A NEW LATE CRETACEOUS GAVIALOID CROCODYLIAN FROM EASTERN NORTH AMERICA AND THE PHYLOGENETIC RELATIONSHIPS OF THORACOSAURS

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ABSTRACT—*Eothoracosaurus mississippiensis*, gen. et sp. nov., is based on a skull and partial skeleton from the Upper Cretaceous (early Maastrichtian) Ripley Formation of Mississippi. Less complete material from the late Campanian or early Maastrichtian of western Tennessee is referred to this taxon. It can be distinguished from late Maastrichtian *Thoracosaurus neocesariensis* on the basis of a wider distance between the supratemporal fenestrae, a long anterior frontal process, and closer apposition of the third and fourth dentary alveoli. Longirostrine crocodylian remains from the later Maastrichtian and earliest Paleocene of New Jersey pertain to a single species (*Thoracosaurus neocesariensis*), as do remains from the early Paleocene of France and Sweden (*Thoracosaurus macrorhynchus*). The basisphenoid in these animals is still an anteroposteriorly thin lamina wedged between the basioccipital and pterygoid, reflecting the "verticalized" condition seen in extant non-gavialoid crocodylians. At least some late Paleocene occurrences from New Jersey, Maryland, and Virginia can be referred to *Thecachampsoides minor* (Marsh, 1870), and a second larger gavialoid may also be present in these units. North American "thoracosaurs" lacked antorbital fenestrae. "Thoracosaurinae" are a paraphyletic grade at the base of Gavialoidea, with *Thecachampsoides* being closer to *Gavialis* than are *Thoracosaurus* or *Eothoracosaurus*. Prior referral of "thoracosaurs" to Tomistominae reflects a typological approach to taxonomy, with longirostrine crocodylians maintaining plesiomorphic rostral states being regarded as tomistomines.

Some of the earliest reported fossil crocodyliforms in the scientific literature had unusually long, slender snouts (e.g., Cuvier, 1824; Geoffroy, 1825; Buckland, 1836)—a condition sometimes viewed as an adaptation for catching fish (Pooley, 1989), though with less ecological justification than often thought (Webb et al., 1983). These fossils inspired some of the most detailed morphological descriptions ever published on the archosaurian skeleton (e.g., D'Alton and Burmeister, 1854) and have played a central role in the ongoing debate over the relationships of extant longirostrine crocodylians (e.g., Antunes, 1964; Hecht and Malone, 1972; Tarsitano et al., 1989; Hass et al., 1992; Brochu, 1997; Harshman et al., 2003; Gatesy et al., 2003; Hua and Jouve, 2004). But despite two centuries of scholarly work, the taxonomy of these crocodylians remains shrouded in ambiguity.

Comparisons were inevitably drawn between fossil longirostrine crocodyliforms and the two most derived modern longirostrine examples, *Gavialis gangeticus* (the Indian gharial) and *Tomistoma schlegelii* (the Indonesian false gharial). Some groups, including the thalattosuchians, pholidosaurids, and dyrosaurids, are now thought to lie outside Crocodylia, though their relationships to each other are a matter of controversy (Buffetaut, 1982a; Clark, 1994; Hua and Buffetaut, 1997; Wu et al., 2001a; Sereno et al., 2001). But eusuchians with narrow rostra, first appearing in the Late Cretaceous and persisting throughout the Cenozoic, were eventually divided into two categories based on similarities with *Gavialis* or *Tomistoma*.

The group including *Gavialis* was based on derived features related to the extremely modified snout—in particular, the presence of enlarged tubera on the basioccipital ventral to the occipital condyle and the separation of the premaxillae and nasals on the dorsal surface of the rostrum (e.g., Kälin, 1955; Hecht and Malone, 1972; Langston, 1973; Steel, 1973; Buffetaut, 1982b). It was also characterized by features that looked primitive in comparison with other living crocodylians, such as an anteroposteriorly broad basisphenoid on the ventral external surface of the braincase (Tarsitano et al., 1989). The earliest known fossil gavialoids were thought to be of late Eocene age or later (Langston, 1965; Hecht and Malone, 1972; Buffetaut, 1982b), but the combination of primitive braincase morphology and extremely derived snout suggested a long history for the group, possibly even as far back as the Jurassic, after it diverged from the lineage leading to all other living crocodylians (Kälin, 1931, 1955; Mook, 1934; Tarsitano et al., 1989).

The tomistomine category was also based on a mixture of primitive and derived characteristics, but in this case, the derived characters seemed to ally it with other crocodylians (especially the crocodylids) and the primitive features reflected a less highly modified rostrum. The nasals and premaxillae were still in contact and the basioccipital lacked enlarged tubera, but the snout was still long and slender. The basisphenoid was visible posteroventrally as a thin slip between the basioccipital and fused pterygoids, the so-called "verticalized" condition thought to characterize non-gavialoid crocodylians (Tarsitano, 1985; Tarsitano et al., 1989).

The oldest fossils putatively allied with *Tomistoma* were the Late Cretaceous and Early Tertiary "thoracosaurs." These are commonly found in marginal marine or shallow marine deposits (e.g., Gallagher, 1993; Mulder, 1997; Zarski et al., 1998; Erickson, 1998). Thoracosaurs were regarded as a distinct family by Cope (1871) and a subfamily by Nopcsa (1928). Although phylogenetic relationships were imprecisely expressed throughout the 1800's, by the late 1900's, a close relationship to *Tomistoma* was generally accepted (or at least implied) in the literature. Rodney Steel's compendium (Steel, 1973), for example, included *Tomistoma* within Thoracosaurinae Nopcsa, 1928.

The largest sample of thoracosaurs comes from the Late Cretaceous and Paleocene of the eastern United States, where they are found in coastal settings in association with marine invertebrates and reptiles (e.g., Troxell, 1925; Gallagher et al., 1986; Schwimmer, 1986; Erickson, 1998). Especially large collections have been built from the Navesink, Hornerstown, and Vincentown formations of New Jersey (Troxell, 1925; Mook, 1931; Miller, 1955; Gallagher et al., 1986; Norell and Storrs, 1986; Gallagher, 1993), but material from these units is typically fragmentary and prone to pyritization. Seventeen species were named from this region between 1842 and 1925, and several are based on fragments of bone and teeth. These fossils are now widely thought to reflect a single species, for which the name *Thoracosaurus neocesariensis* (de Kay, 1842) has priority (Carpenter, 1983).

The supraspecific arrangement of these forms was controversial, though it became customary to divide them into two gen-

era—*Thoracosaurus* and *Holopsisuchus*. *Thoracosaurus* was initially thought to bear openings between the lacrimals and prefrontals, possibly homologous with antorbital fenestrae, and *Holopsisuchus* was thought to lack them (Steel, 1973). Some view the "antorbital fenestrae" as postmortem damage (Carpenter, 1983), but others regard them as natural features (Laurent et al., 2000).

A nearly complete thoracosaur skull from the lower Maastrichtian Ripley Formation of Mississippi affords a unique opportunity to restore the cranial structure of a member of this group. It is more complete than any single specimen from New Jersey sites, most of which are geologically younger. This specimen was described by Carpenter (1983), who referred it to *Thoracosaurus neocesariensis*. He concluded that *T. neocesariensis* was the only thoracosaur known from North America, and that it was more closely related to *Tomistoma* than to *Gavialis*.

A closer examination reveals important differences from other thoracosaurs, including *T. neocesariensis*. Comparison of this specimen, as well as conspecific material from Tennessee, with other thoracosaur specimens from North America and Europe sheds light on numerous conflicts in crocodylian systematics, including the morphology of the ancestral gavialoid braincase, the contrast between clade-based classifications of living crocodylians and grade-based systems formerly used for fossils, and the nature of the thoracosaur "antorbital fenestra."

This paper redescribes the fossil and discuss its importance for understanding early gavialoid phylogeny. It is hoped that the material described herein will encourage further investigations into the long fossil record of Gavialoidea and the phylogenetic relationships of slender-snouted crocodylians from around the world.

The supraspecific taxonomy applied in this paper follows the phylogenetic nomenclatural system for Crocodylia first established by Clark (1986) as reviewed by Brochu (2003). Crocodylia are a node-based group based on the last common ancestor of *Alligator mississippiensis*, *Gavialis gangeticus*, and *Crocodylus niloticus* and all of its descendents. The definition published by Sereno et al. (2001) is a junior synonym; in any case, the definition they prefer (based specifically on the last common ancestor of *C. niloticus* and *G. gangeticus*) would exclude alligatorids from Crocodylia if one accepts trees supported by molecular data. The term Gavialoidea is a stem-based group name based on *Gavialis gangeticus* and any crocodylian closer to it than to *Alligator mississippiensis* or *Crocodylus niloticus*. The last common ancestor of alligatorids and crocodylids defines Brevirostres, the node-based extant sister group of *Gavialis gangeticus*. Traditional Linnean ranks are no longer used.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **ANSP**, Academy of Natural Sciences, Philadelphia; **FMNH**, Field Museum, Chicago; **LO**, Geological Institute, University of Lund, Sweden; **MNHN**, Museum National d'Histoire Naturelle, Paris; **MSU**, Dunn-Seiler Museum, Mississippi State University, Starkville; **NJSM**, New Jersey State Museum, Trenton; **PPM**, Pink Palace Museum, Memphis, Tennessee; **TMM**, Texas Memorial Museum, Austin; **USNM**, United States National Museum of Natural History, Washington, D.C.; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

EUSUCHIA Huxley, 1875
CROCODYLIA Gmelin, 1789
GAVIALOIDEA Hay, 1930
EOTHORACOSAURUS MISSISSIPPIENSIS gen. et sp. nov.

Thoracosaurus neocesariensis (de Kay, 1842) (in part).

Holotype—MSU 3293, nearly complete skull and lower jaw with associated postcranial remains (Figs. 1 and 2) as detailed in Carpenter (1983).

Referred Material—PPM p2001.1.260, posterior portion of skull including braincase (Fig. 3); AMNH 3841, posteriormost portion of skull and incompletely prepared anterior tip of lower jaw (Figs. 4, 5A–D). Isolated postcranial remains at the AMNH (a tibia, two vertebrae, and three partial osteoderms) may also pertain to this taxon, but this is not certain. Likewise, a partial mandible and single caudal vertebra from the Ripley Formation of Georgia (USNM 5783, Fig. 5E, F) are from a slender-snouted eusuchian and may be referable to *Eothoracosaurus*, but diagnostic features are not preserved.

Etymology—Eos, "dawn," in reference to its lower stratigraphic position and more basal phylogenetic position relative to *Thoracosaurus*; mississippiensis, in reference to the state of Mississippi where the holotype was found and to the Mississippi Embayment that evidently included part of the taxon's range.

Horizon—The holotype is from the Ripley Formation of Mississippi. Outcrops of this formation in Mississippi, Alabama, and Georgia are of early Maastrichtian age (Sohl et al., 1991). Referred specimens from western Tennessee are from the Coon Creek Tongue, which is either a formation (e.g., Dunagan and Gibson, 1993; Gibson and Dunagan, 2003) or a member of the Ripley Formation (Wade, 1926; Dockery and Bandel, 2003). Part of the Coon Creek may be of late Campanian age (Cobban and Kennedy, 1993).

Locality—Holotype: Oktibbeha County, Mississippi; specific locality information available at Dunn-Seiler Museum, Mississippi State University. PPM p2001.1.260: Sawmill Site Locality, Decatur County, Tennessee; specific locality information available at Pink Palace Museum, Memphis. Collected by L. Harrell, 1999. AMNH 3841: according to specimen label, "along Coon Cr[eek], Tenn[essee]." The material, collected by A. S. Duckworth in 1931, was acquired from Vanderbilt University. Coon Creek is in northeastern McNairy County, and the specimen is likely to have come from the Coon Creek Tongue. Postcranial material at the AMNH came with a label reading, "This material was sent to Dr. Mook from Dept. of Geology, Vanderbilt Univ., Nashville, Tenn. Wrapped in 1930 newspaper." This argues against direct association with AMNH 3841, which was collected at least one year later, but the remains appear to have come from the same area as AMNH 3841 and suggest an animal of similar size. This sample also includes isolated fish bones, rib fragments, and some amphicoelous vertebrae possibly referable to a dyrosaurid such as *Hyposaurus*.

Diagnosis—Gavialoid crocodylian in which the third and fourth dentary alveoli approach each other closely and are nearly confluent; broad skull table between supratemporal fenestrae, with interfenestral bar approaching half the width of an individual fenestra; extension of nasals between premaxillae for at least one alveolus length; very long rostral process of frontal extending beyond anterior limit of lacrimals to approximately the level of the fourteenth maxillary alveolus; long ventral anterior process of surangular; external mandibular fenestra very small, if present at all.

Description—The skull is largely complete, missing the right lower temporal bar, the right pterygoid wing, and portions of the bones anterior to the orbits. A mass of pyrite coats the surface of the snout immediately anterior to where missing bone has been replaced by plaster (Fig. 1). Sutures are indistinct and difficult to trace.

The premaxillae completely surround the dorsally opening external naris and extend posteriorly to the level of the 4th maxillary alveolus in dorsal view. The ventral surface of each premaxilla is imperfectly preserved, and the margins of the incisive foramen are missing. Each premaxilla bears five ventrally opening alveoli, the fifth being smaller than the other four, which are roughly equal in size to each other. Together, the premaxillae form a wedge on the palatal surface extending back to the level of the 3rd maxillary alveolus.
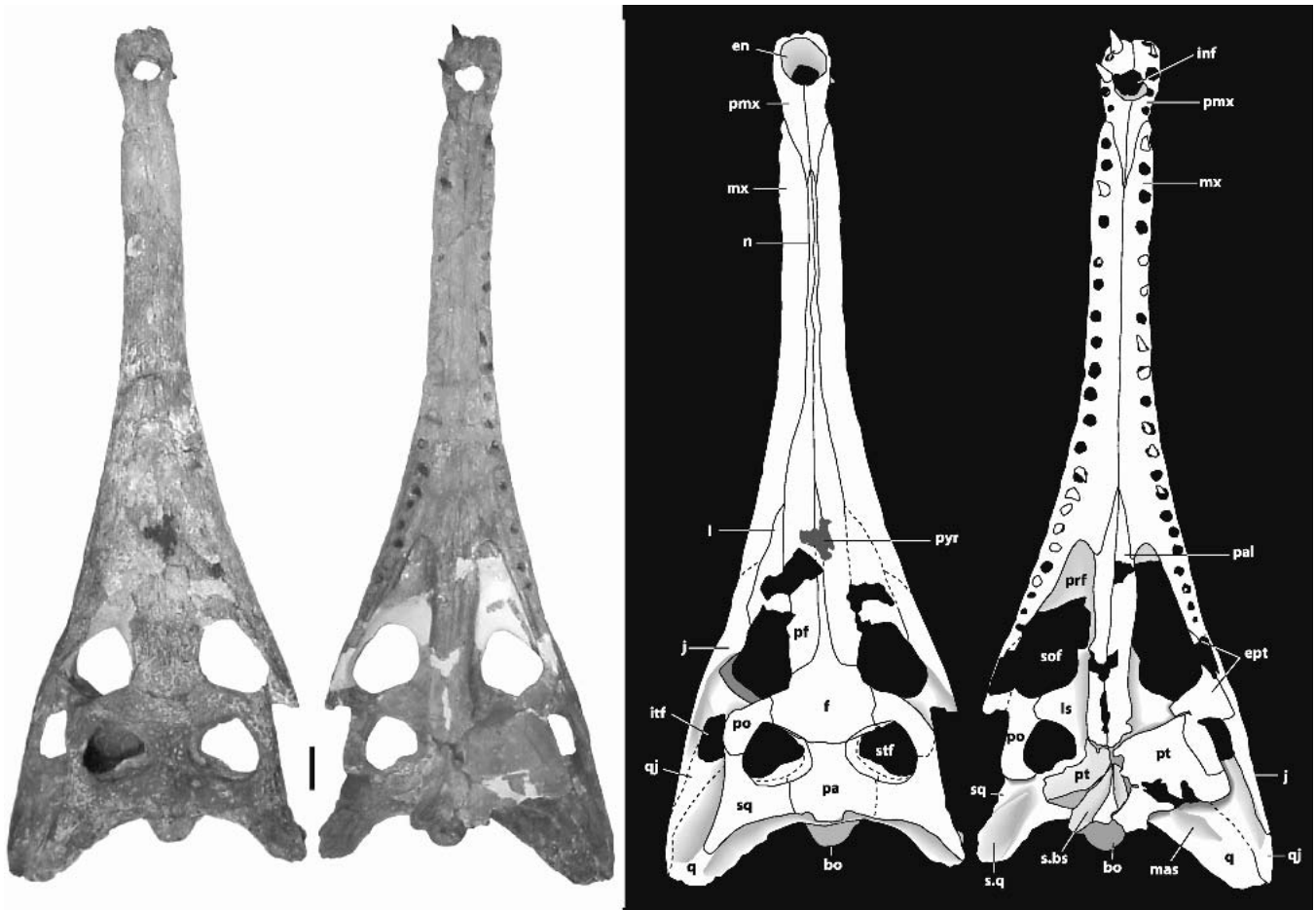
FIGURE 1.   MSU 3293, holotype, *Eothoracosaurus mississippiensis*. Skull in **A** and **C**, dorsal and **B** and **D**, ventral view. Scale equals 5 cm. **Abbreviations**: **bo**, basioccipital; **en**, external naris; **ept**, ectopterygoid; **f**, frontal; **inf**, incisive foramen; **itf**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **ls**, laterosphenoid; **mas**, muscle attachment scar; **mx**, maxilla; **n**, nasal; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **pt**, pterygoid; **pyr**, mass of pyrite; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal; **stf**, supratemporal fenestra; **s.bs**, sutural surface on basioccipital for basisphenoid; **s.q**, sutural surface on squamosal for quadrate.

The nasals extend back from the premaxillae as a pair of thin plates along the midline. They contact the premaxillae (contra Carpenter, 1983) and form a shallow wedge passing between them for approximately 2 cm. The nasals have parallel lateral margins to approximately the level of the 11th maxillary alveolus, after which they expand laterally as they approach the orbits. Contact with other rostral bones is indistinct, and the posteriormost extent of the nasals cannot be seen, but the nasals did not extend as far back as the orbits. The frontal seems to have extended between them for a considerable portion of the rostrum (see below).

The maxillae form most of the tubular snout and contact the premaxillae anteromedially, the nasals medially, the lacrimals and (presumably) the jugals posteromedially, and the palatines and ectopterygoids on the ventral surface. The palatal surface is flat, and other than modest lateral notches between the maxillae and premaxillae, there are no reentrants between any of the alveoli. Although the skull as a whole expands laterally toward the orbits, the maxillae themselves retain a uniform mediolateral width throughout their length in dorsal view, and most rostral expansion is the result of the expanded nasals. The maxillae do widen mediolaterally on the palatal surface.

The number of alveoli in each maxilla is ambiguous; the left maxilla preserves 21, but the right preserves 21 complete alveoli and part of a 22nd at the back of the toothrow. The first alveolus

is smaller than those behind it, and the last seven alveoli become progressively smaller toward the end of the maxillary toothrow, but no other size differences are apparent between alveoli. The alveoli themselves are imperfectly preserved, and precise measurements cannot be taken. Spacing between alveoli is generally uniform, although a diastema separates the fourth and fifth alveoli. Some alveoli retain slender, conical teeth with fluted surfaces and bearing anterior and posterior unserrated carinae.

Sutural contacts with the jugals are not readily seen, except for the jugal-quadratojugal suture within the temporal fossa on the left side and portions of the jugal-lacrimal sutures on both sides. The jugals form the lateralmost part of the orbital margin and presumably contributed to the robust postorbital bars. The postorbital bars merge gradually with the temporal bars laterally, with only a modest sulcus on each temporal bar's dorsal surface extending back beneath the infratemporal fenestrae.

The left lacrimal is a long, triangular bone in dorsal view, forming the anterolateral corners of the left orbit. It contacts the left prefrontal posteromedially, the left nasal anteromedially, and the left maxillae and jugal laterally. The outline of the right lacrimal cannot be traced, and the lacrimal foramen is not preserved on either side.

The prefrontals are imperfectly exposed. They form the anteromedial corners of the orbits and were presumably triangular in outline. Their anteriormost extent is not visible on either side,
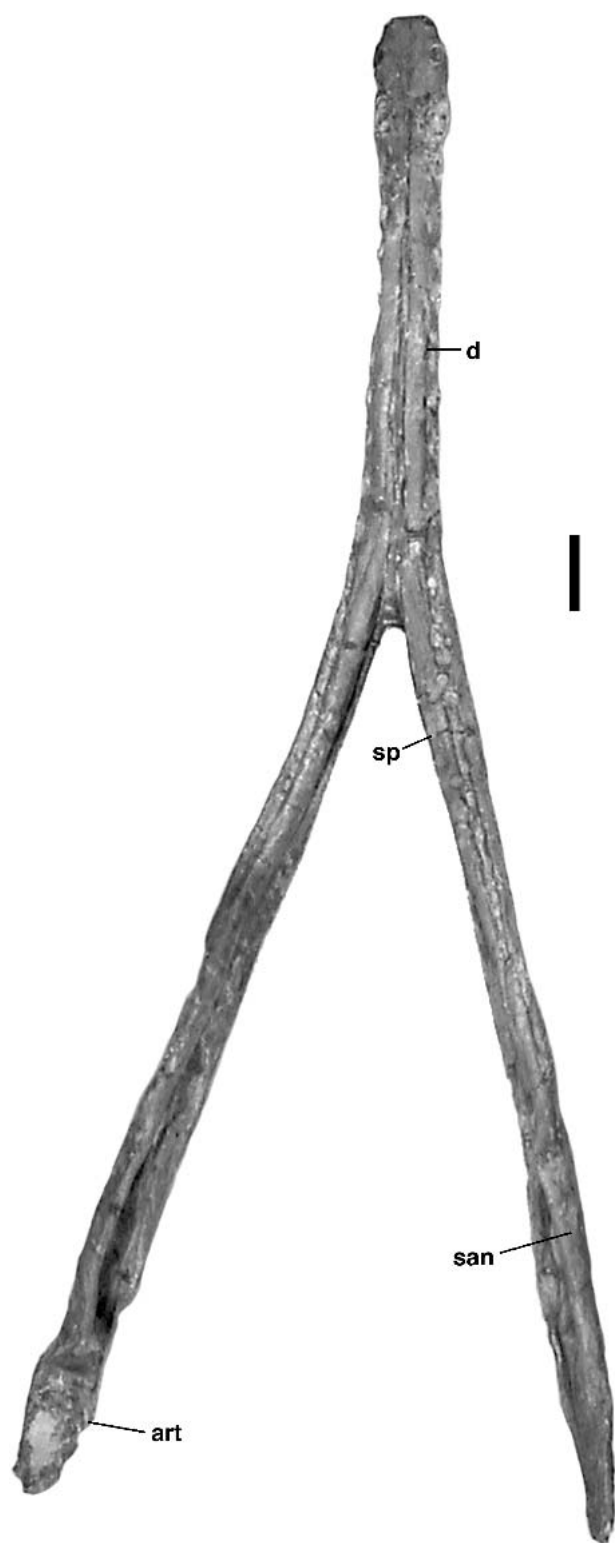
FIGURE 2. MSU 3293, holotype, *Eothoracosaurus mississippiensis*. Mandible in dorsal view. Scale equals 5 cm. **Abbreviations**: **art**, articular; **d**, dentary; **san**, surangular; **sp**, splenial.

The frontal forms the posteromedial corner of each orbit and contacts the prefrontals and nasals anterolaterally, the postorbitals posterolaterally, and the parietal posteriorly. It probably made contact with the laterosphenoids ventrally, but this is not visible. The frontoparietal suture passes deeply through each supratemporal fenestra, and parietal-postorbital contact was minimal. The dorsal surface of the frontal was concave, but only barely so, and the orbital margins were not upturned.

The frontal appears to have extended further forward relative to the nasals than in other gavialoids. The anterior frontal process is very slender and clearly passes anteriorly toward a plaster-filled break in the dorsal surface of the skull and a mass of pyrite on the midline of the skull roof. A pair of sutures between the nasals converges anterior to the pyrite mass. These sutures are here interpreted as the contact between nasals and anterior frontal process. This results in an anterior frontal process twice as long as the main body of the frontal, in contrast with *Thoracosaurus*, in which the process is approximately as long as the body. It is shorter still in other gavialoids.

The slender palatines form the medial margins of each suborbital fenestra and extend anteriorly as an acute wedge between the maxillae to the level of the 13th maxillary alveoli. They evidently extended back behind the suborbital fenestrae; palatine-pterygoid contacts are not preserved, but the palatines are long and extend posterior to the pterygoid margin of each fenestra. They did not contribute to the internal choanae.

The left ectopterygoid is partially preserved in place. The anterior ramus does not extend beyond the last maxillary alveolus. The posterior ramus extends beyond the stout ectopterygoid body and underlies the left pterygoid wing for three-quarters of the anteroposterior length of that wing. It forms the posterolateral corner of the suborbital fenestra. The extent of ectopterygoid contribution to the postorbital bar is unknown.

The pterygoids are incomplete, and only the left border of the choana is preserved on the holotype. Preservation of the pterygoids is better in one of the referred specimens (PPM p2001.1.260), in which the entire circular choana is preserved, showing it to be completely surrounded by the pterygoids and opening posteroventrally, without a midline septum and without the extensive dorsal expansion of the nasopharyngeal duct typically seen in alligatoroids (Norell, 1989; Brochu, 1999).

The pterygoid wing is a flat bony plate extending ventrolaterally from the midline. Its dorsoventral thickness increases at its lateralmost extent, and the lateral margin is rugose and upturned. The posterior margin was concave. The cleft visible on the posterior view of PPM p2001.1.260 (Fig. 3B) is a deep crack in the posterior part of the pterygoid behind the choana.

The postorbitals form the anterolateral corners of the skull table and the dorsalmost portion of the postorbital bars. They also bound the supratemporal fenestrae anterolaterally. The anterolateral margin is rounded, and the skull table consequently lacks the more acute corner seen in *Gavialis*. Contact with the parietal within the fenestrae is limited by the frontal.

The parietal lies immediately behind the frontal, which it meets along a linear suture between the supratemporal fenestrae. It expands laterally behind the fenestrae where it meets the squamosals. Its dorsal surface is flat. Sutural contacts with the braincase are indistinct.

The parietal interfenestral bar is comparatively wider in *Eothoracosaurus* than in any other gavialoid (Fig. 6). In *Eothoracosaurus*, the bar is approximately half the width of one of the fenestrae, compared with slightly less than one-third in *T. neocesariensis* and one-fourth in *T. macrorhynchus*. It is narrower still in *Thecachampsoides*. The relative size of the supratemporal fenestra changes during ontogeny in *Gavialis*, with the fenestra becoming larger relative to the skull table in larger specimens (Kälin, 1933); consequently, relative width of the interfenestral bar diminishes during ontogeny. Even though the interfenestral

but based on the posterior extent of the right nasal and anterior extent of the left lacrimal, the prefrontals did not extend as far forward as the lacrimals. The prefrontal pillars are not preserved.
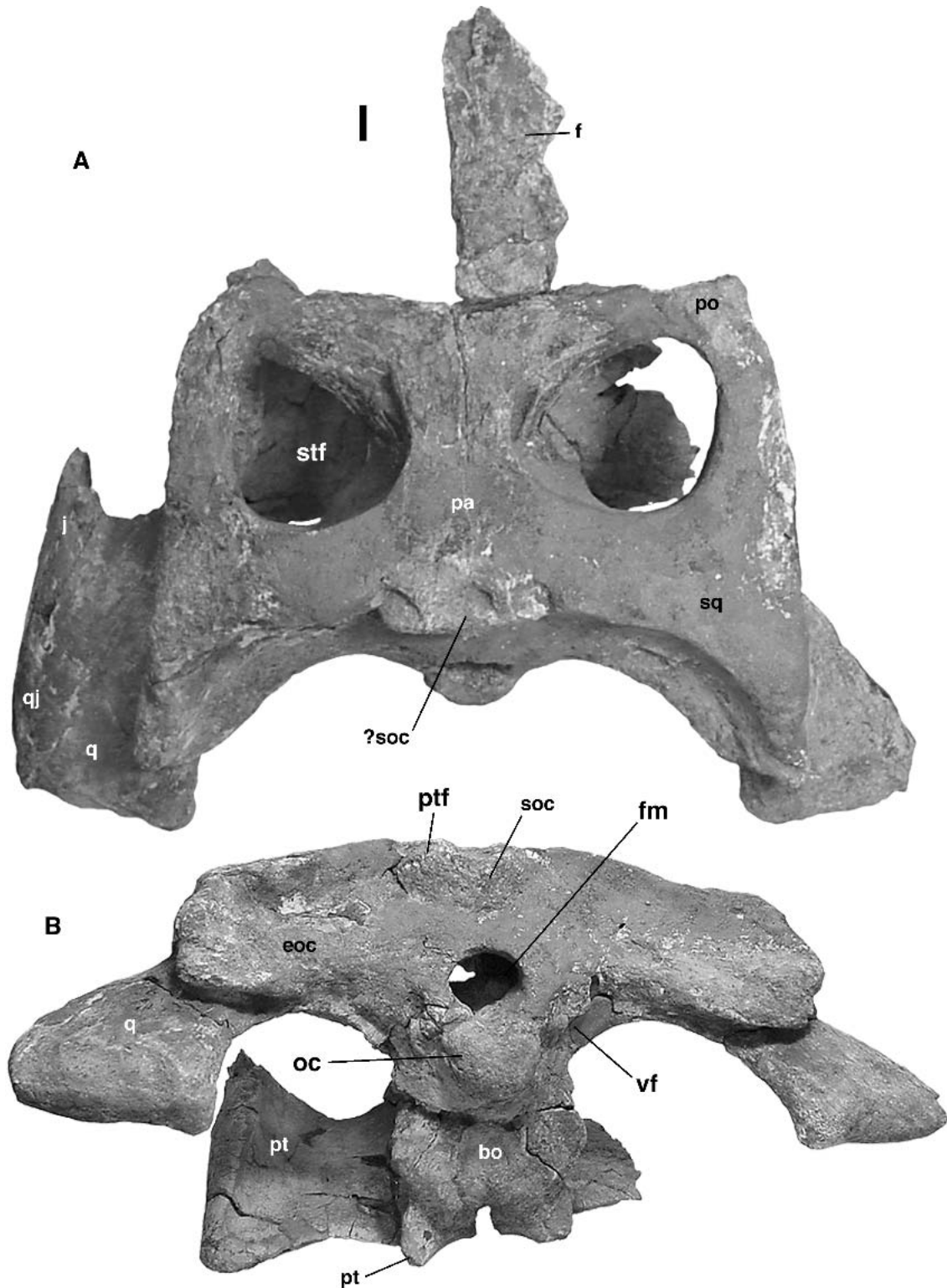
FIGURE 3.   PPM p2001.1.260, *Eothoracosaurus mississippiensis*. Posterior portion of skull in **A**, dorsal and **B**, posterior view. Scale equals 1 cm. **Abbreviations**: **bo**, basioccipital; **eoc**, exoccipital; **f**, frontal; **fm**, foramen magnum; **j**, jugal; **oc**, occipital condyle; **q**, quadrate; **qj**, quadratojugal; **pa**, parietal; **po**, postorbital; **pt**, pterygoid; **ptf**, posttemporal fenestra; **soc**, supraoccipital; **stf**, supratemporal fenestra; **vf**, vagus foramen.

bar visually looks broader in the large *Gavialis* skull in Figure 6F, it is less than a third the width of the fenestra, in comparison with the smaller skull in which the bar is slightly more than one-third the width of the fenestra. Greater relative interfenestral bar width in *Eothoracosaurus* is thus probably not ontogenetic variation—the skulls being compared are roughly the same size, but the type skull of *Eothoracosaurus* is the largest of the skulls in Figure 6.
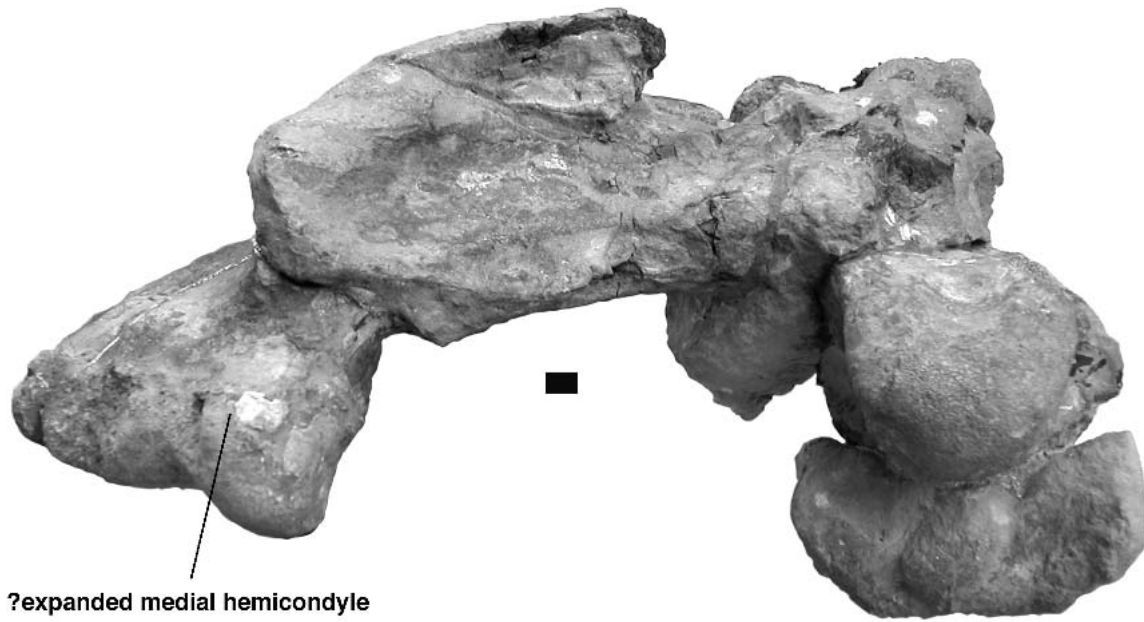
?expanded medial hemicondyle

FIGURE 4.   AMNH 3841, *Eothoracosaurus mississippiensis*. Skull, occipital view. Scale equals 1 cm.

The posterior margin of the parietal is disrupted by three (PPM p2001.1.260) or four (MSU 3293) semicircular depressions. The lateralmost on both correspond with exposure of the supraoccipital on the floors of the posttemporal fenestrae, and the medial depression(s) may correspond with exposure of the supraoccipital on the skull table itself, although sutures are not clearly visible. Whatever the nature of these depressions, the supraoccipital was not exposed as a slender posterior process as in *Gavialis*.

The squamosals form the posterolateral rims of the supratemporal fenestrae, meeting the parietal medially and the postorbitals anteriorly. The dorsal skull table surfaces slope ventrolaterally, resulting in a convex rather than planar skull table. Each squamosal forms the dorsal roof of the external otic recess, and the lateral surface of the roof bears an anteriorly flaring groove. It passes beneath the postorbital, though the anteriormost extent remains unclear. The external otic aperture has a rounded posterior margin and lacks the concavity seen in non-gavialoid crocodylians (Fig. 7). Behind the otic recess, each squamosal bears a long, slender posterolateral process lying above the quadrate ramus and bound posteriorly by the exoccipital.

The temporal foramen within the supratemporal fenestra was a mediolaterally elongate slit, but sutures in its vicinity are not preserved.

Sutural boundaries for the quadratojugals are indistinct, but the quadratojugals contributed little to the quadrate condyles and formed the posteroventral corners of the infratemporal fenestrae.

The quadrate forms the anteroventral margin of the otic aperture, although whether the quadrate-squamosal suture intersected the aperture at its posteroventral corner or externally passed along the posterior margin, intersecting the aperture posteriorly, is unknown. There is no evidence for a preotic siphonial opening. The quadrates did not contribute to the infratemporal fenestrae.

The quadrate rami project behind the occipital surface. Each bears a long, slender muscle attachment scar on the ventral surface. The foramen aereum is located dorsomedially. The cranioquadrate canal opens between the quadrate and the paroccipital process of the exoccipital lateral to the occipital condyle, and it is at the canal that the quadrate and pterygoid make contact.

The quadrate condyles of the holotype and PPM p2001.1.260 are typical for a gavialoid, in that the concave medial hemicondyle is ventrally reflected relative to its convex lateral counterpart. The crocodyloid medial hemicondyle is dorsally expanded, a condition found in tomistomines and providing evidence for a distant gavialoid-tomistomine relationship (Brochu and Gingerich, 2000). The left quadrate of AMNH 3841 seems to have the expanded medial hemicondyle as well (Fig. 6), but it is unclear whether this is natural or the result of postmortem damage to the dorsal surface of the quadrate ramus, with bone removed between hemicondyles producing an apparent "dorsal expansion" of the medial hemicondyle. For purposes of phylogenetic analysis (see below), *Eothoracosaurus* is presumed to lack the expanded medial hemicondyle.

Details of the lateral surface of the braincase are not preserved in the available specimens.

The supraoccipital is exposed as a triangle on the occipital surface, with the dorsolateral margins forming the floors of the posttemporal fenestrae. Sutures are indistinct, but the supraoccipital appears to have been excluded from the foramen magnum.

Each exoccipital forms a robust paroccipital process adjacent to a posterolateral squamosal process. An oblong muscle attachment tubercle lies on the ventral margin of the paroccipital process lateral to the cranioquadrate canal. The exoccipitals form the lateral and dorsal margins of the foramen magnum, and small foramina for cranial nerve XII perforate the exoccipitals immediately lateral to the foramen magnum. The vagus foramen pierces the exoccipital lateral to the occipital condyle, but the lateral carotid foramina are not preserved.

The ventral extent of the exoccipitals on the basioccipital tubera is unclear. In *Gavialis*, each exoccipital bears an anteroposteriorly broad descending process extending almost to the ventral tip of the tuber. This condition is found in *Thoracosaurus* and all other gavialoids. The lateral surface of the basioccipital tuber in *Eothoracosaurus* is broad, but whether the descending process of the exoccipital fills this area is unknown.

The dorsal relationships between the pterygoids and braincase are unclear, but posteriorly, the pterygoids expand laterally as they meet the basisphenoid along a caudally facing vertical sur-
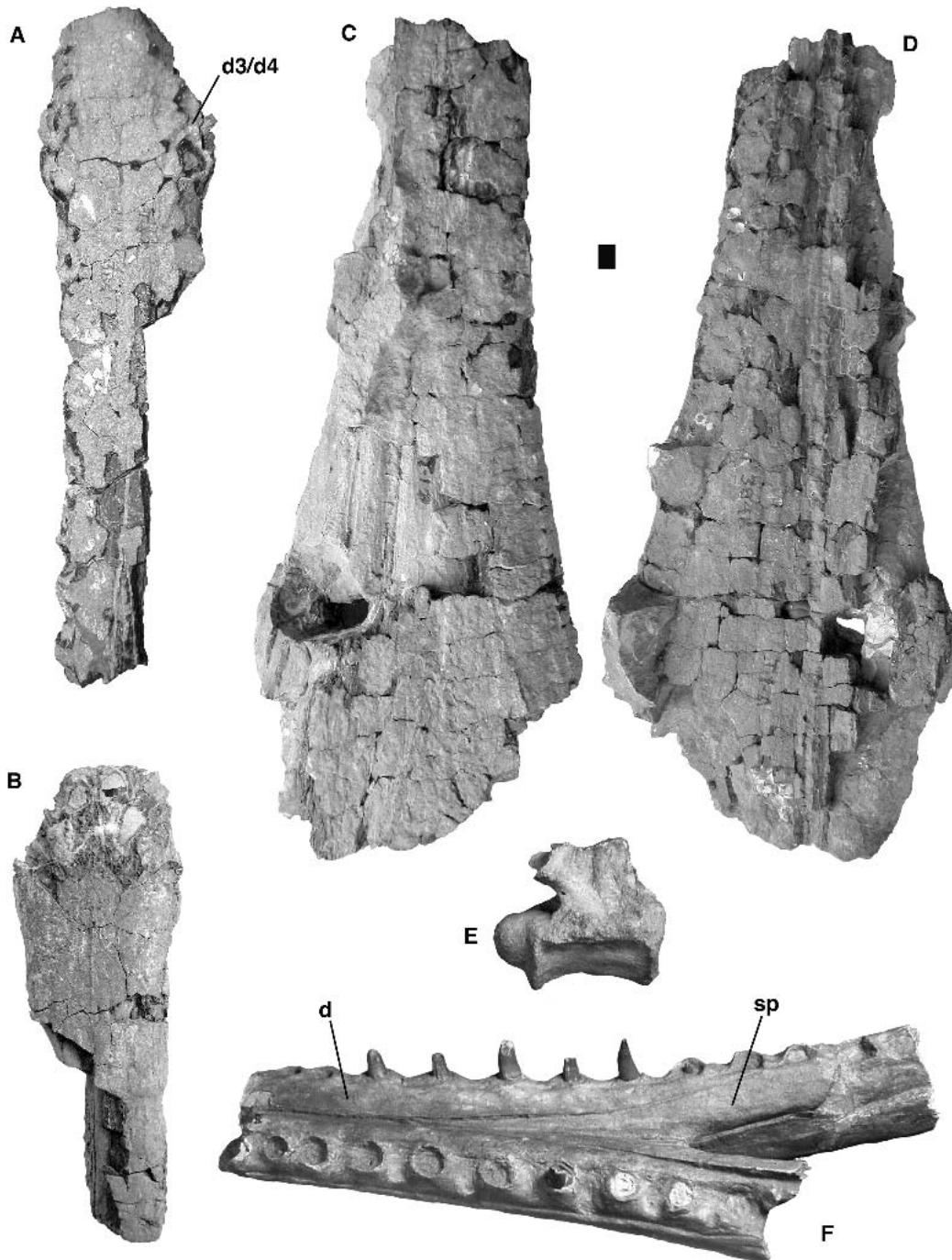
FIGURE 5.   **A–D**, AMNH 3841, *Eothoracosaurus mississippiensis*. Anterior end of dentary in **A**, dorsal and **B**, ventral view; "d3/d4" indicates expanded third and fourth dentary alveoli. Posterior portion of rostrum in **C**, dorsal and **D**, ventral view. **E** and **F**, USNM 5783, caudal vertebra in right lateral view (E) and partial mandible in dorsal view (F) from the Ripley Formation of Georgia possibly referable to *Eothoracosaurus mississippiensis*; **d**, dentary, **sp**, splenial. Scale equals 1 cm.

face. The distinction between basisphenoid, basioccipital, and pterygoid is obscure, but the basioccipital's ventral margin is immediately adjacent to the concave posterior surface of the palate, and the medial eustachian foramen is located between these elements, indicating that the posteriormost exposure of the basisphenoid would have been a thin sheet, not the anteroposteriorly broad element seen in extant *Gavialis*. A similar condition is present in *Thoracosaurus*.

The basioccipital forms the floor of the foramen magnum and

the large, spherical occipital condyle. The bone flares laterally ventral to the condyle, where it bears the lateral basioccipital tubera and an oblong midline tubercle. The median eustachian foramen opens ventrally below the midline tubercle, where the margin of the basioccipital is concave. The lateral eustachian openings cannot be seen.

The dentaries are long, tubular bones with flattened dorsal surfaces (Fig. 2). The right dentary of the holotype bears 26 alveoli, and the alveolar count on the left is unclear. Alveoli are
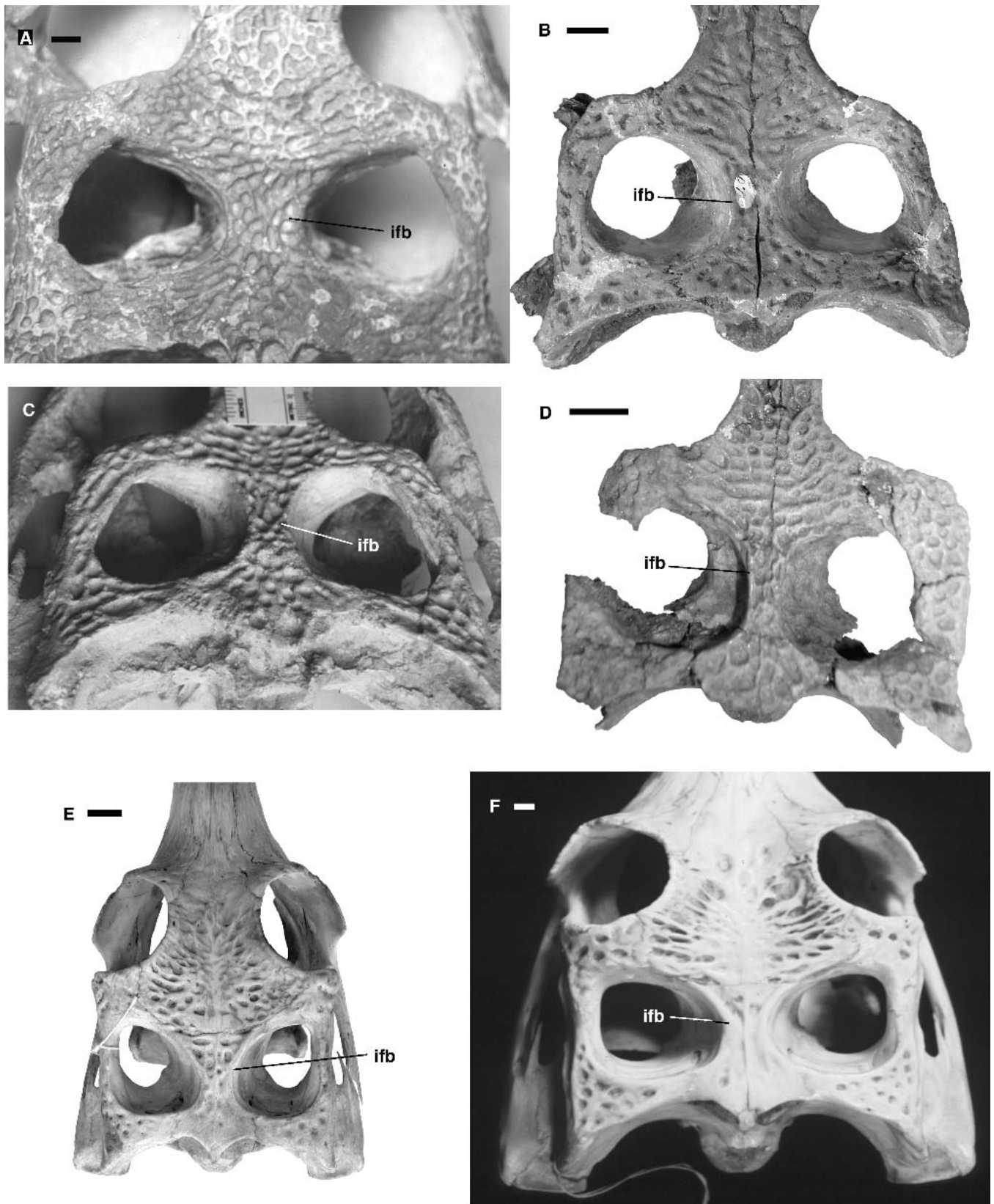
FIGURE 6. Skull tables and interfenestral bars. **A**, *Eothoracosaurus mississippiensis* (MSU 3293). **B**, *Thoracosaurus neocesariensis* (AMNH 2542). **C**, *Thoracosaurus macrorhynchus* (LO 3076T). **D**, *Thecachampsoides minor* (NJSM 15437). **E**, *Gavialis gangeticus* (FMNH 23505). **F**, *Gavialis gangeticus* (TMM m-5485). **ifb**, interfenestral bar.
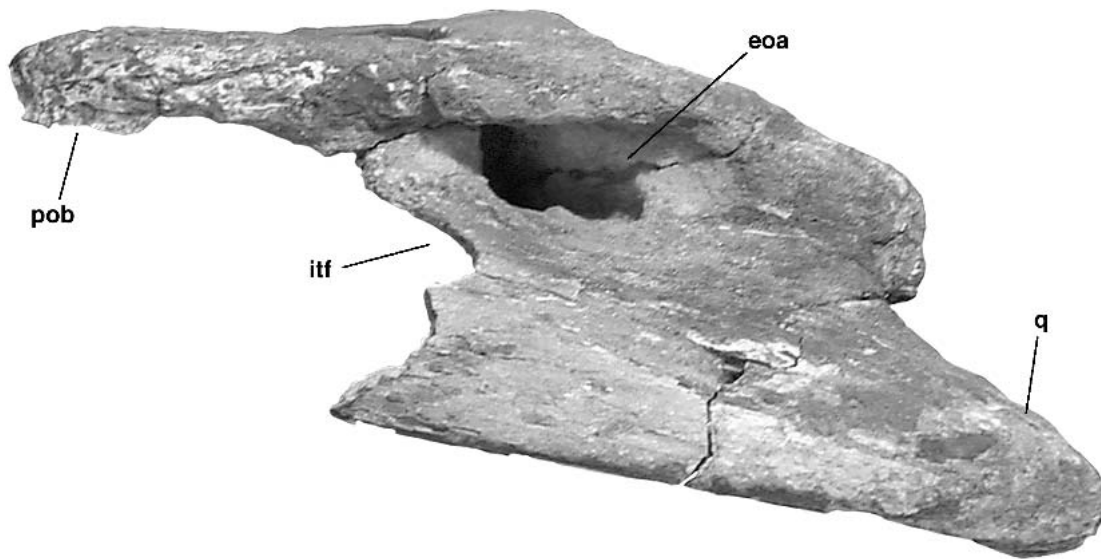
FIGURE 7. PPM p2001.1.260, *Eothoracosaurus mississippiensis*. Left otic region in lateral view. **Abbreviations**: **eoa**, external otic aperture; **itf**, infratemporal fenestra; **q**, quadrate; **pob**, base of postorbital bar.

approximately uniform in diameter until the mandibular rami diverge, after which they sequentially diminish in size. The lateral sides are parallel for much of the dentaries' length with a modest mediolateral expansion at the anterior tip. The third and fourth dentary alveoli are nearly confluent (Fig. 8). These are approximately the same size on both dentaries of the holotype; the third is slightly larger on the right, the fourth on the left. It is less obvious on the dentaries of AMNH 3841, but the region on each dentary corresponding with these alveoli is expanded, suggesting a similar condition. A diastema separates the second alveolus, which is smaller than the third, from the third and fourth, which are located very close together. Another diastema then separates the fourth and fifth alveoli. The third and fourth alveoli are elevated above the dorsal surface of the dentary, giving the impression of sulci separating the closely placed third and fourth alveoli from their neighbors. These alveoli are not "confluent" as in many basal crocodylian lineages, but their arrangement is very similar and suggests that condition. The third and fourth alveoli are more widely separated in *Thoracosaurus neocesariensis*, *T. macrorhynchus*, and all other gavialoids for which the mandible is known. This has interesting phylogenetic implications (see below).

The splenials extend between the dentaries for considerable distance, but plaster obscures the anteriormost and posteriormost limits of the bones. Actual bone extends forward to between the 11th and 12th dentary alveoli, but the actual terminus could have been in front of this. The symphyseal divergence appears to lie between the 15th and 17th dentary alveoli. The splenial symphysis of USNM 5783 (Fig. 5F) extends forward along nearly six alveoli, but we do not know the relative position of these alveoli. The dorsal surfaces of the splenials within the symphysis are flat, but the bones become very thin posterior to the symphysis, and each forms the medial border for the posteriormost 11 or 12 alveoli. There are no foramina on the medial surface of the splenial as exposed.

The surangular extends behind the dentary and lies lateral to the articular, forming the lateral wall of the glenoid fossa. The surangular suture within the fossa lacks the deep indentation seen in crocodyloids. The posterior tips are imperfectly preserved, but the surangular either extended all the way to the posterior tip of the retroarticular process or very nearly did so.

The angular lies below the surangular. It has a convex pos-

teroventral margin and becomes progressively narrow as it approaches the rear tip of the retroarticular process. The anterior interaction between dentary and angular is not preserved on either side, but the angular-surangular suture is dorsally concave on the lateral surface of the jaw. Medially, the angular bears an ascending lamina forming the medial wall of the adductor chamber. Only the posterior and ventral margins of each anteroposteriorly elongate oval foramen intermandibularis caudalis are preserved.

The left articular reveals a rectangular glenoid fossa and a stout descending process lying within the medial sulcus of the angular. The right articular is not preserved, but its articulation facet with the surangular suggests that the lingual foramen lay on the medial articular-surangular contact, not wholly on the surangular, but this is not certain. The medial margin of the retroarticular process is damaged, but the process' dorsal surface bears a modest anteroposteriorly long ridge. The foramen aereum is not preserved.

The coronoid is not preserved.

Two additional remarkable features of the lower jaw involve the postdentary elements. The first is a long inferior anterior process of the surangular. The surangulars of all crocodylians bear a pair of anterior processes, between which lies a small foramen. This is the "interfingering suture" between the surangular and dentary described by Carpenter (1983:6). In most crocodylian groups the superior process, which approaches the dentary toothrow, is much longer than its inferior counterpart. This is the condition in *Gavialis* and in other thoracosaurs. In alligatoroids, the two processes are subequal in length (Brochu, 1999). The superior process is still longer in *Eothoracosaurus*, and it terminates immediately behind the last dentary alveolus, but the inferior process is elongate in a condition suggesting that found in alligatoroids (Fig. 9).

The second involves the external mandibular fenestra, which may not have been present. The margins of the "fenestrae" on both rami are clearly not natural (Fig. 9)—the openings themselves are rectangular rather than oval, the margins are jagged, and surficial bone has flaked away on the medial surfaces of the surangular and angular. The right "fenestra" is larger than its left counterpart. If a mandibular fenestra was present in *Eothoracosaurus*, it probably would have been a very small slit between the surangular and angular. This raises interesting questions about
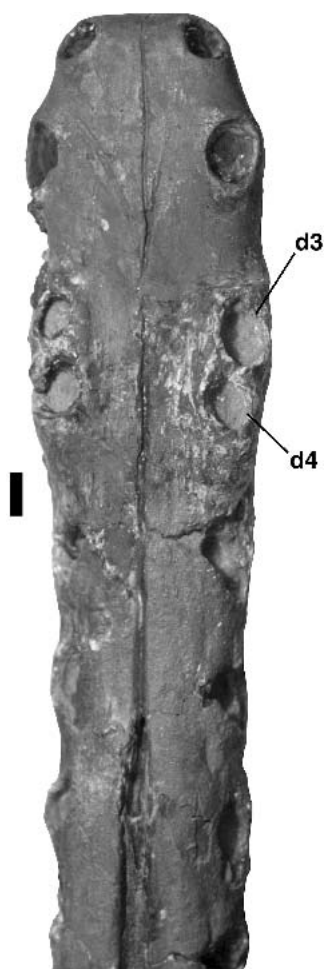
FIGURE 8. MSU 3293, holotype, *Eothoracosaurus mississippiensis.* Anterior end of mandible in dorsal view. Third (d3) and fourth (d4) dentary alveoli are indicated. Scale equals 1 cm.

homology of the crocodylian external mandibular fenestra, as the opening was absent from the jaws of crocodylian outgroups (see below).

The postcranial remains described by Carpenter (1983) include three cervical, 12 dorsal, two sacral, and six caudal vertebrae. The fragmentary vertebrae in the collection of the AMNH, possibly referable to *Eothoracosaurus,* are from the posterior trunk and tail. These are consistent with vertebrae found in other crocodylians. With the exception of the biconvex first caudal, the centra are procoelous; the cervicals bear short, knobby transverse processes that become longer, more planar processes on the trunk vertebrae; and the sacrals bear stout sacral ribs for articulation with the ilia. One of the cervicals has a very short hypapophyseal keel, but its neural spine is inconsistent with that for first postaxial; hence, we do not know the nature of the hypapophysis on the first postaxial.

The scapular blades are not preserved, but the deltoid crest is slender and has an acute lateral tip. The coracoid has a very long, slender blade (Fig. 10), and the coracoid body is anteroposteriorly short and pierced by the coracoid foramen. The ventral half of the glenoid fossa is preserved, but none of the muscle scars usually present on the lateral surface of the coracoid adjacent to the fossa can be seen. The scapula and coracoid were unfused, and other forelimb elements are not preserved.

The pelvic girdle is represented by fragmentary and uninformative pieces of the ilium (interpreted by Carpenter [1983] as

the left element) and ischium. The femur of the holotype is complete except for the distal end, and as described by Carpenter (1983), is consistent with the femur of most extant crocodylians. A left tibia from the AMNH (Fig. 11) is also consistent with homologues from other crocodylians; the proximal end appears to be rather narrow, but this could reflect postmortem damage.

Several osteoderms are preserved with MSU 3293 and the unnumbered AMNH sample. In both cases, the dorsal midline elements are rectangular, unkeeled, and have broad unsculpted anterior articulation facets. They also bear broad anteromedial processes, structures found in outgroups to Crocodylia but not in alligatoroids or crocodyloids. Lateral dorsal osteoderms were square. The number of contiguous dorsal rows is unknown. One AMNH osteoderm resembles the anterior ossification from a ventral element in *Diplocynodon* or *Borealosuchus* (Fig.12). This would be unique for a gavialoid, as most such animals seem to have lacked ventral armor altogether; but identity as a ventral osteoderm, or even association with the cranial remains catalogued as AMNH 3841, is not certain.

PHYLOGENETIC RELATIONSHIPS

Eothoracosaurus mississippiensis was included in an updated version of a character matrix used in previous phylogenetic analyses (Brochu, 1997, 1999; Brochu and Gingerich, 2000). Two additional taxa are added to the analysis—*Thecachampsoides minor* and *Ikanogavialis gameroi.* Details regarding *I. gameroi,* based on a late Miocene skull from Venezuela (Sill, 1970), are discussed in Brochu and Rincón (2004). *Thecachampsoides* is discussed below, along with the other "thoracosaurs" included in the analysis.

Codings for *Eothoracosaurus* are based only on catalogued specimens—i.e., MSU 3293, PPM p2001.1.260, and AMNH 3841. The unnumbered specimens at the AMNH were not included.

Review of Thoracosaurs Included in Analysis

***Thoracosaurus neocesariensis* (de Kay, 1842)**—As applied in this analysis, *T. neocesariensis* refers to the longirostrine crocodylian from the Hornerstown Formation of New Jersey, which straddles the Cretaceous-Tertiary boundary (Staron et al., 2001). Material probably referable to the same species is known from the underlying Navesink Formation (Gallagher, 1993), and specimens from the Maastrichtian of Europe (Laurent et al., 2000; see below) and the Campanian of Georgia (Schwimmer, 1986) have been referred to *T. neocesariensis,* but codings here are based entirely on material from the Hornerstown.

Thirteen species of longirostrine crocodylians have been described from the Cretaceous portion of the New Jersey "greensands" since the earliest reports in the technical literature (de Kay, 1833), the majority of which are based on extremely fragmentary material. Seven of these are known only from postcranial remains. Most holotypes have degraded through pyritization since collection, including the only three—*Thoracosaurus neocesariensis* (de Kay, 1842), *Thoracosaurus mullicensis* Troxell, 1925, and *Thoracosaurus meirsanus* Troxell, 1925—for which substantial cranial material is known. Carpenter (1983) viewed them all as junior synonyms of *Thoracosaurus neocesariensis;* although I agree that these probably represent a single form, most are probably best viewed as nomina dubia.

It was long customary to divide thoracosaurs from the New Jersey Cretaceous into two groups—*Thoracosaurus* and *Holopsisuchus* (a replacement name for *Holops,* which was preoccupied by a fly). *Thoracosaurus* and *Holopsisuchus* are virtually identical (insofar as the scrappy types permitted comparison), with one exception—*Thoracosaurus* was thought to have an antorbital fenestra, or at least some sort of opening anterior to the orbit, and *Holopsisuchus* was thought to lack this feature.
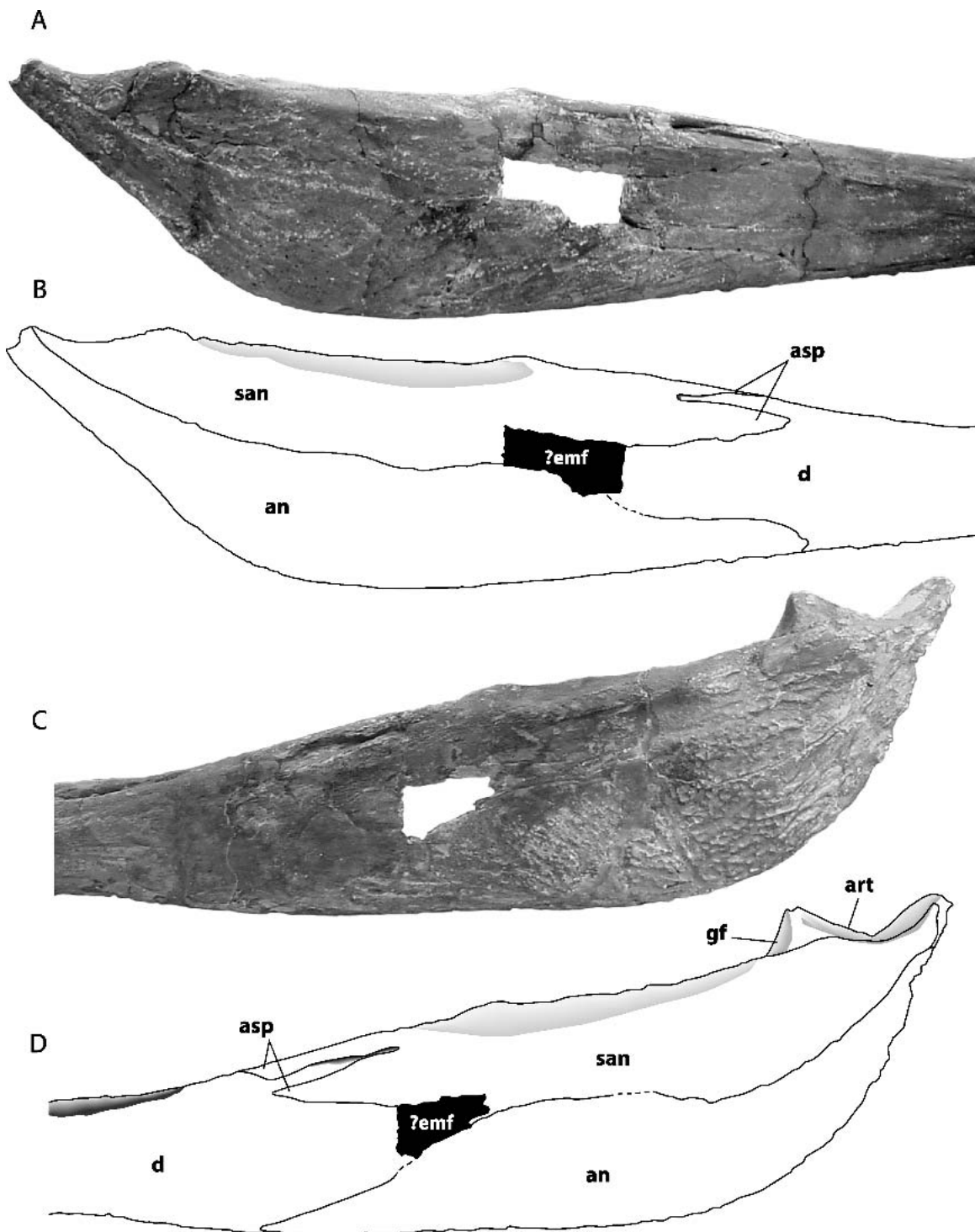
FIGURE 9.   MSU 3293, holotype, *Eothoracosaurus mississippiensis*. Postdentary bones of jaw in lateral view. **A** and **B**, right ramus. **C** and **D**, left ramus. Scale equals 1 cm. **Abbreviations**: **an**, angular; **art**, articular; **asp**, anterior surangular processes; **d**, dentary; **?emf**, possible external mandibular fenestra; **gf**, glenoid fossa; **san**, surangular.

Antorbital fenestrae were present ancestrally in crocodyliforms, but they were lost multiple times within the group and are absent in Neosuchia (Buffetaut, 1982a; Clark, 1994), including the proximate sister taxa to Crocodylia—*Hylaeochampsa*, *Allodaposuchus*, and *Bernissartia* (Buffetaut, 1975; Norell and Clark, 1990; Buscalioni and Sanz, 1990; Clark and Norell, 1992; Buscalioni et al., 2001). No member of Crocodylia is known to have antorbital fenestrae with the possible exception of *Thoracosaurus*. In fact, antorbital fenestrae may be incompatible with the arrangement of the neosuchian dermatocranium; the jugal lies dorsal to the maxilla in a lap joint for a considerable distance, and the triple junction between jugal, maxilla, and lacrimal lies very close to the orbit. If *Thoracosaurus* has antorbital fenestrae, it would be unique among neosuchians.

FIGURE 10. MSU 3293, holotype, *Eothoracosaurus mississippiensis*. Left coracoid, lateral view. Scale equals 1 cm.

FIGURE 11. Left tibia possibly referable to *Eothoracosaurus mississippiensis* at the AMNH in anterior (left) and medial (right) view. Scale equals 1 cm.

Some authors thought the "antorbital fenestra" of *Thoracosaurus* was a preservational artifact and not a real opening (Carpenter, 1983). This renders *Holopsisuchus* synonymous with *Thoracosaurus*. More recently, Laurent et al. (2000) argued that a thoracosaur skull from the Cretaceous of France has genuine openings on the posterior rostrum, though they were thought to be different from antorbital fenestrae as they were between the lacrimal and prefrontal, not the lacrimal and maxilla. The specimen on which this was based was tentatively referred to *Thoracosaurus neocesariensis*.

A closer examination of the evidence indicates that thoracosaurs, at least from North America, do not have this feature. The only North American specimen on which "fenestrae" were observed, ANSP 10079, is not referable to *Thoracosaurus* (see below). The openings on this skull thought to be antorbital fenestrae (Fig. 13) do not have smooth margins. Cortical bone around the rims has flaked away along each circumference. Leidy (1865) stated that each opening was situated between a lacrimal and a prefrontal, but each actually lies almost entirely within a lacrimal, as the lacrimal-prefrontal suture passes medial to each opening. They are not bilaterally symmetrical; the left opening is smaller and situated slightly posterior to its right counterpart. Additional gavialoid skulls from correlative units along the Eastern Seaboard may be referred to the same species (Brochu, 2002), and all of them lack this feature. The "antorbital fenestrae" of ANSP 10079 are best viewed as a postmortem effect.

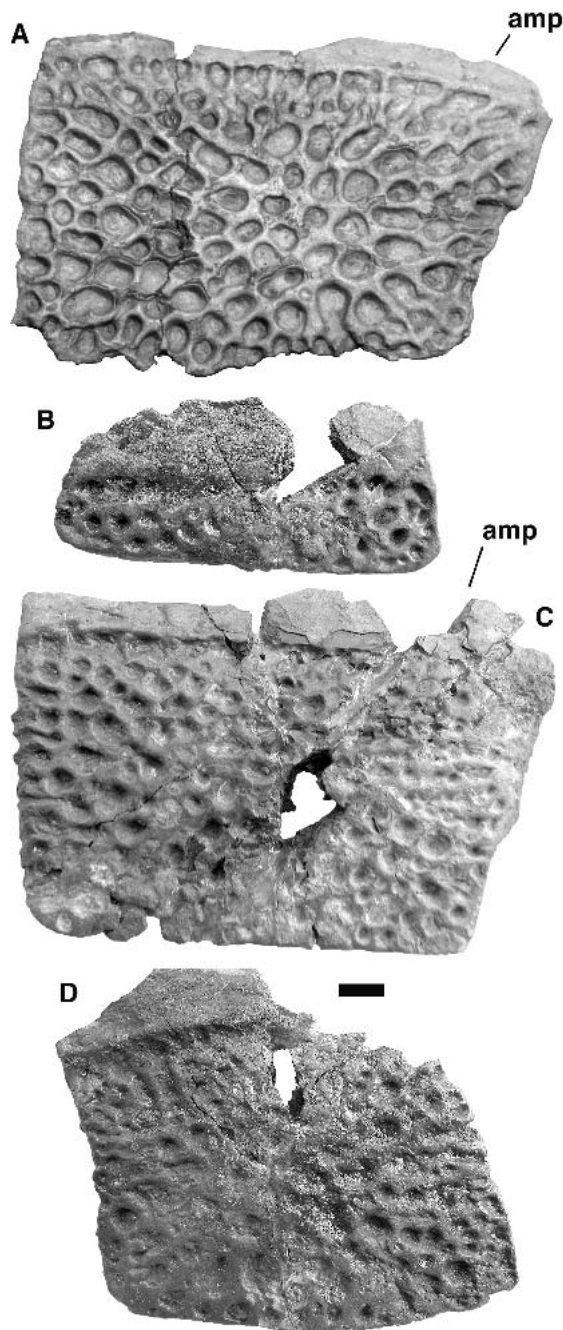To my knowledge, no gavialoid skull from North America

FIGURE 12. *Eothoracosaurus mississippiensis* osteoderms. **A**, MSU 3293, midline dorsal element. **B**, ?AMNH 3841, resembling anterior ventral ossification from *Borealosuchus* or *Diplocynodon*. **C**, ?AMNH 3841, midline dorsal element. **D**, ?AMNH 3841, possible lateral dorsal element. Scale equals 1 cm. **amp**, anteromedial process.

bears openings on the rostrum other than the naris and incisive foramen. This is true not only for the holotype of *Eothoracosaurus mississippiensis*, but also for specimens of *T. neocesariensis* preserving the relevant portion of the skull (e.g., NJSM 12205). We can safely conclude that North American thoracosaurs did not have an antorbital fenestra. If the French skull described by Laurent et al. (2000) has a rostral opening, it is autapomorphic and not referable to *T. neocesariensis*.

***Thoracosaurus macrorhynchus* (de Blainville, 1835)**—Codings are based on specimens from the lowermost Paleocene of

Europe. *Thoracosaurus macrorhynchus* is based on a complete skull and comes from the Paleocene of France (de Blainville, 1850; Gervais, 1859; LeMoine, 1884; Piveteau, 1927). It was initially described as a species of *Gavialis* (de Blainville, 1835) and was first referred to *Thoracosaurus* by Leidy (1865). I follow Piveteau (1927) in regarding *Thoracosaurus scanicus,* based on a skull, mandible, and associated postcranial remains from the Paleocene of Sweden (Troedsson, 1924), as a subjective junior synonym of *T. macrorhynchus*: sutural patterns and proportions in both skulls are identical. Swinton (1938) argued that *T. macrorhynchus* is a subjective junior synonym of *Gavialis* [*Thoracosaurus*] *isorhynchus* Pomel, 1847, but the material described by Pomel apparently came from the Cretaceous, and more detailed comparisons are required before synonymy can be established.

Postcranial material probably referable to *Thoracosaurus* or a close relative is known from the Late Cretaceous throughout Europe (Mulder, 1997; Zarski et al., 1998). Additional cranial material includes a skull referred to *T. neocesariensis* by Laurent et al. (2000) and the holotype of *T. borissiaki* from the Crimean Maastrichtian (Efimov, 1988; Storrs and Efimov, 2000). None of this material is considered in the present phylogenetic analysis.

***Thecachampsoides minor* (Marsh 1870)**—Pending more thorough description of the material used in this study, only a cursory summary of the taxon is provided here. The holotype, YPM 282 (originally *Gavialis minor*), consists of vertebrae and fragments of a skull. Its stratigraphic derivation is unclear—Marsh put it in the Eocene, and Norell and Storrs (1986) specified the Manasquan Formation, which is early Eocene in age (Browning et al., 1997). But all other material referable to this taxon (see below) is derived from the late Paleocene (Cook and Ramsdell, 1991; Fredericksen, 1991), and some of these units were formerly thought to be Eocene (e.g., Miller, 1955). The original localities, if accessible, should be reinvestigated to determine whether YPM 282 is from the Vincentown or Manasquan Formation.

The name *Thecachampsoides* was established by Norell and Storrs (1986), who regarded some features of YPM 282, however fragmentary, as diagnostic—in particular, an enlarged quadrate foramen aereum. The parietal is incompletely preserved, but the preserved portion of the interfenestral bar is very slender, in contrast to the comparatively wider bars in *Thoracosaurus* and *Eothoracosaurus* (Fig. 6). The vertebrae are relatively small, but have closed neurocentral sutures, suggesting a small adult individual.

Much more complete material can be referred to *Thecachampsoides minor* from the Upper Paleocene Vincentown Formation of New Jersey and correlative Aquia Formation of Maryland and Virginia (Brochu, 2002). The "Maryland thoracosaur" studied by Salisbury and Willis (1996) is based on a cast of one of these specimens (USNM 299730). These all share the enlarged quadrate foramen aereum and narrow interfenestral bar with YPM 282, and all represent individuals within the same size range as the type, suggesting individuals no larger than 2.5 meters in total length. Additional diagnostic features include the arrangement of dentary alveoli into discrete "couplets," with pairs of closely spaced alveoli separated by diastemata.

Larger longirostrine crocodylians may be present in both the Vincentown and Aquia formations. These differ from the smaller fossils in several ways—the dentary alveoli are not arranged in the same couplet pattern, and there is no evidence for an enlarged quadrate foramen aereum. The shape and relative size of the supratemporal fenestrae is also different, although this is known to vary ontogenetically in living crocodylians (Kälin, 1933). The postcranial skeleton of the smaller material from these units suggests small adult specimens, and the difference in size between the type of *Thecachampsoides* and the larger Vincentown and Aquia Formation longirostrine crocodylians (which were much more than twice as large) is greater than what would
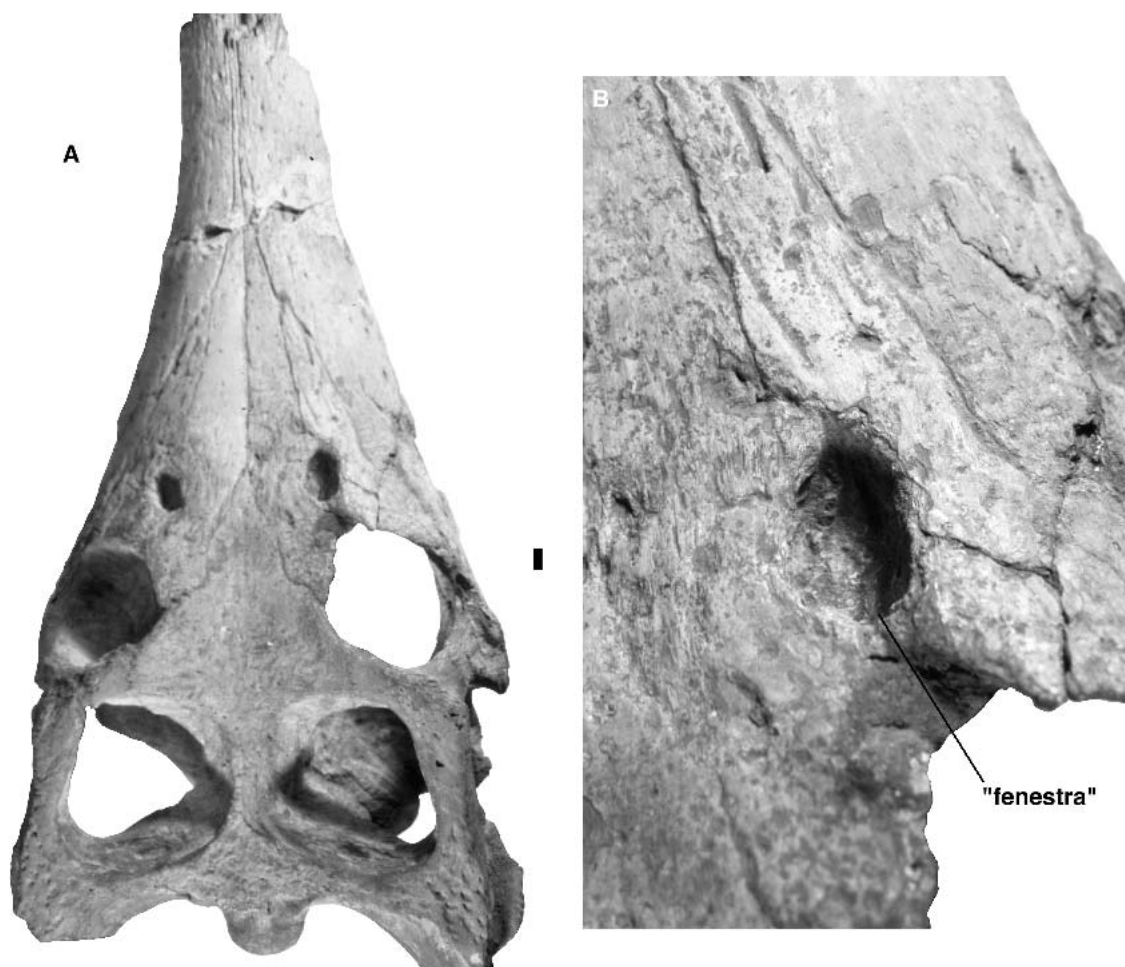
FIGURE 13. ANSP 10079, Late Paleocene gavialoid (?*Thecachampsoides minor*), posterior half of skull showing putative "fenestra" in front of orbit. Scale equals 1 cm.

be seen among adult specimens of extant crocodylians. The weight of available evidence thus suggests that the smaller and larger longirostrine crocodylians from the late Paleocene of eastern North America are two distinct species.

But the presence of two gavialoids in a single formation is unusual, and we cannot completely rule out the possibility that the smaller *Thecachampsoides* are immature versions of the larger specimens. This complicates matters because one of these larger specimens—ANSP 10079, a partial skull from the New Jersey "greensands" (Fig. 13)—is the holotype of *Sphenosaurus clavirostris* (Morton, 1844). This is the partial skull figured by Leidy (1865), who referred it to *Thoracosaurus* and, like his predecessors (including Morton [1844] and Agassiz [1849]) considered it late Cretaceous in age. It was found ". . . in limestone, overlying the ferruginous marl . . . near Vincentown, Burlington County, New Jersey" (Leidy, 1865:5). This corresponds with the Vincentown Formation (Miller, 1955). If ANSP 10079 and YPM 282 are conspecific, *Sphenosaurus clavirostris* (Morton, 1844) would have priority over *Thecachampsoides minor* (Marsh, 1870). The name *Sphenosaurus* is preoccupied (von Meyer, 1847), and so the species would be *Thecachampsoides clavirostris* (Morton, 1844).

Codings in this analysis (Appendix 1) are based entirely on smaller-bodied fossils, most of which included associated vertebrae with closed neurocentral sutures in the trunk and neck. The name *Thecachampsoides minor* is applied to this terminal taxon,

with the understanding that future examination of the larger specimens may require application of a different name and amended codings.

Phylogenetic Analysis

The matrix included 164 discrete morphological characters and 46 ingroup taxa. Only five species of crown-genus *Crocodylus* (*C. rhombifer*, *C. palaeindicus*, *C. porosus*, *C. niloticus*, and *C. cataphractus*) were included, and the alligatoroids were reduced to six (*Leidyosuchus canadensis*, *Diplocynodon darwini*, *Brachychampsa montana*, *Stangerochampsa mccabei*, *Alligator mississippiensis*, and *Caiman yacare*). This eliminated ambiguous portions of the tree remote from the problem at hand and decreased computation time.

The matrix was subjected to maximum parsimony analysis using PAUP* (version 4.0b10; Swofford, 2002). Ten heuristic searches were run with starting order of taxa randomized in each. Nodal support was assessed by calculating decay indices and bootstrap percentages based on 1×10^6 replicate matrices analyzed using fast stepwise addition.

Results—The analysis recovered 9709 equally optimal trees (length = 394, CI without autapomorphies = 0.459, RI = 0.788). The strict consensus tree is consistent with those recovered in previous treatments of the matrix (Fig. 14)—Gavialoidea are basal to a clade including Alligatoroidea, Crocodyloidea,
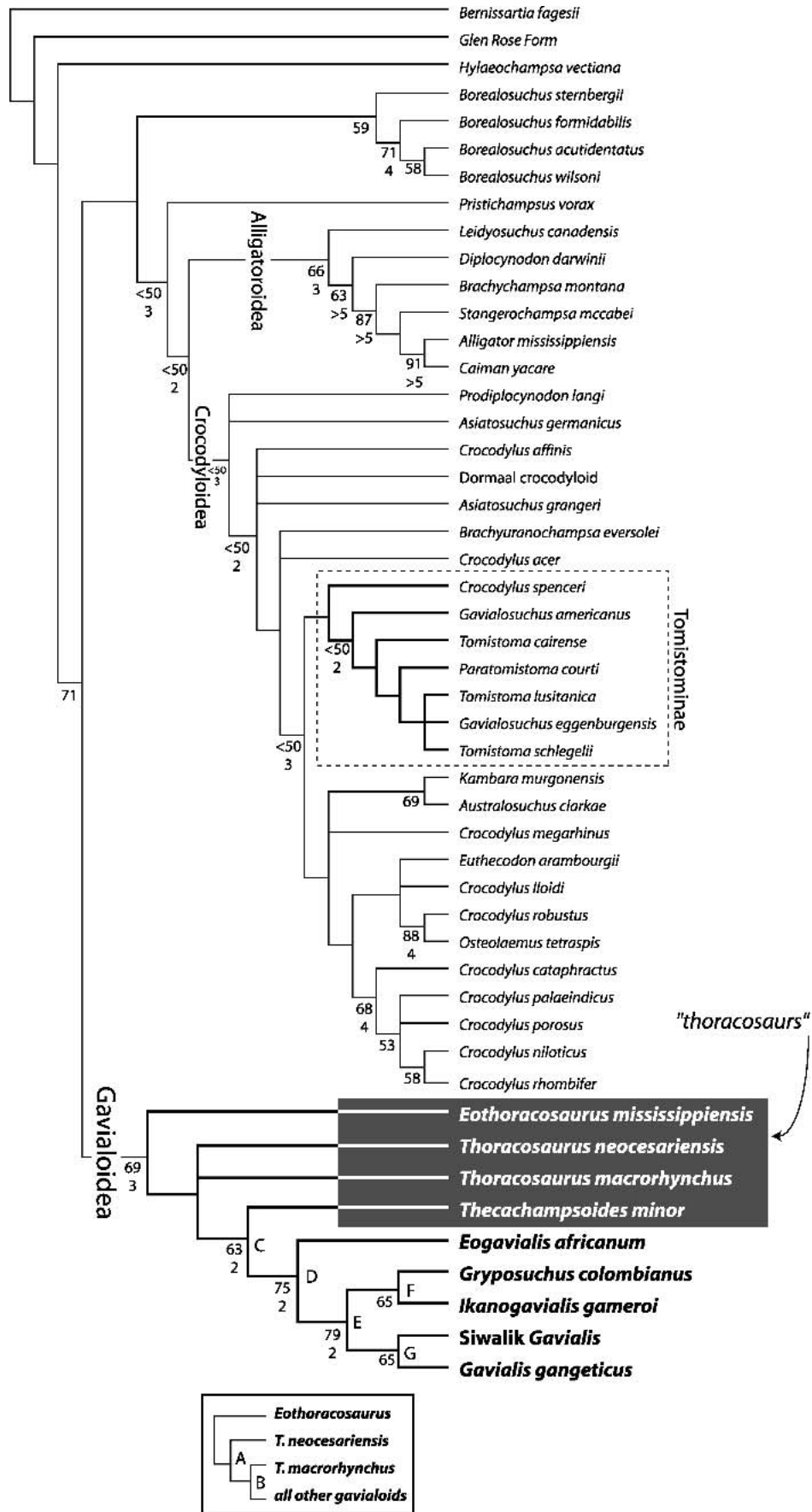
Pristichampsus, and *Borealosuchus*. *Tomistoma* and its closest extinct relatives are crocodylids and distantly related to *Gavialis*.

Harshman et al. (2003) recently argued that some aspects of this matrix obscure relationships between *Tomistoma* and *Gavialis*. In particular, they argued that character 43 (expressing the length and shape of the splenial symphysis) was problematic in that both *Gavialis* and *Tomistoma* have long splenial symphyses, but are coded with different character states because the morphology of the symphysis itself is different. They also argued that character 95 (expressing the relationship between external naris, premaxillae, and nasals) obscured similarity shared by *Gavialis* and *Tomistoma*—the nasals do not contact the naris dorsally in either, but in *Gavialis* the nasals do not even reach the premaxillae. That this latter character state is restricted to the two species of *Gavialis* in the matrix, and that the otherwise extremely similar South American gavialoids share the same character state as *Tomistoma*, renders the latter argument moot; nevertheless, I addressed their concerns by recoding character 43 such that gavialoids and tomistomines all shared the same character state and by ordering character 95. Parsimony analysis of this modified matrix added 14 trees to the set of most parsimonious trees, increased tree length by one step, decreased the CI from 0.459 to 0.455, and supported identical consensus trees to the unmodified matrix.

"Thoracosaurs" form a paraphyletic assemblage at the base of Gavialoidea. *Thecachampsoides minor* is more closely related to *Gavialis* than are *Thoracosaurus* or *Eothoracosaurus*. *Eothoracosaurus* is the basalmost gavialoid, and the two species of *Thoracosaurus* included in the matrix (*T. macrorhynchus* and *T. neocesariensis*) form a polytomy with all other gavialoids.

Eight characters unambiguously diagnose Gavialoidea in this analysis (Appendix 2): a long splenial symphysis exceeding five alveolar lengths and forming a broad "v;" a dentary lacking a concavity in its dorsal outline between the fourth and tenth alveoli; a dorsally projecting external naris; an anteriorly flaring squamosal groove; homodont maxillary dentition, with no enlargement of the fourth or fifth alveoli; a wedge-shaped palatine process terminating in an acute point; the absence of broad basisphenoid exposure ventral to the basisphenoid in posterior view; and premaxillae extending on the dorsal surface of the rostrum back beyond the level of the third maxillary alveolus.

Most of these characters are related to snout elongation. The long splenial symphysis can be seen as a correlate of rostral attenuation, although the shape of the symphysis in dorsal view—a broad "v," in contrast to the constricted "v" seen in tomistomines and Neogene South American gavialoids (Brochu and Rincón, in press)—is unique to gavialoids among eusuchians. The anteriorly flaring squamosal groove, linear dentary, homodonty, wedge-shaped premaxillary process, and long posterior premaxillary processes are also generally seen in longirostrine crocodylians (e.g., Hecht and Malone, 1972; Langston, 1973; Antunes, 1987). That longirostry dominates the character distributions at the root of Gavialoidea reflects two phenomena: the extent to which longirostry impacts cranial morphology and incompleteness of *Eothoracosaurus* and some other basal gavialoids, making it impossible to currently score them for characters not related to snout elongation found widely among gavialoids (see below).

Eight additional characters ambiguously diagnose Gavialoidea. Extant *Gavialis* is characterized by a massive, block-shaped proatlas; a narrow neural spine on the first postaxial vertebra; a dorsoventral flexure to the interclavicle; and a flared dorsal projection of the hyoid cornu. These characters appear elsewhere among crocodylians, and they were not scorable for any fossil gavialoid. Two characters—the absence of a crest on the axial neural spine and a long anterior spur on the splenial bordering the dentary toothrow lingually for at least one alveolar length—are observed in *Gavialis* and *Gryposuchus colombianus* (Langston and Gasparini, 1997) as well as some crocodyloids, but in no other gavialoid. Interfingering dental occlusion is found in all gavialoids, but also in derived members of *Borealosuchus*; it is probably independently derived in both lineages (as well as in crocodyloids), but at present this character's optimization is ambiguous and multiple losses in pristichampsines, alligatoroids, and basal crocodyloids are equally parsimonious. Because a postorbital bar flush with the lateral surface of the jugal, without a deep notch separating the base of the bar from the cheek, is present in some but not all outgroups, this feature (present in all known gavialoids but no other crown-group crocodylian) is also an ambiguous synapomorphy for the group.

A single character state unambiguously diagnoses a clade including all known gavialoids except *Eothoracosaurus*: upturned orbital margins. A mediolaterally oriented capitate process of the laterosphenoid and a deeply forked axial hypapophysis may also diagnose this clade, although they are not presently codable for *Eothoracosaurus*. The former character state may be related to longirostry, but the latter is not.

Jaw Morphology and Ambiguous Character Optimizations— Two aspects of the lower jaw of *Eothoracosaurus* suggest a more complicated evolutionary history for two characters—confluent third and fourth dentary alveoli and the presence of an external mandibular fenestra. The lower jaws are unknown for the basal eusuchians *Hylaeochampsa* and *Allodaposuchus*, but outgroups to Eusuchia (including *Bernissartia* and the Glen Rose Form) generally lack an external mandibular fenestra, and *Bernissartia* has confluent dentary alveoli. Confluent alveoli appear in many noneusuchian lineages, including goniopholidids and at least some thalattosuchians (personal observation), but because the Glen Rose Form lacks confluent alveoli, the most parsimonious distribution of this character state without *Eothoracosaurus* involves multiple gains within Crocodylia—once within *Borealosuchus* and once or twice among alligatoroids. Some less completely known basal alligatoroids, such as *Deinosuchus*, also have this feature; this suggests that alligatoroids ancestrally had confluent alveoli, with a loss among globidontans, but this depends on how *Deinosuchus* is related to other alligatoroids. And in the absence of *Eothoracosaurus*, the external mandibular fenestra arose only once within eusuchians, though whether it diagnoses Crocodylia or a more inclusive clade is unknown.

But if *Eothoracosaurus* is coded as having confluent dentary alveoli (which they almost are) and lacking an external mandibular fenestra, basal conditions throughout Crocodylia for both characters become ambiguous (Fig. 15). This leads to a maximum of four gains or four losses of confluent dentary alveoli in the crown group, and either two independent gains of an external mandibular fenestra or its independent loss in *Eothoracosaurus*. In this case, addition of more information results in less clarity.

This author suspects that confluent dentary alveoli are plesiomorphic for Crocodylia, with multiple losses within the group. The earliest known crocodyloid and pristichampsine jaws are known from the Cenozoic, and so we do not know if the earliest members of these groups—both of which must have existed by the Campanian—lacked confluent alveoli. This condition is also

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FIGURE 14. Strict consensus of 9709 equally optimal trees resulting from maximum parsimony analysis described in this paper. Upper numbers at nodes are bootstrap percentages and lower numbers are decay indices. Letters adjacent to gavialoid nodes, and at nodes in inset tree, indicate node labels used for character state optimizations (Appendix 2).
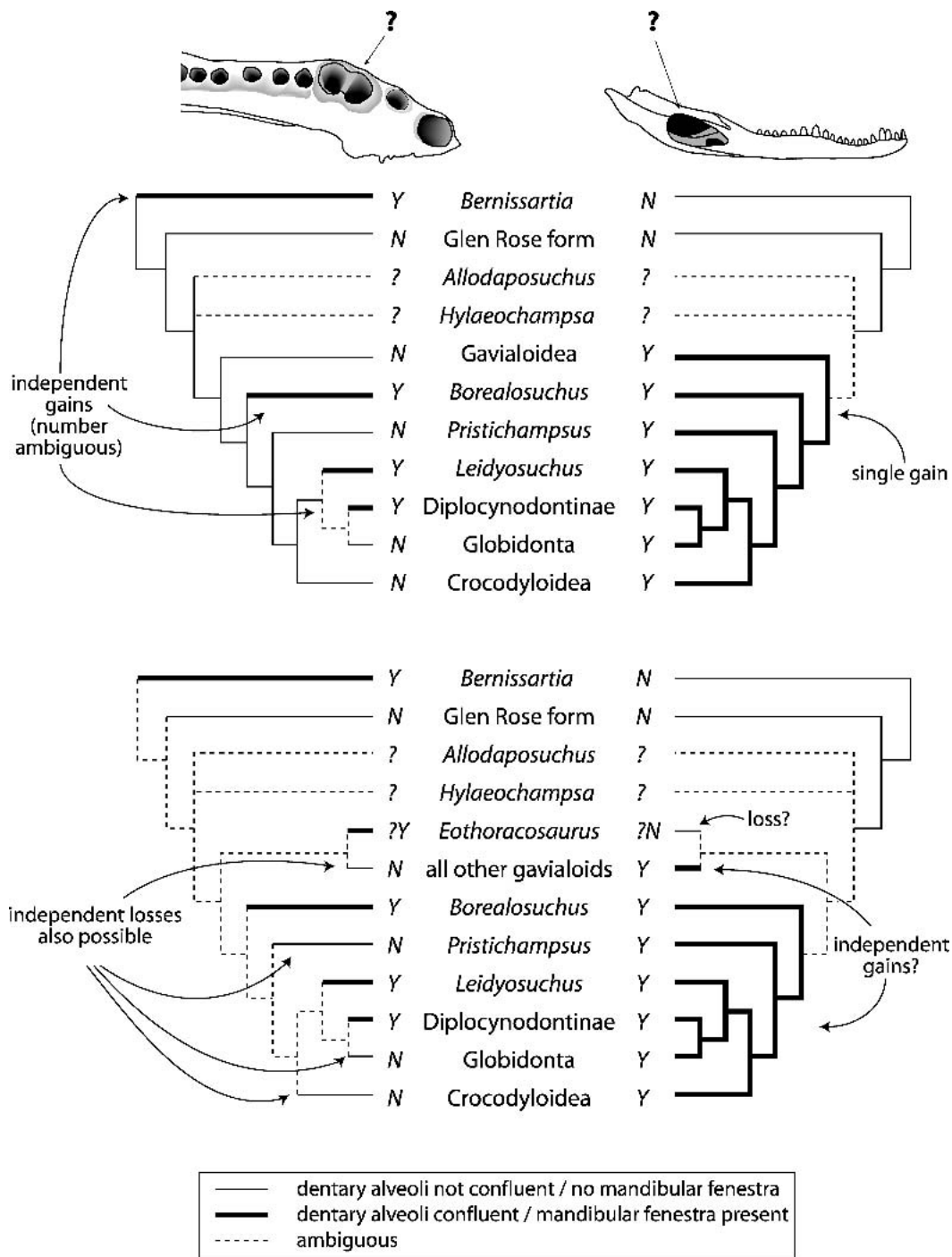
FIGURE 15.   Impact of *Eothoracosaurus* on the optimization of two character states—confluent third and fourth dentary alveoli (left) and presence of an external mandibular fenestra (right). Trees at top indicate optimizations without *Eothoracosaurus*, and trees below indicate optimizations in its presence, assuming it has confluent third and fourth alveoli and lacks a mandibular fenestra.

widely distributed among non-crocodylian crocodyliforms (Buffetaut, 1982a; Norell and Clark, 1990). More complete mandibular material from early crocodylians, and from noncrocodylian eusuchians, is needed to test this hypothesis.

Better mandibular material is also needed to better understand the history of the mandibular fenestra, which was surely more complicated than even the simplified scenario in Fig. 15 suggests. The fenestra was lacking in the putative eusuchian *Stomatosuchus* (Stromer, 1925), but whether it was present in other basal eusuchians is unknown. Most basal crocodylians have well-developed mandibular fenestrae, but a few fossil crocodylians show reduction or loss of the structure. For example, although most species of *Borealosuchus* (including the earliest currently described, the Maastrichtian *B. sternbergii*) have large fenestrae, the fenestra is a very slender slit in the latest known species (*B. wilsoni*). It was either a slit or absent altogether in an undescribed crocodylian from the Campanian of Alabama that has been referred in the literature to either *Diplocynodon* (Parris et

al., 1997) or *Leidyosuchus* (Schwimmer, 2002), but is, in fact, a new species of *Borealosuchus* (personal observation). The external mandibular fenestra is a narrow slit in the basal alligatoroid *Deinosuchus* (see Brochu, 1999:fig. 26) and in the Neogene mekosuchine *Mekosuchus* (Willis, 1997, 2001). This is one reason *Mekosuchus* was initially believed to represent a much more basal lineage outside the crown group (Buffetaut, 1983; Balouet and Buffetaut, 1987). None of this is relevant to the character's polarity at the root of Crocodylia, but it does provide evidence for multiple reductions or losses of the external mandibular fenestra within the group.

Braincase Structure and the Origin of "Verticalization"—The lack of broad basisphenoid exposure ventral to the basioccipital in *Eothoracosaurus* reflects a modification to the gavialoid braincase early in the group's history, and the anteroposterior breadth of the basioccipital tubera suggests, but does not demonstrate, the presence of long, broad, descending processes of the exoccipitals contributing to the tubera. But in other respects, the braincase of *Eothoracosaurus* is primitive. Most importantly, the basisphenoid is exposed broadly neither below nor anterior to the basioccipital.

In all mature crocodylians, the basisphenoid meets the basioccipital along a mediolaterally wide descending lamina that also forms the anterior margins for the eustachian foramina (Fig. 16B). The pterygoids contact this lamina anteriorly. In all mature extant crocodylians except *Gavialis*, this lamina is a thin sheet that extends (to varying degrees) below the ventral limit of the basioccipital. Hatchling crocodylians lack this lamina, and the basisphenoid is a simple plate lying in front of the basioccipital (Fig. 16A). In external view, *Gavialis* seems to retain this condition in adults (Fig. 16C, D). This was compared with the condition in many non-eusuchian crocodyliforms by Tarsitano et al. (1989), who regarded the condition in adult *Gavialis* as primitive and the "verticalized" condition in other crocodylians as derived. But immediate outgroups to Crocodylia have "verticalized" braincases in which the basisphenoid is seen as a thin sheet ventral to the basioccipital. This is the condition, for example, in *Hylaeochampsa* (Clark and Norell, 1992). This suggests that the "verticalized" condition pertains to a group including all eusuchians, and that what looks like an unverticalized braincase in *Gavialis* is a secondary modification.

Eothoracosaurus and *Thoracosaurus* together provide evidence for this view. In both cases, the basisphenoid is not exposed broadly in ventral view. The pterygoids approach the basioccipital very closely, and the basisphenoid can only have been present as a thin lamina (Fig. 16E, F).

Computed tomographic analysis of *Gavialis* also supports this view. The basisphenoid is indeed anteroposteriorly broad in ventral view, but in cross-section, this broad exposure is still in the form of a descending process lying between the basioccipital and pterygoids (Fig. 17B). What looks like an unverticalized braincase may actually be a verticalized braincase modified by dorsoventral compression and anteroposterior elongation. In any case, the condition seen in derived gavialoids is a derived condition within the group and not plesiomorphy separating *Gavialis* from other extant crocodylians.

DISCUSSION

Phylogenetic analysis indicates that the thoracosaurs, including *Eothoracosaurus* and *Thoracosaurus*, are closer relatives of *Gavialis* than of *Tomistoma*. Thoracosaurs form a paraphyletic assemblage at the base of Gavialoidea. Some of the characters supporting a close relationship between *Gavialis* and at least some thoracosaurs are not related to snout elongation.

The earliest fossil alligatoroids place the minimum divergence time between Gavialoidea and Brevirostres—and, by extension, between *Gavialis* and *Tomistoma*—at the base of the Campanian

(Williamson, 1996; Wu et al., 2001b). Material from Georgia referred to *Thoracosaurus* (Schwimmer, 1986) may extend the known range of Gavialoidea further back into the Campanian. Whether *Eothoracosaurus* from Tennessee is of early Maastrichtian or late Campanian age is therefore not critical to dating the split between gavialoids and all other crocodylians—even if the specimens from Georgia are not gavialoid, and even if the portions of the Coon Creek Tongue preserving *Eothoracosaurus* are Maastrichtian, the gavialoid-brevirostrine split must have occurred by the early Campanian. However, *Eothoracosaurus* does demonstrate that gavialoids had adopted the longirostrine condition by the beginning of the Maastrichtian.

A Mesozoic *Gavialis-Tomistoma* divergence conflicts with estimates from various molecular sources, all of which are within the Cenozoic and, sometimes, within the Neogene (Densmore and Dessauer, 1984; Hass et al., 1992; Harshman et al., 2003). This divergence timing is stable even if the matrix is constrained to draw *Gavialis* and *Tomistoma* closer together than to other extant crocodylians (Brochu, 1997) or if a large enough amount of nucleotide sequence data is added to the matrix that the molecular signal, in which *Gavialis* and *Tomistoma* are extant sister taxa, overrides the morphological signal (Brochu, 2003; Gatesy et al., 2003)—Late Cretaceous and Paleocene "thoracosaurs" are closer to *Gavialis* than to *Tomistoma* regardless of how *Gavialis* and *Tomistoma* are placed relative to other extant crocodylians, and the minimum divergence time between *Gavialis* and *Tomistoma* is in the later Campanian or early Maastrichtian.

The characteristics thought to make thoracosaurs closer relatives of *Tomistoma* are plesiomorphic conditions probably found in the basal members of any longirostrine clade. That the nasals fail to reach the external naris on the rostral surface, for example, can be seen as a natural consequence of snout attenuation. The nasals actually reach the naris externally in the basalmost known tomistomine ("*Crocodylus*" *spenceri*) and continue to reach the naris internally in *Tomistoma* (Langston and Gasparini, 1997), but the condition found in the more derived gavialoids, with the nasals not even contacting the premaxillae, is a derived condition relative to what we see in *Tomistoma*, and can be seen as a further modification of the outwardly similar condition found in thoracosaurs.

Ironically, thoracosaur craniology suggests that some features of the gavialoid braincase thought to reflect plesiomorphy—for example, the anteroposteriorly wide basisphenoid adjacent to the medial eustachian foramen—are themselves modifications of the ancestral crocodylian braincase, and that the "verticalized" condition found in other extant crocodylians is actually the primitive condition for the group. Thoracosaurs and tomistomines share yet another plesiomorphic state relative to the highly modified derived gavialoids, although in this case the derived condition externally mimics the morphology found in very distant relatives to Crocodylia.

The assemblage dramatically illustrates the dangerous nature of using combinations of primitive and advanced character states to diagnose supraspecific groups. For decades, systematists puzzled over the apparent primitive nature of *Gavialis*, wondering why the group first appeared in the late Eocene but looked as though it should have arisen in the Mesozoic. The fossils drawing the *Gavialis* lineage back to the Cretaceous were known all along, but because of the typological approach toward group membership that dominated paleontology for much of its history, failure to recognize features held in common with *Gavialis*, along with confusion of primitive features in one group (such as nasal-premaxillary contact) with primitive-looking derived conditions in another (such as the "unverticalized" *Gavialis* braincase) implied a more distant relationship.

Thoracosaurs, including *Eothoracosaurus*, are usually found in marginal marine sediments. This does not, by itself, prove that the earliest gavialoids were marine or coastal animals. But to
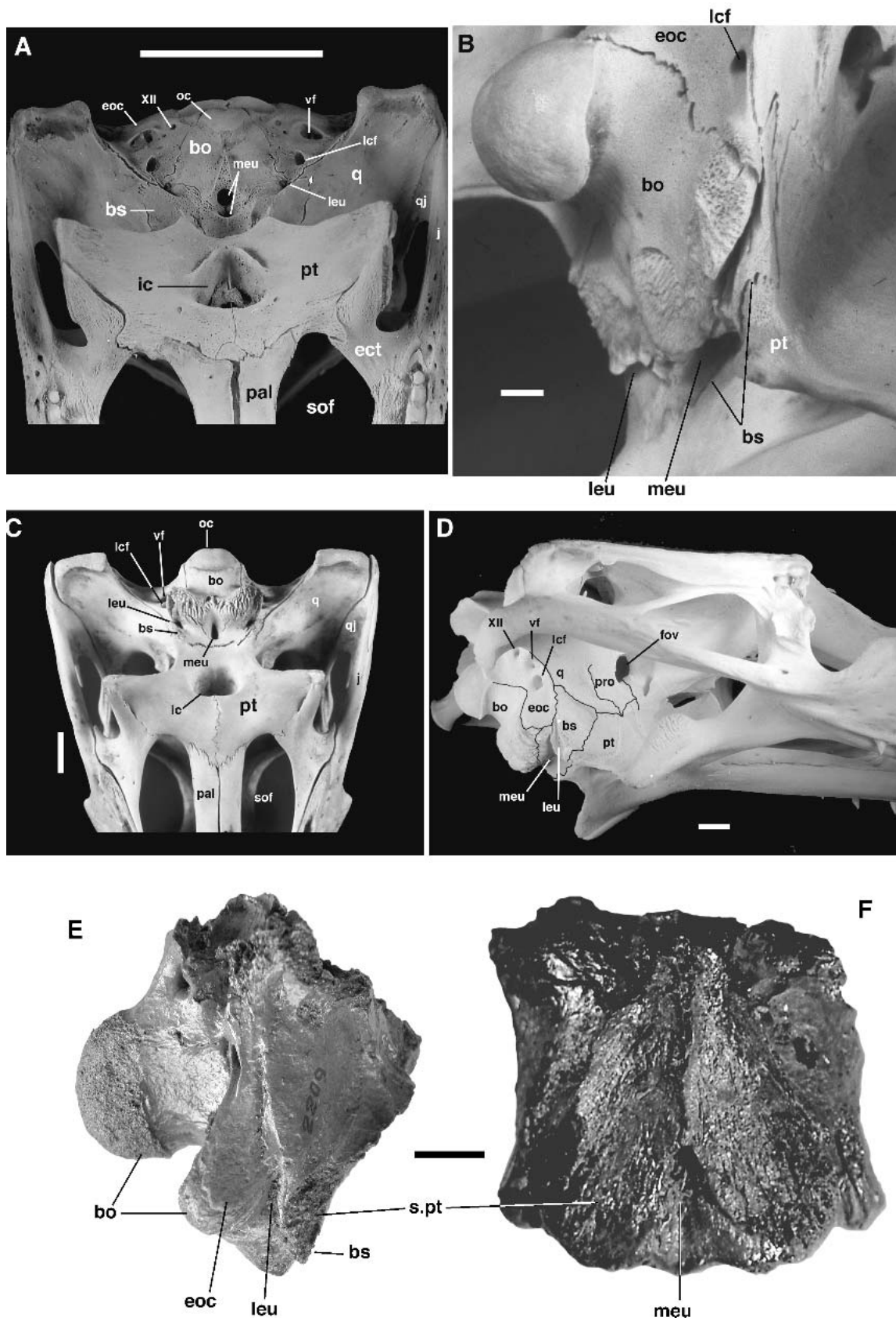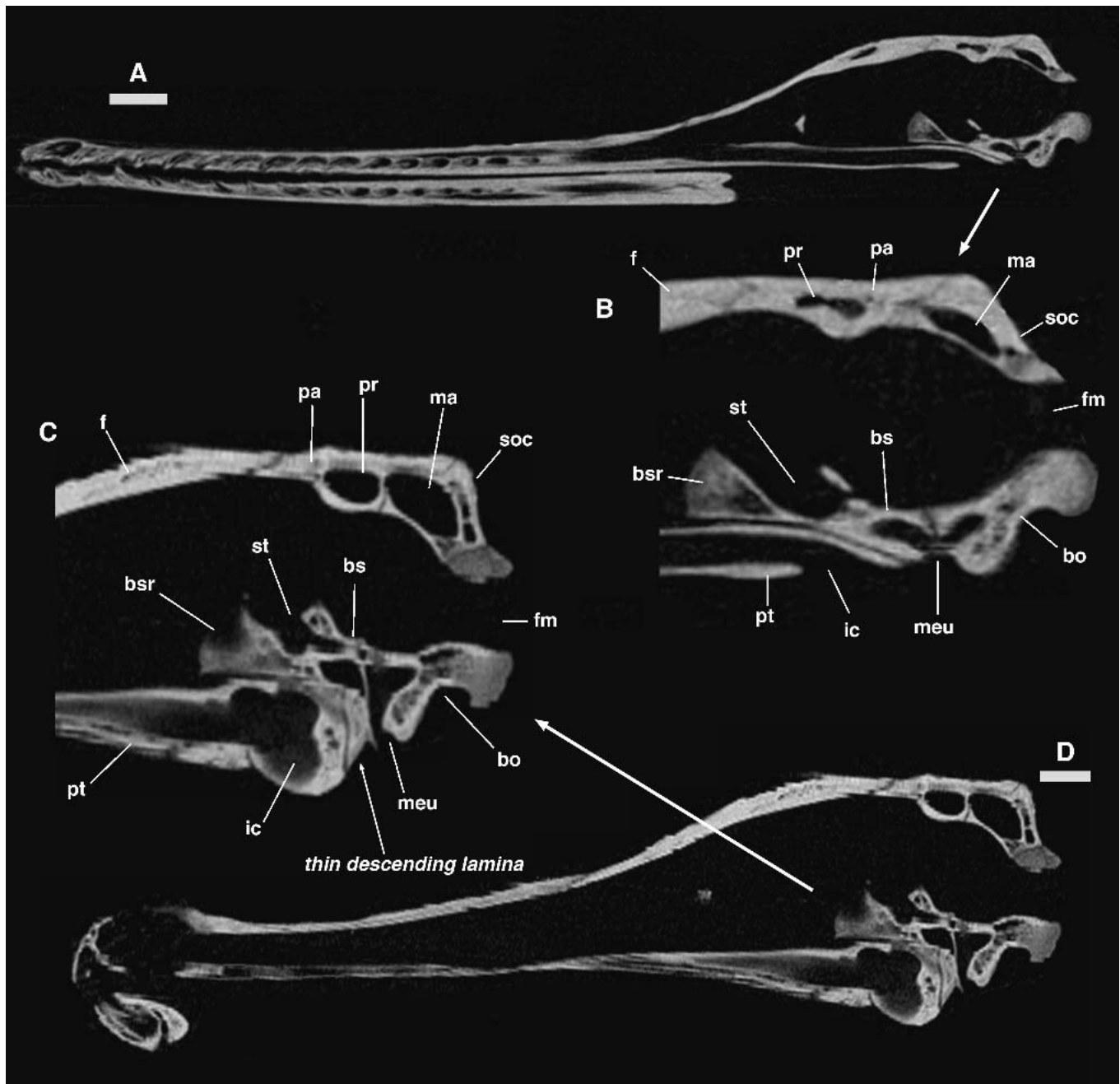
FIGURE 17. Cross-sectional morphology of crocodylian braincase. **A** and **B**, *Gavialis gangeticus* (TMM m-5490). **C** and **D**, *Alligator mississippiensis* (TMM m-983). Images are 250 μm computed x-ray tomographic slices through the sagittal plane of the braincase; see Rowe et al. (1999) for analytical details. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **bsr**, basisphenoid rostrum (cultriform process); **f**, frontal; **fm**, foramen magnum; **ic**, internal choana (in *Alligator*, slice passes through midchoanal septum); **ma**, mastoid antrum; **meu**, medial eustachian opening; **pa**, parietal; **pr**, parietal recess; **pt**, pterygoid; **soc**, supraoccipital; **st**, sella turcica. Scale equals 1 cm.

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FIGURE 16. Crocodylian braincase morphology and "verticalization." **A**, *Caiman crocodilus* (TMM m-837), hatchling, ventral view; basisphenoid is still a flat plate in front of the basioccipital. Anterior and posterior rami of medial eustachian canal visible externally. **B**, *Crocodylus niloticus* (TMM m-1786), adult, ventrolateral view; basisphenoid extends posteroventrally as a thin lamina between the basioccipital and pterygoid, with medial eustachian opening lying between basioccipital and basisphenoid's descending lamina. In adult or near-adult *Gavialis gangeticus* (posterior view, TMM m-5487, **C**; ventrolateral view, TMM m-5485, **D**, the basisphenoid is still visible externally as a broad element between the basioccipital and pterygoid, making it resemble the hatchling condition in A. In adult *Thoracosaurus neocesariensis* (AMNH 2209, [**E**] lateral view, [**F**] anterior view), the basisiphenoid is very thin anterior to the basioccipital, and the sutural surface for the pterygoid is preserved, indicating that the broad exposure seen in *Gavialis* was absent. Scale equals 1 cm. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **ect**, ectopterygoid; **eoc**, exocipital; **fov**, foramen ovale; **ic**, internal choana; **j**, jugal; **lcf**, lateral carotid foramen; **leu**, lateral eustachian opening; **meu**, medial eustachian opening; **oc**, occipital condyle; **pal**, palatine; **pro**, prootic; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sof**, suborbital fenestra; **s.pt**, articulation surface for pterygoid on basisphenoid; **vf**, vagus foramen.

date, nearly all thoracosaur fossils have come from such deposits, and their geographic range suggests a coastal distribution—*Eothoracosaurus* probably lived in or along the Mississippi Embayment, and later thoracosaurs seem to have ringed the early North Atlantic. This supports contentions based on physiology that the freshwater distributions of some extant crocodylian groups, including *Gavialis*, are comparatively recent phenomena (e.g., Taplin et al., 1985; Taplin and Grigg, 1989; Jackson et al., 1996). Vicariance explains gavialoid distribution only if we extend multiple stratigraphic ranges into the Early Jurassic or Triassic. Even if extant *Gavialis* is restricted to freshwater, its distribution is best explained by multiple transoceanic dispersal events, something with which the presence of basal gavialoids in marginal marine deposits is consistent.

Much remains to be done. Most importantly, there are two significant gaps in gavialoid history that could prove pivotal to the *Gavialis-Tomistoma* debate. The first involves the "gharial gap" between the extinction of "thoracosaurs" and the next oldest gavialoid occurrences in the late Eocene. Recognition that the late Paleocene *Thecachampsoides* is a gavialoid closes this gap somewhat, and additional late Paleocene gavialoids are undergoing description (Hua and Jouve, 2004); moreover, some late Paleocene and early Eocene fossils from Europe resemble *Thecachampsoides* and may prove to be close relatives (Brochu, 2002). But we are left to wonder what happened to the group for most of the Eocene. Interestingly, some nucleotide sequence analyses now predict a *Gavialis-Tomistoma* divergence in the early Eocene. Harshman et al. (2003) suggest that the disparity between fossil and molecular divergence estimates for *Gavialis* are resolved if we discount the thoracosaurs as close relatives of *Gavialis*; there is no morphological evidence for this idea, but if the "thoracosaurs" are not related to *Gavialis*, then fossils found in this gap should resolve the matter.

The other gap extends in the other temporal direction—what did pre-Maastrichtian gavialoids look like? Given the distribution of snout shape features among neosuchians, we would expect the last common ancestor of extant crocodylians to have been a generalized animal lacking the long, slender snout found in all fossil gavialoids currently known. The fact that *Eothoracosaurus* is already a highly modified animal, autapomorphies aside, suggests a lengthy unpreserved history for the group. That most characters supporting gavialoid monophyly are related to snout elongation means that basal, nonspecialized members of the group may go unnoticed.

In summary, the thoracosaurs represent a paraphyletic assemblage of basal gavialoids straddling the Cretaceous-Tertiary boundary. They seem to have lived in coastal settings, and a new species of basal gavialoid—*Eothoracosaurus mississippiensis*—may have lived in and around the Mississippi Embayment during the Late Cretaceous. *Eothoracosaurus* preserves character states suggesting very complicated histories for structures in the crocodylian lower jaw, and in combination with other thoracosaur fossils, suggests that the "unverticalized" braincase characterizing derived gavialoids is a derived condition. These fossils continue to support a pre-Cenozoic divergence between *Gavialis* and any other living crocodylian, including *Tomistoma*. Discovery of putative gavialoids in the Eocene and pre-Maastrichtian Cretaceous will prove critical in testing some of the hypotheses explored in this paper.

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APPENDIX 1

Character codings for gavialoids considered in this analysis. Most of the codings used in this analysis are provided in Brochu (1999) and Brochu and Gingerich (2000), along with character descriptions. Codings for *Gryposuchus* were modified as described by Brochu and Rincón (2004).

Eothoracosaurus mississippiensis

```
????? ????? ????? ??1?? ??000 ????? ?00?0 0???0 ??30?
??001 1?1?? ????0 ????? ??2?0 100?0 1021? 00?11 00040
01?02 ?00?0 00000 00000 000?? ?0100 0?0?0 ????? ?0?00
???01 10001 00??? 00??? ????? 00??
```

Thoracosaurus neocesariensis

```
???1? 1?1?? ?00?? ??11? ????? 01?0? ??000 0???0 ??30?
??001 ?11?? ????? ?1?00 0?200 10000 1021? 00011 00040
01002 ?0000 00100 00000 00000 ?010? 00000 00000 0?000
?0?01 10001 00?00 000?? ????? 000?
```

Thoracosaurus macrorhynchus

```
??11? 1?1?? 0???? ??11? ????? 0??0? ??000 0???0 ??300
??001 11??? ????0 ?1000 00200 100?0 10210 00011 10040
01002 ??000 00100 00000 0000? 1010? 00000 0?0?0 ?0000
?0?01 10001 00?10 000?? ????? 000?
```

Thecachampsoides minor

```
???1? 1???? 0???? ??11? ?00?0 ?100? ?0000 00??0 ?0300
00001 1110? 0??00 ?1?00 ?02?0 100?0 10210 10011 00040
01002 ?0000 0?100 00000 031?? ?0100 00000 0?0?1 0000?
0?001 10001 00?1? 100?? ????? 000?
```

Eogavialis africanus

```
????? 1???? ??0?? ???11 ????? ????? ???0? ????0 ?030?
?10?1 111?? ????1 ?1?00 00200 10000 10210 11011 00040
01002 ?0000 00200 00000 00100 00100 000?0 0?0?0 0000?
00011 10001 00?10 1000? ????? 000?
```

Gryposuchus colombianus

```
??1?0 ????? 00??? ??1?? ??000 ????? ????? ????0 ?0300
00001 11110 0??0 01000 00200 10010 10210 10011 10040
01102 ?0200 00200 00000 ?0100 00100 00000 00000 0000?
???12 10001 00?10 100?? ????? 000?
```

Ikanogavialis gameroi

```
????? ????? ????? ????? ????? ????? ????? ????? ??30?
??00? ?11?? ???0 ?1?00 ?02?0 10??? ?020? 200?? 10?40
0?1?2 ?02?0 0?20? ??0?0 ?01?? ?010? 0?00? ??0?? 0??0?
???12 10001 00??0 1???? ????? 00??
```

Siwalik *Gavialis*

```
????? ????? ??0?? ????? ????? ????? ????? ????? ??30?
??0?1 ????? ????? ?1?00 00200 100?0 1?2?0 ?001? ?00?0
0??03 ??20? 00200 0?000 ?010? ??00 000?? 000?? 0000?
???11 1???? 00?10 100?? ????? 000?
```

Gavialis gangeticus

```
02110 10110 00000 00110 00000 01001 0000? 00000 00300
00001 11100 00100 01000 00200 10000 10210 10011 10040
01103 00200 00200 00000 00100 00100 00000 00000 0000?
00011 10001 00010 10000 00000 0000
```

APPENDIX 2

Character state optimizations from phylogenetic analysis. Node labels are indicated in Fig. 14. * ACCTRANS only. ** DELTRANS only.

Gavialoidea 2(2)*, 9(1)*, 12(0)*, 30(1)*, 43(3), 68(2), 61(0)*, 68(2)*, 78(2)**, 79(1), 84(1), 89(4), 118(1), 119(0), 130(0)*, 145(1), 153(0)*

A 19(1)**, 27(1)**, 103(1), 130(0)**, 153(0)**

Thoracosaurus neocesariensis 149(0)*

B 149(1)**

Thoracosaurus macrorhynchus 86(1), 116(1)

C 81(1), 113(1), 151(1)

Thecachampsoides minor 112(3), 130(1)

D 103(2), 139(1)

Eogavialis africanum 20(1), 47(1), 60(1), 82 (1)

E 12(0)**, 61(0)**, 86(1), 93(1), 98(2)

F 54(1)*, 74 (1)*, 140(2)

Gryposuchus colombianus 54(1)**, 74(1)**

Ikanogavialis gameroi 79(0), 81(2)

G 95(3)

Gavialis gangeticus 2(2)**, 9(1)**, 30(1)**, 58(1)**