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COMPARISON OF NEOGENE LOW-CROWNED *HYSTRIX* SPECIES (MAMMALIA, PORCUPINES, RODENTIA) FROM EUROPE, WEST AND SOUTHEAST ASIA

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ABSTRACT

The low-crowned *Hystrix* species known of the Neogene from Europe and Asia and some new finds from Shihuiba near Lufeng, South China, are compared on the basis of numerical data. The taxonomical allocation of the seven species recognised thus far is maintained. The occurrences of two coeval Eurasian late Turolian species is discussed. The material from Lufeng is described and allocated to *Hystrix primigenia* (Wagner, 1848), implicating an area of distribution of this species from S.E. Europe to S.E. Asia in the Turolian. In the northern Chinese Hystricidae the increase of the cheek tooth height is more advanced than in the the West Asiatic and European representatives. The difference in ecological environment of *Hystrix gansuensis* Wang & Qiu, 2002 (North China) and *Hystrix primigenia* from Lufeng (South China), both of Baodean age, is discussed.

Key words: *Hystrix*, Neogene, Europe, Asia, Shihuiba, Lufeng, Gansu, China

INTRODUCTION

All Miocene *Hystrix* species have relatively low-crowned cheek teeth, in the Pliocene both low- and high-crowned porcupines occurred, and from the Pleistocene only high-crowned ones are known. The species *Hystrix primigenia* (Wagner, 1848), *Hystrix parvae* (Kretzoi, 1951) and *Hystrix depereti* Sen, 2001 are known from the Late Miocene of Europe. The species *Hystrix aryanensis* Sen, 2001 has been described from West Asia, Afghanistan. Qiu et al. (1985) mentioned the first finds of a low-crowned porcupine from the Miocene of China at Shihuiba, near Lufeng, Yunnan Province, present in the collections of the Institue of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing. They indicated the extent of these finds, referred to a previous mention of them by Qi Guo-qin (1979) but did not give descriptions. *Hystrix zhengi* Van Weers & Zhang, 1999 is another low-crowned Chinese species reported from the Late Pliocene of Longgupo, Sichuan Province. Recently Wang & Qiu (2002) described the species *Hystrix gansuensis* from the Late Miocene of the Gansu Province in North China and presented measurements of this species. They compared it with a large number of extant and fossil *Hystrix* species without applying numerical data. They also did not give measurements of the thus far undescribed material of the

Table 1. Length of cheek teeth in mm of some fossil *Hystrix* species with means, range and number of teeth. The number of specimens (in parentheses) may be smaller than the number of teeth (n) in the cases where measurements of both left and right teeth from the same serial positions are used.

	P4			M1/2			M3			P4-M3		
	mean	range	n	mean	range	n	mean	range	n	mean	range	n
H. parvae	-	7.3-8.0	3	7.2	6.7-8.1	10	-	-	-	-	-	-
H. depereti	11.7	11.0-12.5	6	10.2	9.2-11.2	19	9.3	8.7-10.0	6	43.2	40.5-45.0	3
H. primigenia	10.9	10.1-11.5	5	9.4	8.7-10.0	12	8.6	8.0-9.3	7	39.2	38.2-41.0	5
Lufeng spec.	10.6	10.0-11.0	3	8.7	7.6- 9.8	10	8.5	8.0-8.9	2	35.2	33.8-36.6	2
H. gansuensis	10.7	10.0-11.4	4(2)	9.5	8.4-10.1	11(7)	8.5	8.1-8.7	3(2)		39.1	1
H. aryanensis		11.0		8.7	8.8-9.0	6(2)		8.4	1		34.8	1
	p4			m1/2			m3			p4-m3		
H. parvae		7.6-8.9	2	7.4	7.1-8.0	8	-	-			30.0	1
H. depereti	12.4	10.7-13.2	8	11.3	10.2-13.1	22	10.2	9.6-10.8	8	46.4	44.0-47.5	4
H. primigenia	11.3	10.7-12.2	8	10.2	8.8-11.6	15	9.8	9.4-10.4	5	40.0	38.2-43.4	5
Lufeng spec.	11.1	10.4-11.4	4	9.1	8.1- 9.8	6	8.9	8.6 - 9.2	3		38.8	1
H. zhengi	11.7	11.0-12.2	4		-			-			-	

porcupine from Lufeng. Lately Lopatin et al. (2003) described *Hystrix caucasica* (Argyropulo, 1939) from the late Pliocene of the Caucasus which originally had been attributed to the Castoridae. The purpose of this paper is to present measurements of the Lufeng porcupine, to compare all the low-crowned *Hystrix* species from the Neogene of Europe and Asia metrically and to establish their taxonomic allocation.

MATERIALS AND METHODS

Cranial characters are not considered because skulls of most species are fragmentary or not available at all. The occlusal patterns of the cheek teeth of all *Hystrix* species, fossil as well as extant, are basically similar. These patterns show individual variation in comparable stages of wear and change greatly as a result of attrition. The homology of islets and folds is often difficult to establish, so the occlusal patterns are of limited use for specific distinction of small samples. For this reason we refrain from detailed morphological descriptions of cheek teeth. Comparisons are made on the basis of the dimensions of the cheek teeth because size and crown height are considered diagnostic characters.

The numerical data presented (Table 1) of *H. parvae*, *H. primigenia*, *H. depereti* and *H. aryanensis* are based on revisions of these species (Van Weers & Montoya, 1996; Van Weers & Rook, 2003). The measurements of *H. gansuensis* are from Wang & Qiu's (2002) original description, those of *H. zhengi* are after Van Weers & Zhang (1999), and the material from Lufeng was measured by the author (Tables 2, 3). A number of teeth in this collection do not belong to *Hystrix*, and some *Hystrix* teeth were not considered because they were either damaged, totally worn, very young or deciduous teeth. The material studied, IVPP 75033, consists of a tooth series P4-M3, a maxillary fragment with P4-M3, a mandible fragment with p4-m3 and some isolated teeth, 1 P4, 6 M1/2, 3 p4, 4 m1/2 and 2 m3. Most of these are figured (Fig. 1, 1-16). The measurements of *H. caucasica* are after Lopatin et al. (2003).

Upper teeth are indicated in upper case, lower ones in lower case. The greatest width and length of each tooth has been taken by Vernier callipers. The largest enamel height (EH) has been measured lingually in the upper cheek teeth, buccally in the lower teeth. The relative height of the cheek teeth (EH/L) is expressed as a percentage of the length.

The wear classes of the upper cheek teeth,

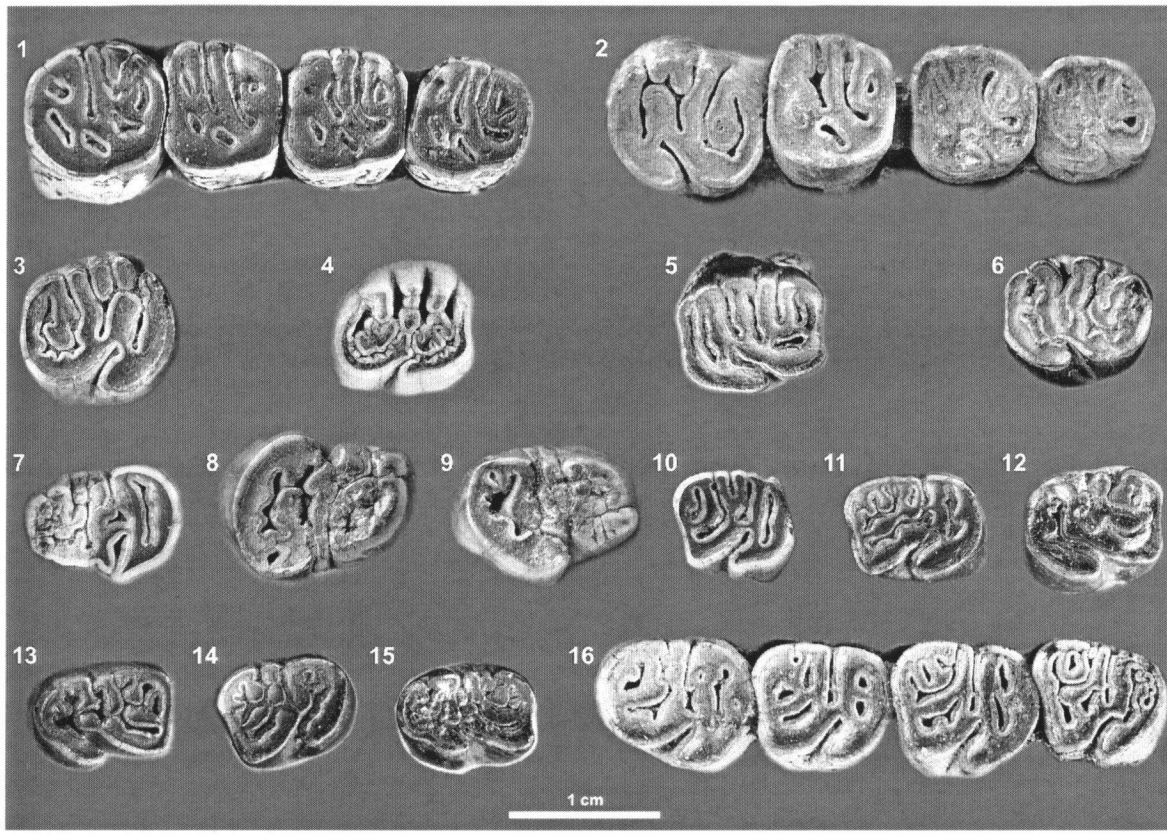

Fig. 1. Occlusal view of cheek teeth of the porcupine from Shihuiba near Lufeng, S. China, coll. IVPP 75033. 1 and 2 = left P4-M3, 3 = right P4, 4 = right M1/2, 5 and 6 = left M1/2, 7 and 8 left p4, 9 = right p4, 10 and 11 = left m1/2, 12 and 13 = right m1/2, 14 = left m3, 15 = right m3, 16 = left p4-m3. For measurements and wear class see Tables 2 and 3.

from unworn to nearly totally worn, are indicated from A to G, the lower teeth from O to T. For the definition and subdivision of these wear classes see Van Weers (1990). The occlusal view of most Lufeng specimens studied are given in Fig. 1, 1-16. In these figures and in the relevant tables (Tables 2, 3 and 4) the classes of wear are given. These classes do not always fit the definitions because these are based on the extant, high-crowned species *H. brachyura* Linnaeus. The occlusal patterns are basically similar in the Neogene species, but often a larger number of the folds and islets that potentially may occur are present in the different stages of wear. Therefore an approximate indication of a class of wear is given by means of a combination of two characters. The distinction between upper and lower molars is partly based on the curved character of upper teeth, but in low-crowned cheek teeth this distinction is difficult. Moreover, in certain stages of wear the occlusal surface of a right upper molar resembles that of a left lower one, so mistakes cannot be excluded.

RESULTS

H. parvae is distinguished from all the species discussed here by its clearly smaller size (Table 1). The mean length of the Lufeng teeth is slightly smaller than in *H. primigenia* and clearly smaller than in *H. depereti* (Table 1). Most of the means of the relative height of the Lufeng teeth (Table 4) are slightly larger than in *H. primigenia*, but they are all below 100%. These dimensions do not differ significantly from *H. primigenia*, so the porcupine from Lufeng is allocated to that species.

The length of the teeth of *H. gansuensis* (Table 1) agrees quite well with *H. primigenia*, but its relative height (Table 4) is higher, even when it is taken into account that the teeth of *H. gansuesis* are nearly unworn (Class A-D). The specific identity of *H. gansuensis* is maintained because its

Table 2. Measurements in mm of upper cheek teeth from the Miocene of Lufeng, China, IVPP 75033, with serial and figure number, length of tooth series, width, length, enamel height and wear class.

P4-M3					
Nr.	Fig.	Alv. Lth.			
1	1	33.8			
26	2	36.6			
P4					
Nr.	Fig.	Wth.	Lth.	E. Ht.	Class
1	1	9.8	10.0	8.0	E
2	3	10.4	11.0	8.9	B
26	2	11.0	10.7	9.0	B/C
M1/2					
1	1	9.4	8.0	5.4	E
1	1	8.8	8.4	6.2	F
3	5	9.2	9.5	9.7	B/C
4	6	8.3	9.8	11.1	B2
5	-	7.5	7.6	8.8	D5
6	4	9.1	9.0	10.4	B
7	-	8.5	8.1	6.2	E
8	-	9.3	8.3	5.6	E
26	2	9.1	9.7	-	D
26	2	8.7	8.2	-	F4
M3					
1	1	8.6	8.9	7.1	G1
26	2	8.0	8.0	9.5	F4

enamel height is larger than in *H. primigenia*, though not as high as in Pleistocene species in which relative heights (EH/L) of more than 250% are reached (Van Weers, 1994).

H. aryanensis is only slightly smaller than *H. primigenia*, and thus smaller than *H. depereti* (Table 1). Its teeth are higher than in *H. primigenia* and the mean (117%) falls within the range (62-150%) of *H. depereti* (Table 4). The species *H. aryanensis* is maintained, not only on the basis of its smaller size and larger tooth height, but also on a character in its occlusal morphology. The strong connection between the second buccal and the lingual fold persists in relatively advanced stages of wear (Sen, 2001). This holds for some teeth of the two specimens which compose the hypodigm of the species, but not for all of them. More material is needed in order to find out if the connection between the second buccal and the lingual fold is a stable character in this species.

The hypodigm *H. zhengi* consists of four p4 only (Table 1). These teeth do not differ significantly in size from *H. primigenia*, but the mean relative crown height of *H. zhengi* (95.7%, range 90-100%, Class P-Q) is larger than that of *H. primigenia* (Table 4). Therefore the species *H. zhengi* is maintained.

In their discussion of the Late Miocene-Early Pliocene porcupines from southern Russia Lopatin et al. (2003) consider the depth of the anteroflexid of the p4 from the northern Caucasus, the type and only specimen of *Hystrix caucasica* (Argyropulo, 1939), to be characteristic for this species. Since we have established that the depth of the anteroflexid is a function of tooth wear, the value of this characteristic is limited. However, this specimen is large, even larger than the largest specimen of *H. depereti*, and has a relatively low crown when the hypsodonty index (H/L= 0.90) is calculated as suggested by Sen (2001), who uses crown height divided by maximum length instead of occlusal length. The type p4 of *H. caucasica* is thus unique in combining a size that is more similar to that of *H. depereti* with a crown height that is similar to that in *H. primigenia*. The name *H. caucasica* is thus considered valid, be it on other grounds than given by Lopatin et al. (2003).

DISCUSSION

Hystrix sivalensis Lydekker, 1878, a name that is based on one low-crowned specimen from the Siwaliks of India, has been synonymised with *Hystrix primigenia* (Van Weers & Rook (2003). Another specimen from the Siwaliks that has been referred to *H. sivalensis* (Colbert, 1935) is an isolated high-crowned m1 that may well represent *Hystrix indica* Kerr, 1792. The same holds for the specimen B.M. 15923 from the Siwaliks (Matthew, 1930).

Qi (1979) and Flynn & Qi (1982) already mentioned the resemblance of the Lufeng fauna with the Late Miocene faunal assemblages of the Siwaliks in India and Pakistan. The vast area of distribution of *H. primigenia*, from S.E. Europe to

Table 3. Measurements in mm of lower cheek teeth from the Miocene of Lufeng, China, IVPP 75033, with serial and figure number, length of tooth series, width, length, enamel height and wear class.

p4-m3					
Nr.	Fig.	Alv. Lth.			
27	16	38.8			
p4					
Nr.	Fig.	Wth.	Lth.	E. Ht.	Class
13	7	8.1	10.4	7.6	O/Q
17	8	8.7	11.6	8.5	O1
18	9	8.8	11.4	8.7	O1
27	16	9.2	10.9	7.0	Q/R
m1/2					
14	10	7.4	8.1	5.9	S
15	11	8.9	9.2	6.5	R
19	12	8.2	9.2	6.3	O3
20	13	7.6	9.3	7.4	O3
27	16	8.3	8.9	5.5	R/S
27	16	8.9	9.8	7.0	Q/R
m3					
16	14	7.8	8.6	6.4	P1
21	15	7.4	9.2	7.4	O
27	16	8.2	8.8	5.8	P

S. China during the Miocene, is not unusual for rodent genera, i.e the gerbil Pseudomeriones and the flying squirrel Miopetaurista, but rare for species (comm. Dr H. de Bruijn). It is therefore quite possible that *Hystrix primigenia* with its conservative dentition embraces different biological species that cannot be recognised on the basis of the available remains.

H. gansuensis is a member of the so-called 'Hipparion Fauna' of northern China (Wang & Qiu, 2002). This mammal assemblage characterises the Baodean Mammal Age which is roughly equivalent to the Turolian of Europe (Qiu & Li, 2003). *H. gansuensis* has higher cheek teeth than *H. aryanensis* from the Turolian of Molayan and *H. depereti* from the early Ruscinian of Rousillon (Table 4). So the increase of tooth height in northern Chinese Hystricidae is more advanced than in the West Asiatic and European representatives. The late Miocene fauna from Shihuiba, Lufeng, S. China, also of Baodean age, reflects a tropical or subtropical forest environment, that of North China a relatively arid temperate steppe or forest-grassland environment (Qiu & Li, 2003). This may correlate with the more advanced development of tooth height in *H. gansuensis*.

Lopatin et al. (2003) criticise our earlier conclusion (Van Weers & Rook, 2003) based on numerical data that two different *Hystrix* species of similar size occurred in Eurasia during the late Turolian. It is correct that not all samples used in our analysis are large enough to be statistically significant, but since six out of the nine samples

Table 4. Relative enamel height (EH/L) expressed as a percentage of the length, with mean, range, the wear classes of the extremes of the range. The number of specimens (in parentheses) may be smaller than the number of teeth (n) in the cases where measurements of left and right teeth in the same serial positions of a specimen are used.

	H. parvae			*H. depereti*			*H. primigenia*			Lufeng spec.			*H. gansuensis*			*H. aryanensis*		
EH/L	mean	range	n	mean	range	n	mean	range	n	mean	range	n	mean	range	n	mean	range	n
P4	98	93-103	3	110	97-132 D-B	3	89	74-94 E-D	5	82	80-84 E-B	3		142 A	1		-	
M1/2	107	72-139	8	105	62-150 G-A	11	67	42-80 G-F	8	91	67-116 E-B	8	143	139-152 A-D	3	117	108-137 D-C	5
M3		-		114	105-121 C-E	2	80	52-99 G-E	5	99	80-119 G-F	2		157 ?	1			
p4	83	80-86	2	87	72-116 R-O	7	68	35-95 T-O	8	72	64-76 R-O	4		-			-	
m1/2	68	41-82	4	68	22-144 T-O	25	51	23-72 T-Q	13	71	62-80 R-O	6		-			-	
m3		-		78	46-109 T-O	6	56	29-97 T-Q	5	74	66-80 P-O	3		-			-	

of probably Turolian age represent *H. depereti*, such a coexistence is strongly suggested. In their discussion about *H. trofimovi* Shevyreva, 1986, Lopatin et al. (2003) moreover implicitly suggest that there have been two coeval species. They found that *H. trofimovi* from the late Pliocene of Tadjikistan agrees with *H. primigenia* in size and morphology of the teeth. That coeval occurrences are not impossible is shown by the extant pendant of *H. brachyura* and *H. crassispinus* occurring on the island of Borneo. These species are more similar in size and tooth morphology than the fossil species discussed above.

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