

# Palaeoenvironmental implications of the giant crocodylian *Mourasuchus* (Alligatoridae, Caimaninae) in the Yecua Formation (late Miocene) of Bolivia

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Outcrops of the Yecua Formation (late Miocene) are exposed for approximately 230 m along the La Angostura section of the Pirá River (50 km southwest of Santa Cruz de la Sierra). These reveal massive (argillic palaeosols) and laminated (quiet-water lacustrine and marsh settings) mudstones interbedded with thin sandstones containing microfossils, molluscs and vertebrate remains. Significantly, the succession hosts a giant crocodylian, *Mourasuchus* (Alligatoridae, Caimaninae), which is represented by both skull and postcranial fragments found in association with freshwater turtles and fishes. *Mourasuchus* was distributed widely from the middle Miocene of Colombia to upper Miocene of Venezuela, Brazil and Argentina, suggesting connections between major fluvial systems and an active mechanism for dispersal of South American freshwater vertebrates during the Miocene.

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THE SUB-ANDEAN system is a thin-skinned fold and thrust belt representing the eastern deformational flank of the central Andes. It is characterized by an asymmetric meridional belt of continuous, parallel mountain ranges. These represent supracrustal loads that depress the lithosphere on both sides of the convergent plate margin, generating accommodation via flexural deflection, i.e., foreland basins (Beaumont 1981, Jordan 1981, Catuneanu 2004).

Since the late Oligocene, compressive tectonics resulted in the formation of the foreland Chaco Basin (Sempere *et al.* 1990, Baby *et al.* 1992, Uba *et al.* 2006), accumulating continental clastic successions exceeding 5000 m in thickness. This basin includes fining-upward successions, characteristic of synorogenic deposits. Sedimentation began in the late Oligocene and is represented by five units: the Petaca (late Oligocene–middle Miocene), Yecua (late Miocene), Tariquíá (late Miocene), Guandacay (late Miocene–early Pliocene)

and Emborozú (Pliocene–Holocene) formations. Their ages were determined via mammalian biostratigraphy and radiometric dating of tuffs (Marshall & Sempere 1991, Marshall *et al.* 1993, Moretti *et al.* 1996, Echavarría *et al.* 2003, Hernández *et al.* 2005, Hulka *et al.* 2006).

The La Angostura section in the Sub-Andean ranges is situated along the Pirá River, 50 km southwest of Santa Cruz de la Sierra (Fig. 1). The Yecua Formation (Padula & Reyes 1958) overlies the continental deposits of the Petaca Formation (late Oligocene–middle Miocene; Marshall *et al.* 1993) and is transitionally overlain by the Tariquíá Formation (Marshall *et al.* 1993). This section (Fig. 2) includes 230 m of reddish to black mudstones, sandstones, calcareous sandstones and yellow–white bioclastic grainstones.

Hulka *et al.* (2006) reported that, in the Angostura section, the Yecua Formation is represented in two outcrops (exposing the lower and upper parts of the section), each 30–35 m thick. Based on sedimentary structures and textures, Hulka *et al.* (2006) proposed two dominant depositional systems: (1) a semi-arid,



Fig. 1. Map of the study area, Río Piráí, Santa Cruz de la Sierra State, central-southern Bolivia. The square indicates the 'La Angostura' area.

low-energy floodplain; and (2) a coastal facies represented by tidal, high-energy shoreline, and shallow marine deposits. Poorly preserved bivalve and ostracod fossils occur in the lower part of the section, with the ostracod *Cyprideis* indicating mixohaline environments. On the other hand, the upper strata contain the ostracod *Heterocypris*, which is diagnostic of freshwater to brackish conditions. The foraminiferal community of the lower La Angostura section includes benthic forms, such as *Anomalinoides*, *Cibicidoides* and *Gyroidina*, implying a shallow marine shelf.

Hernández *et al.* (2005) indicated that the highest diversity of marine organisms in the Yecua Formation was found in outcrops at the 'La Angostura' locality. This led to interpretations of alternating continental lacustrine conditions interspersed with open marine and restricted marine environments (Hernández *et al.* 2005), and concurred with previous reconstructions using heterodontid bivalves (*Corbicula*; Branisa 1970), ostracods (*Cyprideis* sp. aff. *C. floridana* Branisa 1970) and marine foraminifera (Branisa 1970). It also mentioned the presence of marine fossils cirripeds (e.g., *Balanus*), gastropods (e.g., *Natica*) and inarticulate brachiopods (*Orbiculoidea*) in these deposits (see Dalenz Farjat, pers. obs., in Hernández *et al.* 2005, p. 504).

This study provides new evidence on the Yecua Formation depositional setting based on continental vertebrates. In particular, fragmentary skull and postcranial remains of a huge freshwater crocodylian occur in the lower levels of the unit (Fig. 2—Level Y70). These are assigned to *Mourasuchus* Price, 1964, a Miocene alligatorid endemic to South America (Langston & Gasparini

1997), which is known from four species: *Mourasuchus atopus* (Langston, 1965), from the middle Miocene of Colombia; *M. arendsi* Bocquentin-Villanueva, 1984 from the upper Miocene of Venezuela; *M. amazonensis* Price, 1964, from the upper Miocene of Brazil; and *M. nativus* (Gasparini, 1985), from the upper Miocene of Argentina, Brazil and Venezuela (Gasparini 1985, Bocquentin & Souza-Filho 1990, Scheyer *et al.* 2013). *Mourasuchus*, together with *Purussaurus* Barbosa-Rodrigues, 1892, constitute a clade of huge caimans (Alligatoridae: Caimaninae; Brochu 1999, 2003, 2010, Aguilera *et al.* 2006, Bona *et al.* 2013b) whose cranial morphology is well documented (Price 1964, Langston 1965, Bocquentin-Villanueva 1984, Gasparini 1985, Bona *et al.* 2013b). In contrast, detailed descriptions of the postcranial skeleton are scarce: Langston (1965) reported on the scapula, coracoid, humerus, femur, ilium and ischium in *M. atopus*; and Bocquentin-Villanueva (1984) mentioned an incomplete but articulated cervical series in *M. arendsi*. Langston (2008) also later noted vertebrae and osteoderms, probably of *M. arendsi*, from the Urumaco Formation. These records are reassessed here.

## Institutional abbreviations

YPFB-LIT-PAL, Yacimientos Petrolíferos Fiscales Bolivia, Centro de Tecnología Petrolera—Litoteca—Colección de Paleontología, Santa Cruz de la Sierra, Bolivia; CIAAP, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda and AMU-CURS, Alcaldía del Municipio Urumaco, Coro, Venezuela; MLP, Museo de La Plata, La Plata, Argentina; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UFAC, Universidade Federal do Acre, Acre, Brazil.

## Materials and methods

The *Mourasuchus* specimen documented here (YPFB-LIT-PAL-001) incorporates skull fragments, three partial vertebrae and rib components. These were recovered and restored by the MLP. Associated fauna include a pleurodiran turtle shell (YPFB-LIT-PAL-002), proximal fin material (YPFB-LIT-PAL-003) of a siluriform fish cf. Ariidae (Marshall *et al.* 1993), and an indeterminate teleost vertebral centrum (YPFB-LIT-PAL-004), possibly belonging to a large siluriform (Alberto L. Cione pers. comm. 2013). Anatomical terminology follows Hoffstetter & Gasc (1969). Measurements were taken using a Vernier caliper (0–200 mm).

## Sedimentology of the Yecua Formation

The sedimentary facies mapped at the YPFB-LIT-PAL-001 recovery site include thick packages of massive oxidized mudstones with palaeosol overprinting (prismatic, granular and blocky textures), interspersed with

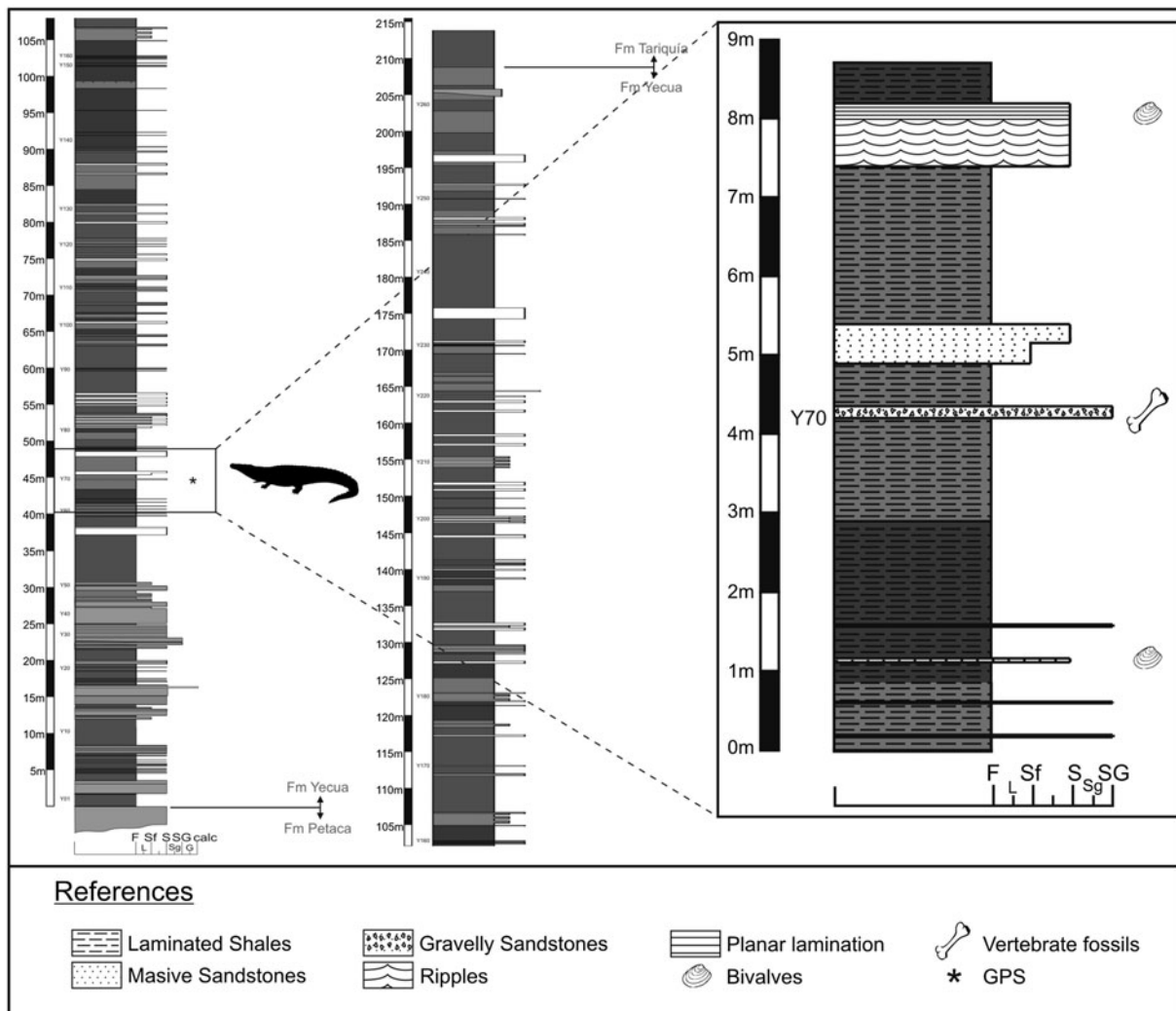


Fig. 2. Geological section of the Yecua Formation in 'La Angostura' locality, where the fossiliferous level (Y70) can be seen; GPS: 18°10'1.85"S, 63°30'49.98"W [\*].

laminated fine-grained sediments of green and purple hues. Horizontal beds of fine-grained sandstones are also intercalated among the pelitic packages. These are traction deposits that lost their primary structure via reworking, and indicate a high (supercritical) flow rate. Symmetrical or slightly asymmetrical ripple layers and sparse interference ripples correspond to a low (subcritical) flow regime. In addition, a discrete bed containing molluscs and microfossils was found associated with the laminated sandstones. In some cases, this level is so fossiliferous that it forms a pale bioclastic grainstone cemented by carbonates. Apparently, monospecific populations of indeterminate corbicullid bivalves are arranged in thin layers of internal moulds (each 15–20 mm long), and preserved together with moulds of elongate gastropod shells (maximum 15 mm long) comprising 6–8 whorls. Associated microfossils include ostracods (Cytherideoidea, Cypridoidea, Darwinuloidea) and foraminiferans (see Dias Nicolaidis & Coimbra 2008), which appear to be allochthonous hydrodynamic accumulations. The taphonomy of these invertebrate beds suggests catastrophic suffocation of *in situ* mollusc

populations by sudden deposition events (obtrusion deposits; Seilacher 1982, Brett & Seilacher 1991). This is inferred by maintenance of shells in life position (autochthonous) with substrate-excitation traces (ichnogenus *Lockeia* isp.). Non-catastrophic accumulation of disarticulated shell valves might be associated, suggesting minimal postmortem transport (parautochthonous) or concentration in postmortem accumulations (allochthonous; Kidwell *et al.* 1986, Kidwell 1991).

The vertebrate fossils were excavated from a green-purple laminate pelitic sequence (level Y70; Fig. 2), consisting of 10–20 cm of very coarse quartzose massive sandstones. The crocodylian elements were not articulated, but preservation of the vertebrae in a continuous life series implies parautochthonous transport and burial by high-energy flows (Fig. 3).

### Systematic palaeontology

CROCODYLIA Gmelin, 1789 (*sensu* Benton & Clark 1988)  
 ALLIGATORIDAE Cuvier, 1807 (*sensu* Norell *et al.* 1994)

**Mourasuchus** Price, 1964

*Type species.* *Mourasuchus amazonensis* Price, 1964.

**Mourasuchus** sp. (Figs 4–7)

*Referred material.* YPFB-LIT-PAL-01, posterior part of right jugal-quadratojugal, distal portion of a left quadrate, three vertebrae and rib fragments.

*Occurrence.* Margin of Pirai River, 50 km southwest of Santa Cruz de la Sierra, Bolivia (GPS: UTM 445620E–

7991224S, Fig. 1). Yecua Formation (Padula & Reyes 1958), middle to late Miocene (Hulka *et al.* 2006), late Miocene (Marshall & Sempere 1991, Marshall *et al.* 1993, Hernández *et al.* 2005).

*Description and comparisons*

*Skull.* The posterior parts of a right jugal and quadratojugal are preserved together with the distal portion of a left quadrate (Fig. 4). These fragments are ornamented by thin interconnected longitudinal lines; the marked pitting otherwise characteristic of caimanines, such as

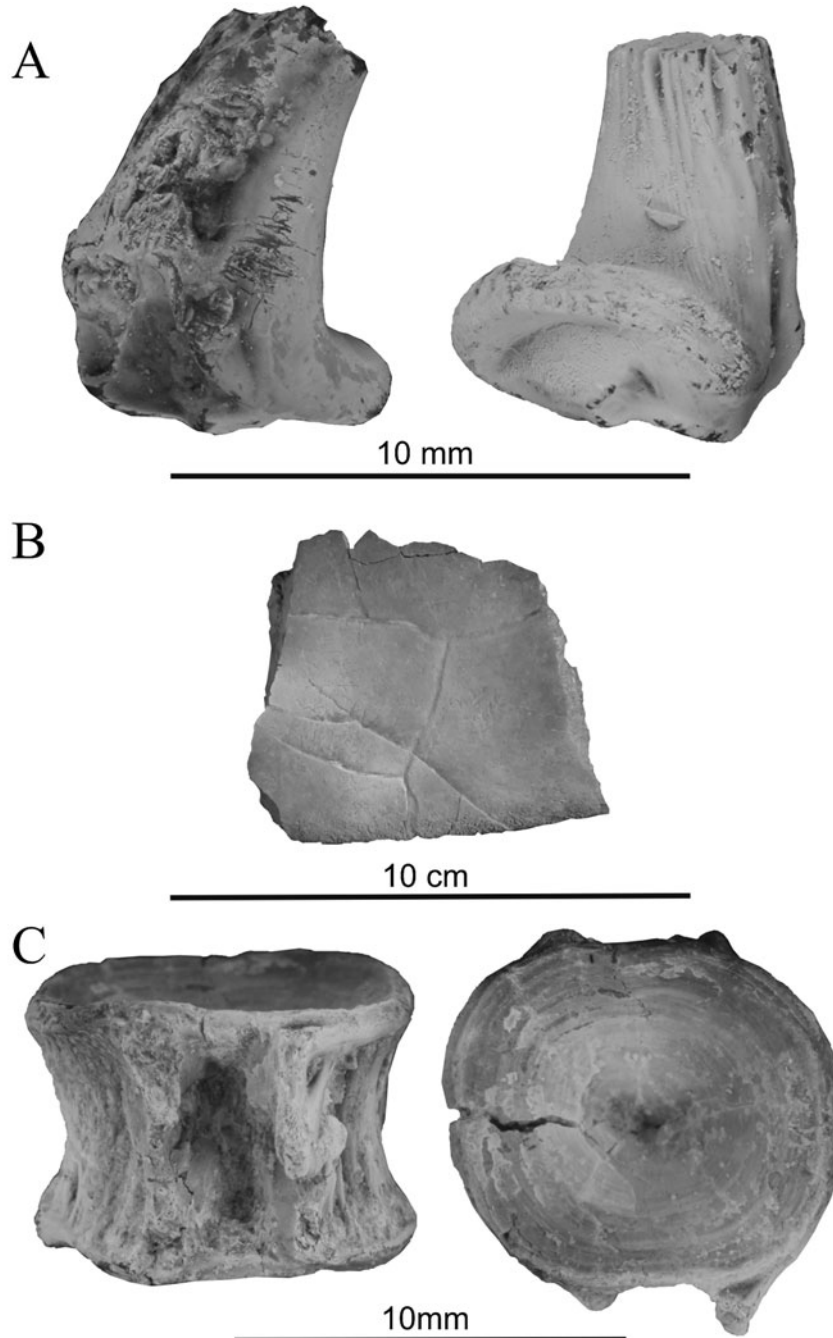


Fig. 3. **A**, Fin fragment of the siluriform cf. Ariidae (YPFB-LIT-PAL-003); **B**, Caparace fragment of the pleurodiran turtle (YPFB-LIT-PAL-002); **C**, Vertebral body of a Teleostei indet. (YPFB-LIT-PAL-004), possibly belonging to a large siluriform.

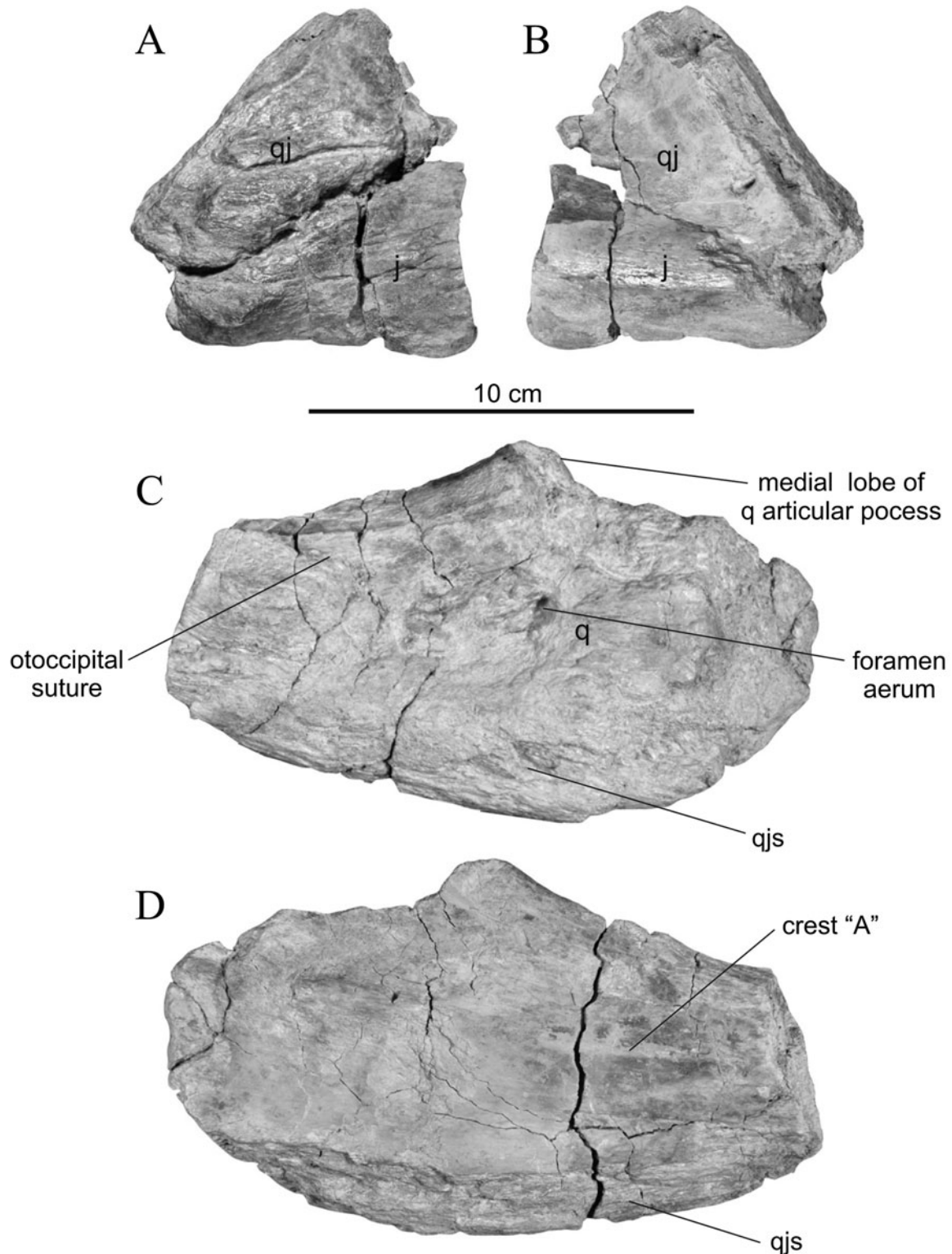


Fig. 4. YPFB-LIT-PAL-01: Skull of *Mourasuchus* sp. A–B, Fragment of right jugal and quadratojugal; A, lateral view, B, medial view. C–D, Distal fragment of left quadrate; C, dorsal view; D, ventral view. j, jugal; q, quadrate; qj, quadratojugal; qjs, quadrate-quadratojugal suture.

*Purussaurus* and *Caiman* (e.g., Bona *et al.* 2013b), is absent (Fig. 8). The quadratojugal component (Fig. 4A–B) is similar to other caimanines in being narrow with sub-parallel lateral margins. The posterior margin of the lateral (infratemporal) fenestra is evident

anteriorly and, as in most crocodylians, delimits the posterior ventral angle of the lateral (inferior) temporal fenestra (e.g., Brochu 1999). In *Mourasuchus*, the temporal fenestrae are expansive and dorsally oriented, such that the distance between the posterolateral corner

of each fenestra versus the posterolateral skull margin is noticeably short (e.g., *M. amazonensis*, Price 1964; *M. nativus* UFAC 1424, Fig. 8A). Indeed, this space is extremely reduced in YPFB-LIT-PAL-01, closely resembling *Mourasuchus* as opposed to *Purussaurus*, *Caiman* and *Melanosuchus* (Bona pers. obs., Fig. 8). There is no evidence of a quadratojugal spine as in Miocene gavialids (e.g., *Gryposuchus colombianus*)

The quadratojugal of YPFB-LIT-PAL-01 articulates with the jugal along a suture that reaches the posterior angle of the skull. This structure is also present in *Mourasuchus*, but differs from *Caiman* and *Purussaurus*, in which the quadratojugal-jugal suture ends at the lateral margin of the skull (Bona pers. obs., Fig. 8).

The lateral margin of the jugal is curved and abruptly divergent, probably correlating with the prominent lateral projection evident on the jugal of *Mourasuchus* (Bona, pers. obs., Fig. 8); there is again no external ornamentation.

The quadrate is incomplete and crushed (Fig. 4C–D). Nevertheless, its medial margin is preserved together with the lateral sutural surface for the quadratojugal. A marked ventral crest (crest ‘A’ of Iordansky 1964) is apparent for the attachment of mandibular adductor muscles.

*Vertebrae.* One cervical and two dorsal vertebrae were recovered and show only slight diagenetic deformation (Figs. 5, 6). As in *Morasuchus arendsi* (Fig. 5G), the cervical vertebra is anteroposteriorly shortened, and contrasts with the condition seen in other alligatorids, which have more elongate cervical centra (e.g., Brochu 1996, Chamero *et al.* 2014). The precise centrum dimensions are 55 mm long (excluding the condyle), 56 mm high (excluding the hypapophysis) and 68 mm wide (measured at the caudal end, excluding the parapophysis). In anterior view, the cotyle is oval and wider than high (75 mm and 62 mm respectively). The anterior ventral surface of the centrum bears an incomplete hypapophysis whose base extends along more than half the length of the centrum (excluding the condyle). The complete left parapophysis bears a wide sub-rectangular surface for articulation of the costal capitulum (Fig. 5F). The parapophyseal bases are anteroposteriorly wide, extending close to the posterior edge of the centrum (excluding the condyle). This is similar to that of the sixth cervical vertebra of *M. arendsi* (CIAAP 1297: Bocquentin-Villanueva 1984, Fig. 5G).

The cervical neural arch measures 139 mm from the neurocentral suture to the tip of the neural spine. The pedicels are robust, dorsoventrally high (61 mm, measured from the neurocentral suture to the base of the neural spine) and anteroposteriorly short (38 mm). As in other adult crocodylians, the base of each pedicel is sutured to the centrum (Brochu 1996, fig. 5F). Ventrolaterally, the neural arch bears a diapophysis, situated just above the midline of the neurocentral suture. The

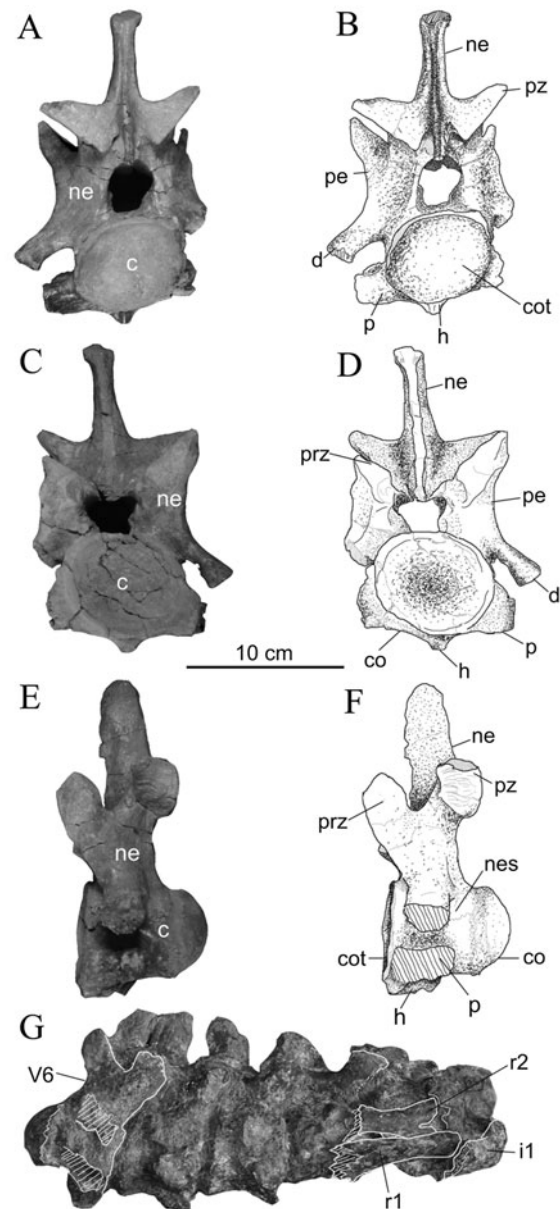


Fig. 5. YPFB-LIT-PAL-01: *Mourasuchus* sp. A–F, Cervical vertebra. A, posterior view; B, outline drawing of posterior view; C, anterior view; D, outline drawing of anterior view; E, left lateral view; F, outline drawing of left lateral view. G, Right lateral view of cervical vertebrae of *Mourasuchus arendsi* (CIAAP 1297, holotype). c, centrum; co, condyle; cot, cotyle; d, diapophysis; h, hypapophysis; i1, first (atlantal) intercentrum; ne, neural arch; nes, neurocentral suture; p, parapophysis; pe, pedicel; prz, prezygapophysis; pz, postzygapophysis; r1, first cervical (atlantal) rib; r2, second cervical (axial) rib; v6, sixth vertebra.

complete left diapophysis is oval in cross-section and ventro-laterally oriented (suggesting placement as the 5th or 6th vertebra in the sequence), bearing an oval facet for lateral articulation with the costal tuberculum. The zygapophyses arise from the top of the pedicel, close to its boundary with the base of the neural spine. They are obliquely oriented, projecting dorsolaterally at 45° from the horizontal. The articular facets are oval in outline with their major axis oriented dorsolaterally. The

prezygapophysis faces dorsally at 60° to the sagittal plane. The cervical neural spine forms a broad, vertical plate-like lamina 62 mm high, and is transversely expanded at its apex (Fig. 5A–D); the dorsal profile is rounded. The posterior ridge of the neural spine is furrowed by a deep groove that extends vertically and separates the postzygapophysis along the midline.

What appear to be the 3rd (=12th vertebra in the column), and a second indeterminate posterior dorsal vertebra were recovered. Both have closed neurocentral sutures with the probable 3rd dorsal (Fig. 6A–D) being 57 mm long excluding the condyle; 69 mm high excluding the hypapophysis, and 66 mm wide anteriorly. The heart-shaped cotyle is dorsoventrally high and mediolaterally narrow. A rudimentary, slightly anteriorly projecting and acute hypapophysis arises from the ventral surface of the centrum. The neural arch is 164 mm high from the base of the pedicels to the tip of the neural spine. The pedicels and centrum are almost equal in length in lateral view. A robust and slightly dorsolaterally erect transverse process arises at the boundary between the pedicels and the base of the neural spine. This would have borne the diapophysial facet for the costal tuberculum, and is broadly blade-like at its proximal extremity becoming narrower and straighter distally (laterally). Although incomplete, the parapophysis was clearly set above the anterior edge of the transverse process (Fig. 6B), similar to the 3rd dorsal of *Caiman yacare* and *Crocodylus niloticus* (Bona pers. obs.). The zygapophyses are obliquely oriented and project dorso-laterally, with their articular facets angled at 50° to the horizontal plane. The neural spine is low (90 mm, measured along its posterior edge), anteroposteriorly short (approximately 57 mm) and slightly posterodorsally inclined with a transversely expanded apex.

The indeterminate posterior dorsal preserves the centrum and the pedicels of the neural arch (Fig. 6E–H) and is large relative to its length: 63 mm long excluding the condyle; 61 mm high; 72 mm wide anteriorly. The centrum is ventrally arched in lateral profile and lacks a hypapophysis. The neural arch is wide and low, with pedicels that are 45 mm long anteroposteriorly, and 22 mm high. The posterior surfaces of the pedicels are excavated for muscle attachment on the lateral and anterior sides of the neural canal. The transverse processes are broken off but their bases suggest a horizontal orientation. The prezygapophyses are dorsolaterally projecting and dorsally angled at 45° to the horizontal: the neural spine is missing.

*Ribs.* The left atlantal, axial and two other cervical rib fragments are preserved together with two sections from the dorsal ribs (Fig. 7). The left atlantal rib (Fig. 7A, B) is flat, broad and holocephalous (180 mm maximum length; 40 mm maximum width). Its medial surface is slightly concave, and the smooth lateral surface is convex. The dorsal margin of the atlantal rib is

anterodorsally expanded towards its proximal end for articulation with the atlantal intercentrum. The dorsal surface is smooth and lacks the conspicuous dorsal process of other alligatoroids (Langston 1965).

The axial rib (Fig. 7C, D) is short (160 mm in maximum length), flat and ‘Y-shaped’, with a sharp ventral edge contributing to a longitudinal lateral crest that delimits a short groove. The capitulum and the tuberculum are well developed as in other caimanines, but contrast with crown crocodylians, such as *Alligator mississippiensis*, *Osteolaemus tetraspis*, *Crocodylus niloticus* and *Tomistoma schlegelii*, which have rudimentary tuberculae (Hoffstetter & Gasc 1969, figs 18, 19). As in *Mourasuchus arendsi* (CIAAP 1297), the axial tuberculum is wide and blade-like, with a thin expanded articular surface for the axial diapophysis (Fig. 7C, D). It is widely separated from the capitulum by a deep U-shaped notch.

A left cervical rib (Fig. 7E) shows that both the capitulum and tuberculum were developed for articulation with the parapophysis and the diapophysis respectively. As in other crocodylians, these form a lateral pleurapophysis (Hoffstetter & Gasc 1969) that contributes to the vertebrocostal canal for the vertebral arteries. The tuberculum is vertically oriented and medially curved where it articulated with the corresponding vertebra. The costal body is short and anteroposteriorly oriented. The anterior tip of the rib is laterally compressed and gently concave on its medial surface. The posterior extremity is otherwise dorsomedially oriented and dorsally concave.

The other cervical rib fragment preserves the tuberculum, which is expanded and triangular distally for contact with the vertebral diapophysis.

The dorsal rib elements include parts of a posterior vertebrocostal, and a possible intercostal rib. The proximal end of the vertebrocostal rib (Fig. 7F) displays an elongate capitulum and short tuberculum indicating derivation from the right side of the body.

## Discussion

The individual represented by YPFB-LIT-PAL-01 was huge (Fig. 8). Similar giant Miocene caimanines include *Purussaurus* and *Mourasuchus* (e.g., Brochu 2010, Bona *et al.* 2013b, Scheyer *et al.* 2013). Although some coeval gavialoids reached comparable proportions, the lack of a quadratojugal spine in YPFB-LIT-PAL-001 favours caimanine affinity. Moreover, the absence of conspicuous cranial ornamentation, the large temporal fenestrae, and orientation of the quadratojugal-jugal suture (Fig. 8) permit more specific referral to *Mourasuchus*. Within the postcranium, the anteroposteriorly short vertebral centra closely resemble *Mourasuchus arendsi* (CIAAP 1297: Bocquentin-Villanueva 1984, fig. 2), and might be diagnostic for the genus (see Langston 2008, p. 15) based on their differentiation from *Purussaurus* (e.g., MPU-CURS-20).

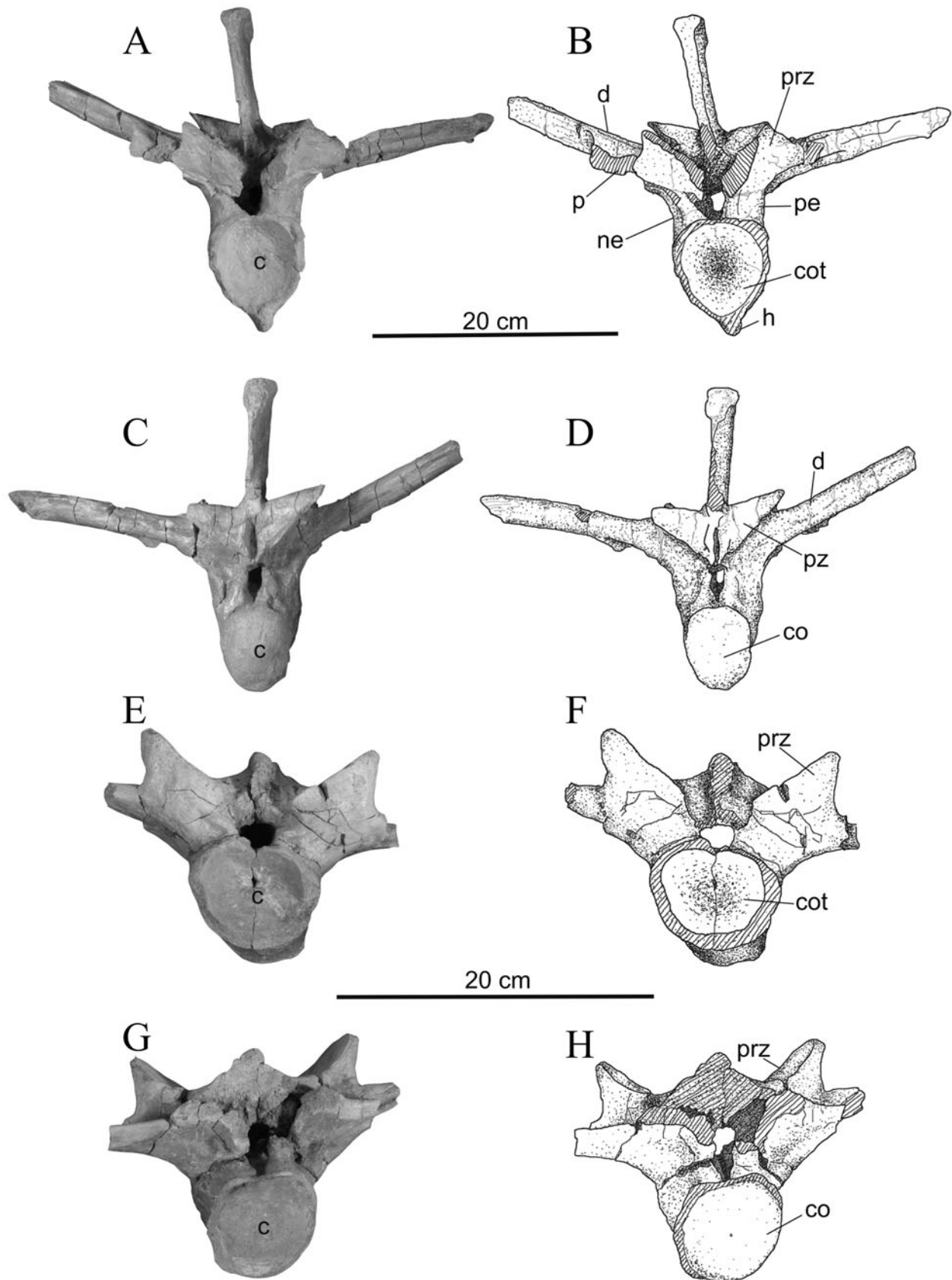


Fig. 6. YPFB-LIT-PAL-01: *Mourasuchus* sp. A–D, Probable third dorsal vertebra. A, anterior view, B, outline drawing of anterior view; C, posterior view; D, outline drawing of posterior view. E–H, Posterior troncal vertebra; E, anterior view, F, outline drawing of anterior view; G, posterior view; H, outline drawing of posterior view. c, centrum; co, condyle; cot, cotyle; d, diapophysis; h, hypapophysis; ne, neural arch; p, parapophysis; prz, prezygapophysis; pz, postzygapophysis.

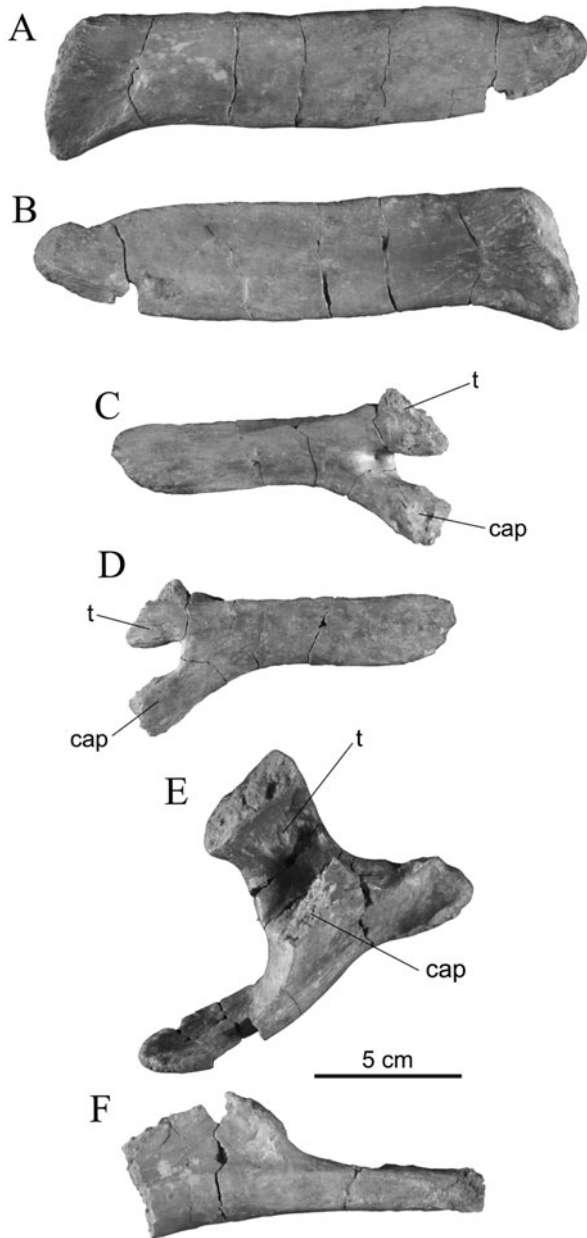


Fig. 7. YPFB-LIT-PAL-01: *Mourasuchus* sp. Cervical ribs. **A, B**, Left atlantal rib. **A**, lateral view; **B**, medial view. **C, D**, Left axial rib; **C**, medial view; **D**, lateral view. **E**, Dorsomedial view of a left cervical rib. **F**, Ventral view of a proximal fragment of a left vertebrocostal piece of troncral rib. cap, capitulum t, tuberculum.

Langston (2008) also inferred a reduced number of cervicals in *Mourasuchus* relative to modern crocodylians, which typically possess nine vertebrae (Hoffstetter & Gasc 1969, Brochu 1996).

The presence of neurocentral sutures on the cervical, but not the dorsals of YPFB-LIT-PAL-001 is coherent with the craniad ossification sequence of crocodylian vertebral ontogeny (Brochu 1996). This is independent of size (Brochu 1996) and suggests that YPFB-LIT-PAL- had not reached maximum somatic maturity.

The atlas–axis complex is incompletely described in *Mourasuchus*, but is comparable with the holotype of

*M. arendsi* (CIAAP 1297: Bocquentin-Villanueva 1984, fig. 2). Based on this and other alligatorids (e.g., *Caiman latirostris*, *C. yacare*, *Alligator mcgrewi*), the atlantal rib of YPFB-LIT-PAL-001 has a similar smooth dorsal margin but lacks a typically prominent dorsal process (Brochu 1999). In general proportions it is almost double the size of the axial rib, and thus comparatively larger than those of *Purussaurus neivensis*, and crocodylians including *Caiman yacare*, *Alligator mississippiensis* and *Crocodylus niloticus* (Bona pers. obs). The tuberculum of the axial rib is well developed as in *M. arendsi* and *P. neivensis*.

#### *Implications for palaeobiology and palaeoenvironment*

The cranial morphology of *Mourasuchus* has been discussed by various authors (e.g., Langston 1965, Riff *et al.* 2010, Bona *et al.* 2013a, Scheyer *et al.* 2013), but the implications for feeding behaviour warrants further exploration; although admittedly this is hampered by a dearth of adequate fossils (Bona *et al.* 2013a). Historically, the species of *Mourasuchus* have been interpreted as filter feeders (e.g., Langston 1965, 73–74; Riff *et al.* 2010). Certainly, the compact neck would have hindered cervical mobility, a necessity for manipulating large prey items. However, the possibility of piscivory remains feasible. Furthermore, assuming that *Mourasuchus* adhered to the conservative vertebral proportions and counts of modern crocodylians (see Hoffstetter & Gasc 1969), the YPFB-LIT-PAL-001 individual probably exhibited length reduction throughout the rest of the vertebral column. The result would have been a skull-length-to-body ratio that was hydrodynamically obverse to typical aquatic crocodylians. Such animals might thus have specialized for lentic and shallow water habitats, their large size coinciding with the warm climatic conditions experienced during the Miocene (Cione *et al.* 2005, Vizcaino *et al.* 2012, Bona *et al.* 2013b).

Both the fossil fauna and sedimentological features of the Yecua Formation are indicative of lowland shallow freshwater lakes and rivers, with an up-section transition from fine-grained siliciclastics to coarser deposits marking active fluvial onset and the lithostratigraphical boundary between the Yecua and Tariquia formations. Invertebrate assemblages also suggest alternating flood–drought cycles in an otherwise low-energy continental setting (Dias Nicolaidis & Coimbra 2008, Tineo *et al.* 2012). The occurrence of *Mourasuchus* in such environments in central Bolivia, Argentina, Brazil and most recently Venezuela (Scheyer *et al.* 2013) not only implies a broad geographic distribution, but also a late Miocene non-marine continuity between the Amazonas and Chacoparanense basins. Such reconstructions contradict proposals for a late Miocene epicontinental incursion into the Yecua Formation (Ihering 1927, Marshall *et al.* 1993, Ramos & Alonso 1995, Hernández *et al.* 2005, Hulka *et al.* 2006), and imply a

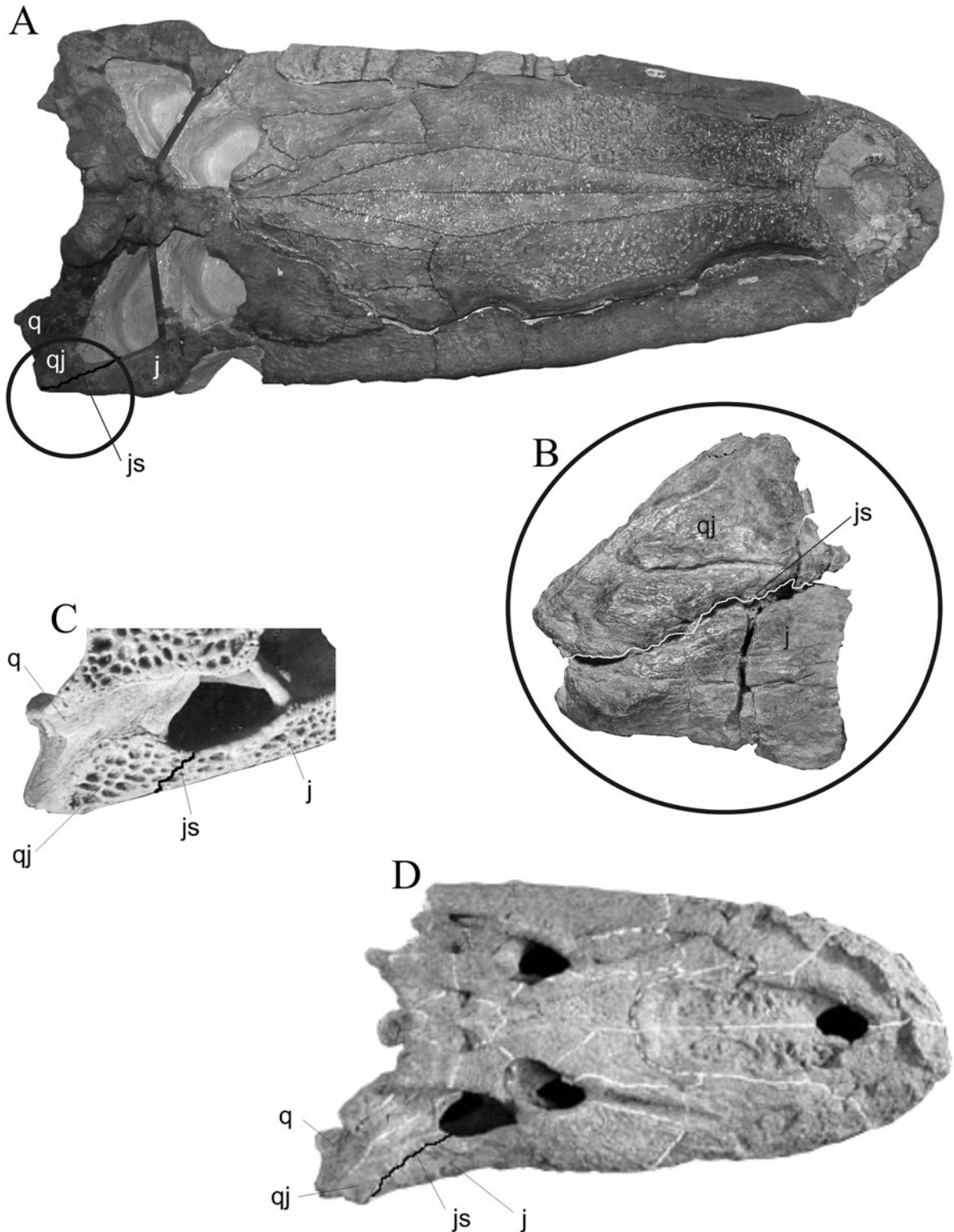


Fig. 8. Caimaninae skulls in dorsal view. **A**, *Mourasuchus nativus* (UFAC 1424); **B**, *Caiman yacare* (detail of the right posterolateral sector); **C**, YPFB-LIT-PAL-01; **D**, *Purussaurus mirandai* (AMU-CURS-1353, modified from Aguilera *et al.* 2006). j, jugal; js, jugal–quadrate suture; q, quadrate; qj, quadratojugal.

network of at least intermittent freshwater systems (Hovikoski *et al.* 2007) that permitted dispersal of indisputably continental vertebrates in a similar manner to the Pantanal of southeast Brazil (Bona *et al.* 2013b).

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