

Fig. 16 Testudines indet. and (non-snake) Squamata from the Vergel Member. **A–E** Testudines indet. **A** Fragment of a right premaxilla (AMU-CURS-1154). **B1, B2** Distal section of a left fibula (AMU-CURS-1160). **C1, C2** Plastron fragment with a bite mark (AMU-CURS-862). **D, E** Shell fragments (**D** AMU-CURS-842 and **E** AMU-CURS-842). **F1–F3** Fragmentary right dentary of *Tupinambis* s.l. (AMU-CURS-721). **G–K** (Non-snake) Squamata indet. **G** Anterior section of a left maxilla (AMU-CURS-1148). **H1, H2** Right jaw fragment preserving three complete teeth (AMU-CURS-1164). **I** Premaxilla fragment with an incomplete tooth (AMU-CURS-1163). **J, K** Two maxilla fragments (**J** AMU-CURS-725 and **K** AMU-CURS-797). Views: anterior (**B2**), external (**C1–E**), left lateral (**G**), right lateral (**A, F2**), mesial (**F3, H2, I–K**), occlusal (**F1, H1**), and posterior (**B1**)

General description, comparisons and remarks: The anterior section of a left maxilla (AMU-CURS-1148) is 1.5 mm in length and its distal section preserves the curved bone surface that forms part of the external narial opening (Fig. 16G). Only an incomplete recurved tooth is preserved, and on the lateral surface of the maxilla, a small foramen is visible. AMU-CURS-1164 is a right jaw fragment 2.8 mm in length preserving three complete teeth (Fig. 16H1, H2). AMU-CURS-1163 is a premaxilla (Fig. 16I) 2.9 mm in length preserving an

incomplete tooth. The other two specimens are maxillary fragments (both specimens less than 1.5 mm in length) preserving one (AMU-CURS-797, Fig. 16K) and two (AMU-CURS-725, Fig. 16J) teeth, respectively. All the specimens have pleurodont dentition, and with the exception of AMU-CURS-1148, teeth are cylindrical and straight. In AMU-CURS-725, both teeth are robust, and one of these preserves a smaller accessory distal cusp. In the specimen AMU-CURS-1164, part of the subdental shelf is preserved with three closely spaced teeth,

which are characterized by a triangular, pointed crown with sharp edges. Approximately, in the middle portion of the teeth, a clear narrow area delimits the transition between the pyramidal crown and the basal section; clear resorption pits are located at the base of the teeth. AMU-CURS-1163 apparently had a tooth with a flattened crown tip and the tooth in AMU-CURS-797 is slender, conical and well pointed (Fig. 16I). Strong differences in the morphology of premaxillary and maxillary teeth, and variation in tooth morphology along maxilla (or dentary) are usual in many lizard taxa. This might suggest that AMU-CURS-1148, AMU-CURS-1163, AMU-CURS-1164, and AMU-CURS-725 would not represent distinct taxa. In contrast, the tooth preserved in AMU-CURS-797 (Fig. 16K), which is small, slender, cylindrical, and well pointed, seems to belong to a different taxon than the above referred specimens. The specimens are not well preserved, and taking into account intraspecific variation, it is not possible to confidently state how many lizard taxa are present in the sample. Nevertheless, the subtle dental differences among AMU-CURS-725 and the other four specimens suggest the presence of at least two taxa.

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Aniliidae Fitzinger, 1826 (sensu Vidal et al., 2009)

Anilius Oken, 1816

Anilius scytale (Linnaeus, 1758)

(Fig. 17A1–A5).

Locality: NCC (conglomerate, Fig. 3B).

Material: An incomplete trunk vertebra (AMU-CURS-1159).

General description, comparisons and remarks: AMU-CURS-1159 is missing part of the neural arch, small portions of the zygosphenes and the right prezygapophysis. The vertebra is slightly wider than it is long (neural arch width: 5.0 mm; centrum length: 4.8 mm). The prezygapophyses are relatively long; they extend well anterolaterally in dorsal view and are dorsolaterally inclined in anterior view, reaching the level of the zygosphenes. The neural arch is strongly depressed in posterior view. The zygosphenes are relatively thin in anterior view. The cotyle is broader than it is high and is larger than the neural canal. The condyle is circular. The postzygapophyseal articular facets are large and ovoidal. The hemal keel is weakly expressed in its medial sector but well defined posteriorly, where it broadens slightly and is posteriorly directed (a groove on each side marks its posterolateral edge). The paradiapophyses are laterally eroded. The diapophysis is much smaller than the parapophysis; they are partially separated by a deep and well-defined groove that

develops from their posterior edge in anterodorsal direction. There are no parapophyseal processes. On the ventral surface, medial to the parapophysis there is, on both sides, a sort of small bony bridge that connects the parapophysis to the cotyle; a foramen opens posteriorly to this bridge delimiting a channel that could be in connection with the deep groove that develops on the anterior surface between the parapophysis and the cotyle. The wide, much depressed, and almost flattened neural arch in posterior view, the elongated and much dorsally inclined prezygapophyses, the rather shallow posterior median notch of the neural arch, and the prominent interzygapophyseal constriction observable in AMU-CURS-1159, are characteristic features of the extant American pipe snake, *Anilius scytale* (Hoffstetter and Rage 1977; Rage 1984, 1998; Smith 2013; Head 2020), which is currently present in Venezuela, though not in Falcón State (Mijares-Urrutia and Arends 2000; Barrio-Amorós et al. 2002).

Anilius (and its sole species *A. scytale*) represents the sole extant taxon of Aniliidae, as recent studies have demonstrated that the extant Asian cylindrophids, anomochilids, and uropeltids (which share several vertebral features in common) are only distantly related and should not be referred to this group (Gower et al. 2005; Vidal et al. 2009; Head 2020; Smith and Georgalis in press). Note that another potential aniliid genus was also present in the Neogene of the Amazonian region, i.e., †*Colombophis* Hoffstetter and Rage, 1977 (Hoffstetter and Rage 1977; Head et al. 2006; see also Hsiou et al. 2010 for a different taxonomic interpretation). The vertebra from the NCC locality further differs from *Colombophis* primarily by its much smaller size and less robust nature, and to a lesser degree by its more depressed neural arch, more slender and pointed prezygapophyses and postzygapophyses, and less thick zygosphenes (Hoffstetter and Rage 1977; Head et al. 2006; Hsiou et al. 2010). We refer this vertebra to *A. scytale*, a taxonomic assignment supported also by geographic and stratigraphic rationale. The specimen AMU-CURS-1159 represents the first fossil occurrence of *Anilius scytale*.

Constrictores Oppel, 1811a (sensu Georgalis and Smith 2020).

Boidae Gray, 1825a

Corallus Daudin, 1803

Corallus sp.

(Fig. 17B1–B5).

Locality: NCC (conglomerate, Fig. 3B).

Material: An incomplete trunk vertebra (AMU-CURS-1157).

General description, comparisons and remarks: AMU-CURS-1157 is missing most of the left prezygapophysis and part of the right prezygapophysis, whereas part of the left side of the zygosphene is damaged. The vertebra is moderately large, with a centrum length of 7.4 mm and a neural arch width of 9.5 mm. The zygosphene is moderately thick in anterior view, with its two lateral edges prominent and extending much dorsally, whereas a distinct convex ridge is present at around its mid-level. In dorsal view, the zygosphene is crenate, with distinct lateral lobes (only the right is preserved). The neural spine is thick in dorsal view, moderately high in posterior view, whereas in lateral view, it is relatively thin, much posteriorly inclined, and its height increased toward the posterior portion of the neural arch. The prezygapophyses are almost horizontal in anterior view, with only slight dorsal inclination. The neural arch is much vaulted in posterior view. The cotyle and condyle are large and almost circular. The hemal keel is wide, denoting that the vertebra apparently originates from the posterior trunk region of the column. The posterior median notch of the neural arch is deep in dorsal view. The wide vertebral centrum, being wider than long in ventral view, the paradiapophyses not divided into diapophyses and parapophyses, the reduced prezygapophyseal accessory processes, the deep posterior median notch of the neural arch, as well as the general shape of the vertebra, being robust, strongly built, and higher than long in lateral view, all denote that AMU-CURS-1157 can be assigned to Boidae (Rage 1984, 2001; Szyndlar and Rage 2003).

Within Boidae, the specimen AMU-CURS-1157 bears strong resemblance with the extant genus *Corallus*, in particular its prezygapophyses being horizontally oriented (almost 180°) in anterior view. Other diagnostic characters are the wide, broad, and strongly vaulted neural arch, the crenate zygosphene in dorsal view with a strong median lobe, the zygosphene in anterior view bearing a prominent median ridge and being wider than the cotyle, the presence of small parazygantral foramina, the high neural spine in lateral view, and the absolute vertebral size (neural arch width less than 10 mm) (Rage 2001; Camolez and Zaher 2010; Onary et al. 2018). *Corallus* is still present in Falcón State (Mijares-Urrutia and Arends 2000).

Eunectes Wagler, 1830

Eunectes sp.

(Fig. 17C1–C5).

Locality: SGOP (conglomerate Ly1, Fig. 3C).

Material: A trunk vertebra (AMU-CURS-1304).

General description, comparisons and remarks: AMU-CURS-1304 is a large specimen with a centrum length

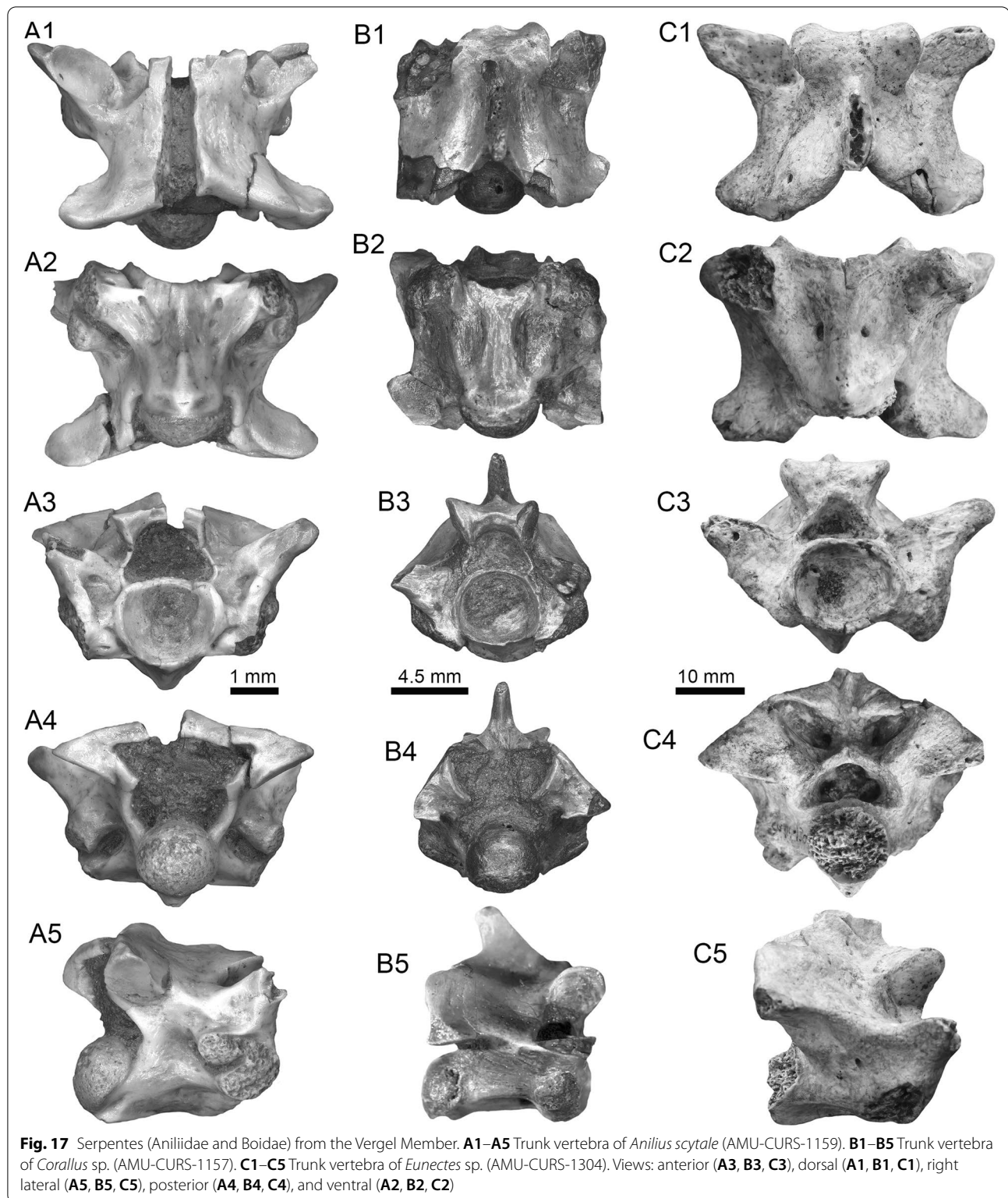
of 18 mm. The vertebra is wider than it is long, with a prominent anterior widening of the centrum. The zygosphene is slightly concave in dorsal view and trapezoidal, relatively thick, and with a median tubercle in anterior view. The prezygapophyses are much laterally projected in anterior view. The interzygapophyseal constriction is distinct and defined. The posterior median notch is deep. The cotyle is large and deep. The neural arch is slightly depressed. The hemal keel is moderately thick and crosses the whole midline of the centrum in ventral view. Two prominent and deep subcentral foramina lie at around the middle of the centrum, one at each side of the hemal keel. Similar to the above *Corallus* specimen (AMU-CURS-1157), specimen AMU-CURS-1304 can be assigned to boids on the basis of a wide vertebral centrum, being wider than long in ventral view, the paradiapophyses not being divided into diapophyses and parapophyses, the relatively reduced prezygapophyseal accessory processes, the deep posterior median notch of the neural arch, and also the general shape of the vertebra, being robust, strongly built, and higher than long in lateral view (Rage 1984, 2001; Szyndlar and Rage 2003). Within boids, AMU-CURS-1304 can be referred to the genus *Eunectes*, commonly known as anacondas, on the basis of its rather robust and large size, the slightly depressed neural arch, the thick zygosphene with a median tubercle, the deep interzygapophyseal constriction, and the laterally projected prezygapophyses (see Hsiou and Albino 2009, 2010; Hsiou et al. 2013). The slightly depressed neural arch and the moderately wide hemal keel further imply a position of the vertebra from the posterior or posterior mid-trunk region of the column. Anacondas of the genus *Eunectes* comprise the largest snakes of South America and among the largest worldwide (Murphy and Henderson 1997). Besides the extant species of the genus, another extinct named species has also been referred: †*Eunectes stirtoni* from the middle Miocene of Colombia (Hoffstetter and Rage 1977). Based on the available new material from the San Gregorio Formation, we refrain from assigning this single vertebra to the species level and prefer to refer it to the genus level only. *Eunectes* is currently present in Venezuela only in the Orinoco River basin (Wallach et al. 2014).

Boidae indet.

(Fig. 18A1–B3).

Locality: NCC (conglomerate, Fig. 3B).

Material: Two isolated vertebrae, one incomplete trunk vertebra (AMU-CURS-1147), and one fragmented specimen of indeterminate position (AMU-CURS-804).



General description, comparisons and remarks: AMU-CURS-1147 is small (centrum length: 4.8 mm), missing portions of both postzygapophyses and the edges of both its prezygapophyses, whereas its paradiapophyses and its condyle are much eroded (Fig. 18A1–A5). The neural arch is vaulted in posterior view. The zygosphene is moderately crenate in dorsal view, with two rather prominent lateral lobes, whereas in anterior view it is thin, convex, and wider than the cotyle. The prezygapophyses are dorsally inclined. The neural spine is moderately high, with its base extending across most of the midline of the neural arch. AMU-CURS-804 lacks the posterior ventral part of the centrum (centrum length: ~1.2 mm), the right prezygapophysis, both postzygapophyses, most of the posterior portion of the neural arch, the neural spine, and part of the zygosphene (Fig. 18B1–B3). The prezygapophyses are dorsally inclined in anterior view, whereas they are rather slender and extend well anterolaterally in dorsal view. Distinct paracotylar foramina are present. The paradiapophyses are rather eroded but seem not to have been divided into diapophyses and parapophyses. A moderately wide hemal keel (or hypapophysis) is present in the ventral surface of the centrum. The overall shape of these two specimens, being relatively strongly built, with the centrum wider than long in ventral view, the paradiapophyses not divided into diapophyses and parapophyses, the relatively reduced prezygapophyseal accessory processes, suggest that they can be referred to Boidae (Rage 1984, 2001; Szyndlar and Rage 2003). A more precise identification is not possible due to the preservational status of the fossils. It has to be noted that AMU-CURS-1147 bears some resemblance with *Epicrates* Wagler, 1830, especially in terms of the dorsal inclination and lateral expansion of prezygapophyses, the shape of the neural spine, and the overall vertebral shape and size (see e.g., Onary et al. 2018). However, we hesitate to definitively assign this incomplete new fossil specimen to that genus. Nevertheless, an assignment of both specimens to *Corallus* (as was the case of the specimen AMU-CURS-1157) seems to be excluded based on the characters described above, most prominently the much dorsally inclined prezygapophyses of these vertebrae. Specimens AMU-CURS-804 and AMU-CURS-1147 could suggest the presence of at least a second taxon of boids in the NCC assemblage.

?Boidae or ?Aniliidae indet.
(Fig. 18C1–C5).

Locality: NCC (conglomerate, Fig. 3B).

Material: An incomplete trunk vertebra (AMU-CURS-1158).

General description, comparisons and remarks: AMU-CURS-1158 is missing part of the posterior portion of the neural arch and the dorsal part of the neural spine, whereas its cotyle, left prezygapophysis, and both paradiapophyses are strongly eroded. The vertebra is wider than long in ventral view (centrum length: 6.4 mm; neural arch width: 9.1 mm), with its prezygapophyses extending anterolaterally. There is a relatively deep interzygapophyseal constriction. The zygosphene is only slightly crenate in dorsal view, whereas in anterior view it is relatively thin and almost straight to slightly convex. The neural arch is moderately vaulted. The sharp hemal keel in ventral view denotes that the vertebra originates from the mid-trunk region of the column. The overall shape of AMU-CURS-1158, being relatively strongly built, with the centrum wider than long in ventral view, the paradiapophyses not divided into diapophyses and parapophyses, and the relatively reduced prezygapophyseal accessory processes are consistent with a referral to Boidae (Rage 1984, 2001; Szyndlar and Rage 2003). However, AMU-CURS-1158 bears also some resemblance to *Colombophis*, a genus that has been referred to aniliids (Hoffstetter and Rage 1977; Head et al. 2006), or simply treated as a basal alethinophidian (Hsiou et al. 2010), especially †*Colombophis spinosus*, from the middle Miocene of Brazil, Colombia and Venezuela (Hsiou et al. 2010). Features shared between AMU-CURS-1158 and *Colombophis* are the deep interzygapophyseal constriction, the rather pointed and dorsally inclined prezygapophyses, the shape of the zygosphene in anterior and dorsal views, the short prezygapophyseal accessory processes, and the neural spine increasing in height in lateral view much posteriorly from the level of the zygosphene (see figures in Hoffstetter and Rage 1977; Head et al. 2006; Hsiou et al. 2010). Nevertheless, AMU-CURS-1158 can still be differentiated from *C. spinosus* by its more vaulted neural arch in posterior view, much more pointed postzygapophyses, more anteriorly inclined prezygapophyses in dorsal view (condition approaching more the type species of *Colombophis*, i.e., †*Colombophis portai* Hoffstetter and Rage 1977), a longer and better defined hemal keel, the orientation of the paradiapophyses, its neural spine not so confined to the posterior portion of the neural arch, and its proportionally much smaller size. Although boid affinities for AMU-CURS-1158 seem to be most likely, based on the existing limited material, we cannot exclude a referral to *Colombophis* or a *Colombophis*-like form.

Caenophidia Hoffstetter, 1939
Colubroides Zaher et al., 2009
Colubroides indet.
(Fig. 18D1–D5).

Locality: NCC (conglomerate, Fig. 3B).

Material: A fragmentary trunk vertebra (AMU-CURS-1161).

General description, comparisons and remarks: A fragmentary trunk vertebra with a centrum length of 1.9 mm (AMU-CURS-1161), missing the zygosphene, its left prezygapophysis, and parts of both postzygapophyses, neural spine, hypapophysis, and right prezygapophysis. The centrum is elongated. A ventrally expanding hypapophysis projects ventrally from the centrum in lateral view, though its exact extent and size cannot be evaluated with certainty. The synapophyses are divided into diapophyses and parapophyses. Paracotylar foramina are present. All the above characters are consistent with the anatomy of Colubroidea. Within Colubroidea, the presence of a hypapophysis instead of a hemal keel throughout all trunk vertebrae is a characteristic, among others, of most taxa of natricids, elapids, and viperids, whereas a hypapophysis is also present in the anterior trunk vertebrae of “colubrids” (Rage 1984; Szyndlar 2012; Smith 2013; Georgalis et al. 2019). The preservation of the specimen AMU-CURS-1161 does not afford any more precise taxonomic attribution, but it confirms the presence of Colubroidea in the fossil assemblage.

Serpentes indet.
(Fig. 18E1–G).

Locality: NCC (conglomerate, Fig. 3B).

Material: A fragmentary trunk vertebra (AMU-CURS-803), another fragmentary trunk vertebra (AMU-CURS-805), and a fragmented prezygapophysis (AMU-CURS-724).

General description, comparisons and remarks: AMU-CURS-803 has a length of ~1.3 mm (Fig. 18E1–E4), missing a large part of the neural arch, the right postzygapophysis, most of the left prezygapophysis, and parts of the neural spine and the right prezygapophysis. The most peculiar feature of this vertebra is the high convexity of its thin zygosphene in anterior view, whereas in dorsal view, three distinct lobes are present at the anterior edge of this structure. The specimen AMU-CURS-805 (Fig. 18G) is also a rather fragmentary trunk vertebra missing most of the left prezygapophysis and both postzygapophyses. In a fragmented prezygapophysis (AMU-CURS-724, Fig. 18F) the completely prezygapophyseal articular facet and the prezygapophyseal accessory process

are preserved. Due to their poor preservational state, these three specimens are little informative. The relatively long prezygapophyseal accessory process present in AMU-CURS-724 hints at possible affinities with Colubroidea, though we refrain from formally assigning this specimen to that group. The overall morphology of AMU-CURS-803, with its relatively wider than long centrum, seems to conform mostly to boids.

Crocodylia Gmelin, 1789 (sensu Benton and Clark, 1988).

Alligatoridae Gray, 1844

Caimaninae Brochu, 2003 (sensu Norell, 1988)

Caiman yacare (Daudin, 1802)

Caiman aff. *C. yacare*

(Fig. 19A1–A3).

Locality: SGOP (conglomerate Ly1, Fig. 3C).

Material: An isolated right maxilla fragment (AMU-CURS-1328).

General description, comparisons and remarks: There are only a few crocodylian fossils from the San Gregorio Formation so far that can be assigned to a species. Of those, AMU-CURS-1328 is among the best-preserved and identifiable skull remains (Fig. 19A1–A3). The bone bears 14 alveoli and the dorsal bone surface is sculptured with ornamental pitting. Just posterior to the largest alveolus, rostral canthi are not present. Rostral canthi are typical for some species of *Caiman*, such as *C. latirostris* (also for *Melanosuchus niger*), but are absent in others, such as *C. crocodilus* or *C. yacare* (e.g., Norell 1988; Brochu 1999). Anteriorly, there is just a remnant of the suture with the premaxilla, whereas posteriorly, the suture with the jugal is well preserved. The anterior border of the suborbital fenestra is oblique, wide, unlike in *C. yacare* and *C. crocodilus*, where it is pointed. In *Caiman c. apaporiensis* from Colombia, the margin is also oblique but much narrower (Medem 1955). Medially, the bone is broken and the smooth internal narial passage is visible. In lateral view, the outline of the maxilla is wavy. In ventral view, the lateral margin of the maxilla from alveolus 7 to 11 is straight rather than slightly convex, which is noteworthy for a presumably adult specimen.

The first three anterior alveoli are of similar diameter, whereas the following fourth alveolus is much larger. The following ten alveoli are small in diameter

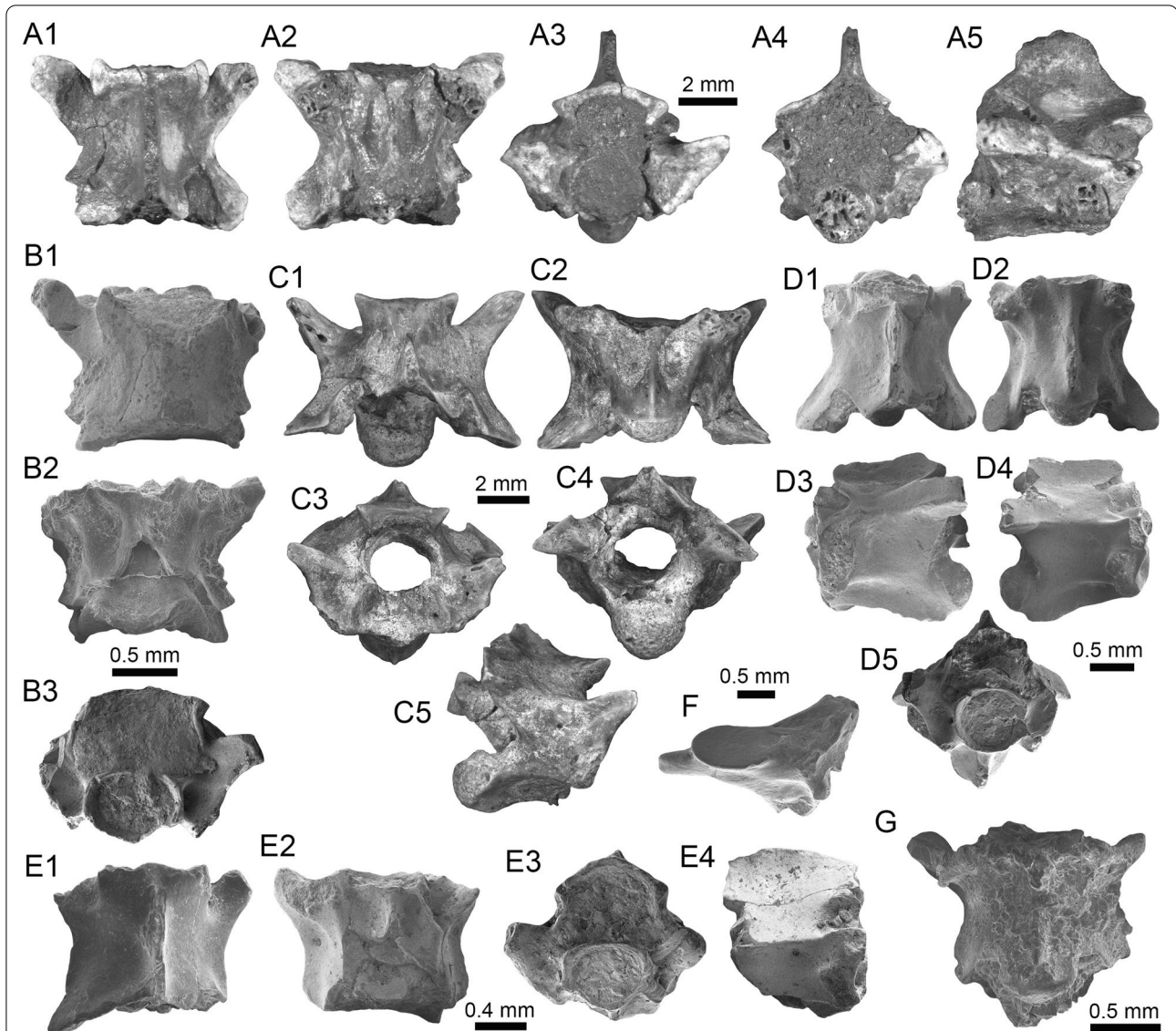


Fig. 18 Serpentes (Boidae and Colubroides) from the Vergel Member. **A1–B3** Trunk vertebra (**A1–A5** AMU-CURS-1147) and specimen of indeterminate position (**B1–B3** AMU-CURS-804) of Boidae indet. **C1–C5** Trunk vertebra of ?Boidae or ?Aniliidae indet. (AMU-CURS-1158). **D1–D5** Trunk vertebra of Colubroides indet. (AMU-CURS-1161). **E1–G** Trunk vertebra (**E1–E4** AMU-CURS-803), fragmented prezygapophysis (**F** AMU-CURS-724), and a trunk vertebra (**G** AMU-CURS-805) of Serpentes indet. Views: anterior (**A3, B3, C3, D5, E3**), dorsal (**A1, B1, C1, D1, E1**), left lateral (**D3**), right lateral (**A5, C5, D4, E4**), posterior (**A4, C4**), and ventral (**A2, B2, C2, D2, E2, G**)

and similar sized. Medial to alveoli 2–3, 3–4, 5–6, 6–7, and 7–8, occlusal pits for the dentary dentition can be seen, with the first one being shallow, the following two pits being deeper and the last one being shallow again. These occlusal pits indicate a complete overbite, as is typical for alligatorids, and are indistinguishable from those of extant *C. yacare* MLP-R 5044. Alveolus 3 and alveoli 9–13 still carry well-preserved teeth (Fig. 19A2, A3). The third tooth is conical and slightly recurved. The teeth in alveoli 9–13 are

straighter and become smaller and more bulbous from anterior to posterior. Bulbous teeth in the posterior portion of the dentary are absent in *C. crocodilus apaporiensis* (e.g., Medem 1955; Escobedo-Galván et al. 2015). The anterior teeth in this series are spaced well apart from each other. The last two alveoli might be confluent as there is no bony separation visible. Teeth 3 and 9–11 show anteroposterior carinae, whereas the more bulbous teeth 12 and 13 have a round crown in cross section. AMU-CURS-1328 has a length of

190 mm, indicating that the maxilla derived from a large skull of ca. 400 mm in length (based on comparisons with extant caimanine skulls). AMU-CURS-1328 appears to combine a mosaic of features that could be ancestral to the modern *C. yacare*, *C. crocodilus*, and *C. c. apaporiensis*. In the absence of further and more complete specimens, we therefore treat AMU-CURS-1328 as aff. *C. yacare*.

Caimaninae Brochu, 2003 (sensu Norell, 1988)

Caimaninae indet.

(Fig. 19B–L).

Locality: NCC (conglomerate, Fig. 3B) and SGOP (conglomerate Ly1, Fig. 3C).

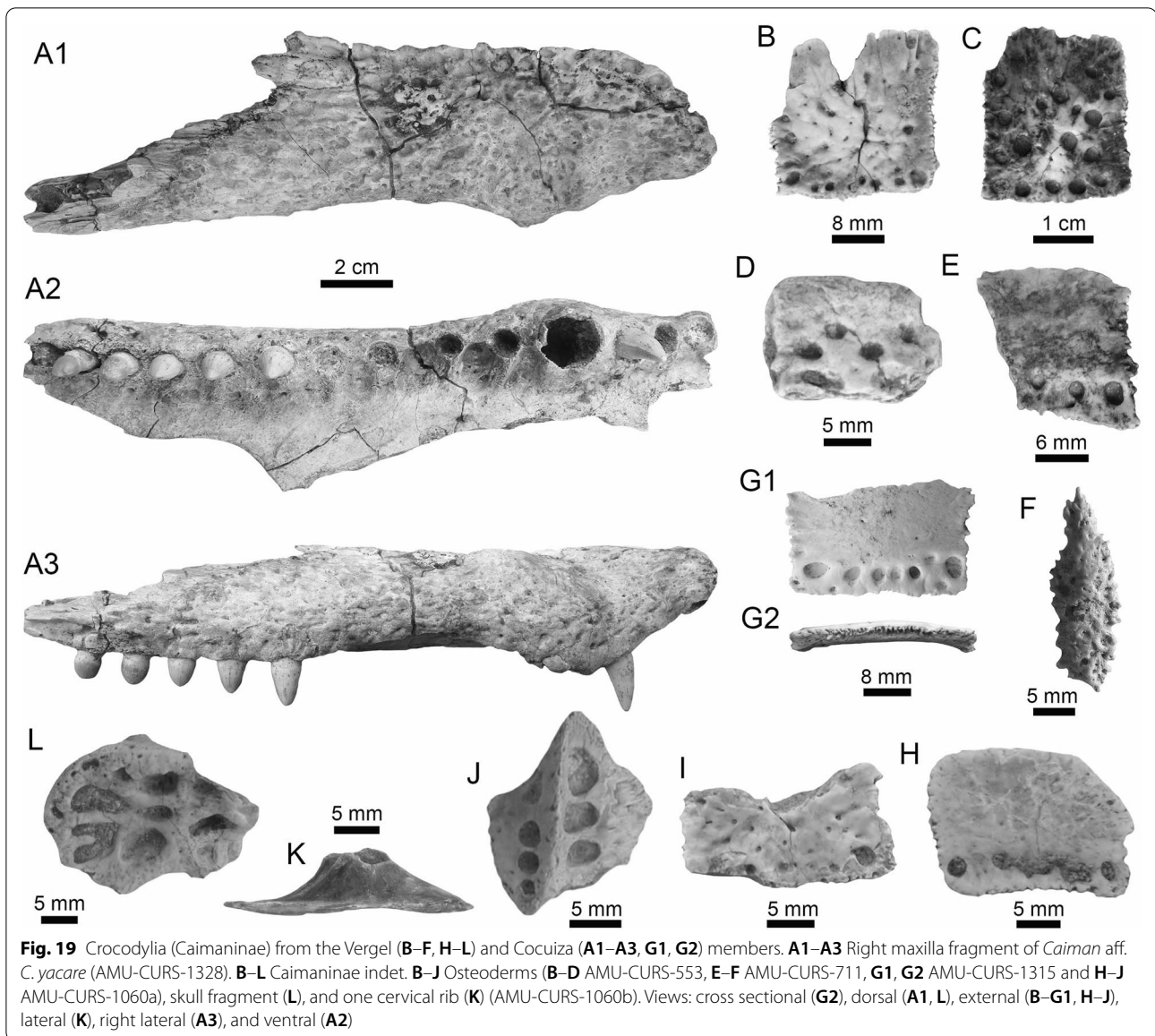
Material: Twelve cranial and postcranial isolated remains from NCC (AMU-CURS-553, -711, and -1060), and SGOP (AMU-CURS-1315) localities.

General description, comparisons and remarks: AMU-CURS-553 includes four crocodylian osteoderms, three of which are flat and one is keeled. The keeled specimen is 23 mm wide and 15 mm long, preserving only the anterior half of the osteoderm (Fig. 19B–D). In this specimen the ornamental pits do not reach the anterior osteoderm margin. The smallest fragment (16 × 17 mm) of the flat osteoderms shows only a few scattered shallow pits on the bone surface and preserves only a small part of the actual bone margin (Fig. 19D). The two-remaining flat osteoderms are of square or almost square shape (26 × 26 mm and 25 × 28 mm), each comprising three strongly sutured margins and one smoother margin (Fig. 19B, C). The two osteoderms differ in the size and distribution of ornamental pits on the bone surface. In one specimen, the largest pits are found distributed along the sutured margins and smaller and less deep pits are scattered over the osteoderm center, whereas in the other specimen, large pits are distributed all over the bone surface with the exception of the thinner, non-sutured margin. Ventrally, all four osteoderms show a cross-hatching pattern of metaplastically ossified structural fibers. The three flat osteoderms are tentatively identified as the posterior ossifications of composite ventral osteoderms prominent in Caimaninae (but see also Brochu et al. 2012 for composite osteoderms in a non-Brevirostres crocodylian).

AMU-CURS-711 comprises two crocodylian osteoderms that were found together. The first one is strongly elongated, with sutural margins, and tapering to anterior and posterior tips. It is 20 mm long and

7 mm wide and carries a low medial ridge (Fig. 19F). The surface of the osteoderm is strongly sculptured by deep pits. The osteoderm likely represents an early stage of a developing dorsal osteoderm (may be from the paravertebral shield), in which the keeled area develops first (Schmidt 1914). The second osteoderm is of rectangular shape (20 mm long and 18 mm wide as preserved) with two sutured margins and one margin tapering into a sharp edge (Fig. 19E). This latter margin of the osteoderm is broken and thus its margin not preserved. The external surface shows a single row of three large and widely spaced pits, opposite the tapering edge margin. Internally, the osteoderm shows some cross-hatching pattern. This osteoderm is identified as the anterior ossification of a composite ventral osteoderm, in which the tapering edge is the anterior margin and the ornamented area is the posterior margin of the ossification. The specimen AMU-CURS-1315 is a partially preserved osteoderm identifiable as the anterior element of a composite ventral osteoderm (Fig. 19G1, G2). This specimen also shows a single row of ventral ornamental pits, three preserved margins with weak sutures, and dorsally a cross-hatching pattern of the bone surface.

AMU-CURS-1060a-b includes an assortment of crocodylian remains, including a skull fragment, one cervical rib, and three fragmentary osteoderms. The skull fragment (AMU-CURS-1060b, Fig. 19L), a right postorbital, has a smoothly convex anterolateral margin, an opposite concave posteromedial margin (forming the margin of the supratemporal fenestra), and shows strong ornamental pitting on its dorsal surface. In anterolateral view, the sutural contacts with the frontal anteriorly and parietal medially and the squamosal posteriorly are preserved, as well as the foramen for the superficial temporal artery (Holliday and Witmer 2007). The bone is 31 mm long (maximum anteroposterior length) and 23 mm wide (maximum mediolateral width). The cervical rib is 31 mm long and 8 mm high and shows the typical double articulation with ventral capitulum and a more dorsally situated tuberculum (AMU-CURS-1060b, Fig. 19K). Of the osteoderms (AMU-CURS-1060a, Fig. 19H–J), two are of rectangular shape and flat, one being the anterior element and the other being the posterior element of a composite ventral osteoderm. Both elements show a crosshatching pattern and few scattered nutrient foramina on the internal bone surface. Whether both elements form a single unit, however, is not clear. The posterior ossification (22 × 13 mm as preserved) shows



three sutured and one broken margin and only small, scattered pits (and one larger pit) over its external bone surface. The anterior ossification (26 × 18 mm) shows three sutured margins, and one margin tapering to a smooth sharp edge. A single row of five pits filled with sediment is present opposite the tapering margin. One small-keeled osteoderm shows two rows of parasagittally arranged pits, with those on one side of the keel being slightly larger than those on the other side (Fig. 19J). This osteoderm is 20 mm long and 16 mm wide. Ventrally it shows a single nutrient foramen. The remaining four osteoderms (or partial skull bones) are very fragmentary. They show strong ornamentation of the bone surface in the form of pitting, but otherwise lack sutural contacts or other diagnostic features.

Crocodylia indet.

(Figs. 20A1–T2 and 21A–P).

Locality: NCC (conglomerate, Fig. 3B) and SGOP (conglomerate Ly1, Fig. 3C).

Material: Over 583 isolated remains, including 524 teeth [522 from NCC (AMU-CURS-19, -167, -302, -558, -574–577, -666, -707, -829, -847, -861, -881–882, -1095, -1121, -1129, and -1201) and 2 from SGOP (AMU-CURS-1322 and -1352)], 35 osteoderms [28 from NCC (AMU-CURS-30, -594, -737, -830, -884, -1029, -1125, -1184, and -1236) and 7 from SGOP (AMU-CURS-1311–1316 and -1321)], and 24 indeterminate skull, lower jaw, and other postcranial bone fragments [21 from NCC (AMU-CURS-21, -561, -578, -593, -743,

-826, -1030, -1062, -1082, -1200, and -1236) and 3 from SGOP (AMU-CURS-1309, -1320, and -1319)].

General description, comparisons and remarks: Many postcranial bones and teeth are recovered from the San Gregorio Formation, but in contrast to larger or more complete cranial elements, these are seldom diagnostic to the generic or specific level. Teeth are represented in different sizes and shapes, ranging from a few millimeters to 63 mm long and 28 mm wide at the base for the largest specimen (e.g., AMU-CURS-1057). Most of the teeth are well preserved with slender, curved, massive, and conical sharp crowns, showing carinae, ornamental ridges, or fine ornamental rugosities of the enamel surface (Fig. 20A1–H). Some tiny curved crocodylian teeth (AMU-CURS-1095, Fig. 20I1, I2) of about 2 and 4 mm in length, with lateral carinae and rugose surface wrinkles on the enamel crown, which might be from a hatchling or very young juvenile specimens.

The osteoderms in general are well preserved, and here the most representative specimens are described. AMU-CURS-030 and AMU-CURS-033 comprise two keeled paravertebral osteoderms of sub-square shape (Fig. 20J1–K2). The surface ornamentation of the osteoderms consists of round to ovoid pits that extend over the complete dorsal surface. Ventrally the osteoderms show scattered nutrient foramina and a strong cross-hatching pattern of metaplastically ossified structural (collagenous) fibers of the deep connective tissue underlying osteoderms of the paravertebral shield (the cingular ligament; see Salisbury and Frey 2001). The osteoderms show sutured margins, with the medial margin being thickened, indicating a close contact with an adjacent osteoderm. AMU-CURS-030 and AMU-CURS-033 could derive from the medial rows of the paravertebral shield (Frey 1988). AMU-CURS-593 contains a fragmentary osteoderm with a tilted keel and a small carinated tooth (13 mm in length) missing the very tip of the crown (Fig. 20L1, L2). The shape of the base of the osteoderm is not discernible due to the lack of preserved marginal areas. AMU-CURS-594 comprises three osteoderms (Fig. 20M, N, Q), of which the largest one is complete and the other two only partially preserved. The smallest specimen (17.5 × 15.5 mm) is flat and of rectangular shape. The preserved margins show sutures and the external surface is sculptured with pits. The mid-sized, only partially preserved specimen and the largest specimen (43 × 36 mm) are keeled osteoderms of ovoid shape. The ornamentation consists of irregularly arranged, larger and smaller pits that reach the margins. The three specimens all show a cross-hatching pattern and scattered nutrient foramina on their internal/visceral bone surface.

AMU-CURS-830 is a single osteoderm of roughly ovoid shape and an off-centered peak (Fig. 20R). Although overall preservation is not great in this specimen, the margins of the osteoderm carry pegs and sockets, indicating

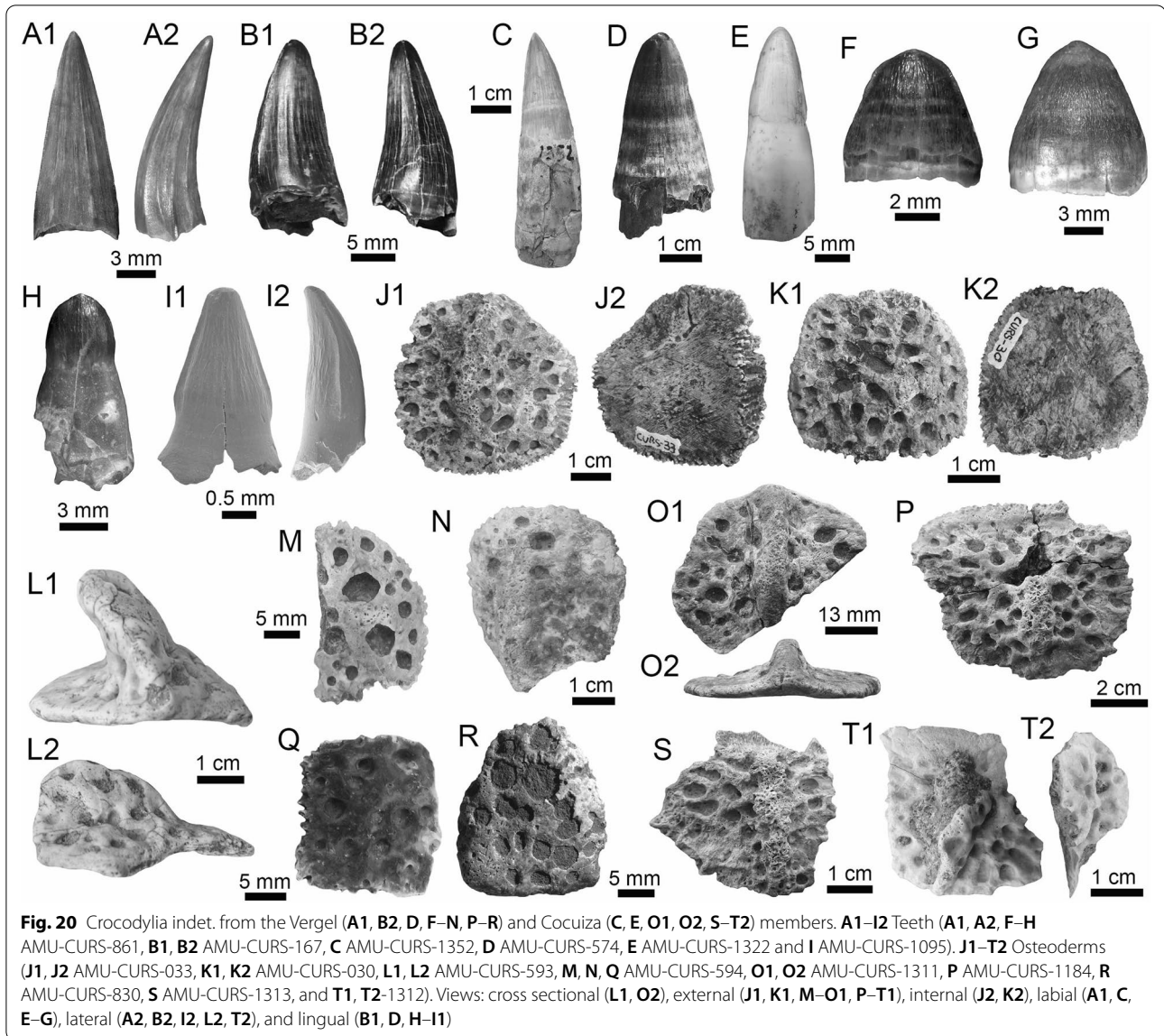
sutured margins on all sides. Ornamentation consists of irregularly arranged larger and smaller pits that reach up to the bone margins. Based on the presence of the off-centered peak, the osteoderm could be from an accessory row on the trunk or from the tail of the animal.

AMU-CURS-1184 is an osteoderm with sub-rectangular base (62 × 78 mm) and a medial keel (Fig. 20P). The posterior margin and one of the lateral margins of the osteoderm show stronger sutures, whereas the sutures are less developed on the anterior and opposite lateral margins. Ventrally, a strong cross-hatching pattern is visible. AMU-CURS-1185 is a keeled osteoderm with a rectangular shape. The lateral margins comprise thickened sutures, indicating articulation with adjacent medially and laterally positioned osteoderms. The bone surface is sculptured with deep pits, except the anterior margin, which remains as a free anterior bar. This specimen (36 mm long × 32 mm wide) pertains to the dorsal paravertebral shield. Due to gypsum incrusting, a cross-hatching pattern and few scattered nutrient foramina are only weakly visible in the ventral bone surface.

AMU-CURS-1311 is a partial osteoderm with an ovoid base and medial keel (Fig. 20O1, O2). Ventrally a slight cross-hatching pattern and a few small foramina are discernible. AMU-CURS-1312 (Fig. 20T1, T2) and -1314 (Fig. 21B) are partial osteoderms with rectangular bases and medial keels. The anterior dorsal margins of the osteoderms taper to a sharp edge and lack ornamental pitting. The ventral base of both osteoderms is slightly concave. A weak cross-hatching pattern and few small foramina can be seen on the ventral bone surface. AMU-CURS-1313 (Fig. 20S) comprises a strongly eroded partial osteoderm with medial keel that lacks the lateral margins, and AMU-CURS-1316 is a strongly weathered flat osteoderm of rectangular shape (Fig. 21C).

Most cranial and postcranial bones are poorly preserved. Cranial bones are represented by small portion of the left dentary (AMU-CURS-1320, Fig. 21D1, D2), possibly preserving the posterior margin of the fourth alveolus to the anterior margin of the seventh alveolus (the fourth one being much larger than the others), and a small portion of either skull or lower jaw (AMU-CURS-1321, Fig. 21E), with strong sculptured pitting pattern on the external bone surface. AMU-CURS-1200 is a fragment that derives from the skull roof and preserves a part of the dorsal and posterodorsal orbital rim of a frontal sutured to a small anterior part of the parietal (Fig. 21F). The dorsal surface of both bone fragments shows ornamental pitting and a smooth ventral bone surface. The frontal part also shows a small foramen laterally. AMU-CURS-1309 comprises the posterior part of a surangular (Fig. 21G).

Postcranial bones include fragmented vertebrae, ribs, and limbs. AMU-CURS-21 is well-preserved vertebral



centra with cotyle and condyle articulations (Fig. 21I1, I2). Anteroventrally, partially preserved hypapophyses and lateroventrally, elongated parapophyses that extend along the anterior margin of the centrum are present, which indicates that these specimens are from the anterior (postaxial) cervical vertebrae. The centrum is 23 mm long, 14 mm wide, and 17 mm high (anteriorly). AMU-CURS-578a corresponds to a centrum of a dorsal vertebra with a condyle and a cotyle as articular surfaces (Fig. 21L1, L2), and one rib fragment (Fig. 21P). The vertebral centrum is 25 mm long and 17 mm wide at mid-centrum. Ventrally, the centrum has a straight and not a concave border and thus represents one of the posterior centra in the dorsal (lumbar) series. The rib fragment (AMU-CURS-578b) is 84 mm long and

12.5 mm wide at the widest and flattened expansion of the rib shaft. AMU-CURS-743 is an isolated humeral shaft (Fig. 21H), where most of the proximal head and distal epiphysis are not preserved, so that the fourth trochanter and a small foramen constitute the only identifiable shaft features. AMU-CURS-826 is a well-preserved vertebral centrum (Fig. 21J1, J2) with cotyle and condyle articulations similar in shape to AMU-CURS-21. AMU-CURS-887 is an isolated vertebral centrum from the dorsal series. The centrum has a cotyle and a condyle and dorsally, the facets for the neural arch and the floor of the neural canal are visible, and zygapophyses are not preserved. AMU-CURS-1030 is another isolated crocodylian vertebral centrum with a cotyle and condyle articulation (Fig. 21K1, K2). The centrum is 41 mm long

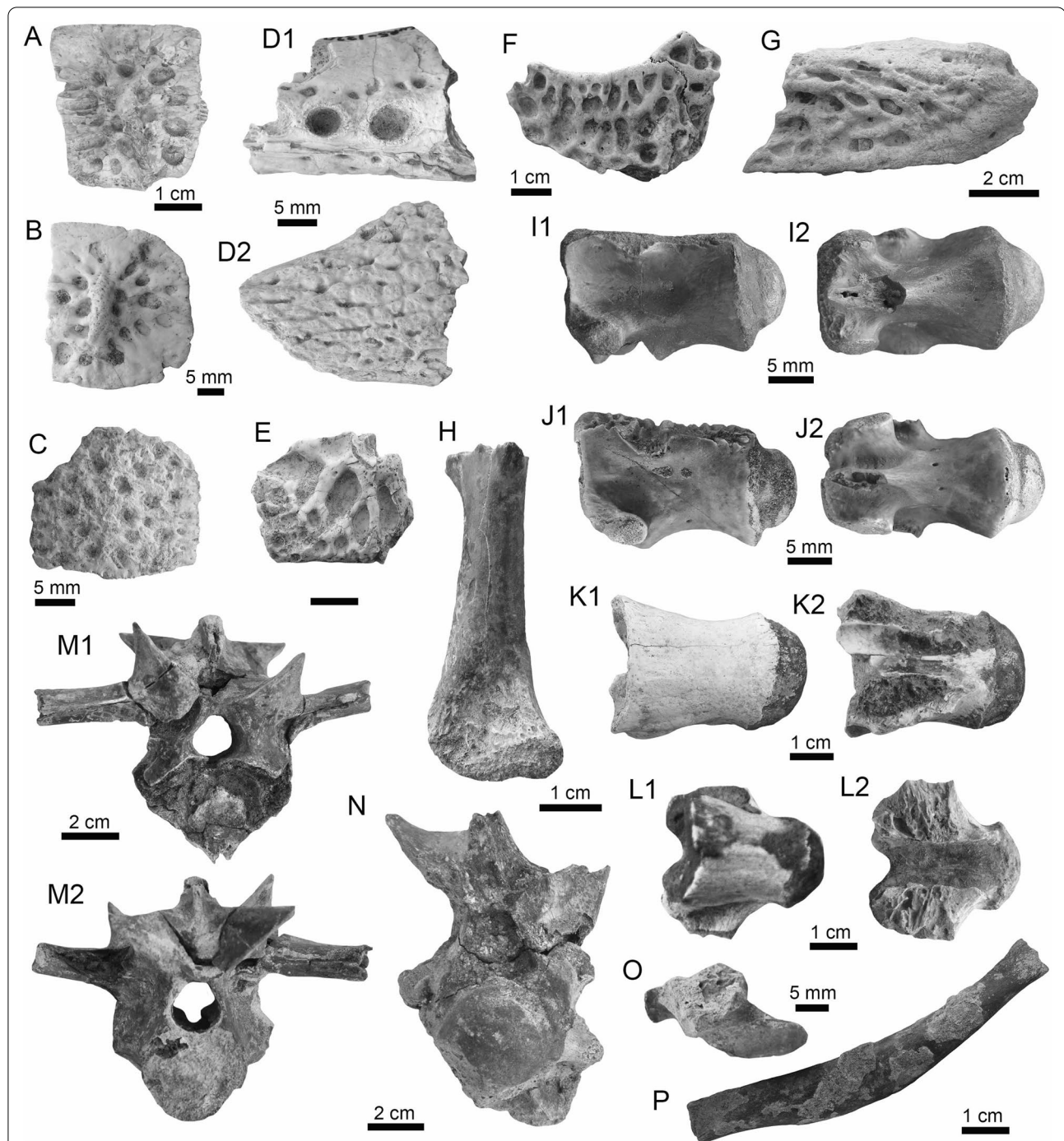


Fig. 21 Crocodylia indet. from the Vergel (A, F, H–P) and Cocuiza (B, C, D1–E, G) members. A–C Osteoderms (A AMU-CURS-1029, B AMU-CURS-1314, and C AMU-CURS-1316). D1, D2 Portion of a left dentary (AMU-CURS-1320). E Portion of either skull or lower jaw (AMU-CURS-1321). F Fragment from the skull roof (AMU-CURS-1200). G Posterior part of a surangular (AMU-CURS-1309). H Humeral shaft (AMU-CURS-743). I1–N Vertebrae (I1, I2 AMU-CURS-21, J1, J2 AMU-CURS-826, K1, K2 AMU-CURS-1030, L1, L2 AMU-CURS-578a and M1–N AMU-CURS-1062). O Isolated prezygapophysis (AMU-CURS-1236). P Rib fragment (AMU-CURS-578b). Views: anterior (M1), dorsal (D1, F, K2, L2, O), external (A–C), left lateral (D2, I1, J1, G), posterior (M2–N), ventral (H, I2, J2–K1, L1), and indet. (E, P)

and 22.5 mm at mid-centrum. This specimen also comes from the posterior part of the dorsal (lumbar) vertebral series. AMU-CURS 1062 comprises two vertebrae of different sizes showing the proximal bases of hypapophyses, and are thus identified as pertaining to the cervical series (Fig. 21M1–N). The smaller vertebra has well-preserved zygapophyses and transverse processes, but the neural spine and the condylar and cotylar articulations of the centrum are strongly weathered (Fig. 21M1, M2). The larger specimen has a better-preserved centrum, but the neural spine and the zygapophyses—with the exception of the left postzygapophysis—are not preserved (Fig. 21N). AMU-CURS-1236 corresponds to an isolated prezygapophysis and five four partially preserved osteoderms, which were not found in association to each other (Fig. 21O). The articulation facet of the isolated prezygapophysis is 15 mm long and 8 mm wide. The very fragmentarily preserved osteoderms show strong ornamentation of the external bone surface in the form of pitting, but otherwise lack sutural contacts or other diagnostic features.

Mammalia Linnaeus, 1758
 Metatheria Huxley, 1880
 Didelphimorphia Gill, 1872
 Didelphidae Gray, 1821a
Didelphis Linnaeus, 1758
 cf. *Didelphis* sp.
 (Fig. 22A1–A3).

Locality: NCC (conglomerate, Fig. 3B).

Material: A partial right humerus (AMU-CURS-1140).

General description, comparisons and remarks: AMU-CURS-1140 has a length of 22 mm, preserving a short portion of the shaft and distal epiphysis, where the entepicondylar foramen (Fig. 22A2, A3), the humeral coronoid fossa (Fig. 22A1), olecranon fossae, and medial epicondyle (Fig. 22A2, A3) are preserved. AMU-CURS-1140 has certain similarities with the humerus of extant species of *Didelphis*; however, the fragmentary nature of the fossils does not permit an identification beyond generic level.

Placentalia Owen, 1837
 Xenarthra Cope, 1889
 Phyllophaga Owen, 1842
 †Megatheriidae Gray, 1821b
 †Megatheriinae Gray, 1821b
 †*Proeremotherium* Carlini, Brandoni and Sánchez, 2006b
 cf. †*Proeremotherium* sp.
 (Fig. 22B1–C3).

Locality: NCC (conglomerate, Fig. 3B) and SGOP (conglomerate Ly1, Fig. 3C).

Material: A nearly complete skull of a ground sloth (AMU-CURS-184), collected from the sandstones overlying the conglomeratic layer in the NCC locality, and an isolated tooth (AMU-CURS-1303) from the SGOP locality.

General description, comparisons and remarks: AMU-CURS-184 is a relatively well-preserved skull with a total length of 455 mm, lacking the jugals, the premaxillae, the left zygomatic process of the squamosal, vertical lamina of the left pterygoid, anterior part of the nasals, anterior part of the maxillae, lateral and partial anterior wall of the alveoli of right Mf1, lateral and anterior wall of the alveoli of left Mf1, and the lateral wall of those of the left tooth row, and teeth (Fig. 22B1–B3). AMU-CURS-184 is broadly similar in size and morphology to that of †*Proeremotherium eljebe* from the underlying Codore Formation in the Urumaco Sequence (Carlini et al. 2006b), but differing in several features such as a longer basicranial area and a more posteriorly projected basioccipital between the condyles (see for details Carlini et al. 2018). The presence of this specimen assigned to cf. *Proeremotherium* in the San Gregorio Formation documents a northern Neotropical occurrence of a megatheriine that addresses issues on intraspecific variation and biogeography (Carlini et al. 2018).

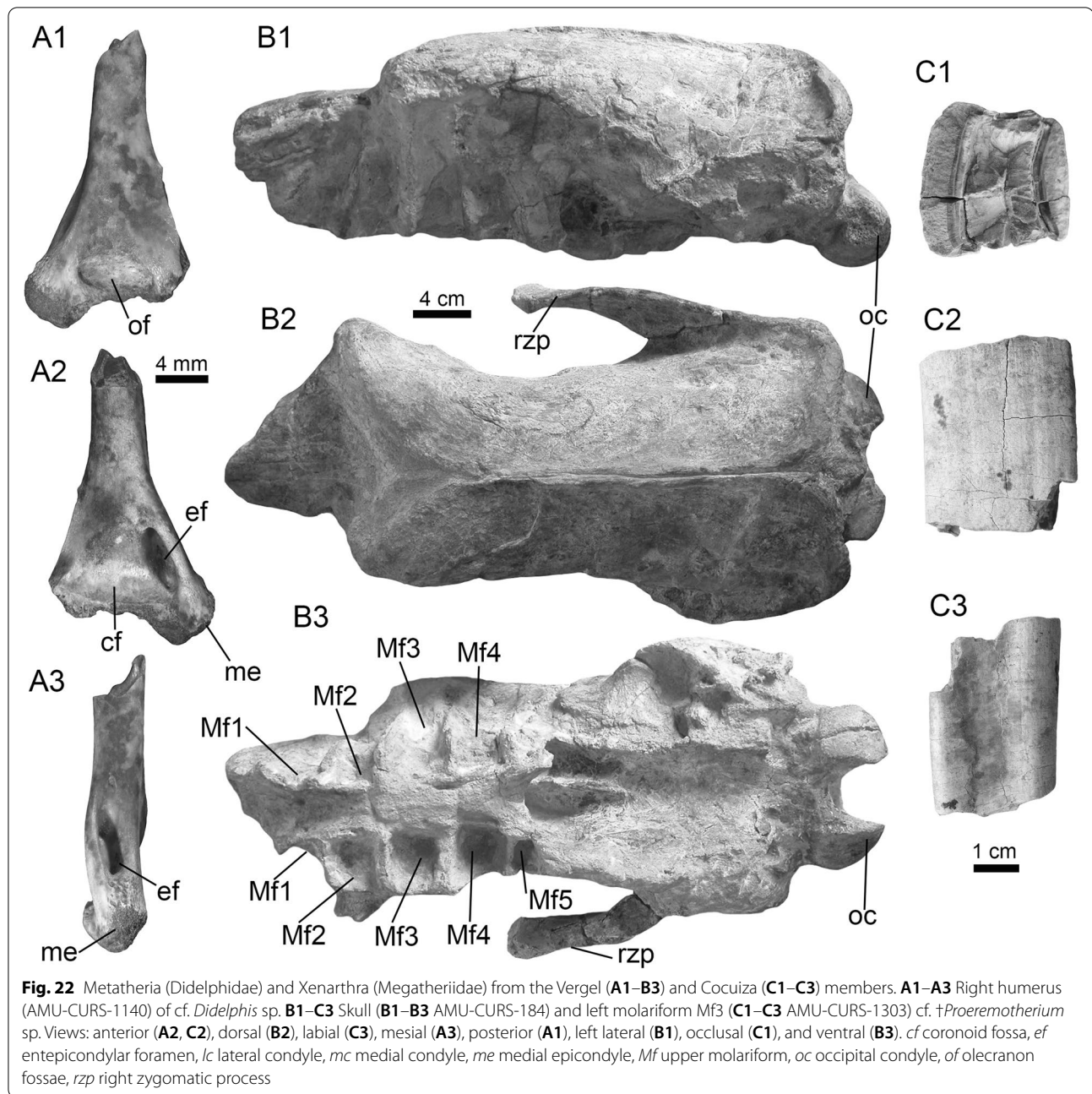
The isolated tooth AMU-CURS-1303 is an incomplete left molariform Mf3 (42 mm height) of indeterminate position (Fig. 22C1–C3). The molariform lacks enamel and it is almost quadrangular in shape (slightly wider than long), with well-marked corners. Although in occlusal view AMU-CURS-1303 is broken and transversal hard dentine (orthodentine) layers are still visible, the two well-developed transversal crests of orthodentine, separated by a deep “V”-shaped valley that characterize cheek teeth (except Mf5) of megatherids (see Carlini et al. 2006b; Bargo et al. 2012), are not preserved.

†Mylodontidae Gill, 1872
 †Mylodontidae indet.
 (Fig. 23A1–A3).

Locality: NCC (conglomerate, Fig. 3B).

Material: A right humerus (AMU-CURS-62).

General description, comparisons and remarks: The specimen AMU-CURS-62 is approximately 450 mm in length. It was collected in the sandstones overlying the conglomeratic layer in the NCC locality (Fig. 2E). As in other mylodontids, like †*Bolivartherium*, †*Lestodon*, or †*Glossotherium*, AMU-CURS-62 has a head that slightly exceeds the height of the major and minor tuberosities (Fig. 23A1, A2), and does not markedly projected posteriorly. The major tuberosity is slightly larger and more



massive than the minor one. The diaphysis is a little wider than in specimens known of the above-mentioned genera. The pectoral and deltoid crests are prominent, placed at the mid-shaft, forming a “V” pointed distally and aligned with the main diaphyseal axes (not as in scelidotherines, where these structures are diagonally set at the beginning of the distal third of the diaphysis).

The entepicondylar foramen is absent and the pronator and supinator processes are not strongly developed but broad, forming a wide and flattened distal third. The projected line that joins its medial most and lateral-most projections being oblique with respect to the line that joins the tuberosities. The olecranial fossa is not deep (Fig. 23A2), and the distal line of the trochlea is slightly

concave. At the distal articular surface, the condyle is bigger mediolaterally than the trochlea.

Cingulata Illiger, 1811

†Glyptodontoidea Gray, 1869

†Glyptodontidae Gray, 1869

†*Boreostemma* Carlini et al., 2008b

aff. †*Boreostemma* sp.

(Fig. 23B, C).

Locality: NCC (conglomerate, Fig. 3B).

Material: Two osteoderms of the carapace region (AMU-CURS-1242).

General description, comparisons and remarks: The osteoderms AMU-CURS-1242 resemble those of *Boreostemma* from the underlying Codore Formation (Pliocene) (see Carlini et al. 2008b); however, the poor preservational condition does not allow a more accurate taxonomic assignation. The complete specimen, which is 43 mm in length (Fig. 23B), can be assigned here to dorsal or postero-dorsal osteoderm of the carapace region. The second specimen is incomplete and precludes a determination of the carapace region (Fig. 23C). The specimens AMU-CURS-1242 correspond to the osteoderms referred previously to aff. †*Boreostemma codorensis* by Vucetich et al. (2010). These osteoderms were not illustrated by Vucetich et al. (2010), and the taxonomical reference by these authors as aff. *B. codorensis* is incorrect, as the correct name of the species is †*Boreostemma pliocena* (see Carlini et al. 2008b). Other specimens assigned to *Boreostemma*? from the NCC locality included at least 14 osteoderms reported by Carlini et al. (2008c) and Zurita et al. (2011).

†Pamphathiidae Paula Couto, 1954

†*Holmesina* Simpson, 1930

†*Holmesina floridanus* Robertson, 1976

aff. †*Holmesina floridanus*.

(Fig. 23D1–G2).

Locality: NCC (conglomerate, Fig. 3B) and SGOP (conglomerate Ly1, Fig. 3C).

Material: Four carapace osteoderms, including two incomplete movable osteoderms from the NCC (AMU-CURS-1063 and -1119) and two fixed osteoderm of pelvic buckler from SGOP (AMU-CURS-1294 and -1295) localities.

General description, comparisons and remarks: Vucetich et al. (2010) referred some osteoderms assigned to aff. *Holmesina floridanus* for the NCC locality; however,

the specimens were not illustrated. The new pamphathere osteoderms collected in the San Gregorio Formation and referred herein belong to a new taxon (sp. 1) under study (in prep.) and aff. to *Holmesina floridanus* (the oldest species recorded as a pamphathere in North America) (Edmund 1987; Scillato-Yané et al. 2005; Carlini and Zurita 2010).

The specimens described herein (Fig. 23D1–E2) are thick, with a peripheral area lower than the main exposed surface, with one or two rounds of depressions that opens radially; the surface is rugose in appearance because of several punctures, on the exposed main surface clear central area elevated, flanked by two shallow and wide depressions. The evidence suggests that a †*Kraglievichia/Holmesina* (or a related intermediate taxon) would have migrated to North America during the GABI, and there the genus *Holmesina* would have differentiated with a single species (*H. floridanus*) for the Blancan (and Irvingtonian?), and other species for the RanchoLabrean (†*Holmesina septentrionalis*, that was sometimes included as a taxon in the Blancan because of labels in collections) (Carlini and Zurita 2010). Similarities between specimens AMU-CURS-1063 (Fig. 23D1, D2), -1119 (Fig. 23E1, E2), -1294 (Fig. 23G1, G2) and -1295 (Fig. 23F1, F2), from the San Gregorio Formation and osteoderms of *H. floridanus* (FLMNH-UF 223813) from the late Blancan late Pliocene of North America, are evident, which support the hypothesis that *Holmesina* is linked to the *Kraglievichia* lineage (Carlini and Zurita 2010), provided these similarities are indeed indication of close relationships. The sequence †*Kraglievichia par-anense* (late Miocene, Tortonian) (Cione et al. 2000)—new “sp.1” of the San Gregorio Formation—*H. floridanus* (late Blancan, late Pliocene) may represent an anagenetic series.

†*Plaina* Castellanos, 1937

aff. †*Plaina* sp.

(Fig. 23H1, H2).

Locality: NCC (conglomerate, Fig. 3B).

Material: An isolated and complete fixed osteoderm of pelvic buckler (AMU-CURS-736).

General description, comparisons and remarks: AMU-CURS-736 (sp. 2) is 35 mm in length, resembling those osteoderms of *Plaina* sp. from the Pliocene of Northwestern Argentina (Gois 2013; Góis et al. 2013; Bonini 2014). It is because AMU-CURS-736 has an almost flat

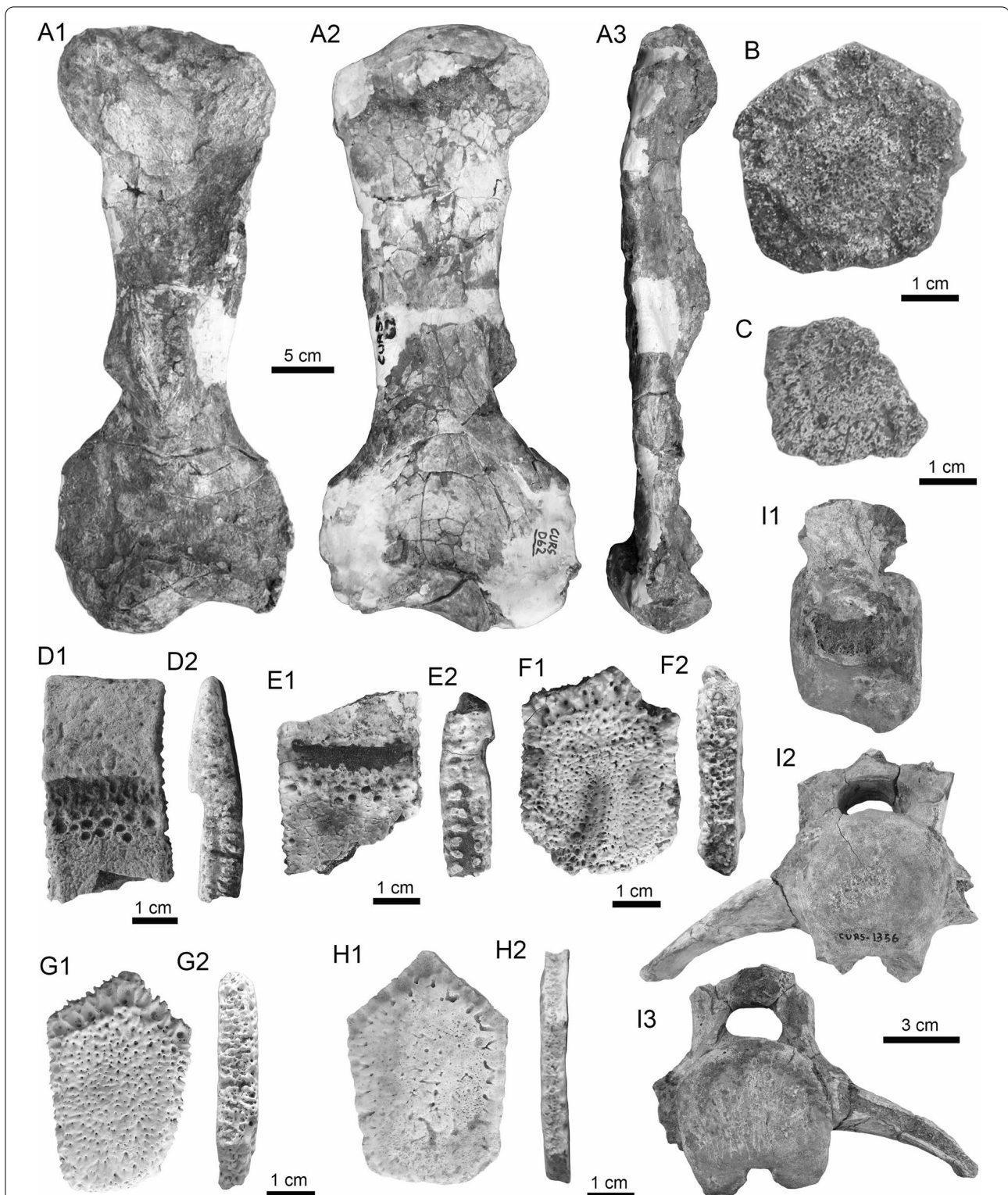


Fig. 23 Xenarthra (Mylodontidae, Glyptodontidae, and Pamphathiidae) from the Vergel (**A1–E2, H1, H2**) and Cocuiza (**F1–G2, I1–I3**) members. **A1–A3** Right humerus (AMU-CURS-62) of Mylodontidae indet. **B, C** Carapace osteoderms (AMU-CURS-1242) of dorsal or postero-dorsal (**B**) and indeterminate position (**C**) of aff. *Boreostemma* sp. **D1–G2** Movable osteoderms (**D1, D2** AMU-CURS-1063, and **E1, E2** AMU-CURS-1119), and fixed osteoderms of pelvic buckler (**F1, F2** AMU-CURS-1295, and **G1, G2** AMU-CURS-1294) of aff. *Holmesina floridanus*. **H1, H2** Fixed osteoderm of pelvic buckler (AMU-CURS-736) of aff. *Plaina* sp. **I1–I3** Incomplete caudal vertebra (AMU-CURS-1356) of Xenarthra indet. Views: anterior (**A1, I2**), cross-sectional (**D2, E2, F2, G2, H2**), external (**B–D1, E1, F1, G1, H1**), left lateral (**I1**), medial (**A3**), and posterior (**A2, I3**)

and smooth exposed surface with few punctuations, and with a shallow and wide depression, that surrounds a slightly elevated and rounded central area (Fig. 23H1). AMU-CURS-736 is thinner (Fig. 23H2) than those of the specimens “sp. 1” referred above to aff. *Holmesina* (AMU-CURS-1063, -1294 and -1295). AMU-CURS-736 is close to half of its thickness for an equivalent surface (e.g., Fig. 23D2, E2, F2 and G2). The presence of this eventual new “sp. 2” in the NCC locality would represent a second lineage of pampatheres.

Xenarthra indet.
(Fig. 23I1–I3).

Locality: SGOP (conglomerate Ly1, Fig. 3C).

Material: An incomplete caudal vertebra (AMU-CURS-1356).

General description, comparisons and remarks: AMU-CURS-1356 corresponds to a caudal vertebra of the anterior region of the series with a centrum of 57 mm in diameter. The right transverse process, hemal facets, and neural arch are preserved; however, the articular facets and spinous process are missing. The right transverse process in AMU-CURS-1356 projects so far ventrally, a morphological feature observable also in some glyptodonts (see Gillette and Ray 1981, figs. 76, 77). Nevertheless, due to the preservational condition of AMU-CURS-1356, for now, we refrain from assigning this specimen to either a terrestrial sloth or a glyptodont.

†Meridiungulata McKenna, 1975
†Liptopterna Ameghino, 1889
†Proterotheriidae Ameghino, 1887
†Proterotheriidae indet.
(Fig. 24A1–B2).

Locality: NCC (conglomerate, Fig. 3B).

Material: A metacarpal (AMU-CURS-742) and a distal epiphysis of a metacarpal (AMU-CURS-1189).

General description, comparisons and remarks: The proterotheriid elements assigned here as a metacarpal (Fig. 24A1–A3) and a distal epiphysis of a metacarpal (Fig. 24B1, B2), likely belonged to a juvenile individual as the epiphysis did not fuse to the shaft. Due the fragmentary condition of these specimens, it is not possible to determine a more precise taxonomic identification. Carrillo et al. (2018) reported proterotheriid specimens from the Algodones Member of the Codore Formation, the new specimens here reported from the NCC locality extend the stratigraphic record to the Vergel Member of the San Gregorio Formation.

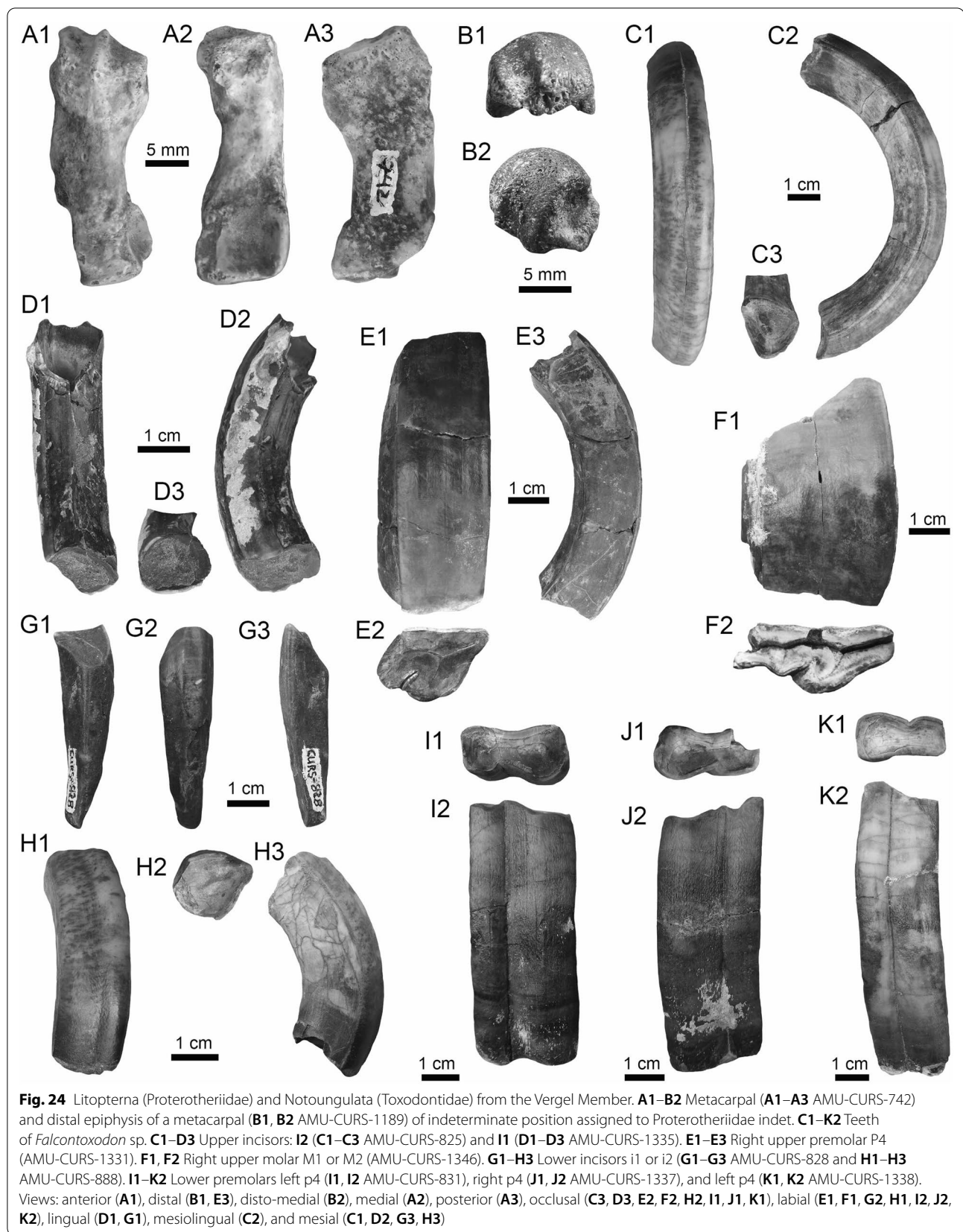
†Notoungulata Roth, 1903
†Toxodontidae Gervais, 1847
†Toxodontinae Trouessart, 1898
†*Falcontoxodon* Carrillo et al., 2018
†*Falcontoxodon* sp.
(Figs. 24C1–K2 and 25A1–E3).

Locality: NCC (conglomerate, Fig. 3B).

Material: Thirty-three dental and postcranial elements, including two upper incisors (AMU-CURS-825 and -1335), two upper premolars (AMU-CURS-1331 and -1332), two upper molars (AMU-CURS-1333 and -1346), five lower incisors (AMU-CURS-828, -888, -1339, -1342, and -1350), 14 lower premolars (AMU-CURS-831–835, -846, -889, -1334, -1336–1338, -1340–1341, and -1343), five lower molars (AMU-CURS-1344–1345 and -1347–1349), two astragali (AMU-CURS-1202 and -1330), and one metatarsal (AMU-CURS-1118).

General description, comparisons and remarks: We report 33 additional dental and postcranial elements of *Falcontoxodon* sp., a taxon reported from the same locality by Carrillo et al. (2018). The second upper incisor (I2) is developed as a tusk; it is triangular in cross section with enamel in the mesial and part of the labial side of the crown (Fig. 24C1–C3). The upper premolars (P4) show an enamel band on the labial side of crown, a second one on the mesiolingual side and a lingual enamel fold with a narrow enamel band (Fig. 24E1, E2). The upper molars are identified as M1 or M2 (Fig. 24F1, F2) because of the absence of a lingual column in the protoloph (Carrillo et al. 2018). They have a primary lingual enamel fold and one broad enamel band on the labial side of the crown and two narrow bands, one on the mesial and one on the lingual side.

The lower incisors (Fig. 24G1–H3) have a broad labial enamel band and a narrow lingual band. In one specimen (AMU-CURS-1342), there is a small lingual enamel fold. The lower premolars (Fig. 24I1–K2) have an enamel band only on the labial side. The specimens with a labial groove are tentatively identified as p4, which is absent in the p3 of the holotype of *Falcontoxodon* (Carrillo et al. 2018). The lower molars (identified as m1 or m2) have a buccal enamel fold on the labial side of the crown, and a meta-entoconid and ento-hypoconulid fold on the lingual side (Fig. 25A1–B3). There is a lingual enamel band that extends from the anterior fold to the hypococonulid, as in the holotype of *Falcontoxodon* (Carrillo et al. 2018). The new postcranial elements include two astragali (AMU-CURS-1202 and -1330, Fig. 25C1–D2) and a metatarsal IV (AMU-CURS-1118, Fig. 25E1–E3). The neck of the astragali is very short and the medial tibial



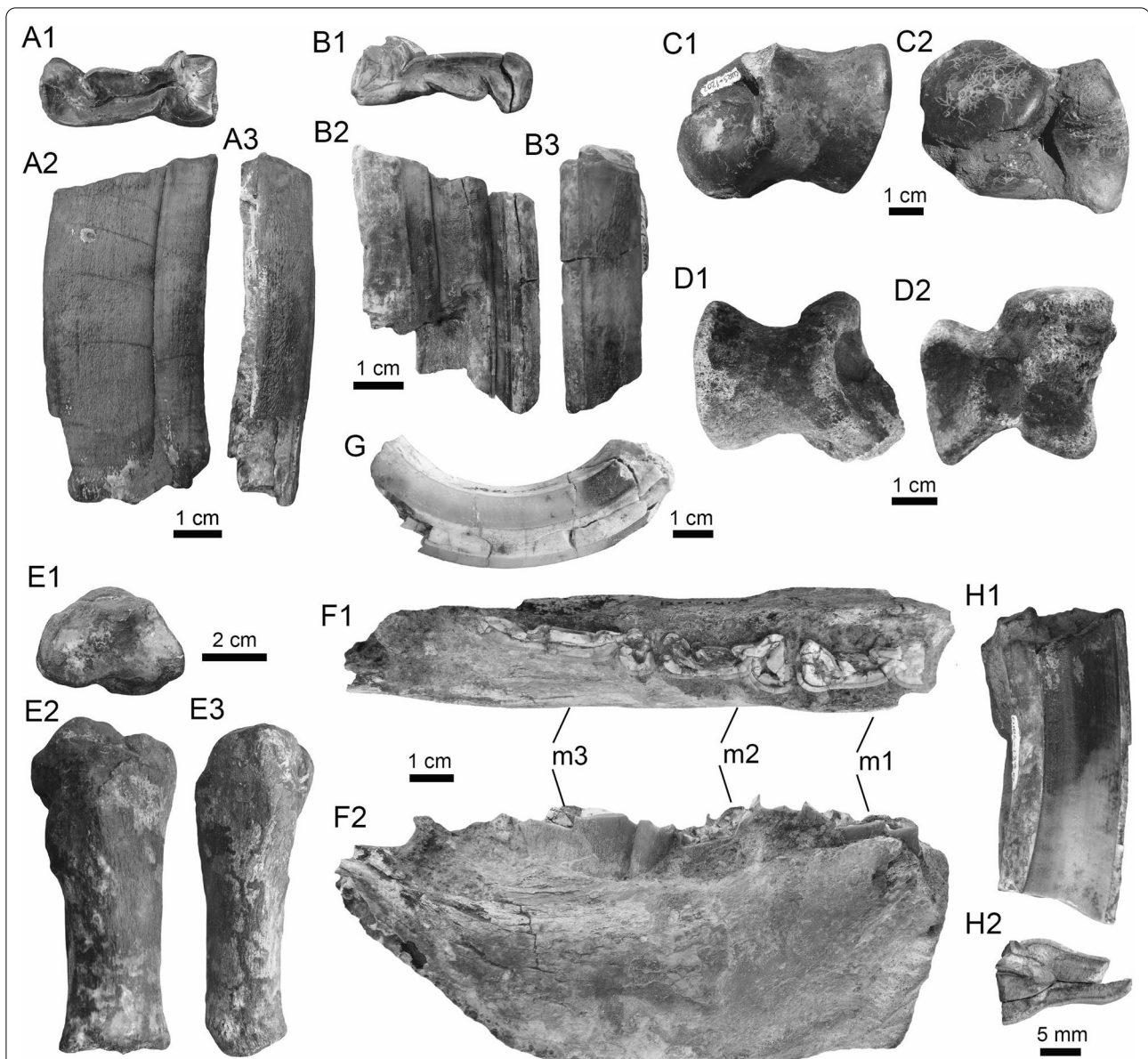
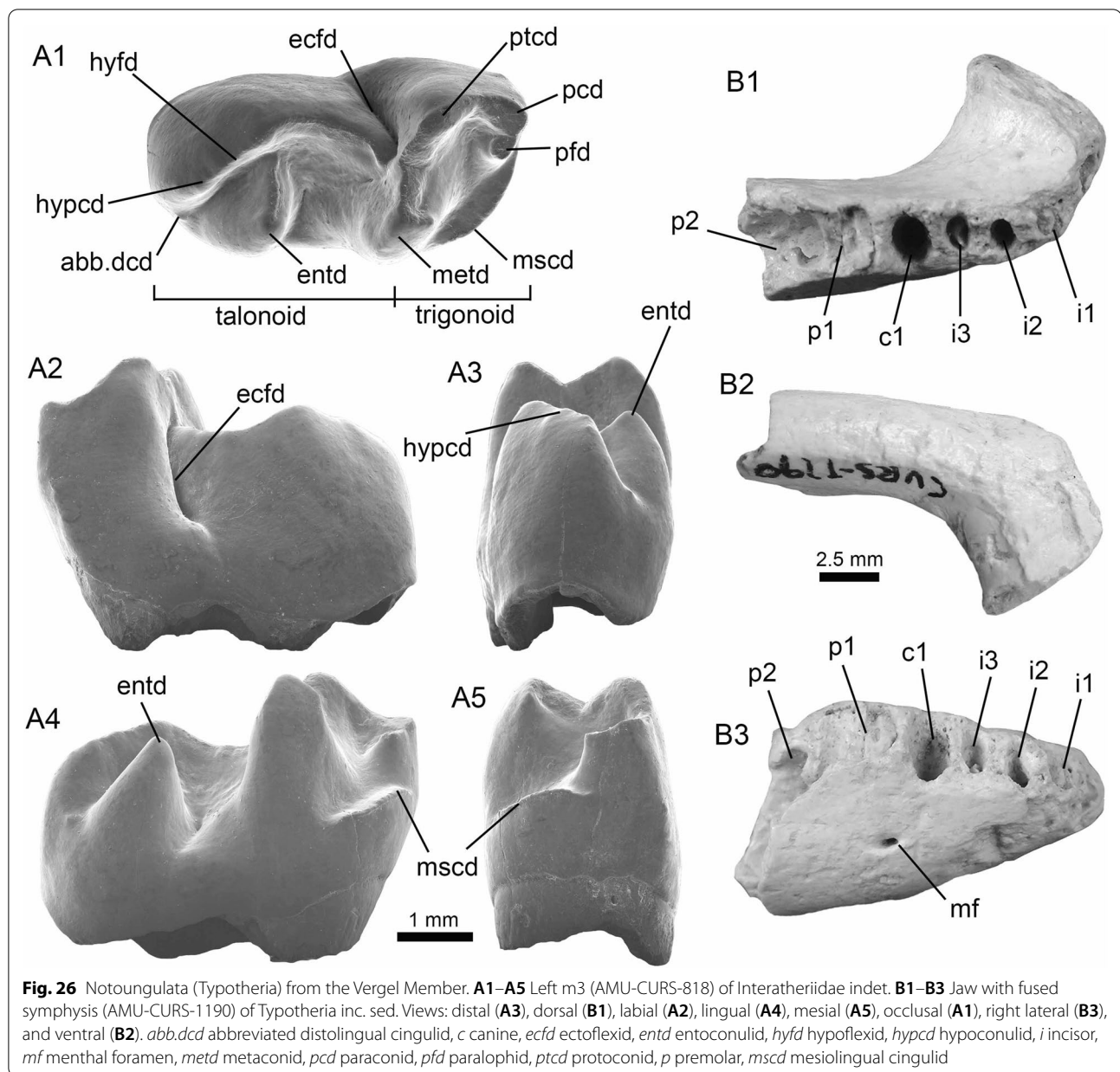


Fig. 25 Notoungulata (Toxodontidae) from the Vergel (A1–E3) and Cociiza (F1–H2) members. A1–E3 *Falcontoxodon* sp. A1–B3 Right lower molars, m1 or m2 (A1–A3 AMU-CURS-1345 and B1–B3 AMU-CURS-1348). C1–D2 Astragali. C1, C2 Left astragalus (AMU-CURS-1202). D1, D2 Right astragalus (AMU-CURS-1330). E1–E3 Metatarsal IV (AMU-CURS-1118). F1–H2 Toxodontinae indet. F1, F2 Right partial mandible (AMU-CURS-1351). G Upper incisor (AMU-CURS-1326). H1, H2 Upper left molar (AMU-CURS-1325). Views: anterior (E1), lateral (E3, F2), distal (A3, B3), dorsal (C1, D1, E2), plantar (C2, D2), labial (A2), lingual (B2, G, H1), and occlusal (A1, B1, F1, H2)

facet is expanded medially, as in the *Falcontoxodon* astragalus described from the same locality (Carrillo et al. 2018). However, in the new astragali, specimens have the sustentacular and navicular facets separated, unlike the

astragalus previously described, which could be related to intraspecific or ontogenetic variation.

†Toxodontinae indet.
(Fig. 25F1–H2).



Locality: SGOP (conglomerate Ly1, Fig. 3C).

Material: An upper incisor (AMU-CURS-1326), an upper left molar (AMU-CURS-1325), and a right partial mandible (AMU-CURS-1351).

General description, comparisons and remarks: The upper left molar AMU-CURS-1325 (Fig. 25H1, H2) is ~80 mm in length, and the right partial mandible (AMU-CURS-1351) of ca. 155 mm in length with m1–m3. The lower molars in AMU-CURS-1351 have a buccal enamel fold, and on the lingual side, the m1 and m2 have a meta-entoconid and an ento-hypoconulid fold

(Fig. 25F1, F2). Parts of the crowns are broken, including enamel bands on the lingual side.

†*Typotheria* Zittel, 1893

†*Interatheriidae* Ameghino, 1887

†*Interatheriidae* indet.

(Fig. 26A1–A5).

Locality: NCC (conglomerate, Fig. 3B).

Material: an isolated crown (AMU-CURS-818).

General description, comparisons and remarks: AMU-CURS-818 is an isolated unworn crown of the left m3

with a length of 4.7 mm. The crown has a distinctive elongated talonid (Fig. 26A1), is nearly hypsodont, and lacks cementum. On the occlusal surface, the crown is lophodont and displays a straight and long transverse metacristid with no distinct longitudinal projection. The trigonid has a distinctive labial reduction of the anterolingual cristid. A deep lingual sulcus separates the paraconid from the metaconid. The metacristid of the metaconid is distinct and projects lingually. The protoconid is connected to the paraconid by a longitudinal ridge. Similar to the m3 of other typotheres, the talonid attaches to the trigonid about midway along the length of the transverse metacristid and forms a labially convex crescent. A discontinuous cingular segment is located distolabially from the hypoconulid. There is a strong mesiolingual cingulid connecting the base of the paralophid with the base of the metaconid. The cristid obliqua is short, low, and rounded and runs parallel to the tooth row.

AMU-CURS-818 is referred to the Notoungulata based on it having a lophodont dentition with two main crescentic crestids (the metalophid and the hypolophid) together with a shorter transverse entolophid derived from the entoconid. The crown lacks cementum and is hypsodont, a distinctive morphology not present in any small-sized notoungulate. It lacks the distinctive tube-like margins present in hypselodont interatheriids with cementum (e.g., †*Miocochilius*). The unreduced second lobe present in the m3 rules out any hegetotheriidae relationships (Cerdeño and Reguero 2015), an interpretation also supported by the lack of cementum, and having a less reduced posterior lobe on m3, the latest only present in Neogene interatheriids. The relative depth of the labial valley between the trigonid and talonid rules out any relationship with other Neogene notoungulate reported in tropical South America. Finally, the presence of an anterolingual cingulid, only preserved in Paleogene †*Notostylops*, suggests an earlier divergence from primitive interatheriids. This small notoungulate has a distinct reduced talonid, and a labially reduced crest connecting the paralophid with the protoconid, features only present in Paleogene notoungulates. The m3 lacks the elongated second lobe present in Neogene mesotheriine specimens, e.g., †*Miocochilus anomopodus* and †*Protypotherium* (Rose 2006; Renvoisé and Michon 2014; Tapaltsyán et al. 2015). The nearly hypsodont crown with no cementum suggests a non-notohippine ancestry (Wyss et al. 2018).

AMU-CURS-818 from the NCC locality is one of the youngest interatheriid fossils in South America. Despite its clear association with fluvial depositional paleoenvironments, the shape of the crown suggests little to no transport prior to burial (Fig. 26A1–A5). However, a distinctive hypselodont dentition cannot be identified in our reduced sample ($N=1$). Despite evident sampling

biases, many of these hypselodont dental morphologies are distinctive of Neogene interatheriids, such as *Miocochilius* or *Protypotherium*. In contrast, the occurrences of notostyloids (typotheres) are restricted to Paleogene sequences in Argentina, Brazil, and Chile (McKenna and Bell 1997; Billet 2011). The absence of cementum rules out any relationship with the Interatheriinae (Vera et al. 2017), while the crown lacks the distinctive flat labial face present in hegetotheriids (Cerdeño and Reguero 2015). The anteroposterior elongation of the second lobe rules out any relationship to basal hegetotheriids, while the m3 has a relatively deep labial sulcus on m3 not present in basal Interatheriinae such as †*Santiagorothia* and †*Proargyrohyrax* (Cerdeño and Reguero 2015).

†Typotheria inc. sed.
(Fig. 26B1–B3).

Locality: NCC (conglomerate, Fig. 3B).

Material: A partial jaw (AMU-CURS-1190).

General description, comparisons and remarks: AMU-CURS-1190 is a partial jaw with fused symphysis of 16.0 mm in length and 13.5 mm in width. The specimen lacks all tooth crowns (Fig. 26B1) but the alveoli for lower i1 and right i1–p2 are preserved. A mental foramen is located about 5.0 mm below the base of the crown for the p1 (Fig. 26B3). The posterior end of the symphysis is located below the root of the p1 (Fig. 26B2). The symphysis is shallower than that of small-sized typotheres, like the hegetotheriid †*Hemihegetotherium trilobus* (Croft and Anaya 2006), and resembles the more gracile Eocene typotheres genus †*Griphitherion* from northwestern Argentina (García and Powell 2011). AMU-CURS-1190 is tentatively referred as a Typotheria inc. sed. based on its small size, shallow symphysis, and completely fused mandible.

Rodentia Bowdich, 1821

Hystricognathi Tullberg, 1899

Caviomorpha Wood, 1955

Cavioidea Fisher von Waldheim, 1817 (sensu Kraglievich 1930)

Caviidae Fisher von Waldheim, 1817

Hydrochoerinae (Gray, 1825a, b) Gill 1872: Weber 1928 (sensu Kraglievich 1930)

†*Hydrochoeropsis* Kraglievich, 1930

?†*Hydrochoeropsis wayuu* Pérez et al., 2017

(Fig. 27A1–B2).

Locality: NCC (Fig. 3B).

Material: A right dentary (AMU-CURS-744) and a left M1 or M2 (AMU-CURS-1222).

General description, comparisons and remarks: The dentary of AMU-CURS-744 is ca. 89 mm in length (Fig. 27A1, A2); it was recovered from the fine sandstone layer about 20 cm below the conglomerate (Fig. 3B). AMU-CURS-744 is quite damaged, but the occlusal surface of the cheek teeth is relatively well preserved (Fig. 27A1, A2). On the medial surface of the dentary, the incisor alveolus forms a salience extended up to the m1 (Fig. 27A2). A prominence projects from the posterior most region of the alveolus in posterior direction, up to the level of the m3, where it is located the mandibular foramen, which penetrates the dentary obliquely (Fig. 27A2). In the lateral view, a small portion of the condylar process is preserved posteriorly to the level of the m3.

The cheek teeth are euhyposodont, formed by prisms or laminae (Fig. 27A1). From the dental series, the p4 and m3 are the best-preserved teeth. The p4 shows the anterior secondary prism (pr.s.a.) with a rounded mesial outline and the tip of the 3rd internal column (c.3e) is oriented distolabially. Lingually, the pr.s.a. shows a wide and shallow 5th internal flexid (h.5i). The secondary external flexid (h.s.e.) is wide and is penetrating obliquely. The pr.s.a. is connected to the pr. I by a thin and short isthmus. The pr. II and I are “y-shaped,” both connected by a short mesiodistally oriented isthmus. The columns of these prisms are transversely oriented, being the tip of the 3rd internal column (c.3i.) located at the same level as the 2nd external column (c.2e.). On the lingual region of the P I and P II, the 3rd internal flexid (h.3i) and 2nd internal flexid (h.2i) have the same deepness, reaching the midline of the tooth, while the 1st internal flexid (h.1i) is more developed, surpassing the midline. The tip of the h.2i is opposite to the fundamental external flexid (h.f.e). The h.f.e. is wide like the h.s.e. but is less deep. The tip of the 1st external column is broken.

In the m1, from the pr. I only the pr. Ib is preserved (Fig. 27A1). The lingual tip of this prism is connected to the pr. II. The lingual tips of the pr. IIa' and IIa'' are broken. The labial tip of the pr. IIa is connected to the pr. IIb. In the m2, only the pr. I is well preserved (Fig. 27A1). The pr. I' and pr. II' are transverse laminae, labially connected, separated by a labiolingually wide tertiary internal flexid (h.t.i.). The m3 is composed of transverse prisms (Fig. 27A1). The pr. I is “U-shaped” and does not preserve the lingual tip of the pr. I'. The pr. I' and pr. I'' are labially united. The pr. II is quite damaged, not preserving the tips of the pr. IIa and pr. IIb'.

The cheek teeth of AMU-CURS-744, as well as the specimen AMU-CURS-1222, were compared with other Neogene and Quaternary hydrochoerines (Vucetich et al. 2005, 2012, 2014, 2015; Deschamps et al. 2007; Pérez et al. 2017; Gomes et al. 2019; Cerdeño et al.

2019). Two morphological traits of the p4 let us to assign AMU-CURS-744 to the hydrochoerine ?*Hydrochoeropsis wayuu*, a taxon recently described from the Pliocene of Colombia (Pérez et al. 2017): (1) the h.2i and h.3i are equally deep (also shared with *Hydrochoeropsis dasseni* from the Pliocene of Argentina); and (2) the fifth internal flexid (h.5i) has the same wide and depth as in ?*H. wayuu*, differing from other known hydrochoerines (see Pérez et al. 2017: p. 115). Besides, the p4 exhibits a symmetric pr. II, with the 3rd internal column at the same level as the 2nd external column, and the tip of the h.2.i opposite to the h.f.e, which are diagnostic traits of this Pliocene hydrochoerines. The only lower tooth of the type series of ?*H. wayuu* is a fragmented p4. Therefore, the material here described is the most complete lower dental series assigned to this species.

The isolated upper tooth (left M1 or M2) AMU-CURS-1222 of 21.6 mm in length (Fig. 27B1, B2) was collected in a fine sandstone layer about 60 m south of the conglomerate outcrop. Although this layer belongs to the Vergel Member and it is included in the same area that we call NCC locality, stratigraphically it could be located about 30 m below the conglomerate. AMU-CURS-1222 is similar to the specimen MUN-STRI-16233, described by Pérez et al. (2017).

The fossil record of hydrochoerines from NCC locality includes †*Cardiatherium* sp. (see Vucetich et al. 2010). However, with the description of ?*H. wayuu* from the Ware Formation, Pérez et al. (2017) suggested that the remains reported by Vucetich et al. (2010) could belong to young specimens of this species. Hence, the specimens here described confirm the presence of ?*H. wayuu* in the San Gregorio Formation and reinforces the biostratigraphic correlation between the two geological units (Moreno et al. 2015).

Hydrochoerinae indet.

(Fig. 27C1–E2).

Locality: NCC (conglomerate, Fig. 3B).

Material: Three fragmentary teeth (AMU-CURS-1186–1188).

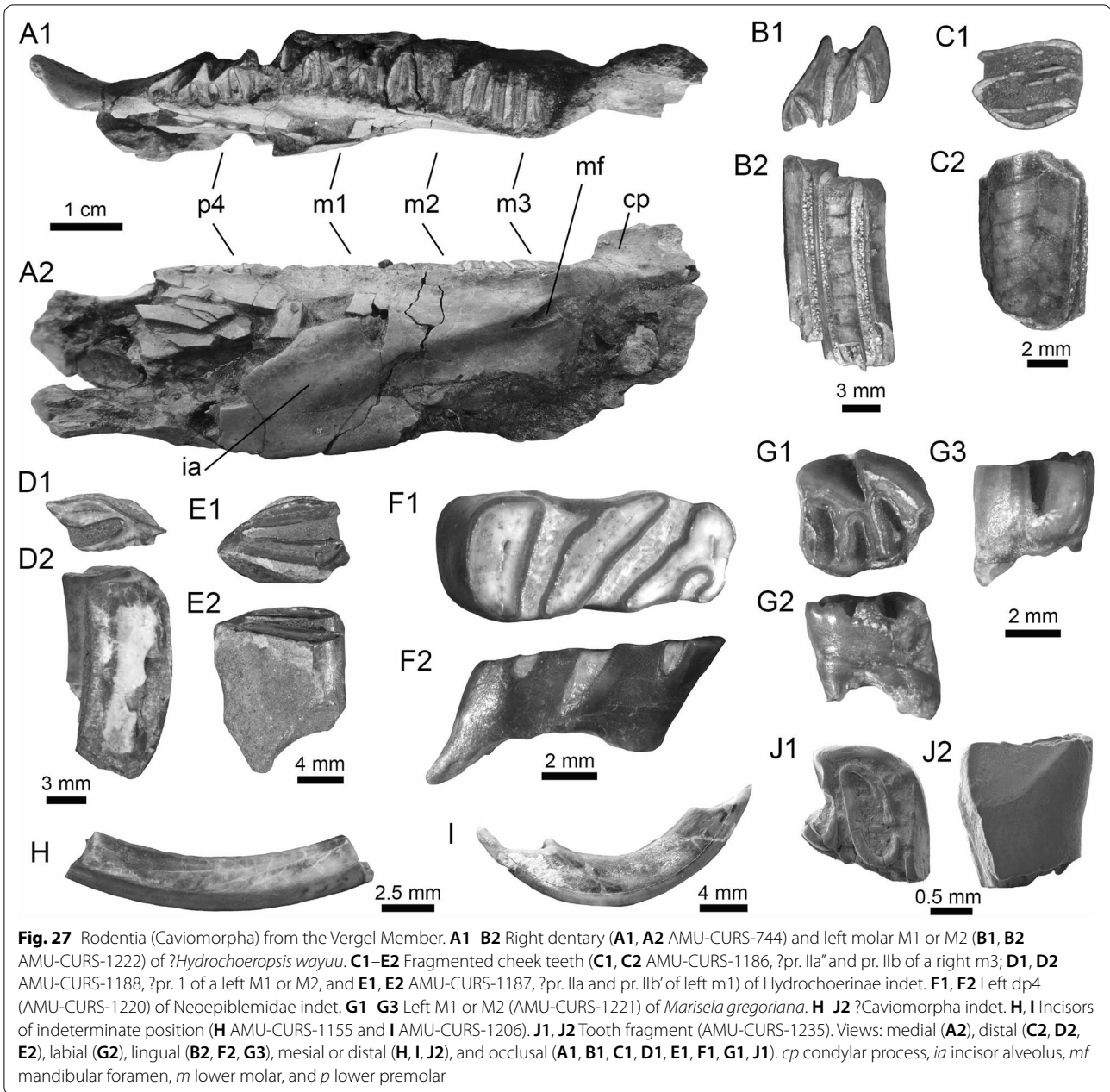
General description, comparisons and remarks: The specimens correspond to fragmentary laminar cheek teeth (AMU-CURS-1186, pr. IIa'' and pr. IIb' of a right m3; AMU-CURS-1187, ?pr. IIa and pr. IIb' of left m1; AMU-CURS-1188, ?pr. 1 of a left M1 or M2), whose state of preservation does not allow a more precise taxonomic determination.

Chinchilloidea Bennett, 1833

†Neopiblemidae Kraglievich, 1926

†Neopiblemidae indet.

(Fig. 27F1, F2).



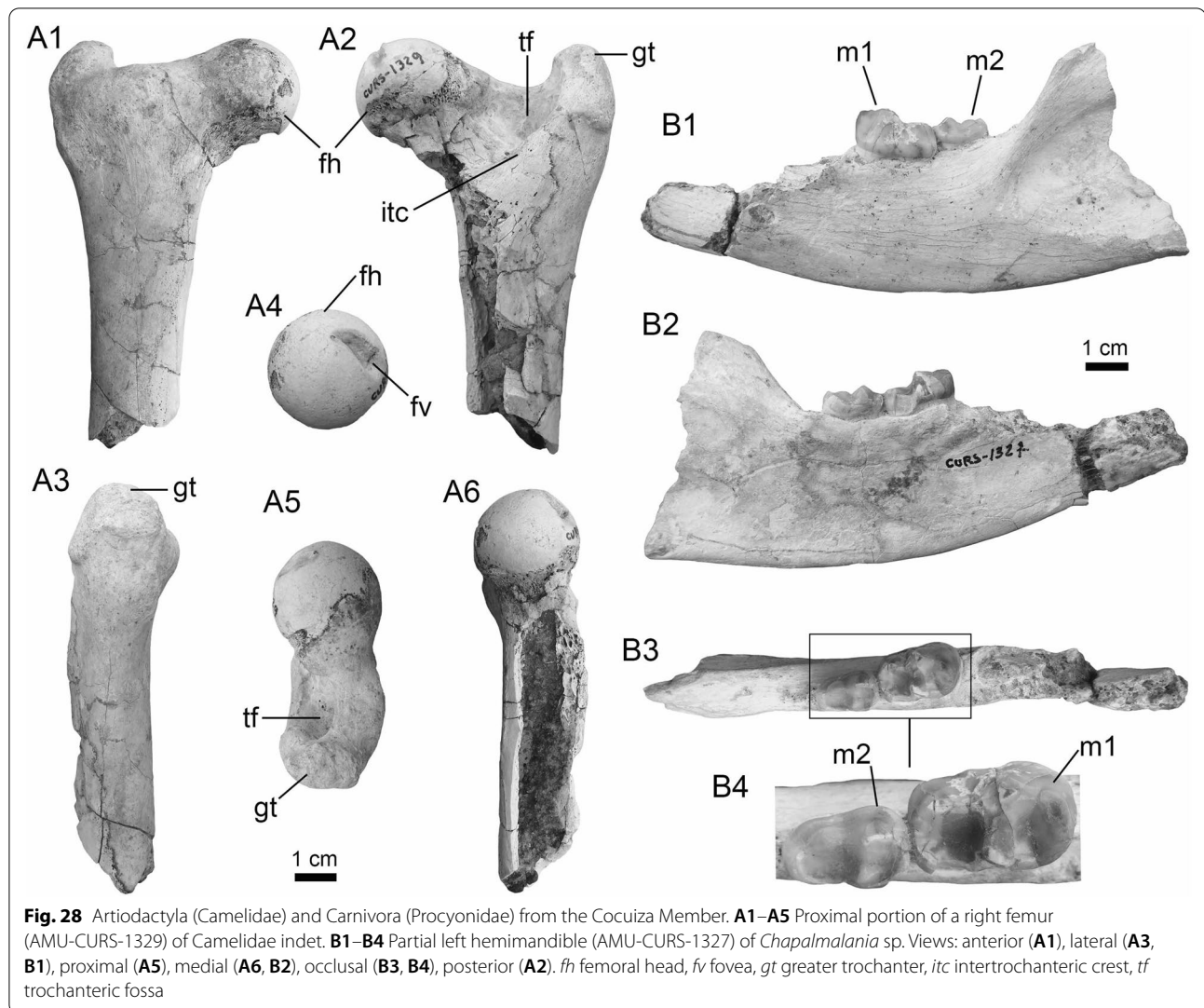
Locality: NCC (conglomerate, Fig. 3B).

Material: An isolated left dp4 (AMU-CURS-1220).

General description, comparisons and remarks: AMU-CURS-1220 corresponds to a left dp4 with 10 mm in length assigned to a neopiblemid rodent (Fig. 27F1, F2). It is a mesiodistally elongated and laminar tooth, with signs of resorption in the apical portion. The occlusal surface is composed of four oblique laminae (Fig. 27F1). The first and second laminae are labially connected. A lingual flexid penetrates between both laminae obliquely, but it does not reach the midline of the tooth. Labially to

the labial tip of the flexid, there is evidence of a closed fossetid. The third lamina is the most oblique and has a greater width. The fourth lamina is labiolingually shorter than the second one, and it is less oblique.

Neogene neopiblemid rodents from the Neotropics include two late Miocene genera: †*Neopiblema* and †*Phoberomys* (Sánchez-Villagra et al. 2003; Horovitz et al. 2006; Kerber et al. 2019), both recorded in the upper Miocene sequence of Urumaco (Carrillo and Sánchez-Villagra 2015). Adult specimens of *Neopiblema* show the lower premolar and molars with three laminae, while



Phoberomys spp. has p4 and molars with three and four laminae, respectively (Rasia and Candela 2018; Kerber et al. 2019). However, juvenile specimens (including *Neoeppiblema*, Kerber, per. obs.) have five or four laminae composing the teeth (Rasia and Candela 2018; Boivin et al. 2019). Due to the absence of more diagnostic features, the material here reported is assigned to *Neoeppiblema* indet. depending on further findings for better taxonomical identification of the San Gregorio neoeppiblemid. Vucetich et al. (2010) reported the presence of *Neoeppiblema* sp. for this unit (specimen UNEFM-VF-54). However, the specimen is quite fragmented for a confident identification. Here, new evidence of the presence of neoeppiblemids confirms the survival of this lineage at the least until the Pliocene. In this sense, San Gregorio Formation neoeppiblemids represent the LAD of this rodent clade.

Octodontoidea Waterhouse, 1839

Octodontoidea?

†*Marisela* Vucetich et al., 2010

†*Marisela gregoriana* Vucetich et al., 2010

(Fig. 27G1–G3).

Locality: NCC (conglomerate, Fig. 3B).

Material: an isolated left M1 or M2 (probably a M2) (AMU-CURS-1221).

General description, comparisons and remarks: The specimen AMU-CURS-1221 is a left M1 or M2 (probably a M2) with 4.4 mm in length, tetralophodont, with a sub-rectangular outline, and unilateral hypsodonty. There are four main lophs separated by three labial flexi (Fig. 27G1). The anteroloph is slightly labiomesially oriented in comparison to the other three lophs, which are transversely oriented. The labial tip of this loph is broken

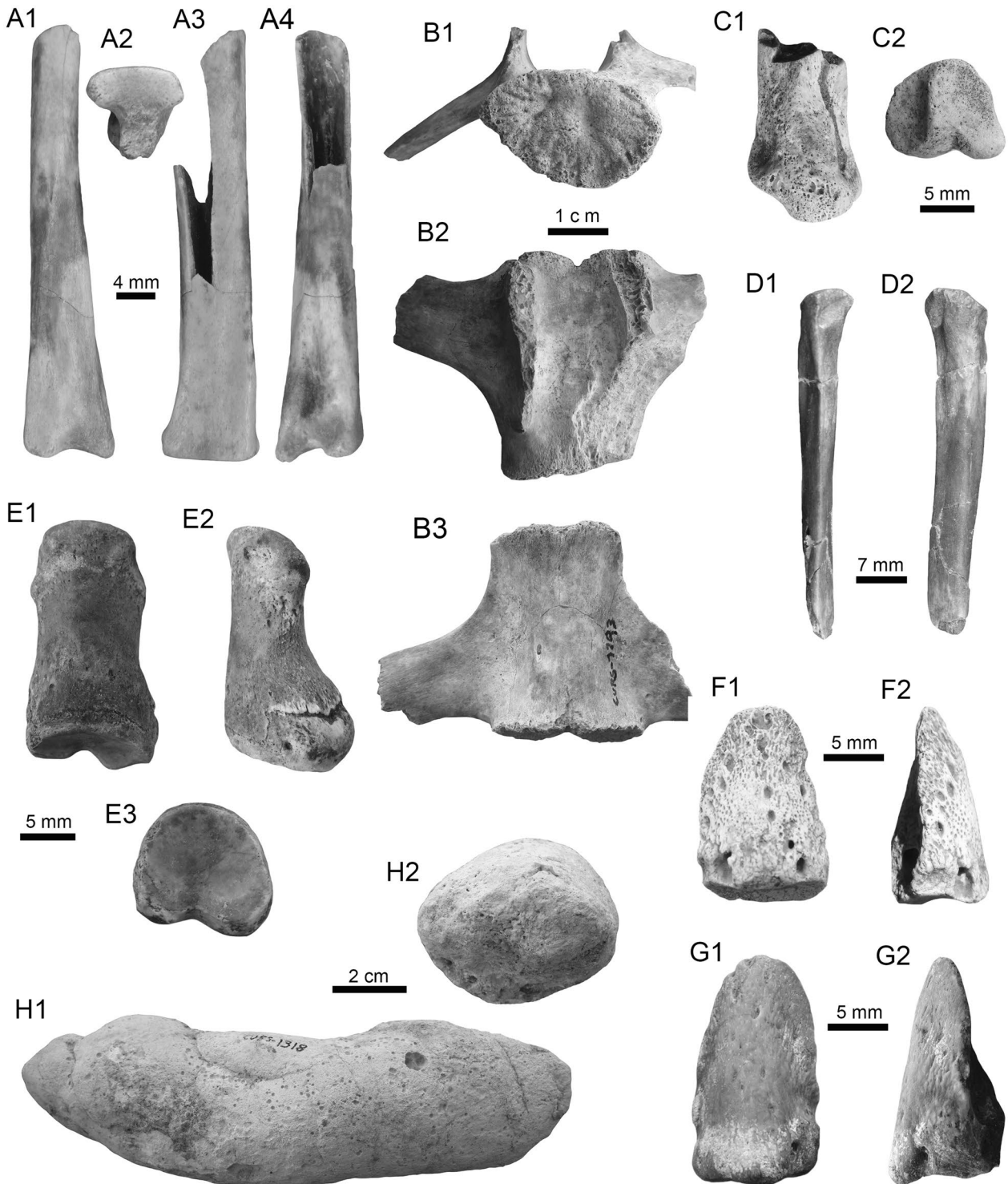


Fig. 29 Indeterminate mammalian remains and coprolites from the Norte Casa Chiguaje (A1–A4, C1–G2) and San Gregorio Oeste del Pueblo (B1–B3, H1, H2) localities. A1–A4 3rd right metatarsal (AMU-CURS-1096). B1–B3 Incomplete ?caudal vertebra (AMU-CURS-1293). C1, C2 Distal portion of a tibia (AMU-CURS-1198). D1, D2 ?right fibula (AMU-CURS-1197). E1–E3 podial phalange (AMU-CURS-1124). F1–G2 Ungual phalanges (AMU-CURS-1127). H1, H2 Presumed crocodylian coprolite (AMU-CURS-1318). Views: anterior (A3, B1, C1, D1), cross sectional (H2), dorsal (B2, E1, F1, G1), distal (C2), lateral (A1, E2, G2, H1), medial (A4, F2), right lateral (D2), proximal (A2, E3), and ventral (B3)

off. The posteroloph is transversely shorter than the protoloph and metaloph. The paraflexus and posteroflexus are slightly more penetrating than the mesoflexus. The posteroflexus is in closure process. Lingually, the hypoflexus is oblique, labiomesially oriented, and its tip is opposite to the second loph (protoloph).

The morphology of AMU-CURS-1221 is quite similar to the holotype of *Marisela gregoriana* (UNEFM-VF-55), but more worn, evidencing an ontogenetic older specimen than UNEFM-VF-55, which according to Vucetich et al. (2010) probably represent a young individual. This rodent of enigmatic affinities is endemic to the San Gregorio Formation. It represents a lineage that evolved in the northern portion of the continent, since there are no related fossils in southern South American deposits (Vucetich et al. 2010).

?Caviomorpha indet.
(Fig. 27H–J2).

Locality: NCC (conglomerate, Fig. 3B).

Material: Three isolated incisor teeth (AMU-CURS-1126, -1155 and -1206) and a small tooth fragment (AMU-CURS-1235).

General description, comparisons and remarks: The incisors (Fig. 27H, I) are between 14 and 22 mm in length, elongated, and curved, with the characteristic enamel layer of rodents covering the distal side of the tooth. Only AMU-CURS-1126 and AMU-CURS-1206 preserve the occlusal chisel-like edge. AMU-CURS-1235 is a small tooth fragment (Fig. 27J1, J2), preserving a portion of the occlusal section where one fossetid can be observed. Due to the absence of diagnostic features in incisors rodent teeth and the fragmentary tooth, these specimens cannot be assigned to any of the referred caviomorphs referred from the Vergel Member.

Artiodactyla Owen, 1848
Camelidae Gray, 1821a
Camelidae indet.
(Fig. 28A1–A6).

Locality: SGOP (conglomerate Ly1, Fig. 3C).

Material: A fragmented right femur (AMU-CURS-1329).

General description, comparisons and remarks: AMU-CURS-1329 corresponds to the proximal portion of a right femur. The proximal width (distance from the greater trochanter to the femoral head) measures 64.1 mm. The femoral head is large, with a diameter of 27.6 mm. The fovea of the head is triangular and elongated. The fovea is deep as in the guanaco (*Lama guanicoe*) and *Lama gracilis* (Cartajena et al. 2010) and not a

small notch as in *Hemiauchenia* (Meachen 2005). The greater trochanter extends proximally to the same level that the head. The trochanteric fossa is wide, deep, and limited laterally by the intertrochanteric crest. Camelids are recorded in South America since the Pliocene (Gasparini et al. 2017; Carrillo et al. 2018). Although the incomplete preservation of AMU-CURS-1329 does not allow a more precise identification, it provides additional evidence of the early presence of camelids in northern South America during the Pliocene (~3.2 Ma) and Early Pleistocene (Carrillo et al. 2018).

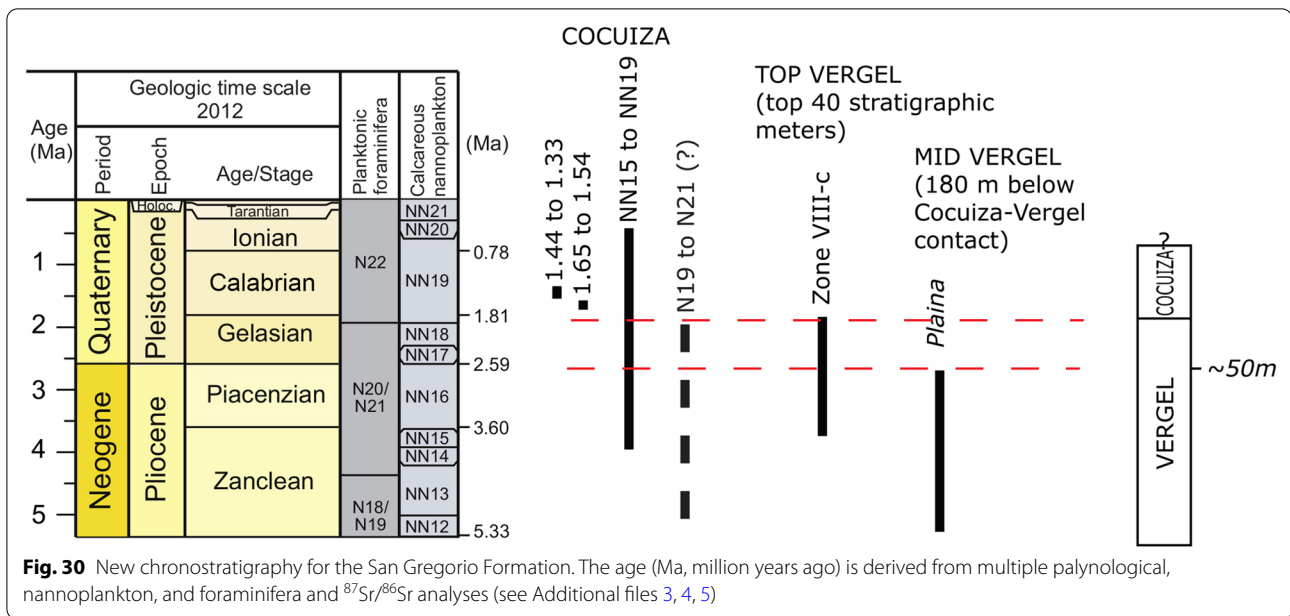
Carnivora Bowdich, 1821
Procyonidae Gray, 1825b
†*Chapalmalania* Ameghino, 1908
†*Chapalmalania* sp.
(Fig. 28B1–B4).

Locality: SGOP (conglomerate Ly1, Fig. 3C).

Material: A partial left hemimandible (AMU-CURS-1327).

General description, comparisons and remarks: AMU-CURS-1327 is a partial left hemimandible of ca. 125.6 mm in length that preserves a fragment of the coronoid process and part of the corpus with the first and second lower molars (m1 and m2). The molars are bunodont (Fig. 28B3, B4). The m1 (17.8 mm in length) has the trigonid cuspids organized in a right-angled triangle, with a less-developed paraconid than the metaconid and protoconid. The paraconid is a single cusp, as in *Chapalmalania* cf. †*Ch. ortognatha* (MLP 91-IV-5-1), †*Cyonasua longirostris* (MACN 8290), and †*Cyonasua lutaria* (MLP 34-VI-20–6), and in the living genera *Bassaricyon*, *Bassariscus*, *Potos*, and *Nasuella*, whereas in *Nasua*, *Procyon*, and some *Cyonasua* (e.g., AMU-CURS-224 and AM: 45985) this structure is bifid. It is not possible to observe the presence of the entoconulid and entoconid because of the deterioration of the material. The hypoconulid is present as a posterior cingulum. The m2 (13.16 mm in length) lacks of paraconid, although the anterior region of the molar extends as a broad cingulum. The metaconid and protoconid have the same height. The entoconid is present and developed, as in *Cy. longirostris*, †*Cy. brevirostris*, †*Cy. pascuali*, which makes it different from *Ch. ortognatha*. The hypoconid and the hypoconulid are absent, but instead, there is a ridge, which runs along the postero-lingual region; the posterior projection observed in *Cyonasua* and some living procyonids is not marked. The ventral edge of the corpus is curved as in *Chapalmalania* cf. †*Ch. altae-frontis* (FMNH 14401), whereas in *Cyonasua* is less curved to straight (e.g., *Cy. brevirostris*).

AMU-CURS-1327 is allocated within the genus *Chapalmalania*, although its morphology does not



resemble the previously species described from South America. In any case, this specimen forms part of a group of procyonids distinctively larger than other living and extinct members (Additional file 6). Prevosti and Forasiepi (2018) indicated that *Chapalmalania* species were the heavier procyonids in South America, with an estimated body mass between 125 and 181 kg. AMU-CURS-1327 represents the first record of this genus from Venezuela, and the second in northern South America (Forasiepi et al. 2014).

Mammalia indet.
(Fig. 29A1–G2)

Locality: NCC (conglomerate, Fig. 3B) and SGOP (conglomerate Ly1, Fig. 3B).

Material: a partial right metatarsal (AMU-CURS-1096), a ?caudal vertebra (AMU-CURS-1293), a fragmented tibia (AMU-CURS-1198), a ?right fibula (AMU-CURS-1197), a podial phalange (AMU-CURS-1124), and two ungual phalanges (AMU-CURS-1127).

General description, comparisons and remarks: AMU-CURS-1096 is a partial 3rd right metatarsal of 45 mm in length (Fig. 29A1–A4). Part of the body and the distal end are missing. The body and proximal end are straight and smooth (Fig. 29A1, A3, A4), resembling the overall shape of this element in Canoidea (i.e., Procyonidae and Canidae), although its proximal processes are less defined. The proximal surface has a distinctive chevron shape (Fig. 29A2), with its dorsal and ventral medial lobes similar in size and shape. Unfortunately, it is not possible

to offer a more detailed taxonomic assignment due to the fragmentary state of the fossil.

AMU-CURS-1293 is an incomplete amphiplatyan ?caudal vertebra of 35 mm in length (Fig. 29B1–B3), from the SGOP locality. AMU-CURS-1198 is a distal portion of a tibia (Fig. 29C1, C2), AMU-CURS-11973 ?right fibula of 50 mm in length (Fig. 29D1, D2), AMU-CURS-1124 a podial phalange (Fig. 29E1–E3), and AMU-CURS-1127 two ungual phalanges (Fig. 29F1–G2), from the NCC locality. Due to their preservation and/or lack of diagnostic characters, these isolated postcranial elements could not be allocated a lower taxonomic level.

Generic richness and sampling completeness

A total of 119 mammal specimens and 509 fish specimens were used to compute the rarefaction and extrapolation plots. The extrapolation of generic richness was estimated for double the reference sample size (238 specimens for mammals and 1018 specimens for fishes). For mammals, 16 genera are observed, 11 identified and five unidentified (Table 1). We estimated that 17 genera (95% confidence interval = [13, 21]) would be recorded with a sampling size of 238 specimens (Fig. 32). For fishes, 15 genera are observed, 11 identified and four unidentified (Table 1). We estimated that 18 genera (95% confidence interval = [13, 24]) would be recorded with 1018 specimens (Fig. 32). Overall, the rarefaction and extrapolation plots indicate that the taxonomic sampling at the genus level for both mammals and fishes is representative of the fauna.

Paleobotanical remains

From the NCC locality, 140 fossil seeds and fruits were collected from the screen-washed sediments, and were grouped into eight morphotypes based on their distinct morphology (Fig. 33). These fossil remains were preserved as limestone casts of the seed/fruit interior, and in many cases, they carry imprints of the internal cellular pattern of the seed coat. Despite the lack of internal anatomical preservation, distinct features and the overall morphology of six of these are sufficient to provide familial affiliations. Among these fossil seeds and fruits, we recognize Poaceae, identified from a caryopsis cast showing a dorsally placed embryo and a flat ventral face and needle-shaped hilum (Morphotype 1, Fig. 33A1, A2) that resembles various taxa of Chloroideae (Liu et al. 2005). Morphotype 2 (Fig. 33B1–C2) includes distinctly compressed, pyriform seeds with impressions of polygonal, elongated cells of the internal seed coat that are identified as Cucurbitaceae (Heneidak and Khalik 2015; Schaefer and Renner 2010). The rounded, subglobose seeds grouped into Morphotype 4 (Fig. 33F1–H) are identified as Amaranthaceae based on a distinct hilar notch and peripheral embryo that surrounds a well-differentiated perisperm, as seen on species of Chenopodioideae (Kühn et al. 1993; Townsend 1993). Asteraceae is also recognized within this assemblage based on an ovoidal, slightly curved and striated cypsela (Morphotype 6, Fig. 33L) with a distinct apical “neck” showing the pappus insertion site (Anderberg et al. 2007; Ghimire et al. 2018). Two seed cast types with limited morphological preservation have tentative affinities to Cleomaceae and Vitaceae. Morphotype 5 (Fig. 33I–K) is interpreted as the cast of a strongly curved, reniform, or horseshoe-shaped seed with an incurved embryo and is identified as *aff.* Cleomaceae, whose seeds have strongly incurved embryos and a deep invagination of the testa (Iltis et al. 2011). Morphotype 7 (Fig. 33M1–O) is identified as *aff.* Vitaceae based on a distinctly elongated scar that resembles the chalazal knot seen in seeds of this family (Chen and Manchester 2011). Morphotype 3 (Fig. 33D1–E2) and morphotype 8 (Fig. 33P1, P2) so far could not be identified.

Discussion

Neogene continental vertebrate faunas of the Urumaco region come from a successive geological sequence that includes the Socorro, Urumaco, Codore, and San Gregorio formations. Their lithological, taphonomic, and paleoenvironmental features are different from each other (see Quiroz and Jaramillo 2010). The new continental vertebrate fauna described here from the Vergel and Cocuiza members of the San Gregorio Formation provide

novel data about the late Neogene diversity in northernmost South America, and the geographical and temporal range of several lineages during the transitional stage that preceded the major climatic shift of the Quaternary.

Age of the San Gregorio Formation

Dating of the San Gregorio Formation has been a long-standing challenge. Several studies estimated its age by stratigraphic position or correlation with other formations (González de Juana et al. 1980; Audemard 2001). Only two previous studies have provided biostratigraphic data: an unpublished MS thesis (Rey 1990) that reported several molluscan taxa of little biostratigraphic value (e.g., *Crassostrea*, *Argopecten*, *Amusium*, *Placuanomia*, *Pecten*, *Anomia*, *Ostrea*, *Anadara*, *Dosinia*, *Chione*, *Solecurtus*, *Macoma*, *Trachycardium*, *Florimetus*, *Conus*, *Epitonium* and *Turritella*), and a palynological study reporting †*Stephanocolpites evansi* in the Cocuiza Member (Hambalek et al. 1994), which indicates that this member cannot be older than late Miocene (Lorente 1986). Additionally, a late Pliocene age has been assigned for the Vergel Member based on its mammalian associations (see Vucetich et al. 2010). A Pleistocene age is suggested for the San Gregorio Formation, based on a compilation derived from multiple foraminifera, nanoplankton, and magnetostratigraphic studies (Carrillo et al. 2018, Fig. 28).

Vergel Member: The last appearance datum (LAD) of †*Bombacacidites nacimientoensis* (senior synonym of *B. bellus* of Lorente 1986), †*Retitrescolpites? irregularis*, and †*Rhoipites guianensis* at the top of the Vergel Member indicates the top of zone VIII-c (interval zone of Echitricolporites–Alnipollenites), as ~1.8 Ma (Lorente 1986). It is important to note that Lorente’s definition of the Pliocene–Pleistocene boundary followed the pre-2012 definition that had the boundary at the base of the Calabrian (1.81 Ma), while currently it is placed at the base of the Gelasian (2.59 Ma) (Hilgen et al. 2012). The presence of the pampatheriid *Plaina* in the NCC locality, approximately 180 m below the Vergel/Cocuiza contact (Fig. 3A), suggests an age no younger than Pliocene (Fig. 30) as *Plaina* has a biochron that spans from the late Miocene to Pliocene (Gois 2013). Therefore, in the NCH section at least the upper ~50 m of the Vergel formation (that is 230 m thick in the NCH section; Fig. 3A, Additional file 1) would correspond to the Early Pleistocene, within the upper zone VIII-c (Fig. 30), while the Pliocene–Pleistocene boundary could be somewhere between stratigraphic meters 130 and 180 of the Vergel Member (Fig. 30).

Cocuiza Member: The $^{86}\text{Sr}/^{88}\text{Sr}$ dating of two samples rendered ages of 1.38 Ma (1.33 to 1.44, $^{87}\text{Sr}/^{86}\text{Sr}=0.709112$) and 1.59 Ma (1.54 to 1.65 Ma, $^{87}\text{Sr}/^{86}\text{Sr}=0.709100$) (Additional file 5), indicating a Calabrian age for the Cocuiza Member (Fig. 30). This age is also supported by the record of nannoplankton. The stratigraphic range of †*Pseudoemiliana lacunosa* is restricted to biozones NN15–NN19 of Martini (1971), which are dated as Pliocene–Pleistocene (Hilgen et al. 2012). The extinction of this species was astronomically calibrated in the eastern equatorial Atlantic, yielding an age of 0.4 Ma (Shackleton and Crowhurst 1997; Backman et al. 2012). The occurrence of †*Helicosphaera sellii* and *Gephyrocapsa* spp. (Additional file 4) also supports a Pleistocene age. The foraminifera, in contrast, indicate an older age, as *Ammonia beccarii*, *Elphidium poeyanum*, and *Melonis barleeaanum* are common in the upper Miocene–Pliocene *Ammonia beccarii* zone in northern South America (Duque 1975; Duque Caro et al. 1996). *Globoturborotalita* cf. *woodii* and *Globoturborotalita* cf. *rubescens* are found in biozones N19–N21 [Zanclean and Gelasian after Kennett & Srinivasan (Kennett and Stott 1991)]. However, the foraminifera assemblage is poorly preserved and it has a large number of reworked taxa. Therefore, our confidence in the age derived on foraminifera is much lower compared to both the Strontium and nannoplankton dating.

The SGOP locality section “S2” of the Cocuiza Member (Figs. 1A and 3C) is characterized by the presence of conglomeratic layers (Fig. 2G, H) that could correspond with those terrigenous sediments reported for the unit by Rey (1990) and Hambalek et al. (1994). It was not possible to correlate the SGOP locality to either the NCH (Figs. 1A and 3A; Additional file 1) or SGRS (Fig. 1A; Additional file 2) sections. Although a more detailed stratigraphic section would be necessary in the future in order to correlate SGOP locality with NCH or SGRS sections, our field observations tentatively suggest that the SGOP locality may belong to the middle section of the Cocuiza Member, which was deposited during the Early Pleistocene (Fig. 30).

Paleodiversity and biostratigraphic affinities

Terrestrial and freshwater vertebrates from the San Gregorio Formation had been reported exclusively from the Vergel Member (Table 1). Previous reports include indeterminate catfishes (Aguilera et al. 2013), crocodylians (Scheyer et al. 2013), terrestrial sloths, glyptodontids, pampatheriids, dasypodid armadillos (Carlini et al. 2008c, 2018; Carlini and Zurita 2010; Vucetich et al. 2010; Zurita et al. 2011; Castro et al. 2014), notoungulates (Carrillo et al. 2018), a procyonid (Forasiepi et al. 2014), and caviomorph rodents (Vucetich et al. 2010). The exception is

†*Crocodylus falconensis* (Scheyer et al. 2013), whose fossiliferous locality is located a few meters above the NCC locality in the NCH stratigraphic section (Fig. 3A). Due to the geographical proximity between *C. falconensis* and NCC localities, Scheyer et al. (2013) recognized the former locality as within the NCC locality area.

Forty-nine aquatic and terrestrial taxa are here reported for the NCC locality (Table 1), where fishes and mammals are the most diverse and abundant groups (Fig. 31). To our knowledge, no other continental late Pliocene deposit in northern South America has shown such a diverse continental aquatic/terrestrial taxonomic richness. Late Pliocene units with aquatic and terrestrial faunas comparable to those of the NCC locality include the Ware Formation in the Cocinetas Basin (Guajira Peninsula, Colombia) in northern South America. Although less diverse, the Ware Formation is characterized by at least eight species of fishes, three reptile taxa, one bird, and 13 mammalian taxa (Aguilera et al. 2013; Moreno et al. 2015; Moreno-Bernal et al. 2016; Carrillo et al. 2018). Hendy et al. (2015) reported a late Pliocene age (mean age of 3.2 Ma) for the Ware Formation, based on $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the shell bed at the top of the unit. The mammalian assemblage of the Ware Formation is characterized by a diversity of herbivores, including sloths (Amson et al. 2016), cingulates, caviomorph rodents (Pérez et al. 2017), toxodontids, and a proterotheriid. It also includes a procyonid (Forasiepi et al. 2014) and a camelid, which are immigrants from North America (Carrillo et al. 2018). The mammalian assemblage of the Ware Formation has a higher richness of terrestrial sloths (with at least five different taxa; see Amson et al. 2016) than the assemblage from NCC (Table 1). In contrast, the NCC locality is more taxon-rich than the Ware assemblage in other mammalian groups, such as cingulates, meridiungulates, and rodents. However, this difference in diversity between both units could be related to taphonomic or sampling biases.

The Ware and San Gregorio formations outcrops are geographically close, less than 140 km in a northernmost portion of South America and probably were part of the same biogeographic province during the Pliocene–Pleistocene. The presence of †*Hydrochoeropsis wayuu* in both Ware Formation (Pérez et al. 2017) and Vergel Member supports the biostratigraphic correlation between these two geological units, as suggested by Moreno et al. (2015). The mammalian assemblages in the Ware Formation and at the Vergel Member are characterized by a predominance of South American native taxa (Carrillo et al. 2018) (Table 1). Immigrants from North America are scarce in both units in spite of their age and proximity to the Isthmus of Panama (Carrillo et al. 2018). Until now, the North American immigrants in the

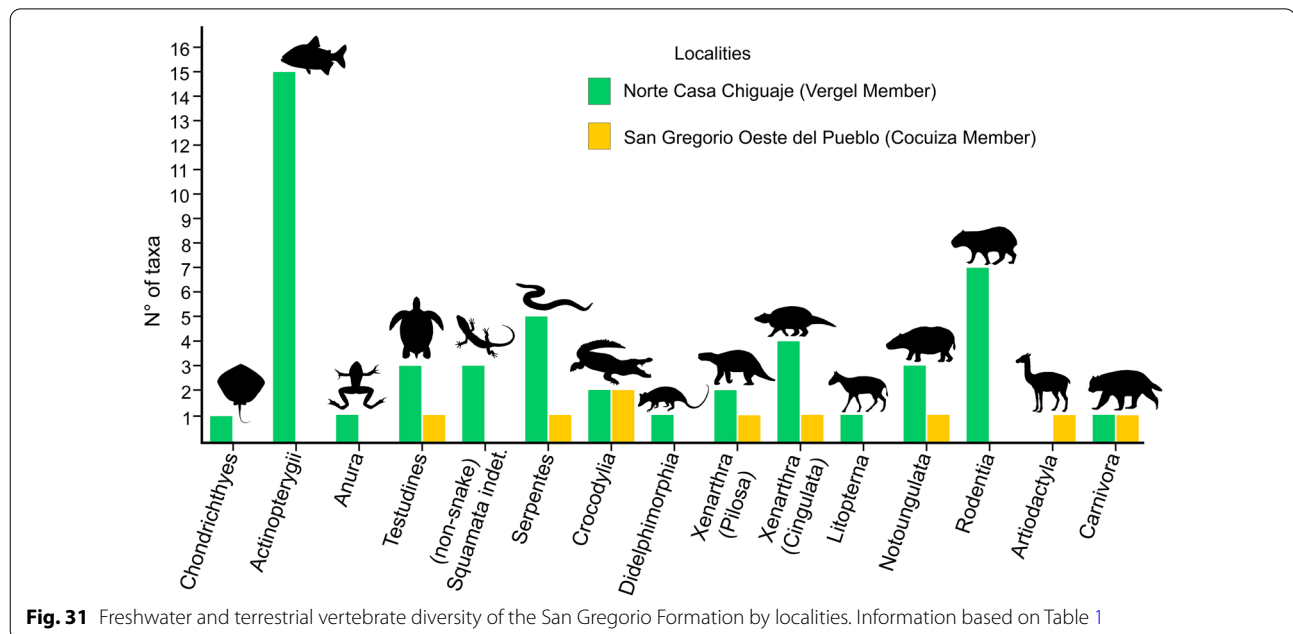


Fig. 31 Freshwater and terrestrial vertebrate diversity of the San Gregorio Formation by localities. Information based on Table 1

Ware assemblage include the procyonid *Chapalmalania* (Forasiepi et al. 2014), and one of the oldest well-dated camelids in South America (Carrillo et al. 2018). The San Gregorio Formation also includes *Chapalmalania* and an indeterminate camelid from the SGOP locality, and *Cyonasua* (Forasiepi et al. 2014) and some Cricetidae rodents with boreal affinities (Ulises Pardiñas, personal communication, March 2020, which are currently under study and reported in Table 1) from NCC locality. The South American cricetids possibly differentiated from other lineages by the middle/late Miocene (see Parada et al. 2013; Leite et al. 2014). Nevertheless, the Neogene fossil record was restricted to fossiliferous localities in Argentina, with a putative record in late Miocene strata (Nasif et al. 2009), and confident records from Pliocene deposits (see Reig 1978; Pardiñas and Tonni 2014; Pardiñas et al. 2002; Verzi and Montalvo 2008; Prevosti and Pardiñas 2009).

Carrillo et al. (2018) placed the Ware Formation and its fauna within the first migration pulse of the Great American Biotic Interchange (GABI, Woodburne 2010), and the San Gregorio Formation (without any differentiation of members) might have overlapped with the second and third migratory pulse, named GABI 2 and GABI 3 (Carrillo et al. 2018, fig. 1). With the late Pliocene age proposed here for most of the Vergel Member (Figs. 3A, 30), the NCC assemblage would have to be reinterpreted within GABI 1 (see Carrillo et al. 2018, fig. 1).

Sampling in the geographic location of the Guajira Peninsula and Falcón region is critical to improving the understanding of the first GABI phases and the timing of the appearance of immigrants from North America into

South America. For example, NCC locality is the only northern Neogene unit in which fossils of caviomorphs and cricetids (under study) are found in the same levels. Since about 41 million years, caviomorphs were the only clade of rodents in South America (Antoine et al. 2012), generating a wide diversification of disparate lineages in morphology, body size, and ecology. After the latest Miocene/early Pliocene several groups of caviomorphs disappeared (e.g., large dinomyids and neopiblemids) (Vucetich et al. 2010, 2015; Kerber et al. 2020), while cricetids arrived from North America. The co-occurrence of caviomorphs, including the last neopiblemids, and cricetids in the NCC fauna, offer an opportunity to better understand the dispersal of cricetids in the tropics of South America as well as the extinction of some caviomorph lineages.

The current and precise temporal allocation of NCC and SGOP localities of the San Gregorio Formation agree with the hypothesis proposed by Carlini et al. (2006a, b, 2008b), and Carlini and Zurita (2010), about possible migration times to Central America. In addition, the San Gregorio *Xenarthra* show anatomical features that are plesiomorphic if compared to those of the late Pliocene–Early Pleistocene taxa recorded in North America and Mexico.

Another fossil-rich (tar pit) locality called El Breal de Orocuá “ORS16,” in Monagas State, northeast of Venezuela, yields an assemblage of terrestrial taxa that exceeds 30 spp. (mostly mammals) (Rincón et al. 2009; Solórzano et al. 2015). The Orocuá fauna is tentatively assigned to the late Pliocene–Pleistocene, based on the

Table 1 Vertebrate paleodiversity of the San Gregorio Formation

Taxonomy					N° Ts		N° Tt		N° TPr	
					NCC	SGOP	NCC	SGOP	NCC	Refs.
Chondrichthyes	Myliobatiformes	Potamotrygonidae	<i>Potamotrygon</i>	sp.	88		1			
		Indet.	Indet.	Indet.	1					
Actinopterygii	Characiformes	Anostomidae	<i>cf. Megaleporinus</i>	sp.	2		1			
			<i>Schizodon</i>	<i>cf. S. corti</i>	70		1			
		Erythrinidae	<i>Hoplias</i>	sp.	248		1			
		Serrasalminidae	<i>Mylossoma</i>	sp.	5		1			
			Indet. ("pacu clade")	Indet.	42					
		Cichliformes	Cichlidae	Indet.	Indet.	10		1		
		Siluriformes	Ariidae	<i>cf. Sciades</i>	sp.	1		1		
			Callichthyidae	Indet.	sp.	6		1		
			Doradidae	<i>cf. Amblydoras</i>	sp.	1		1		
				<i>cf. Scorpiodoras</i>	sp.	1		1		
				Indet.	Indet.	80		1		3 1
			Heptapteridae	<i>cf. Pimelodella</i>	sp.	1		1		
			Loricariidae	Hypostominae	Indet.	12		1		
				Indet.	Indet.	9				
			Pimelodidae	<i>cf. Platysilurus</i>	sp.	3		1		
		Indet.	sp.	2		1				
	Indet.	Indet.	Indet.	99						
Amphibia	Synbranchiformes	Synbranchidae	Synbranchus	sp.	19		1			
	Indet.	Indet.	Indet.	Indet.	195					
	Anura	Pipidae	<i>cf. Pipa</i>	sp.	1		1			
Reptilia	Testudines	Testudinidae	<i>Chelonoidis</i>	sp.	1		1			
		Chelidae	<i>Chelus</i>	sp.	1		1			
		Podocnemididae	Indet.	Indet.	48	3	1	1		
		Indet.	Indet.	Indet.	85					
		Squamata	Teiidae	<i>Tupinambis</i> s.l.	sp.	1		1		
		(non-snake) Squamata	Indet.	Indet.	5		2			
	Serpentes	Aniliidae	<i>Anilius</i>	<i>A. scytale</i>	1		1			
		Boidae	<i>Corallus</i>	sp.	1		1			
			<i>Eunectes</i>	sp.		1		1		
			Indet.	Indet.	2		1			
			?Boidae or ?Aniliidae	Indet.	Indet.	1		1		
			Colubroidea	Indet.	Indet.	1		1		
			Indet.	Indet.	3					
	Crocodylia	Alligatoridae (Caimaninae)	<i>Caiman</i>	aff. <i>C. yacare</i>			1		1	
			Indet.	Indet.	11	1	1			
Crocodylidae		<i>Crocodylus</i>	† <i>falconensis</i>			1		1 2		
	Indet.	Indet.	Indet.	571	12		1			
Mammalia	Didelphimorphia	Didelphidae	<i>cf. Didelphis</i>	sp.	1		1			
	Xenarthra (Pilosa)	†Megatheriidae	<i>cf. †Proeremotherium</i>	sp.	1	1	1	1	1 3	
		†Mylodontidae	Indet.	Indet.	1		1			
	Xenarthra (Cingulata)	Dasypodidae	† <i>Pliodasypus</i>	<i>vergelianus</i>			1		3 4	
		†Glyptodontidae	aff. † <i>Boreostemma</i>	sp.	2		1		14 5,6	
		†Pampatheriidae	aff. † <i>Holmesina</i>	<i>floridanus</i>	2	2	1	1	? 7	
			aff. † <i>Plaina</i>	sp.	1		1			
	Indet.	Indet.	Indet.			1				

Table 1 (continued)

Taxonomy				N° Ts		N° Tt		N° TPr	
				NCC	SGOP	NCC	SGOP	NCC	Refs.
	†Litopterna	†Protheroheriidae	Indet.	Indet.	2	1			
	†Notoungulata	†Toxodontidae	† <i>Falcontoxodon</i>	sp.	33	1	38	8	
			Indet.	Indet.		3	1		
		†Interatheriidae (Typotheria)	Indet.	Indet.	1	1			
		†Typotheria inc. Sed	Indet.	Indet.	1	1			
Rodentia	Cricetidae ^a		Indet.	Indet.	8 ^a	1			
	Hydrochoeridae	† <i>Cardiatherium</i>	sp.			1	1	7	
		cf. † <i>Caviodon</i>	sp.			1	1	7	
		†? <i>Hydrochoeropsis</i>	<i>wayuu</i>		2	1			
			Indet.	Indet.	3				
		†Neopiblemidae	† <i>Neopiblema</i>	sp.		1	1	7	
			Indet.	Indet.	1	1			
		Octodontoidea?	† <i>Marisela</i>	<i>gregoriana</i>	1	1	2	7	
		Caviomorpha	Indet.	Indet.	4				
Artiodactyla	Camelidae		Indet.	Indet.		1	1		
Carnivora	Procyonidae	† <i>Cyonasua</i>	sp.			1	1	9	
		† <i>Chapalmalania</i>	sp.		1	1			
Indet.	Indet.	Indet.	Indet.	Indet.	7				

Localities: Norte Casa Chiguaje (NCC) and San Gregorio Oeste del Pueblo (SGOP). Total number of specimens for locality (N° Ts). Total estimated taxa per locality (N° Tt). Total number of specimens referred in previous publications (N° TPr) and their references (Refs.): (1) Aguilera et al. (2013); (2) Scheyer et al. (2013); (3) Carlini et al. (2018); (4) Castro et al. (2014); (5) Zurita et al. (2011); (6) Carlini et al. (2008c); (7) Vucetich et al. (2010); (8) Carrillo et al. (2018); (9) Forasiepi et al. (2014)

^a Personal communication (Dr. U. Pardiñas)

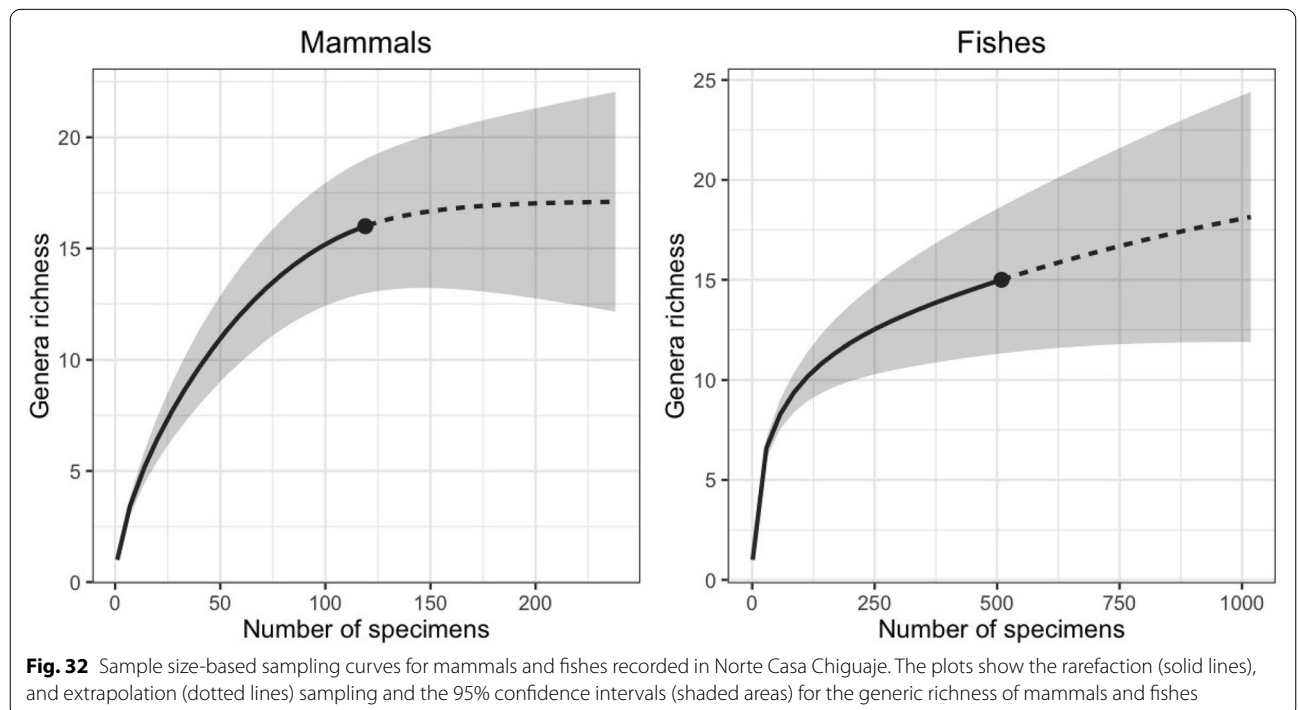


Fig. 32 Sample size-based sampling curves for mammals and fishes recorded in Norte Casa Chiguaje. The plots show the rarefaction (solid lines), and extrapolation (dotted lines) sampling and the 95% confidence intervals (shaded areas) for the generic richness of mammals and fishes

biochron of †*Smilodon gracilis*, †*Pachyarmatherium leiseyi*, and the rodents †*Phugatherium* sp., (Vucetich et al. 2012 considers †*Chapalmatherium* as synonymous of *Phugatherium*), †*Neocavia* sp., and a tetrastylines (Rincón et al. 2009; Solórzano et al. 2015; Czaplewski and Rincón 2020). Additional dating is necessary to confirm the age of the Orocuá assemblage because the biochronology of several mammalian taxa in the tropics is poorly known and it may differ from that of temperate regions. For example, *Chapalmalania* is recorded in Buenos Aires (late Pliocene) and Catamarca (?early Pliocene) in Argentina, and the Guajira in Colombia (late Pliocene) (Ameghino 1908; Reguero and Candela 2011; Forasiepi et al. 2014; Prevosti and Forasiepi 2018). Our field observations suggest that the SGOP locality may belong to the middle section of the Cocuiza Member (and therefore have a Calabrian age, Fig. 30). Therefore, the *Chapalmalania* record in the SGOP would represent the youngest known for the taxon, expanding the biochron of this genus into the Pleistocene (Calabrian).

A wide range of fossil fishes, reptiles, and mammals from the Urumaco sequence (Lundberg et al. 2010; Sánchez-Villagra et al. 2010; Aguilera et al. 2013; Scheyer et al. 2013; Aguirre-Fernández et al. 2017a, b) have been used as unequivocal evidence to support a system with hydrographic connections between western Amazonia and the Proto-Caribbean Sea during the Miocene (e.g., Díaz de Gamero 1996; Hoorn et al. 2010). However, by the late Miocene to early Pliocene, extreme environmental changes and a faunal turnover took place in the region (Sánchez-Villagra et al. 2010; Scheyer et al. 2013). This process has been linked to a major hydrographic restructuring as a consequence of the northern Andes uplift (Mora et al. 2010; Albert et al. 2018), and may have led to the complete isolation of northern peripheral drainages from those of western Amazonia triggering a direct impact (e.g., extinction/extirpation) in fishes, crocodylians, turtles, and some putatively semiaquatic mammals (e.g., rodents) (Lundberg et al. 1998, 2010; Sánchez-Villagra et al. 2010; Scheyer et al. 2013; Cadena et al. 2020). These major changes in the dynamics of the sedimentary and environmental conditions of the Falcón region are documented during the deposition of the Codore Formation (Quiroz and Jaramillo 2010).

Vucetich et al. (2010) proposed the Vergel Member as a “reservoir” for rodent taxa that had gone extinct in southern South America. According to Vucetich et al. (2010), this survival of taxa would be related to the persistence of fluvial environments under warm conditions. Although Vucetich et al. (2010) reported the presence of *Neoeptibema* sp. for the NCC locality, that specimen (UNEFM-VF-54) was in too poor condition for a reliable identification. The new evidence presented here confirms

the survival of this lineage at least until the late Pliocene. However, a “reservoir” hypothesis during the late Pliocene in the Falcón region must be viewed with caution, as there are no other Pliocene–Early Pleistocene fossiliferous localities in the region that can validate or discard this attribution. Additionally, the occurrence of small notoungulates (Interatheriidae and Typotheria inc. sed) in the Pliocene of the Vergel Member (Table 1) represents the first record in the region and suggests the existence of ghost lineages inhabiting tropical areas since the Paleogene.

Thorny catfishes, such as cf. *Amblydoras* and cf. *Scorpiodoras*, have living representative species inhabiting exclusively the cis-Andean (Eastern-slope) rivers from the Orinoco and Amazon basins (Sousa and Birindelli 2011; van der Sleen and Albert 2018). Other freshwater taxa from the NCC locality, such as *Potamotrygon* sp., cf. *Megaleporinus* sp., *Schizodon* cf. *S. corti*, *Mylossoma* sp., and cf. *Platysilurus* sp., were extirpated from the Falcón region. Living representatives of the above-mentioned fishes still inhabit both the cis-Andean (van der Sleen and Albert 2018) and trans-Andean basins, being restricted in the later exclusively to the Magdalena and Lake Maracaibo basins (Pérez and Taphorn 1993; Rodríguez-Olarte et al. 2009). The presence of the above-mentioned stingray, thorny catfishes, and characiform taxa in NCC locality suggests fluvial conditions during the Pliocene time that contrast with those prevailing today in the Falcón region. Aguilera et al. (2013), based on paleoichthyological evidence from the Urumaco and Guajira Peninsula regions, suggested a possible last connection between the Orinoco/Amazon basins and those of the Caribbean region for the Pliocene. However, new geological models support a complete hydrographic isolation between western Amazonia and the Caribbean basins during the Pliocene (Albert et al. 2018).

Extant matamata turtles are represented by two species inhabiting exclusively the Orinoco and Amazon basins (Vargas-Ramírez et al. 2020), whereas that the taxonomic status of some records from the Lake Maracaibo basin is unresolved (Trebba and Pritchard 2016). The fossil record of matamatas is well known from the late Miocene of Urumaco and the Cocinetas basin in Colombia (Sánchez-Villagra et al. 2010; Cadena and Jaramillo 2015). The presence of this taxon can now be extended into the Pliocene of Falcón.

Only a limited number of isolated snake vertebrae have been recovered from the San Gregorio Formation. Nevertheless, these vertebrae provide a glimpse into the ophidian fauna and its evolution in the area. The NCC snake assemblage comprises at least four different species, while the younger Cocuiza Member has yielded only a single vertebra. Among the NCC remains, the

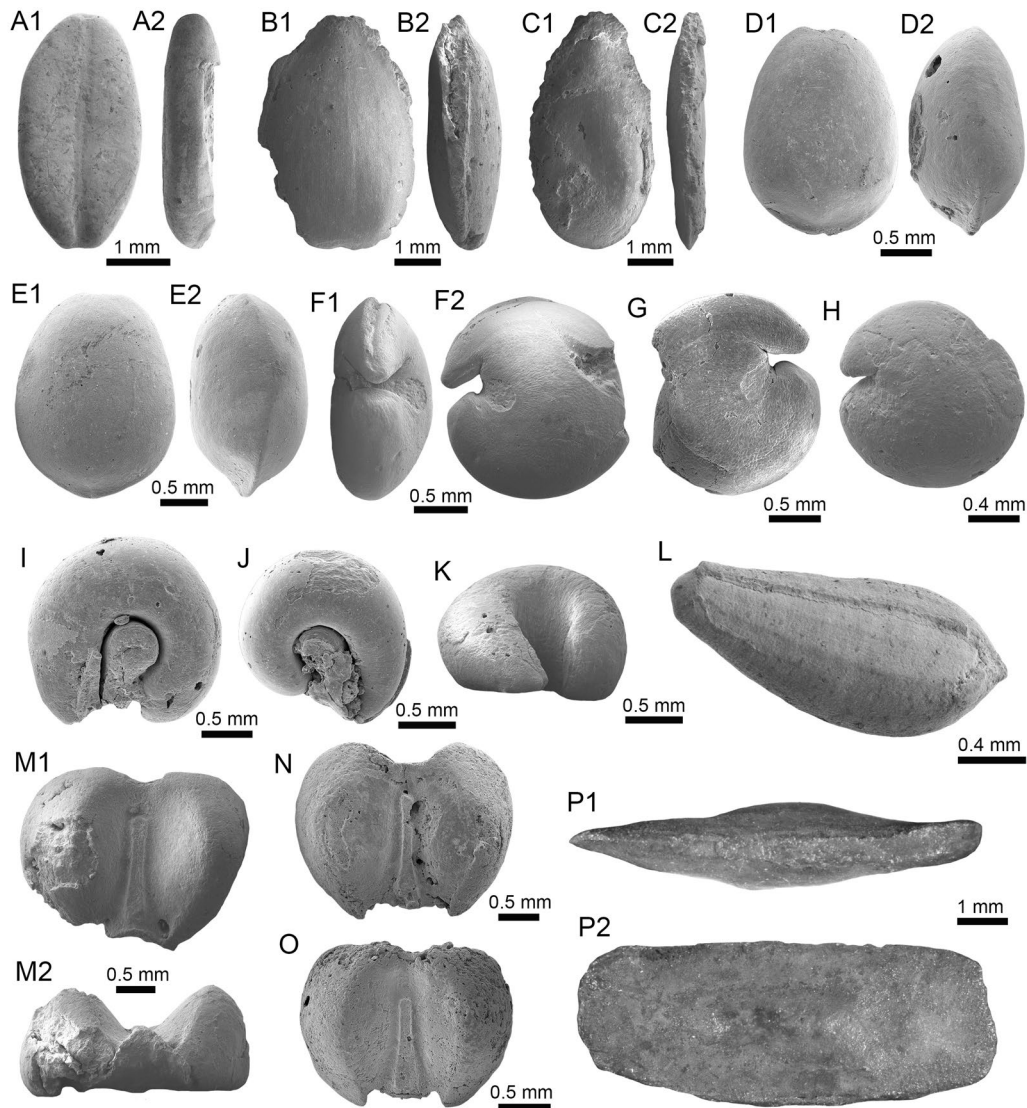


Fig. 33 Internal seed casts from the Norte Casa Chiguaje locality (Vergel Member). **A1, A2** Morphotype 1 (AMU-PB-02), Poaceae *aff.* Chloroideae. **B1–C2** Morphotype 2 (AMU-PB-03), Cucurbitaceae. **D1–E2** Morphotype 3 (AMU-PB-04), of indeterminate affinities. **F1–H** Morphotype 4 (AMU-PB-05), Amaranthaceae. **I–K** Morphotype 5 (AMU-PB-06), *aff.* Cleomaceae. **L** Morphotype 6 (AMU-PB-07), Asteraceae. **M1–O** Morphotype 7 (AMU-PB-09), *aff.* Vitaceae. **P1–P2** Morphotype 8 (AMU-PB-10) of indeterminate affinities

presence of *Anilius scytale* is notable, considering that this cryptic taxon occurs in the extant herpetofauna of northern South America, including parts of Venezuela, but is currently absent from Falcón State and other Caribbean basins (Mijares-Urrutia and Arends 2000). This single NCC record represents, to our knowledge, the sole known fossil occurrence of *Anilius scytale* and can thus offer a fossil calibration point for this species into the late Pliocene. Furthermore, the fact that this Pliocene record lies outside the current geographic range of the species implies a post-Pliocene local extirpation. Boidae in NCC are represented by at least two forms,

one of which is attributed to the extant genus *Corallus*, which is widespread in the Neotropics (Wallach et al. 2014; Reynolds and Henderson 2018), including the Falcón State (Mijares-Urrutia and Arends 2000). *Corallus* represents a relatively ancient lineage, already recorded since the early Cenozoic, as attested by the extinct species †*Corallus priscus* Rage, 2001, from the early Eocene of Itaborai, Brazil (Rage 2001; see Smith and Georgalis in press). The NCC vertebra (AMU-CURS-1158) that bears some resemblance with *Colombophis* is so far inadequate for determining whether this Neogene Neotropic genus was indeed present in the area or if the vertebra belongs

to some other anilioid or boid form. As for Colubroïdes, this is the dominant and most speciose lineage of snakes in extant herpetofaunas, not only in the Neotropics but also all over the globe (Zaher et al. 2009). As such, the single, fragmentary vertebra from NCC that we assigned to Colubroïdes cannot offer any more precise assignment to any of the numerous taxa of that lineage that currently inhabit that area. On the other hand, the single vertebra from the Early Pleistocene of the Cocuiza Member evidences the presence of the giant snake anaconda, i.e., *Eunectes*. This genus is currently absent from the area, and therefore, its herein documentation in the early Quaternary implies a relatively recent extirpation from the region. Based on this limited fossil anaconda material, it is not possible to determine whether this new Venezuelan taxon is phylogenetically closer to the older taxon *Eunectes stirtoni* from the Miocene of Colombia (Hoffstetter and Rage 1977) or to the extant *Eunectes* spp. that currently inhabit the Orinoco and Amazon basins.

Given the fragmentary nature of most crocodylian remains from the San Gregorio Formation, there is little information so far about the connectivity of these fossils and their faunal composition in comparison to the modern fauna of South America. In the case of the cranial remains identified as *Caiman* aff. *C. yacare* and of the well-preserved skull of the *Crocodylus falconensis* (Scheyer et al. 2013), however, some broader implications are warranted. The extant *Caiman yacare*, the southern or Paraguayan spectacled caiman, has a distribution restricted to the southern hemisphere, with a northernmost extension into Bolivia and central/southwestern Brazil (Grigg and Kirschner 2015). The identification of AMU-CURS-1328 as *Caiman* aff. *C. yacare* from the Cocuiza Member tentatively implies that the distribution of the southern spectacled caiman could have had a more extensive northward distribution up to Caribbean, even until the Early Pleistocene (Calabrian). A fossil representative of the northern spectacled caiman, *Caiman crocodylus*, was recently reported from the Pliocene–Pleistocene El Breal de Orocal tar pit in northeastern Venezuela (Cidade et al. 2019b). The overlap of the northern with the southern species of spectacled caimans might thus have been more extensive in the recent past in comparison to today's restricted overlap zone along the northern border of Bolivia with Brazil (e.g., Andrade et al. 2020).

Crocodylidae are represented in South America today only by the American crocodile, *Crocodylus acutus*, ranging from Central America to Colombia and throughout the Caribbean, and the critically endangered Orinoco crocodile, *Crocodylus intermedius*, restricted to Colombia and Venezuela (Grigg and Kirschner 2015). Scheyer et al. (2013) recovered *C. falconensis* from the Pliocene Vergel Member as sister taxon to all New world

crocodyles, including the two extant crocodile species. Together with lower jaw remains identified as *Crocodylus* sp. from the Pliocene Ware Formation of Colombia (Moreno-Bernal et al. 2016), *C. falconensis* is still considered the oldest well-known record of true crocodylids in South America (Cidade et al. 2019a). A recent phylogenetic analysis refined the position of *Crocodylus falconensis* to within the extant New World crocodyles and *Crocodylus intermedius* being the sister taxon to the remaining species (Delfino et al. 2020).

Paleoenvironments

Vergel Member: According to Hambalek et al. (1994), fluvial environments prevailed in the Urumaco region during the deposition of the Vergel Member with depositional environments characterized by alluvial plains and braided rivers (Rey 1990). These conditions were later replaced by a marine incursion that is represented by the deposition of the overlying Cocuiza Member (Hambalek et al. 1994). Foraminifera with low-salinity tolerance indicate the presence of estuaries nearby (Smith et al. 2010).

The conglomeratic layer that bears most of the fossils from NCC Locality (Fig. 3B) is evidence of transportation and accumulation in river channels (Quiroz and Jaramillo 2010). The paleontological evidence, especially the aquatic faunal composition of the NCC assemblage (Table 1), supports this idea and is an unequivocal element supporting the presence of permanent watercourses. The ichthyofauna from NCC assemblage is characterized by a typical tropical-freshwater composition. The habitat preferences of extant taxa related with fossil characiforms (e.g., cf. *Megaleporinus*, *Schizodon* cf. *S. corti*, and *Mylossoma* sp.) and Siluriformes (e.g., cf. *Amblydoras* sp., cf. *Scorpiodoras* sp., cf. *Pimelodella* sp., cf. *Platysilurus* sp., and indeterminate pimeloids and loricariids) suggest flowing waters in a well-oxygenated environment (Additional file 7). The stingray *Potamotrygon* sp. is abundant in the fossil assemblage (Table 1) and although living species are found even in lakes and still waters, they are commonly associated with flowing rivers and particularly on sandy substrates (see Lasso et al. 2014). Although the fossil ichthyofauna from NCC assemblage supports the presence of flowing waters, other environments, such as swampy, ponds, and marginal areas associated with a flooding process, may have also existed. For example, the extant relatives of the armored Callichthyidae catfishes and the freshwater eel *Synbranchus* sp. (Table 1 and Additional file 7) are able to survive also in warm, anoxic, and temporary waters due to their aerial respiration capacity (Lundberg et al. 2010; van der Sleen and Albert 2018). Most of the fossil fish taxa from NCC assemblage have living representatives that exclusively inhabit freshwater environments.

However, the presence of euryhaline species is feasible, especially due to the probable proximity to the marine area during the deposition of the Vergel Member (Hambalek et al. 1994; Smith et al. 2010). A clear example could be the presence of the Ariidae catfish cf. *Sciades*, a genus whose living species have the ability to migrate upstream (Marceniuk and Menezes 2007).

The presence of a pipid amphibian is also indicative of freshwater environments, as Pipidae anurans are strictly linked to aquatic conditions and rarely use terrestrial environments (Wells 2007). Crocodylian (teeth, osteoderms, and vertebrae) and podocnemid turtle remains (shell fragments) are among the most abundant fossils of aquatic vertebrates in the NCC assemblage. The habitat preferences of their extant relatives are freshwater lakes, marshes, swamps, mangroves, and flowing waters (Additional file 7), supporting also the evidence of freshwater environments, although the presence of *Crocodylus falconensis* might imply the existence of estuarine settings nearby. Members of *Crocodylus* live in estuarine or mixed environments (in addition to rivers). Likewise, the environments in which both types of crocodiles (a caiman and a true crocodile) occur today in America are few. For example, the Orinoco or Magdalena River deltas are potentially habitats for both species and could give an idea of the characteristics of the Falcón area in the Pliocene–Pleistocene.

The matamata turtle (*Chelus*) is another example that supports the existence of freshwater environments. The extant species of *Chelus* are associated mainly with slow-moving waters, swamps, and marshes (Trebbau and Pritchard 2016). In addition to the aquatic vertebrate assemblage, the NCC locality yielded abundant remains of freshwater mollusks (Fig. 34A–K) and Trichodactylidae crabs (Fig. 34L–O2) (e.g., Rodríguez 1997). Although mollusks were preserved only by internal molds of bivalves and gastropods, some of the latter could be tentatively allocated to Planorbidae (Fig. 34E–H), which are characteristics of fresh water environments, including slow-moving rivers (Hanley 1980). As for the NCC snakes, *Anilius scytale* is a strictly fossorial form that requires humid soil and proximity to bodies of water (Martins and Oliveira 1999). The boid *Corallus*, on the other hand, is an efficient arboreal dweller and its occurrence indicates the presence of a forested environment (Martins and Oliveira 1999).

Neoepiblemids and hydrochoerines rodents show a fossil record associated with strata formed by permanent bodies of water, such as rivers, lakes, and marshes (Vucetich et al. 2010; Kerber et al. 2017). Their presence in the NCC assemblage is in accordance with wet and humid paleoenvironmental conditions. The presence of terrestrial sloths, glyptodontids, pampatheriids,

and dasypodids in the NCC locality (Carlini et al. 2008c, 2018; Zurita et al. 2011; Vucetich et al. 2010; Castro et al. 2014) (Table 1), and their paleoecological and habitat preferences (e.g., Defler 2019) could suggest forested-grass land areas. This could be supported also by the presence of abundant remains of *Falcontoxodon* (Carrillo et al. 2018) (Table 1), a taxon that is closely related to other toxodontids characterized by a broad ecological flexibility and diet associated with grasslands and/or forested-grassland areas (MacFadden 2005).

The data published by Hambalek et al. (1994) are restricted to the marine Cocuiza Member, with no detailed studies on the Vergel Member palynoflora. Jaramillo et al. (2010) suggested that a xerophyte vegetation dominated the landscape during the accumulation of the Codore Formation in the Urumaco region. However, the palynoflora found in the middle Vergel Member indicates the presence of rainforest elements (Additional file 3), while the palynoflora in the Cocuiza Member, albeit scarce, lacks the rainforest taxa seen in the Vergel member, suggesting a major floristic change toward drier biomes in the Pliocene–Pleistocene transition that also seems to occur in many regions across the Neotropics (Jaramillo 2019). A much wetter precipitation regime for the Urumaco/Ware region had been observed since the early Miocene until at least the middle Pliocene (Scholz et al. 2020; Jaramillo et al. 2020; Pérez-Consuegra et al. 2018) and it is possible that the reduction in precipitation to modern levels occurred at the Pliocene–Pleistocene transition. The small seed and fruit sizes observed in the NCC locality (Fig. 33), in contrast to the pollen, suggest open vegetation environments. In living ecosystems, seeds of small size are most common among herbaceous plants and in grassland environments (Moles et al. 2007). Even though taphonomical processes and the specific depositional environments of the Vergel Member may have biased the selective preservation of small-sized seeds, the natural affinities of this assemblage are also indicative of a low-standing vegetation component in open or partly open environments. These paleobotanical interpretations, the abundance and diversity of freshwater vertebrates, and the ecological preferences of forest-dweller vertebrates described above suggest an environment with mixed forested-grassland areas during the deposition of the Vergel Member (Fig. 35).

Cocuiza Member: In contrast to the Vergel Member a continental paleoenvironment, the Cocuiza Member (the middle portion of the San Gregorio Formation) represents a marine environment associated with marine incursion (Hambalek et al. 1994). The presence of marine microfossils (Hambalek et al. 1994; Smith et al. 2010; Additional file 4), ostreid colonies and several other marine molluscan taxa (Rey 1990), echinoids and

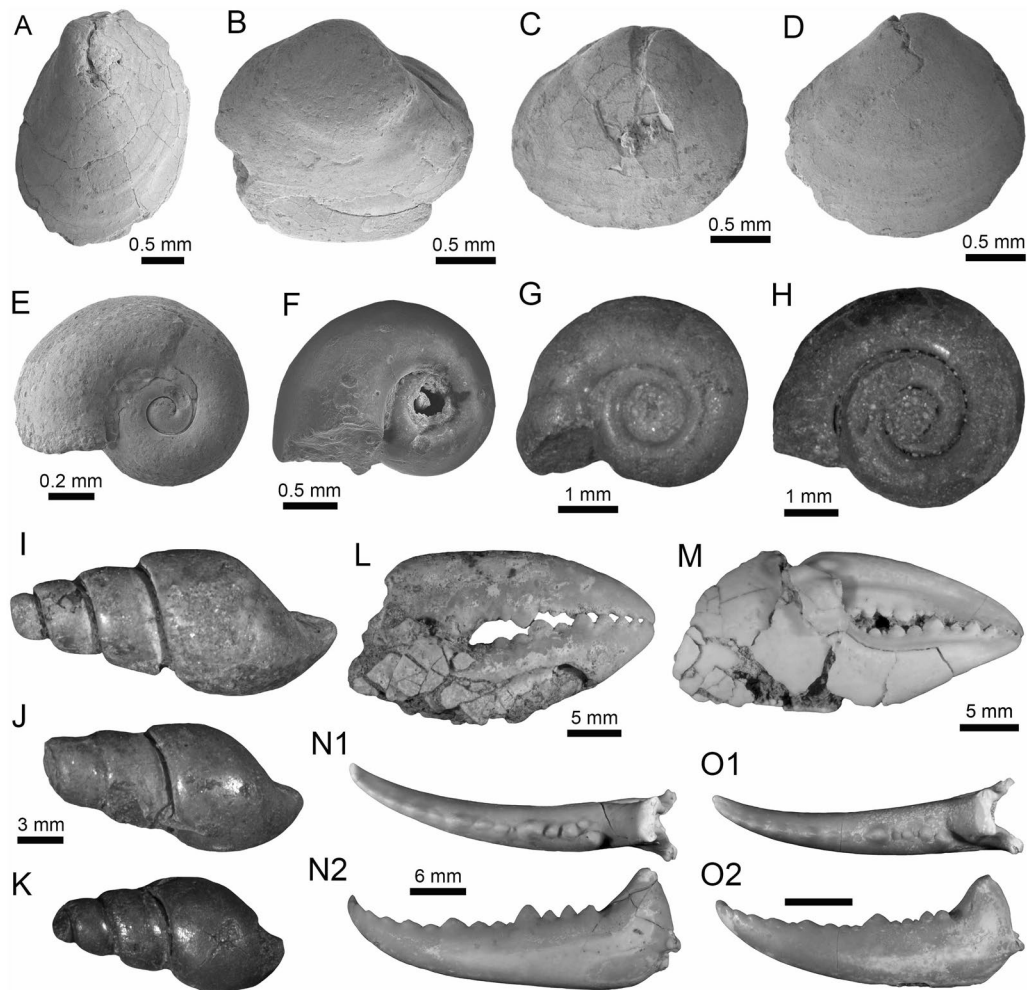


Fig. 34 Freshwater molluscs and crustaceans from the Vergel Member. **A–D** Internal molds of indeterminate bivalves (AMU-PI-81). **E–H** Internal molds of gastropods (AMU-PI-82) presumably related to Planorbidae. **J, K** Internal molds of indeterminate gastropods (AMU-PI-83). **L–O2** Right chelae (**L, M**) and moveable fingers (dactyl: **N1–O2**) of indeterminate freshwater crabs Trichodactylidae (AMU-PI-15)

crustaceans (Aguilera et al. 2010; Mihaljević et al. 2010), and some sharks and bony fishes (Carrillo-Briceño et al. 2018b, table S6; Aguilera et al. 2020) suggests a low to moderate energy coastline environment with an influx of terrigenous sediments (see Rey 1990; Ministerio de Energía y Minas 1997).

The SGOP section (Fig. 3C) is characterized by an interbedding of marine layers (with abundant marine mollusk, crustaceans, rays, and sirenian remains) and lenticular conglomerates (Fig. 2G, H) bearing disarticulated terrestrial vertebrates, suggesting intermittent flows of terrigenous sediments into a littoral environment. For example, the presence of freshwater/terrestrial fauna (including abundant coprolites) in marine sediments (coquinoic limestones) of the Urumaco and Caujarao

formations has been interpreted as the result of the input of streams and rivers from the backshore to the littoral marine environment (see Dentzien-Dias et al. 2018, table 2; Carrillo-Briceño et al. 2018a). Most of the cranial and postcranial remains from the conglomeratic layers of the SGOP locality were collected in situ already in fragmentary and isolated conditions, likely suggesting significant transport and deposition during high-energy episodes. A presumed crocodylian coprolite (Fig. 29H1, H2) was collected in the fine sandstone underlying the conglomeratic layer (Fig. 3C). Although it is difficult to infer the distance of origin and the continental paleoenvironments based on allochthonous terrestrial fossils recovered from marine sediments, the presence of terrestrial sloths, glyptodontids, pampatheriids, toxodontids, camelids, and procyonids in the SGOP locality (Additional file 7) suggests their association with grasslands

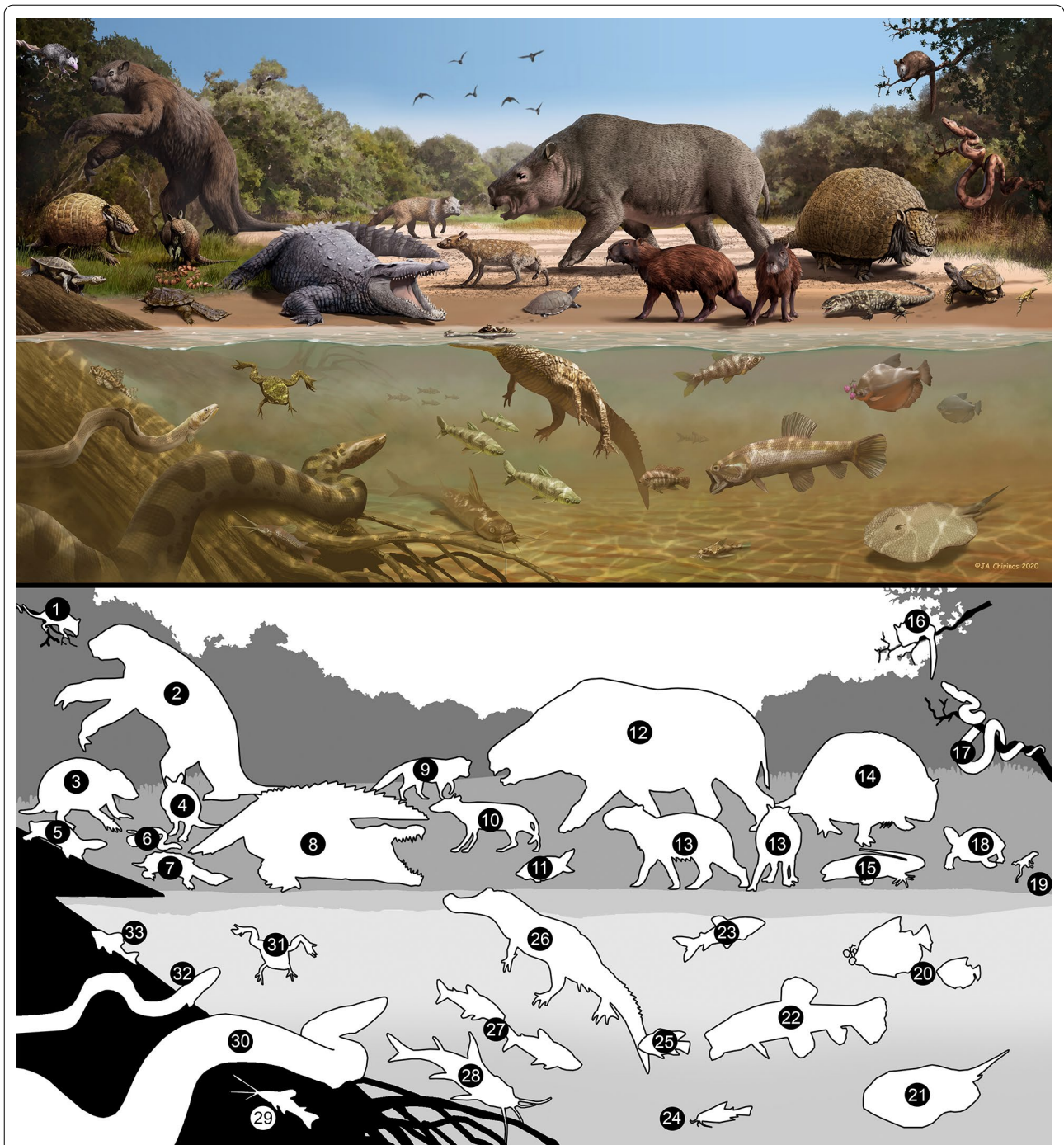


Fig. 35 (Top) Life reconstruction of the San Gregorio Formation faunal assemblage, Falcón Basin, Venezuela. Artist: Jaime Chirinos. (Bottom) Key of the reconstruction. (1) cf. *Didelphis* sp. (2) cf. *†Proeremotherium* sp. (3) aff. *†Holmesina floridanus*. (4) *†Pliodasyus vergelianus*. (5) Podocnemididae indet. (6) *Anilius scytale*. (7) *Chelus* sp. (8) *†Crocodylus falconensis*. (9) *†Cyonasua* sp. (10) *†Interatheriidae* indet. (11) Podocnemididae indet. (12) *†Falcontoxodon* sp. (13) *†?Hydrochoeropsis wayuu*. (14) aff. *†Boreostemma* sp. (15) *Tupinambis* s.l. (16) *†Marisela gregoriana*. (17) *Corallus* sp. (18) *Chelonoidis* sp. (19) Lizard. (20) *Mylossoma* sp. (21) *Potamotrygon* sp. (22) *Hoplias* sp. (23) *Schizodon* cf. *S. corti*. (24) cf. *Amblydoras* sp. (25) Cichlidae indet. (26) Caimaninae indet. (27) cf. *Megaleporinus* sp. (28) cf. *Sciades* sp. (29) Callichthyidae indet. (30) *Eunectes* sp. (31) cf. *Pipa* sp. (32) *Synbranchus* sp. (33) Suckermouth catfish (Hypostominae)

and/or forested-grassland areas (MacFadden 2005; Defler 2019, and references there in). In contrast, the presence of *Caiman* aff. *C. yacare*, *Eunectes*, and podocnemidid turtle remains provides evidence for wetland environments and permanent waters.

Conclusions

A late Pliocene age is here suggested for the Vergel Member based on its stratigraphical position, palynological content, and the presence of the pampatheriid *Plaina*. A Pleistocene age (Calabrian) is suggested for the Cocuiza Member based on its nannoplankton content and the $^{86}\text{Sr}/^{88}\text{Sr}$ dating.

There are fossils of at least 55 aquatic and terrestrial taxa from two different localities of the San Gregorio Formation: 49 taxa from the Vergel Member and 9 taxa from the Cocuiza Member. From the overall paleodiversity, 28 and 18 fossil taxa are reported for the first time in the fossil record of the Urumaco sequence and Venezuela, respectively. Among them are the first fossil records of the freshwater taxa cf. *Megaleporinus*, *Schizodon*, cf. *Amblydoras*, cf. *Scorpiodoras*, and the pipesnake *Anilius scytale*, all from Pliocene strata of the Vergel Member.

The San Gregorio Formation preserves a diverse assemblage of taxa that lived in the Falcón region after the isolation of northern South American and western Amazon basins. Mixed open grassland/forest areas were surrounded by permanent freshwater systems, contrasting with the current dry environments in the Falcón region. The presence of the cis-Andean freshwater catfishes cf. *Amblydoras*, cf. *Scorpiodoras*, podocnemidid and *Chelus* sp. turtles, the *Eunectes* (anaconda) and pipesnake *Anilius scytale* snakes, as well as some caviomorph neopiblemid rodents supports the hypothesis that geographical contraction to their extant distribution in northern South America occurred rapidly during at least the last 1.5 Ma. This could suggest marked environmental changes in the region during the early Quaternary and a subsequent extinction/extirpation process related to major climatic drying.

The rodent fauna from San Gregorio Formation (NCC locality) is the only Neogene unit from northern South America documenting the coexistence of caviomorphs (Hydrochoerinae, Neopiblemidae, and Octodontoidea) and cricetids. This fauna shows the last appearance datum of Neopiblemidae. To date, no dinomyids were found in such strata, a group quite diverse and abundant during the middle-late Miocene, which suggests that they were possibly in decline when the fossiliferous levels of the Vergel Member were accumulated. Cingulate and pilosan (Phyllophaga) xenarthrans from the Vergel Member are more closely related to the earliest South American immigrant taxa in Central and North America around the time

when the Panamá Isthmus was fully established. Carrillo et al. (2018) overlapped the mammalian assemblage of the Vergel Formation with the second and third migratory GABI pulse. However, with the late Pliocene age proposed here for the Vergel Member, this assemblage would have to be reinterpreted within GABI 1.

The occurrence of interatheriids in Pliocene sediments of the San Gregorio Formation could suggest that this mammalian group survived early Neogene climate change inhabiting patchy, likely forested areas in tropical South America. This longer persistence time for basal notoungulates might confirm that tropical areas of northern South America could have been "cradles and museums" of biodiversity (e.g., Jablonski et al. 2006). However, confirmation of these paleobiogeographic patterns requires intensive fieldwork in order to (1) collect, more complete and better-preserved specimens, (2) to increase drastically the sampling effort in the highly vegetated tropics, and (3) for isotaphonomic analysis to rule out any sampling biases in the Neotropics. Based on data from these suggested studies, we will be able to determine whether the tropics were indeed refugia for different clades that inhabited South America.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13358-020-00216-6>.

Additional file 1. Northward Chiguaje Hill section (NCH), San Gregorio Formation, Falcón state, Venezuela.

Additional file 2. San Gregorio Río Seco section (SGRS), San Gregorio Formation, Falcón state, Venezuela.

Additional file 3. Palynological samples from the Vergel Member, San Gregorio Formation.

Additional file 4. Micropaleontological samples from the Cocuiza Member, San Gregorio Formation.

Additional file 5. $^{87}\text{Sr}/^{86}\text{Sr}$ analyses for the Cocuiza Member of the San Gregorio Formation.

Additional file 6. Size of the lower first molar (m1) of AMU-CURS-1327, with respect to other fossil and extinct procyonid genera.

Additional file 7. Habitat preferences of San Gregorio aquatic freshwater taxa based on preferences of extant relatives. Localities: Norte Casa Chiguaje (NCC) and San Gregorio Oeste del Pueblo (SGOP). *Fr* freshwater, *Br* brackish, *Ma* marine.

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Authors' contributions

JDCB, AAC, CJ and MRSV conceived the study. The following authors performed the taxonomic work on the indicated taxa and drafted the description of those fossils: JDCB (rays, bony fishes, anurans, non-snake Squamata and mammals), JLOB (bony fishes), TMS (turtles and crocodylians), MD (anurans, non-snake Squamata and crocodylians), GLG (snakes), EAC (turtles), AAC (xenarthrans), JDC (toxodontids and camelids), LK (rodents), DRR and MCH (Carnivora), AFR (Tyrotheria), and MRC (seeds). JDCB, RS, TMS, JDC, MD, EAC, and AAC, and MRSV conducted fieldwork activities. JDCB processed the sediments, prepared samples, and took photographs. JDCB, JDC, and CJ prepared figures and/or tables. CJ, RTT, FV, and DSJ conceived and performed geochemical analyses and biostratigraphic dating. JDCB, TMS, JDC, MD, GLG, LK, DRR, JLOB, EAC, AFR, MCH, AAC, MRC, CJ, and MRSV wrote drafts of the manuscript. JDCB, and MRSV prepared the final draft. All authors read and approved the final manuscript.

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Availability of data and materials

All the fossil specimens described here are available at the paleontological collections of the Alcaldía Bolivariana de Urumaco (AMU-CURS), Falcón State, Venezuela. All data generated or analyzed during this study are included in this published article and its Additional files.

Competing interests

The authors declare that they have no competing interests.

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