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THE FOSSIL PORCUPINE *HYSTRIX LAGRELLI* LÖNNBERG, 1924 FROM THE PLEISTOCENE OF CHINA AND JAVA AND ITS PHYLOGENETIC RELATIONSHIPS

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ABSTRACT

The Pleistocene *Hystrix vanbreei* from Sangiran, Java, and *Hystrix lagrelli* from the Pleistocene of Henan, China are synonymized. The phylogenetic relationship of *H. lagrelli* with the subgenera *Thecurus, Acanthion* and *Hystrix* s.s. is discussed.

INTRODUCTION

Lönnberg (1924) described *Hystrix (Acanthion) lagrelli* on the basis of a small fossil skull from "Honan" (= Henan), China. The only geological information that came with the type is that the rock matrix is red. Young (1934) supposed that "The geological horizon of the Honan form ..... corresponds to the lower or middle zone of the Reddish Clays (Middle or Late Pliocene) ....", but Teilhard de Chardin (1936) supposed that an origin from the Lower Pleistocene "reddish clays" was more probable. Teilhard de Chardin (1936) and Teilhard de Chardin & Pei (1941) referred the smaller of the two porcupine species from Locality 9 and Locality 13 of "Choukoutien" (= Zhoukoudian near Beijing) to *H. lagrelli*, attributing it an Early Pleistocene age. Zheng Shaohua (1984, Fig.5) suggested an Early to Middle Pleistocene age for the Cricetinae from Locality 9 of Choukoutien, and a Middle Pleistocene age for those from Locality 13. So an Early to Middle Pleistocene age for *H. lagrelli* seems likely.

By far the greater part of all fossil porcupine material consists of isolated teeth and fragments of mandibles and maxillae. The morphology of the cheek teeth in the genus *Hystrix* Linnaeus, 1758 is highly conservative, shows much individual variation and is subject to considerable changes due to attrition. So the morphology of the cheek teeth is of limited diagnostic value

Table 1. Tooth measurements in mm of the type skull and three mandible fragments of *H. lagrelli*, with institute and register number, alveolar length of the tooth series (specimens the same as entered in table 2), occlusal breadth, occlusal length and wear class of the cheek teeth.

Inst. + reg. nr.	Tooth series	Tooth	Occl. b.	Occl. l.	Wear cl. le. / rh.
PMU	P4-M3 l.	P4	5.8	6.1	F1/G5
M3701	22.1	M1	5.7	5.1	G4/G5
(type)		M2	5.8	5.3	G4/G4
		M3	4.3	4.3	C to E
IVPP	p4-m3 l.	m1	4.9	5.6	S3
Loc.13-2	21.8	m2	4.8	5.8	O2
IVPP	-	m1	5.0	5.6	S3
Loc.13-3		m2	5.0	5.8	R
IVPP	p4-m3 l.	p4	5.2	6.7	T1
Loc. 9	20.9	m1	4.3	4.5	T5
		m2	4.8	4.9	T2
		m3	4.3	4.8	S to T

and size is the only diagnostic character if no skull is available. The length of the nasal bones relative to the length of the skull is an important diagnostic character in this family. In the holotype skull of *H. lagrelli* a nearly complete, relatively short nasal bone is present.

The only small *Hystrix* species with relatively short nasals are the extant porcupines of the subgenera *Acanthion* F. Cuvier, 1823 and *Thecurus* Lyon, 1907 from the mainland of S.E. Asia, the Indo-Malayan Archipelago and the Philippines. The species concerned are *H. (A.) javanica* Cuvier, 1823 occurring on Java and the Lesser Sunda Islands, *H. (T.) pumila* Günther, 1879 from Palawan, *H. (Thecurus) sumatrae* from Sumatra and *H. (T.) crassispinis* Günther, 1877 from Borneo. *H. pumila* is the smallest species of the genus, *H. sumatrae* is about as large as *H. lagrelli*, and *H. crassispinis* is larger and concerning spiny covering more specialized than *H. javanica* (van Weers, 1978).

A large number of fossil teeth from Sangiran, Java, in the collections of G.H.R. Von Koenigswald and two teeth from Trinil, Java, in the Dubois collections were described under the name *H. vanbreei* by van Weers (1992). The relationship of *H. vanbreei* and *H. javanica* with *H. lagrelli* could not be established on the basis of the published data of the latter species only.

The opportunity to study both the holotype of *H. lagrelli* from Uppsala and the specimens of this species in Beijing, provided a possibility to compare these forms. The status of *H. vanbreei* will be reconsidered, the relationship of *H. lagrelli* with the subgenera *Acanthion* and *Thecurus* is discussed and a provisional review of the phylogeny of the relevant part of the genus *Hystrix* is represented.

MATERIAL AND METHODS

For the indication of upper cheek teeth, capitals will be used, and for the lower ones small letters.

Specimens studied:

- Holotype of *H. (Acanthion) lagrelli* Lönnberg, 1924, housed in the Palaeontological Museum Uppsala, (PMU), Sweden, Lagrelliska samlingen 263, M3701, 20-4-1921, from Mien-Chih-Hsien N 10 li, "Honan" (= Henan), China, adult skull without mandibles, left nasal bone missing, right one slightly damaged anteriorly, zygomatic arches missing, occiput damaged.
- Two left mandible fragments in the Institute of

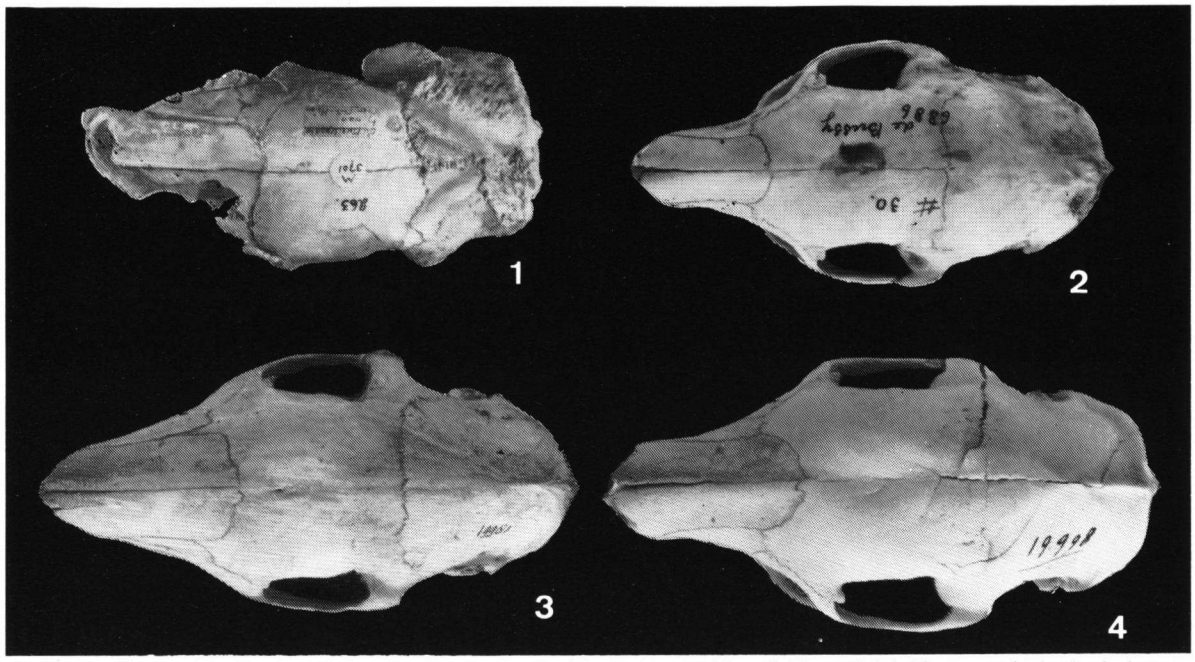

Fig. 1. Dorsal view of skulls of *H. lagrelli* (1), *H. sumatrae* (2), *H. javanica* (3) and *H. crassipinis* (4), respectively the holotype Paleontological Museum Uppsala nr. M3701, Zoological Museum Amsterdam nr. 6886, and National Museum of natural History, Leiden nrs. 19981 and 19998.

Vertebrate Palaeontology and Palaeoanthropology, (IVPP), Beijing,China, from Locality 13 of Zhoukoudian. One of these is nr. 2 in Teilhard de Chardin & Pei (1941, fig. 48b-A), dp4 missing, m3 erupted but not showing wear. The other is nr.3 in Teilhard de Chardin & Pei (1941), m1 and m2 present, not figured in that paper.

- Left mandible in IVPP, Beijing, from Locality 9 of Zhoukudien, figured by Teilhard de Chardin (1936, Fig.10), with p4-m3.

Specimens studied before:

- 45 isolated M1-2 and 55 m1-2 of *H. vanbreei* from the Pleistocene of Sangiran, Java, in the collections of the Senckenberg Museum, Frankfurt am Main (van Weers, 1992).
- 29 skulls of the extant species *H. javanica* from Java and the Lesser Sunda Islands (van Weers, 1979 and 1992).
- 5 skulls of the extant species H. pumila, 31 of *H. sumatrae* and 13 of *H. crassispinis* from the Phillippine Islands, Sumatra, and Borneo respectively (van Weers, 1978).

For the definition of the measurements see van Weers (1976), the wear classes of the cheek teeth are after van Weers (1990). The breadth and length of the cheek teeth were measured at the occlusal surface. All measurements have been taken by the author with Vernier callipers.

RESULTS

In table 1 the toothrow length and the measurements of the teeth of the type skull and the three mandible fragments of *H. lagrelli* from China are presented. The tooth row measurements of table 1 are also presented in table 2, together with the occipito-nasal length and the size of the nasals as relative to the occipito-nasal length of *H. lagrelli* and the four other species in discussion. The figures 1-1 to 1-4 give a dorsal view of the type skull of *H. lagrelli* and of a specimen of *H. sumatrae*, *H. javanica* and *H. crassispinis*.

DISCUSSION AND CONCLUSIONS

CRANIAL DIMENSIONS

The holotype skull of *H. lagrelli* (Fig. 1-1) is rather well preserved and allows to estimate dimensions. The occipito-nasal length and upper toothrow of *H. lagrelli* (Table 2) are only

Table 2. Occipitonasal length of the skull and upper and lower alveolar toothrow length in mm (p4-m3 measurements of *H. lagrelli* are from the same specimens as in table 1), relative length of the nasals as a percentage of the occ.nas.l. (within brackets are after Lönnberg), and relative breadth of the nasals as a percentage of the zygomatic breadth of the skull. Species from top to bottom from Philippines, Sumatra, Borneo, China, and Java together with Bali, Lombok, Sumbawa and Flores. Most dimensions of the holotype of *H. lagrelli* are estimations.

	Occ.nas.l. (mm)	P4-M3 l. (mm)	p4-m3 l. (mm)	Rel.nas.l. (%)	Rel.nas.b. (%)
H.(T.) pumila	87.4-94.5 90.1 n = 5	16.7-20.0 18.7 n = 5	18.3-20.2 19.2 n = 5	27.7-34.9 30.1 n = 5	25.6-29.0 28.1 n = 5
H.(T.) sumatrae	90.1-105.0 98.1 n = 31	17.7-22.2 19.8 n = 27	19.4-24.2 20.9 n = 27	26.1-35.0 29.4 n = 31	22.4-31.5 27.3 n = 27
H.(T.) crassispinis	111.7-119.8 114.9 n = 13	22.7-25.5 24.2 n = 15	24.3-26.6 25.6 n = 13	28.6-35.9 32.4 n = 13	25.7-30.7 27.9 n = 12
H.(A.) lagrelli	100 est. type	22.1 type	20.9-21.8 n = 2	41 (38) est. type	36 est. type
H.(A.) javanica	102.9-127.5 112.7 n = 29	22.3-27.0 24.8 n = 27	23.5-28.1 26.1 n = 26	34.6-43.1 39.3 n = 29	33.4-45.9 39.2 n = 31

slightly smaller than in H. javanica, but the lower tooth-row differs more clearly. Because the sample size of the comparative material of *H. javanica* is relatively large and derives from an extended geographical range, this difference is considered significant. In all extant species such differences of skull dimensions are associated with significant different characters of the spiny covering. As *H. lagrelli* is smaller than *H. javanica* it is considered a valid species.

RELATIVE SIZE OF THE NASALS

Table 2 shows that the size of the skull of *H. lagrelli* agrees with the medium sized species *H. sumatrae* of the subgenus *Thecurus*. Lönnberg (1924) mentioned 35 mm for the actual length of the nasal bone of the type, he estimated the missing front part at 3 mm so supposing an original length of 38 mm. Remeasuring that nasal bone revealed a length of 33.6 mm. My estimation of the original length is 41 mm. Figure 1-1 to 1-4 shows the relation of the size of the nasal bone to the occipito-nasal length. The measurements presented below show that the absolute length of the nasal bone of *H. lagrelli* is larger than in *H. sumatrae* and falls within the range of *H. crassispinis*:

	range	mean	n
H. sumatrae	23.5-34.2	28.9	31
H. crassispinis	32.0-43.0	37.0	14

The latter, however, is a larger species (table 2), so the length of the nasals relative to the occipito-nasal length of *H. lagrelli* of 38 to 41 % agrees with that of *H. javanica*, and the same is found in that table for the relative breadth of the nasals. I therefore conclude that lagrelli is more closely related to subgenus *Acanthion* than to *Thecurus*.

THE STATUS OF *H. VANBREEI*

The breadth and length measurements of the

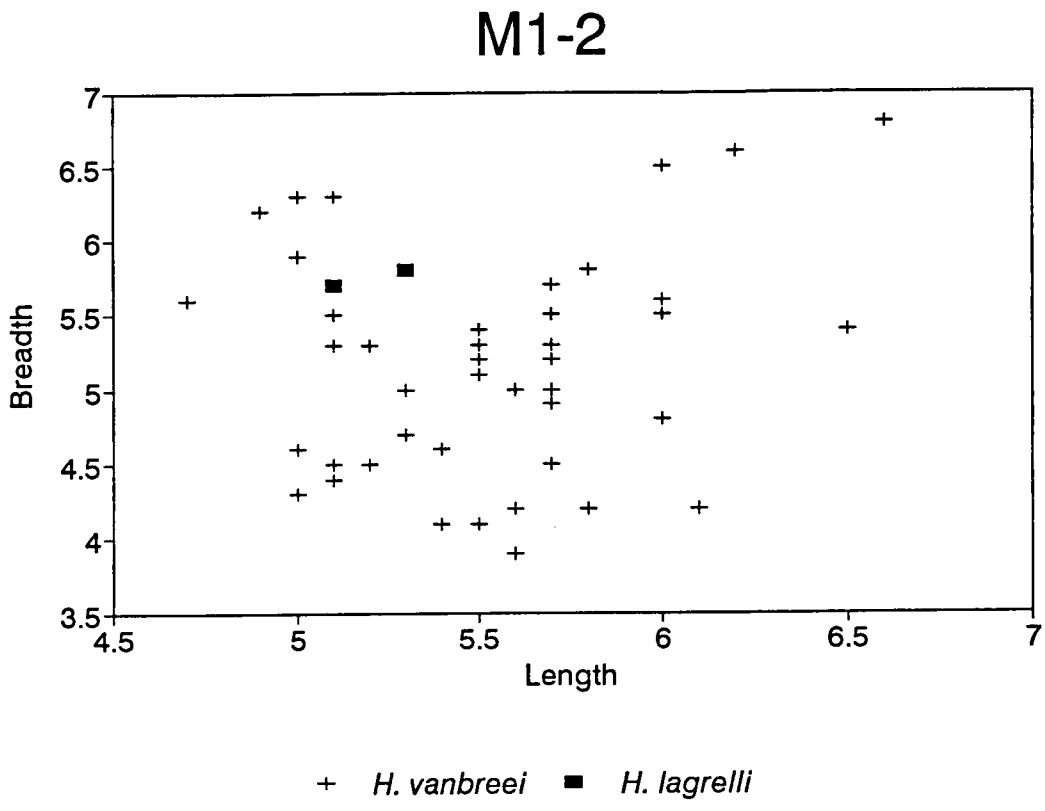

Fig. 2. Diagram with occlusal breadth and length in mm of 45 M1-2 of "*H. vanbreei*" from the Pleistocene of Sangiran, Java, and the M1 and M2 of the holotype of *H. lagrelli* from the Pleistocene of Henan, China.

M1 and M2 of the holotype of *H. lagrelli* are compared with 45 isolated M1-2 teeth of *H. vanbreei* from Sangiran in a scatter diagram (Fig. 2). In another diagram (Fig. 3) the measurements of six m1 and m2 of lagrelli from Zhoukoudian and of 55 m1-2 teeth from Sangiran are presented. Breadth and length measurements of four teeth, a P4, p4, M3 and an m3 of *H. lagrelli* are compared with *H. vanbreei* in table 3. The diagrams and table 3 show that the *H. lagrelli* measurements are all within the range of the *H. vanbreei* sample from Sangiran.

The relative small size of the M3 of the holotype skull, expressed as the ratio occlusal breadth M3/P4 = 0.74 and occlusal length M3/P4 = 0.70, agrees with the Sangiran sample and differs from *H. javanica* (van Weers, 1992: Text-fig. 2).

On these observations *H. vanbreei* is considered a junior synonym of *H. lagrelli.*

THE STATUS OF *THECURUS*

Lönnberg (1924) recognized *Thecurus* as a valid genus and mentioned it in one breath with the less specialized genera *Trichys* Günther, 1877 and *Atherurus* F. Cuvier, 1829. Table 2 shows that the occipito-nasal length of *H. (T.) pumila* is smaller, indeed, on an average,than that of *Atherurus* macrourus (Linnaeus, 1758) which has a range of 87 to 104 mm (van Weers, 1977). However, the much more specialized *H. (Thecurus) crassispinis* was poorly known at that time. There are, moreover, essential cranial and external differences between the Long-tailed

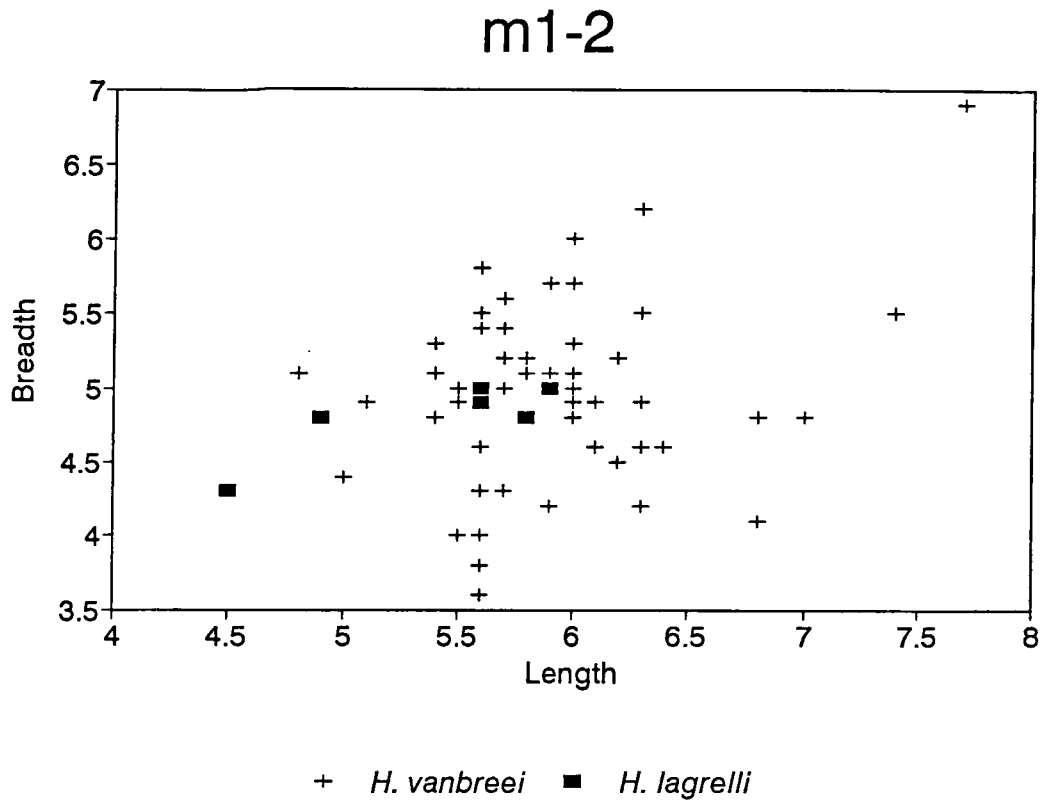

Fig. 3. Diagram with occlusal breadth and length in mm of 55 m1-2 of "*H. vanbreei*" from the Pleistocene of Sangiran, Java and 6 m1 and m2 of *H. lagrelli* from the Pleistocene of Zhoukoudian, China.

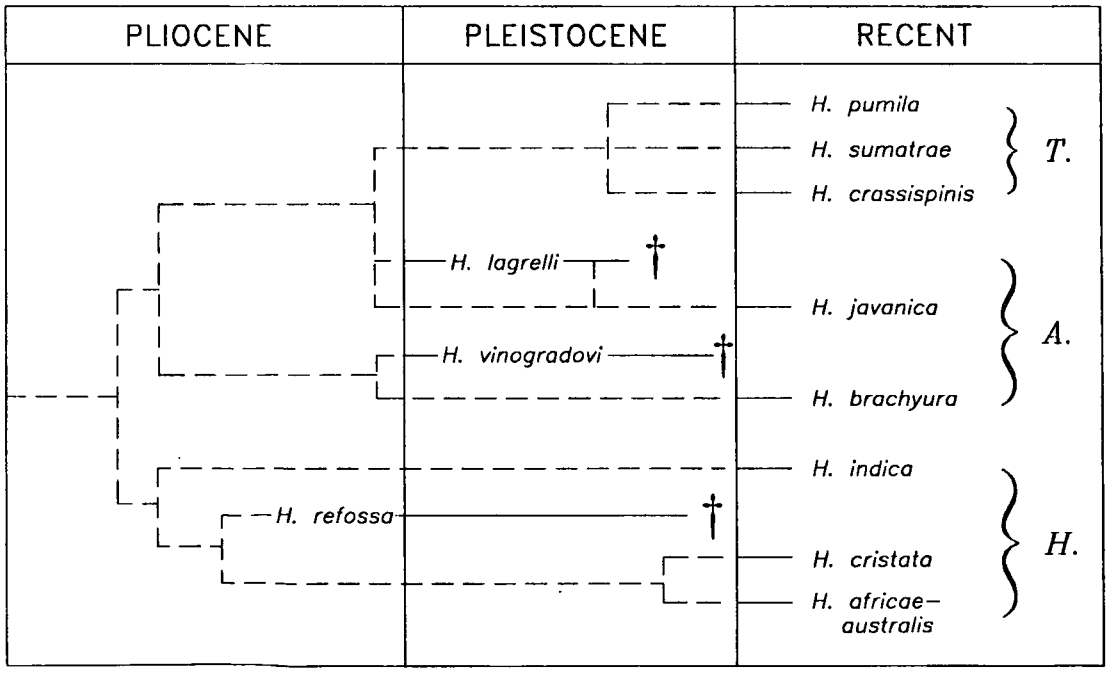

Fig. 4. Diagram presenting a hypothetic phylogeny of a number of species of the genus *Hystrix* with subgenera *Thecurus* (= T.), *Acanthion* (= A.) and *Hystrix* s.s. (H.)

Table 3. Length and breadth measurements of the P4 and M3 of the holotype skull, of the p4 and m3 of mandible IVPP Loc. 9 of *H. lagrelli* from China, and samples of these teeth of *H. vanbreei* from Sangiran.

	H. lagrelli	*H. vanbreei* (Sangiran)
P4 length:	6.1 mm	4.9-7.5 mm (n = 31)
breadth:	5.8 mm	4.5-6.8 mm (n = 31)
p4 length:	6.7 mm	5.6-7.8 mm (n = 21)
breadth:	5.2 mm	4.2-6.2 mm (n = 22)
M3 length:	4.3 mm	4.3-5.0 mm (n = 9)
breadth:	4.3 mm	3.2-4.3 mm (n = 9)
m3 length:	4.8 mm	4.5-6.0 mm (n = 9)
breadth:	4.3 mm	3.4-4.8 mm (n = 9)

porcupines *(Trichys),* the Brush-tailed porcupines *(Atherurus)* and the Short-tailed Porcupines (*Hystrix*). The tails in these genera have unique and different appendices. The least specialized species of subgenus *Thecurus* is *H.(T.) pumila.* Its appendices are beaker-shaped as in *Hystrix* s.s. and its permanent molars are hypsodont, against less hypsodont or brachyodont in *Atherurus* and *Trichys.* So arguments are lacking to consider *Thecurus* a separate genus. In the diagram of figure 4 is expressed that *lagrelli* takes an intermediate position between *crassispinis* and *javanica,* thus underlining that at maximum a subgeneric status may be attributed to *Thecurus.*

TAXONOMIC REVIEW

This review is based on van Weers, 1978, 1979, 1994 and the present study.

Hystrix Linnaeus, 1758

Subgenus *Thecurus*
H. pumila Günther, 1879. Recent, Palawan.
H. sumatrae (Lyon, 1907). Recent, Sumatra.
H. crassispinis Günther, 1877. Recent, Borneo.
Subgenus *Acanthion* F. Cuvier, 1823
H. brachyura Linnaeus, 1758. Recent, Continent S.E. Asia, Sumatra, Borneo.
H. javanica (F. Cuvier, 1823). Recent, Java, Lesser Sunda Islands.
H. lagrelli Lönnberg, 1924. Early and Middle Pleistocene, China, Java.
H. vinogradovi Argyropulo, 1941. Early to Late Pleistocene, Europe.

Subgenus *Hystrix* s.s.
H. cristata Linnaeus, 1758. Recent, Northern half of Africa, Italy.
H. africaeaustralis Peters, 1852. Recent, Southern half of Africa.
H. indica Kerr, 1792. Recent, S.W. Asia.

PHYLOGENETIC RELATIONSHIPS

The cranial differences, besides size, mentioned by Lönnberg (1924) between *H. lagrelli* and the subgenus *Thecurus* and between *H. lagrelli* and H. (A.) javanica, do not hold in the larger material available now. The three species lagrelli, *crassispinis* and *javanica* differ so little that the question arises whether the Early Pleistocene *H. lagrelli* could be the ancestor of both the subgenus *Thecurus* and *H. javanica* . However, *H.(T.) pumila* and *H.(T.) sumatrae* have relatively shorter nasals than *H. lagrelli.* In the evolution of the Hystricidae a clear tendency is supposed in the development from small, less specialized species with relatively short nasals to large, more specialized ones with relatively longer nasals. A reversed development from long to shorter nasals is not probable, so an origin of *Thecurus* from *H. lagrelli* is unlikely. It seems probable that these forms have had a common ancestor, and as *H. lagrelli* already occurred in the Early Pleistocene, this origin may have taken place then or earlier in Pliocene times.

Figure 4 gives the hypothetical phylogenetic

relationships of a number of Plio-Pleistocene *Hystrix* species. The species are arranged according increase in size and relative size of the nasal region. The development of the three endemic species of *Thecurus* on Sumatra, Borneo and Palawan may have taken place in the Pleistocene. A development of *H. javanica* from *H. lagrelli* may date from Pleistocene times but a common, earlier ancestry is considered possible as well. *H. brachyura* is the next of the two extant species recognized in the subgenus *Acanthion* (van Weers, 1979). It occurs from Eastern India to South China and Indonesia, and is the next stage in the development of body size and nasal structure. The nasal structure of the European Pleistocene *H. vinogradovi* is not known, but its dental size cannot be distinguished from *H. brachyura,* so it is allocated to *Acanthion* (van Weers, 1994). As *H. vinogradovi* is known from the Early Pleistocene an origin at that time or in the Pliocene may be possible.

H. refossa Gervais, 1852 from the Plio-Pleistocene of Europe provides an indication to the question in which time the differentiation between *Hystrix* and *Acanthion* took place. This species represents a transitional stage between H. indica Kerr, 1792 and the two highest specialized species of the subgenus *Hystrix* (Van Weers, 1995). So the split up of the genus into the subgenera may have taken place in Pliocene times or earlier.

The Pleistocene species *H. gigantea* van Weers, 1975 from Sangiran and of H. magna Pei, 1987 from Zhoukoudian, both based on very limited material, are not entered in the provisional review of figure 4. Their status is still unclear and awaits the study of a more comprehensive fossil record.

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