

INSIGHTS INTO THE NEOTROPICS PRIOR TO THE GREAT AMERICAN BIOTIC INTERCHANGE: NEW EVIDENCE OF MAMMALIAN PREDATORS FROM THE MIOCENE OF NORTHERN COLOMBIA

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ABSTRACT—A new species of Sparassodonta (Mammalia, Metatheria), *Lycopsis padillai*, sp. nov., is described on the basis of a partial left maxilla with M1–M4 and fragments of lacrimal and jugal. The material comes from the early to early middle Miocene Castilletes Formation, La Guajira Peninsula, Colombia. This specimen represents the northernmost record of a fossil metatherian in South America and integrates a highly diverse vertebrate association, recently discovered in the north of Colombia. The La Guajira specimen is referred to the genus *Lycopsis*, as supported by the results of our phylogenetic analysis. This analysis also demonstrates that species of *Lycopsis* (*L. torresi*, *L. longirostris*, *L. viverensis*, and *L. padillai*) constitute a monophyletic group and are placed as the basal taxon of Borhyaenoidea. *Lycopsis padillai* is a large-sized sparassodont with a body mass of about 22 kg. The presence of *Lycopsis* from La Guajira extends the geographical distribution of the genus to the entire South America, representing the sparassodont with the widest latitudinal distribution.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Cenozoic South American mammals are mostly known from fossils collected in the Southern Cone. This is so both because of the scarcity of paleontologists working on tropical latitudes and the larger outcrops in southern South America: whereas most of the Neotropics are covered by dense vegetation, the southern portion is characterized by cool deserts with sparse vegetation cover. Notwithstanding this, paleontological research in the Neotropics has greatly increased over the past decade.

South American biogeography is divided into two main domains following Morrone (2002, 2006): the Neotropical Region (included in the Holotropical Kingdom) and the Andean Region (included in the Austral Kingdom); the latter is composed of Patagonia and a narrow Cordilleran strip up to the Central Andes. The dual nature of the biogeography and paleobiogeography of South America offers new insights into mammalian evolution on this continent (Goin et al., 2012). The biota was quite distinct in the two South American regions, both in taxonomic and in trophic composition. Taxonomic differences between Neotropical and temperate fossiliferous sites have been explained as a consequence of the latitudinal position of the associations (e.g., Croft, 2007; Carrillo et al., 2015).

The tropics could be seen either as ‘cradles’ (areas of high origination rates) or ‘museums’ (areas of low extinction rates) (e.g., Stenseth, 1984; MacFadden, 2006; Mannion et al., 2014). However, many authors consider that both scenarios can apply to the tropics (e.g., Jablonski et al., 2006; McKenna and Farrell, 2006; Mittelbach et al., 2007; Vucetich et al., 2010; Goin et al., 2012; Rolland et al., 2014). Regarding Metatheria, the middle Miocene La Venta assemblage from Colombia was considered representative of the cradle model to the extent of being interpreted as a hotspot for the Neogene radiation of extant didelphoid opossums (Goin, 1997). The same association gives an example of the museum model with the sparassodont *Hondadelphys*. With many plesiomorphic characters, this taxon is placed in a basal position in sparassodont phylogeny together with Paleogene taxa, but is from the middle Miocene (Forasiepi, 2009).

The most representative fossiliferous sites in northern South America are the mammalian associations from La Venta (middle Miocene) in Colombia (Kay et al., 1997), Urumaco (late Miocene–Pliocene) in Venezuela (Linares, 2004; Sánchez-Villagra and Aguilera, 2006; Sánchez-Villagra et al., 2010), and Acre (late Miocene) in southwestern Amazonia of Brazil, Peru, and Bolivia (Cozzuol, 2006; Antoine et al., 2013; Ribeiro et al., 2013). More recently, a middle Miocene mammalian association has been described from localities of the Fitzcarrald Arch in western Amazonia, Peru (Tejada-Lara et al., 2015); the association was referred to the Laventan South American Land Mammal Age (SALMA). Finally, recent field work undertaken in the

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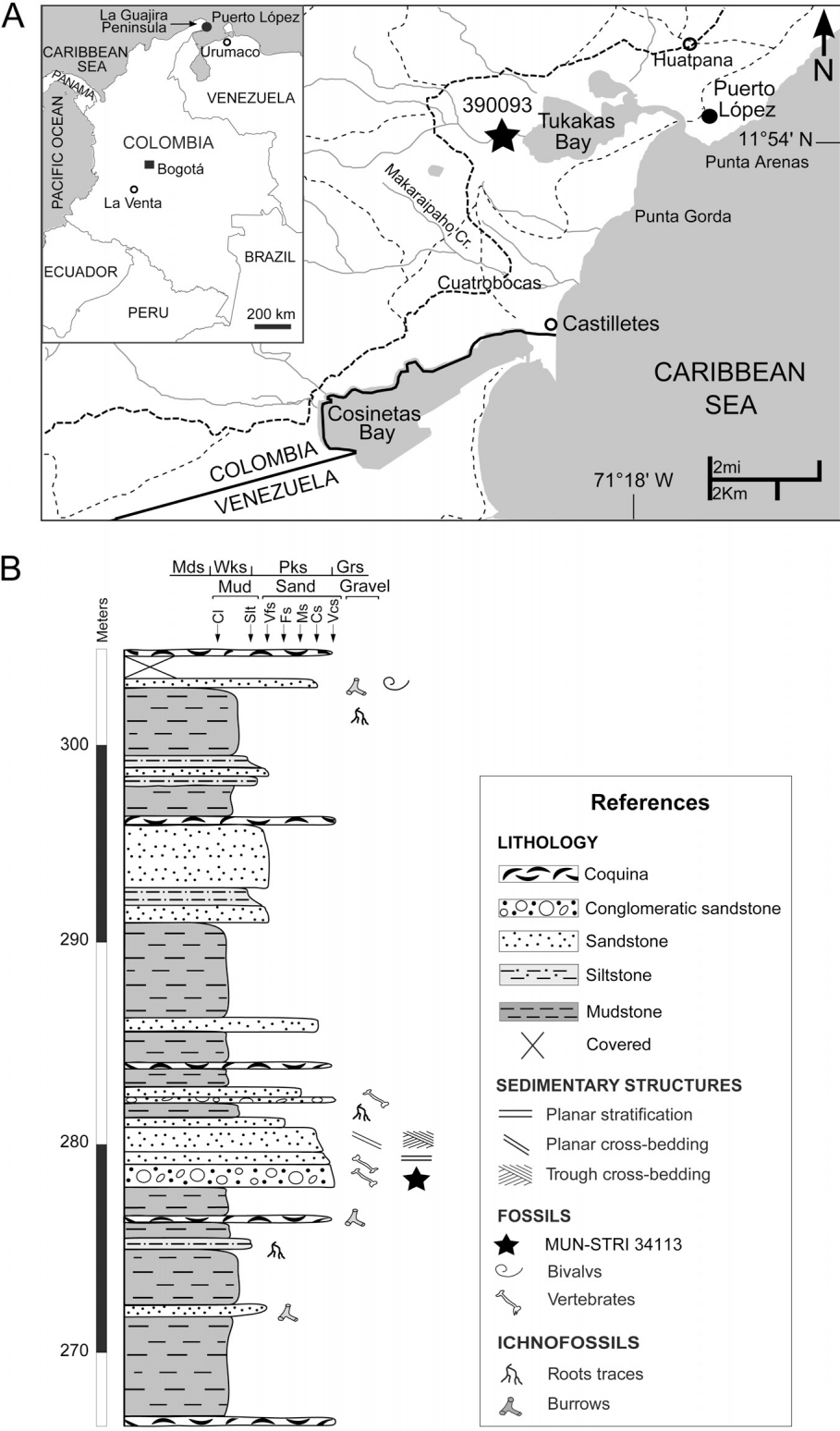


FIGURE 1. **A**, geographical location of the locality Makaraipao (ID: 390093) in La Guajira Peninsula, Colombia, where the specimen MUN-STRI 34113 was collected; **B**, stratigraphic sequence exposed at Makaraipao locality (modified from Moreno et al., 2015), which is part of the middle segment of the Castilletes Formation. **Abbreviations:** Cl, clay; Cs, Coarse sand; Fs, fine sand; Grs, grainstone; Mds, mudstone; Ms, medium sand; Pks, packstone; Slt, silt; Vcs, very coarse sand; Vfs, very fine sand; Wks, wackestone.

La Guajira Peninsula, northernmost Colombia, led to the discovery of new mammalian associations, ranging from the early Miocene to the late Pliocene (Moreno et al., 2015). At about 12°N, bounded by the Caribbean Sea, the La Guajira Peninsula, Colombia, is the northernmost extension of continental South America (Fig. 1A). Previous paleontological research

in the region has been scarce, with only one published work (Becker and Dusenbury, 1958) and few geological studies that include paleontological data (e.g., Bürgli, 1960; Renz, 1960; Rollins, 1965). Since 2009, the Smithsonian Tropical Research Institute has initiated a series of field trips to prospect deposits in the La Guajira Peninsula, resulting in the collection of hundreds of

fossil vertebrates (Moreno et al., 2015). Research at the La Guajira Peninsula offers the opportunity for increasing our knowledge of Neotropical Neogene faunas and recognizing evolutionary aspects of the native biota and the dynamics of the Great American Biotic Interchange (GABI). La Guajira represents the closest South American fauna both in time and space to the Isthmus of Panama.

The Sparassodonta (Mammalia, Metatheria) were the dominant carnivorous mammals in South America during most of the Cenozoic. Unlike other continents, in South America the carnivorous adaptive zone in terrestrial ecosystems was shared by mammals, birds (Phorusrhacoidea), large crocodiles (Sebecidae), large snakes (Madsoidae and Boidae), and occasionally frogs (Marshall, 1977; Marshall and Cifelli, 1990; Head et al., 2009; Degrange, 2012; Degrange et al., 2012; Fernicola and Albino, 2012; Scheyer et al., 2013). The sparassodont record extended for about 60 Ma, from the Paleocene to the late Pliocene, and included diverse morphologies such as the fox-like Hathliacynidae, the dog-like Borhyaenidae, the bone-cracking Proborhyaenidae, and the saber-tooth Thylacosmilidae. Classically, the genus *Lycopsis* has been grouped with *Prothylacynus*, *Pseudolyacynopsis*, *Pseudothylacynus*, *Stylocynus* (e.g., Marshall, 1978, 1979), and later *Dukecynus* (Goin, 1997; Forasiepi et al., 2004) within the Prothylacyninae. However, cladistic analyses have demonstrated that Prothylacyninae is not a monophyletic group (Muisson, 1999; Babot et al., 2002; Forasiepi et al., 2006, 2014; Forasiepi, 2009; Engelman and Croft, 2014). *Prothylacynus*, *Pseudolyacynopsis*, *Pseudothylacynus*, and *Stylocynus* are monospecific, whereas *Lycopsis* at present comprises three species: *L. torresi*, the type species of the genus from the late early Miocene (Santacrucian SALMA) of Patagonia, Argentina (Cabrera, 1927); *L. longirostrus* from the middle Miocene (Laventan SALMA) of Colombia (Marshall, 1977); and *L. viverensis* from the late Miocene (Chasicuan SALMA) of the Pampan region, Argentina (Forasiepi et al., 2003). The monophyly of *Lycopsis* has been questioned, because the features used to characterize this taxon are plesiomorphies (Forasiepi, 2009). However, to date, only *L. longirostrus* has been included in cladistic analyses.

In this contribution, we describe the new species *Lycopsis padillai*, based on a left maxilla with M1–M4 and partial lacrimal and jugal bones. The specimen was collected in the Castilletes Formation, La Guajira Peninsula, Colombia (Langhian, early middle Miocene). We included this taxon in a phylogenetic analysis together with other species of the genus *Lycopsis* to test the affinities of the new species, and estimated its body mass as well. Southern South America has yielded most of our knowledge of Sparassodonta (Forasiepi, 2009); the La Guajira specimen provides an insight into low-latitude Neogene associations of this continent. The studied specimen represents the northernmost South American sparassodont ever recorded, and the first metatherian known from the La Guajira fossil association.

Institutional Abbreviations—MUN, Mapuka Museum of Universidad del Norte, Barranquilla, Colombia (repository); STRI, Smithsonian Tropical Research Institute, Panama City, Panama.

Anatomical Abbreviations—Capital and lower case letters refer to upper and lower teeth, respectively: **M/m**, molar; **P/p**, premolar.

MATERIALS AND METHODS

The nomenclature in the descriptions follows Marshall (1978). Morphological data for comparisons were taken from direct observations on original specimens and casts (Supplementary Data), and published literature (Marshall, 1978, 1979; Forasiepi et al., 2003). Measurements are in millimeters and were taken with digital calipers to the nearest 0.01 mm (Supplementary Data).

The phylogenetic relationship between sparassodont species has been tested through a parsimony analysis conducted in the

program TNT 1.1 (Goloboff et al., 2008). The data matrix is based on Forasiepi (2009) and includes several modifications and additions proposed by Engelman and Croft (2014), Forasiepi et al. (2015), and this paper (Supplementary Data). All the characters are given equal weight. The ingroup has 23 sparassodonts, including all known species of *Lycopsis* (*L. torresi*, *L. longirostrus*, *L. viverensis*, and *L. padillai*, sp. nov.); the outgroup includes 19 non-sparassodont metatherians, and the tree was rooted in *Deltatheridium pretrituberculare*. Following previous approaches, *Thylacinus cynocephalus* was secondarily excluded from the analysis because it is grouped in all the trees within the Sparassodonta due to convergences (see also Forasiepi, 2009; Engelman and Croft, 2014; Forasiepi et al., 2015).

Body mass was estimated using the equations of Myers (2001) for dasyuromorphian species, on the basis of the second upper molar area (2UMA) (Supplementary Data). This variable was calculated by multiplying maximum crown width and length, taken in occlusal view. Additional estimates were calculated using upper molar occlusal row length (UMORL). The estimates were corrected using the Smearing Estimate factor calculated by Myers (2001) for each equation. This factor is expressed by Myers (2001) as a percentage; we made the calculations expressing it as a nonparametric term, following Smith (1993:32), “a typical value for a correction factor, for example 1.085, would indicate that body mass estimates derived from the equation underestimate the arithmetic mean mass for any value of the independent variable by 8.5%.”

GEOLOGIC SETTING

Specimen MUN-STRI 34113 was collected from the Makaraipao locality (ID: 390093), west from Puerto López, La Guajira Department, Colombia (N11°54'32", W71°20'24") (Fig. 1A), from outcrops of the Castilletes Formation (Moreno et al., 2015). The unit is composed of gray massive mudstone, fossiliferous mudstone and siltstone, wackestone to packstone biosparite, and medium-grained to conglomeratic fossiliferous sandstone. Sandy and silty facies increase toward the top of the unit (Moreno et al., 2015). In the locality Makaraipao (Fig. 1A), part of the middle segment of the Castilletes Formation (meter 280 from a total thickness of 440 m) is exposed, corresponding to meter 127 of the Stratigraphic Section Long-150514 (Moreno et al., 2015). The studied specimen comes from conglomeratic sandstones (Fig. 1B).

The Castilletes Formation conformably overlies the Jimol Formation (early Miocene) and is overlaid by the Waré Formation (late Pliocene) in angular unconformity (Moreno et al., 2015). The unit was deposited in a very shallow marine to fluvio-deltaic environment, with strong fluvial influence (Moreno et al., 2015). The Castilletes Formation is rich in marine and terrestrial fossils, including plants, invertebrates, and vertebrates (Moreno et al., 2015). The fossil vertebrates include sharks (Carchariniformes), rays (Myliobatiformes), catfish (Siluriformes), reptiles (Testudines and Crocodylia), and a rich association of mammals (Moreno et al., 2015).

The Castilletes Formation is dated to ~17.3–14.5 Ma, i.e., late early Miocene to early middle Miocene (upper Burdigalian–Langhian), on the basis of macroinvertebrate biostratigraphy and ⁸⁷Sr/⁸⁶Sr isotope chronostratigraphy (Moreno et al., 2015). The locality Makaraipao, where MUN-STRI 34113 was collected, has been correlated with other localities with available ⁸⁷Sr/⁸⁶Sr dating, and it is dated to ~15.3 Ma (range of 15.14 ± 0.13 to 15.43 ± 0.09 Ma) (middle Miocene, Langhian).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
METATHERIA Huxley, 1880
SPARASSODONTA Ameghino, 1894
BORHYAENOIDEA Simpson, 1930
LYCOPSIS Cabrera, 1927

Emended Diagnosis—Medium- to large-sized sparassodonts; P1/p1 implantation parallel to the tooth row; upper molars with protocone large and basined, slightly smaller on M4; stylar shelf very reduced; ectocingulum present, labial to paracone; shallow ectoflexus in the M3, labial to the metacone; mandibular symphysis unfused in adults; lower molars with trenchant protoconid twice as high as paraconid; talonid large and basined on m1–m3 (modified from Marshall, 1979).

Type Species—*Lycopsis torresi* Cabrera, 1927.

Included Species—The type species and *Lycopsis longirostris* Marshall, 1977, *Lycopsis viverensis* Forasiepi et al., 2003, and *Lycopsis padillai*, sp. nov.

LYCOPSIS PADILLAI, sp. nov.
(Fig. 2)

Etymology—*padillai*, in recognition of Carlos Bernardo Padilla, founding member of the Centro de Investigaciones Paleontológicas, Villa de Leyva, Colombia, and promoter of paleontology in Colombia.

Holotype—MUN-STRI 34113, partial left maxilla with M1–M4, partial lacrimal and jugal.

Locality and Stratigraphy—Makaraipao locality (ID: 390093), N11°54'32"/W71°20'24", La Guajira Department, Colombia (Fig. 1A), middle section of the Castilletes Formation (Fig. 1B), ca. 15.3 Ma (middle Miocene, Langian).

Diagnosis—Differing from the other species of *Lycopsis* in size (in the range of *L. torresi*), smaller than *L. longirostris* and larger than *L. viverensis*; more gracile dentition; protocone more mesiodistally compressed and more lingually salient; deeper protocone basin; and vestigial metacone in M4. Differing from *L. torresi* and *L. longirostris* in larger metaconule; more pointed metastylar area in M1; and shallower ectoflexus in M3. Differing from *L. torresi* in flat maxilla behind infraorbital foramen (instead of flaring ‘cheeks’). Differing from *L. viverensis* in more rounded metastylar area in M1; and ectoflexus of M3 deeper and more anteriorly placed, labial to the metacone. Differing from most other sparassodonts in presence of two lacrimal foramina (instead of one).

Description

Specimen MUN-STRI 34113 is a large-sized Sparassodonta with linear measurements similar to those of *L. torresi* and an estimated body mass of around 22 kg (see Supplementary Data). The maxilla is flat as seen in ventral view, similar to the condition of *Acyon myctoderos*, *Lycopsis viverensis*, *Lycopsis longirostris*, and living marsupials, and differing from most sparassodonts (with flaring maxillary ‘cheeks’). Two round palatal pits, to house the lower protoconids when the jaws were closed, are placed lingual to M2–M3 and (the deepest one) to M3–M4. In dorsal view, the maxilla contributes to the floor of the orbit and the floor of the maxillary canal. Small foramina are present in the floor of the orbit to transmit branches of the maxillary nerve and associated vasculature to supply the posterior teeth. Only the lateral border of a broken maxillary canal is preserved above M1–M3. This indicates that the infraorbital foramen opened on the face anterior to the M1. A small fragment of the lacrimal is preserved on the anteroventral border of the orbital rim. There are two partial lacrimal foramina, opening within the orbit, with the ventral foramen larger than the dorsal. One lacrimal foramen is the usual state in Sparassodonta, except in *Arminiheringia* with two foramina and *Callistoe*, which is polymorphic in this feature (Babot, 2005). Alternatively, two foramina are present in many marsupials, such as *Thylacinus cynocephalus*, *Dromiciops glirioides*, *Didelphis albiventris*, and some fossil stem metatherians, such as *Pucadelphys andinus* and *Mimoperadectes houdei* (Marshall and Muizon, 1995; Horovitz et al., 2009). The zygomatic

process of the lacrimal is subtriangular and extends back to the level of the posterior root of M2, as in *Proborhyaena gigantea* and *Thylacosmilus atrox*. Only a small portion of the anterior base of the zygomatic arch is preserved. The maxillary-jugal suture is oblique, extending from the level of the M1/M2 embrasure to M4, with a curved posterior projection at the level of M3 (Fig. 2A). In other sparassodonts, this suture is straight, being alternatively oblique (e.g., *Acyon myctoderos*, *Cladosictis patagonica*, *Sipalocyon gracilis*) or almost vertical (e.g., *Arctodictis sinclairi*, *Prothylacynus patagonicus*, *Thylacosmilus atrox*).

Dentition—The upper molars increase in size from M1 to M3. The M4 is as wide as the M3, as in *L. viverensis*, thus differing from *L. longirostris*, which has the M3 markedly wider than the M4, and *L. torresi* with the M4 wider than the M3 (Supplementary Data). All molars have three roots. The crowns of M1 and M2 are strongly worn, obscuring their morphology. The description is based on M3–M4, comparing with the anterior molars when possible (Fig. 2).

The protocone is large compared with that of other sparassodonts; it is mesiodistally compressed and lingually projected, being more evident towards M4. The protocone basin is shallow. In the M3, the metacone is the dominant cusp, occupying a nearly central position in the crown. In contrast, in the M4 the paracone is the dominant cusp, whereas the metacone is strongly reduced, represented by a vestigial cusp in the posterolingual corner of the tooth. This character differs from *L. torresi*, which has a posterior cingulum instead of a cusp (Cabrera, 1927, suggested a possible homology between this cingulum and the metacone). Alternatively, in *L. longirostris* and *L. viverensis*, the M4 metacone is absent. The labial face of the paracone is convex in M3 and M4, whereas the lingual has two surfaces joint at an acute angle, defining a vertical ridge. The metacone is conical in the M3. The bases of the paracone and metacone are adjoined. The preparacrista is straight, oblique to the main axis of the tooth, and increasing in length from M1 to M4. The postmetacrista is more than twice the length of the preparacrista in M1–M3, and this crest is absent in M4. A vestigial wing-like paraconule and a small metaconule are clearly seen in M3 and M4. These cusps are closer to the paracone and metacone, respectively, than to the protocone. A vestigial anterolabial cingulum (coded in the matrix as ‘preparacingulum’) is present in the M3 and M4; that of the M4 is extremely short and narrow and is clearly disconnected from the (much more lingual) preparacinar crest. The stylar shelf is narrow, with a shallow ectoflexus in the M3, labial to the metacone. An ectocingulum is present in the M3, labial to the paracone.

DISCUSSION

Systematics

Several features present in MUN-STRI 34113 are characteristic of *Lycopsis*: (1) large size; (2) large and basined protocone; (3) reduced stylar shelf; (4) presence of ectocingulum; and (5) shallow ectoflexus in the M3 (see Marshall, 1979, and the emended diagnosis of the genus presented here). None of these characters in isolation or partial combination is exclusive to *Lycopsis*, but the occurrence of all of these characters is unique relative to other sparassodonts (pers. observ.). Several features in the dentition and in the fragmentary skull indicate that the specimen from La Guajira belongs to a new species (*Lycopsis padillai*, sp. nov.; see Diagnosis and Fig. 3). This taxon is morphologically more similar to *L. torresi* than to any other species of the genus, a conclusion also supported by the results of the phylogenetic analysis.

Two most parsimonious trees (consistency index [CI] = 0.370, retention index [RI] = 0.682, length = 1030) were obtained in the phylogenetic analysis. The arrangement within Sparassodonta is the same in both trees. The Bremer index is low for all

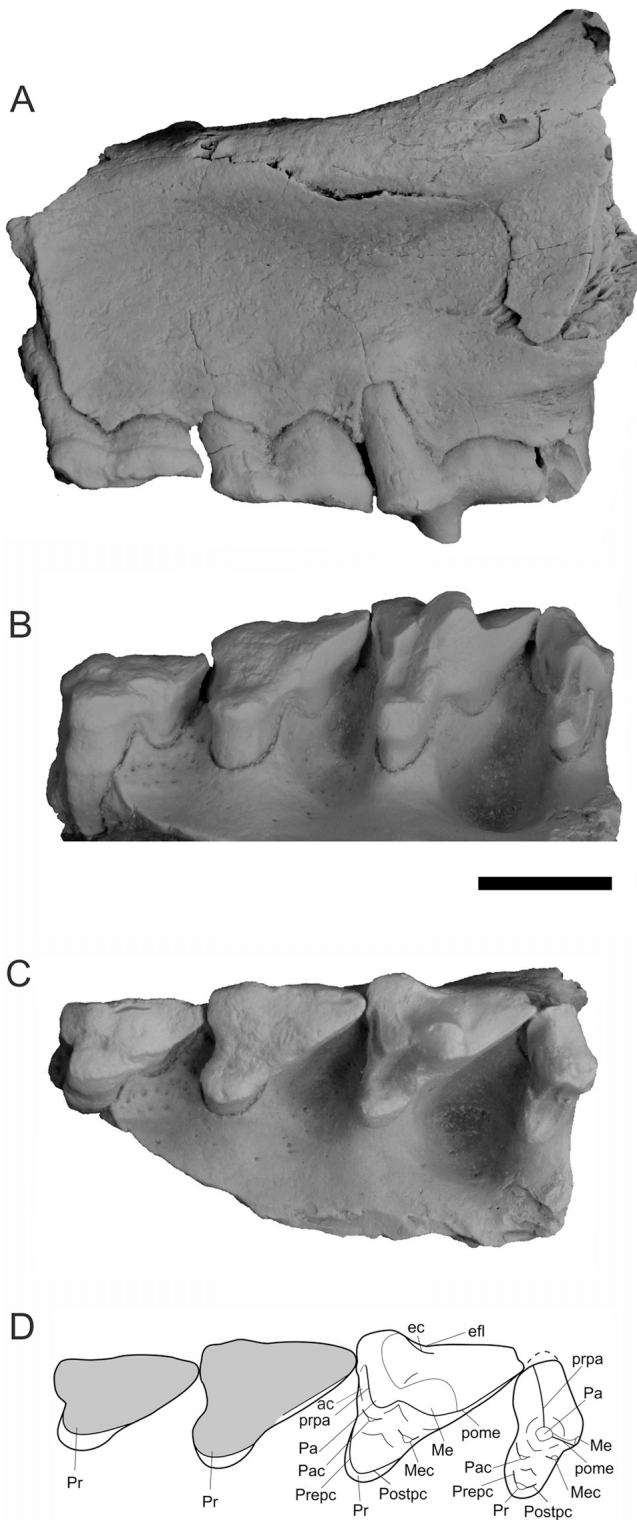


FIGURE 2. *Lycopsis padillai*, sp. nov. Type, MUN-STRI 34113, partial left maxilla with M1–M4. **A**, lateral view; **B**, lingual view; **C**, occlusal view; **D**, line drawing of the upper molars. The labial edge of the M4 was lost after collecting (see Supplementary Data). **Abbreviations:** ac, antero-labial cingulum; ec, ectocingulum; eff, ectoflexus; Me, metacone; Mec, metaconule; Pa, paracone; Pac, paraconule; pome, postmetacrista; Postpc, postprotocrista; Pr, protocone; Prepc, preprotocrista; prpa, pre-paracrista. Scale bar equals 1 cm.

nodes (Fig. 3). Two clades were found within Sparassodonta: Hathliacynidae and Borhyaenoidea, in addition to *Patene*, *Hondadelphys*, and *Stylocynus*, taxa that are basal within Sparassodonta. Within Borhyaenoidea, the genus *Lycopsis* is in a basal position, consistent with recent hypotheses (e.g., Forasiepi, 2009; Engelman and Croft, 2014; Forasiepi et al., 2015). This analysis, which includes all the species of *Lycopsis*, supports the monophyly of the genus (Fig. 3). We recorded two synapomorphies for *Lycopsis*: the location of the infraorbital foramen, anterior or dorsal to the anterior root of the P3 (character 18[0]), and the symmetry of the main cusp on p3, with the anterior edge of the cusp more convex than the posterior (character 129[0]) (Supplementary Data). The relationship between the four species of *Lycopsis* remains stable in the trees. *Lycopsis padillai*, sp. nov., is the sister taxon of *L. torresi*. The sister taxon of *L. padillai* + *L. torresi* is *L. viverensis*, and *L. longirostris* is the sister taxon of all them.

Paleoecology: Body Mass

The body mass for the species of *Lycopsis* was estimated on the basis of the M2 occlusal area (2UMA) (Supplementary Data). Considering the body weight range of 15–35 kg between different specimens of *Thylacinus cynocephalus* (Smith, 1982; Strahan, 1995), our results indicate that *Lycopsis padillai* (ca. 22 kg) lies within the range of *Lycopsis torresi* (ca. 24 kg) and *Lycopsis viverensis* (ca. 16 kg) and is smaller than *Lycopsis longirostris* (ca. 46 kg) (Fig. 4). Additional estimations were made using the upper molar occlusal row length (UMORL) (Supplementary Data), which resulted in similar values: *Lycopsis padillai* (ca. 22 kg) lies within the range of *Lycopsis torresi* (ca. 27 kg) and *Lycopsis viverensis* (ca. 18 kg) and is smaller than *Lycopsis longirostris* (ca. 44 kg). The results based on the UMORL are selected as the best estimates because this equation has better statistical support. Our results are consistent with previous estimates (Ercoli and Prevosti, 2012; Prevosti et al., 2012, 2013).

The body mass estimate of ca. 22 kg for the specimen MUN-STRI 34113 indicates that *Lycopsis padillai* was a large-sized sparassodont, in the size category of Prevosti et al. (2013) for species larger than 15 kg. This is similar to the canid *Lycaon pictus*, with a body mass of about 20–30 kg (Woodroffe and Sillero-Zubiri, 2012), and lies within the range of the marsupial wolf, *Thylacinus cynocephalus* (Smith, 1982; Strahan, 1995).

Neotropical sparassodonts from the middle Miocene La Venta show a body mass range between ca. 4 kg (*Hondadelphys fieldsi*) and ca. 25 kg (*Dukecynus magnus*). In contrast, Sparassodont associations from higher latitudes, such as the early Miocene Santa Cruz Formation from Patagonia, Argentina, show a much wider body mass distribution from 1 kg (e.g., *Pseudonotictis pusillus*) to more than 50 kg (e.g., *Arctodictis munizi*) (Ercoli et al., 2014; Prevosti et al., 2013). Herbivores in Neotropical assemblages (e.g., La Venta; Kay et al., 1997) have a very wide range of body masses, including sizes greater than the prey size estimated for mammalian predators (Ercoli et al., 2014) known to date in those fossil sites. The absence of larger carnivores in the Neotropics does not necessarily indicate a bias in the fossil record that has excluded the preservation of large-sized predatory mammals. It could be a consequence of either a lower collection effort and/or a greater participation of non-mammalian vertebrates in the carnivorous adaptive zone.

Chronostratigraphic and Paleobiogeographic Implications

Specimen MUN-STRI 34113 was collected from a stratigraphic section dated to ~15.3 Ma (range of 15.14–15.43 Ma; Moreno et al., 2015), within the range of the Colloncuren ‘age.’ This informal biochronological unit is based on a

Patagonian mammal association, which has been dated to 15.5–14 Ma (Flynn and Swisher, 1995). With ca. 22 kg of estimated body mass, *Lycopsis padillai* is the third and largest predator mammal species so far described for this time range in South America—the other two species being *Pseudonoticus chubutensis* (ca. 1 kg) and *Patagosmilus goini* (ca. 16 kg) (estimates from Prevosti et al., 2013).

Lycopsis padillai is the sister taxon of *L. torresi* (Fig. 4). *Lycopsis torresi* comes from the older Santacrucian age, 18–16 Ma (Vizcaíno et al., 2012 and literature cited), from Patagonia, Argentina. According to the results of our phylogenetic analysis (Figs. 3, 4), the most basal member of the genus is *Lycopsis longirostris* from the Laventan age, 13.5–11.8 Ma (Madden et al., 1997), from La Venta, Colombia. The overall phylogeny of the genus implies a diversification within (or before) the early Miocene (Fig 4) and the presence of ghost lineages leading to both *L. longirostris* and *L. viverensis*.

The phylogeny indicates that *Lycopsis* had at least two migration events between tropics and temperate regions, and in both instances, there was divergence into new species in the temperate region. The persistence of a basal taxon (*L. longirostris*) of this clade in Neotropical areas in younger ages could be interpreted under the ‘museum’ evolutionary model (other examples in Carlini et al., 1997; Mittelbach et al., 2007; Vucetich et al., 2010). However, we are cautious in assuming this model on the basis of a single species. Additionally, the museum hypothesis predicts that the rate of extinction should be lower toward the tropics, but in this case, *L. viverensis* could have lasted even longer than *L. longirostris*, in spite of being at higher latitude.

Previous studies have documented evidence of faunal provinciality between low- and high-latitude Neogene South American mammal associations (Carlini et al., 1997, 2008; Croft, 2007; Croft et al., 2009; Goin et al., 2012; Carrillo et al., 2015). The record of the genus *Lycopsis* is still too limited to provide insight

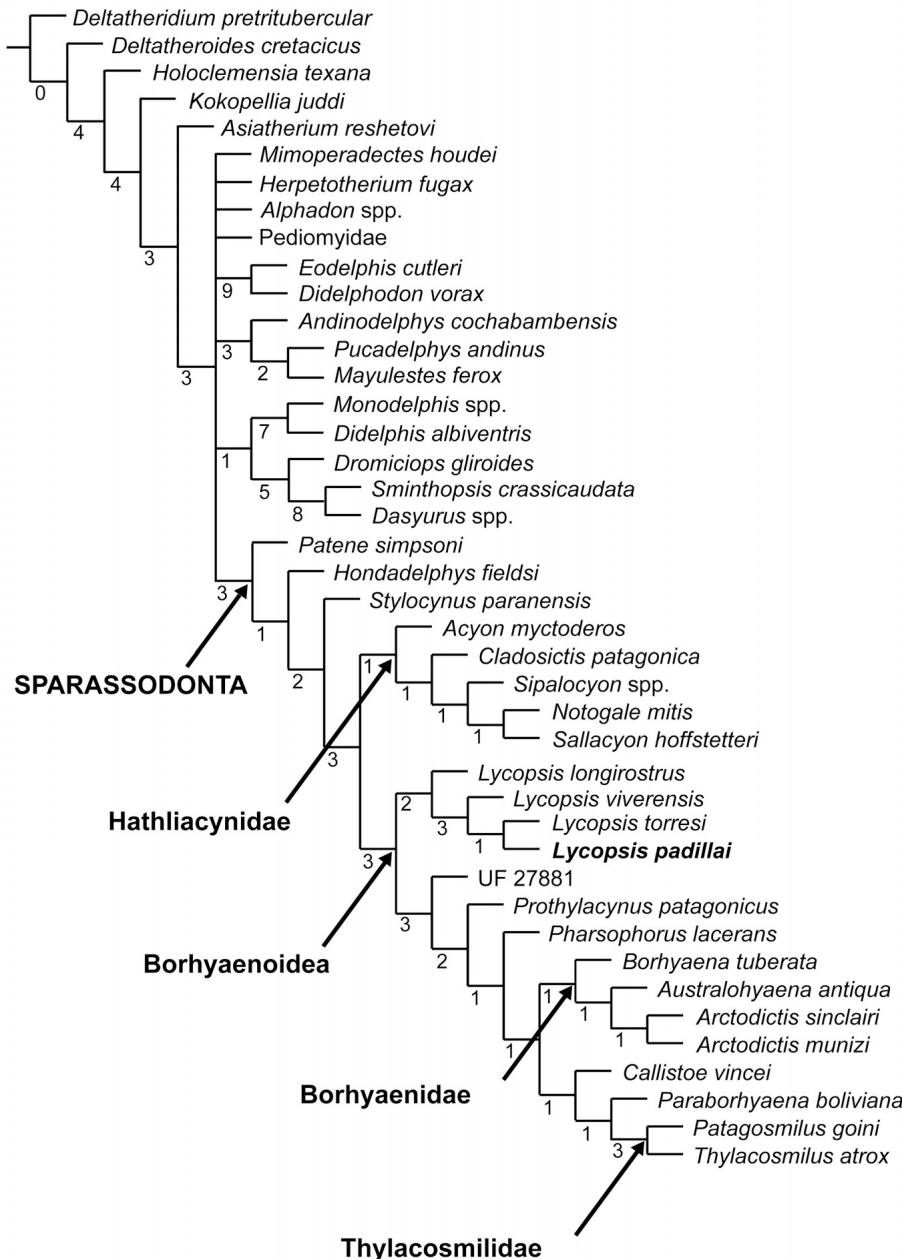


FIGURE 3. Phylogenetic analysis: strict consensus cladogram of two trees obtained with equally weighted characters (1074 steps, CI = 0.355, and RI = 0.660); numbers at nodes indicate Bremer support values.

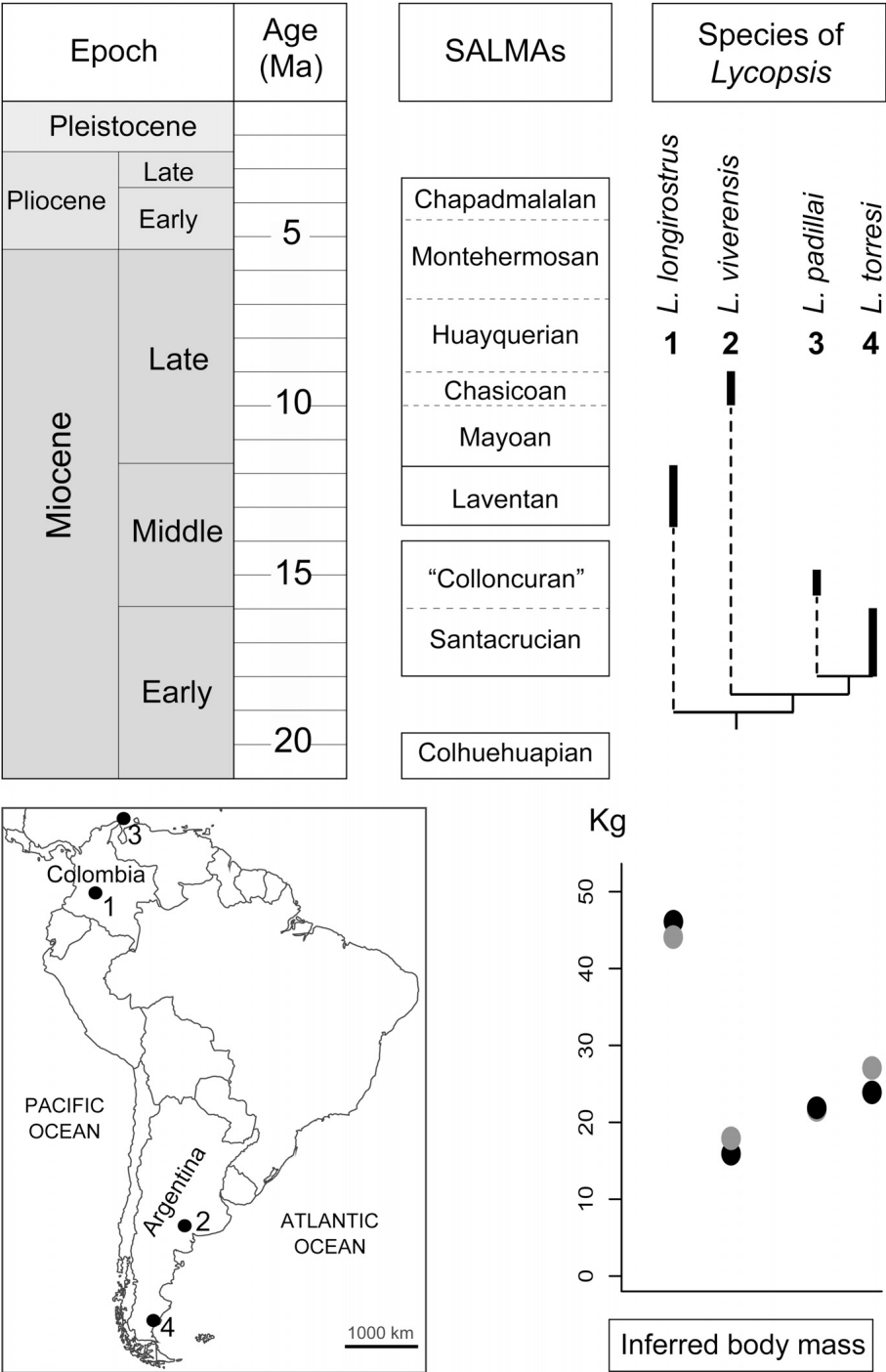


FIGURE 4. Chronostratigraphic and paleobiogeographic distribution of *Lycopsis*, and inferred body mass for each species; black circles in body mass graphic represent estimations using M2 occlusal area; gray circles represent estimations using upper molar occlusal row length.

into provincialism. Each species of *Lycopsis* is represented by a single site (Fig. 4); therefore, the geographic range of each species is still unknown. Sparassodonta includes genera widely distributed across the continent. The genus *Acyon* has been reported at ~22°S (Quebrada Honda, Bolivia) and ~51°S (Patagonia, Argentina) (Forasiepi et al., 2006); *Sipalocyon* at ~12°S (Madre de Dios, Peru), ~47°S (Alto Río Cisnes, Chile), and ~51°S (Patagonia, Argentina) (Marshall, 1990; Antoine et al., 2013); *Borhyaenidium* at ~17°S (Achiri, Bolivia) and ~38°S (La Pampa, Argentina) (Villarroel and Marshall, 1983); *Patene* at ~23°S (Itaboraí, Brazil) and ~45°S (Patagonia, Argentina); and *Lycopsis* with the broadest distribution of any fossil metatherian,

ranging from ~12°N (La Guajira, Colombia) to ~51°S (Patagonia, Argentina) (Fig. 1). Moreover, two sister taxa (*L. torresi* and *L. padillai*) have been recorded at extreme points of the continent. As often happens with living, large-sized mammalian predators, the dual nature of the biogeography and paleobiogeography of South America is not evident in the case of *Lycopsis*: this genus does not show geographical regionalization (Neotropical or Andean), but instead ranges over more than one region in South America.

Not only at the generic level, but even at the species level, living large-sized mammalian predators usually occupy large ranges, such as *Puma* (e.g., *Puma concolor*), *Panthera* (e.g.,

Panthera onca), and *Herpailurus* (e.g., *Herpailurus yagouaroundi*), which are distributed in several biomes along the Americas (Caso et al., 2008a, 2008b, 2008c). This indicates that provinciality might not be reflected in analysis of the distribution of large-sized mammalian predators.

CONCLUSIONS

A new species, *Lycopsis padillai*, sp. nov. (Metatheria, Sparassodonta), is recognized, on the basis of unique features in the dentition and skull. *L. padillai* was a large-sized sparassodont with a body mass of ca. 22 kg.

Our phylogenetic analysis supports the monophyly of the genus *Lycopsis*, which includes four species: *L. torresi*, *L. longirostris*, *L. viverensis*, and *L. padillai*, sp. nov. *L. padillai* is sister taxon to *L. torresi*.

The estimated timing of origin of the genus *Lycopsis* is at or earlier than the early Miocene. According to our phylogenetic analysis, *Lycopsis longirostris*, from the middle Miocene of Colombia, represents the most basal member of the group.

The genus *Lycopsis* had a broad distribution in South America. At least at the generic level, provinciality might not be reflected in analysis of the distribution of large-sized mammalian predators.

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LITERATURE CITED

- Ameghino, F. 1894. Enumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. Boletín de la Academia Nacional en Ciencias, Córdoba 13:259–452.
- Antoine, P. O., M. Roddaz, S. Brichau, J. Tejada-Lara, R. Salas-Gismondi, A. Altamirano, M. Louterbach, L. Lambs, T. Otto, and S. Brusset. 2013. Middle Miocene vertebrates from the Amazonian Madre de Dios subandean zone, Perú. Journal of South American Earth Sciences 42:91–102.
- Babot, M. J. 2005. Los Borhyaenoidea (Mammalia, Metatheria) del Terciario inferior del Noroeste argentino. Aspectos filogenéticos, paleobiológicos y bioestratigráficos. Ph.D. dissertation, Universidad Nacional de Tucumán, San Miguel de Tucumán, Tucumán, Argentina, 454 pp.
- Babot, M. J., J. E. Powell, and C. Muizon. 2002. *Callistoe vincei*, a new Proborhyaenidae (Borhyaenoidea, Metatheria, Mammalia) from the early Eocene of Argentina. Geobios 35:615–629.
- Becker, L. E., and A. N. Dusenbury. 1958. Mio-Oligocene (Aquitanian) foraminifera from the Goajira Peninsula, Colombia. Cushman Foundation for Foraminiferal Research, Special Publication 4:1–48.
- Bürl, H. 1960. Geología de la Península de la Guajira. Servicio Geológico Nacional (Colombia), Boletín Geológico 6:129–168.
- Cabrera, A. 1927. Datos para el conocimiento de los masiúridos fósiles argentinos. Revista del Museo de La Plata 30:271–315.
- Carlini, A. A., S. F. Vizcaino, and G. J. Scillato-Yané. 1997. Armored xenarthrans: a unique taxonomic and ecologic assemblage; pp. 213–226 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. Flynn (eds.), Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D. C., and London.
- Carlini, A. A., A. E. Zurita, G. J. Scillato-Yané, R. Sánchez, and O. Aguilera. 2008. A new glyptodont species from Codore Formation (Pliocene), Estado Falcón (Venezuela), and the ‘*Asterostemma*’ problem. Paläontologische Zeitschrift 82:139–152.
- Carrillo, J. D., A. Forasiepi, C. Jaramillo, and M. R. Sánchez-Villagra. 2015. Neotropical mammal diversity and the Great American Biotic Interchange: spatial and temporal variation in South America’s fossil record. Frontiers in Genetics 5(451):1–11.
- Caso, A., C. Lopez-Gonzalez, E. Payan, E. Eizirik, T. de Oliveira, R. Leite-Pitman, M. Kelly, and C. Valdeirama. 2008a. *Herpailurus yagouaroundi*. The IUCN Red List of Threatened Species, version 2014.2. Available at www.iucnredlist.org. Accessed November 5, 2014.
- Caso, A., C. Lopez-Gonzalez, E. Payan, E. Eizirik, T. de Oliveira, R. Leite-Pitman, M. Kelly, and C. Valdeirama. 2008b. *Panthera onca*. The IUCN Red List of Threatened Species, version 2014.2. Available at www.iucnredlist.org. Accessed November 5, 2014.
- Caso, A., C. Lopez-Gonzalez, E. Payan, E. Eizirik, T. de Oliveira, R. Leite-Pitman, M. Kelly, C. Valdeirama, and M. Lucherini. 2008c. *Puma concolor*. The IUCN Red List of Threatened Species, version 2014.2. Available at www.iucnredlist.org. Accessed October 21, 2014.
- Cozzuol, M. A. 2006. The Acre vertebrate fauna: age, diversity, and geography. Journal of South American Earth Sciences 21:185–203.
- Croft, D. A. 2007. The middle Miocene (Laventan) Quebrada Honda fauna, southern Bolivia and a description of its notoungulates. Palaeontology 50:277–303.
- Croft, D. A., F. Anaya, D. Auerbach, C. Garzione, and B. J. MacFadden. 2009. New data on Miocene Neotropical provinciality from Cerdas, Bolivia. Journal of Mammalian Evolution 16:175–198.
- Degrange, F. J. 2012. Morfología del cráneo y complejo apendicular posterior de aves fororracoideas: implicancias en la dieta y modo de vida. Ph.D. dissertation, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina, 390 pp.
- Degrange, F. J., J. I. Noriega, and J. I. Areta. 2012. Diversity and paleobiology of the Santacrucian birds; pp. 138–155 in S. F. Vizcaino, R. F. Kay, and M. S. Bargo (eds.), Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation. Cambridge University Press, New York.
- Engelman, R. K., and D. A. Croft. 2014. A new species of small-bodied sparassodont (Mammalia, Metatheria) from the middle Miocene locality of Quebrada Honda, Bolivia. Journal of Vertebrate Paleontology 34:672–688.
- Ercoli, M. D., and F. J. Prevosti. 2012. Estimación de masa de las especies de Sparassodonta (Mammalia, Metatheria) de edad Santacrucense (Mioceno temprano) a partir del tamaño del centroide de los elementos apendiculares: inferencias paleoecológicas. Ameghiniana 48:462–479.
- Ercoli, M. D., F. J. Prevosti, and A. M. Forasiepi. 2014. The structure of the mammalian predator guild in the Santa Cruz Formation (late early Miocene). Journal of Mammalian Evolution 21:369–381.
- Fernicola, J. C., and A. Albino. 2012. Amphibians and squamate reptiles from the Santa Cruz Formation (late early Miocene), Santa Cruz Province, Argentina: paleoenvironmental and paleobiological

- considerations; pp. 129–137 in S. F. Vizcaíno, R. F. Kay, and M. S. Bargo (eds.), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, New York.
- Flynn, J. J., and C. C. Swisher III. 1995. Cenozoic South America Land Mammal Ages: correlation to global geochronologies; pp. 317–333 in W. A. Berggren, D. V. Kent, and J. Hardenbol (eds.), *Geochronologies, Time Scales, and Global Stratigraphic Correlation*. Society for Sedimentary Geology, Special Publication 54.
- Forasiepi, A. M. 2009. Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. *Monografías del Museo Argentino de Ciencias Naturales*, new series 6:1–174.
- Forasiepi, A. M., F. J. Goin, and V. di Martino. 2003. Una nueva especie de *Lycopsis* (Metatheria, Prothylacyninae) de la Formación Arroyo Chasicó (Mioceno Tardío) de la provincia de Buenos Aires. *Ameghiniana* 40:249–253.
- Forasiepi, A. M., F. J. Goin, and A. A. Tauber. 2004. Las especies de *Arctodictis* Mercerat, 1891 (Metatheria, Borhyaenidae), grandes metaterios carnívoros del Mioceno de América del Sur. *Revista Española de Paleontología* 19:1–22.
- Forasiepi, A. M., M. J. Babot, and N. Zimicz. 2015. *Australohyaena antiqua* (Mammalia, Metatheria, Sparassodonta), a large predator from the late Oligocene of Patagonia. *Journal of Systematic Palaeontology* 13:503–525.
- Forasiepi, A. M., M. R. Sánchez-Villagra, F. J. Goin, M. Takai, N. Shigehara, and R. F. Kay. 2006. A new species of *Hathliacynidae* (Metatheria, Sparassodonta) from the middle Miocene of Quebrada Honda, Bolivia. *Journal of Vertebrate Paleontology* 26:670–684.
- Goin, F. J. 1997. New clues for understanding Neogene marsupial radiations; pp. 185–204 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C., and London.
- Goin, F. J., J. N. Gelfo, L. Chornogubsky, M. O. Woodburne, and T. Martin. 2012. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds; pp. 20–50 in B. D. Patterson, and L. P. Costa (eds.), *Bones, Clones, and Biomes: An 80-Million Year History of Recent Neotropical Mammals*. University of Chicago Press, Chicago, Illinois.
- Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- Horovitz, I., T. Martin, J. Bloch, S. Ladevèze, C. Kurz, and M. R. Sánchez-Villagra. 2009. Cranial anatomy of the earliest marsupials and the origin of opossums. *PLoS ONE* 4:e8278.
- Huxley, J. S. 1880. On the application of the law of evolution to the arrangement of the Vertebrata, and more particularly to the Mammalia. *Proceedings of the Zoological Society of London* 43:649–662.
- Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.
- Kay, R. F., R. H. Madden, R. L. Cifelli, and J. J. Flynn. 1997. *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C., and London, 592 pp.
- Linares, O. J. 2004. Bioestratigrafía de la fauna de mamíferos de las Formaciones Socorro, Urumaco y Codore (Mioceno medio–Plioceno temprano) de la región de Urumaco, Falcón, Venezuela. *Paleobiología Neotropical* 1:1–26.
- Linnaeus, C. 1758. *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentis, Synonymis, Locis*, 10th edition. Laurentii Salvi, Stockholm, 824 pp.
- MacFadden, B. J. 2006. Extinct mammalian biodiversity of the ancient New World tropics. *Trends in Ecology and Evolution* 21:157–165.
- Madden, R. H., J. Guerrero, R. F. Kay, J. J. Flynn, C. C. Swisher III, and A. H. Walton. 1997. The Laventan stage and age; pp. 499–519 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C., and London.
- Mannion, P. D., P. Upchurch, R. B. Benson, and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution* 29:42–50.
- Marshall, L. G. 1977. A new species of *Lycopsis* (Borhyaenidae, Marsupialia) from the La Venta fauna (late Miocene) of Colombia, South America. *Journal of Paleontology* 51:633–642.
- Marshall, L. G. 1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *University of California Publications in Geological Sciences* 117:1–89.
- Marshall, L. G. 1979. Review of the Prothylacyninae, an extinct subfamily of South American ‘dog-like’ marsupials. *Fieldiana, new series* 3:1–50.
- Marshall, L. G. 1990. Fossil Marsupialia from the type Friasian Land Mammal Age (Miocene), Alto Rio Cisnes, Aisen, Chile. *Revista Geológica de Chile* 17:19–55.
- Marshall, L. G., and R. L. Cifelli. 1990. Analysis of changing diversity patterns in Cenozoic land mammal age faunas, South America. *Palaeovertebrata* 19:169–210.
- Marshall, L. G., and C. de Muizon. 1995. The skull; pp. 21–90 in C. de Muizon (ed.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the Early Paleocene of Bolivia. *Mémoires du Muséum national d'Histoire naturelle* 165.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A. McPeck, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel, and M. Turelli. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10:315–331.
- McKenna, D. D., and B. D. Farrell. 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America* 103:10947–10951.
- Moreno, J. F., A. J. W. Hendy, L. Quiroz, N. Hoyos, D. S. Jones, V. Zapata, S. Zapata, G. Ballen, E. Cadena, A. L. Cárdenas, J. D. Carrillo-Briceno, J. D. Carrillo, D. Delgado-Sierra, J. Escobar, J. I. Martinez, C. Martinez, C. Montes, J. Moreno, N. Perez, R. Sanchez, C. Suarez, M. C. Vallejo-Pareja, and C. Jaramillo. 2015. Revised stratigraphy of Neogene strata in the Cocinetas Basin, La Guajira, Colombia. *Swiss Journal of Paleontology* 134:5–43.
- Morrone, J. J. 2002. Biogeographical regions under track and cladistic scrutiny. *Journal of Biogeography* 29:149–152.
- Morrone, J. J. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology* 51:467–94.
- Muizon, C. 1999. Marsupial skulls from the Deseadan (late Oligocene) of Bolivia and phylogenetic analysis of the Borhyaenoidea (Marsupialia, Mammalia). *Geobios* 32:483–509.
- Myers, T. J. 2001. Prediction of marsupial body mass. *Australian Journal of Zoology* 49:99–118.
- Prevosti, F. J., A. Forasiepi, and N. Zimicz. 2013. The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? *Journal of Mammalian Evolution* 20:3–21.
- Prevosti, F. J., A. M. Forasiepi, M. D. Ercoli, and G. F. Turazzini. 2012. Paleogeology of the mammalian carnivores (Metatheria, Sparassodonta) of the Santa Cruz Formation (late early Miocene); pp. 173–193 in S. F. Vizcaíno, R. F. Kay, and M. S. Bargo (eds.), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, New York.
- Renz, O. 1960. Geología de la parte sureste de la Península de la Guajira (República de Venezuela). III Congreso Geológico Venezolano, Caracas, 1959. *Boletín de Geología, Publicación Especial* 3:317–347.
- Ribeiro, A. M., R. R. Madden, F. R. Negri, L. Kerber, A. S. Hsiou, and K. A. Rodrigues. 2013. Mamíferos fósiles y biocronología en el suroeste de la Amazonia, Brasil; pp. 207–221 in D. Brandoni, and J. I. Noriega (eds.), *El Neógeno de la Mesopotamia Argentina*. Asociación Paleontológica Argentina, Publicación Especial 14.
- Rolland, J., F. L. Condamine, F. Jiguet, and H. Morlon. 2014. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology* 12:e1001775.
- Rollins, J. F. 1965. Stratigraphy and structure of the Goajira Peninsula, Northwestern Venezuela and Northeastern Colombia. *University of Nebraska Studies, New Series* 30:1–102.

- Sánchez-Villagra, M. R., and O. A. Aguilera. 2006. Neogene vertebrates from Urumaco, Falcón State, Venezuela: diversity and significance. *Journal of Systematic Palaeontology* 4:213–220.
- Sánchez-Villagra, M. R., O. A. Aguilera, and A. A. Carlini (eds.). 2010. *Urumaco and Venezuelan Paleontology: The Fossil Record of the Northern Neotropics*. Indiana University Press, Bloomington, Indiana, 286 pp.
- Scheyer, T. M., O. A. Aguilera, M. Delfino, D. C. Fortier, A. A. Carlini, R. Sánchez, J. D. Carrillo-Briceño, L. Quiroz, and M. R. Sánchez-Villagra. 2013. Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics. *Nature Communications* 4:1907. Posted online May 21, 2013. doi: 10.1038/ncomms2940.
- Simpson, G. G. 1930. Post-Mesozoic marsupialia; pp. 1–87 in W. Junk (ed.), *Fossilium Catalogus. I: Animalia*. W. Junk, Berlin, Germany.
- Smith, A. P. 1982. Review of the thylacine (Marsupialia, Thylacinidae); pp. 237–253 in M. Archer (ed.), *Carnivorous Marsupials*. Royal Zoological Society of New South Wales, Mosman, New South Wales, Australia.
- Stenseth, N. C. 1984. The Tropics: Cradle or Museum? *Oikos* 43:417–420.
- Strahan, R. 1995. *Mammals of Australia*. Smithsonian Institution Press, Washington, D.C., 756 pp.
- Tejada-Lara, J. V., R. Salas-Gismondi, F. Pujos, P. Baby, M. Benammi, S. Brusset, D. De Franceschi, N. Espurt, M. Urbina, and P. O. Antoine. 2015. Life in proto-Amazonia: middle Miocene mammals from the Fitzcarrald Arch (Peruvian Amazonia). *Palaeontology* 58:341–378.
- Villarroel, C., and L. G. Marshall. 1983. Two new late Tertiary marsupials (Hathlyacyninae and Sparassocyninae) from the Bolivian altiplano. *Journal of Paleontology* 57:1061–1066.
- Vizcaíno, S. F., R. F. Kay, and M. S. Bargo. 2012. Background for a paleoecological study of the Santa Cruz Formation (late early Miocene) on the Atlantic Coast of Patagonia; pp. 1–22 in S. F. Vizcaíno, R. F. Kay, and M. S. Bargo (eds.), *Early Miocene Paleobiology in Patagonia: High-Latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, New York.
- Vucetich, M. G., A. A. Carlini, O. Aguilera, and M. R. Sánchez-Villagra. 2010. The tropics as reservoir of otherwise extinct mammals: the case of rodents from a new Pliocene faunal assemblage from Northern Venezuela. *Journal of Mammalian Evolution* 17:265–273.
- Woodroffe, R., and C. Sillero-Zubiri. 2012. *Lycaon pictus*. The IUCN Red List of Threatened Species, version 2014.2. Available at www.iucnredlist.org. Accessed November 6, 2014.

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