Swiss Journal of Palaeontology (2019) 138:237–248
https://doi.org/10.1007/s13358-018-0180-y

REGULAR RESEARCH ARTICLE

A new vertebrate continental assemblage from the Tortonian of Venezuela

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Received: 19 October 2018 / Accepted: 22 November 2018 / Published online: 18 December 2018

Abstract

A wide variety of aquatic vertebrates from fluvio-lacustrine facies of northern South America (Colombia and Venezuela) have been used as unequivocal evidence to support hydrographic connections between western Amazonia and the Proto-Caribbean Sea during the Miocene. By the end of the Miocene, changes in the major hydrographic systems of the region produced losses of habitats and a regional faunal turnover, as has been documented in the geological record of the Urumaco region. Here, we report a new Tortonian aquatic and terrestrial vertebrate assemblage from two localities of the Caujarao Formation (El Muaco Member) in western Venezuela. The vertebrate assemblage includes a gharial (cf. †*Gryposuchus pachakamue*), alligatorid crocodylians (†*Purussaurus* and Alligatoridae indet.), a freshwater turtle (*Chelus* sp.), snakes (cf. *Eunectes* sp.), serrasalmids and pimelodids and thorny catfishes, a rodent (†*Potamarchus* sp.), pampatheres (†*Scirrotherium* sp.), sloths, as well as plant remains (coal and amber). Although the Caujarao Formation has been referred to as a fully marine environment, the new assemblage reported here suggests a freshwater input to the coastal area. Taxonomic and biogeographic affinities between the Muaco Member community and that reported from the Miocene proto-Amazonian systems are indicative of the persistence of ecological and hydrographic continuity at minimum until the end of the Miocene in at least an area of northwestern South America.

Keywords Neogene · Miocene · Caujarao Formation · Orinoco River · Biogeography

Introduction

A wide range of fossil fishes, reptiles, amphibians, as well aquatic mammals, from continental, fluvial and brackish facies of what are today arid regions of northern Colombia (Moreno et al. 2015; Cadena and Jaramillo 2015a, b; Moreno-Bernal et al. 2016) and Venezuela (Lundberg et al. 2010; Sánchez-Villagra et al. 2010; Aguilera et al. 2013; Scheyer et al. 2013; Aguirre-Fernández et al. 2017; Delfino and Sánchez-Villagra 2018) have been used as unequivocal evidence to support a hydrographic connections system between western Amazonia and the Proto-Caribbean Sea during the Miocene (e.g., Díaz de Gamero 1996; Hoorn et al. 2010). These connections allowed the dispersal of many aquatic species in equatorial South America, as well the continuum of the Amazonian forest into the coastal areas of Venezuela (Jaramillo et al. 2010). During the latest Miocene and Pliocene, changes in the major hydrographic system of the region occurred, with a consequent loss of habitats and regional faunal turnover (Sánchez-Villagra et al. 2010). The main process that triggered this event has

Editorial Handling: M. R. Sánchez-Villagra.

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been linked to the uplift of the northern Andes, an event that led to the isolation of the previously connected Orinoco and Amazonas systems with northern peripheral drainages, such as those of the western coast of Venezuela, Magdalena and Maracaibo basins (Lundberg 1998; Albert et al. 2006). In western Venezuela, the Castillo Formation (early Miocene), Sierra de la Baragua (Dahdul 2004; Ferreira et al. 2016), and the Socorro (middle Miocene) and Urumaco (late Miocene) formations from the Urumaco sequence (Lundberg et al. 2010; Riff et al. 2010; Sánchez-Villagra et al. 2010; Aguilera et al. 2013; Scheyer et al. 2013; Scheyer and Delfino 2016; Delfino and Sánchez-Villagra 2018) preserve paleontological evidence (e.g., freshwater fishes, reptiles and amphibians) that has been relevant to sustain the hypotheses of the hydrographic connections (but see Rincón et al. 2014). The Urumaco Formation exhibits the most diverse vertebrate fauna in that region, associated with a complex sequence characterized by a variety of paleoenvironments that include terrestrial, riverine, lacustrine and marine facies (Sánchez-Villagra et al. 2010; Aguilera et al. 2013; Scheyer et al. 2013; Carrillo-Briceño et al. 2015). To date, the Urumaco Formation represents the latest Miocene evidence of hydrographic connections between southern Proto-Caribbean and the Orinoco and Amazonas systems.

Here a new, terrestrial and aquatic vertebrate assemblage from the Caujarao Formation in western Venezuela is reported (Figs. 1, 2). Due to the taxonomical and biogeographical affinities of most of the representative taxa here reported from the Caujarao Formation with those fossil and extant taxa of the Orinoco and Amazonas systems, new evidence for the dynamics of hydrographic connections during the Miocene is offered.

Methods

The fossils studied herein (Figs. 3, 4) correspond to 26 cranial and postcranial elements of gharials and alligatorids crocodilians, turtles, snakes and mammals (the freshwater fish assemblage is under study), which were surface-collected from two localities of the El Muaco Member: (1) Quebrada Cucuruchu (11°29′46″N, 69°30′33″W) and (2) Puerto Chávez (11°30′16″N, 69°31′08″W) (Fig. 2). The specimens were extracted from the sediment/rocks mechanically, and these are housed in the paleontological collection of the Museo Ángel Segundo López, Taratara, Falcón State, Venezuela, with the acronym MTT-V. Taxonomic identification involved an extensive bibliographical review and comparative studies of fossil and recent specimens housed at the Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas of the Universidad Experimental Francisco de Miranda (CIAAP, UNEFM-PF); the paleontological collections of the Alcaldía Bolivariana de Urumaco (AMU-CURS), the Museo de Ciencias de Caracas (MCNC), all in Venezuela; the Mapuka Museum of Universidad del Norte (MUN-STRI), Barranquilla, Colombia; the Natural History Museum of National University of San Marcos (MUSM), Lima, Peru; and the Palaeontological Institute and Museum at the University of Zurich (PIMUZ).

Geological setting

The Caujarao Formation crops out in the Coro–La Vela region, with an estimated thickness of 1200 m at its type locality in the vicinity of the Caujarao town, Coro River (Vallenilla 1961). This unit overlays the Socorro Formation, and in the type locality, the lithology is characterized mainly by mudstones and clays, with a smaller proportion of limestones and sandstones (Vallenilla 1961; González de Juana et al. 1980). A fully marine environment and a late Miocene age have been suggested for the Caujarao Formation base on mollusks, foraminifera and nanoplankton (González de Juana et al. 1980; Wozniak and Wozniak 1987; Smith et al. 2010; Carrillo et al. 2018, fig. 29). Kavanagh de Petzall (1959) divided the Caujarao Formation into three members: El Muaco (lower), Mataruca (middle) and Taratara (upper), where the latter one is underlying La Vela Formation (Miocene–Pliocene). The fossiliferous localities here studied belong to the El Muaco Member (Fig. 2), which is 690 m thick and with a lithology characterized mainly by mudstones and clays with some limestones and sandstones well developed at the basal section of the member (Kavanagh de Petzall 1959; Vallenilla 1961). Wozniak and Wozniak (1987) suggested a platform environment for El Muaco Member, whose Tortonian age is assigned based on planktonic foraminifera (Carrillo et al. 2018, fig. 29). The fossiliferous locality in Quebrada Cucuruchu corresponds to a dark-gray mudstone layer of ~ 50 cm with abundant molluscan, ichnofossils and vertebrates remains, which underlay a hard coquinoid layer. The Puerto Chávez fossiliferous locality is located in the coastal line, and it is characterized by a 50 cm thick brown–orange bioturbated coquinoid layer, overlaying a gray mudstone, both with abundant marine invertebrate fragments and marine–continental vertebrates.

Fossil vertebrate assemblage

Crocodylia

Cranial and postcranial elements of gharials and alligatorids (Fig. 3a–q) were found in both Quebrada Cucuruchu and Puerto Chávez localities (Table 1). The gharial (Gryposuchinae) remains are represented by a fragmented skull

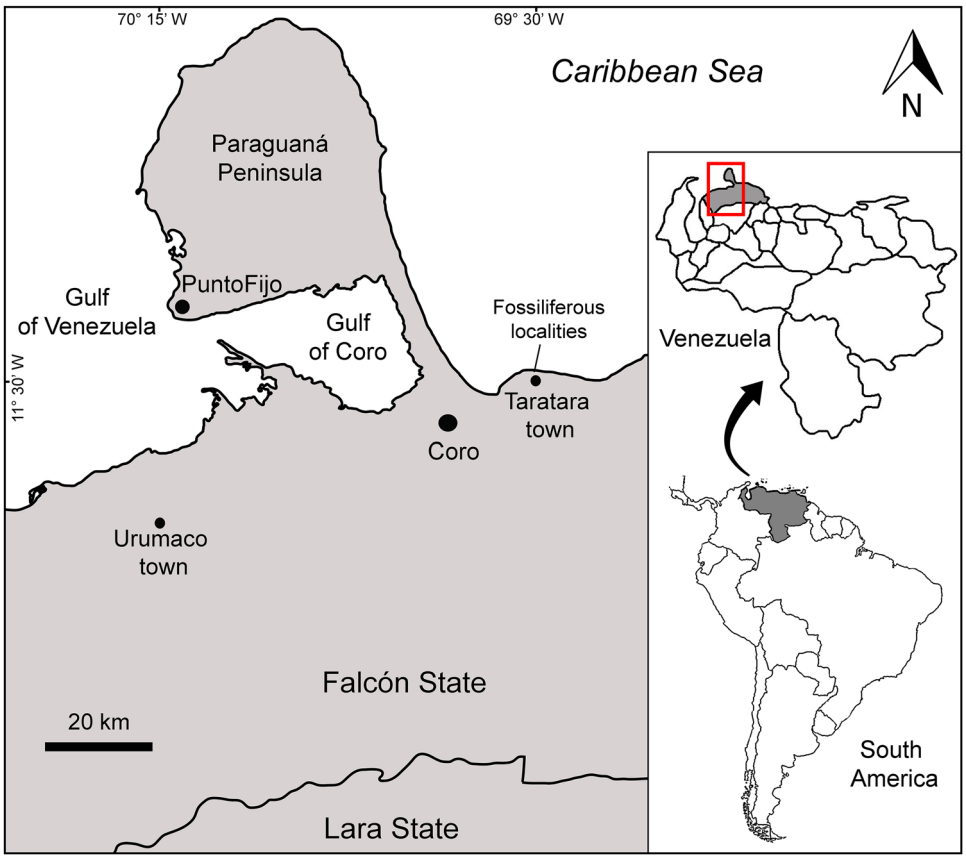

Fig. 1 Geographical location map of the fossiliferous localities of the Caujarao Formation, Western Venezuela

(MTT-V-53, Fig. 3a–f), five isolated long and slender teeth (crown height between 19 and 48 mm) (MTT-V-288-A, Fig. 3i–k) from the Puerto Chávez locality, and three osteoderms of indeterminate position (MTT-V-41, 44–45, Fig. 3g, h) from Quebrada Cucuruchu. The osteoderms are elongated with a rectangular shape and ornamented with pits. The cranial elements (Fig. 3a–f) belong to a single individual and consist of the posterior portion of the skull and fragmentary elements of the rostrum, including fragments of the maxillae, nasals and distal part of both mandibles (Fig. 3c–f). Although the skull is incomplete and fragmented, the shape of the skull table and its relative size are consistent with those of †*Gryposuchus pachakamue* Salas-Gismondi et al. 2016 from the late middle Miocene of Peru. Other †*Gryposuchus* species, such as †*Gryposuchus croizati* Riff and Aguilera, 2008 and †*Gryposuchus colombianus* Langston, 1965, present a broader skull table and widely separated and protruding orbits (see Salas-Gismondi et al. 2018). Therefore, we tentatively assign the Muaco gharial to cf. †*Gryposuchus pachakamue*.

The alligatorid remains are represented by two large, incomplete teeth (MTT-V-144, 295, Fig. 3l, m) referred to †*Purussaurus* Barbosa-Rodrigues, 1892, from Puerto Chávez locality. Additionally, we report two small, slightly blunt caiman-like teeth (crown height about 10–11 mm) (MTT-V-288-B, Fig. 3n, o) and two osteoderms of indeterminate position with a rectangular shape and ornamented with pits (MTT-V-09-10, Fig. 3p, q) from the same locality. The †*Purussaurus* teeth (crown height about 32–34.5 mm) are conical in shape; posteromedially recurved and slightly compressed laterally with distinct serrated carinae (e.g., see Aguilera et al. 2006).

Testudines

The fossil specimens are represented by two shell fragments of the Pleurodira turtle "matamata" (Chelidae: *Chelus* Duméril, 1806) from the Quebrada Cucuruchu. One of the fragments (MTT-V-80, Fig. 3r) corresponds to a carapace fragment preserving the posterior costals 6–8, while the other fragment (MTT-V-80A, Fig. 3s) corresponds to the posterior plastral lobe (xiphiplastra), where portions (most posterior regions) of both hypoplastra are preserved too. Although the two specimens come from the same layer, it is unknown if both belong to a single individual. Considering the age and geographical proximity between the Caujarao and Urumaco formations, it is plausible that these specimens herein referred belong to †*Chelus lewisi* rather than †*Chelus colombianus*, both described by Wood (1976). However, a review of the

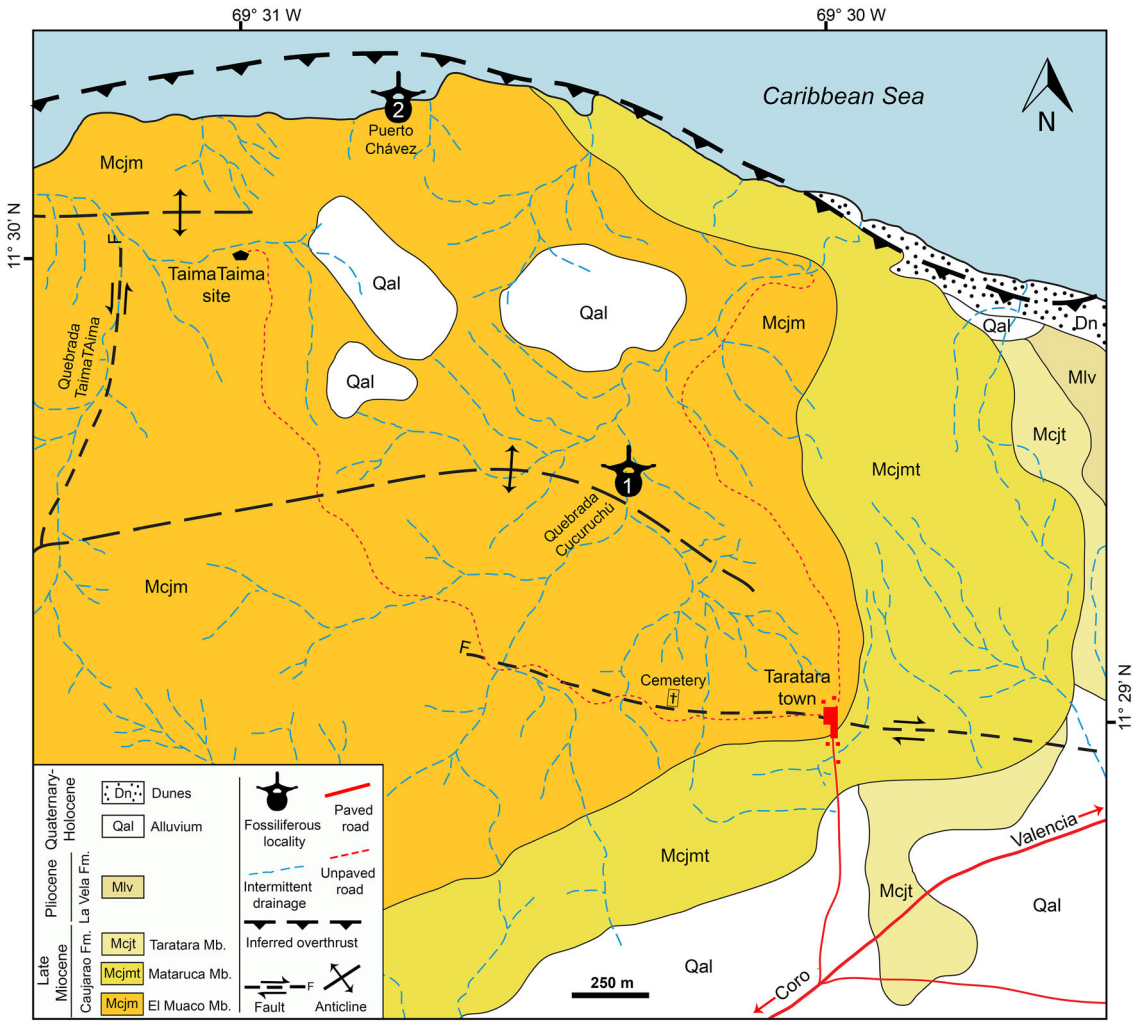

Fig. 2 Generalized geology of the study area. Fossiliferous localities: (1) Quebrada Cucuruchu, and (2) Puerto Chávez. Geological map based and modified from "Mapa geológico de La Vela de Coro–Tarata". Universidad Central de Venezuela, Departamento de Ingeniería, by Clemente González de Juana, 1969 (saber.ucv.ve/handle/123456789/9651)

diagnostic features of the two fossil *Chelus* species suggested that these probably represent intraspecific variation, †*C. lewisi* being a possible junior synonym of †*C. colombianus* (Ferreira et al. 2016). Due to the poorly preserved condition of the specimens from the Caujarao Formation and the wide variation in extant and fossil species of *Chelus*, we, thus, refrain from taxonomic identification at species level.

Squamata

Four large and robust, pre-cloacal vertebrae (Fig. 4a–h), of which three come from the Puerto Chávez locality (MTT-V-32, 301a, b) and one from Quebrada Cucuruchu (MTT-V-386). Three of the vertebrae (MTT-V-301a, b, and MTT-V-386) are incomplete and fragmented (Fig. 4f–h), preserving only their anterior or posterior portions. The specimen MTT-V-32 (Fig. 4a–e) is the largest and most complete with a centrum length of 19 mm and interzygapophyseal constriction width of 27 mm. Large and robust vertebrae with a prominent median tubercle, robust zygosphene and a slightly depressed neural arch are elements that characterized the specimen from Caujarao Formation; features that coincide with previous observations in vertebrae of *Eunectes* Wagler, 1830 (see Hsiou and Albino 2009, 2010). However, due to the scarce number and poorly preserved condition of the specimens, we tentatively assign them to cf. *Eunectes* sp.

Rodentia

The specimen MTT-V-100 (Fig. 4i–l) was collected in Puerto Chávez locality and corresponds to a portion of the left dentary preserving the m2 and m3 of the caviomorph rodent †*Potamarchus* Burmeister, 1885. Both teeth are protohypsodont, lophodont (laminar), and rectangular in

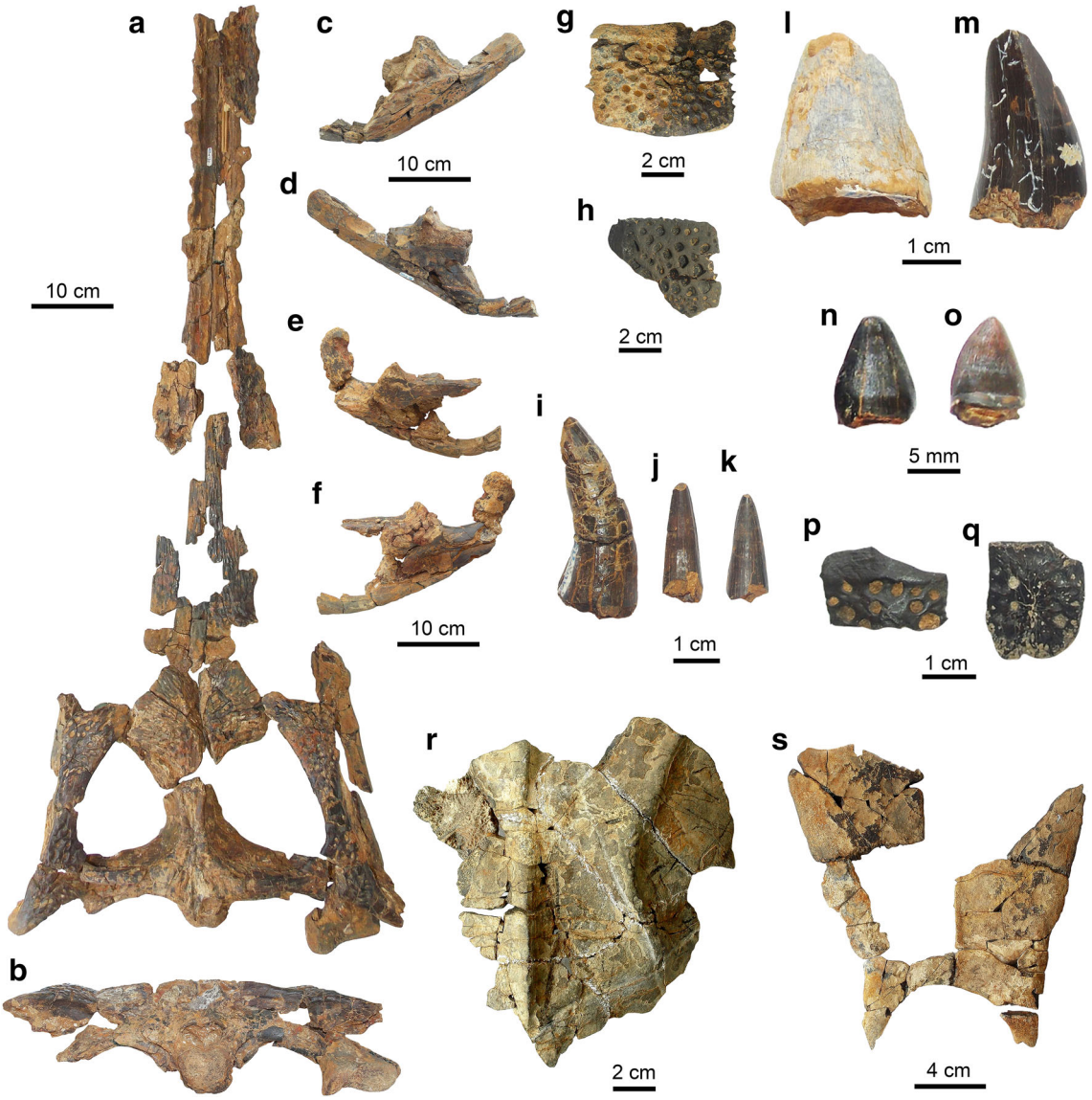

Fig. 3 Crocodylian and chelonian remains from the Caujarao Formation. **a–f** Fragmented skull and posterior portion of the right and left mandibles (MTT-V-53) of cf. †*Gryposuchus pachakamue*. **g–k** Gavialidae indet. **g, h** osteoderms (MTT-V-41, 44–45). **i–k** Isolated teeth (MTT-V-288-A). **l, m** †*Purussaurus* isolated teeth (MTT-V-144, 295). **n–q** Alligatoridae indet. remains. **n, o** Isolated blunt caiman-like teeth (MTT-V-288-B). **p, q** Osteoderms (MTT-V-09-10). **r, s** *Chelus* sp. **r** Carapace fragment preserving the posterior costals 6–8 (MTT-V-80). **s** Plastron posterior lobe (xiphiplastra) (MTT-V-80A)

outline. The m3 is larger than the m2, with a linguolabial width between 9 and 8 mm, respectively. The m3 is 6 mm in mesiodistal length, tetralophodont showing a wear fossetid in the first lophid (Fig. 4l). The m2 is incomplete, especially in its labial section; however, four lophs and a fossetid in the first lophid can be observed. The lophids are oblique and the enamel that outlines the second, third and fourth lophids of both teeth is crenulated mesially and thicker and smoother distally. The morphological features of the specimen MTT-V-100, especially the tooth size, and shape and number of the lophs, coincide with those observed in †*Potamarchus murinus* Burmeister, 1885 and †*Potamarchus adamiae* Kerber et al. 2016, from the late Miocene of Argentina and Brazil, respectively. The analyzed specimen differs from †*Potamarchus sigmodon* Ameghino, 1891 (from the Miocene of Argentina), because the latter is characterized by the absence of crenulations (see Kerber et al. 2016). The poor preservation of the specimen MTT-V-100 does not permit a confident specific identification.

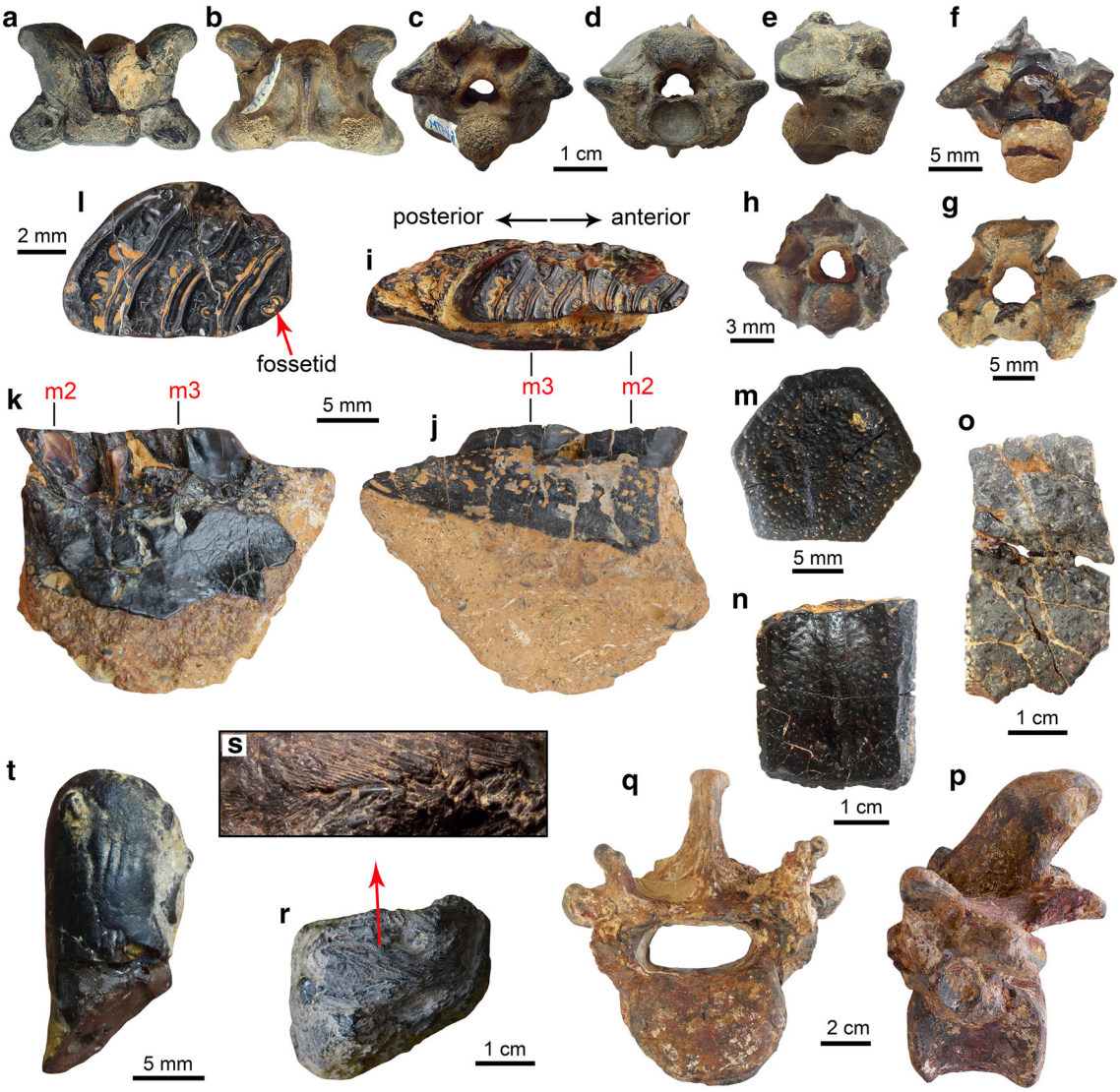

Fig. 4 Squamata, mammals and coprolite remains from the Caujarao Formation. **a–h** Isolated vertebrae of cf. *Eunectes* sp. **a–e** specimen MTT-V-32. **f–h** Broken and incomplete vertebrae (**f, g** MTT-V-301a, b; **h** MTT-V-386). **i–l** Fragmented left dentary portion of †*Potamarchus* sp. (MTT-V-100). **l** m3 in occlusal view. **m–o** Isolated osteoderms of †*Scirrotherium* sp. **m** Buckler osteoderm (MTT-V-307). **n, o** Imbricating osteoderms (**n** MTT-V-148 and **o** MTT-V-34). **p, q** Thoracic vertebra of a terrestrial sloth (MTT-V-142). **r–t** Coprolite fragments. **r, s** Fragment preserving plant remains (MTT-V-s/n). **t** bullet-shape coprolite fragment with longitudinal striations of a potential rodent producer

Cingulata

We report three pampathere osteoderms (Fig. 4m–o), consisting of one fixed buckler osteoderm (MTT-V-307) from the Quebrada Cucuruchu locality and two movable-band osteoderms (MTT-V-34 and MTT-V-148) from the Puerto Chávez locality. The fixed osteoderm (Fig. 4m) is hexagonal in outline, with the anterior margin bearing multiple deep foramina, and a narrow and elongated central elevation. The moveable osteoderm MTT-V-34 (Fig. 4o) is rectangular in outline, almost complete and partially eroded. It preserves the anterior, intermediate and posterior portions (sensu Góis et al. 2013) with abundant anterior and lateral foramina. The other moveable osteoderm MTT-V-148 (Fig. 4n) is broken, preserving part of the posterior portion, where a clear longitudinal central and marginal elevation can be observed. Some foramina are present in the lateral margins. Morphological features of these three osteoderms resemble general features of the pampatherid † *Scirrotherium* Edmund and Theodor, 1997. The genus † *Scirrotherium* ranges from the early to late Miocene of Central and South America (Góis et al. 2013; Rincón et al.

Table 1 New vertebrate faunal assemblage from the El Muaco Member

Order Family Genus/species	El Muaco Member Quebrada Cucuruchu	 Puerto Chávez	Inferred habitat
Crocodylia			
Gavialidae			
cf. †*Gryposuchus pachakamue*		X	?Marine-brackish-fresh
Indet.	X	X	?Marine-brackish-fresh
Alligatoridae			
†*Purussaurus* sp.		X	Freshwater
Indet.		X	Freshwater
Testudines			
Chelidae			
Chelus sp.	X		Freshwater
Squamata			
Boidae			
cf. *Eunectes* sp.	X	X	Terrestrial-Freshwater
Rodentia			
Dinomyidae			
†*Potamarchus* sp.		X	Terrestrial
Cingulata			
†Pampatheriidae			
†*Scirrotherium* sp.	X	X	Terrestrial
Pilosa			
Indet.		X	Terrestrial
Characiformes			
Serrasalmidae (pacu clade) Indet.	X	X	Freshwater
Siluriformes			
Doradidae (thorny catfishes) Indet.		X	Freshwater
Pimelodidae Indet.	X	X	Freshwater

2014), and three nominal species are recognized: †*Scirrotherium hondaensis* Edmund and Theodor, 1997, from the middle Miocene of Colombia, †*Scirrotherium carinatum* Góis et al., 2013, from the late Miocene of Argentina and Brazil, and †*Scirrotherium antelucanus* Laurito and Valerio, 2013, from the late Miocene of Costa Rica. These osteoderms from the Caujarao Formation are confidently referred to †*Scirrotherium*; the enormous variation of osteoderm shapes within individuals precludes a taxonomic identification at the species level.

Pilosa

The specimen MTT-V-142 was collected in the Puerto Chávez locality; it corresponds to one of the last thoracic vertebrae of a large-sized xenathran, preserving the centrum, the neural arch, the articular facets and the spinous and transverse process (Fig. 4p, q). Morphological features of the vertebra resemble mostly those of terrestrial sloths (e.g., Amson et al. 2015).

Coprolites

Abundant vertebrate coprolites (Fig. 4r–t) were collected in the Quebrada Cucuruchu and Puerto Chávez localities. The coprolites are dark brown in color and most of them are in fragmentary condition. One of the specimens preserves what seem to be remains of indeterminate plants (Fig. 4r, s), while another specimen (Fig. 4t) has a typical bullet shape with longitudinal striations, similar to a rodent-coprolite morphotype described for the Urumaco Formation (Dentzien-Dias et al. 2018, fig. 4, table 3).

Discussion and conclusions

During the Miocene, coastal marine areas of what today corresponds to the Falcón state, western Venezuela were influenced by a complex hydrographic system that flowed from southern basins to the Proto-Caribbean Sea (Díaz de Gamero 1996; Aguilera et al. 2013). The paleontological

record of the middle–late Miocene of the Urumaco region (Socorro and Urumaco formations), characterized by abundant remains of freshwater fishes, amphibians, turtles, crocodilians, and aquatic mammals (Lundberg et al. 2010; Riff et al. 2010; Sánchez-Villagra et al. 2010; Scheyer et al. 2013; Aguirre-Fernández et al. 2017; Delfino and Sánchez-Villagra 2018), has been used as unequivocal evidence to support a hydrographic connections between Orinoco and Amazonas systems with northern peripheral drainages (Lundberg 1998). The Urumaco Formation has been referred as correlative with the Caujarao Formation (Quiroz and Jaramillo 2010); however, the latter has been inferred as a fully marine environment (González de Juana et al. 1980), which contrasted with the diverse paleoenvironment facies that characterized the Urumaco Formation (Quiroz and Jaramillo 2010; Carrillo-Briceño et al. 2015). The presence of aquatic fauna in the Caujarao Formation with Orinoquian and Amazonian affinities, such as serraslamids fishes of the ''pacu'' group and pimelodids and thorny catfishes (fish specimens under study), *Chelus* sp. and cf. *Eunectes* sp., are unequivocal evidence that support hydrographic connections during the late Miocene. The fossiliferous localities of the Caujarao Formation from where we collected the new vertebrate assemblage herein described are located a little over 70 km east of the Urumaco region (Fig. 1), and the freshwater fish and reptilian fauna from both geological units share certain faunal similarities. The presence of †*Purussaurus*, *Chelus*, cf. *Eunectes*, serrasalmids fishes (e.g., ''pacu'' group), as well as pimelodids and thorny catfishes with Orinoquian and

Table 2 Associated fish fauna assemblage from the El Muaco Member

Order	El Muaco Member		Inferred habitat
Family Genus/species	Quebrada Cucuruchu	Puerto Chávez	
Lamniformes			
†Otodontidae			
†*Carcharocles megalodon*	X	X	Marine–?brackish
Alopiidae			
†*Anotodus* sp.	X		Marine
Carcharhiniformes			
Hemigaleidae			Marine–?brackish
†*Hemipristis serra*	X		
Carcharhinidae			
Carcharhinus leucas	X	X	Marine-brackish-fresh
†*Galeocerdo aduncus*	X	X	Marine
Negaprion sp.	X	X	Marine-brackish
Sphyrnidae			
Sphyrna mokarran	X	X	Marine-brackish
Sphyrna zygaena		X	Marine-brackish
Rhinopristiformes			
Pristidae			
Pristis sp.		X	Marine-brackish-fresh
Myliobatiformes			
Dasyatidae Indet.	X	X	Marine-brackish
Myliobatidae			
Aetomylaeus sp.	X		Marine-brackish
Perciformes			
Lutjanidae Indet.	X		Marine-brackish
Scombriformes			
Sphyraenidae			
Sphyraena sp.	X		Marine
Tetraodontiformes			
Balistidae			
Balistes sp.	X		Marine
Diodontidae Indet.	X	X	Marine-brackish

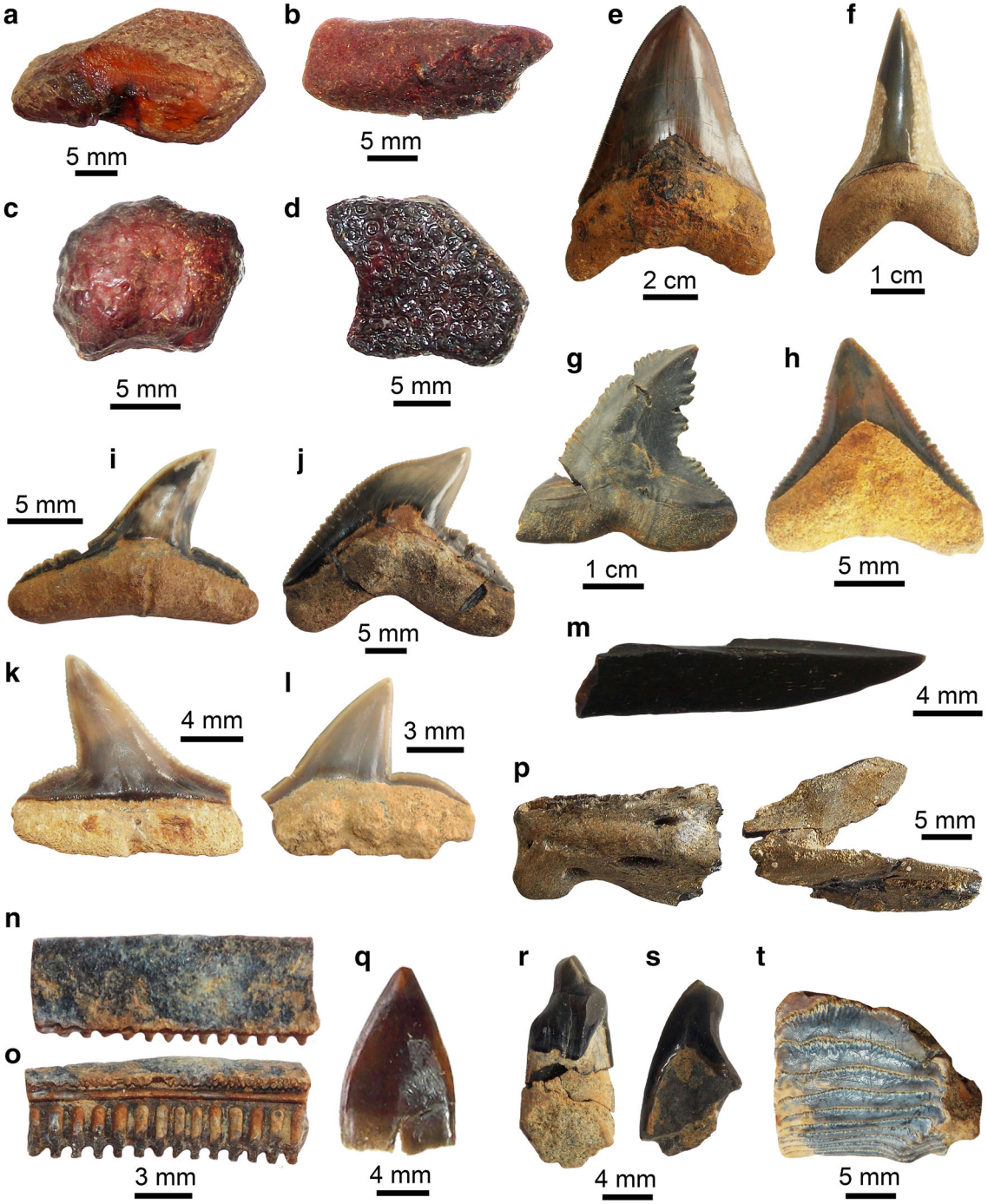

Fig. 5 Plant and marine fish remains found in association in the Quebrada Cucuruchu and Puerto Chávez localities. **a**–**d** Amber fragments (MTT-s/n). **e** †*Carcharocles megalodon* (MTT-V-01). **f** †*Anotodus* sp. (MTT-V-392). **g** †*Hemipristis serra* (MTT-V-127). **h** *Carcharhinus leucas* (MTT-V-104). **i** *Negaprion* sp. (MTT-V-164). **j** †*Galeocerdo aduncus* (MTT-V-117). **k** *Sphyrna mokarran* (MTT-V-377). **l** *Sphyrna zygaena* (MTT-V-377a). **m** *Pristis* sp. (MTT-V-391). **n**–**o** *Aetomylaeus* sp. (MTT-V-124). **p** Lutjanidae Indet., left dentary (MTT-V-495). **q** *Sphyraena* sp. (MTT-V-370). **r**, **s** *Balistes* sp. (MTT-V-130). **t** Diodontidae Indet. (MTT-V-96). Locality: Quebrada Cucuruchu (**f**, **g**, **j**, **n**–**s**), Puerto Chávez (**e**, **h**, **i**, **k**–**m**, **t**)

Amazonian affinities in the Caujarao Formation, increase the paleogeographical distribution of these aquatic taxa in northern South America during late Miocene; suggesting that the freshwater input to the coastal area where El Muaco Member was deposited could have been part of the northern peripheral drainages flowing towards the Proto-Caribbean.

A Tortonian age has been assigned to the El Muaco Member based on the planktonic foraminifera (Carrillo et al., 2018, fig. 29). None of the aquatic and terrestrial vertebrates recovered and described herein from the Quebrada Cucuruchu and Puerto Chávez localities allow us to test this age, due to the wide chronostratigraphic range of most of the taxa. †*Purussaurus*, *Chelus* and *Eunectes* have a record that covers much of the Miocene (Moreno-Bernal et al. 2016; Hsiou and Albino 2009, 2010; Ferreira et al. 2016), with living representatives for the last two. The specimen here assigned to cf. †*Gryposuchus pachakamue* suggests a wider temporal and geographical range that is known for this species described from the late middle Miocene of Peru (Salas-Gismondi et al. 2016). The stratigraphic range of the caviomorph †*Potamarchus* is restricted to the late Miocene of South America (Kerber et al. 2016), and it includes also a report for the Urumaco Formation (Horovitz et al. 2010). The same case could be referred to the pampatherid †*Scirrotherium*, ranging from the early to late Miocene (Góis et al. 2013; Rincón et al. 2014). The presence of †*Scirrotherium* sp. from the Caujarao Formation, together with †*S. antelucanus* from the late Miocene of Costa Rica (Laurito and Valerio 2013) and the western Amazonia of Brazil (Góis et al. 2013), represents the youngest and northern-most records for this taxon.

Different studies based on molluscs and foraminifera concluded that the El Muaco Member was deposited in a marine shallow environment with pelagic influence (Cavanahg de Petzall 1959; Vallenilla 1961; Wozniak and Wozniak 1987). In both Quebrada Cucuruchu and Puerto Chávez localities, together with the fauna described herein (Table 1), abundant marine fish remains including shark teeth and bony fishes were also collected by the authors (Table 2, Fig. 5). It is important to mention that most of the marine shark, ray and bony fish taxa found in association with the fauna described here from the Quebrada Cucuruchu and Puerto Chávez localities have wider environmental preferences with broad salinity tolerances (Table 2). This allows them to be in estuarine areas and in some changes to ascend into rivers (see Carrillo-Briceño et al. 2015, fig. 10). Other shark and bony fish species have also been referred to the Caujarao Formation from the Mataruca and Taratara members (Aguilera 2010; Aguilera and Lundberg 2010; Aguilera et al. 2016; Carrillo-Briceño et al. 2018).

The mixture of marine and freshwater/terrestrial fauna observed in these fossiliferous layers of the Quebrada Cucuruchu and Puerto Chávez localities, which includes amber fragments (Fig. 5a–d) and carbonized vegetation, could be inferred as the result of the input of streams and rivers from the backshore to the littoral marine environment, evidence of mixed coastal marine and fluvial–estuarine environments. Similar deposits have been referred to the Urumaco Formation, as is the case of the "Quebrada Bejucal" locality, a coquinoid layer deposited in an interdistributary bay containing an abundant and diverse mixture of marine/continental fauna that includes: mollusk, crustaceans, sharks and rays, bony fishes, alligatorids, turtles, snakes, sirenians, rodents, sloths, pampatherids, coprolites, among others (e.g., Scheyer et al. 2013, S2 table; Carrillo-Briceño et al. 2015, S1 table; Scheyer and Delfino 2016; Dentzien-Dias et al. 2018, table 2). Although some of the described specimens from Quebrada Cucuruchu and Puerto Chávez localities are fragmentary, this seems to be more associated with the conditions of preservation and exposure to external elements in the outcrops than with transport. Most of the specimens, including the gharial skull, do not show significant transport or erosive evidence, suggesting that they did not suffer transport for long distances and likely were deposited during high energy episodes. The presence of freshwater and continental faunal (e.g., terrestrial sloths and pampatherids) surrounding the littoral area where the Muaco Member was deposited could suggest the presence of rivers with savanna and forest areas.

Acknowledgements We thank to Marcelo Sánchez-Villagra for academic support and for the financial assistance (University of Zurich research monies) that made this work possible. We especially thank the Taratara community, the Museo Ángel Segundo López and the Instituto del Patrimonio Cultural de Venezuela (IPC) for the authorization to collect and study the specimens. To the Alcaldía Bolivariana de Urumaco, the Universidad Experimental Francisco de Miranda, the Museo de Ciencias Naturales de Caracas, in Venezuela, the Mapuka Museum of Universidad del Norte, Colombia; the Natural History Museum of National University of San Marcos, Peru; and the Palaeontological Institute and Museum at the University of Zurich, Switzerland, for their valuable assistance and for access to comparative material. We greatly appreciate comments, suggestions and collaboration provided by Dr. Torsten Scheyer and Dr. Gabriel Aguirre-Fernández. The Editor and reviewers (Dr. Edwin Cadena, Dr. Leonardo Kerber, and Jaime Villafaña) are thanked for their valuable comments and suggestions on the manuscript.

Funding This study was funded/support for the financial assistance of the University of Zurich research monies.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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