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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Early Miocene Insectivores from the Northern Sperrgebiet, Namibia

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Four (or perhaps five) species of insectivores are present in the Early Miocene strata of the Northern Sperrgebiet, two hedgehogs, one tenrecoid and one (possibly two) chrysochloroid. The currently understood diversity of insectivores in Early Miocene deposits of Namibia is lower than that of similarly aged deposits in East Africa where seven genera (eight species) have been recorded. At present erinaceid, tenrecoid and chrysochloroid diversity is much greater in Southern Africa than it is in the tropics, the opposite of the situation in the early Miocene. This difference may well be due to a bias in the fossil record of southern Africa where insectivores are rare and, for the most part, poorly preserved.

A specimen of the large hedgehog *Gymnurechinus* collected at Grillental comprises associated upper and lower jaws and several post-cranial bones. The latter include elements of the ankle and foot that have not previously been available for study, and they reveal that the ankle joint, metapodials and phalanges were more elongated and more gracile than in *Erinaceus* suggesting a more cursorial locomotor repertoire. A pair of caudal vertebra suggests that the tail in this genus was longer than in spiny hedgehogs.

Introduction

Fossil insectivores are rare in the Early Miocene deposits of the Sperrgebiet, and are usually in poor condition. Stromer (1926) did not describe any material, and none was known to Hopwood (1929). The following account describes and interprets material collected by the Namibia Palaeontology Expedition, found mainly by wet screening (isolated teeth) but also by naked eye searches (mandibles and maxillae with more than one tooth and a partial skeleton).

Insectivores have been collected at Elisabethfeld, Grillental and Langental. Their remains are too scarce to show any significant differences in distribution or age between the three sites.

Insectivore classification has been modified greatly in recent years, culminating in the classification proposed by McKenna and Bell (1997). The Sperrgebiet insectivores belong to three separate orders (Chrysochloroidea, Erinaceomorpha and Soricomorpha) in the Grandorder Lypotyphla.

Systematic descriptions

Grandorder Lypotyphla Haeckel, 1866
Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer de Waldheim, 1817
Genus *Gymnurechinus* Butler, 1956

Type species: *Gymnurechinus leakeyi* Butler, 1956

Species *Gymnurechinus leakeyi* Butler, 1956

Referred material: GT 205'96, left i/3; GT 80'06, left mandible containing p/4-m/1; GT 84'06, right mandible fragment containing m/2; GT 217'06, left maxilla and right mandible with almost complete dentitions associated with several post-cranial bones;

LT 70'97, edentulous mandible.

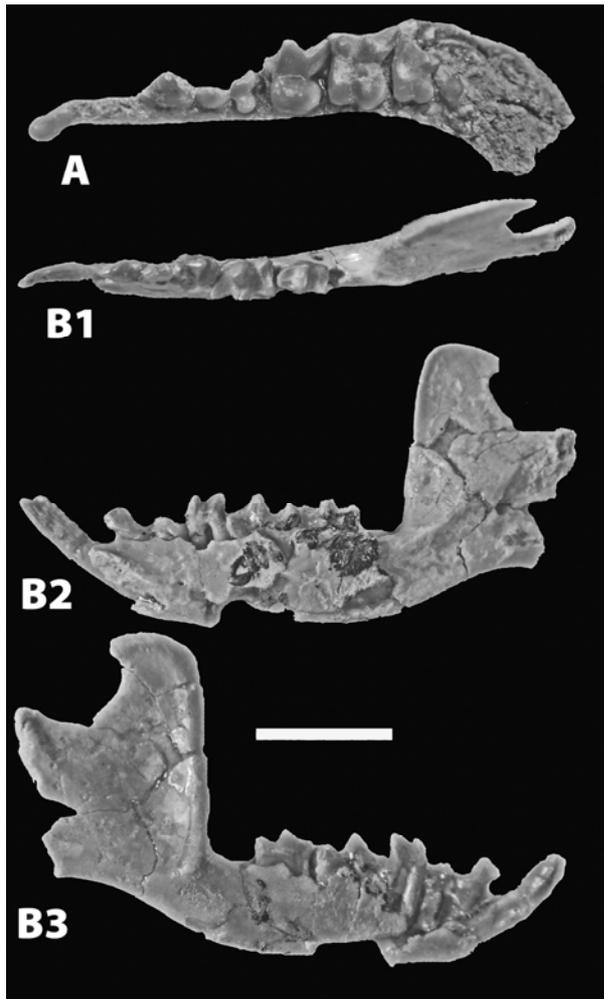**Distribution in Namibia**: Grillental, Langental.

Description. Maxilla and upper dentition (Fig. 1, Table 1). The zygomatic arch departs from the tooth row opposite the contact between M1/ and M2/ and curves distally where it lies beside the jugal and the anterior part of the zygomatic process of the squamosal.

The I3/ has two roots, the distal one being larger than the anterior one. The crown is simple and relatively tall as in material from Rusinga, Kenya (Butler, 1956). The main cusp is anteriorly positioned and has a low crest descending postero-labially. Antero-labially there is a slight swelling but not forming a crest. The basal outline is wide beneath the main cusp and narrows posteriorly. There is a gap of about 3 mm between the I3/ and the upper canine, but this may be exaggerated due to displacement of the I3/ in the sediment. Other erinaceids have a short diastema between these teeth or none at all (Butler, 1956).

The canine is biradiculate and elongated antero-posteriorly. It has a centrally located main cusp with a lingual swelling opposite the main cusp imparting a lozenge shape to the occlusal outline. The distal crest descending from the main cusp terminates in a minute cuspid.

The P2/ is a two-rooted, low crowned tooth with a posterior crest and a very slight buccal swelling in the occlusal outline (Fig. 1).

The P3/ is more molariform with a clear protocone antero-lingually. The paracone has a curved posterior crest which terminates in a small metastyle which recurves slightly anteriorly near cervix. Anteriorly there is a low parastyle. Internally, there is a low postprotocone crista which descends posteriorly towards an incipient hypocone. There is a prominent

Figure 1. GT 217'06, left maxillary dentition and right mandible of *Gymnurechinus leakeyi* from Grillental 6, Northern Sperrgebiet, Namibia (scale 10 mm).

almost at the same buccal level as the parastyle of the M2/. The protocone and hypocone are almost the same height in this medium worn specimen. There is a low cingulum that extends along the anterior and lingual sides of the tooth, terminating in the middle of the distal edge of the crown. There is also a buccal cingulum.

The M2/ has an oblique buccal wall, with the posterior loph being much narrower bucco-lingually than the anterior loph. The parastyle is well developed and points buccally. The metastyle is reduced in dimensions. There is a well developed postprotocone crista that joins the metaconule. The prehypocone crista runs towards the metaconule. There is a clear distal inflection of the cervical outline. The cingula are weak.

The M3/ is blade-like with two low cusplets which according to Butler (1956) are the protocone and paracone, the protocone being slightly higher and broader than the paracone.

Mandible and lower dentition (Fig. 1, 2, Table 1). There are five mandible fragments from the Sperrgebiet, two of which are relatively complete. The body of the mandible is low with a rounded ventral border. The symphysis is unfused, and terminates distally beneath the p/3. The ventral border of the jaw rises posterior to the tooth row before straightening again at the angular process which is stout and projects distally below the level of the cheek teeth. The condyle is low. The anterior margin of the coronoid process rises at an angle of ca 105° near its base but curves distally as it approaches its dorsal extremity. The mandibular foramen is large and located far back, opening slightly above the level of the occlusal surface of the cheek teeth. The oblique crest above the mandibular foramen is oriented at a low angle. This crest serves as the attachment for the posterior part of the mylohyoid muscle and the sphenomandibular ligament (Butler, 1956). The mental foramen is at mid-height of the ramus beneath the contact between p/3 and p/4. The depth of the mandible beneath the p/4 is 5.8 mm, and beneath m/2 it is 6.9 mm.

The i/2 is a high crowned tooth posed on an elongated root that extends into the mandible as far as the level of the p/3. The total height of the tooth is 16.15 mm, the preserved crown height being 5.7 mm. The crown and root are compressed labio-lingually.

The lower canine is uniradiculate. It has a single cusp with anterior and posterior crests. The root, which is in a distal position slopes distally, the anterior half of the crown extending well in front of the root. There is a slight buccal cingulum which rises bucco-distally.

The p/3 (p/2 in Butler, 1956) is biradiculate, the distal root being bigger than the anterior one. The crown is unicuspid, and is lower than the canine. The cervical outline is oval with a slight buccal cingulum.

The p/4 is molariform to the extent of possessing a low but distinct metaconid in the trigonid and a

waist between the buccal and lingual halves of the crown, both the anterior and posterior margins being inflected. There is a short gap between the P3/ and the P4/, probably due to displacement of the teeth in the sediment but also partly due to breakage of the parastyle of the P4/.

The paracone of the P4/ is a high triangular pyramidal cusp with a well developed metastylar blade-like crest which is oriented disto-buccally, terminating in contact with the parastyle of the M1/. The parastyle is damaged. The constriction between the buccal and lingual halves of the tooth is marked. The protocone is higher than the hypocone. The postprotocone crista descends towards the prehypocone crista, forming a continuous wear facet. Distal to the hypocone there is a low cingulum.

The M1/ has well developed paracone and metacone plus a metaconule (Fig. 1). The metaconule is linked to the protocone by a crista obliqua, but is isolated from the hypocone. The prehypocone crista reaches anteriorly to join the protocone. The metastyle does not form an elongated wing, but ends

Table 1. Dimensions (in mm) of the teeth of *Gymnurechinus* from the Northern Sperrgebiet, Namibia, and Songhor and Rusinga, Kenya.

Catalogue N°	Tooth	Length	Breadth 1st loph	Breadth 2nd loph
GT 217'06 (maxilla)	Left I3/	2.62	1.85	
	Right I3/	2.83	1.73	
	Left C1/	2.42	1.52	
	Left P2/	2.44	1.38	
	Left P3/	2.28	2.30	
	Left P4/	3.90	4.54	5.30
	Left M1/	4.88	5.05	6.30
	Left M2/	3.15	4.83	3.48
	Left M3/	1.30	2.90	
Rs 828'47	P3/	2.2	2.0	
	P4/	4.1	3.9	
	M1/	4.2	4.8	
	M2/	3.6	4.7	
Rs 12'32	P3/	2.0	--	
	P4/	3.7	--	
	M1/	3.9	--	
	M2/	3.5	--	
Rs 491'51	P3/	1.9	2.1	
	P4/	3.7	3.3	
	M1/	3.9	4.5	
	M2/	3.4	2.9	
	M3/	--	2.9	
Rs 111'51	P4/	3.8	--	
	M1/	4.1	4.6	
	M2/	3.6	--	
	M3/	--	2.8	
Rs 424	P3/	2.6	2.2	
	P4/	4.6	4.3	
	M1/	4.7	4.8	
	M2/	3.8	4.3	
Sgr 452'48	P3/	2.8	2.2	
	P4/	4.3e	3.5	
	M1/	4.9	4.9	
GT 217'06 (mandible)	Right i/2	2.1	1.48	
	Right c/1	3.60	2.05	
	Right p/3	2.60	1.45	
	Right p/4	3.85	2.33	
	Right m/1	5.53	3.48	3.43
	Right m/2	4.40	2.83	2.60
GT 205'96	Left i/3	2.11	1.62	
GT 80'06	Left p/4	4.01	2.35	
	Left m/1	6.15	2.44 (broken)	
GT 84'06	Right m/2	4.0	2.61	2.18
Rs 864'50	p/4	3.5	2.1	
	m/1	4.5	3.0	
	m/2	3.8	2.7	
	m/3	2.6	1.7	

small talonid. The paraconid is high, almost as high as the protoconid. The roots lean distally. The trigonid is narrower than the talonid, which has a posterior swelling or cingulum-like heel (Butler, 1956). The talonid is 2.84 mm long.

The m/1 has a trigonid with a prominent metaconid. The protoconid is the tallest cusp and is joined to the paraconid by a well formed crest. The metaconid-

paraconid crest is transversely oriented. The talonid is broader than the trigonid and is formed of two cusps, the hypoconid and endoconid, of subequal size.

The m/2 is similar to the m/1 save for the smaller protoconid and the talonid which is narrower than the trigonid.

The m/3 is not represented in the collections, but the alveoli preserved in several mandibles show that it was uniradiculate.

Postcranial skeleton.

The thoracic vertebrae of *Gymnurechinus* possess long neural spines (Butler, 1956), an observation confirmed by the Grillental specimens (Fig. 3A).

The two caudal vertebrae associated with the Grillental specimen, likely come from the middle segment of the tail, probably about the 6th or 7th post-sacral vertebra (Fig. 3). The anterior part of the more complete vertebra possesses apophyses whereas the distal part is devoid of them, showing only the longitudinal crests. This tail vertebra is more elongated and more slender than the 6th or 7th caudal vertebra of *Erinaceus europaeus* (Table 2) suggesting that *Gymnurechinus* possessed a longer, more slender tail than the extant hedgehog.

Butler (1956) reported that the Rusinga skeleton had no trace of the tail, but in fact half a caudal vertebra is associated with the partial skeleton that he described. This vertebra is similar to the Grillental material. On the basis of the sacral morphology Butler (1956) thought that *Gymnurechinus* possibly had a tail that was not enlarged, but the caudal vertebrae now available suggests the presence of a long tail in the genus (Fig. 3B, 3C).

The distal humerus possesses an entepicondylar foramen (Fig. 3D2). Like the fossil from Rusinga, Kenya, there is no epitrochlear foramen in the Namibian specimen contra Butler (1956, Fig. 13) but the depression for the origin of the medial ligament of the elbow (fossa for the origin of the *m. flexor digitorum sublimis* (Verma, 1963)) is present (Fig. 3D1) as in the Rusinga fossil. The distal end of the diaphysis is antero-posteriorly compressed.

The patella of *Gymnurechinus* is proximo-distally elongated and antero-posteriorly slender, contrasting with more solid appearance of the patella of *Erinaceus* (Table 2).

The left calcaneum of *Gymnurechinus* from Grillental 6 is elongated with the articular part slightly longer than the tuber calcis (Table 2, Fig. 3E). This contrasts with the calcaneum of *Erinaceus* which has an articular part that is shorter than the tuber calcis (Romankowowa, 1963; Verma, 1963). The fossil calcaneum is compressed medio-laterally, with a prominent compound facet for the talus and malleolar process of the tibio-fibula (*facies articularis talaris posterior*). The sustentaculum in the fossil is broken. The cuboid facet is narrow.

The left talus from Grillental has a well developed, almost symmetrical trochlea with a deeply ex-
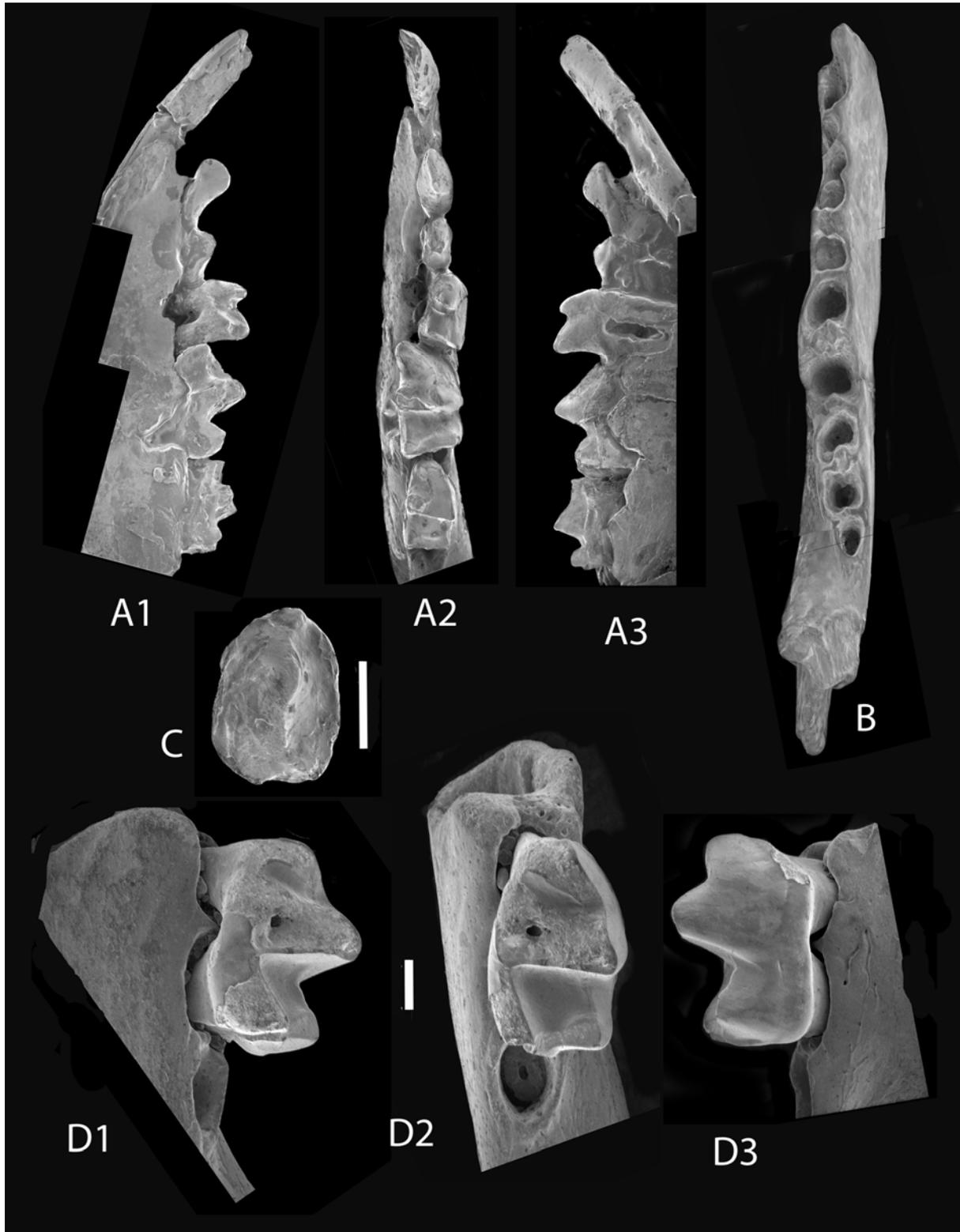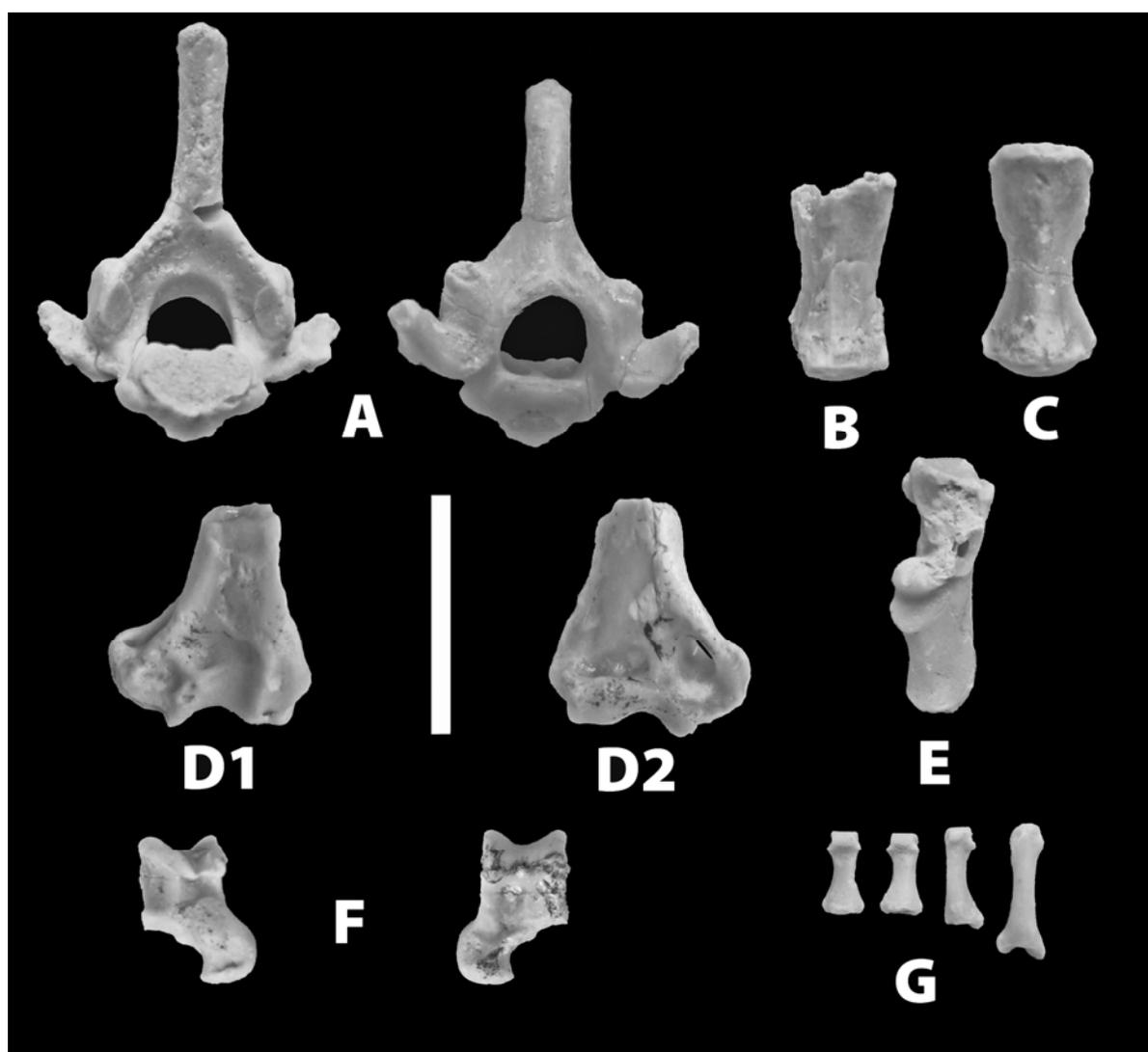
Figure 2. *Gymnurechinus* from the Northern Sperrgebiet, Namibia.
A) GT 217'06, mandible, A1) lingual, A2) occlusal, A3) buccal views; B) LT 70'97, edentulous mandible; C) GT 205'96, left i/3; D) GT 84'06, right mandible fragment containing m/2 (scale 1 mm).

cavated pulley, unlike the shallow pulley that typifies the extant hedgehog *Erinaceus europaeus*. The head and neck lie at a steep angle to the axis of the trochlea (Fig. 3F). The head is ovoid, compressed dorso-ventrally and the neck is elongated (Table 2). The elongation of the talar neck and the articular part of the calcaneum represents a major difference from the morphology expressed in *Erinaceus* in which the corresponding parts are short and squat (Leche, 1902; Butler, 1973).

Butler (1956) provided measurements of a metatarsal associated with the skeleton that he described, although he seems to have been unsure that the specimen belonged to the genus. This specimen appears to have been lost, as it is no longer present in the collections of the NHM, London. A metapodial lacking the distal end found by MP in 2006 in the same block of sediment as the rest of the Rusinga skeleton (NHM

Rs 424'48) measures 15 mm in length as preserved. The original total length of this bone would have been about 17-18 mm taking into account the length of the distal epiphysis, which is about the same length as that of the Rusinga metatarsal (17 mm long by 3.3 mm wide at the distal end) mentioned by Butler (1956). All the metapodials from Grillental are broken, but it is clear from the pieces that remain, that they were more elongated and more slender than those of extant *Erinaceus europaeus* and were similar to the Rusinga material.

The pedal phalanges from Grillental are relatively more elongated and more slender than those of the European hedgehog *Erinaceus europaeus* (Table 2) (Fig. 3G). Butler (1956) reported that a basal phalanx associated with the Rusinga skeleton of *Gymnurechinus camptolophus* was 7 mm long and was shorter in proportion to the metatarsal than is the case

Figure 3. GT 217'06, postcranial bones associated with an upper dentition and mandible of *Gymnurechinus leakeyi* from Grillental 6, Northern Sperrgebiet, Namibia (scale : 10 mm). A - Thoracic vertebra; B, C, Caudal Vertebrae; D - distal right humerus (1) - posterior; 2 - anterior views); E - left calcaneum; F - left talus (plantar and dorsal views); G - Phalanges.

Table 2. Dimensions (in mm) of selected postcranial bones of *Gymnurechinus* from the Northern Sperrgebiet (Namibia) Rusinga (Kenya) and extant *Erinaceus europaeus*.

Measurement	GT 217'06	Rs 424'48°	*Erinaceus*
Humerus total distal medio-lateral breadth	8.0	8.8	11.9
Humerus articular facet most distal medio-lateral breadth	4.9		6.3
Humerus minimal trochlear diameter	1.9		3.5
Patella medio-lateral breadth	3.1		5.1
Patella proximo-distal length	5.4		7.5
Patella antero-posterior thickness	1.8		3.7
Calcaneum total length	9.6		11.4
Calcaneum length of tuber calcis	4.3		5.6
Calcaneum length of articular part	5.3		5.8
Talus breadth of trochlea	3.1		3.7
Talus head medio-lateral diameter	2.4		3.2
Talus head dorso-ventral diameter	1.7		2.2
Talus neck length	1.8		0.7
1st pedal phalanx length	5.1	7*	5.4
2nd pedal phalanx length	3.9		4.2
2nd pedal phalanx length	3.1		3.1
2nd pedal phalanx length	3.1		3.3
Caudal vertebra length (6th or 7th post-sacral)	7.9		4.8
Caudal vertebra minimum diameter (6th or 7th post-sacral)	2.0		3.2

° measurements from Butler (1956).

* the position of this phalanx in the hand or foot is unknown, but Butler (1956) illustrated it as a pedal phalanx.

in *Erinaceus* and *Echinosorex*. Even if that is the case, it would appear that the 1st phalanx from Rusinga is longer than the first phalanges of *Erinaceus* (Table 2).

Discussion: Butler (1984) reduced the diversity of species of *Gymnurechinus* from three to two by indicating that morphological differences between the two species *G. camptolophus* and *G. songhorensis* represented individual variation. The two species are similar in dimensions (Butler, 1984; Butler and Hopwood, 1957). The slightly smaller species *G. leakeyi* was retained by Butler (1984) even though there is a degree of overlap in many of the dental dimensions with those of *G. camptolophus*, because the means and ranges of variation were significantly different (Butler, 1984, Fig. 14, Table 6). Further analysis of these two species is required. The material of *Gymnurechinus* from the Northern Sperrgebiet is homogeneous and falls within the range of metric variation of *G. leakeyi* and *G. camptolophus*.

The talus, calcaneum, metapodials, pedal phalanges and caudal vertebrae of *Gymnurechinus* have not previously been described, the skeletal material illustrated by Butler (1956) comprising much of the axial skeleton, the pelvis and the proximal elements of the limbs, plus a metatarsal and basal phalanx. The new specimens from the Sperrgebiet reveal that *Gymnurechinus* possessed elongated distal limb elements, unlike the more squat and compact talus, calcaneum, metapodials and phalanges of the extant hedgehog

Erinaceus. In addition the trochlea of the talus is deeply pulley-like indicating that movements of the ankle were more constrained to the parasaggital plane than is the case in *Erinaceus*. This suggests that *Gymnurechinus* was more cursorial than *Erinaceus*, from which it is suggested that *Gymnurechinus* may have moved somewhat like macroscelidids with bursts of rapid running with perhaps even an element of springing.

The two caudal vertebrae found with the specimen (Fig. 3B, 3C) are from the middle sector of the tail, probably the 6th or 7th post-sacral vertebrae. The better preserved specimen is more elongated and more slender and less wedge shaped than the corresponding caudal vertebrae of *Erinaceus*, suggesting that *Gymnurechinus* may have been endowed with a long tail.

On account of their relatively great length, Butler (1956) appeared to be concerned that the metapodials from Rusinga might not belong to the skeleton of *Gymnurechinus* that he described. The Grillental metapodials, although none is complete, reveal that indeed the bones were appreciably longer and more gracile than those of *Erinaceus*.

Butler (1956) discussed the differences between *Gymnurechinus* and extant hedgehogs in detail, and postulated that the former may have been hairy along the back rather than spiny. If this is the case, then the ability to move rapidly would have been a necessity for survival.

Genus *Amphechinus* Aymard, 1850

Type species: *Erinaceus arvernensis* de Blainville, 1839

Species *Amphechinus rusingensis* Butler, 1956

Referred material: LT 76'97, right M3/; LT 77'97, m/2 fragment; LT 213'98, left P4/; LT 214'98, left M2/; LT 215'98, left m/1; LT 216'98, left m/1 trigonid; LT 217'98, right m/1 trigonid; LT 218'98, right i/3.

Distribution in Namibia: Langental, Arrisdrift.

Description. Upper dentition. The P4/ (Fig. 4A, Table 3) is represented by two fragments which may belong to the same tooth. The morphology is similar to that of *Gymnurechinus*, but the tooth is appreciably smaller. The parastyle is small, and there is no buccal cingulum. The distal cingulum is weak. The lingual half of the crown has two main cusps, a mesially positioned protocone followed closely by a slightly lower hypocone and a long, distally sloping surface with an invaginated distal contour. The protocone and hypocone are rounded cusps joined by an antero-posterior crest that dips between them. The postero-buccal root is the largest of the roots.

The M2/ (Fig. 4B) is much smaller than the P4/ as in *Amphechinus edwardsi* (Filhol, 1880) from Europe. The buccal part of the cervix is concave in outline, the hypocone is low, round and well separated from the trigon by a low col. There is a clear parastyle and anterior buccal cingulum which fades out along the buccal surface of the tooth. The protocone is in light wear and shows a v-shaped wear facet, the point of the V oriented lingually. There is no sign of a metaconule, but this could be due to its eradication by wear. Butler (1956) mentions the presence of a small metaconule in Kenyan fossils, but in any case the stature of the cusp is less than it is in

Gymnurechinus in which it forms a prominent structure between the hypocone and the metacone. As a consequence, wear of the trigon-metaconule complex is different in the two genera.

The M3/ has an ovoid crown on two roots which are fused throughout their height and which curve anteriorly from cervix to apex. The crown is sectorial, with a protocone higher than the paracone and a low parastyle. The distal surface is concave and there is a cingulum on the mesial side.

Lower dentition. The i/3 (Fig. 4C, Table 3) is a uniradiculate tooth with a distally sloping root. The anterior half of the crown extends well beyond the root. There is a strong buccal cingulum, and the lingual part of the crown is more voluminous than the buccal part. There is a prominant apical wear facet.

The left m/1 (Fig. 4D-F) is lightly worn. The trigonid is elongated and pointed and the paraconid is lower than the metaconid, which is lower than the protoconid. There is a buccal cingulum. The talonid is wider than the trigonid, and the hypoconid is lower than the entoconid. The posterolophid is straight between the hypoconid and the middle of the tooth where it joins the distal cingulum. The latter structure runs from low on the distal surface of the hypoconid towards the summit of the entoconid.

Discussion: The specimens from Langental are appreciably smaller than fossils attributed to *Gymnurechinus* and fall within the range of variation of East African species *Amphechinus rusingensis* (Butler, 1956, 1984). *Amphechinus rusingensis* was already known from the Sperrgebiet, having been recorded at Arrisdrift by Mein and Pickford (2003) on the basis of two mandible fragments and an upper third molar. The dimensions of the Arrisdrift M3/ and m/1 are greater than those from Langental, suggesting that the lineage increased in size over time. However, the quantity of material is too limited for this to be considered a proven tendency.

Table 3. Dimensions (in mm) of the teeth of *Amphechinus rusingensis* from the Northern Sperrgebiet, Namibia and Rusinga, Kenya.

Catalogue N°	Tooth	Length	Breadth 1st loph	Breadth 2nd loph
LT 213'98	Left P4/	2.75	--	
LT 214'98	Left M2/	1.83	2.85	1.87
LT 76'97	Right M3/	0.58	1.38	
Rs 723'47	P3/	1.8	1.2	
	P4/	2.9	2.5	
	M1/	3.0	3.1e	
	M2/	2.2	2.5	
	M3/	--	1.6	
LT 218'98	Right i/3	2.05	1.37	
LT 215'98	Left m/1	3.15	1.90	2.02
LT 216'98	Left m/1 fragment	--	1.85	
LT 217'98	Right m/1 fragment	--	1.96	
Rs 723'47	p/4	1.9	1.5	
	m/1	3.3	2.0	
	m/2	2.7	1.6	

General discussion on Erinaceids from the Sperrgebiet: *Gymnurechinus* has not been reported from the basal Middle Miocene deposits at Arrisdrift (Mein and Pickford, 2003) whereas it is the commoner of the two hedgehog lineages in the Early Miocene strata of the Northern Sperrgebiet. A similar situation appears to have prevailed in East Africa, with *Gymnurechinus* being much better represented in the Early Miocene localities than *Amphechinus*, but seemingly going extinct about 17.5 Ma, whilst *Amphechinus* persisted until at least the level of Fort Ternan (13.7 Ma) (Butler, 1984).

Gymnurechinus has not been recorded outside Africa; indeed it is not even known from the northern half of the continent. In contrast, *Amphechinus* was widespread not only in Africa but also in Eurasia where its fossil record spans a considerable period of time including much of the Oligocene and Miocene. Both *Gymnurechinus* and *Amphechinus* went extinct in Africa by the end of the Middle Miocene if not earlier, and did not give rise to the extant African hedgehogs (*Atelerix*, *Hemiechinus*) (Butler, 1973, 1985).

Order Soricomorpha Gregory, 1910
Family Tenrecidae Gray, 1821
**Genus *Protenrec* Butler and Hopwood, 1957**

Type species: *Protenrec tricuspis* Butler and Hopwood, 1957

Species *Protenrec butleri* Mein and Pickford, 2003

Referred material: Fossils listed in table 4.

Distribution in Namibia: Elisabethfeld, Grillental, Langental, Arrisdrift.

Description: Snout. EF 17'03b (Fig. 5A, Table 4) is a snout containing right I1/-I3/ and left I1/-I2/. It is associated with an auditory bulla and a fragment of left mandible with i/1. The anterior extremity of the snout shows robust premaxillae with vertically implanted incisors. There is no lateral swelling of the premaxillae but there is a gap between the two central incisors. In this space there is a tooth, the isolated right lower central incisor. There is a diastema behind the I3/ marked by a shallow circular fossette.
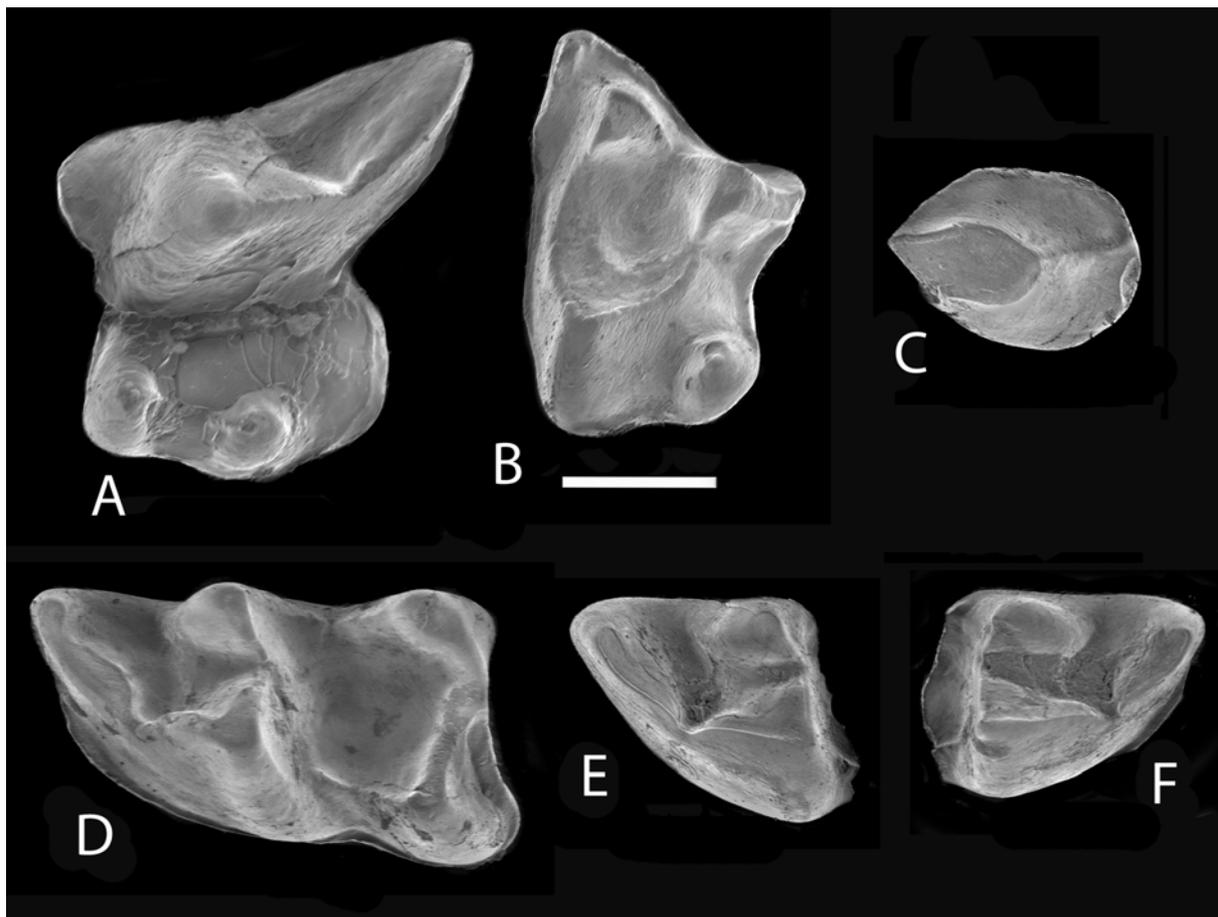
Figure 4. *Amphechinus* from the Northern Sperrgebiet, Namibia
A) LT 213'98, left P4/; B) LT 214'98, left M2/; C) LT 218'98, right i/3; D) LT 215'98, left m/1; E) LT 216'98, left m/1 trigonid; F) LT 217'98, right m/1 trigonid (scale : 1 mm).

Upper dentition. The upper central incisors are caniniform teeth implanted vertically in the premaxilla with their tips recurved slightly rearwards. The tooth is elliptical in section and at the base of the crown there is a slight swelling of the distal crest but not forming a distinct cusp.

The I2/ is lower crowned than the I1/, and differs from it by possessing a well developed lingual cusplet and a mesial cusp in addition to the main cusp.

The I3/ is unicuspid, narrow and pointed and the posterior crest is longer than the anterior one. It is the same height as the I2/.

The incisors of *Protenrec* have not previously been described (Butler, 1984).

The upper molariform teeth (Fig. 5C-E) are antero-posteriorly short and bucco-lingually broad. In the P4/ there is a prominent medially positioned paracone with a hint of a metacone on its distal crest (LT 79'97) which disappears with wear as explained by Butler (1984). LT 79'97 is considered to be a D4/ (Fig. 5E) because its buccal margin is not at right angles to the bucco-lingual axis of the tooth. In addition it possesses a projecting parastyle and there are two prominent stylar cusps buccally, the stylocone and the posterior stylar cusp (Butler, 1984).

Mandible. The mandible LT 284'99, shows two mental foramina, one beneath the anterior root of p/3, the other below the centre of m/1. Both foramina are near mid-height of the ramus. A second mandible fragment, EF 17'03b (Fig. 5F) which was stuck to the snout, has a tiny incisiform tooth with a long root and a tiny crown.

Lower dentition. The lower molariform teeth are characterised by the great difference in height of the trigonid relative to the talonid (Fig. 6H-L). In LT 284'99 (Fig. 6A) all four teeth preserved (p/2-m/1) have two roots. The p/2 and p/3 have a low paraconid poking above the cingulum which extends along the lingual side of the tooth. There is also a small central talonid cusp but no talonid basin. The p/3 is longer and higher than p/2. The p/4 (Fig. 6E) is molariform as it possesses a high metaconid and the paraconid is about 1/3 of the height of the crown. Its talonid is longer than in the p/3 and it is comprised of a centrally positioned hypoconulid which has a crest extending to the centre of the base of the trigonid. The talonid is not basin-like.

The m/1 (Fig. 6F) has a paraconid that is 2/3 the height of the protoconid and at its base there is an accessory cuspid emanating from the cingulum. The talonid forms a basin, the hypoconid having two crests, a prehypoconid cristid which extends to the centre of the tooth behind the trigonid, and a posthypoconid cristid that closes the talonid distally and then curves anteriorly to the base of the metaconid. In an unworn specimen (LT 221'98 (Fig. 6G)) the talo-

Figure 5. *Protenrec* from the Northern Sperrgebiet, Namibia
A) EF 17'03, snout with incisors; B) LT 79'97, left p/3; C) EF 68'96, right upper molariform; D) EF 68'96, right upper molariform lacking much of the crown; E) LT 79'97, right D4/; F) EF 17'03, right mandible fragment with incisor (scale : 1 mm).

nid is seen to comprise a hypoconid and a small ento-conid which would disappear with wear, and the crest linking the two cusps overhangs the cervix distally.

In overall appearance the m/2 (Fig. 6J, 6L) is like the m/1 save for its broader talonid and its antero-posteriorly more compressed trigonid. The m/3 (Fig. 6K) has a reduced talonid.

Discussion. The incisors in the snout EF 17'03b reveal that it is a tenrecoid. Extant *Microgale* and extinct *Erythrozootes* have enlarged upper central incisors that point downwards and backwards and the I2/ possesses a lingual cuspid (Butler and Hopwood, 1957) as in the fossil from Elisabethfeld. Chrysochloroidea do not possess bicuspid incisors.

When Butler and Hopwood (1957) erected the species *Geogale aletris* and *Protenrec tricuspis*, the fossil sample was limited to a single specimen of the former (a snout from Rusinga) and two specimens of the latter (two mandibles from Songhor). It was thus not possible to make comparisons between the species and it could have been argued that the Songhor mandibles and the Rusinga snout belong together. A decade later discoveries at Napak, Uganda, included the first snout of *Protenrec* (Butler, 1969) and additional mandibular specimens from Napak IV, Rusinga and Songhor which showed differences in proportions of the cheek teeth, notably the M3/, which is broader than M2/ in *Protenrec* but about the same breadth as M2/ in *Parageogale*. During the Western Kenya Project, much additional material was discovered at Legetet and Chamtwara (Butler, 1984) which strengthened the case for retaining two genera, the view accepted here.

Overall, the distinctions between the genera *Parageogale* and *Protenrec* are subtle (Butler, 1984; Butler and Hopwood, 1957) especially if only fragments of skulls are available. In fragmentary samples such as the one from the Northern Sperrgebiet, there are few features that can be used to determine the generic position with confidence. The main criteria for attributing the Sperrgebiet fossils to *Protenrec* are the presence of two mental foramina, one beneath the front of p/3 and the other beneath the m/1, and the presence of I3/. *Parageogale* lacks I3/ and P2/ which are present in *Protenrec* (Butler, 1984) and in the fossil from Elisabethfeld. Thus there can be little doubt that the material from the Northern Sperrgebiet belongs to *Protenrec* rather than to *Parageogale*. The dimensions of the teeth reveal that it is smaller than the East African species *Protenrec tricuspis*. The fossils from Langental, Grillental and Elisabethfeld are similar morphologically and metrically to specimens attributed to *Protenrec butleri* from Arrisdrift described by Mein and Pickford (2003).

Order Chrysochloroidea Broom, 1915
Family Chrysochloridae Gray, 1825
Genus *Prochrysochloris* Butler and Hopwood, 1957

Type species *Prochrysochloris miocaenicus* Butler and Hopwood, 1957

Species *Prochrysochloris* cf *miocaenicus* Butler and Hopwood, 1957

Material from the Northern Sperrgebiet: See fossils listed in Table 5.

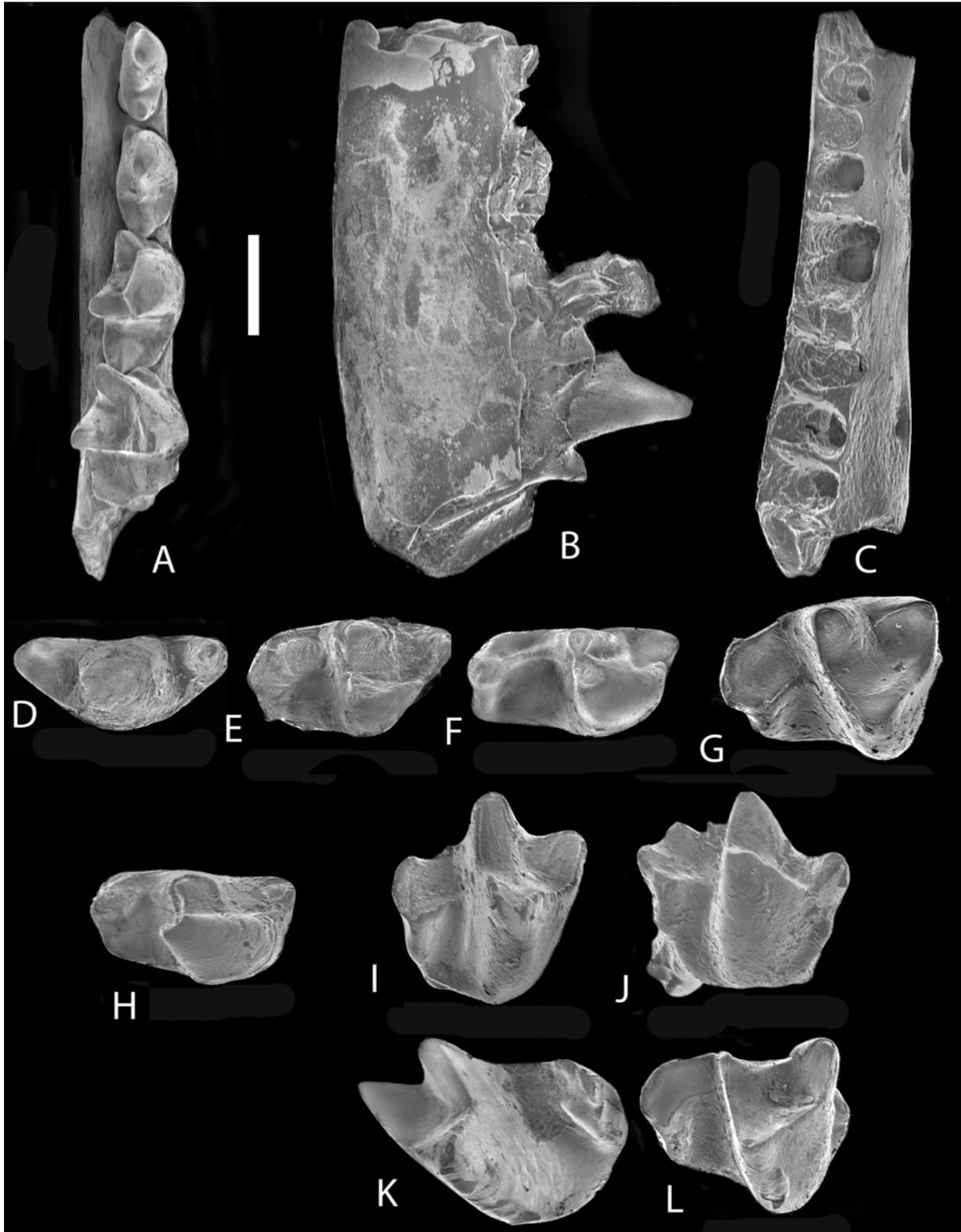**Distribution in Namibia**. Elisabethfeld, Langental, Arrisdrift.

Description. <u>Mandible</u>. A mandible fragment containing three teeth (Fig. 7E) is not complete enough to reveal any significant morphological details of ramal morphology. A second fragment LT 223'98 (Fig. 7D) shows a mental foramen under the m/1 and a vertical root of the coronoid process as in material from Arrisdrift (Mein and Pickford, 2003).

<u>Upper dentition</u>. EF 32'98 (Fig. 7A, Table 5) is an isolated zalamdodont molar with a prominent centrally placed paracone from the apex of which two well defined crests lead buccally enclosing a large fossa, the anterior crest ending in a projecting parastyle. The protocone is low and antero-posteriorly compressed.

<u>Lower dentition</u>. Two isolated caniniform teeth are attributed to this species on the basis of dimensions. The crowns possess a prominent lingual crest running from the apex to the cervix, bordered either side by

Table 4. Measurements (in mm) of teeth from the Northern Sperrgebiet, Namibia, attributed to *Protenrec butleri*.

Catalogue N°	Tooth	Length	Breadth
LT 79'97	Right D4/	1.40	1.90
EF 68'96	Right upper molariform	1.10	2.18
EF 68'96	Left upper molariform	1.19	2.22
EF 32'98	Left M1/	1.13	2.09
LT 79'97	Left p/3	1.36	0.75
LT 79'97	Right p/4	1.34	0.81
LT 79'97	Right m/1	1.32	0.90
LT 221'98	Right p/4	1.27	0.86
LT 221'98	Right m/1	1.36	0.86
LT 221'98	Right m/2	1.28	0.65
LT 221'98	Left m/3	1.24	1.10
GT 1'97	Right m/2	1.32	0.86
GT 1'97	Left p/2	0.91	0.50
EF 69'96	Right m/2	1.29	1.17
EF 69'96	Right m/2	1.33	1.12
LT 284'99	Right p/2 Right p/3 Right p/4 Right m/1	0.98 1.14 1.31 1.37	0.50 0.67 0.87 1.11
EF 23'06	Left m/1 Left m/2	1.16 1.18	-- 1.24

Figure 6. *Protenrec* from the Northern Sperrgebiet, Namibia
A) LT 284'99, right mandible with p/2-m/1; B) EF 23'06, left mandible with m/1-m/2; C) LT 220'98, edentulous mandible; D) LT 79'97, left p/3; E) LT 79'97, right p/4; F) LT 79'97, right m/1; G) EF 69'96, right m/2; H) LT 221'98, right p/4; I) LT 221'98, right m/1; J) LT 221'98, right m/2; K) LT 221'98, left m/3; L) EF 69'96, right m/2 (scale : 1 mm).

grooves. The buccal surface is evenly curved but distally near cervix there is a shallow swelling forming a low heel to the tooth. The crowns of LT 219'98 (Fig. 7B) and LT 79'97 (Fig. 7C) are 1.73 mm and 1.77 mm tall respectively.

The lower molars have a highly compressed tall trigonid in which the paraconid is very close to the metaconid (Fig. 7E, 7F) and the talonid is short, low and does not form a basin. The m/2 is the largest of the molars followed in size by m/1 and then m/3. The molar talonids diminish in breadth from m/1 to m/3. In EF 31'98 (Fig. 7E) the molars form a series of transverse cutting blades functionally similar to those of extant golden moles such as *Eremitalpa*.

Discussion. The Chrysochloridae from the Northern Sperrgebiet are not well preserved, yet the fossils reveal enough information to link them tentatively to the genus *Prochrysochloris*. The dimensions of the specimens reveal an insectivore about the same size as the extant species *Eremitalpa granti*, from which it differs by having less compressed lower molar trigonids. The fossils are compatible is size with the East African Early Miocene species *Prochrysochloris miocaenicus* but there is some residual doubt about the determination due to the generally restricted and fragmentary nature of the Namibian fossils.

Family Chrysochloridae?
Genus and species *incertae sedis*

Material. LT 261'03, upper central incisor?
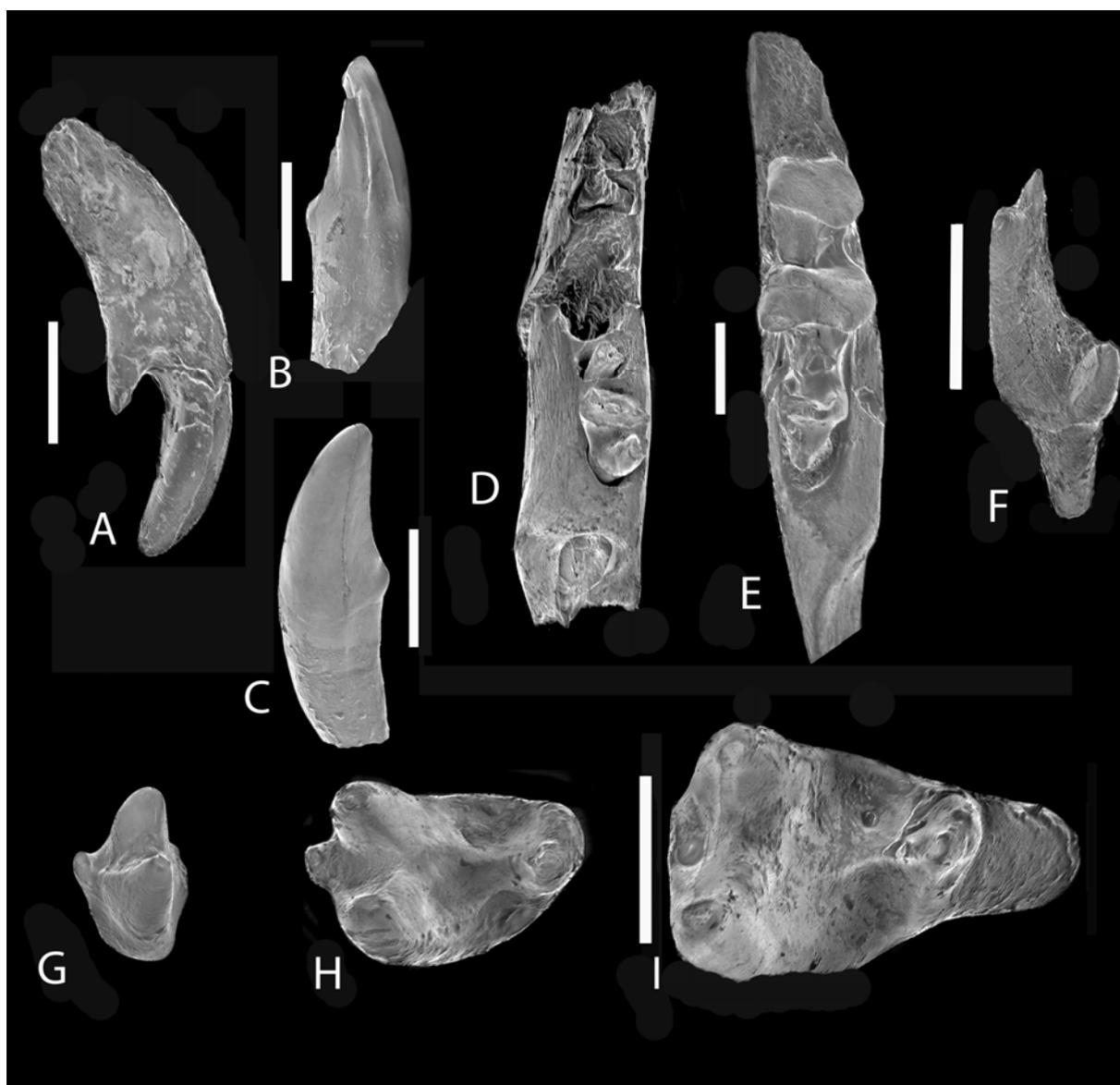
Figure 7. *Prochrysochloris* from the Northern Sperrgebiet, Namibia
A) EF 32'98, left upper incisor; B) LT 79'97, lower canine: C) LT 219'98, lower canine; D) LT 223'98, left mandible with m/3; E) EF 31'98, right mandible with m/3; F) EF 31'98, distal half of right lower molar; G) LT 79'97, lower molar; H) LT 222'98, left m/2; I) LT 222'98, left m/3 (scale : 1 mm).

Description. Specimen LT 261'03 (Fig. 8A-C) is an incisiform or caniniform tooth too large to belong to the chrysochlorids described above. It has a single pulp cavity and the enamel invaginates apically slightly on one side of the tooth. It is a tall, pointed tooth with a prominent crest descending from the apex towards the basal tubercle which bifurcates basally. A second crest descending from the apex a short distance is separated from the main crest by a groove. The crown is lightly curved from cervix to apex. The dimensions are length : 2.78, breadth: 1.75, crown height : 4.60 mm.

Discussion. We tentatively interpret this tooth as a central upper incisor or a canine of a chrysochlorid. In terms of its dimensions it could fit with *Erythrozootes chamerpes*, but the anterior dentition of this species has not been described (Butler, 1969, 1978, 1984, 1985; Butler and Hopwood, 1957). The tooth is unlikely to belong to an erinaceid, as this family does not possess incisors with crests (Butler, 1956) such as the ones developed on the Langental specimen.

This tooth indicates the presence of an additional insectivoran mammal in the Northern Sperrgebiet.

Conclusions

Insectivores from the Early Miocene deposits of the Northern Sperrgebiet are not very diverse, only four genera in three families being recorded (Table 6) compared to seven in the Early Miocene deposits of East Africa (Butler, 1978, 1984).

Out of the seven insectivore genera reported from the Early Miocene of East Africa, only two are known from Eurasia (*Galerix*, *Amphechinus*). All the others are endemic to Africa, although the hedgehog *Gymnurechinus* undoubtedly had an Eurasian ancestor (Butler, 1978, 1984, 1985).

The presence of hedgehogs in the Early and Middle Miocene of the Southern African subcontinent was already reported by Senut *et al.*, (1992) and Mein and Pickford (2003) on the basis of rather poor

material attributed to *Amphechinus*. The fossils from the Northern Sperrgebiet confirm their presence in the region, and add the genus *Gymnurechinus* to the list.

At present, tenrecids do not occur in Southern Africa (Skinner and Smithers, 1990) meaning that their occurrence in Namibia during the Early and Middle Miocene (Mein and Pickford, 2003; Senut *et al.*, 1992) represents a major southwards range extension from the tropics where three extant species in two genera (*Potamogale*, *Micropotamogale*) occur. Tenrecids are highly diverse (8 genera, 21 species) in Madagascar (Wilson and Reeder, 1993). The low diversity of Chrysochloridae in the early Miocene deposits of Namibia contrasts strongly with the high diversity (7 genera) that currently exists in the subcontinent (Wilson and Reeder, 1993) to which should be added the extinct Pleistocene genus from South Africa, *Proamblysomus* Broom, 1941. At present, chrysochlorid diversity diminishes from southern Africa towards the tropics, so it is perhaps understandable that only one genus is known from equatorial Africa during the Early Miocene. The paucity of the available fossil samples from southern Africa is undoubtedly introducing a bias into our understanding of their Miocene diversity, a problem which can only be addressed by further collecting in appropriate locales.
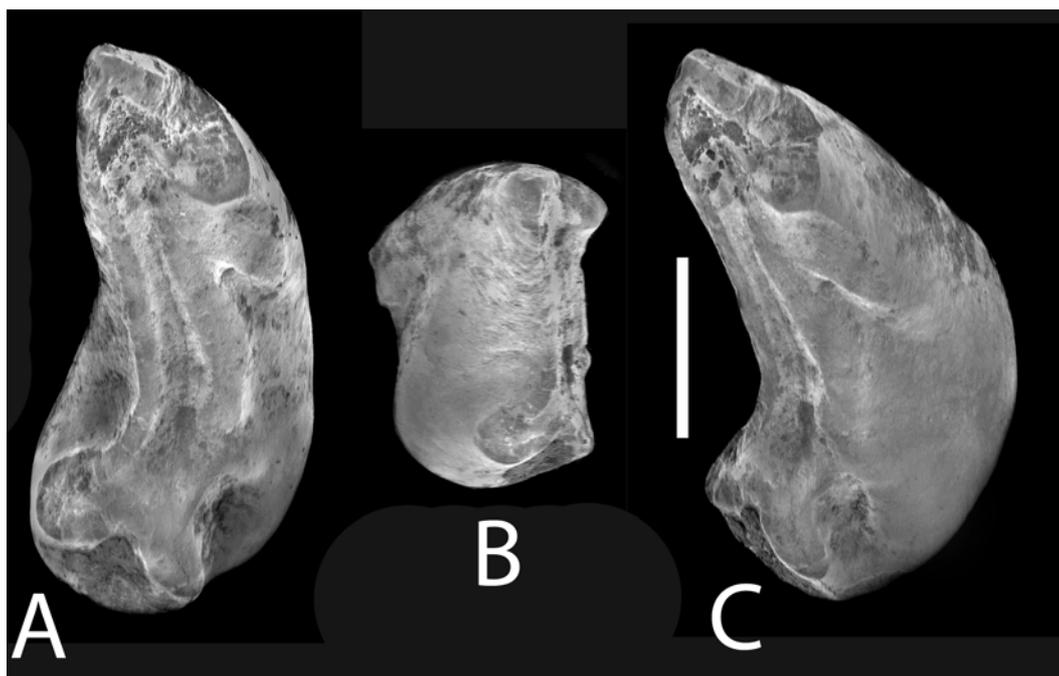
Table 5. Dimensions (in mm) of teeth of Chrysochloridae from the Northern Sperrgebiet, Namibia.

Catalogue N°	Tooth	Length	Breadth
EF 32'98	Left upper molariform	1.10	2.18
LT 79'97	Left caniniform	1.09	0.76
LT 219'98	Left caniniform	1.05	0.68
EF 31'98	Right m/1 Right m/2 Right m/3	1.24 1.43 1.25	1.15 1.34 0.88
LT 222'98	Left m/2	1.45	1.48
LT 222'98b	Left m/3	1.35	1.06
LT 223'98a	Left m/3	1.36	1.21

Figure 8. ?*Erythrozootes* sp. from the Sperrgebiet, Northern Namibia.
A-C) distal, occlusal and oblique buccal views of LT 261'03, upper central incisor? from Langental (scale 1 mm).

Table 6. Diversity of Lypotyphla in Early Miocene deposits of East Africa and Namibia (figures denote the number of species in each genus).

Family	Common name	Genus	East Africa	Namibia
Erinaceidae	Hedgehog	*Galerix*	1	-
	Hedgehog	*Amphechinus*	1	1
	Hedgehog	*Gymnurechinus*	2	1
Tenrecidae	Tenrec	*Protenrec*	1	1
	Tenrec	*Erythrozootes*	1	-
	Tenrec	*Parageogale*	1	-
Chrysochloridae	Golden mole	*Prochrysochloris*	1	1
?Chrysochloridae	?Golden mole	*?Erythrozootes*	1	?1

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