



The snout of *Cricosaurus araucanensis*: a case study in novel anatomy of the nasal region of metriorhynchids

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Metriorhynchids are the only crocodyliforms adapted to pelagic marine life. Snout natural endocasts of the Tithonian (Late Jurassic) metriorhynchid *Cricosaurus araucanensis* indicated that skeletal changes defining the peculiar metriorhynchid body plan were coupled with changes of the soft cephalic anatomy such as the enlarged salt glands and restructuring of the paranasal sinus system. Seven new natural endocasts of the snout and a 3-D reconstruction of *C. araucanensis* are described. Data from these casts and the reconstruction are congruent, and they are combined into an accurate reconstruction that improves our knowledge of the pre-orbital anatomy. The olfactory tract, bulbs, olfactory nasal region and the anterior extension of the antorbital sinus within the maxilla are recognized. Osteological correlates of the salt gland body are also proposed. Palaeobiological inferences are erected based on the integration of natural endocasts and 3-D reconstruction data. It is proposed that *C. araucanensis* nasal salt glands were highly vascularized with a blood supply comparable with those of extant marine birds. Reduced olfactory bulbs and olfactory nasal region indicate that the aerial olfaction, differing from extant crocodylians, was not well developed. □ *Metriorhynchidae*, *natural and digital endocasts*, *olfactory region*, *paranasal sinuses*, *Thalattosuchia*.

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During the last few decades, our knowledge of soft anatomy of the head in extinct forms has radically improved because of X-ray, computed tomography or CT scanning. In the case of antorbital cavity, contributions of L. Witmer *et al.* increased the knowledge of the soft anatomy of extinct archosaurs and its interpretation within phylogenetic frameworks (e.g. Witmer 1997a,b; Sampson & Witmer 2007; Witmer & Ridgely 2008). Traditionally, the exploration of internal skull structures was restricted to the analysis of natural casts or artificial casts obtained through latex injections of skull cavities. Natural endocasts provide relevant information; however, they are rarely preserved.

An unusual situation is represented by the four natural snout endocasts of the metriorhynchine crocodyliform *Cricosaurus araucanensis*. From these endocasts, Fernández & Gasparini (2000) described enlarged nasal glands for salt excretion representing the first direct evidence of this extrarenal osmoregulatory system in an extinct sauropsid. On the basis of this evidence, Fernández & Gasparini (2008) proposed an evolutionary scenario of the gradual adaptation of the thalattosuchian crocodyliforms to the pelagic lifestyle. In 2009, Fernández and Herrera reconstructed the paranasal sinus system of this metriorhynchine, revealing a novel snout anatomy.

In Metriorhynchidae, the external antorbital fenestra is closed due to the internalization of the antorbital cavity, and on the lateral surface of the skull, the opening and oblique fossa, traditionally interpreted as homologous to the antorbital fenestra (and its fossa), correspond to a neomorphic structure for salt gland drainage. This unorthodox hypothesis has been tested and resulted as the most parsimonious explanation both in anatomical (Fernández & Herrera 2009) and phylogenetic frameworks (Leari *et al.* 2012). Since 2009, new material of *C. araucanensis* has been collected, among which there are seven natural snout endocasts. In addition to the natural endocasts and the holotype, *C. araucanensis* is known from several specimens including mainly skull elements. Presently, this species has only been recorded from Tithonian units of the Vaca Muerta Formation (Late Jurassic) outcropping in the Neuquén Basin, Argentina. Particularly interesting among skeletal material is the holotype, because it consists of a 3-D undistorted skull and mandible, as well as postcranial elements. The quality of the skull preservation makes it suitable for a digital reconstruction using CT scanning.

The infrequent situation of having 11 natural snout endocasts and good 3-D skulls of the same species, suitable for digital reconstructions, provides

an excellent case study in the novel snout anatomy of metriorhynchids. Metriorhynchidae are the only group of crocodyliforms to evolve a fully marine lifestyle (Fernández & Gasparini 2008; Young *et al.* 2010, 2011) and are present within a broad geographic range record. Within metriorhynchoids, *Cricosaurus* is among the few genera with a truly cosmopolitan distribution (Young *et al.* 2010). With the shift from one major adaptive zone to another, skeletal changes of metriorhynchids defined a peculiar crocodyliform body plan characterized by a streamlined skull and body, laterally oriented orbits, loss of osteoderm cover, short and paddle-like forelimbs and hypocercal tail. The exquisite preservation of *C. araucanensis* natural snout endocasts indicates that these skeletal changes were coupled with changes in the soft anatomy of cephalic structures with significant physiological impact such as the enlargement of nasal glands for salt excretion. Within this framework, and given the availability of a relatively large sample, we developed a protocol to analyse the peculiar morphology of the preorbital region, generating a background upon which palaeobiological inferences can be made. In this contribution, as a first step, previous reconstructions based on four natural endocasts are compared with those based on the new natural endocasts and completed with further details. Additionally, 3-D reconstructions of the skull, nasal cavities and paranasal sinuses were obtained from CT scan data. As both approaches are completely independent of each other, the natural endocasts are used to validate the 3-D reconstruction. If the information provided by both natural and digital endocasts is congruent, they can be combined into an integrated reconstruction. Finally, palaeobiological hypotheses are built based on the integrated reconstructions to test whether the novel snout anatomy of metriorhynchids could be linked with their marine specialization, which is unparalleled among archosaurs.

Materials and methods

The natural snout endocast sample consists of 11 specimens of *C. araucanensis* (Gasparini & Dellapé 1976): seven undescribed endocasts, five adults (MLP 92-III-6-1, MOZ-PV 7201, MOZ-PV 7202, MOZ-PV 7204 and MOZ-PV 7207) and two subadults (MLP 73-II-27-2 and MOZ-PV 7203) (Figs 1 and 2), and four endocasts previously described (MLP 73-II-27-1, MLP 76-XI-19-1, MLP 84-V-1-1 and MLP 86-XI-10-6; Fernández & Gasparini 2008; Fernández & Herrera 2009) (Figs 3–5). All specimens were recovered from Tithonian beds (Late

Jurassic) of the Vaca Muerta Formation exposed in the Neuquén Basin, northwestern Patagonia, Argentina.

To generate a digital endocast, the skull of the holotype of *C. araucanensis* (MLP 72-IV-7-1) was CT-scanned at the Hospital Paroissien in La Matanza, Buenos Aires, Argentina. The specimen was scanned helically at a slice thickness of 1 mm, 140 kV and 335 mA. CT data provided a clear distinction between fossilized bone and matrix. Data were output from the scanner in DICOM format using eFilm (v. 1.8.3) and then imported into Materialise Mimics software 10.01 (Materialise Inc., Leuven, Belgium), trial version, to create the digital endocast of the nasal cavities and paranasal sinuses. Anatomical terminology follows Witmer (1995a); institutional abbreviations used: MLP, Museo de La Plata, La Plata, Argentina; MOZ, Museo Provincial de Ciencias Naturales ‘Prof. Dr. Juan Augusto Olsacher’, Zapala, Neuquén, Argentina.

Results

Natural endocasts

Among the soft structures within the snout of archosaurs (see Witmer 1995a, 1997a), Fernández & Herrera (2009) identified the following, preserved as natural endocasts in *C. araucanensis*: nasal cavities, paranasal sinuses, as well as nasal glands, and part of their main ducts. The new materials exhibit the same apomorphic pattern of the paranasal system previously reported, that is: the closure of the antorbital fenestra and the internalization of the antorbital cavity that was surrounded dorsally by the prefrontal, laterally by the lacrimal, nasal and maxilla, and ventrally by the maxilla and palatine (Fernández & Herrera 2009). The new material reveals a rostral extension of the antorbital sinus. In all natural endocasts, including most of the new materials, the endocast of the antorbital sinus is broken rostrally at the level of the opening homologous to the internal antorbital fenestra (Figs 1A–C, E, 3A, B). However, in two of the new specimens (MLP 73-II-27-2 and MLP 92-III-6-1), it can be observed that the antorbital sinus extends rostrally and laterally being housed within the maxilla (Fig. 2). In all specimens, the antorbital sinus is medially separated from the nasopharyngeal ducts by a process of the palatine. In one of the new sub-adult specimens (MOZ-PV 7203), the nasopharyngeal ducts have been taphonomically detached, exposing this process as well as the ventral portion of the nasal septum (Fig. 1C). The dorsal portion of the nasal septum has been

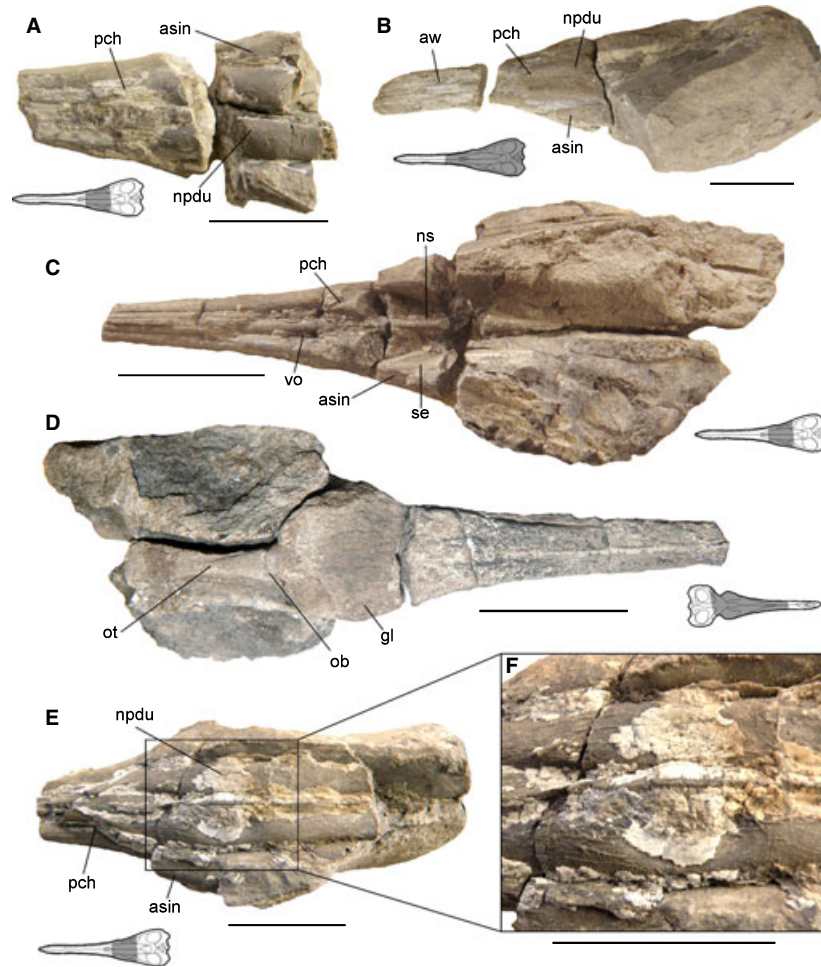


Fig. 1. Natural endocasts of *Cricosaurus araucanensis*. A, MOZ-PV 7201 in ventral view. B, MOZ-PV 7202 in ventral view. C, MOZ-PV 7203 in ventral view. D, MOZ-PV 7203 in dorsal view. E, MOZ-PV 7204 in ventral view. F, detail of vascularization of MOZ-PV 7204. Small sketches show the region preserved as natural endocast and its orientation. aof, antorbital fenestra; aw, nasal airway; asin, antorbital sinus; cnp, nasal cavity proper; co, concavity; de, dentary; en, endocast of brain cavity; gd, duct of the gland; gl, exocrine gland; la, lacrimal; mx, maxilla; na, nasal; nar, external nares; npdu, nasopharyngeal duct; ns, nasal septum; ob, olfactory bulb; olf, olfactory region of the nasal cavity; or, orbit; ot, olfactory tract; pch, primary choana; pl, palatine; prf, prefrontal; pref, preorbital fossa; preo, preorbital opening; sch, secondary choana; se, septum; stf, supratemporal fenestra; ve, vessel; vo, vomer; vs, vestibule. Scale bars = 50 mm.

previously identified as a low ridge on the caudal region of the nasal cavity of MLP 76-XI-19-1 (Fig. 3C).

Close inspection of MLP 76-XI-19-1 and the addition of new material (MOZ-PV 7203) allow us to identify, between the infilling of the orbits, that the olfactory tract is preserved as natural endocast (Figs 1D, 3C). The olfactory tract widens out rostrally forming two small convexities, which in life were probably separated by a non-ossified septum. These convexities, located caudal to the prefrontal pillar, have the same topographic relationship as the olfactory bulbs of extant crocodylians (Hopson 1979) and, therefore, are interpreted here as the endocasts of these structures. The endocasts of the olfactory tract and bulbs fit with a groove ending rostrally in two small concavities preserved on the ventral surface of the

frontal, as observed in the holotype of *C. araucanensis* (MLP 72-IV-7-1). Therefore, the groove and rostral concavities on the ventral surface of the frontal provide an accurate osteological correlate of these structures as proposed by Wenz (1968) for the metriorhynchid *Metriorhynchus superciliosus*. Rostrally, in the endocasts, the olfactory bulbs are in contact with two rostrocaudally elongate convexities, positioned on the caudodorsal region of the nasal cavity and separated from one another by the nasal septum (Fig. 3C). These convexities are medial to the nasal gland and separated by a groove (Figs 3C, 4A). They are positioned caudal to the primary choanae region and are extensively connected to the olfactory bulbs of the brain (Fig. 3C). Based on their position and their connection to the olfactory bulbs, these convexities are interpreted as the olfactory region of the nasal cavity.

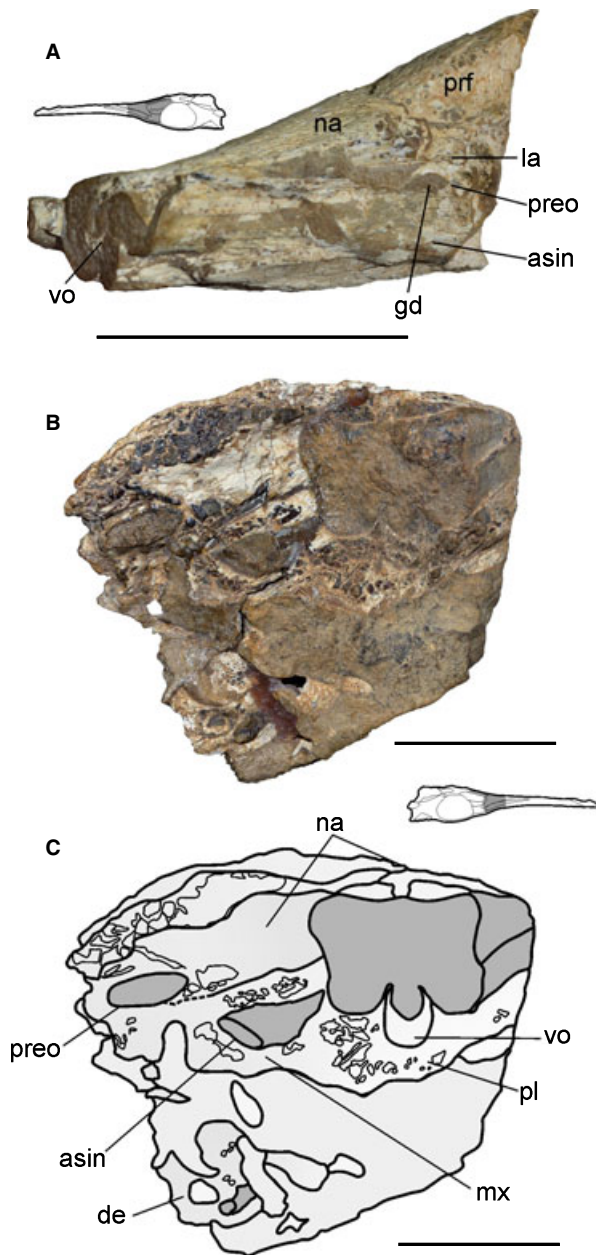


Fig. 2. Preorbital region of *Cricosaurus araucanensis*. A, MLP 73-II-27-2 in left rostralateral view. B, MLP 92-III-6-1 in medial view. C, drawing of MLP 92-III-6-1. Small sketches show the region preserved as natural endocast and its orientation. For abbreviations see Fig. 1. Scale bars = 50 mm.

Rostral to the olfactory region, the nasal cavity proper is enclosed dorsally, laterally and ventrally by the maxilla. The nasal airway is divided ventromedially by the vomer. Two prominent vessel fillings are preserved (Fig. 4B) on the left laterocaudal region of the nasal airway, approximately at the level of the nasomaxillary suture of MLP 84-V-1-1. These vessel fillings have a similar course: they gently curve ventrally, extending antero-posteriorly along the lateral

wall of the nasal airway (Fig. 4B). As pointed by Fernández & Herrera (2009), their locations and courses are similar to the branches of the dorsal maxillary artery described in *Alligator* by Sedlmayr (2002). In the same specimen, over the right ventral region of the airway, two other vessel fillings are preserved.

The nasopharyngeal ducts are partially preserved in all the natural endocasts (Figs 1A–C, E, 3A). The long nasopharyngeal ducts arise rostrally defining the primary choana, at the posterior margin of the preorbital fossa, and end at the secondary choana, positioned slightly rostral to the caudal margin of the orbit (Fig. 3A). In all specimens, the rostral half of the nasopharyngeal ducts are slightly curved ventrally and almost parallel to one another. In MOZ-PV 7204, MLP 76-XI-19-1 and MLP 84-V-1-1 conspicuous impressions of blood vessels have been preserved on the external surface of the nasopharyngeal ducts (Figs 1F, 3B). In these specimens, the major vascular branches are almost parallel and extend rostrocaudally along the ventral surface of the nasopharyngeal ducts, while the small vessel branches have an irregular pattern (Fig. 1F).

The nasal salt gland is caudally displaced, dorsal to the antorbital sinus (Fernández & Herrera 2009) and, as in all sauropsids, it is extracapsular (Witmer 1995a). The same topology is observed in the new specimens (Figs 1D, 2A). These glands are enlarged in metriorhynchids and have previously been identified as salt glands. The presence of salt glands in sauropsids is a prerequisite for inhabiting marine environments to prevent lethal dehydration. Up to now, the most compelling evidence of their presence is the natural endocasts of *C. araucanensis* (Fernández & Gasparini 2000, 2008). Fernández & Herrera (2009) proposed that the osteological correlate that can be used as proxy for developed salt glands is the opening of their ducts on the lateral wall of the snout. These authors also stated that the well-developed depression on the internal surface of the prefrontal and lacrimal observed in one specimen of *Metriorhynchus westermanni* from the Callovian (Middle Jurassic) of Chile would be the place where the body of the salt glands was housed. Gandola *et al.* (2006) described concave teardrop-shaped depressions on the prefrontal of *M. superciliosus* and related these concavities with the location of salt glands in this species. Close examination of MLP 73-II-27-1 reinforces this hypothesis. This specimen is represented by a fragment of rostrum whose left bony wall has been naturally detached exposing the natural endocast of the gland with an external surface composed of many small and rounded lobules (Fig. 5B, C). The detached bony lateral wall shows a

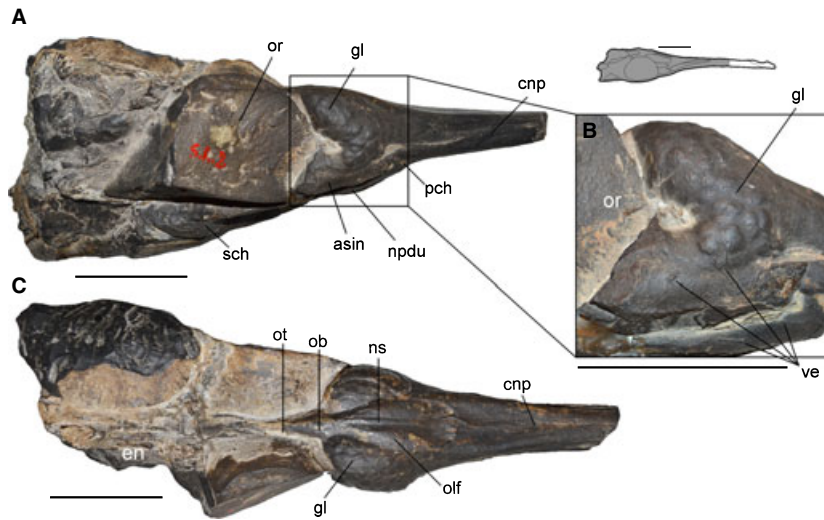


Fig. 3. Natural endocast of *Cricosaurus araucanensis* (MLP 76-XI-19-1). A, right lateral view. B, detail of nasal salt gland in ventrolateral view. C, dorsal view. Small sketch shows the region preserved as natural endocast and its orientation. For abbreviations see Fig. 1. Scale bars = 50 mm.

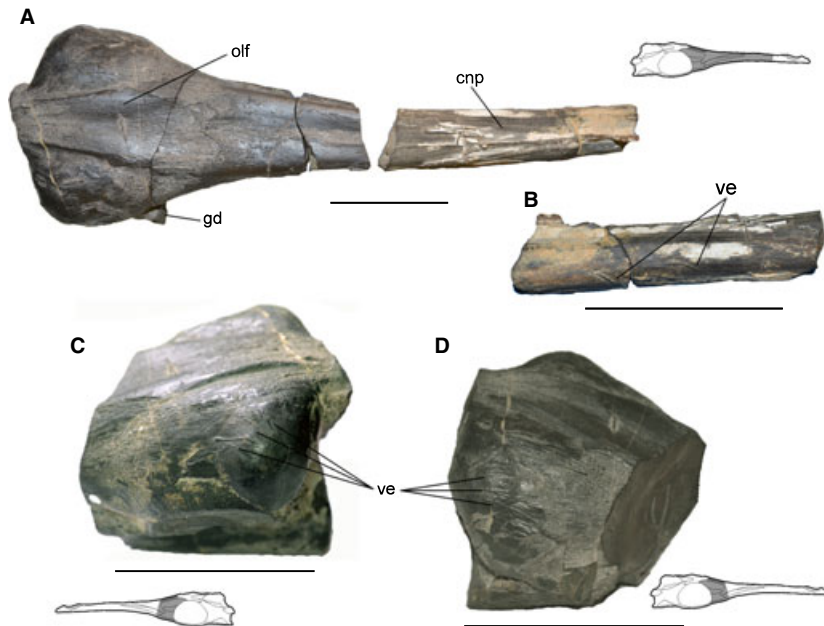


Fig. 4. Natural endocast of *Cricosaurus araucanensis* (MLP 84-V-1-1). A, dorsal view. B, detail of rostral portion of nasal cavity proper in right ventrolateral view. C, detail of left nasal salt gland in lateral view. D, detail of right nasal salt gland in anterolateral view. Small sketches show the region preserved as natural endocast and its orientation. For abbreviations see Fig. 1. Scale bars = 50 mm.

conspicuous triangular depression with a coarse texture, with its apex pointing rostrally, which fits perfectly with the nasal salt gland endocast (Fig. 5C).

On the external surface of the nasal gland of MLP 76-XI-19-1, MLP 84-V-1-1 and MLP 86-XI-10-6, several blood vessels are visible indicating that, as in extant crocodylian adults (Witmer 1995a), nasal glands, as most exocrine glands, are highly vascularized structures (Figs 3B, 4C, D). The nasal salt glands are formed by several rounded lobules

forming roughly concentric semicircles (Fig. 3B). Although the general morphology of the glands can be clearly defined in all the natural endocasts, their lobules are more clear in MLP 73-II-27-1, MLP 76-XI-19-1 and MLP 86-XI-10-6 (Figs 3B, 5A, B).

The structures identified on the new specimens of *C. araucanensis* are consistent with those previously published (see Fernández & Gasparini 2000, 2008; Fernández & Herrera 2009). The presence of the same preorbital morphology in a relatively large

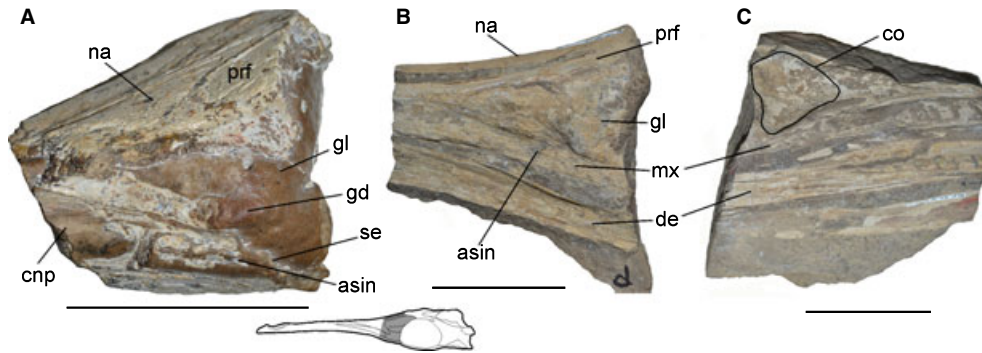


Fig. 5. Preorbital region of *Cricosaurus araucanensis*. A, MLP 86-XI-10-6 in left lateral view. B, C, part and counterpart of MLP 73-II-27-1. B, MLP 73-II-27-1 in left lateral view. C, MLP 73-II-27-1 in medial view. Small sketch shows the region preserved as natural endocast and its orientation. For abbreviations see Fig. 1. Scale bars = 50 mm.

sample (11 natural endocasts), and the same pattern in adults and sub-adults, confirms a constant pattern of the paranasal sinus system in this species. In addition, the examination of the new material along with the re-examination of MLP 76-XI-19-1, MLP 84-V-1-1 and MLP 86-XI-10-6 allowed the identification of other structures such as the nasal airway and the olfactory region of the nasal cavity, as well as the olfactory tract and bulbs.

Digital endocasts and 3-D visualization

Using CT data of MLP 72-IV-7-1, we created 3-D reconstructions of the skull, nasal cavities, paranasal sinuses and nasal gland (Fig. 6). CT data allowed us to reconstruct for the first time the vestibule of the nasal cavity, not preserved as natural endocast. The vestibule is dorsally and laterally bounded by the premaxilla and ventrally by the maxilla. The general morphology of the nasal cavity proper and nasopharyngeal ducts is consistent with the reconstruction based on natural endocasts. The 3-D reconstruction allowed recognition of the rostral extension of the antorbital sinus. Rostral to the opening homologous to the internal antorbital fenestra, the antorbital sinus develops small outgrowths housed within the maxilla (Fig. 6B–D). This anterior extension of the antorbital sinus recovered in 3-D reconstruction is consistent in its location with the infilling of the sinus partially exposed in one of the natural endocasts (MLP 92-III-6-1) (Fig. 2B, C).

Integration of natural and digital endocast data

As the information provided by both approaches is consistent, they can be integrated, thereby improving the reconstruction of the snout anatomy of *C. araucanensis*. The reconstruction of the paranasal sinus system, previously based only on four natural

endocasts (Fernández & Herrera 2009), has been corroborated and improved by 3-D reconstruction, as well as completed. The most significant information provided by the digital endocast of the paranasal sinus is the presence of a relatively long antorbital sinus completely enclosed within the bony snout. In most of the natural endocasts examined, the infilling of this sinus is broken anteriorly, but CT scanning showed the extension of this sinus rostrally within the maxilla. Natural endocasts allowed identification of the areas of the nasal capsules interpreted as the olfactory regions and their topological relationships with olfactory tract and bulbs. After this clear identification, the same structures can be confidently traced in the digital endocast. A similar situation is the identification of salt glands: while natural endocasts permit its identification as exocrine gland through the exquisite preservation of its lobulated morphology, CT scanning (through the identifications of the concavities on the internal surfaces of the prefrontals and lacrimals) permits the recovery of these same structures in skulls without natural endocasts. On the other hand, CT scanning and 3-D visualization generally permit a better and easier interpretation of the relationship between the skull bones and the enclosed soft organs.

Discussion

Information provided by natural endocasts and quality of salt gland preservation

Natural endocasts often provide fine details of loose connective tissues surrounding certain organs, such as the connective perilobular capsule of nasal glands, and/or covering special connective tissues like cartilage capsules. Quite significant are soft structures not completely enclosed by bones, such as the

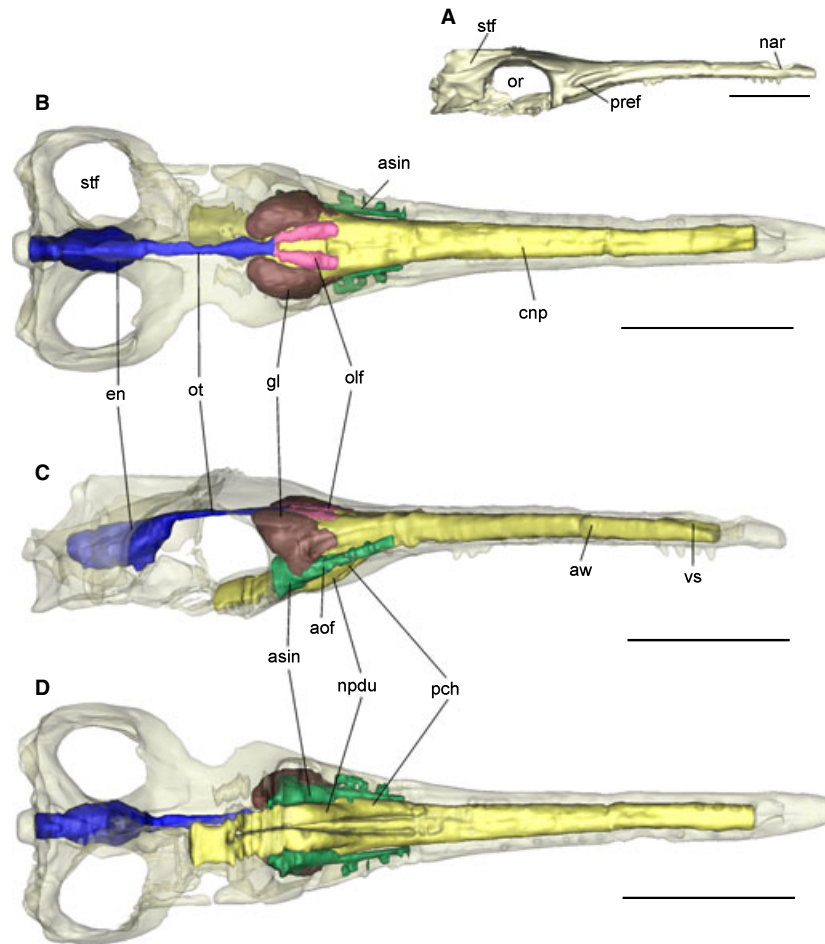


Fig. 6. Reconstructed skull, paranasal sinuses and other cephalic components of *Cricosaurus araucanensis* (MLP 72-IV-27-1). A, skull in right lateral view. B, dorsal view. C, right rostralateral view. D, ventral view. For abbreviations see Fig. 1. Scale bars = 100 mm.

portions of blood vessels that supply blood to the external surfaces of the organs, which can be accurately traced on natural endocasts.

In extant marine sauropsids, salt glands are composed of lobules surrounded by connective tissue, which is continuous with the perilobular capsule of tough connective tissue (Peaker & Linzell 1975). In birds, each gland is composed of longitudinally arranged lobules (Holmes & Phillips 1985), while in the case of non-avian reptiles, the body of the gland consists of branched and rounded lobules. In *C. araucanensis*, the external morphology of the nasal salt glands recovered in natural endocasts is consistent with the general morphology of salt glands of turtles and marine iguana *Amblyrhynchus* (Schmidt-Nielsen & Fänge 1958; Schumacher 1973; Peaker & Linzell 1975). The general morphology of the body of the gland is preserved in all natural endocasts; however, fine details of the lobule morphology are conspicuous only in some of them (MLP 76-XI-19-1, MLP 86-XI-10-6 and MLP 73-II-27-1; Figs 3B, 5A, B). In the others, preservation of

the lobules is much more subtle or not evident at all. One of the specimens (MLP 73-II-27-1) in which the natural endocast has been naturally detached from the bones that surround it laterally shows a concave area housing the body of the gland on the prefrontal and lacrimal (Fig. 5C).

The texture of this bony surface permits to recovery of the general gross morphology of the body of the gland but not its lobules. Fine details of labile tissue require the replication of their morphology by rapid *in situ* growth of minerals (i.e. authigenic mineralization) and, particularly in marine environments, the preservation of labile soft tissues can be compared with a race (Briggs 2003). If decay outpaces mineralization, only the most decay-resistant structures will be preserved (Allison 1988a). A possible explanation for the preservation of the fine lobule morphology observed in MLP 76-XI-19-1 and MLP 86-XI-10-6 is that a similar process to that observed in muscle decay of *Branchiostoma* and other primitive chordates was responsible for the preservation of fine glands in *C. araucanensis*. It has

been demonstrated experimentally that *Branchiostoma* decayed through a series of morphological stages which, although forming a continuum, provide a method of monitoring the degree of decay. Briggs & Kear (1994) recognized five morphological stages in the decay of *Branchiostoma* and, by comparison, they interpreted a pattern of preservation of soft tissues for conodonts and other primitive chordates. One of the final stages is identified by the shrinkage of the V-shaped muscle blocks within the envelopes of connective tissue that accommodate them. Therefore, V-shaped structures observed in fossils of these primitive chordates have been interpreted as muscle blocks preserved as outlines representing myosepta. In the case of fine morphology of the lobules preserved on the gland surfaces of *C. araucanensis* (Figs 3B, 5A, B), a possible explanation could be that glandular tissue could have decayed rapidly, while tough perilobular connective tissue could be more decay resistant. In this way, the connective tissues formed an envelope that, through early diagenetic mineralization, preserved the morphology of the lobules and their original arrangement. Stagnation and rapid burial are considered prerequisite for the preservation of soft tissues in fossils as they promote early diagenetic mineralization (Allison 1988b). Both factors characterized the Vaca Muerta Formation deposits from where *C. araucanensis* endocasts have been recovered (Gasparini *et al.* 1997, 1999; Spalletti *et al.* 1999).

Palaeobiological inferences based on reconstructed soft snout anatomy

As Witmer (1995b, 1997a) pointed out, soft tissue considerations are at the base of a whole host of palaeobiological inferences. He graphically represented this concept as an 'inverted pyramid of inference' where soft tissue inferences are the foundation and justification for higher palaeobiological inferences. We agree with this proposal, and therefore, we used the most accurate reconstruction of soft snout anatomy, resulting from the combination of natural and digital endocasts, to infer physiological aspects of extinct metriorhynchids. Our hypotheses are based on anatomical and physiological aspects, explored experimentally mainly in extant reptiles.

Blood vessels and salt glands. – The natural endocasts allow for the recovery of portions of blood vessel trajectories that did not penetrate the bones, such as vessels on the external surface of the connective tissue surrounding cephalic organs, as well as on the external surface of the nasal capsule cartilage. The blood vessel infill preserved on the external

surface of the nasal salt gland are particularly interesting. These vessels suggest a high vascularization of this structure. The secretory function of salt glands is associated with an elevated blood supply to the gland. In birds and turtles, a positive relationship has been found between the presence of a salt gland, salt secretion rates and blood flow, after salt loading (Hanwell *et al.* 1971; Kaul *et al.* 1983; Reina & Cooper 2000). On the other hand, Cramp *et al.* (2010) found in a recent study of the extant estuarine crocodylian *Crocodylus porosus*, in which the animals were not salt loaded, that secretory rate from the lingual salt glands was not necessarily coupled to changes in blood flow. However, it is worth noting that, according to the evolutionary model of Dunson & Mazzoti (1989), marine adaptations in reptiles were transitional and comprised four stages. The highest stage of marine specialization (fourth stage) was characterized by the enlargement of salt glands capable of maintaining constant plasma osmolality even when, as occurs in turtles, sea water and osmoconforming preys were consumed (Jackson *et al.* 1996). The size and gross morphology of metriorhynchid salt glands are comparable with those of extant turtles, and therefore, it has been suggested that metriorhynchids, like extant sea turtles, represented the fourth stage of Dunson and Mazzoti's model (1989), which corresponds to truly marine (i.e. pelagic) forms (Fernández & Gasparini 2008).

In birds, two branches of the internal carotid artery comprise the major arterial supply to the salt gland (Holmes & Phillips 1985), and the path of the venous drainage from the gland, which follows the same general course as that of the arterial supply (Marples 1932). Blood flow through the avian carotid arteries has been measured indicating an almost 50% diversion of carotid blood to the glands at maximal salt gland secretion (Gerstberger 1991). A conspicuous feature of metriorhynchid skull is the enlarged external carotid foramen compared with other Crocodyliformes (Pol & Gasparini 2009; Young & Andrade 2009; Fernández *et al.* 2011), even to the other basal thalattosuchians of estuarine and/or coastal habits (Hua & de Buffrenil 1996; Fernández & Gasparini 2008). This feature is coupled with an enlargement of the carotid canal (Fernández *et al.* 2011). If the increase in blood flow through the internal carotids was related to an increase of salt gland blood flow to cover functional demands of the glands, then the enlargement of the carotid foramen and canal of metriorhynchids could be regarded as another feature correlated with the achievement of truly pelagic habits in members of this clade unique among crocodyliforms. This hypothesis needs to be tested by subsequent investigation.

In vivo experimental studies of the relationship between the blood flow through and the secretion by the salt glands in a more extensive reptile samples, including detailed observations on correlations between physiological parameters and anatomical features, could allow testing of this hypothesis.

Nasal capsule, olfactory bulbs and olfaction. – Reconstruction of preorbital region of *C. araucanensis* allowed for the delimitation of olfactory tract and bulbs and olfactory region of the nasal cavity proper. According to Witmer *et al.* (2008), telencephalic portions of the brain (e.g. olfactory bulbs) sufficiently fill their region of the endocranial cavity, thus the endocast is a faithful representation of their general size and shape. The olfactory tract in *C. araucanensis*, preserved as natural endocast, is thin and long. We identified the olfactory bulbs as the expansion of the olfactory tract in the rostral region and slightly caudal to the prefrontal pillar. The groove preserved on the ventral region of the frontal of the holotype (MLP 72-IV-7-1) corresponds to the osteological correlate of the olfactory tract. The olfactory region of the nasal cavity is small and positioned caudal to the primary choana and is in contact with the olfactory bulbs of the brain. The olfactory region of the nasal cavity and the olfactory bulbs are conspicuously smaller than those of extant crocodylians (Witmer & Ridgely 2008; Zelenitsky *et al.* 2009). Extant crocodylians have well-developed aerial olfaction, and they are able to distinguish food sources without visual cues (Weldon *et al.* 1990). This behaviour is attributable to the main olfactory system, as the nasal chemical receptor system, the vomeronasal, is absent in adult specimens (Schwenk 2008). The olfactory bulb size has been used as an indicator of olfactory acuity in extant archosaurs (Zelenitsky *et al.* 2009). The small size of olfactory bulbs and olfactory region of the nasal cavity suggests that aerial olfaction in metriorhynchids was not well developed.

Conclusions

New natural endocasts of *C. araucanensis* recovered recently from Tithonian beds of the Vaca Muerta Formation (Neuquén Basin, Argentina) confirm previous observations on the paranasal sinus system of metriorhynchids, which are as follows: internalization of the antorbital cavity and extracapsular enlarged nasal salt glands draining through a preorbital neomorphic opening (Fernández & Herrera 2009).

The 3-D reconstruction derived from the skull of the holotype of *C. araucanensis* and the natural

endocasts provide congruent data on the snout anatomy; however, they provide different details and complementary information. As data from both are congruent, they can be integrated into an accurate reconstruction of the snout anatomy. New information indicates that the antorbital sinus extends rostrally within the maxilla and allows for the identification of olfactory tract and bulbs, the olfactory region of the nasal cavity, the complete morphology of the nasal cavity, as well as osteological correlates of the salt gland bodies.

Exquisite preservations of some natural endocasts provide fine details, such as the salt gland vascularization. The preservation of the individual lobules and their disposition was probably due to rapid *in situ* growth of minerals (i.e. authigenic mineralization).

Based on the reconstruction of the soft anatomy of *C. araucanensis* and comparison with extant reptiles (bird included), we propose that nasal salt glands were highly vascularized. The secretory activity of these glands is associated with a high blood supply. The enlargement of the carotid foramen and canal, unique to metriorhynchids among crocodylians, indicates an increase in blood flow that could be coupled with an increase in blood flow to salt glands at maximal secretion. The reduced size of olfactory bulbs and olfactory region of the nasal cavity proper indicates that, contrary to extant crocodylians, aerial olfaction was not well developed.

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