NEW TOMISTOMINE CROCODYLIAN FROM THE MIDDLE EOCENE (BARTONIAN) OF WADI HITAN, FAYUM PROVINCE, EGYPT

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NEW TOMISTOMINE CROCODYLIAN FROM THE MIDDLE EOCENE (BARTONIAN) OF WADI HITAN, FAYUM PROVINCE, EGYPT

BY

CHRISTOPHER A. BROCHU[1] AND PHILIP D. GINGERICH[2]

Abstract — A partial skull and mandible from the late middle Eocene Birket Qarun Formation of Egypt represents a new genus and species of tomistomine crocodylian, *Paratomistoma courti*. The new taxon can be distinguished from all other tomistomines on the basis of a skull table that slopes laterally from the midline and supratemporal fenestrae having sharp rims along their circumferences. *Paratomistoma courti* is the sister taxon to a clade that includes living *Tomistoma schlegelii,* an assemblage of fossil *Tomistoma* from the Miocene of the Mediterranean region, and *Gavialosuchus eggenburgensis* from the Miocene of Austria. This analysis supports the gavialoid affinities of previously described long-snouted crocodylians from the Gebel Qatrani and Qasr el-Sagha Formations of Egypt, all of which probably represent a single species *(Eogavialis africanum).* The large broad-snouted crocodylian from this region, *Crocodylus megarhinus,* is not descended from the last common ancestor of living *Crocodylus.*

INTRODUCTION

The Fayum Province of Egypt contains an important sequence of middle and upper Eocene strata yielding marine vertebrates that inhabited the Tethys Sea (Beadnell, 1905). This complements a middle Eocene section in the Mokattam Hills of Cairo, and the two sections taken together have yielded marine mammals from the Lutetian, Bartonian, and Priabonian stages of the Eocene (Abel, 1904; Andrews, 1906; Sickenberg, 1934; Gingerich et al., 1990; Gingerich, 1992; Domning and Gingerich, 1994; Gingerich and Uhen, 1996). In addition to mammals, other vertebrates including selachians, teleosts, and reptiles have been studied (Stromer, 1905; Andrews, 1906; Müller, 1927; Peyer, 1928; Case and Cappetta, 1990). The Fayum marine section is overlain by putatively Eocene and Oligocene strata yielding continental vertebrates that inhabited the coastal lowlands of North Africa (Stromer, 1903, 1908; Andrews, 1906; Schlosser, 1911; Simons, 1965,

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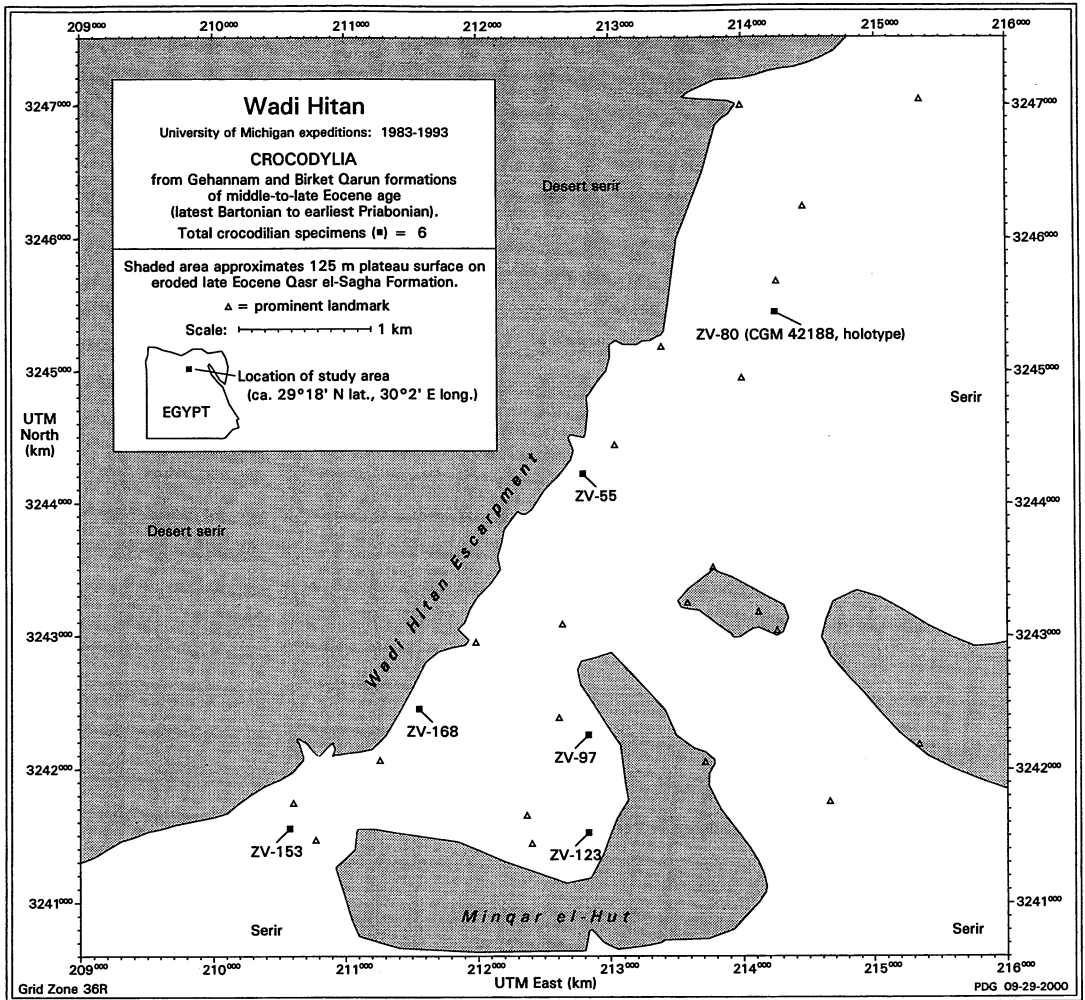
FIG. 1 — Map of Wadi Hitan (Zeuglodon Valley), Egypt, showing locality of the type specimen of *Paratomistoma courti*, new genus and species, field number ZV-80 (CGM 42188). Crocodylian remains are relatively rare in Wadi Hitan. Those mapped here come from the latest Bartonian through earliest Priabonian Gehannam and Birket Qarun Formations of late middle to early late Eocene age. Strata strike NE-SW and dip gently to the northwest. Shaded areas are tablelands rising above crocodylian-bearing strata and capped by indurated and erosion-resistant beds of the late Eocene Qasr el-Sagha Formation. Map is 7 km × 7 km, with specimens located by reference to their position on a triangulated field map, here fit to Universal Transverse Mercator (UTM) coordinates of prominent landmarks (grid zone 36R).

1989, 1990; Simons and Wood, 1968; Simons et al., 1983, 1995; Fleagle et al., 1986; Rasmussen et al., 1987; Simons and Rasmussen, 1990; Kappelman et al., 1992).

Crocodylians are known from these deposits (Andrews, 1901, 1905, 1906; Müller, 1927). And yet, despite the potential systematic significance of these taxa (Langston, 1965; Sill, 1970; Hecht and Malone, 1972; Buffetaut, 1982; Brochu, 1997), comparatively little has been done to revise

the taxonomy of these forms or consider their morphology in the general context of crocodylian phylogenetics. At present, the following crocodylian taxa are recognized from the Egyptian Eocene and Oligocene:

Gebel Qatrani Formation (Rupelian, lower Oligocene)
Eogavialis gavialoides (Andrews, 1905)
Crocodylus megarhinus Andrews, 1905
Crocodylus articeps Andrews, 1905

Qasr el-Sagha Formation (Priabonian, upper Eocene)
Eogavialis africanum (Andrews, 1901)

Lower Mokattam Formation (Lutetian, middle Eocene)
Tomistoma cairense Müller, 1927

A University of Michigan field project was started in 1983 to collect more and better specimens of fossil vertebrates from the marine Eocene of Fayum. The principal area investigated, Wadi Hitan or "Zeuglodon Valley," is named for the fossil whales found there. Most fossils come from shale of the upper part of the Gehannam Formation and are latest Bartonian in age, while others come from sands and sandstones of an overlying barrier bar complex called the Birket Qarun Formation and are earliest Priabonian in age (Gingerich, 1992).

The subject of this report is the partial skull and associated mandible of a new long-snouted crocodylian found in Wadi Hitan in 1987. It came from the Gehannam Formation in the northern part of the valley (Fig. 1). The new specimen is late Bartonian and thus intermediate in age between the crocodylians from the Lower Mokattam and Qasr el-Sagha Formations. Close examination shows that it cannot be referred to any previously published crocodylian taxon, and phylogenetic analysis indicates that whereas long-snouted crocodylians from overlying units in Fayum are gavialoids, the new taxon is a closer relative of living *Tomistoma schlegelii*. The new form is considered in a phylogenetic context, based on a data matrix in Brochu (1999, 2000), and the systematics of tomistomines are discussed. Other Fayum crocodylians are included in the phylogenetic analysis, and thus some discussion of their relationships and potential synonymy is required. Where appropriate their taxonomy is revised.

Taxonomic protocols. — Tomistominae is a stem-based group name based on the Indonesian false gharial *(Tomistoma schlegelii)* and all crocodylians more closely related to it than to any other living crocodylian species. The most recent morphological analysis of crocodylian relationships (Brochu, 1997, 1999) indicated a sister-group relationship between Tomistominae and a group including living *Crocodylus, Osteolaemus,* and several extinct taxa. The name Crocodylinae is used here to refer to the stem-based monophyletic group including *Crocodylus niloticus* (the living Nile crocodile) and all crocodylians more closely related to it than to any other living crocodylian species. Crocodylidae is the node-based monophyletic group including the last common ancestor of Tomistominae and Crocodylinae and all of its descendants, and Crocodyloidea refers to the stem-based group including *Crocodylus* and all crocodylians more closely related to it than to *Alligator* or *Gavialis.*

INSTITUTIONAL ABBREVIATIONS

CGM — Cairo Geological Museum, Cairo, Egypt
TMM — Texas Memorial Museum, Austin
UM — University of Michigan Museum of Paleontology, Ann Arbor

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin 1789
TOMISTOMINAE

Paratomistoma, new genus

Type Species. — *Paratomistoma courti*

Etymology. — *Para,* L., "next to" or "near;" *Tomistoma,* generic name for the only living tomistomine.

Definition. — A stem-based group name including the type species *(P. courti)* and all tomistomines more closely related to it than to *Tomistoma schlegelii, Gavialosuchus eggenburgensis, Tomistoma lusitanica,* or "*Tomistoma*" *cairense.*

Diagnosis. — Derived tomistomine crocodylian differing from all other tomistomines (including *T. cairense* from the underlying Mokattam Formation) in having a skull table that slopes laterally from the midline, acute rims on the supratemporal fenestrae, and laterosphenoid capitate processes with anterodorsal margins perpendicular to the sagittal plane.

Paratomistoma courti, new species
Figs. 2-4

Holotype. — CGM 42188, partial skull and mandible. A cast of the holotype is deposited in the University of Michigan Museum of Paleontology (UM 94813).

Locality. — Wadi Hitan, Fayum Depression, Egypt (Fig. 1).

Horizon and Age. — Gehannam Formation, middle Eocene (Bartonian).

Etymology. — The specific name refers to Nicholas Court, who found the type specimen while visiting the UM camp in Wadi Hitan.

Diagnosis. — As for genus.

DESCRIPTION

General Features. — Most of the rostrum is not preserved, but the posteriormost region of the snout immediately in front of the orbits is present (Figs. 2, 3). The small amount of the palate preserved provides very little information. The jaw is represented by several fragments (Fig. 4), representing a segment of the dentary at the back of the symphysis, parts of the left and right articular regions, and fragments from the anterior region of the dentary.

No cranial bones are fused together. Lack of cranial fusion has been used as indicative of immaturity in the past (e.g., Joffe, 1967), but this criterion is notoriously uninformative (Clark, 1986). CGM 42188 is best interpreted as morphologically mature on the basis of laterosphenoid closure. In hatchling crocodylians, the laterosphenoids are incompletely ossified, and the anterior part of the endocranial cavity is still enclosed by cartilage; as a result, the dry braincases of hatchlings are open anteriorly. During ontogeny ossification in the pile antotica progresses anteriorly until the laterosphenoids meet at the midline. The laterosphenoids are damaged anteromedially, but clearly they either met at the midline or approached each other very closely (Figs. 2, 3). Approximation of the laterosphenoids is an indicator of maturity, but not of maximum size; modern crocodylian skulls that are not maximum size for their species often have medially-meeting laterosphenoids, but skulls bearing this condition generally preserve character states indistinguishable from those in very large individuals.

The medial borders of the orbits are upturned slightly. Dorsally, the supratemporal fenestrae have very sharp rims along their circumference. This is unlike the situation in most crocodylians, in which the postorbital and much of the parietal portions of the supratemporal border are gradual

and smooth. Although the shape of the fenestrae is circular, as in living *Tomistoma,* the sharpness of the fenestral border is more like that in the late Cenozoic long-snouted form *Euthecodon.* There is no overhang of the dermal bones obliterating the supratemporal fossa, as in living caimans and *Osteolaemus.* Consequently, the new taxon was coded with the primitive state (presence of a fossa and absence of dermal overhang) in the character matrix (Appendix 1).

In posterior view, the skull table slopes ventrally from the midline (Fig. 2c). In most living crocodylians, the skull table is inflated in hatchlings, with a domed roof, but the skull table is planar in mature individuals. Lateral sloping is typical of outgroups to Crocodylia (e.g., *Hylaeochampsa* and *Bernissartia,* in which the braincase outwardly resembles that of a young modern crocodylian), and of gavialoids. Because CGM 42188 was a morphologically mature individual, it can be coded as bearing a laterally sloping skull table.

Cranial Bones. — The relationship between the nasals, premaxillae, and external naris cannot be determined; however, each nasal projects posteriorly beyond the anterior limit of the orbits, as in modern *Tomistoma* but unlike most other crocodylians, in which the nasals terminate anterior to the orbits. The nasals are broadest immediately anterior to the prefrontals and taper anteriorly, but whether the lateral sides of the nasals become parallel as they approach the external naris cannot be determined. They are modestly sculpted anteriorly as preserved, but smooth posteriorly.

The maxillae are not well preserved. Three complete and one incomplete alveoli are preserved on the left, and one complete and three incomplete alveoli can be seen on the right. Each preserved alveolus projects posterodorsally into its maxilla, so that the teeth would have projected anteroventrally. There was very little pitting or sculpting on the preserved portions of the maxillae.

Very little can be said of the jugals – only the anteriormost tip of the right element remains. It projects approximately 1.5 cm anterior to the front of the orbits, and the anterior tip is convex, projecting for a short distance into the maxilla.

The lacrymals and prefrontals are both roughly triangular in dorsal view, but the dorsal exposure of the lacrymal is about twice as long as that of the prefrontal. Each lacrymal is broadly convex laterally, where it contacts the maxilla and jugal, and concave medially, where it contacts the nasal. The lacrymals of living *Tomistoma* and *Gavialis* are concave laterally, where they contact the maxillae. There is no posterior process of the maxilla within the lacrymal, as in some crocodylians, including living *Tomistoma.* Dorsally, the prefrontals are heavily pitted except along their lateral margins, where they are smooth. Most of the lacrymal part of the orbit is not preserved, but the lacrymal duct is visible as a transversely-wide opening on the anterior margin of the orbit. As in most non-gavialoid crocodylians, it pierces a medial process of the lacrymal projecting within the prefrontal. The ventral surface of the lacrymal is largely covered by matrix.

In dorsal view, the prefrontals are concave laterally where they contact the lacrymals, and convex medially where they contact the nasals and frontal. They are heavily pitted dorsally. Ventrally, each prefrontal bears a descending process anterior to the orbit that contributed to a prefrontal pillar, the dorsal tips of which were expanded anteroposteriorly, as in non-gavialoid crocodylians. The pillars are not preserved ventrally, and nothing can be said of the medial projections of the pillars.

The relationship between the nasals and frontal is unusual. The nasals project posteriorly farther than in most crocodylians, and the frontal projects farther anteriorly than in most other taxa. Indeed, the frontal and nasals share lateral contact for thirty percent of the frontal's anteroposterior length. Nasals with thin posterior processes are seen in some tomistomines (e.g. *"Crocodylus" spenceri, Gavialosuchus americanus)* and in some derived gavialoids, such as *Gavialis gangeticus,* in which the frontal bears a very thin anterior process passing between two broad nasals.

Dorsally, prominent sculpturing is present on the frontal up to the anterior and lateral margins of the anterior process, which is smooth. A groove is visible ventrally for passage of the olfactory nerve. The frontoparietal suture is concave anteriorly and completely excluded from the supratemporal fenestrae.

The postorbital is incompletely preserved on both sides. The dorsal surface is heavily pitted. The postorbital bar is not complete, but its dorsalmost part indicates that it was slender and
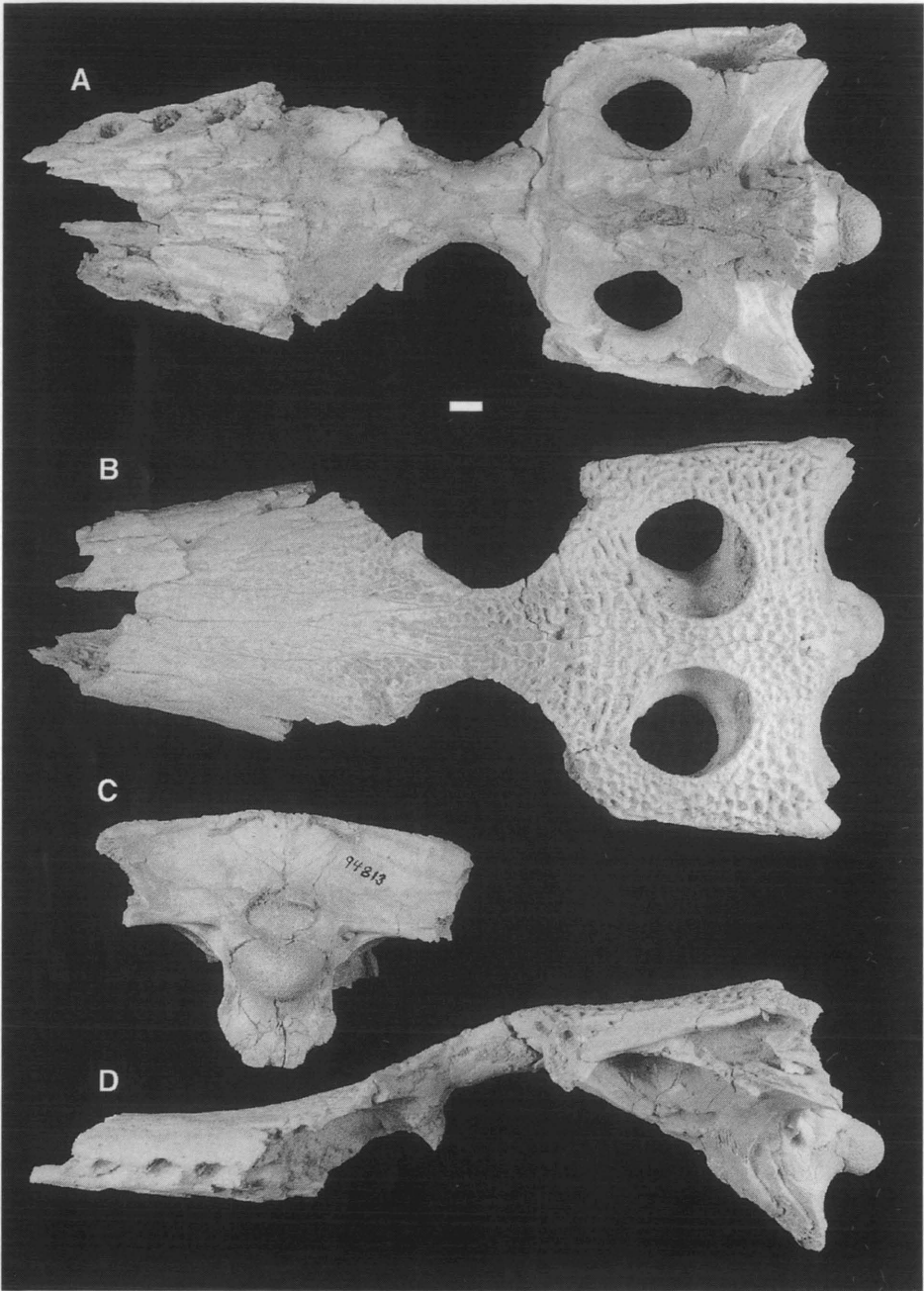
FIG. 2 — *Paratomistoma courti*, skull of holotype (CGM 42188) in ventral (A), dorsal (B), posterior (C), and left lateral (D) views. Scale = 1 cm.

proportioned like those of mature crocodylids. The anterolateral corner appears to have been broadly curved, not sharply angled as in most extant crocodylians, but this portion of the postorbital is damaged on both sides, and the actual shape cannot be recovered. The postorbital border of the supratemporal fenestra is sharp-rimmed, unlike the smoother borders in *Tomistoma* or *Gavialis* but like the more abrupt rims in some alligatorids.
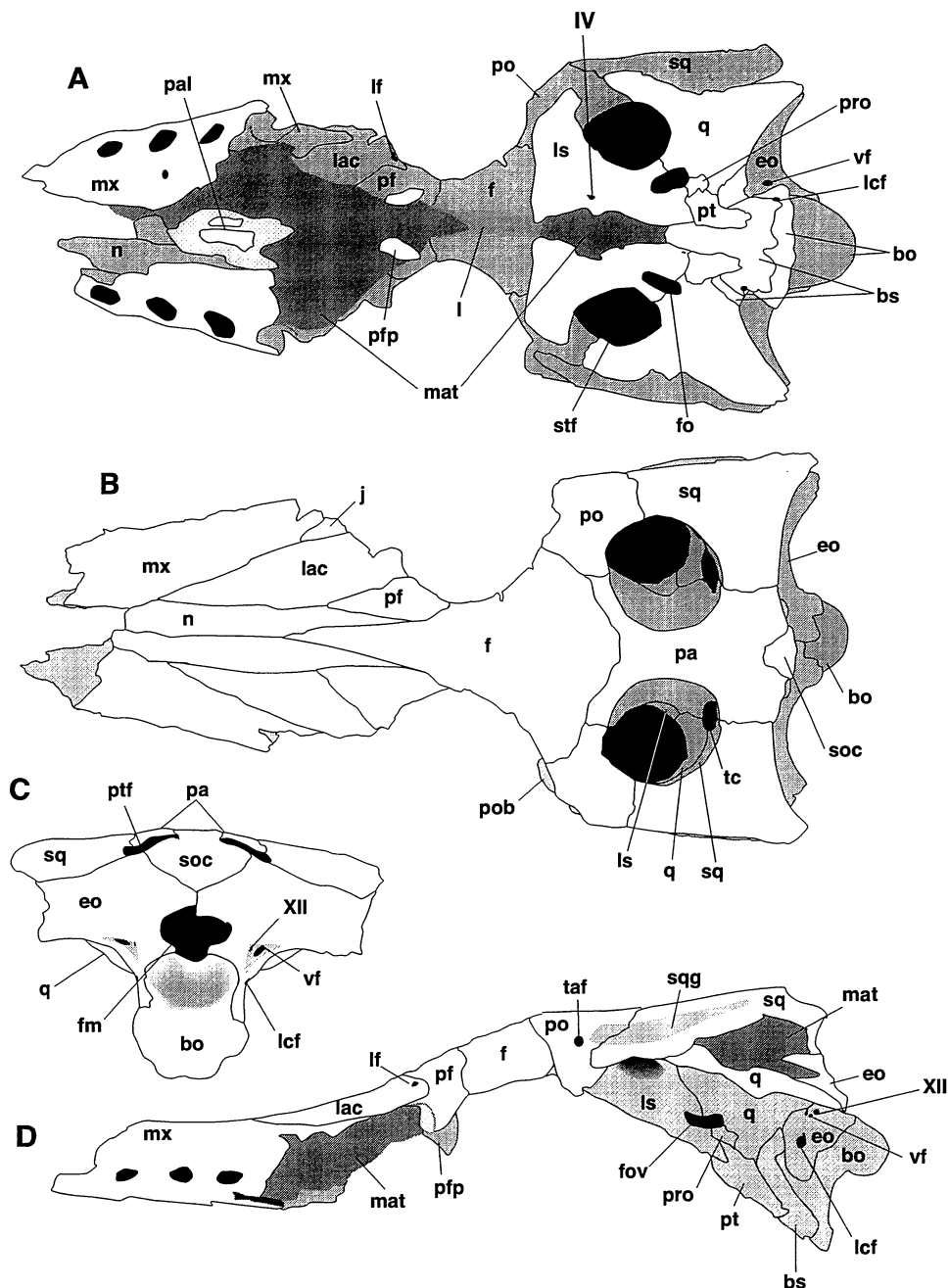
FIG. 3 — *Paratomistoma courti*, diagram of holotype skull (CGM 42188) in ventral (A), dorsal (B), posterior (C), and left lateral (D) views, showing sutural relationships. Abbreviations: *bs*, basisphenoid; *bo*, basioccipital; *eo*, exoccipital; *f*, frontal; *fm*, foramen magnum; *fo*, foramen ovale; *j*, jugal; *lac*, lacrymal; *lcf*, lateral carotid foramen; *lf*, lacrymal foramen; *ls*, laterosphenoid; *mat*, matrix; *mx*, maxilla; *n*, nasal; *pa*, parietal; *pal*, palatine; *pf*, prefrontal; *pfp*, prefrontal pillar; *po*, postorbital; *pro*, prootic; *pt*, pterygoid; *q*, quadrate; *stf*, supratemporal fenestra; *sq*, squamosal; *sqg*, groove on squamosal for external ear muscula-ture; *taf*, foramen for temporal artery; *tc*, temporal canal; *vf*, vagus foramen; *I*, groove on frontal for olfac-tory tract; *IV*, foramen for fourth cranial (trochlear) nerve; *XII*, foramen for twelfth cranial nerve.
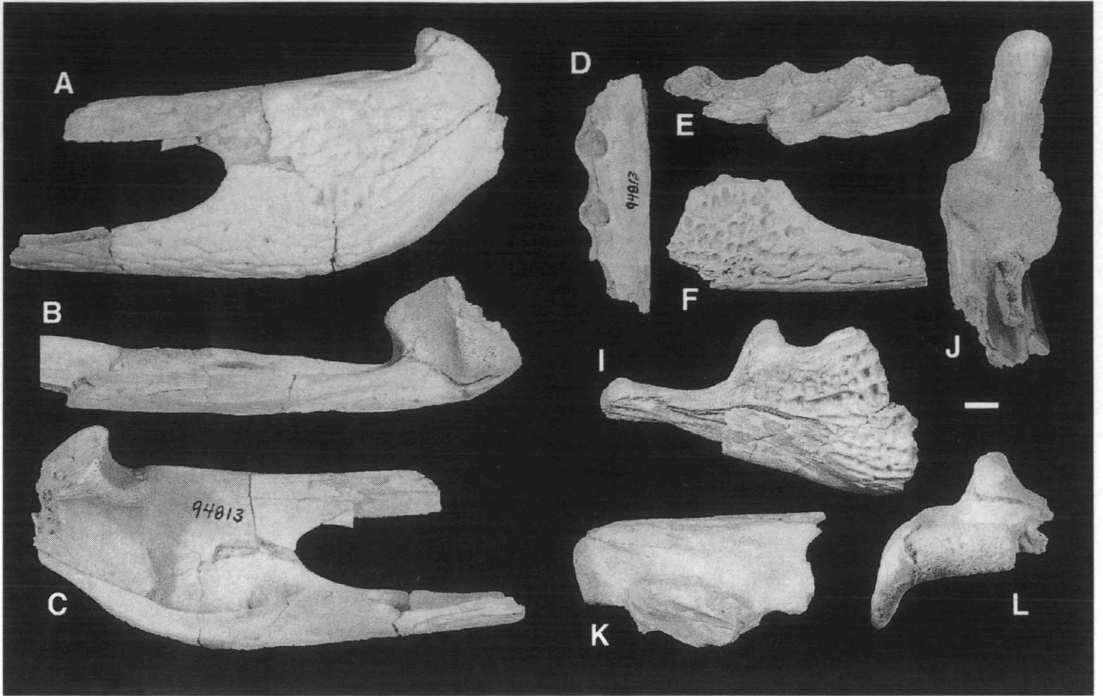
FIG. 4 — *Paratomistoma courti*, fragments of jaw and quadrate of holotype (CGM 42188). A-C, left angular, surangular, and articular in lateral (A), dorsal (B), and medial (C) views. D, fragment of left dentary, dorsal view. E, fragment of right dentary, mediai views. F, right angular, lateral view. I, J, right angular, surangular, and articular in lateral (I) and dorsal (J) views. K, L, left quadrate ramus in dorsal (K) and posterior (L) views. Scale = 1 cm.

The postorbitals are damaged laterally, and whatever contact they may have had with the quadratojugals or jugals cannot be determined. In ventral view, there is a thin postorbital lamina projecting posteriorly toward the squamosal, as in living *Tomistoma, Gavialis,* and alligatorids.

The single parietal is prominently pitted along its dorsal surface. Within the supratemporal fenestra, it makes broad contact with the postorbital, laterosphenoid and – immediately ventral to the temporal canal – the quadrate. The shape of the parietal border of the supratemporal fenestra is like that in extant *Tomistoma,* but, unlike most long-snouted crocodylians, the demarcation between skull table and fenestra is very sharp along the rim of the supratemporal fenestra. In *Tomistoma* and *Gavialis,* the anterior part of the parietal fenestra border is not sharp.

Dorsally, the squamosals form the posterolateral corner of the supratemporal fenestrae. The dorsal surfaces of the squamosals are heavily pitted. The posterior edge of each squamosal is concave, and laterally there is a long groove corresponding to the attachment space for the ear flap muscles (Shute and Bellairs, 1955). This groove flares anteriorly, as in gavialoids, *Gavialosuchus americanus, Gavialosuchus eggenburgensis,* and *Tomistoma lusitanica.*

The distalmost tip of the squamosal, lateral to the otic apterture, is preserved on a fragment of the left quadrate ramus. The ventral suture between the squamosal and quadrate is within the angle between the quadrate ramus and paraoccipital process, and does not extend anteriorly upon the quadrate ramus as in *Osteolaemus* and *Euthecodon.*

The supraoccipital is exposed dorsally on the skull table as a triangular element. It is broad posteriorly, as in nongavialoid crocodylians. Posteriorly, the supraoccipital is excluded from the foramen magnum by the exoccipitals. Its occipital face bears a low sagittal crest. The ventral

surfaces of the posttemporal fenestrae, comprised of the supraoccipitals, are angled dorsolaterally and project posteriorly beyond the occipital surface.

The laterosphenoids are damaged anteromedially, but they would have approached closely. The anterior margins of the capitate processes are oriented mediolaterally. Both foramina ovale are filled with matrix, but the laterosphenoids clearly formed the anterior border for each. There is a small opening on the anterior face of the left laterosphenoid corresponding to the passage for the trochlear nerve.

Each laterosphenoid bears a pair of dorsoventral sulci on its lateral surface. Immediately ventral to the dorsal sulcus is a small process. In most crocodylians, the ventral process of the laterosphenoid extends to the pterygoid and encloses a channel through which the ophthalmic nerve passes. This lamina of the laterosphenoid (the "laterosphenoid bridge") is incomplete in most crocodylids, and the ophthalmic nerve passes along a groove rather than a complete channel. This character is difficult to code, because it is variable within species. The ventral process of the dorsal sulcus in this taxon corresponds with the incomplete bridge seen in most extant crocodylids, and the ventral sulcus corresponds with the pathway for the ophthalmic nerve.

Only the dorsal braincase elements of the pterygoids remain. Each pterygoid made single lateral contacts with the quadrate and prootic and a pair of sutural contacts with the basisphenoid – one with the anterior basisphenoid exposure ventral to the foramen ovale, and another posteriorly. This posterior contact is set within a deep sulcus.

The prootic is exposed on the lateral braincase wall ventral to the foramen ovale (Fig. 3D). Internal details of its morphology cannot be discerned, and boundaries of the prootic are only apparent on the left side.

The basisphenoid was exposed broadly on the anterior wall of the braincase, immediately ventral to the foramen ovale. A small foramen can be seen on the right side. Posteriorly, the basisphenoid is visible as a pair of crescent-shaped exposures anterior to the occipital condyle that lead to a thin lamina anterior and ventral to the basioccipital (Fig. 3). The ventral lamina is incompletely preserved.

The exoccipitals and opisthotics are fused. Each exoccipital bears a broadly concave occipital face and forms half of the roof of the foramen magnum. Lateral to the foramen magnum is a pair of openings – a small medial opening for the twelfth cranial nerve and, lateral to it, the large ventrally-projecting vagus foramen. The lateral carotid foramen (Fig. 3) is ventral to the vagus foramen, which opens posterolaterally and is lateral to the posterior basisphenoid exposure. The ventral processes of the exoccipitals are slender and terminate at the same transverse plane as the ventral margin of the occipital condyle – the exoccipitals do not participate in the basioccipital tubera.

The basioccipital forms the occipital condyle and the floor of the foramen magnum. There is a modest sagittal crest on its posteroventral surface, closely resembling that of *Tomistoma schlegelii*. The medial eustachian opening is large and close to the posterior margin of the basioccipital. The lateral eustachian openings themselves are not preserved, but notches along the ventral margin of the basioccipital indicate that they were dorsal to the median opening.

Little can be said of the quadrate from the skull. Each quadrate bears a robust crest radiating dorsally from the triple junction of the quadrate, basisphenoid, and pterygoid. The quadrates form the ventral margins of the temporal canals within the supratemporal fenestrae. The otic aperture and recess dorsal to the quadrate are covered with matrix.

The left quadrate ramus is represented by an isolated fragment (Fig. 4J,K). The dorsal surface of the ramus is unsculpted. Ventrally, a long crest is visible corresponding with muscle scar D of Iordansky (1973). The lateral quadrate hemicondyle is preserved as a narrow articular surface for the articular, but the medial hemicondyle is not preserved.

The quadratojugal did not participate in the jaw joint. It bears shallow, broad pits along its lateroventral margin, but is smooth dorsally. The posterior tip of the jugal is preserved on the lateral edge of this fragment. The lateral edge of the quadratojugal and jugal projects ventrally from the ventral surface of the quadrate, and the quadrate ramus is deeply concave ventrally.

We cannot tell if the quadratojugal extended to the dorsal angle of the infratemporal fenestra or formed its posterior angle. The anterior edge of the quadratojugal as preserved is concave and bears a worn process, which may be a remnant of the quadratojugal spine; because of the extensive damage in this area, characters relating to the spine and sutural relationships around the infratemporal fenestra are left unscored.

Mandible. — The dentary is represented by fragments. The largest of these is from the posterior part of the symphysis, and bears two complete and one incomplete alveoli. The alveoli project posteroventrally into the dentary, and the teeth would have projected anterodorsally. The alveoli are separated by deep sulci, as in modern *Tomistoma.* The fragment is deeper posteriorly than anteriorly.

Medially, the dentary bore a long groove. A change in the angulation of the medial surface indicates the scar for the splenial, which evidently had a deep symphysis, but the extent and shape of this symphysis cannot be ascertained.

Isolated fragments from the anterior portions of the dentaries indicate only that the alveoli were closely spaced, separated by dorsal sulci, and projected anterodorsally rather than dorsally (Fig. 4).

The only evidence for the posterior extent of the dentary is on the left fragment of the articular region, on which a small triangular process at the end of a long groove represents its posteriormost tip. The groove on the angular for the dentary is preserved on one of the right articular region fragments, but the dentary itself is not preserved. It evidently passed posteriorly along the posterior margin of the external mandibular fenestra, and did not terminate at the anterior margin of the fenestra as in gavialoids.

The angular forms the posteroventral border of the external mandibular fenestra, and laterally it meets the surangular at the posteriormost tip of the fenestra. It is pitted posterior to the fenestra, but ventral to the fenestra these pits become shallow, and the angular is smooth or modestly pitted posterior to the jaw articulation. Medially, it does not project beyond the medialmost extent of the descending process of the articular.

The surangular forms the posterodorsal border of the mandibular fenestra. A piece of the splenial can be seen lapping over the medial surface of the surangular dorsal to the mandibular fenestra. In medial view, the suture between the surangular and angular is concave ventrally; laterally, it is concave dorsally. There is a broad sulcus on the surangular's surface, immediately dorsal to the mandibular fenestra. Posteriorly, there is a deeper sulcus lateral to the glenoid fossa. The contact between the surangular and the articular's descending process is set within a deep sulcus, and the lingual foramen is situated entirely on the surangular. The posteriormost tip of the surangular is not preserved on either of the articular fragments, but the groove for its articulation with the articular and angular can be traced all the way to the tip of the retroarticular process.

The glenoid fossa of the articular can be divided into two sulci separated by an anteromedially-trending ridge. The medial sulcus extends anteriorly beyond its lateral counterpart. The posterior wall of the glenoid extends farther dorsally over the lateral sulcus. The suture between the surangular and articular is bowed medially within the glenoid fossa, and the anterolateral corner of the lateral sulcus is floored by the surangular. The descending process of the articular is mediolaterally narrow and medially concave.

The retroarticular process is best preserved on the right side, where its medial edge is damaged. The process projected posterodorsally. The foramen aereum is not preserved on either side, but the left fragment is broken dorsally, and the passage immediately beneath the surface can be seen, indicating that the foramen would have been situated on the medial edge of the retroarticular process. The dorsal surface of the process was concave, with a long ridge projecting posteriorly from the lateral sulcus to the midpoint of the process.

PHYLOGENETIC RELATIONSHIPS OF *PARATOMISTOMA*

Methods. — *Paratomistoma courti* was added to a matrix of 164 discrete morphological characters (Brochu, 1999, 2000) to explore its relationships to other crocodylians. The analysis con-

sidered 42 ingroup taxa (including *P. courti*) and two outgroups *(Bernissartia fagesii* and an undescribed form from the middle Cretaceous of Texas; see Brochu, 1999). To reduce the number of polytomies in distant parts of the tree and diminish computational time, the alligatoroids were pruned to include only *Leidyosuchus canadensis, Diplocynodon hantoniensis, Brachychampsa montana, Alligator mississippiensis,* and *Caiman crocodilus.*

Taxa not considered in some or all previous analyses were included in this study. *Kambara,* a basal mekosuchine crocodyloid from the lower Eocene of Australia, was coded based on Willis et al. (1993) and Salisbury and Willis (1996); and *Gavialosuchus eggenburgensis* from the Miocene of Austria was coded based on Toula and Kail (1885). Codings for these two taxa are provided in Brochu (2000). This analysis also includes *Thoracosaurus neocesariensis,* a slender-snouted crocodylian from the Late Cretaceous of North America. This had been excluded from previous analyses because it coded redundantly with *Thoracosaurus macrorhynchus* (a basal gavialoid), but is included here to more thoroughly test the relationships among slender-snouted crocodylians. Specimens used to code this taxon are listed in Brochu (1999), and codings are shown in the Appendix, along with those for *Paratomistoma courti.*

Ten heuristic searches were conducted with PAUP (version 4.0b2a; Swofford, 1999), with the starting order of taxa randomized in each search.

Results. — Heuristic searches recovered 1941 equally most parsimonious trees (Fig. 5), with a length of 387 steps and C.I. (excluding uninformative characters) of 0.460. Monophyly of the group including all tomistomines except *"Crocodylus" spenceri* was supported in trees one step longer than optimal, but all nodes within Tomistominae, and Tomistominae itself, collapsed in trees two steps longer. None of the nodes within Tomistominae were considered robust by analysis of 5000 bootstrap replicate data sets. This probably reflects the relatively low number of apomorphies per node, and it is hoped that future surveys of tomistomine morphology will bring more character evidence to bear on relationships within the group.

Paratomistoma courti is deeply nested within Tomistominae. This tree is congruent with others derived from this matrix (Brochu, 1999, 2000). *Paratomistoma* is the sister taxon of a clade including *T. schlegelii, T. lusitanica,* and *Gavialosuchus eggenburgensis.* In the absence of *G. eggenburgensis* and *P. courti* (Brochu, 1997, 1999), *T. schlegelii* and *T. lusitanica* are sister taxa, and *T. cairense* is the sister taxon to (*T. schlegelii + T. lusitanica*).

Tomistoma lusitanica, in this analysis, includes a large number of fossils from the Burdigalian of Europe and northern Africa (Hulke, 1871; Lydekker, 1886; Capellini, 1890; Müller, 1927; Arambourg and Magnier, 1961; Antunes, 1961). The results of this analysis do not refute Rossmann et al.'s (1999) argument for inclusion of this assemblage within *Gavialosuchus,* but neither do they unambiguously support it. But there is a consistent separation between European and North American *Gavialosuchus.* Mook (1921) voiced suspicions that *G. eggenburgensis* was closer to *Tomistoma* than to *G. americanus.*

Much of the character support for Tomistominae is probably related to snout attenuation. Tomistomines are unambiguously united by the presence of a deep, but narrow, splenial symphysis; suborbital fenestrae without a posterior notch; and an acute, wedge-shaped palatine process. The deep splenial symphysis clearly results from elongation of the rostrum, but unlike the wide symphysis of gavialoids, that of tomistomines is very narrow. Moreover, the splenial lacks a foramen intermandibularis oralis in *T. schlegelii;* Langston and Gasparini (1997) reported a foramen in an immature specimen of *T. schlegelii* (TMM m-4720), but the foramen in this specimen is tiny, and other *T. schlegelii* lack this structure (Norell, 1989). The wedge-shaped palatine process and lack of suborbital fenestra notch all occur in other slender-snouted lineages, but they also arise sporadically in other groups, and so nonindependence cannot be demonstrated from these results. Long premaxillary processes occur not only in other narrow-snouted taxa, but also in *"C." acer* and *Brachyuranochampsa,* and so they might be synapomorphies for a more inclusive group that were later reversed in Crocodylinae.

Only a single character unambiguously diagnoses the clade including *Paratomistoma* and more derived tomistomines. In these taxa, the lingual foramen perforates the surangular. This is actually the plesiomorphic condition for Crocodylia, and indeed the condition in *"Crocodylus" spenceri.* The lingual foramen lies on the surangular-articular suture in a few lineages (*Crocodylus, Alligator*),
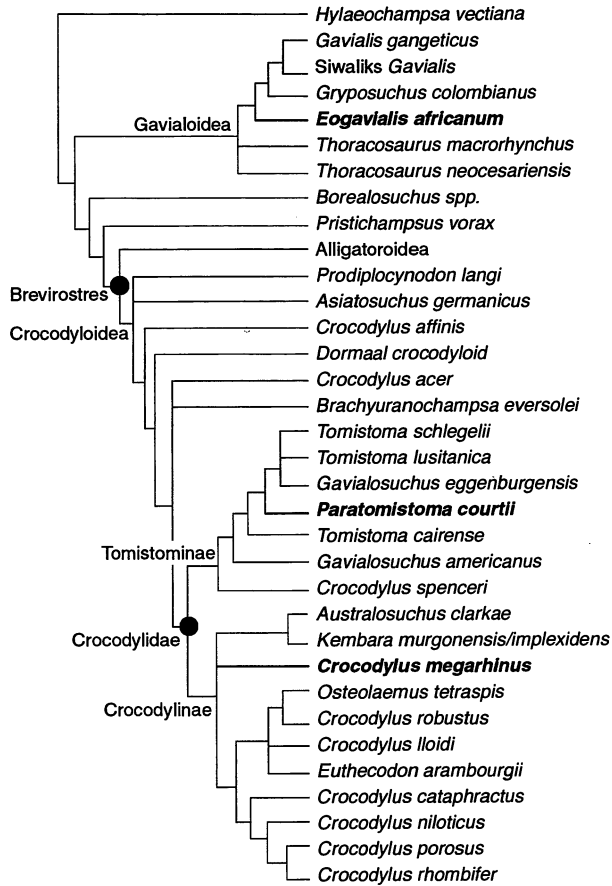
FIG. 5 — Strict consensus of 1,941 equally most-parsimonious trees (length = 387, CI = 0.460). Fayum crocodylians in boldface. Large dots indicate node-based group names.

with the channel passing along the contact surface between the bones before exiting through the surangular, but in *Gavialosuchus americanus* and *Tomistoma cairense* the foramen lies entirely on the descending process of the articular. This is also true in the jaw of *Maroccosuchus*, a tomistomine from the early Eocene of Morocco (Jonet and Wouters, 1977). Because the set of most parsimonious trees places *T. cairense* closer to the crown than to *G. americanus*, placement of the foramen on the surangular becomes the derived condition further up the tree. The condition of the foramen is not known in *T. lusitanica*.

A closer relationship between *T. cairense* and more derived tomistomines is unambiguously supported by only one character – absence of a lamina of the articular along the medial surface of the surangular. Drawing *T. cairense* and *G. americanus* together increases tree length by only a single step. This weakens the conclusions drawn from Fig. 5.

Three characters in the matrix diagnose *Paratomistoma courti*. The skull table slopes laterally from the midline, in contrast with the planar skull tables seen in other mature brevirostrines. The posterior carotid foramen opens lateral to the posterior basisphenoid exposure (Fig. 3) – the condition seen in most crocodylians, but a reversal from the derived state seen in other crocodyloids, where the foramen opens dorsal to the basisphenoid at maturity. Both of these characters are also seen in very immature crocodyloids, but the holotype of *Paratomistoma courti* suggests a mature individual. The third autapomorphy involves a horizontal orientation of the laterosphenoid capitate processes ventral to the frontal – this is seen in gavialoids, but in other crocodylians the pro-

cesses are oriented anterolaterally. This can be seen in Fig. 2B – the anterodorsal margins of the laterosphenoids are perpendicular to the sagittal plane, whereas they intersect this plane at an acute angle in most other crocodylians.

The tree in Fig. 5 has implications for other Fayum crocodylians. That many fossil taxa given the name *Crocodylus* are not descended from the last common ancestor of living species has long been suspected, but some fossils even now conventionally thought to be *Crocodylus* do not belong to that group (Salisbury and Willis, 1996; Brochu, 2000). Andrews (1905, 1906) described two species of *Crocodylus* from the Jebel-el-Qatrani Formation: *Crocodylus articeps* and *Crocodylus megarhinus*. *Crocodylus megarhinus* was based on less complete material, but suggested a larger, broader-snouted taxon than *C. articeps*, and indicated that the region around,the external naris was comparatively larger relative to body size in *C. megarhinus* than in *C. articeps*. More complete cranial material of *C. megarhinus* was described and figured by Mook (1927) and Müller (1927). One of the specimens used in this analysis (AMNH 5076) had been identified as *C. articeps*. This is the anterior end of a mandible from the same locality as AMNH 5061, which is demonstrably *C. megarhinus*, and it cannot be distinguished from the lower jaw associated with AMNH 5061. Indeed, based on other specimens referred to *C. articeps* (AMNH 5095, AMNH 16618, AMNH 16615, AMNH 16613), I question the distinctness of these two names. *Crocodylus megarhinus* may simply represent more mature *C. articeps*.

Mook (1927) considered *C. megarhinus* to be ancestral to extant *C. niloticus*, but other authors have been more cautious (e.g., Müller, 1927; Leakey et al., 1996), acknowledging the similarities between the two taxa, but also recognizing similarity with *C. lloidi* and declining to indicate specific relationships. Tchernov (1986) considered it unrelated to other known African "*Crocodylus*," living or extinct. The relatively narrow snout of specimens identified as *C. articeps* has begged comparisons with the modern African species *C. cataphractus* (Müller, 1927), and Tchernov (1986) considered the two to be ancestor and descendent.

Based on this analysis, *Crocodylus megarhinus* is a crocodyline, but is not a member of crown-group *Crocodylus*. It shares a quadrate participating in the infratemporal fenestra with other crocodylines, but retains a broadly-exposed prootic on the braincase lateral wall and lacks the blind recesses along the lateral wall of the maxillary sinus diagnosing *Crocodylus*.

Eogavialis africanum, which was originally described as *Tomistoma africanum*, is a gavialoid, as suggested by Langston (1965), Sill (1970), Hecht and Malone (1972), and Buffetaut (1982). In this analysis, *E. africanum* includes several other named taxa – *E. gavialoides* (Andrews, 1905), *E. kerunense* (Andrews, 1905), and *E. tenuirostre* (Müller, 1927). These differ only in stratigraphic position and should be regarded as synonyms of *Eogavialis africanum*. Support for a gavialoid affinity of this taxon is strong and based on both cranial and postcranial evidence, not all of which is related to longirostry – the splenial symphysis is deep and wide, maxillary teeth are homodont, the exoccipitals form the robust lateral walls of the basioccipital tubera, the incisive foramen is located far from the premaxillary toothrow, and the orbital margin is telescoped. The axial keel is deeply forked, and the dorsal osteoderms are rectangular and bear a broad anteromedial process.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Most vertebrates from the Gehannam Formation indicate a marine setting (Gingerich, 1992). As such, it is tempting to speculate that *Paratomistoma* was a marine, or at least coastal, crocodylian.

Paratomistoma is not the only tomistomine known from marine deposits. Most North American *Gavialosuchus*, for example, are known from coastal units along the Atlantic Coastal Plain (Cope, 1867; Auffenberg, 1954, 1957; Erickson and Sawyer, 1996). Miocene tomistomines are known from islands in the Mediterranean (e.g., Hulke, 1871), and a specimen possibly referrable to "*Crocodylus*" *spenceri* is known from deposits in Belgium with a strong marine component (Swinton, 1937). That tomistomines enjoy a nearly cosmopolitan distribution during the Tertiary

may be explained by a broad capacity to disperse across marine barriers (Antunes, 1987, 1994; Antunes and Ginsburg, 1989; Taplin and Grigg, 1989; Brochu, in press).

This is also supported by studies of extant crocodylian physiology. Although all living crocodylians can withstand exposure to salt water (Jackson et al., 1996; Moulton et al., 1999), most non-alligatorid forms are known to have specialized osmoregulatory tissues on the tongue and in the cloaca (Taplin, 1988; Taplin and Grigg, 1989; Taplin et al., 1985; Taylor et al., 1995; Pidcock et al., 1997). These allow a crocodylian to maintain osmotic balance in a saline environment. Osmoregulation has not been studied directly in *Tomistoma*, but the anatomy of the buccal cavity is congruent with that of other living crocodylids, and it is reasonable to infer similar osmoregulatory capacity in living false gharials as in other extant crocodylids (Taplin and Grigg, 1989).

Oddly, although most fossil crocodylians from marine deposits are long-snouted forms, extant long-snouted crocodylians are rarely encountered in seawater. *Tomistoma* is distributed throughout Indonesia, suggesting some capacity for swimming between islands, but is usually encountered in freshwater swamps (Thorbjarnarson, 1992). *Gavialis* has never been seen in salt water (Singh and Bustard, 1982; Taplin, 1988). Some fossil gavialoids are known from marine units, and gavialoid paleobiogeography suggests occasional marine dispersal in the past (Langston and Gasparini, 1997; Brochu, in press); hence, the restricted habitats of extant *Tomistoma* and *Gavialis* appear to be relics of a formerly more extensive distribution that, at times, included nearshore environments. Most crocodylians currently found in or near seawater are "generalized" forms with relatively broad snouts, such as the living saltwater crocodile, *Crocodylus porosus*. Fossil "generalized" crocodylians are occasionally encountered in marine deposits (e.g., Angielczyk and Gingerich, 1998), but these are much less common than long-snouted relatives.

ACKNOWLEDGMENTS

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APPENDIX — Character codings for *Thoracosaurus neocesariensis* and *Paratomistoma courti*. A list of characters can be found in Brochu, 1999; see that, and Brochu 2000, for codings of remaining taxa.

	1 11111	11112	22222	22223	33333	33334	44444	44445
	12345 67890	12345	67890	12345	67890	12345	67890	12345 67890
Thoracosaurus neocesariensis	???1? ??1??	??0??	??11?	?????	01?0?	??100	0???0	??3?? ????1
Paratomistoma courti	????? ?????	?????	?????	?????	?????	?????	?????	??00 ?0?01

								1
	55555 55556	66666	66667	77777	77778	88888	88889	99999 99990
	12345 67890	12345	67890	12345	67890	12345	67890	12345 67890
Thoracosaurus neocesariensis	????? ?????	?1?00	?0200	100?0	1021?	?0011	000??	01002 ?0000
Paratomistoma courti	0???? ????0	?1?00	?0??1	???0?	1?2??	20?1?	00???	?10?? ???00

	11111 11111	11111	11111	11111	11111	11111	11111	11111 11111
	00000 00001	11111	11112	22222	22223	33333	33334	44444 44445
	12345 67890	12345	67890	12345	67890	12345	67890	12345 67890
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