BEAUFORTIA

INSTITUTE FOR SYSTEMATICS AND POPULATION BIOLOGY
(ZOOLOGICAL MUSEUM) UNIVERSITY OF AMSTERDAM

Vol. 48, no. 4 August 18, 1998

BIOMETRIC ANALYSIS AND TAXONOMIC ALLOCATION OF PLEISTOCENE *HYSTRIX* SPECIMENS (RODENTIA, PORCUPINES) FROM CHINA

D.J. VAN WEERS* & ZHENG SHAOHUA**

* *Institute for Systematics an d Population Biology (Zoological Museum), University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands.*
** *Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica. P.O. Box 643, Beijing 100044, P.R. China.*

Keywords: *Hystrix*, China, Pleistocene, Nihewanian, Zhoukoudianian, *H. magna, H. kiangsenensis.*

ABSTRACT

Early to Middle Pleistocene *Hystrix* material in the collections of the IVPP in Beijing, has been biometrically studied and compared with other fossil and extant species. The specimens are from Zhoukoudian (Beijing), the Liucheng *Gigantopithecus* cave (Guangxi) and other caves in that province, the Wazhuwan and Yanhui Cave (Guizhou) and from Longgupo (Sichuan). None of the fossil specimens can be allocated to the extant Chinese *Hystrix brachyura subcristata* Swinhoe, 1870, subgenus *Acanthion* F. Cuvier,1823. Most of the collections studied consist of a mixture of two species with overlapping size ranges. Cheek teeth of most *Hystrix* species do not show diagnostic characters other than size, so not every one of them can be assigned with certainty to the larger or the smaller species. Two hypsodont *Hystrix (Hystrix)* species are recognised. The smaller one, *H. kiangsenensis* Wang, 1931, is on average larger than *H. brachyura subcristata.* This smaller species has been recognized in the material from the Provinces Guangxi, Guizhou and Beijing. The second species, *H. magna* Pei, 1987, is on average larger than *H. indica* Kerr, 1792 and is found in essentially the same localities. The stratigraphic range of these species extends from Early Nihewanian (= early Early Pleistocene) to Early Zhoukoudianian (= early Middle Pleistocene). Syntype specimen IVPP nr. V5036.12 is indicated as the lectotype of *H. magna* Pei, 1987. The brachyodont lower premolar collected at Longgupo, Sichuan Province, is provisionally referred to *Hystrix* sp. instead of its allocation to *H. magna* Pei, 1987 given its similarities with Late Miocene to Pliocene *Hystrix* species of Europe and Asia. The relationship of *H. magna* Pei, 1987 with *H. gigantea* van Weers, 1985, *H. refossa* Gervais, 1852 and *H. crassidens* Lydekker, 1886 is discussed.

INTRODUCTION

Pei Wenzhong (1987, posthumous publication) distinguished two *Hystrix* species in the material from the caves in the Province Guangxi, among others from the Liucheng *Gigantopithecus* cave. That material from that province consists of hundreds of isolated cheek teeth and two incom-

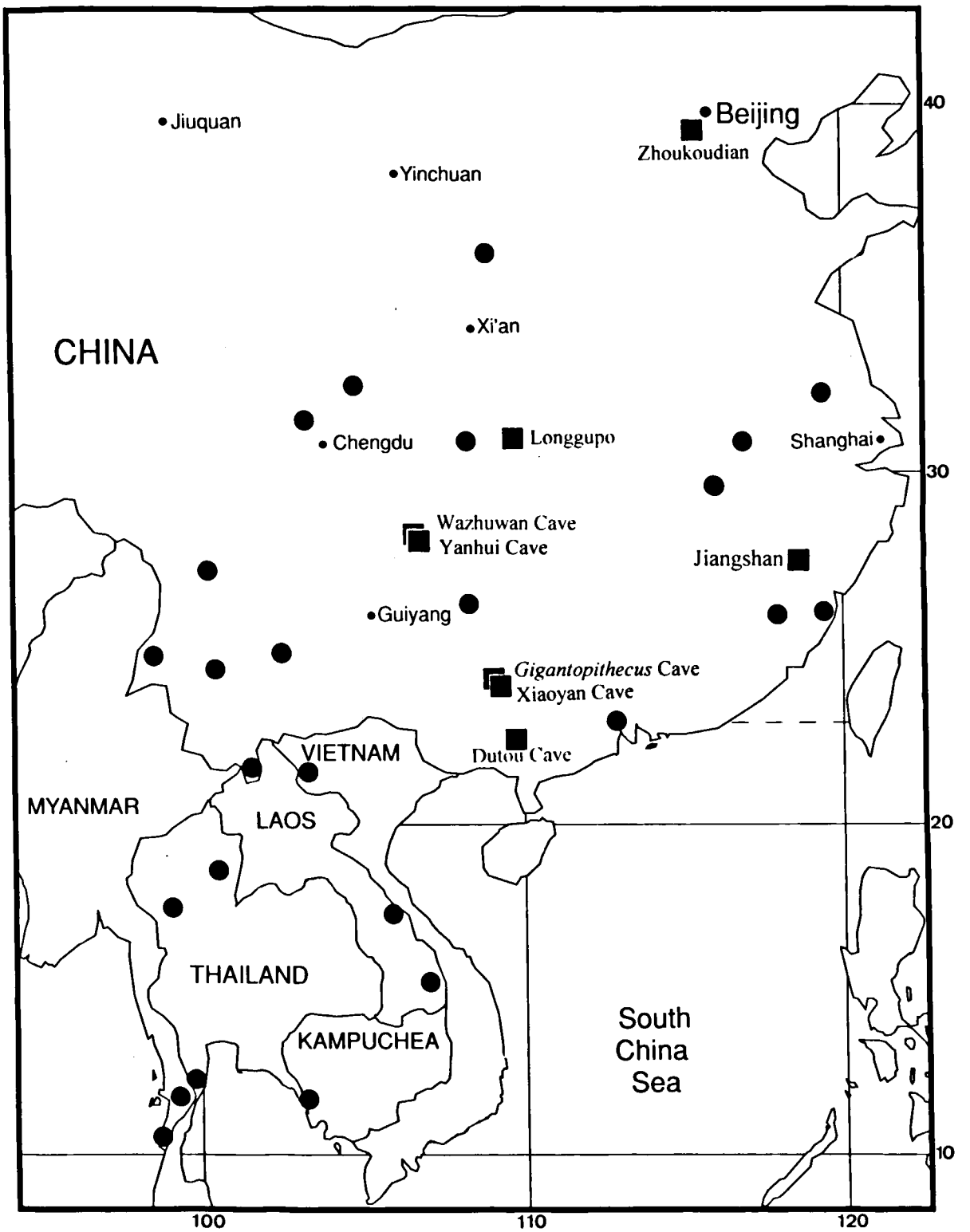

Fig. 1. Localities of fossil *Hystrix* specimens studied (black squares) and of *H. brachyura subcristata* specimens (black dots) used for comparison. The *Gigantopithecus* cave is the type locality of *H. magna* Pei, 1987, Jiangshan that of *H. kiangsenensis*.

plete skulls. The smallest species was allocated to the extant Chinese *Hystrix subcristata* Swinhoe, 1870, with the remark that it concerned a "species of *Hystrix* but not *Acanthion*". However, *H. brachyura subcristata* Swinhoe, 1870 belongs without any doubt to the subgenus *Acanthion* F. Cuvier, 1823 (van Weers, 1979). The use of the name *subcristata* for many Early and Middle Pleistocene *Hystrix* finds in China suggests that this (sub)species remained unchanged up to the present. The fossil specimens, however, have not been compared with a sufficiently large number of specimens of the extant *subcristata* to ascertain its specific identity.

Pei (1987) based the description of a new species, *Hystrix magna*, on the 13 largest out of the more than 200 cheek teeth coming from the *Gigantopithecus* cave in Guangxi. He gave length and breadth measurements of these 13 specimens in a table (Pei, 1987: 89) and figures of the occlusal surface of 9 of these (Pei, 1987: Plate XV, figs. 1-9). The correlation of the specimens in the table and in the figures is not clear from the publication. The morphology of the occlusal surface of the cheek teeth in the Hystricidae does not reveal any character to distinguish species or even (sub)genera. Pei (1987) stated that the crowns of the cheek teeth are rather low and considered *H. magna* intermediate between the brachyodont *Atherurus* F. Cuvier teeth and the hypsodont *Hystrix* teeth. Unfortunately he did not give any height measurements or figures in side view. Zheng (1993) stated that the characteristics of *H. magna* are insufficiently known. Most unfortunately, it appeared to be impossible to identify the type specimens in the relevant collections, except for the upper molar V5036.12, occurring in *Pei's* table (p. 89) and plate XV (fig. 6). However, this tooth, figure 13 in the present paper, cannot be considered low-crowned.
Though the relative enamel height of this specimen is below the mean of the hypsodont *H. brachyura* (van Weers 1996), it is clearly within the range of that species. Within specialised *Hystrix* species the height of the cheek teeth varies greatly. Brachyodont teeth are always rooted, many hypsodont specimens scarcely show roots, but others have clearly developed roots (Lönnberg, 1923: Fig. 1, and Niethammer, 1982: Fig. 196) which affects the height measurement. So the question if *H. magna* is significantly less specialized concerning crown height cannot be answered on the basis of this specimen alone.

Zheng (1993) described a lower premolar from Longgupo with a relative enamel height that falls within the ranges of the brachyodont Miocene species *H. parvae* (Kretzoi, 1951) and *H. primigenia* (Wagner, 1848) and of the species of the primitive extant genera *Trichys* Günther, 1877 and *Atherurus* F. Cuvier, 1829 (van Weers, 1996). Zheng (1993), following Pei's (1987) view that *H. magna* is a brachyodont species, applied that name for his Longgupo specimen. This allocation needs thus to be reconsidered.

Besides the 200 teeth from the *Gigantopithecus* cave, Pei (1987) mentioned 500 isolated teeth from other Caves of Guangxi, varying in age from Early to Late Pleistocene. Besides Pei's material, the taxonomic status of parts of published material from Zhoukoudian (Young, 1934, T. de Chardin & Pei, 1941), Sichuan and Gui-zhou (Zheng, 1993) and of other parts of the collections studied, is not clear. Comparison of these assemblages with extant species of which the range of variation is known is the only basis for an analysis.

The aim of this paper is a biometric comparison of samples from the Pleistocene *Hystrix* specimens in the I.V.P.P. in Beijing. These samples are compared with the extant *H. (Acanthion) brachura* Linnaeus, 1758, - in particular with its Chinese subspecies *subcristata* Swinhoe, 1870, - with the geographically nearest extant S.W. Asian species *H. indica* Kerr, 1792, with the Pleistocene species *H. crassidens* Lydekker, 1886 from India, with *H. gigantea* van Weers, 1985 from Java (Indonesia) and with *H. refossa* Gervais, 1852 from Europe. The low-crowned lower premolar from Longgupo is compared with Miocene and Pliocene *Hystrix* species.

METHODS

Measurements of the premolar and the first and second molar have been used, as only these are present in statistically significant numbers. Upper cheek teeth are indicated in upper case, lower cheek teeth in lower case. Because of the uncertainty in the distinction between isolated

first and second molars, they have been treated as one unit and indicated with M1/2 and m1/2. The identification of the position of an isolated cheek tooth cannot always be done with certainty because contact facets are sometimes not developed. M1/2 and m1/2 teeth have been recognized only when both an anterior and a posterior facet was present. P4 and p4 teeth have been recognised as such when a posterior facet and a rounded anterior side was present. In tables and diagrams no distinction has been made between left and right teeth.

The number of specimens per locality is in most cases too small to enable comparison of teeth in the same stage of attrition. Incidentally the class of wear as defined in van Weers (1990) is given.

The breadth of cheek teeth at the occlusal surface, especially of the curved upper ones, is more liable to change as result of attrition than the length (van Weers, 1990).Yet this variable breadth measurement is used in addition to the length measurements, because only this measurement is available in former studies of extant species with significant numbers of teeth.

The number of specimens of most of the fossil samples studied is marginal from a statistical point of view, so the premolars and molars of the same sample, upper as well as lower ones are involved in the analyses of size.

Chinese fossil *Hystrix* finds are usually referred to *H. subcristata*, type locality Foochow, Fo-kien (= Fuzhou, Fujian). *H. subcristata* is the largest subspecies of *H. brachyura* Linnaeus, 1758 (van Weers, 1979). The fossil specimens are primarily compared with this subspecies *H. b. subcristata* because it is not relevant to compare them with the smaller populations of this species. Incidentally the fossil species are compared with *H. brachyura* as a whole. *H. b. subcristata* reaches its largest size in Southern Burma and Thailand. The data of this subspecies given refer to specimens from localities on the mainland of China, Laos, Cambodia, Thailand and Tenasserim (Burma), indicated in the map (Fig. 1). These are the localities 18 to 24 and 30 to 38 in van Weers (1979), and additional specimens from China are mentioned below.

The data on *H. indica* are after van Weers (1994). The data given in table 1 include those from Corbet & Jones (1965) and Frenkel (1969).

LIST OF SPECIMENS STUDIED

Gigantopithecus cave, Liucheng, Guangxi.

General label "*H. subcristata*, 5704":
- right mand. with p4-m2, nr.V.5029,
- left mand. with alv. dp4, m1, m2 unworn, nr. V.5030,
- M1/2, no nr.,
- M1/2 nr. "xiu/5 V.5036.12", lectotype of *H. magna* Pei, 1987.
- P4, 5704c,
- p4, 5704c.

General label "*H. subcristata*", all individual teeth with nr. 5704:
- 10 M1/2,
- 6 P4.

Wazhuwan cave, Guizhou.

Teeth from coll. V9668, under label "*H. subcristata*":
- 27 M 1/2 selected out of the nrs. 51-63, 69-78, 93-115 and 145-155;
- 9 P4 nrs. 30-34 and 42-45;
- 15 p4 out of the nrs. 226-233 and 240-249.

Yanhui cave, Guizhou.

Teeth from coll. V9668 under label "*H. subcristata*":

- 14 M1/2 out of the nrs.64-66, 116-140 and 156-169;
- 9 P4 nrs. 35-40 and 46-48;
- 9 m1/2 out of the nrs. 258-260, 269 and 291-297;
- 6 p4 nrs. 234-237 and 250-251.

Zhoukoudian, Beijing.

Locality13:

- Fragm. left mand. with p4-m3, nr. CP.270, = "*Hystrix* cf. *subcristata*" in T. de Chardin & Pei (1941, fig. 49).

Locality 1:

"*Hystrix* cf. *subcristata*" in Young (1934, fig. 46):

- Left mand. fragment with p4-m1, nr. C. 1770, B.1:57,
- Left mand. fragment with m1, nr. C.1770, B4.1929,
- M1/2, nr. C.1771,
- m1/2, nr. C.1771.
- Right mand. with p4-m2-alv.m3, nr. C.1772, a 1929 with label "*Hystrix* sp.".
- Left m1/2 with label "*Hystrix* sp., loc.1 of CKT, nr. C.1774".

Unknown localities Guangxi:

15 isol. P4 under label "*H. magna* Pei", selected out of a series of 37 specimens with individual numbers five 5601, one 5612, one 5623, one 5627, two 5651, one 5657, one 5701, one 5702, one 5774 and one 5775.

Xiaoyan Cave, Liujiang, Guangxi:

- Skull nr. V.5082, 5771, fig. 11 in Pei (1987), "*H. subcristata*".

Guangxi, no exact locality:

- Skull nr. V.5083, fig. 12 in Pei (1987), "*H. subcristata*".

Dutou Cave, Chongzuo, Guangxi:

- Skull of very old specimen, nr.V10999, *Hystrix magna* Pei in Guo Jianwei (1997).

Longgupo, Sichuan:

- Left p4, nr. V9669 = "*H. magna* Pei, 1987" in Zheng (1993, fig. 57, a-a1).

India:

- Cast of the right ramus of the type mandible of *Hystrix crassidens* Lydekker, 1886, nr. F. 219a G.S.I. (Geological Survey of India), Calcutta, figured by Dassarma et al. (1982), Late Pleistocene, Kurnool Caves, Andhra Pradesh.
- Fragment of right maxilla G.S.I. 19110, of left maxilla G.S.I 19111 and of left mandible G.S.I. 19113, Late Pleistocene or Early Holo-cene of Babladanga, Bankura district, West Bengal.

Extant *H. brachyura subcristata*:

- Institute of Zoology Beijing: one specimen without number from Sichuan; specimens nrs. 08196 and 08197 from Fujian.
- Kunming Institute of Zoology: nrs. 631426 and 630813 from Guizhou; nrs. 76355, 207, 850002, 850003, 640258 and 640259 from Yunnan.
- Zoological Museum Amsterdam, The Netherlands, nr. 24710, Sekong, Laos.

Extant *H. brachyura brachyura*:

- National Museum of Natural History, Leiden, The Netherlands: 12 specs., nrs. 1112, 1128, 1270, 2543, 4981, 19964, 19966, 19982, 19983, 19993 - 19995, Sumatra.
- Zoological Museum Amsterdam, The Netherlands: 23 specs., nrs. 6848 - 6870, Sumatra.

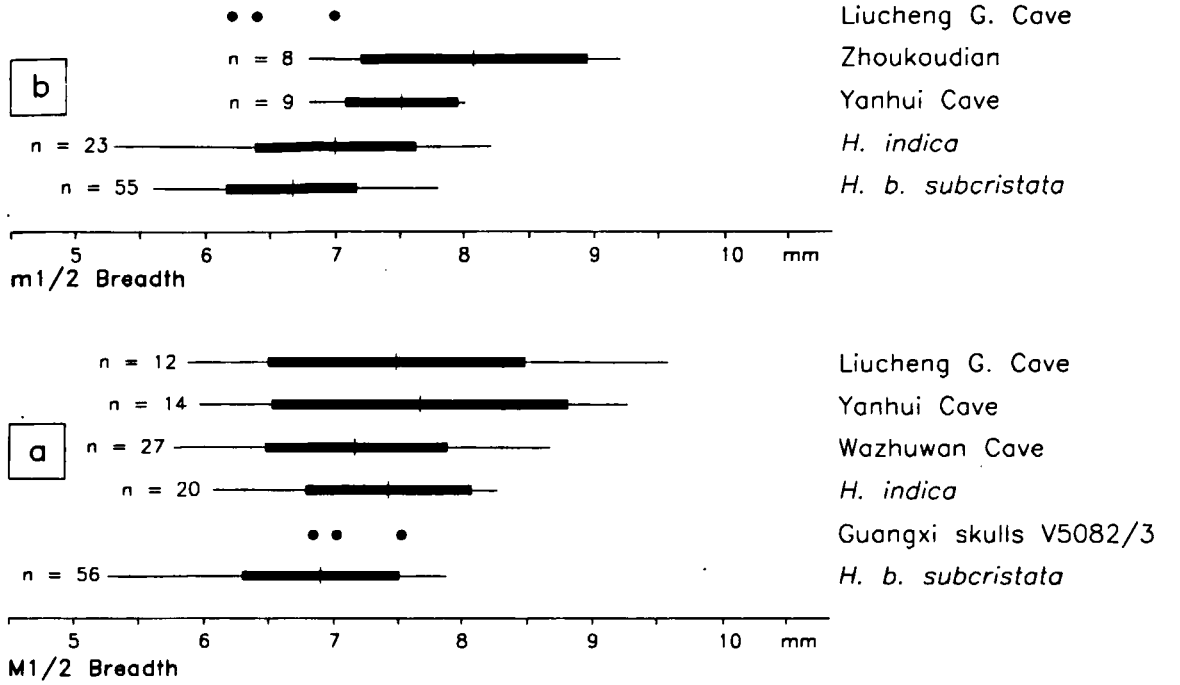

Fig. 2. Breadth of the M1/2 and m1/2 of the fossil *Hystrix* from the localities indicated and the extant *H. brachyura subcristata* and *H. indica* specimens studied, with mean + and - standard deviation, range and sample size (n).

ANALYSIS AND DESCRIPTION OF THE SPECIMENS

COMPARISON WITH *H. BRACHYURA SUBCRISTATA*

The breadth measurements of the M1/2 and m1/2 (Fig. 2a-b) and of the P4 and p4 (Fig. 3a-b) show that the means and the smallest specimens of all fossil samples are always larger than those in the Chinese *subcristata*. Therefore none of the fossil specimens are considered to belong to *H. brachyura subcristata*.

When compared with the entire species *H. (Acanthion) brachyura* Linnaeus, 1758 (sensu van Weers, 1979) these differences are still larger, as shown with the skull dimensions in table 1. In our files (first author) the mean breadth of the M1/2 and m1/2 of *H. brachyura* s.l. is 6.6 mm (n = 191) and 6.3 mm (n = 179) respectively, instead of 6.9 mm (Fig. 2a) and 6.7 mm (Fig. 2b) of the subspecies *subcristata*. So there is no argument to allocate the fossil specimens to the extant *H. brachyura*.

FOSSIL SPECIES

The range of variation in the fossil samples from the Liucheng *Gigantopithecus* cave, the Yanhui cave, the Wazhuwan cave (Fig. 2a) and from Zhoukoudian (Fig. 2b) is larger than the range in the much larger sample of *subcristata*. It is highly improbable that these fossils belong to one species.The samples are therefore considered to be composed of two species, a large one which is on an average larger than *H. indica* and a smaller one on an average larger than *H. brachyura subcristata*.

The large specimens are allocated to *H. (Hystrix) magna* Pei, 1987, type locality the Liu-cheng *Gigantopithecus* cave. In Pei's original description tooth measurements are presented (1987: 89), but with the exception of specimen nr.V5036.12 (M1/2, 10.6 x 9.2 mm) it is not known which measurement belongs to which tooth. The range of variation of the teeth of *H. magna* can only be estimated.

The smaller teeth are considered to belong to

H. (Hystrix) kiangsenensis Wang, 1931, type locality Jiangshan (= Kiangsen). From this species only the measurements of Wangís original description are available (in mm, * = type specimen):

	P4	p4		m1		m2	
length	8.	7.5*	9.6	7.0*	7.4	8.2	8.0
breadth	7.5	6.8*	8.2	-	6.0	6.8	7.6

Table 1. Measurements and ratios of measurements of the extant species *H. brachyura*, separately of its subspecies *H. b. subcristata*, of *H. indica* and of three fossil skulls from the Pleistocene of Guangxi, specimens nr. 5083, 5082 and 10999. Measurements are in millimeters with range, mean and number of specimens. Numbers in italics with * are based on Corbet and Jones (1965) and with ** are from Frenkel (1969). Measurements are: Occipito-nasal length, Basilar length, alveolar length of the upper P4-M3, Nasal length, Nasal breadth, Zygomatic breadth and Height of skull at premolar of alveole. The measurements are of of adult specimens, the ratios are also from sub-adult specimens.

	H. brachyura s.l.	*H. brachyura subcristata*	Guangxi 5083	Guangxi 5082	*H. indica*	Guangxi 10999
Occ.nas length	116 - 146 132 n = 74	125 - 146 136 n = 22	143	150	126 - 158 139.8 n = 12 *127 - 162** 143 *n = 26*	162
Bar.l.	96 - 122 111 n = 70	105 - 122 115 n = 22	117	-	116 - 135 125 n = 8	138
L. P4-M3	22.2 - 31.8 27.6 n = 72	24.0 - 31.8 29.0 n = 28	29.2	31.6	29.6 - 34.8 32.4 n = 10 *31.0 - 34.7*** *32.9* *n = 22*	-
Nas.l./ Occ.n.l.	0.40 - 0.6 1 0.50 n = 73	0.51 - 0.61 0.56 n = 22	0.59	0.60	0.46 - 0.52 0.49 n = 9 *0.45 - 0.56** *0.50* *n = 31*	0.59
Nas.b./ Zyg.b.	0.37 - 0.62 0.49 n = 76	0.47 - 0.61 0.55 n = 28	0.59	0.60	0.47- 0.55 0.50 n = 9	
Hgt./ Occ.n.l.	0.31 - 0.41 0.36 n = 74	0.35 - 0.41 0.38 n = 22	0.41	0.43	0.37 - 0.42 0.40 n = 8 *0.37 - 0.46** *n = 26*	0.45

So of this species too, the range of variation of the teeth can only be estimated.

The means and range of variation of the length of the teeth of the two fossil species, tentatively estimated from the samples studied, are as follows:

		M1/2	m1/2	P4	p4
H. magna	mean	9.0	9.0	9.5	10.0
	range	8.0-10.2	8.0-9.8	9.0-10.0	9.0-11.5
H. kiangsenensis	mean	7.5	7.	8.5	8.5
	range	6.3-8.5	6.0-8.5	7.8-9.0	7.5-9.6

LIUCHENG *GIGANTOPITHECUS* CAVE

In Fig. 4 twelve length and breadth measurements of the M1/2 from the type locality Liucheng are plotted. The two largest ones are considered to belong to *H. magna*, the ten with a smaller tooth length than 8.5 mm are *H. kiangsenensis*. Three m1/2 from this locality (Fig. 2b) are of *H. kiangsenensis*. None of the seven P4 teeth from Liucheng (Fig. 5) can be allocated to *H. magna* with certainty, the three ones around the length of 9 mm may or may not belong to this species. The two p4 teeth from Liucheng (Fig. 3b) are allocated to *H. kiangsenensis*.

WAZHUWAN AND YANHUI CAVE

Zheng (1993) mentioned that the Yanhui teeth are larger than those from Wazhuwan. This difference is reflected in the M1/2 (Fig. 2a) and in the p4 (Fig. 3b), but not in the P4 sample (Fig. 3a). This size difference could be explained by unequal stratigraphical ages of the finds and a taxonomic difference, but statistic tests do not show a high significance of this difference. A more probable explanation is that *H. kinangsenensis* and *H. magna* are not equally represented in the two samples as is clearly shown in Fig. 6. The largest tooth with a length of 9.8 mm is from Wazhuwan, so there is no reason to suppose a systematic difference between the two collections.

Above the M1/2 length of 8.5 mm (Fig. 6), together 10 specimens can tentatively be allocated to *H. magna*, and below the length of about 8 mm, 21 specimens to *H. kiangsenensis*. Roughly between 8 and 8.5 mm 10 specimens cannot be assigned to one of the species. Only four P4 which are clearly longer than 9 mm (Fig. 5) from the two localities are allocated to *H. magna*. Around a length of 9 mm overlap of the two species may be supposed. The three p4 teeth (Fig. 7) with lengths of 10.5 to 10.6 mm are possibly the only ones that can be allocated to *H. magna*.

Remark: The correlation between length and breadth of the cheek teeth in the various diagrams is not always quite clear. This may partly be explained by the changing relation of breadth and length as a result of attrition (van Weers 1990). For the 41 M1/2 from Wazhuwan and Yanhui together, divided in three groups of wear, the relation Occlusal Breadth/Length has been calculated. This shows the the increase of the relative breadth of worn teeth:

wear class	B - D,	mean 0.84,	n = 17
wear class	E - F	mean 0.91,	n = 11
wear class	G,	mean 1.05,	n = 13.

ZHOUKOUDIAN LOCALITY 1 AND 13

The only M1/2 available of Zhoukoudian (breadth 7.2 mm, length 8.1mm) is from Locality 1 and is allocated to *H. kiangsenensis*. The two largest of the 8 m1/2 from Zhoukoudian (Fig. 8) are the m1 and m2 of the lower jaw fragment nr. C.1772, described in detail below. Only these two are allocated to *H. magna*. The 6 smaller ones from Zhoukoudian are of *H. kiangsenensis*, from Locality 1 as well as from Locality 13. No P4 from that locality is available. The p4 in Fig. 3b from Locality 1 is of the *H. magna* jaw fragment of described below, the allocation of the smaller one from Locality 13 in that figure is doubtful.

H. MAGNA P4 FROM UNKNOWN LOCALITIES

From the collection of 33 upper premolars with the label "*H. magna* Pei" 15 specimens have been measured. The origin of this material is unknown. This sample contains the largest P4 measured in this study as appears from breadth mea-

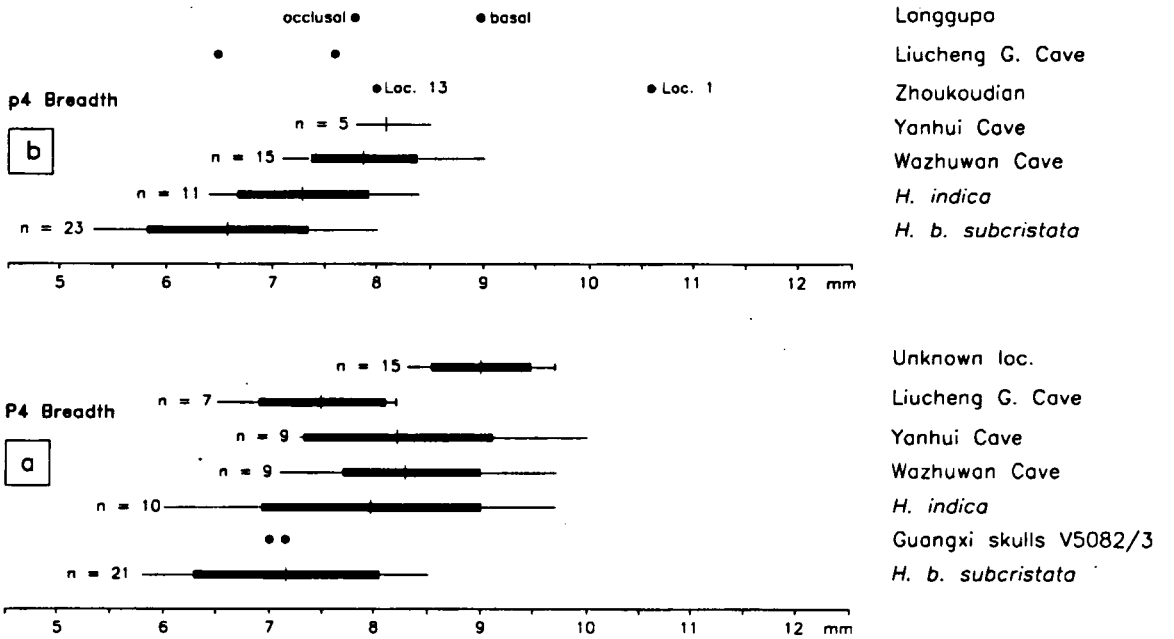

Fig. 3. Breadth of the P4 and p4 of the fossil *Hystrix* from the localities indicated and the extant *H. brachyura subcristata* and *H. indica* specimens studied, with mean + and - the standard deviation, range and sample size (n).

surements (Fig. 3a) and their length range (8.5 - 10.3 mm). Most specimens bear different numbers, suggesting that this P4 sample has been composed by a selection of the largest teeth out of collections from a number of localities. The teeth are clearly hypsodont (Table 2). These teeth are considered to belong to *H. magna.*

LONGGUPO, SICHUAN

A left p4 (nr. V9669) from this locality was described and figured by Zheng (1993) under the name *H. magna* Pei, 1987. The breadth is 7.8 mm at the occlusal surface and 9.0 mm at the base, the length 10.5 mm at the occlusal surface and 12.2 mm at the base. The total height with the only one of the roots left is 17.2 mm, and the height of the enamel crown is 10.2 mm. The breadth is as large as the largest p4 from Wazhuwan (Fig. 3a) and with its length of 12.2 mm it exceeds the largest one in this study (Fig. 7). Its size is within the range of *H. primigenia* (van Weers, 1994) and with the small enamel height (En.h./Lth. = 0.84) the tooth has a degree of brachyodonty like *H. parvae* (Kretzoi, 1951) and *H. primigenia* (van Weers and Montoya, 1996). *H. primigenia* occurred in Europe from Late Miocene up to the Pliocene, Villanyian, MN 16 (Alcala & Montoya, 1998) and was replaced by hypsodont species in the Pliocene (van Weers, 1994).

The Longgupo p4 is about the same size as the clearly brachyodont specimens from the Late Miocene locality of Shihuiba, Lufeng, in the collections of the IVPP listed by Qiu Zhuding et al. (1985) as *Hystrix* sp. Besides similarity with *H. primigenia* and with the geographically nearer Lufeng finds, there is also agreement of the Longgupo tooth with the Late Miocene *H. sivalensis* Lydekker, 1878 from the Siwaliks, India. From this species only the type mandible with m1 and m2 is available. The Longgupo tooth may be referred to these forms rather than to *H. magna* and at present we prefer to provisionally refer it to *Hystrix* sp.

Remark: This p4 is from the same fissure filling as *Mimomys peii* Zheng & Li, 1986 which belongs to the Dachaian fauna (Zheng, 1993), part of the Early Nihewanian, considered to be of the same age as the Late Villanyian (MN 17) of Europe

Table 2. Relative height of cheek teeth, expressed with the ratio Heigt/Lenght with range, mean (m) and sample size (n) of *H. brachyura*, of specimens from the caves of Wazhuwan, Yanhui and Liucheng, from Zhoukoudian, and the specimens "*H. magna*" from one or more unknown localities.

		Height/Length			
		M1/2			
H. brachyura	Wazhuwan	Yanhui	Liucheng	Zhoukoudian	"*H. magna*"
1.4 - 2.4	1.6 - 2.3	1.8 - 2.2	1.7 - 2.	2.1	
m = 2.0	m = 2.0	m = 2.0	m = 1.9		
n = 55	n = 27	n = 13	n = 9	n = 1	
		m1/2			
1.3 - 2.8				1.3 - 2.2	
m = 2.0				m = 1.7	
n = 43				n = 3	
		P4			
1.2 - 2.5	1.7 - 2.5	1.7 - 2.3			1.8 - 2.7
m = 1.9	m = 2.1	m = 2.1			m = 2.2
n = 19	n = 7	n = 9			n = 14
		p4			
1.0 - 2.5	1.8 - 2.4	1.6 - 2.1			
m = 1.9	m = 2.0	m = 1.8			
n = 19	n = 10	n = 5			

(Tong et al., 1995). *Mimomys peii* was brought forward by Huang Wanpo et al. (1995) as one of the indications for the Late Pliocene age of their hominid find from Longgupo. As brachyodont *Hystrix* species have been widespread in Eurasia in Miocene-Pliocene times, the Longgupo *Hystrix* tooth may provide a support for that age assignment.

HEIGHT OF THE CHEEK TEETH

Table 2 presents the relative height of the cheek teeth of the extant hypsodont species *H. brachyura* and of fossil specimens of most of the localities studied. Taking into account the large intraspecific variation and the small size of some samples, no difference in hypsodonty can be detected.

The isolated M1/2 nr.V.5036.12, lectotype of Pei's(1987) *H. magna* from the Liucheng *Gigantopithecus* cave, Fig. 13 in the present paper, has not been entered in Table 2 as the basal part is lacking and the total height can not be measured. This very large tooth with length 10.2 mm has an enamel height of 15 mm, so absolutely and relatively (En.Ht/Lth 1.47) higher than the brachyodont lower molar nr. V9669 from Longgupo (0.84). It is, moreover, in a more advanced stage of attrition than the Longgupo tooth so originally it has been higher. Moreover, it does not have the conical shape of brachyodont teeth. The second large M1/2 (length 9,2 mm) without individual number from Liucheng mentioned in the relevant section, is damaged and its height can therefore not be measured.

No proof could be found that cheek teeth with a certain degree of brachyodonty have been part of Pei's(1987) type series of *H. magna*, nor could one be found in other material from the type locality or from other localities of Guangxi. The specimen V9669 from Longgupo is the only specimen studied wich can be called brachyodont.

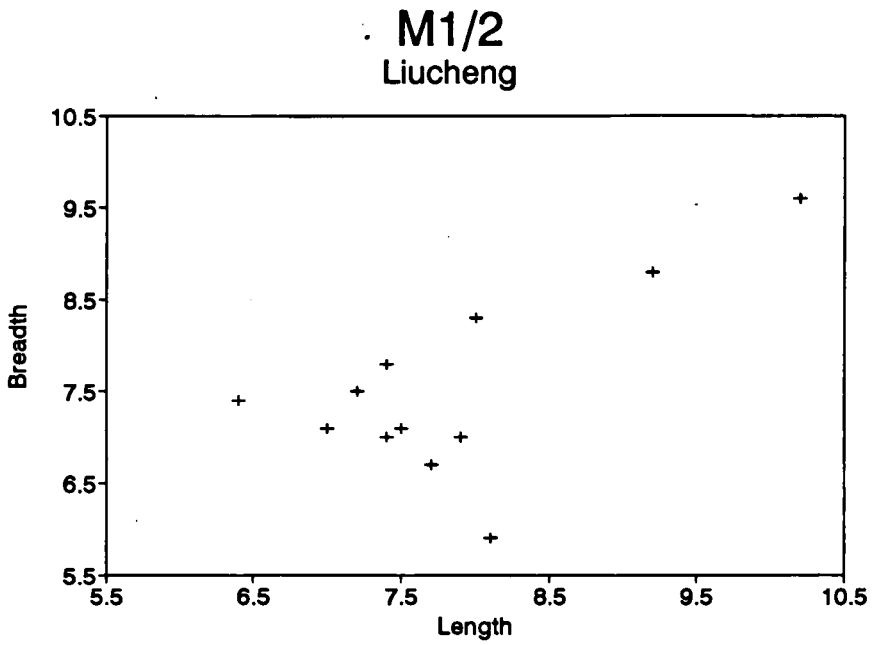

Fig. 4. Diagram of length and breadth in mm of the M1/2 from the Liucheng *Gigantopithecus* cave. The two largest belong to *H. magna*, the 10 smaller ones to *H. kiangsenensis*.

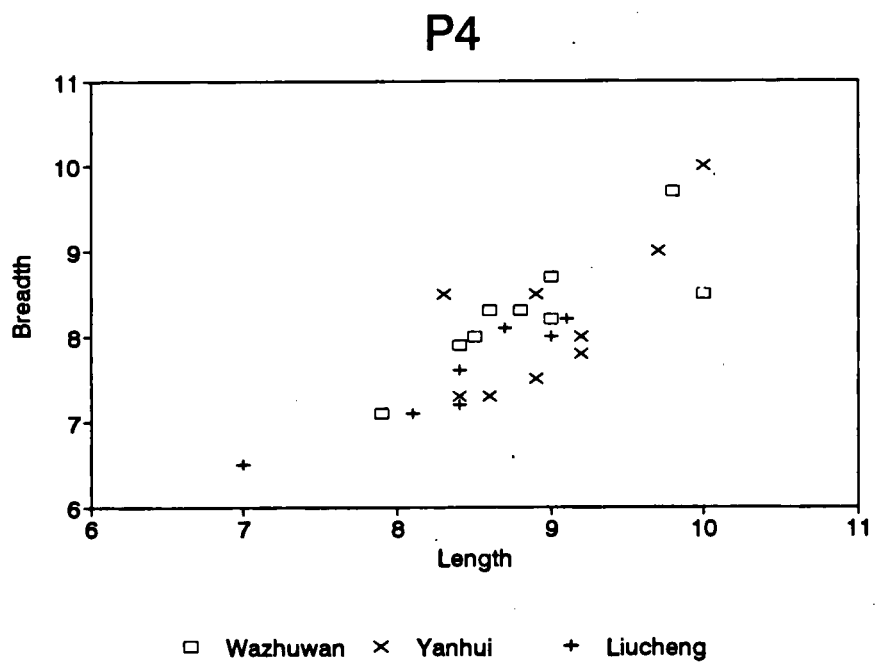

Fig. 5. Diagram of length and breadth in mm of the P4 from the Wazhuwan cave, the Yanhui cave and the Liucheng *Gigantopithecus* cave. The 4 largest specimens belong to *H. magna*, around the tooth length of 9 mm allocation is uncertain, specimens below 8.5 mm are *H. kiangsenensis*.

SKULL CHARACTERS

Specimen nr. V.5082: In Table 3 measurements of this incomplete skull (Pei, 1987: fig. 11) from the Xiaoyan cave near Liujiang, Guangxi, are presented. In Table 1 some of these measurements and ratios between some of them are shown, together with those of *H. b. subcristata* and *H. indica*. The estimated occipito-nasal length of the Xiaoyan skull is larger than all the *subcristata* specimens (n = 22) and is larger than the mean of *indica*. The relative nasal length (Nas.l./Occ. nas.l.) of 0.60 is nearly as large as in the longest *subcristata* specimen (0.61) and clearly larger than in *indica* (max. 0.56). The relative breadth of the nasals (Nas.b./Zyg.b.) of 0.60 is about the same as the broadest *subcristata* specimen and exceeds the maximum of the range (0.55) of *indica*. The relative height of the skull (Hght./Occ.nas.l.), exceeds with 0.43 the highest *subcristata* (0.41) and falls within the range of *indica*. The tooth-row length of this specimen (Table 1 and Fig. 9) is about as large as in the largest *subcristata* specimen (n = 28) and is within the range of *indica*.

This skull is more specialised concerning size, development of the nasals and height of the skull than *subcristata* and differs from *indica* in the nasal structure. On the basis of the size of the skull it represents a species that is on an average larger than *subcristata* and about as large as *H. indica*. On the basis of its tooth dimensions this skull is allocated to *H. kiangsenensis*.

Specimen nr. V.5083: The same comparison as above is made with this incomplete skull (Pei, 1987, fig. 12) from Guangxi, exact locality unknown. The size difference (Table 1) with *subcristata* is less clear than the foregoing specimen, but its estimated occipito-nasal length of 143 mm is well above the mean (136 mm) of that species. The relative nasal length and breadth are both larger than in *indica*, agree with *subcristata* so are not different from the foregoing specimen. The relative height of this skull is similar to the largest one of *subcristata*, but falls within the range of *indica*. The tooth-row length (Table 1 and Fig. 9) is shorter than in *indica* and is about the same as the mean for *subcristata*. This specimen seems to belong to *H. kiangsenensis* also.

Specimen nr. V10999: The very large incomplete skull (Tables 1 and 3) described in detail and figured by Guo Jianwei (1997) from the fissure filling of the Dutou Cave in Guangxi, is apparently from a very old individual because scarcely any suture is left. Therefore some dimensions can only be estimated and others cannot be measured at all. The dental age cannot be seen either since only traces of the roots are left. Hypsodonty could have been established if deep alveoles would have been present. However, in the course of the attrition process alveoles always become filled up with bone tissue and have nearly totally been disappeared when the teeth are worn down. So in this extremely old skull hypsodonty or brachyodonty cannot be established but provisionally it is considered to represent a hypsodont individual. Guo (1997) measures 10.5 x 11 mm for the length and breadth of the alveole of the P4 of his specimen V10999. The actual size of that tooth will have been somewhat larger, so it agrees with the measurements of Pei's(1987: 89) type series of *H. magna* and fits the dimensions of this species.

The estimated occipito-nasal length of 162 mm (Tables 1 and 3) strongly exceeds that of the largest *subcristata* skull and is the same as in the largest *indica* specimen (n = 26, Corbet & Jones, 1965). The estimated relative nasal length (Nas.l./Occ.nas.l. = 0.59) is larger than that of *indica*, and the relative height (Hgt./Occ.n.l. = 0.45) of the skull is nearly the same as the highest *indica* specimen.

For the geological age "Early Pleistocene (?)" has been mentioned (Guo Jianwei, 1997), so there is no contradiction with the supposed age of the *Gigantopithecus* cave material.

Among the hundreds of teeth from Guangxi a medium sized and a large sized species have been distinguished. The two skull types from that province are considered to represent the same two species. So the large skull from the Dutou cave is allocated to *H. magna* Pei, 1987.

Specimen C.1772: A right lower jaw fragment nr.C.1772, labelled *Hystrix* species, Loc.1 of CKT , has not been described thus far. All the molars are broken off and the m3 has almost totally disappeared. The premolar is considered to be the permanent one because it is larger than the m1. Rests of three roots of the p4 are visible, the anterior one with a trace of enamel. Traces of 4 roots of the m1 are visible, the posterior-buccal one with a tiny piece of enamel. The m2 is

Table 3. Measurements of upper skulls from Guangxi, nr. V5082 from Xiaoyan Cave, nr. V5083 exact locality unknown and nr. V10999 from Dutou Cave. Estimations are indicated with *.

	V.5082	V.5083	V10999
Occ.nas.l.	150*	143*	162*
Basilar .l		117	138
Nasal l.	90*	85	96*
Nasal br.	47	41	
Frontal l.	36	31	37*
Palatal l.	79	75*	85
Diastema	44	38	47
Zyg. Br.	79*	70*	85*
Hght. at P4	61	61*	72
Toothr. alv.	31.6	29.2	
Toothr. occl.	30.1	27.5	
Incisor br.	7.6	-	7.2
P4 breadth	7.1	7.0	
length	8.3	7.8	
cl. wear	F4	G1	-
M1 breadth	7.0	7.5	
length	7.2	6.7	
cl.wear	G1	G4	-
M2 breadth	6.9	-	-
length	8.0	-	-
cl.wear	F5	-	-
M3 breadth	5.9	5.8	-
length	7.0	6.3	-
cl. wear	F.	G2	-

broken off on a somewhat higher level, a ring of enamel is visible around the dentine. Only traces of the roots of the m3 are visible. Hypsodonty or brachyodonty cannot be established with certainty. This specimen may be of an old individual whith hypsodont cheek teeth in a progressed stage of wear, with the alveoles largely closed and only rests of the roots left. Length and breadth measurements have been estimated on alveolar level: p4 = 11.5 x 10.6 mm, m1 = 9.3 x 9.1 mm, m2 = 9.8 x 9.2 mm, m3 length = 7.5 mm.

The alveolar length of the tooth-row of this specimen from Locality 1 (39.5 mm) is outside the range of *H. b. subcristata* (26.4 - 33.8 mm, n = 22) and of *H. indica* (32.0 - 38.0 mm, n = 12). On tooth size this specimen C.1772 is allocated to *H. magna.*

Specimen CP.270: The left mandible fragment from Locality 13, nr. CP.270, described by T. de Chardin & Pei (1941, fig 49) has an alveolar tooth-row length of 35.7 mm, occlusal 34.3 mm, so it is larger than *H. b. subcristata*, but not larger than *H. indica.* Measurements and occlusal enamel pattern (classes according van Weers, 1990):

	Breadth	Length	Class
p4	8.0 mm	10.0 mm	S5
m1	7.6 mm	7.7 mm	T1
m2	8.1 mm	8.4 mm	T2
m3	7.2 mm	8.9 mm	S7

This specimen belongs to *H. kiangsenensis.*

STRATIGRAPHIC RANGES

The material from Zhoukoudian (Loc. 1 and 13) is of Early Zhoukoudianian age (Tong et al. 1995). The Zhoukoudianian or Middle Pleistocene in the Chinese stratigraphy, agrees with the Early Toringian in the European biochronology (Tong et al., 1995). The Yanhui and Wazhuan cave fauna is from the Middle Pleistocene (Zheng, 1993). Specimens from the Liucheng *Gigantopithecus* cave are of Early Pleistocene age (Pei, 1987) which is Early Nihewanian in the Chinese biochronology, agreeing with late Villanyian of the European biochronology (Tong et al., 1995). The specimen from Longgupo has an Early Nihewanian age also. So the biochronological distribution of both *H. magna* and *H. kiangsenensis* extends from Earley Nihewanian to Early or Late Zhoukoudianian.

Remarks: De Vos (1984) supposed that the Liucheng *Gigantopithecus* cave finds represent different ages. This was based on Pei's(1958) mention of different layers supposedly connected with climatic changes, and on Gu Yu-min's (1980) mention of six layers in the deposits. Pei (1965), however, states that the fossils were mainly collected from one of the layers. The time range of the deposits which are 2 m thick is unknown. These sediments are much less extensive than those from Longgupo (Zheng, 1993, and Huang et al., 1995).

H. lagrelli is known from Locality 9 and 13 of Zhoukoudian. According to Tong et al. (1995) these localities represent a range from Late Nihewanian to Early Zhoukoudianian, so for an Early Pleistocene assignment (van Weers, 1995) there seems to be no basis.

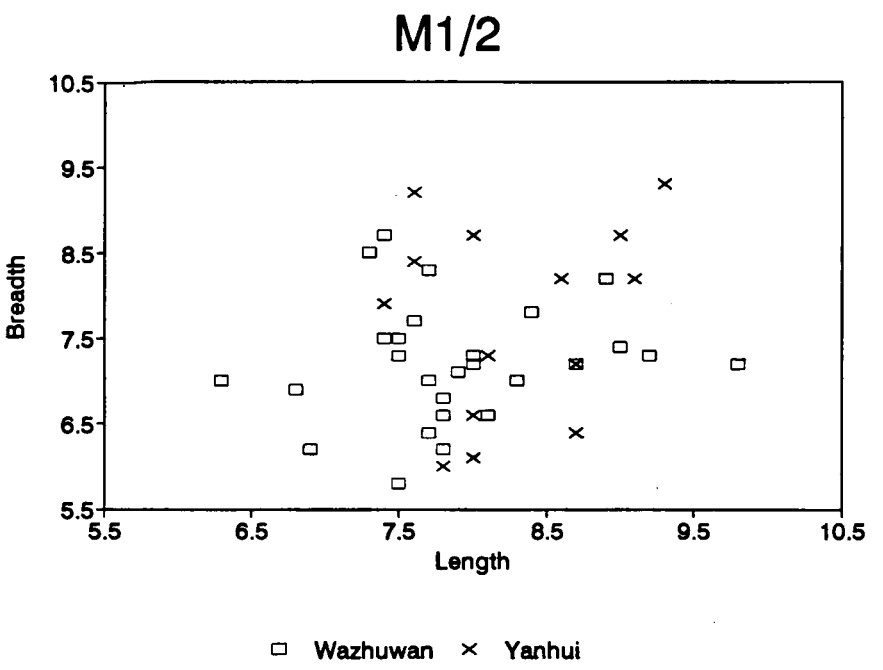

Fig. 6. Diagram of length and breadth in mm of the M1/2 from the Wazhuwan and Yanhui cave. About 10 specimens can be allocated to *H. magna* and 20 to *H. kiangsenensis*. Between the tooth length of 8.0 and 8.5 mm a mixture is supposed.

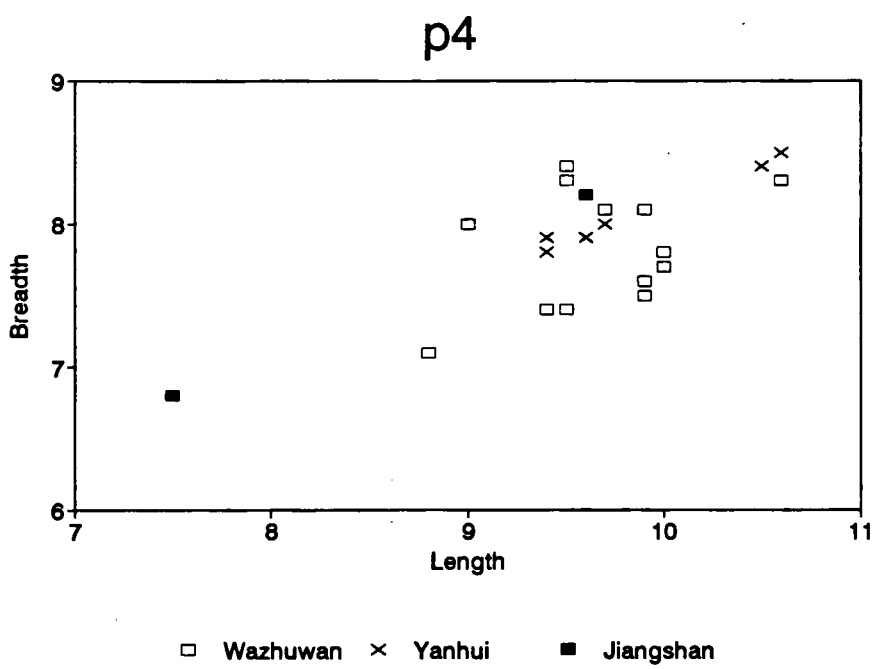

Fig. 7. Diagram of length and breadth in mm of the p4 from the Wazhuwan and Yanhui Cave and from Jiangshan, the type locality of *H. kiangsenensis*. Only the three largest ones are allocated to *H. magna* with certainty, around a length of 10 mm allocation is doubtful.

TAXONOMY

DIAGNOSIS OF *HYSTRIX* LINNAEUS, 1758

Emended diagnosis: Small to large sized porcupines with little to strongly enlarged nasal region and height of the skull, with molars brachyodont to strongly hypsodont.

Differential diagnosis: The smallest *Hystrix* species differ from the genera Trichys Günther, 1877 and *Atherurus* F. Cuvier, 1829 in the possession of hypsodont molars, the larger *Hystrix* species, the hypsodont as well as the brachyodont species, differ from these genera, in their large size, in the larger relative nasal length and the larger relative height of the skull.

(SUB)GENERIC ALLOCATION

Lönnberg (1923) already stated that no satisfactory diagnosis has been published by which the genus *Hystrix* on cranial characters could be divided into a genus *Hystrix* s.s. and a genus *Acanthion*. The only diagnostic character is the different distribution of the colour on the quills, and at maximum the rank of a subgenus may be assigned to *Acanthion* (van Weers, 1979). The Chinese *H. brachyura subcristata* belongs without any doubt to *Acanthion*, so Pei's(1987) application of the name *subcristata* for the two Guangxi skulls is in contradiction with his explicit reference to *Hystrix* s.s. All five species in the subgenera *Acanthion* and *Thecurus* (van Weers 1978 and 1979) are smaller than *Hystrix* s.s. and have the same type of colour distribution on the quills, so apparently this character is correlated with body size. *H. b. subcristata* is very close in size to *H. indica* so it is obvious that specimens which are larger than *subcristata* belong to *Hystrix* s.s. This applies for Pei's skulls from Guangxi and for all samples of teeth discussed here.

SPECIFIC OR SUBSPECIFIC DISTINCTION

A supposition is possible that porcupine species have changed gradually and continuously in size only during Pleistocene times, not allowing specific distinction (Hooijer, 1950). However, size is supposed to be an important adaptation to environmental factors for porcupines, such as a burrowing way of life, type of vegetation, type of food and size of predators. Extant porcupine species that have the same area of distribution, at least show a difference in mean size. Therefore, when a difference in mean size is found between two samples of fossil teeth, these may be supposed to represent different taxonomic units, translated in species from different environments.

Subspecific distinction in the genus *Hystrix* is based mainly based on the morphology of the skull and the development of the spiny covering. As fossil material mainly consists of isolated teeth, only size is left as a diagnostic character. Then distinction below species level is not significant.

DISCUSSION

STATUS OF THE SPECIES NAME *H. MAGNA*.

The oldest, but invalid, mention of this name is of Wu Maolin et al. (1975). These authors mentioned *Hystrix magna* Pei in their list of the fauna from the Yanhui cave without any description, reference to a specimen or to a publication as the source of this species name. They (1975) listed Pei et al. (1965) in their literature references, but the species name *magna* is not mentioned in this publication either. The teeth from the Yanhui cave belong to the largest ones studied and are hypsodont (Table 2). Pei's (1987) description, his table of measurements and the species name *magna*, unmistakably refer to the extremely large size of the species. The Yanhui material may possibly have been the origin of the name *magna* but there is no proof for this supposition. After a thorough research in the relevant collections only one of the syntypes of *H. magna* Pei, 1987 from the Liucheng *Gigantopithecus* cave could be recognised as such, but this specimen cannot be considered brachyodont. The brachyodonty of *magna* in Pei's description is not unambiguous, is not supported by measurements or by a figure showing tooth height and is not supported by other material from the type locality available to the present study. Pei's type series may possibly represent a selection of the lowest ones from the 200 isolated teeth from the *Gigantopithecus* cave. From all the other caves of Guangxi 500 isolated teeth are known among which a very large hypsodont and a clearly smaller hypsodont species can be distinguished. From these caves also the very large skull and two clearly smaller ones discussed

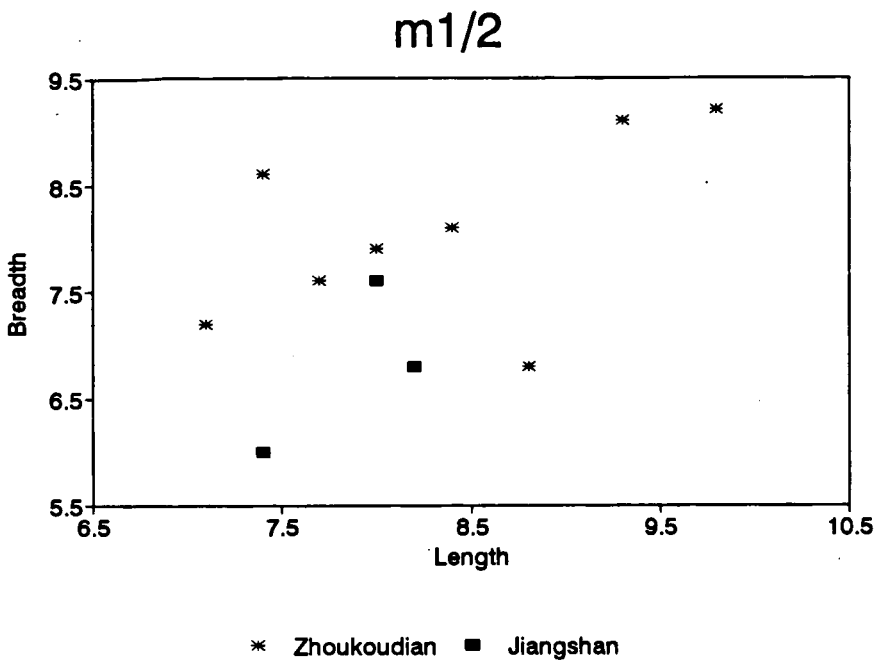

Fig. 8. Diagram of length and breadth of the m1/2 from Zhoukoudian and Jiangshan. The two largest ones are of *H. magna* from Locality 1 of Zhoukoudian, 6 of the 9 smaller ones are of *H. kiangsenensis* from Locality 1 as well as Locality 13, three are from the type locality Jiangshan of *H. kiangsenensis*.

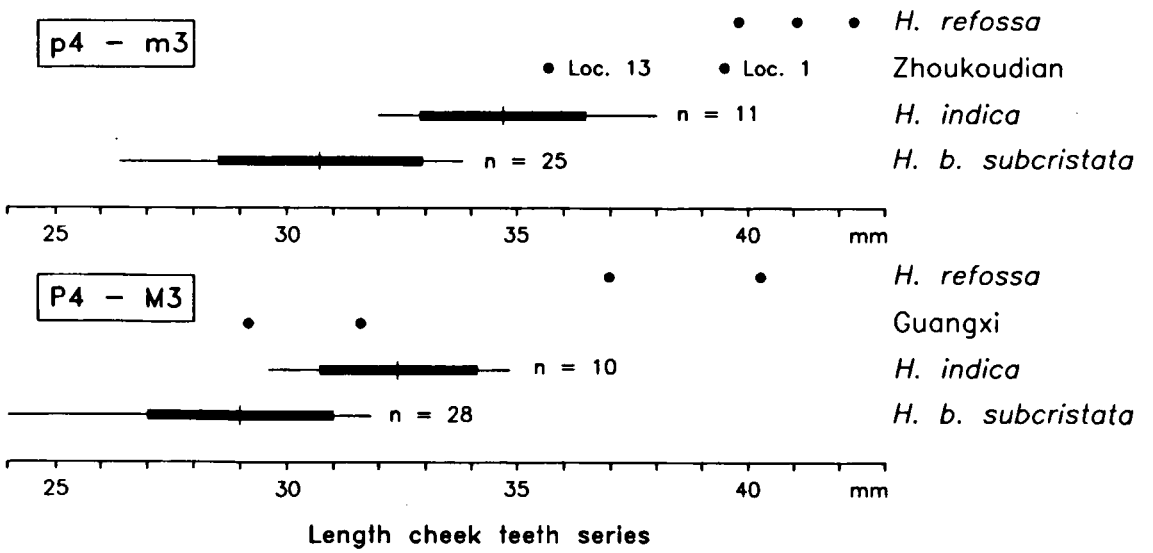

Fig. 9. Alveolar length of upper and lower tooth series of the extant species *H. b. subcristata* and *H. indica* with mean + and - standard deviation, range and sample size (n), with some measurements of specimens from Guangxi and Zhoukoudian and some specimens of *H. refossa*.

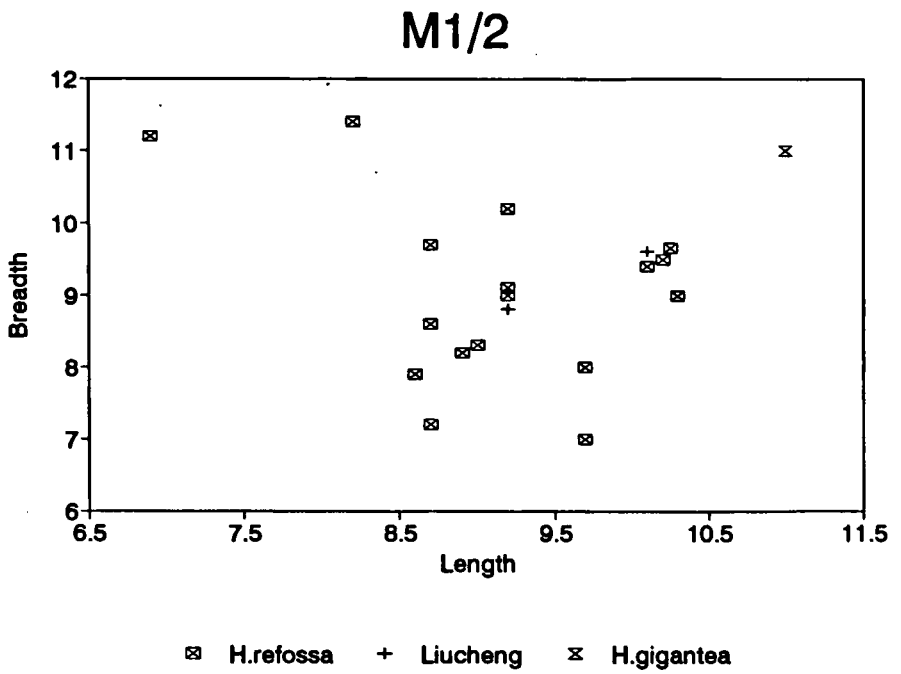

Fig.10. Diagram of length and breadth in mm of M1/2 of 17 specimens of *H. refossa*, one of *H. gigantea* and of two *H. magna* from its type locality the Liucheng *Gigantopithecus* cave.

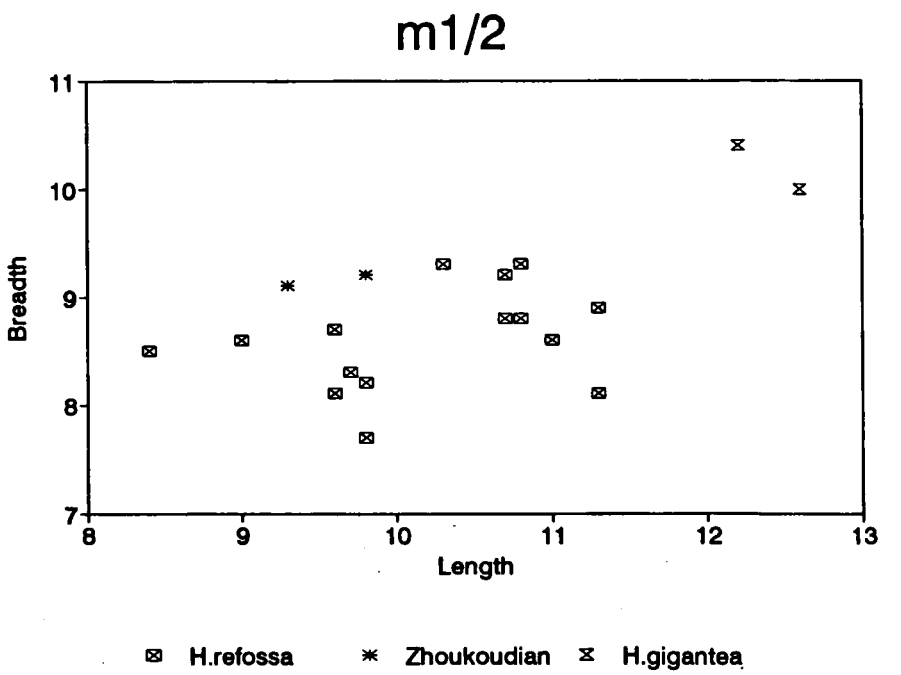

Fig. 11. Diagram of length and breadth in mm of 15 m1/2 teeth of *H. refossa*, two of *H. gigantea* and two of *H. magna* from Zhoukoudian Locality 1.

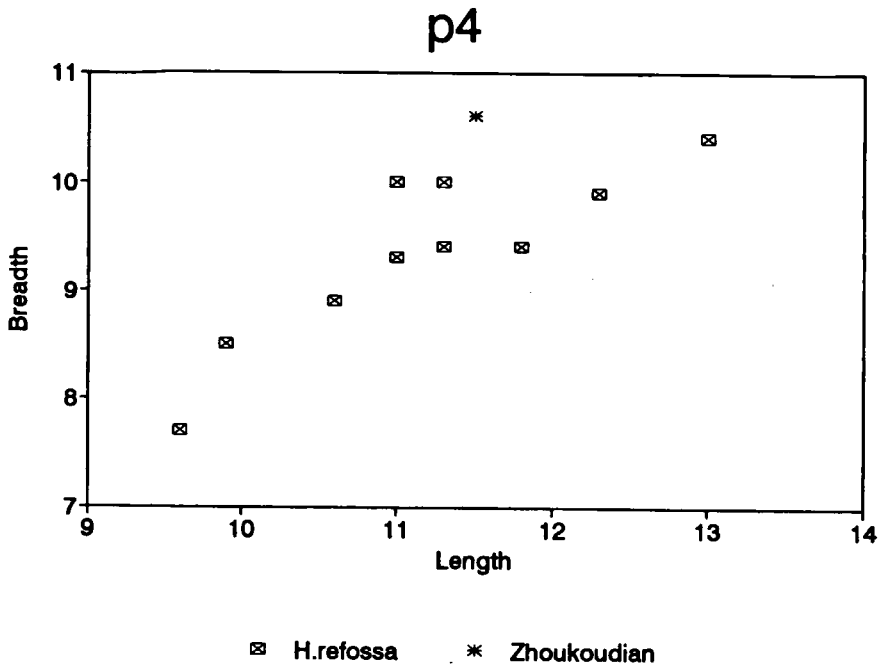

Fig. 12. Diagram of length and breadth in mm of 10 p4 teeth of *H. refossa* and one *H. magna* specimen from Zhoukoudian Locality 1.

above have been obtained. It is assumed that the two types of teeth and the two types of skulls correlate.

The available syntype, the isolated left M1/2 nr.V5036.12 (Pei, 1987: pl. XV, fig. 6), occurring in his table with measurements (p. 89), Fig. 13 in the present paper, is indicated as the lectotype of *H. magna* Pei, 1987.

CO-OCCURRENCE OF *HYSTRIX* SPECIES

In the extant fauna of Sumatra the species *H. sumatrae* (Lyon, 1907) and *H. brachyura* occur together, and on Borneo the same is the case with *H. brachyura* and *H. crassispinis* Günther, 1877. Co-occurrence of the fossil species, *H. refossa* and *H. vinogradovi* Argyropulo, 1941 is known from the Euro-pean Pleistocene of Osztramos 8, Hungary. Co-occurrence of three *Hystrix* species in the Chinese Pleistocene, *H. magna*, *H. kiangsenensis* and *H. lagrelli* Lönnberg, 1924 is not improbable because these three differ greatly in size and probably in biotope. Data from the *H. lagrelli* are from van Weers (1992 and 1995). The size differences are expressed with the approximative occipito-nasal length, the length of an upper or lower tooth-row and the estimated length of some teeth in mm, with range and number of specimens:

	Occ.nas.l.	Tooth-row	M1/2	m1/2	P4	p4
H. magna	160 n = 1	39 n = 1	9.0	9.0	9.5	10.0
H. kiangsenensis	145 n = 2	29-36 n = 2	7.5	7.5	8.5	8.5
H. lagrelli	100 n = 1 n = 45	21- 22 n = 2 n = 55	5.5 4.6-6.6 n = 31	5.9 4.5-7.7 n = 21	6.1 4.9-7.5	6.7 5.6-7.8

COMPARISON OF *H. MAGNA* WITH *H. REFOSSA* AND *H. GIGANTEA*

H. refossa Gervais, 1852: In Fig. 10 the two M1/2 teeth of *H. magna* from Liucheng cannot be distinguished from the European *H. refossa* Gervais, 1852 (van Weers, 1994). In Fig. 11 the two m1/2 of *H. magna* from Zhoukoudian fall within the range of *H. refossa.* In Fig. 12 the dimensions of the p4 of *H. magna,* estimated from the alveole in the mandible from Loc. 1 of Zhoukoudian, does not really differ from *refossa.* In Fig. 9 the length of the lower teeth series of that *H. magna* mandible approaches that of *H. refossa.* These data suggest an agreement between *H. refossa* and *H. magna. H. refossa* has a stratigraphic range in Europe from Early Villanyian to Late Pleistocene, so *H. magna* and *H. refossa* may be synonymous. However, it seems premature to bring the European and Chinese large Pleistocene porcupines under synonymy mainly on tooth dimensions.

H. gigantea van Weers, 1985: In Fig. 10 the M1/2 of this species from Java (nr. 271 in van Weers, 1985, class of wear F) is longer than all 17 refossa specimens and two magna specimens from Liucheng. The two broadest, but very short, *refossa* teeth in this figure are in a progressed stage of attrition (class H and G), the feature mentioned in the Wazhuwan-Yanhui section above. In Fig. 11 the two m1/2 of *H. gigantea* (nrs. 271 and 275 in van Weers, 1985) are clearly larger than the 15 *refossa* specimens and the two *magna* specimens from Loc.1 of Zhoukoudian (m1 and m2 of the mandible V1772). The *H. gigantea* specimens suggest that this species is larger than both *H. magna* and *H. refossa.* On the other hand, the occurrence of the very small *H. lagrelli* and the extremely large *H. gigantea* in the Middle Pleistocene of Java is similar to the presence of *H. lagrelli* and *H. magna* in the Early and Middle Pleistocene of China. However, the number and condition of the Javan specimens provides too poor evidence for bringing *H. magna* under the synonymy.of *H. gigantea.*

COMPARISON OF *H. MAGNA* WITH *H. CRASSIDENS*

Only a cast of an incomplete ramus of an immature mandible of *H. crassidens* Lydekker, 1886 could be studied, probably the right ramus of the complete type mandible F.219.a of which Lydekker (1886) figured the left ramus. This right ramus was also figured by Dassarma et al. (1982). Type locality is the Cathedral Cave, Kurnool district, Andhra Pradesh, India. The age is considered Late Pleistocene (Biswas, 1987). The measurements of the m1 (7.0 x 9.2 mm) and the m2 (7.5 x 9.8mm) are within the range of *H. magna.* However, the chance that considerable differences exist between Early to Middle Pleistocene and Late Pleistocene porcupine species cannot be excluded as in the situation on Java. There the Middle Pleistocene *Hystrix* species from Sangiran and Trinil are totally different from the specimens from Punung which have a Late Peistocene age (Badoux, 1959). The significance of the single specimen from Kurnool is not enough to bring Early and Middle Pleistocene species in the synonymy of this Late Pleistocene species.

Dassarma et al. (1982) described and figured two maxillary and one mandible fragment from the Early Holocene or Latest Pleistocene of Babladanga, Bankura district, West Bengal, India under the name *H. crassidens.* The following measurements have been taken of these specimens:

	M1		M2		P4	
	Breadth	Length	Breadth	Length	Breadth	Length
G.S.I. 19110	7.8	7.1	8.0	8.6	8.0	9.3
G.S.I. 19111	7.2	7.4	7.5	8.8	7.9	-
	m1		m2		p4	
G.S.I. 19113	7.4	8.9	8.0	9.2	7.6	9.1

These dimensions are on an average smaller than those of the measured type mandible of *crassidens* so the allocation to *crassidens* is not certain. They just fit in *H. indica,* so a relationship with this species is more probable than with *H. crassidens.*

The establishment of the relationship of the Late Pleistocene *H. crassidens* with the Early and Middle Pleistocene large porcupines has to await the availability of a more comprehensive material.

PHYLOGENY

In Fig. 14 a review is presented of a hypothetical phylogeny of the genus *Hystrix*. The stratigraphic range of *H. parvae* (Kretzoi, 1951), the smallest and oldest brachyodont *Hystrix* known, is from Late Vallesian (MN 10) to Early Turolian (MN 11). *H. sivalensis* Lydekker, 1878 from the Siwaliks has a Turolian age (Barry & Flynn, 1990), just like the undescribed specimens from Lufeng (Baodean, Tong et al., 1995). *H. primigenia* ranges from the Turolian (MN 12) to the Pliocene (Villanyian, MN 16). *H. primigenia, H. sivalensis,* the specimens from Lufeng and the younger one from Longgupo (Villanyian, MN 17) have a large size and brachyodonty in common, so they may have a common origin.

H. refossa is known from the Pliocene (MN 16). The origin of this species with the other three large hypsodont porcupines, *H. magna, H. gigantea* and *H. kiangsenensis* probably has been in the Pliocene, although not necessarily all simultaneously as suggested in the figure. *H. kiangsenensis* derives its place in the diagram by its size near *H. indica* and its slightly higher specialized skull. The morphology of the skull of *H. indica* is close to that of *H. brachyura* and is less specialised than the other two large extant species. It is also less specialized than the skulls of *H. refossa* (sensu van Weers, 1994) and *H. magna* from Chongzuo (Guo, 1997).

The colour distribution of the spiny covering of *H. indica*, more than one dark ring on each quill, is quite like *H. africaeaustralis* and *H. cristata,* so that character may have a Pliocene origin too.

H. lagrelli and *H. vinogradovi* (Osztramos 8, Jánossy, 1972) occur in the Early Pleistocene. These smaller sized species may have originated in the Pliocene. The three endemic island populations, *H. pumila* Günther, 1879 from the Philippines, *H. sumatrae* (Lyon, 1907) from Sumatra and *H. crassipinis* Günther, 1877 from Borneo may have developed in the Pleistocene from the same ancester. The origin of *H. javanica* (F.Cuvier, 1823) is indicated as Pliocene, but a development from *H. lagrelli* which occurred in the Pleistocene of Java (van Weers, 1995) is also possible. These smaller sized extant species have the colour distribution of one dark part on each quill in common.with *H. brachyura* Linnaeus, 1758.

Fig. 13. Occlusal view (above) and posterior view (below), of the M1/2 nr.V5036.12 in Pei's (1987) table p.89 and plate XV, figure 6, lectotype of *Hystrix magna* Pei, 1987 (x 5).

A common origin of the smaller and the larger sized hypsodont porcupines has probably taken place in the Pliocene. In the Pliocene the brachyodont species were replaced by the hypsodont ones, but the relation between these groups is unclear. The common origin of the genera *Hystrix, Atherurus* and *Trichys,* and the relationship of the family Hystricidae with other families lies in the dark by lack of linking fossils.

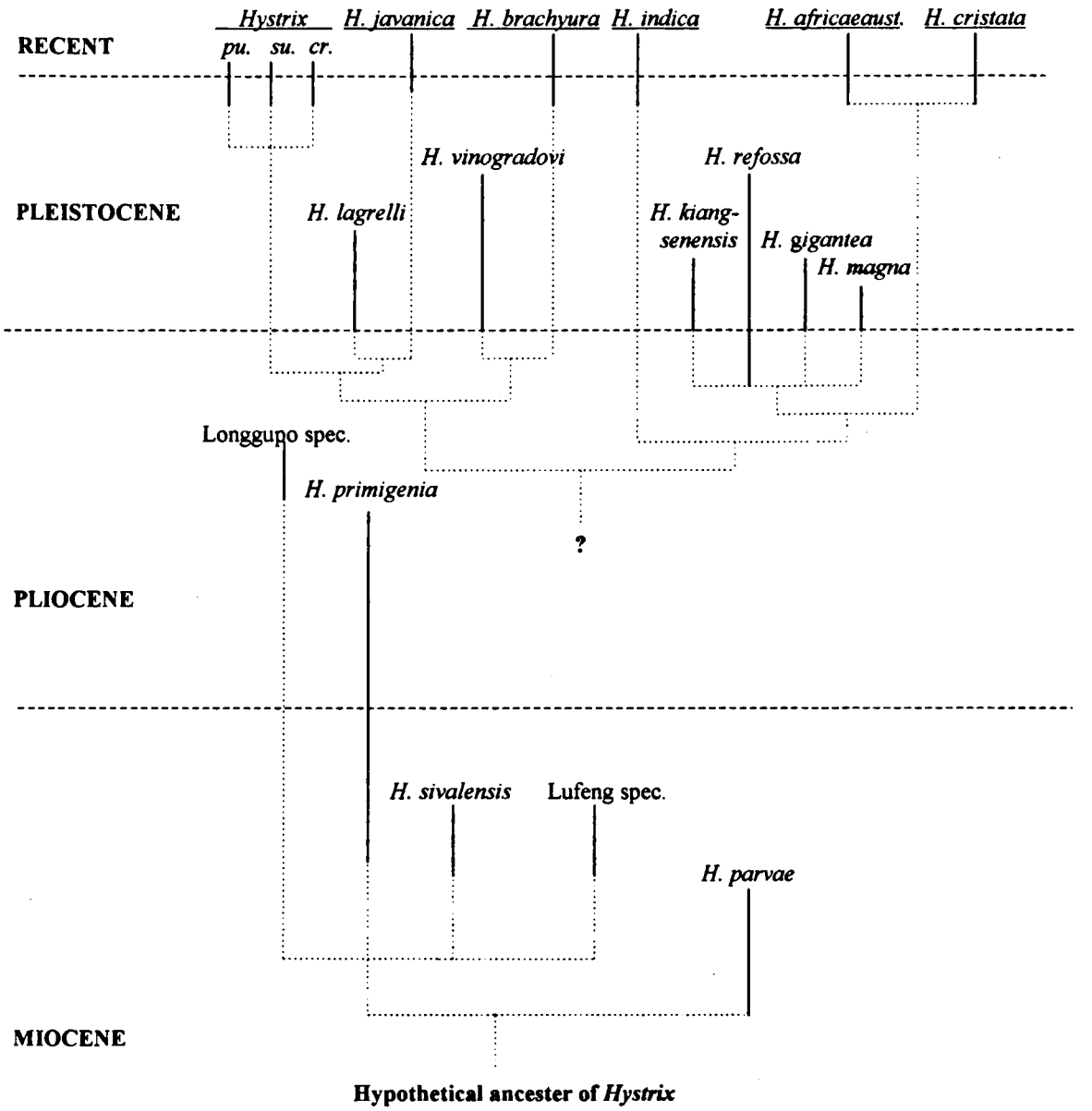

Fig. 14. Review of a hypothetical phylogeny of the genus *Hystrix*. Abbreviations: pu = *H. pumila*, su = *H. sumatrae*, cr. = *H. crassispinis*. Lufeng spec. is based on the collection mentioned in Qiu et al. (1985), Longgupo spec. on specimen V9669 in Zheng (1993). Distances in the figure are not fully proportionate to time, the hypothetical ancester of *Hystrix* lies much farther back in time than suggested in the figure.

CONCLUSIONS

1. None of the specimens in the collections studied belongs to the extant *H. brachyura subcristata* Swinhoe, 1870, subspecies of *Hystrix brachyura* Linnaeus, 1758, subgenus *Acanthion* F. Cuvier, 1823.

2. Neither in the collections from the type locality of *H. magna* Pei, 1987 nor in the other collections studied, brachyodont cheek teeth were

found, except the specimen from Longgupo. Therefore *H. magna* Pei is considered a species with hypsodont rather than with brachyodont teeth.

3. The isolated left M1/2 nr.V5036.12 (Pei, 1987: table p. 89, pl. XV, fig. 6), Fig. 13 in the present paper, kept in the collections of the IVPP in Beijing, is the lectotype of *H. magna* Pei, 1987.

4. The largest specimens from the Pleistocene of the provinces Guangxi, Guizhou and Beijing are allocated to *Hystrix magna* Pei, 1987. Its skull is larger on average than that of *H. indica* and more specialized concerning nasal stucture and height of the skull.

5. The smaller specimens from the collections studied are allocated to *Hystrix (Hystrix) kiangsenensis* Wang, 1931. The skull has about the size of *H. indica* but the nasals are relatively larger

6. The isolated p4 from Longgupo, nr. V9669, described under the name *H. magna* by Zheng, 1993 may represent a different species with lower crowned cheek teeth, more related to the Miocene and Pliocene low-crowned species from Europe and Asia rather than to *H. magna.* The specimen is provisionally referred to *Hystrix* sp.

7. The hypodigm of the Javan *H. gigantea* van Weers, 1985 provides too poor evidence for considering it a senior synonym of *H. magna* Pei, 1987.

8. Too little material of the Late Pleistocene species *H. crassidens* Lydekker, 1886 from Subcontinental India is available to establish its relationship with the Chinese Middle and Early Pleistocene porcupines.

9. The S.E. Asian species *H. magna* and the European Plio-Pleistocene *H. refossa* Gervais, 1852 (sensu van Weers, 1994) may be synonymous, but there are unsufficient data available for nomenclatorial consequences.

ACKNOWLEDGEMENTS

The first author is very grateful to the Drs. Qiu Zhuding, Wu Wenyu and Zheng Shaohua of the IVPP for their kind hospitality, helpful co-operation and care during his stay in Beijing. Many thanks are due for the opportunity to study specimens in their care to the following persons: Prof. Wang Zuwang of the Institute of Zoology, Beijing, Prof. Wang Yingxiang and Mr. Jiang Xuelong, Kunming Institute of Zoology, Kunming, China, Dr. F.N. Mitra and Dr. D.P. Das, Geological Survey of India, Calcutta, India. The criticism of Dr. Hans de Bruijn of the Institute for Earth Sciences Utrecht, provided with much patience, is appreciated very much, and Tom van Hinte of the same institution is thanked for his kind assistance with the figures. Mr. Zhang Jie, IVPP Beijing made the photograph of the lectotype specimen. Dr. P.J.H. van Bree, Zoological Museum Amsterdam, Dr. L.B. Holthuis and Dr. J. de Vos, National Museum of Natural History, The Netherlands gave useful advices. Dr. W. Bergmans added a *H. brachyura* specimen to the reference material. Mrs R.E. Slop is thanked for final corrections in the English text. The first author gratefully acknowledges the financial support (grant R-87-249) of the Netherlands Organisation for Scientific Research (NWO).

REFERENCES

ALCALA, L. & P. MONTOYA, 1998. *Hystrix primigenia* (Wagner, 1848) (Rodentia, Mammalia) del Mioceno Superior MN 13) de Las Casiones (Teruel, EspaÒa). Revista EspaÒola de Paleontologİa, in press.

BADOUX, D. M., 1959. Fossil mammals from two fissure deposits at Punung (Java) with some remarks on migration and evolution of mammals during the Quaternary in South East Asia. Kemink en Zoon N.V., Utrecht: 1-151.

BARRY, J.C. & L.J. FLYNN, 1990. Key biostratigraphic events in the Siwalik sequence: 557-571. In: E.H. Lindsay et al. (eds), European Neogene Mammal Chronology. Plenum Press, New York.

BISWAS, S., 1987. Quaternary mammalian record in peninsular and extra-peninsular India. Indian J. Earth Sciences, 14 (3-4): 296-306.

DASSARMA, D.C., S. BISWAS & A. NANDI, 1982. Fossil vertebrates from the late Quaternary deposits of Bankura, Burdwan and Puralia Districts, West Bengal. Mem. Geol. Survey of India, Palaeontologia Indica, New Series, 14: 1-66.

CORBET, G.B. & L.A. JONES, 1965. The specific characters of the crested porcupines, subgenus *Hystrix.* Proc. Zool. Soc. London, 144 (2): 285-300.

FRENKEL, H., 1970. *Hystrix angressi* sp. nov., a large fossil porcupine from the Levalloiso-Mousterian of the Geula Cave. Israel J. Zool., 19: 51-82.

HUANG WANPO, R. CIOCHON, GU YUMIN, R. LARICK, FANG QIREN, H. SCHWARCZ, C. YONGE, J. DE VOS & W. RINCK, 1995. Early Homo and associated artefacts from Asia. Nature, 378: 275-278.

GU YU-MIN, 1980. Note on the buried and distribution of the *Gigantopithecus* fossils in the *Gigantopithecus* cave of Liucheng, Guangxi. Vertebrata PalAsiatica, 18 (2):151-153 (Chinese) (English abstract. p. 153)

GUO JIANWEI, 1997. Note on a fossil skull of *Hystrix magna* Pei, 1997 (Rodentia, Mammalia) from Chongzuo, Guangxi. Vertebrata PalAsiatica, 35 (2): 145-151 (Chinese) (English summary, p. 151-153).

HOOIJER, D. A., 1950. The study of subspecific advance in the quaternary. Evolution, 4 (4): 360-361.

JÁNOSSY, D., 1972. Ein kleiner *Hystrix* aus dem Altpleistozän der Fundstelle Osztramos 8. (Nordungarn.). Vertebrata Hungarica, 13: 163-182.

LYDEKKER, R., 1886. The fauna of the Karnul Caves. Mem. Geol. Survey India, Palaeontologia Indica, (X), 4 (2): 23-58.

LÖNNBERG, E., 1923. On the chinese porcupine, *Hystrix subcristata* Swinhoe, with remarks on the other members of the genus. Ark. Zoologi, 15 (18): 1-10.

LÖNNBERG, E., 1924. On a new fossil porcupine from Honan with some remarks about the development of the Hystricidae. Palaeontologia Sinica, 1 (3): 1-15.

NIETHAMMER, J., 1982. Familie Hystricidae Burnett, 1830. Altwelt-Stachelschweine. In: Handbuch der Säugetiere Europas, Band2/I. Akademische Verlagsgesellschaft, Wiesbaden: 583-605.

PEI WEN-CHUNG, 1965. Excavation of Liucheng *Gigantopithecus* cave and exploration of other caves in Kwangsi. Mem. Inst. Vert. Palaeont. Palaeoanthrop., 7: 1-36 (Chinese) (English summary, p. 37-54).

PEI WEN-CHUNG, YUAN CHEN-SIN, LIN YI-PU & CHANG YIN-YUN, 1965. Discovery of palaeolithic chert artifacts in Kuan-Yin-Tung cave in Chien-hsi-hsien of Weichow Province. Vertebrata PalAsiatica, 9 (3): 270-279 (Chinese) (English abstract, p. 279).

PEI WENZHONG, 1987. Carnivora, Proboscidea and Rodentia from Liucheng *Gigantopithecus* cave and other caves in Guangxi. Mem. Inst. Vert. Palaeont. Palaeoanthr., Acad. Sinica, 18: 1-94 (Chinese) (English abstract, p. 95-115).

QIU ZHUDING, HAN DEFEN, QI GUOQIN & LIN YUFEN, 1985. A preliminary report on a micromammalia assemblage from the homonoid locality of Lufeng, Yunnan. Acta Anthropologia Sinica, 4 (1): 13-32. (Chinese with English summary).

TEILHARD DE CHARDIN, P. & W.C. Pei, 1941. The fossil mammals from Loc. 13 of Choukoutien. Palaeontologia Sinica, (C), 11 (126): 1-106.

TONG YONGSHEN, ZHENG SHAOHUA & QIU ZHUDING, 1995. Cenozoic mammal ages of China.Vertebrata PalAsiatica, 33 (4): 290-314.

VOS, J. DE, 1984. Reconsideration of Pleistocene cave faunas from South China and their relation to the faunas from Java. Cour. Forsch. Inst. Senckenberg, 69: 259-266.

WANG, K.M., 1931. Die Hohlenablagerungen und Fauna in der Drachen-Maul-Hohle von Kiangsen, Chekiang. Contr. Nation. Research Inst. of Geology Academia Sinica, 1 (4): 41-65.

WEERS, D.J. VAN, 1978. Notes on South-East Asian Porcupines (Hystricidae, Rodentia) III. On the taxonomy of the subgenus *Thecurus* Lyon, 1907 (genus *Hystrix* Linnaeus, 1758). Beaufortia, 28 (344): 17-33.

WEERS, D.J. VAN, 1979. Notes on South-East Asian Porcupines (Hystricidae, Rodentia) IV. On the taxonomy of the subgenus *Acanthion* F. Cuvier, 1823 with notes on the other taxa of the family. Beaufortia, 29 (356): 215-272.

WEERS, D.J. VAN, 1985. *Hystrix gigantea*, a new fossil porcupine species from Java (Rodentia: Hystricidae). Senckenbergiana Lethaea, 66 (1-2): 111-119.

WEERS, D.J. VAN, 1990. Dimensions and occlusal patterns in molars of *Hystrix brachyura* Linnaeus, 1758 (Mammalia, Rodentia) in a system of wear categories. Bijdr. Dierk., 60 (2): 121-134.

WEERS, D.J. VAN, 1992. *Hystrix vanbreei* n. sp., a new fossil porcupine from the Pleistocene of Java, with notes on the extant species of the Indonesian Archipelago. Senckenbergiana Lethaea, 72: 189-197.

WEERS, D.J. VAN, 1994. The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix*. Scripta Geol., 106: 35-52.

WEERS, D.J. VAN, 1995. The fossil porcupine *Hystrix lagrelli* Lönnberg, 1924 from the Pleistocene of China and Java and its phylogenetic relationships. Beaufortia, 45 (2): 17-25.

WEERS, D.J. VAN & P. MONTOYA, 1996. Taxonomy and stratigraphic record of the oldest European porcupine *Hystrix parvae* (Kretzoi, 1951). Proc. Kon. Ned. Akad. Wetensch., 99 (1-2): 131-141.

WU MAOLIN, WANG LING-HONG, CHANG YING-YUN & CHANG SEN-SHUI, 1975. Fossil human teeth and associated fauna from Northern Guizhou. Vertebrata PalAsiatica, 13 (1): 14-23 (Chinese).

ZHENG SHAOHU, 1993. Quaternary rodents of Sichuan-Guizhou area, China. Academia Sinica, Beijing: 1-230 (Chinese) (English summary , p. 231-270).

Received: April 22, 1998