

MACROSCELIDEA, INSECTIVORA AND CHIROPTERA FROM THE MIOCENE OF EAST AFRICA

by
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SUMMARY

The East African Miocene Macroscelidea, Insectivora and Chiroptera are revised on the basis of new material. New taxa proposed are: *Miorhynchocyon*, n. gen. (Macroscelididae); *Miorhynchocyon meswae*, n. sp.; *Pronasilio ternanensis*, n. gen., n. sp. (Macroscelididae); *Hiwegicyon juvenalis*, n. gen. n. sp. (Macroscelididae); *Parageogale*, n. gen. (Tenrecidae); Prochrysochlorinae, n. subfam. (Chrysochloridae); Propottinae, n. subfam. (Pteropodidae); *Chamtwaria pickfordi*, n. gen., n. sp. (Vespertilionidae). *Gymnurechninus songhorensis* is synonymised with *G. camptolophus*.

The new material provides additional information on the dentition, especially of *Myohyrax oswaldi*, *Galerix africanus*, *Amphechinus rusingensis*, *Protenrec tricuspis* and *Parageogale aletris*. Partial skulls are described of *Amphechinus rusingensis*, *Protenrec tricuspis*, *Prochrysochloris miocaenicus* and *Taphozous incognita*.

The oldest member of the Macroscelidinae (*Pronasilio*) is described from Fort Ternan. *Galerix africanus* is closely related to *G. exilis* from Europe. *Amphechinus rusingensis* is compared with Asiatic Oligocene Erinaceinae. The Miocene age of *Crociodura* is rejected. On the evidence of humeri, the following families of Chiroptera are newly reported: Pteropodidae, Nycterididae, Vespertilionidae, Molossidae. *Propotto* is regarded as an offshoot from the Pteropodidae, not ancestral to modern forms. *Chamtwaria* is a primitive vespertilionoid, provisionally placed in the Kerivoullinae.

Erinaceidae probably entered Africa at the beginning of the Miocene, before 20 Ma. Faunistic differences between deposits are largely to be ascribed to differences in local environment.

INTRODUCTION

Mainly because of their important bearing on hominoid evolution, the Miocene deposits of East Africa have been the subject of much palaeontological and geological investigation in recent years (reviewed by Andrews 1981). A considerable amount of fossil material has been collected, much of it from new locations. The purpose of the present paper is to describe the insectivores, macroscelideans and bats obtained mainly between 1967 and 1980. It supplements and revises earlier work on this subject (Butler 1956, 1969; Butler & Hopwood 1957).

The geological history of the area is now much better understood. Reference may be made to Bishop (1968), Van Couvering & Miller (1969), Van Couvering & Van Couvering (1976), Pickford & Andrews (1981), Shipman *et al.* (1981) and Bernor (1983). Radiometric dating (*e.g.* Bishop *et al.* 1969), stratigraphy (Pickford & Andrews 1981) and comparisons of faunas (Pickford 1981) have been used to elucidate the sequence of the deposits, and palaeo-ecological aspects have been discussed by Andrews & Van Couvering (1975), Pickford (1981, 1983), Shipman *et al.* (1981), Evans *et al.* (1981) and Kortland (1983).

The material described in this paper comes from the deposits listed in Table 1. These range in age from about 23.5 Ma (Meswa Bridge) to 14.0 Ma (Fort Ternan), but most of the material dates between 20 and 17.5 Ma (Pickford 1981), approximately equivalent to the late 'Aquitanian' and the 'Burdigalian' land mammal ages of Europe (Laugnac, Estrapouy, La Romieu) (Van Couvering 1972, Bernor 1983). If the age attributed to Meswa Bridge is correct, it would be at the Oligocene-Miocene boundary. The date of 23 Ma given to the Karungu deposit by Bishop *et al.* (1969) is rejected on faunistic grounds by Pickford (1981), who regards it as similar in age to the Hiwegi Formation on Rusinga Island (17.5 Ma). Fort Ternan, at 14.0 Ma (Shipman *et al.* 1981), would be approximately equivalent to La Grive; Maboko is somewhat older (*cir.* 15 Ma, Andrews *et al.* 1981).

Pickford (1981, 1983) classifies the East African Miocene faunas into seven 'sets', based on 'core faunas', of which Songhor, Hiwegi, Maboko and Fort Ternan typify sets I-IV. He points out that the difference between the two 'Burdigalian' faunal sets may be at least partly environmental: all the deposits with set I faunas were formed subaerially, whereas those of set II represent floodplain, swamp and lacustrine environments. The

Ma	Tinderet region	Kisingiri (Rangwa) région	Uganda	Faunal set (Pickford 1981)
14	Fort-Ternan			IV
15	Maboko			III
17.5		Rusinga (Kulu Fm.) Rusinga (Hiwegi Fm.) Karungu Mfwanganu (Kiahera Fm.)		II
19.5	Songhor; Chamtwara (Kapurtay Agglomerates)		Napak	I
20	Legetet Fm. (including Maize Crib) Koru Fm.			
23.5	Meswa Bridge (Muhoroni Agglomerates)			

Table 1

'Burdigalian' deposits are situated geographically in three regions: (1) those associated with the Tinderet volcano (Koru, Legetet, Chamtwara, Songhor) at the eastern end of the Nyanza valley in western Kenya; (2) those related to the Rangwa (Kisingiri) volcano (Karungu, Mfwanganu, Rusinga) at the mouth of the Kavirondo Gulf, about 125 km from (1); (3) Napak, Uganda, some 300 km to the north of (2). Some infraspecific variation is possible at such distances, and barriers to dispersal may have intervened (Andrews & Van Couvering 1975). A closed forest environment seems to have predominated at all these localities, though there is an indication of more open woodland at Koru (Evans *et al.* 1981) and in some areas on Rusinga (Verdcourt 1963, Andrews & Van Couvering 1975).

The distinctiveness of the Fort Ternan fauna is attributable not so much to evolution *in situ* as to the introduction of allochthonous species, due to the drier climate (Evans *et al.* 1981) and to faunistic interchange with Eurasia following the closure of Tethys (Van Couvering 1972, Bernor 1983).

The specimens are housed in the British Museum (Natural History) (registration numbers M...) or in the Kenya National Museum (registration numbers KNM...). In the lists of specimens field numbers are given (in brackets) as well as registration numbers, to permit reference to earlier papers in which field numbers were used. Some specimens, which belong to the Kenya National Museum but are still unregistered at the time of writing, are referred to under field numbers only.

Drawings were made with a camera lucida attached to a 'Wild' stereomicroscope. Scale lines on the figures are graduated in mm.

SYSTEMATICS

Order MACROSCELIDEA BUTLER, 1956

The Macroscelididae, formerly treated as a family of the Insectivora, are now regarded as forming a separate order. McKenna (1975) believed that they originated in Asia from the Palaeocene - Oligocene order Anagalida, which also gave rise to the Lagomorpha, and Szalay (1977) found resemblances to Lagomorpha in the tarsus. Macroscelidea were present in Africa in the Early Oligocene (Patterson 1965).

Family MACROSCELIDIDAE BONAPARTE, 1838

Subfamily RHYNCHOCYONINAE GILL, 1872

MIORHYNCHOCYON nov. gen.

Diagnosis: Differing from *Rhynchocyon* as follows:-Oblique crest (anterior hypoconid crest) on lower molariform teeth ends midway between protoconid and metaconid, instead of joining the metaconid; metastylid absent on dP/4 and M/1; paraconid of P/4 and M/1 higher and more lingually situated; cheek teeth more brachydont; anterior margin of ascending ramus more upright. The skull, known only in *M. clarki*, has primitive characters (Butler & Hopwood 1957).

Type species: *Rhynchocyon clarki* BUTLER & HOPWOOD, 1957.

Remarks: The Miocene species hitherto included in *Rhynchocyon* differ in a number of ways from the living species and it is convenient to separate them generically, although *Miorhynchocyon* is distinguished only by primitive characters and it is probably only an earlier stage in the *Rhynchocyon* lineage.

Miorhynchocyon clarki (BUTLER & HOPWOOD, 1957)

Rhynchocyon clarki, Butler & Hopwood (1957), p. 4, figs. 2, 3; Patterson (1965), p. 309.
cf. *Rhynchocyon clarki*, Butler (1969), p. 5, fig. 2.

Diagnosis: Mandibular specimens are distinguished from *M. rusingae* by their smaller size and by the absence of a protostylid (posterior accessory cusp) on P/3. This distinction is clear in the Hiwégi area of eastern Rusinga (localities R 1, R 3 etc.) (Table 2, fig. 1). However, at Kaswanga, on the western side of the island, there is an apparently unimodal population with teeth intermediate in size between typical *M. clarki* and *M. rusingae*. Only one specimen contains P/3 (KNM.RU 3702), which resembles *M. clarki* in lacking the protostylid. All three forms may occur together at Songhor. As the intermediate form cannot be defined except on a statistical basis, it is provisionally included in *M. clarki* as a large form of that species.

Holotype: M34142 (Sgr 93.47), facial part of a skull with P3,4/.

	Typical <i>M. clarki</i>			Cf. <i>M. clarki</i> Kaswanga			<i>M. rusingae</i>			<i>M. meswae</i> holotype
	N	range	m	N	range	m	N	range	m	
P/2 length				1	2.5		2	3.4, 3.5	3.45	2.8 est.
P/3 length	3	2.6-3.1	2.90	1	3.0		3	3.9-4.5	4.17	3.4
P/4 length	5	3.6-3.8	3.68	4	4.0-4.5	4.33	1	5.1		4.3
P/4 width	4	1.8-2.2	2.00	5	2.2-2.5	2.34	1	2.6		2.5
M/1 length	12	3.0-3.5	3.27	1	3.4		3	4.1-4.7	4.50	
M/1 width	8	1.8-2.2	2.08	2	2.3, 2.4	2.35	3	2.8-3.0	2.93	
M/2 length	7	2.2-2.8	2.51	3	2.5-2.9	2.77	1	3.65		
dP/2 length	1	2.4								
dP/3 length	2	2.6, 2.7	2.65				2	3.9, 4.0	3.95	
dP/4 length	1	4.4					3	5.3-5.6	5.47	
P3/ length	3 _a	3.3-3.5	3.37	1 _b	3.7		1	4.4		
P4/ length	8	3.0-3.6	3.31	3	3.7-3.8	3.77	1 _c	5.1		
P4/ width	8	2.8-3.2	3.03	3	3.1-3.5	3.23	1 _c	4.1		
M1/ length	6	3.0-3.2	3.10	3	3.3-3.4	3.37	2	3.7, 3.9	3.80	
M1/ width	6	3.2-3.3	3.22	3	3.5-3.7	3.60	2	3.8, 4.0	3.90	
M2/ length	1	2.4		3	2.5-2.6	2.57	1	3.0		
M2/ width	2	2.3, 2.5	2.40	3	2.6-2.8	2.70	1	3.2		

a, holotype 3.3. from Songhor - b, specimen from Chamtwara - c, specimen from Fort Ternan.

Table 2 : Measurements (mm) of teeth of *Miorhynchocyon*

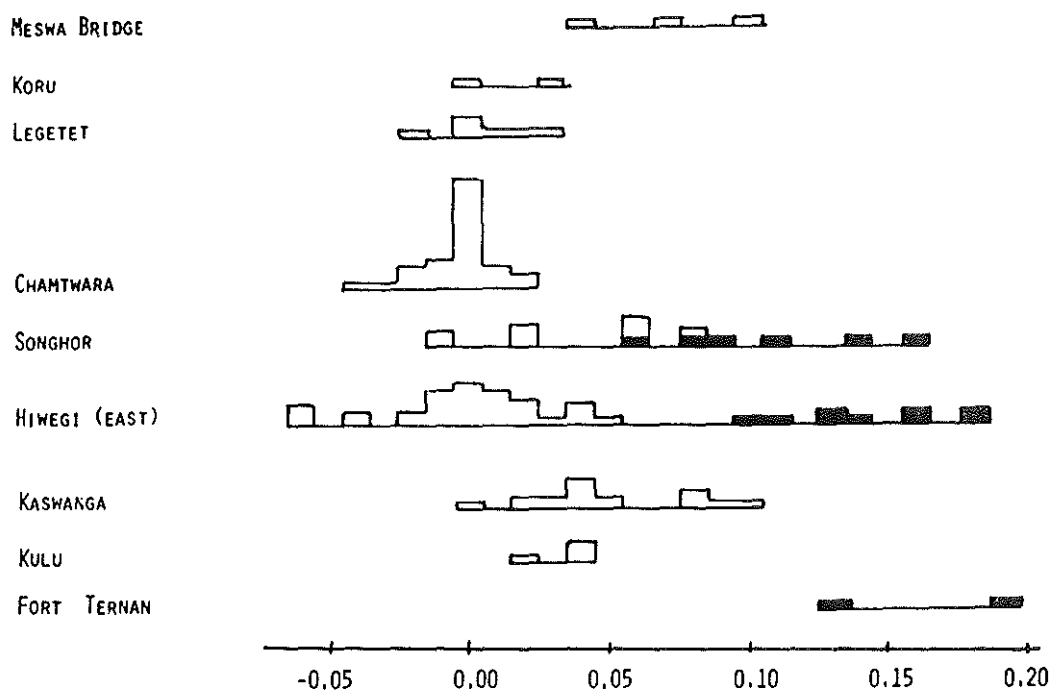


Fig. 1. — Size distribution of *Miorhynchocyon*.

Log measurement — log mean of typical *M. clarki* (from the Hiwegi area of Rusinga (R 1 - 3), Chamtwara and Legetet). Measurements used: length and width of P/4, M/1, P4/ and length of M/2. Specimens referred to *M. rusingae* are indicated in black.

Specimens identified:

Koru Formation.

Locality 25. KNM.LG 1541 (25/62), mandible with M/1.

Legetet Formation.

Locality 10. KNM.LG 1487 (10/549), mandible with P/3-M/1; KNM.LG 1484 10/910), mandible with M/2; KNM.LG 1485 (10/926), mandible with dP/2,3; KNM.LG 1486 (10/931), tibiofibula (?*Myohyrax*).

Locality 21. KNM.LG 841 (21/67), mandible with M/1,2; KNM.LG 867 (21/21), mandible with M/2.

Locality 29. KNM.LG 1528 (29/219), edentulous mandible.

Kapurtay Agglomerates.

Chamtwara (locality 34). KNM.CA 326 (34/194), two mandibles, one with M/1,2, the other edentulous; KNM.CA 1522 and 1523 (34/698), mandibles with M/1; KNM.CA 1551 (34/698), mandible with dP/2,3; KNM.CA 1532 (34/698), ? P/1; KNM.CA 1519 (34/698), P/4; KNM.CA 1976 (34/1523), M/1; KNM.CA 1530 (34/698), ? dP/2; KNM.CA 1916 (34/1281), P/3; KNM.CA 2222 (34/1828), P/3 (large); KNM.CA 2064 (34/716), KNM.CA 1965 (34/1508), KNM.CA 2045 (34/1568) and KNM.CA 1534 (34/698), P4/; KNM.CA 1997 (34/1524), KNM.CA 2003 (34/1530), KNM.CA 2008 (34/1535) and KNM.CA 2047 (34/1570), M1/; KNM.CA 2046 (34/1569), dP4/; KNM.CA 2177 (34/1100), astragalus.

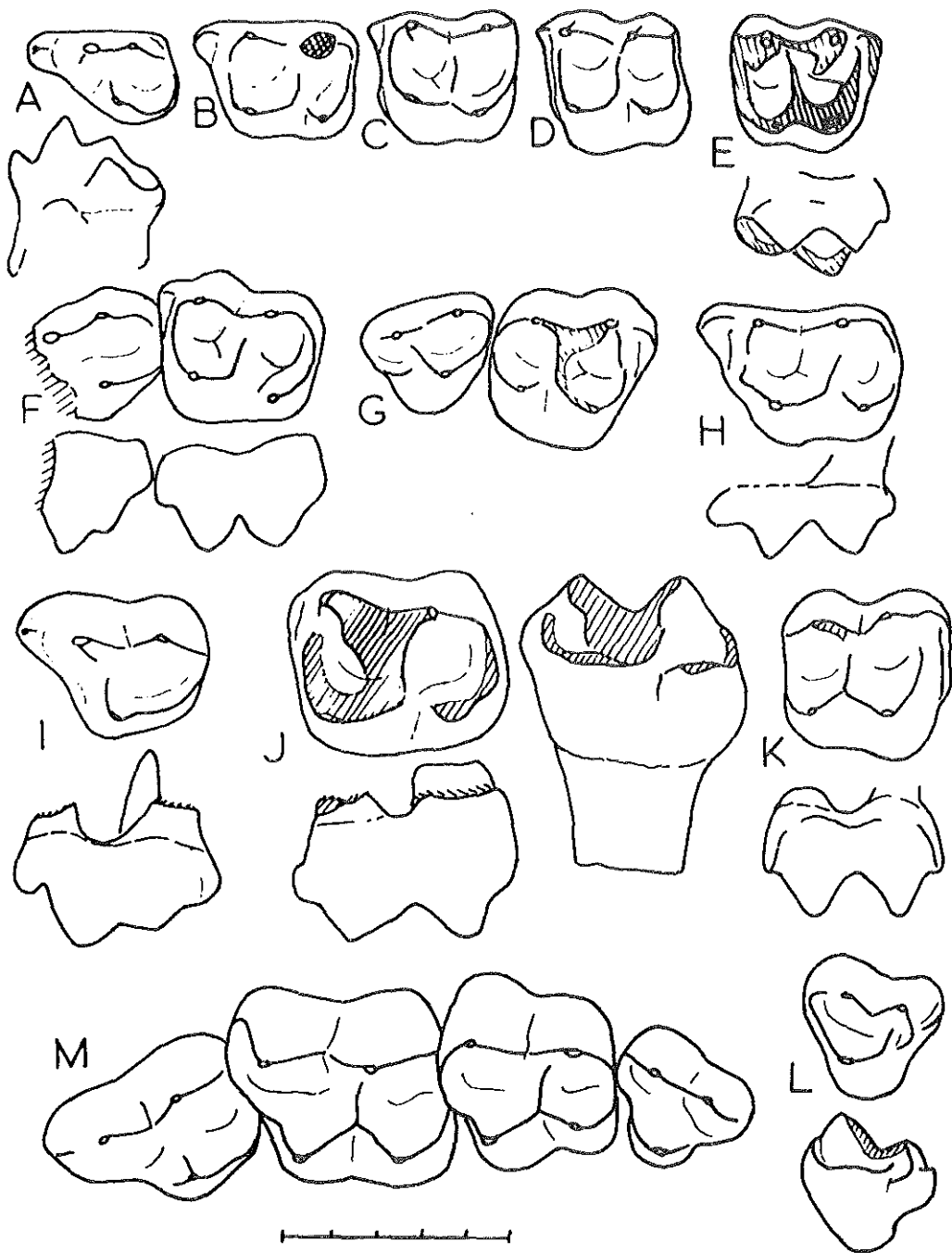


Fig. 2. — Upper teeth of *Miorhynchocyon*.

A-E, *M. clarki*: A, LP3/, KNM.CA 1916; B, LdP4/, KNM.CA 2046; C, LP4/, KNM.CA 2045; D, LM1/, KNM.CA 1535; E, RP4/, KNM.CA 2064.

F-H, *M. clarki* (large form): F, LP3/4/, KNM.RU 3700; G, RM2/3/, KNM.RU 3700; H, LdP4/, KNM.RU 3699.

I-L, *M. rusingae*: I, LP3/, KNM.SO 1405; J, LP4/, KNM.FT 26; K, RM1/, KNM.SO 1419; L, LM2/, KNM.SO 1418.

M, *Rhynchocyon clrnei* (recent), P3/-M2/, BMNH 1938.10.13.6.

Songhor. M 34142 (Sgr 93.47), holotype skull; four mandibles listed by Butler (1969, p. 5); KNM.SO 1424 (Sgr 2737.66), mandible with M/1; KNM.SO 1442 (Sgr 258.70), edentulous mandible; KNM.SO 3540 (Sgr 3065.66), P/4 (large); KNM.SO 1407 (Sgr 2317.66), M/1; KNM.SO 1611 (Sgr 285.72), dP/3; (Sgr 750.72), P3/; KNM.SO 1438 (Sgr 604.66), P4/; KNM.SO 1422 (Sgr 1423.66), dP4/; KNM.SO 1427 (Sgr 642.66), dP4/; KNM.SO 1774, tibiofibula (? this species).

Hiwegi Formation.

Locality R 1. Rs 587.49, mandible with dP/4; Rs 719.47, maxilla with P4/, M1/; M 34105 (Rs 998.50), maxilla with P4/-M2/.

Locality R 1A. KNM.RU 3703 (Rs 1114.71), mandible with P/3-M/2 (from surface); M 34138 (Rs 1265.50), mandible with M/1,2.

Locality R 2 (1956). KNM.RU 4373 (Rs 57.56), mandible with M/1,2; Rs 627.56, mandible with P/4-M/2.

Locality R 3. M 34137 (Rs 1700.50), mandible with M/2; Rs 891.56, maxilla with M1,2/.

Locality A 2. KNM.RU 4374, mandible with P/4, M/1.

Hiwegi area, surface. KNM.RU 3701 (Rs 263.71), mandible with M/1,2.

Kaswanga. All appear to be of the large form. Rs 1970.50, mandible with P/4; M 34139 (Rs 296.49), mandible with P/4, M/1; KNM.RU 3700 maxilla with P3,4/, maxilla with M1,2/, mandible with P/4-M/2, edentulous mandible, symphysis with I/2; KNM.RU 3699, maxilla with M1,2/, isolated M1/, two edentulous mandibles, mandible with P/3,4; KNM.RU 3697, P4/; KNM.RU 3704, M/2; KNM.RU 3705, M/2; KNM.RU 3698, M/2; KNM.RU 4348, M2/; KNM.RU 3702, mandible with P/2-4.

Locality R 106. RU 4287 (Rs 778.47), mandible with P/4 (large).

Kulu Formation.

M 34106 (Rs 903.50), mandible with M/1,2; M 34136 (Rs 904.50), mandible with P/4.

Karungu.

K 459.73, astragalus (? this species).

Description:

The new material provides some additional information on the dentition (Figs 2A-H, 3A-D). Postcranial bones are considered below in conjunction with those of *Myohyrax*.

There are four examples of P3/, one of which is referred to the larger form. The lingual cusp of P3/, interpreted as a hypocone by Butler & Hopwood (1957), is the protocone; a low hypocone frequently differentiates posteriorly to it in *Rhynchocyon*. There are 11 examples of P4/ (3 large) and 10 of M1/ (3 large). P4/ and M1/ are similar, and isolated specimens are not easy to distinguish. P4/ is longer than M1/ but of nearly equal width; it is slightly longer than wide. M1/ is usually narrower posteriorly than anteriorly. The crest from the protocone to the metacone is frequently weak or absent on P4/ but usually well developed on M1/. Four examples of dP4/ show that this tooth is narrower than P4/ and its parastyle is more prominent; the protocone-metacone crest is well developed. In KNM.RU 3699 P4/ is present above dP4/. On P4/, M1/ and dP4/ the protoloph joins the anterolingual side of the paracone, but on M2/ it connects with the parastyle. The paraconule cannot be distinguished on most upper molariform teeth.

The anterior end of a right mandible from Kaswanga (KNM.RU 3700) contains I/2 and the root of I/1 (Fig. 3D). I/2 has a bilobed crown as in *Rhynchocyon*, but the posterior lobe, which is partly worn off, is less high in comparison with the anterior lobe than in the living species. KNM.RU 3702 (Fig. 3A) shows a single alveolus for the canine and two alveoli for P/1, which was larger than the canine but shorter than P/2. KNM.CA

1532 may be an isolated P/1. It is a two-rooted tooth, 2.0 mm in length and with a single cusp 2.2 mm in height. The posterior profile is concave, not straight as in *Rhynchocyon*.

P/2 and P/3 are preserved in KNM.RU 3702, from Kaswanga. They are larger than in the Hiwégi specimen Rs 627.56 (Butler 1969), but agree with that in having no protostylids. There are no other examples of P/2, and three additional specimens of P/3 are too worn or broken for the absence of the protostylid to be confirmed. P/3 appears to vary in the development of the anterior basal cusp: it is largest in the Legetet specimen KNM.LG 1487; distinct in Rs 627.56 (Hiwégi), where it is also present, but smaller, on P/2; indistinct in KNM.RU 3702 (Kaswanga), where it is absent on P/2; absent in M 34136 (Kulu). In *Rhynchocyon* the anterior basal cusp is usually small or absent on P/3 and always absent on P/2.

On P/4 and M/1 the paraconid is higher and more lingually situated than in *Rhynchocyon*. There is no metastylid, and the anterior crest of the hypoconid meets the trigonid near the mid-line of the tooth. There is a well developed cingulum on the anterobuccal side of the trigonid and a posterior cingulum behind the hypoconid. P/4 is somewhat wider across the talonid than across the trigonid, but in most specimens of M/1 the widths of trigonid and talonid are equal. On M/2 the paraconid is reduced, the talonid is narrower than the trigonid, and there is no posterior cingulum.

KNM.CA 1551 is a fragment of mandible containing what are believed to be dP/2 and dP/3 (Fig. 3C). They are comparable in length with P/2 and P/3 but lower and narrower, and they have protostylids and well developed anterior basal cusps. KNM.LG 1485 is a similar specimen from Legetet, in which however dP/3 has lost the protostylid due to wear, and only a fragment of dP/2 remains. KNM.SO 1611 is another example of dP/3. An edentulous fragment (KNM.SO 1442), with the alveoli of dP/3 and dP/4, shows that these teeth had a short middle root between the main anterior and posterior roots.

Miorhynchocyon rusingae (BUTLER, 1969)

Rhynchocyon rusingae, Butler (1969), p. 6, Figs. 2, 3.

Holotype: Rs 711.47, mandible with P/3,4 from Hiwégi, locality R 3.

Specimens identified:

Kapurtay Agglomerates.

Songhor. 4 specimens listed by Butler (1969). Also: KNM.SO 1413 (Sgr 3695.66), mandible with P/4, M/1; KNM.SO 1423 (Sgr 4123.66), mandible with M/1; KNM.SO 1428 (Sgr 786.72), edentulous mandible; KNM.SO 1419 (Sgr 2737.66), maxilla fragment with M1/; KNM.SO 1405 (Sgr 2831.66), isolated P3/; KNM.SO 1418 (Sgr 742.72), M2/. Some of these may belong to the large form of *M. clarki*.

Kiahera Formation, Mfwanganu.

KNM.MW 430 (Mfw 1052.55), distal end of femur (?species).

Hiwégi Formation.

6 specimens listed by Butler (1969), from localities R 1, R 3 and R 3A.

Fort Ternan.

KNM.FT 26, isolated P4/.

Description:

There is some new information on the upper teeth (Fig. 2I-L).

P3/ (KNM.SO 1405) is larger than in *M. clarki*. The protocone is situated more

anteriorly, and it is followed by a ridge that represents the hypocone. The parastyle is distinct, anteriorly prominent, and connected to an anterior cingulum. There are three roots.

P4/, known only from Fort Ternan, is referred to *M. rusingae* on account of its size*. The parastyle is weak; the protoloph connects with the anterolingual face of the paracone; there is no paraconule; the protocone-metacone crest is strong; a curved crest follows the posterior edge of the tooth from the hypocone to the metacone. The tooth is moderately worn, especially in the trigon basin, where dentine is exposed. It differs from *M. clarki* in its proportionately greater length and in the stronger development of the protocone-metacone crest.

KNM.SO 1419 is a fragment of maxilla with M1/. The tooth resembles the specimen described by Butler (1969), but it is a little larger (3.9×4.0 mm). An isolated M2/ (KNM.SO 1418), measuring 3.0×3.2 mm, resembles specimens referred to *M. clarki*, except in size. It is triangular, with three equal roots, the protoloph connects with the parastyle, there is no indication of a paraconule, and the hypocone is very rudimentary.

Miorhynchocyon meswae nov. spec.

Diagnosis: Resembling *M. rusingae* in the possession of a protostylid on the posterior crest of the protoconid of P/3, but smaller in size, P/2,3 smaller in comparison with P/4, and anterior cusp (paraconid) of P/3 about half as high as the protoconid.

Holotype: KNM.ME 21, mandibular fragment with P/3, P/4 and the roots of P/2, from Meswa Bridge. This is the only specimen.

Description (Fig. 3F):

The lengths of P/2 (estimated from the roots) and P/3 are greater than in *M. clarki*, but measurements of P/4 fall into the range of the large form of that species (Fig. 1, Table 2). Compared with *M. rusingae*, P/2 (estimated) and P/3 are proportionately shorter in comparison with P/4: P/3 has 79% of the length of P/4 in *M. meswae*, 75% in *M. clarki* and 88% in *M. rusingae*.

The lingual surface of P/3 has flaked off, but the longitudinal crest and its cusps are preserved. The anterior cusp (paraconid) is better developed than in *M. clarki* and *M. rusingae*, rising to about half the height of the protoconid. P/4 is complete. The paraconid is only a little lower than the metaconid, and placed well forward. It is divided from the protoconid by a notch on the buccal side, below which is a wide anterobuccal cingulum fragment. The talonid is somewhat wider than the trigonid, and fully molariform. The oblique crest joins the middle of the posterior trigonid wall. The entoconid stands somewhat higher than the hypoconid, owing to the downward buccal inclination of the base of the tooth. Behind the hypoconid there is a buccally inclined cingulum. The anterior alveolus of M/1 is visible. The depth of the ramus is 3.7 mm below P/4. The mental foramen is below the middle of P/4.

*Since this paper was written I have come across a P3/ from Fort Ternan (KNM.FT 27), large in size (5.35×3.95 mm) and probably conspecific with the P4/. It is larger than the P3/ from Songhor, and it differs from that in the more posterior position of the protocone. The Songhor specimen may belong to the large form of *M. clarki*.

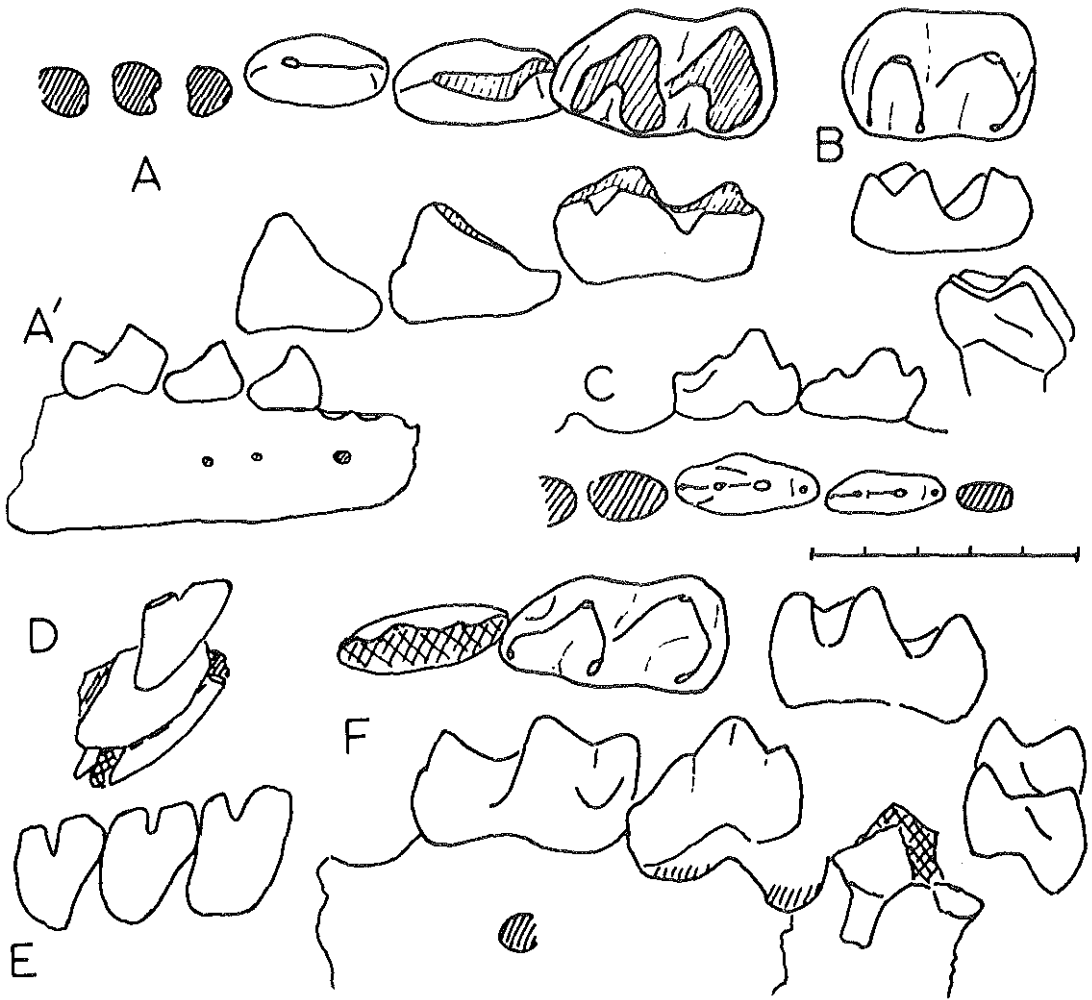


Fig. 3. — Lower teeth of *Miorhynchocyon*.

A, *M. clarki* (large form), RP/2-4 and alveoli of C/1 and P/1, KNM.RU 3702.

A', the same specimen, lateral view, at half the scale.

B, *M. clarki*, RM/1, crown, lingual and posterior views, KNM.SO 1407.

C, *M. clarki*, LdP/3,2, lingual and crown views, KNM.CA 1551.

D, *M. clarki* (large form), fragment with R1/2, KNM.RU 3700.

E, *Rhynchocyon petersi melanurus* (recent), I/1-3, BMNH 63.1854.

F, *M. meswae*, holotype, lateral view; P/3,4, crown view; P/4, lingual and posterior views.

Subfamily MYOHRACINAE ANDREWS, 1914

Originally regarded as hyracoids, *Myohyrax* and *Protypotheroides* were recognised as Macroscelididae by Patterson (1965).

MYOHYRAX ANDREWS, 1914

Myohyrax oswaldi ANDREWS, 1914

Myohyrax oswaldi, Andrews (1914), pp. 169-179, Pl. 28, figs. 4-6; Stromer (1926), pp. 123-124, Pl. 41, figs. 26-28; Whitworth (1954), pp. 26-40, text-figs 9-15, Pl. 5, figs 3, 4, Pl. 6; Patterson (1965), p. 318.
Myohyrax doederleini, Stromer (1926), pp. 120-123, text-fig. 19, Pl. 41, figs. 1-23; Hopwood (1929), p. 6, text-fig. 4.

Holotype: M 10610, mandible with P/2-M/1, from Karungu (Kachuku), not Koru as stated by Patterson (1965).

Distribution:

This species has not been found in the Koru Formation, and the only evidence for its presence in the Legetet Formation is a possible tibiofibula fragment.

Kapurtay Agglomerates.

Chamtwara. Common; more than 30 specimens, mostly single teeth but including four mandibles (KNM.CA 321, 1562, 2042 and 2179) and two astragali (KNM.CA 2043 and 2044).

Songhor. Three specimens only: KNM.SO 1447 and 1448 are mandibular fragments, and KNM.SO 1449 is an isolated M/2.

Kiahera Formation, Mfwanganu.

KNM.MW 196 (Mfw 130.50), a mandible with P/4-M/2.

Karungu. *M. oswaldi* is one of the main constituents of the fauna at this site. I have examined about 50 mandibles and 5 maxillae, as well as a number of isolated teeth and postcranial bones.

Hiwegi Formation. 26 specimens, mainly from the eastern side of Rusinga Island (7 from locality 1A, 5 from locality 3); only four specimens are from the Kaswanga area.

Fort Ternan. KNM.FT 3601, a mandible with (?)M/1,2, is the only specimen.

Description:

New material supplements information on the dentition provided by Whitworth (1954).

KNM.CA 1531 consists of a right mandibular fragment with I/2 and the alveoli of I/1 and I/3, together with an isolated left I/2; K 225.73 contains 8 isolated examples of I/1. I/1 and I/2 are procumbent, with enamel confined to the labial surface. I/1 is broader than I/2. The cutting edges of the lower incisors are not divided into lobes as in other Macroscelididae. A trace of lobulation however exists in the upper incisors, in the form of a slight notch in the cutting edge (Stromer 1926). This notch can be seen (fig. 4 K) in the isolated I1/ (M 21238) described by Whitworth (1954), but it is not shown in his text-fig. 9.

Four specimens show the unworn crown of P/3: KNM.CA 1553, KNM.CA 1554 (Fig. 4A), KNM.KA 114 and (talonid only) KNM.RU 3758. The tooth is a little higher than long, but its cusps occupy only about one-quarter of the height. The cusp pattern is semi-molariform. The trigonid is widely open, its basin represented by a groove on the lingual side between the paraconid and metaconid. These cusps are of equal height and somewhat lower than the protoconid. The paraconid is placed anteriorly and the metaconid postero-lingually to the protoconid. On the talonid there is a hypoconid, connected to the metaconid by a high oblique crest, and a posterolingual entoconid. In two specimens (KNM.CA 1554 and KNM.RU 3758) there is a small entostylid on the anterior crest of the entoconid. The talonid basin opens lingually behind the metaconid; it is not deep, and its sides and floor are complexly wrinkled. Wear removes all traces of

the talonid basin, leaving the talonid as a triangular prism joined to the trigonid by a wall that represents the oblique crest. KNM.KA 114 and KNM.RU 3758 show that P/3 erupts after P/4.

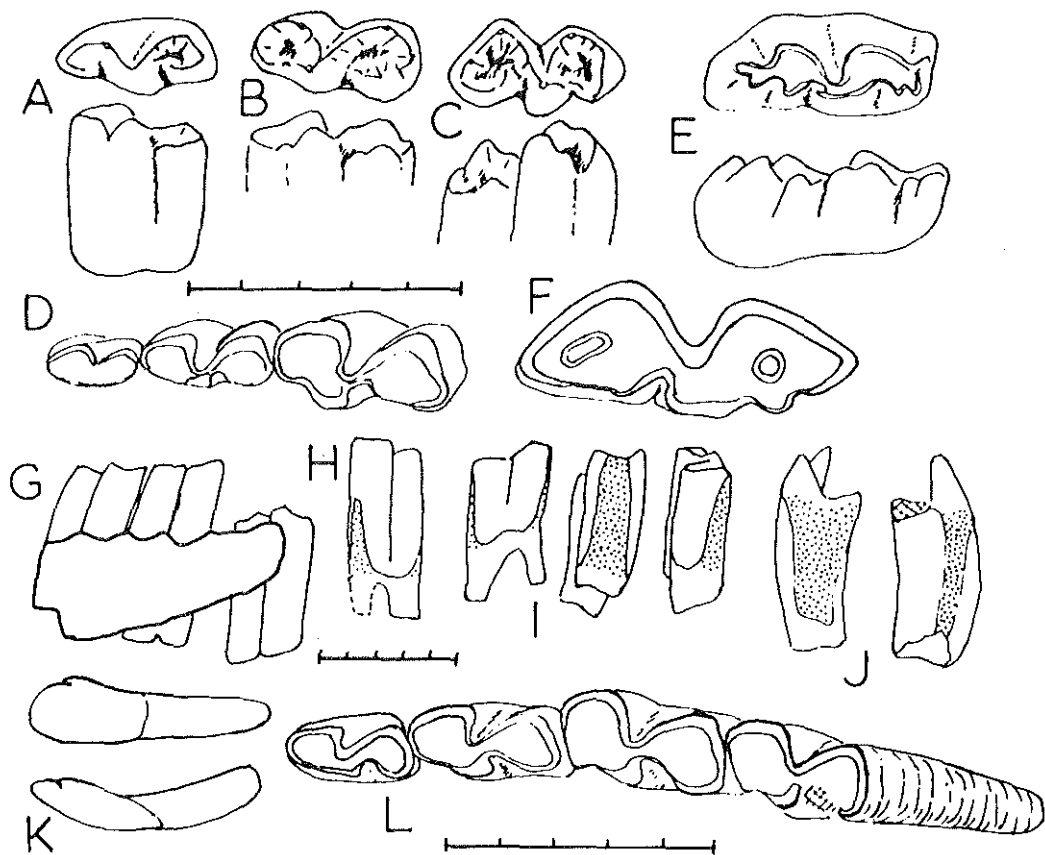


Fig. 4. — Myohyracinae.

A-E, *Myohyrax oswaldi*, lower teeth, crown and lingual views: A, RP/3, KNM.CA 1554; B, RP/4, KNM.RU 3758; C, LM/1, KNM.KA 128; D, RP/2-4, KNM.KA 148; E, LdP/4, KNM.KA 172.

F, *Protypothenoides beetzii*, LP/4, M 36935.

G-K, *M. oswaldi*: G, R fragment with P/4 (unerupted), M/1,2, KNM.MW 196; H, RM/1, lingual view, KNM.SO 1447; I, LM/1, lingual, anterior and posterior views, 34/1346; J, LP4/, anterior and posterior views, KNM.KA 100; K, RI1/, M 21238.

L, *Myohyrax* sp. from Napak, P/3-M/2.

P/4 is unworn in KNM.RU 3758 (fig. 4 B) and KNM.MW 196, and very lightly worn in KNM.KA 137. The maximum height of the crown is about 5.5 mm, compared with about 3 mm in the case of P/3. The two roots develop soon after the crown comes into use. The trigonid is broader than on P/3, and its basin is completed lingually by a crest, which in KNM.RU 3758 bears a small cusp. The paralophid reaches the anterior end of the tooth where it curves lingually, following the tooth margin. The metaconid is divided from the posterior crest of the protoconid by a groove, but as on P/3 it is joined to the

hypoconid by the oblique crest. A hypoconulid is differentiated, and an entostylid is variably developed anterior to the entoconid. The talonid basin opens lingually behind the metaconid as on P/3. Trigonid and talonid basins are both crenulated like the talonid of P/3. Soon after eruption the cusps and basins are removed by wear, giving rise to a prismatic structure. There are no fossettids such as occur in the trigonid and talonid of *Protypotheroides*. Enamel is thick on the buccal and posterior sides of the prisms, but thin on their lingual sides, which wear down faster.

KNM.KA 128 (fig. 4C) is probably an unworn M/1. It differs from P/4 in the paralophid, which turns abruptly towards the lingual side before reaching the anterior end of the tooth, so that the trigonid basin is truncated anteriorly. On M/1 and M/2 a tongue of root cementum extends up the anterior surface of the crown, reaching about halfway up in lightly worn specimens. Enamel is absent over this area, and it consequently disappears from the anterior edge of the occlusal surface when the tooth is sufficiently worn (Whitworth 1954, fig. 15). Another tongue of cementum is present at the posterior end, below the hypoconulid (Fig. 4, H,I). The absence of enamel in these areas, where adjacent teeth touch, would assist in interdental wear and ensure good contact. Cementum does not otherwise appear on the occlusal surface.

Two additional examples of dP/4 (KNM.KA 172) are less worn than the specimen (M 21333) described by Whitworth (1954) (Fig. 4 E). At the anterior end there are three cusps: an anterobuccal cusp, divided from the protoconid by a buccal groove; an anterolingual cusp, probably the paraconid; and a smaller lingual cusp posterior to this. Twinned with the metaconid is the metastylid, connected with the oblique crest. A buccal groove, extending across most of the crown, divides the trigonid from the talonid. On the talonid there are four cusps, the hypoconid, the hypoconulid in a median posterior position, and lingually the entoconid and entostylid. The crown is higher than in *Miorhynchocyon*, and there are four roots: a transversely extended anterior root, a middle root and a pair of posterior roots.

There are no completely unworn upper molariform teeth, but the worn pattern is like that of *Elephantulus* (Butler & Greenwood 1976) (Fig. 5). There is a lingual sinus between the protocone and the hypocone, a fossette between the paracone and the paraconule, and another between the metacone and the metaconule. In addition there are two lingual fossettes, not present in *Elephantulus*, buccal to the protocone and hypocone respectively. The least worn tooth (KNM.CA 2022), a first molar in which the hypocone is unworn (Fig. 5B), shows that the enamel round the posterior lingual fossette is crenulated like the trigonid and talonid basins of the lower teeth, and crenulation is also visible in a small unworn area round the anterior lingual fossette. On this tooth, as on several specimens of P3/ and P4/, the anterior buccal fossette opens anteriorly between the paraconule and the parastyle, becoming closed in the more worn specimens. In *Elephantulus* this is true of P4/, but the anterior buccal fossette is incompletely developed on P3/. The posterior buccal fossette is always present on P2/-M2/ of *Myohyrax*; on P2/ it is the only fossette present. Neither of the buccal fossettes communicates with the lingual sinus, unlike *Elephantulus*, where the anterior fossette frequently does so, and the posterior fossette sometimes joins the sinus on M2/. The anterior lingual fossette of *Myohyrax* is usually absent on P3/, and on P4/ it is smaller than the posterior lingual fossette; on the other hand, on M2/ the posterior lingual fossette unites with the posterior buccal fossette, but the anterior lingual fossette is always present.

	P/3			P/4			M/1			M/2		
	N	range	m	N	range	m	N	range	m	N	range	m
<i>oswaldi</i>												
Chamtwara	4	2.6-3.1	2.80	5	3.0-3.6	3.30	7	3.1-3.6	3.36	5	2.7-3.1	2.90
Songhor				1	3.4		1	3.1		1	3.0	
Mfwanganu				1	3.0		1	3.2		1	3.0	
Rusinga	4	2.7-3.1	2.90	11	3.0-3.5	3.24	13	3.0-3.5	3.26	13	2.7-3.0	2.88
Karungu	9	2.6-3.1	2.91	23	3.1-3.6	3.34	17	3.0-3.6	3.27	17	2.7-3.2	2.91
Fort Ternan										1	2.9	
<i>doederleini</i>												
(Stromer 1926)	1	2.3		2	2.6, 3.0		1	2.9		2	2.5, 2.6	
Napak	1	2.4		1	2.9		1	3.2		1	2.7	

Table 3 : Lengths (mm) of lower teeth of *Myohyrax*, measured on the occlusal surface.

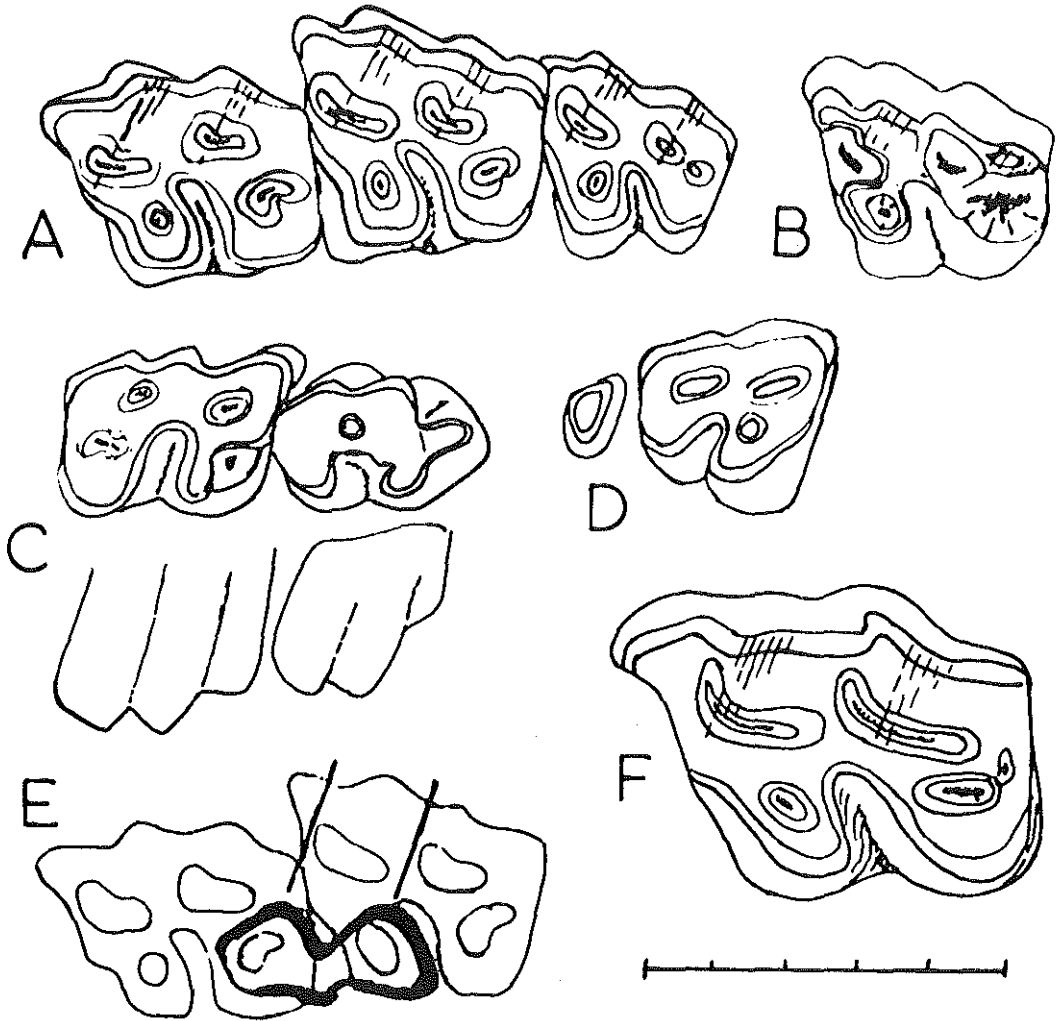


Fig. 5.

A-D, *Myohyrax oswaldi*: A, LP4-/M2/, KNM.KA 88; B, LM1/, KNM.CA 2022; C, RP2,3/, KNM.RU 3764; D, RM2,3/, KNM.RU 3763.

E, occlusion between M/1 and P4/, M1/. The straight lines indicate paths of protoconid and hypoconid.

F, *Protypotheroides beetzi*, LP4/, M 36933.

Occlusal relations are shown clearly by grooves worn in the upper molariform teeth. They are very similar to those of *Elephantulus*. The direction of movement of the lower teeth was obliquely forwards. The buccal fossettes provided additional cutting edges as they were crossed by the buccal enamel edges of the lower teeth (Fig. 5 E). The anterior part of the anterior buccal fossette occluded with a trigonid and the posterior part with a talonid; the posterior buccal fossette functioned anteriorly with a talonid and posteriorly with a trigonid. Facets on the anterior edge of the protocone and the posterior edge of the lingual sinus were produced by contact with the metaconid and the

entoconid respectively. The lingual fossettes were involved in the more horizontal, lingual phase of occlusion, when the talonid passed anterolingually across the protocone and the trigonid across the hypocone. The thick buccal enamel of the lower teeth is bevelled on the buccal side during the buccal phase movement and worn flat at the top during the lingual phase.

The upper cheek teeth increase in buccolingual diameter towards the base, and their occlusal surfaces consequently broaden with age. As on the lower teeth, enamel is deficient in areas where adjacent teeth touch, tongues of root cementum extending down the anterior and posterior surfaces of the crown (Whitworth 1954, fig. 15) (Fig. 4 J).

The upper milk molar identified by Stromer (1926) as dP4/ shows most resemblance to P2/, from which it differs in the much lower crown. It is probably dP2/.

Relationships:

► *Myohyrax doederleini* STROMER (1926), from Namibia, was distinguished from *M. oswaldi* by its smaller size and by the presence of a lingual groove on the trigonid (between paraconid and metaconid). The lingual groove does however occur in some East African specimens of *M. oswaldi*. According to Whitworth (1954) it is more frequent on smaller specimens; it would tend to disappear with wear. Whitworth synonymised *M. doederleini* with *M. oswaldi*. However, nearly all the tooth measurements given by Stromer (1926) are below the range of Kenya specimens, and the matter needs further investigation.

► *Protypotheroides beetzi* STROMER, 1922 (syn: *Myohyrax osborni* HOPWOOD, 1929), also from Namibia, is larger than *M. oswaldi*. Fossettids are present in the trigonids and talonids of P/3-M/2 (fig. 4 F). P/3 closely resembles P/4, and the presence of a fossettoid indicates that its trigonid was basined. P/2 is more high-crowned than in *M. oswaldi*. In the upper molars, the buccal fossettes are longer and narrower than in *M. oswaldi*, and their anterior ends turn buccally to approach the enamel ridge of the ectoloph (Fig. 5 F). P3/ has no parastyle and also lacks the anterior buccal fossette. M2/ is larger relatively to M1/ and it has a separate posterior lingual fossette. M3/ has two roots, whereas in *M. oswaldi* it has one. These differences seem sufficient to justify a generic separation, and I follow Patterson (1965) in rejecting Whitworth's (1954) synonymy of *Protypotheroides* with *Myohyrax*.

► *Myohyrax* sp. from Napak.

M 43553 is a mandibular ramus with P/3-M/2 from Napak IX (Fig. 4 L). Measurements of M/1 and M/2 fall within the range of *M. oswaldi* from Kenya, but they are below the mean size for that species. The teeth are moderately worn (height of M/1, 2.7 mm). There is a lingual bay in the trigonid of P/4 and M/2, but not of M/1, where it has presumably been eliminated by wear. This specimen is distinguished from those from Kenya by its relatively smaller premolars. The length of P/3 and P/4 are below the Kenya range, and they are smaller in proportion to the length of M/1 (Table 3). Whether this difference is to be ascribed to geographical variation or to a difference of geological age is uncertain.

From Stromer's (1926) measurements, the teeth of *M. doederleini* are smaller than those of the Napak specimen, except one example of P/4.

Postcranial bones of *Myohyrax* and *Miorhynchocyon* (Fig. 6).

Astragalus: Seven specimens from Karungu and two from Chamtwara are ascribed to *Myohyrax oswaldi*. They range in length from 4.6-5.9 (mean 5.2) mm. The astragalus



Fig. 6. — Macroscelidean postcranials.

A-D, L astragalus: A, *Myohyrax*, Ka 230.73; B, *Petrodromus* (recent), BMNH 1906.11.8.154; C, *Miorhynchocyon*, Ka 459.73; D, *Rhynchocyon chrysopygus* (recent), BMNH 10.5.281.

E-G, L calcaneum: E, *Myohyrax*, Ka 276.73; F, *Petrodromus*, as B; G, *Rhynchocyon chrysopygus*, as D. H-K, distal end of R tibiofibula, posterior view: H, *Myohyrax*, Ka 272.73; I, *Miorhynchocyon*, KNM.SO 1774; J, *Petrodromus*, as B; K, *Rhynchocyon chrysopygus*, as D.

L, ? *Miorhynchocyon rusingae*, distal end of femur, KNM.MW 430.

of *Myohyrax* was described by Stromer (1926), and Patterson (1965) pointed out its similarity to those of other macroscelidids. The neck occupies about half the length of the bone; it is inclined medially at an angle of about 20° to the plane of rotation at the trochlea. The elongated sustentacular facet is situated towards the medial side. There is no astragalar foramen. This astragalus differs from that of *Rhynchocyon* in that the neck is more slender, and the trochlea is narrower. In these respects it resembles *Petrodromus* and other Macroscelidinae.

Two larger astragali, one from Chamtwara (length 7.5 mm) and one from Karungu (length 7.1 mm), are referred to *Miorhynchocyon clarki*. They resemble *Rhynchocyon chrysopygus*, except for their smaller size.

Calcaneum: Three specimens from Karungu, ranging in length from 7.6 to 8.3 mm, are identified as *Myohyrax oswaldi*. The sustentacular process is not preserved; according to Stromer (1926) it is directed distally, as in *Petrodromus*.

Tibiofibula: The distal end of a tibiofibula from Karungu (width 4.4 mm) is ascribed to *Myohyrax oswaldi*. There is a similar specimen from Legetet, from which teeth of *Myohyrax* have not been reported. A large specimen from Songhor (width 5.4 mm) is probably *Miorhynchocyon clarki*. All these specimens resemble *Rhynchocyon*. In *Petrodromus* and other Macroscelidinae there is a sharp longitudinal ridge on the posterior side of the bone, above the internal malleolus.

Femur: The distal end of a femur from Mfwanganu is very much like *Rhynchocyon*. Its width is 8.2 mm, too large in comparison with the referred tibiofibula and astragalus to belong to *Miorhynchocyon clarki*. It is referred to *M. rusingae*.

Subfamily MACROSCOLIDINAE BONAPARTE, 1838

PRONASILIO, nov. gen.

Diagnosis: P/4-M/2 moderately hypsodont; oblique crest diverted at its anterior end towards the metaconid; talonid lower than trigonid; M/3 present; P/4 trigonid only moderately extended; P/4 talonid incompletely molariform, with reduced entoconid.

Type species: *P. ternanensis* nov. spec.

Pronasilio ternanensis nov. spec.

Diagnosis: With the characters of the genus.

Holotype: KNM.FT 3803, incomplete mandible with P/4, M/1, alveoli of M/2 and part of the M/3 alveolus. From Fort Ternan.

Paratypes: KNM.FT 3409, fragment with M/1, M/2 and alveolus of M/3; M/1 broken off and preserved separately. KNM.FT 3802, fragment with P/4 and M/1. Both from Fort Ternan.

Distribution: Known only from the Middle Miocene of Fort Ternan.

Description (Fig. 7):

P. ternanensis is smaller than *Miorhynchocyon clarki*; the total length of P/4-M/2 is about 6.8 mm, within the range of the living *Elephantulus (Nasilio) brachyrhynchus*. The teeth are moderately high-crowned, as in *Elephantulus*, but they stand upright and do not lean forward as they do in that genus, resembling in this respect *Petrodromus*. KNM.FT 3409 has the least worn molars. The metaconid is a little higher than the

protoconid; it stands a little more posteriorly than the protoconid on M/1, directly opposite it on M/2. The two cusps are joined by a high transverse crest (protolophid) which dips centrally. The anterior margin of the trigonid is formed by the paralophid, an anteriorly convex crest, less high than the protolophid. There is no distinct paraconid, but the paralophid, on reaching the mid-anterior edge of crown, dips abruptly towards the lingual side. The trigonid basin opens lingually between the paralophid and the metaconid, at a rather high level on the tooth. There is a weakly indicated antero-buccal cingulum. The talonid is a little lower than the trigonid. The entoconid is higher than the hypoconid, with which it is connected by a posterior talonid crest (hypolophid). This falls to a minimum level at the middle of the posterior edge of the tooth, where a small angulation of the crest represents the hypoconulid. The oblique crest is high; it bends lingually to join the protolophid near the metaconid. The talonid basin opens lingually by a deep cleft between the entoconid and the metaconid. Wear is confined to the tops of the crests. M/2 is a little smaller than M/1. M/3 is not preserved, but the presence of a single alveolus indicates that it was reduced and simplified as in *Nasilio*.

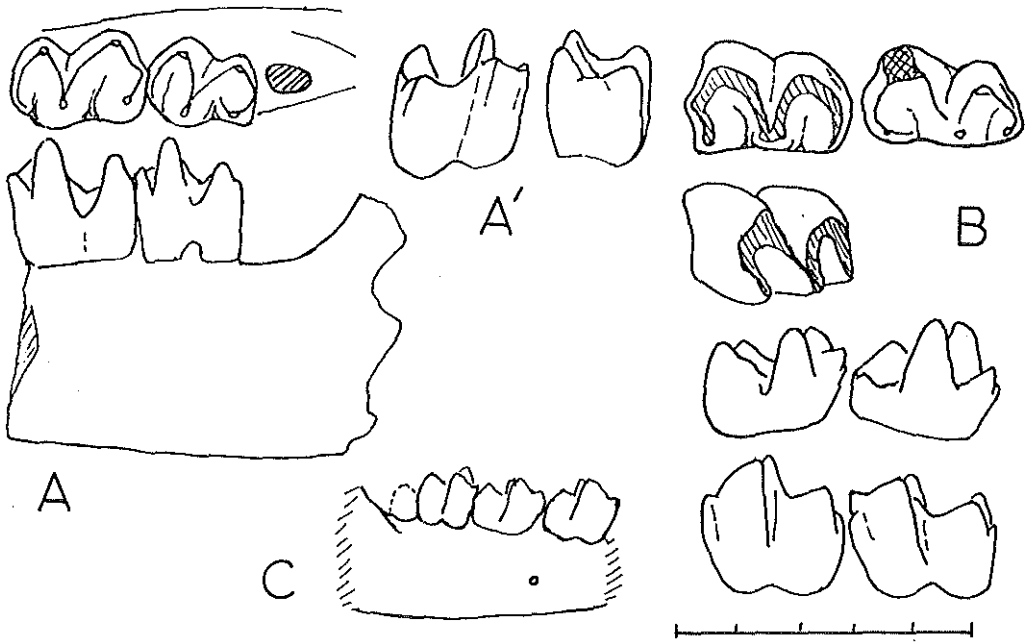


Fig. 7. — *Pronasilio ternanensis*.

A, KNM.FT 3409, crown and lingual views.

A', the same: M/1 in buccal and posterior views.

B, KNM.FT 3802 (holotype): M/1 and P/4 in crown, lingual and buccal views, and oblique posterior view of M/1.

C, reconstruction of cheek teeth from KNM.FT 3802 and 3409, half scale.

P/4 is incompletely erupted and quite unworn in the holotype, and somewhat worn in KNM.FT 3402. It is equal in length to M/1, but the trigonid is longer and the talonid is shorter. The trigonid angle is greater than on M/1, though less than a right angle, and the trigonid is less extended than in living *Macrosclidinae*. The paraconid is in an

anterolingual position; it is much lower than the metaconid. There is a weak anterobuccal cingulum. On the talonid the hypoconid is well developed, but the entoconid is low and indistinct. The oblique crest connects with the metaconid as on the molars.

From the small part of the ascending ramus that is preserved in KNM.FT 3409 it can be seen that its anterior edge rises more steeply than in *Miorhynchocyon*. The depth of the horizontal ramus diminishes forwards from M/3 as in Rhynchocyoninae; in Recent Macroscelidinae the greatest depth is below M/1. There is a foramen below the trigonid of M/1.

Relationships:

M/1 and M/2 of *Pronasilio* closely resemble those of later Macroscelidinae, except that the talonid is a little lower than the trigonid, presumably a primitive feature. The crown is higher than in *Rhynchocyon*, much higher than in *Miorhynchocyon*. The diversion of the oblique crest towards the metaconid occurs in *Rhynchocyon* but not in *Miorhynchocyon*; this resemblance of *Rhynchocyon* to *Pronasilio* is due to parallel evolution. M/3 has been lost in Rhynchocyoninae, but it is retained in some Macroscelidinae (*Palaeothentoides*, *Nasilio*). *Pronasilio* is more primitive than all other known Macroscelididae in the incomplete molarisation of the talonid of P/4.

Because it resembles later Macroscelidinae in derived features of the molar pattern, *Pronasilio* is regarded as a member of that subfamily. Its distinctive features seem to be primitive characters lost in later forms; they do not exclude relationship.

Patterson (1965) very tentatively placed the Early Oligocene *Metoldobotes stromeri* SCHLOSSER in the Macroscelidinae. Though much older than *Pronasilio* it is more advanced in the loss of M/3 and the fully molariform talonid of P/4, characters which it shares with *Miorhynchocyon*. It is more primitive, again like *Miorhynchocyon*, in the low-crowned cheek teeth, in which the oblique crest connects with the middle of the protolophid. The shortened anterior part of the jaw is reminiscent of *Macroscelides*, but this character is not shared with other Macroscelidinae and must be a parallel development. (This part of the jaw is unknown in *Pronasilio*). There is no reason to place *Metoldobotes* in any of the later subfamilies, and until more material comes to light it is best classified as Macroscelididae *incertae sedis*.

Subfamily indeterminate

HIWEGICYON nov. gen.

Diagnosis: M/1 moderately high-crowned; oblique crest on dP/4, and therefore presumably on the molars, runs to the middle of the protolophid; no metastylid on dP/4 or dP/3; dP/3 has a metaconid but no protostylid; anterior lower teeth probably crowded and procumbent.

Type species: *H. juvenalis* nov. spec.

Hiwegicyon juvenalis nov. spec.

Diagnosis: As for the genus.

Holotype: Rs 514.49, an associated pair of juvenile mandibles, from the Hiwegi Formation, locality R 3 (not R 1A as stated by Butler, 1969). Described by Butler (1969, pp. 10-12, fig. 4B) under the heading of 'Macroscelididae of uncertain genus and species'.

A second specimen, KNM.RU 3692 (Rs 2522.52), has been found in the Hiwegi Formation at Kaswanga, (Fig. 8A). It is a right mandibular fragment containing the roots and talonid of dP/2, complete dP/3, and the anterior part of dP/4.

Although this species is represented only by juvenile mandibles, it is clearly distinct, even at the generic level, from other known macroscelideans, and worthy of a name.

Description:

KNM.RU 3692 differs from the type in the presence of a posterobuccal ridge on the protoconid of dP/3. The paraconid of dP/3, broken in the type, is seen to be comparatively high. In these respects the tooth resembles P/3 of M 14284, a problematic fragment from Koru (Butler 1969, fig. 4A), which might belong to this or a related species.

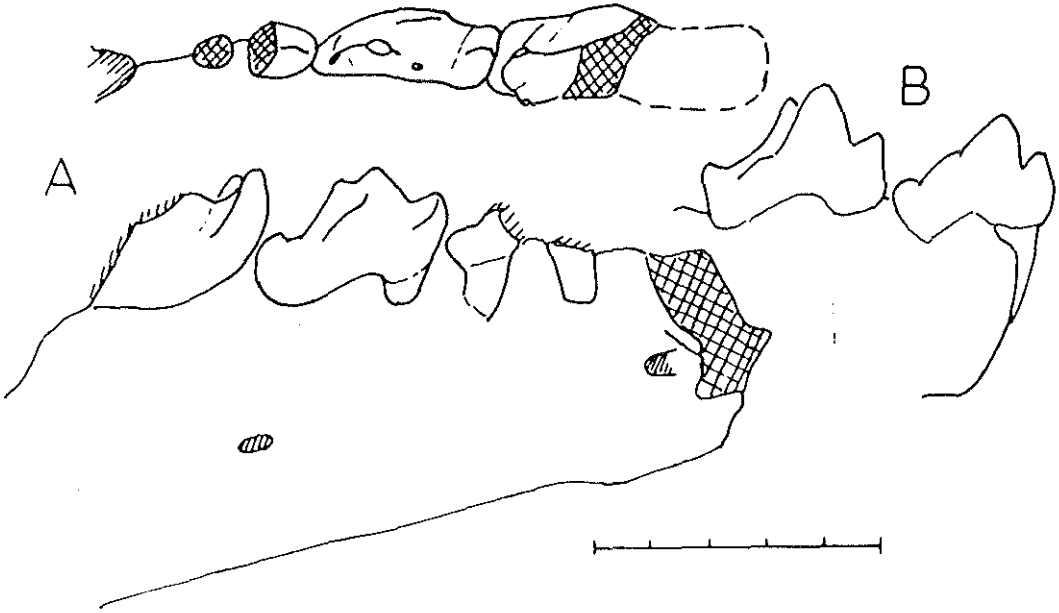


Fig. 8.

A, *Hiwegicyon juvenalis*, crown and buccal views, KNM.RU 3692.
B, Indeterminate macroscelidean from Koru, M 14284.

Relationships:

The unerupted M/1 trigonid, seen in cross-section in the type, agrees in height and width with *Pronasilio ternanensis*, and it is much less high than in *Myohyrax*. On dP/4 the oblique crest does not run towards the metaconid as in Macroscelidinae and *Myohyrax*, but it ends more buccally as in *Metoldobotes* and *Miorhynchocyon*. This is probably a primitive character. The absence of the metastylid of dP/4 is another primitive character, shared with *Miorhynchocyon*. If the Koru specimen is related, its possession of a protostylid on P/2 may indicate a connection with Rhynchocyoninae. On the other hand, the lingual metaconid of dP/3 and the degree of hypsodonty of M/1 do not support such a relationship.

GENERAL REMARKS ON MACROSCOLIDIDAE

The presence of the already specialised *Metoldobotes* in the Early Oligocene shows that the Macroscelididae had undergone in Africa a considerable amount of evolution prior to the Miocene, by which time the three subfamilies, Rhynchocyoninae, Myohyracinae and Macroscelidinae had become differentiated.

The Myohyracinae may be the sister-group of the Macroscelidinae, with which they share a number of derived characters. The second and third premolars are at a higher level of molarisation than in Rhynchocyoninae. The cheek teeth become hypsodont, with a more horizontal type of wear in which enamel edges are used; the enamel pattern is elaborated by the formation of fossettes, and on the lower teeth the oblique crest is diverted lingually to join the metaconid or metastylid. In *Miorhynchocyon* the molar pattern remains primitive, although in the modern *Rhynchocyon* there is some increase of crown height, and the oblique crest is diverted. In Myohyracinae and Macroscelidinae the face is high and narrow, the jaw articulation is elevated, and the ascending ramus is more upright; in Rhynchocyoninae, on the other hand, the face becomes broad and flattened, and the elevation of the condyle is reduced. The hooked sustentacular process of the calcaneum is another character shared by the first two subfamilies but not by Rhynchocyoninae. Apomorphous characters of Rhynchocyoninae are the protostylid of P/2, P/3 and the corresponding milk teeth, and reduction of the upper incisors.

Compared with the Macroscelidinae, the Myohyracinae became precociously specialised in the hypsodont molars, of which the upper one developed additional fossettes, in the expanded angular region of the mandible, and in the incisors. They retained third molars, whereas in Macroscelidinae M3/ is lost and M/3 is present only in *Pronasilio*, *Elephantulus* (subgenus *Nasilio*) and *Palaeothentoides*. Third molars must have been lost several times within the family, for they are also absent in *Metoldobotes* and the Rhynchocyoninae.

As Patterson (1965) pointed out, the Myohyracinae appear to be adapted for an herbivorous diet. The enlarged incisors, kept sharp by the absence of lingual enamel, would be effective for biting off shoots and small fruits. The cheek teeth, with cutting edges of enamel, could reduce fibrous material, including seed-coats. Molarisation of the premolars and retention of the third molars increases the grinding area, and hypsodonty compensates for wear. The mandible resembles that of an ungulate. Living Macroscelididae are mainly insectivorous (Rathburn 1979). *Rhynchocyon* eats mainly beetles, earthworms, termites and insect pupae obtained from litter. The macroscelidines *Petrodromus* and *Elephantulus*, however, in addition to insects eat some plant material, including seeds.

Order INSECTIVORA BOWDICH, 1821 (=LIPOTYPHILA HAECKEL, 1866)

Family ERINACEIDAE FISCHER von WALDHEIM, 1817

Subfamily GALERICINAE POMEL, 1848 (=ECHINOSORICINAE CABRERA, 1925)

GALERIX POMEL, 1948

Includes *Pseudogalerix* GAILLARD, 1897 and *Parasorex* VON MEYER, 1865. Butler (1980) separated *Parasorex* generically from *Galerix* (=Pseudogalerix), but this step has not

been followed by Ziegler (1983) in his monograph of *G. exilis*. Nevertheless, there are significant differences between *G. (Parasorex) socialis* on the one hand and *G. (Galerix) exilis* and *G. (G.) stehlini* on the other, and *Parasorex* is here treated as a subgenus.

Galerix africanus BUTLER, 1956

Galerix africanus, Butler (1956), pp. 62-64, text-fig. 18, Pl. 4, figs 37, 38.

Lanthanותרium sp., Butler (1969), pp. 12-14, fig. 5.

Holotype: M 34148 (Sgr 315.49), mandible with P/3,4 and alveoli of M/1,2; P/3 has subsequently been broken off and lost. From Songhor.

Revised diagnosis: Resembling *G. exilis* and *G. stehlini*, but larger (total length of lower molars about 10 mm), with proportionately shorter and broader premolars, and lacking the posterior crest of the metaconule on the upper molars.

Specimens identified:

Koru Formation.

Locality 25. KNM.LG 1540 (25/133), M/1 trigonid.

Locality 32. KNM.LG 1535 (32/25), mandible fragment with unerupted M/3; KNM.LG 1537 (32/269), 1547 (32/97) and 32/320, edentulous mandibles.

Legetet Formation.

Locality 10. KNM.LG 62 (10/99), mandible with M/1.

Kapurta Agglomerates.

Chamtwaru. KNM.CA 324 (34/13), maxilla with P4/-M2/; KNM.CA 2061 (34/1600), maxilla with M2,3/; KNM.CA 316, CA 1505 and CA 1507 (34/21), isolated M1/; KNM.CA 1506 (34/21), M2/; 34/861, M3/; KNM.CA 1549 (34/698), P4/; KNM.CA 2128 (34/1076), M/2; KNM.CA 2048 (34/1571) and CA 2066 (34/836), edentulous mandibles.

Songhor. KNM.SO 1421 (Sgr 123.71), associated left maxilla and right and left mandibles, with dentition; KNM.SO 1406 (Sgr 2831.66), maxilla with P3/-M1/; KNM.SO 1410 (Sgr 413.72), maxilla with P4/, M1/; Sgr 3114.66 and Sgr 3116.66, associated mandibles with M/1-3; M 34148 (Sgr 315.49), mandible with P/3,4 (holotype); KNM.SO 1415 (Sgr 2627.66), M/1; KNM.SO 1416 (Sgr 281.72), M/3; Sgr 1813.66 and Sgr 3117.66, edentulous mandibles; KNM.SO 1426 (Sgr 696.72), two edentulous mandibles; KNM.SO 1609 (Sgr 490.72), edentulous mandible.

Hiwegi Formation, Hiwegi area. M 33045 (Rs 1201.47), mandible with M/2; M 34102, P4/.

Description:

The most important new specimen is KNM.SO 1421, collected at Songhor by Dr. Peter Andrews in 1971. This is a left maxilla with P2/-M3/, associated with right and left mandibles. The left mandible contains P/2-M/3, the right one P/2-M/1, and both have alveoli of the incisors, the base of the canine, and an alveolus for P/1. (Fig. 9 A). Other new specimens include four partial maxillae with teeth, and several isolated teeth.

From the measurements in Table 4 it may be seen that *G. africanus* is about one-third larger than *G. exilis* and *G. stehlini* from Europe. It falls into the size range of *Lanthanותרium sansaniense*.

The upper dentition anterior to P2/ is unknown; P2/ and P3/ are preserved only in KNM.SO 1421. P2/ is a simple tooth, oval in outline, with an anterior parastyle at cingulum level. It differs from the European species in being proportionately wider and in having a more distinct parastyle. P3/ is a triangular tooth, proportionately wider than

in *G. exilis*. It is subequal to P2/ in length and height, and much lower than P4/. The parastyle forms a low but distinct cusp, better differentiated than in *G. exilis*. There is no metacone, and the posterior crest of the paracone is not angulated or notched. The protocone, directly lingual to the paracone, is followed by a ridge that rises to a small hypocone, as in some specimens of *G. exilis*. There is a posterior cingulum but no anterior cingulum. P3/ has three roots. P4/ is similar to *G. exilis*, except that the parastyle is more distinct, and the posterior cingulum extends round the hypocone. The hypocone is lower than the protocone and stands directly posteriorly to it.

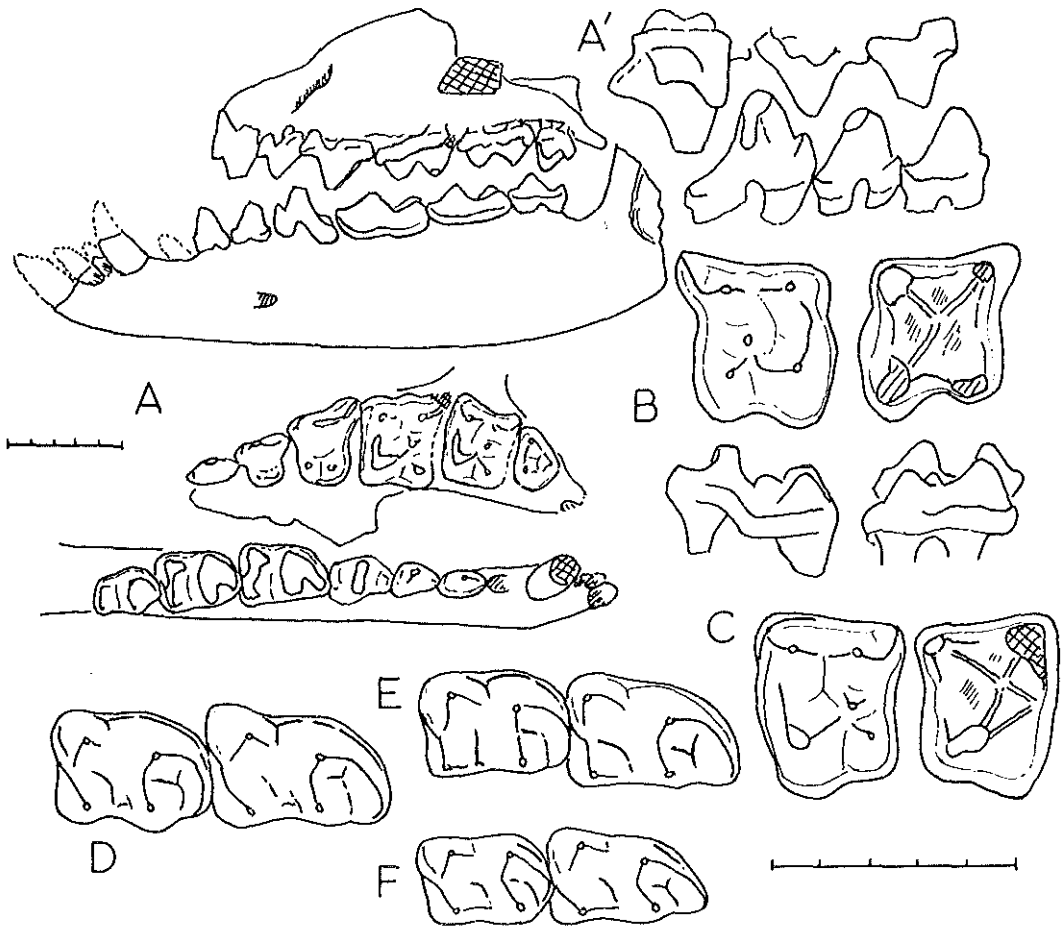


Fig. 9. — *Galerix*.

A-D, *G. africanus*: A, maxilla and left mandible of KNM.SO 1421; A', L premolars, lingual view, KNM.SO 1421; B, RM1/, crown, basal, posterior and lingual views, KNM.CA 316; C, LM2/, crown and basal views, KNM.CA 1506; D, LM/1,2, Sgr 3114.66.

E, *G. stehlini*, LM/1,2, M 5382.

F, *G. socialis*, LM/1,2, specimen from La Grive (Montpellier collection).

There are six examples of M1/ (fig. 9 B). This tooth differs from *G. exilis* in that the metastylar apex is less prominent, so that the ratio of posterior width/ anterior width is smaller (Ratio of means is 1.05, compared with 1.16 in *G. exilis* from Steenburg, Ziegler 1983). The paraconule is absent or very weak. The metaconule is joined to the protocone by a crest, but it lacks the posterior crest; the latter varies in length but is always present in the European species (Ziegler 1983). The hypocone is lower than the protocone, and its anterior crest is lower than the protocone-metaconule crest. The buccal cingulum is well developed, and in some specimens it widens as if to form an incipient mesostyle, producing a slight convexity in the middle of the buccal margin. There is usually a short lingual cingulum between the protocone and the hypocone. The posterior cingulum extends behind the hypocone and in some specimens it connects with the lingual cingulum. Four isolated specimens show the roots. In two of these the lingual root is divided, deep in the jaw, into a longer protoconal and a shorter hypoconal root; the division is incomplete in the third specimen and absent in the fourth. Baudelot (1972, p. 275) states that the lingual root tends to divide in *G. exilis*, but Ziegler (1983) does not mention this. Three interradicular crests arise from the inner sides of the roots and meet at the centre of the base of the crown.

M2/ shows the same characters as M1/, except for the weaker development of its metastyle region (fig. 9 C). The roots can be seen only in KNM.CA 1506, in which the lingual root is grooved but not divided. This specimen has an abnormal arrangement of the interradicular crests: in addition to the usual three, a fourth crest from the central confluence meets a supernumerary crest from the lingual root at a point near the anterior edge of the tooth. M3/ is triangular, wider than long, and with the posterior apex nearer the lingual than the buccal side. The metacone is subequal to the paracone in height, but situated more lingually, and it is joined by a crest to the protocone. The hypocone is represented by a posterolingual cingulum. There are three equal roots.

Alveoli in KNM.SO 1421 show that there were 3 lower incisors, of which I/1 was the largest and I/3 the smallest. The canine, of which only the base is preserved, was moderately robust. There is a single alveolus for the somewhat procumbent P/1, separated from the canine by a short diastema.

P/2 is oval in outline, and proportionately shorter and wider than in *G. exilis*. It is tilted slightly forward in the jaw. It has a rudimentary anterior cusp and a small heel. P/3 is subequal to P/2 in length and height, but it is wider, particularly posteriorly, so that it has a triangular outline. The widening is greater than in *G. exilis*: in two specimens of *G. africanus* the length/width index is 70 and 75, whereas in *G. exilis* its value (calculated from the means) is 53 (Ziegler 1983). The anterior cusp is more distinct on P/3 than on P/2.

The protoconid of P/4 is high and acute, projecting above the molar cusps as in *G. exilis* and *G. stehlini*. The metaconid is a much smaller cusp arising from the lingual surface of the protoconid. The paraconid is a low anterior cusp, not joined to the protoconid by a crest. The talonid is a transverse cingulum, rising to its greatest height somewhat lingually to the mid-line. In these characters P/4 resembles *G. exilis* and *G. stehlini*, but like P/3 it is proportionately shorter and wider than in the European species.

The unworn crown patterns of M/1 and M/2 (fig. 9 D) were described by Butler (1969) as *Lanthanotherium* sp. They closely resemble *G. exilis* (fig. 9 E), except that M/2 is less reduced in size relatively to M/1. Differences from the M/2 referred to *G. africanus* by Butler (1956) are attributable to individual variation. This affects, for example, the development of the buccal cingulum, which may or may not extend round the proto-

conid, and the anterior crests of the hypoconid and entoconid, which are weakly developed in some specimens. The posterior cingulum is continuous in most specimens with the buccal crest of the entoconid. The lingual cuspule between the metaconid and entoconid occurs only in the specimen referred to *Lanthanotherium*, but Ziegler (1983) noted this variation in *G. exilis*. KNM.LG 1540 shows a small paraconid at the lingual end of the paralophid of M/1, not present in other lightly worn specimens. On M/2 and M/3 of *G. africanus*, as in *G. exilis* and *G. stehlini*, the paralophid forms a curved crest that ends at the anterior base of the metaconid, and no paraconid is developed. M/3 is much smaller than M/2, and its talonid is narrower than the trigonid.

Some features of the maxilla can be seen in KNM.SO 1421 and KNM.CA 324. The anteroventral margin of the orbit forms a prominent crest which passes anterior to the lachrymal foramen, so that this opens into the orbit. The infraorbital foramen is above the anterior end of P4/, and the posterior opening of the infraorbital canal is above the M1/-M2/ contact. The zygomatic arch arises opposite the posterior part of M1/ and most of M2/. The palate ends 1.5 mm behind M3/.

The horizontal ramus of the mandible resembles the European species, except that the premolar series is proportionately shorter: the total length of the premolars in KNM.SO 1421 is 77% of the total molar length, while in *G. exilis* the premolar and molar series are of equal length. The symphysis reaches to below P/2, the mental foramen is below P/3, and the greatest depth of the ramus is below M/2. The ascending ramus is incompletely preserved. As in other erinaceids, the alveoli of each tooth from P/4 to M/3 are connected by a groove for the interradicular crest, bordered buccally and lingually by small elevated flanges of alveolar bone.

Relationships:

G. (Parasorex) socialis differs from *G. africanus* in several dental features. P3/ is much larger than P2/, and resembles P4/ in pattern. It has an acute posterior buccal apex which carries a shearing metastylar crest, clearly marked off from the posterior crest of the paracone by an angulation. The protocone is more anteriorly situated in relation to the paracone, and the hypocone is better developed. P4/ and M1/ are arranged more obliquely in relation to the tooth-row: their protocones are more forwardly placed, and their metastylar apices are more prominent. On M1/ the paraconule is retained, and the metaconule possesses a posterior crest, but the crest between the metaconule and the protocone is absent. In the lower jaw, P/3 is much larger than P/2, and P/4 resembles the trigonid of a molar, having a much larger metaconid and paraconid, the latter connected to the protoconid to form the paralophid. P/4 is similar in height to M/1. On the molars (fig. 9 F) the metaconid stands more anteriorly, so that the posterior trigonid wall is somewhat oblique. The paralophid, instead of forming a curve, ends abruptly at the mid-anterior margin of the tooth. These characters relate *G. socialis* with *Schizogalerix*. *G. africanus* is much nearer *G. exilis* and *G. stehlini*, and it is included with these species in the subgenus *G. (Galerix)*.

Galerix was present in Europe in the Burdigalian, but the material has not been described in detail. An unidentified M/3 from Port-la-Nouvelle (Legendre 1982, fig. 7) resembles *G. africanus* except for its smaller size.

Lanthanotherium was probably derived from *G. (Galerix)*, which it resembles in the structure of the lower molars. The premolars are more advanced: on P/4 the protoconid is enlarged and the paraconid and metaconid are obsolescent, while the anterior premolars are reduced. On the upper molars, loss of the metaconule crest is a character shared with *G. africanus*. At least in *L. sawini*, the lingual roots of the upper molars are

		<i>Galerix africanus</i>			<i>G. exilis</i> (Steinberg)	<i>G. stehlini</i>	
		N	range	m	KNM.SO 1421		
P2/	length				2.15	1.63	
	width				1.15	0.79	
P3/	buccal length				2.3	1.88	2.16
	width				2.3	1.43	1.50
P4/	buccal length	3	3.05-3.3	3.20	3.25	2.41	2.71
	posterior width	3	3.7 -3.75	3.72	3.7	2.67	2.90
M1/	buccal length	7	3.0 -3.7	3.38	3.7	2.61	2.93
	anterior width	7	3.45-3.95	3.69	3.9	2.76	3.11
	posterior width	7	3.65-4.0	3.87	4.0	3.20	3.34
M2/	buccal length	4	2.8 -3.2	2.97	3.2	2.33	2.29
	anterior width	4	3.4 -3.9	3.66	3.9	2.76	2.96
M3/	length	3	1.9 -2.0	1.97	1.9	1.36	
	width	3	2.4 -2.9	2.67	2.7	1.92	
P/2	length	2	1.8 , 1.85	1.83	1.85	1.65	1.62
	width	2	1.05, 1.15	1.10	1.15	0.77	0.80
P/3	length	2	1.7 , 2.0	1.85	2.0	1.56	1.47
	width	2	1.2 , 1.5	1.35	1.5	0.82	0.83
P/4	length	3	2.4 -2.6	2.48	2.6	2.03	2.47
	width	3	1.6 -2.2	1.87	2.2	1.26	1.40
M/1	length	4	3.6 -4.0	3.75	4.0	3.06	3.22
	width	4	2.45-2.6	2.54	2.5	1.86	1.98
M/2	length	4	3.05-3.6	3.48	3.6	2.49	2.40
	width	4	2.3 -2.4	2.35	2.4	1.73	1.65
M/3	length	3	2.3 -2.8	2.53	2.8	2.11	2.12
	width	2	1.6 , 2.0	1.80	2.0	1.28	1.20
C-M/3					20.5	16.2	18.9
M/1-M/3					10.3	6.9	7.9
P/1-P/4					8.1	6.9	8.2
Depth of jaw under M/1 (lateral)					4.65	3.7	3.3

Table 4 : Measurements (mm) of teeth of *Galerix africanus*, with comparative measurements of European species (Ziegler 1983).

divided, as in some specimens of *G. exilis* and *G. africanus*. Two species of *Lanthanothe-rium* have been described from the Burdigalian of Europe, but they do not appear to be distinguishable from *Galerix*. *L. (Rubitherium) piveteaui* CRUSAFONT, VILLALTA & TRUYOLS (1955), from the Late Burdigalian of Vallés-Penedés, is known only by M/2 and M/3; the curved paralophids of these teeth do not separate it from *G. (Galerix)*. *L. lactorensis* BAUDELLOT & CROUZEL (1976), from the Early Burdigalian of Navère, is based on a mandible with P/2, P/4, and the alveoli of P/3. P/2 is 77% as long as P/4, and it has two roots; P/4 is much worn and the absence of a metaconid may be due to this,

for its paraconid is comparatively high. Thus the evidence that *Lanthanotherium* existed before the Vindobonian is weak.

The Galericinae are probably of Asiatic origin, derived from a form similar to *Tupaiodon*. They entered Europe after the Grande Coupure; the Oligocene genus *Tetracus* may be ancestral to *Galerix*. *G. africanus* represents an immigration into Africa, after the two subgenera of *Galerix* had separated, and probably not long before the first appearance of the species in the fossil record in the Koru Formation.

AMPHECHINUS AYMARD, 1850

Palaeorimaceus FILHOL, 1879; includes *Parvericius* KOERNER, 1940.

Amphechinus rusingensis BUTLER, 1956

Amphechinus rusingensis, Butler (1956), pp. 54-59, text-fig. 16, 17, Pl. 4, figs 28-31; Butler (1969), p. 17, cranium described as Cf. *Erythrozootes chamerpes*, p. 21-24, fig. 19.

Holotype: M 34096 (Rs 723.47), the facial part of a skull and associated mandibles. From Hiwegi Formation, locality R 1.

Specimens identified:

Legetet Formation.

Maize Crib quarry. M 14316, cranium.

Locality 10. KNM.LG 1515 (10/547), cranium; 10/551, facial skull; KNM.LG 1508 (10/876), maxilla with P4/, M1/; KNM.LG 1510 (10/555), maxilla with P4/-M2/; KNM.LG 1511 (10/553), maxilla with P4/, M1/; KNM.LG 1512 (10/552), mandible with P/4, M/1; KNM.LG 68 (10/108), mandible with M/1.

Locality 21. KNM.LG 1529 (21/117), edentulous mandible.

Locality 29. KNM.LG 1215 (29/72), maxilla with P4/, M1/; KNM.LG 769 (29/55), mandible with P/4-M/2; KNM.LG 1520 (29/311), edentulous mandible.

Kapurta Agglomerates.

Chamtwar. KNM.CA 2002 (34/1529), maxilla with P4/, M1/; KNM.CA 1995 (34/1522), 2026 (34/1021) and 1529 (34/698), mandibles with P4/; KNM.CA 1528 (34/698), juvenile mandible with P/4 erupting; KNM.CA 2174 (34/930), mandible with M/1, M/2; KNM.CA 346 (34/195), mandible with M/2,3; KNM.CA 2024 (34/1349), 1922 (34/1287) and 1550 (34/698), mandibles with M/1; KNM.CA 1549 (34/698), 2182 (34/1098), 2211 (34/1816) and 2221 (34/1826), isolated M/1; 13 edentulous mandibular fragments.

Songhor. M 34143 (Sgr 451.48), facial skull; Sgr 1147.66 and Sgr 1148.66, mandibles with P/4; five edentulous mandibular fragments.

Hiwegi Formation.

Locality R 1. M 34096 (Rs 723.47), facial skull and mandibles (holotype).

Locality R 2 (1956). M 34104 (Rs 409.56), mandible with P/4.

Kaswanga. M 34098 (Rs 1398.50), mandible with P/4-M/2; M 34099 (Rs 553.48), mandible with P/4 (not from R 106 as stated by Butler, 1956).

Locality R 106. M 34100 (Rs 86.48), pair of mandibles with teeth (not from R 105 as stated by Butler, 1969).

Locality unknown. M 34103 (Rs 611.48), mandible with P/2; M 34104 (Rs 1328.50), P/4.

Karungu. KNM.KA 165 (K 223.73) and KNM.KA 168 (K 305.73), isolated M1/; KNM.KA 170 (K 340.73), isolated M2/.

Kulu Formation. M 34097 (Rs 908.50), facial part of skull (not from Hiwegi R 1A as stated by Butler, 1956).

Maboko. KNM.MB 557 (MB 1412.73), mandible with M/1.

Description:

The larger sample now available provides some information supplementary to that given by Butler (1956). (Fig. 10, 11, 12).

Measurements of the teeth (Table 5) show that specimens from Legetet are smaller than those from Chamtwara and Rusinga, indicating an evolutionary increase in size.

P4/ is distinguished from that of *Galerix africanus* by the more extended metastylar blade, and by the anteroposteriorly compressed lingual region, in which the hypocone is situated more lingually than the protocone. The parastylar prominence is usually less developed than in *G. africanus*, and the posterior cingulum does not extend round the hypocone.

M1/ is broader than long: the anterior width averages 7% greater than the length of the buccal edge and 15% greater than the length of the lingual part of the crown. An indentation of the buccal margin is always present. There is no paraconule, but the metaconule is distinct.

P/2 has two separate roots. Alveoli show that the tooth is frequently rotated so that its posterior root is displaced lingually. In 8 out of 15 specimens the posterior alveolus of P/2 is very close to the anterior end of P/4.

P/4 is nearly always widest towards the posterior end and narrowed anteriorly. The metaconid is a small elevation situated midway down the lingual ridge of the protoconid. It is removed by wear, but in some lightly worn specimens it can be seen to be absent as a distinct point, being represented only by an angulation of the ridge (fig. 10 G). The paraconid is intermediate in height between the protoconid and the metaconid; the notch between the paraconid and protoconid varies in depth, but it usually reaches the level of the metaconid. There is a single median talonid cusp. The alveoli of P/4 are not connected by a groove for the interradicular crest, though the groove is always present under M/1 and M/2.

The length of the trigonid of M/1, measured on the lingual side from the notch between metaconid and entoconid, is 60-63% of the length of the tooth. The length/width ratio of the trigonid averages 1.11 (range 1.04 - 1.17). These proportions are probably not significantly different from *A. edwardsi*, to judge from published figures by Viret (1938) and Hürzeler (1944). On unworn teeth the paralophid (anterior trigonid crest) is angled, running at first longitudinally and then turning into an anterolingual direction (fig. 10 D,F). It ends abruptly, but only in one specimen (KNM.CA 1549) is a cusp differentiated at the end of the crest (fig. 10 D). The metaconid is a little more anterior than the protoconid. The talonid is wider than the trigonid; the entoconid is higher than the hypoconid on unworn teeth; there is no hypoconulid. The complete buccal cingulum usually passes round the hypoconid to form the posterior cingulum. This is continuous with the buccal crest of the entoconid.

In four specimens the length of M/2 is 82-85% of the length of M/1; measurements of the alveoli gave a mean proportion of 84%. This proportion is similar to *A. intermedius*, and larger than in *A. edwardsi* (about 75%). The paralophid of M/2 is angled like that of M/1, but it does not reach so far lingually. The posterior cingulum does not connect with the entoconid.

14 specimens show a single alveolus for M/3; only in KNM.CA 1508 is there an

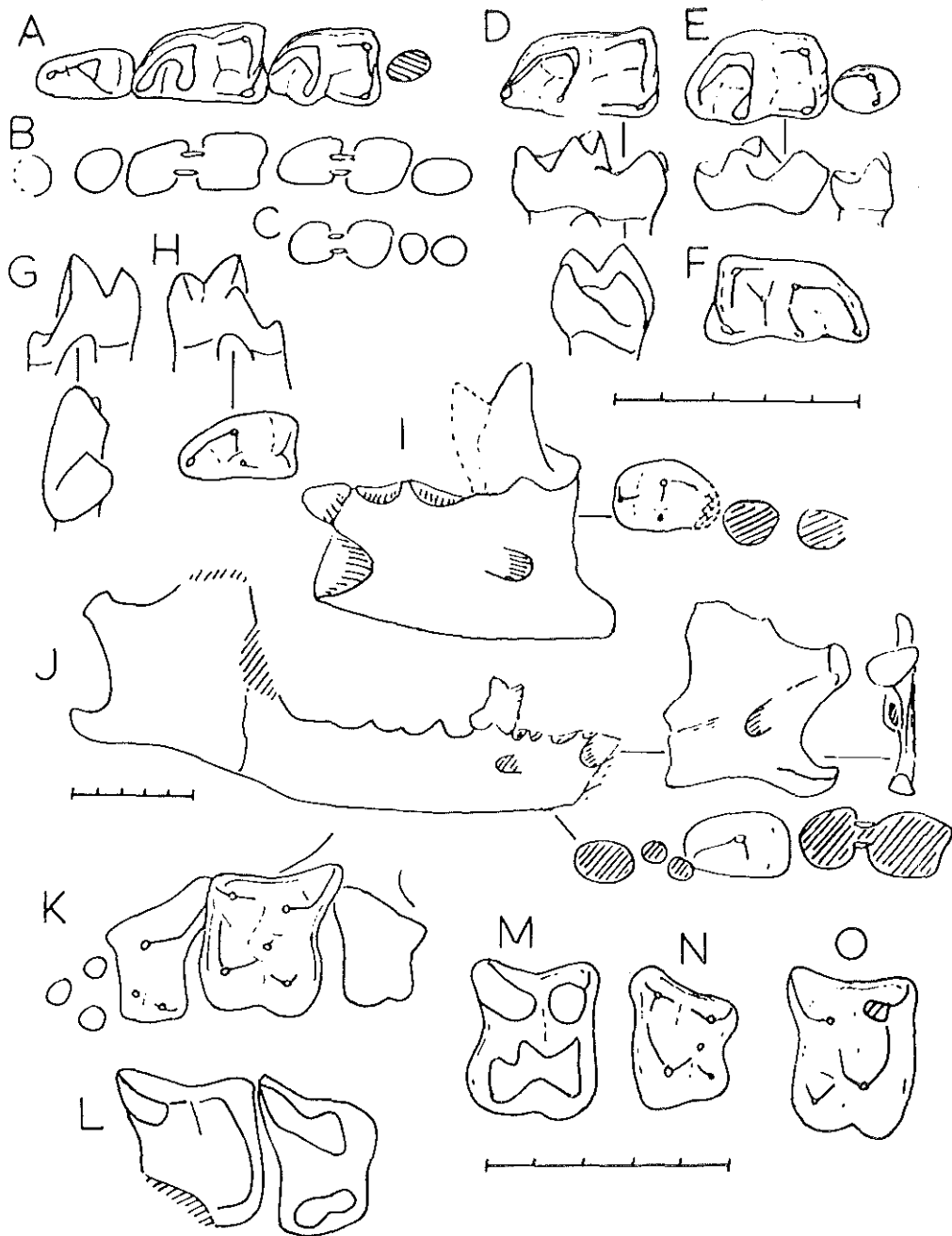


Fig. 10. — *Amphechinus*.

A, B, D-H, J-N, *A. rusingensis*: A, RP/4-M/2, KNM.LG 71; B, alveoli of P/4-M/3, KNM.CA 325; D, RM/1, crown, lingual and posterior views, KNM.CA 1549; E, RM/2,3, crown and lingual views, KNM.CA 346; F, LM/1, KNM.CA 1550; G, LP/4, lingual and posterior views, KNM.CA 1529; H, RP/4, lingual and crown views, KNM.CA 1995; J, R mandible (smaller scale) and C alveolus-M/1 alveolus, KNM.MB 357; K, L upper cheek teeth, composite of KNM.LG 1510 and KNM.LG 1508; L, RP4/ M1/, KNM.CA 2022; M, RM1/, KNM.KA 168; N, LM2/, KNM.KA 170.

C, *Amphechinus* sp. from Koru, alveoli of M/2,3, KNM.KO 81.

I, O, *Amphechinus* sp. from Fort Ternan: I, L fragment with P4/, KNM.FT 3804; O, RM1/, KNM.FT 3641.

	Legetet			Chamtwara			Rusinga		
	N	range	m	N	range	m	N	range	m
P4/ buccal length	4	2.4 -2.5	2.46	3	2.6 -2.9	2.78	2	2.75, 2.95	2.85
posterior width	3	2.95-3.15	3.03	3	3.2 -3.25	3.22	1	3.35	
M1/ buccal length	4	2.6	2.60	2	2.9 , 3.1	3.00	1	3.0	
anterior width	4	2.65-2.9	2.77	2	3.05, 3.1	3.03			
M2/ buccal length	1	2.0					2	2.1 , 2.25	2.17
anterior width	1	2.5					2	2.6 , 2.85	2.73
P/4 length	4	1.9 -2.1	2.01	5	2.0 -2.45	2.27	3	2.2 -2.45	2.30
M/1 length	4	2.85-3.0	2.99	8	2.85-3.55	3.26	2	3.2 , 3.3	3.25
talonid width	3	1.7 -1.85	1.78	8	1.8 -2.1	1.99	2	1.85, 2.1	2.03
M/2 length	2	2.5 , 2.8	2.65	1	2.7		2	2.6	2.60
trigonid width	2	1.55, 1.6	1.57	1	1.8		2	1.6 , 1.8	1.70

Table 5 : Measurements (mm) of teeth of *Amphechinus rusingensis*.

incipient subdivision. The crown of M/3 is fully exposed only in KNM.CA 346; it has no trace of a talonid (fig. 10 E).

In the mandible, the mental foramen is usually under P/4, but its position varies from below the posterior root of P/4 to below P/2. The ascending ramus of the mandible is not complete in any specimen. Re-measurement of the elevation of the anterior edge of the ramus (see Rich & Rasmussen 1973, fig. 11) in the holotype, in which it is best preserved, gave a result of 74° , not 83° as stated in the original description. Elevation of the condyle could be measured only in the Maboko specimen (fig. 10 J), where it is 24° . These elevations are similar to *A. edwardsi* and less than in *A. intermedius*. The width of the condyle in the Maboko specimen is 34% of the total length of the molars, less than in *A. edwardsi* (39-44%) (Butler 1948).

Two partial skulls have been found at Legetet, locality 10. One of these (10/551) contains the left maxillary part of the palate, with the canine roots, P2/, P3/ and part of P4/; dorsally it shows the posterior ends of the maxillae and nasals, and the frontals as far as the end of the olfactory chamber. The second specimen is a cranium KNM.LG 1515), broken off anteriorly at the level of the cribriform plate. Part of the orbital wall is preserved; it agrees with the corresponding region in M 34143, the anterior part of a skull from Songhor, and shows that KNM.LG 1515 belongs to *A. rusingensis*. M 14316, from Maize Crib, was referred to *Erythrozoetes* by Butler (1969), but it agrees closely with KNM.LG 1515 and it must now be identified as *A. rusingensis*.

A reconstruction (fig. 11) shows that the skull differs in a number of ways from that of *A. edwardsi*, described by Viret (1938). The interorbital region, which houses the

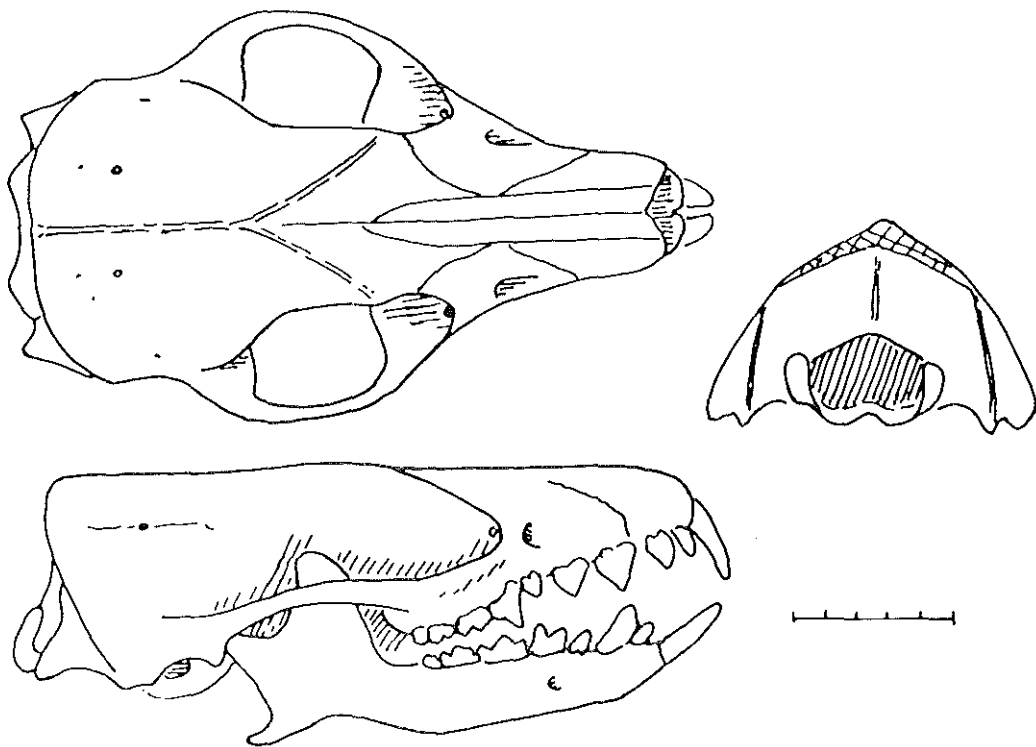


Fig. 11. — Reconstruction of skull of *Amphelchinus rusingensis*, based on specimens from Legetet.

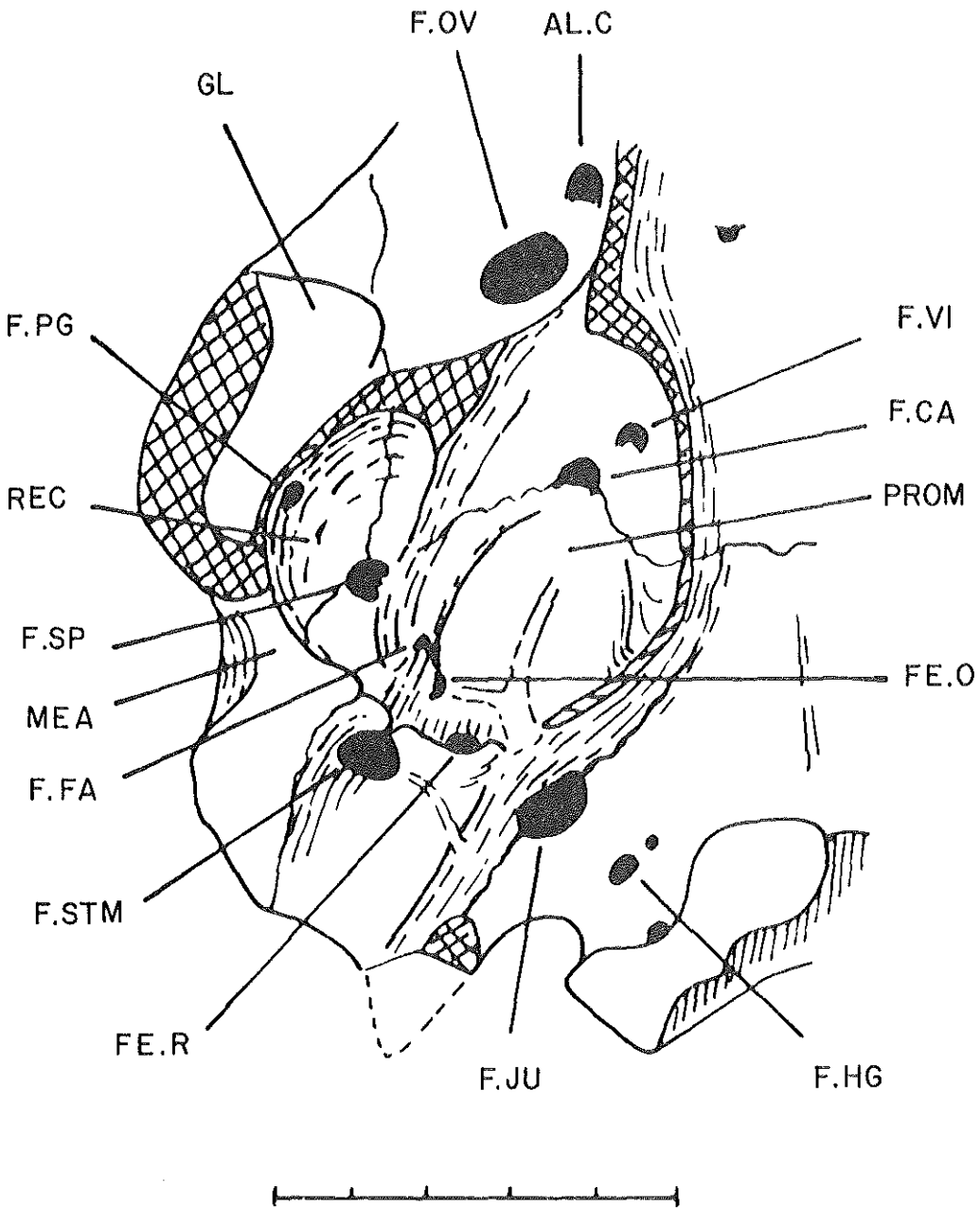


Fig. 12. — *Amphichinus rusingensis*. Middle ear region of KNM.LG 1515.

The anterior and medial walls have broken away. Abbreviations: AL.C, alisphenoid canal. F.CA, carotid foramen (promontorial artery). F.FA, foramen stylomastoideum primitivum (facial nerve). F.HG, foramina for hypoglossal nerve. F.JU, foramen jugulare (lacerum posterius). F.OV, foramen ovale. F.PG, foramen postglenoideum. F.SP, foramen spinosum (middle meningeal artery). F.STM, foramen stylomastoideum. F.VI, posterior opening of vidian canal. FE.O, fenestra ovalis. FE.R, fenestra rotunda. GL, glenoid. MEA, meatus. PROM, promontorium. REC, recessus epitympanicus.

posterior part of the olfactory chamber, is narrow, and postorbital processes are virtually absent. The nasals are longer, reaching as far back as the supraorbital extensions of the maxillae. Temporal and sagittal crests are weak, and in posterior view the skull is lower in comparison with its width. KNM.LG 1515 differs from M 14316 in the presence of a weak median occipital crest and in the emargination of the dorsal edge of the foramen magnum. The condyles resemble those of *A. edwardsi*, but the basioccipital is longer, so that the distance between the tympanic chamber and the condyle is greater. The middle ear region of KNM.LG 1515 (fig. 12) agrees with M 14316, but its lateral portion is better preserved. The area labelled m. stap. by Butler (1969, fig. 10 D) is the roof of the recessus epitympanicus. The postglenoid foramen appears to be smaller than in *A. edwardsi*. The alisphenoid canal is longer than in *A. edwardsi*, its anterior opening being confluent with the sphenorbital foramen. In the orbit, the sinus canal opens below a ridge that is continuous with the dorsal edge of the sphenorbital foramen. A more anterior (ethmoid) foramen, also below the ridge, is for a vessel that passes vertically up the internal face of the frontal, following the cribriform plate. A more dorsal foramen corresponds to one near the postorbital process of *A. edwardsi*. The optic and suboptic foramina are situated immediately anterior to the sphenorbital foramen as in *A. edwardsi*.

Amphechinus sp. from Koru

An edentulous fragment of mandible (KNM.KO 81) has the alveoli of M/2 and M/3 (fig. 10 C). M/2 has the erinaceid character of the groove between the alveoli, but M/3 had two roots. This specimen is within the size range of *A. rusingensis* and too large to belong to *Galerix africanus*. It may represent a primitive stage of *A. rusingensis* that retained a two-rooted M/3.

Amphechinus sp. from Fort Ternan.

Two specimens from Fort Ternan differ in some ways from *A. rusingensis*.

KNM.FT 3804 is a fragment of mandible with P/4 and the alveoli of the more anterior teeth (fig. 10 I). There is only a single alveolus for P/2, as in the European species. The paraconid of P/4 has broken off. There is a small metaconid. The tooth is broadest across the trigonid, unlike most specimens of P/4 of *A. rusingensis* which are broadest near the posterior end, but like the European species. The jaw is broken across immediately behind P/4; the root of I/2 does not appear on the broken surface. The mental foramen is below the middle of P/4. Measurements fall within the range of *A. rusingensis*.

KNM.FT 3641 is an isolated M1/ (fig. 10 O). It is proportionately somewhat broader than in *A. rusingensis*: the anterior width is 17% greater than the buccal length and 30% greater than the lingual length. It also differs from *A. rusingensis* in that the metaconule is indistinct, a resemblance to the European species.

This Middle Miocene form has advanced characters which were present already in *A. arvernensis* in the Late Oligocene of Europe. It is smaller than the European species, resembling *A. rusingensis* in size. It is probably a derivative of *A. rusingensis* that has evolved in parallel with the European species but at a later date. In the jaw from Maboko, which is only about 1 My older than Fort Ternan, P/2 still has two roots like other specimens of *A. rusingensis*.

Relationships of AMPHECHINUS RUSINGENSIS.

The Erinaceinae were widely distributed in Eurasia in the Oligocene. Their centre of evolution was probably in Asia, for the greatest variety of species comes from Mongolia

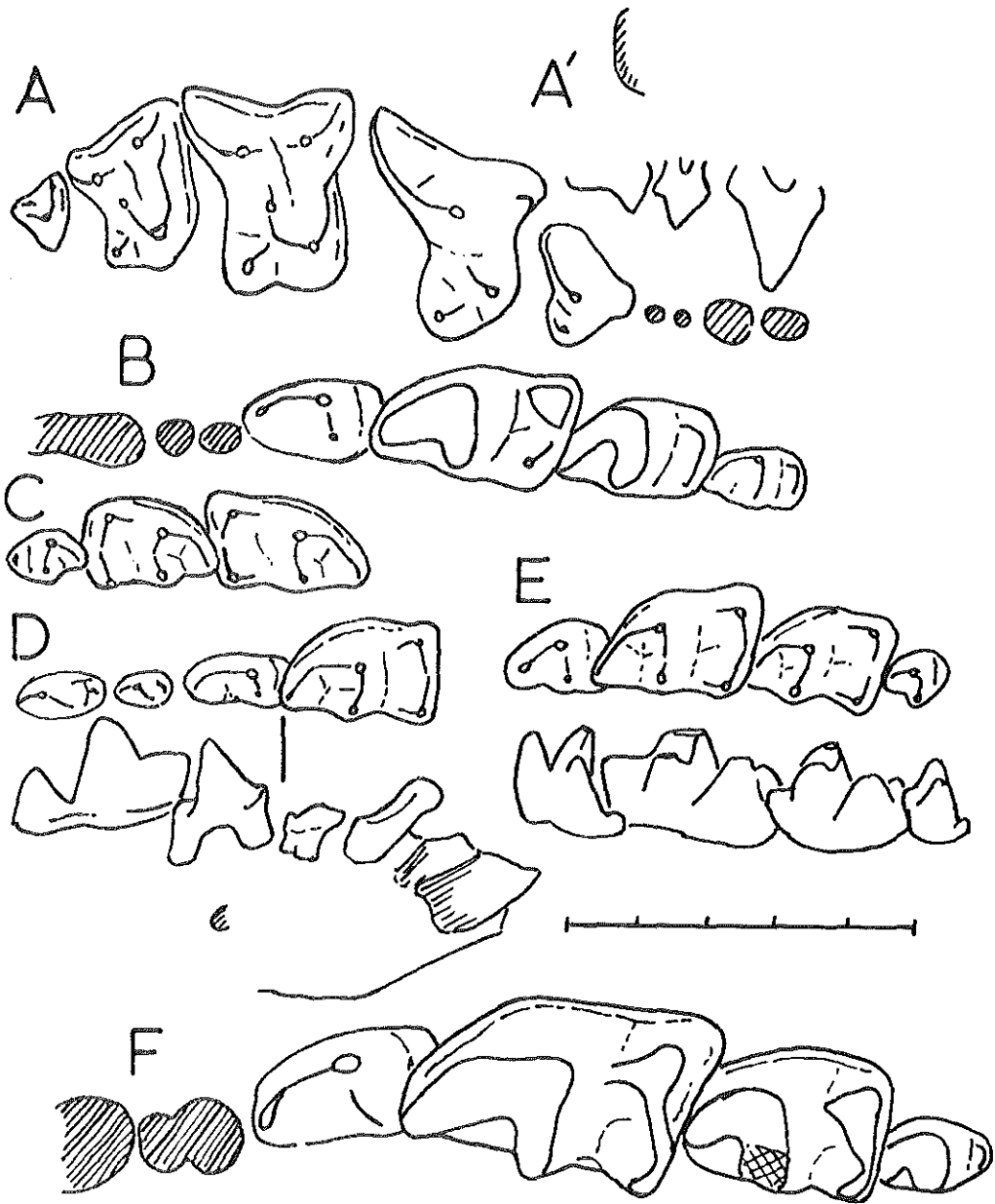


Fig. 13. — Asiatic Oligocene Erinaceidae.

A, *Palaeosceptor acridens*, R upper teeth of AMNH 22080.

A', lateral view of LP3/-C (reversed).

B, *Palaeosceptor acridens*, R lower teeth, Field Museum P 14123.

C, Cf *Amphechinus minimus*, LM/1-3, AMNH 19144; anterior end of M/1 completed from AMNH 19143.

D, Cf *Amphechinus minimus*, RdC-M/1, AMNH 19142.

E, *A. minimus*, RP/4-M/3, holotype (cast).

F, *A. rectus* from Chitan-Gol, Paris Museum.

and China. The most primitive of these is *Palaeosaptor acridens* Matthew & Granger (1924), from the Hsanda Gol Formation (probably Middle Oligocene). I have examined the type material in the American Museum of Natural History. The holotype is broken off in front of P/4, and the authors described the anterior part of the dentition from paratypes, some of which, as is now evident, do not belong to *Palaeosaptor* but to a species of *Amphechinus*, probably *A. montanus* (*A. minimus*) (Fig. 13 C,D). More complete specimens - the material described by Sulimski (1970) and an undescribed specimen in the Field Museum of Natural History, Chicago (P 14213) (fig. 13 B) - have two alveoli between P/4 and the canine, and AMNH 22080 shows that they were occupied by two one-rooted teeth, P/2 and P/3. AMNH 22080 is immature, with P/4 incompletely erupted, as may be seen in a radiograph published by Rich & Rasmussen (1973). AMNH 22081 has a small one-rooted P/3 which reaches only to the level of the cingulum of P/4. In AMNH 22082, another juvenile specimen, figured by Rich & Rasmussen (1973), the tooth in the position of P/3 has two divergent roots, and it might be dP/3. In *Erinaceus* P/3 and dP/3 are represented by uncalcified rudiments (Kindahl 1959).

AMNH 22080 also shows an additional tooth between the canine and the alveolus of I/3. This could be the milk canine. The large incisor of Erinaceinae is generally held to be I/2 on embryological grounds (Leche 1895, Kindahl 1959). McKenna & Holton (1967) and Rich & Rasmussen (1973) call it I/1, being influenced by the fact that I/1 is the largest incisor in Galericinae. If they are right, the extra tooth in AMNH 22080 could be I/3, lost in other Erinaceinae.

The upper dentition of *P. acridens* is preserved in AMNH 22080 (figured by Rich & Rasmussen 1973) and in a skull described by Trofimov (1960). (Trofimov calls the large incisor I2/ and misidentifies I2/-P3/ as I3/-P4/). As in *A. rusingensis*, I1/ is large, I2/ is small, I3/ is two-rooted and larger than I2/, and the canine is two-rooted and a little higher than I3/. However, P2/ is smaller than P3/, which is less reduced than in *A. rusingensis*. P4/-M2/ are more transverse, and M3/ is unique among Erinaceinae in being triangular. Correspondingly, M/3 has a comparatively well developed talonid and two roots (fig. 13 A).

A. rusingensis resembles *Palaeosaptor* in several ways. I/2 is of similar relative size: its transverse diameter is about two-thirds of the length of P/4, and its root ends below the anterior part of P/4. P/4 is widened posteriorly; its metaconid varies in the same way (Sulimski 1970, text-fig. 1). The length/width proportions of the M/1 trigonid are similar (1.06 - 1.13 in 7 specimens of *P. acridens*, 1.04 - 1.17 in *A. rusingensis*). However, in *Palaeosaptor* M/1 is more enlarged (length M/2/length M/1, .70-.80 in *Palaeosaptor*, .82-.85 in *A. rusingensis*). The skull of *Palaeosaptor* (Trofimov 1960) resembles that of *A. rusingensis* in the long, narrow face which widens rapidly to the rounded cranium. Postorbital processes and sagittal crest appear to be weak, but the cranial roof lacks the rugosity present in *A. rusingensis* and other species of *Amphechinus*. Resemblances of *Amphechinus* to *Palaeosaptor* may be regarded as primitive characters within the genus *Amphechinus*.

Three species of *Amphechinus* have been named from the Oligocene of Asia. Of these, *A. kansuensis* (BOHLIN, 1942) is the least known. It differs from *A. rusingensis* in the small size of the canine alveolus, the single root of P/2, the presence of a diastema between P/2 and P/4, and the more anterior position of the mental foramen. *A. rectus* (MATTHEW & GRANGER, 1924) occurs with *Palaeosaptor* in the Hsanda Gol Formation. It is comparatively large, of the size of *A. edwardsi*. I/2 is more enlarged than in *A. rusingensis*, having a diameter of about 85% of the length of P/4, and a root that reaches

well under P/4, causing a swelling on the medial surface of the jaw. P/2 is one-rooted, but the alveolus is partly divided in the specimen described by Teilhard de Chardin (1926) under the name of *Palaeoscaptor acridens* (fig. 13 F). The paraconid of P/4 is elevated. On M/1 the trigonid is more extended (length/width 1.13 and 1.21 in two specimens measured), and M/1 is more enlarged relatively to M/2. M/3 has two roots in some specimens, one in others, and its talonid is reduced and cingulum-like. The upper dentition is unknown. An undescribed cranial fragment (AMNH 21698) shows that the parietal surface is rugose.

A. minutus (BOHLIN, 1942) was based on Late Oligocene material from Taben-buluk. Sulimski (1970) referred to this species some mandibles from Nareen Buluk, of similar age. Specimens from the hypodigm of *Palaeoscaptor acridens* (AMNH 19142-4) are very similar to *A. minutus* in size and proportions and probably belong to the same species (fig. 13 C,D), extending its range back to the Middle Oligocene. Rich & Rasmussen (1973) synonymised *A. minutus* with *Parvericius montanus* KOERNER, 1940, from the Early Miocene (Arikarean) of North America; the name *montanus* has priority over *minimus*. I am grateful to Dr. Rich for a cast of the type of *A. minimus*, which I agree is very much like *P. montanus* (fig. 13 E). I cannot however accept a generic separation of *Parvericius* from *Amphechinus*. It is based on the shorter M/1 trigonid of *A. montanus*, but the difference from *A. rusingensis* is small: from my measurements the length/width ratio is 1.00 - 1.11 in 7 specimens, compared with 1.04 - 1.17 in *A. rusingensis*. In all other respects *A. montanus* falls within the range of *Amphechinus*.

A. montanus is smaller than *A. rusingensis*. I/2 is proportionately similar to *A. rusingensis* and *Palaeoscaptor*. P/2 has only one root. P/4, though widened posteriorly, is not so clearly triangular in outline as in *A. rusingensis*. The metaconid of P/4 varies in size: it is absent in the American specimens. The length of M/2 is about 80% of that of M/1. The Hsanda Gol specimens have a small but distinct talonid on M/3, which is two-rooted; in the later specimens M/3 has one root, and the talonid is reduced to a cingulum which has disappeared in the American specimens. The upper dentition is known only in American specimens. The proportions of P4/-M3/ are like *A. rusingensis*, except that the anterior edge of P4/ is shorter, M1/ is a little more transverse, and the metastylar blades of P4/ and M1/ are more pronounced. The metaconule of M1/ is not clearly developed.

A. rusingensis evidently had a common ancestry with the other species of *Amphechinus*, though it retains some primitive characters, such as the two-rooted P/2, that they have lost. The date of the common ancestor could not have been later than Middle Oligocene. Entry into Africa from Asia could have occurred at any time between Middle Oligocene and earliest Miocene, when the genus was present at Koru. *A. kreuzae* MUNTHE & WEST, 1980, from the Late Miocene Upper Chinji Formation in Pakistan, resembles *A. rusingensis* in retaining a distinct metaconule and low hypocone. It may be a late descendant from the Asiatic stock from which *A. rusingensis* was also derived.

There is an indication of evolution in Africa, provided by the double root of M/3 in the Koru specimen, and the advanced characters of specimens from Fort Ternan.

GYMNURECHINUS BUTLER, 1956

Gymnurechinus leakeyi BUTLER, 1956

Gymnurechinus leakeyi, Butler (1956), pp. 3-30, text-figs. 1-8, Pls 1-4; Butler (1969), pp. 14-16, fig. 6.

Holotype: M 34060 (Rs 12.32), skull and mandibles, from Hiwegi Formation, locality R 12.

Diagnosis: Separation of fragmentary specimens of this species from *G. camptolophus* is dependent mainly on size. 32 specimens from the Hiwegi area of Rusinga (localities R 1, R 1A, R 3, R 3A, R 12 and R 2 (1956) apparently form a uniform sample, which may be taken as the hypodigm of *G. leakeyi*. Coefficients of variation, calculated for 15 measurements of the teeth, range from 3.0 to 8.4 with a median of 5.5 (Table 6; fig. 14).

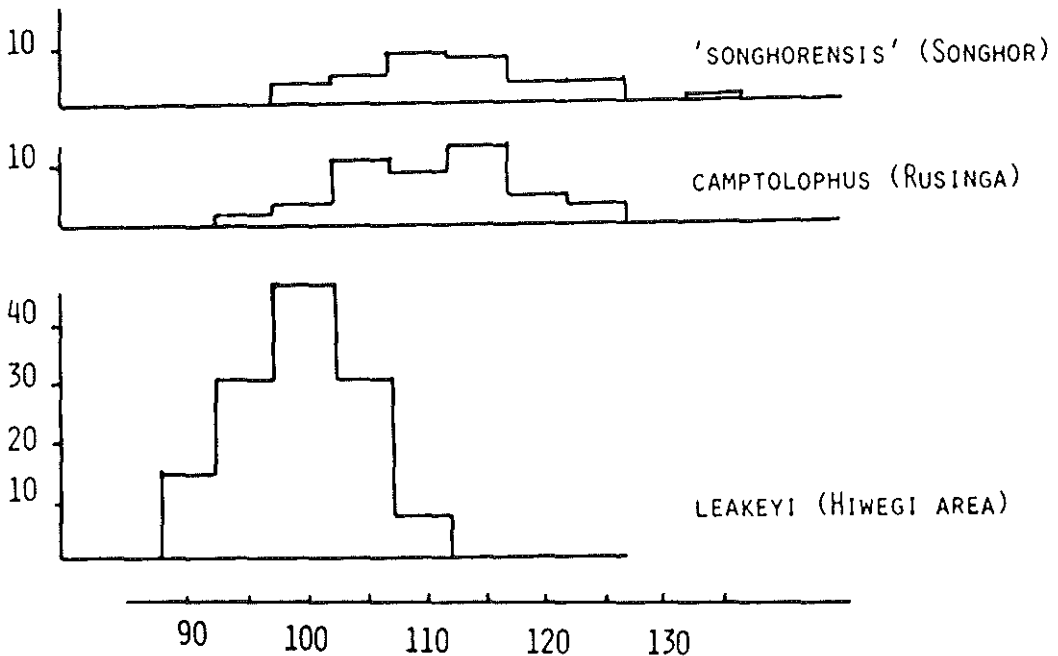


Fig. 14. — Size distribution in *Gymnurechinus*.

Measurements of teeth expressed as percentages of the means of specimens from eastern Rusinga (Hiwegi area).

Specimens identified:

Legetet Formation.

Locality. KNM.LG 1503 (10/627), mandible with P/2-M/1; KNM.LG 1504 (10/886), mandible with P/4.

Locality 14. KNM.LG 1530 (14/165), P/4.

Locality 29. KNM.LG 1213 (29/70), mandible with M/3; KNM.LG 1518 (29/221), M/1.

Locality 45. KNM.LG 333 (45/23), edentulous mandible.

Kapurtay Agglomerates.

	<i>G. leakeyi</i> Hiwegi sample					<i>G. camptolophus</i> (including <i>songhorensis</i>)				
	N	range	m	S.D.	V	N	range	m	S.D.	V
Between I1/ and C1/	1	4.0				1	5.4			
C1/ length	4	2.7	2.70			1	3.5			
P2/ length	1	2.0				1	2.6			
P3/ buccal length	7	1.95-2.25	2.07	0.133	6.4	2	2.35, 2.75	2.55		
Between C1/ and P4/	3	7.0 -7.4	7.23			1	8.4			
P4/ buccal length	9	3.45-4.0	3.80	0.206	5.4	3	3.9 -4.45	4.08		
anterior width	7	3.25-4.1	3.60	0.303	8.4	3	3.6 -3.8	3.70		
posterior width	8	4.2 -5.1	4.61	0.274	6.0	3	4.9 -5.3	5.10		
M1/ buccal length	11	3.75-4.2	4.06	0.180	4.3	3	4.7 -5.0	4.88		
anterior width	10	4.2 -4.9	4.61	0.252	5.5	3	4.75-5.0	4.90		
posterior width	10	4.4 -5.3	4.79	0.307	6.4	3	5.3 -5.4	5.37		
M2/ buccal length	6	3.35-3.8	3.55	0.187	5.3	3	4.05-4.15	4.10		
anterior width	5	4.2 -4.6	4.36	0.182	4.2	3	4.4 -4.8	4.57		
P4/-M2/ length	5	10.4 -11.3	10.92	0.432	4.0	1	11.8			
Posterior I/2 - posterior P/2	3	4.6 -4.8	4.70			2	5.1 , 5.5	5.30		
P/2 length	1	2.7				3	2.9 -3.0	2.97		
P/4 length	7	3.3 -3.6	3.51	0.107	3.0	5	3.7 -4.2	3.88	0.214	5.5
width	7	1.95-2.3	2.12	0.111	5.2	5	2.05-2.4	2.30	0.146	6.3
M/1 length	7	4.3 -5.2	4.76	0.302	6.4	5	4.7 -5.3	5.04	0.256	5.1
trigonid width	5	2.5 -3.1	2.84	0.206	7.3	7	2.8 -3.6	3.21	0.224	7.0
talonid width	6	2.8 -3.3	2.95	0.187	6.3	7	3.0 -3.6	3.27	0.216	6.6
M/2 length	3	3.6 -3.8	3.67			2	4.15, 4.2	4.17		
trigonid width	3	2.5 -3.0	2.80			2	2.7 , 3.35	3.03		
M/3 length	3	2.05-2.4	2.18							
M/1-M/3	2	9.8 , 10.9	10.35			1	11.3			
P/4 -M/2	2	11.5 , 11.9	11.70			1	13.3			

Table 6 : Measurements (mm) of the teeth of *Gymnurechinus*.

- Chamtwara. KNM.CA 2066 (34/836c), edentulous mandible.
 Songhor. KNM.SO 1610 (Sgr 150.72), M/1 trigonid; KNM.SO 1662 (Sgr 66.71), M/1.
 Hiwegi Formation. Most specimens were listed by Butler (1956, 1969); only additions and corrections are detailed here.
 Locality R 1. 8 specimens: 5 previously listed (not Rs 1575.50); M 34086 (Rs 1248.50), maxilla with P3/-M1/ (listed previously as from R 3A); M 34088 (Rs 734.56), maxilla with P4/-M2/ (listed previously as from Kulu-Warengu); M 34089 (Rs 562.51) edentulous mandible (listed as from site unknown).
 Locality R 1A. 2 specimens previously listed.
 Locality R 2 (1956). 3 specimens previously listed.
 Locality R 3. 10 specimens: 7 previously listed; M 34095 (Rs 732.47), mandible with P/4, M/1; KNM.RU 3689 (RU 934.56), mandible with P/2-M/1; M 34052 (Rs 1575.50), M/1 (listed as from R 1).
 Locality R 3A. 6 specimens previously listed (not Rs 1248.50).
 Locality 12. 2 specimens previously listed.
 Kamugere. 1 specimen previously listed.
 Wanyama. 1 specimen previously listed.
 Kaswanga. 4 specimens: 3 previously listed (not Rs 1394.50 and Rs 1539.50); KNM.RU 3696 (Rs 320.71), mandible with P/2-4.
 Locality R 106. 4 specimens. 3 previously listed (not Rs 290.49); KNM.RU 3691 (Rs 933.40), fragment of M1/.
 Locality R 111. 1 specimen previously listed.
 Locality unknown. M 34050 (Rs 32.32), cranium.
 Karungu. KNM.KA 169 (K 365.73), isolated M1/ and M2/.
 Kulu Formation. 3 specimens: M 34048 (Rs 734.48), skull with mandible and atlas vertebra; M 34059 (Rs 735.48), edentulous mandible; M 34067 (Rs 259.49), crushed cranium (previously listed as from locality R 3).

Description (Fig. 15):

There is little to add to the original description (Butler 1956). On P/4 the metaconid is distinct, not merged into the protoconid as is commonly the case in *Amphechinus*. The paraconid is only a little higher than the metaconid; it is upright, and separated from the protoconid by a notch of variable depth. The trigonid of M/1 is usually shorter than wide (length/width in 7 specimens 0.84 - 1.08, mean 0.95), and its length averages 59% of the length of the tooth (range 55-64%). The paralophid is curved, not angled as in *A. rusingensis*; a small paraconid can be seen at its lingual end in unworn specimens. The posterior cingulum of M/1 is usually continuous with the buccal crest of the entoconid, as in *A. rusingensis*.

The upper molars from Karungu (fig. 15 C) differ from typical *G. leakeyi* in that the posterobuccal corner of M1/ is more projecting, and the posterior edge of M2/ is proportionately shorter.

Gymnurechinus camptolophus BUTLER, 1956

Gymnurechinus camptolophus, Butler (1956), pp. 30-50, text-figs. 8-14, Pls. 2, 4.

Gymnurechinus songhorensis, Butler (1956), pp. 50-53, text-figs. 8, 9, 15, Pls. 3, 4; Butler (1969), p. 36, fig. 6.

Holotype: M 34073 (Rs 424a.48), skull from Hiwegi Formation, locality R 105A.

Diagnosis: Re-examination of the specimens leads me to the opinion that *G. songho-*

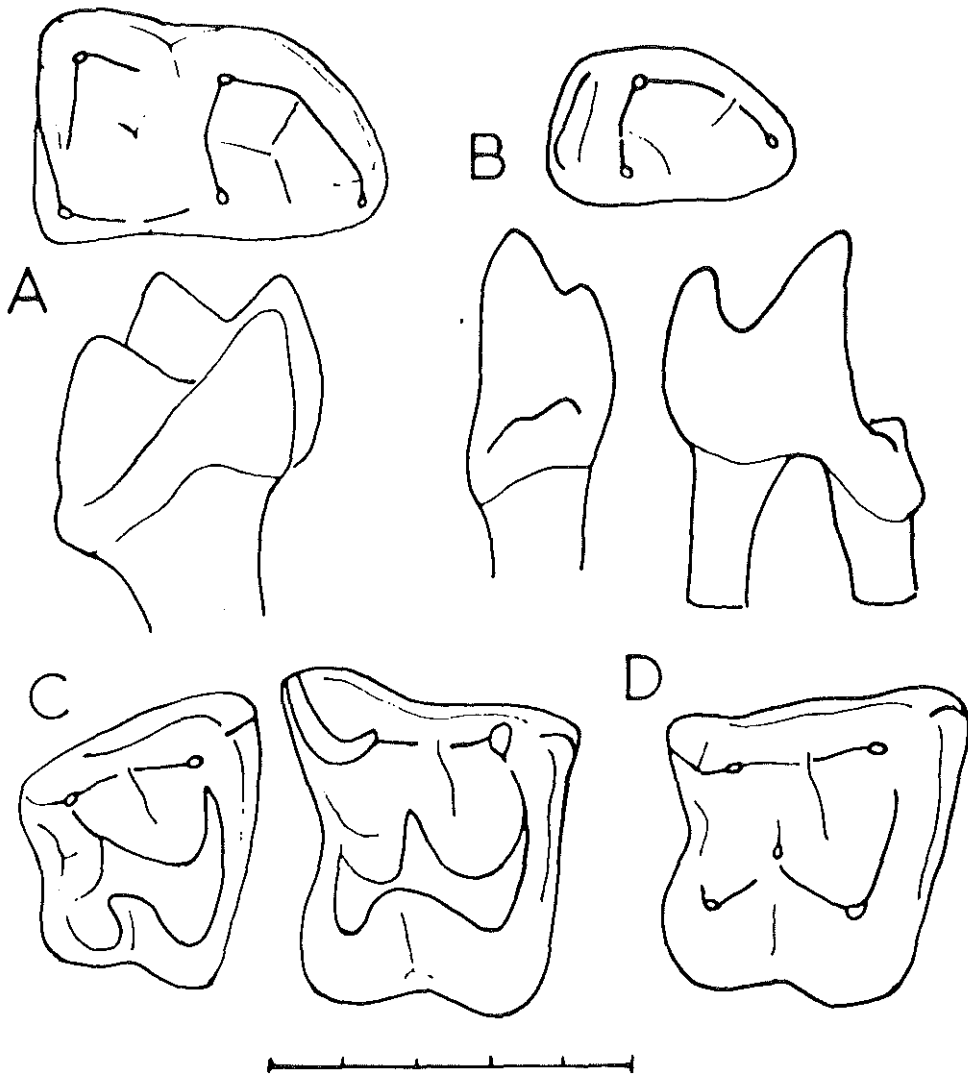


Fig. 15. — *Gymnurechinus*.

A-C, *G. leakeyi*: A, LM/1, crown and posterior views, KNM.LG 1518; B, LP/4, crown, posterior and buccal views, KNM.LG 1504; C, RM1/ and M2/, KNM.KA 169.

D, *G. camptolophus*, RM2/, KNM.RU 3695.

rensis cannot be distinguished from *G. camptolophus*. Specimens from Songhor agree in size with the larger specimens from Rusinga referred to *G. camptolophus*, and when the two samples are combined the coefficients of variation are similar to those of the Hiwegi sample of *G. leakeyi* (fig. 14). Both *G. songhorensis* and *G. camptolophus* differ from *G. leakeyi* in the skull roof, on which the sagittal crest is sharp and the temporal rugosity extends to its base (see Butler 1956, fig. 8). Also, M1/ is not transverse as in *G. leakeyi*, its anterior width being nearly equal to the buccal length.. Characters used to distinguish *G. songhorensis* from *G. camptolophus* were the structure of the posterolateral part of the skull, particularly the small lambdoid area of *G. songhorensis*, and the absence of the

hypocone of P4/ in *G. camptolophus*. These differences, based upon very few specimens, are believed to be individual variations.

Specimens identified:

Kapurtay Agglomerates.

Songhor. 10 specimens recorded previously as *G. songhorensis*.

Hiwegi Formation.

Kaswanga. M 34079 (Rs 1394.50), snout; M 34072 (Rs 290.49), and M 34060 (Rs 1539.50), mandibles (previously recorded as *G. leakeyi*); KNM.RU 3693 (Rs 245.71), mandible with M/1,2; KNM.RU 3695 (Rs 1324.71), isolated M2/, M/1, M/3.

Locality R 105, M 34082 (Rs 212.48), mandible (previously recorded as from R 105A).

Locality R 105A. M 34073 (Rs 424a.48), holotype skull; M 34074 (Rs 424.48), partial skeleton; M 34075 (Rs 424b.48), M1/, M2/, M 34078 (Rs 424c.48), limb bones; KNM.RU 3601 (Rs 900.52), mandible with M/1,2.

Sienga. M 34076 (Rs 564.48) and M 34077 (Rs 595.48), mandibles previously recorded as from R 105A.

Kamathengere (mixed sites). M 34080 (Rs 366.49), mandible with I/3-P/2.

Locality unknown. M 34083 (Rs 32a.32), cranium; M 34094 (Rs 145.41), mandible with M/1.

M 34095 (Rs 732.47), from locality R 3, is now referred to *G. leakeyi*.

Relationships of GYMNURECHINUS

Butler (1956, p. 27ff) listed 20 characters in which *Gymnurechinus* is more primitive than Recent Erinaceinae. Most of them can be found also in *Amphechinus*, *Palaeoscaptor* and Galericinae, indicating that they are plesiomorphous for the family Erinaceidae. At the same time *Gymnurechinus* shares several derived characters with *Amphechinus*: (1) I1/ and I/2 enlarged, I/1 absent; (2) I3/ with two roots, larger than I2/; (3) P1/ and P/1 absent; (4) P/3 absent; (5) metaconule of upper molars without a posterior crest; (6) M3/ transverse, without metacone, and M/3 talonid rudimentary; (7) paraconid of P/4 elevated, metaconid reduced. *Palaeoscaptor* shares all these characters, except (4) and (6), in which it remains primitive. A reasonable inference is that *Gymnurechinus* had a common ancestor with *Amphechinus* and *Palaeoscaptor*, most probably in Asia, and that it entered Africa with *Amphechinus* and *Galerix* in the Oligocene or earliest Miocene.

Rich (1981) grouped *Gymnurechinus* with *Mioechinus*, *Postpalerinaceus*, *Untermannex*, *Protechinus* and the living Erinaceinae in a tribe Erinaceini, opposed to the Amphechhini, which included *Palaeoscaptor*, *Amphechinus* and *Dimylechinus*. The Erinaceini have a relatively small I/2, the root of which does not reach the level of P/4. They also have a shorter M/1 trigonid, a character to which Rich attaches much weight, although the proportions of the trigonid vary between the species of *Amphechinus*, and the range of *A. montanus* (1.00 - 1.11) overlaps with that of *Gymnurechinus leakeyi* (0.84 - 1.08). Other characters, which *Gymnurechinus* shares with some of the species of *Amphechinus*, are probably primitive: the double root of P/2, the posterior widening of P/4, the moderate elevation of the P/4 paraconid, and the relatively large M/2/M/1 ratio. An advanced character of *Amphechinus*, not shared by *Gymnurechinus*, is the more posterior situation of the cheek teeth, P4/ being partly beneath the orbit. In this respect *Palaeoscaptor* appears to be primitive: Trofimov's figure (1960, fig. 1) suggests that P4/ is anterior to the orbit, and according to Rich (1981) the relation of the zygomatic process to the molars is the same as in *Erinaceus*.

Rich (1981) derived the Erinaceini and Amphechini independently from Dormaliidae, ignoring the synapomorphies listed above. It is much more likely that the Erinaceini were derived from a primitive erinaceine related to *Palaeoscaptor*. Some parallel evolution cannot be avoided: if the large I/2 of *Palaeoscaptor* is a synapomorphy with *Amphechinus*, the loss of P/3 and of the metacone of M3/ must have taken place independently in the line that led to the Erinaceini; alternatively, the incisor enlarged independently in *Palaeoscaptor* and *Amphechinus*, unless it was secondarily reduced in Erinaceini.

Stenoechinus tantalus RICH & RASMUSSEN (1973), from the Early Miocene of North America, may be either a primitive member of the Erinaceini or an independent derivative of the ancestral stock of the Erinaceinae. The anterior part of the jaw is poorly known, but there is evidence that the root of I/2 ended well in advance of P/4. Two alveoli closely preceding P/4 might have held a two-rooted P/2. The trigonid of M/1 is short, and the length of M/2 is about 80% of that of M/1. M/3 has two roots, but its talonid is reduced and cingulum-like. M1/ and M2/ are markedly transverse, as in *Palaeoscaptor*, but the metaconule has disappeared. Rich & Rasmussen (1973) suggested a relationship to Brachyericinae, mainly on the basis of the comparatively low P/4 paraconid. There is however no sign of the incisor enlargement that characterises the Brachyericinae; the small P/4 paraconid of that subfamily may be a consequence of the reduction in size of the tooth. The origin of the Brachyericinae may be from a species of *Amphechinus* near *A. rectus*.

Erinaceini appear in Europe in the Late Burdigalian (Zone of La Romieu), after 18 Ma. The genus *Mioechinus*, in which they are provisionally placed, extends to Oeningen (cir. 13 Ma., Van Couvering 1972) and Eskihsar in Turkey (Engesser 1980). *M. butleri*, from the Burdigalian of Spain (Crusafont *et al.*, 1955) is aberrant in its quadrate P4/ and narrow M1/. The later species have advanced characters: the lachrymal foramen opens outside the orbit in *M. tobieni* and *M. sansaniensis* (Engesser 1980), *M. oeningensis* has a basisphenoid pit (Butler 1948), and in *M. sansaniensis* P/2 is one-rooted and the coronoid process is vertical. There is no convincing evidence that these were derived from *Gymnurechinus* as Rich (1981) postulated; more probably they came, like *Gymnurechinus*, from an unknown Asiatic source.

Protechinus salis LAVOCAT (1961), from the Middle Miocene of Beni Mellal, Morocco, is primitive in the relatively transverse molars and the low elevation of the ascending ramus, but it has advanced beyond *Gymnurechinus* in the one-rooted P/2 and the facial position of the lachrymal foramen. Whether it is a descendant of *Gymnurechinus* or an immigrant from Europe cannot be decided on existing evidence.

Family SORICIDAE FISCHER von WALDHEIM, 1817

CROCIDURA WAGLER, 1832

M 34160 (Rs 1875.50), a mandible with M/1 and M/2 (Butler & Hopwood 1957), remains the only specimen of Soricidae. It is from Rusinga, surface of locality R 3A. Very similar to *C. flavescens nyanzae* NEUMANN which now lives in the area, it is considered to be Pleistocene or Recent in date. If this specimen is discarded, the oldest soricid known from Africa is '*Sorex dehmi africanus* LAVOCAT (1961) from Beni Mellal, which is much more primitive.

Family TENRECIDAE GRAY, 1821

Subfamily PROTENRECINAE BUTLER, 1969

PROTENREC BUTLER & HOPWOOD, 1957

Protenrec tricuspis BUTLER & HOPWOOD, 1957

Protenrec tricuspis, Butler & Hopwood (1957), pp. 21-23, fig. 7; Butler (1969), pp. 17-20, figs. 7, 8.

Holotype: M 34149 (Sgr 95.47), mandible with M/1-3, from Songhor.

Specimens identified:

Legetet Formation.

Locality 10. KNM.LG 1493 (10/554, 10/557), facial skull and separate maxilla, probably from the same individual.

Kapurtay Agglomerates.

Chamtvara. KNM.CA 1537 (34/698), mandible with M/1; KNM.CA 1538 (34/698), mandible with M/1,2; KNM.CA 1542 (34/698)/ mandible with M/3; 6 edentulous mandibles.

Songhor. 5 specimens listed by Butler & Hopwood (1957) and Butler (1969); KNM.SO 1404 (Sgr 817.72), juvenile mandible with dentition; KNM.SO 1093 (Sgr 144.72), mandible with P/4-M/3; KNM.SO 1608 (Sgr 300.72), edentulous mandible; KNM.SO 1417 (Sgr 360.66), maxilla with P3/-M3/; KNM.SO 1420 (Sgr 769.72), maxilla with P2/-M3/.

Napak.

Locality IV. M 43552, maxilla with P2/-M3/; M 43551, mandible with P/3-M/3.

Hiwegi Formation.

Locality R 1. Rs 551.49, mandible with P/2-M/1.

Description (Figs. 16, 17):

The upper incisors and canine are unknown. Three new specimens contain upper premolars and molars, hitherto known only from the Napak specimen (Butler 1969).

P2/ has two well separated roots, a paracone, situated somewhat forward, and anterior and posterior basal cusps. P3/ is similar in height and length to P2/, but wider. It is at a low level of molarisation, and contrasts with P4/, which is the largest tooth in the upper dentition. P4/ is less transverse than the molars, owing to its anteriorly prominent parastyle. The protocone is as large as on the molars, but there is no metacone. The styler shelf occupies the posterior half of the buccal edge of the crown; there is a styler cusp (stylocone) directly buccal to the paracone, and a lower elevation more posteriorly. The styler shelf is also present on P3/, though less developed, the stylocone being represented there by a swelling on the buccal surface of the paracone.

In KNM.SO 1417 the little-worn M1/ and M2/ show the metacone, as an elevation of the posterobuccal crest of the paracone (fig. 16A'). The metacone is in a similar position to that of *Potamogale*, but it is less distinct, as the groove that divides it from the paracone, for occlusion with the hypoconid, is not present in *Protenrec*. The protocone, which occupies about 30% of the width of the tooth, is also somewhat smaller than in *Potamogale*. On the buccal edge of the tooth there are a stylocone, directly buccal to the paracone and connected to it by a crest, and a lower styler cusp, posterior to the indentation of the margin (ectoflexus). The ectoflexus is more pronounced on M1/ in the Napak specimen than in those from Kenya. The posterobuccal (metastylar) apex of

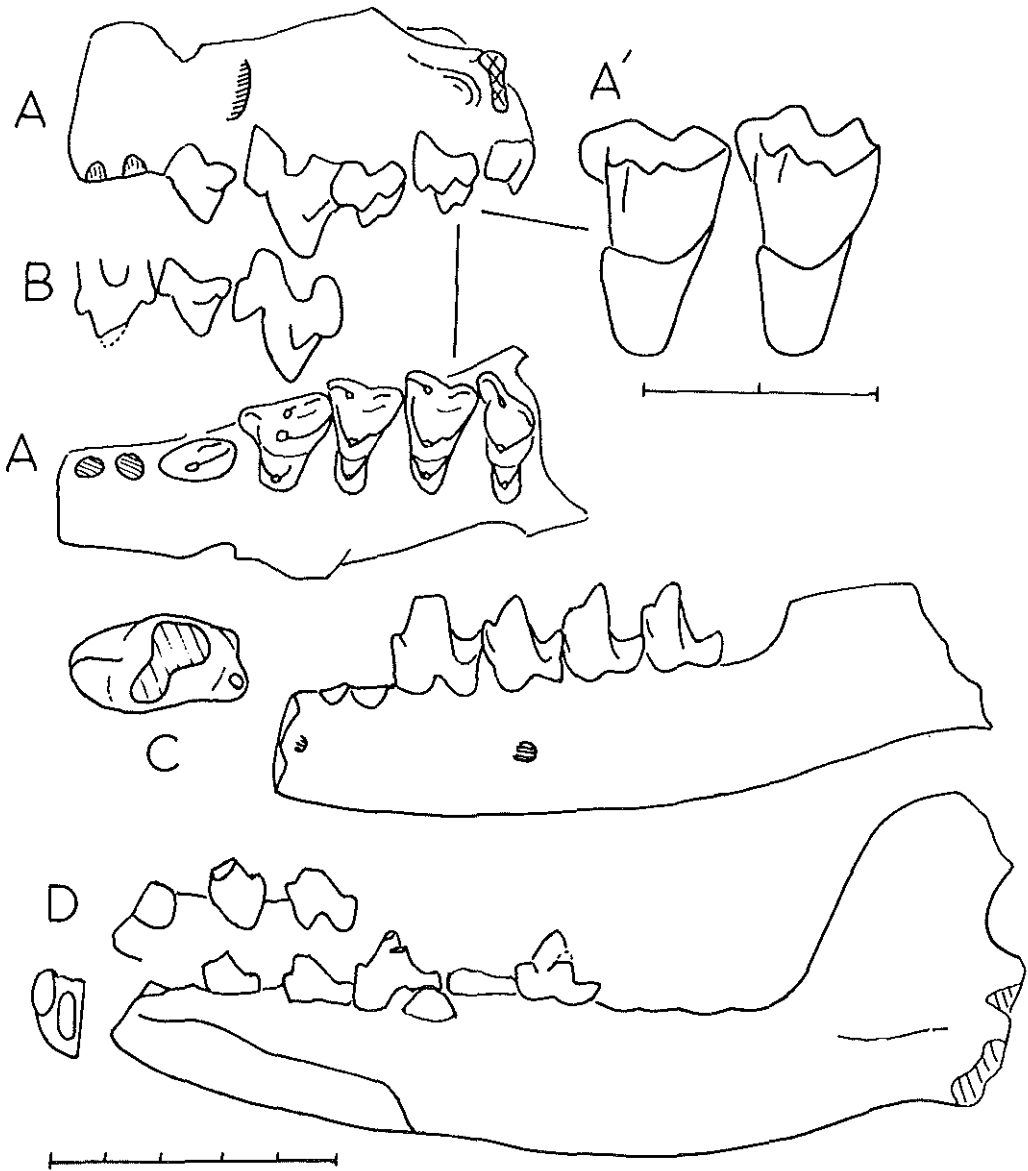


Fig. 16. — *Protenecc tricuspis*.

A, L maxilla, KNM.SO 1417. A', M1, 2/ of the same, oblique lingual view (larger scale).

B, LP2-4/, buccal view, KNM.SO 1420.

C, L mandible and crown view P/4 (larger scale), KNM.SO 1093.

D, Juvenile mandible, KNM.SO 1404: medial view, buccal view of dI/2-dP/2 (reversed), and anterior view showing bases of incisors.

M2/ projects less far laterally than the parastylar apex, unlike most living tenrecids. M3/ is variable in relative width and in the development of the posterobuccal apex.

The anterior part of the mandible is preserved in KNM.SO 1404 (Fig. 16C). M/3 of this specimen is unerupted, and all the antemolar teeth therefore probably belong to the milk dentition; in living tenrecids the permanent antemolars erupt only with or after M/3 (Major 1897). The crowns of the incisors have broken off. The root of Id/1 is flattened and close to the symphysis, and that of Id/2 is broader mediolaterally, but not enlarged as in *Potamogale*. Both teeth are procumbent. Id/3 is absent, but there is a space between Id/2 and the canine, and it is possible that the tooth is still unerupted.

The canine (dC) of KNM.SO 1404 is broken, but it is possible to see that it has a posterior basal cusp, absent from the permanent canine of Sgr 3120c.66. Both teeth are small: the permanent canine is only about as high as P/4. dP/2 of KNM.SO 1404 resembles P/2 of Rs 551.49; it has two roots, a forwardly leaning protoconid and anterior and posterior basal cusps. dP/3 is larger than dP/2 and it has a small metaconid like P/4. Beneath it can be seen the unerupted P/3 which has no metaconid. The corresponding tooth in Sgr 3120c.66 is probably dP/3 rather than P/3, as it has a metaconid (Butler 1969, fig. 7C) and P/4 of that specimen is incompletely erupted. dP/4 of KNM.SO 1404 is poorly preserved, but it appears to be molariform. Two additional examples of P/4 (KNM.CA 1537 and KNM.SO 1093) confirm that the metaconid is small and closely applied to the protoconid, and the paraconid is a low anterior cusp.

On M/1 and M/2 the talonid forms about one-third of the length of the tooth, rather less than in *Potamogale* though more than in other living tenrecids. The talonid basin lies towards the lingual side as in *Potamogale*, but the cusps are less differentiated. The trigonid is less compressed anteroposteriorly than in *Potamogale*; the paraconid is tilted forwards, it is less lingual than the metaconid, and it lacks the anterior basal cusp present in *Potamogale*. In agreement with *Potamogale*, the talonid of M/3 resembles that of M/2, apart from being a little narrower and more pointed posteriorly.

The teeth of the Napak specimens are larger than those from Songhor, Legetet and Rusinga, but the sample sizes are too small to justify a taxonomic distinction.

The skull fragment (KNM.LG 1493) (fig. 17) is broken off anteriorly at about the level of P3/ and posteriorly near the posterior end of the frontals. The left side of the face and the tooth-bearing part of the maxilla on the right side are missing, but a separate left maxillary fragment with P4/-M2/ probably belongs to this skull. The specimen provides information about the skull roof and the medial wall of the orbit.

Only the internasal and interfrontal sutures have closed. The united nasals reach posteriorly beyond the lachrymal foramina, and their posterior end is rounded, not narrowed to a point as in *Potamogale*. The supraorbital extension of the maxilla reaches to the same level as the nasals. The lachrymal is oval, with the foramen near its anterior end. The dorsal surface of the united frontals is flat, with no indication of the sagittal crest. There are no postorbital processes. Between the orbits the sides of the skull converge backwards towards a midcranial constriction at the posterior end of the frontals. The palate is damaged near its posterior end, but it shows the posterior palatine foramen on the left side and the anterior palatine foramen on both sides. A groove continues forward from the anterior foramen towards the maxillary suture. The sphenopalatine foramen is directly dorsal to the posterior palatine foramen. At the posterior end of the specimen a cast of the ventral part of the olfactory chamber is exposed. Next to this is the medial wall of the sphenorbital canal, its lateral wall having broken away. A foramen, probably the suboptic, opens into the canal medially, and dorsally there is a groove that probably represents the sinus canal. There does not

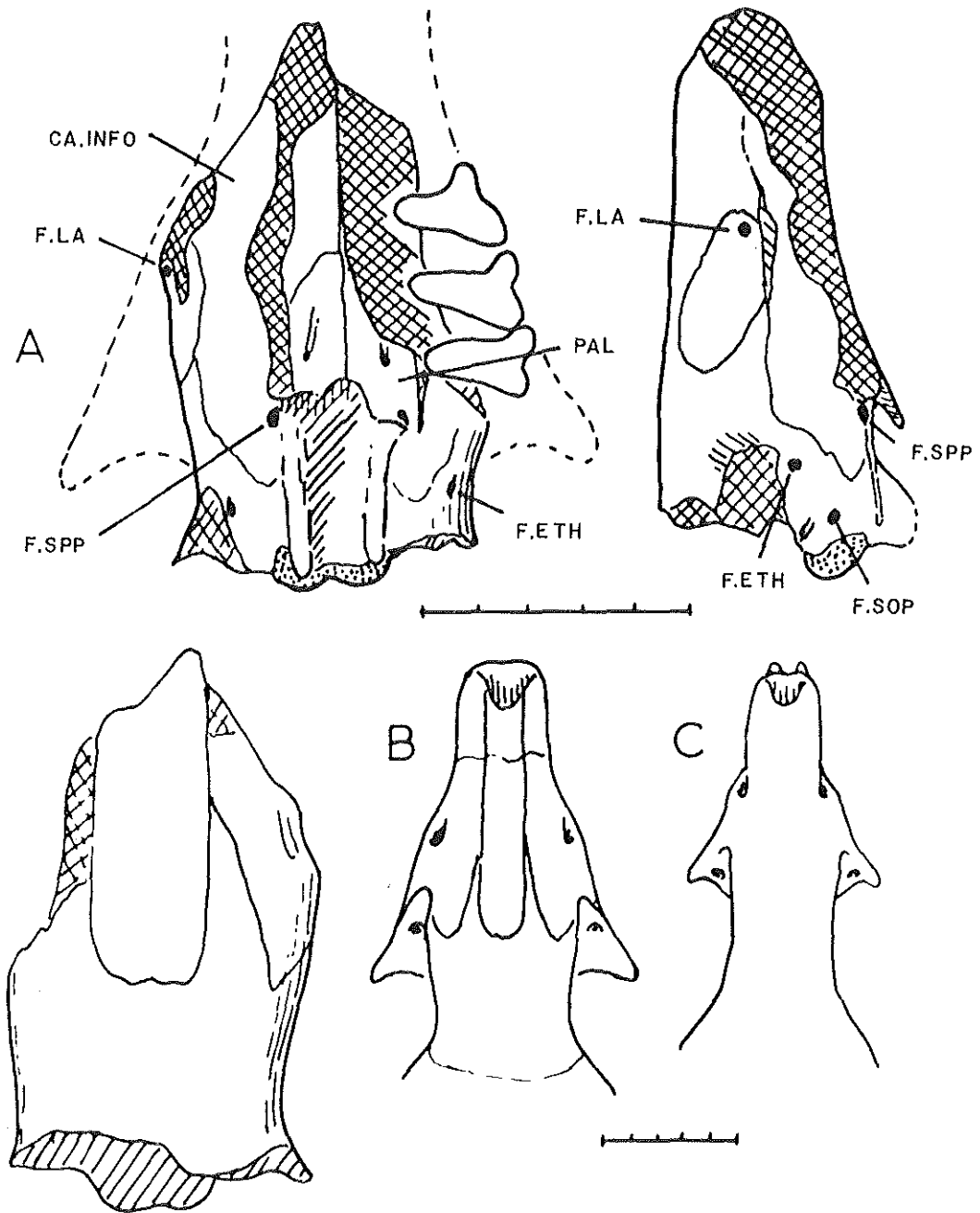


Fig. 17.

A, *Proteneq tricuspis*, skull fragment, KNM.LG 1493, ventral, lateral and dorsal views. Approximate position of P4/-M2/ indicated. Abbreviations: CA.INFO, medial wall of infraorbital canal. F.ETH, ethmoid foramen. F.LA, lachrymal foramen. F.SOP, suboptic foramen. F.SPP, sphenopalatine foramen. PAL, palate.

B, *P. tricuspis*, reconstruction of anterior part of skull.

C, *Geogale aurita* (recent) for comparison.

appear to be a separate optic foramen. A more anterior foramen, above the maxilla-frontal suture, is probably the ethmoid, in a similar position to that of living tenrecids. The maxillae from Legetet and Songhor confirm that the infraorbital canal is long, opening anteriorly to P4/ as in the specimen from Napak.

The coronoid process of the mandible is preserved in KNM.SO 1404, except that the posterior part of the top has broken off. Its anterior edge rises at an angle of 70° from the tooth row. The process is broad at the top, and its posterior edge is somewhat concave. The condyle is not preserved but was evidently low, as in living tenrecids. The mandibular foramen is far back, below the posterior edge of the coronoid process, as in *Micropotamogale* and *Geogale*. There is no masseteric fossa. Mental foramina are below P/2 and M/1. The symphysis is long, reaching to below P/3.

Relationships:

The only surviving Tenrecidae on the African continent are *Potamogale velox* and the two species of *Micropotamogale*, forming the subfamily Potamogalinae. They differ from the Madagascan tenrecids (Geogalinae, Oryzorictinae, Tenrecinae) in several derived characters, such as the loss of the clavicle and the greater ossification of the bulla. *Potamogale* departs from other living tenrecids in its molars, which retain the metacone and possess a relatively well developed protocone and talonid, and thus link the zalambdodont molar pattern with the tribosphenic pattern. Zalambdodonty is a derived character in insectivores (Butler 1972). *Protenrec* is intermediate between *Potamogale* and *Micropotamogale* in molar pattern, having a small metacone which is rapidly worn off. The metacone is a plesiomorphous character that does not denote special relationship; there is a trace of the cusp in some specimens of *Oryzorictes* (Major 1897).

Another primitive character of *Protenrec* is the long infraorbital canal, which it shares with *Geogale* (fig. 16 B,C). In all other living tenrecids, including the Potamogalinae, the infraorbital foramen has retreated to a position below the anterior margin of the orbit, above or posterior to M1/, and the canal has become a mere bridge (fig. 18 H). Shortening of the infraorbital canal took place in other insectivore families, and in Talpidae and Chrysochloridae it is bridge-like as in most Tenrecidae; the Erinaceidae retained a longer canal, and their infraorbital foramen is usually anterior to P4/. The short, bridge-like canal is a synapomorphy that the Potamogalinae share with the Madagascan tenrecids, with the exception of *Geogale*, but it is unknown whether this is due to common ancestry or to parallelism.

The intraorbital lachrymal foramen, with the associated strong antorbital crest, is a primitive character unique to *Protenrec* among Tenrecidae, but found also in Erinaceidae, *Centetodon*, Nyctitheriidae, *Nesophontes* and *Solenodon*. The antorbital crest is weak in *Geogale* and absent in *Potamogale*, but it is rather better developed in some species of *Microgale*, e.g. *M. majori* and *M. longicaudata*, in which it reaches to the anterior edge of the lachrymal foramen.

The mid-cranial constriction is a primitive character of *Protenrec*, shared with Erinaceidae, some Talpidae (e.g. *Desmana*) and *Solenodon*. There is a slight constriction in *Geogale* and *Limnogale*, but in other tenrecids the sides of the mid-cranium are parallel (Potamogalinae, *Nesogale*, *Paramicrogale*, Tenrecinae) or divergent (*Oryzorictes*, *Microgale*, *Leptogale*).

Living tenrecids differ in the relative sizes of the anterior teeth. I1/ and I2 are enlarged and the canines are premolariform in Potamogalinae, *Limnogale* and *Nesogale*, whereas the canines are enlarged in *Oryzorictes* and *Tenrec*. *Protenrec* had small

canines, at least in the lower jaw, and, to judge by the milk teeth, I/2 was probably only moderately enlarged. Its anterior dentition probably resembled that of *Microgale*, which may be regarded as representing the primitive tenrecid condition. *Geogale* differs from other tenrecids in that I/1 is larger than I/2.

Specialisation of P4/ to form a stabbing or puncturing tooth is a common insectivore adaptation, found in erinaceids, geolabids, soricids, nyctitheriids, *Solenodon* and *Nesophontes*. P3/ is then much smaller than P4/ and weakly molarised. This arrangement is present in *Protenrec*, *Geogale* and *Nesogale*, and it may be primitive for the family. In other tenrecids P3/ is more molariform; it is higher than P4/ in Potamogalinae (fig. 18 H), *Limnogale*, *Paramicrogale*, some species of *Microgale*, and especially in *Tenrec*, in which P3/ is much enlarged. At the same time P/3 becomes as high as P/4, and P/4 develops a paralophid, lacking in *Protenrec* and *Geogale*.

In Oryzoricinae the M/3 talonid is not reduced like those of the other molars, but it is elevated to form a crest that shears against the posterior side of M3/. Also, with the exception of *Limnogale*, the Oryzoricinae have an extended metastylar crest on M2/ that shears against the paralophid of M/3. In *Protenrec*, *Geogale* and the Potamogalinae the M/3 talonid functions against the M3/ protocone, and the metastylar apex of M2/ is less prominent, or not more prominent, than that of M1/.

Thus *Protenrec* seems to be not far removed from the tenrecid common ancestor. Though it shows the largest number of resemblances to *Geogale*, these are probably plesiomorphous, reflecting the retention of primitive characters by *Geogale*.

ERYTHROZOOTES BUTLER & HOPWOOD, 1957

Erythrozootes chamerpes BUTLER & HOPWOOD, 1957

Erythrozootes chamerpes, Butler & Hopwood (1957), pp. 24-28, fig. 8.
Cf. *Erythrozootes chamerpes*, Butler (1969), pp. 20-21, fig. 9.

Holotype: M 14314, facial part of skull with dentition, from Legetet Formation, 'Maize Crib' quarry.

Specimens identified:

Koru Formation.

Locality 25. KNM.LG 1542 (25/148), mandible with P/3, dP/4, M/1.

Locality 32. KNM.LG 1536 (32/268), mandible with M/2 and talonid of M/3.

Legetet Formation.

'Maize Crib' quarry. M 14236, holotype.

Locality 10. KNM.LG 1498 (10/884), maxilla, edentulous except for a broken P4/.

Kapurta Agglomerates.

Songhor. Sgr 2491.66, mandible with M/1-3; KNM.SO 1702 (Sgr 2186.66), mandible with M/3.

Napak.

Locality I. M 21831, mandible with P/4-M/3.

The cranium from 'Maize Crib' (M 14316) referred to this species by Butler (1969) is now identified as *Amphechinus rusingensis*.

Description:

There are only four teeth anterior to P3/ in the holotype. The missing tooth could be

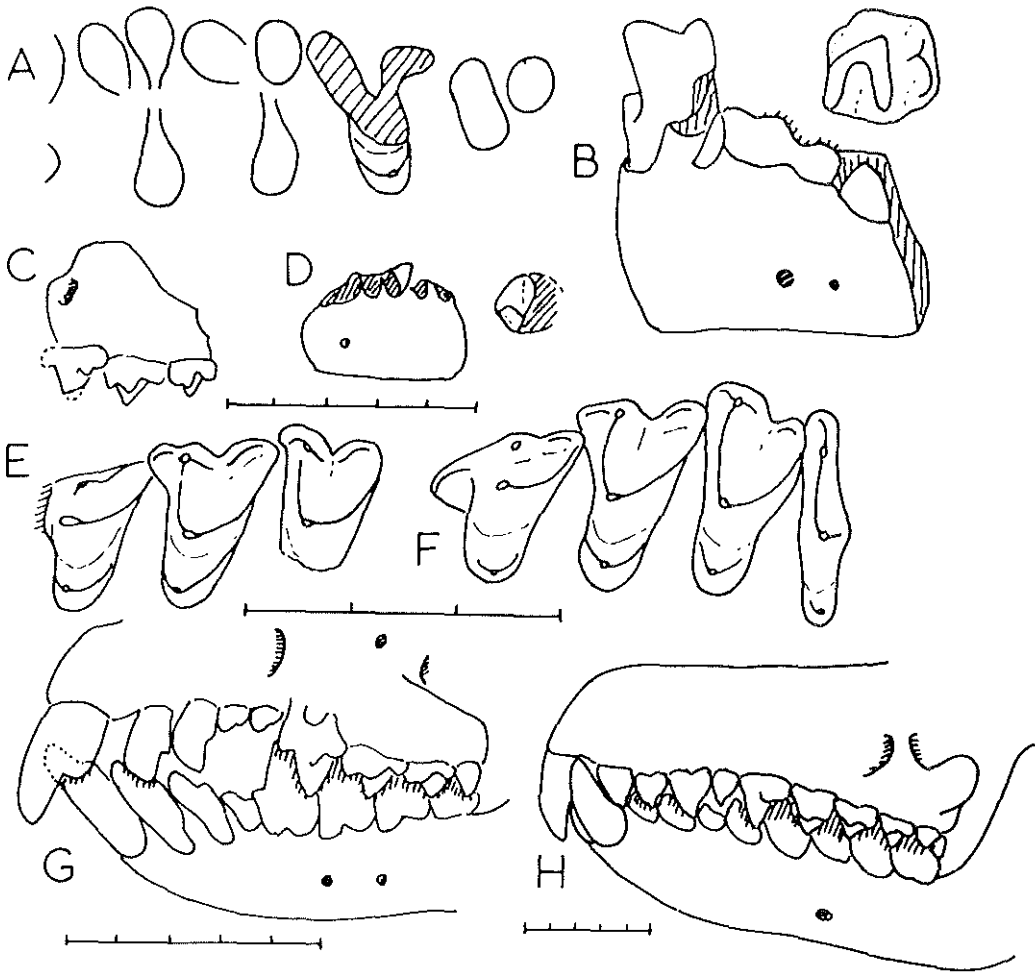


Fig. 18. — Tenrecidae.

A, B, *Erythrozootes chamerpes*: A, alveoli and broken P4/ of KNM.LG 1498; B, fragment with P/3 (unerupted)- M/1, and crown view of M/1, KNM.LG 1542.

C-E, *Parageogale aletris*: C, maxillary fragment, KNM.CA 1548; D, fragment of L mandible, and crown view of molar talonid, KNM.CA 2187; E, LP4/-M2/, KNM.CA 1548.

F, G, *Geogale aurita* (recent), BMNH 3.1.1.1: F, LP4/-M3/; G, teeth in occlusion.

H, *Micropotamogale lamottei* (recent), BMNH 73.170, teeth in occlusion. The large lower incisor (I/2) bites laterally to I1/, whereas in *Geogale* the large lower incisor (I/1) bites medially to I1/.

either I3/ or P2/ (P1/ is absent in all Tenrecidae). Unfortunately the premaxillary suture is not visible. The third tooth is slightly higher and more acutely pointed than the fourth, which is broader and slightly triangular in outline, giving some support to these teeth being the canine and P2/, in which case I3/ would be missing. In Recent tenrecids I3/ is the smallest upper tooth, and it is lost in *Geogale*, *Setifer* and *Echinops*.

KNM.LG 1498 (fig. 18 A) contains the alveoli of P3/, which show that the tooth was less widened than in the holotype, and that its lingual and posterobuccal roots were united, indicative of a lower level of molarisation.

KNM.LG 1542 (fig. 18 B) is a juvenile mandibular fragment with unerupted P/3, the base of dP/4 and a fractured M/1. P/3 consists of a single cusp, with no evidence of metaconid or paraconid, but the basal part of the tooth is uncalcified. dP/4 is equal in length to M/1 but narrower. M/1 shows some details of the unworn pattern. It is as broad as long, the paralophid is more transverse than in *Protenrec*, and the paraconid approaches the metaconid in height; on the talonid, which occupies one-quarter of the length of the tooth, there is a small hypoconid and a still more rudimentary entoconid.

The maxilla, KNM.LG 1498, agrees with the holotype. The infraorbital foramen is above the posterior end of P4/, and the posterior opening of the infraorbital canal is opposite the M1/-M2/ contact. The lachrymal foramen is large and opens on the face. The mandible KNM.LG 1542 has two mental foramina placed closely together: a large foramen under dP/4 and a smaller one anterior to it.

Relationships:

The first upper incisors are large, close together and vertical, as in *Potamogale*, not spaced apart and procumbent as in *Geogale*. By analogy with *Potamogale*, I/2 was probably enlarged. The upper dentition anterior to P3/ is shortened: a tooth (? I3/) has disappeared, and the remaining teeth are all one-rooted, whereas in *Potamogale* the canine and P2/ have two roots. P3/ is less molariform than in *Potamogale*, P4/ resembles *Protenrec* in being the most elevated of the cheek teeth and P/4 lacks a paralophid. The molars are more transverse than in *Protenrec*, and they resemble those of *Micropotamogale* in proportions and in the absence of the metacone. They have the same relation to the orbit as in *Protenrec*, whereas in Potamogalinae they are placed more anteriorly. The infraorbital canal is shorter than in *Protenrec* but much longer than in Potamogalinae. An antorbital crest is present, but it does not pass the lachrymal foramen, which opens on the face; in Potamogalinae the antorbital crest and lachrymal foramen are both absent. The sides of the cranium between the orbits converge backwards as in *Protenrec*, indicating a mid-cranial constriction.

Despite some resemblance in the molars and anterior incisors, *Erythrozootes* is not related to the Potamogalinae. It shares a number of primitive features with *Protenrec*, and it is provisionally included in the Protenrecinae, but it represents an independent line of advance which might justify a subfamily distinction.

Subfamily GEOGALINAE TROUESSART, 1879

PARAGEOGALE nov. gen.

Diagnosis: Differing from *Geogale* as follows: P2/ absent; molars with a trace of the metacone; metastylar lobe of M2/ less reduced; palate extending far behind M3/; infraorbital foramen above paracone of P4/.

Type species: *Geogale aletris* BUTLER & HOPWOOD, 1957.

Parageogale aletris (BUTLER & HOPWOOD, 1957)

Geogale aletris, Butler & Hopwood (1957), pp. 17-21, fig. 6.

Holotype: M 33046 (Rs 764.50), the facial part of a skull, from Hiwegi Formation, locality R 3.

Specimens identified:

Kapurta Agglomerates. Chamtwara. KNM.CA 1548 (34/698), maxilla with P4/-M2/; KNM.CA 2187 (34/1414), mandible with molar talonid; 34/698, edentulous mandible.

Hiwegi Formation. Locality R 3. M 33046 (Rs 764.50), holotype.

Description:

KNM.CA 1548 shows features of the cheek teeth, poorly preserved in the holotype. P4/ resembles *Geogale* and *Protenrec*. The paracone, of which the tip is missing, must have been higher than on M1/. It has a strong posterior crest but no anterior crest; the parastyle has broken off, but the scar shows that it was low. There is a stylocone, partly merged into the buccal surface of the paracone, and a lower posterior style. The protocone occupies about one-third of the width of the tooth through the paracone. M1/, which is complete, is a little less compressed longitudinally than in *Geogale*, and resembles the Napak specimen of *Protenrec*. The posterior crest of the paracone has an angulation at the position occupied by the metacone in *Protenrec*. The parastyle is followed by a stylocone, which is connected by a crest with the paracone, and posterior to the ectoflexus there is a low elevation of the styler ridge. The protocone occupies 28% of the width of the tooth (24% in *Geogale*). M2/ is shorter than M1/, and its metastylar lobe is less prominent, though not as much reduced as in *Geogale*. The protocone of M2/ is not preserved. The infraorbital foramen is small. As in the holotype, it is situated above the paracone of P4/, and farther removed from the teeth than in *Geogale* and *Protenrec*.

The fragments of mandible from Chamtwara are referred to *Parageogale* because of their small size. KNM.CA 2187 (fig. 18 D) contains the roots of three two-rooted teeth, interpreted as P/4-M/2, of which only the talonid of M/1 is preserved. This occupies one-quarter of the estimated length of the tooth. It bears a cusp, from which a low crest runs anteriorly and somewhat lingually, marking off a lingual talonid basin as in *Protenrec*. The other fragment has seven alveoli and part of an eighth, probably for P/4-M/3. In both specimens the mental foramen is below P/4; in *Protenrec* it is below the anterior root of M/1, and in *Geogale* there are foramina below M/1 and M/2.

Relationships:

Parageogale resembles *Geogale* in the enlarged, widely separated first incisors, and in the absence of I3/. In *Geogale* the gap between the first upper incisors receives the tips of the first lower incisors when the jaws close (fig. 18 G). P4/-M3/ of *Parageogale* are much like *Geogale* except that the protocone of M1/ is slightly larger, there is a trace of the metacone, and the metastylar apex of M2/ is less reduced: these are approaches to *Protenrec*. In the skull, *Parageogale* resembles *Protenrec* and *Geogale* in the long infraorbital canal, but the foramen is a little farther back, above P4/ instead of anterior to it, and higher on the face. The sides of the interorbital part of the skull converge posteriorly, indicating the presence of mid-cranial constriction, as in *Protenrec*.

Parageogale is related to *Geogale* but it has some primitive characters that it shares with *Protenrec*. At the same time it diverges from both *Geogale* and *Protenrec* in some ways, including the loss of P2/ and the backward extension of the palate.

Family **CHRYSOCHLORIDAE** GRAY, 1925

Subfamily **PROCHRYSOCHLORINAE** nov.

Diagnosis: Primitive Chrysochloridae in which M2/ is the widest molar, the upper molar protocones are V-shaped, M/1 and M/2 talonids approach the trigonids in length, M/3 talonid is longer and higher than that of M/2, deciduous teeth are replaced early in life, and the mid-cranial base is proportionately narrower than in the modern species.

PROCHRYSOCHLORIS BUTLER & HOPWOOD, 1957

Prochrysochloris miocaenicus BUTLER & HOPWOOD, 1957

Prochrysochloris miocaenicus, Butler & Hopwood (1957), pp. 11-17, figs. 4,5; Butler (1969), pp. 29-34, fig. 11.

Holotype: M 34151 (Sgr 638.49), facial part of skull, from Songhor.

Specimens identified:

Legetet Formation.

Maize Crib quarry. M 14236, facial part of skull (paratype).

Locality 10. KNM.LG 73 (10/103), right side of facial skull, and KNM.LG 72 (10/241), snout (one individual); KNM.LG 1491 (10/585), maxilla with P4/-M2/; KNM.LG 1552 (10/961), maxilla with P4/-M3/; 4 edentulous mandibular fragments.

Locality 29. 29/1155, maxillary fragment with dP3/,4/; KNM.LG 1523 (29/335), edentulous mandible.

Kapurtay Agglomerates.

Chamtwara. KNM.CA 2065 (34/726), maxilla with P4/, M1/; KNM.CA 2057 (34/1572), mandible with M/1; KNM.CA 1520 (34/698), isolated lower molar; 3 edentulous mandibles.

Songhor. M 34151 (Sgr 638.49), facial skull (holotype); KNM.SO 1092 (Sgr 144.72), partial skull with mandible; KNM.SO 1412 (Sgr 306.72), facial skull with P3/-M3/; KNM.SO 1414 (Sgr 1423.66), maxilla with P3/-M1/; Sgr 598.66, facial skull with mandibles; KNM.SO 4844 (Sgr 183.62), mandible with M/3; KNM.SO 4119 (Sgr 3879.66), edentulous mandible.

Description:

The upper cheek teeth are best preserved in KNM.SO 1412, a partial skull with right P3/-M2/ and left P4/-M3/ (fig. 19 A). P3/ has an extended metastylar apex but no parastyle. The styler ridge is confined to the posterior half of the buccal edge, and the stylocone is absent, together with the buccal crest of the paracone (paracrista). The protocone is smaller than on P4/ and the molars, and in KNM.LG 65 it is absent. P4/ is transversely wider than P3/. It has a small parastyle, and the styler ridge is complete, though the stylocone and paracrista are weakly developed. On M1/ and M2/ the parastyle is high, and it projects anteriorly, as in *Amblysomus hottentotus*. The stylocone is united with the parastyle, and there is a lower posterior style. On the middle part of the styler ridge of M1/ are three minor cuspules or crenulations, and one is present on M2/; similar cuspules occur in Recent chrysochlorids. The metastylar apex of M1/ is somewhat less prominent buccally than the parastyle; it is more reduced on M2/ and absent on M3/. The height of the paracone is reduced on M2/ and M3/, but that of the protocone is maintained, so that on M3/ the paracone and protocone are equal. The protocone is V-shaped, and on M1/ and M2/ it occupies one-third of the width of the tooth.

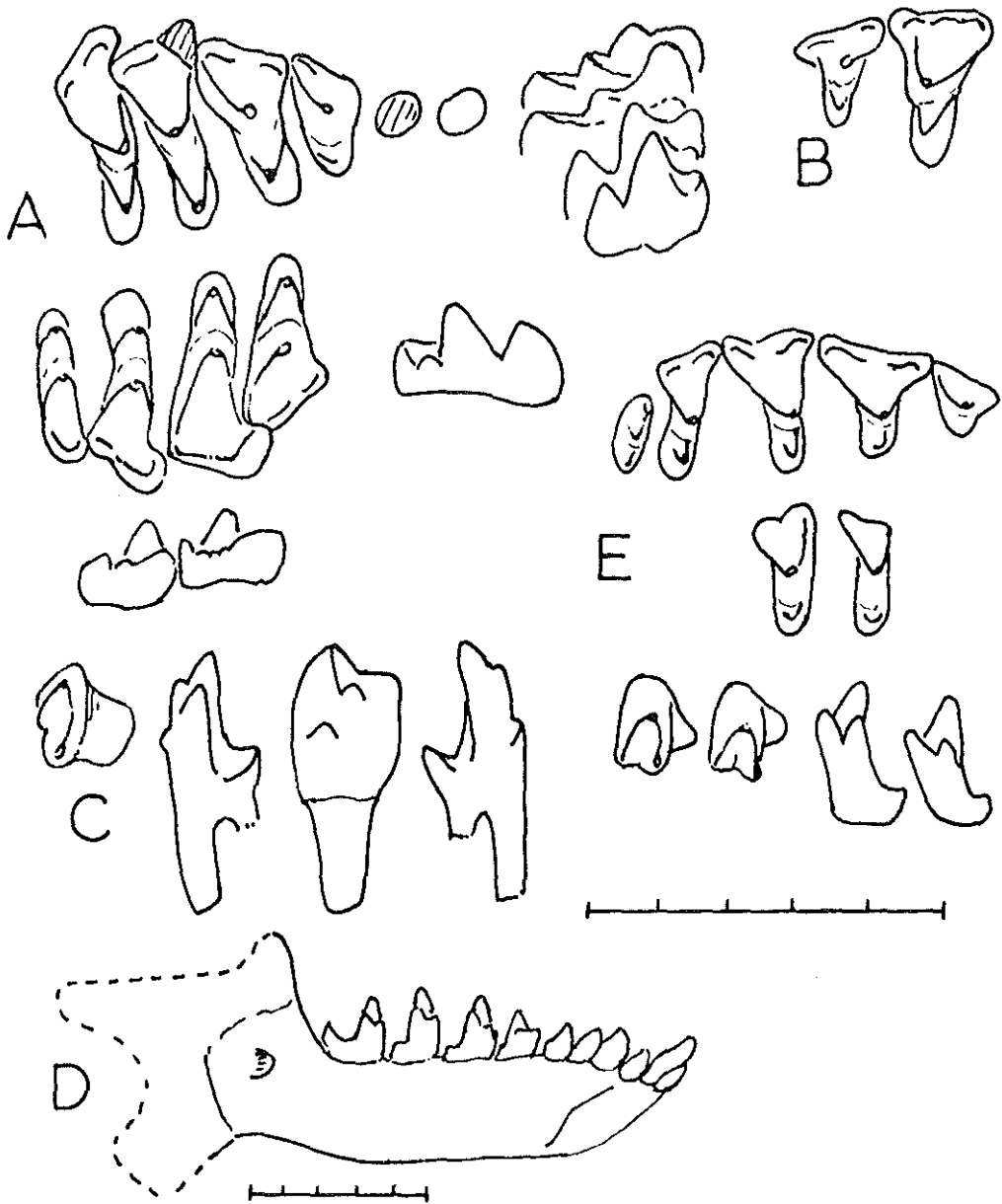


Fig. 19. — *Prochrysochloris miocaenicus*.

A, KNM.SO 1412: RP3/-M2/ and LP4/-M3/, crown view; RP3/-M2/, anterior view; LP4/, anterior view; LM1,2/, buccal view.

B, 29/1155, dP3,4/.

C, lower molar, KNM.CA 1520: crown, lingual, anterior and buccal views.

D, reconstruction of mandible.

E, teeth of *Amblysomus iris corriae* (recent) for comparison: RdP2/-M2/, RP3,4/, RdP/4-M/1 (crown and lingual views).

Two edentulous specimens show two alveoli for P/4, but in three others the alveoli are united. KNM.CA 1520 (fig. 19 C) is an isolated M/1 or M/2 that is quite unworn. The trigonid is high and much compressed anteroposteriorly, the angle between its crests being about 40°. The paraconid is more reduced and less lingual in position than in Recent chrysochlorids (fig. 19 E). The talonid, which is nearly as long as the trigonid, carries a single cusp near the middle of the posterior border. There is a fragment of cingulum anterior to the protoconid. On M/3 (KNM.SO 1702) the talonid is narrower and its cusp more elevated.

A maxillary fragment from Legetet (29/1155) contains dP3/ and dP4/ (fig. 19 B); the germ of P4/ is exposed on the broken posterior surface of the specimen. The milk teeth are similar in length to the corresponding premolars, but they are less widened, their metastylar apices are less prominent, and the parastyles are developed as on the molars. dP3/ has a protocone, and on dP4/ the stylocone is as high as the posterior stylar cusp. KNM.SO 9814, in which M/3 is unerupted, contains the alveoli of dP/3 and dP/4. These show that the milk molars were narrower than the premolars, the root of dP/3 was partly divided, and dP/4 was two-rooted and similar in length to M/1. In Recent chrysochlorids replacement of the milk dentition takes place only after the adult size has been reached, and most museum specimens contain milk teeth (Leche 1904, Thomas & Schwann 1906, Broom 1908). There are 12 specimens of *Prochrysochloris* with premolars but only two with milk molars, and replacement must have occurred earlier in life.

Seven skulls are now known, but in all of them only the anterior part is preserved. All have permanent premolars. The internasal, interfrontal and maxilla-premaxilla sutures are closed in all the skulls; the maxilla-nasal and maxilla-frontal sutures are open in four specimens, and closed in three.

The infraorbital canal is preserved in KNM.LG 63 (fig. 20 A). It is not as short as in the living species, its length being a little less than the vertical diameter of the infraorbital foramen. The antorbital crest is stronger than in the living species. Although the zygomatic arch is not preserved, a broken surface, lateral to the posterior opening of the infraorbital canal, shows that the anterior root of the arch has the same relation to the canal as in other chrysochlorids. Above M2/ there is a scar for muscle attachment (? external masseter) which occurs also in the living species.

KNM.SO 1092 shows the middle part of the base of the skull, and the specimen has been prepared to reveal the interior of the basicranium anterior to the ear region (fig. 20 C). Unfortunately, except for a minute portion of the middle ear chamber, the ear region itself is not preserved. The posterior edge of the palate lies 1.5 mm behind M3/. The palatal crest is represented, as in Recent chrysochlorids, by a pair of prominences on the palatine bones. The ectopterygoid process of erinaceids is represented, as in Recent chrysochlorids, by a flange which passes below the sphenopalatine foramen and is continuous posteriorly with the lateral edge of the sphenorbital foramen. A lateral process is developed midway along the flange; this is also present in some living forms such as *Chrysochloris* and *Eremitalpa*, in which it extends the area of origin of the lateral pterygoid muscle. Ventrally and posteriorly to the sphenorbital foramen the floor of the braincase is thickened and filled with cancellous bone. The foramen ovale, which is well removed from the sphenorbital foramen, as in *Amblysomus hottentotus*, leads from a canal through the cancellous bone for the mandibular nerve. The length of the mid-cranium, measured from the foramen ovale to the sphenopalatine foramen, is 46% of the length of the palate, within the range of the living species (34-50%), but the width across the sphenorbital foramina, compared with the width of the palate across the

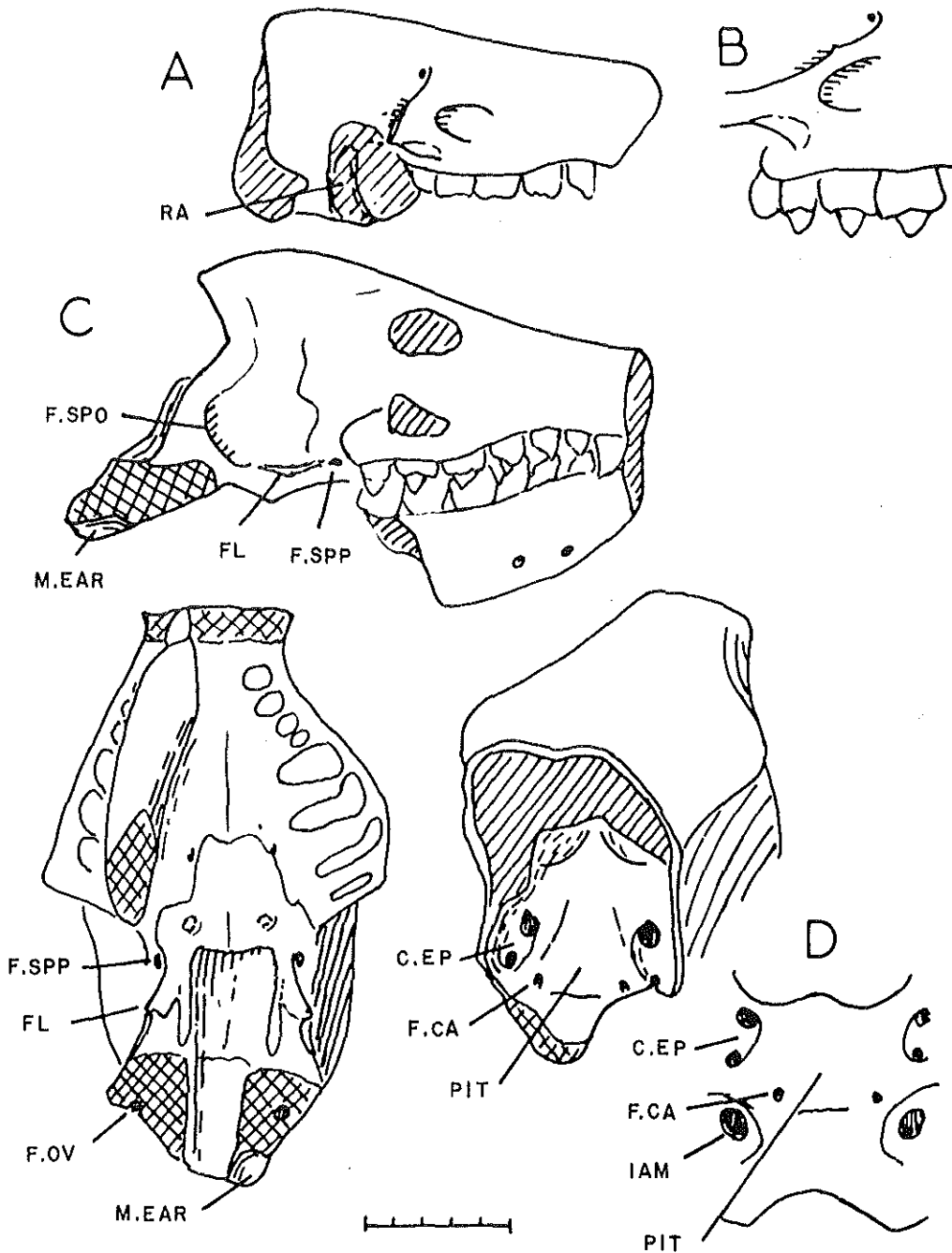


Fig. 20.

A, *Prochrysochloris miocaenicus* skull, KNM.LG 63, showing infraorbital canal.

B, infraorbital canal of *Amblysomus duthiae* (recent), for comparison.

C, *Prochrysochloris miocaenicus*, KNM.SO 1092: lateral and ventral views, and floor of mid-cranium.

D, *Amblysomus hottentotus* (present), floor of mid-cranium, for comparison.

Abbreviations: C.EP, cavum epiptericum. F.CA, carotid foramen. F.OV, foramen ovale. F.SPO, sphenorbital foramen (lacerum anterius). F.SPP, sphenopalatine foramen. FL, flange on lateral pterygoid process. IAM, internal auditory meatus. M.EAR, fragment of middle ear chamber. PIT, pituitary fossa. RA, impression of ascending ramus of mandible.

cheek teeth, is less (50%, compared with 70-90% in the living species). The interior of the mid-cranial floor, exposed in KNM.SO 1092, confirms this difference. There is a shallow pituitary fossa, bounded posteriorly by a low but distinct dorsum sellae, on either side of which are the carotid foramina, as in *A. hottentotus* (fig. 20 D). However, the cavities for the gasserian ganglia (cava epipterica), on either side of the pituitary fossa, are not so widely separated as in *A. hottentotus* and other Recent chrysochlorids, the internal opening of the foramen ovale being much nearer to the carotid foramen. In the Recent forms the basicranium between the olfactory and auditory capsules is proportionately shorter and wider than in *Prochrysochloris*, as if longitudinally compressed.

The lower jaw can be partly reconstructed from fragments (fig. 19 D), but nothing is known of the condylar and angular processes. The lower edge of the horizontal ramus reaches its lowest level below M/2-3, instead of under the premolars as in the Recent species. The position of the mental foramina varies: the anterior one is under P/3 or P/2, the posterior one under the anterior root of M/1 or the posterior root of P/4. In KNM.LG 1523 the posterior foramen is doubled. A mould in KNM.LG shows that the ascending ramus rises perpendicularly from the line of the teeth, closely behind M/3, and it is tilted laterally. The mandibular foramen, seen in KNM.SO 1702, is in line with the teeth and closer to M/3 than in most living species, but it agrees with *Chrysochalax villosus*.

Relationships:

Prochrysochloris differs from all living chrysochlorids in the more posterior emphasis of the cheek teeth, in which M2/ is the widest molar, M3/ and M/3 are comparatively large, P2/ is not molariform, and P3/ and dP3/ are proportionately smaller and less molariform than in living species. The protocone and talonids of the molars are less reduced, and there is an anterobuccal cingulum on the lower molars. The milk dentition was replaced earlier in life. In the skull, the bridge that represents the infraorbital canal is broader, and the midcranial base is less widened. Although all these characters are very probably primitive, the wide difference between *Prochrysochloris* and the living genera demands its separation at the subfamily level.

The comparatively short, broad palate of *Prochrysochloris* may not be primitive. What are believed to be the most primitive living species (Petter 1981), such as *Chrysochalax trevelyani*, *Amblysomus hottentotus* and *A. (Chlorotalpa) duthiae*, have longer palates, with length/width indices in the range 140-155 (Length is measured from the anterior margin of the I1/ alveolus; width is the greatest width across the cheek teeth). The index in *Prochrysochloris* is 113, similar to *Chrysochloris asiatica*, *Eremitalpa granti* and *Amblysomus obtusirostris*, which are in the range 105-125. The species with short palates are divergent in dental morphology, and they have probably been derived independently from forms with long palates. The length of the midcranial base, between the palate and the auditory bulla, is reduced in species with short palates. This would affect the orientation of the pterygoid muscles, and it might explain the development of the process on the lateral pterygoid flange, present in *Prochrysochloris* and living species with short skulls, but absent or rudimentary in long-skulled species.

Order CHIROPTERA BLUMENBACH, 1779

Family PTEROPODIDAE GRAY, 1821

Subfamily PROPOTTININAE nov.

Diagnosis: Lower molars with low relief and poorly differentiated cusps, but posterior trigonid crest retained, and talonid not shortened; M/3 less reduced than in other Pteropodidae, and M3/ probably present; mandible fairly robust.

PROPOTTO SIMPSON, 1967

Propotto leakeyi SIMPSON 1967

Propotto leakeyi, Simpson (1967), pp. 50-51, Pl. i; Walker (1969), pp. 647-648.

Holotype: KNM.SO 508 (Sgr 391.49), mandible with P/3-M/2, from Songhor.

Specimens identified:

Koru Formation.

Locality 25. KNM.KO 101 (25/61), left mandible with P/3-M/3. This is a little larger than the holotype (P/3-M/2 16.5 mm; 14 mm in the holotype), and it differs in some details of the teeth.

Kapurtay Agglomerates.

Chamtwara. KNM.CA 1999 (34/1526), isolated M/1 or M/2.

Songhor. KNM.SO 508 (Sgr 391.49), mandible with P/3-M/2 (holotype; Simpson's specimen R); KNM.RU 2084 (Rs 1.58), mandible with M/2,3 (Simpson's specimen T; not from Rusinga).

Hiwegi Formation.

Locality (?) R 1. KNM.RU 1879 (Rs 579.49), mandible with P/3-M/3 (Simpson's specimen S).

Locality R 3 A. KNM.RU 3690 (Rs 517.49), right mandible with P/3,4 and base of canine.

Description (fig. 21 A-C):

The upper dentition and the lower incisors are unknown. The base of the lower canine is preserved in KNM.RU 3690, and the root is visible in cross-section on the anterior broken surface of the Koru specimen. The canine is relatively larger than in living pteropodids: its greatest diameter is about equal to the length of M/1, and its root reaches at least to below P/3. P/2, known only by its single root, is a small tooth, separated by a short gap from P/3. The protoconid of P/3 is the highest cusp of the post-canine dentition. It is more elevated in the Koru specimen than in the holotype and in KNM.RU 3690, but the difference may be due to wear. There is an anterior crest which is continuous with an anterolingual cingulum. A posterolingual crest, present in the specimens from Songhor and Rusinga, is weak in the Koru specimen. Except for very slight indications in the holotype, paraconid and metaconid are absent. The talonid is short, resembling a wide posterior cingulum, and it bears a low cusp (hypoconid) towards the buccal side. A posterior crest of the protoconid, weak in the Koru specimen, runs to the hypoconid. In the Koru specimen there is a fragment of buccal cingulum near the posterior end of the tooth. P/3 has two roots.

P/4 is quite unworn in KNM.RU 1879 (Simpson's 'S'), in which P/3 is in process of eruption. Compared with P/3, P/4 is more molariform; the protoconid is less elevated;

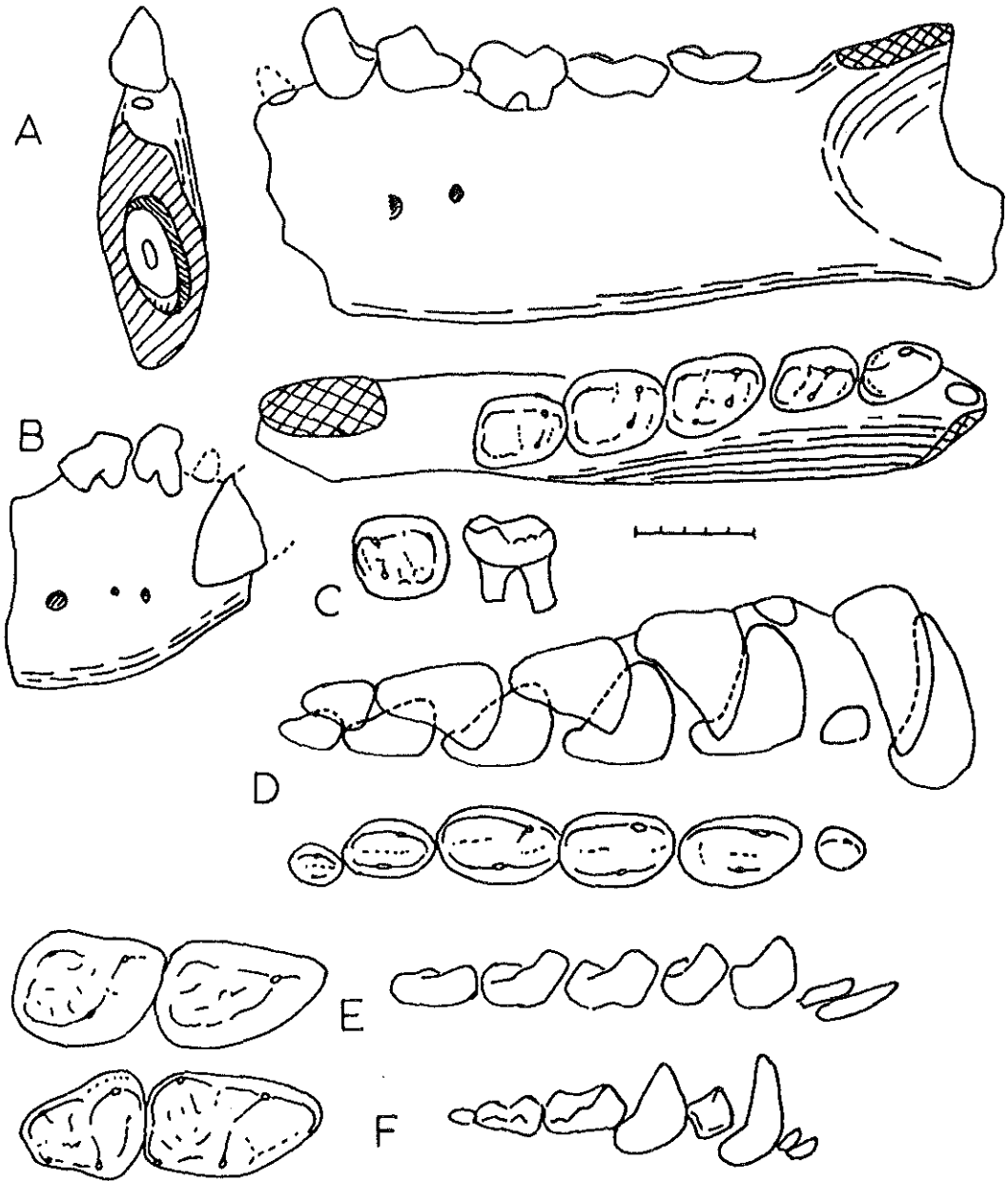


Fig. 21.

A-C, *Propotto leakeyi*. A, KNM.KO 101, L mandible with P/3-M/3, buccal and crown views, and anterior view showing canine root; B, KNM.RU 3690; C, KNM.CA 1999.

D, *Pteropus conspicillatus* (recent), R teeth in occlusion, and LP/2-M/3, crown view.

E, *Cheirogaleus major* (recent), LM/1,2 crown view, and L lower dentition, lingual view.

F, *Artibeus planirostris* (recent), the same.

there is a weakly indicated metaconid on the posterolingual ridge of the protoconid; the anterolingual cingulum is more extensive, reaching to the base of the metaconid, and its edge is crenulated. The talonid is larger; its margin is differentiated into a number of blunt crenulations, of which the most buccal one, representing the hypoconid, is the highest and most distinct.

M/1 and M/2 are longer and wider than P/4. They vary in proportions: M/1 of KNM.RU 1879 is transversely broader than other specimens. Most of the crown is occupied by the shallow talonid basin; the trigonid basin is narrow and oblique, bordered anteriorly by a crenulated paralophid which corresponds to the anterolingual cingulum of the premolars. The protoconid is low and obtuse. The metaconid is weakly differentiated, and posterolingual to the protoconid, the two cusps being joined by a low crest. The hypoconid is the most distinct of the talonid cusps; it is a little lower than the protoconid, and it occupies rather less than half of the buccal side of the crown. There are a number of crenulations on the posterior and lingual edges of the talonid. A short anterobuccal cingulum is present on KNM.RU 1879. M/3 is smaller than M/2, but not as reduced as in living pteropodids, in some genera of which it has been lost. It has a large talonid basin like the other molars, and the posterior margin is somewhat elevated, representing the enlarged hypoconulid of other mammals. This talonid must have functioned against M3/, a tooth which has been lost in the living forms. KNM.RU 1879 contains an unerupted M/3 in a crypt; in this specimen P/3 is in process of eruption and P/4 is in place but unworn.

The ramus of the mandible is deeper and more stoutly constructed than in the living forms. The symphysis reaches to below P/4, whereas in the living forms it does not extend beyond the anterior end of P/3. The masseteric fossa, seen in the Koru specimen, is deeper. KNM.RU 3690 has a foramen under the posterior end of P/4 and two smaller ones farther forward; the Koru specimen has two foramina under P/4.

Relationships:

Originally described as a loroid primate, *Propotto* was recognised as a pteropodid by Walker (1969). It resembles the less specialised of the living fruit-bats such as *Pteropus* in the general organisation of the dentition: large canine; small P/2; protoconid height diminishing from P/3 backwards; metaconid displaced posteriorly in relation to the protoconid. However, the structure of M/3 indicates that M3/ was retained. As Walker (1969) pointed out, the molars show traces of the tribosphenic pattern lost in living pteropodids. A protoconid-metaconid crest divides off the small trigonid basin from the large talonid basin, whereas in modern forms the basins are replaced by a longitudinal valley passing along the length of the tooth, although the metaconid-protoconid connection may persist on the premolars. The hypoconid is still distinct in *Propotto*, but absent or very rudimentary in modern forms; the cusp posterior to the protoconid in *Pteralopex* and *Hypsognathus* is a protostylid. The development of minor cuspules and crenations in *Propotto* contrasts with the simple patterns and smooth enamel of living pteropodids.

In their low relief and loss of cutting edges the molars of *Propotto* resemble those of frugivorous primates such as *Perodicticus*, *Cheirogale* and *Pithecia*, and there is also a resemblance to the phyllostomatid *Artibeus* (fig. 21 E,F). Such teeth function by crushing, irregularities of the surface preventing slipping of the food. The molars of *Pteropus* and other modern pteropodids are constructed in a different way, with a longitudinal median valley flanked by buccal and lingual ridges (fig. 21 D). On the lower molars the ridges are formed by the protoconid and metaconid, and on the upper

molars by the paracone and protocone; the talonid and metacone are reduced. These bats feed by extracting the juices from soft, pulpy fruits, whereas *Artibeus* can eat hard, unripe figs, and *Chirogaleus* and *Perodicticus* are partly insectivorous. It would appear that *Propotto* was capable of dealing with more resistant material than modern pteropodids, and the robustness of its mandible is consistent with this interpretation. Among phyllostomatids, *Sturnira* seems to be adaptively similar to *Pteropus*, though the posterior cusps (metacone, hypoconid) take part in the formation of the ridges.

What little is known of the dentition of *Archaeopteropus transiens*, from the Oligocene of Italy, indicates a considerable difference from *Propotto*. The lower molar drawn in side view by dal Piaz (1937) has high, acute cusps, and it has been compared by Slaughter (1970) with *Harpionycteris* and *Pteralopex*, which he regards as retaining primitive features of the molar pattern. In these modern forms elevation of the cusps and the development of additional cusps (protostylid, metastylid) may be derived features, adapted to piercing the skins of fruits; similar features are present also in *Hypsiphanthus*. Supposedly pteropodid characters of *Archaeopteropus*, such as the second claw on the wing, are primitive chiropteran characters found in *Icaronycteris*, and Russell & Sigé (1970) tentatively included the genus in the Icaronycteridae. If they are followed, *Propotto* would be the oldest known pteropodid. However, Smith & Storch (1981) maintain that *Archaeopteropus* is a pteropodid.

It is unlikely that *Propotto* is ancestral to the living genera. While its molar pattern could be regarded as representing an earlier stage in the evolution of frugivory, much change would be needed to produce the modern pattern: loss of the talonid, and development of the longitudinal groove between the protoconid and the metaconid. Despite differences of detail, all the living forms have this basic pattern. There are more than 20 living genera, and the geographical range extends from Africa to Samoa. It seems unlikely therefore that the common ancestor was as late as the Miocene. The greatest generic diversity is in South-east Asia, suggesting that this may have been the area of origin. The living African genera fall into three distinct groups (classification of Koopman & Jones 1970): (1) the 8 genera of the tribe Epomophorini, confined to Africa; (2) 3 genera of the subtribe Rousettina, tribe Pteropini, one of them (*Rousettus*) widely distributed in Southern Asia and reaching the Solomon Is.; (3) one genus of Macroglossinae, a subfamily of otherwise Indo-Australian distribution. These groups probably represent three invasions from Asia. *Propotto* is interpreted as belonging to an extinct side-branch from the pteropodid stem, and a new subfamily Propottinae is proposed to include it.

Pteropodid humeri

Chiropteran humeri are known from the East African Miocene by fragments in which only the proximal or the distal end of the bone is preserved.

Proximal end:

Kapurta Agglomerates, Chamtwara. KNM.CA 1117 (34/653); KNM.CA 2156 (34/897); KNM.CA 2190 (34/1418c).

Songhor. KNM.SO 5533 (Sgr 3030.66).

Distal end, type A:

Kapurta Agglomerates, Chamtwara. KNM.CA 2178 (34/1101); KNM.CA 2199 (34/1599).

Songhor. KNM.SO 1400 (Sgr 546.72).

Distal end, type B (? same species as proximal end):

Kapurta Agglomerates, Chamtwara. KNM.CA 2197 (34/1538).

Description:

Proximal ends identified as Pteropodidae are similar in size and structure and probably represent one species (fig. 22 A). The width across the trochanters is 4.3 - 4.5 mm, the width of the head is 2.5 - 2.7 mm, and the width of the shaft is 2.15 - 2.25 mm. These measurements are 80-84% of those of a specimen of *Cynopterus sphinx*.

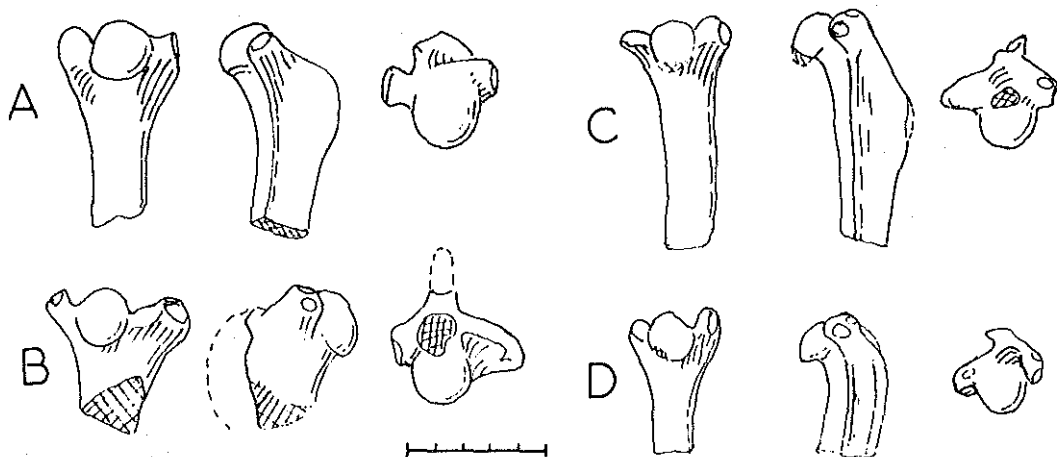


Fig. 22. — Proximal humeri, posterior, lateral and proximal views.

A, Pteropodidae, KNM.SO 5533.

B, Emballonuridae, KNM.SO 5523.

C, Hipposideridae, KNM.CA 1124.

D, Vespertilionidae, KNM.CA 2155.

In most respects the fossils agree with modern pteropodids. The proximal part of the humerus is curved posteriorly. The head is not noticeably compressed, but it is somewhat flattened on the medial side. The articular surface continues across a shallow groove onto the trocheter (greater trochanter), which is truncate and about one-third as wide as the head. There is a conspicuous depression on the lateral surface of the trocheter for *m. infraspinatus*, and distally from the trocheter a ridge extends 4 mm down the shaft. The trochin (lesser trochanter) is wider transversely than the trocheter, but neither of the trochanters reaches proximally beyond the head. The medial edge of the trochin is continued down the shaft as a ridge, to the same level as the distal ridge of the trocheter. The bicipital groove is a deep notch in an anteromedial position between the trochin and a longitudinal crest for *m. pectoralis*. The deltoid crest, most completely preserved in KNM.CA 2156, is moderately prominent; it reaches its greatest prominence near the level of the distal edge of the head, and gradually diminishes distally; its length is about 7 mm.

Cynopterus differs only in that the distal ridge of the trocheter is a little shorter, so that the trocheter appears to be more undercut in anterior or posterior view. The undercutting is more obvious in *Epomophorus* and *Hypsognathus*, and in these genera the groove between the head and the trocheter is almost absent. The deltoid crest is less prominent in *Pteropus* and *Macroglossus*, and higher than in the fossil in *Eidolon* and *Rousettus*.

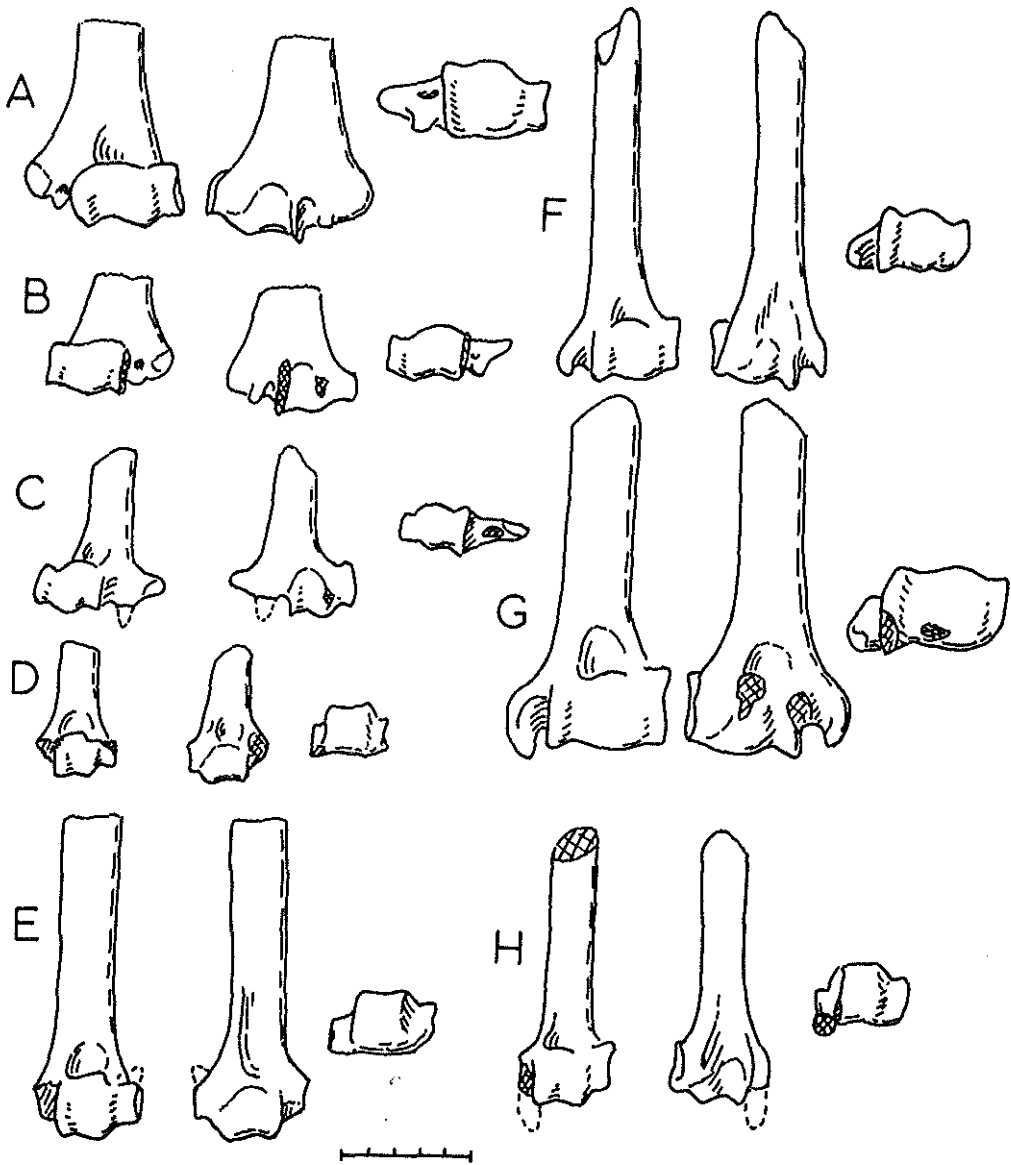


Fig. 23. — Distal humeri, anterior, posterior and distal views.

A, Pteropodidae, type A, KNM.CA 2199.

B, Pteropodidae, type B, KNM.CA 2197.

C, Nycterididae, KNM.CA 2198.

D, Vespertilionidae, type A, KNM.CA 2191.

E, Vespertilionidae, type B, KNM.SO 1399.

F, Emballonuridae, type A, specimen from R 3 (Butler 1969).

G, Emballonuridae, type B, M 34152.

H, Molossididae, M 4355.

There are four examples of the distal end of the humerus. Two from Chamtwara (KNM.CA 2178, 2199) and one from Songhor (KNM.SO 1440) probably belong to one species (fig. 23 A); they have a maximum width of 6.6 - 6.9 mm (93 - 105% of a specimen of *Cynopterus sphinx*). The fourth specimen, from Chamtwara (KNM.CA 2197) is smaller (width 5.1 mm, 78% of *Cynopterus sphinx*). The larger specimens are referred to type A and the smaller one to type B. From its size, type B is the more likely to be conspecific with the proximal humeri. Though poorly preserved, its structure seems to agree with type A, and the following description relates to both.

The epitrochlea is more than half as wide as the articular surface, which is displaced laterally. The tip of the epitrochlea bears a scar for flexor muscles on its anterodistal surface. Nearer to the trochlea there is a small spinous process, placed towards the posterior side, and a pit for a ligament in the anterior surface. The epitrochlea merges proximally into the side of the shaft, its medial profile being slightly concave, as in *Cynopterus*, *Rousettus* and *Eidolon*; in *Pteropus*, *Macroglossus* and *Epomorphus* the concavity is more marked. The keel of the trochlea is about as prominent as in *Cynopterus* and somewhat less so than in *Pteropus*. Lateral to it is the trochlear groove, which extends onto the posterior side of the bone. There is a moderate anterior concavity proximally to the trochlea, but the posterior surface is flat. The capitellum is broad and evenly rounded, and the groove that marks off the lateral capitellar ridge is shallow. On the lateral surface is a deep pit for a ligament, surrounded, except proximally, by a U-shaped articular surface for a sesamoid. In all these features the fossils resemble the living forms.

These humeri are comparable in size with that of *Cynopterus sphinx*, whereas the jaw of *Propotto* is about twice as large. It is therefore unlikely that the humeri belong to *Propotto*, unless the proportion between head and wings was very different from modern pteropodids. This possibility cannot be altogether excluded, as *Propotto* has strongly built, crushing jaws and might be expected to have a large head. Alternatively, the humeri indicate the presence of more typical pteropodids in the African Early Miocene.

Family EMBALLONURIDAE GERVAIS, 1855

TAPHOZOUS GEOFFROY, 1818

Taphozous incognita (BUTLER & HOPWOOD, 1957)

Saccolaimus incognita, Butler & Hopwood (1957), pp. 29-31, fig. 9.

Holotype: M 14222, left half of a facial skull, from Legetet Formation, Maize Crib quarry.

There is a second specimen from the Legetet Formation, from locality 10: KNM.LG 1514 (10/882), facial skull.

Description (Fig. 24 A,B):

KNM.LG 1514 is broken anteriorly, but it contains a fragment of the left canine and part of left P4/. The molars are complete on both sides, but on the left they have been pushed dorsally. Posteriorly the specimen is broken off at the narrowest part of the cranium. Premaxillae and the anterior ends of the nasals are missing, and the postorbital processes have broken off, but the frontal crests are preserved.

The single root of P2/ is present on the right side. It is separated from the canine by a

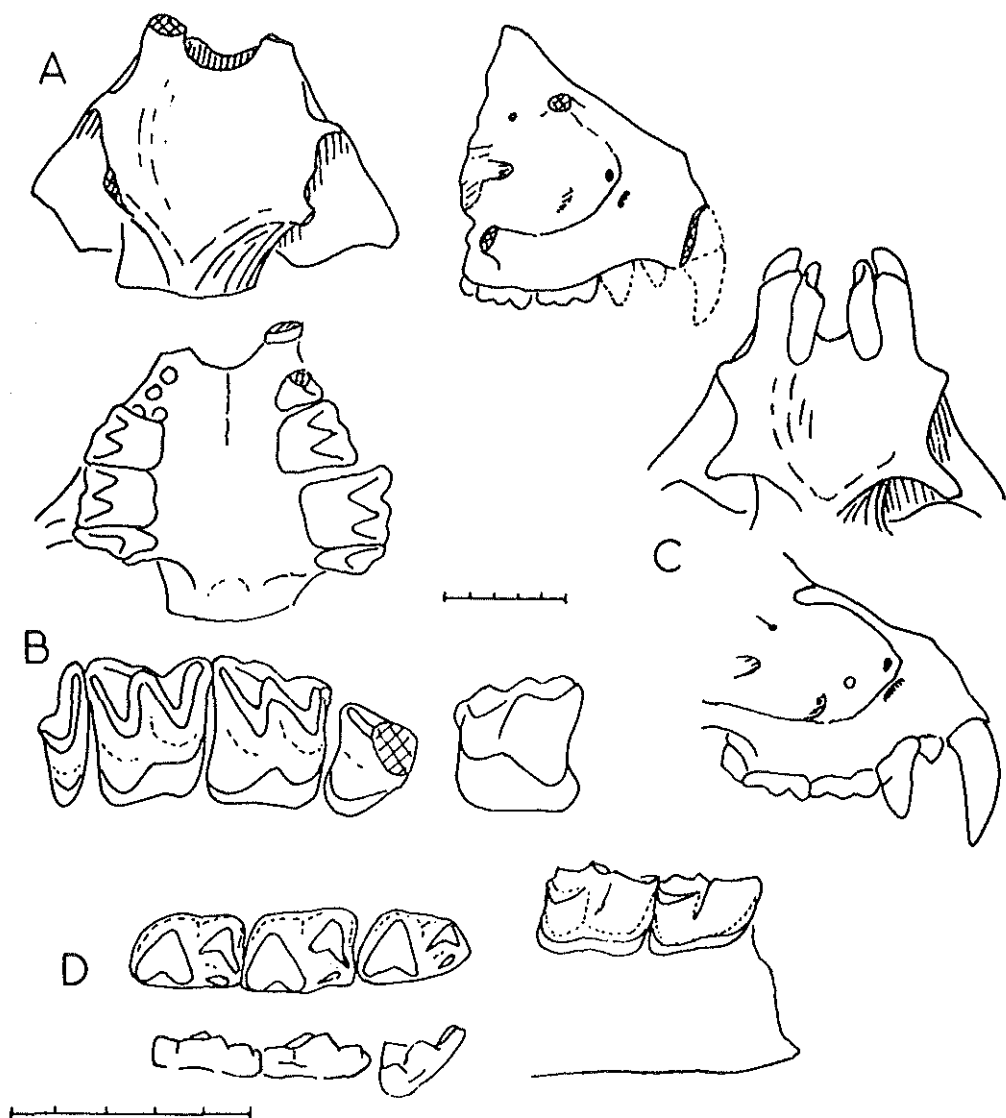


Fig. 24.

A, B, *Taphozous incognita*, KNM.LG 1514. A, facial skull in dorsal, lateral and palatal views. B, RP4-/M3/, and lingual view LM1/.

C, *T (Lironycteris) nudiventris* (recent) for comparison.

D, *Hipposideros* sp., KNM.SO 1392, RM/1-3 in crown and lingual views, and M/1,2 in buccal view.

short diastema. In living species of *Taphozous* P2/ nearly always touches the canine. P4/ has three roots, visible on the right side. On the left side the anterior part of the crown, with the paracone, is missing, but the worn metastylar crest remains. The lingual part of the tooth is occupied by a semicircular talon. The protocone has worn off; a trace is visible in the holotype, in an anterolingual position. P4/ does not appear to differ from that of living species. M1/ is preserved on both sides, though it is worn. As in other

species of *Taphozous* the paracone is V-shaped, with crests to the stylocone and mesostyle; in *Emballonura* and *Coleura* the stylocone and the buccal paracone crest are not developed. There is a forwardly projecting parastyle, but the anterior cingulum is short, as in *Taphozous*; in *Emballonura* and *Coleura* the cingulum connects the parastyle with the protocone. The metacone is higher than the paracone, and the metastylar apex of the crown is prominent. The buccal margin has an indentation anterior to the mesostyle and a smaller one posterior to the mesostyle. The indentations are similar to those of *T. nudiventris*; they are shallower in *T. mauritanicus* and deeper in *T. peli*. The lingual part of the crown, though worn, shows a structure typical of *Taphozous*. The protocone is anteriorly situated; there is a posterior talon at a lower level, but no hypocone is developed; there is no indication of a protocone-metacone ridge, the floor of the trigon passing smoothly into that of the talon. M2/ is a little shorter and wider than M1/, and it is more symmetrical, the metastylar apex being less prominent. The paracone approaches the metacone in height, its buccal crest (to the stylocone) is longer, the parastyle points more buccally, and the buccal indentation anterior to the mesostyle is deeper. These differences between M2/ and M1/ are found in the living species. M3/ agrees with *Taphozous* and differs from *Coleura* and *Emballonura* in having no metacone, and also in the reduction of the protocone, which occupies only one-fifth of the width of the tooth.

The width of the snout, measured across the canines, is greater in proportion to the width across the molars than in the smaller species of *Taphozous*, but not as great as in *T. peli*. The antorbital crest passes in front of the lachrymal foramen, which is thus intraorbital as in some living species such as *T. nudiventris* and *T. theobaldi*; in other species, e.g. *T. peli*, *T. mauritanicus*, *T. perforatus* and *T. longimanus*, there is a gap in the crest near the lachrymal foramen, which opens at the edge of the orbit. The infraorbital foramen is near the lachrymal foramen as in all the living species. The skull roof between the orbits is broad and shallowly depressed as in *T. nudiventris* and *T. peli*, whereas in *T. longimanus*, *T. mauritanicus*, *T. perforatus* and other species the depression is deeper, and the dorsal orbital margins are more deeply concave, reducing the interorbital distance. The frontal crests, arising from the postorbital processes, are strongly developed in *T. incognita*; they converge to meet at an angle of rather less than a right angle, at about the level of the midcranial constriction. They resemble those of *T. peli*. In *T. nudiventris* they follow the same course but are weaker or obsolete posteriorly, owing to swelling of the cranial roof. In the species with a deep interorbital depression the frontal crests are nearly transverse and meet at a wide angle. *T. incognita* has no supraorbital foramina; among living species, these are present only in *T. peli*. In *T. incognita* there is a foramen posteroventral to the postorbital process for the exit of the sinus canal; this is present in the living species. The anterior emargination of the palate reaches to the level of the anterior end of P2/; in the living species, where P2/ is nearer the canine, the emargination ends opposite the middle or posterior edge of P2/. The posterior emargination, lateral to the pterygoid process, reaches the level of the posterior edge of M3/ in KNM.LG 1514, thus not so far forward as in the holotype. The difference is probably due to individual age, as the teeth of the holotype are less worn.

Relationships:

The generic interrelationships of Emballonuridae were investigated by Barghoorn (1977). The oldest and most primitive genus is *Vespertiliavus*, from the Late Eocene — Middle Oligocene of Europe (Revilliod 1920). This has three premolars (P2-4/), but all living emballonurids have lost P3/. A species of *Taphozous* from the Burdigalian of

France, known only by isolated teeth, seems to have retained a small third premolar, at least in the lower jaw (Legendre 1980). According to Barghoorn (1977), *Vespertiliavus* agrees with *Taphozous* (and *Saccolaimus*, which he considers to be generically separate) in the loss of the hypocone from the molars, but Revilliod (1920) states that a very small hypocone is present on M1/ but not on M2/; species of *Vespertiliavus* may differ in this respect. Likewise, the protocone-metacone ridge is absent in Barghoorn's specimens but described as present by Revilliod; a trace is retained in some specimens of *Taphozous*. *Taphozous* is clearly distinguished from the other living genera, as well as from *Vespertiliavus*, by the absence of the metacone of M3/. It resembles *Vespertiliavus*, but differs from the remaining genera, in the presence of the stylocone and the buccal crest of the paracone on M1/. On these criteria, *T. incognita* clearly belongs to *Taphozous*.

Among the living species of the genus, those placed in the subgenera *Saccolaimus* (*T. peli*, *T. saccolaimus*, *T. flaviventris*) and *Liponycteris* (*T. nudiventris*, *T. kashhensis*) most resemble *T. incognita*. The interorbital region of the skull roof is wide and not deeply depressed, and the frontal crests approach each other at an acute angle. *Saccolaimus* differs from *T. incognita* in the marginal position of the lachrymal foramen, the presence of supraorbital foramina, and the deeper buccal indentations on the molars. *Liponycteris* differs in the weaker frontal crests. However, except for the absence of supraorbital foramina shared with *Liponycteris*, the characters that *T. incognita* has in common with *Saccolaimus* and/or *Liponycteris* are also present in *Vespertiliavus* and therefore presumably primitive. Until derived characters are recognized *T. incognita* cannot be allocated to a subgenus. The subgenus *Taphozous* is excluded in any case because of the distinctive characters of its skull roof.

Emballonurid humeri

Proximal end:

Kapurtay Agglomerates. Songhor. KNM.SO 5523.

Distal end, type A (? same species as proximal end):

Legetet Formation. Locality 10. KNM.LG 1507 (10/897).

Hiwegi Formation. Locality R 3. Specimen described by Butler (1969).

Distal end, type B (? *T. incognita*):

Kapurtay Agglomerates. Songhor. M 34152.

Description:

The only specimen of the proximal end (fig. 22 B) measures 5.3 mm in maximum width. It is similar in size to *Taphozous longimanus* and too small to belong to *T. incognita*. The head is less compressed than in *Taphozous* and *Vespertiliavus*, but it is not very different from *T. longimanus*. As in Emballonuridae generally, the trocheter is near the head, from which it is marked off by a groove; it does not project beyond the head proximally. On its proximal surface is a fossa for m. supraspinatus, and laterally there is one for m. infraspinatus. The latter faces slightly posteriorly as in *T. peli*; in *T. longimanus* the posterior orientation is more pronounced, and in *Vespertiliavus* the fossa faces directly posteriorly (Revilliod 1920). The trochin is widely separated from the head, and it is rather more extended than in *Taphozous* and *Vespertiliavus*. Between the head and the trochin there is a deep excavation from the posterior side. Anteriorly to this excavation, a sinuous ridge connects the trochin with the proximal end of the deltoid crest. This crest has broken off, but the broken surface shows that it was narrow and proximally situated, as in other emballonurids. This specimen may represent an unknown genus.

There are two types of distal end. Type A (fig. 23 F) is represented by the specimen from Rusinga described by Butler (1969) and by KNM.LG 1507, a new specimen from Legetet. These agree in size with *T. nudiventris* and probably belong to the same species as the proximal end from Songhor. Type A approaches *Vespertiliavus* in the small size of the styloid process (broken off in the Legetet specimen).

Type B (fig. 23 G) is known by a single specimen from Songhor (M 34152). Its width is 5.9 mm, 89% of that of *Taphozous peli*, and it is thus of a size to belong to *T. incognita*. The distal width is greater in comparison with that of the shaft than in type A or in *T. peli* and *T. longimanus*. The styloid process of the epitrochlea is longer than in type A, reaching distally to the level of the trochlear keel, and resembling *T. longimanus* and *T. nudiventris*; in *T. peli* and *T. saccolaimus* it is not quite so long. The lateral keel of the capitellum is prolonged proximally, unlike type A and *Vespertiliavus*, but in agreement with *Taphozous*.

Family NYCTERIDIDAE VAN der HOEVAN, 1855

Humerus

The distal end of a humerus from Chamtwara (KNM.CA 2198) is very similar to the living *Nycteris thebaica*. Its maximum width is 5.0 mm, that of the joint surface 2.5 mm, and that of the shaft 1.6 mm. The epitrochlea occupies half the width of the distal end, displacing the joint laterally so that the capitellum is entirely lateral to the shaft. A surface for muscle insertion can be seen on the anterior side of the tip of the epitrochlea. The styloid process has broken off, but it was in the same position as in *Nycteris*, at some distance from the trochlea. The trochlear keel is hardly more prominent than the capitellum. The lateral ridge is distinctly marked off from the capitellar condyle by a groove.

This is the oldest known member of the Nycterididae. At present there are 9 species in Africa and S.W. Asia and one species in S.E. Asia, all in the genus *Nycteris*. Five of the African species inhabit forest (Hayman 1967).

Family MEGADERMATIDAE ALLEN, 1864

Genus and species indeterminate

The mandible from the Hiwegi Formation (M 34141), and described by Butler & Hopwood (1957), remains the only representative of this family. It comes from Kaswanga, not R 106 as previously stated.

Family HIPPOSIDERIDAE FLOWER & LYDEKKER, 1891

HIPPOSIDEROS GRAY, 1831

Species indeterminate

KNM.SO 1392 is a fragment of mandible from Songhor with three very worn molars, of which M/3 has been displaced from its original position (fig. 24 D). The estimated total length of the molars is 6.9 mm, about the same as in *H. cyclops* and somewhat less than in *H. commersoni* and *H. diadema*.

M/1 measures 2.2×1.55 mm. All cusps have been removed from the trigonid; its worn surface approximates to an equilateral triangle, the protoconid angle being about 70° and the protoconid-metaconid edge inclining backwards at an angle of about 60° to the long axis of the tooth. The talonid is equal in width to the trigonid. The hypoconid, worn into a crescent, is much lower than the trigonid. Its anterior crest meets the middle of the posterior trigonid wall, and its posterior crest runs posterolingually, turning more posteriorly at its lingual end where a hypoconulid must have stood. A groove separates the hypoconulid from the entoconid; the tooth is nyctalodont (Menu & Sigé 1971). The entoconid was joined to the metaconid by a ridge. The crown is much higher buccally than lingually, owing to a downward buccal inclination of the base, as in other insectivorous bats. There is a wide buccal cingulum, continuous from the paraconid to the hypoconulid. The buccal margin of the tooth is nearly straight, with only the merest indication of an indentation between trigonid and talonid. M/2 resembles M/1, but it is a little wider (measurements: 2.2×1.65 mm) and the trigonid angle is smaller (60°), the anterior edge of the trigonid being more transverse. M/3 is somewhat smaller than M/2 (2.1×1.6 mm) and its talonid is narrowed.

This specimen resembles *Hipposideros cyclops*, *H. abae* and *H. commersoni*, among living African species. In *H. caffer* and *H. camerunensis* the talonid of M/3 is less reduced and the hypoconulid of M/1 and M/2 is less differentiated. In *H. megalotis*, *H. marisae* and *H. jonesi* the teeth are narrower and the buccal indentation is more marked. *H. (Pseudorhinolophus) bouziguensis* SIGÉ, 1968, from the terminal Aquitanian of Europe, is very similar to the Songhor specimen, but slightly smaller (M/1-M/3 6.25-6.65 mm).

Hipposiderid humeri

The only example of the proximal end is KNM.CA 1124 (34/653), from Chamtwara (fig. 22 C). The maximum width is 4.2 mm, and the specimen is thus similar in size to *H. larvatus*; it is much too small to belong to the same species as the mandible from Songhor. The head is less compressed than in living species of *Hipposideros*, but resembles species of the subgenus *Pseudorhinolophus* (*H. (P.) bouziguensis*, *H. (P.) schlosseri*). The trocheter projects proximally beyond the head. Its proximal fossa, for m. supraspinatus, is situated towards the anterior side; the lateral fossa, for m. infraspinatus, faces slightly posteriorly, as in *Pseudorhinolophus* and in the living *H. galeritus*. In *H. commersoni*, *H. larvatus* and *H. diadema* the infraspinatus fossa faces directly laterally. The trochin reaches the level of the head and has a greater mediolateral diameter than the trocheter. The ridge that connects the trochin to the deltoid crest has a slight intermediate elevation. The deltoid crest is wide proximally and narrows as it reaches its greatest height at a level distal to the head.

The distal end of a humerus from Songhor (Sgr 149.66) was described by Butler (1969). There are two more specimens, KNM.SO 1391 (Sgr 1855.66) and KNM.SO 1385 (Sgr 2152.66), also from Songhor, which seem to belong to the same species. The width is 5.4-5.7 mm, much less than in *H. commersoni* (8.6) and *H. diadema* (7.1), and larger than in *H. larvatus* (4.4). These distal humeri therefore seem to be specifically different both from the mandibular specimen and from the proximal humerus.

Family VESPERTILIONIDAE GRAY, 1821

Subfamily KERIVOULINAE MILLER, 1907

CHAMTWARIA, nov. genus

Diagnosis: Resembling *Kerivoula* in having three upper premolars, the middle one (P3/) smaller than the anterior one (P2/) but less reduced than in *Myotis*; differing from *Kerivoula* in the longer, narrower face, nasals extending above canines, infraorbital foramen close to tooth row, the sharp infraorbital crest, and the less elevated paracone of P4/.

Type and only species: *Chamtwarria pickfordi* nov. spec.

Chamtwarria pickfordi nov. spec.

Diagnosis: With the characters of the genus. P2/-M3/ 10.3 mm.

Holotype: KNM.CA 2237, the anterior part of a skull, from Chamtwara. This is the only known specimen.

The species is named after Dr. Martin Pickford.

Description (fig. 25 A,A'):

The skull is broken off posteriorly at the back of the olfactory chamber, and most of the alveolar portion of the maxilla is missing on the right side. On the left side the orbit and the root of the zygoma are preserved, and the three premolars are complete, but the canine and molars are represented only by their broken bases or roots.

Chamtwarria is large for a vespertilionid; in size of molars and width of palate it is comparable with *Scotophilus nigrita* and *S. heathi*, but the postcanine tooth-row is longer.

The face anterior to P4/ is narrower and less depressed than in *Myotis* and *Kerivoula*. Its width, behind the canines, is about equal to the total length of C - P4/, as in *Natalus*. The dorsal surface of the face is flattened, lacking the median concavity of *Kerivoula* and *Myotis* and thus resembling *Natalus*. The profile rises rapidly above the orbits. There are no sutures, except a trace of the internasal suture. Grooves show the position of the ascending processes of the premaxillae, which reached back to above the posterior end of the canines. The nasals are long, extending beyond the canines and reducing the size of the external narial opening. The large anterior emargination of the skull of other Vespertilionidae is absent, but there is more resemblance to *Natalus*. The zygomatic arch arises above M2-3/. Its dorsal edge continues as a sharp crest below and anterior to the orbit, passing in front of the lachrymal foramen, as in *Myotis*; in *Kerivoula* this crest is weak and the lachrymal foramen opens on the face. The lachrymal foramen is above the anterior end of M1/ as in *Kerivoula* and *Myotis*; in *Natalus* it is above M2/. The infraorbital foramen is low on the face above the anterior end of P4/; in *Kerivoula* and *Myotis* it is higher, nearly level with the lachrymal foramen; in *Natalus* it is low but over P3/. The palate is proportionately longer and narrower than in *Kerivoula* and *Myotis*, and also more arched; it resembles *Natalus* in proportions. Its anterior border is not well preserved, but the emargination did not reach beyond mid-canine level. Posteriorly, the lateral part of the palate ends immediately behind M3/; the median part extended back under the nasopharynx, but its posterior edge is not preserved.

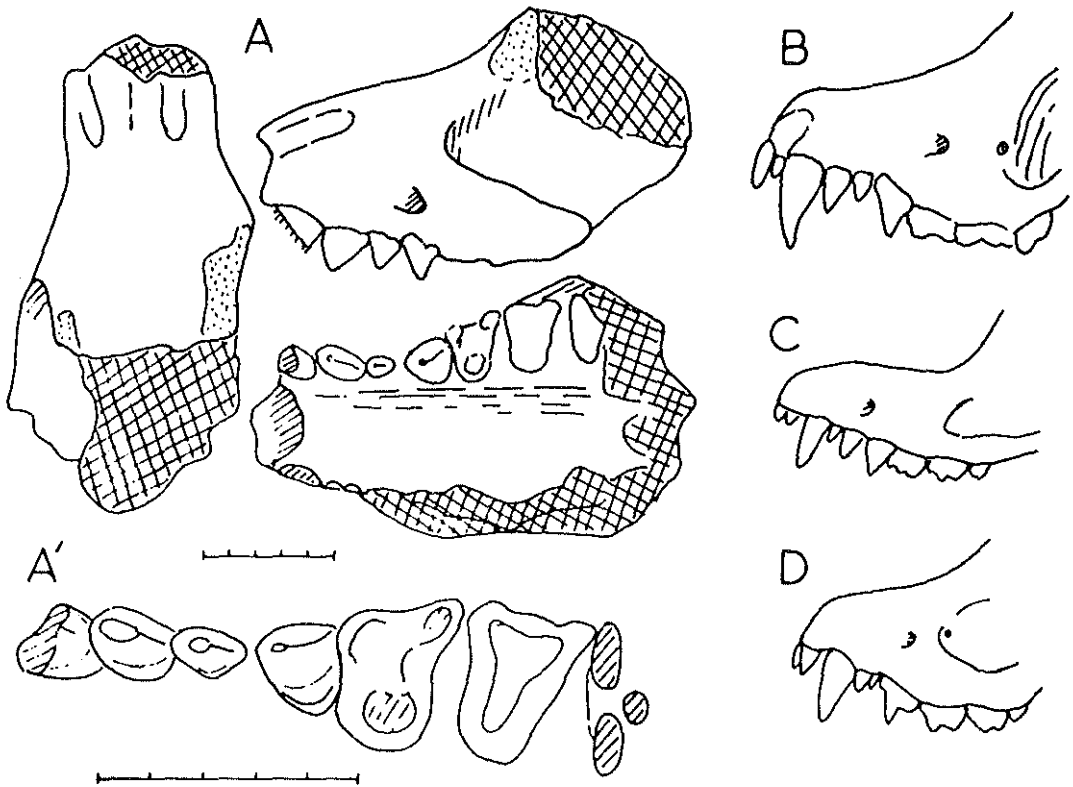


Fig. 25.

A, A', *Chamtwaria pickfordi*, KNM.CA 2237. A, facial skull in dorsal, lateral and palatal views; A', dentition.

B, *Kerivoula cuprosa* (recent).

C, *Natalus major* (recent).

D, *Myotis tricolor* (recent).

To judge by its broken base, the canine seems to have been comparatively small. The first two premolars (P2,3/) are proportionately larger than in *Kerivoula*, so that the total length of the premolar series is 79% of the length of the molar series, compared with 55-65% in *Kerivoula*. In *Myotis* both P2/ and P3/ are reduced, especially P3/ which in some species is minute and displaced lingually. P2/ is larger than P3/ in *Chamtwaria*, as in *Kerivoula* and *Myotis*, but in *Natalus* it is much smaller. Alveoli on the right side of the specimen show that P2/ has two roots. The crown is broadly oval in outline, and less compressed anteroposteriorly than in *Kerivoula*. There is a single cusp, blunted by wear, and buccal and lingual cingula. P3/ is proportionately narrower than P2/, and not compressed as in *Kerivoula*; it is separated from P4/ by a short space. In *Natalus* P3/ is triangular. P4/ of *Chamtwaria* approaches an equilateral triangle in outline; it is much shorter and less wide than M1/. The paracone is not elevated as in *Kerivoula*, but only about as high as on P2/. As far as can be seen from their broken bases, M1/ and M2/ resemble those teeth in *Kerivoula* and *Myotis*. On M1/ the metastylar apex projects farther laterally than the parastyle, and on M2/ parastylar and metastylar apices are

equally prominent. The lingual region is more extended on M1/ than on M2/. The roots of M3/ indicate a short, transverse tooth. In *Natalus* M1/ and M2/ are more quadrate and M3/ is less reduced in length.

Relationships:

The fossil genus that is most like *Chamtwaria* is *Stehlinia*, from the U. Eocene-Oligocene of Europe (Revilliod 1922, Sigé 1975). This agrees in having a long face, with nasals extending above the canines, though the face is flatter and there is a median dorsal concavity; the lower edge of the orbit is sharp; the infraorbital foramen is low, near the teeth. Except the dorsal concavity, these characters are also shared with *Natalus*. The premolars of *Stehlinia* resemble *Natalus* and differ from *Chamtwaria*: P2/ is small and one-rooted; P3/ is a larger, triangular tooth which frequently develops a third root; P4/ is wider in comparison with M1/, and its paracone is elevated. Sigé (1975) considers *Stehlinia* to represent a primitive vespertilionoid stock of which *Natalus* and *Kerivoula* are the least modified living descendants. *Kerivoula* and *Chamtwaria* have advanced beyond *Stehlinia* in the simplification of P3/ and enlargement of P2/. *Myotis* also has P3/ smaller than P2/, but both teeth have diminished in size as the face has shortened, leading to the disappearance of P3/ in other vespertilionids. Thus *Kerivoula* and *Chamtwaria* show in their premolars an early stage in the development of a derived vespertilionid character. *Chamtwaria* is more primitive than *Kerivoula* in skull characters in which it resembles *Stehlinia* and *Natalus*.

How to express these relationships taxonomically is mainly a matter of taste. Sigé (1975) removed *Kerivoula* from the Vespertilionidae and included it with *Stehlinia* in a family Kerivoulidae, but he retained the Natalidae as a separate family. Van Valen (1979) combined Kerivoulidae and Natalidae with Thyropteridae, Furipteridae and Myzopodidae into a single paraphyletic family Natalidae, noting that they lack derived characters of Vespertilionidae, mostly characters of the humerus. Both these arrangements have the disadvantage of obscuring the relationship of *Kerivoula* to *Myotis*. I would therefore retain *Kerivoula* in the Vespertilionidae, subfamily Kerivoulinae, but would exclude *Stehlinia*. *Chamtwaria*, unlike *Stehlinia* but like *Kerivoula*, has advanced in the vespertilionid direction in premolar organisation, and it may also be included in the Vespertilionidae. It is provisionally placed in the Kerivoulinae, though a case might be made for making it the type of new subfamily.

Vespertilionid humeri

There are two similar proximal ends of humeri from Chamtwara, KNM.CA 2155 (34/811) and 2189 (34/1418b) (fig. 22 D). The maximum width of KNM.CA 2155 is 3.3 mm, and the width of the head is 1.5 mm. In KNM.CA 2189 part of the trochin has broken off, but more of the shaft remains; the head width is 1.5 mm and the shaft width is 1.7 mm at a distance of 3 mm below the head. These specimens agree in size and form with *Myotis daubentoni*. The head is relatively large, and nearly spherical. The trocheter projects proximally to a moderate degree, as in *Myotis*. The trochin is smaller than the trocheter, and does not rise above the head. The deltoid crest is not very high; it is wide proximally, where its medial edge overhangs the bicipital groove. The distal ridge of the trocheter extends for most of the length of the deltoid crest. A supraglenoid fossa is present in the proximal surface of the humerus.

There are two types of distal end. Type A, represented by a specimen from Chamtwara, KNM.CA 2191 (34/1418a) (fig. 23 D), may belong to the same species as the proximal ends. The width of the joint is 2.4 mm, and that of the shaft is 1.4 mm. The

epitrochlea is broken, but it seems to have had the same transverse development as in *Myotis*. The groove of the trochlea is very shallow, and the trochlear keel and the capitellar condyle are about equally prominent, together forming an almost cylindrical surface. The ridge of the capitellum is clearly marked off by a groove, deeper than the trochlear groove. The proximal part of the ridge of the capitellum (epicondyle) has broken off. Proximally to the articular surface there is a fossa for the radius, on the anterior side, and a shallower concavity posteriorly. The structure agrees well with *Myotis*.

Type B is represented by a larger specimen from Songhor, KNM.SO 1399 (Sgr 2143.66) (fig. 23 E): maximum width 4.4 mm, joint width 3.4 mm, shaft width 2.3 mm. It is of similar size to *Vespertilio murinus*. It differs from type A in that the shaft is flattened anteroposteriorly as in *Vespertilio* and *Eptesicus*, the trochlear groove is somewhat deeper and the posterior concavity is more pronounced. The epitrochlea is broken and the epicondyle is missing.

Family MOLOSSIDAE PETERS, 1865

Humerus

The distal end of a humerus from Napak, M 43555, is the only specimen referred to the Molossidae (fig. 23 H). Its maximum width is 3.5 mm, joint width 2.9 mm, shaft width 1.6 mm. It is about the size of *Otomops mariensseni*, and larger than *Tadarida aegyptiaca* and the Stampian and Aquitanian species of *Tadarida* from Europe (Sigé 1971). It closely resembles all these in structure. The shaft is deeper (anteroposteriorly) than wide. The joint is in line with the shaft, so that the trochlear ridge is slightly medial, and the ridge of the capitellum slightly lateral to the edges of the shaft when seen in anterior view. The distal part of the epitrochlea, with the styloid process, has broken off, but it was clearly strongly constructed. The trochlear groove is shallow, and the trochlear ridge is hardly more prominent than the capitellum. The condyle of the capitellum occupies about one-third of the width of the joint. The capitellar groove is deeper than the trochlear groove. The lateral ridge of the capitellum is concave laterally, and at its proximal end there is a moderately prominent epicondylar process. Proximally to the condyle the anterior surface is excavated. The trochlear ridge is continued up the posterior side of the bone beyond the smooth area of the joint; another, less prominent ridge continues the lateral ridge of the capitellum, converging towards the trochlear ridge. The area between these ridges is transversely, but not longitudinally, concave, forming a groove that is continuous with the trochlear groove.

This is the oldest recorded African molossid. The family is represented at Beni Mellal (Lavocat 1961) by some indeterminate molar teeth. Unfortunately the very uniform morphology of the molossid humerus, going back to the Oligocene (Sigé 1971), precludes a generic identification of the Napak specimen.

CONCLUSIONS

My previous report (Butler 1969) included material collected up to 1966. Nearly all of it came from Rusinga and Songhor. Subsequent collecting has added several more locations, including Meswa Bridge, Chamtwara, Mfwanganu, Maboko and Fort Ternan, and many more specimens have been found at sites previously known. The total number of identified specimens now approaches 500, almost three times as many as in 1969.

This additional material has provided further information about species already known, but it has not resulted in the discovery of new species of macroscelideans and insectivores, except in the oldest and youngest deposits: Meswa Bridge and Fort Ternan. For the Kapurtay Agglomerates and the Hiwegi Formation the list of species belonging to the two orders must be approaching completion. Knowledge of the Chiroptera however is less complete, for additional collecting has raised the number of species from 5 to at least 14.

The new material covers a range of about 9 Ma (23-14 Ma), but the great majority of specimens are from the Legetet Formation, the Kapurtay Agglomerates and the Hiwegi Formation, which are much closer in time, probably within 3 Ma. There is only one specimen from Meswa Bridge, and only 11 have come from the Koru Formation. Likewise the younger deposits at Maboko and Fort Ternan have produced very few macroscelideans and insectivores, and no bats. Evidence of evolutionary change is therefore limited. *Miorhynchocyon meswae* might be ancestral to *M. rusingae*. The Koru specimen of *Amphechinus* has a two-rooted M/3, there is an increase in the size of *A. rusingensis* between Legetet and Chamtwara, and the Fort Ternan form is more advanced. The *Propotto* from Koru differs in some ways from specimens from Songhor and Rusinga. Most differences between the faunas consist in the presence or absence of species, due partly to immigration or extinction and partly to ecological differences.

The Koru Formation contains, besides the *Amphechinus* and *Propotto* just mentioned, a problematic macroscelidean, perhaps related to *Hiwegicyon*. There are also *Miorhynchocyon clarki*, *Galerix africanus* and *Erythrozoetes chamerpes*, present again in the Legetet Formation. There they are associated with *Amphechinus rusingensis*, probably derived from the Koru form, and with three more insectivores that have not yet been found at Koru: *Gymnurechinus leakeyi*, *Protenrec tricuspis* and *Prochrysochloris miocaenicus*. The Legetet fauna contains three bats: a pteropodid (distal humerus A), *Taphozous incognita*, and a smaller emballonurid (distal humerus A), but not *Propotto*. The list provided by Pickford & Andrews (1981, table 2) shows that 4 species of primate and 8 rodents in the Legetet Formation have not been found in the Koru Formation, and *Proconsul africanus* is subspecifically different in the two deposits. The apparent absence of species from the Koru Formation is no doubt partly due to the small size of the collection, but Evans *et al.* (1981) found evidence of an ecological difference: whereas the Legetet fauna represents a forest community, that of Koru indicates a more open habitat.

Superimposed on the Legetet Formation are the Kapurtay Agglomerates, containing the Chamtwara and Songhor faunas. All the macroscelideans and insectivores known from Legetet are present, and also the bats, if the emballonurid distal humerus B belongs to *Taphozous incognita*. Added to these are *Miorhynchocyon rusingae*, *Gymnurechinus camptolophus*, *Parageogale*, *Myohyrax* (doubtfully present at Legetet), and several bats: *Propotto*, three hipposiderids, a nycterid, *Chamtwaria* and two other vespertilionids.

	Meswa Bridge	Koru	Legetet	Chamtware	Songhor	Napak	MFwanganu	Hiwegi Fm (Hiwegi area)	Hiwegi Fm (west)	Rusinga, site unknown	Karungu	Kulu Fm	Maboko	Fort Ternan
<i>Miorhynchocyon meswae</i>	1													
<i>M. clarki</i>		1	7	20	15			11	11		1			
<i>M. rusingae</i>					10		1	6						1
<i>Myohyrax oswaldi</i>			1	30	3		1	22	4		many			1
<i>Myohyrax</i> sp.						1								
<i>Pronasilio ternanensis</i>														3
<i>Hiwegicyon juvenalis</i>		1 (?cf)						1	1					
<i>Galerix africanus</i>		5	1	10	11			2						
<i>Amphechinus rusingensis</i>		1 (cf)	12	28	8			2	3	2	3	1	1	
<i>Amphechinus</i> sp.														2
<i>Gymnurechinus leakeyi</i>		6	1	2				30	9	1	1	3		
<i>G. camptolophus</i>					10				14	2				
<i>Protenrec tricuspis</i>			1	9	10	2		1						
<i>Erythrozootes chamerpes</i>		2	2		2	1								
<i>Parageogale alettris</i>				3				1						
<i>Prochrysochloris miocaenicus</i>			10	6	7									
<i>Chiroptera</i>		1	4	13	11	1		3	1					

Table 7 : Tally of specimens.

Certain differences between the Songhor and Chamtwara faunas may be noted. Present at Songhor but not Chamtwara are *M. rusingae*, *G. camptolophus*, *Erythrozootes* and five species of bat. At Chamtwara *Myosorex* is much commoner, and there also occur *Parageogale* and four bats that have not been found at Songhor. Most of the differences concern rare species whose absence may well be accidental, but *M. rusingae* and *G. camptolophus* are fairly common at Songhor, with 10 specimens each. Pickford & Andrews (1981, table 2) show that some other mammals, common at Songhor, are absent at Chamtwara: *Rangwapithecus gordonii* (71 specimens from Songhor), *Simonomys genovefae* (42) and *Notocricetodon petteri* (29). Although ecological diversity analysis (Andrews *et al.*, 1979, Evans *et al.*, 1981) indicates that both Songhor and Chamtwara represent predominantly forest faunas like Legetet, the method is insufficiently sensitive to prove that the environment was uniform.

Radiometric data indicate that the Hiwegi Formation on Rusinga Island is younger than the Kapurtay Agglomerates, though the relationship cannot be demonstrated stratigraphically. The fauna contains 4 macroscelideans, 6 insectivores and 3 bats. All are shared with Songhor or Chamtwara or both, except the megadermatid and *Hiwegicyon juvenalis*, known by one or two specimens only. Differences from the Kapurtay faunas that may be significant are the abundance of *Gymnurechinus leakeyi*, the rarity of *Galerix* and *Protenrec*, and the absence of *Prochrysochloris* and *Erythrozootes*. Bats are also scarce: 10 species known from Songhor and Chamtwara have not been found at Rusinga. These differences may be at least partly due to the different modes of deposition: whereas at Songhor and Chamtwara the fossils are mainly from palaeosols, the Rusinga deposits are mainly water-laid silts and sands indicating floodplain and lake-margin conditions (Van Couvering 1972, Andrews & Van Couvering 1975, Pickford 1981).

Within the Hiwegi Formation there are local differences of fauna, particularly between the Hiwegi area (R 1, R 3 etc.) on the eastern side of the island and the Kaswanga area on the western side. The Kaswanga area is characterised by the large form of *Miorhynchocyon clarki* and by *Gymnurechinus camptolophus*, whereas *Miorhynchocyon rusingae* is known only from the Hiwegi area, from which come most specimens of *Myohyrax* and *Gymnurechinus leakeyi*. Andrews & Van Couvering (1975), from an intensive study of a site in the Kaswanga area, concluded that successive layers were environmentally different. They collected the large form of *M. clarki* from layers KB, KF and KG, of which the faunal diversity showed most resemblance to forest (Andrews *et al.* 1979), but not from KH, which represented a more open habitat. Verdcourt (1963) found evidence from the gastropods for the existence of drier conditions (woodland, bush, savanna) at some localities on Rusinga, especially in the Hiwegi area, but species characteristic of forest also occurred at some of the same localities. Mixing of faunas due to flood-plain deposition might explain the occurrence of *M. rusingae* together with the typical form of *M. clarki* at R 1 and R 3. Closely related sympatric species, such as those of *Miorhynchocyon* and *Gymnurechinus*, would be expected to have different habitat preferences. Although the living *Rhynchocyon* is confined to closed forest, this was not necessarily the case with the Miocene form.

At Karungu *Myohyrax oswaldi* is abundant, and *Amphechinus rusingensis*, *Gymnurechinus leakeyi* and *Miorhynchocyon clarki* are present. These four species occur together at Chamtwara, Songhor and Hiwegi, but the fauna as a whole bears most resemblance to Hiwegi (Pickford 1981, 1983). The Karungu sediments are of fluvial origin, and represent a wet flood-plain facies. Evans *et al.* (1981) point to the hypsodonty of *Myohyrax* and of the abundant lagomorph *Kenyalagomys*, which to them suggest a

grazing adaptation and thus indicate an environment in which ground vegetation was dominant. Such conditions might occur in wet as well as in drier areas. If *Myohyrax* fed on seeds and shoots rather than grass it would still be dependent on low vegetation, for its foot bones show that it was a ground-runner like the living macroscelids. *Kenyalagomys* and *Myohyrax* both occur at Rusinga, but whereas *Myohyrax* is found mainly in the Hiwegi area, *Kenyalagomys* is equally abundant in the Kaswanga area. At Chamtwara, where *Myohyrax* is common, *Kenyalagomys* has not been reported.

Myohyrax survived into the Middle Miocene at Fort Ternan, where it is accompanied by *Amphechinus* and *Miorhynchocyon*. A new appearance is *Pronasilio*, the oldest member of the Macroscelidinae. The living members of this subfamily, with the exception of *Petrodromus*, inhabit savanna and grassland, and its occurrence at Fort Ternan is consistent with the change to a more open habitat, postulated by Andrews *et al.* (1979).

Myohyrax, *Protenrec* and *Erythrozootes* have been found at Napak. The *Myohyrax* has proportionately smaller premolars than at Chamtwara and Karungu and it may be more primitive. The *Protenrec* is a little larger than at Chamtwara and Songhor, and there are minor differences in the teeth, but these may be merely individual variations. The mandible of *Erythrozootes* from Napak does not differ significantly from fragments found at Koru and Songhor. The *Myohyrax* suggests that Napak may be somewhat older than the Kapurtay Agglomerates, but the difference might be geographical. The molossid humerus cannot be matched at the Kenyan localities.

The Early Miocene of East Africa provides a picture of the small mammal fauna of Africa which is equalled only in the Late Pliocene and Pleistocene. Four of the five existing families of African macroscelideans and insectivores were present. The Soricidae, now by far the most numerous in species, appear to have been absent: the specimen of *Crocidura* from Rusinga is now regarded as Pleistocene or Recent. Of the bats, seven of the nine African families are now recognised.

The only known Oligocene macroscelidean (*Metoldobotes*) already possessed derived characters, and the order had evidently undergone much diversification prior to the Miocene. Rhynchocyoninae and Myohyracinae were clearly differentiated by Early Miocene time. Macroscelidinae appear only in the Middle Miocene, but they represent a third line of evolution, perhaps going back to a common ancestry with the Myohyracinae in the Oligocene. The Tenrecidae and Chrysochloridae are confined to Africa and must have been present in the Oligocene. The three Miocene genera of Tenrecidae are evidence of an earlier radiation, which would also have produced the ancestor of the Potamogalinae. *Prochrysochloris* already possessed most of the distinctive characters of the Chrysochloridae, and it is widely different from the contemporary tenrecids.

In contrast with these endemic families, the Erinaceidae are clearly an immigrant group. Of the three Early Miocene genera, *Galerix* is represented in the Miocene of Europe, and it is probably related to the Oligocene genus, *Tetracus*; *Amphechinus* was widely distributed in Eurasia in the Oligocene; *Gymnurechinus*, though unknown outside Africa, must have had a common ancestor with *Amphechinus* and *Palaeoscaptor* in Asia, probably in the Early Oligocene. *Galerix* and *Amphechinus* appear in Africa at Koru, in association with other forms of Asiatic origin, including cricetidontids, chalicotheres, rhinoceroses, pigs and tragulids. Their entry indicates the formation of a land-bridge, dividing the Tethys Sea from the Indian Ocean (Bernor 1983), early in the Miocene, perhaps shortly before 20 Ma. This is in accordance with the European appearance of *Brachyodus* in zone MN 3a (Mein 1979), and earlier than the appearance of Proboscidea (MN 3b; 17.5 Ma according to Berggren & Van Couvering 1974) and of hominoid primates (MN 5; 16-15 Ma).

The subsequent history of African macroscelideans and insectivores may be inferred in outline by comparing the Plio-Pleistocene fauna with the Early Miocene fauna (Butler 1978). The Miocene erinaceids died out; the living hedgehogs of the subgenus *Erinaceus* (*Atelerix*) represent a late invasion from the north (Butler & Greenwood 1973). *Miorhynchocyon* is ancestral to *Rhynchocyon*, but the Myohyracinae are extinct. The Macroscelidinae underwent an expansion in the Late Tertiary, with three Plio-Pleistocene genera. The Tenrecidae have survived as the Potamogalinae, but these were not directly derived from known Miocene genera. The nearest living relative of *Parageogale* is *Geogale*, in Madagascar. The Chrysochloridae have diversified. The most significant change in the insectivore fauna was the introduction of Soricidae, which are first known at Beni Mellal, and are now represented by six genera and over 100 species. Their expansion may account for the decline of Tenrecidae.

Less can be said about the history of the Chiroptera. Four families of Microchiroptera appear in Europe, probably as immigrants from Asia, at 44-40 Ma in the Late Eocene (Emballonuridae, Rhinolophidae, Hipposideridae, Vespertilionidae), with the addition of Megadermatidae and Molossidae at 40-37 Ma (Sigé & Legendre 1983). The few bats from the Oligocene of Africa give the impression of endemism: *Provampyrus*, known only by the humerus, is of uncertain affinities, and two vespertilionoids are considered by Sigé (unpub.) to belong to a new family. It would seem that the Tethys Sea prevented the migration of bats from Eurasia to Africa, despite their powers of flight. However, all the families present in the Oligocene of Europe had appeared in Africa by the Early Miocene, with the exception of Rhinolophidae. Nearly all living rhinolophids are found in open country, and this may explain their absence from the Early Miocene deposits, which represent predominantly forest environments. *Rhinolophus* occurs in the Middle Miocene of Beni Mellal. The Nycterididae are unknown in Europe, and they may have evolved in Africa, where all the living species except one are found. The Pteropodidae, to judge from their present distribution, probably evolved in southern Asia. They reached Europe in the Oligocene, if *Archaeopteropus* is a pteropodid. There seems to have been more than one invasion of Africa, including *Propotto* which represents a primitive side-branch of the family.

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