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Caiman gasparinae sp. nov., a huge alligatorid (Caimaninae) from the late Miocene of Paraná, Argentina

PAULA BONA and ARIANA PAULINA CARABAJAL

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Morphological studies of South American alligatorids are scarce, and the phylogenetic relationships within Caimaninae are poorly understood. In this context, systematic revision and detailed morphological description of the enigmatic Argentinean Miocene caimanines are highly relevant. The current record is characterized by numerous species within the genus *Caiman*, although morphological disparity remains unclear. Here, we describe *Caiman gasparinae* sp. nov., which is one of the largest known *Caiman* species from the late Miocene of Argentina. Similar to other *Caiman* species and *Melanosuchus*, the new taxon has orbits larger than the infratemporal fenestrae and small supratemporal fenestrae that are not lost, as in *Paleosuchus*. Together with the absence of conspicuous rostral crests, the shape of the snout distinguishes *C. gasparinae* from *Melanosuchus*. *Caiman gasparinae* can be further distinguished using other cranial characters, such as a broad and low rostrum with a narial opening oriented dorsally, a relatively long interpremaxillary suture, and the occipital surface of the braincase with a poorly developed crista tuberalis exposing the carotid foramina in lateral view.

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Key words: Alligatoridae, *Caiman*, Neogene, South America, Argentina

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THE most complete fossil record of South American crocodyliforms derives from the Miocene pan-Amazonian exposures of La Venta (Colombia), Urumaco (Venezuela), Acre (northwestern Brazil), Fitzcarrald (Peru) and Paraná (northeast Argentina: Fig. 1). These crocodylians (*sensu* Benton & Clark 1988) range stratigraphically upwards from the early Miocene and provide a key perspective on the evolutionary and biogeographical history of South American caimanines and alligatoroids. In particular, the diversity of Miocene gavialids and caimanines in South America was astonishingly high during the Miocene, probably as a result of change in the Western Amazonian wetland from a lacustrine (Pebas System) to fluvial or fluvio-tidal system (Acre System) associated with the Andean orogeny (Riff *et al*. 2010, Bona *et al*. in press).

Northeastern Argentina preserves the most austral late Miocene South American crocodilian fauna, including an unusually high diversity of *Caiman* species relative to other more northern coeval localities (Bona & Riff 2010). The Paraná fossils have been known from the 'Conglomerado Osífero' (Ituzaingó Formation, Herbst 1971) since the middle to late 19th century. However, the taxonomic history of Argentinian Neogene crocodyliforms remains complex (Bravard 1858, Burmeister 1883, Ambrosetti 1887, Scalabrini 1887, Rovereto 1912, Rusconi 1933, 1935, Patterson 1936, Langston 1965, Gasparini 1968, 1973, 1981, 1985, 1996, Langston & Gasparini 1997), and only a few systematic revisions or adequate descriptions have been published (Gasparini 1973, Bona *et al*. 2013, in press). Recently, Bona *et al*. (in press) recognized the gavialoid *Gryposuchus neogeaeus*, and the caimanines *Mourasuchus nativus, Caiman australis, C. latirostris* and *C. lutescens* from Paraná, suggesting that southern Amazonia had been the radiation center for *Caiman* spp. during the Miocene. For this reason, the Paraná crocodylian record is crucial for understanding morphological variation within caimans and testing phylogenetic relationships: DNA sequence analyses of mitochondrial cytochrome b, and nuclear Recombination Activating Gene 1 and the myelocytomatosis oncogene (Hrbek *et al*. 2008) support monophyly of *Caiman*, yet morphology implies generic paraphyly (Norell 1988, Poe 1997, Brochu 1999, 2003, 2010, 2011, Bona *et al*. in press).

Although most of the Paraná remains are extremely fragmentary, some previously undocumented, proportionately large specimens preserve diagnostic cranial components, such as the braincase and rostrum. Therefore, the main goal of this contribution is to review these specimens, here referred to a new *Caiman* species, *C. gasparinae* sp. nov. In addition, we compare the anatomy of the braincase among caimanines and, finally, discuss the

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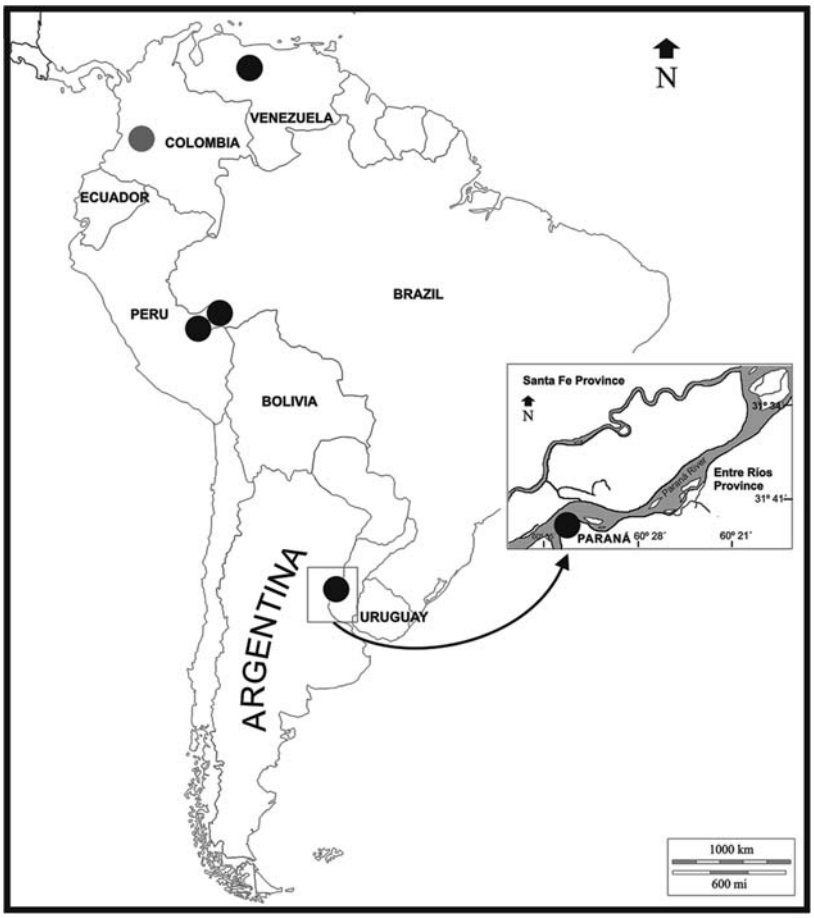

Fig. 1. Location map showing the distribution of Miocene South American Caimaninae. Black circles indicate main late Miocene localities and grey circles indicate main mid-Miocene localities.

implications of our results to increase our understanding about relationships within this group.

Material and methods

Miocene caiman skulls housed at the Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN) were examined. Comparative material of extant species of *Caiman* (88 specimens), *Paleosuchus* (six specimens), *Melanosuchus* (30 specimens) and *Alligator* (three specimens) were also studied; these are deposited in the Zoologische Staatssammlung, Munich (ZSM; Germany), in the MLP and in the MACN. Miocene *Caiman* specimens figured by Langston (1965), Medina (1976), Brochu (1999) and Sánchez-Villagra & Aguilera (2006) were also considered.

To reconstruct soft tissue of endocranial structures in MLP-73-IV-15-1 (Fig. 2), a latex cast was prepared to reveal part of the left inner-ear cavity (Figs 3, 4A–C, 5). Comparative latex endocasts were also made for extant *Caiman yacare* and *C. latirostris* (adult and juvenile specimens, respectively; Fig. 6; Table 1). Assessments of the endocranial structures of other extant crocodylians (Table 1) were based on published descriptions of *Caiman crocodilus* (available information published in http://www.digimorph.org), *Crocodylus siamensis* (Kawabe *et al*. 2009), *C. johnstoni* (Witmer *et al*. 2008), *C. moreleti* (Franzosa 2004) and *Alligator mississippiensis* (Kawabe *et al*. 2009, Witmer & Ridgely 2009). Endocranial volumes of *Caiman* species were calculated by relative water displacement. Measurements of the partial cast of the left labyrinth are listed in Table 2.

Systematic palaeontology

Order CROCODYLIA Gmelin, 1789 (*sensu* Benton & Clark 1988)

Family ALLIGATORIDAE Cuvier, 1807 (*sensu* Norell *et al*. 1994)

Caiman Spix, 1825

Caiman gasparinae sp. nov. (Fig. 2)

1887 *Crocodylus paranensis* Scalabrini, p. 37.
1912 *Alligator? ameghinoi* Rovereto, pp. 360–367 (in part), fig. 16a.
1933 *Xenosuchus paranensis ameghinoi* Rusconi, pp. 78–80 (in part), fig. 9.
1965 *Caiman* sp.; Langston, pp. 121–122.

Holotype. MLP-73-IV-15-1; skull fragments represented by a rostrum with articulated fragments of premaxillae, maxillae, nasals, left lacrymal and a partial braincase lacking the basicranium (Fig. 2A–F).

Referred material. MACN PV 5555; fragment of right premaxilla (Fig. 2G).

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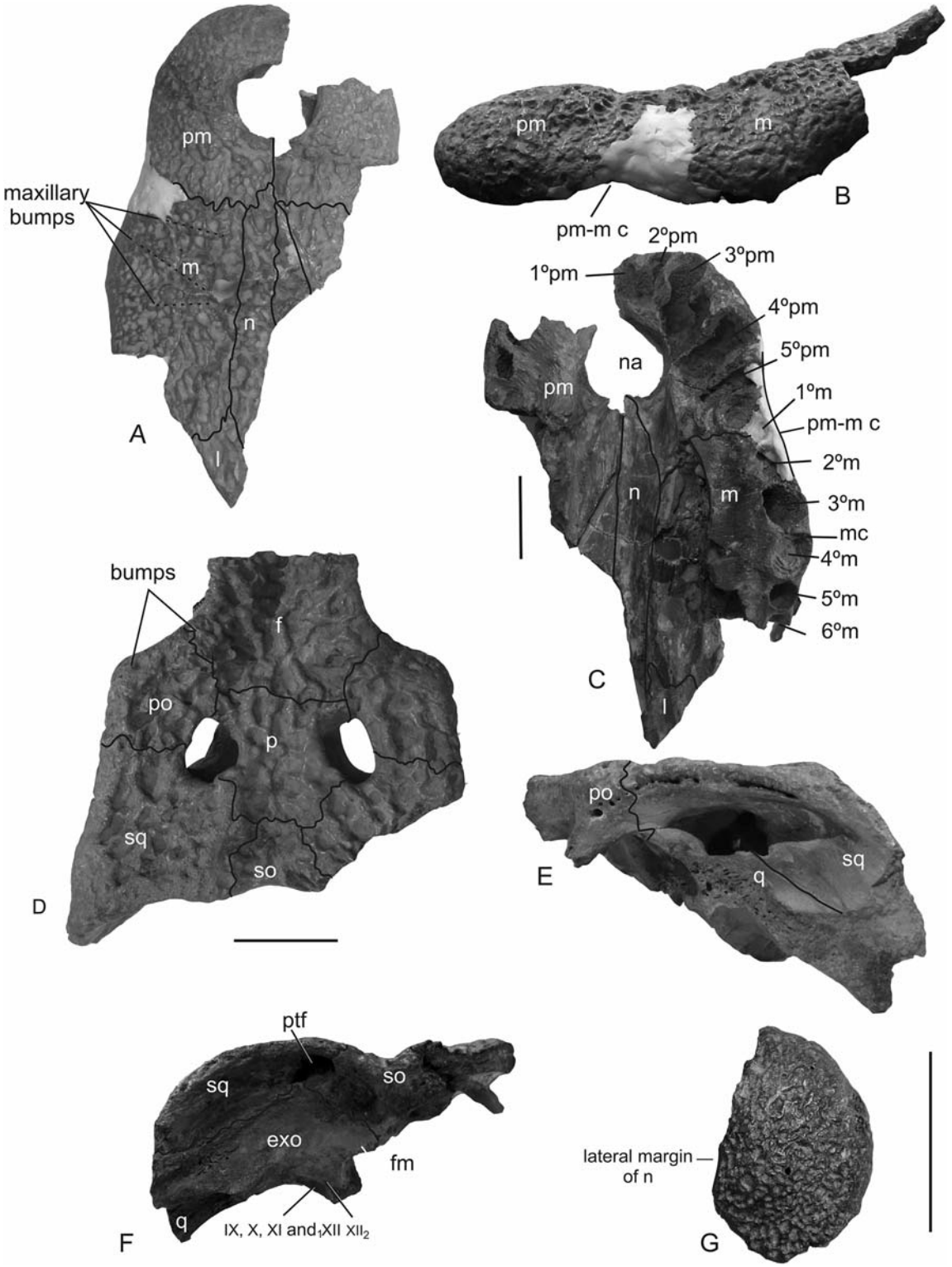

Fig. 2. Cranial osteological morphology of *Caiman gasparinae* sp. nov. MLP-73-IV-15-1 (**A–F**) and MACN PV 5555 (**G**). Snout in dorsal (**A**), left lateral (**B**) and ventral (**C**) views. Braincase in dorsal (**D**), left lateral (**E**) and occipital (**F**) views. Fragment of right premaxilla in dorsal (**G**) view. Abbreviations: exo, exoccipital–opistotic complex or otoccipital; fm, foramen magno; fr, frontal; mx, maxillar; n, narina; na, nasal; pa, parietal; pmx, premaxillar; pmx-mx c, premaxillar–maxillar curvature; po, postorbital; ptf, postemporal foramen; q, quadrate; so, supraoccipital; sq, squamosal; 3°–4° pmx, premaxillar alveoli; IX–XII cranial nerves foramina. Scale bar = 5 cm.

Occurrence. Margin of Paraná River, in the area of Paraná (Entre Ríos province, Argentina; Fig. 1); Ituzaingó Formation (Herbst 1971), upper Miocene (Brandoni & Scillato-Yané 2007, Brandoni 2010).

Etymology. This species is named for Dr Zulma Brandoni de Gasparini, paleoherpetologist at the Facultad de Ciencias Naturales, MLP, who dedicated most of her career to the study of extinct crocodyliforms.

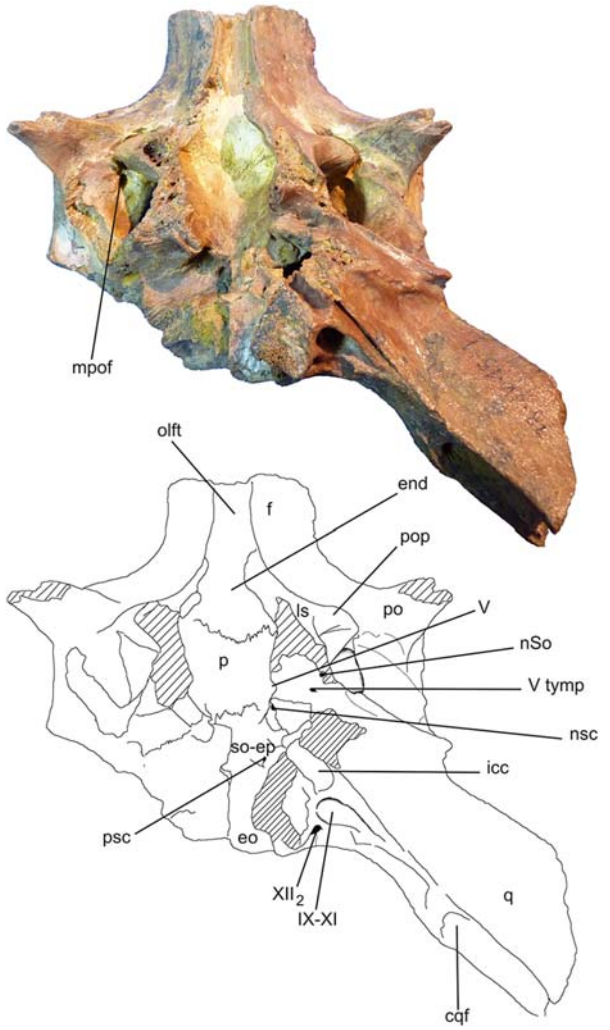

Fig. 3. Braincase of *Caiman gasparinae* sp. nov. (MLP-73-IV-15-1). Ventral view. Abbreviations: cqf, cranioquadrate foramen; endo, endocranial cavity; eo, exoccipital-opisthotic complex; f, frontal; icc, internal carotid canal; ls, laterosphenoid; mpof, medial postorbital foramen; nSo, supraorbital nerve; olft, olfactory tract; p, parietal; po, postorbital; pop, postorbital process of laterosphenoid; psc, posterior semicircular canal of inner ear; q, quadrate; so-ep, supraoccipital–epiotic complex; V tymp, tympanic branch of the trigeminal nerve; IX–XII, cranial nerves. Not to scale.

Diagnosis. Large, broad-snouted caiman with a low rostrum; narial opening oriented dorsally and broadly distanced from the anterior margin of premaxilla; interpremaxillary suture long with respect to the intermaxillary suture. Occipital surface of the braincase with the poorly developed crista tuberalis exposing the carotid foramen in lateral view. The carotid foramen is bounded by the crista tuberalis only posteriorly.

Description and comparisons

Skull. The general morphology of the skull, especially its outline, bone contacts and proportions are similar to other extant *Caiman* species (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232).

Sculpturing of the cranial bones is characterized mainly by crests and depressions that form an irregular surface of marked ridges; these bound interconnected pits to create incomplete 'cell-like' shapes. There are also some ornamental bumps (bony convexities) on the maxilla and the skull table. This pattern of interconnected cells is atypical of extant caimans, in which sculpturing on the rostral part of the premaxilla is distinct from the otherwise smooth and pitted surface of the rest of the skull. The irregular ornamentation extends further rostrally in *C. gasparinae* sp. nov. than in extant caimans, such as *C. latirostris* and *C. yacare* (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232; Fig. 2A, G).

The antorbital section preserved in MLP-73-IV-15-1 belongs to a large, broad-snouted caimanine with a low and short rostrum (Fig. 2A). As in other adult caimans there is a marked premaxillary-maxillary curvature of the lateral margin of the snout in dorsal and lateral views (Fig. 2A, B).

The dermal bones of the skull roof overhang the rims of the relatively small supratemporal fenestrae on the skull table; a morphological feature present in adult individuals of crown *Caiman* (Brochu 1999, p. 68). As in *Caiman* (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232; and supplementary information) and *Melanosuchus niger* (e.g., ZSM 130/1911, ZSM 27/1911, ZSM 87/1911, ZSM 76/1911, ZSM 85/1911, ZSM 84/1911, ZSM 77/1911, ZSM 86/1911, ZSM 83/1911, ZSM 91/1911, ZSM 68/1911, ZSM 14/1911, ZSM 89/1911, ZSM 70/1911, ZSM 80/1911, ZSM 79/1911, ZSM 90/1911, ZSM 73/1911, ZSM 74/1911, ZSM 75/1911, ZSM 3/1911, ZSM 67/1911, ZSM 46/1911), the orbits are larger than the infratemporal fenestrae, and the supratemporal fenestrae are small but not absent as in *Paleosuchus*. The supratemporal fenestra is oval, with shallow grooves at the posterior and anterior margins. The posterior grooves are oriented both posteromedially and posterolaterally; in contrast to the anterior grooves extending anterolaterally and medially (Fig. 4C). The lateral margins of the skull table diverge caudally. The dorsal surface of the skull roof is deeply concave along its midline, especially on the frontal and the supraoccipital. Ornamental bumps are also present at the caudal and caudomedial margins of the orbits (Fig. 2D). The edges of the orbit and both the lateral and caudal margins of the skull table are strongly thickened.

Premaxilla. The premaxillae are laterally and rostrally expanded in dorsal view. The bony nasal aperture

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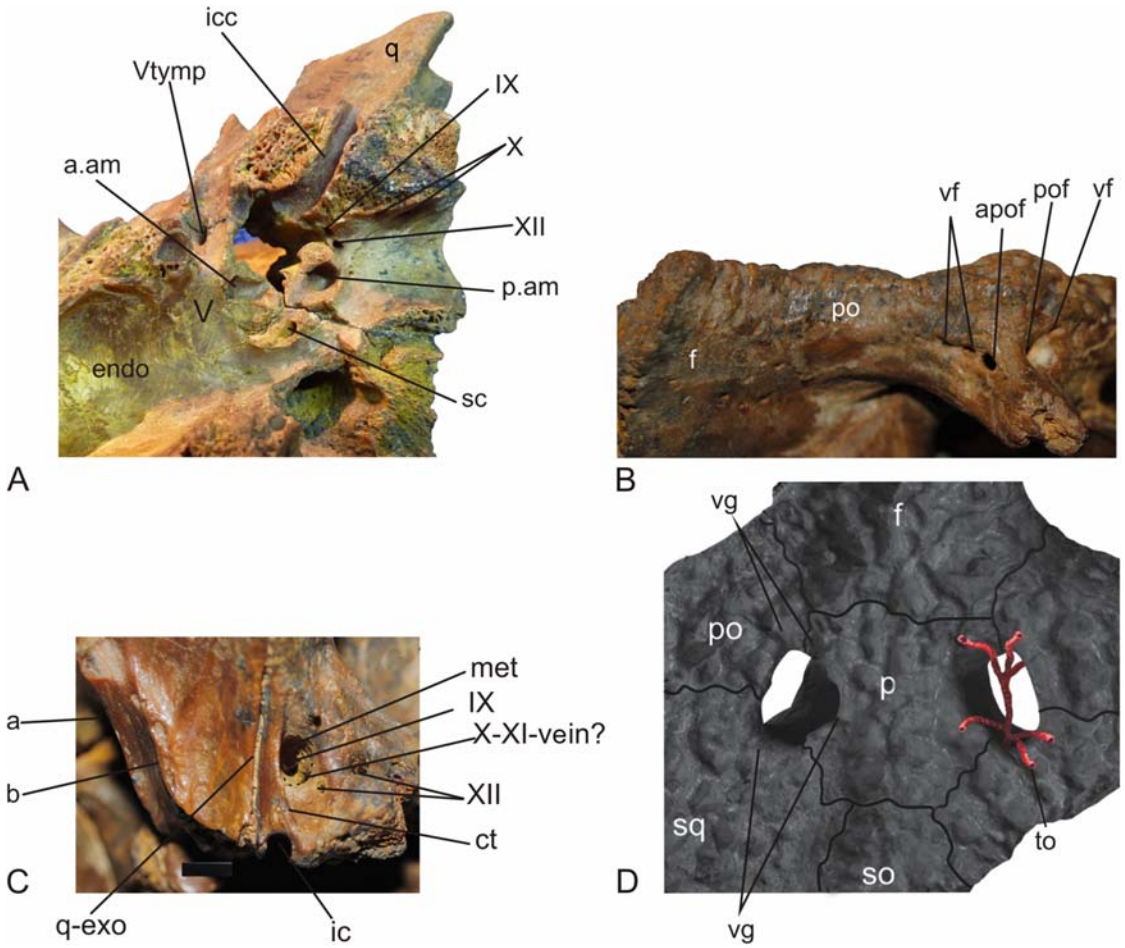

Fig. 4. Details of braincase of *Caiman gasparinae* sp. nov. (MLP-73-IV-15-1). Ventral (**A**) anterolateral (**B**) and dorsal (**D**) views. Detail of otoccipital in posteroventral view (**C**). Abbreviations: a, quadrate crest A; a.am, anterior ampulae of inner ear: b, quadrate crest B; ct, crista tuberalis; endo, endocranial cavity; f, frontal; ic, internal carotid foramen; icc, internal carotid canal; met, metotic foramen for cranial nerves IX–XI and jugular vein; p.am, posterior ampulae of inner ear; po, postorbital; pof, postorbital foramina; q, quadrate; sc, semicircular canal of inner ear; so, supraoccipital; sq, squamosal; to, temporoorbital vessels; vf, vascular foramina; vg, vascular grooves; V, IX–XII, cranial nerves. V tymp, tympanic branch of trigeminal nerve. Not to scale.

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comprises a single sub-circular opening situated dorsally and separated from the anterior margin of the premaxilla by a distance approximately equal to its antero-posterior diameter (Fig. 2A). In lateral view, the premaxillae are low, especially posterior to the narial opening (Fig. 2B). In dorsal view, the premaxillae contact each other posteriorly and exclude the nasals from the posterior margin of the naris. Although the contact of the nasal with the naris varies intraspecifically in extant *Caiman* species (Bona & Desojo 2011), the interpremaxillary suture is relatively long in *C. gasparinae* (Fig. 2A).

In palatal view (Fig. 2C), five premaxillary alveoli are preserved on the left side of the rostrum, showing the same relative size pattern as *Caiman* and *Melanosuchs* species (i.e., the largest alveoli are the 3rd and 4th, with 4th $\geq$ 3rd; Bona & Desojo 2011). Compared with extant *Caiman* species (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232), MLP 73-IV-15-1 has reduced interalveolar spaces, except for the one between the 3rd and 4th alveoli.

Nasal. The nasal bone is similar to that of *Caiman yacare* (e.g., MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603), sub-rectangular with straight and parallel lateral margins that taper rostrally and caudally (Fig. 2A). In contrast to other broad-snouted caimans, such as *C. latirostirs* (e.g., MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232), the nasals of *C. gasparinae* sp. nov are relatively narrow (compared with the broad maxilla) and not involved in the widening of the snout. As observed in several *Caiman* species (e.g., *C. yacare:* MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603), the nasals are separated from the narial openings in dorsal view.

Maxilla. The maxilla is anteroposteriorly elongated. Maxillary crests are absent in this species but common in extant broad-snouted caimans (i.e., *C. latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047,

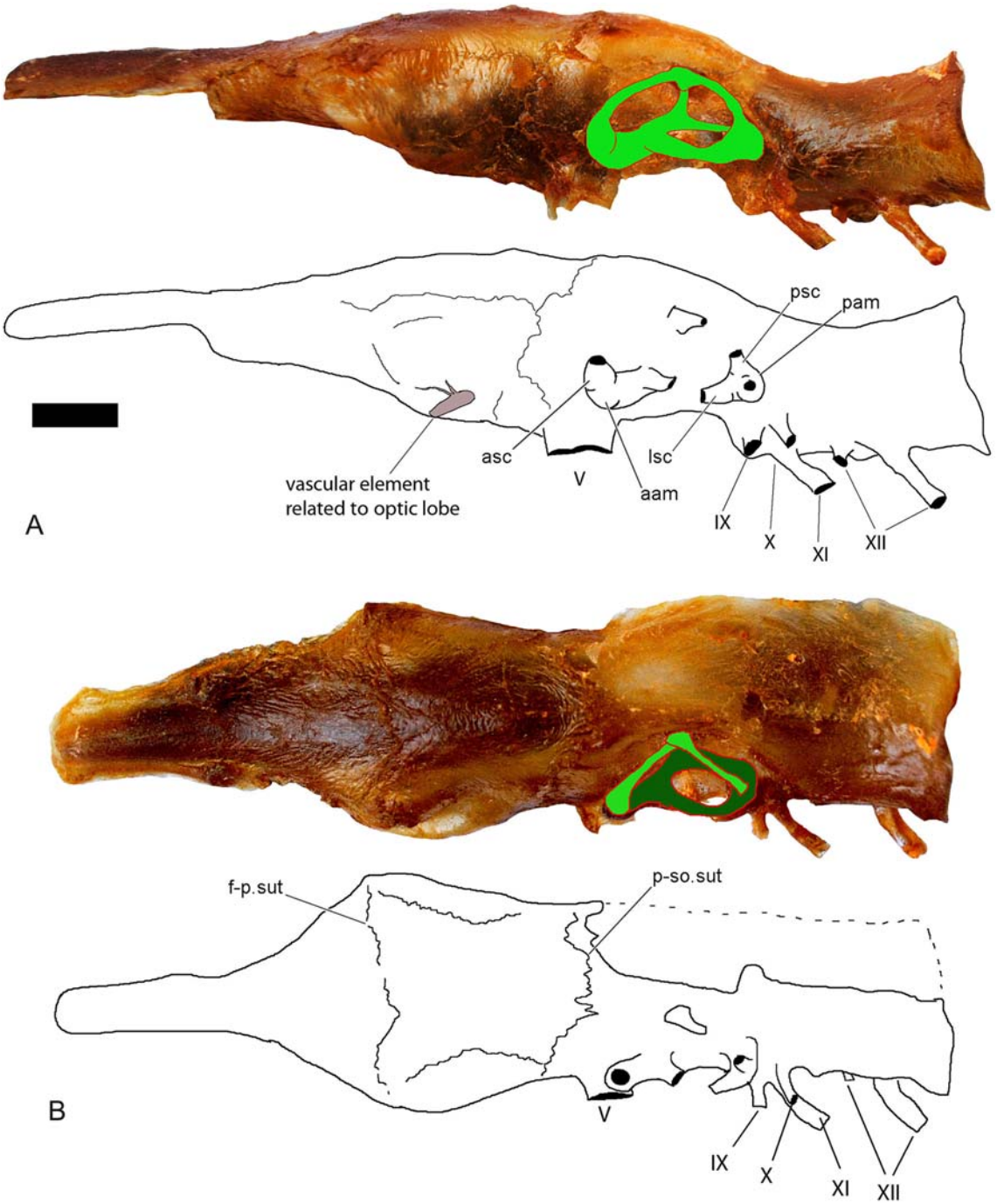

Fig. 5. Latex cranial endocast of *Caiman gasparinae* sp. nov. (MLP-73-IV-15-1). Endocast photo, inner ear reconstruction, and line-drawings in lateral (**A**) and dorsal (**B**) views. Abbreviations: aam, anterior ampulae; asc, anterior semicircular canal; cer, cerebral hemisphere; f-p.sut, frontoparietal suture impression; lsc, lateral semicircular canal; med, medulla oblongata; olft, olfactory tract; p-so suture impression; pam, posterior ampulae; psc, posterior semicircular canal; sut, suture impression; 1, vascular element associated to the optic lobe; V, IX–XII, cranial nerves. Scale bar = 10 mm.

MACN 30610, MACN 15232). However, there are four isolated, elongated and caudomedially to rostrolaterally oriented bumps on the maxilla (Fig. 2A). In palatal view, six maxillary alveoli are preserved on the left side of the rostrum (first to fifth are complete and the sixth incomplete) and follow the general *Caiman* pattern of antero-posterior alveolar diameter and diastema length (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232; Fig. 2C). In *Caiman gasparinae*, the 3rd and 4th alveoli are the largest (see discussion below) with similar antero-posterior diameter and situated at the maxillary curvature, which is strongly pronounced in both dorsal and lateral views (Fig. 2A, B).

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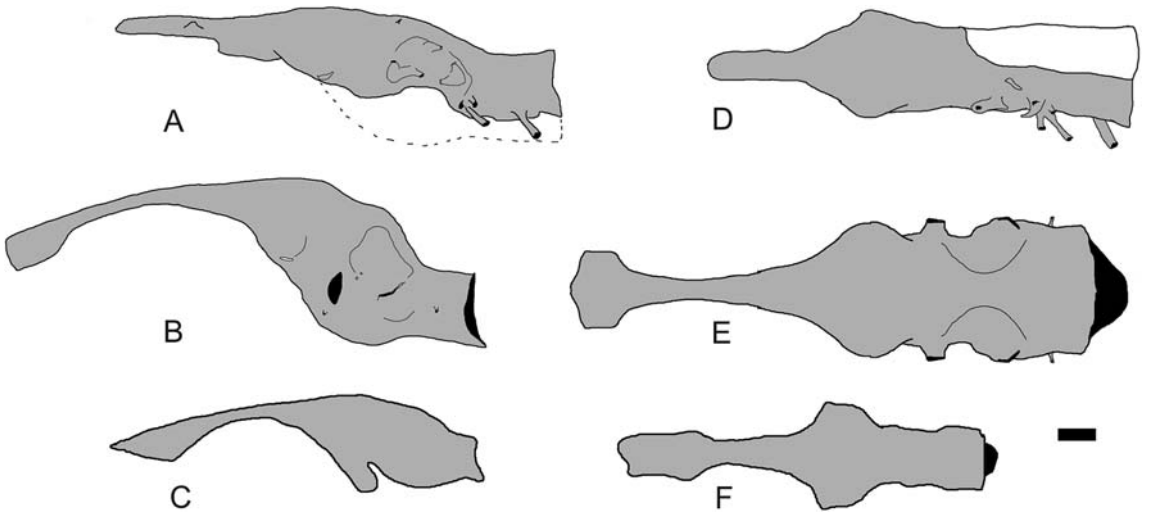

Fig. 6. Cranial endocasts of *Caiman* and *Crocodylus* species. **A, D**, *Caiman gasparinae* sp. nov., MLP-73-IV-15-1; **B, E**, *Caiman yacare*, MLP 603; **C, F**, *Crocodylus johnstoni*. Lateral (**A, B, C**) and dorsal (**D, E, F**) views. (C, F, after Witmer *et al*. 2008). Scale bar = 10 mm.

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Taxon	brain.w	endo.l	ol.tr.w	me.h	lab.w	References
Caiman gasparinae	30	73	8	16♦	20	MLP-73-IV-15-1, this paper
Crocodylus siamensis	26.9	53	5	?	?	Kawabe *et al*. (2009)
Crocodylus johnstoni	27	50	8.9	10.8	?	Witmer *et al*. (2008)
Crocodylus moreleti	27	–	5.8	12.5	15.8	Franzosa (2004)
Alligator mississippiensis	20	47	7.5	?	?	Kawabe *et al*. (2009), Witmer & Ridgely (2009)
Caiman yacare	30	55	7	17	13♦	MLP-603, this paper (Fig. 6)
Caiman latirostris	23	40	5	10	13	MLP-601

Table 1. Endocranial measurements in studied extinct and extant crocodiles (in mm). Abbreviations: brain.w = maximum width at the cerebral hemispheres; endo.l = length of the endocast without the olfactory tract; ♦ = approximately; ol.tr.w = proximal olfactory tract width; me.h = height of the medulla oblongata; lab.w = width of the labyrinth.

	External diameter	Internal diameter	Tube diameter
asc	14.5	9.3	2
psc	12.4	7.8	1.5
lsc	11	7	2

Table 2. Caiman gasparinae sp. nov. (MLP-73-IV-15-1). Inner-ear measurements (in mm). Abbreviations: asc, anterior semicircular canal; lsc, lateral (horizontal) semicircular canal; psc, posterior semicircular canal.

Parietal. As in other crocodylians (e.g., *Gavialis gangeticus, Caiman crocodilus, Crocodylus acutus*; Iordansky 1973), both parietal bones are fused at the midline, forming the anteromedial and medial margins of the supratemporal fenestrae and the medial walls of the supratemporal fossae. The parietal connects anteriorly to the frontal bone, laterally to the postorbital and squamosal, and posteriorly to the supraoccipital. The supraoccipital and the parietal contribute to a shallow depression that is more pronounced at the squamosal surface.

Frontal. As in other eusuchian crocodylians (e.g., *Gavialis gangeticus, Caiman crocodilus, Crocodylus acutus*; Iordansky 1973), both frontal bones are fused at the midline, forming a single bone that medially delimits part of the orbit. Only the posterior section is preserved in MLP 73-IV-15-1. The ventral surface has a medial groove for the passage of the olfactory tract. It contacts the parietal posterio-medially, and the postorbital posterio-laterally (Fig. 2A).

Postorbital. The postorbital bar is subtriangular in section in lateral view (Fig. 2E), similar to some extant *Caiman* species (e.g., *C. yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603). In MLP 73-IV-15-1, there is a conspicuous duct (perhaps a vascular postorbital duct) that runs

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mediolaterally and opens medially within the supratemporal fossa, and laterally at the dorsolateral surface of the postorbital pillar through the postorbital foramen. The medial opening is bounded by the laterosphenoid and the quadrate (Fig. 3). The lateral postorbital foramen in *Caiman gasparinae* communicates with the orbital space region through several foramina along the posterior margin of the orbit (Fig. 4B). Extant caimans (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232) commonly have a single anterior foramen of the postorbital at the orbital rim, which probably corresponds to the largest of the foramina present in *C. gasparinae*.

Squamosal. The squamosal, together with the postorbital, ventrally delimits the supratemporal fenestra. It contacts the postorbital and parietal dorsally, the supraoccipital and exoccipital posteroventrally, and the postorbital and quadrate anteroventrally. In dorsal view, the surface ornamentation comprises deep cells; the lateral and posterior margins of the bone are also expanded. The occipital surface is dorsoventrally elevated, providing a large attachment area for the mandibular depressor and the axial neck muscles (Fig. 2F).

Supraoccipital. As in other caimanines, the supraoccipital extends over the dorsal surface of the skull table (Brochu 1999). Its dorsal surface is deeply concave (especially in occipital view; Fig. 2D, F). In occipital view, the supraoccipital reveals a median vertical crest that separates two distinct oval depressions for the attachment of the transversospinalis capitis muscle (mTSC; *sensu* Cleuren & De Vree 2000).

Laterosphenoid. Both laterosphenoids are incomplete in MLP73-IV-15-1. In ventral view, the laterosphenoid forms the anterolateral wall of the braincase and extends dorsally forming the anteroventral area of the medial wall of the supratemporal fossa. The pyramidal corpus (Holliday & Witmer 2009) is preserved on the left side and is Y-shaped, with a slightly concave rostral margin (Fig. 3). The robust anterior ramus is projected ventromedially. It contacts posteriorly the quadrate and prootic and dorsolaterally the pterygoid, the frontal and postorbital.

Exoccipital-opisthotic complex. In occipital view, otoccipitals and squamosals form a high and dorsoventrally concave surface with a strongly convex dorsal margin for attachment of the neck muscles (Fig. 2F). The crista tuberalis of *C. gasparinae* (MLP 73-IV-15-1) is poorly developed, exposing the carotid foramen in lateral view (Fig. 4D). The carotid canal has a similar trajectory, as in other caimans (Bona *et al*. 2013), but the carotid external foramen is bounded by the crista tuberalis posteriorly instead of anteriorly (Fig. 4D). Furthermore, in other caimans (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232) the crista tuberalis includes an extension of the quadrate (absent in *C. gasparinae*), separating the lateral and posterior faces of the braincase and obscuring observation of the metotic foramen in lateral view (Fig. 4D).

Three foramina occur lateral to the foramen magnum: two correspond to the branches of CN XII to the metotic foramen (providing the exit for cranial nerves IX–XI and the internal jugular vein; see Gower & Weber 1998 and discussion therein). The relative positions of these foramina are similar to other caimans (Bona & Desojo 2011). The external expression of the metotic foramen is a deep recess bounded medially by the exoccipital and laterally by the opisthotic. Two smaller foramina are evident within this recess (Fig. 4D). The most ventrocaudal foramen is for the exit of CN X, XI and the jugular vein. The rostrodorsal foramen is probably for the exit of CN IX only. Endocranially, the three nerves have independent internal openings (see below; Fig. 4A).

Quadrate. Only the proximal section of the quadrate is preserved in MLP 73-IV-15-1. As in other crocodylians (e.g., *Gavialis gangeticus, Caiman crocodilus, Crocodylus acutus*; Iordansky 1973) the quadrate extends posterolaterally in the posterior portion of the skull and is sutured to the surrounding bones, with the exception of the otic sinovial articulation (see Holliday & Witmer 2008; Fig. 3). As in other crocodylians (e.g., *Gavialis gangeticus, Caiman crocodilus, Crocodylus acutus*; Iordansky 1973), the quadrate contacts the exoccipital and squamosal dorsally, and the laterosphenoid and prootic anteriorly. Posteriorly, the quadrate contacts the exoccipital–ophisthotic complex, forming a suture that does not reach the crista tuberalis (Fig. 4C, and see below for discussion and comparison of this condition). A small section of crests A and B (*sensu* Iordansky 1973) is evident on the ventral surface. These crests taper posterodorsally, delimiting a triangular attachment area that protrudes into the adductor chamber.

Endocast and skull recesses. The incomplete braincase exposes the endocranial and inner ear cavities in ventral view. The preserved endocranial impression (Fig. 5) measures 76 mm from the foramen magnum to the base of the olfactory tract. The olfactory tract is 13 mm wide and 38 mm long. Vascular impressions on the ventral surface of the frontal suggest that the cerebral hemispheres filled most of the cavity (Evans 2005); a feature not evident in extant *Caiman yacare* and *C. latirostris* (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN

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I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232). The maximum width of the endocranial cavity (36 mm) is at the level of the cerebral hemispheres, as in extant crocodylians (Table 1). The measured endocranial (minus the olfatory tract, which is particularly broad in caimanines: see Table 1 for comparisons) volume is 26 cm^3, slightly larger than that of *C. yacare* (Table 1)

The cerebral hemispheres of *C. gasparinae* are laterally rounded when viewed in dorsal aspect: this is compatible with *Caiman yacare* and *C. latirostris* (Fig. 6) but unlike the more pointed cerebral outline in *Crocodylus* spp. (Witmer *et al*. 2008, fig. 6.3B). The impression of a blood vessel runs ventrolaterally into the cerebral area of MLP 73-IV-15-1 (Fig. 5A). A similar vascular element occurs immediately posterior of the cerebrum, in *Crocodylus* (Witmer *et al*. 2008), *Caiman yacare* (MLP 603) and *C. latirostris* (MLP 601), whereas it runs behind a shallow protuberance located posteroventrally to the cerebrum (Fig. 5A) in *Caiman gasparinae*.

Although incomplete, MLP 73-IV-15-1 shows that the angles formed by the hindbrain, midbrain and forebrain are similar to those of *Crocodylus* (Witmer *et al*. 2008), and less marked than in *Caiman yacare* (MLP 603) and *C. latirostris* (MLP 601; Fig. 6). Thus, the cranial endocast is sub-horizontal, with the dorsal margin of the medulla oblongata (horizontally oriented) aligned with the base of the olfactory tract (Fig. 6A). In extant caimans (e.g., MLP 601, MLP 603), the dorsal border of the medulla is ventral to the olfactory tract (Fig. 6B, C). There is no evidence of a large dorsal longitudinal sinus as in *Crocodylus* (Witmer *et al*. 2008). Similarly, the optic lobes in the endocast of *C. gasparinae* display no marked separation of the cerebral hemispheres (evident elsewhere in *Crocodylus johnstoni*: Witmer *et al*. 2008) as occurs in *Caiman yacare* (e.g., MLP 603) and *C. latirostris* (e.g., MLP 601). This suggests an enlarged sphenoparietal sinus (Witmer *et al*. 2008), which obscures the dorsal morphology of the endocast in MLP 73-IV-15-1. The left dorsal head vein, that has a small diameter, is preserved posterior to the parietal-supraoccipital suture.

Cranial nerves. Only the dorsal margin of the canal for the trigeminal nerve (CN V) is preserved and measures 5.8 mm in diameter based on the latex endocast. Small foramina for the supraorbital and tympanic branches of the trigeminal nerve are also present on the left side of the braincase, together with the canal for the tympanic branch (plus some other vessels) on the right (Figs 4A, 5A). Two internal foramina (the posterior-most being the largest) for CN XII are observable (Fig. 5A), as are the passages for CN IX–XI. Internally, the latter leave the endocranial cavity through a common foramen (not housed within a crescentic depression as in *C. yacare*, e.g., MLP 603), although externally, the metotic fissure maintains two foramina that open into a deep recess (see above; Fig. 4D).

Inner ear. The semicircular canals of the labyrinth of both inner ears are exposed by fractures. (Fig. 5, Table 2). The labyrinth is 20 mm wide, 12 mm high and triangular with three semicircular canals, two of which are of sub-equal length (Fig. 5). As in other crocodylians (e.g., Rogers 1999, Walsh *et al*. 2009), the anterior ampulae is enlarged resulting in an antero-posterior distance of 3 mm between the confluence of the anterior and lateral semicircular canals. In dorsal view, the angle formed by the posterior and anterior semicircular canals measures approximately 100° (Fig. 5B).

Discussion

Caiman is the most diverse, but least known caimanine genus. Although the pre- and post-Miocene *Caiman* fossil record is poor, a considerable number of South American species are known from relatively complete material of middle and late Miocene age. In particular, the late Miocene taxa from Paraná (Argentina) are highly speciose (Bona & Riff 2010, Bona *et al*. in press) and thus provide an opportunity to explore both cranial morphology and its variability within the genus.

The right premaxillary component of *Caiman gasparinae* (MACN PV 5555) was originally used by Rovereto (1912), together with three isolated vertebrae and a mandibular fragment (1912, p. 364, fig. 6a), to erect the extinct species *Alligator? ameghinoi*. Rovereto (1912) did not assign a type, although Rusconi (1933) chose a dorsal vertebra from Rovereto's material to represent the lectotype of *Xenosuchus paranesis ameghinoi*, defined by its large size. Because no other discrete morphological characters were put forward, Langston (1965, p. 121) reassigned all 'original *paranensis* specimens as *Caiman*'. We clarify this taxonomy further herein by referring the diagnostic premaxillary fragment MACN PV 5555 (Fig. 2G), to a new taxon *C. gasparinae*.

The unpublished doctoral thesis of Brandoni de Gasparini (1973) also attributed MLP-73-IV-15-1 to the extant *Caiman latirostris* without description or justification. Nonetheless, this is morphologically compatible with both MLP 73-IV-15-1 and MACN PV 5555. Therefore, we recognize all of these fossils as belonging to *Caiman gasparinae*.

Taking all of these remains into account, *Caiman gasparinae* can be defined by the following combination of character states: a broad and low rostrum; narial opening oriented dorsally and substantially separated from the anterior margin of the premaxilla; interpremaxillary suture long in relation to the intermaxillary suture; and poor development of the crista tuberalis on the occipital surface of the braincase, thus exposing the carotid foramen in lateral view and bounding the carotid

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foramen posteriorly. The position, development and presence of the crista tuberalis varies widely among archosaurs, crocodyliforms and derived crocodylians (see Säve-Söderbergh 1947): an inconsistency reflected in the multitude of ascribed descriptive names (e.g., 'metotic strut,' Currie 1997; 'metotic process' Gower & Weber 1998; 'crista metotica,' Rauhut 2004). However, the position of the crista tuberalis in *C. gasparinae* (posterior to the carotid foramen) is unique within caimans. The interpremaxillary suture, which is long in *Caiman gasparinae*, is also present in some extant large-sized caimanines, such as the bizarre *Morasuchus* (Bona *et al*. 2013). The dorsal contact of nasals with the narial opening varies intraspecifically in extant caimans (e.g., MLP R 5040 specimen of *Caiman yacare* with nasals in contact; MLP 604 specimen of *Caiman yacare* with nasals not in contact). Nevertheless, the middle contact between both premaxillae is relatively shorter than in the Miocene species (Bona *et al*. 2013).

Other noteworthy features of the new caiman are the conspicuous grooves preserved at the posterior and anterior margins of the supratemporal fenestra in MLP 73-IV-15-1 (Fig. 4C). We interpret these shallow channels as vascular impressions of the temporoorbital vessels (*sensu* Sedlmayr 2002, fig. 10B), which probably communicated with blood sinuses located on the skull roof (Holliday & Gardner 2012, Bona *et al*. 2013). Similar anterolateral and posteromedial grooves occur in several caimanines: *Mourasuchus nativus* (Bona *et al*. 2013); *Caiman yacare* and *C. latirostris* (e.g., *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232). A posteromedial groove has likewise been reported in the extinct crocodyliforms *Aegisuchus witmeri* (Holliday & Gardner 2012), who suggested that concentration of vascularized tissues on the skull roof could confer a thermoregulatory advantage, given that the temporoorbital vessels communicate with the encephalic vessels and ophthalmic rete (see description above).

The generic assignment of *Caiman gasparinae* clarifies the osteological character state definition of *Caiman*. The original list of features provided by Spix (1825) are not exclusive of the genus, and in accordance, subsequent cladistic analyses advocated paraphyly (Norell 1988, Brochu 1999, 2003, 2010, 2011, Poe 1997). The disposition of bones around the supratemporal fenestrae in *Caiman gasparinae* clearly places this taxon within crown Caimaninae (Brochu 1999). In caimanines, the relative proportions of the orbit and supratemporal fenestrae are variable between genera. In *Purussaurus* the orbits are equal or sub-equal to the infratemporal fenestrae (Aguilera *et al*. 2006; figs 2, 3, 5 and 6), whereas in *Mourasuchus*, the orbits are smaller than the infratemporal fenestrae, and the supratemporal fenestrae are reduced (Price 1964, Langston 1965, Bocquentin-Villanueva 1984, Bona *et al*. 2013). In this way, the relative size between the temporal fenestrae and the orbits would represent a character that distinguishes *Caiman* from other genera in the crown group of caimanines. Nevertheless, this is probably a plesiomorphic character within alligatorids.

Caiman gasparinae, Melanosuchus and extant species of *Caiman* (e.g., *Melanosuchus niger*: e.g., ZSM 130/1911, ZSM 27/1911, ZSM 87/1911, ZSM 76/1911, ZSM 85/1911, ZSM 84/1911, ZSM 77/1911, ZSM 86/1911, ZSM 83/1911, ZSM 91/1911, ZSM 68/1911, ZSM 14/1911, ZSM 89/1911, ZSM 70/1911, ZSM 80/1911, ZSM 79/1911, ZSM 90/1911, ZSM 73/1911, ZSM 74/1911, ZSM 75/1911, ZSM 3/1911, ZSM 67/1911, ZSM 46/1911; *Caiman yacare*: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5049, MACN I-15144-3603; *Caiman latirostris*: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232) also share the general pattern of relative size of antero-posterior alveolar diameter and diastema length in the upper jaw; all taxa additionally manifest five premaxillary alveoli with the 3rd and 4th maxillary alveoli the largest in the maxilla tooth row. Furthermore, as in *Melanosuchus niger*, the 3rd and 4th maxillary alveoli in *Caiman gasparinae* are both the largest and have similar antero-posterior diameters. However, in *Caiman gasparinae*, these alveoli are situated over a pronounced maxillary curvature, and the diastema between first and second premaxillary alveoli is almost as large as that segregating the fifth premaxillary from the first maxillary alveolus.

Caiman gasparinae has a distinctive bone surface ornamentation pattern consisting of prominent rostral bumps, arranged to form short crests. This distinguishes the taxon from *Melanosuchus*. However, Mook (1921) suggested that exposure of the vomer on the palate could conform to intrageneric variability observed in *Caiman*, thus rendering the former a junior synonym (see also Schmidt 1928, Poe 1997).

Conclusion

Caiman gasparinae sp. nov. is a broad-snouted caiman from the late Miocene of NE Argentina. The type material belongs to a huge individual (estimated skull length: 45 cm) whose relative proportions of the temporal fenestrae versus the orbits, and the pattern of premaxilla–maxilla alveoli diameters and diastemas are similar to both extant *Caiman* and *Melanosuchus* species (see discussion above). Key to understanding relationships among caimanines is a detailed knowledge of the osteological morphology of extinct and extant species. In particular, it is important to identify the range of morphological variation among and within species. Indeed, our study shows that the braincase morphology in alligatorids (and in other crocodylians) is more variable than previously known. It also shows that features of *Caiman gasparinae*, such as the relative position and

conformation of the crista tuberalis, the orientation of the olfactory tract relative to the dorsal margin of the medulla, and the disposition of the endocranial foramina of CN IX–XI are features that vary among species. Phylogenetic relationships of *Caiman* species and re-diagnosis of the genus should, thus, be inferred using more comprehensive morphological (and molecular) datasets. In this context, this study provides new insights and represents a first step towards much needed systematic revisions and detailed morphological descriptions of the Argentinian Miocene fossil record of caimanines, in general, and of the genus *Caiman* including its extinct species, in particular.

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Appendix A

List of specimens of extant *Caiman* used for morphological comparison in this study

Caiman yacare: MLP R 5046, MLP R 5056, MLP R 5040, MLP R 5042, MLP R 5050, MLP R 5048, MLP R 5053, MLP R 5055, MLP R 5057, MLP R 5049, MLP R 5041, MACN I-15144-3603, MACN 30542, MACN 30532, MACN I-8265-E-1806, MACN 30537, MACN I-8266-E-1806 F, MLP R 5054, MLP R 5052, MLP R 5045, MACN 30538, MACN 30535, MACN 30563, MACN 30540, MACN 30528, MACN 30564, MACN 30534, MACN I-15231, MACN 30562, MACN 30523, MACN 30561, MACN 30551, MACN 30552, MACN 30573, MACN 30596, MACN 30583, MACN 30582, MACN 30593, MACN 30626, MACN 30599.

Caiman latirostris: MACN 30565, MACN I-7021-E-1232, MLP R 5047, MACN 30610, MACN 15232, MACN 30612, MACN 30572, MACN 30611, MACN 7375, MACN I-8270- E-1807, MACN 34420, MACN 30566, MACN 30567, MACN 30613, MLP R 5043.

Caiman yacare: MACN 30578, MACN 30606, MACN 30630, MACN 30576, MACN 30585, MACN 30577, MACN 30631, MACN 30633, MACN 30579, MACN 30603, MACN 30581, MACN 30608, MACN 30580, MACN 30628, MACN 30589, MACN 30594, MACN 30605, MACN 30598, MACN 30591, MACN 30586, MACN 30609, MACN 30588, MACN 30592, MACN 30618, MACN 30575, MACN 30629, MACN 30623, MACN 30587, MACN 30584, MACN 30601, MACN 30600, MACN 30621, MACN 30590.

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