

陕西蓝田晚中新世食肉类

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摘要:陕西省蓝田地区灞河组与蓝田组产出了大量的古哺乳动物化石。其中,晚中新世哺乳动物化石序列为认识该地区自然环境的变化提供了重要的依据。详细描述和研究了其中的食肉类化石。计有鬣狗科3种(*Ictitherium viverrinum*、*Hyaenictitherium* cf. *H. wongii*、*Adcrocuta eximia*)和猫科2种(cf. *Metailurus major*与cf. *Metailurus parvulus*)。在下部的灞河组与上部的蓝田组界线附近,食肉类动物群落组成发生了改变,但引起这种改变的原因仍有待进一步研究确定。

关键词:中国陕西蓝田,晚中新世,灞河组,蓝田组,鬣狗科,猫科

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CARNIVORA FROM THE LATE MIOCENE OF LANTIAN, CHINA

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Abstract Sediments of the Bahe and Lantian formations, Lantian area, Shaanxi Province, China, have produced a large number of mammalian fossils. This Late Miocene sequence provides evidence for a period of major changes in the physical environment of the region. The carnivoran fossils are described and analyzed herein. The following species are present: *Ictitherium viverrinum*, *Hyaenictitherium* cf. *H. wongii* and *Adcrocuta eximia* (Hyaenidae), cf. *Metailurus major* and cf. *Metailurus parvulus* (Felidae). Although a difference in the composition of the carnivoran fauna is noted towards the boundary between the Bahe Formation (lower) and Lantian Formation (upper), the cause of this is yet to be determined.

Key words Lantian, Shaanxi, China, Late Miocene, Bahe and Lantian formations, Hyaenidae, Felidae

1 Introduction

During the years 1997 ~ 2002, a large number of vertebrate fossils were collected from the Late Miocene (Baodean *sensu* Qiu and Qiu, 1995) sedimentary sequence in the Lantian area, Shaanxi Province, China (Fig. 1). The collection has yielded a rich mammalian fauna, including bovids, giraffes, horses and carnivorans. The former groups are treated elsewhere (eg., Zhang et al., 2002), while the purpose of this paper is to describe and analyze the carnivorans in the collection.

The sedimentary sequence at Lantian includes ca. 300 m of continuous sedimentation starting basally with the fluvial deposits of the Bahe Formation and continuing with the aeolian deposits of the Lantian Formation traditionally known as the "Red Clay". The Tertiary sequence

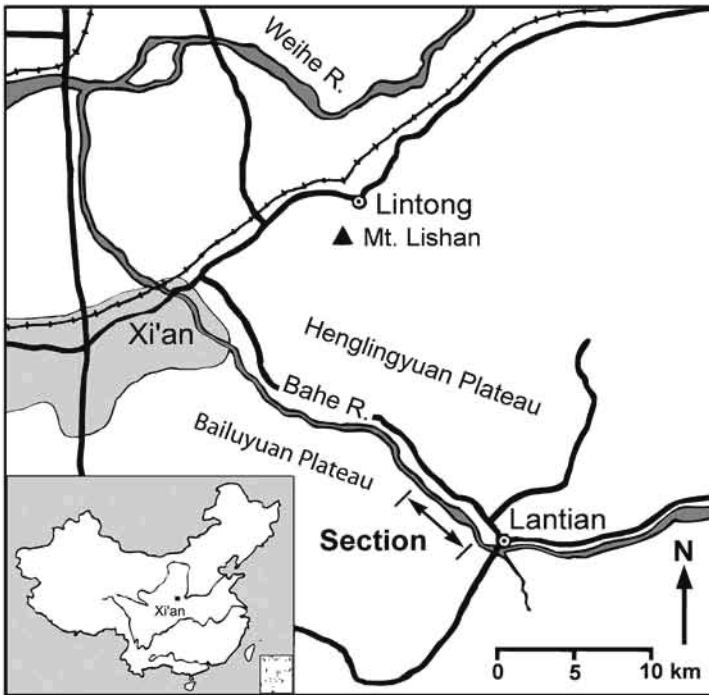


Fig. 1 Map showing the city of Xi'an with adjacent area and the geographic location of the studied section (Redrawn from Andersson, 2004)

is capped by Pleistocene loess deposits. Fossils were mainly collected from the Bahe Formation and the lowest part of the Lantian Formation (Kaakinen and Lunkka, 2003).

This sequence registers a period of increased tectonic activity and climatic change in the region. The Late Miocene uplift of the Tibetan plateau is believed to have triggered and controlled the development of the Northern Asiatic monsoon system (An et al., 2001), leading to aridification to the north and west of the plateau. In Western Eurasia, dramatic changes in the carnivoran fauna during the Late Miocene coincide with changes to the physical environment. Large scale tectonic events, including the Alpine orogeny, the gradual closure of the Paratethys and the Messinian salinity crisis, caused the physical environment to alter dramatically. During this period, there is approximately 90% turnover of the carnivoran fauna of western Eurasia from the Late Miocene to the Early Pliocene (Werdelin and Turner, 1996).

In Eastern Asia and China climatic change and subsequent changes in the mammalian fauna have been recorded (Li et al., 1984; Qiu and Qiu, 1995; Fortelius et al., 2002) and a turnover event has been recorded in the micromammal fauna at Yushe (Tedford et al., 1991). The full extent and dynamics of these changes in the biotic environment are not known. Such analysis is beyond the scope of this paper. To solve this problem, a better understanding of Chinese faunas and their biostratigraphy is needed, and to this the present paper is a contribution.

Liu et al. (1978) reported the presence of three Miocene carnivore taxa in the Lantian region: two large durophagous "hyaenids", *Crocota macrodonta* and *Crocota eximia variabilis* (= *Adrocota eximia* Roth and Wagner, 1854) and one small carnivore, tentatively referred to Viverridae indet. In the present Lantian collection, several more taxa have been added.

Hyaenids and felids are present, with the former numerically dominant. The hyaenas range in size from small jackal-sized ones to one large, durophagous species. Small and medium-sized hyaenids are common elements of Late Miocene faunas throughout Eurasia and they often occur in great numbers (Zdansky, 1924; Solounias, 1981). They have a long and complicated taxonomic history (see e. g., Solounias, 1981; Kurtén, 1982; Werdelin, 1988a, b; Werdelin and Solounias, 1991) and are often informally referred to as "ictitheres". Three small to medium-sized species of this group are common in the Late Miocene of China (Werdelin and Solounias, 1991): *Ictitherium viverrinum* Roth and Wagner, 1854, *Hyaenictitherium wongii* (Zdansky, 1924) and *Hyaenictitherium hyaenoides* (Zdansky, 1924). Other Late Miocene hyaenids reported from China include *Ictitherium kurteni* Werdelin, 1988, *Lycyaena dubia* Zdansky, 1924 and *Palinhyaena reperta* Qiu et al., 1979.

One large bone-cracking hyaenid species, *Adcrocuta eximia* Roth and Wagner, 1854, is currently recognized in the Late Miocene of China (Werdelin and Solounias, 1990, 1991). This species, with its specialized dentition, is distinctly different from "ictitheres" and thus *Adcrocuta* is here analyzed and discussed separately.

2 Material and methods

The carnivoran material analyzed herein is comprised of three isolated skulls, two skulls with associated mandibles, six isolated lower jaws and one isolated tooth. The material also includes three podials and several isolated podial fragments. In addition to these, the collection also contains a couple of broken and fragmentary specimens. All specimens are housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China.

Material from the Lagrelius collection, Museum of Evolution, Uppsala University, the former Paleontological Museum of Uppsala University (PMU) was used as comparative reference material. Measurements used are presented in Table 1 and follow Werdelin and Solounias (1991, p. 7). All measurements were taken by the authors or by the late Björn Kurtén. The information is to be found in Werdelin (1988a, b). Measurements and averages of the four species in the reference sample, *H. hyaenoides*, *H. wongii*, *I. viverrinum* and *A. eximia*, are presented in Table 2. Because of the nature of the fossil record, sample sizes vary depending on species and variable as follows; *H. hyaenoides* ($n = 7 \sim 22$); *H. wongii* ($n = 39 \sim 113$); *I. viverrinum* ($n = 7 \sim 18$); *A. eximia* ($n = 32 \sim 60$).

Table 1 Dental measurements

Lower dentition	
Lp3...4	Length of lower premolars and molars. Measurements taken as the maximum anteroposterior distance of respective tooth.
Lm1...2	Transverse width of lower premolars and molars. Measurements taken as the maximum lingubuccal distance of respective tooth.
Wp2...4	Length of the main cusp of the fourth premolar (p4).
Wm1...2	Length of the trigonid of the first molar (m1).
Upper dentition	
LP3...4	Length of upper premolars and molars. Measurements taken as the maximum anteroposterior distance of respective tooth.
LM1...2	Transverse width of upper premolars and molars. Measurements taken as the maximum lingubuccal distance of respective tooth.
WP3...4	Width of the fourth premolar (P4) at protocone.
WM1...2	Width of the fourth premolar (P4) between the paracone and metastyle.
WaP4	Length of the paracone of the fourth premolar (P4).
WbP4	Length of the metastyle of the fourth premolar (P4).
LpP4	
LmP4	

I Table 2 Dental measurements of the Lantian carnivores and for the species *Hyaenictiterium hyaenoides* (*H. hyae*), *Hyaenictiterium wongü* (*H. wong*), *Ictitherium viverrinum* (*I. viver*) and *Adcrocuta eximia* (*A. exim*) from China* (mm)

Lower dentition												
	Lp3	Wp3	Lp4	Wp4	Lpp4	Lm1	Wm1	Ltm1	Lm2	Wm2	Locality	
V 13121	16.31	8.62	18.86	9.24	8.89	21.24	9.66	16.39	5.10	4.68	42	
V 13122	14.51	7.31	15.93	8.08	7.49	18.77	8.45	13.42	n/a	n/a	42	
V 13123	12.59	6.86	7.22	7.22	6.84	16.75	7.83	11.05	7.41	6.12	42	
V 13124	n/a	n/a	n/a	n/a	n/a	18.92	8.41	13.19	7.84	6.11	42	
V 13125	n/a	n/a	a 13.9	a 6.6	a 8.6	a 18.7	a 6.5	a 13.5	n/a	n/a	42	
V 13126	13.70	7.58	8.24	8.24	7.52	17.45	8.72	12.99	n/a	n/a	42	
V 13130	18.69	12.58	20.67	12.30	10.38	25.44	11.86	21.04	n/a	n/a	42	
V 14329	12.70	6.62	14.50	7.00	6.80	17.40	7.30	11.21	n/a	n/a	42	
<i>H. hyaenoides</i>	17.49	9.48	20.08	10.03	9.05	22.87	10.10	17.59	5.81	4.97	China	
<i>H. wongü</i>	15.31	7.33	17.03	8.24	7.90	20.16	8.56	14.78	5.89	5.07	China	
<i>I. viverrinum</i>	13.09	6.42	14.15	7.21	6.84	17.06	7.42	11.37	7.24	5.41	China	
<i>A. eximia</i>	22.96	13.11	67.35	12.79	10.52	37.97	12.42	21.83	—	—	China	
Upper dentition												
	LP3	WP3	LP4	WaP4	WbLP4	LpP4	LmP4	LM1	WM1	LM2	WM2	Locality
V 13126	16.07	7.81	23.22	12.93	8.75	9.04	8.12	7.87	14.81	5.33	7.84	42
V 13127	n/a	n/a	27.60	15.13	9.78	10.59	11.16	7.87	16.89	4.35	6.48	42
V 13128	13.50	7.53	20.83	13.19	7.58	7.67	7.46	8.90	14.01	6.22	8.73	42
V 13129	15.74	8.11	23.46	13.20	8.70	9.15	8.85	9.01	16.97	5.93	8.37	42
V 13130	20.41	13.89	35.67	15.90	10.58	13.28	13.33	6.47	14.36	—	—	42
V 13133	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	6
<i>H. hyaenoides</i>	19.74	11.38	29.99	17.01	10.37	10.75	11.65	7.95	16.26	4.08	5.62	China
<i>H. wongü</i>	16.66	9.05	25.57	13.94	8.60	9.38	10.01	7.87	15.00	4.44	6.88	China
<i>I. viverrinum</i>	14.25	7.73	19.80	12.18	7.46	7.85	7.24	7.91	13.84	5.69	8.83	China
<i>A. eximia</i>	21.70	15.35	34.96	17.99	11.91	12.66	15.19	5.86	13.11	—	—	China

* See Table 1 for explanation of the measurements. For reference species averages are given. Because of the nature of the fossil record sample sizes vary depending on species and variable. *H. hyae*, average of $n = 7 \sim 22$; *H. wong*, average of $n = 39 \sim 113$; *I. viver*, average of $n = 7 \sim 18$; *A. exim*, average of $n = 32 \sim 60$; n/a = Measurement not available; a = approximate measurement; — = tooth absent on species.

Individual specimens are evaluated through ratio diagrams, following Simpson (1941). Ratio diagrams provide an excellent graphic overview that allows for the simultaneous evaluation of a large number of characters. However, as the number of investigated specimens increases so does the complexity of these graphs. Therefore, ratio diagrams are less suited to situations where intraspecific variation of multiple groups is the main focus. Herein, however, several characters of individual specimens are evaluated against a single reference, and thus the benefits of ratio diagrams are fully exploited.

In a ratio diagram, values are compared to a standard, herein *Ictitherium viverrinum* (Fig. 2). Measurements greater than the standard will result in positive values and smaller ones in negative values. Thus, a specimen larger than the chosen standard, but with the same dental proportions, will result in all positives and a line connecting these, running parallel to that of the standard. See Simpson (1941) for further explanation and discussion of the use of ratio-diagrams. In Fig. 2 the Lantian specimens are plotted against *I. viverrinum*. For *I. viverrinum* the average and ranges of dental measurements are given. Ranges are presented as box-plots, wherein boxes represent the second and third quartiles and whiskers mark the first and fourth. Extreme outliers are plotted individually.

3 Localities: age and stratigraphy

The sediments of the Bahe Formation are made up of facies ranging from massive conglomerates and cross-laminated sandstones to mudstones that were laid down as fluvial and lacustrine deposits. Feeding channel patterns were braided to anastomosing and animal remains

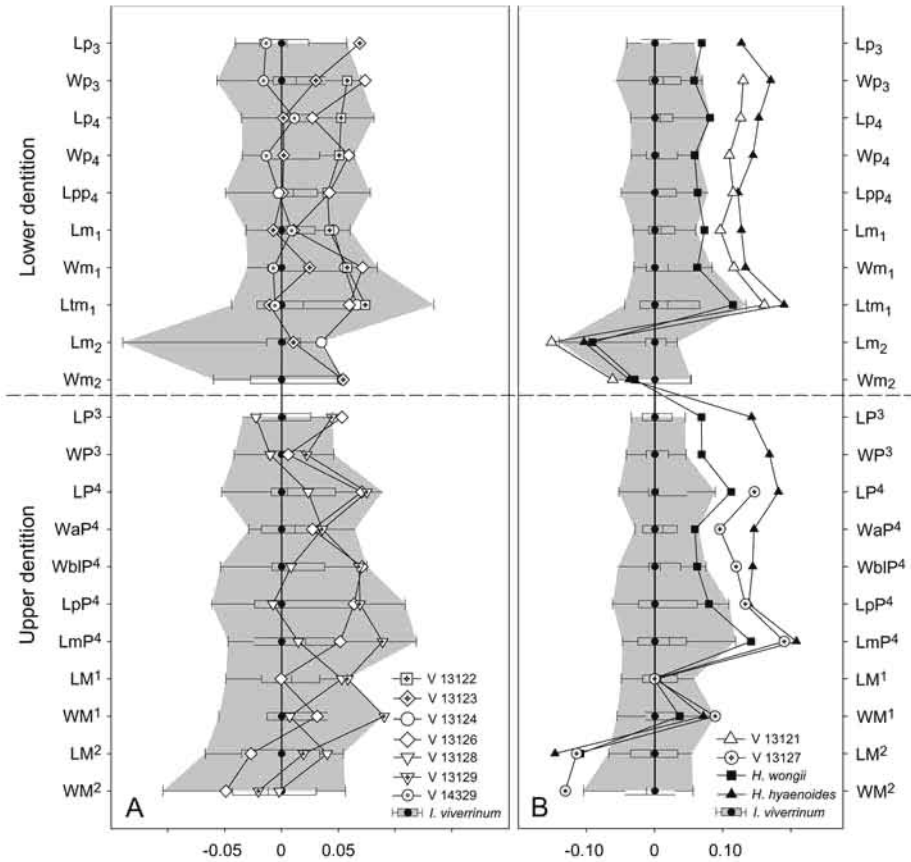


Fig. 2 Ratio-diagrams over Lantian carnivora

A. specimens referred to *Ictitherium viverrinum*; B. specimens referred to *Hyaenictitherium* cf. *H. wongii*. Standard in both A and B is *Ictitherium viverrinum* from China. As reference, averages and ranges of the standard are presented. Bars denote medians; boxes represent the second and third quartiles and whiskers, connected by the shaded area, the first and fourth quartiles. Measurements are \log_{10} -transformed. See Table 1 for explanation of dental variables and Table 2 for measurements

were mainly accumulated through overbank processes (Kaakinen and Lunkka, 2003; Andersson, 2004). Fig. 9 outlines the relative stratigraphic positions of the localities yielding carnivoran fossils. Locality 42 produced an exceptional number of well-preserved and complete fossils. The remains were deposited in a gully-like depression through rapid flow or mass movement (Andersson, 2004). The locality is situated just below the boundary between the Bahe and Lantian Formations.

4 Systematic paleontology

Order Carnivora Bowditch, 1821
Family Hyaenidae Gray, 1869
Genus *Ictitherium* Wagner, 1848

Ictitherium is a genus of medium-sized, omnivorous to moderately carnivorous hyaenids

typical of the later Miocene. The genus is characterized by relatively unreduced molars and short carnassial cutting blades. As currently conceived, the genus includes the following species: *I. viverrinum* Roth and Wagner, 1854; *I. tauricum* Borissiak, 1915; *I. pannonicum* Kretzoi, 1952; *I. intuberculatum* Ozansoy, 1965; *I. ibericum* Meladze, 1967; *I. kurteni* Werdelin, 1988.

Ichtherium viverrinum Roth et Wagner, 1854

1854 *Ichtherium viverrinum* sp. nov. Roth and Wagner, pp. 392 ~ 396, pl. 2:3 ~ 5

1862 *Thalassictis gracilis* sp. nov. Hensel, pp. 566 ~ 567, fig. 5

1924 *Ichtherium gaudryi* sp. nov. Zdansky, pp. 67 ~ 72, fig. 3, pls. 12:5 ~ 6; 13:1 ~ 6

1924 *Ichtherium sinense* sp. nov. Zdansky, pp. 72 ~ 73, pl. 14:1 ~ 2

Age Baodean (~Turolian).

Ichtherium viverrinum is the common species of the genus, with a range extending from China in the east to western Europe. It is well known from numerous skulls and postcranial material from sites such as Pikermi (Gaudry, 1862 ~ 1867).

Referred Lantian material Eight specimens, all from Locality 42, are referred to *I. viverrinum*, as they fall within the range of the species in metrics as well as overall morphology (Fig. 2A). These specimens are IVPP V 13122, a right mandibular ramus with c, p2 ~ m1 (Fig. 3), V 13123, a right mandibular ramus with c ~ m2, lacking the coronoid and angular processes, V 13124, a left mandibular ramus with m1 ~ m2, V 13125, a juvenile right mandibular ramus with dp3 ~ dp4 and roots of dc and dp2, V 13126, a skull and associated lower jaw (Fig. 4), V 13128, a damaged skull with left and right I1 ~ I3, right C, left and right P3 ~ M2 (right M1 damaged), V 13129, a nearly complete skull with dentition, lacking only the right P1 and M1 ~ M2 and metastyle of P4. The following is a composite description of these specimens, and V 14329, a right mandibular ramus with c, p1 alveolus, p2 ~ m1, roots of m2.

The skulls are generally distorted and only a few features are fully determinable. The skull had a distinctly vaulted forehead. The infraorbital foramina are large, slightly wider than tall, and set at the P3 ~ P4 junction. The sagittal crest originates above the retroarticular processes and is relatively low. Towards the posterior end it rises to meet the occipital crest and nuchal crests. The occipital crest is tall but narrow. The occipital condyles are slender.

The I1 is small and longer transversely than anteroposteriorly. It has a distinctly pointed buccal main cusp and a low, cusplless lingual shelf. The I2 is similar to the I1, though taller and more pointed, and about 20% ~ 40% larger. The lingual shelf has a medial cusplet and angles dorsally towards the lateral side. The I3 is larger than I1 and I2 and is distinctly caniniform. The main cusp is buccolingually trenchant and there is a strong cingulum crest running along the median side of the tooth from apex to base. The canines are slender, somewhat mediolaterally compressed, and moderately recurved. The P1 is a small, single-cusped tooth with a slight lingual cingulum. The cusp is distinctly longer than wide, but is blunt and not markedly trenchant. The P2 is long and slender. There is no anterior accessory cusp, while the posterior one is variably developed, ranging from absent to well developed. The main cusp is long and low, with distinct anterior and posterior crests. The P3 is robust and long. It has a small anterior accessory cusp set at the anterolingual corner, making the anterior end of the tooth somewhat bulbous. The main cusp is tall and conical. The posterior accessory cusp is considerably larger than the anterior and set in line with the main cusp. The upper carnassial is robust and short. There is no preparastyle, while the parastyle is a strong and tall cusp. The protocone is large, but considerably lower than the parastyle. The paracone is tall and conical. It is swept backwards, and after a shallow carnassial notch merges with the metastyle, which is of about the same length as or shorter than the paracone. The M1 is

triangular in occlusal view. The parastyle wing is very large relative to the metastyle wing, so that the metacone is positioned at about the middle of the tooth in the buccolingual direction. There are no distinct paracone or metacone cusps, but the protocone, which is large and crest-like, with a distinct cusp. The M2 is more oval than M1 in occlusal view. The metastyle wing is reduced to a small posterior bump, while the parastyle wing is prominent. The protocone makes up about half of the tooth and shows a distinct cusp.

The horizontal ramus is long and slender, with its deepest point posterior to m1. There are two mental foramina, the larger beneath the middle of p2 and the smaller beneath or slightly behind the p2 ~ p3 juncture. The coronoid process is tall and slender, with a square dorsal outline. The masseteric fossa extends to the talonid of m1, or slightly anterior to this point.

The i1 is very small, with an incipient division into two cusps. There is no lingual shelf. The i2 is similar to the i1, but about twice as large and with a more distinct division into a larger median cusp and smaller lateral one. The i3 is larger still, with the median cusp large and the lateral reduced to a crest running from the apex down the lateral side of the tooth. The lower canine is more robust and less compressed and recurved than the upper. The p1 is small and single-rooted. The p2 is slender, with a minute anterior accessory cusp developed as a cingulum cusp. The main cusp is conical but low. The posterior accessory cusp is variably developed, ranging from minute to considerably larger than the anterior accessory cusp. It can have a strong lingual shelf. The p3 is a larger version of p2, but the anterior accessory cusp is less distinct and the posterior lingual shelf narrower and more crest-like. The p4 has a distinct anterior accessory cusp, a tall, conical main cusp, and a strong, crest-like posterior accessory cusp, which is preceded on the posterior margin of the main cusp by a small bump indicative of an incipient cusp. The posterolingual shelf is well developed and crest-like. The m1 is relatively short and has a tall paraconid and protoconid, of which the latter is distinctly taller but shorter. There is sometimes a small cusp at either side of the base of the paraconid. The metaconid is well developed and only slightly lower than the paraconid. The talonid has a number of well developed cusps, including in order of decreasing size entoconid, hypoconid and hypoconulid. The m2 is subrectangular. There are five distinct cusps. The metaconid and protoconid of the trigonid are clearly developed. In the talonid, the entoconid is the largest cusp, followed by the hypoconid and hypoconulid.

In the juvenile specimen, IVPP V 13125, the dp3 is damaged, but had a large, sharp

anterior accessory cusp, a tall, sharp main cusp and a small posterior accessory cusp appressed to the main cusp. There is a small shelf posterior to the posterior accessory cusp. The dp4 is very slender. The protoconid tip is slightly damaged, but this cusp appears to have been slightly taller and longer than the main cusp. The talonid has a tall entoconid, a distinct entoconulid, and a very small hypoconid.

Discussion As seen in Fig. 2A, all these specimens, except the juvenile V 12125, lie within the range of variation



Fig. 3 Mandible of *Ictitherium viverrinum* (IVPP V 13122) from Locality 42
A. lateral view; B. occlusal view

of *I. viverrinum* from China (shaded area in Fig. 2A). This is in contrast to the specimens V 13121 and V 13127 (Fig. 2B; discussed below), which clearly fall outside this range. Despite the individual variation seen in Fig. 2A we conclude that it is reasonable to assign the above listed specimens to *I. viverrinum*, an assignment that also applies to the juvenile specimen, the morphology of which clearly matches that of other juvenile *I. viverrinum*.



Fig. 4 Associated skull and mandible of *Ictitherium viverrinum* (IVPP V 13126) from Locality 42
A. occlusal view; B. ventral view

Genus *Hyaenictitherium* Kretzoi, 1938

As conceived herein, this genus includes as a junior synonym *Hyaenotherium* Semenov, 1989. The latter was used by Semenov (1989) and Werdelin and Solounias (1991) for the species *H. wongii* (Zdansky, 1924). However, it is difficult to make the distinction between the species *H. hyaenoides* and *H. wongii* unless large samples are available, and this argues against placing them in separate genera. In addition, the taxon *H. hyaenoides* was on a branch of zero length in the cladistic analyses of Werdelin and Solounias (1991), i. e., had no distinguishing autapomorphies. This suggests that its position in the cladogram is uncertain, especially relative to its nearest outgroup, which is *H. wongii*. Hence, we believe, following an original suggestion by Qiu Zhanxiang (pers. comm.), that both *H. hyaenoides* and *H. wongii* should be included in *Hyaenictitherium* (the oldest valid genus for these taxa). As currently conceived, this genus further includes the following species: *H. indicum* (Pilgrim, 1910); *H. parvum* (Khomenko, 1914); *H. namaquensis* (Stromer, 1931); *H. pilgrimi* Werdelin and Solounias, 1991; and possibly *H. bessarabicum* (Semenov, 1989).

Hyaenictitherium wongii (Zdansky, 1924)

1924 *Ictitherium wongii* sp. nov. Zdansky, pp. 73 ~ 84, figs. 4 ~ 6, pls. 14:3 ~ 6; 15:1 ~ 4; 16:1 ~ 2

1952 *Hyaenalopex atticus* gen. et sp. nov. Kretzoi, p. 21

1985 *Thalassictis mesotes* sp. nov. Kurtén, pp. 81 ~ 82, figs. 1 ~ 2

1989 *Hyaenotherium magnum* gen. et sp. nov. Semenov, pp. 94 ~ 105, figs. 28 ~ 31

Age Baodean (~Turolian).

Hyaenictitherium wongii is an extremely common hyaenid in the later Miocene of China, being the dominant carnivore in many of the Baodean faunas (Werdelin, 1988a, 1996).

Hyaenictitherium cf. *H. wongii*

Referred Lantian material The following two specimens from Locality 42 are referred to *H. cf. H. wongii* on the basis of morphology and metrics (Fig. 2B).

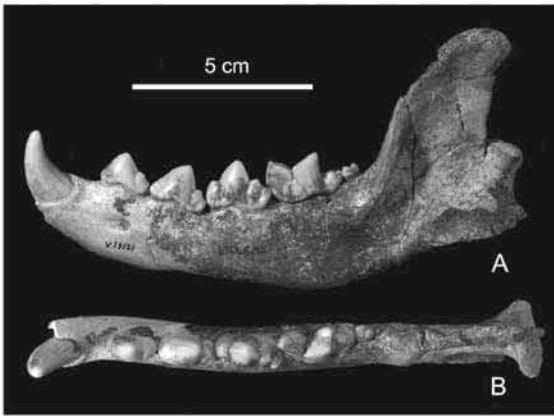


Fig. 5 Mandible of *Hyaenictitherium* cf. *H. wongii* (IVPP V 13121) from Locality 42
A. lateral view; B. occlusal view

IVPP V 13121, an isolated mandibular ramus with c ~ m2 but no evidence for a p1 (Fig. 5). The ramus is long and slender, with a distinct curvature at its deepest point beneath m1. There are two mental foramina, a large one beneath p2 and a much smaller one beneath the anterior end of p3. The coronoid process is tall and slender with a marked dorsal curvature. The c is slender and curved posterad. The p2 lacks an anterior accessory cusp and has a small posterior one appressed to the conical main cusp. The p3 is larger, but otherwise very similar to p2, though the posterior accessory cusp is only slightly larger. The p4 is slender with large anterior and posterior

accessory cusps flanking a conical main cusp. The posterolingual shelf is crest-like. The m1 is tall, with a short talonid. The protoconid is taller than the paraconid, but of about equal length. The metaconid is much smaller than either of the other trigonid cusps. The talonid has three distinct cusps which appear to be hypoconid (largest), entoconid and entoconulid. The m2 is small and round but has three distinct cusps that can probably be identified as protoconid, metaconid and hypoconid.

IVPP V 13127, a nearly complete skull with left I1 ~ I3, C, P4 ~ M2, right I1 ~ I3, P1, P4 ~ M2. The skull is moderately laterally distorted and the left nasofrontal region has been pushed inwards, while the right canine and attendant bone has been lost. Parts of the right parietotemporal region are also damaged, and fragments of the dorsal parts of both zygomatic arches are lost.

The skull is long and slender. Though damaged in the frontal region, this skull probably had only a moderate to small "stoop" of the forehead. The zygomatic arches do not flare out markedly. The occipital crest originates on the parietals and is low and short. The occipital and nuchal crests are more distinct and the occipital region flares outwards and has a clear overhang over the occipital condyles.

The I1 is small and its main cusp is distinctly pointed. The posterior shelf is low and has two cusplets. The I2 is similar to I1, but is 30% larger and its main cusp is more pointed. The

I3 is considerably larger than I1 and I2 and is distinctly caniniform. Its cusp is somewhat trenchant and there is a strong cingulum crest that runs from the apex along its median side. The canine is robust, with distinct posterior and anteromedial salient crests. It is only slightly recurved and mediolaterally compressed. The P1 is a single-cusped tooth. The cusp is somewhat trenchant and there are no anterior and posterior accessory cusps. The upper carnassial is a robust tooth. There is an anterior crest that may be an incipient preparastyle. The parastyle is strong and tall. The protocone is large, but considerably lower than the parastyle. The paracone is tall and conical with distinct anterior and posterior crests emerging from the apex of the cusp. The metastyle is long, slightly higher than the parastyle, but reduced in height from anterior to posterior. It is gently curved. The M1 is transversely elongated. The parastyle wing is very large, with a distinct paracone crest at its buccal end. The protocone is large, with a distinct, pointed cusp. The metastyle wing is very reduced, with a small metacone cusp making up most of its extent. The M2 is a small, oval tooth with distinct but small paracone, metacone and protocone.

Discussion As can be seen from Fig. 2B, the two above-mentioned specimens are intermediate in metrics between *H. wongii* and *H. hyaenoides*. In large samples, such as those at some of the localities from Baode (Werdelin, 1988a), these two species can be readily distinguished, but in small samples, this is nearly impossible when specimens are intermediate in size. On the basis of the morphology of the two specimens, which is relatively slender, it is somewhat more likely that they belong to *H. wongii* than to *H. hyaenoides*, but it is not possible to make this determination with certainty. Therefore, we choose to identify the two as *H. cf. H. wongii*.

Genus *Adcrocuta* Kretzoi, 1938

Adcrocuta is the common large hyaenid of the later Miocene. It appears rather abruptly in MN 10 and goes extinct equally abruptly in MN 13, to be replaced later by the assemblage of large hyaenids we see today. Only one species, *A. eximia* (Roth and Wagner, 1854), is currently recognized.

Adcrocuta eximia (Roth et Wagner, 1854)

1852 *Hyaena eximia* sp. nov. Roth and Wagner, pp. 396 ~ 398, pl. 2:6

1924 *Hyaena variabilis* sp. nov. Zdansky, pp. 93 ~ 103, figs. 11 ~ 13, pls. 18:3 ~ 4; 19:3 ~ 4; 20:1 ~ 4; 21:1 ~ 4; 22:1 ~ 4

1932 *Crocota mordax* sp. nov. Pilgrim, pp. 150 ~ 153, pls. 6:1, 3, 4; 7:10

1938 *Adcrocuta praecursor* sp. nov. Kretzoi, p. 118

1967 *Crocota miriani* sp. nov. Meladze, pp. 31 ~ 34, pls. 3:1 ~ 2; 4:1 ~ 3

1987 *Chasmaporthetes bonisi* sp. nov. Koufos, pp. 913 ~ 920, pl. 1:1 ~ 2, 3C

Age Bahean – Baodean (~ Vallesian – Turolian).

Referred Lantian material The Lantian material includes one specimen from Locality 42 that can confidently be referred to *A. eximia*. In addition, an isolated upper canine fragment from Locality 19 is tentatively referred to the taxon.

IVPP V 13130, a cranium and associated lower jaw (Fig. 6). Both are laterally compressed, and compression at the midline has led to the right side being pushed dorsad approximately 5 mm relative to the left side. The specimen is a juvenile, with deciduous canines still in place, and permanent canines and P2 ~ P3 erupting.

The skull is not fully adult, as judged by the state of eruption of the dentition and by the size relationship between teeth and skull. This, together with the post-mortem compression, makes it difficult to discern useful characters. The orbits are relatively small, as is the zygomatic arch. The sagittal crest is damaged but must have been relatively low. The occipital

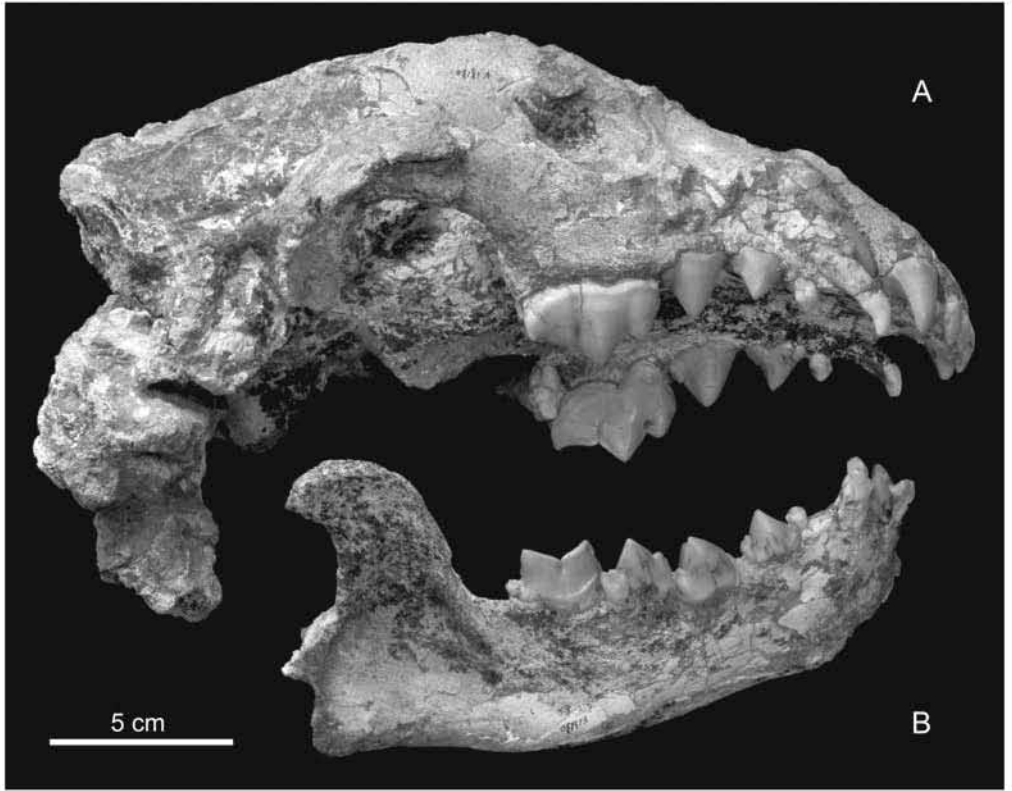


Fig. 6 Associated skull (A) and mandible (B) of *Adcrocuta eximia* (IVPP V 13130) from Locality 42, right lateral view

crest is broken, but would not have extended any significant distance caudal to the occipital condyles. A damaged atlas is attached to the occipital condyles, possibly together with a small part of the axis.

The upper incisors are all present. The first incisors are smallest, with a pointed main cusp and lower, flatter lingual accessory cusp. The second incisors are similar in morphology to the first incisors, but are about half again as large. The third incisors are massive, caniniform teeth with a low lingual cingulum. The deciduous canines are intermediate between incisiform and caniniform, but lack the lingual accessory cusp of the former. They are of about the size of the first incisors. The permanent upper canines are erupting. The crowns of both are visible buccally, where the bone of the maxillae is broken off. The P1 is a small, single-cusped, single-rooted tooth. The P2 is robust, with a small, lingually placed anterior accessory cusp, a large, conical main cusp, and a posterior accessory cusp of about the same size as the anterior one, but placed in the line of the main axis of the tooth. The P3 has a very small, lingually placed anterior accessory cusp, a large, conical main cusp, and a small but well-developed posterior accessory cusp set in a slightly broadened posterior shelf along the midline of the main axis of the tooth. There is a basal cingulum that begins at the anterobuccal corner and continues around the lingual side of the tooth to the posterior accessory cusp. The upper carnassial is robust. There is a minute preparastyle about half way along the anterior face of the parastyle. The parastyle is large and robust and about two thirds the height of the paracone. The latter is a strong, conical cusp with a trenchant posterior crest. The protocone is reduced to a small

swelling at the base of the anterolingual end of the tooth. The metastyle is longer than the paracone and relatively low and straight. There is a basal cingulum that runs on the lingual side from the protocone to the posterior end of the tooth. The M1 is small. The parastyle is robust, and the protocone well developed. The metastyle wing is almost completely reduced, existing as only a small posteromedial swelling with a minute metacone at its center.

The lower jaw includes both rami with coronoid processes, of which the left is damaged apically. Both mandibular condyles are damaged. The rami are robust and deep. The masseteric fossa extends to the posterior end of m1. The first lower incisor is small and somewhat longer (bucco-lingually) than broad (mediolaterally). There is no lingual accessory cusp. The second lower incisor is similar to the first, but about half again as large and has a very small lingual accessory cusp. The third lower incisor is somewhat caniniform, with a sharp central cusp, a low, blunt medial accessory cusp and a somewhat larger and sharper lateral accessory cusp. The deciduous canines are small subcaniniform teeth lacking accessory cusps but with a small crest running from the apex and diagonally, down the lingual side of the tooth. The permanent canines are lodged in their crypts and not visible for study. The p1 is small, single-cusped and single-rooted, with a low central cusp. The p2 has a small anterior accessory cusp, a robust, conical main cusp, and a broad posterior shelf with a small posterior accessory cusp in its center. The p3 is a robust tooth. It is very similar to p2, but is half again as large. The p4 is relatively slender, but with only a weakly marked waist. The anterior and posterior accessory cusps, which flank a robust, conical main cusp, are of about equal size, but the latter is set in a slightly broadened posterior shelf. The m1 has a paraconid and protoconid of about equal size and height. The metaconid is absent. The talonid is short and single cusped and the posterior end of the tooth strongly tapering as a result. There is a cingulum at the base of the paraconid.

cf. *Adcrocuta eximia* (Roth et Wagner, 1854)

IVPP V 14312, a broken isolated right upper canine. Both root and crown are broken, with half the crown and part of the central section of the root entirely missing. Only a small section of enamel remains at what is probably the anterobuccal end. This is a large tooth with a pyramidal crown and substantial, straight root. Since so little remains the attribution of this tooth to *Adcrocuta* must remain tentative

Discussion The presence of *Adcrocuta eximia* is to be expected in any localities of the Chinese Upper Miocene. Together with *H. wongü* it is the most common carnivore in the later Miocene of Eurasia, appearing in western Eurasia in MN 10 and becoming extinct at the end of MN 13 (Werdelin, 1996; Werdelin and Solounias, 1990).

Family Felidae Fischer, 1817

Genus *Metailurus* Zdansky, 1924

Metailurus is a genus of medium-sized saber-toothed felid that is relatively common in the late Miocene of Eurasia. The machairodont adaptations of *Metailurus* spp. are moderate to slight and the genus is generally placed in the tribe Metailurini, together with the genus *Dinofelis*. The species-level taxonomy of *Metailurus* has not been fully resolved, but likely members of the genus are: *M. parvulus* (Hensel, 1862), *M. major* Zdansky, 1924, *M. kansensis* (Hibbard, 1934), *M. mongoliensis* Colbert, 1939, *M. teilhardi* (Crusafont Pairó, 1972), *M. obscura* (Hendey, 1974), and *M. hengduanshanensis* (Zong, 1996).

***Metailurus parvulus* (Hensel, 1862)**

1863 *Machairodus parvulus* sp. nov. Hensel, p. 568

1924 *Metailurus minor* Zdansky, p. 131; 136, pl. 29: figs. 4 ~ 5; 20, pl. 30: figs. 1 ~ 3

1951 *Metailurus parvulus* (Hensel, 1862) Thenius, p. 93, 3

Age Bahean – Baodean (~ Vallesian – Turolian).

Referred Lantian material The Lantian material includes a single cranial specimen from Locality 6 that is tentatively referred to *M. parvulus*.

cf. *Metailurus parvulus* (Hensel, 1862)

IVPP V 13133 (Locality 6), a posterior part of skull, broken anteriorly at about the middle of the orbits (Fig. 7). The zygomatic arches are broken and all that remains are small pieces of their temporal parts. The right parietal is also damaged and has a 5 cm indentation lateral to the occipital crest. The occipital crest itself is broken, but was low and relatively long, originating just anterior to the fronto-parietal suture. The frontals are broad and distinctly inflated. The occipital crest forms a shallow U-shape, broken on the left side. The basicranial region is relatively wide and typically felid. The external auditory meatus is large and not tubular or lipped. The auditory bulla has a tympanic chamber that has grown caudoventrally, to

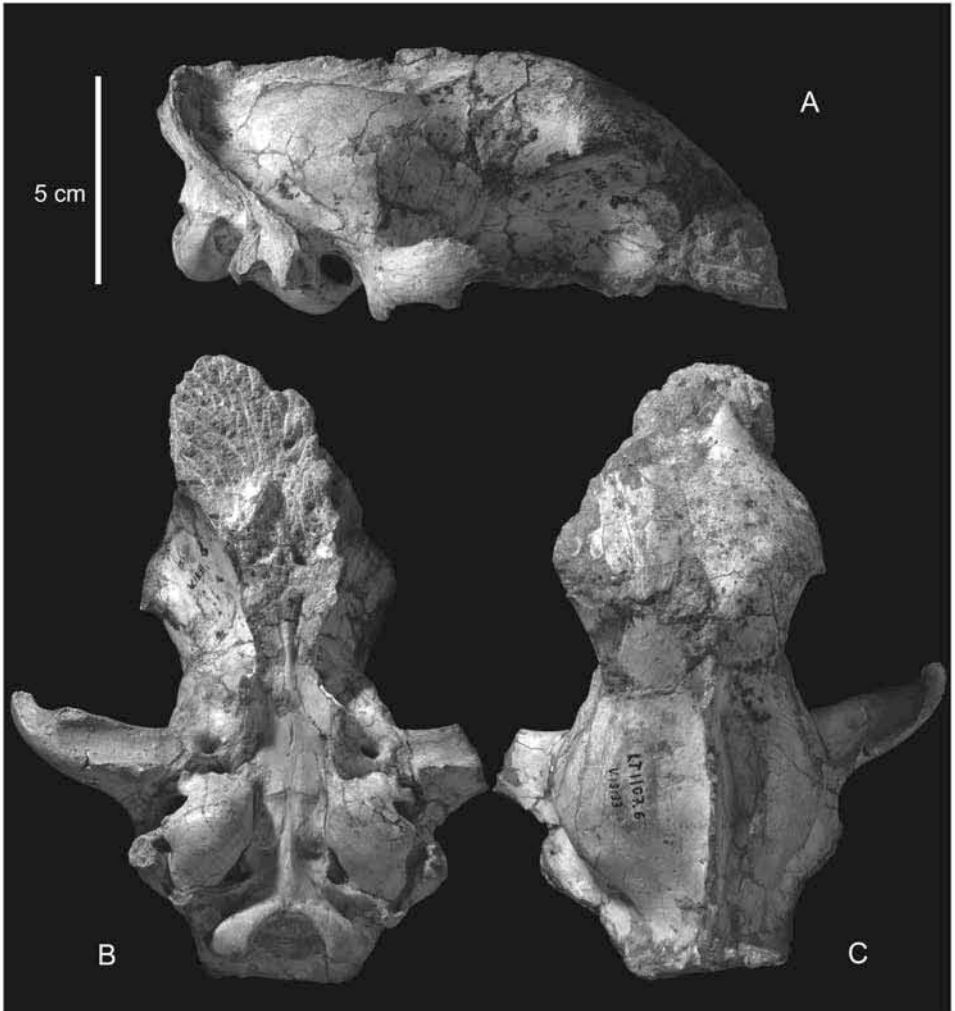


Fig. 7 Skull of cf. *Metailurus parvulus* (IVPP V 13133) from Locality 6
A. right lateral view; B. ventral view; C. dorsal view

envelop most of the caudal ectotympanic chamber. Its relationships to surrounding regions are strongly reminiscent of those seen in *Metailurus*. The sutures do not appear fully closed and the specimen is probably not fully adult.

Discussion Since this specimen lacks the dentition, it is not possible to confirm its taxonomic identity. However, the general morphology of the preserved part is indicative of a machairodont felid, and the size suggests that it should be referred to *M. parvulus*. This species is a relatively common felid in the later Miocene of Eurasia. At several localities it has been found together with its larger congener, *M. major* (see below).

Metailurus major Zdansky, 1924

1924 *Metailurus major* sp. nov. Zdansky, p. 123, pl. 29; figs. 1 ~ 4

Age Bahean – Baodean (~ Vallesian – Turolian).

Referred Lantian material The Lantian material includes several cranial and postcranial specimens from different localities tentatively referred to *M. major*.

cf. *Metailurus major* Zdansky, 1924

IVPP V 14313 (Locality 6), a partial left forelimb (Fig. 8). Elements preserved in this specimen include: proximal radius and ulna, partial manus with carpals, complete metacarpal I and damaged metacarpals II, III, and IV and three unarticulated phalanges. The manus is still in articulation, so not all osteological features could be examined. The scapholunar is broad and flattened, indicating extensive wrist mobility. The metacarpal I has a reduced laterodistal side and an elongated mesiodistal one. Metacarpals II-IV are relatively short and robust. Their shafts are rounded, lacking facets indicating crowding together. All characteristics indicate that this specimen pertains to a medium-sized felid.

IVPP V 14314 (Locality 12), a partial left upper fourth premolar. The tooth is broken behind the parastyle and that cusp and the anterior root are the only parts present.

IVPP V 14315 (Locality 19), a partial left lower canine. Only the apex of the crown is present and a large piece of the lingual side is chipped away. The crown is gently recurved and two ridges run along the anterolingual and posterolingual sides.

Discussion None of these specimens is adequate for positive species identification. A machairodont cat larger than *M. parvulus* is indicated and *M. major* appears to be the most likely candidate of these. Very little postcranial material of *Metailurus* is known, making identification more difficult, but the potential information available from the specimen all the more interesting.

5 Concluding remarks

In addition to the above discussed taxa, the Lantian Carnivoran fauna includes two specimens of the percrocutid *Dinocrocuta gigantean*. Both of these specimens are from Locality 6. They are fully discussed elsewhere (Zhang, in press), and will not be considered further herein.

All of the carnivoran species present in the Lantian material are typical of the later Miocene



Fig. 8 Left forepaw of cf. *Metailurus major* (IVPP V 14313) from Locality 6, in dorsal view

of Eurasia. In fact, the species positively or tentatively identified in the material are among the most common in this time period and region. As such, the material does not provide much information regarding the environment. However, it may be significant that the most common species is *Ictitherium viverrinum*, while *Hyaenictitherium* is less common. This matches the situation seen at Locality 49 of Baode and Pikermi, Greece (Zdansky, 1924; Werdelin, 1988a, b). At other localities, such as Locality 30 at Baode and Samos in Greece the relative abundances between these taxa are reversed (Zdansky, 1924; Solounias, 1981; Werdelin, 1988a, b). The significance of this pattern is at present unknown, but deserves further study.

An interesting feature of the Lantian material is the absence of large machairodont cats. These are very commonly present at Eurasian localities of this time period, including those of Baode (Zdansky, 1924).

Locality 6 and Locality 42 are among the two richest localities in the area. At Locality 6, over 250 fossil specimens were collected from within a couple of meters, making this an unusually rich locality. Taphonomic investigation of the processes active during the formation of this locality indicates that animal remains were transported to, and deposited at this particular site (Andersson, 2004). The accumulation represents a mixture of attritional remains and remains accumulated over a large spatial and temporal space. From a setting like this, it is striking that only moderate-sized felids (cf. *Metailurus major*, cf. *Metailurus parvulus*) were found and no hyaenids (Fig.9).

Locality 42 produced a remarkable number of carnivoran fossils. Taphonomic investigations indicate that this locality was formed through processes limited in time and space. Local environmental or taphonomic conditions at this locality may explain why only hyaenids were found, but precisely what these may have been is not at present clear.

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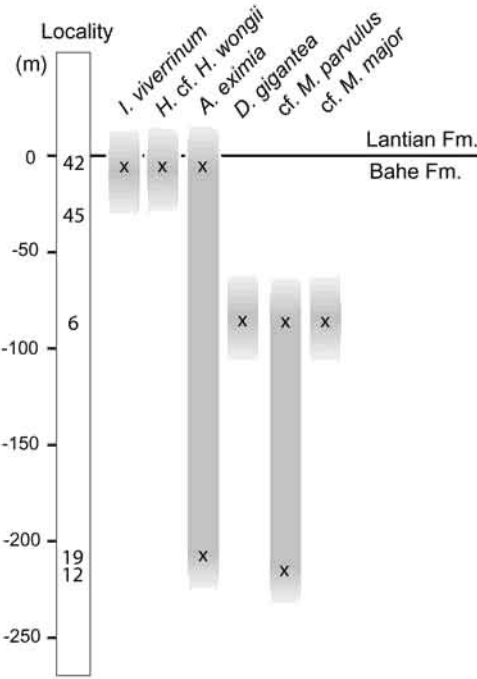


Fig. 9 The ranges of the carnivorous taxa and the position of the localities in the Lantian and Bahe Formation

The x marks the exact stratigraphic position and the shaded area the inferred range of each taxon See Kaakinen and Luncka (2003) for detailed stratigraphy and lithography

coordinating and supervising the project. This work was supported by grants from The Swedish Research Council to LW.

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