Taxonomic affinities of the enigmatic *Prionogale breviceps*, early Miocene, Kenya

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Prionogale breviceps is a tiny carnivorous mammal from the early Miocene of eastern Africa. Originally, specimens were interpreted as the adult morphology of the taxon. The dentition did not obviously align *Prionogale* with the carnivorous lineages present in Afro-Arabia during the early Miocene: Hyaenodonta and Carnivora. When *Namasector* was discovered in Namibia, the small taxa were placed together in Prionogalidae and aligned with Hyaenodonta. In this study, based on comparisons to hyaenodont specimens preserving deciduous dentition, the holotype of *Prionogale* is reinterpreted as preserving dP3 and dP4. Some of the lower dental specimens attributed to the taxon preserve dp4. The holotype of *Namasector* also preserves deciduous dental material. A phylogenetic analysis that includes deciduous dental characters for a broader sample of hyaenodonts resolved Prionogalidae as a clade. Understanding of the deciduous dentition of *Prionogale* allows future analyses to compare homologous morphology, and to explore the environmental factors that shaped carnivorous mammal evolution through the Miocene.

Keywords: Neogene, Africa, ontogeny, phylogeny, Creodonta, Hyaenodonta, carnivory

Introduction

Prionogale breviceps is a small carnivorous taxon known from the early Miocene of eastern Africa, first described by Schmidt-Kittler and Heizmann (1991) as having 'a very strange combination of carnivorous and insectivorous features which do not fit smoothly with any known group' (p. 6; Schmidt-Kittler and Heizmann, 1991). Schmidt-Kittler and Heizmann (1991) provisionally placed the enigmatic taxon in 'Lepticoidea,' adding a new carnivorous mammalian lineage to the already taxonomically crowded eastern African meat-eating guild.

Before the discovery of *Prionogale*, two diverse lineages of distantly related mammalian carnivores were known on the Cenozoic Afro-Arabian landscape: the incumbent Hyaenodonta, present on the continent since at least the middle Paleocene

(Solé et al. 2009); and Carnivora, a more recent arrival that likely dispersed to Afro-Arabia from Eurasia between 25 and 20 Ma (Werdelin 2010). Afro-Arabian hyaenodonts are united by the presence of three adult carnassial pairs (formed between P^4/M_1, M^1/M_2, and M^2/M_3; Rose 2006), whereas taxa comprising the group, Carnivora, are united by the presence of just one carnassial pair (formed between P^4/M_1; Ungar 2010). Notably, early Miocene African hyaenodonts assumed fascinating novel dietary niches, perhaps in response to the arrival of Eurasian carnivoran lineages and the environmental changes associated with tectonic events in the East African Rift System (Borths and Stevens 2017a). But the dental formula of the hypercarnivorous *Prionogale breviceps* as described by Schmidt-Kittler and Heizmann (1991) does not conform to either Hyaenodonta or Carnivora (Werdelin and Cote 2010). The presence of an independent hypercarnivorous mammalian lineage in Afro-Arabia adds complexity to an early Miocene carnivore fauna in flux.

No other taxa resembling *Prionogale* were identified from Afro-Arabia or elsewhere, until the discovery of *Namasector soriae* by Morales et al. (2008). In their description of *Namasector soriae*, the authors noted that *Namasector* shares several dental features with *Prionogale*. The authors erected a new family, Prionogalidae, for a group containing *Namasector* and *Prionogale,* placing Prionogalidae within Hyaenodontidae (equivalent to Hyaenodonta sensu Solé et al. 2015). They based this alignment on the similar proportions of P_4 and M_1 in prionogalids and hyaenodonts. Werdelin and Cote (2010), noting differences in the upper dentition between *Prionogale* and *Namasector*, questioned relationships between these taxa but cautiously elected to retain Prionogalidae. They placed Prionogalidae in Mammalia *incertae sedis* rather than Hyaenodonta until a more detailed analysis of *Prionogale* could be presented.

Recent work on hyaenodont evolution (Solé et al. 2014; Rana et al. 2015; Borths et al. 2016; Borths and Seiffert 2017) has improved systematic interpretations of hyaenodont relationships, affording a phylogenetic context for testing the hyaenodont affinities of *Prionogale* and *Namasector*. Further, recent morphological insights gleaned from detailed work on the deciduous dentition of Afro-Arabian hyaenodonts (Borths and Stevens 2017a; 2017b) offer alternative interpretations of the idiosyncratic dentition of Prionogalidae. In this study, we compare the dentition of *Prionogale* to the dentition of subadult hyaenodonts and carnivorans, and use this novel morphological interpretation to test the phylogenetic affinities of *Prionogale* and *Namasector* within Hyaenodonta.

Materials and methods

To reevaluate the dental homologies of *Prionogale* and perform the phylogenetic analysis, we drew from comparative specimens and casts housed at: BMNH, Natural History Museum, London; DPC, Duke Lemur Center, Division of Fossil Primates, Duke University, Durham, NC; KNM, National Museums of Kenya, Nairobi. Additional materials used for the phylogenetic analysis, including date estimates associated with each taxon, are published in supplemental materials.

Dental terminology and measurements follow Holroyd (1999) and Borths et al. (2016). The phylogenetic analysis is based on the character-taxon matrix initially presented by Borths et al. (2016), expanded to include deciduous dental characters for hyaenodonts (Borths and Stevens 2017b), and to address the morphology of Prionogalidae. The character-taxon matrix used for the phylogenetic experiments performed in this study includes 150 morphological characters and 86 OTUs. Descriptions and references for the characters used in this analysis are published in the

supplemental materials. The character-taxon matrix, formatted for Mesquite (Maddison and Maddison 2015) and is available in the supplementary materials.

Phylogenetic analyses were performed using the same Bayesian 'tip-dating' phylogenetic methods described by Beck and Lee (2014) and applied to hyaenodonts by Borths and Stevens (2017a). This method simultaneously estimates branch length, rate, phylogeny and support for clades recovered in the analysis, a common approach for paleontological systematic analysis (e. g. Beck and Lee 2014; Dembo et al. 2015; Borths et al. 2016; Gorscak and O'Connor 2016; Lund et al. 2016; Turner et al. 2017). Bayesian 'tip-dating' analyses were performed in MrBayes (Ronquist et al. 2012) and MrBayes formatted nexus files with all analytical parameters are included in the supplementary materials.

Two phylogenetic analyses were performed, the first set 18 characters in the analysis as 'ordered' (ordered characters are noted in the supplemental file that contains the list of morphological characters used in the analysis). These 18 ordered characters were also ordered in Borths and Stevens (2017a; 2017b). A second analysis was performed with no ordered characters. Results of these separate phylogenetic analyses are summarized below.

Results

Systematic Paleontology

Mammalia, Linnaeus 1758

Hyaenodonta Van Valen 1967 sensu Solé et al. 2015

Prionogalidae Morales et al. 2008

Diagnosis

Small-bodied hyaenodonts with dental formula interpreted as: I?/2, C?/1, P3?/2, M1?/2. Upper dentition: dP^4 paracone taller than metacone, M1 metacone taller than reduced paracone; mesiodistal axis of metacone buccolingually oriented on dP4 and M1; elongate metastyle on dP4 and M1; dP4 and M1 protocones buccolingually elongate but lacking metaconule and paraconule. Lower dentition: metaconid absent on dp4–m2; talonid developed on dp4 and m1, reduced on m2; m2 preprotocristid mesiodistally elongate. Differs from Carnivora in exhibiting: carnassial formed between $M1/m_2$; dP4/m1 mesiodistally longer than m1 and subequal to m2. Differs from Hyaenodontinae in exhibiting: M1 paracone apex distinct from taller, shearing metacone; dP4/P4 and M1 protocone buccolingually elongate; dp4–m2 paracone more lingually placed relative to protocone; m3 absent. Differs from Hyainailourinae in exhibiting: M1 metacone taller than divergent paracone; m2 preprotocristid significantly longer than postparacristid; m3 absent. Differs from Limnocyoninae in exhibiting: reduced number of premolars; M1 with elongate metastyle and well-developed metacone, much reduced paracone; dp4–m2 metacone absent; m2 talonid very reduced.

Prionogale *Schmidt-Kittler and Heizmann 1991*

Prionogale breviceps *Schmidt-Kittler and Heizmann 1991*

Emended Diagnosis

Small hyaenodont with hypercarnivorous dentition and carnassials formed between P4/m1, M1/m2 (Figure 1, Figure 2, Table 1). Distinct notch on distal face of dP4 and

M1 protocone. m3 absent. Differs from *Namasector soriae* by having: dP3 protocone mesiodistally wider; dP4 paracone and metacone bases unfused; dP4 and M1 metacone lingually placed; dP4 and M1 metastyle shorter and more angled relative to buccal margin; talonid buccolingually wider on dp4 and m1 and hypoconid taller.

Type specimen

KNM-SO 1431, right fragmentary maxilla with dP3, dP4, M1 (originally identified as P3, P4, M1).

Locality and age

The type specimen (KNM-SO 1431) was collected from the early Miocene (~ 19.5 Ma) Songhor locality, Victoria Basin, Kenya. Other specimens have been recovered at Songhor, and from other early Miocene localities in Kenya (Chamtwara, Legetet, and Rusinga), and Uganda (Napak IV) (reviewed in Werdelin and Cote 2010).

Referred specimens

Specimens from Songhor (Kenya) include KNM-SO 1380, KNM-SO 1698, KNM-SO 5056, KNM-SO 8334, KNM-SO 15976, KNM-SO 15977, KNM-SO 15979, KNM-SO 15980, KNM-SO 22192, KNM-SO 22371, KNM-SO 22858, KNM-SO 22857, KNM-SO 22859, and KNM-SO 22946. Specimens from Chamtwara (Kenya) include: KNM-CA 301, KNM-CA 302, KNM-CA 2083, KNM-CA 2731, KNM-CA 2800, and KNM-CA 3164. Specimens from Legetet (Kenya) include: KNM-LG 1554, KNM-LG 2380, KNM-LG 2389, KNM-LG 2395, KNM-LG 2398, and KNM-LG 2402. Specimens from Rusinga (Kenya) include: KNM-RU 15928, and KNM-RU 19690.

Remarks

Several specimens previously identified as p4 are considered by the authors to be dp4 based on comparisons with other hyaenodont dp4 specimens. We here formally refer only those materials that we have been able to personally examine; Werdelin and Cote (2010) report a number of additional missing *Prionogale* specimens from these sites, as well as from the early Miocene Napak IV locality in Uganda.

Emended description

Schmitt-Kittler and Heizmann (1991) initially described the *Prionogale* holotype and many referred specimens, interpreting the holotype to preserve P3, P4, and M1. Based on comparisons to hyaenodont and carnivoran deciduous dentitions (discussed below), we interpret the holotype to instead preserve dP3, dP4, and M1. Likewise, we interpret tooth positions identified as p4 by Schmitt-Kittler and Heizmann (1991) to instead represent dp4. *Prionogale* is here redescribed and compared with other hyaenodont taxa preserving deciduous dentition based on our interpretations.

Upper dentition. KNM-SO 1431 (Holotype, Figure 1) is a right maxilla bearing a worn dP3, and a lightly worn dP4 and M1. The specimen preserves the infraorbital foramen superior to the distal root of dP3 and a portion of the infraorbital canal. The mesial root of dP^4 is exposed buccally, as is a portion of the distal root of dP3. M1 appears partially erupted, with the occlusal surface more distally oriented than is the condition in dP3 and dP4. The dP3 is missing its paracone, but preserves a protocone, with a single distinct cusp projecting lingually and perpendicular to the buccal margin. The dP3 metastyle is mesiodistally short and exhibits a distinct shearing crest, projecting to the same height as the apex of the protocone. The distal edge of the dP3 metastyle contacts the mesial margin of the parastyle of dP4.

The dP4 on the holotype exhibits a distinct parastyle, elongate metastyle, and a divergent paracone and metacone. A thin cingulum connects the mesial margin of the protocone to the parastyle. There is no indication of a paraconule on the dP4 talon basin. The dP4 protocone is mesiodistally wide and triangular in occlusal view. The protocone is mesially shifted relative to the protocone on dP3 and the apex of the protocone is aligned with the parastyle. The dP4 postprotocrista exhibits a slight rise or small metaconule, and the protocone rises above the divergence of the metacone and paracone. The dP4 paracone and metacone are divergent, separated from their bases. The paracone is slightly higher than the metacone, and the metacone is more buccolingually compressed and elliptical in cross section. The metastyle forms a distinct carnassial notch with the distal edge of the metacone. The metastyle and buccal cingulum create a large metastylar shelf buccally. The buccal cingulum is punctuated by small cuspules that terminate at the base of the paracone. The paracone is situated on the buccal margin of the tooth and the metacone is distolingual to the paracone.

M1 is slightly mesiodistally shorter than dP4. The M1 parastyle is mesiodistally expanded and forms part of a broad buccal shelf. The mesial margin of the parastyle connects to the protocone. The protocone base is mesiodistally narrow compared with the protocone base of dP4. The mesial and distal margins of the protocone are parallel on M1, rather than angled towards each other as on dP4. The M1 protocone rises to the same height as the metacone, with a distinct metaconule cusp. The paracone is much reduced relative to the metacone, which is buccolingually compressed into a sectorial cusp with cristae that are parallel to the buccal margin. The metastyle connects to the metacone via a distinct shearing crest that has no distinct carnassial notch. There is a deep ectoflexus formed by the buccal cingulum. As on the dP4, the buccal cingulum is

punctuated by small cuspules. The metacone is mesiodistally aligned with the paracone on M1.

Lower dentition. A composite reconstruction of the lower dentition is presented in Figure 2. Images of all specimens used to construct this composite are contained in supplementary materials. KNM-SO 1380 is a left dentary fragment preserving unworn dp4–m1. The dp4 preserves a paraconid and a protoconid with no indication of a metaconid. The paraconid and protoconid are subequal in height and both are buccolingually compressed, separated by a distinct shearing notch. The paraconid base is mesiodistally longer than the protoconid base. The postprotocristid forms a distinct cristid obliqua with the hypoconid. The hypoconid is the largest of the talonid cusps, rising to the height of the notch formed between the paraconid and protoconid. The hypoconulid is distinct but lower than the hypoconid. There is no indication of an entoconid. Rather, the lingual margin of the talonid is defined by a distinct entocristid that connects the hypoconulid to the base of the paraconid. In occlusal view the talonid is buccolingually wider than the trigonid, and the trigonid tapers mesially.

M_1 is mesiodistally shorter than dp4, the paraconid is slightly lower than the protoconid, and on the buccal aspect of the paraconid there is a distinct buccal keel. The paraconid and protoconid are buccolingually compressed with a blade-like postparacristid that meets a blade-like preprotocristid to form a distinct carnassial notch. The carnassial is oriented obliquely to the mandibular corpus. The postprotocristid meets the hypoconid at a defined cristid obliqua. The hypoconid is more distally positioned than the hypoconid on dp4. The hypoconid is the largest of the talonid cusps. The hypoconulid is placed at the distolingual corner of the talonid and the entocristid slopes from the apex of the hypoconulid to the lingual margin of the talonid with no indication of an entoconid. The entocristid terminates at the base of the paraconid.

The m2 (KNM-SO 22946) is mesiodistally subequal in length to m1 and shorter than dP_4. The m2 is buccolingually more narrow than m1. The protoconid is the tallest cusp on m2 and the mesiodistal length of the paraconid is shorter than the mesiodistal length of the protoconid. The paraconid on m2 is braced between the talonid of m1 and a distinct buccal keel on m2. There is no metaconid present. Both the paraconid and protoconid are buccolingually compressed into blade-like cusps, and both cusps are more compressed than they are on dp4 or m1. The postparacristid slopes to a deep carnassial notch, deeper than the carnassial notch on m1. The carnassial has a more oblique orientation than the carnassial orientation on m1. The preprotocristid is longer than the postparacristid. The distal face of the m2 protoconid is concave and meets a very reduced talonid that is merely an enamel spur on the distal margin of the tooth. The m2 talonid morphology is slightly more distinct on KNM-SO 15977, suggesting variability of m2 talonid expression within the taxon similar to that found in modern carnivorans (Borths and Stevens 2017a). At this time, no specimens can confidently be interpreted as bearing an m3. It is possible that the absence of an m3-bearing specimen is due to the developmentally immature sample recovered thus far. Alternatively, the *Prionogale* lineage lost m3.

The coronoid process (KNM-SO 22371; KNM-SO 15977) rises at an oblique angle from a point immediately distal to the tooth row. It is parabolic in buccal view, forming a broad attachment site for temporalis fibers. The posterior margin of the coronoid process is concave, such that the posterior-most point of the coronoid is superior to the mandibular condyle. The mandibular condyle is mediolaterally expansive, with a width approximately three times its height. A posterior keel connects the lateral extent of the mandibular condyle with the angle of the mandible. The masseteric fossa is well defined anteriorly by a distinct coronoid ridge. The inferior

margin of the masseteric fossa is less distinct. The mandibular symphysis is preserved on KNM-SO 22857, running from a point inferior to i1 and terminating inferior to the alveolus of p1. The alveolus is identified as p1 because this tooth erupts early in ontogeny (Bastl et al. 2011) as a kind of brace against the base of the canine. It is possible the number of premolars was reduced in *Prionogale* and the alveolus was occupied by p2 as it is in some short-faced mustelids (Slaughter 1974). Given the current data, we discuss this tooth position as p1. On the buccal face of the dentary, mental foramina are preserved inferior to p1 and inconsistently inferior to the distal root of dp4.

KNM-SO 22859, a left dentary fragment bearing a heavily worn m1 and the alveoli of m2, preserves distinct pitting characteristic of digestive acid etching, often seen on small mammals preyed upon by raptors and other meat eaters (e.g., Andrews 1990). *Prionogale* is one of the smallest mammalian carnivores known from the Miocene (Borths and Stevens 2017a) and we hypothesize this diminutive hypercarnivore in turn was an opportunistic prey item for larger species.

Morphological comparisons

Deciduous tooth identification

The identification of dP3, dP4, and dp4 is based on comparisons to hyaenodont deciduous dentition reviewed by Bastl et al. (2014) and Borths and Stevens (2017b). The dP3 in hyaenodonts is characterized by a narrow protocone that projects perpendicular to the buccal margin at a point intermediate between the parastyle and metastyle, giving the tooth a 'T' shape in occlusal view. On dP3 the metastyle and parastyle are typically mesiodistally subequal in length, with a small metacone present distal to the paracone. Although the dP3 crown in *Prionogale* is not fully preserved, the

size and orientation of the protocone is consistent with the morphology of other hyaenodont dP3s.

The dP4 differs from P4 in hyaenodonts in retaining both a paracone and metacone. The hyaenodont P4 bears only a paracone, and m1 is the first tooth in the mature tooth row with a metacone. The relationship between the paracone and metacone on dP4 is typically more divergent than their condition on M1. For example, the paracone and metacone on M1 of *Masrasector nananubis* (Borths and Seiffert 2017) are partially fused, but in dP4 (Borths and Stevens 2017b) the cusps remain distinct to their bases. A similar relationship exists between dP4 and M1 in KNM-SO 1431, the holotype of *Prionogale*: the paracone and metacone are distinct and divergent on dP4 and on M1 the metacone is exaggerated with the paracone fused to its base.

The dp4 in hyaenodonts typically resembles m1, the first carnassial-bearing tooth in the adult tooth row. Like m1, dp4 bears both a paraconid and protoconid. The p4 usually bears only the protoconid. On dP4 the paraconid is usually more mesially oriented relative to the protoconid than it is on m1, making the trigonid more buccolingually narrow on dp4 and the carnassial blade closer to parallel with the buccal margin. The tooth identified by Schmidt-Kittler and Heizmann (1991) as p4 exhibits a paraconid and protoconid, a buccolingually compressed trigonid compared with m1, and a carnassial blade close to parallel to with the buccal margin, leading us to conclude the tooth is dp4 rather than p4.

Reevaluating Namasector

Morales et al. (2008) made direct comparisons between *Prionogale* and *Namasector*, placing these two taxa in a distinct family, Prionogalidae. Based on deciduous dental characters, we also propose a reevaluation of the dental positions originally assigned to the holotype and paratype of *Namasector*. On Elisabethfeld specimen EF 118’04, a right

maxilla fragment, dP3 (P3 in Morales et al. 2008) preserves a distinct metacone and centrally positioned protocone that lends the tooth a 'T' shape in occlusal view. The dP4 (P4 in Morales et al. 2008) preserves a metacone that is lower and more divergent than is preserved on M1. Elisabethfeld specimen EF 60'01, a right mandible fragment, dp4 (p4 in Morales et al. 2008) preserves a buccolingually compressed trigonid and carnassial blade that is closer to parallel with the buccal margin than the carnassial blade on m1. Werdelin and Cote (2010) also suggested the holotype and paratype of *Namasector* included deciduous dental material, though they did not raise this possibility for *Prionogale*. The dP4 differs from P4 in hyaenodonts in retaining both a paracone and metacone. The hyaenodont P4 bears only a paracone, and m1 is the first tooth in the mature tooth row with a metacone. The relationship between the paracone and metacone on dP4 is typically more divergent than their condition on M1. For example, the paracone and metacone on M1 of *Masrasector nananubis* (Borths and Seiffert 2017) are partially fused, but in dP4 the cusps remain distinct to their bases (Borths and Stevens 2017b). A similar relationship exists between dP4 and M1 in KNM-SO 1431, the holotype of *Prionogale*: the paracone and metacone are distinct and divergent on dP4 and on M1 the metacone is exaggerated with the paracone fused to its base.

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compressed trigonid compared with m1, and a carnassial blade close to parallel to with the buccal margin, leading us to conclude the tooth is dp4 rather than p4.

Comparisons to Hyaenodonta

Relative to other hyaenodonts, *Prionogale* and *Namasector* share several distinctive dental characters. On both taxa, the dP4 metacone is lower than the paracone, and the M1 metacone is much taller and mesiodistally longer than the paracone, making the metacone the primary, piercing cusp of the carnassial. Two major clades of hyaenodonts – Hyaenodontinae and Teratodontinae – form the upper carnassial from a metacone that is taller than paracone. However, in Hyaenodontinae and Teratodontinae, the paracone is taller than the metacone on dP4 and M1. Further, in these clades the paracone on M1 is fused to the mesial face of the metacone, rather than a small but independent cusp, as the paracone is on the M1 of *Prionogale* and *Namasector*.

In *Namasector* and *Prionogale*, the metaconid is absent on dp4–m2, and the talonid is well-developed on dp4 and m1. This condition is similar to the combination of features found in Apterodontinae, a group that preserves the talonids but lacks or weakly expresses the metaconids. But apterodontines exhibit a well-developed talonid on m2 and m3. This contrasts with the significantly reduced talonid on m2 exhibited by both *Namasector* and *Prionogale*.

The dental formula shared by *Namasector* and *Prionogale*, particularly the absence of m3, is also found in *Thereutherium* and some taxa in the clade Limnocyoninae such as *Limnocyon* and *Thinocyon*. *Thereutherium* exhibits many hypercarnivorous characters shared with *Prionogale*, including the loss of the metaconid and the elongation of the metastyle. *Thereutherium* differs from *Prionogale* by exhibiting an upper carnassial on M1 formed by a fused paracone and metacone. Unlike the tall, leading metacone of *Prionogale*, the tallest cusp on M1 in

Thereutherium is the paracone. On both lower molars, *Thereutherium* retains simple, but mesiodistally elongate talonids. *Prionogale* has an elongate talonid only on m1. Despite these differences from other hyaenodont lineages, both *Namasector* and *Prionogale* share with other hyaenodonts the presence of carnassial pairs formed between dP3/dp4, dP4/m1, and M1/m2, a deeper ectoflexus on M1 than dP4, a dp4 that is mesiodistally longer than m1 and subequal in length to m2, a relatively low coronoid process, and dorso-ventrally narrow mandibular condyle. Compared to other hyaenodonts, the mandibular symphysis of *Prionogale* is short, only extending below the alveoli of p1. On the buccal surface of the dentary, there is one consistent mental foramen below the alveoli of p1 and another between dp4 and m1. This is a relatively distal placement of the second mental foramina compared with other hyaenodonts, but this mental foramen position may also reflect the shortened snout of *Pironogale*.

The only other Afro-Arabian hyaenodonts within the size range of *Prionogale* are *Boualitomus* and *Lahimia* from the early Paleogene, *Masrasector nananubis* from the late Paleogene, and *Isohyaenodon pilgrimi* from the early Neogene. *Tinerhodon*, resolved by Borths et al. (2016) outside of Hyaenodonta, is the only taxon smaller than *Prionogale* and *Namasector* that has ever been attributed to Afro-Arabian hyaenodonts. Finally, the larger *Isohyaenodon pilgrimi* is the only hyaenodont taxon contemporaneous with *Prionogale*. *Isohyaenodon* shares with *Prionogale* the loss of the metaconid on the molars, a shallow slope of the anterior coronoid margin, and a deeply excavated masseteric fossa. *Isohyaenodon* differs from known specimens of *Prionogale* in preserving three lower molars, a buccolingually wider trigonid, a buccolingually narrower and mesiodistally shorter talonid, and a less obliquely oriented m2 carnassial.

Comparisons to Carnivora

Several early Neogene Afro-Arabian carnivores are only slightly larger than *Prionogale* and *Namasector*, including *Mioprionodon pickfordi*, *Stenoplesictis muhoronii*, and *Leptoplesictis rangwai* (Borths and Stevens 2017a). In none of these carnivorans, or indeed any Afro-Arabian carnivoran, is p4 mesiodistally longer than m1. Further, as in all carnivorans, each of these taxa only bears one carnassial pair between P4 and m1. In each of these taxa, where known, m2 is lower than m1 and mesiodistally shorter.

Phylogenetic Results

Previous studies of hyaenodont systematics performed with the character-taxon matrix that forms the basis of the present analysis (Borths et al. 2016; Borths and Seiffert 2017; Borths and Stevens 2017a; 2017b) executed the analysis with multiple ordered characters, following the ordering recommendations of Slowinski (1993). In this study of Prionogalidae, a group defined by character combinations that are uncommon for hyaenodonts, we sought to test the effect of ordered characters on the phylogenetic results by performing two analyses.

In the first analysis (Abbreviated 'allcompat' consensus tree Figure 3; complete consensus tree in supplemental materials), 18 characters were ordered (labelled in supplementary materials). In the ordered analysis, Prionogalidae (*Namasector* + *Prionogale*) was resolved as a clade with robust support (Posterior Probability = 100%). *Thereutherium* was resolved with moderate support (PP = 65%) as the sister taxon of Prionogalidae. The Prionogalidae + *Thereutherium* clade is weakly supported as the sister clade of *Oxyaenoides* (PP = 27%). The clade that includes *Oxyaenoides*, *Thereutherium*, and Prionogalidae is the sister clade of Hyaenodontinae, the moderately supported clade (PP = 61%) that contains both *Propterodon* and *Hyaenodon*.

Prionogalidae is the youngest lineage in the clade that unites Hyaenodontinae and Prionogalidae, and is the only clade that contains Afro-Arabian OTUs.

In the second analysis (Abbreviated 'allcompat' consensus tree Figure 3; complete consensus tree in supplemental materials), all characters were treated as unordered. In this analysis Prionogalidae (*Namasector* + *Prionogale*) is recovered as a clade with robust support (PP = 100%), as it was in the ordered analysis. However, in the unordered analysis, Prionogalidae is not resolved within Hyaenodontinae, but is instead placed within Hyainailourinae. Specifically, Prionogalidae is weakly supported (PP = 26%) as sister to a clade of early Miocene hyainailourines from Afro-Arabia that includes *Isohyaenodon, Mlanyama*, *Hyainailouros*, *Leakitherium*, and *Megistotherium*.

This phylogenetic analysis is the first to incorporate *Thereutherium*, a small-bodied, hypercarnivorous hyaenodont from the Eocene of Europe that lacks an M2/m3 carnassial pair. In neither analysis is *Thereutherium* nested within Limnocyoninae as suggested by Lange-Badré (1979). Rather, as proposed by Morlo and Gunnell (2003), *Thereutherium* is resolved outside of Limnocyoninae as either the sister taxon of Prionogalidae (ordered analysis) or as the earliest diverging lineage in a clade that includes Hyaenodontinae (unordered analysis).

Discussion and conclusions

Based on a reassessment of the material referred to *Prionogale breviceps* we note that the type specimen and some paratype materials preserve deciduous teeth previously interpreted as permanent dentition. *Prionogale breviceps* is certainly 'very strange' (p. 6; Schmidt-Kittler and Heizmann 1991), as stated in the original taxonomic description, combining mesocarnivorous dental features like a well-developed talonid on m1 and a mesiodistally broad M1 protocone, with hypercarnivorous dental features like absent metaconids, mesiodistally elongate metastyles, and a reduced dental formula. Although

this combination of features has not yet been observed in either Afro-Arabian carnivorans or other hyaenodonts, several features nonetheless clearly place *Prionogale* within Hyaenodonta, including multiple carnassials and teeth that increase or are equal in size distally along the tooth row. Morales et al. (2008) recognized these and other features that link *Prionogale* to Hyaenodonta, and further posited dental features to link *Prionogale* with *Namasector*. Indeed, our phylogenetic analyses consistently support a close relationship between *Prionogale* and *Namasector* within Hyaenodonta. As noted by Morales et al. (2008), both *Namasector* and *Prionogale* are hypercarnivores exhibiting mesiodistally elongate carnassials (with hypercarnivorous dental features more exaggerated in *Namasector*).

Polly (1996) was the first to use cladistic methods to demonstrate that multiple lineages of hyaenodonts (Hyaenodontinae and Hyainailourinae) independently converged upon hypercarnivory. Borths et al. (2016) demonstrated there was a shift to exaggerated hypercarnivory within Teratodontinae in the lineage that contains *Dissopsalis* and *Anasinopa*, illustrating differences in carnassial anatomy for each of these lineages. Hyaenodontinae and Teratodontinae, two distantly related clades, build their upper carnassials with an elongate metastyle and tall metacone. In contrast, Hyainailourinae builds the upper carnassial with an elongate metastyle and tall paracone. Prionogalidae, like Hyaenodontinae and Teratodontinae, exhibits a taller metacone than paracone. Yet the relationship between the paracone and metacone in Prionogalidae differs from all other described hypercarnivorous hyaenodonts. In *Prionogale*, the paracone and metacone bases are unfused. This distinction suggests yet another pathway for developing hypercarnivory among the hyaenodonts. Morphologically this distinction may be subtle, but homoplasy of the carnassial dentition can be observed across multiple carnivorous mammalian clades (Muizon and

Lange-Badré 1997; Van Valkenburgh 2007), and subtle differences in carnassial morphology reveal independent adaptive events that yielded functionally comparable dentitions.

Based on our phylogenetic analyses, the position of Prionogalidae within Hyaenodonta is ambiguous, depending on whether characters are ordered or unordered. Many clades are recovered by both ordered and unordered analyses, including Hyainailouroidea, Hyaenodontinae and Limnocyoninae. The position of Prionogalidae is the most dramatic difference between the two consensus trees, either as a clade nested within the Eurasian and North American Hyaenodontinae (ordered) or within the predominately Afro-Arabian Hyainailourinae (unordered). Convergent hypercarnivorous characters are likely supporting both positions, and a stronger Paleogene record is required to more confidently resolve the position of the clade within the hyaenodont tree. A complete, mature dental sample would be particularly useful for comparing Prionogalidae to taxa not known from deciduous material. Depending on the ultimate sister-clade relationships of Prionogalidae, the lineage either represents an endemic Afro-Arabian hyaenodont lineage or an invasive lineage that dispersed (perhaps alongside Carnivora) from Eurasia to Afro-Arabia during the late Paleogene.

Regardless of its continental origins, the combination of distinct characters in Prionogalidae and the long branches supporting the clade in each analysis suggest the clade is another example of independent convergence upon hypercarnivory within Hyaenodonta (Figure 4). The presence of a small-bodied and hypercarnivorous lineage of hyaenodonts in the early Miocene of Afro-Arabia is consistent with patterns observed by Borths and Stevens (2017a) during the Paleogene-Neogene transition. Borths and Stevens (2017a) demonstrated some of the oldest Afro-Arabian carnivorans crowded into small-bodied and mesocarnivorous niche space. The early Miocene hyaenodonts

Isohyaenodon pilgrimi, *Prionogale*, and *Namasector* are tiny hypercarnivores and all are in the same size range as the small, mesocarnivorous, early Miocene carnivorans. Specialized hypercarnivory within Hyaenodonta may be the result of adaptations to the changing carnivore fauna and changing Afro-Arabian environment. However, specialized hypercarnivory may have left hyaenodonts particularly vulnerable to extinction (Holliday and Steppan 2004).

After determining that much of the material referred to *Prionogale* bears deciduous dentition, we reevaluated *Namasector*, noting several features that suggest the Namibian prionogalid is also known only from sub-adult material. It may seem improbable that both prionogalid taxa are known from sub-adult specimens (IDAS 2 using the taxonomy of Anders et al. 2011). However, Mellet (1977) and Bastl and Nagel (2013) demonstrated hyaenodonts erupt their adult dentition relatively slowly compared with carnivorans. A long developmental period allows hyaenodonts to use the dP_4 carnassial for an extensive period, wearing the tooth and preserving the adult molars for extensive wear later in development (Borths and Stevens 2017a; 2017b). A corollary of this developmental strategy is a longer interval of time in which a dentally immature individual may become part of the fossil record. There is taphonomic evidence – pitting and breakage – that some of the micromammal material at Songhor and other early Miocene sites were accumulated by predators (Stevens, pers. obs.). At least one *Prionogale* specimen (KNM-SO 22859) exhibits a distinctly pitted surface, suggesting that these small predators were also prey. Sub-adults may have been particularly vulnerable to predation events, leading to an age-biased record.

Continued examination of the evolutionary history of Prionogalidae requires the discovery and documentation of more complete specimens, exhibiting full adult dentition. Additional materials may reveal whether the clade represents a hyaenodont

lineage that dispersed from Eurasia to Afro-Arabia alongside Carnivora close to the Paleogene-Neogene boundary (the first example of a non-carnivoran carnivore dispersing during this interval), or alternatively whether Prionogalidae represents part of the endemic Afro-Arabian hyaenodont radiation. Although *Prionogale* remains an unusual taxon, reassessment of the taxon in light of new deciduous dentition discoveries provides greater insight into hyaenodont ontogeny and evolution. Future studies of the changing Afro-Arabian ecosystem can now consider the evolutionary conditions that shaped the smallest mammalian predators to scramble through the African Miocene.

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Table 1. Tooth dimensions for *Prionogale breviceps*

	n	Length		Width	
		Mean	Std Dev	Mean	Std Dev
dP3	1	2.84	-	2.08	-
dP4	2	3.96	0.36	2.45	0.21
M1	1	3.44	-	3.36	-
dp4	5	4.22	0.25	1.51	0.22
m1	8	3.33	0.12	1.51	0.11
m2	9	3.03	0.25	1.17	0.07

Table 1. Dental measurements for *Prionogale breviceps*. Measurements in mm; Length, average maximum mesiodistal length of tooth position; Width, average maximum buccolingual width of tooth position; n, number of specimens measured for each tooth position; Std Dev, standard deviation. Individual specimen measurements and additional measurements in Supplementary Materials.

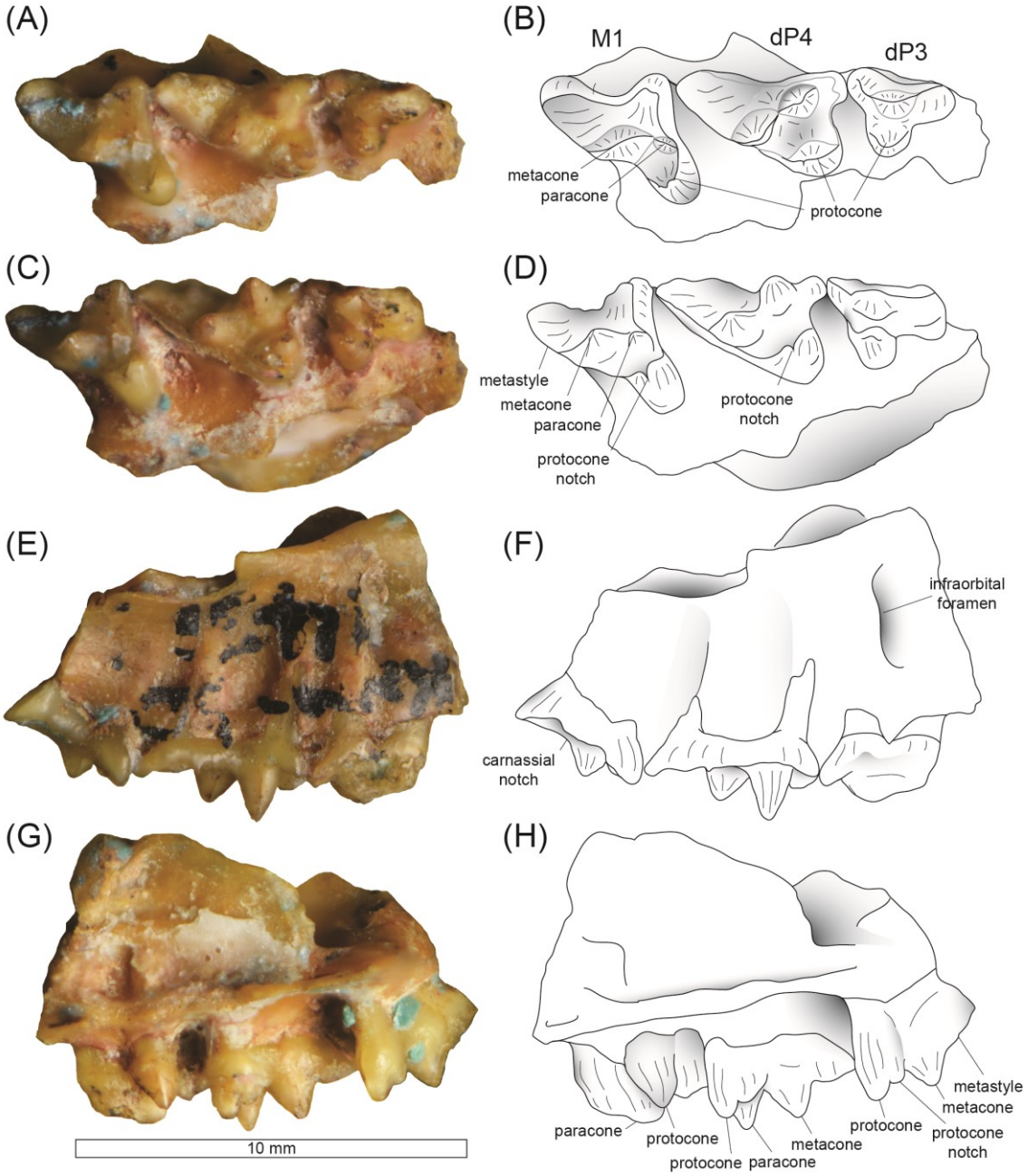

Figure 1. Holotype of *Prionogale breviceps*. KNM-SO 1431, left rostral fragment with dP3, dP4, M1, with specimen photographs (A, C, E, G) and sketches (B, D, F, H) that highlight key morphology. (A) and (B) holotype in occlusal view; (C) and (D) occlusal-lingual view; (E) and (F) buccal view; and (G) and (H) lingual view. Note the paracone is taller than the metacone on dP4 and the metacone is taller than the paracone on M1.

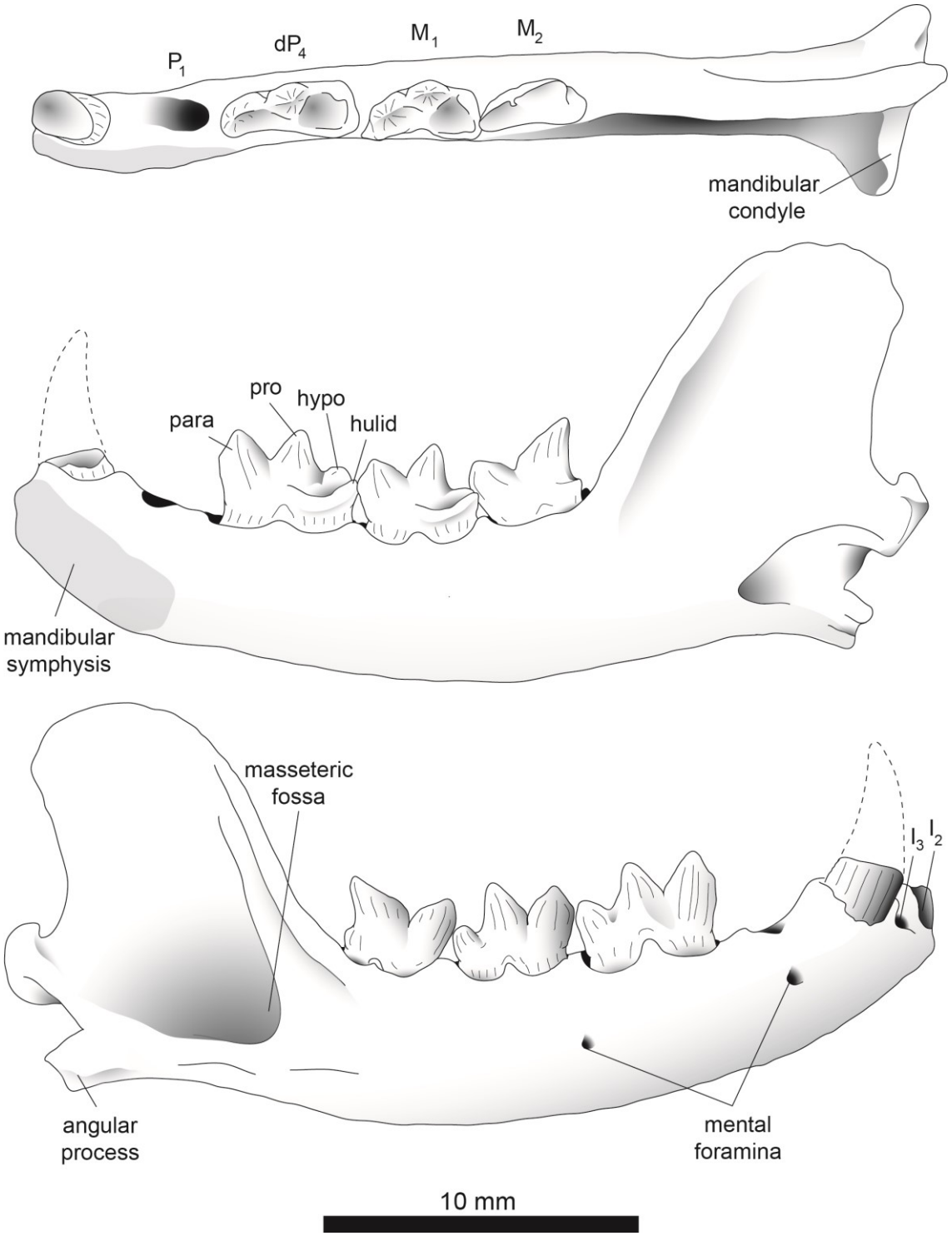

Figure 2. Dentary of *Prionogale breviceps*. A reconstruction of the right dentary and lower dentition of *Prionogale breviceps* based on referred specimens illustrated in Supplementary Materials (KNM-CA 3164, KNM-LG 1554, KNM-RU 19690, KNM-SO 1380, KNM-SO 8334, KNM-SO 15976, KNM-SO 22192, KNM-SO 22371, KNM-SO 22857, KNM-SO 22859, KNM-SO 22946) in occlusal view (A), lingual view (B), and buccal view (C).

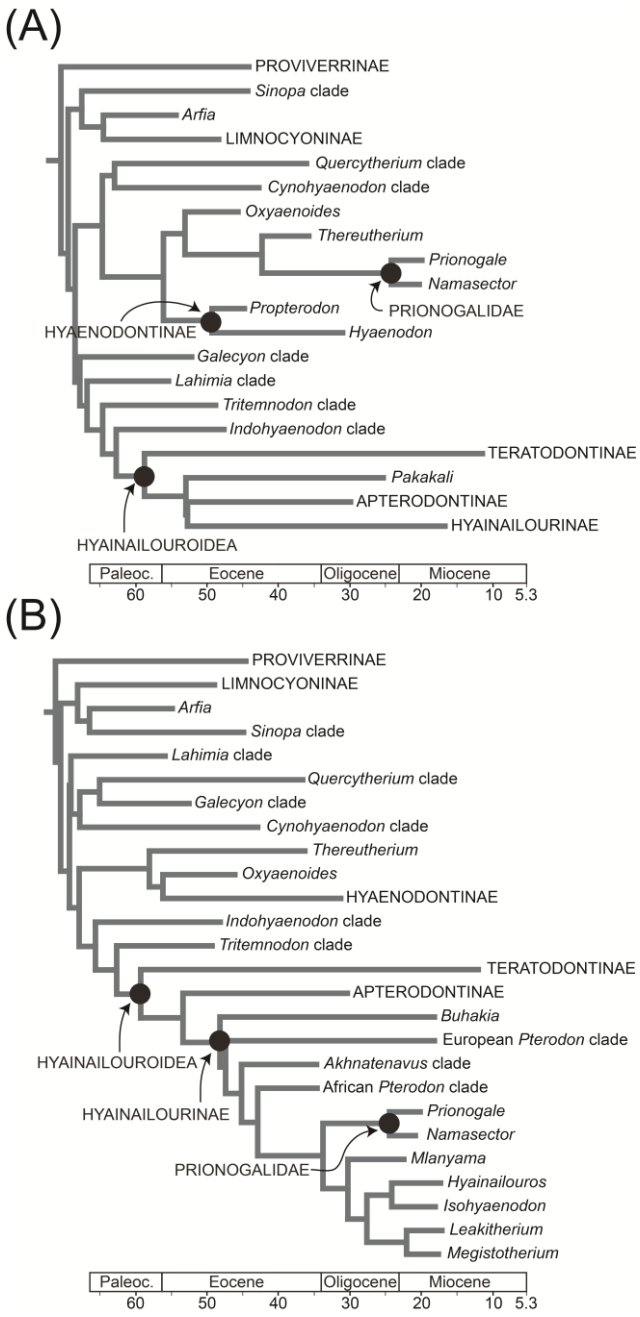

Figure 3. Phylogenetic hypotheses for Prionogalidae. Summarized results of the Bayesian 'tip-dating' analyses performed using 86 OTUs and 150 morphological characters, illustrated using an allcompat summary tree of the analysis performed with 18 ordered characters (A) and with unordered characters (B). Clades were collapsed to make the differing positions of Prionogalidae easier to compare. Divergence dates and terminal ages reflect the median date estimated through the tip-dating analysis. When 18 characters are ordered, as they were in previous Bayesian analyses of Hyaenodonta, Prionogalidae is resolved as the sister clade of *Thereutherium* and nested within the clade that includes Hyaenodontinae (A). When no characters are ordered the alignments of some clades differ, including the placement of Prionogalidae within Hyainailourinae (B). **Paleoc.**, Paleocene; dates on geological timescale expressed in Ma. Complete trees with each OTU in the analysis and dates used for each OTU are presented in Supplementary Materials.

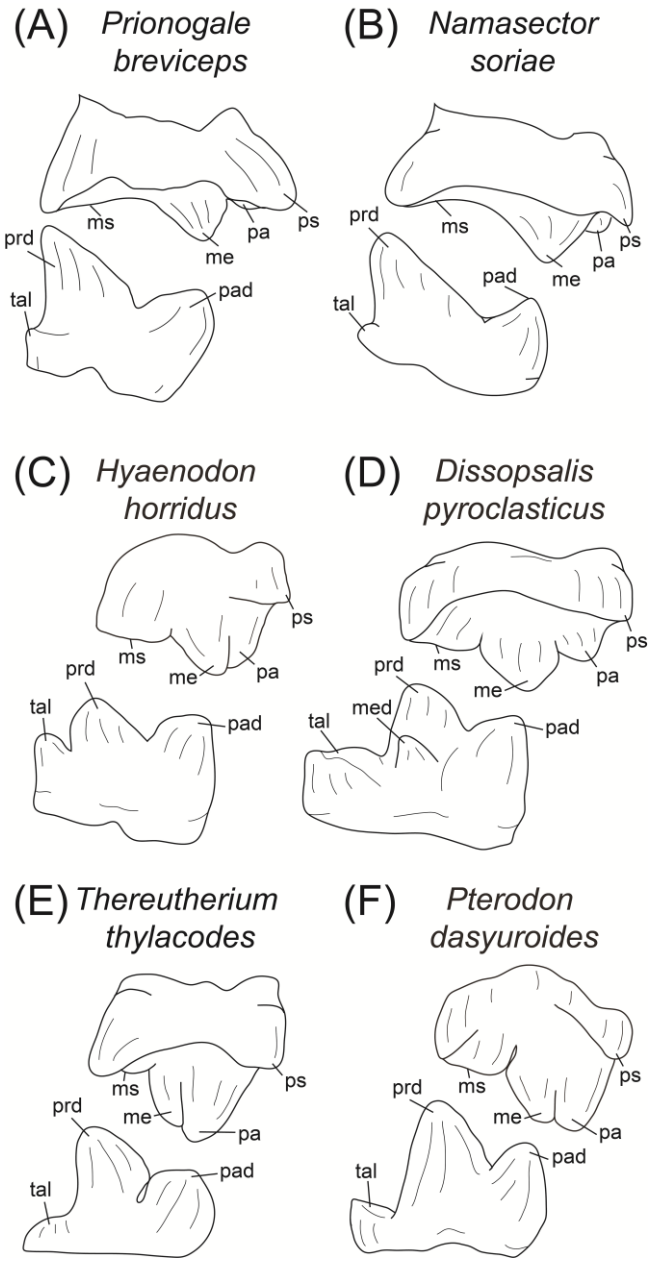

Figure 4. Hypercarnivorous hyaenodont dental comparisons. Upper right M1, shown in buccal view, and lower left m2, shown in lingual view, of hyaenodonts that converged upon hypercarnivorous dental morphology. (A) *Prionogale breviceps* (illustration based on upper KNM-SO 1431 and lower KNM-SO 22192) and (B) *Namasector soriae* (EF 118'04 and EF 60'01) are placed in the clade Prionogalidae with both taxa constructing the carnassial from a tall metacone and very reduced paracone. (C) *Hyaenodon horridus* (AMNH 75699 and AMNH 75704), part of Hyaenodontinae, and distantly related (D) *Dissopsalis pyroclasticus* (KNM-MB 25305 and BMNH M19082) have carnassials similar to Prionogalidae with tall metacones and short paracones. (E) *Thereutherium thylacodes* (MNHN Qu8588 and MNHN Qu8592), recovered in this analysis as part of a clade with Hyaenodontinae, and (F) *Pterodon dasyuroides* (MNHN Qu8669 and MNHN Qu8301), placed in Hyainailourinae, have carnassials with the paracone as the taller, piercing cusp, and the metacone as the lower carnassial cusp. **me**, metacone; **med**, metaconid; **ms**, metastyle; **pa**, paracone; **pad**, paraconid; **prd**, protoconid; **ps**, parastyle; **tal**, talonid.