

A NEW METRIORHYNCHID CROCODYLIAN (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), a clade sometimes 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 Callovian (Andrews 1913; Martill 1986), metriorhynchid crocodilians remain a rarity in the Kimmeridgian (Grange and Benton 1996).

The Kimmeridge 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 pliosaurs *Pliosaurus brachyspondylus* 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.

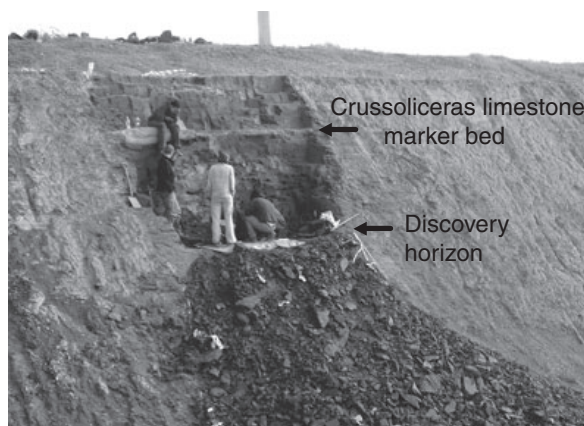
Institutional abbreviations. BMNH, Natural History Museum, London; BRSMG, Bristol City Museum and Art Gallery, Bristol; CAMSM, Sedgwick Museum, Cambridge; GLAHM, Hunterian Museum, Glasgow; HMN, Humboldt Museum für Naturkunde, Berlin; OXFUM, Oxford University Museum; PETMG, Peterborough City Museum and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



TEXT-FIG. 1. Photograph of the postcranial excavation showing the relationship of the discovery horizon to the limestone marker bed, a distance of c. 2 m.

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).

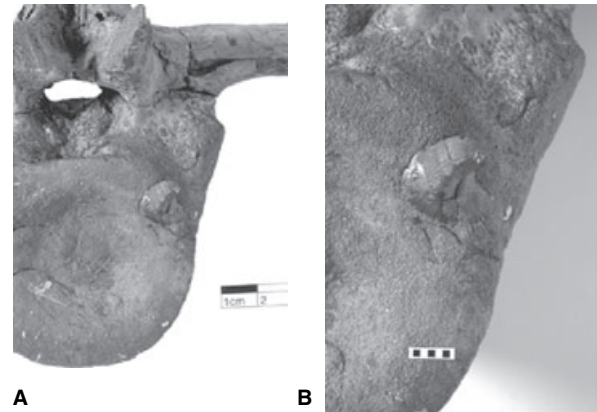
Encrustations are identifiable on both dorsal and ventral surfaces of most of the fossil indicating that the specimen remained exposed on an oxygenated or partially anoxic seabed for a length of time prior to burial (Martill 1985; Dineley and Metcalf 1999). The majority of encrustations are the remains 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



TEXT-FIG. 2. BRSMG Cd7203. A, shell encrustations on vertebra and B, close up view of encrustations seen in A. Scale bars represent 20 mm (A) and 5 mm (B).

DAKOSAURUS Quenstedt, 1856

Dakosaurus carpenteri 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 Ce17365, 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.

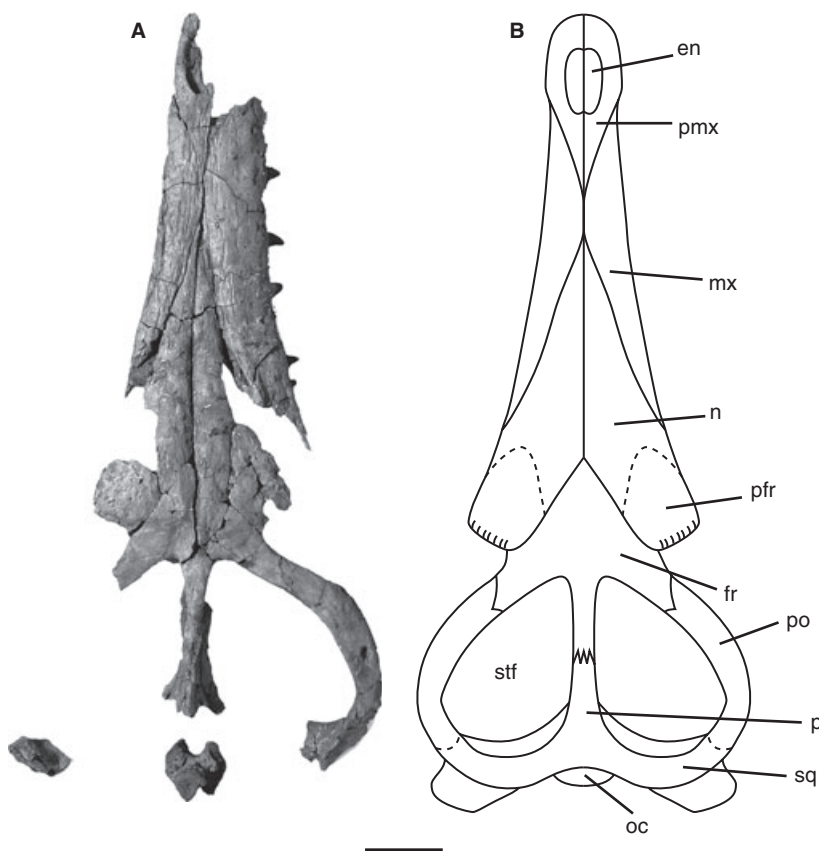
Description

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

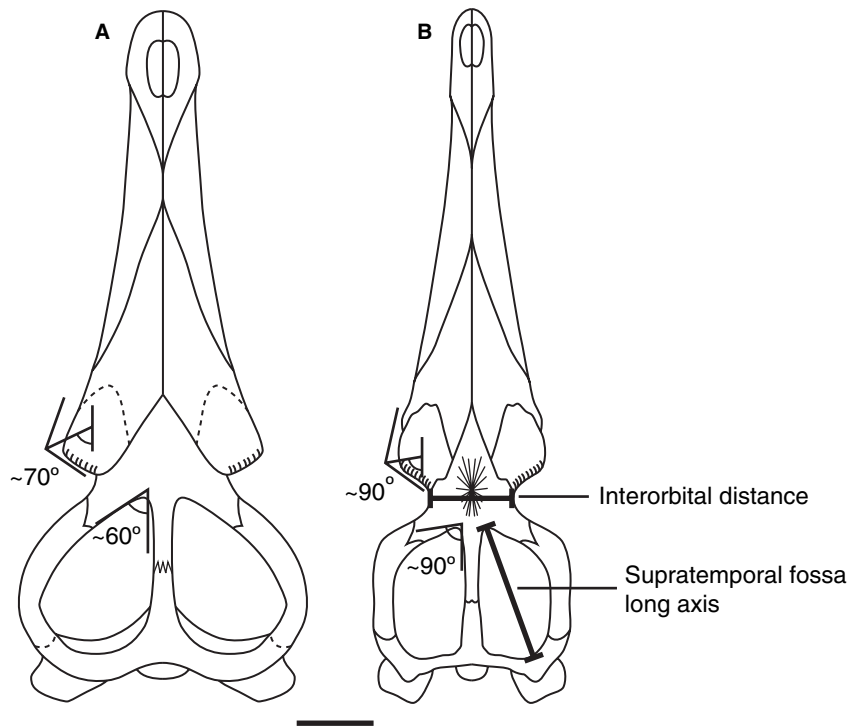
fossae are greatly enlarged, particularly laterally (Text-fig. 4), as the postorbital and the squamosal extend laterally beyond the prefrontal by c. 110 mm compared to just 30 mm in *M. superciliosus* (Andrews 1913; e.g. BMNH R2030). The enlarged postorbital region would have provided an enlarged attachment 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. lissocephalus* CAMSM J. 29419), and *Enaliosuchus* (e.g. *E. macrospondylus* 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.

TEXT-FIG. 4. Diagrammatic sketches of skulls in dorsal view. A, BRSMG Ce17365, the Westbury skull. B, a typical *Metriorhynchus superciliosus* skull. Angles for inflection point and supratemporal fossa indicated. 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 Dellapé 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,

TABLE 1. Cranial dimensions of Late Jurassic species of metriorhynchids.

Taxon	Ris	Ipr	Rss [†]	Afm [‡]
<i>Teleidosaurus calvadosii</i>	0.151	~90°	0.249	~90°
<i>Metriorhynchus casamiquelai</i>	0.183	~90°	0.252	~90°
<i>M. leedsi</i> *	0.136	~90°	0.240	82–91°
<i>M. superciliosus</i> *	0.132	~90°	0.222	86–94°
<i>M. brachyrhynchus</i> *	0.148	~90°	0.243	84–93°
<i>M. acutus</i>	0.126	~90°	0.217	~90°
<i>M. hastifer</i>	0.133	~90°	0.230	~60°
<i>M. superciliosus</i> (Buffetaut 1977)	0.164	~90°	0.226	~60°
<i>M. palpebrosus</i>	0.194	~90°	0.254	~90°
<i>Dakosaurus carpenteri</i>	0.179	~70°	0.315	~60°
<i>D. maximus</i>	0.210	~70°	0.383	~45°
<i>D. andiniensis</i>	0.289	~70°	0.408	~45°
<i>Geosaurus gracilis</i>	0.117	~90°	0.177	~90°
<i>G. suevicus</i>	0.110	~90°	0.227	~45°

*The ratio is the mean of adult skulls of that taxon.

[†]With the long axis defined as that from the rostral-medial corner to the latero-posterior corner.

[‡]The 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 supratemporal 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.

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 *Dako-*

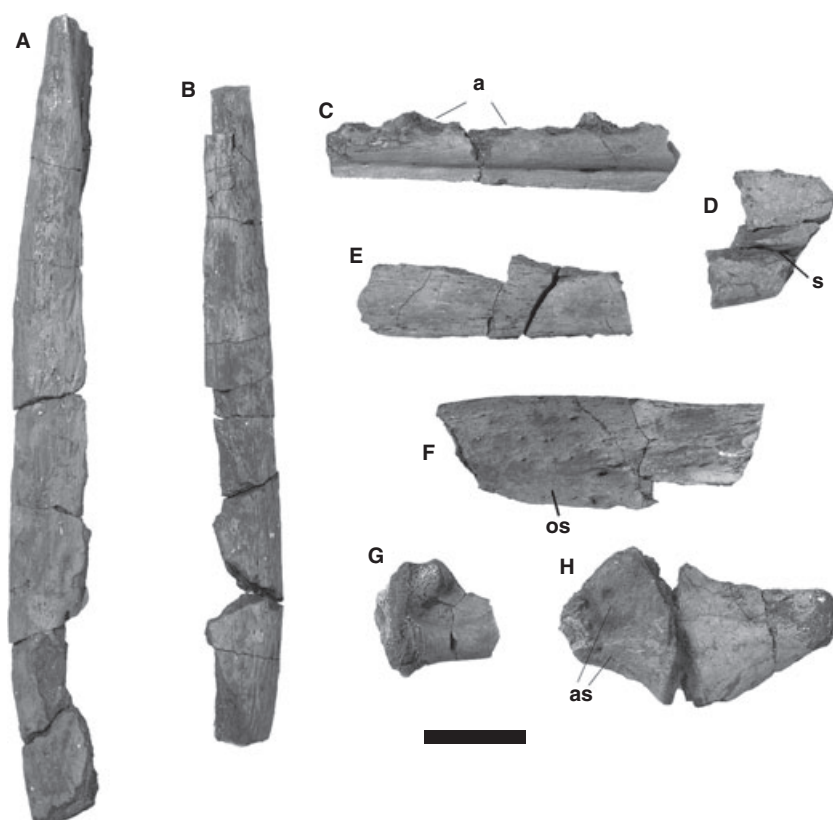
saurus ('c' in Text-fig. 6). The ridges and carinae end abruptly at the gum tissue boundary.

Vertebrae

Cervical vertebrae. Both the first (atlas) and second (axis) vertebrae are missing from the specimen. There should be no more than five post-axial cervical vertebrae in metriorhynchids (Fraas 1902; Andrews 1913; Steel 1973), with the cervicals being identifiable as vertebrae in which the parapophyseal process is located low on the centrum and not associated with the neural arch (Andrews 1913). This is contra to Arthaber (1906) in which he described seven post-axial cervicals on *M. jaekeli* (a junior synonym of *M. superciliosus*: see Vignaud 1995), however Andrews (1913, p. 160) suggests it is more likely that this specimen has vertebrae from other individuals included. This was confirmed by Young (2006, pers. obs.) for *Geosaurus suevicus* (SMNS 9808) and *G. gracilis* (BMNH R. 3948), both of which are preserved within lithographic limestone and have all but the terminal caudals preserved in life-position, and each exhibits only five post-axial cervicals. In addition, specimens of *M. superciliosus* (BMNH R. 1530, R. 2033) and *M. leedsi* (BMNH R. 3014) that preserve both the cervicals and all the anterior dorsals, and are at least as complete as the *M. jaekeli* holotype, possess only five post-axial cervicals. Wu *et al.* (2001) confirm that vertebrae with the parapophysis borne on the centrum are from the cervical series in extant crocodilians, but parapophyseal process position on the final cervical and the first dorsal is very similar, with the parapophysis partly crossing the centrum-neural arch suture on the first dorsal in the spheosuchian *Dibothrosuchus* (Wu and Chatterjee 1993). However, in Metriorhynchidae this issue has not been witnessed in any specimen (Young, pers. obs.) with the parapophysis not only being dorsal to the centrum-arch suture, but is borne above the ventral border of the neural canal. With this being the case, all five post-axial cervicals are present in BRSMG Cd7203. Four of these putative cervicals are very similar and hence the exact order is unknown, but the fifth is very different and is clearly at the boundary between the cervicals and the dorsals, because the parapophyses have passed up the side of the centrum and are situated just below the diapophyseal processes (Text-fig. 7C–D). The articular faces of the cervical vertebrae are oval to circular and moderately concave. Of the cervical vertebrae, the only complete example is the fifth, which has a height of c. 146 mm from the base of the centrum to the tip of the neural spine.

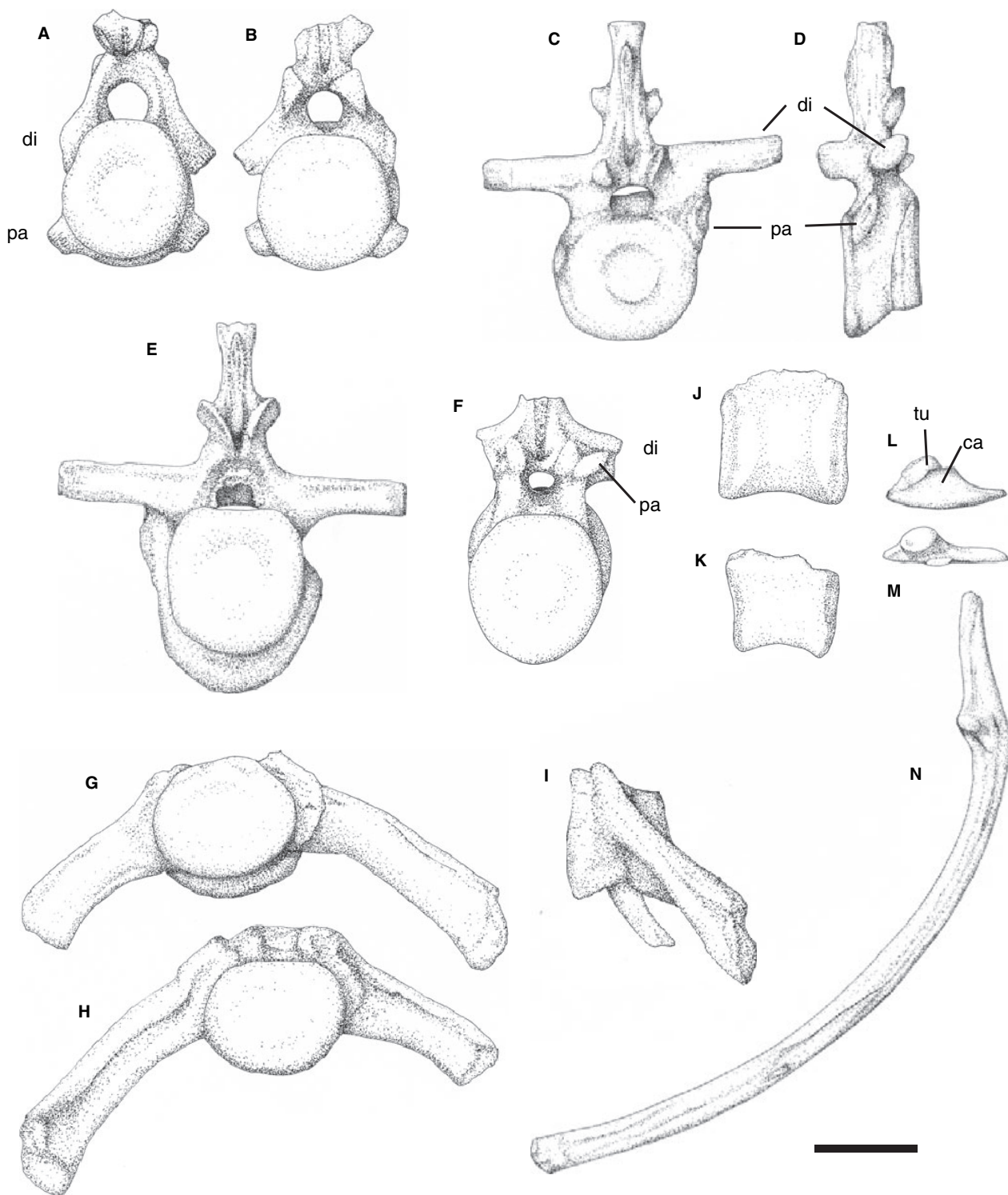
The cervical vertebrae, in general form, closely resemble those of other metriorhynchid crocodiles. In the first four vertebrae, the parapophyseal processes are situated anteriorly and towards the base of the centrum, without protruding beyond the bottom of the centra (Text-fig. 7A–B). The parapophyses are short and at the outer end they bear an articulation surface for attachment with the capitulum of the cervical ribs. The diapophyseal process in these four vertebrae is associated with the neural arch, very small, and angled downwards (Text-fig. 7A–B). Again these processes bear articu-

TEXT-FIG. 5. *Dakosaurus carpenteri* sp. nov., BRSMG Cd7203. Mandibular elements. A, left angular. B, right angular. C, fragment of dentary. D, suture between angular and surangular. E–F, fragments of surangular. G, coronoid process. H, articular. Abbreviations: a, alveoli; as, articulation surface; os, overlapping suture; s, suture. Scale bar represents 40 mm.



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.





TEXT-FIG. 7. *Dakosaurus carpenteri* sp. nov., BRSMG Cd7203. Vertebral elements. A–B, mid cervical vertebrae in A, anterior and B, posterior views. C–E, possible fifth cervical vertebra in C, anterior, D, lateral, and E, posterior views. F, mid dorsal vertebra. G–I, sacral vertebra in G, anterior, H, posterior, I, and lateral views. J, mid caudal vertebra. K, caudal vertebra from fluke region. L–M, mid cervical rib in L, medial and M, dorsal views. N, mid dorsal rib. Abbreviations: ca, capitulum; di, diapophyseal process; pa, parapophyseal process; tu, tuberculum. Scale bar represents 40 mm.

lation surfaces for union with the tubercle, similar to those on the parapophyses.

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 *Metriorhynchus laevis* (BMNH R. 3014, R. 3015), which have a highly lineated 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.

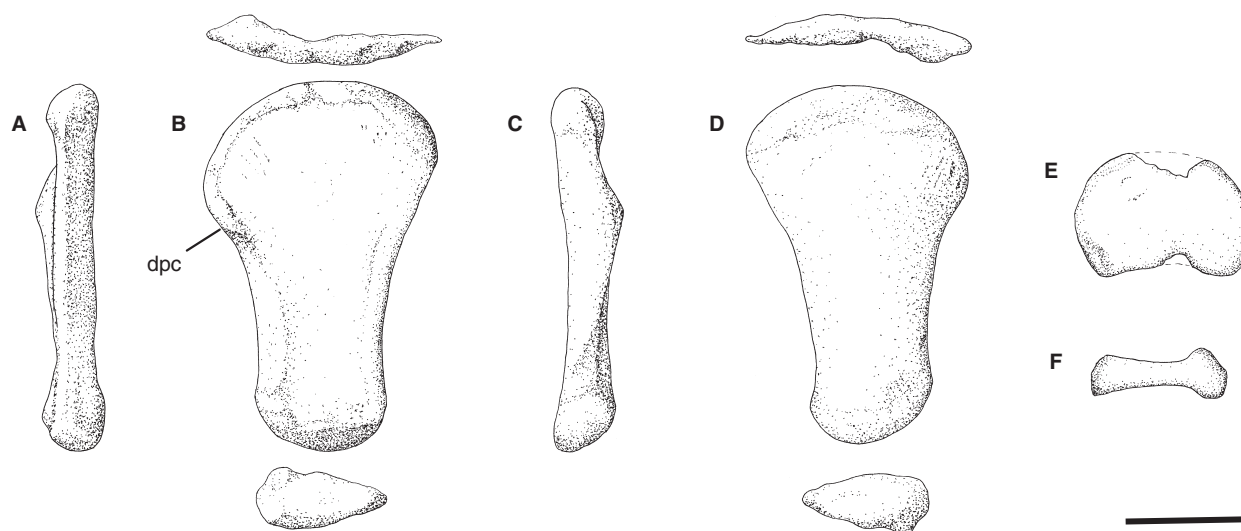
Caudal vertebrae. The caudal series includes a large number of vertebrae of different sizes, with between 33 and 36 elements (Andrews 1913). Only eight caudal vertebrae have been identified, all of which are compressed and lack the neural spines. Seven of the vertebrae are hour-glass shaped, highly depressed 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 vertebrae 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.



TEXT-FIG. 8. *Dakosaurus carpenteri* sp. nov., BRSMG Cd7203. Forelimb elements. A–D, humerus in A, posterior view, B, medial view, with distal and proximal end views, C, anterior view, and D, lateral view, with distal and proximal end views. E, propodial. F, metacarpal. Abbreviation: dpc, deltopectoral crest. Scale bar represents 40 mm.

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 57×40 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.

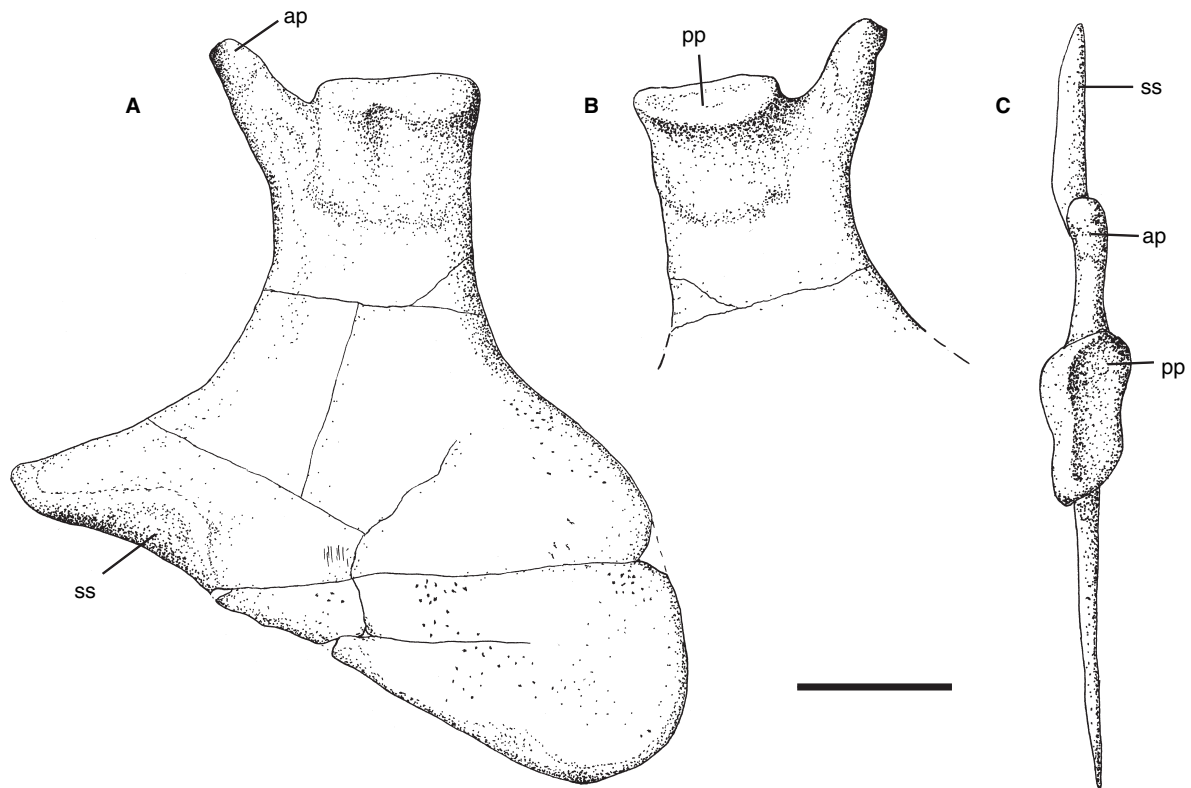
Metacarpals. A very small, thin bone is thought to be a metacarpal. It is 44 mm long and 8 mm wide. Both the proximal and distal heads are enlarged and muscle scarring is visible (Text-fig. 8F).

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



TEXT-FIG. 9. *Dakosaurus carpenteri* sp. nov., BRSMG Cd7203. Ischium. A, lateral view. B–C, proximal processes in B, medial and C, dorsal views. Abbreviations: ap, anterior process; pp, posterior process; ss, sutural surface. Scale bar represents 40 mm.

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

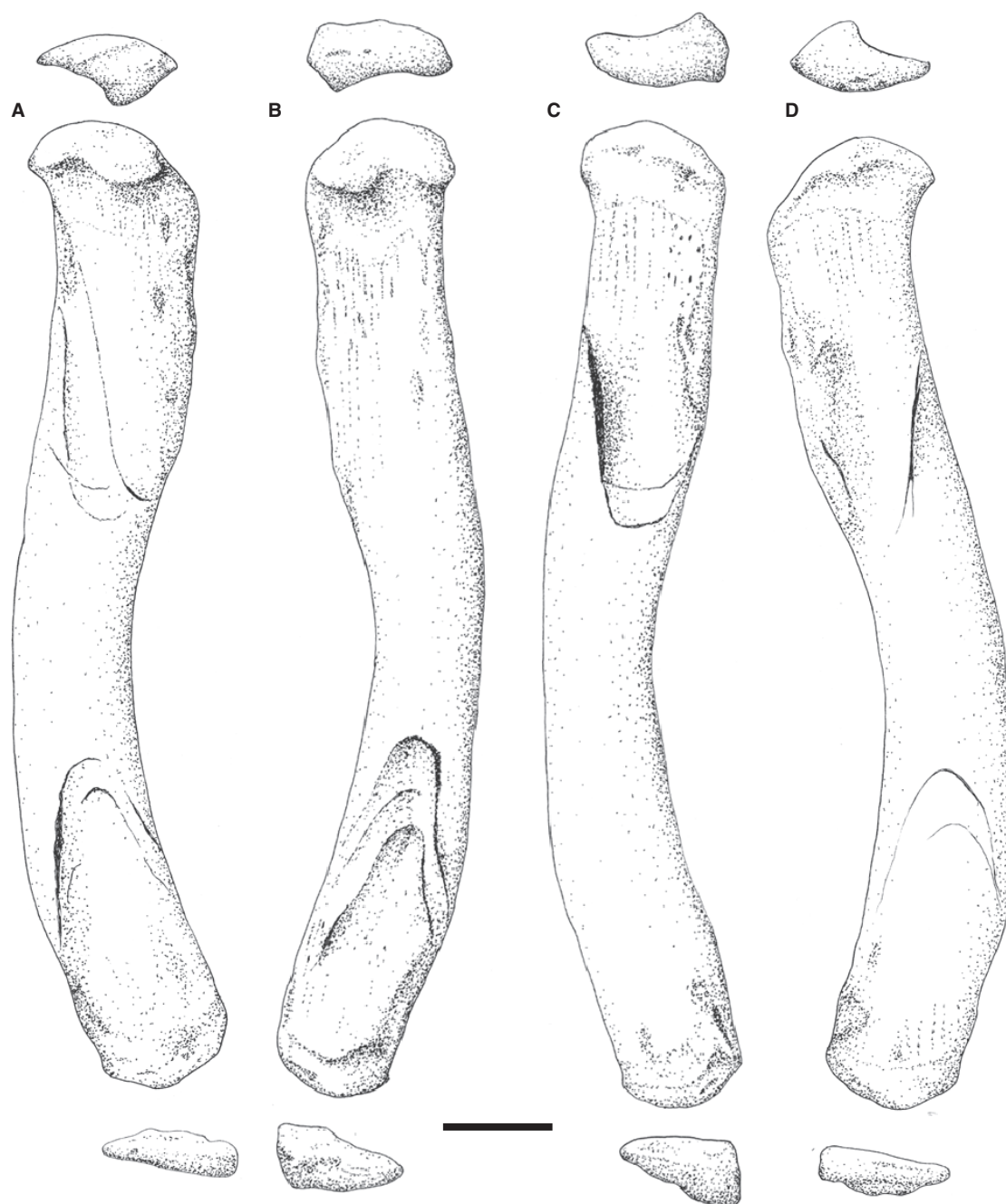
anterior condyle is thinner and distorted anteriorly instead of laterally, suggesting that the left femur has undergone more deformation than the right (Text-fig. 10).

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-Töwe 2005; Gasparini *et al.* 2006), neither of which includes a



TEXT-FIG. 10. *Dakosaurus carpenteri* sp. nov., BRSMG Cd7203. Femora with distal and proximal end views. A, left femur in lateral view. B–C, right femur in B, lateral and C, medial views. D, left femur in medial view. Abbreviation: ra, rugose area. Scale bar represents 40 mm.

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 metri-orhynchid 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*) were 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. andiniensis* (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.*

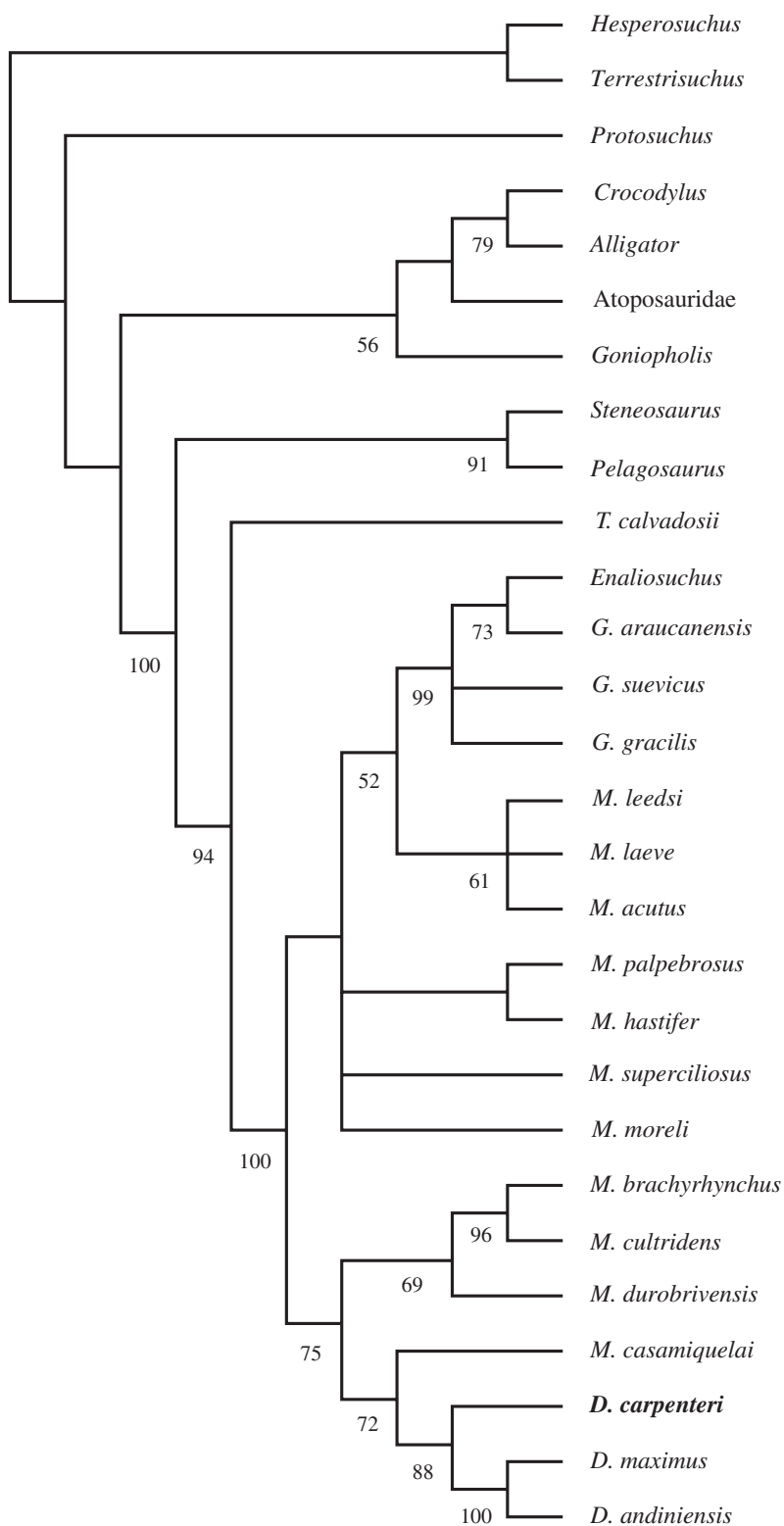
calvadosii fall into two groups: (1) a clade consisting of the brevirostrine *Metriorhynchus* and *Dakosaurus* and (2) a clade consisting of the longirostrine *Metriorhynchus* and *Geosaurus* (with *Enaliosuchus* nested within). With the new characters added, character conflict within the brevirostrine 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. laevis* 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



TEXT-FIG. 11. Strict consensus of 66 most parsimonious cladograms, with bootstrap support for each node. See text for tree statistics.

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 post-orbital 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).

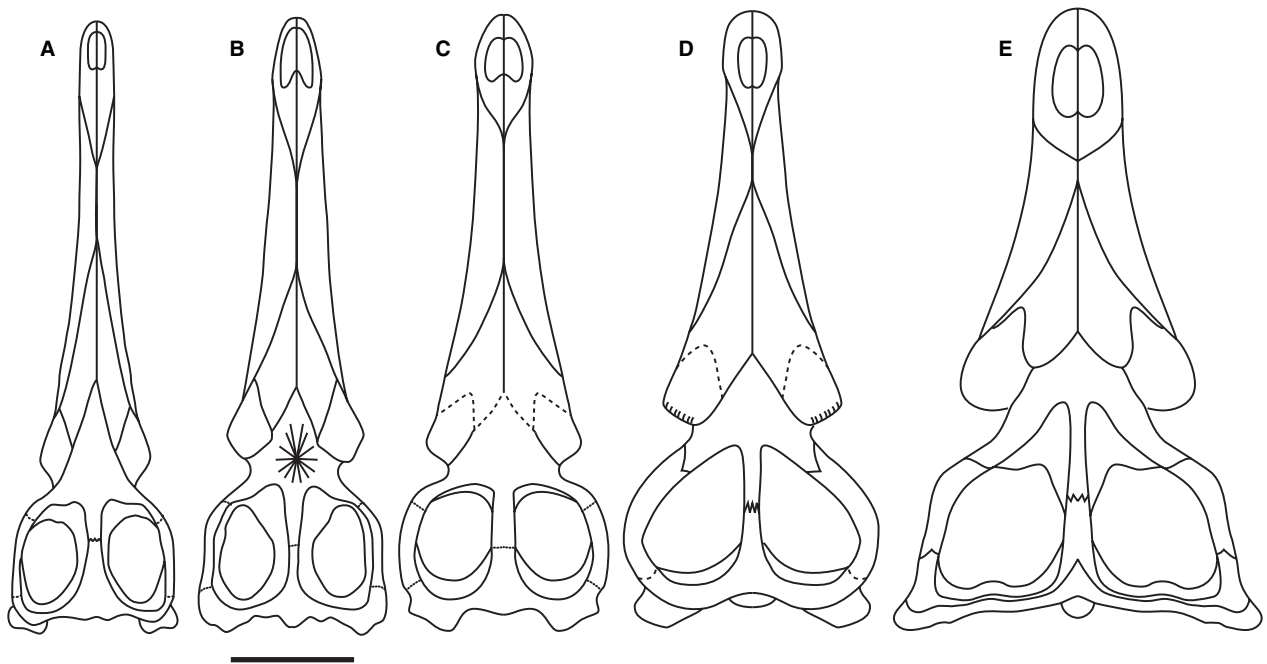
Dakosaurus carpenteri possesses several characters indicative of the genus *Dakosaurus*, and our new cladogram (Text-fig. 11) shows that *D. carpenteri* is more closely related to species of the genus *Dakosaurus* than to *Metriorhynchus superciliosus* or any other *Metriorhynchus* species. The angle 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

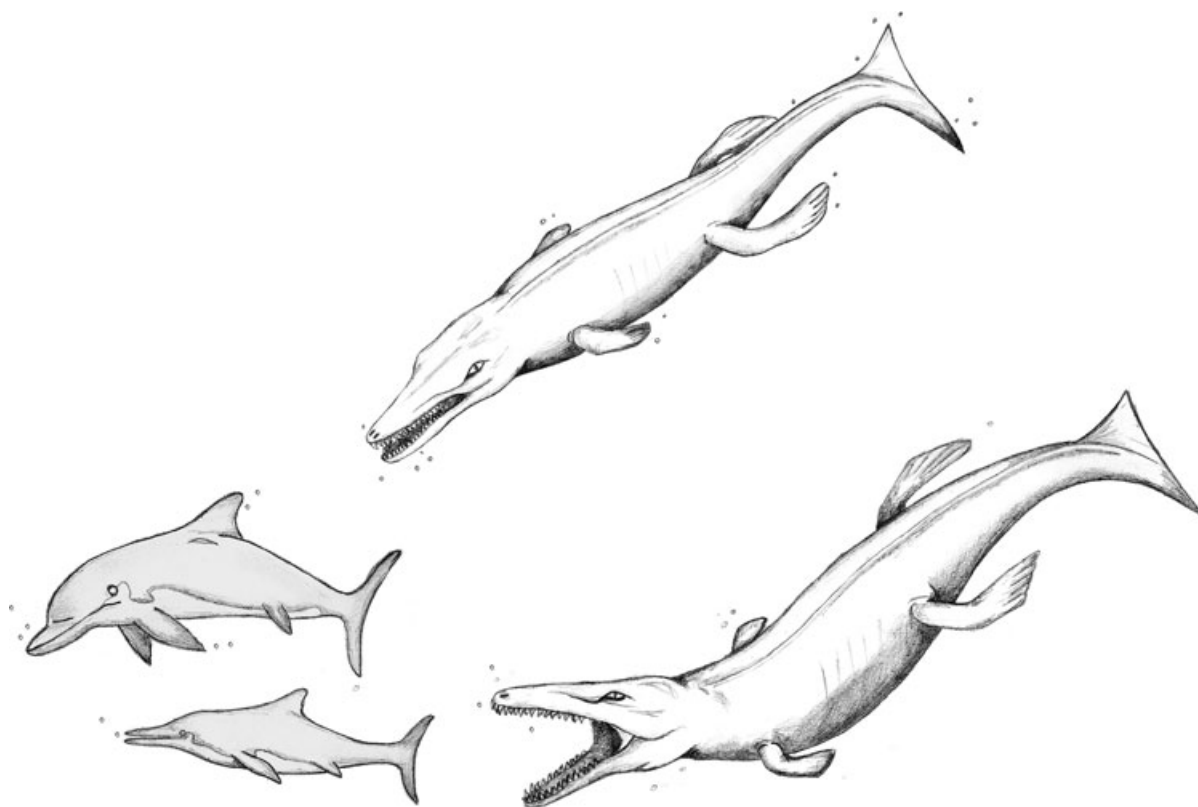
The Kimmeridgian metriorhynchid species

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. geoffroyi*, 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. geoffroyi* 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



TEXT-FIG. 12. Kimmeridgian crocodiles. A, *Metriorhynchus acutus*; B, *Metriorhynchus hastifer*. C, *Metriorhynchus palpebrosus*. D, *Dakosaurus carpenteri* sp. nov. E, *Dakosaurus maximus*. All skulls drawn to same scale for ease of comparison. Scale bar represents 100 mm.



TEXT-FIG. 13. Sketch reconstruction of a pair of *Dakosaurus carpenteri* crocodiles hunting ichthyosaurs.

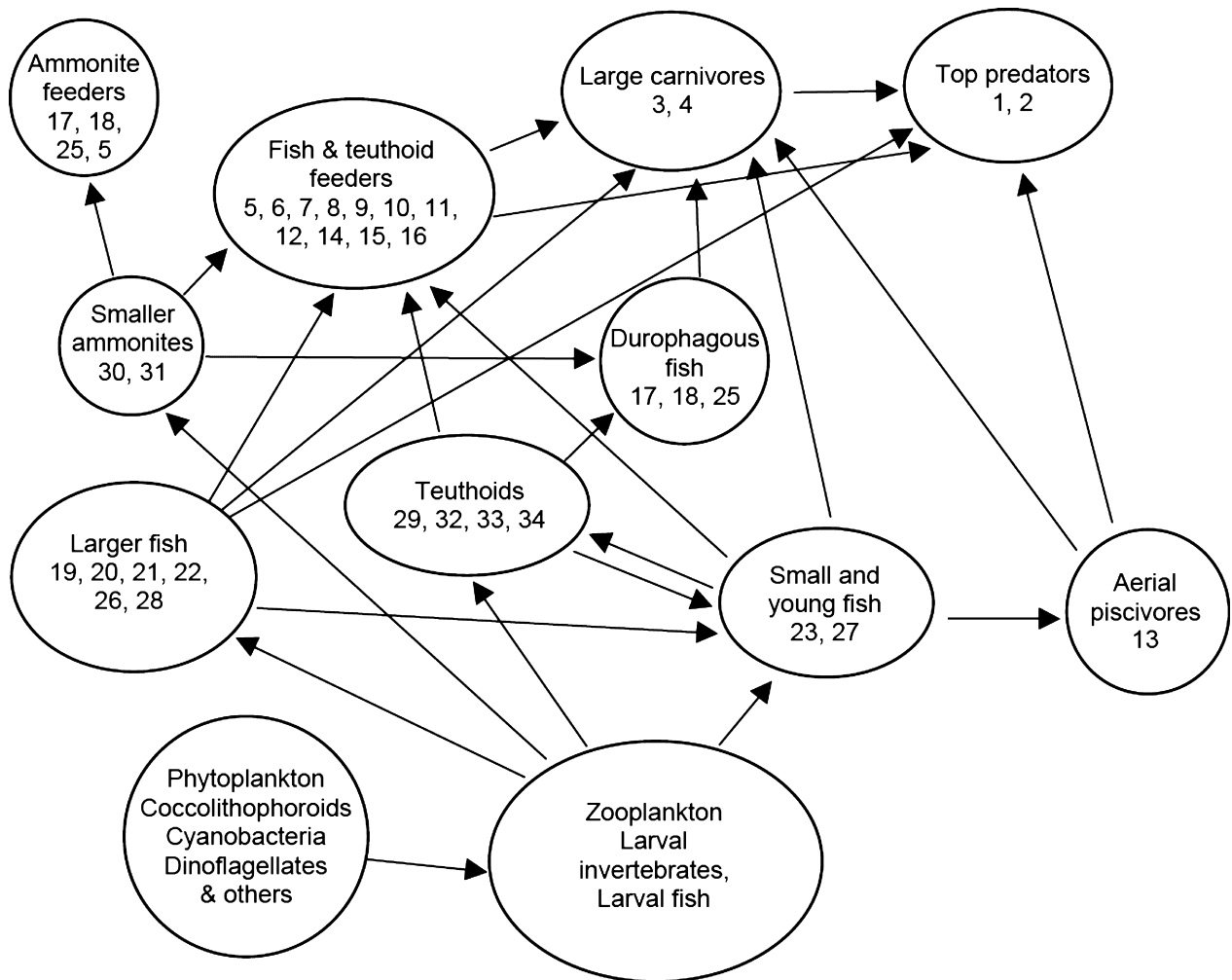
(the holotype of '*D. manselii*'). *Metriorhynchus acutus* has a very slender and gracile skull, and is more reminiscent of *Geosaurus* than *Metriorhynchus*. *Metriorhynchus hastifer* and *M. palpebrosus* are relatively similar, with long snouts and fairly small supratemporal fossae (see Table 1), in 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



TEXT-FIG. 14. Trophic relationships for the genera of the *eudoxus* Zone (Kimmeridgian) thought to feed largely within the upper parts of the water column. Key to numbered taxa: pliosaurs (1, *Liopleurodon*; 2, *Pliosaurus*); crocodilians (3, *Dakosaurus maximus*; 4, *Dakosaurus carpenteri*; 5, *Steneosaurus*; 6, *Machimosaurus*); ichthyosaurs (7, *Macropterygius*; 8, *Nannopterygius*; 9, *Ophthalmosaurus*); plesiosaurs (10, *Colymbosaurus*; 11, *Kimmerosaurus*); turtle (12, *Thalassemys*); pterosaur (13, *Rhamphorhynchus*); hybodont sharks (14, *Asteracanthus*; 15, *Hybodus*); rhinobatid ray (16, *Asterodermus*); bony fishes (17, *Lepidotes*; 18, *Caturus*; 19, *Osteorachis*; 20, *Pachycormus*; 21, *Aspidorhynchus*; 22, *Hypocormus*; 23, *Allothissops*; 24, *Eurycormus*; 25, *Leptolepis*; 26, *Pachytrissops*; 27, *Pholidophorus*; 28, *Thrissops*); ammonites (29, *Orthaspidoceras*; 30, *Aulacostephanus*; 31, *Sutneria*; 32, *Propectinatites*; 33, *Aspidoceras*; 34, *Laevaptychus*). The list of genera is from Birkelund *et al.* (1983), Taylor and Cruickshank (1993), Benton and Spencer (1995), Underwood (2002), Bellwood and Hoey (2004), and the presentation is modified from Martill *et al.* (1994).

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, superseded 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. geoffroyii*) 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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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 orientated 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 posteromedially-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 divided 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 dorsoventral 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 1: 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. Infratemporal 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).

Mandible

43. Symphysis length: short, $\leq 29\%$ of mandible length (0), moderate, 32–38% of mandible length (1), or long, $\geq 40\%$ 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, $\geq 4\%$ 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 posteroventrally 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 midpoint labiolingual width 60–90% distal-medial width (1), or strongly lateromedially compressed, crown midpoint 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 $\pm 5\%$ (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).
68. Scapula/humerus size: humerus longer than scapula (0), humerus and scapula subequal in length (1), or humerus shorter than scapula (2).
69. 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).
70. Metacarpal I: elongate (0), or broadly expanded (1).

Hindlimb and pelvic girdle

71. Ilium size: length of dorsal border at least 30% of femur length (0), or length of dorsal border <21% of femur length (1).
72. Ischium anterior process: developed, with clearly defined articulation facets for pubis and ilium, ≥50% as wide as acetabulum 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).
73. 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).
74. 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 inwards 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).
75. Metatarsal length: metatarsals 1–4 longer than digits (0), or metatarsals 2–4 shorter than digits (1).
76. Metatarsal I: proximal end not enlarged, no more than 10% wider than any other metatarsal (0), enlarged, 20–30% wider (1), moderately enlarged, 46–51% (2), or greatly enlarged, >5% wider (3).
77. Digit lengths: digit lengths in descending order III, IV, II, I (0), or IV, III, II, I (1).

Osteoderms

78. Tail osteoderms: completely surrounded by osteoderms (0), dorsal surface only has osteoderms (1), or lacks any osteoderms (2).
79. Ventral trunk osteoderms: present (0), or absent (1).
80. Dorsal osteoderms: present (0), or absent (1).

Sacral ribs

81. Articulation surface for ilium on sacral rib: wide (0), or narrow (1).

82. Sacral rib curvature: little/none (0), or strong (1).

Character-taxon matrix

Hesperosuchus

100?? ????? ?0000 0110? 00002 01001 1200? ?0000 200?0 010??
?01?2 0210? ?0?0 000?0 ????? ??110 ??

Terristrisuchus

100?? 3000? ?0000 0?102 ?0002 01001 1200? ?0??0 200?0 010??
?0102 02100 000?? 00000 00000 00110 00

Protosuchus

00000 30000 00000 00102 00002 00011 02000 00000 00000
00000 ?11?1 02200 0?000 00000 00000 00000 ??

Atoposauridae

00000 0010? 00000 01001 20001 00012 00000 10100 00020
11102 ?0{1,2}01 0{0,1}{0,1}01 0?000 00000 00000 00010 00

Goniopholis

00000 ?0100 ?0000 01001 00?01 00011 02000 101?? ?0020 11?02
?0101 0100? ????? ????? ????? ????0 ??

Crocodylus niloticus

00000 00100 00000 01001 20001 00012 02000 101?? ?0030 01023
00111 01101 00000 00000 00000 00000 00

Alligator mississippiensis

00000 20100 00100 01000 2?001 00012 02000 101?? ?0000 01023
00111 01100 00000 00000 00000 00000 00

Steneosaurus leedsii

00001 ?01?0 00000 02000 11100 00000 00001 01100 00230 13111
11400 00100 000?0 00010 00000 00100 ??

Pelagosaurus typus

00001 00110 00000 02100 01100 00{0,1}00 00001 01100 00230
13111 ?1300 00100 00000 00010 0000? 00100 ??

Teleidosaurus calvadosii

000?? 001?1 10000 12100 11200 00000 00001 011?? ?0220 10011
?2201 0?1?? ????? ????? ????? ??

Metriorhynchus laeve

11110 101?1 12010 122?0 11300 00100 11111 01221 10231 10111
12401 01100 1?10? 0122? ?211 11211 11

Metriorhynchus leedsii

11110 101?1 12010 12210 ?1?00 00100 11111 01??? ?0?1 10???
?2401 01100 ????? ????? ???11 ??

Metriorhynchus acutus

11??0 ??12? ?2010 122?0 01300 0?00 ?1?? ?2?? ?0??? ????? ?240?
???? ???? ???? ???? ???? ??

Metriorhynchus superciliosus

01110 10111 12010 12210 11300 00100 11111 01221 10221
10111 12301 01100 12101 01121 112?1 11211 11

Metriorhynchus moreli

01110 10111 12010 122?0 11300 00100 11111 01211 10221
10111 12301 01100 ?1?? 0112? 112?? ?211 11

Metriorhynchus palpebrosus

01??? ?0111 ?2110 122?0 11300 00100 1?111 01221 10?21 10111
12301 ?1?? ????? 021?? ?12?? ????1 ??

Metriorhynchus hastifer

01??? ????? ?2110 122?0 11300 2?200 1?1?? 012?? ?0??? ????? ?23??
???? ???? ???? ???? ???? ??

Metriorhynchus durobrivensis

01110 20?1 12120 122?0 1{0,1}301 00100 11101 01221 101?1
1?011 02111 01100 ????? ????? 1?1?? ?211 11

Metriorhynchus cultridens

01110 201?1 12120 122?0 11301 00100 11101 01221 10211 10011
02111 02210 1110? ????? ?1??? ?211 11

Metriorhynchus brachyrhynchus

01110 20131 12120 122?0 1{0,1}301 00100 11101 01221 10211
10011 02111 02210 1110? 0112? 11??? ?211 11

Metriorhynchus casamiquelai

11110 ?2131 12010 122?0 21301 00200 11101 01221 10131 120??
02{1,2}00 ?1100 ????? ????? ????1 ??

Dakosaurus carpenteri

111?? ????? ?2040 122?0 21301 10200 2???? 012?? ?0??? 1???? ?21?1
1110? ?11?? 02??? ?1??? ????1 11

Geosaurus suevicus

111?? ?1??? ?2030 12210 31320 11201 12111 01421 11231 13111
12301 00100 12111 12221 12321 31211 11

Geosaurus gracilis

11110 ?1121 12030 12210 31310 01201 12111 01321 11231
13111 ?2{2,3}?1 00100 12111 12??1 1?311 21211 ?1

Geosaurus araucanensis

11110 11121 12030 122?0 31320 11201 12111 01622 11??? ?31?1
1230? 0???0 ????? ????? ???? ??

Dakosaurus maximus

111?? ?21?1 12051 122?0 21301 1?300 2110? ?13?1 10111 20011
02112 21100 ?11?? 02121 ?1??? ?211 11

Dakosaurus andiniensis

1?1?? ?21?1 12051 12210 21302 10300 21101 01321 10101 20???
?2012 21100 ????? ????? ???? ??

Enaliosuchus macrospandylus

1?1?? ????? ?2030 123?0 30320 112?? ?111? ??622 1???1 13??? ?2204
1110? ?1?? ????? ???? ??

Taxa list and coding sources

Outgroup taxa. *Hesperosuchus agilis*: Clark *et al.* (2000); *Terris-
trisuchus gracilis*: Crush (1984); *Protosuchus*: Steel (1973), Gaspa-
rini *et al.* (2006).

Ingroup taxa. *Goniopholis*: Steel (1973), Gasparini *et al.* (2006); *Alligator mississippiensis*: comparative collection held in the Palaeontology department of BMNH; *Crocodylus niloticus*: comparative collection held in the Palaeontology department of BMNH; *Atoposauridae*: Steel (1973), Gasparini *et al.* (2006); *Steneosaurus leedsi*: BMNH R.2619, BMNH R.3320, BMNH R.3806, BMNH R.5806, Vignaud (1995); *Pelagosaurus typus*: BMNH 19735, BMNH 32599, SMNS 8666, SMNS 17758, SMNS 50374, SMNS 80066, Gasparini *et al.* (2006), Vignaud (1995); *Teleidosaurus calvadosii*: BMNH R.2681, Eudes-Deslongchamps (1867); *Metriorhynchus leedsi*: BMNH R.3540, BMNH R.3899, GLAHM V973-5, PETMG R24, PETMG R72, Vignaud (1995); *Metriorhynchus laevis*: BMNH R.2031, BMNH 2042, BMNH R.3014, BMNH R.3015, CAMSM J64297, Vignaud (1995); *Metriorhynchus moreli*: BMNH R.1666, BMNH R.2032, BMNH R.2044, BMNH R.2049, BMNH R.2054, BMNH R.3900, BMNH R.6860, GLAHM V971, GLAHM V1143, SMNS 10116, Vignaud (1995); *Metriorhynchus superciliosus*: BMNH R.2030, BMNH R.2036, BMNH R.2051, BMNH R.2053, BMNH R.2055, BMNH R.2058, BMNH R.2067, BMNH R.6859, GLAHM V963-6, GLAHM V982-5, GLAHM V987-989, GLAHM V996, GLAHM V1004, GLAHM V1015, GLAHM V1027, GLAHM V1140, GLAHM V1142, PETMG R10, PETMG R17-8, PETMG R20, PETMG R42, PETMG R180, SMNS 10115, SMNS 81689, Vignaud (1995); *Metriorhynchus brachyrhynchus*: BMNH R.3699, BMNH R.3700, BMNH R.3939, GLAHM V978, CAMSM J64267, Vignaud (1995); *Metriorhynchus cultridens*: BMNH R.3051, BMNH R.3804, Vignaud (1995); *Metriorhynchus durobrivensis*: BMNH R.2039, BMNH R.2618, BMNH R.3321, BMNH R.4763, PETMG R19, Vignaud (1995); *Metriorhynchus casamiquelai*: MGHF 1-08573, Gasparini *et al.* (2006); *Metriorhynchus palpebrosus*: OXFUM J29823, OXFUM J55476-9; *Metriorhynchus acutus*: Lennier (1887); *Metriorhynchus hastifer*: Eudes-Deslongchamps (1867); *Dakosaurus carpenteri*: BRSMG Ce17365, BRSMG Cd 7203; *Geosaurus gracilis*: BMNH R.3948; *Geosaurus suevicus*: SMNS 9808, SMNS 90513, Fraas (1902), Gasparini *et al.* (2006); *Geosaurus arauacensis*: Gasparini and Dellapé (1976), Gasparini *et al.* (2006); *Dakosaurus maximus*: BMNH 40103, BMNH 33186, BMNH 35766, BMNH 35835, BMNH 35826, BMNH 3527, CAMSM J. 29419, SMNS 8203, SMNS 80148, Fraas (1902), Gasparini *et al.* (2006); *Dakosaurus andiniensis*: Gasparini *et al.* (2006); *Enaliosuchus macrospendylus*: HMN R1943, HMN R3636.1–6, Koken (1883), Hua *et al.* (2000).

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. Symphysis is long, making at least 40% of mandible length [43-2].

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. Symphysis 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-anterolaterally [16-1].
3. Symphysis depth 4.5–6% of mandible length [44-2].
4. Three teeth in the premaxillae [52-2].

(Longirostrine 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].

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].
12. Antorbital fossa enclosed by lacrimal, maxilla, nasal and jugal [39-2].
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. Parasphenoid 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 enlarged [76-1].
15. Digit IV elongated making it the longest digit [77-1].
16. Tail osteoderms absent [78-2].
17. Dorsal osteoderms absent [80-1].
18. Articulation surface for ilium on sacral rib small [81-1].
19. 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. arauacanensis* + *Enaliosuchus macrospondylus*))):

1. Maxilla-palatine suture: forms an M-shaped orientated posteriorly [6-1].
2. Lacrimal contributing <40% of orbit height [34-1].
3. Surangular extends beyond the orbit along the dorsal margin of the mandible [48-1].
4. Cervical centra length short [62-2].
5. Tibia more reduced, 31–39% of femur length [73-2].

Metriorhynchus palpebrosus + *M. hastifer*:

1. Prefrontals wider than posteriorly directed 'V' of the squamosal created by the posterior margin of the supratemporal fossa [13-1].
2. Humerus greatly reduced, shaft contributing <25% of total length and distal head wider than proximal head [67-2].

(*Metriorhynchus laeve* + *M. leedsi* + *M. acutus*) + (*Geosaurus gracilis* + *G. suevicus* + (*G. arauacanensis* + *Enaliosuchus macrospondylus*)):

1. Smooth frontal [1-1].
2. Internal nares opens out into the buccal cavity in a posterior direction with the palatines creating a broad U-shape with its apex directed anteriorly [9-2].
3. Symphysis depth ~4% of mandible length [44-3].
4. Humerus smaller in length than scapula [68-2].
5. Ischium anterior process greatly reduced and lacking either articulation facet [72-2].

Metriorhynchus laeve + *M. leedsi* + *M. acutus*:

1. More than 28 teeth per maxillae [53-4].

Metriorhynchus acutus:

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

Geosaurus gracilis + *G. suevicus* + (*G. arauacanensis* + *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 arauacensis + *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. Maxilla-palatine suture: forms a broad U-shape pointing anteriorly [6-2].
2. Internal nares opens out into the buccal cavity in a posterior direction with the palatines creating a M-shape on its anterior margin [9-3].
3. Rostrum is broad (dorsoventral diameter $\sim 1.2 \times$ the lateromedial diameter) [25-1].
4. Mandibular symphysis makes up 32–38% of mandible length [43-1].
5. Symphysis depth 7–8% of mandible length [44-1].
6. Coronoid does not project as far as the dentary tooth row [51-0].
7. Maxillary teeth number 12–17 [53-1].
8. Dentary teeth number 18 or less [54-1].
9. Cervical centra length moderate [62-1].

Metriorhynchus durobrivensis + (M. brachyrhynchus + M. cultridens):

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. Paraoccipital 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 premaxilla 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 $\sim 4\%$ 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 carpenteri + (D. maximus + D. andiniensis):

1. Angle between medial and anterior margins of supratemporal fossa: ~ 45 degree angle, or more acute [26-1].
2. Supratemporal fenestra projects more posteriorly than the parietal [31-2].
3. Humerus greatly reduced, shaft contributing <25% of total length and distal head wider than proximal head [67-2].

Dakosaurus carpenteri:

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 ($\pm 5\%$) 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 oreinirostral [25-2].
2. Symphysis depth 10% or more of mandible length [44-0].
3. Less than 11 teeth per maxillae [53-0].