A NEW METRIORHYNCHID CROCODILIAN (MESOEUCROCODYLIA: THALATTOSUCHIA) FROM THE KIMMERIDGIAN (UPPER JURASSIC) OF WILTSHIRE, UK

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Abstract: Recent revision of the marine metriorhynchid crocodilians indicates that a partial skull previously assigned to the species Metriorhynchus superciliosus and newly discovered postcranial elements from the Kimmeridge Clay of Westbury, Wiltshire belong to a new species of metriorhynchid. This material is herein described and referred to a new species of the genus Dakosaurus, characterised by four apomorphies: the size and shape of the enlarged supratemporal fossae; relatively large teeth, and half the number in relatives; the robust and unornamented cranium; and the angle that the prefrontal makes with the long axis of the skull. In a new phylogenetic analysis, Dakosaurus carpenteri sp. nov. is the basal member of a clade containing also D. maximus and D. andiniensis; it is not so short-snouted and its teeth are not so few and large as in the other two species, but the new form illustrates the ecological transition among metriorhynchids from a piscivorous diet to high-order carnivory.

Key words: Metriorhynchidae, Kimmeridgian, Jurassic, England, Metriorhynchus, Dakosaurus, Thalattosuchia.

The Crocodylia (crocodilians and their extinct relatives) have had a long and eventful evolutionary history, with many notable groups such as the Thalattosuchia, the only group of archosaurs entirely adapted to living in the marine realm (Neill 1971). The Thalattosuchia appear in the Lower Jurassic, diversifying and dispersing throughout the Jurassic, with specimens found worldwide, and eventually becoming extinct during the Early Cretaceous (Hua and Buffetaut 1997; Gasparini et al. 2000, 2005; Pierce and Benton 2006). Note that we use the term Crocodylia Gmelin, 1789 to refer to the least inclusive clade containing Protosuchus richardsoni and Crocodylus niloticus, the general usage through the nineteenth and twentieth centuries (Martin and Benton 2008), and renamed Crocodyliformes Hay, 1930 (Benton and Clark 1988).

The Thalattosuchia consists of two families (Ginsburg 1970; Buffetaut 1980), the Teleosauridae and the Metriorhynchidae, both of which are represented by species with long, narrow bodies and muscular tails (Massare 1988). Whereas the teleosaurids were relatively unspecialised in their body plan, the metriorhynchids had evolved extreme adaptations to living in a marine environment (Lydekker 1890; Fraas 1901). They evolved hydrofoil-like forelimbs and reduced, paddle-like hind-limbs; they lost their osteoderms, and the tail evolved to become laterally compressed and hypocercal, allowing efficient propulsion through the water (Massare 1988).

Although the Thalattosuchia appeared in the Early Jurassic, the Metriorhynchidae spanned from the Bajocian (Middle Jurassic) to the Hauterivian (Lower Cretaceous) (Grange and Benton 1996; Gasparini et al. 2005). Regardless of the abundant remains found in the Cretaceous (Andrews 1913; Martill 1986), metriorhynchid crocodilians remain a rarity in the Kimmeridgian (Grange and Benton 1996). The Kimmeridgian Clay of England outcrops in a long, narrow strip that runs from Dorset on the south coast, through central England to Yorkshire in the northeast, with Westbury, Wiltshire currently being the only sizable inland exposure (Grange et al. 1996). The site has provided an abundance of marine vertebrate fossils, the majority of which are housed in private collections and of which only a handful have been formally described, so the true quantity of material is hard to assess. However, reported finds include thalassemyid turtles, the common Kimmeridgian ichthyosaur Ophthalmosaurus sp., several plesiosaurs including Kimmerosaurus sp., and the giant plesiosaurs Pliosaurus brachypterylus and Liopleurodon sp. (Birkelund et al. 1983; Grange et al. 1996; S. Carpenter,
pers. comm. 2006). The Westbury clay pits have also yielded crocodilian remains that include fragmentary materials of *Dakosaurus maximus* (Hulke, 1869; Grange et al. 1996), but the most notable crocodilian fossil is a skull discovered in 1991 that was provisionally assigned to the species *Metriorhynchus superciliosus* by Grange and Benton (1996). Upon re-examination, it is clearly not assignable to that species, as the skull possesses a shorter, more robust snout with much larger teeth. In 2005, an assortment of postcranial material was also discovered, together with parts of a mandible that contains teeth of identical size, shape, and banding patterns to those in the skull discovered earlier. A recently revised metriorhynchid phylogeny reveals that this is a new species (Young 2006).

The aim of this paper is to describe the mandible and the postcranial material of the new metriorhynchid crocodilian and to assess the relationship between this material and the skull discovered in 1991. We will identify autapomorphies of the species and consider its palaeobiology.

**Institutional abbreviations.** BMNH, Natural History Museum, London; BRSMG, Bristol City Museum and Art Gallery, Bristol; CAMSM, Sedgwick Museum, Cambridge; GLAHM, Hunterian Museum, Glasgow; HMN, Humboldt Museum für Naturkunde, Berlin; OXFUM, Oxford University Museum; PETMG, Peterborough City Museum and Art Gallery, Peterborough; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

**GEOLOGICAL SETTING**

The postcranial material was discovered in the ‘new quarry’ at the Lafarge cement works (formerly Blue Circle Industries) in Westbury, Wiltshire (National Grid Reference ST 8817 5267) in July 2005. The Westbury clay pits expose over 40 m of Kimmeridge Clay, which includes the upper *cymodoce* Zone, all of the *mutabilis* Zone and the majority of the *eudoxus* Zone (Birkelund et al. 1983; Grange and Benton 1996; Grange et al. 1996) and thus represents a large section of the middle Kimmeridgian.

The material lay *in situ* c. 2 m below the *Crussoliceras* limestone marker bed of Birkelund et al. (1983), a lithologically persistent horizon found throughout the English Kimmeridgian (Taylor and Cruickshank 1993), and thus the material comes specifically from the *eudoxus* Zone (E5). The traditional stratigraphy for the Kimmeridgian is no longer considered valid; the International Commission on Stratigraphy has reclassified the Upper Kimmeridge Clay Formation as part of the Early Tithonian. The ammonite Zone *eudoxus* originally marked the middle to upper Lower Kimmeridgian, it is now situated towards the top of the Kimmeridgian as a whole (Morgans-Bell et al. 2001).

The site of discovery lay on the rim of the pit, and so the remains had to be excavated quickly to avoid the risk of further disturbance. Collection of the specimen became progressively harder as the excavation moved further into the quarry face and clay overburden increased (S. Carpenter, pers. comm. 2006). A second more thorough excavation into the quarry face in April 2006 yielded few remains (Text-fig. 1).

**MATERIALS AND METHODS**

Approximately 40 per cent of the postcranial skeleton is preserved in BRSMG Cd7203. The collection comprises elements of the mandible, including fragments of dentary, angular, surangular, articular, and several isolated teeth. Thirty-six vertebrae are preserved in total, including five cervicals, 12 dorsals, one sacral, and eight caudals, and of the ribs, three cervical and approximately 12 dorsals are present. The pectoral girdle is not represented in the collection, and only isolated bones of one forelimb are present, which includes one humerus, a possible propodial, and a possible metacarpal. The pelvic girdle is represented only by the left ischium, and both femora are present.

The similarity between the teeth of the mandible of BRSMG Cd7203 and those of BRSMG Ce17365 (the 1991 skull) suggests strongly that they belong to the same species of crocodilian. The teeth in both the 1991 and 2005 specimens are larger and more robust than those of other metriorhynchids. Both the postcranial material and the skull were also found at the same broad stratigraphic level, although the vertical distance between the two discovery horizons is about one metre. The spatial distance between the two, however, is more problematic. The skull was found in the old quarry, whereas the postcranial material was found in the new quarry, several 100 m away (S. Carpenter, pers. comm. 2007). Although skulls do disarticulate easily from the rest of the body during degradation
(Schäfer 1972; Grange and Benton 1996), it is unlikely to have travelled such a large distance. Therefore, we assume that although they both represent the same species, they do not represent parts of the same individual.

**Preparation and conservation**

All preparation and reconstruction of BRSMG Cd7203 was undertaken by Mr S. Carpenter. A solution of Paraloid B72 dissolved in acetone was used for both surface consolidation and as an adhesive. Care was taken to avoid removing encrusting organisms and to preserve the many delicate surface features (S. Carpenter, pers. comm. 2006).

**Taphonomy and preservation**

The postcranial material is fragmented, disarticulated, and missing large areas of the skeleton. This is likely to be the result of a combination of damage prior to burial and destruction of the material by quarry machinery at the site of discovery. It is evident that the bones have been through a great deal of deformation post-deposition, and this is particularly clear in the vertebrae, of which many are crushed, and in the femora, which have a characteristic curved, step-like deformation pattern. This shearing deformation can be attributed to the pressure produced by the overlying clay. The skull has also undergone deformation from overburden pressure (Grange and Benton 1996), as have those of other marine reptiles from Westbury and elsewhere, indicating that these processes are a fairly common occurrence (Martill 1986; Carpenter 1995; Grange and Benton 1996).

Encrustations are identifiable on both dorsal and ventral surfaces of most of the fossil indicating that the specimen remained exposed on an oxygenated or partially anoxic seabed for a length of time prior to burial (Martill 1985; Dineley and Metcalf 1999). The majority of encrustations are the remains of unidentifiable shell colonisations, but in a few cases (Text-fig. 2) the shell has remained attached to the surface and can be identified as an ‘oyster’ (Nanogyra? sp.; Grange and Benton 1996).

**SYSTEMATIC PALAEONTOLOGY**

**Order CROCODYLIA Gmelin, 1789**

**Infraorder THALATTOSUCHIA Fraas, 1901 (sensu Ginsburg, 1970)**

**Family METRIORHYNCHIDAE Fitzinger, 1843**

**DAKOSAURUS Quenstedt, 1856**

**Dakosaurus carteri** sp. nov.

*Text-figs 2–10*

**Derivation of name.** Named in honour of Mr. Simon Carpenter, who discovered the holotype and subsequent postcranial material, yielding ‘Carpenter’s tearing lizard’.

**Holotype.** BRSMG Cc17365, an incomplete skull that consists of maxilla, partial premaxilla, prefrontals, frontals, parietal, nasal, postorbitals, and squamosal.

**Paratype.** BRSMG Cd7203, mandibular fragments; 36 vertebrae, including five cervicals, 12 dorsals, one sacral and eight caudals; ribs, including three cervical and approximately 12 dorsals; humerus; possible propodial and metacarpal; left ischium; left and right femora.

**Diagnosis.** A metriorhynchid crocodilian distinguished from other species of *Dakosaurus*, and from *Metriorhynchus*, by four apomorphies: the supratemporal fossae are enlarged and project further forward than in other species; the teeth are somewhat smaller than those of other species of *Dakosaurus*, but larger than those of all species of *Metriorhynchus*; the cranium is robust and lacks ornamentation; and the prefrontal makes a greater angle with the long axis of the skull than in *Dakosaurus* (50 degrees), but less than in species of *Metriorhynchus* (60–70 degrees). Further, the new species has a similar number of teeth in each jaw ramus (estimated at 14) compared to *D. maximus* and *D. andiniensis* (12–16), but far fewer than in any species of *Metriorhynchus* (typically 22–29).

**Locality and horizon.** Westbury, Wiltshire, UK. Upper Kimmeridgian, Upper Jurassic (upper *mutabilis* to upper *eudoxus* Zones) of the Kimmeridge Clay Formation.
Description

Skull. The skull of the new specimen was not preserved, and a full description of the skull discovered in 1991 (BRSMG Ce17365; Text-fig. 3) is given in Grange and Benton (1996). In the description, the skull was provisionally assigned to the species *Metriorhynchus superciliosus*, but here we list the evidence suggesting otherwise and expand on several points not covered in the original description.

*Metriorhynchus superciliosus* is a common longirostrine metriorhynchid from the Callovian Oxford Clay formation. It possessed a slender, long snout in which up to 28 teeth line each side of the upper and lower jaws (Andrews 1913; Adams-Tresman 1987). Upon viewing, it is immediately clear that BRSMG Ce17365 is brevirostrine, with a shorter, wider, more robust snout (Text-fig. 4), and there are at least 14 teeth in each upper tooth row. On the left side, there are three premaxillary alveoli, four maxillary teeth, and six empty alveoli, and on the right side, nothing of the premaxillary portion, nine maxillary teeth, and one empty alveolus. The teeth are also larger than expected, with all crowns higher than 20 mm, with the largest being 32 mm; the typical tooth crown height for *M. superciliosus* of comparable size is 15–17 mm (BMNH R2030; GLAHM V987, V1004; PETMG R10). In the original description, the supratemporal fossae were identified as being unusually large, and in fact they are much larger than those of any specimen of *M. superciliosus* (Young, pers. obs.). Here the supratemporal fossae are greatly enlarged, particularly laterally (Text-fig. 4), as the postorbital and the squamosal extend laterally beyond the prefrontal by c. 110 mm compared to just 30 mm in *M. superciliosus* (Andrews 1913; e.g. BMNH R2030). The enlarged postorbital region would have provided an enlarged attachment for the *M. adductor mandibulae externus* muscle group, indicating a more powerful bite force than for *M. superciliosus* (Massare 1988).

The supratemporal fossae in the Westbury skull also differ in shape from those of *M. superciliosus*, with the anterior margin (formed by the posterior and lateral processes of the frontal) forming an angle of c. 60 degrees. This is more typical of the acute angle seen in *Geosaurus* (e.g. *G. suevicus* SMNS 9808, *Geosaurus* sp. OXFUM J.1431), *Dakosaurus* (e.g. *D. manselii* BMNH 40103, *D. liscocephalus* CAMSM J. 29419), and *Enaliosuchus* (e.g. *E. macrospodium* Hua et al. 2000; *E. schroederi* Karl et al. 2006) rather than that of many species of *Metriorhynchus*, in which the angle is c. 90 degrees (Text-fig. 4). The exception to this is *M. hastifer* from the early Kimmeridgian (Eudes-Deslongchamps 1867), and the late Oxfordian skull referred to *M. superciliosus* by Buffetaut (1977), in which the angle is similarly acute (see Table 1). BRSMG Ce17365 also has larger and more prominent prefrontals than would be expected for *M. superciliosus*.

The inflection point on the outer margin in dorsal view projects backwards, forming an angle of c. 70 degrees to the central line, as opposed to c. 90 degrees seen in *M. superciliosus* (Text-fig. 4, Table 1).

**TEXT-FIG. 3.** *Dakosaurus carpenteri* sp. nov., BRSMG Ce17365. Skull in dorsal view. A, photograph and B, diagrammatic sketch. Abbreviations: en, external nares; fr, frontal; mx, maxilla; n, nasal; oc, occipital condyle; p, parietal; pfr, prefrontal; po, postorbital; pmx, premaxilla; sq, squamosal; stf, supratemporal fossa. Scale bar represents 100 mm.
Whereas *M. superciliosus* typically has at least some ornamentation on its cranial bones, particularly in the frontal, prefrontal, and nasal regions (Andrews 1913), BRSMG Ce17365 has no ornamentation in these regions. The variability of this character has been long known (Andrews 1913; Wenz 1968). Its taxonomic significance was doubted (Adams-Tresman 1987), but Vignaud (1995, 1997) recognises two species of longirostrine taxa from the Oxford Clay, *M. superciliosus* and *M. leedsi*, largely based upon the exceptionally high maxillary tooth count of the latter. It must be noted that if this taxonomic decision is adopted then *M. superciliosus* has at least some ornamentation upon the frontal, whereas *M. leedsi* does not (Young, pers. obs.).

The brevirostrine taxa of the Callovian show a similar distinction, in which those from the Oxford Clay of England have cranial ornamentation to a varying degree (Andrews 1913; Wenz 1968; Adams-Tresman 1987), whereas *M. casamiquelai* of the Middle Callovian of Chile exhibits none (Gasparini and Dellape 1976). The only cranial ornamentation witnessed in this specimen is the characteristic pitting and grooving seen on the lateral edges of the maxilla (Grange and Benton 1996).

*Mandible.* Several dentary fragments are preserved from both mandibular rami in BRSMG Cd7203. The dentaries are easy to distinguish from the rest of the mandibular fragments by the row of alveoli along the oral surface of the fragment, some of which cut deeply into the dentary (‘a’ in Text-fig. 5C). The teeth sit within the alveoli and this association is present in several fragments (Text-fig. 6). The lateral sides of the dentaries are heavily pitted and grooved, with the more anterior fragments being less grooved than those that are more posterior. The tip of the left dentary is present in association with the first dentary tooth; on the lateral edge is the articulation surface for the union with the right dentary. Posteriorly the dentary tapers away; it presumably occupied a lateral depression present at the anterior ends of the angular and the surangular.

Large parts of both angulars are preserved (Text-fig. 5A–B). The angular is a long, robust bone that curves slightly inwards towards the tip of the mandible and upwards towards the articular. The angular contains a large deep groove, which rotates from the top at the anterior end of the angular to inside more posteriorly, in which the dentary sits. The lateral side of the angular is highly grooved, with the left side possessing larger grooves, some of which protrude from the surface quite dramatically. The angular articulates with the dentary, the surangular, and the splenial, but the only evidence of these contacts preserved is the one with the surangular (Text-fig. 5D).

A fragment of the surangular clearly shows a band at its base of lighter coloration that represents the overlapping suture between the surangular and the angular, in which the surangular would have been positioned on top of the angular (‘os’ in Text-fig. 5F). There is no evidence on either the surangular or the angular of an external mandibular fenestra, a feature lacking in all metriorhynchid skulls, which may be because of reduction of the *M. intramandibularis*, the muscle involved in helping to keep the mouth open during basking in extant crocodilians (Hua and Buffetaut 1997). The coronoid process, which forms the summit of the coronoid angle lies on the upper border of the surangular, of which a small fragment of the right side is preserved (Text-fig. 5G).

The articular is a massive bone, which articulates with the quadrate to form the jaw joint. Part of the left articular remains,
and consists of two concavities, separated in the middle by a low ridge (‘as’ in Text-fig. 5H), for the reception of the quadrate. Behind the articular surface is a prominent flat process projecting posteriorly which terminates with a rounded, rugose area for attachment of the M. adductor mandibulae posterior (Endo et al. 2002). The right retroarticular process is also preserved; this process forms the very back of the mandible and provides a long lever arm for the insertion of the M. depressor mandibulae (Taylor and Cruickshank 1993).

Dentition. There are several isolated teeth, six of which are complete (Text-fig. 6). Four teeth are associated with dentary fragments. Among these is the first dentary tooth associated with the tip of the dentary (‘fd’ in Text-fig. 6). This tooth has been rotated and protrudes from the outermost tip of the dentary. The teeth are robust and large with a typical crown size of >20 mm, greater than those of typical Callovian metriorhynchids (Adams-Tresman 1987). They are weakly lateromedially compressed and curve distally. The enamel displays fine longitudinally aligned ridges that become coarser away from the smooth apex. Carinae are visible on mesial and distal sides of the teeth, but they are not serrated, unlike those of other species of Dakosaurus (‘c’ in Text-fig. 6). The ridges and carinae end abruptly at the gum tissue boundary.

<table>
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<th>Taxon</th>
<th>Ris</th>
<th>Ipr</th>
<th>Rss</th>
<th>Afm</th>
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<td><em>Metriorhynchus casamiquelai</em></td>
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*The ratio is the mean of adult skulls of that taxon.

1With the long axis defined as that from the rostro-medial corner to the latero-posterior corner.

2The angle between the lateral and medial processes of the frontal that bound the anterior-medial margin of the supratemporal fossa is used in preference to the angle between the lateral and medial margins of the supraocular fossa (which laterally would include the postorbital) as when the skull is dorsoventrally compressed the postorbital tends to displace laterally exaggerating that angle.

Ris, ratio of interorbital distance across the frontals to skull length; Ipr, infection point of the prefrontals along the lateral margin in dorsal view compared to long axis of the cranium; Rss, ratio of supratemporal fossae long axis to skull length; Afm, angle between frontal lateral and medial processes.

TEXT-FIG. 6. Dakosaurus carpenteri sp. nov., BRSMG Cd7203. Teeth and dentigerous elements. Abbreviations: c, carina; fd, first dentary tooth. Scale bar represents 20 mm.
The fifth cervical vertebra can be identified as both the diapophyseal and parapophyseal processes have moved up the centra. The left parapophyseal process appears higher than the right (Text-fig. 7C–D), but this difference may have been amplified by deformation. The diapophyses are located at the same level as the anterior prezygapophyses, and have lengthened to form transverse processes (Text-fig. 7C–E), which are compressed slightly from above and have an overall length of 144 mm. They have an oval cross section with an approximate diameter of 17 mm. The diapophyses have a smooth anterior edge, unlike the cervicals of M. superciliosus (BMNH R. 1530, R. 2033, R. 2051, R. 2775; GLAHM V990), which have a highly lined anterior edge, and the posterior edge typically possesses a deep groove.

The zygapophyses are present only on the fifth cervical and are again typical of other metriorhynchid crocodiles. The prezygapophyses are large and strongly developed, projecting vastly beyond the centrum, each with an articulation surface that is flat (Text-fig. 7D). They are separated from each other in the midline by a very deep fossa beneath which the neural canal runs. The postzygapophyses are closer together than the prezygapophyses and they are separated by a smaller fossa (Text-fig. 7E). They also project beyond the centrum, but not as far as the prezygapophyses, and the articulation surface of each is slightly concave. The neural spine projects vertically, becoming thinner (width 13 mm) towards the extremity but becoming thicker (width 16 mm) again at the very tip of the spine.

**Dorsal vertebrae.** The first dorsal is identifiable as the first vertebra in which the parapophysis passes wholly or partly onto the neural arch, but still arises separately from the diapophysis (Andrews 1913). There are 12 identifiable dorsal vertebrae, all of which are highly deformed and incomplete, and only two preserve the bases of neural arches. The shape of the centra of these vertebrae ranges from circular, similar to that of the cervical vertebrae, to more elongate and oval. Whereas the anterior articulation surface of the centra is notably concave, the posterior surface is only faintly concave. The neural arches of the dorsal vertebrae appear to differ only slightly from the fifth cervical, except that the parapophysis is no longer borne on the centra (Text-fig. 7F). The affinity of the parapophysis, however, is unknown on the dorsals because none of the vertebrae is complete; in metriorhynchids, however, the parapophysis typically forms a step-like prominence on the anterior edge of the transverse process (Text-fig. 7F; Andrews 1913).

**Sacral vertebrae.** Only the second of the two sacral vertebrae is present, and it lacks the neural spine and the tip of the right sacral rib (Text-fig. 7G–I). The centrum is round to oval in shape, with a width of 56 mm and height of 49 mm. It is concave anteriorly and almost flat posteriorly, but this flattening may be the result of deformation. The sacral ribs are large and more robust than those of M. superciliosus (BMNH R. 1530, R. 2033, R. 2051, R. 2775; GLAHM V990), and they curve downwards so far that their outer ends are considerably lower than the ventral edge of the centra (Text-fig. 7G–H). The ribs also have a backwards curvature, the typical feature in metriorhynchids (Andrews 1913), and so the articulation surface of the rib extends further backwards than the posterior centrum face (Text-fig. 7I). The anterior margin of the rib is rounded, whereas the posterior edge bears a deep groove that runs the length of the rib (Text-fig. 7G–H). Towards the distal tip of the rib, the width increases from an average thickness of 25 mm in the centre to 35 mm at the extremity, and culminates in an articulation surface for contact with the ilium. The articulation bears concave facets that face laterally and downwards.

**Caudal vertebrae.** The caudal series includes a large number of vertebrae of different sizes, with between 33 and 36 elements (Andrews 1913). Only eight caudal vertebrae have been identified, all of which are compressed and lack the neural spines. Seven of the vertebrae are hour-glass shaped, highly depressed in the centre (Text-fig. 7J), and possess round concave faces, in which the width of the centra is less than the length of the vertebrae. They have an average length of 50 mm and width of 44 mm. One of the vertebrae, however, is much smaller (length 40 mm, width 15 mm), has highly elongated, concave surfaces, and it appears less square-shaped in lateral view. The articular surfaces of this vertebra are at a slight angle to the sagittal plane and the neural spine projects slightly forward, hence it is thought that this vertebra formed part of the caudal fluke (Text-fig. 7K).

**Ribs**

The ribs associated with the atlas and axis are missing, as are the ribs from the caudal series and associated chevrons.

**Cervical ribs.** Two of the ribs are anterior to mid-cervical in origin, and represent a left and a right rib. The tubercular (diapophyseal) process is larger and oval in cross section with a slightly concave articulation surface, whereas the capitular (parapophyseal) process is smaller and highly compressed (Text-fig. 7L–M). The outside of the rib projects slightly in front of the processes and extends back further, culminating in a point, and has an overall length of 58 mm. Part of another cervical rib is also present, probably from a mid- to posterior cervical vertebra because of its size.

**Dorsal ribs.** In the anterior dorsals, the anterior limb of the rib is reduced to a crest, whereas the posterior portion is elongated and forms the main part of the rib (Andrews 1913). Anteriorly, the region between the capitular (parapophyseal) and tubercular (diapophyseal) elements form a distinct angle, whereas further back in the series the tubercular process reduces to form a step-like structure on the posterior face (Andrews 1913), as seen in the majority of examples in this collection (Text-fig. 7N). The ribs are circular to oval in cross section with an average diameter of 12 mm, and they possess a small ridge running on the posterior edge from the tubercular facet to the end of the rib (Text-fig. 7N). The distal end of the rib is rounded and fairly indistinct.
Forelimb

Humerus. The humerus is a short, stocky bone, unlike the more slender humerus of *M. superciliosus* (BMNH R1530, R3016; GLAHM V1140), *M. leedsi* (BMNH R3015) and *M. palpebrosus* (OXFUM J.55476-8), with a length of 115 mm, and a width of 72 mm at the proximal end, 40.5 mm at the distal end, and a shaft 37.5 mm in diameter (Text-fig. 8). The shaft is flattened, and expands proximally. The distal end is triangular in outline, pointed at the posterior margin, and rounded at the anterior (Text-fig. 8B, D). The articulation surface is rounded, with no obvious inner and outer condyle.

The proximal end of the humerus is curved and rounded, with no obvious differentiation between the deltopectoral crest and the proximal articulation surface (‘dpc’ in Text-fig. 8B). This humerus has a rounded proximal margin towards the deltopectoral crest as opposed to a straighter edge seen in *M. superciliosus*, *M. leedsi*, and *M. palpebrosus*. The anterior margin of the shaft is flattened, whereas the posterior margin is more rounded. On the lateral surface, in the region of the deltopectoral crest, there are strong rugosities for the attachment of muscles (Text-fig. 8D), most likely *M. deltoideus clavicularis*, the major muscle involved in flexion of the forelimb during swimming (Meers 2003). Similarly there are roughened areas both externally near the distal end and internally near the proximal extremity for the attachment of lesser muscles (Meers 2003).

Propodial. A small, flattened disk-like bone is probably a propodial, either a radius or ulna. The bone is an oval disk measuring $57 \times 40$ mm (Text-fig. 8E). The bone thickness is uniformly c. 2–4 mm thick, except for a slight enlargement on one side, possibly the articulation surface for the humerus. Faint rugosity is apparent on the external surface around the margin.

Metacarpals. A very small, thin bone is thought to be a metacarpal. It is 44 mm long and 8 mm wide. Both the proximal and distal heads are enlarged and muscle scarring is visible (Text-fig. 8F).

Pelvis

Ischium. The pelvic girdle is represented by the left ischium, which is roughly triangular in shape (Text-fig. 9A). The overall shape is similar to that of *Metriorhynchus superciliosus* and other Callovian metriorhynchids, except that the outer margin is much more rounded. The neck of the ischium is narrow, measuring c. 47.5 mm, and widens ventrally to a broad blade-like expansion with a width of 175 mm. The blade is extremely thin, generally only c. 2–4 mm thick.

The proximal end of the ischium is divided into two processes separated by a deep notch (Text-fig. 9A–B). The anterior process is slender, more so than that of *M. superciliosus* (BMNH R. 2054, R. 2775, R. 6859), nearly circular in cross section, and projects from the neck of the ischium head at an angle of 45 degrees (Text-fig. 9A). This slender process extends higher than the posterior process by c. 11 mm. The tip of the anterior process terminates in a smooth, convex surface with no obvious articulation surfaces for either the ilium or the upper end of the pubis, and hence it is thought there was cartilage in this area (Andrews 1913). The width of this process is less than half that of the posterior process, the typical state in metriorhynchids, whereas a width of <25 per cent that of the posterior process is characteristic of *Geosaurus* (SMNS 9808).

The posterior process has a concave articulation surface that is dorsomedially directed (‘pp’ in Text-fig. 9B–C) and surrounded by fine striations for articulation with the ilium. The ischiadic wing is flat except for a slight increase in thickness on the ventral margin, indicating the sutural surface for union with...
the right ischium (‘ss’ in Text-fig. 9A, C). This ventral margin is much thicker and striated in *M. superciliosus* (BMNH R. 2054, R. 2775, R. 6859). On both the lateral and medial margins of the ischiadic wing are numerous striations and rugosities for attachment of various muscles (Romer 1923).

**Hindlimb**

**Femur.** The femur is a robust-looking bone with the classic sigmoidal shape seen in all metriorhynchids in which the proximal and distal extremities are twisted at about 160 degrees to each other (Text-fig. 10). In comparison to *Dakosaurus* (BMNH 40103a), however, the femur here is less sigmoidal. The fourth trochanter is absent, a character shared by all metriorhynchids (Andrews 1913). The lengths from the proximal to the distal extremities are 349.5 and 351 mm for the left and the right femora, respectively, and the widths at the thickest points of the shaft are 23.5 and 22.5 mm.

Both femora may be from the same individual, and the slight differences in measurements probably result from subtle deformation. The proximal end of the left femur appears flatter with a more pronounced crest on the inside than the right. The proximal head consists of two condyles that protrude laterally (Text-fig. 10A–B), and that are separated by a curved indentation, with the larger condyle on the inside. However, on the left femur, the anterior condyle is thinner and distorted anteriorly instead of laterally, suggesting that the left femur has undergone more deformation than the right (Text-fig. 10).

On the interior edge of both femora is a flattened, highly rugose area that extends one-third down the shaft (‘ra’ in Text-fig. 10A–B), and this area appears somewhat reduced in *M. superciliosus*. This large region is associated with the attachment of several muscles, including the *M. caudofemoralis longus* (Romer 1923; Gatesy 1990) and *M. pubo-ischio-femoralis* (Romer 1923). Scarring is also visible on both sides of the femora and is associated with the attachment of lesser muscles (Romer 1923). At the distal end a ridge is visible on the lateral sides of both femora, yet is more pronounced on the right. Otherwise, the distal extremities of the femora are rounded and fairly indistinct.

**PHYLOGENETIC ANALYSIS**

**Methods**

Phylogenetic relationships within Metriorhynchidae are still to be fully resolved. Currently there are two published phylogenies for Metriorhynchidae (Muller-Toewe 2005; Gasparini et al. 2006), neither of which includes a
large number of taxa, nor do they show a consistent topology. The Muller-Töwe (2005) study shows an unresolved polytomy consisting of *Dakosaurus maximus*, *Geosaurus giganteus*, a clade consisting of three species of *Geosaurus*, and a monophyletic *Metriorhynchus* (also consisting of three species). However, as no brevirostrine species of *Metriorhynchus* were included, the monophyly of this genus was not convincingly demonstrated. The Gasparini *et al.* (2006) study included only six metriorhynchid species, two of *Geosaurus*, two of *Dakosaurus*, one longirostrine *Metriorhynchus*, and one brevirostrine *Metriorhynchus*. Here the two *Metriorhynchus* species did not form a monophyletic grouping, but formed a polytomy with a *Geosaurus-Dakosaurus* clade. As these two

topologies only have three species in common (Metriorhynchus superciliosus, Dakosaurus maximus, and Geosaurus suevicus) nothing conclusive can be noted about metriorhynchid evolution from studying these two analyses alone.

In order to better assess the phylogenetic position of the new taxon, it was incorporated into a new cladistic analysis of metriorhynchid crocodilian relationships. This analysis is an extension of Young (2006) with new characters and taxa added (see the Appendix), bringing the total of characters to 82 and taxa to 28. All new characters were established by MTY after first-hand examination of specimens housed in various European institutions. Twenty-five ingroup taxa, of which the majority (19) were metriorhynchids, and three outgroup taxa (Hesperosuchus, Terristrisuchus, Protosuchus) where coded, making this the most detailed analysis on metriorhynchid crocodiles to date. The data matrix was analysed in PAUP* v.4.0b10 (Swofford 2002), using a branch-and-bound search. Nodal support was generated using non-parametric bootstrapping, also in PAUP* v.4.0b10, here with 1000 replicates of branch-and-bound searching.

Results

Sixty-six most parsimonious cladograms were generated with a tree length of 197 (CI = 0.73, RI = 0.88, RC = 0.64). The strict consensus (Text-Fig 11) of the fundamental cladograms is highly resolved. Thalattosuchia were found to be basal mesoeucrocodylians, but, as longirostrine metasuchians were not included in this analysis, the ambiguity over the phylogenetic position of Thalattosuchia is not addressed here (see Benton and Clark 1988). Very high bootstrap support was found for the nodes Thalattosuchia (100%), Teleosauridae (91%), Metriorhynchidae (94%), Metriorhynchidae more derived than Teleidosaurus calvadosii (100%), Geosaurus + Enaliosuchus (99%), Metriorhynchus cultridens + M. brachyrhynchus (96%), and Dakosaurus maximus + D. andinienensis (100%). The position of Pelagosaurus as the sister taxon to Steneosaurus is consistent with the findings of both Muller-Töwe (2005) and Gasparini et al. (2006). In agreement with Muller-Töwe (2005), Teleidosaurus calvadosii was found to be the basal-most metriorhynchid, and as with Muller-Töwe (2005) and Gasparini et al. (2006), a Geosaurus clade is recovered (however, Geosaurus is found to be paraphyletic with regard to Enaliosuchus). However, the internal relationships found here do not support the hypotheses of either Muller-Töwe (2005) or Gasparini et al. (2006).

In expanding the taxon and character data set, the broad topology of Young (2006) is retained, but with better resolution. All metriorhynchids more derived than T. calvadosii fall into two groups: (1) a clade consisting of the brevirostrine Metriorhynchus and Dakosaurus and (2) a clade consisting of the longirostrine Metriorhynchus and Geosaurus (with Enaliosuchus nested within). With the new characters added, character conflict within the brevirostrine clade (which in Young 2006, resulted in poor resolution of interrelationships) is now fully resolved. Dakosaurus, including D. carpenteri, is found to be monophyletic. Metriorhynchus casamiqualei is found to be the next closest taxon to Dakosaurus, whereas the Oxford Clay brevirostrine forms (M. brachyrhynchus, M. durobrivensis and M. cultridens) comprise a basal monophyletic group within the brevirostrine clade. Interestingly, M. brachyrhynchus and M. cultridens form a clade, which is the sister taxon of M. durobrivensis. Our results support the geometric morphometric analysis that Young (2006) found separated the brevirostrine forms into two species: namely M. durobrivensis and M. brachyrhynchus. Nodal support is generally high for all nodes in this clade.

Within the longirostrine clade nodal support is much poorer than that of the brevirostrine clade, with the exception of the Geosaurus clade. At the base of this clade there is a polytomy of a clade of Kimmeridgian species (M. palpebrosus and M. hastifer), M. superciliosus, M. moreli, and a clade consisting of the hyper-dentate Metriorhynchus and Geosaurus + Enaliosuchus. The taxonomic decision of Vignaud (1995) and Young (2006) in separating the Oxford Clay longirostrine Metriorhynchus into two species, M. superciliosus and M. leedsi, is also supported here. Metriorhynchus superciliosus and M. moreli are found in an unresolved position at the base of this clade, coding identically for all characters, whereas M. laeve and M. leedsi form an unresolved polytomy with the Kimmeridgian species M. acutus. As such, the smooth-skulled, hyper-dentate forms of the Oxford Clay are found to be more closely related to Geosaurus than to M. superciliosus.

The demonstrated non-monophyly of Metriorhynchus, and the large neglect of this family until comparatively recently, means a full taxonomic revision the family is badly needed. A larger and more comprehensive analysis of metriorhynchids by MTY is currently underway.

Discussion of phylogenetic conclusions

Synapomorphies of Thalattosuchia, such as possession of a non-planar skull table, the presence of diapophyses on the neural arch of the axis, the hindlimb being much longer than the forelimb, no palpebrals present in the orbit, and the vomer not exposed on the palate (Vignaud 1995; Larsson and Sues 2007), cannot be observed in the new taxon. However, Dakosaurus carpenteri clearly possesses several synapomorphies of Metriorhynchidae: three
teeth in the premaxilla (Andrews 1913), participation of the nasal in the antorbital fenestra, and an elongated, narrow, and obliquely orientated antorbital fossa (Vignaud 1995). There is no evidence of osteoderms near the body of the crocodile, nor of an external mandibular fenestra on the surangular and the angular, the sacral ribs have the typical ventrally-orientated curvature, and the pectoral girdle is somewhat reduced (Andrews 1913). In the skull,
the orbits are positioned laterally and are rostrally overhung by the lateral expansion of the prefrontals, the postorbital is longer than the squamosal, and the frontal part of the supratemporal crest is thicker than that of the parietal (Clark 1994). The tooth shape is also typical of metriorhynchids, being weakly lateromedially compressed and curved distally (Vignaud 1995).

_Dakosaurus carpenteri_ possesses several characters indicative of the genus _Dakosaurus_, and our new cladogram (Text-fig. 11) shows that _D. carpenteri_ is more closely related to species of the genus _Dakosaurus_ than to _Metriorhynchus superciliosus_ or any other _Metriorhynchus_ species. The angle between the lateral and medial processes of the frontal in _D. carpenteri_, at c. 60 degrees, is more similar to that of _Dakosaurus_, which is typically c. 45 degrees, rather than that of other metriorhynchids in the brevirostrine clade, which is typically closer to 90 degrees due to the reduced size of the supratemporal fossa (Gasparini et al. 2006) (see Table 1). Although the tooth shape and lack of denticles in _D. carpenteri_ is similar to those of other metriorhynchids, the number of teeth and size are closer to _Dakosaurus_: _D. maximus_ has approximately 16 teeth in each side of the upper jaw (SMNS 8203) and _D. andiniensis_ possesses 13–14 (Gasparini et al. 2006); while this crocodile has at least 14, in contrast to the 20–30 observed in most other metriorhynchids (Vignaud 1995).

**DISCUSSION**

_The Kimmeridgian metriorhynchid species_

The Westbury crocodile has already been shown not to belong to the common Callovian metriorhynchid species _Metriorhynchus superciliosus_. In order to justify the erection of a new species name, we compare it with the four other metriorhynchid species from the Kimmeridgian (Text-fig. 12): _Metriorhynchus acutus_, _M. hastifer_, and _M. palpebrosus_ from the early Kimmeridgian (cymodoce Zone), and _Dakosaurus maximus_ from the eudoxus Zone of the Kimmeridgian to the hybonotum Zone of the Early Tithonian (Vignaud 1995; Benton and Spencer 1995).

Hence _Dakosaurus maximus_ is the only species contemporaneous with the new crocodile. The type species of _Metriorhynchus_, _M. geoffroyii_, is also known from the cymodoce Zone of the Kimmeridgian (Vignaud 1995), but only the snout is preserved. Based upon comparative analysis of the shape of the external nares among metriorhynchids (Young, pers. obs.), it is very probable that _M. geoffroyii_ and _M. palpebrosus_ are synonymous, but this is beyond the scope of the current study.

All four Kimmeridgian species are similar in size to the Westbury skull at c. 0.8 m in length (Text-fig. 12). _Dakosaurus maximus_, however, has been found to have a wide range of skull sizes, with the largest being over 1 m long.
(the holotype of ‘D. manselii’). *Metriorhynchus acutus* has a very slender and gracile skull, and is more reminiscent of *Geosaurus* than *Metriorhynchus. Metriorhynchus hastifer* and *M. palpebrosus* are relatively similar, with long snouts and fairly small supratemporal fossae (see Table 1), in which the backs of the skulls appear somewhat box-shaped. *Dakosaurus maximus*, on the other hand, is much more robust, with a short, broad snout and very large supratemporal fossae. Its skull is also more triangular in shape because of the lateral and backwards expansion of the supratemporal fossae, whose posterior margin extends as far as the occipital condyle. It is clear that the Westbury skull is distinct from the other four metriorhynchid species (Text-fig. 12). The Westbury skull appears to fill the morphological gap between the more gracile metriorhynchids and *D. maximus*, with its fairly robust snout and relatively triangular appearance, although neither the snout is as short and broad as that of *Dakosaurus* nor is the skull so strongly triangular.

The dentition of the Westbury skull is also unique, not only in size, but in number of teeth for a Kimmeridgian skull. *Metriorhynchus acutus* has the highest number of teeth of any Kimmeridgian species, with 28–29 teeth per side in the upper jaw (Vignaud 1995). *Metriorhynchus hastifer* and *M. palpebrosus* have a similar number of teeth, with 22–24 on each side of the upper jaw (Vignaud 1995). The Westbury skull and *Dakosaurus maximus* share low numbers of teeth: *Dakosaurus* has 16 teeth on each side of the upper jaw (BMNH 40103), whereas the Westbury skull is estimated to have at least 14. In this respect the Westbury skull is more similar to *Dakosaurus* than to any other *Metriorhynchus* species, and is clearly not of the same species as any other Kimmeridgian crocodile.

**Palaeoenvironment**

During the Mid Jurassic, shallow epicontinental seas covered much of central and southern England. During the Late Jurassic, however, sea levels began to rise, reaching a high point during the Kimmeridgian (Taylor and Sellwood 2002). The sediments of the *eudoxus* Zone are thick, laterally uniform mudrock deposits that can be traced from southern England to Greenland, indicating that this deepening effect was large-scale, probably a result of basin subsidence following a phase of crustal extension (Hallam and Sellwood 1976; Taylor et al. 2001). Presence of oil-shales during the *eudoxus* Zone suggests that water depth had increased enough to allow prolonged stratification of the water column (Aigner 1980). During the Late Jurassic Wiltshire, England was approximately 30 degrees north of the palaeo-equator, equivalent
to the latitudes of the Mediterranean and Black Sea today. Rare fossil wood indicates that a landmass (perhaps the London landmass or Cornubia) might have been close by (Dineley and Metcalf 1999; Wright and Cox 2001).

**Palaeobiology**

Extreme marine adaptations, including modified hydrofoil-like forelimbs and a hypocercal tail, suggest that *D. carpenteri* was very much at home in the water and rarely, if ever, graced the land. Unlike teleosaurs and modern crocodilians, metriorhynchids had lost their surface osteoderms, allowing for more flexible body movement and tail-propelled swimming, possibly axial-undulatory (Massare 1988), but more likely generated by vertical movements (Krebs 1962). The caudal fin, to some extent, superceded the hind paddle as the main means of propulsion (Andrews 1913).

The general trend to long, thin snouts in most crocodilian groups reaches an extreme in the Thalattosuchia, ideal for preying upon small agile prey, such as cephalopods and fishes (Massare 1988). The *Dakosaurus* lineage appears to have secondarily shortened the snout, resulting in a lar-
ger, more robust jaw (Gasparini et al. 2006). With a shorter, more robust snout than most metriorhynchids, the skull of D. carpenteri was more like that of Dakosaurus, and they probably shared a similar mode of life. The ribs of D. carpenteri are long, indicating a large, deep-bodied animal, the supratemporal fossae are enlarged to accommodate larger jaw adductor musculature, and the robust articular indicates that D. carpenteri had a powerful bite (Massare 1988). These features, coupled with the larger teeth, indicate that D. carpenteri was less of a specialised piscivorous predator, like other metriorhynchids, and perhaps more of a generalist carnivore (Text-fig. 13).

The eudoxus Zone fauna of the English Kimmeridgian consists of an abundance of microscopic and invertebrate fauna, as well as a diversity of marine reptiles (Benton and Spencer 1995). The upper part of the water column was dominated by the large carnivorous pliosaurs and thalattosuchians, Dakosaurus carpenteri and D. maximus, the only two metriorhynchid species presently known from the eudoxus Zone (Text-fig. 14). In contrast to the five or six pliosaur species in the Callovian (Benton and Spencer 1995), only three pliosaur species are known from the Kimmeridgian (Grange et al. 1996; Benton and Spencer 1995) none of them medium-sized. If this is not a taphonomic artefact, then the absence of medium-sized pliosaurs in the Kimmeridgian might have left a niche for metriorhynchids to evolve a more robust skull, so enabling larger prey to be tackled. The Late Kimmeridgian metriorhynchids that would have occupied the fish/teuthoid-feeding niche are rare. The only definitively referable specimens are a complete mandible (CAMSM J29475) from the eudoxus Zone of Ely, Cambridgeshire, England (Benton and Spencer 1995) and an incomplete skull from the austissiodorensis Zone of Boulogne-sur-mer, France (SMNS 56999).

In order to understand the shifts in metriorhynchid niche occupation, food webs of the Callovian and Kimmeridgian are compared. Martill et al. (1994) presented a thorough food web for the Callovian of Peterborough, including four species of metriorhynchids, Metriorhynchus leedsi, M. superciliosus, M. brachyrhynchus, and M. durobrivensis. These were grouped, together with the pliosaurs Liopleurodon, Pliosaurus, and Simolestes, in a 'gigantic carnivore' group. However, in order to better represent the interactions among species, the gigantic carnivore group should be split in two, creating a top predator group and a large carnivore group. Liopleurodon and Pliosaurus were the top predators, with Simolestes and the brevirostrine metriorhynchids (M. brachyrhynchus and M. durobrivensis) being the large carnivores. Metriorhynchus brachyrhynchus and M. durobrivensis, however, should also be placed in the fish/teuthoid-feeding group, probably their dominant role. Metriorhynchus leedsi and M. superciliosus are clearly not large carnivores, and so they should be positioned in the fish/teuthoid feeding niche. It is clear that the majority of Callovian metriorhynchids occupied the fish/teuthoid-feeding niche.

This pattern continues into the cymodoce Zone of the early Kimmeridgian, in which the metriorhynchids, Metriorhynchus acutus, M. palpebrosus (M. geoffroyi) and M. hastifer, fill the fish/teuthoid-feeding niche, as in the Callovian. Interestingly, there are no medium-sized pliosaurs in the large carnivore niche, which appears to be empty, and so this might have provided an opportunity for the metriorhynchids D. maximus and D. carpenteri to fill that niche by the Late Kimmeridgian (eudoxus Zone). Apart from this major shift in the ecological role of metriorhynchids, the late Kimmeridgian food web (Text-fig. 14) is similar to that of the Callovian (Martill et al. 1994).

The late Kimmeridgian pattern continues into the early Tithonian (hybonotum Zone) where two of the metriorhynchids, Geosaurus gracilis and G. suevicus, occupied the fish/teuthoid-feeding niche, and the other two, G. giganteus and D. maximus, the large carnivore niche (Vignaud 1995). The gigantic carnivores Liopleurodon and Pliosaurus occupy the top predator role (Benton and Spencer 1995). Again, no medium-sized pliosaurs are present at this time, and large carnivorous crocodiles apparently continue to occupy their ecospace.

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REFERENCES


APPENDIX

List of characters. This list is an updated version of that in Young (2006).

Skull

1. Frontal: ornamented (0), or smooth (1).
2. Frontal-parietal between supratemporal fossa in dorsal view: frontal and parietal subequal in width (0), or parietal width is narrower than that of frontal (1).
3. Frontal-postorbital suture in dorsal view: irregular and straight or gently curved (0), or frontal splitting the postorbital in a V-shape directed posteriorly (1).
4. Parasphenoid: not visible in palatal view (0), or visible in palatal view forming a ridge along the pterygoids meeting the basisphenoid posteriorly (1).
5. Basisphenoid: in palatal view it never projects to a more anterior position than the quadrates (0), or projects further than the quadrates by more than 10% of its total length (1).
6. Maxilla-palatine suture: forms a V-shaped pointing anteriorly (0), M-shaped oriented posteriorly (1), or a broad U-shape pointing anteriorly (2) or no contact along the midline, lateral contact only (3).
7. Orientation of paraoccipital process in occipital view: horizontal (0), dorsal-laterally directed at a 45 degree angle (1), or medial edge horizontal, then terminal third sharply inclined dorsal-laterally at a 45 degree angle (2) or curve downwards strongly, so that they terminate ventral to the occipital condyle (3).
8. Palatal secondary palate: palatines of primary palate exposed and do not contact one another secondarily on midline (0), or palatines meet on midline forming a secondary palate (1).
9. Internal nares: open directly onto the palatal roof (0), open out into the buccal cavity in a posterior direction with the palatines creating a V-shape with its apex directed anteriorly (1), same but with palatines creating a broad U-shape on the anterior edge of the nares (2), or with palatines creating an M-shape on the anterior margin (3).
10. Position of foramen for cranial XII nerve: above the occipital condyle, in line with the foramen magnum (0), or below the foramen magnum (1).
11. Foramen for the internal carotid artery: similar in size to the openings for cranial nerves IX–XI (0), or extremely enlarged (1).
12. Prefrontal lateral development: reduced, flush with the rim of the orbit (0), incipient enlargement, extending laterally over the orbit by approximately 5% of its width (1), or enlarged, extending laterally over the orbit by >15% of its width (2).
13. Prefrontals: not wider than posteriorly directed V of the squamosal created by the posterior margin of the supratemporal fossa (0), or are wider (1).
14. Prefrontal shape: quadrilateral with irregular outline (0), teardrop-shaped with a convex outer margin (1), teardrop-shaped, with dorsal margin forming a 90 degree angle having a distinct triangular shape (2), teardrop-shaped with a smooth convex outer margin not exceeding the jugal bar in dorsal view (3), teardrop-shaped with the inflexion point directed posteriorly at approximately 70 degree angle from the antero-posterior axis of the skull (4), or teardrop-shaped with medial and lateral edges parallel with the inflexion point directed posteriorly at approximately a 50 degree angle from the antero-posterior axis of the skull (5).
15. Prefrontal length-width: longer than wide in dorsal view (0), or subequal in dorsal view (1).
16. Prefrontals anterior to the orbits: elongate, oriented parallel to antero-posterior axis of the skull (0), or short and broad, oriented posteriorly-medially-anterolaterally (1).
17. Palpebrals: two large palpebrals in orbit (0), one large palpebral (1), or absent (2).
18. Orbit position: dorsal (0), fully lateral and clearly visible in dorsal view (1), or fully lateral but the orbit shape is only clear in lateral view (2).
19. Sclerotic ossicles: absent (0), or present (1).
20. Ventrally opened notch on palatal surface of the rostrum near premaxilla-maxilla contact: absent (0), present as a notch (1), or present as a large fenestra (2).
21. Premaxilla length posterior to external nares: >67% of premaxilla total length is posterior to the external nares (0), between 50–65% of total length (1), 36–45% of total length (2), or ≤28% (3).
22. Nasal-premaxilla contact: present (0), or absent (1).
23. External nares shape: circular or division by nasals create two semi-circles (0), transverse ellipsoid (1), in dorsal view posterior edge straight (2), or spoon-shaped elongate ellipse (dorsal width <40% of antero-posterior length) (3).
24. External nares: either undivided or dived by nasal intrusion (0), almost completely separated in two by a premaxillary septum (1), or completely separated by a premaxillary septum (2).
25. Rostral proportions: nearly tubular (lateromedial and dorso-ventral diameters subequal ±5%) (0), broad, dorsoventral diameter ≥1.2 × lateromedial one (1), or oreinirostral, snout depth >33% of snout length, with a convex upper margin (2).
26. Angle between medial and lateral processes of the frontal: approximately 90 degree angle (0), approximately 45 degree angle, or more acute (1), or approximately 70–60 degree angle (2).
27. Lateral process of the frontal forming the beginning of the supratemporal arch: level with the medial process of the frontal starting the intertemporal bar (0), lower than the intertemporal bar, or not involved with the supratemporal arch (1).
28. Supratemporal fossa in dorsal view: anterior margin posterior to the postorbital (0), anterior margin reaches between the anterior and posterior points of the frontal-postorbital suture (1), reaches at least as anteriorly as the postorbital (2), or projects more anteriorly than the postorbital and reaches the intraorbital minimum distance (3).
29. Supratemporal roof dorsal surface: complex (0), or dorsally flat ‘skull table’ developed, with postorbital and squamosal with flat shelves extending laterally beyond quadrate contact (1).
30. Supratemporal fenestra in dorsal view: longer in length than the orbit (0), subequal in length as the orbit (1), or smaller than the orbits (2).
31. Supratemporal fenestra in dorsal view 2: does not exceed the parietal posteriorly or reach the supraoccipital (0), does not exceed the parietal, but does reach supraoccipital (1), or more posterior than the parietal (2).

32. Infracraniiform fenestra in lateral view: considerably longer in length than the orbit (0), equal/subequal in length than the orbit (1), or shorter in length than the orbit (2).

33. Lacrimal position: dorsal and lateral (0), or only lateral and not visible in dorsal view (1).

34. Lacrimal size: large, in lateral view at least 45% of orbit height (0), or smaller, <40% of orbit height (1).

35. Postorbital-jugal contact: postorbital medial to jugal (0), or postorbital lateral to jugal (1).

36. Postorbital bar: transversely flattened (0), or cylindrical (1).

37. Relative length between squamosal and postorbital: squamosal is longer (0), or postorbital is longer (1).

38. External nares position: at the tip of the snout, not exceeding the first premaxillary alveolus (0), at the tip of the snout, stretching between premaxillary alveoli (1), stretches to beginning of the first maxillary alveolus (2), starts just after the first premaxillary alveolus and does not exceed the 1st maxillary alveolus (3), or stretches to approximately the end of the second maxillary alveolus (4).

39. Jugal: separated from margin of antorbital fossa (0), or participates in the margin of antorbital fossa (1).

40. Nasal participation in antorbital fenestra: no (0), or yes (1).

41. Shape of antorbital fossa: subcircular or subtriangular (0), or elongated, narrow and oriented obliquely (1).

42. Parietal shape between parietal-squamosal sutures on either side in dorsal view: forms a anteriorly directed curve (0), or forms a straight line with an enclave for the supraoccipital (1).

43. Symphysis length: short, ≤29% of mandible length (0), moderate, 32–38% of mandible length (1), or long, ≥40% of mandible length (2).

44. Symphysis depth: deep, 10% or more of mandible length (0), moderate, 7–8% of mandible length (1), narrow, 4.5–6% of mandible length (2), or very narrow, ≥4% of mandible length (3).

45. External mandibular fenestra: present (0), or absent (1).

46. Pronounced groove on lateral surface of the dentary and surangular: absent (0), shallow and poorly developed (1), or deep and strongly developed with a large foramen at both ends (2).

47. Angular and surangular in lateral view: angular extends beyond the orbits, but surangular does not (0), neither bones extend beyond the orbits (1), surangular extends beyond the orbits, but angular does not (2), or both bones extended rostrally beyond the orbits (3).

48. Surangular in dorsal view: does not extend beyond the orbit along the dorsal surface of the mandible (0), or does (1).

49. Splenial involvement in symphysis: slight <10% of symphysis length (0), or extensive >20% of symphysis length (1), or not involved (2).

50. Retroarticular process: very short, broad, and robust (0), posteriorly elongated, triangular-shaped and facing dorsally (1), or posterovertrally projecting and paddle-shaped (2), or posteriorly elongated, dorsally facing and concave, with the posterior tip of the process elevated above the rest of the mandible (3).

51. Coronoid: does not projecting as far as the dentary tooth row (0), or projects further anteriorly than the caudalmost alveoli (1).

Dentition

52. Premaxilla tooth count: five (0), four (1), or three (2).

53. Maxilla tooth count: with no more than 11 teeth (0), 12–17 teeth (1), 18–20 (2), 20–28 teeth (3), or >28 teeth per side (4).

54. Dentary tooth count: 20 or more teeth per rami (0), or 18 or less teeth per rami (1). Although this character is expected to covary with character 53, M. casamiquelai has more teeth in the dentary than in its maxilla.

55. Tooth margins: without carinae, (0), smooth carinae (1), or denticulate carinae (2).

56. Maxillary teeth crown size: crowns not enlarged, <3.0 cm long (0), moderately enlarged, 3.0–3.8 cm long (1), or enlarged, >6 cm long (2).

57. Maxillary teeth: not lateromedially compressed (0), weakly lateromedially compressed, crown midipoint labiolingual width 60–90% distal-medial width (1), or strongly lateromedially compressed, crown midipoint labiolingual width >60% distal-medial width (2).

58. Tooth curvature: none, crown apical/subapical, 89–91 degrees (0), weakly recurved, 82–88 degrees (1), or strongly recurved, >80 degrees (2).

59. Maxillary teeth: no ‘constriction’ (pale band) at base of crown (0), or has a ‘constriction’ (1).

60. Dentary teeth posterior to tooth opposite premaxilla-maxilla contact: equal in size (0), or enlarged dentary teeth opposite to smaller teeth in maxillary tooth row (1).

Vertebrae

61. Caudal vertebrae downwards deflection: absent (0), or present (1).

62. Cervical vertebrae relative centra length: long (0), moderate, length-width subequal ±5% (1), or short, length <0.95 the centrum width (2).

63. Post-axial cervical vertebrae number: seven (0), or five (1).

64. Caudal vertebrae number: between 30–40 (0), or >48 (1).

Forelimb and pectoral girdle

65. Radius: elongate (0), or greatly reduced (1).

66. Humerus deltopectoral crest: present (0), or absent (1).

67. Humerus shape: proximal wider or subequal to distal head in width, distal head articulation surface almost straight
shaft contributing >50% of total length (0), same as before
except shaft contributes between 35–38% of total length (1),
or distal head wider than proximal head (>7%), distal end
articulation surface convex, with shaft making <25% of total
length (2).
6. Scapula/humerus size: humerus longer than scapula (0),
humerus and scapula subequal in length (1), or humerus
shorter than scapula (2).
7. Coracoid shape: neither ends are fan-shaped, having angular
margins (0), ventral end convex forming a gentle fan-shape,
and scapula-articular end triangular in shape with blunt
ends (1), or ventral and scapula-articular ends convex both
being a gentle fan-shape (2).
8. Metacarpal I: elongate (0), or broadly expanded (1).

Hindlimb and pelvic girdle
9. Ilium size: length of dorsal border at least 30% of femur length
(0), or length of dorsal border <21% of femur length (1).
10. Ischium anterior process: developed, with clearly defined
articulation facets for pubis and ilium, ≥50% as wide as aceto-
abalum width (0), reduced, lacking either articulation facet
and is 30–50% as wide as acetabulum width (1), or highly
reduced, lacking either articulation facet and is <25% as wide
as acetabulum width (2).
11. Tibia: long, >45% of femur length (0), medium, 40–45% of
femur length (1), short, 31–39% of femur length (2), or very
short, <30% of femur length (3).
12. Calcaneum tuber: well developed, with long neck (subequal
in length to main body of calcaneum ±5%), distal end wider
than main body of calcaneum and projects into the body at
>80 degrees (0), poorly developed, short neck (<half
length of calcaneum main body), distal end <half the width
of calcaneum main body width and projects out straight
from calcaneum (1), or absent/vestigial (2).
13. Metatarsal length: metatarsals 1–4 longer than digits (0),
or metatarsals 2–4 shorter than digits (1).
14. Metatarsal I: proximal end not enlarged, no more than 10%
widter than any other metatarsal (0), moderately enlarged, 20–30% wider
(1), or greatly enlarged, >5% wider (2).
15. Digit lengths: digit lengths in descending order III, IV, II, I
(0), or IV, III, II, I (1).

Osteoderms
16. Tail osteoderms: completely surrounded by osteoderms (0),
dorsal surface only has osteoderms (1), or lacks any osto-
derms (2).
17. Ventral trunk osteoderms: present (0), or absent (1).
18. Dorsal osteoderms: present (0), or absent (1).

Sacral ribs
19. Articulation surface for ilium on sacral rib: wide (0), or nar-
row (1).

Character-taxon matrix

Hesperosuchus

Terristrisuchus
100?? 3000? ?0000 0210? 0002 01001 1200? ?0?0 200?0 010?? ?012 02100 00000 00110 00

Protosuchus
00000 30000 00000 00102 00002 00011 02000 00000 00000 00000 ?11?1 02200 00000 00000 00010 00

Atoposauridae
00000 0010? 00000 001001 20001 00012 00000 10100 00020 11102 ?0{1,2}1 0[0,1][0,1]0[1]0[0]00 00000 00000 00100 00

Goniopholis
00000 0?000 01002 00000 02000 00000 02000 00000 00000 00000 ?11?1 02200 00000 00000 00010 00

Crocodiles niloticus
00000 00100 00000 001001 20001 00012 02000 101?? ?0030 01023 00111 01101 00000 00000 00000 00000 00

Alligator mississippiensis
00000 00100 00010 00000 02000 20000 00100 02000 010?? ?0030 01023 00111 01101 00000 00000 00000 00000 00

Stenoceraud leedsi
00000 0100? 00000 02000 01100 00000 00000 01100 00230 13111 11400 00100 000?0 00010 00000 00100 ?

Pelagosaurus typus
00000 00110 00000 02100 01100 00010 00100 01100 00230 13111 11300 00100 00000 00010 00000 00100 ?
Teleidosaurus calvadosii

Metriorhynchus laeve

Metriorhynchus leedsi

Metriorhynchus acutus

Metriorhynchus superciliosus

Metriorhynchus moreli

Metriorhynchus palpebrosus

Metriorhynchus hastifer

Metriorhynchus durobrivensis

Metriorhynchus cultridens

Metriorhynchus brachyrhynchus

Metriorhynchus casamiquelai

Dakosaurus carpenteri

Geosaurus suevicus

Geosaurus gracilis

Geosaurus araucanensis

Dakosaurus maximus

Dakosaurus andiniensis

Enaliosuchus macrospondylus

Taxa list and coding sources


8. Dentary and surangular possess a groove on the lateral surface which is shallow and poorly developed [46-1].
9. Splenial involvement in symphysis extensive [49-1].
10. Coronoid projects further anteriorly than the caudal most alveoli [51-1].

Pelagosaurus + Steneosaurus:
1. Basisphenoid (palatal view): projects further than quadrates by >10% of total length [5-1].
2. Cranial XII nerve foramen above the foramen magnum [10-0].
3. External nares is oval & dorsal width >10% longer than antero-posterior length [23-1].
4. Symphys depth ~4% of mandible length [44-3].
5. Angular and surangular extend rostrally beyond the orbits [47-3].
6. Surangular extends beyond the orbit along the dorsal margin of the mandible [48-1].
7. Teeth lack carinae [55-0].
8. Maxillary teeth not lateromedially compressed [57-0].

Pelagosaurus:
1. More than 67% of premaxilla total length is posterior to the external nares [21-0].

Steneosaurus:
1. Orbit dorsal [18-0].
2. More than 28 teeth per maxillae [53-3].

Teleidosaurus + (Longirostrine Metriorhynchus + (Geosaurus, Enaliosuchus)) + (Dakosaurus + brevirostrine Metriorhynchus)):
1. Foramen for the internal carotid artery extremely enlarged compared to the openings for cranial nerves IX–XI [11-1].
2. Prefrontals anterior to the orbits short and broad, oriented posteromedially-antrolaterally [16-1].
3. Symphys depth 4.5–6% of mandible length [44-2].
4. Three teeth in the premaxillae [52-2].

(Alongirostrine Metriorhynchus + (Geosaurus + Enaliosuchus)) + (Dakosaurus + brevirostrine Metriorhynchus):
1. Frontal-parietal crest in dorsal view: parietal width is <75% of frontal width [2-1].
2. Fronto-postorbital suture in dorsal view, frontal pushes the postorbital in a V-shape directed posteriorly [3-1].
3. Prefrontals greatly enlarged [12-2].
4. Prefrontal teardrop-shaped with a convex outer margin [14-1].
5. Orbit fully lateral but the orbit shape is only clear in lateral view [18-3].
6. External nares spoon-shaped elongate ellipse [23-3].
7. Supratemporal fossa in dorsal view, anterior margin reaches between the anterior and posterior points of the frontal-postorbital suture [28-1].
8. Supratemporal fenestra does not exceed parietal, but does reach supraoccipital [31-1].

Apomorphy list for thalattosuchian taxa

Thalattosuchia:
1. Premaxilla posterior to external nares: 50–65% of premaxilla total length [21-1].
2. Nasal-premaxilla contact absent [22-1].
3. Rostrum nearly tubular [25-0].
4. Supratemporal roof dorsal surface: complex [29-0].
5. Postorbital-jugal contact: postorbital lateral to jugal [35-1].
6. Relative length between squamosal and postorbital: postorbital is longer [37-1].
7. Symphys depth ≥4% of mandible length [43-2].
9. Infratemporal fenestra equal/subequal in length with the orbit [32-1].
10. Lacrimal lateral and not visible in dorsal view [33-1].
11. External nares reaches to the beginning of the first maxillary alveolus [38-2].
13. Antorbital fenestra is enclosed by lacrimal posteriorly, nasal dorsally and the maxilla ventrally [40-1].
14. Antorbital fossa is elongated, narrow and oriented obliquely [41-1].
15. External mandibular fenestra absent [45-1].
16. Maxillary teeth number 20–28 [53-3].

Equivocal-synapomorphies with *Teleidosaurus calvadosii*:
1. Paraphrenoid visible in palatal view forming a ridge along the pterygoids meeting the basisphenoid posteriorly [4-1].
2. Hypocercal tail [61-1].
3. Five cervical vertebrae [63-1].
4. Radius greatly reduced and oval in shape [65-1].
5. Humerus reduced, with the shaft contributing 35–38% of total length [67-1].
6. Humerus subequal in length to scapula [68-1].
7. Coracoid fan-shaped with both ends convex [69-1].
8. Metacarpal I broadly expanded [70-1].
9. Ilium dorsal border small [71-1].
10. Ischium anterior process reduced and lacking either articulation facet [72-1].
11. Tibia reduced, 40–45% of femur length [73-1].
12. Calcaneum tuber poorly developed [74-1].
13. Metatarsals II–IV shorter than digits [75-1].
14. Metatarsal I proximal end moderately enlarged [76-2].
15. Dorsal osteoderms absent [80-1].
16. Articulation surface for ilium on sacral rib small [81-1].
17. Sacral rib strongly curved ventrally [82-1].

*Metriorhynchus superciliosus + M. moreli + (M. palpebrosus + M. hastifer) + ((M. laeve + M. leedsi + M. acutus) + (Geosaurus gracilis + G. suevicus + (G. araucanensis + Enaliosuchus macrospondylus))):
1. More than 67% of premaxilla total length is posterior to the external nares [21-0].

*Metriorhynchus acutus*:
1. More than 28 teeth per maxillae [53-4].

*Geosaurus gracilis + G. suevicus + (G. araucanensis + Enaliosuchus macrospondylus)*:
1. Paraoccipital process is directed dorsal-laterally at a 45 degree angle [7-1].
2. Prefrontal teardrop-shaped with a smooth convex outer margin not exceeding the jugal bar in dorsal view [14-3].
3. Twenty-eight per cent of premaxilla total length is posterior to the external nares [21-3].
4. Lateral process of the frontal forming the beginning of the supratemporal arch: lower than the intertemporal bar [27-1].
5. Supratemporal fossa in dorsal view reaches at least as anteriorly as postorbital [28-2].
6. Supratemporal fenestra subequal in length as the orbit [30-1].
7. Infratemporal fenestra shorter in length than the orbit (at <25%) [32-2].
8. Between parietal-squamosal sutures the parietal is straight, with an enclave for the supraoccipital [42-1].
9. Angular and surangular extend rostrally beyond the orbits [47-3].
10. Maxillary teeth not lateromedially compressed [57-0].
11. Increased caudal vertebrae number [64-1].
12. Humerus deltopectoral crest absent [66-1].
13. Humerus greatly reduced, shaft contributing <25% of total length and distal head wider than proximal head [67-2].
14. Tibia highly reduced, <30% of femur length [73-3].

*Geosaurus gracilis*:
1. External nares is almost completely separated in two by a premaxillary septum [24-1].
2. External nares begins just after the first premaxillary alveolus but does not exceed 1st maxillary alveolus [38-3].
3. Metatarsal I proximal end moderately enlarged [76-2].
**Geosaurus arauacanensis** + **Enaliosuchus macrospondylus**:
1. External nares reaches to at least the end of the third maxillary alveolus [38-6].
2. Antorbital fenestra is enclosed by lacrimal and nasal, excluding the maxilla [40-2].

**Enaliosuchus macrospondylus**:
1. Maxillary teeth number 18–20 [53-2].
2. Moderately enlarged maxillary teeth (3.0–3.8 cm long) [56-1].
3. Teeth weakly compressed [57-1].

**Metriorhynchus durobrivensis** + (**M. brachyrhynchus** + **M. cultridens**): (**M. casamiquelai** + **Dakosaurus**):
1. Prefrontals wider than posteriorly directed ‘V’ of the squamosal created by the posterior margin of the supratemporal fossa [13-1].
2. Prefrontal teardrop-shaped, with dorsal margin forming a 90 degree angle having a distinct triangular shape [14-2].

**Metriorhynchus brachyrhynchus** + **M. cultridens**:
1. Mandibular symphysis makes up >40% of mandible length [43-2].
2. Maxillary teeth strongly lateromedially compressed [57-2].
3. Tooth crowns strongly recurved [58-2].
4. Maxillary teeth has a constriction at its base [59-1].

**Metriorhynchus casamiquelai** + **Dakosaurus**:
1. Smooth frontal [1-1].
2. Paroccipital process begins horizontal, terminal third sharply inclines dorsal-laterally at a 45 degree angle [7-2].
3. Thirty-six to forty-five per cent of premaxillary total length is posterior to the external nares [21-2].
4. Supratemporal fossa in dorsal view reaches at least as anteriorly as postorbital [28-2].

**Metriorhynchus casamiquelai**:
1. Symphysis depth ~4% of mandible length [44-3].
2. Surangular extends beyond the orbits, but the angular does not [47-2].
3. Dentary teeth number 20 or more [54-0].
4. Teeth lack carinae [55-0].

**Dakosaurus carponenti** + (**D. maximus** + **D. andiniensis**):
1. Prefrontal teardrop-shaped with the inflexion point directed posteriorly at ~70 degree angle from the antero-posterior axis of the skull [14-4].
2. Maxillary tooth crowns moderately enlarged (3.0–3.8 cm long) [56-1].

**Dakosaurus maximus** + **D. andiniensis**:
1. Prefrontal teardrop-shaped with medial and lateral edges parallel with the inflexion point directed posteriorly at approximately a 50 degree angle from the antero-posterior axis of the skull [14-5].
2. Prefrontal length-width subequal (±5%) in dorsal view [15-1].
3. Supratemporal fossa in dorsal view projects more anteriorly than the postorbital and reaches the intraorbital minimum distance [28-3].
4. External nares starts just after the 1st premaxillary alveolus and does not exceed the 1st maxillary alveolus [38-3].
5. Pronounced groove on lateral surface of the dentary and surangular deep and strongly developed with a large foramen at both ends [46-2].
6. Large denticulate serrations creating the dental carinae [55-2].
7. Maxillary teeth crowns extremely enlarged (>6 cm long) [56-2].

**Dakosaurus andiniensis**:
1. Rostrum is oreinostral [25-2].
2. Symphysis depth 10% or more of mandible length [44-0].
3. Less than 11 teeth per maxillae [53-0].