

The porcupine *Hystrix (Acanthion) brachyura punungensis* subsp. nov. from Late Pleistocene fissure deposits near Punung, Java

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A large number of isolated cheek teeth and a mandibular fragment of porcupines from the Late Pleistocene fissure deposits near Punung, Java, are compared with extant *H. (Acanthion) brachyura* Linnaeus, 1758 (southeast Asia) and *H. (Acanthion) javanica* (F. Cuvier, 1823) (Java). Middle Pleistocene and Holocene specimens from Java are compared with the latter species. The Punung specimens belong to one species and are considered a new subspecies, *Hystrix brachyura punungensis* subsp. nov. The Middle Pleistocene specimens are allocated to *Hystrix brachyura* subsp. and those from the Holocene to *Hystrix javanica*.

Contents

Introduction	217
Material and methods	218
Comparison and discussion	219
Systematic palaeontology	222
Conclusions	224
Acknowledgements	224
References	224

Introduction

Dr. John de Vos of the National Museum of Natural History, Leiden (RGM), working on the Upper Pleistocene fauna of Punung, drew my attention to the porcupine material formerly present in the collections of the Geologisch Instituut, Utrecht. Hundreds of isolated *Hystrix* teeth and one right mandible were collected by Dr. G.H.R. von Koenigswald in the years 1936-1937 in two fissure deposits near Punung, a village some 10 miles north of Patjitan, Java. The fauna is dated to c. 80,000 BP (Long *et al.*, 1996). Badoux (1959) studied this material when it was still in Utrecht and established that the collections of the two fissures were mixed and could not be separated. He suggested that the Punung teeth consist of a large and a smaller form, indicating the right mandible with "*Acanthion* spec." and the smaller sized teeth with "Genus indet. (cf. *Acanthion) brachyurus javanicum* Cuvier." Bosma (1967) also studied this collection, but did not distinguish two species in this material and identified all of them as *Acanthion brachyurus javanicum* Cuvier. The applied nomenclature reflects the confusion about the taxonomy of these species. Later, the Punung collection was partly entered in the Dubois collection of National Museum of Natural History in Leiden and partly

in the Senckenberg Museum in Frankfurt am Main (SMF). The relevant porcupine teeth are now kept in Frankfurt. Although the material did not bear labels with an indication to the actual locality, from Bosma's (1967) report it is unmistakably clear that we have to do with von Koenigswald's collection from Punung. The aim of this study is to describe this material, to establish if either one or two species are involved and to determine its specific identity. The taxonomic allocation of the Middle Pleistocene and Holocene specimens from Java in the Dubois collection (RGM) will be established.

Material and methods

The serial position of all teeth from Punung has been re-established on morphology, and presence of anterior and posterior contact facets. From a study of complete skulls (Weers, 1990) it appeared that nearly 10% of the first and second molars showed only one contact facet, apparently because these were not yet developed at a young age, or in older teeth had disappeared by the process of attrition. Only the teeth with both an anterior as well as a posterior facet have been recognised as first or second molars. This may cause an under representation of very young and older teeth. Only the positively recognised teeth have been selected and a considerable number of teeth with a doubtful serial position, including those that are damaged, have been put aside. Upper teeth are indicated in upper case, lower ones in lower case. The M1/2 and m1/2 with an anterior as well as a posterior facet could be determined with great certainty. The determination of the P4, p4, M3 and m3 is not possible with absolute certainty because of the possible occurrence of M1/2 and m1/2 teeth without a posterior facet. The deciduous premolars are left out of consideration because of their low numbers.

The mandible fragment in the Punung collection, registered as SMF/PA/F6639, was described by Badoux (1959) and Bosma (1967). Its relatively large size may have been the reason that Badoux (1959) attributed a different specific identity to the mandible than to the isolated teeth. However, as the size of its teeth is not significantly different from the size range of the isolated cheek teeth, the mandible is considered conspecific with the teeth. The mandible is chosen as the type for a new subspecies. The following specimens of the teeth have been selected for this study.

- - **52 P4**, nrs. 11, 20, 31, 33, 34, 36-38, 40, 43, 44, 48, 58, 62, 68, 70, 71, 72, 74, 78, 81, 87, 88, 90, 93, 100, 107, 118, 143, 151, 154, 163, 167, 174, 180, 182, 250, 295, 299, 303, 317, 338, 380, 386, 473, 486, 489, 497, 498, 601 and the nrs. X and Z.
- - **74 M1/2**, nrs. 5, 12, 22, 23, 27-29, 39, 45, 46, 50, 53, 57, 60, 85, 87, 96, 103, 105, 164, 227, 244, 261, 265, 270, 271, 275, 276, 278, 281, 284, 287, 290, 291, 293, 298, 300, 306, 315, 319, 322, 331, 371, 394, 396, 404, 408, 414, 425, 437, 438, 439, 442, 447, 449, 452, 453, 455, 459, 462, 465, 472, 483, 487, 490, 495, 496, 499, 510, 514, 515, 526, 604, 609.
- - **33 M3**, nrs. 218, 237, 247, 252, 255, 255*, 269, 285, 294, 302, 303, 309, 310, 313, 314, 320, 326, 329, 330, 333, 335, 340, 342, 358, 417, 465, 502, 504, 610-614.
- - **16 I**, nrs. 127-132, 538, 546, 547, 549, 550, 555-558, 627.
- - **55 p4**, nrs. 14, 18, 21, 25, 64, 77, 83, 94, 99, 104, 110, 114, 115, 119, 120, 122-124, 128, 130, 137, 139, 140, 141, 142, 146, 148, 150, 155, 161, 165, 168, 169, 171, 172, 177, 181, 183, 185, 186, 203, 262, 381, 397, 402, 407, 412, 415, 419, 431, 457, 503, 617-619.
- - **72 m1/2**, nrs. 6, 9, 16, 17, 32, 51, 55, 63, 69, 75, 80, 101, 109, 111, 117, 1256, 127, 129,

136, 138, 145, 158, 160, 166, 178, 188, 192, 195, 209, 211, 220, 223, 230, 232, 256, 264, 273, 274, 283, 308, 311, 323, 332, 344, 360, 361, 362, 365, 369, 370, 372, 375, 379, 385, 387, 388, 399, 405, 406, 409, 429, 444, 461, 474, 484, 523, 600, 621-625.

- - **20 m3**, nrs. 187, 204, 207, 208, 214, 221, 235, 240, 242, 246, 263, 266, 321, 327, 341, 346, 352, 378, 491, 506.
- - **13 i**, nrs. 134, 135, 537, 542, 543, 544, 545, 548, 551, 553, 554, 560, 562.

The Punung material is compared (Table 1) with the extant *H. (Acanthion) javanica* (F. Cuvier, 1823) from Java and of *H. brachyura* Linnaeus, 1758, in the concept of Weers (1979) based on specimens from the total area of distribution from Borneo and Sumatra to southern China, eastern India and Nepal. The data of the latter species are completed with the specimens of the Zoological Reference Collection Singapore (ZRCS), nrs. 4.1598, 4.1603-1606, and 4.1634. Six subfossil fragments Dub.10047a-f, from Goa Djimbe, Java, were studied. Subfossil specimens a-b-c were figured by Hooijer (1946, figs. 6, 9, 19). A mandible fragment Dub.1488a from Bangle, two m1/2 Dub.1488b-c from Soember Kepoeh near Bangle and an m3 Dub.1661a from Pati Ajam, all from Java, are Middle Pleistocene (John de Vos, pers. comm.). These specimens were also figured by Hooijer (1946, figs. 12-15).

Comparison and discussion

Hystrix (Acanthion) brachyura Linnaeus, 1758, does not exist on Java at the present day. Comparison of the Punung material with *H. (Acanthion) javanica* (F. Cuvier, 1823) is obvious, because this extant species occurs on Java. The problem with specific distinction of porcupine teeth is that the occlusal morphology of *Hystrix* has changed little from the Miocene and Pliocene to the Recent. Moreover, occlusal morphology varies individually and shows extreme changes in the successive stages of wear. As a consequence, only size and tooth height can be used for specific distinction. As the relative tooth height of *H. brachyura* and *H. javanica* is the same, and as there is a considerable overlap in size, it is impossible to distinguish each individual tooth specimen of these species. However, *H. javanica* is, beside its smaller mean size, considered a valid species (Weers, 1979) on the lesser development of the spiny covering and structure of the skull. As mainly cheek teeth are available from Punung, only the mean sizes of the samples are informative in the present study.

The special situation of this study is that the teeth from Punung comprise a large sample which can be compared statistically (Student's T-test) with a large sample of teeth of *H. brachyura* and with a relatively large number of specimens of *H. javanica* (Table 1). The mean length of the P4, M1/2 and m1/2 of the Punung teeth are only slightly larger than those of *H. brachyura*, and the means of the M3 and m3 of the Punung teeth and *H. brachyura* do not differ in these samples. However, the mean length of the p4 of Punung is larger than that of *H. brachyura* and statistical tests show that this difference is highly significant. The width of the teeth shows the same tendency. The mean width of all teeth from Punung is on average slightly larger than those of *H. brachyura*. The mean width of the p4 of the two samples also shows a highly significant difference. Comparison of the standard deviations of the length measurements of the M1/2 and m1/2 (Table 1) of the teeth from Punung with those of *H.*

brachyura shows that the variation in the latter species is larger. That makes it improbable that a considerable number of the smaller teeth of *H. javanica* or of another smaller species has been mixed up in the Punung collection. The length difference between the p4 teeth is shown by the plots (Fig. 1) in which the boxes represent 50% of the values of the samples. The median, smallest and largest values of both samples, and two outlying values of the Punung sample, are shown. The latter values are considered to represent aberrant individuals. The somewhat larger individual variation in the sample of *H. brachyura* may be explained by these specimens originating from the total area of distribution of the species, whereas the Punung specimens are from one locality only.

Most of the teeth in the mandible from Punung agree in size with the largest ones in the size ranges of the isolated teeth and, consequently, the alveolar length of the tooth row is strikingly large. With 34.4

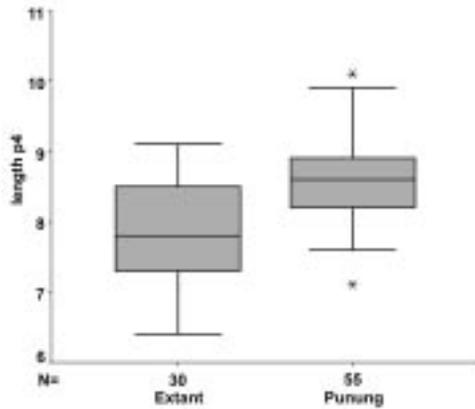


Fig. 1. Boxplots of tooth length in mm of 30 p4 of *Hystrix brachyura* Linnaeus, 1758, from their total area of distribution, compared with 55 specimens from the Punung fissure deposits, showing the median, the 25th to 75th percentile, the smallest and largest value and two outlying values (*)

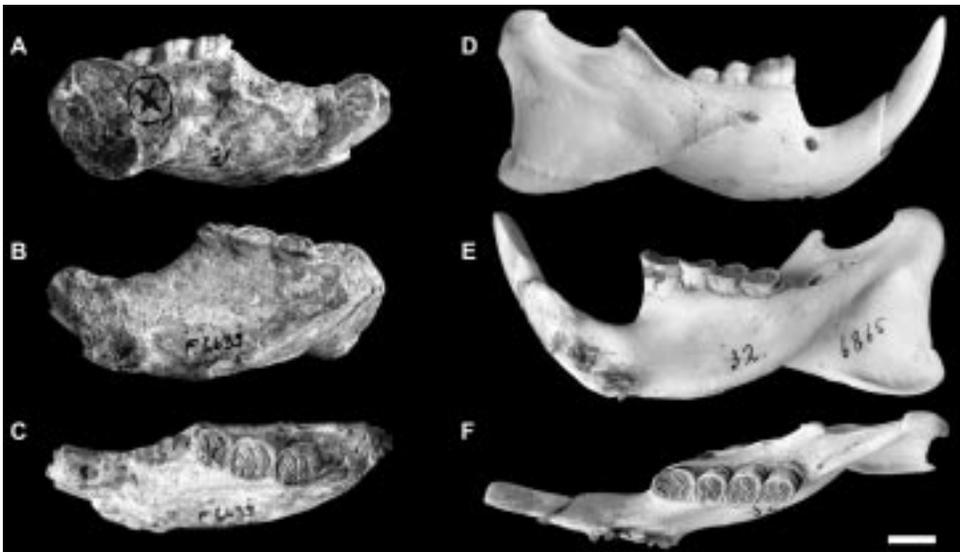


Fig. 2. Buccal (A), lingual (B) and occlusal view (C) of the fragment of the right ramus mandibularis (SMF/PA/F6639) with m1-m3 and part of the alveole of the p4, holotype of *Hystrix brachyura punungensis* subsp. nov., compared with the same views (D-F) of the extant subspecies *H. b. brachyura* from Sumatra (STET ZMA 6865). Scale bar represents 10 mm.

Table 1. Length of cheek teeth of *H. javanica* from Java, of *H. brachyura* from Sumatra and Borneo to eastern India and Nepal, and of the fissure finds from Punung, with range, mean and number of specimens (n), in mm.

<i>H. brachyura</i>	P4	M1/2	M3	p4	m1/2	m3
Mean	7.4	6.6	6.2	7.9	7.1	6.7
Range	5.3-8.5	4.7-8.0	5.2-7.3	6.4-9.1	4.6-8.9	5.5-8.1
n	32	91	35	30	87	31
St. dev.	0.62	0.77	0.49	0.71	0.83	0.55
Punung collection						
Mean	7.6	6.7	6.2	8.6	7.3	6.7
Range	6.2-8.7	5.2-8.0	4.8-7.5	7.1-10.1	5.5-8.7	5.8-7.5
n	52	74	33	55	72	20
St. dev.	0.52	0.66	0.61	0.60	0.78	0.41
<i>H. javanica</i>						
Mean	6.8	6.1	5.6	7.0	6.5	5.8
Range	6.3-7.8	5.4-6.8	5.2-6.1	6.2-8.2	5.7-7.4	5.4-6.5
n	13	31	14	13	31	14
St. dev.	0.43	0.36	0.36	0.50	0.39	0.39
Holocene of Java						
Mean				7.8	6.6	6.1
Range				7.6-7.9	6.1-7.0	5.8-6.2
n				2	9	3
St. dev.					0.27	
Middle Pleistocene of Java						
Mean					7.3	
Range				7.5	6.9-7.8	6.7
St. dev.						
n				1	4	1

mm it is larger than the maximum in a large series of *H. brachyura* (22.8-33.8 mm, n = 86). Although relatively large, it is not different from what can be expected when the size ranges of the isolated cheek teeth are taken into account.

The size range of the four Middle Pleistocene m1/2 (Table 1) exceeds the range of the much larger sample (n = 31) of the extant *H. javanica* (Table 1), and the only available m3 of Middle Pleistocene age exceeds the largest of 14 *H. javanica* specimens. This suggests that there may be an early representative of *H. brachyura* on Java. This is not surprising because an earlier *H. brachyura* subspecies is known from the Upper Pliocene or Lower Pleistocene of Longgupo in China (Weers, 2003). The length of the only available P4 (8.8 mm) from that locality exceeds the largest one (8.5 mm) in the range of *H. brachyura*. That is nearly the same as the maximum size of Punung P4 (8.7 mm; Table 1). However, the specimens from Java as well as that from Longgupo are too scanty to determine their subspecific identity.

Hooijer (1946) attributed the Holocene material from Goea Djimbe to "*Acanthion brachyurus* (L.) subspecies." The four mandible fragments 10047b-c-d-e from that locality show a range in the tooth-row length of 26.2-27.2 mm (m = 26.7 mm). They agree with the range in *H. javanica* specimens from Java (24.8-28.1 mm, m = 26.8 mm, n = 16; Weers, 1979). The measurements (Table 1) of the individual teeth of the Holocene specimens are similar, so the Goea Djimbe material is allocated to *H. javanica* (F. Cuvier, 1823).

The width of the largest upper incisor of the Punung teeth is 6.5 mm (n = 16) and of the lower incisor 7.4 mm (n = 13). Incisor size depends on age, the age composition of the Punung sample is unknown and insufficient data of *H. brachyura* are available. Therefore, incisor size cannot contribute to the comparison.

Systematic palaeontology

Order Rodentia Bowdich, 1821
Family Hystricidae, Fischer, 1817
Genus *Hystrix* Linnaeus, 1758
Subgenus *Hystrix* Linnaeus, 1758

Remarks — This subgenus is comprised of the larger *Hystrix* species, with high crowned as well as low crowned cheek teeth, and with relatively large nasals and high skulls. The extant species show more than one black ring on the quills.

Subgenus *Acanthion* F. Cuvier, 1823

Remarks — This subgenus contains the relatively smaller *Hystrix* species with comparatively smaller nasals. The extant species have only one black ring or coloured part on the quills.

Included taxa — *Hystrix (Acanthion) javanica* (F. Cuvier, 1823); *Hystrix (Acanthion) brachyura* Linnaeus, 1758; *Hystrix (A.) b. brachyura* Linnaeus, 1758; *Hystrix (A.) b. hodgsoni* Gray, 1847; *Hystrix (A.) b. subcristata* Swinhoe, 1870; *Hystrix (A.) b. punungensis* subsp. nov.

Hystrix brachyura punungensis subsp. nov.

- 1959 "Acanthion spec. indet."; "Genus indet. (cf. *Acanthion*) *brachyurus javanicum* Cuvier" – Badoux, p. 16, pl. 1, figs. 3A, B.
1967 *Acanthion brachyurus javanicum* Cuvier – Bosma, p. 24.
1983 *Acanthion brachiurus longicaudum* – Vos, p. 422.
1985 *H. brachyura* – Weers, p. 113.
1996 *Acanthion brachyurus* – Long *et al.*, p. 103.

Holotype — Fragment of the right ramus mandibularis SMF/PA/F6639 with m1-m3 and part of the alveole of the p4 (Fig. 2A-C). The mandible fragment is chosen as the type because it contains more morphological information for future research than an arbitrary chosen single cheek tooth. Teeth discussed above are all designated paratypes.

Diagnosis — The dimensions of the cheek of *Hystrix brachyura punungensis* show an overlap with those of the *Hystrix brachyura* subspecies recognised thus far, but are on average larger, in particular the p4.

Differential diagnosis — The cheek teeth of *H. b. punungensis* are on average larger than those of *H. b. brachyura*, *H. b. subcristata* and *H. b. hodgsoni*. Other differences from

these extant subspecies are not relevant because their subspecific distinction is based on cranial and external characters. The average size difference with the cheek teeth of *Hystrix javanica* is larger still than with those of *H. brachyura*.

Description — The alveolar length of the tooth row of the holotype is 34.4 mm and approaches the maximum value what can be expected on the basis of the sizes in the isolated cheek teeth. The occlusal width of the m2 and m3 in the mandible is unusually large with a thin rim on the lingual side, caused by a relatively large angle of the occlusal surface with the length axis of the tooth. This is considered an individual variation. Width measurements below that surface may be more representative for the size of the teeth and are given here separately. The length measurements are more important for comparison because they are less liable to individual variation in the course of attrition: —

	Width occlusal	Width below occlusal	Length	Wear class
m1	7.1	7.1	7.5	T3
m2	8.1	7.8	8.4	T2
m3	7.0	6.5	7.5	T1

The type mandible fragment (Fig. 2A-C) is compared with a mandible of the extant *H. brachyura* (Fig. 2D-F) from Sumatra (Zoological Museum Amsterdam, ZMA 6865) in a slightly more advanced stage of attrition. The alveolar length of the tooth series (29.0 mm) of the extant mandible represents the mean of the species, whereas the type mandible may approach the maximum of the subspecies. The length of the incomplete tooth series m1-m3 of the type is 23.7 mm, that of the specimen from Sumatra 19.0 mm. The difference in shape between the specimens in this figure is mainly caused by the absence in the type mandible of the p4 with its alveole and by missing fragments of the anterior part of that mandible. The isolated cheek teeth are delineated by the measurements in Tables 1 and 2, and Figure 1.

Age — Late Pleistocene, 80,000 year before present (Long *et al.*, 1996).

Table 2. Width of *H. brachyura* from Sumatra and Borneo to eastern India and Nepal, and of the fissure finds from Punung, with range, mean and number of specimens (n), in mm.

<i>H. brachyura</i>	P4	M1/2	M3	p4	m1/2	m3
Mean	6.7	6.6	5.5	6.2	6.3	5.6
Range	4.9-8.5	4.5-8.5	3.8-7.5	4.7-8.0	4.4-7.8	4.4-7.0
n	71	203	83	68	190	77
St. dev.	0.90	0.77	0.62	0.79	0.61	0.55
Punung collection						
Mean	7.0	6.8	5.8	7.0	6.4	5.8
Range	5.3-8.1	4.8-8.4	4.2-7.0	5.4-8.5	4.2-7.6	5.0-6.4
n	52	73	33	55	72	20
St. dev.	0.52	0.85	0.61	0.57	0.71	0.34

Conclusions

The porcupine material from Punung is considered to belong to one species. It represents a porcupine that is very close to *H. brachyura* Linnaeus, 1758, but with on average slightly larger cheek teeth, in particular the p4. On this difference this form is considered a new subspecies, *Hystrix brachyura punungensis*. It is most probable that the porcupine from Punung is the forerunner of the extant *H. b. brachyura* in the Malay Archipelago. As the Punung fauna is dated to about 80,000 year B.P. (Long *et al.*, 1996), the decrease of the teeth size may have taken place during that time.

The Middle Pleistocene porcupine teeth from Bangle and Pati Ajam may be allocated to *H. brachyura*, being the oldest record of this species in the Malay Archipelago. The material is too scanty to judge a relationship with the Chinese Plio-Pleistocene *Hystrix brachyura* species of Longgupo or with the Late Pleistocene porcupine of Punung.

The specimens from Goea Djimbe show that *H. javanica* (F. Cuvier, 1823) occurred on Java during the Holocene. Because this species is less specialised, it is unlikely that it was derived from *H. brachyura*. Descent from the less specialised Early to Middle Pleistocene *H. lagrelli* Lönnberg, 1924 (Weers, 1995), which also occurred in the Middle Pleistocene of Sangiran and Trinil on Java, is more probable.

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