

SYSTEMATICS AND TAXONOMY OF EOCENE TOMISTOMINE CROCODYLIANS FROM BRITAIN AND NORTHERN EUROPE

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Abstract: The holotype of *Dollosuchus dixonii* (Owen) from the Early–Middle Eocene Bracklesham Beds of England is a set of mandibular fragments that cannot be distinguished from corresponding parts of other longirostrine crocodylians. An isolated humerus from the Bracklesham Beds is consistent with a gavialoid, but it cannot be referred to the holotype of *D. dixonii*. The name *Dollosuchooides densmorei* is established for the well-preserved skull and skeleton of a tomistomine from the Middle Eocene of Belgium that had

been referred to *D. dixonii*. It can be clearly distinguished from the basal tomistomine ‘*Crocodylus*’ *spenceri* Buckland from the Lower Eocene of England, which cannot be referred to *Dollosuchooides* and is provisionally referred to *Kentisuchus* Mook. Although basal within Tomistominae, *Dollosuchooides* is more closely related to *Tomistoma* than to *Kentisuchus*.

Key words: Crocodylia, Tomistominae, *Dollosuchooides*, *Kentisuchus*, systematics, Eocene, Europe.

SOME of the most important fossils for understanding the origins of modern long-snouted (longirostrine) crocodylians are from Late Paleocene and Early Eocene deposits in Britain and Europe. These were historically allied with *Tomistoma* (the Indonesian false gharial; Kuhn 1936; Swinton 1937; Steel 1973), but basal relatives of both *Tomistoma* and *Gavialis* (the Indian gharial) are represented in the region (Brochu 2004, 2006; Hua and Jouve 2004; Kotsakis *et al.* 2004; Delfino *et al.* 2005). These are found within the stratigraphic window in which some molecular data predict *Tomistoma* and *Gavialis* last shared a common ancestor (Harshman *et al.* 2003), and they preserve combinations of primitive and derived features critical to ongoing debates about their phylogenetic relationships.

Two of these forms have been included in published phylogenetic analyses. One, *Eosuchus lerichei* Dollo, 1907 from the Upper Paleocene of France adjacent to the Belgian border, is a gavialoid (Delfino *et al.* 2005; Brochu 2006). The other is ‘*Crocodylus*’ *spenceri* Buckland, 1836 from the Ypresian of England, which is now considered to be the basalmost known tomistomine (Brochu and Gingerich 2000; Delfino *et al.* 2005).

Although not a member of *Crocodylus*, previous phylogenetic analyses continued to call the English Ypresian fossil ‘*Crocodylus*’ *spenceri* because at least four different generic names in the literature might have applied, and

it was unclear which was the most appropriate. The oldest name applied, *Eosuchus* Dollo, 1907, can now be ruled out, as it is based on a very different animal belonging to a different clade. The next is *Dollosuchus* Swinton, 1937, which was established for *Gavialis dixonii* Owen, 1849, a species based on fragmentary remains from the Lower or Middle Eocene of England. Mook (1955) later established two additional generic names, one (*Megadontosuchus*) for ‘*Crocodylus*’ *arduini* de Zigno, 1880 from the upper Middle Eocene of Italy and another (*Kentisuchus*) for ‘*Crocodylus*’ *spenceri*. These are all very similar to each other, but in the absence of a detailed comparison of the holotypes, it was difficult to decide on the most appropriate name for any of them.

Close examination of two sets of specimens allows a partial resolution of this problem. The first is the holotype of *Dollosuchus dixonii*, which cannot be distinguished from most longirostrine crocodylians and should be regarded as a *nomen dubium* (see below). The second is IRSNB 1748, a nearly complete, well-preserved skull and skeleton from Belgium described and referred to *D. dixonii* by Swinton (1937). Phylogenetic analysis supports a basal placement among tomistomines, albeit more closely related to *Tomistoma* than to ‘*C.*’ *spenceri*, from which it can be clearly distinguished. For this reason, ‘*C.*’ *spenceri* is here provisionally referred to *Kentisuchus* and a new

taxon name, and *Dollosuchoides densmorei*, is established for the Belgian specimen.

This paper is not intended to be a thorough evaluation of the phylogenetic relationships among tomistomines or of the morphological evidence regarding the relationships of *Tomistoma* and *Gavialis*. Additional taxa must be added before a comprehensive study can be completed. It is, however, timely to clarify the taxonomy among crocodylians that have featured prominently in recent work (Table 1).

Institutional abbreviations. BMNH, the Natural History Museum, London; IRSNB, Institut Royal des Sciences Naturelles de Belgique/Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels.

Anatomical abbreviations. an, angular; art, articular; boc, basi-occipital; d, dentary; emf, external mandibular fenestra; en, external naris; eoc, exoccipital; ept, ectopterygoid; f, frontal; fae.q, quadrate foramen aereum; fic, foramen intermandibularis caudalis; fm, foramen magnum; gf, glenoid fossa; ic, internal choana; if, incisive foramen; itf, infratemporal fenestra; j, jugal; lac, lacrimal; lcf, lateral carotid foramen; mx, maxilla; n, nasal; p, parietal; pal, palatine; path, pathological portion of dentary; pmx, premaxilla; po, postorbital; pp, anterior palatine process; ppc, cleft at anterior tip of palatine process; prf, prefrontal; ps, sulcus on dorsal surface of parietal; pt, pterygoid; ptb, pterygoid bulla; q, quadrate; qj, quadratojugal; sa, surangular; soc, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; stf, supratemporal fenestra; v, foramen for trigeminal nerve; vf, vagus foramen; xii, foramen for twelfth cranial nerve.

TABLE 1. Systematic review of slender-snouted crocodylians described from the Paleocene and Eocene of Europe.

	Holotype	Status	Comments
LONDON CLAY, EARLY EOCENE (YPRESIAN), ENGLAND			
<i>Crocodylus delucii</i> Gray, 1831	cervical vertebra	<i>nomen dubium</i>	'Crocodile de Sheppey' of Cuvier (1824)
<i>Crocodylus spenceri</i> Buckland, 1836	BMNH 19633, partial skull	<i>Kentisuchus spenceri</i> (Buckland, 1836)	Referred to <i>Kentisuchus</i> by Mook (1955). Basal tomistomine.
<i>Crocodylus toliapicus</i> Owen, 1849	BMNH R1753, skull and jaws encased in haematite	junior subjective synonym of <i>Kentisuchus spenceri</i>	Synonymized with <i>C. spenceri</i> by Lydekker (1887); condition of pyritized holotype limits comparisons.
<i>Crocodylus champsoides</i> Owen, 1849	BMNH 38975, skull	junior subjective synonym of <i>Kentisuchus spenceri</i>	Synonymy first proposed by Lydekker (1887)
<i>Eosuchus</i> sp.	BMNH R41, rear portion of skull		Referred by Lydekker (1888) to <i>Crocodylus spenceri</i>
BRACKLESHAM BEDS, EARLY–MIDDLE EOCENE, ENGLAND			
<i>Gavialis dixonii</i> Owen, 1849	BMNH 26125, 26126, dentary fragments	<i>nomen dubium</i>	Possible gavialoid based on humerus (33238a) referred to type material, but cannot be diagnosed. Swinton (1937) included isolated femur (26128) and vertebral centrum (26129) as part of holotype, but it is unclear whether Owen intended these to form part of the type. All but 26125 have '?' between <i>Gavialis</i> and <i>dixonii</i> on the labels.
LATE PALEOCENE (THANETIAN), FRANCE			
<i>Eosuchus lerichei</i> Dollo, 1907	IRSNB 1740, skull and partial skeleton	<i>Eosuchus lerichei</i> Dollo, 1907	Later described by Swinton (1937). Gavialoid.
MIDDLE EOCENE (LUTETIAN), BELGIUM			
<i>Dollosuchoides densmorei</i> sp. nov.	IRSNB 1748, skull and skeleton	<i>Dollosuchoides densmorei</i>	Referred by Swinton (1937) to <i>Gavialis dixonii</i> Owen, 1849, but moved to a new genus. Tomistomine.
EOCENE, ITALY			
<i>Crocodylus arduini</i> de Zigno, 1880		<i>Megadontosuchus arduini</i> (de Zigno, 1880)	Referred to <i>Megadontosuchus</i> by Mook (1955)

SYSTEMATIC PALAEOLOGY

CROCODYLIA Gmelin, 1789, *sensu* Clark in Benton and Clark 1988

CROCODYLOIDEA Fitzinger, 1826, *sensu* Brochu 2003

TOMISTOMINAE Kålin, 1955, *sensu* Brochu 2003
(morphological context)

Genus KENTISUCHUS Mook, 1955

Kentisuchus spenceri (Buckland, 1836)

Text-figures 1–2

Synonyms. *Crocodylus spenceri* Buckland, 1836, *Crocodylus champsoides* Owen, 1849, *Crocodylus toliapicus* Owen, 1849, *Kentisuchus champsoides* (Owen, 1849), *Kentisuchus toliapicus* (Owen, 1849).

Holotype. BMNH 19633, partial skull (Text-fig. 1).

Referred specimens. BMNH 37717, 38975 (holotype, *Crocodylus champsoides* Owen, 1849; Text-fig. 2), R1753 (holotype, *Crocodylus toliapicus*), 38978, 38990, 38991. Additional uncatalogued material at the Sedgwick Museum, Cambridge University, UK, can also be referred to this species.

Diagnosis. Prefrontal nearly as long as lacrimal; cleft in lacrimal sutural outline at anteriormost extent of bone; skull table has an M-shape in posterior view because the dorsal surfaces of the squamosals slope ventrally at their posterolateral corners and the parietal has a dorsal sulcus behind supratemporal fenestrae.

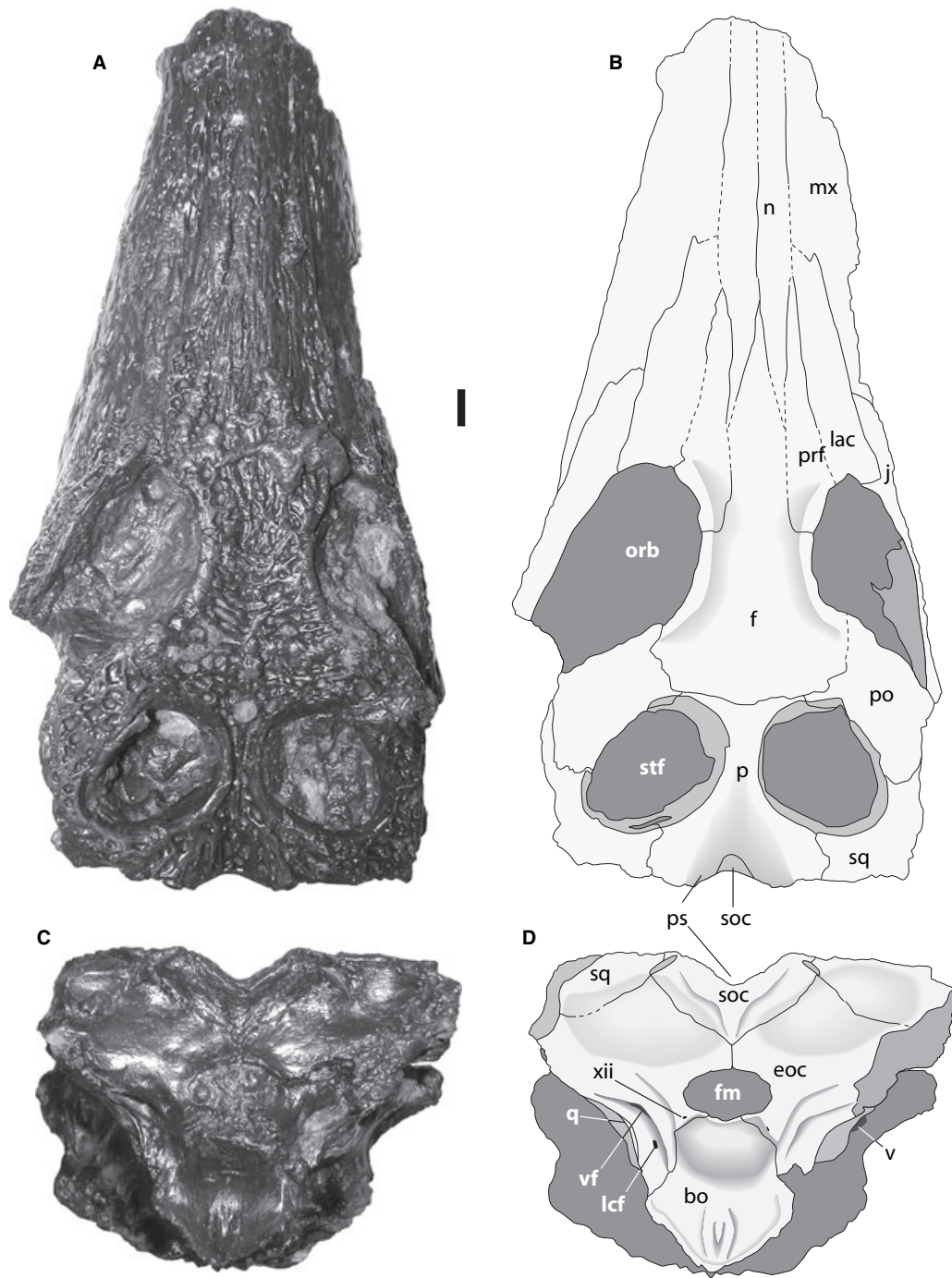
Remarks. Mook (1955) established the generic name *Kentisuchus* for *Crocodylus toliapicus* Owen, 1849 and viewed his referral of *C. spenceri* as provisional. Owen (1850) argued that Cuvier used the name *toliapicus* in reference to a crocodile from the Isle of Sheppey prior to 1841 and that, if the material described by Buckland (1836) was conspecific, *toliapicus* had priority over *spenceri*. Owen did not specify the publication in which this occurred, but he stated that the second edition of ‘Ossimens Fossiles’ (Cuvier 1824a) was the first publication in which crocodylians from the Isle of Sheppey were mentioned, and therefore implied that the name *toliapicus* appeared there. However it does not appear in either the second (1824a) or fourth (1836) editions of ‘Ossimens Fossiles’, nor is it in a shorter note on fossil crocodiles published in 1824 (Cuvier 1824b). Regardless, the material observed by Cuvier was limited to isolated vertebrae that are insufficient to establish a crocodyliform species. A gavialoid is known from the London Clay on the Isle of Sheppey (Brochu in press), and it is not known whether the vertebrae studied by Cuvier are from

a gavialoid or tomistomine. Moreover, according to Mook (1955), Cuvier’s supposed use of *toliapicus* was informal. Buckland (1836) was the first to refer specifically to a diagnosable type specimen and apply a binomial; as a result, *Crocodylus spenceri* Buckland, 1836 should be given priority.

The type skull of *C. toliapicus* is largely complete, but the jaws are fixed in place and the entire specimen is covered with pyrite (Owen 1849). Sutures are thus impossible to trace. Nevertheless, it shares with the holotype of *C. spenceri* a characteristic skull table morphology. The dorsal surfaces of the squamosals are reflected posteroventrally, and there is a conspicuous triangular sulcus on the parietal and supraoccipital behind the supratemporal fenestrae (Text-figs 1–2). As a result, the dorsal margin of the skull table in posterior view is M-shaped (Text-fig. 1C–D). This does not occur in any other tomistomine, and the skull table is planar in posterior view in IRSNB 1748. The skull table has a linear posterior profile in other crocodyloids. The holotypes are virtually identical in all other ways, at least as far as preserved portions overlap.

Mook (1955) also provisionally referred *Crocodylus champsoides* Owen, 1849 to *Kentisuchus*. The holotype of *C. champsoides* (Text-fig. 2) is more complete than that of *C. spenceri*, and sutures are much more discernible than in the type of *C. toliapicus*. It also preserves an M-shaped skull table outline. In addition, the types of *C. spenceri* and *C. champsoides* share a distinctive sutural pattern on the dorsal surface of the skull. The anterior frontal process is acute and long, extending forward for a distance nearly equal to the anteroposterior diameter of the orbit. It appears to exceed the diameter of the orbit in BMNH 38975. The lacrimal and prefrontal are also both long, with the lacrimal extending forward slightly further. The margin of the lacrimal is disrupted by a posterior process of the maxilla, a structure found in many crocodylians and diagnostic for Tomistominae (see below), but in this case the cleft in the lacrimal margin is at the anteriormost extent of the lacrimal. The anterior frontal process of IRSNB 1748 is also long, but it does not extend nearly as far forward relative to other elements, and the lacrimal is considerably longer than the prefrontal with a maxillary process on the anterolateral margin.

I agree with Lydekker (1888) that *C. toliapicus* and *C. champsoides* are junior subjective synonyms of *C. spenceri*. The name *Kentisuchus* Mook, 1955 is provisionally applied pending direct comparison with *Megadontosuchus arduini* (de Zigno, 1880) from the Bartonian of Italy. Mook (1955) established both *Megadontosuchus* and *Kentisuchus* in the same paper, but *Megadontosuchus* appears first. Published figures of *M. arduini* suggest a more robust skull with comparatively larger and more rectan-

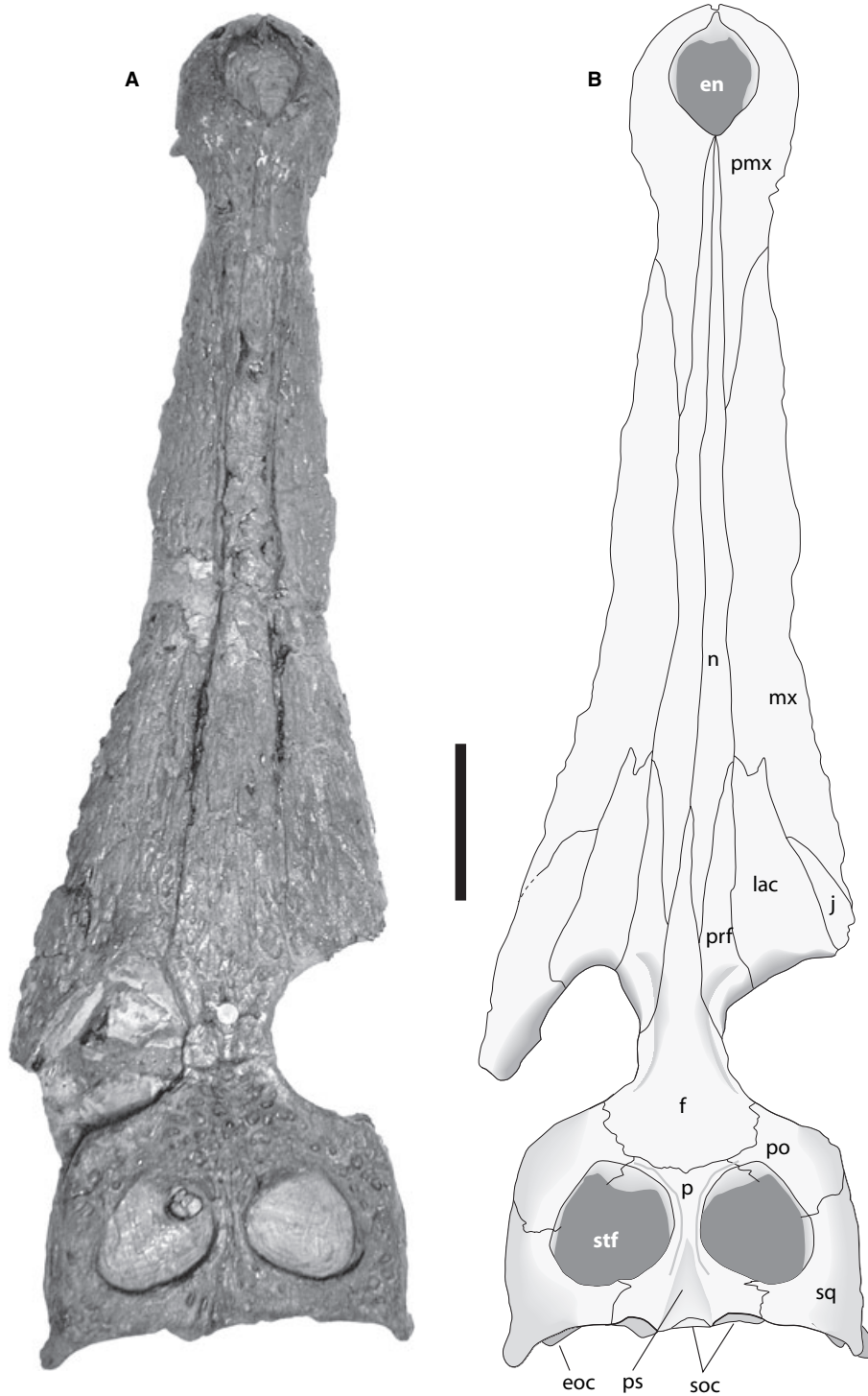


TEXT-FIG. 1. BMNH 19633, holotype, *Kentisuchus spenceri* (Buckland, 1836), in A–B, dorsal, and C–D, ventral views. Scale bar represents 1 cm.

gular supratemporal fenestrae, but it is unclear whether these are real differences or preservational artefacts. The nasals evidently contributed to the narial rim in the Italian form (de Zigno 1880), as they do in *K. spenceri*, and the anterior frontal process appears to be quite long in *M. arduini*. Although Lydekker (1887) regarded

M. arduini and *K. spenceri* as conspecific, a recent review of Italian crocodylians (Kotsakis *et al.* 2004) maintained them as distinct species.

Occurrence. London Clay, Isle of Sheppey, England; Early Eocene.



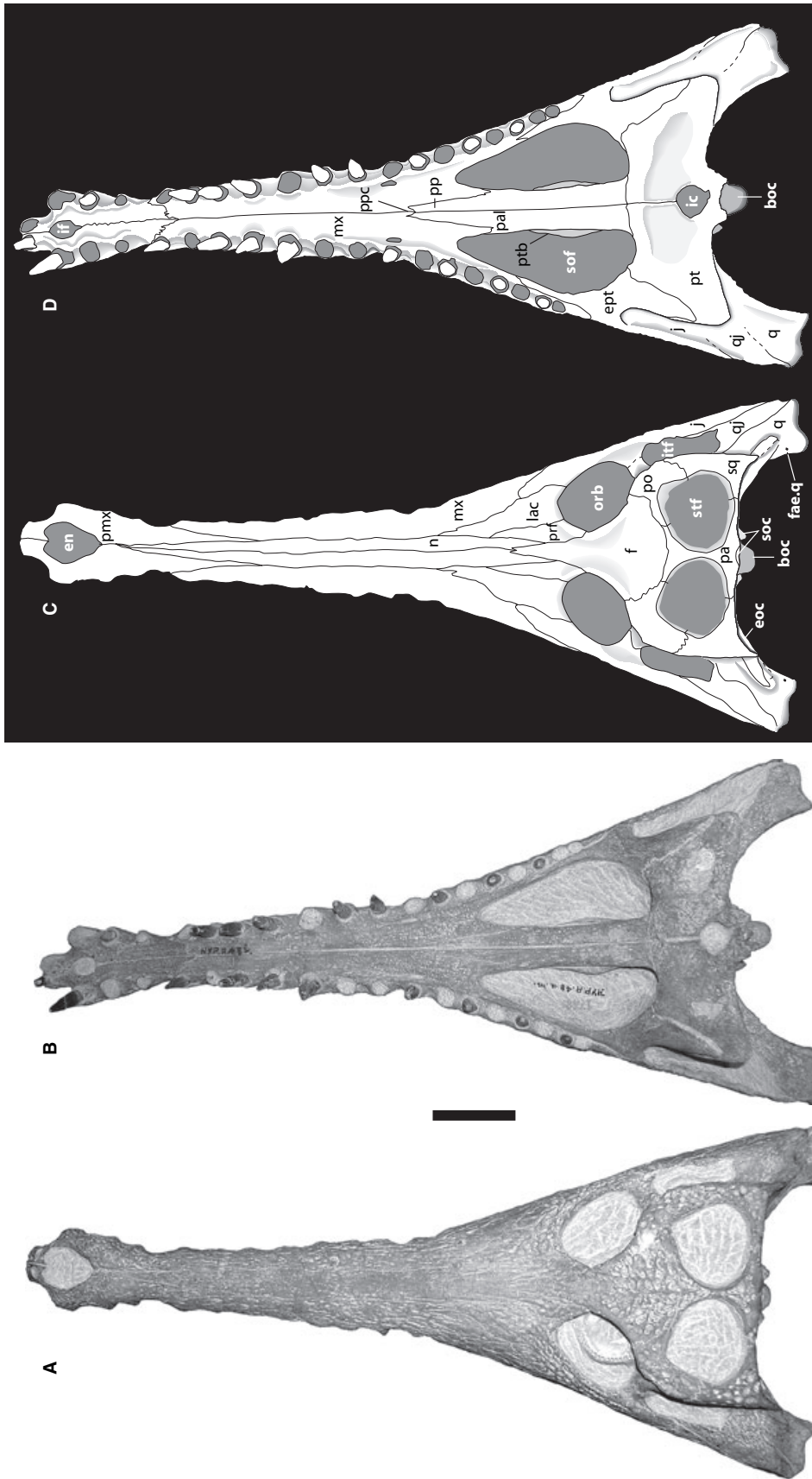
TEXT-FIG. 2. BMNH 38975, *Kentisuchus spenceri*, dorsal view. Scale bar represents 5 cm.

Dollosuchoides densmorei tax. nov.

Text-figures 3–4

Synonyms. *Dollosuchus dixonii* (Owen, 1849), *Gavialis dixonii* Owen, 1849 (in part).

Derivation of name. *Dollosuchooides*, ‘resembling Dollo crocodile’; *densmorei*, after Llewellyn D. Densmore, who resurrected the field of crocodylian systematics. Unused museum labels at the IRSNB indicate that Dollo intended to apply the name *Europaeosuchus* to this fossil, which Swinton (1937, p. 5) rejected as



TEXT-FIG. 3. IRSNB 1748, holotype, *Dollosuchooides densmorei*, skull in A, C, dorsal, and B, D, ventral views. Scale bar represents 5 cm.

'cumbrous'. I have opted to minimize confusion by erecting a name similar to that under which the Belgian fossil has long been referred.

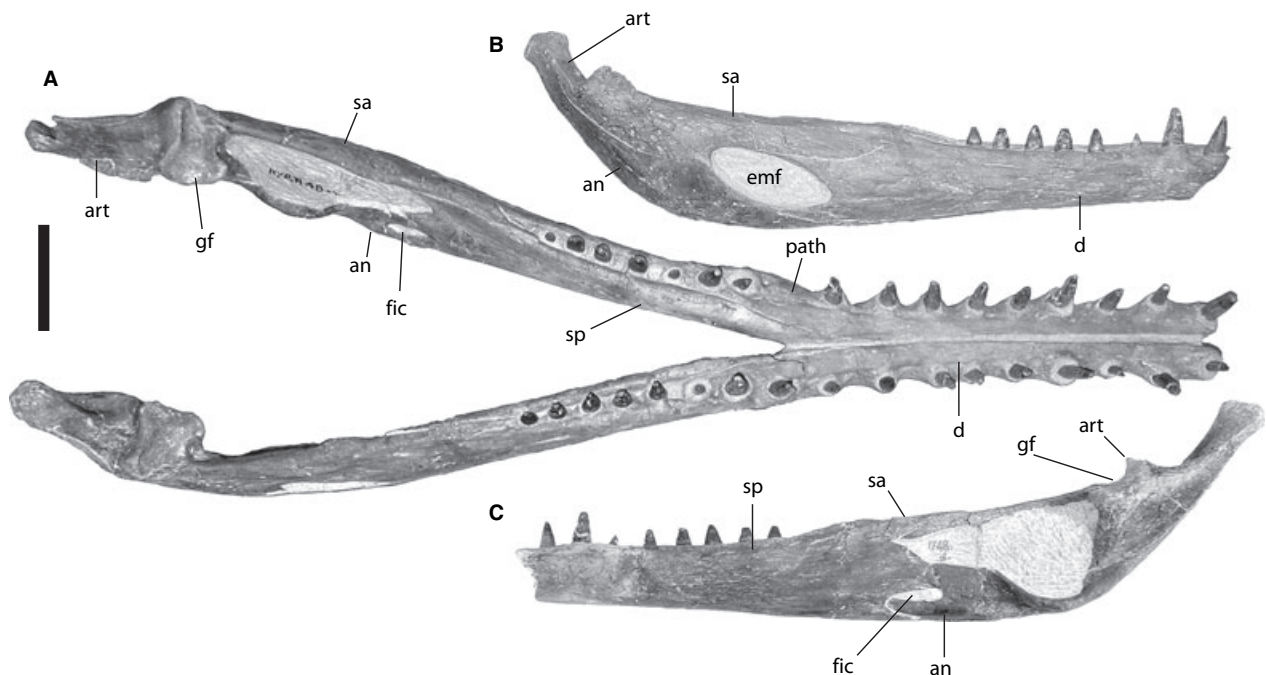
Holotype. IRSNB 1748, skull (Text-fig. 3), jaws (Text-fig. 4), and associated skeleton described by Swinton (1937).

Diagnosis. Large, nearly circular supratemporal fenestrae; interfenestral bar hourglass-shaped and narrow at the midpoint compared with other tomistomines; skull table behind supratemporal fenestrae also comparatively slender, with minimal flat dorsal surface. Maxillary and dentary alveoli separated by distinct sulci. Third and fourth premaxillary alveoli similar in diameter. Unlike other tomistomines for which the atlas-axis complex is known, the anterior half of the axial neural spine is horizontal and the neural spine lacks a posterior crest. The pterygoids of the holotype bear inflated bullae above the palatines that have not been observed in any other tomistomine, but this is a sexually dimorphic feature in some extant crocodylians and may not be diagnostic for this species.

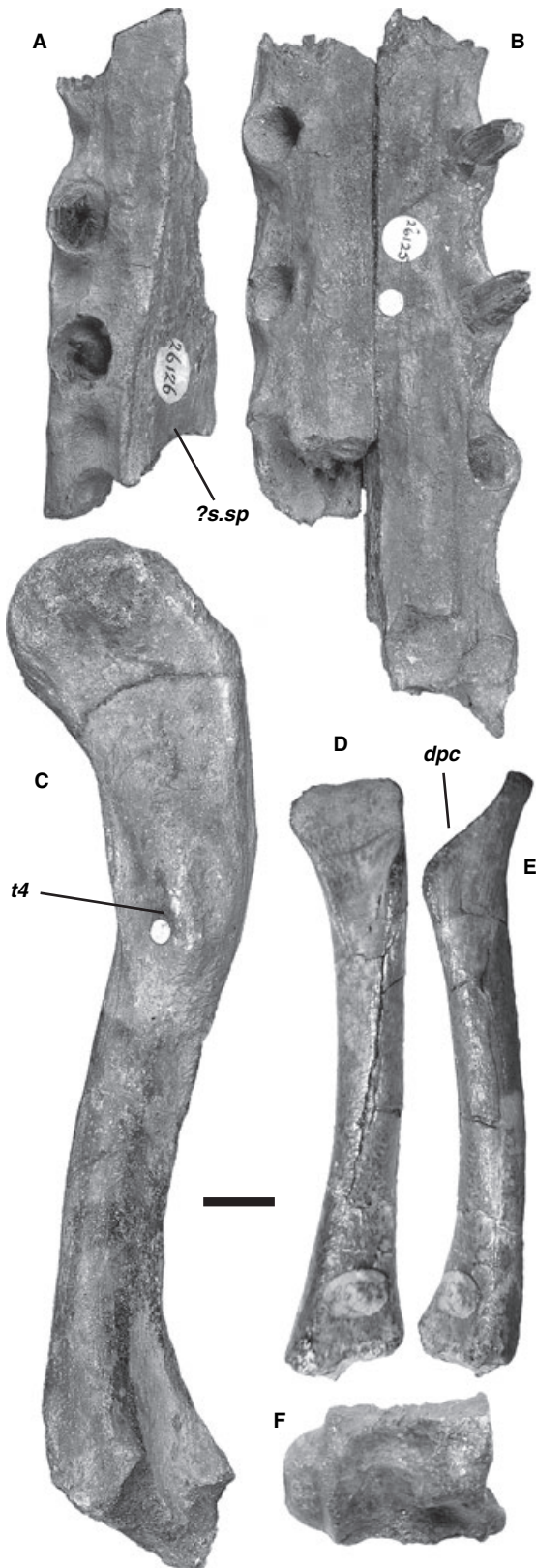
Remarks. *Gavialis dixonii* Owen, 1849 is based on fragments of a snout, an isolated cervical vertebra, and isolated limb elements representing multiple individuals from the Early–Middle Eocene Bracklesham Group of southern England (Text-fig. 5). Swinton (1937) later referred IRSNB 1748 to this species. He recognized that the material did not belong to *Gavialis* and erected the new generic name *Dollosuchus*.

Swinton (1937) explicitly designated IRSNB 1748 as the 'genotype' for *Dollosuchus*. However, based on the principle of coordination, genus names are based on type species rather than specimens. It is the type species that is based on a type specimen. It follows that the specimens forming the basis of *Dollosuchus* are the holotypes of *Gavialis dixonii* (BMNH 26125 and 26126, Text-fig. 5A–B), which are insufficient for adequate diagnosis. The mandibular fragments are consistent with the dentaries of IRSNB 1748, *Eosuchus*, *Thoracosaurus*, or even young *Gavialis* and *Tomistoma*. Additional material from Bracklesham referred to *G. dixonii*, with one exception (see below), is likewise not diagnosable beyond the level of *Crocodyliiformes*.

The only limb bone referred by Owen (1849) to *D. dixonii* was a right femur now catalogued as BMNH 26128 (Text-fig. 5C), but the same collections also include a left humerus (BMNH 33238a, Text-fig. 5D–E) from a much smaller individual. This was not mentioned in later publications specifying the type material (Lydekker 1888; Swinton 1937). Interestingly, if BMNH 33238a pertains to *D. dixonii*, then IRSNB 1748 does not. On the Bracklesham specimen, the proximal surface of the deltopectoral crest is linear and merges gradually with the head of the humerus. This is the ancestral condition for *Crocodylia* and is found in most gavialoids and *Borealosuchus* (Brochu 1997). In alligatoroids and crocodylioids (including tomistomines), the proximal surface is concave, resulting in a more abrupt transition between deltopectoral crest and humeral head. This would suggest that the Bracklesham crocodylian is a gavialoid.



TEXT-FIG. 4. IRSNB 1748, holotype, *Dollosuchooides densmorei*. A, mandible in dorsal view. B, postsymphysal portion of right ramus, lateral view. C, postsymphysal portion of right ramus, medial view. Scale bar represents 5 cm.



Regardless, IRSNB 1748 has a humeral morphology consistent with that of other tomistomines and inconsistent with that of the Bracklesham form. This would also argue against the Bracklesham crocodylian(s) being a form of *Eosuchus*, as *Eosuchus* is the only gavialoid known to have a proximally concave deltopectoral crest (Brochu 2006).

There are several points of difference between *Kentisuchus* and *Dollosuchooides*. *Dollosuchooides* has a comparatively more slender rostrum; the ratio of snout width at the level of the fifth maxillary alveoli to skull table width is 0.536 for BMNH 38975 (*K. spenceri*) but 0.395 in IRSNB 1748. The maxillary and dentary alveoli are separated by shallow sulci in *Dollosuchooides*. The nasals closely approach the external naris in *Dollosuchooides*, but unlike *Kentisuchus*, they do not actually penetrate the dorsal narial rim. *Dollosuchooides* lacks the elongate prefrontal characteristic of *Kentisuchus*, and its lacrimal has a maxillary process on its anterolateral rather than anteriormost margin. The circular supratemporal fenestrae of *Dollosuchooides* are comparatively large, and the hourglass-shaped interfenestral bar is comparatively thin at its midpoint. The dorsal surface of the skull table is flat and lacks the deep posterior sulcus found in *Kentisuchus*.

The mandibular symphysis of *Dollosuchooides* extends to a level between the ninth and tenth right dentary alveoli. The left dentary is pathological, and what would have been the tenth alveolus is missing (Text-fig. 4). The splenial portion of the symphysis extends forward to the eighth dentary alveolus. Although it is impossible to know how many dentary alveoli are adjacent to the symphysis in *Kentisuchus*, the symphysis (which has a splenial component) as a whole is relatively shorter than that of *Dollosuchooides* (pers. obs.).

Sulci between maxillary and dentary alveoli are prominent in *Dollosuchooides*, not to the degree seen in the African osteolaemine *Euthecodon* (Fourtau 1920; Tchernov 1986) or the South American gavialoid *Ikanogavialis* (Sill 1970), but similar to those found on the dentary of *Charactosuchus kugleri* Berg, 1969 from the Lower Eocene of Jamaica (Text-fig. 4). *Charactosuchus kugleri* also has a mandibular symphysis extending to just behind the ninth alveoli with the splenial portion extending anteriorly to the seventh. This is unlike the condition in the type species of *Charactosuchus* (*C. fieldsi* Langston, 1965), in which the splenial symphysis is much shorter (Langston 1965) or completely absent (pers. obs.), which is consistent with the suggestion

TEXT-FIG. 5. Type and referred material of *Dollosuchus dixonii* Owen, 1849 in the BMNH. A, BMNH 26126, partial left dentary, dorsal view. B, BMNH 26125, partial dentaries. C, BMNH 26128, right femur, ventral view. D, BMNH 33238A, left humerus, ventral view. E, BMNH 33238A, left humerus, anterior view. F, BMNH 26129, cervical vertebral centrum, right lateral view. Scale bar represents 1 cm.

made by Domning and Clark (1993) that *C. kugleri* might instead be referable to *Dollosuchus*.

The postorbital bar is robust compared with those of many other tomistomines (Text-fig. 3). This independently mimics the condition found in gavialoids, in which the robust postorbital bar reflects the plesiomorphic condition at the level of Crocodylia, but the postorbital bar of *Dollosuchoidea* does not have the pair of anterolateral protuberances also found plesiomorphically in gavialoids. Robust postorbital bars can also be observed in large specimens of Western Hemisphere *Gavialosuchus* (pers. obs.), but this might be an allometric effect; postorbital bars become comparatively more robust in all crocodylians with increasing size, and large *Gavialosuchus* skulls are larger than the skulls of most modern crocodylians.

Occurrence. Belgium, Middle Eocene.

PHYLOGENETIC ANALYSIS

Methods

Previous phylogenetic analyses of crocodylian relationships were augmented by the addition of *Dollosuchoidea densmorei* to a matrix of 165 morphological characters (Brochu 1999, 2004). Codings for *Dollosuchoidea* are provided in Brochu (2006). Multistate characters were left unordered, and all characters were equally weighted. *Bernissartia fagesii* and *Hylaeochampsia vectiana* were used as sequential outgroups. The ingroup included 59 terminal taxa. The matrix was subjected to maximum parsimony analyses using PAUP* (version 4.0b10; Swofford 2002). These applied 100 heuristic searches with the input order of terminal taxa randomized in each search.

Results

The parsimony analysis recovered 114,824 equally most parsimonious trees (length, 425; CI without uninformative characters, 0.426; RI, 0.804). The strict consensus tree (Text-fig. 6) is consistent with those from previous analyses (Brochu 2004). There is a basal split between *Gavialis* and its closest relatives (Gavialoidea) and a clade including all other extant crocodylians. *Eosuchus* is a gavialoid crownward of *Thoracosaurus*. Tomistomines, including *Dollosuchoidea* and *Kentisuchus*, are nested within Crocodylidae. *Kentisuchus* is the basalmost tomistomine in the analysis, and *Dollosuchoidea* is more closely related to other tomistomines.

Of the three unambiguous synapomorphies for Tomistominae, two are presumably related to snout shape: a long splenial symphysis and a wedge-like palatine process.

The splenial symphysis is constricted in dorsal view (and this can sometimes be discerned in ventral view as well), in contrast to the comparatively broader structure found in most gavialoids (Brochu and Rincon 2004). Most slender-snouted crocodylians have an acute, wedge-like palatine process, but in *Kentisuchus* and *Dollosuchoidea* it has a deep notch at its anteriormost extent. The same is true of some basal gavialoids (Brochu 2004, 2006).

A third unambiguous synapomorphy for the group, a distinct re-entrant on the anterior margin of the lacrimal for a short maxillary process, does not appear to be related to snout attenuation. The presence or absence of a maxillary process within the lacrimal (or between the lacrimal and prefrontal in some forms) does not vary within extant crocodylian populations (pers. obs.). This is a problematic character, as some derived forms (e.g. '*Tomistoma*' *cairensis*, *Paratomistoma courti*) lack this structure, but others (including extant *Tomistoma schlegelii*) retain it.

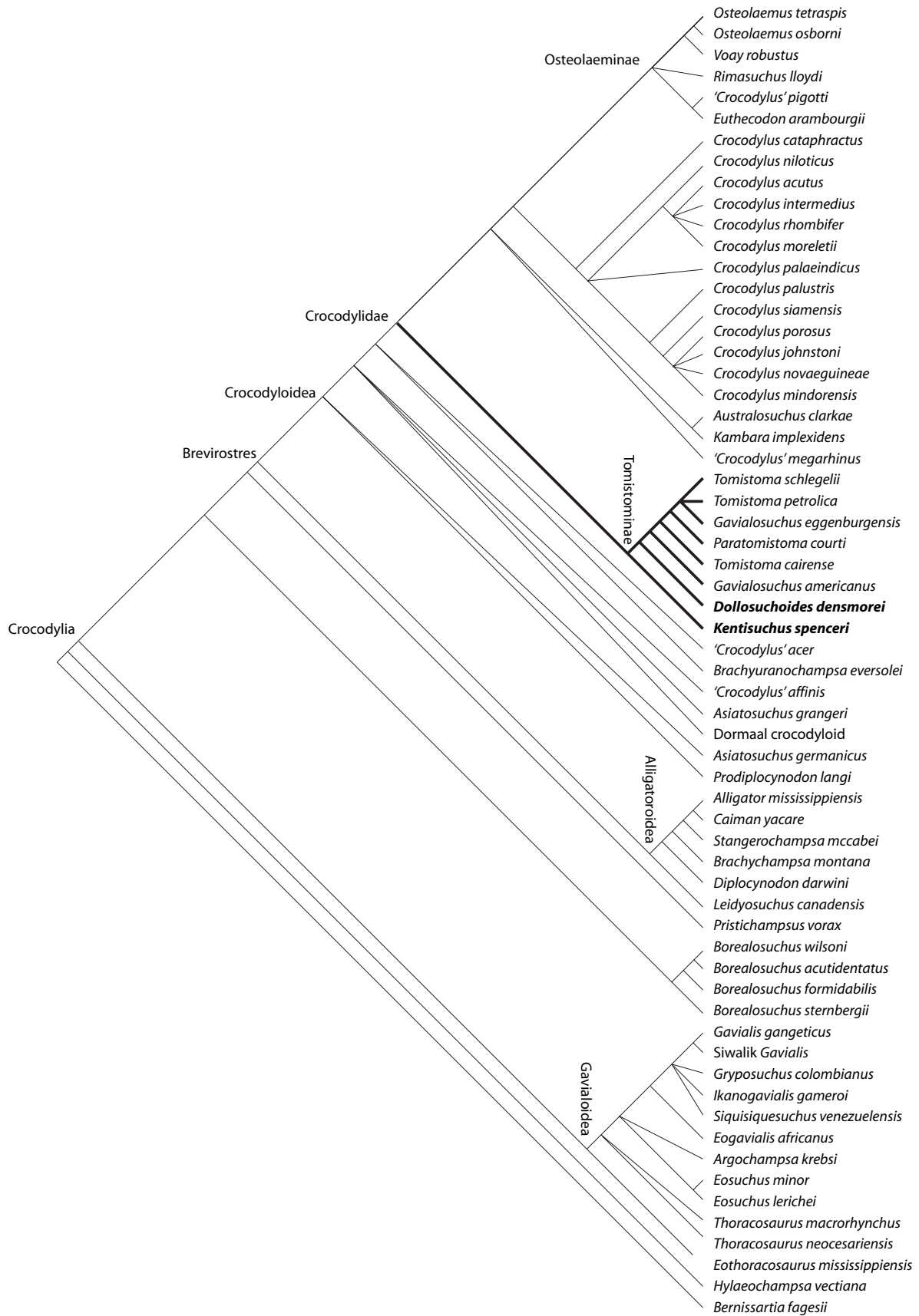
Two character states draw *Dollosuchoidea* closer to *Tomistoma* than is *Kentisuchus*: an anteriorly flaring lateral squamosal groove and complete exclusion of the nasals, at least dorsally, from the margin of the external naris. Both of these are commonly found in longirostrine crocodyliforms, including gavialoids. Anterior flare to the lateral squamosal groove is absent (and is most parsimoniously viewed as a loss) in *Tomistoma schlegelii*. Moreover, the nasals of *T. schlegelii* actually penetrate the narial chamber as a thin process ventral to the narial rim itself (Iordansky 1973). This is in contrast to the condition in *Gavialis*, in which the nasals are completely excluded from the narial aperture. The condition in *T. schlegelii* may pertain to any extinct tomistomine and possibly some basal gavialoids, but known material is insufficiently preserved to make a determination.

Tomistomines crownward of *Dollosuchoidea* share a proatlas with a blocky rather than boomerang shape and the absence of a sulcus on the dorsal dentary surface posterior to the fourth alveolus.

DISCUSSION

Kentisuchus spenceri and *Dollosuchoidea densmorei* are primitive tomistomines, but they can be clearly distinguished from each other. *Kentisuchus* has a characteristic dorsal skull table morphology and retains nasals that externally disrupt the narial aperture. *Dollosuchoidea* has comparatively larger supratemporal fenestrae and a more slender rostrum.

Arambourg (1934) described incomplete crocodylian mandibular material from the Ypresian of Morocco that he later referred to *Crocodylus* aff. *spenceri* (Arambourg 1952). Comparisons with British material are difficult because the only complete jaw of *Kentisuchus spenceri* is



the pyritized object fixed to the skull of *C. toliapicus*. However, this material is very similar to that of *Maroccosuchus zennaroi*, a slender-snouted crocodyloid from the same deposits in Morocco (Jonet and Wouters 1977; pers. obs.). Referral of the material described by Arambourg to *M. zennaroi* is more reasonable.

A mandibular fragment originally described as *Asiatosuchus zajsanicus* Efimov, 1982 was later referred to *Dollosuchus* (Efimov 1988, 1993). The type and only known specimen, from the Middle Eocene of Kazakhstan, consists of a fragment of dentary including the posterior-most portion of the symphysis. Efimov (1982) specified that the symphysis extends to the level of the sixth dentary alveolus, which indicates a comparatively shorter symphysis than in *Dollosuchoides*, but the anteriormost end of the dentary is not preserved. The splenial (what I presume is meant by 'squamosal' in the published English translation of Efimov 1982) evidently reached the symphysis, though whether the splenials actually met at the midline is unclear. Available material of *D. zajsanicus* may be insufficient to permit precise taxonomic assignment, but a closer look is clearly warranted.

Also warranted is a more thorough examination of the phylogenetic relationships of these forms. Although current evidence favours a close relationship with *Tomistoma* and a much more distant relationship with *Gavialis*, there are some interesting commonalities between early tomistomines and early gavialoids, not all of which are obvious reflections of snout shape. Most of these forms show an anterior cleft in the palatine process, for example. Moreover, the gavialoid *Eosuchus* shares a derived deltopectoral crest with brevirostrine crocodylians.

Inclusion of additional known taxa, such as *Megadontosuchus*, *Maroccosuchus*, and an undescribed Middle Eocene tomistomine from the Messel locality in south-east Germany (Rossmann 2002), and more intensive field collection of slender-snouted crocodylians from this critical block of time, are clearly necessary. If, as molecular data predict, *Tomistoma* and *Gavialis* diverged during this time, we should find fossils that exhibit the hierarchical acquisition of morphological reversals currently thought to be plesiomorphic conditions in Neogene gavialoids (Gatesy *et al.* 2003). On the other hand, if *Gavialis* really does represent a more basal crocodylian lineage unrelated to *Tomistoma*, new Eocene fossils should clarify the morphological transition between a basal but autapomorphic form such as *Eosuchus* and post-Eocene gavialoids.

Also needed are more detailed morphological studies of the skulls of Paleocene and Eocene gavialoids and tomistomines. The most tantalizing similarities between these forms are rostral, whether related to snout attenuation or

not, and the most significant differences are chondrocranial and postcranial features allying tomistomines, including early forms, with crocodyliids. Are the developmental pathways uniform in taxa currently assumed to share homologous character states? Is it possible that *Gavialis* and *Tomistoma* really are extant sister taxa, even if both lineages developed the slender-snouted condition independently? Some of these fossils (especially the holotype of *Dollosuchoides densmorei*) are extremely well preserved and might provide informative computed tomographic imagery. Without such work, current efforts to reconcile disparate sources of data regarding living longirostrine crocodylians are less likely to succeed.

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TEXT-FIG. 6. Strict consensus of 114 824 most parsimonious trees (length, 425; CI without uninformative characters, 0.426; RI, 0.804). Trees were rooted using *Hylaeochampsia* and *Bernissartia*.

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