Active airflow of the paranasal sinuses in extinct crocodyliforms: Evidence from a natural cast of the thalattosuchian *Dakosaurus andiniensis*

Marta S. Fernández | Yanina Herrera

CONICET, División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina

**Correspondence**
Yanina Herrera, Facultad de Ciencias Naturales y Museo, Unidades de Investigación Anexo Museo, Av. 60 y 122, B1900 La Plata, Argentina.
Email: yaninah@fcnym.unlp.edu.ar

**Funding information**
Agencia de Promoción Científica y Tecnológica, Grant/Award Numbers: PICT 2016-0267, PICT 2016-1039; Universidad Nacional de La Plata, Grant/Award Number: Proyectos de Incentivos Docentes

**Abstract**
The evolution of Thalattosuchia documents the unique shift among Crocodylomorpha from aquatic continental/coastal habitats to a fully pelagic lifestyle. This transition was coupled with deep modification of their skeletons, such as hydrofoil forelimbs, hypocercal tail, and loss of osteoderms. The natural snout casts of the rhacheosaurin *Cricosaurus araucanensis* showed that it also included changes in the internal anatomy of the snout like the enlargement of nasal glands (probably for salt excretion) and the rearrangement of the paranasal sinus system, including the internalization of the antorbital sinus. Here we described the snout natural cast of the geosaurin *Dakosaurus andiniensis* from the Late Jurassic of Patagonia. The information provided by it indicates that, despite having different external morphologies and ecology, *D. andiniensis* and *C. araucanensis* share the same facial anatomy. The new cast preserves a suborbital diverticulum of the antorbital sinus protruding into the orbit through the postnasal fenestra. Its location indicates that it was interleaved with jaw adductor muscles suggesting an active airflow in the paranasal sinus. We provide a putative functional interpretation of this peculiar arrangement where below pumps actions of musculature may help drain salt glands. The rearrangement of the paranasal sinuses predates the transition to a completely pelagic-lifestyle. We proposed a stepwise evolutionary scenario of Thalattosuchia, implying changes in the preorbital region (and orbit orientation) where the internalized antorbital sinus via its subsidiary diverticulum was co-opted for helping nasal glands drainage. Further scrutiny of facial anatomy of a larger sample of thalattosuchians will help to test this hypothesis.

**KEYWORDS**
antorbital sinus, Jurassic, Metriorhynchidae, suborbital diverticulum, Vaca Muerta Formation

### 1 INTRODUCTION

Oceanic environments seem to be elusive adaptive zones for crocodylomorphs. Despite their previously high ecological diversity, the dominance of amphibious/aquatic forms, and even the phenotypic plasticity to acclimate to changes in environmental salinity of extant crocodiles (Cramp, Meyer, Sparks, & Franklin, 2008), only once in...
their long evolutionary history and broad ecological radiations did crocodylomorphs successfully colonized the open sea. Wilberg, Turner, and Brochu (2019) analyzed the complex pattern of major habitat shifts in Crocodylomorpha and recognized at least four independent origins of salt water tolerance in Crocodylomorpha plus several transitions from terrestrial to marine habits. However, from the four clades (Pholidosauridae, Crocodylia, Dyrosauridae, and Thalattosuchia) represented by fossils found in marine sediments (Bardet et al., 2014), only derived metriorhynchoid thalattosuchians show changes in their morphology that could be linked with adaptation to living in pelagic or oceanic environments. Thalattosuchia is one of the most interesting lineages of Crocodylomorpha as its subclades (Teleosauroidea and Metriorhynchoidea) documented the unique shift from predominantly continental aquatic/coastal (shores and estuaries) to oceanic or pelagic lifestyle. Like in their pelagic avian relatives, this shift from coastal to marine lifestyles must have required changes not only of their morphology and physiology but also of their behavior and demography (Hémery, 2001; Kristoffersen, 1999).

The last two decades have witnessed a renewed interest in thalattosuchians triggered by new material, revisions of historical collections but, mainly, by using new technical approaches for anatomical explorations and phylogenetic analyses. Although the understanding of their diversity and evolutionary history increased significantly (e.g., Barrientos-Lara, Alvarado-Ortega, & Fernández, 2018; Foffa, Young, Brusatte, Graham, & Steel, 2018; Herrera, Fernández, & Vennari, 2021; Herrera, Gasparini, & Fernández, 2015; Johnson, Young, & Brusatte, 2020a, 2020b; Martin et al., 2019; Parrilla-Bel, Young, Moreno-Azanza, & Canudo, 2013; Wilberg, 2015; Young et al., 2012; Young & Andrade, 2009; Young, Andrade, Etches, & Beatty, 2013), changes associated with the transition from littoral/in-shore to offshore habitats have received less attention (Brusatte et al., 2016; Herrera, Leardi, & Fernández, 2018; Schwab et al., 2020). The differences that could be inferred as functionally linked with the shifts from coastal/inshore teleosauroids to pelagic metriorhynchosids are conspicuous in bone histology (Hua & de Buffrenil, 1996) and postcranial features such as hypocercal tail, the lack of osteoderms and hydrofoil limbs (e.g., Andrews, 1913; Fernández et al., 2020; Fraas, 1902; Young, Brusatte, Ruta, & Andrade, 2010). Although a tendency towards reducing size, thickness, and ornamentation of osteoderms has been documented in some teleosauroids (Foffa, Johnson, Young, Steel, & Brusatte, 2019), no osteoderms have been reported associated with metriorhynchid skeletons. As the anatomy of the postcranial skeleton of most metriorhynchosids is still poorly known, it is difficult to evaluate if these modifications were present in basal metriorhynchosids or if they evolved later within metriorhynchosids. Pelagosaurus typus and Magyarosuchus fitosi retain the osteoderm cover. Also, Magyarosuchus fitosi presents a rudimentary hypocercal tail (Ösi, Young, Galácz, & Rabi, 2018), and Zoneait nargorum, the sister taxon to Metriorhynchoidea, depicts no particular forelimb modification (Wilberg, 2015). In the case of cranial features, it is not clear which were the changes (if any) associated with the shift from littoral to definitive pelagic lifestyle. Recently, significant information has been yielded by the analyses and reconstructions of the otic region. In particular, the reconstructions of the inner ear of thalattosuchians demonstrate that teleosauroids and basal metriorhynchosids differ from pelagic thalattosuchians (i.e., metriorhynchosids) in the vestibular system morphology. These findings suggest that during the evolution of the lineage, the transition from coastal/inshore to offshore environments was coupled with changes in at least the hearing and balance parts of the cranial sensory systems (Pierce, Williams, & Benson, 2017; Schwab et al., 2020). The rostrum, particularly the preorbital region of the snout between the posterior constriction of the snout (i.e., the point where the snout becomes broader to accommodate the orbits, Pierce, Angielczyk, & Rayfield, 2009) and the orbits (PrOS from hereon), also shows morphological changes from teleosauroids to metriorhynchosids with basal metriorhynchosids depicting some intermediate conditions. The most conspicuous feature is the broadening of the dorsal cranial surface adjacent to the orbit and the lateralization of the orbits. This last change implies vision changes, a sense that among other Mesozoic Marine reptiles such as ichthyosaurs and mosasaurs was dominant for gathering information from the outside world (Motani, Rothschild, & Wahl Jr, 1999; Yamashita, Konishi, & Sato, 2015). A taphonomical advantage of the PrOS is that, as indicated by finite element analysis (Pierce et al., 2009), it corresponds to a strong part of the skull between points of natural weakness, and it is one of the most commonly preserved parts of the metriorhynchid skull. Natural casts of the snout of Cricosaurus araucanensis from the Tithonian (Late Jurassic) of the Vaca Muerta Formation exposed at different localities of northwest Patagonia (Herrera, Fernández, & Gasparini, 2013) provided direct evidence of several soft structures housed within it, such as parts of the cartilaginous nasal capsule, paranasal sinus system, and enlarged nasal glands. This species was a longirostrine piscivorous/teutophagous metriorhynchid. In 2008, part of the snout, teeth, palate, natural casts of the snout and orbit, associated with a hind limb of a
large metriorhynchid, was found at Mallín Quemado locality in Neuquén Province (Argentina). The graphic superposition of the parts of the cranium and mandible, teeth, and natural cast of this specimen match with the most complete and best-preserved skull of *Dakosaurus andiniensis* (MOZ-PV 6146; Pol & Gasparini, 2009), and comparable elements of the new specimen are also consistent with the morphology of the fragmentary holotype of this species (MHNSR PV 344). The skull morphology and dentition of *D. andiniensis* indicates that this metriorhynchid was hypercarnivorous and used more aggressive behaviors than long-snouted forms such as *Cricosaurus* (Pierce et al., 2009; Young et al., 2012). One of the most interesting aspects of the cast of *Dakosaurus andiniensis* snout is that it preserves the infilling of the left orbit and ventral to it, the infilling of a diverticulum extending backward and passing through the postnasal fenestra (i.e., the suborbital diverticulum). The new specimen permits us to explore the internal snout anatomy of *D. andiniensis*, compare it with that of *Cricosaurus*, and explore the putative osteological correlations of the soft structures preserved as natural casts. The preserved parts of the paranasal sinus system ventral to the infilling of the orbits permit us to hypothesize that, contrary to extant crocodylians (Witmer, 1995, 1997), the airflow of the paranasal sinuses of metriorhynchids (as in birds and other nonavian theropods) was actively ventilated.

Institutional abbreviations. MDA, Museo del Desierto de Atacama, Antofagasta, Chile; MGHF, Museo Geológico H. Fuenzalida, Universidad Católica del Norte, Antofagasta, Chile; MHNSR, Museo de Historia Natural de San Rafael, San Rafael, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MOZ, Museo Provincial de Ciencias Naturales “Prof. Dr. Juan A. Olsacher”, Zapala, Argentina.

# MATERIALS AND METHODS

## 2.1 Materials

The specimen MOZ-PV 058 was collected ex-situ from a naturally broken calcareous nodule at Mallín Quemado locality from the Vaca Muerta Formation (Neuquén Basin, Neuquén Province, Argentina). Another calcareous nodule was found in-situ a few meters apart from MOZ-PV 058, which contains an articulated hind limb. However, this specimen has not been collected yet, and we cannot confidently assign it to the same specimen (Figure S1). Ammonite-based biostratigraphy indicates a late Tithonian age (*Corongoceras alternans* ammonite Zone; Leanza, 1975; Garrido, Parent, & Brambilla, 2018) for the hind limb.

The MOZ-PV 058 specimen consists of the anterior portion of the snout, from the posterior region of the external nares to the posterior margin of the premaxilla-maxilla suture, the natural cast of the preorbital region, the nasopharyngeal ducts, the infilling of the orbital region, a partially preserved mandibular ramus, and other isolated and broken fragments of the skull and teeth (Figures 1 and 2).

Comparable elements of the specimen MOZ-PV 058 with *Dakosaurus andiniensis* holotype (MHNSR 344) and the specimen MOZ-PV 6146 show that the new specimen shares with those a proportionally high rostrum, a high and robust mandibular ramus, and large and labiolingually compressed teeth with well-developed denticles on their margins. As in MHNSR 344 and MOZ-PV 6146, the ventral margin of the dentaries is straight, except for its anterior-most part, where the margin rises anterodorsally. Finally, the profile of MOZ-PV 058 perfectly fits that of the skull of MOZ-PV 6146. On this basis, the specimen MOZ-PV 058 can be confidently referred to as *Dakosaurus andiniensis* (Figure 1).

## 2.2 Methods

Three-dimensional models were created by two methods. A three-dimensional model of the skull was sculpted using the software Blender 2.91.0, based on the 2D reconstructions of the specimen MOZ-PV 6146 of *Dakosaurus andiniensis* published by Pol and Gasparini (2009), whereas the reconstruction of the soft structures is based on the specimen MOZ-PV 058. The three-dimensional models of the preorbital and orbital regions and the nasopharyngeal ducts of MOZ-PV 058 were created using a NextEngine 3D scanner HD Desktop (Supplementary Material). Image data manipulation was carried out using ScanStudio HD software. An interactive 3D model is available here: https://sketchfab.com/3d-models/my-sketchfab-mesh-d4df9ab0558c4f6793dc75f10f1fad5f.

## 2.3 Habits of Thalattosuchia

Assessing lifestyles of extinct species is always difficult, even in lineages with extant representatives like Crocodylomorpha. Though, it is not necessarily expected that the extant ecological and behavioral diversities mirror past diversities. In this contribution, to characterize the habits of extinct aquatic crocodylomorphs in general, and thalattosuchians in particular, we define animals inferred to expend most of their life cycle in littoral and inshore environments (including estuaries and ponds) as aquatic continental/coastal forms. We restrict oceanic or pelagic species to forms that are inferred to spend their whole...
(or at least the most important part of it) at the offshore (or oceanic) zone. These oceanic are also thought to possess adaptations for fully marine lifestyles, including hydrofoil limbs, hypocercal tail, and the lack of osteoderms.

### 3 | DESCRIPTION

#### 3.1 | Skull

The bony elements preserved in the specimen MOZ-PV 058 consist of an incomplete rostrum in articulation with the lower jaw. The left side of the snout is better and more completely preserved than the right one. The anterior end of the snout is weathered, and the external surface of the bones preserved (premaxillae, maxillae, dentaries, and splenials) are damaged.

The premaxilla-maxilla suture is partially preserved; it is interdigitated and, in dorsal view, seems to be perpendicular to the sagittal axis of the skull (Figure 1a,b), as in MHNSR PV 344 (Vignaud & Gasparini, 1996), and not U-shaped as in MOZ-PV 6146 (Pol & Gasparini, 2009). Only the posterior portion of the narial fossa is preserved. It is separated by a stout premaxillary internarial bar (Figure 1b); however, it is not possible to assess if this bar extends further anteriorly, completely

![Figure 1](image-url)
separating the external nares. External nares completely divided by a premaxillary process are only known for Rhacheosaurini (see for example, Young et al., 2020). The posterior margin of the narial fossa is posterior to the first maxillary alveoli’s anterior margin, as in MOZ-PV 6146. Only a small portion of the left maxilla is preserved; it is high and presumably short (Figure 1a), as in the specimens MHNSR PV 344 and MOZ-PV 6146. The anterior portion of the mandible preserves the anterior-most part of the mandibular symphysis (Figure 1c). The splenials contribute to the mandibular symphysis, contrary to MOZ-PV 6146, where the symphysis seems to be formed exclusively by the dentaries (Pol & Gasparini, 2009).

3.2 | Dentition

In the specimen MOZ-PV 058, some teeth are partially preserved. The three premaxillary and three maxillary teeth are preserved interlocked with the dentary elements, as in MOZ-PV 6146. The left premaxilla bears three partially preserved teeth. Only the distal part of the premaxillary teeth is preserved and shows the lingual surface of the enamel. The maxillary and dentary teeth are partially preserved from the crown’s base, but the labial enamel surface is eroded in all of them. As mentioned before, teeth are large and labiolingually compressed with well-developed denticles on their margins (Figure 1a).

3.3 | Description and interpretation of the snout cast

3.3.1 | General

The facial anatomy preserved as a natural cast comprises the preorbital segment of the rostrum from approximately the sutural anterior contact (in dorsal view) between the maxilla and the nasal, the left orbit, and the complete nasopharyngeal ducts. The orbital region is slightly laterally compressed, but the constitutive parts of the head (i.e., cast of individual organs) maintain their original pattern of connectivity. The cast has been naturally broken by recent weathering in three main blocks (Figure 2): block 1 contains part of the cartilaginous nasal capsule (probably corresponding to part of the concha/postconcha), nasal (salt) glands, anterior portion of both nasopharyngeal ducts from the primary choana up to the anterior margin of the orbits, a fragment of the left antorbital sinus which is enclosed in the snout and the almost complete segment of the right antorbital sinus enclosed in the skull (Figure 2a–c); block 2 includes the infilling of the left orbit and the left suborbital diverticulum (Figure 2d); block 3 comprises the infilling of both nasopharyngeal ducts (Figure 2e).

The general aspect of the cast and all the structures preserved are compatible with those described in *Cricosaurus araucanensis* (Fernández & Herrera, 2009; Herrera et al., 2013). This section describes the main structures identified on *Dakosaurus andiniensis* cast (Figures 2 and 3), based principally on the comparison with previously described *C. araucanensis* natural casts.

3.3.2 | Nasal capsule

As in *Cricosaurus araucanensis*, the posterodorsal region of the nasal capsule of *Dakosaurus andiniensis* has two elongate convexities that could be identified as the part of the capsule bearing olfactory epithelium as proposed by Herrera et al. (2013). Although Wenz (1968) first identified the osteological correlate of them as concavities on the ventral
surface of the frontal of *Thalattosuchus superciliosus* as olfactory bulbs, the enormous size does not reflect the expected diminished olfactory senses of these pelagic species. Herrera et al. (2013), based on natural casts of the snout of *Cricosaurus*, proposed an alternative hypothesis and interpreted them as the olfactory region of the nasal cavity. They also identified two small protuberances anterior to the olfactory tract and identified them as the cast of reduced olfactory bulbs.

### 3.3.3 | Nasal salt glands

As in *Cricosaurus araucanensis* (Fernández & Gasparini, 2000, 2008), the casts of nasal salt glands are located lateral to the cartilaginous nasal capsule (Figures 2a–c and 3b,e). As depicted on the graphic superposition of the dorsal views of the cast and the specimen MOZ-PV 6146, the glands fit in the internal concavities of the ventral surfaces of the prefrontals (sketches on Figure 1). The prefrontal concavities housing the glands can be seen on a specimen of *Metriorhynchus westermanni* (MDA 1) that has been acid-prepared (Figure 4a,b). The relative size and general form of *Dakosaurus* glands are nearly identical to those of *Cricosaurus araucanensis*. On the anterolateral surface of the left gland, an ovoid anterodorsally oriented mark indicates the rim of the preorbital opening (Figure 2c). On the right side, this rim, although present, is less distinctive.

### 3.3.4 | Antorbital sinus and suborbital diverticulum

Ventral to the left gland, and separated by a thin layer of bone, is the antorbital cavity. Most of the infilling of this cavity (i.e., the cast of the antorbital sinus and previously described as “diverticulum 2” by Fernández &
Herrera, 2009, p. 709) has been naturally detached, leaving exposed the thin layer of the bone surrounding most of the dorsal and medial walls of the cavity and separating the infilling of the antorbital sinus from the salt glands. This bone layer is also partially observed on the right side and corresponds to the “septum” described in the natural casts of other metriorhynchids in former contributions (Fernández & Herrera, 2009; Herrera et al., 2013; Figures 2b,c and 3e). This layer is so delicate that it is challenging to observe it in CT scans and to determine the identity of the bones forming it. It is medially confluent with the dorsal processes of palatines enclosing the nasopharyngeal ducts and possibly formed by the palatines and/or the prefrontals. On the left side, the infilling of the antorbital sinus extends posteriorly, forming a suborbital diverticulum passing through the postnasal fenestra and ending ventral to the posterior border of the infilling of the left orbit. This diverticulum lays parallel to the left nasopharyngeal duct (Figures 1d, 2d–f, and 3).

In the case of Cricosaurus, based on the CT scan of the skull, Fernández and Herrera (2009) identified a “cul-de-sac” diverticulum housed within a maxillary recess (“diverticulum 1”). The presence of this second diverticulum in Dakosaurus andiniensis cast cannot be confirmed, and it is pending until the skulls of this taxon could be scanned.

3.3.5 Nasopharyngeal ducts

Both ducts are completely and exceptionally well preserved (Figures 2b,e and 3a,b,d,e). The anterior extreme of both marks the exact location of the primary choana.
opposite to the extreme where the antorbital sinuses evaginate from the nasal cavity (Figure 3b). The nasopharyngeal ducts are taller than wide, as in other metriorhynchids (Figure 5). In posterior view of block 1 (Figure 2b), the cross-section of the ducts enclosed in the snout has the same pattern as in the *Dakosaurus andiniensis* holotype (Figure 5c). The portion of the ducts passing ventrally to the orbits has been plastically deformed, and, in anterior view, the cross-section of the left duct is sigmoidal and higher and narrower than the right one (Figure 3d).

4 | DISCUSSION

The interpretation of the soft structures housed within the snout and their corresponding bony correlates has important implications for understanding the evolution of the thalattosuchians for two main reasons. First, the interpretation of soft structures is intimately linked with the homology of bony structures expressed as taxonomic characters used to build phylogenies (e.g., antorbital fenestra and fossa). Second, the morphology of the PrOS is also a source of systematic information, and it housed and/or determined the orientation of vital organs such as the salt glands and the eyes. Therefore, changes in the PrOS are significant for understanding changes linked with the major habitat shifts in crocodylomorphs evolution as it is the adaptation to living in oceanic environments.

4.1 | Preorbital snout region of the metriorhynchid: Rearrangement of the paranasal sinus system, the internalization of the antorbital cavity, and orbit orientation

The lateral external surface of *Dakosaurus andiniensis* PrOS differs from that of *Cricosaurus araucanensis* (Figure 4c,d). The preorbital fossa, as in all metriorhynchids, is elongated and obliquely oriented with the anterior end of the main axis more dorsal than the posterior, but in *D. andiniensis*, the fossa is conspicuously deep and concave with a well-defined external rim, and the anterior end is continuous with a slight and short depression on the external surface of the maxilla forming a canal that vanishes from the dorsal surface of the snout (Figure 4c). Despite the disparate morphology of the stout- and short-snouted geosaurin *Dakosaurus* and the delicate long-snouted rhacheosaurin *Cricosaurus*, the natural infillings of their snouts depict the same arrangement of soft structures preserved as casts suggesting that this pattern is conservative among metriorhynchids. In both, the cast of enlarged glands is placed lateral to the cartilaginous nasal capsule, in front of the orbits, and separated by a ventral thin bony septum from the infilling of a diverticulum located lateral to the nasal capsule. This diverticulum is connected with the main nasal cavity through an opening located directly opposite to the primary choana. The location and connectivity of this diverticulum agree with the condition hypothesized by Witmer (1997, p. 25) of the antorbital sinus of the common ancestor of Archosauria and, on this basis, Fernández and Herrera (2009) identified it as the antorbital sinus in *Cricosaurus araucanensis*. The antorbital sinus of these metriorhynchids is partially enclosed within the skull; the septum that separates it from the nasal gland does not completely enclose the antorbital sinus in all of its extension. Also, the most posterior portion passes through the postnasal fenestra forming a suborbital diverticulum. The natural cast of *Dakosaurus andiniensis* confirms that the connectivity pattern and location of the antorbital sinus and its subsidiary diverticulum is the same as in *C. araucanensis* and suggests that the internalization of the antorbital cavity was a common feature of metriorhynchids (for further information, see Fernández & Herrera, 2009). The internalization of the antorbital cavity was previously hypothesized in the metriorhynchoids *Thalattosuchus superciliosus* and *Pelagosaurus typus* (Witmer, 1997) and

![Figure 5](image-url)
the teleosaurid *Teleosaurus cadomensis* (Jouve, 2009). If so, this feature was acquired early in the evolution of metriorhynchoids, at least since the Early Jurassic, or even it was already present in basal thalattosuchians.

The bony opening on the lateral surface of the metriorhynchid skulls has been traditionally identified as the antorbital fenestra until Fernández and Herrera (2009) proposed, based on natural snout casts, that this opening was for the drainage of the enlarged salt nasal glands and that the opening homologous to the internal antorbital fenestra is located within the skull. The antorbital region of metriorhynchid skulls is distinct from those of other archosaurs as the fenestra opening on the lateral wall is surrounded by the nasal, the lacrimal, and, with a minor contribution, by the maxilla. Additionally, the fenestra is directed posteromedially rather than laterally, so in lateral view, the opening is hidden (Witmer, 1997, figure 27). Besides these differences, the most significant feature is that the opening is not connected to the infilling identified as the antorbital sinus. Also, in two metriorhynchid natural casts (Herrera et al., 2013, figure 5), part of the duct leaving the gland body and passing through this opening have been preserved as casts. It is noteworthy that using other evidence and even assuming different homology of the opening, the most compelling interpretation of the snout anatomy of metriorhynchoids is that, as in extant crocodilians, the antorbital cavity was internalized (Fernández & Herrera, 2009; Witmer, 1997). Whether this major change in the organization of the paranasal sinuses system was acquired more than once during the evolution of Crocodylomorpha or if it is a common feature of Neosuchia depends on the phylogeny selected. Using dynamic homology approach for testing the alternative hypotheses on the primary homology (Ramirez, 2007) of the opening (i.e., the opening of metriorhynchids correspond to the antorbital fenestra of all crocodylomorphs or the opening is a neomorphic structure) in different phylogenetic frameworks resulted in the rejection of the former hypothesis and found as most parsimonious assuming that the opening in metriorhynchids is a neomorphic structure (Leardi, Pol, & Fernández, 2012). It is still unclear the homology of the snout lateral openings of non-metriorhynchid thalattosuchians (e.g., Pierce et al., 2017). In some teleosaurids, the opening is extremely reduced or even absent (e.g., Johnson et al., 2020a). Further analyses using different macroevolutionary analysis approaches will provide a better understanding of this topic.

Independent of the primary homology of the lateral opening, a striking feature of the metriorhynchid snout is the structural disposition of the main components of the PrOS. The most conspicuous morphological changes of the PrOS, compared with non-metriorhynchid thalattosuchians, include an elongated preorbital fossa (with variable morphology among metriorhynchids), the maxilla not exposed dorsally, lacrimal laterally oriented, dorsal surface of the prefrontal thick and laterally expanded, descending process of prefrontals mediolaterally expanded partially delimited the orbit anteriorly, and stout prefrontal pillars contacting the palate and forming the dorsal and dorso-medial edges of the postnasal fenestra. This gross pattern determines an almost rectangular cross-section of the PrOS that roughly resembles extant crocodilian embryos before nasal rotation (Witmer, 1995, figure 17a). The postnasal fenestra is almost vertical (dorso-ventrally oriented) and it is as high as or slightly higher than the cross-section of the nasopharyngeal ducts. A similar cross-section of the PrOS, except for a comparative larger postnasal fenestra, characterizes the metriorhynchid *Zoneait nargorum* (Wilberg, 2015, figure 4a), which also depicts a trend to lateralization of the orbits. The PrOS pattern of basal metriorhynchoids reinforces the idea that the internalization of the antorbital cavity occurred early in the evolution of the group and previous to changes in forelimb morphology as proposed by Wilberg (2015). The distinct arrangement of the metriorhynchid PrOS seems to be coupled with the lateralization of the orbits. The orbits oriented more laterally than dorsally also characterized other metriorhynchoids such as *Pelagosaurus typus* and *Opisuchus meieri* (Aiglstorfer, Havlík, & Herrera, 2020). The morphological changes of the PrOS—mainly the enlargement and lateral expansion of the prefrontals and the ventral extension of the descending process—would have two main functional consequences. First, it generates free space in the snout for housing the enlarged salt glands. Second, the bony wall formed by the enlarged descending processes of the prefrontal forces the lateral reorientation of the orbits with the consequent changes in the visual range. Laterally oriented orbits are more beneficial in pelagic environments such as those hypothesized for metriorhynchids. In contrast, the plesiomorphic condition of more dorsolaterally oriented orbits is better suited for hunting land-based prey from a submerged/partially submerged position (MacIver, Schmitz, Mungan, Murphey, & Mobley, 2017), as is hypothesized for teleosaurids.

### 4.2 The suborbital diverticulum and the active airflow

In natural snout casts of *Cricosaurus araucanensis* and in the cast of *Dakosaurus andiniensis*, the paranasal sinuses are consistently preserved as elongated structures with
almost rounded cross-sections. In one specimen of *C. araucanensis* (MLP 76-XI-19-1, Fernández & Herrera, 2009, figures 1 and 7) and better preserved in *Dakosaurus andiniensis* (Figures 2 and 3), the posterior extension of the antorbital sinus passing through the postnasal fenestra and forming a suborbital diverticulum ventral to the infilling of the orbit, have been preserved as natural cast. In specimens with partially preserved snout casts, the presence of this posterior extension of the antorbital sinus can be inferred based on auxiliary taphonomic information, as is the abrupt end of the infilling of the antorbital sinus at the postnasal fenestra and/or at least part of the antorbital sinus preserved (Figure 5).

The suborbital diverticulum and the antorbital sinus of metriorhynchids are not as large as those of birds or other nonavian theropods (Witmer & Ridgely, 2008). In birds, the suborbital diverticulum interleaves between jaw adductor muscles (e.g., m. dorsal pterygoideus, m. adductor mandibulae externus and m. pseudotemporalis; Witmer, 1995). Based on its location and posterior extension, we propose that the metriorhynchid suborbital diverticulum could be interleaved with those jaw adductor muscles. The pattern of the paranasal system of metriorhynchids, contrary to that of extant crocodilian and similar to birds, implies that the antorbital sinus was actively ventilated as there is no way to prevent the airflow actively moving when jaws are moved. If there is any, the advantages of active ventilation in theropods are still not clear but interesting; as Witmer and Ridgely (2008) pointed out, the suborbital diverticulum may have been widely distributed among extinct archosaurs regardless of whether it confers any advantage. Its presence is difficult to infer except for a few cases like *Majungasaurus*, *Tyrannosaurus*, and dromeosaurids, where bone recesses provide positive evidence of it (Witmer & Ridgely, 2008). In the case of metriorhynchids, the natural snout cast provides even more compelling evidence than those of the recesses of extinct theropods. In both *C. araucanensis* and *D. andiniensis*, the gland casts are connected with the outside through the preorbital opening, and they are ventrally separated from the infilling of the antorbital sinus by a thin septum. This septum can be seen on the left side of *D. andiniensis* cast, where the infilling of the antorbital sinus has been broken by recent weathering, leaving the septum exposed (Figures 2 and 3). The same occurs in other specimens of *C. araucanensis* and “*Metriorhynchus* casamiquelai” (Figure S2; Fernández & Herrera, 2009, figure 6c,d). Witmer (1997) described the mechanical effect of adduction and abduction of the mandible on the suborbital diverticulum of birds as a bellows pump device. The jaw muscles’ contractions set up positive and negative pressures within the air sac that can be transferred throughout the system where air would flow back and forth. This mechanism is surprisingly suitable also for phylogenetically and ecomorphologically distant metriorhynchids.

The enlargement and modification of cephalic glands for salt excretion have significant advantages (e.g., contrary to kidneys, their activity can stop when not demanded, Withers, 1992). However, they also require two main changes: first, cephalic glands need extra free space to be housed and cannot be enclosed by rigid walls as they greatly change their volume even in few hours (Hughes, Bennett, & Sullivan, 2002; Peaker & Linzell, 1975); second, when salt glands excrete in the air like birds and marine iguanas, they need a mechanism to avoid encrustation blocking the ducts (Withers, 1992). Extant sauropsids with nasal salt glands resolve the first problem by displacing the main body of the glands backward above the orbits as in birds (Marple, 1932; Schmidt-Nielsen & Fange, 1958) or by broadening the nasal region as in iguanas (Hazard, 2001; Peaker & Linzell, 1975). The second problem (i.e., avoiding salt encrustations) is resolved in birds by shaking their heads or through strong sneezes in marine iguanas. Both mechanisms are unlikely in the case of metriorhynchids. In metriorhynchids, the space for housing enlarged glands is created by broadening the PrOS and the strong concavity of the prefrontal interior surfaces (Figure 4a,b). The antorbital sinus is reduced and extruded through the postnasal fenestra into the orbit, where the subsidiary suborbital diverticulum interleaved with jaw adductor muscles (e.g., m. dorsal pterygoideus, m. adductor mandibulae externus, and m. pseudotemporalis). The adduction and abduction of the mandible on the suborbital diverticulum could have acted (as in birds) like bellows pumps pushing the air forward, “inflating” the antorbital sinus and pushing up the septum pressing the gland above it (Figure 6). Even the same effect could be caused by contractions of muscles without jaw movements. The septum separating both organs is extremely thin and could permit this movement without the risk of breaking. In some exquisite preserved natural gland cast of other metriorhynchids (Figure S3), it could be seen how the gland can be expanded and the sinus reduced without the septum breaking. In this way, the differences in pressures within the paranasal system could produce an effect similar to the sneeze of marine iguanas and could help drain the salt glands when animals went to the sea surface for breathing (Figure S4).

As natural casts of nonmetriorhynchid thalattosuchians are unknown, it is difficult to determine if the enlargement of nasal glands occurs early in the evolution of the lineage. The internalization of the antorbital sinus can be inferred based on compelling osteological evidence provided by the teleosauroid *Teleosaurus*
*cadomensis* and the metriorhynchoids *Pelagosaurus typus* and *Zoneait nargorum* (Jouve, 2009; Wilberg, 2015; Witmer, 1997). The internalization was probably not related to the enlargement of nasal glands. Depositional environments and the body plan (particularly the post-cranium) of teleosauroids, and basal metriorhynchoids, do not indicate adaptations to a definitely pelagic lifestyle, as it is also suggested by bone histology (Hua & de Buffrenil, 1996) and inner ear morphology (Schwab et al., 2020). Recent revisions of Teleosauroida also showed an interesting diversity of ecomorphotypes (Johnson et al., 2020a, 2020b). It could be expected that these forms were euryhaline. Some populations of teleosauroids and basal metriorhynchoid species inhabiting brackish, estuarine, or even littoral habitats, could have been able to tolerate limited exposure to sea water by selectively drinking only fresh water (like estuarine populations of *Alligator mississippiensis*; Jackson, Butler, & Brooks, 1996; Taplin, Grigg, Beard, & Pulsford, 1999; Cramp et al., 2008) or by salt-secreting glands of low secretory capacity combined with selective drinking (like *Crocodylus porosus*, *C. acutus*, and *C. johnstoni*) (Taplin & Grigg, 1981; Taplin, Grigg, & Beard, 1983).

On the other hand, the pelagic lifestyle of metriorhynchids must have required salt-secreting glands of high secretory capacity allowing them to drink sea water and include osmoconforming preys in their diet (e.g., Martill, 1985, 1986). This hypothetical scenario of marine adaptations of thalattosuchians is based on the stepwise model of extant reptile marines proposed on a physiological basis by Dunson and Mazzotti (1989) and Mazzotti and Dunson (1989). The model includes four major transitional stages (1, behavioral osmoregulation represented by aquatic-freshwater forms; 2, forms that tolerate limited exposure to sea water reduction in net salt uptake and water loss by selective drinking of fresh water only represented by estuarine forms; 3, behavioral osmoregulation combined with salt glands of low secretory; 4, forms with well-developed salt glands with high secretory capacity allowing drinking sea water and feed on osmoconforming preys) and some populations of teleosaurid species could represent stage two and/or three and metriorhynchids stage four. It is unlikely, or at least unclear if the internal antorbital sinus conferred any advantage to basal thalattosuchians related to marine adaptations. Likewise, the closing of the external antorbital fenestra may have provided potential advantages reducing the skull stress in forms with a tubular or oreinirostral snout (Rayfield, Milner, Xuan, & Young, 2007). By the Middle Jurassic, when derived

**FIGURE 6** (a) Head reconstruction and (b-c) schematic illustration of the hypothesized volume changes of the nasal gland, antorbital sinus, and suborbital diverticulum of *Dakosaurus andiniensis* during jaw (b) abduction and (c) adduction.
metriorhynchoids were definitely adapted to a pelagic lifestyle, the internal antorbital sinus could have been co-opted and transformed in a bellow pump system for helping in salt gland drainage. In this context, the presence of a suborbital diverticulum would have represented a great advantage for pelagic metriorhynchids.

4.3 | Evolutionary scenario for the adaptation of metriorhynchids to pelagic environments

A putative stepwise evolutionary scenario of the transition to fully pelagic lifestyle among Thalattosuchia, congruent with major morphological changes (Figure 7), could be that from terrestrial ancestors with lateral orbits and external lateral antorbital fossa, semiaquatic teleosauroids diversified in coastal and brackish, and even littoral marine environments in where the orbits oriented more dorsally were advantageous for a lifestyle similar to extant estuarine crocodilians. Noteworthy, this scenario is also consistent if other relationships among thalattosuchia and the rest of crocodylomorphs are assumed (i.e., Thalattosuchia is nested within Neosuchia, Pol & Gasparini, 2009). The diversity of deposition environments where teleosauroids are found suggested that at least some of them must have been euryhaline forms, and they could be able to tolerate limited exposure to hyperosmotic sea water by selectively drinking only fresh water complemented by other osmoregulatory mechanisms involving renal-cloacal-salt gland complex (like extant estuarine crocodilians, Taplin, 1984; Taplin & Grigg, 1981; Taplin et al., 1999). This osmoregulatory strategy of teleosauroids is consistent with the second and third stages of Dunson and Mazzotti (1989) model of marine adaptations in reptiles. The salt glands of low

**FIGURE 7** Simplified phylogeny showing major morphological changes discussed in the text. Modified from Wilberg (2015), Aiglstorfer et al. (2020), and Schwab et al. (2020)
secretory capacity should not necessarily have been large and with accessory mechanisms for their drainage. The internalization of the antorbital cavity in teleosauroids, as proposed by Jouvé (2009), could have occurred independently of the development of enlarged salt glands. Basal metriorhynchoids represent the intermediate stage to a fully marine pelagic or oceanic lifestyle represented by metriorhynchids. This transition to pelagic environments was coupled with the broadening of the PrOS and the lateralization of the orbits. These changes may have had two functional advantages generating space for enlarged salt glands and relocating the eyeballs (with the consequent change in the vision field) similar to the more lateral orbit location of most vertebrates with underwater vision (Kröger & Katzir, 2008; Walls, 1942). The “internalization” of the antorbital cavity occurred before the shift to a definitively pelagic lifestyle as documented by PrOS architecture of Pelagosaurus typhus and Zoneait nargorum (see Wilberg, 2015; Wittmer, 1997). The co-option of the internal antorbital sinus as bellows pumps would have represented an advantage for salt gland drainage in pelagic forms. With high secretory activity, the enlarged glands would have allowed them to drink sea water (and they would not have to go back to continents to drink fresh water as extant estuarine crocodylians do). The inner ears (Schwab et al., 2020) and the postcranial morphology (e.g., Wilberg, 2015) provide convergent lines of evidence supporting a stepwise evolutionary scenario for the unparalleled adaptation of metriorhynchids to pelagic environments among crocodylomorphs. It is also very interesting that all functional changes of the PrOS and orbit orientation could have been archived via a single heterochronic process, as it is the lack of nasal rotation described by Witmer (1995). In this framework, it would be worthy of an empirically test this hypothesis of evolutionary integration (i.e., morphological changes of two distinct units as the snout and the orbits were evolutionarily integrated and functionally overlapped) as it has been tested, for example, functional coupling and evolutionary integration of morphological units in the evolution of suction feeding and gill ventilation of some marine teleost (Farina, Knope, Corn, Summers, & Bemis, 2019). Morphological and functional integration of the skull units (rostrum and postrostrum) have been explored in crown Crocodylidae and produced interesting results (Piras et al., 2014) and, in a broader context, evolutionary integration of the archosaur skull has been analyzed by Felice et al. (2019). In this context, it would be worth further exploring evolution integration of the skull focused on the change of the PrOS and orientation of the orbits related to the exploration of new habitats (e.g., oceanic environments) along with the evolution of crocodylomorphs.

Comprehensive anatomical analysis of the thalattosuchian paranasal sinuses is being made (Cowgill et al. in this issue), so these pending issues may be resolved in the future.

5 | CONCLUSIONS

Information provided by natural snout casts indicates that, despite having very different external morphologies, Dakosaurus andiniensis and Cricosaurus araucanensis share the same facial anatomy suggesting that this pattern was common to metriorhynchids.

The arrangement of the soft organs in the snout of D. andiniensis brings additional support to the hypothesis of the internalization of the antorbital cavity and that the opening on the lateral surface of the snout was for salt gland drainage.

The new cast provides positive evidence of the evagination of the antorbital sinus via a subsidiary suborbital diverticulum protruding into the orbit through the postnasal fenestra. The excellent preservation of the suborbital diverticulum permits us to define it better, and it is larger than that described previously in C. araucanensis.

The location and extension of this diverticulum suggest an active airflow in the paranasal sinus. We provide a putative functional interpretation of the peculiar arrangement of sinuses in metriorhynchids where bellow pumps actions of jaw musculature may help drain salt glands.

For adaptation to the pelagic life of Thalattosuchia, we proposed a stepwise evolutionary scenario that implies changes in the preorbital region of the skull (PrOS) and orbits orientation. Further scrutiny of the facial anatomy of a larger sample of thalattosuchians will help to test if the morphological changes of the PrOS and lateralization of the orbits were evolutionarily integrated and if these changes were functionally coupled with adaptation to living in oceanic environments on an almost permanent basis.

ACKNOWLEDGMENTS

We would like to thank the editors for the invitation to be part of this special issue. We also thank L. Campos (MLP) for assistance with scan optimization, A. Ruella (MLP) for the 3D models, J. Gonzalez for the illustration of Dakosaurus andiniensis in Figure 6, and A. Garrido and B. Bollini (MOZ) for access to the specimen. C. Holliday is sincerely thanked for the English grammar corrections and his helpful comments on an earlier draft of this manuscript. We also thank D. Pol and an anonymous reviewer for their valuable review helping us improve the quality of the manuscript.
CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Marta Fernández: Conceptualization; formal analysis; funding acquisition; methodology; writing-original draft; writing-review & editing. Yanina Herrera: Conceptualization; formal analysis; methodology; writing-original draft; writing-review & editing.

ORCID
Marta S. Fernández https://orcid.org/0000-0001-6935-7575
Yanina Herrera https://orcid.org/0000-0002-2020-1227

REFERENCES
Aiglstorfer, M., Havlik, P., & Herrera, Y. (2020). The first metriorhynchid crocodyliform from the Aalenian (Middle Jurassic) of Germany, with implications for the evolution of Metriorhynchoidea. Zoological Journal of the Linnean Society, 188, 522–551.

Andrews, C. W. (1913). A descriptive catalogue of the marine reptiles of the Oxford clay. London: British Museum of Natural History.

Bardet, N., Falconnet, J., Fischer, V., Houssaye, A., Jouve, S., Pereda Suberbiola, X., … Vincent, P. (2014). Mesozoic marine reptile palaeobiogeography in response to drifting plates. Gondwana Research, 26, 869–887.

Barrientos-Lara, J. I., Alvarado-Ortega, J., & Fernández, M. S. (2018). The marine crocodile Maledictosuchus (Thalattosuchia, Metriorhynchidae) from the Kimeridgian deposits of Tlaxiaco, Oaxaca, southern Mexico. Journal of Vertebrate Paleontology, 38, 1–14.

Brusatte, S. L., Muir, A., Young, M. T., Walsh, S., Steel, L., & Witmer, L. M. (2016). The braincase and neurosensory anatomy of an early Jurassic marine crocodylomorph: Implications for crocodylian sinus evolution and sensory transitions. The Anatomical Record, 299, 1511–1530.

Cramp, R. L., Meyer, E. A., Sparks, N., & Franklin, C. E. (2008). Functional and morphological plasticity of crocodile (Crocodylus porosus) salt glands. The Journal of Experimental Biology, 211, 1482–1489.

Cowgill, T., Young, M. T., Schwab, J. A., Walsh, S., Witmer, L. M., Herrera, Y., Dollman, K. N., Choiniere, J. N., & Brusatte, S. L. (in press). Parasinal sinus system and upper respiratory tract evolution in Mesozoic pelagic crocodylomorphs. The Anatomical Record.

Dunson, W. A., & Mazzotti, F. J. (1989). Salinity as a limiting factor in the distribution of reptiles in Florida bay: A theory for the estuarine origin of marine snakes and turtles. Bulletin of Marine Science, 44, 229–244.

Farina, S. C., Knopf, M. L., Corn, K. A., Summers, A. P., & Bemis, W. E. (2019). Functional coupling in the evolution of suction feeding and gill ventilation of sculpins (Pericroformes: Cottoidei). Integrative and Comparative Biology, 59, 394–409.

Felice, R. N., Watanabe, A., Cuff, A. R., Noirault, E., Pol, D., Witmer, L. M., … Goswami, A. (2019). Evolutionary integration and modularity in the Archosaur cranium. Integrative and Comparative Biology, 59, 371–382.

Fernández, M., & Gasparini, Z. (2000). Salt glands in a Tithonian metriorhynchid crocodyliform and their physiological significance. Lethaia, 33, 269–276.

Fernández, M., & Gasparini, Z. (2008). Salt glands in the Jurassic metriorhynchid Geosaurus: Implications for the evolution of osmoregulation in Mesozoic marine crocodyliforms. Naturwissenschaften, 95, 79–84.

Fernández, M. S., & Herrera, Y. (2009). Parasinal sinus system of Geosaurus araucanensis and the homology of the antorbital fenestra of metriorhynchids (Thalattosuchia: Crocodylomorpha). Journal of Vertebrate Paleontology, 29, 702–714.

Fernández, M. S., Vlachos, E., Buono, M. R., Alzugayar, L., Campos, L., Sterli, J., … Paolucci, F. (2020). Fingers zipped up or baby mittens? Two main tetrapod strategies to return to the sea. Biology Letters, 16, 20200281.

Foffa, D., Young, M. T., Brusatte, S. L., Graham, M. K., & Steel, L. (2018). A new metriorhynchid crocodylomorph from the Oxford Clay Formation (Middle Jurassic) of England, with implications for the origin and diversification of Geosaurini. Journal of Systematic Palaeontology, 16, 1123–1143.

Foffa, D., Johnson, M. M., Young, M. T., Steel, L., & Brusatte, S. L. (2019). Revision of the Late Jurassic deep-water telesauroid crocodyliform Telosaurus megarinus Hulke, 1871 and evidence of pelagic adaptations in Telesaurusidae. PeerJ, 7, e6646.

Fraas, E. (1902). Die Meer-Krocodiller (Thalattosuchia) des oberen Jura unter spezieller berucksichtigung von Dacosaurs und Geosaurus. Paleontographica, 49, 1–72.

Garrido, A. C., Parent, H., & Brambilla, L. (2018). Tithonian stratigraphy and ammonite fauna of the Vaca Muerta Formation in Mallin Quemado (Neuquén Basin, Argentina), with remarks on the Andean chronostratigraphy. Volumina Jurassica, 16, 1–26.

Hazard, L. C. (2001). Ion secretion by salt glands of desert iguanas (Dipsaurus dorsalis). Physiological and Biochemical Zoology, 74, 22–31.

Hényery, G. (2001). Biodiversity and adaptations of extant marine birds: An overview. In J.-M. Mazin & V. de Buffrénil (Eds.), Secondary adaptation of Tetrapods to life in water (pp. 119–139). München: Verlag Dr. Friedrich Pfeil.

Herrera, Y., Fernández, M. S., & Gasparini, Z. (2013). The snout of Cricosaurus araucanensis: A case study in novel anatomy of the nasal region of metriorhynchids. Lethaia, 46, 331–340.

Herrera, Y., Gasparini, Z., & Fernández, M. S. (2015). Purranisaurus potens Rusconi, an enigmatic metriorhynchid from the Late Jurassic–Early Cretaceous of the Neuquén Basin. Journal of Vertebrate Paleontology, 35, e904790.

Herrera, Y., Leardi, J. M., & Fernández, M. S. (2018). Braincase and endocranial anatomy of two thalattosuchian crocodylomorphs and their relevance in understanding their adaptations to the marine environment. PeerJ, 6, e6586.

Herrera, Y., Fernández, M. S., & Vennari, V. V. (2021). Cricosaurus (Thalattosuchia, Metriorhynchidae) survival across the J/K boundary in the High Andes (Mendoza Province, Argentina). Cretaceous Research, 118, 104673.

Hua, S., & de Buffrenil, V. (1996). Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). Journal of Vertebrate Paleontology, 16, 703–717.

Hughes, M. R., Bennett, D. C., & Sullivan, T. M. (2002). Effect of saline drinking water on the size and water content of the gut
Walls, G. L. (1942). The vertebrate eye and its adaptive radiation. Bloomington Hills: Cranbrook Inst. New York: Ilañer.

Wenz, S. (1968). Contribution a l’étude du genere Metriorhynchus: crâné et moulage endocranien de Metriorhynchus superciliosus. Annales de Paléontologie, 54, 148–191.

Wilberg, E. W. (2015). A new metriorhynchoid (Crocodylomorpha, Thalattosuchia) from the Middle Jurassic of Oregon and the evolutionary timing of marine adaptations in thalattosuchian crocodylomorphs. Journal of Vertebrate Paleontology, 35, e902846.

Wilberg, E. W., Turner, A. H., & Brochu, C. A. (2019). Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. Scientific Reports, 9, 1–10.

Withers, P. C. (1992). Comparative animal physiology. Sydney: Saunders College Publishing.

Witmer, L. M. (1995). Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. Journal of Morphology, 225, 269–327.

Witmer, L. M. (1997). The evolution of the antorbital cavity in archosaurs: A study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Mem 3. Journal of Vertebrate Paleontology, Suppl 1, 1–73.

Witmer, L. M., & Ridgely, R. C. (2008). The paranasal air sinuses of predatory and armored dinosaurs (Archosauria: Theropoda and Ankylosauria) and their contribution to cephalic structure. The Anatomical Record, 291, 1362–1388.

Yamashita, M., Konishi, T., & Sato, T. (2015). Sclerotic rings in mosasaurs (Squamata: Mosasauridae): Structures and taxonomic diversity. PLoS One, 10, e0117079.

Young, M. T., & Andrade, M. B. (2009). What is Geosaurus? Redescription of Geosaurus giganteus (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. Zoological Journal of the Linnean Society, 157, 551–585.

Young, M. T., Brusatte, S. L., Ruta, M., & Andrade, M. B. (2010). The evolution of Metriorhynchioidea (Mesoeucrocodylia, Thalattosuchia): An integrated approach using geometrics morphometrics, analysis of disparity and biomechanics. Zoological Journal of the Linnean Society, 158, 801–859.

Young, M. T., Brusatte, S. L., Andrade, M. B., Dessojo, J. B., Beatty, B. L., Steel, L., ... Schoch, R. R. (2012). The cranial osteology and feeding ecology of the metriorhynchid crocodylomorph genera Dakosaurus and Plesiosuchus from the Late Jurassic of Europe. PLoS One, 7, e44985.

Young, M. T., Andrade, M. B., Etches, S., & Beatty, B. L. (2013). A new metriorhynchid crocodylomorph from the Lower Kimmeridge Clay Formation (Late Jurassic) of England, with implications for the evolution of dermaticranium ornamentation in Geosaurini. Zoological Journal of the Linnean Society, 169, 820–848.

Young, M. T., Sachs, S., Abel, P., Foffa, D., Herrera, Y., & Kitson, J. J. N. (2020). Convergent evolution and possible constraint in the posterodorsal retraction of the external nares in pelagic crocodylomorphs. Zoological Journal of the Linnean Society, 189, 494–520.

SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Fernández, M. S., & Herrera, Y. (2021). Active airflow of the paranasal sinuses in extinct crocodyliforms: Evidence from a natural cast of the thalattosuchian Dakosaurus andiniensis. The Anatomical Record, 1–16. https://doi.org/10.1002/ar.24678