

A reassessment of *Prionogale* and *Namasector* (Prionogalidae, Hyaenodonta, Mammalia) with descriptions of new fossils from Napak, Uganda and Koru, Kenya

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Abstract: New fossils of *Prionogale breviceps* found at the early Miocene site of Napak IV, Uganda, at Koru, Kenya, together with a re-examination of the dentition of *Namasector soriae* from the early Miocene of Elisabethfeld, Namibia, confirm the peculiar morphological combination of these two species which are attributed to the hyaenodont family Prionogalidae. The new material of *Prionogale breviceps* includes a molariform tooth interpreted as a D4/, the morphology of which differs from the upper molariform teeth previously known in the holotype maxilla of the species, which can therefore be interpreted as the M2/ and M1/. The implication of this discovery is fundamental for positioning the family Prionogalidae among the Hyaenodonta with two pairs of carnassial molars comprised of m/3-M2/ and m/2-M1/, and an additional pair m/1-P4/ which also fulfils the same function, considerably augmenting the length of the cutting blade. Study of several mandibles of *Prionogale* and the maxilla and mandible of *Namasector* via tomographic CT-Scan indicates that there are no dental germs corresponding to permanent premolars. The suppression of premolars and the highly derived morphology of the molar dentition of the two species of Prionogalidae render it difficult to determine the systematic position of this clade of hypercarnivores, which comprise part of the radiation of Hyainailouroidea of the Miocene of Africa.

Key words: Miocene; Africa; Hyaenodonta; Prionogalidae; Systematics; CT-scan tomography.

To cite this paper: Morales, J. & Pickford, M. 2018. A reassessment of *Prionogale* and *Namasector* (Prionogalidae, Hyaenodonta, Mammalia) with descriptions of new fossils from Napak, Uganda and Koru, Kenya. *Communications of the Geological Survey of Namibia*, **20**, 114-139.

Introduction

Prionogale breviceps Schmidt-Kittler & Heizmann, 1981, and *Namasector soriae* Morales, Pickford & Salesa, 2008, are among the most peculiar carnivorous mammals thus far recognised in the fossil record, not only because of their diminutive dimensions equivalent to the smallest extant carnivore *Mustela nivalis*, but also because of the extreme carnivorous adaptation of some of the molars, in particular the m/3 (equivalent to the carnassial tooth in the Order Carnivora) in which the angle α (Crusafont & Truyols, 1956) is clearly greater than 90°, a value which only approaches some species of the family Felidae, and a few hyaenodonts such as *Hyaenodon*, *Apataelurus* and *Patriofelis* (Denison, 1938; Scott, 1938). These features, together with other morphological peculiarities of the dentition of *Prionogale*

led the first authors to propose an informal *Prionogale* clade distinguished from the creodonts and carnivores by the unusual combination of carnassial teeth; P4/-m/1 and M1/-m/2 (Schmidt-Kittler & Heizmann 1981). This interpretation was followed by Morales *et al.* (2008) who, when describing the fossils from Elisabethfeld, Namibia, accepted a homologous dental position as that of *Prionogale breviceps*, and proposed a formal family name Prionogalidae to include the two species within Creodonta *sensu lato*. Werdelin & Cote (2010) accepted the new family, but were reticent to retain it within Creodonta, preferring to classify it as *Incertae sedis*. They also raised the possibility “that the anteriormost of the preserved (P3/ and p/4 above) teeth might be deciduous”. The interpretation of the meristic position of the teeth in

Prionogale and *Namasector* and whether they are deciduous or permanent was discussed recently by Borths & Stevens (2017a). For the latter authors, the teeth in the holotype maxilla of *Prionogale breviceps* previously identified as the P3-/M1/ were interpreted to be the D3-/D4-/M1/, while the mandibular teeth previously thought to be the p/4-m/1-m/2, were interpreted to be the d/4-m/1-m/2. As a consequence, Borths & Stevens (2017a), even though in the revised diagnosis of *Prionogale* they mentioned that the carnassial function was performed by the P4-/m/1 and M1/-m/2 (as had been proposed by Schmidt-Kittler & Heizmann, 1981) in the body of the text the same teeth were identified as the D4/-m/1 and M1/-m/2, which implies long-term retention of the D4/. The same proposal was applied to *Namasector soriae* Morales *et al.* (2008) who, in the original description of the species, adhered to the interpretation of

tooth positions proposed by Schmidt-Kittler & Heizmann (1981). The basis for the argument employed by Borths & Stevens (2017a) regarding the reinterpretation of the dentition of *Prionogale* and *Namasector* is fundamentally morphological, itself leaning on new data concerning the deciduous dentition published by Bastl *et al.* (2011, 2014) and Borths & Stevens (2017b).

The aims of the present paper are to reassess the dentition of *Namasector soriae* and to describe new fossils of *Prionogale breviceps* from Napak IV (Uganda) and Koru (Kenya). The latter record is the first from the site, and we utilise tomographic images obtained by CT-scan to illustrate the material. Our results refute the previous hypothesis which considers that the meristic position of teeth in the two genera is homologous, and that the posterior carnassials are respectively M2/-m/3, whereas the anterior carnassial pair could be M1/-m/2.

Materials and Methods

The fossils described herein are housed at the Museum of the Geological Survey of Namibia (GSN), Windhoek, Namibia; Orrorin Community Organisation (OCO), Kipsaraman, Baringo County, Kenya, the Kenya National Museum (KNM), Nairobi, and the Uganda Museum (UM), Kampala, Uganda.

Namasector soriae tooth measurements were estimated from Scanning Electron Microscope images (Morales *et al.*, 2008).

The *Prionogale breviceps* teeth were measured with a "Nikon Measuroscope 10 5x microscope with an incorporated micrometer of an accuracy of 0.025 mm". Scans were made by the Servicio de Técnicas No Destructivas: Microscopía Electrónica y Confocal y Espectroscopía del MNCM-CSIC, Madrid. Scan Tomographic images were obtained by VGStudio MAX 3.0 software.

Abbreviations:

AMNH American Museum of Natural History, New York, USA

GSN Geological Survey of Namibia, Windhoek, Namibia

KNM National Museum of Kenya, Nairobi, Kenya

NHMUK Natural History Museum, London, United Kingdom

MNHN Muséum Nationale d'Histoire Naturelle, Paris, France

OCO Orrorin Community Organisation, Kipsaraman, Baringo County, Kenya

UM Uganda Museum, Kampala, Uganda

Dental nomenclature

For identifying the meristic position of teeth we employ the method of Pickford, 2017. Upper teeth are referred to by capital letters (I - Incisor, C - Canine, P - Premolar, M - Molar, D - Deciduous cheek tooth)

while lower teeth are presented in lower case letters (i, c, p, m, d). In order to avoid confusion due to typographical errors, the position of the tooth is given relative to a forward slash (/) which represents the

occlusal plane (P4/ - upper fourth pre-molar). For lower teeth the numbers are

below the forward slash (m/3 - lower third molar).

Systematic Palaeontology

Superorder Ferae Linnaeus, 1758

Order Hyaenodonta Van Valen, 1967

Superfamily Hyainailouroidea Pilgrim, 1932

Family Prionogalidae Morales, Pickford & Salesa, 2008

Diagnosis: In Morales *et al.* (2008) and Borths & Stevens (2017a).

Emended diagnosis: Dwarf Hyainailouroidea with shortened facial zone, hypercarnivorous dentition with dental formula ?I-?Ii, C-c, 2P-1p, 3M-3m, the carnassial function being performed by two pairs of teeth, M2/-m/3 and M1/-m/2. Protocones of M3/-M1/ and P4/ well-developed; M2/-M1/ with paracone and metacone well separated from each other, with their apices far apart, with parastyle prominent and projecting

buccally. M2/ with paracone in lingual position between the parastyle and protocone and notch between metastyle and metacone completely suppressed. Lower molariform teeth without metaconids, m/2-m/1 tricuspid buccally (paraconid-protoconid and hypoconid), m/3 with paraconid and protoconid forming a cutting blade, and the apex of the protoconid projecting distally.

Genus *Prionogale* Schmidt-Kittler & Heizmann, 1981

Species *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981

Diagnosis: In Schmidt-Kittler & Heizmann (1981) and Borths & Stevens (2017a).

Emended diagnosis: Prionogalidae with M2/ almost triangular with the metastyle less elongated than in *Namasector*, parastyle prominent, mesostyle in the middle of the buccal wall. Protocone large and joins to the rest of the crown via a broad isthmus. M1/

with metastyle-metacone-paracone placed in a V-shape, P4/ short. Lower molars strongly imbricated, talonid of m/1-m/2 with a wide and deep valley which extends lingually to the base of the paraconid.

Type locality: Songhor, Kenya.

Age: Early Miocene

Holotype: KNM SO 1413, maxilla containing P4/-M2/ (reported as P3/-M1/ in Schmidt-Kittler & Heizmann, 1981, and

reinterpreted as D3/-M1/ by Borths & Stevens, 2017a).

New material from Napak IV (Uganda)

UM NAP IV 159'12, right maxilla fragment with M1/. UM NAP IV 72'05 left D4/ with broken protocone. NAP IV 74'14, left m/2 (L= 4.25, W=1.75). UM NAP IV 58'18, right mandible with broken m/3, m/2 roots and alveolus for m/1, p/1 and canine. UM NAP IV 79'18, fragment of left mandible with m/3. NAP IV 22'08, left mandible with m/3 and m/2, biradicate alveoli of the m/1, uniradicate alveolus for the p/1 and a large alveolus for the

canine and another smaller one for an incisor. UM NAP IV 63'11, fragment of right mandible with m/3-m/2.

UM NAP IV 159'12 (Fig. 1) a right M1/ is a molariform tooth with sectorial morphology, the protocone is quite broad and dome-shaped. It is linked to the rest of the tooth via a sharp, broad isthmus. The anterior crista of the protocone is tall and sharp, the lingual crista is low and weakly separated from the main cusp by a notch.

This lingual crista blends into the basal cingulum which backs onto the base of the lingual wall of the metacone. The parastyle is well-developed and buccally is separated from the paracone by a deep depression. The paracone is conical, large and taller than the other cusps. The metacone is sectorial and is separated from the metastyle by a notch. The metastyle and the metacone are displaced lingually in such a

way as to produce a broad postero-buccal concave platform bordered by a tall buccal crest which blends into the basal part of the paracone. The occlusal morphology of the tooth is characteristic, with two anterior depressions (buccal and lingual) separated from each other by the paracone and a third depression postero-buccally, separated from the anterior ones by the metacone-paracone.

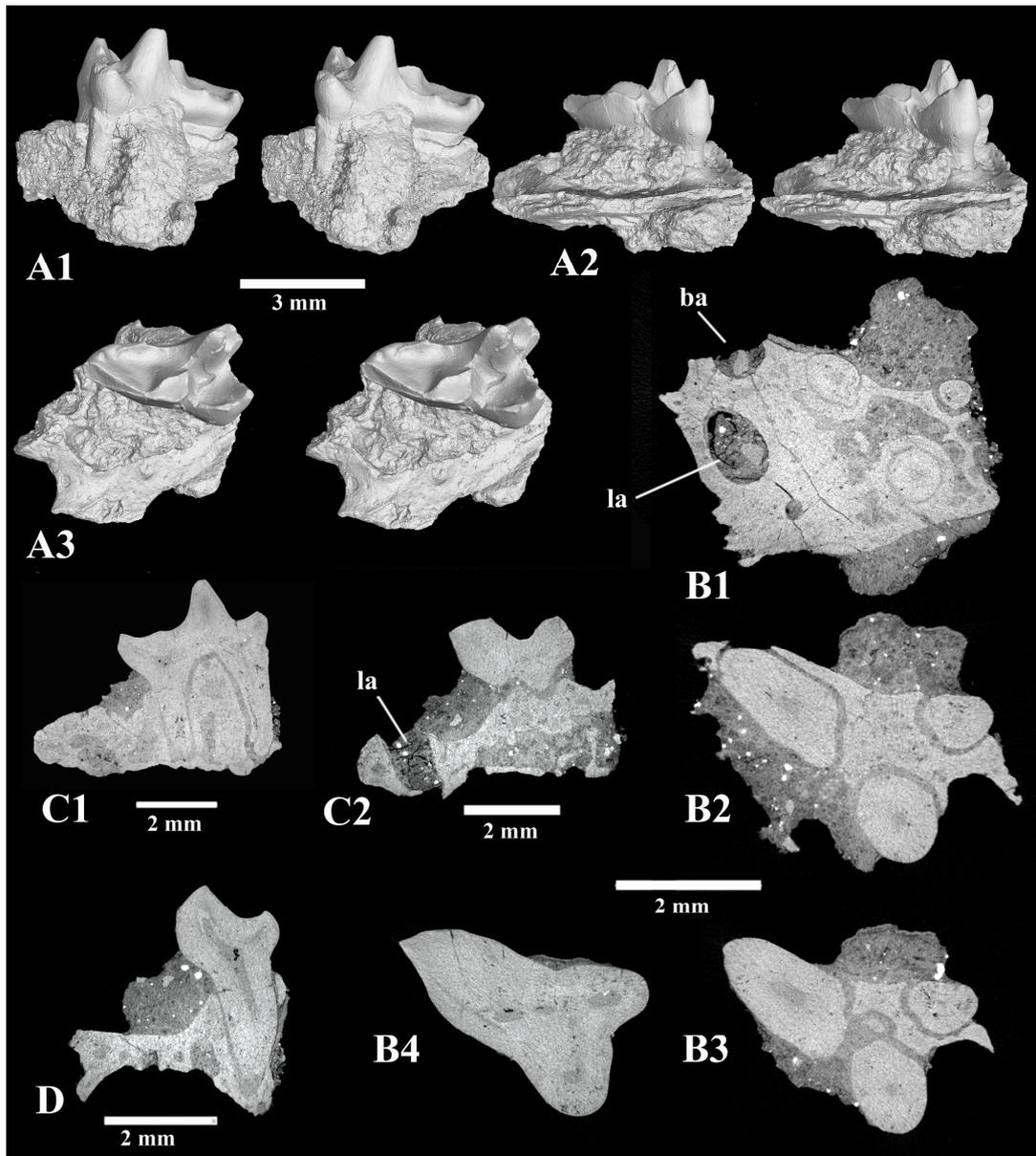


Figure 1. *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981, from Napak IV, Uganda. A) Right maxilla fragment with M1/ (UM NAP IV 159'12). A1) buccal view, A2) lingual view, A3) occlusal view (stereo pairs). B1-B4) transverse section, from near the base of the roots to gingival plane. C) antero-posterior cross section, C1) buccal, C2) lingual. D) anterior bucco-lingual cross section. ba= M2/ anterior buccal alveolus, la= M2/ lingual alveolus.

UM NAP IV 72'05 (Fig. 2), a left D4/ is slightly smaller than the M1/ described above, and is noticeably more gracile. The protocone is broken, but its base suggests that it would have been quite broad and in a position similar to the protocone in the M1/. The paracone and metacone are tall, coniform and well individualised, and the metastyle extremely sectorial. The parastyle is flattened and its base is deeper than the other buccal cusps. The styler area is reduced in such a way as to accent the sectorial aspect of the metastyle. Only the antero-buccal root is preserved, being somewhat compressed suggesting that its inner part was likely poorly mineralised.

UM NAP IV 58'18 (Fig. 3) is a right mandible, broken off behind the posterior border of the canine. The body of the mandible is gracile and buccally shows a prominent mental foramen beneath the alveolus of the p/1, and a second subdivided foramen is developed beneath the anterior half of the m/1, the anterior

aperture connecting to the mandibular canal, while the posterior one is channelled and probably connects to the anterior aperture. The posterior part of the jaw is broken, the angular process is almost completely lost, the base of the coronoid process is preserved and much of the masseteric fossa is present which is quite deep. The m/3 has a broken paraconid, the protoconid is tall and its apex projects posteriorly. The talonid is diminutive, and is only visible lingually in the form of a cingulum which extends anteriorly. Only the roots of the m/2 are preserved, but the crown would have been broader and longer than the m/3. There are two alveoli in front of the roots of m/2 as in other examples of *Prionogale* indicating a generous m/1. The m/1 alveoli are separated from the alveolus of the p/1 by a short diastema. The p/1 (or d/1) is uniradicate and is immediately behind the canine alveolus, the anterior part of which is broken off.

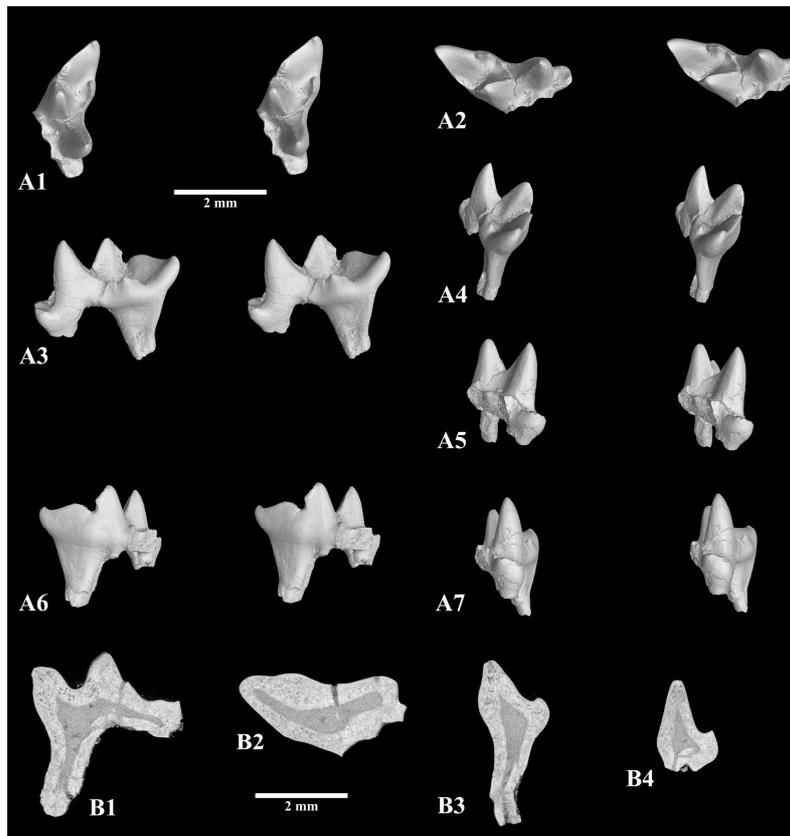


Figure 2. *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981, from Napak IV, Uganda. Left D4 (UM NAP IV 72'05). A1) occlusal view, A2) occlusal view, A3) lingual view, A4) posterior view, A5) anterior view, A6) buccal view, A7) anterior view (stereo pairs). B1) antero-posterior cross section, B2) transverse cross section near the gingival plane, B3) posterior bucco-lingual cross section, B4) anterior bucco-lingual cross section.

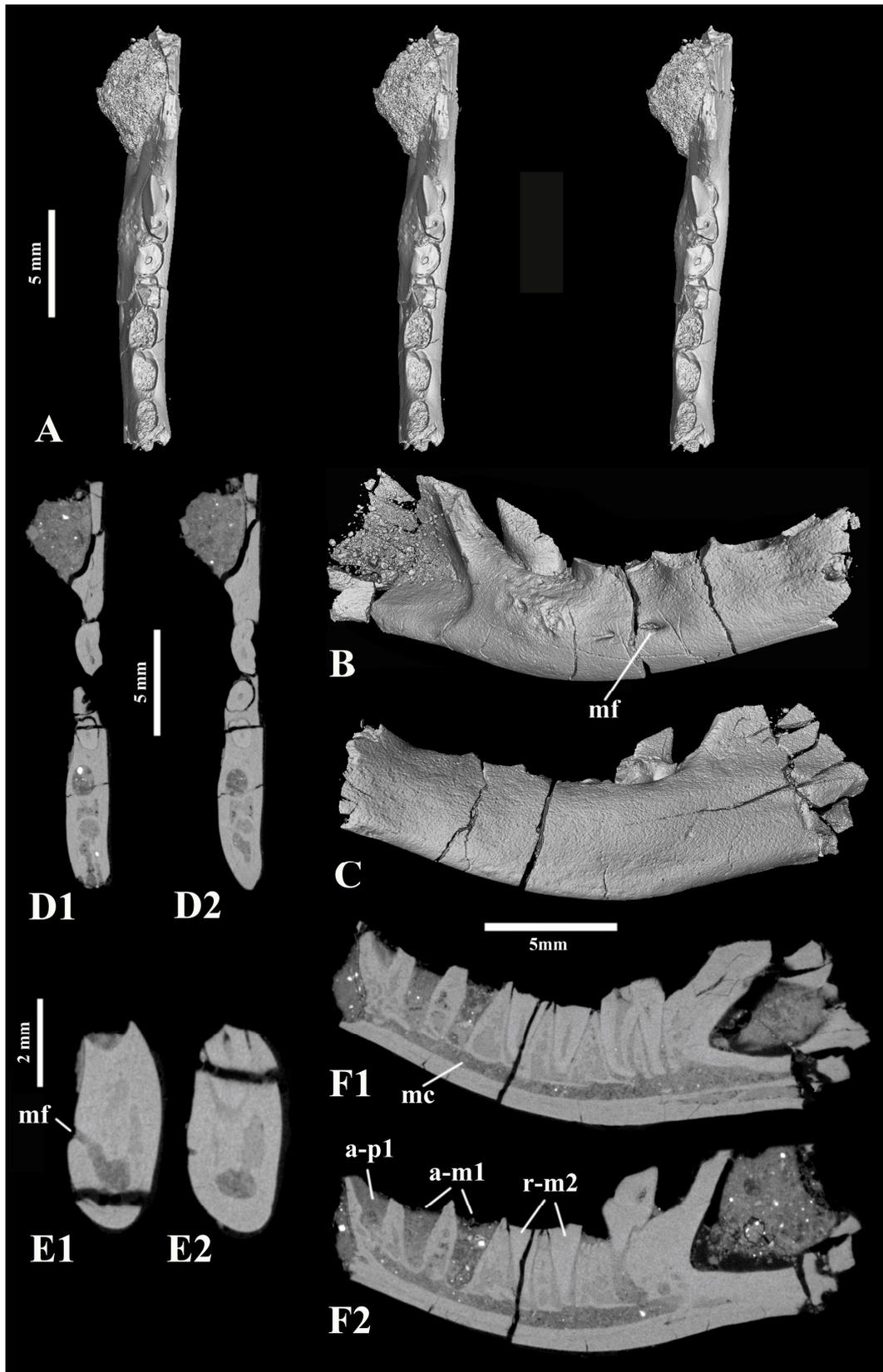


Figure 3. *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981, from Napak IV, Uganda. A) right mandible with m/3, m/2 roots, and canine and incisor alveoli (UM NAP IV 58'18). A) occlusal view (stereo pairs). B) buccal view. C) lingual view. D1-2) transverse section. E1-2) bucco-lingual cross sections. F1-2) antero-posterior cross sections. a-p1= p/1 alveolus, a-m1= m/1 alveoli, r-m2= m/2 roots, mc= mandibular canal, mf= mental foramen.

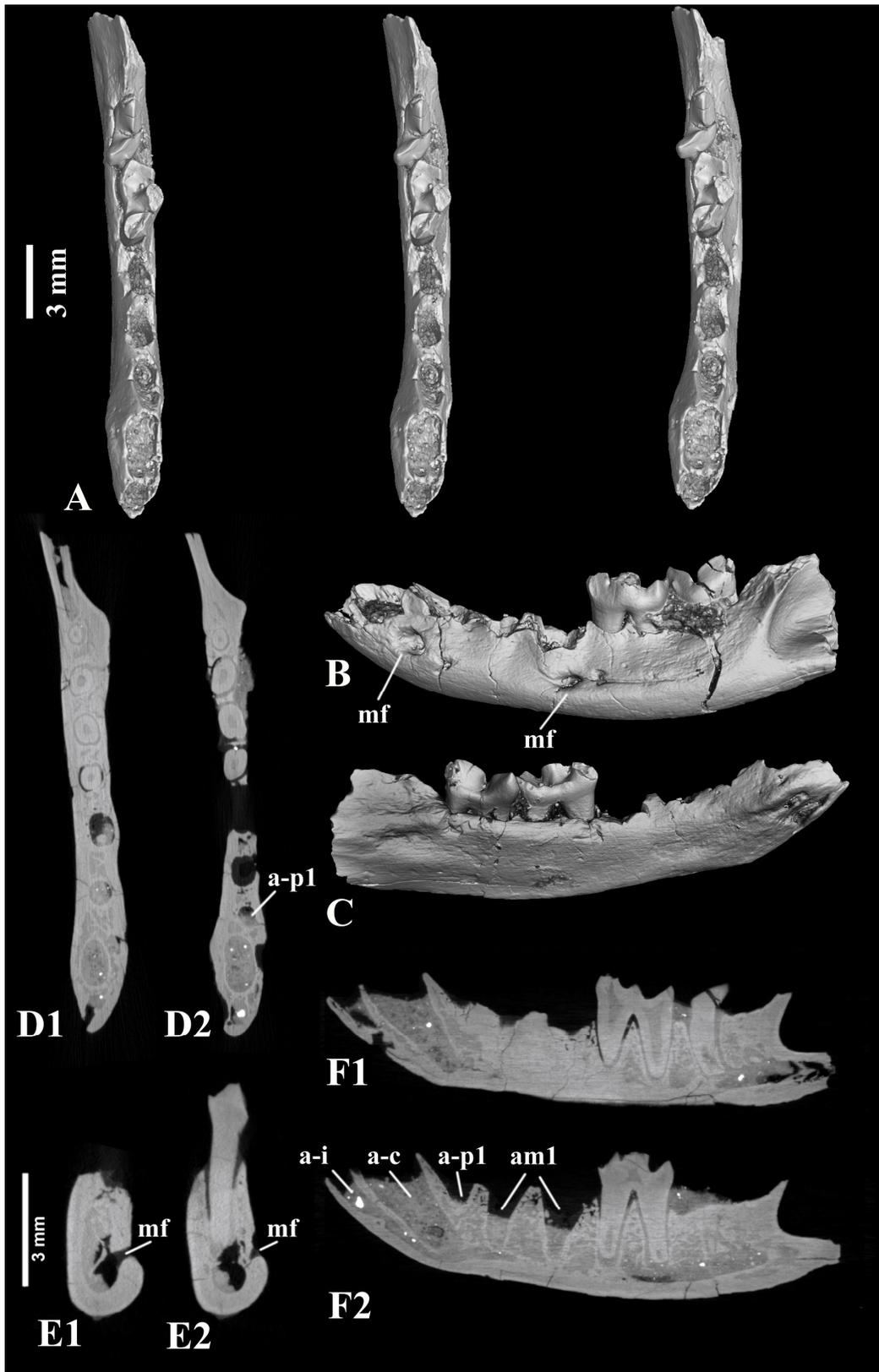


Figure 4. *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981, from Napak IV, Uganda. A) left mandible with m/3-m/2, biradicate alveoli of the m/1, and p/1 alveolus (UM NAP IV 22'08). A) occlusal view (stereo pairs). B) buccal view. C) lingual view. D1-2) transverse section. E1-2) bucco-lingual cross sections F1-2) antero-posterior cross sections. a-c= canine alveolus, a-i= incisor alveolus, a-p1= p/1 alveolus, a-m1= m/1 alveoli, mf= mental foramen.

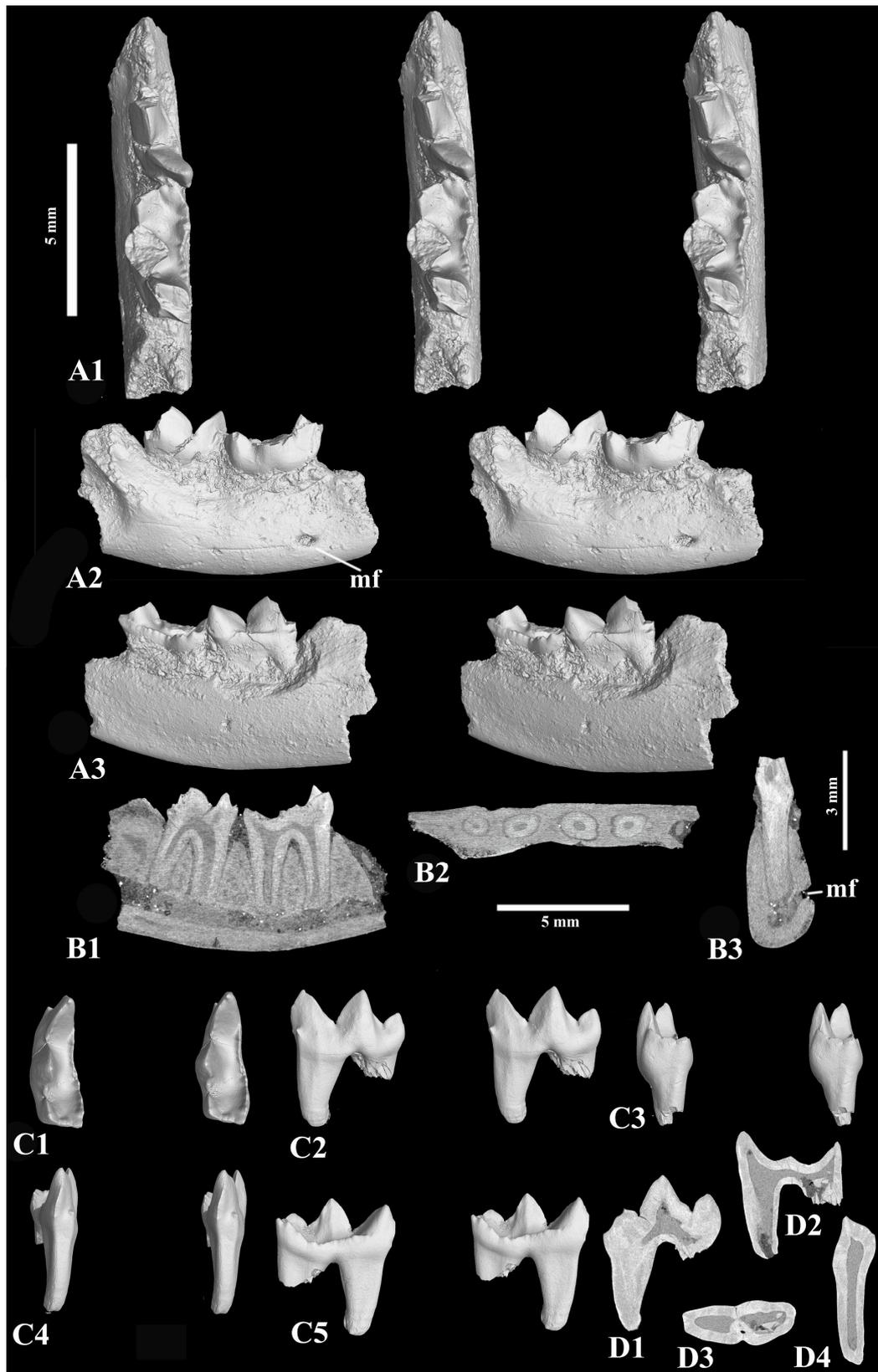


Figure 5. *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981, from Napak IV, Uganda. A) right mandible with m/3-m/2, (UM NAP IV 63'11). A1) occlusal view, A2) buccal view, A3) lingual view (stereo pairs). B1) antero-posterior cross section, B2) transverse section, B3) anterior bucco-lingual cross section. C) right m/1 (UM NAP IV 74'14). C1) occlusal view, C2) buccal view, C3) posterior view, C4) anterior view, C5) lingual view (stereo pairs). D1-2) antero-posterior cross sections, D3) transverse cross section, D4) anterior bucco-lingual cross section. mf= mental foramen.

UM NAP IV 22'08 (Fig. 4) is a left mandible with m/3-m/2, the biradicate alveoli of the m/1, a uniradicate alveolus for the p/1 and alveoli of the canine and an incisor.

The morphology of the jaw is the similar to that of the specimen described immediately above, but this specimen preserves the canine alveolus as well as one for an incisor. The genial tuberosity is weakly expressed and the symphysis is ploughed by a pair of deep canals. The m/3 is extremely sectorial, with a residual talonid, the protoconid is tall and its apex leans distally to such an extent that it overhangs the talonid. The paraconid is much lower, but is similar in length to the protoconid, and on its buccal wall it has a vertical tubercle which touches the hypoconulid of the tooth in front. The axis of the crown is twisted with respect to the antero-posterior axis of the mandible, in such a way that the anterior margin of the paraconid imbricates with the talonid of the preceding tooth.

The m/2 is characterised by the presence of quite a deep basin which occupies almost the entire lingual part of the crown, from the posterior margin of the talonid (formed of a small entoconid, a hypoconulid and a hypoconid, the last being quite tall) to the base of the paraconid. There is no metaconid, and in the posterior part of the basin, there is a small circular depression caused by contact with the protocone of the occluding upper tooth. Lingually, this basin

is bordered by a cristid which distally blends into the entoconid and anteriorly melds into the antero-buccal cristid of the paraconid. As in the posterior tooth, the axis of the crown is twisted, with the paraconid reaching lingually such that the paraconids of the m/3 and m/2 lie parallel to each other. The alveoli of the m/1 suggest that the tooth would have been somewhat longer than the m/2, and was separated by a short diastema from the uniradicate alveolus of the p/1. The latter tooth was close to the canine alveolus. On the buccal aspect of the ramus there are two clear mental foramina, the posterior one beneath the m/2-m/1, the anterior one between the alveoli of the p/1 and canine. Dorso-ventral and transverse scans of the mandible reveal that there are no signs of teeth or germs of teeth hidden inside the ramus. The alveoli of the m/1 are deep and positioned at the same level as the roots of the erupted molars, the canine and the incisor. In contrast, the alveolus of the p/1 is not deep.

UM NAP IV 63'11 (Fig. 5 A-B) is a right mandible fragment with m/2-m/3. It differs from the previous specimens in that the posterior mental foramen is not subdivided but has a smooth posterior canal. The posterior molar is missing the protoconid part and the second molar lacks the paraconid and protoconid. The buccal basin of this molar is bordered by an irregularly crenulated cristid.

Table 1. Measurements (in mm) of the upper teeth (A) and lower teeth (B) of *Namasector soriae* Morales *et al.* 2008 and *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981.

Abbreviations: EF - Elisabethfeld, Namibia. NAP - Napak, Uganda. KO - Koru, Kenya.

L – antero-posterior diameter; W – width. *alveolus measure, **estimated measure.

A	Specimen	LM3/	WM3/	LM2/	WM2/	LM1/	WM1/	LP4/	WP4/	LD4/	WD4/
	EF 118'01			2.8	2.2	3.1	2.00	2.5	1.3		
	EF 118b'01					2.8	1.8				
	NAP IV 159'12					4.30	2.65				
	NAP IV 72'05									4.30	2.20**
	KO 489'05	1.56	2.67								
	KO 528'05					4.41	2.60**				

B	Specimen	Lm/3	Wm/3	Lm/2	Wm/2	Lm/1	Wm/1
	EF 60'01	2.7	1.1	2.3	1.1	3.2	1.2
	NAP IV 22'08	3.1	1.23	3.44	1.77	3.87*	1.51*
	NAP IV 63'11	2.95	1.11	3.51	1.74		
	NAP IV 74'14					4.28	1.77
	KO 495'05	2.75	1.26				
	KO 488'05	2.67**	1.57				

UM NAP IV 79'18, is a fragment of left mandible with m/3. The paraconid in the m/3 is broken. The mandible fragment

preserves part of the angular process, in which can be seen the opening of the mandibular canal.

UM NAP IV 74'14 (Fig. 5 C-D) is a right m/1 the morphology of which is close to that of the m/2 in mandible UM NAP IV 22'08, described above, but it is slightly longer. The anterior root is complete, and is oriented vertically with the apex curving slightly to the rear (i.e. towards the midline of the tooth) and the part of the posterior root preserved is robust. The lingual valley is broad and has been slightly enlarged by

wear against the corresponding upper teeth. As in the m/2 in UM NAP IV 22'08, in the lingual basin the part corresponding to the talonid is marked by a characteristic circular depression caused by wear against the protocone of the M1/. Notable are the greater dimensions of the paraconid which is taller than the homologous cuspid in the m/2.

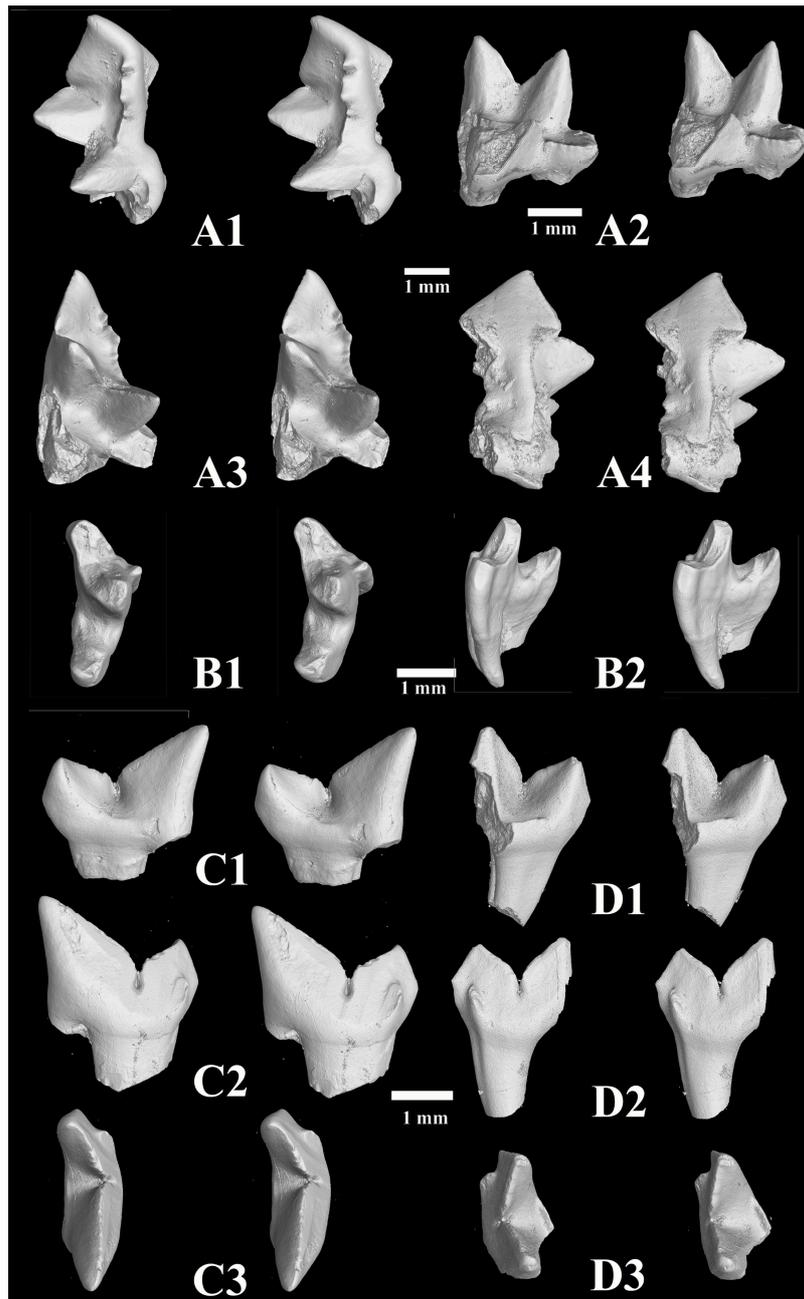


Figure 6. *Prionogale breviceps* Schmidt-Kittler & Heizmann 1981 from Koru, Kenya. A) right M1/ (OCO KO 528'05). A1) buccal view, A2) anterior view, A3) occlusal view, A4) lingual view (stereo pairs). B) left M3/ (OCO KO 489'05) B1) occlusal view, B2) posterior view (stereo pairs). C) right m/3 (OCO KO 495'05). C1) lingual view, C2) buccal view, C3) occlusal view (stereo pairs). D) left m/3 (OCO KO 488'05). D1) lingual view, D2) buccal view, D3) occlusal view (stereo pairs).

New material from Koru (Kenya)

OCO KO 528'05 (Fig. 6 A) a left M1/, is a carnassial with a broken protocone, but which was quite broad. Despite the damage, one can make out the broad and sharp isthmus which linked the protocone to the rest of the tooth. The parastyle is also partly broken, but was quite well-developed, and buccally is separated from the paracone by a deep depression. The paracone is conical, large and taller than the other cusps. The metacone is sectorial and is separated from the metastyle by a deep notch. The metastyle and metacone are displaced lingually to the extent that a broad postero-buccal platform is formed, bordered by a tall serrated buccal crest which blends into the basal part of the paracone. The occlusal morphology of the tooth is characteristic, with two basins, one antero-lingually the other postero-buccally, separated by the metacone-paracone complex which is oriented diagonally to the long axis of the tooth.

The left M3/, OCO KO 489'05 (Fig. 6 B) is reduced and its morphology is similar to the specimen described and figured by Morales *et al.* (2008) as an M3/ of *Metapterodon stromeri* from the locality of Elisabethfeld, Namibia. It is formed of a moderately worn central cusp which extends diagonally to the position of the parastyle. A small postero-buccal cusplet occupies the position of the metastyle,

which borders a buccal platform which extends as far as the end of the parastyle. Lingually the crown is prolonged by a narrow, relatively flat platform on which there is a weak semilunate protocone and an elevated buccal cingulum.

OCO KO 495'05 (Fig. 6 C) is a right m/3 which has lost the posterior root and part of the base of the distal margin of the protoconid. The protoconid is tall and its apex leans towards the rear to the extent that it overhangs the posterior margin of the tooth. The paraconid is quite low but is similar in length to the protoconid, and on its buccal surface there is a vertical tubercle which occludes with the talonid of the m/2. The paraconid has developed a smooth lingual cristid which borders a moderately developed lingual valley, analogous to the one observed in the m/1s of *Prionogale*, but less developed. The buccal wall of the tooth has a vertical wear facet between the protoconid and paraconid in the zone where the two cusps meet each other.

OCO KO 488'05 (Fig. 6 D) is a left m/3 which has lost the posterior part of the crown, the root and the basal part of the protoconid. The preserved part is morphologically close to the specimen described above, and it confirms the presence of moderately developed lingual valley which extends to the base of the paraconid.

Genus *Namasector* Morales, Pickford & Salesa, 2008 **Species *Namasector soriae* Morales, Pickford & Salesa, 2008**

Diagnosis: In Morales *et al.* (2008)

Emended diagnosis: Dentition more hypercarnivorous than *Prionogale*, M2/ with elongated metastyle fused with the metacone without notch. Parastyle enlarged and together with the paracone forms a second cutting crest, almost transversely oriented to the metastyle-metacone. M1/ is also clearly elongated, but the metastyle is separated from the metacone by a notch, parastyle is as strong as the protocone. P4/ has a much elongated buccal wall marked by a prominent

paracone, a possible weakly expressed metacone and a moderately long metastyle, the protocone is smaller than in the two anterior molars and is positioned centrally. The m/3 is a very sectorial carnassial with a small and low talonid, m/2 with the talonid quite well-developed and the protoconid taller than the paraconid, m/1 is bigger and more robust than the m/2, with a very tall paraconid.

Type locality: Elisabethfeld, Namibia.

Age: Early Miocene

Holotype: GSN EF 118'01, fragment of skull which includes the zygomatic arch and part

Paratype: GSN EF 60'01, right mandible.

Description

GSN EF 118'01 holotype (Fig. 7). In lateral view, one observes the strong development of the infraorbital canal which is located very close to the orbit and which opens in front of it. The infraorbital foramen is located above the anterior root of the P4/. Above the infraorbital canal, the orbital margin is narrow and of a tubular shape, prolonged anteriorly around the lachrymal foramen which is located in a

of the right maxilla, including the palatine process.

shallow depression. This disposition implies that the orbit is very close to the anterior extremity of the maxilla, which is swollen to house the canine root. As a consequence, the maxilla is reduced in antero-posterior dimensions, which implies a foreshortened snout. The surface of the maxilla between the anterior margin of the infraorbital canal and the canine jugum is quite concave.

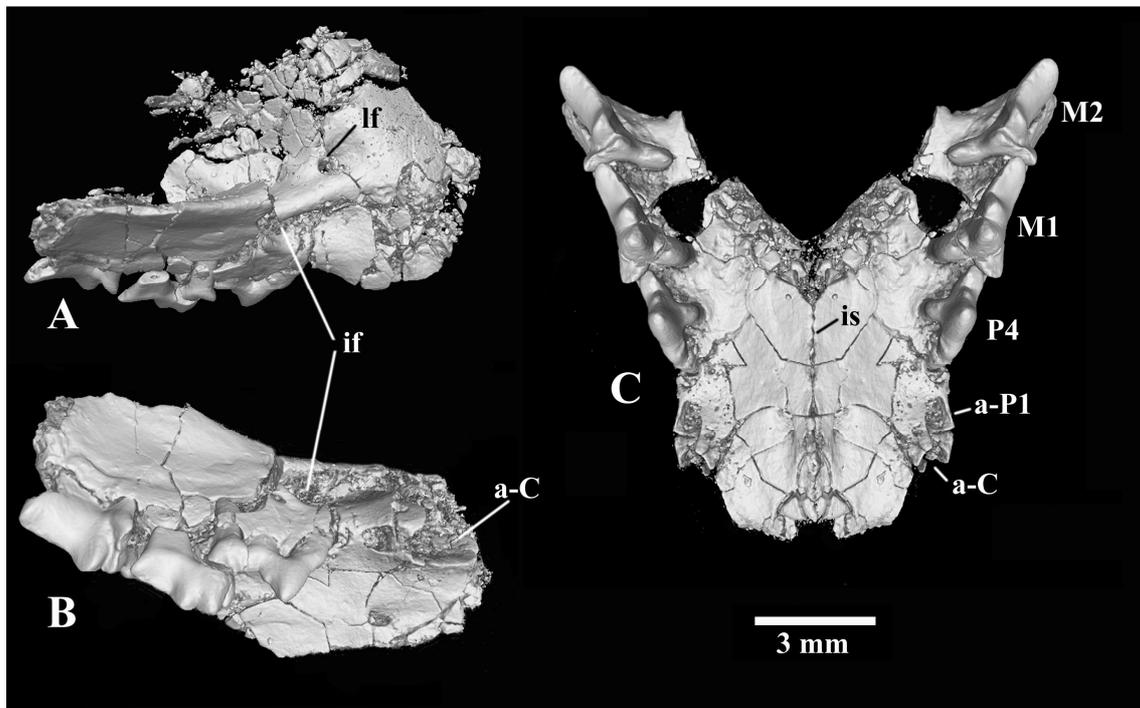


Figure 7. *Namasector soriae* Morales *et al.* 2008, from Elisabethfeld, Namibia. Right skull fragment with maxilla (holotype GSN EF 118'01). A) dorso-buccal view, B) ventro-buccal view, C) ventral view, with the mirror image. a-C= Canine alveolus, a-P1= P1 alveolus, if= infraorbital foramen, is= inter-palatine suture, lf= lacrimal foramen.

In ventral view, the palatine bone is not preserved, but the transverse maxillo-palatine suture is partly present, marked by a series of small fragments of bone which delimit its margin. The palatine process of the maxilla is almost complete, clearly showing the inter-palatine suture which anteriorly separates the incisive foramina, in a similar way to that observed in *Kerberos langebadrae* (Solé *et al.* 2015, figs 7 and 13). Anteriorly, the incisive

foramen separates the palatine process of the maxilla from the premaxilla which is broken off.

The upper dentition of *Namasector soriae* (Fig. 8) comprises two molariform teeth M2/-M3/, and a premolariform tooth P4/, separated by a short diastema from a uniradicate alveolus. Dorso-ventral and transverse scans of the dental series reveals that there are no teeth or germs of teeth hidden in the interior of the maxilla above

the erupted teeth. The roots of the erupted teeth are well-developed and show similar densities. The three teeth have buccal roots that are parallel or slightly convergent towards their apices.

The P4/ is a premolariform tooth with a well-developed centrally positioned protocone. The paracone is well-developed and tall, without an anterior cusplet and a weak

parastyle. The post-crista is of medium height and is interrupted by a notch which separates the paracone from a low cusplet which is weakly developed and interpreted as a metacone (Borths & Stevens, 2017a). A tall, well-developed cusp occupies the posterior part of the crown. The protocone is located in a central position opposite the paracone. There is no basal cingulum.

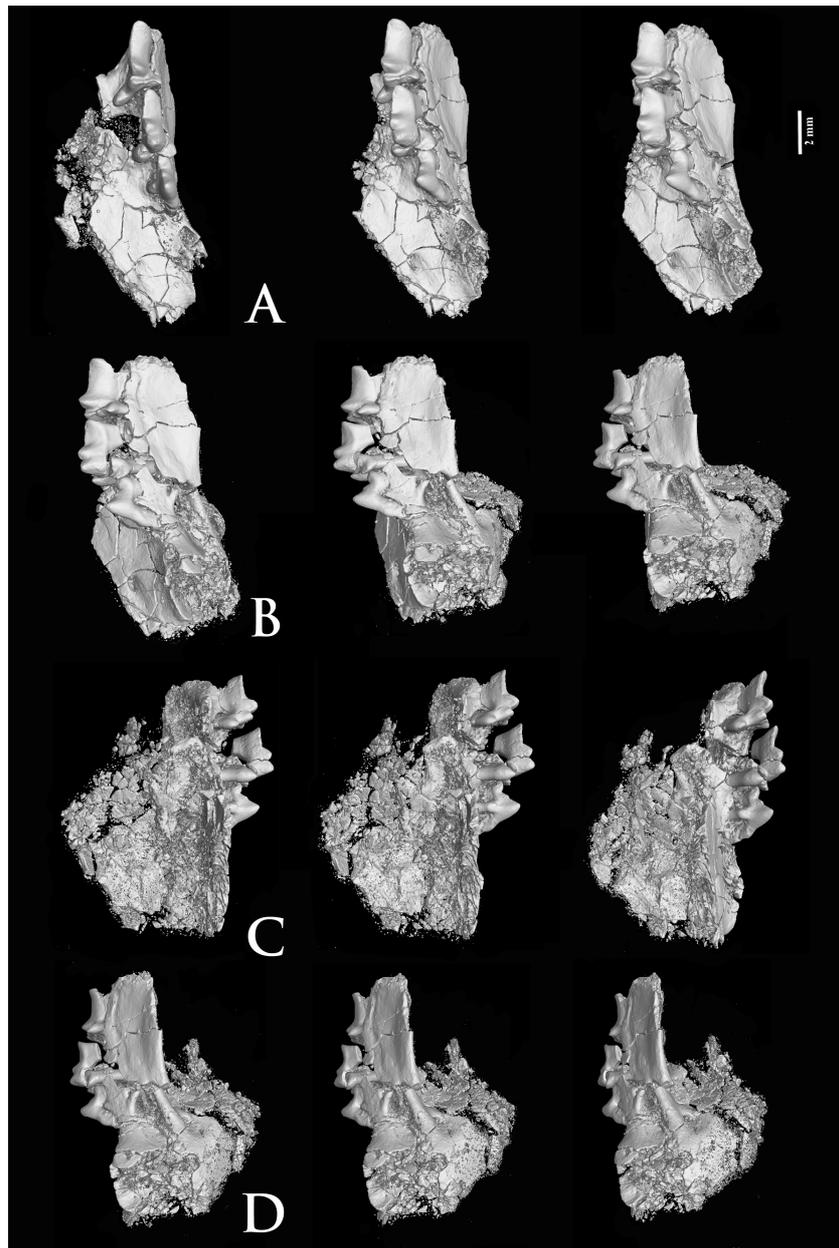


Figure 8. *Namasektor soriae* Morales *et al.* 2008, from Elisabethfeld, Namibia. Right skull fragment with M2/-M1/- P4/, P1/ alveolus and broken C1/ alveolus (holotype GSN EF 118'01). A1) occlusal view, A2) buccal view, A3) lingual view, A4) dorso-buccal view (stereo pairs).

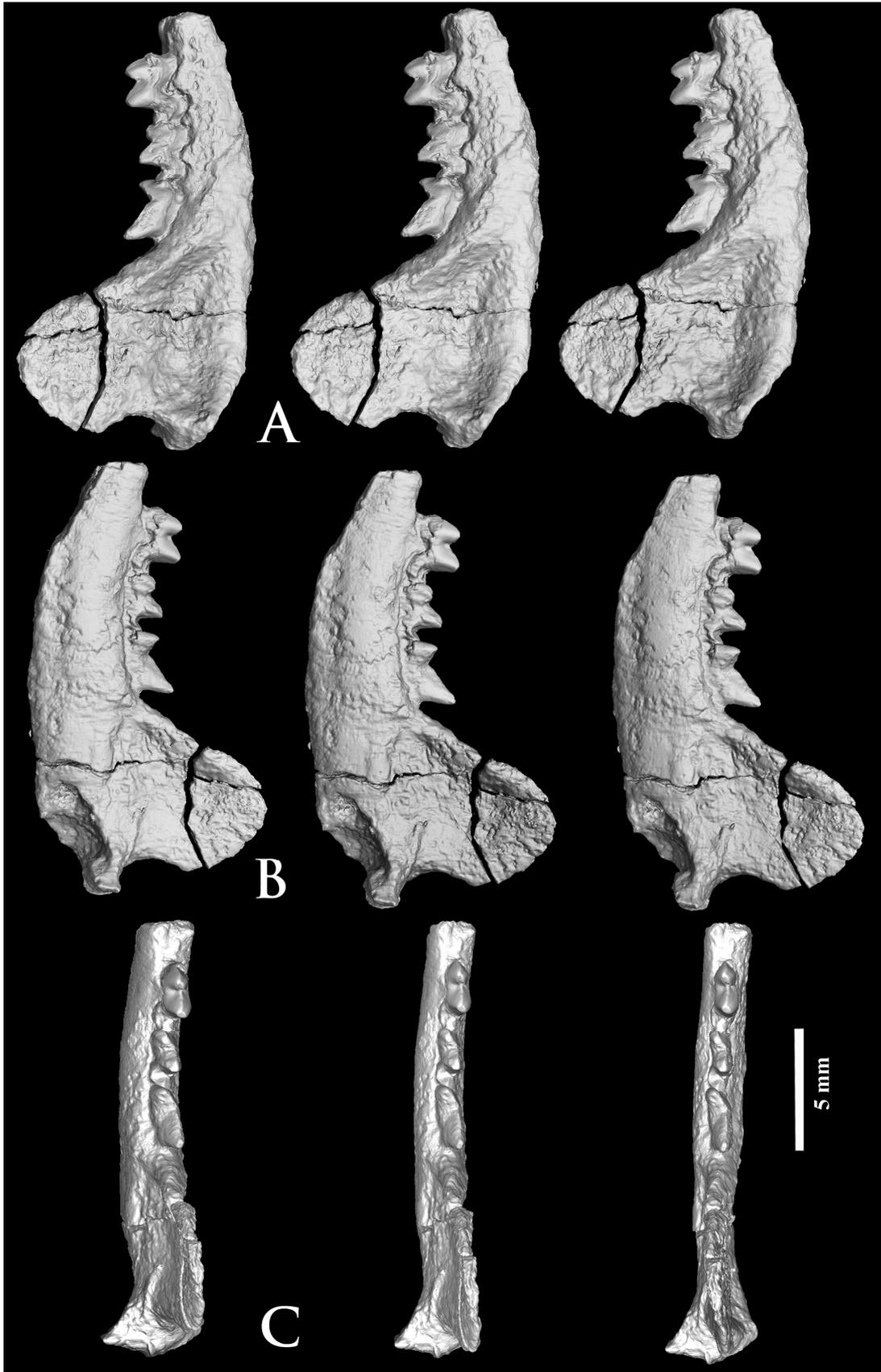


Figure 9. *Namasector soriae* Morales *et al.* 2008, from Elisabethfeld, Namibia. Right mandible with m/3, m/2 and m/1 (Paratype GSN EF 60'01) B1) buccal view, B2) lingual view, B3) occlusal view (stereo pairs).

The M1/ is a molariform tooth with carnassial structure. The protocone is globular, quite strongly developed and linked to the base of the paracone by a narrow isthmus and it projects antero-lingually. The paracone is voluminous and similar in height to the metacone, the two cusps joining basally, but well-separated from each other apically. The parastyle is well-developed, tall and projects antero-buccally, forming a cusp which is almost a mirror image of the protocone, in such a way that the front of the crown between the two cusps is concave. The metacone is moderately sectorial and extends distally to the long metastyle, the notch between the two cusps being weak. The paracone, metacone and metastyle are arranged in a straight line antero-posteriorly. There is no sign of basal cingula.

The M2/ is a carnassial. The protocone is smaller than M1/, and it projects strongly antero-lingually and is linked to the paracone via a long, narrow isthmus. The parastyle is well-developed and projects buccally and is joined to the paracone via a sharp transversely oriented crest. The metacone-metastyle complex is separated from the paracone by a deep semicircular valley. The metacone is taller than paracone, as in the M1/, is moderately compressed, and continues distally with no sign of notch from the sectorial metastyle. There is no basal cingulum.

GSN EF 60'01 is a right mandible (Fig. 9) paratype of the species. The ascending ramus is preserved as is a large part of the horizontal branch, but the angular process is missing. The mandibular foramen is quite well-developed. The dentition comprises three molariform teeth, in front of which there is a diastema. Longitudinal and transverse scans clearly indicate that there are no dental germs hidden in the jaw beneath the erupted teeth.

The lower teeth, m/3-m/1 correspond perfectly with what is known about the

maxilla, and it is likely that there would have been an additional premolar close to the canine as in the maxilla of *Namasector soriae* described above and in the mandibular reconstruction of *Prionogale breviceps* (Schmidt-Kittler & Heizmann, 1981; Borths & Stevens, 2017a) and confirmed in the present study.

The m/3 is a very sectorial carnassial with the protoconid more developed in size and height than the paraconid, and with its apex clearly slanting distally. A small, low talonid is present posteriorly, arranged such that the posterior cristid of the protoconid appears to be slightly curved. Lingually, at the base of the paraconid, there is a small vertical cristid which touches the talonid of the m/1, in such a way that the two teeth are slightly imbricated.

The m/2 has similar morphology to m/1, with the talonid quite well-developed, the protoconid taller than the paraconid, but less so than in the m/3. As in m/3, there is a small vertical cristid at the base of the paraconid which occludes with the talonid of the tooth in front, producing slight imbrication between the teeth.

The m/1 is bigger and more robust than the m/2, with a very tall paraconid but is overall rather similar in morphology to the m/2.

The three teeth are disposed in a straight line, but as described above the bases of the paraconids of m/3 and m/2 are imbricated with the talonids of the preceding teeth. In side view, the cutting edges of the three teeth form a clearly concave complex, a consequence of the lesser height of the protoconid and paraconid of the m/2 with respect to the teeth in front and behind it. In contrast, in the upper dentition, the cusps of the M1/ are taller than those of the P4/, producing a cutting edge that is convex in side view, thereby occluding in a precise way with the concave cutting edge of the lower dentition (Fig. 7, A-B).

Interpretation of tooth positions

Prionogale breviceps

Most specimens of this species, known from Songhor (the type locality), Chamtwara, Legetet, Rusinga and Koru (Kenya) and Napak IV (Uganda) consist of

lower teeth, many contained in mandibles. The lower dentition from all these localities, with the exception of the anterior portion of a mandible containing a broken

canine (KNM SO 22957), is represented only by three types of molariform teeth; the first kind, located at the rear of the jaw (m/3) is extremely sectorial and formed of the paraconid and protoconid, the other two kinds (m/2 and m/1) have the same basic morphological pattern comprising three cusps aligned along the buccal side of the crown (paraconid, protoconid, and hypoconid) and a capacious lingual depression bordered posteriorly by the hypoconuid-entoconid and lingually by a crest that extends to the base of the paraconid. The main difference between these two teeth apart from the greater length and more gracile form of the anteriormost one, is that in this tooth the paraconid is more robust and taller than the protoconid, the opposite of the situation in the succeeding tooth. This molariform tooth

was interpreted by Borths & Stevens (2017a) to be a d/4, but now, by correlation with the upper dentition, is considered to be an m/1.

The mandible UM NAP IV 74'14 confirms the reconstruction of the jaw of *Prionogale breviceps* proposed by Schmidt-Kittler & Heizmann (1981, fig. 16) and by Borths & Stevens (2017a, fig. 2). The lower dentition comprised three molariform teeth, a residual premolar (p/1 or d/1) represented by a shallow alveolus, a canine and at least two incisors. UM NAP IV 74'14 has lost the anterior molariform tooth (m/1), but the empty alveoli are preserved. Scans clearly indicate that there are no signs of dental germs hidden in the interior of the jaw (Fig. 10). The same appears to be the case with the mandible KNM SO 22192, in which the two anterior molariform teeth are missing.

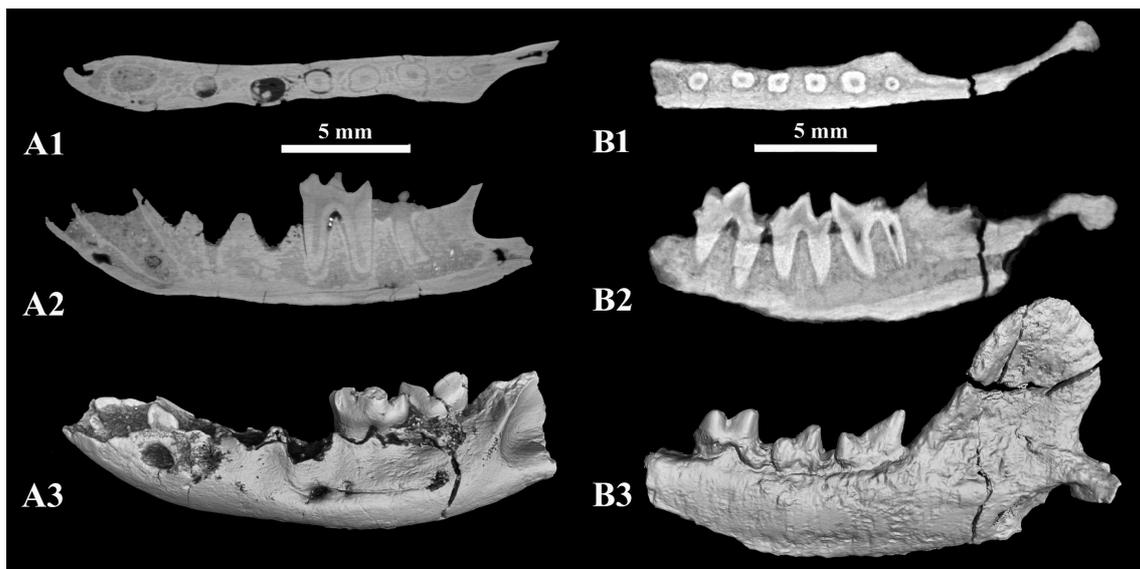


Figure 10. A) *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981, from Napak IV, Uganda. Left mandible (UM NAP IV 159'12). A1) transverse section, A2) longitudinal section, A3) superficial buccal view. B) *Namasektor soriae* Morales *et al.* 2008, from Elisabethfeld, Namibia. Right mandible (Paratype GSN EF 60'01) B1) transverse section, B2) longitudinal section, B3) superficial lingual view.

The data concerning the upper teeth are more limited, but what is available shows a similar situation. In addition to the holotype of *Prionogale breviceps* from Songhor, which is the most complete specimen with the molariform teeth and a single premolariform one, there are two fragments of maxilla preserving the anterior molariform tooth from Legetet (Schmidt-Kittler & Heizmann, 1981) and Napak IV

(Fig. 1) and there are isolated molariform teeth from Songhor, Napak IV and Koru. In the re-description of the holotype from Songhor, Borths & Stevens (2017a) did not mention any information about tooth germs inside the maxilla (in this case the P4/ and P3/), which theoretically ought to exist if the erupted teeth are the D4/-D3/, as can be observed in other maxillae in which at least one permanent molar has erupted (Borths &

Stevens, 2017b). The molariform tooth UM NAP IV 72'05, here interpreted as a right D4/ (Fig. 11), reveals that this tooth differs morphologically from the teeth identified as D4/ by Schmidt-Kittler & Heizmann (1981) and Morales *et al.* (2008) and Borths & Stevens (2017b). The position of the tooth in the dental series means that it can only be an M1/, meaning that the posterior tooth only known in the holotype of the species

Namasector soriae

Namasector soriae probably had the same kind of dental series as *Prionogale breviceps*. In the two available mandibles of the Namibian species only the posterior part is preserved containing three molariform teeth and part of the diastema in front of them. The information yielded by the scans (Fig. 10) indicates that there are no teeth within the jaws that could replace the tooth interpreted by Borths & Stevens (2017a) as deciduous ones, and it is possible to observe that the three erupted teeth have similar development of roots. In the maxilla fragment, the scans also show that there are

no germs of tooth crowns hidden inside (Fig. 12). If some of the teeth in the maxilla of *Namasector* really are deciduous, (D3/-D4/) as deduced by Borths & Stevens (2017a), there ought to be indications of developing teeth inside the maxilla. To these observations, can be added that the upper canine in the left maxilla, even if the crown is broken, was quite large with an ovoid section (Morales *et al.* 2008 Pl.1, Fig. 5), therefore with adult morphology. In conclusions the dental formula of *Namasector soriae* would be similar to that of *Prionogale breviceps*.

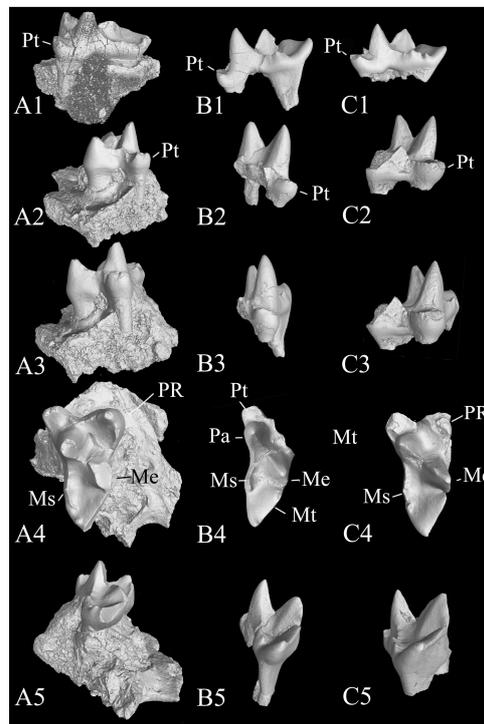


Figure 11. *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1981, D4/-M1/ morphology. A) Napak right maxilla fragment with M1/ (UM NAP IV 159'12). B) Napak left D4/ with broken protocone (UM NAP IV 72'05). C) Koru right M1/ with protocone partially broken (OCO KO 528'05). 1) buccal view, 2) anterior view, 3) lingual view, 4) occlusal view, 5) posterior view. Me= Metacone, Ms= Mesostyle, Mt= Metastyle, Pa= Paracone, Pt= Parastyle.

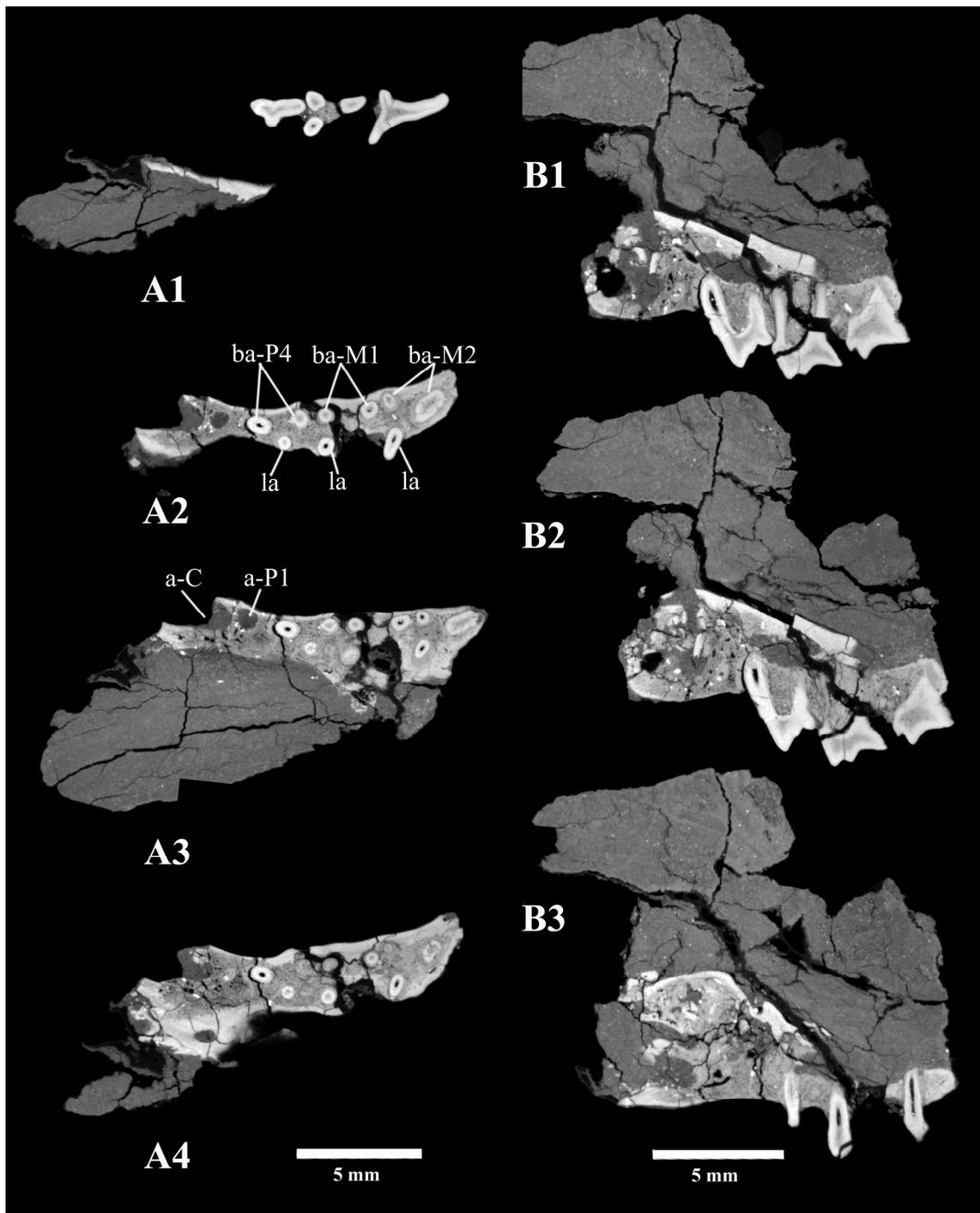


Figure 12. *Namasector soriae* Morales *et al.* 2008, from Elisabethfeld, Namibia. Right skull fragment with maxilla (holotype GSN EF 118'01). A1) transverse section at gingival plane, A2) transverse section below gingival plane, A3) Transverse section at half the height of the roots, A4) transverse section near the base of the roots. B1) longitudinal section near teeth buccal side, B2) longitudinal section near teeth lingual side, B3) longitudinal section at protocones of teeth. a-C= Canine alveolus, a-P1= P1 alveolus, ba= buccal alveoli, la= lingual alveolus.

Comparison between *Namasector soriae* and *Prionogale breviceps*

Together with the loss of premolars, *Namasector* and *Prionogale* share several characters such as: the infraorbital foramen

is located in a posterior position such that the anterior margin of the orbit overhangs it. In both genera the snout was shortened.

Whereas the anterior maxillary teeth are unknown in *Prionogale*, in *Namasector* it is the anterior teeth of the mandible which are missing. Nevertheless, it is possible to infer with reasonable confidence that they had the same number of dental elements. The overall dental morphological pattern is similar; the upper molars have the paracone and metacone well separated from each other, with their apices far apart, the protocones of the three maxillary teeth are well-developed and in the two molariform teeth the parastyles are prominent and project buccally. In the M2/ the paracone is in a very lingual position between the parastyle and protocone, and the notch between metastyle and metacone has been completely suppressed. In the lower dentition, the three molariform teeth lack metaconids, are tricuspid buccally (paraconid-protoconid and hypoconid), and the two anterior molariform teeth m/1-m/2 possess a well-developed talonid, whereas in the m/3 the paraconid and protoconid comprise a cutting blade, and the apex of the protoconid projects distally.

However, despite the overall similarity in dental structural pattern, there are notable differences: *Namasector* possesses a dentition which is more hypercarnivorous than that of *Prionogale*, in that the M2/ not only has an elongated metastyle but also has fused it with the metacone thereby forming a long cutting edge, analogous to the situation in extant *Mustela nivalis* and other hypercarnivorous mustelids. In addition, in this molar the parastyle is enlarged and together with the paracone forms a second cutting crest, almost transversely oriented to the metastyle-metacone. The M1/ is also clearly elongated, but the metastyle is separated from the metacone by a notch, and the parastyle is as strong as the protocone whereas in the M1/ the parastyle is closer to the paracone than in the M1/. The P4/ has a much elongated buccal wall marked by a prominent paracone, a possible weakly expressed metacone and a moderately long metastyle, the protocone is smaller than in the two molariform teeth and is positioned centrally.

Prionogale is less hypercarnivorous and has more conventional dental morphology than *Namasector*. The M2/ is almost triangular with the metastyle less elongated than in *Namasector*, the parastyle is prominent and there is a buccal cusp (mesostyle) in the middle of the buccal wall. The protocone is better-developed than in *Namasector* and joins the rest of the crown via a relatively broad isthmus. The M1/ is similar to that of *Namasector*, even though it is less sectorial, such that the occlusal plan of the metastyle-metacone-paracone is V-shaped, whereas in *Namasector* these three cusps are arranged in a straight line. Similarly, the P4/ is quite a bit shorter than in *Namasector*. In the lower dentition, the differences are of the same kind, *Namasector* having more sectorial, scarcely imbricated teeth, whereas in *Prionogale* they are strongly imbricated and the two anterior molariform teeth (m/2-m/1) possess a talonid with a wide and deep valley which extends lingually to the base of the paraconid.

In our opinion, as was already discussed by Morales *et al.* (2008), *Namasector* and *Prionogale* belong to the same systematic group, defined at the family level, Prionogalidae. However, the two genera show divergent trends, *Namasector soriae* to such an extent that it is one of the most hypercarnivorous known members of the Ferae. *Prionogale*, even though it is hypercarnivorous in the reduction of the premolars, the shortening of the snout and the elongation of the metastyle in the upper molars, the loss of the metaconid in the lower molars and the very sectorial morphology of the m/3, is less advanced in this direction than *Namasector soriae*. Other characters accord with this interpretation, including the primitive occlusal pattern of the M2/, the lesser elongation of the M1/ and P4/, the disposition of the three cusps of the trigon of the upper molars in a V-shape (related to its occlusal form) and the development of capacious buccal depressions in the upper molars and lingual ones in the m/1 and m/2 (Fig. 13).

Systematic Relationships

The systematic position of the Prionogalidae is difficult to elucidate, despite knowing, that except for the D4/ (UM NAP IV 72'05), all teeth described in the previous work are permanent. The reasons for the difficulties are varied, but

fundamentally reside in the peculiar character of their dentitions, in which there is extreme reduction of the premolar series and the extraordinary morphology of the molars, in which there is a mixture of primitive and derived characters.

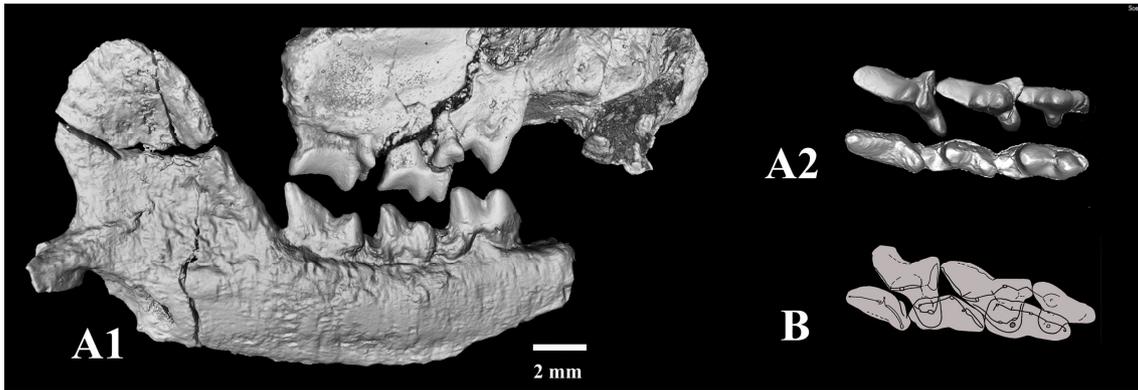


Figure 13. Occlusion of upper and lower dentition of Prionogalidae. A) *Namasector soriae* A1) buccal view, A2) occlusal view, B) *Prionogale breviceps* after Schmidt-Kittler & Heizmann (1991, Fig. 18).

1. The extreme reduction of the premolar series in Prionogalidae was evoked by Schmidt-Kittler & Heizmann (1991) and Borths & Stevens (2017), but in a way was minimized because of the identification of the anterior molariform teeth as premolars, herein interpreted as m/1-M/1. Because of this the dental formula was considered by these authors to be $I?/i2, C?/,1, P3/p2, M1/m2$, but in our interpretation should be $I?/i2, C1/c1, P2/p1, M3/m3$, with the anterior premolar much reduced. The model of the jugal dentition approaches that of several groups of rodents, in which the deciduous dentition and premolars have been notably reduced (Nievelt & Smith 2005). In the order Carnivora the hypercarnivorous dentition is associated with a reduction of several elements of the premolar series; with reduction of the P2/-P1/ and p3-p/1, the case in some families of Feliformia, especially the machairodont felids (Turner *et al.* 2011). However, the most hypercarnivorous species of Hyaenodonta do not show significant reduction or

loss of premolars, but which however do occur in other creodonts. For instance, the hypercarnivorous forms of Machaeroidini such as *Apataelurus* (Scott, 1938) and *Machaeroides* (Matthew, 1909; Gazin, 1946; Dawson *et al.* 1986), even though in both these genera the symphysis is not shortened as a consequence of the great development of the canines, they converge with the 'sabre-toothed tigers' (Machairodontinae, Nimravidae, Barbourfelidae). Several very specialised Oxyaenidae, such as *Patriofelis* and *Sarkastodon* have shortened the rostrum and the mandible, losing or reducing the anterior premolars (Denison, 1938), but the dental morphology of these genera is markedly different from that of the *Prionogale*, showing a bone-crushing dental model. Whatever the case these forms are separated from the Prionogalidae by the reduction of the molar series (loss of m/3 and M3/, and reduction of M2/) which results in the carnassial function being undertaken by the m/2-M1/.

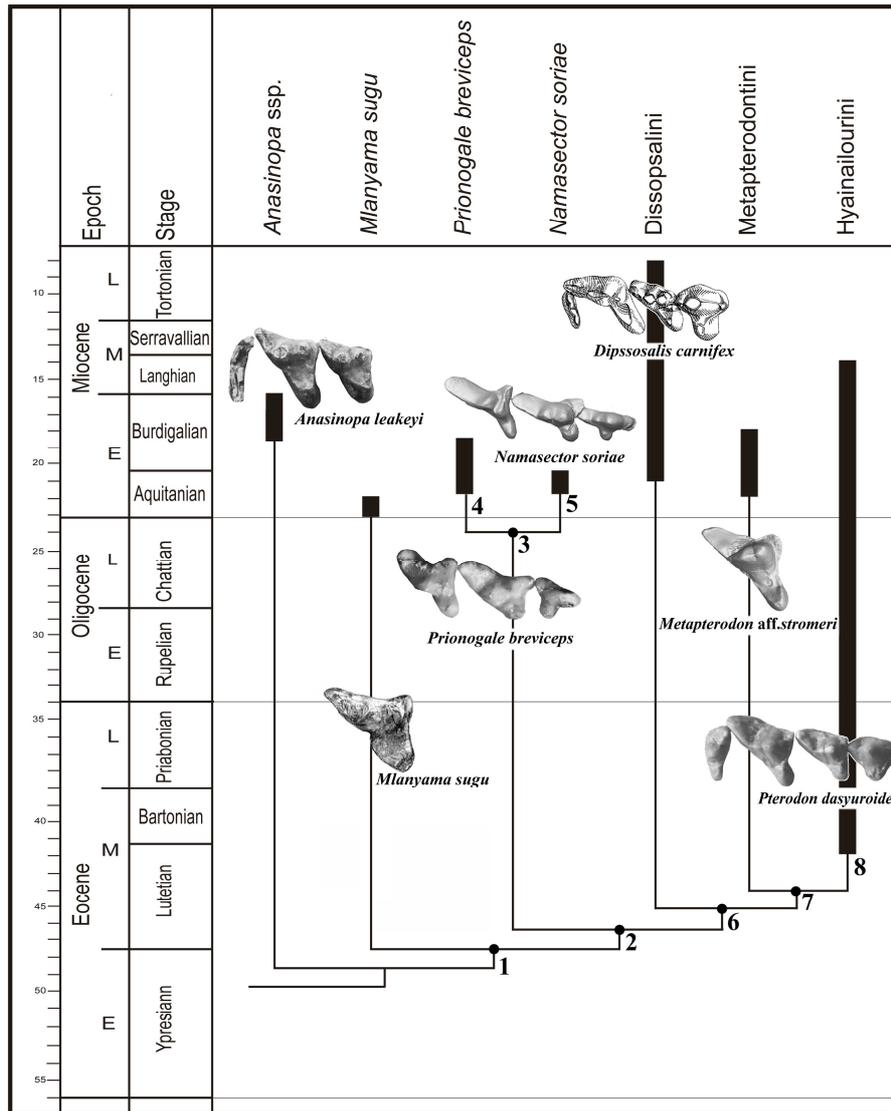


Figure 14. Biochronology and hypothesis of phylogenetic relationships (see Morales & Pickford, 2017) of Prionogalidae with other Hyainailouroidea. Chronostratigraphic data from Cohen *et al.* (2013). **Specimens figured:** *Anasinopa leakeyi* Savage, 1965, NHMUK M 19081b, right maxilla with M1-/M2/ and alveoli of M3/ from Rusinga, Kenya. *Mlanyama sugu* Rasmussen & Gutiérrez 2007, KNM-NW 46831, left M1/ from Nakwai, Kenya (redrawn). *Prionogale breviceps* Schmidt-Kittler & Heizmann, 1991, KNM-S0 1431, left maxilla with M2-/P4/ from Songhor, Kenya (redrawn from Borths & Stevens, 2017a, Fig. 1a). *Namasector soriae* Morales *et al.* 2008, GSN EF 118'01, left M2-/P4/ from Elisabethfeld, Namibia. *Dissopsalis carnifex* Pilgrim 1910, AMNH 19401, left M3-/P4/ from Lower Siwaliks, Pakistan (mirrored, redrawn from Colbert, 1933, Fig. 2). *Metapterodon aff. stromeri* Morales *et al.* 1998, UM NAP V 121'08, right M2/ from Napak V (Morales & Pickford, 2017, Pl. 2). *Pterodon dasyuroides* Blainville, 1839, MNHN Qu 8737, left P4-/M3/ from Quercy, France (mirrored). **Character selection:** 1- Sectorial lower molars, loss of metaconid in m/3, reduction of metaconid in m/1-m/2. 2- Sectorial upper molars with protocone placed anteriorly. 3- Prionogalidae: loss of premolars (p/2-p/4 and P3-/P2/), loss of metaconid in lower molars, high protoconid in m/3, with the apex projected posteriorly, m/1 with high paraconid, M2/ paracone placed in antero-lingual position, M1-/M2/ with parastyle buccally projected, loss of notch between metacone-metastyle in M2/. 4- *Prionogale*: m/1-m/3 strongly imbricated, m/1-m/2 with basined talonid, and cingulum extending to the base of paraconid. 5- *Namasector*: very sectorial molars; M1-/M2/ with metastyle elongated and protocone narrow; m/3 with protoconid elongated. 6- Reduction of parastyle in upper molars; M2/ elongated with narrow protocone. 7- Metacone-paracone fused in upper molars. 8- Protocone reduction in upper molars, complete loss in some species. Metacone-paracone undifferentiated in some species.

2. The hypercarnivorous morphology of the molar battery of the Prionogalidae combines characters that *a priori* could be primitive with other more specialized ones, some of them unique at the level of the order Hyaenodonta. As was discussed above, there seems to be no close analogue to any other lineage of hyaenodonts. Currently, hypercarnivory in hyaenodonts is interpreted to be an adaptation that evolved several times independently in diverse lineages (Polly, 1996; Solé *et al.* 2014; Rana *et al.* 2015, Borths *et al.* 2016). Concerning the Prionogalidae, Borths & Stevens (2017) suggested that they represent another clade that acquired hypercarnivory independently within the Hyaenodonta. This idea was implied indirectly by Schmidt-Kittler & Heizmann (1981) when they proposed to exclude the family from the “Creodonta” and Carnivora. Furthermore, Morales *et al.* (2008) proposed a model close to *Thereutherium thylacodes* Filhol (1876) from the late Oligocene of France, considered as a Limnocyoniidae by Lange-Badré (1979), but the presence of two upper carnassial teeth (M1/ and M2/) in the Prionogalidae excludes any close relationship with this species. The more hypercarnivorous forms of hyaenodonts are classified into two clades Hyaenodontinae and Hyainailourinae, which present notable parallelisms, in which there are species in which the lower molars lose the metaconid and reduce the talonid, while the upper molars (with the exception of the M3/, which is usually greatly reduced) tend to fuse the metacone and paracone into a single cusp, to reduce the protocone and enlarge the metastyle (Borths *et al.* 2016; Morales & Pickford, 2017). In the Prionogalidae, even though there is a lingual cingulum in the m/2-m/1 of *Prionogale*, the molars, including the m/3 are extremely sectorial, the m/3 comprising only a paraconid and protoconid, whereas in the m/2 and m/1 a sectorial hypoconid is present. In this their teeth do not differ greatly from those of Hyaenodontinae and Hyainailourinae. However, the upper molars (M1/ and M2/) possess well separated paracone and metacone, retain a strong protocone and possess large parastyle which projects buccally. From

this it flows that the separation of *Prionogale* from other other Hyaenodontidae would have taken place before the split between the Hyaenodontinae and Hyainailourinae (sensu Borths *et al.* 2016).

3. An alternative systematic scheme for the Prionogalidae is to search for possible relationships among the hypercarnivorous hyaenodonts of “Proviverrinae grade” some of which, including *Oxyaenoides* Matthes (1967), could belong to Hyaenodontinae according to Polly (1996), on the basis that the metaconid is lost in all the lower molars. But among all the modifications associated with the development of hypercarnivorous dentitions, the loss of the metaconid is the most frequent cause of homoplasy. For Solé (2013) and Solé *et al.* (2014) the most sectorial “proviverrines” comprise the subfamily Proviverrinae, which underwent an important radiation in Europe during the Eocene. However, in the phylogenetic analysis of Borths *et al.* (2016) they appear to be paraphyletic, with the group *Oxyaenoides-Quercytherium* together with Hyaenodontinae forming the clade Hyaenodontidae, and the remainder (*Proviverra*, *Morlodon*, etc.) related to other species that Solé (2013) grouped in the subfamily Sinopinae. The molar battery of *Oxyaenoides bicuspidens* (Matthes, 1967) apparently possessed an overall structure close to that of *Prionogale*; with M1/ broader than M2/, the two molars with well-developed metacones, as large as or greater than the paracone, protocone well-developed and buccally projecting parastyle, especially strong in M2/. In the lower molars the metaconid has been suppressed and the lingual bases of the paraconid and protoconid of the m/1-m/2 are fused, thereby closing the lingual valley between the two cuspid (Lange-Badré & Haubold, 1990). In *Oxyaenoides lindgreni* (Rich, 1971) this fusion is clearly visible in the holotype mandible (Solé *et al.* 2014, fig. 2-E). However, the differences are also important, *Prionogale* distancing itself from *Oxyaenoides* by the position of the paracone of the M2/ which is displaced lingually with respect to the metacone, and the absence of a notch between the metacone and parastyle, and, in the M1/ by

the more buccal position of the paracone and the individualisation of the metacone. However, other proviverrines of the clade, *Allopterodon* (Solé *et al.* 2014) like *Proviverra typica* Rüttimeyer, 1862 and *Allopterodon torvidus* (Van Valen, 1965) present an arrangement of the cusps of the M1/ similar to those of *Prionogale*, but differ in being less sectorial (Van Valen, 1965). It is possible that the Prionogalidae are a clade derived from the most basal Proviverrinae, which acquired hypercarnivory in parallel with the clade *Oxyaenoides*.

4. Relationship with Hyainailouroidea. Unlike the Hyaenodontoidea which experienced a profound crisis at the end of the Palaeogene, which drastically reduced their diversity, the Hyainailouroidea experienced an important adaptive radiation during the Oligocene and Miocene in África, which was less evident in Asia. The Prionogalidae would have participated in this radiation of the African hyainailouroids, but as mentioned above they were clearly separated from the Hyainailourinae (sensu Borths *et al.* 2016), equivalent to the Hyainailourini sensu Solé *et al.* (2015). According to Morales & Pickford (2017) two groups of hypercarnivores separated from these Hyainailourini, the Dissopsalini (*Dissopsalis*, *Leakitherium* and *Buhakia*) and the Metapterodontini (only represented by *Metapterodon*). Both tribes diverge from the Hyainailourini by the persistence in the upper molars of strong protocones and clear separation of the buccal cusps (the case with *Metapterodon*), and additionally in the Dissopsalini by a greater individualisation between the metacone and paracone, and a metacone better developed than the paracone, as occurs in the M2/ of the Prionogalidae. *Metapterodon stromeri* has very sectorial lower molars, with loss of the metaconid and reduction of the talonid (Morales *et al.* 1998), whereas in Dissopsalini the lower molars are also sectorial, but m/2 and m/1 nevertheless retained the metaconid, even though it is reduced in dimensions (Barry, 1988; Morlo *et al.* 2007; Morales & Pickford, 2017). In a way, the two groups shared this mixture of

analogous characters as those discussed about thehyaenodonts of the *Oxyaenoides* type. It is possible that the Prionogalidae separated from the Metapterodontini and Dissopsalini, by the disappearance in the M2/ of the notch between the metastyle and the metacone, the antero-lingual position of the paracone and the greater buccal projection of the parastyle. Finally, *Mlanyama sugu* Rasmussen & Gutiérrez, 2009, was related by these authors to *Dissopsalis pyroclasticus* Savage, 1965. It is characterised by a very sectorial m/3, without a metaconid and a reduced talonid, similar to the m/3 of *Metapterodon stromeri*, and somewhat more distant from that of *Dissopsalis pyroclasticus*. The unique molar of *M. sugu* known, possesses a well-developed protocone and its unión with the buccal cusps is broad and long, a feature which differentiates it from *Metapterodon*, *Dissopsalis* and the Prionogalidae. For this reason, *M. sugu* seems to be far from these clades, despite the sectorial character of its lower dentition (Morales & Pickford, 2017).

5. Analogous antagonistic phylogenetic scenarios were published by Borths & Stevens (2017a) but the weak resolution of their analyses, described by the authors as ambiguous “*depending on whether characters are ordered or unordered*”, could be caused by misinterpretation of tooth positions. However, the interpretation of the systematic position of *Prionogale* and *Namasector*, which eliminates a possible relationship to *Thereutherium*, renders it less likely that there is a close systematic relationship to the Hyaenodontidae, owing to an enormous temporal gap of nearly 20 million years between the Prionogalidae and any potential proviverrine ancestors. In contrast, the African fossil record reveals the existence of an important radiation of Hyainailouroidea during the Palaeogene and much of the Miocene. The potential ancestors of the Prionogalidae may be recognised in this African fossil record with greater likelihood than among the Hyaenodontidae (Fig. 14). However, confirmation of the systematic position of *Prionogale* requires a more complete fossil record.

Conclusions

New fossils of *Prionogale breviceps* from early Miocene localities Napak IV, Uganda, and Koru, Kenya, together with restudy of the dentition of *Namasector soriae* from the early Miocene of Elisabethfeld, Namibia, confirm the peculiar combination of dental morphologies in the two species. The interpretation by Borths & Stevens (2017a) that the cheek teeth in the available samples of the two species are deciduous is not confirmed by the present study, because a D4/ of *Prionogale breviceps* from Napak IV shows different morphology from the M1/ (=D4/ in the interpretation of Borths & Stevens, 2017a) and because scans of the mandible of *Prionogale* and a maxilla and mandible of *Namasector* indicates that there

are no tooth germs beneath the supposed deciduous teeth. As a consequence, the dentitions of both taxa hitherto interpreted as juvenile, are in fact adult and comprise the dental formula: I²/i², C1/c1, P2/p1, M3/m3. The combination of three pairs of carnassials comprising respectively m/3-M2/, m/2-M1/ and m/1-P4/, the reduction of the premolars and the highly derived morphology of the molar battery of these two genera of Prionogalidae is unique among the Hyaenodonta. Whereas a relationship with the Hyaenodontidae is possible, it is more likely that the Prionogalidae are more closely related to the Hyainailouroidea (in which they comprise a distinct family) which proliferated in Africa during the Miocene.

Acknowledgements

We appreciate the organisation of the Namibia Palaeontology Expedition (co-leader B. Senut), and the support of the Geological Survey of Namibia (G. Simubali, A. Nguno, V. do Cabo, H. Mocke), The Namibian National Heritage Council (H. Elago), the Uganda Palaeontology Expedition, the Uganda Museum (R. Mwanja, S. Musalizi, C. Ssebuyongo), the Uganda National Council for Science and Technology, The Kenya Palaeontology Expedition, the Orrorin Community Organisation (J. Kipkech, M. Cherutoi, S. Cheptumo, D. Chebor, N.

Kiptalam) the Kenya Ministry for Higher Education, Science and Technology, the French Ministry of Foreign Affairs, the Muséum National d'Histoire Naturelle, Paris, Sorbonne Université, Paris, and the French CNRS. The Spanish Research Project CGL 2015-68333-P (MINECO/FEDER-UE) and the Research Groups CSIC 64 1538 and CAM-UCM 910607 funded aspects of this research. We thank the Servicio de Técnicas No Destructivas: Microscopía Electrónica y Confocal y Espectroscopía del MNM-CSIC, Madrid, for making the scans.

References

- Barry, J.C. 1988. *Dissopsalis*, a middle and late Miocene proviverrine creodont (Mammalia) from Pakistan and Kenya. *Journal of Vertebrate Paleontology*, **8**: 25–45.
- Bastl, K., Nagel, D. & Peigné, S. 2014. Milk tooth morphology of small-sized *Hyaenodon* (Hyaenodontidae, Mammalia) from the European Oligocene - evidence of a *Hyaenodon* lineage in Europe. *Palaeontographica, Abteilung A: Palaeozoology - Stratigraphy*, **303** (1-3), 61-84 DOI 10.1127/pala/303/2014/61.
- Blainville, H. M. D. de, 1839. Sur l'*Hyaenodon leptorhynchus* (de Laizer) nouveau genre de Carnassiers fossiles d'Auvergne. *Annales français et étranger d'Anatomie et Physiologie*, **3**, 17-31.
- Borths, M.R., Holroyd, P.A. & Seiffert, E.R. 2016. Hyainailourine and teratodontine cranial material from the late Eocene of Egypt and the application of parsimony and Bayesian methods to the phylogeny and biogeography of Hyaenodonta (Placentalia, Mammalia). *PeerJ* **4**: e2639; DOI 10.7717/peerj.2639.

- Borths, M.R. & Stevens, N.J. 2017a. Taxonomic affinities of the enigmatic *Prionogale breviceps*, early Miocene, Kenya, *Historical Biology*, DOI: 10.1080/08912963.2017.1393075.
- Borths, M.R. & Stevens, N.J. 2017b. Deciduous and dental eruption of Hyainailouroidea (Hyaenodonta, Placentalia, Mammalia). *Palaeontologia Electronica*. <https://doi.org/10.26879/776>.
- Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X. 2013 (updated). The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199-204. URL: www.stratigraphy.org/ICSchart/ChronostratChart2018-07.
- Colbert, E.H. 1933. The Skull of *Dissopsalis carnifex* Pilgrim, a Miocene Creodont from India. *American Museum Novitates*, **603**, 1-8.
- Crusafont-Pairó, M. & Truyols-Santonja, J. 1956. A Biometric study of the evolution of fissiped Carnivores. *Evolution*, **10**, 314-332.
- Dawson, M.R., Stucky, R.K., Krishtalka, L. & Black, C.C. 1986. *Machaeroides simpsoni*, new species, oldest known sabertooth creodont (Mammalia), of the Lost Cabin Eocene *Contributions to Geology, University of Wyoming, Special Paper*, **3**, 177-182.
- Denison, R.H. 1938. The broad-skulled Pseudocreodi. *New York Academy of Sciences, Annals*, **37**, 163-256.
- Filhol, H. 1876. Mammifères fossiles nouveaux provenant des dépôts de phosphate de chaux du Quercy. *Comptes Rendus de l'Académie des Sciences de Paris*, **82**, 288-289.
- Gazin, C.L. 1946. *Machaeroides eohen* Matthew, the saber-tooth creodont of the Bridger Eocene. *United States National Museum, Proceedings*, **96**, 335-347.
- Granger, W. 1938. A giant Oxyaenid from the Upper Eocene of Mongolia. *American Museum Novitates*, **969**, 1-5.
- Lange-Badré, B. 1979. Les créodontes (Mammalia) d'Europe occidentale de l'Éocène supérieur à l'Oligocène supérieur. *Mémoires du Muséum National d'Histoire Naturelle*, **42**, 1-249.
- Lange-Badré, B. & Haubold, H. 1990. Les Créodontes (Mammifères) du gisement du Geiseltal (Eocène Moyen, RDA). *Geobios*, **23**, 607-637.
- Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. Holmiae: Laurentius Salvius. 823 pp.
- Matthes, H.W. 1967. Erstmaliger Nachweis eines Vertreters der Oxyaeninae Trouessart 1885 (Creodonta) in Europa. *Geologisches Jahrbuch*, **16**, 452-456.
- Matthew, W.D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. *Memoirs of the American Museum of Natural History*, **9**, 291-576.
- Morales, J. & Pickford, M. 2017. New hyaenodonts (Ferae, Mammalia) from the Early Miocene of Napak (Uganda), Koru (Kenya) and Griliental (Namibia). *Fossil Imprint*, **73** (3-4), 332-359, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).
- Morales, J., Pickford, M. & Salesa, M.J. 2008. Creodonta and Carnivora from the Early Miocene of the Northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**, 291-310.
- Morales J., Pickford M., Soria, D. 1998. A new creodont *Metapterodon stromeri* nov. sp. (Hyaenodontidae, Mammalia) from the early Miocene of Langental (Sperrgebiet, Namibia). *Comptes Rendus de l'Académie des Sciences, Paris, Série Sciences de la Terre et des Planètes*, **327**, 633-638.
- Morlo, M., Miller, E.R., & El-Barkooky, A.N. 2007. Creodonta and Carnivora from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology*, **27**, 145-159.
- Nievelt, A. F. H. van & Smith, K. K. 2005. To replace or not to replace: the significance of reduced functional tooth replacement in marsupial and placental mammals. *Paleobiology*, **31**, 324-346.
- Pickford, M. 2017. Revision of « peccary-like » Suoidea (Artiodactyla: Mammalia) from the Neogene of the Old World. *Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, **46**, 1-144.
- Pilgrim, G.E. 1910. Notices of new mammalian genera and species from the Tertiaries of India. *Records of the Geological Survey of India*, **40**, 63-71.
- Pilgrim, G.E. 1932. The fossil Carnivora of India. *Memoirs of the Geological Survey*

- of India, *Palaeontologica Indica*, New Series, **18**, 1-232.
- Polly, P.D. 1996. The skeleton of *Gazinocyon vulpeculus* gen. et comb. nov. and the cladistic relationships of Hyenodontidae (Eutheria, Mammalia). *Journal of Vertebrate Paleontology*, **16**, 303-319.
- Rana, R., Kumar, K., Zack, S.P., Solé, F., Rose, K., Missiaen, P. Singh, L., Sahni, A. & Smith, T. 2015. Craniodental and postcranial morphology of *Indohyaenodon raoi* from the early Eocene of India, and its implications for ecology, phylogeny, and biogeography of hyaenodontid mammals. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2015.965308.
- Rasmussen, D.T. & Gutiérrez, M. 2009. A Mammalian Fauna from the Late Oligocene of Northwest Kenya. *Palaeontographica*, Abt. A, **288**: 1-52.
- Rich, T.H.V. 1971. Deltatheridia, Carnivora and Condylarthra (Mammalia) of the Early Eocene, Paris Basin, France. *University of California Publications in Geological Sciences*, **88**, 1-72.
- Rütimeyer, D.M. 1862. Eocäne Säugethiere aus dem Gebiet des schweizerischen Jura. *Neue Denkschriften der Allgemeinen schweizerischen Gesellschaft für die gesammten Naturwissenschaften*, Zurich, **19**, 1-98.
- Schmidt-Kittler, N. & Heizmann, P.J. 1991. *Prionogale breviceps* n. gen. n. sp.: Evidence of an unknown major clade of eutherians in the Lower Miocene of East Africa. *Münchner Geowissenschaftliche Abhandlungen*, **19**, 5-16.
- Savage, R.J.G. 1965. The Miocene Carnivora of East Africa. *Fossil Mammals of Africa*, **19**, 239-316.
- Scott, W.B. 1938. A problematical cat-like mandible from the Uinta Eocene, *Apataelurus kayi*, Scott. *Annals of the Carnegie Museum*, **27**, 113-120.
- Solé, F. 2013. New proviverrine genus from the early Eocene of Europe and the first phylogeny of late Palaeocene–middle Eocene hyaenodontidans (Mammalia). *Journal of Systematic Palaeontology*, **11**, 375–398.
- Solé, F., Amson, E., Borths, M., Vidalenc, D., Morlo, M. & Bastl, K. 2015. A new large Hyainailourine from the Bartonian of Europe and its bearings on the evolution and ecology of massive hyaenodonts (Mammalia). *PLoS ONE* **10(9)**:e0135698.doi:10.1371/journal.pone.0135698
- Solé, F., Falconnet, J. & Yves, L. 2014. New proviverrines (Hyaenodontida) from the early Eocene of Europe; phylogeny and ecological evolution of the Proviverrinae. *Zoological Journal of the Linnean Society*, **171**, 878-917.
- Turner, A., Antón, M., Salesa, M.J. & Morales, J. 2011. Changing ideas about the evolution and functional morphology of Machairodontine felids. *Estudios Geológicos*, **67**, 255-276.
- Van Valen, L. 1965. Some European Proviverrini (Mammalia, Deltatheridia). *Palaeontology*, **8**, 638-665.
- Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. *Bulletin of the American Museum of Natural History*, **135**, 217-284.
- Werdelin, L. & Cote, S.M. 2010. Prionogalidae (Mammalia *Incertae Sedis*). In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, Los Angeles, London, University of California Press, pp. 561-562.