Skull Anatomy of the Bizarre Crocodylian *Mourasuchus nativus* (Alligatoridae, Caimaninae)

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ABSTRACT

Mourasuchus is a Miocene alligatorid endemic to South America, and is represented by four species. Together with the closely related *Purussaurus*, it is a peculiar crocodylian taxon of neogene Caimaninae and one of the most bizarre forms among eusuchian crocodiles. The phylogenetic relationships between *Mourasuchus* species have not been explored, and detailed skull descriptions are scarce. The goal of this study is to provide new data on skull morphology and cranial recesses in *Mourasuchus nativus*, including a new tomography analysis (3D modeling). We observed that several diagnostic characters of *Purussaurus*, such as lack of contact between the nasal and lacrimal, separation of the nasal and frontal by the prefrontals, and the posterior dorsal margin of the skull table, are shared with *Mourasuchus*. *M. nativus* is characterized by the presence of solid transverse squamosal eminences, large posttemporal fenestrae, and a quadrate laterocaudal bridge separating V_2-V_3 trigeminal openings. Compared with other crocodylians, the endocast of *M. nativus* is similar in shape but quite sigmoid in lateral view, the canal of the supraorbital ramus of V_2 is more vertically oriented, the thick tympanic branch canal opens in a large foramen aligned with trigeminal foramen, and the canal of the vagal (X) tympanic ramus is also very wide. Contrary to extant alligatorids, the median pharyngeal recess remains paired throughout its course and only connects its opposite fellow near the external ventral opening. The knowledge of the internal skull anatomy of *Mourasuchus* contributes to the understanding of the general morphology of alligatorids, Caimaninae, and their variation. Anat Rec, 296:227–239, 2013.   © 2012 Wiley Periodicals, Inc.

Mourasuchus Price 1964 is an alligatorid endemic to South America (Langston and Gasparini, 1997), and is represented by 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. *Mourasuchus*, together with *Purussaurus* Barbosa-Rodrigues 1892, represent a very peculiar crocodylian clade of South American Neogene alligatorids and perhaps one of the most bizarre forms among eusuchian crocodiles (Brochu, 1999; Aguilera et al., 2006; Figs. 1, 2).

Recent cladistic analysis shows *Mourasuchus* is a caiman (Alligatoridae: Caimaninae) (Brochu, 1999, 2003, 2010;

Aguilera et al., 2006; Fig. 1). However, the phylogenetic relationships between *Mourasuchus* species have not been explored and each taxon is only briefly described in a few works (Price, 1964; Langston, 1965, 2008; Gasparini, 1985;
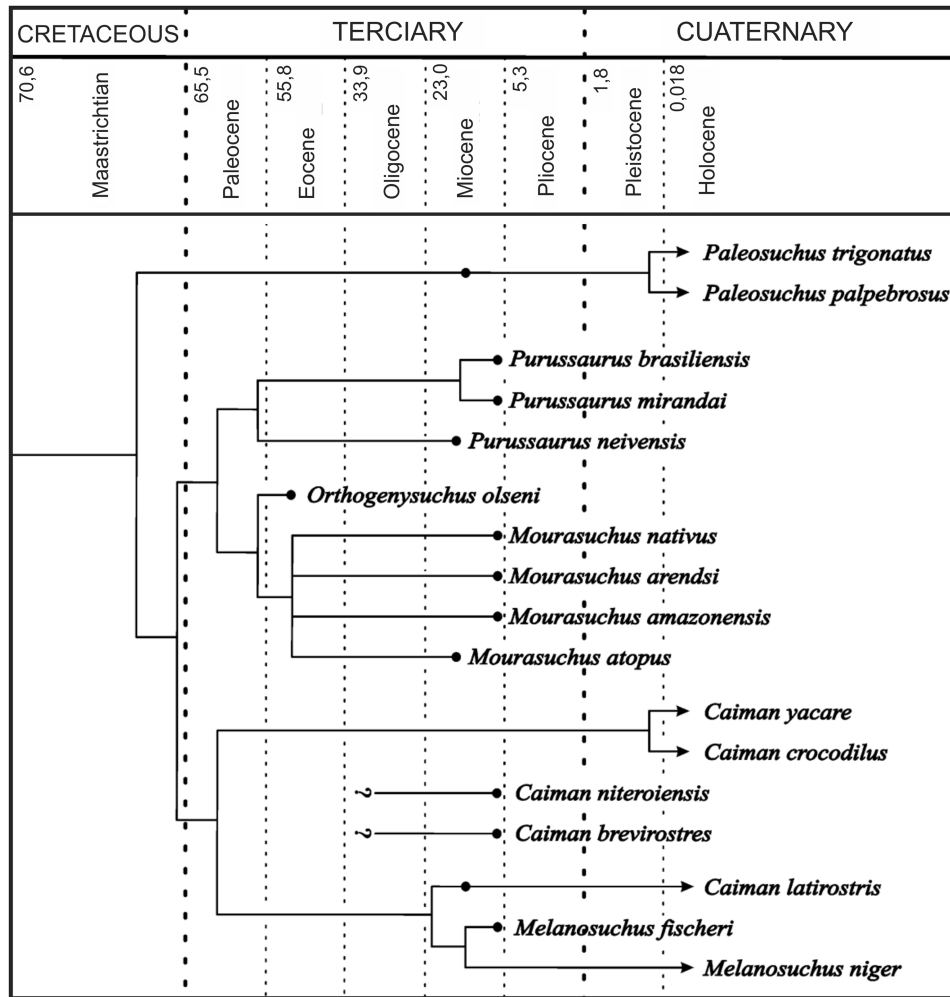
Fig. 1. Cladogram of Caimaninae showing the phylogenetic relationships of *Mourasuchus*. Modified from Riff et al. (2010).

Bocquentin-Villanueva and Souza-Filho, 1990). Moreover, its sister group relationship with the North American Eocene taxon *Orthogenysuchus olseni* Mook 1924 is supported by recent phylogenetic analysis but deserves further investigation (Brochu, 1999, 2010; Aguilera et al., 2006; Riff et al., 2010). In that phylogenetic scenario, the caimanines *Purussaurus* plus *Mourasuchus* and *Orthogenysuchus* comprise a clade. If so, the presence of *Purussaurus* and *Mourasuchus* lineages extend back to Eocene and multiple dispersal events between North and South America are necessary to explain the biogeographic history of this lineage (Brochu, 1999, 2010). Future phylogenetic revisions and detailed anatomical studies of *Mourasuchus* and *Orthogenysuchus* should clarify this situation.

Despite the original anatomical descriptions (Price, 1964; Langston, 1965; Bocquentin-Villanueva, 1984; Gasparini, 1985) and some postcranial descriptions published later (e.g., *M. arendsi*; Langston, 2008), there are no detailed anatomical analyses comparing the species of *Mourasuchus*. Detailed skull descriptions of *Mourasuchus* are scarce (i.e., *M. atopus* described by Langston, 1965) and *M. nativus* is known by the early descriptions given by Gasparini (1985) and Bocquentin-Villanueva and Souza-Filho (1990). These last authors referred and figured new cranial material, but provided only a very brief description. The main goal of this study is to provide new morphological data of the skull and cranial recesses of *M. nativus*, including a new computed tomography analysis. Although the exploration of paleobiological implications related to the cranial morphology of *M. nativus* is beyond the scope of the present contribution (but see below), accurate anatomical descriptions should include comprehensive descriptions of internal anatomical structures. Among crocodiles, and particularly in Alligatoridae, there is little published information of cranial anatomy for comparative studies. CT methods offer a nondestructive option to visualize and reconstruct such morphology, which is especially useful in fossils. Features related to brain, nerves, and ear may indicate functional significance or specific behavioral attributes (e.g., Pearson, 1972; Sherry and Duff, 1996; Garamszegi et al., 2002; Macphail, 2002; Nowicki et al., 2002; Jacobs, 2003, Picasso et al., 2010) useful in paleobiological, paleoecological, evolutionary, and phylogenetic studies. Knowledge of the internal anatomy of the skull contributes to our understanding of the general morphology and its
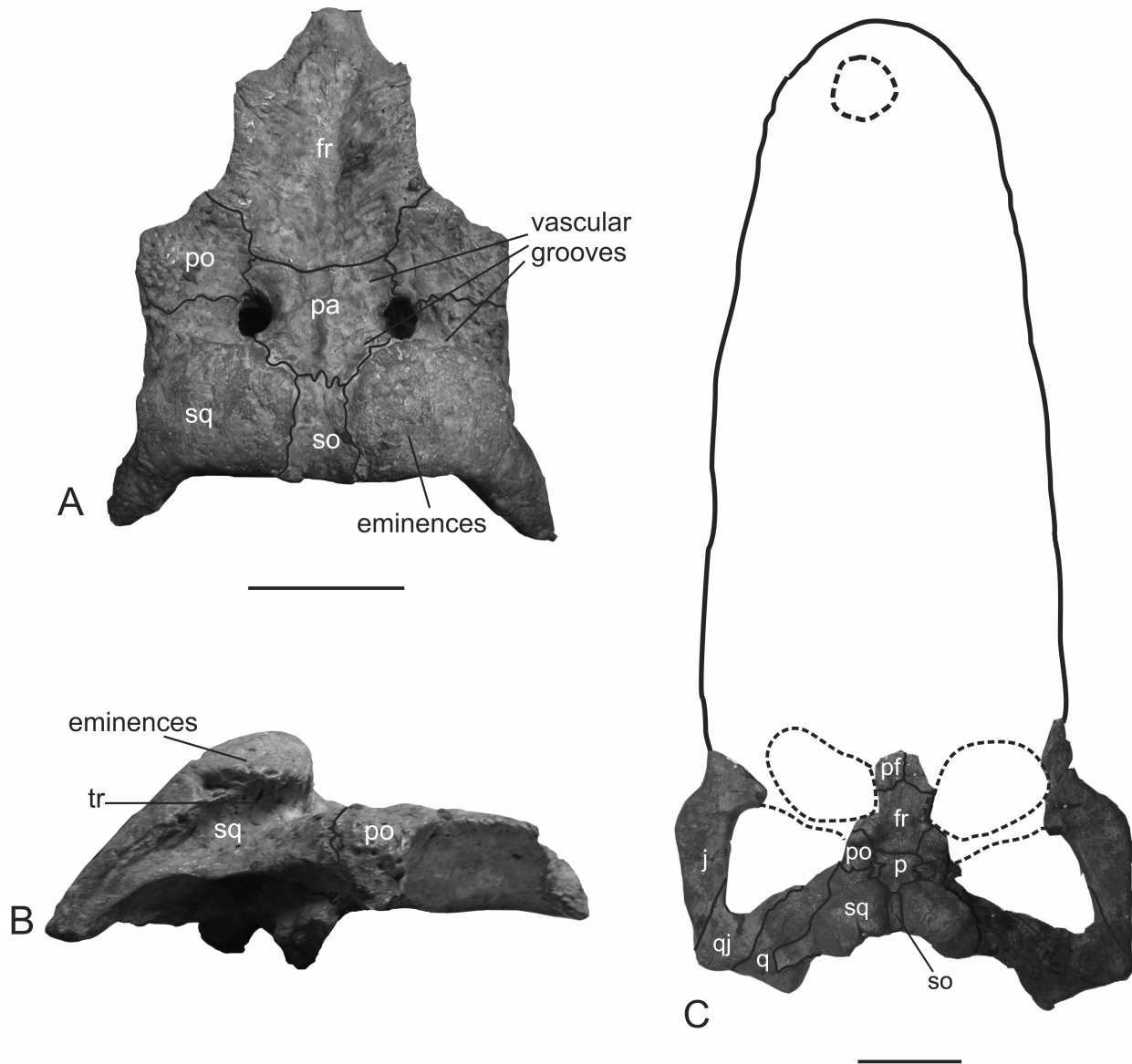
Fig. 2. *Mourasuchus nativus*: MLP 73-IV-15-8, Holotype; (**A**) dorsal and (**B**) lateral views; scale bar = 5 cm. (**C**) Outline drawing restoration of *M. nativus* in dorsal view based on unpublished material housed at UFAC and part of the skull of the specimen UFAC 1424, published by Bocquentin-Villanueva and Souza-Filho (1990); scale bar = 15 cm.

variation. This study provides a source of external and internal bony characters whose implications in systematics, evolution, and paleobiology should be tested.

Institutional Abbreviations

MACN PV, Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia," Paleontología Vertebrados, Buenos Aires, Argentina. MLP, Museo de La Plata, Buenos Aires, Argentina. UFAC, Universidade Federal do Acre, Rio Branco, Acre, Brasil.

Anatomical Abbreviations

bo, basioccipital; bs, basisphenoid; bsr, basisphenoid recess; c, cochlea, cap, capitate process; cb, caudal bridge of laterosphenoid; cer, cerebral hemisphere; cer dl, cerebral dorsal protuberence; cf, carotid foramen; cq, cranioquadrate canal; cr A, crest A; cr B, crest B; crc, crus communis; cr cot, cotylar crest of laterosphenoid; ctp, cavum tympanicum proprium; ctr, caudal tympanic recess; dtr, dorsal tympanic recess; exo, exoccipital; exop, exoccipital process; f IX-X-XI, foramen for glossopharyngeal, vagus, and accesory nerves; fnSO, foramen for supraorbital nerve; fr, frontal; f XII 1-2, foramen for hypoglossal nerve branches; f V, trigeminal foramen; fV_1, ophthalmic trigeminal foramen; f V_2, maxillary trigeminal foramen; f V_3, mandibular trigeminal foramen; f Vtymp, tympanic trigeminal foramen; g V, trigeminal groove; hfo, hypophyseal fossa; itr, intertympanic recess; IX-X-XI, common canal for glossopharyngeal, vagus, and accesory nerves; j, jugal; lab, endosseous labyrinth; lcb,
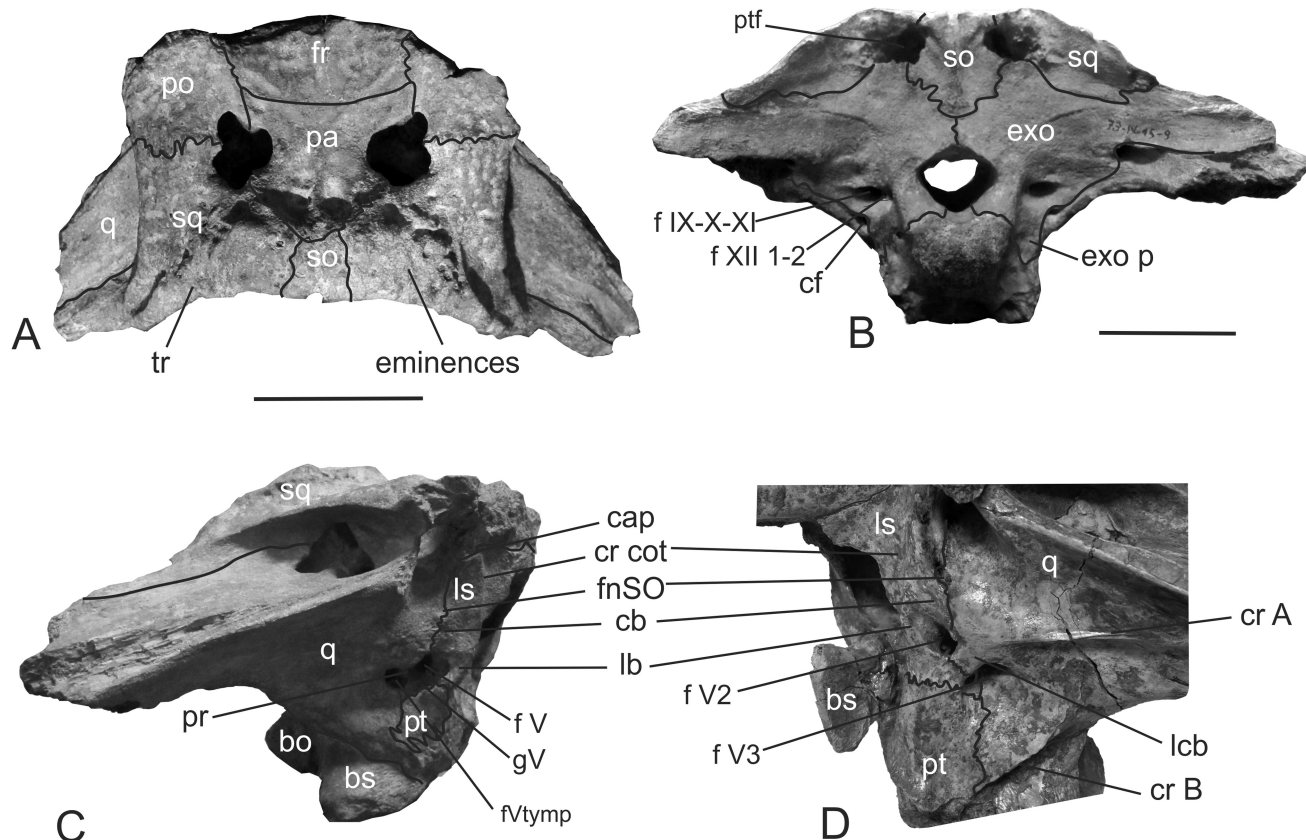
Fig. 3. *Mourasuchus nativus*. MLP 73-IV-15-9, fragment of posterior sector of the skull; (**A**) dorsal, (**B**) occipital, and (**C**) lateral views. UFAC-2515; (**D**) details of the left lateral view. Scale bars = 5 cm.

laterocaudal bridge of quadrate; lb, lateral bridge of laterosphenoid; ls, laterosphenoid; lsc, lateral (horizontal) semicircular canal; mAME, *musculus adductor mandibulae externus*; mAMEM, *musculus adductor mandibulae externus medialis*; mAMP, *musculus adductor mandibulae posterior*; mpr, median pharyngeal recess; nSO, supraorbital nerve canal; pa, parietal; pf, prefrontal; po, postorbital; pr, prootic; pt, pterygoid; ptc, posttemporal canal; ptf, posttemporal fenestra; ptr, pharyngotympanic (=Eustachian) recess; q, quadrate; qj, quadratojugal; rsc, rostral (anterior vertical) semicircular canal; s, siphonium; sq, squamosal; so, supraoccipital; th, torcular herophili; tr, transverse ridge; ts, transverse sinus; V_1, ophthalmic canal of trigeminal nerve; V_2, maxillary canal of trigeminal nerve; V_3, mandibular canal of trigeminal nerve; Vtymp, tympanic branch canal of trigeminal nerve; XII, hypoglossal canal; Xtymp, tympanic branch canal of vagus nerve.

MATERIALS AND METHODS

The skull redescription of *M. nativus* presented here is based mainly on the holotype (MLP 73-IV-15-8) and a subadult specimen (MLP 73-IV-15-9). Both specimens are represented only by skull material including a braincase and skull table, respectively, from the Upper Miocene ("Conglomerado Osífero" level from the Ituzaingó Formation) of Paraná, Argentina, and housed at the Museo de La Plata, Argentina. Intraspecific morphological comparisons were made using published figured material of *M. nativus* (Boc-

quentin-Villanueva and Souza-Filho, 1990; Figs. 2–4) and the study of unpublished cranial material of 13 new specimens from Upper Miocene of Acre, housed in the UFAC (photographs provided by Douglas Riff). Comparisons with cranial material of other fossil taxa (e.g., *Purussaurus* and other species of *Mourasuchus*) were also made using those materials figured by Price (1964), Langston (1965), Bocquentin-Villanueva (1984), Gasparini (1985), Bocquentin-Villanueva and Souza-Filho (1990), Brochu (1999), Aguilera et al. (2006), and personal photographs. Cranial comparative material of extant alligatorids species used in this analysis belongs to herpetological collections housed in the MLP and the MACN.

CT scans were obtained in the transverse plane of *M. nativus* MLP 73-IV-15-9 by means of spiral computed tomographies performed at Tomografías Computadas Ipensa, La Plata, Argentina (General Electric Medical Systems; HiSpeed CT scanner, 120 kV, 112 mA, 1 mm slice thickness). The DICOM images were processed, and the reconstruction of the three-dimensional (3D) models of the endocast, inner ear, and air sinuses was made using Materialise Mimics software 10.01 (Materialise, Leuven, Belgium), trial version.

Description

Skull morphology. In dorsal view (Figs. 2A, 3A), the skull table shows straight and parallel lateral margins, caudolaterally oriented because of the squamosal
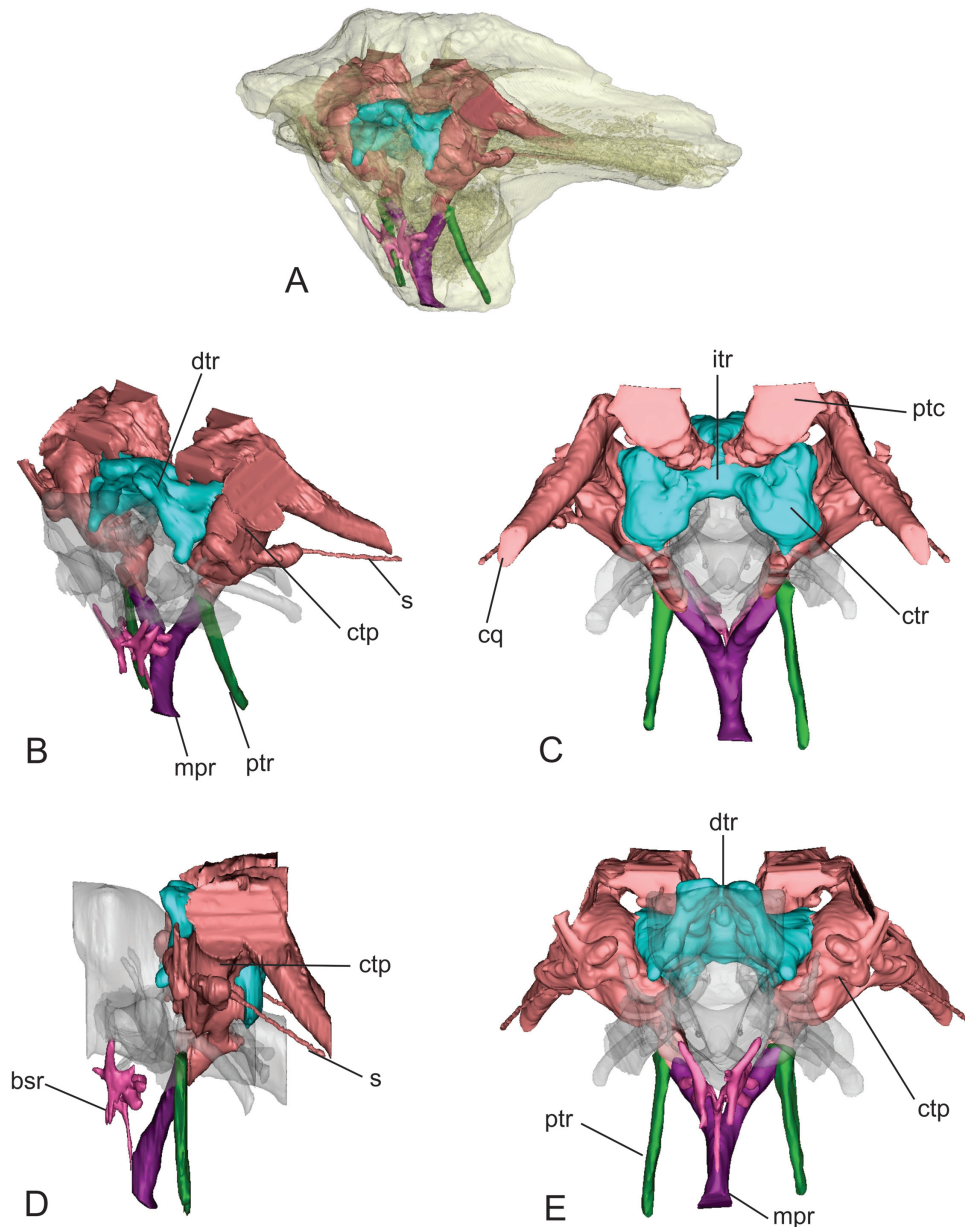
Fig. 4. Pneumatic sinuses and other recesses of the braincase region of *Mourasuchus nativus* (MLP 73-IV-15-9) based on CT scanning followed by segmentation and 3D visualization. (**A**, **B**) Rostrolateral, (**C**) caudal, (**D**) lateral, and (**E**) rostral views. Bone is rendered semitransparent in A and endocast is rendered semitransparent (except in A).

projections at the paraoccipital processes. The posterior margin of the skull table in *M. nativus* is similar to that in extant caimanines. In lateral view (Fig. 2B), the skull table surface is particularly high because of the abrupt elevation of parietals, deeply convex squamosals, and supraoccipital bones. These bones together form paired eminences, whose size varies with ontogeny, situated over a robust, transverse ridge at the posterior margin of the skull table. Although the sizes of the squamosal eminences vary with the skull size, this ridge is developed in all young and adult specimens of *Mourasuchus*. CT scan images show that these eminences are solid and

not internally invaded by the paratympanic sinus system as in other archosaurs (see below). The squamosal eminences are surrounded by vascular grooves which become more pronounced the larger the bumps become. Unlike *M. atopus* and *M. amazonensis*, the supratemporal fenestrae are rostrally bounded by the parietals and postorbitals. In *M. nativus*, these fenestrae have different sizes and shapes that vary from trilobed with a medial, rostrolateral, and caudolateral lobes (e.g., MLP 73-IV-15-9) to subcircular (e.g., MLP 73-IV-15-8). The three curvatures of the margins of the supratemporal fenestra communicate with grooves extending

over the skull roof, here interpreted as vascular marks. The rostrolateral lobe of the margin of the fenestra relates to a shallow groove that is directed rostrally toward the caudomedial margin of the orbit. The caudolateral and medial lobes are related to caudolaterally and caudomedially directed grooves, respectively, which surround the squamosal eminences. The larger the specimen, the more marked the caudolateral groove and squamosal eminences become (Fig. 2).

As in young specimens (i.e., juvenile or subadult) of most of the extant caimanine species, MLP 73-IV-15-9 has a rostral opening of the posttemporal canal that is exposed in dorsal view within the supratemporal fenestra and is obliquely oriented. In MLP 73-IV-15-8, the rostral opening of the posttemporal canal is vertically oriented and covered by the dermal skull roof, a synapomorphy of the crown group caimans, observed in adult specimens (Brochu, 1999: 68). Both infratemporal fenestrae are almost completely preserved in UFAC 1424 (Fig. 2C). In *M. nativus*, the quadratojugal forms the posterior part of the lateral margin of these fenestrae and the lateral margin of jugal presents a marked notch. These fenestrae are wider than long, triangular in shape, and wider than the skull table width. As in other *Mourasuchus* species, the orbits are smaller than the infratemporal fenestrae and the supratemporal fenestrae are reduced (probably a synapomorphy of the genus). However, in *M. nativus*, the rostral margin of the orbits is smooth and lacks the knob found in orbits of *M. amazonensis, M. arendsi*, and *M. atopus*.

The occipital region dorsal to the foramen magnum is tall (Fig. 3B). As Gasparini (1985) pointed out, the dorsal margin of squamosal descends abruptly at the level of the paraoccipital processes. The supraoccipital is also tall and narrow and delimits the posttemporal fenestrae medially. These fenestrae are large (see comments below), similar in size with the supratemporal fenestrae (probably an autapomorphy of this taxon), and bounded by exoccipitals ventrally, medially, and dorsomedially by supraoccipital and laterally and dorsolaterally by the squamosals. Unlike most extant caimans, the skull ornamentation is reduced, with bone surfaces particularly smooth, with crests and isolated cells and pits.

In occipital view, the basioccipital plate is rectangular shaped. The ventral margin (=basioccipital-basisphenoid suture) is horizontal and straight and as in other crocodylian delimits the median (singular) and lateral (paired) openings of the Eustachian tube (=median pharyngeal recess and pharyngotympanic recess, respectively; Witmer et al., 2008). The basioccipital tubera extend along the ventral and lateral margins of the basioccipital plate, which bears a marked medial crest. In crocodiles, this crest together with the tubera serve as attaching surface for the tendons of the *M. basioccipitovertebralis* (=*M. rectus capitis anterior*) and the *M. occipitotransversalis profundus* (*M. longissimus capitis*) (Iordansky, 1973: 226). The basioccipital forms the occipital condyle and the medial portion of the ventral margin of foramen magnum. It extends rostrally forming the posterior floor of the cerebral cavity and contacts the exoccipital dorsally in occipital view.

As in other crocodiles, exoccipitals meet at the midline delimiting dorsally the foramen magnum and extending laterally forming the paraoccipital processes. These processes are formed by opisthotics which are confluent with exoccipitals (otoccipital, s*ensu* Iordansky, 1973: 226). In occipital view, exoccipitals are sutured with the squamosals dorsolaterally and the supraoccipital dorsomedially and form the floor of the posttemporal canal for the passage of the temporal artery and vein (Sedlmayr, 2002). Ventrally, exoccipital processes are short and do not extend over the basioccipital tubera as occur in other Caimaninae (Brochu, 1999). The cranioquadrate canal is delimited by paraoccipital process and quadrate (Fig. 3B) and runs from the middle ear cavity to the occipital surface (Fig. 4). It provides passage for the main branch of the facial nerve (VII), the orbitotemporal artery and the lateral cephalic vein (*sensu* Iordansky, 1973), the stapediall artery and vein (*sensu* Sedlmayr, 2002), and the ceratohyal nerve (*sensu* Romer, 1956) plus the tympanic branch of the glossopharyngeal nerve (*sensu* Hasse, 1873). In crocodylians, the temporo-orbital artery and the larger temporo-orbital vein (branches of the stapedial vessels) pass through the middle ear space and enter to the supratemporal fossa where these vessels connect with the temporal artery and vein (Sedlmayr, 2002). As stated above, the temporal artery and vein run through the posttemporal canal which opens at the occipital region by the posttemporal fenestra. In *M. nativus*, the cranioquadrate canal, the posttemporal canal, and the posttemporal fenestra are huge (see below).

The huge cranioquadrate opening is surrounded by the otoccipital and quadrate. In *M. nativus*, the otoccipital-quadrate suture is entirely exposed at the occipital surface (Fig. 3B).

At the otoccipital and lateral to the foramen magnum, there are four foramina. The ventrolateral foramen represents the external ostium of the osseous cranial carotid canal (Sedlmayr, 2002: 214; "foramen carotids" *sensu* Romer, 1956) for the internal carotid passage. The internal carotid artery passes rostrodorsomedially through this canal from the occipital opening to the middle ear space (Sedlmayr, 2002: 214; Fig. 5). The osseous carotid canals are not completely ossified. The middle part of its trajectory toward the hypophysis is absent and was probably occupied by a cartilaginous tube, like in *Alligator mississippiensis* (Daudin 1801) (Sedlmayr, 2002). Rostrally, this canal extends ventromedially and then dorsomedially through the basisphenoid to the hypophyseal fossa. The other three foramina are horizontally aligned. The lateral and larger one is the foramen vagus (Romer, 1956) for the passage of the IX, X, and XI nerves and the jugular vein. The medial ones are the foramina hypoglossi for the passage of the XII nerve (Figs. 3B, 5).

The otoccipitals form the posterior part of the lateral walls of the cerebral cavity, and together with supraoccipital and prootic, form the "bulla tympani" (Iordansky, 1973).

As in other species of *Mourasuchus* (e.g., *M. arendsi*), the supraoccipital of *M. nativus* is a high and narrow bone that delimits the posttemporal fenestra medially. The shape of this bone differs from that of other crocodylians where supraoccipital is flat and laterally expanded, and shows a well-developed median crest for the attachment of the cervical muscles. In crocodylians, ventral to the posttemporal fenestra the supraoccipital forms a pair of posteriorly directed processes (Iordansky, 1973: 227; *processus postoccipitales* of Kälin, 1933) which serve as the attachment surface of the tendons of the *M. spinalis capitis* (Iordansky, 1973). These processes are practically absent in *M. nativus*, so the tendons of this
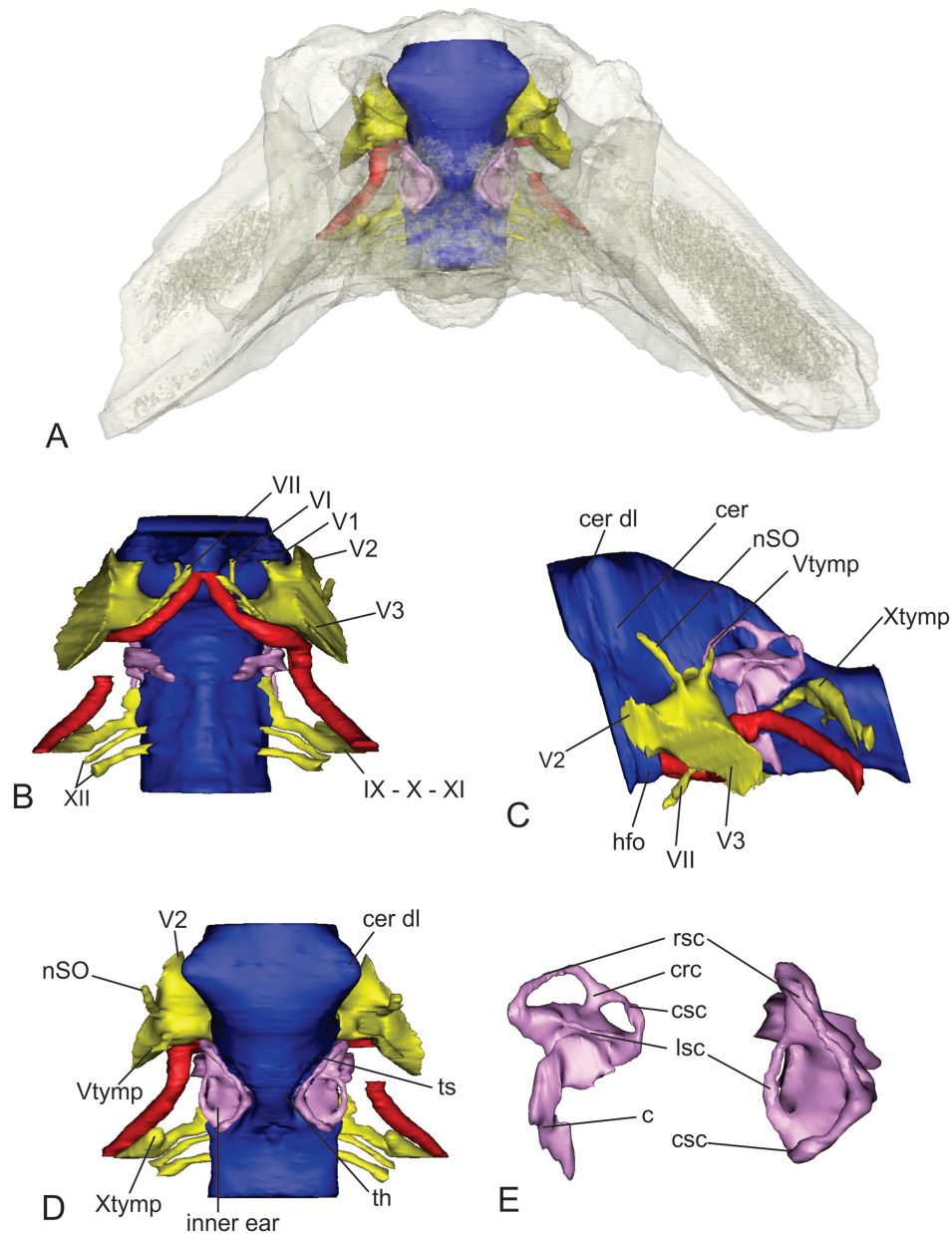
Fig. 5. Cranial endocast (blue), nerve canals (yellow), carotid canals (red), and endosseous labyrinth of the inner ear (pink) of *Mourasuchus nativus* (MLP 73-IV-15-9) derived from surface renderings of CT scan data. (**A**, **D**) Dorsal, (**B**) ventral, and (**C**) lateral views. (**E**) Endosseous labyrinth of the left inner ear on lateral (left) and dorsal (right) views. Bone is rendered semitransparent in A.

muscle may have attached dorsally to the posttemporal fenestra at the squamosal. In this species, the area of attachment of the longitudinal axial musculature (cervical muscles) at the occipital aspect of the squamosals is large and extends dorsal and dorsolateral to the huge posttemporal fenestra. This area is more developed in huge specimens with large squamosal eminences (e.g., MLPIV15 8). As in Caimaninae, the supraoccipital extends anteriorly over the skull table. In MLP 73-IV-15-9, the supraoccipital is not pneumatized by the paratympanic air sinuses system (see below).

The basisphenoid forms the rostral surface of the cerebral cavity. It is preserved in the cranial fragment of the speci-men MLP 73-IV-15-9 and is exposed in lateral and anterior view. The pterygoids are partially preserved in this specimen and are visible in lateral view. The lateral sutural surface between the basisphenoid and pterygoids is covered by the quadrate caudodorsally and the laterosphenoid rostrodorsally (Fig. 3C). It is exposed at the posterior part of the lateroventral skull surface and the basisphenoid-basioccipital suture is visible posterior to it at the lateral margin of the occipital surface. The rostral projection of the basisphenoid (i.e., basisphenoid rostrum) is not preserved in this specimen, but it can be observed in UFAC-2515 (Fig. 3D).

In anterior view, a deep oval-shaped hypophyseal fossa is exposed. The openings for the VI nerve are

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located dorsolaterally to the fossa. As in other crocodylians, the caudal wall of the hypophyseal fossa is pierced by a large pair of *foramina carotica antericus* (the anterior opening of the carotid canal).

The laterosphenoids form the rotrolateral wall of the cerebral cavity and as in other crocodylians, the rostral border of trigeminal foramen, which is caudally delimited by the prootic (Fig. 3C,D; Holliday and Witmer, 2009). Dorsally, the postorbital process of the laterosphenoid (the primary site of the attachment for the *pseudotemporalis superficialis* muscle in crocodiles; Holliday and Witmer, 2009: Fig. 3) is sutured caudally to the quadrate and rostrodorsally with the frontal. The surface of the dorsal aspect of laterosphenoid bears a marked rostral longitudinal oblique crest for the attachment of the *pseudotemporalis* muscle (Iordansky, 1964; Holliday and Witmer, 2007; Bona and Desojo, 2011). In *M. nativus*, this crest (cotylar crest of laterosphenoid; Holliday and Witmer, 2009) is more vertically oriented than in other caimans, extending from the dorsal aspect of the postorbital process of laterosphenoid ventrally toward the cranial margin of the laterosphenoid lateral bridge (Fig. 3C,D). Caudodorsally, the laterosphenoid bears a capitate process (Fig. 3C). As in other crocodylians, this contact is not sutural (see Iordansky, 1973: 228; Holliday and Witmer, 2007, 2009). The lateral and caudal bridges of laterosphenoid are present. As in other caimanines (e.g., *Caiman, Paleosuchus*, and *Melanosuchus*), the caudal bridge is typically short, robust, and encloses the supraorbital branch of the trigeminal nerve (Holliday and Witmer, 2009; Bona and Desojo, 2011; Figs. 3C,D, 5C,D). The lateral bridge is complete and caudoventrally sutured with pterygoid and with the basisphenoid rostrally. It forms the rostrolateral bony limit of the *cavum epiptericum* and provides the passage of the ophthalmic ramus of the trigeminal nerve (V_1). The opening of the trigeminal fossa to the adductor chamber is bounded by laterosphenoid (rostrally), quadrate (caudally and dorsally), and pterygoid (ventrally) and is dorsorostrally–ventrocaudally oriented. In *M. nativus*, the quadrate forms a robust caudolateral bridge (Fig. 3D), a process that is ventrally sutured to the laterosphenoid. The ventral surface of the quadrate in *M. nativus* is more laterally facing and crest "A" and "B" (Iordansky, 1964) are more laterally and caudally oriented than in other caimanines, respectively. It can be inferred that the mAME (see Holliday and Witmer, 2007; Figs. 4B, 8) was more laterally positioned in this species. The huge opening of the trigeminal fossa lies just at the area of attach of this muscle. The presence of a quadrate bridge at this level probably serves as a bony surface of attachment, especially for the mAMEM, which in extant Crocodylia is caudoventrally attached to the lateral trigeminal foramen (Holliday and Witmer, 2007; Bona and Desojo, 2011). It is clear that in *M. nativus* the quadrate bridge also divides the maxillary (V_2) and mandibular (V_3) trigeminal branches. Contrary to other camanines, in this species, the opening of the branch V_3 is caudoventrally oriented, not caudolaterally and ventrally oriented. Given the caudal orientation of crest "B," these features indicate that mAMP (see Holliday and Witmer, 2007; Figs. 1, 4B) attached more caudally than in other caimanines. These features of the orientation of adductor muscles, bony attachments, and nerve osteological

correlates fit with the presence of a flat and elongated skull in this species (see below).

The prootic in *M. nativus* is more laterally exposed at the posterior sector of trigeminal foramen than in other Caimaninae and crocodylians (Fig. 3C) and forms the caudal margin of the trigeminal foramen and the medial wall of the trigeminal fossa. The prootic also forms the rostral margin of the lateral foramen for the passage of the tympanic trigeminal branch (Holliday and Witmer, 2009), which is bounded by the quadrate caudally. In *M. nativus*, this foramen is particularly large (it size is almost equal to that of the trigeminal foramen), completely exposed in lateral view and horizontally aligned with the trigeminal foramen (Fig. 3C). Through this orifice, and in a rostrodorsal position, the medial foramen for the passage of the tympanic ramus of the trigeminal into the otic space can be observed in the prootic (Figs. 3C, 5). In extant crocodylians, the small tympanic branch of the trigeminal nerve passes from a small lateral tympanic foramen, bounded by prootic and quadrate and situated caudodorsally to the trigeminal foramen (and ganglion), into the otic region (see Witmer et al., 2008; Holliday and Witmer, 2009: Fig. 4A, and literature cited therein).

As in all crocodylians, the parietals are fused at the midline. In *M. nativus*, this bone is wider than long and bears a moderately developed median longitudinal crest (Figs. 2A, 3A). Rostrally, the parietals contact the single broad frontal, which does not project by a rostral process as in several alligatorids. In *M. nativus*, the frontal and nasals are not in contact because of the mid-line contact of prefrontals (Fig. 3). In some material from Acre, figured by Bocquentin-Villanueva and Souza-Filho (1990: 232; Fig. 3A; UFAC 1424; Fig. 3D), some palatal elements can be observed. In palatal view, the pterygoids are broad forming part of the caudal margin of the suborbital fenestra.

Braincase and Main Skull Cavities

Three-dimensional reconstruction of the CT data of *M. nativus* revealed a brain cavity, middle ear, and inner ear cavities and Eustachian system similar in morphology to those of extant crocodylians (Figs. 4, 5).

Endocast of brain cavity. As in other reptiles, the brain did not fill the endocranial cavity and many of the brain parts are obscured by the overlying dural venous sinuses and the dura itself (Jerison, 1973; Hopson, 1979; Witmer et al., 2008). As is observed in the 3D reconstruction (Fig. 5), the endocast includes the caudal part of the forebrain and the hindbrain. As stated above, it seems to be dominated by large dura and venous sinuses that cover much of the brain structure, especially dorsally (Witmer et al., 2008; Witmer and Ridgely, 2009) and many of the brain details are not visible (Witmer et al., 2008). As in other crocodylians, the dorsal longitudinal sinus is expanded caudally in a central venous sinus, the *torcular herophili* (Sedlmayr, 2002), which in this specimen is huge with an "hourglass" outline diverging caudally (Fig. 5D). The *torcular herophili* is located in the center of the endocranial aspect of the parietal at the parietal fossa. Caudally it continues into the occipital venous sinus (not well marked in this specimen), which drains much of the blood and exits through the

foramen magnum (Witmer et al., 2008). Rostrolaterally, a pair of transverse sinus, which drains into the *torcular herophili*, is poorly delimited.

The endocast presents the typical sigmoid morphology of Crocodylia (see discussion below) (Fig. 5C). Although the brain is hidden by the overlaying dura and venous system in dorsal view, the caudal portions of the telencephalic hemispheres are visible. Caudodorsally, the endocast of *M. nativus* is characterized by the presence of a pair of pointed lumps (Fig. 5C,D). The optic tectum of the mesencephalon (optic lobule) as well as the cerebellum is not visible.

Cranial nerve canals. Only the canals of the V, VI, IX, X, XI, and XII and part of VII nerves were recognized and reconstructed, allowing identification of the corresponding entry foramina (see osteological description above). The trigeminal canals (V) are represented by the V_1, V_2, V_2 supraorbital, V_3, and tympanic branches (Fig. 5B,C). The base of the canal for V_1 is ventromedial to the rostrally oriented canal for V_2, which is directed rostrally, and its supraorbital branch is rostrodorsally oriented. In this specimen, the tympanic trigeminal nerve canal is wide, its base is dorsolaterally directed, whereas the main ramus is caudodorsally oriented (Fig. 5C,D). The reconstructed part of the canal of the VII nerve is extended more ventrally than in *Crocodylus*, passing ventrally to the carotid canals (Fig. 5B,C). The canals of cranial nerves IX, X, XI and cranial nerves XII are located at the lateral portion of the endocast corresponding to the hindbrain (Fig. 5B,D). The nerves IX, X, and XI pass into a common canal, except for the tympanic branch of the vagus nerve (X), which in this specimen passes into a large differentiated canal (Fig. 5C,D). As it was mentioned previously, all of these nerves pass together through the vagus canal that opens in the vagal foramen at the occipital surface. Caudal to these nerves, the paired canals of the hypoglossal nerve branches are observed. The rostral one corresponds to the branch XII_1 that innervates most of the muscles of the tongue and exit the skull laterally to the posterior branch XII_2 (Bona and Desojo, 2011).

Endosseous labyrinth of the inner ear. The rostral, caudal, and lateral semicircular canals, crus communis, cochlea, and part of the vestibule were reconstructed (Fig. 5E), although reconstruction of the fenestrae vestibuli was not possible. The general aspect of the endosseous labyrinth is similar to that present in extant crocodylians (i.e., simple and triangular vestibular apparatus and elongated cochlea). The rostral and caudal semicircular canals form a 94-degree angle. In dorsal view, the rostral canal is almost twice as long as the caudal canal (Fig. 5E).

Tympanic and pharyngotympanic recesses. As with many archosaurians, this specimen shows bony recesses from the cranial system of air-filled sinuses that pneumatized the skull (Witmer, 1990, 1995, 1997; Witmer et al., 2008; Witmer and Ridgely, 2009) (Fig. 4). Like in other crocodylians, the paratympanic and the pharyngeal sinuses in *M. nativus* pneumatize several bones of braincase and otic region generating several bony recesses.

In crocodiles, the paratympanic sinuses, which are those formed by middle-ear diverticulae, are extended into the recesses they excavate, generally known as tympanic recesses (Witmer, 1997). These recesses in this specimen are particularly large, similar to the situation present in young specimens of *A. mississippiensis* (Daudin 1802) (Dufeau, personal communication). Although the *cavum tympanicum propium*, the recess of the quadrate sinus, and the pharyngotympanic (=Eustachian) recess were reconstructed, the boundaries between them could not be established. In this specimen, the caudal and the dorsal tympanic recesses were observed (Fig. 4B,C). As in other crocodylians [e.g., *Crocodylus johnstoni* (Krefft 1873), *A. mississippiensis*], the caudal tympanic recess is broadly confluent with the very extensive dorsal tympanic recess. They are excavated mainly in the otoccipital and epiotic bones, respectively, and medially communicated by a broad intertympanic recess (Witmer et al., 2008; Fig. 4C). Their general morphology is similar to that present in other alligatorids as *A. mississippiensis*, and *Caiman latirostris* (Daudin 1802). As in other crocodyliforms, in *M. nativus* the paratympanic sinuses also pneumatize the quadrate and probably the articular. The resultant bonny recess, the quadrate recess, is preserved and communicates with the long and thin siphonial tube, which in extant crocodylians passes through the quadrate on its way to the articular (Fig. 4B,D).

The pharyngeal sinus system derived from pneumatic outgrowths of the roof of the pharynx occupies the median pharyngeal and the pharyngotympanic or Eustachian recesses (Colbert, 1946; Witmer et al., 2008). The 3D reconstruction shows that the median pharyngeal recesses descend rostromedially, connecting to each other near the external ventral opening, between the basisphenoid and basioccipital bones (Fig. 4C,E) where both symmetrical tubes are connected. This recess presents a dorsorostral projection, the basisphenoid recess, which pneumatizes the basisphenoid (Fig. 4D) and has no communication with the tympanic system. This recess presents a very complex morphology which is typical of caimanines. Only the distal part of the Eustachian recess could be reconstructed.

DISCUSSION

Although its paleobiological implications are beyond the scope of this article, the cranial morphology of *M. nativus* is amongst the most bizarre of any alligatorid. *Mourasuchus* presents an unusual skeletal morphotype. All species are represented by large specimens with skull with around 1 m in length, characterized by having an extremely broad, long, and dorsoventrally compressed (duck-faced) rostrum with many small teeth, a slender mandible, tiny mandibular symphysis, and a relatively small skull table contrasting with the large infratemporal fenestrae (Riff et al., 2010). This skull morphology and the presence of short cervical vertebrae with poorly developed hypapophyses and cervical spine suggesting the incapacity of strong flexing and lateral movements of the neck to capture large prey have led others to interpret *Mourasuchus* as a filter-feeding animal (Langston, 1965, 2008; Bocquentin-Villanueva, 1984; Riff et al., 2010).

Accurate anatomical descriptions should include comprehensive descriptions of internal anatomical

structures. Among crocodiles, and particularly in Alligatoridae, there is little published information of cranial anatomy for comparative studies. CT methods offer a nondestructive option to visualize and reconstruct such morphology, which is especially useful in fossils. Features related to brain, nerves, and ear may indicate functional significance or specific behavioral attributes (e.g., Pearson, 1972; Sherry and Duff, 1996; Garamszegi et al., 2002; Macphail, 2002; Nowicki et al., 2002; Jacobs, 2003, Picasso et al., 2010) useful in paleobiological, paleoecological, evolutionary, and phylogenetic studies. As a result of the detailed anatomical study of *M. nativus*, we provide new morphological information to anatomically diagnose this species to clarify its relationships in future phylogenetic analysis.

Osteology

As a result of the present comparative morphological study, we have observed that, as in *Purussaurus*, the caudal margin of the skull table in *M. arendsi* and *M. amazonensis* is deeply concave "V" or "U" shaped because the caudal margin of squamosal is oblique in all its length (Rovereto, 1912; Price, 1964; Brochu, 1999; Aguilera et al., 2006). In *M. nativus*, this feature varies from a "V" or "U" shaped to a "half-hexahedron" outline. According to Mook's description (1924: 4, Fig. 2) of *Orthogenysuchus*, the caudal margin is distinctive and medially convex with two notches lateral to the supraoccipital bone. Several diagnostic characters of *Purussaurus* given by Aguilera et al. (2006) are shared with *Mourasuchus*, including their large size, the presence of enlarged and wide skull and wide narial aperture surrounded by a large narial fossa formed by developed rostral canthi (at least in *M. amazonensis*), an oval incisive foramen entirely surrounded by the premaxillae, nasal, and lacrimal bones not in contact, squamosal bone tall and long caudally, and caudal dorsal margin of the skull table (squamosal and supraoccipital) strongly concave. Because of this problematic scenario, it seems necessary to rediagnose both genera (i.e., *Purussaurus* and *Mourasuchus*) morphologically. Differing from other caimanines, *Mourasuchus* species share the presence of a dentary that is linear between the fourth and tenth alveoli (Brochu, 1999; character 68-2; also present in other non-alligatoroid crocodylians, such as *Tomistoma, Thoracosaurus, Eosuchus, Gavialis, Gryposuchus*, and *Hesperogavialis*), orbits that are smaller than the infratemporal fenestrae, and reduced supratemporal fenestrae. *M. nativus* differs from *M. amazonensis, M. arendsi*, and *M. atopus* by the absence of marked knob at the margin of the orbit, and from *M. atopus* and *M. amazonensis* by the presence of a supratemporal fenestra surrounded rostrally by the postorbital and parietal (and not only by postorbital as in those species). As stated above, the skull table of *M. nativus* is also characterized by the presence of paired squamosal eminences (Gasparini, 1985). Similar features are also present in some crocodylids such as *C. rhombifer* Cuvier 1807, *C. niloticus* (Laurenti 1768), *Voay robustus* (Grandidier and Vaillant 1872), and in the Alligatoridae *Caiman niteroiensis* (Souza-Filho and Bocquentin-Villanueva 1991) and *Ceratosuchus burdoshi* (Schmidt 1938). Nevertheless, in all those species, the eminences are always parallel to the sagittal plane, mainly at the laterocaudal margin of the squamosal bones, and not transversely situated as in *M. nativus*. The presence of these solid transverse eminences at the caudal margin of the skull is diagnostic of this species (Gasparini, 1985). They are associated with vascular grooves (Figs. 2, 6) and their robusticity varies with ontogeny (see below). *M. nativus* also shows distinctive large posttemporal fenestrae Gasparini (1985), and a likely autapomorphic caudolateral bridge formed by a robust descending process of quadrate, sutured to the laterosphenoid and separating V_2-V_3 trigeminal openings. Together with this feature, the skull of *M. nativus* shows several distinctive characters. Differing from several caimanines (e.g., *C. latirostris* and *C. yacare*) and other crocodylians like *Crocodylus niloticus, M. nativus* shows an exoccipital-quadrate suture entirely exposed at the occipital surface. Although in Caimaninae the exoccipital extends ventrally by a long exoccipital process that forms part of the occipital tubera (Brochu, 1999), in *M. nativus* these processes are short as in *Alligator*. In lateral view, *M. nativus* also shows a distinctive large foramen for the passage of the tympanic ramus of the trigeminal nerve, horizontally aligned with the trigeminal foramen

Skull Recesses and Main Cranial Cavities

The endocast of *M. nativus* shows the same general morphology of those of other crocodylians but is quite sigmoidal shaped in lateral view, with a pronounced caudodorsal concavity at the caudal aspect of the cerebellum (Fig. 5C). Only the trigeminal nerve shows significant differences in its morphology when compared with extant taxa. In *M. nativus*, the supraorbital ramus of V_2 is more vertically orientated and the V_3 ramus is more caudally orientated than in living crocodiles. The caudal disposition of the V_3 branch is probably related with the adductor muscle arrangement (see below), similar to those of other flat-headed crocodyliforms such as *Aegisuchus witmeri* (Holliday and Gardner, 2012).

In *M. nativus*, the canal of the tympanic branch is thick, opening in a large foramen aligned with the trigeminal foramen (Figs. 3C,D, 5). The canal of the tympanic ramus of the vagus nerve is also very large compared with that of other crocodiles such as *Crocodylus*.

Contrary to the condition seen in some *Crocodylus* species and like other alligatorids such as *C. latirostris* and *A. mississippiensis*, the carotid canals converge rostrally (in *C. johnstoni* both canals become parallel before entering at the hypophyseal fossae). These bony canals are clearly interrupted in the middle portion, being incompletely ossified.

The general pattern of recesses determined from computed tomography and 3D modeling in this species is similar to that present in extant alligatorids. Despite the fact that there are few studies and reconstructions of the cranial recesses of crocodiles, it can be stated that derived alligatorids, such as the caimanines *C. latirostris*, *C. crocodylus*, and *M. nativus*, have complexes cranial recesses. The relatively large sizes of the dorsal, caudal, and intertympanic recesses (Fig. 4) in the juvenile specimen MLP 73-IV-15-9 are similar to the condition found in young specimens of extant alligatorids such as *A. mississippiensis* (Dufeau, personal communication).

Among extant Archosauria, the intertympanic recess is present only in crocodylians. It communicates with the dorsolateral portion of the tympanic recesses
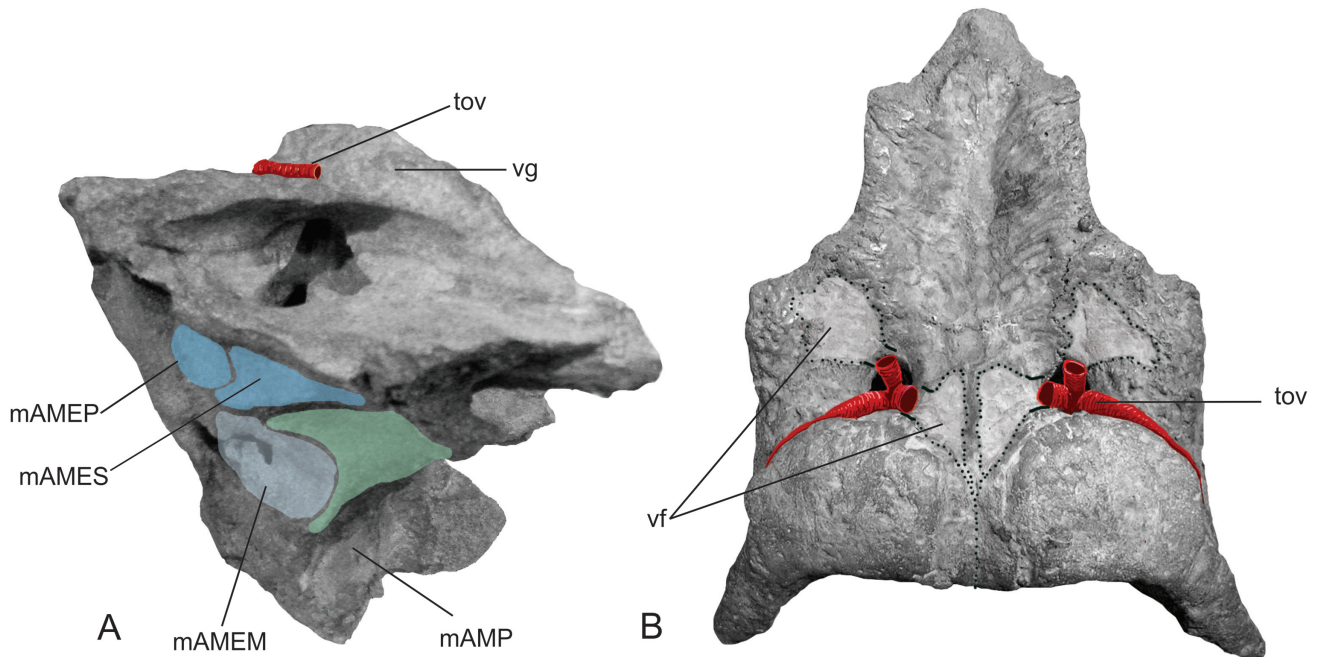
Fig. 6. Soft tissues reconstructions of *Mourasuchus nativus*. (**A**) Attach areas of jaw muscles of MLP 73-IV-15-8 in left lateral view. (**B**) Vascular vessel at the skull roof of MLP 73-IV-15-9 in dorsal view.

(Fig. 4C) and in *M. nativus* extends through the otoccipitals without reaching the supraoccipital, contrary to the condition pointed out by Iordansky, 1973: 227, for crocodiles [i.e., "the (supraoccipital) bone is much pneumatized and the transverse canal connecting the right and left middle ear cavities passes through it"].

The origin and adaptive significance of the median pharyngeal system of cavities is poorly understood. It has been recognized in several archosaurs but its function remains unclear (e.g., Witmer and Ridgely, 2009). Contrary to *C. crocodilus* and *A. mississippiensis*, the median pharyngeal recess in *M. nativus* remains paired in almost all its extension and only connects its symmetrical tube near the external ventral opening. As a result, the horizontal tube that connects both lateral pharyngotympanic recesses present in *C. johnstoni* (Witmer et al., 2008) is absent in *M. nativus* (Fig. 4B,C,E). The median pharyngeal sinuses represent a poorly known group of sinuses (Witmer and Ridgely, 2009), which probably derive from a diverticulum of the pharynx separate from the middle ear sac (Witmer and Ridgely, 2009), producing two typical sinuses, both median in position: the subsellar and basisphenoid recesses. The dorsorostral projection that pneumatizes the basisphenoid corresponds to the basisphenoid recess which has no communication with the tympanic system. This recess shows a very complex and intricate morphology, but if this condition is a juvenile feature seems to be speculative. There is no evidence of a subsellar recess.

Interpretations About the Soft Tissues of *Mourasuchus* and Their Significance

The most peculiar morphological features of *M. nativus* to be discussed are the anatomical arrangements of the adductor musculature, the correlated bony structures of attachment (such as the robust quadrate bridge), and the inferred vasculature emerging from the dorsotemporal fossa circumscribing the transverse squamosal eminences (Fig. 6).

Although the anatomy of jaw muscles of living alligatorids follows the same general pattern, there are some specific differences on the attaching areas and the fiber inclinations of the muscles, related with minor differences on the skull morphology among taxa (Bona and Desojo, 2011). To interpret the disposition of jaw muscles in *M. nativus*, we used multiple criteria including the attachment areas and the orientation of the trigeminal nerve osteological correlates (see Holliday and Witmer, 2007). As stated above, *Mourasuchus* is peculiar because of its flat and elongate skull, wide rostrum, slender lower jaw, and the huge, dorsally oriented infratemporal fenestra, bounded by the laterally expanded jugal, quadratojugal, and quadrate. The flat and wide temporal region and the lateral orientation of the ventral surface of quadrate indicate a derived position of the jaw musculature. The ventral surface of the quadrate is more laterally oriented than in other caimans, generating a different orientation of crest "A" and "B" and thus mAME and mAMP. The fibers of the mAME (Fig. 6A) would be more horizontally oriented than in extant crocodiles, passing from the lateral wall of the skull to the dorsal aspect of surangular bone and transiliens cartilage (Iordansky, 1973; Bona and Desojo, 2011). The fibers of the mAMP (Fig. 6A) would have been more caudally directed, passing from the caudal portion of the lateral skull wall to the medial border of the articular, the medial margin of the angular, the medial area of the surangular, and the caudal portion of the transiliens cartilage (Iordansky, 2000; Bona and Desojo, 2011). The different orientations of these adductor muscles are consistent with that of the V_2 and V_3 trigeminal branches

(rostrally and caudally oriented, respectively), inferred by the outline and the disposition of the huge trigeminal fossa (Fig. 3C,D).

The general morphological pattern of *Mourasuchus* resembles that of some rare Cretaceous crocodyliforms such as *A. witmeri* (Holliday and Gardner, 2012). As the authors pointed out, in this species, the mAMEP is oriented more horizontally compared with that of other crocodyliforms, and mAMEM appears to be much larger relative to those of other crocodyliforms. As in *M. nativus*, the lateral opening of the trigeminal fossa is large and bilobate, indicating a rostral and caudal directed V_2 and V_3 trigeminal branches.

In *M. nativus*, the trigeminal fossa is huge and divided by a conspicuous bony bridge from the quadrate separating V_2 and V_3 openings similar to that found in some large crocodylians (*Crocodylus palustris*; Holliday and Witmer, 2009, Fig. 4C) (Figs. 3D, 5). This quadrate bridge is absent in other giant caimanines as *Mourasuchus*'s sister taxon *Purussaurus*, and thus not associated with a huge body size. The absence of braincases preserved in three dimensions of other species of *Mourasuchus* does not allow compare this character between the genus.

The presence of a large trigeminal fossa indicates either the presence of a large trigeminal ganglion but also possibly the hypertrophy of surrounding trigeminal vasculature. Although the trigeminal fossa extends into the normal attachment region of mAME, the robust quadrate bridge would have permitted the musculature to maintain potentially lost attachment surface area (Fig. 6A).

Together with the peculiar stomatosuchids, a poorly represented clade of Cretaceous giant and flat-snouted crocodyliforms (Sereno and Larsson, 2009; Holliday and Gardner, 2012), *Mourasuchus* present one of the most peculiar skull morphotypes of crocodyliforms. *A. witmeri* from the Late Cretaceous of Morocco is characterized by an especially flat skull, adaptations for strong jaw opening, and what appears to be a cranial, vascular integumentary structure at midline on the skull roof (Holliday and Gardner, 2012). As in that species, there is evidence of superficial vascularization on the head in *M. nativus*, such as the marked vascular grooves associated with the lobed supratemporal fenestrae but surrounding in this case the squamosal eminences (Fig. 6B; see below). The huge posttemporal and cranioquadrate canals and the large openings associated with the passage of blood vessels (e.g., posttemporal fenestra and foramen vagus) indicate that the vascular system of this species was capable of transmitting a large volume of blood, potentially related to a physiological mechanism such as thermoregulation. As Holliday and Gardner (2012) pointed out, potential roles for vascularized tissues on the skull roof could be related to a thermoregulatory adaptation, given that the temporo-orbital vessels communicate with the encephalic vessels and ophthalmic rete.

The conspicuous bony eminences and distinctive cranial ornamentation in *M. nativus* may also be display structures. Comparing both the holotype (MLP 73-IV-15-8) and the specimen MLP 73-IV-15-9 (which is a subadult animal), Gasparini (1985) concluded that their different sizes were related to sexual dimorphism and that the huge "horns" were present in males and related to sexual behavior. However, the horn size also increases with the skull size and thus may simply be ontogenetic variation. Finally, this bony ornamentation may be associated with

the significant amount of superficial vasculature associated with the skull roof (Fig. 6), a concept forwarded by Gasparini (1985) for the genus "*Carandaisuchus*."

Despite those morphological peculiarities, feeding behavior of *M. nativus* requires further discussion. Historically, species of *Mourasuchus* has been seen as filter-feeder animals (e.g., Langston, 1965: 73–74; Riff et al., 2010); however, there is not any biomechanical study to support that hypothesis. Inferences in feeding biomechanics in *Mourasuchus* remain challenging because of the lack of key cranial material such as teeth, postdentary mandible, and hyoid. *Mourasuchus* has been inferred to be a filter-feeder (e.g., Langston, 1965: 73–74; Riff et al., 2010). However, there are no biomechanical studies to support this hypothesis.

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