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Notes on Southeast Asian Porcupines (Hystricidae, Rodentia) II On the taxonomy of the genus *Atherurus* F. Cuvier, 1829

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ABSTRACT

The individual and geographical variation of the Brush-tailed Porcupine, *Atherurus* F. Cuvier, 1829 from eastern India, Burma, Thailand, Laos, China, Hainan, Peninsular Malaysia and some adjacent islands has been studied from material in European and American museums. Information about this material is presented and the status of ten specific and subspecific names is discussed. Only one species, *Atherurus macrourus* (Linnaeus, 1758) is recognized and insufficient arguments were found for the distinction of subspecies on the basis of the small samples at present available. An error in Van Weers (1976: 19) concerning the name of the type species of *Trichys* Günther, 1877, is corrected in a foot note.

INTRODUCTION

Seba (1734: 84, pl. 52 figs. 1 and 2) described and figured the Brush-tailed Porcupine, "Porcus, aculeatus, sylvestris, seu Hystrix, Orientalis, singularis," thereby unambiguously characterizing the peculiar tail brush by comparing the swellings in its hairs to grains of rice. Linnaeus (1758: 57) gave the name *Hystrix macroura* to this taxon, quoting Seba thus: "Porcus aculeatus s. Hystrix orientalis. Seb. mus. 1. p. 84. t. 52. f. 1. Habitat in Asia." F. Cuvier (1829: 483) used the generic name *Atherurus* for these porcupines with origin "Des Indes orientales" and described them as follows: ". . . leur queue est longue et terminée par un faisceau de lanières cornées, aplaties et étranglées d'espace en espace, de manière à représenter un chapelet", which corresponds with Seba's description. Lyon (1906: 199) stated that *Hystrix macroura* Linnaeus is the type species for the porcupine with the beaded tail bristle as it was the only available name at the time of Cuvier's description, and the same author (Lyon, 1907: 584) restricted the type locality of *macroura* to Malacca.

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This species lacks a holotype and individual variation within it is poorly understood. Until now there have been only a few Malayan specimens scattered over some European and American museums. On occasion, only one arbitrary specimen from the Malay Peninsula has been available for comparison with samples from other localities in Southeast Asia, and in other cases, newly described species were based on no more than one single specimen. This has led to the description of a number of doubtful species and subspecies. Mohr (1964) brought the number of names among Asiatic *Atherurus* to ten with the publication of two new ones. She distinguished three species and quoted eight subspecific names, whereas Ellerman (1961) recognized only one species with two subspecies, at the same time stating: "Probably if a large number of specimens for this genus were collected, it would be impossible to divide it into subspecies".

The aim of the present paper is a critical examination of the status of these species and subspecies and to present some information about the morphology of these taxa as far as is possible with the material of European and American museums that has been available to me.

Material and methods

Sources. — The list of specimens studied comprises 53 skins and 59 skulls of adult specimens and 14 skins and 16 skulls of non-adult ones, available 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.
IRSNB = Institut Royal des Sciences Naturelles, Bruxelles.
MNHN = Muséum National d'Histoire Naturelle, Paris.
MSNG = Museo Civico di Storia Naturale di Genova, Genoa.
RMNH = Rijksmuseum van Natuurlijke Historie, Leiden.
USNM = National Museum of Natural History, Washington.
UZMC = Universitetets Zoologiske Museum, Copenhagen.
ZMA = Zoölogisch Museum, Amsterdam.

Geographical areas. — The area of distribution of the specimens studied ranges from Assam in India to Vietnam and from the Malay Peninsula to Szechwan in China. To enable an analysis of the data gathered, a number of geographical areas, based on the distances and geographical barriers between groups of localities, have been distinguished and are presented in table I.

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

Measurements. — Cranial and external measurements are defined by Van Weers (1976: 17—19). These are the same as those used in the present

paper, except the definition of the tail bristles. In *Atherurus* these are highly modified flattened hairs, alternately expanded and contracted from one to six times.

Table I. Geographical areas with locality numbers (see map fig. 1) as used in the analysis of the data gathered and number of adult specimens studied.

Geographical area	Loc. numbers	Skins	Skulls
Malay Peninsula	1— 4	5	6
Pulau Terutau	5	1	1
Pulau Penang	6	—	1
Pulau Aur	7	7	8
Pulau Pemanggil	8	1	1
Pulau Tioman	9	4	5
Tenasserim, Burma	10	1	1
Southern Laos	11—12	3	3
Annam, Vietnam	13	3	3
Thailand	14—15	1	2
Central Laos	16—17	2	2
Tonkin, Vietnam	18—20	6	6
Hainan, China	21	6	6
Northern Burma	22—27	6	6
Assam, India	28	1	1
Wanhsien, China	29	1	1
Unknown localities	—	5	7

Specimens examined

The numbers before the localities in this list of specimens examined correspond with the numbers of the localities on the distribution map and in the histograms and tables in the present paper. The grouping of the localities in geographical areas is the same as presented in table I. The coordinates are given in the Gazetteer. Abbreviations: HB = length of head and body, Tl = length of tail, Hf = length of hindfoot, E = ear, Wt = weight.

Malay Peninsula

1. Skeats camp, G. Tahan, Malaya, BMNH 55.3206, skull, adult ♂, coll. no.5.
2. Province of Wellesley, Malay Peninsula, BMNH 54.10.5.8, skin and skull, adult ♂, E. J. Comp. no. 880 b, Dr. Cantor.
   —, UZMC M-493, skin and skull, adult, Aschlund 27-IX-1848 no. 5.
   —, UZMC M-492, skin and skull, young, Aschlund 27-IX-1848 no. 4.
3. Jalor, Malay Peninsula, BMNH 3.2.6.75, skin and skull, adult ♂, H. C. Robinson and N. Annandale no. 182.
4. Trong, Malay Peninsula, USNM 84433, skin and skull, adult ♀, W. L. Abbott 22-1-1897, HB 17.5, Tl 9, Wt 9.75 lbs., uterus contained one fetus 1.5 inch in length.

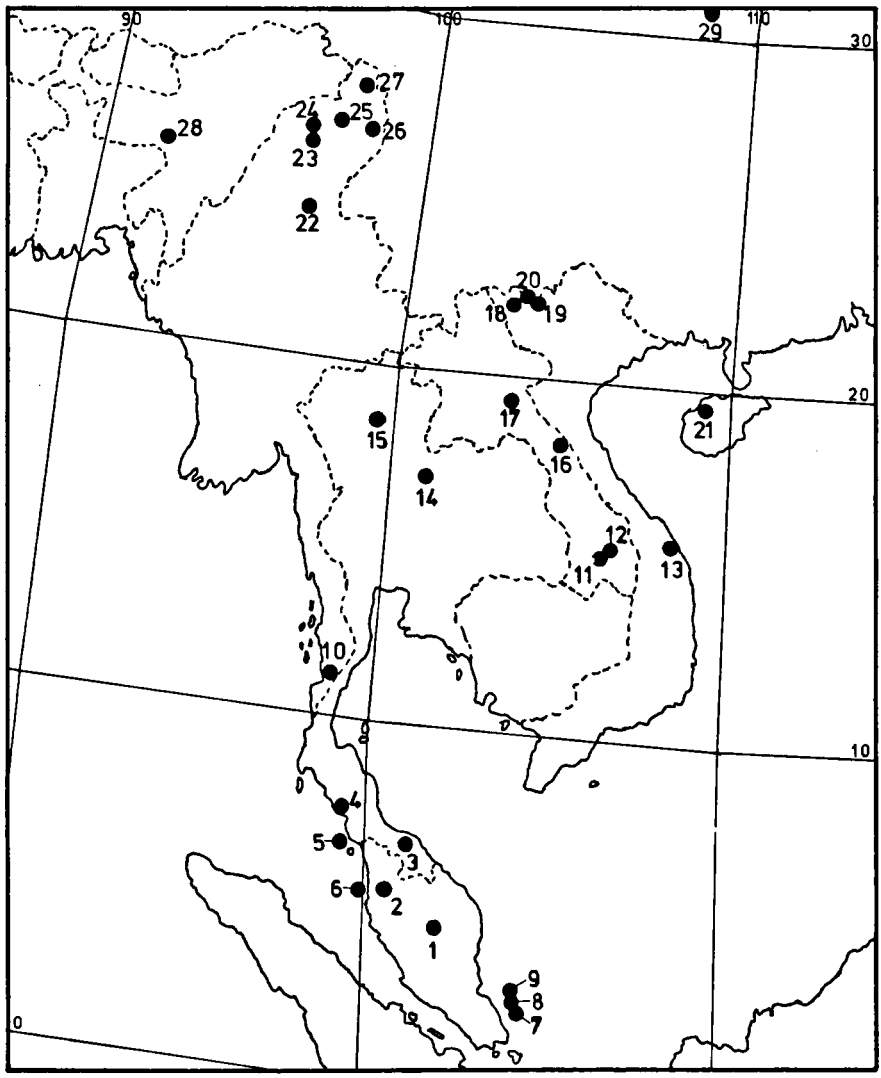

Figure 1. Range of the Southeast Asiatic *Atherurus* forms as determined by specimens examined. The numbers of plotted localities correspond with the numbers in the list of specimens examined and with those in the histograms of the figs. 2, 3 and 4 and the tables I and III.

—, USNM 49498, skull and skeleton, adult ♀, 6-II-1897.
—, USNM 83500, skin and skull, subadult ♀, W. L. Abbott 2-XI-1896, length to anus 19, tail from anus 8, Wt 7 lbs.
Malacca, RMNH 20020, skin, Diard, (= Jentink's, 1888, *Atherura macrura* no. b).

PULAU TERUTAU

5. Pulo Terutau, USNM 123971, holotype of *Atherurus terutaus* Lyon, 1907, skin and skull, adult ♂, W. L. Abbott 10-IV-1904 no. 3223, HB anus 440, Tl from anus 110, Wt 6.76 lbs.

PULAU PENANG

6. Pulo Pinang, UZMC M-494, skull, adult, Dr. Cantor 16-VII-1846.
— , UZMC M-491, skin and skull, subadult ♂, Dr. Cantor 16-VII-1846 no. 20.
— , BMNH 79.11.21.639, skin and skull, subadult, Dr. Cantor 880c no. 54.
— , BMNH 60.5.4.76, skin and skull, young ♀, E. India House Coll.

PULAU AUR

7. Pulo Aor, South China Sea, USNM 112429, holotype of *Atherura zygomatica* Miller, 1903, skin and skull, adult ♀, W. L. Abbott 6-VI-1901, HB 520 mm, Tl 200 mm, Wt 9 lbs.
— , USNM 112431, paratype of *A. zygomatica* Miller, W. L. Abbott 7-VI-1901 no. 1014, HB 500 mm, Tl from anus 145 mm, Wt 10 lbs.
— , USNM 112432, paratype of *A. zygomatica* Miller, skin and skull (sawed through lengthwise), adult ♂, W. L. Abbott 7-VI-1901, HB 485 mm.
— , USNM 112434, paratype of *A. zygomatica* Miller, skin and skull, adult ♀, W. L. Abbott 7-VI-1901 no. 1022, HB 500 mm.
— , USNM 49602, paratype of *A. zygomatica* Miller, skull and skeleton, adult, W. L. Abott 8-VI-1901.
— , BMNH 8.1.25.30, skin and skull, adult ♀, H. C. Robinson 16-VI-1906, F.M.S. no. 326/06, HB 516, Tl 209, Hf 64, E 36.
— , BMNH 55.3208, skin and skull, adult ♂, H. C. Robinson 15-VI-1912 no. 5017, F.M.S. no. 347/12, HB 457, Tl 190, Hf 68, E 37.
— , BMNH 55.3207, skin and skull, adult ♂, H. C. Robinson no. 4886, F.M.S. no. 349/12, HB 469, Hf 68, Tl 213, E 36.
— , USNM 112430, paratype of *A. zygomatica* Miller, skin and skull, subadult ♀, W. L. Abbott 6-VI-1901 no. 1010, HB 470 mm, Tl 190 mm, Wt 7.75 lbs.

PULAU PEMANGGIL

8. Pulau Pemanggil, South China Sea, BMNH 49.435, holotype of *Atherurus macrourus pemangilis* Robinson, 1912, skin and skull, adult ♀, H. C. Robinson no. 5014, F.M.S. no. 341/12, HB 456, Hf 64, E 34.
— , BMNH 55.3212, paratype of *A: m. pemangilis* Robinson, skin and skull, subadult, H. C. Robinson, F.M.S. no. 344/12, HB 487, Tl 203, Hf 67, E 34.5.

PULAU TIOMAN

9. Juara Bay, Pulau Tioman, South China Sea, BMNH 8.1.25.21, holotype of

Atherurus tionis Thomas, 1908, ♂ skin only, skull assumed to be lost, H. C. Robinson 13-VI-1906, F.M.S. no. 325/06, HB 516, Tl 176, Hf 66, E 35.
— , BMNH 8.1.25.52, paratype of *A. tionis* Thomas, skull only, skin in the collections of the University of Singapore, adult ♀, H. C. Robinson no. 323.
— , BMNH 8.1.25.51, paratype of *A. tionis* Thomas, adult ♂, H. C. Robinson no. 324.
— , BMNH 55.3209, skin and skull, adult ♂, H. C. Robinson 79, F.M.S. no. 438/15, 27-VI-1915, HB 378, Tl 138, Hf 56, E 34.
— , BMNH 55.3211, skin and skull, adult ♀, H. C. Robinson 24-VI-1915 no. 6612, F.M.S. no. 440/15, HB 434, Tl 148, Hf 68, E 38.
— , BMNH 55.3210, skin and skull, adult ♂, H. C. Robinson 24-VI-1915 no. 6613, F.M.S. no. 442/15, HB 452, Hf 68, E 34.

TENASSERIM, BURMA

10. Thoungyah, Tenasserim, BMNH 85.8.1.340, skin and skull, adult ♂, J. Darling, Allen O. Hume.

SOUTHERN LAOS

11. Plateau Bolovens, Laos, AMNH 87585, skin and skull, adult ♀, T. D. Carter no. 448, leg. Indo-China Exped. 1-II-1932, total length 750, Tl 250, Hf 60.
— , AMNH 87586, skin and skull, adult ♂, T. D. Carter no. 449, leg. Indo-China Exped. 1-II-1932, total length 840, Tl 265, Hf 70.
12. Thateng, Laos, FMNH 37992, skin and skull, adult ♂, J. Delacour 14-XII-1931 no. 109, total length 680, Tl 250, Hf 71.

QUANG NAM, VIETNAM

13. 2.5 km W., 0.5 km S. Mt. Sontra, Prov. Quang Nam, Vietnam, USNM 356571, skin and skull, adult ♂, T. J. Mc Intyre no. 607, 15-III, prep. 21-III-1966, length 610, Tl 210, Hf 65, E 33, alt. 200 m.
— , USNM 356572, skin and skull, adult ♀, T. J. Mc Intyre no. 660, 25-V-1966, length 634, Hf 63, Tl 218, E 38.
— , USNM 356573, skin only, T. J. Mc Intyre no. 662, 13-V-1966, length 620, Hf 66, Tl 205, E 35.

THAILAND

14. Lomlo Mtn., Dansai, Loei, USNM 300170, skin and skull, adult ♂, R. E. Elbel 29-III-1954, R. E. 3512, 730—250—70—40.
15. Doi Sutep, West Siam, UZMC 14152, holotype of *Atherurus angustiramus* Mohr, 1964, skull only, adult, evergreen forest, 1000 m, det. 1-XI-1959.

CENTRAL LAOS

16. Nape, Laos, BMNH 28.7.1.144, skin and damaged skull, adult ♂, W. Lowe no. 843, 29-I-1928, HB 485, Tl 205, Hf 79, E 38.

17. Xieng-Khouang, Laos, BMNH 26.10.4.192, skin and damaged skull, adult ♀, J. Delacour-W. Lowe no. 173, 12-I-1926, HB 530, Tl 175, Hf 78, E 37.

TONKIN, VIETNAM

18. Lai Chau, Tonkin, FMNH 32516, skin and skull, adult ♂, R. E. Wheeler 1-IV-1929, Kelley-Roosevelt Exp. no. 5399, 696—190—78.
19. Chapa, Tonkin, BMNH 33.4.1.490, skin and skull, adult ♀, J. Delacour-W. Lowe no. 1495, 30-XI-1929, alt. 5000 ft., HB 515, Tl 235, Hf 77, E 40.
— , BMNH 33.4.1.491, skin and skull, adult ♂, J. Delacour-W. Lowe no. 1654, 11-XII-1929, alt. 5000 ft., HB 505, Tl 225, Hf 73, E 41.
— , USNM 259437, skin and skull, adult ♀, J. Delacour-W. Lowe no. 1557, alt. 5000 ft., HB 515, Tl 240, Hf 74, E 38.
— , BMNH 33.4.1.493, skin and skull, subadult ♀, J. Delacour-W. Lowe no. 1518, alt. 5000 ft., HB 455, Tl 200, Hf 76, E 36.
— , BMNH 33.4.1.492, skin and damaged skull, adult ♂, J. Delacour-W. Lowe no. 1724, HB 510, Tl 245, Hf 75, E 42.
— , BMNH 33.4.1.494, skin and skull, young ♀, J. Delacour-W. Lowe no. 1570, 6-XII-1929, alt. 5000 ft., HB 370, Tl 180, Hf 69, E 37.
20. Ngai-Tio, Tonkin, BMNH 25.1.1.93, holotype of *Atherurus stevensi* Thomas, 1925, skin and skull, adult ♀, H. Stevens no. 156, 8-VI-1924, alt. 4800 ft., HB 525, Tl 228, Hf 75, E 36.

HAINAN, CHINA

21. Hainan, China, AMNH 26641, holotype of *Atherurus hainanus* Allen, 1906, skin and skull, adult, IX-1902.
— , Nodoa, AMNH 60143, skin and skull, adult ♀, C. Pope no. 558.
— , Nodoa, AMNH 60145, skin and skull, adult ♀, C. Pope no. 663, 25-I-1923.
— , Nodoa, AMNH 60147, skin and skull, adult ♀, C. Pope no. 676, 27-I-1923.
— , Nodoa, AMNH 60045, skeleton, young.
— , Nodoa, AMNH 117640, skin and skull, adult ♂, C. Pope.
— , Nodoa, AMNH 60043, skin and skull, adult ♂, C. Pope no. 398, 11-I-1923.

NORTHERN BURMA

22. 50 miglie Est di Bhamò, Dint. di Mongioch, Birmania, MSNG 34177, skull, skin no. 34176, young, L. Fea 1885.
23. Haibum, N.O. Burma, AMNH 113485, skin and skull, adult ♀, H. C. Raven 25-II-1935, Vernay-Hopwood Exped. no. 300, 625—125—69.
— , AMNH 113486, skin and skull, adult ♂, H. C. Raven 25-II-1935, Vernay-Hopwood Exped. no. 301, 650—140—70.
— , AMNH 113487, skin and skull, adult ♀, H. C. Raven 25-II-1935, Vernay-Hopwood Exped. no. 302, 670—185—70.
— , AMNH 113483, skin and skull, subadult ♀, H. C. Raven 29-I-1935, Vernay-Hopwood Exped. no. 145, 655—187—71.

24. Dalu, N.O. Burma, AMNH 113484, skin and skull, young ♀, H.C. Raven, 15-II-1935, Vernay-Hopwood Exped. no. 244, 610—180—72.
25. Hkampti Plain, Upper Burma, BMNH 32.11.168, skull, adult ♀, Lord Cranbrook-F. Kingdon Ward no. 392.
— , FMNH 41048, damaged skull, adult ♂, Lord Cranbrook.
— , FMNH 41047, skull, subadult ♀, Lord Cranbrook no. 393, 16-XII-1931, 1500 ft.
26. Ningma, Upper Burma, BMNH 50.705, skin and incomplete skull, young ♀, R. Kaulback no. 503, 15-I-1939, N 26.33, E 97.43, 1300 ft.
27. Nam Tamai Valley, Upper Burma, BMNH 50.702, skin and skull, adult ♂, R. Kaulback no. 157, 13-IX-1938, 470 (anus)-187—72—35, N 27.42, E 97.54, 5000 ft.
— , BMNH 50.704, skin, R. Kaulback no. 387, 5-XII-1938, N 27.42, E 97.58, 3000 ft.

ASSAM, INDIA

28. Cherrapunji, Upper Assam, BMNH 20.11.1.77, holotype of *Atherurus assamensis* Thomas, 1921, skin and skull, adult ♂, H. W. Wells no. 563, HB 420, Tl 220, Hf 65, E 34, Wt 4.5, alt. 4500 ft.
— , Mawphlang, Assam, FMNH 758772, damaged skin and skull fragments, young ♀, D. Wal-N. Koelz 24-XII-1952, length 474, Tl 153, Hf 62, E 32.

WANHSIEN, CHINA

29. Szechuan, Wanhsien, AMNH 58369, skin and skull, adult ♂, Walter Granger no. 449, 535—240—80—40.

UNKNOWN, LOCALITIES

IRSNB 13918, holotype of *Atherurus retardatus* Mohr, 1964, skin and skeleton, adult ♀, Soc. Roy. Zool. Anvers 18.I.1963.
IRSNB 15177, paratype of *A. retardatus* Mohr *), skeleton, adult ♂, Soc. Roy. Zool. Anvers 23-XI-1963.
RMNH 19420, paratype of *A. retardatus* Mohr *), skin and skull, adult ♂, zoological garden Rotterdam 12-I-1967.
RMNH 19897, paratype of *A. retardatus* Mohr *), skin and skull, adult ♀, zoological garden Rotterdam 13-II-1968.
RMNH 20782, paratype of *A. retardatus* Mohr *), skin and skull, adult ♂, zoological garden Rotterdam 8-IV-1969.
ZMA 5092 B (not 5292 as Mohr 1964: 107 recorded), paratype of *A. retardatus* Mohr, zoological garden "Natura Artis Magistra" Amsterdam 22-IX-1962.
MNHN 1962.2231, skull, adult, Indo-Chine, Capitaine Bonifacy, a vécu du 27 mars 1902 au janvier 1903.
BMNH 81.11.23.1, Malayan region, skin and skull, adult, E. Gerrard 880c, presumed Pulo Aor.

*) At the moment the holotype was studied by Mohr, these specimens were still alive in the Antwerp and Rotterdam Zoo.

Results

Genus **Atherurus**

Atherurus F. Cuvier, 1829: 483

Type species. — *Hystrix macroura* Linnaeus, 1758, type by monotypy.

Range. — Malay Peninsula and adjacent small islands, Thailand, Laos, Vietnam, Hainan and Szechwan (China), Burma, Assam (India) and tropical Africa (extra-limital).

Diagnosis. — Differing from the more primitive genus *Trichys* *) Günther in the number of dorsal vertebrae, 14 in *Atherurus* against 16 in *Trichys*. The tail is shorter on average, one quarter to half the length of the head and body with about 19 to 23 caudal vertebrae as against about 22 to 25 in *Trichys*. As for the skull characters, there is scarcely a postorbital process and the postorbital breadth is always larger than in *Trichys*. The longest spines are always larger than those of *Trichys*. From the least specialized representatives of the genus *Hystrix*, subgenus *Thecurus* Lyon, 1907, it differs in the permanent molars showing visible roots when in place and in the quite different tail structure. This genus is fully characterized by its peculiar caudal bristles, alternately expanded and contracted from one up to six times.

According to Yong Hoi-Sen *et al.* (1973), *Atherurus macrourus* has a diploid number of 54 chromosomes against 46 chromosomes in *Trichys fasciculata*.

Remarks. — *Hystrix macroura* Linnaeus, 1758, is the type by monotypy as pointed out by Jentink (1894: 207) and Lyon (1906: 199) and not by subsequent designation by Lyon (1907: 584) as mentioned by Delany (1975: 113).

Shaw's (1801) *Hystrix fasciculata* from Malacca, has sometimes been associated with *Atherurus* (Günther, 1889; Thomas, 1889 and 1907; Bonhote, 1900). This has been refuted thoroughly by Jentink (1894), Mohr (1963), more recently by Van Weers (1976), and the designation of a Malayan *Trichys* specimen as neotype for *H. fasciculata* by the latter author definitely has taken away the basis for this confusion.

The five nominal taxa from the African part of the range should probably be regarded as one species, *A. africanus* Gray, 1842, according to Delany (1975) and Kingdon (1974) but are not listed here.

List of nominal taxa:

Hystrix macroura Linnaeus, 1758: 57

Type. — No holotype designated.

Type locality. — "Habitat in Asia". Lyon (1907: 584) restricted the type locality to Malacca, obviously used as a synonym of Malay Peninsula and taken as such in the present paper.

*) The type species of this genus is *Trichys lipura* Günther, 1877, type by monotypy, and not "*Trichys fasciculata* (Shaw, 1801)" as erroneously recorded by Van Weers (1976: 19).

Atherura zygomatica Miller, 1903: 42
Holotype: USNM 112429, skin and skull, adult ♀.
Type locality: Pulo Aor. (Loc. no. 7 in map fig. 1)

Atherurus hainanus Allen, 1906: 470
Holotype: AMNH 26641, skin and skull, adult.
Type locality: Hainan. (Loc. no. 21 in fig. 1)

Atherurus terutaus Lyon, 1907: 587
Holotype: USNM 123971, skin and skull, adult ♂.
Type locality: Pulo Terutau. (Loc. no. 5 in fig. 1)

Atherurus tionis Thomas, 1908: 105
Holotype: BMNH 8.1.25.21, ♂ skin.
Type locality: Juara Bay, Pulau Tioman. (Loc. no. 9 in fig. 1)

Atherurus macrourus pemangilis Robinson, 1912: 590
Holotype: BMNH 49.435, skin and skull, adult ♂.
Type locality: Pulau Pemanggil. (Loc. no. 8 in fig. 1)

Atherurus assamensis Thomas, 1921: 598
Holotype: BMNH 20.11.1.77, skin and skull, adult ♂.
Type locality: Cherrapunji, Assam. (Loc. no. 28 in fig. 1)

Atherurus stevensi Thomas, 1925: 505
Holotype: BMNH 25.1.1.93, skin and skull, adult ♀.
Type locality: Ngai-Tio, Tonkin. (Loc. no. 20 in fig. 1)

Atherurus retardatus Mohr, 1964: 105
Holotype: IRSNB 13918, skin and skull, adult ♀.
Type locality: Unknown, from Zoo Rotterdam.

Atherurus angustiramus Mohr, 1964: 108
Holotype: UZMC 14152, skull, adult, skin of head and tail with brush.
Type locality: Doi Sutep, Chengmai, Thailand. (Loc. no. 15 in fig. 1)

Cranial measurements:

Measurements of 15 cranial dimensions for 16 samples from the geographic areas given in table I, are presented in table II. Some of them, and some cranial characters not included in this table, are further discussed below. The remaining cranial dimensions presented in table II, reflect mainly the differences as already expressed by the cranial length measurements.
Cranial length. — The occipito-nasal length and the bassilar length are also presented in two histograms, figures 2 and 3. Both histograms show the considerable differences in skull size. All the island populations are distinctly smaller (occ. nas. l. 87—94 mm) than the populations of Tenasserim, Laos, Thailand, Tonkin and Wanhsien (97—109 mm). However, the samples of the continental populations from Annam, N. Burma and Assam are equally

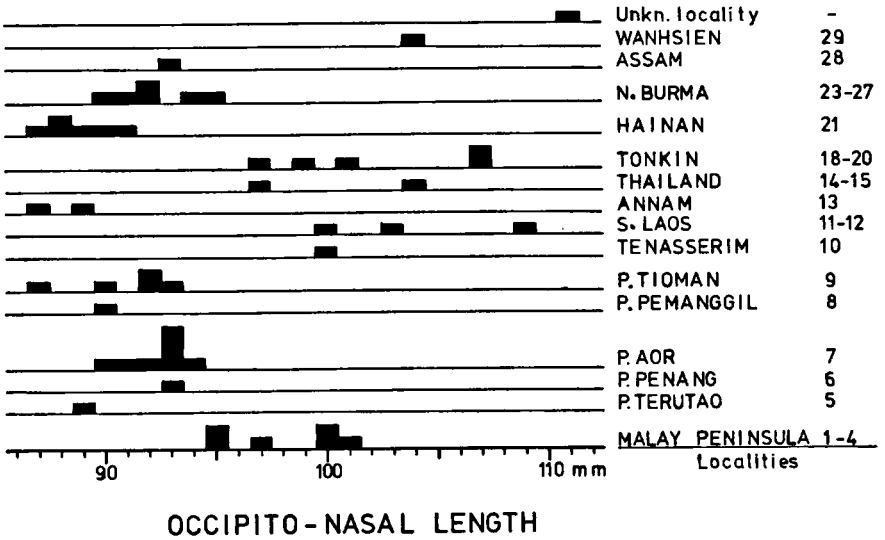

Figure 2. Frequency distribution of the occipito-nasal length of skulls of *Atherurus macrourus*. Adult specimens only. Locality numbers correspond with those on the distribution map (fig. 1). Specimen from unknown locality is MNHN 1962.2231.

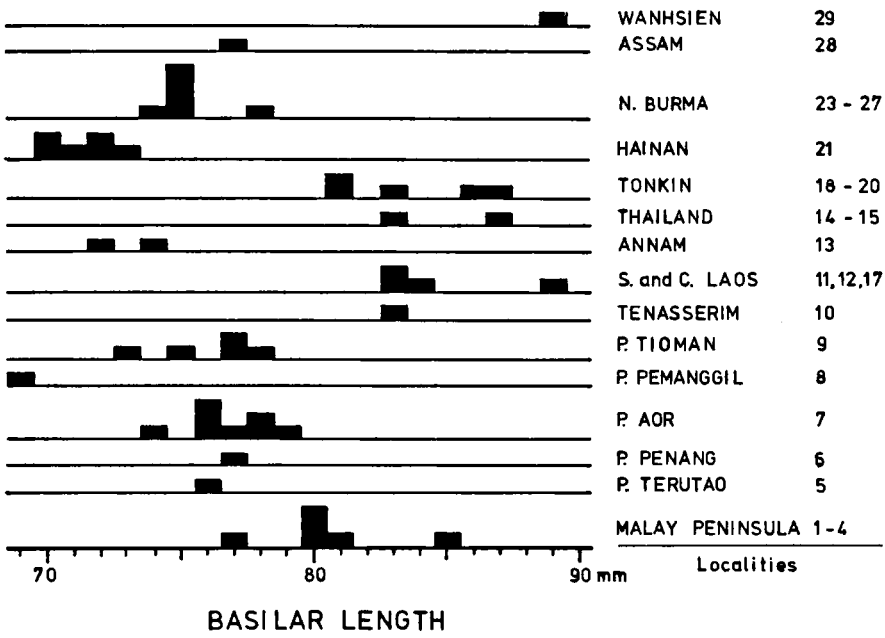

Figure 3. Frequency distribution of the basilar length of skulls of *Atherurus macrourus*. Adult specimens only. Locality numbers correspond with those on the distribution map (fig. 1).

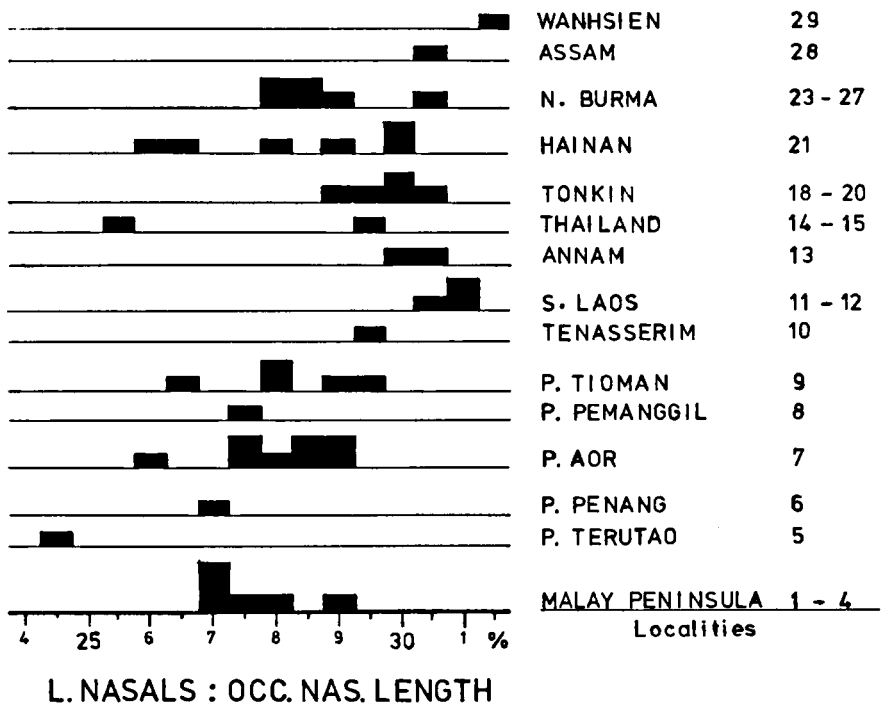

Figure 4. Frequency distribution of the relative size of the nasals of *Atherurus macrourus*, expressed as a percentage of the occipito-nasal length of the skull. Adult specimens only. Locality numbers correspond with those on the distribution map (fig. 1).

small and that from the Malay Peninsula is intermediate in size (95—101 mm). The basilar length measurements reflect these proportions in the same way (respectively 69—79 mm, 81—89 mm and 77—85 mm). Therefore, it would be quite arbitrary to divide these populations into two or more taxonomic units on cranial length alone.

Nasal length. — In most of the original descriptions of Asiatic *Atherurus* species the nasal length has been used as a diagnostic character. Therefore, the relative length of the nasals, expressed as a percentage of the occipito-nasal length, is presented in a histogram (fig. 4). This relative measure has been chosen because the absolute size differences have been stressed sufficiently by the two cranial length measurements. The holotype of *A. terutaus* Lyon, 1907 has absolutely, as well as relatively, the smallest nasals (21.7 mm, 24,4%). But since it is the only specimen available from that locality, no conclusions as to its specific or subspecific status on this character are justified. The same can be said of the specimen from Wanhsien, China, representing the upper extremity of this measurement in table II and fig. 4 (33.0 mm, 31.7%). There is a clear difference between the relative nasal sizes of the sample from S. Laos (30.3—31.0%) and those of the

Malayan specimens (26.9—28.1%), but the measurements of all the other continental populations are intermediate between these two. The relative size of the nasals of the five remaining island populations varies from 26 to 30% so it is obvious that this character is of little use for diagnostic purposes.

Nasal breadth. — In Thomas' (1925) description, the nasals of *A. stevensi* are called narrower, eespecially their posterior breadth. When compared with the Malay Peninsular population, this character does not hold good. The posterior breadth of the combined nasals of the holotype from Tonkin is 43.5% of the nasal length while in six Malayan specimens this ratio varies from 40.7 to 52.0% and in five specimens from Tonkin from 43.3 to 51.2%.

The most important diagnostic character in Mohr's (1964) description of *A. angustiramus* is the difference between the posterior and anterior breadth of the nasals, in the holotype respectively 12.4 and 16.4 mm. However, these dimensions fall within the range of variation of the Asiatic speciees as may appear from table II, and extremer ratios are found in a specimen from Malaya (11.2 and 15.4 mm) and in one from Laos (11.7 and 16.5 mm).

Lachrymal bone. — According to Miller's description (1903), there is a constant difference between the form of the lachrymal bone of *A. zygomaticus* and that of the mainland animal. Miller gives fully 8 mm for the lateral dimension of the latter's lachrymal bone, but of the six Malayan specimens available three are below that value (5.5—10 mm, m= 7.5 mm). The same author mentions measurements of about 5 mm for *zygomaticus* from Pulau Aor, but the seven available measurements range from 5 to 9 mm (m= 6.1), so this difference is not constant and is smaller than originally described.

According to Miller (1903) again, the forward extension of the lachrymal bone in the dorsal skull surface in *zygomaticus* is scarcely visible when the skull is viewed from above. Measurements of the *zygomaticus* specimens show lengths from 0 to 4.4 mm and the Malayan sample 3 to 7.5 mm. So there is some overlap, and in 36 measurements of the remaining Asiatic samples the dorsal length of this bone appears to vary from 0 to nearly 8 mm, obviously correlated with cranial length. Therefore, the population of Pulau Aor cannot be distinguished from the continental populations on this character.

Zygoma shape. — Miller (1903) stated that the zygoma of his *A. zygomatica* is shorter than that of the mainland animal. Expressed as a percentage of the basilar length, the zygoma length (measured from the posterior rim of the infraorbital foramen to the posterior edge of the zygomatic process of the squamosum) of seven specimens from Pulau Aor ranges from 38.2 to 40.7% (m= 39.3%) and six Malayan specimens vary from 37.4 to 43.8% (m= 39.6%), so these samples do not differ at all in this respect.

Miller (1903) also stated that, compared with the continental forms, the zygoma of the Pulau Aor form is deeper in proportion to its length. To test this statement, the height of the jugal bone at the anterior jugal suture of part

Table II.

Cranial measurements in millimetres of adult specimens of *Atherurus macrourus* from geographic areas as distinguished in the present study with range, mean of sample in parentheses, number of measurements (n) and the standard deviation (s). For the definitions of the measurements see Material and Methods. P.=Pulau, Tu.=Terutau, Pg=Penang, Pl.=Pemanggil, Ten.=Tenasserim, Vm.=Vietnam, Ass.=Assam, Wanh.=Wanhsien, Un.l.=unknown locality (MNHN 1962.2231).

	Malay Peninsula	P. Tu.	P. Pg.	Pulau Aur	P. Pl.	Pulau Tioman	Ten.	Southern Laos
Occ. nas. 1	94.7—101.4 (97.9) n=6 s=2.85	88.8	93.3	90.1—94.0 (92.3) n=8 s=1.28	89.6	86.7—92.8 (90.7) n=5 s=2.41	100.2	100.0—109.0 (104.1) n=3
Basilar 1.	77.0—85.5 (80.6) n=6 s=2.77	75.8	77.4	73.8—78.1 (76.7) n=8 s=1.73	68.6	72.6—77.7 (75.8) n=5 s=2.10	82.9	83.3—89.0 (85.3) n=3
L. nasals	25.4—28.1 (27.0) n=6 s=1.06	21.7	25.3	24.3—27.1 (25.9) n=8 s=0.89	24.7	24.2—27.3 (25.6) n=5 s=1.40	29.4	31.0—33.8 (32.0) n=3
L. frontals	34.6—41.6 (39.1) n=6 s=2.48	36.5	35.0	33.5—37.0 (35.5) n=8 s=1.13	35.9	32.6—36.3 (34.0) n=5 s=1.74	43.4	39.00—40.3 (39.7) n=3
Palatal 1.	44.5—52.1 (48.0) n=6 s=2.71	45.1	46.7	41.6—48.8 (46.5) n=7 s=2.31	42.3	44.2—46.1 (45.4) n=5 s=0.74	52.2	51.3—55.0 (52.7) n=3
L. diast.	26.4—31.0 (28.8) n=6 s=1.48	28.0	27.6	26.0—27.7 (27.1) n=7 s=0.65	23.9	25.8—28.1 (27.4) n=5 s=0.94	29.8	30.0—34.3 (31.6) n=3
B. nas. po.	11.2—14.3 (12.8) n=6 s=1.17	10.3	12.8	12.0—13.5 (12.6) n=7 s=0.52	11.5	11.6—13.6 (12.4) n=5 s=0.88	14.5	13.7—14.2 (14.0) n=3
B. nas. ant.	14.7—16.7 (15.2) n=6 s=0.76	14.6	13.6	12.8—14.1 (13.6) n=7 s=0.67	13.5	13.3—15.5 (14.6) n=5 s=0.82	15.8	14.8—17.0 (15.7) n=3
Postorb. b.	25.9—29.1 (27.6) n=6 s=1.17	24.6	26.4	24.4—26.7 (25.5) n=7 s=0.86	25.1	25.8—27.4 (26.4) n=5 s=0.63	28.0	26.3—28.8 (27.8) n=3
Zygom. b.	46.0—50.3 (48.0) n=6 s=1.70	45.5	44.0	44.2—47.0 (45.6) n=7 s=0.85	45.2	47.1—48.8 (48.0) n=5 s=0.68	50.0	47.5—48.8 (48.2) n=3
Height sk.	25.0—27.0 (26.0) n=6 s=0.94	23.9	24.0	24.5—26.6 (25.3) n=8 s=0.65	23.4	22.6—25.4 (24.2) n=5 s=1.10	26.8	25.1—28.1 (26.8) n=3
L. mandible	60.8—64.0 (62.2) n=6 s=1.35	56.7	57.0	55.6—59.4 (57.9) n=8 s=1.21	55.3	55.0—59.2 (57.7) n=5 s=1.68	60.0	63.5—66.6 (64.6) n=3
H. mandible	22.0—25.2 (23.3) n=4	22.6	—	24.1—26.0 (25.3) n=5 s=0.73	—	—	—	24.3—26.5 (25.3) n=3
Alv. P4—M3	17.0—19.3 (18.0) n=6 s=0.82	16.2	18.2	15.0—17.4 (16.5) n=6 s=0.89	16.8	15.7—16.8 (16.2) n=5 s=0.43	18.5	17.1—18.3 (17.7) n=3
Alv. p4—m3	18.9—20.6 (19.8) n=6 s=0.74	17.8	19.8	17.2—18.1 (17.6) n=7 s=0.32	—	17.6—18.3 (17.8) n=5 s=0.29	19.2	19.0—19.6 (19.2) n=3

Table II. Continued.

	Annam, VM.	Thailand	C. Laos	Tonkin, Vietnam	Hainan, China	N-Burma	Ass.	Wanh.	Un.l.
Occ. nas. l.	87.2—89.3 n=2	97.5—103.7 n=2	—	97.4—107.1 (102.1) n=5 s=4.17	87.3—91.0 (88.9) n=6 s=1.48	90.0—94.9 (92.5) n=6 s=1.83	93.1	104.1	111.3
Basilar l.	72.0—73.7 n=2	83.2—86.9 n=2	83.4	81.4—86.6 (83.7) n=5 s=2.62	69.7—73.5 (71.4) n=6 s=1.31	74.0—78.0 (75.4) n=6 s=1.36	76.8	89.2	88.0
L. nasals	26.4—26.9 n=2	25.0—30.4 n=2	29.0—29.5 n=2	28.7—32.6 (30.4) n=5 s=1.59	23.2—27.5 (25.1) n=6 s=1.69	25.7—27.8 (26.7) n=6 s=0.77	25.8	33.0	32.0
L. frontals	31.8—32.9 n=2	39.2—41.9 n=2	42.4	36.5—42.5 (39.0) n=5 s=2.50	33.8—39.5 (35.0) n=6 s=2.22	34.8—39.2 (36.9) n=5 s=1.93	35.0	38.5	40.0
Palatal l.	44.0—45.0 n=2	49.7—55.6 n=2	51.5—51.9 n=2	50.5—54.9 (52.2) n=5 s=1.92	42.5—45.6 (44.2) n=5 s=1.26	41.8—46.0 (45.0) n=6 s=1.61	46.7	56.5	55.0
L. diast.	25.4—27.0 n=2	31.5—31.9 n=2	30.4—31.7 n=2	30.0—31.9 (31.1) n=5 s=0.80	24.2—26.7 (25.5) s=1.08	25.6—29.7 (27.4) n=6 s=1.53	28.0	30.7	33.0
B. nas. po.	11.4—12.2 n=2	12.4—13.7 n=2	11.7—13.5 n=2	12.7—14.7 (14.1) n=5 s=0.79	9.2—12.2 (10.9) n=6 s=0.98	11.6—14.5 (13.2) n=6 s=1.00	12.7	13.5	13.4
B. nas. ant.	13.2—13.8 n=2	16.0—16.4 n=2	16.5—17.0 n=2	14.4—16.7 (15.5) n=5 s=0.83	11.8—15.5 (13.0) n=6 s=1.39	13.8—15.3 (14.5) n=6 s=0.63	14.0	15.8	—
Postorb. b.	24.2—24.5 n=2	26.8—27.5 n=2	27.9—28.4 n=2	27.5—29.2 (28.4) n=5 s=0.65	24.7—27.1 (25.8) n=5 s=0.88	25.3—29.6 (26.8) n=5 s=1.64	25.4	25.9	25.7
Zygom. b.	42.7—43.3 n=2	51.5—52.2 n=2	50.0—50.3 n=2	49.0—51.8 (49.6) n=5 s=1.22	42.6—45.0 (43.8) n=6 s=0.84	44.5—47.9 (46.4) n=6 s=1.60	43.3	48.8	48.2
Height sk.	22.7—24.1 n=2	25.7—27.4 n=2	27.4 —	23.8—26.9 (25.7) n=5 s=1.23	23.0—24.0 (23.7) n=6 s=0.38	23.4—26.9 (25.3) n=6 s=1.46	23.6	27.5	27.0
L. mandible	54.0—55.1 n=2	62.8—64.7 n=2	63.5—63.9 n=2	61.8—67.0 (63.2) n=4	53.2—56.8 (54.7) n=6 s=1.27	55.0—59.9 (57.3) n=6 s=2.09	55.9	66.1	65.0
H. mandible	20.1—22.5 n=2	24.4—26.5 n=2	— —	24.8—25.4 n=2	20.0—22.7 (21.5) n=6 s=0.98	21.5—22.9 (22.2) n=4	—	24.0	—
Alv. P4—M3	14.0—15.5 n=2	16.6—19.5 n=2	17.4—17.5 n=2	16.1—18.7 (17.7) n=5 s=1.07	15.0—16.4 (15.7) n=5 s=0.52	16.2—18.1 (17.3) n=6 s=0.97	16.4	20.8	17.3
Alv. p4—m3	14.5—16.1 n=2	19.6—19.7 n=2	19.0—19.0 n=2	17.6—20.1 (19.3) n=4	16.3—17.0 (16.6) n=5 s=0.27	16.4—18.3 (17.6) n=5 s=0.72	17.3	22.2	19.0

of the material studied has been measured and expressed as a percentage of the zygoma length. In six Malayan specimens this character varies from 25.7 to 28.9% (m= 27.6%) and in seven specimens from Pulau Aor from 29.9 to 31.7% (m= 30.7%), so in this respect these samples differ significantly indeed. Nevertheless, in this character, too, there is much variation throughout the total Asiatic population. Five specimens from Pulau Tioman have relative heights of the jugal of 24.8—28.5%, three specimens from South and Central Laos of 26.5—32.0% and four specimens from N. Tonkin of 24.6—30.1%. Moreover, one specimen (BMNH 81.11.23.1) from unknown locality with a most clear "toothlike process" at the zygoma (see below), has a relative zygoma height of 28.4%, so either the latter character in *zygomaticus* shows more variation or the former character is more widespread. So on the basis of the zygoma height with the individual and geographical variation as represented, no satisfying division of the species is possible now.

The lower contour of the jugal was described by Miller (1903) as follows: "... broken by a strongly developed concavity beneath posterior jugal suture, this concavity terminating anteriorly on the posterior upper surface of a well-marked tooth-like projection." The sample from Pulau Aor is distinguished more clearly by this character, indeed, than by those discussed before, but it is not developed equally strongly in the eight *zygomaticus* specimens studied, neither is it quite unique for this population. Although not all samples were studied on this character, a specimen with a more or less clearly developed concavity with toothlike process was found in the Tonkin and in the Annam sample (FMNH 32516 and USNM 356571) and in a larger number of specimens this character was found more or less slightly indicated.

External characters

Body size. — The length of head and body of the Asiatic *Atherurus* species as appears from 35 collector measurements recorded in the list of specimens studied ranges from 38 to 57 cm with a mean of 48 cm. Further analysis of these measurements has not been undertaken because of the uncertainty about the way in which they have been obtained.

Tail length. — The length of the tail in 31 collector measurements varies from 11 to 26 cm, being 25 to 52% of the length of head and body, mean 40%.

In dry skins the anterior border of the tail is not easily definable because of the different ways the skins have been prepared. Therefore the length of the scaly part of the tail of dry skins has been measured (table III). In Lyon's (1907: 587) description of *A. terutaus* the shorter tail was mentioned as diagnostic character. The length of the scaly part of the tail of the holotype (40 mm) is extremely small indeed, when compared with the Malayan specimens (130—150 mm). But the measurements in table III show an individual variation in the sample from Pulau Aor of 70 to 140 mm, in that

from Hainan of 60 to 130 mm and in the N. Burmese sample of 60 to 110 mm. Against the background of the individual and geographical variation of the tail length as presented in table III, one single specimen is insufficient proof for a different species or race on Pulau Terutau.

Hindfoot. — The length of a hindfoot in 29 collector measurements varies from 65 to 80 mm with a mean of 71 mm.

Ear. — The length of the ears in 29 collector measurements varies from 33 to 42 mm with a mean of 37 mm.

Colour. — The individual variation in the blackish-brown colour of back and sides is mainly caused by a different frequency of visible white parts of the spines and tactile bristles. This exposure of white parts of spines, however, may be influenced by shrinkage or stretching of a skin during preparation. Both individual variation and this phenomenon, interfere with the judgement of geographical variation.

Mohr's (1964) *A. retardatus* is mainly based on the presence of light and dark longitudinal stripes along the back and sides of adult animals. According to this author, all other Asiatic Brush-tailed Porcupines only show longitudinal stripes at birth which disappear after three or four weeks. However, little is known about the development of the colour pattern during life and there is nothing that affirms Mohr's statement. These dark and light stripes are found from rather clearly to at least slightly perceptible in all the Asiatic *Atherurus* specimens studied and the type series does not differ in this respect.

Thomas (1921) mentions of his *assamensis*: "colour above rather darker", but considering the individual variation as observed in all the other Asiatic samples, this single specimen does not prove that the population in Assam is different in this respect. In a very light-coloured skin from Tonkin (BMNH 33.4.1.490) nearly 50% of the large spines of the back have white tips of up to 25 mm in length. This is probably not common in this geographic area. The holotype of *A. stevensi* Thomas, 1925, from Tonkin does not possess white-tipped spines, but unfortunately this skin is damaged and nearly half of its large spines are lacking. Other skins from that area, however, show these white spines in a much less conspicuous degree.

Miller (1903) and Thomas (1921 and 1925) used a lighter or darker colour of the underside as a diagnostic character for respectively *zygomaticus* of Pulau Aor, *assamensis* from Assam and *stevensi* from Tonkin. Chin, throat and chest between the forelegs are whitish in all the specimens of the whole Asiatic material studied, but there is, indeed, some variation in the colour of the belly. In some specimens from the Malay Peninsula the belly is light brown with the spines with a pale brown middle part and a whitish tip, whereas others have more white on the belly. Some specimens from Pulau Aor have the same light brown belly as the darkest specimens from Malaya, whereas others from that island have the belly more darkly mottled. Thomas' (1925) type of *stevensi* has a white belly, but other specimens from Tonkin have light brown bellies, dirty white or light brown with a narrow white strip

in the middle. Apparently there is so much variation in the colour of the underside that its use as a diagnostic character in the small samples available is open to question.

Spines and tactile bristles. — The measurement of the longest spine and tactile bristle is somewhat subjective because it is not always possible to know whether in fact the longest spine or bristle of a skin has been measured. Therefore, although these measurements provide a good method of comparing the development of the spiny covering, no mean or standard deviation is recorded and only the ranges of the samples are presented in table III. The relation between skull size and development of spiny covering shows the following tendency. The samples with the largest skulls from Tenasserim, Laos, Thailand and Tonkin (see figs. 2 and 3) have the highest developed spiny covering with spines of 80 to 117 mm and tactile bristles of 120 to 160 mm, against spines of 70 to 75 mm and tactile bristles of 80 to 110 mm (see table III) in the samples from Annam and Hainan with smaller skulls. This tendency is far from constant. From the figs. 2 and 3 and table III it appears that the specimen from Wanhsien, China, with nearly the largest skull, has relatively short spines and bristles (respectively 7 mm and 110 mm). Further, the specimens from Pulau Aor with smaller skulls on an average than those from the Malay Peninsula, have spine lengths of 90 to 108 mm against 75 to 100 mm in the Malayan animals. Moreover, the sample from N. Burma with a relatively small skull length (figs. 2 and 3) has rather large tactile bristles (120 to 135 mm).

The largest spine in a skin varies in thickness from 1.2 to 2.2 mm in the total material studied, and its breadth ranges from 1.8 to 3.0 mm. These long spines on the posterior upper part of the back differ in form from the majority of the smaller spines in a skin. The long spines are thicker, and the shorter ones are broader and thinner as may be demonstrated with the measurements of a specimen chosen arbitrarily (BMNH 3.2.6.75), in mm:

length	thickness	breadth
100	2.1	2.2
97	1.8	2.3
50	1.6	2.5
45	1.3	2.6
32	0.9	2.6

The largest tactile bristle in the skins of all the specimens studied has a thickness near the basis of 1.0 to 1.8 mm.

Tail brush. — The length of the largest tail bristle in the total material studied, varies from 50 to 130 mm, the greatest number of expansions in one bristle varies from two to six, the size of the expansions is in most cases about 10 mm and ranges from 8 mm in some smaller beads to 25 mm in terminal ones which are generally somewhat larger.

Table III. Length of the longest spine, length of the longest tactile bristle and length of the scaly part of the tail in the skins of *Atherurus macrourus* studied. Adult specimens only. The locality numbers correspond to those in the map of fig. 1, measurements in millimetres, n= number of skins available.

	Loc. number	L. spines	Tact. br.	Scaly p. tail	n
Malay Peninsula	1—4	75—100	110—150	130—150	5
P. Terutau	5	90	130	40	1
P. Penang	6	80—85	110—140	110	2
P. Aur	7	90—108	110—130	70—140	7
P. Pemanggil	8	87—89		120	2
P. Tioman	9	76—87	110—120	100—130	4
Tenasserim	10	87	120	155	1
Laos	11, 12, 16, 17	97—110	125—140	90—140	5
Annam	13	70—75	100—105	120—130	2
Thailand	14, 15	105	160	160	1
Tonkin	18—20	80—117	120—160	130—170	7
Hainan	21	70—72	80—110	60—130	4
N. Burma	23—27	76—85	120—135	60—110	4
Assam	28	82	85	140	1
Wanhsien	29	75	110	150	1

Lyon (1907: 588) mentioned the caudal bristles with only one expansion in the tail brush of the holotype and only specimen of his new species *terutaus* and supposed that the worn appearance of the bristles might account for this feature. This implies that each bristle should have lost one or more beads, but the form and length of the expansions suggest that these are terminal ones. This adds to the probability of Mohr's (1964: 104) supposition that this specimen had totally shed its bristles and was forming new ones. Nevertheless, individual or geographical variation as a possible explanation may not be left out of consideration. A re-examination of this specimen yielded one bristle with two expansions, length 8 and 12 mm. A tail brush with bristles having only two expansions is found in one specimen in the sample from Pulau Aor, remaining specimens having four or five expansions, and also one in the Hainan sample, remaining specimens having three expansions. The available data suggest that there is a correlation between tail length and number of expansions in the bristles. As discussed before, this specimen from Pulau Terutau has the shortest tail of all the specimens studied, so it is not necessarily an aberrant individual. But considering the individual variation of this character in the Asiatic material, this single specimen cannot be accepted as sufficient proof for a different species or subspecies on that island.

Wool-hairs. — The original description of *A. stevensi* Thomas, 1925, reads: "Upper surface with much greater development of the close coat of wool-hairs beneath the spines." Each porcupine skin possesses something of an undercoat of wool-hairs, in most cases only perceptible when the spines are separated and sometimes more clearly visible. The type skin, however, has

lost the greater part of its spines on the middle and posterior part of the back, thus exhibiting these wool-hairs in quite an unusual way and making it difficult to compare the frequency of these hairs with other specimens. Two specimens from northern Tonkin do not show this character as described by Thomas, whereas in four others from that geographical area the wool-hairs are more abundant. The specimen from southern China does not show this character very conspicuously and southwards the specimens from Laos do not differ in this respect from the Malayan skins. But with the material available, it is not possible to decide whether the Tonkin sample differs or not, on an average, from others with regard to the development of wool-hairs.

Conclusions

All the Asiatic Brush-tailed Porcupines belong to one species *Atherurus macrourus* (Linnaeus, 1758). With the material currently available, a satisfactory division into subspecies is not possible and all the subspecies distinguished up to this moment are poorly characterized. The results of this study support the probability of Ellerman's supposition (1961) that it would be impossible to divide this species into subspecies if a larger number of specimens was collected.

Atherurus macrourus (Linnaeus, 1758)

Hystrix macroura Linneaus, 1758: 57

Type. — No type designated.
Type locality. — Original type locality "Habitat in Asia", restricted to Malacca by Lyon (1907: 584), considered a synonym of Malay Peninsula in the present paper.
Distribution. — The Asiatic range of the genus in the list of nominal taxa.
Synonyms. — Subjective synonyms as enumerated in the list of nominal taxa.
Characters. — Ellerman (1961: 292—295) gives a detailed description of external and cranial characters. A number of characters with their individual and geographical variation is discussed in the present paper (see Results). This species differs from the African form in the total absence of quills (long and thick spines, circular in cross-section and with the largest diameter about mid-length). As far as I know, some of these quills are always present in the skins of African brush-tailed porcupines and are missing only when they have been shed. In *A. macrourus* there is no inflation of the frontals, and the heights of the skulls, expressed as a percentage of the basilar length, range from 29.2 to 35.6% (n=51, m=32.3%). East African populations are *macrourus*-like in this respect, whereas West African specimens show some inflation of the frontal region. The holotype of *A. africanus* Gray, 1842, exceeds the range of the Asiatic series with a relative height of the skull of

36.1% and in a specimen from Cameroun (BMNH 48.1297) this is even more clearly with 38.8%.

Status of the named forms

A. zygomaticus of Pulau Aor was compared by Miller (1903) with Malayan specimens and was characterized as follows: lachrymal bone smaller, zygoma shorter, jugal deeper, jugal with posterior concavity and a toothlike process, whitish areas less developed. As discussed before (see Results), the difference in zygoma length is not borne out by the present study, the other differences appeared to be smaller than originally described and none is absolute when compared with the total Asiatic material. Considering the individual variation in this sample, the small sample size and the enormous variation in all the cranial and external characters in this species, a nomenclatorial recognition of this population, in my opinion, is not justified now.

A. hainanus was diagnosed by Allen (1906) with the following differences from the mainland animal: smaller size, darker colour, shorter spines and tail. The occipito-nasal length of the Hainan sample is very small indeed, but it does not differ in this respect from the samples of the five small Malay islands, Annam and northern Burma (figs. 2 and 3). The spines are very small too, but not different from the spine lengths of the Annam specimens (table III), the tail length is not smaller than in the remaining samples with smaller cranial size (table III) and the colour is probably not outside the range of variation in the species. Therefore, it is apparent that *A. hainanus* is insufficiently characterized for subspecific recognition.

A. terutaus was characterized (Lyon, 1907), among others by shorter nasals, smaller lachrymal bone, more pronounced orbital constriction and a shorter tail with shorter bristles. The development of lachrymal bone and orbital constriction falls within the range of variation of the species but the length of the nasals and the length of the tail are the shortest measured in this species (fig. 4 and table III). However, with the large amount of variation in this species in mind, this single specimen is considered insufficient proof for the existence of a different subspecies on Pulau Terutau.

A. tionis was said (Thomas, 1908) to have a shorter tail, a lower skull and rather large nasals. However, when compared with continental samples the tail is not short (table III), the nasals are not large (fig. 4) and the relative heights of the skulls in five specimens available (30.2—33.1% of the basilar length) fall within the range of the total Asiatic material (29.2—35.6%, n=51). An insufficient number of differences could be found in this sample to consider the populations of Pulau Tioman a different subspecies.

A. macrourus pemangilis was compared in Robinson's (1912) diagnosis with a number of rather variable characters of *zygomaticus, tionis* and Malayan specimens. The only remark that can be made about the holotype and at the same time only adult specimen that has been available to me, is that its

cranial size approaches the lower limit of the range of variation of the species (figs. 2 and 3). This basis is insufficient for maintaining subspecific rank for the population of Pulau Pemanggil.

The main characters of *A. assamensis* from Cherrapunji, Assam, as given in the original publication (Thomas, 1921), are highly variable in the Asiatic *Atherurus* species, such as the breadth of the skull, form of the nasals, form of the zygoma, colour, etc.... Compared with the geographically nearest population, that of northern Burma, it has the same cranial size (figs. 2 and 3) and scarcely longer nasals (fig. 4). The relative zygomatic breadth of the skull, expressed as a percentage of the basilar length, is smaller (56.4%, against 59.3—63.9% in the Burmese sample) but is not outside the range of the species (54.8—65.9%). So this, the only available adult specimen, does not show enough differences to justify subspecific recognition.

Cranial size, length and breadth of the nasals, colour of the back and belly and development of the wool-hairs of *A. stevensi* were discussed before. Other, merely trivial skull characters have been mentioned in the original description (Thomas 1925), such as the upper profile of the skull, form of palatal foramina and posterior palate, etc. On the characters studied the Tonkin sample cannot be distinguished from the others, except on larger size, but this character alone, as stated before, produces a rather artifical classification of the Asiatic Brush-tailed Porcupines.

A. retardatus Mohr, 1964, is based on the presence of light and dark longitudinal stripes along the back and sides of six living adult specimens in the zoological garden "Blijdorp" in Rotterdam in 1959. The original description is based on one of these specimens which came into the collections of the Institut Royal des Sciences Naturelles in Brussels after it had died, and on a specimen in the collections of the Zoölogisch Museum Amsterdam (ZMA 5092 B) obtained from the zoological garden "Artis" in Amsterdam (not ZMA 5292 as Mohr erroneously recorded). The specimens from Rotterdam came "via Singapore" and the geographical origin of the latter specimen is quite unknown. Three of the remaining specimens in Rotterdam came into the collections of the Rijksmuseum van Natuurlijke Historie in Leiden (RMNH 19420, 19897 and 20782). According to Mohr (1964), the holotype (IRSNB 13918) had lost its stripes before the preparation and concerning the paratype ZMA 5092 B, nothing is known about the presence of stripes during life. Little or nothing is known about alterations in the colour pattern of the Asiatic Brush-tailed Porcupines and the type series of *retardatus* does not differ at all from other samples (see also Results: colour), so there is no reason at all for maintaining this specific or subspecific name.

The form of the nasals of the holotype of *A. angustiramus* Mohr, 1964, from Thailand has been discussed before (see Results). The breadth of the orbital process of the maxilla, the most important diagnostic character, is really very small, 2.9 mm, against 3.2—6.8 mm in twenty nine other Asiatic specimens measured. The geographical nearest specimen (USNM 300170) in Thailand

has a more normal orbital process of 5 mm, so it is very probable that the narrow orbital process of the holotype is an accidental, individual variation. Apparently this name must be considered a synonym too.

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Gazetteer

The following geographic names are those from the list of specimens studied. Different spellings of 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 published information of the collectors.

Malay Peninsula (with adjacent islands):

Gunung Tahang	4.23 N 102.24 E
Jalor	6.30 N 101.10 E
Pulau Aor, (Pulo Aur)	2.27 N 104.31 E
Pulau Pemanggil	2.35 N 104.20 E
Pulau Pinang, (Pulo Penang)	5.30 N 100.28 E
Pulau Terutao, (Pulo Terutau; Ko Tarutao)	6.35 N 99.40 E
Pulau Tioman	2.48 N 104.11 E
Trang, (Trong)	7.33 N 99.36 E
Wellesley	5.25 N 100.25 E

Thailand (mainland):	
Doi Suthep, (Doi Sutep)	18.48 N 98.55 E
Lomlo Mt., (Lom lo Phu)	17.01 N 101.05 E
Laos:	
Nape	18.18 N 105.07 E
Plateau Bolovens, (Phouphieng Bolovens)	15.20 N 106.20 E
Thateng	15.26 N 106.22 E
Xieng-Khouang	19.21 N 103.23 E
Vietnam:	
Chapa, (Cha Pa)	22.21 N 103.50 E
Lai Chau	22.04 N 103.10 E
Ngai-Tio (Osgood 1932: pl. 9)	22.44 N 103.36 E
Qang Nam	15.40 N 108.00 E
Sontra, (Son Tra)	15.23 N 108.46 E
Burma:	
Dalu, (Dalu Ga; Taro)	26.21 N 96.11 E
Hai Bum (Carter 1943: map)	26.04 N 95.52 E
Hkampti Plain	25.—27.N 97.00 E
Nam Tamai Valley	27.42 N 97.54 E
Thaungyah, (Thoungyah)	11.22 N 98.44 E
Assam, India:	
Cherrapunji	25.16 N 91.48 E
Mawphlang	25.28 N 91.46 E
China:	
Nodoa, (Na-ta)	19.31 N 109.33 E
Wanhsien, (Wan-Hsien)	30.49 N 108.24 E

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