



A reassessment of *Nemolestes* (Mammalia, Metatheria): Systematics and evolutionary implications for Sparassodonta

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Accepted: 27 April 2023 / Published online: 7 June 2023

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Abstract

Nemolestes and *Procladosictis* are Eocene sparassodonts of controversial affinities. Nevertheless, despite the poor preservation of their holotypes, several other specimens have been tentatively assigned to these genera, as exemplified by some isolated teeth from the Itaboraí and Laguna Fría faunas. Here, we revise specimens referred to *Nemolestes* and *Procladosictis* from Itaboraí, Laguna Fría and Ameghino's collection. *Nemolestes* differs from *Patene* in its more reduced metaconid, and "carnassialized" m4 (with reduced talonid and talonid cuspids, except the hypoconulid), features that make it possible to identify specimens from Itaboraí and Laguna Fría as *Nemolestes*. This taxon occurred from the early Eocene (Itaboraian SALMA) to the middle Eocene (Casamayoran SALMA). *Nemolestes* represents the oldest known hypercarnivorous sparassodont. The inclusion of *Nemolestes* and *Procladosictis* in a comprehensive phylogenetic analysis recovered them in a polytomy as the sister taxa of Borhyaenoidea and a new unnamed clade that includes *Lycopsis*, *Dukecynus*, Hathliacynidae, *Hondadelphus* and *Stylocynus*. *Nemolestes* shares with these taxa, but not *Patene*, the presence of a "carnassialized" m4. *Nemolestes* differs from known borhyaenoids in the absence of a medially positioned protoconid and short anterolabial cingulid. Therefore, *Nemolestes* is an early lineage of Sparassodonta. "*Procladosictis erecta*" is a lower premolar of the unnamed clade, as it shows symmetric walls and a small precingulid. "*Procladosictis erecta*" should be, in fact, referred to *Procladosictis*. Our phylogenetic analysis indicates that during the early middle Eocene (Laguna Fría and La Barda faunas), the unnamed clade and Borhyaenoidea had already diverged. Therefore, the evolutionary history of these groups is older than previously thought.

Keywords Hypercarnivory · Itaboraian · Paleogene · South America · Teeth

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Introduction

Sparassodonts are a group of endemic South American carnivorous metatherians (Prevosti et al. 2013; Prevosti and Forasiepi 2018) that inhabited South America from the Paleocene to the Pliocene (Muizon et al. 2018; Prevosti and Forasiepi 2018). However, despite the long evolutionary history of this group, their early evolution (i.e., pre-late Oligocene) is still poorly known (Engelman et al. 2018, 2020b; Engelman and Croft 2021).

Among Eocene sparassodonts, *Nemolestes* is currently considered a monotypic genus, as the type species, *Nemolestes spalacotherinus* from the middle Eocene (Casamayoran SALMA), Argentina (see Prevosti and Forasiepi 2018), is the only currently recognized taxon. *Nemolestes spalacotherinus* is only known from its holotype, MACN-A 10330, which consists of two broken molar trigonids MACN-A 10330a and MACN-A 1033b and the tip of a canine MACN-A 10330c (Ameghino 1902).

Nevertheless, despite the poor preservation of the holotype of *Nemolestes spalacotherinus*, several other sparassodont specimens have been tentatively assigned to this genus. These include: MN 1344-V, a left m4 from the early Eocene fauna of Itaboraí (Marshall 1978; Bergqvist et al. 2009); LIEB-PV 1038, an incomplete right m4 from the middle Eocene Laguna Fría local fauna, Argentina (Tejedor et al. 2009); MCN.P.1259, an incomplete left dentary with p2-m3 from the middle Eocene Guabirota Formation of southern Brazil (Sedor et al. 2017); and AMNH 29433, a left m2 or m3 from the late Eocene (Mustersan) beds at Cerro del Humo, Argentina (Simpson 1948; Marshall 1981) (Fig. 1). These specimens are widely distributed across space and time (Itaboraian to Mustersan SALMAs, early Eocene to late Eocene), and do not share any features that would allow them to be assigned to a single taxon aside from general arguments based on “stage of evolution”. Thus, *Nemolestes* as currently defined is essentially a “wastebasket” taxon.

Nemolestes was originally considered to be a borhyaenid by Marshall (1978) (= Borhyaeninae of that author). However, Zimicz (2012), Carneiro and Oliveira (2017), Carneiro (2018), Prevosti and Forasiepi (2018), and Rangel et al. (2019) considered *Nemolestes* to be an early sparassodont, diverging prior to the major sparassodont clades of Hondadelphidae, Hathliacynidae and Borhyaenoidea. The controversial affinities of this taxon are largely due to the fragmentary nature of the holotype, which limits direct comparisons with other sparassodonts and makes it unclear if the other material assigned to *Nemolestes* pertains to this taxon. Another key taxon in this context is *Procladosictis anomala*, whose holotype may constitute the upper dentition of *Nemolestes*. *Procladosictis anomala* is a late Eocene (Mustersan SALMA) taxon that is only known by the type specimen, MACN-A 10327, a fragment of a right maxilla with P3-M3 (Marshall 1981).

Of the additional material currently referred to as *Nemolestes*, the fossils from the Itaboraí fauna (Bergqvist et al. 2009) are probably the most important, because it consists of well-preserved molars, it allows for direct comparisons with the fragmentary specimens of *Nemolestes spalacotherinus* and other incomplete Eocene sparassodonts. The *Nemolestes* specimens from Itaboraí are also some of the oldest known sparassodont fossils in South America (alongside *Patene simpsoni* from the same fauna). The sparassodont fauna of Itaboraí is particularly important in how it pertains to the initial diversification of the group and is only represented by a small number of small-bodied, generalist species. By contrast, in the younger middle Eocene faunas of Laguna Fría and La Barda (between 49.26 ± 0.30 Ma and 43.50 ± 1.14 Ma; see Gosses et al. 2021), generalized early-diverging sparassodonts like *Nemolestes* are found together with larger hypercarnivorous sparassodonts with putative affinities to hathliacynids? and borhyaenoids (Tejedor et al. 2009). Sparassodonts exhibit a striking increase in size and ecological diversity during the middle-late Eocene, and in this respect the specimens from Itaboraí and “Paso del Sapo” local faunas could help to elucidate the early evolution of the group and how it may be linked with abiotic events such as the Paleocene-Eocene Thermal Maximum.

Based on this, the goals of this contribution are to: (1) present a redescription of the specimens assigned as cf. *Nemolestes* sp. from the Itaboraí and Laguna Fría local faunas in order to evaluate their affinities with *Nemolestes*, *Patene* and other sparassodonts; (2) provide a taxonomic review of other incomplete sparassodonts from the Eocene (*Procladosictis*, “*Procladosictis erecta*” and “*Pseudocladocictis determinabile*”); and (3) re-evaluate the occurrence of some of the late Oligocene-Neogene groups of sparassodonts (e.g., Hathliacynidae) during the Eocene in South America.

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; LIEB-PV, Laboratorio de Investigaciones en Evolución y Biodiversidad – Vertebrate Paleontology Collection, Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia “San Juan Bosco”, Esquel, Argentina; 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, Museu de Ciências da Terra, fossil mammal collection, Rio de Janeiro, Brazil (replacing DGM, Divisão de Geologia e Mineralogia); MN, Museu Nacional, Rio de Janeiro, Brazil; MPEF-PV, Sección Paleontología Vertebrados, Museo Paleontológico “Egidio Feruglio”, Trelew, Argentina.

Other abbreviations Hpo, relative height of the protoconid on m3-4; Lm, lower molar length; M, upper molars with the numbers corresponding to its positioning (M1-4); m, lower molars with the numbers corresponding to its positioning



Fig. 1 Map of South America indicating *Patene*, *Nemolestes* and *Procladosictis*-bearing localities by a star: **1**, Itaboraí fauna, Itaboraí Formation, Itaboraian SALMA (early Eocene), Brazil (*Patene simpsoni* and *Nemolestes brasiliensis* sp. nov.); **2**, Sarmiento Formation, Gran Barranca (south slope of the Colhué-Huapi Lake), Barrancan sub-SALMA (middle Eocene), Argentina (*Patene coluapiensis* and “*Pseudocladosictis determinabile*”); **3–4**, El Tonco Valley and Quebrada Grande, Los Cardones National Park, Quebrada de Los Colorados Formation, Barrancan sub-SALMA (middle-late Eocene), Argentina (*Patene coloradensis*); **5**, Santa Rosa local fauna, ?Yahuarango

Formation (early Oligocene), Peru (*Patene campbelli*); **6**, Laguna Fría local fauna, La Huitrera Formation (middle Eocene), Argentina (*Nemolestes lagunafriensis* sp. nov.); **7**, Sarmiento Formation, Gran Barranca (north slope of the Colhué-Huapi Lake), Casamayoran SALMA (middle-late Eocene), Argentina (*Nemolestes spalacotherinus* and “*Procladosictis erecta*”); **8**, Musters Formation and Roth’s “Lago Musters” locality, Cerro del Humo, Mustersan SALMA (late Eocene), Argentina (cf. *Nemolestes*?/cf. *Procladosictis*?); **9**, Guabirota local fauna, Guabirota Formation, Barrancan sub-SALMA (middle Eocene), Brazil (*Nemolestes* sp. indet.)

(m1-4): **MPT**, Most parsimonious Tree: **P**, upper premolars with the numbers corresponding to its positioning (P1-3): **p**, lower premolars with the numbers corresponding to its positioning (p1-3): **PETM**, Paleocene-Eocene Thermal Maximum: **SALMA**, South American Land Mammal Age: **SEM**, scanning electron microscope: **St**, stylar cusp.

Materials and methods

The Brazilian specimens are accessioned at MCT.M and MN. The specimen LIEB-PV 1038 is repositated at LIEB-PV. The holotypes of *Nemolestes spalacotherinus* and *Procladostictis anomala* are repositated at the MACN. Information about the localities of studied specimens is presented as Table 1. The complete list of studied specimens is included in the Online Resource 1: Appendices 1 and 2.

For *Nemolestes*, which is known only by isolated lower molars, estimation of body mass (BM) was based on the regression equations of Gordon (2003) obtained from a pooled sample of marsupials (Didelphidae, excluding *Caluromys*, and Dasyuridae). For this taxon, we calculated BM based on m4 length. For *Patene simpsoni* and *P. coloradensis*, we used the equations of Myers (2001), who considered the upper and lower molar series length or the alveolar length when molars were not preserved in situ. These formulae, the specimens that were used, and calculated body masses are included in Online Resource 1: Appendix 3. The body mass estimates (BM) of other sparassodonts were obtained from Zimicz (2012), Prevosti et al. (2013), and Prevosti and Forasiepi (2018).

The morphological data matrix followed Oliveira et al. (2021), Engelman et al. (2020b) and Muizon and Ladevèze (2020, 2022), which is included in the Online Resource 1. It comprises 576 characters and 80 therian taxa, including 72 metatherians and closely related 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 with TNT 1.5 (Goloboff and Catalano 2016) using the sectorial, ratchet, drift, and tree-fusing strategies with 100 replications. Bremer supports and tree scores were calculated with TNT 1.5. Two analyses were performed: (1) with all characters treated as unordered and (2) with some characters treated as ordered (see the ordered data matrix file for the list of ordered and unordered characters). The list of characters (Online Resource 1: Appendix 4), characters by taxon of the unordered (Online Resource 1: Appendix 5) and the ordered (Online Resource 1: Appendix 7) matrixes, and synapomorphies of the unordered (Online Resource 1: Appendix 6) and ordered (Online Resource 1: Appendix 8) matrixes are included in the Online Resource 1. The data matrix is repositated at Morphobank and can be accessed by the following link: https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4509.

Systematic paleontology

Mammalia Linnaeus, 1758
 Metatheria Huxley, 1880
 Marsupialiformes Vullo et al., 2009
 Sudameridelphia Szalay, 1994
 †Pucadelphyda Muizon et al., 2018
 †Sparassodonta Ameghino, 1894
 †*Nemolestes* Ameghino, 1902
 (Figs. 2–3, 5).

Type species. *Nemolestes spalacotherinus*.

Included species. *Nemolestes brasiliensis* sp. nov. and *N. lagunafriensis* sp. nov.

Type locality and horizon. Sarmiento Formation, Barranca Norte de Lago Colhue Huapi, Chubut, Argentina. Middle Eocene, Casamayoran SALMA, “Couches á *Notostylops*” local fauna (Prevosti and Forasiepi 2018).

Locality and horizon. Itaboraí Basin, Rio de Janeiro, Brazil (Bergqvist et al. 2009). Early Eocene, Itaboraian SALMA, Itaboraí local fauna (Woodburne et al. 2014); Tuffs filling of Laguna Fría, Chubut, Argentina. Middle Eocene, Laguna Fría local fauna (Tejedor et al. 2009) (between 49.26 ± 0.30 Ma and 43.50 ± 1.14 Ma; Gosses et al. 2021); Sarmiento Formation, Barranca Norte de Lago Colhue Huapi, Chubut, Argentina. Late middle Eocene, Casamayoran SALMA, “Couches á *Notostylops*” local fauna (Prevosti and Forasiepi 2018).

Diagnosis. Emended from Ameghino (1902) and Marshall (1978). Medium-sized, South American, Eocene sparassodont with a body mass greater than 4.06 kg (see e.g., 6.5 kg, Zimicz 2012; ~5.00 kg, Prevosti et al. 2013; 5.72 kg, Prevosti and Forasiepi 2018). Differs from *Patene* based on its evident larger size (the smallest of its species, *Nemolestes brasiliensis*, is as larger as *P. coluapiensis*, the largest species of *Patene*, and ca. 26% larger than *P. simpsoni*), m4 with talonid mesiodistally much shorter than the trigonid (i.e., between 25–27% of m4’s length and ca. 44% in *Patene*), and m4 with the metaconid much more reduced than the paraconid (less than 50% of paraconid height). Differs from *Patene simpsoni*, but not *P. coloradensis*, in the presence of a centrally positioned hypoconulid on m4. Differs from *Chlorocyon* in the inferred absence of a m4 with talonid reduced to a “heel-like” structure (i.e., talonid lacking a distinct hypoconulid or simple, non-basined “heel”; see Engelman et al. 2018). Differs from *Hondadelphys* in the protoconid distinctly wider at mid-height than at base, and height of protoconid relative to length in m3 (Hpo/Lm) > 0.90 (see Muizon et al. 2018) (lower than 0.90 in *Hondadelphys*). Differs from hathlyacinids in the presence of an identifiable metaconid on all lower molars and protoconid not medially positioned (=protoconid at midline of tooth/trigonid basin floor lost, see Engelman et al. 2020b), retaining the “subtriangular” shape

Table 1 Localities with *Nemolestes*, *Procladosictis*, cf. *Nemolestes* sp., “*Procladosictis erecta*” and “*Pseudocladocictis determinabile*”

Taxon	Locality	Geographic location	SALMA/fauna	Estimated age	Geologic age	Geologic unit	Geographic coordinates	Main reference
<i>Nemolestes brasiliensis</i>	São José de Itaboraí	Rio de Janeiro, Brazil	Itaboraian	?	Early Eocene	Itaboraí Basin	22° 45' 9.9" S, 42° 51' 53.5" W	Bergqvist et al. (2009)
<i>Nemolestes lagunafriensis</i>	Laguna Fría	Chubut, Argentina	Paso del Sapo fauna	49.26 ± 0.30–43.50 ± 1.14 Ma	Middle Eocene	La Huitrera Formation	42° 43' 31.5" S, 69° 51' 36.1" W	Tejedor et al. (2009)
<i>Nemolestes spalacotherinus</i>	Couches à <i>Notostylops</i> , Gran Barranca (north slope of the Colhué-Huapi Lake)	Chubut, Argentina	Casamayoran	?	Middle Eocene	Sarmiento Formation	?	Prevosti and Forasiepi (2018)
“ <i>Procladosictis erecta</i> ”	Partie supérieure des couches à <i>Notostylops</i> , Gran Barranca (north slope of the Colhué-Huapi Lake)	Chubut, Argentina	Casamayoran	?	Middle Eocene	Sarmiento Formation	?	Ameghino (1902)
“ <i>Pseudocladocictis determinabile</i> ”	Partie supérieure des couches à <i>Notostylops</i> , Gran Barranca (south slope of the Colhué-Huapi Lake)	Chubut, Argentina	Casamayoran	?	Middle Eocene	Sarmiento Formation	?	Ameghino (1902)
<i>Nemolestes</i> sp. indet./ <i>Nemolestes spalacotherinus</i>	Guabirota	Paraná, Brazil	Barrancan	?	Middle Eocene	Guabirota Formation	25° 30' 30" S, 49° 20' 30" W	Sedor et al. (2017)
<i>Procladosictis anomala</i>	Couches à <i>Astraponotus</i>	Chubut, Argentina	Mustersan	?	Latest middle-earliest late Eocene	Musters Formation	?	Prevosti and Forasiepi (2018)
cf. <i>Nemolestes</i> sp./cf. <i>Procladosictis</i> sp.	Roth's “Lago Musters” locality	Cerro del Humo, Chubut, Argentina	Mustersan	?	Late Eocene	Musters Formation	?	Simpson (1948)

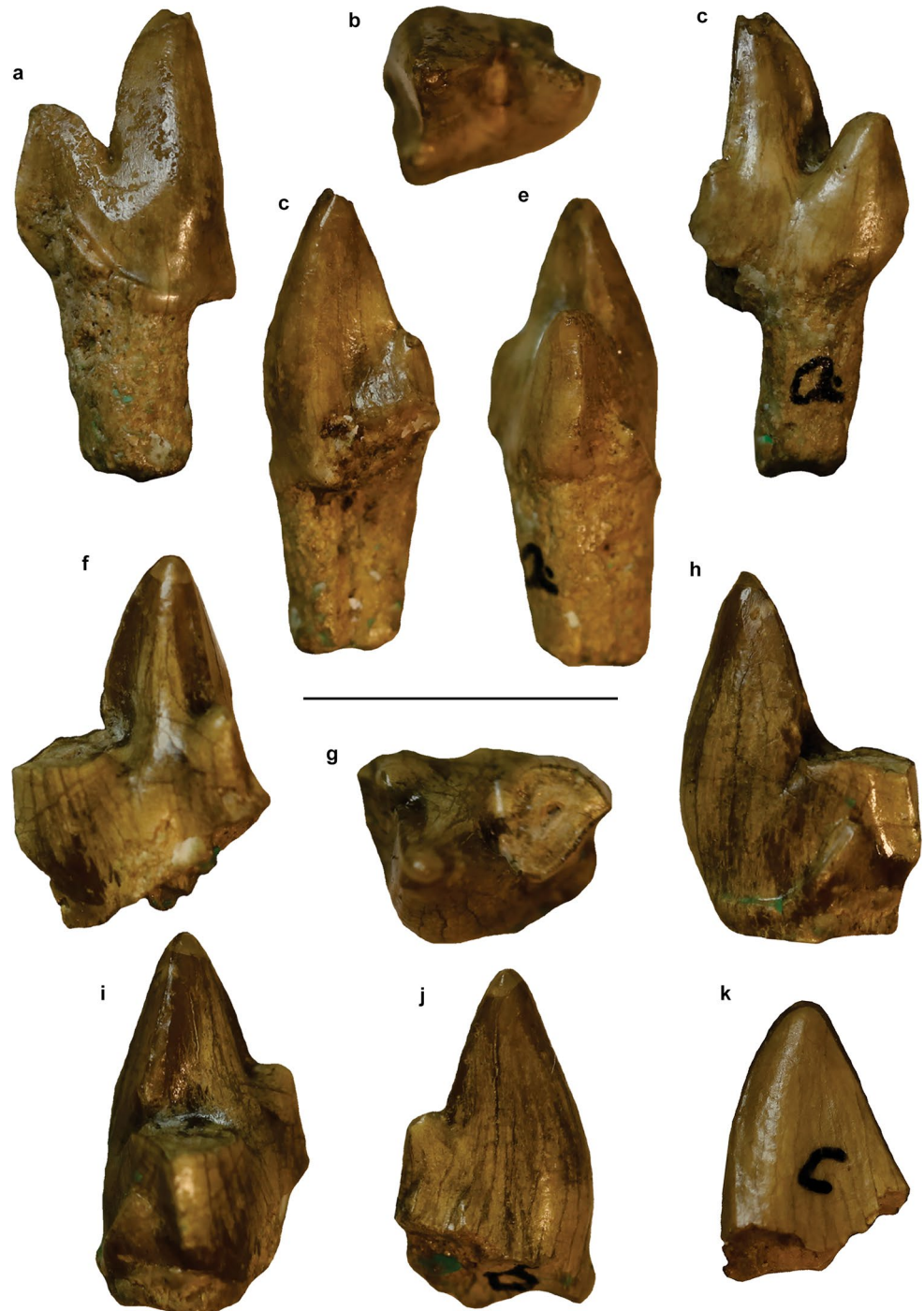
of the trigonid on the lower molars (i.e., labially/buccally placed protoconid). Differs from borhyaenoids in the absence of a m4 with talonid reduced to a “heel-like” structure, protoconid not medially positioned and anterobasal cingulid more developed, reaching the protoconid.

Remarks. *Nemolestes* was a very enigmatic taxon, mostly known by the very fragmentary condition of its type species. Originally, the specimens of this taxon were considered as representing a Paleogene lineage of Spalacotheriidae, a

Cretaceous group of mammals (Ameghino 1902). However, Simpson (1948: p. 46) and Marshall (1978: p. 26) included *Nemolestes* within Metatheria, as the two molars preserved only the trigonid. Despite its fragmentary condition, *Nemolestes* can be identified from other Eocene taxa. Therefore, *Nemolestes* is here considered as a valid taxon.

†*Nemolestes spalacotherinus* Ameghino, 1902
Fig. 2

Fig. 2 *Nemolestes spalacotherinus*. Photographs of referred specimens: **a–e**. MACN-A 1033a, left m2, in labial (**a**), occlusal (**b**), lingual (**c**), distal (**d**) and mesial (**e**) views; MACN-A 1033b, right m4: in labial (**f**), occlusal (**g**), lingual (**h**), mesial (**i**) and distal (**j**) views; MACN-A 1033c, isolated protoconid (**k**). Scale bar equals 10 mm



Holotype. MACN-A 1033a, a left m2 trigonid (Fig. 2a-e); MACN-A 1033b, a right m4 trigonid (Fig. 2f-j); MACN-A 1033c, a broken tip of a lower canine (Fig. 2k).

Hypodigm. The type only.

Locality and horizon. “Couches á *Notostylops*” local fauna, Sarmiento Formation, Barranca Norte de Lago Colhue Huapi, Chubut, Argentina (Middle Eocene, Casamayoran SALMA; see Prevosti and Forasiepi 2018).

Diagnosis. Emended from Ameghino (1902) and Marshall (1978). Differs from *Nemolestes brasiliensis* based on its larger size and metaconid reduced to a tiny cuspid. Differs from *N. lagunafriensis* based on its larger size.

Description. The trigonid of m2 MACN-A 1033a shows a paraconid that is markedly taller and more robust than the metaconid, which is reduced to a tiny cuspid. The paraconid shows a mesial keel (sensu Muizon and Ladevèze 2020, character 254, state 1), similar to *Patene* and *Nemolestes*. The protoconid is the largest cuspid of the trigonid. The labial side of the protoconid is convex in distal view (Fig. 2d). The anterolabial cingulid is moderately developed and extends from the paraconid to the labial wall of the protoconid (=developed or long; see Muizon et al. 2018, ch. 81, state 0). The length ratio between the trigonid of MACN-A 1033a and the trigonid of MACN-A 1033b (m4) is 0.82, which is compatible with an expected size ratio between m2/m3 or m2/m4 of sparassodonts, as an m1 would be smaller (see Online Resource 1: Appendix 9). Therefore, this tooth is suggested to be an m2 based on its relative size and presence of a slightly mesiodistally elongated paraconid that is somewhat obliquely oriented.

The trigonid of m4 MACN-A 1033b is visibly broader and more robust than the preserved m2. The paraconid is damaged, lacking most of its structure; even so, it is significantly more robust than the metaconid. Based on its preserved base, the paraconid is shorter than the protoconid (Fig. 2f). The metaconid is reduced to a very short cuspid and is by far the smallest cuspid of the trigonid. The metaconid is placed at the disto-lingual wall of the protoconid. The protoconid is the largest cuspid of the trigonid. The labial side of the protoconid is convex in distal view (Fig. 2j). The anterolabial cingulid extends from the paraconid to the labial wall of the protoconid. This specimen is here identified as a m4 due to its dimensions, reduced metaconid and enlarged somewhat mesially oriented paraconid.

The trigonid of MACN-A 1033b is very similar to MN 1344-V (here regarded as a m4 of *Nemolestes brasiliensis*, see below). Therefore, we suggest that MACN-A 1033b should represent the same molar locus as MN 1344-V (i.e., m4). The m3 of *Nemolestes* sp. indet. from the Guabirota fauna (MCN.P.1259) has developed talonid cuspids and a talonid

that represents ca. 44% of the trigonid length and about 30% of the lower molar length. MN 1344-V differs from the m3 of MCN.P.1259 in the reduced talonid cuspids, except the hypoconulid; and reduced talonid (i.e., less than 30% of the length of m4). Consequently, we suggest that MACN-A 1033b represents the same locus as MN 1344-V. Therefore, MACN-A 1033b is here considered as a m4 trigonid.

Measurements. See Table 2.

Remarks. Ameghino (1902) described specimens of *Nemolestes spalacotherinus* recovered from the “Couches á *Notostylops*” locality (at the north slope of the Colhué-Huapi Lake, Gran Barranca, Chubut, Argentina), along with a broken tooth, MACN 10331, of a medium-sized sparassodont, “*Argyrolestes peralestinus*”. Simpson (1948) described this tooth as presenting a large metacone, a small but distinct worn paracone, and a broken but identifiable protocone. He compared it with *Patene*, which differs from “*Argyrolestes*” in the presence of a stronger external cingulum (=ectocingulum? sensu Forasiepi et al. 2015). The size dimensions of this specimen (see Simpson 1948) are compatible with *N. spalacotherinus*. Later, Marshall (1978) suggested that “*Argyrolestes peralestinus*” might represent a M1 of *Nemolestes*, a hypothesis that should not be neglected. Unfortunately, this specimen is currently lost, which led Prevosti and Forasiepi (2018) to consider this taxon a *nomen dubium*.

Some authors have suggested that MACN-A 1033 may not pertain to a single animal (Simpson 1948; Marshall 1978). Nevertheless, the trigonid size and shape of the specimens MACN-A 1033 are compatible with different lower molar locus of a single taxon, in which MACN-A 1033a represents a m2 and MACN-A 1033b would be a m4. The increase in the dimensions of the trigonid from m1 to m4 and the reduction in the size of the metaconid through the lower molar series is observable for *Patene* (Rangel et al. 2019), *Nemolestes* sp. indet. from the Guabirota fauna (Sedor et al. 2017) and *Chlorocyon* (Engelman et al. 2018). In short, on the lower molar series of early sparassodonts, the trigonid increases in length and width, whereas the metaconid reduces in size from m1 to m4 (Engelman et al. 2018). Therefore, it is more likely to consider MACN-A 1033a and 1033b as belonging to a single taxon. Furthermore, Marshall (1978) considered MACN-A 1033c as a broken tip of a lower canine (Fig. 2k), an observation that cannot be securely made due to lack of reliable evidence.

†*Nemolestes brasiliensis* sp. nov.

1961 cf. *Arminiheringia* sp. Paula Couto, p. 331, Fig. 11

1978 cf. *Nemolestes* sp. Marshall, p. 26.

Fig. 3

ZooBank Life Science Identifier (LSID)—urn:lsid:zoobank.org:act:71216E91-323E-4B4F-9353-69A27E35C9B4.

Derivation of name. “*brasiliensis*”, in reference to its discovery in Brazil.

Holotype. MCT.M.657, a left m2 (Fig. 3a, b).

Hypodigm. The type and MN 1344-V, a left m4 (Fig. 3c, d).

Locality and horizon. The specimen MCT.M.657 was recovered in the Itaboraí Basin in 1967 and MN 1344-V was recovered from one of the fissures explored in 1948–49 in the Itaboraí Basin, municipality of Itaboraí, State of Rio de Janeiro, Brazil (Bergqvist et al. 2009). Early Eocene, Itaboraian SALMA.

Diagnosis. Differs from *Nemolestes spalacotherinus* in its smaller size (see Table 2), metaconid exceeds half of the paraconid height, and base of paraconid and metaconid closely spaced (i.e., trigonid basin very short in lingual view). Differs from *Nemolestes lagunafriensis* sp. nov. in the presence of a hypoconid on m4 (absent on *N. lagunafriensis*), smaller hypoconulid on m4 (enlarged on *N. lagunafriensis*), cristid obliqua contacting the distal wall of the trigonid below the carnassial notch (*N. lagunafriensis* has

a more lingual contact—at metaconid and not below the carnassial notch).

Description. The m2 (MCT.M.657) has a trigonid ~3× taller than the talonid. The paraconid is taller and more robust than the metaconid, which is short (mesio-distally compressed). The paraconid shows a well-developed basal mesial keel. The metaconid is moderately developed, exceedingly more than the half of paraconid height. The protoconid is the largest cuspid of the trigonid. The labial side of the protoconid is convex on distal view. The talonid has ca. 66% of the trigonid length and about 41% of the tooth length. The hypoconid does not preserve its apex, so its height cannot be determined. The entoconid is flattened (i.e., with some degree of labiolingual compression) and less developed when compared with the hypoconid. The hypoconulid is the largest talonid cusp and is placed slightly more labial than the entoconid. The entocristid is short and bears a carnassial notch at the mesial wall of the entoconid. The cristid obliqua is weakly developed and contacts the distal wall of the trigonid below to the carnassial notch. The anterolabial cingulid is developed (i.e., present on paraconid and protoconid).

Fig. 3 *Nemolestes brasiliensis* sp. nov. SEM images of the referred specimens: MCT.M.657 (Holotype), left m2: in lingual (a) and occlusal (b) views; MN 1344-V, left m4: lingual (c) and occlusal (d) views. Scale bars equals 2 mm

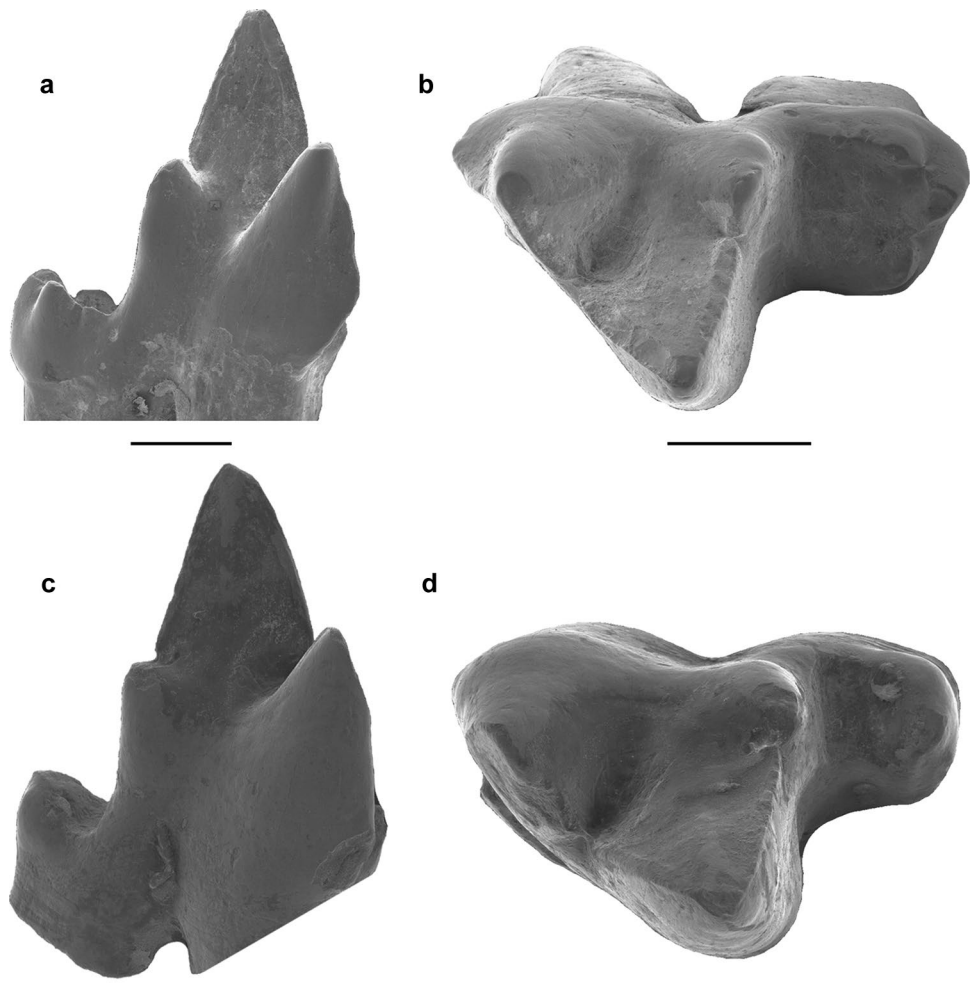


Table 2 Dental measurements (in mm) of *Nemolestes* and *Procladocictis*. The holotypes are highlighted in bold. An asterisk (*) indicates a measurement based on the trigonid (i.e., talonid was not preserved); parentheses indicate talonid length or width

Taxon	Lp3	Wp3	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm4	Wm4	Lm1-4
MCT.M.657					4.27 (2.96)—7.23	3.78 (2.78)					
MN 1344-V									5.90 (2.19)—8.09	5.12 (2.12)	
LIEB-PV 1038									6.38 (2.12)—8.50	4.50 (2.12)	
MACN-A 1033a					6.90*	5.30					
MACN-A 1033b							8.50*	6.20			
Taxon	LP3	WP3	LM1	WM1	LM2	WM2	LM3	WM3	LM4	WM4	LM1-4
MACN-A 10327	8.50	4.00	6.50	7.00	7.50	9.50	6.00	10.50			

The m4 (MN 1344-V) differs from MCT.M.657 in its larger size, its trigonid being more lingually “open” (=trigonid basin floor is visible at lingual view), its metaconid being shorter and less voluminous than the paraconid, its less developed paraconid mesial keel, its talonid being relatively shorter than the trigonid, reaching less than half of the length of the trigonid. The talonid has ca. 37% of the trigonid length (about 27% of the tooth length). The hypoconid is very low and the entoconid is vestigial. The hypoconulid is nearly central and is the largest of the talonid cuspids. The talonid basin is narrow, shallow, and short. The entocristid is very low but much longer than the cristid obliqua. A carnassial notch is present very close to the distal wall of the metaconid. The cristid obliqua is very short and low, probably a consequence of the reduction of talonid. The anterolabial cingulid is developed and the posterobasal cingulid is very short. This tooth is identified as an m4 based on the reduced condition of the entocoid and hypoconid, and the very mesiodistally short talonid.

Measurements. See Table 2.

Remarks. The m4 of *Nemolestes brasiliensis* (MN 1344-V) was identified previously as *Arminiheringia* sp. by Paula Couto (1961), and cf. *Nemolestes* sp. by Marshall (1978) and Bergqvist et al. (2009). The m2 (MCT.M.657, holotype) was previously referred to as borhyaenid indet. by Paula Couto (1970). MCT.M.657 was excluded from *Patene* based on its much larger size (about 2 mm larger than the largest molar of *Patene simpsoni*; see Rangel et al. 2019 and Table 2). Based on the evident size difference (Fig. 4)

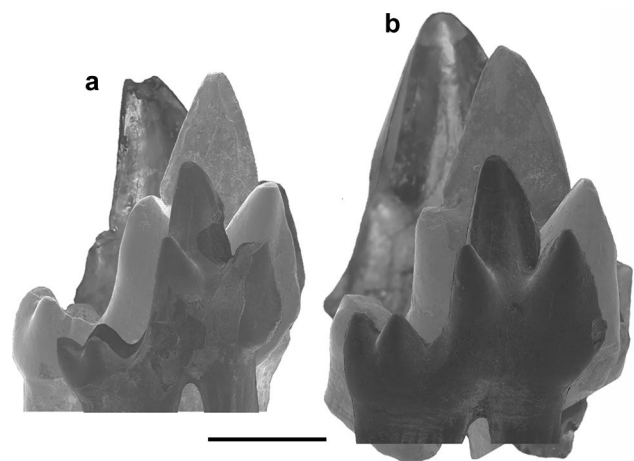


Fig. 4 Size comparisons of the lower molars of *Patene simpsoni*, *Nemolestes brasiliensis* sp. nov., and *N. spalacotherinus*: **a.** m2, from front to back: *P. simpsoni* (MCT.M.801, reversed right m2); *N. brasiliensis* (MCT.M.657, left m2, holotype; middle); *N. spalacotherinus* (MACN-A 1033a, left m2); **b.** m3/m4 size comparison: *P. simpsoni* (MCT.M.798, left m3, in front); *N. brasiliensis* (MN 1344-V, left m4, at the middle); *N. spalacotherinus* (MACN-A 1033b, reversed right m4, type specimen, behind). Scale bar equals 3 mm

Table 3 Relative length of the talonid of Eocene small to medium-sized sparassodonts. The values correspond to a ratio between talonid/lower molar length (Rmxtal/mxL) and talonid/trigonid length (Rmxtal/mxtri). For *Patene simpsoni*, the number within parenthesis () indicates the number of considered specimens for each locus. The values of *Chlorocyon phantasma* considered the measurements provided by Engelman et al. (2018). Holotypes are in bold. Abbreviations: **(l)**, left; **L**, length; **m**, lower molar with number corresponding to its locus; **(r)**, right; **R**, ratio; **tal**, talonid; **tri**, trigonid. An asterisk (*) indicates estimated values calculated based on the distances between the upper molars of an upper molar series (see Zimicz 2012)

Taxon	Rm1tal/ m1L	Rm1tal/ m1tri	Rm1taW/ m1triW	Rm2tal/m2L	Rm2tal/m2tri	Rm2taW/ m2triW	Rm3tal/m3L	Rm3tal/m3tri	Rm3taW/ m3triW	Rm4tal/m4L	Rm4tal/m4tri	Rm1taW/m1triW
MCN.P.1259 <i>Nemolestes</i> sp. indet				0.35	0.54	0.89	0.30	0.44	0.75			
MCT.M.657 <i>Nemolestes</i> <i>brasiliensis</i>				0.41	0.66	0.73						
MN 1344-V <i>Nemolestes</i> <i>brasiliensis</i>							0.27	0.37	0.41			0.41
LIEB-PV 1038 <i>Nemolestes</i> <i>lagunaf-</i> <i>riensis</i>							0.25	0.33	0.47			0.47
MACN-A 10327 <i>Proclad-</i> <i>ostictis</i> <i>anomala</i>			0.85*	0.38*	0.62*	0.70*	0.34*	0.51*	0.61*			
SGOPV 6200 <i>Chlorocyon</i> <i>phantasma</i>				0.26(l)/0.25(r)	0.36(l)/0.34(r)							
AMNH 28448 <i>Patene colu-</i> <i>apiensis</i>			0.89*	0.43*	0.75*	0.68*	0.41*	0.69*	0.60*	0.42*	0.72*	0.44*
PVL 2618 <i>Patene colo-</i> <i>radensis</i>	0.43(l)	0.77(l)	0.96(r)	0.45(l)	0.83(l)	0.73(r)	~0.42(l)/0.41(r)	~0.73(l)/0.70(r)	0.75(l)/0.76(r)	0.44(l)/0.45(r)	0.80(l)/0.82(r)	0.55(l)/0.59(r)
<i>Patene</i> <i>simpsoni</i>	0.43–0.45 (3)	0.76–0.83 (3)	0.99–1.12 (3)	0.40–0.47 (6)	0.67–0.89 (6)	0.66–0.92 (6)	0.39–0.41 (3)	0.65–0.71 (3)	0.87 (1)	0.44 (1)	0.78 (1)	0.73 (1)

and described morphology, MCT.M.657 and MN 1344-V are here assigned to *Nemolestes brasiliensis* sp. nov.

Marshall (1978: p. 27) rejected affinities between MN 1344-V and *Arminiheringia* due to the smaller size of MN 1344-V, presence of a much larger, fully basined talonid, fully basined; and presence of a distinct metaconid, and a large anterolabial cingulid. Marshall (1978: p. 27) considered MN 1344-V as *Nemolestes*, a conclusion followed in this revision. However, we did not follow Marshall's (1978) hypothesis that *Nemolestes* should be included within Borhyaenidae or Borhyaenoidea (see the results of our phylogenetic analysis and associated discussion).

The talonid of *Nemolestes* shows a similar pattern to those of *Patene* and *Nemolestes* sp. indet. (MCN.P.1259), in which the talonids of m1-2 are proportionally longer than the one of m3. The m4 of *Patene* is not "carnassial-like" and the m4 is not preserved in MCN.P.1259, which restricts comparisons with *Nemolestes*. Nevertheless, the similarities between *Nemolestes*, *Patene* and *Nemolestes* sp. indet. supports the talonid of m4 as the shortest of the lower molar series (Table 3). In addition, on *Patene simpsoni*, *P. coloradensis* and *Nemolestes* sp. indet. from the Guabiro tuba fauna (MCN.P.1259), the talonid cuspids are identifiable and developed on m1-3. On the contrary, on the m4 of *P. simpsoni*, *P. coloradensis* and other sparassodonts, the entoconid and hypoconid are much reduced, similar to MN 1344-V and LIEB-PV 1038, described below. Therefore, we suggest that MN 1344-V and LIEB-PV 1038 represent two m4s of *Nemolestes*.

The MCT.M.657 is here considered as a m2 due to its trigonid/talonid proportions (ca. 66% of the trigonid length and 41% of the tooth length) and presence of well-developed cuspids on the talonid; hypoconid, entoconid and hypococonid. The proportions presented by this tooth is more like the one presented by the m2 of *Nemolestes* sp. indet. from Guabiro tuba MCN.P.1259 (see Table 3).

†*Nemolestes lagunafriensis* sp. nov.
2009 cf. *Nemolestes* Tejedor et al., p. 12

Fig. 5 *Nemolestes lagunafriensis* sp. nov., digital photographs of LIEB-PV 1038 (holotype), a left m4: lingual (a), occlusal (b), and labial (c) views. Scale bars equal 2 mm



Fig. 5

ZooBank Life Science Identifier (LSID)—urn:lsid:zoobank.org:act:CFC681E7-FCFC-4644-A925-8B8E42D7C4EE.

Derivation of name. "*lagunafriensis*", in reference to its discovery in Laguna Fría local fauna, Argentina.

Holotype. LIEB-PV 1038, a left m4 (Fig. 5).

Hypodigm. The type only.

Locality and horizon. Tuffaceous sediments of Laguna Fría, Chubut, Argentina. Middle Eocene, Laguna Fría local fauna (Tejedor et al. 2009) (between 49.26 ± 0.30 Ma and 43.50 ± 1.14 Ma; see Gosses et al. 2021).

Diagnosis. Differs from *Nemolestes spalacotherinus* in its smaller size (see Table 2). Differs from *N. brasiliensis* sp. nov. in its talonid basin nearly absent on m4, absence of a hypoconid on m4 (present on *N. brasiliensis*), enlarged hypoconulid that occupies most of the talonid (more reduced on *N. brasiliensis*), more lingual contact of the cristid obliqua, reaching the metaconid (on *N. brasiliensis*, it contacts the carnassial notch), and broader labial cingulid due to a more lingual contact of the cristid obliqua.

Description. The trigonid is $\sim 3\times$ taller than the talonid. The protoconid and metaconid are damaged, not allowing a comparison of their height with the paraconid. Nevertheless, based on the preserved bases of these cuspids, the metaconid is the smallest of them. The talonid has ca. 33% of the trigonid length and about 25% of the tooth length (Table 3). The talonid basin is nearly absent due to the presence of an enlarged hypoconulid. The hypoconulid is the only identifiable cuspid, entoconid and hypoconid are absent). The anterolabial cingulid is broad, in occlusal view, and extends to the protoconid. This tooth is identified as a left m4 based on the presence of a cristid obliqua with a lingual contact with the trigonid, very short talonid and absence of entoconid and hypoconid.

Measurements. See Table 2.

Remarks. The LIEB-PV 1038 was originally considered as a possible m4 by Tejedor et al. (2009: p. 12), a conclusion

followed in this study, based on the presence of a very short talonid and the unicuspid condition of the talonid, only hypoconulid. The size and morphology, developed anterolabial cingulid and very short talonid, of this specimen support its referral to a third species of *Nemolestes*. Nevertheless, the more reduced condition of the talonid and the enlargement of the hypoconulid of *N. lagunafriensis* support its identification as a different species from *N. brasiliensis*.

†*Procladosictis* Ameghino, 1902

Type species. *Procladosictis anomala* Ameghino, 1902.

Included species. The type only.

Locality and horizon. “Couches á *Astraponotus*”, Chubut Province, Patagonia, southern Argentina. Latest middle-earliest late Eocene, Mustersan SALMA (see Prevosti and Forasiepi 2018).

Diagnosis. Emended from Marshall (1981). Medium-sized, South American, Paleogene sparassodont with body mass of about 8.90 kg (see e.g., Zimicz 2012; Prevosti and Forasiepi 2018). Differs from other sparassodonts in the presence of a metastylar lobe much broader than the parastylar lobe of the stylar shelf on M3, well-marked ectoflexus on M3, postmetacrista perpendicular to the tooth row on M3, and mesio-distally compressed M3. Differs from *Patene simpsoni* and *P. coluapiensis* in the presence of a much lower and narrower protocone on M3; and from *P. simpsoni*, in the P3 with a small posterolabial cingulum, absent on *P. simpsoni*, and disto-medial crest less developed, sharp and tall on *P. simpsoni*. Differs from *Hondadelphys* in the larger StB on M2 and narrower protocone. Differs from *Stylocynus* in the smaller size, much narrower protocone and broader stylar shelf. Differs from hathliacynids in the larger StB on M2.

Remarks. Simpson (1948: p. 45) and Marshall (1981: p. 18) tentatively assigned an isolated tooth, AMNH 29433, found at Roth’s “Lago Musters” locality, Cerro del Humo, Argentina (Mustersan SALMA), to *Procladosictis*. Simpson (1948) and Marshall (1981) mentioned that its size is comparable and the structure apparently harmonious with *Procladosictis*. AMNH 29433 has a minute metaconid, a basined, narrow talonid, with a long external slope, and a hypoconulid that is poorly distinguishable from the entoconid. Marshall (1981: p. 18) measured this tooth as 9.80 mm in length and 4.90 in trigonid width and 4.90 in talonid width. Later, Forasiepi et al. (2015: p. 18, Fig. 10A) referred AMNH 29433 to cf. *Nemolestes* sp. but did not discuss this identification in detail. Engelman et al. (2018) considered this tooth as cf. *Nemolestes*/cf. *Procladosictis*. Finally, Sedor et al. (2017) mentioned that this tooth differs from *Nemolestes* sp. indet. from Guabiro tuba (MCN.P.1259) in the smaller metaconid and narrow basined talonid.

Furthermore, the subequal trigonid and talonid of AMNH 29433 would prevent an association with *Nemolestes*, as the trigonids of this taxon are wider than the talonids on m2 and m4. Therefore, AMNH 29433 clearly does not pertain to *Nemolestes*. This tooth would belong to another small to medium-sized sparassodont from the middle-late Eocene, such as *Procladosictis* or *Chlorocoyon* due to its compatible dimensions (see discussion of *Procladosictis*’ affinities).

Tejedor et al. (2009: p. 12, Fig. 3H) described and figured a “Hathliacynidae indet.” (LIEB-PV 1036, a right fragment of maxilla with M3?) from the faunas of Laguna Fría and La Barda (between 49.26 ± 0.30 Ma and 43.50 ± 1.14 Ma; see Gosses et al. 2021). This specimen is very similar to the M2 of *Procladosictis anomala* in the following features: slightly reduced stylar shelf, marked ectoflexus, small parastyle, large, conical StB, short preparacrista oriented to StA, well distally oriented postmetacrista, metacone much larger than the paracone, reduced conules and mesio-distally compressed protocone but with developed protoconal basin. The major difference is an apparently greater separation between the paracone and metacone. If a M3, this tooth would represent a different taxon to *Procladosictis* due to the presence of an obliquely oriented postmetacrista and shallower ectoflexus on M3. Nevertheless, if a M2, it could be assigned to *Procladosictis*. Therefore, we consider the identification of LIEB-PV 1036 as an older species of *Procladosictis* or one closely related to this taxon.

Goin et al. (2010: p. 73) described and figured an upper molar lacking the protocone of an indeterminate “hathliacynid” (MPEF-PV 4345), originally considered as a possible M1. This specimen shows a narrow stylar shelf, shallow ectoflexus, small parastyle, large StB, subequal to the paracone, StC absent, and small, labiolingually compressed StD located near the distal end of the postmetacrista, reduced preparacrista that contacts the StB, well-developed postmetacrista, and metacone slightly taller than the paracone. This same combination of features is present on the M2 of *Procladosictis anomala* (MACN-A 10327). Therefore, we do not reject the possibility that this tooth represents a M2 instead of a M1 (see a similar conclusion in Engelman and Croft 2022). The similarities between MPEF-PV 4345 and the M2 of *P. anomala* indicate that this tooth could represent a new species of *Procladosictis* due to its evidently smaller size (MPEF-PV 4345 length: 4.95 mm; *P. anomala* LM2: 7.50 mm) or a closely related taxon to this one.

†*Procladosictis anomala* Ameghino, 1902

Fig. 6

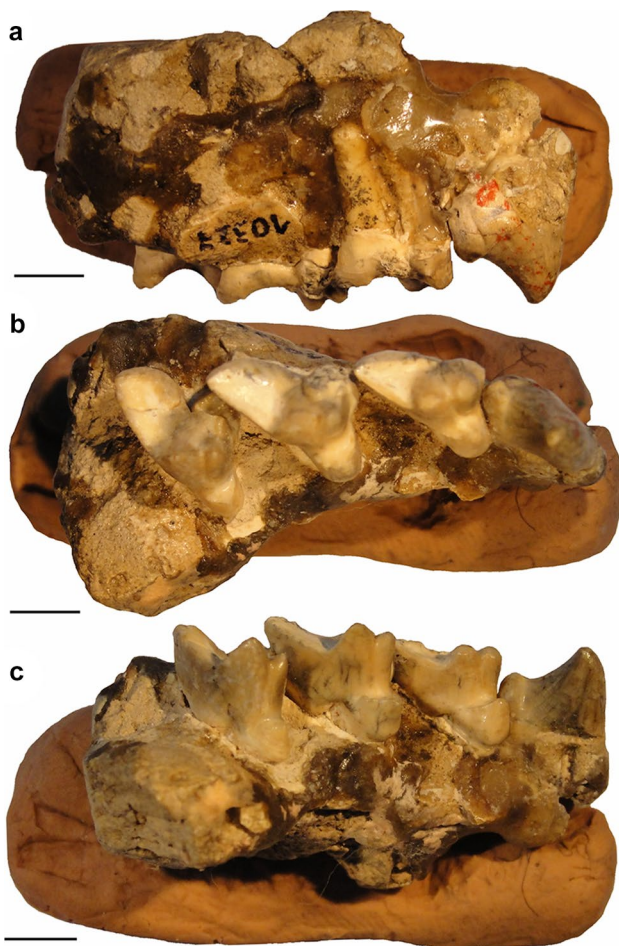


Fig. 6 *Procladosictis anomala*. Digital photographs of the type specimen, MACN-A 10327, a fragment of a right maxilla with P3-M3, in labial (a), occlusal (b), and lingual (c) views. Scale bars equals 5 mm

Holotype. MACN-A 10327, a fragment of a right maxilla with P3-M3 (Fig. 6).

Hypodigm. The type only.

Locality and horizon. As for the genus.

Diagnosis. As for the genus.

Description. The P3 shows a well-developed posterolingual cingulum and a reduced labial cingulum. Its posterobasal heel does not present a developed posterobasal cusp but only a small elevation on the crown, more likely, a reduced posterobasal cusp. The disto-medial crest of the main cuspid extends from its apex to the reduced posterobasal cusp but is poorly developed (not tall or sharp). The P3 is narrower than, but as long as, M1.

The M1 has a small StB, and a roll of reduced cusps can be identified on the posterior styler shelf (the largest of these is very likely StD). The anterior styler

shelf is greatly reduced to a narrow rim and the posterior styler shelf equivalent to the metastyler area, extends well distally. The paracone and metacone are fused. The centrocrista is straight, weak, and noticeably short. The postmetacrasta is long and oblique to the tooth row. The conules are vestigial or absent. The protocone is mesiodistally compressed. The paracingulum is complete and narrow. The metacingulum is absent.

The M2 is similar in description to M1 but differs in some features: the paracone is relatively smaller, the preparacrista is more developed and appears to contact the mesiolingual base of StB (i.e., somewhat oriented to StA); and StB is much larger. Other styler cusps are absent, in exception for two reduced cusps on the posterior edge of the posterior styler shelf.

The M3 is also similar in its features to the previous upper molars but it shows a relatively longer preparacrista, which is oriented to StA; the paracone is even smaller and more labiolingually compressed, StB is vestigial (similarly to M1), StD is slightly better developed, the protoconal basin is very narrow and shorter, the postmetacrasta is nearly perpendicular to tooth row and the posterior styler shelf is broader.

Measurements. See Table 2.

Remarks. Simpson (1948: p. 5) and Marshall (1981: p. 17–18) mentioned that the oblique position of MACN-A 10327's P3 should be a direct consequence of its restoration with wax. Consequently, this condition is not a diagnostic feature of this taxon.

Procladosictis anomala is a Mustersan SALMA (late Eocene) taxon and is only known by the type specimen, MACN-A 10327, a fragment of a right maxilla with P3-M3. Marshall (1981) noticed that this taxon shows a very deep ectoflexus, a specialization not found in other Borhyaenidae. For him, this feature makes *P. anomala* very distinct, excluding it as an "ancestor" for other later taxa. Then, Marshall (1981: p. 18) stated: "Based on present evidence, *P. anomala* is regarded as a dead-end offshoot of an early Tertiary hathiacynine radiation. It apparently represents a slightly larger specialized descendant of a population of *Patene coluapiensis*". However, see the results of our phylogenetic analysis.

Phylogenetic analysis and systematic implications

The unordered and ordered phylogenetic analyses recovered nine MPTs (Steps: 1,997; CI: 0.330; RI: 0.660) and similar topologies but differ in the Bremer support values of some clades (Fig. 7). Following the results, *Nemolestes* was recovered in a polytomy with *Procladosictis*, *Patene*, and a large clade composed of unnamed clade A (composed of

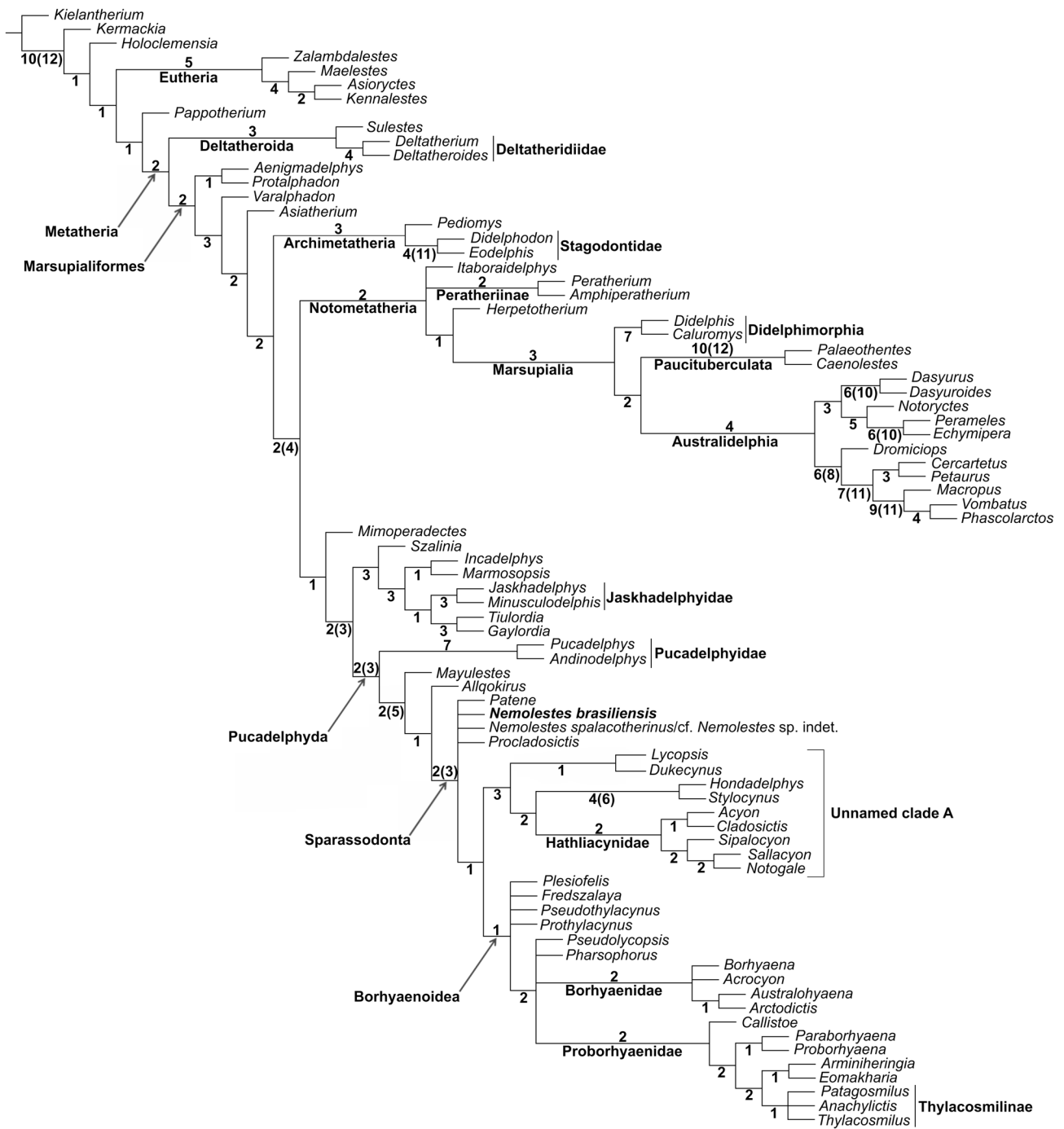


Fig. 7 Strict consensus tree of the nine most parsimonious trees found in the phylogenetic analyses. Numbers below and above the branches indicate similar Bremer support values for both unordered and ordered phylogenetic analyses. The number inside parentheses

() represent the Bremer values of the ordered phylogenetic analysis when they differ from the unordered analysis. *Nemolestes brasiliensis* is highlighted in bold

Lycopsis and *Dukecynus*, *Stylocynus* and *Hondadelphys*, and *Hathliacynidae* plus *Borhyaenoidea* based on the absence of StE (character 22, state 0), presence of posterior lobe of the stylar shelf broader than the parastylar lobe of the stylar shelf (ch. 29, state 2), and paraconid lingually aligned with

the metaconid (ch. 39, state 0). The affinities of *Nemolestes* and *Procladosictis* will be discussed in detail later.

Pucadelphyidae was recovered as the sister taxon of *Mayulestes*, *Allqokirus*, and *Sparassodonta* with these clades forming *Pucadelphyda* (see Muizon et al. 2018). For

a complete list of synapomorphies of Pucadelphyda, Pucadelphyidae and Sparassodonta, see Online Resource 1.

Muizon et al. (2018) recovered *Mayulestes*, *Allqokirus* and *Patene* as representatives of a group they named Mayulestidae. However, other studies (e.g., Rangel et al. 2019; Engelman et al. 2020b) did not recover a monophyletic Mayulestidae. Rangel et al. (2019) recovered *Mayulestes*, *Allqokirus*, and *Patene* as successively diverging lineages at the stem of Sparassodonta, whereas Engelman et al. (2020b) recovered *Mayulestes* and *Allqokirus* as sister taxa (i.e., a more narrowly defined Mayulestidae) and *Patene* as more closely related to other sparassodonts. We recover a result similar to Rangel et al. (2019), with *Mayulestes* and *Allqokirus* not forming a clade, due to the following features shared by *Allqokirus* and Sparassodonta to the exclusion of *Mayulestes*: a postmetacrista oblique to the tooth row (ch. 34, state 1), Lm1/Lm2 proportion lower than 0.90 (ch. 83, state 2; see Carneiro 2018), paraconid taller than metaconid on m4 (ch. 133, state 1), absence of midline contacts of pterygoids (ch. 264, state 1) and large tuberculum tympani (ch. 297, state 1).

The phylogenetic analysis recovered a sister relation between *Hondadelphys* and *Stylocynus*, similar to Engelman et al. (2020b), based on the following features: paracone labial to metacone (ch. 39, state 1), bases of paracone and metacone separated (ch. 40, state 0), somewhat expanded protocone (ch. 47, state 2), protocone greater than or equal than 60% of para/metacone height (ch. 48, state 1), m1 trigonid with paraconid, protoconid and metaconid (ch. 74, state 0), protoconid height does not exceed 90% of the molar length on m3-4 (ch. 98, state 0), talonid wider than trigonid on m2-3 (ch. 107, state 2), cristid obliqua in a lateral contact with the distal wall of the trigonid (i.e., contacts the disto-labial wall of the protoconid) (ch. 123, state 4), posterior mental foramen below p3/m1 embrasure (ch. 202, state 1) and absence of a flaring of maxillary "cheeks" behind infraorbital foramen (ch. 237, state 1).

The phylogenetic analysis supported the monophyly of Hathliacynidae based on the following features: reduced cristid obliqua (ch. 115, state 1), diastema between c and p1 (ch. 167, state 1), lacrimal anterior extent restricted to orbit (ch. 234, state 0), absence of epitympanic wing (ch. 273, state 0), ventral aperture of the hiatus fallopii (ch. 279, state 0), well-defined groove between hypoglossal foramina and foramen for the inferior petrosal sinus (ch. 356, state 1), and absence of a median keel in basioccipital (ch. 357, state 0). The phylogenetic analysis also recovered Hathliacynidae and Hondadelphidae as sister taxa, which has never been proposed before in the literature. These clades share a m4 hypoconulid as tall as other talonid cuspids (ch. 138, state 0), P1/p1 parallel to tooth row (ch. 160, state 0), one palatal pit between the penultimate and ultimate molar (ch. 257, state 1), alisphenoid tympanic wing poorly to moderately

developed (ch. 307, state 1), and absence of a glenoid process of alisphenoid (ch. 329, state 0).

Moreover, the phylogenetic analysis recovered *Lycopsis* and *Dukecynus* as sister taxa based on a long skull (ch. 219, state 1). These two taxa were recovered as the sister taxa of Hondadelphidae + Hathliacynidae (i.e., these taxa are grouped in the unnamed clade A) based on the following synapomorphies: StB reduced to absent (ch. 5, state 1), m1 cristid obliqua contacting the labial wall of the protoconid (ch. 80, state 3), cristid obliqua on m2-3 with labial contact with the distal wall of the protoconid (i.e., not completely labial as the one of Hondadelphidae) (ch. 123, state 3), posterobasal cingulid reduced to absent (ch. 127, state 0) (with the exceptions of *Sallacyon* and *Notogale*), well-developed post-orbital process (ch. 221, state 1), palate and basicranium at same level (ch. 263, state 1), presence of alisphenoid canal (ch. 305, state 1), braincase longer than wide at base (ch. 357, state 2; this character could not be evaluated for Hondadelphidae), anteroventrally projecting post-tympanic and/or paracondylar processes (ch. 363, state 1), distal end of deltoid crest merging with diaphysis (ch. 432, state 0), and absence of a astragalo-cuboid facet on the astragalar head (ch. 570, state 1).

Borhyaenidae was supported based on the following synapomorphies: pseudotalonid on m1 (ch. 81, state 1), hypoconulid vestigial to absent (ch. 124, state 4), m2-3 with pseudotalonid (ch. 128, state 1), p3 inflated and bulbous (ch. 151, state 1), three upper incisors (I2-4) (ch. 188, state 2), small crescentic and rounded anteriorly facial process of the lacrimal (ch. 244, state 0; this character was not coded for *Acrocyon*), petrosal crest absent (ch. 296, state 0; this character was not coded for *Acrocyon* and *Australohyaena*), postglenoid foramen medial to postglenoid process (ch. 333, state 0; this character was not coded for *Acrocyon*), dorsal anteroposterior orientation of sustentacular facet (ch. 502, state 0; this character was coded only for *Borhyaena*, *Arctodictis* and *Thylacosmilus* among Borhyaenoidea), tuber calci longer than the body of the calcaneus (ch. 515, state 0 – this character was coded only for *Borhyaena*, *Arctodictis* and *Thylacosmilus* amongst Borhyaenoidea), and cleft ungual phalanges (ch. 576, state 1).

Close affinities between *Pharsophorus* and *Borhyaena* were originally proposed by Ameghino (1897) and later by Marshall (1978) and Goin et al. (2007). This hypothesis supports in part the conclusion of Forasiepi et al. (2015), who recovered this taxon as more closely related to Borhyaenidae and Proborhyaenidae (sensu Engelman et al. 2020b, i.e., with *Thylacosmiliinae* as a subfamily of Proborhyaenidae), but differs from Engelman et al. (2020b), who recovered *Pharsophorus* as the sister taxon of *Prothylacynus*, Borhyaenidae + Proborhyaenidae. In addition, our phylogenetic analysis did not recover *Pharsophorus* as a member of Borhyaenidae; however, we consider this taxon as a closely

related taxon to Borhyaenidae due to the presence of pseudotalonids on m3-4 (= talonid is fused with the posterobasal and labial cingulids; see Goin et al. 2007). It could be possible that the inclusion of *Pseudolycoopsis*, a taxon only known by upper molars, could be “responsible” for the polytomy between *Pharsophorus*, Borhyaenidae, Proborhyaenidae and *Pseudolycoopsis*.

Pseudolycoopsis was recovered in a polytomy with *Pharsophorus*, borhyaenids and proborhyaenids based on the presence of the following features: StB reduced to absent (ch. 5, state 1; nevertheless, a developed StB can be identified for some Borhyaenidae and Proborhyaenidae; see e.g., Babot et al. 2002; Goin et al. 2007), styler shelf reduced to a narrow rim labial to paracone and metacone (ch. 28, state 3), centrocrista reduced or absent (ch. 44, state 2), hypoco-nulid on m4 absent (ch. 137, state 1), and P3 with lingual cingulum (ch. 154, state 0).

Goin et al. (2007: pp. 64–65) discussed the presence of a sharp crest between the hypoconid and the metaconid on *Pseudothylocynus* and *Plesiofelis*, which was suggested to represent a synapomorphy of this clade, as this crest is not present among borhyaenids and proborhyaenids. We identified this crest as a postprotocristid, which is oriented towards the hypoconid on m1-2 and to the hypoco-nulid on m3-4 on *Plesiofelis* and *Pseudothylocynus*. For *Prothylocynus*, this condition is less observable, but the m3-4 appears to have a similar morphology for the other two taxa. This crest is here regarded as a postprotocristid because it descends from the distal wall of the protoconid and does not contact the very reduced metacristid on m3-4 (see discussion in Goin et al. 2007, who first suggested a possible association of this crest with the postprotocristid).

The phylogenetic analysis does not support the assignment of *Fredszalaya* within Borhyaenidae, based on the following features: reduced but not vestigial styler shelf, presence of a moderately developed StB, StC and other supernumerary styler cuspules, and protocone is small but not reduced as identified within borhyaenid. However, we do not rule out a closely relation between *Fredszalaya*, *Pharsophorus* and Borhyaenidae due to the apparent presence of inflated crown and roots of P3, and absence of an alisphenoid canal (see Shockey and Anaya 2008). The major dental synapomorphy of Borhyaenidae is the presence of a pseudotalonid on m1-4 (present on m3-4 of *Pharsophorus*), but the lower molars of *Fredszalaya* are currently not known.

Proborhyaenidae (sensu Engelman et al. 2020b) was recovered based on the following synapomorphies: presence of prominent median sulci on labial faces of canines (ch. 180, state 1), presence of open pulp cavity of canines (ch. 186, states 1–2), rostrum between 1/3 and 1/2 of the skull length (ch. 220, state 1), palate and basicranium at same level (ch. 263, state 1), absence of the glenoid process

of alisphenoid (ch. 329, state 0), upper incisor arcade compressed transversely (ch. 350, state 3), anteroventrally projecting post-tympanic and/or paracondylar processes (ch. 363, state 1), presence of a concave process of alisphenoid contributing to antero-dorsal portion of hypotympanic sinus (ch. 364, state 1), absence of a median crest of basisphenoid/presphenoid (ch. 368, state 0), presence of an anterior expansion of the middle ear sinus within the lateral wall of the braincase (ch. 383, state 1), Atlas, posterior extent of transverse process extends caudally far beyond level of caudal facet for axis (ch. 390, state 2), and presence of a C5 transverse process displaying two heads (ch. 401, state 1). Proborhyaenidae included *Callistoe*, *Proborhyaena*, *Paraborhyaena*, *Arminiheringia*, *Eomakharia*, *Patagosmilus*, *Anachylictis* and *Thylacosmilus*.

The phylogenetic analysis recovered a sister relation between *Eomakharia* + *Arminiheringia* based on the following features: dentary below m4 clearly higher than below m1 (ch. 198, state 1; see similar observation in Zimicz 2012), and presence of one or two mental foramina (ch. 203, state 0). These two taxa share a high dentary, similar to *Callistoe* (ch. 197, state 2). Based on this, the previous hypothesis about the proborhyaenid affinities of *Arminiheringia* is supported (see e.g., Babot et al. 2002), and we are the first to recover in the context of a phylogenetic analysis a sister-relationship between *Arminiheringia* and *Eomakharia* based mostly on the jaw shape.

The analysis also recovered that *Thylacosmiliinae* has shallower and straighter dentaries (ch. 197, states 0–1), enlarged, saber-like upper canines (ch. 184, state 1), symphyseal flange subvertical and with radially oriented, lingual bone striations (ch. 200, state 1) and maximum maxilla with a length/width ratio less or equal to 1.5 (ch. 254, state 0). Therefore, based on our results, *Eomakharia* and *Arminiheringia* should be considered as the sister taxa of *Thylacosmiliinae*. Our results trace back the origin of *Thylacosmiliinae*'s clade to the middle Eocene, as *Arminiheringia* occurred during this sub-epoch (Prevosti and Forasiepi 2018).

The phylogenetic analysis recovered *Szalinia*, *Incadelpophys*, *Marmosopsis*, *Tiulordia/Mizquedelphys*, *Gaylordia*, *Jaskhadelpophys*, *Minusculodelphis* and *Kiruwamaq* within a clade that is the sister taxon of *Pucadelphyda* (i.e., *Pucadelphyidae* plus *Sparassodonta*; see Muizon et al. 2018), as previously recovered by Rangel et al. (2019). The validity of a clade comprising these taxa has been considered by Oliveira and Goin (2011), Carneiro (2018, 2019), Rangel et al. (2019) and Oliveira et al. (2021). This clade was supported by the phylogenetic analysis based on the following synapomorphies: paracone and metacone closely spaced but not in contact (ch. 40, state 2), M3 mesiodistally compressed (ch. 69, state 1), lacrimal foramen within the orbit (ch. 240, state 0), and posterior expansion of the palate behind last molar (ch. 261, state 0).

Varalphadon and *Aenigmadelphys* were not recovered as part of Pucadelphyda, restricting this clade to South America contra Carneiro (2018) and Muizon and Ladevèze (2020, 2022). *Itaboraidelphys* was recovered as more closely related to Peratheriinae, Herpetotheriidae and Marsupialia than to Pucadelphyda, as previously considered by Oliveira and Goin (2011), Carneiro (2018, 2019), Rangel et al. (2019) and Oliveira et al. (2021). The assignment of this taxon within Pucadelphyda (Muizon et al. 2018; Muizon and Ladevèze 2020, 2022) was based mostly on the assignment of the petrosal morphotype II (PII) (Ladevèze 2004) from the Itaboraí fauna to this taxon. Nevertheless, the hypothesis that proposed the assignment of PII to *Epidolops ameghinoi* (Beck 2017) has not been extensively discussed.

Discussion

Systematic affinities of *Nemolestes*

Nemolestes is a medium-sized sparassodont that occurred in the faunas from the early Eocene (Itaboraian SALMA) to the middle Eocene (Casamayoran SALMA). This taxon differs mostly from *Patene* based on its more “carnassialized” m4, which bears a small metaconid, very short talonid, vestigial entoconid and reduced hypoconid. In *Patene*, the m4 does not differ much from the condition of *Mayulestes* and *Allqokirus*, in which the talonid is shorter than the trigonid but not reduced, the metaconid is not small, and the talonid cuspids are more developed (see Muizon 1994, 1998; Muizon et al. 2018; Rangel et al. 2019).

Nemolestes and *Patene* share several similar lower molar features (m4 not considered), such as the subtriangular shape of the trigonid, a moderately developed metaconid, and developed anterolabial and posterolabial cingulids, talonid, entocoid, hypoconid and hypoconulid. In exception of m4, the lower molars of these two taxa differ mostly in their dimensions, in which *Nemolestes* is larger and *Patene* smaller.

Nemolestes is similarly sized to *Chlorocyon* from the late Eocene of Chile (Engelman et al. 2018); however, the fragmentary condition of *Nemolestes* and the poor state of preservation of the holotype of *Chlorocyon* restrict comparisons between them. *Chlorocyon* is considered to have a “heellike” talonid on m4, a condition confidently absent on *Nemolestes* due to the presence of a well-developed hypoconulid, small hypoconid and developed entocristid on *N. brasiliensis* and an enlarged hypoconulid on *N. lagunafriensis*. Moreover, Engelman et al. (2018) observed the probable absence of a metaconid on m1 but not on m2–4 in *Chlorocyon*, which supports its assignment to Borhyaenoidea, unnamed clade A or as more closely related to them than to *Patene* and *Nemolestes* (i.e., sister taxon of Borhyaenoidea and Unnamed clade A).

Marshall (1978) considered *Nemolestes* as a borhyaenid (= Borhyaeninae of that author). Nevertheless, several authors did not follow this hypothesis and considered *Nemolestes* to be an early sparassodont (e.g., Zimicz 2012; Carneiro and Oliveira 2017; Prevosti and Forasiepi 2018; Carneiro 2019; Rangel et al. 2019). *Nemolestes* differs from Borhyaenidae and *Pharsophorus* (a taxon closely related to Borhyaenidae) in the absence of a pseudotalonid (sensu Goin et al. 2007), protoconid not medially positioned on the trigonid, retention of the “subtriangular” shape of the trigonid on the lower molars; metaconid not evidently distal to the protoconid (= not placed at the distolingual wall of the protoconid), anterolabial cingulid reaching the protoconid (= developed/long), and entocristid lingual to the trigonid (sensu Engelman et al. 2020b).

Nemolestes should not be referred to Borhyaenoidea as it lacks a protoconid medially positioned on the trigonid, short anterobasal cingulid (= only on paraconid; see Muizon et al. 2018), entocristid lingual to the trigonid, and m4 talonid reduced to a “heel-like” structure (i.e., unbasined sensu Engelman et al. 2018). *Nemolestes* should not be considered closely related to the clade that includes *Lycopsis* and *Dukecynus* due to the absence of a protoconid medially positioned on the trigonid, presence of metaconid, trigonid wider than the talonid on m2, and cristid obliqua reaching the carnassial notch (lacks a more labial contact). *Nemolestes* should not be referred to the clade of *Hondadelphys* and *Stylocynus* due to the talonid narrower than the trigonid on m2–3 (subequal to wider on *Hondadelphys* and *Stylocynus*), and cristid obliqua contacting the distal wall of the trigonid below the carnassial notch (labial contact on *Hondadelphys* and *Stylocynus*). *Nemolestes* should not be referred to Hathliacynidae due to the presence of a metaconid (absent on hathliacynids), longer cristid obliqua (very short to nearly absent on hathliacynids), and protoconid not medially positioned on the trigonid.

Furthermore, *Nemolestes* represented an early lineage of Sparassodonta not directly related to any of the major clades (Borhyaenoidea and unnamed clade A). Nevertheless, *Nemolestes* shares more closely affinities with Borhyaenoidea and unnamed clade A than to *Patene* due to the presence of a reduced talonid and talonid cuspids on m4 (“carnassialized” m4).

Systematic affinities of *Procladosictis*

Procladosictis is a medium-sized sparassodont that occurs in a fauna from the late Eocene (Mustersan SALMA). This taxon was found in “Couches à *Astraponotus*”, Chubut, Argentina, but further information about this locality had not been provided by Ameghino (1902). Originally, this taxon was considered as a hathliacynid (Ameghino 1902). Later, Marshall (1981) tentatively considered *Procladosictis* as an early hathliacynine or as an early lineage of

Sparassodonta. Nevertheless, no further conclusion has been reached regarding its affinities.

Procladosictis shows several symplesiomorphies for Sparassodonta: broad stylar shelf and deep ectoflexus on M3, and large StB on M2. However, none of these features can be properly evaluated for some Eocene sparassodonts due to the absence of associated upper dentition. Consequently, direct comparisons between them cannot be made. This is the case of *Nemolestes* and *Chlorocyon*, which are known only by lower dental elements, whereas *Procladosictis* is represented by upper dental elements. Moreover, no study has ever demonstrated that the upper molars of *Procladosictis* could not be referred to *Nemolestes* (for the case of *Chlorocyon*, see Engelman et al. 2018). Compared with *Patene*, *Procladosictis* clearly differs on its greater mesio-distal compression of M2-3, deeper ectoflexus on M3, and relatively narrower protocone (see Table 3).

Procladosictis anomala shows a moderately broad protocone on M2 and a much narrower one on M3, which recover a moderately developed talonid on m2 and a shorter talonid on m3. The m2 of *Patene simpsoni*, *P. coloradensis*, *Nemolestes brasiliensis* and *Nemolestes* sp. indet. from Guabiro-tuba (MCN.P.1259) show relatively developed talonids. The protocone of *P. anomala* is proportionally narrower than the one of *P. simpsoni* and *P. coluapiensis* on M2 and M3, which suggests proportionally shorter talonids on its lower molars (for talonid proportions see Table 3).

Zimicz (2012) calculated the RGA (Relative Grinding Area: $\sqrt{\text{talonid area}/\text{trigonid length}}$ of the carnassials; see Van Valkenburgh 1991) of metatherians that are only known by upper dentition based on the distances between M2-3. The trigonid length is correlated with the distance between the metacone of M2 and the paracone of M3 (Lpa-me), and the talonid length would be equivalent to the distance between the protocones (Lpts) subtracted from the distance between the metacone of M2 and paracone of M3 (i.e., talonid length = Lpts—Lpa-me). The width of the talonids is estimated based on the distance between the apex of the protocone and the medial point of the centrocrista (i.e., the central point of the space between the paracone and metacone) (Zimicz 2012). The trigonid width is estimated by the distance between the apex of the protocone (which represents the lingual wall of the lower molar) and the mesial wall of the parastyle (i.e., the labialmost point of the protoconid). The schematic drawing of these measurements is provided as a supplementary material (Online Resource 1: Appendix 10). Therefore, estimations about the dimensions of the lower molars of *Procladosictis* can be inferred and compared with other Eocene small to medium-sized sparassodonts.

Considering the measurements obtained from MACN-A 10327 (Table 3), *Procladosictis anomala* has more similar estimated values to those calculated for *Nemolestes brasiliensis* (MCT.M.657) than to *Patene* spp., *Nemolestes* sp.

indet. from Guabiro-tuba (MCN.P.1259) and *Chlorocyon phantasma*. This indicates that the M2 of *N. brasiliensis* would have a protocone as developed as the one of *P. anomala*. *Patene coluapiensis* would have a similar trigonid/talonid width proportion but longer talonids than *P. anomala*. The other two species of *Patene* (*P. simpsoni* and *P. coloradensis*) have greater values, indicating relatively longer and wider talonids in comparison to *P. anomala*. *Procladosictis anomala* would have lower molars more similar in proportions to *N. brasiliensis*, with a talonid moderately shorter and narrower than the trigonid (Fig. 8).

Considering MCN.P.1259 from the Guabiro-tuba local fauna, its lower molars have a unique morphology in comparison to *Patene*, *Nemolestes brasiliensis* and *Procladosictis*: its lower molars have proportionally shorter but relatively wider talonids. This occlusal pattern suggests that the upper molars of this taxon show a more reduced protocone and a more lingually shifted parastyle (more reduced stylar shelf?) in comparison to *Patene*, *Nemolestes brasiliensis* and *Procladosictis*. Therefore, we infer that the upper molars of MCN.P.1259 should resemble those of the hathliacynid *Chasicostylus* from the Arroyo Chasicó Formation (Chasicóan SALMA, late Miocene), Buenos Aires, Argentina (see Reig 1957; Marshall 1981) more than any other small to medium-sized sparassodont. In addition, this specimen also bears more developed posterolabial and labial cingulids than *Patene* and *Nemolestes brasiliensis* on m2, which may indicate that its upper molars could have more developed ectocingula (ectocingulum sensu Forasiepi et al. 2015). Based on this, we did not recognize a co-generic association between MACN-A 10327 (holotype of *P. anomala*) and MCN.P.1259 (*Nemolestes* sp. indet.).

We noticed that the trigonid of MCN.P.1259 is remarkably like the one of *Nemolestes spalacotherinus*, an observation also considered by Sedor et al. (2017) and Carneiro (2019). The fragmentary state of the holotype of *Nemolestes spalacotherinus* (MACN-A 1033) restricts comparisons with MCN.P.1259, which led us to consider this taxon as *Nemolestes* sp. indet. in this present study. Nevertheless, we are confident that this specimen clearly differs from *Patene*, *Nemolestes brasiliensis* and *Procladosictis*, being more likely a new species of *Nemolestes* (see Sedor et al. 2017) or the most complete specimen of *Nemolestes spalacotherinus* known so far (see Carneiro 2019).

Moreover, Engelman et al. (2018) made comparisons between *Procladosictis* and the similarly sized *Chlorocyon*, concluding that they did not belong to a single taxon due to an incongruent occlusal relation between the protocone of *P. anomala* and the talonid of *C. phantasma*. We calculate the ratio proportions of the m2 talonid of *C. phantasma* based on the measurements provided by Engelman et al. (2018). As discussed by them, the talonid of *Chlorocyon* is proportionally much shorter than expected for *Procladosictis* (see Table 3). Therefore, considering the results of Engelman

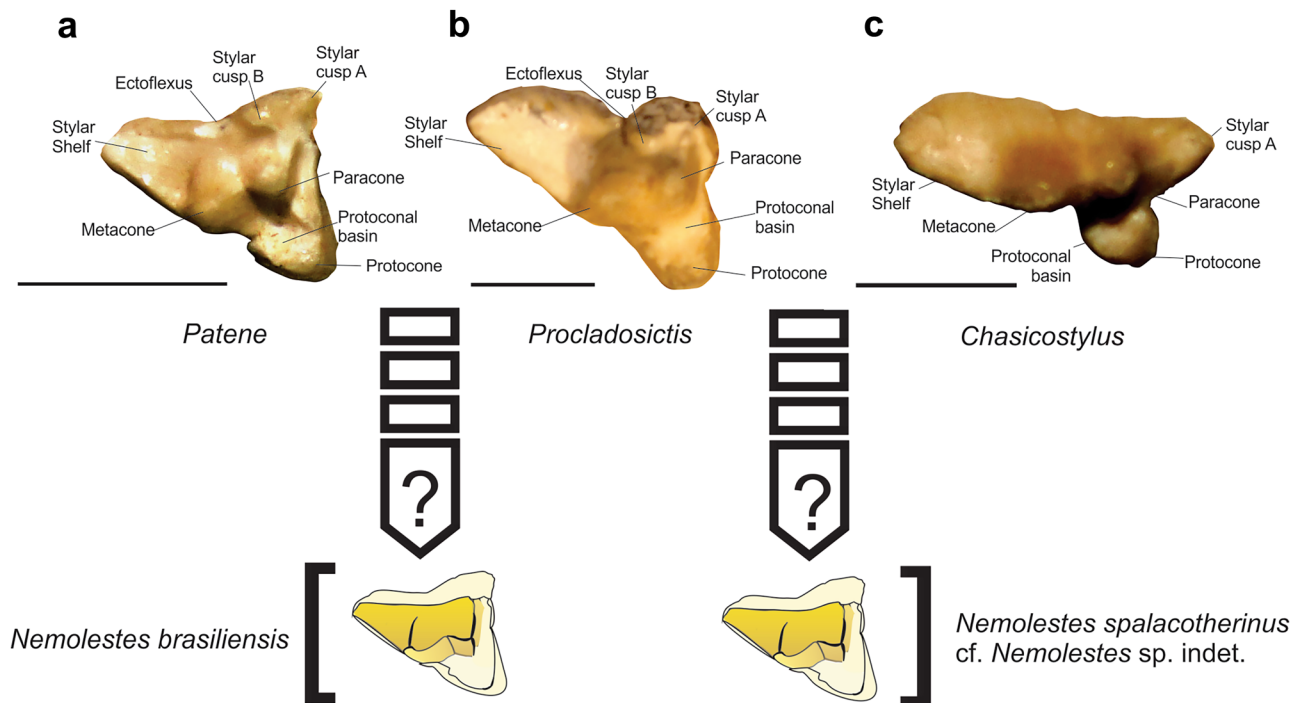


Fig. 8 Schematic inferences of the probable second upper molar shape of *Nemolestes brasiliensis* and *Nemolestes spalacotherinus*/*Nemolestes* sp. indet. (MCN.P.1259). The M2 of *N. brasiliensis* would be more like a “mosaic” between the one of *Patene* and *Procladosictis*; whereas the one of *N. spalacotherinus*/*Nemolestes* sp. indet. would be a “mosaic”

between the one of *Procladosictis* and *Chasicostylus*. **a.** M2 of *Patene* (holotype, MN 1331-V, a right maxilla with P3-M4); **b.** M2 of *Procladosictis* (holotype, MACN-A 10,327, a right maxilla with P3-M3); **c.** M2 of *Chasicostylus* (holotype, MLP 57-XI-9-2, a left maxilla with M1-2). Scale bars equal 5 mm

et al. (2018), the possibility that *Procladosictis* represents the upper dentition of *Chlorocyon* is unlikely.

Furthermore, the isolated lower molar (AMNH 29433) from Cerro del Humo (Mustersan biochron) appears to be incompatible with *Procladosictis*. This tooth is considered to be a m2 or m3 and has subequal trigonid and talonid in width but trigonid much longer than the talonid. As discussed, the m2 and m3 of *P. anomala* would have talonids shorter and narrower than the trigonids.

In short, *Procladosictis* is a valid taxon in which its lower molars would have more developed talonids than *Nemolestes* sp. indet. and *Chlorocyon* but less developed ones than *Patene*. The talonid proportions of its lower molars would be more like those of *Nemolestes brasiliensis* than to any other sparassodont known so far (see Table 3).

Systematic affinities of “*Procladosictis erecta*”

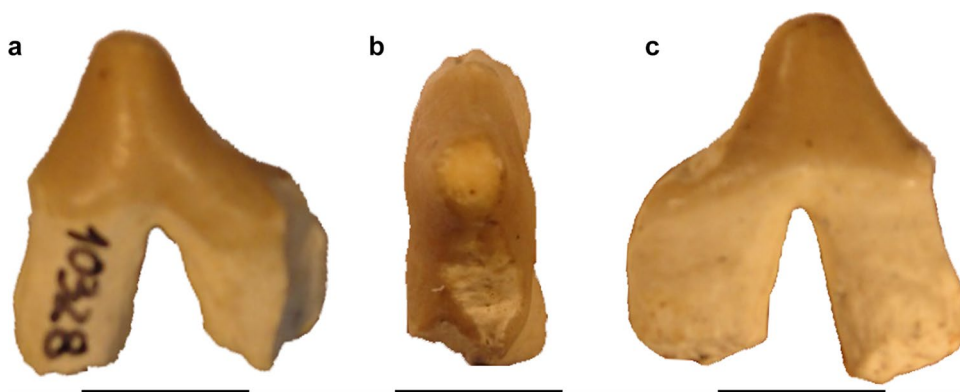
“*Procladosictis erecta*” is another enigmatic taxon from the middle Eocene of southern Argentina. This “dubious” taxon is recognized only by an isolated p2 (MACN-A 10328). This tooth was found in the locality named as “partie supérieure des couches á *Notostylops*”, north of Lago Colhue-Huapi,

Chubut Province, Argentina (Ameghino 1902). Currently, this locality has been considered as middle Eocene (Casamayoran SALMA) in age. Later, Simpson (1967: p. 64) considered “*Procladosictis erecta*” a *nomem vanum*, a conclusion followed by Marshall (1981: pp. 18–19).

MACN-A 10328 has symmetric mesial and distal walls, a small precingulid, and a developed posterobasal heel with a reduced posterobasal cuspid (its base is identifiable but no erected cuspid is observed). This premolar has little to no development of crests, especially on the mesial wall of the protoconid. Its roots are greatly preserved, showing a more robust posterior root than the anterior one (Fig. 9). This tooth is identified as a p2, as its main cuspid has a distal wall that extends strongly posteriorly, unlike a p3, that has a more “vertical” distal wall (see comments in Engelman et al. 2020a).

The symmetric walls of MACN-A 10328 are very similar to those of *Hondadelphys* and, especially, *Hathliacyonidae* (in fact, we did not observe these concave walls in any other group of Sparassodonta; see a similar conclusion in Engelman et al. 2020a). Moreover, the phylogenetic analysis recovered the presence of symmetric walls on p2 as a synapomorphy of the clade that comprehends *Hathliacyonidae*, *Hondadelphys* and *Stylocynus* (despite

Fig. 9 “*Procladosictis erecta*” nomem vanum. Digital photographs of MACN-A 10328, left p2, in labial (a), occlusal (b), and lingual (c) views. Scale bars equal 5 mm



the independent loss in *Stylocynus*; Engelman et al. 2020a observed that symmetric walls on p2 is a peculiar feature of hathliacynids and *Hondadelphys*. Therefore, MACN-A 10328 should be a member of this clade or a closely related taxon to these two groups.

Regarding the presence of precingulids, Engelman et al. (2018) provided a list of sparassodonts that present this feature on p2. The presence of a precingulid on MACN-A 10328 suggests affinities with the unnamed clade A, as most of its representatives show precingulids on p2, in exception of *Stylocynus* (this condition could not be observed for *Dukecynus*); and with the borhyaenoids *Prothylacynus* and some borhyaenids (*Arctodictis* and *Australohyaena*). However, the lower premolars of *Prothylacynus* and borhyaenids are more robust than the slender shape of MACN-A 10328. Therefore, MACN-A 10328 should not be assigned to a borhyaenoid.

The phylogenetic analysis recovered a precingulid on p2 as a synapomorphy of the unnamed clade A, as it is identified in hathliacynids, *Hondadelphys* and *Lycopsis* (but not *Stylocynus*). This feature was independently acquired by *Prothylacynus* and by the borhyaenids *Arctodictis* and *Australohyaena* (this condition is unknown for *Acrocyon*).

The MACN-A 10328 and the p2 of hathliacynids share little to no development of crests, concave symmetric walls of the main cuspid, and a reduced posterobasal cuspid on the posterobasal heel (see discussion in Engelman et al. 2020a). Following Engelman et al. (2020a), these features would represent synapomorphies of Hathliacynidae, a result supported by the phylogenetic analysis. However, MACN-A 10328 differs from hathliacynids in its greater inflation of P3 (PS = 0.47) (hathliacynids have lower values; see a complete list of calculated PS for several sparassodonts in Online Resource 1: Appendix 11) and relatively longer posterobasal heel on p2. These two features prevent the inclusion of “*Procladosictis erecta*” within Hathliacynidae but do not discard closely affinities between them.

MACN-A 10328 should be assigned to a small to medium-sized sparassodont of the unnamed clade A.

Considering the diversity of small to medium-sized sparassodonts from the middle to late Eocene, the dimensions of MACN-A 10328 (Table 4) are like the P3 of *Procladosictis anomala* (MACN-A 10327) and *Nemolestes* sp. indet. from Guabiro tuba (MCN.P.1259) but are larger than expected for *Chlorocyon phantasma* (see Engelman et al. 2018: p. 12, table 2). *Angelocabrerus*, *Arminiheringia*, *Callistoe* and *Plesiofelis* are larger than MACN-A 10328 and are recognized as borhyaenoids, a group with more robust premolars (PS > 0.58) in comparison with “*Procladosictis erecta*”.

The symmetric concave walls of MACN-A 10328 prevent associations with *Patene* and *Nemolestes* sp. indet. (MCN.P.1259). The presence of a precingulid does not allow its assignment to *Patene*, *Nemolestes* sp. indet. from Guabiro tuba or *Chlorocyon*, as these taxa lack this feature (see Engelman et al. 2018). In addition, *Chlorocyon* is considered to be an early borhyaenoid (Engelman et al. 2018), whereas MACN-A 10328 is identified as belonging to a closely related taxon to Hathliacynidae and *Hondadelphys*. The best candidates for the referral of MACN-A 10328 are *Nemolestes* and *Procladosictis*, as their lower premolars are unknown. Nevertheless, Sedor et al. (2017) and Carneiro (2019) identified MCN.P.1259 from Guabiro tuba fauna as *Nemolestes* sp. indet. and *N. spalacotherinus*, respectively. Moreover, the size proportions calculated for MCN.P.1259 and MACN-A 10327 support that they belong to different taxa. Therefore, *Procladosictis* is the only known middle to late Eocene taxon in which an association with MACN-A 10328 can be considered due to its similar dimensions (see

Table 4 Dental measurements (in mm) of the holotypes (bold) of “*Pseudocladodictis determinabile*” nomem vanum and “*Procladosictis erecta*” nomem vanum

	Taxon	L	W
MACN-A 10325	“ <i>Pseudocladodictis determinabile</i> ” nomem vanum	8.50	5.50
MACN-A 10328	“ <i>Procladosictis erecta</i> ” nomem vanum	8.50	4.00

Table 4) and compatible morphology (e.g., gracile shape of P3), as originally considered by Ameghino (1902).

Despite the possible argument of “a great number of symplesiomorphies for Sparassodonta on the upper dentition of *Procladosictis*” as precluding its assignment as a member of the unnamed clade A, we call attention to the fact that other early sparassodonts (*Nemolestes*) and early borhyaenoids (*Chlorocyon*) have no preserved upper molars. This fragmentary condition restricts comparisons between these taxa and the members of the unnamed clade A and Borhyaenoidea. In addition, *Sallacyon* and *Notogale* (Villarroel and Marshall 1982) from the Salla Beds (late Oligocene; Deseadan SALMA) of Bolivia are the oldest known members of the unnamed clade A, which identifies a long ghost-lineage between them and *Procladosictis*. Based on this, possible upper molar modifications during the evolution of this clade (e.g., loss of StB, reduction of the styler shelf width) cannot be confidently evaluated based on the current fossil record knowledge (the common ancestor of the unnamed clade A had a large StB?). Therefore, we did not consider the “symplesiomorphic upper molar features” of *Procladosictis* as a preventing argument for its inclusion as a member of the unnamed clade A.

Furthermore, if *Procladosictis* were a member of the unnamed clade A, this would push back the origin of the group that comprises Hathliacynidae, *Hondadelphys* and *Stylocynus* to the middle-late Eocene. Moreover, we call attention to the similarities between the “Hathliacynidae indet.” from Laguna Fría and La Barda with *Procladosictis*, as discussed. These specimens could represent the oldest known members of the unnamed clade A, as originally suggested by Tejedor et al. (2009) (“hathliacynid indet.” of those authors), dating back the origin of this group to the earliest middle Eocene. This observation represents a compatible result with the occurrence of a borhyaenoid in La Barda fauna and the results of our phylogenetic analysis that recovered a sister relation between the unnamed clade A and Borhyaenoidea.

Systematic affinities of “*Pseudocladosictis determinabile*”

The holotype of “*Pseudocladosictis determinabile*” (MACN-A 10325) was found in the upper part of the “Couches á *Notostylops*” from the south slope of the Colhué-Huapi Lake (Ameghino 1902), Gran Barranca, Chubut, Argentina (Middle Eocene, Casamayoran SALMA; see Prevosti and Forasiepi 2018). Originally, this tooth was described by Ameghino as a lower premolar. Later, Simpson (1948: p. 46) suggested that this tooth would better represent an upper premolar and considered “*Pseudocladosictis determinabile*” a *nomem vanum*. These conclusions were followed by Marshall (1981: pp. 18–19).

MACN-A 10325 is somewhat inflated, shows a multicusped posterobasal heel, developed lingual and labial cingula (Marshall 1981) (Fig. 10). Based on its shape and features, we recognize this tooth as a P3 or p3. This tooth is similarly sized to the P3 of *Procladosictis anomala* and p2 of “*Procladosictis erecta*” but is relatively wider (see Table 4).

MACN-A 10325 differs from other small to medium-sized Eocene sparassodonts on its more inflated morphology (i.e., greater PS value) (Table 5). This tooth clearly differs from the P3 of *Patene simpsoni* and *Procladosictis anomala*, which are more gracile (= lower PS) and lack a multicusped posterobasal heel. A similar conclusion can be observed for the lower premolars of *Patene coloradensis* and *Nemolestes* sp. indet. from Guabiro-tuba (MCN.P.1259), which shows gracile p2-3. Moreover, MACN-A 10325 differs from *Patene simpsoni* in the presence of a well-developed lingual cingulum and more reduced labial cingulum. Its labial cingulum is less developed than the lingual one, similarly to *Procladosictis anomala* but its crown is relatively more inflated. Furthermore, we observe that this tooth should not be assigned to *Patene*, *Nemolestes* sp. indet. from Guabiro-tuba or *Procladosictis*.

Fig. 10 “*Pseudocladosictis determinabile*” *nomem vanum*. Digital photographs of MACN-A 10325, right P3, in lingual (a), occlusal (b), and labial (c) views. Scale bars equal 5 mm

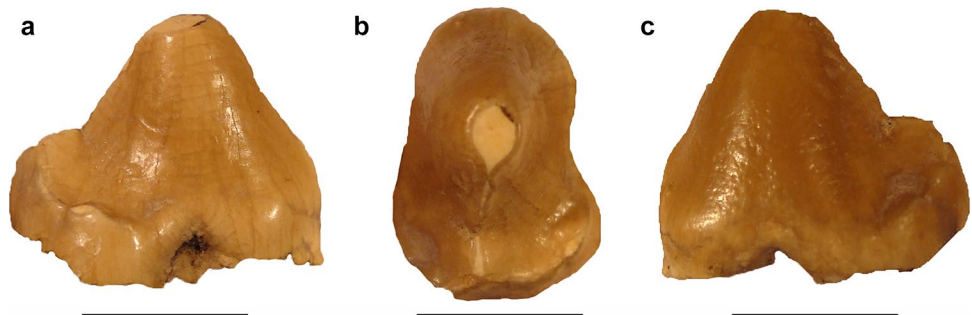


Table 5 Premolar shape (PS) of small to medium-sized Eocene sparassodonts. The values of PS for *Angelocabrerus*, *Arminiheringia* and *Plesiofelis* were provided by Zimicz (2012); for *Callistoe*, see Babot et al. (2022); and for *Eomakharia molossus*, see Engelman et al. (2020a, b). Abbreviations: (l), left; (r), right; ~, estimated value due to the broken condition of the specimen

Taxon	PSP3	PSp2	PSp3
<i>Patene simpsoni</i>	0.46	0.43	0.46–0.47
<i>Patene coloradensis</i>		0.35	0.42
<i>Nemolestes</i> sp. indet.		0.39	~0.43
<i>Procladosictis anomala</i>	0.47		
" <i>Procladosictis erecta</i> "		0.47	
" <i>Pseudocladocictis determinabile</i> "	0.64		
<i>Callistoe vincei</i>			0.53
<i>Arminiheringia</i> spp.			0.54–0.74
<i>Eomakharia molossus</i>	0.57(l)/0.55(r)	0.65(r)/	0.56(l)/0.54(r)
<i>Plesiofelis schlosseri</i>		0.59	0.59
<i>Angelocabrerus daptēs</i>			0.60

The representatives of the unnamed clade A show less robust premolars (*Lycopsis*, *Hondadelphys*, *Stylocynus* and hathliacynids) in comparison with borhyaenoids, except *Pseudothylacynus rectus* (see a complete list of calculate PS of several sparassodonts in Online Resource 1: Appendix 11). Therefore, the assignment of this premolar to a representative of the unnamed clade A is also unlikely.

Comparing MACN-A 10325 with borhyaenoids, a group that shares more robust premolars than early sparassodonts and unnamed clade A, this tooth is smaller than expected for the upper premolars of *Callistoe*, *Arminiheringia*, *Angelocabrerus* and *Plesiofelis* (see a list of measurements of studied specimens in Online Resource 1: Appendix 12). It cannot be assigned to Borhyaenidae, as it lacks a developed posterolabial cusp. Moreover, considering its dimensions and the Eocene diversity of small to medium-sized sparassodonts, MACN-A 10325 would be similarly sized to *Chlorocyon phantasma*. *Chlorocyon* was considered as an early borhyaenoid by Engelman et al. (2018); therefore, we did not discard the possibility of this association.

In short, it is very likely that MACN-A 10325 is a premolar of a small to medium-sized borhyaenoid (*Chlorocyon*?), as its great PS value (PS = 0.64) excludes associations with *Patene*, *Nemolestes* sp. indet. and *Procladosictis* (and, by consequence, with the unnamed clade A).

***Nemolestes*, an Eocene mammalian predator**

Nemolestes has been considered a hypercarnivorous metatherian (Zimicz 2012; Prevosti et al. 2013; Prevosti and Forasiepi 2018) based on its calculated value of RGA (but see Croft et al. 2018 and references therein for cautions and caveats in using this approach for clades that lack extant representatives). The RGA calculated for *N. brasiliensis* (RGA = 0.36) (RGA = 0.39; Zimicz 2012) and for *N. lagunafriensis* (RGA = 0.33) are indicative of a hypercarnivorous

diet (Zimicz 2012; Forasiepi et al. 2015). *Nemolestes brasiliensis* has a lower RGA index value than the contemporaneous *Patene simpsoni* (RGA = 0.73), which has been considered as a mesocarnivorous sparassodont. The younger *Patene coloradensis* is also in the range of mesocarnivory (RGA = 0.55).

Nemolestes brasiliensis is one of the largest metatherians in the Itaboraí fauna, being similarly sized to *Eobrasilia coutoi* and larger than *Carolocoutoia ferigoloi*. *Nemolestes brasiliensis* weighed about 4 kg. It is here proposed that *Nemolestes* represented the top mammalian predator of the Itaboraí fauna, as *Carolocoutoia* is considered as a strict frugivorous taxon (Goin et al. 1998; Oliveira and Goin 2011; Zimicz 2012), and *Eobrasilia* is considered a taxon specialized for durophagy (Carneiro and Oliveira 2017).

Considering the fauna from Laguna Fría, *Nemolestes lagunafriensis* shared the hypercarnivorous niche with a "putative hathliacynid" (unnamed clade A?) and a borhyaenoid (see Tejedor et al. 2009). Other metatherian members of this fauna, such as derorhynchids and "peradectoids", are considered insectivorous (Zimicz 2012; Goin et al. 2016; Oliveira et al. 2021); *Protodidelphis*, *Procaroloameghinia*? and *Palangania* are considered as insectivorous/frugivorous (Goin et al. 1998; Oliveira and Goin 2011; Zimicz 2012; Carneiro 2019); and *Itaboraidelphys* is considered a hypocarnivorous/omnivorous taxon (see Zimicz 2012).

Therefore, sparassodonts were the only hypercarnivorous mammals known from Itaboraí, Laguna Fría and La Borda local faunas (Zimicz 2012). This group occupied the role of main mammalian predators in South America from the early Eocene until the Pliocene (Prevosti et al. 2013; Prevosti and Forasiepi 2018). Moreover, *Patene simpsoni* and *Nemolestes brasiliensis* from the Itaboraí fauna are the oldest known sparassodonts, which identifies *N. brasiliensis* as the oldest known sparassodont to exhibit dental features specialized for hypercarnivory (Fig. 11).



Fig. 11 Artistic life reconstruction of *Nemolestes brasiliensis* with a recently captured metatherian prey. Designed by Sérgio Lages dos Reis from the Universidade Federal de Minas Gerais (UFMG)

The Paleocene-Eocene Thermal Maximum (PETM) and the evolution of Sparassodonta

Sparassodonta was represented during the Eocene by early lineages (*Patene* and *Nemolestes*), early members of the unnamed clade A (*Procladosictis*?), early borhyaenoids (*Chlorocyon*? and *Plesiofelis*), borhyaenids (*Angelocabrerus*?) and proborhyaenids (*Callistoe*, *Arminiheringia* and *Eomakhaira*) (Simpson 1970; Babot et al. 2002, 2022; Tejedor et al. 2009; Engelman et al. 2018, 2020b; Prevosti and Forasiepi 2018; Rangel et al. 2019). The fauna from Itaboraí preserved only early lineages of Sparassodonta (*Patene* and *Nemolestes*) (Paula Couto 1952, 1961, 1962, 1970; Marshall 1978, 1981; Bergqvist et al. 2009; Rangel et al. 2019). Nevertheless, the occurrence of a “hathliacynid-like taxon” (unnamed clade A?) from Laguna Fría and La Barda local faunas and a borhyaenoid from La Barda local fauna (see Tejedor et al. 2009) indicate that the dichotomy between Borhyaenoidea and the unnamed clade A had already

occurred during the middle Eocene. Therefore, the Eocene diversity of sparassodonts should be greater than expected (see a similar conclusion in Croft et al. 2018; Engelman et al. 2018).

Furthermore, the apparently “short-time” evolutionary history of sparassodonts in South America should be directly linked with the paleoenvironmental changes resulted from the events of the Paleocene-Eocene Thermal Maximum (around 55.5 Ma; Bowen et al. 2015), which increased global temperatures and tropical biomas throughout South America during the early Eocene (Woodburne et al. 2014; Goin et al. 2016), mostly due to the increase in the global temperatures (see e.g., Tarquini et al. 2022). The results of our phylogenetic analysis argue in favor of the hypothesis that linked the increase in diversity of metatherians with the climatic modifications during the early Eocene (see Tarquini et al. 2022), which has been linked to the increase in abundance of polydolopimorphians (Goin et al. 2016) and increase in diversity of protodidelphids (Carneiro 2019).

Conclusions

Nemolestes was an early to middle Eocene (Itaboraian to Casamayoran) sparassodont. This taxon is the oldest known small hypercarnivorous metatherian from South America. *Nemolestes* has three identified species: *Nemolestes brasiliensis* (Itaboraí fauna—Itaboraian biochron), *N. lagunafriensis* (Laguna Fría fauna; Riochican biochron) and *N. spalacotherinus* (“Couches à *Notostylops*” fauna; Casamayoran biochron).

Nemolestes cannot be included within Hathliacynidae, Hondadelphidae or Borhyaenoidea. This taxon represents an early lineage of hypercarnivorous sparassodonts more closely related to the unnamed clade A and Borhyaenoidea than to *Patene*. If the identification of “*Procladosictis erecta*” as *Procladosictis* were confirmed, then *Procladosictis* would be more closely related to *Hondadelphys*, *Stylocynus* and hathliacynids, as with a late Eocene member of the unnamed clade A.

The results of the phylogenetic analysis suggest that during the early middle Eocene, the faunas from Laguna Fría and La Barda preserved the oldest representatives of the unnamed clade A and Borhyaenoidea. Therefore, the major groups of Sparassodonta have already diverged during the middle Eocene. This “short time” diversification of sparassodonts can be linked to the PETM, as the early Eocene fauna from Itaboraí preserved only early lineages of Sparassodonta (*Patene* and *Nemolestes*) and the faunas from Laguna Fría and La Barda preserved a greater diversity of clades (*Nemolestes*, unnamed clade A and Borhyaenoidea).

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s10914-023-09663-7>.

Acknowledgements We would like to express our gratitude to Luciana Carvalho (MN), Rodrigo R. Machado (MCT), Rafael C. Silva (MCT), who allowed the study of Brazilian taxa; and Laura Chornogubsky, Stella Alvarez and Alejandro Kramarz (MACN), who allowed the study of Argentine specimens. We thank Nelson Novo and D. Podestá (CONICET-CENPAT) for taking the photographs of LIEB-PV 1038. We thank Laura Chornogubsky for sending images of *Nemolestes spalacotherinus* for Caio C. Rangel. We thank Analia Forasiepi for sending images of *Hondadelphys* for Leonardo M. Carneiro. We would like to thank Bruno M. G. Guimarães for sending images of *Lycopsis longirostris*, *L. torresi* and *Pseudothylacynus rectus*. We are grateful for Francisco J. Goin (MLP) for reading and revising the manuscript in its early stages. We also would like to express our gratitude to Russel K. Engelman, Robin M. D. Beck and one anonymous reviewer of this paper, who provide important contributions to this study. This work was supported by the National Council of Scientific and Technological Development (CNPq) [CNPq, 140891/2020-0—GD], Postgraduate Program in Geosciences of Universidade Federal de Pernambuco (UFPE).

Author contributions CCR, LMC, LPB, MFT and EVO wrote the main manuscript text and prepared figures and tables. All authors reviewed the manuscript.

Funding The authors were supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq (305281/2020–8 and 303610/2020–4) and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (E-26/201.108 /2022).

Data availability The Morphobank link is https://morphobank.org/index.php/Projects/ProjectOverview/project_id/4509.

Declarations

Competing interests LPB and EVO are members of the Editorial Board of the JME but was not involved in evaluation of this manuscript.

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