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Osteology of a North American goniopholidid (*Eutretauranosuchus delfsi*) and palate evolution in Neosuchia

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ABSTRACT

The goniopholidid *Eutretauranosuchus delfsi* is currently known from two skulls from the Late Jurassic Morrison Formation of Colorado. Here we present a detailed osteology for a third *Eutretauranosuchus delfsi* specimen (AMNH FARB 570), consisting of a skull and fragmentary postcranium from Bone Cabin Quarry, Wyoming (Morrison Formation). Additional preparation, computed tomography (CT), and three-dimensional processing of CT images reveal matrix-covered structures on AMNH FARB 570, provide new information on goniopholidid cranial anatomy, and allow for the first description of an articulated North American goniopholidid braincase. These new data, along with restudy of the palatal anatomy in *Eutretauranosuchus*, provide valuable insight into the phylogenetic history of goniopholidid crocodyliforms. The skull of AMNH FARB 570 is extremely similar to other specimens of *E. delfsi* and *Amphicotylus* spp., especially in details of the architecture of the palate. In these Morrison Formation goniopholidids the secondary palate is incomplete such that the nasopharyngeal passage has no ventral floor. Additionally, there is a complex septum, constructed from the vomers and pterygoid, which extends ventrally near to the plane of the secondary palate. Characters diagnosing *Eutretauranosuchus delfsi* include: (1) an elongate, platyrostral skull; (2) a prominent depression on the posterolateral surface of the alveolar process of the maxilla; (3) minimal lateral undulation of the maxillary tooth row; (4) broad-

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ening of the nasals anterior to the prefrontals; (5) nasals that do not contact external nares; (6) a broad, flat interfenestral bar with raised rims along the supratemporal fenestrae; (7) a nasopharyngeal septum formed from diverging vomeral processes anteriorly and a midline pterygoid process posteriorly (also in *Amphicotylus lucasii*, AMNH FARB 5782); and (8) a vomeral septal complex that forms an X shape in cross section.

Based on a revised phylogenetic analysis of 88 crocodylomorph taxa, a novel phylogenetic hypothesis is proposed in which a clade of *Calsoyasuchus* + *Sunosuchus* is sister to a clade of *Goniopholis baryglyphaeus* + (*Goniopholis simus* + (*Amphicotylus lucasii* + *Eutretauranosuchus delfsi*)). Examination of secondary palate characters in Goniopholididae suggests that this group "experimented" with changes to the bony secondary palate a number of times, resulting in morphologies not seen other mesoeucrocodylian clades.

INTRODUCTION

Goniopholididae is a clade of Jurassic and Cretaceous neosuchian crocodyliforms characterized by platyrostral snouts and prominent depressions on the posterolateral surfaces of the maxillae. Goniopholididae are of importance in understanding the origin of the modern crocodylian body plan, because they represent the earliest crocodyliforms known to exhibit a flattened (= platyrostral) rostrum and to exploit a freshwater, semiaquatic habitus (Averianov, 2000; Tykoski et al., 2002). Richard Owen (1842) was the first to report on this group with the description of a partial skeleton of *Goniopholis crassidens* from the Early Cretaceous of Swanage, Dorset, United Kingdom. Numerous additional species have been named and assigned to the Goniopholididae (e.g., Marsh, 1877; Cope, 1888; Mook, 1925, 1967; Wiman, 1932), but no extensive review of species historically referred to the clade exists. Most recent systematic studies recover a well-supported, monophyletic Goniopholididae nested within Neosuchia. These analyses include several Asian, European, and North American taxa temporally ranging from the Early Jurassic to the Late Cretaceous (e.g., Pol et al., 2009; Turner and Sertich, 2010; Andrade et al., 2011). Nevertheless, other recent papers consider the possibility that goniopholidids are a paraphyletic grade within Neosuchia (Jouve et al., 2006). Ecologically, goniopholidids are regarded as modern crocodylian analogs (Foster, 2009) although, as we learn more about the disparate habits in the extant taxa, exactly what this means is unclear.

Although nearly all goniopholidids are characterized by platyrostral snouts (albeit subtle in *Calsoyasuchus valliceps* Tykoski et al., 2002) and maxillary depressions (possibly reversed in the putative goniopholidid *Denazinosuchus kirtlandicus* Lucas and Sullvian, 2003), goniopholidids exhibit high degrees of variation in their palatal anatomy. Taxa from the Cretaceous of Europe (e.g., *Goniopholis simus* Owen, 1878; *G. kiplingi* Andrade et al., 2011) exhibit a conservative mesoeucrocodylian palatal morphology in which a secondary bony palate, formed by the palatal processes of the maxillae and palatines, forms the floor of the bony nasopharyngeal canal (Salisbury et al., 1999). This contrasts with the morphology present in species of the Asian *Sunosuchus* (e.g., Young, 1948; Wu et al., 1996) and the North American *Amphicotylus*, *Eutretauranosuchus*, and *Calsoyasuchus* (Tykoski et al., 2002). It should be noted that North American species traditionally referred to the genus *Goniopholis* (e.g., Foster, 2009) are herein

FIG. 1. Panel mount of *Eutretauranosuchus delfsi* AMNH FARB 570. The skull has been removed, and the right mandible and cervical region remain.

referred to *Amphicotylus*, based on recent phylogenetic hypotheses (Allen, 2010; Andrade et al., 2011). In *Sunosuchus miaoi* and *S. junggarensis*, the secondary palate is marked by prominent ventral openings into the nasopharyngeal passage within the sutures of the palatal processes of the maxillae with the palatal processes of the palatines (Young, 1948; Buffetaut, 1986; Wu et al., 1996). In *Amphicotylus, Eutretauranosuchus*, and *Calsoyasuchus* the palate is more open because the maxillae and palatines fail to contact such that the bony nasopharyngeal passage is exposed in ventral view (Mook, 1967; Tykoski et al., 2002; Allen, 2010; Smith et al., 2010). This is unique among mesoeucrocodylians, but a similar ventrally opened nasopharyngeal trough is present in some basal crocodyliforms (e.g., *Orthosuchus stormbergi* Nash, 1968, and *Hsisosuchus dashanpuensis* Gao, 2001). However, in these taxa, the palatines and maxillae are widely separated, whereas American goniopholidids possesses a much narrower ventral cleft for the nasopharyngeal passage. The details of this condition have been addressed only in the description of *C. valliceps*, but it should be noted that many sutural relationships in the holotype of *C. valliceps* (TMM 43631-1) are unclear due to poor preservation of the palate.

The braincase osteology in goniopholidids is poorly understood. Damaged, isolated braincase elements were described for *Sunosuchus junggarensis* from the Late Jurassic Shishugou Formation of Xinjiang, China (Wu et al., 1996). Edinger (1938) described an endocast of *Goniopholis pugnax* and partial braincases for *G. pugnax* and *G. minor* from Wealden deposits in the U.K. (according to Salisbury et al., 1999, these specimens are now lost). Smith et al. (2008) briefly described the endocast of another specimen of *Eutretauranosuchus delfsi*, noting similarities with modern crocodylians. However, the braincase of a North American goniopholidid has yet to be described in detail. With the recent focus on braincase/endocast anatomy in Crocodyliformes (e.g., Brochu et al., 2002; Sereno and Larsson, 2009; Kley et al., 2010), braincase osteology will likely continue to be a rich source of new characters for phylogenetic analysis.

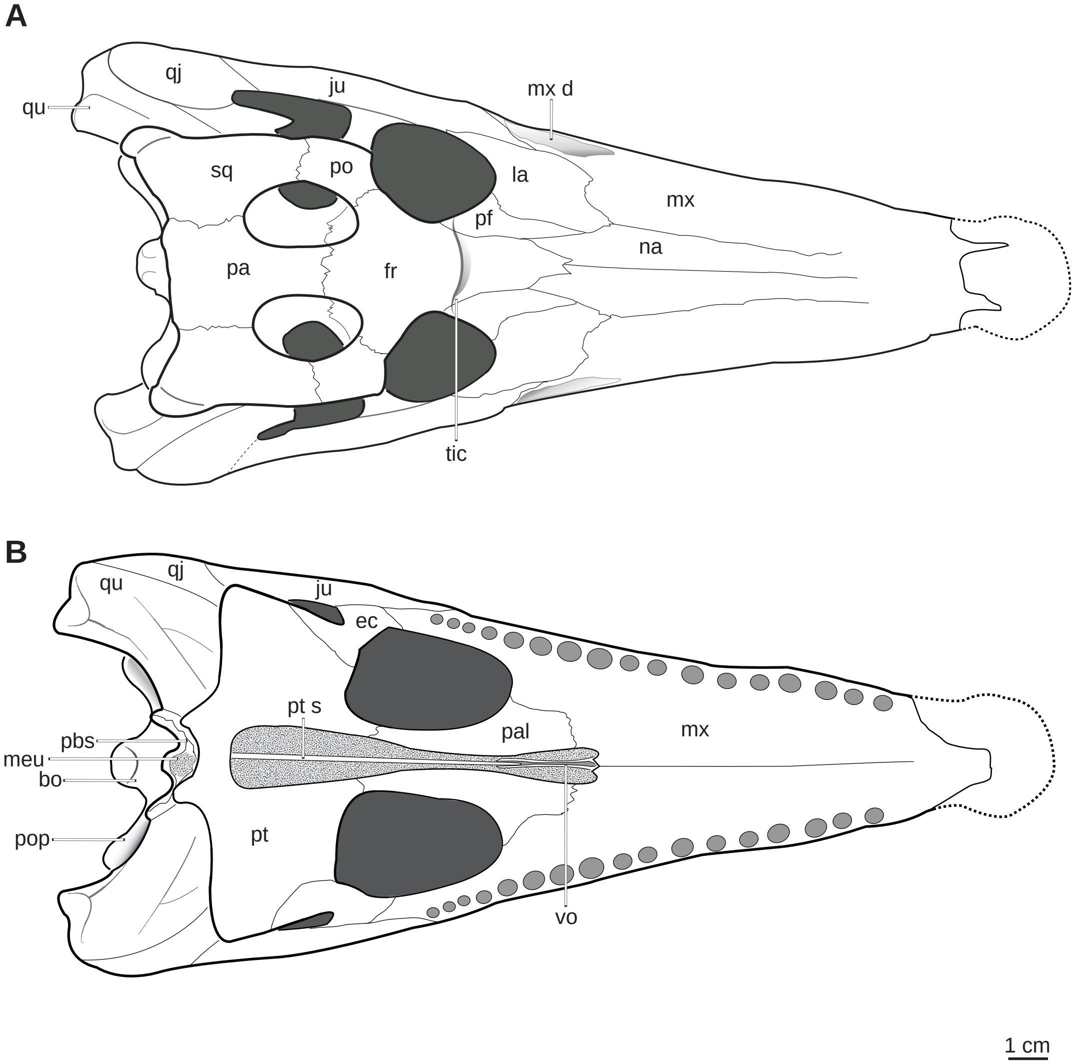

FIG. 2. Holotype of *Eutretauranosuchus delfsi* CMNH 8028 in **(A)** dorsal and **(B)** ventral view. See appendix 2 for abbreviations.

Here we expand anatomical studies of Goniopholididae with the description of AMNH FARB 570, an undescribed crocodyliform specimen referable to *Eutretauranosuchus delfsi* (fig. 1). AMNH FARB 570 consists of a nearly complete skull, partial cervical series, right hemimandible, and fragmentary postcranium. CMNH 8028, the holotype of *E. delfsi*, was first described by Mook (1967) based on a nearly complete skull (missing the premaxillae) and complete hemimandibles (figs. 2, 3). This specimen was the first neosuchian known to possess a ventrally exposed nasopharyngeal passage. A larger and more complete skull (BYU 17628) attributed to *Eutretauranosuchus* was recently described (Smith et al., 2010). Yet even with these remarkable specimens, the bizarre palate condition in *E. delfsi* has not been fully described.

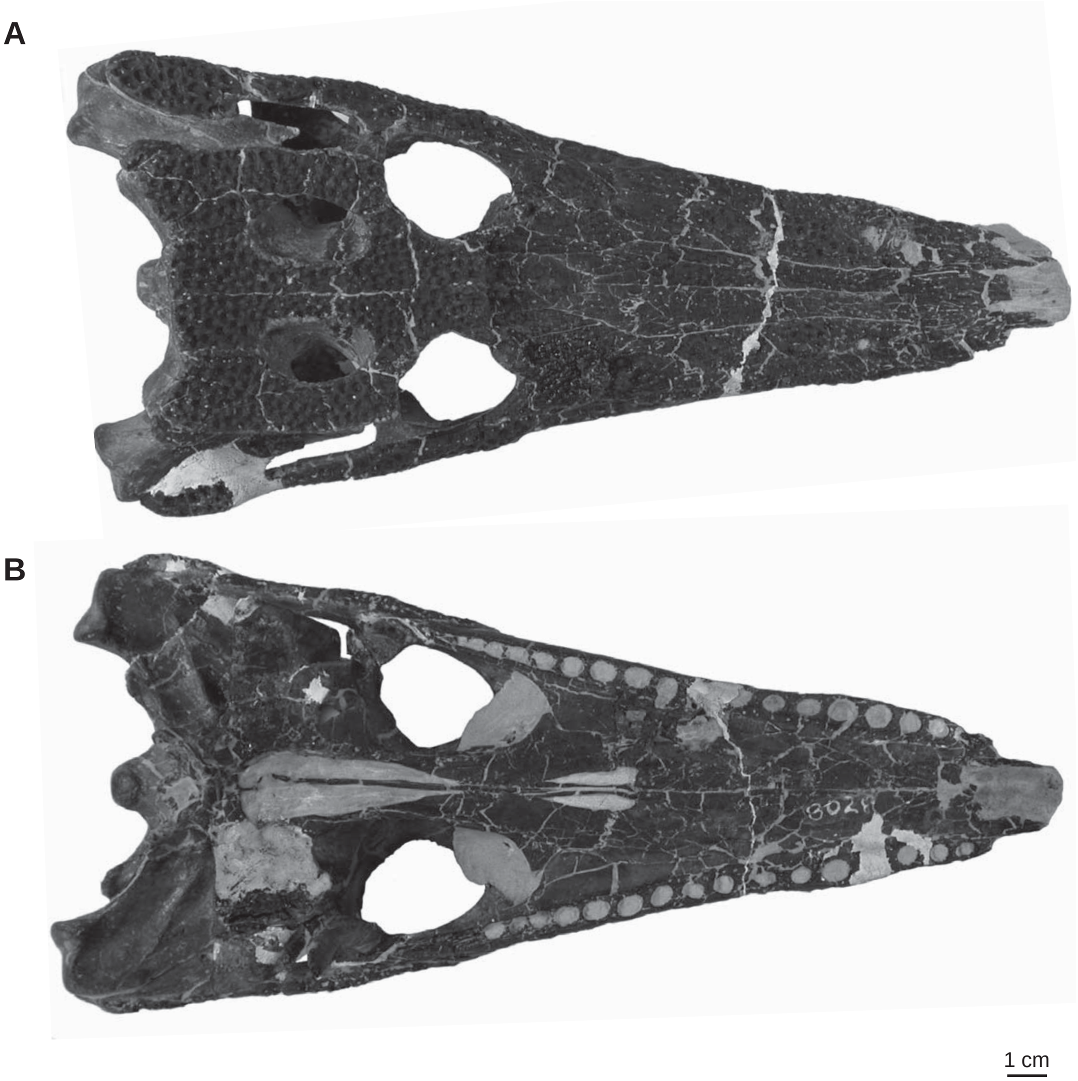

FIG. 3. Holotype of *Eutretauranosuchus delfsi* CMNH 8028 in **(A)** dorsal and **(B)** ventral view.

Preparation and CT scanning of AMNH FARB 570 allows for an extensive description of almost all cranial elements, including those of the palate and braincase. We discuss the diversity of palatal conditions among goniopholidids and analyze character transformations that preceded the derived condition in *E. delfsi.*

Although at the time undescribed, AMNH FARB 570 has served as an exemplar for *Eutretauranosuchus delfsi* in several cladistic analyses of mesoeucrocodylian interrelationships (e.g., Pol et al., 2004; Pol et al., 2009; Turner and Buckley, 2008; Turner and Sertich, 2010), beginning with Pol and Norell (2004a, 2004b).

Descriptive terminology is derived from Kley et al. (2010) unless otherwise noted and anatomical abbreviations are listed in appendix 2. Institutional acronyms may be found in appendix 3.

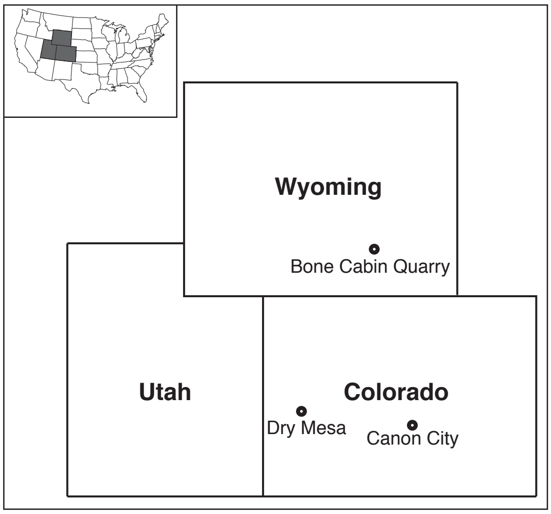

FIG. 4. Locality map highlighting sites with material of *Eutretauranosuchus delfsi*.

Discovery and Geological Context

Field catalogs indicate that AMNH FARB 570 was discovered by Peter Kaisen at the Bone Cabin Quarry site in the Morrison Formation of Wyoming in July 1900. AMNH FARB 570 is labeled "crocodile skull" in the field catalog, although subsequent catalog notes attribute several postcranial elements to the specimen. The same catalog note indicates that the specimen was initially attributed to *Goniopholis* by Walter Granger, with the first attribution of this material to *Eutretauranosuchus delfsi* by Pol and Norell (2004a) in their phylogenetic analysis.

The holotype of *Eutretauranosuchus delfsi* was discovered from Morrison Formation deposits in Red Canyon, north of Cañon City, western Colorado in 1957. This is adjacent to the locality of the holotype and neotype of *Amphicotylus lucasii* (Cope, 1878, 1888; Mook, 1942). The recently described second specimen of *Eutretauranosuchus delfsi* (Smith et al., 2010) is also from the Morrison Formation (Brushy Basin Member) deposits ~250 miles to the west of Cañon City at Dry Mesa Quarry in Colorado. With the addition of AMNH FARB 570 to *E. delfsi*, this taxon is now known to have occurred across a broad geographic range, spanning present day central and western Colorado to southeastern Wyoming (fig. 4).

Computed Tomography

The skull of AMNH FARB 570 was CT scanned on a GE Lightspeed VCT scanner at the Stony Brook University Medical Center. The entire skull of AMNH FARB 570 was scanned in the transverse plane, resulting in a total of 1095 slices, each 0.625 mm thick, with an interslice spacing of 0.200 mm, and a pixel resolution of 512 × 512. For greater detail, the braincase of AMNH FARB 570 was scanned in the transverse plane, resulting in a total of 1399 slices, each 0.625 mm thick with an interslice spacing of 0.125 mm and a pixel resolution of 512 × 512. Avizo 3D imaging software (Visualization Sciences Group, Version 6.3.1) was employed to examine matrix-covered elements of AMNH FARB 570. Slice archive data is available upon request from the lead author.

Preparation Materials and Methods

Detailed preparation notes are not available for most of the original 1900 preparation and subsequent installation into a cement mount with the mandible and material. The original preparators also applied a supportive matrix to the anterior portion of the rostrum for stabilization. Subsequent preparation of AMNH FARB 570 was conducted in 2004 by Jeanne Kelly (AMNH) and in 2011 by Virginia Heissy (Stony Brook University). A preparation record is held at the AMNH Division of Paleontology for 21st-century preparatory work on the specimen.

SYSTEMATIC PALEONTOLOGY

Crocodylomorpha Hay, 1930 (sensu Walker, 1970)

Crocodyliformes Hay, 1930 (sensu Clark, 1986)

Neosuchia Clark, 1986

Eutretauranosuchus delfsi Mook, 1967

Holotype: CMNH 8028, nearly complete skull and complete mandibles (figs. 2, 3).

Referred Specimens: BYU 17628, complete skull and articulated mandibles.

Newly Referred Specimen: AMNH FARB 570, complete skull (figs. 5–15); partial right hemimandible (fig. 16); partial cervical series with associated osteoderms (fig. 1), three isolated osteoderms, distal portion of a left femur (fig. 17).

Emended Diagnosis: (1) Elongate, platyrostral skull; (2) prominent depression on posterolateral surface of alveolar process of maxilla; (3) subtle emargination of maxillary tooth row, with only a single lateral undulation; (4) broadening of nasals anterior to prefrontals; (5) nasals do not contact external nares; (6) broad, flat interfenestral bar with raised medial rims along supratemporal fenestrae (from Mook, 1967, and Smith et al., 2010: shared with *Amphicotylus lucasii* [AMNH FARB 5782]); (7) anteroposteriorly elongate palatal opening due to partial contact of palatal processes of maxillae and noncontact of palatal processes of palatines, exposing entire nasopharyngeal canal in ventral view (shared with *Calsoyasuchus valliceps* [TMM 43631-1]); (8) nasopharyngeal septum formed from diverging vomeral processes anteriorly and midline pterygoid process posteriorly (present in *Amphicotylus lucasii* [AMNH FARB 5782]); and (9) vomeral septal complex forms X shape in cross section (shared with *Amphicotylus lucassii* [AMNH FARB 5782]).

Locality: Bone Cabin Quarry, Morrison Formation (Brushy Basin Member), Wyoming, United States of America (fig. 4). Upper Jurassic (Kimmeridgian) (Foster, 2009).

COMPARATIVE DESCRIPTION

The Skull

Superficial Anatomy and Cranial Openings: The skull of AMNH FARB 570 is elongate and platyrostral (figs. 5 and 6), resembling specimens of *Amphicotylus* and *Goniopholis* (Mook, 1942; Salisbury et al., 1999). The specimen experienced some dorsoventral compression during diagenesis, evinced by small transmitting fractures in the preorbital region (figs. 5C, 6C), a ventral depression on the frontal and left postorbital, and plastic deformation and lateral

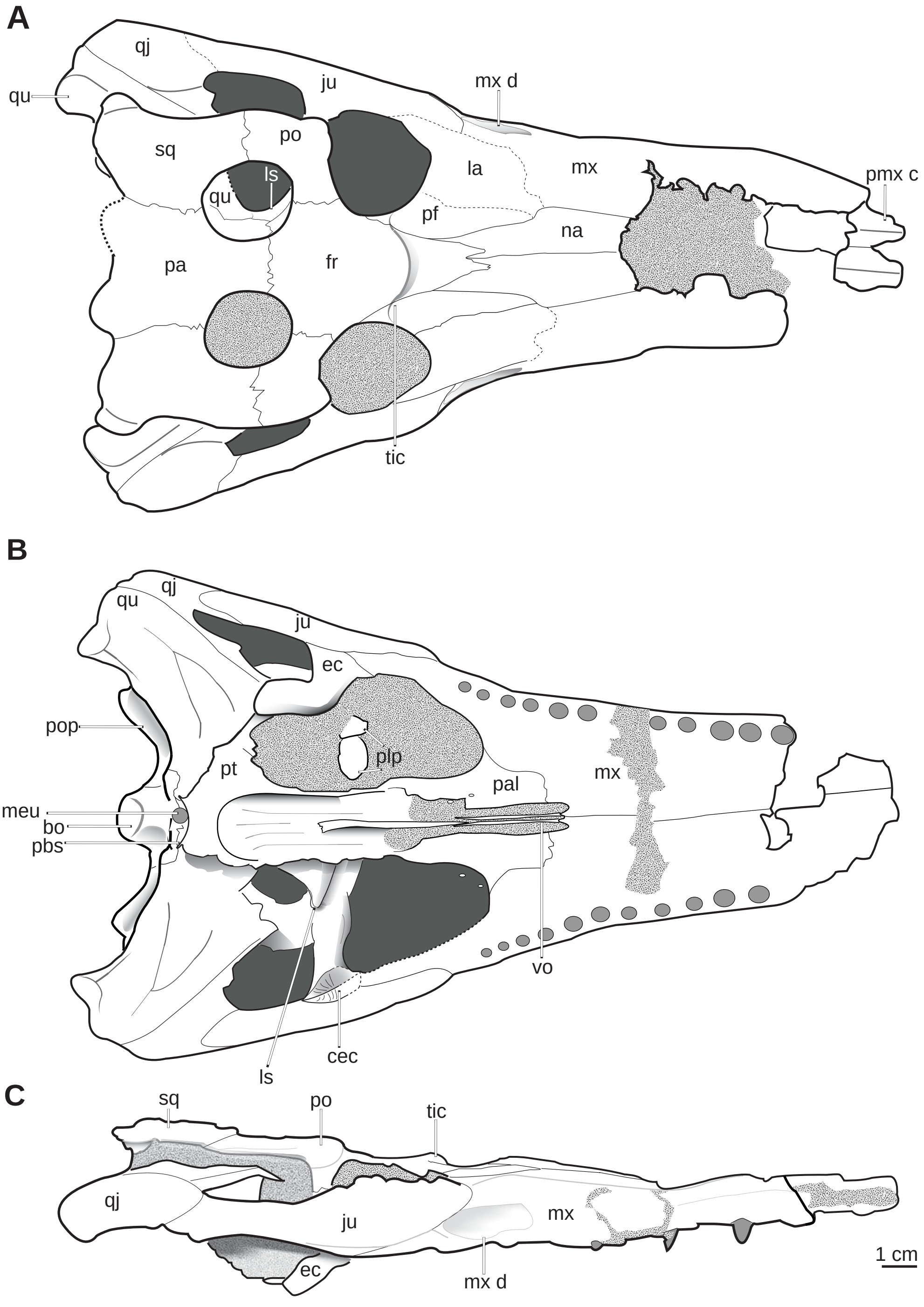

FIG. 5. *Eutretauranosuchus delfsi* AMNH FARB 570 in **(A)** dorsal, **(B)** ventral, and **(C)** right lateral views. See appendix 2 for abbreviations.

FIG. 6. *Eutretauranosuchus delfsi* AMNH FARB 570 in **(A)** dorsal, **(B)** ventral, and **(C)** right lateral views.

displacement of the left jugal. Although the skull appears strongly dorsoventrally compressed, additional preparation and CT data indicate that little crushing deformation has occurred. AMNH FARB 570 is generally well preserved; however, the snout anterior to the prefrontals exhibits several displaced bone fragments held in place by supportive matrix (figs. 5A, 6A). The nasals anterior to the eighth maxillary alveolus are eroded, as are much of the ascending processes of the maxillae. As in the holotype (figs. 2A, 3A), the premaxillae are not preserved (Mook, 1967). The positions of CT slices described below are shown in figure 7.

The palate of AMNH FARB 570 is well preserved anterior to the anteroposterior midpoint of the suborbital fenestrae (figs. 5B, 6B). On the palatal surface a prominent fracture extends through the palatal processes of the maxillae at the level of the eighth alveolus. This crack is continuous with damage on the dorsum of the rostrum (fig. 5A). The palate is incised, so that the maxillae and palatines are separated to create a ventrally open nasopharyngeal passage. A similar choanal trough is evident in *Amphicotylus gilmorei* (CAMNH 1339), *A. lucasii* (AMNH FARB 5782), *A. stovalli* (OMNH 2392), *Calsoyasuchus valliceps* (Tykoski et al., 2002), an undescribed Morrison goniopholidid specimen (YPM 1263), and possibly in *Sunosuchus shuhanensis* (Fu et al., 2005) and *Siamosuchus phuphokensis* (Lauprasert et al., 2007). The nasopharyngeal passage is elevated dorsal to the plane of the secondary palate, as reported by Smith et al. (2008). In AMNH FARB 570, near the anteroposterior midpoint of the suborbital fenestra, the anterior process of the pterygoid is displaced somewhat dorsally. This displacement has elevated the parabasisphenoid rostrum, such that it sits between the anterolateral laminae of the laterosphenoids.

The anterior borders of the suborbital fenestrae are well preserved. The left ectopterygoid and most of the transverse processes of the pterygoid are not preserved (figs. 5B, 6B). On the right side, the ectopterygoid is partially preserved with the posteromedial portion of the palatal process broken away. The transverse process of the right pterygoid is represented by a few fragments. As such, the posterior margins of both suborbital fenestrae are not preserved.

In contrast to the condition in *Calsoyasuchus* (Tykoski et al., 2002), there is neither a sizeable antorbital fenestra nor an antorbital fossa present in AMNH FARB 570. A tiny opening may have been present as described for CMNH 8028 by Buffetaut (1982), but such a fenestra cannot be identified in this specimen. Prominent depressions are present on the alveolar processes of both maxillae (figs. 5C, 6C), a character common to goniopholidids (Wu et al., 1996; Salisbury et al., 1999; Smith et al., 2010; Andrade et al., 2011) and certain pholidosaurids (Martin and Buffetaut, 2012). The orbits are relatively small and circular in dorsal view. There is no indication of a palpebral ossification integrated into the medial orbital margin, in contrast to the massive palpebral ossifications in *Amphicotylus lucasii* (AMNH FARB 5782; Mook, 1942) and *Goniopholis simus* (NHMUK R 41098; Salisbury et al., 1999; Andrade and Hornung, 2011). The supratemporal fenestrae are subcircular and slightly smaller than the orbits, as opposed to the transversely narrow oval-shaped supratemporal fenestrae in CMNH 8028 (Mook, 1967). BYU 17628 exhibits an intermediate condition (Smith et al., 2010). The infratemporal fenestrae in AMNH FARB 570 are similar in size to the orbits and roughly trapezoidal in shape.

The occipital surface of the skull is well preserved (fig. 14). The left paroccipital process is slightly displaced and reoriented such that its dorsal margin is pushed anteriorly underneath the descending process of the left squamosal. Several prominent cracks run through the supraoccipital, shattering it, but the fragments are preserved in situ. Vascular and nervous foramina are well preserved and easily visible. The left aspect of the basioccipital and left otoccipital are cracked so that the external opening of the carotid foramen is not preserved.

The external surface of the skull is ornamented with variable pits and grooves. The snout is characterized by pits and anastomosing grooves, whereas the skull table exhibits larger pits and smaller grooves. Such a pattern is widespread among neosuchians and occurs in some other more basal mesoeucrocodylians. The ornamentation in AMNH FARB 570 is more strongly developed than in the holotype of *Eutretauranosuchus delfsi* (Mook, 1967).

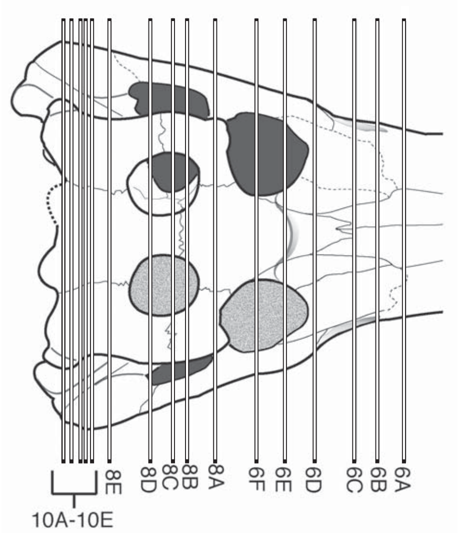

FIG. 7. Positions of figured transverse CT slices on AMNH FARB 570 in dorsal view. Alphanumerics refer to figures in this paper, infra.

Dermatocranial Bones: The **maxillae** in AMNH FARB 570 are elongate and dorsoventrally short, forming most of the lateral and dorsal aspects of the rostrum and much of the secondary palate (figs. 5, 6). Each maxilla consists of three components: an alveolar process, an ascending process, and a palatal process. The alveolar process of the maxilla in AMNH FARB 570 is dorsoventrally short. The surface of the alveolar process is characterized by tiny (~1 mm in diameter) pits surrounded by thick, anastomosing ridges. The right alveolar process is broken anterior to the fourth maxillary alveolus, whereas the left process is broken at the level of the first maxillary alveolus (figs. 5A, 6A). Anterior to the ninth maxillary alveolus, each alveolar process forms a strongly dorsolaterally curved surface. Also, anterior to the ninth alveolus, the alveolar process exhibits a dorsolaterally placed groove, which extends anteriorly as far as the maxillae are preserved.

Posterior to the ninth maxillary alveolus, the dorsolateral curvature along the dorsum of the alveolar process gives way to a sharp, dorsolaterally positioned angle. This angle marks the distinction between the dorsal and alveolar maxillary processes. Posteriorly, the alveolar process possesses a shallow, roughly circular depression. On both the left and right maxillae, the depressions are positioned between the 10th and 15th alveolus. Neither depression is well preserved in AMNH FARB 570; the anterior margin of the left depression is obscured by subtle medial crushing of the alveolar process in that area, and the medial wall of the right depression is largely broken away. The lateral surface of the depression features subtle, anteroposteriorly oriented striations. Similar depressions are present in almost all goniopholidids including *Anteophthalmosuchus hooleyi* (NHMUK R3876), *Goniopholis simus* (Salisbury et al., 1999), *Amphicotylus lucasii* (Mook, 1942), *Sunosuchus junggarensis* (Wu et al., 1996), *Sunosuchus miaoi* (Young, 1948; Buffetaut, 1986), *Sunosuchus shartegensis* (Efimov, 1988), *Sunosuchus shunanensis* (Fu et al., 2005), and *Siamosuchus phuphokensis* (Lauprasert et al., 2007). Maxillary depressions are unknown in the putative Late Cretaceous gonipholidid *Denazinosuchus kirt-*

landicus (Lucas and Sullivan, 2003). Lateral facial depressions are also apparent in some pholidosaurids (e.g., *Pholidosaurus purbeckensis* and *Sarcosuchus imperator*), although these occur on both the maxilla and the jugal (Martin and Buffetaut, 2012).

The lateral margin of the alveolar process of the maxilla in AMNH FARB 570 is anterolaterally convex between the first and fifth alveolus on the left side (figs. 5, 6). On both maxillae, the lateral margins of the alveolar processes are straight between the fifth and ninth alveolus and anterolaterally concave posterior to the ninth alveolus. A similar curvature pattern is found in *Sunosuchus junggarensis* (Wu et al., 1996) and a more sinusoidal lateral border is present in *Amphicotylus* (Mook, 1942, 1964, 1967), and *Siamosuchus phuphokensis* (Lauprasert et al., 2007). Along the ventral margin of the alveolar process, anterior to the ninth maxillary alveolus, there is a row of deep nutrient foramina. Each nutrient foramen is oval and anteroposteriorly elongate. CT scans of AMNH FARB 570 reveal the presence of a canal within each maxilla (fig. 8C). This passage likely transmitted the superior alveolar branches of the maxillary nerve (second division of the trigeminal nerve).

The left superior alveolar canal is nearly complete throughout the preserved length of the maxilla (fig. 8). The right canal is obscured between the sixth and ninth maxillary alveolus where the right maxilla is damaged. The canal lies dorsal to the maxillary dentition, and each maxillary nutrient foramen passes laterally and slightly posteriorly to reach the surface of the alveolar process of the maxilla. The anteriormost nutrient canals project more ventrally than the posterior canals.

Posteriorly, the alveolar process contacts the jugal. The broad, flat plate of the anterior process of the jugal overlies the alveolar process just posterodorsal to the maxillary depression (figs. 5B, 6B). This contact is preserved on both sides in AMNH FARB 570. In ventral view, the alveolar process terminates after wedging between the anterior process of the jugal laterally and the anterior projection of the lateral process of the ectopterygoid medially. In AMNH FARB 570, the ectopterygoid-maxilla contact is preserved only on the right side (fig. 5B). The left alveolar process is not preserved medial to its jugal contact and posterior to the 13th alveolus.

The ascending processes of the maxillae (sensu Kley et al., 2010) are dorsoventrally flat in AMNH FARB 570. The right ascending process is missing on the right side anterior to the ninth maxillary alveolus (figs. 5A, 6A). The left ascending process is broken anterior to the fourth alveolus. Between the fourth and eighth maxillary alveolus, the medialmost portion of the ascending process of the maxilla is cracked and broken on both sides.

Anterior to the ninth maxillary alveolus, the ascending processes are textured with small (~1 mm in diameter) pits surrounded by thick, anastomosing ridges. The lateral margins of both ascending processes anterior to the ninth alveolus feature a dorsolaterally placed curvature that terminates at a groove along the dorsum of the alveolar process. Posterior to the ninth alveolus, the surface of the ascending process of the maxilla bears pits that are smaller and shallower than those farther anteriorly.

The ascending process contacts the lateral aspect of the nasals along the length of the rostrum. The contact is a simple, straight suture, and it is only preserved posterior to the ninth maxillary alveoli on both sides in AMNH FARB 570. Posterolateral to the maxilla-nasal con-

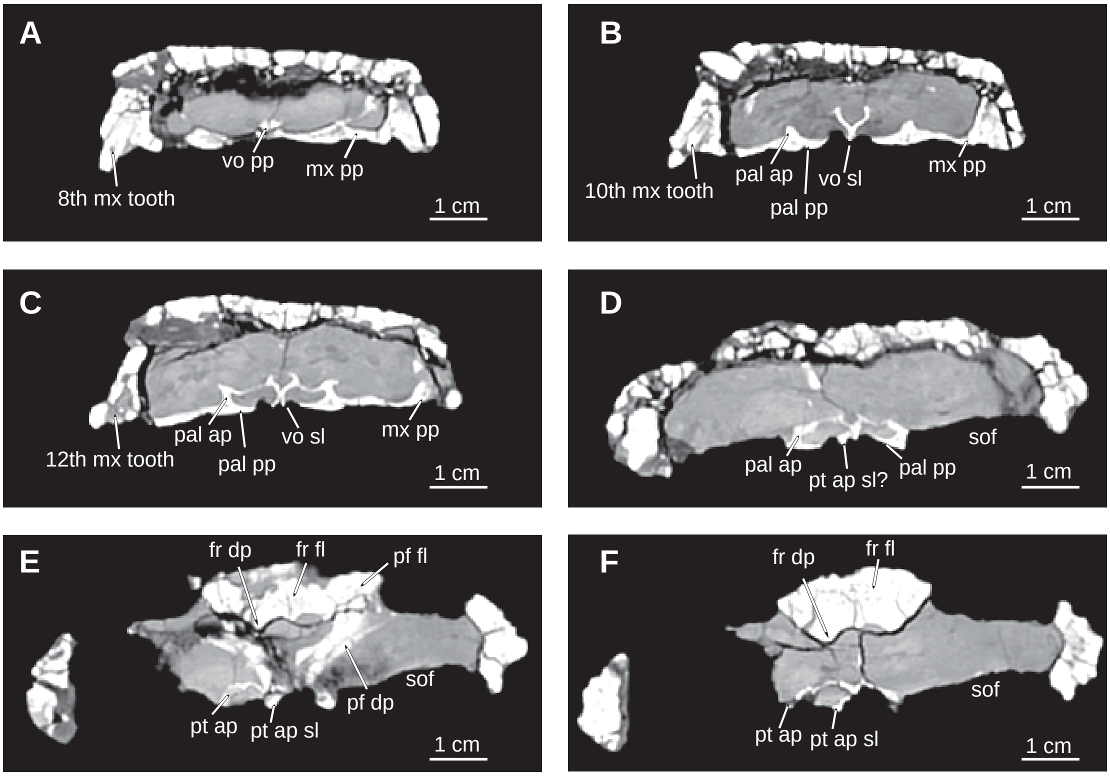

FIG. 8. Transverse CT sections through the skull of *Eutretauranosuchus delfsi* AMNH FARB 570. (**A**) Tra 359, (**B**) Tra 400, (**C**) Tra 435, (**D**) Tra 555, (**E**) Tra 585, (**F**) Tra 616. See appendix 2 for abbreviations.

tact, the ascending process of the maxilla meets the lacrimal. This contact is well preserved on the left side in AMNH FARB 570, whereas a small portion of the ascending process of the maxilla is broken away on the right side. The broken surface exposes a striated, sutural portion of the lacrimal that underlies the maxilla.

In AMNH FARB 570 the palatal processes of the maxillae are similar to those in other mesoeucrocodylians. Each forms a flat plate that contacts its opposite along a straight longitudinal midline suture anterior to the level of the 11th maxillary alveolus (figs. 5B, 6B). At this level, the palatal processes diverge from one another, forming the heart-shaped anterior margin of the choanal groove. The anterior margins of the vomers (fig. 8A) contact the dorsal surface of the palatal processes of the maxillae rostral to the anterior margin of the choanal groove. A similar divergence of the palatal processes of the maxillae is evident in *Amphicotylus lucasii* (AMNH FARB 5782, possibly YPM 1263), *Sunosuchus miaoi* (Buffetaut, 1986), and *Sunosuchus junggarensis* (Wu et al., 1996). In *Calsoyasuchus valliceps*, the shape of this divergence is unclear (Tykoski et al., 2002).

Lateral to the choanal groove the palatal process of the maxilla contacts the palatal process of the palatine along a sigmoidal suture (figs. 5B, 6B). The suture is transversely oriented and interdigitates at the level of the 12th maxillary alveolus. The suture is sigmoidal lateral to this transverse contact, extending posterolaterally to the anterior margin of the suborbital fenestra. The shape resembles that of the palatine-maxilla contact in adult *Alligator mississippiensis* (AMNH R 9112; Iordansky, 1973).

The palatal process contributes to the anterolateral margin of the suborbital fenestra posteriorly to the level of the 15th maxillary alveolus (figs. 5B, 6B). In AMNH FARB 570, there is no contact between the posterolateralmost aspect of the palatal process of the maxilla and the anteriormost margin of the lateral process of the ectopterygoid. In many other mesoeucrocodylian taxa, the anterior projection of the ectopterygoid forms much of the lateral margin of the suborbital fenestra (see Iordansky, 1973; Turner and Sertich, 2010). For example, in *Mahajangasuchus* the anterior projection forms nearly the entire lateral border of the suborbital fenestra (Turner and Buckley, 2008).

The **nasals** are transversely slender, flat plates that contact one another along a straight suture on the midline (figs. 5A, 6A). Both nasals are preserved in AMNH FARB 570 posterior to the eighth maxillary alveoli. The contribution of the nasals to the external naris is unclear as this region of the skull is poorly preserved. More posteriorly, the paired nasals expand transversely up to the level of the 11th maxillary alveoli. Anterior to this level, each nasal is laterally in contact with the ascending process of the maxilla at a straight suture.

Posterior to the 11th maxillary alveolus, the conjoined nasals taper. At that level, the maxilla-nasal contact gives way to a short contact between the medial margin of the lacrimal and the lateral margin of the nasal (figs. 5A, 6A). At the level of the 12th maxillary alveolus, the nasal contacts the medial margin of the prefrontal along a straight suture. At the 13th maxillary alveolus, the paired nasals diverge from one another where the anterior processes of the frontal wedge between them. The contact between the nasals and the frontal forms a jagged, anteriorly pointed, W-shaped suture in the midline. Among goniopholidids this shape is evident in the holotypes of *Eutretauranosuchus delfsi* (CMNH 8028) and *Amphicotylus felix* (YPM 517).

The **lacrimal** is composed of a facial lamina contributing to the preorbital portion of the rostrum and an orbital lamina forming part of the anterior margin of the orbit. The facial lamina is a trapezoidal, flat plate that tapers anteriorly to the level of the 10th maxillary alveolus. The right facial lamina in AMNH FARB 570 is complete, and the left facial lamina is broken anterolaterally (fig. 6A). The anterior and lateral margins of the facial lamina contact the maxilla. Posterior to the 13th maxillary alveolus, the contact of the facial lamina with the maxilla gives way to a lacrimal-jugal contact that persists to the posterolateral terminus of the facial lamina of the lacrimal.

Between the 11th and 12th maxillary alveolus, the facial lamina has a small anteromedial contact with the nasal. Posterior to the 12th alveolus, the facial lamina contacts the prefrontal along a long and straight suture that extends posteriorly to the anterior orbital margin. The facial lamina of the lacrimal extends anterior to the anteriormost margin of the prefrontal, as in CMNH 8028 (Mook, 1967), gavialoids, and crocodyloids (Iordansky, 1973).

The orbital lamina of the lacrimal in crocodyliforms typically forms a dorsoventrally short, vertically oriented surface that contributes to the anterior margin of the orbit. In AMNH FARB 570, the orbital lamina is broken away on the left side but visible in CT slices on the right (fig.

8C, D). The posterior opening of the nasolacrimal canal is preserved on the posterolateral margin of the right orbital lamina. The nasolacrimal canal is visible throughout its course in CT reconstructions (fig. 8C), traveling anteromedially and opening into the nasal cavity near the lacrimal-nasal contact at the 11th maxillary alveolus. A small portion of the anterior portion of the left nasolacrimal canal is also visible in the CT slices (fig. 8C).

Each **prefrontal** consists of a rostrally exposed facial lamina, an orbital lamina, and a descending/palatal process that projects ventromedially from the orbital lamina. Both the right and left prefrontals are complete in AMNH FARB 570.

The facial lamina of the prefrontal forms an elongate, triangular plate contributing to the dorsal surface of the rostrum (figs. 5A, 6A). The preorbital portion is an anteroposteriorly elongate, isosceles triangle–shaped plate with its anterior tip reaching the level of the 11th maxillary alveolus. The preorbital portion of the prefrontal contacts the nasal anteromedially, the frontal posteromedially, and the lacrimal laterally; all three contacts forming straight sutures. The shape of the prefrontal facial lamina varies among species of crocodyliforms, but triangular and rectangular variants are common. A triangular lamina is present in crocodyloids and gavialoids, whereas most alligatoroids have a rectangular lamina (Iordansky, 1973).

In the interorbital region of AMNH FARB 570, the facial lamina of the prefrontal contributes to the anteromedial margin of the orbit. This portion of the facial lamina tapers to the midpoint of the orbital margin. All portions of the facial lamina of the prefrontal are textured with large pits (~2 mm in diameter) surrounded by low and anastomosing ridges. A palpebral is not coossified to the lateral margin of the facial lamina of the prefrontal (figs. 5B, 6B) as in *Amphicotylus lucasii* (AMNH FARB 5782) and many European goniopholidids (Andrade and Hornung, 2011). In certain European goniopholidids (e.g., *Goniopholis simus* and *G. baryglyphaeus*), the palpebral has been misidentified as a posterior extension of the prefrontal facial lamina that excluded the frontal from the medial margin of the orbit (see Andrade and Hornung, 2011). The left facial lamina of the prefrontal in AMNH FARB 570 preserves a lightly textured surface on its medialmost aspect. This surface may indicate the position of a palpebral facet. The equivalent site on the right prefrontal is not preserved.

The orbital laminae of both prefrontals in AMNH FARB 570 are partially preserved; the left lamina is broken laterally, whereas the right is complete but remains embedded in matrix (fig. 8E). Each lamina is smoothly textured and oriented slightly ventromedially. The medial margin of the orbital lamina of the prefrontal is continuous with the orbital lamina of the lacrimal. The left orbital lamina terminates at a vertically oriented suture with the descending process of the left frontal near the anteroposterior midpoint of the orbit.

The descending or palatal processes of the prefrontals are well preserved in AMNH FARB 570, but only the lateralmost margin of the left process is fully exposed. Hence, description of the descending process is derived mostly from CT data (fig. 8E).

The descending process of the prefrontal in AMNH FARB 570 projects posteroventromedially from the anteromedial corner of the orbit to the dorsal surface of the ascending process of the palatine near the level of the posteriormost maxillary alveolus. The process is transversely broad at its dorsal origin and tapers as it descends to contact the palatine. In transverse section, the descending process follows a strongly ventromedial course as it extends toward the palate. Just dorsal to the prefrontal-palatine contact, each descending process sends off a medial projection that meets its opposite at the midline. The descending process of the prefrontal is anteroposteriorly thick at its medial margin. The lateral margin of the descending process is anteroposteriorly thin and laminar. Among goniopholidids, the prefrontal pillar complex has been described in *Sunosuchus junggarensis, Eutretauranosuchus delfsi* (BYU 17628), and *Goniopholis simus* (Salisbury et al., 1999). In another *E. delfsi* specimen (BYU 17628) the pillar is described as laterally indented (Smith et al., 2010). In *S. junggarensis* the descending process was only briefly characterized, as it is obscured in all described specimens (Wu et al., 1996). The descending processes in *G. simus* are described as rounded in cross section (Salisbury et al., 1999).

The **frontal** is complete in AMNH FARB 570 and unpaired as in all other mesoeucrocodylians (Turner and Sertich, 2010). The element consists of a dorsal lamina, two anterior processes that wedge between the nasal bones, and bilateral descending processes.

The two conjoined, but unfused anterior processes form a transversely narrow, tapering prong that lies anterior to the rostral margins of the orbits (figs. 5A, 6A). The anterior processes are complete in AMNH FARB 570. Each anterior process is in contact with the prefrontal along the lateral margin of the orbit. Large shallow pits (~2 mm in diameter) surrounded by low anastomosing ridges ornament both anterior processes.

The dorsal lamina is a broad and flat plate that forms the majority of the interorbital portion of the skull, the posteromedial borders of the orbits, and the anteromedial borders of the supratemporal fenestrae. All portions of the dorsal lamina are preserved on both sides of AMNH FARB 570. There is no external evidence of a midline suture on the dorsal lamina, although CT scans of AMNH FARB 570 demonstrate one between the deeper, more ventral portions of the frontal (fig. 8F).

Anteriorly, the juncture between the anterior processes and the dorsal lamina is marked by a large, anteriorly curved, transversely oriented ridge (transverse interorbital crest sensu Andrade and Hornung, 2011). The ridge has its lateral margins on the facial lamina of the prefrontal near the anteroposterior midpoint of the orbit. It continues onto the frontal, with the anteriormost point of its curvature at the midline corresponding to the level of the anterior margin of the orbit (fig. 9).

Transverse interorbital crests are present in *Amphicotylus gilmorei* (Holland, 1905), *A. lucasii* (AMNH FARB 5782), *A. stovalli* (OMNH 2392; Mook, 1964), and *Goniopholis simus* (IPB R359, NHMUK R41098; Andrade and Hornung, 2011). In *Sunosuchus junggarensis* (Wu et al., 1996) and possibly *Siamosuchus phuphokensis* (Lauprasert et al., 2007), the dorsal lamina is marked by a midline ridge running anteroposteriorly along the length of the bone. In *Calsoyasuchus valliceps* the frontal bears an anteroposteriorly oriented depression on the midline (Tykoski et al., 2002).

In the interorbital region of AMNH FARB 570, the dorsal lamina of the frontal is excluded from the anteromedial border of the orbit by its contact with the facial lamina of the prefrontal (figs. 5A, 6A). This contact terminates near the rostrocaudal midpoint of the orbit, after which point the dorsal lamina forms the entire posteromedial border of the orbit. The postorbital contribution of the frontal terminates at a subtle and interdigitating sutural contact with the anteromedial process of the postorbital. Posteriorly, the dorsal lamina contributes to much of the anteromedial margins of the supratemporal fenestrae. The dorsal lamina posteriorly sutures to the parietal in a prominent interdigitating contact positioned well posterior to the anterior margins of the supratemporal fenestrae, as in *Calsoyasuchus valliceps* (Tykoski et al., 2002), *Goniopholis simus* (Salisbury et al., 1999), and *Sunosuchus shartegensis* (Efimov, 1988).

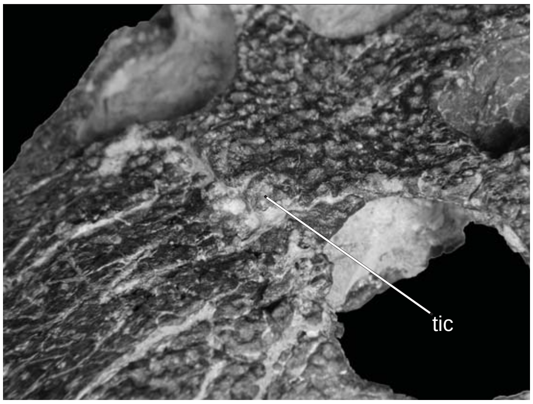

FIG. 9. *Eutretauranosuchus delfsi* AMNH FARB 570. Interorbital region in oblique dorsolateral view See appendix 2 for abbreviations.

Among goniopholidids, the frontoparietal contact has been reconstructed as lying anterior to the supratemporal fenestrae in *Amphicotylus lucasii* (Mook, 1942), *Denazinosuchus kirtlandicus* (Lucas and Sullivan, 2003), and *Sunosuchus miaoi* (Young, 1948). Our reexamination indicates that the frontoparietal contact identified for *A. lucasii* by Mook (1942) is actually a transversely oriented depression at the anterior margins of the supratemporal fenestrae in AMNH FARB 5782. The actual frontoparietal suture in that specimen is positioned near the anteroposterior midpoint of the supratemporal fenestrae, much as in specimens of *Eutretauranosuchus delfsi*. Sutural relationships are unclear in *Denazinosuchus* such that the frontoparietal suture cannot be observed in this taxon (Irmis et al., in press). A frontoparietal contact anterior to the supratemporal fenestrae is characteristic of derived crocodylians (e.g., *Alligator* and *Crocodylus*) and would be unexpected among basal neosuchians (Turner and Sertich, 2010).

The ventral surface of the frontal in AMNH FARB 570 features dorsoventrally short descending processes (cristae cranii frontalis). The left descending process is partly exposed, whereas the right descending process is embedded in matrix (fig. 8E). Each is smoothly textured, similar to the braincase elements. The processes descend from the level of the prefrontal pillar complex and expand ventrally and laterally as transversely broad, ventrally tapering triangles in transverse section (fig. 8A). They form dorsolateral walls for the olfactory tracts. The descending processes grow dorsoventrally thinner toward the posterior aspect of the frontal within the borders of the supratemporal fenestrae (fig. 8C). Just posterior to the orbits, each descending process contacts the dorsal surface of the ipsilateral laterosphenoid. The contact between these elements continues to the posterior end of the frontal.

The **parietal** is unpaired, consisting of a single dorsal lamina (that part exposed dorsally) and two descending processes (cristae cranii parietalis). The parietal is well preserved in AMNH FARB 570, aside from damage to its left posterior margin.

The dorsal lamina is flat and transversely narrow between the supratemporal fenestrae (figs. 5A, 6A). It expands broadly posteriorly to form curved posteromedial borders for each of the supratemporal fenestrae. The dorsal surface is heavily sculptured with large pits (~2 mm in

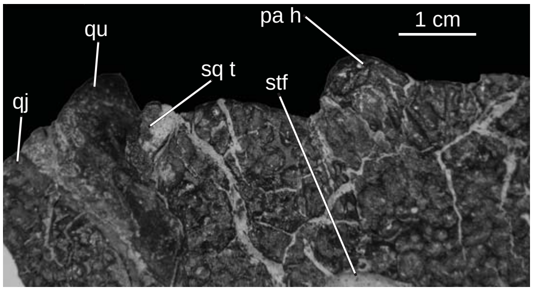

FIG. 10. *Eutretauranosuchus delfsi* AMNH FARB 570. Right posterior skull table in dorsal view. See appendix 2 for abbreviations.

diameter) surrounded by prominent, anastomosing ridges. Near the transverse midpoint of each supratemporal fenestra, the dorsal lamina contacts the medial process of the squamosal. In AMNH FARB 570 the contact is minimally interdigitating, each being marked instead by an anteroposteriorly oriented pair of straight bony ridges. Posteroventrally, the parietal is in contact with the dorsal margin of the supraoccipital. On the right side, just lateral to this midline contact, the parietal is posteriorly expanded into a small and posteriorly rounded hornlet that forms a prominent shelf over the supraoccipital and paroccipital processes (fig. 10). The broken base of a presumably similar structure is present on the left side. The hornlet projects laterally to the lateral margin of the parietal, just medial to the parietal-squamosal contact. Similar projections are present in other *Eutretauranosuchus* specimens (Mook, 1967), *Amphicotylus lucasii* (AMNH FARB 652, AMNH FARB 5782), *Goniopholis kiplingi* (Andrade et al., 2011), and *G. simus* (NHMUK R41098; Salisbury et al., 1999). They are absent in illustrated specimens of *Sunosuchus junggarensis* (Wu et al., 1996). In *Fruitachampsa* (Clark, 2011: fig. 4D) there is a series of spiny osteoderms along the occipital surface of the parietal and squamosal. These are also present in shartegosuchids from the Shishugou Formation (Clark, personal commun.) The hornlets in goniopholidids could be similar osteoderms fused to the parietal.

In AMNH FARB 570, the hornlet is posteriorly curved. The texturing on the parietal anterior to the hornlet is distinctive, marked by thick, posteriorly directed ridges and an absence of the ordinary pitting. Posteriorly the hornlet is smoothly textured and marked only by scant, small pits, a texturing that is present dorsally, posteriorly, and ventrally.

The paired descending processes of the parietal are similar to those of the frontal and form portions of the dorsolateral walls of the braincase as in modern crocodylians (Iordansky, 1973) and extinct crocodyliforms (Colbert and Mook, 1951; Turner, 2006; Kley et al., 2010). In AMNH FARB 570, the lateral portion of the left descending process is well exposed and smoothly textured as in braincase elements. The contributions of the processes to the deeper walls of the supratemporal fenestrae are prominent and ventrolaterally inclined (fig. 11). The right descending process is obscured by rock matrix (fig. 12D).

Three sutures are observable on the exposed left descending process. Anterodorsally, the descending parietal encounters the descending process of the frontal along a vertically oriented suture (fig. 11). Anteroventrally, it encounters the posterodorsal corner of the posterolateral lamina of the laterosphenoid at a posteroventrally inclined suture. Posterior to the laterosphenoid-parietal contact, the descending process of the parietal broadly contacts the dorsum of the anterodorsal process of the quadrate (sensu Kley et al., 2010). This suture continues posteriorly to the transverse midpoint of the supratemporal fenestra, where it is replaced by a quadrate-squamosal contact. Such a sutural pattern within the medial margin of the supratemporal fenestrae is common to most mesoeucrocodylian taxa (e.g., Brochu et al., 2002; Kley et al., 2010). A notable exception is in thalattosuchians, where the prootic is prominently exposed on the medial wall of the supratemporal fenestra (Jouve, 2009).

Posteriorly the descending processes of the parietal are in contact with the anterodorsal surface of the supraoccipital, although the details of this contact are unclear both under direct observation and in CT scans. In occipital view, the dorsal lamina of the parietal sits atop the dorsalmost portion of the occipital face of the supraoccipital. Unlike the condition in a number of modern crocodylians (e.g., caimanines, Iordansky, 1973; *Trilophosuchus*, Willis, 1993), *Mahajangasuchus* (Turner and Buckley, 2008), and *Simosuchus* (Kley et al., 2010) the supraoccipital lacks exposure on the skull table.

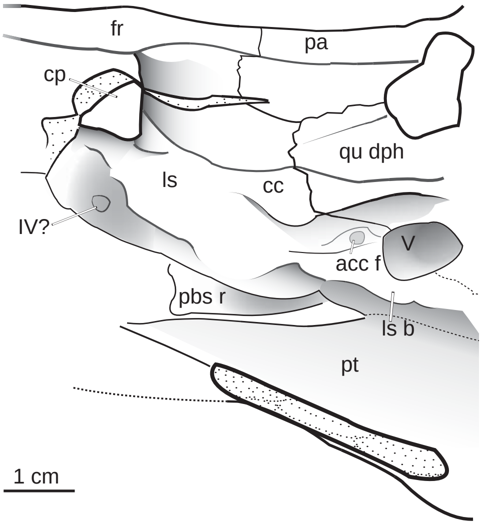

FIG. 11. Braincase of *Eutretauranosuchus delfsi* AMNH FARB 570 in left lateral view. See appendix 2 for abbreviations.

As in modern crocodylians (Iordansky 1973) and at least some basal mesoeucrocodylians (e.g., Turner, 2006), the body of the parietal in AMNH FARB 570 is pneumatic. The pneumatic space is visible in CT slices and lies anterior to the anteroposterior midpoint of the supratemporal fenestrae (fig. 12C, D). The pneumaticity continues posteriorly to the occipitalmost surface of the parietal, where it communicates with the posterodorsal contribution to the mastoid air cavities that are lateral expansions of spaces in the supraoccipital and otoccipitals.

The **squamosal** in AMNH FARB 570 consists of two primary surfaces: a flat dorsal lamina contributing to the surface of the skull table and a descending process that contributes to the occipital face of the skull (figs. 5A, 6A). Unlike the condition in most neosuchians, the squamosal does not exhibit an extensive contact between the descending process and dorsum of the quadrate body to frame the lateral aspect of the cranioquadrate canal (e.g., Iordansky, 1973; Brochu et al., 2002). The absence of this expansion can also be seen in *Amphicotylus lucasii* (AMNH FARB 5782). The dorsal lamina overall resembles other skull table bones in AMNH FARB 570, as it is marked by similar prominent pits and ridges. The dorsal lamina is triradiate, consisting of separate anterior, posterior, and medial processes. On both the right and left squamosals, there is a prominent anteroposteriorly running crack that obscures much of the dorsal surface of the bone.

The dorsal laminae of the squamosals contribute to the posterolateral borders of the supratemporal fenestrae and the posterolateral portions of the skull table itself. The anterior process of the dorsal lamina contributes to the lateral border of each supratemporal fenestra. On both sides in AMNH FARB 570, there are distinct sutural contacts (on the left it can be seen as interdigitating) between the anterior process of the squamosal and the posterior process of the postorbital (figs. 5A, 6A). The medial portion of the suture is positioned anterior to the antero-

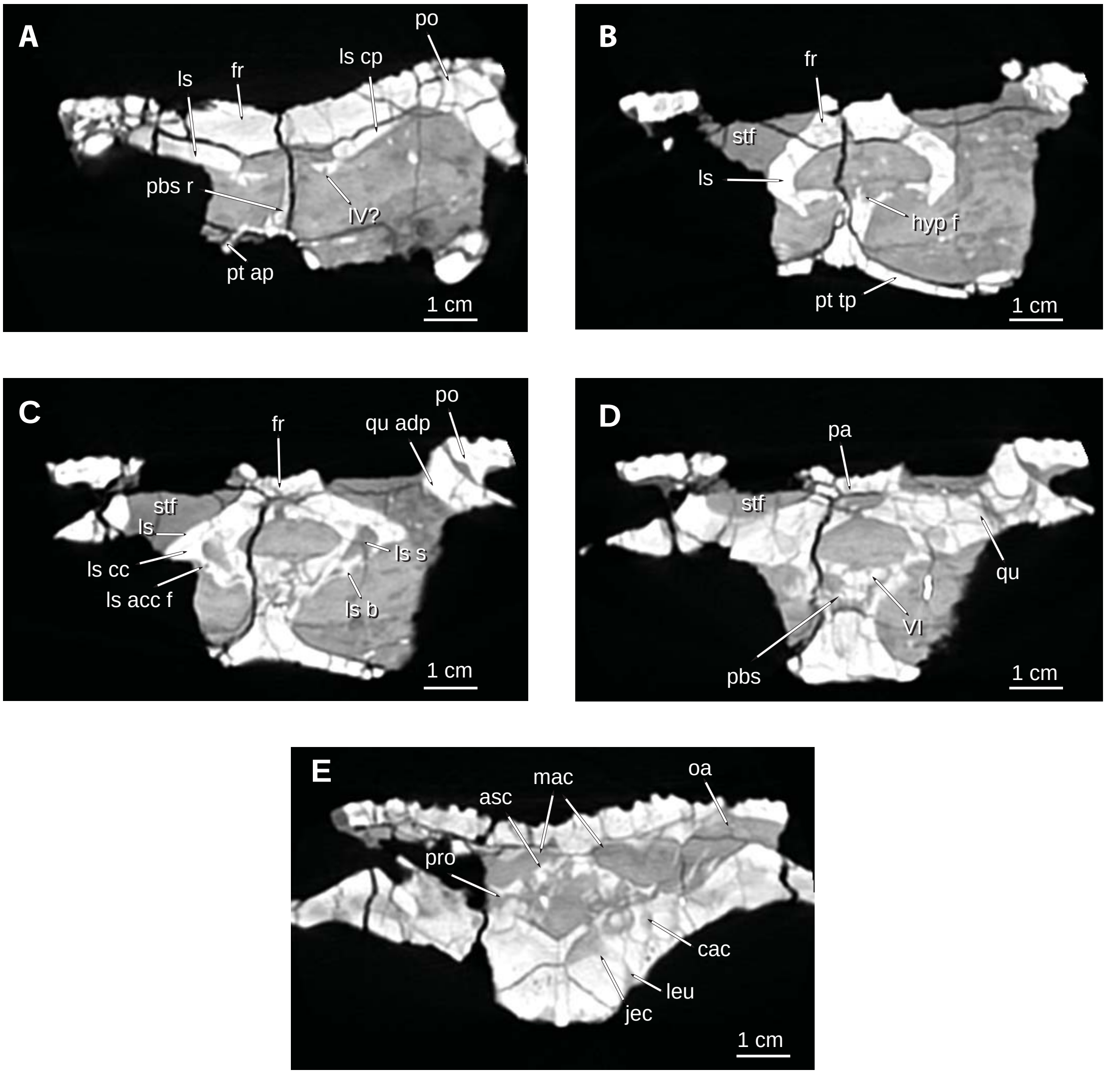

FIG. 12. Transverse CT sections through the skull of *Eutretauranosuchus delfsi* AMNH FARB 570. (**A**) Tra 574, (**B**) Tra 770, (**C**) Tra 878, (**D**) Tra 936, (**E**) Tra 1036, (**F**) Tra 1116. See appendix 2 for abbreviations.

posterior midpoint of the supratemporal fenestra. Lateral to this point, the suture projects slightly anterolaterally. As such, the anterior process of the squamosal contributes more length to the lateral margin of the supratemporal fenestra and the lateral aspect of the skull table than does the posterior process of the postorbital.

The medial process of the dorsal lamina of the squamosal is transversely narrow and anteroposteriorly elongate (figs. 5A, 6A). The medial process contacts the dorsal lamina of the parietal near the transverse midpoint of the supratemporal fenestra. Posteriorly, the medial process of the squamosal prominently overhangs the paroccipital process and the occipital surface of the skull. Farther laterally, the posterior inclination of the paroccipital process results in a lateral termination of this overhang by the dorsal lamina of the squamosal. This condition

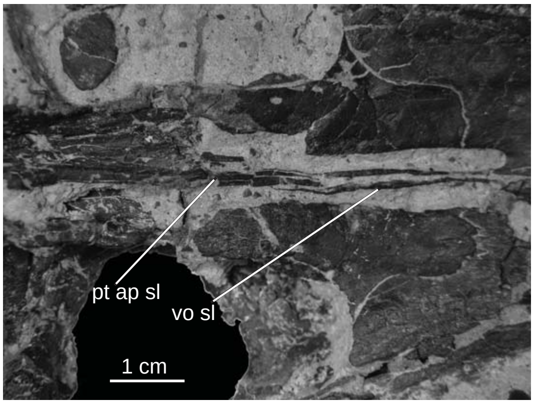

FIG. 13. *Eutretauranosuchus delfsi* AMNH 570. Palatal trough in ventral view.

is similar to that in *Amphicotylus lucasii* (AMNH FARB 5782) and *G. simus* (Salisbury et al., 1999), and contrasts with that in most neosuchians (Iordansky et al., 1973; Wu et al., 2001; Pol et al., 2009).

In AMNH FARB 570, the posterior process of the squamosal is a flat expansion of the dorsal lamina overhanging the posterolateralmost margin of the paroccipital process. Overall the process is textured like the other elements of the skull table. A similar process is present in *Goniopholis simus* (Salisbury et al., 1999; NHMUK R41098), possibly *G. willetti* (Salisbury and Naish, 2011), *Amphicotylus lucasii* (Mook, 1942), and *Sunosuchus junggarensis* (Wu et al., 1996). On the lateralmost tip of the process, there are prominent rounded tuberosities (fig. 10). Both tuberosities are partially obscured by breaks and matrix. The preserved portions of the tuberosities are smoothly textured and resemble the parietal hornlets. Only the portion of the posterior process bearing the tuberosity forms a shelf over the occipital face of the skull and the remainder of the posterior process directly overlays the ipsilateral paroccipital process. These resemble the osteodermal protuberances on the parietal in AMNH 570 and the osteoderms fused to the posterior margin of the skull table in *Fruitachampsa* (Clark, 2011).

The descending process of the squamosal is a dorsoventrally short, transversely broad plate. In AMNH FARB 570, it projects ventrally from the posterior margins of both the medial and posterior processes of the squamosal (fig. 14). The portion arising from the medial process is inset on the occiput with the dorsal surface of the squamosal overhanging it. This contrasts with the common condition in modern crocodylians in which the descending process is flush with the posteroventral margin of the medial process (Iordansky, 1973). Along its length, the descending process contacts the dorsal surface of the paroccipital process. Medially, the descending process of the squamosal forms the lateral border of the posttemporal fenestra as is demonstrated on the well-preserved right side. There is no indication of contact between the descending process of the squamosal and the lateralmost margin of the supraoccipital.

The **postorbital** consists of a flat dorsal lamina and a descending process. The dorsal lamina contributes to the anterolateral corner of the skull table giving it a squared-off appearance. The dorsal lamina is textured like other skull table bones. In AMNH FARB 570, the left dorsal lamina is marred by an anteroposteriorly running crack (figs. 5A, 6A).

The dorsal lamina of the postorbital can be divided into two separate processes: an anteromedial process and a posterior process. The anteromedial process contributes to the anterior margin of the supratemporal fenestra and the posterior orbital margin. The process tapers slightly along its medially directed course. Near the transverse midpoint of the supratemporal fenestra, the anteromedial process contacts the lateral aspect of the dorsal lamina of the frontal

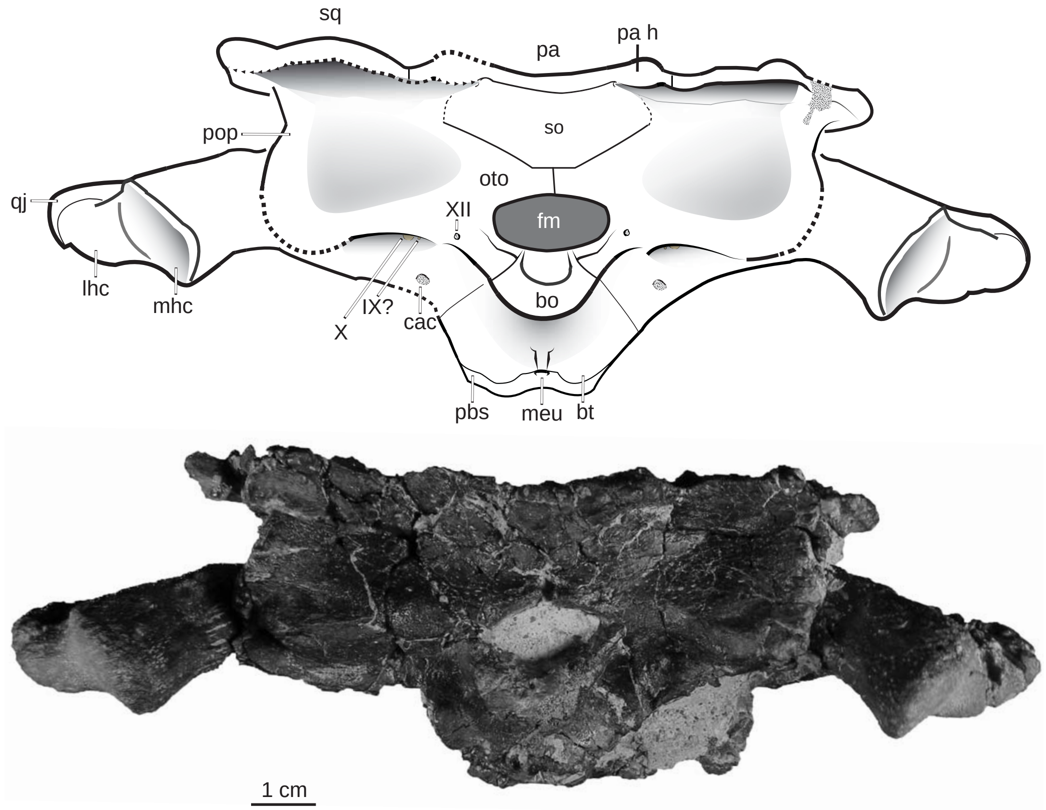

FIG. 14. Occiput of *Eutretauranosuchus delfsi* AMNH FARB 570 in posterior view. Dashed lines indicate reconstructed sutures and surfaces. See appendix 2 for abbreviations.

at an interdigitating suture. Ventrally, the anteromedial process is in contact with the anteromedial lamina and the capitate process of the laterosphenoid. This contact is visible in CT scans and it is exposed on the left side in AMNH FARB 570 (fig. 12A).

The posterior process of the dorsal lamina of the postorbital is broader than the anteromedial process, forming a small portion of the lateral border of the supratemporal fenestra (figs. 5A, 6A). It meets the squamosal anterior to the anteroposterior midpoint of the supratemporal fenestra along an interdigitating contact. On the left side of the skull in AMNH FARB 570, the ventral aspect of the posterior process of the postorbital is visible. The element is smoothly textured ventrally. Although partially obscured by matrix in AMNH FARB 570, the ascending process of the quadratojugal and the dorsolateral portion of the anterodorsal head of the quadrate clearly contact the ventral aspect of the posterior process on the right side of the skull. A similar contact is present throughout Crocodyliformes (Turner and Sertich, 2010), but it is not apparent in thalattosuchians (Jouve, 2009; Pol and Gasparini, 2009).

The descending process of the postorbital forms the dorsal part of the postorbital bar, which is columnar in form (figs. 5C, 6C). It is laterally exposed on both the right and left sides and completely exposed on the left side in AMNH FARB 570. The exposed left descending process is reconstructed. In cross section the descending process forms a semicircle; the anterior margin of the process is flattened, whereas its posterior aspect is posteriorly convex. The right descending process possesses a prominent lateral tuberosity.

The descending process of the postorbital contacts the ascending process of the jugal to form a complete postorbital bar. Although this is certainly the case in AMNH FARB 570, no trace of the postorbital-jugal suture is visible on either side of the skull. On the left side, this is likely due to reconstruction. Along its medial aspect, the descending process of the postorbital meets the capitate process of the laterosphenoid. The two elements are not sutured to one another.

Just posterior to the descending process, the postorbital bears an additional small, triangular, ventrally directed projection. This element is visible in CT scans only on the right side of AMNH FARB 570 (fig. 12C). The ascending process of the quadratojugal and associated quadrate appear to be appressed against the descending process of the postorbital just medial to this accessory process, as in other Crocodyliformes.

The **jugal** is a large element that contributes to the ventral and posterior margins of the orbit and the anterior and ventral margins of the infratemporal fenestra. Each element is triradiate with a broad anterior process, a cylindrical ascending process, and a slender posterior process. In AMNH FARB 570, both jugals are preserved but the left jugal is dorsoventrally crushed and displaced laterally.

The anterior process resembles an anteriorly pointed teardrop in lateral aspect (figs. 5C, 6C), as is the case in most goniopholidids and other neosuchians (Mook, 1942; Iordansky, 1973; Salisbury et al., 1999; Pol et al., 2009; Smith et al., 2010). It laterally overlies the alveolar process of the maxilla up to the level of the 15th alveolus. This contact is well preserved on the right side in AMNH FARB 570, whereas it is incomplete on the left side due to the poorer preservation of the left maxilla. Laterally, the anterior tip of the jugal sits dorsal to the posterior margin of the maxillary depression, as in other goniopholidids (Salisbury et al., 1999; Smith et al., 2010).

Laterally, the anterior process is strongly convex and heavily ornamented. The ornamentation pits tend to be wide (~2 mm in diameter) and deep like the skull table. Ridges are tall and anastomosing. A small portion of the medial surface of the left jugal is preserved and visible within the suborbital fenestra, indicating that the surface for contact with the maxilla was smoothly textured and medially concave.

The ascending jugal process contributes to the ventral portion of the postorbital bar. The left ascending process is fragmented and extensively repaired. The ascending process is inset from the lateral surface of the jugal (figs. 5C, 6C). As discussed with the postorbital, the nature of the jugal-postorbital suture is unclear on both sides of AMNH FARB 570. The bar projects slightly medially at its base before turning dorsally to contact the descending process of the postorbital. Due to its lateral displacement, the ascending process of the left jugal in AMNH FARB 570 follows a medial direction. Both ascending processes of the jugal are marked by smooth-textured bone, as is the case in the descending processes of the postorbitals. Slender, smooth-textured postorbital bars are prevalent in goniopholidids (Young, 1948; Salisbury et al., 1999; Smith et al., 2010). The postorbital bar in *Calsoyasuchus* is notably thick and sits much closer to the lateral margin of the jugal (Tykoski et al., 2002).

In ventromedial aspect there is a prominent suture for the lateral process of the ectopterygoid located where the anterior and ascending processes contact (figs. 5B, 6B). The anterior portion of the contact would have been present on the posteromedial margin of the alveolar process of the maxilla. The suture is exposed on the left side in AMNH FARB 570, whereas the lateral process of the ectopterygoid is preserved in situ on the right side. The exposed portion of the suture is very small and teardrop shaped and extends slightly dorsally onto the ascending process of the jugal. The suture does not extend anteriorly beyond the level of the postorbital bar. The sutural surface is marked by striations. A similarly small ectopterygoid contact is preserved in *Amphicotylus lucasii* (AMNH FARB 5782). The lateral ectopterygoid contact is significantly longer anteroposteriorly in modern crocodylians (Iordansky, 1973) and hylaeochampsids (Clark and Norell, 1992; Ösi, 2008).

The posterior process of the jugal begins at the juncture between the anterior and ascending processes of the jugal (figs. 5C, 6C). Both posterior processes are preserved in AMNH FARB 570, though the right process was extensively reconstructed after postpreservational damage. The posterior process is cylindrical in cross section and forms the ventral margin of the infratemporal bar. On its lateral surface, the posterior process is textured with small pits (~1 mm in diameter) and thick ridges, a marked distinction from the larger pits along the anterior process. This lateral portion of the posterior process terminates in a posteroventrally inclined straight suture with the central plate of the quadratojugal. Dorsally, the quadratojugal-jugal contact extends anterior to the posterior margin of the infratemporal fenestra. Ventrally, the contact stretches just posterior to the posterior margin of the infratemporal fenestra. This contact is similar to that described in *Goniopholis simus* (Salisbury et al., 1999).

Medially, the posterior process is not textured and it contacts the anterior process of the quadratojugal at an anteriorly pointed, triangle-shaped contact. The contact extends anteriorly to the anteroposterior midpoint of the infratemporal bar.

The **quadratojugal** consists of three primary divisions: a slender ascending process associated with the lateral aspect of the anterodorsal head of the quadrate, a small anterior process, and a thick central plate (figs. 5C, 6C).

The ascending process is cracked and broken on both sides in AMNH FARB 570 (fig. 5C). The right ascending process is more exposed and severely shattered, whereas the left process is encased in matrix, but some information can be garnered from direct observation and through CT data. The ascending process forms much of the posterodorsal border of the infratemporal fenestra. The ascending process is transversely narrow along its length, although it tapers as it passes dorsally toward the skull table. On both sides of AMNH FARB 570, there is a lateral expansion of the ascending process near the posterior margin of the infratemporal fenestra. This projection is marked by broken bone anteriorly on both sides, indicating that these were the bases for anteriorly projecting quadratojugal spines (fig. 5A). Similar spines are present in many modern crocodylians (Iordansky, 1973), *Leidyosuchus* (Brochu, 1997), and *Borealosuchus* (Brochu, 1997). Among goniopholidids, quadratojugal spines are apparent in *Goniopholis simus* (NHMUK R41098). As previously stated, CT scans reveal the contact between the right ascending process and the ventral aspect of the postorbital, but details of this contact cannot be assessed.

At the posterior margin of the infratemporal fenestra, the ascending process arises from the dorsum of the central plate of the quadratojugal. The juncture between ascending process and central plate creates a convex posteroventral corner to the infratemporal fenestra (fig. 5A).

In ventral view, the central plate is largely obscured by the ventral aspect of the quadrate, so only a posteriorly tapered triangle of bone is visible. The exposed ventral portion of the central plate is smoothly textured with tiny irregular pits. Overall, the texturing is similar to that on the ventral surface of the quadrate.

Dorsolaterally the central plate forms a very prominent ovoid element that overlies much of the lateral aspect of the quadrate. Laterally, the central plate is variably textured and the dorsolateral surface has prominent pits (~2 mm in diameter). In dorsal view, this heavily ornamented part of the central plate overlies the dorsolateral portion of the quadrate all the way to the posteriormost corner of the lateral quadrate hemicondyle. In posterior view, the central plate is distinctly visible, covering the dorsal and lateral surfaces of the lateral quadrate hemicondyle. *Goniopholis simus* (Salisbury et al., 1999), *Sunosuchus shuhanensis* (Fu et al., 2005), and other *Eutretauranosuchus* specimens (Smith et al., 2010) bear similar ovoid central plates.

The anterior process of the quadratojugal is small and projects anteriorly from the anteromedial aspect of the central plate. In AMNH FARB 570, the right anterior process is well preserved whereas the left anterior process is reconstructed. The anterior process is restricted to the medial aspect of the infratemporal bar. It abuts the medial aspect of the posterior process of the jugal, with which it forms a triangle-shaped, anteriorly pointed suture. Both the left and right anterior processes are smooth in texture in AMNH FARB 570.

Each **vomer** consists of an anteriorly positioned palatal process and a complex septal lamina (in part homologous with the ascending process described by Kley et al., 2010). Both vomers are well preserved and in articulation in AMNH FR 570 (figs. 5C, 6C, 13). The ventralmost portions of the septal laminae are visible in ventral view whereas the remaining parts, although obscured by matrix, are visible in CT reconstruction (fig. 8C, D).

The palatal process of the vomer is a small and transversely narrow horizontal plate. The palatal processes contact each other along the midline where they overlie the conjoined palatal processes of the maxillae just anterior to the ventrally open choanal passage (fig. 8A). The primary choanae are positioned lateral to the palatal processes of the vomers. The palatal processes have no palatal exposure in goniopholidids (Young, 1948; Mook, 1967; Salisbury et al., 1999; Smith et al., 2010), unlike the condition in *Simosuchus* (Kley et al., 2010) and *Melanosuchus* (Iordansky, 1973) where a polygonal exposure of the palatal process is situated in the midline between the palatal process of the premaxillae and the palatal process of the maxillae.

The septal lamina projects posteriorly from the posteromedial aspect of a palatal process (fig. 8B). Between the anterior margin of the choanal groove and the prefrontal pillars, these laminae form the medial and dorsomedial boundaries of the osseous nasopharyngeal canal.

Just posterior to the anterior margin of the choanal opening, the septal laminae are conjoined and rectangular in cross section. Each lamina expands dorsolaterally as it continues posteriorly resulting in a Y-shaped element in cross section (fig. 8B). Slightly farther posteriorly the two dorsolateral prongs of the Y project small lateral accessory processes. These accessory processes meet the ascending process of the ipsilateral palatine (fig. 8C). A similar vomeral septal complex is visible in *Calsoyasuchus* (Tykoski et al., 2002), although without any posterior bifurcation of the Y as in AMNH FARB 570.

Continuing posteriorly, the ventralmost portion of the Y septum bifurcates to form a ventrally narrow X-shaped septal complex (fig. 8C). Near the level of the posteriormost maxillary alveolus, a thin projection of the anterior process of the pterygoid lies between the ventral stems of the X-shaped septal complex. Near the anterior margin of the orbit, the vomeral septal complex appears to terminate, giving way to a Y-shaped complex comprised solely of the pterygoid (fig. 8D, E). No CT scans are as yet available for other specimens of *Eutretauranosuchus* (Mook, 1967; Smith et al., 2010), *Amphicotylus lucasii* (AMNH FR 5782), or *Amphicotylus stovalli* (Mook, 1964); however, all show bilateral septal laminae anteroventrally within the nasopharyngeal passage. This suggests that all these species bear the peculiar vomeral septal complex exhibited by AMNH FARB 570. *Calsoyasuchus* exhibits only a single midline septum that does not reach as far ventrally as the *Eutretauranosuchus*-style septa (Tykoski et al., 2002).

Each **palatine** is a bipartite structure, consisting of a broad palatal process and an internal ascending process. The palatal processes in AMNH FARB 570 do not contact along the midline (figs. 5B, 6B, 8A–D, 13) allowing for the ventrally open nasopharyngeal canal. This character state is shared with all other reported specimens of *Eutretauranosuchus* (Mook, 1967; Smith et al., 2010) and an undescribed skull attributed to this taxon from the Morrison Formation of Dinosaur National Monument (Tykoski et al., 2002). Similar architecture is evident in *Amphicotylus* (Mook, 1964), *Calsoyasuchus* (Tykoski et al., 2002), and *Sunosuchus shuhanensis* (Fu et al., 2005). In all of these taxa the palatal processes of the palatines form small shelves at the ventrolateral margin of the nasopharyngeal trough. The palatines are medially separated in *Simosuchus clarki*, but in that taxon the space is filled by palatal exposures of the vomer and the anterior process of the pterygoid; there is no ventral opening to the nasopharyngeal canal (Kley et al., 2010).

The palatines closely resemble those of most other mesoeucrocodylians. The contacts between the maxilla and the palatal processes of the palatines are transversely rectangular and narrow (figs. 5B, 6B). Just anterior to the suborbital fenestra, the palatal process has a lateral projection that forms the anteromedial margin of the suborbital fenestra. The contact between the palatal maxillae and these elements produces the sigmoid suture discussed above. The anteromedial margin of the palatine-maxilla contact is interdigitating, whereas the curved anterolateral contact is smooth. In AMNH FARB 570, the left palatal process of the palatine extends farther anteriorly than on the right side.

Posteriorly, near the terminus of the vomeral septa, the palatines are damaged. The better-preserved left palatal process tapers to a point along the ventrolateral margin of the nasopharyngeal canal. Medially this tapered portion of the left process is fragmented. On the right side, the tapered portion of the palatine is heavily cracked medially (figs. 5B, 6B). In CMNH 8028, the palatal process of the palatine tapers more significantly. Near the posterior margin of the suborbital fenestra, it terminates at a short, transverse suture with the anterior process of the pterygoid, which sits lateral to the nasopharyngeal trough (Mook, 1967).

On the posterolateral margins of the palatal processes, there is a pair of ovoid foramina (figs. 5B, 6B). These are better preserved on the right side in AMNH FARB 570. The anterior foramen sits at the level of the 13th alveolus, whereas the posterior foramen sits at the level of the ultimate alveolus. CT scans indicate that each foramen is connected to a canal that passes dorsomedially through the palatine connecting with the nasopharyngeal passage (fig. 8B).

The ascending process of the palatine projects dorsally from the dorsal surface of the palatal process of the palatine (fig. 8B). Both palatine ascending processes are preserved in AMNH FARB 570. These are visible only in CT reconstructions. The ascending process is first visible at the level of the anterior margin of the suborbital fenestra. Beginning as a stout, dorsally rounded prominence, the ascending process increases in height posteriorly. Small, medially direct prongs arise from the ascending process, resulting in the structure resembling an inverted L in cross section (fig. 8C, D). It is these prongs that contact the septal lamina of the ipsilateral vomer to form the dorsolateral wall for the nasopharyngeal canal (fig. 8C). This contact can be seen clearly in the holotype of *Calsoyasuchus valliceps* where the nasopharyngeal passage is entirely prepared (Tykoski et al., 2002). The contact between the ascending process of the palatine and the vomer terminates at the level of the prefrontal pillars.

Farther posteriorly, the ascending processes become dorsoventrally shorter and persist to the level of the prefrontal pillars. Although the contact is obscured in AMNH FARB 570, they likely met the lateral portion of the anterior process of the pterygoid at, or very near to, this level (fig. 8D) considering the shape of this contact in modern crocodylians (e.g., Iordansky, 1973). The posteriormost portion of the ascending process of the palatine meets the ventralmost portion of the descending process of the prefrontal (fig. 8E). The dorsal margin of the anterior process of the pterygoid also contacts the descending prefrontal creating a tripartite prefrontal pillar complex.

The **pterygoid** is a large unpaired element with no evidence of a midline suture. It is roughly tetraradiate with a midline anterior process, two prominent laterally projecting transverse processes, and dorsoventrally short ascending processes. Both sides of the pterygoid are partially preserved in AMNH FARB 570, although the left transverse process is not preserved. In palatal view all portions of the pterygoid are smoothly textured.

The anterior process of the pterygoid is well preserved in AMNH FARB 570. The portion anterior to the prefrontal pillars is visible only in CT scans. As discussed above, this portion of the anterior process is Y-shaped in cross section and extends posteriorly to the level of the prefrontal pillars (fig. 8D). Posterior to the prefrontal pillars, the anterior process forms the dorsolateral borders of the nasopharyngeal passage (fig. 8E, F).

Posterior to the pillars, the anterior process of the pterygoid develops prominent lateral walls for the nasopharyngeal passage. In cross section this portion of the bone resembles the numeral 3 with its convex portions facing dorsally (fig. 8E, F). In AMNH FARB 570, the midline septal portion is offset to the left due to breakage. The exposed roof of the nasopharyngeal groove is marked by multiple parallel, anteroposteriorly running grooves. Along much of its length, the lateral limbs of the anterior process are overlain by the posterior lengths of the palatal processes of the palatines (fig. 8F).

The midline septum terminates at the level of the anterior tip of the infratemporal fenestra. Fractures indicate that the septum is broken and would have extended more posteriorly. Farther posteriorly the anterior process becomes dorsoventrally shorter, resulting in a shallowing of the nasopharyngeal trough (fig. 8F). Posteriorly, the terminus of the nasopharyngeal trough is marked by a curved shallow wall. This causes the pterygoid to border the posterior and posterolateral margins of the choanal opening in AMNH FARB 570 as in *Amphicotylus stovalli* (Mook, 1964), *Goniopholis simus* (Salisbury et al., 1999), and the atoposaurid *Theriosuchus* (Schwarz and Salisbury, 2005; NHMUK R48330). A small, flat pterygoid plate sits posterior to the terminus of the choanal trough. The pterygoid plate is posteroventrally inclined and has a slight, posterior concavity.

The transverse processes are poorly preserved in AMNH FARB 570 (figs. 5B, 6B). The right process is preserved as a dorsoventrally shallow plate of bone. It is broken both anteriorly and posteriorly, resulting in a medially broad and laterally narrow triangular structure. The lateralmost tip of the right transverse process contacts the palatal process of the ectopterygoid. On the left, the transverse process is missing with only its fractured base preserved.

The transverse process of the pterygoid would have extended from the lateral surface of the anterior process of the pterygoid. Neither process has a well-preserved base, and the anteroposterior length of the element is thus unclear. However, the base was anteroposteriorly elongate and dorsoventrally flat, indicating that the complete transverse processes would have been broad, flattened plates as in most crocodyliforms (Turner and Sertich, 2010). The partially preserved right transverse process exhibits a slight posteroventral inclination along its length, as would be expected in a crocodyliform. The preserved portion of the element is dorsoventrally flattened. CT slices show no pneumatic spaces in the interior of the right transverse process (fig. 12B, C).

The ascending processes of the pterygoid consist of two flat plates that ascend along the ventrolateral margins of the braincase. In AMNH FARB 570, the right ascending process is largely embedded in matrix and is exposed only at its posterior margin. The left ascending process is well exposed and makes a small contact with the posterolateral margin of the dorsal primary head of the quadrate. In AMNH FARB 570 a sutural contact is visible on the right side; damage to the quadrate makes the suture indistinct on the left side. The process for quadrate contact is narrow and lacks grooves. Anterior to the pterygoid-quadrate contact, the ascending process appears to make contact with the ventral aspect of the laterosphenoid bridge (fig. 8C). This contact is exposed only on the left side, and the suture is poorly preserved. Posteriorly, the ascending process fits lateral to both the parabasisphenoid and the basioccipital. In posterior view the basioccipital and basisphenoid are underlain only by the pterygoid. In AMNH FARB 570 the left ascending process is badly broken, which exposes the lateral aspect of the basioccipital plate.

Only the right **ectopterygoid** is preserved in AMNH FARB 570 (figs. 5B, 6B). It consists of a lateral process for contact with the jugal and maxilla, a palatal process for contact with the transverse process of the pterygoid, and a central body connecting the elements. The lateral process further consists of an anterior prong and a posterior projection (possibly homologous with the anterior and posterior processes of Kley et al., 2010). The dorsomedial surface of the bone is entirely embedded in supporting matrix and is visible in CT scans. The preserved ectopterygoid is smoothly textured, lacking any pitting or sculpturing.

The lateral process contacts the posteromedial margin of the alveolar process of the maxilla and the anteromedial margin of the anterior process of the jugal. This is similar to the central contact point for the lateral process in modern crocodylians (Iordansky, 1973) and most mesoeucrocodylians (Turner and Sertich, 2010). The anterior and posterior prongs are very weakly developed in AMNH FARB 570, projecting only a very short distance from the central point of contact for the lateral process (figs. 5B, 6B). The anterior projection does not reach the level of the posteriormost margin of the tooth row, and the posterior projection reaches the level of the posterior margin of the postorbital bar. There is no dorsally oriented projection for contact with the medial margin of the postorbital bar. No modern crocodylian has such a similar small lateral ectopterygoid contact (Iordansky, 1973). Such a structure is present in *Amphicotylus lucasii* (AMNH FARB 5782) and *Sunosuchus junggarensis* (Wu et al., 1996). A small foramen is present on the ventral surface of the anterior projection.

The body of the ectopterygoid is oriented ventromedially. The distinction between the body and palatal process is demarcated by a marked inflection point, with the palatal process following a posteroventral inclination. In AMNH FARB 570 the palatal process is broken anterodorsally and the anterior face is missing. The dorsalmost preserved portion of the palatal process appears to be flattened anteriorly, whereas the more ventral preserved portion is convex anteriorly. In AMNH FARB 570 only a tiny piece of the right transverse process remains in articulation with the posteromedial face of the palatal process. Posterior to the contact, the palatal process terminates at a posteriorly rounded margin. The shape and orientation of the palatal process and central body are similar to that in *Amphicotylus lucasii* (AMNH FARB 5782) and *Sunosuchus junggarensis* (Wu et al., 1996).

Palpebrals: Two flattened, oval-shaped ossifications are preserved within the supporting matrix in the right suborbital fenestra (figs. 5B, 6B). The exposed surfaces are smooth and these are interpreted as disarticulated and displaced palpebrals, resembling those found above the orbits of juveniles of extant crocodylians and adult alligatorines (Nesbitt et al., in press). The palpebrals in *Amphicotylus lucasii* (AMNH FARB 5782) and many European goniopholidids (Andrade and Hornung, 2011) are similarly oblong, though they tend to be broader posteriorly than anteriorly. Additionally, in some goniopholidid taxa (e.g., *Goniopholis simus*) the palpebrals appear to be strongly integrated into the orbital margin (Andrade and Hornung, 2011).

Chondrocranial Elements: The **laterosphenoid** is a prominent bone forming the anterolateral and anteroventral portion of the braincase (fig. 11). The element consists of two flattened laminae (anterolateral and posterolateral) divided by a cotylar crest. Dorsolaterally, the cotylar crest contributes to a well-developed capitate process. The left laterosphenoid is encased in matrix, but the right laterosphenoid is partially exposed with only its ventralmost aspect embedded in matrix. Most of following description will come from the exposed right laterosphenoid.

The anterolateral lamina forms the anterior portion of the braincase. The lamina faces ventrally in AMNH FARB 570, similar to the condition in *Eosuchus minor* (Brochu, 2006), and is dorsally in contact with the descending process of the frontal. Only one small foramen is exposed on the right anterior lamina, which may correspond to the exit for the trochlear nerve (CN IV) (fig. 12A). In AMNH FARB 570 the left laterosphenoid is embedded in matrix ventral to the trochlear foramen. CT scans reveal that the ventral half of the anterolateral lamina projects strongly medially toward the midline (fig. 12A). On both sides, the medial tips of the anterolateral laminae contact the lateral aspect of the parabasisphenoid rostrum (fig. 12A, B). Similar anterolateral laminae with a strong medial inclination are present in *Gavialis* (AMNH R 88316, AMNH R 110145) and in *Eosuchus minor* (Brochu, 2006).

The posterolateral lamina of the laterosphenoid has a strong posterodorsal inclination in AMNH FARB 570 with much of the lamina visible within the supratemporal fenestra (figs. 5A, 6A). This portion of the laterosphenoid makes dorsal contacts with the descending processes of the frontal anterodorsally and the parietal posterodorsally. Posteriorly, the laterosphenoid contacts the quadrate along a dorsoventrally oriented suture. The bone is dorsoventrally short and elongate in comparison to modern crocodylians, although the element is not as elongate as in *Rhabdognathus aslerensis* (Brochu et al., 2002; Jouve, 2007).

A prominent cotylar crest marks the boundary between the laminae of the laterosphenoid. On the right side of AMNH FARB 570, a distinct, suturelike crack runs along the cotylar crest. Dorsolaterally, the crest and the two laterosphenoid laminae contribute to a prominent, transversely elongate capitate process (fig. 12A). This process integrates dorsally with the ventral aspect of the anteromedial process of the postorbital. In sagittal section the left capitate process forms an anteriorly pointed equilateral triangle, whereas the right capitate process forms an anteroposteriorly elongate rectangle. A rounded lateral margin is visible on both capitate processes where each fits against the dorsomedial aspect of the descending process of the postorbital (fig. 11).

Posteriorly, the cotylar crest expands into a broad, laterally facing plate. CT scans show a large pneumatic cavity in the anterior portion of this plate (fig. 12C). In coronal section, the cavity is roughly triangular and pointed laterally. A small passage extends anteroventrally from this pneumatic space toward the anterior margin of the laterosphenoid, lateral to the hypophyseal fossa.

Posteriorly the cotylar plate has a strongly curved posterior margin contributing to the anterior margin of the trigeminal foramen. Anteroventral to the trigeminal foramen, the laterosphenoid forms a prominent platelike process (fig. 12C). This is the laterosphenoid bridge, which forms the lateral wall of a canal through which passes the opthalmic division of the trigeminal nerve (CN V1) after it leaves the trigeminal foramen. The canal contacts the anterodorsal margin of the ascending process of the pterygoid and the dorsolateral margin of the parabasisphenoid. There is no indication of an epipterygoid, as described in some mesoeucrocodylian taxa (Holliday and Witmer, 2009; Kley et al., 2010).

On AMNH FARB 570 only the posterior margin of the left laterosphenoid bridge is exposed. The exposed element has a strong posteromedial inclination toward a sutural contact with the ascending process of the pterygoid. Anterior to this posterior exposure, the laterosphenoid bridge is visible in CT reconstructions (fig. 12C). The anterior portion is cracked along its length, distorting the element, so that it is angled farther medially.

The **prootic** forms much of the proximal margin of the trigeminal foramen and the anteroventral portion of the otic capsule. In AMNH FARB 570, a small lateral portion of the left prootic is partially exposed laterally. The right prootic remains entirely embedded in matrix. The prootics in AMNH FARB 570 resembles those of modern crocodylians. Laterally, the element is seen to contact the laterosphenoid anterolaterally and the quadrate posterolaterally within the trigeminal foramen. The left prootic-laterosphenoid suture is clear in the anterior border of the trigeminal foramen in AMNH FARB 570. The posterior portion of the left trigeminal foramen is damaged, so details of the quadrate-prootic contact are obscured. However, it appears that, as in *Alligator* and *Caiman* (Iordansky, 1973), the prootic did not contribute to the lateral surface of the braincase, instead being recessed within the trigeminal foramen.

In CT reconstruction, the contribution of the prootic to the otic capsule is difficult to interpret due to damage and lack of contrast in this area. A series of slender struts, however, are visible where the prootic contributes to the borders of the mastoid air cavities (fig. 12E). These struts would contact the supraoccipital medially and the otoccipital ventrolaterally. The poor preservation in this region suggests that the tympanic region and paratympanic sinuses were formed by a thin, fragile, bony plate as noted by Smith et al. (2008).

The **parabasisphenoid** is a midline element. It should be noted that, although it is discussed here with other chondrocranial elements, the element is the result of fusion between the endochondral basisphenoid and the dermal parasphenoid (Romer, 1956). The element is comprised of an anterior parabasisphenoid rostrum and a posterior braincase contribution (fig. 12A, B). The parabasisphenoid has only a small posterior exposure in posterior view, whereas most of the element is visible only in CT slices.

The parabasisphenoid sits atop the pterygoid, with the ascending processes of the pterygoid fitting lateral to it. Posteriorly, the parabasisphenoid sutures to the basioccipital plate (fig. 14). A small circular opening, the ventral opening of the median eustachian foramen, is formed by the contact between the parabasisphenoid and basioccipital. CT scans of AMNH FARB 570 reveal that the opening forms a bony median eustachian canal that rises toward the ventral aspect of the foramen magnum (fig. 12E).

Ventrally only an anteroposteriorly short exposure of the parabasisphenoid is visible in AMNH FARB 570. The small posterior exposure of the parabasisphenoid is reminiscent of gavialoids (AMNH R 88316). In CT scans of AMNH FARB 570, the contribution of the parabasisphenoid to the ventral aspect of the braincase is clearly visible (fig. 12D). The element is still laterally bordered by the ascending processes of the pterygoid at the level of its braincase contribution. The pterygoid-parabasisphenoid contact is akinetic. The otoccipital, prootic, and laterosphenoid contact the parabasisphenoid posterolaterally, laterally, and anterolaterally, respectively. Near the anteroposterior level of its anterior contact with the laterosphenoid, the braincase contribution of the parabasisphenoid terminates. Near the anterior terminus of the braincase contribution of the parabasisphenoid, two small canals are visible exiting the ventral surface of the braincase and traveling anteriorly. These are interpreted as passages for the left and right abducens nerves (CN VI) (fig. 12D).

At its anteriormost extent the parabasisphenoid forms a small cavity for the pituitary gland (the hypophyseal fossa) (fig. 12B). The cavity appears to be unframed anterodorsally, although this may be the result of damage. Within the posterior aspect of the hypophyseal fossa in AMNH FARB 570, two large and bilateral dark-colored cavities are visible medially. These are interpreted as the anteriormost passages for the internal carotid arteries, which have traveled from the otic region to the hypophyseal fossa, as in modern crocodyliforms. Lateral to the carotid canals, two tiny foramina are visible. These are interpreted as the anterior extent of the canals for the abducens nerves, as they are continuous with the anteroventral foramina in the braincase floor described previously (fig. 12D).

Anteroventral to the hypophyseal fossa, a tall and transversely thin structure projects anteriorly which we interpret as the parasphenoid rostrum. Just anterior to the hypophyseal fossa small medial projections from the anterolateral lamina of the laterosphenoid are apparent. These contact the dorsolateral margins of the parasphenoid rostrum. Anterior to this laterosphenoid-parasphenoid contact, the rostrum becomes transversely narrow. It terminates at an anteriorly curved edge, well posterior to the prefrontal pillar complex (fig. 12A, B).

Posterior to the prefrontal pillars, the anterior process of the pterygoid is in contact with the parasphenoid rostrum ventrally (fig. 12B). In AMNH FARB 570 the nasopharyngeal passage appears displaced, being positioned just lateral to the left of the parasphenoid rostrum. Farther posteriorly the nasopharyngeal canal shifts, so that it is positioned ventral to the parasphenoid rostrum, although a prominent crack running through both the parasphenoid and anterior process of the pterygoid obscures this contact in AMNH FARB 570.

The **basioccipital** is a midline element that forms the posteroventral portion of the braincase, the ventral portion of the occiput, and the ventral border of the foramen magnum (fig. 14). It consists of a ventral basioccipital plate and a dorsal condylar process. Both portions are well preserved in AMNH FARB 570. The basioccipital faces posteriorly as is common among neosuchians (Turner and Sertich, 2010).

The condylar process of the basioccipital is anteroposteriorly elongate. Dorsally, there is a sulcus running the entire anteroposterior length of the condyle. The occipital condyle itself forms a fattened U shape in posterior view (fig. 14). In AMNH FARB 570 the posterior aspect of the condyle is cracked in several places. The texture of the preserved condyle is smooth. Along its entire dorsolateral margin, the condyle is in contact with the exoccipital portion of the otoccipital. Ventrally, there is a prominent demarcation between the occipital condyle and the “neck” of the condyle supported by the basioccipital. The surface of the ventral condyle is marked by minuscule pits and has a spongy appearance. A sharp groove separates this element from the otherwise smooth-textured surface on the ventral aspect of the condylar neck. A pair of bilateral ridges run from the ventral aspect of the condylar neck toward the more ventrally placed basioccipital plate.

The neck of the occipital condyle runs continuously into the platelike occipital portion of the basioccipital. In posterior view, the occipital surface is roughly pentagonal. Anteroventrally, the basioccipital contacts the posterior aspect of the parabasisphenoid. A circular gap between the two elements forms the opening of the median eustachian foramen (figs. 5B, 6B). In AMNH FARB 570 the ventralmost surface of the basioccipital exhibits a slight dorsally directed curvature, which exposes the median eustachian foramen posteriorly. As such, the ventral aspect of the basioccipital plate is bilobate. The two ventrally rounded eminences surrounding the median eustachian foramen are the basal tubera. Each tuber is marked by roughened, dorsoventrally striated bone ventrally. These are small and have limited curvature, unlike the significantly larger tubera found in thalattosuchians and gavialoids (Hua and Jouve, 2004; Pol and Gasparini, 2009). Dorsal to the median eustachian foramen in AMNH FARB 570 the basioccipital exhibits a dorsoventrally short midline crest, a common feature in neosuchians (Turner and Sertich, 2010).

Anterolaterally, the occipital plate of the basioccipital contacts the posterior part of the ascending processes of the pterygoid. This contact is broken slightly on the left side. Though no external opening is visible, there is a distinct lateral eustachian canal visible between the basioccipital and parabasisphenoid (fig. 12E). The canal is dorsally inclined to the level of the foramen magnum, from which it diverges medially to meet the dorsolaterally directed diverticulum of the median eustachian canal. In AMNH FARB 570 the lateral eustachian canal is broken on the left side of the skull. The left lateral aspect of the basioccipital is partly exposed due to breakage of the left ascending pterygoid process.

The **otoccipitals** are paired in AMNH FARB 570; a groove dorsal to the foramen magnum indicates the site of the midline suture between the elements (fig. 14). The otoccipital consists of an exoccipital portion, which laterally frames the foramen magnum and a more complex opisthotic part that forms much of the posterior surface of the occiput. Dorsal to the foramen magnum the otoccipitals meet and entirely exclude the supraoccipital from the border of the foramen. The supraoccipital-otoccipital contact forms a ventrally directed curve in posterior view.

The exoccipital portion of the otoccipital consists of bilateral struts that sit lateral to the foramen magnum. A small foramen is positioned just lateral to this strut and the dorsoventral midpoint of the foramen magnum (fig. 14). The foramen is present on both sides of AMNH FARB 570, though it is externally cracked on the left. In CT reconstructions, a canal can be seen connecting this foramen directly to the posteriormost surface of the braincase suggesting the position of the hypoglossal foramen (CN XII). Ventrally, the struts of the exoccipital expand posteriorly to form a small portion of the dorsolateral margin of the occipital condyle. They adopt some of the "spongy" texturing of the posterior occipital condyle. A straight, ventrolaterally oriented suture is visible between the elements.

Lateral to the exoccipital portion of the otoccipital, the bone flares into a broad paroccipital process that forms most of the surface area of the occipital plate (fig. 14). Both paroccipital processes are well preserved in AMNH FARB 570, although the right process is slightly anterodorsally displaced and both are laterally cracked. Along their lengths the paroccipital processes show a marked posteroventral inclination. Dorsally, the paroccipital processes fit against the descending processes of the squamosal. Posteroventrally the paroccipital processes support a shelf of bone. This shelf anterodorsally contacts the posterior margin of the quadrate along a straight suture that is visible ventrally. This bony shelf encloses three passages that transmit cranial nerves IX–XI and the internal carotid artery, as is typical among crocodyliforms (Turner and Sertich, 2010). The courses for each structure are visible in CT slices on the right side of AMNH FARB 570 (fig. 15).

The glossopharyngeal foramen (CN IX) is the most medially positioned of the foramina (fig. 15), lying just lateral to the medialmost margin of the paroccipital process. It is small (~1 mm in diameter), and the course of the glossopharyngeal canal runs anterodorsally through the body of the otoccipital. The glossopharyngeal canal quickly encounters the more laterally positioned vagal canal (CN X).

The vagal foramen is the lateralmost foramina and is positioned lateral to the glossopharyngeal foramen (fig. 15C–E). The vagal foramen is larger (~3 mm across) than the other occipital cranial nerve foramina and roughly ovoid in shape. Its canal follows a slightly more medially directed course before merging with the glossopharyngeal canal. The two appear to join into a single canal that extends dorsally through the otoccipital. The canal terminates internally posterior to the crushed prootic, presumably at the metotic foramen (fig. 15C).

The carotid foramen (which transmitted the internal carotid artery) is positioned ventral to the other foramina, just dorsal to the ventral contact of the otoccipital with the basioccipital. In AMNH FARB 570, the external opening of this foramen is only preserved on the right, due to cracking of the ventromedial otoccipital on the left. The opening is directed nearly ventrally. The right carotid canal is easily visible in the CT slices of AMNH FARB 570 (fig. 15A–D). It passes anteromedially, extending to the otic capsule where it disappears due to poor preservation in this region.

The **supraoccipital** is a midline element positioned dorsally on the occipital surface. In AMNH FARB 570 the bone is nearly completely preserved but heavily fragmented, making sutural details and morphology indistinct (fig. 14). The supraoccipital is trapezoidal in posterior view, with a narrow margin ventrally contacting the dorsal surface of the otoccipital and a broader margin dorsally contacting the parietal. The otoccipital-supraoccipital contact is indistinct, but does appear to be curved ventrally.

The otoccipital-supraoccipital suture may be visible on the right side in AMNH FARB 570 where it appears to be oriented dorsolaterally. No contact is apparent on the left side. The suture between the parietal and the supraoccipital is clear and forms a straight suture medial to the parietal hornlets (fig. 14). The hornlets project posteriorly past the level of the parietal-supraoccipital contact.

A ventromedially oriented crack between the otoccipital and supraoccipital may indicate the position of the contact between these elements on the right side (fig. 14). Damage on the left side obscures any comparison. The possible contact extends from the ventral aspect of the left parietal hornlet to a point dorsolateral to the dorsalmost tip of the foramen magnum.

The supraoccipital-parietal contact is distinct on the right side of the occiput, running transversely between the posttemporal fenestrae. Laterally, the parietal hornlets broadly overhang the supraoccipital (fig. 14). Closer to the midline, the supraoccipital-parietal contact is in the same transverse plane as the back of the skull table.

It is unclear in the CT reconstructions whether a distinct supraoccipital contribution to the mastoid air cavities is present in AMNH FARB 570 (fig. 15A). However, considering the

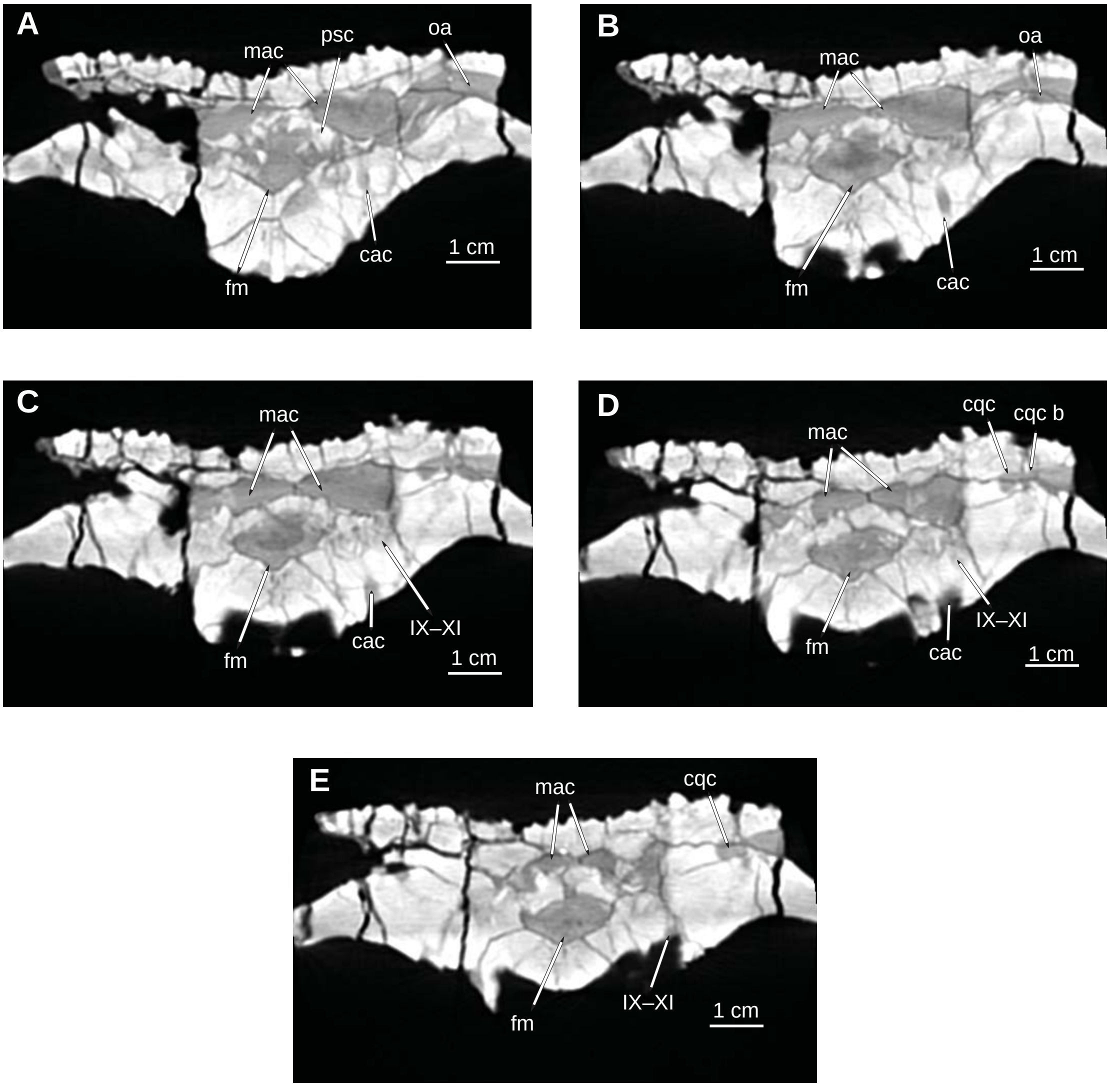

FIG. 15. Transverse CT sections through the skull of *Eutretauranosuchus delfsi* AMNH FARB 570. (**A**) Tra 1124, (**B**) Tra 1159, (**C**) Tra 1177, (**D**) Tra 1184, (**E**) Tra 1195, (**F**) Tra 1216. See appendix 2 for abbreviations.

passage of a transverse pneumatic canal through the posteriormost skull table, the supraoccipital must be pneumatized to allow such a passage to exist.

Splanchnocranial Elements: The **quadrate** closely resembles that of derived mesoeucrocodylians in that it is solidly appressed to the lateral aspect of the braincase (figs. 11, 12). The quadrate consists of a posteriorly positioned quadrate body (incorporating the quadrate condyle) and a broad dorsal primary head. The dorsal primary head possesses an anterodorsal process for contact with the ventral surface of the skull table and a pterygoid process. In AMNH FARB 570, the right quadrate is nearly complete but marred by a longitudinal crack. The left quadrate is similarly cracked and also has extensive damage on the ventral surface of the dorsal primary head.

In ventral view both quadrates are angled more laterally than in CMNH 8028, but this is likely the result of distortion of the jugals and infratemporal bars in AMNH FARB 570.

The body of the quadrate is smoothly textured both dorsally and ventrally. The body curves strongly posterolaterally away from the lateral aspect of the braincase as in most mesoeucrocodylians (Turner and Sertich, 2010). The quadrate hemicondyles are directed posteriorly with a slight lateral inclination (fig. 14). The lateral hemicondyle is the smaller of the two and terminates at a ventromedially inclined intercondylar sulcus. The medial hemicondyle is twice as tall as the lateral hemicondyle and bears a dorsomedially curved medial margin. There is a large crack through the right lateral hemicondyle. The hemicondyles both bear a spongy texture similar to that of the occipital condyle. The condylar morphology in AMNH FARB 570 closely resembles that of *Amphicotylus lucasii* (AMNH FARB 5782).

Laterally, the quadrate body is in contact with the central body and ascending process of the quadratojugal. The central body of the quadratojugal is visible posteriorly, broadly overlying the dorsolateral margin of the lateral hemicondyle. However the quadratojugal does not extend as far posteriorly as in dyrosaurids (Brochu et al., 2002).

Dorsally, the quadrate body is marked by a thick ridge that runs anterodorsally toward the posteroventral margin of the otic aperture (fig. 14). Along its course, the ridge becomes dorsoventrally shorter. Laterally on both sides of AMNH FARB 570, the quadrate body is marked by anteroposteriorly running striations. This is interpreted as the original extent of the otoccipital-quadrate contact exposed due to damage of the paroccipital processes on the right side. On both the right and left sides in AMNH FARB 570, the cranioquadrate canal (for passage of CN VII and the orbitotemporal artery) is apparent as a gap between the anteriormost margin of the paroccipital processes and the posteriormost margin of the quadrate body (fig. 15D, E). On the right side of AMNH FARB 570, the lateralmost margin of the paroccipital process exhibits slight anterolateral curvature that approaches the lateralmost margin of the striations. The complete contact may have enclosed the cranioquadrate canal close to the lateral margin of the skull table. Damage obscures the external anatomy of the cranioquadrate passage on the left side, but it is visible in CT slices on the right. It appears to be enclosed by a contact of quadrate, squamosal, and otoccipital near the otic aperture (fig. 15). However, this contact terminates quickly and there is no broad contact between the three elements as in modern crocodylians. The configuration of these elements in AMNH FARB 570 is uncommon among mesoeucrocodylians, although it is present in thalattosuchians (Turner and Sertich, 2010) and in *Goniopholis simus* (Salisbury et al., 1999).

Ventrally the quadrates are smoothly textured, but marked by large crests resembling those of other mesoeucrocodylians (figs. 5B, 6B). The lateralmost crest is homologous with Iordansky's crest A (Iordansky, 1973). It curves anteromedially, running from a position anterior to the lateral hemicondyle to a point just posterior to the level of the posterior margin of the supratemporal fenestra. A second, more medial crest (crest B of Iordansky, 1973) begins posteriorly at the same point as crest A. However, this crest arcs farther medially, crossing the quadrate to reach the medial margin of the pterygoid process of the quadrate. There is a slight platform between crests A and B. Both quadrates preserve crests in AMNH FARB 570. However, their medial aspects are embedded in matrix on the right side and the medialmost margin of crest B is broken on the left. The crest arrangement is very similar to the condition in other *Eutretauranosuchus* specimens (Mook, 1967), *Sunosuchus junggarensis* (Wu et al., 1996), and *Amphicotylus lucasii* (AMNH FARB 5782). *Goniopholis baryglyphaeus* (Schwarz, 2002) also possesses similar crests A and B, although it also has a strong crest C (sensu Iordansky, 1973) farther posteriorly. Posteromedial to the origins of crests A and B, there lies a small raised eminence. This region is marked by small anteroposteriorly oriented muscle scars. Slight pitting marks the ventral portion of the quadrate body just proximal to the hemicondyles.

The dorsal primary head of the quadrate sweeps medially to contact the lateral wall of the braincase (figs. 11, 12D). Posteromedially it frames the lateral margin of the otoccipital. This posterior margin terminates in the prominent and descending pterygoid process. In AMNH FARB 570, the pterygoid process is well preserved only on the left side of the skull, where it is embedded in matrix. On the left side the quadrate-braincase contact is medially damaged, so contacts are difficult to discern (fig. 12). The pterygoid process clearly contributes to the posteroventral border of the trigeminal foramen (fig. 11). On the left side, the pterygoid process contacts the posterodorsal margin of the ascending process of the pterygoid. Farther anteriorly the pterygoid process contacts the prootic and laterosphenoid. The prootic is interpreted here as having no lateral exposure as the pterygoid process of the quadrate ventromedially overlaps it. Anteroventrally, the pterygoid process contacts the ventral ramus of the laterosphenoid bridge, so that the trigeminal foramen is externally bordered by the laterosphenoid anteriorly and the pterygoid process of the quadrate posteriorly.

Dorsomedially the dorsal primary head slots firmly against the lateral wall of the braincase dorsal to the trigeminal foramen (fig. 11). This portion of the dorsal primary head sutures to the laterosphenoid posteriorly. Dorsally, the dorsal primary head contacts the descending process of the parietal. In AMNH FARB 570, this suture is visible within the left supratemporal fenestra (figs. 5A, 6A).

The anterodorsal process of the quadrate forms a contact between the quadrate and the ventral surface of the skull table. It is well preserved and embedded in matrix on the right side of the skull, whereas the left process is not preserved. The right anterodorsal process is visible as it slots against the ventral aspect of the posterior process of the postorbital (fig. 12C).

SEMICIRCULAR CANALS: Only one semicircular canal is distinctly visible in the CT reconstructions of AMNH FARB 570, which we interpret as the anterior semicircular canal (fig. 12E). As preserved, the structures sit dorsolaterally alongside the posterior margin of the braincase. Both the right and left canals are oriented dorsomedially within the skull. Along its course the canal passes anteroposteriorly through the prootic and the supraoccipital. The right anterior canal is slightly posterior to the left canal. At the absolute posterior margin of both anterior semicircular canals, there are slight posterolaterally inclined cavities within the supraoccipital. These may indicate the presence of the posterior semicircular canals, given that the preserved cavities do have a distinct dorsal arcing along their lengths and are significantly shorter than the anterior semicircular canals (fig. 15A). However, because these are poorly preserved, it is not possible to confidently identify these structures as posterior semicircular canals.

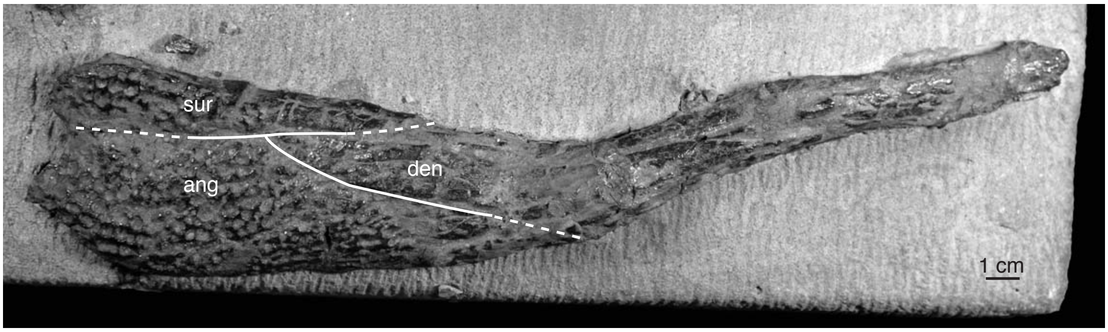

FIG. 16. *Eutretauranosuchus delfsi* AMNH FARB 570. Right hemimandible in lateral view. See appendix 2 for abbreviations.

Mandible

The right ramus of the mandible of AMNH FARB 570 is embedded in a cement panel mount that previously held the skull as well (fig. 16). The anterior half of the mandible shows signs of damage followed by reconstruction with brown cement. Due to this damage and alteration, it is unclear whether the entire anterior end of the dentary is preserved. Along the alveolar margin, poor preservation precludes the identification of the location and number of alveoli in the mandible. Likewise, no details of the medial surface of the mandible are available. Based on the available data it seems that this surface may not have been preserved in whole or even in part.

The mandible is dorsoventrally short anteriorly but rises in height near the midpoint and is tallest for the last third of its length. As in CMNH 8028 (Mook, 1967: pls. 4, 5), the posterior portion is roughly three times the height of the anterior half of the mandible (fig. 16). Few features are discernible on the anterior half of the mandible. The lateral surface is textured by a series of anastomosing grooves. A single prominent groove, just ventral to the alveolar margin begins 4 cm posterior from the preserved anterior end of the dentary. This groove runs nearly the entire length of the mandibular ramus, ending roughly 5 cm before the end of the preserved portion of the mandible. The groove terminates at the junction of the dentary with the surangular and angular.

As in CMNH 8028 (Mook, 1967: pls. 4, 5), the dentary extends dorsally as a pointed process that divides the surangular and angular along their anterior margins. The posterior suture of the dentary with the angular is along a dorsally sloping contact (fig. 16). Although the region is poorly preserved, there is no indication that the dentary extended between branches of the angular. In contrast to the holotype of *Eutretauransuchus delfsi* (CMNH 8028), AMNH FARB 570 appears to lack an external mandibular fenestra. If an external mandibular fenestra is present it is very small and located at the posteriormost tip of the lateral surface of the dentary. The external mandibular fenestra in BYU 17628 is smaller than in CMNH 8028. This seems to indicate that the size of the external mandibular fenestra is variable among individuals of *Eutretauranosuchus*.

Among goniopholidid taxa, the presence and/or size of external mandibular fenestrae are variable. *Goniopholis baryglyphaeus* (Schwarz, 2002) and *G. simus* (Salisbury et al., 1999) lack external mandibular fenestrae. One specimen of *Amphicotylus lucasii* (AMNH FARB 534) appears to lack an external mandibular fenestra. *Sunosuchus* sp. (Maisch et al., 2003), *Goniopholis simus* (Owen, 1878), and *Sunosuchus junggarensis* (Wu et al., 1996) all have clear external mandibular fenestrae.

The surangular is triangular in shape with the posterior end being the broadest and the anterior end tapering gradually toward the contact with the dentary. The surangular has a straight dorsal margin up to the point that it is broken posteriorly near where the retroarticular process would have begun. At this point the surangular is weakly convex dorsally. The surangular is textured with deep pits. The lateral surface of the bone curves medially along its dorsal border, and this surface is smooth, lacking the pitting seen on the remainder of the lateral surface. A slight, raised ridge is present on the dorsolateral surface of the surangular.

The angular is nearly three times the height of the surangular as in CMNH 8028, *Sunosuchus* sp. (Maisch et al., 2003), *Sunosuchus junggarensis* (Wu et al., 1996), *Goniopholis simus* (Salisbury et al., 1999), and *Goniopholis baryglyphaeus* (Schwarz, 2002). The lateral surface is textured with deep pits like the surangular and most of the skull table. The angular contacts the surangular along a horizontal suture visible on the lateral surface of the mandible. Anteriorly, the dorsal margin of the angular begins to curve ventrally, tracking along the diagonal contact with the dentary. The ventral margin of the angular is flat for much of its length before curving dorsally at the posterior terminus of the mandible as in many early neosuchians (e.g., *Goniopholis baryglyphaeus* [Schwarz, 2002], *Sunosuchus miaoi* [Young, 1948]).

Postcranial Skeleton

A partial postcranium was collected with the skull (figs. 17, 18). The block that held the skull and partial mandible also encases most of the cervical vertebral series covered completely in heavily weathered osteoderms (fig. 1). No details of the cervical vertebrae are apparent and the weathering of the osteoderms is so severe that no morphological details can be characterized.

Also collected and included with AMNH FARB 570 are a partial left femur, a single proximal phalanx, and four fragments of dorsal osteoderms from the trunk. The **femur** is incomplete, lacking the proximal end from the head to the fourth trochanter. The remainder of the femoral shaft is straight until the distal end where the femur expands to form the two distal condyles, which are separated by a broad and shallow popliteal space (fig. 17A–D).

The **phalanx** included in AMNH FARB 570 (fig. 18) does not belong to the same animal as the other material. Proportionally it is much larger than would be expected for a neosuchian with a femur the size of AMNH FARB 570. Moreover, based on the anatomy of the element it is likely that the phalanx does not belong to a crocodylomorph. The phalanx is widest proximally and is most constricted at the midpoint. Unlike nearly all crocodylomorphs, especially ones showing the typical aquatic skull adaptations of AMNH FARB 570, the distal articular surface is not mediolaterally broad and dorsoventrally compressed. Furthermore, the distal articular surface forms a well-defined trochlea with sharply defined medial and lateral edges. The dorsal surface of the trochlea extends dorsally above the level of the phalangeal shaft and the extensor pits on both sides are dorsally displaced. Proximally on the ventral surface there is a medially displaced extensor ridge. Taken together, these features suggest this phalanx is a right proximal phalanx of a theropod dinosaur (most likely from digit II).

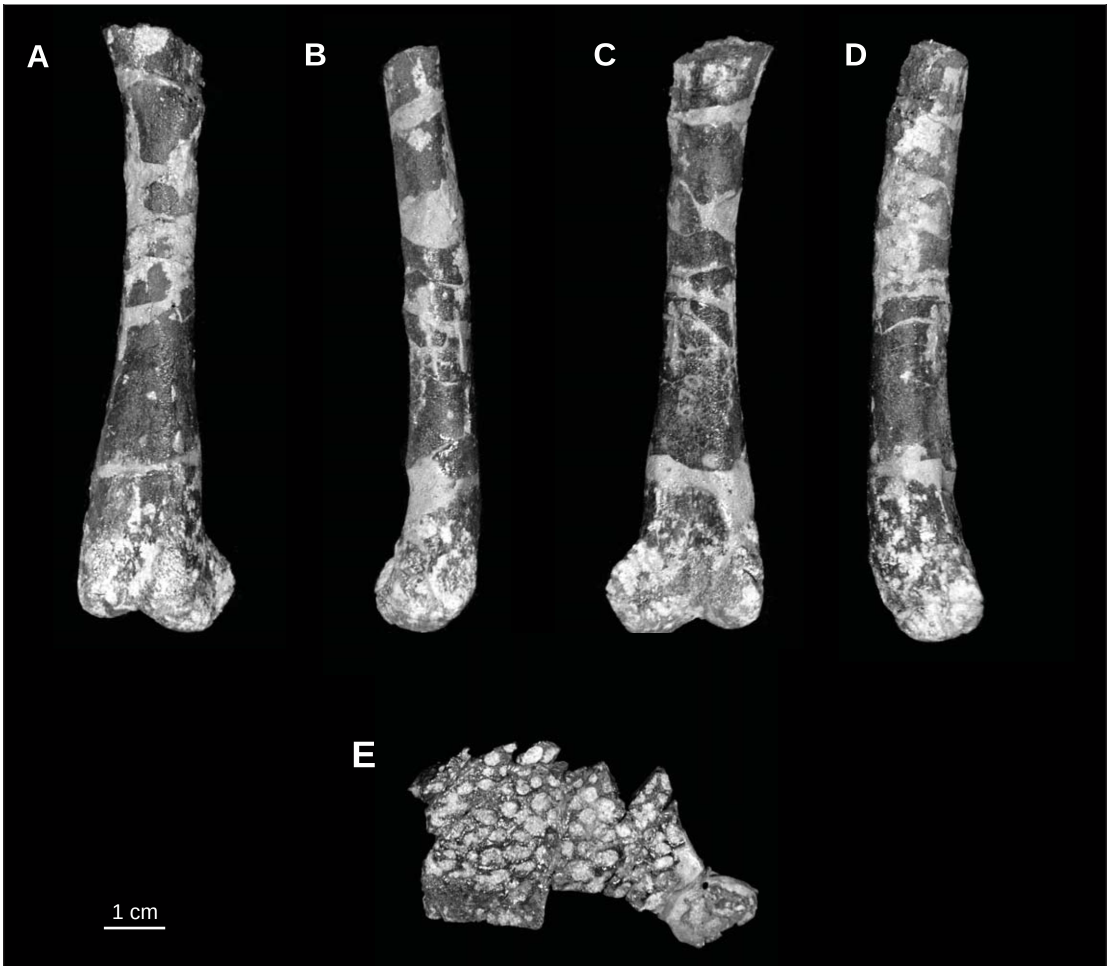

FIG. 17. *Eutretauranosuchus delfsi* AMNH FARB 570 postcranial elements. Partial right femur in **(A)** dorsal, **(B)** medial, **(C)** ventral, and **(D)** lateral views. Partial dorsal osteoderm in **(E)** dorsal view.

The dorsal trunk **osteoderms** are extremely fragmentary (fig. 17E). What little is preserved indicates that the osteoderms have a smooth anterior bar, likely for articulation with the next anterior osteoderm. They are weakly dorsally convex as is typical for most neosuchians. Additionally, the dorsal surfaces of the osteoderms are ornamented with extensive deep irregular pits like that seen in other goniopholidids.

PHYLOGENETIC RELATIONSHIPS

Phylogenetic Analysis

The character set and matrix used in this analysis are adapted from Turner and Sertich (2010) and incorporates character modifications discussed below, AMNH FARB 570, and *Goniopholis baryglyphaeus*. The complete dataset includes 88 crocodylomorph taxa plus *Graci-*

lisuchus stipanicicorum as an outgroup used to root the phylogenetic trees. Taxa and specimens added to the original Turner and Sertich (2010) analysis can be found in appendix 1. This matrix is available upon request from the lead author.

This phylogenetic data set was analyzed with equally weighted parsimony using TNT v. 1.0 (Goloboff, 2003; Goloboff et al., 2008a, 2008b). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using random addition sequences) followed by TBR branch swapping (holding 10 trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994). An additional New Technology Search, also run in TNT v. 1.0, using the "ratchet" and "drift" options (1000 replicates) recovered an identical topology.

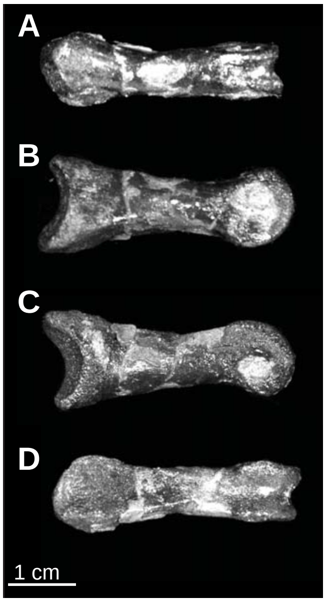

FIG. 18. Phalanx included in AMNH FARB 570 material, herein referred to Theropoda incertae sedis in **(A)** dorsal, **(B)** right lateral, **(C)** left lateral, and **(D)** plantar views.

CHARACTER MODIFICATIONS

CHARACTER 271 (modified from Turner, 2006: character 126 by Pol et al., 2009): Ventral surface of choanal septum: smooth to slightly depressed (0), marked by an acute groove (1), or vomeral choanal septum divided into bilateral laminae (2).

This character, pertaining to the ventral surface of the choanal septum, initially had two states: (0) smooth to slightly depressed and (1) marked by an acute groove. Only *Araripesuchus buitreraensis*, *Araripesuchus gomesii*, and *Araripesuchus patagonicus* were coded with state (1). *Eutretauranosuchus delfsi* and *Amphicotylus lucasii* (AMNH FARB 5782) clearly possess vomeral choanal septa that are divided into separate bilateral laminae. As such the following new state (2) is added to account for this distinction: "vomeral choanal septum divided into bilateral laminae."

CHARACTER 276: Transverse ridge crossing frontal anteromedial to orbits: absent (0), present as ridge (1), prominent anteriorly curved shelf (transverse interorbital crest sensu Andrade and Hornung, 2011) present (2), or anteroposteriorly oriented crest on frontal (3).

This character focuses on the morphology of ridge systems on the dorsal surface of the frontal with the following states: 0, transverse ridge absent; and 1, transverse ridge present. Initially, only the Glen Rose Form exhibited state 1, and all other taxa were coded as 0. We introduce two new states for this character to describe the frontal ridges found throughout Goniopholididae. *Eutretauranosuchus*, *Amphicotylus*, and *Goniopholis* all possess a prominent anteriorly curved prominence on their frontals (transverse interorbital crest of Andrade and Hornung, 2011). We employ the following descriptor for state 2: "prominent anteriorly curved shelf (transverse interorbital crest sensu Andrade and Hornung, 2011) present." In addition to its shape, this crest is positioned between the orbits, distinguishing it from the Glen Rose

Form's preorbital crest. *Sunosuchus junggarensis* was described as bearing a prominent anteroposteriorly running crest on its frontal. Such a crest was employed for state 3: "anteroposteriorly oriented crest on frontal."

Character 284: Exposure of vomer on palate: vomer contributes flattened plate to secondary palate (0), or vomer forms no contribution to secondary palate (1).

In *Simosuchus clarki* (Kley et al., 2010) and *Melanosuchus niger* (Iordansky, 1973) the vomers contribute to the secondary palate, each contributing a flattened palatal process that together form an elliptical plate positioned between the palatal processes of the premaxillae, palatal processes of the maxillae, and the palatal processes of the palatines. By contrast, the vomers in American goniopholidids and certain early crocodylomorphs (e.g., *Orthosuchus*, the Kayenta *Edentosuchus*) are exposed in palatal view only because of the ventral opening of the nasopharyngeal passage.

In the analyses of Buckley et al. (2000) and Turner and Sertich (2010), both *Simosuchus* and *Eutretauranosuchus* were coded as state 0 for this character. However, as discussed above, the exposure of the vomers in these taxa are not homologous. State 1 has been modified to account for the homology of the ventral "exposure" of the vomers in *Amphicotylus* spp., *Calsoyasuchus valliceps*, and *Eutretauranosuchus delfsi* with the vomeral contribution to the nasopharyngeal septum in all mesoeucrocodylians.

Results of Phylogenetic Analysis

The phylogenetic analysis resulted in 38 most parsimonious trees of 1322 steps (CI = 0.285, HI = 0.715, RI = 0.673, RCI = 0.192), found in 52 out of the 1000 replicates (fig. 19). Character support for the nodes present in the most parsimonious reconstructions was calculated using Bremer support (Bremer, 1988, 1994) which evaluates node stability/sensitivity by exploring suboptimal tree solutions in order to determine how many additional steps must be allowed in searching for topologies before the hypothesized clade is no longer recovered. Bremer support was calculated using negative constraints through the use of the BREMER.RUN script supplied with TNT. The dataset was then jackknifed with 1000 replicates and a character removal probability of 20%. Jackknife values are presented as relative frequency differences (GC values).

The strict consensus tree resulting from this analysis yielded a novel topology for the interrelationships of Goniopholididae. In most prior analyses using an earlier version of this dataset (e.g., Pol et al., 2009; Turner and Sertich, 2010) *Goniopholis simus* is sister to a clade of ((*Eutretauranosuchus* + *Amphicotylus*) + (*Calsoyasuchus* + *Sunosuchus*)). Here the clade of *Calsoyasuchus* + *Sunosuchus* is sister to a clade of *Goniopholis baryglyphaeus* + (*Goniopholis simus* + (AMNH FARB 570 + *Amphicotylus*)). The close relationship between European *Goniopholis* to *Amphicotylus* was recovered by Andrade et al. (2011), although these authors suggested a close relationship between *Eutretauranosuchus* and *Sunosuchus junggarensis*.

Goniopholididae has a Bremer support of 4 and a frequency difference of 44. The *Calsoyasuchus* + *Sunosuchus* clade has a Bremer support of 3 and a frequency difference of 38. The *G.*

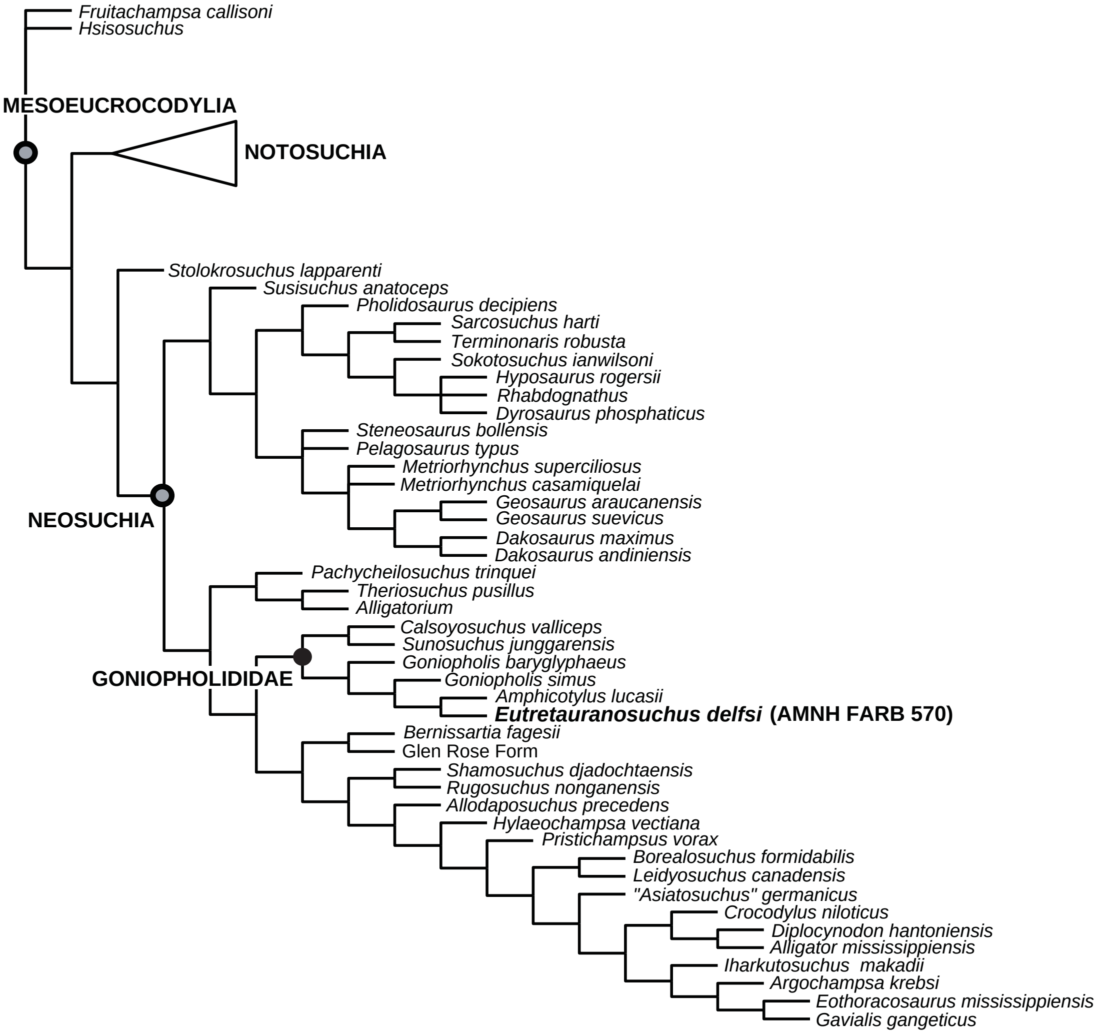

FIG. 19. Phylogenetic placement of *Eutretauranosuchus delfsi* (in bold) shown in a strict consensus of mesoeucrocodylian interrelationships from 38 most parsimonious trees of 1322 steps found in our phylogenetic analysis of 301 characters and 88 taxa. The topology of non-mesoeucrocodylian crocodylomorph interrelationships is identical to that presented in Turner and Sertich (2010). CI = 0.285; rescaled CI = 0.192; homoplasy index = 0.715; RI = 0.6858.

baryglyphaeus + (*Goniopholis simus* + (*Amphicotylus* + *Eutretauranosuchus*) clade has a Bremer support of 1, whereas the *G. simus* + (*Amphicotylus* + *Eutretauranosuchus*) clade has a Bremer support of 1 and a frequency difference of 8. The *Amphicotylus* + *Eutretauranosuchus* clade has a Bremer support of 1 and a frequency difference of 61.

Goniopholididae is supported by five unambiguous synapomorphies: (10.1) palatal processes of the maxillae failing to meet posteriorly; (13.1) nasals not contributing to the posterior border of the nares; (101.0) osteoderms with longitudinal keels on the dorsal surface; (171.0) supraoccipital not exposed on the dorsal skull roof; and (207.1) presence of a smooth-walled depression on the posterolateral surface of the maxilla.

The clade of *Calsoyasuchus* + *Sunosuchus* is supported by one synapomorphy: (7.0) premaxillae do not contact posterior to the incisive foramen.

The newly recognized clade of "*Goniopholis*" *baryglyphaeus* + (*G. simus* + (*Amphicotylus* + *Eutretauranosuchus*) is supported by a single synapomorphy, broadened premaxillae anterior to the nares (5.1). In *Sunosuchus* and *Calsoyasuchus* the premaxillae form a narrow anterior portion to the rostrum. The novel *Goniopholis simus* + (*Amphicotylus* + *Eutretauranosuchus*) clade is supported by a double undulation of the lateral border of the upper tooth row (78.2) and the *Amphicotylus* + *Eutretauranosuchus* clade is supported by a failure of the palatal processes of the palatines to meet along the midline (37.1). As with the topology presented by Andrade et al. (2011), the topology presented here is more stratigraphically consistent than most prior analyses addressing goniopholidid interrelationships, which resolved the Early Cretaceous *Goniopholis simus* as sister to all other goniopholidid taxa including the Early Jurassic *Calsoyasuchus*, suggesting a ~45 million year ghost lineage for *G. simus* (Allen, 2010; Smith et al., 2010; Tykoski et al., 2002).

DISCUSSION

Palatal Evolution within Goniopholididae

Palate Diversity among Goniopholidids: For decades following the discovery of the holotype, *Eutretauranosuchus delfsi* was recognized as a unique taxon in terms of its palatal morphology. Indeed all of the three preserved skulls referred to *Eutretauranosuchus* possess the same ventrally open nasopharyngeal trough (Mook, 1967; Smith et al., 2010). Nevertheless, additional analysis has revealed the presence of multiple goniopholidid taxa with similar palatal morphologies.

The taxonomy of Goniopholididae, including the North American taxa, is poorly understood. Allen (2010) regarded North American taxa referred to *Goniopholis* as paraphyletic with respect to *Goniopholis simus*. Following the usage of Andrade and Hornung (2011) and Andrade et al. (2011), we have referred all North American *Goniopholis* species to *Amphicotylus* but maintain the original species epithets.

AMNH FARB 5782, a skull of *Amphicotylus* (=*Goniopholis*) *lucasii* Cope, 1878, was described in Mook (1942). In the original illustrations by Mook, the secondary palate shows maxillary palatal processes and palatines contacting their opposites along the midline. Reexamination of AMNH FARB 5782 shows that the portion of the "palate" of the fossil posterior to the level of the 11th maxillary alveolus is in fact made up of poorly preserved bone fragments held together by matrix. However, near the level of the 12th maxillary alveolus, two bilateral vacuities are present in the palate closely resembling the condition in *Eutretauranosuchus delfsi* (AMNH FARB 570, CMNH 8028). Separating the two vacuities are slender, paired, bilateral laminae. Thus, we concur with Salisbury et al. (1999) that *A. lucasii* resembled *Eutretauranosuchus* in its palatal architecture. Contra Smith et al. (2010), it is likely that a choanal trough was indeed present in *Amphicotylus lucasii,* as in specimens referred to *Eutretauranosuchus delfsi*. The holotype specimen of *Amphicotylus* (= *Goniopholis*) *stovalli* (OMNH 2392) as figured in Mook (1964) has palatines that definitely do not meet in the midline, exposing bilateral septal laminae. The holotype of *Amphicotylus* (= *Goniopholis*) *felix* (YPM 517) does not preserve a palate.

The Early Jurassic taxon *Calsoyasuchus valliceps* is the earliest known taxon referred to Goniopholididae and indeed Neosuchia (Tykoski et al., 2002). Although the form of its rostrum differs from other American goniopholidids in being more tubular, resembling extant *Crocodylus johnstoni*, *Calsoyasuchus valliceps* has a palate quite similar to AMNH FARB 570 and *Amphicotylus* specimens. The nasopharyngeal canal is open ventrally, so that the primary choana is exposed at its anterior margin. Farther posteriorly, the vomeral septal laminae and ascending processes of the palatines can be seen contributing to the roof and lateral walls of the nasopharyngeal canal. The palate is unpreserved posterior to the suborbital fenestrae, so nothing can be said about the pterygoid contribution to the nasopharyngeal passage.

Taxa referred to *Sunosuchus* exhibit a wide range of palatal morphologies. Wu et al. (1996) reconstructed the palate of *Sunosuchus junggarensis* based on numerous specimens. That taxon is reconstructed with bilateral, ovoid vacuities positioned between the palatal processes of the maxillae and palatal processes of the palatines, near the midline. In *Sunosuchus junggarensis*, the palatal processes of the palatines are reconstructed as making midline contact, as in most mesoeucrocodylians. A virtually identical construction is found in *Sunosuchus miaoi* (Young, 1948; Buffetaut, 1986). In that taxon, a septum is evident between the anterior palatal vacuities. Buffetaut (1986) considered these to be thin laminae derived from the palatal processes of the maxillae, although considering the present observations on AMNH FARB 570 it is more likely that anterior nasopharyngeal septa are derived from the vomers. The Middle Jurassic *Sunosuchus shuhanensis* possesses a ventrally open nasopharyngeal passage (Fu et al., 2005). The high degree of palatal variability and extensive temporal range of attributed *Sunosuchus* species suggest that a review of that genus is also needed.

SECONDARY PALATE EVOLUTION: Ancestral states were examined for four palate characters from Turner and Sertich (2010). A second cladistic analysis was run with the same TNT parameters discussed above, in which "*Goniopholis*" *baryglyphaeus* was excluded from the analyzed trees, because the palate of this taxon could not be coded due to poor preservation. This analysis resulted in 38 most parsimonious trees of 1320 steps (CI = 0.286, HI = 0.714, RI = 0.674, RCI = 0.193). The tree topology for Goniopholididae remains the same as in the primary phylogenetic analysis even with the exclusion of *"G." baryglyphaeus*. The clade of *Sunosuchus* + *Calsoyasuchus* was resolved as sister to a clade of *Goniopholis simus* + (*Amphicotylus lucasii* + AMNH FARB 570).

For all 38 MPTs, ancestral states were studied using parsimony optimization in the Trace Character History module included in Mesquite v. 2.74 (build 550) for Mac OSX (Maddison and Maddison, 2010). The recovered character histories did not differ among topologies (fig. 20) and are discussed below.

Character 10 (fig. 20A): The Goniopholididae nest within neosuchian taxa with unambiguously closed palatal processes of the maxillae. The condition at the root of Goniopholididae and the branch leading to the *Goniopholis* + (*Amphicotylus* + AMNH FARB 570*)* clade is

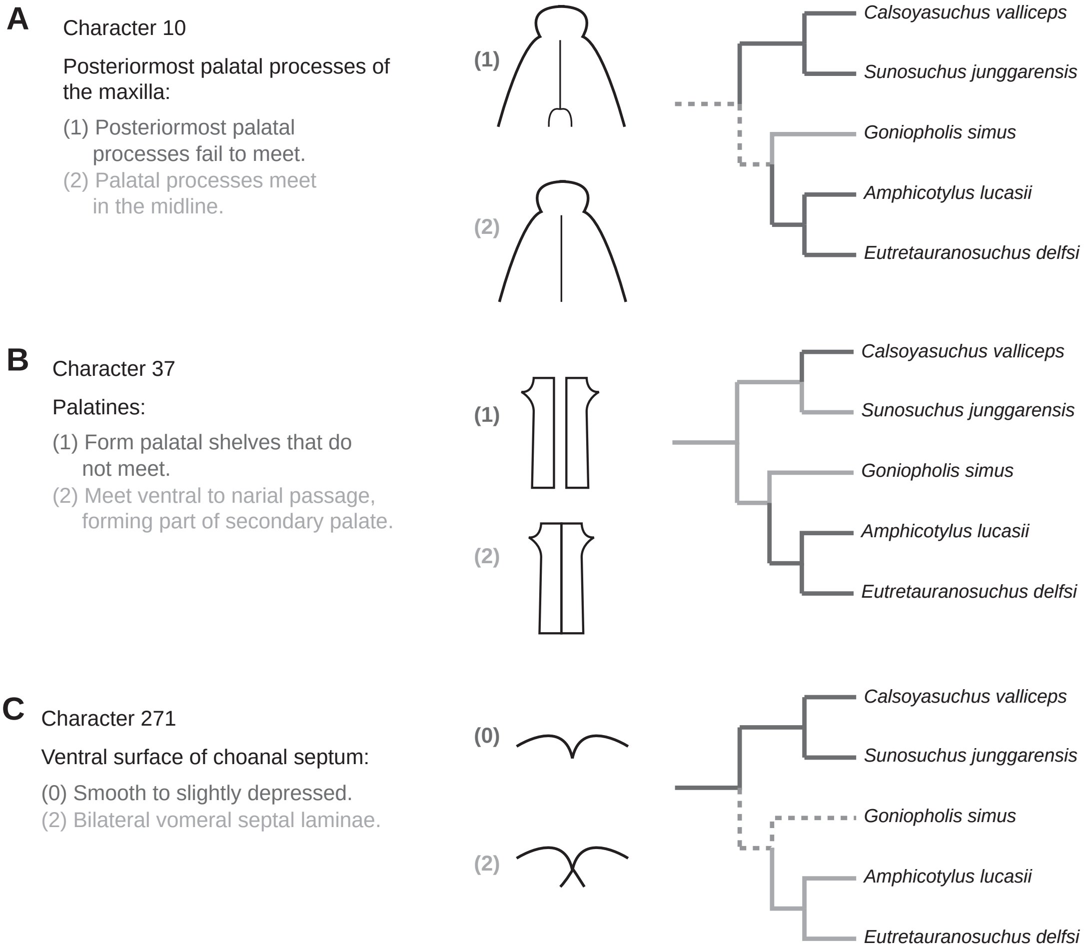

FIG. 20. Tracing of ancestral palatal character states (**A**) 10, (**B**) 37, and (**C**) 271 for Goniopholididae. Each row features a description of the character, a cartoon of relevant character states, and a color-coded phylogeny displaying the distribution of the character within Goniopholididae. The palates illustrated in A and B are drawn in ventral view, whereas the vomeral complex in C is drawn in transverse section. Color-coding on the phylogeny is equivalent to the colors used to indicate relevant states on the cartoons. Dotted lines indicate ambiguous reconstruction.

ambiguous: the palatal processes of the maxillae may or may not have have been in contact. The clades *Sunosuchus junggarensis* + *Calsoyasuchus* and *Amphicotylus* + *Eutretauranosuchus* are unambiguously reconstructed with posteriorly unfused maxillae.

Character 37 (fig. 20B): The presence of entirely unfused palatines is characteristic of *Amphicotylus*, *Calsoyasuchus*, and *Eutretauranosuchus*. Interestingly, this reconstruction resolves an independent derivation of unfused palatines in *Calsoyasuchus* and the branch leading to *Amphicotylus* + AMNH FARB 570. All other nodes within Goniopholididae are resolved as unambiguously bearing fused palatal processes of the palatines.

Character 271 (fig. 20C): Goniopholididae is reconstructed as lacking bilateral vomeral septal laminae. The branch of the clade *Goniopholis* + (*Amphicotylus* + *Eutretauranosuchus*) is ambiguously reconstructed with septal laminae (the complete secondary palate in *Goniopholis* renders observations of the vomers difficult as these skulls are yet to be CT scanned). *Amphicotylus* + AMNH FARB 570 unambiguously possess the laminae.

The sequences of character change suggest a complex pattern of palatal character acquisition within Goniopholididae. In other mesoeucrocodylian groups, (e.g., sphagesaurids, mahajangasuchids), palatal osteology is variable; however, no other mesoeucrocodylian lineage varies so strongly in the construction and reopening of the secondary palate. Considering that a number of goniopholidids have yet to be included in a phylogenetic analyses (e.g., *Sunosuchus shuhanensis*), it is likely that the topology of Goniopholididae and perhaps the pattern of character acquisition will change. Nevertheless, even with the comparatively small number of taxa analyzed here, an unparalleled level of palatal variation is apparent.

The presence of prominent ventrolaterally positioned shelves constructed from the palatines to form a partial bony floor for the choanal passage in AMNH FARB 570 suggests that soft-tissue structures likely floored the nasopharyngeal canal, maintaining the separation between the choanal passage and the oral cavity. Similar evidence and the prominent vaulting of the nasopharyngeal canal roof were cited by Nash (1975) as evidence of a membranous secondary palate in the "protosuchian" *Orthosuchus stormbergi*.

Functional explanations for the evolution of the bony secondary palate in crocodyliforms focus on feeding adaptations (Huxley, 1875). Recent analyses suggest that a bony secondary palate may act to decrease stress during unilateral biting or biting involving the midtooth row (Langston, 1973; Clark and Norell, 1992; Busbey, 1995; Daniel and McHenry, 2001; Turner and Buckley, 2008). Stress reduction throughout the secondary palate has also been associated with the adoption of weaker platyrostral skull morphology by mesoeucrocodylians (Rayfield and Milner, 2008; Turner and Buckley, 2008). However, goniopholidids with *Eutretauranosuchus*-type palates run counter to this pattern. They successfully combined a platyrostral snout with an incomplete bony secondary palate.

Among known mesoeucrocodylian lineages, no other group exhibits the extremes of bony palate variation observed in Goniopholididae. Taxa in the group range from having complete secondary palates to the ventrally opened condition exhibited by AMNH FARB 570. The distinctiveness of Goniopholididae is key to understanding the selective pressures for a complete, bony secondary palate. The extreme plasticity in palatal characters suggests that goniopholidids were unlike other known mesoeucrocodylians in their habits. Taxa with incomplete palates (e.g., *Eutretauranosuchus*, *Calsoyasuchus*) maintained a generalized neosuchian bauplan, suggesting multiple scenarios: (1) open-palate goniopholidids circumvented the functional advantages conferred by a complete bony palate; (2) the palatal morphology in goniopholidids was functionally identical to that in living crocodyliforms; or (3) the open-palate condition conferred an unknown functional advantage, distinct from that in modern crocodyliforms.

Further analysis of goniopholidid palatal diversity, additional taxon sampling for phylogenetic analysis, and reconstruction of goniopholidid feeding mechanics are key to understanding palate evolution among neosuchians. Future modeling of crocodyliform cranial stresses (through FEA) should incorporate modified secondary palates (e.g., open nasopharyngeal passages and anterior palatal fenestration) to examine craniofacial stress responses. Models could be further modified to include the laminar septum, a structure potentially at risk during feeding.

Ontogeny

Multiple features suggest that AMNH FARB 570 had not reached adult somatic maturity. Several sutures on the cranial table are visible (postorbital-squamosal, frontoparietal) and associated teeth are slender and recurved as would be predicted of a young individual (Mook, 1921). Similar features were cited by Joffe (1967) as evidence that the holotype of *Nannosuchus gracilidens*, originally described as a dwarfed crocodyliform, was not an adult. AMNH FARB 570 also lacks a fully fused occipital condyle, where the exoccipital-basioccipital contact is clearly visible on both sides. Similar morphologies are present in both CMNH 8028 and BYU 17628 and were recently cited as evidence that they were not fully grown (Smith et al., 2010). Additionally, the posterior process of the squamosal bears an unsculpted lobe in AMNH FARB 570, a feature associated with subadult status in *Sunosuchus junggarensis* (Wu et al., 1996). The proposal by Smith et al. (2010) that *Eutretauranosuchus* may be a subadult *Amphicotylus* is plausible. However, a confident referral will require a detailed study of the size-related variation within goniopholidid specimens and a comprehensive revision of goniopholidid taxonomy.

CONCLUSIONS

Novel information on the anatomy of goniopholidid crocodyliforms is presented based on AMNH FARB 570, a skull referable to *Eutretauranosuchus delfsi*. In general, the braincase resembles that of other derived mesoeucrocodylians. The position of bones and the placement of nerve foramina suggest a neurovascular organization similar to modern crocodylians (Smith et al., 2008). The anteroposterior elongation of the laterosphenoid and anteroposteriorly elongate and laterally prominent cotylar crest are notable. The bony secondary palate is incompletely formed, with a prominent ventral opening that exposes the nasopharyngeal passage. The septum of the nasopharyngeal passage extends far ventrally. The anterior septum is formed by bilateral vomeral laminae, whereas its posterior portion is formed by a midline lamina of the pterygoid. Such a condition appears to be common to *Eutretauranosuchus* (CMNH 8028, BYU 17628), *Amphicotylus lucasii* (AMNH FARB 5782), and *Amphicotylus stovalli* (OMNH 2392).

Goniopholidids are a prominent mesoeucrocodylian group in the Jurassic and Cretaceous fauna of Laurasia. They have generally been regarded as analogs of modern crocodylians within their respective ecosystems (Foster, 2009). However, the diversity of palatal morphologies in the goniopholidid lineage suggests that this ecologic explanation may be oversimplified. Further revision of goniopholidid taxonomy and phylogeny are needed to resolve detailed complexities of character evolution within the group, and new biomechanical analyses, such as finite element analysis, could examine differences in feeding mechanics among the distinctive goniopholidid cranial morphologies.

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REFERENCES

Allen, E.R. 2010. Phylogenetic assessment of goniopholidid crocodyliforms of the Morrison Formation. Journal of Vertebrate Paleontology 30: 52A.

Andrade, M.B., and J.J. Hornung. 2011. A new look into the periorbital morphology of *Goniopholis* (Mesoeucrocodylia: Neosuchia) and related forms. Journal of Vertebrate Paleontology 31 (2): 352–368.

Andrade, M.B., E. Edmonds, M.J. Benton, R. Schouten. 2011. A new Berriasian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England and a review of the genus. Zoological Journal of the Linnean Society 163: S66–S108.

Averianov, A.O. 2000. *Sunosuchus* sp. (Crocodylomorpha, Goniopholididae) from the Middle Jurassic of Kirghisia. Journal of Vertebrate Paleontology 20: 776–779.

Blainville, H.M. 1853. Lettres sur les crocodiliens vivants et fossils. Mémoires de la Société Linnéenne de Normandie 9: 109–183.

Bremer, K. 1988. The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Bremer, K. 1994. Branch support and tree stability Cladistics 10: 295–304.

Brochu, C.A. 1997. A review of "*Leidyosuchus*" (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. Journal of Vertebrate Paleontology 17 (4): 679–697.

Brochu, C.A. 2006. Osteology and phylogenetic significance of *Eosuchus minor* (Marsh, 1870) new combination, a longirostrine crocodylian from the Late Paleocene of North America. Journal of Paleontology 80 (1): 162–186.

Brochu, C.A., M.L. Bouaré, F. Sissoko, E.M. Roberts, and M.A. O'Leary. 2002. A dyrosaurid crocodyliform braincase from Mali. Journal of Paleontology 76 (6): 1060–1071.

Buckley, G.A., C.A. Brochu, D.W. Krause, and D. Pol. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. Nature 405: 941–944.

Buffetaut, E. 1982. Radiation évolutive, paléoécologie, et biogéographie des crocodiliens mesosuchiens. Mémoires de la Société Géologique de France 142: 1–88.

Buffetaut, E. 1986. Remarks on the anatomy and systematic position of *Sunosuchus miaoi* Young 1948, a mesosuchian crocodilian from the Mesozoic of Gansu, China. Neues Jahrbuch für Geologie und Paläontologie 1986: 641–647.

Busbey, A.B. 1995. The structural consequences of skull flattening in crocodilians. *In* J.J. Thomason (editor), Functional morphology in vertebrate paleontology: 173–192. Cambridge: Cambridge University Press.

Clark, J.M. 1986. Phylogenetic relationships of the crocodylomorpha archosaurs. Ph.D. dissertation, University of Chicago, Chicago, Illinois, 556 pp.

Clark, J.M. 1994. Patterns of evolution in Mesozoic Crocodyliformes. *In* N. Fraser and H.-D. Sues (editors), In the shadow of the dinosaurs: Early Mesozoic tetrapods: 84–97. New York: Cambridge University Press.

Clark, J.M. 2011. A new shartegosuchid crocodyliform from the Upper Jurassic Morrison formation of western Colorado. Zoological Journal of the Linnean Society 163: S152–S172.

Clark, J.M., and M.A. Norell. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. American Museum Novitates 3032: 1–19.

Coddington, J.A., and N. Scharff. 1994. Problems with zero-length branches. Cladistics 10: 415–423.

Colbert, E.H., and C.C. Mook. 1951. The ancestral crocodile *Protosuchus*. Bulletin of the American Museum of Natural History 97 (3): 143–182.

Cope, E.D. 1878. Descriptions of new extinct Vertebrata from the Upper Tertiary and Dakota formations. Bulletin of the United States Geological and Geographical Survey of the territories 4: 379–396.

Cope, E.D. 1888. *Goniopholis* in the Jurassic of Colorado. American Naturalist 22: 1106–1107.

Daniel, W.J.T., and C. McHenry. 2001. Bite force to skull stress correlation—modeling the skull of *Alligator mississippiensis*. *In* G.C. Grigg, F. Seebacher and C.E. Franklin (editors), Crocodilian biology and evolution: 135–143. Chipping Norton, NSW, Australia: Surrey Beatty and Sons.

Edinger, T. 1938. Über Steinkerne von Hirn-und Ohr-Höhlen der Mesosuchier *Goniopholis* und *Pholidosaurus* aus dem Bückeburger Wealden. Acta Zoologica 14: 467–503.

Efimov, M.B. 1988. On the fossil crocodilians from Mongolia and the USSR. Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii 34: 81–90.

Foster, J. 2009. Jurassic West. Bloomington: Indiana University Press.

Fu Q., Ming S., and P. Guang-Zhao. 2005. A new species of *Sunosuchus* from Zigong, Sichuan, China. Vertebrata PalAsiatica 43 (1): 76–83.

Gao, Y. 2001. A new species of *Hsisosuchus* from Dashanpu, Zigong, Sichuan. Vertebrata PalAsiatica 39 (3): 177–184.

Goloboff, P.A., J.S. Farris, and K. Nixon. 2003. TNT: tree analysis using new technologies. Program and documentation available from the authors and online (http://www.zmuc.dk/public/phylogeny).

Goloboff, P., J.S. Farris, and K.C. Nixon. 2008a. TNT: tree analysis using new technology, vers. 1.1 (Willi Hennig Society edition). Program and documentation available online (http://www.zmuc.dk/public/phylogeny/tnt).

Goloboff, P., J.S. Farris, and K.C. Nixon 2008b. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.

Holland, W.J. 1905. A new crocodile from the Jurassic of Wyoming. Annals of the Carnegie Museum of Natural History 3 (3): 431–434.

Holliday, C.M., and L.M. Witmer. 2009. The epipterygoid of crocodyliforms and its significance for orbitotemporal region of eusuchians. Journal of Vertebrate Paleontology 29 (3): 715–733.

Hua, S., and S. Jouve. 2004. A primitive marine gavialoid from the Paleocene of Morocco. Journal of Vertebrate Paleontology 24 (2): 341–350.

Huxley, T.H. 1875. On *Stagonolepis robertsoni*, and the evolution of the Crocodilia. Quarterly Journal of the Geological Society 31: 423–431.

Iordansky, N.N. 1973. The skull of Crocodilia. *In* C. Gans and T.S. Parsons (editors), Biology of the Reptilia 4: 201–262. London: Academic Press.

Irmis, R.B., J.H. Hutchison, J.J.W. Sertich, and A.L. Titus. In press. Crocodyliforms from the Late Cretaceous of Grand Staircase-Escalante National Monument and vicinity, southern Utah, U.S.A. *In* A.L. Titus and M.A. Loewen (editors), The Late Cretaceous in Utah. Bloomington: Indiana University Press.

Joffe, J. 1967. The 'dwarf' crocodiles of the Purbeck Formation, Dorset: a reappraisal. Palaeontology 10 (4): 629–639.

Jouve, S. 2007. Taxonomic revision of the dyrosaurid assemblage (Crocodyliformes; Mesoeucrocodylia) from the Paleocene of the Iullemmeden Basin, West Africa. Journal of Paleontology 81: 163–175.

Jouve, S. 2009. The skull of *Teleosaurus cadomensis* (Crocodylomorpha; Thalattosuchia), and phylogenetic analysis of Thalattosuchia. Journal of Vertebrate Paleontology 29 (1): 88–102.

Jouve, S., M. Iarochène, B. Bouya, and M. Amaghzaz. 2006. A new species of *Dyrosaurus* (Crocodylomorpha, Dyrosauridae) from the early Eocene of Morocco: phylogenetic implications. Zoological Journal of the Linnean Society 148: 603–656.

Kley, N.J., et al. 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *In* D.W. Krause and N.J. Kley (editors), *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagsacar. Society of Vertebrate Paleontology Memoir 10. Journal of Vertebrate Paleontology 30 (6): 13–98.

Langston, W. 1973. The crocodilian skull in historical perspective. *In* C. Gans and T.S. Parsons (editors), Biology of the Reptilia 4: 263–284. London: Academic Press.

Lauprasert, K., G. Cuny, E. Buffetaut, V. Suteethorn, and K. Thirakhupt. 2007. *Siamosuchus phuphokensis*, a new goniopholidid from the Early Cretaceous of northeastern Thailand. Bulletin de la Société Géologique de France 178 (3): 201–216.

Lucas, S.G., and R.M. Sullivan. 2003. A new crocodilian from the Upper Cretaceous San Juan Basin, New Mexico. Neues Jahrbuch für Geologie und Paläontologie 2003 (2): 109–119.

Maddison, W.P., and D.R. Maddison. 2010. Mesquite: a modular system for evolutionary analysis, version 2.5. Available online (http://mesquiteproject.org/mesquite/mesquite.html).

Maish, M.W., A.T. Matzke, and H. Stöhr. 2003. *Sunosuchus* (Archosauria, Crocodyliformes) from the Toutunhe Formation (Middle Jurassic) of the southern Junggar Basin (Xinjiang, NW-China). Geobios 36: 391–400.

Marsh, O.C. 1877. Notice of some new vertebrate fossils. American Journal of Science and Arts 14 (81): 249–256.

Martin, J.E., and E. Buffetaut. 2012. The maxillary depression in Pholidosauridae: an anatomical study. Journal of Vertebrate Paleontology 32 (6): 1332–1446.

Mook, C.C. 1921. Individual and age variations in the skulls of recent Crocodilia. Bulletin of the American Museum of Natural History 44 (7): 51–66.

Mook, C.C. 1925. A revision of the Mesozoic Crocodilia of North America. Bulletin of the American Museum of Natural History 51:319–438.

Mook, C.C. 1942. Skull characters of *Amphicotylus lucasii* Cope. American Museum Novitates 1165: 1–5.

Mook, C.C. 1964. New species of *Goniopholis* from the Morrison of Oklahoma. Oklahoma Geology Notes 24: 283–287.

Mook, C.C. 1967. Preliminary description of a new goniopholid crocodilian. Kirtlandia 2: 1–10.

Nash, D.S. 1968. A crocodile from the Upper Triassic of Lesotho. Journal of Zoology 156: 163–179.

Nash, D.S. 1975. The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho. Annals of the South African Museum 67: 227–329.

Nesbitt, S.J., A.H. Turner, and J.C. Weinbaum. In press. A survey of skeletal elements in the orbit of Pseudosuchia and the origin of the crocodylian palpebral. Earth and Environmental Transactions of the Royal Society of Edinburgh.

Ösi, A. 2008. Cranial osteology of *Iharkutosuchus makadii*, a Late Cretaceous basal eusuchian crocodyliform from Hungary. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 248: 279–299.

Owen, R. 1842. Report on British fossil reptiles, part II. Report of the British Association for the Advancement of Science 11: 60–204.

Owen, R. 1878. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement no. VIII. Crocodilia (*Goniopholis*, *Petrosuchus*, and *Suchosaurus*). Monograph of the Paleontographical Society 32 (149): 1–15, pls. 1–6.

Pol, D., and M.A. Norell. 2004a. A new crocodyliform from Zos Canyon, Mongolia. American Museum Novitates 3445: 1–36.

Pol, D., and M.A. Norell. 2004b. A new gobiosuchid crocodyliform taxon from the Cretaceous of Mongolia. American Museum Novitates 3458: 1–31.

Pol, D., S. Ji, J.M. Clark, and L.M. Chiappe. 2004. Basal crocodyliforms from the Lower Cretaceous Tugulu Group (Xinjiang, China), and the phylogenetic position of *Edentosuchus*. Cretaceous Research 25: 603–622.

Pol, D., A.H. Turner, and M. Norell. 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. Bulletin of the American Museum of Natural History 324: 1–103.

Rayfield, E.J., and A.C. Milner. 2008. Establishing a framework for archosaur cranial mechanics. Paleobiology 34 (4): 494–515.

Romer, A.S. 1956. The osteology of the Reptilia. Chicago: University of Chicago Press, 772 pp.

Salisbury, S.W., and D. Naish. 2011. 24. Crocodilians. *In* D.J. Batten (editor), English Wealden fossils: 305–369. Palaeontological Association Field Guide to Fossils 14. London: Palaeontological Assocation.

Salisbury, S.W., P.M.A. Willis, S. Peitz, and P.M. Sander. 1999. The crocodilian *Goniopholis simus* from the Lower Cretaceous of North-Western Germany. Special Papers in Palaeontology 60: 121–148.

Schwarz, D. 2002. A new species of *Goniopholis* from the Upper Jurassic of Portugal. Palaeontology 45 (1): 185–208.

Schwarz, D., and S.W. Salisbury. 2005. A new species of *Theriosuchus* (Atoposauridae, Crocodylomorpha) from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. Geobios 38: 779–802.

Sereno, P.C., and H.C.E. Larsson. 2009. Cretaceous crocodyliforms from the Sahara. Zookeys 28: 1–143.

Smith, D.K., D. Dufeau, K.R. Sanders, R. Ridgley, and L. Witmer. 2008. The cranial endocast of *Eutretauranosuchus delfsi* (Crocodyliformes, Goniopholididae) and its relationship to other cephalic spaces. Journal of Vertebrate Paleontology 28 (3): 144A.

Smith, D.K., E.R. Allen, R.K. Sanders, and K.L. Stadtman. 2010. A new specimen of *Eutretauranosuchus* (Crocodyliformes, Gonipholididae) from Dry Mesa, Colorado. Journal of Vertebrate Paleontology 30 (5): 1466–1477.

Turner, A.H. 2006. Osteology and phylogeny of a new species of *Araripesuchus* (Crocodyliformes: Mesoeucrocodylia) from the Late Cretaceous of Madagascar. Historical Biology 18: 255–369.

Turner, A.H., and G.A. Buckley. 2008. *Mahajangasuchus insignis* (Crocodyliformes: Mesoeucrocodylia) cranial anatomy and new data on the origin of the eusuchian-style palate. Journal of Vertebrate Paleontology 28 (2): 382–408.

Turner, A.H., and J.J.W. Sertich. 2010. Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *In* D.W. Krause and N.J. Kley (editors), *Simosuchus* *clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagsacar. Society of Vertebrate Paleontology Memoir 10. Journal of Vertebrate Paleontology 30 (6): 177–236.

Tykoski, R.S., T.B. Rowe, R.A. Ketcham, and M.W. Colbert. 2002. *Calsoyasuchus valliceps*, a new crocodyliform from the Early Jurassic Kayenta Formation of Arizona. Journal of Vertebrate Paleontology 22 (3): 593–611.

Walker, A.D. 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. Philosophical Transactions of the Royal Society B 257: 323–372.

Willis, P.M.A. 1993. *Trilophosuchus rackhami* gen. et sp. nov., a new crocodilian from the early Miocene limestones of Riversleigh, northwestern Queensland. Journal of Vertebrate Paleontology 13 (1): 90–98.

Wiman, C. 1932. *Goniopholis kirtlandicus* n. sp. aus der oberen Kreide in New Mexico. Bulletin of the Geological Institution of the University of Uppsala 23: 181–189.

Wu, X.-c., D.B. Brinkman, and A.P. Russell. 1996. *Sunosuchus junggarensis* sp. nov. (Archosauria: Crocodyliformes) from the Upper Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 33: 606–630.

Wu, X.-c., A.P. Russell, and D.B. Brinkman. 2001. A review of *Leidyosuchus canadensis* Lambe, 1907 (Archosauria: Crocodyliformes) and an assessment of cranial variation based on new material. Canadian Journal of Earth Sciences 38: 1665–1687.

Young, C. 1948. Fossil crocodiles of China, with notes on dinosaurian remains associated with the Kansu crocodiles. Bulletin of the Geological Society of China 28 (3–4): 255–286.

APPENDIX 1

ADDED TAXA AND NEW SPECIMENS USED IN PHYLOGENETIC ANALYSIS

The following represent taxonomic additions to and new literature and specimens consulted for this phylogenetic analysis. For all other taxa, see the taxon list from Turner and Sertich (2010).

*Amphicotylus lucasii (*coded as *"Goniopholis" stovalli* in Turner and Sertich, 2010)—Mook, 1942; AMNH 5782.

Calsoyasuchus valliceps—Tykoski et al., 2002; TMM 43631-1.

Eutretauranosuchus delfsi—Mook, 1967; Clark, 1986, 1994; AMNH FARB 570.

Goniopholis baryglyphaeus—Schwarz, 2002.

APPENDIX 2

ANATOMICAL ABBREVIATIONS

IV	foramen for cranial nerve IV
V	foramen for cranial nerve V
VI	foramen for cranial nerve VI
IX	foramen for cranial nerve IX

X	foramen for cranial nerve X
XI	foramen for cranial nerve XI
XII	foramen for cranial nerve XII
ang	angular
asc	anterior semicircular canal
bo	basioccipital
bt	basal tubera
cac	canal for the carotid atery
cqc	cranioquadrate canal
cqc b	cranioquadrate canal border
den	dentary
ec	ectopterygoid
fm	foramen magnum
fr	frontal
fr dp	descending process of the frontal
fr fl	facial lamina of the frontal
hyp f	hypophyseal fossa
jec	junction of the eustachian canals
ju	jugal
la	lacrimal
leu	lateral eustachian canal
lhc	lateral hemicondyle
ls	laterosphenoid
ls b	laterosphenoid bridge
ls acc	laterosphenoid accessory foramen
ls cc	laterosphenoid cotylar crest
ls cp	laterosphenoid capitate process
ls s	laterosphenoid sinus
mac	mastoid air cells
meu	median eustachian foramen
mhc	medial quadrate hemicondyle
mx	maxilla
mx d	maxillary depression
mx pp	palatal process of the maxilla
na	nasal
oa	otic aperture
oto	otoccipital
pa	parietal
pa h	parietal “hornlet”
pal	palatine
pal ap	ascending process of the palatine

pal pp	palatal process of the palatine
pbs	parabasisphenoid
pbs r	parabasisphenoid rostrum
pf	prefrontal
pf dp	descending process of the prefrontal (prefrontal pillar)
pf fl	prefrontal facial lamina
plp	palpebral
pmx c	contact for premaxilla
po	postorbital
pop	paroccipital process
pro	prootic
psc	posterior semicircular canal
pt	pterygoid
pt ap	anterior process of the pterygoid
pt ap sl	septal contribution of the anterior process of the pterygoid
pt s	pterygoid choanal septum
pt tp	transverse process of the pterygoid
qj	quadratojugal
qu	quadrate
qu adp	anterodorsal process of the quadrate
qu dph	dorsal primary head of the quadrate
so	supraoccipital
sof	suborbital fenestra
sq	squamosal
sq t	squamosal tuberosity
stf	supratemporal fenestra
sur	surangular
tic	transverse interorbital crest
vo	vomer
vo pp	palatal process of the vomer
vo sl	septal lamina of the vomer

APPENDIX 3

Institutional Acronyms

AMNH FARB	American Museum of Natural History; Fossil Amphibians, Reptiles, and Birds Collection (New York, NY)
AMNH R	American Museum of Natural History; Herpetological Collection (New York, NY)

BYU	Brigham Young University (Provo, Utah)
CAMNH	Carnegie Museum of Natural History (Pittsburgh, PA)
CMNH	Cleveland Museum of Natural History (Cleveland, OH)
IPB	Institute of Natural Sciences (Brussels, Belgium)
NHMUK	Museum of Natural History of the United Kingdom (London, U.K.)
OMNH	Oklahoma Museum of Natural History (Norman, OK)
TMM	Texas Memorial Museum (Austin, TX)
YPM	Yale Peabody Museum of Natural History (New Haven, CT)

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