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ON THE TOOTH MORPHOLOGY OF THE LONG - TAILED PORCUPINE *TRICHYS FASCICULATA* (HYSTRICIDAE: RODENTIA), WITH NOTES ON THE GENERA *ATHERURUS* AND *HYSTRIX*

Désiré J. van Weers

ABSTRACT. - The primitive and rare Long-tailed Porcupine *Trichys* occurs on the Malay Peninsula, Sumatra and Borneo. The morphology of the teeth of this monospecific genus is poorly known. Occlusal patterns of the teeth are described and dimensions are presented. Comparisons are made with the less primitive genus *Atherurus* and the highly specialised genus *Hystrix*.

INTRODUCTION

The genus *Trichys* Günther, 1877, with only one species, *T. fasciculata* (Shaw, 1801), occurs on the Malay Peninsula, Borneo and Sumatra only. The species is rare and poorly represented in museum collections. Its morphology and biology are insufficiently known. The taxonomy of this genus was revised by Van Weers (1976), but liitle attention had been paid to the morphology of the teeth. In Dutch institutions only a few skulls are present, but additional specimens, kindly made available by the National University of Singapore and by the Director-General for Wildlife and National Parks of Kuala Lumpur, enabled me to fill this gap.

Ellerman (1940) mentioned the presence of one inner and three outer folds in the upper cheek teeth and the reverse pattern in the lower series in the family Hystricidae, but this is only validfor an incidental stage of wear (Van Weers, 1990). This incomplete description was repeated by Woods (1984). Stehlin & Schaub (1951) figured and discussed only the occlusal pattern of one single *Trichys* specimen, not knowing the individual variation or involving other morphological characters of the cheek teeth in their study. Differences from the taxonomically nearest and more specialized genus *Atherurus* F. Cuvier, 1829, have not yet been described. All Pleistocene porcupines are attributed to *Hystrix*, fossils of *Trichys* have not yet been found or have not been recognized as such. This paper aims at making the dentition of *Trichys* better known.

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MATERIAL AND METHODS

Specimens studied. - Skulls from the following institutions have been studied. DGWK = Directory General for Wildlife and National Parks, Kuala Lumpur; NNML = National Natural History Museum, Leiden; ZMA = Zoological Museum Amsterdam; ZRC = Zoological Reference Collection, National University of Singapore; RMAC = Royal Museum for Middle Africa, Tervuren, Belgium. The dental age classses (Van Weers, 1990) of the skulls listed are indicated in brackets. For the discussion of occlusal patterns three specimens with dental ages from III to V are used. In younger dentitions only a few unworn teeth are present, and the older ones have already lost many details of the occlusal structure.

Malay Peninsula: DGWK WD0233, (IV), Hutan Simpan, Bukit Lanjan, Selangor. — ZRC 4.1620, (VII), Kuala Lumpur, Selangor. — ZRC 4.1623, (II), Sungei Buloh, Selangor.

Borneo: NNML 20018, fragment, (VI), Mt. Kalulong, Sarawak. — ZMA 22.224, (V), Lanjak-Entimau area, S.E. Sarawak. — ZRC 4.1622, (III), Kiau, Mt. Kinabalu, Sabah. — NNML 20019, (IV), Mt. Kenepai, Kalimantan.

Sumatra: NNML 737, (VI), Padang, W. Sumatra. — NNML 1846, (VI), exact locality unknown. — ZMA 8883, (V), Deli.

Atherurus africanus. - 10 skulls, RMMA coll. 83006 M, Zaïre, Kisangani, Africa.

Measurements. - The occlusal breadth, occlusal length, 'height' and 'crown height' of the cheek teeth have been measured with vernier callipers (Table 1). The 'height' of a cheek tooth was taken as defined in Van Weers (1990), is indicated in figure 1 (ht.) and is in fact the total height with the roots. The 'crown height' has been measured as indicated in the same figure (cr.ht.) and is the height of the body of the tooth without the roots. For practical reasons that measurement was chosen instead of the enamel height. The enamel border is not always clear, especially in fossil specimens, and sometimes covered with cement, so this measurement is less easy to take and less reproducible. In the genus *Atherurus* two species are recognized, and specimens of one of these, *A. africanus* Gray, 1842, specimens could be studied. In Table 2, measurements of that species are presented to enable comparison of the relative molar height with *Trichys* . The breadth and length of the incisors was measured near the cutting end (table 3). Only one out of the two measurements from a pair of teeth was used. In the case of a difference between a left and a right tooth, the average was taken. The upper teeth are indicated in capital, the lower ones with small letters.

From a former *Trichys* study (Van Weers, 1976) tooth breadth measurements were available and these are entered in Table 1. In a single case is referred to individual specimens specified in that study.

Hystrix *as a reference.* - In the present paper *Hystrix* is used as a reference. Therefore the description of occlusal patterns in *Trichys* is prefaced by the following discussion of the basic *Hystrix* pattern. The terminology of parts of the cheek teeth is after Van Weers (1990). In figure 2A, an unworn M1 of *Hystrix*, the folds I to VI are present. With continued wear these folds will lose contact with the outer enamel and generally be transformed in the islands 1 to 6, a situation

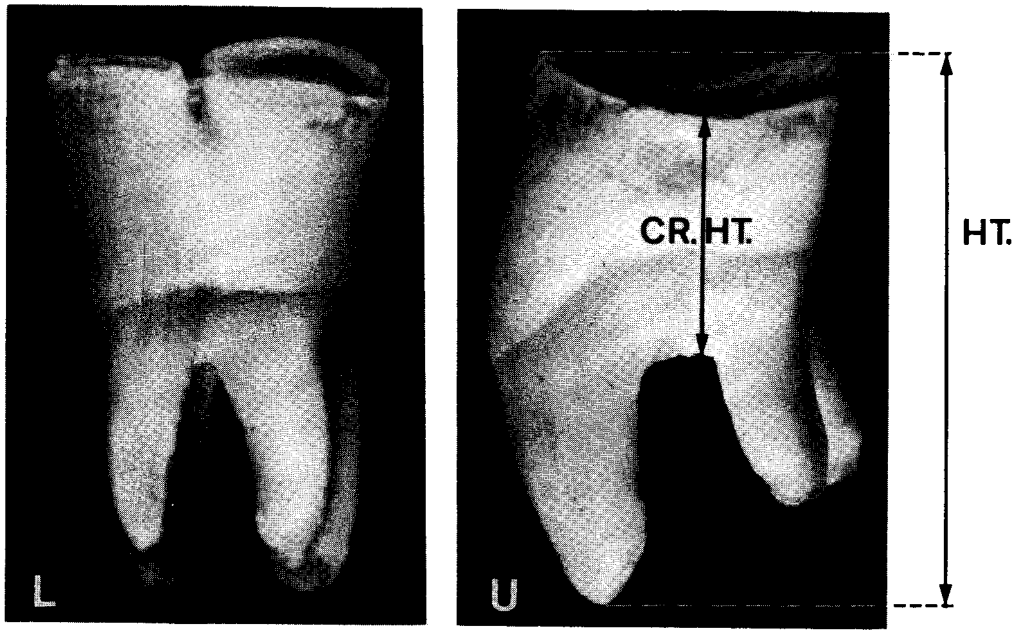

Fig. 1. Lingual view of a right m1 (L) and posterior view of left M1 (U) of *Trichys* specimen DGWK WD 0233, with indication of the measurements 'heigth' (HT.) and 'crown height' (CR. HT.). Figure ± x7.

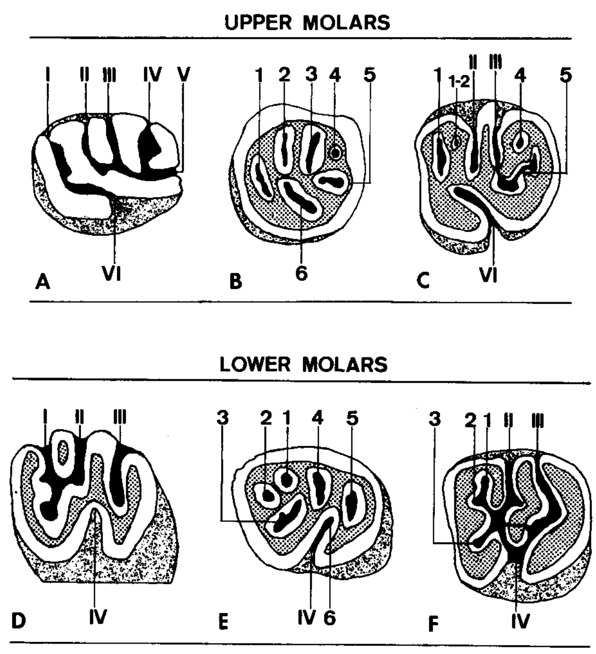

Fig. 2. Comparison of occlusal patterns in different stages of wear of upper and lower cheek-teeth of *Hystrix* (A, B, D, E) and *Trichys* (C, F) specimens. Upper molars: A = M1 of *H. brachyura* (ZMA 1270) with folds I - VI, B = M2 of *H. brachyura* (ZMA 6855) with islands 1 - 6, C = M1 of *Trichys fasciculata* (ZRC 4.1622) with folds and islands. Lower molars: D = m3 of *H. brachyura* (ZMA 6870) with folds I - IV, E = m2 of *H. brachyura* (ZMA 1128) with islands 1 - 5 and fold VI, and F = m1 of *Trichys fasciculata* (ZRC 4.1622) with folds and potential islands. All molars are left ones and not figured to the same scale. Indication of folds and islands after Van Weers (1990).

Table 1. Measurements of occlusal breadth, occlusal length, height, crown height in mm, and the ratios height/length and crown-heigt/length of cheek-teeth of *Trichys*, with range, mean, number of specimens (n) and standard deviation (s).

	breadth	length	height	cr.ht.	ht./l.	cr.ht./l.
			UPPER MOLARS			
D4	2.8-3.5	3.1-3.5	4.9-5.7	1.8-2.5	1.4-1.7	0.51-0.74
	3.1	3.3	5.4	2.2	1.6	0.63
	n = 5	n = 4	n = 3	n = 3	n = 3	n = 3
P4	3.3-4.8	3.2-4.4	6.1-8.2	2.8-4.4	1.7-2.0	0.64-1,09
	4.1	3.8	7.4	3.4	1.9	0.89
	n = 26	n = 6	n = 6	n = 6	n = 6	n = 6
	s = 0.38	s = 0.44	s = 0.72	s = 0.55	s = 0.10	s =0.15
M1	3.1-4.7	3.3-3.8	5.0-7.2	2.0-3.6	1.4-1.9	0.61-0.95
	3.9	3.6	6.3	3.0	1.7	0.82
	n = 33	n = 10	n = 9	n = 9	n = 9	n = 9
	s = 0.42	s = 0.16	s = 0.67	s = 0.47	s = 0.16	s =0.10
M2	3.2-4.8	3.3-4.0	5.0-6.8	2.0-3.4	1.5-1.9	0.61-0.94
	4.0	3.6	6.1	2.9	1.7	0.81
	n = 30	n = 9	n = 8	n = 8	n = 8	n = 8
	s = 0.43	s = 0.19	s = 0.50	s = 0.43	s = 0.11	s = 0.11
M3	3.0-4.0	3.0-3.7	4.8-5.9	2.2-3.4	1.4-1.6	0.59-1,06
	3.6	3.3	5.2	2.6	1.5	0.80
	n = 26	n = 6	n = 6	n = 6	n = 6	n = 6
	s = 0.30	s = 0.24	s = 0.36	s = 0.41	s = 0.08	s =0.14
			LOWER MOLARS			
d4	2.8-3.1	3.4-3.7	5.4-6.5	2.5-2.7	1.5-1.9	0.69-0.79
	2.9	3.5	6.1	2.6	1.7	0.74
	n = 4	n = 4	n = 3	n = 3	n = 3	n = 3
p4	2.9-4.3	3.3-4.5	6.5-8.4	2.6-4.0	1.7-2.3	0.60-1,09
	3.7	3.9	7.7	3.3	2.0	0.86
	n = 25	n = 6	n = 6	n = 6	n = 6	n = 6
	s = 0.35	s = 0.41	s = 0.65	s = 0.49	s = 0.23	s =0.15
m1	3.3-4.4	2.9-4.0	5.0-7.0	2.4-3.8	1.5-1.9	0.65-0.97
	3.9	3.7	6.2	2.9	1.7	0.77
	n = 32	n = 10	n = 10	n = 10	n = 10	n = 10
	s = 0.31	s = 0.31	s = 0.65	s = 0.44	s = 0.12	s = 0.10
m2	3.2-4.6	3.3-4.3	4.3-6.1	2.2-3.5	1.3-1.5	0.58-0.94
	4.0	3.8	5.4	2.9	1.4	0.78
	n = 29	n = 9	n = 9	n = 9	n = 9	n = 9
	s = 0.37	s = 0.25	s = 0.48	s = 0.41	s = 0.08	s = 0.12
m3	2.1-4.6	3.2-3.8	4.0-5.6	2.2-3.4	1.2-1.6	0.59-1,03
	3.5	3.5	4.7	2.8	1.4	0.94
	n = 27	n = 8	n = 8	n = 8	n = 8	n = 8
	s = 0.44	s = 0.20	s = 0.54	s = 0.37	s = 0.14	s = 0.13

Table 2. Measurements of occlusal breadth, occlusal length, height, crown height in mm, and the ratios height/length and crown-height/length of specimens of *Atherurus africanus* with range, mean and number of specimens.

	breadth	length	height	cr.ht.	ht./l.	cr.ht./l.
			UPPER MOLARS			
P4	3.8-5.0	3.6-4.8	7.5-8.7	4.3-5.0	1.7-2.4	0.96-1.39
	4.2	4.4	8.2	4.7	1.9	1.09
	n = 6	n = 6	n = 5	n = 5	n = 5	n = 5
M1	3.4-5.5	4.0-5.3	6.6-9.1	3.4-5.0	1.6-2.1	0.85-1.16
	4.1	4.3	7.7	4.2	1.8	0.98
	n = 12	n = 12	n = 8	n = 7	n = 8	n = 7
M2	3.5-4.5	4.0-5.3	6.3-9.2	3.5-5.5	1.5-2.0	0.83-1.04
	4.0	4.3	7.3	4.1	1.7	0.94
	n = 12	n = 12	n = 9	n = 8	n = 8	n = 8
M3	3.0-4.1	3.1-4.3	5.6-7.1	2.4-5.0	1.4-1.8	0.65-1.43
	3.4	3.7	6.2	4.1	1.7	1.12
	n = 9	n = 9	n = 9	n = 6	n = 9	n = 6
			LOWER MOLARS			
p4	3.5-4.5	4.1-5.5	8.6-9.3	4.1-5.6	1.6-2.3	0.75-1.37
	4.0	4.7	9.0	4.7	1.9	1.03
	n = 5	n = 5	n = 4	n = 4	n = 4	n = 4
m1	3.3-4.8	4.2-5.6	7.0-8.0	3.7-5.2	1.3-1.8	0.84-1.16
	3.9	4.6	7.2	4.3	1.6	0.97
	n = 12	n = 12	n = 5	n = 5	n = 5	n = 5
m2	3.3-4.5	3.5-5.5	5.8-7.6	4.0-4.8	1.3-1.7	0.89-1.23
	3.9	4.5	6.4	4.5	1.5	1.03
	n = 12	n = 12	n = 8	n = 7	n = 8	n = 7
m3	3.2-3.7	3.7-4.5	5.2-6.3	4.1-5.1	1.2-1.6	0.96-1.32
	3.4	4.1	5.5	4.7	1.4	1.15
	n = 9	n = 9	n = 7	n = 7	n = 7	n = 7

Table 3. Breadth and length measurements in mm of upper and lower incisors of ten *Trichys* specimens, arranged in order of the dental development classes II (young, DP - M1) to VII (old, P4 - M3).

Specimen	Dental	Upper Incisors		Lower Incisors	
	Age	Breadth	Length	Breadth	Length
ZRCS 4.1623	II	1.3	1.9	1.2	1.6
ZCRS 4.1622	III	2.0	3.5	1.8	3.5
NNML 20019	IV	2.0	3.4	1.7	3.6
WD 0233	IV	2.0	2.8	1.9	3.2
ZMA 22.224	V	2.1	3.9	2.3	4.2
NNML 8883	V	2.1	3.3	1.9	3.6
NNML 20018	VI	2.6	4.0	2.1	4.6
NNML 737	VI	2.4	3.7	2.2	3.1
NNML 1846	VI	2.3	3.3	2.0	3.8
ZRC 4.1620	VII	2.2	3.3	2.0	3.3

presented in figure 2B, an M2 of *Hystrix*. Fold V is seldom developed, fold IV mostly becomes closed in an early stage of wear and in most cases fold I is the next to lose its connection with the outer enamel border. The 'islands', in three-dimensional sense tube-like enamel invaginations from the enamel surface, may split up in a deeper level of the tooth which results in a larger number of islands in the worn tooth. In the medium sized *H. brachyura* Linnaeus from Sumatra (Van Weers, 1990, n = 35) more than six islands have rarely been observed, whereas in the larger *H. cristata* Linnaeus this is not exceptional. In Van Weers (1992: fig. 1.4) an extremely large P4 (10.8 x 12.7 mm) with eight islands from a *H. cristata* specimen has been figured. The available data suggest that there is a correlation between absolute size of a tooth and the complexity of the dental pattern.

In the lower cheek teeth of *Hystrix* the relation between islands and folds is more complicated than in upper teeth. Here the four original folds (fig. 2D) usually result in six islands. In figure 2E five are present, fold IV has not yet been transformed into the sixth island. Rarely, and in a very early stage of wear only, other weakly developed folds may be distinguished. The pattern with four folds in figure 2D is also shown in the m3 of Niethammer's (1982: fig. 193) figure of a *H. cristata* tooth row. That pattern, however, is not very common because in most cases fold I is not developed.

DESCRIPTIONS AND DISCUSSION

The occlusal patterns of the upper cheek teeth. - The upper dentition of *Trichys* specimen ZMA 22.224 with P4 - M2 (M3 is missing) in figure 3A, shows a clear similarity with the occlusal pattern of *Hystrix*. In the slightly worn P4 folds I to IV and VI are present. In the M1 a trace of fold II, the islands 1, 2, 3, 5 and 6 are present and of island 4 a light spot is left. In the M2 the folds have disappeared and all the islands 1 to 6 are present. The upper dentition of *Trichys* specimen ZRC 4.1622 (age class III) also shows a more than average similarity with the basic *Hystrix* pattern. The M1 of that specimen (fig. 2C) shows the folds II, III and VI and the islands 1 and 4 can easily be recognized. An accessory island is indicated with '1-2' to suggestits supposed original connection with island 1 or 2, and the developing island 5 in that figure seems to be splitting into two islands. The D4 in figure 4A shows fold II and VI clearly, relics of I and III, island 4 and a trace of island 5. In the M2 fold I is closed buccally but lingually still connected with the other ones, II and VI are present, III and IV can be recognised and islands have not yet been developed.

Specimen DGWK WD0233 in figure 5A (D4 - M3, age class IV) shows a later stage of wear. This holds for the D4 and M2 but not fully for the M1. In that tooth fold I still opens buccally, whereas in the younger specimen (figures 2C and 4A, age class III) this fold is transformed already into the island 1. In the unworn M3 all the potential folds are slightly indicated at least.

Not all specimens resemble the common *Hystrix* patterns to the same extent. The early disappearance or fusion of islands or folds, causes a larger variability of the dental pattern. This may be due to the brachyodonty of the *Trichys* cheek teeth, but in my opinion it is more strongly correlated with the smaller absolute size of these teeth. This variation in number of details occurs in the dentition of a *Trichys* specimen figured by Stehlin & Schaub (1950: fig. 43). In the M1 the folds II and III are nearly fused and in the M2 the only island may be a fusion of 3, 4 and 5. This large individual variation is illustrated below by the numbers of folds and islands in the M1 in four skulls of about the same dental development:

	number of folds	number of islands
ZMA 22.224	rudiments	5
USNM 144216	3	none
USNM 34.785	1	5
USNM 144218	4	1

As a consequence in this sample it is impossible to distinguish wear categories for teeth as has been done for *Hystrix brachyura* (Van Weers, 1990). Only unworn teeth with folds only, considerably worn teeth in which only island are left, and a middle group with folds as well as islands can be distinguished. However, the overall conclusion is that the occlusal pattern of *Trichys* does not differ fundamentally from the basic pattern in *Hystrix*.

The occlusal patterns of the lower cheek teeth. - For the patterns in the lower cheek teeth it is less easy to determine the homology with the *Hystrix* plan. In figure 3B of specimen ZMA 22.224 in the p4 the folds II and IV can be recognised and the buccal island is probably nr. 3. That island has had a buccal opening, which is an individual variation. In the m1 the islands are probably the numbers 1 to 3 and 4 or 5, fold IV is still present. In the m2 fold IV is still deeply penetrating, and the two anterior islands may be the numbers 1 to 4. In the m3 the islands 1 and 3, and perhaps 4 are fused.

In figure 4B of *Trichys* specimen ZRC 4.1622, the d4 is much too worn to be analysed. The m1 in this figure, and figure 2F, show a clear similarity with the pattern in *Hystrix*. The folds II, III and IV are still present and the loci of the potential islands 1 to 3 are indicated. The structure of the m2, in an early stage of wear, is not so easy to homologize as the as the m1. Four folds seem to be present, but in this stage, their homology is far from clear.

The d4 of specimen WD0233 in figure 5B is much too worn for an analysis. In the m1 fold II is present, III is closed but still connected with IV, and islands have not yet developed. The m2 is somewhat less worn than the m1 and fold III still has its buccal opening. The m3 is very little differentiated and only the folds II and IV can be recognised.

Although the lower teeth of the studied *Trichys* specimens show a somewhat more reduced pattern than *Hystrix*, they do not differ essentially.

Number of roots. - The upper molar in figure 1 (U) shows the normal situation for the M1 and M2 with one broad lingual and two buccal roots. Four-rooted M1 and M2 are not uncommon and in some a small threadlike fifth one may be present.

The lower molar in figure 1 (L) shows the for *Trichys* common situation with four roots in the m1 and m2. The d4 and p4 have always three roots. The m3 mostly has three roots, sometimes a fourth is present.

In *Hystrix* the maximal number of roots of the hypsodont teeth is three. As for skeletal characters, structure of the skull and development of the spiny covering, *Trichys* is the most primitive genus of the Hystricidae (Van Weers, 1976). The brachyodonty of the cheek teeth is also considered to be the primitive condition. Fossil evidence, however, is lacking to consider the larger number of roots in *Trichys* as original and the broad lingual root of the upper teeth as a fusion of two smaller ones, or to consider it as a derived condition.

Dimensions and outline of cheek teeth. - In Table 1 the dimensions of the upper and lower

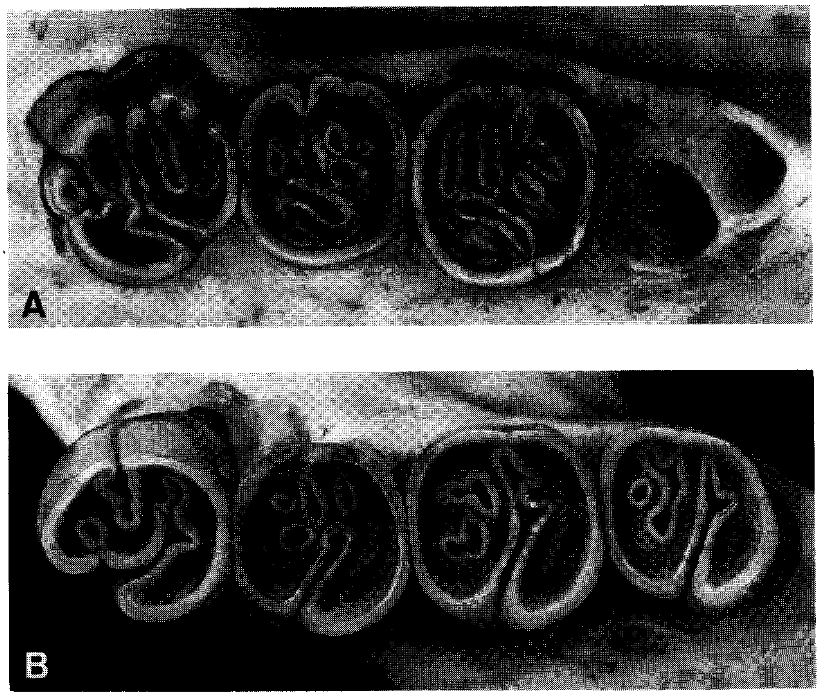

Fig. 3. Left P4 - M2 (A) and p4 - m3 (B) figured as a left one, *Trichys fasciculata*, specimen ZMA 22.224 from Sarawak, Borneo. Protocone, respectively protoconid directed to the bottom of the page, figures ±x7.

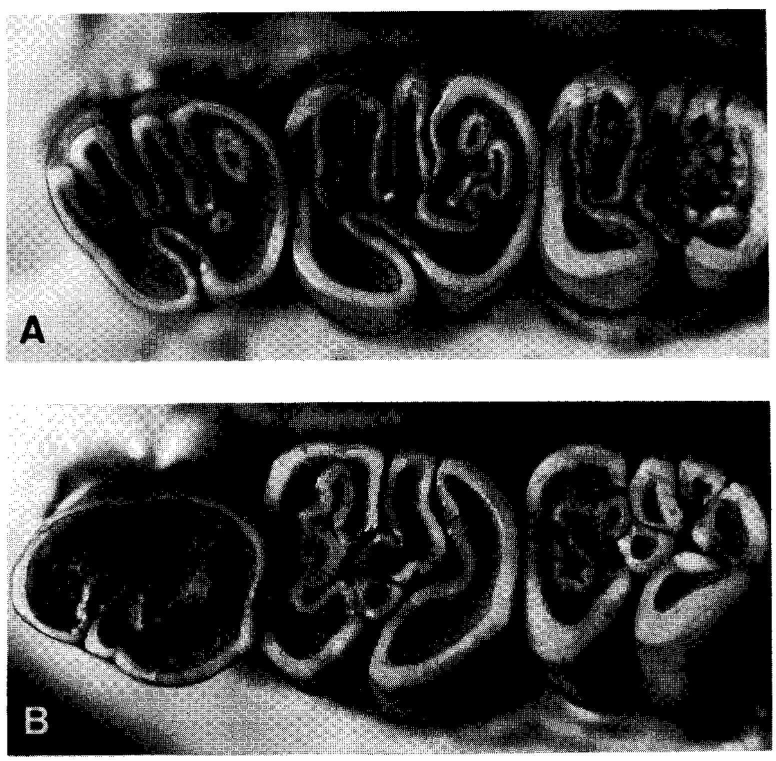

Fig. 4. Left D4 - M2 (A) and d4 - m2 (B) of *Trichys fasciculata*, specimen ZRCS 4.1622 from Mt. Kinabalu, Borneo. Protocone respectively protoconid directed to the bottom of the page, figures ± x7.

cheek teeth are presented. From this table can be seen that the occlusal breadth of the M1 and M2 together vary from 3.1 to 4.8 mm. The increase of the occlusal breadth of the upper cheek teeth of *Hystrix* through wear is discussed in Van Weers (1990). Although our *Trichys* sample does not allow the distinction of wear classes, it is clear that worn teeth are wider than unworn ones. In unworn M1-2 with only folds the mean breadth is 3.5 mm (range 3.4 - 3.8 mm, n = 5) against 4.3 mm in worn M1-2 in which only islands are present (range 3.8 - 4.7 mm, n = 11).

The cheek teeth of *Trichys* are always, and those of *Atherurus* mostly, multi-rooted and brachyodont. Mones (1982) tried to improve the inadequate terminology related with cheek tooth growth and proposed an equivocal nomenclature. However, in the family Hystricidae, from *Trichys* to *Hystrix*, a gradual transition from brachyodonty to extremely hypsodonty ("protohypsodonty" after Mones, 1982) occurs. Therefore a quantative expression is a better solution than the use of terms solely. For the expression of brachyodonty the ratio crown-height/ length (cr.ht./l.) is preferred to the expression of the crown height as a percentage of the total height. The former index has the advantage that it can be used for fossil teeth with damaged roots also.

Of the two species of *Atherurus*, sufficient specimens could be studied of the African *A. africanus* Gray, 1842 (Table 2). The dentition of that genus is more specialized than *Trichys* because the teeth are less brachyodont as appears from table 2. All the molars have a larger relative crown height than those of *Trichys* (Table 1). In *Hystrix* the shape of the molars varies from more or less cylindrical, in which a distinction between 'crown' (as defined in the present paper) and 'root' is not possible, to a situation with one large and two smaller roots. This

Fig. 5. Left D4 - M3 (A) and d4 - m3 (B) of *Trichys fasciculata*, specimen DGWK WD0233 from Selangor, Malay Peninsula. Protocone respectively protoconid are directed to the bottom of the page, figures ± x7.

variation is clearly shown by Niethammer (1982: fig.196). Therefore, besides the index cr.ht./l., the ratio total height/length (ht./l.) is chosen. For *Trichys* and *Atherurus* the latter index does not really differ (table 1 and 2). In *H. brachyura* in the M1-2 it varies from 1.4 to 2.4 (mean 1.9, n = 56), and in the m1-2 from 1.3 to 2.8 (mean 1.9, n = 43), data which are derived from the same specimens as studied in Van Weers (1990). Instead of the relation of height and length of the teeth, the ratio between the height and the occlusal breadth could have been chosen. The disadvantage of the latter is that the breadth is more affected by wear than the length.

Dimensions of incisors. - In table 3 breadth and length measurements near the cutting end of the incisors of the ten *Trichys* specimens studied are presented. As incisors are ever growing teeth, a correlation between age of the specimen and the dimensions of its incisors is expected. Although the number of specimens is rather small, that relation is shown in Table 2.

EVOLUTIONARY RELATIONSHIP

Stehlin & Schaub (1951) derived the occlusal pattern of the Hystricidae from the Theridomyidae (Europe, Eocene to late Oligocene). There is, indeed, considerable agreement in the basic plan of the upper cheek teeth of the Hystricidae with that of the "Theridomysplan" (Stehlin & Schaub: 42), but for the lower teeth the similarity is less convincing (Stehlin & Schaub: 230). However, this agreement loses much of its significance when it is realized that the Theridomyidae are sciurognathous. Although the Theridomyidae and the Hystricidae have a hystricomorph masseter structure, there is strong evidence that this character was developed independently (Wood, 1985). Moreover, the micro-structure of the incisor enamel in the Theridomyidae is pauciserial or uniserial, against multiserial in the Hystricidae (Wood, 1985). The suggestion of affinity of the Hystricidae with Eocene Ctenodactyloidea (Hussain *et al.*, 1978) is stronger but still has the character of a working hypothesis (De Bruijn *et al.*, 1982, Lucket & Hartenberger, 1985), because fossils linking the two groups are missing.

CONCLUSIONS

The occlusal pattern of the cheek teeth in *Trichys* does not differ essentially from the basic pattern in *Hystrix.*

In the Hystricidae there seems to be a correlation between the absolute size of the cheek teeth and the occlusal pattern. In some of the largest *Hystrix* molars a larger number of structural elements occurs than in the basic pattern, whereas in *Trichys* specimens that number may be reduced.

The larger number than three roots of the cheek teeth of *Trichys* differs from *Hystrix* and from rodent cheek teeth in general. It cannot be decided whether this is a derived or a specialized condition.

It is preferable to quantify the tooth height development in the Hystricidae with ratios as crown-height/length and total height/length instead of using adjectives only.

The relative crown height (cr.ht./l.) in the upper cheek teeth of *Trichys* in our sample is lower (51 to 109 %) than in *Atherurus* (65 to 143 %); ~~for the~~ lower cheek teeth these values are 58 to 109 % against 75 to 137 %.

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