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THE FIRST RECORD OF THE LATE MIOCENE *HYAENICTITHERIUM HYAENOIDES* ZDANSKY (CARNIVORA: HYAENIDAE) IN INNER MONGOLIA AND AN EVALUATION OF THE GENUS

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ABSTRACT—New dental material of the hyaenid *Hyaenictitherium hyaenoides* Zdansky, 1924 from the late Miocene Baogeda Ula Formation in central Inner Mongolia is described. An evaluation of the morphological trends and spatial and temporal ranges of the genus *Hyaenictitherium* follows. The unworn isolated teeth described here represent a nearly complete set of dentition. Furthermore, the Baogeda Ula material is the eastern-most record of this genus, and the only hyaenid record in eastern Asia associated with a layer of basalt capping the fossil producing sediments. Previous studies of the capping basalt and associated small mammal fauna constrain the age of the Baogeda Ula hyaenid at 8–7 Ma. In addition to the Baogeda Ula material, other occurrences of the genus in eastern Asia include Gansu, Shanxi and Shaanxi provinces of northern China. Of the ten species currently thought to belong to the genus, two (*H. intuberculatum* and *H. minimum*) appear more primitive than the others. The rest seem to follow a morphological trend of increasing size and robustness of the teeth, as well as reduction of the trigonid of m1. This trend is observed roughly from *H. wongi* (MN9) to *H. namaquensis* (MN14). The genus appears to be a cursorial form and first appeared in western Eurasia in MN9. Subsequent range expansion occurred in northern Asia, southern Asia, and in Africa from MN12 on. The observed phylogenetic and morphological gaps between *H. namaquensis* and *H. minimum* prevent a clear interpretation of *Hyaenictitherium* immigration into Africa.

INTRODUCTION

The Tunggur strata in central Inner Mongolia have long been known from the extensive collection of middle Miocene fossil mammals made by the American Museum Central Asiatic Expeditions (Spock, 1929; Osborn and Granger, 1932; Wang et al., 2003). These expeditions established the region as a classic locality for studying middle Miocene mammals of Eurasia. Fossil records from the late Miocene of Inner Mongolia, on the other hand, are rarer. Early discoveries by Andersson (1923), later described by Schlosser (1924), established the Ertemte fauna as an important latest Miocene assemblage; additionally, Teilhard de Chardin (1926a, b) found some miscellaneous *Hipparion* fauna along Huiteng River area. Beside these, however, a large gap of several million years in the fossil record has persisted through much of the 20th century. Such a gap is especially apparent in the record of hyaenid evolution. Archaic hyaenids and hyaenid-like forms such as *Tungurictis* and *Percrocuta* from the Tunggur Formation (middle Miocene) are very instructive about the origin and early diversification of the family (Colbert, 1939; Hunt and Solounias, 1991; Wang, 2004), but late Miocene hyaenids, which underwent an explosive radiation in much of Eurasia (Werdelin and Solounias, 1991), are almost completely unknown in Inner Mongolia.

In the late 1970s, Chinese geologists reported a *Hipparion* fauna near the village of Baogeda Ula (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region, 1991), a lead that was followed by one of us (XW) in the mid 1990s to the present. Our field efforts in the past few years have yielded a moderate fossil assemblage of large and small mammals. Among the large mammals is a nearly complete dentition of a *Hyaenictitherium hyaenoides* Zdansky, 1924, which forms the basis of this report. The Inner Mongolian specimen possesses a prominent posterolingual cusp and crest on p4, a large anterior accessory cusp free of the main cusp on p4, three well-developed talonid cusps on m1, m1 with paraconid and protoconid subequal in height, long P4 metastyle relative to the paracone, and a protocone subequal in size and in line with the parastyle on P4. These features are consistent with current understanding of the species (Werdelin, 1988; Werdelin and Solounias, 1991).

The new record of *Hyaenictitherium hyaenoides* from Inner Mongolia is the first such occurrence in the region and permits a glimpse of early hyaenine radiations in the region. The presently described specimen also represents the eastern-most record of this genus. The Baogeda Ula record is also important because it is the only hyaenid record in eastern Asia that is associated with a layer of basalt that caps the fossil producing sediments. The basalt was dated to 7.11 ± 0.48 Ma (Luo and Chen, 1990), and together with small mammals, helps to constrain the underlying Baogeda Ula Formation to an age range of ca. 8–7 Ma (Qiu et al., 2006).

Chinese records of *Hyaenictitherium* are important not only because they are on the eastern end of its Eurasian range but also because the genus appears to persist slightly longer here

than in the rest of Eurasia. We thus review Chinese records of the genus along with records elsewhere in the world.

Institutional Abbreviations—**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **UPM**, University of Uppsala Museum of Evolution, Uppsala, Sweden. **Abbreviations for Mammal Zones**—**MN**, European Neogene Mammal Zones; **NMU**, Chinese Neogene Mammal Faunal Unit (Qiu et al., 1999).

Measurements—All follow Werdelin and Solounias (1991). **L**, maximal anteroposterior length; **LmP4**, P4 metastyle length; **Lpp4**, length of primary cusp of p4; **LpP4**, P4 paracone length; **Ltm1**, trigonid length of m1; **W**, maximal transverse width; **WaP4**, anterior P4 width at protocone and parastyle; **WblP4**, P4 width between paracone and metastyle.

METHODS

Teeth were measured with Mitutoyo Absolute digital calipers to the nearest 0.01 mm. Log ratio diagrams of individual and sample measurements were constructed as in Simpson (1941). The absolute measurement values of *Hyaenictitherium hyaenoides* were converted to log values before they were compared to log-transformed values of a sample of *Hyaenictitherium wongi*. All comparative measurements were taken from Werdelin (1988). Tooth measurements of the holotype of *H. hyaenoides*, UPM M3852–3855, were kindly provided to us by Lars Werdelin. Data used are summarized in Table 1.

A cladistic analysis was run using PAUP (Swofford, 1991) with the exhaustive search option. Eight taxa and 14 characters were coded in a data matrix. *Ictitherium viverrinum* was coded as the outgroup taxon. The character list is provided in Appendix 1; the data matrix and taxa used are listed in Appendix 2.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family HYAENIDAE Gray, 1869
Genus *HYAENICTITHERIUM* Kretzoi, 1938
HYAENICTITHERIUM HYAENOIDES (Zdansky, 1924)
(Fig. 1)

Material—IVPP V14737: upper dentition: left and right I1, left I2, partial right I2, right I3, P1, left and right P2, partial left P3, right P3, partial left and right P4; lower dentition: right i1–3, partial right c1, right p2, partial left p3–4, right p4, right m1. IVPP V14738, right p4. Both specimens were collected by Gerhard Storch on July 7, 2000.

Locality—Baogeda Ula, probably near IVPP IM9602 locality (N 44° 08′ 26.3′, E 114° 35′ 38.1′), 3 km northeast of Baogeda Ula Sumu, Abaga Qi, Inner Mongolia.

Stratigraphy and Age—The Baogeda Ula Formation consists of approximately 110 m of light gray to reddish, yellowish, or greenish mudstones and sandstones capped by a 5 m basalt (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region, 1991; Qiu and Wang, 1999; Wang et al., 2003; Qiu et al., 2006). Although the precise stratigraphic level where the new hyaenid specimens were collected is not clear, they probably come from the middle or lower part of the section not far from a previously established locality (IVPP IM9602) from which two *Hipparion* teeth were collected in 1996. The middle to lower part of the section has produced a modest fauna of small and large mammals including *Parasoriculus* sp., two erinaceids, Gliridae indet., *Lophocricetus* cf. *L. gansus*, *Paralactaga* sp., *Dipus* sp. nov., *Kowalskia* sp., *Nannocricetus* sp., *Sinocricetus* sp., *Microtoscoptes* sp., *Pararhizomys* sp., *Hansdebruijnia perpusilla*, *Abudhabia* sp., *Prosiphneus* sp., *Alilepus* sp., *Ochotona* cf. *O. lagreli*, *Hipparion* sp., *Palaeotragus* sp., in addition to *Hyaenictitherium* presently described. This fauna was initially suspected

TABLE 1. Dental measurements of Baogeda Ula *Hyaenictitherium hyaenoides*, the holotype specimen, and samples of *H. hyaenoides* and *H. wongi* from China.

	H. hyaenoides Baogeda Ula IVPP V14737	*H. hyaenoides* Holotype UPM M3852-3855†	*H. hyaenoides* China* mean	*H. hyaenoides* China* range	*H. wongi* China* mean	*H. wongi* China* range
Lp2	14.06	13.2	14.27	12.4–15.7	12.20	10.6–13.6
Wp2	7.36	7.2	7.73	7.1–8.8	5.94	5.0–7.0
Lp3		16.2	17.49	15.5–19.2	15.30	13.4–17.1
Wp3		8.2	9.51	8.2–10.3	7.31	6.2–8.5
Lp4	18.47	19.1	20.08	18.3–21.8	17.04	14.7–19.0
Wp4	9.49	9.5	10.05	8.8–11.3	8.23	7.1–10.3
Lpp4	8.24	9	9.01	8.2–10.1	7.88	6.1–9.2
Lm1	21.71	20.6	22.87	19.0–25.1	20.25	17.7–23.1
Wm1	9.98	9.2	10.10	9.0–11.2	8.57	7.4–10.2
Ltm1	16.58	16.1	17.59	13.7–19.6	14.81	12.0–17.0
Lm2		5.9	5.39	4.7–6.6	5.82	4.8–7.0
Wm2		5.6	4.97	4.3–5.6	5.07	4.0–5.8
LP2	15.45	14.8	15.44	14.0–17.2	13.30	11.1–15.1
WP2	8.41	8.1	8.57	7.4–10.0	6.46	5.4–7.7
LP3	19.92	18	19.74	18.0–22.5	16.66	14.3–19.0
WP3	11.52	10.6	11.38	9.8–13.1	9.02	7.4–10.8
LP4	28.46	28.2	29.99	27.4–33.4	25.53	23.1–29.2
WaP4	15.33	16	17.01	15.5–19.2	13.95	11.2–16.8
Wb1P4	9.51	9.1	10.37	9.1–11.8	8.59	7.2–10.6
LpP4	11.07	10.9	10.75	9.2–12.4	9.35	8.2–11.0
LmP4	11.22	11.6	11.65	10.6–13.6	9.98	8.5–11.4
LM1		8.1	7.95	7.0–8.9	7.87	6.0–9.2
WM1		15.8	16.26	14.3–18.7	15.03	13.2–18.1
LM2		4.4	4.08	3.1–5.0	4.46	3.1–5.6
WM2		5.6	5.62	4.7–6.2	6.90	4.5–8.6

For source localities of Chinese samples see Werdelin (1988). See text for abbreviations.
All measurements are in millimeters.
*Data from Werdelin (1988).
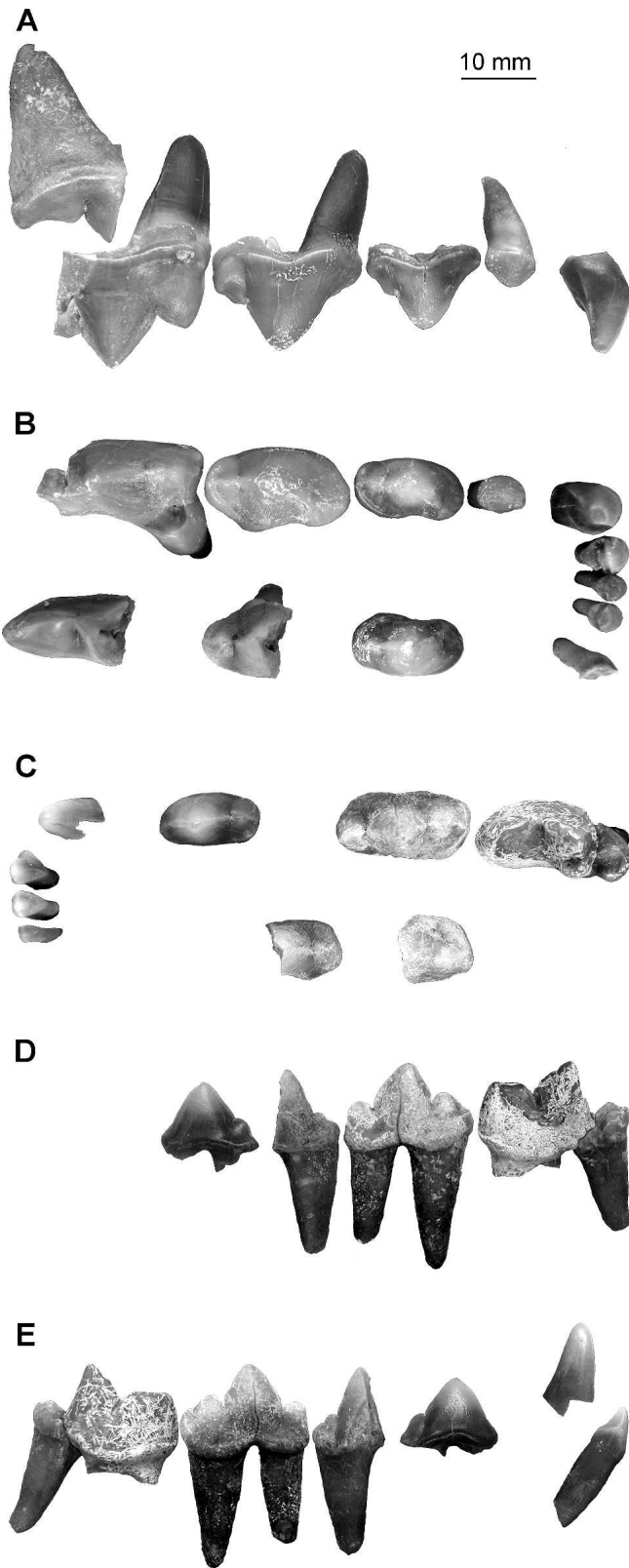†Data from Lars Werdelin, taken by Björn Kurtén.

FIGURE 1. *Hyaenictitherium hyaenoides*, IVPP V14737. **A**, labial view of the upper right dentition I3, P1–4 and lingual view of left P4; **B**, occlusal view of the upper dentition: right I1–3, right P1–P4, left I1–3, left P2–4; **C**, occlusal view of the lower dentition: right i1–c1, right p2, right p4–m1, left p3–4; **D**, lingual view of the lower dentition: right p2, left p3, right p4–m1; **E**, labial view of the lower dentition: right i3–c1, right p2, left p3, right p4–m1.

to be close in age to the Shala Fauna of Inner Mongolia based on limited comparisons with a small portion of that fauna (Qiu and Wang, 1999), but it is now thought to be somewhat younger (Qiu et al., 2006). The capping basalt at the top of the Baogeda Ula section has been dated to 7.11 ± 0.48 Ma (sample B48 of Luo and Chen, 1990). Given the above faunal considerations and radiometric age constraint, Qiu and colleagues (2006) considered the fossiliferous horizons to be middle Miocene in age, approximately 8–7 Ma.

Description—The Baogeda Ula hyaenid material is composed solely of isolated teeth. The minimum number of individuals represented is two, there being two right p4s. All dental material described in this study was collected in close proximity; the similar wear stages of the teeth and the almost complete tooth count makes the presence of more than two individuals highly improbable. Thus, one specimen number was assigned to the set of teeth, and another number to the extra right p4. All cheek teeth show little or no wear, with the upper incisors exhibiting only slight wear. Tooth size increases from I1 to I3, and there is a robust ridge that runs down the posterolingual wall of the I3. P1 is unicuspid, the anterior crest of the cusp being more shallowly sloped than the posterior crest; the tooth is roughly ovoid, being slightly longer in the sagittal axis. P2 has a posterior accessory cusp but no anterior accessory cusp; a prominent cingulum runs from the posterior edge of the tooth around the lingual side to just anterior to the main cusp, where it meets a ridge running anterolingually down slope from the main cusp. P3 is very similar to P2 in morphology except that P3 is larger and also relatively wider. The left P3 is represented by the posterior portion of the crown associated with the posterior root. The anterior faces of both P2 and P3 are slightly concave in lateral profile. The parastyle and the protocone of P4 are subequal in size; a crest runs lingually from the unworn apex of the parastyle to the apex of the protocone. The paracone blade of the right P4 (LpP4 = 11.27 mm) is slightly longer than the metastyle blade of the left P4 (LmP4 = 11.05 mm). The partial right P4 includes the crown and root anterior to the carnassial notch between the paracone and metastyle. The partial left P4 is a portion of the tooth just posterior to the apex of the paracone.

In lower dentition, tooth size increases from i1 to i3, as in the upper incisors, but the degree to which i3 is enlarged relative to the other incisors is not nearly as obvious as that observed for I3. The partial right i2 includes the posterior half of the tooth and is broken along the lateral axis of the main cusp down to the root. The right c1 is represented by the tip only. There is a crest along the long axis of c1 on the lingual side; no evidence of the wear facet associated with occlusion of the upper and lower canines is visible. There is a posterior accessory cusp on p2, but not an anterior one. The anterior edge of p2 has a slight bump which appears to be a short cingulum; there is also a short cingulum posterior to the posterior accessory cusp. The left p3 and p4 each include the posterior portion of the crown and root. The posterior accessory cusp of p3 is relatively smaller to that of p2; there is a short robust cingulum that surrounds the buccal, posterior, and lingual sides of the p3 posterior accessory cusp. Two of the p4s show clearly discernable variation in shape, one being more slender (longer and narrower) than the other. The p4 has prominent anterior and posterior accessory cusps that are subequal in size; a posterior cingulum runs around the lingual but not buccal side of the posterior accessory cusp. Between the posterior cingulum and the posterior accessory cusp there is a small bump connecting the two structures; this is present in all three p4s. There is a notch between the posterior accessory cusp and the main cusp on two of the p4s (the more robust ones), and this is similar to the one between the paraconid and protoconid of m1. The lower carnassial (Lm1 = 21.66 mm) is about 25% shorter than the length of the upper carnassial (LP4 = 28.76 mm). A small but prominent metaconid is present on the m1; the proto-

conid is shorter and slightly taller than the paraconid, and both are unworn; the hypoconid, hypoconulid, and entoconid are all present, being connected by crests.

Comparison to Other Taxa—The protocone and parastyle of P4 are subequal in size and in line with each other, perpendicular to the long axis of the tooth in the Baogeda Ula *Hyaenictitherium hyaenoides*, whereas in *Protictitherium*, *Plioviverrops*, and *Tungurictis* the protocone of P4 is placed anteriorly relative to the parastyle; in *Adcrocuta* and "*Leecyaena*" *bosei* the P4 protocone is situated posteriorly relative to the parastyle (Werdelin and Solounias, 1991). The metastyle may be slightly longer than the paracone on P4 as in more derived taxa in both the *Chasmaporthetes* and *Crocuta* clades. The length of P4 was estimated from the anterior right P4 and posterior left P4; thus this character was used only in conjunction with other characters that were unambiguously assigned.

Both the anterior and posterior accessory cusps of p4 are prominent, differing from *Palinhyaena*, *Ikelohyaena*, *Belbus*, *Parahyaena*, *Hyaena*, and *Crocuta*. In those taxa, the anterior accessory cusp is reduced relative to the main cusp of p4. The anterior accessory cusp of p4 is also appressed to the main cusp in the above taxa, a trend that is associated with relative widening of the tooth as occurs in taxa approaching the bone-cracking morphology of *Crocuta crocuta*. The posterolingual cusp and crest of p4 are clearly present, differing dramatically from the reduction of the cusp and crest in more hypercarnivorous and cursorial *Lycyaena*, *Hyaenictis*, and *Chasmaporthetes* (Werdelin and Solounias, 1991). Furthermore, a log-ratio diagram comparison (not shown) between the Baogeda Ula *H. hyaenoides* and a sample of *Lycyaena dubia* from Werdelin (1988) indicates lengthening of premolars in *L. dubia* compared to *H. hyaenoides*. This trend is consistent with the interpretation of *Lycyaena*, *Hyaenictis*, and *Chasmaporthetes* being more hypercarnivorous and possessing a slender, slashing dentition.

The paraconid and protoconid of m1 are subequal in height; in *Ictitherium* and *Thalassictis* the m1 paraconid is clearly lower than the protoconid (Werdelin and Solounias, 1991). The Baogeda Ula m1 retains all three cusps of the talonid (hypoconid, hypoconulid, entoconid) whereas in more derived taxa (*Leecyaena*, *Chasmaporthetes*, *Adcrocuta*, *Pachycrocuta*, *Pliocrocuta*, *Parahyaena*, *Hyaena*, and *Crocuta*) the number of talonid cusps is reduced to two or one (Werdelin and Solounias, 1991). Taxa such as *Chasmaporthetes* and *Crocuta* tend to also show the derived condition of the absence of m1 metaconid; the Baogeda Ula hyaenid retains a robust m1 metaconid. Neither M2 nor m2 were found, though the degree of reduction of the second molars might provide some insight into the inferred level of specialization in the Baogeda Ula hyaenid towards the hyaenine clade.

Of the congeneric taxa, the only specimen of *Hyaenictitherium indicum* is a maxilla, now missing, that was not figured in the original publication (Werdelin and Solounias, 1991). Thus no comparison could be made to this species. The P4 protocone of *H. pilgrimi* is placed posteriorly relative to the parastyle, whereas in the Baogeda Ula *H. hyaenoides* the P4 protocone is in line with the parastyle. As discussed by Werdelin and Solounias (1991), the material representing *H. parvum* is probably synonymous with *H. wongi* or *H. hyaenoides*. The specimens of *H. wongi* are in general somewhat smaller than those of *H. hyaenoides* (Bonis, 2005), and a log ratio diagram (Fig. 2) shows that the measurements of the Baogeda Ula *H. hyaenoides* fall between those of the type specimen (UPM M3852–3855) and a sample of Chinese *H. hyaenoides*, both summarized by Werdelin (1988). It should be noted here that the morphological similarity between *H. wongi* and *H. hyaenoides* clearly suggest they are congeneric; thus, we follow Bonis (2005) and Zhang and colleagues (2002) in placing *H. wongi* in *Hyaenictitherium* and not *Hyaenotherium*. In addition to overall larger size, the premolars of *H. namaquensis* are relatively wider than those of *H. hyae-*

noides, including the Baogeda Ula material. The premolars of *H. ? barbarum* (Geraads, 1997) are wider, more robust, and its carnassials are both shorter and wider compared to the Baogeda Ula *H. hyaenoides*. There is doubt as to whether *H. ?barbarum* should belong in the genus (L. Werdelin, pers. comm., September 2006), but pending a reevaluation of the single lower jaw representing the species, this taxon is included in this study for now. One of the earliest occurrences of *Hyaenictitherium* in Africa, *H. minimum* from the late Miocene (~7–6 Ma) of Chad (Bonis et al., 2005), has a very small anterior accessory cusp on p4 whereas the accessory cusp is prominent in the Baogeda Ula *H. hyaenoides*. Furthermore, *H. minimum* also has a larger m1 talonid relative to the trigonid compared to *H. hyaenoides*. The late Miocene *H. intuberculatum* from Turkey (Bonis, 2004) also has a relatively longer talonid compared to the Baogeda Ula *H. hyaenoides*, along with a more robust and prominent m1 metaconid.

Discussion—The Baogeda Ula *H. hyaenoides* has larger and wider premolars compared to the archaic middle Miocene hyaenid *Tungurictis spocki* (Colbert, 1939; Hunt and Solounias, 1991; Wang, 2004) from the Tunggur Formation of Inner Mongolia. The new material represents a transitional form from ancestral taxa such as *Tungurictis*, *Ictitherium*, and *Thalassictis*, in which the dentition resembles those of viverrids, to two major clades that occur after the late Miocene. One of the clades represents a highly cursorial and hypercarnivorous group (e.g., *Chasmaporthetes*) which has a slashing dentition resembling those of extant hunting dogs. The other clade represents the stereotypical hyena with robust premolars capable of cracking large bones (e.g., *Crocuta*). The split of the two major clades is highlighted by changes in the morphology of accessory cusps of p4, as illustrated by Werdelin and colleagues (1994:fig. 7).

Werdelin (1988) observed a relatively high variability of the degree of reduction in the posterior non-carnassial molars in *H. wongi* and *H. hyaenoides*. Although the major familial pattern is toward more reduced posterior molars and talonid of m1, the trend is not entirely straightforward, and the younger hypercarnivorous, cursorial genus *Hyaenictis* has a variable presence of m2 (Werdelin and Solounias, 1991). The occurrence of posterior molars in the more derived taxa theoretically represents either retentions or evolutionary reversals, but there is no strong evidence favoring one or the other. Although m2 and M1–2 are not available for the Baogeda Ula *H. hyaenoides*, the material from Baogeda Ula does seem to indicate that the Inner Mongolia *H.*
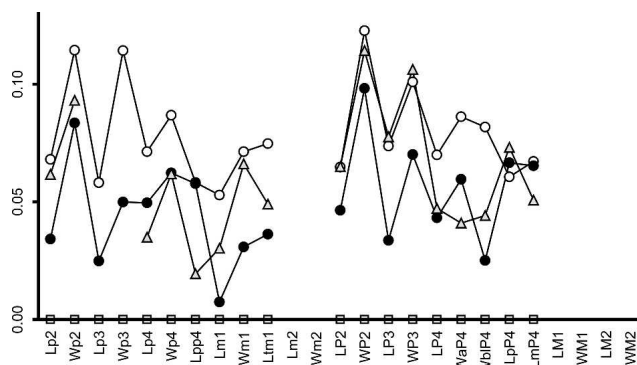

FIGURE 2.   Log ratio diagram comparing *Hyaenictitherium hyaenoides* IVPP V14737 from Baogeda Ula (triangles), *H. hyaenoides* type specimen UPM M3852–3855 (filled circles), a Chinese sample of *H. hyaenoides* (open circles), and a Chinese sample of *H. wongi* (squares). Data for the Chinese samples were taken from Werdelin (1988). For abbreviations of dental measurements see text. M1–2 and m1 were not found with the Baogeda Ula material and therefore measurements for those teeth were removed from comparative data.

hyaenoides evolved prior to the split of *Chasmaporthetes-Hyaenictis-Lycyaena* and hyaenine clades (Werdelin et al., 1994).

MORPHOLOGICAL TRENDS IN *HYAENICTITHERIUM*

A phylogenetic analysis was performed using the data matrix presented in Appendix 2. An exhaustive search returned three trees (10,395 evaluated), and the strict consensus tree is shown in Figure 3. The species *H. parvum* and *H. indicum* were not included in the analysis for lack of information on their character states.

Although species referred to *Hyaenictitherium* may well be paraphyletic (Werdelin and Solounias, 1991)—as transitional taxa often are—an examination of spatial and temporal distributions of of such a taxon should nevertheless be instructive for revealing evolutionary trends during the transition to the hyaenid ecomorphological split (i.e., into the hypercarnivorous *Chasmaporthetes* clade and the bone-cracking hyaenine clade). The earliest occurrences of the genus, both in MN9 of western Eurasia, include *H. intuberculatum* from Turkey (Bonis, 2004) and *H. wongi* from Höwenegg, Germany (Bernor et al., 1980; Beaumont, 1986; Werdelin and Solounias, 1991; Swisher, 1996). The morphology of *H. intuberculatum* more closely resembles *H. minimum* than any other species; the latter is from the latest Miocene (equivalent to MN13) of Chad. Both *H. intuberculatum* and *H. minimum* retain a prominent m1 trigonid and a strong m1 metaconid. These characters are generally considered to be ancestral features in hyaenid evolution (Werdelin and Solounias,

1991); their presence in *H. intuberculatum* and *H. minimum* is compatible with their probable morphological position between other *Hyaenictitherium* taxa, and the morphologically less derived *Ictitherium* (Fig. 3).

The period during the late Miocene from MN11 to MN 13 (and equivalent ages outside Europe) is marked by the presence of six species that all fall along a morphological gradient of increasing size and robustness, starting from *H. wongi* (Fig. 3). Specimens of *H. hyaenoides* have been shown by Werdelin (1988) to be statistically distinct from samples of *H. wongi*. These two species were contemporaneous during MN11–12 in Kazakhstan, Iran, Ukraine, possibly Turkey, and NMU10–12 in China. Furthermore, the two species are almost always found in the same localities in China (Werdelin and Solounias, 1991). Although m1 paraconid and protoconid height are generally more similar in *H. wongi* than in *H. hyaenoides*, possibly representing a derived condition relative to *H. hyaenoides*, the overall dental morphology of *H. hyaenoides* appears to be slightly more derived than that of *H. wongi*; the premolars are wider in *H. hyaenoides*, and specimens of *H. hyaenoides* are in general larger than *H. wongi*.

No illustration of *H. indicum* has been published. According to Werdelin and Solounias (1991), the holotype of *H. indicum*, the only specimen of the species, was never figured in Pilgrim's (1910) original description. All other specimens previously referred to *H. indicum* were transferred to *H. pilgrimi* by Werdelin and Solounias (1991). Based on the ratio diagram of Werdelin
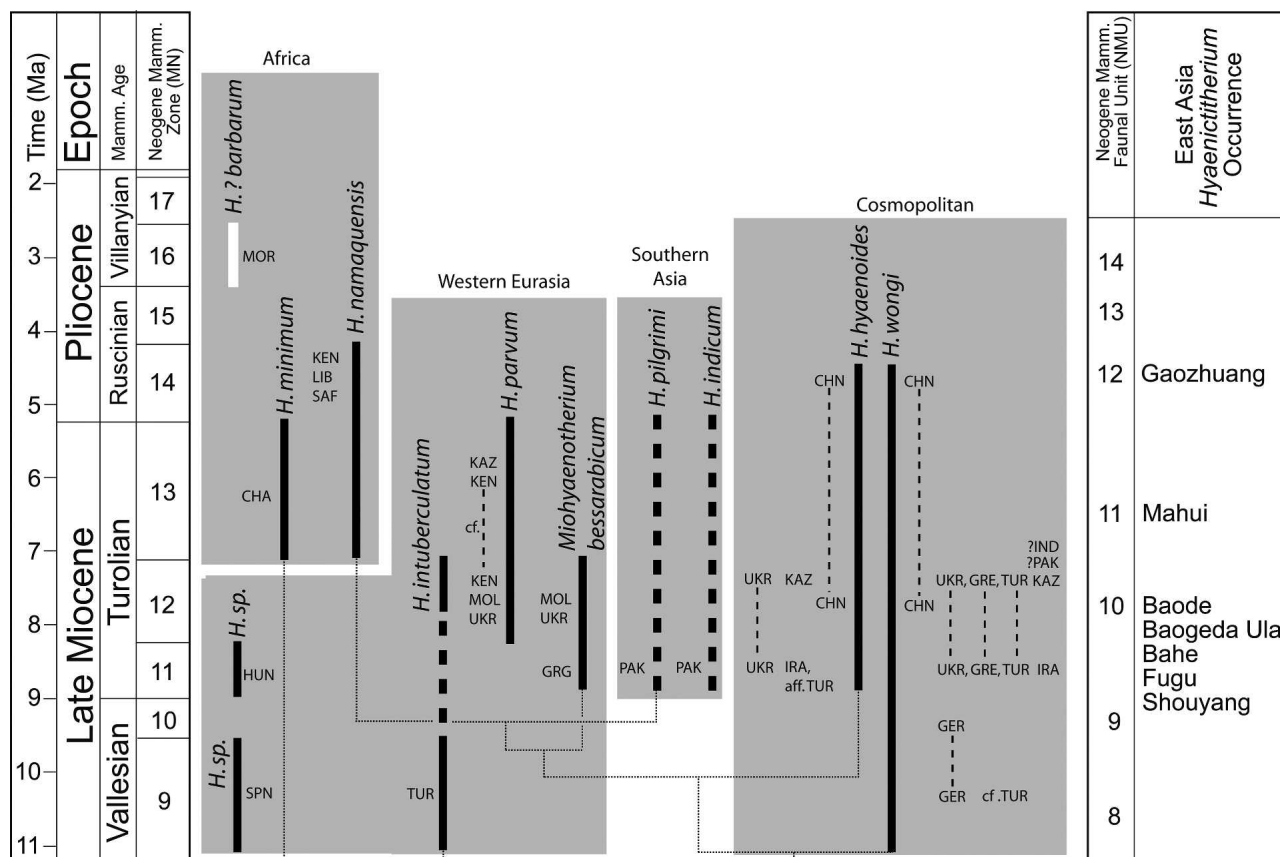

FIGURE 3. Proposed phylogenetic and zoogeographic relationships within the genus *Hyaenictitherium*. Countries and temporal ranges are indicated for each species. Thin vertical dashed lines between country names indicate possible occurrences in both MN zones. Occurrence of *H. hyaenoides* in Turkey (Bonis, 2004) is probable but not confirmed. Age resolution is lacking for the Siwaliks localities in which *H. pilgrimi* and *H. indicum* were found. *H.? barbarum* is questionably included here for completeness. **Abbreviations**: **CHA**, Chad; **CHN**, China; **GER**, Germany; **GRE**, Greece; **GRG**, Georgia; **HUN**, Hungary; **IND**, India; **IRA**, Iran; **KAZ**, Kazakhstan; **KEN**, Kenya; **LIB**, Libya; **MOL**, Moldova; **MOR**, Morocco; **NAM**, Namibia; **PAK**, Pakistan; **SAF**, South Africa; **SPN**, Spain; **TUR**, Turkey; **UKR**, Ukraine.

(1988), the p4 dimentions of *H. indicum* appear to be more similar to those of *H. hyaenoides* than *H. wongi*. The only other character separating *H. indicum* from *H. hyaenoides* is the posteriorly placed protocone on P4, a tooth similar in size to *H. hyaenoides*. The Pakistani material (from the middle Siwaliks group) may thus be an offshoot of either *H. wongi* or *H. hyaenoides*, the latter being less likely if the Pakistani material turns out to be contemporaneous with the earliest occurrence of *H. hyaenoides*. The age of the type locality of *H. indicum*, Hasnot in the Dhok Pathan Formation, is still being studied (see Barry et al., 2002). The provisional range of *H. indicum* and *H. pilgrimi* is therefore late Miocene through early Pliocene. Along the same line, the relative ages of sister species *H. namaquensis* and *H. pilgrimi* cannot be resolved without constraint on the temporal occurrence of the latter taxon. Given the uncertain temporal occurrence of *Hyaenictitherium* in Pakistan, the dispersal of ancestral *H. pilgrimi/indicum* from central Eurasia could have occurred from either east or west of the Himalayas into India/ Pakistan during the late Miocene, as *H. wongi* was present in most of Eurasia by MN11.

Type specimens of *Miohyaenotherium bessarabicum* and *H. venator* (= *H. parvum*), as described and illustrated by Semenov (1989), appear very similar to each other as well as to *H. wongi*. Werdelin and Solounias (1991) suggested all three may all be conspecific, but difficulties in specimen access prevented those authors from synonymizing them. We consider both *M. bessarabicum* and *H. parvum* to be closely related to, if not conspecific with, *H. wongi*, the species of the genus with the largest geographical distribution. Assuming this close relationship, Eurasian *Hyaenictitherium* immigrated into Africa during the Mio-Pliocene transition, and is best represented by the Pliocene species *H. namaquensis*. Werdelin (2003) described hyaenid fossils that he referred to *Hyaenictitherium cf. H. parvum* from the Lothagam fauna of Kenya (Nawata Formation, 7.0–6.0 Ma). This occurrence predates *H. namaquensis*, which is found in Kenya, Libya, Namibia, and South Africa during the latest Miocene and early Pliocene (Fig. 4). A species questionably referred to the genus, *H. ?barbarum*, is also found only in Africa, in the MN16 of Morocco. *H. ?barbarum* shows relative shortening of the premolars, appearing more robust than *H. namaquensis*. Both are larger than *H. parvum*, *H. wongi*, and *H. hyaenoides*. The mor-

phological trend from *H. wongi*, along with its morphologically similar forms in Eurasia, to the Pliocene *H. namaquensis* and *H. ?barbarum*, shows enlarged size and increased robustness of the dentition consistent with the general hyaenid evolutionary trend proposed by Werdelin and Solounias (1991). This group of species could thus represent a continuous progression towards larger size and more robust premolars, putting them closer to the ancestral condition of the hyaenid clade that eventually evolved into forms such as the large *Adcrocuta eximia* and the extant spotted hyena *Crocuta crocuta*. The question of how *H. intuberculatum* and *H. minimum* fit into the morphological trend observed in the rest of the genus remains to be answered, as the relatively hypocarnivorous morphology of these two taxa places them apart from the other species of *Hyaenictitherium* (Fig. 3).

HYAENICTITHERIUM IN CHINA

Species of *Hyaenictitherium* in China are represented by two morphologically very similar forms: *H. wongi* and *H. hyaenoides*. These two species were up until now only found in northern China in Gansu, Shaanxi and Shanxi provinces (Table 2). The Baogeda Ula *H. hyaenoides* is geographically further north and east than all previously described Chinese *Hyaenictitherium*. So far the material described in this report represents the only hyaenid from Baogeda Ula; thus it is not clear whether *H. wongi* also occurs in Inner Mongolia. Both *H. wongi* and *H. hyaenoides* are found in many of the Shanxi localities in Baode and Shouyang, which are probably late Miocene in age (Deng et al., 2004a; Yue et al., 2004), similar to Baogeda Ula. The Shaanxi locality of Fugu, which includes *H. wongi*, might be somewhat earlier in age. Andersson and Werdelin (2005) described *Hyaenictitherium cf. H. wongi* from Locality 42 of the Bahe and Lantian Formations of Lantian, Shaanxi Province, which has been dated at 7.67 Ma by Kaakinen (2005). Overall, the Lantian carnivores represent a typical early Baodean fauna, and the hyaenid specimens are either *H. wongi* or *H. hyaenoides*. In the youngest occurrence of the genus, both species are found in the Gaozhuang Formation in the early Pliocene, and *H. hyaenoides* is additionally found in the Mahui Formation in the late Miocene of Yushe Basin, Shanxi Province. The Gaozhuang Fauna has been paleomagnetically calibrated to 5.3–3.9 Ma (Flynn et al., 1991; Tedford et al., 1991), placing it in the early Pliocene (Qiu and Qiu, 1995). Its *Hyaenictitherium* occurrence thus represents the last occurrence of the genus in the Pliocene of Eurasia, approximately contemporaneous with the terminal African species *H. namaquensis* (Fig. 3). For a list of localities, see Tables 2 and 3.

PALEOBIOGEOGRAPHY OF *HYAENICTITHERIUM*

The genus *Hyaenictitherium* has a wide geographic range in the late Miocene; in Eurasia, it has been reported from China, Ukraine, Moldova, Pakistan, Iran, Turkey, Romania, Greece, Germany, Hungary, and Spain, among others (Werdelin and Solounias, 1991 and references therein; Werdelin et al., 1994; Bonis, 2005). These Eurasian records range in age from ~10.6–5.2 Ma (Werdelin, 2003). In Africa, two late Miocene taxa (possibly conspecific), *H. minimum* (Bonis et al., 2005) and *Hyaenictitherium* cf. *H. parvum* (Werdelin, 2003), have been recorded, followed by *H. namaquensis* in the early Pliocene of Libya, South Africa, and Kenya (Werdelin and Solounias, 1991; Werdelin et al., 1994; Morales et al., 2005). The new record of *H. hyaenoides* from the Baogeda Ula Formation in Inner Mongolia broadens the geographic distribution of *Hyaenictitherium* as it represents the eastern-most record of the genus.

Hyaenictitherium first appeared in western Eurasia in MN9; specimens from Germany and Spain have not been identified to species, but *H. intuberculatum* is present in Turkey (Fig. 4; Table 3). The genus greatly expanded its geographic range in Eurasia between MN11 and MN13 (and equivalent ages outside of Eu-
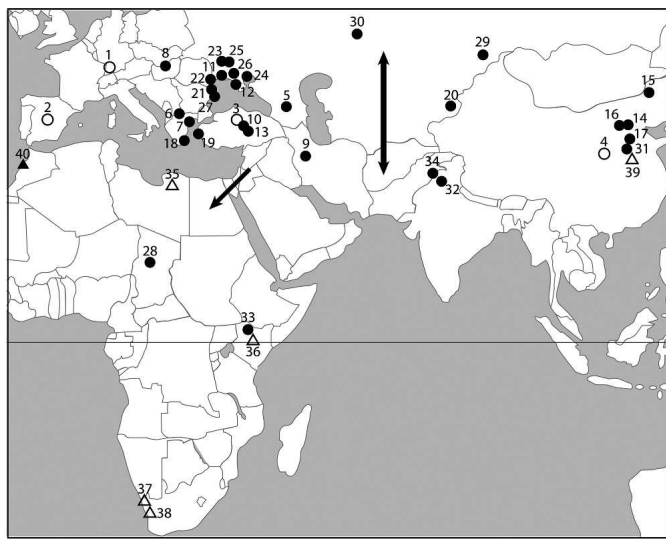

FIGURE 4. Geographical and temporal distribution of the genus *Hyaenictitherium*. Localities are coded by age: open circles, early late Miocene; filled circles, latest Miocene; open triangles, early Pliocene; filled triangles, late Pliocene. For locality names and countries, see Table 3.

TABLE 2. List of localities in which species considered to be within the genus *Hyaenictitherium* have been recorded.

Taxon	Localities
H. ? barbarum	Ahl al Oughlam (2.5 Ma MOR) (Geraads, 1997)
H. hyaenoides	Grossulovo (MN11 UKR); Kuçukyözgat (MN11 TUR) (Bonis, 2004); Maragheh (9–7.6 Ma IRA) (Bernor et al., 1996); [UPM] Sangjialianggou (=Sang-Chia-Liang-Kou; Loc. 43), Shenshuzui (=Shen-Shu-Tsui; Loc 44), Yangmugou (=Yang-Mu-Kou; Loc. 49), Chenjiamaogou (=Chen-Chia-Mao-Kou; Loc. 108), Huanglugou (=Huang-Lu-Kou; Loc. 109), [AMNH] Chin Kou; Liao Wan Kou (8–5.3 Ma Baode, CHN) (Werdelin, 1988; Deng et al., 2004a; Yue et al., 2004); Dashengou, Yangjiashan (Baodean Hezheng, CHN)*; [UPM] Zhaozigou (=Chao-Tzu-Kou; Loc. 116) (Baodean Qingyang, CHN) (Zdansky, 1924); [UPM] Hung-Kou (Baodean Wuxiang, CHN) (Kurtén, 1952); [AMNH] Hsiao Kou Chan, Lu Kao Ling, Nan Ho, Pai Tao Tsun, Ta Tung Kou (late Baodean Shouyang, CHN) (Werdelin, 1988); Baogeda Ula (8–7 Ma Inner Mongolia, CHN) [This paper]; Mahui (NMU11, Yushe, Shanxi, CHN)†; Novaja Emetovka 2 (MN12 UKR); Kalmakpai (MN12 KAZ); Gaozhuang (NMU12/~5.2–3.4 Ma Yushe, Shanxi, CHN)†
H. indicum	Hasnot (MN11–13 Siwaliks, PAK)
H. intuberculatum	Sinap Loc. 7, 8, 91 (10–9 Ma TUR) (Kappelman et al., 2003; Bonis, 2004); Sinap Loc. 42 (MN12 TUR) (Viranta and Werdelin, 2003)
H. minimum	Toros-Menalla (7–6 Ma CHA) (Vignaud et al., 2002; Bonis et al., 2005)
H. namaquensis	Kleinzee, Langebaanweg (latest Miocene to early Pliocene SAF) (Langebaanweg: Hendey, 1981); Sahabi (~5.2 Ma LIB) (Bernor and Scott, 2003); Tugen Hills 95.0–4.5 Ma KEN) (Morales et al., 2005)
H. parvum	Belka, Novaja Emetovka 2 [7.43–7.09 Ma] (Steininger et al., 1996), ?Novoelisavetovka (MN12 UKR); Taraklia, Tudorovo (MN12 MOL); Pavlodar (MN13 KAZ)
H. pilgrimi	Bhandar, Hasnot, Nila (MN11–13 Siwaliks, PAK)
H. wongi	Höwenegg (~10.3 Ma GER) (Swisher, 1996); Sinap Loc. 4 (~10 Ma TUR) (Kappelman et al., 2003; Viranta and Werdelin, 2003); Bahe (NMU9 Shaanxi, CHN) (Andersson and Werdelin, 2005); ?Grebeniki (MN11 UKR); Maragheh (MN11 IRA); Ravin des Zouaves 5, Vathylakkos 2-3 (MN11 GRE); Akkaşdaği (MN11–12 TUR) (Bonis, 2005); [UPM] Daijiagou (=Tai-Chia-Kou; Loc. 30), Loc. 35, Sangjialianggou (=Sang-Chia-Liang-Kou; Loc. 43), Yangmugou (=Yang-Mu-Kou; Loc. 49), Chenjiamaogou (=Chen-Chia-Mao-Kou; Loc. 108), Huanglugou (=Huang-Lu-Kou; Loc. 109), Wangjialianggou (=Wang-Chia-Liang-Kou; Loc. 110), Nanlianggou (=Nan-Liang-Kou; Loc. 111), Chi Tsu Kou, [AMNH] Chin Kou, Chou Chia Kou, He Tsui Kou, Hsi Mao Kou, Hsin Yao, Jen Tse Kou, Kou Chia Ta, Lao Yeh Mao Kou, Liao Wan Kou, Lou Wan Kou, Ma Chi Liang Kou, Tu Kou (8–5.3) Ma Baode, CHN) (Kurtén, 1952; Werdelin, 1988; Deng et al., 2004a; Yue et al., 2004); Dashengou, Yangjiashan (Baodean Hezheng, CHN)*; [UPM] Loc. 115, Zhaozigou (=Chao-Tzu-Kou; Loc. 116) (Baodean Qingyang, CHN) (Zdansky, 1924; Kurtén, 1952); [AMNH] Hsiao Kou Chan, Lu Kao Ling, Nan Hao Hsiz, Nan Ho, Pai Tao Tsun (late Baodean Shouyang, CHN) (Werdelin, 1988); [AMNH] Kuer Shan (8–7 Ma Fugu, CHN) (Werdelin, 1988; Xue et al., 1995); [AMNH] ?Dhok Pathan, ?Hasnot (MN11–13 Siwaliks, PAK); [AMNH] ?Hari Talyangar, ?Kalka (?MN11–13 Siwaliks, IND); Bota-Maynok (MN12 KAZ); Cherevichnoe (MN12 UKR); Pikermi (8.3–8.2 Ma GRE) (Bernor et al., 1996), Samos (~7.6–7.1 Ma GRE) (Swisher, 1996); Gaozhuang (5.2–3.4 Ma Yushe, Shanxi, CHN)†
M. bessarabicum	Udabno (MN11 GRG); Belka (MN12 UKR); Çimislia (MN12 MOL)

Localities are ordered by age then alphabetically or numerically. Locality information is from Werdelin and Solounias (1991) unless otherwise noted. UPM and AMNH localities are distinguished for Chinese occurrences. Chinese locality names in Zdansky (1924) are updated using current Pinyin System of spelling, with original spelling and locality number in parentheses. Ages for Chinese localities follow Qiu and Qiu (1995) and Qiu and colleagues (1999) unless otherwise noted. Country abbreviations as in Figure 3.
*No published descriptions available; from faunal list in Deng and colleagues (2004b).
†Unpublished data from Qiu Zhanxiang and R. H. Tedford.

rope), reaching China to the east and the Indian subcontinent to the south sometime during the late Miocene. The expansion was mainly a latitudinal one; the genus was already present in mid-latitudes as early as the earliest late Miocene. The earliest records of the genus on the African continent are *Hyaenictitherium* cf. *H. parvum* from Lothagam, Kenya (Werdelin, 2003), and *H. minimum* from Chad (Bonis et al., 2005). By the Miocene-Pliocene boundary the genus had reached the southern tip of the continent, represented by *H. namaquensis* in South Africa. Migration into Africa does not appear to have occurred through the Strait of Gibraltar during intermittent land bridge formation in the late Miocene. The two localities opposite the strait, Los Valles de Fuentidueña to the north and Ahl al Oughlam to the south, represent the oldest and (questionably) youngest occurrences of *Hyaenictitherium*, respectively (Fig. 4). The occurrence of *Hyaenictitherium* in Los Valles de Fuentidueña, Spain, was recorded only as *Hyaenictitherium* sp. (Werdelin and Solounias, 1996). Thus, based on the large temporal gap on either side of the Strait of Gibraltar, and on the basis of morphological continuity of *Hyaenictitherium* as a clade, we conclude that immigration of the genus into Africa most likely occurred in an eastern route through the Sinai Peninsula (Fig. 4). This immigration event, however, is complicated by the phylogenetic positions of the African *H. namaquensis* and *H. minimum* (Fig. 3). *Hyaenictitherium namaquensis*, one of the most derived species, is separated from *H. minimum* by morphologically intermediate species in Eurasia. Thus, two possible scenarios are: (1) the two taxa

immigrated into Africa independently; and (2) there was only one *Hyaenictitherium* immigration event and although morphological intermediates between *H. minimum* and *H. namaquensis* exist in Africa, they have not been discovered. The dental morphology of *H. minimum* indicates a hypocarnivorous diet relative to other contemporaneous *Hyaenictitherium*, whereas *H. namaquensis* shows the derived condition of enlarging bone-cracking premolars. This problem clearly needs further work, but its resolution is beyond the scope of this study. Overall, the available fossils of *Hyaenictitherium* seem to indicate that the genus was widespread in western Eurasia by MN9 and subsequently spread to northern Asia, southern Asia, and Africa by as early as 7.0 Ma (Fig. 4, Table 3). The range of *Hyaenictitherium* expanded in Africa until MN16, the latest appearance of this moderately sized genus of ten described species.

CONCLUSION

New material of *Hyaenictitherium hyaenoides* Zdansky from the Baogeda Ula Formation of Inner Mongolia is described. The late Miocene (~8–7 Ma) occurrence of the species is the first record of the genus in Inner Mongolia. Furthermore, the Baogeda Ula hyaenid represents the eastern-most record of the genus. The widening of the premolars and the degree of reduction of the m1 talonid place the Baogeda Ula specimen above the stage of morphological evolution observed in taxa such as *Thalassictis* and *Ictitherium*. The retention of prominent anterior and poste-

TABLE 3. *Hyaenictitherium* localities ordered by age, country, and then locality name.

#	Locality	Country	Age	Ma
1	Höwenegg	GER	MN9	10.3
2	Los Valles de Fuentidueña	SPN	MN9	
3	Sinap (5)	TUR	MN9-12	
4	Bahe	CHN	NMU9	11–6.8
5	Udabno	GRG	MN11	
6	Ravin des Zouaves 5	GRE	MN11	
7	Vathylakkos 2,3	GRE	MN11	
8	Czákvár	HUN	MN11	
9	Maragheh	IRA	MN11	9.0–7.6
10	Kuçukyözgat	TUR	MN11	
11	Grebeniki	UKR	MN11	
12	Grossulovo	UKR	MN11	
13	Akkaşdaği	TUR	MN11-12–14	
14	Baode (21)	CHN	NMU10	8–5.3
15	Baogeda Ula	CHN	NMU10	8~7
16	Fugu	CHN	NMU9-10	8~7
17	Shouyang (6)	CHN	NMU10	
18	Pikermi	GRE	MN12	8.3–8.2
19	Samos	GRE	MN12	7.6–7.1
20	Bota-Maynok	KAZ	MN12	
21	Çimislia	MOL	MN12	
22	Taraklia	MOL	MN12	
23	Belka	UKR	MN12	
24	Cherevichnoe	UKR	MN12	
25	Novoelisavetovka	UKR	MN12	
26	Novaja Emetovka 2	UKR	MN12	7.43–7.09
27	Tudorovo	UKR	MN12	
28	Toros-Menalla	CHA	L. Mio.	7.0–6.0
29	Kalmakpai	KAZ	MN13	
30	Pavlodar	KAZ	MN13	
31	Mahui (Yushe)	CHN	NMU11	
32	Middle Siwaliks (2)	IND	L. Mio.	
33	Nawata Fm. (Lothagam)	KEN	L. Mio.	7.0–6.0
34	Middle Siwaliks (4)	PAK	L. Mio.	
35	Sahabi	LIB	E. Plio.	5.2
36	Mabaget Fm. (Tugen Hills)	KEN	E. Plio.	5.0–4.5
37	Kleinzee	SAF	E. Plio.	
38	Varswater Fm. (Langebaanweg)	SAF	E. Plio.	5.3–5.0
39	Gaozhuang (Yushe)	CHN	NMU12	5.2–3.4
40	Ahl al Oughlam	MOR	L. Plio.	2.5

Ages of western Eurasian localities are in European MN zones; Chinese localities are in Chinese NMU units (Qiu et al., 1999). Numerical ages are given for African localities where available. Locality numbers correspond to Figure 4. Parenthetical values following locality names indicate the number of *Hyaenictitherium* localities in the general area.
Country abbreviations as in Figure 3.

rior accessory cusps of p4 positions *H. hyaenoides* basal to the split of the family into *Chasmaporthetes*-like and *Crocuta*-like clades. The premolars of Baogeda Ula *H. hyaenoides* are more robust than the late Miocene *H. wongi*, but do not reach the degree of widening observed in Pliocene forms such as *H. ?barbarum* and *H. namaquensis*. An overall trend of increasing premolar size and robustness in *Hyaenictitherium* places the genus morphologically closer to the ancestral stock leading up to the major hyaenid clade (including *Crocuta*)—in which prominent bone-cracking dentition evolved—than to the more hypercarnivorous *Chasmaporthetes* clade. The genus appears to be already widespread in early late Miocene in western Eurasia. Subsequent expansion to northern Asia, southern Asia, and Africa occurred in the latest Miocene.

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APPENDIX 1. Description of dental characters used in the cladistic analysis.

Character states were treated as unordered. **WS#**: characters used by Werdelin and Solounias (1991) in their phylogenetic analysis, where applicable.

(1) Relative positions of P4 protocone and parastyle: protocone anterior (0); protocone in line (1); protocone posterior (2). [WS9]
(2) Prominence of anterior accessory cusp of p4: subequal to posterior accessory cusp (0); minor (1). [WS13]
(3) m1 talonid: half as long as trigonid (0); less than half as long as trigonid (1).

(4) Prominence of m1 metaconid: as high crowned as protoconid, prominent in size (0); reduced relative to m1 protoconid and paraconid (1).

(5) Reduction of M1 relative to P4: (ranked in order by ratio of LP4 to WM1): 1.39 (0); 1.66 (1); 1.70 (2); 1.84 (3); 1.87 (4). [WS6]

(6) Number of talonid cusps on m1: three (0); two (1). [WS7]

(7) Lower premolar toothrow shape: straight (0); curved (1).

(8) Relative lengths of P4 paracone and metastyle: equal (0); metastyle longer (1). [WS11]

(9) Carnassial placement in toothrow in line (0); off-set (1). [WS12]

(10) Anterior face of p3: concave/straight (0); convex (1). [WS15]

(11) m2 presence: present (0); lost (1). [WS1]

(12) Relative width of p3 (ranked in order by ratio of Wp3 to Lp3): 0.46~0.47 (0); 0.48 (1); 0.51 (2); 0.54 (3); 0.56 (4). [WS16]

(13) Relative width of p4 (ranked in order by ratio of Wp4 to Lp4): 0.48 (0); 0.50 (1); 0.52~0.53 (2).

(14) Relative width of P3 (ranked in order by ratio of WP3 to LP3): 0.54~0.55 (0); 0.56 (1); 0.58 (2); 0.64 (3).

APPENDIX 2.   Character-taxon matrix used for cladistic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
H. hyaenoides	1	0	1	1	3	0	0	0	0	1	0	3	1	2
H. intuberculatum	1	0	0	0	1	0	?	1	0	0	0	0	2	1
H. minimum	1	1	0	0	?	0	?	?	0	1	0	0	0	?
H. namaquensis	0	0	1	1	4	1	1	0	1	1	0	4	2	3
H. pilgrimi	2	1	1	1	?	0	1	?	1	?	0	?	2	?
H. wongi	1	0	1	1	2	0	0	0	0	1	0	1	0	0
M. bessarabicum	0	0	1	?	?	?	?	1	0	1	?	?	0	?
I. viverrinum	1	1	1	0	0	0	0	0	0	0	0	2	2	0

For character and character state descriptions see Appendix 1. **Abbreviations**: **H**, *Hyaenictitherium;* **I**, *Ictitherium;* **M**, *Miohyaenotherium.*