

EOSUCHUS (CROCODYLIA, GAVIALOIDEA) FROM THE LOWER EOCENE OF THE ISLE OF SHEPPEY, ENGLAND

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ABSTRACT—A partial skull from the early Eocene London Clay of the Isle of Sheppey, England, is referable to the gavialoid clade *Eosuchus*, otherwise known from the late Paleocene of continental Europe and North America. It differs slightly from Paleocene forms, but there is insufficient material on which to base a new species. This extends the range of *Eosuchus* beyond the Paleocene and represents the first unambiguous occurrence of a gavialoid in the early Eocene.

INTRODUCTION

Part of the controversy surrounding the relationships of the two living gharials—*Gavialis gangeticus* (Indian gharial) and *Tomistoma schlegelii* (Indonesian false gharial)—involves time of divergence. Morphological data view them as distant relatives, with *Tomistoma* nested within Crocodylidae and *Gavialis* basal to all other crocodylians, implying that their last common ancestor was in the Mesozoic (e.g., Kälin, 1931; Mook, 1934; Norell, 1989; Tarsitano et al., 1989; Brochu, 1997; Hua and Jouve, 2004). Molecular data, on the other hand, usually regard them as living sister taxa with a divergence in the Cenozoic. Molecular divergence estimates range from the early Eocene through the Neogene (Densmore, 1983; Densmore and Dessauer, 1984; Hass et al., 1992; Harshman et al., 2003).

The oldest known tomistomine, “*Crocodylus*” *spenceri* (Buckland, 1836), is of Ypresian age. Other tomistomines are known throughout the Eocene of the Northern Hemisphere (Müller, 1927; Swinton, 1937; Berg, 1969; Bramble and Hutchison, 1971; Li, 1975; Brochu and Gingerich, 2000; Rossmann, 2002; Kotsakis et al., 2004). Fossils now thought to be gavialoids first appear in the Campanian and are found through the Maastrichtian into the Paleocene of the North Atlantic region (Troxell, 1925; Piveteau, 1927; Carpenter, 1983; Schwimmer, 1986; Gallagher et al., 1986; Zarski et al., 1998; Laurent et al., 2000; Brochu, 2004; Robb, 2004; Delfino et al., 2005), but they then vanish from the record and reappear in the latest Eocene (Andrews, 1906; Hecht and Malone, 1972; Buffetaut, 1982). This “gharial gap” occurs in the stratigraphic window in which some nuclear DNA sequence data predict a *Gavialis*–*Tomistoma* divergence (Harshman et al., 2003).

The lower boundary of the gap is based on three late Paleocene gavialoids—*Argochampsia krebsi* Hua and Jouve, 2004, from Morocco, and two species of *Eosuchus*, one from northwestern Europe (*Eosuchus lerichei* Dollo, 1907) and another from the eastern United States (*Eosuchus minor* [Marsh, 1870]). *Eosuchus* was formerly classified as a relative of *Tomistoma* (Swinton, 1937), but this was based on a combination of coarse derived morphology (the slender snout) and detailed plesiomorphy (e.g., contact between the premaxillae and nasals). Phylogenetic analyses place *Eosuchus* within Gavialoidea (Delfino et al., 2005; Brochu, 2006).

A review of crocodylians from the London Clay of the Isle of Sheppey, England, reveals a partial skull referable to *Eosuchus*. It differs slightly from Paleocene *Eosuchus*, but whether the differences represent diagnostic features, intraspecific variation, or taphonomic artifacts is unclear. Although previously referred to the basal tomistomine “*Crocodylus*” *spenceri*, also from the London Clay (Lydekker, 1887, 1888), it is not a crocodyloid. The London Clay is of early Eocene (Ypresian) age (King, 1981, 1984; Sumbler, 1996), and the specimen described here provides the first clear occurrence of a gavialoid in the early Eocene. Although this does not close the gharial gap, it demonstrates the potential for improved sampling within this critical stratigraphic span.

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789, sensu Clark in Benton and Clark, 1988
GAVIALOIDEA Hay, 1930, sensu Brochu, 2003
EOSUCHUS Dollo, 1907

Referred Specimen—Natural History Museum, London (BMNH) R41, partial skull consisting of braincase and skull table, with a fragment of the lower jaw and the atlas intercentrum attached to the ventral surface (Figs. 1, 2).

Occurrence—Lower Eocene (Ypresian) London Clay, Isle of Sheppey, southeastern England.

Description—Only the posteriormost portions of the maxillae are preserved. Two complete alveoli and the posterior half of a third are preserved on the right element, indicating that the maxillary tooth row extended lateral to the suborbital fenestra, though the posterior extent is not known. The only portion of the jugal identified is the dorsal-most portion of the ascending jugal process of the right postorbital bar.

The nasals cannot be traced on the dorsal surface, and although the frontal extended forward of the orbits, the sutures bounding the anterior process of the frontal become indistinct close to the broken surface. In late Paleocene *Eosuchus*, the nasals pass between the prefrontals, the frontal extends past the anterior margin of the orbits, and the anterior process of the frontal is relatively short; in the present specimen, the anterior process of the frontal appears to be comparatively longer.

Sutural relationships between the lacrimals, prefrontals, and frontal are difficult to trace anterior to the orbits. Their arrangement around the orbital rims is consistent with that in *E. lerichei* and *E. minor*. The lacrimal is an anteroposteriorly elongate element forming the anterior margin of the orbit. It lies medial to the jugal and maxilla and lateral to the prefrontal and nasal. The prefrontal is crescentic in dorsal outline. It forms the anteromedial margin of the orbit. It contacts the lacrimal laterally and the frontal and nasal medially. There is a shallow sulcus at the posterior end of the prefrontal between the orbit and frontal.

The anterior process of the frontal becomes indistinct anteriorly, and its anterior limit cannot be seen. However, it is clear that the process extended at least as far as the anterior margin of the orbits. The frontal is flat between the orbits, and its sutures with the prefrontals emerge from the orbital rim at an acute angle. The frontoparietal suture is concave anteriorly and does not enter the supratemporal fenestrae.

The anterolateral corner of the skull table, comprised of the postorbital, is broad and U-shaped. The dorsal surface of the postorbital slopes anteroventrolaterally dorsal to the inset postorbital bar. The postorbital portion of the postorbital bar is similar to that of *E. lerichei* and almost triangular in cross section, with comparatively flat lateral and anterior surfaces meeting at a right angle ventral to a prominent anterolateral tubercle.

The parietal is constricted between the supratemporal fenestrae, forming a dorsally flat interfenestral bar that expands laterally anterior and posterior to the fenestrae. It thickens along the fenestral rims. The pa-

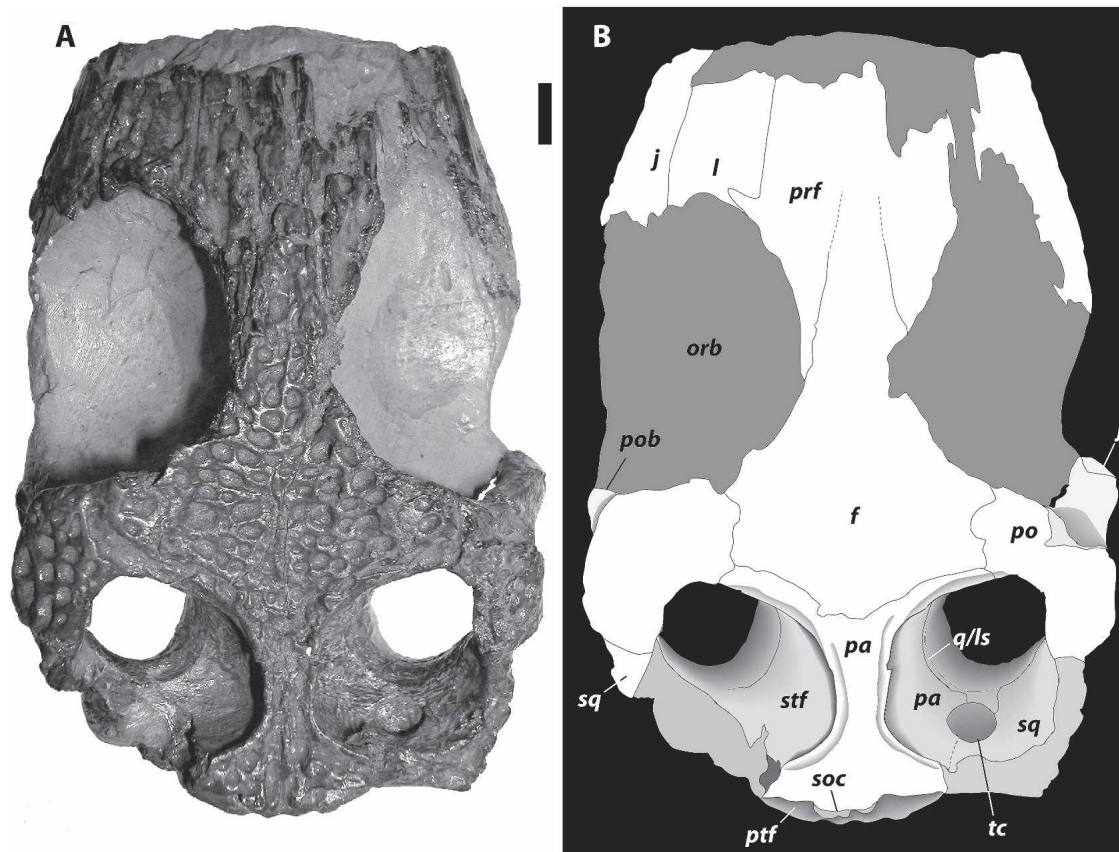


FIGURE 1. BMNH R41, *Eosuchus* sp., skull table and braincase in dorsal view. **A**, photograph. **B**, line interpretation. **Abbreviations:** **f**, frontal; **j**, jugal; **l**, lacrimal; **orb**, orbit; **pa**, parietal; **po**, postorbital; **pob**, postorbital bar; **ptf**, floor of posttemporal fenestra; **q/ls**, quadrate/laterosphenoid (suture separating them not preserved); **soc**, supraoccipital; **sq**, squamosal; **tc**, opening of temporal canal. Scale bar equals 1 cm.

rietal also forms the medial walls of the supratemporal fossae, contacting the laterosphenoids and quadrates ventrally. Along with the quadrate and squamosal, the parietal forms a large, circular temporal canal on the posterior wall of the supratemporal fenestra. Sutural separation between the quadrate and laterosphenoid is not preserved on the lateral braincase wall (see below), but the parietal and squamosal did not meet ventral to the temporal canal, indicating that the quadrate contributed to its margin.

The squamosals are imperfectly preserved on both sides, but they formed the posterolateral margins of the supratemporal fenestrae and had flat dorsal surfaces behind the postorbitals. The lateral squamosal grooves are incomplete, but they appear to flare anteriorly as they approach the postorbital bar.

The palatines formed a bar between the suborbital fenestrae with linear lateral margins and a flat ventral surface. They extend anterior to the fenestrae to form an anterior palatine process. The palatine-maxillary sutures appear to converge abruptly, which suggests a wedge-shaped palatine process, but the anterior end of the process is not preserved.

The pterygoid wings and internal choanae are not preserved, although the posteroventral surface of the pterygoids as preserved is anteriorly reflected, presumably indicating the posterior wall of the nasopharyngeal duct and the approximate location of the choana. The pterygoid continues anteriorly dorsal to the palatines, forming a midline septum within the nasopharyngeal duct.

Sutural relationships on the lateral braincase wall cannot be reconstructed. The vagus foramen is circular. Posterior to it, on what is presumably the quadrate, is a thin crest extending from the ventral surface of the quadrate ramus along the braincase to approximately the point at which the descending process of the exoccipital and quadrate diverge to expose the basisphenoid. A similar structure is seen in *Eosuchus lerichei* and *E. minor* (Brochu, 2006), but in this case the crest does not extend ventrally to merge with the basioccipital tuber and form the lateral wall

of the lateral eustachian canal. Whether this is real morphology or the result of damage is unclear.

The supraoccipital is triangular in posterior view. It forms the floor of each slit-like post-temporal fenestra, both of which can be seen along the posterior margin of the skull in dorsal view (Fig. 1). The supraoccipital is also exposed as a very thin element immediately posterior to the parietal on the skull table. A shallow, dorsoventrally elongate sulcus extends from the medial limit of the posttemporal fenestra. A low midline crest separates the sulci.

On the occipital surface, the exoccipitals meet at the midline to exclude the supraoccipital from the foramen magnum. A single foramen for cranial nerve XII pierces each exoccipital on the lateral wall of the foramen magnum. A deep groove lateral to the foramen magnum forms the dorsal and medial surfaces of the vagus foramen, and the lateral carotid foramen lies below this. The anteroposteriorly wide descending process of the exoccipital extends ventrally to the basioccipital tuber.

The basioccipital forms the hemispherical occipital condyle and the floor of the foramen magnum. It has a pair of crescentic tubera that nearly meet at the midline, a feature found in *E. lerichei* and *E. minor*.

The basisphenoid lies as a thin lamina on the anterior surface of the basioccipital behind the median eustachian foramen. The foramen itself is circular and is bound on all sides by the basisphenoid, which becomes anteroposteriorly thick around it. Although the lateral eustachian foramen itself cannot be seen, a groove on the right side of the braincase forward of the right basioccipital tuber probably indicates the location of the channel.

A fragment of the lower jaw is attached to the ventral surface of the skull, comprised of parts of the dentary, splenial, and the anterior-most part of the surangular. Two alveoli are visible in anterior view, one of which houses a conical tooth. The splenial is a flat plate presently lying against the palate, but originally medial to the dentary. The only part of the surangular preserved is the spur that, in other crocodylians, ap-

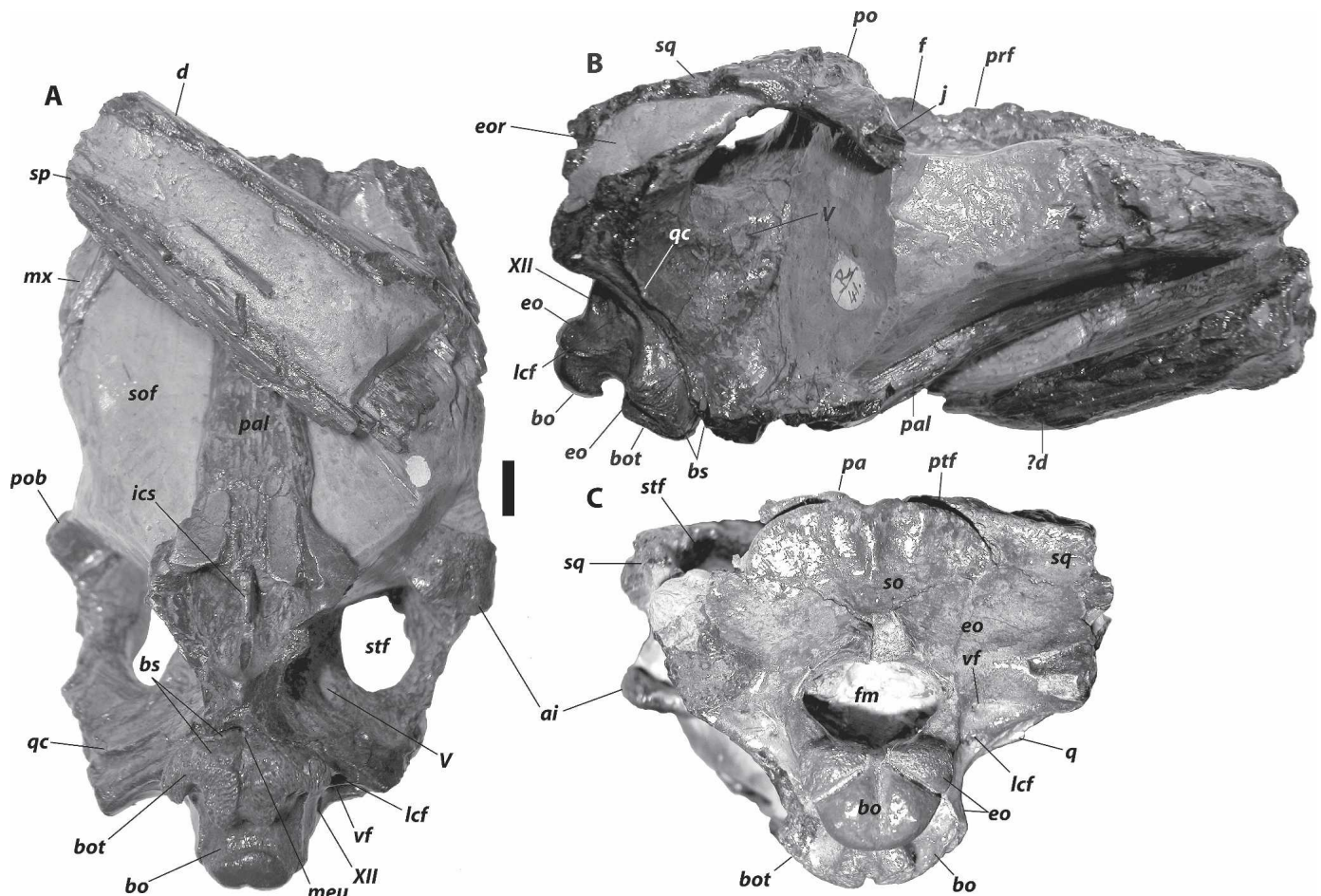


FIGURE 2. BMNH R41, *Eosuchus* sp., braincase and skull table in ventral (A), right lateral (B), and posterior (C) views. **Abbreviations:** ai, atlas intercentrum; bo, basioccipital; bot, basioccipital tuber; bs, basisphenoid; d, dentary; eo, exoccipital; eor, external otic recess (filled with matrix); f, frontal; fm, foramen magnum; ics, intrachanoal septum; j, jugal; lcf, lateral carotid foramen; meu, median eustachian foramen; mx, maxilla; pa, parietal; pal, palatine; po, postorbital; pob, postorbital bar; prf, prefrontal; ptf, posttemporal fenestra; q, quadrate; qc, quadrate crest; sof, suborbital fenestra; sp, splenial; sq, squamosal; stf, supratemporal fenestra; V, trigeminal foramen; vf, vagus foramen; XII, opening for 12th cranial nerve. Scale bar equals 1 cm.

proaches the dentary tooth row, and in the present case the spur does not pass medial to any of the alveoli.

The atlas intercentrum is the only postcranial fragment preserved with the specimen. As with other non-alligatoroid crocodylians, the intercentrum is an anteroposteriorly flattened plate, concave posteriorly and convex anteriorly, with a modest anteroposterior expansion dorsally. It bears a concave articulation facet for the occipital condyle on its dorsal surface. The ventral margin is divided into a pair of short processes, each separated from its counterpart by a deep sulcus on the anterior surface, and each ending in a convex articulation facet for an atlantal rib.

DISCUSSION

Referral of BMNH R41 to *Eosuchus* is supported by several derived features, most notably the characteristic basioccipital tuber comprised of a pair of crescentic structures on the ventral surface of the basioccipital (Fig. 2). The dorsal surfaces of the postorbitals slope anterolaterally immediately dorsal to the stout postorbital bars. The deeply concavoconvex frontoparietal suture does not enter the supratemporal fenestrae, a feature that is unique among gavialoids. The temporal canal is large and circular. There is a prominent midline septum within the nasopharyngeal duct, and a crest runs along the ventrolateral surface of the braincase, presumably indicating the location of the quadrate crest found in other specimens of *Eosuchus*. These features are all apomorphic for *Eosuchus* (Brochu, 2006).

Lydekker (1887, 1888) referred BMNH R41 to "*Crocodylus*" *spenceri*, a reasonable assignment given the much greater abundance of "*C.*" *spenceri* in the London Clay, but "*C.*" *spenceri* is a basal tomistomine and can be distinguished clearly from gavialoids generally and *Eosuchus* (including BMNH R41) in particular. Derived gavialoid features are absent, including a descending process of the exoccipital that reaches the basioccipital tubera. The basisphenoid is anteroposteriorly expanded at the level of the median eustachian foramen in *Eosuchus* (Brochu, 2006), but is plesiomorphically thin in "*C.*" *spenceri*. Conversely, derived brevirostrine or crocodyloid features are present, such as a less robust postorbital bar and placement of the lateral eustachian foramen dorsal to the posterolateral basisphenoid exposure.

Features diagnostic of *Eosuchus* are also lacking in "*C.*" *spenceri*. In particular, "*C.*" *spenceri* does not have the double-crescent basioccipital tubera or quadrate crest characteristic of *Eosuchus* and seen in BMNH R41; even if the quadrate crest is much less pronounced in BMNH R41 than in other specimens of *Eosuchus*, it is unambiguously absent in "*C.*" *spenceri*.

The skull table of "*C.*" *spenceri* bears a distinct midline sulcus, whereas the skull table of *Eosuchus* lacks this sulcus and slopes laterally from the midline. The dorsal surface of the frontal between the orbits is concave in "*C.*" *spenceri*, but flat in *Eosuchus*, and the frontoparietal suture between the supratemporal fenestrae is linear rather than concavoconvex in "*C.*" *spenceri*. The posttemporal fenestrae are more widely separated in "*C.*" *spenceri* than in *Eosuchus*. Unlike *Eosuchus*, "*C.*" *spenceri* has a large semilunate exposure of the supraoccipital on the skull table.

The present specimen differs from late Paleocene *Eosuchus* in a few subtle ways. The anterior frontal process appears to extend farther forward of the orbits, but sutures are very difficult to trace on the specimen. The anterolateral corners of the postorbitals are more acutely angular, the dorsal surface of the frontal is more concave, and the temporal foramen within the supratemporal fenestra is more circular. However, it is unclear whether these reflect species-level differences or population-level variation, and because BMNH R41 is incomplete, postmortem distortion cannot be ruled out. For this reason, it is premature to base a new species on the available material.

A more significant difference involves the quadrate crest. In *E. minor* and *E. lerichei*, the quadrate crest is a thin but laterally broad lamina extending ventrally to the basioccipital tuber. It forms the anterolateral wall of the lateral Eustachian channel, and the posterolateral exposure of the basisphenoid normally seen dorsal to the basioccipital tuber in most crocodylians lies within the deep sulcus formed by the crest and the lateral braincase wall. In BMNH R41, the quadrate crest is not nearly as laterally extensive, and it does not extend as far ventrally. That this is the result of postmortem damage, and not a diagnostic feature, is supported by two observations: first, that the preserved portion of the quadrate crest has an irregular lateral surface; and second, that the lateral eustachian openings are absent, indicating that channel was probably located adjacent to the now-missing ventral extension of the quadrate crest.

Although the holotype of *Eosuchus minor* was initially thought to be of Eocene age (Marsh, 1870; Miller, 1955; Norell and Storrs, 1986), the precise locality from where it was collected is unknown, and its preservation closely mirrors that seen in other specimens of *E. minor* from the region, all of which are from the late Paleocene (Brochu, 2006). Likewise, *E. lerichei* is from units formerly thought to be from the early Eocene (Swinton, 1937), but now thought to be late Paleocene (Staub, 1998; Delfino et al., 2005). The specimen described in this manuscript is thus the only unambiguous gavialoid occurrence in the early Eocene.

Fragmentary material from the early Eocene of Virginia, including a pair of premaxillae, was referred to *Eosuchus* by Weems (1999). The arrangement of alveoli resembles that in *Eosuchus*—the second and third alveoli are close in size, and the fourth is larger. The second through fifth alveoli are also arranged in an almost linear parasagittal array, mirroring the condition in *Eosuchus* (Brochu, 2006) and contrasting with the condition in *Argochampsia*, in which the first through third form a row perpendicular to the midline (Hua and Jouve, 2004). The arrangement is more arcuate in basal tomistomines. However, the Virginia specimen appears to have a much more significant prenasal rostrum—the anterior margin of the naris is behind the third alveoli in the Virginia material, but anterior to the third in *E. lerichei* and possibly to the second in *E. minor*. The specimen described by Weems (1999) may thus pertain to a gavialoid, but referral to *Eosuchus* is less certain.

Eosuchus minimally last shared a common ancestor with more derived gavialoids, including *Gavialis*, in the late Paleocene. Thus, even if BMNH R41 demonstrates the presence of gavialoids in the early Eocene, the lower bound of the gharial gap remains in the late Paleocene. Discovery of an Eocene fossil closer to *Gavialis* than to *Eosuchus* is required to reduce the gap.

So far, other long-snouted crocodylians from the early-middle Eocene have been most parsimoniously viewed as tomistomines. These include: “*Crocodylus*” *spenceri*; a skull and skeleton from the middle Eocene of Belgium referred to *Dollosuchus dixonii* (Swinton, 1937; Delfino et al., 2005; Brochu, 2006); “*Crocodylus*” *arduini* de Zigno, 1880, from the early Eocene of Italy (Kotsakis et al., 2004); and some middle Eocene African forms (Brochu and Gingerich, 2000). Several others, including *Charactosuchus kugleri* Berg, 1969, from Jamaica and *Tomistoma petrolica* Yeh, 1958, from China, also appear to be tomistomines but require further testing.

Expansions and improvements to morphological data sets have been unable to overturn the prevailing hierarchical signal in which *Gavialis* is basal to all other extant crocodylians (Norell, 1989; Salisbury and Willis, 1996; Brochu, 1997, 2004; Buscalioni et al., 2001; Hua and Jouve, 2004). Either this is the correct signal (a possibility at variance with a growing amount of molecular data), or the observations that could cause morphology to support a different result have not yet been made. If the morphological signal is to be overturned with improved taxon sampling, key taxa are likely to be found within the gharial gap. The specimen described here reveals the need for increased sampling and analysis of longirostrine crocodylians within this stratigraphic window.

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