

For the outline shape, the crenulated crown of (SC6-2) surface is without a preprotocrista and has an oval and elongated outline shape with a more flared lingual crown surface.

For the P⁴, the presence of distinct accessory cusp behind and in front of the protocone, a hypocone and a protoconule, respectively has been reported by Hooijer (1948) for a small number of upper P⁴s from Padang (for example, Figs. 3, 5 and 6, Plate. VI). The marginal borders around the protocone for all the upper P⁴s are smooth and without indication of any accessory cusp, as is the situation seen in most of the Padang fossils. The upper P⁴s of Vietnam assigned to either *P. p. kahlkei* or *P. hooijeri* (Schwartz *et al.*, 1995) are distinctly less crenulated than our samples and those of modern species. Even the heavily worn specimen (BDC 1-28U) with crenulations is only weakly discernible and shows a degree of crenulations greater than the teeth reported in Schwartz *et al.* (1994 & 1995). Neither specimen seems to have any cingulum developments on either lingual or buccal surfaces whereas a lingual cingulum has been noted for a specimen from Guangdong Province (YFG 01, Gu *et al.*, 1987).

For the M³, the subtriangular shape of (CC 6-3) is typical of an upper M³ and is different from the more triangular outline (owing to a more reduced vestigial metacone) of the upper M⁴ reported from the Padang materials (Hooijer, 1948). This is the only *Pongo* specimen showing signs of dental pathology in our collection. A carious lesion seems to have developed from the anterior interproximal area and later expanded into the nearby occlusal surface, causing the collapse of part of the enamel crown around the protocone and exposing the underlying dentine. Carious teeth have been reported from both fossil (Hooijer, 1948) and modern wild-captured *Pongo* (Stoner, 1995). Among the fossil great apes, *Gigantopithecus* from Guangxi and Hubei Provinces of China had been reported to show a high prevalence of this disease (Woo, 1962; Han & Zhao, 2002).

For the lower I_2 , Hooijer (1948) observed that the lateral border of the lower I_2 is more rounded than its mesial surface, allowing identification of (SC 3-4) as from the right side. The central vertical ridge on the lingual surface is clear but not as developed as Coll. Dub. No.11499/5 (Hooijer, 1948, Fig. 10, Plate II). It is more similar in general shape to specimen Coll. Dub. No. 11499/6 (Hooijer, 1948, Fig. 11, Plate II) but does not bear a tubercle on its latero-incisal angle. A few lower I_2 s had been reported from sites in Vietnam and South China but the asymmetrical form seems to be consistent with our specimen. Bacon and Long (2001) however noted that the lingual cingulid is less cervically positioned, almost at the mid-section of the crown, than the Padang series. Specimen (SC 3-4) is characterized by a lower lingual cingulid and therefore seems to be closer to those from Padang and modern *Pongo*.

The large series of lower P_3 samples from Padang exhibits variable development in some dental features, including the cingulid, metaconid and trigonid basin. These features are only moderately developed in (BDC 1-10L). A minor cusp in the postero-external border of (BDC 1-10L) may represent the vestigial hypoconid. No entoconid, as noted in Coll. Dub. No. 11548/25 and the Hoa Binh specimens, is observable. The presence of a vertical groove in the trigonid basin resembles some modern specimens (Swindler and Olshan, 1988) and fossils from Padang and *P. p. ciochoni* and *P. p. devosi* (Schwartz *et al.*, 1995). For the lower P_4 , SC 3-3 has a smaller trigonid basin than that of (BDC 1-19U) owing to the closer proximity of protoconid to metaconid in the former. The distance between these two cusps and the extent of the anterior fovea are shown to be variable among some specimens from Padang (Hooijer, 1948) and also reported by later authors, for example Bacon and Long (2001) and Swindler (2002).

Hypoconids are vestigial in both teeth, and in contrast to materials reported by (Hooijer, 1948) for Padang and (Bacon *et al.*, 2008b) for Duoi U'Oi Cave (Vietnam), no entoconid or hypoconulid are seen. Neither tooth is elongated in shape as are recorded among some of the Punung materials. Only two lower posterior premolars were reported from Tham Khuyen (Schwartz *et al.*, 1994), both assigned later to a new species, *P. hooijeri* (Schwartz *et al.*, 1995) but these are characterized by a lack of enamel crenulations and a squarer shape than the present samples. No lingual cingulid is seen either on (SC 3-3) or (BDC 1-19U) but a slightly developed enamel ledge on the postero-buccal surfaces of both teeth seems to suggest the presence of an incipient cingulid. Both lingual and buccal cingulids have been noted for some specimens from caves in South China (Gu *et al.*, 1987 and Ho *et al.*, 1995) but have not been recorded in teeth from other fossil sites or modern *Pongo* (Swindler & Olshan, 1988).

For the lower M_1/M_2 , Hooijer (1948) observed that there are certain features that can be used to differentiate the lower M_1 from M_2 . Among the features noted are: (1) a more obtuse angle between anterior and lingual surfaces and (2) more prominent entoconid corner in M_1 than M_2 . (BDC 5-3) and (VC 4-4) are therefore referred to M_1 and M_2 , respectively. Both have interproximal contact facets in their mesial and distal surfaces but this does not resolve the question of which molar in a dental row they may represent. Furthermore, the complete reliance on the occurrence of contact facets in determining serial position of isolated molars has been questioned by Badoux (1959). Only (VC 4-4) has the C6 and C7 accessory cusps on the postero-lingual border. Among modern samples, a higher prevalence of C6 is found in M_2 than in M_1 (7.2% of 293 cases in M_2 compared to 2% of 300 cases in M_1) and a higher prevalence of C7 (36.3% of 124 cases in M_2 and 10.3% of 126 cases in M_1) (Swindler, 2002).

The presence of these cusps has been noted for some lower molars from Padang (Hooijer, 1948), and a lower M₂ from Sangiran (C7 only) (Kaifu *et al.*, 2001). Swindler and Olshan (1988) reported a decrease in the incidence of C6 in modern-day populations compared with Pleistocene Orangutans while C7 remains little changed. As with many of the fossil and modern non-human hominoid samples, the Y-5 '*Dryopithecus*' pattern of cusp and groove distribution is well-marked in (VC 4-4) and (BDC 5-3). They do not possess any structure suggesting the presence of buccal cingulid, unlike some teeth reported from Padang (Hooijer, 1948), Punung (Koenigswald, 1982) and Sangiran (Kaifu *et al.*, 2001). The Vietnamese materials reported by Schwartz *et al.* in 1994 from Tham Khuyen are markedly less crenulated than my samples. A variable position of the hypoconulid has also been observed among the material from Duoi U'Oi Cave (Bacon *et al.*, 2008b).

3.2.2.1.3 A new chronology for *Pongo* in Peninsular Malaysia

The first evidence of *Pongo* in Peninsular Malaysia is here associated with numerical ages that determine the deposition of *Pongo* in rich fossiliferous breccia at two different localities in this region in two phases: in the Middle Pleistocene before 500 ka in Lenggong, Perak and in the Late Pleistocene between 66 - 33 ka in Batu Caves, Selangor. They also represent significant southward extensions of the ancient Southeast Asian continental range of fossil *Pongo* during these two key periods of the Quaternary.

The recognition that living Orangutans were represented by two species was originally based on morphometric characters (Groves, 2001a). So far, however, no features of dental morphology have been recognized to distinguish isolated teeth of the Sumatran and Bornean species *P. abelii* and *P. pygmaeus*, respectively (Uchida, 1998; Smith *et al.*, 2011& 2012), and quantitatively there is a considerable overlap between the two.

The dimensions and morphological features of the new Peninsular Malaysian fossil teeth from two spatially and chronologically different localities do not show a consistent and unambiguous clustering pattern with any other Pleistocene taxa. The small sample size is an additional impediment to assigning these fossils to any existing or extinct taxon.

Molecular evidence has pointed to a date for the last common ancestor of the two living species at 400 ka (Locke *et al.*, 2011), Specimens antedating the presumed divergence of the two are therefore likely to be a common ancestor, for which the prior species name is *P. pygmaeus* (L.).

The Late Pleistocene material from Batu Caves is subsequent to the molecular separation date of the two extant *Pongo* clades. Although there is no supporting palaeontological evidence, the most economical conclusion from a biogeographical point of view is that the ancestral *P. pygmaeus* lineage was already present in an eastern sector of Quaternary Sundaland, and was periodically isolated on Borneo during high sea levels of subsequent interglacials and the Holocene (Voris, 2000). The *P. abelii* lineage must have occupied an area west of the Quaternary environmental barrier dividing Sundaland (see below), and was presumably already established in Sumatra by the late Quaternary, if not earlier. The extinct large-toothed taxon *P. palaeosumatranus* Hooijer 1948, dated 80 - 60 ka, should therefore now be assigned to the species *P. abelii*. Although lowered sea levels of the terminal Pleistocene ice age could have facilitated gene exchange via land connections between Sumatra and Peninsular Malaysia (Voris, 2000), as shown above, dental anatomy does not convincingly allocate the Batu Caves material to the contemporaneous *P. abelii palaeosumatranus*. On Borneo three geographically separated subspecies of *P. pygmaeus* have been recognized (Groves, 2001a).

Although the present population of *P. abelii* is monotypic, this species may also have been labile in the past. While the applicable species name for the Batu Caves specimens is therefore *P. abelii*, it appears probable that they represent an extinct independent clade.

Although this interpretation might be clearer if it was reflected in nomenclature, the material is inadequate to define a new taxon. For clarity, the Batu Caves specimens can be identified as *P. abelii* subsp. indet.

The Middle Pleistocene specimens from Badak Cave C fall into this category. The small sample provides no features consistently identifying these teeth with any Middle Pleistocene taxon previously described. The generally accepted Middle Pleistocene chronosubspecies, *P. p. weidenreichi* Hooijer 1948 of southern China, is larger in dental dimensions than the Badak C specimens of Middle Pleistocene taxa described by Schwartz *et al.* (1995) on the basis of collections of isolated teeth from different cave sites in Vietnam, *P. hooijeri* uniquely among the genus lacks crenulations of the molars, a character present in all the Peninsular Malaysian specimens. Chronometrically, the indicated ages of additional Middle Pleistocene taxa described as subspecies of *P. pygmaeus* i.e., *P. p. ciochoni*, *P. p. devosi*, *P. p. kahlkei* and *P. p. fromageti* (Schwartz *et al.*, 1995) are subsequent to the Badak C. The different characterizations of these taxa are not matched by the Badak C *Pongo* series. Subject to the reservation that they may represent yet another clade, the Badak C teeth can be identified as *Pongo pygmaeus* subsp. indet.

3.3 ORDER RODENTIA Bowdich, 1821

3.3.1 Family Hystricidae Fischer, 1817, Plate 2

This family contains three extant genera:

- *Trichys* Günther, 1877, contains one species:

- Long-tailed Porcupine *Trichys fasciculata* (Shaw, 1801), in Peninsular Malaysia, Sumatra, and Borneo.

- *Atherurus* Cuvier, 1829, one species in Asia:

- Brush-tailed Porcupine (Figure 3.6, A), *Atherurus macrourus* (Linnaeus, 1758), in Vietnam, Laos, Peninsular Malaysia, Myanmar, Thailand, and China.

- *Hystrix* Linnaeus, 1758, in Southeast Asia region, this genus is divided into two subgenus:

Subgenus *Acanthion* including:

- Malayan Porcupine (Figure 3.6, B), *Hystrix (Acanthion) brachyura* Linnaeus, 1758; synonymous with *Hystrix subcristata* Swinhoe, 1870, in Nepal, Myanmar, Thailand, Laos, Cambodia, Vietnam, Peninsular Malaysia, Sumatra, and Borneo and central and southern China.

- Sunda Porcupine *Hystrix (Acanthion) javanica* (F. Cuvier, 1823), endemic to Java and the Lesser Sunda Islands (Corbet & Hill, 1992).

Subgenus *Thecurus* including:

- Thick-spined Porcupine *Hystrix (Thecurus) crassispinis* (Günther, 1877), in Borneo.

- Palawan Porcupine *Hystrix (Thecurus) pumila* (Günther, 1879), endemic to the island of Palawan in the Philippines.

- Sumatran Porcupine *Hystrix (Thecurus) sumatrae* (Lyon, 1907), endemic to Sumatra.

The current distribution suggests that southern Asia was the centre of origin of this family (Weers, 2005).



Figure 3.6 *Atherurus macrourus* (A) and *Hystrix brachyura* (B), source: zooinstitutes.com & nationalgeographicstock.com

Porcupines were present in some of the Pleistocene cave or fissure faunas of Southeast Asia in great abundance. In North Thailand, Pope *et al.* (1981) discovered *Hystrix* sp. from Khao Panam cave breccias while Ginsburg *et al.* (1982) reported *Hystrix hodgsoni* from Thum Wiman Nakin Cave.

Hystrix sp. and *Hystrix subcristata* fossils were recorded from different localities in South China by Kalkhe (1961) and Colbert & Hooijer (1953), while in Vietnam, *Hystrix subcristata*, *Atherurus macrourus* and *Hystrix brachyura* were reported from different sites by Olson & Ciochon (1990), de Vos & Long (1993) and Bacon *et al.* (2006 & 2008b) and in Laos *Hystrix subcristata* and *Hystrix brachyura* teeth was reported from south Tam Hang by Bacon *et al.* (2008a & 2011).

Teeth of porcupines are prevalent in the Late Pleistocene prehistoric caves in the Padang Highlands in Sumatra and almost every tooth or bone of other animals in the Sumatran collection bears evidence of the gnawing habits of these animals (Hooijer, 1946a).

Hystrix cf. *brachyura* and *Trichys fasciculata* were found in Niah cave in Sarawak, Borneo, (Cranbrook, 2010) and the later species was also present in the Madai caves in Sabah. It was not possible to separate between *Hystrix* sp. and *Thecurus* sp. in Madai caves collection (Cranbrook, 1988a). The Asiatic Brush-tailed Porcupine *Atherurus macrourus* is absent in Borneo (Cranbrook (1988a, & 2010) but present in both Peninsular Malaysia and Sumatra (Cranbrook, 1988b).

Hystrix and *Hystrix brachyuran* remains from the Middle Pleistocene in Trinil (Java) were mentioned by Dubois (1907) and Medway (1972) respectively. A tooth of *Hystrix* from Sangiran II was mentioned by Von Koenigswald (1934). The Pleistocene porcupine from Goea Djimbe, Java with the same dental dimensions as the modern day Sumatran porcupine was identified as *Acanthion brachyurus longicaudum* (Marsden) and *H. b. brachyura* by Weers (1979) in Corbet & Hill (1992). It is intermediate in size and geographical position between *H. b. brachyura* of the Malay Peninsula and *A. b. javanicum* Cuvier or *H. b. javanica* of Java (Hooijer, 1946a). Hooijer believed that the Javan fossils were indistinguishable from those of the Sumatran subspecies but suggested to leave the form unnamed until the possibility to separate them from the recent Sumatra subspecies is settle while Weer (2003) allocated these to *H. javanica* as the individual teeth measurements are similar to those of the modern day Sunda porcupine. Weers in the same publication also allocated the Middle Pleistocene specimens to *H. brachyura* subsp. and named a new subspecies, *H. brachyura punungensis* for the Late Pleistocene materials from Punung fissures.

From Trinil, (Stremme, 1911 in Hooijer, 1946a) identified a tooth as the right M² of a small species of *Hystrix* which Hooijer, (1946a) identified provisionally as *Thecurus sumatrae* Lyon subsp. Materials from Java have been identified as *H. lagrelli* Lönnberg, 1924 from

Gunung Dawung near Punung, and *H. gigantea* Van Weers, 1985 from Sangiran (Weers, 2005).

The *Hystrix* fossils recorded much greater in number compared to the poor fossil record of *Atherurus*. Weers (2002) related this to the cave dwelling habitats of *Hystrix*, whereas *Atherurus* is more typical of forest habitats and the smaller species like *Trichys fasciculata* with its smaller ecological range in swampy habitats (Lim *et al.*, 1989) had smaller chances of fossilization.

The distribution of the Hystricidae in Southeast Asia is probably the result of several migrations of *Hystrix* species from the Asian mainland into Sundaland and is not considered to be the result of 'in situ' evolution (Weers, 2005). The porcupines in current study are *Atherurus macrourus* and *Hystrix brachyura* as in (Table 3.5).

Table 3.5 Dimensions of the upper and lower teeth attributed to porcupine in this study.

	Tooth Type	No.	L	W
<i>Atherurus macrourus</i>	Upper I (sin.)	CC EX14	2.5	3.5
	Upper I?	BDC EX21	4.4	5.1
	Lower I (sin.)	BDC 1-25U	3.4	4.4
	M ₁ /M ₂ (sin.)	BDC 1-22U	5.2	4.6
<i>Hystrix brachyura</i>	Upper I (sin.)	BDC 2-1	6.0	8.7
	M ¹ /M ² (dex.)	BDC 1-21U	8.0	6.4
	P ₄ (sin.)	BDC 5-16	7.6	5.6
<i>Hystrix</i> sp. indet.	Upper I (sin.)	BDC EX6	3.5	5.3
	dP ₄ (sin.)	BDC 1-17U	6.9	5.0

No.= specimens field number; L= mesio-distal length; W= bucco-lingual width. All measurements are in mm. Incisor measurements are from the cutting end.

3.3.1.1 Teeth description (Figure 3.7)

A. *Atherurus macrourus* in Batu Caves

One sample identified as *Atherurus macrourus* recovered from Batu Caves:

Upper incisor

CC EX14 (sin.)

This is the only porcupine fossil recovered from Batu Caves. It is a complete upper incisor, semicircular in outline with an open root. Its incisive surface is oval in shape. The posterior surface is rather flat compared to the convex antero-labial surface.

B. *Atherurus macrourus* in Lenggong Valley

Three samples of *Atherurus macrourus* collected from Badak Cave C in Lenggong Valley site, these samples are:

Upper incisor

BDC EX21 (?)

This tooth is the incomplete with only part of the anterior portion of the incisor. The incisive surface is semi- rounded in shape with a sharp edge. Its enamel layer is orange red in colour.

Lower incisor

BDC 1-25U (sin.), Plate 2 (A1)

This is a slender incisor broken into two parts. The incisive surface is elongated in shape with a flat edge. The enamel layer is orange red in colour for the upper two-thirds of the tooth.

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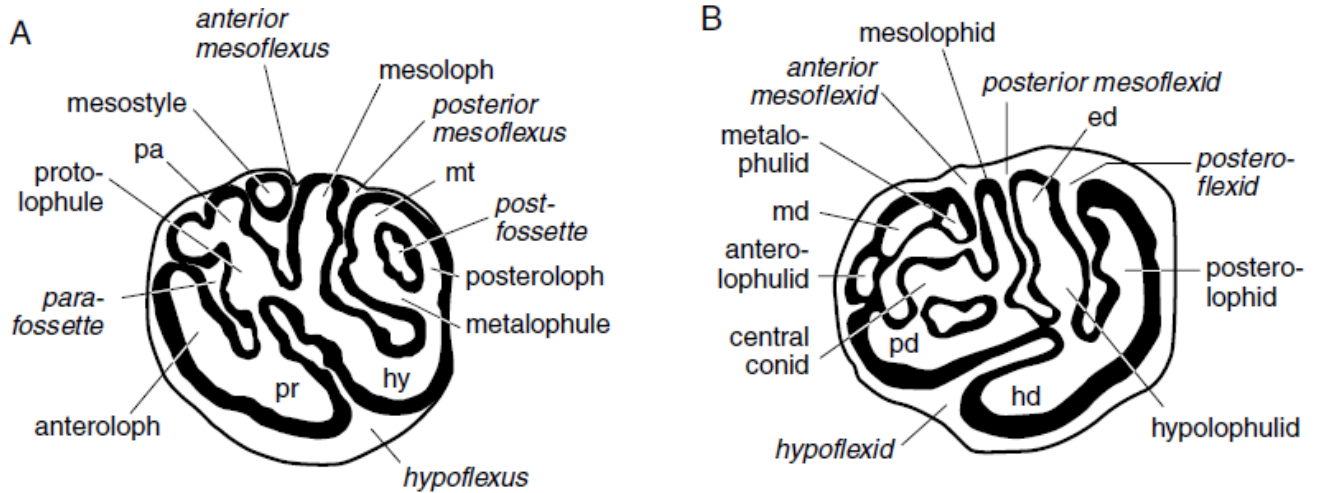


Figure 3.7 Nomenclature to describe cheek teeth structures of Hystricidae modified from SEN (2001); **A**, upper cheek teeth; **B**, lower cheek teeth. Abbreviations: **ed**, entoconid; **hd**, hypoconid; **hy**, hypocone; **md**, metaconid; **mt**, metacone; **pa**, paracone; **pd**, protoconide; **pr**, protocone.

Lower molar

M₁/M₂; BDC 1-22U (sin.), Plate 2 (A2)

This is a very small moderately worn low crowned cheek tooth. The hypoflexid is clear on occlusal surface and blocked by a small tubercle at its entrance on the buccal surface. The metaconid, metalophulid and anterolophulid are fused together with the protoconid. The mesolophid and central conid are also fused together. Both the anterior and posterior mesoflexids are still open at the lingual side. The posteroflexid is closed on the lingual surface. Small contact facets are present on the anterior and posterior surfaces. Judging from the root remnants it seems that there is one large root at the posterior end, one small one on the antero-buccal side somewhat fused to the posterior root and one tiny isolated root on the antero-lingual side.

***C. Hystrix brachyura* in Lenggong Valley**

Hystrix brachyura represented by three samples, all collected from Badak Cave C, these samples are:

Upper incisor

BDC 2-1 (sin.), Plate 2 (B1)

Parts of incisor broken into two parts with a triangular cross section and the incisive shape not clear (broken).orange red colour enamel.

Upper molar

M¹/M²: BDC 1-21U (dex.), Plate 2 (B2)

A high crowned cheek tooth only moderately worn without roots. The base of the crown curve slightly towards buccal side. Hypoflexus running down only one-third of the entire height of the lingual surface. Protocone, protoloph and anteroloph are connected to one another, thereby isolated the parafochette into a completely closed island. Mesoloph has not yet fused with hypocone and there are still clear anterior and posterior mesoflexuses opening into the buccal surface. Metaloph and posteroloph is still separated from hypocone. The two lophes surrounding the postfochette but not yet totally isolated it into an island. Small contact facets on anterior and posterior surfaces.

Lower premolar

P₄: BDC 5-16 (sin.), Plate 2 (B3)

Crown and parts of the roots preserved. One large root in the front part of the tooth while there are two smaller at the back (the lingual root was lost). Worn low crowned tooth,

hypoflexid still visible on occlusal surface and cutting the buccal surface down to its base. There are five fossettids visible on the occlusal surface. Crown narrower in front than at the back, with interproximal contact facet on posterior surface.

D. *Hystrix* sp. indet. in Lenggong Valley

Two samples from Badak Cave C identified generally as *Hystrix* sp. indet. these are:

Upper incisor

BDC EX6 (sin.), Plate 2 (C1)

This specimen is semi-circular in outline without any trace of a root. It has a flat posterior surface and smoothly curved antero-labial surface. The incisive surface is oval in shape. The enamel on its labial surface is orange red in colour.

Lower premolar

dP₄: BDC 1-17U (sin.), Plate 2 (C2)

This is an unworn, possibly just erupted, tooth. It is low crowned without any roots. The hypoflexid is clearly marked on the occlusal surface and runs down to almost two-thirds of the entire height of the buccal surface. Other synclines and lophids are not so clearly discernible in such an early stage of dental development.

3.3.1.2 Remarks

All the porcupine materials recovered in this study are from Lenggong Valley site (Badak Cave C) except for the one upper incisor CC EX14 from Batu Caves (Cistern Cave) (Table 3.5). No porcupine remains were recovered from Swamp Cave or Villa Cave.

However, several samples of other mammals collected from the latter sites at Batu Caves have of gnaw marks attributable to the activity of these rodents.

It could be that the carcasses were probably exposed outside the caves and gnawed before being washed in to the caves. This is a well-known phenomenon in Pleistocene and Holocene caves of Southeast Asia (Hooijer, 1946a; Tougard, 1998; Zeitoun *et al.*, 2005).

In order to establish some specific morphological characters to distinguish between the different species, I believe a greater number of recent specimens should be examined before these characters could be considered as taxonomically meaningful characteristics but unfortunately this is not possible with the limited number of specimens available.

Most of the researchers use the structure of the skull and development of the spiny covering to distinguish between the members of this family (Weers, 1993).

The occlusal pattern of cheek teeth is considered useless for subgenera and species determination as already mentioned by Weers (1994 & 2005), because it seems that the occlusal patterns are strongly changed by wear and may also be by age. The occlusal morphology of *Hystrix* has changed little from the Miocene and Pliocene to the Recent (Weers, 2003) suggesting that only the size and tooth height can be used for specific distinction. When only tooth material is available, the subgenera *H.* (*Hystrix*), *H.* (*Acanthion*) and *H.* (*Thecurus*) cannot always be distinguished by size due to the overlap of their size ranges and the heights of the crowns of all Pleistocene forms does not differ from that of the extant species (Weers, 2005).

Fossil and living porcupines have semi-hypsodont to hypsodont cheek teeth. Their hypsodonty is unequal: the lingual portion of upper cheek teeth is higher crowned than the labial portion, with the inverse being the case in lower cheek teeth.

There is a gradual transition from brachyodont to extremely hypsodont cheek teeth from *Trichys* to *Hystrix*. *Atherurus* teeth are less brachyodont than *Trichys*. The complete upper incisor is more curved in general than the lower incisor.

The depth of the hypoflexus is a characteristic feature in *Hystrix* in relation to the evolutionary stage of the species. Most researchers used the serial length or width of porcupine teeth for comparative studies. De Vos & Long (1993) mentioned that to use the serial molar length is much clearer than to use only the dimensions of the isolated molars as there is an overlap between the species but the serial measurements are not useful in this study because all the samples are isolated teeth.

The Lenggong Valley lower molar fits within the range of recent *Atherurus macrourus* material in the Natural History Museum (London) and with the fossils from Lang Trang Caves (Table 3.6). Moreover the *Hystrix* measurements differ from the others in its considerably larger dimensions. The upper molar in this study falls again within the limits of the *Hystrix brachyura* Lang Trang teeth and with those from the Sumatran caves. It is the same with the P₄ dimensions falling within the *Hystrix brachyura* ranges (Table 3.6).

The width and the length of the incisor are not reliable because they are influenced by the way of the measurements and size of the incisor that is dependent on age (Weers, 2003). Incisors are therefore, unsuitable for comparative studies although their dimensions are presented in (Table 3.6). Two specimens not included in the table mentioned above, BDC EX6 and BDC 1-17U, are under identified generally as *Hystrix*. The first sample is an upper incisor with length overlapping with that of *Atherurus macrourus* but fitting within *Hystrix* sp. indet. of the Sumatran caves specimens in the National Museum of Natural History (Leiden). This is the same with BDC 1-17U, dP₄ which has very similar morphology and measurements to the juvenile mandibles (registration no. 889h & 734i) in the Leiden Museum making it better to attribute these two specimens to *Hystrix* sp. indet.

Table 3.6 Comparative measurements of well-preserved porcupine teeth in this study with other modern and prehistoric material.

	Upper incisor	M¹	M²	Lower incisor	P₄	M₁	M₂
<i>Atherurus macrourus</i>							
Modern							
Zoological Museum University of Malaya							
N	3	2	1	3	3	3	2
L	2.4 - 3.7	3.6 - 4.4	4.1	2.4 - 2.9	5.2 - 5.6	4.8 - 5.7	5.0-5.3
W	3.7 - 4.4	4.8 - 5.6	4.8	2.7 - 3.6	4.1 - 5.1	4.0 - 5.0	4.7-5.2
Zoological Museum (Amsterdam) ¹							
N	17	46*		18		44*	
L	3.1 - 4.7	3.4 - 5.2		3.4 - 4.3		3.7 - 5.5	
W	2.5 - 3.0			2.5 - 3.3			
Natural History Museum (London)							
N						6	6
L						4.7 - 5.3	4.0-4.6
W						4.5 - 5.8	3.7-4.4
Material from Southeast Asia ²							
N		20	20			20	20
L							
W		3.8 - 6.1	3.6-5.6			3.6 - 5.0	3.7-5.1
Prehistoric							
Lang Trang Caves (Vietnam) ³							
N		1*				3*	
L		4.8				4.6 - 5.3	
W		5.6				4.6 - 4.9	
In this study							
Batu Caves [^]							
N	1						
L	2.5						
W	3.5						
Lenggong Valley [^]							
N	1			1		1*	
L	4.4			3.4		5.2	
W	5.1			4.4		4.6	

Table 3. 6, continued

	Upper incisor	M¹	M²	Lower incisor	P₄	M₁	M₂
<i>Hystrix brachyura</i>							
Modern							
Zoological Museum (University of Malaya)							
N	3	4	2	3	3	3	3
L	5.4 - 5.9	5.0 - 7.7	7.6 - 7.7	5.0 - 5.9	6.9 - 7.6	5.0 - 8.1	5.7-6.4
W	6.2 - 7.0	7.5 - 8.0	6.6 - 7.0	4.8 - 6.3	6.3 - 6.7	5.3 - 7.2	5.3-7.6
Sumatran recent materials ³							
N		58*			18	56*	
L		4.7 - 7.9			6.4 - 9.0	4.6 - 8.5	
W		4.8 - 5.8			4.7-7.1(N=16)	4.4 -7.6 (N=46)	
Material from Southeast Asia ⁴							
N		91*			30	87*	
		4.7 - 8.0			6.4 - 9.1	4.6 - 8.9	
Prehistoric							
National Museum of Natural History (Leiden)							
Lida Ajer/ Sibrambang Caves (Sumatra)							
N	7•	18•			1•		
L	3.6 - 8.3	7.0 - 8.2			7.7		
W	4.0 - 6.3	5.4 - 6.7			7.3		
Punung (Java) ³							
N		10*			10	12*	
L		5.7 - 7.6			6.6 - 9.6	5.6 - 8.7	
W		4.8 - 7.8			5.4 - 7.8	4.5 - 8.2	
Lang Trang Caves (Vietnam) ³							
N		20*			10	23*	
L		6.7 - 8.4			8.0 - 10.1	7.5 - 9.2	
W		6.3 - 8.2			6.0 - 7.6	6.2 - 8.3	
Duoi U'Oi Cave (Vietnam) ⁵							
N					22	30*	
L					7.2 - 9.1	8.4 - 11.9	
W					5.5 - 7.3	6.5 - 9.8	

Table 3.6 ,continued

	Upper incisor	M¹	M²	Lower incisor	P₄	M₁	M₂
Ma U'Oi Cave (Vietnam) ⁶							
N					1	2*	
L					8.3	8.1	
W					5.2	5.9 - 6.0	
American Museum of Natural History (A.M.N.H.) (Yenckingkou fauna, China) ⁷							
N						1	
L						7.6	
W						6.7	
In this study							
Lenggong Valley [^]							
N	1	1*			1		
L	6.0	8.0			7.6		
W	8.7	6.4			5.6		

N= number of samples, L= mesio-distal length; W= bucco-lingual width. All measurements are in mm after:

¹ Weers (2002)

² Weers (1977) in de Vos & Long (1993)

³ De Vos & Long (1993)

⁴ Weers (2003)

⁵ Bacon *et al.* (2008b)

⁶ Bacon *et al.* (2006)

⁷ Colbert & Hooijer (1953) ; identified as *Hystrix subcristata*

* Identified as M¹/M² or M₁/M₂

[^] Refer to the (Table 3.5) for more details

• The materials are identified as *Hystrix* sp. indet.