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Notes on Southeast Asian Porcupines (Hystricidae, Rodentia) III. On the taxonomy of the subgenus *Thecurus* Lyon, 1907 (genus *Hystrix* Linnaeus, 1758)

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ABSTRACT

The characters of the short-tailed porcupines with small nasals from Sumatra, Borneo and the Philippines, genus *Hystrix* Linnaeus, 1758, subgenus *Thecurus* Lyon, 1907, have been studied. As a result three species are recognized, namely: *H. crassispinis* Günther, 1877, *H. pumila* Günther, 1879, and *H. sumatrae* (Lyon, 1907). Evidence is brought forward for the valid specific status of these forms and data are presented to supplement the scarce information known about these species.

INTRODUCTION

The specific characters in the subgenus *Thecurus* Lyon, 1907, are poorly known. When Lyon described his new genus and species *Thecurus sumatrae* from Sumatra, specimens neither of *Hystrix crassispinis* Günther, 1877, from Borneo, nor of *Hystrix pumila* Günther, 1879, from the Philippines, were available to him. At that time he supposed that *pumila,* but not *crassispinis,* possibly was a species of his new genus. Later, Lyon (1911) stated that G. S. Miller, having compared the type of *H. crassispinis* with specimens of *H. sumatrae,* considered these two forms congeneric but distinct species. Chasen (1940), on the other hand, stated that differences between these two forms had yet to be demonstrated, and Ellerman (1949) and Ellerman & Morrison-Scott (1955) also considered them to be a single species. Mohr (1965), however, treated them as different species but there are no indications that this opinion was based on the study of specimens of both forms. The validity of *H. pumila,*although cranially much less different from *H. sumatrae* than *H. crassispinis,* has never been queried as far as I know.

In the present paper, evidence is brought forward for the valid specific status of these forms, and data about external and cranial features and the

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geographical distribution are presented to supplement the scarce information about this subgenus. The taxonomic status of *Thecurus* as well as those of the remaining nominal genera in the family Hystricidae will be discussed in the next paper in this series.

MATERIAL AND METHODS

Specimens. — The specimens examined comprised 24 skins and 52 skulls of adults and 6 skins and 17 skulls of juveniles from the collections of the institutions mentioned below:

AMNH = American Museum of Natural History, New York.
BMNH = British Museum (Natural History), London.
MNHN = Muséum National d'Histoire Naturelle, Paris.
RMNH = Rijksmuseum van Natuurlijke Historie, Leiden.
SMF = Senckenberg Museum, Frankfurt/Main.
USNM = National Museum of Natural History, Washington.
ZMA = Zoölogisch Museum, Amsterdam.
ZMB = Zoologisches Museum, Berlin.

Dental age. — The dental age groups adult, subadult and young are defined by Van Weers (1976: 17). The number of non-adult specimens is too small to enable comparisons, so that only data for adult specimens appear in the tables and figures.

Sexual dimorphy. — No indications for sexual differences were observed, neither in cranial characters nor in colouration.

Caudal vertebrae. — The number of caudal vertebrae is difficult to determine because the last rudimental vertebrae are very insignificant and often get lost in the preparation. It is not always possible to know whether a skeleton is complete or not, and, moreover, there is some individual variation. So the number of caudal vertebrae, established for four *H. crassispinis* and three *H. sumatrae* skeletons with different degrees of certainty, can only be indicated approximately.

Cranial measurements. — The cranial measurements presented, are defined by Van Weers (1976: 17-19), with the exception of the posterior breadth of the nasals which has a slightly modified definition here.

Breadth of the nasals posterior: greatest breadth of the combined nasals between, or posterior to, the left and the right conjunction point of the nasal-premaxillary suture and the premaxillary-frontal suture.

External measurements. — On each skin the length and diameter of the longest quill, tactile bristle and the hollow part of the longest rattle-quill were measured.

Spines: stiff, flattened and grooved bristles.

Quills: long, thick and very little flexible bristles, circular in cross-section with the largest diameter about mid-length.

Tactile bristles (term after Banks, 1932: 41; tactile sense function

suggested by Mohr, 1965: 23) : very flexible bristles, circular in cross-section with the largest diameter near the base, some of these bristles in each skin always considerable longer than the longest quill.

Rattle-quills: hollow capsule-like structures, open at end, sometimes closed ones with pointed top present, secured to the terminal part of the tail by a thin stalk.

Collector's measurements: the measurements from the labels of the specimens studied, presented in the list of specimens examined.

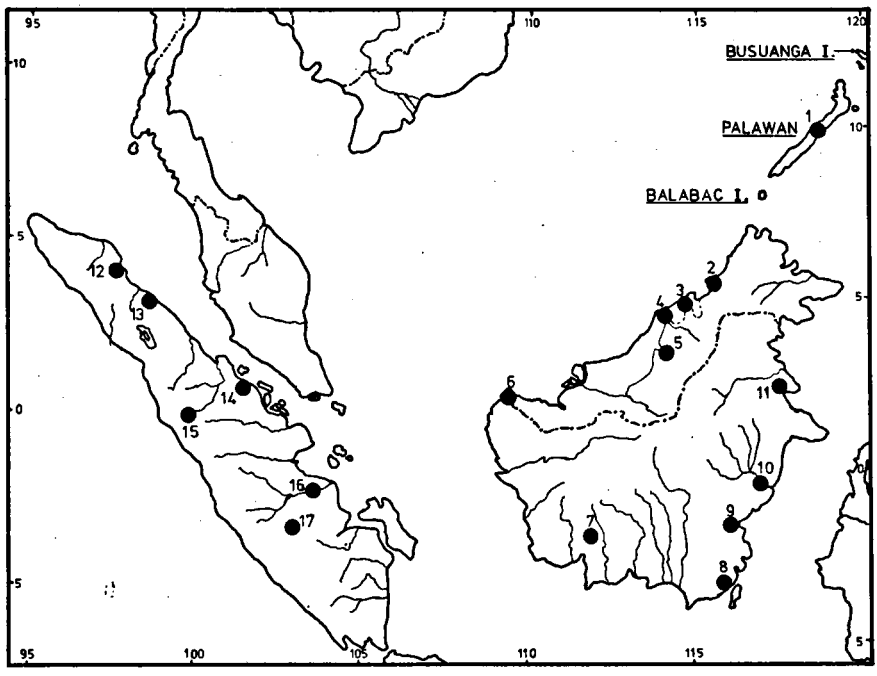

Figure 1. Distribution map of *Hystrix pumila* (1), *Hystrix crassispinis* (2—11) and *Hystrix sumatrae* (12—17). The numbers of the plotted localities correspond with the numbers in the lists of specimens examined. For coordinates see Gazetteer.

Specimens examined

The numbers before the localities in this list of specimens examined, correspond with the numbers of the map of figure 1. The coordinates are given in the Gazetteer. Sex, collector's measurements and other data are mentioned as far as known.

Abbreviations: HB = length of head and body, T = length of the tail, Tot. l = total length, Hf = lenght of a hindfoot, E = lenght of an ear, Wt = weight. Localities within quotation marks could not be located.

Hystrix pumila

1. Puerto Princesa, Paragua, Philippines, BMNH 79.5.3.9, selected as the lectotype of *Hystrix pumila* Günther, 1879 in the present paper, skin and skull, young ♀, coll. Everett 1704a.
   —, BMNH 79.5.3.17, paralectotype of *H. pumila*, skull without lower jaw, adult ♂, coll. Everett 1704.
1. Palawan, BMNH 94.2.1.15, skin and skull, adult, coll. Everett.
1. Paragua, MNHN 1883-1290, skull, adult, coll. Marche.
1. Palawan, Maojan, SMF 26113, skin and skull, adult ♂, Bregulla 1965.
1. Palawan, USNM 396591, skin and skeleton (tail incomplete), adult ♀, R. A. Wilson, from Manilla Zoo via San Diego Zoo, 580 (probably HB), 64, 69 and 31.

Hystrix crassispinis

2. N. W. Borneo, opposite Labuan, BMNH 76.9.20.15, lectotype of *Hystrix crassispinis* Günther, 1877, skin and skull with damaged occiput and left zygoma missing, adult, coll. H. Low.
   —, BMNH 76.9.20.16, paralectotype of *H. crassispinis*, skull with damaged left side, adult ♂, coll. H. Low.
   —, BMNH 76.9.20.13, paralectotype of *H. crassispinis*, skin with skull inside, coll. H. Low.
   —, BMNH 76.9.20.14, paralectotype of *H. crassispinis*, skin with skull inside, coll. H. Low.
2. Mengalong, RMNH 19998, skin and skull, adult, Everett X-92.
3. Tutong River, Brunei, N. Borneo, RMNH 19997, skeleton, adult, coll. Waterstraat II-98, bought from H. Rolle, Berlin I-1899.
4. Baram, E. Sarawak, BMNH 92.10.1.5, skull, subadult ♀, pres. by C. Hose 4-XII-89.
   —, N. E. Sarawak, BMNH 92.9.6.17, skin and skeleton, adult, coll. Everett 27-IX-91.
5. Mt. Dulit, Sarawak, BMNH 0.2.2.10, skeleton, adult ♀, coll. C. Hose.
6. La Datu, Borneo, ZMB A85.10, skull, young, Dr. Pagel 22-VII-07.
7. Riam, S. W. Borneo, Kotawaringen, AMNH 106287, skin and skull, adult ♀, coll. J. J. Menden, jungle, 300 m, HB = 618, T = 190, Hf = 85, E = 42 mm.
8. Pagatan, Borneo, ZMB A3752, skull, subadult, F. J. Grabowsky, Königsberg, 9-X-82.
   —, S. O. Borneo, ZMB 14123, skull, young, Grabowsky XII-09.
9. Tanah Grogot, E. Borneo, BMNH 40.626, skin and skull, adult ♀, coll. W. J. C. Frost no. 11.
10. Samarinda, Borneo, USNM 196777, holotype of *Thecurus major* Schwarz, 1939, skin and skull, adult ♂, H. C. Raven no. 118, 8-VII-1912, HB = 570, T = 160 mm.
11. Birang River, W. bank, USNM 196778, paratype of *Thecurus major*,

skull, subadult ♂, H. C. Raven no. 412, 12-I-1913.

Eastern Borneo:
"Landas", USNM 197640, paratype of *Thecurus major*, skin and skeleton, adult ♀, H. C. Raven no. 911, 15-VII-1913, Schwarz's (1939) reg. no. 196640 is probably erroneous, HB = 580, T = 162, Hf = 87 mm.
Northern Borneo:
"Badang", N. E. Borneo, AMNH 103751, skin and skull, adult ♀, Victor von Plessen I-VI-1935, no. 121, Tot. l. = 761, T = 112, Hf. = 87, E = 39 mm.
"Entoyut River", E. Sarawak, 1000 ft, BMNH 95.5.7.7, skeleton, subadult ♂, coll. C. Hose X-94, purchased from E. Gerard.
"Spitang River", N. Borneo, BMNH 92.9.6.16, skin and skeleton, adult, coll. Everett.
Sarawak, BMNH 84.5.19.7, skin and skull, young, presented by Rajah Brooke.
N. Borneo, ZMB without reg. number, Rolle no. I, adult skull.
N. Borneo, ZMB without reg. number, Rolle no. II, adult skull.
Unknown localities:
Borneo, ZMB without reg. number, Dr. Pagel no. I, 5-II-01, subadult skull.
Borneo, ZMB without reg. number, Dr. Pagel no. II, 5-II-01, subadult skull.
RMNH 4104, skin and skull, adult male, Zoo Rotterdam, 23-X-39.

Hystrix sumatrae

12. Aru Bay, East Sumatra, USNM 143432 (holotype), 143430, 143433, skins and skulls, adult ♂♂; USNM 49870, skeleton, adult ♂; USNM 143435, 143436, 143438, 143439, skins and skulls, adult ♀♀; collected by W. L. Abbott from 22-XI-1905 to 26-I-1906.

13. Serdang, Sumatra, ZMA 6872—6891 and 5599, skulls only, 17 adult, 1 subadult and 3 young specimens, collected by L. P. le Cosquino de Bussy from 1905 to 1917.
13. Deli, Sumatra, RMNH 19990, skeleton, adult, B. Hagen 1885, is Jentink's (1887: 232) "*A. javanicum*" no. d.
—, Tandjong Morawa, RMNH 19991 and 19992, skulls, respectively adult and young, are Jentink's (1887: 232) "*A. javanicum*" ns. i and j.
14. Sungei Mandau, Sumatra, USNM 49932, skeleton, adult ♀, W. L. Abbott no. 4916, 26-XI-1906, HB = 485, T = 90 mm, Wt = 9 lbs.
—, USNM 144220, skin and skull, adult ♂, W. L. Abbott no. 4915, 26-XI-1906, HB = 485, Hf = 70 mm, Wt = 9 lbs.
15. Taloe, W. Sumatra, BMNH 40.625, skin and skull, adult ♂, coll. W. J. C. Frost no. 8, 900 ft, 2-V-39, HB = 560, T = 90, Hf = 75, E = 30 mm.
16. Kompei, Sumatra, USNM 144222, skin and skull, adult ♀, W. L. Abbott no. 5086, 1-III-1907, HB = 472, T = 90, Hf = 73 mm, Wt = 9 lbs.
17. Batang Putih, Central Sumatra, ZMB without reg. number, Dr. Moskowski no. 17, A. 14,08, adult skull.

Unknown locality:
Sumatra, BMNH 40.624, skull without lower jaw, damaged skin, young, W. J. C. Frost no. 9.

Specimen not assignable with certainty to any species:
"S. Pulu Atas", ZMB without reg. number, Aug. 02, M. Schmidt 18-VI-02, Hystrix, adult ♀.

Results

Subgenus **Thecurus** Lyon, 1907

Thecurus Lyon, 1907: 582.

Type species.— *Thecurus sumatrae* Lyon, 1907, by original designation.
Range. — Sumatra, Borneo, Philippines.
Diagnosis. — Tail shorter than in *Atherurus* F. Cuvier, 1829, in most specimens between 15 and 20 % of the length of head and body against 25 to 50 % in *Atherurus*, with about 17 to 19 tail vertebrae (n = 7) against about 19 to 23 in *Atherurus* (n = 6). The tail bears a cluster of rattle-quills at its end, most of them open at the tip, quite different from *Atherurus'* tail-brush. The permanent molars generally do not show visible roots when in place, whereas in *Atherurus* the molars show evidence of being multi-rooted (respectively termed "hypsodont" and "brachyodont" molars by Ellerman, 1940: 202). *Thecurus* differs from the subgenus *Acanthion* F. Cuvier, 1823, probably in the number of tail vertebrae (about 15 to 16 in the latter subgenus, n = 4) and in the very small dimensions of the nasals, length 26 to 36% of the occipito—nasal length of the skull against probably always longer than 36% in *Acanthion*, breadth 22 to 32% of the zygomatic breadth against probably always broader than 33% in *Acanthion*.

Hystrix pumila Günther, 1879

Hystrix pumila Günther, 1879: 106.

Type specimens. — BMNH 79.5.3.9, herewith designated as the lectotype, skin and skull, young ♀, coll. Everett no. 1704a. One paralectotype, BMNH 75.5.3.17, skull, adult ♂, coll. Everett no. 1704.
Type locality. — Puerto Princessa, Paragua, Philippines.
Distribution. — Palawan (Paragua), Philippines. From Busuanga Island specimens were described by Taylor (1934) and from Balabac Island they were recorded by Hollister (1913). Figure 1 shows these localities. Mohr's record (1965: fig. 87) of the Philippin Island Luzon is probably based on the stuffed specimen in the museum in Leiden, RMNH 19999, the label of which records "Manilla", but there is considerable doubt that this is actually the place where this animal was collected as appears from information from the relevant institution.

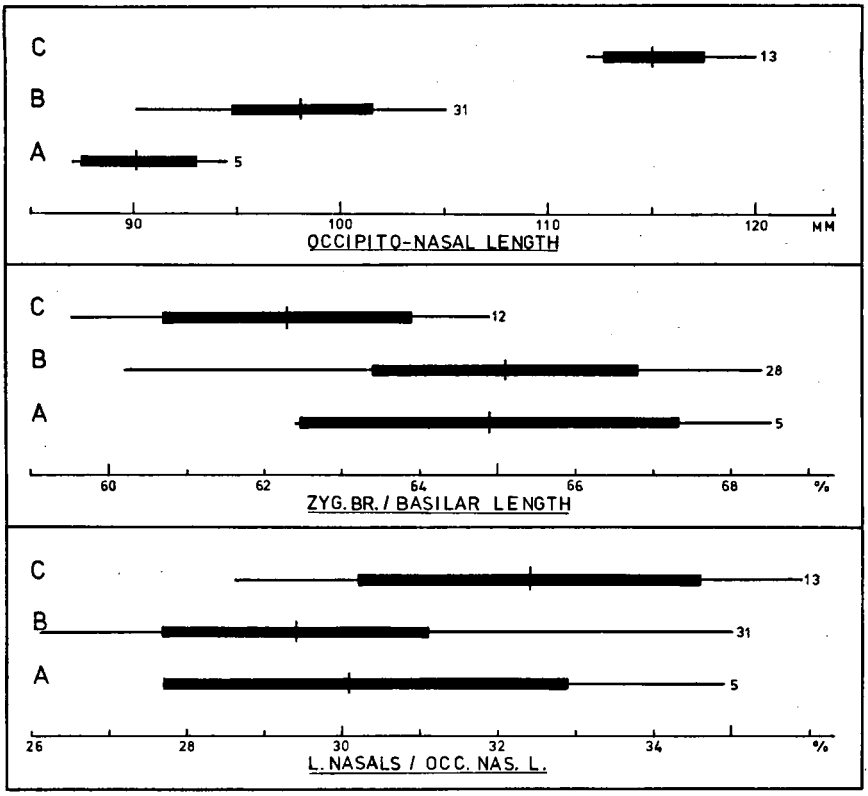

Figure 2. Graphs of the occipito-nasal length of the skull, relative breadth of the skull and the relative length of the nasals of *H. pumila* (A), *H. sumatrae* (B) and *H. crassispinis* (C). Horizontal line, range; solid bar, one standard deviation on each side of the mean; sample size at right of the range.

Diagnosis. — Smallest *Hystrix* form, on average smaller than *H. sumatrae*, spiny covering poorly developed with very small quills, tactile bristles and rattle-quills and only a small number of quills on the back, colouration quite different from *H. sumatrae* as well as from *H. crassispinis* by the absence of white tips to the quills.

Body size. — Günther's type specimen has a length of head and body of 370 mm but this is a young specimen in which the fourth molar is still undeveloped. The only further measurements available from adult specimens are the length of head and body (450 mm) measured from a dry skin (BMNH 94.2.1.15), the estimated total length (480 mm) of a specimen described by Taylor (1934) and the collector's measurements of USNM 396591 (head and body 580, tail 64, hindfoot 69, ear 31 mm). These data suggest an animal smaller on average than *H. sumatrae*.

Cranial characters. — Table I shows a statistically significant difference between the means of the occipito-nasal length of *H. pumila* and *H. sumatrae*.

In table II only the relative height of the skulls of these two species seems to be different, but the sample of *H. pumilis* is too small to justify any further conclusion. Measurements of five adult specimens available are presented in table IV.

Table I. Cranial measurements in millimetres of adult specimens of *Hystrix pumila* *Hystrix sumatrae* and *Hystrix crassispinis*, with range, mean of the sample in parentheses, number of measurements (n) and standard deviation (s). For definitions of the measurements see Material and methods.

	pumila	*sumatrae*	*crassispinis*
Occ.nas.l.	87.4 — 94.5 (90.1) n = 5 s = 2.90	90.1 — 105.0 (98.1) n = 31 s = 3.29	111.7 — 119.8 (114.9) n = 13 s = 2.43
Basilar l.	77.4 — 83.7 (80.6) n = 5 s = 2.83	75.2 — 87.6 (81.6) n = 30 s = 2.81	93.4 — 102.4 (97.6) n = 13 s = 2.56
L. nasals	24.5 — 31.0 (27.1) n = 5 s = 2.63	23.5 — 34.2 (28.9) n = 31 s = 2.09	32.0 — 43.0 (37.0) n = 14 s = 2.96
L. frontals	34.5 — 35.0 n = 2	33.2 — 39.5 (35.2) n = 20 s = 1.52	35.7 — 44.4 (39.9) n = 14 s = 2.41
Palatal l.	44.8 — 49.3 (47.6) n = 4	45.2 — 51.7 (48.9) n = 30 s = 1.68	55.3 — 63.0 (59.0) n = 15 s = 2.25
L. diastema	26.0 — 28.5 (26.8) n = 5 s = 1.02	23.2 — 28.6 (25.6) n = 29 s = 1.56	28.1 — 33.7 (31.3) n = 15 s = 1.89
Br.nas.po.	13.1 — 15.5 (14.7) n = 5 s = 0.93	12.4 — 16.8 (14.5) n = 27 s = 1.23	15.3 — 19.5 (17.2) n = 15 s = 1.22
Postorb.br.	29.1 — 30.4 (29.8) n = 5 s = 0.55	28.8 — 33.9 (31.3) n = 27 s = 1.34	31.9 — 39.0 (35.3) n = 14 s = 1.84
Zygom. br.	51.0 — 53.7 (52.3) n = 5 s = 1.24	48.8 — 55.6 (53.1) n = 29 s = 1.82	57.9 — 63.5 (60.9) n = 12 s = 1.58
Height sk.	29.6 — 32.0 (30.7) n = 5 s = 1.12	26.3 — 32.1 (29.8) n = 30 s = 1.41	33.2 — 39.3 (35.7) n = 15 s = 1.66
L. mandible	61.8 — 63.5 (62.9) n = 3	60.3 — 70.0 (64.1) n = 27 s = 2.40	69.7 — 81.3 (75.5) n = 11 s = 3.15
H. mandible	27.3 — 29.8 n = 2	25.2 — 30.8 (27.0) n = 26 s = 1.36	28.1 — 33.3 (31.6) n = 9 s = 1.67
Alv. P4-M3	16.7 — 20.0 (18.7) n = 5 s = 1.46	17.7 — 22.2 (19.8) n = 27 s = 1.15	22.7 — 25.5 (24.2) n = 15 s = 0.87
Alv. p4-m3	18.3 — 20.2 (19.2) n = 3	19.4 — 24.2 (20.9) n = 27 s = 1.32	24.3 — 26.6 (25.6) n = 13 s = 0.76

External characters. — From table III it appears that *H. pumila* is a form with a much less developed spiny covering, with quills and tactile bristles on average thinner and shorter in comparison with *H. thecurus* and *H. crassispinis*. A datum not apparent from this table is the strikingly smaller

number of quills on the back. The colouration of the skin of this species is quite different from that of *H. sumatrae* and *H. crassispinis*. All the quills and tactile bristles are quite black up to the tip, except for a small non-visible white base. There are no quills or tactile bristles with a white tip, the spines, too, having black tips. The white tips of the spines which give the speckled appearance to *H. crassispinis* and *H. sumatrae* are absent here. Most of the few visible white parts in these skins are the white basal halves of spines on the sides and lower parts, sometimes there are a few white-tipped spines on the lower parts. See also figure 4.

Hystrix sumatrae (Lyon, 1907)

Thecurus sumatrae Lyon, 1907: 583.

Holotype. — USNM 143432, skin and skull, adult male, W. L. Abbott no. 4637.

Type locality. — Aru Bay, East Sumatra.

Distribution. — Sumatra. The localities of the specimens examined are plotted on the map of figure 1, numbers 12—17.

Diagnosis. — Intermediate as to size and development of the quills between *H. pumila* and *H. crassispinis*. Differs greatly from *H. pumila* with regard to the colouration of the spiny covering by the possession of white-tipped quills and spines, and differs from *H. crassispinis* primarily in the dimensions of the skull.

Body size. — The body sizes as appear from collector's measurements (n = 11) in millimetres are as follows: head and body 455—560 (m = 506), tail 90—110 (m = 94), hindfoot 68—75 (m = 72), weight 3.8—5.4 kg (m = 4.7 kg).

Cranial characters. — The morphological limits of the skull of this species, are presented primarily in the tables I and II and in the figures 2 and 3. Some cranial differences with *H. pumila* are discussed above and comparisons with *H. crassispinis* will be made below. Measurements of the holotype and a second specimen are presented in table IV.

External characters. — Diameter and length of the quills, tactile bristles and rattle-quills are presented in tabel III. A large number of quills is developed on the posterior part of the back, considerable more than in *H. pumila* and a somewhat smaller number than in *H. crassispinis*. The number of the white-tipped quills is eitther equally large as that of the quills with black tips, or can be clearly smaller. The length of the white tip varies from 10 to 30 mm, being almost always shorter than in *H. crassispinis*.

The number of tactile bristles is small, about two to six ones which are longer than the quills of the same skin. The skins are distinctly speckled by the white tips of the spines on cheeks, neck, shoulders, flanks and anterior part of the back. As appears from table III, the rattle-squills are very small, no larger than in *H. pumila* and always shorter than in *H. crassispinis* in our

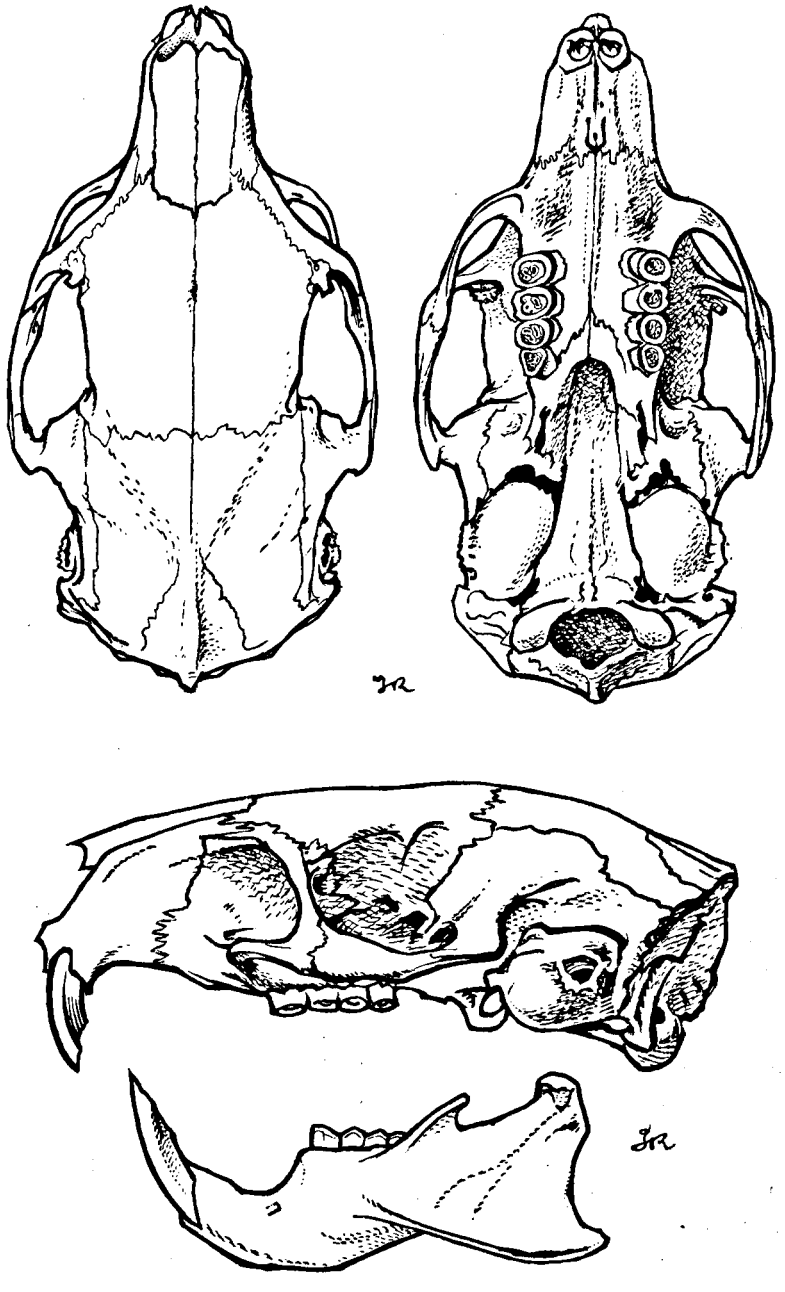

Figure 3. Dorsal (left), ventral (right) and lateral (below) views of the skull of *Hystrix sumatrae* Lyon, 1907, ZMA 5599. Drawings by Mr. Jos Ruting - ZMA.

Table II. Relative measures of skulls and nasals of *Hystrix pumila, Hystrix sumatrae* and *Hystrix crassispinis*. The zygomatic breadth is expressed as a percentage of the basilar length, the height of the skull as a percentage of the basilar length, the length of the nasals as a percentage of the occipito-nasal length and the breadth of the nasals as a percentage of the zygomatic breadth. Adult specimens only.

	pumila	*sumatrae*	*crassispinis*
Zyg. br./Basilar l.	62.4 — 68.5% m = 64,9% n = 5 s = 2.45	60.2 — 68.4% m = 65.1% n = 28 s = 1.68	59.5 — 64.9% m = 62.3% n = 12 s = 1.58
Height/Basilar l.	35.7 — 40.4% m = 38.1% n = 5 s = 1.67	35.0 — 38.5% m = 36.5% n = 29 s = 10.5	35.5 — 38.4% m = 36.8% n = 13 s = 0.93
L. nasals/Occ.nas.l.	27.7 — 34.9% m = 30.1% n = 5 s = 2.83	26.1 — 35.0% m = 29.4% n = 31 s = 1.71	28.6 — 35.9% m = 32.4% n = 13 s = 2.20
Br.nasals/Zyg. br.	25.6 — 29.0% m = 28.1% n = 5 s = 1.46	22.4 — 31.5% m = 27.3% n = 27 s = 2.14	25.7 — 30.7% m = 27.9% n = 12 s = 1.79

material. For further comparison with the latter species see below.

Hystrix crassispinis Günther, 1877

Hystrix crassispinis Günther, 1877: 736, pl. 70, figs. 1 and 1a.
Thecurus major Schwarz, 1939: 246. Subjective synonym.

Type specimen. — BMNH 76.9.20.15, lectotype (Ellerman, 1940: 211), skin and skull, adult, sex unknown, collector H. Low.
Type locality. — N.W. Borneo opposite Labuan.
Distribution. — Borneo. The localities of the specimens examined, are plotted on the map of figure 1, the numbers 2—11. Chasen & Kloss (1932) record specimens from Bettotan, and Davis (1962) from Dandulit and Sandakan, Northeast Sabah.
Diagnosis. — Largest form of this subgenus with larger quills, tactile bristles and rattle-quills. Quills extremely thick with more and longer white tips. Skull always larger than that of *H. sumatrae* with slightly longer nasals and other minor differences.
Body size. — The body sizes as they appear from collector's measurements (n=6) in millimetres, are as follows: head and body 550—665 (m = 610), tail 90—190 (m = 123), hindfoot 80—90 (m = 84), ears 35—42 (m = 38), obtained from specimens examined and from published sources (Schwarz 1939, Chasen & Kloss 1932, Davis 1962). The individual measurements are recorded in the list of specimens examined.
Cranial characters. — The skull of *H. crassispinis* is always larger than that of *H. sumatrae* as appears from the cranial measurements presented in

Table III. Measurements in millimetres of diameter and length of the longest quill, tactile bristle and rattle-quill in skins of *Hystrix pumila, Hystrix sumatrae* and *Hystrix crassispinis* with range, mean (m) and number of measurements (n).

	pumila	*sumatrae*	*crassispinis*
Quills			
diameter	4.5 — 5.2	5.0 — 7.0	6.3 — 8.3
	m = 4.8	m = 6.0	m = 7.3
	n = 3	n = 10	n = 12
length	123 — 130	115 — 155	140 — 200
	m = 126	m = 137	m = 172
	n = 3	n = 10	n = 11
Tactile bristles			
diameter	1.0 — 1.7	1.8 — 2.8	2.2 — 3.6
	m = 1.4	m = 2.5	m = 3.0
	n = 3	n = 10	n = 9
length	112 — 142	130 — 165	140 — 240
	m = 127	m = 144	m = 187
	n = 3	n = 10	n = 11
Rattle-quills			
diameter	2.4 — 2.5	2.4 — 3.8	3.5 — 4.6
		m = 3.2	m = 4.0
	n = 2	n = 9	n = 7
length	10 — 11	8 — 10	12 — 16
		m = 9.2	m = 13.8
	n = 2	n = 9	n = 11

table I. Relative measures of table II show that, on average, the skull of *H. crassispinis* is relatively narrower than that of *H. sumatrae* (mean of zyg. br./basilar l. = 62.3% against 65.1% in *H. sumatrae*), and that, on average, the nasals of *H. crassispinis* are relatively longer than those of *H. sumatrae* (mean of l. nasals/occ. nas. l. = 32.4% against 29.4% in *H. sumatrae*). Both these differences are statistically significant. Measurements of the lectotype and a second specimen are given in table IV.

External characters. — *Hystrix crassispinis* has enormous thick quills of up to 8.3 mm, which are thicker than in the largest specimens of the subgenus *Acanthion* studied by me, and probably as thick as those of the highest specialized forms of the subgenus *Hystrix*. The dimensions of quills, tactile bristles and rattle-quills are presented in table III. All these data reflect that *H. crassispinis* clearly is a larger form than *H. sumatrae*. The large quills of the posterior part of the back have a white tip of about 25—65 mm, or a blackish part all up to the tip. In most skins the number of white-tipped quills is largest and in a few of the specimens there are about as many quills with a white terminal part as with a dark one. jin *H. sumatrae*, on the contrary, quills with dark tips are more numerous in many cases and, moreover, the length of the white tips (10—30 mm) is smaller on average than in *H. crassispinis*. The number of tactile bristles is small; on the back

Table IV. Cranial measurements of five specimens of *Hystrix pumila*, two of *Hystrix sumatrae*, two of *Hystrix crassispinis* and one not assigned with certainty to any species. Measurements in millimetres, adult specimens only. 1. BMNH 79.5.3.17, paralectotype; 2. BMNH 94.2.1.15; 3. MNHN 1883—1290; 4. SMF 26113; 5. USNM 396591; 6. USNM 143432, holotype; 7. ZMA 6872; 8. BMNH 76.9.20.15, lectotype; 9. RMNH 19998; 10. ZMB without reg.nr.

	H. pumila					*H. sumatrae*		*H. crassispinis*		Not assigned
	1	2	3	4	5	6	7	8	9	10
Sex	♂	—	—	♂	♀	♂	—	—	—	♀
Occ.nas.l.	87.4	91.5	88.3	94.5	88.8	103.4	94.0	—	111.7	124.3
Basilar l.	80.4	83.3	77.4	83.7	78.4	85.3	80.1	92	95.9	106.4
L. nasals	25.0	26.7	24.5	28.2	31.0	29.5	28.0	33.0	39.4	39-41
L. frontals	—	34.5	—	35.0	—	39.5	33.3	38.9	35.7	41
Palatal l.	49.3	48.4	44.8	—	47.8	51.1	48.0	56.0	58.5	63.8
L. diastema	26.1	28.5	26.5	27.0	26.0	28.0	24.2	29.0	30.9	34.8
Br.nas.po.	14.8	15.1	13.1	15.0	15.5	14.6	14.7	17.2	18.8	16.6
Postorb.br.	29.1	30.0	29.4	30.4	30.2	31.8	28.9	37.9	37.6	37.0
Zygom. br.	51.0	52.0	51.2	53.4	53.7	55.4	51.7	—	61.5	68.4
Height sk.	30.4	29.7	29.6	32.0	31.7	32.1	29.2	34.5	36.0	39.6
L.mandible	—	63.4	—	61.8	63.5	69.2	—	69.7	76.5	85.8
H.mandible	—	27.3	—	—	29.8	30.8	27.4	30.7	—	—
Alv.P4-M3	20.0	17.7	16.7	19.9	19.3	19.1	20.3	24.1	23.6	24.7
Alv.p4-m3	—	19.0	18.3	20.2	—	19.5	21.1	24.3	24.4	25.2

there are up to five which are longer than the quills in that skin. The rattle-quills of *H. crassispinis* are always longer than those of *H. sumatrae*. The skins are distinctly speckled by the white tips of the spines on cheeks, neck, shoulders, flanks and sometimes on the anterior part of the back. The head, just as *H. pumila* and *H. sumatrae*, does not show any trace of a crest of hairs.

Remarks. — There is a remarkable contradiction between Lyon's treatments of Günther's *H. crassispinis* in 1907 (: 581) and 1911 (: 173). Lyon (1911) stated: "In 1907 I applied Günther's name *crassispinis* to the Bornean *Acanthion.*", but this statement can only be understood if one reads it the other way round. In fact, Lyon (1907) has applied the name *Acanthion* to Günther's *Hystrix (Thecurus) crassispinis.*

As contrasted with our observations, Chasen & Kloss (1932: 38) found a few white hairs on the nape of an adult male, representing a crest.

In table IV, no. 10, measurements are presented of a relatively large skull which could not be assigned with certainty to *H. crassispinis*. See also the end of the list of Specimens examined and Discussion.

Discussion

Ellerman (1940: 211) considered *H. pumila* a valid species because the spiny covering is at its lowest development among true Porcupines, and he affirmed this classification on a later occasion (1949: 3). Although Chasen

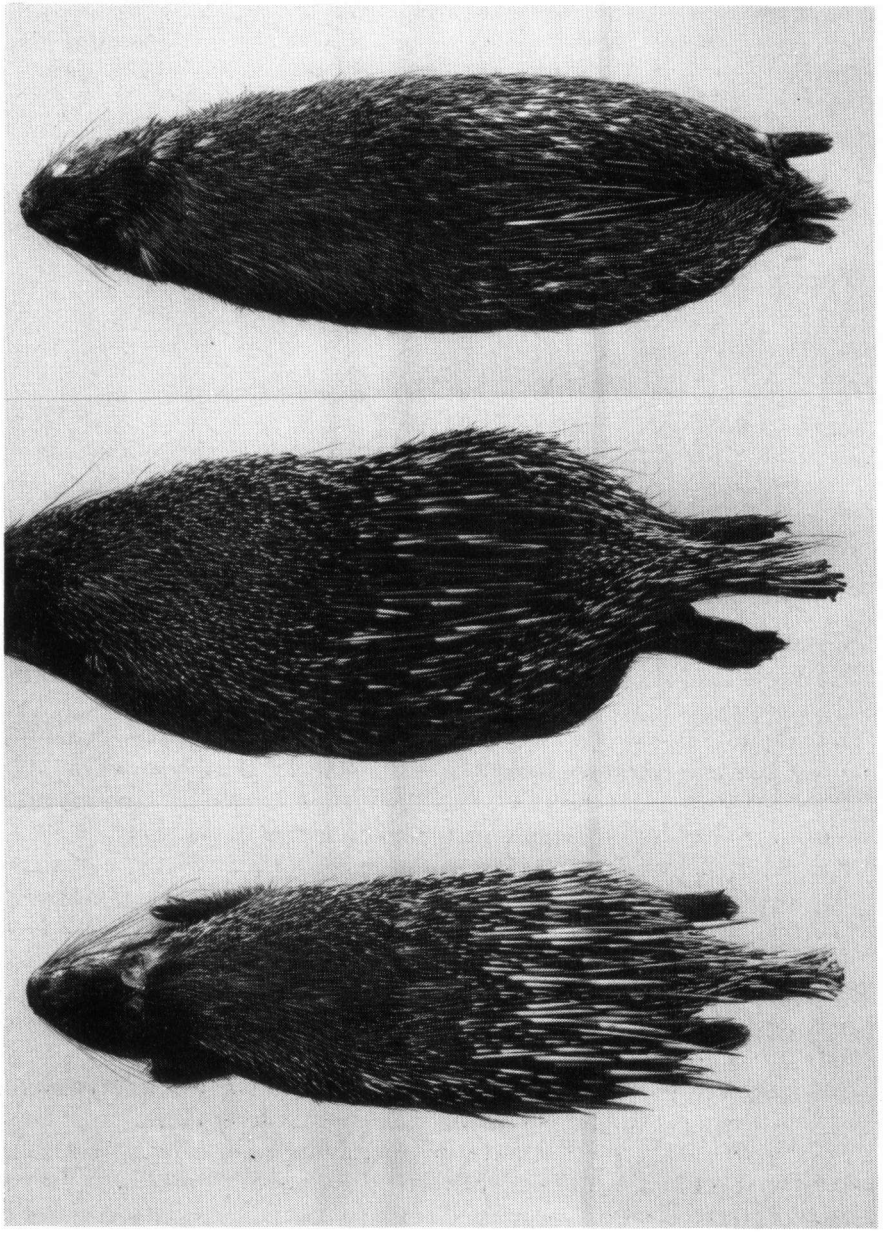

Figure 4. Photographs of skins of *Hystrix pumila* (above, USNM 396591), *Hystrix sumatrae* (middle, USNM 144222) and *Hystrix crassispinis* (below, USNM 197640). Not figured to the same scale, for dimensions see list of specimens examined.

(1940: 187) did not have the opportunity of comparing specimens of *H. crassispinis* and *H. sumatrae*, he classified these forms as races of the same species, a view which was accepted by Ellerman (1949: 3) and by Ellerman & Morrison-Scott (1955: 40). In my opinion, Ellerman's classification of *H. pumila* as a valid species must be maintained on the characters noted by him, but from the information presented in the present paper, it appears that *H. sumatrae* is as different from *H. crassispinis* as it is from *H. pumila*. Therefore I will consider these three forms valid species.

The three species in the present subgenus are treated as monotypic. Considering the small size of the samples and the enormous amount of individual variation (Chasen 1940: 187), it is impossible to distinguish between individual and geographical variation at this moment. It remains a possibility that the *H. pumila* populations of the various islands of the Philippines are not the same, but meaningful differences have yet to be demonstrated. To facilitate comparisons, the cranial measurements of all five adult specimens available are presented in table IV.

Unfortunately, the locality "S. Pulu Atas" of a skull in the collections of the Zoologisches Museum Berlin could not be traced in the files of that institution, nor on any map nor in any gazetteer. The extremely large size of this skull (i.e. for this subgenus), the fact that it is apparently from an island, together with the circumstance that no skin is available, make it impossible to assign this skull to *H. crassispinis*, or to any other species with confidence. It is always possible, of course, that the range of variation of *H. crassispinis* is larger than hitherto known but more reliable data than are obtainable from the Berlin specimen would be necessary to confirm this point.

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Gazetteer

The following geographic names are those from the list of specimens studied. Different spellings or synonyms are enclosed in parentheses. Most of the coordinates were taken from the "Official Standard Names Gazetteer" of the United States Board on geographic Names, Washington, some of them were derived from "The Times Atlas of the World", ed. 5, 1975, London, or from the "Atlas van tropisch Nederland", Kon. Ned. Aardr. Gen., 1938, Batavia.

Philippines:		
Paragua (Palawan Island)		
Puerta Princesa	9°46′ N	118°45′ E
Borneo:		
Baram, cape and est.	4°36′ N	113°59′ E
Birang River	2°11′ N	117°28′ E
Datu Mt.	2°03′ N	109°37′ E
Dulit, hill	3°18′ N	114°11′ E
Labuan	5°20′ N	115°10′ E
Mengalong	5°01′ N	115°28′ E
Pagatan	3°36′ S	115°56′ E
Riam	1°50′ S	111°25′ E
Samarinda	0°30′ S	117°08′ E
Tanahgrogot	1°55′ S	116°14′ E
Tutong	4°51′ N	114°40′ E
Sumatra:		
Aru Bay	4°09′ N	98°12′ E
Deli (Labuhandeli)	3°45′ N	98°41′ E
Kumpeh, sungai (S. Koempeh)	1°33′ S	103°39′ E
Mandau, sungai	0°48′ N	101°47′ E
Putih, sungai	2°30′ S	103°10′ E
Serdang, the former sub-recidency of	3°30′ N	99°00′ E
Talu (Taloe)	0°13′ N	99°59′ E

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