

PROCYONIDAE (MAMMALIA, CARNIVORA) AND THE GREAT AMERICAN BIOTIC INTERCHANGE

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ABSTRACT Members of the family Procyonidae were the first placental carnivorans to migrate from North America to South America, during the first part of the Great American Biotic Interchange (ProtoGABI). The *Cyonasua* group is an endemic South American radiation of procyonids, known from the Late Miocene to Middle Pleistocene. It includes *Cyonasua argentina*, perhaps four species of *Amphinasua*, one of *Brachynasua*, and two species of the remarkable, bear-like *Chapalmalania*. Some of the characters used to distinguish these taxa are likely caused by individual variation and sexual dimorphism. Early records of the *Cyonasua* group include fossils collected in 1926–27 by an expedition from the Field Museum of Natural History to Catamarca Province, Argentina. We illustrate and discuss the most important of these specimens. The *Cyonasua* group is the sister taxon of the North American Middle and Late Miocene *Arctonasua*. The extant genera *Nasua* and *Procyon* have a Pliocene record in North America and first occur in South America in the Early-Middle Pleistocene. The fossil record indicates that, for the most part, the genera of procyonids evolved in North America before migrating to South America. Divergence dates determined from the fossil record are younger than those of the molecular clock.

KEYWORDS Miocene, Pliocene, GABI, Carnivora, *Cyonasua*

INTRODUCTION

In the Late Miocene, land mammals from North and South America began crossing the narrowing gap between Central and South America, first by island hopping and later along the dry land corridor of the Isthmus of Panama (Simpson, 1950, 1952, 1980). This exchange and interaction of northern and southern taxa greatly altered the Neotropical and Nearctic faunas and floras. The “heralds” of the Great American Biotic Interchange (GABI) included ground sloths migrating northward from South America and procyonids migrating southward from North America (Webb, 1985). Woodburne et al. (2010) placed the heralds in the pre-GABI followed by GABI 1 to 4. We follow Cione et al. (2015) in dividing the Interchange into the Late Miocene to Early Pliocene ProtoGABI and the Late Pliocene to Early Holocene GABI 1 to 4 (Fig. 1).

The extant Procyonidae include 14 species and 6 genera of small to medium size, mainly Neotropical carnivorans (e.g.,

Koepfli et al., 2017). Procyonids are adapted to terrestrial and arboreal habitats, and their dietary ecology ranges from frugivory (*Potos*, *Bassaricyon*), to omnivory (*Nasua*, *Nasuella*, *Procyon*), and to omnivory, but with a significant proportion of insects and small vertebrates (*Bassariscus*) (e.g., Kays, 2009; Koepfli et al., 2017; Kitchener et al., 2017). Beginning in the Late Miocene (ca. 7 Ma) to middle Pleistocene (ca. 1 Ma), the extinct procyonids of the *Cyonasua* group diversified in South America (e.g., Patterson & Pascual, 1968; Simpson, 1980; Webb, 1985; L. Soibelzon & Prevosti, 2007; Forasiepi et al., 2014; Cione et al., 2015). During GABI 1–4, extant procyonids migrated south and diversified in South America (e.g., Simpson, 1980; Woodburne, 2010; Forasiepi et al. 2014). The aim of our present research is to summarize the diversity of fossil procyonids in the Americas, update the taxonomic attributions, and summarize the evolutionary history of the procyonids, placing special emphasis on the *Cyonasua* group.

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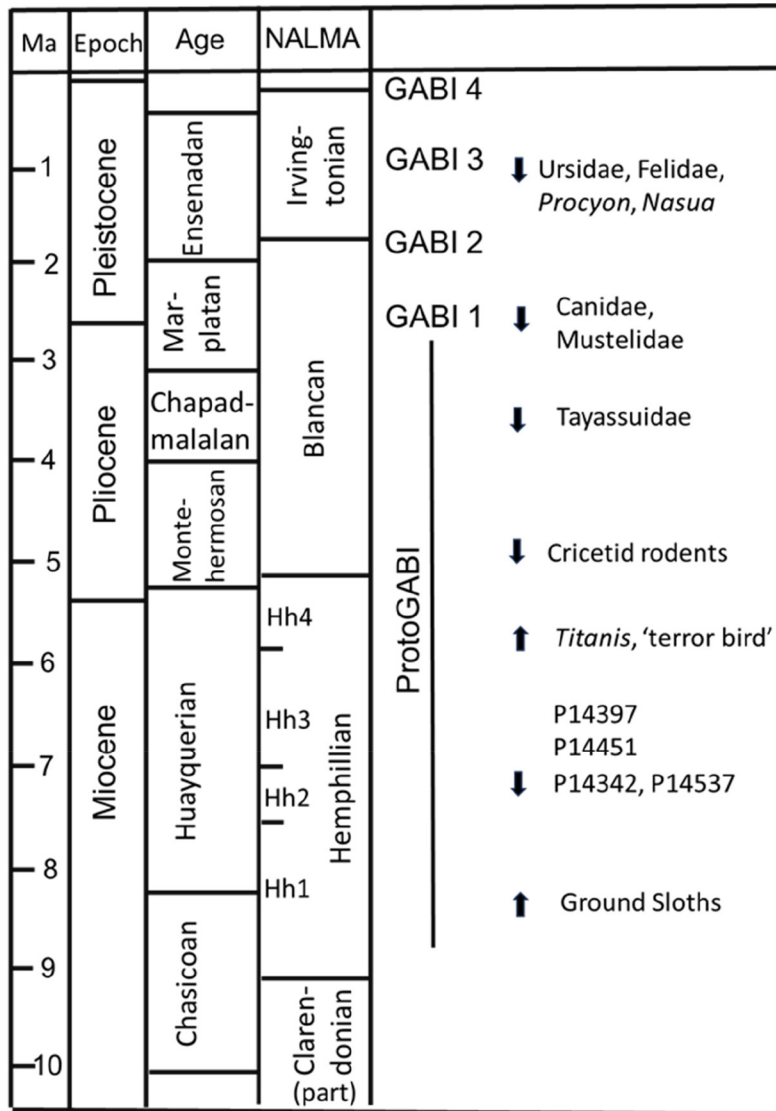


FIGURE 1. Biostratigraphic and chronostratigraphic chart of migration events to South America (↓) and to North America (↑) during the GABI and stratigraphic occurrence of FMNH P specimens.

Abbreviations — AMNH F:AM, Frick Collection, Division of Vertebrate Paleontology, American Museum of Natural History, New York City, USA; FMNH, Field Museum of Natural History, Chicago, USA; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales ‘Lorenzo Scaglia’, Mar del Plata, Argentina; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; UCMP, University of California Museum of Paleontology, Berkeley, USA; UF, Vertebrate Paleontology Collection of the Florida Museum of Natural History (FLMNH), University of Florida, Gainesville,

USA; GABI, Great American Biotic Interchange; NALMA, North American Land Mammal Age.

SYSTEMATIC PALEONTOLOGY

Family PROCYONIDAE (Gray, 1825)

Included Taxa — *Broiliana* Dehm 1950, Procyoninae Gill, 1872, and Potosinae, Trouessart 1904.

Distribution — Early Miocene (MN3, Orleanian and Agenian) of Europe; Early Miocene-Recent (Hemingfordian-Recent) of North America; Late Miocene-Recent (Huayquerian-Recent)

of South America.

Diagnosis — In the Procyonidae and Ailuridae, the dental formula is I3/i3, C1/c1, P4/p4, M2/m2. The procyonid and ailurid dentition is distinguished from that of primitive mustelids in having the second molars enlarged. The m2 has a short trigonid and an elongated talonid. The m1 primitively has a relatively prominent metaconid and a basined talonid. P4 has a lingual internal cingulum and a small parastyle. M1 retains a postprotocrista and metaconule, the primitive arctoid state. Procyonids are derived relative to ailurids in having a Type B auditory bulla (Hunt, 1974) with an inflated entotympanic, greater separation of the posterior lacerate and posterior carotid foramina, a deep suprameatal fossa, and loss of the alisphenoid canal. Relative to *Broiliana*, the New World Procyonidae (Potosinae + Procyoninae) are further derived in having P4 with a better developed parastyle, and m2 hypoconulid postero-lingual and anterior cingulum reduced.

Discussion — In his classification of mammals, Gray (1825) listed, without comments, the Tribe Procyonina for *Procyon*, *Nasua*, and *?Potos*. The Tribes Procyonina, Ursina (bears), and the Gulonina, Myadina, and Taxina (various mustelids) were placed in the Family Ursidae. Turner (1848) discussed the cranial and dental characters uniting *Procyon*, *Bassariscus* (= *Bassariscus*), *Nasua*, and *Cercoleptes* (= *Potos*) in the ursid subfamily Procyonina. Bonaparte (1850) established the Family Procyonidae for the Procyonina (*Potos* was placed in its own family Cercoleptidae), Melina (certain mustelids) and Ailurina (red panda). Flower (1869) restricted Procyonidae to *Procyon*, *Bassariscus* (= *Bassariscus*), *Nasua*, and *Cercoleptes* (= *Potos*) and discussed characters that united this family. Pocock (1921) added *Bassaricyon* and further discussed the 18th and 19th century history of the recognition and diagnosis of members of this family. Koepfli et al. (2017) elaborated further on this and added developments in the 20th century.

Subfamily PROCYONINAE Gill, 1872

Distribution — Early Miocene-Recent (Hemingfordian-Recent) of North America; Late Miocene-Recent (Huayquerian-Recent) of South America.

Diagnosis — Primitive Procyoninae are distinguished from primitive Potosinae in having M1 with a more posteriorly situated hypocone, M1 with a better developed metaconule, and bulla with a more inflated entotympanic. The extinct South American procyonines of the *Cyonasua* group share with the

extant *Nasua*, *Nasuella*, and *Procyon* the following characters: m1 with an entoconulid and a low trigonid with paraconid and metaconid close together; m2 with entoconid, a postero-lingual hypoconulid forming a heel, and a reduced anterior shelf; P4 with enlarged protocone and parastyle and with shortened metaconid blade; and M2 with broadened protocone.

Comment — Gill (1872) established this subfamily solely for *Procyon*, with *Nasua* placed in its own procyonid subfamily, and *Potos* and *Bassariscus* in own families. The Procyoninae was later expanded to include many more genera (e.g., Simpson, 1945).

CYONASUA GROUP Patterson & Pascual, 1968

Diagnosis — Medium to very large-sized procyonids with a shortened rostrum (relative to *Procyon*) and deep mandible, I3 enlarged, P4 triangular with hypocone absent and with reduced to absent parastyle and reduced metacone (=metastyle), M1 and M2 with greatly reduced to absent hypocone, and m1 with a complex paraconid except in the most primitive species.

Comments — Patterson & Pascual (1968) coined the term *Cyonasua* group for the endemic South American Late Miocene to Middle Pleistocene (Huayquarian to Ensenadan Ages) procyonids. From the late 19th into the 21st century the systematics of this group has been contentious. The two most important 20th century works describing and illustrating the members of the *Cyonasua* group are Kraglievich & Reig (1954) and Kraglievich & Olazábal (1959). Berta & Marshall (1978) provided a useful summary of the synonymies and references concerning South American fossil procyonids up to that time. In the 21st century, Argentinian paleontologists have greatly increased our knowledge of this group. Prevosti & Forasiepi (2018) includes the most comprehensive review of South American fossil procyonids to date and should be consulted for further information. *Cyonasua argentina* was the first member of this group to be described (F. Ameghino, 1885). F. Ameghino noted the similarity of *Cyonasua* to *Nasua*, the coatimundi. F. Ameghino (1891) synonymized *Amphinasua brevirostris* (Moreno & Mercerat, 1891) with *C. argentina*, but later (1906) considered *Cyonasua*, *Amphinasua*, and *Pachynasua* (F. Ameghino, 1904) distinct genera from different time periods forming a lineage to *Ailurus*, the red panda. C. Ameghino & Kraglievich (1925) placed their new genus *Brachynasua* in the Potosinae. *Cyonasua* was recognized as the senior synonym of *Amphinasua* and *Pachynasua* (Riggs &

Patterson, 1939; Kraglievich & Reig, 1954; Kraglievich & Olazábal, 1959). Kraglievich & Olazábal (1959) determined that the bear-sized *Chapalmalania* (F. Ameghino, 1908a) was a procyonid (rather than an ursid) that was very closely related to *Cyonasua*. Berman (1994) added *Brachynasua* to the junior synonyms of *Cyonasua*. Baskin (2003, 2004) retained four genera in this group, with *Cyonasua* the primitive sister taxon of *Amphinasua*, *Brachynasua* and *Chapalmalania*. Others (e.g., Berman, 1994; L. Soibelzon & Prevosti, 2007; J. Tarquini et al., 2018) recognized only two valid genera: *Cyonasua* with at least eight valid species (*C. argentina*, *C. brevisrostris*, *C. longirostris*, *C. clausa*, *C. pascuali*, *C. groeberi*, *C. lutaria*, and *C. meranii*) and *Chapalmalania*, with two, *Ch. ortognatha* and *Ch. altaefrontis*. Prevosti & Forasiepi (2018) included seven species in *Cyonasua*, with *C. longirostris* a junior synonym of *C. brevisrostris*. L. Soibelzon, (2011, fig. 1) displayed the temporal distribution of these taxa. We recognize those species assigned to *Cyonasua* as belonging to *Cyonasua*, *Amphinasua*, and *Brachynasua*.

CYONASUA F. Ameghino, 1885

Type species — *Cyonasua argentina* F. Ameghino, 1885, p. 17

Holotype — MLP 10-171, left mandible with a broken canine and p2-p3; MLP 69-XII-14-1, anterior mandible with p4 (L. Soibelzon, & Bond, 2013, figs. 2.1, 2.2).

Type locality — Lower Member of the Ituzaingó Formation (Late Miocene; traditionally known as “Mesopotamiense” or “Conglomerado osífero”; Brunetto et al. 2013), Barrancas del río Paraná, Department of Paraná, Entre Ríos Province (Cione et al., 2000; L. Soibelzon, & Bond, 2013). The fossil mammals of the Conglomerado osífero are the basis for the Piso Mesopotamiense (Ameghino, 1883). Cione et al. (2000) assigned the “Mesopotamiense” to the Huayquerian Age. Schmidt et al. (2020) further discussed the different interpretations of the age of the “Mesopotamiense.” Sr-isotope dates of 11.9 to 6.00 Ma for the underlying Paraná Formation set a maximum age for the Ituzaingó Formation (del Río et al., 2018; Schmidt et al., 2020).

Diagnosis — The most primitive genus of the *Cyonasua* group. Medium-sized procyonid with paraconid of m1 simple, conical; p1 present; p2-p4 with poorly-developed posterior accessory cusps.

Distribution — *Cyonasua* (*sensu* Kraglievich & Reig, 1954)

is well represented in the Late Miocene to Pliocene of Argentina (e. g., Berta & Marshall, 1978; Berman, 1994; J. Tarquini et al. 2016). Elsewhere it is known from the Late Pliocene of Venezuela (Forasiepi et al., 2014), Late Miocene of Uruguay (L. Soibelzon, et al., 2019), Late Miocene of Bolivia (L. Soibelzon, et al., 2020), and Late Miocene of Peru (J. Tarquini et al., 2020). Huayquerian, Montehermosan, and Chapadmalan Ages.

Comments — F. Ameghino (1885) distinguished *Cyonasua* from *Nasua* and provided measurements of the type material. While this material was sufficient to diagnose the genus, it is insufficient to determine if any of the other nominate species of *Cyonasua* are junior synonyms of the genotype. However, *C. argentina* has only been recorded with certainty in the “Mesopotamiense” (L. Soibelzon, & Bond, 2013). MACN-A-53-6 is a mandible fragment with m1, m2 of *Cyonasua* from Paraná. The m1 has “V”-shaped trigonid, the paraconid is a simple cuspid, and the entoconid prominent (Kraglievich & Reig, 1954, fig. 4). This can be used to diagnose the species. Although the illustration makes the m1 appear smaller than the other specimens, the m1 lengths are similar (Kraglievich & Reig, 1954, unnumbered table). Other specimens of *C. argentina* from Catamarca Province (Kraglievich & Reig, 1954; Kraglievich & Olazabel, 1959) are discussed below.

AMPHINASUA Moreno & Mercerat, 1891

Type species — *Amphinasua brevisrostris* Moreno & Mercerat, 1891:235.

Included species — *Amphinasua brevisrostris*, *A. clausa*, *A. lutaria*, *A. groeberi*, *A. pascuali*.

Diagnosis — Medium- to large-sized procyonids with paraconid of m1 complex as result of the development of at least a lingual crest of the paraconid; paracone of m1 situated anterolingually. Characters of the skull and upper dentition are discussed with *Amphinasua brevisrostris*. An m1 with a complex paraconid also characterizes *Chapalmalania* (Kraglievich & Reig, 1954; Kraglievich & Olazabel, 1959).

Amphinasua brevisrostris Moreno & Mercerat, 1891

Holotype — MLP 10-52.

Type locality — “bajo de Andalhualá” near Valle Santa María, Catamarca Province.

Additional material — MACN 8209, holotype of *Amphinasua*

longirostris Rovereto, 1914, p. 81; MACN 8210, holotype of *Pachynasua? robusta* Rovereto, 1914, p. 82.

Diagnosis — Medium-sized procyonid with m1 paraconid situated antero-lingually close to the metaconid and with a low crest extending postero-lingually; I3 much larger than I1 or I2; P1/p1 reduced to absent; P4 with a low protocone directly opposite the subcentral paracone, which is flanked by a very small parastyle and metacone; M1 with hypocone very reduced to absent; M2 relatively small; cranium with expanded frontal sinuses.

Distribution — Andalhuala and Chiquimil Formations, Catamarca Province, Huayquerian Age.

Descriptions — The holotype of *Amphinasua brevirostris* is a skull with a damaged rostral region (Moreno & Mercerat, 1891, Lamina IX; Reguero & Candela 2011, fig. 4). The P1 is small; P2 and P3 are simplified, lacking accessory cusps; P4 is triangular, with the paracone situated subcentrally on the buccal margin opposite a low protocone, a very small metacone, that is shorter than the parastyle, and no hypocone; M1 with buccal cingulum absent and a narrow posterolingual hypoconal shelf; M2 triangular, with a relatively prominent posterolingual hypoconal shelf.

The holotype of *Amphinasua longirostris* is a skull with two hemimandibles (Rovereto, 1914, plate VII, figs. 5, 5a, 5b). It has P1 small, P2/p2 and P3/p3 without accessory cusps, and m1 paraconid antero-medial, with a low postero-lingual extension (see Foresiepi et al., 2014, fig. 2D). Baskin (2004) interpreted this as a paraconid with a lingual extension from an illustration of the m1 (Kraglievich & Reig, 1954, fig. 4 A) and from a poor-quality plaster cast (UCMP 38435). The holotype of *Pachynasua? robusta* is an anterior mandible with c1, p3, p4 (Rovereto, 1914, plate VII, figs. 6a). The mandible is deep, the canine is broken, p1 is absent, and the worn p3 and p4 do not have accessory cusps.

Comments — The holotypes of *Amphinasua brevirostris*, *A. longirostris*, and *Pachynasua? robusta* are from unknown levels of the Andalhuala Formation, Valle de Santa María, Catamarca Province. Although there are morphological differences between the first two (Foresiepi et al., 2014) and the third consists of a worn, anterior dentition “without any systematic value” (Soibelozon et al. (2019, p. 368), we follow Kraglievich & Reig (1954) in synonymizing the three.

Moreno & Mercerat (1891) compared *Amphinasua brevirostris* favorably to *Cyonasua* and *Nasua*. F. Ameghino (1891, p. 204–207) synonymized *A. brevirostris* with *C. argentina*. He

illustrated the skull of *A. brevirostris* with a hemimandible attributed to *C. argentina* from Paraná (F. Ameghino, 1891, fig. 76). To the best of our knowledge, the provenance of that jaw has not been published. Ameghino emphasized that *Cyonasua* had the four premolars and two molars of procyonids rather than three premolars and three molars used in the descriptions of *A. brevirostris*. Mercerat (1895) defended the distinctness of the two genera, having previously noted *Amphinasua* was most similar to *Nasua* and that an antiquated tooth numbering system was used for the cheek teeth.

Forasiepi et al (2014) constructed a data matrix with 78 characters based on Ahrens (2012) with the addition of members of the *Cyonasua* group. *Cyonasua brevirostris* and *C. longiramus* (represented by the type specimens) have a deep zygomaticus muscle fossa in orbital wall (derived) relative to its absence in *Chapalmalania altaefrontis*. The P4 hypocone is present (scored as derived) in *A. longirostris* and absent (scored as primitive) in *A. brevirostris*, the only difference of these sister taxa. The m1 paraconid of *A. longirostris* is scored as not divided.

Amphinasua clausa (F. Ameghino, 1904 p. 268)

Holotype — MACN 7955. Mandible with left i1, i3 c1, p2–m2; right i2, i3, p3–m2 described as *Pachynasua clausa*, new genus and species (F. Ameghino, 1904). Figure in Rovereto (1914, fig. 67). Measurements in Sobelzon et al. (2020, table 1).

Type locality — “Farola Monte Hermoso”, Buenos Aires Province, Argentina, the type locality of the Monte Hermoso Formation. L. Soibelzon, (2011) described eight deciduous teeth of *Cyonasua* sp. collected by Sergio Bogan from the ‘Miembro de las Limolitas claras’ of the Monte Hermoso Formation, close to the site where MACN 7955 was found. The Miembro de las Limolitas claras had been assigned to the Chapadmalalan Age (Cione & Tonni, 1996). Tomassini et al. (2013) assigned *Amphinasua clausa* to the *Eumysops laeviplicatus* Zone, the only biozone of the Montehermosan Age. The Montehermosan is Early Pliocene, 4.7–3.7 Ma (Prevosti et al., 2021).

Description — MACN 7955 is from an old individual with a very worn dentition, such that the cusp patterns are not visible (Rovereto, 1914, fig. 67). The p1 alveolus is very small. The p2 and p3 are crowded and set at an angle. *Amphinasua clausa* is similar in size to *A. groeberi* and *A.*

brevirostris. The offset and overlapping p2 and p3 are similar to those of *A. lutaria* (Cabrera, 1936) which is smaller and lacks p1.

Comment — Because the dentition is so worn, *Cyonasua clausa* has been considered *Cyonasua incertae sedis* (Kraglievich & Reig, 1954) and “without any systematic value” (Soibelzon et al., 2019, p. 368). However, the holotype of *Amphinasua clausa* is at least as informative as the holotype of *Cyonasua argentina*.

Amphinasua lutaria (Cabrera, 1936, p. 304)

Holotype — MLP 34-VI-20-6, left premaxilla and maxilla with i3-m2; left and right mandible with i1-m2; right tibia and fibula (Tarquini, 2018). It was described as a new species of *Pachynasua* and later transferred to *Cyonasua* (Kraglievich & Reig, 1954).

Type locality — Atlantic coast of Miramar, *Paraglyptodon chapadmalensis* biozone of the Chapadmalal “formation”, Buenos Aires Province (Cione & Tonni, 1995; Cenizo et al., 2016).

Description — P1/p1 absent; P4 with small parastyle and larger metacone flanking the prominent paracone, small twinned cuspules posterolingually placed to the protocone; M1 with a reduced lingual cingulum and a small parastyle; lower premolars with prominent posterior accessory cuspids; p2 and p3 crowded and offset in the mandible, and m1 with a complex paraconid (Prevosti & Reguero, 2000, fig. b, c; Forasiepi et al., 2014, fig. 4a, c; Engelman & Croft, 2019, figs. 3A, 4A).

Amphinasua groeberi (Kraglievich & Reig, 1954, p. 217)

Holotype — MMP S-645, left mandible with p2-m2 and anterior right mandible c1, p2, and partial p3. Described as *Cyonasua groeberi* (Kraglievich & Reig, 1954).

Type locality — Tuclame Quarry, La Playa Formation of Córdoba Province, Huayquerian–Montehermosian in age (Bondesio & Pascual, 1981) or younger (Deschamps et al., 2013).

Description — The p1 alveolus is for a small, single-rooted tooth. The premolars are wider posteriorly. The p3 and p4 possess well-developed anterior and posterior accessory cuspids. The m1 has a complex paraconid. (Kraglievich & Reig, 1954, figs. 1-3, 4D).

Amphinasua pascuali (Linares, 1982, p. 118)

Figure 2

Holotype — AMNH F:AM 45985, right mandible with p2-m2. Described as *Cyonasua pascuali* (Linares, 1982, figs. 3, 4c; L. Soibelzon, 2020, fig. 4) from the Huayquerías Formation, Mendoza Province is Huayquerian in age, greater than 5.8 Ma (Marshall, 1985). *Amphinasua* cf. *pascuali* has been reported from the Huauquerian Tariquía Formation of Bolivia (L. Soibelzon, et al., 2020).

Referred specimens — AMNH F:AM 45984, left mandible with p2 and broken dentition, possibly from the same individual as AMNH F:AM 45985; AMNH F:AM 45986, right mandible with broken p3, and complete p4-m2.

Type locality — San Carlos, Mendoza, Huayquerías Formation.

Description and Comparison — AMNH F:AM 45985 is significantly smaller than the holotypes of other species of *Cyonasua*. There is no alveolus for a p1. The posterior accessory cusp is absent on p2, weakly developed on p3, and better developed on p4. The p4 has a very small anterior accessory cusp. The premolars are not expanded posterolingually. The m1 has a small antero-lingually situated paraconid with a prominent lingual extension. In the m1 talonid, the hypoconid is the most prominent cusp, followed by the entoconid (identified by Linares, 1982, as the entoconulid), and a smaller hypoconulid. The m2 metaconid is situated distinctly posterior to the protoconid and the protoconid is separated from the hypoconid by a V-shaped notch, and the hypoconulid is situated postero-centrally.

AMNH F:AM 45986 is larger than AMNH F:AM 45985, with a p2-m1 length similar to *Cyonasua lutaria* but with a longer m1 and a longer m2 (Table 1). The p4 length and width are similar to the holotype of *Cyonasua argentina*. The p4 lacks an anterior accessory cusp. The m1 has a better developed antero-internal cingulum of the paraconid than AMNH F:AM 45985; the hypoconid is the largest cusp of the talonid; and the entoconid is connected anteriorly to a small entoconulid and posteriorly to a small hypoconulid. The m2 metaconid is situated almost opposite the protoconid; the protoconid and hypoconid are connected by a narrow ridge; and the hypoconulid is situated postero-lingually.

Causes of Variation

Rodríguez et al. (2016) have pointed out that for *Cyonasua*



FIGURE 2. *Amphinasua pascuali* from San Carlos, Mendoza, Argentina, Huayquerias Formation. A-C. AMNH F:AM 45985, right hemimandible in buccal (A), lingual (B), and occlusal (C) views; D. AMNH F:AM 45984, left hemimandible with p2 and broken dentition in buccal (D), lingual I, and occlusal (F) views; G-I. AMNH F:AM 45986, right hemimandible from Mendoza in buccal (G), lingual (H), and occlusal (I) views.

(*sensu lato*) a “large number of taxa have been described for a relatively short time span, collected from a restricted geographical area, and based on badly preserved specimens raises reasonable doubt about the validity of these taxa.” They proposed that

sexual dimorphism was a factor for some of these differences. Males of *Nasua* are consistently larger than females (Decker, 1991). Adult males of *Bassariscus astutus* were significantly larger than females for 12 of 17 cranial and dental measurements

TABLE 1. Measurements (mm) of AMNH 45986; the holotypes of *Cyonasua pascuali* (AMNH F:AM 45985), *C. argentina* (MLP 69-XII-14-1), *C. longirostris* (MACN 8209), *C. lutaria* (MLP 34-VI-20-6), *C. clausa* (MACN 7955), and *C. groeberi* (MMMP S-645), data from Soibelzon et al., (2020); *A. brevisrostris* (FMNH P14342 and P14397); and *C. argentina* (MACN 6689, 13284), and *C. cf. argentina* (MACN 6692) from the “Araucanense” of Catamarca Province as identified in Kraglievich and Reig (1954)

	p4L	p4W	p4W/p4L	m1L	m1W	m2L	m2W	p2m2	p4L/m1L	m2L/m1L
AMNH F:AM 45986	9.6	6.2	0.64	12.1	7.3	9.6	5.9	43.0	0.79	0.79
<i>C. pascuali</i>	7.1	4.0	0.56	8.9	4.8	7.0	3.9	34.0	0.80	0.79
<i>C. argentina</i>	9.5	6.0	0.63							
<i>C. longirostris</i>				12.5	7.1	9.8	5.6	47.8		0.78
<i>C. lutaria</i>	9.5	5.4	0.57	10.8	6.0	8.4	5.4	43.0	0.88	0.78
<i>C. clausa</i>	9.8	6.9	0.70	12.5	7.2	8.6		49.0	0.77	0.69
<i>C. groeberi</i>	10.8	7.6	0.70	12.2	7.7	8.7	6.0	48.5	0.89	0.71
FMNH P14342	9.2	6.4	0.70	11.3	6.6	9.9	4.9	48.0	0.81	0.88
FMNH P14397	11.0	6.0	0.55	12.2	7.0	9.6	5.3	48.2	0.90	0.79
MACN 6689	9.1			10.7		8.8		45.0	0.85	0.82
MACN 13284	9.2	5.8	0.63					42.0		
MACN 6692	9.3	6.1	0.66	11.6	6.5	9.5	5.0	44.5	0.80	0.83

(Stangl et al., 2014). The 52% body size difference in two specimens of the ailurid *Pristinailurus bristoli* from the Hemphillian Gray Fossil Site in Tennessee is most plausibly explained by sexual dimorphism (Fulwood & Wallace, 2015). The borophagine canid *Epicyon saevus* from the late Clarendonian of Florida varies in the development of accessory cusps and size of the lower premolars (Baskin, 1998a). The following are examples where further research is needed to determine whether size (Table 1) and/or morphological differences may represent different, possibly new, species or are evidence of individual variation or sexual dimorphism.

Linares (1982) did not include AMNH F:AM 45986 in the hypodigm of *Cyonasua pascuali* or discuss it in his paper. The catalogue label from AMNH states it came from the locality of San Carlos (Mendoza). Although AMNH F:AM 45986 has a 34% greater m1 length and a 26% greater p2-m2 length than AMNH F:AM 45985, the width to length proportions for the p4, for the m1, and for the m2, respectively, are similar.

Two species of *Cyonasua* were presumed present in the “Araucanense” of Catamarca Province (Kraglievich & Reig, 1954; Kraglievich & Olazabel, 1959). *Cyonasua argentina*, the smaller of the two (Table 1), has a lower horizontal ramus, more complicated premolars, m1 with a simple conical paraconid and talonid without well-defined cuspids on the margins, and m2 proportionally well-developed. MACN 6692,

illustrated by F. Ameghino (1906, fig. 259) as *Amphinasua brevisrostris*, was reidentified as *Cyonasua cf. argentina* by Kraglievich & Reig (1954). *Cyonasua brevisrostris* (represented by the holotype of *Amphinasua longirostris*) is larger with simpler premolars; m1 with paraconid formed by two to three cusps, metaconid more reduced, the talonid postero-lingual border with an entoconid and hypoconulid; and m2 tending to be proportionately reduced in size (Kraglievich & Reig, 1954, p. 224, fig. 4A). These differences may be of taxonomic significance or may represent individual variation or sexual dimorphism within *Amphinasua brevisrostris*.

Both *Amphinasua clausa* (F. Ameghino, 1904) and *A. lutaria* (Cabrera, 1936) were first assigned to *Pachynasua*. Both have premolars that are offset. *Amphinasua clausa* is 14% larger than *A. lutaria*. *Amphinasua lutaria* lacks p1 and there are no gaps between the premolars. The stratigraphic ranges of *Amphinasua clausa* and *A. lutaria* may have overlapped (L. Soibelzon, 2011, fig. 1b).

Problematic Taxon Names

Parahyaenodon argentinus (F. Ameghino, 1904, p. 266) and *Tetraprothomo argentinus* (F. Ameghino, 1908b) are from unknown levels of the Monte Hermoso Formation (Tomassini et al., 2013). *Parahyaenodon argentinus* is a procyonid allied to *Cyonasua*, not a metatherian borhyaenid carnivore

(Forasiepi et al., 2007). The holotype of *Tetraprothomo* is a procyonid femur (Bordas, 1942; Forasiepi et al., 2007). Examples of *Cyonasua* recorded as *Cyonasua* sp., with little or no further information, make it difficult to determine anything further.

The holotype and only specimen of *Oligobunis argentinus* is an anterior mandible fragment with i3, c1, p2-p3 (Burmeister, 1891, p. 378, plate VII, fig. 2; L. Soibelzon, & Bond 2013, fig. 2.3). It is from Ituzaingó Formation at Barrancas del río Paraná, Entre Ríos Province (L. Soibelzon, & Bond, 2013), the same general locality as the holotype of *Cyonasua argentina*. Burmeister (1891) named his species *Oligobunis argentina* but labeled the figure caption (Burmeister, 1891, p. 400) *Oligodens argentinus*. He compared his specimen favorably to the North American *Oligobunis crassivultus* (Cope, 1881). Cope considered his species a canid and had initially assigned it to *Icticyon*. *Icticyon* is a junior synonym of *Speothos*, the hypercarnivorous Latin American bush dog. However, *Oligobunis crassivultus* is an oligobunine mustelid (Valenciano et al., 2016). Ameghino (1891) recognized Burmeister's species as a junior synonym of his *Cyonasua argentina*. Later work which distinguished the two referred to it as *C. argentinus*. Its provenance suggests it is *C. cf. argentina*.

MACN-PV 6229 is an incomplete skull, mandible with canine and molars, and astragalus (Kraglievich & Olazábal 1959; J. Tarquini et al., 2018) from the Huayquerian, Epecuén Formation, La Pampa province, Argentina (Tonni et al., 1992). One of us (JB) made brief observations of it and other specimens at the MACN. It has the m1 (Kraglievich & Reig, 1954, fig. 4E) paraconid smaller and lower than the metaconid. The paraconid and metaconid are close together almost closing off the trigonid. The paraconid has a slightly more lingual, very small accessory cuspid. And very close to the slightly smaller and lower metaconid. In a footnote, Kraglievich & Olazábal (1959, p. 39) suggested it might be a new species. Zetti (1972) proposed a name in his dissertation, but never published it (J. Tarquini et al., 2020). Because m1 lacks a prominent cingulid extending from the paraconid, it is tentatively referred to *C. cf. argentina*.

BRACHYNASUA C. Ameghino & Kraglievich, 1925

Type and only species — *Brachynasua meranii* C. Ameghino & Kraglievich, 1925.

Diagnosis — A procyonid of the size of *A. pascuali*; very

short rostrum, P1/p1 absent; no postcanine diastema; P2/p2 anterior root offset; P4 with virtually no parastyle anterior to the paracone, the metacone is a small, very low cusp, the protocone is low, and the tooth is relatively wide posterobuccally; and the M1 has no paraconule or metaconule, the paracone is larger than the metacone, both lingual and buccal cingula are present, and the lingualcingulum is slightly expanded posterolingually; M2 very small to absent (Zetti, 1966).

Distribution — “las toscas del Río de La Plata” (E. Soibelzon et al. 2008), Buenos Aires Province. Ensenadan Age (middle Pleistocene).

Comment — The illustrated holotype lacks the M1 (C. Ameghino & Kraglievich, 1925, p. 185). However, an M1, probably collected at a later date, is present in the specimen (Kraglievich & Olazábal, 1959). *Brachynasua* has many features that are convergent with *Potos* which led C. Ameghino & Kraglievich assigning it to the Potosinae. Kraglievich & Olazábal (1959) stated that *Brachynasua* was likely more closely related to *Procyon* than to *Potos*. The fossil record shows that these features developed independently and much earlier in the North American lineage that gave rise to *Potos* and possibly *Bassaricyon* (Baskin, 2003).

CHAPALMALANIA F. Ameghino, 1908a

Type species — *Chapalmalania ortognatha* F. Ameghino, 1908a, p. 424.

Included species — *Chapalmalania ortognatha* F. Ameghino, 1908a; *Ch. altaefrontis* Kraglievich & Olazábal, 1959.

Distribution — Buenos Aires Province, Mendoza Province, and Catamarca Province, Argentina; Ware Formation, Colombia; and San Gregorio Formation, Venezuela. Late Pliocene (Chapadmalalan to Marplatan Ages).

Diagnosis — A bear-sized procyonid, with a short, broad rostrum and a high skull; P1/p1 present; P1-P3 offset, expanded transversely; P4 with a well-developed buccal cingulum and with very low parastyle and metacone. M1 without a hypocone, but with well-developed lingual and buccal cingula and the paracone and metacone are close together. The M2 is a relatively small, transversely elongated tooth. The p1 alveolus is small. The m1 with bifid paraconid and reduced metaconid.

Comment — F. Ameghino (1908a) created the Piso Chapalmalense for the fauna collected from the coastal cliffs between Mar del Plata and Miramar in Buenos Aires Province.

Kraglievich (1952) named this unit the Chapadmalal Formation. The fauna of this unit, including *Chapalmalania ortognatha*, defined the Chapadmalalense (Chapadmalalan in English) Age (Cione & Tonni, 1996; Tonni, 2009). Since the mid 1990's some references to *Chapalmalania* have spelled it *Chapadmalania*. According to the rules of the International Commission on Zoological Nomenclature (ICZN, 1999), "The original spelling of a name is the "correct original spelling", unless it is demonstrably incorrect" (Article 32.2), such as "an inadvertent error, such as a lapsus calami or a copyist's or printer's error" (Article 32.5).

Discussion — *Chapalmalania* is known exclusively from cranial and dental remains, the postcranial skeleton is unknown (J. Tarquini et al., 2018). The type specimen of *Chapalmalania ortognatha* is an anterior rostrum with incisors and a canine (F. Ameghino, 1908a; Kraglievich & Olazábal, 1959, fig. 3a; Agnolín, 2022, fig. 1A) that Ameghino thought was from a giant short-faced bear. The type specimen is from the Chapadmalal Formation, Buenos Aires Province, Argentina, and is 'probably no older than 2.8 Ma' (Marshall et al., 1986, p. 456). A P4 of *Chapalmalania* cf. *ortognatha* (Kraglievich & Olazábal, 1959, fig. 4) is from the Chapadmalal Formation or from the Uquian (=Marplatan) Age Barranca de los Lobos Formation (Marshall et al., 1986). There is an undescribed, but illustrated, skull of *Ch. ortognatha* from the Chapadmalal Formation (Berman, 1994; Prevosti et al., 2013, fig. 4j). Berman (1993) noted a mandible of *Ch. ortognatha* from the Vorohué Formation (Marplatan Age) in the Miramar region, that he discussed in detail in his dissertation (Berman, 1994).

The larger *Ch. altaefrontis* is based on a partial skull from the Tunuyán Formation, Mendoza Province (Kraglievich & Olazábal, 1959). It was initially considered Montehermosan in age (Kraglievich & Olazábal, 1959). Marshall (1985; et al., 1986) interpreted this specimen came from between two tuffs, dated at 2.4 and 2.6 Ma. Yrigoyen (1994) regarded that this specimen came from approximately 180 m below the lower tuff, and to be probably older than 3.8 Ma, but Chapadmalalan in age. North of Argentina, *Chapalmalania* sp. occurs in the Late Pliocene San Gregorio Formation, Venezuela (Carrillo-Briceño et al., 2021) and Late Pliocene Ware Formation, Colombia (Forasiepi et al. 2014).

Berman (1994) suggested that *Chapalmalania* could be seen as a scavenger. De los Reyes et al. (2013) described a skull of a glyptodont from sediments in Buenos Aires Province that are Chapadmalalan or younger in age that had bite marks that

correspond to the dentition of *Chapalmalania* sp. They inferred that *Chapalmalania* was an omnivore with hyena-like scavenger habits.

Procyonids with a North and South American Fossil Record

PROCYON Storr, 1780

Fossil Distribution — late Hemphillian to Rancholabrean of United States of America; Rancholabrean of Canada; Irvingtonian and Rancholabrean of Mexico; Lujanian of Argentina (L. Soibelzon et al., 2010); Pleistocene of Brazil (Rodriguez et al., 2013); and Marplatan? of Venezuela (Ruiz-Ramoni et al., 2018). See Prevosti & Forasiepi (2018) for complete information.

Diagnosis — Rostrum of skull not greatly elongate; P2-3/p2-3 tall, anterioposteriorly compressed; P4 subquadrate, with prominent hypocone and parastyle; M1 with prominent metaconule posterior to protocone; m1 with closed trigonid; angular process of dentary above level of tooth row.

NASUA Storr, 1780

Fossil Distribution — late Hemphillian (Latest Miocene) to Rancholabrean of United States of America; Marplatan? of Venezuela (Ruiz-Ramoni et al., 2018); Late Pleistocene (Lujanian?), Brazil (Rodrigues et al., 2014); Middle Pleistocene, (?Ensenadan), Bolivia (Berta & Marshall, 1978). Prevosti & Forasiepi (2018) conclude that earliest South American record of *Nasua* is Late Pleistocene.

Diagnosis — Cranium with elongate and laterally compressed rostrum; Canines compressed, upper canines buccally laterally flared; P1 two-rooted; P4 subquadrate, with prominent hypocone and parastyle; M1 with prominent metaconule posterior to protocone; m1 with closed trigonid; angular process of dentary above level of tooth row.

PROCYONIDAE AND THE GREAT AMERICAN BIOTIC INTERCHANGE

First Appearances of members of the *Cyonasua* group

Procyonids, the first placental carnivorans in South America, dispersed across a narrowed seaway between Panama and Colombia as heralds of the GABI (Patterson & Pascual, 1968; Simpson, 1980; Webb, 1985; Woodburne et al., 2006; Cione et

al., 2015). Their oldest records are from the Huayquarian Age in Argentina (Prevosti et al., 2021). In 1926, Elmer Riggs led a paleontological expedition for the Field Museum of Chicago to Catamarca Province, Argentina (Riggs & Patterson, 1939; Butler et al., 1984). There they made extensive collections of fossils from the “Araucanense”, including, most famously, the saber-toothed marsupial *Thylacosmilus atrox* (Riggs, 1934) and a nearly complete skeleton of the “terror-bird” *Andalgalornis ferox* (Patterson & Kraglievich, 1960; Marshall, 1978). The procyonids they collected were only briefly mentioned (Riggs & Patterson, 1939) and it wasn’t until radiometric and paleomagnetic dating assigned absolute ages to them that their significance was recognized (Marshall et al., 1979).

FMNH P14342 and P14537 were collected from units XVIIIa and XIX, respectively, of the Chiquimil Formation near Chiquimil (Entre Ríos), in the Valle de Santa María, (Marshall et al., 1979). Reguero & Candela (2011) reported FMNH P14342 and P14537 (nec P14357) were from a few meters above the base of the Andalhuala Formation at Chiquimil. They are instead from the El Jarillal Member, the uppermost member of the Chiquimil Formation (Esteban et al., 2014; Prevosti et al., 2021). They were initially assigned an average age date of 6.02 Ma (Marshall et al., 1979; Butler et al., 1984). The radiometric dates have been revised to 7.31-7.14 Ma, making them the oldest securely dated procyonids in South America (Esteban et al., 2014; Prevosti et al., 2021). These two are “morphologically similar and resemble *C. brevirostris*” (Tedford in Marshall et al., 1979, p. 275). In FMNH P14342 (Figure 3A-H), the dentition is moderately worn. The p2 and p3 do not have anterior and posterior accessory cuspids. The p4 has a lingually situated posterior accessory cuspid and a well-developed heel. The postero-lingual extension of the paraconid of the left m1 is expanded terminally into a smaller cusp. The trigonid of the right m1 is damaged. The talonid has an entoconid and entoconulid. The m2 is large, but not as large as m1. The forelimb was described by J. Tarquini et al. (2019).

In FMNH P14537 (Fig. 3 I-J; Hough, 1948, figs. 7, 8; Prevosti et al., 2013, fig. 4f-h), the teeth are heavily worn. P1/p1 are apparently absent, perhaps as a result of age. The worn and damaged P4 appears to be triangular in shape and lacking a hypocone. The premolars are separated by diastemata. Because of wear, it is not possible to determine the presence of accessory cusps.

FMNH P14451 and FMNH P14397 were collected at Puerta de Corral Quemado from two levels of the “Araucanense”

Formation (Butler et al., 1984), now the Andalhuala Formation (Reguero & Candela, 2011). Marshall et al. (1979) had wrongly assigned them to the younger Corral Quemado Formation (Butler et al., 1984). FMNH P14451, a lower jaw with deciduous dentition (Fig. 4), is from just above unit 14 of the Andalhuala Formation (Reguero & Candela, 2011) and has been age dated at 7.0 to 7.5 Ma (Butler et al., 1984), making it one of the oldest well-dated members of the *Cyonasua* group. This deciduous dentition is not further identifiable beyond *Cyonasua* sp. (Marshall et al., 1979). FMNH P14397 (Fig. 5) is from unit 16 or 17 of the Andalhuala Formation, age dated at 6.4 to 6.9 Ma (Marshall et al., 1979; Butler et al., 1984). The p1 alveolus is very small. The p2 has a weakly developed posterior accessory cuspid. The p4 anterior accessory cuspid is small; the prominent posterior accessory cuspid is situated postero-labial to the protoconid; and the talonid has two small cuspid on its posterior margin. The m1 protoconid is the most prominent cusp; the metaconid is lower than the protoconid; the hypoconid is the most prominent cusp of the talonid, entoconid and smaller entoconulid are distinct cuspid.

FMNH P14397 was described as having “a simple connate m1 paraconid rather than the more complex divided cuspid present in the type of *C. lutaria*” or the bifid m1 paraconid of *Amphinasua groeberi*; and in having “longer and more complex lower premolars bearing stronger anterior and posterior cuspid and having a shorter m2 than m1” (Marshall et al., 1979, p. 276). We interpret that the m1 paraconid is complex: the paraconid is a small cusp situated on the antero-medial flank of the protoconid at the front of the tooth. A low ridge extending posteriorly from it terminates in a lower cusp on the lingual margin; this extension of the paraconid is separated from the metaconid by a narrow gap. Although the anterior and posterior accessory cusps of p4 are prominent as in *Amphinasua groeberi*, the dimensions of the m1 and m2 are more similar to those of the type *Amphinasua longirostris* (Table 1). The complex m1 paraconid suggests assignment to *Amphinasua brevirostris*.

Other early examples of the *Cyonasua* group include *Amphinasua pascuali* (Linares, 1982), from the Huayquerias Formation, Mendoza Province, which is 5.8 Ma or older (Marshall et al., 1986). *Cyonasua* has been recorded from three localities of the Cerro Azul Formation, Salinas Grandes de Hidalgo, La Pampa Province (Goin et al., 2000; Romano et al., 2023). Salinas Grandes de Hidalgo has a median inferred age of 6.83 Ma (range 7.31-6.47 Ma); Quehué, 6.61 Ma (range



FIGURE 3. *Amphinasua brevirostris* from Valle de Santa María and Río Corral Quemado, Catamarca Province, Argentina. A-H. FMNH P14342. Fragmented skull, mandibles and postcranial skeleton. Skull in occlusal view (A), detail of the dentition in occlusal view (B), left humerus in cranial view (C), and right femur in cranial view (D); Right hemimandible with p2-m2 in buccal (E), lingual (F) and occlusal (G) views. Left hemimandibles with p4-m2 in occlusal view (H); I-J. FMNH P14537. Skull and mandible in lateral view (I), detail of the maxilla, note upper canines are reconstructed (J). Bar scales shared in (B, E-H, J), and (C, D, I).

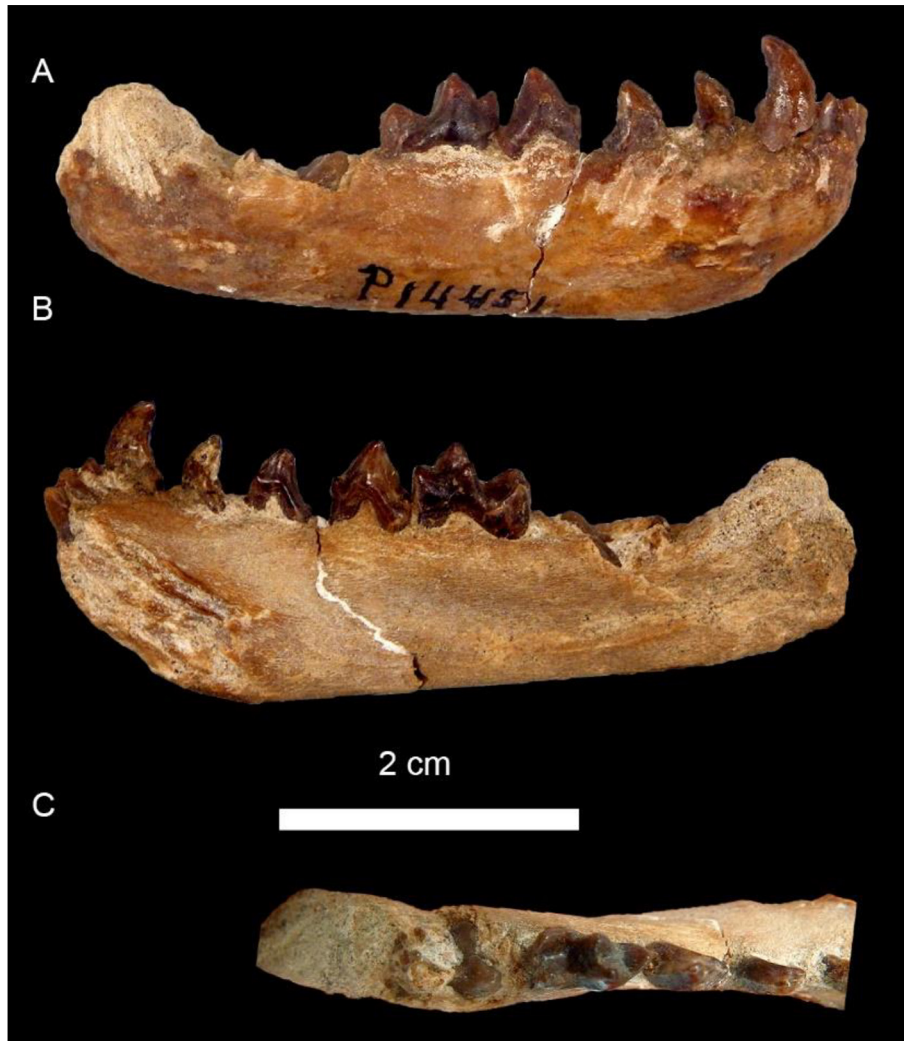


FIGURE 4, FMNH P14451, right hemimandible with deciduous dentition comprising dc, dp1-dp4 of *Cyonasua* sp. in buccal (A), lingual (B) and occlusal views (C).

7.05-6.32 Ma); and Telén, ca. 7.09 Ma (range 7.21-6.95 Ma) (Prevosti et al., 2021; Romano et al., 2023). Berman (1989) noted *Cyonasua* n. sp. from the Maimará Formation, Jujuy province. Although the specimen is currently lost, its estimated age is between c. 6.6 and c. 6.4 Ma (Candela et al., 2023). In Peru, postcranial elements of *Cyonasua* sp. from two levels in the Pisco Formation have been age dated at 6 to 7 Ma (J. Tarquini et al. (2020). L. Soibelzon, et al. (2019) accepted that 11-9 Ma was the best estimate available at the time for the Late Miocene Camacho Formation of Uruguay which has produced an m2 of *Cyonasua* sp. del Río et al. (2018) and del Río & Martínez (2021) assigned age dates of 7.20 Ma-6.92 Ma for the San Pedro Member of the Camacho Formation. This widespread distribution around 7 Ma suggests they may have

entered South America earlier in the Huayquerian. Those evidences clearly demonstrate that the *Cyonasua* group of procyonids preceded the entrance of other members of the Carnivora from North America to South America by approximately five million years (Fig. 1), as has been noted by many others beginning with Patterson & Pascual (1968).

FMNH P14401, a left mandible (Fig. 6) of *Chapalmalania* cf. *altaefrontis* (Kraglievich & Olazábal, 1959, fig. 11b; Prevosti et al., 2013, fig.4i), may represent the first occurrence of *Chapalmalania*. It was collected from the Corral Quemado Formation at Puerta de Corral Quemado Catamarca Province by the Riggs expedition (Riggs & Patterson, 1939; Marshall et al. 1979). It is presumably from level 21, which has been dated at 5.4-5.8 Ma (Butler et al., 1984), but according to Marshall



FIGURE 5. FMNH P14397, *Amphinasua brevirostris* from unit 16 or 17 of the Andalhuala Formation, in buccal (A), lingual (B) and occlusal views (C).

& Patterson (1981), could be as old as unit 15 (6.5 Ma) or as young as unit 32 (younger than 3.5 Ma). Reguero & Candela (2011) included *Chapalmalania* in the Andalhuala Formation Fauna of the Montehermosan to Chapadmalalan Ages. Accurately determined occurrences of *Chapalmalania* are limited to the Chapadmalalan with a possible younger occurrence in the Marplatan Age (L. Soibelzon, 2011, fig. 1; L. Soibelzon & Prevosti, 2012; Forasiepi et al., 2014).

Origin of the *Cyonasua* group

The *Cyonasua* group is not directly related to the extant procyonids. Baskin (1982, 2004) proposed a sister-group relationship for it and the North American Barstovian to Hemphillian Miocene *Arctonasua*. Forasiepi et al. (2014) strongly supported the monophyly of the *Cyonasua* group but

rejected a sister-group relationship of it with *Arctonasua*. The *Cyonasua* group and *Arctonasua* share nine possible synapomorphies (Baskin, 1982, 1989, 2004). *Arctonasua* differs from *Cyonasua* in having an elongate rostrum, P4 with a more anteriorly placed and larger protocone, upper molars with a better developed hypocone, m2 with the protoconid smaller than the metaconid, and a simple paraconid on m1, all primitive characters. *Cyonasua* may be derived from a taxon similar to the early Barstovian (ca. 16 Ma) *Arctonasua minima* (Baskin, 1982; Fig. 7). The P4 of *A. minima* has a greatly reduced hypocone, approaching the state of the *Cyonasua* group. However, in this species the P4 metacone is absent, an even more derived condition than in primitive *Amphinasua*. The m1 of *Arctonasua minima* is similar in size and morphology to that of FMNH P14397 from Catamarca (Fig.

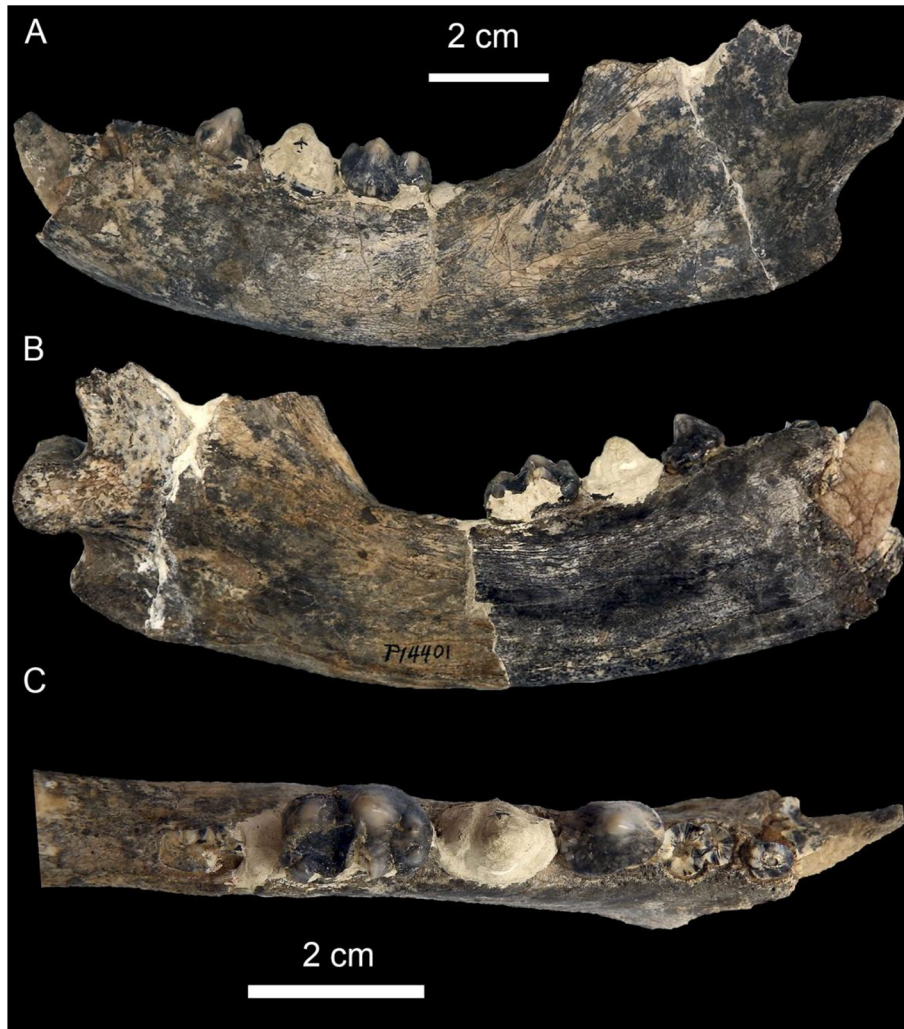


FIGURE 6. *Chapalmalania* cf. *altaefrontis* FMNH P14401; from Corral Quemado, level 2, Catamarca (Argentina), left mandible with fragmented c, complete p3, p4 (reconstructed) and fragmented m1, in buccal (A), lingual (B) and occlusal views (C) Scale bar is the same in A and B.

5). In FMNH P14397, the paraconid is somewhat more separated from the metaconid (but is situated mostly at the same level labial to the metaconid) and the entoconid and entoconulid are less bulbous than in *A. minima*. The mandible is much more massive.

Chapalmalania and *Amphinasua* share the unique morphology of the m1 paraconid (which is unknown in *Brachynasua*). C. Ameghino & Kraglievich (1925) suggested that *Brachynasua* was related to *Potos*. Kraglievich & Olazábal (1959, p. 45) concluded *Brachynasua* was more closely related to *Procyon*. Baskin (1990) suggested it was more closely related to *Cyonasua*. *Brachynasua* is interpreted to be the sister taxon of advanced *Amphinasua* such as *A. lutaria*, because of loss of P1/p1 and similar P4 and M1 morphology.

Chapalmalania is also similar to *Brachynasua* in having P4 with parastyle greatly reduced to absent. However, in *A. lutaria*, the parastyle is reduced, approaching the condition of *Brachynasua*. Linares (1982) stated that the Clarendonian (Late Miocene) *Protoprocyon* was ancestral *Cyonasua* group and to *Nasua*, *Procyon*, and *Bassaricyon*. However, in our opinion *Protoprocyon* is most closely related to *Paranasua*, *Nasua*, and *Procyon* (Figure 8) on the basis of the shared derived m2 morphology.

Morphological vs. molecular phylogenies of the Procyonidae

Decker & Wozencraft (1991) used 37 cranial characters, 14 dental characters, seven postcranial characters, and six soft tissue characters of extant procyonids to generate the following



FIGURE 7. *Arctonasua minima* from Observation Quarry, Dawes County, Nebraska, Olcott Formation equivalent, early Barstovian. A-C. AMNH F:AM 49116, left hemimandible with p2 and m1 in buccal (A), lingual (B), and occlusal (C) views; D. AMNH F:AM 25378, left m1 in occlusal view; E-F. AMNH F:AM 105249, left P4 in occlusal (E) and anterior (F) views; G. AMNH F:AM 61006a, left M1 in occlusal view.

tree: (*Potos-Bassaricyon*)-(*Bassariscus*-(*Procyon*-(*Nasua-Nasuella*))). Ahrens (2012) used 78 cranial and dental characters to develop similar trees supporting the homology of the morphological characters. In addition to dental characteristics (which may be the result of convergence for a frugivorous diet). Decker & Wozencraft (1991) used nine cranial synapomorphies to unite *Potos* and *Bassaricyon* in the Potosinae. Ahrens (2012) recognized eight unambiguous synapomorphies, including cranial characters, uniting *Potos* and *Bassaricyon* in the Potosinae. *Potos* is in many ways the most specialized of the procyonids, having New World primate post-cranial characters such as a prehensile tail (Ford & Hoffmann, 1988).

Baskin (1982) developed a phylogenetic tree based on dental characters of living and fossil procyonids: (*Potos*)-(*Bassariscus*-(*Cyonasua-Arctonasua*)-(*Bassaricyon*-(*Procyon*-(*Nasua-Nasuella*))). His 1989 and 1998b phylogenies omitted *Potos* and *Bassaricyon*, but were otherwise similar. Baskin (2004) added *Parapotos* (Baskin, 2003), *Bassaricyonoides* (Baskin, 2003), and *Bassaricyon* to the Potosinae and expanded the discussion of the sister-group relationship of *Arctonasua* and *Cyonasua* to include the other three genera of the *Cyonasua* group.

DNA phylogenies of extant procyonids produce different results from morphological ones. In them *Bassariscus* is the sister taxon of *Procyon*; *Bassaricyon* is the sister taxon of

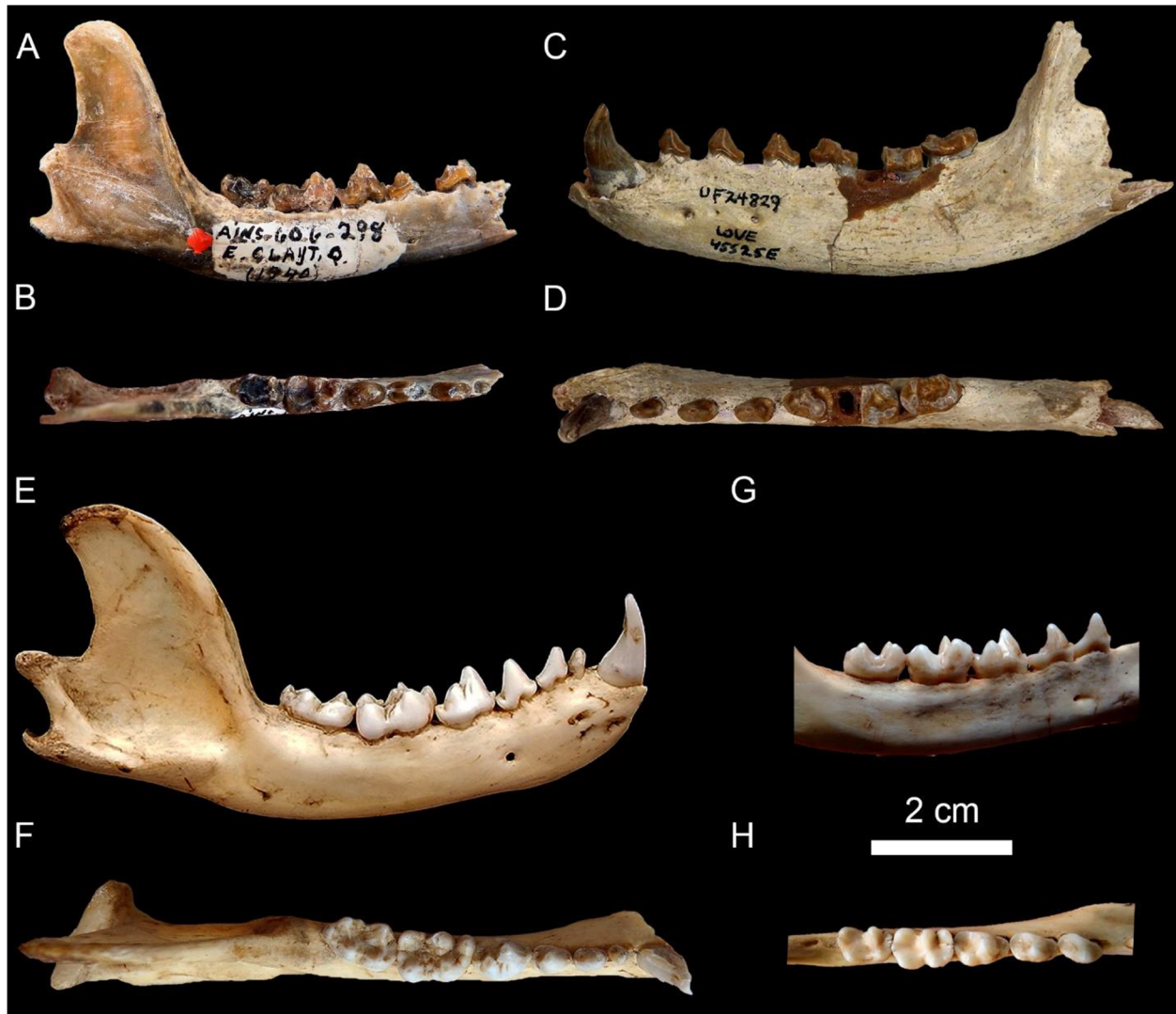


FIGURE 8. Mandibles of extinct and extant procyonids. A-B. *Protoprocyon savagei* AMNH F:AM 25210 (Holotype) from E. Clayton Quarry (Brown County, Nebraska, Early Clarendonian) in buccal (A), and occlusal (B) views; C-D. *Paranasua biradica* UF 24829 (Holotype) from Love Bone Bed (Alachua County, Florida, latest Clarendonian) in buccal (C), and occlusal (D) views; E-F. Extant *Procyon lotor* (raccoon) NRM-MA582011 in buccal, (E) and occlusal (F) views; G-H. Extant *Nasua nasua* (coati) NRM-MA585504, in buccal (G), and occlusal (H) views.

Nasua. These four genera are the sister-group of *Potos* (Fulton and Strobeck, 2007; Koepfli et al. 2007, 2017; Eizirik et al., 2010). According to Koepfli et al. (2017), similarities of dental characters, such as those uniting *Procyon* and *Nasua*, are not shared derived characters, but are caused by developmental genetic correlation. This caused the morphology-based phylogenies to differ from the molecular phylogeny. We cannot offer further evidence on which phylogenies may be more accurate and we agree “that a substantial portion of the procyonid fossil record may yet be uncovered” (Koepfli et al., 2017, p. 89). The molecular clock divergence between the *Nasua* and the

Bassaricyon lineages and the molecular clock divergence between the *Procyon* and the *Bassariscus* lineages averages 11-12 Ma; that between the (*Nasua-Bassaricyon*) and the (*Procyon-Bassariscus*) lineages averages 18-20 Ma; and that between *Potos* and the other procyonids is in the Early Miocene or perhaps the Oligocene, ca. 21-25 Ma (Koepfli et al., 2007). The fossil record places the divergence of *Procyon* and *Nasua* at 10-12 Ma (i.e., at least 6 Ma younger than the molecular date); that of (*Procyon-Nasua*) and *Bassariscus* at 12-14 Ma (i.e., similar to the *Procyon* and *Bassariscus* molecular divergence date); and that of the Potosinae and Procyoninae at

18-20 Ma (Baskin, 2003, 2004).

Origin of the present-day genera and species of Procyonidae found in South America

Procyon (raccoons) is widely distributed throughout the Americas, from Canada to northern Argentina. *Nasua* (coatis) ranges from the southwestern United States to Uruguay and northern Argentina. *Nasuella* is endemic to South America, in the Andes of Colombia, Ecuador and Venezuela (Helgen et al. 2009). It has recently been considered a junior synonym of *Nasua* (Ruiz-García et al., 2022a, 2022b). *Bassaricyon* and *Potos* are restricted to Central and South America. Koepfli et al. (2017:90) noted that molecular data leave unanswered whether “the lineages representing the extant procyonid genera evolved and diversified first in North America, South America, or some combination of the two.” *Nasua narica* is known from southern Arizona, New Mexico, and Texas to far northwestern Colombia. It is widespread in Mexico and Central America. Nigenda-Morales et al. (2019) used molecular evidence to demonstrate that *Nasua narica* is more closely related to the South American endemic *Nasuella* than it is to the South American endemic *Nasua nasua*, both of which are allopatric to *N. narica*. The mitochondrial DNA also indicated the following (Nigenda-Morales et al., 2019): (1) the most recent common ancestor of the coatis most likely occurred in South or Central America around 6 Ma; (2) the diversification of other extant procyonid lineages may have occurred in South America; (3) the dispersal of *N. narica* was south-to-north beginning in the Pliocene of South America; and (4) the diversification of extant procyonid lineages may have occurred in South America. Ruiz-García et al. (2022a, b) concluded that the mitochondrial DNA diversification of the coatis began around 13 Ma in the Northern Andes where *N. narica* originated and then later migrated to Central America.

The fossil record demonstrates that most of, if not all of, the direct ancestors of the extant genera of procyonids evolved in North America or Central America during the Miocene. During the Late Pliocene and Pleistocene, they crossed the Panamanian land bridge and further diversified in South America. Some species may have migrated back into Central and perhaps North America. *Bassariscus* has an extensive fossil record in North America, from the Barstovian (middle Miocene, 16 Ma) to Recent of North America and the Recent of Central America (Baskin, 2004), but is only known from a few Late Pleistocene localities in Mexico, and none from

Central or South America. It is morphologically the most primitive of the living procyonids (Decker and Wozencraft, 1991; Baskin, 2004; Ahrens, 2012). The late Clarendonian (Late Miocene, 9 Ma) genus *Paranasua* is the sister taxon to *Procyon* and *Nasua* (Baskin, 1982). The oldest records of *Procyon* are from the Late to Latest Miocene (ca. 5 Ma) of North America: *?Procyon* sp. from the late Hemphillian Mt. Eden Local Fauna in southern California (Baskin, 1982); *Procyon* sp. from the late Hemphillian Modesto Local Fauna, Mehrten Formation of California (Wagner, 1976, 1981); and *Procyon* sp. from the latest Hemphillian of Florida (Baskin, 1982; Webb et al. 2008). *Procyon rexroadensis* (Hibbard, 1941), from the early Blancan (Early Pliocene, 3-5 Ma) Rexroad Formation of Kansas, was synonymized with the extant *P. lotor* because of its lack of distinguishing characteristics (Emmert & Short, 2018). *Procyon gipsoni* and *P. megalokolos* are from the late Blancan (late Pliocene, 2-3 Ma) of Florida (Emmert & Short, 2018). *Procyon* sp. has been reported from numerous other Blancan and Irvingtonian localities in the United States. *Procyon lotor* is widespread in the Pleistocene of North America (Kurtén & Anderson, 1980).

Nasua sp. is present in the latest Hemphillian of Florida (Baskin, 1982; Webb et al. 2008). *Nasua pronarica*, described from a p4, is from the early Blancan Beck Ranch Local Fauna of Texas (Dalquest, 1978); *Nasua mastodonta* is from the late Blancan (Late Pliocene) of Florida (Emmert & Short, 2018). *Nasua narica* and *P. lotor* are known from the Late Pleistocene of Mexico (Ferrusquía-Villafranca et al., 2010). *Procyon* and *Nasua* have been reported from several Pleistocene localities in South America (see references in Ruiz-Ramoni et al., 2018). Their possible earliest occurrences in South America are from the Late Pliocene-Early Pleistocene (Marplatan) of El Breal De Orocuál of Venezuela (Ruiz-Ramoni et al., 2018). The Marplatan Age is dated at ca. 3.2-2.0 Ma (Cione & Tonni, 2005) and correlates with the late Blancan NALMA (Woodburne et al., 2006). However, the tar deposits at Orocuál range in age from Late Pliocene to Late Pleistocene (Solórzano et al., 2015). The earliest well-dated (and not contentious) records for *Procyon* are from the Late Pleistocene of Argentina and Brazil (L. Soibelzon, et al. 2010; Rodriguez et al. 2013; Prevosti & Forasiepi, 2018).

Emmert & Short (2018) noted that because there are similar and older records in North America, a North American origin more likely, supporting an entry into South America after the completion of the land bridge during GABI I (Woodburne,

2010; Cione et al., 2015). *Potos* and *Bassaricyon* are not represented in the fossil record. As discussed above, molecular evidence indicates *Bassaricyon* is a procyonin, the sister taxon of *Nasua*; morphological evidence, a potosin, the sister taxon of *Potos*. Both are arboreal frugivores and we would not be surprised if their dental and skeletal similarities are the result of ecological convergence. *Bassaricyonoides* (Hemingfordian, Early Miocene of Panama, Nevada, and Florida) and *Parapotos* (Barstovian, middle Miocene) of Texas are the only known fossil Potosinae (Baskin, 2003). Besides several derived dental characteristics, *Parapotos* and *Potos* have a mandible that is massive, deeper anteriorly and with a large symphyseal region, unlike the unspecialized mandible of *Bassaricyon*. Although the fossil record is limited, this does support a North American origin.

CONCLUSION

During the Late Oligocene, primitive musteloids (such as *Amphictis ambigua*, *Pseudobassariscus riggsi*, and *Stromeriella franconica*) with affinities to the Procyonidae and Ailuridae appear in Europe (e.g., Cirot & de Bonis, 1993; Wolsan & Lange-Badré, 1996; Wang et al., 2023). *Broiliana nobilis* from the Early Miocene (MN3) of Germany (Dehm, 1950) is the sister taxon of the New World Procyonidae (Baskin, 1982, 1989). *Bassaricyonoides* from the Hemingfordian (Early Miocene, ca. 17-19 Ma) of Nevada, Florida, and Panama is the earliest record of the Potosinae. A second potosine, *Parapotos tedfordi*, is present in the middle Miocene (Barstovian) of Texas (Baskin, 2003). The presence of a New World monkey in the Early Miocene (late Arikarean) Las Cascadas Formation of Panama (Bloch et al., 2016) and *Bassaricyonoides* in the overlying Hemingfordian Centenario Fauna (MacFadden et al., 2014) raises the possibility that potosin procyonids entered South America before ProtoGABI.

The Hemingfordian *Edaphocyon lautus* from the Running-water Formation of Nebraska (Baskin, 1982), *Bassariscus antiquus* from the Mascall Formation of Oregon (Barrett et al., 2020), and cf. *Probassariscus* from the Thomas Farm Local Fauna of Florida (Holte, 2008) are the earliest Procyoninae. The Barstovian is the Last Appearance Datum for *Edaphocyon* and *Probassariscus* and First Appearance Datum for *Arctonasua* (Baskin 1982, 1998b, 2004). *Protoprocyon* (Linares, 1982; Baskin, 1989) is restricted to the Clarendonian; *Paranasua*, to the Clarendonian and Hemphillian (Baskin 1982). The late

Hemphillian is the Last Appearance Datum for *Arctonasua* (Baskin 1982). The latest Hemphillian (Hh4, Early Pliocene) is the first definite record of the extant *Procyon* and *Nasua*. Thus, the fossil record reveals that the ancestors of the extant genera of procyonines evolved in North America or Central America during the Miocene, crossed the Panamanian land bridge in the Pleistocene, and underwent further diversification in South America.

The *Cyonasua* group, composed of *Cyonasua argentina*, *Amphinassua* spp., *Brachynassua meranii*, and *Chapalmalania* spp., is an endemic South American radiation of Late Miocene to Middle Pleistocene (Huayquarian-Ensenadan) procyonids. *Amphinassua brevirostris* from the Chiquimil Formation, Cartamarca Province, Argentina (FMNH P14342 and P14537, 7.31-7.14 Ma), is the oldest record of a procyonid (and the Carnivora as well) in South America (Marshall et al., 1979; Reguero & Candela, 2011; Prevosti et al., 2021). The arrival of procyonids in South America coincided with the decline of the Sparassodonta, a group of borhaenid marsupials (Soibelzon, 2011, fig. 1). Although the Huayquerian members of the *Cyonasua* group were more carnivorous than extant procyonids other than *Bassariscus*, they were more omnivorous than the larger, hypercarnivorous sparassodonts (Forasiepi et al., 2007; Prevosti et al. 2013). Engelman and Croft (2019) posit that ecological dissimilarity enabled the *Cyonasua* group to successfully invade and diversify in South America without competition from the sparassodonts. Competitive replacement was also probably not a factor in the extinction of the *Cyonasua* group. The last appearance of *Amphinassua* in the Chapadmalalan preceded the first appearance in the Marplatan of the Canidae, Mustelidae, *Nasua*, and *Procyon* (Fig. 1). The extinction of *Chapalmalania* in the Pliocene preceded the appearance of Ursidae in South America. The presumably frugivorous *Brachynassua meranii* is known from a single Ensenadan record. Because the frugivorous *Potos* and *Bassaricyon* lack a fossil record in South America, it cannot be shown if there was competition with *Brachynassua*. Climate change was an important factor in the extinction of the hathiacynid sparassodonts (Zimicz, 2014). S. Tarquini et al. (2022) attributed the extinction of the sparassodonts to multiple factors, including uplift of the Andes, not to competition. Pino et al. (2022) concluded that regional climatic change caused by the uplift of the Andes led to the extinction of the sparassodonts. The last members of the *Cyonasua* group, other than *Brachynassua*, occurred at the same time as the last

sparassodonts (Cione et al., 2015), perhaps going extinct for the same reasons.

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Dedication to LLJ by JB. I met Louis Jacobs in 1972 when he was a second year and I was a new Master's student in the Department of Geosciences at the University of Arizona. Our theses, supervised by Everett Lindsay (the "Dock") were both on small mammals, mostly rodents, from the Hemphillian of Arizona. I learned a lot from Louis and both of us a lot from the Dock, whose dissertation was on small mammals, especially rodents, from the Barstow Formation. Dock and his students formed the "Red Fireballs", a group whose mission was to socialize together and help each other with our research. In furthering these two aims we met on Friday afternoons at the home of George Simpson, who had retired to Tucson and was on our thesis committees. One of the topics

Dr. Simpson discussed with us was the history of the mammalian fauna of South America. Louis and I became more interested in what Simpson (1950, 1953) termed the third major stratum of mammalian immigrants to South America, consisting of "late island-hoppers" and "late immigrants", what is now called the Great American Biotic Interchange. Louis has a continuing interest in faunal interchange between zoogeographic realms, including the role of sigmodontine rodents in the GABI (Jacobs & Lindsay, 1981, 1984; Jacobs & Flynn, 2005; Lindsay et al., 2006). Whatever group of fossils Louis has studied, be it North American cricetid rodents, South Asian murid rodents, dinosaurs from Texas and Malawi, mosasaurs from Texas, Angola and the Netherlands, a snake with limbs, etc., etc., etc., he has tackled with great enthusiasm which he brings to all of us who have heard him talk about his research.

AUTHOR CONTRIBUTIONS

JB developed the initial concept for the research and wrote the first draft of the manuscript. JB and AV performed the data collection, the analysis and wrote the final draft.

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