

Naturwissenschaften (2014) 101:965–974
DOI 10.1007/s00114-014-1237-4

ORIGINAL PAPER

Carnivorans at the Great American Biotic Interchange: new discoveries from the northern neotropics

Analia M. Forasiepi · Leopoldo H. Soibelzon ·
Catalina Suarez Gomez · Rodolfo Sánchez · Luis I. Quiroz ·
Carlos Jaramillo · Marcelo R. Sánchez-Villagra

Received: 17 July 2014 / Revised: 1 September 2014 / Accepted: 2 September 2014 / Published online: 17 September 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract We report two fossil procyonids, *Cyonasua* sp. and *Chapalmalania* sp., from the late Pliocene of Venezuela (Vergel Member, San Gregorio Formation) and Colombia (Ware Formation), respectively. The occurrence of these pre-Holocene procyonids outside Argentina and in the north of South America provides further information about the Great American Biotic Interchange (GABI). The new specimens are recognized in the same monophyletic group as procyonids found in the southern part of the continent, the “*Cyonasua* group,” formed by species of *Cyonasua* and *Chapalmalania*. The phylogenetic analysis that includes the two new findings support the view that procyonids dispersed from North

America in two separate events (initially, previous to the first major migration wave—GABI 1—and then within the last major migration wave—GABI 4—). This involved reciprocal lineage migrations from North to South America, and included the evolution of South American endemic forms.

Keywords Procyonidae · South America · Neotropics · Pliocene

Introduction

Fossils are relevant to understand the timing and dynamics of the Great American Biotic Interchange (GABI), a major natural experiment resulting from the land proximity and later connection between the continents of North and South America during the late Neogene (Webb 1985; Woodburne 2010). The palaeontological record of the Late Neogene is mostly restricted to the southern parts of South America, primarily Argentina (Pascual and Ortiz Jaureguizar 1990; Cione et al. 2007). Tropical sites, as in Colombia and Venezuela, either predate the GABI (Kay et al. 1997; Sánchez-Villagra et al. 2010) or record the Holocene (Rincón 2006; Prevosti and Rincón 2007; Soibelzon and Rincón 2007; Rincón et al. 2011), and there is a significant gap in the tropical record spanning most of the GABI. The principal waves of the interchange started at ca. 3 Ma (GABI 1 sensu Woodburne 2010), although some mammalian groups (Campbell et al. 2000, 2010; Prothero et al. 2014), including procyonids—raccoons and their relatives—began to expand their distribution into South America before that time (Marshall et al. 1979). By integrating the fossil findings, radioisotopic and magnetostratigraphic data, Reguero and Candela (2011) suggested that the earliest South American fossil procyonids are from about 7.1–7.3 Ma. These findings in the Argentinean deposits are more than 4000 km away from the Panama

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-014-1237-4) contains supplementary material, which is available to authorized users.

A. M. Forasiepi

Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, CCT-Mendoza, CONICET, Av. Ruiz Leal s/n°, 5500 Mendoza, Argentina

L. H. Soibelzon · C. S. Gomez

División Paleontología Vertebrados, Museo de La Plata, Consejo Nacional de Investigaciones Científicas y Técnicas, Paseo del Bosque s/nro, 1900 La Plata, Argentina

R. Sánchez · L. I. Quiroz · C. Jaramillo (✉)

Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancón, Republic of Panamá
e-mail: JaramilloC@si.edu

L. I. Quiroz

Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK S7N 5E2, Canada

M. R. Sánchez-Villagra (✉)

Palaeontological Institute and Museum, University of Zürich, Karl Schmid-Strasse 4, Zürich 8006, Switzerland
e-mail: m.sanchez@pim.uzh.ch

isthmus, the likely route through which the first carnivorans would have reached South America. Here, we describe two fossil procyonids collected from the late Pliocene of Venezuela and Colombia, approximately 600 km west of the Panama isthmus (Fig. 1), and we place them in the context of the GABI migration dynamics.

Materials and methods

The nomenclature for the dentition follows Ahrens (2012) and Baskin (1982, 1989). The comparative material, measurements, and institutions that house the specimens compared are provided in the [electronic supplementary material](#).

The biochronology refers to the South American Land Mammal Ages (SALMA). Huayquerian SALMA (~9 to ~5.3 Ma), Chasicoan/Huayquerian boundary at ~9 Ma following Marshall et al. (1979), Cione et al. (2007), and Woodburne (2010); Huayquerian/Montehermosan boundary recently calibrated in 5.28 Ma by Tomassini et al. (2013). Montehermosan SALMA (~5.3 to 4.5/5 Ma) boundaries after Tomassini et al. (2013). Chapadmalalan SALMA (4.5/5 to ~3.3 Ma), Chapadmalalan/Marplatan boundary at 3.2 Ma after Cione et al. (2007) and Woodburne (2010) or 3.3 Ma after Deschamps et al. (2013) and Tomassini et al. (2013). Marplatan SALMA (~3.3 to ~1.8 Ma), Marplatan/Ensenadan boundary at about 1.8 Ma (between 1.95 and 1.77 Ma after Tonni 2009). Ensenadan SALMA (~1.8 to 0.4 Ma) boundaries after Tonni (2009). Bonaerian SALMA

(400 to 128 Ka), boundaries after Tonni (2009). Lujanian SALMA (128 to 8.5 Ka), boundaries after Tonni (2009). Platan SALMA (8.5 Ka to 1492 AD), boundaries after Cione and Tonni (1999) and Tonni (2009).

The phylogenetic relationships were explored through a maximum parsimony analysis using TNT 1.1 (Goloboff et al. 2008). The data matrix was taken from Ahrens (2012); it includes 78 morphological characters (35 from skull, 3 from dentary, and 43 from dentition) and 26 terminal taxa. All characters were equally weighted and treated as unordered. Four taxa were considered as outgroup, rooted in *Urocyon cinereoargenteus*. The ingroup covers 22 taxa (including the red panda *Ailurus fulgens*, following Ahrens 2012). The South American fossil procyonids *Cyonasua brevisrostris*, *Cyonasua longirostris*, *Chapalmalania altaefrontis*, *Chapalmalania ortognatha*, together with the new specimens *Cyonasua* sp. (AMU-CURS 224) and *Chapalmalania* sp. (SGC STRI-34114) were added in the analysis ([electronic supplementary material](#)) to test their affinities with other procyonids. We employed heuristic searches with 500 replicates of a random addition sequences, followed by tree bisection reconnection branch swapping (TBR), and saving 20 trees per round. The first analysis included all the extant and extinct taxa with the new specimens AMU-CURS 224 and SGC STRI-34114 from Venezuela and Colombia. The second analysis assumed the monophyly of the species of *Arctonasua*, *Chapalmalania*, and *Cyonasua*, which were merged as composite taxa

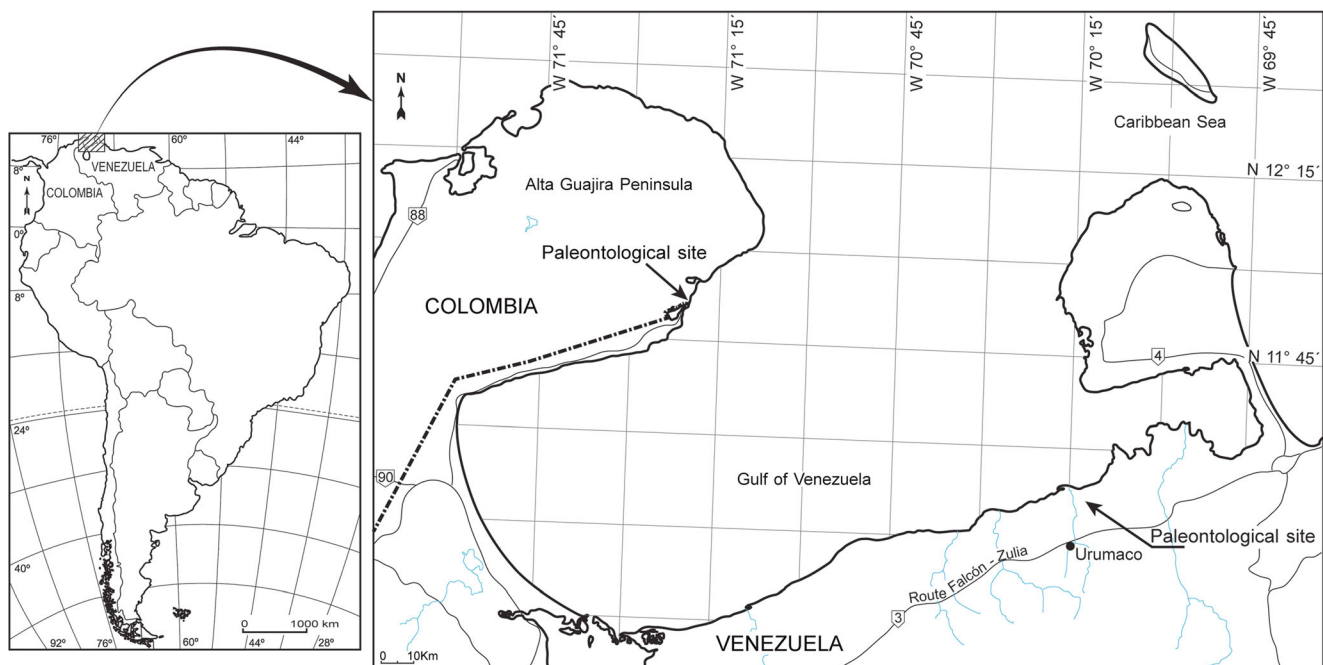


Fig. 1 Map with the paleontological sites in Venezuela and Colombia where *Cyonasua* sp. (AMU-CURS 224) and *Chapalmalania* sp. (SGC STRI-34114) were recovered

(*Arctonasua* included the scorings of *Arctonasua fricki* and *Arctonasua gracilis*; *Chapalmalania* included *Ch. altaefrontis*, *Ch. ortognatha*, and SGC STRI-34114; and *Cyonasua* included *Cy. longirostris*, *Cy. brevirostris*, and AMU-CURS 224). Additional searches were performed with extant and extinct procyonids with more than 25 % and more than 50 % of the characters scorable (electronic supplementary material), following the analyses of Ahrens (2012).

Geological settings

The *Cyonasua* sp. specimen AMU-CURS 224 (Fig. 2) was collected from the Vergel Member, at the base of the San Gregorio Formation, Falcón State, northwestern Venezuela (Fig. 1). The sedimentary sequence represents the accumulation in distal alluvial fans and includes primarily mudstone and intercalations of fine- to coarse-grained sandstone with discontinuous beds of pebbly conglomerate (Quiróz and Jaramillo 2010; Vucetich et al. 2010). The fossil vertebrate assemblage from the Vergel Member includes one crocodile (*Crocodylus falconensis*: Crocodylia), turtles, four xenarthrans (*Pliodasypus vergelianus*: Dasypodidae, Pampatheriidae aff. *Holmesina floridanus*, Glyptodontidae aff. *Boreostemma codorensis*, and Megatheriidae indet.), one notoungulate (Toxodontidae indet.), and caviomorph rodents (*Cardiatherium* sp. and cf. *Caviodon*: Hydrochoeridae, *Neoepiblema* sp.: Neoepiblemidae, and *Marisela gregoriana*: Octodontoidea?), and the procyonid studied here (Carlini and Zurita 2010; Vucetich et al. 2010; Zurita et al. 2011; Scheyer et al. 2013; Castro et al. 2014). A late Pliocene age was estimated for the Vergel Member of the San Gregorio Formation based on the stratigraphic position and the mammalian association (Carlini and Zurita 2010; Zurita et al. 2011; Castro et al. 2014, who tentatively suggested an approximate age of 3.5 Ma).

The *Chapalmalania* sp. specimen SGC STRI-34114 (Fig. 3) was recovered from the locality 470061, “Estación de Policía,” stratigraphic meter 4.3 of the Ware Formation, La Guajira Department, northeast Colombia (Fig. 1). The Ware Formation is composed mostly by fine-grained to muddy sandstone, and pebbly conglomerate, and records the fill of estuarine channels and bays. Conglomerates very rich in vertebrates dominate the base of the sequence. The fossil vertebrate assemblage includes sharks (Carcharhiniformes), rays (Rajiformes and Myliobatiformes), and representatives of three fish (Characiformes, Perciformes, and Siluriformes), two reptile (Crocodylia and Testudines), and six mammalian orders (Rodentia, Xenarthra, Notoungulata, Litopterna, Artiodactyla, and the Carnivora studied here) (Moreno-Bernal et al. 2012; Moreno-Bernal 2014). The top of the unit has been dated as 2.7 Ma using $^{87}\text{Sr}/^{86}\text{Sr}$ geochronology (Moreno et al. in prep).

Systematic paleontology

Mammalia Linnaeus 1758

Carnivora Bowdich 1821

Procyonidae Gray 1825

Cyonasua Ameghino 1885

Cyonasua sp.

Fig. 2

Type species: *Cyonasua argentina* Ameghino 1885 (holotype MLP 10–171)

Temporal range Late Miocene–Early Pleistocene (Huayquerian to Ensenadan SALMAS).

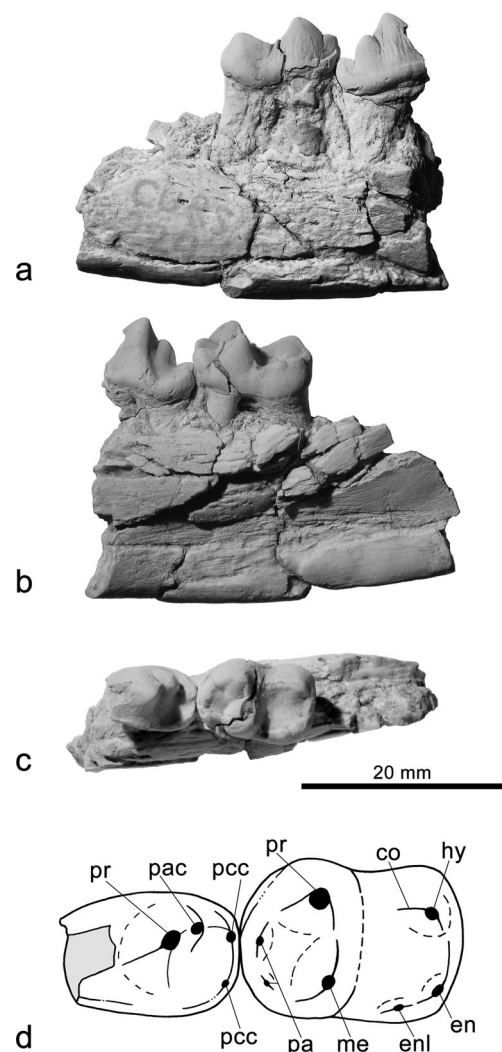


Fig. 2 *Cyonasua* sp. (AMU-CURS 224) from northwestern Venezuela, San Gregorio Formation (Late Pliocene). Right dentary with p4–m1 in labial (a), lingual (b), and occlusal (c) views. The line drawing (d) shows the morphological features mentioned in the text. *co* crisid obliqua, *en* entoconid, *enl* entoconulid, *hy* hypoconid, *me* metaconid, *pa* paraconid, *pac* posterior accessory cusp, *pcc* posterior cingular cusplet, *pr* protoconid

Geographic distribution Argentina (Buenos Aires, Catamarca, Córdoba, Entre Ríos, Jujuy, La Pampa, and Mendoza provinces) and Venezuela (Falcón State).

Referred specimen AMU-CURS 224, fragment of right dentary with p4–m1 from San Gregorio, Falcón State, Venezuela (N11° 17' 49.4" / W70° 13' 54.4"). Vergel Member of the San Gregorio Formation, Late Pliocene.

Description and comparisons AMU-CURS 224 is comparable in size to other species of *Cyonasua* (except for *Cyonasua pascuali* which is very small), but the m1 is noticeably wider than in other species. The mandible is labiolingually narrow and deep, representing more than twice the height of the molar crown (Fig. 2a, b).

The teeth are bunodont. The protoconid is the dominant cusp of p4 similar in size as the m1 protoconid. An anterior cingulid cusp on the mesial face of the protoconid, present in other procyonids (e.g., Linares 1981 and Baskin 1989), cannot be confirmed due to breakage. The posterior accessory cusp is large, slightly labiolingually compressed, and located on the labial border of the tooth. There is a broad posterior cingular shelf attached to the base of the protoconid, forming a talonid. This is broader lingually, shorter than it is wide, and includes a shallow basin (Fig. 2c). There are two posterior cingular cusplets on the labial and lingual borders of the tooth, with the labial the larger.

The m1 trigonid and talonid are clearly differentiated by height. The trigonid cusps are arranged in an angle of 70° with the paraconid and metaconid close to each other (Fig. 2c). The protoconid is the tallest cusp of the trigonid followed by the metaconid. The paraconid is small, anteroposteriorly compressed, and labially displaced. An extra, smaller cusp develops lingual to the paraconid. This cusp originates from the anterointernal cingulum according to Baskin (1982, 1989; alternative interpretation in Linares 1981), and gives the appearance of a bifid paraconid. Except *Cy. argentina* (Kraglievich and Reig 1954; Baskin 1989) and *Cy. longirostris* with single paraconid, a bifid paraconid is found in *Cy. pascuali*, *Cy. groeberi*, and *Cy. lutaria* (Fig. 4a). This feature could not be confirmed for *Cy. argentinus* and *Cy. clausa* because in the holotypes the molars are heavily worn. Carnassial notches are between the main cusps of the trigonid.

The talonid is almost as wide as the trigonid (Table S1, electronic supplementary material) and has a very deep basin. The hypoconid is the tallest cusp of the talonid, similar in size to the metaconid and is on the posterolabial corner of the tooth. The cristid obliqua is labial to the carnassial notch. There is no hypoconulid. A crest borders the talonid posteriorly. The entoconid and entoconulid are well-differentiated and separated from each other (Fig. 2c).

Both cusps are slightly labiolingually compressed. The entoconid is on the posterolingual corner of the talonid and slightly larger than the entoconulid. The entoconulid is mesial to the entoconid. A low crest descends from its tip towards the metaconid, and forms the lingual border of the talonid basin.

The main differences between the p4 of AMU-CURS 224 and *Cy. argentina*, *Cy. pascuali*, *Cy. robusta*, *Cy. groeberi*, and *Cy. lutaria* are that the posterior accessory cusp is conical in these species and the crest descending from this cusp to the posterior cingular labial cusplet is absent in *Cy. groeberi* and *Cy. lutaria* (Fig. 4a). The m1 of AMU-CURS 224 is noticeably wider than in other species of *Cyonasua*. The main differences with *Cy. pascuali*, *Cy. lutaria*, and *Cy. groeberi* are in the talonid. In *Cy. lutaria*, the hypoconid is conical and blunt, the hypoconulid is present, the entoconid is larger and conical, and the entoconulid is absent. In *Cy. pascuali*, the hypoconid resembles AMU-CURS 224, but the entoconid is larger, the entoconulid is absent, and the hypoconulid is bifid. In *Cy. groeberi* and *Cy. longirostris*, the hypoconid is conical and massive, the hypoconulid is bifid, the entoconid is present, and also have three small cusplets that may be homologous with the entoconulid.

Chapalmalania Ameghino 1908

Chapalmalania

Fig. 3

Type species: *Chapalmalania ortognatha* Ameghino 1908 (holotype MACN 6164)

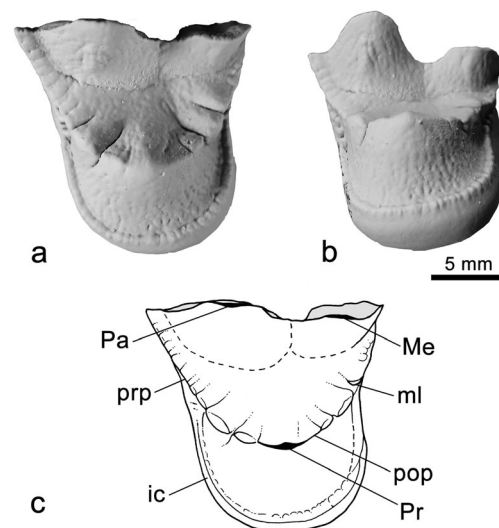


Fig. 3 *Chapalmalania* sp. (SGC STRI-34114) from northeast of Colombia, Ware Formation (Late Pliocene). Left M1 in occlusal (a) and lingual views (b). The line drawing (c) indicates the morphological features mentioned in the text. *ic* internal cingulum, *Me* metacone, *ml* metaconule, *Pa* paracone, *pop* postprotocrista, *Pr* protocone, and *prp* preprotocrista

Temporal range Late Pliocene (Chapadmalalan to Marplatan SALMAs)

Geographic distribution Argentina (Buenos Aires and Mendoza provinces) and Colombia (La Guajira Department)

Referred specimen SGC STRI-34114, fragmentary left M1 from locality 470061, “Estación de Policía,” north of Bahía Cocinetas, La Guajira Department, Colombia (N11° 50' 55.32" / W71° 19' 27.48"). Lower Ware Formation, Late Pliocene.

Description and comparisons The M1 is almost complete except for lacking the labial portion of the crown (Fig. 3a, b). Roots are not preserved. The tooth has no wear, suggesting that it corresponds to a juvenile or young adult. The lingual side of the paracone and a small portion of the metacone base are preserved. According to their bases, the paracone was the tallest cusp of the crown. The lingual side of the paracone is vertical and flat. The protocone is conical and blunt. The preprotocrista and postprotocrista border a deep and wide protocone basin. The preprotocrista is oblique, runs towards the paracone mesial face, and has two tiny cusplets. The postprotocrista is also oblique, runs towards the distal metacone base, and has three tiny cusplets. The most labial cusplet, homologous to the metaconule, connects to the metacone by a short metacristid. A thin wide and crenulated internal cingulum surrounds the mesial, lingual, and distal base of the protocone.

SGC STRI-34114 and the holotype of *Ch. altaefrontis* are very similar in size and shape (Fig. 4d). The crown (measured at the protocone level) is 6 % shorter, and the protocone is 3 % longer, 3 % narrower, and 2 % higher in SGC STRI-34114 (Table S2, electronic supplementary material). Differences are that in *Ch. altaefrontis*, the lingual side of the paracone is oblique and divided in two faces by an enamel ridge that runs from the tip to the base of this cusp. The protocone basin is

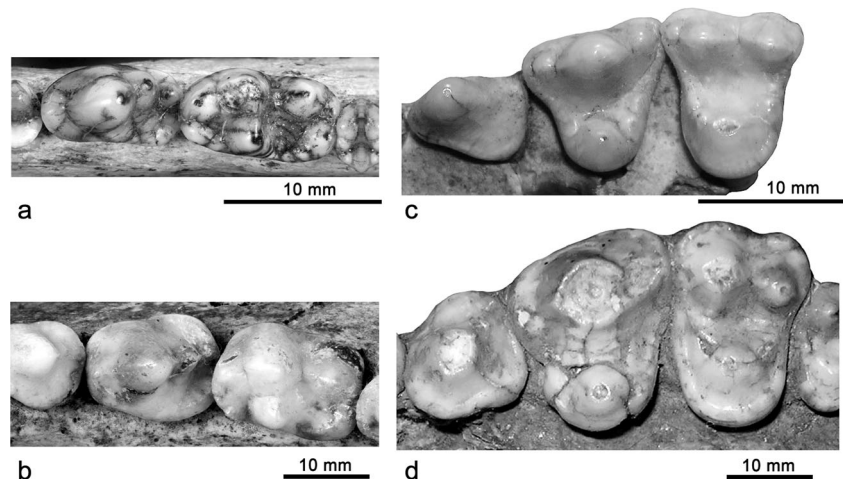
deeper, shorter, and wider in *Ch. altaefrontis* (9 % longer and 27 % narrower in SGC STRI-34114) (Table S2, electronic supplementary material).

Taxonomical comments The species of *Cyonasua* and *Chapalmalania* differ clearly in their sizes (Fig. 4). Specimens of *Cyonasua* are generally 30–50 % smaller than specimens of *Chapalmalania* based on linear dental measurements (Fig. 4). The estimated body mass of *Cyonasua* is between 3 and 13 kg while *Chapalmalania* is about 22 kg (Soibelzon and Prevosti 2007; Prevosti et al. 2013). *Chapalmalania* has molarized carnassial teeth (Fig. 4b, d) and larger posterior molars compared to the carnassials (Kraglievich and Olazabal 1959; Berman 1994), suggesting convergences with ursids. Because of the deep dentary, m1 bifid paraconid, and medium size (Table S1, electronic supplementary material), we refer AMU-CURS 224 to *Cyonasua*. In contrast, SGC STRI-34114 is about 40 % larger than *Cyonasua* sp. (Table S2, electronic supplementary material), with the M1 internal cingulum around the protocone, more developed in SGC STRI-34114 than in any *Cyonasua* sp. (Fig. 4c), and similar to species of *Chapalmalania*.

Phylogenetic analyses Our first analysis including all the extant and extinct taxa resulted in 19 most parsimonious trees (208 length, CI 0.442, RI 0.654; Fig. 5a). Two main groups were found within Procyonidae: one containing the coatis (*Nasuella* and species of *Nasua*, which are shown paraphyletic) and the other with the extinct South American procyonids *Cyonasua* spp. and *Chapalmalania* spp., including the new specimens from Venezuela and Colombia.

Our analysis that treated *Arctonasua*, *Chapalmalania*, and *Cyonasua* as composite taxa resulted in three most parsimonious trees (205 length; CI, 0.449; RI, 0.663; Fig. 5b). The general topology shows the extinct South American procyonids as monophyletic, one group with *Potos* and *Bassaricyon* (Potosinae), and another group with *Procyon*,

Fig. 4 South American procyonids. Lower dentition with detail of p4–m1 in occlusal view of *Cyonasua lutaria* (holotype, MLP 34-VI-20-6), right dentition (a) and *Chapalmalania* cf. *ortognatha* (MLP 91-IV-5-1), left dentition inverted (b). Upper dentition with detail of P3–M1 in occlusal view of *Cy. lutaria* (holotype, MLP 34-VI-20-6), left dentition (c) and *Chapalmalania altaefrontis* (holotype, MLP 54-V-17-1), right dentition inverted (d)



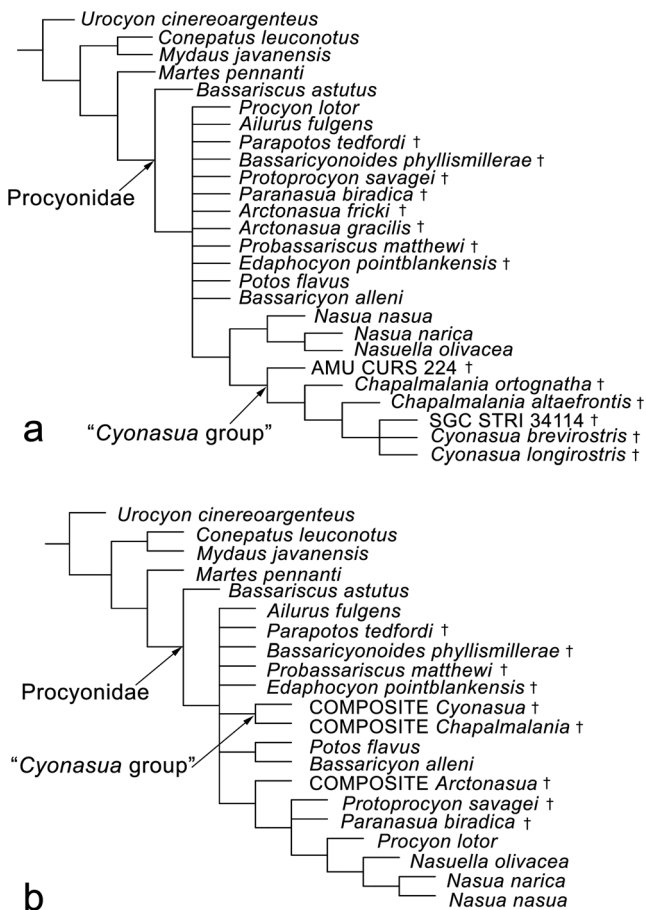


Fig. 5 Strict consensus tree from 19 most parsimonious trees recovered by heuristic search of the extant and extinct procyonids (length, 208; CI, 0.442; RI, 0.654) (**a**). Strict consensus tree from three most parsimonious trees recovered by heuristic search of the extant and extinct procyonids, considering *Arctonasua* spp., *Chapalmalania* spp., and *Cyonasua* spp. as composite taxa (length, 205; CI, 0.449; RI, 0.663) (**b**). Dagger extinct taxa

Nasua and *Nasuella*, and the extinct *Arctonasua*, *Paranasua* and *Protoprocyon* (partial Procyoninae). The groups obtained in both analyses have very weak or no support (electronic supplementary material) and are sensitive to whether taxa are included or excluded.

Discussion

The two pre-Holocene procyonids specimens from northern South America possess diagnostic features of *Cyonasua* and *Chapalmalania*, although the taxonomy of these genera is unstable given the incompleteness of their records. Our phylogenetic analyses (Fig. 5a, b) support the monophyly of a clade of the extinct South American procyonids, as did previous assessments (Baskin 1989, 2004) that recorded this assembly as the “*Cyonasua* group” (Baskin 2004, see also Patterson and Pascual 1972). The “*Cyonasua* group” is characterized by a short rostrum, deep dentary, and m1 with well-

developed anterointernal cingulum that produce in some taxa a bifid paraconid (Baskin 1989, 2004). In our analysis, we recorded the p4 and m1 protoconid equally in height [character 66(1)] and presence of entoconulid [character 70(1)] as synapomorphies (electronic supplementary material). The “*Cyonasua* group” was also recorded when *Arctonasua*, *Chapalmalania*, and *Cyonasua* were treated as composite taxa (Fig. 5b) and it was recovered in some of the most parsimonious trees that include the taxa with more than 25 % of the characters scorable (electronic supplementary material). When considering the taxa with more than 50 % of the characters scorable, the monophyly of the “*Cyonasua* group” is lost: *Cy. brevirostris* and *Cy. longirostris* are sister taxa, while *Ch. altaefrontis* is grouped together with living raccoons and coatis (electronic supplementary material).

The analysis that includes all the extant and extinct taxa suggests that the “*Cyonasua* group” shares a common ancestor with living procyonids (i.e., coatis; Fig. 5a). A similar result was obtained when including the taxa with more than 25 and 50 % of the characters scorable: the South American fossil procyonids formed a monophyletic group with raccoons and coatis (electronic supplementary material). None of our trees showed close affinities of the “*Cyonasua* group” with *Arctonasua* spp. The *Arctonasua* sp., from the middle Miocene–Pliocene (Early Barstovian to Late Hemiphillian NALMAs) of North America, were previously recognized as the sister taxon of the “*Cyonasua* group” (Baskin 1982, 1989, 2004). In most of our searches, the phylogenetic position of *Arctonasua* is ambiguous (*Arctonasua* is placed as part of a large polytomy within procyonids; Fig. 5a and electronic supplementary information); the only exception is by treating *Arctonasua*, *Cyonasua*, and *Chapalmalania* as composite taxa (Fig. 5b). In this search, *Arctonasua* is placed in a monophyletic group together with the extinct North American procyonids *Paranasua* and *Protoprocyon*, living raccoons and coatis (the monophyly of *Paranasua*, *Protoprocyon*, raccoons, and coatis was already recovered by Baskin 1989, 2004). In turn, the “*Cyonasua* group” is placed in this search alternatively as the sister taxon of a group formed by *Arctonasua*, *Protoprocyon*, *Paranasua*, *Procyon*, *Nasua*, and *Nasuella*, the sister taxon of all of them plus *Edaphocyon*, or the sister taxon of *Edaphocyon* (the “*Cyonasua* group” is part of a large polytomy in the consensus of Fig. 5b). *Edaphocyon* is an extinct North American procyonid from the Early–Middle Miocene (Early Hemingfordian to early Barstovian NALMAs) (Baskin 1982) with a generalized dental morphology and it was considered a basal Procyoninae by Baskin (1989, 1982). If close phylogenetic relationships exist between *Edaphocyon* and the “*Cyonasua* group,” the extinct South American procyonids may represent a basal lineage within this monophyletic group, as already suggested by Baskin (1989, 2004), sharing a distant common ancestor with raccoons and coatis.

The alpha taxonomy of the extinct South American procyonids is still unresolved. Large intraspecific variation has been recognized in extant procyonids (Rodríguez et al. 2013) and this could be also the case for the fossil species. In fact, what is treated here as *Cyonasua* (e.g., Riggs and Patterson 1939; Kraglievich and Reig 1954; Soibelzon 2011) was considered by some authors as different genera (e.g., Baskin, 2004). We followed Patterson and Pascual (1972), Berman (1994), Soibelzon and Prevosti (2007), Soibelzon (2011), Prevosti and Soibelzon (2012), and Prevosti et al. (2013) in considering two valid genera for the South American extinct procyonids, although our phylogenetic analysis failed to recognize the monophyly of *Chapalmalania* (Fig. 5a). *Ch. altaefrontis* and *Ch. ortognatha* are successive sister taxa of the group that includes *Cy. longirostris* and *Cy. brevirostris*. AMU-CURS 224 with a morphology that compares favorably with *Cyonasua* spp. is at the base of the “*Cyonasua* group,” and SGC STRI-34114 that compares favorably with *Chapalmalania* spp. is grouped with *Cyonasua* sp. The consensus in Fig. 5a would seem to be against the traditional view of the recognition of two genera for the fossil South American procyonids, a view also followed here. However, when the monophyly of *Chapalmalania* (formed by *Ch. altaefrontis*, *Ch. ortognatha*, and SGC STRI-34114) and *Cyonasua* (formed by *Cy. longirostris*, *Cy. brevirostris*, and AMU-CURS 224) are forced on purpose, only two more extra steps are obtained to the original 208-step length of the most parsimonious trees. In addition, in the consensus of the analysis that includes the taxa with more than 50 % of the characters scorable, *Ch. altaefrontis* locates in another group than the monophyletic *Cy. longirostris* and *Cy. brevirostris* (electronic supplementary material), supporting the traditional view of two valid genera for these species. In summary, we recorded conflicting hypotheses in our analyses about the validity of the genus *Chapalmalania*. We follow the traditional view of recognizing *Chapalmalania* and *Cyonasua* as valid genera, as we consider that more complete fossils are needed to solve the alpha taxonomy of the extinct South American procyonids. As such, we assigned SGC STRI-34114 and AMU-CURS 224 from Colombia and Venezuela to *Chapalmalania* and *Cyonasua*, respectively, and provide in each case diagnostic characters.

The general tree topologies obtained in our analyses resemble previous phylogenetic hypotheses based on morphological data (Fig. 5a and Ahrens 2012 Fig. 36; Fig. 5b and Baskin 1989, 2004; Decker and Wozencraft 1991; Ahrens 2012). However, molecular data analyses (Koepfli et al. 2007; Eizirik et al. 2010) have contested the groupings obtained with morphological data alone by considering that morphology-based assessments reflect convergences associated with similar lifestyles and diets rather than ancestry. These inconsistencies provide a debatable scenario while further studies hopefully provide better evidence.

Procyonids and the Great American Biotic Interchange

Procyonidae first appear in the fossil record in the late Oligocene of Europe (Wolsan and Lange-Badré 1996; Baskin 2004). Most of their evolutionary history excludes South America with the first record in this continent dating back to the late Miocene, at about 7.1–7.3 Ma, following Reguero and Candela (2011; Fig. 6a).

The classic biogeographic model considered that the first main GABI migration wave between North and South America dates back to the Late Pliocene, ca. 3 Ma (Woodburne 2010 and references there). Fossil evidence demonstrated that the procyonids predate this episode and are among the first North American immigrants recorded in South America (Marshall et al. 1979; Linares 1981; Baskin 1982; Berman 1994; Soibelzon and Prevosti 2007, 2012; Woodburne 2010; Prevosti and Soibelzon 2012). A full closure of the Central American Seaway (or CAS, the oceanic pathway along the tectonic boundary between South America and the Panama Block) occurred by 12–10 Ma, ending the exchange of deep and intermediate waters between the Caribbean and the Pacific (Coates et al. 2004; Montes et al. 2012a, b; Sepulchre et al. 2014). Intermittent exchange of shallow waters between the Pacific and the Caribbean continued in the 10- to 3.5-Ma interval, along places other than the CAS, greatly enhancing the dispersal of biota across the isthmus (Jaramillo et al. 2014), previous to its full closure that occurred at about 4.2–3.5 Ma (Haug et al. 2004). This is contemporaneous with the taxonomic radiation of the “*Cyonasua* group” in South America (Fig. 6a–c). The Pliocene procyonids from Venezuela and Colombia that we reported here are part of this first event. Both new specimens belong to the same monophyletic group (Fig. 5a, b) as the taxa recovered in Argentina, found more than 4000 km distant (Fig. 6b, c). This suggests a broad geographical distribution of the fossil taxa, also recorded in extant procyonid species (e.g., *Procyon cancrivorous* and *Nasua nasua*), ranging in South America from tropical environments of Colombia and Venezuela to the north of Argentina (Kays 2009; Fig. 6d).

These new specimens of *Cyonasua* and *Chapalmalania* in the Pliocene of northern South America partially fill a gap in the fossil record. The rare evidence of this group in lowlands of northern South America raise the question whether this is the result of a bias in the fossil record, or alternatively, that the group migrated south throughout the tropical belt using the Andes as a corridor. The major uplift of the Northern Central and Northern Andes occurred during the 10- to 6-Ma interval (Mora et al. 2010) and the mountain belt was already available as a migration route (Patterson et al. 2012 and references therein).

During the Pliocene, at about 2.6–2.4 Ma, the GABI began its major event of faunal exchange (GABI 1; Marplatan) and had major pulses at ~1.8 Ma (GABI 2; early Ensenadan),

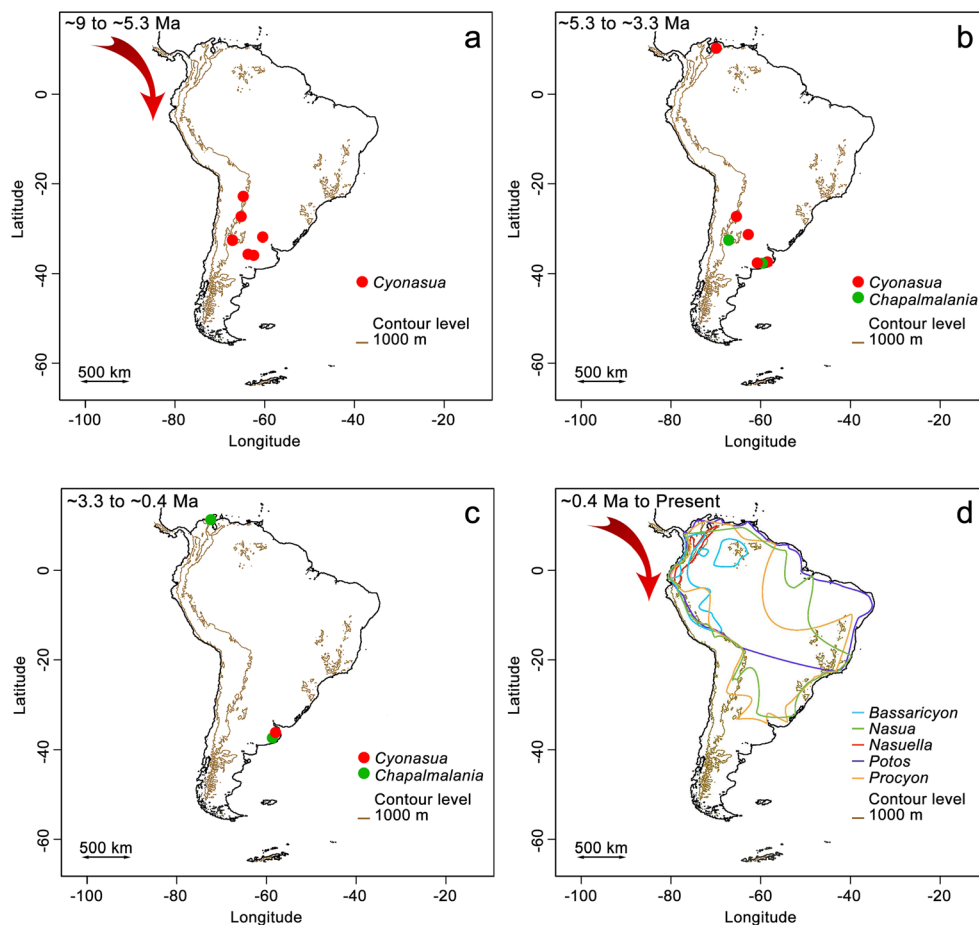


Fig. 6 Biogeographical distribution of fossil and extant South American Procyonidae. **a** Late Miocene (Tortonian–Messinian) to earliest early Pliocene (Zanclean), Huayquerian SALMA (~9 to ~5.3 Ma), including the paleontological sites of Paraná (Ituzaingó Formation), La Pampa (Cerro Azul Formation), Buenos Aires (Epecuén Formation), Huayquerías (Huayquerías Formation), Valle de Santa María (Andalhuala Formation), and Maimará (Maimará Formation) with record of *Cyonasua*. **b** Early to late Pliocene (Zanclean–Piacenzian), Montehermosan to Chapadmalalan SALMAs (~5.3 to ~3.3 Ma), including the paleontological sites of Montehermoso (Montehermoso Formation), Playas de Córdoba (Montehermosan), Valle de Santa María (Corral Quemado Formation), and hills between Mar del Plata and Miramar (Chapadmalal Formation), and Falcon State (San Gregorio Formation) with record of *Cyonasua*; Huayquerías (Tunuyán Formation), and hills between Mar del Plata and Miramar (Montehermoso and Chapadmalal

formations) with record of *Chapalmalania*. **c** Late Pliocene (Piacenzian) to middle Pleistocene, Marplatán to Ensenadan SALMAs (~3.3 to 0.4 Ma), including the hills between Mar del Plata and Miramar (Vorohue Formation), and “Estación de Policía” (Ware Formation) with record of *Chapalmalania*, and Toscas del Río de La Plata (Ensenadan) with record of *Cyonasua*. This diagram encompasses GABI 1 at ~2.6–2.4 Ma, GABI 2 at ~1.8 Ma, and GABI 3 at ~1 Ma (Woodburne 2010). **d** Middle Pleistocene to Present, Bonaerian, Lujanian, Platan SALMAS (last 0.4 Ma), biogeographical distribution of the genera *Bassaricyon*, *Nasua*, *Nasuella*, *Potos*, and *Procyon*. This diagram encompasses GABI 4 at ~0.12 Ma (Woodburne 2010). Fossil data points were taken from Berman (1994). Extant data points were accessed through The Global Biodiversity Information Facility (GBIF; August 2013). Arrows indicates the two different occasions that procyonids dispersed from North America to South America according to the fossil record

~1 Ma (GABI 3; Ensenadan), and ~0.12 Ma (GABI 4; Lujanian) (Woodburne 2010). For carnivorans, the most abrupt taxonomic increase was recorded in the Lujanian (Prevosti and Soibelzon 2012; Prevosti et al. 2013). By then, a second episode of migration was recognized for procyonids with the entrance of the extant components of the South American fauna (Fig. 6d). The biochron of *Procyon* and *Nasua* in South America dates back to the Lujanian (~58,000 years AP; Soibelzon et al. 2010; Rodríguez et al. 2013). More than half a million year gap in the fossil record separates the last *Cyonasua* in the Ensenadan (~1.8 to 0.4 Ma; Tonni 2009) and the first *Procyon* and *Nasua* in the Lujanian (Fig. 6d, e). Other factors resulted in

a second wave of procyonid migration long after the full closure of the Panama isthmus, as physical connection between the Americas was present at ca 3 Ma. However, molecular studies have demonstrated that the diversification leading to the extant Procyonidae occurred in the early Miocene (~20 Ma), while the divergence times between coatis and raccoons occurred in the late Miocene (~8–7 and 5.7–5 Ma, respectively) (Koepfli et al. 2007; Eizirik et al. 2010) well before the full closure of the Panama isthmus. This scenario requires a clear bias in the fossil record, long ghost lineages, and an evolutionary history of the living taxa that precedes the GABI.

The South American procyonids are the result of a complex evolutionary history. Different lineages may have independently invaded the continent (see Prevosti 2006 with another example within South American carnivores), with different arrival timings. Endemic forms evolved from disparate lineages, such as the extinct species of the “*Cyonasua* group” and the extant *Nasuella* sp., living in the high elevations of the Andean Mountains of northern South America (electronic supplementary material). Bidirectional migrations (i.e., movements of taxa that originated in South America to North America) are also possible (Prevosti and Soibelzon 2012).

Acknowledgments We gratefully thank Francisco Prevosti, Adriana Candela, and Agustín Martinelli for helpful comments and discussions, two anonymous reviewers for useful suggestions to improve the manuscript, Jorge D. Carrillo-Briceno for support in the field and in the lab, Andrés Cárdenas for producing the fossil and extant distribution maps, Torsten Scheyer for technical help, Simon Kay for assistance in revising the English text, Instituto del Patrimonio Cultural of the República Bolivariana de Venezuela and the Alcaldía del Municipio Urumaco for support during this research, coworkers of the Smithsonian Tropical Research Institute that participated in the field trip, and the Wayúú Community for access to their lands and support during the field work. The Swiss National Fund SNF 31003A-149605, PICT 2011–0309, Smithsonian Institution, National Geographic Society, The Anders Foundation, Gregory D. and Jennifer Walston Johnson, Universidad del Norte, and NSF EAR 0957679 help to support this work. We acknowledge having used the Willi Hennig Society edition of TNT.

References

- Ahrens HE (2012) Craniodental characters and the relationships of Procyonidae (Mammalia: Carnivora). *Zool J Linn Soc* 164:669–713
- Baskin JA (1982) Tertiary Procyoninae (Mammalia: Carnivora) of North America. *J Vert Paleontol* 2:71–93
- Baskin JA (1989) Comments on new world tertiary Procyonidae (Mammalia, Carnivora). *J Vert Paleontol* 9:110–117
- Baskin JA (2004) *Bassariscus* and *Probassariscus* (Mammalia, Carnivora, Procyonidae) from the early Barstovian (Middle Miocene). *J Vert Paleontol* 24:709–720
- Berman WD (1994) Los carnívoros continentales (Mammalia, Carnivora) del Cenozoico en la provincia de Buenos Aires. Dissertation, Universidad Nacional de La Plata
- Campbell KE, Frailey CD, Romero-Pittman L (2000) The late miocene Gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: implications for the great american faunal interchange. *INGEMMET, Serie D, Bol* 23:1–152
- Campbell KE, Prothero DR, Romero-Pittman L, Hertel F, Rivera N (2010) Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. *J South Am Earth Sci* 29: 619–626
- Carlini AA, Zurita AE (2010) An introduction to cingulate evolution and their evolutionary history during the Great American Biotic Interchange: biogeographical clues from Venezuela. In: Sánchez-Villagra MR, Aguilera OA, Carlini AA (eds) Urumaco and Venezuelan Paleontology: the fossil record of the northern Neotropics. Indiana University Press, Bloomington, pp 233–255
- Castro MC, Carlini AA, Sánchez R, Sánchez-Villagra MR (2014) A new *Dasyopodini* armadillo (*Xenarthra*: Cingulata) from San Gregorio formation, Pliocene of Venezuela: affinities and biogeographic interpretations. *Naturwissenschaften* 101:77–86
- Cione AL, Tonni EP (1999) Biostratigraphy and chronological scale of upper-most Cenozoic in the Pampean area, Argentina. In: Rabassa J, Salemme M (eds) Quaternary of South America and Antarctic Peninsula 12:23–51
- Cione AL, Tonni EP, Bargo S, Bond M, Candela AM, Carlini AA, Deschamps CM, Dozo MT, Esteban G, Goin FJ, Montalvo CI, Nasif N, Noriega JI, Ortiz Jaureguizar E, Pascual R, Prado JL, Reguero MA, Scillato-Yané GJ, Soibelzon L, Verzi DH, Vieytes EC, Vizcaíno SF, Vucetich MG (2007) Mamíferos continentales del Mioceno tardío a la actualidad en la Argentina: cincuenta años de estudios. *Publicación Especial Ameghiniana 50° aniversario*. APA, Buenos Aires, pp 257–278
- Coates AG, Collins LS, Aubry MP, Berggren WA (2004) The geology of the Darien, Panama, and Miocene-Pliocene collision of the panama arc with northwestern South America. *Geol Soc Am Bull* 116:1327–1344
- Decker DM, Wozencraft WC (1991) Phylogenetic analysis of recent procyonid genera. *J Mammal* 72:42–55
- Deschamps CM, Vucetich MG, Montalvo CI, Zárate MA (2013) *Capybaras* (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the late Miocene–Pliocene sequences of South America. *J South Am Earth Sci* 48:145–158
- Eizirik E, Murphy WJ, Koepfli K-P, Johnson WE, Jerry W, Dragoo JW, Wayne RK, O’Brien SJ (2010) Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Mol Phylogenet Evol* 56:49–63
- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786
- Haug G, Tiedemann R, Keigwin L (2004) How the isthmus of Panama put ice in the Arctic. *Oceanus* 42:94–97
- Jaramillo C, Moreno E, Ramirez V, da Silva S, Barrera A, Barrera A, Moron S, Herrera F, Escobar J, Koll R, Manchester S, Hoyos N (2014) Palynological record of the last 20 million years in Panama. *Monogr Syst Bot Mo Bot Gard* 68:134–251
- Kay RF, Madden RH, Cifelli RL, Flynn JJ (1997) Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta. Smithsonian Institution Press, Washington
- Kays R (2009) Family Procyonidae (Racoons). In: Wilson DE, Mittermeier RA (eds) Handbook of the mammals of the world. Carnivores. Lynx Editions, Barcelona, pp 504–531
- Koepfli K-P, Gompper ME, Eizirik E, Ho C-C, Linden L, Maldonado JE, Wayne RK (2007) Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology and the Great American Interchange. *Mol Phylogenet Evol* 43:1076–1095
- Kraglievich JL, Olazabal AG (1959) Los prociönidos extinguidos del género *Chapalmalania* Ameghino. *Rev Mus Argent Cienc Nat (Zool)* 6:1–59
- Kraglievich JL, Reig OA (1954) Un nuevo prociönido del Plioceno de las Playas (Provincia de Córdoba). *RAGA* 9:210–231
- Linares OJ (1981) Tres nuevos carnívoros prociönidos fósiles del Mioceno de Norte y Sudamérica. *Ameghiniana* 10:113–121
- Marshall LG, Butler RF, Drake RE, Curtis GH, Tedford RH (1979) Calibration of the Great American Interchange. *Sci* 204:272–279
- Montes C, Bayona G, Cardona A, Buchs DM, Silva CA, Morón S, Hoyos N, Ramirez DA, Jaramillo CA, Valencia V (2012) Arc-continent collision and orocline formation: closing of the Central American seaway. *J Geophys Res* 117. doi:10.1029/2011JB008959
- Montes C, Cardona A, McFadden R, Morón SE, Silva CA, Restrepo-Moreno S, Ramirez DA, Hoyos N, Wilson J, Farris D, Bayona GA, Jaramillo CA, Valencia V, Bryan J, Flores JA (2012b) Evidence for middle Eocene and younger land emergence in central Panama: implications for isthmus closure. *Geol Soc Am Bull* 124:780–799

- Mora A, Baby P, Roddaz M, Parra M, Brusset S, Hermoza W, Espurt N (2010) Tectonic history of the Andes and Sub-Andean zones: implications for the development of the amazon drainage basin. In: Hoorn C, Wesselingh FP (eds) Amazonia, landscape and species evolution: a look into the past. Blackwell Publishing, Hoboken, pp 38–60
- Moreno-Bernal JW (2014) Fossil crocodylians from the high Guajira Peninsula of Colombia, and the history of Neogene crocodylian diversity in tropical South America. Dissertation, University of Nebraska
- Moreno-Bernal JW, Moreno F, Vallejo-Pareja MC, Jimenez-Campos L (2012) Neotropical late Miocene-early Pliocene vertebrates from the castilletes formation, northern Colombia. *J Vert Paleontol* 32(Suppl 1):145
- Pascual R, Ortiz Jaureguizar E (1990) Evolving climates and mammal faunas in Cenozoic South American. *J Hum Evol* 19:23–60
- Patterson B, Pascual R (1972) The fossil mammal fauna of South America. In: Keast A, Erk FC, Glass B (eds) Evolution, mammals and southern continents. State University of New York Press, New York, pp 274–309
- Patterson BD, Solari S, Velazco PM (2012) The role of the Andes in the diversification and biogeography of Neotropical mammals. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: an 80-million year history of modern Neotropical mammals. University of Chicago Press, Chicago, pp 351–378
- Prevosti FJ (2006) New material of Pleistocene cats (Carnivora, Felidae) from Southern South America, with comments on biogeography and the fossil record. *Geobios* 39:679–694
- Prevosti FJ, Rincón AD (2007) A new fossil canid assemblage from the late Pleistocene of northern South America: the canids of the incierte asphalt Pit (Zulia, Venezuela), fossil record and biogeography. *J Paleo* 81:1053–1065
- Prevosti FJ, Soibelzon LH (2012) Evolution of the South American carnivores (Mammalia, Carnivora): a paleontological perspective. In: Patterson BD, Costa LP (eds) Bones, clones, and biomes: an 80-million year history of modern Neotropical mammals. University of Chicago Press, Chicago, pp 102–122
- Prevosti FJ, Forasiepi AM, Zimicz N (2013) The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? *J Mamm Evol* 20:3–21
- Prothero DR, Campbell KE, Beatty BL, Frailey CD (2014) New late Miocene dromomerycine artiodactyl from the amazon basin: implications for interchange dynamics. *J Paleo* 88:434–443
- Quiróz LI, Jaramillo C (2010) Stratigraphy and sedimentary environments of Miocene shallow to marginal marine deposits in the Urumaco trough, Falcón basin, western Venezuela. In: Sánchez-Villagra MR, Aguilera OA, Carlini AA (eds) Urumaco and Venezuelan Palaeontology: the fossil record of the northern Neotropics. Indiana University Press, Bloomington, pp 153–172
- Reguero MA, Candela AM (2011) Late Cenozoic mammals from the northwest of Argentina. In: Salfity JA, Marquillas RA (eds) Cenozoic Geology of the Central Andes of Argentina. SCS Publisher, Salta, pp 411–426
- Riggs ES, Patterson B (1939) Stratigraphy of late Miocene and Pliocene deposits of the provincia de Catamarca (Argentina) with notes on the faunas. *Physis* 14:143–162
- Rincón AD (2006) A first record of the Pleistocene saber-toothed cat *Smilodon populator* Lund, 1842 (Carnivora: Felidae: Machairodontinae) from Venezuela. *Ameghiniana* 43:499–501
- Rincón AD, Prevosti FJ, Parra GE (2011) New saber-toothed cat records (Felidae: Machairodontinae) for the Pleistocene of Venezuela, and the great american biotic interchange. *J Vert Paleontol* 31:468–478
- Rodriguez SG, Soibelzon LH, Rodrigues S, Morgan CC, Bernardes C, Avilla L, Lynch E (2013) First record of *Procyon cancrivorus* (G. Cuvier, 1798) (Carnivora, Procyonidae) in stratigraphic context in the late Pleistocene of Brazil. *J South Am Earth Sci* 45:1–5
- Sánchez-Villagra MR, Aguilera OA, Carlini AA (2010) Urumaco and Venezuelan Paleontology: the fossil record of the northern neotropics. Indiana University Press, Bloomington
- Scheyer TM, Aguilera OA, Delfino M, Fortier DC, Carlini AA, Sánchez R, Carrillo-Briceño JD, Quiroz L, Sánchez-Villagra MR (2013) Crocodylian diversity peak and extinction in the late Cenozoic of the northern neotropics. *Nat Commun* 4:1907. doi:10.1038/ncomms2940
- Sepulchre P, Arsouze T, Donnadiou Y, Dutay J-C, Jaramillo C, Le Bras J, Martin E, Montes C, Waite AJ (2014) Consequences of shoaling of the Central American seaway determined from modeling Nd isotope. *Paleoceanography* 29:176–189
- Soibelzon LH (2011) First description of milk teeth of fossil South American procyonid from the lower Chapadmalalan (Late Miocene–Early Pliocene) of “farola monte hermoso”, Argentina: paleoecological considerations. *Paläontol Z* 85:83–89
- Soibelzon L, Prevosti FJ (2007) Los carnívoros (Carnivora, Mammalia) terrestres del Cuaternario de América del Sur. In: Pons GX, Vicens D (eds) Geomorfología Litoral i Quaternari: Homenaje a Joan Cuerda Barceló. *Mon Soc Hist Nat Balears* 14:49–68
- Soibelzon LH, Prevosti F (2012) Fossils of South American Land Carnivores (Carnivora, Mammalia). In: Ruiz M, Shostell J (eds) Molecular population genetics, evolutionary biology and biological conservation of neotropical carnivores. Nova Science Publisher, New York, pp 509–530
- Soibelzon LH, Rincón A (2007) The fossil record of the short-faced bears (Ursidae, Tremarctinae) from Venezuela. Systematic, biogeographic, and paleoecological implications. *N Jb Geol Paläont (Abh)* 245: 287–298
- Soibelzon LH, Zurita AE, Morgan CC, Rodríguez S, Gasparini GM, Soibelzon E, Schubert BW, Miño-Boilini AR (2010) Primer registro fósil de *Procyon cancrivorus* (G. Cuvier, 1798) (Carnivora, Procyonidae) en la Argentina. *Rev Mex Cienc Geol* 27:313–319
- Tomassini RL, Montalvo CI, Deschamps C, Manera T (2013) Biostratigraphy and biochronology of the monte hermoso formation (Early Pliocene) at its type locality, Buenos Aires Province, Argentina. *J South Am Earth Sci* 48:31–42
- Tonni E (2009) Los mamíferos del Cuaternario de la Región Pampeana de Buenos Aires, Argentina. In: Ribeiro AM, Bauermann SG, Cherer CS (eds) Cuaternario Do Rio Grande do Sul: integrando conocimientos. Monografias da Sociedade Brasileira de Paleontologia, Porto Alegre, pp 193–205
- Vucetich MG, Carlini AA, Aguilera OA, Sánchez-Villagra MR (2010) The tropics as reservoir of otherwise extinct mammals: the case of rodents from a new Pliocene faunal assemblage from Northern Venezuela. *J Mamm Evol* 17:265–273
- Webb SD (1985) Late Cenozoic mammal dispersals between the Americas. In: Stheli FG, Webb SD (eds) The Great American Biotic Interchange. Plenum Press, New York, pp 357–386
- Wolsan M, Lange-Badré B (1996) An arctomorph carnivoran skull from the Phosphorites du Quercy and the origin of the procyonids. *Acta Palaeontol Pol* 41:277–298
- Woodburne MO (2010) The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *J Mamm Evol* 17:245–264
- Zurita AE, Carlini AA, Gillette D, Sánchez R (2011) Late Pliocene Glyptodontinae (Xenarthra, Cingulata, Glyptodontidae) of South and North America: Morphology and paleobiogeographical implications in the GABI. *J South Am Earth Sci* 31:178–185