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Neogene vertebrates from Urumaco, Falcón State, Venezuela: diversity and significance

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SYNOPSIS The first palaeontological discoveries in Urumaco were made more than half a century ago. Several research groups have worked in the region, but new vertebrate fossils are still being found in this area of northwestern Venezuela. The most conspicuous elements of the fauna are reptiles, because of their size and abundance, although fishes are by far the most diverse group. Among South American Neogene assemblages the whole fauna is most similar to those of Acre in Brazil and Entre Rios in Argentina. The crocodile fauna includes at least 12 species representing diverse ecomorphological types; most of them lived sympatrically, a unique case in worldwide crocodylomorph assemblages. At least four turtle species provide unique palaeobiogeographical or palaeobiological information. Several freshwater species, including Serrasalminae fish, thorny catfishes, silver croaker, redtail catfishes, matamata turtle, river dolphin and probable sirenians, are consistent with the hypothesis that a tributary and/or delta of the Orinoco existed in this area of north-western Venezuela during late Miocene times.

KEY WORDS Miocene, crocodile, turtle, fish, Orinoco, Caribbean

Introduction

The Falcon Basin in northwestern Venezuela has long been known as a source of Neogene vertebrate fossils. As well as Pleistocene sites in the vicinity of Coro, some associated with well-known archaeological and palaeontological finds (Bryan *et al*. 1978; Aguilera 2005), ample exposures of late Miocene deposits around the town of Urumaco, which is located approximately 100 km west of Coro, have been known for some time and have produced several significant findings (e.g. Royo y Gómez 1960; Wood 1976*a*, *b*; Lundberg *et al*. 1988; Lundberg & Aguilera 2003; Sánchez-Villagra *et al*. 2003; Aguilera 2004).

Many geologists and palaeontologists have been attracted to the productive oil fields of Falcón for more than seven decades. Oil companies were operating in the 1930s near Urumaco. An important centre of operation was the oil camp of El Mamón, located in one of the richest palaeontological areas. The first reports of fossil vertebrates were made in the 1950s during exploration by the Texas Petroleum Company, which donated the first fossil vertebrate to the Universidad Central de Venezuela (Aguilera 2004). This would later be described as a new gharial genus and species, *Ikanogavialis gameroi* from the locality of Tío Gregorio (Sill 1970). Inspired by these first discoveries, Dr Royo y Gómez (Fig. 1), Professor of Geology at the Universidad Central de Venezuela in Caracas, conducted the first two expeditions in 1958 and 1959. Among the specimens collected were fish skulls and teeth, turtle shells, crocodile scutes and vertebrae and a mammalian skull and vertebrae (Royo y Gómez 1960). Since the pioneering studies of Royo y Gómez, several teams of investigators or individuals have worked in Urumaco, resulting in an important and diverse fossil fauna, one of only a few from the northern neotropical Cenozoic (Table 1). In what follows, we discuss the significance of the fauna and summarise some of the highlights of discoveries made to date.

Geological formations with fossil vertebrates in the Urumaco area

Three geological formations in the Urumaco area contain fossil vertebrates. The most fossiliferous is the Urumaco Formation (Aguilera 2004), of late Miocene age and probably encompassing the Chasicoan–Huayquerian South American land mammal ages (Díaz de Gamero & Linares 1989). Most palaeontological work to date in Urumaco has been done in this Formation.

The Urumaco Formation is characterised by diverse faunal associations in continental (savannas), freshwater (swamps and rivers), estuarine (brackish) and marine (coastal lagoon, salt marsh and sandy littoral) environments. Each assemblage can be correlated with a distinctive sedimentary environment. The following facies are apparent: shallow water marine rich in molluscs and fishes, brackish water rich in marine catfish and swampy palaeoenvironments rich in crocodilians, freshwater and marine turtles and freshwater

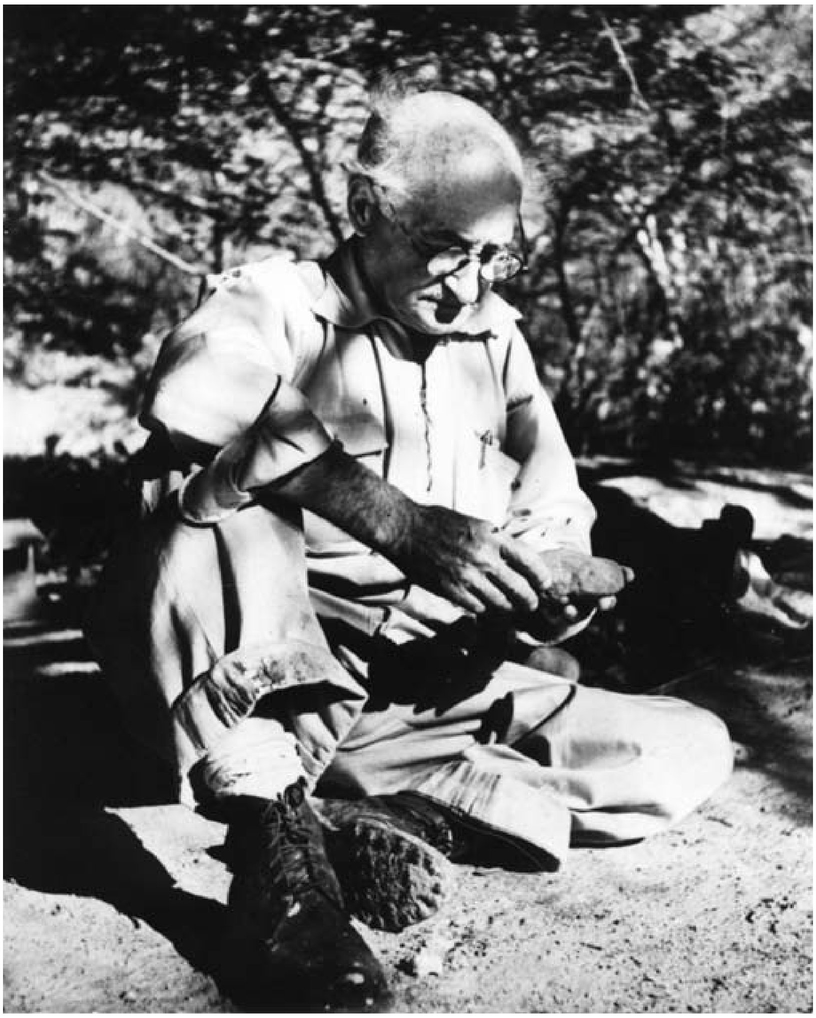

Figure 1 José Royo y Gómez, Universidad Central de Venezuela, in the mid- 1950s, contemplating one of the many fossils he collected during extensive explorations in northwestern Venezuela.

catfish. This general sequence repeats several times in the outcrop, with the whole formation reaching a total thickness of between 1700 and 2000 m (Aguilera 2004).

In addition to Urumaco, two other formations contain fossil vertebrates as reported in several papers in this volume. Overlying the Urumaco Formation is the Codore Formation, containing two members, the upper one marine and with marine invertebrates that suggest an early Pliocene age, while the lower member contains fossil vertebrates that suggest more continental environments (Ministerio de Energía y Minas 1997).

Underlying the Urumaco Formation is the Socorro Formation, the geology and biostratigraphy of which is summarised by Hambalek *et al*. (1994). Based on numerous previous studies of foraminifera and their studies of palynomorphs, they assigned a middle Miocene age to the formation. The upper part of Socorro Formation is where fossil vertebrates reported in this volume have been found. It includes limestone with molluscs, especially in the eastern sector of the Formation, to the east of Urumaco River, which has an estimated thickness of 700 m. The definition of the lower limit of the Urumaco Formation, which is characterised by limestone, is therefore a more or less arbitrary decision and has been somewhat different for each author who has published on this matter (Díaz de Gamero & Linares 1989 and references therein). Considering that mostly deltaic and fluvial deposits are represented in a great portion of the Socorro Formation (Hambalek *et al*. 1994), more so than in the Urumaco Formation, the former is probably more relevant for testing the large river hypothesis discussed below (Díaz de Gamero 1996) and for future exploration for continental mammals and microvertebrates.

Comparison with other faunas in South America

As listed in Table 1, the Urumaco fauna contains at least 77 vertebrate taxa, making it one of the best-documented tropical Miocene fossil vertebrate faunas in the world.

There is a widespread false assumption that fossils are not to be found in tropical areas because of difficulties in preservation, perhaps because most tropical areas are covered by vegetation. In fact southern South America now encompasses many arid regions where extensive rock exposures are common and fossils can be found with relative ease. Northern Venezuela presents a further problem when searching for continental vertebrates. In parallel with the situation in

Table 1 Vertebrate biota from the Socorro, Urumaco, and Codore Formations, Venezuela.

- *CHONDRICHTHYES*
  - LAMNIDAE
    - (1) *Carcharodon megalodon*
  - HEMIGALEIDAE
    - (2) *Hemipristis serra*
  - CARCHARHINIDAE
    - (3) *Carcharhinus* sp.
    - (4) *Galeocerdo cuvier*
    - (5) *Negaprion eurybathrodon*
    - (6) *Rhyzoprionodon* sp.
  - PRISTIDAE
    - (7) *Pristis* aff. *pectinata*
  - DASYATIDAE
    - (8) *Dasyatis* sp.
  - MYLIOBATIDAE
    - (9) *Aetobatus arcuatus*
    - (10) *Myliobatis* sp.
    - (11) *Pteromylaeus* sp.
    - (12) *Rhinoptera* sp.
  - RHINOBATIDAE
    - (13) *Rhynchobatus* sp.
- *OSTEICHTHYES*
  - PIMELODIDAE
    - (14) *Phractocephalus nassi*
    - (15) cf. *Pseudoplatystoma* sp.
  - DORADIDAE
    - (16) Gen et sp. indet.1
    - (17) Gen et sp. indet.2
    - (18) Gen et sp. indet.3
  - ARIIDAE
    - (19) *Aspistor quadriscutis*
    - (20) *Aspistor kessleri*
    - (21) *Aspistor rugispinis*
    - (22) *Bagre marinus*
    - (23) *Sciades couma*
    - (24) *Sciades dowii*
    - (25) *Sciades herbergii*
    - (26) *Sciades troscheli*
  - SERRASALMIDAE
    - (27) *Piaractus* sp.
  - (28) ERYTHRINIDAE indet.
  - SCIAENIDAE
    - (29) *Cynoscion* sp.
    - (30) *Equetus* sp.
    - (31) *Larimus* sp.
    - (32) *Micropogonias coatesi*
    - (33) *Ophioscion lundbergi*
    - (34) *Plagioscion urumacoensis*
  - HAEMULIDAE
    - (35) *Haemulon* sp.
  - SERRANIDAE
    - (36) *Epinephelus itajara*
- *SAUROPSIDA*
  - AVES, Ciconiiformes, CICONIIDAE
    - (37) *Jaribu* sp. nov.
- *CROCODYLOMORPHA*
  - ALLIGATORIDAE
    - (38) *Caiman brevirostris*
    - (39) *Caiman lutescens*
    - (40) *Melanosuchus fisheri*
    - (41) *Purussaurus mirandai*
  - CROCODYLIDAE
    - (42) *Thecachampsa* sp.
  - GAVIALIDAE
    - (43) *Brasilosuchus mendesi*
    - (44) *Gryposuchus jessei*
    - (45) *Gryposuchus* sp. nov.
    - (46) *Hesperogavialis cruxenti*
    - (47) *Ikanogavialis gameroi*
  - NETTOSUCHIDAE
    - (48) *Mourasuchus arendsi*
- SQUAMATA, OPHIDIA
  - ANILIIDAE
    - (49) *Colombophis* cf. *Colombophis portai*
  - BOIDAE, (50) BOINAE gen. et sp. indet.
    - (51) ALETHINOPHIDIA gen. et sp. indet.
- TESTUDINES
  - PODOCNEMIDIDAE
    - (52) *Bairdemys venezuelensis*
    - (53) *Stupendemys geographicus*
  - (54) TRIONYCHIDAE indet.
  - CHELIDAE
    - (55) *Chelus lewisi*
- *MAMMALIA*
  - *MARSUPIALIA, (56) BORHYAENIDAE indet.
  - CETACEA, (57) Odontocete indet.
  - XENARTHRA
    - MEGATHERIIDAE
      - (58) *Urumacotherium garciai*
      - (59) *Urumaquia robusta*
      - (60) *Proeremotherium eljebe*
    - MEGALONYCHIDAE
      - (61) *Pronothrotherium* sp.
    - MYLODONTOIDEA
      - (62) *Mirandabradys socorrensis*
      - (63) *Mirandabradys urumaquensis*
      - (64) *Mirandabradys zabasi*
      - (65) *Bolivartherium urumaquensis*
      - (66) *Bolivartherium codorensis*
    - SIRENIA, (67) DUGONGIDAE indet.
    - LITOPTERNA, PROTHEROTHERIIDAE, MEGADOLODINAE
      - (68) *Bounodus enigmaticus*
    - NOTOUNGULATA
    - *TYPOTHERIA (69) Interatheriidae indet.
    - *HEGETOTHERIA (70) Hegetotheriidae indet.
    - (71) TOXODONTIDAE indet.
    - (72) *ASTRAPOTHERIA indet
    - RODENTIA, CAVIOMORPHA
      - (73) *Phoberomys pattersoni*
      - (74) ***Eumegamys* sp.
      - (75) **Tetrastylus* sp.
      - (76) **Kiyutherium octolaminatus*
      - (77) *?*Cardiatherium* sp.

Sources: Aguilera (1994, 2004); Aguilera & Rodrigues de Aguilera (2004*a*, *b*, *c*); Bocquentin Villanueva (1981, 1983, 1984*a*, *b*, *c*, 1988); Bocquentin, Villanueva & Buffetaut (1981); Bondesio, Bocquentin & Villanueva (1988); Díaz de Gamero & Linares (1989); Gaffney & Wood (2002); Lundberg *et al.* (1988); Lundberg & Aguilera (2003); Medina (1976); Mones (1980); Pascual & Díaz de Gamero (1969); Royo y Gómez (1960); Sánchez-Villagra *et al.* (1995, 2003); Sill (1970); Wood (1976*a*, *b*); Wood & Díaz de Gamero (1971); Wood & Patterson (1973); S. Walsh (pers. comm.).

Collections of vertebrates from the Urumaco region are deposited at the Universidad Nacional Experimental Francisco de Miranda (UNEFM), Alcaldía del Municipio Urumaco (AMU-CURS), Universidad Simón Bolívar (USB) and Universidad Central de Venezuela (UCV). Taxa marked with an asterisk refer to specimens that were not revised by us but were mentioned by Linares (1990) in a conference abstract. The rodent marked with a double asterisk was cited by Wood & Díaz de Gamero (1971).

other areas of the Caribbean, in particular the Greater Antilles (Iturralde-Vinent & MacPhee 1999), it seems highly likely that the northwestern coast of Venezuela was subject to several transgressions during the Neogene. Terrestrial environments certainly existed during the Neogene, land perhaps being developed for short periods of time throughout the period. Similar to other localities in the Caribbean (MacPhee & Iturralde-Vinent 1994), continental mammals are rare. Work in Urumaco involves surface collecting and in few places is there a high concentration of fossils.

The most common fossils in Urumaco are shark teeth, ray tooth plates and caudal spines, fish skulls and otoliths, turtle carapaces and crocodile skeletons. Mammals are much less common and we currently know of only 22 species. This is probably the result of preservational and, to some extent, sampling biases and is unlikely to reflect true faunal composition.

Cozzuol (2006), based on a comparison of the faunas using a variety of similarity coefficients, showed that there are strong affinities between the Urumaco fauna and those of Acre in Brazil and the Argentinian Mesopotamian. These three faunas are more closely related to each other than to the La Venta fauna in southern Colombia. Part of the reason is temporal, as the La Venta fauna is of middle Miocene (Laventan) age (Madden *et al.* 1997), while the vertebrate fossils from Acre and Urumaco are, for the most part, late Miocene. Further discoveries in the older Socorro Formation in Urumaco will be important for comparisons between what is today northwestern Venezuela and central Colombia in the middle Miocene.

Cozzuol (2006) summarised the information available on amniotes and reported 125 genera from the Mesopotamian of Entre Ríos (Cione *et al.* 2001), 51 for Acre and 76 from La Venta (Kay *et al.* 1997), but many more are being described from the latter. The diversity in Urumaco is lower (Table 1), with approximately 35 genera, in large part because of the lack of microvertebrates in the fauna, which are so abundant in La Venta after many years of intensive sampling (Kay *et al.* 1997). Some differences are also most probably the result of the different palaeoenvironments sampled. The stratigraphic sequence in Urumaco includes a lot of marine and near-shore marine deposits, mostly lacking in the localities from Brazil, Colombia and Argentina discussed here. The mammals of La Venta are very well known, while most of those from Urumaco consist of poorly preserved fragments and/or remain unstudied, with the notable exception of *Phoberomys pattersoni* (Sánchez-Villagra *et al.* 2003) and of the numerous xenarthrans described in this volume (Carlini *et al.* 2006*a*, *b*). In view of the dearth of fossil mammals from the northern Neotropics (MacFadden 2006), discoveries of mammals from Urumaco are significant.

Significance of the Urumaco fauna for the reconstruction of fluvial history of South America

At present, the Falcón and Lara basins are practically isolated from the Orinoco basin, but some of the fossil taxa clearly indicate hydrographic relationships that do not exist today. Some portions of the sequence of Urumaco Formation, in particular much of the upper member, contain fluvial deposits, as shown by palynological studies (Hambalek *et al.* 1994) and by the presence of several vertebrate groups.

The freshwater fauna of Urumaco include species (Lundberg *et al.* 1988; Sánchez-Villagra *et al.* 1995; Aguilera & Rodrigues de Aguilera 2000, 2003, 2004*a*; Lundberg & Aguilera 2003; Aguilera 2004) that have been cited in conjunction with geological evidence (Díaz de Gamero 1996; Lundberg *et al.* 1998) to support the hypothesis that the proto-Orinoco River ran in a south-north direction and flowed into the Caribbean Sea in what is now west Falcón (Díaz de Gamero 1996; Lundberg *et al.* 1998). The species of fish recovered so far that are indicative of Orinoquian affinites (Fig. 2) are: redtailed catfish *Phractocephalus*, thorny catfishes Doradidae spp. indet., cachama *Piaractus,* shovelnose catfish cf. *Pseudoplatystoma* and freshwater croakers *Plagioscion* and *Pachyurus*.

Among the sea catfishes (Aguilera & Rodrigues de Aguilera 2004*a*) and as with many other elements of the Urumaco Formation fauna, there are also forms which today live in the brackish waters of the Orinoco and Amazon River deltas (Cervigón *et al.* 1993; Ponte *et al.* 1999), such as the couma sea catfish *Sciades couma* and the bressou sea catfish *Aspistor quadriscutis*.

Further support for a connection of the ancient Orinoco River with what is today northwestern Venezuela was recently reported from older deposits than those of Urumaco, the early Miocene Castillo Formation fauna of Cerro La Cruz in Lara State, some 100 km South of the town of Urumaco. This fauna contains freshwater cachama fish and croakers (Aguilera & Rodrigues de Aguilera 2003; Dahdul 2004) and a sirenian (Sánchez-Villagra *et al.* 2004). Reconstructions of the changing course of the Orinoco during the Cenozoic (Díaz de Gamero 1996) would predict the discovery of early Miocene freshwater forms in Lara.

Reptilian diversity in the Urumaco Fauna

With the exception of some snake remains first described in this volume (Head *et al.* 2006), the reptilian fauna of Urumaco consists of crocodiles and turtles. Because of the diversity and uniqueness of these groups in this locality, they deserve special mention.

Crocodyliforms are the most diverse amniote components of the Urumaco fauna, with at least 12 species distributed in the middle and upper members of the Urumaco Formation and at least three species also known from the Socorro Formation (Fig. 3). Knowledge and sampling of the range of each species in the Urumaco sequence is still incomplete, so it is possible, if not likely, that the12 species were not all sympatric.

The Urumaco crocodile fauna is one of the most diverse of any region, past or present (Riff & Aguilera 2005). It includes species representing very diverse ecomorphological types, some with no modern analogues (Brochu 2001). This includes species of distantly related clades within Crocodylia, such as Netosuchidae, Alligatoridae and Gavialidae (Gasparini *et al.* 1991). This unique assemblage is comparable only with a locality in the Cretaceous of Madagascar (Buckley *et al.* 1997) that shows a similar pattern of co-occurrence, but with fewer species. The La Venta assemblage contains nine species. The Acre fauna potentially contains 17 species (Cozzuol 2006), but stratigraphic control is problematical and obviously several different strata and, apparently, ages are included in what is

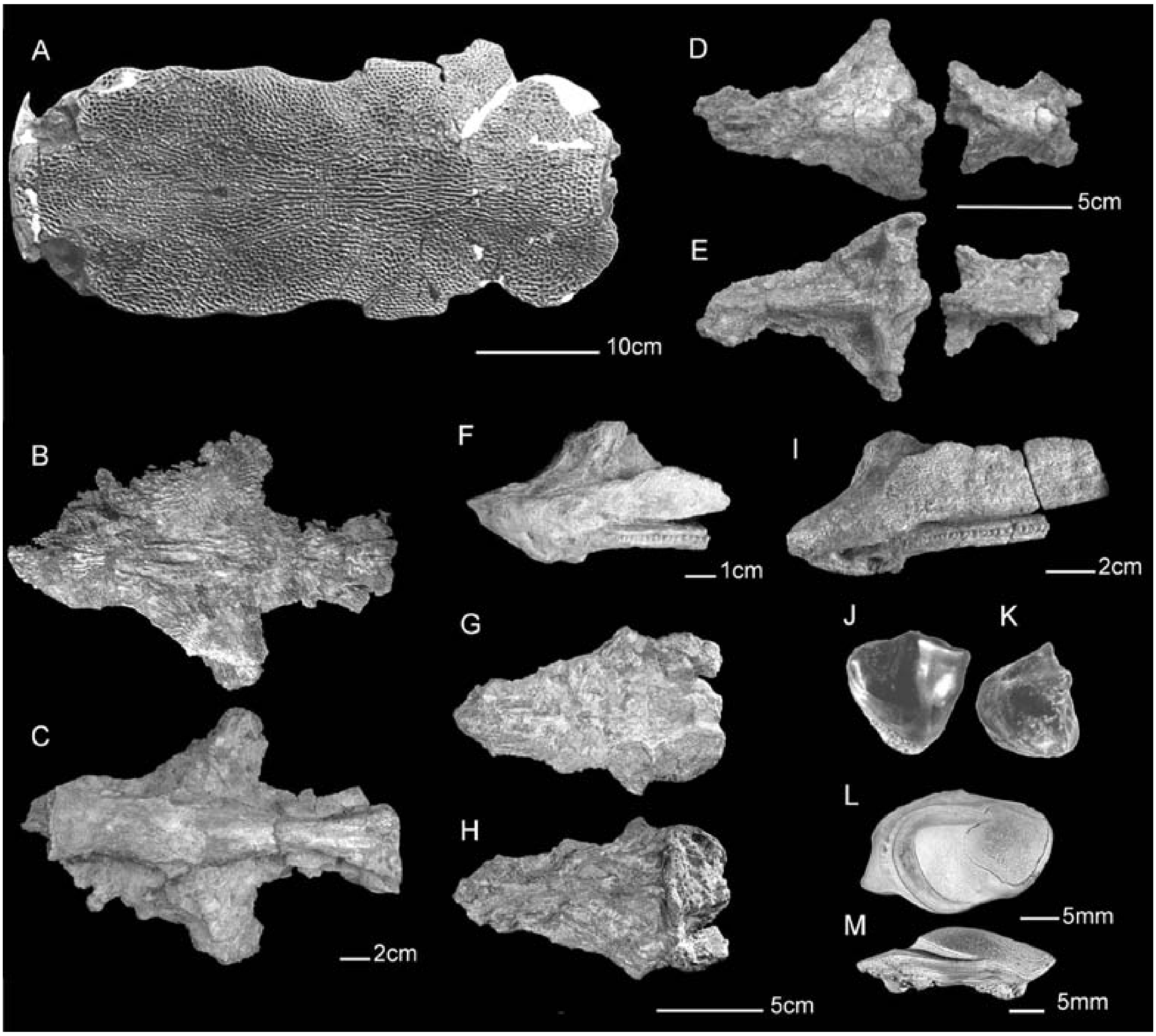

Figure 2 Fishes from the Urumaco Formation with Orinoquian affinites. See Aguilera (2004) for information on fossil localities. **A**, *Phractocephalus nassi*, MC USBOL-2142 (skull in dorsal view), El Mamón; **B, C**, cf. *Pseudoplatystoma*, UNEFM-PF-412 (skull in dorsal and ventral view), Tío Gregorio; **D, E**, Doradidae gen. et sp. indet.1, UNEFM-PF-412 (skull in dorsal and ventral view), Las Huertas; **F**, Doradidae gen. et sp. indet.1, UNEFM-PF-278 (left pectoral girdle), Tío Gregorio; **G, H**, Doradidae gen. et sp. indet.2, UNEFM-PF-411 (left pectoral girdle), El Hatillo; **I**, Doradidae gen. et sp. indet.3, MCNC-37-72V (skull in dorsal and ventral view), Corralito; **J, K**, *Piaractus*, MCNC-52-72V (teeth), Corralito; **L, M**, *Plagioscion urumacoensis*, UNEFM-PF-49 (otolith), El Hatillo.

called the Acre fauna (Frailey 1986; Latrubesse *et al.* 1997; Cozzuol 2006).

The extant neotropical crocodilian species occupy niches generally restricted to longitudinal segments of river systems. Six species of crocodiles are present in the Orinoco and Amazon basins, but it is unusual for more than three species to frequent the same stretch of river or tributary (Langston & Gasparini 1997). It is very likely that many crocodile species that lived in Urumaco inhabited brackish waters. Today there are just eight crocodile species for the whole of South America and of these, five or six occur in northern Venezuela.

The same points raised by Cozzuol (2006) when considering the high crocodile diversity of Acre apply to Urumaco, in that its extraordinary crocodile diversity 'can only be explained if the region had a high primary productivity, long term environmental stability and habitat fragmentation. The last two conditions can be deduced from the large number of endemic lineages and the variety of ecotypes.'

The turtle fauna from the Urumaco Formation in Venezuela is remarkable because of singular occurrences and exceptional species (Aguilera 2004). Perhaps the most spectacular example is *Stupendemys geographicus,* a Podocnemididae first described by Wood (1976*a*) as the "world's largest turtle", based on fairly complete carapace material. In fact, the largest and most recently excavated specimen of this species has a straight carapace length of 3.3 m and a maximum carapace width of 2.18 m (Aguilera 2004). This species has been subsequently reported from Miocene deposits in Acre, Brazil (Lapparent de Broin *et al.* 1993; Gaffney *et al.* 1998). Ongoing studies on the carapace histology of *S. geographicus* by Scheyer & Sánchez-Villagra (2005) indicate that this turtle shows extensive weight-reduction through lightweight construction of

Figure 3 Crocodile diversity in Urumaco. All specimens are from the Urumaco Formation, except for **T–U**, which is from the Socorro Formation. See Aguilera (2004) for information on fossil localities. **A–C**, *Purussaurus mirandai*, UNEFM-CIAAP-1369 (skull with associated mandibles in dorsal and ventral view; mandible in occlusal view), El Hatillo; **D, E**, *Mourasuchus arendsi,* UNEFM-CIAAP-1297 (skull with associated mandibles in dorsal view; mandible in occlusal view), Southeastern Corralito; **F, G**, *Melanosuchus fisheri,* MCNC-243 (skull in dorsal view), Corralito; **H, I**, *Caiman brevirostris,* MCNC (skull in latero-dorsal, latero-ventral view). **J, K**, *Ikanogavialis gameroi,* UCV-VF-1165 (skull in dorsal view) and UCV-VF-1166 (mandibles in occlusal view), Tío Gregorio; **L, M**, *Gryposuchus* sp. nov., MCNC-77-72V (skull with associated mandibles in dorsal and ventral view), 500 m North from the El Picache and 50 m eastern from the Chiguaje fault; **N, O**, *Hesperogavialis cruxenti,* UNEFM-CIAAP-320 (mandible in occlusal and ventral view), North-western of El Mamón; **P, Q**, *Caiman lutescens*, AMU-CURS-49 (right premaxilla and maxilla in dorsal and occlusal view), Corralito; **R, S**, *Hesperogavialis* sp., AMU-CURS-01 (skull in dorsal and ventral view), Northeast of the Urumaco bridge; **T, U**, *Thecachampsa* sp. 1, AMU-CURS-34 (skull with associated mandibles in dorsal and ventral view), Quebrada Honda; **V, W**, *Thecachampsa* sp. 2, AMU-CURS-12 (skull in dorsal and ventral view), Agua Blanca dome, **X, Y**, *Gryposuchus jessei*, UNEFM-CIAAP-617 (premaxilla and maxilla in dorsal and occlusal view), Corralito; **Z, AA**, *Brasilosuchus mendesi*, MCNC-126-72V (premaxilla and maxilla in dorsal and occlusal view), between La Paz valley and the Macunare fault.

the carapace, although not to the degree seen in deep marine species. Furthermore, the giant size was not based upon a novel mode of carapace bone formation that differs greatly from that of other turtles in general, and *S. geographicus* is likely to have grown at high rates for at least three decades in order to reach its giant size.

Another singular occurrence in Urumaco is that of a soft-shelled turtle or trionychid (Wood & Patterson 1973), a highly specialised group with no living representatives in South America. This animal was first reported more than 30 years ago based on an isolated portion of the plastron. Since then no other remains have been found, leading to the suspicion that the report in Urumaco is the result of waif dispersal from North America. However, Sánchez-Villagra *et al*. (2004) also reported this group from the early Miocene Castillo Formation in northwestern Venezuela and there are remains of this group from the early Pliocene of Margarita Island (Head *et al*., in press). This suggests that trionychids were present in northern South America during the Neogene and, unlike living species of the group, inhabited near-shore marine environments.

Other turtles from Urumaco include a fossil species of the matamata, *Chelus lewisi* (Wood 1976*b*; Bocquentin Villanueva 1988; Sánchez-Villagra *et al*. 1995) and the podocnemidid *Bairdemys venezuelensis* (Wood & Díaz de Gamero 1971; Gaffney & Wood 2002), the latter being the most common and best-known turtle species in this area. *Bairdemys* is known from complete shells and, as reported by Winkler & Sánchez-Villagra (2006), based on the discovery of a nesting site with eggs, it provides the first direct evidence of marine adaptations in a pelomedusoides, a group whose living species are strictly fresh-water dwellers.

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