



NEW HYAENODONTS (FERAE, MAMMALIA) FROM THE EARLY MIOCENE OF NAPAK (UGANDA), KORU (KENYA) AND GRILLENTAL (NAMIBIA)

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Morales, J., Pickford, M. (2017): New hyaenodonts (Ferae, Mammalia) from the Early Miocene of Napak (Uganda), Koru (Kenya) and Grillemtal (Namibia). – *Fossil Imprint*, 73(3–4): 332–359, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Recent palaeontological surveys in Early Miocene sediments at Napak (Uganda), Koru (Kenya) and Grillemtal (Namibia) have resulted in the collection of a number of small to medium-sized hyaenodonts and carnivorans, some of which were poorly represented in previous collections. The present article describes and interprets the hyaenodonts from these localities. The new fossils permit more accurate interpretation of some of the poorly known taxa, but new taxa are also present. The fossils reveal the presence of a hitherto unsuspected morphofunctional dentognathic system in the Hyaenodontidae which is described and defined, along with previously documented dentognathic complexes. Two new tribes, three new genera and one new species are diagnosed.

Key words: Hyaenailurinae, Hyaenodontia, Creodontia, Systematics, Miocene, Africa

Received: May 24, 2017 | Accepted: November 13, 2017 | Issued: December 31, 2017

Introduction

The Miocene Hyaenodonts of Africa are relatively poorly understood, in contrast to the true carnivores. This is partly because they were only abundant during the Early Miocene after which their diversity declined rapidly, the order finally disappearing completely from the continent by the beginning of the Late Miocene. The publication by Savage (1965), despite the limitations of the fossil record at the time that he worked, remains a fundamental source of information for understanding these carnivorans.

Savage's (1965) results were soon discussed by van Valen (1967), who pointed out that the holotype mandible of *Isohyaenodon andrewsi* could represent the lower dentition of *Leakitherium hiwegi*, although he mentioned the slight differences in dimensions between them. As a consequence he proposed that *Isohyaenodon* was a synonym of *Leakitherium*. In addition, the same author discussed the maxillae described by Savage (1965) as *Metapterodon kaiseri* STROMER and *Metapterodon zadoki* SAVAGE, and stressed the morphological similarities between them, indicating that they could not be distinguished at the species level, on which basis he proposed that *Metapterodon* and *Pterodon* were synonyms. In much the same way, Mellet (1977: 124–125) indicated that *Isohyaenodon* possessed a dentition of *Pterodon* grade, and that therefore it could not

be considered a *Hyaenodon*. For this author *Isohyaenodon* could be retained as a valid subgenus of *Pterodon*, but apparently true *Hyaenodon* never reached Africa. Other authors such as Dashzeveg (1985) glossed superficially over the problems, but nevertheless abandoned the idea that *Metapterodon* was a synonym of *Pterodon*. Morales et al. (1998a) discussed the two maxillae attributed by Savage (1965) to *Metapterodon*, indicating a possible morphological correspondence with the larger species defined by the author as the subgenus *Isohyaenodon*, which was elevated to generic rank, and they proposed uniting *Metapterodon zadoki* and *Isohyaenodon matthewi*. They also stressed the distinctiveness of *Metapterodon* and *Pterodon*, rejecting synonymy between them. Holroyd (1999) reported the presence of the genus *Metapterodon* in the Palaeogene of Africa, defining two new species. This author revised the previous identification of *Isohyaenodon andrewsi* based on C.8812-13 from the Fayum, Egypt (Savage 1965) and she included it in her new species *Metapterodon schlosseri*. We accept the distinctiveness of *Metapterodon*, not only from *Hyaenodon* but also from *Pterodon*. More recently, Lewis and Morlo (2010) adopted an eclectic position, accepting *Isohyaenodon* as a valid genus, but pointing out the requirement for a revision of these two genera. The essence of the problem was highlighted in papers by Solé et al.

(2014, 2015) in which the authors argued for the separation of the genera into two subfamilies: *Metapterodon* (subfamily Koholiinae CROCHET, 1988) and *Isohyaenodon* (subfamily Hyainailourinae BIEDERMANN, 1863 (Pilgrim 1932)). Borths et al. (2016) did not encounter any difficulties with this separation.

The new sample of hyaenodonts from Napak, Koru and Grillental is important for this debate. On the one hand, it substantiates the presence of *Metapterodon* in the Early Miocene of Uganda, previously based on doubtful or erroneous identifications. On the other hand, it permits us to report the presence of a new dental morphological complex in the panoply of hyaenodonts. The difficulty of determining the correspondence between upper and lower dentitions, already pointed out by Lewis and Morlo (2010), is without doubt one of the main contributors to the complexity of the existing systematics of the group. Table 1 resumes the current state of systematics of the African hyaenodonts discussed in the present work. It is evident that there have been problems of correlating upper and lower dentitions, already experienced by Savage (1965), with the exception of *Teratodon spekei*, *Anasinopa leakeyi* and *Isohyaenodon pilgrimi*. The last taxon, although based on a lower dentition, could reliably have an upper molar attributed to it on the basis of its minuscule size.

Material and methods

Geological, palaeoenvironmental and palaeoecological contexts

The richly fossiliferous localities of Napak (Uganda), Koru (Kenya) and Grillental (Namibia) are of Early Miocene age. The first two localities are associated with carbonatite-nephelinite volcanoes, the fossils occurring in palaeosols which developed on the flanks of the volcanic edifices. Details of the fossiliferous sites at Napak can be found in Musalizi et al. (2009) and those concerning Koru were published by Pickford (1986a, 2009). Radio-isotopic age determinations of the subjacent volcanic deposits provide accurate age estimates for the deposits (Pickford 1986b, c) – both sites are close to 20 million years old, and being quite close neighbours (the distance between the localities is about 260 km) they share many animal taxa.

The palaeoenvironments at Koru were dominated by humid forest as shown by the terrestrial gastropod assemblages, comprising over 48 taxa (Pickford 2009) whereas Napak, with 22 snail taxa, was slightly drier (Pickford 2004) with some open grassy patches interspersed in upland forest growing on the slopes of the volcano.

Both Koru and Napak have yielded a high diversity of mammals, dominated by rodents and primates, but also with

Table 1. Current state of systematics of the Miocene African hyaenodont species discussed in this paper. Shaded boxes indicate the species holotype.

Species	Type locality	Lower dentition	Upper dentition	References
<i>Teratodon spekei</i>	Koru	Yes	Maxilla P4, M1 – M2	Savage (1965)
<i>Teratodon enigmae</i>	Songhor	Yes	Maxillary region	Savage (1965)
<i>Anasinopa leakeyi</i>	Rusinga	Maxilla P4 – M2	Mandible c – m3	Savage (1965)
<i>Anasinopa libyca</i>	Gebel Zelten	Mandible m1 – m3	Not known	Morales et al. (2010)
<i>Metasinopa napaki</i>	Napak 1	Mandible m3	Maxilla P3 – P4	Savage (1965)
<i>Dissopsalis pyroclasticus</i>	Rusinga	Mandible p4 – m3	Not known	Savage (1965)
<i>Leakitherium hiwegi</i>	Rusinga	Not known	Maxilla M1 – M2	Savage (1965)
<i>Buhakia mogharaensis</i>	Wadi Moghara	Mandible d4 – m2	Not known	Morlo et al. (2007)
<i>Africanictis hyaenoides</i>	Arrisdrift	m2	Not known	Morales et al. (2003)
<i>Isohyaenodon andrewsi</i>	Ombo	Mandible m1 – m3	Not known	Savage (1965)
<i>Isohyaenodon matthewi</i>	Songhor	Mandible m2 – m3	Not known	Savage (1965)
<i>Isohyaenodon pilgrimi</i>	Rusinga	Mandible p2 – m3	M1	Savage (1965)
<i>Metapterodon kaiseri</i>	Elisabethfeld	Maxilla P3 – M2	Not known	Stromer (1926)
<i>Metapterodon schlosseri</i>	Fayum	Mandible p2 – m3	Maxilla P2, P4 – M2	Holroyd (1999)
<i>Metapterodon markgrafi</i>	Fayum	Not known	Maxilla P4 – M2	Holroyd (1999)
<i>Metapterodon kaiseri</i>	Karungu	Not known	P3-M2	Savage (1965)
<i>Metapterodon zadoki</i>	Rusinga	Not known	Maxilla M1 – M2	Savage (1965)
<i>Metapterodon stromeri</i>	Langental	Yes	M2	Morales et al. (1998a)
<i>Hyainailouros napakensis</i>	Napak 1	Not known	P4 – M2	Ginsburg (1980)
<i>Pterodon nyanzae</i>	Ombo	Not known	P4	Savage (1965)
<i>Hyainailouros fourtaui</i>	Wadi Moghara	Not known	P4	Koenigswald (1947)
<i>Megistotherium osteothlastes</i>	Gebel Zelten	Not known	Skull	Savage (1971)
<i>Megistotherium osteothlastes</i>	Wadi Moghara	Mandible p4 – m3	Not known	Rasmussen et al. (1989)
<i>Hyainailouros sulzeri</i>	Arrisdrift	Mandible m1	M1	Morales et al. (1998b, 2003)

many macroselidids, insectivores, perissodactyls, artiodactyls, hyracoids and even proboscideans. In addition there was a healthy avian fauna as well as lizards, chamaeleons and gastropods (Morales et al. 2016). There was thus a vast variety of potential food resources for carnivorans, ranging in size from mice to elephants, including ground dwellers (fossorial and above ground dwellers) as well as arboreal species. It is thus not surprising to find that the carnivoran faunas at both these localities were highly diverse, not only taxonomically, but also in terms of the size spectra of the species represented. The tiny carnivoran, *Prionogale* (family Prionogalidae) for example was about the size of the smallest extant carnivores (*Mustela*) whereas the largest (the creodont *Hyainailourus*) was larger than a lion (*Panthera leo*). In between there was a high diversity of other hyaenodonts and fissipeds (amphicyonids, felids, viverrids, mustelids) collectively spanning the range of body sizes between these extremes.

Phylogenetic analysis

In order to understand the phylogenetic relationships of the Miocene Hyainailourinae we have performed a cladistic analysis comprising 17 taxa (Tabs 2–3). The taxa included are for the most part Miocene, for which we could obtain at least some information about the teeth. Thus, some forms, such as *Metasinopa napaki*, *Isohyaenodon andrewsi* and *Dissopsalis pyroclasticus* were excluded from the analyses, whereas *Isohyaenodon andrewsi*, the type species of the genus is tentatively related to *Isohyaenodon matthewi*. Furthermore, we included forms such as *Brychotherium ephalmos* BORTHS et al., 2016, *Masrasector nananubis* BORTHS et SEIFFERT, 2017, *Pterodon africanus* ANDREWS, 1906 and *Metapterodon schlosseri* HOLROYD, 1999 all from the Late Eocene of the Fayum (Egypt) and *Mlanyama sugu* RASMUSSEN et GUTIÉRREZ, 2009 from the Early Miocene of Kenya (Reynoso 2014) (originally thought to be Late Oligocene) in order to place the Miocene Hyaenodonts in a broader context. The analysis was rooted using *Cimolestes magnus* CLEMENS et RUSSELL, 1965 (additional data from Lillegraven 1969) as the outgroup.

The cladistic analysis includes 26 equally weighted and unordered dental characters (17 binary characters and 9 multistate characters; Tabs 2–3). Some of them were used by Egi et al. (2005), Solé et al. (2015) and Borths et al. (2016) with few new character definitions. The choice of characters was gleaned from the molars (M1 – M2 and m3 – m2), which, in the majority of species analysed, acted like doubled carnassials, although dominated by M2 – m3 more than M1 – m2, and the attribution to hypo- and hyper-carnivorous adaptations was based on these pairs of teeth. To a lesser degree, we included several characters associated with the premolar rows, but in such cases, the information was more limited, and the correlations between isolated dentitions was difficult to establish. Cladistic analysis was performed using in PAUP* 4.0b10 (Swofford 2002).

Abbreviations

Collections

AMNH	American Museum of Natural History, New York, USA
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

CMF	Coryndon Museum Fossil collection at the National Museum of Kenya, Nairobi, Kenya (old register numbers)
DPC	Duke University Primate Center, Durham, North Carolina, USA
GSN	Geological Survey of Namibia, Windhoek, Namibia
GSP	Geological Survey of Pakistan, Quetta, Pakistan
KNM	National Museum of Kenya, Nairobi, Kenya
NHMUK	Natural History Museum, London, United Kingdom
MNHN	Museum Nationale d'Histoire Naturelle, Paris, France
OCO	Orrorin Community Organisation, Kipsaraman, Baringo County, Kenya
UM	Uganda Museum, Kampala, Uganda

Others

L – anteroposterior diameter
H – height
W – width

Systematic palaeontology

Superorder Ferae LINNAEUS, 1758
Order Hyaenodonta VAN VALEN, 1967
Family Hyaenodontidae LEIDY, 1869
Subfamily Hyainailourinae PILGRIM, 1932

Diagnosis. See Lewis and Morlo (2010).

Genus *Mlanyama* RASMUSSEN et GUTIÉRREZ, 2009

Type species. *Mlanyama sugu* RASMUSSEN et GUTIÉRREZ, 2009 (type locality: Nakwai, Kenya). Holotype is left dentary with symphysis, incisor alveoli, canine alveolus, p1 – m1, alveolus for m2, and the anterior portion of right dentary with symphysis and anterior alveoli, with a fragment of the canine (KNM-NW 46832).

Age. Early Miocene according to Reynoso (2014) (originally correlated to the Late Oligocene).

Diagnosis. See Rasmussen and Gutiérrez (2009).

Discussion. *Mlanyama sugu* differs from *Anasinopa* species by the broadening of the metastyle in the M1/ and the reduction and narrowing of the isthmus linking the protocone to the buccal cusps. The m/3 of *M. sugu* is very sectorial, with strong reduction of the talonid and absent metaconid, a cusp which is present but reduced in the other molars. Rasmussen and Gutiérrez (2009) related it closely to *Dissopsalis pyroclasticus* in particular because of the transverse orientation of the anterior premolars.

Tribe Dissopsalini trib. nov.

Type genus. *Dissopsalis* PILGRIM, 1910.

Diagnosis. Hyaenodontidae with elongated upper molars (M1 – M2), with strong protocone separated from the buccal cusps by a narrow isthmus, long in the type genus *Dissopsalis*, shorter in the other genera of the tribe, metacone

better developed than the paracone, the two cusps separated from each other by a well-marked vertical groove. Lower dentition with very sectorial m3 without a metaconid and a reduced talonid, m2 with greatly reduced, even residual, metaconid, wide talonid with hypoconid and entoconid, m1 with strong metaconid and wide accented talonid. Robust anterior premolars (P4 and p4). Anterior premolars not broadened.

Included genera. *Dissopsalis* PILGRIM, 1912, *Leakitherium* SAVAGE, 1965 and *Buhakia* MORLO et al., 2007.

Genus *Dissopsalis* PILGRIM, 1910

Type species. *Dissopsalis carnifex* PILGRIM, 1910 (with type locality Chinji Formation, near Chinji Village, Pakistan).

Diagnosis. See Barry (1988).

Other species. *Dissopsalis pyroclasticus* SAVAGE, 1965.

***Dissopsalis pyroclasticus* SAVAGE, 1965**

Holotype. Right mandible containing p4, m1 – m3 and alveoli of canine and p1 – p3 (NHMUK M 19082).

Type locality. Maboko, Kenya (erroneously given as Kaboor (error for Kabua = alternative name for Maboko)), Northern Frontier District, Kenya by Savage (1965).

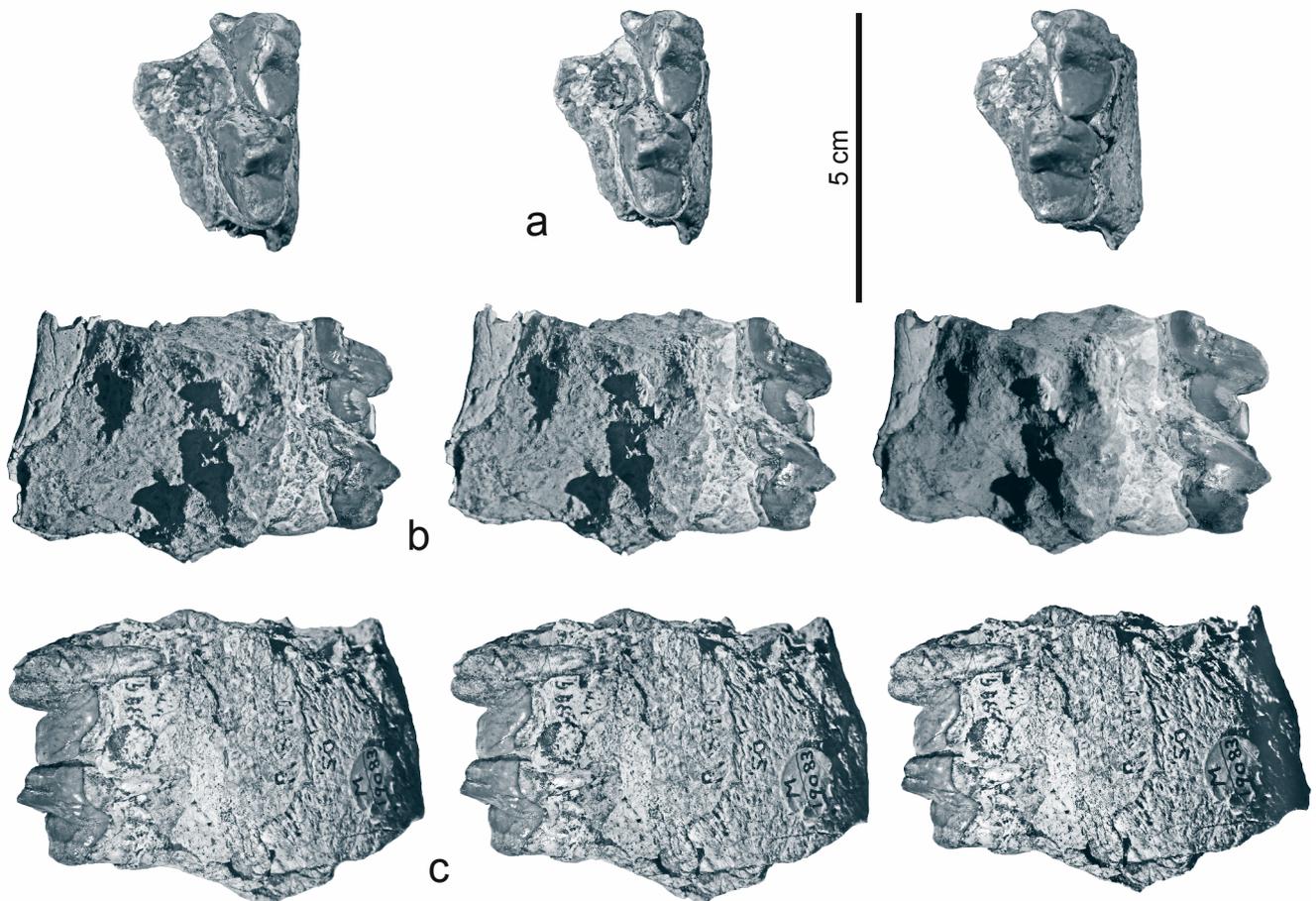
Age. Basal Middle Miocene, ca. 15 Ma.

Diagnosis. See Savage (1965).

Discussion. Barry (1988) cited several quite obvious differences between the lower dentitions of *Dissopsalis carnifex* PILGRIM, 1910 and *Dissopsalis pyroclasticus*. Among these were the more pronounced metaconid in the molars of *D. pyroclasticus*, the differences in length of the p4 and m3, and the taller crown and the diminutive talonid of the m3 of *D. pyroclasticus*. To these differences could be added the greater size of the m2 with respect to the m3 in *D. pyroclasticus*. These differences, although important, do not exclude the possibility of the two species being classified in the same genus. Borths et al. (2016: supplementary tab. 2) included, but did not describe, additional upper and lower dentitions in this species, the study of which would, without doubt, help to clarify the relationship between the two species.

Genus *Leakitherium* SAVAGE, 1965

Type species. *Leakitherium hiwegi* SAVAGE, 1965.



Text-fig. 1. *Leakitherium hiwegi* SAVAGE, 1965 from Rusinga, Kenya. NHMUK M 19083 (holotype), left maxilla with M2 – M1. a: occlusal view, b: lingual view, c: buccal view (stereo pairs).

***Leakitherium hiwegi* SAVAGE, 1965**

Text-fig. 1

H o l o t y p e. Left maxillary fragment with M1 – M2 (NHMUK M 19083) (Text-fig. 1).

T y p e l o c a l i t y. Rusinga, Kenya.

A g e. Early Miocene.

D i a g n o s i s. See Lewis and Morlo (2010).

D i s c u s s i o n. As for *Dissopsalis pyroclasticus*, Borths et al. (2016: supplementary tab. 2) cited the existence of additional unpublished teeth, comprising both

upper and lower dentitions. The lingual wall of the M2 in the holotype maxilla of the species is heavily worn, which partly obscures proper assessment of its characters, just as in a second individual, attributed to this species but which shows important differences from the holotype, rendering its identification doubtful. Therefore, it is not strange to find that its systematic position is erratic. It is possibly related to *Isohyaenodon andrewsi* (van Valen 1967, Dashzeveg 1985) or to *Hyainailouros napakensis* (Morales et al. 1998a) or to the more hypercarnivorous species of the subfamily Hyainailourinae (Solé et al. 2014, Borths et al. 2016).

Another possible correlation for *Leakitherium hiwegi*, not only morphological, but also dimensional, could apply to *Dissopsalis pyroclasticus*, which has a robust lower dentition. The two forms also share the presence of wrinkled enamel and in addition have posterior molars (M2 – M1 and m3 – m2) which are similar in length. This is highly divergent from the interdental proportions in *Dissopsalis carnifex*, in which the M2 and the m3 are noticeably larger than the M1 and m2. In fact, Morlo et al. (2007) indirectly suggested the possible generic separation of these taxa in their interpretation of *Buhakia* from Wadi Moghara, a new genus proposed by the authors, which they considered to be closer to *D. carnifex* than to *D. pyroclasticus*, but the separation was not formally proposed (Lewis and Morlo 2010). In their supplementary table 2, Borths et al. (2016) pointed out that the protocones in the holotype of *Leakitherium hiwegi* “suggest larger talonid basins are expected on the lower dentition...”. This is possible as indicated above. Even though the holotype of *Leakitherium hiwegi* has a heavily worn lingual wall of the M2, the impression is that the protocone would have been at least as well-developed as in the M1. Another important feature is the strong groove between the paracone and metacone visible in the buccal side of the two cusps. The metacone is much better developed than the paracone in both molars, a condition also found in other taxa such as *Dissopsalis carnifex*. An analogous morphology, even though the teeth are more robust, occurs in the maxilla from Karungu described by Savage (1965) as *Metapterodon kaiseri*, which we here interpret as an indeterminate species of *Buhakia*, and therefore relatively close to *Dissopsalis*.

Table 2. Character list.

1	M1/M2 occlusal shape: quadrangular (0), isosceles triangle (1), rectangle (2), linear (3)
2	M1/M2 protocone size: large (0), medium (1), reduced (2)
3	M1/M2 protocone isthmus: wide (0), narrow (1), reduced (2)
4	M2 L/W ratio: <0.85 (0), between 0.86 – 1.15 (1), between 1.16 – 1.35 (2), >1.35 (3)
5	M1 L/W ratio: <0.85 (0), between 0.86 – 1.15 (1), between 1.16 – 1.35 (2), >1.35 (3)
6	M1/M2 protocone position: in front of parastyle/paracone (0), anterior position to parastyle/paracone (1)
7	M2 metacone/paracone: partially separated (0), fused with vertical separation groove (1), fused without separation groove (2)
8	M1 metacone/paracone: partially separated (0), fused with vertical separation groove (1), fused without separation groove (2)
9	M2 metastyle: small (0), short (1), long (2), very long (3)
10	M1/M2 paracone/metacone morphology: coniform (0), sectorial (1)
11	M1/M2 parastyle: present (0), reduced or absent (1)
12	M1/M2 buccal cingulum: present (0), reduced or absent (1)
13	M1/M2 buccal styler area: present (0), reduced or absent (1)
14	M1/M2 paracone/metacone relative size: paracone larger than metacone (0), paracone somewhat larger than metacone (1), metacone larger and taller than paracone (2)
15	M1/M2 trigon valley: wide (0), narrow (1)
16	P4 L/W ratio: <1.1 (0), >1.1 (1)
17	P3 W/L ratio: >0.55 (0), <0.55 (1)
18	m3 metaconid: present (0), absent (1)
19	m3 W/L ratio: >0.60 (0), <0.60 (1)
20	m2 metaconid: present or residual (0), absent (1)
21	m2 talonid morphology: basined with hypoconid, hypoconulid and entoconid (0), narrow with hypoconid in central position (1)
22	m2 talonid size: well-developed (0), reduced (1)
23	p4 talonid morphology: basined (0), narrow, hypoconid in central position (1)
24	p3 W/L ratio: <0.65 (0), >0.65 (1)
25	p4 W/L ratio: <0.57 (0), >0.57 (1)
26	p2/p3 orientation with respect to axis of mandible: linear (0), transversal (1)

Genus *Buhakia* MORLO, MILLER et EL-BARKOOKY, 2007

T y p e s p e c i e s. *Buhakia moghraensis* MORLO, MILLER et EL-BARKOOKY, 2007 (type locality: Wadi Moghra, Egypt).

D i a g n o s i s. See Morlo et al. (2007).

A g e. Basal Middle Miocene

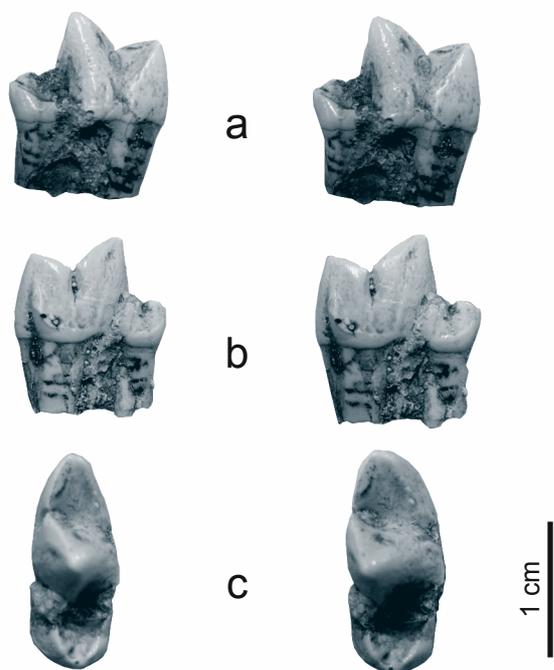
O t h e r s p e c i e s. *Buhakia hyaenoides* (MORALES et al., 2003), Arrisdrift, Namibia. *Buhakia* sp., Karungu, Kenya (Savage 1965), *Buhakia* sp., Grilental VI, Sperrgebiet, Namibia.

***Buhakia hyaenoides* (MORALES et al., 2003)**

Text-fig. 2

2003 *Africanictis hyaenoides*; Morales et al., p. 183.

H o l o t y p e. Left m2 (GSN AD 241'99) (Text-fig. 2).



Text-fig. 2. *Buhakia hyaenoides* (MORALES et al., 2003) from Arrisdrift, Sperrgebiet (Namibia). GSN AD 241'99 (holotype), left m2. a: lingual view, b: buccal view, c: occlusal view (stereo pairs).

Type locality. Arrisdrift, Namibia.

Age. Basal Middle Miocene.

Discussion. Morales et al. (2003) defined *Africanictis hyaenoides* at the locality of Arrisdrift (Namibia) on the basis of a suspected m1 with specialised features (loss of the metaconid, narrow, cutting trigonid and reduced talonid, although it possesses a hypoconid and entoconid) thereby differing from the type species of the genus, *Africanictis meini* (Morales et al. 1998b). Among the carnivores described by Morlo et al. (2007) from Wadi Moghra, Egypt, there was a new creodont, *Buhakia moghraensis*, based on a subadult mandible of which the dentition was interpreted to be dp4, m1 and m2. In particular, the last molar in this specimen is morphologically quite close to the Arrisdrift species, which is only slightly larger (Text-fig. 3). The Arrisdrift molar is unworn, and has open roots, indicating its subadult status, similar in age to the individual of *B. moghraensis*. The Arrisdrift molar has a basal cingulum on the buccal side of the paraconid which sweeps upwards along the anterior margin and swells such that occlusion with the talonid of the preceding molar (m1) is via this cingulum and the anteriormost extremity of the paraconid, a conformation visible in *Buhakia moghraensis* and frequent in hyaenodonts in which the molars are imbricated. Other characters common to the two species are the loss of the metaconid and the presence of cutting talonid and hypoconid.

***Buhakia* sp. I**

1965 *Metaterodon kaiseri* Stromer; Savage, pp. 270 – 271.

1998 *Isohyaenodon* sp.; Morales et al., p. 636.

2010 *Metapterodon kaiseri* Stromer; Lewis and Morlo, p. 551.

Locality. Karungu, Kenya.

Age. Early Miocene.

Material. Maxilla with P3 – M3 (Savage 1965: text-fig. 28, pl. 4, fig. 2, Lewis and Morlo 2010: fig. 26.5).

Discussion. The species *Metapterodon kaiseri* was recorded by Savage (1965) at the locality of Karungu. The maxilla from this site differs from that of *M. kaiseri* (holotype from Elisabethfeld) and *M. stromeri* from Langental (Morales et al. 1998a) by the scalene triangle occlusal outline of the M2, in which the protocone-parastyle is quite a bit shorter than the length of the parastyle-metastyle. This is related to the lesser development of the isthmus which unites the protocone to the base of the paracone. The M1 and P4 of the holotype of *M. kaiseri* also have more developed and individualised protocones than the Karungu form, and in addition, the latter form possesses a stronger, very robust P3, which contrasts with the extremely gracile P3 of *M. kaiseri* (holotype; Pl. 2, Fig. 4). Like Morales et al. (1998a) we conclude that none of the forms attributed by Savage (1965) to *Metapterodon*, belong to this genus.

An alternative interpretation of the Karungu maxilla is that it could correspond to a form akin to *Dissopsalis*, a genus which has a peculiar admixture of characters, among which we emphasize the strong development of the protocone in the upper molars (M1 – M2), which agrees with the relatively strong development of the talonid of m2. As we saw above, it is one of the few characters clearly observed in the genus *Buhakia*, which were described by Morlo et al. (2007) and Lewis and Morlo (2010). The dimensions of the Karungu maxilla suggest that it could correspond to the available lower dentition of *Buhakia*. Additionally, the Karungu maxilla falls outside the known range of variation of *Dissopsalis carnifex*, with which it shares the robustness of the premolars (P3 – P4), and the linear disposition of the buccal cusps of the upper molars (M1 – M2), such that the metacone is more developed than the paracone.

***Buhakia* sp. II**

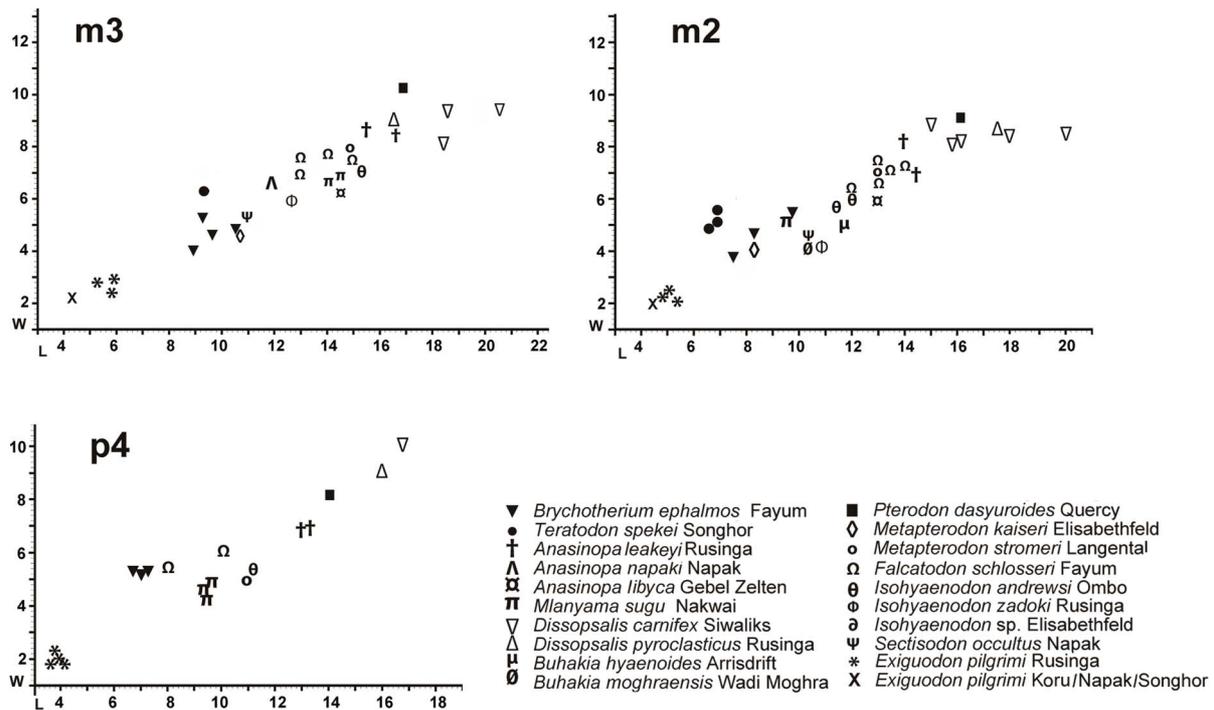
Pl. 1

Locality. Grillental VI, Sperrgebiet (Namibia).

Age. Early Miocene.

Material. Right mandible with the p2 – m1 and the alveolus of the m2 and the anteriormost part of the alveolus of m3 (GSN GT VI 22'17). Measurements p3 (L = 9 mm, W = 4.5 mm), p4 (L = 9.15 mm, W = 5 mm), m1 (L = ca. 8.3 mm, W = ca. 4.2 mm), alveolus m2 (L = 10 mm, W = 4.8 mm) (Pl. 1).

Description. GT VI 22'17 is a right mandible with the p2 – m1 and the alveolus of the m2 and the anteriormost part of the alveolus of m3. The front of the p2 and the lingual side of the m1 are broken. The talonid of the m1 is relatively short but it would have been broad, with a strong, tall hypoconid. The p4 is quite a bit bigger than the m1 with a well-developed, tall main cusp. The anterior and



Text-fig. 3. Bivariate plots of the lower teeth (m3 – m2) of small to medium sized Miocene hyaenodonts from African localities. Data source: Pilgrim (1912, 1932), Colbert (1935), Savage (1965), Barry (1988), Morales et al. (1998a, 2003, 2007, 2008, 2010), Holroyd (1999), Morlo et al. (2007), Rasmussen et al. (2009), Borths et al. (2016), Borths and Seiffert (2017).

posterior cristids are almost vertical and are well-marked, especially the anterior one. There is no anterior cuspid. The

talonid is short but relatively broad, and the hypoconid is strong and occupies the buccal half of the talonid, and a

Table 3. Character matrix of taxa analysed (see Table 3 for the corresponding list of characters and character states).

	1	10	20	26
Cimolestes magnus	0	0	0	0
Teratodon spekei	0	0	0	0
Masrasector nananubis	1	0	0	1
Brychotherium elphamos	1	0	0	1
Mlanyama sugu	1	0	0	1
Anasinopa leakeyi	1	0	0	1
Buhakia sp.	2	0	0	2
Dissopsalis carnifex	2	0	0	3
Leakitherium hiwegi	2	0	1	2
Pterodon africanus	2	1	1	3
Metapterodon spp.	2	0	0	1
Hyainailouros spp.	2	1	1	2
Falcatodon schlosseri	2	1	1	2
Isohyaenodon zadoki	2	1	1	3
Sectisodon markgrafi	3	1	2	3
Sectisodon occultus	3	2	2	3
Exiguodon pilgrimi	2	2	2	3

low crest forms the lingual border. A moderate cingulum is irregularly developed around the premolar, more marked on the anterior part of the tooth. The p3 is almost as large as the p4 but is lower with less vertical cristids. Like the p4 it has no anterior cuspid and the talonid is short, almost reduced to a posterior cingulum. The p2 has lost the anterior extremity but its basic morphology seems to be like that of the p3, and it is appreciably smaller. The two anterior premolars overlap and are oriented obliquely with respect to the p4. The mandibular ramus is deep and the symphysis very rugose, with its posterior margin at the level of the posterior root of the p3. On the buccal side of the jaw there are two foramina visible at half the height of the jaw beneath the gap between the p3 and p4. Of these the anterior one is strong and oval, the posterior one small and circular.

Discussion. The premolars of the Grillental VI jaw are robust and big, the two anterior premolars (p2 and p3) being only slightly smaller than the p4. The p4 is quite peculiar because of its tall main cusp with almost vertical, concave anterior cristid, and the absence of a paraconid. In effect, it is quite close in morphology to the p4 of *Dissopsalis carnifex* (Barry 1988: fig. 2) and *Dissopsalis pyroclasticus* (Savage 1965: pl. 3), even though the tooth is smaller than in these two species. In contrast if we attribute the p2 or p3 to *D. carnifex* (GSP 16036; Barry 1988: fig. 3) the differences from the Grillental specimen would be important. Unfortunately, in *D. pyroclasticus* the anterior premolars are not preserved although the alveoli suggest that they would have been large relative to the p4. It is possible that the p3 attributed to *Dissopsalis carnifex* mentioned above could be a P3 as it is morphologically close to the P3 in the maxilla from Karungu, here identified as *Buhakia* sp., sharing the presence of a weakly developed posterior cuspid, and above all a characteristic postero-buccal cingulum or basal swelling.

Some information can be obtained from *Anasinopa leakeyi* (Savage 1965) in which the p4 possesses a structure similar to that described in *Dissopsalis*, although it differs from it by the lower height of the main cusp and the less vertical anterior cristid, as well as the greater development of the talonid. The p2 and p3 of *D. pyroclasticus* have a more usual morphology similar to that in the Grillental VI specimen, even though, at least in the p3 the main cusp is lower than in the Namibian form. In conclusion, the mandible from Grillental VI has several features more specialised than in *Anasinopa leakeyi*, a characteristic of the tribe Dissopsalini, as we point out in this paper. The dimensions of the Grillental VI specimen are smaller than *Dissopsalis* or *Leakitherium hiwegi*, and could correspond closely to *Buhakia* (Morales et al. 2003, Morlo et al. 2007). The alveoli of the m2 in GT VI 22'17 measure about 11 mm, which suggests that the tooth would have been close in dimensions to the m2 of *B. moghraensis* or *B. hyaenoides*. However, in this genus the lower premolars are unknown, and as mentioned previously, they are poorly represented in the larger genus *Dissopsalis*. But, we can have a reasonable idea about the characters of the premolars in this group that we call Dissopsalini which are remarkably divergent from those of the very bunodont genus *Teratodon*, approaching the hyaenid pattern, tall and robust premolars. This morphological pattern is clearly

recognisable in the mandible from Grillental VI, from which we deduce that its inclusion in Dissopsalini is the most plausible hypothesis. In contrast, it differs in size from the species of *Dissopsalis* and *Leakitherium*, and is closer to species of *Buhakia*, which is for the moment, the only clear representative of this size in this tribe. For these reasons, and in the hope of finding new material in the Early Miocene sites of the Sperrgebiet, Namibia, we prefer to classify this fossil as *Buhakia* sp., following the same reasoning that we used for the controversial maxilla from Karungu. Nevertheless, some doubt remains concerning the specific identification of the two fossils.

Tribe Metapterodontini trib. nov.

Type genus. *Metapterodon* STROMER, 1926.

Diagnosis. Hyainailourinae with sectorial upper molars (M2 – M1) with the paracone and metacone subequal in size and fused together, nevertheless with a moderate vertical groove between the two cusps. It has a strong protocone united to the rest of the tooth by a long, narrow isthmus. Lower molars with metaconid, with unicuspidate talonid which is very reduced in the m3. Premolars gracile.

Included genera. Type genus only.

Genus *Metapterodon* STROMER, 1926

1967 *Pterodon* Blainville, 1839; van Valen, p. 252.

1985 *Pterodon* Blainville, 1839; Dashzeveg, p. 234.

Type species. *Metapterodon kaiseri* STROMER, 1926 (with type locality: Elisabethfeld, Sperrgebiet, Namibia). Holotype is left maxillary fragment with M2 – P3 (BSPG Nr.1926X1).

Age. Early Miocene.

Diagnosis. *Metapterodon*, being the only known genus in the tribe, has the same diagnosis as the tribe.

Other species. *Metapterodon stromeri* MORALES, PICKFORD et SORIA, 1998 from the Early Miocene of Langental, Sperrgebiet, Namibia.

Metapterodon aff. *stromeri* MORALES et al., 1998a

Pl. 2, Fig. 1

Locality. Napak V, Uganda.

Age. Early Miocene.

Material. Right M2 (L = 12.8 mm, W = 12.2 mm) (NAP V 121'08).

Description. The occlusal outline is an obtuse isosceles triangle, in which the two equal sides are formed of the posterior surface (protocone-parastyle) and the buccal surface (parastyle-metastyle), while the unequal side is longer and extends from the paracone to the metastyle. Outstanding is the strong development of the protocone, in the shape of a pointed clog, which extends well forwards. The parastyle is strong and basally is contiguous with the moderately well-developed buccal cingulum. The paracone and metacone are largely fused together, but are slightly

separated at their apices by a shallow incision on the buccal surface and are transversely compressed. The metastyle is similar in size to the paracone-metacone. The lingual cingulum is weak.

Discussion. The occlusal morphology and the great development of the protocone (Pl. 2, Figs 1–2) approach this molar to that of *Metapterodon kaiseri* STROMER, 1926 and *Metapterodon stromeri* MORALES et al., 1998a. It differs from the former by its greater dimensions (ca. 10%) and by the greater development of the parastyle. It differs from *M. stromeri* by its smaller dimensions (ca. 15%; Text-fig. 4).

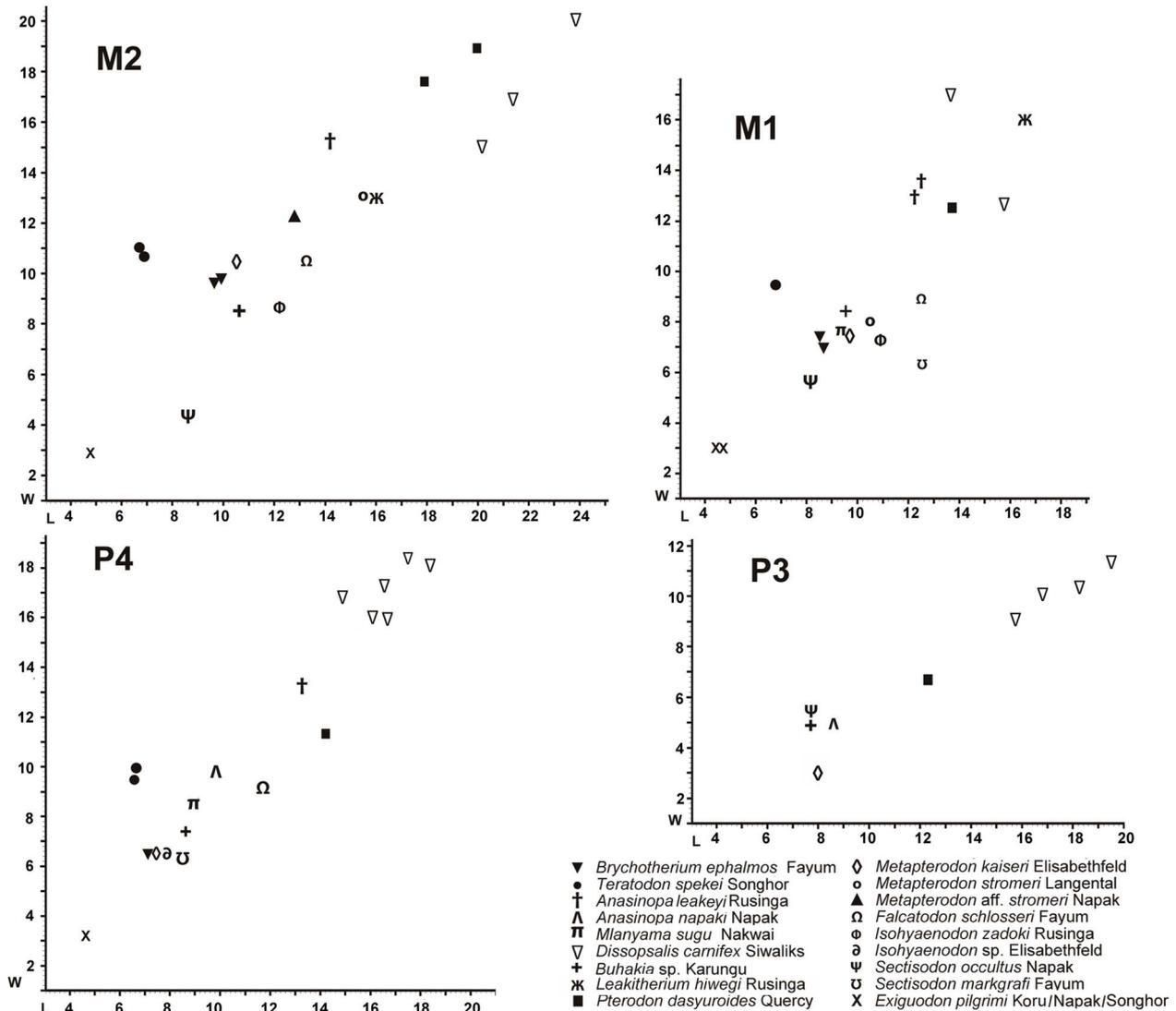
Holroyd (1999) included three species from the Eocene-Oligocene of the Fayum, Egypt, in *Metapterodon*, but she raised reasonable doubts concerning the generic attribution. In particular, in the two species represented by upper dentitions (and thus comparable to the holotype of *Metapterodon kaiseri*) there are important differences, noted in the descriptions by Holroyd (1999: 12, 14). According to this author, the molars of *M. schlosseri* and *Metapterodon*

markgrafi are strongly modified for cutting, with a small protocone in the first species and none in the second, and in addition, the two species possess long metastyles. These differences prevent the use of *Metapterodon* as a possible genus for these Palaeogene forms. In contrast, as we will see later, the species could be related to *Isohyaenodon*, an idea indirectly supported by Savage (1965) who included in *I. andrewsi* one of the mandibles later identified as *M. schlosseri* by Holroyd (1999).

Tribe Hyainailourini GINSBURG, 1980

Type genus. *Hyainailouros* BIEDERMANN, 1863.

Diagnosis. Hyainailourinae with sectorial upper molars (M2 – M1) with the paracone somewhat larger than the metacone, generally fused together, some genera retain a moderate vertical sulcus between the two cusps, but which can be completely lost. Protocone is in general reduced, in some genera it is relictual or even absent. Lower molars



Text-fig. 4. Bivariate plots of the upper teeth (M2 – P3) of small to medium sized Miocene hyaenodonts from African localities. Data source: Pilgrim (1912, 1914, 1932), Colbert (1935), Savage (1965), Barry (1988), Morales et al. (1998a, 2007), Holroyd (1999), Rasmussen et al. (2009), Borths et al. (2016), Borths and Seiffert (2017).

without metaconid and with talonid very reduced or absent.

Included genera. Miocene: *Hyainailouros* BIEDERMANN, 1863, *Isohyaenodon* SAVAGE, 1965, *Sectisodon* gen. nov. and *Exiguodon* gen. nov. Eocene (after Solé et al. 2015): *Akhnatenavus* HOLROYD, 1999, *Kerberos* SOLÉ et al., 2015, *Parapterodon* LANGE-BADRÉ, 1979, *Pterodon* BLAINVILLE, 1839, *Falcatodon* gen. nov.

Genus *Hyainailouros* BIEDERMANN, 1863

Type species. *Hyainailouros sulzeri* BIEDERMANN, 1863 (with type locality Veltheim, Switzerland).

Diagnosis. See Ginsburg (1980).

African species. *Hyainailouros napakensis* GINSBURG, 1980 and *Hyainailouros osteothlastes* (SAVAGE, 1973).

Hyainailouros napakensis GINSBURG, 1980

Text-fig. 5

- 1965 *Pterodon africanus* Andrews; Savage, p. 272.
1965 *Pterodon nyanzae* sp. nov.; Savage, p. 274.
1999 *Pterodon nyanzae* Savage; Holroyd, p. 7.
2009 *Hyainailouros* sp.; Rasmussen and Gutiérrez, p. 35.
2010 *Hyainailouros napakensis* Ginsburg; Lewis and Morlo, p. 547.
2010 *Hyainailouros nyanzae* Savage; Lewis and Morlo, p. 547.

Holotype. Left maxilla with P4 – M2 (NHMUK M 19090) described and figured by Savage (1965).

Type locality. Napak I, Uganda.

Age. Early Miocene.

Diagnosis. See Ginsburg (1980).

Other localities. Ombo, Rusinga, Kenya (Savage 1965), Losodok, Meswa Bridge, Kenya (Rasmussen and Gutiérrez 2009). With reserve, given the incomplete nature of the material, we may include the localities of Grillental and Elisabethfeld, Namibia (Morales et al. 2007).

Hyainailouros sulzeri BIEDERMANN, 1863

Text-fig. 6

- 1965 *Pterodon nyanzae* sp. nov.; Savage, p. 274.

Locality. Arrisdrift, Namibia. Morales et al. (1998b) and Morales et al. (2003) referred an M1 (Text-fig. 5c), an upper canine and a mandible with m1 and unerupted molar (Text-fig. 6) to this species.

Age. Basal Middle Miocene.

Hyainailouros osteothlastes (SAVAGE, 1973)

- 1920 *Hyaena* sp. indet.; Fourtau, p. 91.
1947 *Hyaenaelurus fourtaui*; Koenigswald, p. 292.
1973 *Megistotherium osteothlastes*; Savage, pp. 485–486.
1989 *Megistotherium osteothlastes* Savage; Rasmussen et al., p. 443.

- 2007 *Hyainailouros bugtiensis* Pilgrim; Morlo et al., p. 147.
2010 *Megistotherium osteothlastes* Savage; Lewis and Morlo, p. 550.

Holotype. Skull (NHMUK M 26173).

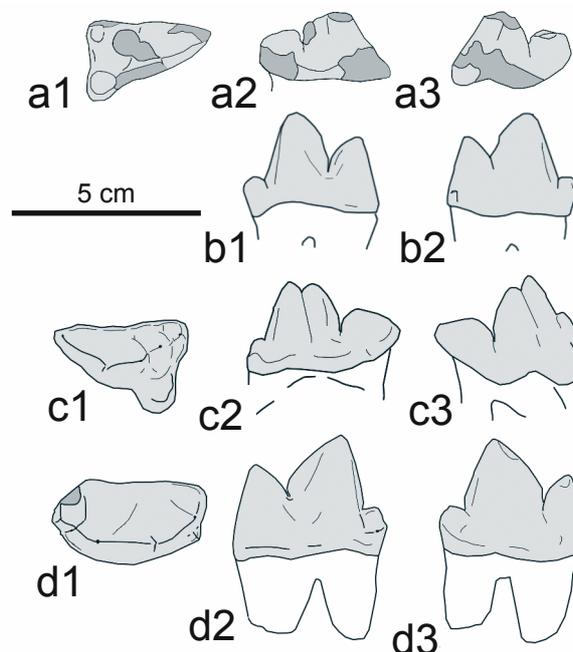
Type locality. Gebel Zelten, Libya.

Diagnosis. See Savage (1973).

Age. Basal Middle Miocene.

Other localities. Wadi Moghara, Egypt (Fourtau 1920, Koenigswald 1947, Rasmussen et al. 1989, Morlo et al. 2007); Cheparawa, Muruyur Formation (ca. 14.5 Ma), Tugen Hills, Kenya (Morales and Pickford 2008); Fort Ternan, Kenya (ca. 13.7 Ma) (Savage 1973); Bartule, Ngorora Formation, Member A (ca. 13–12.5 Ma) and Kabarsero, locality 2/10, Ngorora Formation, Member D (ca. 12 Ma), both Kenya (Morales and Pickford 2005).

Discussion. *Hyainailouros* has a long and complicated history of study, influenced by two opposing aspects; on the one hand, it is quite rare in the fossil record, and on the other, its gigantic size makes it easily recognisable even with little material. The sample of the type species described from the Swiss locality at Veltheim by Biedermann (1863) was revised by Helbing (1925), to which he added other fossils from Europe and Asia. Later, Beaumont (1970) revised the fossils from the type locality, and fossils from Chevilly Aérotrain, France, were added to the hypodigm (Ginsburg 1980) which are the most complete dental remains



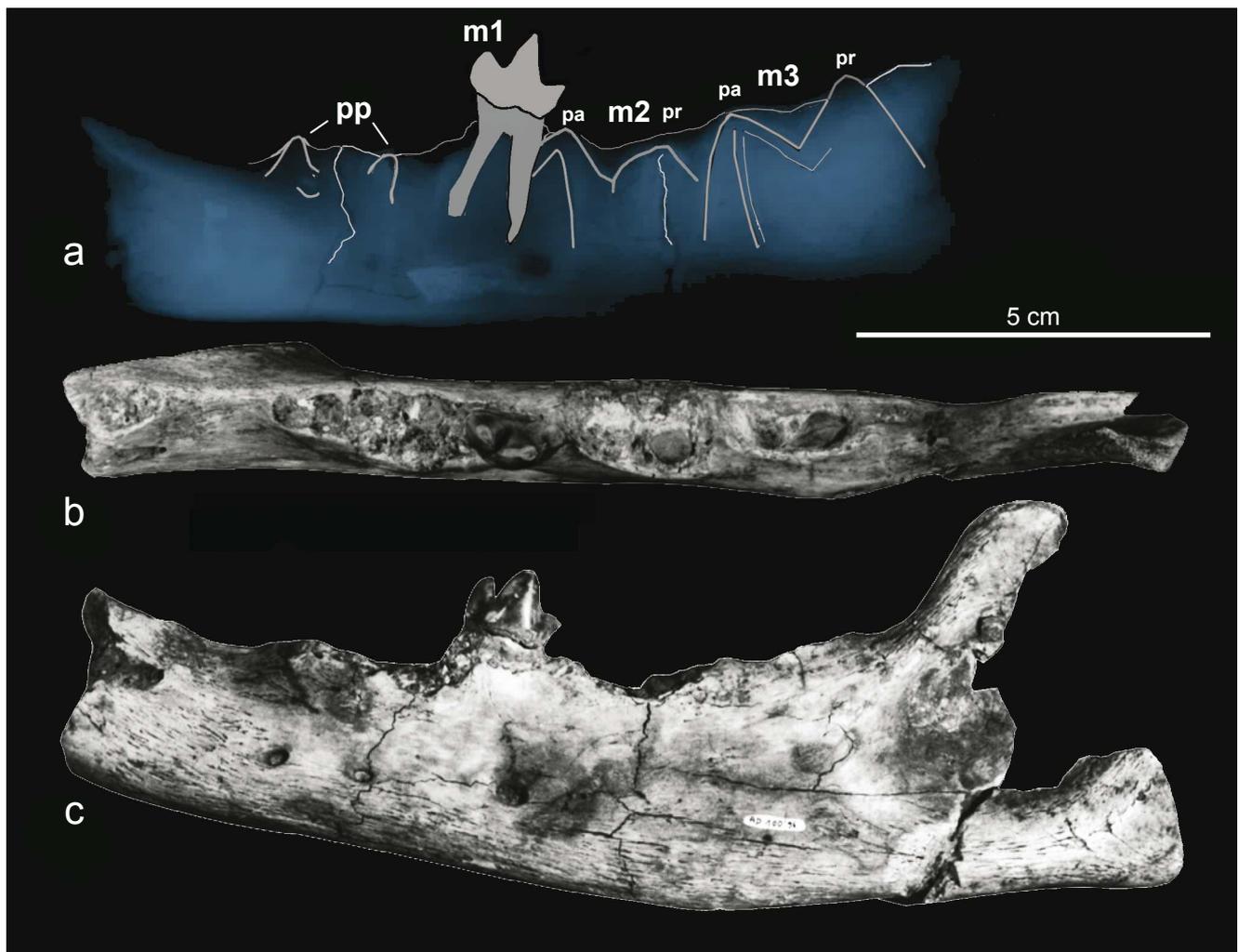
Text-fig. 5. *Hyainailouros napakensis* GINSBURG, 1980. a: NHMUK M 19090, left M1 from Napak (Uganda), 1: occlusal view, 2: buccal view, 3: lingual view. b: KNM-ME 22, left m2 from Meswa Bridge (Kenya), 1: buccal view, 2: lingual view. *Hyainailouros sulzeri* BIEDERMANN, 1863. c: GSN AD 375'94, right M1 from Arrisdrift (Namibia), 1: occlusal view, 2: buccal view, 3: lingual view. d: MNHN Tav 167, right m2 from Tavers (France), 1: occlusal view, 2: buccal view, 3: lingual view.

associated with elements of the postcranial skeleton. Two additional Miocene genera were attributed to *Hyainailouros* on the basis of their large dimensions and their resemblance to this genus; the first was *Megistotherium* SAVAGE, 1973 and the second was *Sivapterodon* erected by Ginsburg (1980) for the species *Hyainailouros lahirii* PILGRIM, 1932. The latter species is known only by a fragment of mandible with m2 – m3 close in size to *Hyainailouros sulzeri*. According to its creator, the genus is based on the greater reduction of the paraconid in the molars (m2 – m3). However, the two molars are poorly preserved “both of them considerably worn and damaged in their anterior halves” (Pilgrim 1932: 170) which prevents us from taking this character seriously, and the same applies to the apparent robusticity of the m3, which could have been over-estimated due to the damage to the anterior part of the crown. The great reduction of the talonid of the m3, which is almost obsolete, is comparable to that in the fossils of *H. sulzeri* from Chevilly Aérotrain. In the current state of our knowledge, it is difficult to sustain the validity of *Sivapterodon*.

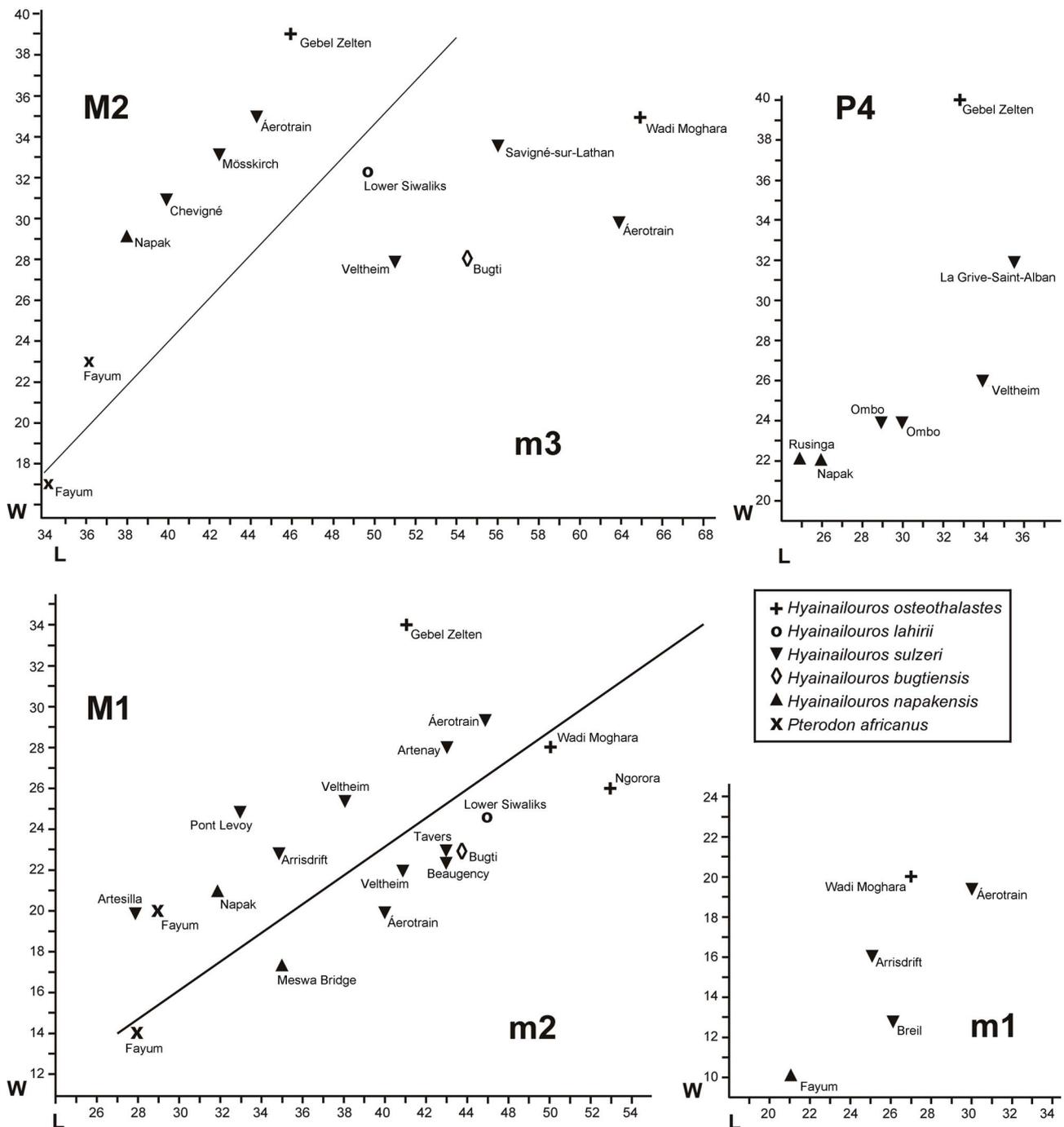
Megistotherium was erected by Savage (1973) for cranial and post-cranial material collected at Gebel Zelten, Libya. The holotype is a magnificent skull which unfortunately lacks most of the dentition, preserving only the almost complete

right P2 and parts of the two M2s. As such, comparisons with *Hyainailouros* are limited. The dimensions of the molars (M1 – M2) estimated from the roots clearly exceed those of the largest specimens of *Hyainailouros sulzeri* (Text-fig. 7). Despite the greater dimensions, there are no other criteria which support of generic distinction between *Megistotherium osteothlastes* and the type species of *Hyainailouros*. In addition, Ginsburg (1980) realised that some of the post-cranial elements attributed to *Megistotherium* by Savage (1973) belong in fact to a large species of *Amphicyon*. Nevertheless, the metatarsal UB 20758 (Savage 1973: fig. 17) corresponds closely in morphology and dimensions to the specimen from Chevilly Aérotrain illustrated by Ginsburg (1980). Morlo et al. (2007) and Lewis and Morlo (2010) maintained the validity of these two genera, but unconvincingly.

The scarcity of material renders it difficult to obtain a reliable estimate of the range of metric variation of the dentition (Text-fig. 7). The variation, with exceptions, is not very great especially when compared to other large hyaenodonts such as *Pterodon dasyuroides* (Lange-Badré 1979). The smaller form comprises *Hyainailouros napakensis*, plus an M1 from the Spanish site of Artesilla (Azanza et al. 1993) and an m2 (KNM ME 12) from Meswa Bridge, Kenya



Text-fig. 6. *Hyainailouros sulzeri* BIEDERMANN, 1863 from Arrisdrift, Sperrgebiet, Namibia. GSN AD 106'99, left mandible with m1. a: radiograph showing unerupted m3 and m2, b: occlusal view, c: buccal view. pp = undetermined premolars, pa = paraconid, pr = protoconid.



Text-fig. 7. Bivariate plots of the upper teeth (M2, M1, P4) and lower teeth (m3, m2, p4) of large Miocene hyaenodonts from Eurasian and African localities. Data source: Stromer (1926), Savage (1965), Barry (1988), Ginsburg (1999), Holroyd (1999), Morales et al. (2003, 2007, 2008, 2010), Morlo et al. (2007), Rasmussen and Gutiérrez (2009), Borths et al. (2016).

Rasmussen and Gutiérrez (2009). *Hyainailouros napakensis* is also the oldest known species in the genus, to which can be attributed an m1 from Meswa Bridge (KNM ME 12) classified as *Hyainailouros* sp. by Rasmussen and Gutiérrez (2009: fig. 15C) which, in our opinion, corresponds better with an m2, the dimensions of which accord well with the Napak species (Text-fig. 5b). It is also possible that a posterior fragment of an m3 from Losodok attributed by the same authors to *Hyainailouros* sp. can be included in *H. napakensis*. The maxilla of *H. napakensis* is only slightly

smaller than the specimen of *Hyainailouros sulzeri* from Arrisdraft, Namibia, comparisons between the samples being limited to the M1, which are close in morphology, with the metacone and paracone well separated from each other, with a strong parastyle and the protocone not reduced. However, two significant differences are highlighted; 1) in *H. napakensis* the protocone is located in a very anterior position, in front of the parastyle, whereas, in the Arrisdraft fossil, the protocone is more distally positioned in front of the protocone; 2) in *H. sulzeri* from Arrisdraft the sectorial

part of the M1, formed of the paracone+metacone-metastyle is more compressed transversely than in *H. napakensis* (Text-fig. 5c). In both these features, the M1 from Arrisdrift approaches the M1 from Artesilla (Azaña et al. 1993). Furthermore, the juvenile mandible from Arrisdrift (GSN AD 106'99) with the unerupted molar (Morales et al. 2003) indicates the presence of a large m3, approaching 50 mm in length, a size which corresponds well with *Hyainailouros sulzeri*. It is notable that the locality of Artesilla has yielded mammals with clear African affinities (Azaña et al. 1993, Pickford and Morales 1994, Morales et al. 2001).

The opposite extreme of the size spectrum is occupied by the huge species *Megistotherium osteothlastes*. The upper dentition is known only from the holotype skull, which, as mentioned previously, is incomplete and damaged, measurements being obtained from the roots or alveoli. However, the specimen indicates that the teeth were large, much longer than other specimens of *Hyainailouros* (Text-fig. 7). Lower teeth attributed to this species were published by Rasmussen et al. (1989) and Morales and Pickford (2005) from Wadi Moghara, Egypt, and Ngorora, Kenya, respectively. The differences in dimensions from the maximal values of *H. sulzeri* are not great, but they fall outside the range of variation of this species. It is possible that the metric differences could correspond to extreme intra-specific variability, within which the specimens of *H. osteothlastes* would be the largest (perhaps males with hypertrophic canines), but it is also possible that, without denying the existence of dimorphism or great variability, there could be two or three species with overlapping dimensions. Morphological comparisons do not resolve the problems because of the meagre quality of the teeth of *H. osteothlastes*, impossible to observe in the upper dentition, and very limited for the lower teeth. The mandible from Wadi Moghara described by Rasmussen et al. (1989) has an m3 missing the posterior part, and an m2 with a reduced talonid, similar to the m2 of *H. sulzeri* and to an m2 from Ngorora (Morales and Pickford 2005).

Genus *Falcatodon* gen. nov.

Type species. *Metapterodon schlosseri* HOLROYD, 1999.

Derivatio nominis. From “falcate”, the cutting sword used by the Iberians.

Diagnosis. Medium sized Hyainailourinae, differing from *Metapterodon* by the reduction of the protocone in the upper molars (M1 – M2), which is located in a very anterior position. It differs from *Hyainailouros* by the more sectorial morphology of the upper molars, with more advanced fusion of the paracone-metacone with, nevertheless, a groove separating the cusps visible in the M1. Lower molars sectorial with reduced talonid and without a metaconid. It differs from *Isohyaenodon*, *Sectisodon* and *Exiguodon*, by the lesser reduction of the protocone in the upper molars which, above all, retain a stretched out subtriangular occlusal outline.

***Falcatodon schlosseri* (HOLROYD, 1999)**

Holotype. Left dentary containing canine alveolus, p2 – m3 (DPC 4877).

Type locality. Quarry V, upper sequence of Jebel Qatrani Formation, Fayum Province, Egypt.

Age. Rupelian (Seiffert 2010).

Diagnosis. The same as for the genus.

Discussion. Holroyd (1999) recognized that “although the Eocene-Oligocene species referred here to *Metapterodon* may ultimately prove to be a separate genus from *M. kaiseri*, I have here united them in an attempt to demonstrate their distinctiveness from both *Hyaenodon* and *Pterodon*, and their probable closer relationship to one another than to contemporaneous species of *Pterodon*”. The weaker development of the isthmus between the protocone and paracone and the more distal position of the protocone in the upper molars of *Falcatodon schlosseri* are closer to *Isohyaenodon zadoki* than to *Metapterodon* spp. but in any case, are different from both genera.

Genus *Isohyaenodon* SAVAGE, 1965

1985 *Leakitherium* Savage; Dashzeveg, p. 234.

1999 *Metapterodon* Stromer; Holroyd, p. 11.

Type species. *Isohyaenodon andrewsi* SAVAGE, 1965 (holotype: right mandible with m1 – m3 (M-15048); type locality: Ombo, Kenya).

Diagnosis. See Morales et al. (1998a).

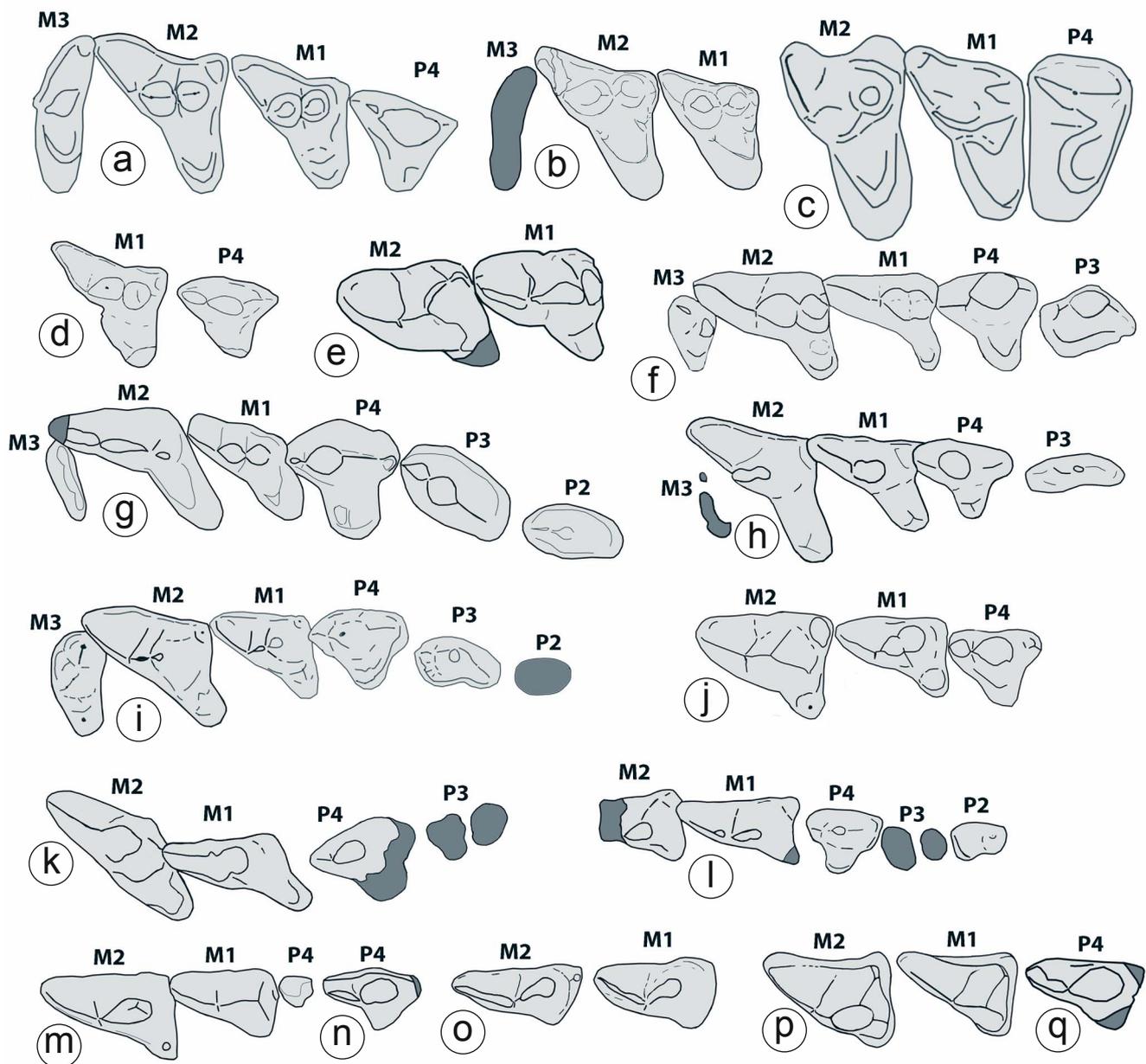
Other species. *Isohyaenodon zadoki* SAVAGE, 1965 (= *Isohyaenodon matthewi* SAVAGE, 1965) and *Isohyaenodon* sp. (Morales et al. 2008).

N.B. Part of Savage's (1965) hypodigm of *Isohyaenodon matthewi* (CMF 4060 NHMUK M 2947), left m2 in a mandible fragment, fits perfectly onto a specimen attributed by the same author to *Isohyaenodon andrewsi* (CMF 4023 NHMUK M 2948) a left m3 in a mandible fragment. Both fragments came from site R3, Rusinga Island and represent a single individual.

Discussion. Soon after its creation, this genus, as was mentioned in the introduction, was the subject of discussion by van Valen (1967) and subsequently by Morales et al. (1998a, 2007) and Lewis and Morlo (2010). The holotype mandible is similar in dimensions (at least the m3) to *Metapterodon stromeri* from the locality of Langental (Morales et al. 1998a). However, there are morphological reasons for separating the two species, *I. andrewsi* possesses a slightly more sectorial m3, with a moderate tendency to enlarge the protoconid. The two species share the absence of the metaconid and the greatly reduced talonid in the m3. But in *M. stromeri* the m2 retains a more developed talonid. Reasonably, the mandible of *I. andrewsi*, which shows a greater sectorial tendency, could correspond to the upper dentitions more sectorial than the *Metapterodon* species. Borths et al. (2016: supplementary table 2) support the speculation that *Isohyaenodon andrewsi* and *Metapterodon* represent the lower and upper dentition of the same taxon based on the size of the occluding carnassial portion of the upper and lower dentitions. However, very sectorial lower teeth are known in Africa from the Late Eocene in the Fayum succession, the case with the species previously

identified as *Metapterodon schlosseri* by Holroyd (1999). This was realised by Savage (1965), when he included in *Isohyaenodon* one of the Fayum mandibles described by Andrews (1906). The upper teeth of this species are known from a single maxilla (Holroyd 1999: fig. 8B) which differs from species of *Metapterodon* by the reduction of the protocone and the extension of the metastyle in the M1 – M2 (Text-fig. 8k). This morphological pattern can be seen in the form described by Savage (1965: text-fig. 29, pl. 4, fig. 2) as *Metapterodon zadoki* from the site of Rusinga, Kenya,

which could correspond to the lower dentition of the species *Isohyaenodon matthewi* from the locality of Songhor, Kenya (Savage 1965: text-figs 41–43). Apparently, *M. zadoki* seems to have progressed further in the reduction of the protocone of the molars, as was noted by Savage (1965), which are also more robust and without a parastyle (Pl. 3, Fig. 1). To a certain extent, these characters approach *Isohyaenodon* to the new genus *Sectisodon* gen. nov., but the difference in robustness of the M1 is more than noticeable. It is evident that the solution is not easy, as there exists a whole range of



Text-fig. 8. Drawings of upper dentition in occlusal view of African Miocene Hyainailourinae. Comparison with other selected Hyaenodontida taxa. a: *Brychotherium ephalmos*, b: *Anasinopa leakeyi*, c: *Teratodon spekei*, d: *Mlanyama sugu*, e: *Leakitherium hiwegi*, f: *Buhakia* sp. from Karungu, g: *Dissopsalis carnifex*, h: *Metapterodon stromeri*, i: *Pterodon dasyuroides*, j: *Hyainailouros napakensis*, k: *Falcatodon schlosseri*, l: *Sectisodon markgrafi*, m: *Isohyaenodon zadoki*, n: *Isohyaenodon* sp. from Elisabethfeld, o: *Sectisodon occultus*, p–q: *Exiguodon pilgrimi*, p: from Napak, q: from Koru.

morphologies in the upper teeth which do not correspond directly to the sectorial lower teeth. Thus, we propose to restrict the species content of *Isohyaenodon* to *I. andrewsi* and *Isohyaenodon zadoki* (= *I. matthewi*) from Kenya, as well as *Isohyaenodon* sp. (Pl. 3, Fig. 2) from Elisabethfeld, Namibia (Morales et al. 2008) in the hope that new fossil finds may clarify the characteristics of this genus.

Genus *Sectisodon* gen. nov.

Type species. *Sectisodon occultus* sp. nov. (with type locality Napak V, Uganda).

Derivatio nominis. From the Latin “sectis” meaning cutting.

Diagnosis. Hyainailourinae of small dimensions, M1 and M2 of similar length. M2 with paracone and metacone fused together, tall and pointed. Protocone very reduced, flattened and extending basally beyond the base of the paracone. Anterior cingulum with a well-defined parastyle with a moderate buccal cingulum. M2 and M1 with the metastyle quite a bit longer than the paracone-metacone. P3 short, with tall main cusp, posterior cusplet moderate, and much reduced protocone. Basal lingual cingulum strong, weaker on the buccal side. Lower molars with protoconid bigger than the metaconid, m2 with talonid present, much reduced in the m3.

Other species. *Sectisodon markgrafi* (HOLROYD, 1999), Fayum, Egypt.

***Sectisodon occultus* sp. nov.**

Pl. 4

2007 *Isohyaenodon zadoki* (Savage, 1965); Morales et al., pp. 72–74.

Holotype. Right M2 (UM NAP V 178'08).

Type locality. Napak V, Uganda.

Age. Early Miocene.

Other localities. Napak I and Napak IV, Uganda.

Description. NAP IV 72'04, right P3 (L = 7.75 mm, W = 5.46 mm, H paracone = 7.01 mm). This is a narrow premolar with the main cusp tall and sharp. There is a small posterior cusplet and a well-marked basal cingulum completely encircling the tooth. The protocone is reduced to a lingual bulge in the middle of the tooth joined to the cingulum and quite a bit deeper than the base of the main cusp. The morphology is analogous to that seen in the protocones of the molars.

NAP IV 01'09, right M1 (L = 8.1 mm, W = 5.58 mm, H paracone = 6.19 mm, metastyle length = 3.63 mm). Short molar with tall cusps. Paracone and metastyle of similar size. The protocone is greatly reduced, flattened and extending low down beyond the base of the paracone. Reduced parastyle included in the anterior cingulum. Basal cingula almost imperceptible. The molar has a vertical wear facet on the lingual surface of the paracone and the metastyle (Pl. 4, Fig. 2a).

NAP V 178'08, right M2 (L = 8.57 mm, W = 4.32 mm, H paracone = 5.52 mm, Mestastyle length = 3.85 mm). This specimen is morphologically similar to the preceding

one, similar in length, but narrower and with lower cusps. The parastyle and protocone seem to be quite big and the metastyle elongated. There is a small interstitial facet at the posterior part of the base of the metastyle (Pl. 4, Fig. 3a) probably produced by contact with a small M3.

Discussion. *Sectisodon* represents a more advanced sectorial adaptation than other hyaenodonts from the Miocene of Africa, with the exception of *Exiguodon*. The upper molars (M1 – M2) almost lack protocones, which differentiates them from those of *Metapterodon*, in which the M2 has a hyper-developed protocone. With respect to *Exiguodon* described in this work, apart from the reduction of the protocone in the upper molars, the morphological differences are important, in particular the strong development of the cingulum and the buccal platform that occurs in this genus.

***Sectisodon markgrafi* (HOLROYD, 1999)**

1909 ?*Metasinopa*; Osborn, p. 423.

1965 *Metasinopa* (?); Savage, p. 264.

1999 *Metapterodon markgrafi*; Holroyd, p. 11.

Holotype. Left maxilla containing alveoli for C – P1, roots of P2 – P3, partial P4, M1 and partial M2 (AMNH 14452).

Type locality. Fayum, Egypt.

Diagnosis. See Holroyd (1999).

Discussion. As defined by Holroyd (1999) *Sectisodon markgrafi* possesses highly sectorial molars with complete fusion of the paracone-metacone and strong reduction of the protocone, which is nevertheless visible in occlusal view. It is quite a bit larger than the Napak species, and the greater development of the protocone in the upper molars differentiates it from *S. occultus*.

Genus *Exiguodon* gen. nov.

Type species. *Hyaenodon (Isohyaenodon) pilgrimi* SAVAGE, 1965.

Derivatio nominis. From the Latin “exiguus” meaning exiguous.

Diagnosis. Hyainailourinae of diminutive dimensions, lower molars (m3 – m2) with greatly reduced talonid; protoconid and paraconid similar in size. Paraconid of the molars lingually oriented. M2 and M1 close in size and morphology. Occlusal outline sub-triangular, with greatly reduced protocone, which appears like an antero-lingual cingulum which extends anteriorly and buccally. Presence of a strong parastyle in an antero-buccal position, united to the apex of the paracone by a well defined crista. The buccal cingulum borders a wide buccal platform, particularly large in the M2. Paracone tall and narrow, elongated blade-like metastyle. P4 broadened, with reduced protocone and presence of a notch between the main conical cusp and the blade-like posterior cusp.

***Exiguodon pilgrimi* (SAVAGE, 1965)**

Pls 5, 6

1965 *Hyaenodon (Isohyaenodon) pilgrimi*; Savage, p. 284

- 1998 *Isohyaenodon pilgrimi* Savage; Morales et al., p. 636.
 2007 *Isohyaenodon pilgrimi* Savage; Morales et al., p. 72.
 2010 *Isohyaenodon pilgrimi* Savage; Lewis and Morlo, p. 548.

Holotype. Mandible with both rami and part of the neurocranium attached to the seven cervical vertebrae (NHMUK M 19100a-c; Pl. 5).

Type locality. Site R 114, (Whitworth's Pothole), Rusinga Island, Kenya.

Age. Early Miocene.

Diagnosis. The same as for the genus.

Other localities. Songhor and Koru, Kenya and Napak IV, Uganda.

Description of Koru fossils. KO38'04 (Pl. 6, Fig. 1) is a right mandible with m3 (L = 4.7 mm, W = 2.3 mm) and m2 (L = 4.4 mm, W = 2 mm). In the m3 the paraconid and protoconid are robust, sub-equal in size and morphology. The paraconid is located in quite a lingual position, such that the molar appears to be inclined with respect to the antero-posterior axis of the dental series. There is no sign of a metaconid, and the talonid is reduced to a small tubercle at the base of the crown in a posterior-lingual position. The notch that separates the paraconid from the protoconid is deep. In the paraconid a basal vertical tubercle develops on the antero-buccal surface that serves to lodge the talonid of the m2. The buccal surface shows a vertical wear facet, while lingually a deep valley is developed at the base of the paraconid-protoconid. The m2 is somewhat worn anteriorly, and is smaller than the m3, although its morphology is similar. The talonid is quite well-developed and possesses a small sharp hypoconid.

KO 466'04 (Pl. 6, Fig. 3) is a left P4 (L = 4.6 mm, W = 3.2 mm). The protocone and the postero-buccal border are lightly worn. It is quite sectorial with a reduced protocone located in front of the main cusp, which is conical. The posterior cusplet is strongly developed and approaches the morphology of the metastyle of the upper molars. There is a clearly visible notch between the protocone and the posterior cusp.

Discussion. The upper dentition attributed to *E. pilgrimi* differs completely from the rest of the known morphotypes in species of hyaenodonts from the Miocene of Africa, which prompts us to erect a new genus. *Exiguodon pilgrimi* possesses a highly original upper dentition, as shown in the diagnosis above, which is based mainly on the maxilla from Napak NAP IV-64 (Pl. 6, Fig. 2), described and figured by Morales et al. (2007: figs. 1-3 and 3-1), and which, combined with the much smaller dimensions of the molars, can be summarised as a combination of primitive features such as the presence of a strong buccal cingulum and a broad buccal shelf, with more derived ones such as the extreme reduction of the protocone, the broadening of the metastyle and the compression of the paracone.

Systematic analysis of African Miocene hyaenodonts

The systematics and phylogenetic relationships of most of the Miocene hyaenodonts have been the subject of several

Table 4. Summary of the systematics of the Miocene African hyaenodont species proposed in this paper. Taxa described in present paper in bold.

Original determination	Locality	Holotype	Other specimens	References	Present determination
<i>Metastinopa napaki</i>	Napak I	Mandible m3	Maxilla P4 – P3	Savage (1965)	<i>Anasinopa napaki</i>
<i>Africanictis hyaenoides</i>	Arrisdrift	m2		Morales et al. (2003)	<i>Buhakia hyaenoides</i>
<i>Metapterodon kaiseri</i>	Karungu		Maxilla P3 – M2	Savage (1965)	<i>Buhakia</i> sp.
<i>Pterodon africanus</i>	Napak I	Maxilla P4 – M2		Savage (1965), Ginsburg (1980)	<i>Hyainailouros napakensis</i>
<i>Pterodon nyanzae</i>	Ombo	P4		Savage (1965)	<i>Hyainailouros napakensis</i>
<i>Hyainailouros fourtaui</i>	Wadi Moghara	P4		Koenigswald (1947)	<i>Hyainailouros osteothlastes</i>
<i>Megistotherium osteothlastes</i>	Gebel Zelten	Skull		Savage (1971)	<i>Hyainailouros osteothlastes</i>
<i>Hyainailouros</i> sp.	Mestwa Bridge		m2	Rasmussen and Gutiérrez (2009)	<i>Hyainailouros napakensis</i>
<i>Metapterodon schlosseri</i>	Fayum	Mandible p2 – m3	Maxilla P2, P4 – M2	Holroyd (1999)	<i>Falcatorodon schlosseri</i>
<i>Metapterodon zadoki</i>	Rusinga	Maxilla M1 – M2		Savage (1965), Morales et al. (1988)	<i>Isohyaenodon zadoki</i>
<i>Isohyaenodon matthewi</i>	Songhor	Mandible m3		Savage (1965), Morales et al. (1988)	<i>Isohyaenodon zadoki</i>
<i>Metapterodon markgrafi</i>	Fayum	Maxilla P4 – M2		Holroyd (1999)	<i>Sectisodon markgrafi</i>
<i>Isohyaenodon zadoki</i>	Napak I		Mandible m3 – m2	Morales et al. (2007)	<i>Sectisodon occultus</i>
<i>Isohyaenodon pilgrimi</i>	Rusinga	Mandible p2 – m3	M1 (Songhor)	Savage (1965)	<i>Exiguodon pilgrimi</i>
<i>Isohyaenodon pilgrimi</i>	Napak IV		Maxilla M2 – M3	Morales et al. (2007)	<i>Exiguodon pilgrimi</i>

recent publications, including in-depth scenarios by Solé et al. (2014, 2015), and Borths et al. (2016). Our analysis focuses on the Miocene species, and is thus more limited in its scope than previous analyses, which were useful in a general way, but in which the phylogenetic relationships of Miocene hyaenodonts were quite limited. The description of additional creodont fossils from the Early Miocene of Africa substantially alters the systematics of the group, not only because there are new genera in the samples, but also because the content of several existing taxa needed to be modified (Tab. 4). In particular, the genera *Metapterodon* and *Isohyaenodon* are markedly affected by these changes. The former, *Metapterodon*, is now restricted to the Miocene, separated from the Palaeogene species from the Fayum, described by Holroyd (1999). One of them is classified in the new genus *Sectisodon* as *S. markgrafi*, but the other two, especially the relatively abundant *M. schlosseri*, is attributed to the new genus *Falcatodon* as its type species. For this reason, even though the genus is currently known only from the Palaeogene, it is included in this revision. The second affected genus, *Isohyaenodon*, poses special problems. On the one hand, the type species *I. andrewsi* came from relatively young deposits (Ombo, Kenya ca. 15 Ma), and was based on a young adult mandible with m3 – m1. The teeth are very sectorial, comparable to other Miocene forms, but as yet, with no possibility of establishing a clear

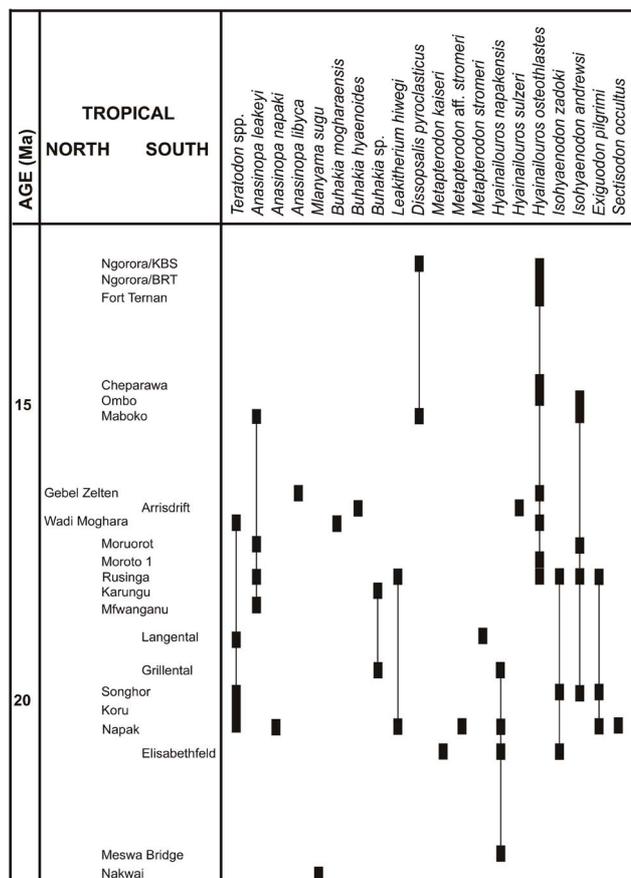
correspondence to the upper dentition. Thus, the inclusion of *Isohyaenodon zadoki* in this genus is indirect and is based on the compatibility in size with *Isohyaenodon matthewi* (Morales et al. 1998a), but further evidence is required from the fossil record in order to confirm this hypothesis (Text-fig. 9)

In addition, among the re-classified forms, there is the Karungu maxilla containing P3 – M2 described by Savage (1965) as *Metapterodon kaiseri* which presents affinities with *Dissopsalis*. The dimensions and morphology of this maxilla could correspond to the lower dentition of *Buhakia* (Morlo et al. 2007). This genus, and the problematic form *Leakitherium* (at least the holotype maxilla described by Savage (1965: text-fig. 36)) are included in the new tribe Dissopsalini (Text-figs 10–11).

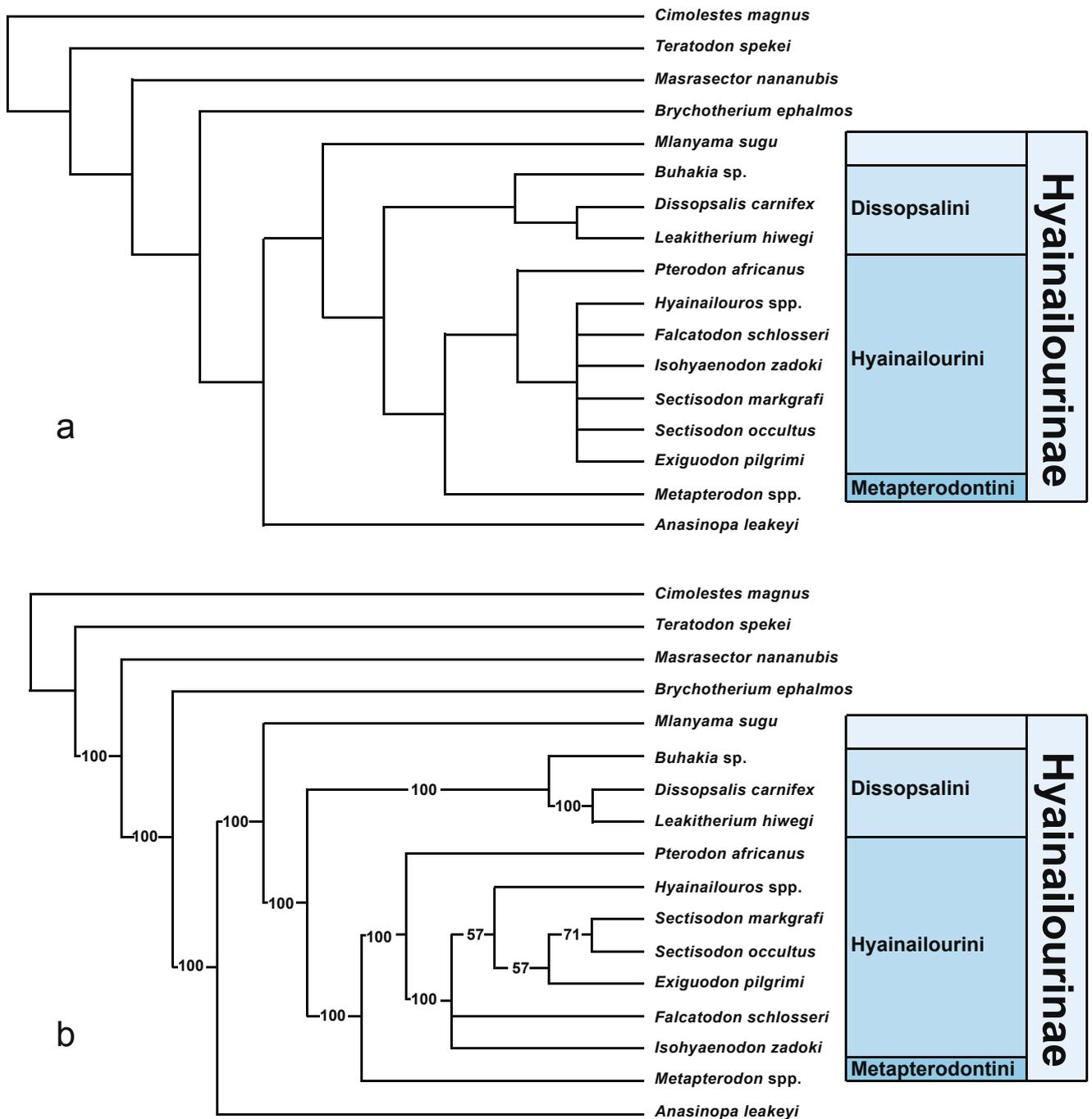
The most hypercarnivorous Miocene hyaenodonts appear to comprise a monophyletic group Hyainailourini, at the base of which occurs *Pterodon africanus* with *Sectisodon* and *Exiguodon* as the terminal forms. These two genera with *Hyainailouros* represent the extremes of size, the latter being the largest creodont (indeed carnivorous mammal) known and *Exiguodon* one of the smallest (with the exception of the peculiar genera *Prionogale* SCHMIDT-KITTLER et HEIZMANN, 1991, and *Namasektor* MORALES et al., 2008). *Pterodon africanus* represents a morphological pattern close to that of *Pterodon dasyuroides*, whereas *Exiguodon pilgrimi* possesses a highly sectorial dentition, with lower and upper molars almost reduced to the cutting cusps paraconid-protoconid and metastyle-paracone/metacone respectively. In between these two extremes occur four genera, *Falcatodon*, *Isohyaenodon*, *Hyainailouros* and *Sectisodon* which present more or less sectorial tendencies up to hypercarnivory, giving rise to a small cladogenesis which was probably interrupted by the dispersal of fissiped carnivores to the African continent.

Text-fig. 10 shows the strict consensus trees and 50% majority-rule of the 7 trees obtained. The differences between them are obvious, focusing on the Miocene species in Hyainailourini, as was already seen by Borths et al. (2016). Probably, this results from the incomplete knowledge of taxa such as *Sectisodon markgrafi* and *Isohyaenodon zadoki*. *Sectisodon* and *Exiguodon* appear to be sister-taxa in the majority rule cladogram and together with *Hyainailouros* occur in a monophyletic group, evidencing the evolution of the most sectorial groups of the analysed species. *Falcatodon* and *Isohyaenodon* appear to be closely related to this group and with *Pterodon africanus* occur in a monophyletic clade characterized by an advanced grade of sectorialisation of the buccal cusps (paracone+metacone-metastyle) that defined the tribe Hyainailourini. *Metapterodon* spp. share with Hyainailourini the sectorialisation of the molar, but retaining primitive characters in the upper dentition, the most telling being the presence in M1 – M2 of a long isthmus leading to the protocone. This association of characters is unique among Hyainailourinae and allows us to distinguish *Metapterodon* spp. as a single clade named Metapterodontini.

These two clades link to the Dissopsalini forming a larger clade, the Hyainailourinae in which the basal genus *Mlanyama* occurs. The separation of the Teratodontinae from the Hyainailourinae, in the sense already defined, must have occurred a long time ago (Text-fig. 11), probably as early as the Early Eocene (Solé et al. 2014). Inclusion



Text-fig. 9. Biostratigraphy of African Miocene localities, with the temporal ranges of the diverse species of hyaenodonts found therein. See Pickford (1986a), Pickford and Senut (2003), Reynoso (2014) and Werdelin (2010).

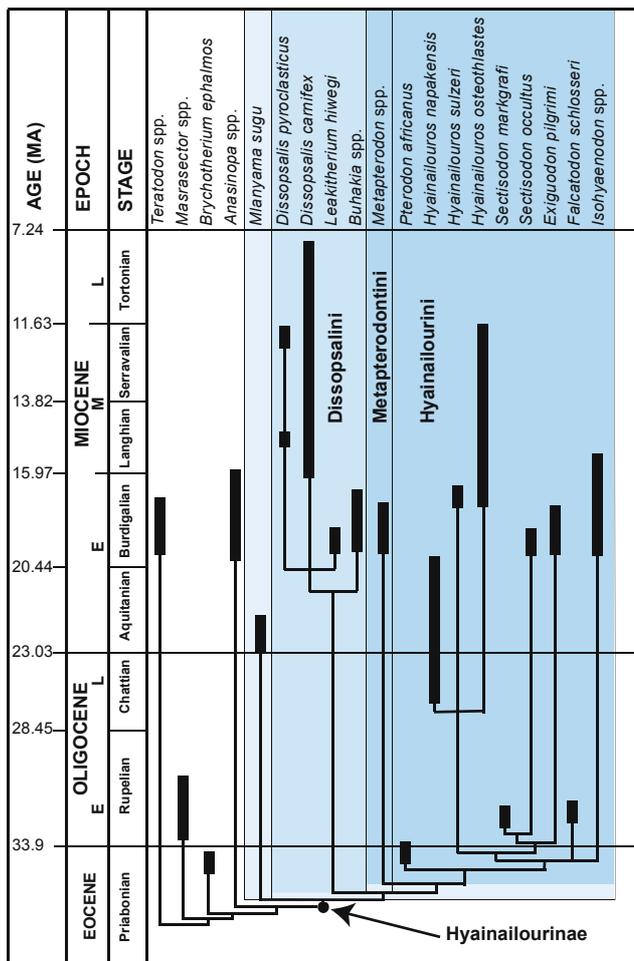


Text-fig. 10. Phylogenetic relationships of Miocene hyaenodonts (for definitions of character states see Table 2). The data matrix was compiled in MacClade 4.05 and run in PAUP 4.0b10 (Macintosh version). We chose *Cimolestes magnus* CLEMENS et RUSSELL, 1965, (additional data from Lillegraven 1969), as the outgroup. The unordered and unweighted analysis produced 16 trees. **a:** Majority-rule consensus. **b:** Strict consensus. Consistency index (CI): 0.5882; Homoplasy index (HI): 0.4118; Retention index (RI): 0.7742.

of Dissopsalini in this subfamily is not supported in our analysis, and highlights the difficulty of defining the subfamily Teratodontinae, as a group sharing primitive characters, but with the derived characters distributed in a mosaic pattern (Solé et al. 2014). One of the problems resides in the extreme singularity of the type genus of the family, *Teratodon*, which in effect means that the subfamily is diagnosed on the basis of an admixture of primitive characters observed in the molars (the M2 resembles much older species such as *Prototomus minimus* SMITH et SMITH,

2001) and derived characters seen in the hypertrophied anterior premolars. However, in *Dissopsalis*, and to a lesser extent in the other two genera of the tribe, the specialisation occurs in the molar rows whereas the posterior premolars are moderately robust (similar to those of Miocene hyaenas) far from the great specialisation seen in *Teratodon*. Because of this, it is difficult to envisage the Dissopsalini forming part of the subfamily Teratodontinae.

The Hyainailourini appear to have been well diversified at the Eocene/Oligocene boundary, and in a general way



Text-fig. 11. Biochronology and hypothesis of phylogenetic relationships of the Miocene and Palaeogene species of hyaenodonts based on the majority consensus tree (Text-fig. 10a). Chronostratigraphic data after Cohen et al. (2013). Temporal ranges of Miocene species as in Text-fig. 9. Temporal ranges of Palaeogene species based on Holroyd (1999), Seiffert (2010) and Borths et al. (2016).

the subsequent Miocene groups are recognisable. The same does not apply to the Dissopsalini, and only *Mlanyama sugu* (Rasmussen and Gutiérrez 2009) appears to be the basal taxon of the group. It is evident that better knowledge of the Oligocene fossil record of the hyaenodonts would yield major insights into the later phase of radiation of the order during an epoch which witnessed the disappearance of the group over broad expanses of the Old and New Worlds.

Conclusion

The African Miocene fossil record of hyaenodonts is still scarce and mainly composed of mandibles and isolated teeth which are difficult to interpret. New fossils from the Early Miocene localities of Napak (Uganda), Koru (Kenya) and Grillental (Namibia) clarify the systematics of the Miocene hyaenodonts. The descriptions of the new taxa; *Falcatodon* gen. nov., *Sectisodon occultus* gen. et sp. nov. and *Exiguodon* gen. nov. underline the importance of the hypercarnivorous hyaenodonts during the Ealy Miocene in Africa, just as

the Feliformia carnivores began to diversify. Phylogenetic analysis allows the recognition of four different Miocene hyaenodont clades: Hyainailourini, Metapterodontini and Dissopsalini (Hyainailourinae) and Teratodontinae.

Acknowledgements

The Spanish Research Project CGL2015-68333-P (MINECO/FEDER-UE) and the Research Groups CSIC 641538 and CAM-UCM 910607 funded aspects of this research. We thank Gertrud Rössner (SNSB-BSPG) Helke Mocke (Geological Survey of Namibia), Sarah Musalizi (Uganda Museum, Kampala), Pip Brewer (NHMUK) and Christine Argot (MNHN Paris) for providing access to collections in their care. Special thanks to Brigitte Senut for her help at all times, and Jan Wagner and Ivan Horáček for the invitation to participate in the volume in honour of Prof. Oldřich Fejfar. We also thank Floréal Solé for useful comments and suggestions, which improved the original manuscript.

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Explanations of the plates

PLATE 1

Buhakia sp. II from Grillental VI, Sperrgebiet, Namibia

1. Right mandible with alveolus of m2, m1 – p2 (GSN GT VI 22'17);
 - a: occlusal view (stereo pairs),
 - b: buccal view,
 - c: lingual view.

PLATE 2

Metapterodon aff. *stromeri* MORALES et al., 1998a from Napak V, Uganda

1. Right M2 (UM NAP V 121'08);
 - a: occlusal view (stereo pairs),
 - b: lingual view (stereo pairs),
 - c: buccal view (stereo pairs),
 - d: posterior view, I.F. = interstitial facet for M3.

Metapterodon stromeri MORALES et al. (1998a) from Langental, Sperrgebiet, Namibia

2. Right M2 (holotype; GSN LT 527c'96);
 - a: occlusal view,
 - b: lingual view,
 - c: buccal view.
3. Left m3 (GSN LT 526c'96);
 - a: occlusal view,
 - b: buccal view,
 - c: lingual view.

Metapterodon kaiseri STROMER, 1926 from Elisabethfeld, Sperrgebiet, Namibia

4. Left maxillary fragment with M2 – P3 (holotype; BSPG Nr.1926X1);
 - a: occlusal view,
 - b: buccal view,
 - c: lingual view.

PLATE 3

Isohyaenodon zadoki SAVAGE, 1965 from Rusinga, Kenya

1. Right maxilla with M2 – M1 and P4 fragment (holotype; NHMUK M 19094);
 - a: occlusal view (stereo pairs),
 - b: buccal view (stereo pairs),
 - c: lingual view (stereo pairs).

Isohyaenodon sp. from Elisabethfeld, Sperrgebiet, Namibia

2. Left P4 (GSN EF 208'01);
 - a: occlusal view,
 - b: buccal view.

PLATE 4

Sectisodon occultus gen. et sp. nov. from Napak, Uganda.

1. Right P3 (UM NAP-IV 72'04);
 - a: lingual view (stereo pairs),
 - b: buccal view (stereo pairs),
 - c: occlusal view (stereo pairs).
2. Right M1 (UM NAP-IV 01'09);
 - a: postero-lingual view, O.F. = occlusal facet,
 - b: occlusal view (stereo pairs),
 - c: lingual view (stereo pairs),
 - d: buccal view (stereo pairs),
 - e: anterior view (stereo pairs).
3. Right M2 (holotype; UM NAP-V 178'08);
 - a: postero-lingual view, I.F. = interstitial facet for M3,
 - b: occlusal view (stereo pairs),
 - c: lingual view (stereo pairs),
 - d: buccal view (stereo pairs),
 - e: anterior view (stereo pairs).

PLATE 5

Exiguodon pilgrimi (SAVAGE, 1965) from Rusinga, Kenya

1. Left mandible (holotype; NHMUK M 19100a-c);
 - a: lingual view (stereo pairs),
 - b: occlusal view (stereo pairs),
 - c: buccal view (stereo pairs).
2. Right mandible (holotype; NHMUK M 19100a-c);
 - a: lingual view (stereo pairs),
 - b: occlusal view (stereo pairs),
 - c: buccal view (stereo pairs).
3. Part of the neurocranium attached to the seven cervical vertebrae (holotype; NHMUK M 19100a-c);
 - a: ventral view,
 - b: dorsal view.

PLATE 6

Exiguodon pilgrimi (SAVAGE, 1965)

1. Right mandible with m3 – m2 from Koru, Kenya (OCO KO 38'04);
 - a: lingual view (stereo pairs),
 - b: buccal view (stereo pairs),
 - c: occlusal view (stereo pairs).
2. Left maxilla with M2 – M1 from Napak, Uganda (UM NAP-IV 64);
 - a: buccal view,
 - b: lingual view,
 - c: occlusal view.
3. Left P4 from Koru, Kenya (OCO KO 466'04);
 - a: occlusal view (stereo pairs),
 - b: buccal view (stereo pairs),
 - c: lingual view (stereo pairs).

PLATE 1



1a



1b



1c

1 cm

PLATE 2

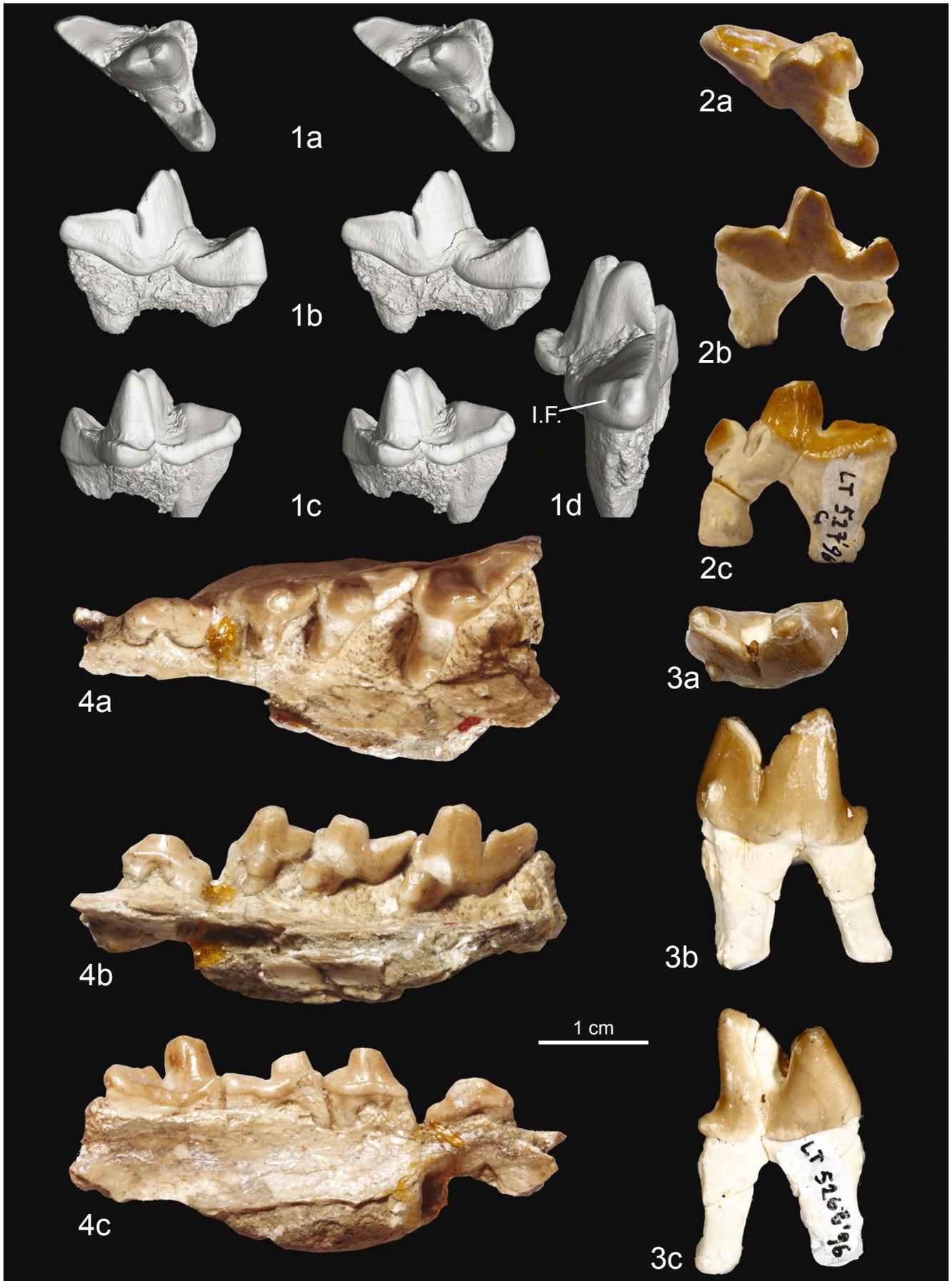


PLATE 3

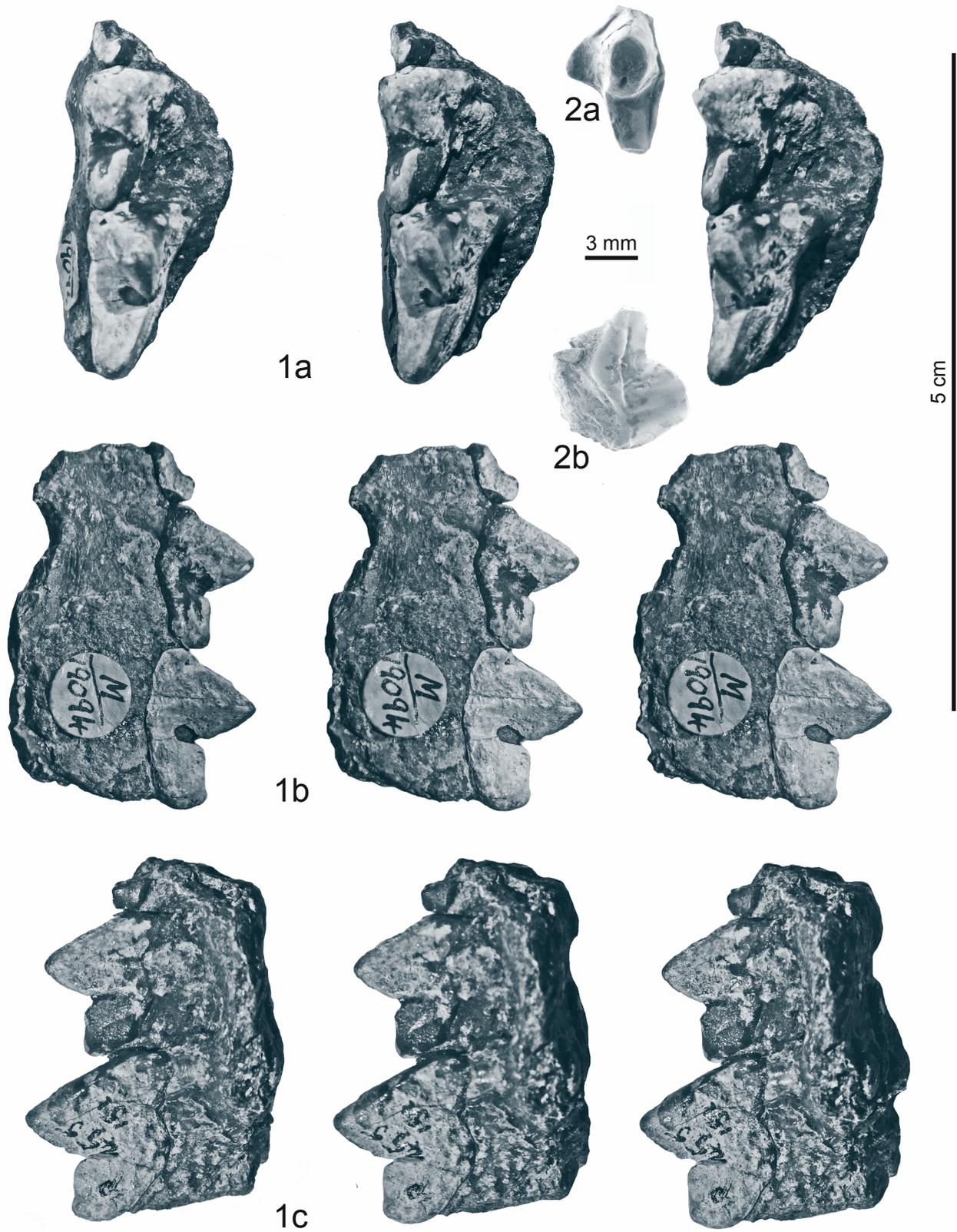


PLATE 4

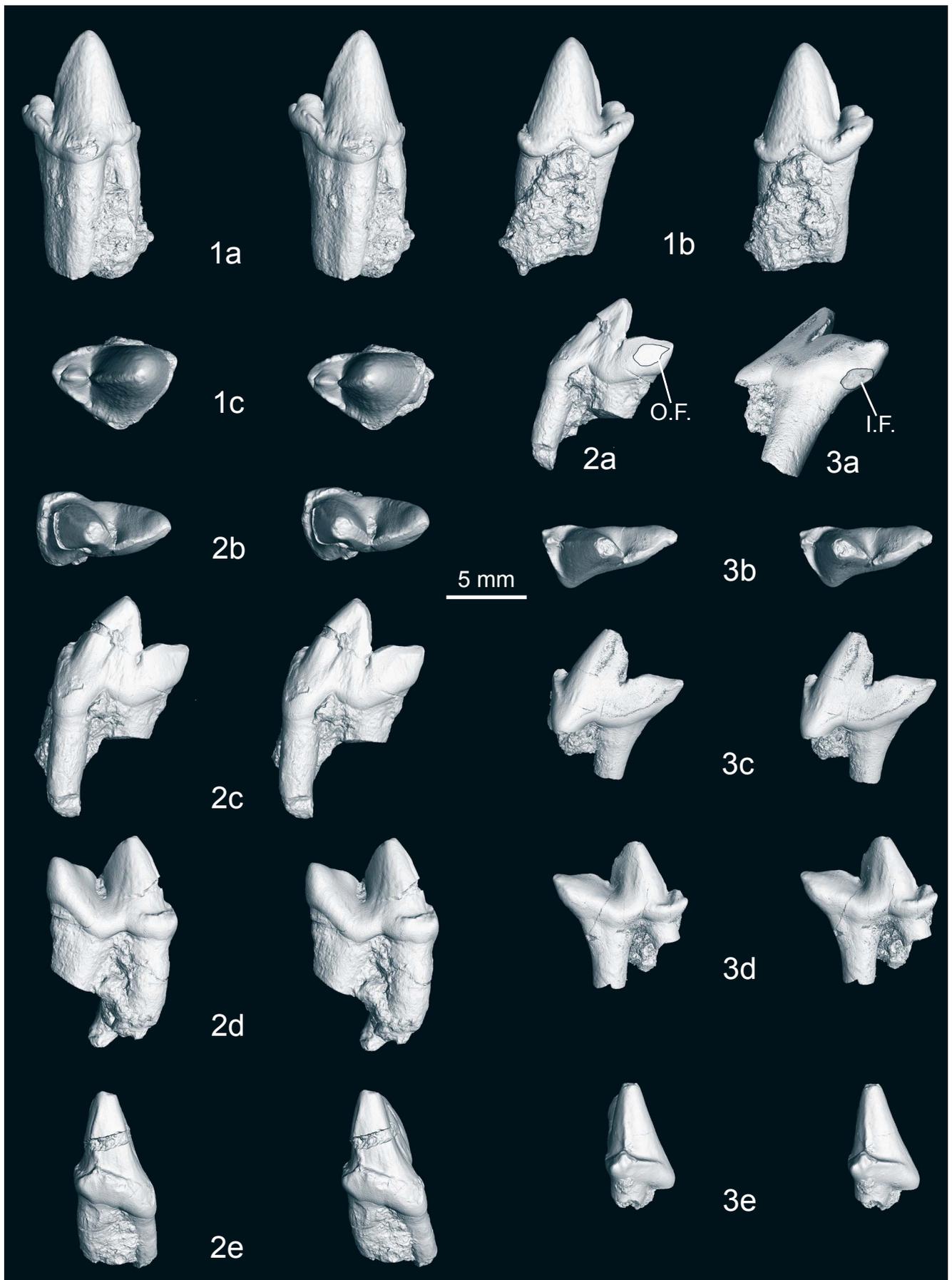


PLATE 5



PLATE 6

