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Convergent Evolution of a Eusuchian-Type Secondary Palate within Shartegosuchidae

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ABSTRACT

Shartegosuchids are a poorly known, early-branching group of Asian and North American crocodylomorphs. Shartegosuchids have been hypothesized to have eusuchian-type secondary palates, but a paucity of described material makes assessing this difficult. Our fieldwork in western Mongolia recovered cranial material of a new *Shartegosuchus* specimen from the Ulan Malgait Formation, which we CT-scanned and digitally reconstructed to investigate its palatal morphology. We then incorporated this new anatomical information into a revised phylogenetic dataset to assess its affinities. Our study confirms that *Shartegosuchus* has a posteriorly placed choana that is fully enclosed by the pterygoids, but differs from Eusuchia in possessing a secondary palatal fenestra and reduced palatine bones. *Shartegosuchus*, together with *Adzhosuchus*, *Fruitachampsa*, and *Nominosuchus*, forms the monophyletic group Shartegosuchidae. Shartegosuchidae is nested within a larger clade Shartegosuchoidea, and this clade is an earlier-diverging lineage than Eusuchia, showing that a eusuchian-type secondary palate evolved multiple times in crocodylomorphs, including very early in the group's evolutionary history. The co-occurrence of *Nominosuchus* in the Ulan Malgait Formation and the Shishigou Formation allows us to assign an early Oxfordian age to *Shartegosuchus*. The independent evolution of a eusuchian-type secondary palate in an oreinorostral group suggests that the link between platyrostry and a closed secondary palate has been overstated.

KEYWORDS: Crocodylomorpha, palatal fenestra, pterygoid, Ulan Malgait Formation, Mongolia

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INTRODUCTION

The secondary palate of extant crocodylians and their eusuchian relatives is a derived anatomical feature that may serve as an adaptation to aquatic habits, and whose functionality has been a subject of speculation for nearly 150 years. Macroevolutionary hypotheses for the evolution of this derived palatal construction generally involve a series of intermediate conditions (Langston, 1973). The early diverging members of Crocodylomorpha, "protosuchians," are often described as having a "protosuchian" palate (Langston, 1973; Buffetaut, 1982), which is open and has the choana positioned anteriorly between the palatine and a maxillary secondary palate. More crownward extinct taxa are considered to have a "mesosuchian" palate (hereinafter: "palatine secondary palate"), formed from the maxilla and palatines, with a posteriorly positioned choana bordered anteriorly by the palatines and posteriorly by the pterygoid. Finally, eusuchians have a fully closed, bony secondary palate with the choana positioned posteriorly on the palate and enclosed entirely by the pterygoids (hereinafter: "pterygoid secondary palate") (Huxley, 1875; Langston, 1973).

Several recent studies have shown that the construction of the crocodylomorph secondary palate and position of the choana have complex evolutionary histories, with multiple convergences and reversal events and with many different palatal structure formations (Turner and Buckley, 2008; Pritchard et al., 2013; Wilberg, 2015). A palatine secondary palate is present in many groups, including some shartegosuchids (*Nominosuchus* and *Fruitachampsa*), thalattosuchians, and goniopholidids, although some members of the latter taxon have an open nasopharyngeal duct, e.g., *Eutretauranosuchus* (Pritchard et al., 2013). A pterygoid secondary palate is present in Eusuchia, *Mahajangasuchus*, and reportedly in the shartegosuchids *Shartegosuchus* and *Adzhosuchus* (Efimov et al., 2000). Thalattosuchia is generally considered to be a part of a pelagic clade deeply nested within Crocodyliformes, e.g., Clark (1994). However, there is some evidence that supports Thalattosuchia as sister to Crocodyliformes, which would imply that the palatine secondary palate arose in thalattosuchians and was lost in early-branching crocodyliforms (Benton and Clark, 1988; Jouve, 2009; Pol and Gasparini, 2009; Wilberg, 2015). Goniopholidids are nested among neosuchian taxa and exhibit significant diversity in their palatal anatomy: some forms possess a complete palatine secondary palate; others possess an open nasopharyngeal duct separating the palatines medially (Tykoski et al., 2002; Pritchard et al., 2013). The phylogenetic position of *Mahajangasuchus* is uncertain, but under all analyses it is recovered far from Eusuchia (Turner and Buckley, 2008; Sereno and Larsson, 2009; Turner and Sertich, 2010; Pol and Powell, 2011). This implies that the pterygoid secondary palate of *Mahajangasuchus* is not homologous with that of eusuchians, which is supported by many differences in its anatomy (e.g., the expanded pterygoid septum forms the anterior border of the choana, excluding the palatines).

Early hypotheses for the posterior position of the choana and the closed secondary palate in eusuchians focused on the role it plays in separating the nasal passage from the oral cavity (Huxley, 1875; Langston, 1973). More recently, the development of a closed eusuchian-type palate was hypothesized as a means of strengthening the platyrostral skull against strains placed on it during feeding (Busbey and Gow, 1984; Rayfield and Milner, 2008), with the posteriorly

placed choana being a by-product of this functional constraint. The observation of a closed palate and a posteriorly placed choana in *Shartegosuchus* (Efimov et al., 2000), a crocodylomorph with an oreinorostral snout, calls into question the strength of the functional relationship of a closed palate and a posteriorly placed choana with a platyrostral skull.

Shartegosuchids are a poorly known clade of small-bodied crocodyliforms from Asia and North America. Some shartegosuchids possess an unusual, well-developed palate that is thick and heavily sculptured, such as *Adzhosuchus*, *Shartegosuchus*, and *Fruitachampsa* (Efimov et al., 2000; Clark, 2011). An incomplete, "mesosuchian" palatine secondary palate is present in *Nominosuchus* and *Fruitachampsa*, but interestingly, the later-branching taxa *Shartegosuchus* and *Adzhosuchus* have been described as possessing a pterygoid secondary palate. Additionally, some forms (e.g., *Fruitachampsa* and *Shartegosuchus*) also possess two palatal openings: an anterior palatal fenestra and a posterior opening likely homologous to the choana. Thus, shartegosuchids present a rare instance in which the evolutionary transformation sequence between the two palatal constructions is seen within a lineage (Efimov, 1996; Efimov et al., 2000; Clark, 2011).

The 2010 Mongolian-American Expedition to the early Late Jurassic exposures in the western Gobi recovered several well-preserved specimens of basal crocodylomorphs, including new specimens of *Shartegosuchus asperopalatum* from the Ulan Malgait Formation. Here we present the results of CT-scanning and digital reconstruction of a well-preserved snout of *Shartegosuchus* (IGM 200/50), and discuss its implications for palatal evolution within Crocodylomorpha.

METHODOLOGY

A partial skull of *Shartegosuchus asperopalatum* (IGM 200/50) was CT-scanned at the American Museum of Natural History Microscopy and Imaging Facility. Individual skull bones, including all palatal elements, were segmented into separate regions using the region-growing tool in VG Studio Max 3.0. The scan was compared to previous descriptions of the palates of other crocodylomorphs (Iordansky, 1973; Busbey and Gow, 1984; Efimov et al., 2000; Gow, 2000; Tykoski et al., 2002; Turner and Buckley, 2008; Clark, 2011; Pritchard et al., 2013).

The relationship of *Shartegosuchus* to other crocodylomorphs was tested in a matrix developed by Pol and Gasparini (2009) and modified by Clark (2011). The data matrix was compiled and edited using Mesquite v3.10 (Maddison and Maddison, 2018). One new character was added concerning the position of the choana relative to the suborbital fenestra. Characters 200 and 258 were amended to introduce more specific information concerning the sculpturing of palatal elements, and the size of the palatine and its participation in the margins of the suborbital fenestra.

The taxonomic sample used in Clark (2011) was maintained, which included the shartegosuchid genera *Shartegosuchus*, *Adzhosuchus*, *Fruitachampsa*, and *Nominosuchus*. *Gracilisuchus* was specified as the outgroup. New anatomical information described for IGM 200/50 was incorporated into a coding of *Shartegosuchus asperapalatum* (which included PIN 4171/2). Twenty-three character codings for *Shartegosuchus* that were previously unknown were scored,

and four additional character scores were amended (see online supplementary information at https://doi.org/10.5531/sd.sp.31).

The data matrix was analyzed in TNT version 1.5 to heuristically search for shortest length topologies (Goloboff and Catalano, 2016). Memory was set to 10,000 trees and 100 MB of RAM. The data matrix was analyzed with the following parameters: tree bisection and reconnection (TBR) as a heuristic search strategy; 1000 Wagner builds with a random seed of 1; keep two trees per replication; and replace existing trees when more optimal trees were discovered. An additional round of branch swapping on shortest-length topologies was then performed using the trees in memory and holding up to 10,000 trees of shortest length. Support for the strict consensus tree topology was assessed using Bremer support, jacknife, and bootstrap. Bremer support was calculated in TNT by a round of TBR swapping on the optimal topologies, saving trees up to 10 steps longer than the MPT's and stopping when the tree buffer contained 10,000 topologies of any length. Jacknife and bootstrap support measures were calculated in TNT using GC frequencies. Jacknife analysis used 36 removal probability and 100 replicates. Bootstrap analysis used a standard resampling strategy (with replacement) and 100 replicates. An additional analysis constraining Thalattosuchia as the sister-taxon of Crocodyliformes was performed to evaluate how the position of Thalattosuchia affects inferences of palate evolution within Crocodyliformes, given the new data collected on shartegosuchids. The constrained analysis was completed by defining tree constraints in TNT and repeating the analysis using the same search parameters outlined above.

SYSTEMATIC PALEONTOLOGY

Crocodyliformes Hay 1930 (sensu Clark, in Benton and Clark, 1988)

Shartegosuchoidea Efimov, 1988

Shartegosuchidae Efimov, 1988

Revised Familial Diagnosis (* denotes revised diagnostic features): *pterygoid, palatine and maxilla are sculptured with concentrated, deep, irregular-shaped pitting; posterior maxillary teeth and postcaniniform dentary teeth with flat, horizontal cusp and vertical crenulations extending proximally; mandibular fenestra absent, *dentary anteriorly edentulous.

Shartegosuchus asperopalatum Efimov, 1988

Holotype: PIN 4174/2 a dorsoventrally crushed skull and mandible of a juvenile individual.

Type Locality: Ulan Malgait Formation, Shar Teg, Mongolia.

Referred Material: IGM 200/50, an anterior portion of the skull including rostrum and palatal and dentary bones recovered from Ulan Malgait Formation, Shar Teg, Mongolia.

Revised Genus and Species Diagnosis: *Palatines small and enclose anterior palatal fenestra; *mediolaterally narrow and anteroposteriorly elongate anterior palatal fenestra; *anterior palatal

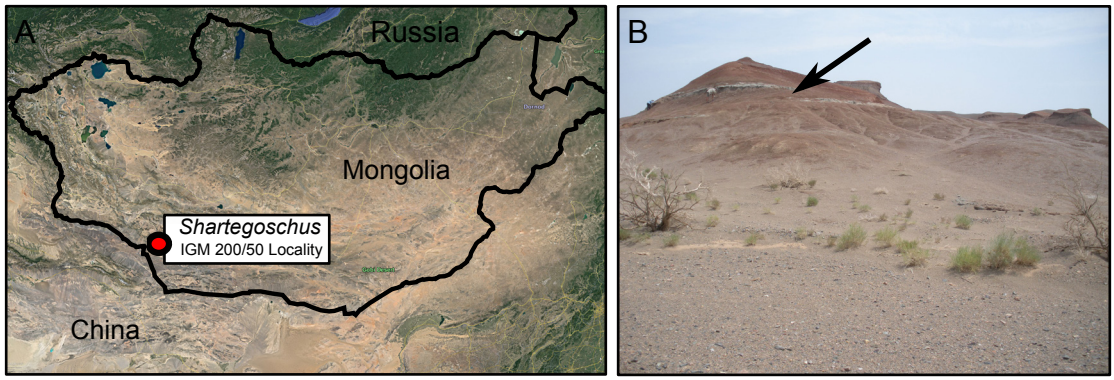

FIGURE 1. **A.** Map of Mongolia with marker indicating the locality of *Shartegosuchus asperapalatum* (IGM 200/50). **B.** Photograph of locality of *Shartegosuchus asperapalatum* (IGM 200/50) with arrow indicating the position the specimen was recovered from.

fenestra begins at level of midpoint of suborbital fenestra and ends beyond anterior margin of suborbital fenestrae; *choana positioned posteriorly on the palate and enclosed by pterygoids.

The name Shartegosuchoidea is proposed for the clade Shartegosuchidae + *Shantungosuchus*, *Sichuanosuchus*, and *Zosuchus*, and we define it here as the least-inclusive clade including *Shartegosuchus*, *Shantungosuchus*, *Zosuchus*, and *Sichuanosuchus*. The definition of Shartegosuchidae is revised as the most inclusive clade that includes *Shartegosuchus* and *Nominosuchus* but not *Zosuchus*.

RESULTS

Stratigraphy

The *Shartegosuchus* specimen (IGM 200/50) was discovered in a gray, medium-coarse-grained sandstone lag deposit at the Bor Ukhaa locality within the reddish mudrock strata of the lower part of the Ulan Malgait Formation exposed at Shar Teg in Gobi Altai Aimag (fig. 1A).

The Ulan Malgait beds have yielded fossil remains of fish, turtles, crocodyliforms, dinosaurs, a tritylodontid, molluscs, and ostracods (Gubin and Sinitza, 1996; Watabe et al., 2004; Watabe et al., 2007). Remains of both *Shartegosuchus* and *Nominosuchus* have been recovered at this locality (Efimov et al., 2000). Gubin and Sinitza (1996) assigned the Ulan Malgait beds to the Upper Jurassic based on the fossil fauna assemblages found at the Shar Teg locality.

The cooccurrence of the shartegosuchid *Nominosuchus matutinus* (Efimov et al., 2000) in the upper part of the Shishigou Formation at Wucaiwan, China (Clark and Xu, 2009a; 2009b), and the Ulan Malgait Formation strongly suggest these formations are coeval. Identification of Shishigou *Nominosuchus* individuals is based on descriptions by Efimov (1996) of Shar Teg specimens and a study of the original material by James Clark. Future anatomical investigation of the *Nominosuchus* specimens from both localities will confirm or revise their taxonomic identifications. Radiometric dating of tuffs at the Shishigou Formation indicate these beds are 159.7+/-0.3 and 162.2+/-0.2 Ma (Choiniere et al., 2014), which suggests that the *Shartegosuchus* specimen from the Ulan Malgait Formation is in the early Oxfordian stage near the beginning of the Late Jurassic (Gradstein, 2012).

Description and Comparisons

Only the rostrum, anterior rim of the orbits, palate, and the anterior portion of the mandible are preserved. The bone is white, preserved in a medium-to-fine-grained yellow sandstone matrix. The dorsal bones of the rostrum are fragmentary and posteriorly only their impression in matrix remains. The anterior section of the mandible is preserved in tight occlusion with the cranium. The lower jaws have been broken anterior to the mandibular fenestrae, preserving no detail of the fenestrae or of the articular region.

The antorbital fossa, described as the "maxillary depression" by Efimov et al. (2000), is a large fossa on the lateral surface of the rostrum, anterior to the orbit (figs. 2, 4). The depression is in a similar position as the antorbital fossa found in non-shartegosuchoid "protosuchians," e.g., *Orthosuchus* (Nash, 1975) and *Hemiprotosuchus* (Bonaparte, 1971), however, it fails to open into a large antorbital fenestra. The depression is circular in outline and the surface of the fossa is unsculptured. An antorbital fossa is also described for *Adzhosuchus* and *Nominosuchus* at the confluence of the maxilla, lacrimal, and jugal (Efimov, 1996). Similar depressions are present within goniopholidids (Tykoski et al., 2002; Pritchard et al., 2013) and some pholidosaurs (Martin and Buffetaut, 2012), although they are unlikely to be homologous, based on the phylogenetic distribution of these groups in Crocodylomorpha (Turner and Buckley, 2008). The depression is absent in *Fruitachampsa* (Clark, 2011). Shartegosuchids appear to lack an antorbital fenestra except for *Nominosuchus*, which has a small opening. Within shartegosuchoids, *Sichuanosuchus* has a small antorbital fenestra that opens from a shallow antorbital fossa (Wu et al., 1997), *Zosuchus* has a small antorbital fenestra that is not surrounded by an antorbital fossa (Pol and Norell, 2004), but unknown within *Shantungosuchus* (Young, 1961; Wu et al., 1994).

The palatal fenestra is positioned on the midline of the palate and enclosed entirely by the palatines (fig. 3). The palatal fenestra is an oblong slit with the minor axis oriented mediolaterally and the major axis oriented anteroposteriorly. Posteriorly, the palatal fenestra begins at the level of the midpoint between the suborbital fenestrae, and it extends anteriorly beyond the anterior margin of the suborbital fenestrae. In contrast, the palatal fenestra of *Fruitachampsa* is positioned anterior to the level of the suborbital fenestra and is circular, whereas the palatal fenestra of *Nominosuchus* is a mediolaterally narrow slit confluent with the choanal opening posteriorly (Efimov et al., 2000; Clark, 2011).

The suborbital fenestra is enclosed by the maxilla anteriorly and laterally, the pterygoid medially and posteriorly, and presumably the ectopterygoid posterolaterally. The suborbital fenestra is oblong in shape, with the posterior margin approximately twice as wide as the anterior margin.

The choana is oval in outline, with a raised, unsculptured surface rimming its anterior and lateral edges. It is enclosed entirely by the pterygoid, and positioned posteriorly on the palate medial to the pterygoid flanges (fig. 3). The major axis is oriented along the longitudinal axis of the skull.

Maxilla: The body of the maxilla is divided into a facial portion and a palatal process. The facial portion of the maxilla extends dorsally and curves medially, contacting the premaxilla anteriorly, nasal dorsomedially, and the lacrimal posterodorsomedially where it forms the lateral wall and a portion of the dorsal roof of the rostrum (fig. 4). Posteriorly, the maxilla

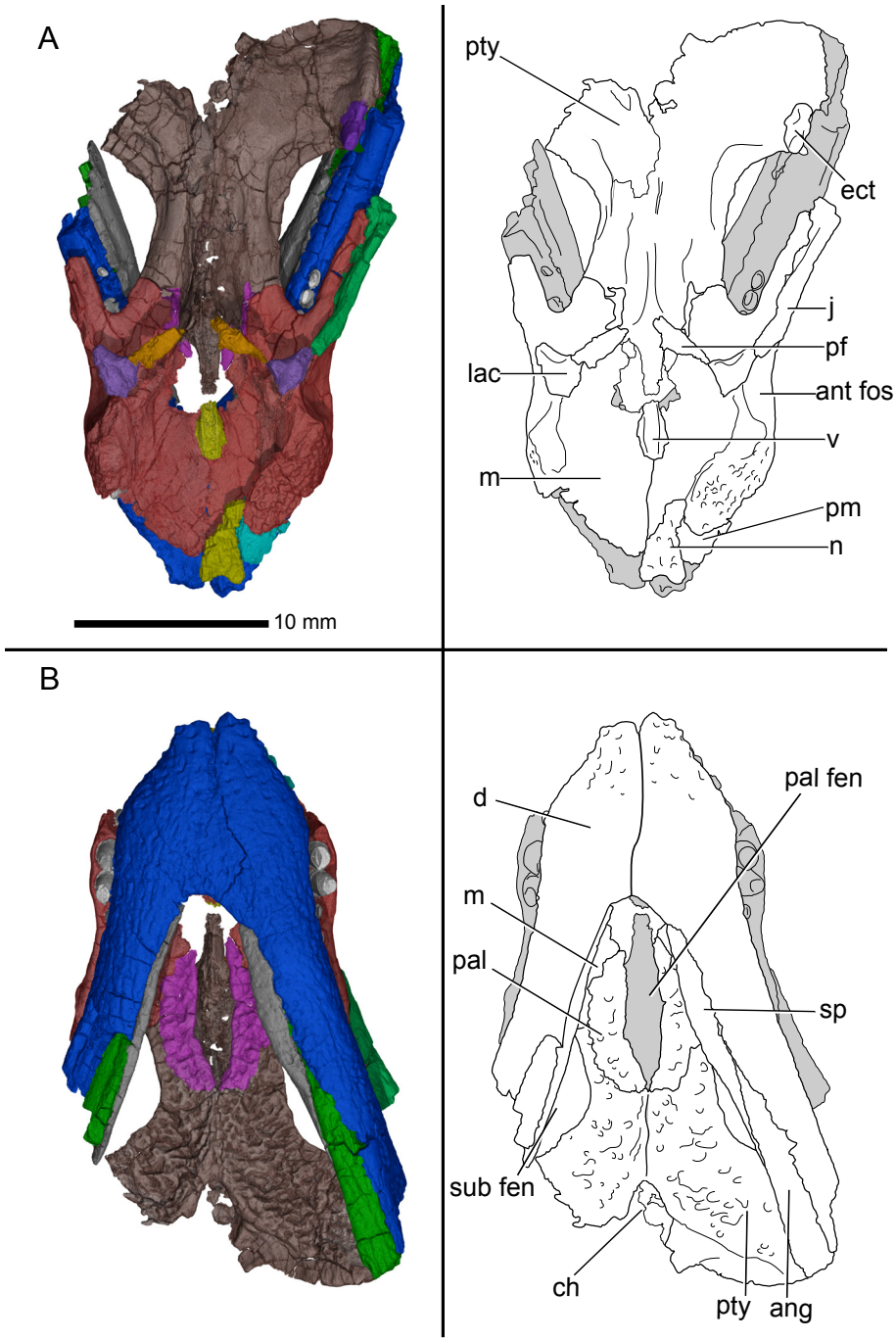

FIGURE 2. Digital reconstructions and line drawings of *Shartegosuchus asperapalatum* (IGM 200/50) in **A,** dorsal view, **B,** ventral view of *Shartegosuchus asperapalatum* (IGM 200/50). Abbreviations: **ang,** angular; **ant fos,** antorbital fossa; **ch,** choana; **d,** dentary; **ect,** ectopterygoid; **j,** jugal; **lac,** lacrimal; **m,** maxilla; **n,** nasal; **pal,** palatine; **pal fen,** palatal fenestra; **pf,** prefrontal; **pm,** premaxilla; **pty,** pterygoid; **sub fen,** suborbital fenestra; **sp,** splenial; **v,** vomer.

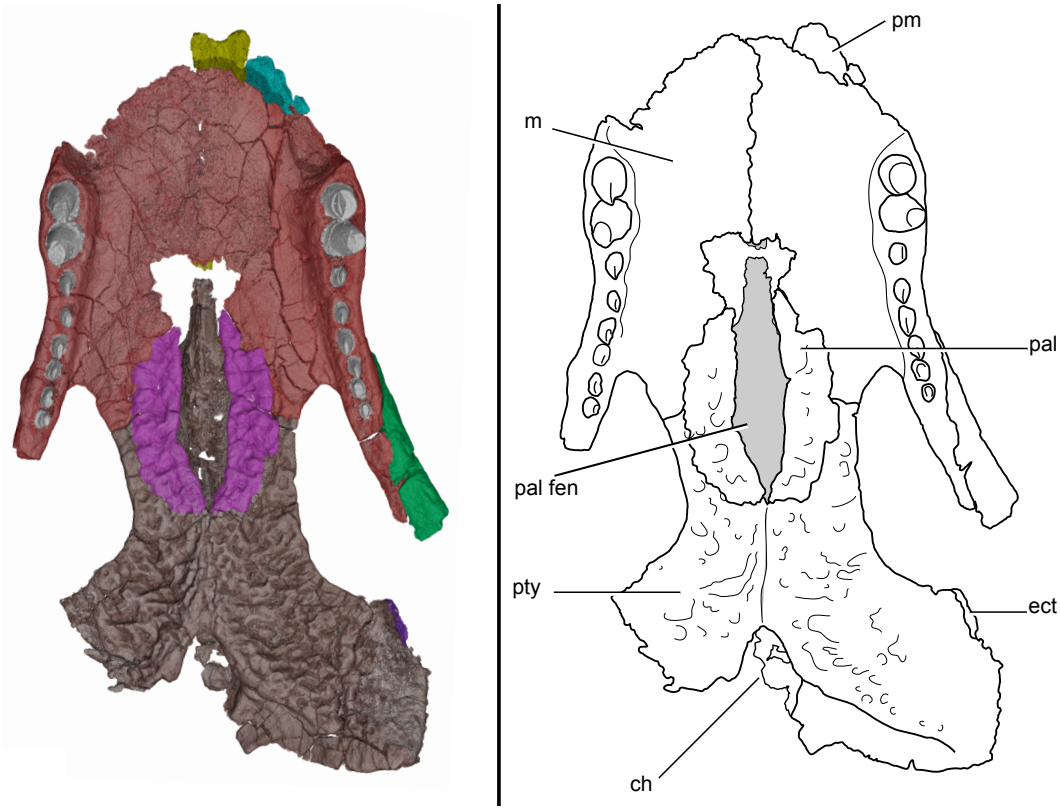

FIGURE 3. Digital reconstructions and line drawings of *Shartegosuchus asperapalatum* (IGM 200/50) in ventral view of the palate. Abbreviations: **ch,** choana; **ect,** ectopterygoid; **m,** maxilla; **pal,** palatine; **pal fen,** palatal fenestra; **pty,** pterygoid.

contacts the jugal ventrally along the anterior edge of the orbit. The facial surface of the maxilla is marked by a large antorbital fossa. The unsculptured surface of the fossa is in contrast with the remaining rostral surface of the maxilla, which is marked with extensive pitting.

The palatal shelves of the maxillae, together with the missing portion of the premaxillae, contact to form the anterior end of the palate (fig. 3). Posteriorly, the maxillae are not in contact at the midline, being separated by the palatines and palatal fenestra, but there is still a considerable contribution of this portion of the maxillary shelf to the secondary palate. In non-shartegosuchoid "protosuchians" the palatal shelves of the maxilla are separated posteriorly by the choana, which is positioned anteriorly on the palate. The vomers in non-shartegosuchoid "protosuchians" are also exposed in ventral view of the palate, a condition not apparent within shartegosuchoids.

Unlike the palatine and pterygoid, the ventral surface of the maxillary palatal shelves is unsculptured, except along the contact with the palatine and pterygoid where the maxilla is sculptured with pitting and ridges. The maxilla does not appear to participate in the palatal fenestra margins, however, there is a fracture along this region and an apparent missing portion of the maxillary palatal shelf along the midline of the skull and another missing portion along

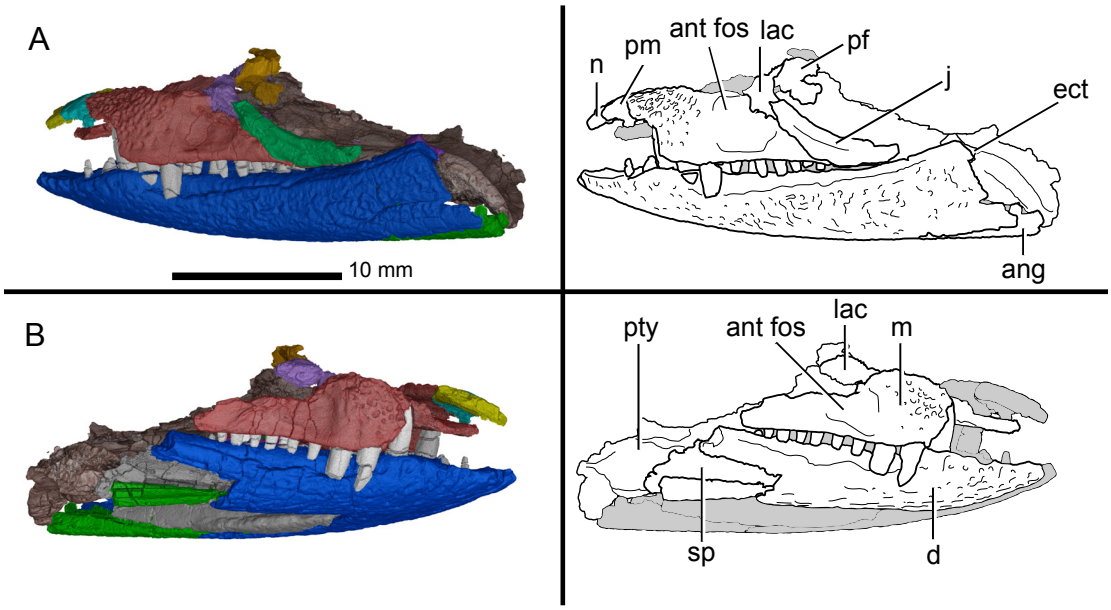

FIGURE 4. Digital reconstructions and line drawings of *Shartegosuchus asperapalatum* (IGM 200/50) in **A.** left lateral view, **B.** right lateral view of *Shartegosuchus asperapalatum* (IGM 200/50). Abbreviations: **ang,** angular; **ant fos,** antorbital fossa; **d,** dentary; **ect,** ectopterygoid; **j,** jugal; **lac,** lacrimal; **m,** maxilla; **n,** nasal; **pf,** prefrontal; **pm,** premaxilla; **pty,** pterygoid; **sp,** splenial.

the anterior edge of the palatines. In *Nominosuchus* and shartegosuchoids *Sichuanosuchus* and *Shantungosuchus*, the margins of the palatal fenestra are formed by both the maxilla and palatine (Wu et al., 1994; Wu et al., 1997; Efimov et al., 2000; Clark, 2011). The maxilla forms the anterior, lateral, and the rostral half of the medial margin of the suborbital fenestra. This is different from the condition described for non-shartegosuchoid "protosuchians," where the maxilla is excluded from the anteromedial edge of the suborbital fenestra by an anterolateral maxillary process of the palatines. The maxilla has eight alveoli, the first two of which are large, housing two large caniniform teeth. The more posterior alveoli are much smaller and gradually decrease in diameter posteriorly. The first and second alveoli are joined and circular in cross section, the remaining smaller alveoli are oval in cross section and are separated by bony septa. The rostral surface of the maxilla bulges laterally to accommodate the two large caniniform teeth. The remaining anterior surface of the maxilla that abuts the premaxilla is incomplete.

Lacrimal: The lacrimal is a small bone that contacts the jugal posteriorly, the maxilla ventrally and anteriorly, and the prefrontal medially. The lacrimal forms the posterodorsal surface of the antorbital fossa. The posterior edge of the dorsal surface of the lacrimal is cupped, presumably to articulate with a corresponding facet on a palpebral.

Prefrontal: The prefrontal is a small, rectangular bone that contacts the lacrimal anterolaterally and the pterygoid ventromedially. The prefrontal pillar of *Shartegosuchus* IGM 200/50 is preserved as a thin sheet of bone that extends ventromedially from the body of the prefrontal to form a weak contact with the lateral area of the dorsal surface of the pterygoid (fig. 4). This

is unlike the prefrontal pillar observed in extant crocodylians wherein the prefrontal forms a robust contact with the dorsal surface of the palatines (Iordansky, 1973).

Jugal: Only the anterior ramus of the left jugal is preserved (fig. 4A). It curves strongly dorsally as it extends anteriorly, so that the dorsal margin is concave. This margin forms the ventral and anteroventral margin of the orbit. The tip of the anterior ramus of the jugal overlaps the ventralmost extension of the lacrimal for a short distance. The lateral surface of the jugal is incised by a shallow groove that extends anteroposteriorly along the anteroventral margin of the orbit. Dorsal to this groove, the jugal is unsculptured, and ventral and posterior to the groove, the jugal is ornamented with shallow pitting.

Palatine: The palatine is restricted to the medial portion of the palate as a small, crescent-shaped element. The ventral surface of the palatine is highly sculptured with pitting, except along the margin of the palatal fenestra, where it is lacking. The palatal sculpturing consists of small circular or oblong shallow pits that are either linked or separated by a series of shallow ridges. The pits closer to the midline of the palate are more circular in shape. The pits become more oblong laterally on the palate. Also, posteriorly on the palate, the pitting becomes more deeply incised and the ridging more pronounced.

The palatine is excluded from the margins of the suborbital fenestra by the posterior extension of the palatal shelf of the maxilla and the anterior ramus of the pterygoid. The palatines enclose an opening, the palatal fenestra, which is positioned on the midline of the palate and medial to the suborbital fenestra.

Pterygoid: The fused pterygoids form the posterior surface of the palate. A ridge running along the midline of ventral palatal surface extending anteroposteriorly from posterior edge of the palatal fenestra to the anterior edge of the choana could be interpreted as a suture between the pterygoids. However, in CT cross section the suture between individual pterygoid bones cannot be observed, revealing that the pterygoid is completely fused. The palatal surface of the pterygoid is heavily sculptured with pits and ridges, which become more pronounced posterolaterally along the pterygoid flange (fig. 3). Pitting is also noted on the palatal surface of shartegosuchoids *Shantungosuchus* but not *Sichuanosuchus*, and extensive on the palatal surface of shartegosuchid *Fruitachampsa*. Efimov (1996) illustrates *Nominosuchus* as also having a sculptured palatal surface of the pterygoid (holotype PIN 4174/4), however, study of referred specimen IVPP 14392 shows a small amount of sculpturing of the palatal surface of the pterygoid, palatines, and maxilla.

The pterygoid has an anterior ramus that contacts the prefrontal, maxilla, palatine, and vomer and a posterolateral ramus that forms the pterygoid flange. The anterior ramus of the pterygoid forms the posterior portion of the medial edge of the suborbital fenestra. Anteriorly, along the margins of the suborbital fenestra, the pterygoid contacts the maxilla in mediolaterally transverse suture. The medial surface of the anterior ramus of the pterygoid is concave and sutured to the convex edge of the palatine. The anterior ramus of the pterygoid has a tall ridge on the dorsal surface of the pterygoid that extends anteroposteriorly along the midline of the palate over the palatal fenestra. The ridge is tallest at the contact point with the prefrontal pillars (fig. 4A). The anterior tip of the dorsal ramus is incomplete, but appears to have contacted the posterior edge of the vomer along the anterior edge of the palatal fenestra (fig. 2A). In CT

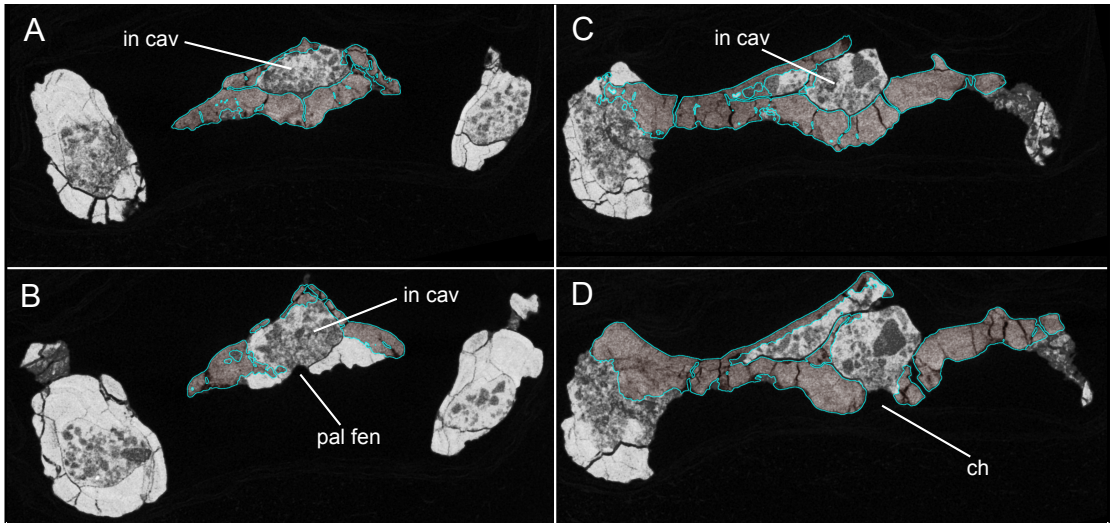

FIGURE 5. CT scan cross sections through the pterygoid of *Shartegosuchus* (IGM 200/50). The blue line demarcates the boundary of the pterygoid. **A.** anterior to palatal fenestra; **B.** posterior to palatal fenestra; **C.** through palatal fenestra; **D.** through choana. Abbreviations: **ch,** choana; **in cav,** internal cavity; **pal fen,** palatal fenestra.

cross sections the dorsal ramus of the pterygoid is hollow, presumably to allow air to flow from the nasal opening to the choana (fig. 5).

The posterolateral ramus of the pterygoid, or pterygoid flange, is a broad, sculptured sheet of bone. The anterolateral edge of the flange sutures to the ectopterygoid. The choana (of which only the anterior half is preserved) is positioned on the posterior end of the palate between the fused pterygoids. The right pterygoid preserves a small area posterior to the choana, which is less sculptured and angled posterodorsally to the palatal surface. The right posterior corner near the edge of the choanal opening is depressed and oriented ventrally and medially. A thin, unsculptured surface projects laterally from the choana along the posterior surface of the pterygoid flange, separated from the sculptured region of the palate by a small ridge. A median ridge on the palatal surface is also noted for *Shantungosuchus* and *Sichuanosuchus*, although their ridges extend posteriorly from the choanal opening, unlike *Shartegosuchus*, in which the ridge is positioned anterior to the choana.

Ectopterygoid: Only a small portion of the pterygoid process of the ectopterygoid remains, which abuts the anterolateralmost edge of the pterygoid flange without extending a posterior process further over the surface of the flange. Although the ectopterygoid is incomplete, the anterolateral direction of the remaining portion of neck indicates it would have contacted the medial surface of the jugal, the maxilla, or both, and formed the posterolateral edge of the suborbital fenestra.

Vomer: The medial contact between the fused vomers is indiscernible in CT scans. The vomer is preserved as contacting the dorsal palatal surface of the maxilla and positioned immediately anterior to the palatal fenestra. Presumably, the posterior process of the vomers would have contacted the anterior tip of the dorsal ramus of the pterygoid. The vomers are characterized by a deep medial depression edged by two parallel ridges on the dorsal surface that continues

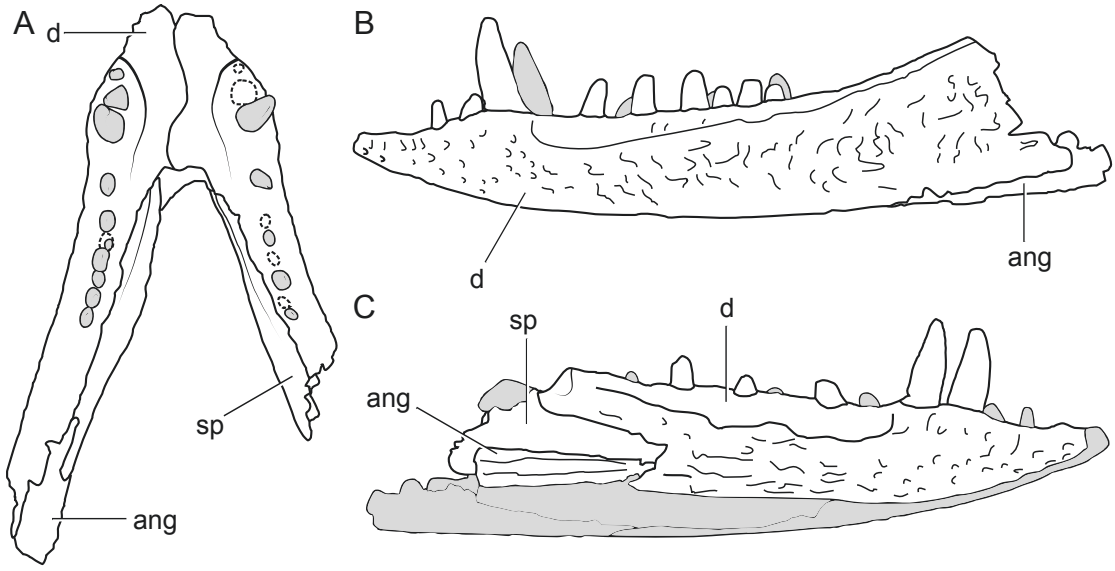

FIGURE 6. Line drawings of the mandible *Shartegosuchus asperopalatum* (IGM 200/50) in **A.** dorsal view, **B.** left lateral view, and **C.** right lateral view. Abbreviations: **ang,** angular; **d,** dentary; **sp,** splenial.

along their anteroposterior length (fig. 2A). The groove is mediolaterally wide, encompassing the dorsal surface of the bone.

Dentary: The dentary is only preserved anterior to the mandibular fenestra. The preserved portion of the dentary has 10 alveoli and is edentulous anteriorly. All known shartegosuchoids with the exception of *Shantungosuchus* and *Zosuchus* are edentulous anteriorly on the dentary (Wu et al., 1994, 1997; Pol and Norell, 2004; Clark, 2011). In dorsal view, the surface of the dentary symphyseal region is broad and subtriangular in outline. The lateral surface of the dentary is heavily sculptured with pits and grooves. A long groove on the lateral surface of the dentary commences from below the first maxillary caniniform and continues posteriorly along its remaining length. Dorsally to the groove the lateral surface of the dentary is less sculptured, lacking any pitting.

The first dentary alveolus is located opposite the posterior end of the premaxilla. The dentary flares out laterally to accommodate two enlarged caniniforms in the second and third alveoli. A deep Meckelian canal incises the medial surface of the dentary, opening between the splenial and dentary.

Splenial: The splenial is a dorsoventrally broad sheet of bone that forms the medial surface of the mandible, contacting the dentary laterally and the splenial posteriorly. The splenial is not involved in the dentary symphysis, and forms the medial wall of the Meckelian canal.

Angular: Only the anterior portion of the angular remains. It is preserved as a long splintlike element. It starts as a sharp point that is wedged between the ventral edge of the splenial and dentary, contributing to the floor of the Meckelian canal. The Meckelian canal continues posteriorly along a shallow groove on the dorsal surface of the angular. As the angular becomes exposed on the ventral surface of the mandible it gains external sculpturing, continuous with the dentary.

Dentition: The dentition resembles that described for *Fruitachampsa* (Clark, 2011), but the dental count differs, with *Shartegosuchus* having eight teeth per maxilla as opposed to the nine teeth of *Fruitachampsa*. *Shartegosuchus* possesses 10 dentary teeth, the first of which is smaller than the others. Two large caniniforms occupy maxillary alveoli one and two and dentary alveoli two and three. The caniniforms are oval in cross section, slightly recurved, with keels on their anterior and posterior edges, lacking serrations on any tooth as in *Fruitachampsa*. Both the maxillary and dentary caniniforms are seated in joined alveoli. Unlike *Fruitachampsa*, all other teeth are seated in individual sockets. The postcaniniform teeth are similar in size, rectangular in lateral view and labiolingually compressed. As with *Fruitachampsa*, *Adzhosuchus*, and *Nominosuchus* (Efimov, 1996; Clark, 2011), the postcaniniform teeth have an anteroposteriorly long horizontal tip with vertical crenulations extending ventrally from it.

Phylogenetic Relationships

Our analysis resulted in five most parsimonious topologies (length = 897, CI = 0.360, RI = 0.712). Bremer support for Shartegosuchoidea is poor with a support value of 1, although Shartegosuchidae is better supported with a Bremer value of 3. Bootstrap and jacknife values also show that Shartegosuchoidea is poorly supported, with a bootstrap value of 7 and a jacknife value of 18. However, Shartegosuchidae is relatively well supported with a bootstrap value of 59 and jacknife value of 69 (fig. 7).

All trees show a paraphyletic "Protosuchia," which includes the monophyletic groups Gobiosuchidae, Protosuchidae, and Shartegosuchoidea. Shartegosuchoidea includes the taxa *Zosuchus*, *Shantungosuchus*, *Sichuanosuchus*, *Nominosuchus*, *Fruitachampsa*, *Shartegosuchus*, and *Adzhosuchus*. The relationships within Shartegosuchoidea are identical to those observed by Clark (2011). This group is supported by a small palatine that is excluded from the margin of suborbital fenestra by the maxilla and pterygoid (char. 200). This character is present in all shartegosuchoids with the exception of *Fruitachampsa*, in which it is absent, and *Zosuchus*, in which the condition is unknown.

Nested within Shartegosuchoidea is the monophyletic group Shartegosuchidae, consisting of *Nominosuchus*, *Fruitachampsa*, *Shartegosuchus*, and *Adzhosuchus*. Shartegosuchidae are united by synapomorphic posterior maxillary and postcaniniform teeth that have apically flat cusps with apicobasally oriented crenulations extending proximally from it (char. 262). Within Shartegosuchidae, *Fruitachampsa*, *Adzhosuchus*, and *Shartegosuchus* form a clade united by a palatal fenestra that is separated from the choana (char. 263) and an edentulous anterior end of the dentary (char. 259). In these three taxa, the choana is positioned posterior to the suborbital fenestrae. In shartegosuchoids outside this group (except *Zosuchus*), the palatal fenestra is continuous with the choana by a mediolaterally narrow slit. Within Shartegosuchidae, *Shartegosuchus* and *Adzhosuchus* are sister taxa, supported by the choana continuous with the ventral surface of the pterygoid and positioned near the posterior end of the pterygoid flanges (chars. 39 and 44).

Outside Shartegosuchidae, the relationship between *Shantungosuchus*, *Sichuanosuchus*, and *Zosuchus* is unresolved in the strict consensus tree. However, the results from the

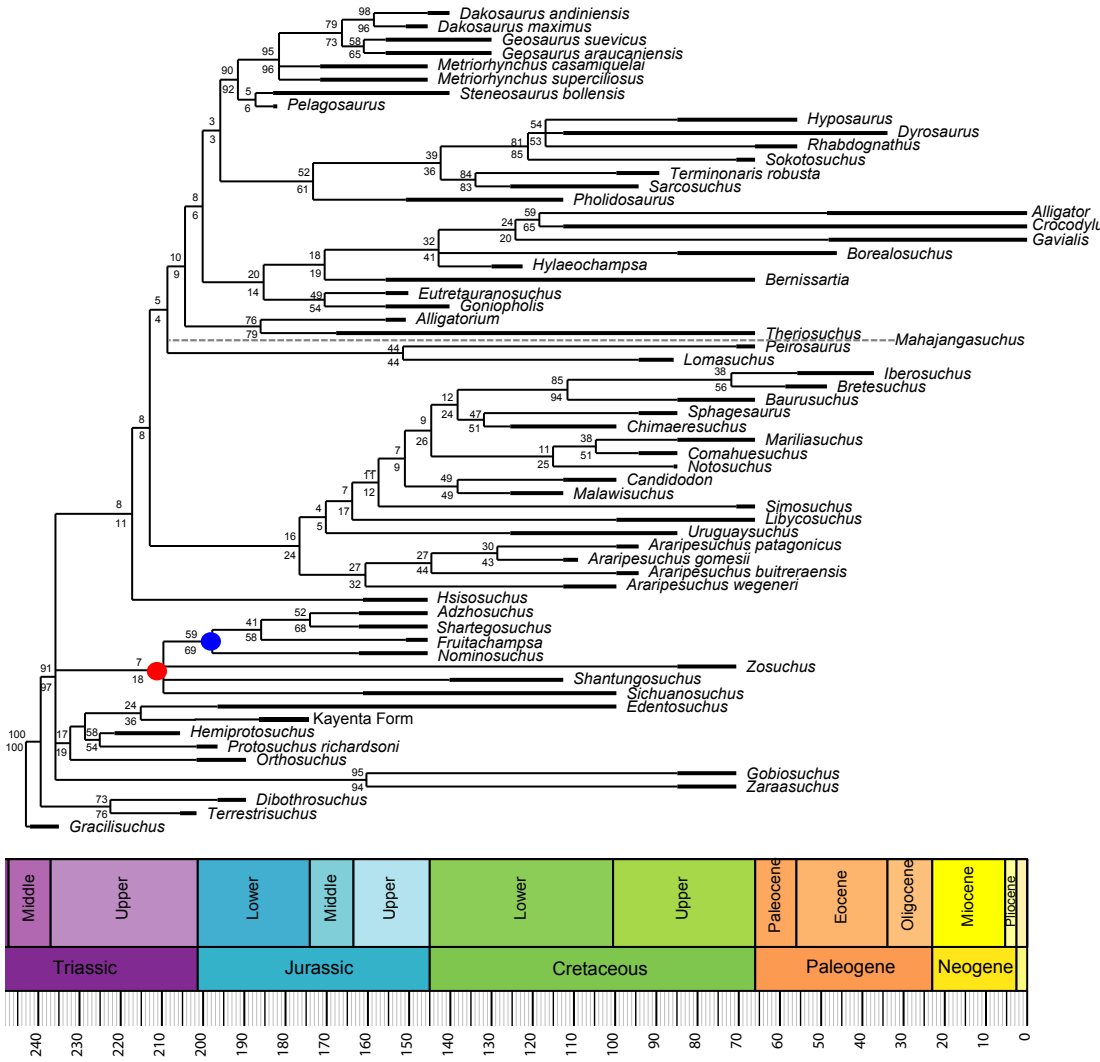

FIGURE 7. Time calibrated strict consensus tree (length = 897, CI = 0.360, RI = 0.712). A red circle indicates the node Shartegosuchoidea and a blue circle indicates the node Shartegosuchidae. Bootstrap values are listed above each node, and jacknife values below each node. *Mahajangasuchus* added a posteriori to tree, based on a position hypothesized in Turner and Buckley's (2008) work.

analysis show that in some most parsimonious topologies these three taxa form another monophyletic group within Shartegosuchoidea, sister to Shartegosuchidae (fig. 8). There are two possible synapomorphies to support a group that includes these three taxa: the angular shifted to the ventral surface of the mandible posterior to the mandibular fenestra (char. 201); and the posterolateral edge of the quadratojugal has a sinusoidal ventral edge with the posterior edge overhanging the lateral surface of the quadrate (char. 211).

A recent phylogenetic analysis of Crocodylomorpha found support for Thalattosuchia in a much more basal position than usually found (Wilberg, 2015). An identical search protocol

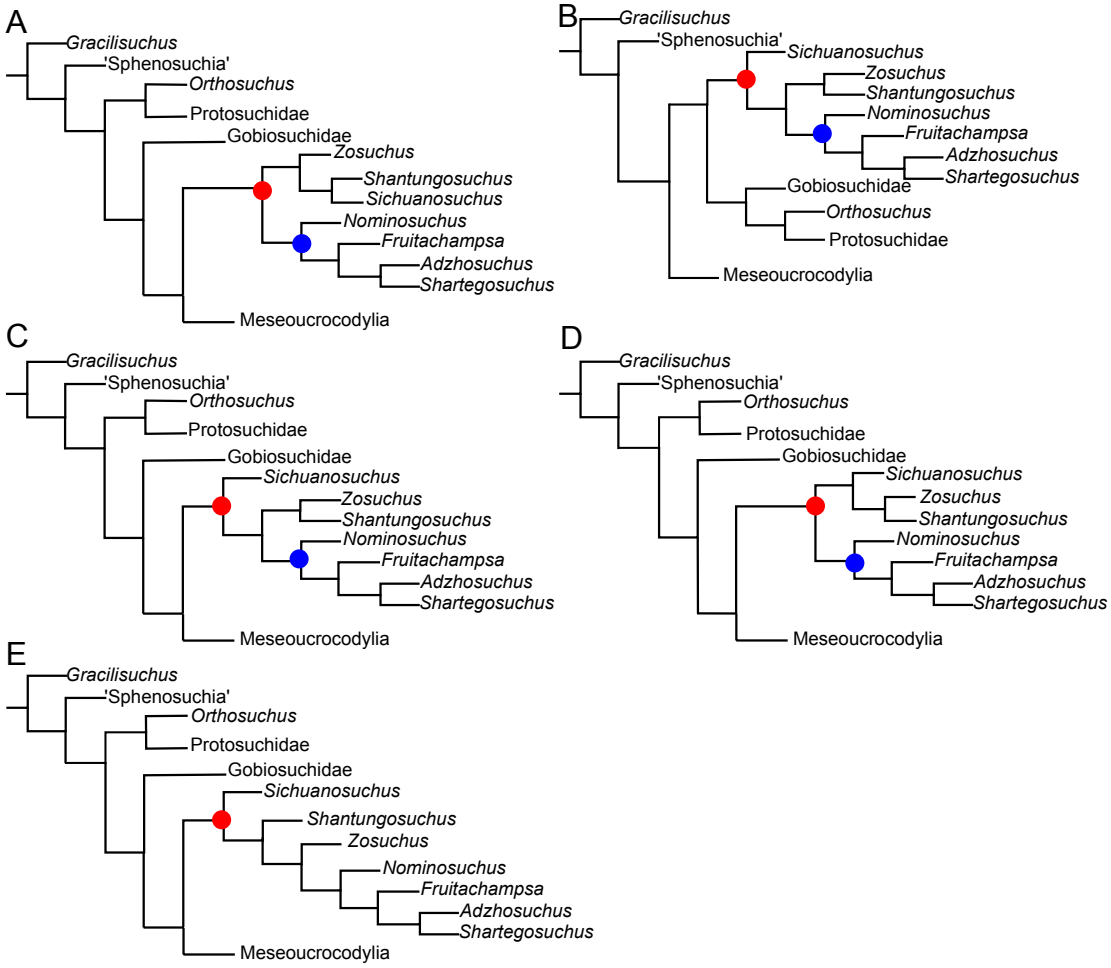

FIGURE 8. The five most parsimonious trees from the analyses (length = 897). Red circles indicate the node Shartegosuchoidea and blue circles indicate the node Shartegosuchidae.

with Thalattosuchia constrained as the sister taxon to Crocodyliformes returned six most parsimonious trees with a length of 903. All trees in this constrained analysis hypothesize a monophyletic Shartegosuchoidea, which is in turn sister to Protosuchidae, and which together form a monophyletic Protosuchia.

When Thalattosuchia is constrained as the sister taxon of Crocodyliformes (fig. 9), Protosuchia is monophyletic and the palatine secondary palate then optimizes as a synapomorphy of Thalattosuchia + Crocodyliformes, which is later lost in Protosuchidae; this result is similar to that of Clark (1994). It implies that the palatine secondary palate evolved once at the base of Thalattosuchia + Crocodyliformes, was retained as a symplesiomorphy within Shartegosuchoidea and modified into a eusuchian-type palate within Shartegosuchidae, but lost within Protosuchidae. It could also imply that a palatine secondary palate evolved independently from Crocodyliformes within Thalattosuchia, and then evolved

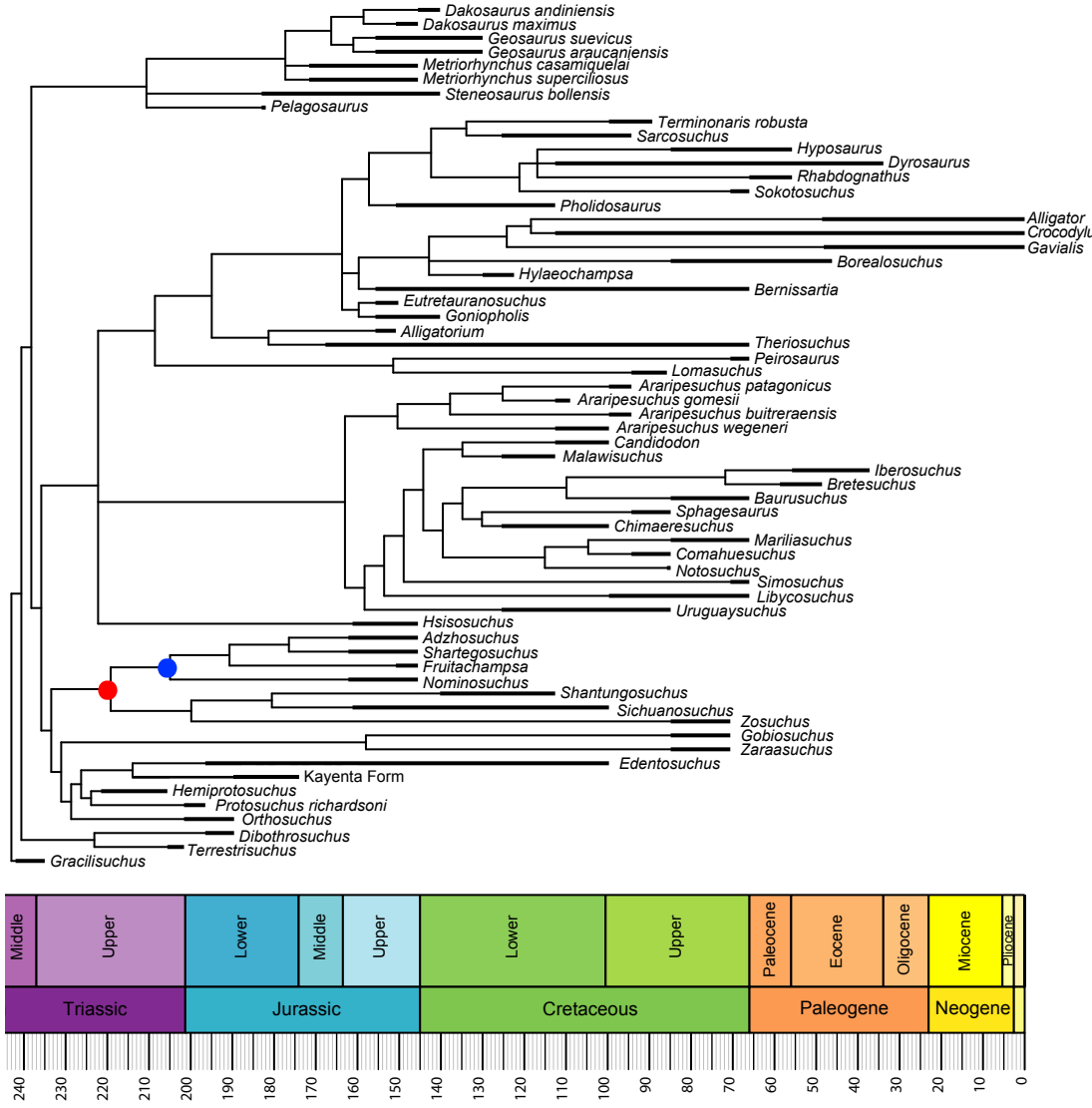

FIGURE 9. Strict consensus tree with Thalattosuchia constrained as a sister group to Crocodyliformes (length = 903). A red circle indicates the node Shartegosuchoidea and a blue circle indicates the node Shartegosuchidae.

later independently within Shartegosuchoidea and Mesoeucrocodylia, although this hypothesis is less parsimonious.

DISCUSSION

The presence of a palatine and pterygoid secondary palate within Shartegosuchidae, a clade that is far outside of Eusuchia, provides an opportunity for further evaluating the homology relationships of palatal constructs across Crocodylomorpha (fig. 10), an ongoing process that other research has commenced (Turner and Buckley, 2008).

Choanal Position and Palatal Fenestra Function

Several lines of evidence support homology of the posterior palatal opening of *Shartegosuchus* with the choana of other crocodylomorphs. First, the posterior opening of *Shartegosuchus* is elliptical in shape, standing in marked contrast to the elongated, slitlike morphology of the palatal fenestra. Throughout Crocodylomorpha, the choanal opening generally is an elliptical structure as it opens from the palate, although a more slitlike choana has been described for *Candidodon* (Andrade et al., 2006). Furthermore, the posterior opening in *Shartegosuchus* has a raised rim, triangular, depressed surfaces along the posteroventral margins, and a smoothed anterior margin that extends dorsally into the airway. These features are nearly ubiquitous on crocodylomorph choanae, and are conspicuously absent on the palatal fenestra of *Shartegosuchus*.

This raises the question of whether the presence of a palatal fenestra in shartegosuchids is retained for functional reasons or is an artifact of a transitional stage in the evolution of a closed secondary palate. Embryonic crocodylian palates as well as macroevolutionary transformation series have the potential to provide evidence one way or the other about the latter hypothesis.

Rieppel (1993) describes the developmental stages of a secondary palate within embryonic alligators. Most relevant to this study are the palatal constructs from 41 days onward, which in some ways resemble the shartegosuchid condition. After 41 days, the secondary palate of an embryonic alligator resembles the palatal construct described for the shartegosuchid *Nominosuchus*, whereby the palatines do not meet along the skull midline. Additionally, the pterygoids of both the embryonic alligator and *Nominosuchus* do meet along the midline of the palate and form the roof of the choanal tubes.

After 47 days, the palatines have developed a long contact along the midline of the skull and form the anterior edge of the choana, resembling the condition in *Fruitachampsa*. However, although the maxillae of the alligator embryo has formed palatal shelves after 47 days, they do not meet along the midline of the palate (as in *Fruitachampsa*). Therefore, the anterior palatal fenestra of the embryonic alligator is enclosed by the palatines posteriorly, the maxilla posterolaterally and laterally, and the premaxilla anteriorly. This is different from the palatal fenestra described for *Fruitachampsa*, which is enclosed by the palatines posteriorly and the maxilla laterally and anteriorly.

After 50 days, the embryonic alligator develops pterygoid flanges that meet along the midline of the skull and enclose the anterior edge of the choana, resulting in a choana enclosed entirely by the pterygoids. As the embryo develops, the choana moves further posteriorly, resembling the choanal position in *Shartegosuchus*. However, the obvious distinction between the two palatal morphologies is the presence of a palatal fenestra that is enclosed by the palatines together with a choana enclosed entirely by the pterygoids, which is observed in *Shartegosuchus* but not within the embryonic alligator. This suggests that either the *Shartegosuchus* specimen IGM 200/50 is not a juvenile exhibiting an ontogenetic feature, or the recapitulation is not perfectly represented in the embryonic alligator.

It is interesting to note that in Efimov et al. (2000) reconstruction of *Adzhosuchus*, the palatines are illustrated as larger, with a long, medial contact extending anteriorly along the

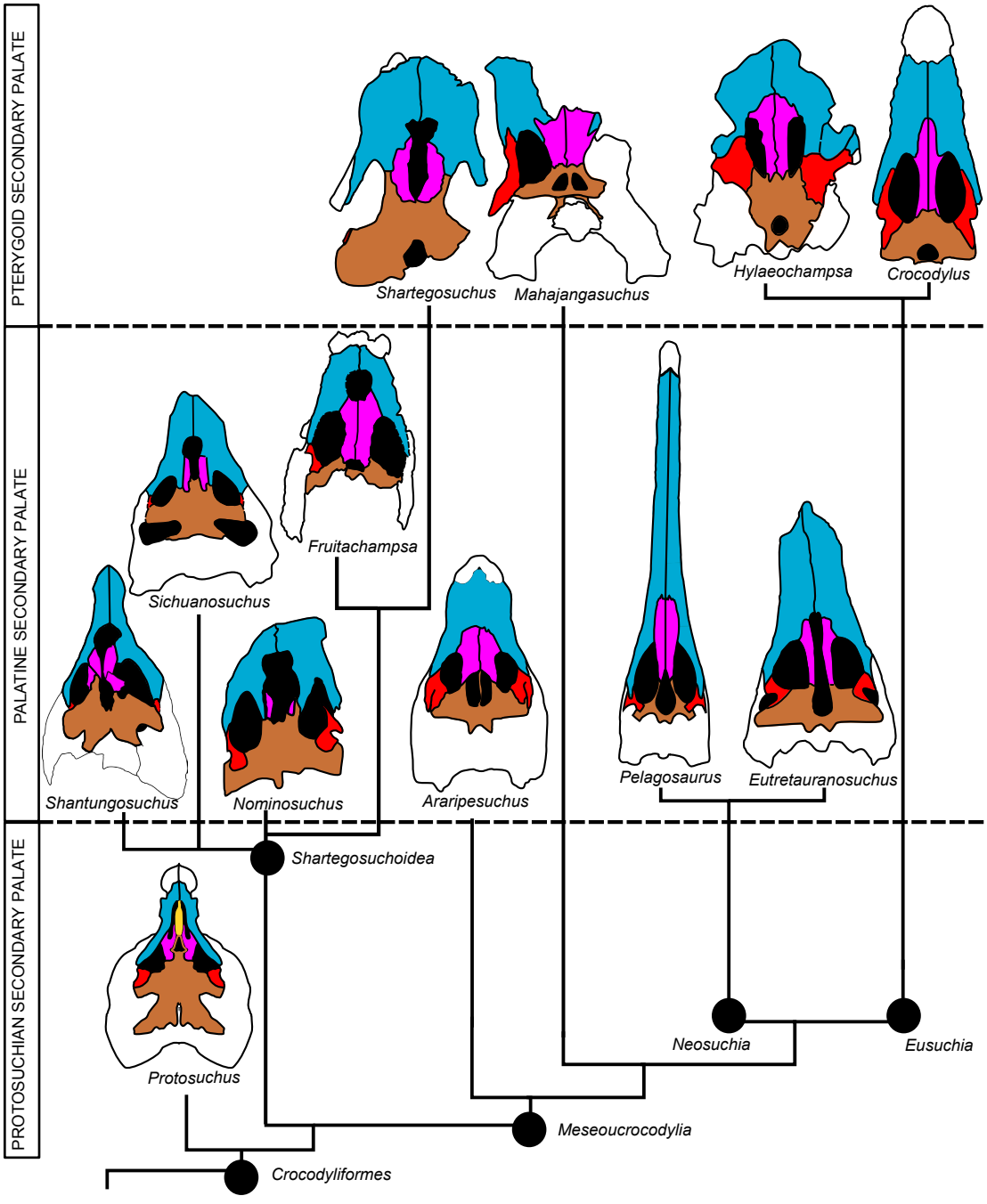

FIGURE 10. Simplified phylogenetic tree mapping the stages in the evolution of the secondary palate in Crocodylomorpha. Palatal bones are colored as follows: maxilla, blue; palatine, pink; ectopterygoid, red; pterygoid, brown; and vomer, yellow.

skull midline. Also, the palatal fenestra of *Adzhosuchus* is positioned further anteriorly than in *Shartegosuchus*, a condition more closely resembling the embryonic alligator.

It could be proposed that palatal fenestra of shartegosuchids has no functional purpose and is covered in soft tissue to separate the oral from nasal cavity. The differences in the palatal morphologies between shartegosuchids and embryonic alligators may be a result of a differences in the evolutionary development of a closed palate, a concept that has already been noted for mammalians with multiple convergent occurrences of a closed secondary palate with variances in palatal constructs (Cluvier, 1971).

The Evolution of a Pterygoid Secondary Palate

A pterygoid secondary palate was first proposed by Huxley (1875) to have evolved to prolong the nasal passage, and thus allowing a posteriorly positioned choana. More recently a biomechanics-based hypothesis has been proposed to explain the evolution of a pterygoid secondary palate as an adaptive response to the torsional strains placed on platyrostral skulls (Busbey, 1995; Rayfield and Milner, 2008).

Turner and Buckley's (2008) work on *Mahajangasuchus*, a non-eusuchian crocodylomorph with a pterygoid secondary palate and a platyrostral skull, supports a biomechanical motivation. Previous evaluations of the relationship between rostral shape and biomechanical performance resolved that platyrostry is inefficient in resisting dorsoventral torsional stresses. Rather, platyrostry is optimized to decrease hydrodynamic resistances on the lateral movements of the skull, allowing for predation on more small, agile prey (i.e., fish) (McHenry et al., 2006; Pierce et al., 2008).

Shartegosuchus remains have been recovered within deposits that include aquatic turtles and molluscs, which suggests a wet environment (Gubin and Sinitza, 1996; Watabe et al., 2004; Watabe et al., 2007; Watabe et al., 2008) and indicates that *Shartegosuchus* may have exhibited a semiaquatic lifestyle, as hypothesized by Efimov et al. (2000). However, the short, oreinorostral snout of *Shartegosuchus* is inconsistent with piscivory. The extant crocodylian species with the anteroposteriorly shortest and dorsoventrally tallest rostral profile are *Paleosuchus palpebrosus*, *Paleosuchus trigonatus*, and *Osteolaemus tetrapis*. These extant taxa predate on aquatic invertebrates and terrestrial prey rather than on more agile fish (Riley and Huchzermeyer, 2000; Magnusson and Campos, 2010).

An argument could be made that the feeding habits of *Shartegosuchus* would resemble those of *Paleosuchus* and *Osteolaemus* based on similarities in rostral shape, although they are many times larger than the largest specimens of *Shartegosuchus.* However, the unusual palatal and dental morphologies observed in *Shartegosuchus* (the sculptured palate, the anteriorly edentulous dentary and unusual dental morphology) suggest that shartegosuchids used their snouts for a predation activity for which there is no modern analog within extant crocodylians. Therefore, it is also possible that this feeding activity imposed stress loadings on the skull that mimic those observed in platyrostral crocodylians and thus required similar reinforcement strategies. This hypothesis is supported by the presence of additional features within *Shartego-*

suchus, such as thick palatal bones and lack of antorbital fenestrae, which have been proposed to assist in reducing strain on platyrostral skulls (Busbey, 1995; Preushscoft and Witzel, 2002). However, in *Shartegosuchus* the prefrontal pillar forms only a weak contact with the dorsal surface of the palate; in extant crocodylians this pillar forms a robust contact with the dorsal surface of the palatine to provide additional structural reinforcement to the rostrum (Iordansky, 1973). Furthermore, *Shartegosuchus* possesses an anterior palatal fenestra that results in an incomplete closed secondary palate. It could be that the need for a robust prefrontal pillar and a complete secondary palate within *Shartegosuchus* is circumvented by the presence of a more tabular cross section of the rostrumthat, according to basic beam theory and prior Finite Element (FE) modeling of rostral shape, is a more stress-resistant structure (McHenry et al., 2006; Pierce et al., 2008; Rayfield and Milner, 2008). It could also be that the stresses were focused on a small area at the posterior end of the rostrum, and so only required a more localized structural reinforcement for the rostrum.

In the future, evaluating the mechanical performance of the skulls of shartegosuchids and comparing them to extant crocodylians will more clearly evaluate the relationship between rostral shape, ecology, multiple palatal morphologies, and the posterior movement of the choana. It is evident from the data presented in this study and from prior studies that these characteristics are more intertwined than previous assumptions held.

CONCLUSION

Shartegosuchoidea is a monophyletic clade that branches much earlier than Eusuchia and that independently evolved a pterygoid secondary palate (a choana posteriorly positioned and enclosed fully by the pterygoid). Furthermore, the presence of a pterygoid secondary palate within *Shartegosuchus*, a taxon with an oreinorostral snout, calls into question biomechanical motivations for the evolution of a pterygoid secondary palate to support platyrostry. The presence of unusual palatal and dental features within *Shartegosuchus* suggests it had feeding habits that imposed stress loadings on the skull that required similar reinforcement strategies observed in eusuchians (thick palatal bones and lack of antorbital fenestra). However, *Shartegosuchus* possesses an anterior palatal fenestra and a weak contact between the prefrontal and palate (additional reinforcement features observed in extant crocodylians). The need for these additional features may have been circumvented by the presence of oreinorostry within shartegosuchids, a rostral shape that has inherent higher mechanical performance. Future research would require FE models to evaluate stress distributions across shartegosuchid skulls, to evaluate their mechanical performance against extant crocodylians to infer further details about ecology, biomechanical performance, and its relationship with rostral shape.

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