

A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family

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Abstract

Measurements of many hundreds of the high-crowned cheek teeth of *Hystrix* specimens from the Euro-Asiatic Pleistocene in the collections of European and Asiatic institutions have been compared with extant species for a revision of the genus. A review is given about the extant genera and species of the family. The number of recognisable Euro-Asiatic species in the fossil record is reduced from eight to five. The European *H. (A.) vinogradovi* Argyropulo, 1941 is here considered to be a synonym of *H. (A.) brachyura* Linnaeus, 1758, and the three Asiatic species *H. (H.) crassidens* Lydekker, 1886, *H. (H.) gigantea* Van Weers, 1985 and *H. (H.) magna* Pei, 1987 are synonymized with *H. (H.) refossa* Gervais, 1852. Most of the Chinese fossil specimens are properly allocated to *H. (H.) kiangsenensis* Wang, 1931 instead of '*H. subcristata*', and a neotype is indicated for this species. The distribution of the Indonesian *Hystrix* species is the result of several migration waves into Sundaland, and is not considered to be the result of 'in situ' evolution. Comparison of the Miocene material from the Siwaliks in India, described as *Sivacanthion complicatus* Colbert 1933, with extant and Pleistocene *Atherurus* results in allocation of this species to *Atherurus karnuliensis* Lydekker, 1886.

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Introduction

The extant porcupines and their distribution

In the classification of the Hystricidae followed here, the family contains three, all extant, genera: *Trichys* Günther, 1877, *Atherurus* F. Cuvier, 1829, and *Hystrix* Linnaeus, 1758, which are distinguished by different degrees of specialisation. *Trichys*, with only one species, is the least specialised and the only one that is limited to Southeast Asia. *Atherurus*, occurring in Africa as *A. africanus* Gray, 1842 and represented in Southeast Asia with *A. macrourus* (Linnaeus, 1758), takes an intermediate position. *Hystrix* is the most specialised genus and is divided in the subgenera *Hystrix*, *Acanthion* F. Cuvier, 1823, and *Thecurus* Lyon, 1907. *Hystrix* s.s. is represented by two species in Africa (*H. cristata* Linnaeus, 1758 and *H. africae-australis* Peters, 1852), and one in Asia: *H. indica* Kerr, 1792. The distribution of the genera and subgenera of the Hystricidae in Southeast Asia is indicated in Fig. 1. The subgenus *Acanthion* F. Cuvier, 1823 contains two species, *H. (A.) brachyura* Linnaeus, 1758 and *H. (A.) javanica* (F. Cuvier, 1823). In *H. (A.) brachyura* the subspecies *H. (A.) b. brachyura* Linnaeus, 1758, *H. (A.) b. subcristata* Swinhoe, 1870 and *H. (A.) b. hodgsoni* (Gray, 1847) are distinguished. The least specialised subgenus *Thecurus* Lyon, 1907 includes three species: *H. (T.) sumatrae* (Lyon, 1907), *H. (T.) crassispinis* Günther, 1877 and *H. (T.) pumila* Günther, 1879. On the basis of their current distribution it is generally supposed that southern Asia was the centre of origin of this family. The taxonomy of the extant species of the genus

Dr Dees J. van Weers passed away on 12 February 2006 at the age of 72. He drew consolation from the notion that several of his colleagues had reviewed his last work and that it could be finished 'in time'.

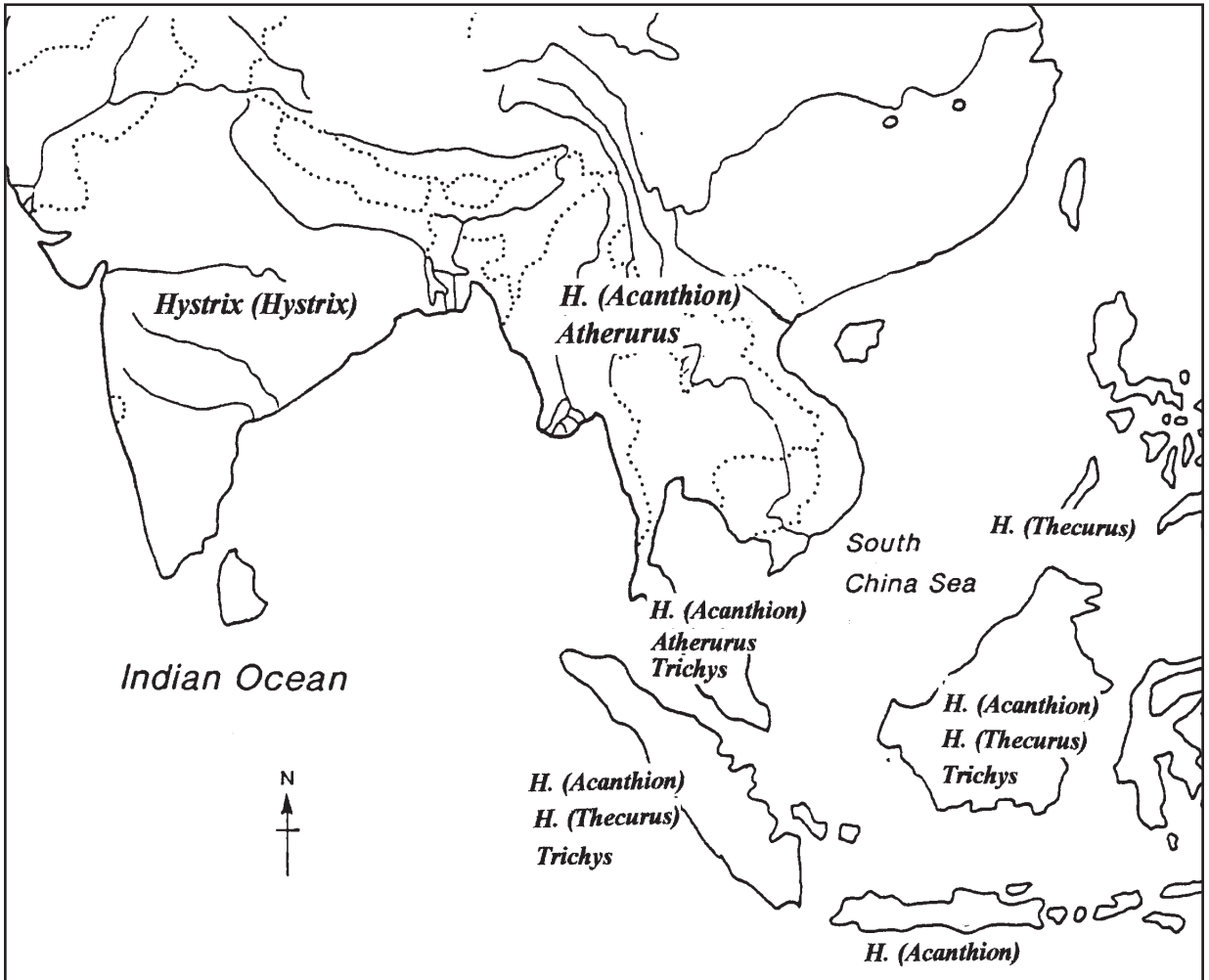


Fig. 1. Map of Southeast Asia broadly indicating the distribution of the extant genera and subgenera of the family Hystricidae. Subgenus *Hystrix*: India. Subgenus *Acanthion*: the continent (south of 35°N), Malay Peninsula, Java, Sumatra and Borneo. Subgenus *Thecurus*: Sumatra, Borneo and Palawan. Genus *Trichys*: Malay Peninsula, Sumatra and Borneo. Genus *Atherurus*: the continent (south of 30°N) and the Malay Peninsula.

Hystrix is based on cranial characters and on their spiny covering. The morphology of the cheek teeth is unusable for the distinction of subgenera and species, because the occlusal patterns strongly change by wear, even so that a left and a right tooth in the same position in a skull may differ. When only tooth material is available, the subgenera *H. (Hystrix)*, *H. (Acanthion)* and *H. (Thecurus)* cannot always be distinguished by size due to the overlap of their size ranges. An additional problem is that the occlusal morphology of the geologically oldest known species (from the Miocene) is, except the crown height, not really different from the extant representatives.

The Pleistocene porcupines

Because the spiny covering does not fossilize and finds of skulls are very rare, the taxonomy of the Pleistocene Hystricidae is necessarily based on the size of the cheek teeth. Unfortunately, many of the described species are based on a small number of specimens and their size variation is not known. Moreover, the height of the crown of all Pleistocene forms does not differ from that of the extant species. Cave fillings in China, Vietnam and Indonesia yield associations of many hundreds of specimens. Those from China show, in comparison with the variabil-

ity within extant species, an extreme size variation (Van Weers and Zheng, 1998). Therefore, we have to take into account that these associations may include several species. These Asiatic finds were never sufficiently compared with those from Europe. As a consequence a revision of the eight Euro-Asiatic species (recognised by Van Weers and Zheng, 1998; van Weers, 2003a) has become necessary. In this study the variation in size within and between the mostly overlapping associations are evaluated. This leads to a taxonomic revision of the Pleistocene species of the genus *Hystrix*. Finally, a short discussion is given about the evolution and paleogeography of the family.

Material and methods

Material from a number of institutions has been measured for this study, and data from preceding publications have been used. The length measurement of the cheek teeth has been preferred to that of the

width because it does not change in an extreme way in the course of attrition. The length diminishes gradually by wear but the occlusal width of a cheek tooth increases by wear to a size disproportional to the other dimensions of the tooth. The measurements are presented in Figs. 2-4 with range, mean, standard deviation and sample size. The upper cheek teeth are presented in upper case, the lower ones in lower case, ‘1/2’ is used because isolated first and second cheek teeth cannot be distinguished. The alveolar length of the P4-M3 and p4-m3 (Fig. 2), the length of the P4 and p4 (Fig. 3) and that of the M1/2 and m1/2 (Fig. 4), although correlated dimensions, are all presented to enable a better comparison. The measurements of the milk teeth and the third molars are not used because of their statistically small numbers. For convenience of comparison of the large number of assemblages, the measurements of some smaller collections are discussed but not represented in the relevant figures. The measurements are indicated in the figures with the current species names or with the locality name of the assemblages for which the spe-

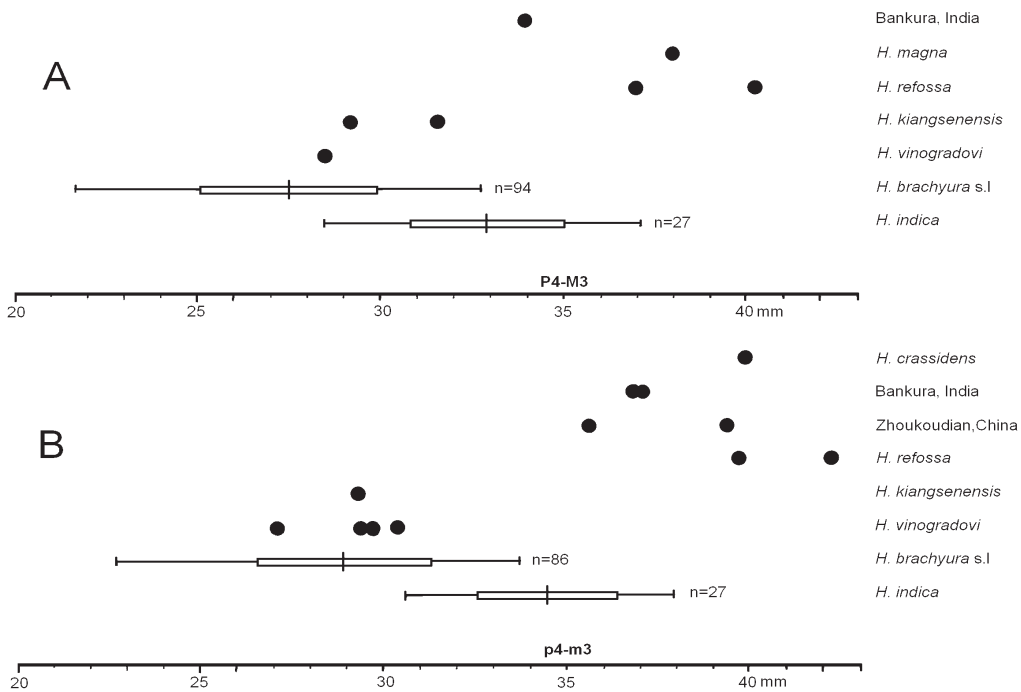


Fig. 2. Alveolar length of the P4-M3 (A) and p4-m3 (B) of the extant species *H. (Hystrix) indica* and *H. (Acanthion) brachyura* s.l., of a number of fossil species recognised thus far and of specimens from localities not yet allocated to a species, with mean, range, standard deviation and number of specimens (n). The extant species are presented with open bars. For the current specific allocation see the relevant text.

cific distinction was not clear. Data of the extant Asiatic species *Hystrix (Acanthion) brachyura* and *Hystrix (H.) indica* are represented in the figures as a reference for the variability in the fossil forms. Data of *H. (A.) brachyura* are from Van Weers (2003b) which include the subspecies from the Malay region to southern China and Nepal. Those of *H. (H.) indica* are from 32 specimens from the total area of distribution of this species. These two considerably differing species nevertheless show a clear overlap as for the size of the teeth (Figs. 2-4). This illustrates that other morphological characteristics that are not fossilized may have existed between fossil assemblages. The results are presented for each geographic region and subdivided on the basis of the thus far current specific names.

Institutional abbreviations: AMNH, American Museum of Natural History; IAH, Institute of Archeology, Hanoi; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MHNG, Muséum d’Histoire Naturelle de Genève; NHML, Natural History Museum London; NNMN, Nationaal Natuurhistorisch Museum Naturalis, Leiden; GSDB,

Geological Survey Division, Bangkok; GSI, Geological Survey India, Calcutta; ZMNH, Zhejiang Museum of Natural History, China.

Results

Europe

Hystrix refossa Gervais, 1852.

Localities. Perrier, St. Vallier and Ratonneau (France), Val d’Arno and Pirro (Italy), Venta Micena (Spain), Gombasek (Slovakia) and Ostramos (Hungary). Data are from Van Weers (1994, map fig. 3).

Hystrix vinogradovi Argyropulo, 1941.

Localities. Binagady (Azerbaijan), Kudaro (Georgia), Brassóv (Romania), Ostramos, Kiskohat, Varbó and Csobánka (Hungary), Medvednica (Slovenia), Ostrov and Kotlarce (Czech Republic), Siegmansbrunn (Germany). Data are from Van Weers (1994, map fig. 3), and new material from the Cave of Chênelaz (France, MHNG).

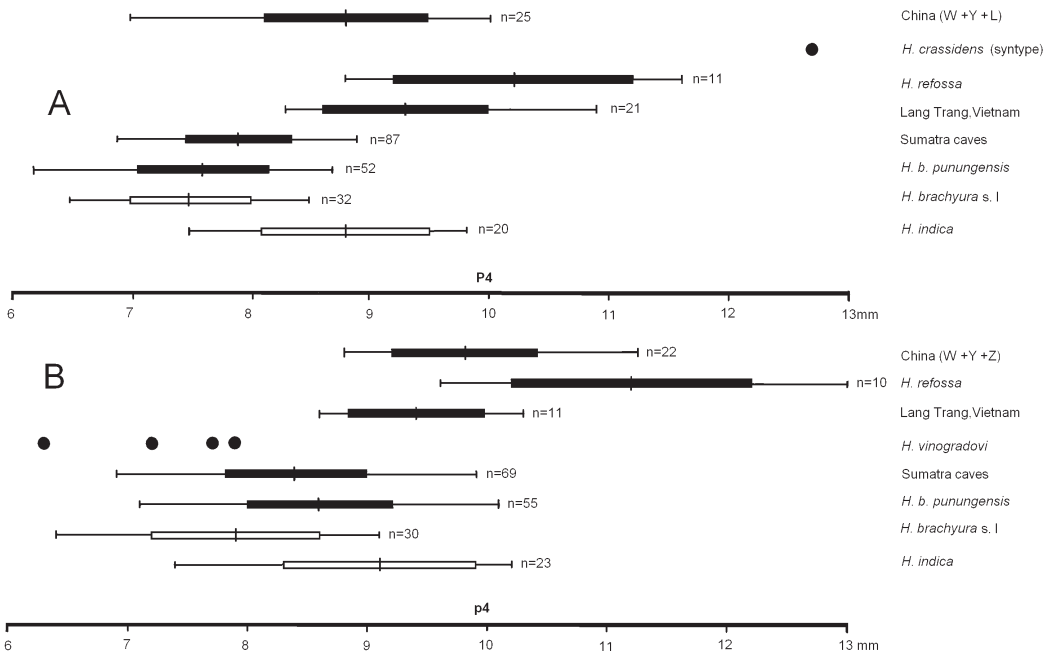


Fig. 3. Length of the P4 (A) and p4 (B) of the extant species *H. (Hystrix) indica* and *H. (Acanthion) brachyura* s.l., of fossil species recognised thus far and of specimens from localities not yet allocated to a species, with mean, range, standard deviation and number of specimens (n). The extant species are presented with open bars. W = Wazhuan, Y = Yanhui, L = Liucheng, Z = Zhoukoudian. For the current specific allocation see the relevant text.

Analysis and conclusions. *Hystrix refossa* is clearly larger than *Hystrix vinogradovi*. The length measurements of the P4-M3 (Fig. 2a) of *H. vinogradovi*, those of the p4-m3 (Fig. 2b), the p4 (Fig. 3b) and the M1/2 (Fig. 4a) fall nearly totally within the range of variation of the extant species *Hystrix (Acanthion) brachyura*, Linnaeus, 1758. Therefore the latter is considered the valid name for the smaller European porcupine.

Age of the assemblages. The stratigraphic range of *H. refossa* is from the Late Pliocene to Late Pleistocene (Van Weers, 1994). The European *H. brachyura* is from the Early Pleistocene (Janossy, 1972) to the Late Pleistocene (Malez, 1963, Schweitzer, 2002), and Recent.

India

H. crassidens Lydekker, 1886.

Most of the type material of this species from the Karnul (= Karnool) district (India) has not been available. Some of the presented data (Figs. 2a, 3b) are

from the original description. Lydekker figured the left mandible (GSI no. F219a, pl. 8, fig. 17) in which the milk premolar has not yet been shed and the m3 is scarcely erupted. A cast of the right mandible (GSI no. F219a), quite agreeing with Lydekker’s description of the left one, was available for this study. A collection (NHML M3448, a-g) from the type locality contains two mandible fragments (a and b), an M1/2 (c), an upper and a lower incisor (d and e), an unworn tooth (f) and an m1/2 (g).

Material from the Bankura district in India has also been allocated to *H. crassidens* (Dassarma *et al.*, 1982). The right P4-M3 (GSI 19110) was mentioned as a “left maxilla” by these authors, the right mandible (GSI 19111) as a “right maxilla”, and the left p4-m3 (GSI 19113) as a “lower right tooth row”. The length measurements of these tooth rows are estimations because of the space between the teeth in these reconstructed specimens.

Analysis and conclusions. Lydekker (1886) considered the large difference between the width of the upper and lower incisor (8.1 and 6.3 mm respectively) as

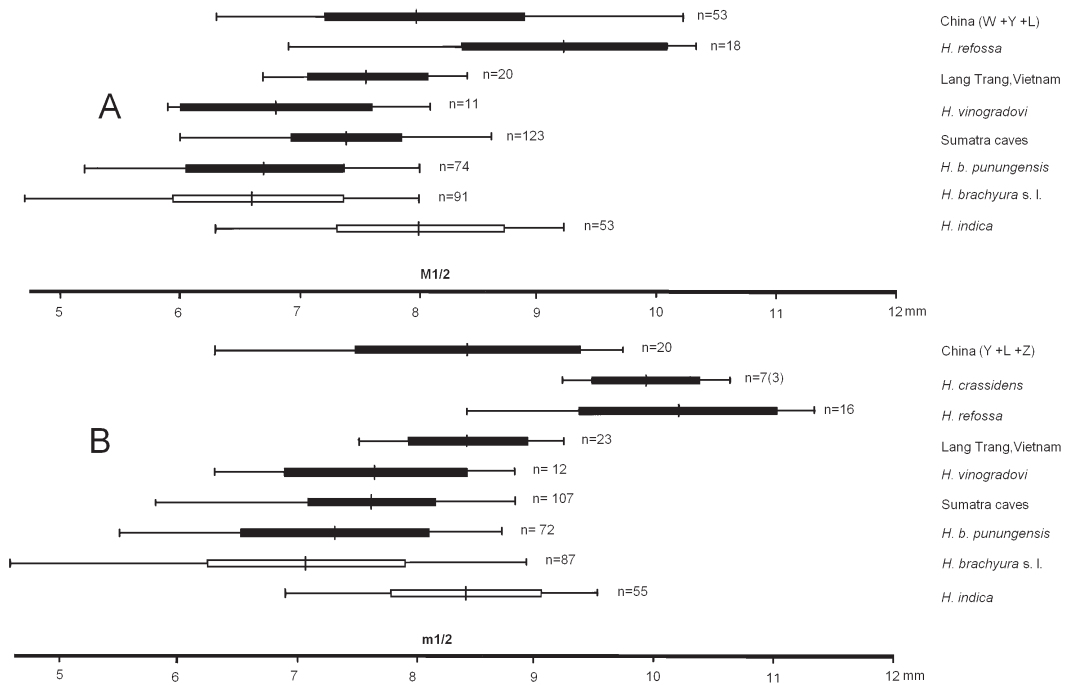


Fig. 4. Length of M1/2 (A) and m1/2 (B) of the extant species *H. (Hystrix) indica* and *H. (Acanthion) brachyura* s.l., of fossil species recognised thus far and of specimens from localities not yet allocated to a species, with mean, range, standard deviation and number of specimens(n). The extant species are presented with open bars. W = Wazhuan, Y = Yanhui, L = Liucheng, Z = Zhoukoudian. For the current specific allocation see the relevant text.

an important specific character. The isolated upper incisor (NHML M3448d) is also rather large. However, the most evident explanation for the difference between upper and lower incisors is that these are represented by remains of young and extremely old animals. The alveolar length of Lydekker's young type mandible (GSI no. F219a) is measured from the cast. On that basis, the length of an adult specimen is estimated at not smaller than 40 mm (Fig. 2b). Lydekker's P4 (GSI no. F220), at 12.7 mm is also extremely large (Fig. 3a). There is no clear difference of Lydekker's *H. (H.) crassidens* from *H. (H.) refoffa* Gervais, 1852 of Europe, so it is allocated to the latter species.

The alveolar length of the two p4-m3 tooth rows from Bankura (GSI 19111 and 19113) is estimated to 37 mm (Fig. 2b), and that of the maxilla 34 mm (Fig. 2a). The measurements of the m1 and m2 in the mandibles GSI 19111 and 19113 from Bankura (not in the graphics) can be compared with those from Karnool. Karnool: mean = 9.7 mm, range 9.2-10.6 mm, number of molars seven from three specimens. Bankura: mean = 8.6 mm, range 7.7-9.2 mm in four molars from two specimens. So the molars from Bankura are smaller on average, but for these small samples an allocation to *H. (H.) refoffa* cannot be excluded. However, assignment as Pleistocene occurrence of *H. (H.) indica* Kerr, 1792 or *H. (H.) kiangsenensis* seems to be more probable.

Age of the assemblages. Biswas (1987) mentions a "Pleistocene and later age" of the Karnool material. Dassarma *et al.* (1982) mention "later than Upper Pleistocene" for the Bankura material.

China

H. lagrelli Lönnberg, 1924.

This is the smallest Chinese species, described at length by Van Weers (1992, 1995) on material from Henan and Zhoukoudian (China) and Sangiran (Indonesia). It is distinguished from all other forms by its small size with the length of the upper and lower tooth rows not exceeding 22.1 mm and therefore not involved in the graphic figures.

Hystrix subcristata Swinhoe, 1870.

This porcupine now occurring in China is considered to be a subspecies of *H. (A.) brachyura* Linnaeus, 1758. Most finds of fossil porcupine remains in

China have been allocated to '*Hystrix subcristata*' and, remarkably enough, even recently by Tong (2005) for the Late Pleistocene-Holocene finds from the Tanyuan Cave near Zhoukoudian. The occurrence of *H. brachyura* has been shown, indeed, in the Plio-Pleistocene deposits of Longgupo (Van Weers, 2003a) so an occurrence in the large samples from the sites of Zhoukoudian (Fangshanxian), Liucheng Cave (Guangxi), Wazhuan Cave and Yanhui Cave (Guizhou) cannot be excluded. However, Van Weers and Zheng (1998) showed that the isolated cheek teeth from these localities are on average larger than the extant *H. (A.) b. subcristata* and they considered the majority of them to belong to *H. (H.) kiangsenensis* Wang, 1931.

H. kiangsenensis Wang, 1931.

This species, of which the type material is lost, was based on the length of a P4 (8.4 mm), M3 (7.3 mm), p4-m3 alveolar length (29.4 mm), two p4 (7.5 and 9.6 mm), two m1 (7.0 and 7.4 mm), two m2 (8.2 and 8.0 mm). These measurements are larger, on average, than *H. (A.) b. subcristata* and agree well with the material from the above mentioned localities allocated to *H. (H.) kiangsenensis*. The same is the case with two skulls from Guangxi, southern China, (IVPP V5082 and V5083) figured by Pei (1987: 115, pl. XV, figs. 11 and 12) and perceptively characterised by him as "species of *Hystrix* and not *Acanthion*". Van Weers and Zheng (1998) mentioned the larger average size, larger relative length and width of the nasals, and a larger relative height of these skulls (Van Weers and Zheng, 1998, table 1) and allocated them, confirming Pei's (1987) subgeneric assignation, to *H. (Hystrix) kiangsenensis*. The skull IVPP V5082 is here indicated as the neotype of this species. In the preceding study of the assemblages from Zhoukoudian, Liucheng, Wazhuan and Yanhui (Van Weers and Zheng, 1998, figs. 2 and 3) the samples are presented separately in their graphics. Because of the similarity then demonstrated, in the present study (Figs. 3 and 4) they are presented as if they were one species. The p4-m3 length of the type mandible is given in Fig. 2b, the P4-M3 length of the two skulls in Fig. 2a.

Besides the material of the localities mentioned above, finds from Zhejiang (not in the graphics) have been studied. A young and an old mandible from Hemuda (ZMNH, YHC771 and YH7701) have dp4-m3 and p4-m3 lengths of 32 mm. A mandible from

the Huyan cave (ZMNH 1263) has also a p4-m3 length of 32 mm. These values are higher than the mean of a large sample (n = 86) of *H. brachyura* (Fig. 2b).

The measurements of the cheek teeth from the Late Pleistocene-Holocene Tianyuan Cave (Tong, 2005, table 3), and those of the Luobidong Cave at Hainan with the same age (Hao and Huang, 1998, table 5.12), show a larger mean size than the large samples from the total area of distribution of *H. brachyura* as presented by Van Weers (2003b).

All assemblages from this large number of localities ranging from Zhoukoudian to South China and Hainan show that the majority of the Pleistocene Chinese *Hystrix* differ from the extant *Hystrix b. subcristata* by a larger mean size, and are assigned to *H. kiangsenensis*.

Hystrix magna Pei, 1987.

Pei (1987) based this species on nine large cheek teeth, apparently selected arbitrarily, from a large number of teeth from southern Chinese cave deposits. Only one of these syntypes, an M1/2 from the Liucheng cave, is left (the others are lost) and is indicated as the lectotype of this species by Van Weers and Zheng (1998). Its length is the maximum value in the size range in Fig. 4a (10.2 mm, n = 53), representing the clustered assemblages of Liucheng, Wazhuan and Yanhui. This shows the mixed character of these assemblages but probably a very few specimens of these samples do belong to *H. magna*.

From Jiande, Zhejiang, two P4 (ZMNH, M1135 and M1135-3) have a length of 11.2 and 10.1 mm respectively (not depicted in the graphics). Comparison with Fig. 3b shows that they agree with *H. (H.) refossa*. Guo (1997) estimated the P4-M3 length of an extreme old skull from Guangxi with nearly fused sutures (IVPP, V10999) at 38 mm (Fig. 2a). This skull, with the occipito-nasal length of 162 mm has the size of *H. refossa*.

Analysis and conclusions. The mean of the M1/2 length of the cheek teeth of Wazhuan, Yanhui and Liucheng (Fig. 4a, n = 53) is clearly larger than *H. brachyura*. This is also the case for the P4 of Wazhuan, Yanhui and Liucheng (3A) and the p4 of Wazhuan, Yanhui and Zhoukoudian (Fig. 3b). Because also the smaller, apparently unmixed, samples from Hemuda, Huyan, Tianyuan and Hainan have

mean sizes which are larger than *H. (A.) brachyura*, all these assemblages are allocated to *H. (H.) kiangsenensis*, and only an unknown, insignificant number of specimens are supposed to belong to *H. magna*.

The length of the M1/2 of the lectotype of *H. magna* approaches with 10.2 mm the maximum of *H. refossa* (Fig. 4a). The largest alveolar length of the p4-m4 of Zhoukoudian Loc. 1 (IVPP, C1772) approaches with 39.5 mm (Fig. 2b) that of *H. refossa*. Therefore the very large porcupine of the Chinese Pleistocene is allocated to *Hystrix (Hystrix) refossa* Gervais, 1852.

Remarks. From Figs. 3 and 4 a clear similarity appears in the tooth size of *H. indica* and the assemblages from the Chinese caves which are allocated to *H. kiangsenensis*. However, the two skulls IVPP V5083 and V5082 allocated to the latter species have a morphology that differs from *H. indica* in its nasal structure (Van Weers and Zheng, 1998, tab. 1) which makes an allocation to the latter species not probable.

Age of the assemblages. Wang (1931) mentions a Late Pliocene or Early Pleistocene age for *H. kiangsenensis*, and Van Weers (2003b) mentions the same age for *H. (A.) brachyura* from Longgupo. For *H. lagrelli* from China Van Weers (1995) mentions Early to Middle Pleistocene. Pei (1987) gives Early Pleistocene for the finds of Liucheng, and Middle to Late Pleistocene for the remaining localities of southern China. Zheng (1993) mentions the Middle Pleistocene for the Yanhui and Wazhuan caves. The *H. kiangsenensis* finds from the Huayan cave in Zhejiang are of Late Pleistocene age (Zhang, 1984). Dr Jin Xingsheng (pers. comm.) mentions a Late Pleistocene age (50 ky) for the *H. magna* (or *H. refossa*) cheek teeth of Jiande.

Indonesia

H. lagrelli Lönnberg, 1924.

See preceding China section. The species is recently described from Gunung Dawung near Punung, Java (Storm *et al.*, 2005)

H. b. punungensis Van Weers, 2003.

The Late Pleistocene material (NNMN) from Punung (Figs. 3-4) has been described as *H. brachyura*

punungensis Van Weers, 2003. Dubois collected in 1888-1890 large numbers of teeth in the Sibrambang cave and cave A91 in the Padang Highlands (NNMN). The exact locality of cave A91 is not known, and the material of these two caves together is indicated in the graphics (Figs. 3-4) with ‘Sumatra caves’.

Hystrix gigantea Van Weers, 1985.

The lower jaw molars SMF no. 274 and 275 with the lengths 12.2 and 12.6 mm and assigned to *H. gigantea* Van Weers, 1985 from Sangiran, Java (not in graphic figures) do not differ from *H. refossa* (Fig. 3b).

Analysis and conclusions. The P4 (Fig. 3a) of the extant *H. brachyura* s.l., of *H. b. punungensis* from Java and those of the Sumatran caves do not differ much. The p4 of *H. brachyura punungensis* differs slightly more (Fig. 3b). The similarity between these assemblages is large and therefore the fossil material of Java and Sumatra is allocated to *H. brachyura punungensis* Van Weers, 2003.

H. gigantea is considered a synonym of *H. refossa* Gervais, 1852.

Age of the assemblages. Gunung Dawung is Late Pleistocene. Long *et al.* (1996) mention an age of 80 ky for the comparable faunas of Punung and Sumatra, part of Sundaland at that time. For the Pleistocene ‘*H. gigantea*’ of Java no more detailed age is known.

Thailand

Species of *Hystrix*.

From northern Thailand finds from the Pha Bong cave and the Snake cave have been available (GSDB). The samples of both localities are small, do not differ significantly, are considered as a whole and not represented in the graphics.

Analysis and conclusions. The M1/2 (mean 8.0 mm, n = 11) and m1/2 (mean 8.7 mm, n = 15) approach the mean values of *H. indica* (compare Fig. 4a-b). This may indicate a Pleistocene occurrence of a species *H. indica* but an allocation to *H. kiangsenensis* is possible as well. Without skull material showing the morphology of the nasal region a definite identification is not possible.

Age of the assemblages. Esposito *et al.* (2002) mention “a Late Middle Pleistocene age” for the faunal assemblage of the Snake Cave, and “the main fossiliferous level is older than about 160 ky”. From the Pha Bong cave no data are known.

Vietnam

Species of *Hystrix*.

From Vietnam specimens have been studied from the Tham Om cave, Nghe An province, the Tham Khuyen cave, Lang Son province and from the Lang Trang cave, Thanh Moa province (IAH). From the Lang Trang cave the largest sample is available, and this is the only sample presented in the graphics. The mean length of the P4 from Lang Trang (Fig. 3a, n = 21) as well as that of the p4 (Fig. 3b, n = 11) is larger than the teeth of *H. indica* but this is not valid for the other teeth of this locality. The mean of M1/2 (Fig. 4a, n = 20) is smaller than that of *H. indica*, and the mean of the m1/2 (Fig. 4b, n = 23) is as large. Apparently the relation between the size dimensions of the teeth in a dentition in this population is not the same as in *H. indica*. The porcupine of Lang Trang is clearly larger than *H. brachyura* (Figs. 3 and 4) but not clearly different from *H. indica*.

The smaller number of specimens from the Tham Khuyen cave in Vietnam have not been presented in the graphics. The length of the P4 (mean 9.1 mm, n = 6) does not differ from that of Lang Trang (Fig. 3a, mean 9.3 mm, n = 21). The M1/2 van Tham Khuyen (mean 8.0 mm, n = 11) does not differ too from that of Lang Trang (Fig. 4a, mean 7.6, n = 20).

The measurements of the Tham Om cave are not presented in the graphics either. The P4 (mean 8.7 mm, n = 9) does not really differ from that of Lang Trang (Fig. 3a), and the M1/2 (mean 7.6 mm, n = 13) is the same (Fig. 4a).

Analysis and conclusions. Summarising it can be stated that in the Pleistocene of Vietnam a porcupine occurred that can be allocated to *H. indica* Kerr, 1792. A similarity exists in size with *H. kiangsenensis* but without skull material showing the morphology of the nasal region a definite identification is impossible.

Age of the assemblages. Ciochon (pers. comm.)

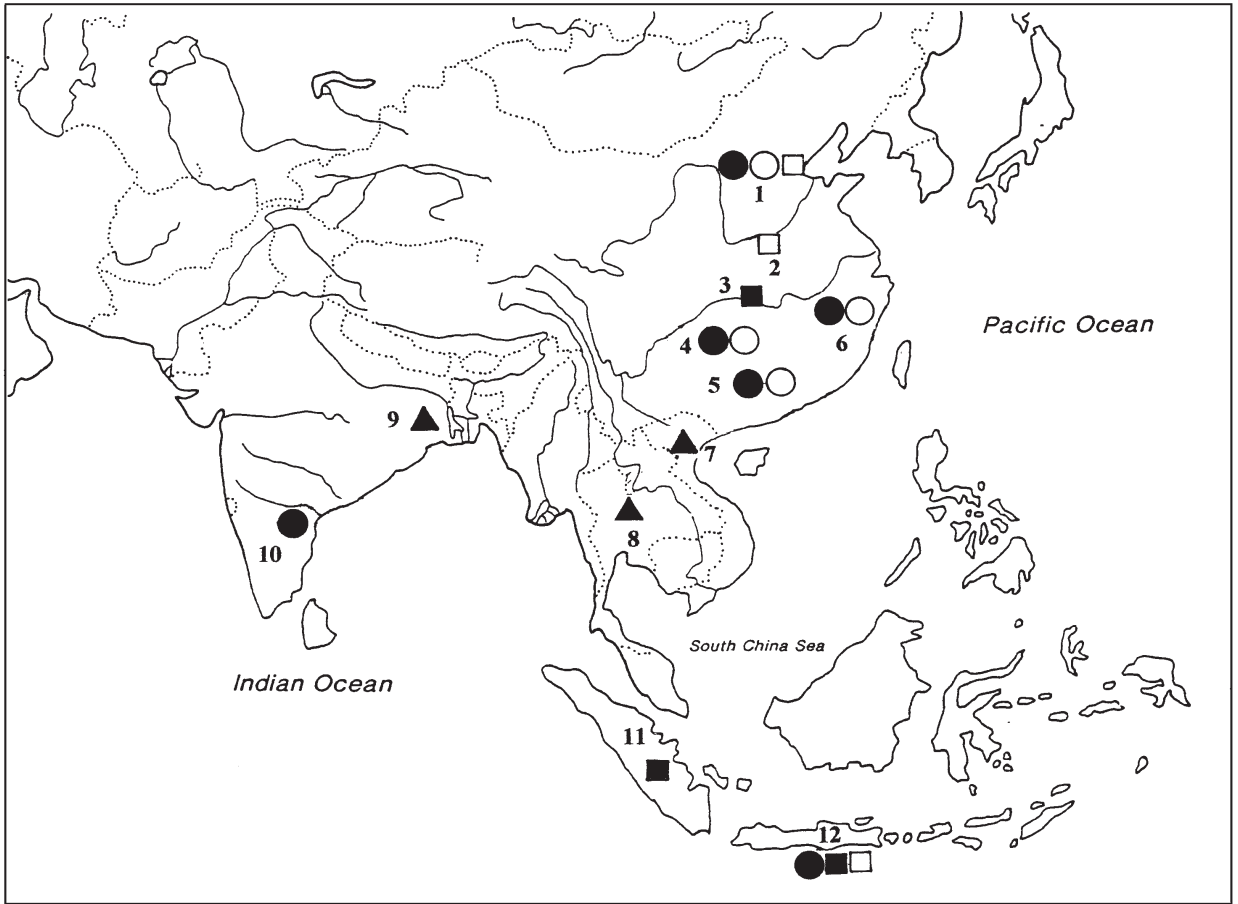


Fig. 5. Map of Southeast Asia indicating the species and geographic areas of Pleistocene species studied. Solid circles = *H. (H.) refossa*. Open circles = *H. (H.) kiangsenensis*. Open squares = *H. (A.) lagrelli*. Solid squares = *H. (A.) brachyura*. Triangles = *H. (H.) indica*. 1 = Zhoukoudian. 2 = Henan Prov. 3 = Longgupo. 4 = Guizhou Prov. 5 = Guangxi Prov. 6 = Zhejiang Prov. 7 = Lang Trang. 8 = North-east Thailand. 9 = Bankura Distr. 10 = Karnul Distr. 11 = Sumatra caves. 12 = Sangiran and Punung.

mentions the provisional results of ESR research of samples from Lang Trang of 180 ky to 350 ky and characterises the site as “Late middle Pleistocene”. Olsen Ciochon (1990) give the same age for the Tham Om cave. Ciochon *et al.* (1996) mention an age of the fauna of the Tham Khuyen cave of 475 ky.

Taxonomy of the Pleistocene *Hystrix* species

Based on the presented data five *Hystrix* species can be distinguished in the Pleistocene of Asia: *H. (A.) lagrelli* Lönnberg, 1924, *H. (A.) brachyura* Linnaeus, 1758, *H. (H.) kiangsenensis* Wang, 1931, *H. (H.) refossa* Gervais 1852 and probably *H. (H.) indica* Kerr, 1792, (Fig. 5), and two species in the Pleistocene of

Europe: *H. (A.) brachyura* Linnaeus, 1758 and *H. (H.) refossa* Gervais, 1852.

The revised taxonomy of the Pleistocene *Hystrix* species from Europe and Asia is thus as follows:

Order Rodentia Bowdich, 1821

Family Hystricidae Fischer, 1817

Genus *Hystrix* Linnaeus, 1758

Subgenus *Hystrix (Hystrix)* Linnaeus, 1758

H. (H.) indica Kerr, 1792

H. (H.) refossa Gervais, 1852

Synonyms:

H. major Gervais, 1859

H. crassidens Lydekker, 1886

H. etrusca Bosco, 1898

H. angressi Frenkel, 1970

H. gigantea Van Weers, 1985

H. magna Pei, 1987

H. (H.) kiangsenensis Wang, 1931

Subgenus *Hystrix (Acanthion)* F. Cuvier, 1823

H. (A.) lagrelli Lönnberg, 1924

Synonym:

H. (A.) vanbreei Van Weers, 1992

H. (A.) brachyura Linnaeus, 1758

Synonym:

H. vinogradovi Argyropulo, 1941

Subspecies:

H. (A.) b. punungensis Van Weers, 2003

Remarks on evolution and paleogeography

Molecular research hypothesizes that the genera *Trichys* and *Atherurus* of the family Hystricidae originated in the Paleocene from an unknown hystricognath ancestor in Asia (Huchon and Douzery, 2001). *Trichys* is not known from fossil assemblages. The oldest occurrence of *Atherurus* is from a Miocene assemblage from the Lower Siwaliks, described as *Sivacanthion complicatus* by Colbert (1933). Landry (1957) judged that it was similar with *Atherurus* based on the morphology of the mandible. An occlusal photograph (Fig. 6) of the right m1 of a cast of this specimen (AMNH 19626) shows the presence of the four characteristic lingual inflections which may occur in a certain stage of wear in *Atherurus* cheek teeth. The length of the m1 (5.3 mm) of this specimen falls within the range of *A. karnuliensis* Lydekker, 1886 from the Pleistocene of Southeast Asia (Van Weers, 2002), so it is allocated to this species. The oldest *Hystrix* remains are of *H. parvae* (Kretzoi, 1951) from the Miocene, Vallesian of Hungary (Van Weers and Montoya, 1996). Because these oldest records of Hystricidae represent already highly specialised animals, it is not possible to establish the origin of this family.

All Miocene *Hystrix* species are relatively low-crowned with a H/L ratio of the cheek teeth generally not much above 1.0. A most probable ancestor of the high-crowned Pleistocene *Hystrix* species may be *H. gansuensis* Wang and Qiu, 2002 from the Late Miocene in the Gansu province, China. The H/L ratio 1.4–1.5 of the M1/2 of this species (Van Weers, 2004) shows some overlap with that of the extant

H. brachyura which has a H/L ratio of 1.4–2.4 (Van Weers and Zheng, 1998). Therefore the origin of the high-crowned species may lie in the Late Miocene or Early Pliocene. This early origin is also suggested by the occurrence of *H. refossa* in Europe and *H. brachyura* in Asia, already distinct in the Late Pliocene. The three endemic species of the least specialised subgenus *Thecurus*, *H. (T.) sumatrae*, *H. (T.) crassispinis* and *H. (T.) pumila* occur on Sumatra, Borneo and Palawan respectively. A possibility is that they originated from a common Late Pleistocene ancestor when these islands were part of Sundaland. However, *H. (Acanthion) lagrelli* from the Early to Middle Pleistocene of northern and Central China has a skull that represents a transitional stage between the extant subgenera *Acanthion* and *Thecurus* (Van Weers, 1995). That makes it probable that also *Thecurus* had that more northern Pliocene origin compared to its current distribution. Moreover, Hooijer (1949) and Badoux (1959) mention that the differences between Pleistocene ancestors and extant species seldom range beyond subspecific level. The small differences of the Late Pleistocene finds of Punung (Java) and the Sumatran caves compared with the extant species (Figs. 2 and 3) confirm this observation. An early origin of the *Thecurus* species with a number of different migrations is therefore more probable and agrees with the statement of De Vos (1984) who supposes four different migrations into the Indonesian archipelago. An early migration may also hold for the endemic *H. (Acanthion) javanica* from Java, which is the least specialised species of this subgenus. Chaimanee (1998) mentions the extreme difficulty to reconstruct the paleogeography of Sundaland during the glacial stages. The distribution of the Hystricidae in Southeast Asia is probably the result of several migrations of *Hystrix* species from the Asian mainland into Sundaland. However, due to the limited material, a precise reconstruction of the paleogeography is not possible here.

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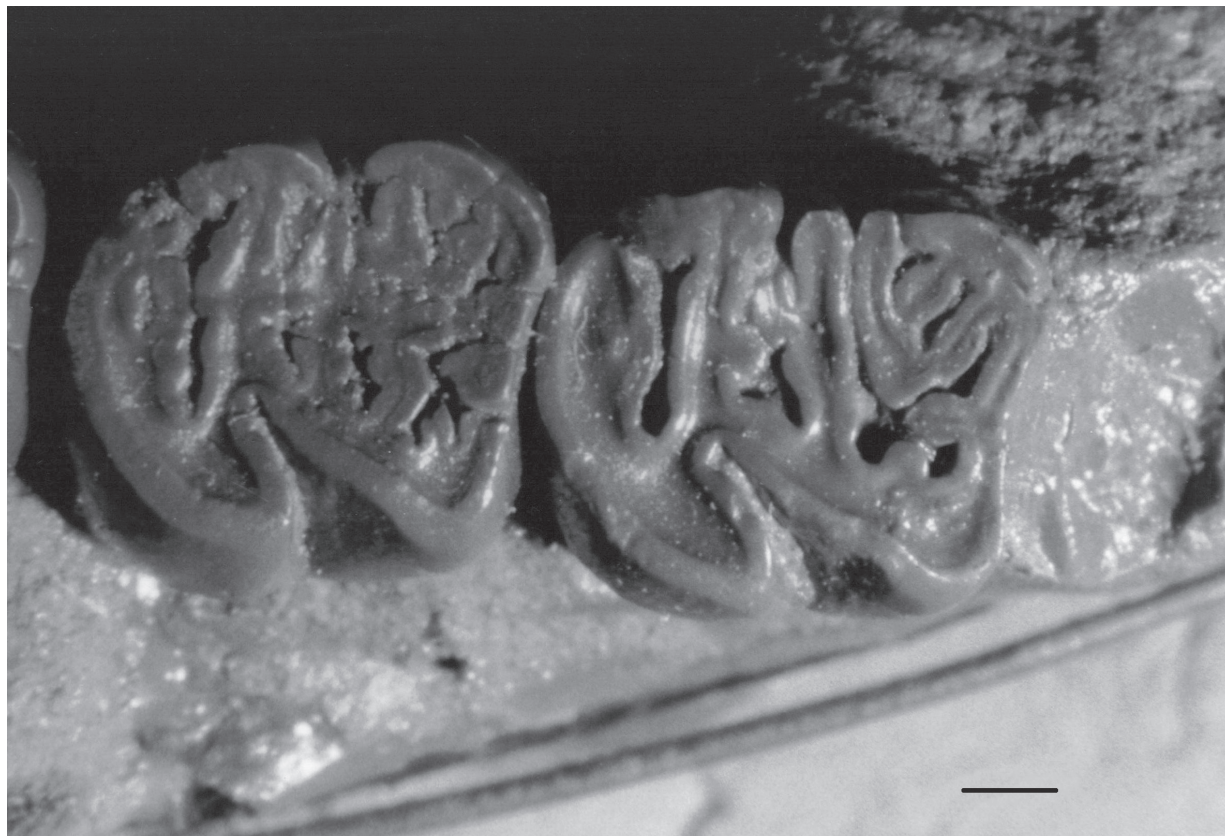


Fig. 6. Photograph of a cast of the right ramus (AMNH 19626) with m1 and m2 of the holotype of *Sivacanthion complicatus* Colbert, 1933 from the middle Miocene of the Siwaliks, India, now allocated to *Atherurus karnuliensis* Lydekker, 1886. (Scale bar = 1 mm)

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