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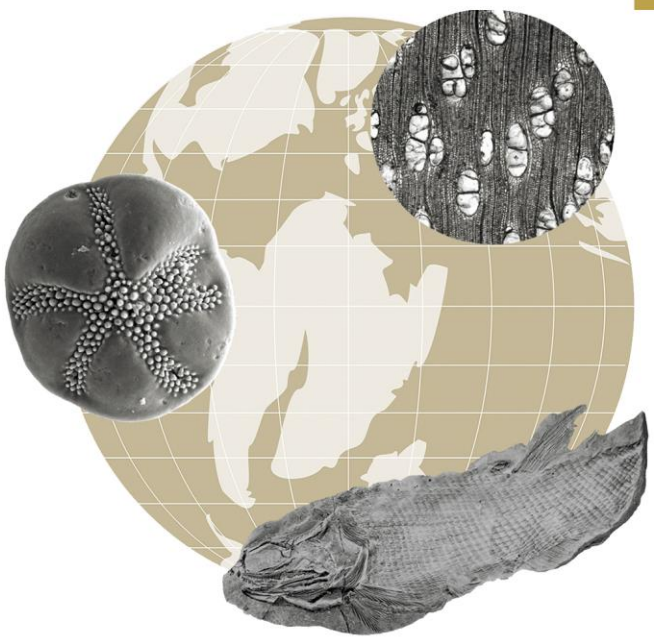

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New evidence on the nasopharyngeal and paranasal systems in sebecid crocodyliforms: the case of *Sebecus ayrampu*

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Running Header: Bravo et al.: Internal rostral anatomy of *Sebecus ayrampu*.

Short Description: This study describes the internal rostral anatomy of *Sebecus ayrampu* using CT data, detailing its general internal nasal structures.

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Abstract. Sebecidae is a clade of notosuchian crocodyliforms that includes mainly terrestrial predators from the Paleogene of South America. Its anatomical features are mostly known from external cranial morphology, whereas the neurocranial and internal anatomy remain largely unexplored. Here, we investigate the internal rostral anatomy of *Sebecus ayrampu* based on computed tomography (CT) data, in order to better understand the nasopharyngeal ducts and paranasal sinus system in this enigmatic group, as well as the implications for the evolution of these structures in Crocodyliformes. In this way, we expand the sampling within Notosuchia and provide new insights into their cranial pneumaticity, the development of glandular structures, and functional morphology.
Key words. Mealla Formation. Northwestern Argentina. Paleocene. Notosuchia. Sebecoidea. Sebecidae.

Resumen. Nueva evidencia sobre los sistemas nasofaríngeo y paranasal en cocodriliformes sebécidos: el caso de *Sebecus ayrampu*. Sebecidae es un clado de crocodyliformes notosuquios que incluye principalmente depredadores terrestres del Paleógeno de América del Sur. Sus rasgos anatómicos son conocidos principalmente por su anatomía craneal externa, mientras que su anatomía neurocraneana e interna permanecen poco exploradas. En este trabajo, investigamos la anatomía interna del rostro de *Sebecus ayrampu* basándonos en datos de tomografía computada (TC), con el fin de comprender el conducto nasofaríngeo y el sistema de senos paranasales en este enigmático grupo, así como las implicaciones para la evolución de estas estructuras en Crocodyliformes. En este sentido, expandimos el muestreo dentro de Notosuchia y aportamos nuevos conocimientos sobre la neumaticidad craneal, el desarrollo de estructuras glandulares y morfología funcional.
Palabras clave. Formación Mealla. Noroeste argentino. Paleoceno. Notosuchia. Sebecoidea. Sebecidae.

Introduction

Sebecidae constitutes an extinct clade of notosuchian crocodyliforms characterized by distinctive morphological adaptations that markedly differentiate them from extant crocodylians (Colbert, 1964; Gasparini, 1984; Buffetaut & Marshall, 1991; Gasparini et al., 1993; Pol & Powell, 2011; Kellner et al., 2014; Sellés et al., 2020; Bravo et al., 2021; Martin et al., 2023). Sebecids, along with some related non-South American forms clustered in Sebecoidea (Bravo et al., 2025), were the only notosuchians that survived the end Cretaceous mass extinction event. During the Cenozoic, sebecids occupied a prominent ecological role as terrestrial predators in different regions of South America (Bravo et al., 2025, and the references cited therein). Their tall, laterally compressed, and elongated skull, ziphodont dentition, along with the presence of proportionally long limbs has traditionally been interpreted as evidence of an active ambulatorial predatory lifestyle in predominantly continental environments (Paolillo & Linares, 2007; Pol et al., 2012; Kellner et al., 2014; Sellés et al., 2020; Martin et al., 2023).

Despite the growing interest this group has received in recent decades, numerous aspects of their internal cranial anatomy, particularly in the rostral region, are insufficiently understood (Sellés et al., 2020; Bravo et al., 2022). This lack of information is particularly relevant given the differing hypotheses regarding the phylogenetic position of Sebecidae within Notosuchia (sensu Leardi et al., 2024). Several studies have recovered sebecids as the sister group of Baurusuchia within Sebecosuchia (e.g., Pol & Powell, 2011; Kellner et al., 2014; Leardi et al., 2018; Bravo et al., 2025), whereas others have proposed a closer relationship with Peirosauridae, placing both clades within Sebecia (e.g., Larsson & Sues, 2007; Pinheiro et al., 2018, 2023; Geroto & Bertini, 2019). Previous studies have primarily focused on external cranial morphology or broad phylogenetic analyses, often overlooking the detailed examination of rostral elements and their associations with internal structures in

the nasal cavity and secondary palate (Colbert, 1964; Gasparini, 1984; Buffetaut & Marshall, 1991; Gasparini et al., 1993; Pol & Powell et al., 2011; Kellner et al., 2014; Bravo et al., 2021; Martin et al., 2023).

The nasal cavity of extant crocodylians, as in other archosaurs, comprises a complex system of respiratory and olfactory passages extending from the external naris to the pharynx (e.g., Parsons, 1959, 1970; Saint Girons, 1979; Witmer, 1995). The external naris opens into a vestibular region that continues posteriorly into the cavum nasi propium, which includes an anterior respiratory portion and a more dorsal and posterior olfactory region (e.g., Saint Girons, 1979). Ventral to the nasal cavity, the primary choana communicates with the nasopharyngeal duct, which extends posteriorly to the secondary choana and the pharynx (Parsons, 1970; Witmer, 1995). In addition, extant crocodylians possess a series of paranasal recesses associated with the maxilla, lacrimal, prefrontal, palatine, and other rostral bones, forming a complex pneumatic system whose osteological correlates can be recognized in fossil archosaurs (Witmer, 1995; Witmer & Ridgely, 2008; Bourke & Witmer, 2023).

Consequently, the study of internal cranial anatomy can provide valuable information for reconstructing soft-tissue organization, airflow pathways, and evolutionary modifications of the rostral region in extinct crocodyliforms. Recent advances in computed tomography and digital reconstruction techniques have greatly improved the study of internal cranial anatomy in fossil archosaurs, allowing detailed examinations of the relationships between osteological structures and the nasal cavity (e.g., Witmer & Ridgely, 2008; Fonseca et al., 2020; Cowgill et al., 2022; Puértolas-Pascual et al., 2022; Serrano-Martínez et al., 2025). These studies have demonstrated there is considerable variation in the morphology of the nasal cavity and associated paranasal recesses among crocodyliforms and other archosaurs and can provide important information regarding their cranial evolution, phylogenetic relationships, and ecological adaptations. However, despite the growing body of information available for

several crocodyliform lineages, the internal organization of the nasal cavity and associated rostral structures in Sebecidae remains poorly documented (e.g., Busbey, 1995; Sellés et al., 2020; Bravo et al., 2022).

The rostral region of sebecids can provide insights into their ecology and feeding strategies and can also represent a valuable source of characters for resolving their phylogenetic relationships within Notosuchia. This study aims to provide a detailed description of the rostral anatomy of *Sebecus ayrampu* Bravo et al., 2021 (specimen PVL 2606), in order to contribute to the understanding of cranial morphology in the group and to discuss its functional and systematic implications.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; **BP**, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa; **MMP**, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia," Mar del Plata, Buenos Aires, Argentina; **PVL**, Paleontología de Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Tucumán, Argentina.

Anatomical abbreviation. al, alveolus; **ants**, antorbital sinus; **aod**, antorbital depression; **aspp**, ascending process of the palatine; **ch**, choana; **dml**, dorsal margin of lacrimal; **dt**, dentary; **en**, external narina; **lac**, lacrimal; **lcd**, nasolacrimal duct; **lcs**, lacrimal sinus; **mch**, meckelian canal; **md**, neurovascular canal for the maxillary division of the trigeminal nerve (V2); **msph**, mandibular symphysis; **mx**, maxilla; **mxs**, maxillary sinus; **n**, nasal; **nc**, nasal cavity; **ng**, nasal gland; **nvd**, neurovascular canal; **pal**, palatine; **pas**, palatine sinus; **pfs**, prefrontal sinus; **phd**, nasopharyngeal duct; **phs**, nasopharyngeal septum; **pmx**, premaxilla; **pt**, pterygoid; **pts**, pterygoid sinus; **pvs**, postvestibular sinus; **sp**, splenial; **th**, tooth; **thr**, tooth root.

Materials and methods

Material. The present study is based on the holotype specimen of *Sebecus ayrampu*, housed in the paleontological collection of the Facultad de Ciencias Naturales e Instituto Miguel Lillo (PVL 2606), and collected in the Mealla Formation in northwestern Argentina (Jujuy province; see Bravo et al. 2021). The specimen consists of a well-preserved partial skull, including most of the rostral region, with elements such as the premaxillae, maxillae, nasals (among other), and elements of the secondary palate. In this study, partially preserved elements not described in the original publication of *Sebecus ayrampu* were identified, including the lacrimal, prefrontal, and vomer (Figs. 1, 2A-I).

Methods. In order to investigate the internal morphology of the rostrum, the specimen was scanned using a medical-grade computed tomography (CT) scanner (Siemmens Healthineers scanner; 500 slices of 0.6 mm thickness, voltage of 130 kVp, pixel size 0.461781 mm, X-Ray tube current 103 mA) at Radiological center Mendez Collado, Tucumán, Argentina. The CT results were used to describe the internal anatomical features in detail. Anatomical terminology follows the conventions established in recent crocodyliform cranial studies (e.g., Kley et al., 2010; Pol et al., 2014; Darlim et al., 2021). The resulting images were visualized and segmented using Materialise Mimics v. 21 (Materialise NV, Leuven, Belgium), in which all measurements were subsequently obtained (Table 1). The measurement protocol and data table (Table S1) are provided in the Supplementary Online Information.

The description of the internal cranial morphological features primarily follows the terminology adopted in recent studies and key reference works on Crocodyliformes (e.g., Witmer & Ridgely, 2008; Dias et al., 2020; Fonseca et al., 2020; Bourke & Witmer, 2023). Interpretations of soft-tissue-related structures were based on the Extant Phylogenetic Bracket (EPB) approach (Witmer, 1995) and comparisons with osteological correlates observed in extant crocodylians.

Systematic Paleontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone & Whybrow, 1983

Notosuchia Gasparini, 1971 [Leardi et al., 2024]

Sebecoidea Simpson, 1937 [Bravo et al., 2025]

Sebecidae Simpson, 1937 [Leardi et al., 2024]

Sebecus Simpson, 1937

Type species. *Sebecus icaeorhinus* Simpson, 1937

Included species. *Sebecus icaeorhinus* Simpson, 1937; *Sebecus querejazus* Buffetaut y Marshall, 1991; *Sebecus huilensis* Langston, 1965; *Sebecus ayrampu* Bravo et al., 2021.

Sebecus ayrampu Bravo et al., 2021

Figures 1-4

Holotype—PVL 2606, anterior portion of the skull and mandible. Distal fragment of a left femur.

Stratigraphic and geographic occurrence—Mealla Formation, late Paleocene, western slopes of the Sierras de Mal Paso, near the locality of Mina Aguilar, Jujuy Province, Argentina.

Diagnosis— A sebecid mesoeucrocodylian characterized by the following unique combination of features (autapomorphies marked with an asterisk): palatal surface of the premaxilla markedly concave; sagittal maxillary torus extending from the premaxillae*; alveolar region of the premaxilla vertically descending relative to the rest of the palatal surface of the maxilla*; deep lateral premaxillary fossa for the hypertrophied dentary tooth, with a well-defined anterior crest-like margin*; rostral ornamentation pattern shifting from

semicircular pits in the anterior region to elongated grooves in the posterior region; palatine with a long and gracile posterolateral process ending in a blunt tip; anterior margin of the choana V-shaped; presence of a diastema posterior to the fifth mandibular tooth; and hypertrophied development of the second maxillary tooth*.

Description and comparisons

Premaxilla. The preserved portion corresponds to the posterior third of the premaxillae (Fig. 1A). In this region, a posterior expansion behind the external nares is observed, from which the third and fourth premaxillary alveoli emerge (Fig. 2A-B), as seen in other sebecoid taxa (e.g., *Ayllusuchus fernandezi* Gasparini, 1984, *Bretesuchus bonapartei* Gasparini et al., 1993, *Sebecus icaeorhinus* and *Ogresuchus furatus* Sellés et al., 2020). The roots of the left third and fourth premaxillary teeth are preserved. In the pulpar cavity of third premaxillary teeth of *Sebecus ayrampu*, up to two replacement teeth can be observed (Fig. 1B). The height of these roots is notable, extending dorsally to almost reach the nasal contact, resulting in an extraordinarily deep alveolar cavity (Figs. 1B; 2A). A similar deep alveolar cavity is present in most crocodyliforms that have a hypertrophied posterior premaxillary tooth (e.g., *Notosuchus*; Lecuona and Pol, 2008). The premaxilla bears neurovascular canals connecting to the external and palatal foramina, which would have supplied and innervated the rostral integument and the soft palate (Fig. 2B). Additionally, there is a neurovascular canal originating from the foramen–maxilla palatal located over the premaxilla contact. This latter feature is shared among most notosuchians (e.g., *Ayllusuchus*, *Comahuesuchus* Bonaparte, 1991, *Baurusuchus* Price, 1945, *Montealtosuchus* Carvalho et al., 2007, *Araripesuchus* Price, 1959), with the exception of sphagesaurids, in which this palatal foramen is absent.

Maxilla. The maxillary alveoli are equidistant and decrease progressively in size posteriorly, except for the second maxillary tooth (m2) that is hypertrophied relative to the first (Figs. 1B;

S1A). The dental roots are slightly posterodorsally curved and, up to the third tooth, are deeply embedded within the maxilla (Figs. 1B; 2D; S1A). In *Sebecus ayrampu*, the root of the hypertrophied maxillary tooth reaches 70% of the maximum rostral height at the level of the corresponding alveolus (Fig. 1B). In the analysed *Sebecus icaeorhinus* specimen (MMP 235), the root of the hipertrophied third tooth is not preserved (Fig. S1B). This condition is shared with *Bretesuchus bonapartei*, in which it is evidenced by the lateral bulge of the maxilla produced by the enlarged tooth root, and is similar in *Barinasuchus alverloi* Paolillo and Linares, 2007 (60%). In contrast, in *Ogresuchus furatus*, the tooth root reaches 50% of the maximum height of the maxilla (Fig. S1C). In the other oreinirostral notosuchians, such as baurusuchids, the root of the hypertrophied maxillary tooth can exceed 70% (e.g., *Campinasuchus dinizi* Carvalho et al., 2011, 76%; *Aphaurosuchus scarafacies* Darlim et al., 2021, 82% Fig. S1D). The posterodorsal extension of the dental roots within the maxilla produces protuberances on the lateral surface of the rostrum in sebecids and baurusuchians. In *Sebecus ayrampu* and Lumbrera form, this largest protrusion is located in the hypertrophied second tooth root, whereas in *Bretesuchus* and *Barinasuchus* it is located at the hypertrophied third tooth root, as in *Ogresuchus furatus* and baurusuchians (e.g., *Aphaurosuchus scarafacies*, *Baurusuchus salgadoensis* Carvalho et al., 2005). In peirosaurids (e.g., *Montealtosuchus*) and uruguaysuchids (e.g., *Araripesuchus gomesii* Price, 1959) the third maxillary tooth is the one with the largest development (Soto et al., 2011; Pol et al., 2014), although their protuberances are less developed. Posteriorly, the root height of *Sebecus ayrampu* decreases gradually toward the last maxillary tooth (Fig. S1A) as in *Sebecus icaeorhinus* (Fig. S1B), a common feature in Crocodyliformes. In contrast, some eusuchians exhibit a biphasic pattern correlated to variations in tooth size, with root height decreasing to mid-rostrum, increasing in the posterior third, and subsequently decreasing

again toward the end of the tooth row (e.g., *Alligator mississippiensis* Daudin, 1802; Fig. S1E).

In the pulpar cavity of first maxillary teeth of *Sebecus ayrampu*, there are up to two replacement teeth, arranged vertically, with one developing within the root of its predecessor (Fig. 1B). This pattern is also observed in *Notosuchus terrestris* Woodward, 1896 even though only a single replacement tooth per pulp cavity is recorded (Navarro et al., 2022). This suggests the presence of more frequent tooth replacement rate in sebecids relative to *Notosuchus*.

Two neurovascular canals run parallel to the nasopharyngeal duct of *Sebecus ayrampu*, extending anteroposteriorly along the alveolar margins (Fig. 2C-F). These canals correspond to passages for the maxillary division of the trigeminal nerve, from which smaller neurovascular branches arise and open onto the surfaces of the palatal and lateral processes of the premaxilla and maxilla. Due to the limited resolution of the CT data, the smaller neurovascular canals cannot be followed in detail, preventing a precise reconstruction of their trajectories and their respective entry and exit points within the rostrum. In peirosaurids (e.g., *Gasparinisuchus peirosauroides* Martinelli et al., 2012 and *Uberabasuchus terrificus* Carvalho et al., 2004), the canal to passage for the maxillary division of the trigeminal nerve shows a greater degree of branching than in any other notosuchians (Barrios, pers. obs.), resembling to some extent that of the Crocodylia.

Lacrimal. The lacrimal of *Sebecus ayrampu* exhibits features similar to those of the lacrimal of Lumbrera form. These bear a smooth-surfaced antorbital depression (aod; Fig. 1B), bounded by well-defined margins as in *Ayllusuchus fernandezi*, and possibly in *Sebecus querejazus* Buffetaut and Marshall, 1991. On the internal side of this depression, on the left lacrimal, a nasolacrimal duct can be observed (Fig. 3A-B, D-E), running obliquely anterodorsally and opening into a nasal cavity.

Although neither the anterior margin of the lacrimal nor the posterior margin that forms the anterior edge of the orbit has been preserved, the dorsal margin is complete. This dorsal margin contacts the nasal and prefrontal and bears a crest that forms a shelf over the antorbital depression, which would have formed part of the facet for the anterior palpebral.

Prefrontal. The prefrontals are poorly preserved but are positioned in the dorsal plane, dorsal to the oblique crest of the lacrimal. Internally and medial to the nasolacrimal duct, there are small diverticula, corresponding to the prefrontal sinus, as commonly present in other mesoeucrocodylians (e.g., *Araripesuchus*, *Uberabasuchus*, *Alligator*, *Caiman* Spix, 1825; Turner, 2006; Witmer & Ridgely, 2008; Fonseca et al., 2020).

Palatine. Both palatines are completely preserved in *Sebecus ayrampu.* This element is composed by a horizontal lamina and an ascending dorsal process that forms the base of the lateral wall of the nasopharyngeal duct as in other notosuchians (e.g., *Sebecus icaeorhinus*, *Aphaurosuchus scarafacies*, *Lomasuchus palpebrosus* Gasparini et al., 1991, *Uruguaysuchus aznarezi* Rusconi, 1933). The ascending process of *Sebecus ayrampu* extends dorsomedially towards the pterygoid contact. However, the contact region is fractured/crackled, making it impossible to determine the suture between both elements.

Pterigoid. In *Sebecus ayrampu*, only the region forming the laterodorsal wall of the choanal fossa is preserved. The lateral wall of the choanal fossa is obliquely oriented forming an angle of 45° relative to the sagittal axis, as in other sebecids, such as *Sebecus icaeorhinus* and *Sahitisuchus fluminensis* Kellner et al., 2014. This condition is similar to that observed in peirosaurids (e.g., *Montealtosuchus arrudacamposi* and *Lomasuchus palpebrosus*) and uruguaysuchids (e.g., *Araripesuchus buitreraensis* Pol & Apesteguia, 2005, *Anatosuchus minor* Sereno et al., 2003). Although no pneumatopore is visible, its absence cannot be confirmed due to poor preservation of this element.

Vomer. As in other Crocodylomorpha, the vomers are paired, laminar, and very delicate bones. These elements can be recognized in *Sebecus ayrampu* through the computed tomography (Fig. 2D-F). Unlike extant crocodylians, the vomers in this taxon are particularly tall, especially along their midlength. In *Notosuchus terrestris*, a broad but subhorizontally oriented vomer has been described (Barrios et al., 2017; 2021a), suggesting the presence of marked morphological differences in the vomer among crocodyliforms.

Nasal cavity and nasopharyngeal duct. The nasal cavity is well preserved in *Sebecus ayrampu*, it is longer than wide and gradually tapers anteriorly. It extends posteriorly from the external nares, which are formed by the premaxillae and nasals, and continues as the nasopharyngeal duct between the nasals, maxillae, vomers, palatines, and pterygoids. The nasopharyngeal duct ultimately opens into the choana, which is enclosed by the palatines and pterygoid. The nasal cavity is dorsoventrally divided into two regions: the dorsal *cavum nasi proprium* (nc; Fig. 3) and the ventral nasopharyngeal duct (phd; Fig. 3) (*sensu* Witmer and Ridgely, 2008). This division becomes particularly evident at the level of the fourth maxillary tooth.

The true nasal cavity (*cavum nasi propium*) is anteroposteriorly divided into two regions, the respiratory region (anterior) and the olfactory region (posterodorsally) (Fig. 3B). The latter region is evidenced by the widening in the posterior half of the endocast of the nasal cavity. It communicates anterolaterally with the paranasal sinuses (postvestibular and antorbital; see below), and posteriorly, it would have connected with the olfactory bulb (*sensu* Witmer & Ridgely, 2008). The respiratory region, on the other hand, is anteroposteriorly long but transversely narrow. The olfactory region partially preserved in *Sebecus ayrampu*, corresponds to the posterodorsal part, which is the widest part of the nasal cavity (Tabla 1). The olfactory region has a globular morphology similar to that observed in other notosuchians, such as baurusuchids (*Campinasuchus, Aphaurosuchus, Wargosuchus*

298 Martinelli & Pais, 2008), sphagesaurians (*Caipirasuchus* Iori & Carvalho, 2011, *Notosuchus*,
299 *Yacarerani* Novas et al. 2009), uruguaysuchids (*Araripesuchus*), and peirosaurids
300 (*Uberabasuchus*, *Lomasuchus*, *Gasparinisuchus*) (e.g., Fonseca et al., 2020; Darlim et al.,
301 2021). In *Uberabasuchus terrificus*, the olfactory region is well developed, but it is less
302 expanded than in *Campinasuchus dinizi*, in which it is comparable to the condition observed
303 in *Sebecus ayrampu*.
304 The ventral region of the nasal cavity corresponds to the nasopharyngeal duct, which
305 is dorsoventrally tall and bounded by the laterodorsal walls of the vomers, maxillae,
306 palatines, and pterygoids. Along its anteroposterior course, the duct gradually expands
307 dorsoventrally while the dorsal half narrows lateromedially. In *Sebecus ayrampu*, the highest
308 portion of the nasopharyngeal duct exceeds 50% of the maximum height of the nasal cavity
309 (Fig. 3A, Table 1). A dorsoventrally tall nasopharyngeal duct was also described in the
310 baurusuchid *Campinasuchus dinizi* (Fonseca et al., 2020). In contrast, in peirosaurids such as
311 *Lomasuchus palpebrosus* and *Gasparinisuchus peirosauroides*, the highest portion of the
312 nasopharyngeal duct is below 50% of the maximum height of the nasal cavity (Barrios, pers.
313 obs.). In addition, when standardized the volumetric proportion of the nasopharyngeal duct
314 and nasal cavity is comparatively low relative to extant Crocodylia (Table 1), which we
315 interpret as reflecting a dorsoventrally expanded and relatively enlarged olfactory region of
316 the nasal cavity. In cross-section, the nasopharyngeal duct has a subtriangular shape with
317 rounded vertices. Dorsally, it is bounded by the vomers (anterior portion), the palatines
318 (posterior portion), and the pterygoids (the most posterior portion). At the level of the
319 palatines, the duct is divided by a tall median septum formed by the pterygoids, a common
320 feature among Crocodyliformes.
321 Within the nasal cavity of *Sebecus ayrampu*, just ventral to the nasal bones, there are
322 protuberances that represent the cast of elongated structure extending along the nasomaxillary

suture. Among notosuchians, the osteological correlates in the nasals of a similar structures have been observed in, for example, *Campinasuchus dinizi*, *Aphaurosuchus scarafacies*, *Araripesuchus gomesii*, and *Yacarerani boliviensis* Novas et al., 2009; however, in all these notosuchians these are proportionally shorter relative to the total length of the nasals than in *Sebecus ayrampu*. Based on its morphology and position, this structure is interpreted as the cast of the nasal glands *sensu* Witmer (1997), which are present in all extant sauropsids (see below).

Paranasal sinuses. The maxilla of *Sebecus ayrampu* is characterized by the presence of pneumatic sinuses in the palatal branch and in the lateral walls, which corresponds to the paranasal sinuses (maxillary, postvestibular and antorbital respectively) described for other crocodyliforms (e.g., extant eusuchians and baurusuchians; Witmer and Ridgely, 2008; Fonseca et al., 2020; Young et al., 2024). These sinuses are connected and occupy the anterior and middle sectors of the maxilla, being reduced in the posterior half (Fig. 3A-C). In *Sebecus ayrampu*, as in other notosuchians (e.g., *Gasparinisuchus peirosauroides*, *Simosuchus clarki* Buckley et al., 2000), this sinuses are partially subdivided by trabeculae, resembling the condition of Crocodylia, although not reaching the degree of development present in that clade.

The maxillary sinus can be recognised between the postvestibular and antorbital sinuses, internally in the palatal branch of the maxilla. It is present but is small and extends between the first and third maxillary teeth, as in *Campinasuchus dinizi* (mxs in Fig. 3C). This differs from *Simosuchus clarki*, where maxillary sinus is more extensive posteromedially. In *Araripesuchus buitreraensis* (MPCA-PV 515), the maxillary and palatine sinuses are exposed due to a fracture (Fernandez Dumont et al., 2020). The sinus within the maxilla appears to be well developed and corresponds to the maxillary sinus.

In *Sebecus ayrampu*, a postvestibular sinus is recognized immediately posterior to the premaxilla–maxilla contact, oriented vertically up to the vicinity of the premaxilla–nasal–maxilla contact (pvs in Fig. 3A-D). The postvestibular sinus continues and opens (without clearly defined boundaries) into the antorbital sinus. In *Campinasuchus dinizi* a postvestibular sinus is developed anterior to the third tooth of the maxilla, but it is not possible to determine how developed it is due preservation of this region (Fonseca et al., 2020). Both in *Sebecus ayrampu* and baurusuchians (e.g., *Campinasuchus dinizi* and *Aphaurosuchus escharafaciesi*), the postvestibular sinus is formed by small diverticula separated by trabeculae, whereas in peirosaurids (e.g., *Uberabasuchus terrificus*) the postvestibular sinus is present as a single cavity. Although the maxilla of *Araripescuhcus tsangatsangana* Turner, 2006 was described as lacking internal struts and sinuses (Turner, 2006), CT data reveal the presence of a postvestibular sinus in one of the analyzed specimens.

The antorbital sinus of *Sebecus ayrampu* extends posterodorsally at the lateral level of the primary choana (ants in Fig. 3A-D) and includes numerous smaller cavities or diverticula. These are distributed within the anterior half of the maxilla and posteriorly between the maxilla and the lacrimal. This sinus extends into the palate only to a limited extent, with small diverticula restricted to the anterior margins of the palatine. In the peirosaurids (e.g., *Lomasuchus palpebrosus*, *Gasparinisuchus peirosauroides*, *Uberabasuchus terrificus*) the antorbital sinus is comparatively poorly developed. In *Campinasuchus dinizi*, the antorbital sinus is more limited, extending within the ventral half of the maxilla, from the level of the fourth tooth to just past the fifth (Fonseca et al., 2020). In addition, in *Notosuchus terrestris*, paranasal sinuses are practically absent.

The palatine is pneumatized and the palatine sinus is located at the base of the ascending process (lateral to the nasopharyngeal duct) and the medial half of the horizontal palatal lamina (pas in Fig. 3A-C), as in *Sebecus icaeorhinus* (MMP 235), *Simosuchus clarki*

(Kley et al., 2010), *Araripesuchus buitreraensis* and living crocodylians (Witmer & Ridgely, 2008). However, in *Araripesuchus* and extant taxa (e.g., *Caiman*, *Crocodylus* Laurenti 1768), the pneumatization is more developed, with broader cavities spanning the entire lateromedial length of the palatines.

Dorsal to the choana, the palatine sinus of *Sebecus ayrampu* expands and continues into the pterygoid sinus (pts in Fig. 3A-B, E), which extensively invades the preserved anterior portion of the pterygoid and communicates with the nasopharyngeal duct, as in *Sebecus icaeorhinus* and *Campinasuchus dinizi*. In sphagesaurids, such as species of *Caipirasuchus* Iori & Carvalho, 2011 (e.g., *C. paulistanus* Iori & Carvalho, 2011, *C. montealtensis* Andrade & Bertini, 2008), the primary pterygoid chamber forms a type of paranasal sinus, whereas a secondary pterygoid chamber appears to represent an internal recess of the pterygoid bone (Dias et al., 2020), thereby developing a more complex pterygoid sinus system than in other notosuchians described to date.

Below the nasolacrimal duct, a sinus is identified, suggesting that the lacrimal is somewhat pneumatized, at least in its posteroventral portion (lcs in Fig. 3A-E), as evidenced for *Campinasuchus dinizi* (Fonseca et al., 2020) and *Aphaurosuchus escharafacies*. The presence of a lacrimal sinus in these taxa contrasts with the condition of the peirosaurids (e.g., *Gasparinisuchus peirosauroides*, *Uberabasuchus terrificus*), which do not have a pneumatized lacrimal. The prefrontal sinus in *Sebecus ayrampu* is located anterior to the prefrontal pillar of the left side of the rostrum. Due to the degree of preservation of the prefrontal, it is not possible to determine its total extent. In *Araripesuchus tsangatsangana*, the prefrontal sinus (prefrontal recess; Turner, 2006) is smaller with respect to the extant neosuchians, while *Campinasuchus dinizi* and *Aphaurosuchus escharafacies* lack the prefrontal sinus.

Mandible. Internally, the mandibular rami of *Sebecus ayrampu* are cracked and filled with sediment. However, the neurovascular structures and Meckelian canal can be recognized (mch; Fig. 4). The splenial is a laminar element that contacts the dentary anteroposteriorly both dorsally and ventrally, forming the medial wall of the Meckelian canal and the mandibular canal (Fig. 4C). Immediately posterior to the mandibular symphysis, the *foramen intermandibularis oralis* can be identified. This foramen is elongated (slot-like) as in *Baurusuchus salgadoensis*, and has a similar position to that of other notosuchians (e.g., *Sebecus huilensis* Langston, 1965, *Baurusuchus salgadoensis*, *Hamadasuchus* Buffetaut, 1994; *Caipirasuchus stenognathus* Pol et al., 2014), except in some basal notosuchians (e.g., *Araripesuchus gomesii*, *Anatosuchus minor*), in which the foramen lies just posteriorly to the splenial-splenial suture at the mandibular symphysis. The dentary is also a laminar element, though dorsally it forms a narrow alveolar margin and ventrally is lateromedially broader and houses the canal for the mandibular division of the trigeminal nerve, which projects anteriorly and internally through the dentary (ndv; Fig. 4). Additionally, the dentary contributes to the lateroventral wall of the Meckelian and mandibular canals.

Discussion

Nasal cavity and nasopharyngeal duct. The internal anatomy of the rostrum of *Sebecus ayrampu* resembles in some features that of the baurusuchian *Campinasuchus dinizi* and *Aphaurosuchus escharafacies*, revealing a set of morphological features that can be interpreted as supporting the monophyly of Sebecosuchia or as convergences due to their oreinirostral condition. These alternative interpretations depend on the phylogenetic placement of sebecoids, which is a topic still debated in recent phylogenetic analyses (Larsson & Sues, 2007; Pol et al. 2012; Geroto & Bertini, 2019; Pinheiro et al., 2018, 2023; Bravo et al., 2021, 2025). Among these features are (i) a lateromedially narrow and dorsoventrally high nasal cavity and nasopharyngeal duct (Table 1); (ii) the presence of a

broad posterior olfactory region; (iii) well-developed postvestibular and antorbital sinuses within the anterior half of the maxilla (compared with other notosuchians); (iv) a relatively reduced maxillary sinus developed within the anterior half of the maxilla (compared with Crocodylia); (v) the presence of poorly developed lacrimal sinuses; and (vi) a reduced degree of branching of the neurovascular canal for the maxillary division (V2) of the trigeminal nerve (CN V). These traits may provide an important source of new characters for evaluating phylogenetic hypotheses within Notosuchia and for assessing the relationships of Sebecidae in future studies of Crocodyliformes.

In *Sebecus ayrampu*, the nasal cavity is dorsoventrally undivided along the anterior half of the rostrum. Along the posterior half, the nasal cavity is divided dorsally into the olfactory region and ventrally in the nasopharyngeal duct. The narrow and high nasal cavity, mainly in the respiratory region, is a feature shared among sebecids, such as *Sebecus icaeorhinus* and the Lumbrera form (see Bravo et al., 2022). This particular structural organization, possibly associated with airflow dynamics, appears to be less complex than in other notosuchians, such as Peirosauridae (e.g., *Lomasuchus palpebrosus*) and Baurusuchia (e.g., *Campinasuchus dinizi*), in which ethmoidal elements are more developed (Barrios et al., 2021b). Although many notosuchians preserve the rostral region and there is significant external morphological variation in this region, the lack of tomographic data have resulted in the internal anatomy receiving little attention, and its potential functional or evolutionary implications remain largely unexplored. Recent studies of notosuchian internal anatomy indicated that at least some taxa (such as *Simosuchus*, Peirosauridae, Baurusuchia, Sphagesauria) have a relatively expanded olfactory region compared to neosuchians (Fonseca et al., 2020; Fachini et al., 2025). Because this region corresponds to the region of the nasal cavity associated with the olfactory epithelium, its relative expansion may potentially reflect an increase in the available sensory surface involved in odor detection (e.g., Dille et al.,

2025). Consequently, the dimensions of the olfactory region have been used as a proxy for the relative development of the olfactory system in crocodyliforms (e.g., Fonseca et al., 2020). In an ecological context, such expansion could be consistent with variation in the reliance on airborne chemical cues among taxa with contrasting lifestyles, given the importance of olfactory capabilities in terrestrial environments (e.g., Barrios, 2021b; Barrios et al., 2022; Fonseca et al., 2020). In contrast, aquatic or semi-aquatic taxa (such as thalattosuchians and living crocodylians) have proportionally smaller olfactory regions, and their nasal cavity is cylindrical and elongated, likely reflecting a shift toward other sensory modalities, such as mechanoreception and vision (e.g., Herrera et al., 2013; Pierce et al., 2017; Bowman et al., 2022; Bourke et al., 2022; Lessner et al., 2023; Young et al. 2024).

An considerably high nasopharyngeal duct (see Table 1) is likely related to a higher ventilation rate, allowing an increased airflow through the nasal passage, as previously suggested for the baurusuchid *Campinasuchus dinizi* and other archosaurs such as theropod dinosaurs and metriorhynchids (Witmer & Ridgely, 2008; Fonseca et al., 2020; Cowgill et al., 2022; Young et al., 2024). A larger air passage and greater inspiratory and expiratory volumes are likely associated with increased oxygen supply (elevated aerobic capacity), which would have important implications for sebecid physiology. However, osteological correlates alone are insufficient to infer metabolic rate. Available histological evidence indicates that some notosuchians do not exhibit the bone tissue organization typically associated with sustained high metabolic rates, suggesting that they did not reach endotherm-like metabolic levels (Cubo et al., 2020; Sena et al., 2025). Furthermore, the physiology of Notosuchia more broadly remains far from fully understood. Among extant reptiles, large terrestrial predators such as varanids (e.g., *Varanus komodoensis* Ouwens, 1912) display relatively high aerobic and metabolic capacities compared to most reptiles, yet they remain within the ectothermic physiological spectrum (Wood et al., 1977; Thompson &Withers,

1997; Clemente et al. 2009; da Silva et al., 2013). This comparison highlights that increased respiratory capacity does not necessarily imply endothermy, but may instead reflect elevated aerobic performance within an ectothermic framework.

Paranasal sinuses system. Paranasal pneumaticity in *Sebecus ayrampu* is represented by the postvestibular, antorbital, maxillary, palatine, pterygoid, lacrimal, and prefrontal sinuses, comparable to those of *Campinasuchus* and *Sebecus icaeorhinus* (e.g., Fonseca et al., 2020; Bravo et al., 2022; Young et al., 2024). These paranasal sinuses of these taxa are reduced relative to that observed in other notosuchia taxa such as *Simosuchus clarki*, *Caipirasuchus stenognathus*, and *Caipirasuchus paulistanus* Iori & Carvalho, 2011, in which it is more expanded and complex (Kley et al., 2010; Witmer & Ridgely, 2008; Dias et al., 2020) and resemble the condition of extant crocodylians.

In tetrapods, the paranasal sinuses are generally more developed in continental forms than in marine ones. In the case of Crocodylomorpha, thalattosuchians (particularly the pelagic metriorhynchids) exhibit a reduced sinus system compared with that of some notosuchians and eusuchians (Witmer & Ridgely, 2008; Kley et al., 2010; Fonseca et al., 2020; Cowgill et al. 2022). The morphology and distribution of the paranasal sinuses in the oreinirostral *Sebecus ayrampu* and *Campinasuchus dinizi* are intermediate between those of tubular longirostrine thalattosuchians (e.g., *Cricosaurus* Wagner, 1858) and platyrostral eusuchians (e.g., *Caiman*).

Several functions (e.g., respiratory, weight reduction, vocal resonators, thermal insulators) have been proposed for the paranasal sinuses, but none of these have been convincingly demonstrated for the different amniotes in which they are present (e.g., Witmer, 1997). On the other hand, the reduced paranasal pneumaticity in comparison with that of platyrostral crocodylians, may be linked to structural and biomechanical requirements of the narrow and high oreinirostral snout of *Sebecus ayrampu*, and other notosuchians (e.g.,

Campinasuchus dinizi, *Baurusuchus salgadoensis*; *Araripesuchus gomesii*, *Caipirasuchus paulistanus*). Unlike the platyrostral snout of extant crocodylians (that also lack an antorbital fenestra), an oreinirostral snout (such as that of *Sebecus*) is poorly suited to withstand torsion movements and tolerate better flexion movements (Rayfield & Milner, 2008). In fact, recent finite element analyses indicate that the oreinirostral skull of several notosuchians had greater overall resistance to vertical feeding-induced loads and tend to exhibit lower stress magnitudes than platyrostral skulls (Nieto et al., 2021; Srinivas et al., 2025). This increased resistance has been interpreted as a consequence of the dorsoventrally expanded and compact architecture of oreinirostral rostra, which efficiently dissipates stresses generated during biting and pull-back feeding behaviors (Moreno et al., 2008; Rayfield & Milner, 2008; Srinivas et al., 2025). A similar functional interpretation was previously suggested by Busbey (1986), who noted that the extant *Varanus komodoensis*, a large terrestrial predator with bladed teeth and a laterally compressed skull, tends to employ a bite-and-pull-back feeding strategy. Such behavior minimizes torsional stresses on the snout resulting from struggling prey and maximizes resistance to compressive forces. Hence, Busbey therefore suggested that similar cranial architectures in large terrestrial crocodyliform (e.g., Sebecidae and Baurusuchia) predators may reflect comparable feeding strategies. The specific biomechanical implications of the distinctive sebecid cranial morphology with reduced pneumaticity, however, remains to be investigated to better understand the ecology and paleobiology of this group, as well as their functional differences with Cretaceous oreinirostral notosuchians.

Nasal gland. In adult crocodylians, the nasal gland is relatively long with a dorsal position under the nasal bones (along the naso-maxillary suture) and medially to the nasolacrimal duct (Parsons, 1970; Dunson, 1976; Witmer, 1995, 1997). In *Sebecus ayrampu*, we interpret the two parasagittal eminences on the dorsal surface of the nasal cavity endocast, connecting the

nasolacrimal duct with the vestibule in the external naris, as the space that would have been occupied by the nasal gland. This is a groove running under the nasals and along the naso-maxillary suture as osteological correlates of the nasal gland (e.g., Witmer, 1995, 1997). . Also, the presence of such groove in the internal surface of the naso-lacrimal suture and the nasal cavity of *Sebecus ayrampu* suggests the first mention the presence of nasal glands in a notosuchian, as this osteological correlate is present in other taxa (e.g., *Araripesuchus gomesii* AMNH 24450, *Caipirasuchus montealtensis*, *Aphaurosuchus scarafacies*). Analogous structures have been described in other extinct crocodyliforms, primarily thalattosuchians in which they are hypertrophied as salt gland (e.g., *Pelagosaurus typus* Bronn, 1841, *Geosaurus araucanensis* Gasparini & Dellapé, 1976; Fernández & Gasparini, 2000, 2008; Gandola et al., 2006), in gavialoid neosuchians (e.g., *Argochampsa krebsi* Hua & Jouve 2004, *Portugalosuchus azenhae* Mateus et al., 2018; see Puértolas-Pascual et al., 2022 and Pligersdorffer et al., 2024), and in the protosuchid *Protosuchus haughtoni* Whetstone & Whybrow, 1983 (BP/1/4770; Cowgill et al., 2023). In most extant crocodylians, such as species of *Crocodylus rhombifer* Cuvier, 1807, *Gavialis gangeticus* Gmelin, 1789, and *Tomistoma schlegelii* Müller, 1838 the nasal glands occupy small concavities on the ventral surface of the nasals along the nasomaxillary suture (Taplin & Grigg, 1981; Taplin et al., 1982, 1985; Cowgill et al., 2023). The presence of a nasal gland in *Sebecus ayrampu* raises questions regarding the need for osmoregulation in Sebecidae (and more generally in Notosuchia), which should be examined in detail with further evidence. In fact, even in extant and extinct terrestrial reptiles, many aspects of their osmoregulatory physiology remain poorly understood and are insufficiently studied (e.g., homology, secretion mechanisms, regulation, distribution, embryology, evolution; Peaker & Linzell, 1975; Osmólska, 1979; Dantzler & Bradshaw, 2009; Babonis & Brischoux, 2012).

Conclusion

In this study, we present new anatomical information of *Sebecus ayrampu* based on data obtained through computed tomography (CT) scanning, including the first description of the nasal endocast anatomy of a sebecid. Among the novel features, we highlight the following: a transversely narrow respiratory region and a wide olfactory region of the nasal cavity; a dorsoventrally tall and broad nasopharyngeal duct occupying approximately 50% of the mean height of the nasal cavity; a nasolacrimal duct directed anteriorly ventral to the nasomaxillary crest; and an elongated parasagittal nasal gland connecting the nasolacrimal duct with the vestibule in the external naris, constituting the first anatomical interpretation of nasal gland osteological correlates in Notosuchia.

The paranasal pneumaticity of *Sebecus ayrampu* is comparable to that described for other continental notosuchians, principally with the baurusuchid *Campinasuchus dinizi* with identifiable postvestibular, maxillary, antorbital, lacrimal, which are less developed in comparison with the neosuchians. In *Sebecus ayrampu* also are observable a prefrontal, palatine and pterygoid sinuses.

Data accessibility

The three-dimensional reconstruction of the internal structure of the holotype of *Sebecus ayrampu* is available in the MorphoSource repository: https://www.morphosource.org/concern/media/XXXXXX.

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Figure captions

Figure 1. Holotype of *Sebecus ayrampu* (PVL 2606) from the Mealla Formation (Jujuy province, Argentina). **A**, Left lateral view; **B**, Dental implantation of the premaxillary and maxillary teeth (colored) in lateral view of the semitransparent rostrum; Roots of the functional teeth are highlighted in yellow, whereas replacement teeth are highlighted in red.

Abbreviations: aod, antorbital depression; dml, dorsal margin of the lacrimal; lac, lacrimal; mx, maxilla; m1-5, maxillary root; pal, palatine; pmx, premaxilla; pt, pteryogid; p3-4, premaxillary root. Scale bar equals 20 mm.

Figure 2. Transverse CT sections of the rostrum of *Sebecus ayrampu* (PVL 2606), with a reference image indicating the position of each section (**A**–**I**) along the horizontal axis. Abbreviations: al, alveolus; ants, antorbital sinus; aspp, ascending process of the palatine; ch, choana; dt, dentary; lac, lacrimal; lcd, nasolacrimal duct; lcs, lacrimal sinus; md, maxillary neurovascular canal; mx, maxilla; n, nasal; nc, nasal cavity; nvd, neurovascular canal; pal, palatine; pas, palatines sinus; pcm, maxillary pneumatic cavity; pfs, prefrontal sinus; phd, nasopharyngeal duct; phs, nasopharyngeal septum; pmx, premaxilla; pt, pterygoid; pts, pterygoid sinus; pvs, postvestibular sinus; th, tooth; thr, tooth root; v, vomers. Scale bar equals 20 mm.

Figure 3. Rostral endocranial anatomy of *Sebecus ayrampu* (PVL 2606) in **A**, lateral; **B**, dorsal; **C**, ventral; **D**, anterior; **E**, posterior views with rostrum rendered transparent. Blue, nasal cavity; violet, nasopharyngeal duct; green, paranasal sinuses; pink, nasolacrimal duct. Abbreviations: ants, antorbital sinus; ch, choana; en, external nares; lcd, lacrimal duct; lcs, lacrimal sinus; mxs, maxillary sinus; nc, nasal cavity; ng, nasal glands; pas: palatine sinus pfs, prefrontal sinus; phd, nasopharyngeal duct; pts, pterygoideal sinus; pvs, postvestibular sinus. Scale bar equals 20 mm.

Figure 4. Transverse CT section of the mandible of *Sebecus ayrampu* (PVL 2606), with a reference image indicating the position of each section (**A**-**C**) along the horizontal axis. Abbreviations: al, alveolus; dt, dentary; mch, meckelian channel; msph, mandibular symphysis; nvd, neurovascular duct; sp, splenial; th, tooth; thr, tooth root. Scale bar equals 20 mm.

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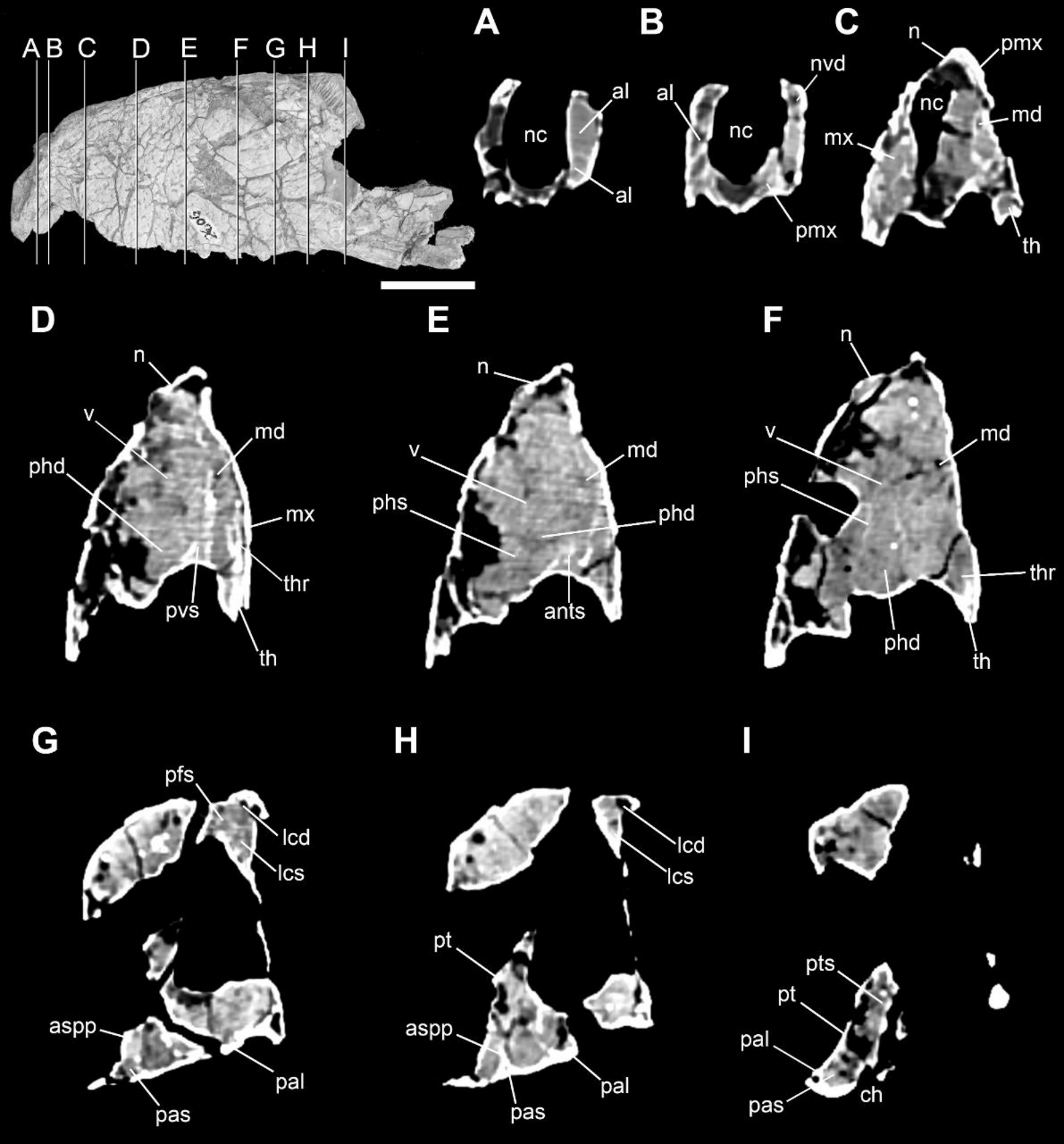
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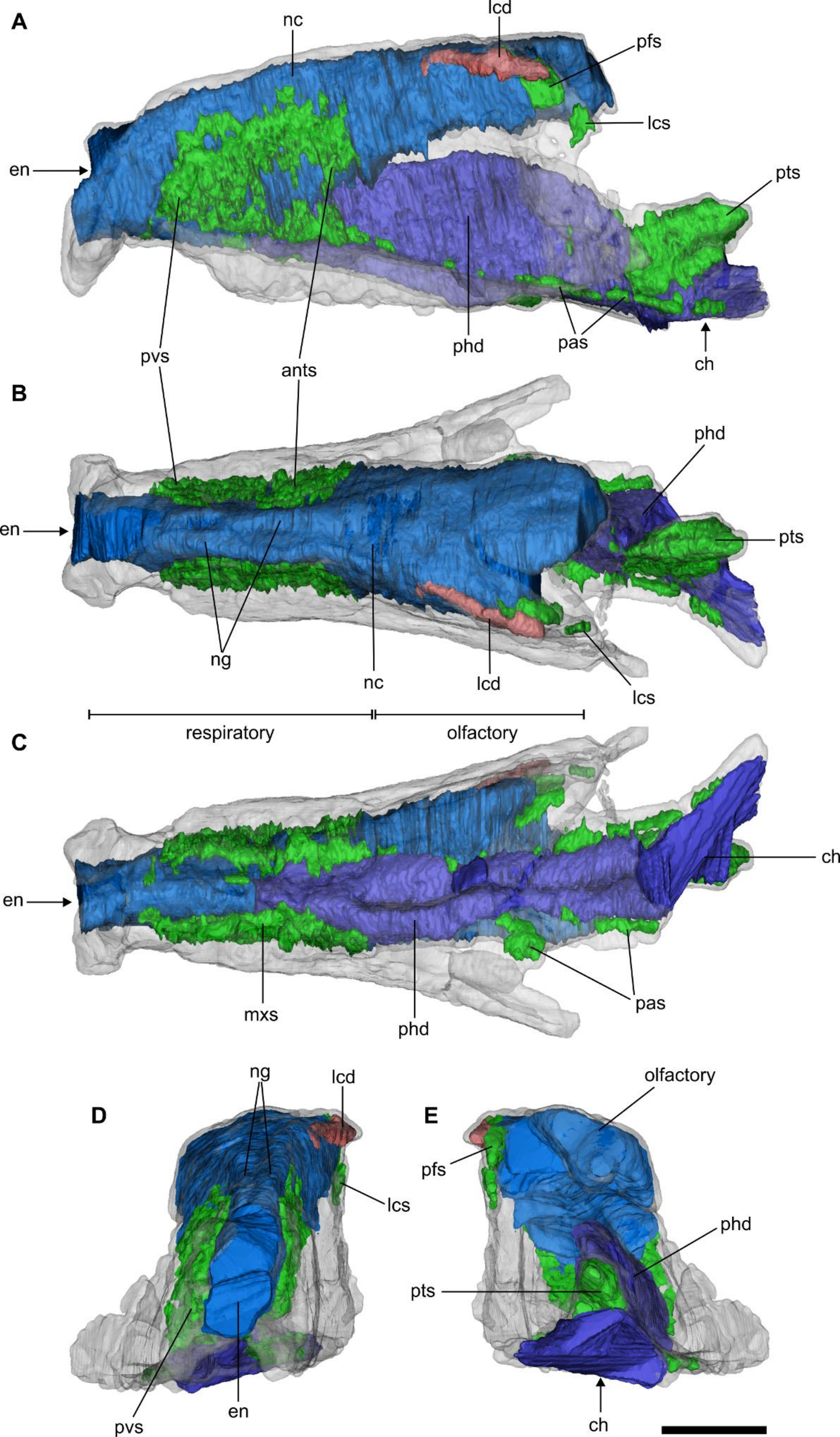
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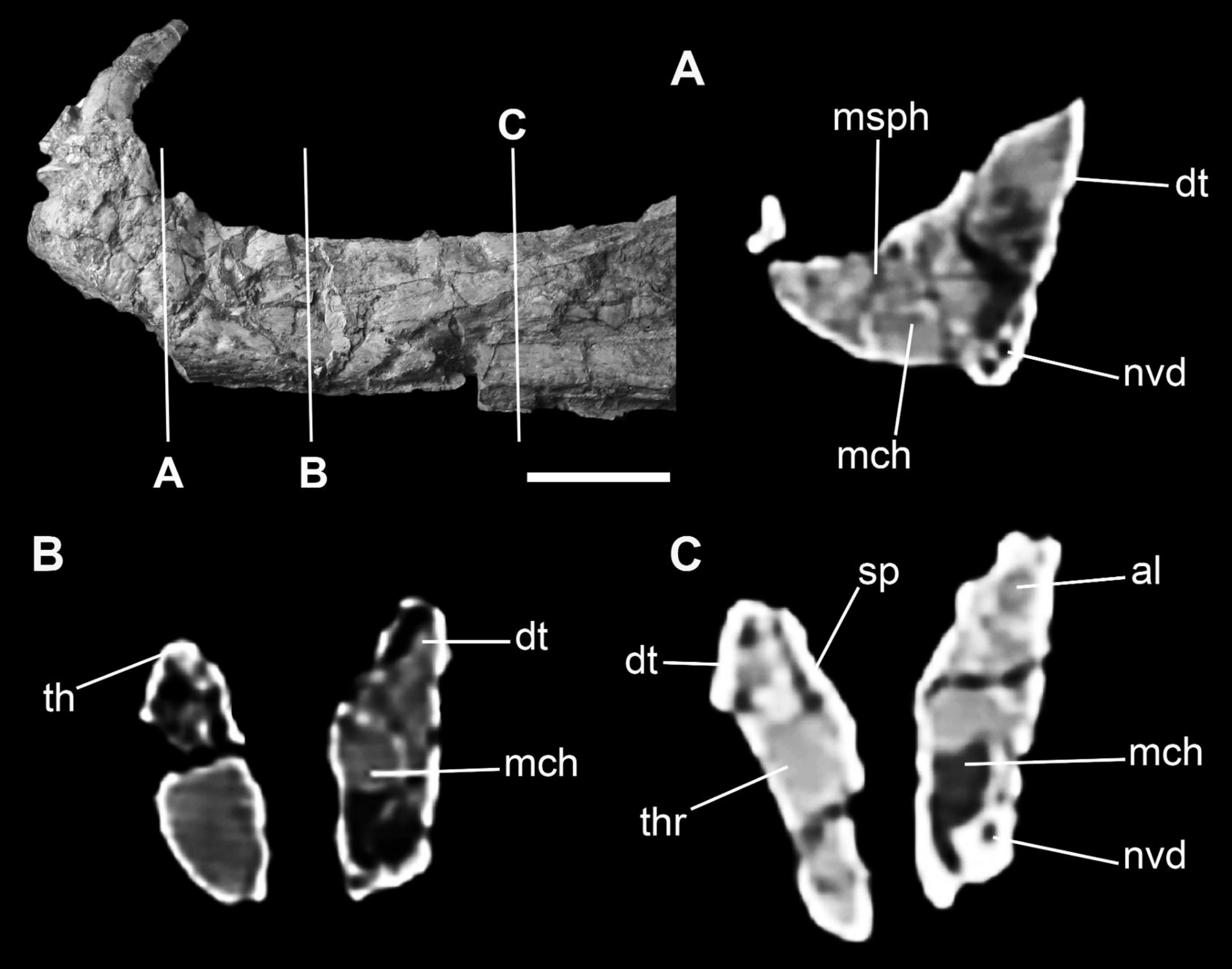
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Table 1. Measurements of the nasal cavity and nasopharyngeal duct in a comparative sample of Crocodyliformes.

Taxon	Nasal cavity height[b] (mm)	Nasal cavity width[b] (mm)	Nasal cavity ratio (height/width)	Nasal cavity vol (mm^3)	Nasopharyngeal duct vol (mm^3)	Nasopharyngeal duct croos-section area (mm^2)[c]	Nasopharyngeal duct height (mm)[c]	Nasopharyngeal ratio[d]
Sebecus ayrampu	42.4	28.6	1.48	47.791	12.039	85.8	24.5	0.25
Notosuchus terrestris	31.6	36.9	0.85	32.145	9.258[a]	26.0	9.74	0.28
Simosuchus clarki	38.2	44.0	0.86	49.505	7.490	81.0	11.4	0.15
Alligator mississippiensis	29.5	60.6	0.48	121.024	44.400	108.6	12.1	0.37
Caiman yacare	33.5	50.3	0.66	96.192	48.600	86.7	11.5	0.50
Crocodylus niloticus	50.2	74.6	0.67	432.006	161.080	213.7	22.7	0.37

[a] Partially preserved

[b] Width and height máximum of the olfactory region, between frontal, prefrontal, lacrimal, maxilar, pterygoids, and palatines bones; immediately in front of the prefrontal pillars

[c] Same level as the previous measure between pterygoids, and palatines; only on one side

[d] Nasopharyngeal duct vol / nasal cavity vol