelf is set more posteriorly than the anterolingual edge of the tooth, and the total width of the protocone shelf is equivalent to the width of the parastyle adjacent to it. Overall, the labial P4 cusps are aligned on a linear axis, which is approximately parallel to the sagittal axis. The P2 and P3 are slightly imbricated, with anterior ends tilting towards the midsagittal axis at a shallow angle. The RM1 is at least triple-rooted, with a large labial root and two smaller lingual roots; the lingual and posterior faces of the alveolus are broken, thus the dimension of the tooth cannot be estimated (Fig. 2C).

The lower left dentary preserves all three incisor alveoli, which are stacked, with i2 positioned caudally to the other two incisors (Fig. 3). The canine alveolus is large but incomplete. There is a diastema (~15 mm) between c1 and p2; a rugose sulcus is present, connecting the two teeth, dividing the diastema into a medial and a lateral portion. The mandibular symphysis is oval in shape, rugose, and extends the length of the ramus body from below the diastema to the rostral border of the incisor alveoli (Fig. 3D). Three mental foramina are present: the largest, main foramen is positioned just rostral to the anterior root of p2, halfway down the depth of the body; the second foramen is small, and immediately caudal to the first. The third foramen is smaller still, and located more ventrally on the mandibular body, at the position between p2 and p3. The p2 is an elongate tooth, with a slight posterolingual widening; the anterior accessory cusp (AAC) is very small compared with the large and distinct PAC. No basal cingulum is present. The p3 is broken at the roots, but the occlusal view indicates a proportionally larger tooth than p3. Only labial p4 crown is preserved, showing a symmetrical tooth from lateral view, with equally enlarged AAC and PAC. The m1 crown is partially complete, but all cusps are preserved and allow observation of its dental morphology: the paraconid is longer than the protoconid, but the latter is higher crowned; both cusps are slightly bulbous in profile, and exhibits slight labial wear at the tips. The talonid basin is composed of a single, centrally located hypoconid, which is trenchant and aligned with the trigonid blades. A bulbous posterolingual cingulum projects continuously from the posterior face of the hypoconid, and is differentiated at its lingual end into a small cusp in the position of the entoconid. The overall occlusal shape of the tooth row is convex, with the apex near the posterolabial region of the p2. The masseteric fossa is deep and distinct, and ends rostrally

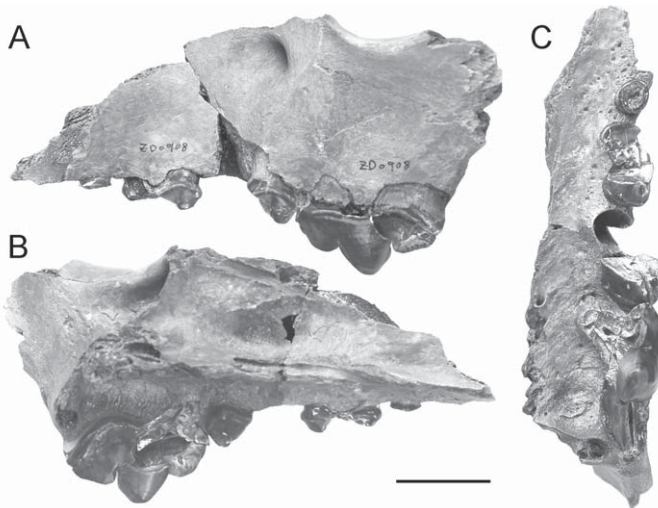


FIGURE 2. IVPP V18566.1, partial left maxilla of *Chasmaporthetes gangriensis*, with partially preserved LP1–P4. **A**, lateral view; **B**, medial view; **C**, occlusal view. Scale bar equals 20 mm.

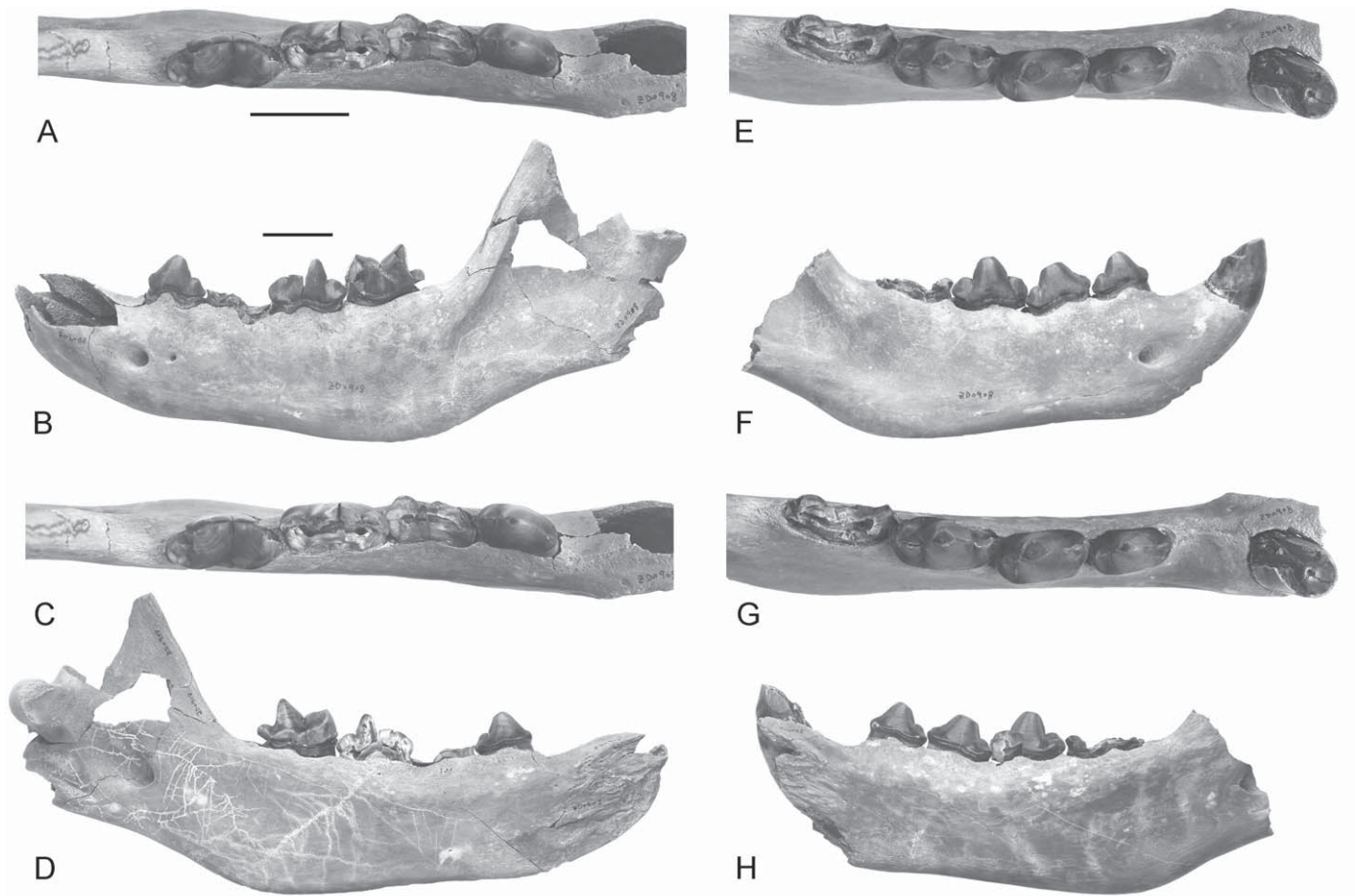


FIGURE 3. IVPP V18566.3–4, left and right dentaries of *Chasmaporthetes gangsriensis*. **A, C**, stereoscopic pair of occlusal view of left dentary; **B**, lateral view of left dentary; **D**, medial view of left dentary; **E, G**, stereoscopic pair of occlusal view of right dentary; **F**, lateral view of right dentary; **H**, medial view of right dentary. Upper scale bar is for stereoscopic pairs, lower scale bar is for lateral and medial views; both equal 20 mm.

just behind the last tooth (m1) in the tooth row. The ascending ramus is broken dorsocaudally just above the condyloid process. The ventral profile of the mandible curves dorsally after the m1 position and ends in a break where the missing angular process would be located. A large mandibular foramen is present on the medial side of the ramus immediately ventral to the ascending part.

The right dentary preserves much of the same morphological characteristics as the left dentary, with the addition of well-preserved p2–4 (Fig. 3E–H). One main difference is the presence of a single, large mental foramen on the right dentary at the same position as the left one, with a very small opening immediately caudal to it. The p2 and p3 are identical in morphology, with the latter being proportionally larger than the former. The preservation of the posterolingual p4 shows a short but strong cingulum leading from the posterior face of the PAC and extending for a short distance (~4.5 mm) lingually. The Rm1 is broken at the roots, but is very similar in overall shape to the left one. An isolated condyloid process is preserved without any bones of the ascending ramus.

The right metatarsal II (mt.II) and phalanges are distinctly hyaenid in characters, with the shape of the metatarsal closely matching those found in other *Chasmaporthetes* (Fig. 4). The proximal end of mt.II is broken off, thus the total length of the bone is unknown. However, the preserved part is already longer than

the corresponding complete element in modern hyaenids, indicating a more cursorial form (Berta, 1981). The medial-plantar surface closer to the proximal end of the shaft has an oval rugosity for the ligament connecting the bone to mt.I (Berta, 1981). The body of the bone has a visible curvature with the head curving medially in dorsal view. There is a deep sesamoid fossa on the dorsal side just proximal to the head, and two shallower sesamoid depressions on the plantar side. The proximal phalanx is elongate, and



FIGURE 4. IVPP V18567.1–3, right metatarsal II, proximal and distal phalanges (from left to right) of *Chasmaporthetes gangsriensis*. **A**, dorsal views; **B**, lateral views; **C**, ventral views. Scale bar equals 20 mm.

TABLE 1. Measurements of *Chasmaporthetes gangsriensis*.

Dimension	IP1	wP1	IP2	wP2	IP3	wP3	IP4	lpaP4	lmtP4	wP4	
Left	7.3*	6.1*	18.0	9.7	20.6*	12.4*	32.1	11.8	12.4*	17.2*	
Right			17.6*	8.7*							
	lc1	wc1	lp2	wp2	lp3	wp3	lp4	wp4	lm1	ltrm1	wm1
Left			17.4	9.4	20.0*	10.3*	22.3	10.3*	23.2	18.7	11.2
Right	16.2	11.5	17.3	9.2	20.0	10.7	22.0	10.6	23.4*		
	Right mt.II			Proximal phalanx			Distal phalanx				
Length	>80.0			34.4			24.8				
Proximal width				12.6			11.3				
Shaft width	9.5			7.4			8.1				
Distal width	13.0			10.8			11.9				

All values are in mm. *Estimated from alveolus dimensions.

tapering at the distal end in lateral view; the distal phalanx has a shallow shaft and wide proximal and distal ends, forming a distinctly saddle-shaped head similar to modern hyaenids. As pointed out by Berta (1981), the proximal articulation of the proximal phalanx in hyaenids has a more angular border than the very rounded border seen in felids.

Comparison

The reduced m1 talonid, reduced posterior cingulum and symmetrical arrangement of AAC and PAC on the p4, and the elongate outline of the cheek teeth preclude *C. gangsriensis* from membership in less derived genera such as *Ictitherium* or *Hyaenictitherium*. Blade-like m1 hypoconid, slender premolars with aligned accessory cusps, and non-imbricated tooth rows also preclude designation to robust hyaenine genera such as *Adcrocuta* or *Pliocrocuta*. This combination of characteristics are consistent with those present in the four genera of the ‘*Chasmaporthetes*’ lineage: *Lycyaena*, *Hyaenictis*, *Lycyaenops*, and *Chasmaporthetes* (Werdelin, 1999). The most distinguishing feature of *C. gangsriensis* from other congeneric species, the relatively wide and short m1, is shared with *Lycyaenops rhomboideae* and *Hyaenictis hendeyi*. However, species of *Lycyaenops* (*L. rhomboideae* and *L. silberbergi*) have rectangularly shaped posterior p2 and p3, unlike the long-oval premolar shape in *C. gangsriensis* (Fig. 3). *Hyaenictis*, as revised by Werdelin et al. (1994), is diagnosed by its presence of m2, which is absent in *C. gangsriensis*; furthermore, *Hyaenictis* has a less derived p4 morphology than that observed in *Chasmaporthetes*, with less reduced posterior cingulum (Werdelin et al., 1994). *Lycyaena*, the most basal genus of the ‘*Chasmaporthetes*’ lineage, has more slender premolars and also the retention of a stronger p4 posterior cingulum than *C. gangsriensis* and all other *Chasmaporthetes*; *Lycyaena* also retains the m1 metaconid, which is absent in *C. gangsriensis*. In combination, *Chasmaporthetes gangsriensis* exhibits m1 shape and morphology that are derived beyond *Lycyaena* but at a similar stage among *Hyaenictis*, *Lycyaenops*, and *Chasmaporthetes*, and at the same time shows the trenchant premolar morphology that allies the new species with other *Chasmaporthetes*. As will be demonstrated below, we interpret *C. gangsriensis* to be a basal form among Plio-Pleistocene *Chasmaporthetes*.

Kurtén and Werdelin (1988) compared the metric dimensions of known *Chasmaporthetes* cheek teeth and showed that the measurements of Asian and European *Chasmaporthetes lunensis* are statistically indistinguishable. In lower p3 dimensions, *C. gangsriensis* is in the center of the distribution bracketed by European and Asian *C. lunensis*. For its given width, *C. gangsriensis*

has a relatively shorter m1 than all *Chasmaporthetes* material examined by Kurtén and Werdelin (1988), regardless of their overall size (Table 1; Supplementary Data, Tables S1, S2). Minimum M1 length approaches values observed for the large Chinese sample of *Hyaenictitherium hyaenoides* from Werdelin (1988). P3 dimensions in *C. gangsriensis* are within the *C. lunensis* distribution towards the lower (smaller) end. P4 length and width in *C. gangsriensis* are in the center of the distribution for *Chasmaporthetes*; however, the relative length of the P4 metastyle in *C. gangsriensis* is at the lower end of the distribution, and closer to values observed in *H. hyaenoides* than other *Chasmaporthetes* specimens. These comparisons show that whereas premolar dimensions are well within the typical ranges observed for *Chasmaporthetes*, the shearing components of the carnassials in *C. gangsriensis* are closer to plesiomorphic conditions observed in *Hyaenictitherium* (Table 1).

Because of the fragmentary nature of the holotype material of *C. gangsriensis*, much of the differentiating cranial characters discussed in depth by Qiu (1987) and Qiu et al. (2004) cannot be evaluated. However, a few morphological features that are preserved prompt some modification of Qiu et al.’s (2004) emended diagnosis of the genus *Chasmaporthetes*: they indicated that the infraorbital foramen in species of *Chasmaporthetes* is located dorsally over the P4 anterior root, or immediately dorsorostral of it; in *C. gangsriensis*, the foramen is situated dorsal of the posterior P3 root, a more plesiomorphic feature in their framework (Qiu et al., 2004). By comparison, the infraorbital foramen is situated between P3 and P4 in the complete *C. lunensis* skull from La Puebla de Valverde (Antón et al., 2006), being more posterior than *C. gangsriensis*; in correspondence, the orbit is also further rostrally placed in *Chasmaporthetes gangsriensis*, and the ventral-most rim of the orbit is just above the P4 paracone, not the P4 metastyle as in the La Puebla de Valverde specimen. The morphology shown in *C. gangsriensis* therefore expands the range of variation in relative P4–infraorbital foramen position in *Chasmaporthetes*. Admittedly, the relative positions of dental and cranial features are influenced by ontogenetic age of the individual specimens, and as many of the known *Chasmaporthetes* specimens show subadult features (e.g., Khomenko, 1932). Therefore, we did not include this character in our amended diagnosis for the genus, pending additional data.

Chasmaporthetes exhibit an elongate P4 metastyle, probably a trait towards hypercarnivory shared among some *Lycyaena* and *Hyaenictis*, being derived from less elongate conditions in icitheres (Kurtén and Werdelin, 1988). Some geologically younger species of *Chasmaporthetes* (e.g., *C. ossifragus*) show the reversed condition and do not have very elongate P4 metastyle (Werdelin, 1988). *Chasmaporthetes gangsriensis* has a P4 metastyle that is

39% of P4 total length; this percentage is low for *Chasmaporthetes*, and resembles *Lycyaena dubia* (39%) and *L. macrostoma* (38%). Given that *C. gangsriensis* is similar in overall size to Chinese *Hyaenictitherium hyaenoides*, which has a metastyle proportion of 39% (Werdelin, 1988), and that other plesiomorphic features such as a residual m1 entoconid are also present, the metastyle length in *C. gangsriensis* is more likely part of a suite of plesiomorphies rather than derived as in *C. ossifragus*.

The ratio between the lengths of p4 and m1 (lp4/lm1) has been used to characterize *Chasmaporthetes* morphotypes in Europe and Asia, and was once thought to separate the longer p4 forms (94–98.7%) in the former region with shorter p4s (85–88%) in the latter (Kurtén and Werdelin, 1988; Sotnikova, 1994). However, review of additional *Chasmaporthetes* material from Asia demonstrated that both morphotypes in fact existed in this region (Sotnikova, 1994). Contrary to previous interpretation of the shorter p4 forms replacing the plesiomorphic longer p4 ones, the latter was not entirely replaced, and both groups were present in the later Pliocene and Pleistocene deposits of Asia. The lp4/lm1 ratio in *C. gangsriensis* is 0.96, well within the range of the 'long' morphotype, again consistent with other plesiomorphic features.

The lateral profile of Rp4 in *Chasmaporthetes gangsriensis* is symmetrical, indicating comparable development of the anterior and posterior accessory cusps. This is consistent with evolutionary trends in the *Lycyaena-Hyaenictis-Chasmaporthetes* lineage, where accessory cusps become well developed in premolars, which became increasingly symmetrical at the expense of the posterior cingulum. Rp4 morphology in *C. gangsriensis* is less derived than the condition in *C. ossifragus*, in which the cingulum has all but disappeared; however, the posterolingual cingulum on the p4 of *C. gangsriensis* is still present, strong, and raised in its center to resemble a small cusp. Compared with p4, relatively less symmetrical occlusal shape in anterior premolars of *C. gangsriensis* further represents the plesiomorphic condition in the clade (Werdelin et al., 1994).

Kurtén and Werdelin (1988) diagnosed *Chasmaporthetes* as having a single cusp on the m1 talonid, and Qiu et al. (2004) suggested that in addition to a centrally positioned hypoconid cusp in the m1 talonid, additional cusps are only rarely present in *Chasmaporthetes*. Sotnikova (1994) demonstrated that the presence of multiple talonid cusps is not as uncommon as other workers have suggested. Our examination of the morphological data below agree with Sotnikova (1994); *Chasmaporthetes gangsriensis* exhibits the plesiomorphic condition of multiple cusps on the m1 talonid, a character shared by *Lycyaena*, *Hyaenictis*, and the outgroup *Hyaenictitherium* (Werdelin and Solounias, 1991). Other Ruscian and earliest Villafranchian occurrences of *Chasmaporthetes* also retain multiple cusps in the m1 talonid in addition to the hypoconid, those additional cusps usually located on the talonid cingulum (Sotnikova, 1994). However, the later Villafranchian *Chasmaporthetes* are supposed to have unicuspid m1 talonids. Kurtén and Werdelin (1988) suggested that the blade-like hypoconid in the m1 talonid basin is a unifying character for all species of *Chasmaporthetes*, being distinct from the conical and more cusp-like hypoconid in the *Crocutea* lineage. This interpretation is still uniformly supported by all available m1 specimens, regardless of the number of additional small cusps in the talonid. The earliest geologic occurrence of *Chasmaporthetes* in Asia, that of *C. exielus* from the late Miocene Qingyang locality of Gansu Province, China, is represented by a palate only; thus, it is unknown whether the trenchant m1 hypoconid is truly an autapomorphy of the genus. *Chasmaporthetes bonisi* from MN13 of the Axios Valley in Greece shows this trenchant condition of the m1 hypoconid, and it also retains a small entoconid (Koufos, 1987; De Bonis and Koufos, 1994). Similarly, the late Miocene (~7.0 Ma) *Chasmaporthetes cf. C. australis* from Toros-Menalla

has a reduced bicuspid talonid (de Bonis et al., 2007). In Africa, the talonid became unicuspid by the Mio-Pliocene, as observed in the Langebaanweg *C. australis* (Hendey, 1978). In Europe, *C. lunensis* from MN16 deposits of Odessa Catacombs still maintain one to two talonid cusps in addition to the hypoconid. In Asia, the early Pliocene *C. lunensis* from Yushe Basin also maintain multiple cusps in the talonid (Qiu, 1987; Qiu et al., 2004). In the Villafranchian of Europe, *C. lunensis* (Kurtén and Werdelin, 1988) tend to have a single-cusped talonid, and this characteristic is shared with contemporaneous materials in Mongolia, Beregovaya, and Shouyang in northern China (Galiano and Frailey, 1977; Sotnikova, 1994). In North America, only the material from Cita Canyon (Blancan IV of Texas) and Inglis IA (Blancan V of Florida) have the m1 preserved, and both have the unicuspid talonid condition (Berta, 1981; Sturton and Christian, 1940). Thus, Sotnikova (1994) is correct that the presence of small cusps in the talonid in addition to the trenchant hypoconid is not a diagnostic difference of species, but a feature that becomes less common in more derived (i.e., geologically younger) occurrences of *Chasmaporthetes*. The lower number of talonid cusps is a more derived condition in later *Chasmaporthetes* from all localities, with the more slender-toothed and trenchant forms losing all but the hypoconid.

The robust premolars in *Pliocrocutea*, *Pachycrocutea*, *Adrocutea*, and *Crocutea* show varying degrees of crown inflation, with development of a basal band of cingulum around the crown; *Chasmaporthetes gangsriensis*, and all other species of *Chasmaporthetes*, do not show such development of the premolars, and furthermore has a straight axis along the main and accessory cusps, unlike the lingually deflected anterior accessory cusp/cingulum in the group of robust hyaenids. In some *Chasmaporthetes* (e.g., *C. borisiaki* from Dermedzhi in Moldavia; *C. lunensis* from La Puebla de Valverde in Spain, Shamar in Mongolia, Schernfeld in Germany; *C. nitidula* from Swartkrans in the Transvaal Caves), the posterolingual cingulum of P2 and P3 is strong, and often supported by a third root. This does not appear to be the case in *C. gangsriensis*, in which the P3 is two-rooted, and the posterolingual cingulum is not greatly expanded lingually. In this regard, *C. gangsriensis* is similar to '*Chasmaporthetes*' *bonisi* from the late Miocene Greek locality of Dytiko (De Bonis and Koufos, 1994) and *C. exielus* from the late Miocene Chinese locality of Qingyang (Kurtén and Werdelin, 1988). One might interpret a lack of a third root as a more basal condition based on the older geologic ages of these specimens, but the late Miocene occurrence of *Chasmaporthetes cf. C. australis* from Toros-Menalla (de Bonis et al., 2007) clearly has a third root, whereas the type specimen of *C. lunensis* from the MN17 Italian locality of Olivola does not (Del Campa, 1914). Furthermore, an expanded posterolingual cingulum and third root, apparently absent in *Hyaenictitherium*, is present in some *Lycyaena* specimens. Even though the distribution of this character is unclear at the present, the presence of a laterally expanded base of the posterior P3 would nevertheless render the tooth more robust, and may be functionally advantageous for durophagy. This character is absent in *C. gangsriensis*.

Sotnikova (1994) diagnosed *Chasmaporthetes* as always having a single mental foramen on each dentary; given the fact that mental foramen count variation in another hyaenid, *Adrocutea eximia*, seems to be the norm rather than the exception (Werdelin and Solounias, 1991), it is not surprising to find mental foramen count to be variable in *Chasmaporthetes*. In *Chasmaporthetes gangsriensis*, the left dentary has a single large mental foramen, whereas the right dentary has a smaller mental foramen posterior to the main one. Another mandible character that supposedly has diagnostic value is angular process morphology. Qiu (1987) demonstrated through comparison of the angular processes of *Chasmaporthetes* specimens, as also noted by Berta (1981), that a dorsoventrally

expanded and ventrally curving angular process is a common feature of *Chasmaporthetes*. The angular process is missing at its tip in the left dentary of *C. gangsriensis* (IVPP V18566.3); even so, the lateral profile of the ventral ramus curves up and towards the posterior end of the jaw, without much indication of ventrocaudal curvature or expansion to the extent seen in examples of *Chasmaporthetes lunensis* and *C. ossifragus* observed by Qiu (1987). An increased ventral deflection of the caudal ramus could be a more derived trait in geologically younger *Chasmaporthetes*, even though neither the Dytiko nor the Toros-Menalla specimens have the angular processes preserved, a slightly younger complete dentary of *C. australis* (SAM PQ-L22204) from Langebaanweg shows an upward curvature of the ventral ramus rostral to the angular process, which has a clear ventral curvature (Hendey, 1978), more closely resembling the shape in *C. gangsriensis*, *Lycyaena*, and more basal *Hyaenictitherium*. Thus, the degree of ramus curvature and deepening at the angular process may be an evolutionarily derived trait within *Chasmaporthetes*, and *C. gangsriensis* retained the plesiomorphic condition of a shallow caudal ramus (Fig. 3).

Log-ratio diagrams were constructed for lower dentition (p2–m1) measurements to show the relative changes in *Chasmaporthetes* from their purported ancestral type: larger icittheres such as *Hyaenictitherium* (Werdelin et al., 1994) (Fig. 5; Supplementary Data, Tables S1, S2). The typical *C. lunensis* shows a variably enlarged (i.e., the tooth can be either relatively longer or wider compared with *Hyaenictitherium*) p2, almost invariably longer p3 and p4, and proportional increase in overall m1 size with a disproportionate elongation of the m1 trigonid (Fig. 5A). From this main *C. lunensis* group, a set of specimens can be distinguished by their relatively longer m1; these specimens make up what Sotnikova (1994) referred to as *C. lunensis kani*. This group of specimens are not only united by their elongate m1, but also by more uniformly enlarged premolars compared with the *Hyaenictitherium* condition (Fig. 5B). They could potentially represent a distinct group, as discussed in more detail in the species classification section below (“How Many *Chasmaporthetes* Species Are in Asia?”).

The African *C. australis* is separated from the *C. lunensis* group by larger overall size, proportionally enlarged p2–3, wider p4, and less elongation of m1 trigonid. These features are plesiomorphic, because only proportional enlargement, but not elongation, of the tooth row is observed in *C. australis* compared with *Hyaenictitherium*. The North American *C. ossifragus* is distinct from both *C. australis* and *C. lunensis*, sharing proportionally enlarged pre-

molars with *C. australis*, but has a very long m1 trigonid without greatly enlarging the dimensions of m1, as in *C. lunensis*. *Chasmaporthetes gangsriensis* exhibits a pattern that is different from all of the groups described above, by having progressively less enlargement from p2 to p4, with slight elongation, and a distinct widening of the m1 (Fig. 5). In contrast to the proportional enlargement of the premolar tooth row seen in *C. australis*, which could be interpreted as a basal late Miocene *Chasmaporthetes* evolving from icittheres mainly in body size, the premolars in *C. gangsriensis* appear to be closer to each other in size, with relatively more enlarged anterior teeth, than other *Chasmaporthetes*. This difference could indicate a generalization of the dentition for a more generalized diet in *C. gangsriensis*, where the anterior premolars would share the task of cracking food items usually done with p3–p4 in the larger bone crackers. Galiano and Frailey (1977) have already observed this phenomenon as a potential convergent trait between some hyaenids and the borophagine canid *Aelurodon*. The widening of the m1 also supports this interpretation, whereby the carnassials play a larger role in crushing by having a more bulbous base like the premolars. In this regard, m1 shape in *C. gangsriensis* approaches that of *Hyaenictis hendeyi* and *Lycyaenops rhomboideae*, which are both considered basal to *Chasmaporthetes* (Werdelin et al., 1994; Werdelin, 1999).

To examine the evolutionary perspective on character and size changes among species of *Chasmaporthetes*, dental measurements and ratios are placed within a stratigraphic context (Fig. 6). All comparative specimens are placed in their estimated geological age of occurrence, using combined data from biostratigraphy and chronology studies (Supplementary Data, Table S3). The ratio between width and length of P3 (wP3/lP3) showed an increasing trend among *C. lunensis*, with the late Miocene *C. australis* and Pliocene *C. ossifragus* having relatively narrower P3. *Chasmaporthetes gangsriensis* has an estimated ratio of 0.60, falling in the middle of the distribution of Ruscinian *C. lunensis* (Fig. 6A). The relative length of the P4 metastyle (% of total P4 length) showed an increasing trend across the stratigraphic sequence, with longer metastyles and overlapping distributions across Pleistocene species (Fig. 6B). *Chasmaporthetes gangsriensis*, again, falls within the mid-range value (0.39) with contemporaneous *C. lunensis*. Raw P4 length shows a mixed pattern, mostly providing information about variation in absolute size. The late Miocene *C. australis* is larger than all geologically younger *Chasmaporthetes*, which showed no obvious trend in P4 length except for an increase in the range of variation in younger samples (Fig. 6C). *Chasmaporthetes gangsriensis* has a shorter P4 than other *Chasmaporthetes* of

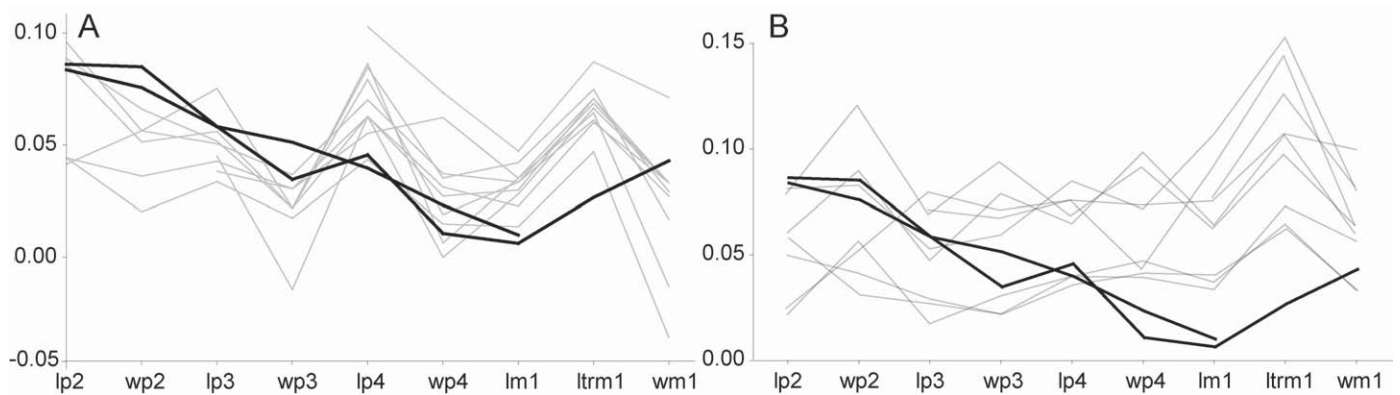


FIGURE 5. Log-ratio diagrams of *C. gangsriensis* (in bold), with data from **A**, *Chasmaporthetes lunensis* samples from Europe and Asia, and **B**, Group ‘B’ *Chasmaporthetes* samples from Asia (both in light gray). Mean measurement values of the lower dentition for *H. hyaenoides* from Werdelin (1988) were used as the standard of comparison. Note the relatively wide width of m1 in *C. gangsriensis*. **Abbreviations:** l, length; ltr, length of the m1 trigonid; m1, first molar; p2–p4, second to fourth lower premolars; w, width. For raw data values, see Supplementary Data, Table S2.

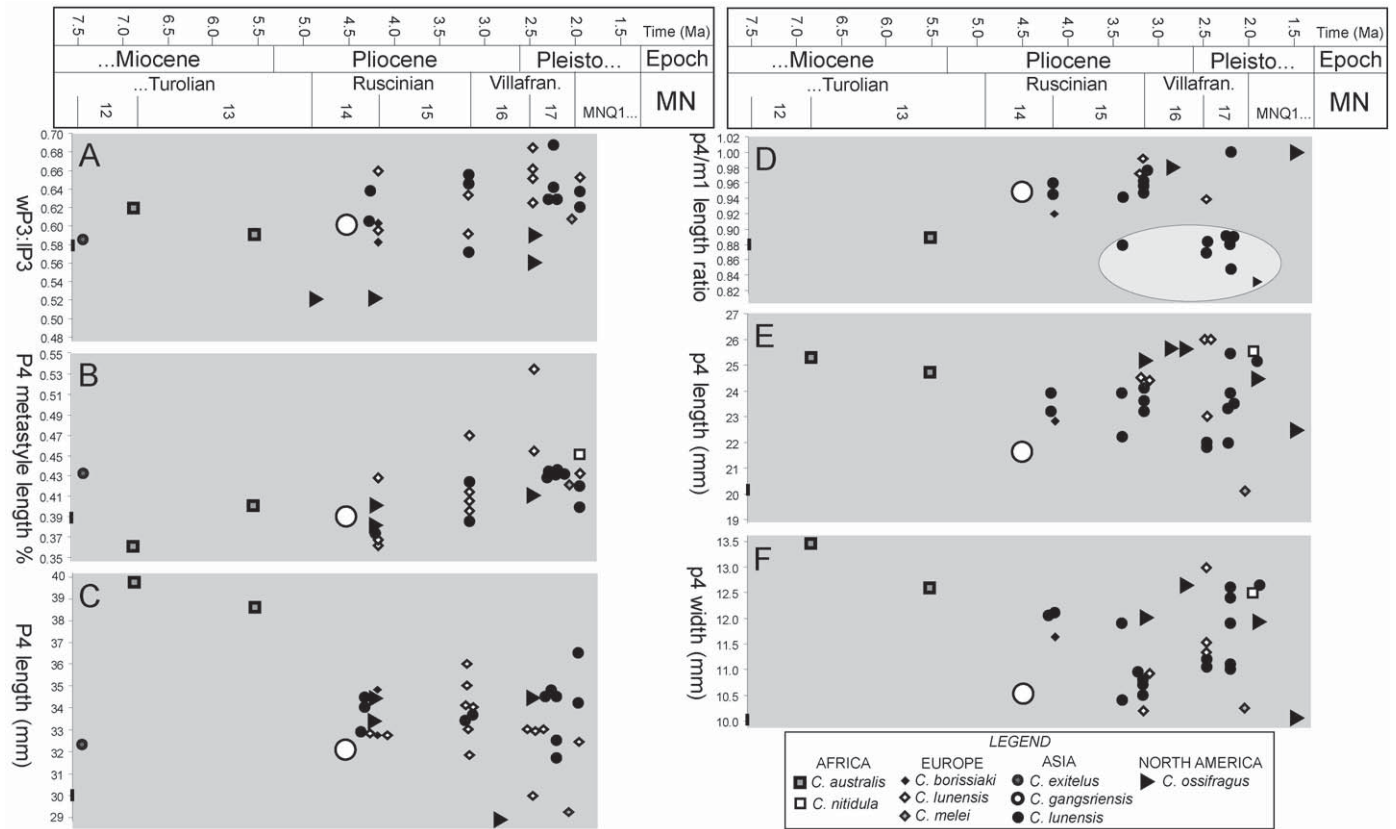


FIGURE 6. Dental measurements and ratios of *Chasmaporthetes* plotted by relative stratigraphic occurrences of the respective specimens. **A**, ratio of P3 width to P3 length; **B**, the length of P4 metastyle as a percentage of total P4 length; **C**, P4 length; **D**, ratio of p4 length to m1 length; **E**, p4 length; **F**, p4 width. Note clustering of Group 'B' *Chasmaporthetes* by low p4/m1 length ratio in part **D**, indicated by light gray oval. Mean values for the less derived hyaenid *Hyaenictitherium hyaenoides*, taken from Werdelin (1988), are indicated on the y-axes by a black bar. For sources of stratigraphic and age data values, see Supplementary Data, Table S3.

Ruscinian-age deposits. The ratio of p4/m1 lengths started low in the late Miocene, and split into two groups in the Plio-Pleistocene: one group formed the clade *C. lunensis*-*C. ossifragus*, and the other group is composed of a mix of Asian and North American specimens with elongate m1, as also distinguished in the log-ratio diagram analysis (Figs. 5, 6D). *Chasmaporthetes gangsriensis* has an average value of 0.95, well within the range of the former clade. Length of the p4 showed no clear trend across the stratigraphic column, except for the obviously smaller island form *C. melel* of the Plio-Pleistocene (Fig. 6E). Width of p4, on the other hand, is more variable within the *C. lunensis* group, and some specimens of *C. lunensis* as well as *C. ossifragus* have values overlapping those of *C. melel*. *Chasmaporthetes gangsriensis* has a short p4 among Ruscinian forms, and is average for p4 width (Fig. 6F).

DISCUSSION

Biostratigraphy and Paleozoogeography

The examination of morphological characters in a stratigraphic framework clarified several issues regarding plesiomorphic and apomorphic characters in the classification and comparison of *Chasmaporthetes*. Here we briefly discuss the current fossil record on which our interpretation of character evolution is based. The oldest identified *Chasmaporthetes* are currently known from the later Miocene deposits of Greece, Chad, and China; the materials

are fragmentary, and thus a thorough comparison of their evolutionary positions is not possible at this point. However, the genus was already widespread at the time of their earliest record around 7 Ma. By the early Pliocene, *Chasmaporthetes* had spread to North America. Ruscinian *Chasmaporthetes* are found from four localities in Europe, and ~13 localities are known in MN16-17 (Fig. 7; Supplementary Data, Table S3). The majority of European specimens have been at one time referred to *C. lunensis*, with two specimens from Dermedzhi (Moldavia) and Perpignan (France), respectively, assigned to *C. borissiaki*, which may be synonymous with the former (Rook et al., 2004). In the Pleistocene, species diversity in Europe increased slightly by the addition of an insular island form *C. melel* on Sardinia (Rook et al., 2004). In Africa, the two known species appear distinct from the European *C. lunensis* (albeit by only a few dental characters) and are separated by a significant temporal gap. This may be explained by a poorer Pliocene fossil mammal record in Africa compared with other time periods, compounded by dating issues (Werdelin, 2010). *Chasmaporthetes australis* is known from the late Miocene and the Mio-Pliocene boundary, whereas *C. nitidula* is known from Villafranchian equivalent deposits. In North America, a single species *C. ossifragus* is known through the entire Blancan North American land mammal age (NALMA), and into the Irvingtonian. In Asia, the taxonomy is not as resolved, partly because the region contains some forms similar to European *C. lunensis* and others to the North American *C. ossifragus* (Fig. 7).

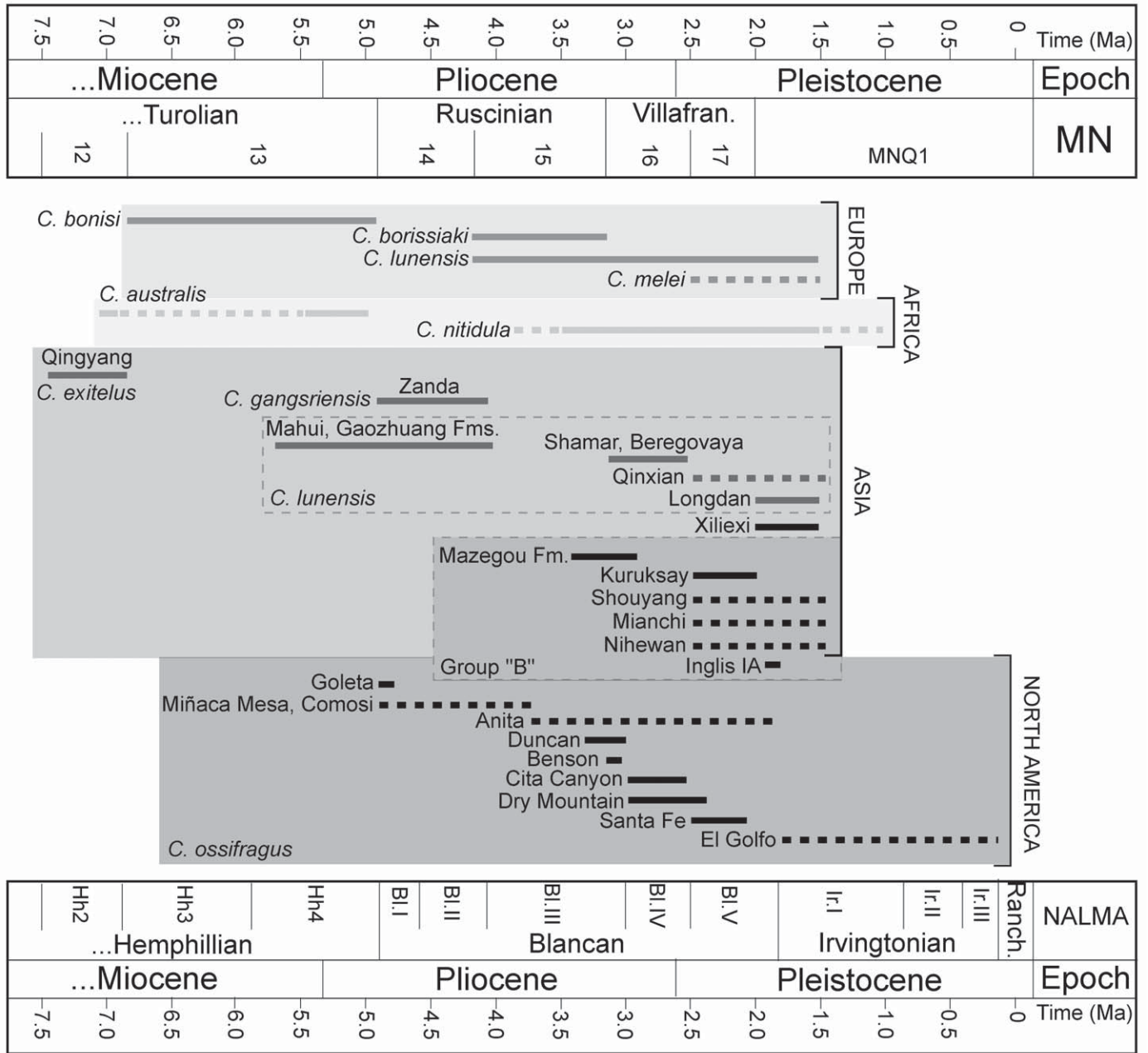


FIGURE 7. Stratigraphic occurrences of *Chasmaporthetes* across the African, Eurasian, and North American continents. Locality names are listed for Asian and North American localities only. For sources of stratigraphic and age data values, see Supplementary Data, Table S3.

At least four forms have been named in Asia, beginning with the late Miocene occurrence of *C. exitelus* from Qingyang, Gansu Province (China). *Chasmaporthetes 'kani'* is known from the Pliocene Yushe Basin, as well as Plio-Pleistocene Shouyang district; forms attributed to *C. 'kani'* was reported from Kuruksay, Tadjikistan (Sotnikova, 1994), but see additional discussion below. *Chasmaporthetes* cf. *C. ossifragus* have been reported from the late Pliocene part of the Yushe Basin, as well as Plio-Pleistocene Mianchi and Nihewan localities. *Chasmaporthetes 'progressus'* was originally described from Qinxian, and has more recently been found in Longdan (Qiu et al., 2004). Lastly, Sotnikova (1994) and

Tseng et al. (2008) referred material from Mongolia/Russia and Huainan (central China) to *C. lunensis*, respectively.

How Many *Chasmaporthetes* Species are in Asia?

Different perceptions of intra- versus interspecific variation are a principal factor in the current state of divergent taxonomic opinions regarding *Chasmaporthetes*. Species have been erected on meager dental criteria, but there has been no consensus on what level of variation is acceptable for species diagnosis, even though tooth measurements can be more variable than cranial

measurements in carnivorans (Dayan et al., 2002). Here we summarize the main differences in taxonomic opinions about Asian *Chasmaporthetes*, and evaluate some of the morphological characteristics used in different interpretations. We concentrate mainly on Asian occurrences of *Chasmaporthetes* because of their relevance to the presently described *C. gangriensis*.

Material formerly identified as *Euryboas* have been reported in Asia from Mongolia (Shamar), Russia (Beregovaya), Kuruksay (Tadjikistan), and the Odessa Catacombs in Ukraine (Sotnikova, 1994). All those occurrences under this genus, as well as those of *Euryboas* in Europe, have been synonymized with *Chasmaporthetes* by Kurtén and Werdelin (1988). Researchers have largely agreed on this assessment (but see Galiano and Frailey, 1977), and thus we will discuss these and other relevant specimens and occurrences under the synonymized genus *Chasmaporthetes*.

North America—Because of potential links between Asian and North American forms, we begin with a discussion of the New World record of *Chasmaporthetes*. The taxonomy of *Chasmaporthetes* species in the New World was most recently summarized by Werdelin and Solounias (1991), who recognized almost all materials from the United States and Mexico as *C. ossifragus*, and the material from Florida to be a new species. Kurtén and Werdelin (1988) first proposed a distinct identity for the Florida material, which was assigned to *C. ossifragus* by Berta (1981), based on a long m1 relative to the p4. Based on our analysis, the p4 dimensions of the lone dentary from Florida (Inglis IA; UF 18088) fall between those of the Irvingtonian El Golfo and the Blancan IV Cita Canyon specimens. Furthermore, even though the p4/m1 length ratio of the Inglis IA dentary is extreme among North American material, intermediate values found in China (Shouyang, Mianchi, Nihewan, and Qinian; Fig. 6) demonstrate that this character is a continuum, and therefore by itself not species diagnostic. However, if the length and width ratios of the lower dentition are compared on a log-ratio diagram, some differences do emerge that separate out the Florida and some Chinese specimens along with what Sotnikova (1994) referred to as *Chasmaporthetes lunensis kani* (Fig. 5A vs. 5B). Specifically, in addition to the elongate m1, the lower premolars do not show the relatively long and narrow condition observed in all other *C. lunensis*; this group (hereon called Group 'B,' as distinct from the main group of *C. lunensis* specimens) is known only from the Villafranchian-equivalent deposits of Asia and North America. Even though the metric profiles of the lower dentition in Group 'B' appear distinct from the main sample of *C. lunensis*, we refrain from naming this group of specimens because of the paucity of additional cranial characters to support a distinct form (Werdelin and Solounias, 1991). However, it is nevertheless interesting to postulate that if the Florida specimens should be shown to share identity with Asian specimens of Group 'B,' the later geologic occurrence of this form in North America would suggest a separate dispersal to the New World from *C. ossifragus*, which are known in the New World by the early Blancan NALMA (Fig. 7). An alternative explanation for this phenomenon would be that they are extreme variants evolving independently in the Old and New Worlds, respectively.

Werdelin and Solounias (1991) maintained species-level distinction between the North American and Eurasian *Chasmaporthetes*, citing relatively narrower P3 and relatively shorter P4 metastyle in North American forms, demonstrated by Kurtén and Werdelin (1988) using metric measurements. Specifically, the early Blancan Mexican occurrences (La Goleta, Miñaca Mesa) of *C. ossifragus* have relatively narrower P3 than contemporaneous Eurasian occurrences, and the Blancan V specimens in Florida (Santa Fe) have relatively narrower P3 compared with MN17 *Chasmaporthetes*, except for the holotype specimen of *C. lunensis* from Olivola (IGF 4377). In our analysis, P4 metastyle lengths (relative to total P4 length) of all *C. ossifragus* fall within the range of vari-

ation observed for Eurasian *Chasmaporthetes* (Fig. 6B). Based on these results, the P3 and P4 characteristics alone do not unambiguously diagnose North American *Chasmaporthetes* from Old World species.

Eurasia—Recently, Qiu et al. (2004) described new material of *Chasmaporthetes* from the Chinese early Pleistocene Longdan locality in Gansu Province; they pointed out that the paucity of cranial material was a factor in the complicated state of species classification in the genus, and that few morphological differences can be discerned among the available dental material. They also downplayed the significance of absolute size in classification, and as our analysis here shows, univariate measurements do not separate out the bulk of *Chasmaporthetes* material except for the large African *C. australis* and the small Sardinian *C. melei* (Fig. 6). Instead, Qiu et al. (2004) emphasized the utility of nasal bone shapes in species classification, differences among which, as we show below, can be more parsimoniously explained by intraspecific or populational variation, rather than a proxy for true species-level differences.

Using a combination of cranial and dental characters, Qiu et al. (2004) concluded that there are at least four species in Eurasia; however, their classification did not include discussion of the late Miocene *C. exitelus* from Qingyang (Gansu Province, China) or *C. bonisi* from Dytiko (Axios Valley, Greece). *Chasmaporthetes kani*, in their concept, is diagnosed by a 'Type I' nasal shape (Fig. 8A, C), lower premolar crown height, weak to lack of anterior accessory cusp (AAC) on p2, and presence of multiple cuspids in addition to hypoconid in the m1 talonid; all but the crown height character have been shown to be highly variable across geographic samples (Sotnikova, 1994; this paper). *Chasmaporthetes progressus* is diagnosed by a 'Type II' nasal shape (Fig. 8A, C), higher crown height, well-developed accessory cusps in premolars, elongate P4 metastyle, and a single-cusped m1 talonid; furthermore, Qiu et al. (2004) suggested that all Asian materials of this species are smaller in size than European ones formerly referred to it. We found no evidence of crown height differences between the available material of *C. progressus* and *C. kani*; in fact, the holotype specimen of *C. kani* (F:AM 99789) is higher-crowned than the holotype of *C. progressus* (IVPP V7279). In addition, Qiu et al.'s (2004) statement about smaller Asian materials is simply not the case when larger samples are considered (Fig. 6C). The variability of premolar accessory cusps and m1 talonid cusp numbers, the latter decreasing with younger geologic ages in *Chasmaporthetes* specimens, coupled with lack of strong evidence for elongate P4 metastyle, bring morphological differences between *C. progressus* and *C. kani* into question.

Chasmaporthetes bielawskyi was diagnosed by Qiu et al. (2004) by its 'Type III' nasal shape (Fig. 8A, C), overall size equal to or smaller than *C. kani*, higher crowned than *C. kani*, with a long P4 metastyle and a single-cusped m1 talonid; based on the variable characters noted above, crown height is, again, the only character that could potentially diagnose this species based on their criteria. Lastly, *C. lunensis* is diagnosed to be a large species with 'Type II' nasal shape that is more elongate than those in *C. progressus*, with high crowned teeth and well-developed AAC. Crown height, again, is the only unconfirmed character that could diagnose this species. Because there is currently no quantitative measure for crown height estimates in hyaenids that take into account the substantial tooth wear some species exhibit, species criteria based on crown height will have to be considered tentative, pending more concrete data. To evaluate the nasal bone types, we examined nasal bone shape in more detail below.

Geometric Morphometrics Analysis of Nasal Shape

Qiu (1987) outlined three types of nasal morphology in *Chasmaporthetes*, which Qiu et al. (2004) reiterated and used as key

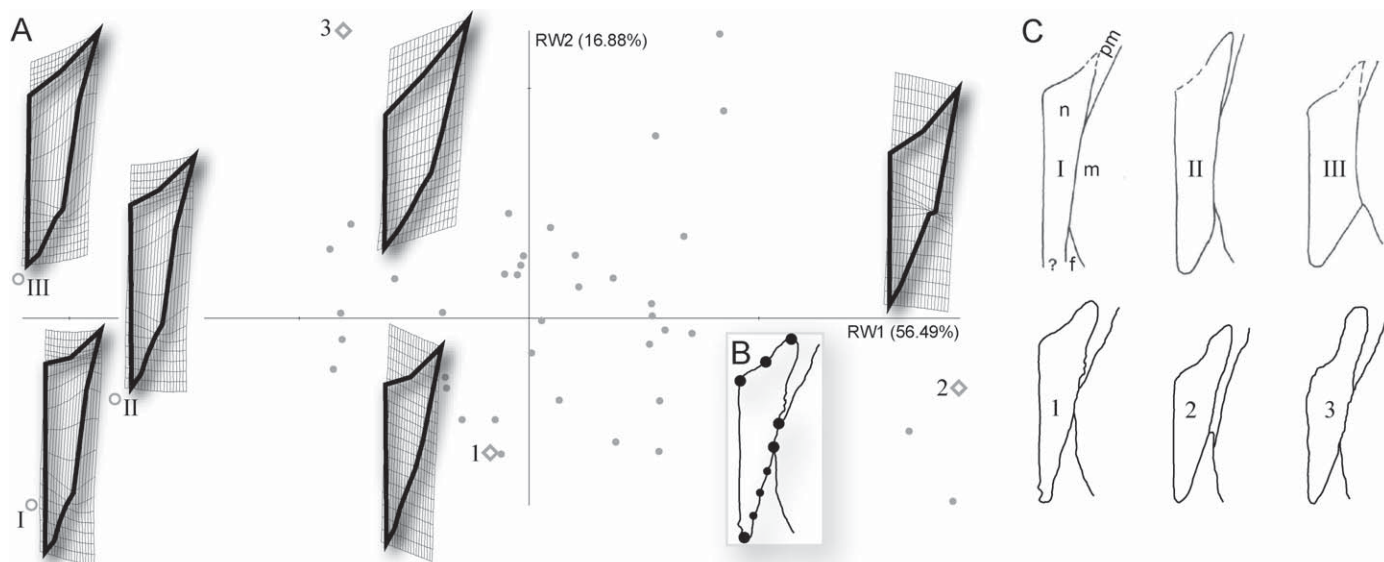


FIGURE 8. Geometric morphometrics analysis of nasal bone shape in extant *Crocuta crocuta* and comparison with *Chasmaporthetes* nasal bone types described by Qiu (1987). **A**, plot of the first two relative warp axes, which account for 73.37% of shape variation in the sample; deformation grids show nasal bone types (I–III) of Qiu (1987) and representative extreme shapes within the *Crocuta* population (1–3); **B**, anatomical landmarks and semilandmarks used in the geometric morphometrics analysis; **C**, comparison of nasal bone types of Qiu (1987) for *Chasmaporthetes* species (I–III) and intraspecific variation observed in modern *Crocuta* (1–3, corresponding to numbered data points in **A**). Image data for *Crocuta* were taken from Tseng and Wang (2011), and nasal bone types from Qiu (1987).

criteria for recognizing four Eurasian *Chasmaporthetes* species that have all been considered under a single species, *C. lunensis*, in other works (Kurtén and Werdelin, 1988; Rook et al., 2004). The characteristics highlighted in the different nasal types are the overall shapes of the bone (slender and long or wide and short) and the degree to which the lateral border of the bone is angled towards the midsagittal axis. Using a sample ($n = 41$) of extant *Crocuta crocuta* skull images from Tseng and Wang (2011), we conducted a shape analysis of nasal bone variation using geometric morphometrics, by digitizing six landmarks and three semilandmarks around the border of the nasal bone (Zelditch et al., 2004). Landmarks were digitized using TPSDig 2.05 (Rohlf, 2006a), and then superimposed using a Procrustes fit. Relative warp analysis was performed on the aligned data set using TPSRelw (Rohlf, 2006b). The results show that within a relatively homogeneous modern population of juvenile and adult hyenas, the shape of the nasal can vary widely, encompassing and exceeding the range of variation covered by the three nasal types in *Chasmaporthetes* proposed by Qiu (1987) (Fig. 8A). One caveat to this analysis is that the simple landmarks chosen did not include variation in nasal bone curvature at the position between the premaxilla-maxilla-nasal and the frontal-maxilla-nasal sutures; nonetheless, observation of the modern sample showed a range of variation for that region as consistent with the numerical analysis (Fig. 8C). Therefore, nasal morphology is an ambiguous and poor character for species-level distinction in hyaenids. Without more quantitative justification for diagnostic crown height differences, the four species recognized by Qiu et al. (2004) should all be considered *C. lunensis*, in line with the broader concept of the species (Kurtén and Werdelin, 1988; Sotnikova, 1994).

Other Eurasian *Chasmaporthetes*

Kurtén and Werdelin (1988) referred essentially the entire known sample of European *Chasmaporthetes* to *C. lunensis*, and

placed those specimens under the geographic subspecies *C. l. lunensis*. Two specimens, one from Perpignan (France) and the other from Dermedzhi (Moldavia), both Ruscian in age, were referred to *C. borissiaki*; however, there is suggestion that these specimens may be conspecific with *C. l. lunensis* (Rook et al., 2004). For the Asian material, *C. l. honanensis* was established based on occurrences in China (Yushe Basin, Shouyang, and Henan), Mongolia (Shamar), and Central Asia (Kuruksay, Beregovaya). Differential diagnosis between the European and Asian forms were based on relatively shorter p4 in the Asian specimens compared with European ones (Kurtén and Werdelin, 1988). This difference, though very slight, is also observed in our analysis for contemporaneous early Villafranchian as well as late Villafranchian samples of *Chasmaporthetes*. However, if Chinese specimens from the study of Qiu (1987) are included (data that were not available to Kurtén and Werdelin, 1988), the range of p4/m1 relative lengths overlaps extensively between the Asian and European samples (Fig. 6E). A simple t-test returned a P value of 0.31, indicating no statistical significance, contra the original test with a smaller Asian sample conducted by Kurtén and Werdelin (1988). Thus, intraspecific variation may be adequate in explaining differences among various European and Asian occurrences of a single species, *C. lunensis*.

Tseng et al. (2008) described a partial dentary attributed to *C. lunensis* from the Xiliexi fissure cave site in Dajushan, Anhui Province, China, that is supposed to be early Pleistocene in age based on artiodactyl biochronology (Dong, 2006, 2008). Even though the metric measurements of the Dajushan specimen are in all regards more similar to North American *C. ossifragus* than any Eurasian samples of the genus, they assigned the specimen to *C. lunensis* based on the geographic separation of the two species. We reexamined the specimen in question (IVPP V15162), and conclude that it is almost identical in dental morphology and size to the Cita Canyon specimen of *C. ossifragus* (PPM 2343). Thus, this particular Chinese occurrence could represent an occurrence of

the North American form in Asia, and lacking older confirmed records of a similar form in China, evidence for a reversed dispersal of the North American species westward into Asia. Additional materials from China as well as other contemporaneous sites in Asia are needed to verify this interpretation.

Kurtén and Werdelin (1988) named a new species, *C. exitelus*, on the basis of a partial palate from the late Miocene of Qingyang (China). Diagnostic characters are relatively broad P4 and M1, and narrow palate. Based on our analysis, the P4 dimensions of the holotype (F:AM 26369) is well within the range of variation for European *C. lunensis*. The width of the palate in hyaenids is dependent, in part, on ontogeny, and there is considerable cranial shape change even after the permanent dentition has erupted in the modern *Crocota crocuta* (Tanner et al., 2010). The supposed old age (late Miocene) of the specimen is dependent on adequate documentation (which is lacking) of locality and geological information from Otto Zdansky's field work in northern China, during which time the specimen was collected (Kurtén and Werdelin, 1988). Without additional material from the original locality to provide more information about the morphological affinity of this lone specimen, the importance of this species cannot be further resolved.

To summarize, cranial characters previously used to justify taxonomic separation among the majority of Asian *Chasmaporthetes* specimens, as well as metric analyses of the dentition, both offer insufficient evidence with which to unambiguously diagnose species or subspecies. These results support the interpretation that most Asian specimens belong to *Chasmaporthetes lunensis*, forming one sample of a widespread Palearctic carnivoran along with European occurrences. The distinct dental metric profile of the Group 'B' *Chasmaporthetes* may in fact indicate a distinct species, but additional materials are needed to support this interpretation.

Relationship between *Chasmaporthetes gangsiensis* and other Chinese *Chasmaporthetes*

Deng et al. (2011) proposed an 'out of Tibet' hypothesis for the origin of some species of Pleistocene mammalian herbivores, citing Pliocene fossil evidence from the Zanda Basin for early plateau occurrences of cold-adapted species such as the woolly rhino, wild yak, Tibetan antelope, and Tibetan bharal. How does the Tibetan *C. gangsiensis* fit in to this hypothesis? The estimated early Pliocene age of *C. gangsiensis* is contemporaneous with *C. lunensis* from the Mahui and Gaozhuang formations of Yushe Basin in northern China (Fig. 7). Several Yushe specimens (IVPP V7274, V7275, V7277, V7278) contemporaneous with *C. gangsiensis* share less reduced P4 protocone, less pronounced symmetry of the AAC and PAC on p4, and non-imbricated tooth alignment with the Zanda species, in contrast to the more reduced P4 protocone, pronounced p4 accessory cusp symmetry, and clearly imbricated upper teeth in geologically younger specimens of *C. lunensis* from Yushe (e.g., IVPP V7279). All of these features are more developed still in Pleistocene *Chasmaporthetes*, in China and elsewhere, than the Pliocene forms. In terms of several plesiomorphic features, the presence of multiple talonid cusps on m1 is shared by the Yushe *C. lunensis* and the Zanda *C. gangsiensis*; however, the short and wide m1 trigonid of *C. gangsiensis* is distinct from all aforementioned occurrences of *Chasmaporthetes*. This m1 shape in *C. gangsiensis* is instead shared with *Hyaenictis* and *Lycyaenops*, and may be a symplesiomorphy at the clade level. Based on this combination of characters, we suggest that *C. gangsiensis* exhibits symplesiomorphic m1 features with other genera in the *Chasmaporthetes* lineage, and at the same time shares common features with other Pliocene *Chasmaporthetes* in China that are plesiomorphic within the genus; this interpretation places *C. gangsiensis* as the most basal among the Pliocene

Chasmaporthetes in China, and is consistent with the 'out of Tibet' hypothesis in terms of stratigraphic and morphological data.

The 'Cursorial' Hyenas and Morphological Concept of the Clade

The fragmentary nature of the new materials described in this study, the highly uneven representation of *Chasmaporthetes* craniodental material across species, and the paucity of identified postcranial material of *Chasmaporthetes* and related hyaenid genera undermine the utility of a cladistic analysis specifically for the 'cursorial clade'; therefore, we did not attempt to analyze a character matrix. However, a discussion of currently recognized morphological differences is nevertheless informative about the concept of this clade. Werdelin (1999) reexamined specimens of *Lycyaenops rhomboideae* and suggested that the clade of cursorial hyenas should include four genera: *Lycyaena*, *Hyaenictis*, *Lycyaenops*, and *Chasmaporthetes*. This clade is monophyletic according to a family-level cladistic analysis (Werdelin and Solounias, 1991). De Bonis et al. (2007) apparently omitted *Lycyaenops* in their discussion of clade-level distinction among the cursorial hyenas, but which will be included here as a relevant genus.

As a clade, the four genera exhibit varying degrees of enlarging size and tooth row reduction, at the same time maintaining relatively slender cheek teeth and prominent accessory cusps on p3/p4. These traits, except for the last, are shared between the cursorial hyenas and the hyaenines, the latter evolving towards wider and more bulbous premolars (Werdelin and Solounias, 1991). Larger size, coupled with reduction of the foremost premolars and the posterior molars, distinguish these two clades from the more jackal- and wolf-like 'ictitheres,' *Ictitherium*, *Thalassictis*, and *Hyaenictitherium*, from which the two clades evolved (Werdelin, 1988). The morphological differences between the hyaenines and the cursorial forms are relatively clear-cut, even at the base of the divergence. The earliest hyaenines, *Palinhyaena reperta*, retains both p1 and m2, whereas these two teeth are not simultaneously present in the cursorial genera.

Generic-level distinction within the cursorial clade, on the other hand, is much less resolved. In part, this has been propagated by overly restrictive (but becoming less so) generic diagnoses and a lack of clarity in character distribution in the clade. It is probably also true that starting from an evolutionary stage similar to a large *Hyaenictitherium*, the cursorial clade show rather continuous variation towards larger size and more reduced tooth rows, thereby evolving more as grades rather than distinct groups with discrete synapomorphies. To disentangle what is potentially a continuous gradient in some aspects, we suggest that genus-level diagnoses for *Lycyaena*, *Hyaenictis*, *Lycyaenops*, and *Chasmaporthetes* be based on less subjective presence/absence morphological characters, as summarized here.

The four genera within the cursorial clade each show a unique combination of dental characters in the lower dentition, and with *Hyaenictitherium hyaenoides* as an outgroup, the polarity of the characters can readily be determined: in *Hyaenictitherium*, both p1 and m2 are present, as well as the m1 metaconid and a full set of three cusps in the m1 talonid basin. *Lycyaena* have variable presence of p1, but with absence of m2 and presence of m1 metaconid, and possess two to three m1 talonid cusps. *Hyaenictis* have variable presence of p1, but with presence of m2 and absence of m1 metaconid, and have two to three m1 talonid cusps. *Lycyaenops* show absence of both p1 and m2, but with m1 metaconid present, and two (may be variable) m1 talonid cusps. Finally, *Chasmaporthetes* show absence of p1 and m1 metaconid in the majority of specimens, m2 is also absent, and m1 has one to two m1 talonid cusps (Table 2). These are the minimum sets of characters from literature that separate the four genera.

TABLE 2. A summary of character distribution in the lower dentition of *Lycyaena*, *Hyaenictis*, *Lycyaenops*, and *Chasmaporthetes*.

Tooth	(Outgroup)	<i>Lycyaena</i>	<i>Hyaenictis</i>	<i>Lycyaenops</i>	<i>Chasmaporthetes</i>
p1	Present	Variable	Variable	Absent	Absent
m1 metaconid	Present	Present	Absent	Present	Absent
m1 talonid cusp	3	3~2	3~2	2	2~1
m2	Present	Absent	Present	Absent	Absent

Unfortunately, even though several previous studies have discussed cranial characteristics that may be more diagnostic of species differences in a given genus (Qiu, 1987), there is no comparable skull material to include additional characters for all four genera in the clade (Werdelin et al., 1994). Furthermore, the questionable utility of certain cranial characters in distinguishing species of *Chasmaporthetes* is an indication of the additional work that is required to resolve cranial morphology evolution in this clade.

Age-Specific Mortality in *Chasmaporthetes*

Unlike many Quaternary cave and fissure sites where robust hyaenids *Crocota* or *Pachycrocota* are found in large numbers of

individuals representing a broad age structure (e.g., localities in China and England), the isolated occurrences of *Chasmaporthetes* tend to represent younger individuals with little tooth wear. The causes of mortality that may differ between a highly social species (e.g., *Crocota*) and presumably more solitary hunters like *Chasmaporthetes* could be a factor that creates bias towards preservation of younger individuals of *Chasmaporthetes*. Older individuals in large social groups may be able to survive into more advanced age by their high social ranks and priority in the pecking order before succumbing to disease or hunger, whereas individuals of more solitary species are more significantly affected by availability of seasonal resources, with less security from conspecifics to procure food (Kruuk, 1972, 1976; Mills and Mills, 1978). This phenomenon could differentiate the two groups by the age of peak mortality



FIGURE 9. Life reconstruction of a pair of *Chasmaporthetes gangsriensis* sp. nov. in the Pliocene Zanda Basin. The discovery of this cursorial hyaenid species provides additional evidence for open environments in the western Himalayan foothills no later than the Pliocene, as consistent with previous evidence from Zanda Basin's fossil horses and herbivore enamel isotope analyses. Artwork by Julie Selan.

in their respective life histories, thereby affecting the likelihood of their preservation as fossils at different ontogenetic ages. This idea, of course, requires further testing with larger single-locality samples of *Chasmaporthetes*. Furthermore, this interpretation is dependent on potential differences between the degrees of tooth wear in the two hyaenid ecomorphs, which are proxies for individual age; the gracile build of the *Chasmaporthetes* skeleton have long been interpreted to be indicative of cursorial hunting habits, which may be correlated with less bone consumption (Khomeenko, 1932; Galiano and Frailey, 1977; Berta, 1981). Tseng et al. (2011) compared the masticatory capability of extant spotted hyenas and *Chasmaporthetes* using skull models and finite element analysis to demonstrate that body size, rather than bone-cracking capability per se, may be a more important factor by which robust hyaenines differ from *Chasmaporthetes* in ecology, in combination with cursorial adaptations in the latter. More rigorous analyses of the available taphonomic and paleoecological data are required to address this interesting question.

Conclusion

A new species, *Chasmaporthetes gangsriensis*, is described from materials collected in the Pliocene sequence of the Zanda Basin in southwestern Tibetan Plateau. The relatively undifferentiated premolars and the short and wide m1 of this species, along with its smaller size, distinguish *C. gangsriensis* from all known materials in the genus *Chasmaporthetes*. Comparison of currently available Asian *Chasmaporthetes* fossils indicates that the bulk of the specimens can be divided into two morphotypes. The first morphotype is that of *C. lunensis*, a species shared between the Europe and Asian regions. The second group (Group 'B') has relatively longer m1s and proportionally enlarged premolars, clearly differentiated from typical *C. lunensis*. The presence of Group 'B' in North America at the Inglis IA locality may either indicate a distinct New World species, parallel examples of populational variants in a widespread Holarctic carnivoran species, or a second dispersal event distinct from that of *C. ossifragus*, which arrived in North America at the beginning of the Blancan NALMA. The Tibetan *C. gangsriensis* exhibits plesiomorphic features belonging to both the *Chasmaporthetes* lineage and to the genus itself, which place it as the most basal among Pliocene *Chasmaporthetes* in China, consistent with the 'out of Tibet' hypothesis in morphological and stratigraphic data.

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