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安徽淮南晚新生代鬣狗类化石[1)]

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摘要：记述了安徽淮南地区晚新生代洞穴、裂隙堆积中发现的鬣狗化石。材料系2003年至2006年间由本文作者之一（金昌柱）等在淮南市八公山区进行地层古生物调查时，于大居山老洞、西裂隙及大顶山裂隙的堆积物中采集到的。与鬣狗伴生的其他哺乳动物属种多样，并具有一定的地质断代意义。大居山老洞有 *Pliopentalagus huainanensis*、*Kowalskia* sp.、*Nannocricetus mongolicus* 等，西裂隙有 *Sericolagus* sp.、*Mimomys* sp.、*Equus sanmeniensis* 等，大顶山裂隙则有 *Lepus* sp.、*Ailuropoda* sp.、*Homotherium ultima* 等。

所发现的鬣狗化石包括 *Adcrocuta eximia*、*Chasmaporthetes lunensis* 和 *Crocuta crocuta* 三种。其中 *Crocuta crocuta* 至少包括三个个体；其他两种则只有一个个体。淮南的鬣狗种类跨越了晚中新世至晚更新世。*Adcrocuta eximia* 为欧亚大陆晚中新世的特有种，为鬣狗科中朝食骨方向演化的类群；体型和前臼齿主尖与晚中新世较原始的属种（如 *Hyaenictitherium*）相比，都有壮大的趋势。*Chasmaporthetes* 地理分布最广，除欧亚大陆有多处化石记录外，还出现于北美洲的晚上新世至中更新世动物群中。修长的肢骨与尖利的颊齿表明了其擅长奔跑的能力和主动猎食的习性。该属在淮南的出现突出反映了一种相对开阔的古地理环境。*Crocuta crocuta* 在大居山西裂隙与大顶山裂隙中都有发现。斑鬣狗分布于中国多处的中－晚更新世地点，包括台湾的澎湖列岛。在前臼齿的形态上，*C. crocuta* 与 *Pachycrocuta* 相似，比 *A. eximia* 的宽大，具有更为进步的特征。这说明在早更新世晚期至中更新世早期，*Crocuta* 极可能完全取代了 *Pachycrocuta*。迄今在安徽 *Pachycrocuta* 仅发现于和县与繁昌的洞穴堆积中，由于目前确定高分辨率的洞、裂隙堆积物的地层年代较为困难，安徽的有关动物群是否记录了这个替代事件有待于进一步工作。淮南的鬣狗化石至少涉及了两个不同时期的动物群：一为 *Adcrocuta eximia* 所代表的晚中新世动物群，二为 *Crocuta* 所代表的晚上新世－更新世动物群。*Chasmaporthetes lunensis* 的出现对于年代的确定并无太大帮助，但具有草原习性的 *Chasmaporthetes* 却为动物群的古生态环境分析和重建提供了一些证据。

关键词：安徽淮南，晚中新世－更新世，鬣狗科

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FOSSIL HYAENIDAE (MAMMALIA: CARNIVORA) FROM HUAINAN, ANHUI PROVINCE, CHINA

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Abstract Three species of the family Hyaenidae (Mammalia: Carnivora) from cave or fissure fillings near Huainan, Anhui Province, are described. The bone-cracking hyaenines are represented by *Adcrocuta eximia* and *Crocuta crocuta*. The cursorial or hunting hyaenids are represented by *Chasmaporthetes lunensis*. The presence of *Adcrocuta* indicates a Late Miocene component in the Huainan faunas, whereas *Crocuta* represents a Late Pliocene to Pleistocene faunal element. The occurrence of *Chasmaporthetes* provides evidence for the presence of open habitats, such as grasslands.

Key words Anhui Province, Late Miocene-Pleistocene, Hyaenidae

1 Introduction

Systematic excavation during the past three years by the Institute of Vertebrate Paleontology and Paleoanthropology resulted in a collection of fossil mammals from cave or fissure fillings of Bagong Hill area, northwest of Huainan City, Anhui Province (Fig. 1). Preliminary identification from three localities (Laodong cave, Xiliexi fissure, and Dadingshan fissure) includes *Pliopentalagus huainanensis*, *Kowalskia* sp., and *Nannocricetus mongolicus* from Laodong; *Sericolagus* sp., *Mimomys* sp., and *Equus sanmeniensis* from Xiliexi, and *Lepus* sp., *Ailuropoda* sp., and *Homotherium ultima* from Dadingshan (Jin, 2004). This study describes the hyaenids from the Bagong fissure or cave fillings, including specimens from all three localities.

All three fossiliferous deposits of Bagong Hill are within Ordovician limestone, with sandstone and sandy mudstone fillings. The sediments are reddish to yellowish in color. All three localities have alternating sequences of sandstone and mudstone, ranging from four to six layers. The openings of the fissures or caves range from 6 to 15 meters in width and visible depth. Preliminary interpretation of geologic age puts the localities at the Late Miocene (Laodong), Early Pleistocene (Xiliexi), and Middle Pleistocene (Dadingshan), respectively.

Because of their large geographical distributions in the fossil record, the hyaenids are not good indicators of the environmental and/or faunal affinities of the Huainan faunas. However, morphological differences between taxa of different time periods provide rough estimates of the ages represented by the faunas. The maximum temporal range indicated by the fossil hyaenids described herein spans the Late Miocene to the Holocene. The Huainan faunas, given their location in the region between the Palearctic and Oriental mammalian faunas, probably represent transitional faunas in the zone between the two biogeographic regions of East Asia.

All dental measurements were taken using a Mitutoyo Absolute digital calipers to the nearest 0.01 mm. Log ratio diagrams were constructed for comparison as described in Simpson (1941). No stratigraphic information are known for the specimens described here; thus, ages listed in the systematics section for each respective taxon are known ranges taken from literature.

Tooth abbreviations: c1, lower canine; C1, upper canine; i1, i2, i3, lower incisors; I1, I2, I3, upper incisors; Measurement abbreviations: as in Werdelin and Solounias (1991); Lp2, Lp3, Lp4, Lm1, maximal anteroposterior length of the respective lower tooth; Wp2, Wp3, Wp4, Wm1, maximal transverse width of respective lower tooth; LP2, LP3, LP4, LM1,

maximal anteroposterior length of respective upper tooth; WP2, WP3, WP4, WM1, maximal transverse width of respective upper tooth; Institutional abbreviation: CJ, Dadi Fossil and Mineral Museum, Tainan, Taiwan, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LACM, Department of Mammalogy, Natural History Museum of Los Angeles County, Los Angeles, California, United States; UPM, University of Uppsala Museum of Evolution, Uppsala, Sweden.

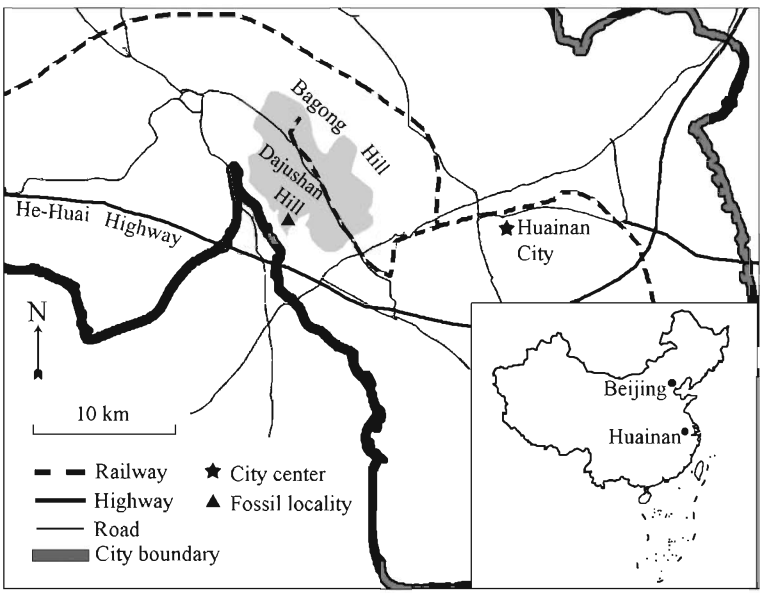

Fig. 1　A local area map of Huainan, Anhui Province showing the localities in the Bagong Hill

2　Systematics

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1869
Genus *Adcrocuta* Kretzoi, 1938
Adcrocuta eximia (Roth & Wagner, 1854)

(Fig. 2; Table 1)

Hyaena eximia Roth and Wagner, 1854
Hyaena variabilis Zdansky, 1924
Adcrocuta eximia Kretzoi, 1938

Material　A right mandibular fragment with p2–4 and broken m1 (IVPP V 15161) from the Laodong cave, Dajushan Hill (32°35′47″N, 117°01′49″E), Huainan, Anhui Province, China, known as latest Miocene age.

Measurement　(see Table 1)

Description　The right mandible is broken both anteriorly and posteriorly, preserving only the region around and below the p1–m1 toothrow. The p1 position is represented only by the alveolus, which is approximately 4 mm in diameter. The enamel margin of p2 is chipped off, except for the medial region. The main cusp of p2 is inflated, but it is impossible to tell whether anterior and posterior accessory cusps were present. The enamel margin of p3 is missing

except for the anterior and medial regions. The main cusp is large relative to the posterior accessory cusp; there is no anterior accessory cusp. The anterior slope of the p3 is outlined by a ridge, which appears straight (as opposed to convex or concave) in lateral profile view. The p4 is missing the anterior and lateral enamel margins, but the anterior and posterior accessory cusps are still visible. The anterior accessory cusp is smaller than the posterior one. There is a cingulum that leads from the posterior edge of the posterior accessory cusp, along the postero-medial margin of the tooth, and ends in a small cusp. Just lateral of this minor cusp is another small cusp that rests just postero-medially of the main cusp. The medial margin of the crown shows a slight bulging above each root in occlusal view. There is very little enamel preserved on the m1; only the dentine portion of the base of the crown, and the roots, are visible. All cheek teeth appear to have two roots, except p1, which has only one root.

Comparison The presence of p1, coupled with robust p2–3 and large size, are diagnostic of the Late Miocene *Adcrocuta eximia*. It is the only taxon with size and dental morphology trending toward larger bone-cracking predators that retains p1; possesses reduction of anterior accessory cusps on p2–3, with relatively large area posterior to the main cusp to accommodate the prominent posterior accessory cusp; and retains both anterior and posterior accessory cusps on p4, with additional accessory cusps postero-medially of the main p4 cusp.

Although all three teeth in this specimen are missing the enamel rim around the enamel-dentine junction (Fig. 2), several characters still distinguish this species from other hyaenid taxa of Anhui. Compared with *Pachycrocuta brevirostris* (known in Anhui from Fanchang and Hexian), the right p4 of V 15161 has a less prominent anterior accessory cusp; that tooth is relatively narrower in *Adcrocuta*, and it possesses two minor medial posterior accessory cusps. In *Pachycrocuta brevirostris*, only one posterior accessory cusp is present, and there is a flat plateau immediately medial to that cusp. The right p3 of the specimen is also narrower in occlusal profile view, and as far as the eye can tell, the enamel-dentine border does not appear to bulge out around each root, as in *Pachycrocuta*. The right p4 is smaller than that of *Pachycrocuta brevirostris*. Even though the ramus itself is fragmentary, it does appear to be both narrower and shallower than those of *Pachycrocuta*.

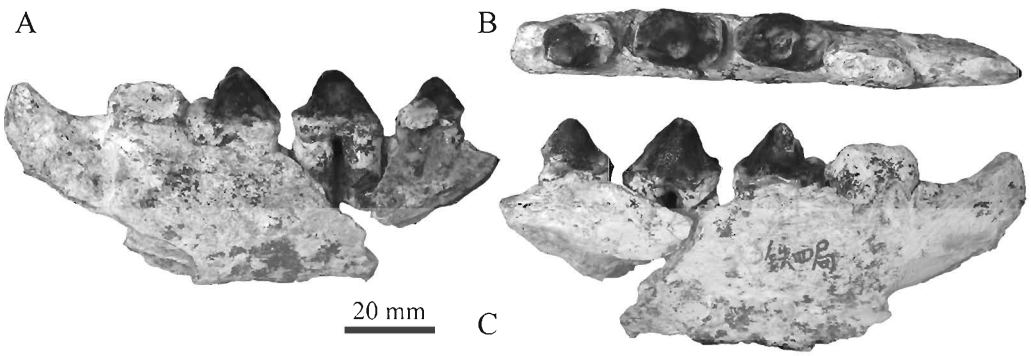

Fig. 2 *Adcrocuta eximia*, partial right mandible with p2–4 and broken m1 (V 15161)
A. lateral view; B. occlusal view; C. medial view

Compared to *Crocuta crocuta*, V 15161 has a smaller p4 posterior accessory cusp, lack of bulging crown bases on p3, a lower-crowned p3, narrower p2, and a more slender ramus.

Compared to *Chasmaporthetes lunensis* from Huainan, the length of p4 on V 15161 is shorter; the main cusp is more prominent at the expense of the anterior and posterior accessory

cusps. This trend is observed in some transitional hyaenids such as *Hyaenictitherium*, and interpreted to be a feature correlated with buttressing the cheek teeth for bone-consumption. The anterior accessory cusp in V 15161 is minute compared to *C. lunensis*. The premolars show no sign of anterior tapering in occlusal profile of the teeth, which is observed in *C. lunensis*. The material of *C. lunensis* described from Yushe, Shanxi Province by Qiu (1987) have prominent p4 accessory cusps. In V 15161, the anterior accessory cusp is small, with no cingulum, and appressed to the main cusp.

Compared with *Adcrocuta* samples from Baode (Localities 30, 49, 108), Shouyang (Xiaokoushan, formerly Hsiao Kou Shan) in Shanxi Province, China, and Pikermi, Greece (Werdelin and Solounias, 1990), the dental dimensions of the Anhui *Adcrocuta* are within measurement ranges (Table 1). The width measurements of V 15161 are underestimates; the medial and lateral enamel margins of the cheek teeth are more incomplete than the antero-posterior margins. Zdansky (1924) has demonstrated the variability in both size and dental morphology in the sample of *A. eximia* from Baode. Thus, it is completely within reason to suggest that the true dental dimensions of V 15161 are within the variation observed for the Baode sample. Log ratio diagram was not constructed for *Adcrocuta* comparisons, because accurate dental dimensions could not be measured with the missing enamel margins.

Table 1　Measurements of the lower premolars p2 through p4 of *Adcrocuta eximia* V 15161 from Huainan, Baode (Shanxi), Shouyang (Shanxi), and Pikermi (Greece)[1)]　(mm)

	Anhui	Baode		Shouyang		Pikermi	
	IVPP	Loc. 30,49,108		(Xiaokoushan)			
	V 15161	mean	range	mean	range	mean	range
Lp2	16.60	16.33	14.8 ~ 17.7	16.33	16.0 ~ 16.6	16.25	15.1 ~ 16.9
Wp2	10.68	11.71	10.6 ~ 13.3	11.43	11.2 ~ 11.8	11.18	10.0 ~ 11.9
Lp3	21.43	19.98	19.1 ~ 21.0	20.35	19.7 ~ 21.0	19.67	18.4 ~ 21.3
Wp3	12.79	13.83	13.2 ~ 14.9	—	—	13.53	12.5 ~ 14.0
Lp4	21.59	20.85	21.7 ~ 22.9	21.65	21.6 ~ 21.7	21.52	18.7 ~ 24.0
Wp4	12.20	13.68	12.2 ~ 14.6	13.17	12.9 ~ 13.6	13.38	12.4 ~ 13.9

1) Sample means and ranges are from Werdelin and Solounias (1990); the Baode and Shouyang samples are from the Uppsala Lagrelius and American Museum Frick Collections.

Genus *Chasmaporthetes* Hay, 1921
Chasmaporthetes lunensis (Del Campana, 1914)

(Fig. 3; Table 2)

Lycyaena lunensis Del Campana, 1914
Lycyaenops lunensis Kretzoi, 1938
Euryboas bielawskyi Schaub, 1941
Chasmaporthetes kani Galiano and Frailey, 1977

Material　A right mandibular fragment with p2–m1 (IVPP V 15162) from Xiliexi, Dajushan Hill (32°35′47″N, 117°01′49″E), Huainan, Anhui Province, China, known as Late Pliocene to Pleistocene age.

Measurement　(see Table 2)

Description　The right mandible is broken anteriorly below p2; posteriorly the ascending ramus is missing, but with the anterior margin of the masseteric fossa still present. The premo-

lars (p2-4) are somewhat teardrop-shaped in occlusal view; the anterior margin of the tooth tapers and is narrower than the posterior margin. The anterior slope of the p2 main cusp has no accessory cusp, but a ridge is present; there is a bulging, prominent posterior accessory cusp on p2. The p3 has a minor anterior accessory cusp, and a prominent posterior accessory cusp. The anterior and posterior accessory cusps of p4 are equal in size, both very prominent even after moderate wear. The lateral and lingual sides of m1 are broken off; the paraconid is slightly longer than the protoconid. The extent of the talonid basin is difficult to observe, since most of it is missing. The premolars all exhibit moderate degree of wear, the p3 being relatively more worn than p2 or p4. From medial view, the toothrow appears to be slightly concave ventrally; the point between p3 and p4 appears to be the shallowest region of the mandibular body.

Table 2 Measurements of the lower premolars p2 through m1 of *Chasmaporthetes lunensis* from Huainan, Anhui; compared with Asian and European samples of *C. lunensis*, *C. ossifragus* from the United States, and *C. borissiaki* from Moldavia[1)] (mm)

	Anhui	*C. lunensis*	*C. lunensis*	*C. ossifragus*		*C. borissiaki*
	IVPP	Asia	Europe	United States		Moldavia
	V 15162	mean	mean	mean	range	
Lp2	17.44	16.11	16.77	17.83	17.4 ~ 18.6	15.80
Wp2	9.90	9.00	9.26	9.87	9.7 ~ 10.2	8.40
Lp3	21.40	19.20	20.00	21.63	20.0 ~ 22.5	19.30
Wp3	11.69	10.61	10.97	11.53	10.8 ~ 12.3	10.20
Lp4	25.15	22.50	24.28	25.20	25.0 ~ 25.5	22.80
Wp4	12.64	11.31	11.88	12.27	12.0 ~ 12.6	11.60
Lm1	—	25.05	25.06	28.10	26.1 ~ 29.5	24.80
Wm1	11.87	11.01	11.53	12.00	11.8 ~ 12.1	9.80

1) All comparative data are from Kurtén and Werdelin (1988). Measurement ranges were not available for the *C. lunensis* comparisons. The sample size of each dimension measurement in the Asian sample ranged from seven to ten; in the European sample it ranged from three to nine.

Comparison The described specimens in most characters correspond to the diagnosis of the genus *Chasmaporthetes*. These characters are the deep and narrow mandible with non-bulged main cusps on premolars; the minor anterior accessory cusps on p2 and p3, compared to more prominent posterior accessory cusps; the large anterior and posterior accessory cusps on p4; the longer paraconid than the protoconid on m1, with reduced talonid basin. In addition, slight bulging is visible on the medial margins of enamel-dentine border of lower premolars.

There are at least seven recognized species of *Chasmaporthetes* since the genus was reviewed by Kurtén and Werdelin (1988): *C. progressus*, *C. borissiaki*, *C. exitelus*, *C. lunensis*, *C. melei*, *C. nitidula*, and *C. ossifragus*. *Chasmaporthetes melei* is an endemic island form from Late Pliocene-Early Pleistocene fissure fillings of Sardinia, Italy (Rook et al., 2004). *Chasmaporthetes borissiaki* is a small form from the Early Pliocene of Moldavia (Khomenko, 1932). The absence of p2 anterior accessory cusp and the minor p3 anterior accessory cusp in the Anhui specimen are distinct from the well developed p2-3 accessory cusps of *Chasmaporthetes nitidula* from the Early Pleistocene of South Africa. A comparison is made between the Anhui *Chasmaporthetes* and *C. borissiaki*, *C. ossifragus*, and European and Asian samples of *C. lunensis* (for detailed description see Kurtén and Werdelin, 1988) using a log ratio diagram (Fig. 4). From dimensions of the lower dentition, the Anhui specimen is clearly closer to the

mean measurements of *C. ossifragus* than either the European or Asian *C. lunensis*; it approaches *C. ossifragus* in its larger size and increased robustness of the cheek teeth. Although *C. ossifragus* from North America may be very similar to *C. lunensis*, Werdelin and Solounias (1991) kept them as separate taxa. This was based on the argument that by synonymizing *C. lunensis* and *C. ossifragus* the resulting taxon would stretch the species concept established by studies of well-known hyaenids such as *Hyaenictitherium wongi* (Werdelin, 1988). The current taxonomy of *Chasmaporthetes* appears to be heavily regionalized, and an evaluation of inter-regional variation is probably required to clarify these issues. No attempt will be made here to revolve the taxonomy, as they are beyond the scope of this study. Thus, only the relationship between the Anhui specimen and known Chinese *Chasmaporthetes* will be considered.

Kurtén and Werdelin (1988) reviewed the then known species of *Chasmaporthetes*, and named *C. exitelus*. Along with *C. lunensis honanensis*, *C. exitelus* represents the Chinese *Chasmaporthetes*. Whereas *C. exitelus* occurs in the Late Miocene of China, *C. lunensis* occurs during the Nihewanian (Late Pliocene-Pleistocene). *Chasmaporthetes exitelus* was described from an incomplete palate, and other than the fact that it has narrower palatal width than *C. lunensis*, the dental dimensions are otherwise similar between the two species (Kurtén and Werdelin, 1988). From the relatively deep mandibular body of V 15162, it is referred to the more robust form *C. lunensis*, rather than *C. exitelus* (Fig. 3). However, discovery of the lower dentition of *C. exitelus* could change this conclusion. The other Chinese form, *Chasmaporthetes progressus*, was raised from subspecific status within *C. kani* (= *C. lunensis* sensu Kurtén and Werdelin, 1988) by Qiu et al. (2004) based on differences in the morphology of the nasal bones and larger size. Qiu et al. (2004) listed ten *Chasmaporthetes* species, but only compared four of them in their description of *C. progressus*. An important feature in Qiu et al.'s (2004) discussion included the shape of the nasal bones; their morphology apparently provides an interpretation of species differences in disagreement from Kurtén and Werdelin (1988). The only lower teeth known for *C. progressus* are from Shanxi (Qiu, 1987), including a pair of p4–m1. Both p4s (IVPP V 7279; lengths 25.3 and 25.6 mm, widths 12.0 and 11.8) are longer and narrower than the Anhui specimen. For m1, the only comparable measurement is its width, which are similar between the Anhui (11.87 mm) and Shanxi (11.9 mm) *Chasmaporthetes*. Thus, the Anhui specimen is still most similar to the American *C. ossifragus* in the robustness and size of its teeth than the Chinese *C. progressus*.

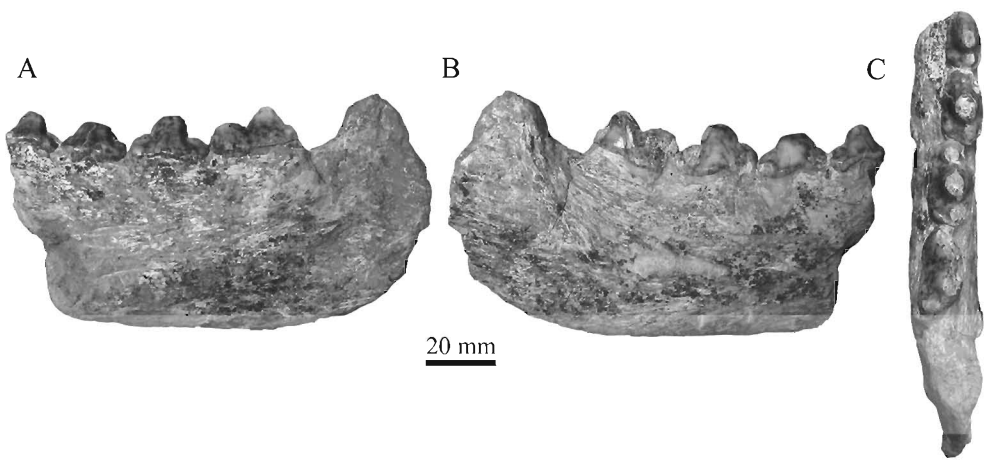

Fig. 3　*Chasmaporthetes lunensis*, partial right mandible with p2–m1 (V 15162)
A. medial view; B. lateral view; C. occlusal view

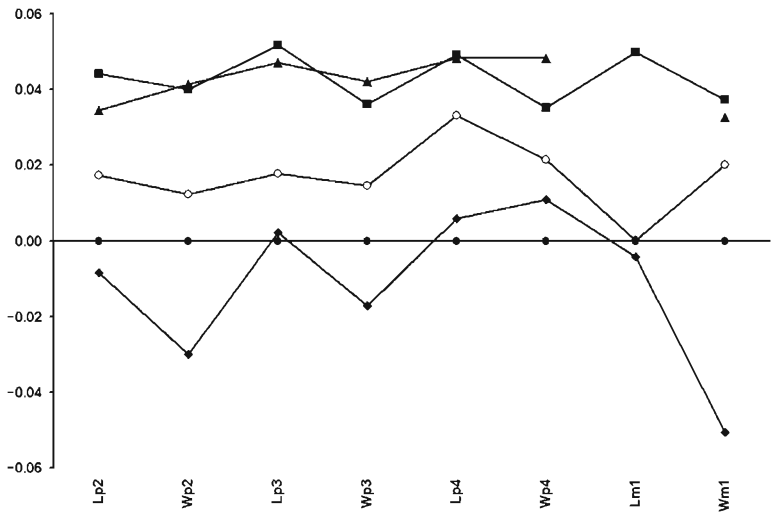

Fig. 4 Log ratio diagram comparing the lower teeth of *Chasmaporthetes lunensis* V 15162 from Huainan (triangle), *C. ossifragus* sample from the United States (square), European sample of *C. lunensis* (open circle), Chinese sample of *C. lunensis* (filled circle; as standard), and *C. borissiaki* (diamond) from Moldavia Comparative measurement data were taken from Kurtén and Werdelin (1988); the length of m1 of V 15162 is not plotted; the talonid basin is broken, thus an accurate measurement could not be made

Genus *Crocuta* Kaup, 1828

Crocuta crocuta (Erxleben, 1777)

(Figs. 5-8; Table 3)

Canis crocuta Erxleben, 1777
Crocuta crocuta Kaup, 1828
Hyaena ultima Matsumoto, 1915
Hyaena ultima Zdansky, 1927
Hyaena ultima Pei, 1934
Crocuta ultima Huang, 1989

Material A right mandibular fragment with p2 - 4 (V 15160) from Dadingshan (32°35′47″N, 117°01′49″E, ~2 km northwest of Dajushan Hill); a left mandibular fragment with c1 - p4 (V 15163), a premaxilla and anterior maxillary fragment with left and right I1 - C1 (V 15164.1), a left maxillary fragment with P3 and anterior P4 (V 15164.2), a mandibular fragment with left p2 (V 15164.3), a mandibular fragment with partial left m1 (V 15164.4), a right c1 (V 15164.5), a right c1 (V 15164.6) from Xiliexi, Dajushan Hill; known as Late Pliocene age to Recent.

Measurement (see Table 3)

Description The anterior jaw (V 15164.1) has two parallel anterior palatal foramina that diverge posteriorly at the premaxilla-maxilla suture border; I1 - 2 have two accessory cusps immediately posterior to the spatula-shaped main cusp; I2 is slightly larger than I1; I3 is more than twice the size of I1 or I2; it has both a lingual and a labial ridge that runs from the tip of the cusp to the base of the tooth, the ridges are connected posteriorly by a horizontal ridge running parallel to the enamel-dentine border (Fig. 5). The upper canines are oval in cross-section; the long axis is antero-posteriorly oriented, with ridges on both the anterior and posterior slopes of the teeth. Upper cheek teeth are represented by left P3 and partial left P4 (V 15164.2). P3 has both anterior and posterior accessory cusps; the anterior one is offset lingually, and ap-

pears appressed to the large main cusp. The posterior accessory cusp on P3 is independent of the main cusp, and is border posterior by a low cingulum.

Table 3　Dental dimensions of *Crocuta crocuta* from Huainan; comparisons are made to *C. crocuta* from Zhoukoudian (Pei, 1940), Yushe (Qiu, 1987), Penghu (Ho et al., 1997), and Henan (Zdansky, 1924)[1)]　(mm)

	Huainan, Anhui Province			Zhoukoudian	Yushe
	V 15164.3-4	V 15160	V 15163		V 7296
Lp2	15.52	16.47	15.70	17.30	14.30
Wp2	10.10	11.64	11.69	13.50	9.50
Lp3		22.75	21.99	24.01	19.40
Wp3		16.74	14.56	16.40	13.50
Lp4		23.99	23.96	25.20	21.90
Wp4		14.49	14.52	15.00	13.30
Lm1	24.44			35.50	24.20
Wm1	13.11			14.60	12.60
	Huainan	Penghu	Zhoukoudian	Henan	
	V 15164.2	CJ-0013		UPM M1975	
LP3	22.12	23.73			
WP3	17.20	18.28			
LP4			42.90	35.40	
WP4	21.16		21.00	20.50	

1) Zhoukoudian and Penghu specimens have been assigned to *C. crocuta ultima*; Yushe and Henan specimens were assigned to *C. crocuta honanensis*.

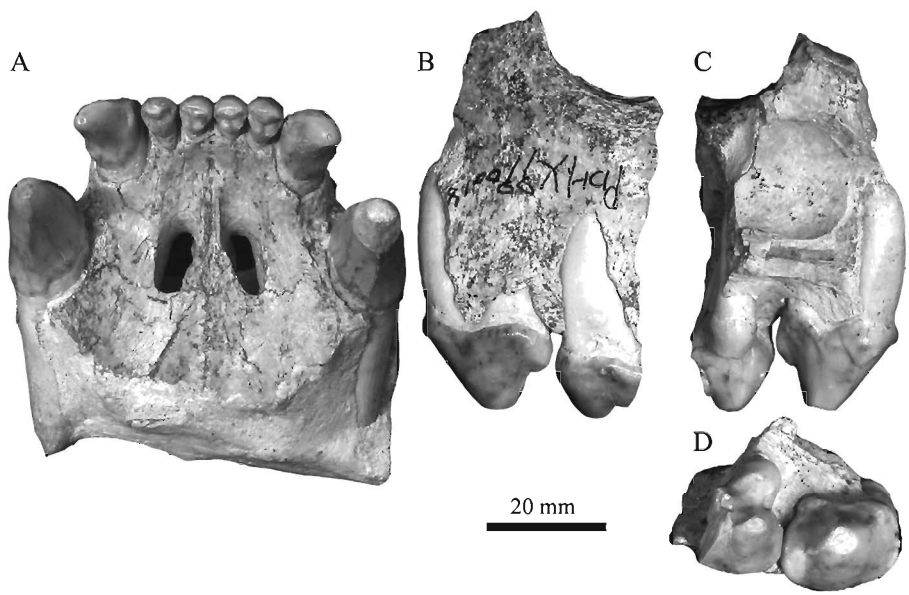

Fig. 5　*Crocuta crocuta*

A. anterior maxillary and premaxillary fragment, with left and right I1-C1 (V 15164.1); B-D. left maxillary fragment with P3 and partial P4 (V 15164.2), B. lateral view, C. medial view, D. occlusal view

V 15164.3 and V 15164.4 are two lower left mandibular fragments (Fig. 6). The smaller fragment contains p2 and a small portion of the horizontal ramus, preserving a single, large

mental foramina directly below p2; the tooth has a small anterior accessory cusp, and a large posterior accessory cusp. The margins of p2 are bulging around each root in occlusal view. The large mandibular fragment has a partial m1 with paraconid preserved; the jaw is deep, and convex medially in cross-section. The very anterior tip of the masseteric fossa is preserved, appearing as a deep indentation on the lateral side of the mandible. The postero-lingual region of the m1 is missing, but from the labial side a small talonid basin can be discerned. From occlusal view, the tooth appears wider anteriorly and tapers off posteriorly, but the missing enamel contributed to this appearance. Two isolated left c1s (V 15164.5 and V 15164.6) are found along with other fragments; both appear little worn, and have two labial ridge down the length of the tooth. The ridges run from the anterolabial and posterolabial faces of the tooth to the enamel-dentine border, respectively.

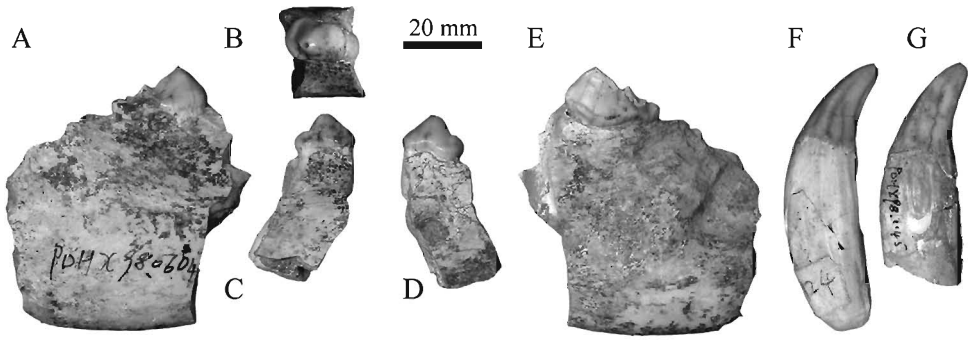

Fig. 6 *Crocuta crocuta*
A–E. left mandibular fragment with p2 (V 15164.3) and left mandibular fragment with partial m1 (V 15164.4), A, C. medial view, B. occlusal view of p2, D, E. lateral view; F. right c1 (V 15164.5), lingual view; G. right c1 (V 15164.6), lingual view

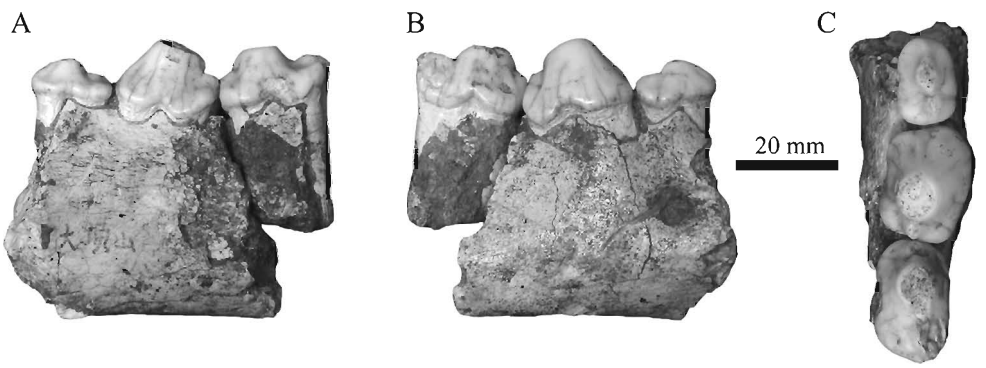

Fig. 7 *Crocuta crocuta*, right mandibular fragment with p2–p4 (V 15160)
A. medial view; B. lateral view; C. occlusal view

The lower mandibular fragment with p2–4 (V 15160) shows moderate wear on the tooth occlusal surfaces (Fig. 7). The p2 has a small anterior accessory cusp and a larger posterior accessory cusp. The p3 has only a posterior accessory cusp; the anterior slope of the main cusp is marked by a ridge which widens near the enamel-dentine border to form a short cingulum antero-lingually. The p4 has a small anterior accessory cusp, and a large posterior accessory cusp that's twice in size; a narrow cingulum runs from the posterior edge of the posterior accessory

cusp lingually to form a minor cusp at the postero-lingual border of the tooth. The p3 is wider than p4; both show bulging margins above the root on the lingual side. The mandibular fragment is roughly oval in cross-section; the anterior face shows a circular cross-section of the canine root. There is a single, large mental foramen below the p2.

Another lower mandible (V 15163) shows more extensive wear on the teeth (Fig. 8). The c1 is heavily weathered, with only a small amount of enamel left on the anterior and labial facies of the tooth. The anterior edge of p2 is worn, and it is impossible to tell whether an anterior accessory cusp was present; the posterior accessory cusp is present on the unworn p2. The p3 is worn down to within 10 mm of the enamel-dentine border; there is no anterior accessory cusp, and the main cusp has worn to the degree that a large dentine lake combines the posterior accessory cusp with the main wear surface. Both accessory cusps and the main cusp are worn on p4; the wear surfaces have connected on all three cusps. The p4 does not appear much wider than p3 in occlusal view. The mandibular fragment is broken posterior of the p4 position; there is a diagonally oriented, rugose mandibular symphysis just medial of the canine. There is one large mental foramen below p2. The mandible appears convex lingually below the p4 position, whereas it is roughly oval in cross-section below the p2-3 positions.

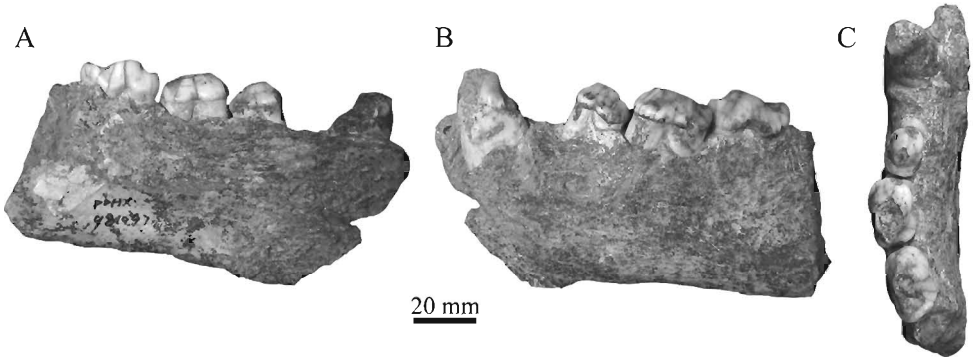

Fig. 8　*Crocuta crocuta*, left mandibular fragment with c1-p4 (V 15163)
A. medial view; B. lateral view; C. occlusal view

Comparison　The specimens described above are referred to the genus *Crocuta* by possession of the following characters: a large-sized hyaenid, but smaller than *Pachycrocuta*; P4 protocone and parastyle being equal in size, and the protocone being not reduced as in *Adcrocuta*; P3 and p3 having small or no anterior accessory cusps, a condition contrasting the prominent anterior accessory cusps of *Chasmaporthetes* premolars; talonid basin of m1 being very reduced, more so than in *Pachycrocuta*, which retains the entoconid; the enamel margins above each root on the premolars being not as bulbous in occlusal view as observed in *Pachycrocuta*.

Compared to a recent specimen of *Crocuta crocuta*, the Huainan *C. crocuta* are slightly larger in overall size, but very comparable in most dimensions (Fig. 9). They are somewhat smaller when compared to a specimen from Zhoukoudian, Beijing. Within China, two subspecies, *C. crocuta honanensis* and *C. crocuta ultima* have been recognized (Huang, 1989), although Qiu et al. (2004) maintains the specific status of *C. honanensis*. A specimen from Yushe, Shanxi Province that was identified as *Crocuta crocuta honanensis* by Qiu (1987) is smaller than any of the other *C. crocuta*. In addition, the specimens of *C. honanensis* (= *C. crocuta honanensis*) from Longdan (Qiu et al., 2004) are smaller than the Anhui specimens. Therefore, if subspecific status was to be assigned to the Huainan specimens, they would be closer to *C. crocuta ultima* represented in Figure 9 by the Zhoukoudian specimens. The similarity in dental measurements of Huainan *Crocuta* and samples of *C. crocuta ultima* can also be seen in Table 3.

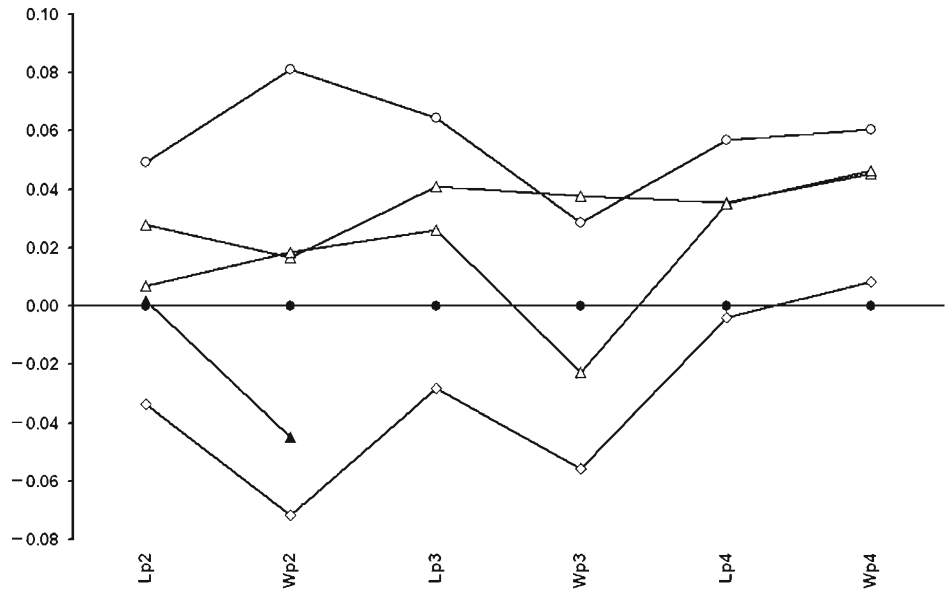

Fig. 9 Log ratio diagram comparing dimensions of the lower teeth p2–p4 of *Crocuta crocuta* from Huainan with specimens from other Chinese localities; measurements of a recent specimen of *C. crocuta* from Kenya serves as the standard (LACM 30655; filled circle)
The Huainan specimens are IVPP V 15160 (open triangle), V 15163 (shaded triangle), V 15164.3 (black triangle); *Crocuta crocuta* from Zhoukoudian, Beijing (Pei, 1940) is open circle; *C. crocuta* from Yushe, Shanxi Province (Qiu, 1987) is diamond

3 Discussion

All three taxa of hyaenids described in this study are first occurrences within Anhui Province. The other known occurrences of hyaenids in Anhui are in the Renzidong fissure fillings of Fanchang County (Jin et al., 2000) and cave deposits of the hominid site in Hexian (Huang et al., 1982), both being *Pachycrocuta brevirostris*. The new occurrences extend the temporal range of hyaenids in Anhui to Late Miocene-Holocene, broader than what was previously represented by *Pachycrocuta*, which is only Late Pliocene to Middle Pleistocene in age.

Judging from the known temporal ranges of the hyaenids occurring in Huainan, at least two time periods are represented by the three taxa. The Late Miocene is represented by *Adcrocuta eximia*, which has not been found, with absolute dates, in the Plio-Pleistocene (Werdelin and Solounias, 1991). Although this species is found with other hyaenids of Plio-Pleistocene affinity, it would be unreasonable to extend the range of *A. eximia* in the absence of detailed stratigraphic information. The cave or fissure fillings at Huainan could very well represent time-averaged faunas that have accumulated since the Mio-Pliocene; this is supported by the presence of multiple layers of sandstone and sandy mudstone at Huainan.

The other hyaenids (*Chasmaporthetes* and *Crocuta*) are both known as Plio-Pleistocene forms. *Crocuta* represents one of the most widespread bone-cracking hyaenids of the Old World during the Plio-Pleistocene (Werdelin, 1999); the genus has been found from western Europe to South Africa, and to coastal East Asia. This genus also coexisted with the larger *Pachycrocuta brevirostris* in many localities throughout Eurasia for the better part of Late Pliocene-Early Pleistocene. But sometime during the Early to Middle Pleistocene, *Pachycrocuta* was completely replaced by *Crocuta* (Pei, 1934, 1940), which then persisted until as late as 7 815 years before

present in China (Ma and Tang, 1992). The age range of *Crocuta* is consistent with an age of Early to Middle Pleistocene, as indicated by the other mammalian taxa in the Xiliexi and Dadingshan localities. This age cannot be more resolved at the present time; even though both *Pachycrocuta brevirostris* and *Crocuta crocuta* are found in Anhui Province in fissure or cave fillings, the possible time-averaging effects of fissure or cave accumulation prevents the clarification of this replacement event locally in Anhui.

The genus *Chasmaporthetes* reached its taxonomic as well as geographic climax during the Plio-Pleistocene, occurring in North America for the first time in hyaenid family history (Hendey, 1975). No other genera of hyaenids were ever able to range outside of Eurasia and Africa. Although the genus has been known to occur since the Late Miocene (Kurtén and Werdelin, 1988), the Chinese species *C. lunensis honanensis* (= *C. lunensis*) is found only from the Plio-Pleistocene. Thus, the occurrence of this species in Huainan further supports the Late Plio-Early Pleistocene age represented by *Crocuta*.

In addition, the known postcranial skeletons of *Chasmaporthetes* indicate a highly cursorial hyaenid group. The teeth also demonstrate a trend towards hypercarnivory (Kurtén and Werdelin, 1988). These are all indicators of an open-terrain predator, much like the modern-day cheetah (*Acinonyx jubatus*) in Africa. The central location of Huainan within China suggests that the entire region might have been something of an ecotone between the northern, open terrain Palearctic fauna and the southern, tropical Oriental fauna. The interpretation from the hyaenid guild in Huainan would suggest the presence of grassland faunal components during at least part of the Plio-Pleistocene of Huainan.

In conclusion, there are three currently recognized species of hyaenids from Bagong cave or fissure fillings near Huainan, Anhui Province, China: 1) *Adcrocuta eximia* representing a Late Miocene bone-cracking hyaenid, 2) *Chasmaporthetes lunensis* representing a Plio-Pleistocene cursorial hunting hyaenid, and 3) *Crocuta crocuta* representing a medium to large-sized bone-cracking hyaenid from the Pliocene into the Holocene of China. These hyaenids represent at least two faunas, one being Late Miocene in age, and the other Plio-Pleistocene. In addition, the presence of *Chasmaporthetes lunensis* represents the presence of open terrain in Huainan during part of the Plio-Pleistocene.

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