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Notes on Southeast Asian Porcupines (Hystricidae, Rodentia) IV. On the taxonomy of the subgenus *Acanthion* F. Cuvier, 1823 with notes on the other taxa of the family

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ABSTRACT

Arguments are presented to demonstrate that Lyon's (1907) division of the Old World porcupines, family Hystricidae, into two subfamilies is superfluous and provides a distorted classification. Evidence is presented for the point of view that the generic status of *Thecurus* Lyon, 1907 has been based on quite insufficient arguments, and this taxon is not accorded a higher rank than that of a subgenus. Only three genera are recognized in this family: *Trichys* Günther, 1877, *Atherurus* F. Cuvier, 1829, and *Hystrix* Linnaeus, 1758 with the subgenera *Hystrix* s.s., *Acanthion* F. Cuvier, 1823 and *Thecurus* Lyon, 1907. Data about some south-western Asiatic specimens of *Hystrix indica* Kerr, 1792 are presented. The main subject of the present paper is the specific distinction within the subgenus *Acanthion*. Two species are recognized in this taxon: *Hystrix brachyura* Linnaeus, 1758 from the continent of Southeast Asia and the Malay Archipel, and *Hystrix javanica* (F. Cuvier, 1823) from Java and a number of the small Sunda Islands. Individual and geographic variation in these species is described. *H. javanica* is considered monotypic and in *H. brachyura* at least three subspecies can be recognized. However, a number of specimens cannot be assigned to one of these subspecies and the data available strongly suggest that many differences may be likely to be bridged by intergrading forms when specimens from intermediate localities become available.

INTRODUCTION

The porcupines of the family Hystricidae occur on the greater part of the African Continent and in Southern Palearctic and Oriental Asia. In the present study three genera in this family are recognized: the Long-tailed Porcupine *Trichys* Günther, 1877, the Brush-tailed Porcupine *Atherurus* F. Cuvier, 1829, both with relatively long tails, and the short-tailed genus *Hystrix* Linnaeus, 1758. Lyon (1907) proposed to divide this family into two subfamilies the "Atherurinae" comprising *Atherurus* and *Trichys*, and the "Hystricinae" with three short-tailed genera. In the present paper evidence

will be presented to demonstrate that the morphological break between these two "subfamilies" is less obvious than Lyon supposed, that the mutual differences between the "genera" of Lyon's "Hystricinae" are much smaller than he assumed and that, consequently, the division of the Hystricidae into subfamilies is superfluous and provides a distorted classification.

Lyon (1907) recognized three genera in the short-tailed porcupines: *Thecurus* Lyon, 1907, *Acanthion* F. Cuvier, 1823 and *Hystrix* Linnaeus, 1758. Cuvier (1823) used the name *Acanthion* for the porcupines with less convex head and nasals shorter than two fifths of the skull length. Lönnberg (1923) studied the characters used until then for the distinction of this group from *Hystrix* s.s. and discussed the form and dimension of premaxilla, palatum and nasals, the height of the skull, the development of the roots of the molars and the presence of a crest of bristles on the neck. He pointed out that the use of all these characters leads to bizarre classifications and stated that no satisfactory diagnosis had been published justifying the division of the genus *Hystrix* into a genus *Hystrix* s.s. and a genus *Acanthion*. Only one difference between these groups can be absolutely established: the possession of quills with only one dark ring in *Acanthion* against quills with more than one ring in *Hystrix*. After Lönnberg's paper, for most authors one distinctive feature appears to have been too weak a basis to divide the genus. Osgood (1932), Allen (1940), Chasen (1940), Ellerman (1940, 1961), Ellerman & Morrison-Scott (1951, 1955) and Laurie & Hill (1954) do not assign a higher rank to *Acanthion* than that of a subgenus, and this view is adopted in the present study.

The generic status of *Thecurus* Lyon, 1907, with the least specialized short-tailed porcupines from Sumatra, Borneo and the Philippines possessing very small nasals, has never been the subject of a thorough discussion as was the case with *Acanthion*. However, there are undoubtedly fewer arguments for the separation of this group than Lyon (1907) put forward when he described the type species *Thecurus sumatrae*. This originally monotypic genus was based on differences of body size, structure of the spinal column, dimensions of the cranial bones and development of the spiny covering, between Lyon's relatively primitive *T. sumatrae* and the more specialized representatives of *Acanthion*. Most of these differences, however, as will be argued in the present paper, are bridged by the much more specialized *Hystrix* (*Thecurus*) *crassispinis* Günther, 1877, and by *Hystrix* (*Acanthion*) *javanica* (F. Cuvier, 1823), the least specialized member of the nominal genus *Acanthion*. No specimens of *javanica* nor of *crassispinis* were available to Lyon in 1907 and he did not even associate Günther's (1877) description of the latter species with his genus *Thecurus*. Chasen (1940) indicated a close external resemblance of *crassispinis* to *javanica*. He did not recognize the genus *Thecurus* as appears from his application of names, but differed in this respect from the authors mentioned above. Therefore, in this paper ample arguments are presented to dispute the status of *Thecurus* at a generic level.

The specific characters in the genera *Trichys* Günther, 1877 and *Atherurus* F. Cuvier, 1829 were outlined by Van Weers (1976 and 1977), those in the subgenus *Hystrix* Linnaeus, 1758 were clearly pointed out by Corbet & Jones (1965) and the specific characters in the subgenus *Thecurus* Lyon, 1907 were recently described by Van Weers (1978). The specific distinction in the subgenus *Acanthion* is, besides a revision of the generic distinction in the family Hystricidae and notes about the subgenus *Hystrix*, the main subject of the present paper.

MATERIAL AND METHODS

Specimens. — 52 Skins and 97 skulls of adult, 11 skins and 25 skulls of subadult, and 25 skins and 46 skulls of young specimens were studied from the collections of the institutions mentioned below:

- AMNH = American Museum of Natural History, New York.
- BMNH = British Museum (Natural History), London.
- FMNH = Field Museum of Natural History, Chicago.
- MAKB = Museum Alexander Koenig, Bonn.
- MHNLR = Muséum d'Histoire Naturelle La Rochelle, France.
- MNHN = Muséum National d'Histoire Naturelle, Paris.
- MSNG = Museo Civico di Storia Naturale di Genova, Genoa.
- MZB = Museum Zoologicum Bogoriense, Bogor.
- NMW = Naturhistorisches Museum Wien, Vienna.
- NRS = Naturhistoriska Riksmuseet, Stockholm.
- 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.
- ZSIC = Zoological Survey of India, Calcutta.
- ZSM = Zoologische Staats-Sammlung München, Munich.

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

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

Cranial measurements. — The cranial measurements presented, were defined by Van Weers (1976: 17—19), with the exception of the posterior breadth of the nasals for which the definition is slightly modified 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. — Mohr (1964 and 1965) used, for the description of the various forms of modified hairs, the following terms: “Borsten”, “Stachelborsten”, “Stacheln”, “Stilett-Stacheln”, “Spiesz”, “Borstenstacheln” and “Tastborsten”. Because transitional forms between

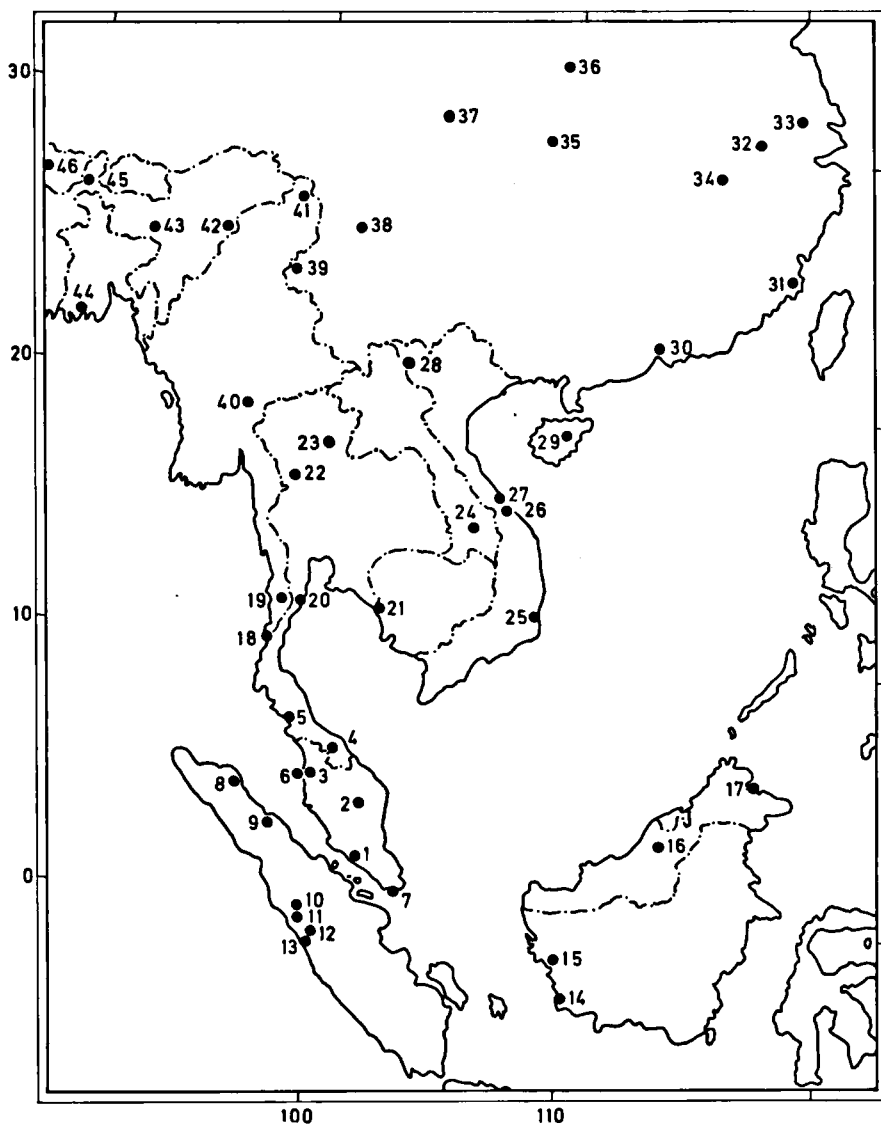


Fig. 1. Range of *Hystrix brachyura* in Southeast Asia as determined by specimens examined. The numbers of the plotted localities correspond with the numbers of the list of specimens examined. 1—17 = *H. b. brachyura*; 18—24, 28—38 and 40—42 = *H. b. subcristata*; 39 = *H. b. yunnanensis*; 45 and 46 = *H. b. hodgsoni*; 25—27, 43, and 44 (“*H. bengalensis*”) cannot be assigned with certainty to any subspecies.

all these types occur, distinctive definitions are hardly possible, and for this reason mainly Ellerman's (1940) terminology is followed.

Spines = stiff, flattened and grooved bristles with a sharp point.

Quills = long and thickest modified hairs, very little flexible, circular in cross-section with the largest diameter about midlength and with a very sharp point. Findlay (1977) used the term "quill" in a broader sense.

Tactile bristles (term after Banks, 1932: 41) = very flexible modified hairs, circular in cross-section with the largest diameter near the base, some very short, some of these bristles in each skin always considerably longer than the longest quill, diameter on average considerable smaller than that of the quills. This definition partly fits Mohr's "Borstenstachel" and "Tastborsten", and seems to be synonym with Findlay's "whip type quill" and Ellerman's (1940) "hair-like quills".

Transitional quills = intermediate forms between the former two ones as for length, diameter and flexibility, sometimes with a cylindrical body portion with equal thickness. This description is much like Findlay's "needle type 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.

On each skin the length and diameter of the longest quill, tactile bristle and the hollow part of the longest rattle-quill, the length and place of the blackish parts of the quills, the greatest length of the hairs of the crest on the head and their white tips were measured.

SPECIMENS EXAMINED

The numbers before the localities in this list of specimens examined, correspond with the numbers of the plotted localities on the relevant map of the figures 1 and 2. A dash indicates specimens from localities not plotted on the maps, or specimens with unknown exact locality. The coordinates are given in the Gazetteer. Localities within quotation marks could not be located. Sex, collector's measurements and other data are mentioned as far as known.

Abbreviations: HB = length of head and body, T = length of tail, Tot. l. = total length, Hf = length of a hindfoot, E = length of an ear, Wt = weight.

Hystrix indica

Southwest Asia

- Jerusalem (Emmaus, Ellerman 1940), ZSM AM/1279, holotype of *H. hirsutirostris aharoni* Miller, 1911, skull, subadult.
- Ajeleth Hashakhar, Huleh area, (Palestine, see Gazetteer), MAKB 58.94,

- skull, adult, Prof. Georg Haas.
 — Kaukasus, MAKB 36.1, skin and skull, adult ♀, Zoo Köln 4-I-1936.
 — Shacha sumbil, Susa Steppe, Chusistan, Iran, ZSM 1957/285, skin and skull, adult ♀, J. Popp 25-IX-1957, HB = 810, T = 75, Hf = 120, E = 48 mm.

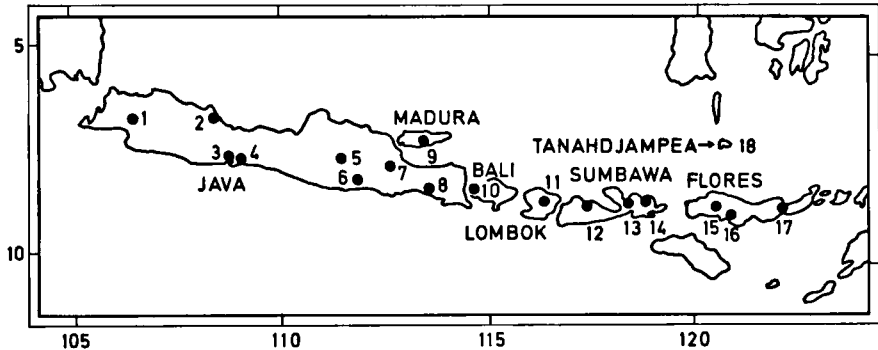


Fig. 2. Range of *Hystrix javanica* in Indonesia as determined by specimens examined. The numbers of the plotted localities correspond with the numbers of the list of specimens examined.

Hystrix brachyura

Malay Peninsula

1. Malacca, BMNH 49.12.7.1, holotype of *Acanthochoerus grotei* Gray, 1866, skull and mounted skin, 889c, young.
 —, BMNH 79.11.21.533, skin, probably adult, Dr. Cantor, ex Indian Mus. coll.
2. Kuala Tahan, Pahang, Malaya, BMNH 55.3204, skin and skull, subadult ♀, Survey Vert. Fauna Malay Peninsula 19-VII-1920.
3. Wellesley, Province, BMNH 79.11.21.199, skull, adult, ex Indian Mus. coll.
4. Mabek, Jalor, Malay peninsula, BMNH 3.2.6.73, skin and skull, adult ♂, H. C. Robinson and N. Annandale, 28-VII-1901, no. 105.
 —, BMNH 3.2.6.74, skin and skull, adult ♀, H. C. Robinson and N. Annandale, 25-VI-1901, no. 106.
5. Trong, Lower Siam, USNM 83519, skin and skull, adult ♀, W. L. Abbott 15-XII-1896, HB = 25, T = 2.5 inch, Wt = 26 lbs.
 —, USNM 83521, skin and skull, adult ♂, W. L. Abbott 15-XII-1896, no. 148, HB = 28, T = 4.5 inch, Wt = 27 lbs.
 —, USNM 49465, skull, subadult, W. L. Abbott.
 — "Salak", North Malaya, BMNH 55.3205, skull, adult ♂, 128/14.

Malay Islands

6. Pinang, BMNH 79.11.21.638, skin with skull inside, probably adult, Cantor.

7. Singapore, BMNH 5.9.27.1, skull, adult, H. N. Ridley.

Sumatra

8. Perlak, O. Atjeh, N. Sumatra, RMNH 19982, skull, adult ♂, H. J. V. Sody 1930, no. F140.
—, RMNH 19983, skull, subadult, IV-1932.
9. Serdang, Sumatra, ZMA 6848—6850 and 6852—6870, skulls only, 9 adult, 3 sub-adult and 10 young specimens, L. Ph. le Cosquino de Bussy 1907—1908.
—, “Klein Soengei Karang”, RMNH 1128, skull, adult, F. C. van Heurn 1920.
—, Bangoeng Poerba, Deli, RMNH 2543, skull, adult, P. J. Nieuwdorp 6-X-1936.
—, Deli, RMNH 19994, skeleton, adult ♀, Zoo Rotterdam II-1896.
—, “Tandjong Morawa”, Deli, RMNH 19995, skull, adult, B. Hagen 1882, Jentink’s (1887: 232) “*A. javanicum*” no. h.
10. Loeboeksikaping, W. Sumatra, BMNH 48.18, skin and skull, adult ♂, W. J. C. Frost I-V-1939, no. 2, alt. 2400 ft, HB = 580, T = 110, Hf = 90, E = 40 mm.
—, BMNH 48.17, skin and skull, young ♂, W. J. C. Frost I-V-1939, no. 1, HB = 580, T = 120, Hf = 90, E = 40 mm.
11. Maninjau Lake, W. Sumatra, BMNH 48.15, skin and skull, adult ♂, W. J. C. Frost 3-V-1939, no. 4, alt. 2000 ft, HB = 540, T = 100, Hf = 90, E = 40 mm.
—, BMNH 48.16, skin and skull, adult ♀, W. J. C. Frost 3-V-1939, no. 3, alt. 2000 ft, HB = 630, T = 80, Hf = 95, E = 40 mm.
11. Karbou Gat, W. Sumatra, BMNH 48.12, skin and skull, adult ♂, W. J. C. Frost 4-V-1939, no. 7, alt. 2600 ft, HB = 610, T = 95, Hf = 90, E = 40 mm.
—, BMNH 48.13, skin and skull, adult ♀, W. J. C. Frost 4-V-1939, no. 5, alt. 2600 ft, HB = 600, T = 100, Hf = 90, E = 40 mm.
—, BMNH 48.14, skin and skull, adult ♀, W. J. C. Frost 4-V-1939, no. 6, alt. 2600 ft, HB = 600, T = 130, Hf = 80, E = 40 mm.
12. Sinkarah, W. Sumatra, RMNH 4981, skull, adult ♀, E. Dubois 29-VIII-1941.
13. Padang-besi, Sumatra, RMNH 19993, skeleton, adult, syntype of *Hystrix mülleri* Marshall in Sclater, 1871, Jentink’s (1887: 232) *Acanthion mülleri* no. a, S. Müller.
—, RMNH 19964, skin and skull, young ♀, syntype of *Hystrix mülleri* Marshall in Sclater, 1871, Jentink’s (1888: 104) *Acanthion mülleri* no. a (“Femelle adulte monté”), S. Müller.
—, RMNH 19965, skin with skull inside, probably adult, ♂, syntype of *Hystrix mülleri* Marshall in Sclater, 1871, Jentink’s (1888: 104) *Acanthion mülleri* no. b, Jardin Zoologique la Haye 1878.
13. Padang, W. Sumatra, RMNH 1112, skin and skull, young ♂, Zoo

Rotterdam 15-XI-1921.

—, RMNH 1270, skin and skull, young, Zoo Rotterdam 12-XI-1923.

—, NMW 1474, skull, subadult, Konsul Schild VIII-1904.

- RMNH 19966, skin and skull, young, syntype of *Hystrix mülleri* Marshall in Sclater, 1871, Jentink's (1888: 104) *Acanthion mülleri* no. c.
- RMNH 19967, skin with skull inside, young, syntype of *Hystrix mülleri* Marshall in Sclater, 1871, Jentink's (1888: 104) *Acanthion mülleri* no. d, Zoo Rotterdam 26-XI-1875.

Borneo

14. Kendawangan River, S.W. Borneo, USNM 153737, skin and skeleton, adult ♂, W. L. Abbott 20-IX-1908, no. 6176, Wt = 22 lbs.
 - , USNM 153974, skull, young ♂, W. L. Abbott 10-VII-1908, no. 6049.
15. Semandang River, W. Borneo, USNM 145572, skull, young ♂, W. L. Abbott no. 5434.
16. Mt. Dulit, Baram District, Sarawak, BMNH 0.2.2.9, skin with skull inside, ♀, C. Hose 23-X-1897, 3000 ft.
 - , BMNH 92.9.4.11, skin and skull, young ♂, C. Hose.
 - , BMNH 1900.3.30.7, skeleton, adult ♀, C. Hose V-1894, 3000 ft.
17. Sandakan, N. Borneo, MZB 2734, skull, young ♀, C. B. Kloss and F. N. Chasen 15-VIII-1927, no. 3270.
 - "Long Petah", N.E. Borneo, MZB 1177, skull, adult ♀, H. C. Siebers 16-IX-1925, Tot. l. = 740, T = 133, E = 39 mm.
 - "Sandaren Baagoe", Borneo, USNM 197641, skin and skull, young ♂, H. C. Raven 29-III-1913, no. 494, HB = 570, T = 122, Hf = 89 mm, Wt = 16 lbs.
 - "Tandjong Seglu", Borneo, USNM 197642, skin and damaged skull, young ♀, H. C. Raven I-VIII-1913, no. 932, HB = 580, T = 100, Hf = 87 mm.

Southern Burma

18. Southern Tenasserim, Bankachon, BMNH 14.12.8.224, skull, adult, G. C. Shortridge no. 4720.
 - , Champang, USNM 124020, skin and fragments of skull, adult ♀, W. L. Abbott 22-XII-1903, no. 2928, HB = 725, T = 140 mm, Wt = 29 lbs.
19. Tenasserim Town, BMNH 14.12.8.223, skin and skull, adult ♂, holotype of *Acanthion klossi* Thomas, 1916, G. C. Shortridge no. 4905.

Thailand

20. S. Siam, 12°00' N 99°50' E, BMNH 14.8.22.31, skull, adult, K. G. Gairdner.
21. Klong Yai, S. E. Siam, BMNH 15.11.4.220, skin and skull, adult ♂, C. B. Kloss 1857, HB (?) = 850 (Tot. l. dry skin 770 mm), T = 115, Hf = 93, E = 44—47 mm.

22. "Me Taqua", Raheng District, USNM 253537, skin and skull, adult ♂, J. H. Chambai 6-IX-1924, no. 78, HB = 670, T = 142, Hf = 89, E = 43 mm, 800 ft.
23. Meh Lem, Nord Siam, NRS 3983, skull, adult, N.G. 10-III-1912.

Laos

24. Thateng, Laos, FMNH 37990, skin and skull, subadult ♂, J. Delacour 22-XII-1931, no. 178, Tot. l. = 830, T = 160, Hf = 95 mm.

Vietnam

25. Ninh Hoa, near Nhatrang, Annam, BMNH 6.11.6.37, skin and skull, young ♀, J. Vassal 25-XII-1905, no. 15, HB = 310, T = 67, Hf = 104, E = 33 mm, alt. = 0.
25. Nha-Trang, Annam, MHNLR — M756, skull, adult, J. Durand 1951.
26. Hué, Annam, BMNH 27.12.1.204, skin and skull, subadult ♂, J. Delacour and W. Lowe 28-I-1927, no. 554.
—, BMNH 26.10.4.191, skin, young ♂, J. Delacour and W. Lowe, no. 221, HB = 410, T = 74, Hf = 64, E = 36 mm.
27. "Phouc Mon", Quangtri, Annam, FMNH 31043, skin and skull, young ♀, R. W. Hendee 30-I-1929, Kelley-Roosevelt Expedition no. 5122, HB = 480, T = 55, Hf = 72 mm.
28. Muong muon, south of Lai Chau, FMNH 32514, skin and skull, young ♀, R. E. Wheeler 2-IV-1929, Kelley-Roosevelt Expedition no. 127, HB = 590, T = 90, Hf = 85 mm.
— Annam, BMNH 26.10.4.201, skull, young ♂, J. Delacour and W. Lowe.

Hainan (China)

29. Nodoa, Hainan, AMNH 60048, skin and skull, adult ♂, holotype of *Acanthion subcristatus papae* G. M. Allen, 1927, C. Pope, Third Asiatic Expedition, no. 599.
—, AMNH 60154, skin and skull, adult ♂, C. Pope, Third Asiatic Expedition, no. 219.
—, AMNH 60153, skin and skull, adult ♀, C. Pope, Third Asiatic Expedition, 8-XII-1922, no. 53.
—, FMNH 39453, skin and skull, adult ♀, C. Pope, Third Asiatic Expedition, 22-I-1923, no. 636.

China (Continent)

30. Tungwahn, Kuangtung, ZMB 43346, skin and skull, adult ♀, R. Mell 30-V-1919.
31. Futsing, Fukien, AMNH 45561, skin and skull, adult ♂, Second Asiatic Expedition, no. 1212.
—, AMNH 84466, skin and skull, adult ♀, C. Pope, Third Asiatic Expedition, XI-1925, no. 199.

- , AMNH 84470, skull, subadult ♂, C. Pope, Third Asiatic Expedition, no. 339.
32. "Yeh-Shan", T'ung-Ling-Hsien, Anhui, NRS 6144, skin and skull, young ♀, J. G. Anderson 4-IV-1920, no. 865.
—, NRS 6143, skin and skull, adult ♂, J. G. Anderson 4-IV-1920, no. 864.
33. Chin-Kiang, Yang-tse, BMNH 19.12.22.21, skull, adult, J. O. la Jouibz.
34. Kiu-Kiang, Kiang-Si, MNHN 1874—548, skin and skull, young, A. David.
34. Kiukiang, BMNH 8.11.14.6, skull, adult, W. Styan.
35. "Yen-Ching-Kou", Wanhsien, Szechwan, AMNH 84357, skin and skeleton, adult ♂, W. Granger 17-III-1926, Third Asiatic Expedition no. G 573.
36. Shen-si meridional, MNHN 1873—63 (in register no. 1873—69), skull, subadult, A. David.
37. Szechwan, USNM 268874, skull, adult, D. C. Graham 1938, no. 1452.
—, Wen Chuan, USNM 268875, skull, adult, D. C. Graham 1938, no. 1454.
38. Lichiang, Yunnan, AMNH 43169, skin and skull, subadult ♂, 11-X-1916.
— "Ha Pa", Yunnan, AMNH 43170, skull fragments, 22-XI-1916.
— S. China, BMNH 1570a, damaged skull, adult, holotype of *Hystrix subcristata* Swinhoe, 1870, R. Swinhoe.
39. Kakhyen Hills, Yunnan, ZSIC 15687, skin and skull, young, holotype of *Hystrix yunnanensis* Anderson, 1878, J. Anderson, Indian Museum Cat. no. a, label: "Yunnan collection skull taken out for comparison 11th April 1869".

Burma

40. Carin Bia, MSNG 5825, skull, subadult ♂, VIII-1880, 1000 m.
40. Yado mountains east of Tounghoo, MSNG 10429 skin and MSNG 10430 skull, subadult ♂, L. Fea 22-XII-1887, 1000 m.
41. Upper Burma, BMNH 50.708, skull, adult, R. Kaulback no. 1.
—, Nam Tamai Valley, 27.42 N 97.54 E, BMNH 50.707, skin and skull fragments, young ♀, R. Kaulback 19-IX-1938, no. 177, HB = 345, T = 78, Hf = 65, E = 36 mm, 4000 ft.
— "Gangfang", N. Burma, AMNH 115577, skull, adult, H. E. Anthony, 5200 ft.
— Burma, AMNH 54637, skull, adult, A. S. Vernay.

Eastern India, Bangladesh

42. Naga Hills, "Sangrachu", BMNH 21.7.16.4, skull ♀, holotype of *Acanthion millsii* Thomas, 1922, J. P. Mills VIII-1920, 3500 ft.
—, "Okatsa", BMNH 22.12.22.20, skull, adult ♂, J. P. Mills.
—, "Okatsa", BMNH 22.12.22.21, skull, adult ♂, J. P. Mills.
—, "Changsii", BMNH 22.12.22.22, skull, subadult, J. P. Mills.

- , "Longpa", BMNH 21.8.2.26, skin and skull, young, J. P. Mills 29-IV-1920, no. 372, 3500 ft.
- BMNH 22.12.22.23, skull, adult, J. P. Mills.
43. Mawphlang, Assam, India, FMNH 75873, skin and skull, young ♂, W. N. Koelz 13-I-1953, HB = 582, Hf = 70, E = 39 mm.
- "Mangpu", Bengal Presidency, India, FMNH 35667, skin and skull, subadult ♂, H. Stevens 28-XII-1930, no. 629, HB = 655, T = 65, Hf = 84, E = 36 mm, Wt = 14 lbs, 2500 ft.
- , FMNH 35668, skin and skull, young ♀, H. Stevens no. 618, 3000 ft.
44. Sunderbuns?, ZSIC 10034, skin and skull, young, holotype of *Hystrix bengalensis* Blyth, 1851, E. Lindstedt, A.S.B. Cat. no. 422B.

Nepal, Sikkim

45. Sikim, BMNH 91.10.7.146, skin, probably adult, L. Mandilli.
- , BMNH 48.6.11.6, skull fragment, young.
- , Darjiling, "Gopalthaja", ZMB 33650, skull, young, H. Stevens no. 2212.
46. Hathiban, Nepal, BMNH 21.10.4.35, skin and skull, adult ♂, N. A. Baptista 25-IV-1921, no. 212.
- Nepal, BMNH 47.7.22.9, skin and skull, subadult, lectotype of *Acanthion hodgsoni* Gray, 1847, B. H. Hodgson 887 b.
- , BMNH 45.1.8.8, skull, adult, paralectotype of *Acanthion hodgsoni* Gray, 1847, B. H. Hodgson 887 a.
- , BMNH 53.8.16.11, skin and skull, adult, lectotype of *Hystrix alophus* Hodgson, 1847, B. H. Hodgson.
- , BMNH 58.6.24.36, skin and skull, adult, B. H. Hodgson 887 c.
- , BMNH 79.11.21.637, skin and skull, adult ♂, B. H. Hodgson.
- , SMF 11227, skin and skull, subadult, Ostind. Compagnie 1853.
- , RMNH 19996, skin and skull, young, B. H. Hodgson, Jentink's (1888: 103) *Hystrix leucura* no. b.

Hystrix javanica

Java

1. Buitenzorg, RMNH 19974, skull, adult, H. J. V. Sody.
- , Tjileungsi, RMNH 19971, skin, probably adult, ♂, H. J. V. Sody 13-XI-1931, Tot. 1. = 720, T = 130, Hf = 84, E = 35 mm.
- , Tjileungsi, RMNH 19972, skin, ♂, H. J. V. Sody 13-XI-1931, Tot. 1. = 560, T = 100, Hf = 70, E = 32 mm.
- , Tjileungsi, "Tjibarsesan", RMNH 19975, skull, subadult ♂, H. J. V. Sody 28-I-1932, Tot. 1. = 677, T = 110, Hf = 84, E = 37 mm.
- , RMNH 19976, skull, subadult, H. J. V. Sody.
- , RMNH 19977, skull, young, H. J. V. Sody.
- , Bogor, NMW 11974, skull, adult, Th. Adensamer 1893, No. 53.
- , Bogor, NMW 5006, skeleton, young, Th. Adensamer 1893.

2. Cheribon, AMNH 102034, skin and skull, adult ♂, J. J. Menden 25-III-1933, HB = 542, T = 102, Hf = 73, E = 35 mm, alt. 600 m.
—, AMNH 106324, skin and skull, adult ♂, J. J. Menden 5-I-1936, no. 786, HB = 518, T = 120, Hf = 75, E = 38 mm.
3. Pangandaran, "Dirk de Vries Bay", BMNH 9.1.5.802, skull, young ♀, G. C. Shortridge no. 1631.
4. Tjilatjap, BMNH 9.1.5.804, skull, young ♀, G. C. Shortridge.
5. Madioen, E. Java, BMNH 40.619, skin and skull, subadult ♂, W. J. C. Frost no. 4.
6. Toeloeng Agoeng, RMNH 4982 and 4983, adult skulls, sex respectively unknown and ♂, E. Dubois 29-VIII-1941.
7. Tretes, E. Java, BMNH 40.620 and 40.621, skins and skulls, adults, ♂ and ♀, W. J. C. Frost 4-X-1938, nrs. 5 and 6, 3000 ft.
8. Rambipoedji Besoeki, E. Java, RMNH 19973, skull, adult, H. J. V. Sody 20-VI-1929, no. Z3.
— Java, RMNH 1282, skull, subadult ♂, Zoo Rotterdam 7-I-1924.
— Java, RMNH 1715 and 1721, skins and skulls, adults, ♀, C. Blazer Rotterdam, 5-XII-1928.
— RMNH 11813, skin and skull, subadult ♀.
— West-Java, RMNH 19968, skin and skull, adult, Diard 1864.
— West-Java, RMNH 19970, skin, Diard 1864.
— West-Java, RMNH 20014, skull, adult ♀, E. Jacobson 18-I-1938.
— Java, RMNH 19984 and 19985, skeletons, adult, Jentink's (1887: 232) *Acanthion javanicum* nrs. a and b.
— Java, RMNH 19960, skin with skull inside, Jentink's (1888: 103) *Acanthion javanicum* no. a.
— Java, RMNH 19986, 19987, 19988 and 19989, respectively a young skeleton, two young skulls and an adult skull, Jentink's (1887: 232) *Acanthion javanicum* nrs. c, e, f and g, N.A.M. Amsterdam 1872, Junghuhn 1864, unknown, and Van Raalten 1825.
— ZMB 8944, skull, adult.

Madura

9. Madura Island, N. E. Java, BMNH 40.618, skin and skull, young ♂, W. J. C. Frost 25-IX-1938, no. 3.

Bali

10. "Sendang", W-Bali, RMNH 19978, skull, young ♂, H. J. V. Sody 16-VII-1930, no. E45, HB = 455, T = 90, Hf = 73, E = 33 mm.
—, RMNH 19979, skull, adult ♂, H. J. V. Sody 16-VII-1930, no. E47, HB = 505, T = 80, Hf = 71, E = 32 mm.
—, RMNH 19980, skull, adult ♂, H. J. V. Sody 18-VII-1930, no. E59, HB = 500, T = 100, Hf = 74, E = 36 mm.
—, RMNH 19981, skull, adult ♀, H. J. V. Sody 21-VII-1930, no. E75, HB = 521, T = 124, Hf = 75, E = 34 mm.

Lombok

11. Lombok, Rindjani-Vulcan, SMF 4740, skin and skull, nearly adult, J. Elbert 26-V-1909, no. 3352, alt. 800 m.
—, SMF 4739, skin, J. Elbert.

Sumbawa

12. Soembawa, Soembawa, MZB 931, skull, subadult ♂, Berkholz III-1925.
13. Dompoe, Sumbawa, SMF 833, skin and skull, adult ♀, holotype of *Acanthion sumbawae* Schwarz, 1911, J. Elbert 24-XII-1909, no. 301.
14. Bima, Sumbawa, MZB 493, skull, adult, H. A. v. Meckl VII-1923.

Flores

15. Ruteng, Flores, RMNH 26825, skin and skull, adult ♂, J. A. J. Verheijen 26-I-1960.
16. Badiawa, Flores, BMNH 40.617, skin and skull, adult ♂, W. J. C. Frost no. 2, alt. 5100 ft.
—, BMNH 40.622, skin, ♂, HB = 450, T = 50, Hf = 75, E = 40 mm, alt. 5100 ft.
17. East Flores, Sika, RMNH 19969, damaged skin and parts of skull, H. ten Kate IX-1891.
—, Maumeri, ZMA 6871, skeleton and some spines, adult, P. Calon, don. M. Weber.
— “Baowac”, Flores, BMNH 40.616, skin and skull, adult ♀, W. J. C. Frost no. 1.

Tanah Djampea

18. Tanah Djampea, BMNH 40.623, skin and skull, young ♀, W. J. C. Frost, no. 10, HB = 430, T = 75, Hf = 55, E = 35 mm.

REVIEW OF THE FAMILY HYSTRICIDAE

Genus *Trichys* Günther, 1877

Genus *Atherurus* F. Cuvier, 1829

Genus *Hystrix* Linnaeus, 1758

Subgenus *Hystrix* Linnaeus, 1758

Subgenus *Acanthion* F. Cuvier, 1823

Subgenus *Thecurus* Lyon, 1907

Discussion. — Lyon (1907: 578 and 584) based his distinction of the subfamily “Hystricinae” from the subfamily “Atherurinae” principally on the possession of well developed dorsal quills in the former group. This argument is invalid, however, because clearly developed quills are always present in the African Brush-tailed Porcupine, *Atherurus africanus* Gray, 1842. A second character mentioned by Lyon was the number of four sacral vertebrae in the “Hystricinae” against three in the “Atherurinae”. In point

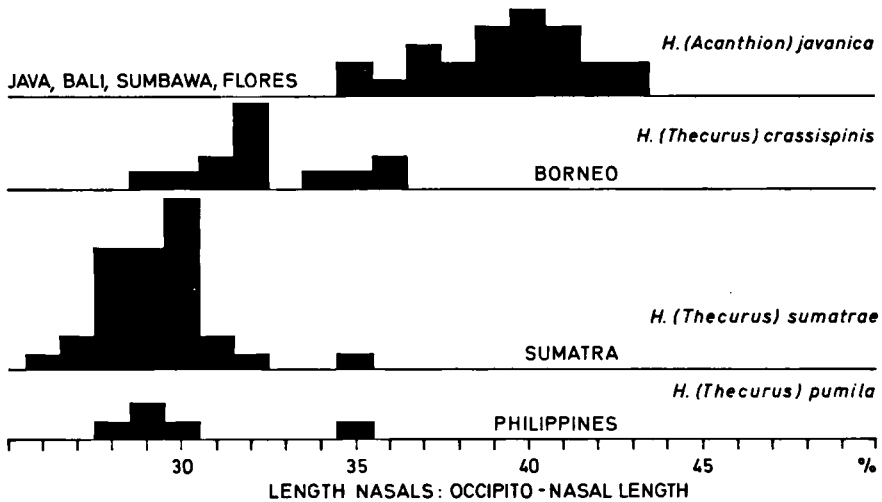


Fig. 3. Frequency distribution of the relative length of the nasals of three species of the subgenus *Thecurus*: *H. pumila*, *H. sumatrae* and *H. crassispinis*, and one species of the subgenus *Acanthion*: *H. javanica*, expressed as a percentage of the occipito-nasal length of the skull. Adult specimens only.

of fact four were found in seven specimens studied of the subgenus *Acanthion* but in eight specimens of the subgenus *Thecurus* I found four skeletons with four sacral vertebrae and four with three sacral vertebrae. Another diagnostic character, according to Lyon (1907), was the presence of rootless, hypsodont molars in the "Hystricinae" and rooted, brachyodont molars in the "Atherurinae". There are, indeed, clear differences between the molars in the genera *Atherurus* and *Hystrix* but not in such an absolute sense as stated by Lyon, for all porcupine molars have smaller or larger roots. The deciduous premolars of *Hystrix* always show visible roots whereas in many specimens of the genus *Atherurus* the roots of molars in place are invisible. From the foregoing it may be evident that the morphological break between the long-tailed and short-tailed porcupines is less obvious than presented in Lyon's diagnoses (1907: 578 and 584). Ellerman (1940: 198) stated already that there appear to be too many essential characters common to those groups, such as the structure of the feet, the pattern of the cheekteeth and other cranial characters, for this division to be maintained.

Lyon's division of the family into subfamilies was prompted by the far smaller differences between the short-tailed genera recognized by him (*Thecurus*, *Acanthion* and *Hystrix*), than between these and the remaining genera (*Atherurus* and *Trichys*). Consequently, if it is demonstrated that there are insufficient grounds for the division of the short-tailed porcupines into separate genera, as will be done below, no arguments are left for the division of the family into subfamilies.

The diagnostic characters used by Lyon (1907) for his genus *Thecurus* are discussed here successively. According to him its body size is about half that

of *Acanthion*, but *H. (Thecurus) crassispinis* with a mean length of head and body of 610 mm (range 550—665, n = 6) is even larger than *H. (Acanthion) javanica* with 537 mm (500—600, n = 11). He also stated that the quills were shorter and much less numerous than those of *Acanthion* (Lyon 1907: 582) but this does not hold good, either, when *H. crassispinis* is compared with *H. javanica*. The peculiar “tri-prismatic” neural spine on the axis as described by Lyon (1907: 582), is quite an individual feature of the single *H. sumatrae* skeleton studied by him, since in other specimens this spine is as much laterally compressed as in *Acanthion*. The skeletons available of the subgenera *Thecurus* and *Acanthion* cannot be distinguished on this character, which is also the case with respect to the form of the seventh cervical vertebra as described by Lyon. Apparently, the individual variation in these features is so large that they are of no use for diagnostic purposes. Lyon stated that *Thecurus* was cranially very similar to *Atherurus*, and Ellerman (1940: 209) mentioned its short nasals, which he found were even smaller than the frontals. The latter statement holds true for *H. sumatrae* but not for four out of fifteen measurements in our series of *H. crassispinis*. The relative length of the nasals as a percentage of the occipito-nasal length presented here, show that the nasals of *H. sumatrae* are not much longer, it is true, than those of *Atherurus macrourus*, but also that in this respect *H. crassispinis* to a certain extent bridges the gap between *H. sumatrae* and *H. javanica* and that there is even a slight overlap (see also figure 3):

	mean	range	n	s
<i>Atherurus macrourus</i>	28.6 %	24.4—31.7 %	50	1.54
<i>H. (Thecurus) sumatrae</i>	29.4 %	26.1—35.0 %	31	1.71
<i>H. (Thecurus) crassispinis</i>	32.4 %	28.6—35.9 %	13	2.20
<i>H. (Acanthion) javanica</i>	39.4 %	34.6—43.1 %	25	2.39

Ellerman’s statement (1940: 209): “skull appearing flatter than in any *Hystrix* seen”, can be tested with our relative height measurement (height as percentage of the basilar length):

<i>H. crassispinis</i>	36.8 %	35.5—38.4 %	13	0.93
<i>H. javanica</i>	40.8 %	37.4—45.8 %	25	2.42

Obviously, the means of these two species differ significantly, but there is a clear overlap, so from Ellerman’s statement it cannot be inferred that the *Thecurus* skull is always lower than that of *Acanthion*. Ellerman (1940: 209) also stated that *Thecurus*: “is not very well separated from the smaller species of *Hystrix* like *javanicum*”, and, in the discussion about the (sub-)generic status of *Acanthion* (1940: 213): “It is quite clear that on nasal structure alone this genus will not divide into two”. Starting from these statements, I cannot but conclude from the evidence presented above, that in my opinion the generic status of “*Thecurus*” is based on quite insufficient arguments.

Consequently I will not accord it a higher taxonomic rank than that of a subgenus.

In the introduction to the present paper the acceptance of a subgeneric rank of "*Acanthion*" has already been mentioned. Summarizing, it is possible to conclude from what has been adduced in this paper that the most balanced division of the family Hystricidae is the recognition of three genera, *Trichys* Günther, 1879, *Atherurus* F. Cuvier, 1829 and *Hystrix* Linnaeus, 1758, without division into subfamilies.

Key to the genera and subgenera:

- 1 a. Tail long, one quarter to half the length of head and body, without rattle-quills; molars less high-crowned, in most cases showing roots when in place: 4
- b. Tail short, less than one fifth of head and body length, bearing a cluster of rattle-quills at its end; molars high-crowned, permanent molars not showing roots when in place: 2, Genus *Hystrix*
- 2 a. Quills with more than one blackish ring: Subgenus *Hystrix*
- b. Quills with only one blackish ring: 3
- 3 a. Number of tail vertebrae about 17 to 19, length of the nasals 26 to 36 percent of the occipito-nasal length, breadth of the nasals less than 32 percent of the zygomatic breadth: Subgenus *Thecurus*
- b. Number of tail vertebrae about 15 to 16, length of the nasals nearly always larger than 36 percent of the occipito-nasal length, breadth of the nasals always larger than 33 percent of the zygomatic breadth: Subgenus *Acanthion*
- 4 a. Tail half the length of head and body, bearing a cluster of flattened bristles without expansions and contractions at its end; skull with a well-marked postorbital process and interorbital constriction, prominent horizontal groove on the surface of the jugal: Genus *Trichys*
- b. Tail one quarter to half the length of head and body, bearing a cluster of alternately expanded and contracted bristles at its end; skull without, or with scarcely marked, postorbital process and little orbital constriction, jugal without horizontal groove: Genus *Atherurus*

TAXONOMY OF THE GENUS *Hystrix*

- Hystrix* Linnaeus, 1758: 56.
- Acanthion* F. Cuvier, 1823: 425. Valid as a subgenus.
- Oedocephalus* Gray, 1866: 308.
- Acanthochoerus* Gray, 1866: 309.
- Thecurus* Lyon, 1907: 582. Valid as a subgenus.

Type species. — *Hystrix cristata* Linnaeus, 1758 by subsequent designation (Sclater 1901: 89). Linnaean tautonomy, as suggested by Thomas (1911: 144) and Delany (1975: 111), does not apply here because the conditions of the Code article 68D(i) are not fulfilled.

Range. — Africa, Italy, Southern Palearctic region and Oriental Asia.

Diagnosis. — Porcupines with short tail, less than one fifth of head and body length, bearing a cluster of rattle-quills at its end. Molars high-crowned, permanent molars not showing roots when in place.

Subgenus *Hystrix* Linnaeus, 1758

For this extralimital subgenus the taxonomy of Corbet & Jones (1965) is presented here.

***Hystrix cristata* Linnaeus, 1758**

Hystrix cristata Linnaeus, 1758: 56.

Synonyms. — For synonymy see Corbet & Jones (1965: 296) and Ellerman (1940: 219—220).

Type locality. — Asia, restricted to Rome by Thomas (1911: 144).

Range. — Italy, North, West, Northeast and East Africa, in Tanganyika sympatric with *Hystrix africae australis* Peters, 1852.

Diagnosis. — Nasals long, over 57 percent of the occipito-nasal length, frontal: nasal ratio 23—38 percent; premaxillae of medium width, less than 40 percent of the nasal width; hairs of crest predominantly white; rattle-quills short, usually under 50 mm, and slender; midline of the rump black or mottled.

***Hystrix africae australis* Peters, 1852**

Hystrix africae australis Peters, 1852: 170.

Synonyms. — For synonymy see Corbet & Jones (1965: 295) and Ellerman (1940: 219).

Type locality. — Querimba coast and Tete, Mozambique.

Range. — South, Southwest, Central and East Africa, in Tanganyika sympatric with *Hystrix cristata* Linnaeus, 1758.

Diagnosis. — Nasals of medium length, 51 to 58 percent of the occipito-nasal length, frontal: nasal ratio 49 to 68 percent; premaxillae narrow, less than 23 percent of the nasal width; hairs of crest predominantly white; rattle-quills long, usually over 60 mm, and white; tail entirely white below; mid-line of rump white.

***Hystrix indica* Kerr, 1792**

Hystrix indica Kerr, 1792: 213.

Synonyms. — For synonyms see Corbet & Jones (1965: 297) and Ellerman & Morrison-Scott (1951: 519—520).

Type locality. — India.

Range. — Corbet and Jones (1965) studied specimens from Turkey, Irak, Iran, Aden, Pakistan, India and Ceylon. Ellerman & Morrison-Scott (1951) also mentioned Palestine, Syria, Transcaucasia, Southern and Eastern Russian Turkestan, Kashmir and Nepal.

Diagnosis. — Nasals short, under 57 percent of the occipito-nasal length, frontal: nasal ratio 45 to 70 percent; premaxillae wide, over 44 percent of the nasal width; hairs of crest entirely or predominantly brown; rattle-quills short and wide, shorter than 60 mm; mid-line of rump white.

Remarks. — Corbet & Jones (1965) had available only five specimens from Southwest Asia (Iran, Irak, Turkey and Aden) to determine any evidence for clinal variation in the specific characters of the North African and Asiatic *Hystrix* forms. A study of four other specimens from this intervening zone (Palestine, Iran and the Caucasus) enabled me to verify their provisional conclusions. The data about Corbet & Jones' samples given here, are taken from their histograms (1965: figs. 5, 6 and 8).

The ratio of nasal to occipito-nasal length in Corbet & Jones' Southwest Asiatic specimens (48—50 %) did not show an approach to the North African condition (58—68 %), and the same is seen in our measurements (46—51%).

Corbet & Jones stated that the data about the relation of frontal to nasal length of their Southwest Asiatic specimens (61—66%) did not show a tendency towards convergent clinal variation between *H. cristata* (23—40%) and *H. indica* (45—70%), and our measurements (55—78%) are quite in agreement with this statement.

The range in the relative width of the nasals (greatest width as a percentage of the length of the nasals) in Corbet & Jones' Southwestern Asiatic specimens (56—63%) is quite the same as in our series of four specimens (56—62.5%).

Corbet & Jones' measurements of the width of the premaxilla of their Southwest Asiatic sample (45—58% of the greatest breadth of the nasals), is intermediate between *H. cristata* (19—36%) and the East Asiatic *H. indica* sample (57—78%). Our measurements (50—66%) reduce the difference between the Western Asiatic and the Indian sample.

One of the cranial characters of *H. indica* and *H. cristata* with different means but with a clear overlap, is the height of the skull (respectively 37—46% and 41—52% of the occipito-nasal length). Both Corbet & Jones' and our own Southwest Asiatic sample average rather low (respectively 38—42% and 38—40%), and they cannot be said to be "in any way intermediate between the Indian and African groups".

Summarizing it can be stated that Corbet & Jones' conclusion, that *H. indica* should be considered specifically distinct from the African species, is confirmed by our observations.

Subgenus *Acanthion* F. Cuvier, 1823

Type species. — *Acanthion javanicum* F. Cuvier, 1823 by original designation.

Range. — Nepal, Eastern India, Bangla-Desh (?), Burma, Southern China, Hainan, Thailand, Laos, Vietnam, Malay Peninsula, Sumatra, Borneo, Java and some of the Lesser Sunda Islands.

Diagnosis. — Spiny covering less specialized than in the nominal subgenus. Only quills with one dark ring or dark apical part, no many-ringed quills as in *Hystrix* s.s. Differs from the subgenus *Thecurus* in the larger nasals, nearly always longer than 36% of the occipito-nasal length (range 35—60%) against 26—36% in *Thecurus*, always broader than 33% of the zygomatic breadth against 22—32% in *Thecurus*.

Remarks. — In the introduction of the present paper the acceptance of the subgeneric rank of *Acanthion* by a number of authors has already been mentioned. Yong (1973) studied the karyotype of a specimen of *Hystrix (Acanthion) brachyura* Linnaeus, 1758 and found a diploid number of 66, the same as reported by Wurster *et al.* (1971) for *Hystrix cristata*, thus supporting the taxonomic unity of these groups.

Hystrix brachyura Linnaeus, 1758

Hystrix brachyura Linnaeus, 1758: 57.

Hystrix longicauda Marsden, 1811: 118.

Acanthion hodgsoni Gray, June 1847: 101. Valid as a subspecies.

Hystrix alophus Hodgson, August 1847: 771.

Hystrix bengalensis Blyth, 1851: 170.

Acanthochoerus grotei Gray, 1886: 310.

Hystrix subcristata Swinhoe, 1870: 638. Valid as a subspecies.

Hystrix mülleri Marshall in Sclater, 1871: 235.

Hystrix yunnanensis Anderson, 1878: 332.

Acanthion klossi Thomas, 1916: 139.

Acanthion millsi Thomas, 1922: 431.

Acanthion subcristatus papae G. M. Allen, 1927: 3.

Distribution. — Specimens examined from Nepal, Eastern India, Bangla-Desh (?), Burma, Southern China, Hainan, Thailand, Laos, Vietnam, Malay Peninsula, Sumatra, Borneo and the Malay islands Pinang and Singapore.

Diagnosis. — Larger, on an average, than *H. javanica*, another species in this subgenus. The occipito-nasal length varies from 116 to 148 mm ($n = 64$) against 103 to 127 mm ($n = 25$) in *H. javanica*. The nasals are larger on an average; the relative length is 41—60% of the occipito-nasal length against 35—43% in *H. javanica*; the relative breadth is 37—62% of the zygomatic breadth against 33—46% in *H. javanica*. The crest of hairs on the head and nape of the neck varies from just perceptible to quite well developed, differing in this respect from *H. javanica* which does not show a trace of a crest. The spines of back, shoulders and sides are brown without white tips,

Table I. Cranial measurements in millimetres of adult specimens of *Hystrix brachyura* from geographical areas as distinguished in the present study with range, mean of the sample in parenthesis, number of measurements (n) and the standard deviation (s). For the definitions of the measurements see Material and methods.

	Sumatra	Borneo	Malay Peninsula	Tenasserim-Thailand	Vietnam
Occ. nas. I.	126.7—137.9 (132.7) n = 21 s = 3.03	123.1—131.8 (128.8) n = 4	130.5—137.0 (135.0) n = 6 s = 3.76	131.8—146.0 (139.2) n = 6 s = 4.75	117.7
Basilar I.	104.0—117.3 (110.9) n = 21 s = 3.64	101.1—116.1 (107.5) n = 4	106.5—116.5 (112.6) n = 6 s = 3.85	114.3—121.8 (118.0) n = 6 s = 2.89	95.6
L. nasals	51.0—63.0 (57.2) n = 21 s = 2.88	53.7—62.5 (58.5) n = 4	57.0—63.0 (59.3) n = 6 s = 2.10	71.0—79.5 (74.0) n = 6 s = 3.29	59
L. frontals	35.0—43.6 (38.8) n = 14 s = 2.79	34.3—36.5 (35.3) n = 3	35.3—41.0 (38.5) n = 6 s = 2.43	27.0—35.3 (31.8) n = 6 s = 3.09	29
Palatal I.	63.8—72.2 (68.0) n = 19 s = 2.44	63.9—69.3 (66.7) n = 4	63.1—71.0 (68.1) n = 6 s = 2.90	70.4—78.8 (75.5) n = 7 s = 3.00	61.2
L. diastema	31.2—38.0 (35.1) n = 19 s = 1.84	34.2—38.1 (35.0) n = 4	34.2—38.2 (36.2) n = 6 s = 1.65	35.7—40.6 (38.1) n = 7 s = 1.69	30.0
Br. nas. post.	23.8—29.0 (26.8) n = 21 s = 1.62	26.7—27.6 (27.1) n = 4	25.6—31.7 (28.5) n = 6 s = 2.31	35.6—42.3 (38.4) n = 6 s = 2.38	30.2
Postorb. br.	39.0—46.5 (42.1) n = 19 s = 1.94	43.3—46.4 (44.1) n = 4	43.2—47.4 (45.2) n = 5 s = 1.67	41.7—48.4 (45.4) n = 6 s = 3.17	38.7
Zygom. br.	63.4—72.5 (67.0) n = 21 s = 2.26	64.0—69.7 (65.9) n = 4	65.0—71.6 (67.8) n = 6 s = 3.03	69.4—75.0 (73.1) n = 6 s = 2.08	62.4
Height sk.	40.3—49.1 (44.8) n = 21 s = 1.93	42.4—45.6 (44.0) n = 4	46.0—50.4 (47.8) n = 6 s = 1.45	49.0—56.0 (51.5) n = 6 s = 2.47	45.0
L. mandible	84.5—92.6 (88.1) n = 17 s = 2.51	82.0—90.0 (85.3) n = 4	85.3—90.6 (88.8) n = 6 s = 1.84	85.0—99.7 (93.4) n = 7 s = 5.18	79.0
H. mandible	36.0—40.9 (38.7) n = 18 s = 1.45	35.6—40.8 (37.7) n = 4	35.4—42.8 (38.1) n = 6 s = 2.77	35.6—42.7 (39.2) n = 7 s = 2.93	—
Alv. P4—M3	22.2—30.0 (26.5) n = 19 s = 2.12	22.4—26.2 (24.1) n = 3	24.6—28.9 (27.5) n = 5 s = 1.69	29.4—31.8 (30.8) n = 6 s = 1.09	23.0
Alv. p4—m3	22.8—30.6 (27.7) n = 20 s = 2.10	24.3—26.4 n = 2	27.0—29.5 (28.4) n = 5 s = 0.97	29.5—33.5 (31.6) n = 7 s = 1.38	25.8

	East India-North Burma			Sub-Himalayas			Hainan			China		
	Mean	s	n	Mean	s	n	Mean	s	n	Mean	s	n
Occ. nas. l.	125.3—136.0 (131.6)	4.45	n = 7	115.7—118.1 (117.1)	1.09	n = 5	118.1—130.7 (122.0)		n = 4	129.2—140.5 (132.7)	4.48	n = 9
Basilar l.	110.4—115.3 (112.5)		n = 4	99.0—102.1 (100.8)		n = 5	99.5—110.7 (102.8)		n = 4	104.7—119.0 (113.8)		n = 9
L. nasals	65.5—77.0 (71.1)	3.79	n = 7	60.3—64.0 (62.7)	1.83	n = 5	63.7—74.0 (68.0)		n = 4	72.6—80.0 (76.0)	2.30	n = 10
L. frontals	25.2—33.3 (30.6)		n = 7	21.0—24.5 (22.7)		n = 3	24.7—33.4 (28.4)		n = 4	23.3—32.3 (29.0)	2.57	n = 10
Palatal l.	70.0—73.2 (71.4)	1.35	n = 7	58.5—64.5 (62.2)	2.22	n = 5	61.5—71.2 (64.6)		n = 4	66.0—79.3 (73.3)	3.79	n = 10
L. diastema	34.3—36.4 (35.3)	0.81	n = 7	30.5—33.2 (31.5)	1.10	n = 5	29.2—33.5 (31.3)		n = 4	31.5—38.0 (35.4)	2.20	n = 10
Br. nas. post.	37.6—42.9 (39.5)	2.35	n = 7	31.7—38.8 (34.3)	3.04	n = 5	34.7—39.3 (36.7)		n = 4	36.1—41.8 (39.7)	2.00	n = 10
Postorb. br.	45.2—48.4 (46.8)	1.22	n = 7	37.7—39.8 (38.8)	0.77	n = 5	42.3—44.8 (43.4)		n = 4	43.4—50.0 (46.8)	2.12	n = 10
Zygom. br.	68.6—74.2 (70.5)	2.28	n = 6	60.4—63.5 (62.0)	1.32	n = 5	62.5—63.7 (63.2)		n = 4	67.2—72.3 (70.7)	1.81	n = 10
Height sk.	47.7—53.5 (50.8)	2.33	n = 7	40.5—42.5 (41.3)	0.86	n = 5	45.7—49.3 (45.7)		n = 4	50.4—54.6 (52.3)	1.48	n = 10
L. mandible	85.0—90.6 (87.2)	1.89	n = 7	75.1—78.8 (77.3)		n = 4	74.9—85.7 (79.8)		n = 4	85.5—97.8 (91.4)	4.00	n = 10
H. mandible	34.0—40.8 (38.4)	2.54	n = 6	30.7—32.7 (31.6)		n = 4	31.5—34.7 (33.2)		n = 4	36.1—43.4 (38.7)	2.33	n = 8
Alv. P4—M3	25.3—31.7 (28.4)	1.94	n = 7	23.4—27.8 (25.9)	1.70	n = 5	27.7—29.7 (28.7)		n = 4	26.6—31.3 (28.5)	1.60	n = 9
Alv. p4—m3	29.0—33.7 (30.0)	1.65	n = 7	24.6—28.1 (26.6)		n = 4	28.0—28.8 (28.3)		n = 3	26.4—33.4 (29.6)	2.46	n = 9

whereas the *H. javanica* skins make a speckled impression because of the distinctly white-tipped spines. The quills, tactile bristles and caudal rattle-quills are as a rule larger than in *H. javanica*.

Infra-specific variation

In the tables I and II and in the histograms of the figures 4 to 7, information is presented about the individual and geographical variation within this species. For these tables and figures nine geographical areas are distinguished, chosen on the basis of distances, geographical barriers and observed morphological differences of the samples. The localities in these areas are plotted on the map of figure 1 and are indicated with numbers corresponding to those in the list of specimens examined. In the histograms of the figures 4 to 7, four cranial characters are compared of mainly adult and some subadult specimens, which successively will be discussed below. The dimensions of the skulls of some subadult specimens in the largest sample from a limited geographical area, that from Sumatra, are not much smaller than the adult ones and fall within their range of variation. This is connected with the criteria for these age-classes and with the fact that the deciduous premolar is shed relatively late in life. Hence, we may assume that subadult specimens in other samples too, do not differ very much from adult ones. In table I fourteen cranial measurements of merely adult specimens are presented, and in table II data about the spiny covering of adult or probably adult, and some subadult specimens are given, which will be discussed below as well.

Occipito-nasal length. — From figure 4 it appears that the populations from the Malay Peninsula, Sumatra and Borneo have about the same skull length and show an essential overlap with the specimens from Tenasserim, Thailand and Laos which are on an average larger. The sample from the westernmost area, East India and North Burma, averages only slightly lower than those from the Malay Peninsula and China. The sample from Hainan averages clearly lower than that from continental China, but the Sub-Himalayan and Vietnamese specimens are still more distinguished by their small size. The largest skull of the total material studied is that of a subadult specimen (MNH 1873—63) from “Shen-si méridional”, China, the northernmost locality of this subgenus. Its occipito-nasal length of 148.5 mm seems to be an extreme value in the series from China. The principal conclusion derived from these data is that there seems to be a quite random distribution of the skull sizes of the several populations over the total geographical range.

Nasal length. — The relative length of the nasals, expressed as a percentage of the occipito-nasal length and presented in the histogram of figure 5, shows that the populations from the Malay Peninsula, Sumatra and Borneo form a unity with respect to this character. Their length does not exceed 48% of the occipito-nasal length (range 39.5—48.0%) whereas in nearly all continental specimens the nasals are longer than 49% of the

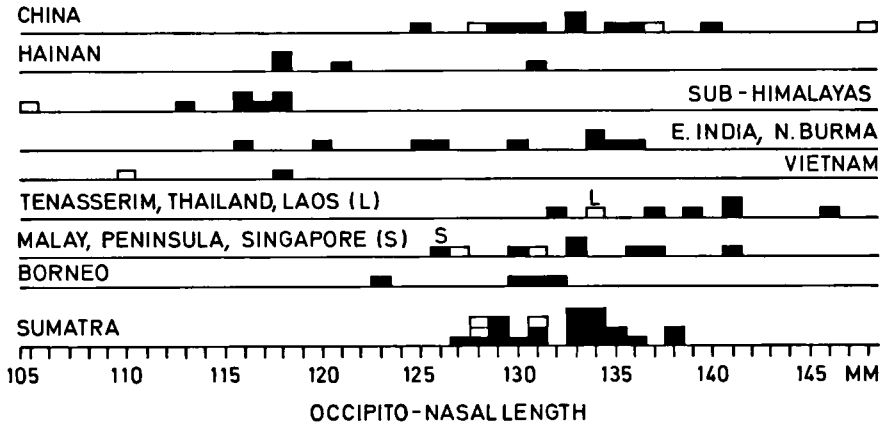


Fig. 4. Frequency distribution of the occipito-nasal length of the skulls of *Hystrix brachyura*. Solid rectangles represent adult, open rectangles subadult specimens.

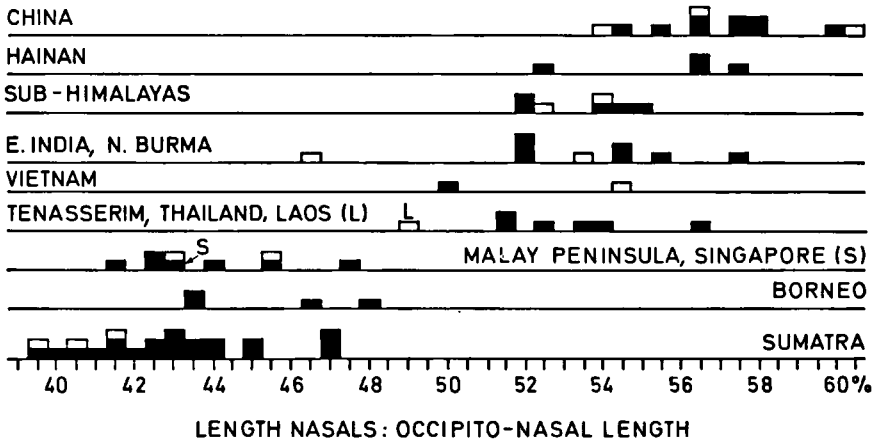


Fig. 5. Frequency distribution of the relative length of the nasals of *Hystrix brachyura*, expressed as a percentage of the occipito-nasal length. Solid rectangles represent adult, open rectangles subadult specimens.

occipito-nasal length (range 50.0—60.0%). On this cranial character only, these populations were regarded a valid species by Ellerman (1940: 214) under the name *H. brachyura*, together with *H. javanica* forming the “short-nasal group” of this author. However, clear external differences between these two forms on the one hand, and external similarities between the Malayan and continental populations on the other hand will be shown in the present paper. Other specimens with comparatively short nasals in figure 5 are a subadult specimen from the former Bengal Presidency in India, with 46.5% being within the range of variation of the Malayan sample, and a subadult specimen from Laos with 49.1%. Not inserted in this histogram is the relative nasal length of 40.3% of a young specimen from Nahrang,

Table II. Measurements in millimetres of some dimensions of the quills, tactile bristles, rattle quills and hairs of the crest of *Hystrix brachyura*, and some data about the presence of quills with black tips, presence of transitional quills and development of the crest. For the definitions of the measurements see Material and methods.

	Sumatra (n = 7)	Borneo (n = 2)	Malay Peninsula (n = 6)	Tenasserim- Thailand-Laos (n = 5)	Hainan (n = 3)	China (n = 6)	Nepal-Sikkim (n = 7)
QUILLS							
diameter	4.9-6.6 5.7	5.7-6.1	5.7-6.6 6.3	6.1-7.3 6.8	5.2-6.4 5.7	5.7-6.7 6.3	4.5-5.6 4.9
length	155-190 177	160-185	180-233 197	170-210 197	155-180 170	175-220 201	105-190 139
black rings	25-35	16-25	25-75	30-90	45-75	50-90	40-75
black tips	none or few	none	none or few	few -50%	50% or more	few -50% or more	50% or more
TACTILE BRISTLE							
length	190-240 212	180-270	185-320 247	220-320 282	200-350 273	270-340 312	165-350 222
TRANSITIONAL QUILLS	none	none	none or few	present	present	present	present
RATTLE-QUILLS							
diameter	4.4-5.3 5.1	6.5-7.2	5.4-6.3 5.8	6.5-7.2 6.8	5.8-6.5 6.2	6.5-7.7 7.2	4.1-5.2 4.6
length	20-24 22.5	31-35	20-28 25.6	23-27 24.8	20-27 23	25-34 28.2	16-19 17.2
CREST							
length hairs	55-63	50-65	45-165	110-155	100-150	85-230	55-110
white tips	5-27	8-20	25-85	70-110	30-90	55-150	10-55
development	rudimental	rudimental	rudimental to clear	clear	clear	clear to conspicuous	rudimental

Vietnam. Progressive enlargement of the nasal bones must be taken into account, but comparison with young specimens of the sample from Sumatra shows that its nasals have about the same relative length, so rather small for a continental specimen. Quite anomalous is the relative nasal length (38%) of the skull of the holotype (see figure 17) of *H. yunnanensis* Anderson, 1878 from Yunnan, China. The nasal length of this young individual is not inserted in figure 5 and this puzzling form will be discussed below. The specimen with the longest nasals is the subadult one from the northernmost locality, Shensi, China, mentioned above.

Breadth nasals. — Figure 6 shows that the relative breadth of the nasals of the populations of the Malay Peninsula, Sumatra and Borneo is nearly always smaller than 46% of the zygomatic breadth of the skull (range 37—46%) and that the remaining populations have the nasals larger than 46% of the zygomatic breadth (range 47—64%) with mean differences and considerable overlaps.

Height of the skull. — This dimension is expressed in figure 7 as a percentage of the basilar length. The Sumatran sample averages clearly lowest but its range still includes the Bornean and Malayan specimens. The small number of Himalayan specimens averages much lower than the Chinese sample which has the highest skulls and it averages also clearly lower than the East Indian and Northern Burmese specimens whose localities are relatively near to those of the Himalayan specimens.

Body size. — The few body size measurements available correspond with the differences in skull size already noticed. The largest specimens studied are from Trong, Peninsular Thailand (HB = 710 mm, Wt = 27 lbs), Tenasserim (HB = 725 mm, Wt = 29 lbs), Thailand (Tot. l. = 850 mm) and Laos (Tot. l. = 830 mm). The specimens from Sumatra and Borneo vary from 540 to 630 mm head and body length (n = 10).

Quill size. — In table II, data of six skins from the Malay Peninsula are given. Two of them are from Jalor (locality nr. 4) and one of these two (BMNH 3.2.6.74) is quite different from the other five. This specimen has quills with lengths up to 233 mm, the other five from 180 to 200 mm. Other characters in which it is much like the continental forms will be discussed below.

The quills of the specimens from Tenasserim, Thailand and Laos (n = 5) are relatively large. The longest quill in the four specimens from Tenasserim and Thailand have a length of 200—210 mm and diameters of 6.8—7.3 mm, which is about as long as in the Chinese sample, but clearly thicker. The quills of the form from Nepal and Sikkim clearly show the lowest development.

Colouration of quills. — Unlike the continental forms, the skins of the specimens from Sumatra, Borneo and some of the Malay Peninsula can be

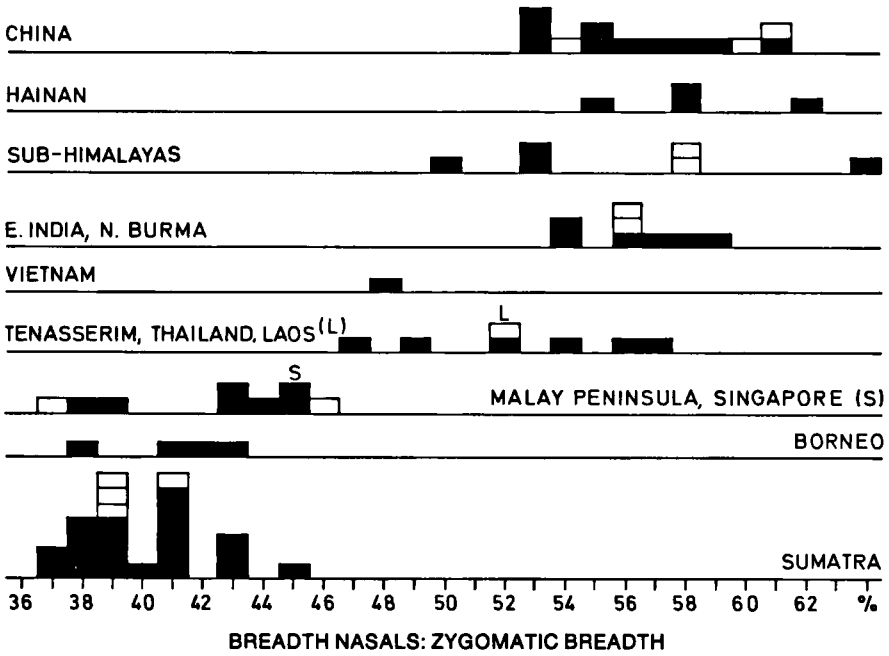


Fig. 6. Frequency distribution of the relative breadth of the nasals of *Hystrix brachyura*, expressed as a percentage of the zygomatic breadth. Solid rectangles represent adult, open rectangles subadult specimens.

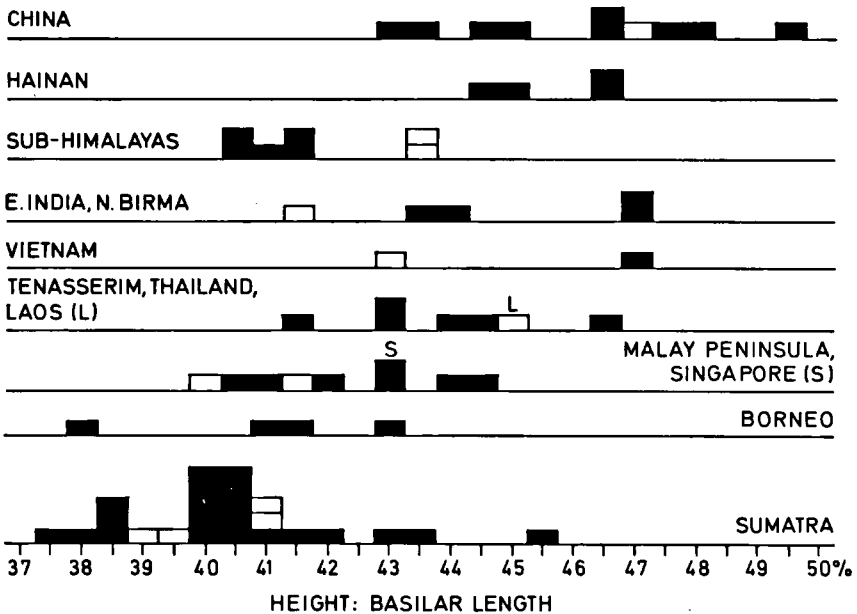


Fig. 7. Frequency distribution of the relative height of the skulls of *Hystrix brachyura*, expressed as a percentage of the basilar length. Solid rectangles represent adult, open rectangles subadult specimens.

easily described. Nearly all the large quills are white with a small blackish ring about midlength of 20 to 35 mm length, the white apical halves with a maximal length of 70 to 110 mm (figure 11-left). One of the two Peninsular specimens from Jalor, locality nr. 4 (figure 11-right), has blackish rings from 20 to 75 mm which are broader on an average, and, covered by the superficially situated white-tipped quills, a number of quills with a blackish part to the tip up to 95 mm length. In these respects, and in others discussed below, this specimen closely resembles the continental forms. The two Peninsular specimens from Trong (locality nr. 5) are much like the more southern specimens in respect of the small length of the blackish rings on the quills (25—30 mm), but resemble the continental forms, just as the Jalor specimen, as to the possession of a number of quills with black tips of 40 to 45 mm. The two specimens examined from Tenasserim possess black rings from 25 to 45 mm length, see figure 12-left for the one from Champang (locality nr. 18). They have some quills with black tips up to 60 mm but the majority of the quills have white tips. This also holds good for the specimen from Southeast Thailand (locality nr. 21), but the skin from West Thailand (locality nr. 22) and that from Laos (locality nr. 24) have about as many quills with a black tip as white-tipped ones. In the samples from the remaining areas a number of black-tipped quills is also found, varying from clearly less than fifty percent of the large quills of a skin to predominance of the black-tipped ones. The skin in figure 12-right from Anhui, China (locality nr. 32) gives a darker impression than the one to the left from Tenasserim, because the former has quills with a blackish ring of 25 to 90 mm and about as many quills with a black tip as white-tipped ones. One of the six Chinese skins studied, that from Wanh sien (locality nr. 35), is rather light because most of the rings are relatively short (30—40 mm) and most of the quills have white tips, whereas a specimen from Kiang-Si (locality nr. 34) is very dark with most of the quills having a black extremity up to 100 mm long. The photograph of figure 13 shows a specimen from Sikkim (locality nr. 45) having short (maximal 115 mm) and thin (maximal 4.5 mm) quills with small black rings (maximal 40 mm) and roughly as many quills with black extremity as with a white tip (maximal 25 mm), which is more or less representative of most of the seven skins from the sub-Himalayan region that were studied. The photograph of figure 14 represents a specimen from Hathiban, Nepal (locality nr. 46) which illustrates the enormous individual variation in these forms, having thicker (5.6 mm) and longer (190 mm) quills with broader black rings (65 mm) and longer white tips (55 mm). The latter skin, with the exception of the quite rudimental crest, is very much like a small version of a Chinese or Thai form. The large number of tactile bristles of this Nepalese specimen, also contributes to this impression.

Tactile bristles. — In the skins from Sumatra, Borneo and in five of the six specimens from the Malay Peninsula (locality nrs. 1—5) the maximal length of these bristles varies from 180 to 285 mm. In the sixth Peninsular

specimen, that one from Jalor (locality nr. 4) discussed before, a length of 320 mm is attained as is the case in a specimen from Tenasserim and one from Thailand. The longest bristle (350 mm) is measured in the specimen from Hathiban (photograph figure 14) discussed before and also in one from Hainan, that is in the smaller forms of this species. In the skins studied, the roughly estimated number of tactile bristles with greater length than the quills varies in all samples from one or two to some ten or more. Of the Peninsular animals, the specimen from Jalor (figure 11-right) has the largest number of tactile bristles (10—15), about the same number as in the Tenasserim specimens. In the specimen from Hathiban (figure 14) about twenty tactile bristles are found and in the Chinese specimens up to about thirty.

Transitional quills. — These are wanting in the Sumatran, Bornean and some Malayan specimens, a few can be found in the more northern specimens of the Malay Peninsula (locality nrs. 4 and 5) and considerably more occur in most specimens of all other areas, sometimes as many as there are tactile bristles.

Rattle-quills. — From table II it appears that the diameter of the rattle-quills averages lowest in the sample from Nepal and Sikkim and that in this sample they are always shorter than in any other population. The dimensions of the rattle-quills of two adult specimens from Borneo are, with the exception of two Chinese specimens, the largest in this species. That of a third, subadult specimen from Borneo is equally large (6.6 mm thick and 32 mm long).

Crest. — The conspicuousness of the crest of hairs on the head and nape of the neck depends on the length of these hairs, on the length of their white terminal parts, and is particularly determined by the frequency of the hairs. Measurements of the first two features are presented in table II, and the degree of development of the crest is subjectively qualified with the terms "rudimental", "clear" and "conspicuous". A crest qualified "conspicuous", for example that of figure 12-right, however, does not possess crest hairs in such great masses and as long as in specimens of the subgenus *Hystrix* where they reach a length of 350 mm and probably longer. In this character too, the Peninsular specimen from Jalor (figure 12-right) resembles part of the continental forms. Its longest hair measures 165 mm with a 85 mm long white tip, against hairs of 45—70 mm with white tips of 25—35 mm in the remaining five Peninsular specimens.

The status of taxa and populations

Although some clearly different populations can be recognized, the whole of the material available to study this species with its extreme divergence as to all its characters, is so scanty and taken from such widely scattered localities that full subspecific distinction is unwarranted. The morphological and

geographical limits of the recognizable populations cannot sufficiently be established and the nomenclatorial recognition of other populations seems to be necessary. However, the data available strongly suggest that many differences may be likely to be bridged by intergrading forms when specimens from intermediate localities will become available, and in this situation I reject the naming of new taxa. Within the limitations of these considerations and in the light of the preceding results the status of taxa and populations will be established.

***Hystrix brachyura brachyura* Linnaeus, 1758**

Hystrix brachyura Linnaeus, 1758: 57. Malacca.

Hystrix longicauda Marsden, 1811: 118. Sumatra.

Acanthochoerus grotei Gray, 1866: 310. Malacca.

Hystrix mülleri Marshall in Sclater, 1871: 235. Sumatra.

Type. — No type designated.

Type locality. — Malacca, based on Linnaeus' reference to Seba (1734): "Porcus aculeatus s. *Hystrix malaccensis*. *Seb. mus.* I p. 81. t. 51. f. 1.", also the type locality of *Acanthochoerus grotei* Gray after Sclater's (1871: 234) restriction: "... received from Malacca, having procured for Mr. Grote from the jungles of that settlement...".

Distribution. — Malay Peninsula, Malay islands Pinang and Singapore, Sumatra, Borneo. The localities of the specimens are plotted on the map of figure 1, numbers 1—17.

Diagnostic characters. — Skull with occipito-nasal length of 123—138 mm, nasals small, length 51—63 mm, relative length of the nasals 39.5—47.9% of the occipito-nasal length, breadth of the nasals 23.8—31.7 mm, relative breadth of the nasals 36.6—45.2% of the zygomatic breadth of the skull, skull low on an average, mean relative height 45.3% of the basilar length ($n = 31$). A photograph of a skull from Sumatra is presented in figure 18. The longest quill in a skin varies from 155—200 mm, the blackish rings about midlength of the large quills on the back are very small, nearly always between 20 and 35 mm, and as a consequence there are always many long white tips present of 70—110 mm, there are practically no large quills with black point nor are there any transitional quills. The maximal length of the tactile bristles varies from 180—285 mm, the crest is rudimental with hairs of 45—70 mm and white tips of 5—35 mm length.

Remarks. — The above mentioned data are based only on five of the six skins available from the Malay Peninsula and not on the sixth one from Jalor (BMNH 3.2.6.74). This specimen (figure 11-right) belongs cranially to this subspecies but looks externally more like the northern forms, so in fact it cannot be allocated to one of the two races. It has longer quills, broader blackish rings on the quills, possesses black-tipped quills and some transi-

tional quills, has longer tactile bristles and a clearly developed crest. A second specimen from this locality, however, is quite like the southern ones.*)

The specimens USNM 83519 and 83521 from Trang, locality nr. 5, are similar to the next subspecies too with respect to the possession of a number of black-tipped quills, and the first of these two also possesses a clearly developed crest, not in the first place determined by the length of the hairs (60 mm, white tips 20 mm) but by their frequency (more than a hundred). These conditions demonstrate the close relationship of the Malayan form with that of Tenasserim (type locality of *A. klossi* Thomas, 1916) which is externally more or less intermediate between the Malayan form and the Thai and Chinese populations but cannot be distinguished cranially from the latter.

***Hystrix brachyura subcristata* Swinhoe, 1870**

Hystrix subcristata Swinhoe, 1870: 638. Foochow, Fokien, China.

Acanthion klossi Thomas, 1916: 139. Tenasserim, southern Burma.

Acanthion millsii Thomas, 1922: 431. Assam, India.

Acanthion subcristatus papae G. M. Allen, 1927: 3. Nodoo, Hainan, China.

Holotype. — BMNH 1570-a, skull, adult, occiput damaged, R. Swinhoe. As contrasted with Allen's mention (1940: 1105), no evidence could be found that the type skin has ever been in the collections of the British Museum (Natural History).

Type locality. — Foochow, Fokien, China.

Distribution. — Tenasserim (Burma), Thailand and Laos: map figure 1, locality nrs. 18—24; Tonkin (Vietnam), Hainan (China), mainland of China: locality nrs. 28—38; mainland of Burma, eastern Assam (India): locality nrs. 40—42.

Diagnostic characters. — Occipito-nasal length of the skull variable, on an average smaller (Hainan), about the same size (east India, north Burma, China) or slightly larger (Tenasserim, Thailand) than *H. b. brachyura*. Differs from this subspecies in the larger nasals, relative length 51.4—60.5% of the occipito-nasal length, relative breadth 47.5—61.7% of the zygomatic breadth of the skull. Skull higher, relative height as a percentage of the basilar length in the Tenasserim and Thailand sample slightly larger (43.6%, $n = 6$) than the former subspecies and largest in the sample from China (45.9%, $n = 9$). A photograph of a skull from Anhui, China is presented in figure 19. The quills

*) After submission of this article, Dr Alfred Feiler of the Staatliches Museum für Tierkunde in Dresden drew my attention to a third specimen from Mabek, Jalor, in the collections of his institution, and through his kind cooperation I have been able to study this skin (reg. no. B 4359, without skull, H. C. Robinson, 1903). By the poor development of the crest and the development and colouration of the quills. this specimen is quite like the form from Malacca.

of the Hainan sample have about the same length as those of the nominal subspecies (155—180 mm, $n = 3$) and those of the remaining specimens are somewhat longer (170—220 mm, $n = 11$), the breadth of the blackish rings on the quills are larger (maximal 40—90 mm) and the white tips are shorter (35—90 mm), always at least some quills are present with a black extremity, in most specimens about half of them have black tips and in some specimens the black-tipped ones are in the majority. The tactile bristles are longer on an average (200—350 mm) than in the former subspecies, some, or a considerable number of transitional quills occur, often forming a gradual transition from quills to tactile bristles. Crest always clearly to quite conspicuous present, with hairs of 85—230 mm and white tips 30—150 mm length, though not as largely developed as in the subgenus *Hystrix*.

***Hystrix brachyura hodgsoni* (Gray, 1847)**

Acanthion hodgsoni Gray, June 1847: 101. Nepal.

Hystrix alophus Hodgson, August 1847: 771. Nepal.

Type-specimen.— BMNH 47.7.22.9, lectotype, skin and damaged skull, subadult, B. H. Hodgson 887-b. One paralectotype, BMNH 45.1.8.8, skull, adult, B. H. Hodgson 887-a.

Type locality. — Nepal.

Distribution. — Sub-Himalayas, including Nepal with the only exact locality Hathiban, Sikkim, and Darjeeling (India). Perhaps also at "Mangpu", a locality in the former Bengal Presidency of India which could not be located.

Diagnostic characters. — Judged from the occipito-nasal length (115.7—118.1 mm, $n = 5$) this form is the smallest within the species. The relative height of the skull (mean 41.0% of the basilar length) is smaller than that of *H. b. subcristata* and is about the same as that of *H. b. brachyura*. As to its nasal structure, this form with a relative nasal length of 52.0—55.1% of the occipito-nasal length and a breadth of 49.9—63.6% of the zygomatic breadth, is not at all different from *H. b. subcristata*. As regards the spiny covering, however, the sub-Himalayan form shows the lowest degree of development within this species. The quills are on an average thinner (maximal diameter 4.5—5.6 mm) and shorter (maximal length 105—190 mm), with large blackish rings (40—75 mm) and relatively short white tips (20—55 mm) in proportion to their length. The rattle quills are always shorter (16—19 mm) than those of the remaining forms of this species, and only a rudimental crest is present with hairs of 55—110 mm maximal length and white tips of 10—55 mm.

Remarks. — Very little is known about the geographical and morphological limits of this sub-Himalayan race. Ellerman (1961: 300, 305) mentioned *hodgsoni* from Longpa in the Naga Hills, N. E. Assam, evidently based on specimen BMNH 21.8.2.26 which is registered as *H. hodgsoni* and bears a

label "*Acanthion bengalensis*". The identification of the skin and skull of this young animal with only the deciduous premolar, however, is very doubtful. Judging from the measurements of the skull and the colouration of the quills, there is more reason to refer this specimen to *H. b. subcristata*, undoubtedly occurring in this area. A young specimen (FMNH 75873, M3 not yet erupted) from Mawphlang, Assam (locality nr. 43) cannot be identified either. The cranial dimensions and the vestigial crest could possibly correspond with *H. b. hodgsoni*, but white extremities of quills of 85 mm length do not agree with *hodgsoni* as known from Nepal. A subadult specimen from "Mangpu, Bengal Presidency, India" (FMNH 35667) offers a better opportunity for comparison, although that locality, unfortunately, cannot be located on any map or gazetteer. On the evidence of the occipito-nasal length of 116 mm, and the size and colouration of the quills (largest diameter 5.5 mm, length 160 mm, rings 30—60 mm, white tip 55 mm), the small rattle-quills (diameter 4.7 mm, length 16 mm) and the rudimental crest (75 mm, 45 mm white), it can be asserted that it is quite like the sub-Himalayan form, but this specimen has remarkable short nasals (46.6% of the occipito-nasal length). It is evident that these specimens from the zone between the sub-Himalayan area and Burma cannot be assigned with certainty to one of the subspecies diagnosed until this moment, and that the identification of this material will have to wait until more information from this area becomes available.

Little evidence is available, too, for the sympatric occurrence of the species under consideration and *Hystrix indica* Kerr, 1792. Inglis *et al.* (1919: 824) mentioned, besides the "Crestless Himalayan Porcupine", the occurrence of a second species "other than the crestless one" in the Jalpaiguri district, south of Sikkim, but even if this observation was correct, it cannot be decided whether a *subcristata*-type of animal or *H. indica* has been observed. According to Hodgson (1847: 772—774) *H. indica* as well as *H. b. hodgsoni* occurred in all regions of the Himalayan states, the former were quite numerous, the latter much more rare, and he collected specimens of both species but no exact localities are known. The only *H. indica* specimen with exact locality known to me is a mounted skin from Dakhna Bagh in extreme western Nepal (28°50'N 80°05'E) in the collections of the Naturhistorisches Museum Wien, and from a cursory study of this specimen no differences appeared between this specimen and the western Asiatic form.

The porcupine of Bengal

Blyth (1851) described the "common Bengal Porcupine" under the name *Hystrix bengalensis* and characterized it as "the small crested species" in comparison with the "sub-Himalayan crestless Porcupine". Kloss (1916: 60) observed: "It is remarkable how little information we have concerning *Hystrix bengalensis*". He borrowed the type skull from the former Indian

Museum at Calcutta and his conclusions were that, until topotypes of *bengalensis* were available, nothing could be said about the relationship of this form. Thomas (1916: 137) inferred from Blyth's description: "Possibly, indeed, *bengalensis* is not distinct from *hodgsoni*, but this must be settled later", and in 1922 (: 432) he stated: "Blyth's *bengalensis* is certainly the same as *hodgsoni* as I have been able to prove by some measurements of its type". Ellerman & Morrison-Scott (1951: 519) listed this species name, preceded by a questionmark, in the synonymy of *Hystrix hodgsoni hodgsoni* (Gray, 1847) and Ellerman (1961: 304) did not doubt Thomas' identification and synonymized it with this subspecies too. Thanks to the kind cooperation of the authorities of the Zoological Survey of India at Calcutta, who lent me the type skin and skull, I was able to make a more detailed comparison than my predecessors. Blyth did not mention the exact locality of his type. The label of the holotype records "? Sunderbuns", and Kloss (1916: 60) mentioned that it is "supposed to come from the Sunderbunds", so there is some doubt as to its geographic origin. The Sundarbans, mouth area of the Ganges, is indicated in the present paper as locality nr. 41. The skull of the holotype (register nr. 10034: figure 20) has an incomplete dentition with the M3 just erupted and not yet showing wear. The occipito-nasal length is 112.4 mm, length of the nasals 57.2 mm (50.9% of occ. nas. 1.), breadth of the nasals 34.8 mm (60.0% of zygomatic br.) and the height of the skull is 41.5 mm (45.1% of the basilar l.). The skin (figure 15) has quills with a maximal length of 145 mm, diameter 5.3 mm, black rings up to 50 mm, none of the white tips is longer than 30 mm with the exception of one of 50 mm length, the majority of the quills have a black tip. There are about five long tactile bristles, the longest 250 mm. The length of the rattle-quills is maximal 20 mm and the diameter 5.7 mm. The distinct crest has hairs with a maximal length of 127 mm and white tips of 60 mm. Comparison with skulls of about the same dental age from Sumatra and Malacca and subadult specimens from Nepal, only leads to the conclusion that this specimen, proportionally to its age, is probably too large for *H. b. hodgsoni* and very small for *H. b. subcristata*. The height of the skull is clearly above the range of variation of the sub-Himalayan sample, so not different from *subcristata*. With respect to the development of the quills and tactile bristles and the colouration of the quills, the skin is more like *hodgsoni*, the rattle-quills are more or less intermediate while the crest has broadly the same development as *subcristata*.

In short it can be stated that "*bengalensis*" is based on only one young specimen from an uncertain locality and unites characters of *hodgsoni* and *subcristata*. This is an affirmation of Ellerman's (1940: 214) statement regarding these forms: "probably intergradation would take place in these external characters if enough specimens came to hand". There is, however, very little material available from the area west of Burma and south of the sub-Himalayan area, and therefore the best thing we can do is to refrain from assigning *H. bengalensis* Blyth, 1851 to any subspecies and to maintain provisionally the subspecies as recognized thus far.

The porcupine of Yunnan

J. Anderson (1878) described a specimen from "... the mountains to the east of the Kakhyen hills...", Yunnan, South China, under the name *Hystrix yunnanensis*. By the kind cooperation of the authorities of the Zoological Survey of India at Calcutta I was able to study this holotype as well. This young animal (figure 21), with the third permanent molar just erupted, has but one remarkable peculiarity and that is the exceptionally small size of the nasals (length 45.6 mm, 38.0% of the occ. nas. 1, breadth 27.1 mm, 43.2% of the zyg. br.). Thus, those are shorter than in three specimens of *H. b. brachyura* (relative length 41.7—42.8%) of about the same dental age and fully within the range of *H. javanica* (F. Cuvier, 1823). Ellerman & Morrison-Scott (1951) listed this form with a question-mark as *H. b. yunnanensis* and Lekagul & McNeely (1977: 490), too, synonymized it with the Malayan *H. brachyura*. The latter authors also supposed the possibility of a misidentification or a poor understanding of the east Asian *Hystrix*. If one considers the possibility of a mistake, then, on the basis of the very small nasals, it might be supposed that the skull that was described, belonged to a specimen from Java, but this is highly improbable because of the large size of the skull (occ. nas. 1. 120.4 mm) in relation to its dental age. The skin is damaged but the most important parts are in good condition (figure 16). As far as can be judged from this young animal externally it does not differ from *H. b. subcristata*. The quills have a maximal diameter of 5.5 mm and a length of 132 mm with black rings between 30 and 55 mm, most of the quills have white tips of 50—60 mm and some smaller quills have black tips of about 60 mm. The tactile bristles are up to 280 mm long and have, as the transitional quills, much longer white parts. The rattle-quills have a maximal diameter of 4.9 mm and a length of 20 mm. There is a thin but clearly perceptible crest with hairs of maximal 115 mm and white tips of 65 mm, quite different from *H. javanica* in which the crest is totally absent. Anderson's remarkable specimen might be considered either to be an aberrant individual, or to belong to quite a different population in Yunnan, the existence of which we will have to assume, or a much larger variation in the continental *Hystrix* forms must be supposed than is known up to the present. As it is, there is no evidence for any of these suppositions, so I will provisionally regard it a subspecies of *Hystrix brachyura* as here understood.

The porcupine of Vietnam

From the area of Nha Trang, Hue and Quang Tri (locality nrs. 25, 26 and 27) in Annam, Vietnam, four skins and five skulls of six specimens have been studied of which four are young, one is subadult and one adult. The cranial measurements of the adult specimen are presented in table I and those of the adult and the subadult also in the relevant histograms. The measurements of the young specimens have been compared with those of the specimens of

H. b. brachyura of about the same dental age. From these data it appears that all these specimens are very small, probably as small as *H. b. hodgsoni*. They are undoubtedly smaller than the only specimen available (FMNH 37990) from south Laos (locality nr. 24), a subadult with an occipito-nasal length of 134.3 mm and a development of the spiny covering which is quite like that of *H. b. subcristata*, and also smaller than the only specimen (FMNH 32514) from Tonkin, Vietnam (locality nr. 28). This specimen is a very young one with the M2 not yet erupted, but its occipito-nasal length of 104.2 mm is large in proportion to its age and the other characters of skull and skin show that it is much like *H. b. subcristata*. One of the specimens (BMNH 6.11.6.37) from Nha Trang (locality nr. 25), a young one with the M2 not yet erupted and an occipito-nasal length of 76.9 mm, was mentioned before by Ellerman (1940: 200): "a very small juvenile..... which has for its size surprisingly developed caudal quills and quite conspicuous crest". The rattle-quills are not longer than 17 mm but the largest diameter is 6.5 mm and the crest hairs have a maximal length of 95 mm with a 45 mm long white tip. Another remarkable character of this specimen is the small size of the nasals (40.3% of the occ. nas. 1.), the same as in specimens of *H. b. brachyura* of the same dental age. A second specimen from Nha Trang (MHNLR-M756), skull without skin, adult, has a relative nasal length of 50.1%, and so is exactly between the ranges of variation of *H. b. brachyura* and *H. b. subcristata*. A subadult specimen (BMNH 27.12.1.204) from Hue with an occipito-nasal length of 110.1 mm, thickest quill 5.1 mm with a length of 105 mm, however, has longer nasals (54.5% of occ. nas. 1), less conspicuous rattle-quills and fewer and shorter crest hairs (maximal 70 mm). A second skin of unknown age (BMNH 26.10.4.191) from the same locality has a crest with hairs of 100 mm maximal.

Summarizing, it can be stated that in Vietnam porcupine populations occur with the small body size and the development of the spiny covering of *H. b. hodgsoni*, with a nasal size somewhere between that of *H. b. brachyura* and *H. b. subcristata*, with rattle-quills larger than those of *H. b. hodgsoni*, with a crest of hairs clearly larger than *H. b. brachyura* and perhaps smaller on an average than that of *H. b. subcristata*. These specimens cannot be designated to any of the subspecies recognized thus far, and I regard this situation, again, as an indication that subspecific distinction within this species may prove to be impossible when collections from many more localities in Southeast Asia become available.

Hystrix javanica (F. Cuvier, 1823)

Acanthion javanicum F. Cuvier, 1823: 431. Java.

Hystrix torquata van der Hoeven & de Vriese, 1836: 110. Java.

Hystrix ecaudata van der Hoeven & de Vriese, 1836: 110. Java.

Hystrix brevispinosa Wagner in Schreber, 1844: 20. Java.

Acanthion sumbawae Schwarz, 1911: 639. Dompu, Sumbawa.

Table III. Cranial measurements in millimetres of *Hystrix javanica* from Indonesia with range, mean of the sample in parenthesis, number of measurements (n) and the standard deviation (s). Adult specimens, except the one from Lombok (subadult). For the definitions of the measurements see Material and methods.

	Java	Bali	Lombok	Sumbawa	Flores
Occ. nas. l.	103.8—127.5 (116.2) n = 16 s = 5.54	104.0—110.7 (107.0) n = 3	102.9	107.7	108.8—110.5 n = 3 (109.5)
Basilar l.	88.5—106.8 (97.8) n = 16 s = 5.02	90.1—95.2 (92.2) n = 3	88.1	94.1	89.7—93.7 n = 3 (91.7)
L. nasals	41.8—55.0 (46.6) n = 16 s = 3.36	38.5—42.8 (40.5) n = 3	37.8	39.0	42.7—48.1 n = 5 s = 1.95
L. frontals	30.8—39.0 (35.1) n = 15 s = 2.62	31.4—33.3 n = 2	30.0	36.2	31.0—31.5 n = 2
Palatal l.	55.8—63.5 (60.1) n = 16 s = 2.93	52.6—54.0 n = 2	53.3	55.4	56.8—58.4 n = 5 s = 0.65
L. diastema	28.7—34.7 (31.4) n = 16 s = 1.62	28.4—30.1 n = 2	26.5	29.6	28.3—30.0 n = 5 s = 0.66
Br. nas. post.	21.4—28.0 (24.8) n = 16 s = 1.99	19.3—21.7 (20.7) n = 3	22.5	24.5	20.3—24.8 n = 5 s = 1.97
Postorb. br.	32.7—44.8 (37.0) n = 15 s = 2.81	31.0 n = 1	33.6	35.6	31.9—35.2 n = 4 (33.7)
Zygom. br.	57.7—69.3 (62.0) n = 16 s = 3.00	56.0—56.6 (56.8) n = 3	56.2	60.4	54.0—60.5 n = 4 (57.9)
Height sk.	36.2—46.2 (40.6) n = 16 s = 2.46	34.1—35.6 (34.8) n = 3	33.9	38.0	36.0—38.8 n = 4 (37.8)
L. mandible	73.5—84.4 (77.9) n = 14 s = 3.38	70.9—73.4 (72.2) n = 3		73.0	72.8—75.9 n = 4 (74.5)
H. mandible	31.8—41.0 (34.7) n = 14 s = 2.71	29.5—32.7 (31.4) n = 3		31.3	31.2—34.7 n = 4 (33.3)
Alv. P4—M3	23.1—27.0 (25.3) n = 16 s = 1.18	23.1—23.9 n = 2	23.3	23.3	22.3—26.6 n = 4 (24.2)
Alv. p4—m3	24.8—28.1 (26.8) n = 16 s = 0.96	23.9 n = 1	23.5	23.5	23.6—27.2 n = 4 (25.0)

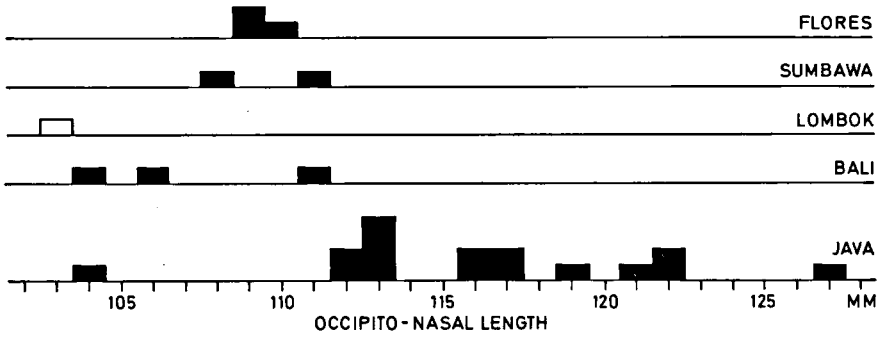


Fig. 8. Frequency distribution of the occipito-nasal length of the skulls of *Hystrix javanica*. Solid rectangles represent adult, open rectangles subadult specimens.

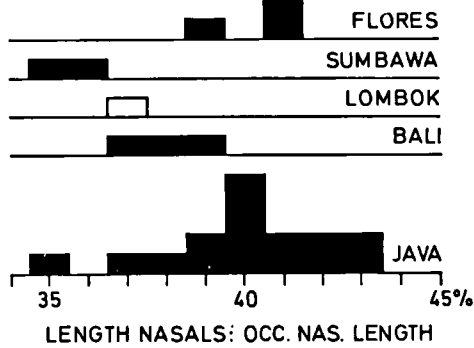


Fig. 9. Frequency distribution of the relative length of the nasals of *Hystrix javanica*, expressed as a percentage of the occipito-nasal length. Solid rectangles represent adult, open rectangles subadult specimens.

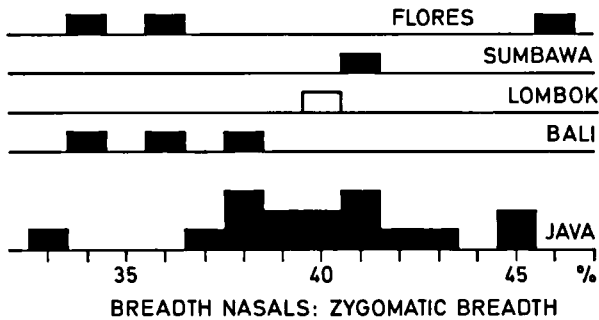


Fig. 10. Frequency distribution of the relative breadth of the nasals of *Hystrix javanica*, expressed as a percentage of the zygomatic breadth. Solid rectangles represent adult, open rectangles subadult specimens.

Holotype. — Despite the kind co-operation of the authorities of the Muséum National d'Histoire Naturelle at Paris and a thorough search, F. Cuvier's holotype could not be found.

Type locality. — Java.

Range. — Java, Madura, Bali, Lombok, Sumbawa, Flores, Tanahdjampea. The localities of the specimens studied are plotted on the map of figure 2, and the numbers correspond with those of the list of specimens examined. This species is also recorded from Celebes by Jentink in Weber (1890: 121) who supposed that it had been introduced there from Flores a long time ago and who mentioned a case of a transfer of a living porcupine from that island in a proa.

Diagnostic characters. — With a length of head and body of about 455—590 mm ($m = 524$ mm, $n = 8$) this species is on an average smaller than *H. crassispinis* ($m = 610$ mm, $n = 6$) and only slightly larger than *H. sumatrae* ($m = 506$ mm, $n = 11$). The occipito-nasal length of the skull varies from 103.8—127.5 mm ($m = 113.2$ mm, $n = 25$) which is nearly always smaller than in the neighbouring populations of *H. b. brachyura* as may appear from the histograms in figures 4 and 8. Judging from cranial size, *H. javanica* is scarcely any smaller than the sub-Himalayan *H. b. hodgsoni*, but this subspecies is much more specialized by its large nasals which are always over 50% of the occipito-nasal length. The length of the nasals of *H. javanica* varies from 34.6—43.1% of the occipito-nasal length ($m = 39.4\%$, $n = 25$) and the breadth of the nasals from 33.4—45.9% of the zygomatic breadth ($m = 39.6\%$, $n = 26$). The relative length of the nasals shows a considerable overlap with *H. b. brachyura*, but externally *H. javanica* can always be distinguished at a glance from the neighbouring populations of Borneo, Sumatra and the Malay Peninsula. The quills are very weakly developed. The diameter of the thickest quill varies from 3.5—6.1 mm ($m = 5.1$ mm, $n = 18$) and the length of the longest quill varies from 80—155 mm ($m = 126$ mm, $n = 18$) against 155—233 mm in *H. b. brachyura*. These small quills have relatively broad black rings of mostly 40—50 mm and relatively short white tips, in many cases between 25 and 35 mm, sometimes up to 50 mm. Moreover, there are always a considerable number of quills with a black tip with a maximum length of 40—65 mm, and in many skins these black-tipped quills account for fifty per cent or more of the quills. This colouration of the exposed parts of the quills gives a dark appearance to the skin of *H. javanica*. White-tipped bristles on the cheeks, shoulders, sides and sometimes on the foremost part of the back, give a speckled impression to the skin of this species (figure 17). This character has been observed, to a much lesser degree, in only one young specimen of *H. b. brachyura* from Sumatra (RMNH 19966) and never in any specimen from the continent. The rattle-quills, with the diameter of the largest one from 3.1—4.8 mm ($m = 4.0$, $n = 15$), are still less developed than in *H. b. hodgsoni* although the length does

not differ very much (range 15—20 mm, $m = 17$ mm, $n = 15$). The crest is totally absent in this species. On the head and nape of the neck some white-tipped bristly hairs are sometimes present, but they are not longer than those of the sides of head and body and cannot be regarded as even a suggestion of a crest.

Geographical variation. — The cranial dimensions of the various populations of this species are presented in table III and in the histograms of figures 8, 9 and 10. The photograph in figure 22 shows a skull from Sumbawa (MZB 493) with the smallest nasals in this species. Schwarz (1911) based his *Acanthion sumbawae* on a number of cranial characters concerning the general shape and proportions of the skull and nearly all its component parts, as well as on its small size. These characters, however, are quite individual and vary in the specimens of all populations. Except for a distinct smaller mean size of the samples from the Lesser Sunda Islands when compared with that from Java, I could not perceive any significant difference neither in cranial nor in external characters. A smaller size alone, however, does not justify nomenclatorial recognition of populations in this subgenus.

DISCUSSION

Ellerman (1961) treated the short-tailed porcupine from the Malay Peninsula and Archipelago as a separate species, *H. brachyura* Linnaeus, 1758 and brought the remaining forms of the continent of Southeast Asia under the name *H. hodgsoni* Gray, 1947. This classification was mainly based on the length of the nasal bones which are always below 50% of the occipito-nasal length of the skull in *H. brachyura*, whereas they are clearly above 50% in the continental populations. However, this author also stated (1940: 213) that: "... external characters (development of quills, etc.) must be regarded as being just as important as any cranial character". When, as in the present paper, all the continental forms are assigned to *H. brachyura* on the basis of the gradual transition of the external characters of the Malayan form into those of the continent, the question arises whether *H. javanica* must be considered to belong to the same species, too, as was the point of view of Chasen (1940: 188). An argument in support of this opinion is that this form is as small as *H. b. hodgsoni* which has more or less the same poorly developed spiny covering. *H. javanica*, however, is a still less specialized form with very small nasals whose measurements even show an overlap with those of the subgenus *Thecurus* Lyon, 1907 (figure 3). Moreover, the skin of *H. javanica* does not possess a trace of a crest which is always at least indicated in *H. brachyura*, the caudal rattle-quills are smaller still, and the speckled appearance, caused by the presence of white-tipped bristles is never met with in such a degree in *H. brachyura*. Therefore, in my opinion *H. javanica* must stand as a separate species.

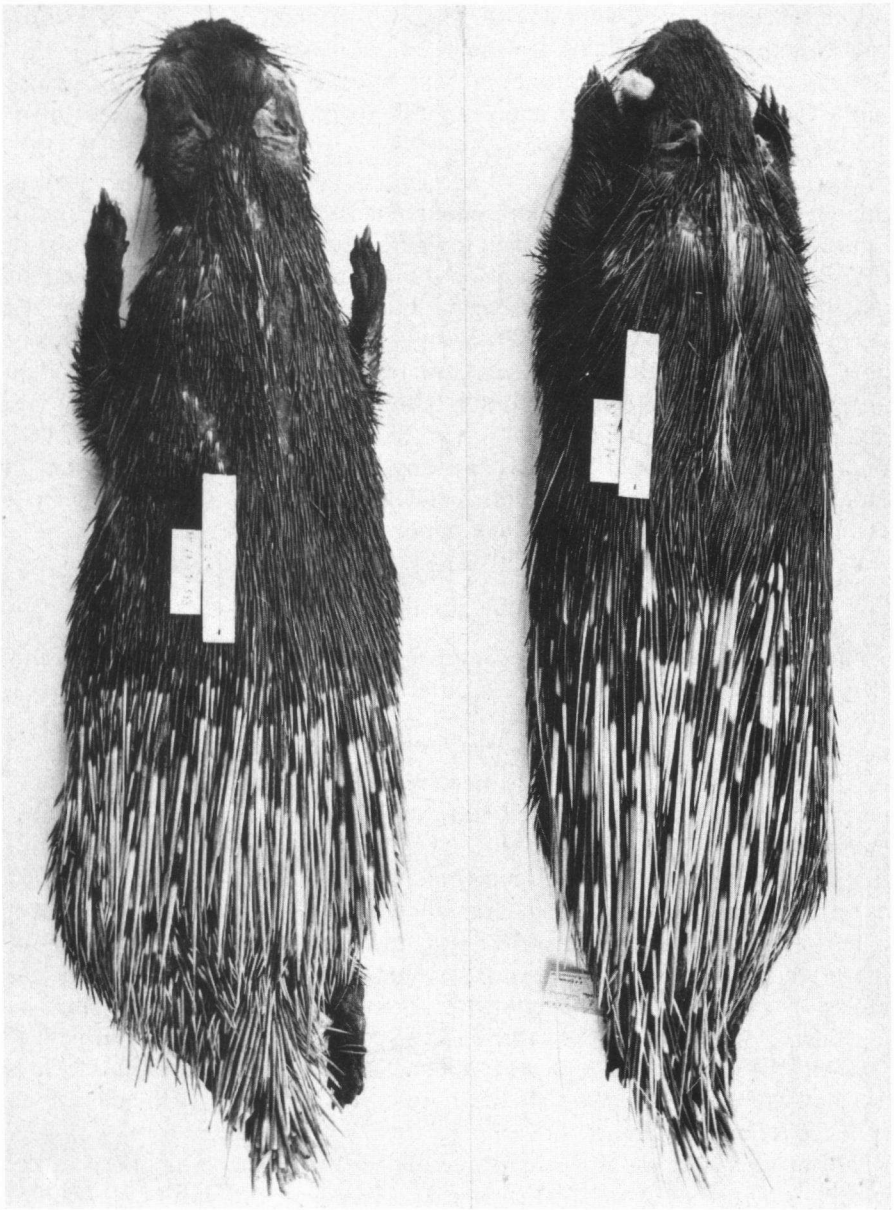


Fig. 11. Photographs of skins of *H. b. brachyura*. Left: specimen from Malacca, locality no. 1, (BMNH 79.11.21.533). Right: specimen from Peninsular Thailand, locality no. 4, (BMNH 3.2.6.74).

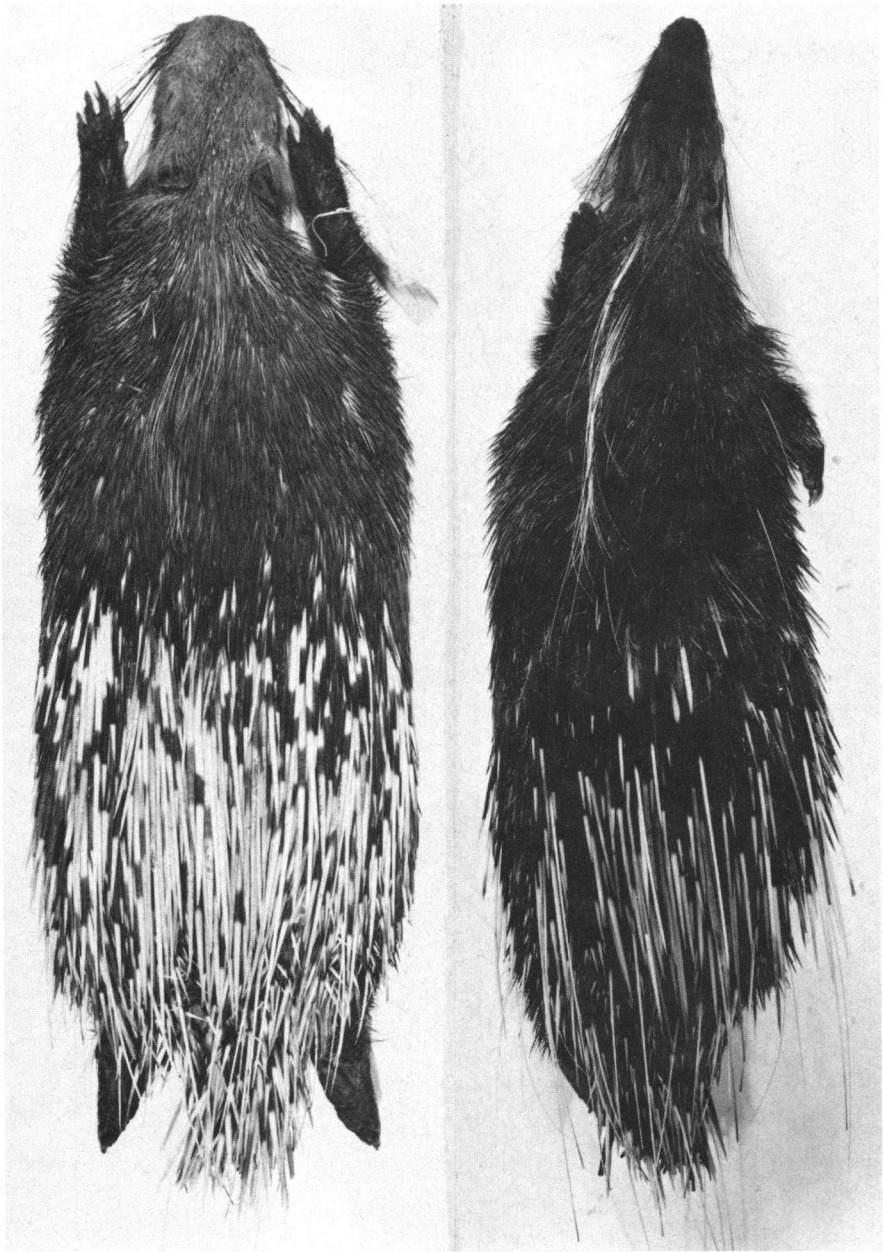


Fig. 12. Photographs of skins of *H. b. subcristata*. Left: specimen from Tenasserim, locality no. 18, (USNM 124020), photograph USNM. Right: specimen from China, locality no. 32, (NRS 6143), L. R. Hafkamp (ZMA) fecit.

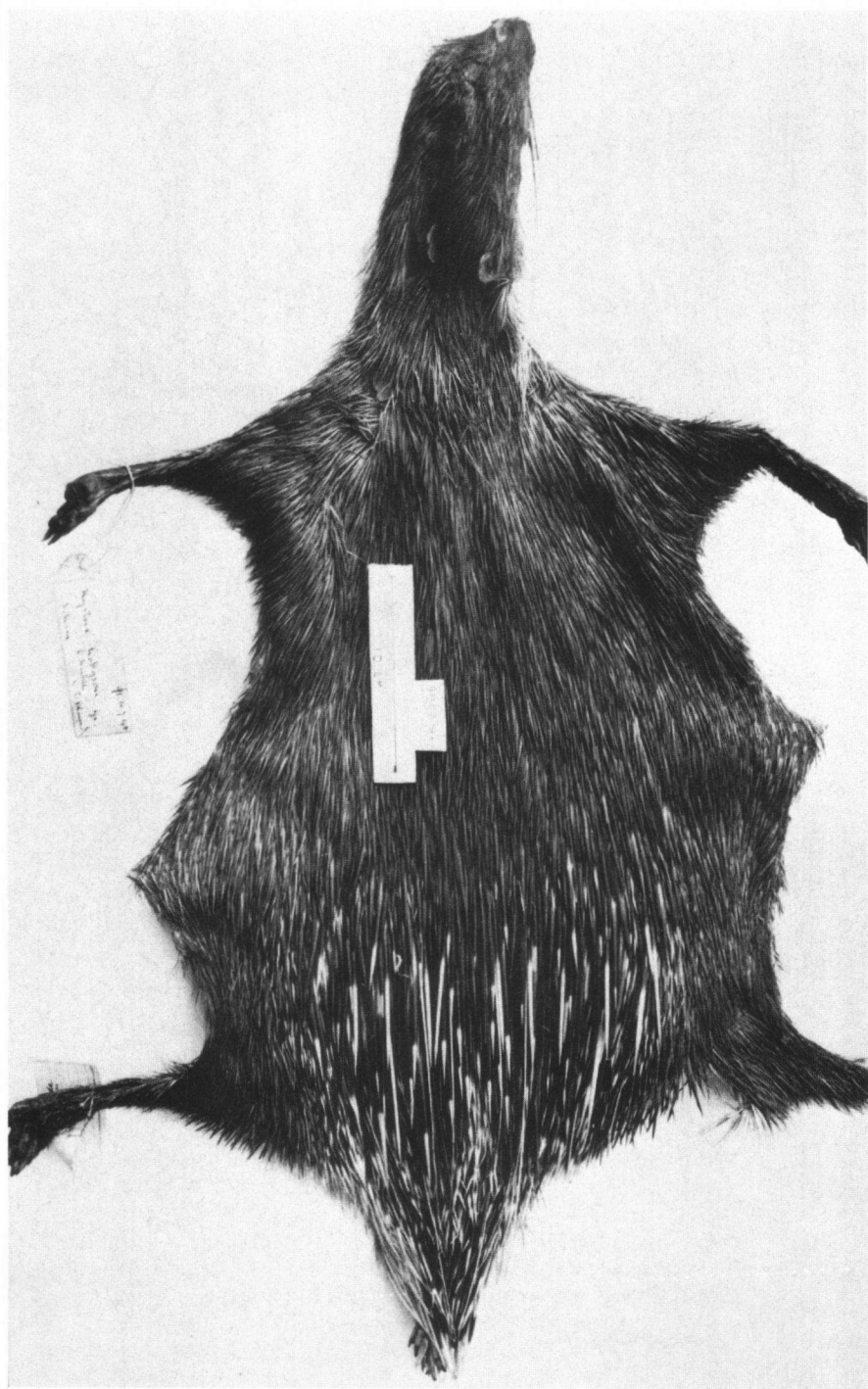


Fig. 13. Photograph of a skin of a specimen of *H. b. hodgsoni* from Sikkim, locality no. 45, (BMNH 91.10.7.146).

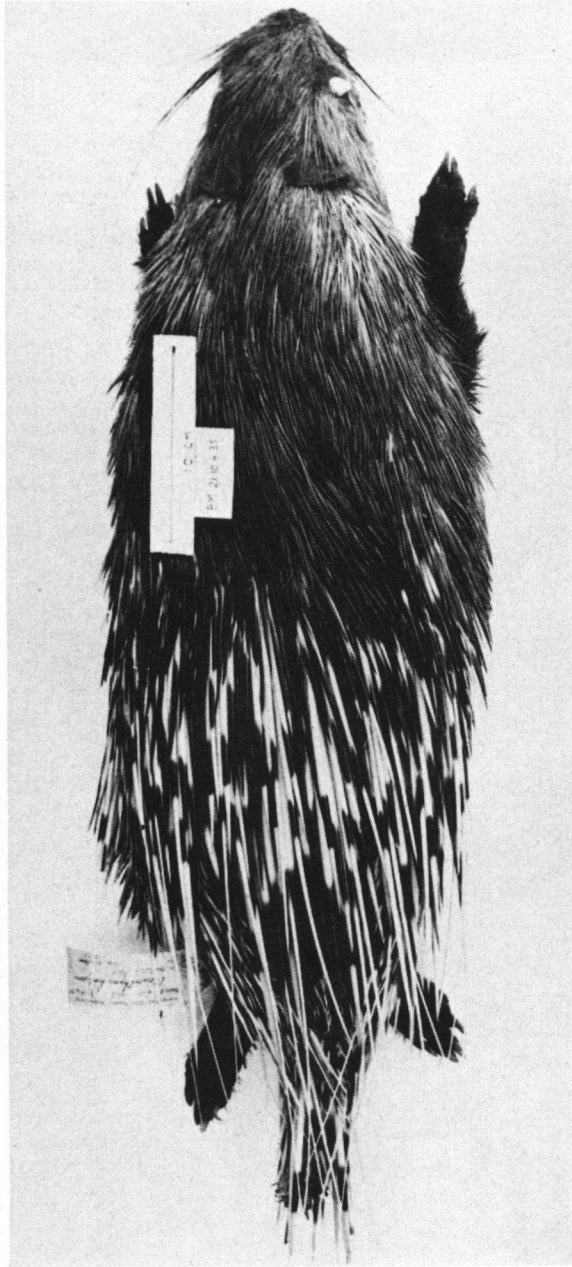


Fig. 14. Photograph of a skin of a specimen of *H. b. hodgsoni* from Nepal, locality no. 46, (BMNH 21.10.4.35).



Fig. 15. Photograph of the skin of the holotype of *Hystrix bengalensis* Blyth, 1851, (ZSIC 10034), A. L. van der Laan (ZMA) fecit.



Fig. 16. Photograph of the skin of the holotype of *Hystrix yunnanensis* Anderson, 1878, (ZSIC 15687), A. L. van der Laan (ZMA) fecit.



Fig. 17. Photograph of a mounted specimen of *Hystrix javanica* from Java, (RMNH 1721). Photograph of RMNH.

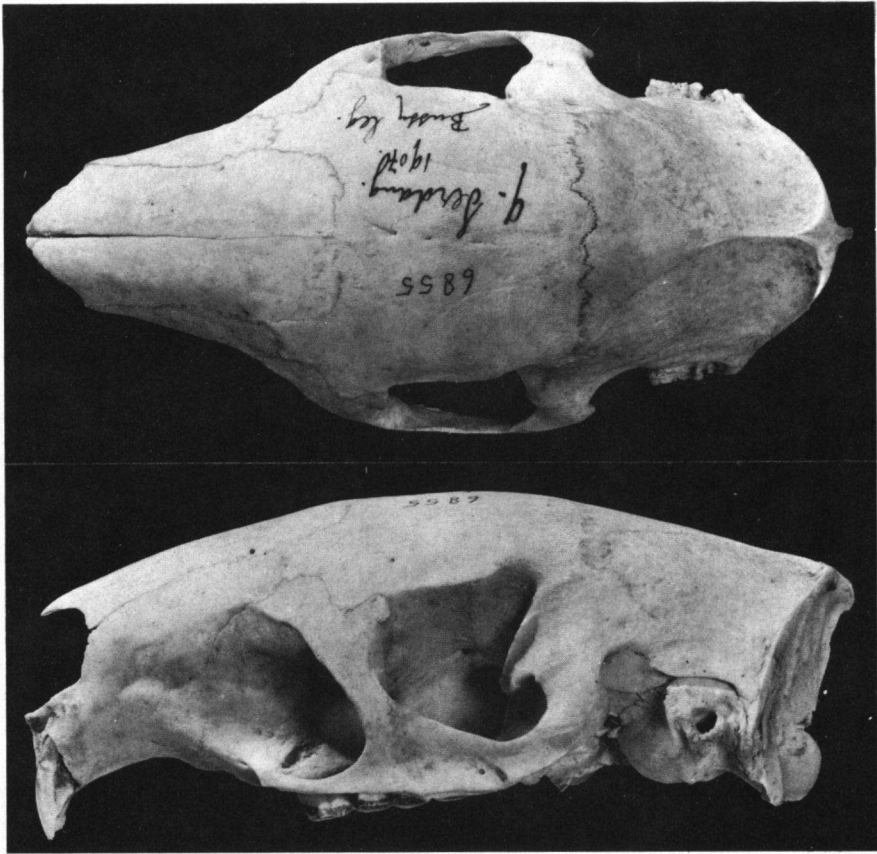


Fig. 18. Photographs of the skull of a specimen of *H. b. brachyura* from Sumatra, (ZMA 6855), A. L. van der Laan (ZMA) fecit.

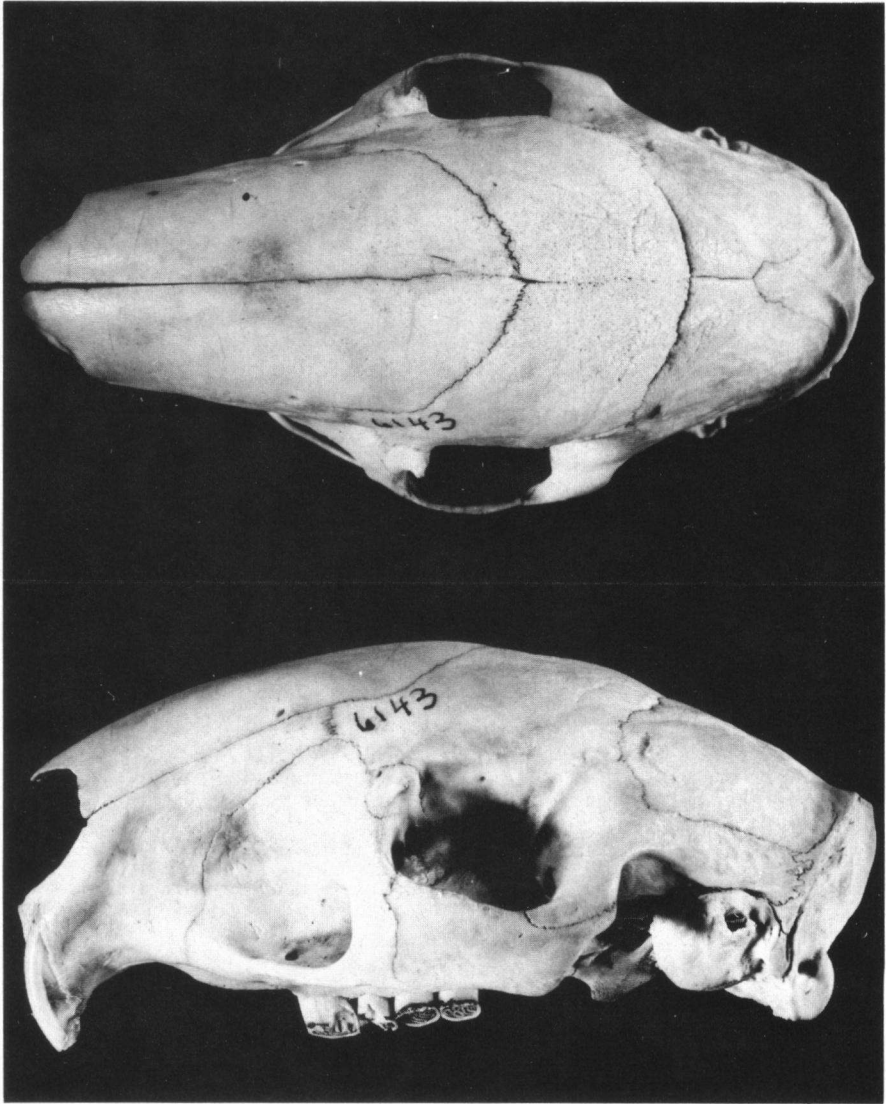


Fig. 19. Photographs of the skull of a specimen of *H. b. subcristata* from China, locality no. 32, (NRS 6143), L. R. Hafkamp (ZMA) fecit.

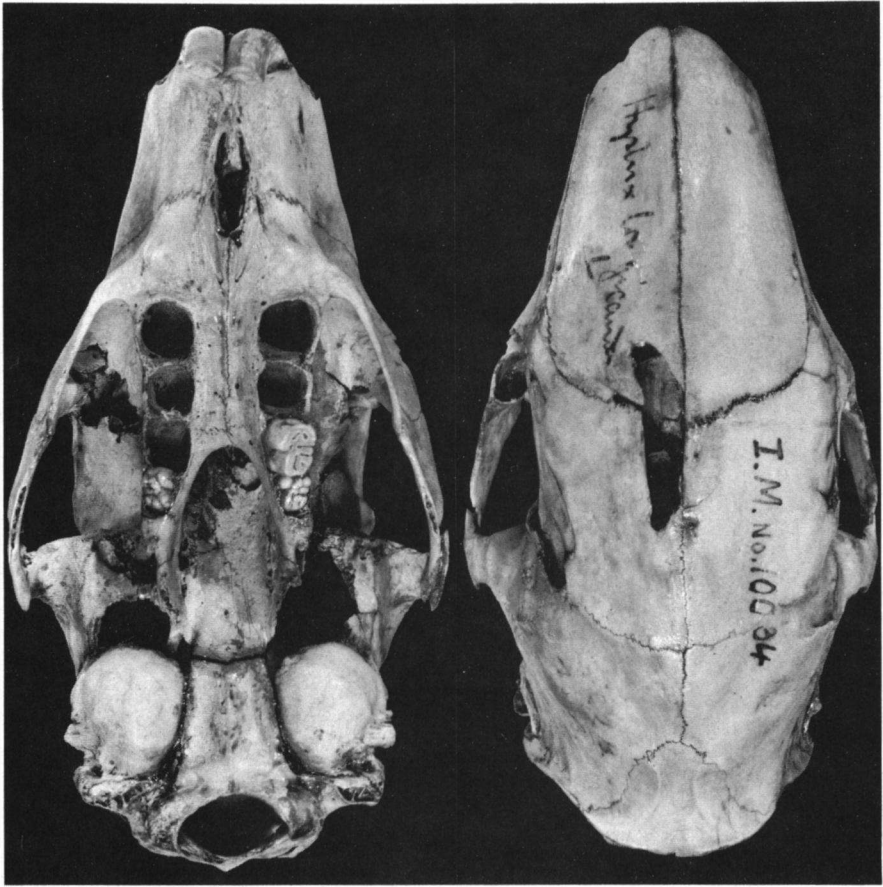


Fig. 20. Photographs of the skull of the holotype of *Hyrax bengalensis* Blyth, 1851, (ZSIC 10034), A. L. van der Laan (ZMA) fecit.

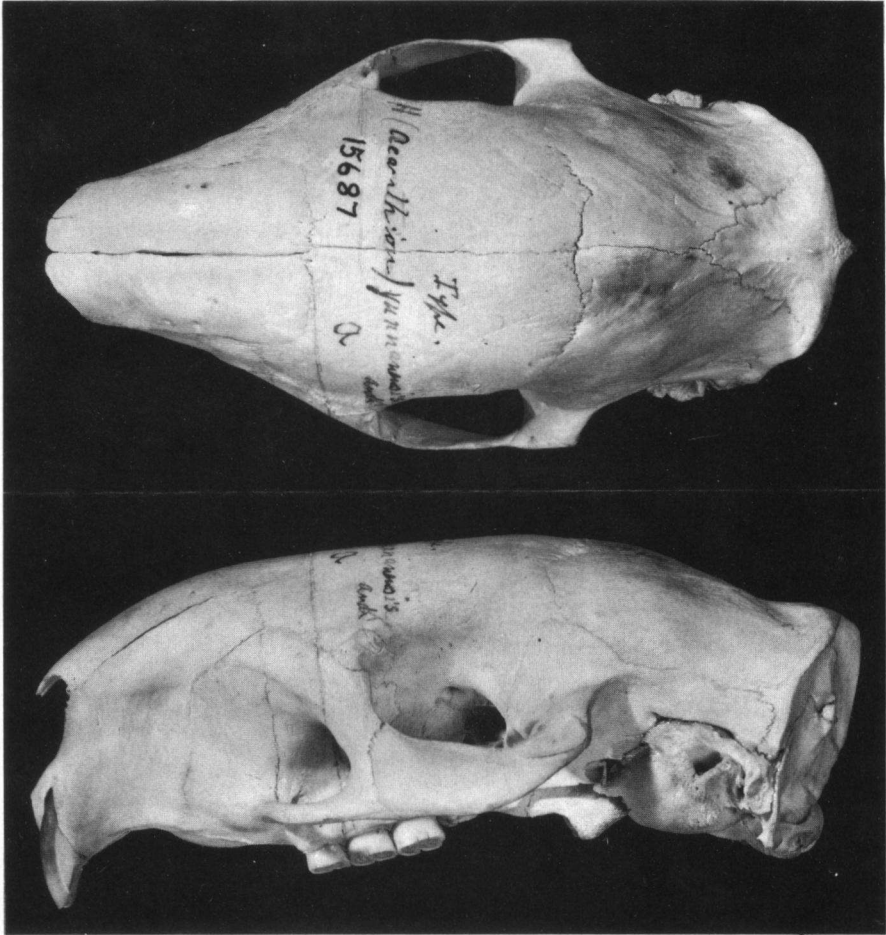


Fig. 21. Photographs of the skull of the holotype of *Hystrix yunnanensis* Anderson, 1878, (ZSIC 15687), A. L. van der Laan (ZMA) fecit.

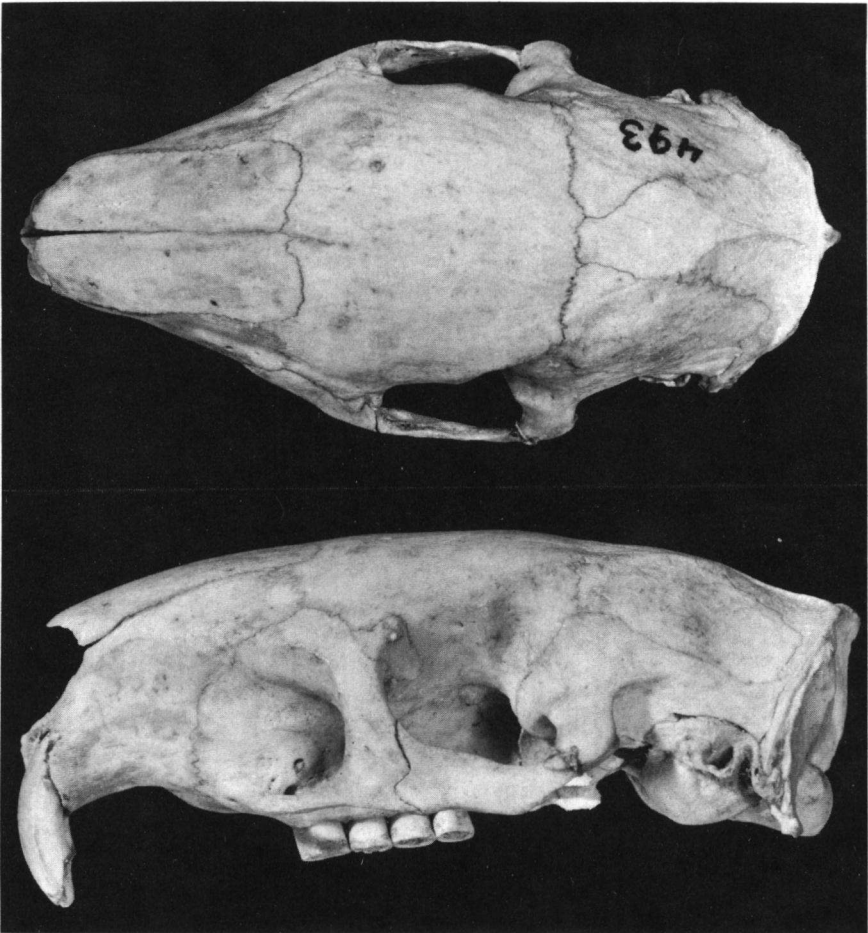


Fig. 22. Photographs of the skull of a specimen of *Hystrix javanica* from Sumbawa, (MZB 493), A. L. van der Laan (ZMA) fecit.

ACKNOWLEDGEMENTS

I am most grateful to Dr. P. J. H. van Bree, Curator of the Mammal Department, Zoölogisch Museum Amsterdam, to whom I am much indebted for his encouragement to continue and finish this series. Many thanks are owed to Mr. C. M. Sep (Alkmaar) who spent much time and patience on the correction of my English text. I am greatly indebted to the following persons for allowing me to study specimens under their care, for lending me material and for co-operation: Dr. S. Anderson (American Museum of Natural History, New York), Dr. Renate Angermann (Zoölogisches Museum Berlin), Dr. K. Bauer (Naturhistorisches Museum Wien), Dr. U Bergström (Naturhistoriska Riksmuseet Stockholm), Dr. I. R. Bishop, Dr. G. B. Corbet and Dr. J. E. Hill (British Museum (Natural History), London), Dr. Boedi (Museum Zoologicum Bogoriense, Bogor), Dr. P. K. Das (Zoological Survey of India, Calcutta), Dr. R. Duguay (Muséum d'Histoire Naturelle, La Rochelle), Dr. H. Felten (Senckenberg Museum Frankfurt/Main), Dr. C. P. Groves (Department of Prehistory and Anthropology, Canberra), Dr. Th. Haltenorth (Zoologische Staats-Sammlung München), Dr. Å. Holm (Zoologiska Institutionen Uppsala), Dr. A. M. Husson, Dr. Chr. Smeenk and Mr. J. Schouten (Rijksmuseum van Natuurlijke Historie, Leiden), Dr. F. Petter and Dr. M. Tranier (Muséum National d'Histoire Naturelle, Paris), Dr. H. W. Setzer (National Museum of Natural History, Washington), Prof. Dr. L. Silén (Zoologiska Institutionen Stockholm), Dr. L. de la Torre (Field Museum of Natural History, Chicago) and Dr. H. Wolf (Museum Alexander Koenig, Bonn). I am also grateful to Dr. I. R. Ball and to Dr. Ronald H. Pine for reading the paper critically and for their comments.

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GAZETTEER

The following geographic names are those from the list of specimens examined. 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.

Southwest Asia

Ayelette, Hashackar (Ayyelet, Hashahar)	33°01'N	35°34'E
Emmaus (Imwas)	31°50'N	34°59'E
Susa (Shüsz)	32°12'N	48°20'E

Malay Peninsula

Jalor	06°30'N	101°10'E
Kuala Tahan	04°23'N	102°24'E
Malacca	02°12'N	102°15'E
Pinang, island (Pulo Penang)	05°30'N	100°28'E
Trong (Trang)	07°33'N	99°36'E
Wellesley, province	05°25'N	100°25'E

Sumatra

Karbou Gat	00°12'S	100°11'E
Loeboeksikaping (Lubuksikaping)	00°08'N	100°10'E
Maninjau, lake	00°20'S	100°11'E
Padang	00°58'S	100°22'E
Perlak (Peureulak)	04°48'N	97°50'E
Sinkarah (Sinkarak)	00°42'S	100°36'E

Borneo

Dulit, hill	03°18'N	114°11'E
Kendawangan, river	02°32'S	110°12'E
Sandakan	05°50'N	118°07'E
Semandang, river	01°04'S	110°04'E

Tenasserim (S. Burma)

Bankachon	10°09'N	98°36'E
Champang	10°13'N	98°31'E
Tenasserim	12°05'N	99°01'E

Thailand

Klong Yai, river	11°46'N	102°54'E
Meh Lem, river	18°20'N	100°20'E
Raheng (Tak)	16°51'N	99°08'E

Laos

Thateng	15°26'N	106°22'E
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Vietnam

Hué (Hue)	16°28'N	107°36'E
Muong Mouen (Muong Muon)	21°40'N	103°04'E
Nha-Trang	12°15'N	109°11'E
Ninh Hoa	12°30'N	109°07'E
Quang Tri	16°46'N	107°11'E

China

Anhui, province (An-hui Sheng)	32°00'N	117°00'E
Chin-Kiang (Chinkiang = Chen-Chiang)	32°13'N	119°26'E

Futsing (Fu-ch'ing)	25°43'N	119°22'E
Kakhyen	about 26° N	99° E
Kiangsi, province (Chiang-hsi Sheng)	28°00'N	116°00'E
Kiu-Kiang (Chiu-chiang)	29°41'N	116°03'E
Lichiang (Li-chiang)	26°48'N	100°16'E
Nodoa (Na-ta)	19°31'N	109°33'E
Shen-si, province (Shen-hsi Sheng)	36°00'N	109°00'E
Szechwan, province (Ssu-ch'uan Sheng)	30°00'N	103°00'E
T'ung-Ling-Hsien	30°56'N	117°47'E
Tung-wan	23°00'N	113°50'E
Wen Chuan (Wen-Ch'uan)	31°22'N	103°33'E
<i>Burma</i>		
Carin, hills (Karennee)	19°30'N	97°00'E
Nam Tamai Valley	27°42'N	97°54'E
Yado, mountains	19°19'N	96°50'E
<i>Assam, India</i>		
Mawphlang	25°28'N	91°46'E
Naga Hills	26°00'N	95°00'E
<i>Nepal and Sikkim</i>		
Darjiling (Darjeeling)	27°02'N	88°20'E
Hathiban, locality near Kathmandu (Hinton & Fry, 1923)		
Kathmandu	27°42'N	85°19'E
<i>Java</i>		
Besoeki	07°45'S	113°41'E
Buitenzorg (Bogor)	06°35'S	106°47'E
Cheribon (Tjirebon)	06°43'S	108°35'E
Madioen (Madiun)	07°37'S	111°31'E
Pangandaran	07°41'S	108°39'E
Rambipoedji	08°13'S	113°36'E
Tjilatjap	07°44'S	109°01'E
Tjileungsi (Tjileungsir)	06°24'S	106°57'E
Tretes	07°43'S	112°36'E
<i>Sumbawa</i>		
Bima	08°27'S	118°45'E
Dompoe	08°30'S	118°28'E
Soembawa (Sumbawa)	08°28'S	117°26'E
<i>Flores</i>		
Badiawa (Badjawa)	08°47'S	120°59'E
Maumeri (Maumere)	08°37'S	122°14'E
Sikka (Sika)	08°45'S	122°12'E

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