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New cranial remains of the broad-nosed crocodile *Elosuchus* (Pholidosauridae; Mesoeucocodrylia) and its paleoecological implications

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Abstract

Sometimes Natural History Museums unknowingly treasure singular specimens in their collections for decades. The re-discovery of such elements allows the description of previously unknown features of well-known taxa. Here, we describe a nearly complete left premaxilla attributed to the pholidosaurid *Elosuchus*. Specimen IPS3303 shows some remarkable differences with previously known premaxillae of *Elosuchus*, especially concerning the relative position of the fifth premaxillary tooth and the premaxilla-maxilla sutural surface morphology. Because of the scarcity of current data, it is difficult to evaluate the significance of such differences. The described element is about 40% larger than the largest premaxilla of *Elosuchus* known so far, suggesting that this taxon could achieve remarkable body size proportions. The preliminary analyses of the dentition and the neurovascular system of the premaxilla provide new insight into the paleoecology of this riverine crocodylomorph from the Cretaceous of Africa.

Keywords: Pholidosauridae, *Elosuchus*, paleoecology, Cretaceous, Museum Collection.

INTRODUCTION

Aside from performing public outreach and educational missions, one of the pivotal points of any Natural History Museum is to curate unique specimens that hold critical information for evolutionary sciences. Due to the large number of specimens that usually manage NHM collections, sometimes accounting for thousands of elements, it is not surprising that some specimens “get lost” or remain hidden for decades. There are several examples of that, but once re-discovery and re-evaluation, these hidden treasures either come out as new species or additional specimens of previously described taxa (e.g. Boersma and Pyenson 2016; Chapelle et al. 2019; Borths and Stevens 2019; Smitha et al. 2021; Spiekman et al. 2021), while other times they represent new remains of an already known but rare taxon (i.e. Prieto-Márquez and Wargne 2013; Prieto-Márquez and Gutarra 2016).

Funded in 1965 as the Institut de Paleontologia de Sabadell (IPS) and re-named as Institut Català de Paleontologia Miquel Crusafont (ICP) in 2006, the ICP has acted as a pool of attraction and a state reference in the preservation of vertebrate fossils from all eras. Consequently, it is not rare that time to time enthusiastic, amateur, and private collectors end up giving their collections to the institution. To date, the ICP collection accounts for up to 126,000 specimens. In 1992, the ICP Museum received the private collection of an amateur paleontologist from Barcelona (Sr. Andreu), who donated two specimens –a left premaxilla of a crocodylomorph (IPS3303) and a tooth of *Spinosaurus* sp. (IPS3304)– from an unknown locality of the southern Er-Rachdia Province, close to the Morocco-Algeria boundary (J. Agustí per. com.). The two specimens remained stored in the museum collections for more than 30 years, without anyone knowing of its existence since a review made by one of the authors (A.S) brought the remains to light.

Here, we describe a new nearly complete premaxilla (IPS3303) attributed to the pholidosaurid *Elosuchus*. Despite the fragmentary nature of the finding, it is the largest premaxilla known for this taxon so far and provides new clues about the paleoecology of this pholidosaurid species.

Institutional abbreviations. — ICP-Museum of Institut Català de Paleontologia - Miquel Crusafont, Sabadell, Spain; MNHN-Muséum national d'Histoire Naturelle, Paris, France.

MATERIAL AND METHODS

The element of interest of the present study is a nearly complete left premaxilla of a putative large crocodylomorph (IPS3303), which is housed in the paleontological collections of the

Museum of the Institut Català de Paleontologia Miquel Crusafont. All anatomical measures were taken using a digital caliper Mitutoyo 15CPX with a range of error of 0.005 mm. Anatomical descriptions follows the morphological nomenclature of previous studies on pholidosaurid crocodylomorphs (Jouve 2005; Young et al. 2016; Meunier and Larsson 2017).

A three-dimensional model of the studied fossil specimen was produced following the photogrammetric protocol of Mallison and Noble (2016), and using Agisoft Photoscan Pro (v. 1.2.4, www.agisoft.com), to perform scaling and alignment.

Alanyses of the topographic relieve and neurobascular densty were perfomerd using ImageJ software (Schneider et al. 2012)

SYSTEMATIC PALAEONTOLOGY

Superorder: Crocodylomorpha Hay 1930

Clade: Neosuchia Benton & Clark 1988

Family: Pholidosauridae von Zittel & Eastman 1902

Genus: *Elosuchus* de Lapparent de Broin 2002

Elosuchus sp.

Specimen

IPS3303, a nearly complete left premaxilla.

Locality and age

Unknown fossil site near the southern border of Er Rachida Province, Morocco. Kem Kem Group; late Albian-early Cenomanian (see Ibrahim et al. 2020 for further details).

Description and Comparison

IPS3303 is a nearly complete left premaxilla, only lacking the most rostromedial part of the bone, including most of the first and half of the second premaxillary alveolar region, and the ventral palatine process.

In dorsal view, the main body of the premaxilla is strongly sculptured with numerous ridges and pits that vary in size and shape. The anterior margin of the premaxilla is rounded in shape, and transversally broad (Fig 1). The maximal width of the element is at the level of the fourth premaxillary alveolus, as in *Elosuchus* (de Lapparent de Broin 2002; Young et al. 2016), *Meridiosuchus* (Fortier et al. 2011), *Pholidosaurus* (Martin et al. 2016), and *Oceanosuchus* (Hua et al. 2007). Except from the embayment of the external nares, the medial side of the bone is nearlt streaigh. The resulting "half pan-like" shape of IPS3303 resembles that of *Pholidosaurus* (Martin et al. 2016), *Chalawan* (Martin et al. 2013), *Meridiosaurus* (Fortier et al. 2011), and *Elosuchus* (de Lapparent de Broin 2002; Young et al. 2016). Despite the absence of nasal bone, given that the premaxilla-nasal sutural surface extends until the posterior edge of the external nares (Fig 1), it is likely that the premaxilla did not contact each other medially and therefore nasals contributed to the posterior margin of the opening of the nares. Such anatomical configuration is, so far, only reported in *Elosuchus* (de Lapparent de Broin 2002; Young et al. 2016).

The dorsally facing external naris is more expanded lateromedially than anteroposteriorly, occupying about 33% of the maximum transverse width of the premaxilla (Fig 1). This feature is shared by other broad-nose pholidosaurids such as *Oceanosuchus* (Hua et al. 2007), *Terminonaris* (Shimada and Parris 2007), and *Elosuchus* (Young et al. 2016), but not as developed as in *Sarcosuchus* (Sereno et al. 2001) and *Chalawan* (Martin et al. 2013). The anterior margin of the external nares exhibits a small posteriorly directed bump (Fig 1) like in *Terminonaris* (Shimada and Parris 2007) and *Elosuchus* (Young et al. 2016).

A set of neurovascular foramina arranged in a semicircular distribution surrounds the lateral margin of the external nares. A prominent rim surrounds the anterior margin of the external nares (Fig 1), as in the most well-preserved specimen of *Elosuchus* (MNHN.F SAM 129 and MNHN.F MRS 334; Young et al. 2016). An enlarged, laterodorsally semi-rounded fossa for the accommodation of the first dentary teeth, named "elosuchid fossa" by Mourier and Larsson (2016), is located in the anterior half of the premaxilla, near the lateral edge of the bone (Fig 1), a feature only reported in the African pholidosaurid *Elosuchus* (de Lapparent de Broin 2002; Young et al. 2016).

In palatal view, the premaxilla displays five alveoli oriented lateroventrally (Fig 1), as *Pholidosaurus, Terminonaris,* and *Elosuchus* (Shimada and Parris 2007; Young et al. 2016; Martin et al. 2016). The morphology of the premaxilla and alveoli form a broad rosette dentition. Despite being partially broken, the second alveolus (P2) seems to be the smallest of the premaxillary series, followed by the P5, P4 and P3 being the largest one as in *Pholidosaurus* (Martin et al. 2016) and *Elosuchus* (Young et al. 2016). The first two alveoli (P1 and P2) are located anteromedially to the large "elosuchid fossa" (Fig 1), as in *Elosuchus* (Young et al. 2016). This fossa, intended to the reception of the enlarged first dentary tooth (D1), separates the P2 from the P3 alveolus (Fig 1). Although similar notches are present in other pholidosaurids (e.g. Mook 1933; Sereno et al. 2001; Lepage et al. 2008; Fortier et al. 2011), the position of this opening that splits the premaxillary tooth series into distinct units is considered autapomorphic of *Elosuchus* (Young et al. 2016).

The third and fourth premaxillary alveoli are widely separated from each other by a deep concave interalveolar space. P5 is located posteromedially relative to the P4 alveolus, as in *Elosuchus* (de Lapparent de Broin 2002; Fortier et al. 2011; Young et al. 2016), and *Chalawan thailandicus* (Martin et al. 2013), while P5 is posterolateral to the P4 alveoli in most pholidosaurids (e.g. Mook 1934; Sereno et al. 2001; Wu et al. 2001; Hua et al. 2007;

Lepage et al. 2008; Fortier et al. 2011). The posterolateral position of the fifth premaxillary tooth regarding the tooth row was proposed as a synapomorphy of Pholidosauridae by Fortier et al. (2011), but the medial 'migration' of the last premaxillary alveolus could be characteristic of a more inclusive clade within pholidosaurids (Young et al. 2016). The gap between the P4 and P5 alveoli is proportionally smaller than the P3–P4 interalveolar space. This condition is similar to that of MNHN.F INA 30 (Young et al. 2016), while the P4-P5 interalveolar space seems much larger in *E. cherifiensis* (MNHN.F MRS 334; de Lapparent de Broin 2002). The interalveolar space between P3-P4, and P4-P5 alveoli would have accommodated the second and third dentary teeth respectively.

Only the third replacement tooth is preserved in place in IPS3303 (Fig 1), although fragments of the fifth premaxillary tooth are observed within the alveolus. The third premaxillary tooth is conical in shape, and circular in cross-section (Fig 1). While most of the crown is covered by smooth enamel with fine apicobasal striation, the apex is ornamented with anastomosing enamel (Fig 1). There is no evidence of carinae. This ornamental pattern resembles that of *Elosuchus* and *Chalawan* (de Lapparent de Broin 2002; Martin et al. 2013) and differs from the curved cone-like tooth with carinae and apicobasal ridges of *Terminonaris*, *Pholidosaurus*, and *Sarcosuchus* (Sereno et al. 2001; Shimada and Parris 2007; Martin et al. 2016). It is worth noting that the dental features of IPS3303 and *Elosuchus* strongly resemble that of the thalattosuchid *Machimosaurus* (Young et al. 2014).

The ventral palatine process of the premaxilla is broken, and its extinction can only be assessed from the scar left on the medial edge of the palatine, which expands from the posterior margin of the "elosuchid fossa" to the level of the posterior margin of the P4. A series of neurovascular foramina are present on the palatal shelves, mainly surrounding the medial margins of the alveoli. The posterior process tapers posteriorly to the fifth premaxillary alveolus. Three large foramina are located at the anterior premaxilla-maxilla sutural surface, which seems to be related to the trigeminal nerve (CN V; Fig 1). The trigeminal nerve seems to extend along all the anteroposterior length of the premaxilla.

In lateral view, the premaxilla is beak-shaped, with the anterior margin oriented anteroventrally (Fig 1), a characteristic feature of pholidosaurids. Several neurovascular foramina cover most of the lateral surface of the bone. The premaxilla-maxilla sutural surface, which is curved posterodorsally, is restricted to the most posterior part of the lateral edge of the premaxilla (Fig 1).

Finally, the straight premaxilla-nasal sutural surface is the most salient structure in the medial side of the premaxilla, occupying more than half of the total length of the element and reaching at the level of P4 (Fig 1).This sutural surface is depicted by a strongly sculptured rectangular surface consisting of anteroventrally ridges (Fig 1). The inner margin of the external naris displays five neurovascular foramina, being the largest one located in the posterior border.

The combination of the above-described character in IPS3303–transversally broad beak-like premaxilla, strong posterior constriction of the posterior process, rosette-like alveolar region, a large "elosuchid fossa" and nasal contributing to the posterior margin of external nares–allow us to tentatively assign the studied specimen to the pholidosaurid genus *Elosuchus*.

[FIGURE 1 SHOULD BE PLACED HERE]

DISCUSSION

Taxonomic attribution and morphological variability

Pholidosauridae is a group of specialized longirostrine crocodylomorphs adapted to aquatic environments (Hua et al. 2007). Throughout their evolutionary history, pholidosaurid achieved a wide geographic distribution, being present in Europe, Africa, North America, and South America. It is also worth noting that the family expanded several millions of years, from 167Ma to 61Ma, proving that the clades survived to the K-Pg biotic mass extinction (Jouve and Jalil 2020).

Elosuchus is perhaps one of the most controversial pholidosaurid taxa described so far due to its complex history. The original material was collected in 1951 by the French paleontologist René Lavocat to the north of Gara Sbaa (SE of Morocco). Initially identified as '*Thoracosaurus' cherifiensis* (Lavocat 1955), the type material was re-described years later by de Lapparent de Broin (2002), who concluded that the taxon discovered by Lavocat should be attributed to a new genus: *Elosuchus*. In the same study, de Lapparent de Broin described a new elosuchid species –'*Elosuchus' felixi*– and erected the family 'Elosuchidae', which initially included *E. cherifiensis*, '*E'. felixi* (currently *Fortignathus felixi*, Young et al. 2016) and *Stolokrosuchus lapparenti* (Larsson and Gado 2000). However, Jouve (2005) was the first in noting that such grouping was inconsistent. He observed that *Stolokrosuchus* lacked the 'elosuchid fossa', that several alleged premaxillary 'elosuchid' characters were also apomorphie of Peirosauridae, and that *E. cherifiensis* –as defined by de Lapparent de Broin (2002)– shared several characters with basal dyrosaurids.

In a posterior re-evaluation of the genus, Meunier and Larsson (2017) proposed to restrict *E. cherifiensis* to Morocco, defined *E. broinae* from Argelia, and questioned the validity of '*E'. felixi*. By the same time, the latter taxon was re-assessed by Young et al. (2016) to the genus *Fortignatus*. In consequence, the purported family 'Elosuchidae' sensu de Lapparent de Broin (2002) is currently questioned by several authors (Jouve 2005; Young et al. 2016; Meunier and Larsson 2017).

Therefore, the genus *Elosuchus* currently includes two species: *E. cherifiensis* and *E. broinae*. Ibrahim et al. (2020) noted that they only differ in minor anatomical characters, but none of them pertaining to the morphology of the premaxilla (Young et al. 2016). As a result, the attribution of IPS3303 to a lower rank than the genus level is impossible here.

Nevertheless, it is worth noting that there are some anatomical differences between IPS3303 and other premaxillae attributed to *Elosuchus* (Fig 2). First, the intra-alveolar space between P4 and P5 of IPS3303 is similar in size to MNHN.F INA 30, but they both are smaller than in MNHN.F MRS 334. This feature can be quantified as the distance between the posterior margin of the P4 alveolus and the anterior edge of the alveolus P5 (Fig 2). In turn, the difference in the spacing is also reflected in the relative position of the fifth premaxillary alveolus, which is located more medially in MNHN.F MRS 334 and FSAC-KK 10 than in MNHN.F INA 30 and IPS 3303 (Fig. 2)

In addition, in dorsal view, the premaxilla-maxilla sutural surface in IPS3303 differs from the other known *Elosuchus* premaxillae (Fig 2). In that it extends anterolaterally in the IPS specimen, while in other specimens seems limited to the axial plane of the snout. With the current data at hand, it is difficult to establish if such differences may correspond to interspecific variations (even sexual dimorphism), ontogenetic changes, or taxonomic differences. Whatsoever, the unexpected discovery of a large premaxilla attributed to the pholidosaurid *Elosuchus* in the IPS collections provides new ecological information to this enigmatic taxon.

[FIGURE 2 SHOULD BE PLACED HERE]

Body size

Body size is one of the most fundamental biological traits because it affects virtually all aspects of an organism's physiology and ecology. To date, with a basal skull length of 94 cm (measured from the tip of snout to the posterior side of the occipital condyle in MNHN SAM

129; Meunier and Larsson 2017), *Elosuchus* is considered a mid-length pholidosaurid, almost a half of its relative *Sarcosuchus* (skull length of 178 cm; Sereno et al. 2001).

Judging by the graphic information available of the most complete premaxillae (see de Lapparent de Broin 2002; Meunier and Larsson 2007), MNHN SAM 129 has a total anteroposterior length of about 16.3 cm, being that of MNHN SAM 334 just slightly smaller. In this regard, IPS3303 is the largest premaxilla attributed to the genus *Elosuchus* so far, being 143.7% larger than MNHN SAM 129 (see Supplementary Table 1).

By assuming a similar cranial morphological ontogenetic trajectory of *Elousuchus* than the extant long-snout *Gavialis gangeticus* (Piras et al. 2010; Hone et al. 2020) for *Elosuchus*, the total skull length of IPS3303 would likely measure about 135 cm in length, almost twice the skull size of the current Nile crocodiles. If so, *Elosuchus* could be as large as *Chalawan* (Martin et al. 2013) but smaller than the gigantic skull of *Sarcosuchus* (Sereno et al. 2001). Consequently, *Elosuchus* could be recognized as the third-largest species of pholidosaurid known so far.

Paleoecological implications

The occurrence of a premaxillary tooth in the IPS3303 provides new insights into the potential dental variability and feeding strategy in *Elosuchus*. Overall, the premaxillary tooth of IPS3003 resembles the maxillary teeth of MNHN MRS 1112 and SAM 129. All of them show a similar conical-shaped crown with apical ornamented enamel consisting of anastomosing ridges, but the premaxillary tooth does not have carinae as the maxillary ones, it is less curved vocally, and the anastomosing texture covers more surface of the tooth crown (Fig 3).

Similar morphology differences are recognized along the jaw in extant crocodiles, putative semiaquatic dinosaurs (Ibrahim et al. 2014), and mosasaurs (Street et al. 2021). In fact, it is noteworthy that the false denticulations and anastomosing enamel texture are produced by the same amelogenesis process (Sander 1999, 2000) –in which the underlying dentine does not contribute to the relieve development, but as a differential thickening of the enamel–, and because of that it is not surprising to find them coexisting in the same tooth.

While the anastomosing enamel texture covering the apical region of the crowns favor the increase of the grip during biting, the conical morphology of the premaxilla teeth are ideal for gripping, crushing, and pulling. The combination of these features suggests that the premaxillary teeth of *Elosuchus* were able to deal with hard-biting elements (i.e. bones or shells). In contrast, the ziphodont maxillary teeth seem primarily intended to slice the meat (Hornung and Reich 2015). Such heterodonty is consistent with a bite-and-swallow feeding style (O'Connor et al. 2010), similar to that of the extant *Crocodylus niloticus*.

[FIGURE 3 SHOULD BE PLACED HERE]

The external surface of IPS3303 is strongly sculpured with several sinuous grooves (Fig 4a,c), some of them allocating neurovascular foramina of different sizes and shapes (Fig 4b,d). The distribution of these neurovascular foramina is uneven and they are predominantly concentrated around the labial margin of the mouth (n=44; Fig 4b,d) and surrounding the external nares (n=14; Fig 4d). This topographic distribution resembles that of extant crocodiles, whose foramina are associated with a high-resolution mechanosensory system linked to the terminal innervations of the ophthalmic premaxillary branch (CN V1) of the trigeminal nerve (Leitch and Catania 2012; George and Holliday 2013). Pending further analyses, in IPS3303 the preserved ophthalmic division of trigeminal nerve (CN V1) cavities extend rostrally through all the craniocaudal length of the premaxilla (Fig 4) and suggest the presence of a complex neurovascular system intender for detecting waterborne vibrations and optimal temperature of nesting site (Brazaitis and Watanabe 2011; George and Holliday 2013), as in extant crocodylians.

The combination of relatively large body size, a highly sensitive sensorial system, and a specialized dentition leads suggest that *Elosuchus* could likely be a remarkable ambusher predator of its time. Hidden underwater, *Elosuchus* could feel vibrations and pressure changes produced by its potential prey underwater. Once attacking, it could grasp its prey with the bulbous massive conic premaxillary teeth, until it pull part of the prey and sliced with the posterior ziphodont dentition. Although its primary food source could be fishes, it is also likely that *Elosuchus* could easily prey upon mid-sized vertebrates, such as turtles –the Kem Kem Group has plenty of turtles remains of *Dirqadim Hamadachelys*, or *Galianemys*– or even small dinosaurs –most likely young *Rebbachisaurus*.

[FIGURE 4 SHOULD BE PLACED HERE]

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FIGURE CAPTIONS

Figure 1. IPS3303. Left premaxilla of *Elosuchus* sp. in a) dorsal, b) palatal, d) medial, and e) lateral view. c) Detail of the posterior process of the premaxilla showing the anatomic configuration of the maxilla and nasal sutural surface and details of the neurovascular foramina. f) Close-up view of the third premaxillary replacement tooth showing the

characteristic anastomosing wrinkle of the enamel at the apex of the tooth (white arrow) running until the mid-high of the tooth crown (black arrow).

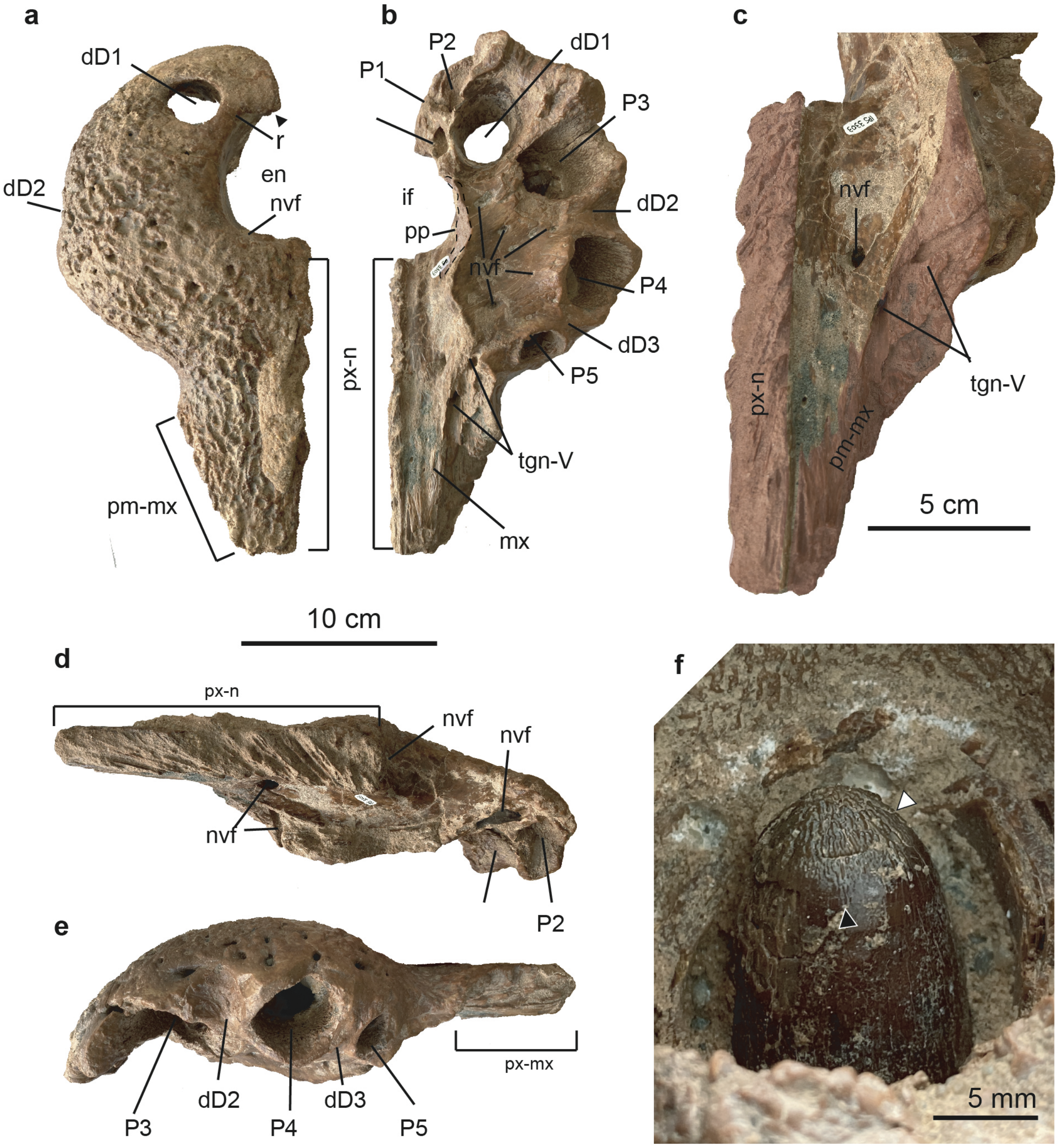
The black triangle in “a” indicates the possible location of an incipient anterior narial bar. *Abbreviations:* dD1,dD2,dD3-diastema for the reception of the dentary teeth; en-external nares; if- inferior fossa ;nvf-neurovascular foramen; pp-palatine process; px-mx- premaxilla-maxila sutural surface; px-n- premaxilla-nasal sutural surface; P1 to P5 -premaxillary tooth position; r-rimtgn-V- trigeminal nerve or cranial nerve V. [double-column; color only in electronic version]

Figure 2. Features comparison between premaxillae attributed to the pholidosaurid *Elosuchus* in palatal (upper row) and dorsal (lower row) views. Dashed black lines and triangles illustrate the lateromedial displacement of P5 regarding P4. Dashed grey lines and triangles show the craniocaudal spacing between P4 and P5. Dashed black lines and triangles in the lower row show the layout of the premaxilla-maxilla sutural surface in dorsal view. Schemes are not at scale. *Abbreviations:* mx-maxilla; n-nasal; px-premaxilla. [double-column]

Figure 3. Dental features of *Elosuchus*. Schematic illustration showing the dental morphology variations on the upper jaw of *Elosuchus*, in both having marginal carinae (fc) and relative contribution of enamel types within each tooth. Note that anastomosing enamel has a relative more contribution on the apex of the premaxillary tooth than in maxillary one. Tooth schemes are not at scale. [one-column]

Figure 4. Neurovascular system distribution in IPS3303. Colored topographic relieve showing the distribution of the sculpturing grooves in (a) dorsal and (c) lateral views. Red

points illustrate the presence of a neurovascular foramina (NVF). Density map distribution of neurovascular foramina upon a tridimensional model in the (b) dorsal surface and (d) the lateral surface of the premaxilla. Note the higher concentration of foramina around the external nares and the labial margin of the bone, just above the alveolar region. [double-column; color only in electronic version]


a
dD1
r
en
nvf
dD2
px-n
pm-mx
b
P2
dD1
P1
P3
if
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dD2
P4
dD3
P5
px-n
tgn-V
mx
c
nvf
px-n
pm-mx
tgn-V
5 cm
10 cm
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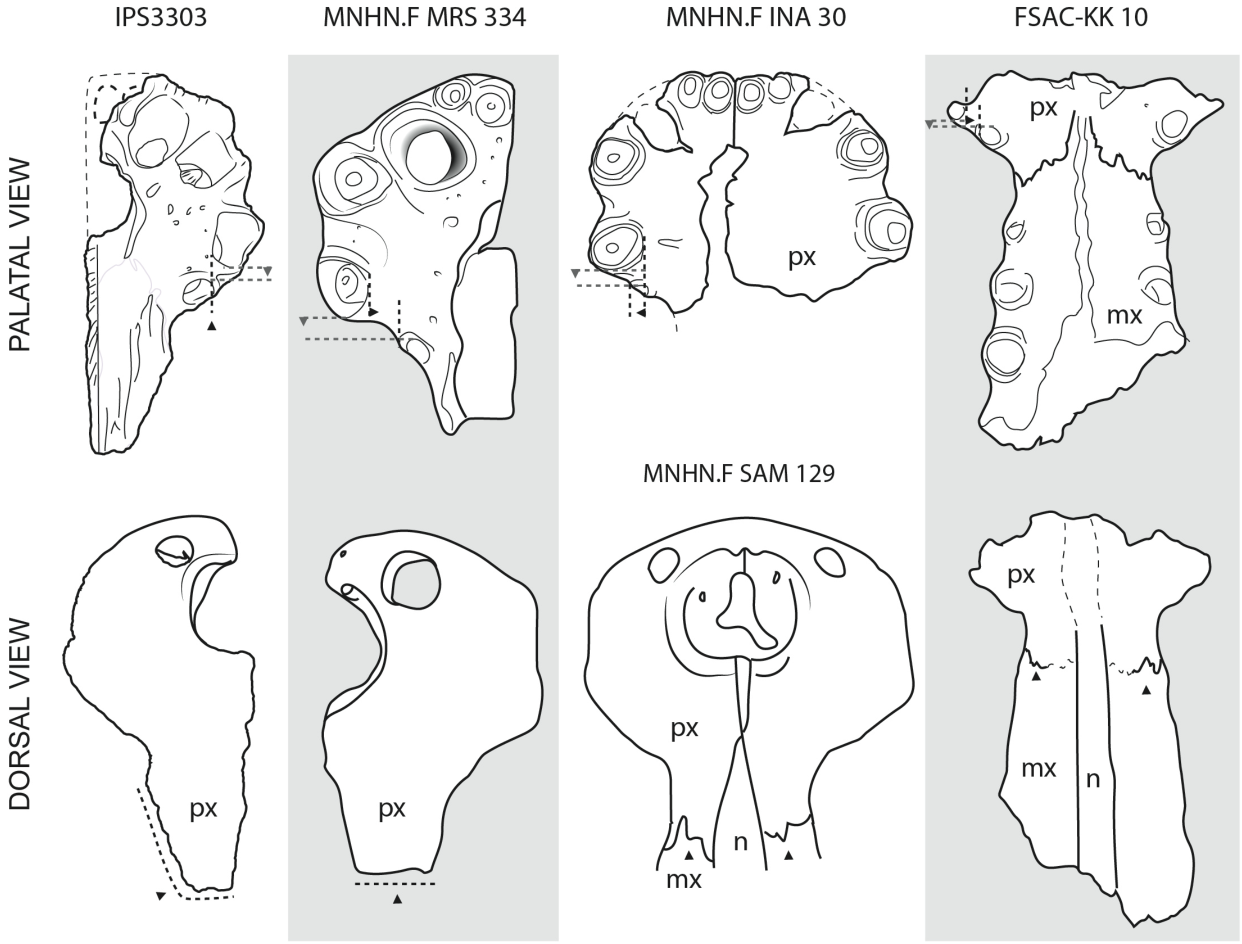
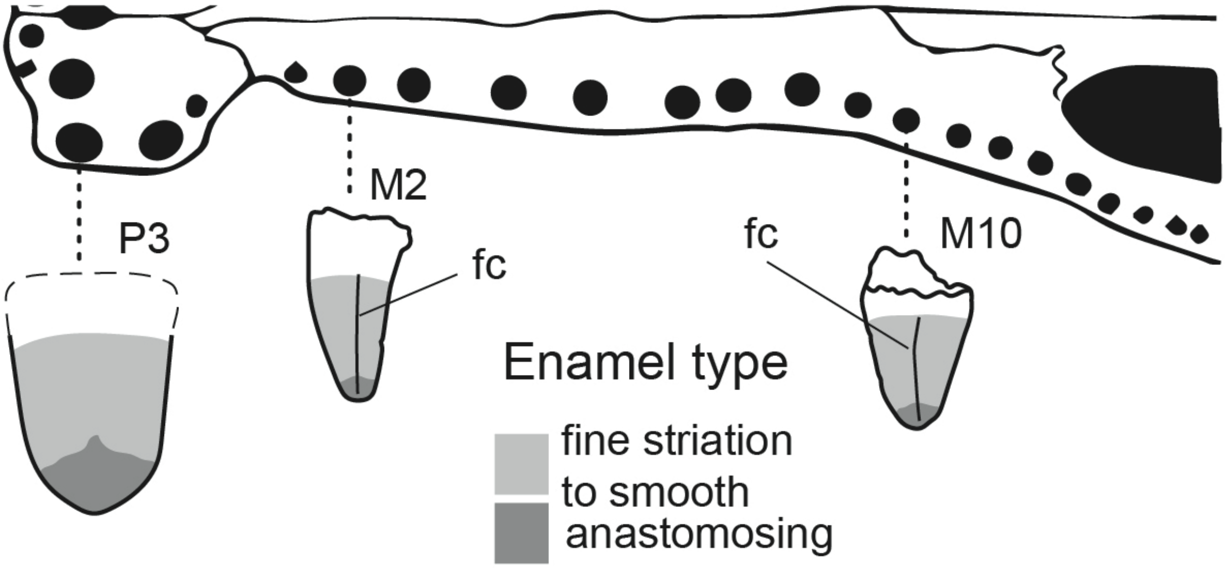
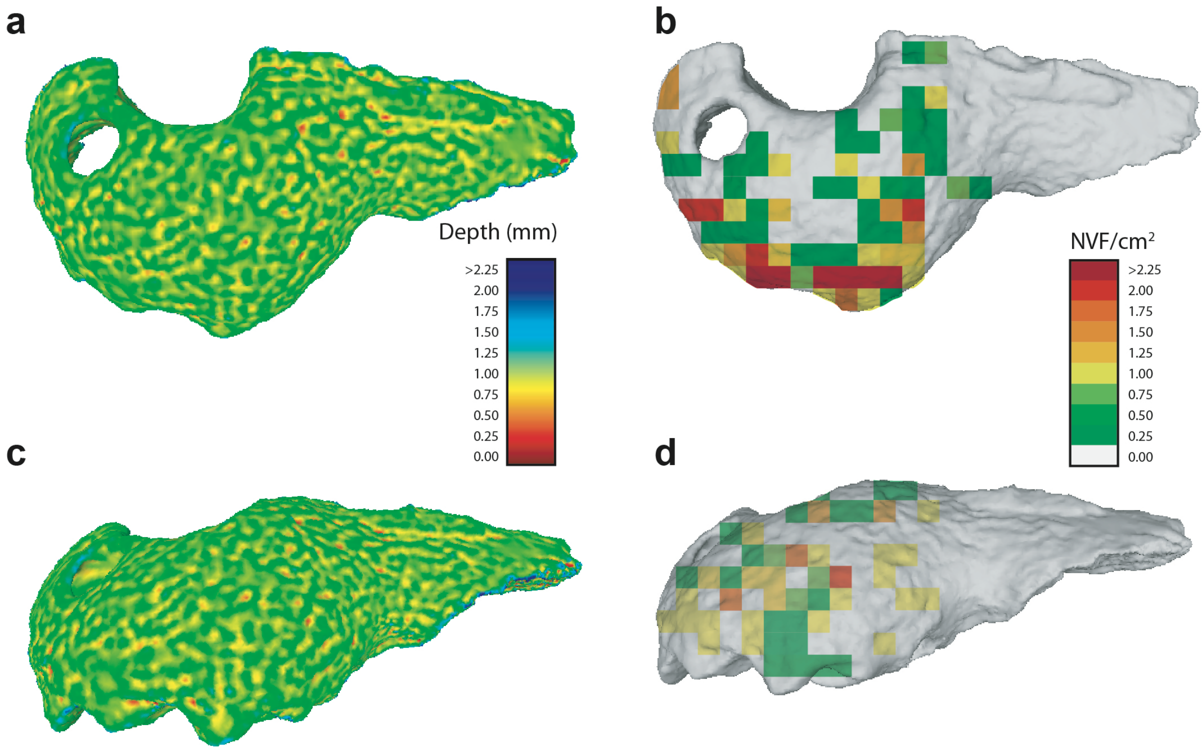
px-mx
f
5 mm


IPS3303
MNHN.F MRS 334
MNHN.F INA 30
FSAC-KK 10
PALATAL VIEW
px
px
mx
MNHN.F SAM 129
DORSAL VIEW
px
px
px
mx
n
px
mx
n


P3
M2
fc
fc
M10
Enamel type
fine striation
to smooth
anastomosing


a
b
Depth (mm)
>2.25
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
NVF/cm²
>2.25
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
c
d

Supplementary Table 1. Measures of premaxillae attributed to the genus *Elosuchus*. Width measurements were taken considering just one premaxillary bone (half of the total rostrum width). All measures are in cm. Measures are taken from: de Lapparent de Broin, 2002; Meunier and Larsson, 2016; Young et al. 2016; Ibrahim et al., 2017.

*Values extrapolated by using ImageJ software.

**Value calculated using linear regression.

	IPS3303	MNHN SAM 129	MNHN MRS 334	MNHN FINA 30	FSAC-KK 10
max. length	23.43	16.45*	16.98*	-	-
max. width	11.25	8.93*	11.22*	6.87*	-
min. width (posterior to P5)	5.28	3.99*	4.6*	3.06*	4.28*
max. nares length	5.07	5.27*	5.31*	5.26*	-
max. nares width	3.2	2.7*	3.01*	2.40*	-
Skull length	135.12**	94*	-	-	-