

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

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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

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(*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).

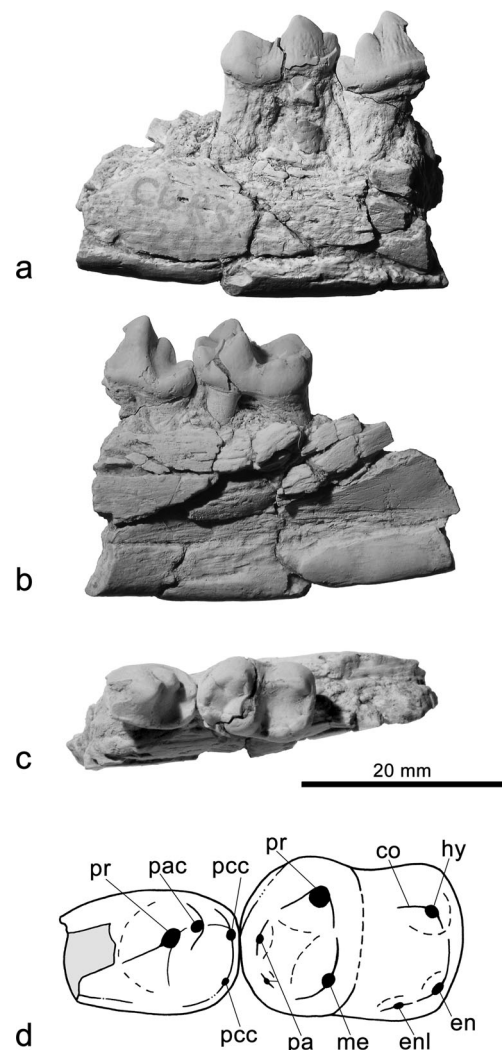


Fig. 2 *Cyonasua* sp. (AMU-CURS 224) from northwestern Venezuela, San Gregorio Formation (Late Pliocene). Right dentary with p4–m1 in labial (a), lingual (b), and occlusal (c) views. The line drawing (d) shows the morphological features mentioned in the text. *co* cristid obliqua, *en* entoconid, *enl* 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)

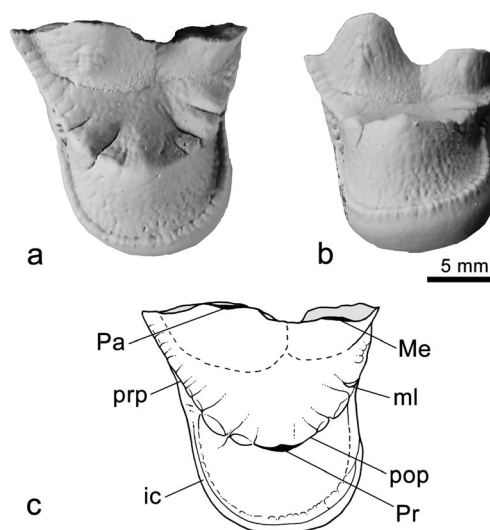


Fig. 3 *Chapalmalania* sp. (SGC STRI-34114) from northeast of Colombia, Ware Formation (Late Pliocene). Left M1 in occlusal (a) and lingual views (b). The line drawing (c) indicates the morphological features mentioned in the text. *ic* internal cingulum, *Me* metacone, *ml* metaconule, *Pa* paracone,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

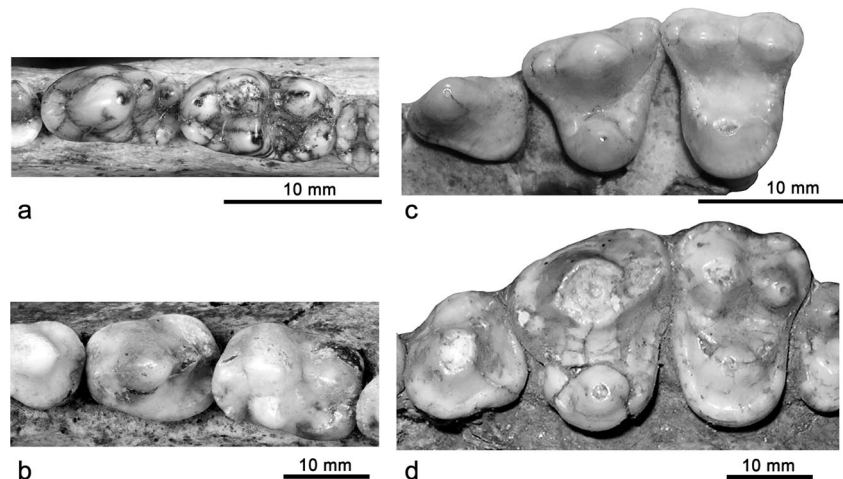
deeper, shorter, and wider in *Ch. altaefrontis* (9 % longer and 27 % narrower in SGC STRI-34114) (Table S2, electronic supplementary material).

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)



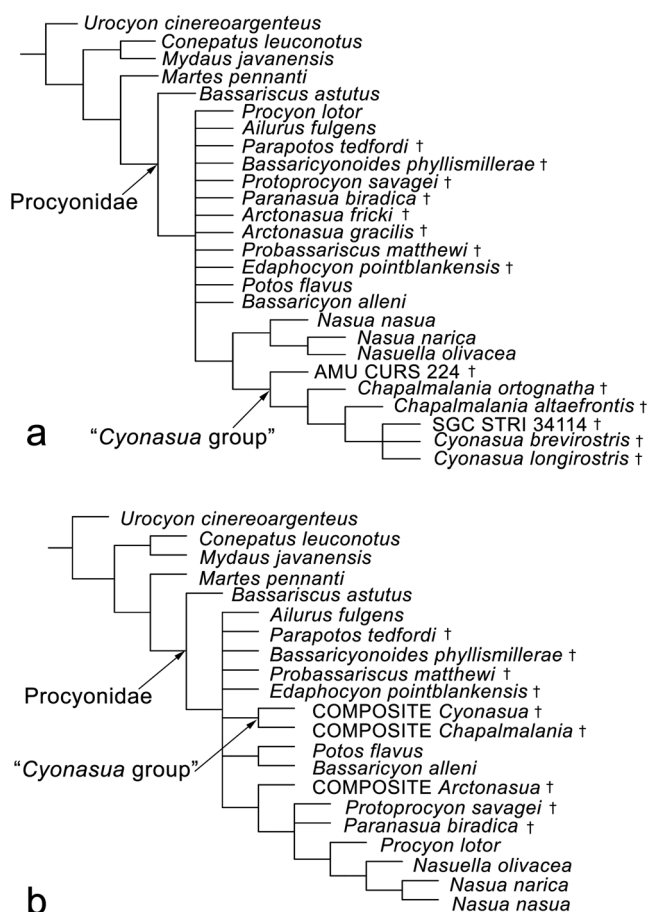


Fig. 5 Strict consensus tree from 19 most parsimonious trees recovered by heuristic search of the extant and extinct procyonids (length, 208; CI, 0.442; RI, 0.654) (**a**). Strict consensus tree from three most parsimonious trees recovered by heuristic search of the extant and extinct procyonids, considering *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),

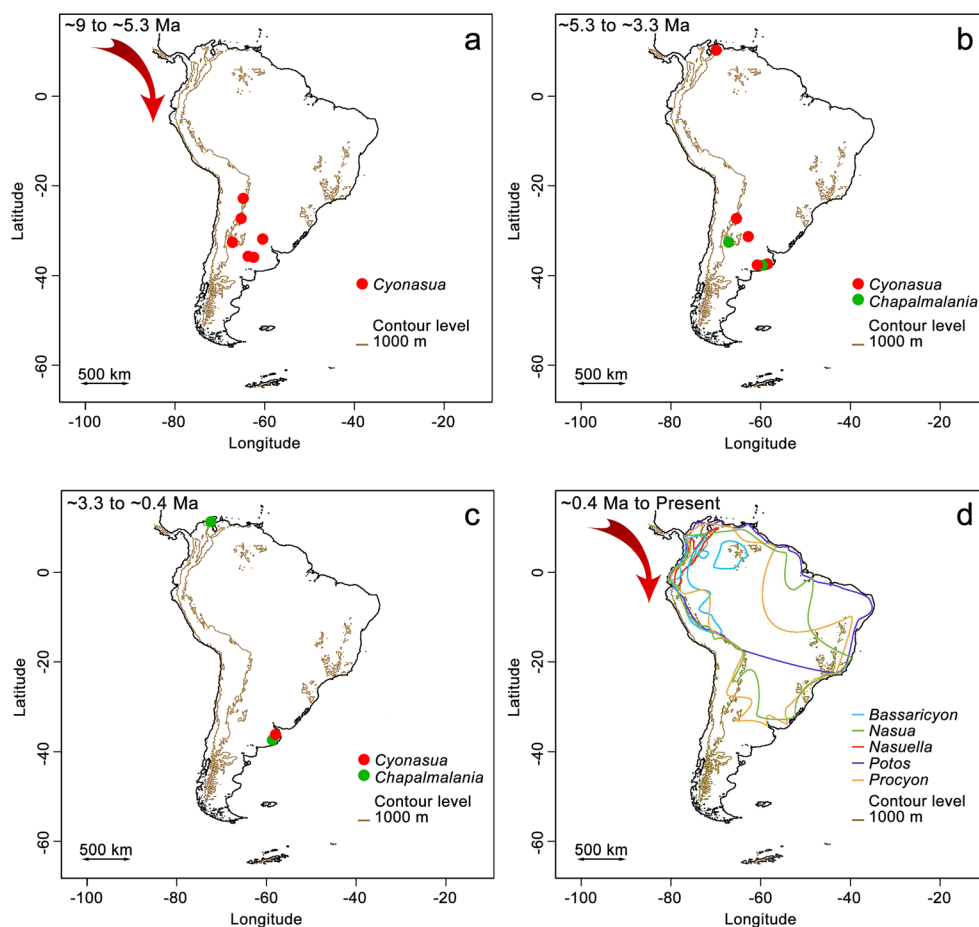


Fig. 6 Biogeographical distribution of fossil and extant South American Procyonidae. **a** Late Miocene (Tortonian–Messinian) to earliest early Pliocene (Zanclean), Huayquerian SALMA (~9 to ~5.3 Ma), including the paleontological sites of Paraná (Ituzaingó Formation), La Pampa (Cerro Azul Formation), 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 indicate 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).

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