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INSECTIVORA AND CHIROPTERA
FROM THE MIOCENE ROCKS
OF KENYA COLONY

BY

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INSECTIVORA AND CHIROPTERA FROM THE MIOCENE ROCKS OF KENYA COLONY

By P. M. BUTLER and A. TINDELL HOPWOOD

INTRODUCTION

In this paper are described a number of Insectivora and two bats from Lower Miocene sites in Kenya Colony. Incomplete skulls of two insectivores and a bat were found at Koru in 1931, and subsequently several specimens were obtained from Songhor and Rusinga Island. Detailed accounts of the sites are given by Kent (1944), Le Gros Clark & Leakey (1951) and Shackleton (1951).

At the present time the Insectivora are represented in Africa by five families: Erinaceidae, Soricidae, Macroscelididae, Chrysochloridae and Tenrecidae. All these families are represented in the Lower Miocene, and the Erinaceidae have already been described by Butler (1956). The distribution of the specimens belonging to the remaining families is as follows :

	KORU	SONGHOR	RUSINGA
SORICIDAE			
<i>Crocidura</i> sp.			1
MACROSCELIDIDAE			
<i>Rhynchocyon clarki</i>		1	6
CHRYSOCHLORIDAE			
<i>Prochrysochloris miocaenicus</i> . .	1	1	
TENRECIDAE			
<i>Geogale alettris</i>			1
<i>Erythrozootes chamerpes</i>	1		
<i>Protenrec tricuspis</i>		2	

The bats appear to belong to families still living in Africa : Emballonuridae and Megadermidae. Each is represented only by a single specimen, from Koru and Rusinga respectively.

SYSTEMATIC DESCRIPTIONS

Order **INSECTIVORA**
 Family **SORICIDAE**
 Genus *CROCIDURA* Wagler, 1832

Species indeterminate
 (Text-fig. 1)

MATERIAL.—Coryndon Museum, Rs.1875.50, an incomplete mandible containing M_1 and M_2 , from Rusinga Island (site 3a).

DESCRIPTION.—The posterior part of the jaw is missing, but it is possible to see part of the deep fossa for the temporal muscle and, below it, the canal leading from the mandibular foramen. On the medial side near the posterior end of the specimen is a shallow depression for the pterygoid muscle. The horizontal ramus is moderately deep. The symphysis extends back to the posterior end of P_4 . The mental foramen is below the posterior part of P_4 , and opens into a groove which passes forwards to near P_1 .

The dental formula is $i1, co, p2, m3$. No trace of pigmentation is visible on M_1 and M_2 ; the remaining teeth are represented by their alveoli. The alveoli show

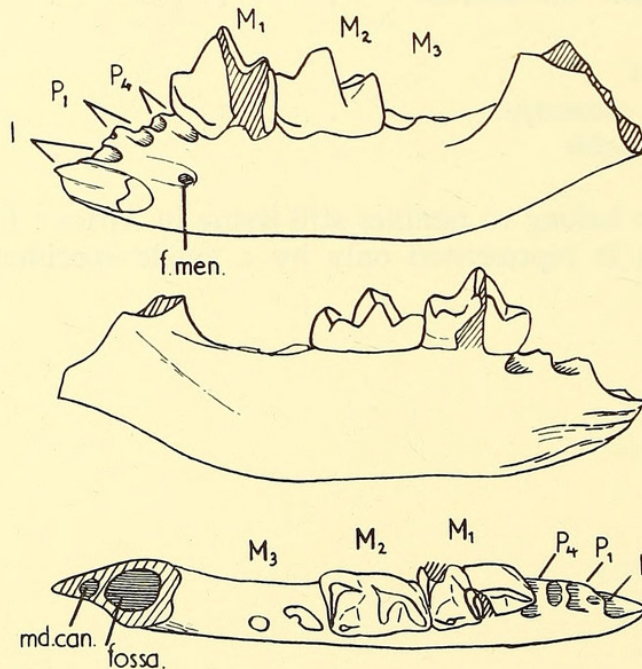


FIG. 1. *Crocidura* sp., Rs 1875.50. Outer, inner and upper views of lower jaw. $\times 14$. Fossa, fossa for temporalis muscle; *f.men.*, mental foramen; *md.can.*, mandibular canal.

that the large incisor had two roots, and that, on the labial side, the exposed part of the tooth extended back below P_1 to the level of the middle part of P_4 . P_1 and P_4 were procumbent; each had a large posterior root and a small anterior one. P_4 was probably somewhat broader than P_1 . M_1 is badly fractured, but the crown of M_2 is intact. On both molars, the trigonid is higher than the talonid, and the paraconid is well developed and trenchant, but lower than the metaconid. The entoconid is low but distinct; the hypoconulid is not developed as a distinct cusp, but is represented merely by the lingual end of the posterior crest of the hypoconid. There is a narrow antero-buccal cingulum, but the lingual cingulum is not distinct. The talonid of M_2 is shorter than the trigonid, and the same is probably true of M_1 . The posterior border of M_2 is oblique, being inclined forwards lingually, though not so much as in *Sylvisorex*. The metaconid and entoconid are more anterior than the protoconid and hypoconid respectively. M_3 has two roots, of which the anterior is obliquely elongate in cross-section, with a groove on its posterior side, whereas the posterior root is circular in cross-section.

TABLE I
CROCIDURA

	Rs 1875.50	<i>C. sericea</i>
Alveolar length M_1 - M_3	5.0 mm.	4.4 mm.
Base of coronoid process—anterior end of jaw	8.5	7.3
Internal height below M_1	2.9	2.1
Lingual edge M_2	1.8	1.6
Posterior width M_2	1.5	1.3

RELATIONSHIPS.—Stirton (1930) divided Recent shrews into five groups, which he separated by the characters of the lower jaw and teeth. Most of the distinguishing characters used by Stirton cannot be made out in the *Rusinga* specimen, but in every respect in which it can be compared with the lower jaws of Recent shrews it agrees with members of the *Crocidura* group (*Crocidura*, *Suncus*, *Surdisorex*, *Sylvisorex*, *Myosorex*). The shortness of the talonid, the obliquity of the posterior edge of the molar, and the position of the metaconid further forward than the protoconid, seem to be diagnostic of the *Crocidura* group. The position of the mental foramen below P_4 , rather than M_1 , also distinguishes the *Crocidura* group from other Recent shrews, but it is found in Aquitanian species of "*Sorex*" (Stehlin 1940; Viret & Zapfe 1951). The relatively short symphysis, ending below P_4 , and the backward extension of the crown of I_1 only to below P_4 , are characters found in the *Crocidura* group, in *Sorex* and in *Neomys*; *Sylvisorex* is exceptional for its group in its more extensive symphysis. Only in the primitive species of "*Sorex*" (Stehlin 1940; Viret & Zapfe 1951) and in *Domnina* (Patterson & McGrew 1937) is the incisor smaller.

The *Rusinga* specimen must therefore be placed in the *Crocidura* group, and is referred provisionally to the genus *Crocidura*, pending the discovery of its upper dentition. The only other Miocene species of the genus is *C. schlosseri* (Roger) from Sansan, re-described by Filhol (1891). This agrees with the *Rusinga* specimen in size, but the fragmentary nature of the material does not permit detailed comparison.

Family MACROSCOLIDIDAE

Genus *RHYNCHOCYON* Peters 1847*Rhynchocyon clarki* sp. nov.

(Text-figs. 2, 3)

DIAGNOSIS.—A primitive species of *Rhynchocyon* differing from the Recent members of the genus in the following characters : facial region flatter ; tooth rows more divergent ; extra-nasal processes of premaxilla well-developed ; facial part of lachrymal less extensive ; olfactory bulbs placed further back in relation to the orbits ; P² with anterior basal cusp (parastyle) ; M² less reduced. P¹ – M² 17.5 mm.

The species is named after Professor Sir Wilfred Le Gros Clark, F.R.S.

HOLOTYPE.—Coryndon Museum, Sgr. 93.47, the anterior part of a skull, from Songhor. (Text-fig. 2).

REFERRED MATERIAL.—A number of fragments from Rusinga Island, which cannot be directly compared with the holotype, probably belong to this or a closely related species. They are Rs.998.50, a fragment of maxilla containing P⁴ – M², from site R.1 ; and a number of mandible fragments, namely, Rs.903.50, Rs.904.50 and Rs.1265.50, from site R.1a, Rs.1700.50, from site R.3, and Rs.296.49, from site R.106.

DESCRIPTION OF SKULL.—The holotype consists of the uncrushed facial part of a skull, which has been broken across anteriorly in front of P¹ and posteriorly at the narrowest part of the interorbital region, behind the olfactory lobes.

It is much smaller than *Rhynchocyon petersi* and only a little larger than *Petrodromus tetradactylus* (Table II). The facial part of the skull is broad and flat, as in Recent species of *Rhynchocyon*, and contrasts with *Petrodromus* and other Macroscelidinae. The height of the skull is less, in proportion to length and breadth, than in *R. petersi*. The tooth-rows are slightly more divergent than in *R. petersi*, but not so divergent as in *Petrodromus*. The olfactory bulbs, which in Macroscelididae are pushed forward between the orbits, are situated slightly further back in relation to the anterior borders of the orbits than in Recent *Rhynchocyon* or *Petrodromus*. The backward extension of the maxillary sinus at the sides of the olfactory bulbs is much less than in *R. petersi*. There is a groove for the lateral muscles of the snout at the sides of the face, as in *R. petersi*, but the convexity above it, containing an expansion of the maxillary sinus, is less pronounced. As in *R. petersi*, only M² is below the orbit, whereas in *Petrodromus* the orbit extends over M¹. The infraorbital canal is long, opening above the anterior part of P⁴, as in *R. petersi* ; in *Petrodromus* it opens above M¹, only just in front of the orbit.

The nasals are rounded posteriorly, as in *R. petersi*, whereas in *Petrodromus* their posterior ends are squared off. They are bordered anteriorly by the extra-nasal processes of the premaxillae, very weakly developed in *R. petersi*, but present in *Petrodromus*. A foramen, probably for the alveolar nerve, opens into the infero-medial wall of the infraorbital canal, near its anterior end. In the region of the lateral groove, the maxilla appears to extend back almost to the orbital margin, but

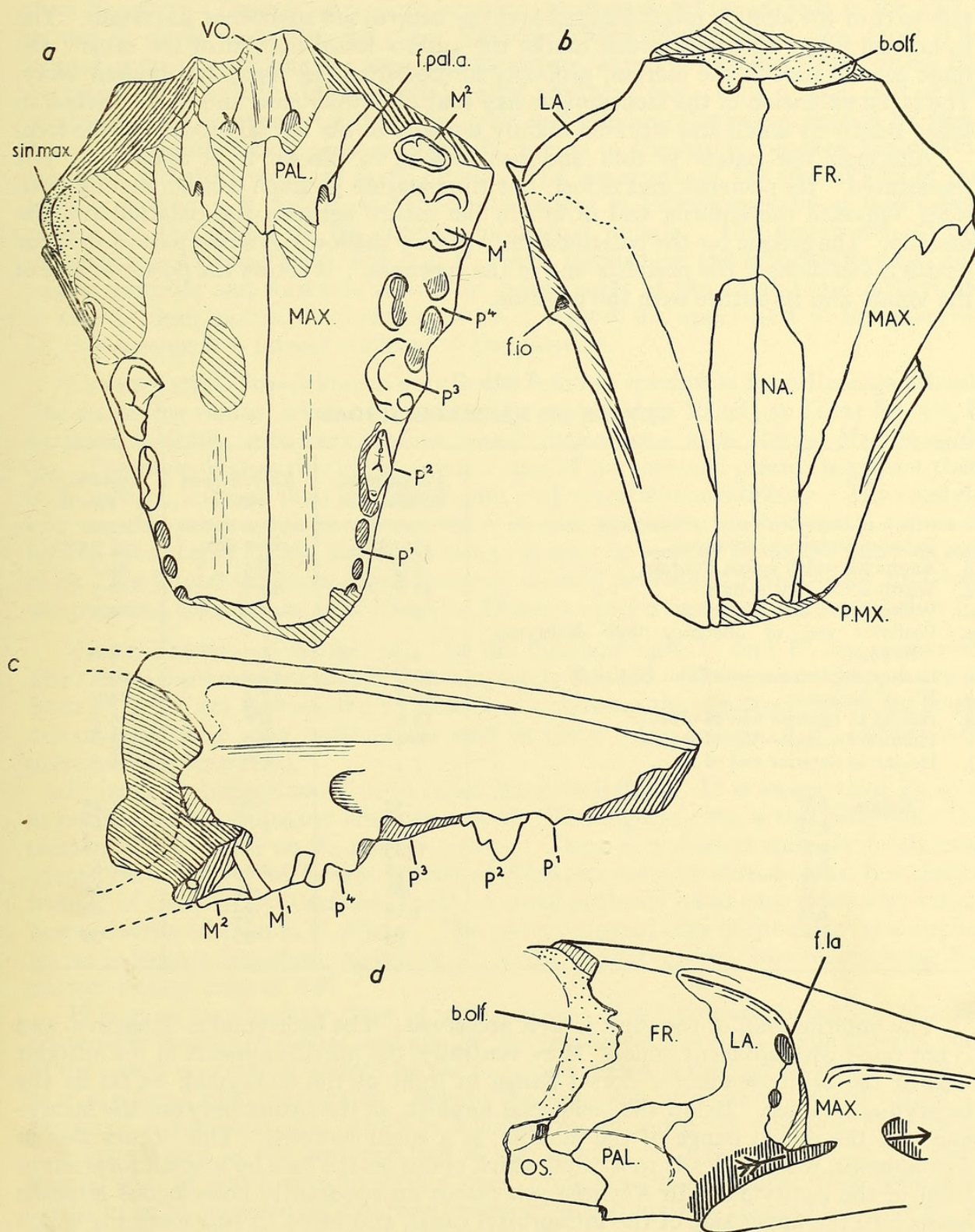


FIG. 2. *Rhynchocyon clarki* sp. nov. HOLOTYPE, Sgr 93.47. (a), (b), (c) palatal, dorsal and lateral views of skull, $\times 8$. (d) posterolateral view of orbit, $\times 10$. FR, frontal; LA, lachrymal; MAX, maxilla; NA, nasal; OS, orbitosphenoid; PAL, palatine; PMX, premaxilla; VO, vomer. b.olf, cast of olfactory bulbs; f.io, infraorbital foramen; f.la, lachrymal foramen; f.pal.a, anterior palatine foramen; sin.max, cast of maxillary sinus. Arrow through infraorbital canal.

this part of the skull is much fissured and the sutures are somewhat uncertain. The lachrymal forms the crest which marks the antero-dorsal margin of the orbit ; the more central part of the margin, probably formed from the jugal, has broken away. The facial extension of the lachrymal is like that of *Petrodromus* and *Macroscelides* in being relatively small and situated mainly dorsally to the lateral groove on the face.

Although the palate is thin and has broken in places, it is apparently not fenestrated. Its posterior end is lost, but the palatine foramen can be seen on both sides, opposite the anterior end of M², in the suture between the palatine and the maxilla. The groove for the palatine artery is very shallow. A small part of the true palate is visible near the posterior end of the specimen ; it shows the posterior end of the vomer and its suture with the palatine.

TABLE II
SKULLS OF MACROSCOLIDIDAE

	<i>Petrodromus tetradactylus</i>	<i>Rhynchocyon clarki</i>	<i>Rhynchocyon petersi</i>
a. Between lachrymal foramina	11.0 mm.	16.5 mm.	25.0 mm.
b. Maximum width across frontals	9.7	17.5	26.3
c. Width across first molars	11.2	10.3	12.3
d. Width across first premolars	9.0	8.9	12.9
e. Posterior end of olfactory bulb—lachrymal foramen	4.5	5.7	4.0
f. Lachrymal foramen—anterior end of P ¹	12.7	17.0	22.5
g. M ² —P ¹ inclusive	16.7	17.5	24.0
h. Height at anterior end of orbit	13.0	9.8	15.3
i. Palatine foramen—top of frontal	10.4	9.0	13.8
j. Height at anterior end of P ¹	7.3	4.6	8.5
Ratios:—b/c57	1.09	1.25
c/d	1.88	1.80	1.63
e/f35	.34	.18
h/j	1.78	2.13	1.80
j/d81	.52	.66
h/a	1.18	.59	.61
i/a94	.55	.55

The anterior wall of the orbit is well preserved. The lachrymal is extensive, and is not fused with adjacent bones. More ventrally, the maxilla appears in the anterior wall of the orbit, sending a dorsal flange in front of the lachrymal, as far as the lachrymal foramen. Below the lachrymal foramen, in the suture between the lachrymal and the dorsal flange of the maxilla, is a small foramen. This occurs also in *Petrodromus*, where it leads to a canal which opens on the face by a small foramen in front of the lachrymal. In *Rhynchocyon petersi* an apparently homologous foramen opens into the upper side of the infraorbital canal, and leads to two foramina which open on the face in the anterior suture of the lachrymal. The relations of the lachrymal and maxilla in the orbit of *R. clarki* resemble *Petrodromus* more closely

than *R. petersi*. There is no contact between the frontal and the maxilla in the orbit ; in this *R. clarki* resembles the other Macroscelididae (Muller 1934 : 209, 219). The frontal meets the palatine in a long, oblique suture, as in *Petrodromus* ; in *R. petersi* the exposure of the palatine in the orbital wall is relatively less. Only a small part of the orbitosphenoid is preserved, and the optic and suboptic foramina cannot be seen. A small foramen, facing postero-ventrally, occurs in the suture between the orbitosphenoid and the frontal, as in *R. petersi*. The lower part of the rostral wall of the orbit is marked in *R. petersi*, and to smaller extent in *Petrodromus*, by an impression caused by the origin of the internal pterygoid muscle. The upper edge of the impression is a curved crest, which in *R. petersi* begins near the suboptic foramen and passes upwards and forwards across the lower parts of the frontal and lachrymal. It may be seen also in *R. clarki*, in which it crosses the upper part of the palatine. In *Petrodromus* it is largely confined to the palatine.

LOWER JAW.—This is known only in the referred specimens from Rusinga Island. The ascending ramus, which is incompletely preserved in Rs.903.50 (Text-fig. 3*b*), is flattened laterally, with very shallow muscle impressions, as in Recent Macroscelididae. The angle of elevation of the anterior edge of the coronoid process is greater than in *R. petersi*, but less than in *Petrodromus* and other Macroscelidinae. The condyle and angular process are not preserved. In this specimen the horizontal ramus is broken off anterior to M_1 , but in Rs.904.50 it may be seen as far as the anterior end of P_3 . The lateral surface is slightly convex, as in *R. petersi* and *Petrodromus*, and does not possess a lateral crest as in *Nasilio*. There is a posterior mental foramen below P_4 .

UPPER TEETH.—(Text-fig. 3*a*). In the holotype only P^2 and P^3 are preserved. Their crowns are unworn, and P^2 is incompletely erupted. The remaining upper teeth, from P^1 to M^2 , are represented by their roots, showing that replacement of the milk-molars took place after both molars were in place. The crowns of $P^4 - M^2$ are well preserved in Rs.998.50.

P^1 has two distinct roots, as in other Macroscelididae. P^2 is longer than P^1 , oval in outline, and presumably also two-rooted. The highest cusp is the paracone ; the metacone is situated on its posterior slope. There is a distinct anterior basal cusp (parastyle) as in Pd^2 of Recent species of *Rhynchocyon* and *Petrodromus*, but absent from P^2 of these forms (Carlsson, 1909). A small posterior basal cusp is present, rather better developed than in *R. petersi*. The postero-lingual edge of the crown is occupied by an indistinct cingulum, absent in P^2 of the Recent species, but representing the postero-lingual cusp of Pd^2 .

P^3 is at an intermediate stage of molarisation. It is triangular in outline, broader posteriorly than in *R. petersi*, and apparently possesses three roots. The anterior part of the crown is occupied mainly by the paracone, which is the highest cusp. In front of it is a basal cusp (parastyle). Behind the paracone, and closely united with it at the base, is the metacone, which is followed by an indistinct posterior basal cusp. The lingual part of the posterior half of the crown is occupied by a basin, the most lingual edge of which rises to form a cusp, probably the hypocone. The protocone seems to be represented by a narrow antero-lingual cingulum, absent in *R. petersi*; in *Petrodromus* and other Macroscelidinae the protocone of P^3 is a distinct cusp. No buccal cingulum is present on P^2 or P^3 .

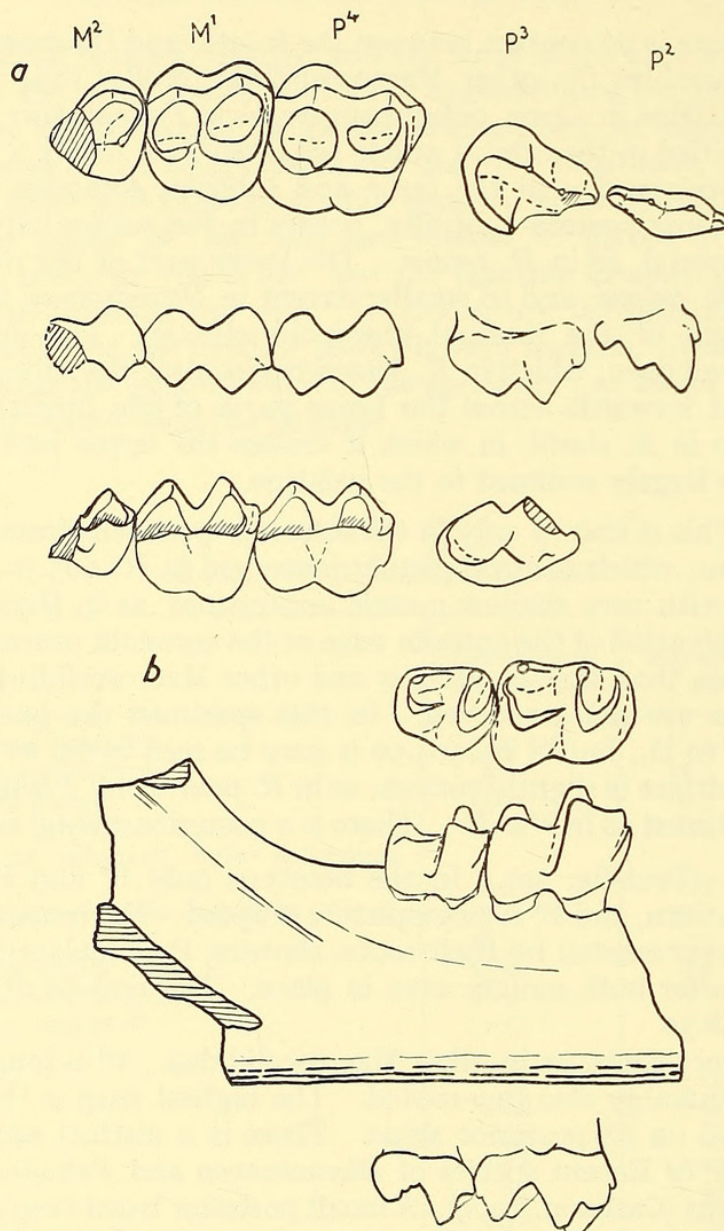


FIG. 3. *Rhynchocyon clarki* sp. nov. (a) Crown, buccal and lingual views of right upper cheek-teeth. P⁴ — M² from Rs 998.50, P² and P³ from Sgr 93.47 (P³ reversed). $\times 10$. (b) Lower jaw fragment, Rs 903.50, lateral view, and M₁₋₂ in crown and lingual views. $\times 10$.

P⁴, as seen in Rs.998.50, is fully molariform, and is the largest of the cheek teeth. In comparison with *R. petersi* it is slightly broader in proportion to its length, and its buccal cusps are less elevated. The subequal paracone and metacone are placed near the buccal edge, and there is no buccal cingulum. The crown is moderately worn, and the original shape of the lingual cusps cannot be determined. The protocone is connected by a crest to the antero-lingual side of the paracone. Anterior to this crest is a short cingulum, continuous with the parastyle. In *R. petersi*, judging from somewhat worn specimens, this cingulum is continued lingually up to the tip of the

protocone ; in *Petrodromus* the cingulum is broadened and elevated to form a small cusp, and the crest from the protocone runs directly to the tip of the paracone. Posteriorly, the protocone is connected with the hypocone by a crest, the bay on the lingual side being much more weakly indicated than in *R. petersi* or *Petrodromus*. A transverse crest links the protocone with the antero-lingual face of the metacone, dividing the central part of the crown into two basins, of which the posterior is somewhat lower than the anterior, as in *R. petersi*. The hypocone seems to be somewhat lower than the protocone, as in *R. petersi*, whereas in *Petrodromus* the hypocone is equal to or higher than the protocone on somewhat worn teeth. There is no lingual cingulum.

M¹ resembles P⁴, except that the posterior part of the crown is narrower than the anterior part, the groove on the lingual side between the protocone and hypocone is somewhat deeper, and the metacone is lower than the paracone. Similar differences between the two teeth are found in *R. petersi* ; in *Petrodromus* the reduction of the posterior part of the crown is less marked. Like P⁴, M¹ is borne on three roots, of which the lingual one is much the largest.

M² is much smaller than M¹, but it is slightly less reduced in comparison with M¹ and P⁴ than in *R. petersi*, though more reduced than in *Petrodromus*. It is narrowed posteriorly, and thus has a triangular outline, with an oblique buccal edge. The lingual root is subequal to the buccal roots. The protocone and paracone resemble those of M¹ ; the posterior part of the crown has broken away, but must have been much reduced, as in *R. petersi* and *Petrodromus*.

TABLE III
TEETH OF MACROSCOLIDIDAE

	<i>Petrodromus tetradactylus</i>	<i>Rhynchocyon clarki</i>	<i>Rhynchocyon petersi</i>
Upper teeth (length × breadth)		(Sgr 93.47)	
P ²	2.9 × 1.5 mm.	3.0 × 1.3 mm.	3.1 × 2.6 mm.
P ³	3.0 × 2.3	3.6 × 2.7	4.6 × 3.1
		(Rs 998.50)	
P ⁴	4.2 × 3.4	3.6 × 3.1	4.7 × 4.0
M ¹	3.5 × 3.5	3.2 × 3.1	4.2 × 4.2
M ²	2.8 × 3.0	2.1e × 2.4	2.7 × 2.9
Lower teeth (length)		(Rs. 904.50)	
P ₃	3.0	3.0	4.4
P ₄	3.8	3.5	5.2
		(Rs. 903.50)	
M ₁	3.4	3.3	4.3
M ₂	2.9	2.5	2.7

LOWER TEETH.— P_3 is preserved in Rs.904.50, in which however it is much worn. In Recent species of *Rhynchocyon* this tooth possesses a crest from the protoconid to the postero-buccal apex of the crown, and there is no metaconid, though a posterior accessory cusp is present. In *Petrodromus* the crest is postero-lingual, and it bears a small metaconid, the posterior accessory cusp being absent. In *R. clarki* a postero-lingual crest is present, and the posterior accessory cusp appears to be absent, as in *Petrodromus*, but the worn crown shows no evidence of a metaconid. P_4 is longer than P_3 ; its talonid is molariform, but its trigonid is not preserved.

M_1 is present almost unworn in Rs.903.50 (Text-fig. 3*b*). It resembles that of Recent *Rhynchocyon* in that the paraconid is nearly in line with the metaconid and entoconid, whereas in the Macroscelidinae it is more buccal. The tooth shows distinctive features: the anterobuccal cingulum is more distinct than in Recent *Rhynchocyon* or *Petrodromus*; the anterior crest of the hypoconid stops short at the base of the posterior face of the trigonid, whereas in Recent forms it reaches nearly to the tip of the metaconid; the posterior cingulum, behind the hypoconid, is more distinct. Similar features may be seen on the talonid of P_4 .

M_2 is well preserved in Rs.1700.50 and in Rs.903.50. It is not so much reduced in proportion to M_1 as in *R. petersi*, but more so than in *Petrodromus*. The paraconid is less lingual than on M_1 , so that it resembles M_2 of *Petrodromus* rather than Recent *Rhynchocyon*. As in Recent forms, the talonid is smaller in proportion to the trigonid than in M_1 . There is no trace of M_3 .

RELATIONSHIPS.—The holotype resembles Recent species of *Rhynchocyon* and differs from the Macroscelidinae in the broad flattened face, the rounded posterior ends of the nasals, the long infraorbital canal, the unfenestrated palate, the position of M^1 in front of the orbit, and the shape of P^3 . It resembles *Petrodromus* rather than *Rhynchocyon* in size, in the development of the extranasal process of the premaxilla, in the reduced facial extension of the lachrymal, and in details of the anterior wall of the orbit. In other respects it is intermediate between the two genera: the divergence of the tooth-rows, the presence of a rudimentary protocone on P^3 , and the degree of reduction of M^2 . It seems to be more primitive than any living member of the family in the more posterior position of the anterior end of the cranial cavity in relation to the orbits, and in the presence of a parastyle on P^2 .

The Rusinga specimens show a similar mixture of characters. As in *Rhynchocyon*, the hypocone of P^4 is lower than the protocone, and the paraconid of M_1 is relatively lingual. As in *Petrodromus*, the posterior accessory cusp of P^3 is lacking, and the paraconid of M_2 is more buccal than the metaconid. In the elevation of the coronoid process, the anterior crest of the protocone of P^4 and M^1 , and the reduction of M^2 and M_2 , the Rusinga form is intermediate between the two genera. It is more primitive than Recent Macroscelididae in the less hypsodont teeth, the weaker separation of the protocone and hypocone on P^4 , the presence of small antero-buccal and postero-buccal cingula on M_1 , and the character of the anterior crest of the hypoconid on the lower molars.

Such a mixture of characters is to be expected in an early member of the *Rhynchocyon* lineage. *R. clarki* already shows some of the characteristic specialisations of *Rhynchocyon*, and indicates that the Rhynchocyoninae and Macroscelidinae had

separated before the Miocene. It is however nearer to the common ancestor of the two groups, and possesses a number of primitive characters which have been lost in Recent representatives of both subfamilies.

Rhynchocyon clarki throws no light on the relationships of *Pseudorhynchocyon cayluxi* Filhol (1892), based on the posterior part of a mandible without teeth, from the French Phosphorites (probably L. Oligocene). This form was compared with *Rhynchocyon* because of the weak development and backward inclination of the coronoid process. *R. clarki* indicates, however, that this specialisation of the Rhynchocyoninae was less marked in Miocene times, and that the Oligocene ancestors probably resembled *Petrodromus* in the possession of a more vertical coronoid process. The presence of such a high degree of inclination in a Lower Oligocene form cannot therefore be considered as evidence of affinity, and the reference of *Pseudorhynchocyon* to the Macroscelididae is most improbable.

Palaeothentoides africanus Stromer (1931), from the Pliocene of South Africa, is not a marsupial as supposed by Stromer, but a member of the Macroscelididae. It shows much resemblance to *Nasilio*, for example, in the retention of a small M_3 . Stromer mistook the molariform P_4 for the first molar, and hence concluded that there were four molars.

Family CHRYSOCHLORIDAE

Genus *PROCHRYSOCHLORIS* nov.

DIAGNOSIS.—Dental formula 3.1.3.3. ; M^2 the widest upper tooth; P^3 at an early stage of molarisation, comparable with P^2 of Recent genera ; lingual cusp of upper molars (protocone) relatively large and V-shaped.

TYPE SPECIES.—*Prochrysochloris miocaenicus* sp. nov.

Prochrysochloris miocaenicus sp. nov.
(Text-figs. 4, 5)

DIAGNOSIS.—Greatest width across the upper cheek-teeth about equal to the length of the palate ; length of upper dental series about 12 mm.

HOLOTYPE.—The anterior part of a skull, broken off just behind the cribriform plate. Coryndon Museum Sgr.638.49. Lower Miocene of Songhor, Kenya Colony.

PARATYPE.—A specimen in a similar state of preservation to the holotype, but lacking the snout anterior to P^3 , and showing the crown of right P^3 and M^1 (Brit. Mus. Geol. Dept. M.14236). Lower Miocene of "Maize Crib", Koru, Kenya Colony.

DESCRIPTION OF SKULL.—The following species of Recent Chrysochloridae have been studied for comparative purposes : *Chrysospalax trevelyani*, *Amblysomus hottentottus*, *Chlorotalpa duthiae*, *Chrysochloris asiatica*, and *Eremitalpa granti*.

In the length of the upper dental series, *P. miocaenicus* exceeds all these species other than *C. trevelyani*. In proportion to this length, the palate and the midcranial region are very broad, resembling *E. granti* and *C. asiatica* (Table IV). Judging by the

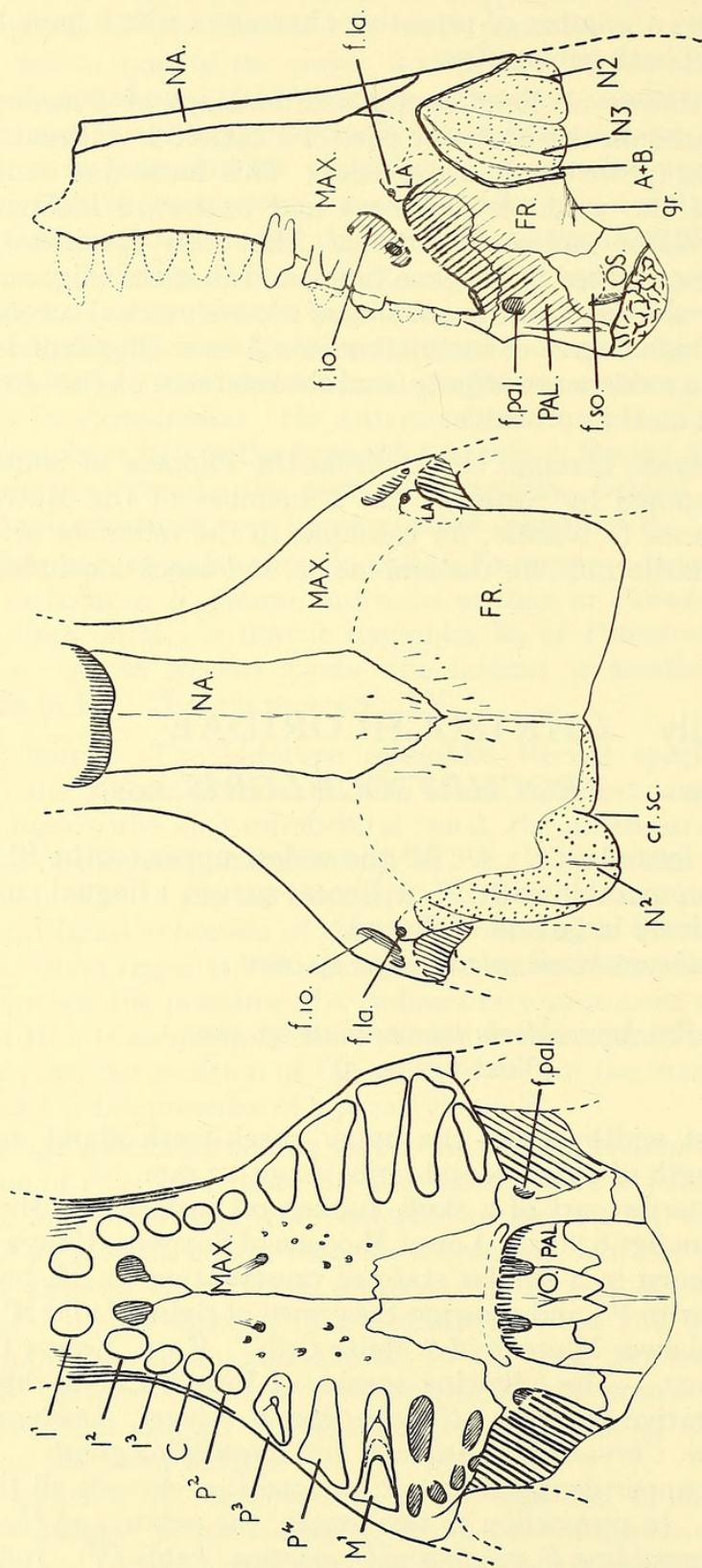


FIG. 4. *Prochrysochloris miocaenicus* gen. et sp. nov. Partial reconstruction of skull: palatal, dorsal and left lateral views. $\times 10$. Part of the frontal bone is represented as removed, to show the cast of the olfactory chamber. FR, frontal; LA, lachrymal; MAX, maxilla; NA, nasal; OS, orbitosphenoid; PAL, palatine; VO, vomer. *cr.sc*, crista semicircularis; *f.io*, infraorbital foramen; *f.la*, lachrymal foramen; *f.pal*, palatine foramen; *f.so*, sphenorbital foramen; *gr*, venous groove on frontal.

proportionate length of the olfactory chamber behind the lachrymal foramen, the midcranial region was not elongated as in *C. trevelyani*. The interorbital part of the olfactory chamber is relatively lower than in *C. asiatica* and *E. granti*, and the upper profile of the face does not rise so steeply in relation to the tooth-row as in these species, but resembles *C. duthiae*.

In Recent Chrysochloridae most of the sutures of the skull close early in life. In *C. miocaenicus*, although M^3 has erupted, most of the sutures remain open, as may be seen in both specimens. The only sutures which have united are the interfrontal suture, the suture between the maxilla and the premaxilla, and the internasal suture (still partly open however in the paratype). It is of course possible that neither specimen is completely mature.

The nasals are parallel-sided bones, overlapped laterally by the maxillae and posteriorly by the frontals. The median suture is represented by a groove in the holotype, but its posterior end remains open in the paratype. The united frontals possess a very slight median crest; they extend forwards laterally to the posterior ends of the nasals to meet the maxillae, which they partly overlap.

The extreme tip of the snout is missing in the holotype, but there is an indication of the broadening of this region found in Recent forms. The premaxilla cannot be distinguished from the maxilla on the face, the suture between the two bones having completely closed. The medial palatal process between the incisive foramina is however suturally distinct from the maxilla.

The infraorbital canal was very short, as in Recent forms, but its lateral wall is broken away on both specimens. Some foramina open into its medial side, perhaps for branches of the superior alveolar nerve. The zygomatic process is not preserved. The lachrymal foramen opens immediately dorsally to the infraorbital foramen, in the suture between the maxilla and the small lachrymal. As in Recent Chrysochloridae, therefore, the lachrymal duct does not pierce the lachrymal bone (Roux, 1947). The maxilla extends on to the anterior wall of the orbit, below the lachrymal, and meets the frontal and palatine.

There are many scattered foramina in the palatine part of the maxilla, of which one on each side, placed opposite P^2 , is larger and apparently carried the main branch of the palatine nerve. Similar foramina occur in Recent Chrysochloridae, opposite P^2 in *C. trevelyani*, *A. hottentottus* and *E. granti*, opposite the canine in *C. duthiae* and *C. asiatica*. The palatine bones terminate anteriorly in a transverse suture, opposite M^1 . The posterior part of the palate is broken away in both specimens, but it certainly did not extend back far behind the posterior molar as it does in *C. trevelyani* and *A. hottentottus*.

The medial wall of the orbit is visible in both specimens, the sutures being clearly indicated. The palatine meets the frontal in a horizontal suture at about half the height of the maxilla. The palatine foramen is placed near the suture with the maxilla. The lateral wall of the sphenorbital canal is broken away in both specimens, but the floor of the canal is clearly preserved in the paratype. There is a vertical groove on the orbital part of the frontal, following the edge of the eribriform plate, and representing a venous foramen which in Recent forms opens into the dorsal side of the sphenorbital canal. There is no trace of the optic foramen in the portion of the orbitosphenoid, that is preserved, and it was probably absent, as in Recent forms.

TABLE IV
SKULLS OF CHRYSOCHLORIDAE

	<i>Prochrysochloris mocaenicus</i>		<i>Eremitalpa granti</i>	<i>Chrysochloris asiatica</i>	<i>Chlorotalpa duthiae</i>	<i>Amblysomus hottentottus</i>	<i>Chrysofalax trevelyani</i>
	Holotype	Paratype					
a. Greatest width across cheek teeth	mm. 11.4	mm. 12.0	mm. 8.1	mm. 8.0	mm. 7.5	mm. 8.3	mm. 14.0
b. Width across posterior part of olfactory chamber	9.7	10.2	7.4	8.3	6.6	8.3	10.6
c. Length of upper dental series . .	11.8	—	8.3	10.0	10.1	10.7	17.3
d. Lachrymal foramen—anterior end of alveolus for I ¹	9.7	—	6.7	8.4	8.4	10.5	14.7
e. Lachrymal foramen—postero-dor- sal end of olfactory chamber . .	5.0	5.5	3.1	4.0	3.7	6.0	10.4
f. Palatine foramen—upper side of frontal	6.3	7.0	5.6	6.5	5.4	6.0	9.7
Ratios:—a/c97	—	.98	.80	.74	.78	.81
b/c82	—	.89	.83	.65	.78	.61
e/d52	—	.46	.48	.44	.57	.71
f/e	1.26	1.28	1.81	1.63	1.46	1.00	.93
f/b65	.69	.76	.78	.82	.72	.91

The cribriform plate is visible in posterior view in both specimens (Text-fig. 5). Its main part is orientated at about 70° to the upper surface of the skull. There is a somewhat convex median region, with a slight crista galli. Dorsally there is a median foramen through which the sagittal vein passed out of the olfactory chamber, and on each side of this, at the edges of the median region of the cribriform plate, is a foramen for the anterior ethmoidal nerve. The distance between the latter foramina is about half the width of the cribriform plate. The lateral regions of the plate are concave, the line of junction with the side wall of the skull being nearly vertical. The posterior and ventral part of the plate, forming the tectum posterior nasi, is approximately horizontal. The only Recent species of which comparative material is available is *A. hottentottus*: in this species, the median region of the cribriform plate is relatively narrower, and the ethmoid foramina are therefore closer together in

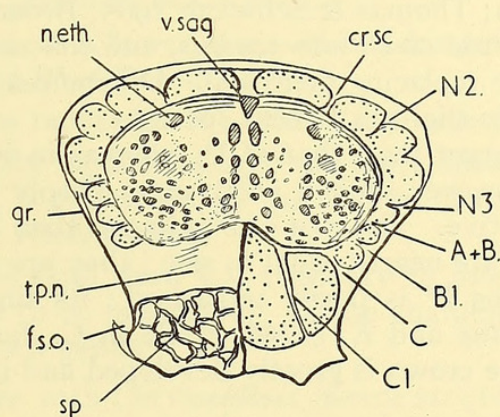


FIG. 5. *Prochrysochloris miocaenicus* gen. et sp. nov. Reconstruction of cribriform plate and adjacent parts, seen from behind. $\times 10$. On the right side the cupula posterior is represented as having been opened by removal of the tectum posterior nasi. *cr.sc*, crista semicircularis; *f.so*, sphenorbital foramen; *gr*, venous groove on frontal; *n.eth*, foramen for anterior ethmoidal nerve; *t.p.n*, tectum posterior nasi; *v.sag*, foramen for sagittal vein; *sp*, spongiosa in orbitosphenoid.

proportion to the width of the plate as a whole, but otherwise the differences appear to be slight. In both the Recent and the fossil forms the floor of the brain-cavity immediately behind the cribriform plate slopes down rapidly, forming the posterior wall of the cupula posterior of the olfactory capsule. At the bottom of the slope in the Recent form is a transverse groove for the optic chiasma. This region is broken away in the fossils, but the paratype shows that the interior of the presphenoid is filled with spongy bone as in *A. hottentottus* and other Recent Chrysochloridae (Forster-Cooper, 1928).

Some features of the internal structure of the olfactory capsule can be made out, but no differences from Recent forms were noticed. The nasoturbinal is placed under the suture between the maxilla and the nasal, and lateral to it is a groove, visible in the holotype, marking the internal opening of the lachrymal duct. The holotype also shows an incomplete median septum formed by the prevomerine processes of the premaxillae. The maxillary sinus extends back to about 1 mm. behind the lachrymal foramen. Where the superficial bone has broken away, both specimens show natural

casts of the chambers for the ethmoturbinals. Most dorsally is a chamber on the medial side of the crista semicircularis. Next to this are spaces for two bifurcate ectoturbinals in the recessus superior: the first ectoturbinal (N2) is attached near the dorsolateral extremity of the olfactory capsule, and the second (N3) is placed lower down on the side wall. The ventral chamber of the second ectoturbinal is small. Beneath it is the line of attachment of the first endoturbinal (A & B; posterolateral sulcus of Roux, 1947). There are four more chambers, separating three more turbinals, the most ventral turbinal (C1) being situated in the cupula posterior of the olfactory capsule.

UPPER TEETH.—In the holotype all the crowns are broken off, but the roots of ten teeth on either side may be interpreted as *i*3, *c*1, *p*3, *m*3. The paratype shows something of the crowns of P³ and M¹. In Recent forms, replacement of the milk teeth takes place very late in life, and they are present in the majority of the skulls in collections (Leche 1904; Thomas & Schwann 1905; Broom 1908). It is impossible to say whether this was true of *P. miocaenicus*, and the antemolar teeth are named as if they belonged to the replacing dentition. Differences between the teeth of the two sets are comparatively slight in Recent species.

The root of I¹ is no larger than that of I², whereas in Recent forms it is always enlarged; the skull is however broken away more deeply near I¹ than I², and the appearance may be deceptive. The root of I² is longer than broad. I³, C and P² have nearly circular roots and are nearly equal in size; they are shorter anteroposteriorly than I². In Recent forms P² is partly molarised: its single root is triangular in *C. trevelyani*, *A. hottentottus* and *E. granti*, while in *C. duthiae* and *C. asiatica* the postero-buccal apex of the crown is greatly developed and is supported by a distinct root.

P³ of *P. miocaenicus* is a triangular tooth with apparently incompletely divided roots, resembling P² rather than P³ of Recent species. The postero-buccal apex is prominent, and the posterior edge is the longest (1.7 mm.), but the tooth does not depart greatly from an equilateral triangle. On the crown the highest cusp is lingual in position, and there was apparently a strong postero-buccal style. P⁴ is a transverse, molariform tooth, though not so wide as M¹, and having the postero-buccal apex more prominent than the antero-buccal apex, as in P³ of Recent forms. It has three roots, of which the transversely elongated lingual one supports the greater part of the crown. The posterior edge of the tooth measures 2.6 mm. in the paratype.

M¹ is the most symmetrical molariform tooth. In the paratype the crown, though damaged, shows a central V-shaped paracone and a lingual protocone, as in *C. trevelyani* and *A. hottentottus*. The protocone, however, forms about 40% of the width of the crown, compared with about 25% in *C. trevelyani*; it was evidently much higher than in Recent forms, and more definitely V-shaped, being continuous with cingula on the anterior and posterior faces of the paracone. The tooth is 1.2 mm. long and 3.3 mm. broad in the paratype.

M² and M³ are known only from the roots or alveoli. M² is broader than M¹, its antero-buccal apex projecting beyond the postero-buccal apex of M¹. M³, though smaller than M², is less reduced in size than in Recent Chrysochloridae.

Between the cheek teeth, beginning at the space between P³ and P⁴, the maxilla is pitted to receive the trigonids of the lower teeth when the jaws are closed.

RELATIONSHIPS.—In spite of the considerable advances in our knowledge of the group made by Broom, Roberts and Forster-Cooper, the taxonomy of the Chrysochloridae is still somewhat confused. Most of the described species appear to be of very limited distribution, and it seems likely that a large proportion will eventually be reduced to sub-specific status. The tendency has been to put most of the well-marked species into separate genera, based on such characters as the presence or absence of M^3 and M_3 , the development of the talonid on the lower molars, the proportions of the skull, the shape and size of the malleus, and the shape of the feet e.g. Roberts (1924). Forcart (1942) attempted to reduce the number of genera, mainly by making some of them sub-genera of *Chrysochloris*, but Broom (1946) objected to this, at least in the case of *Eremitalpa*.

Prochrysochloris miocaenicus is the first golden mole to be described from pre-Pleistocene deposits. It differs from all members of the family hitherto known in the possession of a number of primitive characters :—

- (1) The premolars are at a lower stage of molarisation, P^3 and P^4 resembling respectively P^2 and P^3 of Recent forms.
- (2) The molars are less reduced, so that M^2 is the widest tooth.
- (3) The protocone of the molars is larger and more definitely V-shaped ; in correlation with this it is probable that the talonid of the lower molar was better developed than in Recent forms.
- (4) The sutures of the skull show less tendency to fuse (unless both the known specimens happen to be immature). These characters would seem to justify the creation of a new genus.

Prochrysochloris agrees with *Chrysochloris* (sensu stricto) and *Eremitalpa* among Recent golden moles, in the short, broad skull, but this may well be an adaptive character associated with burrowing habits, and does not necessarily imply special affinity. *Prochrysochloris* throws little light on the relationships of the family, except to show that nearly all the distinctive features of the anterior part of the head had already been acquired in the Lower Miocene.

Family TENRECIDAE

Genus *GEOGALE* M.-Edw. & Grandid., 1872

At the present time, this genus is confined to Madagascar. The type species is *G. aurita* M.-Edw. & Grandid. As shown by Heim de Balsac (1955), *Cryptogale australis* Grandidier (1928) is very close to *G. aurita*, of which it is probably to be regarded as a subspecies.

Geogale aletris sp. nov.
(Text-fig. 6)

DIAGNOSIS.—A species of *Geogale* differing from *G. aurita* in the absence of P^2 , the larger postero-buccal lobe of M^2 , and the greater backward extension of the palate behind the teeth. $I^1 - M^3$ inclusive, 8.3 mm.

HOLOTYPE.—The facial part of a skull. Coryndon Museum, Rs.764.50, from site R.3, Rusinga Island. This is the only known specimen.

SKULL.—The specimen on which this species is based consists of the anterior part of a skull, broken off just behind the cribriform plate, and showing the palate, with either the upper teeth or their roots. The roof of the skull has flaked away, exposing the interior of the olfactory chamber as a cast. The skull is a little larger than in *G. aurita*, and resembles in size that of *Microgale cowani*. The snout is even shorter than in *G. aurita*.

A small part of the premaxilla remains, showing that its posterior suture is not closed as in Recent adult Tenrecidae. The comparatively small infraorbital foramen is placed above P^4 : in *G. aurita* it is just anterior to P^4 , but in other Oryzorictinae it is above M^1 . In front of the infraorbital foramen, shortly behind the canine, is a small foramen in the maxilla, which seems to be represented by two small foramina in this

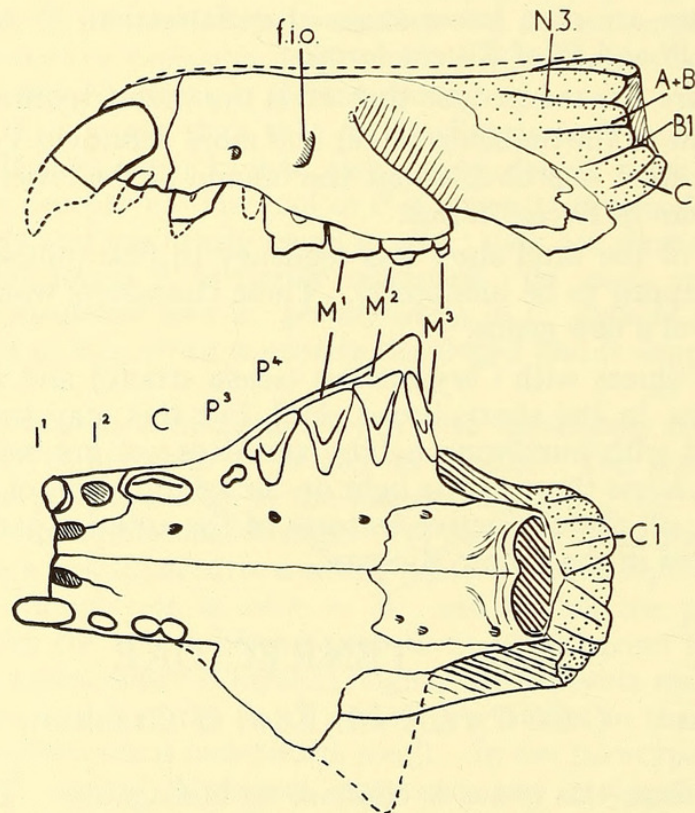


FIG. 6. *Geogale aletris* sp. nov. HOLOTYPE, Rs 764.50. Left lateral and palatal views. $\times 11$. *f.io.*, infraorbital foramen.

region in *G. aurita*; in other Oryzorictinae and in *Potamogale* there is a foramen farther back, usually over P^4 , which may correspond to it. The infraorbital canal, although much longer than in most Tenrecidae, is not unlike that of *G. aurita*. Its posterior opening is over M^2 . Owing to a fracture, the lachrymal foramen cannot be made out. The short zygomatic process is placed outside M^3 , and is directed outwards as in *G. aurita* and other Tenrecidae.

The palate is not perforated. Unlike other Tenrecidae, it extends backwards for some distance (1.3 mm.) behind M^3 , where it is thickened to form a transverse crest. The suture between the palatine and maxilla is not closed ; it is situated opposite M^2 . There is a postero-lateral palatine foramen.

The inner wall of the orbit is too poorly preserved for the sutures to be determined with certainty. Owing to lengthening of the palate, the olfactory chamber does not extend so far behind the palate as in Recent *Oryzorictinae*.

The chambers for the ethmoturbinal conchae agree with those of *Prochrysochloris*. There seem to have been two bilaminar ectoturbinals (N_2 and N_3) in the dorso-lateral recess. Below the lower wall of this recess (lateral attachment of A & B) are two small chambers, for turbinals B_1 and C respectively. The chamber for the bifurcated turbinal C_1 is below the horizontal part of the cribriform plate. The ventral turbinal chambers, unlike those of *Prochrysochloris*, do not meet in the middle line, but are separated by a cast of the posterior part of the respiratory passage, visible on either side of the median septum. Judging from skulls seen in transparency by a bright light, a similar arrangement occurs in *Microgale* and *Oryzorictes*.

UPPER TEETH.—The dental formula is i_2, c_1, p_2, m_3 . Dobson (1882) gave the formula of *G. aurita* as i_2, c_1, p_3, m_3 . Leche (1907) regarded the third tooth as an incisor ; with good magnification, however, it is possible to confirm Dobson's statement that the closed premaxillary suture passes anterior to this tooth, which must therefore be the canine.

I^1 is greatly enlarged, but only the root is preserved. It is flattened laterally, so as to form a long oval in cross-section, and the root curves backwards to above the canine. I^1 is well separated from the corresponding tooth on the other side ; this is also seen in *G. aurita*, where the large anterior lower incisors bite between the upper ones. I^2 is a smaller tooth, represented only by its root.

Separated from I^2 by a short diastema is the canine, the crown of which is considerably worn. The canine is antero-posteriorly elongated, and has a single root which is deeply grooved on the buccal side. Behind the canine is a diastema equal to about half the length of the tooth. This is followed by the root of a small tooth, presumably P^3 , but owing to a fracture of the skull in this region it is not certain whether P^3 had more than one root. P^2 is absent, whereas in *G. aurita* it is present, though minute.

TABLE V
GEOGALE

	<i>G. aletris</i>	<i>G. aurita</i>
Palatal crest—anterior end of alveolus for I^1	9.6 mm.	8.4 mm.
Anterior end P^4 —anterior end of alveolus for I^1	4.0	4.4
P^4 — M^3 inclusive	4.3	3.7
Width across paracones of first molars	6.7	5.7
Width across anterior incisors	3.1	2.6
Width across zygomatic processes	9.4	7.8
Palatal crest—top of frontal	3.8	3.5

$P^4 - M^3$ are of zalambdodont structure, though their crowns are greatly worn and details of the pattern cannot be made out. P^4 is triradiate, with three roots. The paracone occupies a central position, and is joined by a strong shearing crest to the metastyle; the postero-buccal lobe of the outline is well developed. On the anterior and lingual lobes there seem to have been a low parastyle and a low protocone respectively, but they have been rounded off by wear.

M^1 is broader than P^4 . The protocone must have been small and low; the paracone is displaced towards the lingual side as in other Tenrecidae, and forms the lingual apex of an elevated triangular area. M^2 is more transverse than M^1 , and a bay is visible in its buccal edge. The postero-buccal apex of the crown is somewhat more prominent than the antero-buccal apex, as in *Microgale*, whereas in *G. aurita* it shows signs of reduction. The pattern of M^2 is like that of M^1 . M^3 is a very transverse tooth, as in *G. aurita*. Its postero-buccal lobe is greatly reduced, the root being placed about midway between the lingual and antero-buccal roots. The crown bears a low lingual protocone and a high median paracone.

RELATIONSHIPS.—The zalambdodont upper molar teeth suggest comparison with the two African families now possessing such teeth, the Chrysochloridae and the Tenrecidae.

In all the existing Chrysochloridae the infraorbital canal is very short, opening above M^1 . The zygomatic process arises in most species opposite M^1 (in *Chrysochloris trevelyani* opposite M^2); it passes back to form a complete zygomatic arch. Although the median upper incisors are enlarged, they are broader transversely than in the Rusinga specimen, and touch in the middle line, the lower incisors biting behind them. The incisors are more spaced, and I^1 is more vertical. No chrysochlorid shows reduction of P^2 , but on the contrary there is a tendency for the tooth to become molariform. The emphasis of the cheek teeth is further forward, and M^2 and often also M^1 show signs of reduction. There seem therefore to be no grounds for placing the specimen in the Chrysochloridae.

Until recently the only Tenrecid known to be living on the African continent was *Potamogale velox*. This is often placed in a distinct family, Potamogalidae, but the differences from the Madagascan Tenrecidae, such as the loss of the clavicles and of the lachrymal foramen, seem to be mainly adaptive to an aquatic mode of life; we therefore follow Weber (1928) in uniting *Potamogale* with the Tenrecidae. *P. velox* differs from the Rusinga fossil in its much longer and narrower snout; its palate does not extend much beyond M^3 , and lacks a posterior crest; there is no small foramen in the maxilla in front of the infraorbital foramen; the large anterior incisors are close together, and are broadened transversely as in Chrysochloridae; I^2 and I^3 are not reduced; the canine has two distinct roots; P^2 and P^3 are not reduced; the protocones of the molars are probably somewhat larger. Characters which *Potamogale* shares with the Rusinga species are also found in Madagascan Tenrecidae: the short zygomatic process, placed far back, directed outwards and not forming a zygomatic arch; the narrow mid-cranial region, the width across the posterior part of the olfactory chamber being about half the greatest width across the cheek teeth (also in *Geogale* and *Limnogale*); the enlarged I^1 , with backwardly curving root (also in *Geogale*, *Limnogale*, and to a lesser extent in *Microgale*); the well-developed postero-buccal lobe of M^2 (found in *Limnogale*, *Microgale*, *Oryzorictes* and *Tenrec*).

A second species of *Potamogale*, *P. ruwenzorii*, has recently been described by de Witte & Frechkop (1955). This approaches *G. aletris* in its shorter snout, which is, however, less slender than in the fossil form. It agrees with *P. velox* in dental formula and in the semi-molariform condition of P^3 , but approaches *G. aletris* in the form of M^3 . *Micropotamogale lamottei* Heim de Balsac (1954), is known only from a single immature specimen, in which M^2 is described as erupting. As there is no trace of a third molar, it is possible that this animal has only five post-canine teeth, as in *G. aletris*. Although three incisors are present, I^3 is described as more reduced than in *Potamogale*.

None of the living African Tenrecidae resembles the Rusinga species as closely as the Madagascan *Geogale aurita*. The two forms agree with each other and differ from other Tenrecidae in the short snout, the relatively long infraorbital canal, the presence of foramina in the maxilla in front of the infraorbital foramen, and the shape and degree of separation of the large anterior incisors. Because of these special resemblances, the fossil is placed in the genus *Geogale*. It is probably more primitive than *G. aurita* in the better development of the postero-buccal lobe of M^2 . It is more progressive than the living species in the loss of P^2 and the prolongation of the palate behind M^3 . Unless its resemblances to *G. aurita* are the deceptive result of parallel evolution, the discovery of *G. aletris* provides evidence for the African origin of the Madagascan Tenrecidae.

Genus *PROTENREC* nov.

DIAGNOSIS.—Talonids of lower molars smaller and simpler than in *Potamogale*, but not so much reduced as in Madagascan Tenrecidae ; posterior end of lower jaw apparently resembling *Potamogale*.

TYPE SPECIES.—*P. tricuspis* sp. nov.

Protenrec tricuspis sp. nov.
(Text-fig. 7)

DIAGNOSIS.—This is the sole species : the characters are those of the genus. $M_1 - M_3$ 4.9 mm.

HOLOTYPE.—A fragment of lower jaw, containing M_1 , M_2 and part of M_3 . Coryndon Museum, Sgr.95.47, from Songhor.

REFERRED MATERIAL.—A fragment of lower jaw, containing M_1 and M_2 . Sgr.602.49, from Songhor.

DESCRIPTION.—The teeth are a little larger than those of *Oryzorictes tetradactylus*, and a little smaller than those of *Limnogale mergulus*. The skull must have been at least 20 per cent. larger than that of *Geogale aletris*. The lower molars fit between the upper teeth of *Prochrysochloris miocaenicus*.

The horizontal ramus has been lost in front of P_4 ; the remainder is slender, with a nearly straight lower edge, except for a slight posterior rise beginning under M_3 . The extreme posterior end of the jaw, with the tips of the coronoid and angular processes and the condyle, is missing, but the elevation of the posterior part of the jaw

is clearly less than in Madagascan Tenrecidae, and resembles that of *Potamogale velox*. As in *Potamogale*, the mandibular foramen is below the level of the teeth, the anterior edge of the coronoid process rises nearly vertically, the depression on the inner side for the temporal muscle is shallow, and the ridge forming the lower border of this depression, passing above the mandibular foramen, is faint. The outer surface of the coronoid process is nearly flat, as in Tenrecidae in general. The posterior mental foramen is below the middle of M_1 : in other Tenrecidae it is a little further back, below the posterior end of M_1 or below M_2 , or, as in most specimens of *Microgale* and *Oryzorictes*, it is absent.

The roots of P_4 are present in Sgr.602. The tooth was about as long as M_1 .

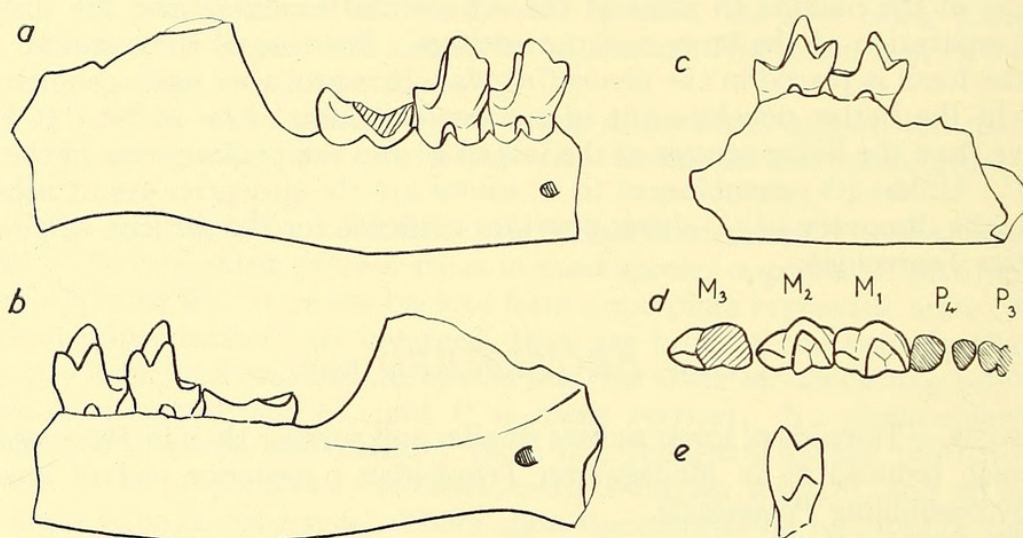


FIG. 7. *Protenrec tricuspis* gen. et sp. nov. $\times 13$. (a) and (b) Outer and inner views of jaw fragment, with M_{1-3} . HOLOTYPE, Sgr 95.47. (c) Inner view of jaw fragment with M_1 and M_2 . Sgr 602.49. (d) Crown view of cheek teeth; M_3 from Sgr 95.47, the remainder from Sgr 602.49. (e) Posterior view of M_2 , Sgr 602.49.

M_1 is present in both specimens; in Sgr.602 it is only slightly worn. The protoconid is somewhat, but not greatly, higher than the metaconid, as in other Tenrecidae. The paraconid is lower than the metaconid, and is situated directly anterior to it. The trigonid angle is about 60° . In *Potamogale* a small cusp is developed on the anterior face of the paraconid (Butler 1939), but in *Protenrec* it is very rudimentary, as in the Madagascan forms. An antero-buccal cingulum is present, not connected to the paraconid, and falling rapidly towards the buccal side, where it fades out on the buccal side of the protoconid. The talonid is much lower than any of the trigonid cusps. Its length is about two-thirds of the length of the trigonid, thus less than in *Potamogale* but more than in the Madagascan Tenrecidae. The only talonid cusp is the hypoconulid, placed at the extreme posterior end. A crest passing forward from the hypoconulid forms the buccal edge of a rudimentary talonid basin, confined to the lingual half of the talonid. The hypoconid is not differentiated. The buccal side of

the talonid slopes down sharply to form, with the posterior face of the protoconid, a groove in which worked the tip of the paracone of M^1 . No postero-buccal cingulum can be made out. There are two equal roots.

M_2 is similar to M_1 , except that the trigonid angle is smaller (about 45°), and the trigonid is more elevated. The trigonid of M_3 is broken off in the holotype; the talonid is longer than on M_2 , but its pattern is similar, except that the hypoconulid is higher. The posterior root of M_3 is longer in cross-section than the anterior root.

TABLE VI
PROTENREC TRICUSPIS

	(Sgr 95.47)
Length of lower molars	4.9 mm.
Length of M_1	1.6
Length of M_2	1.7
Length of M_3	1.6
Width of trigonid of M_1	1.3
Width of trigonid of M_2	1.3
Lingual height of mandible below M_1 .	2.5

RELATIONSHIPS.—*Protenrec tricuspis* is probably a tenrecid rather than a chrysochlorid. In Recent Chrysochloridae the lower border of the jaw does not rise posteriorly, the horizontal ramus is deeper, the mental foramen is below P_3 or P_4 instead of M_1 , the concavity for the masseter muscle is usually much deeper, the mandibular foramen is situated higher up in relation to the tooth-row, the trigonids of the lower molars are much more elevated and compressed antero-posteriorly, and the talonids are more reduced.

Protenrec shows a number of resemblances to *Potamogale*, particularly in the shape of the posterior end of the lower jaw, and in the relatively large talonids of the lower molars. However, there are a number of differences: in *Potamogale*, the talonids are better developed, with rudimentary hypoconids and larger talonid basins; the paraconid of M_1 is as large as the metaconid, and the cusp on its anterior face is more distinct; M_2 is more like M_1 in *Potamogale* than in *Protenrec*.

Protenrec differs from the Madagascan Tenrecidae in the larger talonids of M_1 and M_2 , but the talonid of M_3 is more comparable, because in *Microgale*, *Oryzorictes*, *Geogale*, *Tenrec* and other Madagascan forms it is less reduced than those of M_2 and M_1 .

In its lower molar pattern, *Protenrec* is intermediate between *Potamogale* and the Madagascan Tenrecidae, and resembles *Micropotamogale*. It thus supports the view that *Potamogale* and the Madagascan forms have been derived from a common African stock. Owing to the incompleteness of the material, it cannot be compared with *Geogale aletris*.

Genus *ERYTHROZOOTES* nov.

DIAGNOSIS.—Dental formula 3.1.2.3 ; protocone of upper molariform teeth about as strongly developed as in *Potamogale* ; differing from *Geogale* in that the anterior incisors of the two sides are not widely separated, and in the short infraorbital canal.

TYPE SPECIES.—*Erythrozootes chamerpes* sp. nov.

Erythrozootes chamerpes sp. nov.
(Text-fig. 8)

DIAGNOSIS.—Palatal width across the last molars about 15 mm. ; palatal length about 20 mm.

HOLOTYPE.—A snout and palate containing most of the teeth on either side. Brit. Mus. Geol. Dept. M.14314. Lower Miocene of "Maize Crib", Koru, Kenya Colony.

This was referred to by Hopwood (1933) as being "very close to *Potamogale*".

DESCRIPTION OF SKULL.—The holotype consists of an uncrushed palate and snout broken off shortly behind the third molar ; the anterior margins of the orbits and the root of the right zygomatic arch are preserved. All the teeth are present except the first two incisors on the right side and the first and third incisors on the left. In the course of preparation the outer roots of the teeth from I¹ to P⁴ have been exposed on the left side.

The snout is comparable in size with that of *Chrysospalax trevelyani* ; it is larger than *Limnogale* but smaller than *Potamogale velox*.

All the sutures are closed, as is usual in adult Chrysochlorids and Tenrecids. Careful examination in a very strong light reveals a fine groove, which represents the suture between the two nasal bones, and, on either side of it, a band of bone which is of a paler colour than the rest. These bands, which are symmetrical with regard to the groove, indicate the nasal bones themselves. As they are traced from front to back these indications die away to leave the length and posterior width of the bones in doubt, but there is reason to think that the nasals do increase in width as they pass backwards, as in *Microgale* and some other Tenrecids. The anterior ends are each cut obliquely to come to a point against the maxillae ; in consequence there is a single central notch at the upper margin of the broadly oval, somewhat backwardly inclined anterior nares. In Chrysochloridae and many Tenrecidae the anterior ends of the nasals are transverse, but *Microgale* and *Nesogale* resemble *Erythrozootes* in this respect. The tip of the snout shows no signs of the widening characteristic of the Chrysochlorids. The face is pinched in from the sides and bears no trace of the dorsal flattening which is so noticeable in Chrysochlorids and present to a smaller degree in *Limnogale* and *Geogale* ; in general appearance the face approaches most nearly to *Microgale*, but it is shorter in proportion to its height and width.

The most anterior part of the orbital margin is situated above the posterior part of M¹, as in Chrysochloridae and in *Geogale* ; in other Tenrecidae it is further back, above M² or M³. There is a slight supraorbital crest, not visible in the Recent forms examined. The lachrymal foramen is on the face near the anterior margin of the orbit. Slightly anterior and ventral to it is the round infraorbital foramen, of which

TABLE VII
SKULLS OF TENRECIDAE

	<i>Erythrozootes chamerpes</i>	<i>Geogale aurita</i>	<i>Nesogale dobsoni</i>	<i>Linnogale mergulus</i>	<i>Oryzorictes tetradactylus</i>	<i>Potamogale velox</i>
a. Width across third molars . . .	mm. 14.5	mm. 5.9	mm. 9.7	mm. 10.8	mm. 8.0	mm. 18.3
b. Interorbital width . . .	9.0	3.7	6.6	11.9	6.2	8.3
c. Length of upper dental series . . .	18.3	8.1	15.7	15.0	13.6	32.0
d. Lachrymal foramen—anterior end of alveolus for I ¹ . . .	13.8	6.3	12.5	13.2*	13.6	29.7*
e. Palatine foramen—upper surface of frontal . . .	7.5	2.9	6.0	4.7	5.9	13.0
Ratios:—c/a . . .	1.26	1.37	1.62	1.39	1.70	1.75
b/a62	.63	.68	1.10	.78	.46
d/a94	1.07	1.29	1.22	1.70	1.62
e/b83	.70	.91	.40	.95	.57

*In *Potamogale* and *Linnogale* this measurement is taken from the anterior border of the orbit, the lachrymal foramen being absent.

the posterior margin is above the posterior part of P^4 ; it is anterior to P^4 in *Geogale*, more posterior in the other Tenrecidae and Chrysochloridae. The infraorbital canal is short, as in all members of these two families except *Geogale*.

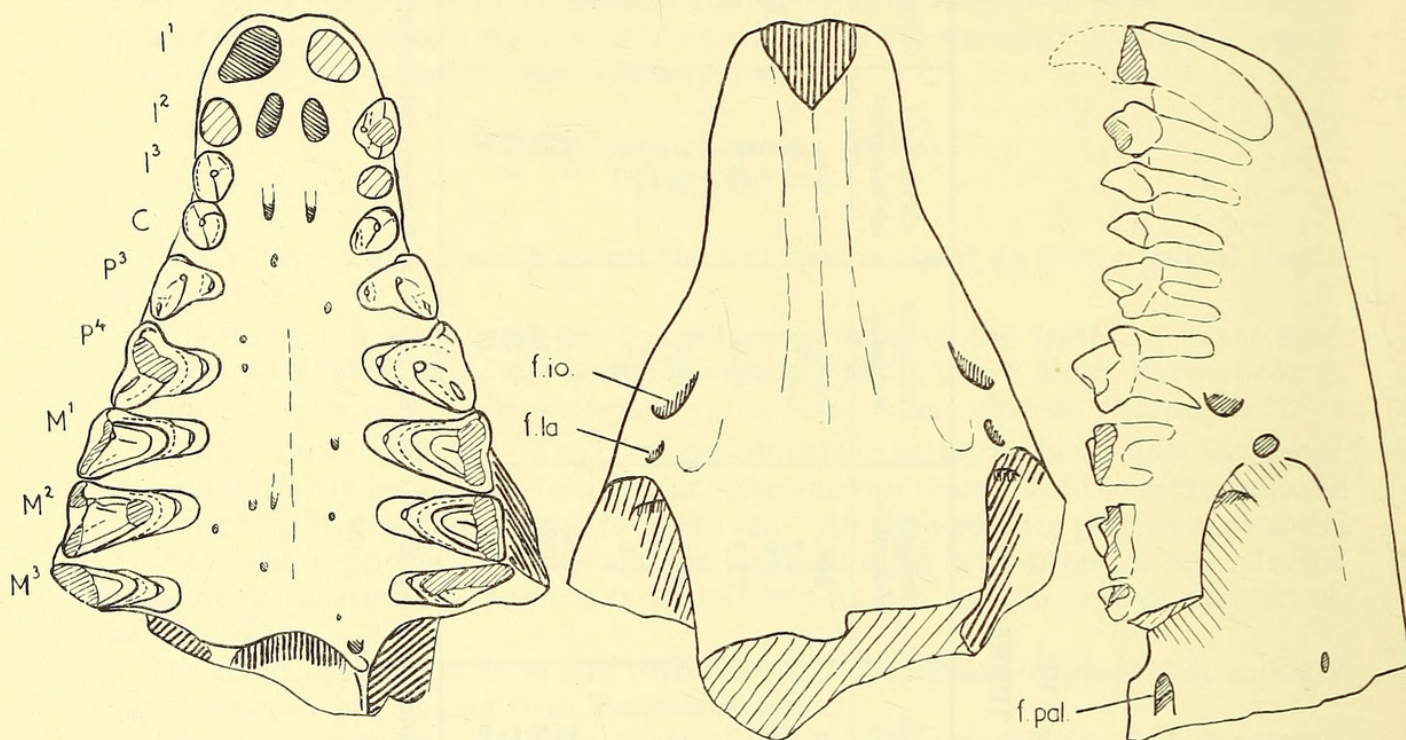


FIG. 8. *Erythrozoetes chamerpes* HOLOTYPE, B.M. M14314, $\times 8$. Palatal, dorsal and left lateral views. *f.io.*, infraorbital foramen; *f.la.*, lachrymal foramen; *f.pal.*, palatine foramen.

The palate is comparatively narrow, and the tooth-rows are only slightly divergent; the general appearance of the palate resembles that of the Tenrecidae rather than the Chrysochloridae. There is an indistinct posterior crest shortly behind M^3 , and on the left side a foramen may be seen just anterior to this crest. The incisive foramina are at the level of I^2 . The palate is perforated by numerous small foramina, of which a pair near the middle line opposite the canine appear to be larger than the others, and correspond to those found in a similar position in *Potamogale*, *Limnogale* and the Chrysochloridae. The palatine (orbito-nasal) foramen is visible on the side of the skull just above the posterior end of the palate.

UPPER TEETH.—The anterior incisor on the right side is represented only by a large, round alveolus which measures 2×1.8 mm. That on the left side has lost its crown, but the single stout root is the strongest of the three incisor roots exposed by dissection. Enlargement of I^1 is usual in Chrysochloridae and Tenrecidae. The alveoli of the anterior incisors are separated in the middle line by a gap of 1 mm., and judging by the mesial inclination of the root it is probable that the crowns touched.

I^2 is preserved on the left side. It is a stout cone, which has lost its tip by breakage. Small anterior and posterior basal cusps are present, the anterior one being slightly higher on the crown. On the lingual side there is a higher cusp, closely applied to the main cusp, and joined to the anterior basal cusp by a cingulum ledge. The presence

of a lingual cusp on I^2 is common in the Tenrecidae : it occurs in *Oryzorictes*, *Geogale*, *Microgale* and *Nesogale*, and a lingual cingulum is present on this tooth in *Potamogale*.

TABLE VIII
TEETH OF *ERYTHROZOOTES CHAMERPES*

	Antero-posterior	Transverse	Height of paracone over external enamel margin	Height of protocone over internal enamel margin
I^1	1.8 mm.	1.6 mm.	— mm.	— mm.
I^2	1.9	1.5	1.9	—
I^3	1.7	1.3	1.9	—
C	1.5	1.5	1.9	—
P^3	2.1	2.4	1.7	0.8
P^4	2.9	3.3	2.0	1.7
M^1	2.2	3.8	1.3	2.0
M^2	2.1	4.0	1.3	2.0
M^3	1.4	4.1	1.0	1.8

Only the right third incisor retains its crown. It is the smallest of the three and consists of a single stout cone with anterior and posterior crests passing down into the cingulum. This is a basal ridge which can be traced all round the tooth, but is best developed postero-lingually, where it forms a marked shelf.

The canine, which is the first tooth to be preserved on either side of the palate, is closely similar to I^3 . It has nearly the same height as I^3 , but is somewhat broader, and is rotated so that the posterior end is displaced inwards. There is a vertical crest on the lingual side, passing down to a somewhat basined postero-lingual cingulum. A small posterior cingulum cusp is present, and a faint cingulum can be made out on the buccal side, extending round the anterior end of the crown. In Recent Tenrecidae the canine is to a varying extent larger than I^3 , but the two teeth are nearly equal in size in the Chrysochloridae.

The anterior premolar, which is interpreted as P^3 , is a stout cone standing on a triangular base, supported by two buccal roots and a lingual root. There is a large, relatively high, central cusp (paracone), which is joined to the postero-buccal corner of the crown by a strongly developed posterior crest. This crest forms the lingual border of a postero-buccal basin. There is a low cingulum round the antero-buccal corner of the tooth. The lingual part of the crown is occupied by a wide cingulum which bears a small protocone. This tooth is similar to P^3 of *Potamogale* and *Limnogale*, though it is smaller in proportion to P^4 . In *Geogale* P^3 is much more reduced and simplified, and in *Nesogale*, *Microgale* and *Oryzorictes* it is at a lower level of molarisation. In Recent Chrysochloridae P^3 is more molariform, and P^2 , which most closely resembles P^3 of *Erythrozootes*, differs from it in the absence of the protocone. P^3 of *Prochrysochloris* also appears to have no protocone.

P^4 is approaching the molariform condition, and resembles P^4 of *Limnogale*. It differs from P^3 in its larger size, the paracone being particularly stout and elevated,

in the presence of a distinct though low parastyle, and in the greater size of the protocone, which resembles that of M^1 . P^4 differs from M^1 in its greater antero-posterior length, due largely to the prominence of the antero-buccal apex, bearing the parastyle, and in the absence of the style immediately buccal to the paracone ("anterior buccal cusp" of Butler, 1937).

M^1 is thus identified because it is more worn than P^4 , and because the lingual lobe, bearing the protocone, is narrower in antero-posterior diameter than in P^4 , but resembles that of M^2 and M^3 . It is a transversely triangular tooth, with the posterior edge longer than the anterior. The higher parts of the crown are worn away, but the paracone was evidently situated slightly lingually to the middle of the crown, and there appears to have been a complete series of stylar cusps along the buccal edge, as in Tenrecidae. The protocone is crescentic in shape, resembling *Prochrysochloris* rather than the living Chrysochloridae; it is lower than the paracone, but larger than in all living Tenrecidae except *Potamogale*.

M^2 apparently resembled M^2 in pattern. It is wider transversely, but as in M^1 the posterior edge is slightly longer than the anterior edge. There are signs of a high anterior buccal cusp directly outside the paracone and behind the parastyle, and probably connected to the tip of the paracone by a strong crest as in other zalambdodonts.

M^3 is the widest tooth, its parastyle projecting slightly beyond M^2 as in *Potamogale*, *Microgale*, *Nesogale* and *Tenrec*. Also as in these, its posterobuccal apex is greatly reduced, so that the posterior edge is only half as long as the anterior edge, and the buccal edge faces mainly backwards. The posterobuccal root is displaced lingually to a position nearly midway between the other two roots.

RELATIONSHIPS.—Among Tenrecidae, *Erythrozootes* resembles *Potamogale velox* in the relatively large size of the protocone, perhaps a primitive character. In its relatively short face it approaches *P. ruwenzorii*, de Witte & Frechkop (1955), but the tip of the snout is broader than in either. In the absence of a metacone it approaches *P. ruwenzorii* but differs from *P. velox*. However, *Erythrozootes* differs from both species of *Potamogale* in the loss of P^2 , the more anterior position of the orbit in relation to the teeth, and the presence of a lachrymal foramen.

Detailed comparison with *Micropotamogale lamottei* Heim de Balsac (1954) is impossible owing to the incomplete description of this species, which is known from a single immature specimen. *Erythrozootes* and *Micropotamogale* agree in the absence of the metacone. It is possible that they have the same dental formula: the fifth post-canine tooth is in process of eruption in the holotype of *Micropotamogale*, but there is no trace of a more posterior tooth. However, the anterior milk-molar of *Micropotamogale* is a non-molariform tooth like Pd^2 of *Potamogale*, and since in the Tenrecidae the milk-molars resemble the premolars in general form, it is probable that the anterior premolar is also not molariform. It would therefore differ from P^3 of *Erythrozootes*, which resembles P^3 of *Potamogale* in being semi-molariform.

Erythrozootes resembles *Geogale alettris* in the absence of P^2 and in the relation of the cheek teeth to the orbit, but differs in the short infraorbital canal, the closer approximation of the anterior incisors, and the greater development of P^3 . Except for the absence of P^2 and the large size of the protocone, *Erythrozootes* resembles the Recent Madagascan genera *Microgale* and *Nesogale*.

Order **CHIROPTERA**Family **EMBALLONURIDAE**Genus *SACCOLAIMUS* Lesson, 1842*Saccolaimus incognita* sp. nov.

(Text-fig. 9)

DIAGNOSIS.—A species of *Saccolaimus* of fairly large size, a little larger than *S. nudiventris* ($P^2 - M^2$ inclusive 8.2 mm.) ; differing from *S. nudiventris* in the less divergent frontal crests, the larger size of P^2 , and the position of the zygomatic root opposite M^2 .

HOLOTYPE.—The left half of a rostrum lacking much of the bone, but showing the interior of the orbit and part of the crowns of P^4 and M^2 . Brit. Mus. Geol. Dept., M.14222. From the Lower Miocene of "Maize Crib", Koru, Kenya Colony.

SKULL.—The part of the skull that is preserved is slightly larger than *S. nudiventris* and smaller than *S. peli*. It agrees fairly closely in proportions with *S. nudiventris*. In the description that follows it is compared with these two species, and also with *S. perforatus*, *S. mauritanus*, *Coleura afra* and *Emballonura atrata* : all these Recent species are from Africa, except the last, which is a Madagascan form.

The frontal crest makes a smaller angle with the middle line than in Recent species of *Saccolaimus*, and the degree of divergence of the crests must have been about the same as in *Emballonura*. There is a concavity in the roof of the skull between the orbits, about as deep as in *S. nudiventris* or *Coleura*. Behind the concavity the profile rises steeply, but the skull is broken off at the level where the frontal crests unite to form the sagittal crest. The postorbital process is broken off, but its base shows that it was strongly constructed, as in other Emballonuridae.

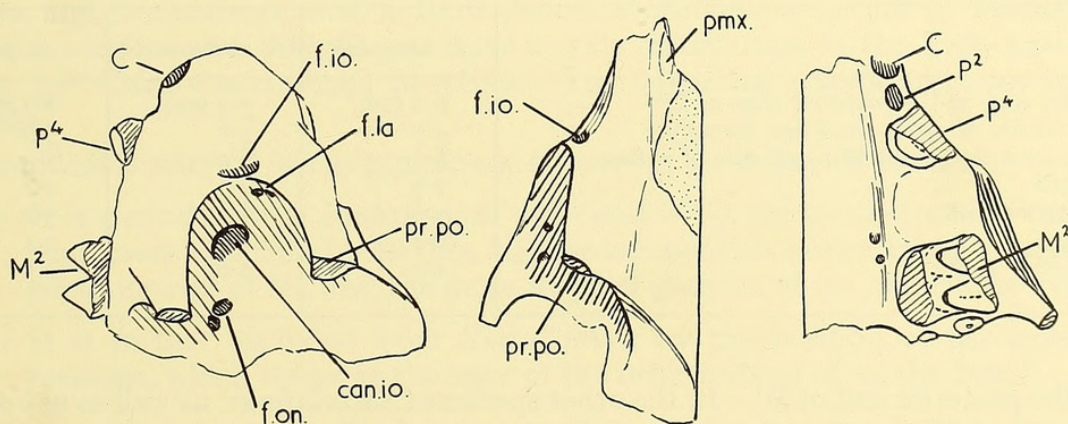


FIG. 9. *Saccolaimus incognita* sp. nov. HOLOTYPE, B.M. M14222, $\times 8$. Left lateral, dorsal and palatal views. *can.io.*, posterior opening of infraorbital canal; *f.io.*, infraorbital foramen; *f.la.*, lachrymal foramen; *f.on.*, orbitonasal foramen; *pmx.*, facet for articulation of premaxilla with nasal; *pr.po.*, postorbital process.

The nasal has broken away anteriorly, but the natural cast of its inner surface shows a moderate dorsal inflation of the region medial to the nasoturbinal attachment. The premaxilla is not preserved, but a facet where it articulated with the maxilla at the side of the external nares is present. The supra-orbital crest is about as strongly developed as in *Coleura afra*, *S. nudiventris* and *S. perforatus*. It appears to have been notched for the lachrymal foramen, as in *Saccolaimus* and *Coleura*, whereas in *Emballonura* the foramen opens on the face. Immediately below the lachrymal foramen and in front of the crest which marks the edge of the orbit, is the infraorbital foramen, which is situated above P⁴. In this part of the skull, *S. incognita* closely resembles the Recent species of *Saccolaimus*: in *Emballonura atrata* the infraorbital foramen is placed farther back than the lachrymal foramen, whereas in *Coleura afra* the infraorbital foramen is farther forward, above the diastema between P² and P⁴.

Much of the palate has broken away, but two foramina are visible, one opposite the posterior part of M¹, the other opposite the anterior part of M². In the Recent species, one or two foramina may occur on each side, but their exact position is probably subject to individual variation. In the fossil, as in Recent species of *Saccolaimus*, the palate ends opposite the posterior end of M²; in *Coleura* and *Emballonura* it extends further back, in association with the larger size of M³. The zygomatic root arises opposite M² in *S. incognita*; in Recent species it is situated farther back, in *Saccolaimus*, opposite the posterior part of M² and part of M³, and in *Coleura* and *Emballonura* mainly opposite M³.

Inside the orbit may be seen the orbito-nasal foramen (posterior opening of the palatine canal) and the posterior opening of the infraorbital canal. These are situated as in *S. nudiventris*, the former at the level of the posterior end of M², and the latter

TABLE IX
SACCOLAIMUS

	<i>S. incognita</i>	<i>S. nudiventris</i>	<i>S. peli</i>
Posterior edge of C—posterior edge of M ²	8.2 mm.	7.3 mm.	8.7 mm.
Upper border of orbit—mid-line dorsally	4.7	3.6	5.6
Postero-buccal apex of M ² —mid-line of palate	6.7	6.0	7.5
M ² length	2.7	2.6	2.8
M ² posterior width	3.0	3.0	3.2
P ⁴ length	2.1	1.9	2.1
P ¹ posterior width	2.0	2.0	2.5

over the posterior end of M¹. In the other species of *Saccolaimus*, as well as in *Coleura*, the infraorbital canal opens nearer to the anterior end of the orbit, whereas in *Emballonura* the opening of the palatine canal is situated more posteriorly. A small foramen is situated above the teeth in the floor of the orbit, probably for the alveolar nerve; similar foramina occur in the Recent forms.

TEETH.—Nothing is known of the incisors. The canine is represented only by its broken alveolus.

P² is placed immediately behind the canine. It has a single, oval root, apparently relatively larger than in Recent species. The crown is not preserved.

The next premolar, P¹, is placed immediately behind P², without any intervening diastema. It is triangular in outline, relatively narrower than in *Coleura* or *Saccolaimus peli*, but resembling *Emballonura atrata* and the other species of *Saccolaimus*. The buccal part of the crown is broken away; the part that is preserved shows a postero-lingual basin, the rim of which rises anteriorly to form a lingual cusp (protocone).

M¹ is missing. From the space left it appears to have been slightly longer than M². M² has lost the buccal edge of the crown and part of the postero-lingual portion, but what remains shows that the pattern of this tooth was of the normal chiropteran type. Both the paracone and the metacone are V-shaped, the metacone being slightly the higher cusp. There is a narrow anterior cingulum, almost obsolete in front of the paracone, but widening lingually to form the protocone, which is about half the height of the paracone. The outline of the tooth is quadrate, with a shallow bay in the posterior edge. The narrow posterior cingulum widens out lingually to form a talon, which is damaged in the specimen, but which probably carried a hypocone in the form of an antero-posterior ridge, connected with the protocone. M² thus agrees very closely with that of the existing *Emballonuridae*.

M³ is represented only by fragments of root, but, to judge by the limited space available, it was evidently much reduced, and thus resembled *Saccolaimus* rather than the other genera.

RELATIONSHIPS.—The close resemblance in many details to Recent *Emballonuridae* leaves no doubt as to the family to which this specimen should be referred. Although the postorbital process has broken off, it was evidently well-developed in the manner characteristic of the *Emballonuridae*.

The Recent members of the family found in Africa are referred to the genera *Coleura* and *Saccolaimus*, and a third genus, *Emballonura*, occurs in Madagascar. Both *Saccolaimus* and *Emballonura* have a wide distribution in the Indo-Australian region, but *Coleura* is confined to Africa. The remaining genera are from tropical America.

The fossil is referred to the genus *Saccolaimus* for the following reasons :—

- (1) It is excluded from *Emballonura* and *Coleura* by the small size of M³ and the characters associated with this, e.g. the termination of the palate opposite the posterior end of M², and the more forward position of the root of the zygoma.
- (2) It is further excluded from *Emballonura* by the position of the lachrymal foramen, which opens at the edge of the orbit instead of on the face.

S. incognita differs from Recent species of *Saccolaimus* in the smaller divergence of the frontal crests, the larger size of P², and the more anterior position of the zygomatic root. It resembles *S. nudiventris* rather than the other species in the position of the opening of the infraorbital canal into the orbit.

Family MEGADERMIDAE

Genus and species indeterminate

(Text-fig. 10)

MATERIAL.—A mandibular fragment with weathered $M_1 - M_3$. Rs. 171.47, from site R. 106, Rusinga Island, Lake Victoria.

DESCRIPTION.—The jaw fragment is broken anteriorly in front of M_1 , and posteriorly it shows only the beginning of the coronoid process.

It is comparatively large for a bat : $M_1 - M_3 = 8.3$ mm., internal depth of ramus below $M_1 = 4$ mm.

The anterior edge of the coronoid process is nearly vertical. The process seems to have been stout, with a deep excavation for muscle attachment on the lateral side. The horizontal ramus is deeper than in Recent Megadermidae, but resembles that of the Emballonurid *Saccolaimus peli*, with which it also agrees in size.

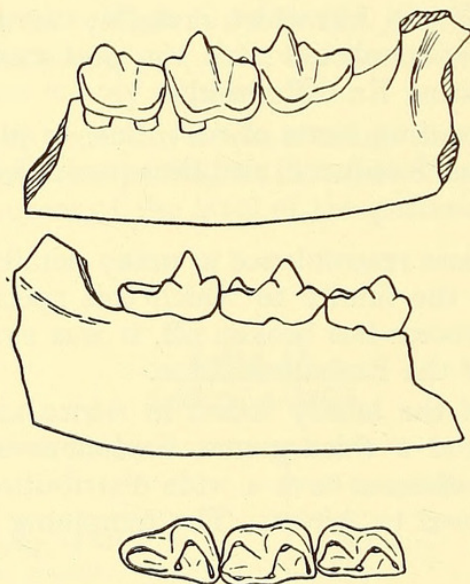


FIG. 10. Megadermid, Rs 171.47, $\times 8$. Outer and inner views of jaw fragment, and crown views of M_{1-3} .

The enamel of the molars has been damaged by weathering, but the main features of the pattern can be made out with some assurance. The protoconid is the highest cusp. The metaconid is widely separated from the somewhat lower paraconid, especially on M_1 . The metaconid is placed farther back on the crown than the protoconid, more so on M_1 than on M_2 or M_3 . The talonid is shorter than the trigonid; the V-shaped hypoconid is lower than the metaconid. There is a small hypoconulid on the posterior border, and near it a small entoconid is present, at least on M_2 . The talonid is reduced in width on M_3 , but a trace of the basin remains. On all three

molars there is a buccal cingulum, which is especially wide antero-buccally to the protoconid. M_1 differs from M_2 in being slightly shorter and narrower, and in the more widely open angle of the trigonid.

TABLE X
MEGADERMID, Rs 171.47

M_1 — M_3 inclusive	9.5 mm.
Internal depth of mandible below M_2	4.0
M_1 , ap \times tr	2.8 \times 1.7
M_2 , ap \times tr	3.0 \times 1.9
M_3 , ap \times tr	2.9 \times 1.8

RELATIONSHIPS.—The lower molar pattern, with backwardly displaced metaconid and reduced talonid, is found in the families Megadermidae, Nycteridae, Rhinolophidae and Hipposideridae among Old World bats. A reduction of the talonid of M_3 to the extent seen in the Rusinga specimen is found in some members of most families except, apparently, the Vespertilionidae. Only in the Megadermidae is M_1 shorter than M_2 , and the specimen is therefore referred to that family.

According to Anderson & Wroughton (1907) the Recent Megadermidae fall into two groups, one African, consisting of the genera *Lavia* and *Cardioderma*, and the other Oriental and Australian, with the genera *Megaderma*, *Eucheira* (*Lyroderma*) and *Macroderma*. Of the two African genera, *Lavia* differs from the Rusinga form in the less reduced talonid and smaller trigonid angle, but the molar patterns of the fossil agree quite closely with *Cardioderma*, as well as with the Oriental *Megaderma*.

Among fossil forms, the Rusinga specimen agrees most closely with *Necromantis*, from the French Phosphorites (re-described and figured by Revilliod, 1920). In *Necromantis*, however, M_1 is as long as M_2 . *Miomegaderma* Gaillard (1929) differs from the Rusinga form in the more widely open trigonid of M_1 , the metaconid of which is greatly reduced.

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