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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Creodonta and Carnivora from the Early Miocene of the Northern Sperrgebiet, Namibia

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Between 1993 and 2007 the Namibia Palaeontology Expedition collected a variety of carnivorous mammals in the Northern Sperrgebiet, comprising six species of Creodonta and the same number of Carnivora. Although carnivoran remains tend to be rare in the Sperrgebiet, some significant discoveries were made including a new genus and three new species. The Sperrgebiet carnivorans range in size from a tiny hypercarnivorous creodont discovered in 2001 at Elisabethfeld, which is the smallest known carnivorous mammal reported from Africa, to gigantic *Hyainailouros*, the largest known creodont. Several fissipeds belonging to Amphicyonidae, Viverridae and Felidae were collected, but the only ones which are well preserved are two new species of *Leptoplesictis*.

Introduction

The fossiliferous valley-fill sediments of the Northern Sperrgebiet, Namibia, have traditionally been attributed to the Early Miocene (Stromer, 1926) and the results of the NPE (Pickford and Senut, 2000) confirm that they are aged about 21-19 Ma, being faunally similar to East African sites such as Songhor, Koru and Napak ranged in Faunal Set PI, for which radio-isotopic ages of between 19 and 20 Ma have been reported (Bishop *et al.*, 1967).

From 1993 to 2007 surface collections and excavations yielded a variety of carnivores from Elisabethfeld, Grillental, Fiskus and Langental. In 2001 the Namibia Palaeontology Expedition excavated at Elisabethfeld, and collected a rich and diverse microfauna. Among the small mammals from the E-Feld "Tortoise" site, several specimens of a tiny, hypercarnivorous creodont were found, possibly representing a single individual. Additional fossils that might represent the same species were found at other outcrops in the same deflation basin, but they are poorly preserved, having suffered from sand blasting after eroding out of the strata. The most notable features of the new creodont are its minuscule size and the extremely hypercarnivorous dentition. This is by far the smallest creodont ever recorded from Africa, being similar in size to the enigmatic carnivorous mammal from East Africa known as *Prionogale breviceps* (Schmidt-Kittler and Heizmann, 1991) which we consider may well be related to the new Namibian species. It is also the most hypercarnivorous. The species is smaller than the smallest extant carnivore, *Mustela nivalis*. A new family is created for this group of tiny creodonts. Four medium sized creodonts belonging to Teratodontidae, and the hyaenodonts *Metapterodon* and *Isohyaenodon* were also found.

At the opposite end of the size spectrum, remains of the largest known creodont *Hyainailouros / Megistotherium* were collected from Grillental and Elisabethfeld and to fill the size continuum, three medium sized species belonging to Hyaenodontidae and Teratodontidae were found at various sites. Among the fissiped Carnivora, the expedition found an amphicyonid, four species of viverrid and a felid. The ratio of creodonts to carnivores described in the northern Sperrgebiet is thus equal at 6/6.

Systematic descriptions
Order Creodonta Cope, 1875
Family Hyaenodontidae Leidy, 1869
Genus *Metapterodon* Stromer, 1924
Species *Metapterodon kaiseri* Stromer, 1924

Locality: Elisabethfeld.

New material: EF 7'06, right mandíble with partly erupted m/3, alveoli of m/2, and poorly preserved d/4 or m/1. EF 93'01, fragment of left mandíble with m/1 (or d/4) and alveoli of the p/4 and p/3 (incomplete). EF 90'01, anterior fragment of right mandible with canine and incomplete alveoli of the p/2, p/3 and p/4.

Description: EF 7'06, a right mandible (Pl. 2, Fig. 6) with the partly erupted m/3 (L = 10.4 mm, B = ca. 5 mm) has the apices of the cusps of the m/3 broken off. It is a highly sectorial tooth formed of a transversely compressed paraconid with an almost vertical anterior crest, and a well-developed protoconid which is less transversely compressed. The protoconid reaches a vertical crest in the postero-buccal position (position of the metaconid) which basally joins the posterior cingulum and this crest is better developed than the posterior one, which makes contact with the small cuspid of the talonid. The paraconid and protoconid are separated by a strong, deep notch, and they are disposed in different planes which form an open angle. Buccally the paraconid possesses a vertical basal cuspid which is quite strong. The talonid is reduced, formed of a minuscule cuspid associated with a broadening of the posterior cingulum, and it is slightly buccally positioned. In front of this tooth there is a biradiculate alveolus for the m/2 (L = 8.2

mm, B = 4.1 mm) and in front of this there is a broken molariform tooth with a strong talonid and a robust paraconid-protoconid complex. The latter tooth corresponds to the m/1 or perhaps the d/4 (L = 6.7 mm, B = 3.5 mm).

EF 93'01, is a left mandible with m/1 or d/4 (L = ca. 6.5 mm, B = ca 3 mm). The tooth has lost all the morphological details, but judging from its size and aspect, it could be close to EF 7'06 described above. The anterior alveolus for the p/4 has the following dimensions (L = 8.8 mm, B = 4 mm).

EF 90'01, is a right mandible with the canine and incomplete alveoli for p/2, p/3 and p/4 (Pl. 2, Fig. 5). The most outstanding feature of the specimen is the length of the symphysis which extends as far backwards as the anterior alveolus of p/3. In contrast, out attention is called to the shallowness of the mandibular ramus and the development of the root of the canine which enters the mandible as far as the level of the alveoli of p/2. The canine crown (L = 7.2 mm, B = 4.6 mm) is small compared to the size of the root and is strongly curved, but even so it is inclined relative to the axis of the mandible. The alveoli of the p/2 (L = 9.7 mm, B = 3.8 mm) and p/3 (L = 9 mm, B = 3.5 mm) are preserved, and in both cases the anterior alveolus is smaller than the posterior one and almost circular in outline.

Discussion: *Metapterodon kaiseri* Stromer (1924, 1926) was hitherto known only by its holotype, a maxilla, and it is thus not possible to make direct comparisons with the new specimens attributed to the species. However, the dimensions of the three mandibles correspond reasonably well with a species the size of *M. kaiseri*. Morphologically the m/3 EF 7'06 is close to the m/3 attributed by Morales *et al.* (1998) to *Metapterodon stromeri*. The differences between the two species reside in the dimensions and the smaller m/3 talonid and in the greater development of the postero-buccal cristid of the protoconid in EF 7'06. However, the morphology of the two m/3s is closely similar, with the disposition of the paraconid and protoconid in slightly divergent planes. In this feature it differs from *Isohyaenodon andrewsi* Savage, 1965 in which the m/3 has the paraconid-protoconid complex almost aligned in the same plane, a disposition that accentuates the cutting function of the carnassial.

Species *Metapterodon stromeri* Morales, Pickford and Soria 1998

Material: LT 6'01, left M3/.

Locality: Langental.

Description: LT 6'01, a left M3/ (L = 10.1 mm, B = 4 mm) has a kidney-shaped outline (Fig. 2.5). It is a peculiar molar with two buccal lobes clearly separated by a deep valley; the anterior cusp is probably a well developed parastyle and the posterior one the metacone which is joined to a large buccal lobule which does not form a separate cusp although its highest part is occupied by a crest (protocrista).

Discussion: The morphology of this molar is strange, and it can be interpreted as an M3/ of a creodont with a tendency towards reduction. Its morphology *grosso modo* would fit with the alveolus of the M3/ of the holotype of *Metapterodon kaiseri* Stromer (1926) although it is clearly larger, which is why it is likely to belong to *Metapterodon stromeri*.

Genus *Hyainailouros* Biedermann, 1863, or *Megistotherium* Savage, 1973
Species *Hyainailouros* or *Megistotherium* indet.

Locality: Elisabethfeld (EF 6'04) and Grillental (GT 53'06, GT 58'06).

Description: GT 53'06 is a fragmented lower carnassial of a huge creodont. Although very fragmentary, the protocristid and anterior basal cusplet are preserved, showing similar dimensions and morphology to an m/2 from Ngorora, Kenya, recently described by Morales and Pickford (2005). The protocristid is bordered each side by a sharp but shallow furrow, as in the Ngorora fossil, and the enamel is lightly wrinkled in the style of *Megistotherium* carnassials. The anterior basal cusplet is broader than long, with expanded buccal and lingual halves, also as in the Ngorora specimen.

EF 6'04, a left pisiform (Table 1; Pl. 4, Fig. 4) is massive, short and markedly flattened laterally. In the dorso-distal border there is a large and round articular facet for the ulna. In the medial face, the medial projection of the dorsal border can be observed, due to the medial expansion of the articular facet for the

Table 1: Measurements (in mm) of the pisiform of Creodonta from the Elisabethfeld (APL, antero-posterior length; LMW art, latero-medial width of the articular facet; APL tub, antero-posterior length of the posterior tubercle; LMW tub, latero-medial width of the posterior tubercle).

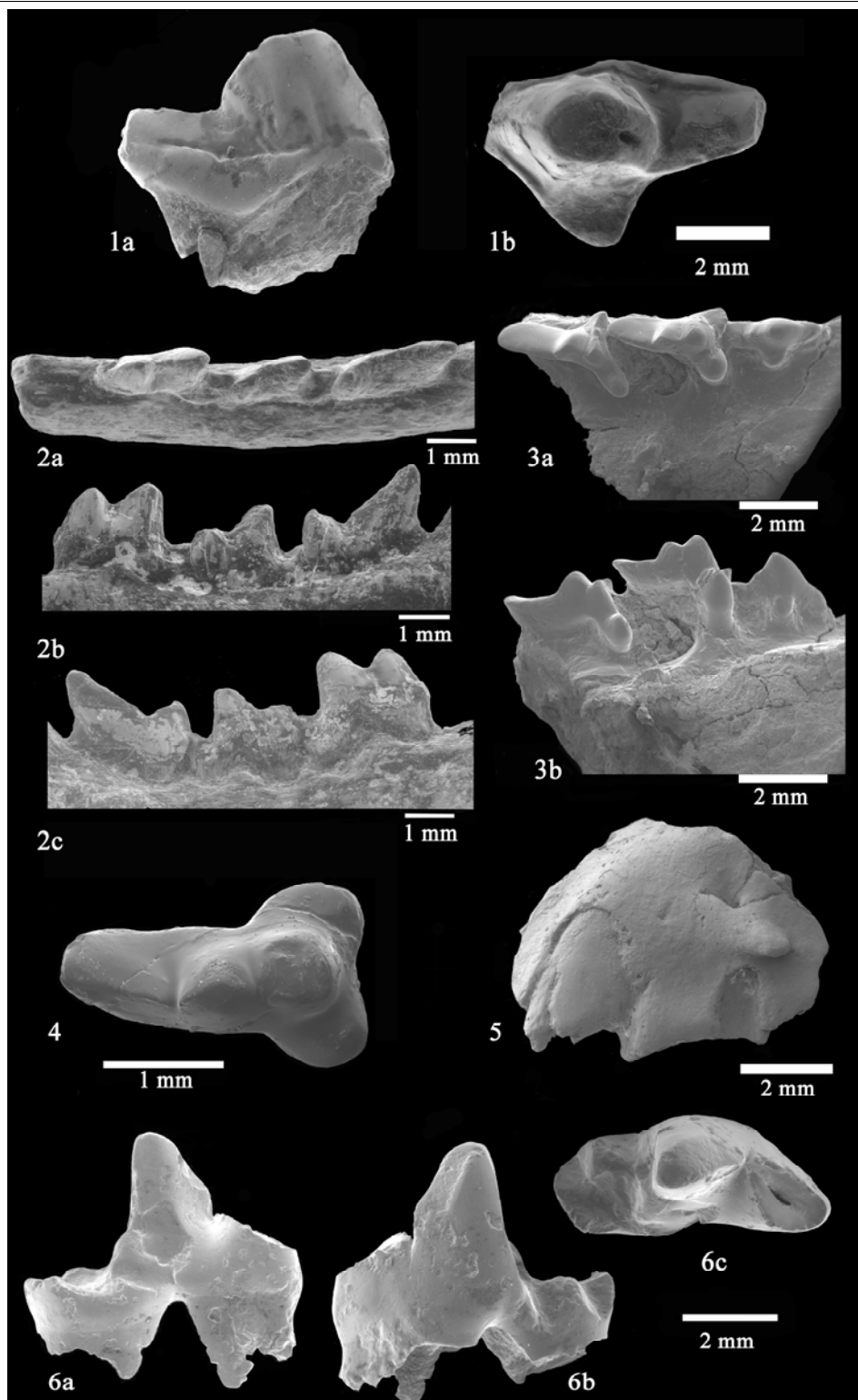| Catalogue number	Specimen	Taxon	APL	LMW art	PDL tub	LMW tub
EF 6'04	Pisiform	*Hyainailouros* sp.	24.0	14.8	20.1	11.4

Plate 1: Dentognathic remains of Sperrgebiet carnivorans.

1.- *Isohyaenodon* sp., Elisabethfeld, EF 208'01, left P4/; a) buccal view, b) occlusal view.

2.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 60'01, right mandible with m/2-p/4; a) occlusal view, b) lingual view, c) buccal view.

3.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04, (holotype) right maxilla with M1/-P3/; a) occlusal view, b) lingual view.

4.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04, right P4/; occlusal view.

5.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04, fragment of left maxilla, buccal view.

6.- Viverridae gen. et sp. indet. I, Elisabethfeld, EF 45'93, left m/1 or d/4; a) lingual view, b) buccal view, c) occlusal view.

Table 2: Measurements (in mm) of the radius of Creodonta from Grillental (TL, total length; APL prox, antero-posterior length of the proximal epiphysis; LMW prox, latero-medial width of the proximal epiphysis; APL dist, antero-posterior length of the distal epiphysis; LMWdist, latero-medial width of the distal epiphysis).

Catalogue number	Specimen	Taxon	TL	APL prox	LMW prox	APL dist	LMW dist
GT 58´06	Radius	*Hyainailouros* sp.	286.6	32.4	-	39.7	41.5

pyramidal. This facet for the pyramidal is square in outline, elongated medio-laterally. The palmar tubercle of the bone is flattened and rough.

GT 58´06, is a right radius (Table 2; Fig. 1) with the distal half partially reconstructed, and both proximal and distal epiphyses damaged and partially restored. The overall morphology and size of the bone are similar to the radius of *Hyainailouros sulzeri* figured by Ginsburg (1980). The diaphysis is relatively slender, and slightly curved posteriorly. The proximal epiphysis is antero-posteriorly flattened; its articular surface shows a medial facet, flat and medially oriented, and a strongly concave lateral facet. A bicipital tuberosity is not clearly developed, but there is a rough, postero-laterally located surface for the attachment of muscle *biceps brachii* below the proximal epiphysis. The distal epiphysis shows an elliptic and concave articular surface, slightly antero-posteriorly compressed.

Discussion: In overall morphology and size, the radius GT 58'06 is close to a specimen of *Hyainailouros sulzeri* figured by Ginsburg (1980).The fragmentary lower molar (GT 53'06) is from a huge creodont, similar in size to specimens attributed to *Megistotherium osteothlastes* Savage, 1973 by Morales and Pickford (2005).

On the basis of this rather meagre material we are unable to decide whether there is a single species of huge creodont in the Northern Sperrgebiet deposits, or whether two taxa are preserved. The uncertainty is aggravated by the fact that the huge creodonts of Europe and Africa require revision, *Megistotherium* possibly being a synonym of *Hyainailouros* (Morales and Pickford, 2005).

Genus *Isohyaenodon* Savage, 1965
Species *Isohyaenodon* sp.

Material: EF 208'01, left P4/.

Localities: Elisabethfeld (EF) and Grillental (GT)

Description: EF 208'01, a left P4/ (L = ca. 7 mm, B = 6.5 mm) has the anterior margin slightly eroded, even though the impression is that the damage is slight and the tooth extended only a little anteriorly (Pl. 1, Fig. 1). The main cusp is high and transversely compressed, its anterior crista is smooth and the posterior one quite worn by use. It is clearly separated from the posterior cusp of the tooth which is wide and in the shape of a cutting blade. Buccally the tooth has a strong basal swelling which is worn by occlusion with the m/1. The lingual cingulum is strong but buccally the cingulum is only present at the anterior base of the basal expansion, extending as far as the anterior border.

GT 58'07, a right mandible with the roots of m/3-p/4, corresponds in dimensions with the P4/ from Elisabethfeld described above.

Discussion: *Isohyaenodon* sp. from Elisabethfeld is slightly smaller than *Metapterodon kaiseri* Stromer, 1924, described from the same site. Morphologically, it differs from the latter species by the smaller extent of the basal expansion and by the greater compression and development of the posterior cusp. As a result, the P4/ identified as *Isohyaenodon* sp. appears to be more hypercarnivorous than the homologous tooth of *Metapterodon kaiseri*. This more hypercarnivorous morphology characterises the species of *Isohyaenodon* Savage (1965) although the species described here is not the same size as any of the species attributed to this genus by Savage (1965) and Morales *et al.* (1998).

Family Teratodontidae Savage, 1965
Genus and species Teratodontidae indet.

Material: LT 125'04, fragment of left maxilla with the crowns of the molars (M3/-M1) damaged by erosion.

Locality: Langental.

Description: LT 125'04 is a maxilla fragment with the crowns of the molars damaged by wind-blown sand (Pl. 2, Fig. 1). The roots of the teeth appear to be quite robust. What remains of the crowns indicates that the specimen is a creodont. The M3/ seems to have only two roots (lingual and buccal) suggesting that it was somewhat reduced, with a crown that was wider than long as occurs in creodonts that possess M3/s. The M2/ is triangular in occlusal outline, and is also broader than long. Finally the M1/ is likely to be incomplete, lacking the anterior part, but even so, it is possible to see that it was also a broad tooth, with strong development of the protoconal area and with a deep inflexion in the centre of its posterior border.

Figure 1: *Hyainailouros* sp., Grillental, GT 58'06, right radius; a-d) proximal, lateral, medial, and distal views.

Discussion: The morphology of the molars agrees with what is known in two genera from the Early Miocene of East Africa, *Teratodon* Savage (1965) and *Anasinopa* Savage (1965). Both genera possess three molars, with the M3/ transversal. Also, in both genera the M2/ and M1/ are triangular in occlusal outline with the protocones strongly developed. The molars of these two genera differ from each other, those of *Anasinopa* having M2/ and M1/ with small parastyles and well developed metastyle, whereas in species of *Teratodon*, although the metastyle is strong, the parastyle is also well developed, which imparts, at least to the M2/, an outline which is an isosceles triangle, whereas in *Anasinopa* the outline is a scalene triangle. In these features the Langental specimen is closer to *Teratodon* than to *Anasinopa*, and this, together with the massivity of the roots, in particular those of M1/, indicate to us that this material belongs to a small species in the family Teratodontidae, although given the poor preservation of the teeth, some doubt must remain about this attribution.

Family Prionogalidae nov.

Diagnosis: Dwarf creodonts, shortened facial zone, hypercarnivorous dentition with dental formula ?I/2I, C/C, 3P/2P, 1M/2M, the carnassial function being performed by two pairs of teeth, M1/m2 and P4/m1.

Genus *Namasector* nov.
Species *Namasector soriae* nov.

Holotype: EF 118'01, maxilla with M1/-P3/, alveolus of P2/.

Paratypes: EF 50'01 and EF 60'01, left and right mandibles, EF 118'01 right P4/ and EF 118'01 right maxilla fragment with the canine root and the alveoli of P2/ and P3/. Probably all the material referred to this species belongs to the same individual.

Derivatio nominis: The generic name refers to the Nama region of Namibia and the sectorial nature of the carnassials. The species name is in memory of Dolores Soria.

Type locality: Elisabethfeld (Tortoise Site) Sperrgebiet, Namibia.

Age: Early Miocene, ca 20-21 Ma.

Diagnosis: Very small hypercarnivorous creodont, comparable in size to *Thereutherium* and *Prionogale*, M1/-m/2 and P4/-m/1 functioning as highly specialised carnassials. P3/ elongated with a strong linguo-basal cuspid, P4/ and p/4 elongated with morphology similar to M1/ and m/1 respectively.

Differential diagnosis: *Namasector* is relatively close to *Prionogale*, with which it shares the two
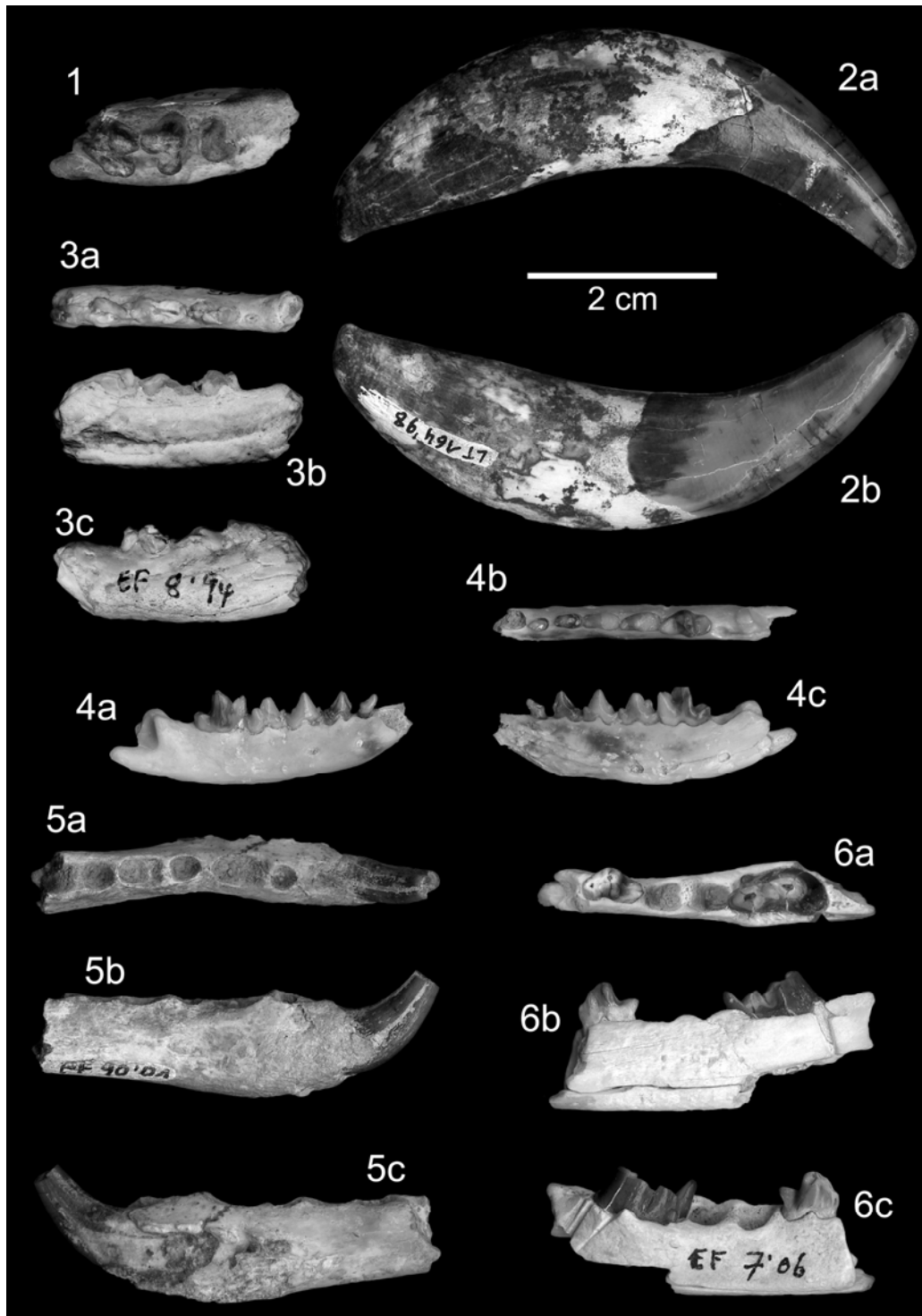
Plate 2:

Dental remains of Sperrgebiet carnivorans : Teratodontidae indet. (Fig. 1) *Ysengrinia* sp. (Fig. 2) Viverridae indet. sp. 2 (Fig. 3) *Leptoplesictis senutae* sp. nov. (Fig. 4) and *Metapterodon kaiseri* (Figs 5, 6).

1.- Teratodontidae indet. Langental, LT 125'04, fragment of left maxilla with M1, M2 and M3, occlusal view.

2.- *Ysengrinia* sp. Langental, LT 164'98, right lower canine, a-b) lingual and labial views.

3.- Viverridae indet. sp. II Elisabethfeld, EF 8'94, fragment of left hemimandible with roots of c, p2-p4, a-c) occlusal, lingual and buccal views.

4.- *Leptoplesictis senutae* sp. nov., holotype right mandible, a) buccal, b) occlusal, and c) lingual views.

5.- *Metapterodon kaiseri* Stromer, 1924, Elisabethfeld, EF 90'01, fragment of right hemimandible with canine and the alveolus of p/2-p/4 (the latter, incomplete) a) occlusal view, b) buccal view, c) lingual view.

6.- *Metapterodon kaiseri* Stromer, 1924, Elisabethfeld, EF 7'06, fragment of hemimandible with d/4 (or m/1) alveolus of m/2 and broken m/3, a) occlusal view, b) lingual view, c) buccal view.

pairs of carnassials in homologous positions and the probable reduction of the anterior dentition. It differs by the much greater hypercarnivorous specialisation, especially by the strong development of the metastyle of the M1/, the in-line position of the paracone-metacone-metastyle complex in the P4/ and the great elongation of the P4/. In the lower dentition it differs by the strong development of the trenchant blade of the protoconid of the m/2 and the reduction of the talonids of m/1 and p/4.

Description: Holotype. EF 188'01, left maxilla with M1/-P4/, alveoli of P3/ and C1/ (Fig. 2.1-2.3; Pl. 1, Figs 2-5). The M1/ is elongated with a very obvious development of the metastyle into a trenchant blade, which occupies almost the entire distal half of the tooth, without any sign of an incision (notch) between it and the metacone. The anterior part of the tooth is dominated by a high and voluminous metacone, whereas the paracone is of moderate size and continues as an antero-buccal parastyle. The protocone is well developed and prominent.

The P4/ has a typical carnassial morphology, differing from the M1/ by having the anterior part of the tooth dominated by a voluminous paracone, behind which is found the metacone separated from the metastyle by an incision. These three elements are disposed in a line. The parastyle is prominent and the protocone is slightly less strongly developed than in the M1/.

The P3/ is premolariform, comprised of a high central cusp which occupies the anterior two thirds of the tooth, and a posterior talonid cuspid which fits snug up against the anterior part of P4/, between the protocone and parastyle. There is a strong lingual expansion in the middle of the tooth.

There is a small uniradiculate alveolus in front, and another larger alveolus further forwards which we interpret to be the P2/ and C1/ respectively.

The disposition of the upper molariform series is peculiar, in that the crown of the P4/ is higher than that of M1/ and P3/ making the cutting edge of the series convex, as in a guillotine. This disposition of the cusps is reflected in the lower molariform series, in which the crown of the m/1 is lower than those of the m/2 and p/4.

EF 118'01, an isolated P4/ is similar in size and morphology to the holotype.

EF 118'01, a maxilla with the canine and roots of P2/ and P3/ corresponds well with the holotype, but it is better preserved. The upper canine is well developed with an oval section. The alveolus of the P2/ is uniradiculate, but of large dimensions, the alveoli of P3/ is broken anteriorly and opened externally. The infra-orbital foramen is located above the alveolus of the P3/ and is small and is partly covered by a bony apophysis which leans backwards.

Mandible. (EF 50'01, EF 60'01). The two available specimens are similar to each other, and belong to different sides. EF 60'01 is the best preserved (Pl.

2, Fig. 3). The m/2 is a narrow, cutting tooth, formed of a high paraconid separated by an incision from the protoconid, which is clearly hypertrophied and which occupies almost two thirds of the total length of the tooth. It has no talonid.

The m/1 is also greatly elongated being formed of a paraconid that is almost the same size as the protoconid, and separated from it by an incision. In buccal view, the wall is flat, in lingual view it is less trenchant than the m/2. The talonid is short and relatively high.

The p/4 is bigger than the m/1, and is morphologically similar to it, but the separation between the paraconid and protoconid is wider, without the typical incison of carnassials. The cuspids are less trenchant and the talonid is quite a bit bigger.

Discussion : *Namasector soriae* is a tiny hypercarnivoran mammal, comparable in size to *Prionogale breviceps* Schmidt-Kittler and Heizmann (1991) but with a much more sectorial dentition. The advanced degree of hypercarnivory in comparison with *P. breviceps*, is reflected in particular in the more aligned disposition of the cutting cusps of the upper and lower teeth (M1/, P4/, P3/ and m2/, m/1, p/4) and the major development of the metastyle of the M1/ into a slicing blade, in the antero-posterior alignment of the paracone-metacone in the P4/ and the lengthening of the cusps of the P3/. Similarly, in the lower dentition it is reflected in the elongation of the protoconid of m/2 – the morphology of which resembles that of the m/3 of species of *Hyaenodon* – and in general the transversal compression of the three molariform teeth (m/2, m/1 and p/4). In its exaggerated sectorial specialisation, *N. soriae* approaches *P. breviceps*, not only by its diminutive size, but if the interpretation of Schmidt-Kittler and Heizmann (1991) is correct, then also by the development of two pairs of carnassials, M1/m2 and P4/m1. In both genera the m/1 is smaller than the m/2 and the p/4, and the premolar row is very reduced.

Schmidt-Kittler and Heizmann (1991) saw in this carnivorous adaptation, a new clade distinct from both creodonts and carnivores. The weightiest argument in support of this hypothesis resides in the interpretation of the cutting function of the carnassials which in Carnivora is restricted to the P4/m1, whereas in Creodonta it is expressed exclusively between the molars. The interpretation of the two upper molars of *Prionogale breviceps* as P4/ and M1/ is based on the different position of the paracone in the two teeth, and if the anterior tooth is interpreted as a P4/ then its position is lingual, whereas if it is considered an M1/ this cuspid is displaced buccally. This point is not so evident in *Namasector soriae*, in which the two molariform teeth share a similar morphological pattern, although the position of the paracone of the posterior molar is more buccal than in the anterior one. But together, the two upper molars of *Namasector soriae* are not very different from the
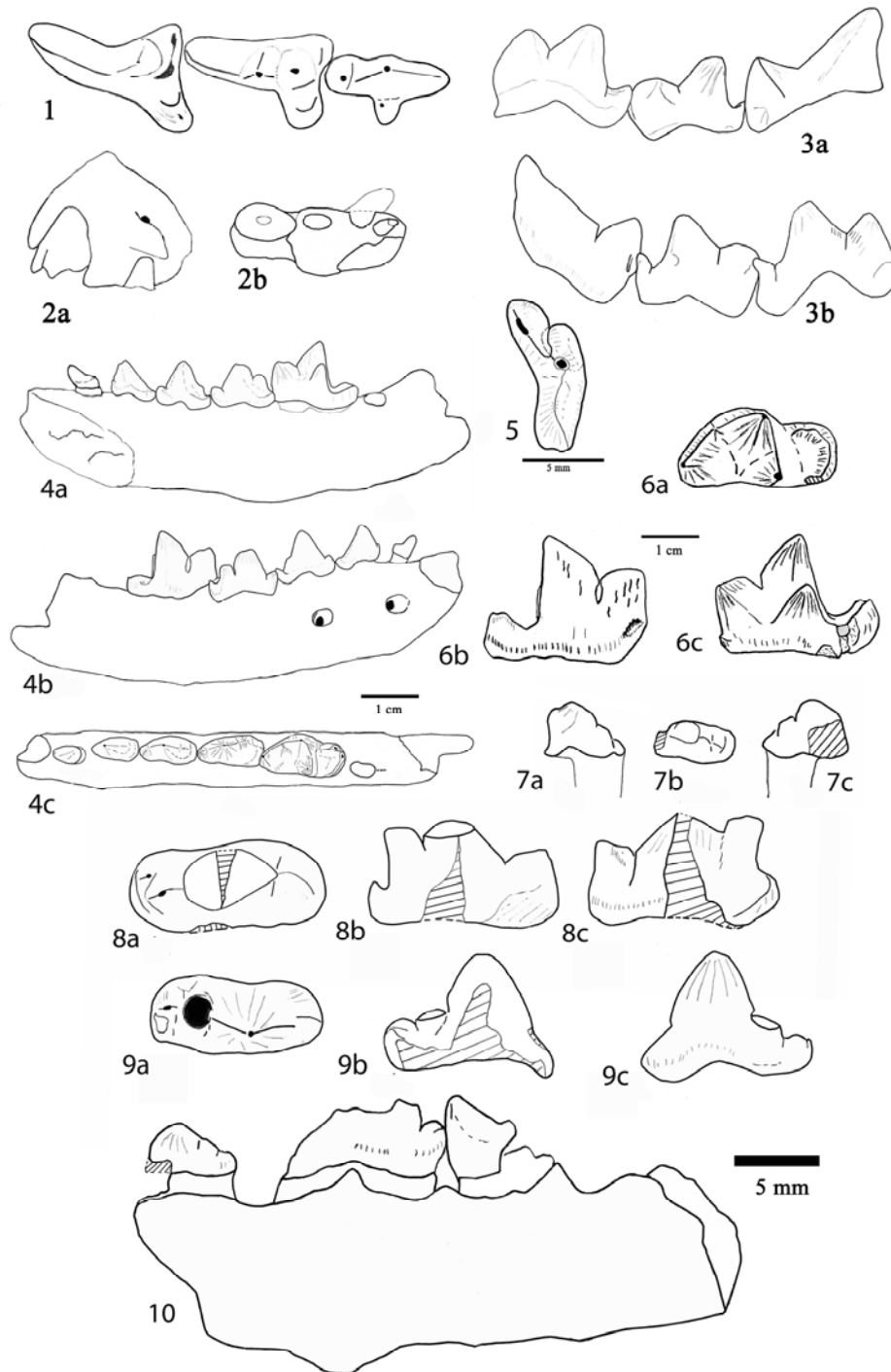
Figure 2: Dento-gnathic remains of Sperrgebiet carnivorans.

1.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04 (holotype) right maxilla with M1/-P3/; a) occlusal view.

2.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 118'04 fragment of left maxilla; a) buccal view, b) occlusal view

3.- *Namasector soriae* nov. gen. nov. sp., Elisabethfeld, EF 60'01 right mandible with m/2-p/4; a) lingual view, b) buccal view.

4.- *Leptoplesictis senutae* sp. nov., GT 1'06 holotype right mandible; a) lingual, b) buccal, and c) occlusal views.

5.- *Metapterodon stromeri* Morales, Pickford & Soria (1998) Langental, LT 6'01 left M3/, occlusal view.

6.- *Leptoplesictis namibiensis* sp. nov., LT 50'07 holotype right m/1; a) occlusal, b) buccal and c) lingual views.

7.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, right p/2; a) buccal view, b) occlusal view, c) lingual view.

8.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, right p/4; a) occlusal view, b) lingual view, c) buccal view.

9.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, left p/3; a) occlusal view, b) buccal view, c) lingual view.

10.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30'01, right mandible; buccal view.

corresponding teeth of hypercarnivorous Hyaenodontidae, as can be observed in the species *Metapterodon kaiseri* and *Metapterodon stromeri* described from sites in the Sperrgebiet (Stromer, 1924, 1926; Morales *et al.*, 1998).

If the molariform upper teeth of *Prionogale breviceps* are considered to be P4/ and M1/ the corresponding teeth in the mandible would be the m/1 and m/2. Not only *Prionogale breviceps* but also *Namasector soriae*, show that the most posterior molar is very different from the two anterior ones (absence of talonid and tendency to elongate the protoconid) whereas in the anterior ones the talonid is well developed in *P. breviceps*, but even more reduced in *N. soriae*. Given the advanced grade of hypercarnivory of the two species, it is not easy to decide whether the three molariform teeth correspond to m/2, m/1 and p/4 as interpreted by Schmidt-Kittler and Heizmann (1991) or as m/3, m/2 and m/1, an alternative hypothesis, in which case the upper molariform teeth would be M2/ and M1/. In *Prionogale breviceps* these two molariform teeth, supposedly m/1 and p/4 are quite worn and present no metaconid, a cusp which is also missing in the molariform teeth of *N. soriae*. As such, a molarised premolar could easily be confused with a hypercarnivorous molar. An argument in support of the hypothesis of Schmidt-Kittler and Heizmann (1991) could reside in the smaller dimensions of the second lower molar with respect to the third and first. In many Hyaenodontidae such as *Hyaenodon* or *Pterodon* the m/1 is small compared to p/4 and m/2, (Mellett, 1977; Lange-Badré, 1979) as is also the case in several creodonts which have lost the m/3, such as *Oxyaena gulo* Matthew (1915) *Patriofelis ferox* (Marsh, 1872) and *Limnocyon verus* Marsh (1872) to cite a few examples (Denison, 1938 ; Matthew, 1909). Certainly, these genera are not as hypercarnivorous as *Prionogale* or *Namasector*, but they reveal how the P4/ is molarised. This is also the case in the small species *Thereutherium thylacodes* Filhol (1876) which shows progressive reduction of the premolar dentition, m/1 smaller than m/2, and equal in size or smaller than p/4. In contrast, the P4/ in *Thereutherium* is slightly less molarised than in the species mentioned above, although it shows an elongation of the posterior half, as well as the protocone remaining in an anterior position, giving the tooth the aspect of a carnassial.

No matter which of the two hypotheses about the molariform teeth of *Prionogale breviceps* and *Namasector soriae* is accepted, these two species share an extreme development of hypercarnivory which is unknown in any other creodont, at least among those that preserve a well developed premolar row. McKenna and Bell (1997) classified *Prionogale breviceps* as *incertae sedis* among the creodonts. The small forms from Africa which were previously said to be related to forms such as Limnocyoninae Wortman (1902) or Oxyaeninae Wortman (1902) subfamilies that some authors consider to be due to Wortman

(1902) or Matthew (1915) are included in a single family Oxyaenidae Cope (1877). For Denison (1938) the two subfamilies resemble each other in the retention of primitive creodont characters due to a similar adaptation leading to parallelism. We suppose that the latter aspect refers to the loss of the third molars and to the development of a carnassial function in the M1/ and m/2, in contrast with the M2/ and m/3 of typical hyaenodontids. *Namasector* and *Prionogale* show a well developed hypercarnivory which clearly separates them from the generally accepted families of creodonts. For this reason, we propose a new family, Prionogalidae, for this group of tiny African creodonts, leaving open, for the moment, the question of its relationships at a higher taxonomic level.

Order Carnivora Bowdich, 1821
Family Amphicyonidae Haeckel, 1866
Genus *Ysengrinia* Ginsburg 1965
Species *Ysengrinia* sp.

Material: Langental, LT 164'98: right lower canine, LT 135'03: right pyramidal, LT 2´06: right scapholunar, LT 41'03: proximal fragment of left Mc II, LT 165'98: proximal epiphysis of left Mc III, LT 123'96: left Mt I, LT 230'99: first phalanx, LT 121'96: left Mt II, LT 122'96: proximal epiphysis of right Mt III , LT 5'01: left Mt IV, Elisabethfeld, EF 196'01: left Mc II, Fiskus, FS 17'03: fragmented right calcaneum, Grillental, GT 4'04: right Mt IV.

Description: Dentition. LT 164'98, a right lower canine has a robust curved root that is larger in antero-posterior dimensions than the crown (Pl. 2, Fig. 2). The lingual side of the root is flattened with a longitudinal groove. Despite the fact that the apex of the root is closed, the crown shows only minor apical wear and none on the two crests that descend from the apex towards the cervix. These two crests are positioned distally and medially, and have a slightly wrinkled appearance but are not crenulated. Mesially there is a slight contact facet caused by abrasion against the upper lateral incisor. The cervix descends rootwards on the buccal side, but rises on the lingual side to form an open v-shape immediately distal to the medial crest. At cervix the dimensions are ap 14 x tr 10.4 mm, and buccally the crown and root are both 35 mm tall.

Table 3: Measurements (in mm) of the pyramidal of *Ysengrinia* sp. from Langental (PDL, proximo-distal length; LMW, latero-medial width).

Catalogue number	Specimen	Taxon	PDL	LMW
LT 135'03	Pyramidal	*Ysengrinia* sp.	17.0	15.2

Table 4: Measurements (in mm) of the calcaneum of Carnivora from the northern Sperrgebiet (TL, total length; APL tub, antero-posterior length of the tuber calcis; LMW tub, latero-medial width of the tuber calcis; LMW art, latero-medial width of the articular surface).

Catalogue number	Specimen	Taxon	TL	APL tub	LMW tub	LMW art
FS 17'03	Calcaneum	*Ysengrinia* sp.	70.3	-	-	30.5
EF 9'94	Calcaneum	Viverridae sp. 2	22.2	5.8	5.0	9.4

Table 5: Measurements (in mm) of the metapodials and phalanges of Carnivora from the Sperrgebiet localities (TL, total length; APL prox, antero-posterior length of the proximal epiphysis; LMW prox, latero-medial width of the proximal epiphysis).

Catalogue N°	Specimen	Taxon	TL	APL prox	LMW prox
EF 196'01	Mc II	*Ysengrinia* sp.	53.9	18.3	10.3
LT 41'03	Mc II	*Ysengrinia* sp.	-	-	8.6
LT 165'98	Mc III	*Ysengrinia* sp.	-	20.0	12.6
LT 123'96	Mt I	*Ysengrinia* sp.	37.7	-	-
LT 121'96	Mt II	*Ysengrinia* sp.	56.9	16.1	9.9
LT 122'96	Mt III	*Ysengrinia* sp.	-	17.4	13.8
LT 5'01	Mt IV	*Ysengrinia* sp.	71.3	18.1	9.8
GT 4'04	Mt IV	*Ysengrinia* sp.	68.7	16.2	-
LT 230'99	Ist Phalanx	*Ysengrinia* sp.	22.7	7.9	10.2
LT 25'04	Ist Phalanx	*Afrosmilus africanus*	19.7	5.5	7.0
LT 228'99	Mc V	*Afrosmilus africanus*	39.4	8.7	8.2
GT 77'07	Mt II	*Afrosmilus africanus*	36.6	6.7	7.4
GT 78'07	Ist Phalanx	*Afrosmilus africanus*	-	7.1	7.8

Postcranial skeleton (Tables 4, 5; Fig. 3; Pl. 3, Figs 1-6, 8; Pl. 4, Figs 1-3). *Forelimb*. LT 135'03, a right pyramidal (Table 3) has a more or less rounded shape, and its morphology is typical of an amphicyonid, with a lateral surface divided into two by a marked distally oriented ridge, and a medial surface mostly occupied by a concave and smooth articular surface for the unciform.

LT 2'06, a right scapholunar, lacks the proximal surface and part of the palmar tubercle. Nevertheless, the distal articular surface is that of a medium-sized amphicyonid. The articular surfaces for the unciform and magnum are separated by a smooth ridge, with the facet for the magnum being much larger than that for the unciform. The facet for the trapezoid is triangular, with its plane almost completely oriented medially. The posterior tubercle is not complete, but it seems to be proximally oriented.

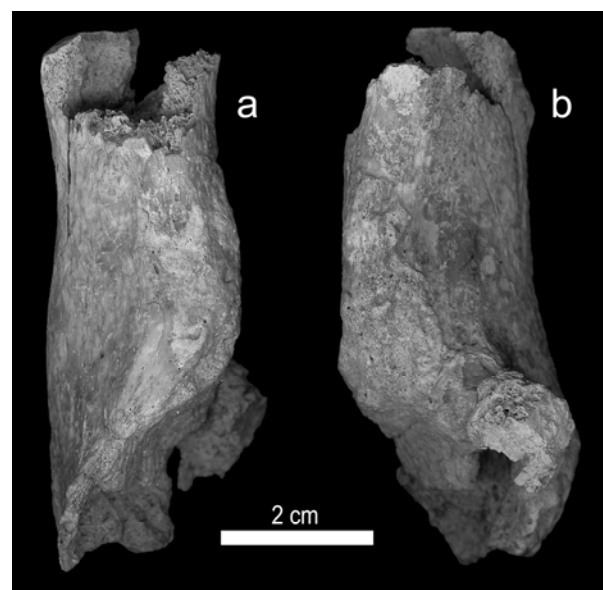EF 196'01, a left Mc II, has a short diaphysis which is straight and lacks any flattening; it has a

Figure 3: *Ysengrinia* sp., Fiskus, FS 17'03, right calcaneum; a-b) lateral and medial views.

Plate 3: Metapodials of *Ysengrinia* sp. (Figs 1-6, 8) and *Afrosmilus africanus* (Fig. 7, 9).

1.- *Ysengrinia* sp. Elisabethfeld, EF 196'01, left metacarpal II, a-c) lateral, medial and dorsal views.
2.- *Ysengrinia* sp. Grillental, GT 4'04, right metatarsal IV, a-c) lateral, medial and dorsal views.
3.- *Ysengrinia* sp. Langental, LT 5'01, left metatarsal IV, a-c) lateral, medial and dorsal views.
4.- *Ysengrinia* sp. Langental, LT 121'96, left metatarsal II, a-c) lateral, medial and dorsal views.
5.- *Ysengrinia* sp. Langental, LT 165'98, left metacarpal III, a-c) lateral, medial and dorsal views.
6.- *Ysengrinia* sp. Langental, LT 122'96, right metatarsal III, a-c) medial, lateral and dorsal views.
7.- *Afrosmilus africanus* (Andrews, 1914) Langental, LT 228'96, left metacarpal V, a-c) lateral, medial and dorsal views.
8.- *Ysengrinia* sp. Langental, LT 41'03, left metacarpal II, a-c) lateral, medial and dorsal views.
9.- *Afrosmilus africanus* (Andrews, 1914) Grillental, GT 77'07, left metatarsal II, a-c) lateral, medial and dorsal views.

large tuberosity in its proximo-medial border, corresponding to the attachment of the muscle *extensor carpi radialis longus*. The distal epiphysis is slightly asymmetrical, corresponding to a medial metapodial.

The proximal articular surface has an irregular shape, elongated dorso-palmarly, with the dorso-lateral border markedly projected dorsally in relation to the dorso-medial one. Palmarly, this surface develops a small tuberosity for the attachment of one of the two tendons of the muscle *flexor carpi radialis*. The medial face of the proximal epiphysis has a central rough depression that probably articulates with a reduced Mc I. Occupying most of the lateral face there is a large, concave and smooth articular facet for the Mc III.

LT 41'03, a proximal fragment of left Mc II, possesses morphology similar to that of EF 196'01, but it is much smaller. The proximal articular surface is damaged, but its shape is close to that of the latter specimen. Nevertheless, LT 41'03 lacks the tuberosity for the muscle *extensor carpi radialis longus*, although the bone is thicker in this area. Given the small dimensions and the morphological difference, this piece probably belongs to a sub-adult individual.

LT 165'98, a proximal epiphysis of a left Mc III, in which most of the proximal surface is severely damaged, retains just the dorsal border. In the medial face there is a partially broken large dorsal facet for the articulation of Mc II; it is wide and smooth, occupying the dorso-proximal border. In the palmar border of this face, a large facet for the muscle *flexor carpi radialis* can be clearly observed. Between the two articular facets, there is a rough depression. The lateral face of the epiphysis shows a central rough tuberosity and part of the dorsal groove for the articulation of the Mc IV.

LT 230'99, a first phalanx, is relatively short and robust, with a slight medial curvature. The lateral and medial borders of the proximal epiphysis are strongly projected. Based, in this morphology, this piece probably corresponds to the first phalanx of the thumb.

Hindlimb. FS 17'03, a fragmented right calcaneum (Table 4, Fig. 3) is poorly preserved; the *tuber calcanei* and the distal and talar facets are broken, so they cannot be described. The overall morphology of this specimen is that of a medium-sized amphicyonid, with a well developed but not especially projecting sustentaculum tali, similar to the specimen of *Haplocynoides suevicus* from the Lower Miocene of Germany, figured by Peigné and Heizmann (2003 : fig. 14e).

LT 123'96, a left Mt I, in which the proximal and distal epiphyses are poorly preserved, and cannot be described. The diaphysis is slender, slightly flattened dorso-plantarly and plantarly curved.

LT 121'96, is a left Mt II, in which the diaphysis is slightly flattened dorso-plantarly in its distal half. The proximal surface is triangular, elongated dorso-plantarly, slightly inclined medially, and ending plantarly in a rounded tubercle for the attachment of the muscles *peroneus longus* and *adductor obliquus hallucis*. The medial face of the proximal epiphysis is rough, with a plantar facet for the articulation of the Mt I. The lateral face shows a pair of rounded and large facets for the articulation of the Mt III, separated by a smooth and shallow groove.

LT 122'96, is a proximal epiphysis of right Mt III, in which the proximal surface is typically T-shaped and clearly inclined medially. The dorsal half of the surface is wider than the plantar half, which finishes in a smooth plantar facet for the attachment of the muscle *adductor obliquus hallucis*. The medial facets for the articulation of the Mt II are poorly preserved, but they seem to have been small and restricted respectively to the dorsal and plantar border of this medial surface. The lateral facets for Mt IV are also in a poor state of preservation; the dorsal one is concave and almost plantarly oriented, probably producing a not very rigid articulation between Mt III and IV; the plantar facet for Mt IV is smaller and placed just below the level of the proximal surface.

LT 5'01, is a left Mt IV, in which the diaphysis is slightly dorso-plantarly flattened and curved. The specimen shows pathologic growth of bone on the dorsal surface of the diaphysis and part of the proximal epiphysis. The distal epiphysis is slightly displaced medially, being more or less symmetrical in distal view. The proximal surface of the proximal epiphysis is rectangular, with a convex dorsal half and a concave plantar one. In the distal end of this epiphysis, there is a rounded and smooth surface for the attachment of the muscle *adductor obliquus hallucis* and the long plantar ligament. There are two medial articulatar facets for the Mt III : the dorso-medial one is smooth, rounded, dorsally oriented and separated from the proximal surface by a low notch; the plantar facet for Mt III is medially oriented, smooth, and proximo-distally elongated. There is a marked notch separating the two medial facets. The lateral face of the proximal epiphysis shows a large central depression for the articulation of the medial face of Mt V; there are also two articular facets for the Mt V, one of them placed all along the proximal border, and another one, much smaller and proximo-distally elongated, located in the plantar border.

GT 4'04, a right Mt IV, has the same size and similar morphology to LT 5'01, although it lacks any pathological growth and thus shows a more slender and smoother diaphysis than the latter specimen.

Discussion: Specimens of *Ysengrinia* from the localities of Grillental, Fiskus, Langental and Elisabethfeld are close in size and morphology to material of *Ysengrinia ginsburgi* from Arrisdrift published by Morales *et al.* (2003). Some elements, for example the calcaneum, are slightly smaller than those from the latter locality, but the differences can be considered to fall within the range of size variation of this amphicyonid.

Family Viverridae Gray, 1821
Genus *Leptoplesictis* Major, 1903
Species *Leptoplesictis senutae* nov.

Locality: Grillental, Sperrgebiet, Namibia.

Age: Early Miocene.

Derivatio nominis: In honor of Brigitte Senut.

Holotype: GT6 - 1'06 right mandible with p/1-m/2.

m /1	L=6.0	B=3.0
p /4	L=5	B=2.5
p /3	L=4.3	B=2.1
p /2	L=3.4	B=2.0
p /1	L=1.5	B=1.6

Diagnosis: m/1 large in comparison with the premolar series, with high metaconid, almost as high as the paraconid; p/4 with cusps aligned oblique to the long axis of the mandible and the talonid enlarged lingually; p/3 with weak anterior cusp and uniradiculate p/1.

Differential diagnosis: *Leptoplesictis senutae* differs from *Leptoplesictis aurelianensis* (Schlosser, 1888) type species of the genus, by the morphology of the p/4 (smaller anterior cusp and better developed talonid) and by the greater development of the m/1 compared to the p/4. It differs from *Leptoplesictis rangwai* (Schmidt-Kittler, 1987) and from *Leptoplesictis mbitensis* (Schmidt-Kittler, 1987) by the more hypercarnivorous morphology of the m/1, in which the trigonid is more transversely compressed. In addition, it differs from *Leptoplesictis rangwai* by the greater development of the m/1 compared to the p/4, the higher metaconid of the m/1 and the lesser development of the anterior cusp of p/4. It also differs from *Leptoplesictis mbitensis* by the absence of the lingual cusplet of the talonid in the p/4.

Description: The holotype, GT6 - 1'06 is a right mandible lacking the ascending ramus (Fig. 2.4; Pl. 2, Fig. 4). The m/2 is lost, but its alveolus indicates that it was reduced and was uniradiculate. The m/1 is quite a narrow and sectorial carnassial, with a high trigonid in which the protoconid stands out by its greater height compared to the paraconid and metaconid which are of similar height to each other, even though the metaconid is smaller than the paraconid. The posterior part of the metaconid and the protoconid form a continuous posterior wall, which is slightly inclined with respect to the long axis of the tooth. The paraconid and protoconid are disposed in such a way as to form a slicing blade and are separated from each other by a deep, vertical notch. The talonid is short, being formed of a high hypoconid of which the anterior cristid is short, but is well developed and contacts the internal base of the protoconid

in such a way as to form a small undulating valley in the lingual base of the talonid between the hypoconid and the protoconid. The posterior cristid of the hypoconid is shorter and contacts the entoconid, which continues round the posterior part of the talonid as a peripheral crest which almost reaches the base of the metaconid. The p/4 has a sharply pointed anterior cusp of modest dimensions, a transversely compressed main cusp and a high but moderately sized posterior cusp. These three cusps are aligned with each other but are oblique to the long axis of the jaw. Buccally, the talonid is short, but lingually it is well developed. The p/3 is a single-cusped tooth, with small anterior and posterior cusplets, and a short talonid, and differs from the p/4 because the cusps are aligned with the long axis of the mandible. The p/2 is reduced, having a single cusp with a tiny anterior cusplet. The reduced p/1 is a single cusped, uniradiculate premolar.

Discussion: *Leptoplesictis senutae* is close to *Leptoplesictis rangwai* and *Leptoplesictis mbitensis* in the morphology of its p/4, in which the strong development of the talonid stands out, as does the alignment of the cusps oblique to the long axis of the mandible (Schmidt-Kittler, 1987). The three species share the m/1 with short talonid, formed of a hypoconid endowed with an anterior cristid and a peripheral entoconid. The presence of a uniradiculate, reduced p/1 is another feature shared by *L. senutae* and *L. rangwai*, but the condition of this tooth is unknown in *L. mbitensis*.

However, *L. senutae* differs from *L. rangwai* and *L. mbitensis* by the more compressed morphology and thus more sectorial trigonid of the m/1. In this character the two species from Rusinga approach extant species of *Herpestes*, and this hypercarnivorous morphology is also found in *Leptoplesictis aurelianensis* (Viret, 1951; Beaumont, 1973). These differences might justify generic separation of the more hypercarnivorous species (*L. senutae* and *L. aurelianensis*) from *L. rangwai* and *L. mbitensis*, but a better fossil record is necessary to decide, in particular concerning the upper dentition and cranial anatomy, so far unknown in the three African species.

Leptoplesictis was considered to be a synonym of *Herpestes* by McKenna and Bell (1997) but the morphological differences between the type species *L. aurelianensis* and *Herpestes* (and in general all the extant forms classified in the family Herpestidae) are considerable, indicating that they belong to different genera. The lower dentition of *L. aurelianensis* is in some respects closer to that of *Genetta genetta* than to that of *Herpestes*, with elongated, narrow premolars, reduced talonid in the p/4, and a sectorial carnassial with a narrow protoconid-paraconid blade and a metaconid with a tendency towards reduction. This hypercarnivorous tendency of the lower dentition accords with the maxilla from La Grive, France, de-

scribed by Beaumont (1973, plate I, fig. 6) and appears to indicate a closer relationship of *Leptoplesictis* with the family Viverridae than with the Herpestidae.

Species *Leptoplesictis namibiensis* nov.

Type locality: Langental, Sperrgebiet, Namibia.

Age: Early Miocene.

Holotype: LT 50'07, right m/1.

m /1   L=8.3   B=4.4

Diagnosis: *Leptoplesictis* of large size, m/1 with high and short trigonid. Talonid small, with simple morphology, comprising a high peripheral crest in which cusplets are imperceptible. Talonid valley deep.

Differential diagnosis: *Leptoplesictis namibiensis* differs from other species of *Leptoplesictis* by its notably greater dimensions. In addition it differs from *Leptoplesictis rangwai* (Schmidt-Kittler, 1987) and *Leptoplesictis mbitensis* (Schmidt-Kittler, 1987) by the more hypercarnivorous morphology of the m/1. It differs from *Leptoplesictis senutae* nov. sp. and *L. aurelianensis* by the construction of the talonid, which is simpler morphologically and is higher.

Material: Holotype, LT 50'07, right m/1 (Fig. 2.6).

Description: The trigonid of m/1 is high and narrow, with the buccal walls of the protoconid and paraconid forming a slicing blade with a well marked incision between the cusps. The protoconid is higher than the paraconid. The metaconid has a pyramidal morphology, and is lower than the paraconid, and its lingual wall is aligned with the lingual wall of the paraconid, such that the overall cutting aspect of the trigonid is accentuated. The posterior walls of the paraconid and protoconid are almost transversely oriented with respect to the long axis of the tooth, such that the trigonid is clearly separated from the talonid. The talonid is short with a deep central valley, bordered posteriorly by a high, sharp crest in which a small hypoconid can be distinguished on its buccal sector. The lingual crest of the hypoconid is low and extends to the internal base of the protoconid. Lingually, the posterior crest of the talonid as low and terminates near the base of the metaconid. Quite a strong cingulum extends along the buccal base of the paraconid.

Discussion: Knowledge of viverrids *sensu lato* from the Early Miocene of Africa is obscure, in particular for the species included by Schmidt-Kittler (1987) in the genera *Herpestides* and *Leptoplesictis* (originally defined in Europe). The former was positioned by Beaumont (1967) at the base of the radiation of the family Hyaenidae and with the Viverridae by Hunt (1991) possessing a talonid in the m/1 normally comprising at least three well separated cusplets; a hypoconid, an entoconid and an additional cusp located between them. This morphology occurs in the majority of Hyaenidae (except for the more specialised species) and in extant and fossil species of the *Viverra* group. In *Leptoplesictis namibiensis*, the morphology of the talonid of m/1 is completely different from that of *Herpestides antiquus*, and is closer to that of some species of *Herpestes*. *Herpestides aequatorialis*, to judge from the figures published by Schmidt-Kittler (1987) appears to have an m/1 close to that of *L. namibiensis*. The two species can be differentiated from other species of *Leptoplesictis* and could be included in another genus, which however, for the reasons evoked above, cannot be *Herpestides*. In the absence of a better fossil record, or a more detailed revision of the African viverrids, we provisionally include all these species in *Leptoplesictis*, although we are aware that this is not an ideal option.

Viverridae gen. et sp. indet. I

Locality: Elisabethfeld.

Material: EF 45'93, left m/1 or d/4 (L = 6.6 mm, B = ca. 3 mm).

Description : The tooth is well preserved, although the apex of the paraconid is broken, and it is damaged in the area of the metaconid and is missing the postero-buccal part of the talonid, and it has suffered some erosion of the anterior wall of the protoconid (Pl. 1, Fig. 6). The roots of the molar indicate that it was a young animal at the time of death. In spite of the damage, a general idea of the morphology of the tooth can be obtained. It possesses a long trigonid, which is sectorial and very compressed transversely, with a blade-like paraconid and sharp protoconid. The metaconid area is broken, but a swelling in the medial part of the internal wall of the protoconid indicates to us that it would have had a certain size and that it was retired with respect to the base of the protoconid. The talonid is relatively large, being formed of a voluminous hypoconid (broken posteriorly) provided with an anterior cristid which runs to the base of the separation between the protoconid and metaconid, in such a way as to make a small undulating valley at the lingual base of the talonid between the hypoconid and protoconid. In the postero-buccal corner there is a vertical, subdivided entoconid. The gap between the entoconid and metaconid is eroded, but the impression is that the two cusps were well separated.

Discussion: The overall morphology of this tooth is similar to that of the m/1 in the Grillental mandible described above as *Leptoplesictis senutae* nov. sp. However, there are some differences, including the

fact that EF 45'93 is more elongated and narrower, the metaconid appears to be more retired and the talonid is quite different, with a more voluminous hypoconid and a higher entoconid. These differences are sufficient to exclude it from *L. senutae*. In addition, the Elisabethfeld molar seems to be more hypercarnivorous than that of *L. senutae*, which runs counter to the larger dimensions of the talonid. This fact makes us prudent not to eliminate the possibility that it could represent a deciduous tooth, d/4. Whatever the case we are in the presence of a probable species of Viverridae larger than *L. senutae*.

Viverridae gen. et sp. indet. II

Material: EF 8'94, a fragment of right mandible with c/1-p/4 in a poor state of preservation, and EF 9'94, associated left calcaneum and astragalus.

Locality: Elisabethfeld.

Description : EF 8'94 is a fragment of a modestly sized but quite robust mandible (Pl. 2, Fig. 3). The symphysis is high and it is possible to see that the canine root is robust, although it doesn't extend beyond the alveolus of the p/1, which is small and uniradiculate.Between the p/1 and the canine there is a long diastema, and a shorter one occurs between p/2 and p/3. The other three premolars are interpreted as p/2-p/4, but on account of their lamentable state of preservation none of them show any morphological details, although they seem to increase in size from p/2 to p/4 and were probably robust.

EF 9'94 is an associated left calcaneum and astragalus belonging to the same individual. These specimens were found in anatomical connection, being cleaned and separated in order to describe the talar facets. Both pieces are eroded, and the original morphology of some structures is not readily observed. The overall size and morphology of the calcaneum (Table 4; Pl. 4, Fig. 5) is similar to that of the extant viverrid *Genetta genetta*. The *tuber calcanei* is slightly longer in EF 9'94 than in the genet, with a thicker dorsal border; its proximal tip is deeply eroded, making it impossible to appreciate the development of the lateral and medial expansions, present in *G. genetta*. The degree of projection of the *sustentaculum tali* and lateral margin is very similar to that of *G. genetta*, although in EF 9'94, the small tubercle for the attachment of the long lateral collateral ligament is slightly displaced distally in relation to its disposition in the genet; the surface of this small tubercle is smooth and flat, as in *G. genetta*, different from the grooved surface that occurs in felids. The attachment surface for the muscle *quadratus plantae*, on the lateral surface, is more marked in the genet, although it is clearly present in EF 9'94. The talar facet of the coracoid process seems to be more proximally elongated in the genet than in EF 9'94, whereas that of the *sustentaculum tali* is very similarly shaped

Table 6. Measurements (in mm) of the astragalus of Viverridae from Elisabethfeld (PDL, proximo-distal length; LMW troc, latero-medial width of the trochlea).

Catalogue number	Specimen	Taxon	PDL	LMW troc
EF 9'94	Astragalus	Viverridae indet.	14.8	8.0

in both species, being clearly separated from that of the coracoid process, whereas in felids both facets are more closely placed. The *sinus tarsi* is shorter in EF 9'94 and *G. genetta* than in felids. The distal articular facet for the cuboid is partially broken, but its morphology and development is similar to that of *G. genetta*.

The astragalus of EF 9'94 (Pl. 4, Fig. 8) is similar to that of *G. genetta* (Table 6). In dorsal view, the trochlea is medio-laterally wider in the former, with a more concave distal border in the latter. The astragalar neck of EF 9'94 is also wider and shorter than that of a genet. The talar facets of the astragalus are very similar to those of the genet, with that for the *sustentaculum tali* of the calcaneum being placed on the neck surface, whereas in felids this facet is more proximally located.

Discussion: The mandible and associated astragalus/calcaneum correspond to a viverrid somewhat more robust than extant *Genetta genetta*. Among the forms known from the Early Miocene of East Africa the fossil material is similar in size to *Herpestides aequatorialis* Schmidt-Kittler (1987) and *Stenoplesictis muhoronii* Schmidt-Kittler (1987). It differs from the former by the uniradiculate condition of its p/1, but in *Stenoplesictis muhoronii* we do not know the state of this feature, nor of most of the lower dentition. Under the circumstances, it is better to leave the identification of these Sperrgebiet fossils as Viverridae indet.

Family Felidae Fischer von Waldheim, 1817
Subfamily Barbourofelinae Schultz, Schultz and Martin, 1970
Tribe Afrosmilini Morales *et al.*, 2001
Genus *Afrosmilus* Kretzoi, 1929
Species *Afrosmilus africanus* (Andrews, 1914)

Localities: Fiskus : FS 35'93, fragment of mandíble with p/2, fragment of p/3 and anterior part of p/4; FS 30'01, associated fragments of right mandibular symphysis, right p/2, left p/3, right p/4 and anterior part of left p/4. Langental : LT 25'04, first phalanx; LT 228'99, left Mc V. Grillental : GT 77'07 left Mt II; GT 79'07, left scapholunar.

Description: Dentition (Figs 2.7-2.10). FS 35'93, a p/2, is a reduced tooth, with the anterior part somewhat broken. Its morphology is simple with a low, rounded main cusp with the posterior part of the tooth
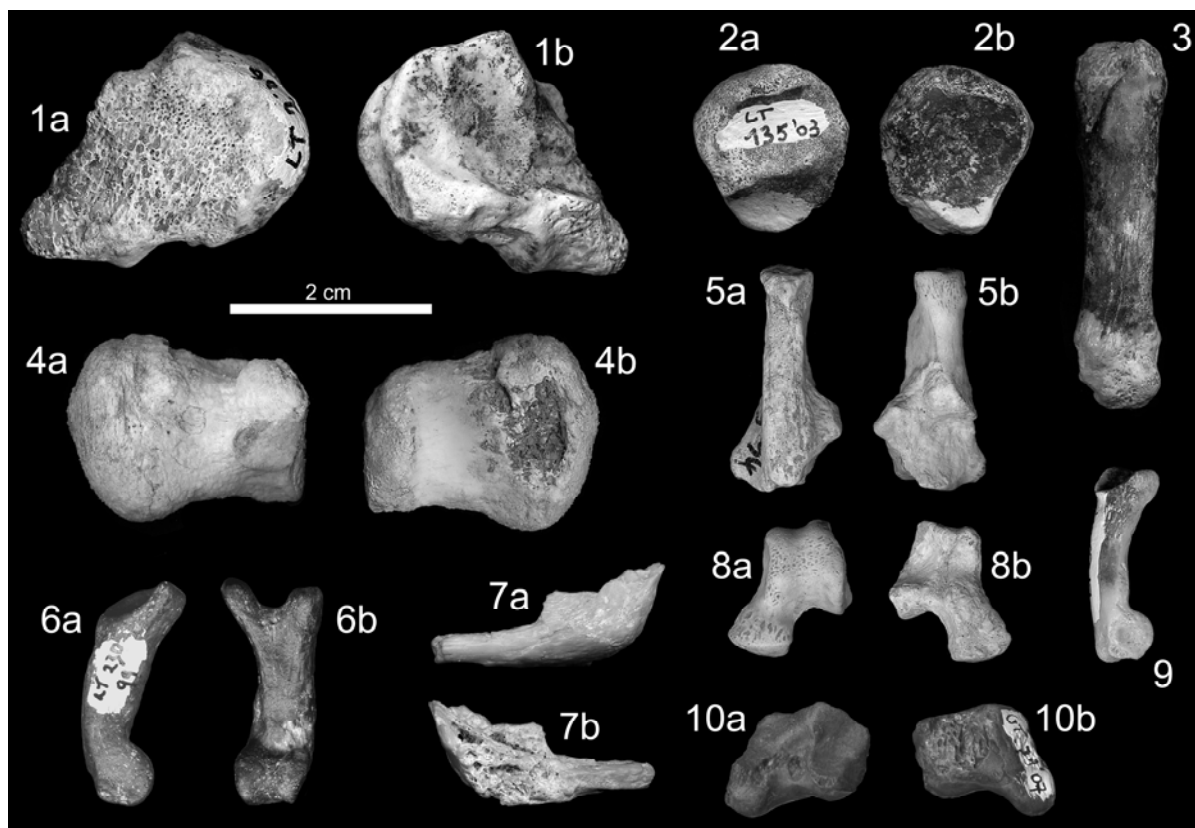
Plate 4:

Postcranial remains of *Ysengrinia* sp. (Figs 1-3, 6) Viverridae indet. (Figs 5, 8) *Afrosmilus africanus* (Figs 7, 9, 10) and *Hyainailouros* sp. (Fig. 4).

1.- *Ysengrinia* sp. Langental, LT 2´06, right scapholunar, a-b) proximal and distal views.

2.- *Ysengrinia* sp. Langental, LT 135´03, right pyramidal, a-b) lateral and medial views.

3.- *Ysengrinia* sp. Langental, LT 123´96, left metatarsal I, dorsal view.

4.- *Hyainailouros* sp. Elisabethfeld, EF 6´04, left pisiform, a-b) medial and lateral views.

5.- Viverridae sp. indet. II Elisabethfeld, EF 9'94, left calcaneum, a-b) plantar and dorsal views.

6.- *Ysengrinia* sp. Langental, LT 230'99, first phalanx of the thumb, a-b) lateral and volar views.

7.- *Afrosmilus africanus* (Andrews, 1914) Fiskus, FS 30´01, fragment of right mandibular symphysis, a-b) lateral and lingual views.

8.- Viverridae sp. indet. II Elisabethfeld, EF 9'94, left astragalus, a-b) anterior and posterior views.

9.- *Afrosmilus africanus* (Andrews, 1914) Langental, LT 25´04, first phalanx, lateral view.

10.- *Afrosmilus africanus* (Andrews, 1914) Grillental, GT 79´07, left scapholunar, a-b) distal and proximal views.

longer than the anterior and it has small posterior and basal cusplets. A short diastema separates the p/2 from the p/3 (L = 9.8 mm, B = 4.4 mm). The latter tooth has all the buccal wall damaged, although we discern a relatively strong posterior cuspid and a well-developed talonid with a small cusplet in its centre. Only a minor part of the front of the p/4 (L = ca 12 mm, B = ca 5.8 mm) is preserved as is the posterior alveolus.

FS 30'01 comprises several fragments of bone and teeth, of which the best preserved are a fragment of right symphysis which shows a clear machairodontine profile (Pl. 4, Fig. 7) and the right p/2 (L = 5.2 mm, B = 2.1 mm) which shows the absence of the anterior cusplet, and the greater development of the posterior part of the tooth, as in the specimen described above. The left p/3 (L = 9.9 mm, B = 4.4 mm) has an eroded buccal wall, and its main cusp is high,

sharp and is displaced anteriorly. There seems to have been no anterior cusplet although this part of the tooth is not well preserved. The posterior cusplet is strong and is close to the base of the tooth, and the talonid is relatively strong. The right p/4 (L = ca 10.6 mm, B = 6.3 mm) is reconstructed from two halves that were separated, which have a contact between the upper part of the buccal wall. There is a vertical, strong and transversely compressed anterior cusp which is separated by a notch from the main cusp. The posterior cusp is high but is smaller than the anterior one, while the talonid is short, but is swollen by a posterior cingulum.

Postcranial skeleton (Pl. 3, Figs 7, 9; Pl. 4, Figs 9, 10). GT 79'07, a left scapholunar slightly smaller than that of *Lynx pardina*, is almost complete, showing a broken proximal surface. The distal articular surface is similar to that of a felid, although the facet

for the unciform is more laterally oriented, and that for the magnum is wider, shallower, and does not surpass the level of the palmar margin. The palmar tubercle is relatively shorter than that of *L. pardina*, and dorso-palmarly shows a proportionally longer articular facet for the trapezium developed on its distal surface.

LT 228'99 is a left Mc V (Table 5) in which the proximal epiphysis is partly broken, but in which it is clear that it was less distally projected than in a felid of similar size, such as *Lynx*. The diaphysis is more dorso-palmarly flattened and less laterally curved than that of a *Lynx*. Nevertheless, the overall morphology is felid-like, and the proximal epiphysis is similar to that of *Lynx*. In proximal view, this proximal epiphysis has a semicircular shape, with a rounded lateral border, and a straight medial one; its palmar border develops a small expansion for the attachment of the muscle *flexor carpi ulnaris*, an expansion which is not present in *Lynx*, but which is well developed in other larger felids. The lateral face of this epiphysis shows a partly damaged tuberosity for the attachment of the muscle *extensor carpi ulnaris*. Most of the medial face of the proximal epiphysis is occupied by the articulatar surface for the Mc IV, which is smooth and develops a medially projected bony sheet in the centre of the articular surface.

This specimen fits well with the manus of *Afrosmilus* from Napak figured by Schmidt-Kittler (1987) but it is larger. We attribute the Napak material to *Ginsburgsmilus napakensis* Morales *et al.*, (2001). As there are some dento-gnathic remains of *A. africanus* in the Sperrgebiet sites, then it is probable that the Mc V and the phalanx, LT 25'04, belong to this species.

LT 25'04, a first phalanx (Table 5) is slender, straight and slightly curved palmarly, which fits well into the morphology of a first phalanx of the Vth digit of the forelimb of a *Lynx*-sized felid.

GT 77'07, a left Mt II (Table 5) collected in two pieces, lacks a small portion of the diaphysis. Both pieces are rounded and the proximal epiphysis is slightly dorso-palmarly flattened. The specimen is slightly smaller than the Mt II of *Lynx pardina*, and much more robust. The proximal articular surface is widened in comparison to that of *L. pardina*, due to the lateral projection of the dorso-lateral margin. This projection produces a lateral face markedly different from that of *L. pardina* and other felines : in the former, the articular facet on the dorsal border of the lateral face is clearly divided into a proximal part for the ectocuneiform, and a distal one for the Mt III; in GT 77'07 the facet for the ectocuneiform is placed along the proximal border, which is not seen in felids, but is present in viverrids. The medial articular facet for Mt I, absent in felids, is developed from the dorsal border to the origin of the palmar tubercle, and is dorso-palmarly lengthened in comparison to that of *G. genetta*, in which it is restricted to the dorsal border of the medial face. Nevertheless, the dimesions of

GT 77'07 prevents its assignment to Viverridae, as no fossil viverrids of such a large size are known in the Lower Miocene of Africa.

GT 79'07, an almost complete left scapholunar, is slightly smaller than that of *Lynx pardina*, showing a broken proximal surface. The distal articular surface is similar to that of a felid, although the facet for the unciform is more laterally oriented, and that for the magnum is wider, shallower, and does not surpass the level of the palmar margin. The palmar tubercle is relatively shorter than that of *L. pardina*, and on its distal surface shows a proportionally dorso-palmarly longer articular facet for the trapezium. It measures 7.1 mm proximo-distal length by 13.7 mm medio-lateral breadth.

Discussion: The felid material from the Northern Sperrgebiet is fragmentary and not well preserved. Nevertheless, on the basis of the small but characteristic fragment of symphysis, we can affirm that we are in the presence of a machairodont felid. Furthermore, the sectorial premolars with high cusps accord with the morphology of the symphysis, in particular, the morphology of the p/4 with an anterior cusplet, the sectorial paraconid and a high posterior cusp similar to that in the holotype of *Afrosmilus africanus* (Andrews, 1914). The dimensions, interpreted with caution, considering the state of preservation of the specimens, are similar to those of *A. africanus*, and are somewhat greater than those of *Afrosmilus turkanae* Schmidt-Kittler (1987) and what can be inferred from the lower dentition of *Ginsburgsmilus napakensis* Morales *et al.*, (2001). The Mc V accords well with the manus of *Afrosmilus turkanae* figured by Schmidt-Kittler (1987) but it is larger.

General discussion and conclusions

The adaptive radiation that appears to have occurred among African creodonts during the Tertiary, resulted in gigantic forms such as *Hyainailouros* and *Megistotherium* (if these two genera are not synonyms) and tiny ones like *Prionogale* and *Namasector*, which are the smallest known carnivores in the African fossil record, passing by intermediate sized forms such as *Metapterodon* and *Isohyaenodon*. The creodont list from the Sperrgebiet is less diverse than that of East Africa, but it is nevertheless quite diverse with six species (Table 7).

The fissiped carnivores from the Northern Sperrgebiet are much less diverse than the fauna known in East African deposits spanning the same time period (Table 7). A single species of amphicyonid is accompanied by four viverrids and a felid, making a total of six species, of which two are new, and three indeterminate, due to limitations of the material. The ratio of creodonts to carnivores is 6-6 (Table 7) which is more equal than in the fauna from Arrrisdrift, Namibia, (ca 17.5 Ma) which is dominated by fissipeds Morales *et al.*, (2003).

Table 7: Carnivoran faunas from the Northern Sperrgebiet, Namibia (x = present).

TAXON/LOCALITY	ELISABETH-FELD	LANGEN-TAL	GRILLENTAL	FISKUS
Metapterodon kaiseri	X			
Metapterodon stromeri		X		
Hyainailouros sp.	X		X	
Isohyaenodon sp.	X			
Teratodontidae indet.		X		
Namasector soriae gen. et sp. nov.	X			
Ysengrinia sp.	X	X	X	X
Leptoplesictis senutae sp. nov.			X	
Leptoplesictis namibiensis sp. nov.		X		
Viverridae indet. I	X			
Viverridae indet. II	X			
Afrosmilus africanus	X	X	X	X

In Namibia, between 19 and 17.5 Ma there seems to have occurred a drastic reduction in creodont diversity. The change in diversity could be related to an increase in seasonality and a decrease in vegetation cover accompanying the onset of aridification in the Namib between 21 and 17 Ma. A comparable diminution of creodont diversity took place in East Africa, but it occurred more slowly and seems to have started later than in the Sperrgebiet. This is undoubtedly due to the fact that East Africa remained more humid, less seasonal and better vegetated for longer than Namibia. From this it is concluded that the majority of creodonts were adapted to forested environments, and that, apart from a few lineages such as *Megistotherium*, were inadapted to open vegetation and seasonal climates. Fissipeds, in contrast, seem to have been equally well adapted to forest and open country, and in the fullness of time came to dominate and eventually to displace entirely the creodont fauna which went extinct in Africa by the end of the Middle Miocene (Morales and Pickford, 2005).

Aridification occurred earlier in southwestern Africa than in East Africa (Pickford and Senut, 2003) with marked consequences on the carnivoran fauna. It is clear that other lineages of mammals and lower vertebrates were equally affected by these climatic changes, with Namibia being in the lead in terms of extinctions as well as in evolution of new lineages with particular adaptations evolving for survival in more seasonal and unstable climates, and more open vegetation types, including savannah, steppe and desert. As such, the southwestern part of the continent was a crucible of evolution, with poorly adapted lineages being weeded out much more rapidly than they were in East Africa with its more equable climate and denser vegetation types, and adaptable lineages evolving new strategies for dealing with changed vegetation and climate and all that that means in terms of environmental and ecological impact. The carnivores, being at the summit of the food chain, were particularly susceptible to the changes, the creodonts were more adversely affected than the fissiped carnivores, and this is reflected not only in the lower total diversity of carnivores in the south compared with the equatorial regions of the continent, but also in the rapidity and precocity of the changes that occurred in the south.

Acknowledgements

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