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Article

THE 'SWAMP MONSTER' OF THE TREMEMBÉ FORMATION (TAUBATÉ BASIN, BRAZIL; LATE OLIGOCENE): A DESCRIPTION OF A CARNIVOROUS METATHERIAN (SPARASSODONTA, PROBORHYAENIDAE)

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ABSTRACT – Sparassodonta is an extinct clade of South American metatherians that occupied the role of carnivorous predators on the continent during the Cenozoic Era. The Oligocene was a significant period for the diversification of several mammalian lineages, being the time when the largest sparassodonts, such as several Proborhyaenidae evolved. Among the known localities with fauna from this epoch, the Taubaté Basin (late Oligocene, Deseadan SALMA), located in the State of São Paulo, southeastern Brazil, is the only one from Brazil dated to this period. The fauna from this locality is represented by Metatheria, Chiroptera, Rodentia, Cingulata, Astrapotheria, Litopterna, Notoungulata, and Pyrotheria. Here, we describe specimen MHNT.VT.2075, a lower canine of a large sparassodont from this fauna. This canine is assigned to the Proborhyaenidae based on the presence of an open root and labial and lingual midline sulci. This record increases the diversity of large mammals in this locality. Overall, the Tremembé Formation is a significant geological and paleontological resource that provides valuable insights into the final stages of the Paleogene period in intertropical South America.

Keywords: Paleogene, sulci, procumbence, canine, phylogenetic analysis.

INTRODUCTION

Sparassodonta is an extinct clade of metatherians endemic to South America that presented the main terrestrial mammalian predators on this continent during Cenozoic times. Their evolution included two major diversification events, firstly in the Eocene and posteriorly in the Miocene (Goin *et al*., 2010, 2016; Prevosti *et al*., 2013; Muizon *et al*., 2018; Prevosti & Forasiepi, 2018). The Oligocene is characterized by lower temperatures compared to the late Eocene and Miocene. This global cooling event led to significant environmental changes, which in turn caused a faunal turnover in South America, including the extinction and diversification of several metatherian clades (see Bond & Pascual, 1983; Babot, 2005; Zimicz, 2012; Goin *et al*., 2016).

The oldest borhyaenoids are recorded in the middle Eocene (*Callistoe*) and the Borhyaenidae is understood to have started in the Oligocene, with the basal *Pharsophorus* (Marshall, 1978; Forasiepi *et al*., 2015; Prevosti & Forasiepi, 2018) from La Cantera fauna at Gran Barranca, which predates the Deseadan SALMA (Goin *et al*., 2010; Ré *et al*., 2010; Dunn *et al*., 2013). In addition to *Pharsophorus*, other Sparassodonta from the Oligocene (Deseadan SALMA) have proportions ranging from medium to large sized such as *Australohyaena*, *Eomakharia*, *Fredszalaya*, *Proborhyaena*, *Paraborhyaena*, *Notogale* and *Sallacyon* (Mones & Ubilla, 1978; Bond & Pascual, 1983; Hoffstetter & Petter, 1983; Reguero & Escribano, 1996; Shockey & Anaya, 2008; Forasiepi, 2009; Forasiepi *et al*., 2015; Engelman *et al*., 2020).

The phylogenetic history of Sparassodonta is widely debated, with its origin proposed from *Mayulestes*, *Allqokirus* and *Patene* as representatives of the Mayulestidae, as well as phylogenetic arrangements in which *Mayulestes*, *Allqokirus*, and *Patene* are recovered as diverging stem lineages at Sparassodonta (*e.g*., Muizon *et al*., 2018; Rangel *et al*., 2019; Engelman *et al*., 2020; Beck *et al*. (2022). Despite this discussion, most phylogenetic analyses recover three main lineages of Sparassodonta: an early lineage, an unnamed Clade A, and the superfamily Borhyaenoidea (*sensu* Marshall *et al*., 1990; Muizon *et al*., 1997; Babot *et al*., 2002; Forasiepi *et al*., 2004, 2015; Muizon *et al*., 2018; Rangel *et al*., 2023a, b). The Borhyaenidae is represented by *Acrocyon*, *Arctodictis*, *Australohyaena*, *Borhyaena* and *Fredszalaya* (*e.g*., Forasiepi & Carlini, 2010; Engelman & Croft, 2014; Engelman *et al*., 2018, 2020; Muizon *et al*., 2018; Rangel *et al*., 2019, 2023a, b; Guimarães *et al*., 2024). Some phylogenetic hypotheses recover Borhyaenidae as being closely related to Proborhyaenidae, which includes the Thylacosmilinae (*e.g*., Engelman *et al*., 2018, 2020; Rangel *et al*., 2023a, b; Guimarães *et al*., 2024). Other phylogenetic arrangements recover Borhyaenidae as a group closer to Thylacosmilidae and Proborhyaenidae (*e.g*., Babot *et al*., 2002; Babot, 2005; Forasiepi *et al*., 2015; Suarez *et al*., 2023). Finally, Suarez *et al*. (2025) recognize two main clades within the Borhyaenoidea: the Thylacosmiliformes, which branch from their sister group, which includes Borhyaenidae and Proborhyaenidae.

In Brazil, sparassodonts are recorded from the Itaboraí (early Eocene, *sensu* Woodburne *et al*., 2014), Curitiba (Guabirotuba Formation, middle Eocene, *sensu* Sedor *et al*., 2017), and Taubaté (Tremembé Formation, late Oligocene, Deseadan SALMA, *sensu* Couto-Ribeiro, 2010) basins. These basins, along with the locality of PRJ-33 in the State of Acre (Western Amazonia, Eocene–Oligocene transition; see Marivaux *et al*., 2023), are the only units in Brazil with Paleogene continental mammal records. Within these units, only the Tremembé Formation presents a specimen identified as a Borhyaenoidae (Couto-Ribeiro, 2010). However, there is still a need for additional investigations to understand which Sparassodonta truly comprise the Tremembé fauna.

The Tremembé Formation is the only late Oligocene fossiliferous unit in Brazil that preserves mammal fossils, with a diverse fauna and autochthonous taxa. In this context, we present the specimen MHNT.VT.2075, an isolated canine from the Tremembé Formation, which is identified and evaluated in terms of its taxonomic affinities, with a focus on its implications for the Tremembé fauna. Comparing the Tremembé Fauna with other well-known localities fosters new discussions on the evolutionary history of South American mammals, as well as the paleoclimatology and paleogeography scenarios that shaped South America at the end of the Paleogene.

Abbreviations: AMNH, American Museum of Natural History, New York, USA; **FUNAT,** Fundação de Apoio à Ciência e Natureza, Taubaté, Brazil; **MACN-A**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Ameghino's Collection, Buenos Aires, Argentina; **MCN**, Museu de Ciências Naturais da Universidade Federal do Paraná, Paraná, Brazil; **MCT.M** (ex **DGM**, Divisão de Geologia e Mineralogia), Museu de Ciências da Terra, Rio de Janeiro, Brasil; **MHNT-VT**, Museu de História Natural de Taubaté "Doutor Herculano Alvarenga", Taubaté, São Paulo, Brazil; **MPEF-PV**, Museo Paleontológico "Egidio Feruglio" Sección Paleontología de Vertebrados, Trelew, Argentina. **SALMA,** South American Land Mammal Age.

GEOLOGICAL, STRATIGRAPHIC AND PALEONTOLOGICAL CONTEXTS

The Taubaté Basin is located in the State of São Paulo in southeastern Brazil and extends from the municipalities of Cachoeira Paulista to Jacarei (geographic coordinates 22°56'60.00"S, 45°31'60.00"W; Figure 1). It is approximately 150 km in length and 10 to 20 km in width (Brito, 1979), in a graben between the mountain range of Serra do Mar and Serra da Mantiqueira (Leinz & Amaral, 1989). Currently, three stratigraphic units are recognized in this basin: the Resende, Pindamonhangaba and Tremembé formations (Riccomini *et al*., 2004). The latter is a stratigraphic unit of lacustrine origin and of greater paleontological significance among the formations that comprise the Taubaté Basin (Cogné *et al*., 2013; Voltani *et al*., 2023). The Tremembé Formation is composed of pyrobituminous shales deposited during the late Oligocene, approximately 23 million years ago (Riccomini *et al*., 1996). However, studies on fossil content, based on a relative dating concept with other deposits, due to the impossibility of absolute dating (see

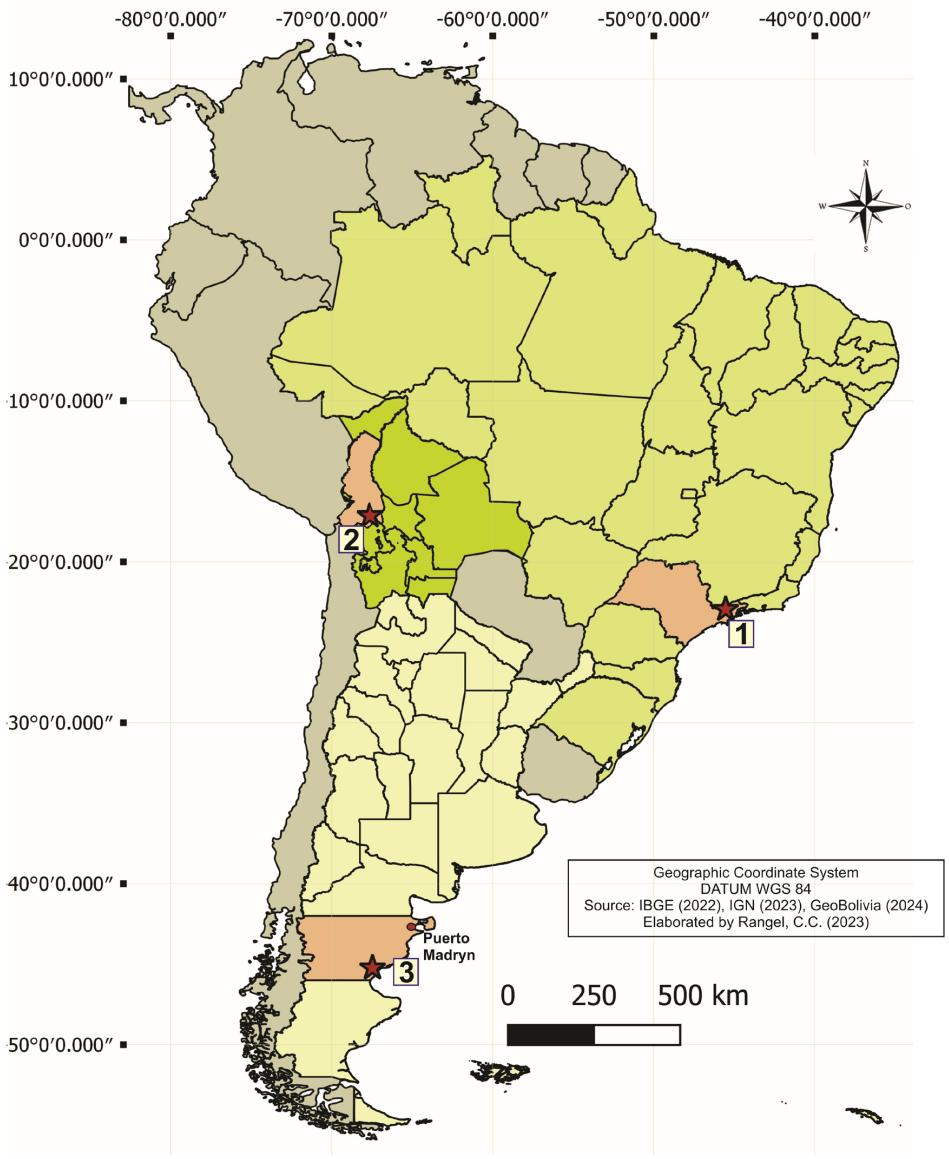

Figure 1. Map of South America indicating the Oligocene (Deseadan SALMA *Australohyaena*, *Fredszalaya*, *Notogale*, *Pharsophorus* and *Sallacyon*-bearing localities by a red star: **1**, Tremembé Formation, Brazil (MHNT.VT.2075); **2**, Estratos Salla, Salla Luribay Basin, Bolívia (*Fredszalaya hunteri* Shockey & Anaya, 2008; *Notogale mitis* Ameghino, 1897; *Sallacyon hoffstetteri* Villarroel & Marshall, 1982); **3**, Sarmiento Formation, Argentina (*Australohyaena antiqua* Forasiepi, Babot & Zimicz, 2014; *Notogale mitis*; *Pharsophorus lacerans* Ameghino, 1897 and *Pharsophorus tenius* Ameghino, 1897).

Marshall, 1985; Marshall *et al*., 1986), allow us to attribute an age that ranges from the late Oligocene to the early Miocene (Couto-Ribeiro, 2010).

Numerous studies have been carried out on the sedimentology, stratigraphy, and geomorphology of the Tremembé Formation (see Setzer, 1955; Suguio, 1969; Riccomini, 1989). In addition to invertebrate and plant fossils (Galego & Mesquita, 2000; Bernardes-de-Oliveira *et al*., 2002; Bergue *et al*., 2018; Martine *et al*., 2023; Carmo *et al*., 2024), this unit is known for its highly fossiliferous deposits mainly preserving the remains of fishes, birds and mammals (see Alvarenga, 1982, 1985, 1988, 1990, 1993a, b, 1995, 1997, 1999; Figueiredo & Costa-Carvalho, 1999; Olson & Alvarenga, 2002; Alvarenga *et al*., 2005; Malabarba & Lundberg, 2007; Melo, 2007). The Tremembé Formation also contains fossil evidence of other extinct animals, such as crocodiles, turtles, and a caecilian amphibian (see Kellner & Campos, 1999; Santos *et al*., 2024). These fossils significantly contribute to the Paleogene Brazilian fossil record, which is otherwise poorly known in this region. Among vertebrates, mammals are the most diverse group, although they are much less abundant than fish. The following groups of mammals are reported for the Tremembé Formation: Metatheria (Proborhyaenidae and Hathliacynidae), Chiroptera (Molossidae), Rodentia (Echimyidae), Cingulata (Dasypodidae),

Astrapotheria, Litopterna (Proterotheriidae), Notoungulata (Leontiniidae and Notohippidae) and Pyrotheria (Couto-Ribeiro, 2010). Overall, the Tremembé Formation is an important geological and paleontological resource that provides valuable information about the latter part of the Paleogene, due to the paleoenvironmental and biogeographical conditions evidenced in coprolites and parasites (see Fernandes *et al*., 1988, Carmo *et al*., 2023) and faunal similarities it shares with other late Oligocene deposits, such as the Salla beds from Bolivia, the locality of Quebrada Fiera from Argentina, the Fray Bentos Formation of northwestern Argentina and Uruguay, and Sarmiento Formation of Southern Argentina (Shockey, 1997, 2005; Cerdeño *et al*., 2012; Cerdeño & Vera, 2015).

MATERIAL AND METHODS

The studied specimen, MHNT.VT.2075 is housed in the paleontological collection of the Museu de História Natural de Taubaté "Doutor Herculano Alvarenga" linked to Fundação de Apoio à Ciência e Natureza (FUNAT). The radiography and tomography of the studied specimen were made using a dental X-ray machine unit and CT-scan by technician V.A.S. Bueno.

MHNT.VT.2075 was included in a phylogenetic analysis to test its affinities with other sparassodonts. The morphological data matrix used by Guimarães *et al*. (2024) is included as Supplementary Materials 1, 2 and 3. It comprises 727 characters (312 dental, 28 jaw, 183 cranial, and 202 post-cranial characters) and 110 therian taxa, including 102 metatherian taxa, from the Cretaceous and Cenozoic of North America, Asia, South America, Antarctica, Europe, and Australia. The matrix was submitted to a new technology search using TNT 1.5 (Goloboff & Catalano, 2016), employing the sectorial, ratchet, drift, and tree-fusing strategies with 100 replications. Bremer supports and tree scores were calculated with TNT 1.5. The list of characters, characters by taxon, and synapomorphies are presented as Supplementary Materials 1, 2 and 3. The data matrix is hosted at Morphobank and may be accessed by the following link: http://morphobank.org/permalink/?P5688. The password is: taubate.

The degree of curvature angle of the canine was measured by the angle formed between the final part of the canine root and the apex of the crown in MHNT.VT.2075. This approximate value was obtained using the protractor tool of the CorelDRAW software. This same method was applied to the lower canines of various sparassodonts, such as *Arctodictis* (MLP-85-VII-3-1), *Proborhyaena* (MACN-A-52-382), *Cladosictis* (MACN-A-5927) and *Prothylacinu*s (MACN-A-706-720). These measurements allowed for the classification of the canine as having an obtuse, straight, or acute angle, which in turn helped interpret the wear facets present in the teeth, indicating whether it could have a straight or procumbent orientation. Pronounced procumbence of the lower canine is a characteristic associated with Proborhyaenidae. The compared specimens had the lower canines still remaining in the dentary. Thus, the measurements were taken from the apex of the canine relative to the alveolus in the dentary . This act proved to be interesting , as it suggests that Proborhyaena underwent taphonomic alterations due to frontal compression of its canine , which presents an obtuse angle and a non-procumbent (straight) shape , not typical in Proborhyaenidae.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
METATHERIA Huxley, 1880
MARSUPIALIFORMES Vullo *et al.*, 2009
†PUCADELPHYDA Muizon *et al.*, 2018
†SPARASSODONTA Ameghino, 1894
†BORHYAENOIDEA Simpson, 1930
†PROBORHYAENIDAE Ameghino, 1897

Gen. et sp. indet.
(Figure 2)

Referred specimen. MHT.VT.2075, an isolated lower right canine.
Locality . Eastern State of São Paulo, Brazil; coordinates 22° 56'60.00"S, 45°31'60.00"W (Figure 1).
Horizon. Lower part of the Tremembé Formation, Taubaté Basin.
Age. Late Oligocene, Deseadan SALMA (*sensu* Marshall *et al*., 1983).
Measurements. The specimen MHNT.VT.2075 measures 57.3 mm maximum length (crown height + root), 32.19 mm of crown (height, circa of 56%), 19.4 mm mesiodistally (length), and 8.17 mm labiolingually (width) (see Table 1).
Description. This tooth is posteriorly and lingually curved and laterally compressed with a length/width ratio of 2.37 and a slight angle of ≅64° in relation to the cervical line. In mesial view, it presents a 5° labial displacement of the tip of its apex relative to the base (Figure 2E). The apex of the tooth is not pointed ("crushed", Figure 2F). It has a distolingual wear facet due to occlusion against the lingual side of the antagonistic upper canine (Figure 2C–D), as well as another wear facet parallel to this. This principal wear facet is oval and long, apparently smooth and oblique, extending from the distal to the labial face and well defined by sharp borders (Figure 2C–D). The apical region bears an enamel coating which thins towards its base and disappears before reaching the cervical line, i.e., the enamel coating is only evident in the apex (Figure 2A–C, E–F). Several longitudinal striae are present along the entire length of the canine, mainly on the lingual and distal sides, parallel to each other and without much proximity, being more numerous towards the base of the tooth along the root (Figure 2A). There are two sulci, one on the labial surface and another on the lingual surface. Among these sulci, the deepest is the lingual median sulcus (Figure 2A–B), which is thick, deep, and widest at the base of the root, ending close to the apex (Figure 2A, G–H). The labial sulci are thin and shallow that begins at the base of the tooth and ends in the initial third of the apex (Figure 2B–C). The cervical line (Figure 2C–D) is evident, indicating the end of the crown and beginning of the interalveolar portion. The pulp cavity is wider in the base and tapers slightly towards the

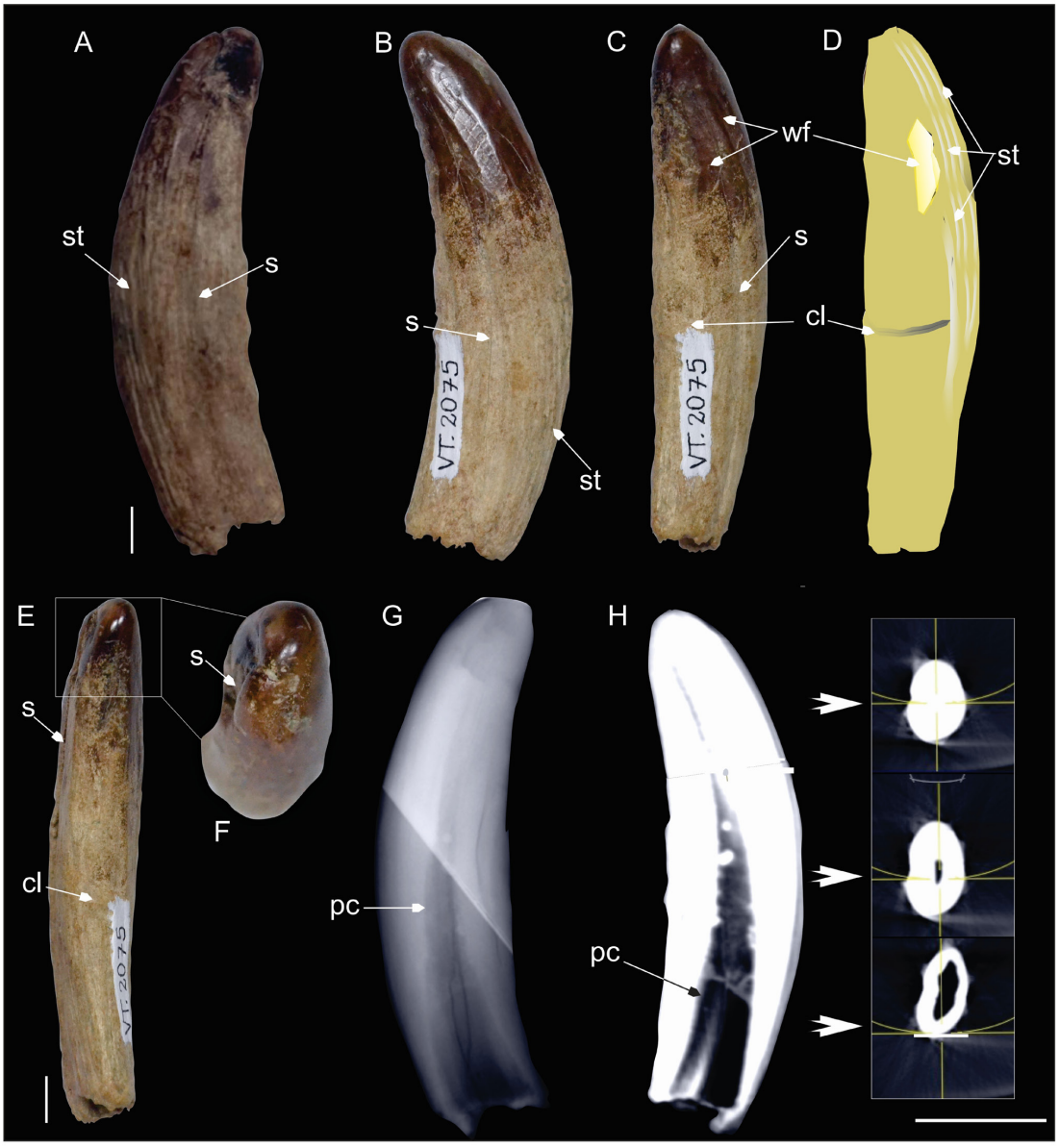

Figure 2. Right lower canine, MHNT.VT.2075: **A**, lingual view; **B**, labial view; **C**, mesio-lateral view; **D**, mesio-lateral view illustration; **E**, mesial view; **F**, apical detailed view; **G**, lingual radiography of canine and **H**, lingual tomography of base, medium and apex regions. **Abbreviations: cl**, cervical line; **pc**, pulpar cavity; **s**, median sulcus; **st**, striae; **wf**, wear facet. Scale bars: A–E = 5 mm; H = 20 mm.

Table 1. Measurement (in mm) and L/W Ratio comparison of specimens with lower canines preserved attributed to Deseadan Borhyaenidae and Proborhyaenidae taxa. **Symbols:** * represents a partial specimen. ** represents measurements based on the scale bar of images. - represents missing measurements.

Taxa	Specimen	Height	Length mesiodistal	Width labiolingual	L/W Ratio- Lower canine
Studied specimen	MHNT.VT.2075	57.3 (32.19 crown)	19.4	8.17	2.37
Australohyaena antiquua	FMNH P13633*	65.8**	28,44**	-	-
Australohyaena antiquua	UNPSJB PV 113	41.30 (right)/38.18 (left)**	33.66 (right)/35.64 (left)**	16.61 (right)/15.89 (left)**	2.02 (right)/ 2.24 (left)
Eomakharia molossus	SGOPV 3490	53.57**	5.8**	3.0	1.89
Pharsophorus lacerans	MPEF- PV 4190	61.02 (32.34 crown) **	19,01**	-	-
Pharsophorus lacerans	MACN A 52-391- Holotype	9.4 (worned crown)/37.16 (root)	15.61	11.61	1.4
Proborhyaena gigantea	MACN-A-52382	126.38 (69.39 crown)	30.0	20.0	1.5

apex (Figure 2H). The specimen is open-rooted as can be seen in the CT imagery (Figure 2H).

Remarks. A distolingual facet from occlusion against of the lingual side of antagonist upper canine is observable (Figure 2C–D), as in other proborhyaenids (*e.g.*, *Callistoe vincei*; Babot *et al*., 2022, p.474; and *Proborhyaena gigantea*; Engelman *et al*., 2020, p. 58; and Proborhyaenidae indet.; Guimarães *et al*., 2024, p. 3), demonstrating that MHNT.VT.2075 represents a lower canine (see other lower canines with a similar wear face). The distolabial wear facet could have been caused by friction with the lingual side of the upper canine (Figure 3), which affects its shape. The insertion or procumbence of the canine in the dentary significantly influences the shape and degree of wear, as it is determined by the angular relationship between the upper and lower dental arches (Figure 4). The procumbence observed in the canine of specimen MHNT.VT.2075 associated with evident wear in the crown, suggests a frequent use probably related to the capture or active processing of prey in an adult individual. The angular relationship between the upper and lower dental arches influenced occlusal dynamics, reflecting functional adaptations for delivering powerful anterior bites or securing struggling prey.

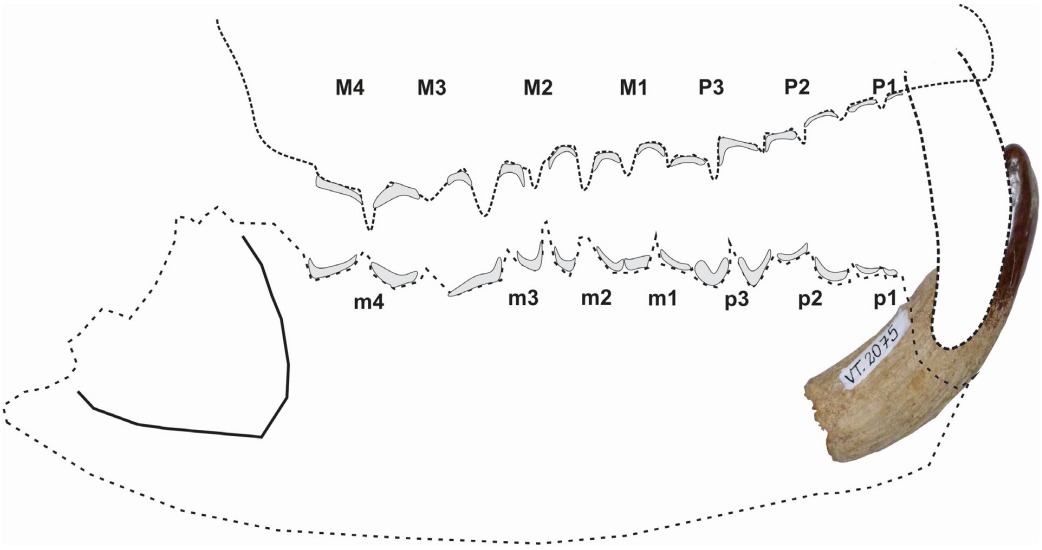

Figure 3. Hypothetical reconstruction in right labial view of the position of the canine, based on the cervical line and dental series. Antagonism to the right upper canine produces the wear facet. **Abbreviations: P/p**, upper/lower premolars *loci*; **M/m**, upper/lower molars *loci*.

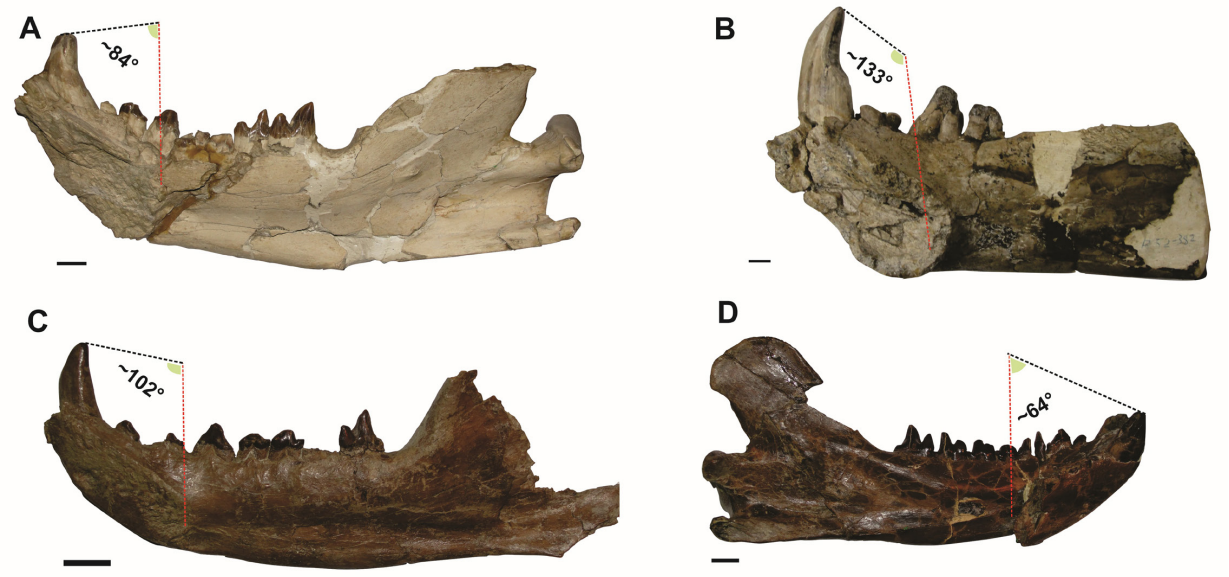

Figure 4. Degrees of inclination between the root of the lower canine and the tip of the canine in different Sparassodonta: **A**, *Arctodictis* (MLP-85-VII-3-1); **B**, *Proborhyaena* (MACN -A-52-382); **C**, *Cladosictis* (MACN-A-5927); **D**, *Prothylacinus* (MACN-A-706-720). Scale bars = 1cm.

Phylogenetic analysis

Following the results of the phylogenetic analysis, MHNT.VT.2075 was recovered in a polytomy with IGM 251108, *Thylacosmilus*, and *Anachylictis* + *Patagosmilus*, within the subfamily Thylacosmilinae subfamily. Therefore, MHNT.VT.2075 is identified here as a possible member of Thylacosmilinae (Figure 5).

The Thylacosmilidae apply a relationship very close to the Proborhyaenidae (Muizon, 1998; Babot *et al*., 2002; Babot, 2005). The subfamily Thylacosmilinae was reported for Engelman *et al*. (2020) and reiterated in Rangel *et al*. (2023a, b). Suárez *et al*. (2023, 2025) first considered Thylacosmilidae to be an independent clade and close to Proborhyaenidae (*i.e*., the classical family Thylacosmilidae), according to previous works, and more recently recognized a clade with a stock of characteristics similar to thilacosmilids, giving it the name Thylacosmiliformes. This remains a topic of debate, as our results did not permit a definitive conclusion regarding the supra-generic taxonomic rank of this clade (Thylacosmilinae or Thylacosmilidae). Based on this, we considered the abduction reasoning to use Thylacosmilidae instead of Thylacosmilinae, which is the most conservative explanation.

Suárez *et al*. (2023) identified several distinctive features of thylacosmilids canines, including: 1) hypertrophied (saber-like) upper canines, 2) upper canines clearly more developed than the lower ones, and 3) upper canines very compressed (ratio length/width greater than 1.60). These features are based on upper canines, whereas MHNT.VT.2075 is a lower one. This condition restricts comparisons between this specimen and thylacosmilines. However, lower canines of thylacosmilines lack an open root on adult individuals (Riggs, 1934; Babot *et al*., 2002; Forasiepi & Carlini, 2010). This character condition in lower canine roots is observable in MHNT.VT.2075, thus suggesting the hypothesis that it could be a Thylacosmilinae/Thylacosmilidae.

Engelman *et al*. (2020) included *Eomakhaira* within Thylacosmilinae, supported by the ch. 61, a supramental foramen character. Rangel *et al*. (2023a, b) recovered *Eomakhaira* as the sister taxon of *Arminiheringia* through sharing the ch. 180, the relation of entoconid x hypoconulid height on m2–3, with both as the sister taxa of Thylacosmilinae. If confirmed, *Arminiheringia* should also be considered a member of the Thylacosmilinae (but see Suárez *et al*., 2023). Moreover, Suárez *et al*. (2023) recovered *Eomakhaira* as the sister taxon of Thylacosmilinae in some analyses, whereas other topologies found these two taxa to be not closely related. Although we found *Eomakhaira* with similar proceedings in some trees, our results are inconclusive regarding the hypotheses mentioned above, which led us to consider *Eomakhaira* as a non-Thylacosmilinae proborhyaenid, as it was not confidently recovered in the clade that encompasses IGM 251108, *Thylacosmilus*, and *Anachylictis* + *Patagosmilus* (Thylacosmilinae/Thylacosmilidae).

Therewith, we do not consider MHNT.VT.2075 as a member of Thylacosmilinae based on its curvature (the lower canine is more conical and erect in thylacosmilines), and the presence of lingual and labial sulci (which are absent in thylacosmilines). Nevertheless, the hypothesis that MHNT.VT.2075 represents a taxon more closely related to thylacosmilines than to *Proborhyaena*, *Paraborhyaena*, *Callistoe*, *Arminiheringia* and *Eomakhaira* cannot be excluded based on the results of the phylogenetic analysis.

Furthermore, the affinities between proborhyaenid and thylacosmilid taxa remain inconclusive. Thus, a more conservative approach was considered regarding the affinities of MHNT.VT.2075. The phylogenetic hypothesis presented by Engelman *et al*. (2020), Rangel *et al*. (2023a, b) and

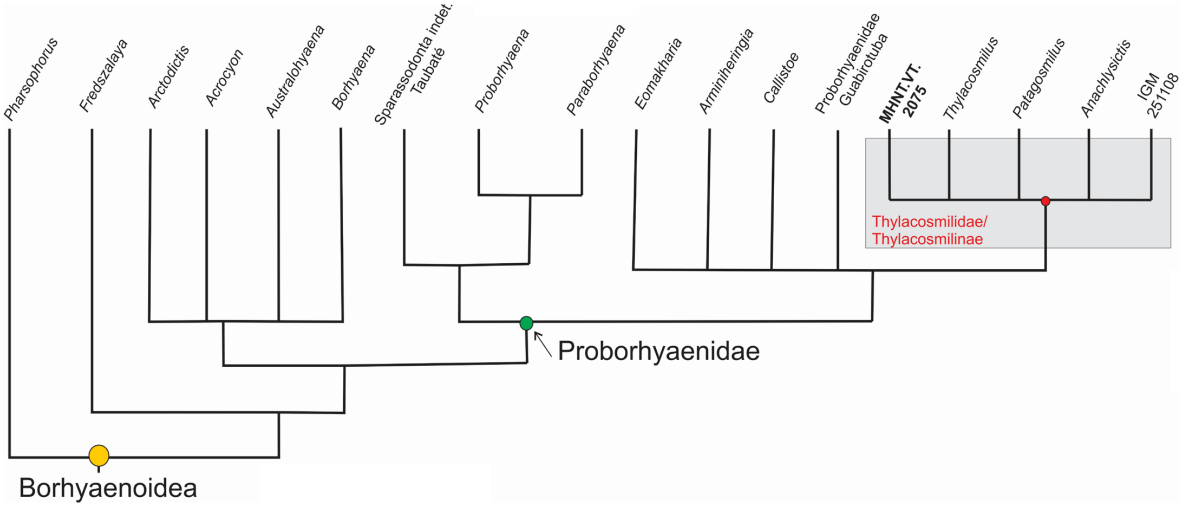

Figure 5. Simplified strict consensus tree of the seven most parsimonious trees (steps: 2614; CI: 0,303; RI: 0,670; RC: 0,203) recovered in the phylogenetic analysis. MHNT.VT.2075 is highlighted in bold. Thylacosmilidae/Thylacosmilinae is highlighted in grayish and marked by a red node. Proborhyaenidae is marked by a green node. Borhyaenidoidea is marked by a yellow node.

Guimarães *et al*. (2024) presents Proborhyaenidae as the clade that comprehending *Arminiheringia*, *Callistoe*, *Eomakhaira*, *Paraborhyaena*, *Proborhyaena* and Thylacosmilidae/Thylacosmilinae (IGM 251108, *Thylacosmilus*, and *Anachylictis* + *Patagosmilus*). Suárez *et al*. (2023) regarded the phylogenetic position of *Eomakhaira* uncertain, primarily due to the fragmentary aspect of the material, which limits the assessment of morphological characters and leads to conflicting interpretations across different analytical methods, such as implied weighted, equal weighted or Bayesian inference.

Finally, our results support the specimen MHNT. VT.2075 as a non-Thylacosmilinae/Thylacosmilidae member of Proborhyaenidae (see the mereophyletic groups of Proborhyaenidae and Thylacosmilinae in our phylogenetic analysis, Figure 4).

DISCUSSION

The specimen MHNT.VT.2075 (Figure 2) has a distinct distolingual wear facet on its apex, which indicates that this specimen is a lower canine of a young individual. In addition, the presence of striae (=grooves) and labial and lingual midline sulci identifies and characterizes this canine as a borhyaenoid sparassodont. This specimen displays several features associated with proborhyaenids: large size, less conical apex, posteriorly curved teeth, open-rooted, deep median sulcus on lingual face and shallow sulcus in labial face, striae on the base of the tooth, and enamel present on the apex, thickening downwards its base, becoming absent on most of the tooth. The body mass of the specimen couldn't be estimated.

The presence of open-rooted canines has been considered as a synapomorphy of Proborhyaenidae (*e.g*., Marshall, 1978; Babot *et al*., 2002, 2022; Babot, 2005; Engelman *et al*., 2020; Rangel *et al*., 2023a, b; Guimarães *et al*., 2024). Some authors have associated the open-rooted condition with the restriction of the enamel to the apical region, lacking in most of the crown (von Koenigswald, 2011, 2018; Madden, 2015; Engelman *et al*., 2020; Babot *et al*., 2022), while others have noted a direct relationship with cranial ontogeny (Argot, 2003; Gaillard *et al*., 2023). Specimen MHNT.VT.2075 provides new evidence associated with the first hypothesis.

Proborhyaenids have open roots, posteriorly curved canines, with lingual and labial sulci. Meanwhile, thylacosmilids/thylacosmilines only retain open roots on upper canines. It has been discussed that the closed roots on lower canines are a reversal from a proborhyaenid condition caused by the hypertrophy of the upper canines, which would be ever-growing in time (Babot *et al*., 2002; Forasiepi & Carlini, 2010; Engelman *et al*., 2020). In summary, these facts are intrinsically related to the structural integrity aspect of the tooth (see Folinsbee *et al*., 2007; Orr *et al*., 2007; Turvey, 2010). The presence of striae and sulci in the canines is common in large sparassodonts (*e.g*., *Arctodictis*, *Borhyaena*, *Callistoe*, *Paraborhyaena* and *Proborhyaena*) (Forasiepi *et al*., 2015). Both Folinsbee *et al*. (2007) and Orr *et al*. (2007) suggested the hypothesis that longitudinal sulci (or the margins that define the sulci) may act to increase the structural integrity of the canine, either by providing greater surface area for enamel or as a secondary consequence of selection for longitudinal striae or ridges to buttress the tooth.

As for labial sulci, Babot *et al*. (2002) noticed that the labial sulcus was generally shallower than the lingual in proborhyaenids, while Suarez *et al*. (2023) observed that labial sulci are absent on Thylacosmilinae lower canines (*i.e*., *Anachlysictis*). Based on this combination of features (*i.e*., presence of open roots and labial sulci), the specimen MHNT.VT.2075 cannot be identified as a thylacosmiline/thylacosmilid sparassodont. Therefore, MHNT.VT.2075 is more closely related to the Proborhyaenidae or non-thylacosmiline/thylacosmilid proborhyaenids (Figure 5).

The tooth section pattern, in longitudinal or transverse section, provides interesting information about the internal structure. The cross-section tomography of MHNT.VT.2075 (Figure 2H) presents an 8-shaped configuration. Babot *et al*. (2002) observed such an 8-shaped pattern, which is often considered diagnostic for Proborhyaenidae, this being caused by the deep median sulci. Engelman *et al.* (2020, suppl. inf., p. 60) indicated that canine median sulci are much more widely distributed in sparassodonts than previously thought, occurring in *Pharsophorus lacerans*, *Arctodictis munizi*, *Arctodictis sinclairi*, *Australohyaena antiquua*, *Borhyaena macrodonta*, although non-proborhyaenid sparassodonts only bear the lingual sulcus (except *Arctodictis*). The specimen MNHT.VT.2075 exhibits a deep median lingual sulcus and a shallow median labial sulcus, resembling the 8-shaped set described by Babot *et al*. (2002).

During the Oligocene, three proborhyaenids are formally recognized: *Eomakhaira molossus*, *Paraborhyaena boliviana* and *Proborhyaena gigantea*. *Eomakhaira* occurs in the Abanico Formation, in the central region of Chile (Engelman *et al*., 2020), probably dated as early Oligocene (?Tinguiririan SALMA, but see Croft *et al*., 2008). *Paraborhyaena boliviana* is only recorded from the Estratos Salla of Salla-Luribay Basin at western Bolivia, dated as late Oligocene (Deseadan SALMA; see Hoffstetter & Petter, 1983, Shockey & Anaya, 2008). *Proborhyaena gigantea* was also recorded for the Fray Bentos Formation from Santa Lucia Basin in Uruguay (*Proborhyaena* cf. *gigantea*) and Sarmiento Formation from San Jorge Basin in Argentina, which are all dated as late Oligocene (Deseadan SALMA; see Bond & Pascual, 1983; Mones & Ubilla, 1978; Forasiepi, 2009)

Specimen MHNT.VT.2075 shares a larger combination of features with *Eomakhaira* than with *Proborhyaena* and *Paraborhyaena*. MNHT.VT.2075 and *Eomakhaira* share the presence of thin enamel layer present on the apex of the canine, the lingual sulcus, lower canine rounded, reniform aspect (incipient 8-shaped) in cross-section, a widening of the root edge outwards in cross-section that connecting the pulp cavity to the tooth, open-rooted, the striae in base (*sensu* Engelman *et al*., 2020), however the proportions of the teeth are much different (see Table 1). Based on the results of the phylogenetic analysis, it's possible that these features and morphology represent the

simplesiomorphic condition of Proborhyaenidae. Therefore, the similarities between specimen MHNT.VT.2075 and *Eomakhaira* are more than one labial sulcus and lower canine L/W Ratio.

Australohyaena antiqua occurs in the Sarmiento Formation, in Patagonia region from Argentina (Forasiepi *et al*. 2015), dated as late Oligocene (Deseadan SALMA, but see Croft *et al*., 2008). *Fredzalaya hunteri* occurs in Salla Beds of Salla-Luribay Basin at western Bolivia, dated as late Oligocene (Deseadan SALMA; see Shockey & Anaya, 2008). Finally, *Pharsophorus lacerans* and *Pharsophorus tenax* occur in the Sarmiento Formation, in the Patagonia region, Argentina (Reguero & Escribano, 1996; Forasiepi *et al*., 2015), dated as late Oligocene (Deseadan SALMA, but see Croft *et al*., 2008) and Salla Beds from Bolivia (Patterson & Marshall, 1978; Hoffstetter & Petter, 1983).

Furthermore, MHNT.VT.2075 is more similar in size to *Pharsophorus* than to other non-proborhyaenid borhyaenoid of the Oligocene, however it differs morphologically. Out of the two species of *Pharsophorus*, only *P. lacerans* has preserved lower canines. The lower canine of *P. lacerans* is corrugated with small striae and grooves on canine surface of the roots, absent prominent median sulci canine on labial faces, presence of a prominent median sulci on lingual face, single-rooted lower canine, without compression or slightly compressed canine (length/width <1.60), lateral compression and closed roots in adults, vertical procumbence, with moderately to thick enamel layer on the tooth. Furthermore, there is no labial sulcus in *Pharsophorus*, as well as the other non-proborhyaenid borhyaenoids mentioned above.

The temporal distribution of the Proborhyaenidae/non-thylacosmilinae proborhyaenids is from the Eocene to the Oligocene, while Thylacosmilidae/Thylacosmilinae from the Miocene to the Pliocene thus further suggesting the association of MHNT.VT.2075 with Proborhyaenidae/non-thylacosmilinae proborhyaenids. Regarding the geographic aspect, the Tremembé Formation and the Salla Beds (Oligocene, Deseadan SALMA), where *Australohyaena*, *Fredszalaya*, *Notogale*, *Pharsophorus* and *Sallacyon* are recorded both occur at almost the same latitude (20°S), which may be indicative of a similar paleoenvironment, at a time when the Andean uplift was not at its peak, which affected the entire South American Cenozoic.

Moreover, the identification of a lower canine of a proborhyaenid in southeastern Brazil extends the geographic distribution of this clade and adds a second record of a member of this clade in Brazil (see Couto Ribeiro, 2010). Proborhyaenids are considered as the largest hypercarnivorous mammals during the Oligocene (*e.g*., Prevosti & Forasiepi, 2018). Based on this, the specimen MHNT.VT.2075 can be considered as a possible apex predator of the Taubaté local fauna, which was composed of large herbivores, such as Astrapotheria, Notoungulata and Pyrotheria.

In summary, the results of the phylogenetic analysis place MHNT.VT.2075 within the Proborhyaenidae, although the polytomy restricts further conclusions regarding whether it is closer to the Thylacosmilinae/Thylacosmilidae or Proborhyaenidae/non-thylacosmilinae proborhyaenids. The presence of open root and median sulci on both lingual and labial faces helped exclude comparisons with borhyaenids (as described in *e.g*., Babot *et al*., 2002, 2022; Engelman *et al*., 2020). The Thylacosmiliformes clade proposed by Suarez *et al*. (2025) supports the interpretation that MHNT.VT.2075 belongs within Proborhyaenidae, the sister lineage of the Thylacosmiliformes.

CONCLUSIONS

The specimen MHNT.VT.2075, a lower canine recovered from the Tremembé Formation. Taubaté Basin, Oligocene of southeastern Brazil (Deseadan SALMA) represents a proborhyaenid sparassodont. This specimen can be confidently attributed to a Proborhyaenidae non-thylacosmiline/Thylacosmilidae based on combinations of features, such as, the presence of an open root, a graduation from coarse apical to thin basal enamel layer, curved lower canine, and presence of median labial and lingual sulci. The phylogenetic analysis places MHNT.VT.2075 as a stem Proborhyaenidae in a polytomy with the Thylacosmilinae/Thylacosmilidae. This new record supports the presence of a large sparassodont predator in the swamp/lacustrine depositional environment of the Tremembé Formation and suggests it possibly has occupied the role of apex predator of the Taubaté mammalian fauna.

DATA AVAILABILITY STATEMENT

Data will be available upon request.

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AUTHOR CONTRIBUTIONS

Caio César Rangel: writing – original draft, methodology, editing, visualization, investigation, formal analysis, software,

resources, data curation. Graziella do Couto-Ribeiro: writing – original draft, methodology, editing, visualization, investigation, formal analysis, software, resources, data curation. Bruno Mauricio Graichen Guimarães: editing, investigation, formal analysis. Édison Vicente Oliveira: review. Elizabeth Höfling: review. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used generative AI in scientific writing.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Material

Supplementary material accompanies this paper.

Supplementary Material 1. Characters and states of phylogenetic analysis. Characters and states used in the phylogenetic analysis. Characters are coded with respect to Kielantherium gobiense as outgroup. All characters are treated as unordered.

Supplementary Material 2. MatrixCoutoRibeiro_et_al_Canine_Proborhyaenidae.

Supplementary Material 3. MatrixCoutoRibeiro_et_al_Canine_Proborhyaenidae+(1).

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