The evolution of Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics

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Metriorhynchoid crocodylians represent the pinnacle of marine specialization within Archosauria. Not only were they a major component of the Middle Jurassic–Early Cretaceous marine ecosystems, but they provide further examples that extinct crocodilians did not all resemble their modern extant relatives. Here, we use a varied toolkit of techniques, including phylogenetic reconstruction, geometric morphometrics, diversity counts, discrete character disparity analysis, and biomechanical finite-element analysis (FEA), to examine the macroevolutionary history of this clade. All analyses demonstrate that this clade became more divergent, in terms of biodiversity, form, and function, up until the Jurassic–Cretaceous boundary, after which there is no evidence for recovery or further radiations. A clear evolutionary trend towards hypercarnivory in *Dakosaurus* is supported by phylogenetic character optimization, morphometrics, and FEA, which also support specialized piscivory within *Rhacheosaurus* and *Cricosaurus*. Within Metriorhynchoidea, there is a consistent trend towards increasing marine specialization, with the hypermarine *Cricosaurus* exhibiting numerous convergences with other Mesozoic marine reptiles (e.g. loss of the deltopectoral crest and retracted external nares). In addition, biomechanics, morphometrics, and character-disparity analyses consistently distinguish the two newly erected metriorhynchid subfamilies. This study illustrates that together with phylogeny, quantitative assessment of diversity, form, and function help elucidate the macroevolutionary pattern of fossil clades.

INTRODUCTION

The morphological diversity of living members of the clade Crocodylia (extant crocodylians and their extinct relatives; *sensu* Martin & Benton, 2008) represents only a small proportion of the extraordinary variety of body shapes and sizes exhibited by this group of archosaurs during its long evolutionary history. In particular, Jurassic and Cretaceous crocodylians evolved numerous anatomical modifications, and novel functional adaptations and lifestyles not seen in any modern species. For instance, the clade Notosuchia is often cited as an example of the wide range of ecophenotypes present in Cretaceous crocodylians. Notosuchians include terrestrial hypercarnivores (e.g. Baurusuchidae; Carvalho, Campos & Nobre, 2005), terrestrial herbivores (e.g. *Chimaerasuchus*; Wu, Sues & Sun, 1995), omnivores showing propaliny (fore-and-aft movement of the mandible; e.g. *Mariliasuchus*; Nobre *et al.*, 2008), carnivores with mammalian carnassial-like molariform teeth (*Malawisuchus*; see Andrade & Bertini, 2008 and

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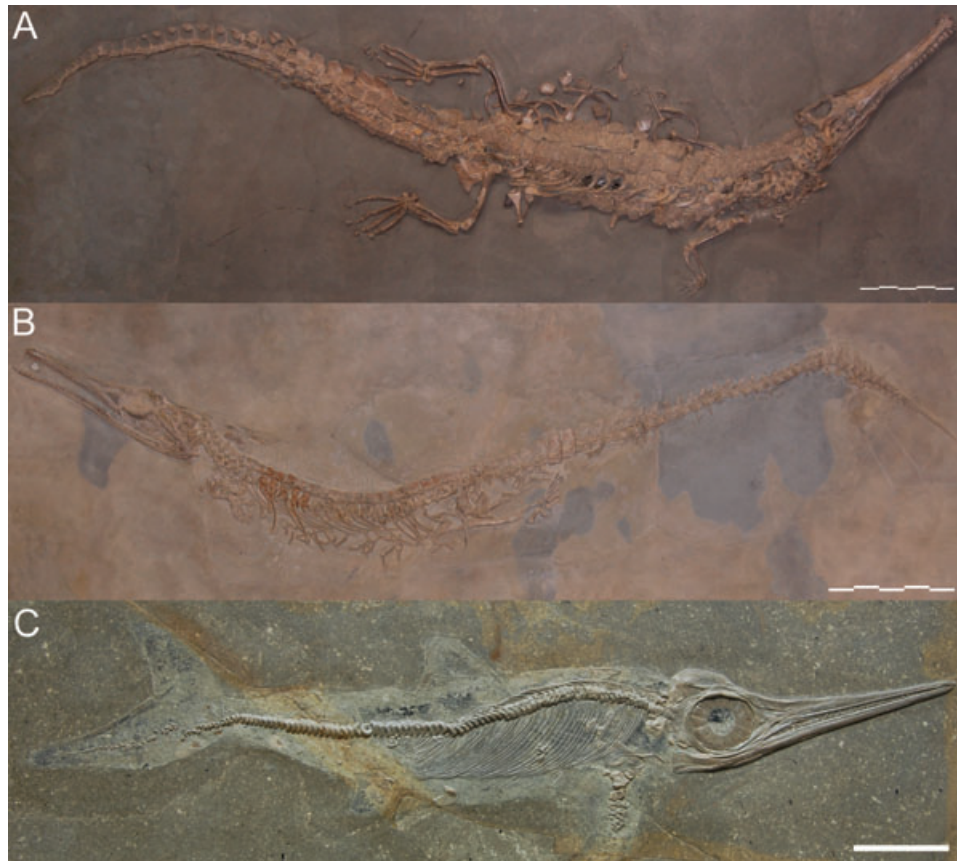
Figure 1. Two extinct marine crocodylians, and an ichthyosaur, showing the extensive morphological adaptations to a pelagic lifestyle in metriorhynchids: *Platysuchus* SMNS 9930 (A), a teleosaurid, displays the comparatively heavier body typical of semi-aquatic teleosaurids, goniopholidids, pholidosaurids and eusuchians; in contrast to the hydrodynamic metriorhynchids, such as *Cricosaurus suevicus* SMNS 9808 (B). The ichthyosaur *Stenopterygius* SMNS 81841 (C) has similar adaptations to metriorhynchids, i.e. hydrofoil-like forelimbs, hypocercal tail, and the reduction in limb girdle size. Scale bar = 50 mm.

references therein), heavily armoured 'armadillo-like' forms (*Armadilosuchus*; Marinho & Carvalho, 2009), and Sphagesauridae, with their mammal-like lower jaw motion (possibly capable of lateral and propalinal movements) and tooth crown morphology (heterodonty with unilateral occlusion; Pol, 2003; Andrade & Bertini, 2008; Marinho & Carvalho, 2009). This variety of morphofunctional specializations defies the still widely held concept of crocodylians as large, heavily armoured, semiaquatic predators that have remained morphologically conservative since the Jurassic.

Although less well-known than notosuchians, the extinct crocodylians of the family Metriorhynchidae (Fitzinger, 1843) are perhaps the most divergent from the widely held 'typical crocodylian bauplan'. Metriorhynchids are the only archosaurian group that successfully adapted to, and radiated within, the marine realm (Langston, 1973; Steel, 1973); although certain extant birds, such as penguins, have extensively adapted to moving and feeding in a marine environment (e.g. Bengtson, Croll & Goebel, 1993; Watanuki *et al.*, 2006). The adaptations of metriorhynchids to pelagic life are convergent upon those of other Mesozoic marine reptiles (Fig. 1), and include: hydrofoil-like forelimbs, elongated body, well-developed sclerotic ossicles, and hypocercal tail (Fraas, 1902; Arthaber, 1906, 1907; Auer, 1907; Andrews, 1913, 1915); evidence for hypertrophied nasal salt glands (Fernández & Gasparini, 2000, 2008; Gandola *et al.*, 2006); highly streamlined skull, in which the prefrontals expand laterally over the orbits (convergently acquired in mosasaurs; Langston, 1973); the osteoporotic lightening of skull, femora, and ribs (Hua, 1994; Hua & Buffrénil, 1996); and a re-arrangement of bones in the pelvic girdle, resulting in a significant increase in its diameter (analogous with that observed in viviparous nothosaurs; Cheng, Wu & Ji, 2004). In addition, metriorhynchids lost the external mandibular fenestrae and osteoderm cover

(Lydekker, 1888), and their pectoral and pelvic girdles became extremely reduced (Andrews, 1913) in comparison with those of other crocodylians.

Despite the remarkable adaptations, taxonomic richness, and morphological diversity of metriorhynchids, research on this clade has been neglected for many years. Although they were among the first groups of fossil reptiles to be discovered [e.g. *Geosaurus giganteus* (von Sömmerring, 1816)], metriorhynchids were eclipsed by the discoveries of dinosaurs and the extraordinarily complete skeletons of Liassic ichthyosaurs and plesiosaurs, all of which captured the imagination of the Victorian era (e.g. Cadbury, 2002). The stratigraphic range of metriorhynchids is comparable in duration with that of the Upper Cretaceous mosasaurs (see Lindgren & Jagt, 2005; Caldwell & Palci, 2007), spanning at least 35 Myr, from the Middle Jurassic to the Lower Cretaceous: *Metriorhynchus* sp., early Bajocian (Gasparini, Vignaud & Chong, 2000), to *Cricosaurus macrospondylus* (Koken, 1883), late Valanginian (Karl *et al.*, 2006) (see Fig. 2). Geographically, they are well known from Europe, and new discoveries from Argentina, Chile, Cuba, Mexico, and Russia have further extended our knowledge of this group.

In total, metriorhynchids represent a morphologically distinctive, long-lived, and widespread clade. They offer a unique opportunity to investigate patterns of evolutionary transformation and range of functional adaptations in a well-defined group of extinct archosaurs, for which a detailed database of morphological characters has been assembled (Young & Andrade, 2009). In addition, they represent a case study into the quantitative investigation of craniofacial trends observed in various clades of marine amniotes (e.g. cetaceans, ichthyosaurs, plesiosaurians, and mosasaurids), namely long-rostral and short-rostral morphologies. Here, we undertake a multidisciplinary investigation of metriorhynchid evolution that applies several analytical protocols to examine in detail the taxonomic diversity, morphological disparity, craniofacial biomechanics, and evolutionary dynamics of an outstanding radiation of early crocodylians.

PHYLOGENETIC RELATIONSHIPS OF METRIORHYNCHOIDEA

The evolutionary relationships of the Metriorhynchidae were elucidated by Young & Andrade (2009), with a comprehensive cladistic analysis that considered all currently known valid taxa in the Metriorhynchoidea (Metriorhynchidae *s.s.* and their closest relatives). Young & Andrade's (2009) analysis included 38 metriorhynchids, five species of Teleosauridae (the sister taxon to Metriorhynchidae), representatives from numerous metasuchian clades, as well as more basal crocodylomorphs (*Protosuchus*, three species of sphenosuchians), and with *Erpetosuchus* as an out-group. The resultant strict consensus, here simplified to show only the interrelationships of Metriorhynchoidea (Fig. 2), is well resolved.

Young & Andrade (2009) proposed a phylogenetic definition for both Metriorhynchidae and related family groups. Their terminology, which is used throughout, defines the superfamily Metriorhynchoidea as all species more closely related to *Metriorhynchus geoffroyii* von Meyer, 1830 than to *Teleosaurus cadomensis* (Lamouroux, 1820) (i.e. the teleosaurids). They restricted the family Metriorhynchidae to the least inclusive clade consisting of *M. geoffroyii* and *Ge. giganteus*, and regarded the two clades into which Metriorhynchidae are split as subfamilies (Figs 2 and 3). The first subfamily, Metriorhynchinae, is defined as all metriorhynchids closer to *M. geoffroyii* than to *Ge. giganteus*; whereas the second, Geosaurinae, consists of all metriorhynchids closer to *Ge. giganteus* than to *M. geoffroyii*. In addition, the genera considered valid in this study follow the recent taxonomic changes introduced by Young (2006, 2007) and Young & Andrade (2009), and we herewith erect two new genera (*Eoneustes* gen. nov. and *Gracilineustes* gen. nov.; see Appendix). Note that we use Crocodylia Gmelin, 1789 as defined by Martin & Benton (2008), i.e. the least-inclusive clade containing *Protosuchus richardsoni* (Brown, 1933) and *Crocodylus niloticus* Laurenti, 1768. This clade has at times been referred to as Crocodyliformes Hay, 1930 (*sensu* Benton & Clark, 1988).

PREVIOUS CHARACTERIZATIONS OF METRIORHYNCHID MORPHOLOGICAL DIVERSITY

Historically, metriorhynchids have been assigned to two broad groups, the 'longirostrines' (long rostrum) and 'brevirostrines' (short rostrum), based on cranial shape and proportions (e.g. Andrews, 1913; Wenz, 1968; Adams-Tresman, 1987; Pierce, 2007; Pierce, Angielczyk & Rayfield, 2009a). According to Busbey's (1995) classification of crocodylian cranial shape, the 'long' condition is defined as one in which the rostrum contributes 70% or more to basicranial length (longirostrine *s.s.* herein), whereas in the 'short' condition, the rostrum contributes 55% or less to basicranial length (brevirostrine *s.s.* herein). Using this set of definitions, most metriorhynchids fall between the two categories, and will be referred to as mesorostrine hereafter. Only four taxa cannot be regarded as showing the mesorostrine condition, namely the longirostrine *Gracilineustes acutus* (Lennier, 1887) comb. nov., *Gracilineustes leedsi* (Andrews, 1913) comb. nov. (most specimens), *Rhacheosaurus gracilis* von Meyer, 1831, and the brevirostrine *Dakosaurus andiniensis*
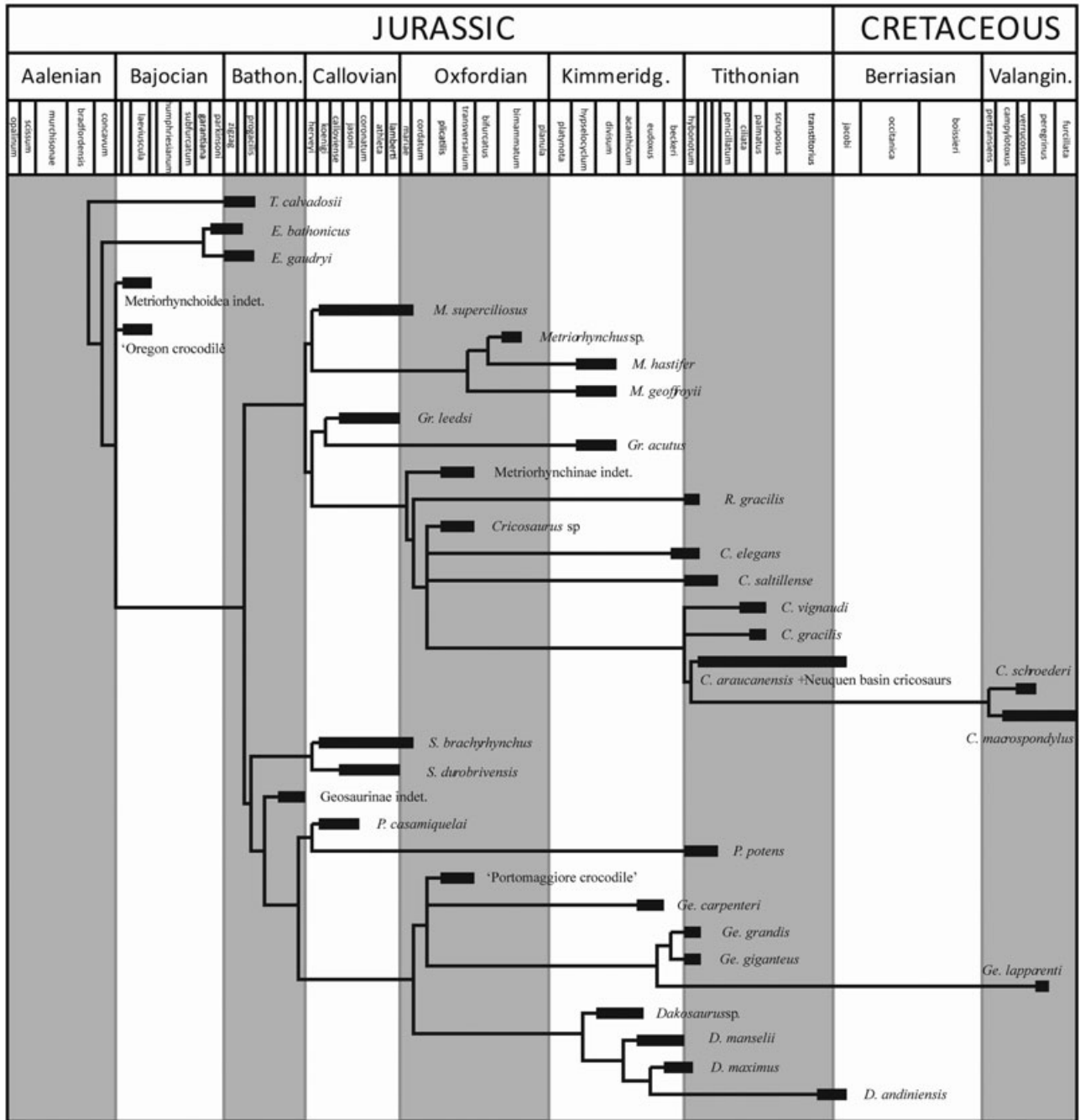
Figure 2. Strict consensus of Metriorhynchoidea from Young & Andrade (2009), calibrated by Tethys ammonite zones. See the Appendix for further details regarding genera and taxonomy.

Vignaud & Gasparini, 1996 (Table 1). On average, the difference in rostral contribution between brevirostrine and longirostrine taxa is only 5% of the basicranial length (M.T. Young, unpubl. data). The previously used 'brevirostrine' and 'longirostrine' groups correspond approximately, but not exactly, to Geosaurinae and Metriorhynchinae, respectively, in the phylogeny of Young & Andrade (2009).

The dorsoventral height of the rostrum is of little use in ascribing metriorhynchids to phylogenetically delimited clades (Table 1). Gasparini, Pol & Spalletti (2006) compared rostral length with rostral height in five species of metriorhynchids [*Metriorhynchus superciliosus* (Blainville, 1853), *Purranisaurus casamiquelai* (Gasparini & Chong, 1977), *Cricosaurus araucanensis* (Gasparini & Dellapé, 1976), *Dakosau-*

Table 1. Taxonomic discrimination is possible using rostral length and depth

		Rostral length		
		Brevirostrine	Mesorostrine	Longirostrine
Rostral depth	'Shallow'	–	*Cricosaurus* **Gracilineustes** gen. nov.	*Rhacheosaurus* **Gracilineustes** gen. nov.
	'Moderate'	–	All other metriorhynchoids	–
	'Deep'	–	*Dakosaurus*	–
	Oreinirostral	*Dakosaurus andiniensis*	–	–

See text for definition of terms; oreinirostral is definied as a deep snout with a convex upper margin (Busbey, 1995).

rus maximus (PLIENINGER, 1846), and *Dakosaurus andiniensis* Vignaud & Gasparini, 1996]. *Metriorhynchus* and *Purranisaurus*, both basal members of their respective subfamilies, possess a mesorostrine length and moderate rostral depth [as do *Suchodus brachyrhynchus* (Eudes-Deslongchamps, 1868) and the basal-most metriorhynchoid *Teleidosaurus calvadosii* (Eudes-Deslongchamps, 1866); M.T. Young, unpubl. data]. *Cricosaurus* possesses a relatively 'shallow' rostral depth, as do other derived metriorhynchines, such as *Rhacheosaurus* (M.T. Young, unpubl. data). *Dakosaurus*, in contrast, displays a deeper rostrum (Gasparini *et al.*, 2006). These findings indicate that basal metriorhynchoids and metriorhynchids show comparatively similar snout depths, whereas the derived members of both subfamilies display opposite evolutionary trajectories regarding rostral depth: in Geosaurinae the rostrum becomes increasingly deeper and more robust, whereas in Metriorhynchinae it becomes increasingly thinner and more gracile.

As the previous two examples show, simple bivariate comparisons lack the resolution that is necessary to discriminate and quantify craniofacial diversity within Metriorhynchoidea (Table 1). That is why several previous workers have undertaken ordination (morphometric) analyses in order to distinguish the craniofacial proportions of various taxa. Analytical methods have included principal co-ordinates analysis (PCO, Adams-Tresman, 1987), principal components analysis, (PCA, Vignaud, 1995), and cluster analysis (Grange, 1997). Unfortunately, several methodological flaws in the analysis of Adams-Tresman (1987) invalidate her taxonomic and morphological conclusions. As mentioned by Young (2006), many of the linear measurements used by Adams-Tresman (1987) directly overlap one another. This measurement strategy amplifies the relative allometric increase or decrease in size of that region of the skull. Her measurement of nasal bone length is suspect; examining her diagram of linear measurements (Adams-Tresman, 1987: 181, text and fig. 1), the length of both the nasal and maxilla in dorsal aspect

is recorded. This in turn overlaps with her measurements A, B, C, D, and E. In addition, she never took any measurements of the supratemporal fossae or fenestrae. As the results herein show (see below), the supratemporal region experiences shape variation between the brevirostrine and longirostrine skull forms (increasing in size in the brevirostrine forms).

Grange (1997) used a variety of linkage methods in his cluster analysis, but the three methods that, according to him, gave 'reasonable' results did not in fact yield consistent, statistically supportable consensus. This is most likely to be a result of his limited taxon sampling. Only the analysis of Vignaud (1995) stands up to scrutiny (his measurement regime is valid: see Young 2006). However, application of PCA (and PCO) to morphometric analyses suffers from the confounding effect of size when multivariate analysis is carried out on raw measurements (as it was by both Adams-Tresman, 1987 and Vignaud, 1995). In other words, the primary axis of variance in PCA captures mostly size increase (e.g. Livezey, 1988; Young, 2006), whereas the remaining axes capture aspects of shape change. As such, it is hardly surprising that both Adams-Tresman (1987) and Vignaud (1995) were unable to discriminate any further than 'longirostrine' and 'brevirostrine', as the second most important axis of variation in their respective analyses expressed the transition between these cranial forms (Young, 2006, reported the same effect in the PCA discussed therein). As geometric morphometric techniques allow shape to be compared, independent of size (i.e. through Procrustes fitting; Dryden & Mardia, 1998), they may therefore be suitable for interpreting shape variation effectively. Methodological flaws aside, the above studies were carried out without reference to a well-constrained phylogeny or a detailed understanding of character change. For the first time, the availability of a global phylogeny of Metriorhynchoidea (Young & Andrade, 2009) permits a detailed investigation into cranial shape, taxonomic diversity, and morphological disparity in this clade. In addition, recent revisions of the metriorhynchoid

fossil record (Young, 2006; Young & Andrade, 2009) allow for well-constrained temporal and biogeographic distributions, which were also unavailable to previous authors.

Using this remarkable volume of new data, we set out to address the following issues. First, we use a recent phylogenetic analysis to document patterns of character evolution within Metriorhynchoidea, especially those characters related to a pelagic and hypercarnivorous lifestyle. Second, we plot profiles of taxonomic richness for Metriorhynchoidea as a whole using phylogenetic information to assess differences between observed (standard) and inferred (corrected through phylogenetic interpolation) diversity through time. Third, we characterize the main patterns of shape variation in the skull roof of Metriorhynchoidea using geometric morphometrics. Fourth, we use phylogenetic data to quantify disparity (i.e. morphological diversity). Finally, we discuss the biomechanical properties of the metriorhynchid skull from an engineering standpoint using finite-element analysis.

INSTITUTIONAL ABBREVIATIONS

The following institutional abbreviations have been used throughout: BRSMG, Bristol City Museum & Art Gallery, Bristol, UK; BSPG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; CAMSM, Sedgwick Museum, Cambridge, UK; GLAHM, Hunterian Museum, Glasgow, UK; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MGHF, Museo Geologico H. Fuenzalida, Universidad Catolica del Norte, Antofagasta, Chile; MLP, Museo de La Plata, La Plata, Argentina; MMGLV, Mindener Museum für Geschichte, Landes- und Volkskunde, Minden, Germany; MOZ, Museo Profesor J. Olsacher, Zapala, Argentina; NHM, Natural History Museum, London, UK; NMING, National Museum of Ireland, Dublin, Ireland; NMW, National Museum of Wales (National Museum Cardiff, Amgueddfa Genedlaethol Caerdydd), Cardiff, UK; OXFUM, Oxford University Museum, Oxford, UK; PETMG, Peterborough Museum & Art Gallery, Peterborough, UK; RMS, Royal Museum, Edinburgh, UK; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

CHARACTER EVOLUTION

Adaptations to a marine lifestyle and acquisition of specialized feeding strategies (e.g. hypercarnivory) have long been recognized as key aspects of metriorhynchid evolution. However, little attention has been devoted to the evolution of character complexes in the group as a whole (see Young, 2006). The character complexes of special interest for our understanding of the ecological and functional adaptations of this group are detailed below.

GENERAL FEATURES

The generalized metriorhynchid body plan is exemplified by the abundance of basal metriorhynchine and geosaurine material from the Peterborough Member of the Oxford Clay Formation (Leeds Collection: CAMSM, GLAHM, NHM, NMING, PETMG, RMS; middle Callovian–lower Oxfordian). All genera recorded from this formation (*Metriorhynchus*, *Gracilineustes* gen. nov., and *Suchodus*) exhibit a shortened neck, elongate and hypocercal tail, shortened humeri, sclerotic ossicles, prefrontals expanded laterally over the orbits, and a loss of both external mandibular fenestrae and osteoderm cover (Figs 4, 5). There is also evidence for hypertrophied nasal salt glands (Gandola *et al.*, 2006), and osteoporotic lightening of the skull, femora, and ribs (Hua, 1994; Hua & Buffrénil, 1996). The pectoral and pelvic girdles are extremely reduced, whereas the propodia–epipodia joint surfaces are planar, and this presumably limits the possible planes of movement at the joint in life (Fig. 5). All limb bones are flattened to some degree (not a taphonomic artefact), whereas several of them are discoid or oval in shape (because of a loss of perichondral bone ossification). The pes is paddle-like in overall morphology; however, the forelimb morphology is unknown, except in *Metriorhynchus* and more-derived metriorhynchines. A hydrofoil-like morphology of the manus is observed exclusively in *Rhacheosaurus* and *Cricosaurus*.

MARINE ADAPTATIONS

The transition from a semiaquatic to a pelagic lifestyle in metriorhynchoids is difficult to document, because of the lack of postcrania in basal members and their general rarity. Basal members of both metriorhynchid subfamilies already exhibit morphological adaptations to marine life (e.g. hypocercal tails; reduced girdles; the loss of external mandibular fenestrae, osteoderms, and the posterior process of the ilium). By contrast, close out-group taxa (teleosaurids) apparently did not evolve extensive adaptations to a pelagic lifestyle. The cranium of the basal taxon *T. calvadosii* (early–middle Bathonian of Normandy, France; Eudes-Deslongchamps, 1866; Vignaud, 1995) retains two characters that suggest they were not fully adapted to aquatic life: large external mandibular fenestrae and the lack of antorbital fenestrae (Fig. 6A).

A large external mandibular fenestra is associated with a terrestrial lifestyle in some archosaurs because
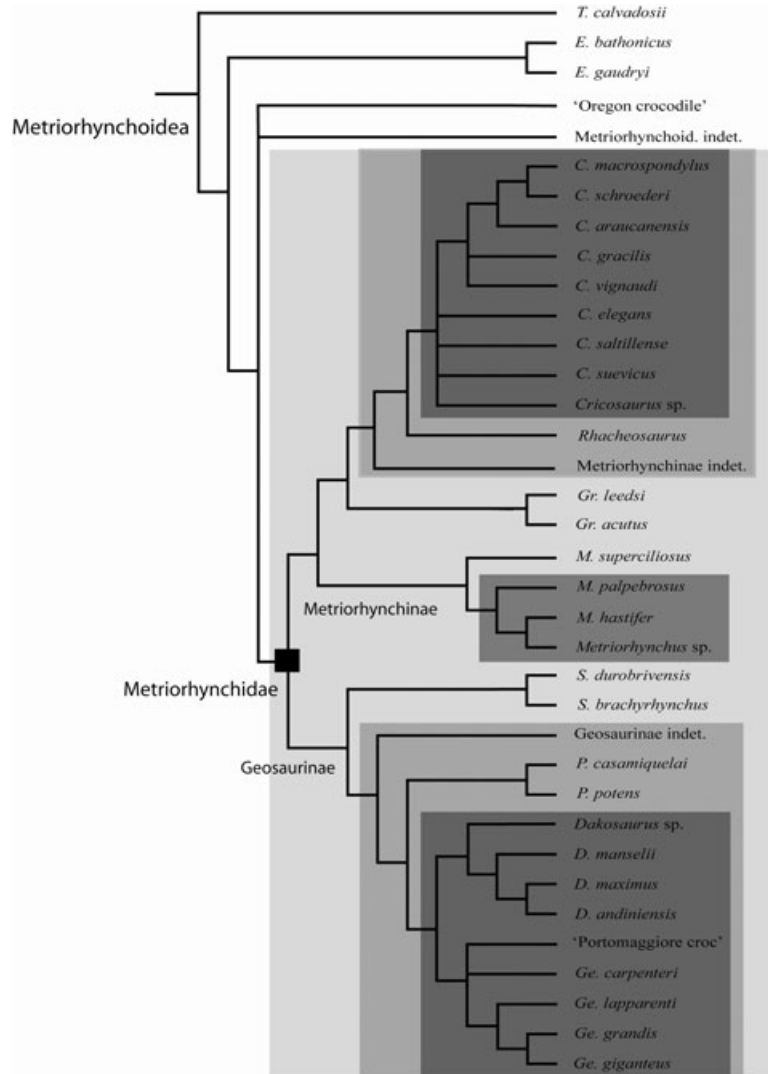
Figure 3. Metriorhynchoidea phylogeny, with character complexes relating to marine adaptation mapped by shading. The light-grey shading indicates taxa demonstrating the 'typical' adaptations of metriorhynchids, i.e. hypocercal tails, no osteoderms, and no external mandibular fenestrae. The mid-grey shading refers to taxa with dorsally inclined paroccipital processes and verticalized squamosals; whereas the dark-grey shading highlights taxa with streamlined crania (lateral processes of the frontal reoriented caudally, creating an acute angle between the medial and lateral processes of the frontal) and more flattened humeri.

it is associated with gape basking on land. The loss, or extreme reduction, of the external mandibular fenestra is observed in certain marine crocodylians (e.g. the Upper Cretaceous dyrosaurids and Oceanosuchus, with these taxa exhibiting less specialized marine adaptations than metriorhynchids), and has been linked to a regression of the musculus intramandibularis (Hua & Buffetaut, 1997; see Holliday & Witmer, 2007 for the homology of this muscle in relation with the musculus pseudotemporalis). The mandibular fenestrae in extant crocodylians are only filled by the musculus intramandibularis (Dodson, 1975), as the mandibular adductor musculature attachments to the medial mandibular fossae are largely tendinous (Iordansky, 1964; the musculus adductor mandibulae posterior also inserts into the medial mandibular fossae in lizards, despite the lack of external mandibular fenestrae in this group; see Holliday & Witmer, 2007). In addition, the musculus intramandibularis of extant crocodylians acts to fix the jaws in a gaping position (Dodson, 1975), a behaviour associated with thermoregulation (e.g. Diefenbach, 1975; Spotilia, Terpin & Dobson, 1977; Loveridge, 1984; Downs, Greaver & Taylor, 2008). The mouth-gaping basking behaviour in *Cr. niloticus* is important for elevating body temperature, leading to the hypothesis that a higher body

Figure 4. Comparative metriorhynchid cranial morphology. A, ***Eoneustes gaudryi* comb. nov.**, holotype, NHM R.3353. B, *Geosaurus araucanensis*, holotype, MLP 72-IV-7-1. C, *Cricosaurus suevicus*, lectotype, SMNS 9808. D, *Enaliosuchus schroederi*, holotype, MMGLV#. E, *Suchodus durobrivensis*, referred specimen, NHM R.2618. F, *Metriorhynchus superciliosus*, referred specimen, MNHN 1908-6. G, *Geosaurus giganteus*, referred specimen, NHM 37020. H, *Dakosaurus maximus*, neotype, SMNS 8203. Scale bars: 20 mm. We thank N. Knötschke for photograph (D), and P. Hurst and P.M. Barrett for photograph (G).
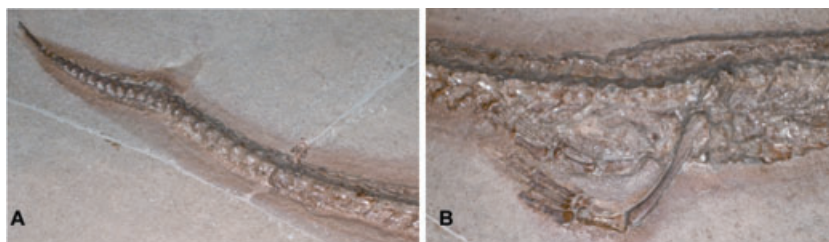
Figure 5. Postcranial marine adaptations of metriorhynchids (*Rhacheosaurus gracilis* NHM R.3948): (A) tail fluke with an impression of the fleshy upper lobe (the only specimen preserving this feature); (B) hindlimbs, note the high proportion that the pes makes, compared with the tibia–fibula, and how poorly developed the pelvis is.
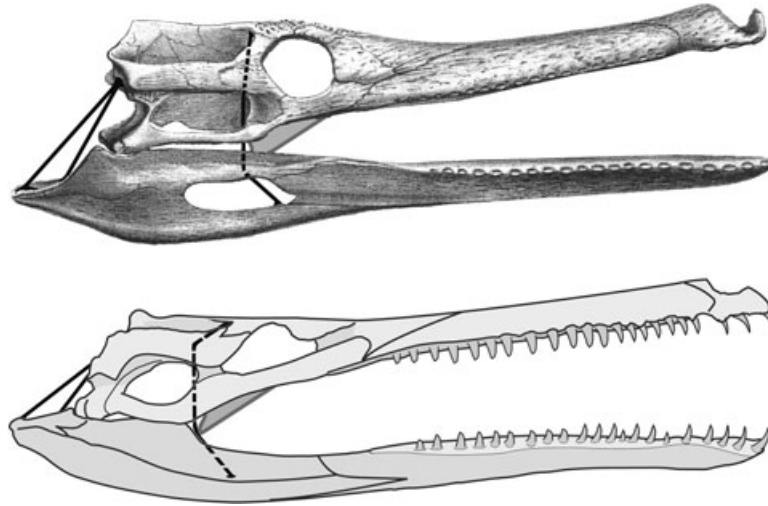
Figure 6. Lateral aspect cranial reconstructions, with the muscle line of action indicated: (A) *Teleidosaurus calvadosii* (modified from Eudes-Deslongchamps, 1867–1869); (B) *Metriorhynchus superciliosus* (composite based upon specimens from NHM and MNHN). The broken line represents the musculus pseudotemporalis–intramandibularis, whereas the solid black line is the musculus depressor mandibulae. The pterygoids are reconstructed based upon teleosaurids.

temperature enables optimal performance when they return to the water (see Downs *et al.*, 2008, and references therein). Therefore heat-avoiding and heat-seeking behaviours, both on land and in water, are the principal methods of thermoregulation in extant crocodylians (Seebacher, Grigg & Beard, 1999; Downs *et al.*, 2008). As *Teleidosaurus* retains external mandibular fenestrae that are similar in size to those of some extant crocodylians, we infer that this taxon could still mouth-gape, and presumably ventured ashore to perform this thermoregulatory behaviour.

Metriorhynchids, in contrast, not only lack external mandibular fenestrae, but possess a foreshortened retroarticular process (Fig. 6B). With a shorter retroarticular process, the lever arms of the jaw-closing muscles –musculus depressor mandibulae – become shortened, thereby reducing the gape (see Antón *et al.*, 2003, and references therein). However, it must be noted that jaw joint morphology and cervicocranial musculature also have a significant bearing on gape. Nevertheless, shorter jaw-opening muscles coupled with the musculus intramandibularis being unable to bulge outwards (thereby fixing the mouth agape), make it highly unlikely that metriorhynchids employed mouth-gaping basking behaviour. As bone histology shows metriorhynchids (specifically *M. superciliosus*; Hua & Buffrénil, 1996) to have been ectothermic, they presumably evolved different thermoregulatory behaviours.

The lack of antorbital fenestrae is associated with a terrestrial lifestyle in some archosaurs because without them the skull cannot accommodate the large salt glands required for physiological regulation in a marine environment (see Gandola *et al.*, 2006). If this functional interpretation is correct, then the absence of antorbital fenestrae/fossae suggests that *Teleidosaurus* lacked large hypertrophied salt glands, which are common in secondarily marine tetrapods (Fernández & Gasparini, 2008). This lends further support to the hypothesis that *Teleidosaurus* was not fully adapted to pelagic life. However, complete postcranial remains are required to corroborate this hypothesis.

Contra Young & Andrade (2009), no metriorhynchoid possesses true antorbital fenestrae (which are essentially paired holes through the skull in front of the orbits). As discussed by Witmer (1997), the fenestrae in *M. superciliosus* are internalized, and lack an internal paranasal chamber. This has the effect of creating a 'pseudofenestra', in which the antorbital chamber is enclosed (i.e. its medial surface is closed off). This results in a deep antorbital fossa, which, depending upon the state of preservation, may give the impression that a true fenestra was present in life. If the hypothesis that hypertrophied nasal salt glands possessed an excretory duct connecting them to the 'antorbital fenestra' (Gandola *et al.*, 2006), then this could explain the presence of this unusual structure. Therefore, the internalization and closure of the antorbital fenestrae is a metriorhynchoid synapomorphy, whereas the 'antorbital pseudofenestra' is potentially an osmoregulatory adaptation in taxa more derived than *T. calvadosii*.

Another basal taxon, *Eoneustes* gen. nov. (from the late Bajocian–middle Bathonian of France; see Appendix), possesses 'antorbital pseudofenestrae', whereas the shallow fossae surrounding them have the same

elongate and obliquely oriented outline as observed in Metriorhynchidae (Fig. 4A). The lack of any mandibular or postcranial remains prevents any discussion of the possible marine adaptations of this genus.

The basal metriorhynchoids from the early Bajocian of Chile and Oregon, USA, are the most closely related species to Metriorhynchidae *s.s.* Unfortunately, the cranial material from Chile is poorly preserved (Gasparini *et al.*, 2000), again preventing discussion of marine adaptations. A recently discovered taxon from the Snowshoe Formation of Oregon, the 'Oregon crocodile' (currently under description; E. Wilberg, pers. com., 2008), preserves both cranial and postcranial remains. Its cranial geometry is very similar to that of Metriorhynchidae *s.s.*, but further discussion of its palaeoecology must await its full description.

Perhaps one of the most convincing indications of marine adaptations in metriorhynchids is the complete loss of body osteoderms, a unique feature among Crocodylia. Undoubtedly, it reflects the pelagic predatory lifestyle of this clade, as the reduction in body mass would have aided acceleration and improved hydrodynamic efficiency by minimizing friction drag (the main drag component in streamlined bodies) (Hua & Buffetaut, 1997). Furthermore, the loss of osteoderms is interesting, as they have been hypothesized to be involved in thermoregulation (Seidel, 1979), furthering our contention that metriorhynchids evolved distinct thermoregulatory behaviours. In addition, osteoderms provide a rigid central axis for parts of the epaxial muscle to attach to, thereby possibly playing a role in terrestrial locomotion (Seidel, 1979; Frey, 1984). We do not know when osteoderms were lost in metriorhynchoid evolution. All metriorhynchids lack osteoderms, but the absence of postcranial remains in basal metriorhynchoids does not allow us to determine whether such a loss occurred in more basal portions of the metriorhynchoid phylogeny.

Cranial adaptations to a presumed marine lifestyle in Metriorhynchidae *s.s.* included enlarged orbits (orbital anteroposterior length > 17% of basicranial length), suggesting that vision was their primary sense of perception (see Motani, Rothschild & Wahl, 1999 and Motani, 2005 for a discussion on orbit and eye size in vertebrates, and its importance to vision). Extant phocid pinipeds, ichthyosaurs, the fossil mysticete *Janjucetus*, and the fossil odontocete *Odobenocetops* all have enlarged orbits, and have been interpreted as vision-based marine predators (McGowan, 1973; Wartzok & Ketten, 1999; Schusterman *et al.*, 2000; Muizon, Domning & Ketten, 2002; Kear, 2005; Fitzgerald, 2006). Lateral orientation of the orbits (another metriorhynchid apomorphy) would have provided a wider field of vision for metriorhynchids, which is advantagous for vision-based predators in a nonturbid environment (see Massare, 1988; Hua, 1994; Martill,

Taylor & Duff, 1994), especially for those foraging for prey on the same level of the water column as themselves, as at a certain distance their prey would 'merge' into the background either through light diffusion or water turbidity (Martill *et al.*, 1994) (i.e. they would have had an increased likelihood of observing a prey item near them). The third cranial adaptation is the presence of an unornamented shallow fossa within the external nares, which forms a continuous border around the narial opening laterally and posteriorly (e.g. see Fig. 4B and Wilkinson, Young & Benton, 2008: text and fig. 3A). In specimens where the external nares are poorly preserved or has matrix infill, this feature is obscured (e.g. see Fig. 4E, D and Pol & Gasparini, 2009). The only extant crocodylians with a shallow fossa within the external nares are mature male gavials (with an anterior fossa), whereas separate anterior and posterior fossae are observed in the fossil gavialid *Rhamphosuchus* (Martin & Bellairs, 1977). The gavial fossa has been linked to the narial excrescence, a secondary sexual characteristic of males (see Martin & Bellairs, 1977). Therefore, using the gavial as an extant analogue, the narial fossae correlate with soft tissue hypertrophy (conntective tissue in the case of the gavial). However, the position of the fossa in metriorhynchids suggests that it is the constrictor and dilator musculature that is hypertrophied (see Bellairs & Shute, 1953; Parsons, 1970; Martin & Bellairs, 1977; for anatomy and discussion of crocodylian narial musculature). If this is indeed the case, then the narial closing musculature would be hypertrophied, modifying them into valves that can close the nostrils and exclude water while they are submerged (much like extant marine mammals; see Reidenberg & Laitman, 2008).

A similar cranial construction in Callovian metriorhynchids previously led to their inclusion within the same genus (*Metriorhynchus*; e.g. Andrews, 1913; Adams-Tresman, 1987) (compare Fig. 4E with F). However, although derived genera exhibit similar craniofacial constructions, similarities can now be interpreted as convergences (probably associated with independent acquisitions of increasing marine adaptations within each of the two metriorhynchid subfamilies). Similar skull morphologies formerly provided the basis for hypothesizing a sister-taxon relationship between *Dakosaurus* and *Geosaurus* (as then defined; *Cricosaurus* after Young & Andrade, 2009), proposed by Vignaud (1995) and Gasparini *et al.* (2006). The *Cricosaurus* + *Rhacheosaurus* clade, the *Geosaurus* + *Dakosaurus* clade, and derived species in the genus *Metriorhynchus* all independently evolved an increasingly streamlined cranium. This was achieved through a caudal reorientation of the lateral processes of the frontal, and the consequent formation of an acute angle between the medial

and lateral processes of the frontal (Fig. 4B–D). In addition, the aforementioned clades developed a more flattened humerus, with a short shaft and a strongly convex proximal margin (Fig. 3). Such cranial and humeral modifications are absent in the Callovian species of *Metriorhynchus*, as well as in *Gracilineustes* gen. nov. and *Suchodus*. Moreover, both metriorhynchines and geosaurines progressively evolved the following adaptations: (1) smooth cranial bones; (2) rostral extension of the intertemporal flange; (3) verticalization of the squamosal; and (4) dorsal inclination of the paroccipital processes. The entire suite of the six aforementioned adaptations are observed in the metriorhynchine *Cricosaurus* (*Rhacheosaurus* lacks the streamlining of the cranium and rostral extension of the intertemporal flange), and the geosaurines *Geosaurus* and *Dakosaurus*.

In specimens lacking the rostrum and complete prefrontals, the crania of derived metriorhynchines and geosaurines look remarkably similar (e.g. the holotypes of *Dakosaurus lissocephalus* Seeley, 1869 CAMSM J.29419, and *Cricosaurus gracilis* (Philips, 1871) OXFUM J.1431]. This is especially true of juvenile specimens. In both clades of derived metriorhynchids, the order of character acquisition is very similar. However, within Metriorhynchinae, the cranial bones become smooth prior to the acquisition of dorsally inclined paroccipital processes, whereas the reverse pattern is seen in Geosaurinae. Subsequent character evolution in both subfamilies followed parallel trends, including: verticalization of the squamosal and simultaneous dorsal inclination of the paroccipital processes (less pronounced in geosaurines, but more extensive in metriorhynchines), cranial streamlining, and rostral extension of the intertemporal flange. However, because of the lack of preserved humeri, the timing of evolutionary change of this bone is unknown, although in metriorhynchines a shortened–flattened humerus is acquired by the time of squamosal verticalization. It is not clear why a step-wise acquisition of these traits prior to cranial streamlining is observed in derived metriorhynchids but not in derived species of *Metriorhynchus* [i.e. *Metriorhynchus hastifer* (Eudes-Deslongchamps, 1868) and *Metriorhynchus palpebrosus* (Philips, 1871)]. However, even in these species of *Metriorhynchus*, the cranium is not as streamlined as in contemporary species of *Cricosaurus*, *Geosaurus*, or *Dakosaurus*. Interestingly, this entire suite of adaptations had evolved by the middle Oxfordian in *Cricosaurus* and *Geosaurus*; unfortunately, no reasonably complete *Dakosaurus* crania are known before the upper Kimmeridgian.

The marine adaptations of the Metriorhynchoidea reach their zenith in the genus *Cricosaurus*. Loss of the deltopectoral crest on the humerus is a characteristic observed convergently in other marine reptiles (e.g. ichthyosaurs; e.g. Motani, 1998), and is indicative of a reorganization of the forelimb musculature. In basal sauropterygians (pachypleurosaurs) there is still a well-developed deltopectoral crest, whereas in the nothosaurs *s.l.*, the crest is reduced in size, being lost in pistosaurids, plesiosaurs, and pliosaurs (Rieppel, 1998; Rieppel, Sander & Storrs, 2002). This progression in sauropterygian evolution is a hallmark of the transition from a semiaquatic to fully pelagic existence. Grange (1997) discussed forelimb movement in *Metriorhynchus*, with reference to the muscles attaching to the deltopectoral crest. He noted that the prominent deltopectoral crest on the leading edge of the humerus implied that the musculus deltoides scapularis provided backwards leverage (retraction). Potential synergists (musculus pectoralis and musculus coracobrachialis) contacted the underside of the crest and medial area of the shaft, thereby providing accessory adducting forces as the humerus retracted during swimming. The loss of the crest therefore is correlated with limiting the ability of forelimb retraction, and adapting the forelimb to act as a hydrofoil.

The forelimbs of both *Rhacheosaurus* and *Cricosaurus* lack the pisiform in the wrist. In extant crocodylians the musculus flexor carpi ulnaris inserts onto a prominence on the pisiform (Meers, 2003). This muscle is involved with flexion and abduction of the carpus, stabilization of the elbow joint, and adduction of the antebrachium. The loss of the pisiform is therefore correlated with a regression of the musculus flexor carpi ulnaris, and the aforementioned functions, which provides further evidence of forelimb adaptation to an exclusively marine lifestyle.

In *Cricosaurus*, the external nares became progressively retracted posterodorsally throughout the evolutionary history of the genus (Fig. 4B–C); this is also observed in other clades with sustained swimmers (e.g. ichthyosaurs and cetaceans; see Massare, 1994 and references therein). This transition is most extreme in *C. macrospondylus*, in which the entire naris is positioned caudal to the premaxilla (Hua *et al.*, 2000). However, the retraction only occurred after the development of a premaxillary septum, which bifurcates the external nares, and presumably improves the efficiency of respiratory airflow (i.e. less turbulence; see Hua *et al.*, 2000). Interestingly, all Mesozoic marine reptiles that exhibit narial retraction possess bifurcated external nares.

The bones of the mesopodia in *Cricosaurus* continue to become more flattened and plate-like, and the marginal perichondral bone is lost (this is another adaptation to an aquatic lifestyle that has been observed in other marine reptiles; see Caldwell, 2002). In the tarsus, the calcaneum tuber completely regresses. This is an essential component of the

third-class lever system that acts during terrestrial locomotion (analogous with the mammalian 'heel bone' and the 'hooked fifth metatarsal' of various diapsid groups; see Robinson, 1975; Lee, 1997). There is also an increase in caudal vertebrae number within *Cricosaurus*, which results in the longest tails, proportionally, of any metriorhynchid (> 52 caudals). In addition, after the tail fluke there is an increase in caudal number. The holotype of *Neustosaurus* (see Raspail, 1842) has the deepest hypocercal tail of the entire family. By the Valanginian, *Cricosaurus* [*C. macrospondylus*, *Cricosaurus schroederi* (Kuhn, 1936), and the *Neustosaurus* holotype] possessed the following characters: very deep hypocercal tails; retracted and bifurcated external nares; orbits that are at least 20% of the basicranial length; and a robust sclerotic ring that fills the orbit. All of these adaptations are suggestive of *Cricosaurus* becoming stronger, sustained swimmers, possibly mesopelagic, but certainly shifting away from epipelagic ambush predation.

The increased adaptation to marine life may have reduced competition with other genera of metriorhynchids, although it is likely to have increased competition with other piscivorous marine reptiles, such as ichthyosaurs. The skull and dentition of *C. schroederi* (see Karl *et al.*, 2006; Young & Andrade, 2009; Fig. 4D) is highly reminiscent of an ichthyosaur, suggesting the possibility of morphospace overlap and competition between these two groups during the Lower Cretaceous. The increase in marine adaptation of *Cricosaurus* coincides with their taxic diversity increase during the Tithonian (see below). By the lower Tithonian, its geographic range included Argentina, Mexico, Western Europe, and Russia. Together with *Dakosaurus*, *Cricosaurus* is one of very few metriorhynchoids exhibiting a truly cosmopolitan distribution.

Although marine adaptations within Geosaurinae are currently poorly understood, the genera *Geosaurus* and *Dakosaurus* were the deepest-bodied metriorhynchids (characterized by their long, robust ribs). As explained by Massare (1988), body shape has a large impact upon swimming capabilities, with deeper bodies minimizing drag, thereby increasing swimming efficiency. Massare (1988) found *Dakosaurus* to be the most efficient swimmer of the metriorhynchids that she included in her study. This suggests that the hypercarnivorous genera (*Dakosaurus* and *Geosaurus*) were better able to sustain fast swimming speeds for longer periods of time than other metriorhynchids. Further support of this hypothesis for *Geosaurus* comes from the sclerotic ring of *Ge. giganteus* (NHM R.1229, NHM 37020; Fig. 4G). It is the second largest and second most robust sclerotic ring of any known metriorhynchid (after *C. schroederi*), occupying most of the orbit. As such, it would have offered good support for the eye, suggesting that *Geosaurus* was either a fast swimmer and/or ventured on deep dives (Young & Andrade, 2009).

FEEDING ADAPTATIONS

Gullet size, dental morphology (Taylor, 1987; Massare, 1987), and osmoregulatory physiology (Fernández & Gasparini, 2000, 2008) are the main factors that constrain prey selection in marine predators. The hypertrophied nasal salt glands of metriorhynchines (Fernández & Gasparini, 2000, 2008; Gandola *et al.*, 2006) would have allowed the ingestion of large numbers osmoconforming prey (i.e. cephalopods). Although the presence of these excretory glands cannot be confirmed in Geosaurinae, such glands were undoubtedly present. Buchy *et al.* (2007) notes that in a Mexican specimen of *Dakosaurus* the chamber housing the salt glands are preserved. Therefore, the evolution of hypertrophied nasal salt glands enabled not only an increase in metriorhynchid marine specialization, but extended their range of possible prey items.

Within Metriorhynchidae, there is a diverse array of tooth crown morphologies (Fig. 6), and, by inference, feeding behaviours. A conical bicarinate tooth crown with a sharp apex and a homodont dentition represents the ancestral condition for Metriorhynchoidea (Eudes-Deslongchamps, 1867–1869), and for both metriorhynchid subfamilies (Eudes-Deslongchamps, 1867–1869; Vignaud, 1997). However, derived members in both subfamilies display different dental morphologies (e.g. von Sömmerring, 1816; Gasparini *et al.*, 2006; Young & Andrade, 2009).

Dental morphology, including tooth wear patterns, sharp apices, and small basal crown diameters, place all metriorhynchines within the pierce guild of Ciampaglio, Wray & Corliss (2005), and place most metriorhynchine genera within Massare's (1987) pierce-II guild (Figs 7–8). The exceptions are the genus *Metriorhynchus* and *C. macrospondylus*, which would be classified as 'general', as they have a slightly greater basal crown diameter and a blunter apex, and *Rhacheosaurus*, which possess teeth that are consistent with Massare's pierce-I guild (fragile crowns with a very sharp apex and narrow basal crown diameter). Massare (1987) considered the pierce guilds to be more indicative of soft-bodied feeders (e.g. shell-less neocoleoid cephalopods), than that of the 'general' guild (which may have preyed upon shelled belemnoid cephalopods, supported by the presence of belemnite hooklets found within the body cavity of *Metriorhynchus* from the Oxford Clay; Martill, 1985). *Rhacheosaurus* and *Cricosaurus* dentition is characterized by the loss of the dental carinae (cutting edges; Fig. 8E), although the Valanginian species *C. macrospondylus* possessed autapomorphic unicarinate crowns.
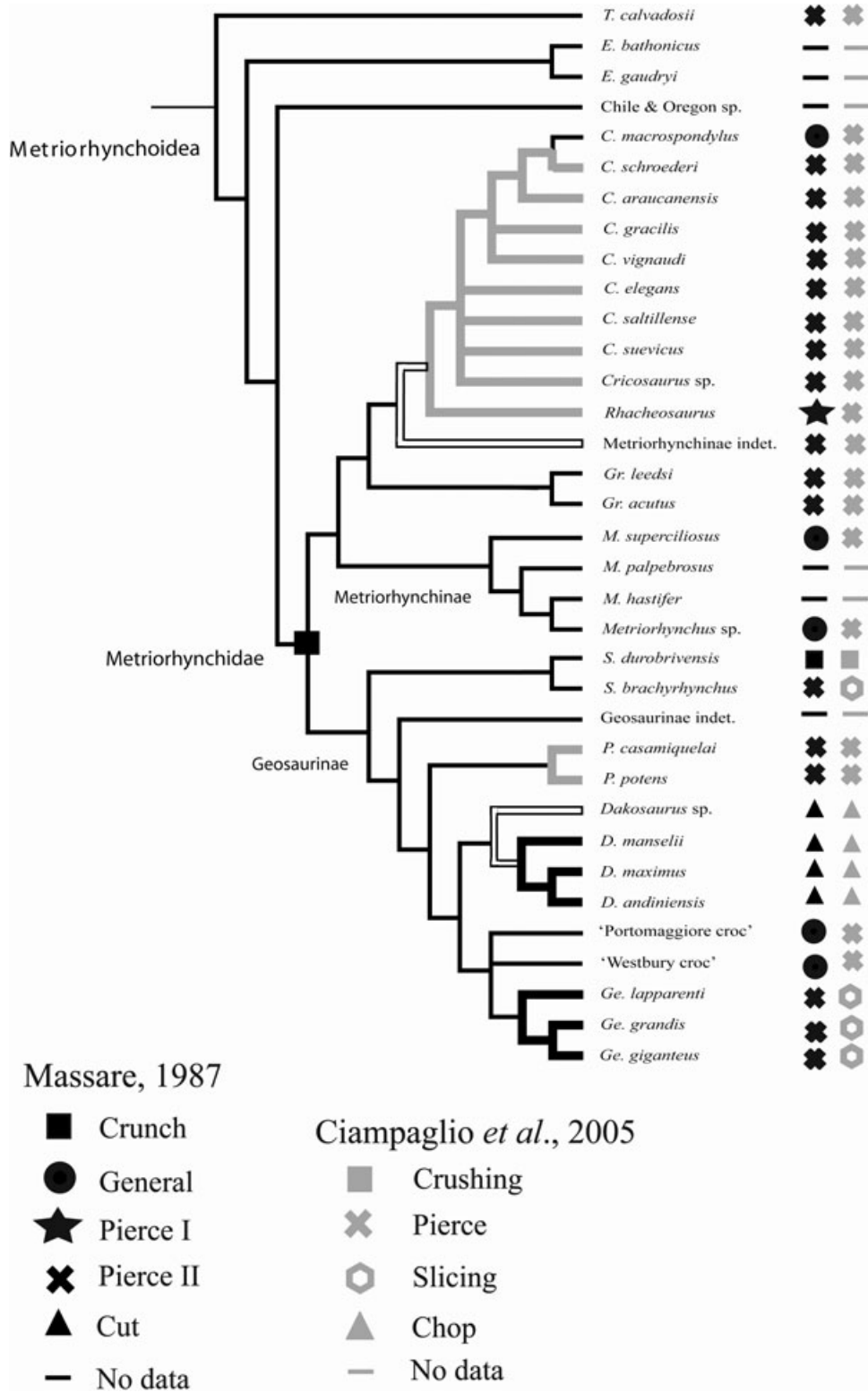
Figure 7. Metriorhynchoidea phylogeny, with dental characters mapped. The thin branches refer to smooth carinated crowns, whereas the bold black lines refer to denticulate carinae. The bold grey indicates crowns lacking carinae. The symbols refer to tooth morphology guilds from Massare (1987) and Ciampaglio *et al.* (2005).
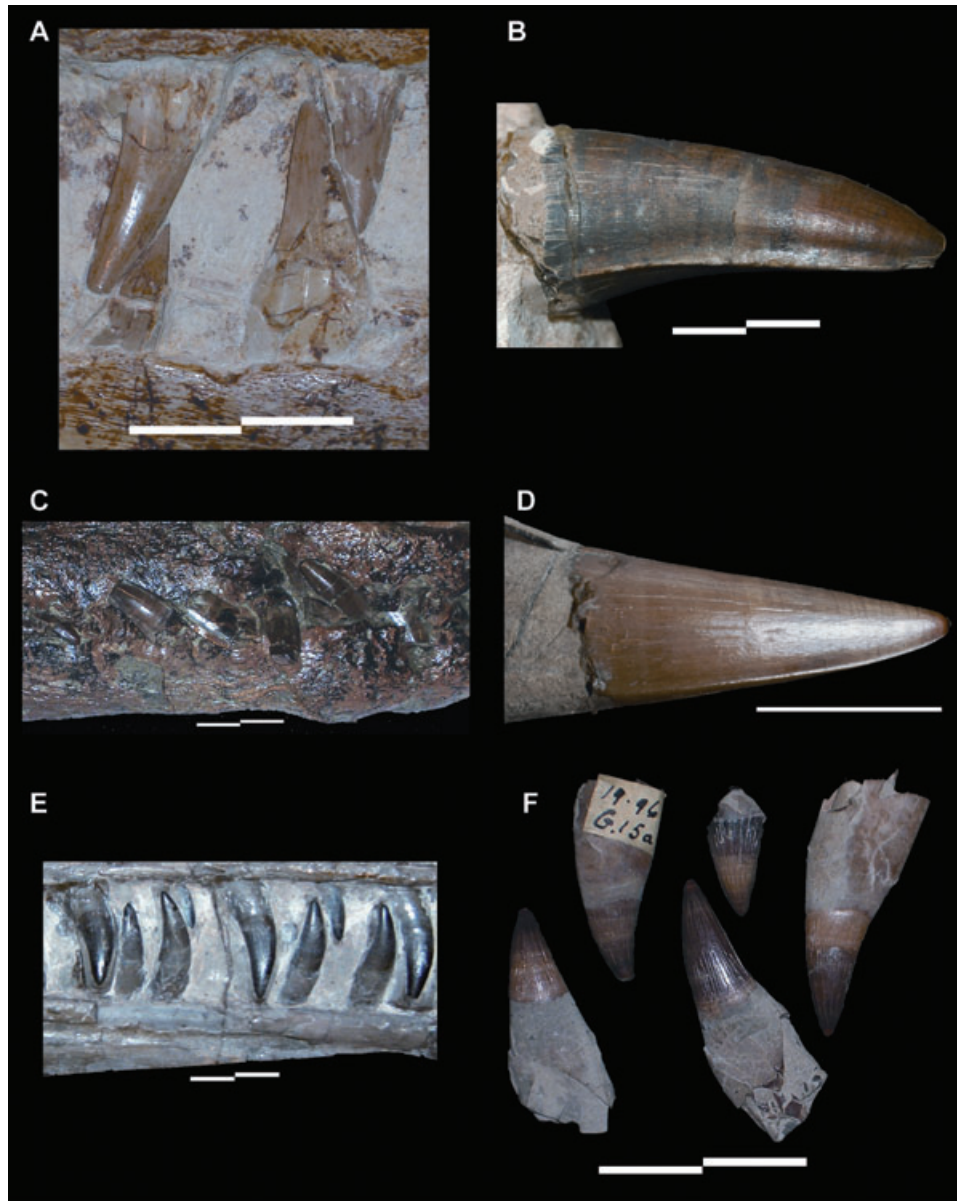
Figure 8. Comparative metriorhynchid dental morphology: (A) in situ crowns of *Geosaurus giganteus* NHM R.1229; (B) isolated crown of *Dakosaurus maximus* HMN R.4313; (C) in situ crowns of *Suchodus durobrivensis* NHM R.2618; (D) isolated crown of *Suchodus brachyrhynchus* HMN R.3386.2; (E) in situ crowns of *Cricosaurus schroederi* MMGLV#; (F) isolated crowns of *Metriorhynchus superciliosus* NMW 19 96 G15a. Scale bars: 10 mm. We thank for N. Knötschke for photograph (E).

The long snout-to-basicranial length and the procumbent orientation of the crowns indicate that metriorhynchines fed upon soft-bodied cephalopods and thin-scaled fish (a diet also proposed by Hua, 1994). The retention of the dental carinae most likely indicates that basal metriorhynchines were opportunistic predators, and were not specialist piscivores (much like the extant *Crocodylus johnsoni* Krefft, 1873). It is the derived metriorhynchine genera (*Rhacheosaurus* and *Cricosaurus*) that most resemble the extant *Gavialis* morphologically, with their narrower and less-deep snouts. Coupled with the lack of dental carinae, the snout morphology suggest that both genera were opportunistic predators of small aquatic prey, with differences in snout length allowing for dietary partitioning between contemporary species, e.g. the longirostrine *Rhacheosaurus gracilis* von Meyer, 1831, and the mesorostrine *Cricosaurus elegans* (Wagner, 1852), from the early Tithonian of Germany.

Geosaurine dental morphology is far more varied than that of the metriorhynchines (Fig. 8A–D). Geosaurines occupy four of Massare's (1987) guilds (pierce II, general, crunch, and cut), and, in the terminology of Ciampaglio *et al.* (2005), four guilds are held (pierce, slice, crush, and chop) (Fig. 7). The crunch guild of Massare (1987) and crush guild of Ciampaglio *et al.* (2005) are both held exclusively by *Suchodus durobrivensis* Lydekker, 1890a, which has unrecurved teeth with blunt and rounded apices (Fig. 8C). These teeth are considered to be adapted for crushing organisms with a harder exoskeleton or cuticle (i.e. thicker scaled fish or thin-shelled ammonoid cephalopods; Massare 1987). Its contemporary *S. brachyrhynchus* is one of the two geosaurine taxa with slicing dentition (along with derived species of *Geosaurus*) (Fig. 8A, D). Its crowns are strongly lateromedially compressed, distinctly triangular in labial and lingual views, and remarkably blade-like. Basal species of *Geosaurus* possess dentition very much like *Metriorhynchus* (general guild), except that the crowns are approximately twice the basi-apical length. *Purranisaurus* independently lost dental carinae, and possessed a crown morphology that is superficially similar to that of *Cricosaurus*. Finally, the cut and chop guilds are exclusively held by *Dakosaurus*. This dental morphology is distinctly robust, with a large basal diameter and well-developed carinae (Fig. 8B), and is observed in other high-order marine predators (e.g. extant orcas, mosasaurs, and pliosaurs; see Massare, 1987).

As the skulls of geosaurines are proportionally broader and have shorter snouts than those of metriorhynchines, it is probable that there is dietary partitioning between the subfamilies (see Henderson, 1998 for a similar example in theropod dinosaurs), with the geosaurines better able to feed upon larger prey, such as other marine reptiles. Further evidence for this hypothesis is provided by bite marks on vertebrae of the plesiosaur *Cryptoclidus eurymerus* (Phillips, 1871) (Forrest, 2003), which are consistent with the teeth of the basal geosaurine *S. brachyrhynchus*.

The genus *Dakosaurus* has recently been shown to be highly atypical for currently known marine crocodylians (Gasparini *et al.*, 2006). With its theropod dinosaur-like dentition, and robust skull, it is presumably adapted to feeding upon other marine reptiles via a torsional feeding strategy [a similar feeding strategy has been proposed for Mesozoic pliosauroids, the Oligocene basal mysticete *Janjucetus*, and the extant leopard seal, *Hydrurga leptonyx* (de Blainville, 1820); see Fitzgerald, 2006 and references therein]. A number of characters support this feeding strategy, including: deeply rooted, large (apicobasal length > 6 cm), denticulate teeth; a deep, bulbous mandibular symphysis; a well-developed quadrate distal head; and robust articular (see Gasparini *et al.*, 2006: fig. 1;

Figs 4H and 8B). Furthermore, their skulls feature both the greatest cross-sectional thickness of bone and the largest muscle origination sites for the musculus adductor mandibulae externus group and musculus pseudotemporalis superficialis of all other metriorhynchids (see Holliday & Witmer, 2007 for a discussion on reptilian comparative jaw musculature; see Young, 2006 and Buchy, 2007 for a discussion on metriorhynchid cranial architecture). *Dakosaurus* was adapted for hypercarnivory, and was characterized by a powerful bite force (aided by the reduction in rostral length, which increases the mechanical advantage of the adductor musculature; Freeman, 1979; Henderson, 1998; Metzger & Herrel, 2005), a strengthened jaw joint, dentition adapted for breaking bone (Massare, 1987), and the largest skulls (~1.1 m in length, NHM 40103; and by assumption body size) of any metriorhynchid. Thus, bone cracking and osteophagy within Metriorhynchidae was limited to *Dakosaurus*. Wroe, McHenry & Thomason (2005) found that for terrestrial mammals, skull and dentition constrain the biomechanics of osteophagy more strongly than muscle forces do. In order to achieve material failure of bone, a concentration of high loads is required on a limited area of the prey (Wroe *et al.*, 2005). Based upon overall morphology, we posit that *Dakosaurus* would be able to deliver such a load on to a potential prey item; furthermore, its skull would be able to withstand the stresses involved. However, this hypothesis requires additional testing using computer-aided tomography scanning of metriorhynchid skulls, and finite-element analysis. Regardless of whether or not *Dakosaurus* was able to crack bone, its strong and powerful skull and mandible would have reduced the time taken to process prey, making larger organisms more energetically feasible prey items (Verwaijen, Van Damme & Herrel, 2002).

This evolutionary trend towards presumed bone crunching 'culminates' with *D. andiniensis*, which is characterized by a robust, wide oreinirostral skull, with the shortest and deepest snout and mandible of any known metriorhynchid (Gasparini *et al.*, 2006; see Fig. 4). *Dakosaurus andiniensis* would therefore have benefited from greater resistance to both torsional and bending stresses (see Rayfield *et al.*, 2007b), the highest mechanical advantage for adductor musculature, and the most deeply rooted teeth of any metriorhynchid.

However, *Geosaurus* also exhibits an independent evolutionary trend towards pelagic hypercarnivory. When most reptilians bite upon a food item, the upper and lower jaws approach one another vertically, subjecting the food item to compression (see Sinclair & Alexander, 1987 for details on reptilian jaw muscle force theory). In animals lacking fore-and-aft movements of the mandible and/or cranial element kinesis

(e.g. propaliny and streptostyly), shearing is introduced by the dentition if the teeth crowns of the upper and lower jaws interlock. This is the case in extant crocodylians and most thalattosuchians. However, in *Ge. giganteus*, the dentition is arranged as opposing blades; therefore, during a bite ,the food item would be subjected to shearing between the two tooth rows, as well as between the individual teeth (Young & Andrade, 2009; Fig. 8A). This improves the efficiency of slicing through soft tissue, such as muscle (especially as there is no lingual curvature to their teeth). Coupled with the strong lateromedial compression of the dentition, and their serrated carinae (see Frazzetta, 1988; Abler, 1992 for further details on serrations and tooth shape theory), the derived *Geosaurus* would have been adapted to a mode of feeding involving gouging and slicing flesh off prey.

In the progression towards hypercarnivory, both *Dakosaurus* and *Geosaurus* evolved true ziphodonty (teeth with denticulate serrated carinae; see Prasad & de Broin, 2002). The nonhomology of this trait is possible because of the difference in their detailed structure (Andrade & Young, unpubl. data), and from the results of character optimization on the global phylogeny (Young & Andrade, 2009). This is currently the focus of another study (Andrade & Young, unpubl. data). *Geosaurus* (*sensu* Young & Andrade, 2009) has a geological range from the lower Oxfordian to the lower Valanginian. However, denticulate carinae are only observed on teeth from the uppermost Kimmeridgian onwards. In contrast, the earliest known teeth of *Dakosaurus* (lower Oxfordian) possess denticulate carinae.

In many mesoeucrocodylians, true ziphodonty correlates with a crown morphology described as theropodomorph (i.e. large, robust, and recurved, as in large theropod dinosaurs; Abler, 1992). These morphologies have evolved multiple times, primarily in taxa that are considered to have been terrestrial hypercarnivores, such as the Baurusuchidae, Peirosauridae, and Pristichampsidae (e.g. Price, 1945, 1955; Langston, 1975; Carvalho, Ribeiro & Avilla, 2004; Carvalho *et al.*, 2005; Pinheiro *et al.*, 2008). The ziphodont metriorhynchids have very different crown morphologies (see Fig. 8A–B) [interestingly, metriorhynchids were left out of Prasad & de Broin's (2002) review of ziphodonty in crocodylians]. *Dakosaurus* is the only example of a marine ziphodont mesoeucrocodylian with theropodomorph teeth, whereas ziphodont *Geosaurus* had triangular (in lateral view), blade-like crowns (the theropodomorph designation for *Dakosaurus* is apt, as its teeth were originally considered to belong to the theropod *Megalosaurus*; von Quenstedt, 1843). Thus, there is convergence upon serrations, but divergence upon overall crown morphology. Therefore, both genera became more effi-

cient carnivores, but were able to feed and process food differently, which presumably indicates that they were exploiting different prey. The only known co-occurrence of ziphodont metriorhynchids was in the Solnhofen Sea (Young & Andrade, 2009).

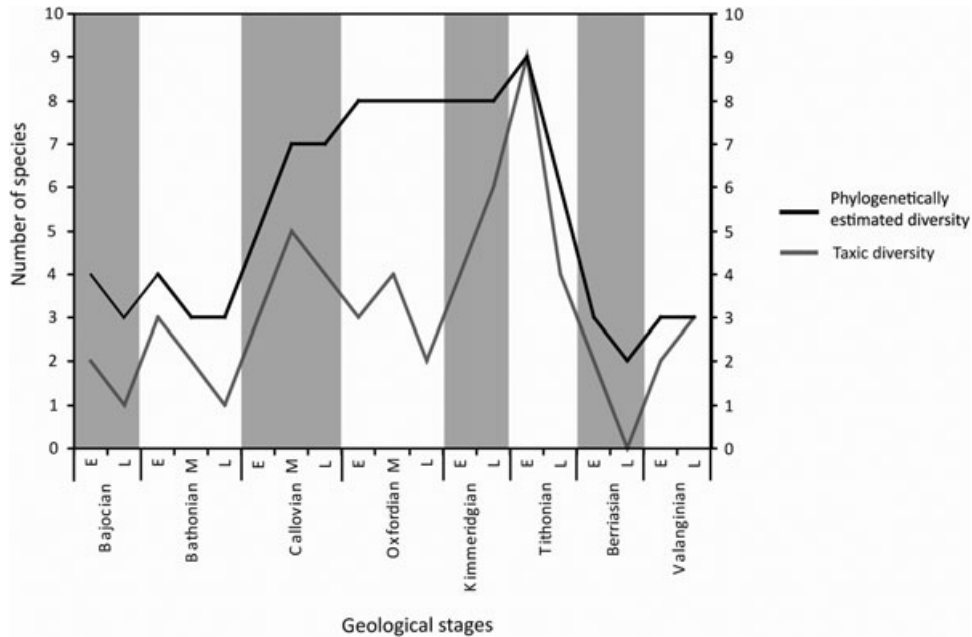## DIVERSITY OF METRIORHYNCHOIDEA
METHOD

Counts of taxonomic diversity (taxic diversity) have come under increasing criticism, as biases in the rock record invariably engender an underestimate of palaeobiodiversity (see Lane, Janis & Sepkoski, 2005 and the references therein). To correct for this bias, phylogeny-based approaches (which take into account 'ghost lineages' and 'range extensions' implied by the phylogeny) have been introduced (e.g. Norell, 1992; Smith, 1994). As a comprehensive cladistic treatment for Metriorhynchoidea is now available, diversity can be investigated using phylogenetic interpolation. A new compendium of metriorhynchoid taxic diversity (see Appendix) was compiled based upon an exhaustive literature search and specimen examination. Phylogenetic diversity was compiled using the phylogeny of Young & Andrade (2009) to correct for ghost ranges and range extensions. Taxic and phylogenetically estimated diversity measures were then plotted against time (Bajocian–Valanginian; based upon Ogg, Ogg & Gradstein, 2008).

RESULTS

Both observed and inferred curves of diversity track each other well during the Bajocian to the middle Callovian, and during the Tithonian to the late Valanginian (Fig. 9). During the Bajocian–Bathonian, metriorhynchoid diversity was comparatively low (three or four species when phylogenetically corrected). However, during the Callovian there is a sharp rise in diversity, reaching seven species by the middle Callovian. From the late Callovian to late Kimmeridgian, the observed diversity departs considerably from the inferred diversity. In particular, the greatest underestimate is observed during the late Oxfordian (a fourfold underestimation). This is largely in agreement with Bardet (1994), who found that the fossil record of marine reptiles during the Oxfordian is only 44% complete. There is a sharp decline in metriorhynchid diversity beginning in the late Tithonian, which continues throughout the Berriasian, and is then followed by a slight increase in the Valanginian.

Based upon the divergence between the taxic and phylogenetic diversity curves, we conclude that there are many more species of metriorhynchids still to be discovered. The Kimmeridgian–Berriasian deposits of La Casita and La Caja formations of Mexico are a

Figure 9. Species diversity of Metriorhynchoidea (both taxic and phylogenetically corrected) for each stage subdivision.

good example of the rich metriorhynchid fauna yet to be fully unearthed (see Buchy, 2007, 2008a, b; Buchy *et al.*, 2007).

CRANIAL SHAPE VARIATION WITHIN METRIORHYNCHIODEA: GEOMETRIC MORPHOMETRICS

METHOD

Geometric morphometric techniques are suitable for quantifying morphological variation in a group of organisms, as they allow for the reduction of a complex shape into a set of measurements using collections of 2D (or 3D) co-ordinate positions (i.e. landmarks). In this paper, geometric morphometrics is employed to quantify shape variation in the skull roof of metriorhynchoids, which allows for a much more detailed examination of cranial form than that obtained with the previous analyses, which take into account proportional measurements (e.g. 'longirostrine' and 'brevirostrine' clusters) (see Dryden & Mardia, 1998 and Zelditch *et al.*, 2004, for a review of geometric morphometrics, and see Stayton & Ruta, 2006; Pierce, Angielczyk & Rayfield, 2008; Pierce *et al.*, 2009a, for cranial dorsal aspect 2D geometric morphometric analyses).

Landmark and sample selection
All the landmarks (see Fig. 10 and Table 2) used for relative warp analysis (RWA) were digitized from
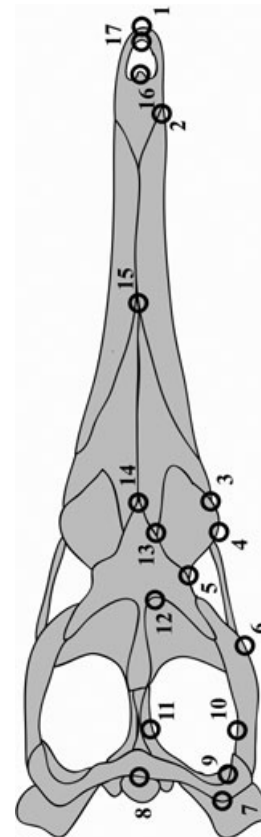
Figure 10. Dorsal view of a generalized metriorhynchid skull, with the landmarks measured shown (see Table 4). Image redrawn from Frey *et al.* (2002).

Table 2. Relative warp landmarks, with a description

Number	Description
1	Anteriormost point of the premaxilla
2	Premaxilla–maxilla suture along dorsal outline
3	Nasal–prefrontal suture along dorsal outline
4	Inflexion point of the prefrontal
5	Prefrontal–frontal suture along dorsal outline
6	Inflexion point of the postorbital
7	Posteriormost point of the squamosal
8	Posteriormost point of the parietal along the midline
9	Lateralmost point of the maximum distance of the supratemporal fossa
10	Lateralmost point of the minimum distance of the supratemporal fossa, perpendicular to the maximum distance
11	Medialmost point of the minimum distance of the supratemporal fossa, perpendicular to the maximum distance
12	Medialmost point of the maximum distance of the supratemporal fossa
13	Sutural contact between the frontal, prefrontal, and nasal
14	Frontal–nasal midline suture
15	Nasal–maxilla midline suture
16	Posteriormost point of the external nares
17	Anteriormost point of the external nares

photographs, or were scanned from the literature using Image Pro Plus v5.1.0.20 (Media Cybernetics, http://www.mediacy.com). Photographs were taken by M. T. Young using a Canon IXUSi digital camera, or were kindly provided by colleagues (see Table 3 for a list of all specimens and the source details). Landmarks used to describe the dorsal aspect of a metriorhynchid skull were chosen in order to maximize the quantity of shape information using the smallest number of points. A landmark for the suture between the maxilla and nasal along the dorsal edge was initially considered, but was later rejected as the suture does not lie along the margin of the skull of *Cricosaurus* in dorsal aspect. It is important to note that there is an over-representation of specimens from the genera present in the Oxford Clay Formation (namely *Metriorhynchus*, *Gracilineustes* gen. nov., and *Suchodus*) (see Table 3). Unfortunately, this cannot be helped as there have been more skulls discovered from the Oxford Clay Formation than all other metriorhynchid-bearing formations combined.

Cranial bone arrangements on either side of the skull dorsal midline are not exact mirror images of each other (Stayton & Ruta, 2006). Moreover, additional asymmetry is introduced by taphonomic deformation (most especially in those from the Oxford Clay Formation of England). Deformation is evidenced by dorsoventral compression of the cranium; however, for our purposes the landmark constellation chosen (in dorsal aspect) suffers the least from this dorsoventral compression. Nevertheless, some specimens were excluded from this analysis. In order to increase the sample size, some specimens in which one half had not undergone deformation were chosen for the analysis. Landmark co-ordinates were taken from the nondeformed half, with the images being flipped (reversed) to ensure that in all specimens they were taken in the same orientation. Mirroring the landmarks was not considered necessary, as it added no further information, and an increased cosmetic representation was not desired.

Geometric morphometrics: relative warps analysis
The metriorhynchoid cranial form was analysed with RWA (Rohlf, 1993), which removes the conflating effects of size when constructing a landmark-constellation morphospace. The freeware program tpsRelw v1.42 (Rohlf, 2005) was used for the analysis.

When undertaking the RWA, the first step (in tpsRelw v. 1.42) was to take the aforementioned landmarks from the digital images and conduct a Procrustes generalised orthogonal least-squares alignment. First, the landmark configuration for each taxon was scaled to unit centroid size, the square root of the sum of squared distances from all landmarks to the centroid of the configuration (Bookstein, 1991). The taxon landmark configurations were then centred and rotated, thereby minimising the sum of the squared distances between the landmarks of each configuration compared to the corresponding landmarks of the reference configuration (the mean landmark configuration of all taxa).

Next, an interpolation technique, the thin-plate spline function (Bookstein, 1991) was used to express the shape differences between the reference configuration and the Procrustes aligned configurations in terms of the bending energy matrix. The eigenvectors of the energy bending matrix are referred to as principal warps (Bookstein, 1991). The matrix of partial warp scores is derived by projecting the Procrustes aligned configurations onto the principal warps. Partial warps are the non-affine (non-uniform) shape changes modelled by the thin-plate spline that describe local variation in shape, with a principal components analysis of the partial warp score matrix referred to as a relative warps analysis (Rohlf, 1993).

In order to plot the positions of landmark coordinates derived from the actual specimens, the x, y configurations derived from the relative warps analysis are projected orthogonally onto a plane that is tangential to the shape space at the point occupied by

Table 3. Specimens used in the relative warp analysis

Species	Source (specimen or reference)
Cricosaurus araucanensis	Photograph of MLP 72-IV-7-1 provided by Z. Gasparini
Cricosaurus suevicus	SMNS 9808
Cricosaurus vignaudi	Frey *et al.* (2002: 1469, fig. 2B)
Dakosaurus andiniensis	Photograph of MOZ 6146P provided by Z. Gasparini
Dakosaurus manselii	NHM 40103
Dakosaurus maximus	Composite of Fraas (1902: 10, fig. 10) and SMNS 8203
Geosaurus carpenteri	BRSMG Ce17365
Geosaurus grandis	BSPG-AS-VI-1
Gracilineustes acutus comb. nov.	Lennier (1887: pl. 20, fig. 1)
Gracilineustes laeve comb. nov.	NHM R.2042
	NHM R.3014
	NHM R.3015
	NHM R.4762
Gracilineustes leedsi comb. nov.	NHM R.3540
Metriorhynchus hastifer	Eudes-Deslongchamps (1867–1869: pl. 24, fig. 5)
Metriorhynchus moreli	NHM R.2032
	NHM R.2044
	NHM R.2049
	NHM R.2054
	NHM R.6860
Metriorhynchus palpebrosus	OXFUM J.29823
'*Metriorhynchus superciliosus*'	Buffetaut (1977: 257, fig. 1)
Metriorhynchus superciliosus	NHM R.2030
	NHM R.2033
	NHM R.2051
	NHM R.2056
	NHM R.3016
	CAMSM unnumbered
	GLAHM V966
	GLAHM V983
	GLAHM V1027
	GLAHM V1142
	Photograph of NMING F21731 provided by J. Liston
	RMS M150
Purranisaurus casamiquelai	Photograph of MGHF 1-08573 provided by Z. Gasparini
Rhacheosaurus gracilis	NHM R.3948
Suchodus brachyrhynchus	NHM R.3699
	NHM R.3700
	NHM R.3939
	PETMG R176
Suchodus cultridens	NHM R.3804
Suchodus durobrivensis	NHM R.2618
	NHM R.3321
	NHM R.4763
Teleidosaurus calvadosii	NHM R.2681

the mean skull shape (e.g. Dryden & Mardia, 1998; Zelditch *et al.*, 2004). To be able to determine whether or not any significant distortion occurred during this projection, the Procrustes distances were regressed against the Euclidean distances (e.g. Dryden & Mardia, 1998; see Stayton & Ruta, 2006 for methods), using the program tpsSmall v1.20 (Rohlf, 2003). In order for skull shape morphospace to be characterized, we focused on the most important relative warp axes (i.e. the ones that explained most of the variance). The morphospace of each genus was delimited by convex hulls (the smallest convex set containing the coordinate points of a particular genus – i.e. a closed polygonal chain) in order to aid visualization.
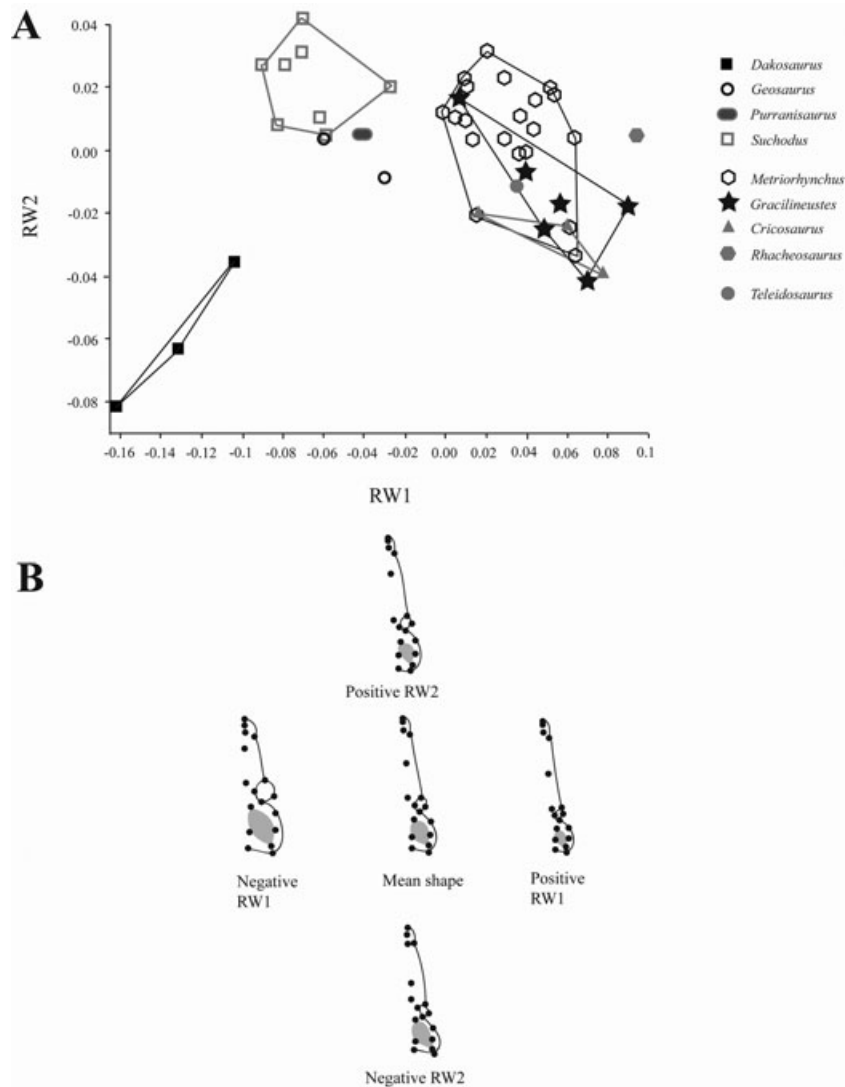
Figure 11. A, relative warps cranial morphology morphospace, delimited by the first two axes. B, shape changes corresponding to the mean shape, and the extremes of both of the first two axes.

The statistical significance between the disparity of Metriorhynchinae and Geosaurinae was assessed using NPMANOVA (nonparametric multivariate analysis of variance), which tests for significant differences in the distribution of groups in morphospace (Anderson, 2001). NPMANOVA, the multivariate (and nonparametric) equivalent of ANOVA, was calculated in PAST v1.78 (Hammer, Harper & Ryan, 2001). One of the strengths of NPMANOVA is that as a nonparametric statistical test, it does not assume or require normality from the multivariate data.

RESULTS

The regression of Procrustes distance against Euclidean distance for each pair of landmarks gave a high correlation coefficient ($r > 0.99$). Thus, distortion did not prevent the interpretation of results from the relative warp morphospace. It is important to remember the limitations of our sample (e.g. overrepresentation of specimens from the Oxford Clay Formation, and the lack of specimens from the Valanginian) in our discussion regarding relative warp morphospace occupation.

Relative warp axes one and two account for 56.87 and 11.32%, respectively, and 68.19% cumulatively, of the variation around the mean shape (Fig. 11). The first relative warp axis (RW1) summarizes the brevirostrine to longirostrine transition. Negative RW1 values are characterized by: (1) the landmarks around the supratemporal fossa being widely dispersed, (2) the landmarks that delimit the prefrontal

being laterally and anteroposteriorly dispersed, (3) the nasal–maxilla suture landmark occupying its most anterior position out of all significant RW axes, and (4) the distance between the prefrontal–nasal suture along the dorsal margin and the anterior of the premaxilla being proportionally short. Positive RW1 values show the opposite: (1) the landmarks around the supratemporal fossa being proportionally closer together, (2) the nasal–maxilla suture occupying a much more posterior position, (3) the prefrontal landmarks being closer together, and (4) the distance between the prefrontal–nasal suture and the anterior of the premaxilla being proportionally much greater.

The second relative warp axis (RW2) characterizes the second most important shape differences (Fig. 11). Increasingly negative RW2 values reflect the progressive shifting backwards of the nasals, the premaxilla–maxilla suture being in line with the posterior margin of the external nares, and the suture of the nasal, maxilla, and prefrontal being anterior to the inflexion point of the outer angle of the prefrontal. Positive RW2 values place the premaxilla–maxilla suture more posterior along the dorsal margin of the skull, and the suture between the nasal, maxilla, and prefrontal posterior to the inflexion point of the outer angle of the prefrontal, coming close to the suture between the prefrontal and frontal along the dorsal margin.

Metriorhynchine and geosaurine subfamilies occupy statistically distinct areas of the morphospace (Figs 3, 11; NPMANOVA, $P < 0.0001$, $F = 70.3$, 50 000 permutations), which was expected from the historical tradition of separating metriorhynchids into 'brevirostrine' and 'longirostrine' forms (see also Pierce *et al.*, 2009a). The landmark-based skull shape morphospace delimited by the first two RW axes (Fig. 11) shows a separation between the brevirostrine genera (Geosaurinae) and the longirostrine genera (Metriorhynchinae and *T. calvadosii*) along RW1 (recording the differences between *Rhacheosaurus* and *Dakosaurus*). The morphospace occupied by *Dakosaurus* and the more mesorostral geosaurines are distinct from both one another and all other metriorhynchoid taxa. *Dakosaurus* skull morphospace is separated from the other geosaurines, as it is characterized by more negative RW1 and RW2 values (with RW2 recording the differences between *Suchodus* and *Dakosaurus*). Within the longirostrine genera there is extensive overlap in morphospace occupation. The sole *Teleidosaurus* skull landmark configuration falls within both *Metriorhynchus* and *Gracilineustes* gen. nov. morphospace. Although the *Teleidosaurus* specimen falls within the convex hulls of both genera, it does not necessarily mean that *Teleidosaurus* morphologically overlaps with either genera (e.g. if the overlap takes place in a sparsely populated region, such as with *Gracilineustes* gen. nov., the overlap

might appear very distinct; however, there is a distinction between genuine overlap and apparent overlap resulting from projection).

TEMPORAL TRENDS

Temporal patterns were characterized by examining the two most significant axes of variation from the RWA in three separate time bins (Callovian; Oxfordian–Kimmeridgian; Tithonian–Berriasian; Fig. 12). As we only have a single data point for nonmetriorhynchid metriorhynchoids (*T. calvadosii*), only the temporal trends for the Metriorhynchidae could be investigated.

During the Callovian, metriorhynchids can be easily separated into 'brevirostrine' and 'longirostrine' forms, which also represents the distinction between the Geosaurinae and Metriorhynchinae, respectively. The area of morphospace occupation is comparable for both *Metriorhynchus* and *Suchodus*, even though *Metriorhynchus* is known from twice as many specimens. The Metriorhynchinae skull morphospace is as dispersed along the RW1 axis, as with the brevirostrine forms, but it is in the RW2 axis that metriorhynchine skull morphospace is expanded, notably negatively in *Gracilineustes* gen. nov. The negative RW2 region is characterized by the nasal occupying a posterior position, the maxilla 'moving' closer to the external nares, and the back of the skull becoming more pointed around the squamosal. It is the crania of *Gracilineustes laeve* (Andrews, 1913) comb. nov. (a junior synonym of *Gr. leedsi*) that demonstrate this morphology. Of all of the Callovian specimens, they have the proportionally longest rostrum and smallest prefrontals, but have the narrowest cranium.

As the sample size is smaller post-Callovian, it is divided here into two subdivisions: Oxfordian–Kimmeridgian and Tithonian–Berriasian (unfortunately there are no complete crania for Valanginian taxa). For both subdivisions the occupation of the morphospace is very similar. In the Oxfordian–Kimmeridgian relative warp morphospace, the evolution of *Dakosaurus* begins a trend of increasingly negative RW1 and RW2 values. *Geosaurus* occupies the same region of morphospace that *Suchodus* did in the Callovian; *Metriorhynchus* shifts to a more negative RW2 region, much like that occupied by *Gracilineustes* gen. nov. in the Callovian; whereas *Gracilineustes* gen. nov. itself, represented by only *Gr. acutus*, occupies the most positive position on RW1. This taxon (known only from a skull that was lost during the Second World War) had a highly gracile cranium, with one of the proportionally longest rostra of any metriorhynchid, suggestive of a more specialist teuthophagous–piscivorous lifestyle.

Finally, during the Tithonian–Berriasian, the overall pattern of skull morphospace occupation is not
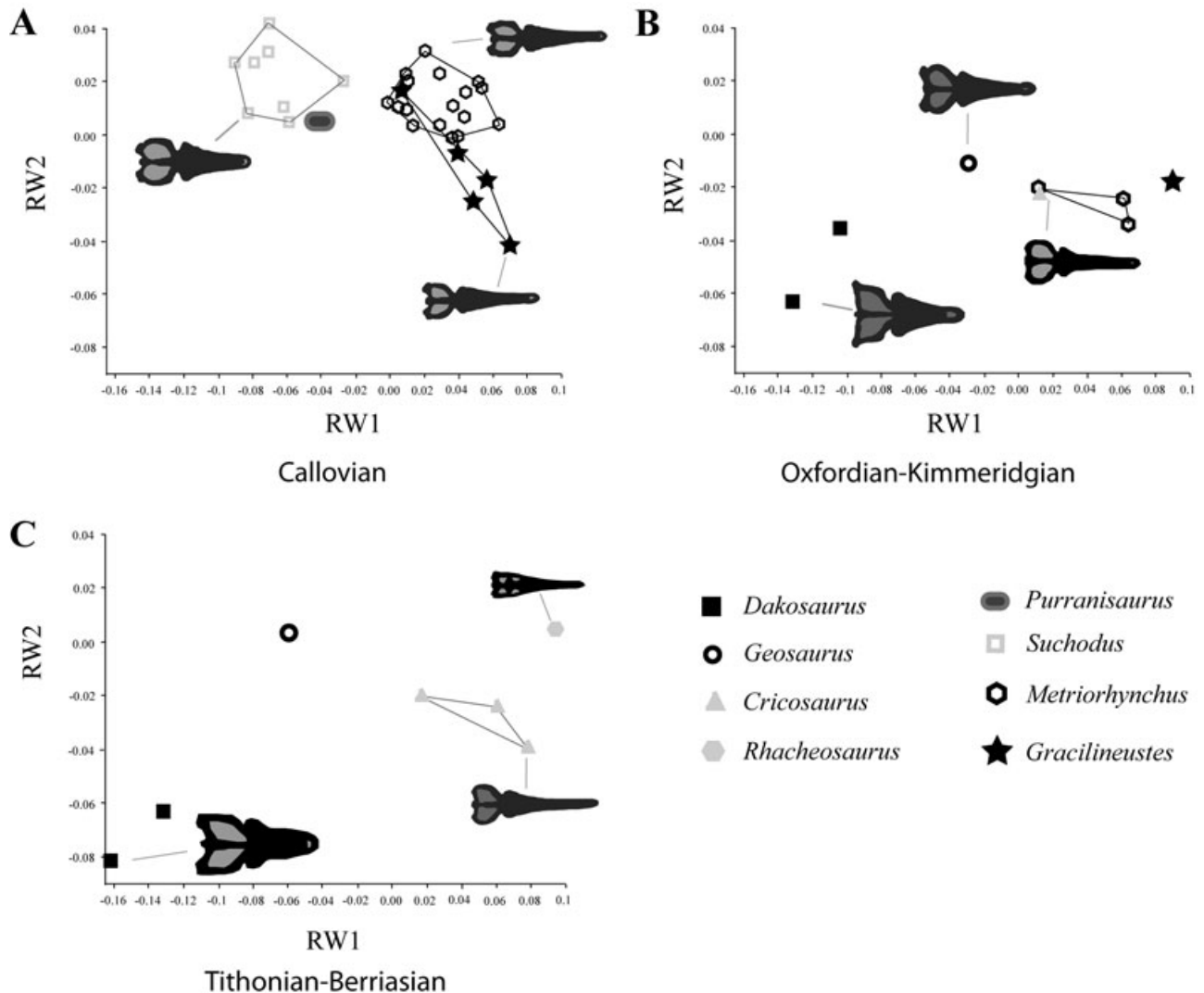
Figure 12. Relative warps morphospace subdivided into three time bins: (A) Callovian; (B) Oxfordian–Kimmeridgian; (C) Tithonian–Berriasian.

very different from the previous time bin, although there is a change in generic composition. *Dakosaurus andiniensis* extends metriorhynchid morphospace into a highly negative RW1 and RW2 region, as this genus evolved a brevirostrine–oreinirostral cranium, with larger prefrontals than other taxa. *Geosaurus* continued to occupy the same morphospace region as *Suchodus* did during the Callovian. Within Metriorhynchinae at the end of the Kimmeridgian, both *Metriorhynchus* and *Gracilineustes* gen. nov. became extinct. Interestingly, the morphospace occupied by the *Cricosaurus* skull is almost identical with that of *Metriorhynchus* in the Oxfordian–Kimmeridgian, whereas *Rhacheosaurus* occupies the highly positive RW1 region that *Gracilineustes* gen. nov. previously held. However, instead of occupying a negative RW2 region, *Rhacheosaurus* occupies a positive region,

being the first metriorhynchine to do so since *Metriorhynchus* in the Callovian. This suggests that although longirostry evolved in both *Rhacheosaurus* and *Gracilineustes* gen. nov., the changes were achieved independently, and in very different ways morphologically.

The continuing divergence in morphospace occupation throughout the Jurassic and into the Cretaceous leaves the mean shape unoccupied (in contrast to the Callovian), thereby displaying a classic radiation pattern. All four Tithonian–Berriasian genera occupy different regions of morphospace without any overlap, a continuation of the trend observed since the Oxfordian. Therefore, after the Callovian, the high generic diversity of metriorhynchids is maintained by their evolution of distinct cranial morphologies.

DISPARITY OF METRIORHYNCHOIDEA: DISCRETE CHARACTER APPROACH

Geometric morphometrics enables the construction of a morphospace, but the above analysis only takes into account the shape of the skull in dorsal aspect, and only in the sample currently available. Although these shape differences have long been used to define metriorhynchoid taxa, and appear to be closely tied to different dietary and ecological strategies, they are a limited source of data for examining the larger macroevolutionary patterns in the group. An alternative data set for investigating such patterns is the set of discrete characters used in the phylogenetic analysis, as these have the advantage of sampling the entire skeleton, and include important variation that is difficult to quantify in geometric morphometrics (which is a largely phenetic form of comparison). Discrete cladistic characters can be used to define a morphospace and calculate metrics of disparity, which quantify morphological diversity, and the overall range of body plan variability (Foote, 1994; Wills, Briggs & Fortey, 1994; Erwin, 2007). These metrics, which can be tracked over time or compared between different taxonomic groups, can reveal and describe macroevolutionary changes such as the evolution of new body plans and shifts in ecological structure (Foote, 1993, 1996, 1997; Wesley-Hunt, 2005; Adamowicz, Purvis & Wills, 2008; Brusatte *et al.*, 2008a, b).

METHOD

The metriorhynchoid cladistic data set from Young & Andrade (2009) was used to derive a Euclidean distance matrix, which was then subjected to principal coordinates analysis (PCO), a multivariate approach that combines information from the entire data set (166 characters) into a smaller and more manageable set of variables (37 axes). As with many other phylogenetic analyses on vertebrates, there is a bias towards cranial characters, with 76.5% of the 166 characters coding cranial variation, and 23.5% representing postcranial variation. In addition, 47.4% of the matrix is missing data. Principal coordinates, as opposed to principal components, or other methods, is well-suited to disparity analyses because it can better handle inapplicable characters and missing data (Wills *et al.*, 1994; Lupia, 1999; Stockmeyer Lofgren, Plotnick & Wagner, 2003). The PCO analysis served two purposes: (1) to ordinate taxa into a taxon-defined empirical (*sensu* McGhee, 1999) morphospace (Fig. 13), and (2) to produce a set of variables (axes) that could be subjected to disparity analysis.

Disparity metrics were calculated using the first 28 PCO axes, which encompass 85% of the cumulative variance. Four disparity metrics were calculated for several taxonomic and temporal bins: the sum and product of the ranges and variances on the 28 axes (Wills *et al.*, 1994). Each metric gives an indication of the volume of morphospace occupied. However, range measures quantify the entire spread of morphological variation, or the 'absolute extent of body plan variety' (Wills, 1998: 471), whereas variance measures indicate the average dissimilarity among forms. The range measures are more sensitive to sample size, whereas the variance measures are more sensitive to taxonomic practice, but are robustly insensitive to sample size (Wills *et al.*, 1994). All metrics were calculated using the software program Rare (Wills, 1998), and multiplicative measures were normalized by taking the 28th root. The statistical significance between the disparity of different bins was assessed in two ways: by the overlap or non-overlap of 95% bootstrap confidence intervals (calculated by Rare with 1000 replications), and by the conservative NPMANOVA test.

RESULTS

Metriorhynchine and geosaurine subfamilies occupy statistically distinct areas of morphospace (Fig. 13; NPMANOVA, $P < 0.0001$, $F = 2.439$, 10 000 permutations), which is expected, as the analysis is based on cladistic characters with a phylogenetic structure. Basal metriorhynchoids do not fall within the morphospace of either subfamily, but are closer to the Metriorhynchinae. Neither subfamily is significantly more disparate than the other (Fig. 13; Table 4). In other words, neither subfamily has a significantly larger morphospace, which is borne out by visual examination of Figure 13. Interestingly, both subfamilies seem to have a morphospace of approximately the same size, shape, and orientation. Thus, the overall metriorhynchoid morphospace is not dominated by the contribution of a single subfamily [e.g. compare the morphospace occupation of Crurotarsi with Avemetatarsalia in Brusatte *et al.* (2008a, b), where either one clade or the other dominates, depending on time interval].

Range- and variance-based measures give a slightly different picture of metriorhynchoid disparity through time (Table 5), most likely as a result of the strong sample-size biases of the range metrics. The variance metrics exhibit a relatively static profile (Fig. 14), and no differences between time intervals are significant. The sum of variances peaks in the Callovian, whereas the product of variances peaks in the Tithonian (Table 5). On the other hand, the range metrics show a more oscillatory trend. Both the sum and the product of ranges are lowest in the Bathonian, with a statistically significant increase in the Callovian. Thus, metriorhynchoid morphospace expanded in the Callovian, as basal metriorhynchoids became extinct, and
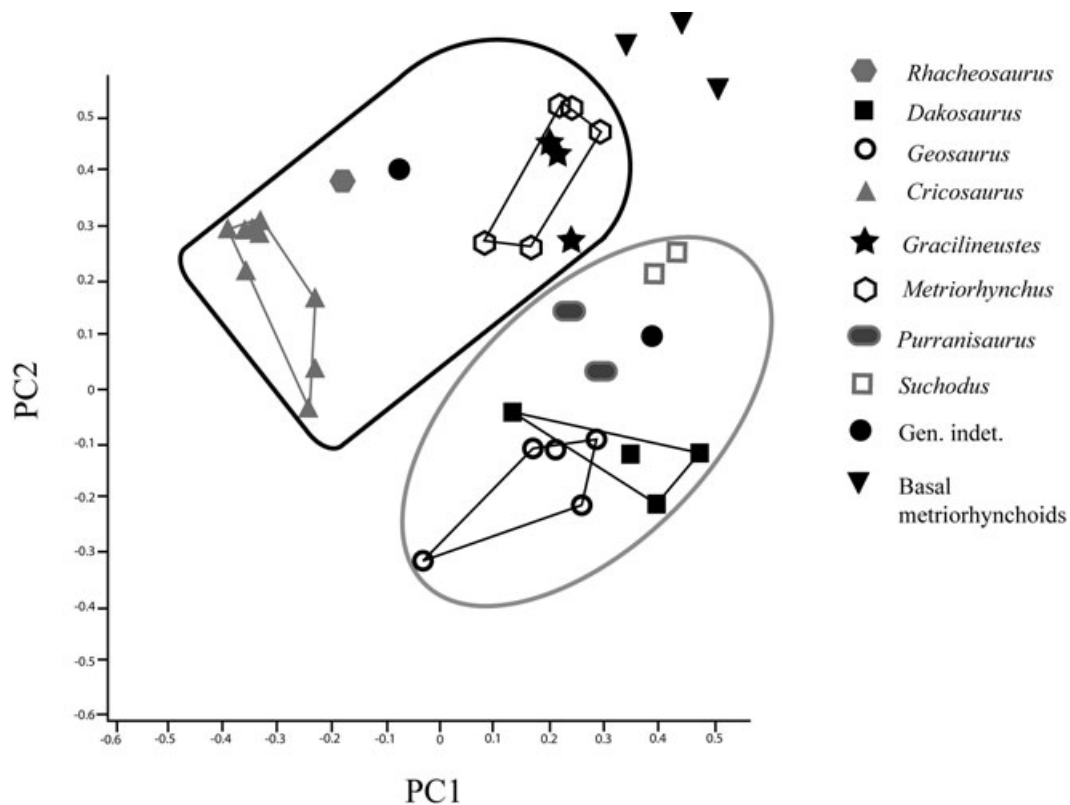
Figure 13. Principle coordinates cladistic character morphospace, delimited by the first two axes. The black ellipse contains the metriorhynchine taxa, whereas the grey ellipse contains the Geosaurinae.

Table 4. Morphological disparity for metriorhynchid subgroups: Metriorhynchinae ($N = 20$) and Geosaurinae ($N = 17$)

Metric	Taxon	Value	95% error bars
Sum of ranges:	Metriorhynchinae	174.09148	159.00455, 187.85016
	Geosaurinae	162.63872	145.09767, 176.32956
Product of ranges:	Metriorhynchinae	6.08770	5.34061, 6.45995
	Geosaurinae	5.55424	4.72824, 5.88132
Sum of variances:	Metriorhynchinae	104.40413	93.65547, 113.20937
	Geosaurinae	103.24130	89.56734, 115.88481
Product of variances:	Metriorhynchinae	3.12786	2.58062, 3.34123
	Geosaurinae	2.77056	2.24972, 2.94645

Product measures are normalized by taking the 28th root. None of the differences are significant, judging by the overlap of 95% bootstrap confidence intervals.

both subfamilies radiated. At this time, each subfamily contained at least two genera, and was geographically widespread, with metriorhynchines present across Europe and geosaurines distributed globally. A slight decrease in disparity is seen in the Oxfordian and Kimmeridgian, but this is likely to be the result of small sample size, as complete specimens are poorly known from this interval. The range metrics reach a peak in the Tithonian, which is the time of cosmopolitan genera such as *Cricosaurus* and *Dakosaurus*, and

then crash in the Early Cretaceous. The difference between the Tithonian peak and the Early Cretaceous dip is marginally significant (Fig. 14).

In general, the range metrics show a similar temporal profile to the observed taxonomic diversity of metriorhynchoids over time (Fig. 9). This may merely be the result of sampling biases, as range-based metrics are sensitive to sample size (Wills *et al.*, 1994). However, rarefaction curves show that the relative pattern of the sum of ranges is consistent

Table 5. Morphological disparity for Metriorhynchoidea and the two subfamilies over time

Age	Sum range	Product range	Sum variance	Product variance
All Metriorhynchoidea				
Bajocian–Bathonian	72.91314	2.73167	87.11022	1.63837
Callovian	128.20621	4.32523	112.91052	2.54768
Oxfordian	110.51837	4.01625	94.55165	2.56901
Kimmeridgian	119.96784	4.30784	94.08383	2.64308
Tithonian	150.69921	5.32735	103.95687	2.86930
Early Cretaceous	97.13214	3.36568	99.28333	2.02216
Metriorhynchinae				
Middle Jurassic	67.89794	2.14075	73.79968	1.07373
Oxfordian–Kimmeridgian	116.09469	4.26819	87.12955	2.56762
Tithonian	94.15218	3.41176	71.33376	1.79166
Early Cretaceous	50.44655	1.70538	65.75679	0.83700
Geosaurinae				
Middle Jurassic	92.17334	3.17688	92.14514	1.81858
Oxfordian–Kimmeridgian	84.58560	2.99263	70.47027	1.63646
Tithonian	93.44251	3.34668	87.20547	2.03299
Early Cretaceous	62.25460	1.46536	114.26548	1.07365

Product measures are normalized by taking the 28th root. Few of the differences are significant, judging by the overlap of the 95% bootstrap confidence intervals (see Fig. 14). The small sample sizes for the Early Cretaceous in both subgroups renders the values ambiguous.

down to a sample size of three (Fig. 15). That is, even with a small sample size, disparity is lowest in the Bathonian, spikes in the Callovian, peaks in the Tithonian, and crashes in the Early Cretaceous. Thus, depending on the metric used, metriorhynchoid disparity either shows a similar trend to diversity (range metrics) or is static through time, thus showing no clear relation to diversity (variance metrics). In the first case, peak disparity occurs in concert with peak diversity, whereas in the latter case, peak disparity (or near peak disparity) is seen early in the history of the clade, before the period of greatest taxonomic diversity. This pattern is consistent with an early onset of high disparity relative to diversity, which has often been noted in major taxonomic groups (Foote, 1994; Wills *et al.*, 1994; Wagner, 1997; Erwin, 2007).

Temporal trends in the two subfamilies are less clear, largely because of the small sample size in some time bins. This is especially true of Geosaurinae, as demonstrated by the large error bars for both range and variance metrics (Fig. 14). Variance measures for Metriorhynchinae show a generally static trend, similar to that of the entire clade of Metriorhynchoidea. However, range measures show a significant increase in metriorhynchine disparity from the Bathonian–Callovian to a peak in the Oxfordian–Kimmeridgian, a slight decrease in the Tithonian, and then a crash in the Early Cretaceous that is significant relative to the peak levels of the clade.

Finally, the PCO analysis enables the construction of a morphospace that is based on a more complete data set than the relative warps morphospace discussed above (Fig. 13). The PCO morphospace shows that the basal metriorhynchoids, metriorhynchines, and geosaurines all occupy distinct and non-overlapping regions. The basal genera of both subfamilies are closer in position than the derived genera (*Cricosaurus*, *Rhacheosaurus*, *Geosaurus*, and *Dakosaurus*), a pattern which becomes more pronounced through time. This pattern is repeated within each subfamily, as the derived genera become successively positioned in more negative regions of the two PC axes. In metriorhynchines, *Cricosaurus* 'moves' into the negative region of PC1, although in PC2 they range from 0.3 to −0.05, whereas the geosaurines *Geosaurus* and *Dakosaurus* migrate to the negative region of PC2 [*Geosaurus lapparenti* (Debelmas & Strannoloubsky, 1957) is the only negative PC1 and PC2 geosaurine].

Comparison between the dorsal-aspect cranial RWA morphospace and the whole-body cladistic character PCO morphospace shows some striking parallels. Both metriorhynchid subfamilies occupy distinct, and non-overlapping, areas of both morphospaces, and throughout the Jurassic and into the Cretaceous, the morphospace occupation of the subfamilies becomes increasingly distinct, with each genus occupying their own discrete region (Fig. 16). However, there are some important distinctions: in the RWA morphospace ordination, *Dakosaurus* occupies a region very distinct from all other metriorhynchoids; basal metriorhynchoids fall within the region also occupied by metriorhynchines; while the Late Jurassic
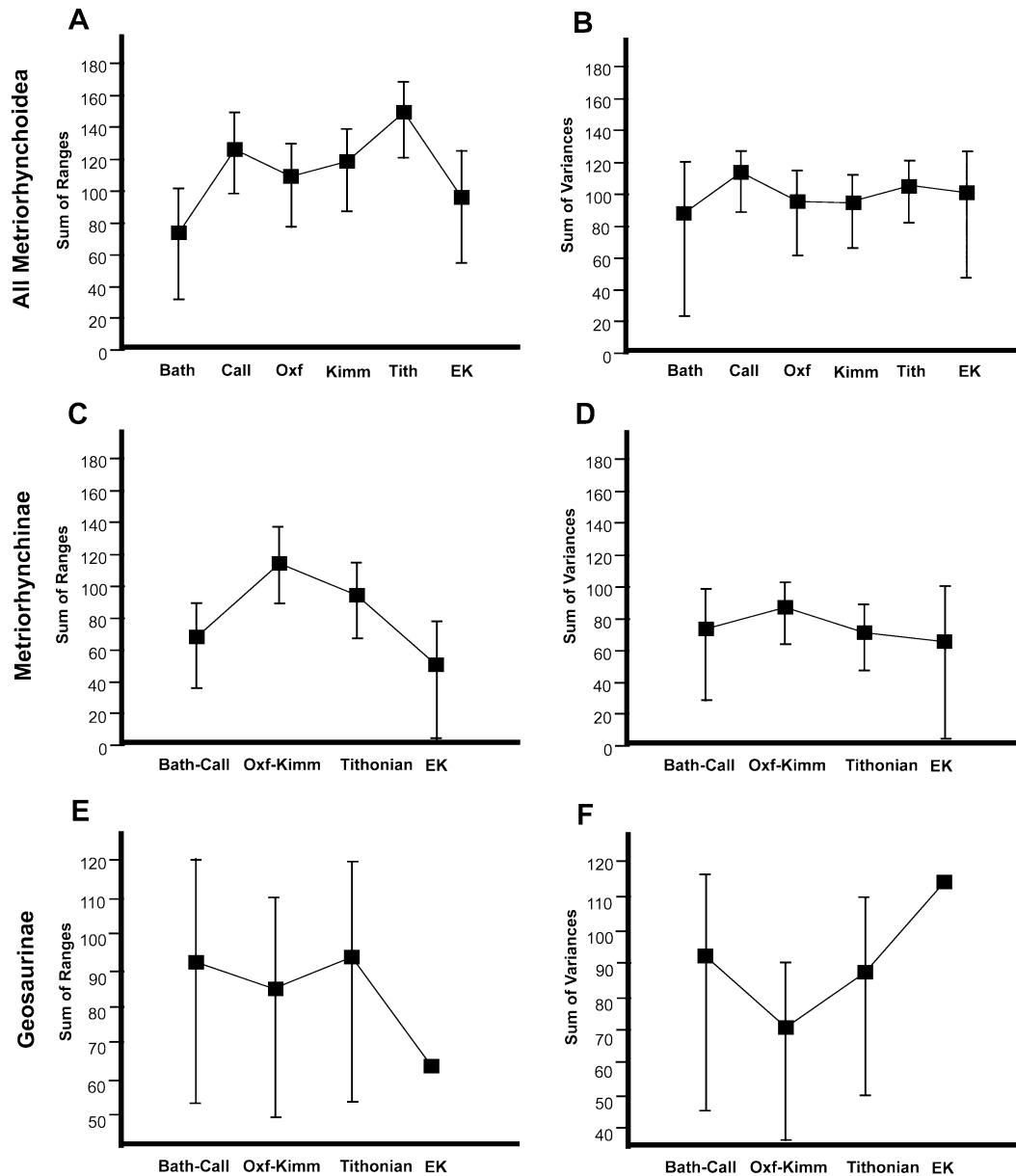
Figure 14. The disparity (morphological diversity) of metriorhynchoids through time, based on two metrics (sum of ranges and sum of variances, derived from a PCO analysis; see text for details). A, B, disparity of all metriorhynchoids through time. C, D, disparity of metriorhynchines through time. E, F, disparity of geosaurines through time. Squares represent the disparity metric and error bars denote 95% confidence intervals, based on bootstrapping. There are no error bars for the Early Cretaceous geosaurines because of the small sample size ($N = 2$).

specimens of *Metriorhynchus* and Tithonian specimens of *Cricosaurus* occupy essentially the same region of dorsal craniofacial form space. None of these are paralleled in the cladistic character space. *Dakosaurus* and *Geosaurus* occupy very similar regions of morphospace, *Cricosaurus* is very distinct even early in its evolution, and the basal metriorhynchoids do not overlap with any metriorhynchids (although in position they are closer to metriorhynchines).

CRANIAL BIOMECHANICS: FINITE ELEMENT ANALYSIS

Fundamental to the tenets of bone modelling, and remodelling, is that the skeleton is a dynamic structure capable of modifying both its shape (form) and its biology in response to applied loads (e.g. Moore, 1965; Jones *et al.*, 1977; Corruccini & Beecher, 1982; Lieberman, 1997; Rayfield, Jasinoski & Young, 2007a; and
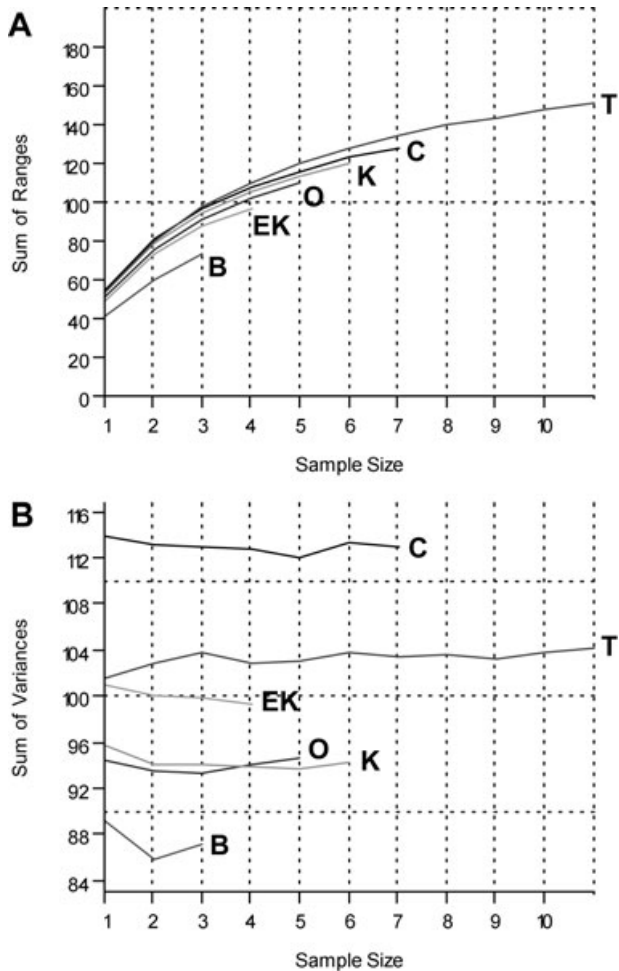
Figure 15. Rarefaction plots for two metrics (sum of ranges and sum of variances) that measure metriorhynchoid disparity (all taxa) throughout time. A, sum of ranges. B, sum of variances. The sum of variances shows little obvious relationship with sample size, in keeping with the theoretical robustness of the measure to differences in sample size (see Wills *et al.*, 1994). The sum of ranges curve suggests that, although this measure is highly sensitive to sample size (Wills *et al.*, 1994), the patterns for metriorhynchoids are robust. Notably, the relative ordering of disparity measures from high (Tithonian) to low (Bathonian) is seen at all sample sizes, from $N = 3$ upwards. Abbreviations: B, Bathonian; C, Callovian; EK, Early Cretaceous; K, Kimmeridgian; O, Oxfordian; T, Tithonian.

references therein). Although the principle of bone remodelling is accepted, the mechanism by which this occurs and the exact signature it leaves upon the skeleton is less understood (e.g. deviations from Wolff's Law; Meers, 2002). Nevertheless, the process of remodelling induces adaptations to applied loads at various structural levels within bone, whether it is at the level of overall morphology or microstructure (see Currey,

2002). As such, within bony tissue there is a signature of loading history, or function. As the skeleton experiences a variety of loads during different behaviours, we might expect there to be certain trade-offs with regards to the resistance of some loading compared with others. Biomechanical modelling, using finite element analysis (FEA), has enabled biomechanical hypotheses related to feeding and locomotion to be investigated within palaeontology, in both an inductive and deductive manner (for a review see Rayfield, 2007). Finite element analysis is a computational technique used to assess the mechanical behaviour of complex geometries (structures, fluid dynamics, etc.), and is implemented in fields as diverse as aerospace design, orthopaedics, and dentistry.

PREVIOUS FEA STUDIES

Recent comparative analyses on the rostra of extant crocodylians and theropod dinosaurs have presented quantitative insights into the evolution of cranial morphology in relation to feeding behaviour (Pierce *et al.*, 2008; Rayfield *et al.*, 2007b; Rayfield & Milner, 2008). Using FEA as a way to test hypotheses of biomechanical function, the biomechanical performance of FEA models with and without the secondary palate for platyrostral taxa (e.g. *Alligator*), tubular snouted taxa (e.g. *Gavialis*), and oreinirostral taxa (e.g. theropods), were compared. These FEA models suggest that general snout morphology influences the biomechanical impact that the loss of the secondary palate has upon the cranium. In the alligator, a secondary palate resists torsional stresses, but does little to lower bending stresses, whereas the snout in the gavial had a reduced susceptibility to bending stress. Interestingly, in the theropod snout, the secondary palate reduces both torsional and bending stresses. This supports the results by McHenry *et al.* (2006), which suggested that the more oreinirostral extant crocodylians have a better overall mechanical performance in orthal and twist feeding bites than platyrostral species.

Using the FEA results of these previous studies as a proximate guide to cranial function, the metriorhynchines possess a tubular snout much like the extant *Gavialis*, suggesting that they too were better adapted to resist bending forces than torsional ones. Cranial remains attributed to *Geosaurus* and *Dakosaurus* do not fall neatly within any of the platyrostral, tubular, or oreinirotral categories (with the exception of *D. andiniensis*, where the oreinirostral theropod skull is a good analogue). Their crania are broad, but are not platyrostral as in Neosuchia. However, using the *Alligator* FEA model as a guide, the *Geosaurus* and *Dakosaurus* skulls are better adapted to withstanding torsional stresses than those of the tubular-snouted
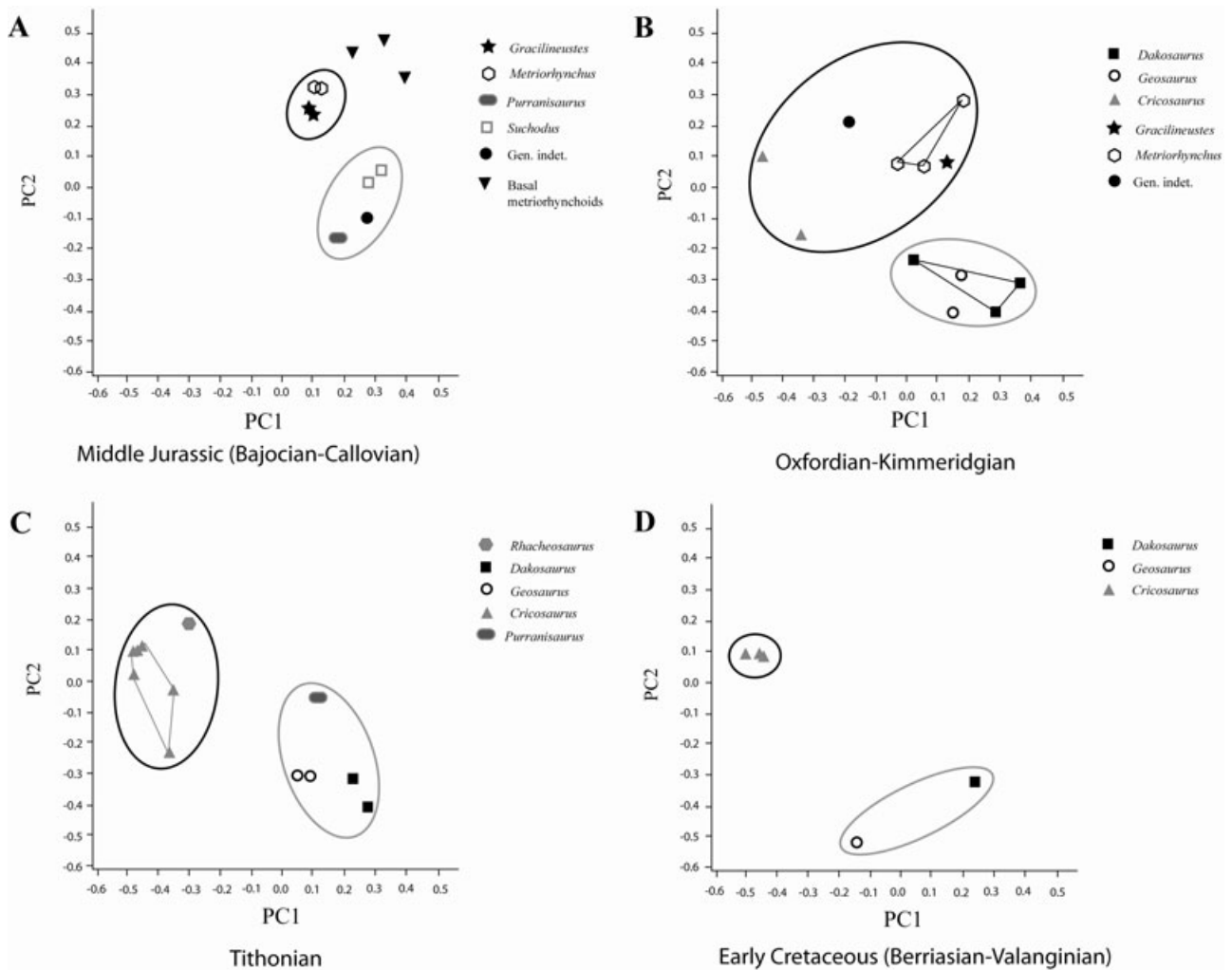
Figure 16. Principle coordinates morphospace subdivided into four time bins: (A) Middle Jurassic (Bajocian–Callovian); (B) Oxfordian–Kimmeridgian; (C) Tithonian; (D) Early Cretaceous (Berriasian–Valanginian). The black ellipse contains the metriorhynchine taxa, whereas the grey ellipse contains the Geosaurinae.

species (although perhaps not to the same extent as extant broad-snouted forms). This would therefore suggest that both *Geosaurus* and *Dakosaurus* could occasionally adopt the 'twist-and-rip' method employed by large extant crocodilians, and would be able to feed upon large-bodied prey (crania attributed to *Dakosaurus* are both broader and have a thicker cross section of bone than any attributed to *Geosaurus*).

The evolution of the secondary palate in Crocodylia has largely been explored in relation to the platyrostral condition and resistance to applied loads (e.g. Langston, 1973; Busbey, 1995; Daniel & McHenry, 2001; McHenry *et al.*, 2006; Rayfield *et al.*, 2007b; Turner & Buckley, 2008), and, in particular, the structural adaptations to rotational feeding and applied torque (torsional and rotational bending stresses). Recent 3D FEA results (McHenry *et al.*, 2006; Rayfield *et al.*, 2007b; Rayfield & Milner, 2008) demon-

strate that platyrostry is not the 'best cranial design' for rotational feeding. As discussed by McHenry *et al.* (2006), platyrostry may be a trade-off between (1) hydrodynamic efficiency, as taller skulls experience greater drag during lateral head sweeps, making catching small, agile prey difficult, and (2) enabling large terrestrial prey (coupled with large body size as in *Cr. niloticus*) to be incorporated into the diet. A recent 2D FEA study by Pierce *et al.* (2008) on extant crocodylians supports this hypothesis. Therefore, the mesorostrine platyrostral skull is well suited to generalist feeding on small to large-bodied animals, in both the water and at the waterside. Thus, this supports Witmer (1997), who suggested that platyrostral rostra are predisposed to high torsional stresses during rotational feeding. Consequently, the evolution of a brevirostrine–oreinirostral skull within *Dakosaurus* (i.e. *D. andiniensis*) is indicative of torsional

feeding behaviour, and that it was no longer predating upon small, agile aquatic prey.

During a bite, the tensile strain peaks at the posterior margin of the palate (Daniel & McHenry, 2001). As shown by *in vivo* (e.g. Buckland-Wright, 1978; Jaslow, 1990; Jaslow & Biewner, 1995; Herring & Teng, 2000) and FEA studies (Rayfield, 2004, 2005a; Moazen *et al.*, 2009), sutural contacts and the soft tissues therein can act as shock absorbers, dissipating potentially damaging tensile strain. In crocodylians where the secondary palate is most developed, i.e. when the choana is entirely enclosed by the pterygoids (Eusuchia and *Mahajangasuchus*; Turner & Buckley, 2008), the extensive palatine–pterygoid contact would have acted as a shock-absorber, further increasing the mechanical strength of the palate. No metriorhynchine or basal geosaurine (i.e. *Suchodus*) displays a eusuchian-style palate morphology. However, the palate of derived geosaurines is very poorly known, with the only described palate being that of the genus *Purranisaurus* (no complete palates are known for *Geosaurus* or *Dakosaurus*). Rusconi (1948, 1955) illustrates *Purranisaurus potens* Rusconi, 1948 (currently under redescription; Pol & Gasparini, 2007) as possessing a choana positioned posterior to the anterior margin of the supratemporal fenestra in palatal view (i.e. the greatest development of the secondary palate currently known within Metriorhynchoidea), further supporting the hypothesis for a shift in this subfamily towards hypercarnivory.

METHOD

Our primary objective here was to quantitatively assess the biomechanical performance of 2D metriorhynchid crania using linear static FEA. We used the RWA digitized landmark data to construct dorsal-aspect FEA models, whereas lateral-aspect models were constructed by digitizing data from Gasparini *et al.* (2006). Although there have been relatively few 2D FEA studies undertaken within palaeontology and zoology (Rayfield, 2004, 2005a, b; Pierce *et al.*, 2008), within dentistry, their use has been demonstrated widely (e.g. Joshi *et al.*, 2001; MackAldener & Olsson, 2002; Dejak, Młotkowski & Romanowicz, 2003). If the feeding hypotheses as set previously are correct, the crania of *Dakosaurus* should be more resistant to the high stresses generated during feeding than other metriorhynchids, whereas those of *Rhacheosaurus* and *Cricosaurus* should be less resistant to extreme feeding stresses. Although the exact material properties, constraints, and loading regimes cannot be modelled with true accuracy (see Richmond *et al.*, 2005), by subjecting all FEA models to the same set of boundary conditions, here, we use FEA as a comparative tool (much like Rayfield, 2005b).

Model construction

The methodology used to create these models is similar to that of Rayfield (2004). Freeware ImageJ (http://rsb.info.nih.gov/ij) was used to capture the (x, y) co-ordinates from photographs and figures from the literature. These were imported directly into the Cosmos FEA package (v2.95, 256K; http://www.cosmosm.com). Creating the mesh within Cosmos, all planar FEA models were composed of less than 13 000 three-noded triangular elements.

Material properties

Cranial bone was the only tissue modelled, and was treated as a homogenous and isotropic material. Currey (1987) determined the Young's modulus for the *Crocodylus* frontal and prefrontal, giving a range of 5.6–7.7 GPa. However, because of the osteoporotic nature of metriorhynchid crania (e.g. *M. superciliosus*; see Hua, 1994; Hua & Buffrénil, 1996), we took the lowest value (5.6 GPa) for the Young's modulus. Nevertheless, we are aware this could be an overestimate of metriorhynchid cranial stiffness, but as we are conducting a comparative study within Metriorhynchidae, and not comparing or making inferences to extant forms, this is not an issue. As cranial bone material properties are very poorly known, we based our Poisson's ratio value upon the transverse axis, rather than the longitudinal axis, of vertebrate long bones (0.29–0.41; Reilly & Burstein, 1975). We took the lowest value so as not to overestimate the cranial strength.

Boundary conditions

The meshes were constrained by preventing translation at the quadrates (jaw joint). This prevented the FEA models rotating whilst loaded. A 1000 N bilateral bite was applied to the nodes corresponding to the anterior maxillary teeth. This arbitrary load was used as we are interested in making relative comparisons between extinct taxa. Although bite force data from extant crocodilians (e.g. *Alligator* Erickson, Lappin & Vliet, 2003; Erickson *et al.*, 2004) are available, extant crocodylian skulls vary in terms of absolute size, geometry, and muscle proportions (Endo *et al.*, 2002). Consequently, different crocodylians are likely to have very different bite forces. In order to visually compare the FEA models, von Mises stress was plotted, as it indicates regional deformation as a function of the three principal stresses σ_1, σ_2, and σ_3 (Dumont, Piccirillo & Grosse, 2005).

RESULTS

Visual inspection of the contour plots in both lateral and dorsal aspect show a clear demarcation of metriorhynchines and geosaurines (Fig. 17; results comparable to Pierce *et al.*, 2009b). Higher stresses are
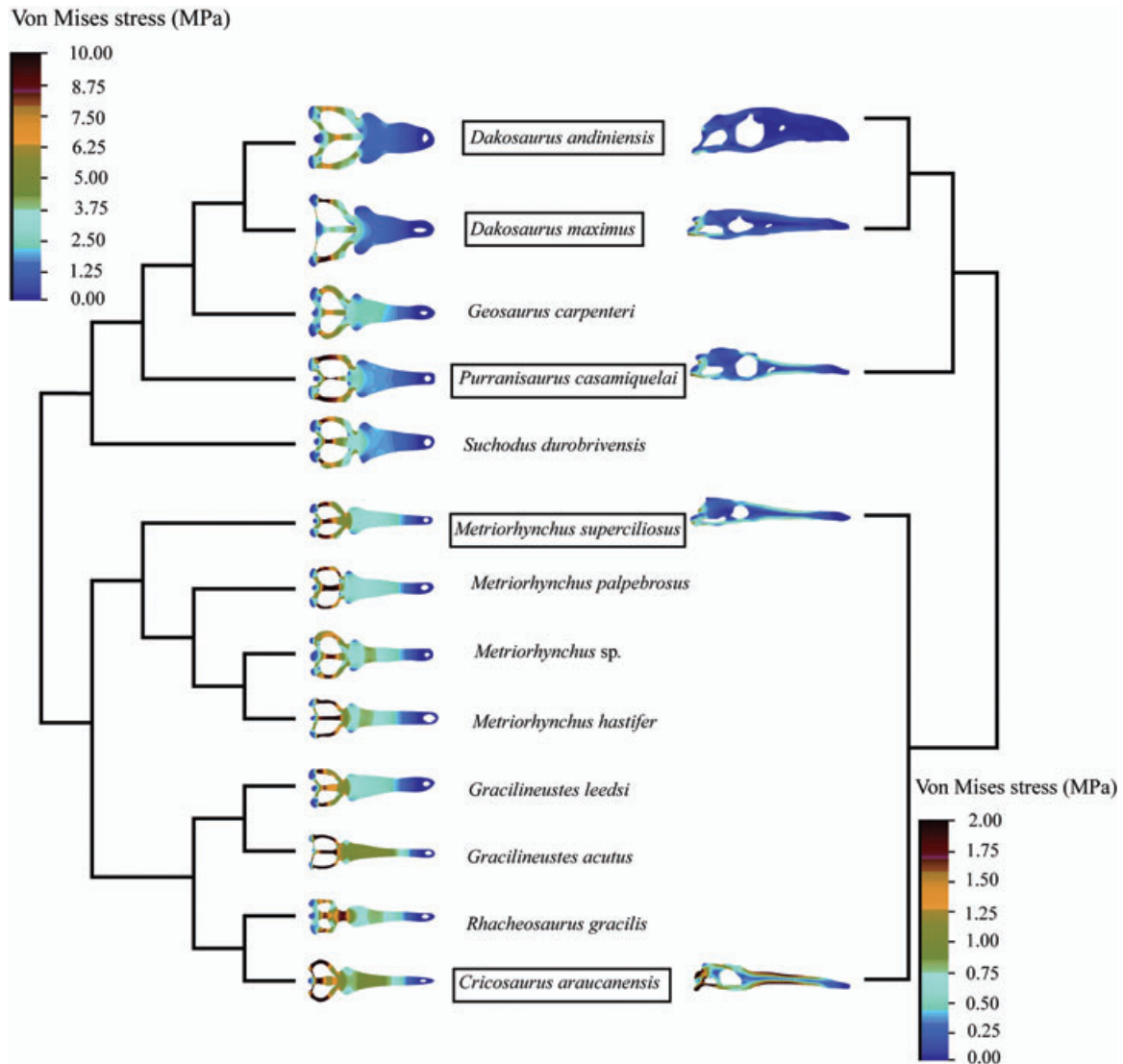
Figure 17. von Mises stress contour plots for each taxon placed within the phylogenetic context. The left-hand models are those in dorsal aspect (with the appropriate scale), whereas those on the right are the lateral-aspect models (with their own respective scale).

observed within the crania of metriorhynchines. Within the metriorhynchine snout, high stresses are observed at its posterior end (immediately in front of the orbits). Interestingly, several metriorhynchine specimens of the NHM Leeds Collection (Oxford Clay Formation, England) have been broken post-mortem in this region. Therefore, this region appears to be a zone of weakness in metriorhynchine skulls. Indeed, Hua & Buffrénil (1996) found the bone histology of this region to be highly cancellous.

In dorsal aspect, with the arbitrary values listed above, stress in the snouts of geosaurines does not exceed 2.5 MPa, whereas in Callovian metriorhynchines (*M. superciliosus* and *Gr. leedsi*), snout stresses can reach up to 3.8 MPa. In derived *Metrio-*

rhynchus species this increases to 4.4 MPa, and exceeds 5.5 MPa in *Gracilineustes* gen. nov., *Rhacheosaurus*, and *Cricosaurus*. Thus, throughout the Jurassic the metriorhynchine cranial strength decreased in three different lineages (*Metriorhynchus*, *Gracilineustes* gen. nov., and *Rhacheosaurus* + *Cricosaurus*). In derived geosaurines a different pattern is observed. The *Dakosaurus* cranial strength is clearly greater, with snout stress peaking at 1.5 MPa. *Geosaurus*, however, has higher cranial stress than any other geosaurine, with stress in the snout peaking at 3.2 MPa. Therefore, within Geosaurinae there are two trends: cranial strengthening within *Dakosaurus*, and a comparative weakening in *Geosaurus*.

In lateral view, we are limited to five taxa, but the same general trends that are evident in dorsal view are replicated. Basal metriorhynchines and geosaurines have similar cranial stresses, whereas *Dakosaurus* exhibits cranial strengthening and *Cricosaurus* exhibits cranial weakening.

The localized decrease in stress is observed in dorsal view at the prefrontals. Basal metriorhynchines and geosaurines have moderately expanded prefrontals, which correspond with a moderate localized decrease in von Mises stress. In both *Rhacheosaurus* and *Cricosaurus*, the decrease in prefrontal lateral expansion corresponds with an increase in snout stress, whereas the opposite is true in *Dakosaurus*. It would appear that the enlargement of the prefrontal and its expansion over the orbits acted as a stress sink, lowering cranial stress and increasing strength in front of the orbits. In those metriorhynchids that are hypothesized to be more piscivorous, this expansion is less-developed, whereas in the hypercarnivore *Dakosaurus* it is at its greatest development. Analogous, but less extensive, lateral expansions of the prefrontals are observed in mosasaurs and basal ichthyosaurs (i.e. *Utatsusaurus*; Maisch & Matzke, 2000), and by the frontals in polycotylid plesiosaurs, presumably fulfilling a similar function. Similarly, terrestrial sebecosuchian crocodilians (Colbert, 1946), large theropod dinosaurs (Brusatte & Sereno, 2008), and large carnivorous 'rauisuchian' crurotarsans (Brusatte, 2007), also exhibit a thickened expansion in this region.

Interestingly, the streamlining of the cranium and the increase in the size of supratemporal fossae do not seem to be linked to an increase in cranial strength. Compared with *M. superciliosus*, the derived species of *Metriorhynchus* (*M. hastifer* and *Metriorhynchus* sp.) have a weaker cranium; the same pattern is observed within *Gracilineustes* gen. nov. *Geosaurus* and *Cricosaurus* both have weaker crania than more basal forms in their respective subfamilies. It is only *Dakosaurus* that exhibits a stronger cranium. It could be that cranial streamlining in most metriorhynchids correlates with a shift away from feeding on large prey; however, both the dentition and increased cross-sectional thickness of cranial bone in *Geosaurus carpenteri* (Wilkinson *et al.*, 2008) would suggest that this was not the case. Further analyses (3D FEA) are required to assess if there could be a trade-off between cranial strength and streamlining in most metriorhynchids, and if it is the distinctly robust architecture of *Dakosaurus* crania that reverses this trend.

It should be noted, however, that the feeding hypothesis set out for *Geosaurus* – gouging the flesh of prey – would not require high bite forces. With teeth possessing serrated edges and a very sharp tip, the energy required to penetrate food would be signifi-cantly reduced (Freeman & Weins, 1997; Evans & Sanson, 1998). Increasing the sharpness of the tip and the edges (along with its lateromedially compressed triangular shape) increases the stress in the food item (Evans & Sanson, 2003). Therefore, it would take less energy to initiate and propagate a 'crack' in the surface of a prey item, especially one in which the prey is not brittle. As such, the bite force needed to penetrate the prey item is decreased, with muscle action being used to help propagate the 'crack' in the prey item (aided in this case by the tooth rows in *Geosaurus* being arranged as opposing blades). 'Double-bladed' (upper and lower) dentition is the optimal design to break food with a high fragmentation criterion [(food toughness/Young's Modulus)$^{0.5}$; see Lucas (2004: 103], such as vertebrate soft tissue, whereas contact between the two blades as they pass through a food particle ensures it will separate in two (Lucas, 2004: 105). An example from Lucas (2004: 113) illustrates this nicely: 'A free-running crack in rat skin has a toughness of 14–20 kJ m^{-2} (Purslow, 1983), while that cut with scissors (blade sharpness ~1.6 µm) is only ~0.59 kJ m^{-2} (Pereira *et al.*, 1997)'. With this in mind, it is not surprising that the cranial strength of *Geosaurus* is lower than that initially expected. Based upon the osteoporotic lightening of the cranial bones in *M. superciliosus* (and metriorhynchids in general), doubt was cast upon their ability to prey on large-bodied animals (Hua & Buffrénil, 1996), thus supporting the hypothesis of metriorhynchids being epipelagic stalking predators feeding on fast-moving fish and cephalopods (Hua, 1994). The stress magnitudes and distribution observed here concur with that assessment. In particular, we can conclude that teuthophagy–piscivory became more specialized within Metriorhynchinae after the Callovian, as their inability to accommodate large feeding loads suggests moving away from large- and medium-bodied prey. The hypothesis that *Dakosaurus* could tackle larger prey is also supported by our FEA results.

When comparing the patterns of FEA stress distributions with the cranial shape (morphometric) and cladistic character (disparity) morphospaces, striking parallels are observed. In the cranial shape morphospace, taxa occupying highly positive RW1 regions have the weakest crania (*Rhacheosaurus*, *Gr. acutus*, and *C. araucanensis*), whereas those that occupy the highly negative RW1 regions have the strongest crania (*Dakosaurus*); RW2 values do not exhibit such a clear trend. For geosaurines, movement from positive to negative regions of RW2, cranial strength increases. The converse is true for metriorhynchines. As mentioned above, the trend between cranial weakening and streamlining appears to be subsumed within this axis (the more negative taxa are *Dakosaurus* and *Cricosaurus*). This furthers

our observation that the evolution of *Dakosaurus* requires additional exploration.

DISCUSSION

The continuous development and refinement of techniques that can quantify morphological variation, a prerequisite in our understanding of form, has enabled the investigation of macroevolutionary questions that were hitherto difficult or impossible to address. The 'form' of an organism is here considered to be a synonym of its phenotype, and its structural/geometric morphology. Therefore, techniques that examine structural morphology (i.e. morphometrics and character-based disparity analysis) can be thought of as elucidating aspects of form. This is herein contrasted with functional morphology (or 'function'), which methodologies such as beam theory and FEA are well suited to investigate.

In any analysis of form, phylogenetic inertia must be considered. The question of whether distinct morphospace-cluster/finite-element contour plots represent the diversity/disparity of a monophyletic group, or are evidence of convergence with the clade of interest, can only be answered if a robust phylogeny has been generated a priori to undertaking morphological analyses (both structural and functional). All of our discussion regarding dietary specializations are from a 'mechanistic' and evolutionary standpoint (*sensu* Ferry-Graham, Bolnick & Wainwright, 2002), as ecological interactions, although possible to infer, are very rarely preserved in the fossil record (one notable exception is the 'death pose' of *Velociraptor* and *Protoceratops*; Kielan-Jaworowska & Barsbold, 1972). This furthers our point that form, and the controls upon it, can never be truly understood in isolation from function and phylogeny.

CONVERGENCE, COMPETITION, AND FAUNAL SUCCESSION

Although overall cranial morphology became more divergent throughout metriorhynchid evolution, convergence (character homoplasy) was rampant. There are several examples of this, from the dentition (ziphodonty in *Dakosaurus* and derived geosaurs; loss of carinae in *Purranisaurus* and *Rhacheosaurus* + *Cricosaurus*; triangular, blade-like dentition in *S. brachyrhynchus* and derived geosaurs) to the skull (as mentioned above; very thin mandibular symphysis in *Purranisaurus* and *Gracilineustes* gen. nov. + *Rhacheosaurus* + *Cricosaurus*). In the postcranium, the only example of convergence is that of the humerus given above, but postcranial elements are poorly known for many metriorhynchids, especially Geosaurinae.

The suggestion by Wilkinson *et al.* (2008) that the evolution of *Dakosaurus* was linked to the lack of medium-sized pliosaurs post-Callovian is intriguing. The crown basi-apical height of pre-Oxfordian metriorhynchids was less than 2 cm (M.T. Young, pers. observ.). However, in the lower Oxfordian, the crown basi-apical height for both *Geosaurus* and *Dakosaurus* exceeds 3 cm (i.e. a doubling in length), and the teeth became far more robust than those of other genera. By the upper Oxfordian, *Dakosaurus* teeth reached 12 cm in height [e.g. *Dakosaurus nicaeensis* (Ambayrac, 1913)]. Although there is a general lack of marine reptile fossils known from the Oxfordian (Bardet, 1994), post-Callovian medium-sized pliosaurs (3–6-m long) were lacking in the seas that metriorhynchids inhabited. By the Bathonian, the rhomaleosaurid pliosaurs had become extinct, and, until the Oxfordian, their niche was held by pliosaurid pliosaurs (*sensu* Smith & Dyke, 2008). From then onwards, metriorhynchids held the medium-sized marine carnivore niche, until their extinction. Specimens referred to Leptocleidoidea (a clade of smaller-bodied pliosauroids; *sensu* Druckenmiller & Russell, 2008; Smith & Dyke, 2008) are currently only known after the extinction of the metriorhynchids (i.e. *Leptocleidus*; Cruikshank, 1997).

All of the different analyses indicate that during the Oxfordian there was a shift in metriorhynchid evolution. From the phylogenetic analysis, *Dakosaurus*, *Geosaurus*, *Cricosaurus*, and *Rhacheosaurus* (by extension of its ghost range) all evolved, each demonstrating extensive adaptations to more specialist feeding, and increasing marine specializations, than basal metriorhynchids. The relative warp morphospace indicates that early in the evolution of these genera there was divergence in craniofacial form, whereas FEA demonstrates that each of these forms possessed distinctive distributions of (and by extension, reaction to) stress from mechanical loading. The cladistic character PCO morphospace similarly visualizes the divergence between the derived metriorhynchines (*Cricosaurus* + *Rhacheosaurus*) and the more basal taxa. The phylogenetically corrected diversity curve shows a very modest increase in the lower Oxfordian, and then prolonged stasis until the lower Tithonian. However, the PCO disparity metrics show that there is no overall increase in morphospace size during the Oxfordian. Two factors may be responsible for the diversity–disparity patterns. Firstly, metriorhynchid sampling is very poor for the Oxfordian. Here, we have not corrected disparity for missing portions of metriorhynchid evolution (such as those implied by ghost ranges and range extensions). However, note that the extinction of *Suchodus* minimizes the impact that the radiation of derived metriorhynchids has on diversity (in terms of species

number) and disparity measures. Secondly, this was only the beginning of the radiation. The more biologically interpretable event, the progressive dispersion into morphofunctionally non-overlapping 'functional spaces', did not occur until the lower Tithonian.

With the evolution of the four derived genera (*Rhacheosaurus*, *Cricosaurus*, *Geosaurus*, and *Dakosaurus*), there are several faunal successions (i.e. extinction of the basal endemic genera). During the lower Oxfordian there is a shift in Europe between a *Suchodus* fauna to a *Geosaurus* and *Dakosaurus* fauna. By the middle Oxfordian the only European geosaurine fossils are attributable to *Geosaurus* and *Dakosaurus* (M.T. Young, pers. observ.). This raises the question of what impact the evolution of both *Geosaurus* and *Dakosaurus* had upon the European marine reptile fauna. They first appear after both medium-sized pliosaurs and *Suchodus* specimens are no longer found (in the *cordatum* ammonite zone; M.T. Young, pers. observ.). However, whether their evolution towards a high-order carnivore morphology was triggered by niche availability (opportunism) or by out-competing the pliosaurs and *Suchodus*, or if this observed pattern is merely the result of taphonomic biases, cannot be currently answered. However, in Western Europe there was a ~5–7 °C sea-surface temperature drop from the late Callovian to the early Oxfordian (see Dromat *et al.*, 2003).

The genus *Purranisaurus*, endemic to South America (Chile and Argentina), survived for longer than the endemic European geosaurines (lower Tithonian). However, in the upper Tithonian, the only geosaurines in the geographic region were *Dakosaurus*. Whether there was co-existence between *Purranisaurus* and *Dakosaurus* will require further discoveries.

The metriorhynchine faunal succession in Europe occurs later than that of the geosaurines. The metriorhynchine genera of Europe (*Metriorhynchus* and *Gracilineustes* gen. nov.) were endemic, based upon current knowledge (M.T. Young, unpubl. data), although so far, no other Jurassic–Cretaceous marine basin has been found with an endemic metriorhynchine fauna (in contrast with that of the geosaurines). The oldest *Cricosaurus* fossils are known from the Middle Oxfordian of Cuba, but there is no evidence of more derived metriorhynchines in Europe until the end of the Kimmeridgian [*Cricosaurus suevicus* (Fraas, 1901) from Nusplingen; Fraas, 1901, 1902]. Up until the end of the Kimmeridgian in Europe, there are still fossil remains of both *Metriorhynchus* and *Gracilineustes* gen. nov., but in the lower Tithonian both genera are absent. The morphometric results show that *Metriorhynchus* and *Cricosaurus* both occupied essentially the same region of skull morphospace, as did *Gracilineustes* gen. nov. and *Rhacheosaurus*. With the more extensive marine and piscivorous adaptations of *Cricosaurus* and *Rhacheosaurus*, it is possible that the dramatic shift to a fauna centred on these genera from one dominated by *Metriorhynchus* and *Gracilineustes* gen. nov. was driven by competition, rather than by the opportunistic filling of vacant niches. However, there is still a lack of fossils in key ammonite zones to rigorously assess this hypothesis.

As the Oxfordian was a period of geographic, taxonomic, and morphological expansion for the metriorhynchids, it is curious that they were absent from the Sundance Sea (Sundance Formation) of North America. Most marine reptiles from this age are known from the Redwater Shale Member (lower Oxfordian), which was deposited during a shallow, open-shelf environment (Wahl, Ross & Massare, 2007). The fauna is ichthyosaur dominated, with two species of cryptocleidoid plesiosaurs and the giant pliosaur *Megalneusaurus* (Wahl *et al.*, 2007). As this represents the last of the marine transgressions forming the 'Sundance Sea', it is possible that the geographic range of metriorhynchids never expanded there, until after the transgression, but basal metriorhynchoids from the upper Aalenian–lower Bajocian of Oregon would suggest this to be unlikely (Stricker & Taylor, 1989; E. Wilberg, pers. comm., 2008).

One final note regards the Solnhofen limestones of Germany, and the strata proceeding and succeeding this unit (the *Beckeri* and *Hybonotum* ammonite zones; latest Kimmeridgian and earliest Tithonian). The Solnhofen Sea was shallow and hypersaline, lacked pliosaurs and plesiosaurs, and was home to only small ichthyosaurs (Bardet & Fernández, 2000). The apex predator of this sea was *Dakosaurus maximus* (Plieninger, 1846), and all marine reptiles of 2 m in length or more were metriorhynchids. This is currently the only known metriorhynchid-dominated marine fauna. The deeper Kimmeridge Clay Sea, which covered England at the same time, was not only dominated by pliosaurs and plesiosaurs, but also had larger metriorhynchids [with the skull of *Dakosaurus manselii* (Hulke, 1870) being at least 1.1 m in length] (Taylor & Benton, 1986; Taylor & Cruickshank, 1993; Wilkinson *et al.*, 2008). This demonstrates that metriorhynchids were an important clade of Mesozoic marine reptiles, the neglect of which in many studies has hampered our understanding of the ecology and evolution of marine reptile faunas.

METRIORHYNCHOID EXTINCTION

Metriorhynchoidea, along with their sister group, the Teleosauridae, appear to have become extinct at the end of the Valanginian. The causes of this extinction are currently unknown; however, the impact of marine transgressive-regressive phases on metriorhynchoid evolution must be mentioned. Global sea

levels were at their highest in the Jurassic, during the lower Tithonian (Hallam, 1988, 2001), which coincided with the peak of metriorhynchid species diversity, the peak in diversity of cranial form and function, and the peak in disparity. During the Tithonian, and continuing into the Early Cretaceous, global sea levels fell (Hallam, 1988, 2001), during which time metriorhynchid diversity and disparity also fell (Figs 9 and 15). Obviously, the reduction of marine outcrop area will have a decisive influence upon the discovery of new fossils, and comparing the taxic diversity curve with that of global sea levels explains some of the troughs. The decline in taxic diversity in the late Bathonian and the Oxfordian coincided with sea-level drops, suggesting that the reduction of marine outcrops is to blame. However, the Valanginian transgression (Surlyk, 1991) in Europe demonstrates how limited metriorhynchid diversity was at the end of their fossil record. Therefore, the crash in metriorhynchid diversity during the Tithonian could be explained by habitat loss (i.e. the regression of shallow epeiric seas).

Questions over rock biases aside, the continuing survival of metriorhynchids without recovery in the Cretaceous makes them a candidate for Jablonski's (2002) 'Dead Clade Walking' status. With this in mind, the change in marine ecosystem composition that occurred during the Early Cretaceous could have played a major role in their extinction. The radiation of the teleosts, and their 'replacement' of many Jurassic 'holostean'-grade fish, was suggested by Steel (1973) to have been a possible cause of the metriorhynchid extinction. The great diversification in teleosts during the Late Jurassic–Early Cretaceous was in part enabled by the mobility of the upper jaw and the subsequent adaptive radiation of feeding mechanisms (Schaeffer & Rosen, 1961). However, whether the new teleost radiation had improved the swimming efficiency of the fish, making them more difficult to catch, is unknown.

Another clade undergoing a major radiation during the latest Jurassic and early Cretaceous were the neoselachians, whereas the batoids (rays, skates, etc.) became more abundant in this period (Kriwet, 2003; Rees, 2005). Although the pre-Albian Cretaceous fossil record for sharks is poor (Underwood, 2006), teeth from the Valanginian of Poland (Rees, 2005) provide the oldest evidence for lamniforms, and the evolution of modern, large, predatory sharks. By the Barremian, lamniforms and batoids had rapidly diversified, heralding the beginning of a modern shark fauna (Rees, 2005; Underwood, 2006).

A major fall (> 50 m) in sea levels occurred during the late Valanginian–early Hautervian, which has been hypothesized as a response to the formation of polar ice-caps (see McArthur *et al.*, 2007). At the Valanginian–Hautervian boundary, the Tethys sea-surface temperatures reached a low of 11 °C (van de Schootbrugge *et al.*, 2000). As sea temperatures dropped, an influx of Boreal sea belemnoid and ammonoid cephalopods south into the Tethys resulted in a shift in the composition of cephalopod abundance, i.e. from a Duvaliidae-dominated belemnoid fauna to a Mesohibolitidae-dominated one (Janssen & Clément, 2002). Therefore, there are numerous potential causal agents involved in the extinction of metriorhynchids, ranging among habitat loss, climate change, and new biotic interactions (with newly radiating prey items and possible competitors).

CONCLUSION

Metriorhynchid crocodylians were a consistent component of the Middle Jurassic–Lower Cretaceous marine reptile faunas. They were taxonomically and morphologically diverse, evolving a range of sophisticated feeding behaviours, bizarre cranial morphologies, and extensive adaptations to pelagic life. Despite the importance of the clade to Mesozoic marine ecosystems, the evolution of form within Metriorhynchoidea has remained, until now, very poorly understood because of: (1) the lack of in-depth comparative studies; (2) an inadequate understanding of their taxonomy and palaeobiology; and (3) an absence of a rigorous global phylogenetic analysis. Recent work (Gandola *et al.*, 2006; Gasparini *et al.*, 2006; Young, 2006, 2007; Buchy *et al.*, 2007; Buchy, 2008a, b; Fernández & Gasparini, 2008; Gasparini, Paulina-Carabajal & Chong, 2008; Pierce, 2007; Pierce *et al.*, 2009a, b; Wilkinson *et al.*, 2008; Young & Andrade, 2009) has helped to rectify these issues, facilitating the analyses presented herein.

This study demonstrates the potential of the quantitative techniques now available to palaeontologists. The main conclusions from this paper are: (1) cladistic character disparity analysis, morphometrics, and biomechanics consistently subdivide metriorhynchids into the same two clades found by Young & Andrade (2009); (2) both subclades show increasing marine specializations, reaching their most extreme in *Cricosaurus*; (3) phylogenetic character optimization, morphometrics, and biomechanics support the hypotheses that *Dakosaurus* was hypercarnivorous, and that *Rhacheosaurus* and *Cricosaurus* were specialized piscivores; (4) diversity curves show that with the evolution of Metriorhynchidae, metriorhynchoid biodiversity significantly increased; (5) the high diversity of the contemporaneous Late Jurassic genera were maintained by progressively distinct cranial shapes and biomechanics; (6) the evolution of *Geosaurus*, *Dakosaurus*, and *Cricosaurus* in the Oxfordian, alongside novel morphologies, demonstrates that this is a key

age of metriorhynchid evolution; (7) all analyses demonstrate that metriorhynchids became more divergent in terms of biodiversity, form, and function up until the Jurassic–Cretaceous boundary, after which there is no evidence for recovery or further radiations.

Three key problems to our continuing understanding of metriorhynchoid evolution remain: (1) the scarcity of basal metriorhynchoid specimens; (2) the lack of complete skeletons, which would allow character complexes to be more fully dissected and trait acquisition to be better understood, and (3) the lack of in-depth comparative biomechanical analyses (e.g. 3D dynamic linear FEA, multibody dynamics analysis, and inverse kinematics), thereby preventing the quantification of functional aspects of their evolutionary morphology, and the fit between form and function.

As large-scale macroevolutionary studies can only proceed gradually, we hope that further fossil discoveries and the application of new methods will test the hypotheses advocated in this paper, and continue to reveal information on the evolutionary history of this important, but neglected, group.

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REFERENCES

Abler WL. 1992. The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology* **18:** 161–183.

Adamowicz SJ, Purvis A, Wills MA. 2008. Increasing morphological complexity in multiple parallel lineages of the Crustacea. *Proceedings of the National Academy of Sciences of the United States of America* **105:** 4786–4791.

Adams-Tresman SM. 1987. The Callovian (Middle Jurassic) marine crocodile *Metriorhynchus* from Central England. *Palaeontology* **30:** 179–194.

Ambayrac H. 1913. Une mâchoire de grand reptile du Jurassique supérieur. *Compte Rendu de L'Association Française pour l'avancement des Sciences* **42:** 97–98.

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26:** 32–46.

Andrade MB, Bertini RJ. 2008. A new *Sphagesaurus* (Mesoeucrocodylia: Notosuchia) from the Upper Cretaceous of Monte Alto City (Bauru Group, Brazil), and a revision of the Sphagesauridae. *Historical Biology* **20:** 101–136.

Andrews CW. 1913. *A descriptive catalogue of the marine reptiles of the Oxford Clay, Part Two*. London: British Museum (Natural History).

Andrews CW. 1915. Fore-paddle of *Metriorhynchus* from the Oxford Clay. *Geological Magazine, Decade 6* **2:** 444–447.

Antón M, Sánchez IM, Salesa MJ, Turner A. 2003. The muscle-powered bite of *Allosaurus* (Dinosauria; Theropoda): an interpretation of cranio-dental morphology. *Estudios Geológicos* **59:** 313–323.

Arthaber G. 1906. Beiträge zur kenntnis der organisation und der anpassungserscheinung des genus *Metriorhynchus*. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* **19:** 287–320.

Arthaber G. 1907. Ueber die hinterextremität von *Metriorhynchus*. *Centralblatt für Mineralogie, Geologie und Paläontologie* **1907:** 502–508.

Auer E. 1907. Die extremitäten von *Metriorhynchus*. *Centralblatt für Mineralogie, Geologie und Paläontologie* **1907:** 536–538.

Bardet N. 1994. Extinction events among Mesozoic marine repiles. *Historical Biology* **7:** 313–324.

Bardet N, Fernández M. 2000. A new ichthyosaur from the Upper Jurassic lithographic limestones of Bavaria. *Journal of Paleontology* **74:** 503–511.

Bellairs AD, Shute CCD. 1953. Observations on the narial musculature of Crocodilia and its innervations from the sympathetic system. *Journal of Anatomy* **87:** 367–378.

Bengtson JL, Croll DA, Goebel ME. 1993. Diving behaviour of chinstrap penguins at Seal Island. *Antarctic Science* **5:** 9–15.

Benton MJ, Clark JM. 1988. Archosaur phylogeny and the relationships of Crocodylia. In: Benton MJ, ed. *The phylogeny and classification of the tetrapods*. Oxford: Clarendon Press, 295–338.

Bizzarini F. 1996. Sui resti di coccodrillo del rosso ammonitico veronese di sasso di asiago (Altopiano dei Sette Comuni, Prealpi Venete). *Annali del Museo Civico di Rovereto* **11:** 339–348.

Blainville HD de 1853. Letter by H. D. de Blainville. In: Eudes-Deslongchamps JA, ed. Lettres sur les crocodiles vivants et fossiles. *Bulletin de la Société Linnéenne de Normandie (Années 1849–1853)* **IX:** 109–120.

Bookstein FL. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. New York: Cambridge University Press.

Brusatte SL. 2007. *The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida)*. Unpublished MSc thesis, University of Bristol, Bristol, 170 pp.

Brusatte SL, Benton MJ, Ruta M, Lloyd GT. 2008a. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* **321:** 1485–1488.

Brusatte SL, Benton MJ, Ruta M, Lloyd GT. 2008b. The first 50 mya of dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biology Letters* **4:** 733–736.

Brusatte SL, Sereno PC. 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Palaeontology* **6:** 155–182.

Buchy M-C. 2007. *Mesozoic marine reptiles from north-east Mexico: description, systematics, assemblages and palaeobiogeography*. Unpublished PhD dissertation, Universität Karlsruhe, Karlsruhe, 98 pp.

Buchy M-C. 2008a. New occurrence of the genus *Dakosaurus* (Reptilia, Thalattosuchia) in the Upper Jurassic of northeastern Mexico with comments upon skull architecture of *Dakosaurus* and *Geosaurus*. *Neues Jahrbuch für Geologie und Palaeontologie. Abhandlungen* **249:** 1–8.

Buchy M-C. 2008b. Reevaluation of the holotype of *Plesiosaurus* (*Polyptychodon*) *mexicanus* Wieland, 1910 from the ?Upper Jurassic of Mexico: a thalattosuchian, not a sauropterygian. *Revista Mexicana de Ciencias Geológicas* **25:** 517–522.

Buchy M-C, Stinnesbeck W, Frey E, Gonzalez AHG. 2007. First occurrence of the genus *Dakosaurus* (Crocodyliformes, Thalattosuchia) in the Late Jurassic of Mexico. *Bulletin de la Société Géologique de France* **178:** 391–397.

Buchy M-C, Vignaud P, Frey E, Stinnesbeck W, González AHG. 2006. A new thalattosuchian crocodyliform from the Tithonian (Upper Jurassic) of northeastern Mexico. *Comptes Rendus Palevol* **5:** 785–794.

Buckland-Wright JC. 1978. Bone structure and the patterns of force transmission in the cat skull (*Felis catus*). *Journal of Morphology* **155:** 35–62.

Buffetaut E. 1977. Sur un crocodilien marin *Metriorhynchus superciliosus*, de l'Oxfordien supérieur (Rauracien) de l'Ile de Ré (Charente-Maritime). *Annales de la Société des Sciences Naturelles de la Charente-Maritime* **4:** 252–266.

Buffetaut E, Thierry J. 1977. Les Crocodiliens fossiles du Jurassique moyen et superieur de Bourgogne. *Géobios* **10:** 151–193.

Busbey AB. 1995. The structural consequences of skull flattening in crocodilians. In: Thomason JJ, ed. *Functional morphology in vertebrate paleontology*. Cambridge: Cambridge University Press, 173–192.

Cadbury D. 2002. *Terrible Lizard: The first dinosaur hunters and the birth of a new science*. New York: Henry Holt and Company.

Caldwell MW. 2002. From fins to limbs to fins: limb evolution in fossil marine reptiles. *American Journal of Medical Genetics* **112:** 236–249.

Caldwell MW, Palci A. 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) to Slovenia with a review of mosasauroid phylogeny and evolution. *Journal of Vertebrate Paleontology* **27:** 863–880.

Carvalho IS, Campos ACA, Nobre PH. 2005. *Baurusuchus salgadoensis*, a new Crocodylomorpha from Bauru Basin (Cretaceous), Brazil. *Gondwana Research* **8:** 11–30.

Carvalho IS, Ribeiro LCB, Avila LS. 2004. *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. *Gondwana Research* **7:** 975–1002.

Cheng Y, Wu X, Ji Q. 2004. Triassic marine reptiles gave birth to live young. *Nature* **432:** 383–386.

Ciampaglio CN, Wray GA, Corliss BH. 2005. A toothy tale of evolution: convergence in tooth morphology among marine Mesozoic – Cenozoic sharks, reptiles, and mammals. *The Sedimentary Record* **3:** 4–8.

Colbert EH. 1946. *Sebecus*, representative of a peculiar suborder of fossil Crocodilia from Patagonia. *Bulletin of the American Museum of Natural History* **87:** 217–270.

Collot L. 1905. Reptile Jurassique (*Teleidosaurus gaudryi*) trouvé à Saint-Seine l'Abbaye (Côte-d'or). *Mémoire Academy de Sciences, Arts et Belles-Lettres Dijon, (4th series)* **10:** 41–45.

Cope CD. 1869. On the reptilian orders, Pythonomorpha and Streptosauria. *Proceedings of the Boston Society of Natural History* **12:** 250–266.

Corruccini RS, Beecher RM. 1982. Occlusal variation related to soft diet in a nonhuman primate. *Science* **218:** 74–76.

Cruikshank ARI. 1997. A lower Cretaceous pliosauroid from South Africa. *Annals of the South African Museum* **105:** 206–226.

Currey J. 1987. The evolution of the mechanical properties of amniote bone. *Journal of Biomechanics* **20:** 1035–1044.

Currey JD. 2002. *Bones: structure and mechanics*. Princeton, NJ: Princeton University Press.

Cuvier G. 1824. Sur les ossements fossiles de crocodiles, 5. In: Dufour G, D'Occagne E, eds., *Recherches sur les ossements fossiles*, 2nd édn. Paris, 143–160.

Daniel WJT, McHenry CR. 2001. Bite force to skull stress correlation – modelling the skull of *Alligator mississippiensis*. In: Grigg GC, Seebacher F, Franklin CE, eds. *Crocodilian biology and evolution*. Surrey: Beatty & Sons, 135–145.

Debelmas J. 1952. Un crocodilien marin dans l'Hauterivien

des environs de Comps (Var) *Dacosaurus maximus* Plieninger var. *gracilis* Quenstedt. *Travaux Laboratoire de Géologie l'université de Grenoble* **29:** 101–116.

Debelmas J, Strannoloubsky A. 1957. Découverte d'un crocodilien dans le Néocomien de La Martre (Var) *Dacosaurus lapparenti* n. sp. *Travaux Laboratoire de Géologie de l'université de Grenoble* **33:** 89–99.

Dejak B, Młotkowski A, Romanowicz M. 2003. Finite element analysis of stresses in molars during clenching and mastication. *Journal of Prosthetic Dentistry* **90:** 591–597.

Diefenbach CO da C. 1975. Thermal preferences and thermoregulation in *Caiman crocodilus*. *Copeia* **3:** 530–540.

Dodson P. 1975. Functional and ecological significance of relative growth in Alligator. *Journal of Zoology* **175:** 315–355.

Downs CT, Greaver C, Taylor R. 2008. Body temperature and basking behaviour of Nile crocodiles (*Crocodylus niloticus*) during winter. *Journal of Thermal Biology* **33:** 185–192.

Dromat G, Garcia J-P, Gaumet F, Picard S, Rousseau M, Atrops F, Lecuyer C, Sheppard SMF. 2003. Peturbation of the carbon cycle at the Middle/Late Jurassic transition: geological and geochemical evidence. *American Journal of Science* **303:** 667–707.

Druckenmiller PS, Russell AP. 2008. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. *Zootaxa* **1863:** 1–120.

Dryden I, Mardia KV. 1998. *Statistical shape analysis*. Chichester: John Wiley and Sons.

Dumont E, Piccirillo J, Grosse I. 2005. Finite-element analysis of biting behavior and bone stress in the facial skeletons of bats. *The Anatomical Record Part A* **283A:** 319–330.

Endo H, Aoki R, Taru H, Kimura J, Sasaki M, Yamamoto M, Arishima K, Hayashi Y. 2002. Comparative functional morphology of the masticatory apparatus in the long-snouted crocodiles. *Anatomia Histologia Embryologia* **31:** 206–213.

Erickson GM, Lappin AK, Parker T, Vliet KA. 2004. Comparison of bite-force performance between long-term captive and wild American alligators (*Alligator mississippiensis*). *Journal of Zoology* **262:** 21–28.

Erickson GM, Lappin AK, Vliet KA. 2003. The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *Journal of Zoology* **260:** 317–327.

Erwin DH. 2007. Disparity: morphological pattern and developmental context. *Palaeontology* **50:** 57–73.

Eudes-Deslongchamps E. 1867–1869. *Notes Paléontologiques*. Caen and Paris: 320–392.

Eudes-Deslongchamps E. 1869. Mémoire sur les téléosauriens de la Normandie. *Bulletin de la Société Linnéenne de Normandie, Série 2* **3:** 124–221.

Eudes-Deslongchamps JA. 1864. Mémoire sur les téléosauriens de l'époque Jurassique du Calvados. *Mémoires de la Société Linnéenne de Normandie* **13:** 1–138.

Eudes-Deslongchamps JA. 1866. Description d'une espèce inédite de Téléosaure des environs de Caen. *Bulletin de la Société Linnéenne de Normandie (Années 1864–1865)* **X:** 193–223.

Eudes-Deslongchamps JA. 1868a. Remarques sur l'os de la mâchoire inférieure des Téléosauriens, désigné sous le nom de complémentaire. *Bulletin de la Société Linnéenne de Normandie, Série 2* **1:** 112–118.

Eudes-Deslongchamps JA. 1868b. Note sur un groupe de vertèbres et d'écailles rapportées au *Teleosaurus hastifer* et provenant des assises kimméridgiennes du Cap de la Hève. *Bulletin de la Société Linnéenne de Normandie, Série 2* **1:** 146–155.

Evans AR, Sanson GD. 1998. The effect of tooth shape on the breakdown of insects. *Journal of Zoology* **246:** 391–400.

Evans AR, Sanson GD. 2003. The tooth of perfection: functional and spatial constraints on mammalian tooth shape. *Biological Journal of the Linnean Society* **78:** 173–191.

Fernández M, Gasparini Z. 2000. Salt glands in a Tithonian metriorhynchid crocodyliform and their physiological significance. *Lethaia* **33:** 269–276.

Fernández M, Gasparini Z. 2008. Salt glands in the Jurassic metriorhynchid *Geosaurus*: implications for the evolution of osmoregulation in Mesozoic crocodyliforms. *Naturwissenschaften* **95:** 79–84.

Ferry-Graham LA, Bolnick DI, Wainwright PC. 2002. Using functional morphology to examine the ecology and evolution of specialization. *Integrative and Comparative Biology* **42:** 265–277.

Fitzgerald EMG. 2006. A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. *Proceedings of the Royal Society B* **273:** 2955–2963.

Fitzinger LJFJ. 1843. *Systema reptilium*. Wien: Braumüller et Seidel.

Foote M. 1993. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* **19:** 185–204.

Foote M. 1994. Morphological disparity in Ordovician-Devonian crinoids and the early saturation of morphological space. *Paleobiology* **20:** 320–344.

Foote M. 1996. Ecological controls on the evolutionary recovery of post-Paleozoic crinoids. *Science* **274:** 1492–1495.

Foote M. 1997. The evolution of morphological diversity. *Annual Review of Ecology and Systematics* **28:** 129–152.

Forrest R. 2003. Evidence for scavenging by the marine crocodile *Metriorhynchus* on the carcass of a plesiosaur. *Proceedings of the Geologists' Association* **114:** 363–366.

Fraas E. 1901. Die Meerkrokodile (Thalattosuchia n. g.) eine neue sauriergruppe der Juraformation. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* **57:** 409–418.

Fraas E. 1902. Die Meer-Krocodilier (Thalattosuchia) des oberen Jura unter specieller berücksichtigung von *Dacosaurus* und *Geosaurus*. *Paleontographica* **49:** 1–72.

Frazzetta TH. 1988. The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). *Zoomorphology* **108:** 93–107.

Freeman PW. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. *Journal of Mammalogy* **60:** 467–479.

Freeman PW, Weins WN. 1997. Puncturing ability of bat canine teeth: the tip. In: Yates TL, Gannon WL, Wilson DE,

eds. *Life among the muses: papers in honor of James S Findley*. Albuquerque, NM: The Museum of Southwestern Biology, 225–232.

Frey E. 1984. Aspects of the biomechanics of crocodilian terrestrial locomotion. In: Reif W-E, Westphal F, eds. *Third symposium of Mesozoic Terrestrial Ecosystems*. Tübingen: ATTEMPTO Verlag, 93–97.

Frey E, Buchy M-C, Stinnesbeck W, López-Oliva JG. 2002. *Geosaurus vignaudi* n. sp. (Crocodylia, Thalattosuchia), first evidence of metriorhynchid crocodilians in the Late Jurassic (Tithonian) of central-east Mexico (State of Puebla). *Canadian Journal of Earth Sciences* **39:** 1467–1483.

Gallinek E. 1895. Ueber den weissen Jura von Inowraclaw. *Jahres-Bericht der Schlesischen Gesellschaft für Vaterländische Cultur* **72** (*for 1894*); II, Abtheilung, Naturwissenschaften: a, Naturwissenschaftliche Section, 23.

Gandola R, Buffetaut E, Monaghan N, Dyke G. 2006. Salt glands in the fossil crocodile *Metriorhynchus*. *Journal of Vertebrate Paleontology* **26:** 1009–1010.

Gasparini ZB. 1973. Revisión de '? *Purranisaurus potens*' Rusconi, 1948 (Crocodila, Thalattosuchia). Los Thalattosuchia como un nuevo infraorden de los Crocodilia. *Actas del congreso Geológica Argentino* **3:** 423–431.

Gasparini ZB. 1980. Un nuevo cocodrilo marino (Crocodylia, Metriorhynchidae) del Caloviano del norte de Chile. *Ameghiniana* **17:** 97–103.

Gasparini ZB. 1985. Los reptiles marinos jurásicos de América del Sur. *Ameghiniana* **22:** 23–34.

Gasparini ZB, Chong G. 1977. *Metriorhynchus casamiquelai* n. sp. (Crocodilia, Thalattosuchia) a marine crocodile from the Jurassic (Callovian) of Chile, South America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **153:** 341–360.

Gasparini ZB, Dellapé D. 1976. Un nuevo cocodrilo marino (Thalattosuchia, Metriorhynchidae) de la Formación Vaca Muerta (Jurasico, Tithoniano) de la Provincia de Neuquén (República Argentina). *Congreso Geológico Chileno* **1:** c1–c21.

Gasparini ZB, Iturralde-Vinent M. 2001. Metriorhynchid crocodiles (Crocodyliformes) from the Oxfordian of Western Cuba. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **9:** 534–542.

Gasparini ZB, Paulina-Carabajal A, Chong G. 2008. Un nuevo espécimen de cocodrilo marino del Jurásico Medio del norte de Chile: revalidación de *Metriorhynchus westermanni* (Crocodyliformes: Metriorhynchidae). *Revista Geológica de Chile* **35:** 335–346.

Gasparini ZB, Pol D, Spalletti LA. 2006. An unusual marine crocodyliform from the Jurassic-Cretaceous boundary of Patagonia. *Science* **311:** 70–73.

Gasparini ZB, Vignaud P, Chong G. 2000. The Jurassic Thalattosuchia (Crocodyliformes) of Chile: a paleobiogeographic approach. *Bulletin de la Société Géologique de France* **171:** 657–664.

Geoffroy Saint-Hilaire ÉG. 1825. Recherches sur l'organisation des gavials. *Mémoires du Muséum national d'Histoire naturelle* **12:** 97–155.

Geoffroy Saint-Hilaire ÉG. 1831. Recherches sure de grands sauriens trouvés a l'état fossile aux confins maritimes de la Basse-Normandie, attributes d'abord au crocodile, puis déterminés sous les noms de *Teleosaurus* et *Steneosaurus*. *Mémoires de l'Academie des sciences* **12:** 1–138.

Gervais P. 1876. Crocodile gigantesque fossile au Brésil. *Journal de Zoologie* **5:** 232–236.

Giebel CGA. 1846. *Palaeozoologie*. Merseburg, 360 pp.

Giebel CGA. 1870. Ueber *Dakosaurus amazonicus* n. sp. *Zeitschrift für die gesammten Naturwissenschaften* **35:** 170–171.

Giebel CGA. 1876. *Dakosaurus amazonicus* ist neuerdings von Gervais als *Dinosuchus terror* beschrieben. *Zeitschrift für die gesammten Naturwissenschaften* **48:** 307.

Gmelin JF. 1789. Caroli a Linné, Systema Naturae. In: Beer GE, ed. *Tome. I. Pars III*. Leipzig: 1033–1516.

Grange DR. 1997. *Adaptations of Jurassic marine crocodilians*. Unpublished PhD dissertation, University of Bristol, Bristol.

Gray JE. 1831. *Synopsis Reptilium: or short descriptions of the species of reptiles. Synopsis Reptilium Part 1: tortoises, crocodiles and enaliosaurians*. London, **III:** 85 pp.

Hallam A. 1988. A re-evaluation of Jurassic eustasy in the light of new data and the revised Exxon curve. In: Wilgus CK, Hastings BS, Kendall CGC, Posamentier HW, Ross CA, Van Wagoner JC, eds. *Sea-level changes – an integrated approach, SEPM SPec. Publ* **42:** 261–273.

Hallam A. 2001. A review of the broad pattern of Jurassic sea-level changes and their possible causes in the light of current knowledge. *Palaeogeography Palaeoclimatology Palaeoecology* **167:** 23–37.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: palaeontological Statistics software package for education and data analysis. *Palaeontologia Electronica* **4:** 9.

Hay OP. 1930. *Second bibliography and catalogue of the fossil vertebrata of North America 2*. Washington, DC: Carnegie Institute Washington.

Henderson DM. 1998. Skull and tooth morphology as indicators of niche partitioning in sympatric Morrison Formation theropods. In: Perez-Moreno BP, Holtz T, Sanz JL, Moratalla J, eds. *Aspects of theropod palaeobiology, Gaia* **15:** 219–226.

Herring SW, Teng S. 2000. Strain on the braincase and its sutures during function. *American Journal of Physical Anthropology* **112:** 575–593.

Holl F. 1829. Handbuch der Petrefactenkunde. Erstes Bändchen. *Allgemeine Taschenbibliothek der Naturwissenschaften* **9:** 115 pp.

Holliday CM, Witmer LM. 2007. Archosaur adductor chamber evolution: integration of musculoskeletal and topological criteria in jaw muscle homology. *Journal of Morphology* **268:** 457–484.

Hua S, Atrops F. 1995. Un Crane de *Teleidosaurus* cf. *gaudryi* (Crocodylia, Metriorhynchidae) dans le Bajocien superieur des environs de Castellane (Sud-Est de la France). *Bulletin de la Société Géologique de France* **166:** 643–648.

Hua S, Buffetaut E. 1997. Crocodylia. In: Callaway JM, Nicholls EL, eds. *Ancient marine reptiles*. San Diego, CA: Academic Press, 357–374.

Hua S, Buffrénil V. 1996. Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate Paleontology* **16:** 703–717.

Hua S. 1994. Hydrodynamique et modalitée d'allègement chez *Metrorhynchus supercilosus* (Crocodylia, Thalattosuchia): implications paléologique. *Neues Jahrbuch für Geologie und Palaontologie Abhandlungen* **193:** 1–19.

Hua S, Vignaud P, Atrops F, Clément A. 2000. *Enaliosuchus macrospondylus* Koken, 1883 (Crocodylia, Metriorhynchidae) du Valanginien de Barret-le-Bas (Hautes Alpes, France): un cas unique de remontée des narines externes parmi les crocodiliens. *Géobios* **33:** 467–474.

Hulke JW. 1869. Notes on some fossil remains of a gavial-like saurian from Kimmeridge Bay collected by J.C. Mansel, Esq., establishing its identity with Cuvier's deuxième gavial d'Honfleur, tête à museau plus court (*Steneosaurus rostrominor* of Geoffroy St. Hilaire) and with Quenstedt's *Dakosaurus*. *Quarterly Journal of the Geological Society* **25:** 390–401.

Hulke JW. 1870. Note on a crocodilian skull from Kimmeridge Bay, Dorset. *Quarterly Journal of the Geological Society London* **26:** 167–172.

Iordansky NN. 1964. The jaw muscles of the crocodiles and some relating structures of the crocodilian skull. *Anatomischer Anzeiger* **115:** 256–280.

Jablonski D. 2002. Survival without recovery after mass extinctions. *Proceedings of the National Academy of Sciences of the United States of America* **99:** 8139–8144.

Janssen NMM, Clément A. 2002. Extinction and renewal patterns among Tethyan belemnites in the *Verrucosum* Subzone (Valanginian) of southeast France. *Cretaceous Research* **23:** 509–522.

Jaslow CR. 1990. Mechanical properties of cranial sutures. *Journal of Biomechanics* **23:** 313–321.

Jaslow CR, Biewner AA. 1995. Strain patterns in the horncones, cranial bones and sutures of goats (*Capra hircus*) during impact loading. *Journal of Zoology* **235:** 193–210.

Jentzsch A. 1884. Über den Jura der Gegend von Inowrazlaw. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg i/Pr* **24** (for 1883)**:** 41–45.

Jones HH, Priest JD, Hayes WC, Tichenor CC, Nagel DA. 1977. Humeral hypertrophy in response to exercise. *Journal of Bone and Joint Surgery* **A59:** 204–208.

Joshi S, Mukherjee A, Kheur M, Mehta A. 2001. Mechanical performance of endodontically treated teeth. *Finite Elements in Analysis and Design* **37:** 587–601.

Karl H-V, Gröning E, Brauckmann C, Knötschke N. 2006. Revision of the genus *Enaliosuchus* Koken, 1883 (Archosauromorpha: Metriorhynchidae) from the Early Cretaceous of Northwestern Germany. *Studia Geologica Salmanticensia* **42:** 49–59.

Kear BP. 2005. Cranial morphology of *Platypterygius longmani* Wade, 1990 (Reptilia: Ichthyosauria) from the Lower Cretaceous of Australia. *Zoological Journal of the Linnean Society* **145:** 583–622.

Kielan-Jaworowska Z, Barsbold R. 1972. Narrative of the Polish-Mongolian paleontological expeditions. *Paleontologica Polonica* **27:** 5–13.

Koken E. 1883. Die reptilian der norddeutschen unteren Kreide. *Zeitschrift deutschen Geologischen Gesellschaft* **35:** 735–827.

Kotsakis T, Nicosia U. 1980. Il «coccodrillo di Portomaggiore» (Ferrara). In: *I vertebrati fossili italiani – Catalogo della Mostra Verona*: 103–104.

Kriwet J. 2003. Neoselachian remains (Chondrichthyes, Elasmobranchii) from the Middle Jurassic of SW Germany and NW Poland. *Acta Palaeontologica Polonica* **48:** 583–594.

Kuhn O. 1936. *Crocodilia*. Fossilium Catalogus I: Animalia 75. Gracenhage: Junk.

Lamouroux JVF. 1820. Sur le crocodile fossile trouvé dans les carrière du bourg. *Annales Générales des Sciences Physiques* **3:** 160–163.

Lane A, Janis CM, Sepkoski JJ Jr. 2005. Estimating paleodiversities: a test of the taxic and phylogenetic methods. *Paleobiology* **31:** 21–34.

Langston W. 1973. The crocodilian skull in historical perspective. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, Vol. 4. London: Academic Press, 263–284.

Langston W. 1975. Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), a new combination, from Eocene of North America. *Fieldiana, Chicago, Série Geologie* **33:** 291–314.

Lee MSY. 1997. The evolution of the reptilian hindfoot and the homology of the hooked fifth metatarsal. *Journal of Evolutionary Biology* **10:** 253–263.

Lennier G. 1887. Description des fossils du Cap de la Heve. *Bulletin de la Société Géologique de Normandie, Le Harve* **12:** 17–98.

Leonardi P. 1956. Notizie preliminari sul «Coccodrillo di Portomaggiore». *Bollettino della Società Geologica Italiana* **75:** 88–90.

Lieberman DE. 1997. Making behavioral and phylogenetic inferences from hominid fossils: considering the developmental influence of mechanical forces. *Annual Review of Anthropology* **26:** 185–210.

Lindgren J, Jagt JWM. 2005. Danish mosasaurs. *Netherlands Journal of Geosciences* **83:** 315–320.

Livezey B. 1988. Morphometrics of flightlessness in the Alcidae. *The Auk* **105:** 681–698.

Loveridge JP. 1984. Thermoregulation of the Nile crocodile Crocodylus niloticus. *Symposia of the Zoological Society of London* **52:** 443–467.

Lucas PW. 2004. *Dental functional morphology, how teeth work*. Cambridge: Cambridge University Press.

Lupia R. 1999. Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. *Paleobiology* **25:** 1–28.

Lydekker R. 1888. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History), Cromwell Road, S.W., Part 1. Containing the Orders Ornithosauria, Crocodilia, Dinosauria, Squamta, Rhynchocephalia, and Proterosauria*. London: British Museum of Natural History.

Lydekker R. 1889. On the remains and affinities of five genera of Mesozoic reptiles. *Quarterly Journal of the Geological Society* **45:** 41–59.

Lydekker R. 1890a. On a crocodilian jaw from the Oxford Clay of Peterborough. *Quarterly Journal of the Geological Society, London* **46:** 284–288.

Lydekker R. 1890b. *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History), Cromwell Road, S.W., Part 4. Containing the Orders Anomodontia, Ecaudata, Caudata, and Labyrinthodontia; and supplement*. London: British Museum of Natural History.

McArthur JM, Janssen NMM, Reboulet S, Leng MJ, Thirlwall MF, van de Schootbrugge B. 2007. Palaeotemperatures, polar ice-volume, and isotope stratigraphy (Mg/Ca, δ18O, δ13C, 87Sr/86Sr): the Early Cretaceous (Berriasian, Valanginian, Hauterivian). *Palaeogeography, Palaeoclimatology, Palaeoecology* **248:** 391–430.

McGhee GR Jr. 1999. *Theoretical morphology. The concept and its applications*. New York: Columbia University Press.

McGowan C. 1973. The cranial morphology of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. *Bulletin of the British Museum (Natural History)* **24:** 1–109.

McHenry CR, Clausen PD, Daniel WJT, Meers MB, Pendharkar A. 2006. Biomechanics of the rostrum in crocodilians: a comparative analysis using finite-element modeling. *The Anatomical Record Part A* **288A:** 827–849.

MackAldener M, Olsson M. 2002. Analysis of crack propagation during tooth interior fatigue fracture. *Engineering Fracture Mechanics* **69:** 2147–2162.

Maisch MW, Matzke AT. 2000. The Ichythosauria. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* **298:** 1–159.

Marinho TS, Carvalho IS. 2009. An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil. *Journal of South American Earth Sciences* **27** (1)**:** 36–41.

Martill D. 1985. The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society of London B* **311:** 155–165.

Martill DM, Taylor MA, Duff KL, with contributions by Riding JB, Brown PR. 1994. The trophic structure of the biota of the Peterborough Member, Oxford Clay Formation (Jurassic), UK. *Journal of the Geological Society, London* **151:** 173–194.

Martin BGH, Bellairs AD. 1977. The narial excrescence and pterygoid bulla of the gharial, Gavialis gangeticus (Crocodilia). *Journal of Zoology* **182:** 541–558.

Martin JE, Benton MJ. 2008. Crown clades in vertebrate nomenclature: correcting the definition of Crocodylia. *Systematic Biology* **57:** 173–181.

Massare JA. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* **7:** 130–131.

Massare JA. 1988. Swimming capabilities of Mesozoic marine reptiles: implications for methods of predation. *Paleobiology* **14:** 187–205.

Massare JA. 1994. Swimming capabilities of Mesozoic marine reptiles: a review. In: Maddock L, Bone Q, Rayner JMV, eds. *Mechanics and physiology of animal swimming*. Cambridge: Cambridge University Press, 133–149.

Meers MB. 2002. Cross-sectional geometric properties of the crocodylian humerus: an exception to Wolff's Law? *Journal of Zoology* **258:** 405–418.

Meers MB. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. *The Anatomical Record, Part A* **274A:** 891–916.

Mercier J. 1931. Présentation d'une tête de *Teleidosaurus*. *Bulletin de la Société Linnéenne de Normandie, Série 8* **4:** 45–46.

Mercier J. 1933. Contribution à l'étude des Métriorhynchidés (crocodiliens). *Annales de Paléontologie* **22:** 99–119.

Metzger KA, Herrel A. 2005. Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. *Biological Journal of the Linnean Society* **86:** 433–466.

von Meyer CEH. 1830. Achte Versammlung der Naturforscher und Aerzte zu Heidelberg im September 1829. *Isis von Oken* **1830:** 517–519.

von Meyer CEH. 1831. Neue fossile Reptilien aus der Ordung der Saurier. *Nova Acta Academiae Leopoldino-Carolinae, Curios* **15:** 173–184.

von Meyer CEH. 1832. *Palaeologica zur Geschichte der Erde und ihrer Geshopfe*. Frankfurt: 560 pp.

von Meyer CEH. 1842. *Brachytaenius perennis* aus dem dichten gelben Jurakalk von Aalen in Würtembertg. In: Meyer CEH von, Althaus GB, Münster G, eds. *Beiträge zur Petrefacten-kunde*. Bayreuth: 22–23, & plate 7.

von Meyer CEH. 1859. *Der königlich Bayerischen akademie der Wissenschaften in München zur feiler ihres hundertjährigen bestehens*. Dargebracht: 132 pp.

Moazen M, Curtis N, O'Higgins P, Jones MEH, Evans SE, Fagan MJ. 2009. Assessment of the role of sutures in a lizard skull: a computer modelling study. *Proceedings of the Royal Society B* **276:** 39–46.

Moore WJ. 1965. Masticatory function and skull growth. *Journal of Zoology* **146:** 123–131.

Motani R. 1998. First complete forelimb of the ichthyosaur *Grippia longirostris* from the Triassic of Spitsbergen. *Palaeontology* **41:** 591–599.

Motani R. 2005. Evolution of fish-shaped reptiles (Reptilia: Ichthyopterygia) in their physical environments and constraints. *Annual Review of Earth and Planetary Sciences* **33:** 395–420.

Motani R, Rothschild BM, Wahl W Jr. 1999. Large eyeballs in diving ichthyosaurs. *Nature* **402:** 747.

Mueller-Töwe IJ. 2005. Phylogenetic relationships of the Thalattosuchia. *Zitteliana* **A45:** 211–213.

Muizon C de, Domning DP, Ketten DR. 2002. *Odobenocetops peruvianus*, the walrus-convergent delphinoid (Mammalia: Cetacea) from the Early Pliocene of Peru. *Smithsonian Contributions to Paleobiology* **93:** 223–261.

Nobre PH, Carvalho IS, Vasconcellos FM, Souto PR. 2008. Feeding behavior of the Gondwanic Crocodylomorpha *Mariliasuchus amarali* from the Upper Cretaceous Bauru Basin, Brazil. *Gondwana Research* **13:** 139–145.

Norell MA. 1992. Taxic origin and temporal diversity: the effect of phylogeny. In: Novacek MJ, Wheeler QD, eds.

Extinction and phylogeny. New York: Columbia University Press, 88–118.

Ochev VG. 1981. [Marine crocodiles in the Mesozoic of Povolzh'e] (in Russian). *Priroda* **1981:** 103.

Ogg JG, Ogg G, Gradstein FM. 2008. *The concise geologic time scale*. Cambridge: Cambridge University Press.

Owen R. 1884a. *A history of British Fossil reptiles*. London: Cassel.

Owen R. 1884b. On the cranial and vertebral characters of the crocodilian genus *Plesiosuchus*, Owen. *Quarterly Journal of Geological Society London* **40:** 153–159.

Parsons TS. 1970. The nose and Jacobson's organ. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, Vol. 2. London: Academic Press, 99–191.

Pereira BP, Lucas PW, Swee-Hin S. 1997. Ranking the fracture toughness of thin mammalian soft tissues using the scissors cutting test. *Journal of Biomechanics* **30** (1): 91–94.

Philips J. 1871. *Geology of Oxford and the Valley of the Thames*. Oxford: Clarendon Press.

Pictet FJ. 1845. *Traité élémentaire de paléontologie: ou, Histoire naturelle des animaux fossiles considérés dans leurs rapports zoologiques et géologiques. Tome Second*. Paris: Impr. De J-G Fick.

Pierce SE. 2007. *Morphospace occupation and mechanical performance in extant and extinct crocodile skulls: A combined geometric morphometric and finite element modelling approach*. Unpublished PhD thesis, University of Bristol.

Pierce SE, Angielczyk KD, Rayfield EJ. 2008. Patterns of morphospace occupation and mechanical performance in extant crocodilian skulls: a combined geometric morphometric and finite element modeling approach. *Journal of Morphology* **269:** 840–864.

Pierce SE, Angielczyk KD, Rayfield EJ. 2009a. Morphospace occupation in thalattosuchian crocodylomorphs: Skull shape variation, species delineation, and temporal patterns. *Palaeontology* **52:** 1057–1097.

Pierce SE, Angielczyk KD, Rayfield EJ. 2009b. Shape and Mechanics in Thalattosuchian (Crocodylomorpha) Skulls: Implications for Feeding Behaviour and Niche Partitioning. *Journal of Anatomy* **215:** 555–576.

Pierce SE, Rayfield EJ, Angielczyk KD. 2006. Morphospace occupation in extant and extinct crocodiles. *Journal of Vertebrate Palaeontology* **23:** 110A.

Pinheiro AEP, Bertini RJ, Andrade MB, Martins Neto RG. 2008. New specimen of *Stratiotosuchus maxhechti* (Baurusuchidae, Crocodyliformes) from the Adamantina Formation (Upper Cretaceous), Southeastern Brazil. *Revista Brasileira de Paleontologia* **11:** 37–50.

Plieninger T. 1846. Prof. Dr. Th. Plieninger hielt nachstehenden vortrag über ein neues Sauriergenus und die Einreihung der Saurier mit flachen, schneidenden Zähnen in eine Familie. Pp. 148–154 in: Zweite Generalversammlung am 1. Mai 1846 zu Tübingen. *Württembergische naturwissenschaftliche Jahreshefte* **2:** 129–183.

Pol D. 2003. New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Journal of Vertebrate Paleontology* **23:** 817–831.

Pol D, Gasparini ZB. 2007. Crocodyliformes. In: Gasparini ZB, Salgado L, Coria RA, eds. *Patagonian Mesozoic Reptiles (Life in the Past)*. Bloomington, IN: Indiana University Press, 116–142.

Pol D, Gasparini ZB. 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Palaeontology* **7:** 163–197.

Prasad GVP, de Broin FL. 2002. Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Annales de Paléontologie* **88:** 19–71.

Price LI. 1945. A new reptile from the Cretaceous of Brazil. *Notas Preliminares e Estudos – DGM* **25:** 1–8.

Price LI. 1955. Novos crocodilídeos dos arenitos da Série Bauru. *Cretáceo do Estado de Minas Gerais. Anais da Academia Brasileira de Ciências, Rio de Janeiro* **27:** 487–498.

Purslow PP. 1983. Measurement of fracture toughness of extensible connective tissues. *Journal of Material Sciences* **18:** 3591–3598.

von Quenstedt FA. 1843. *Das Flötzgebirge Württembergs: mit besonderer rücksicht auf den Jura*. Tübingen: Laupp.

von Quenstedt FA. 1852. *Handbuch der Petrefaktenkunde*. Tübingen: Laupp.

von Quenstedt FA. 1856. *Sonst und Jetzt: Populäre Vortäge über Geologie*. Tübingen: Laupp.

Raspail E. 1842. *Observations sur un nouveau genre de saurian fossile, le Neustosaurus gigondarum*. Paris: 56 pp.

Rayfield EJ. 2004. Cranial mechanics and feeding in *Tyrannosaurus rex*. *Proceedings of the Royal Society of London B* **271:** 1451–1459.

Rayfield EJ. 2005a. Using finite-element analysis to investigate suture morphology: a case study using large carnivorous dinosaurs. *The Anatomical Record Part A* **283A:** 349–365.

Rayfield EJ. 2005b. Aspects of comparative cranial mechanics in the theropod dinosaurs *Coelophysis*, *Allosaurus* and *Tyrannosaurus*. *Zoological Journal of the Linnean Society* **144:** 309–316.

Rayfield EJ. 2007. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. *Annual Review of Earth and Planetary Sciences* **35:** 541–576.

Rayfield EJ, Jasinoski SC, Young MT. 2007a. Using Abaqus to explore form and function in living and extinct animals. *Proceedings of the 21st Abaqus UK Regional User Meeting* **2007:** 171–185.

Rayfield EJ, Milner AC, Bui Xuan V, Young PG. 2007b. Functional morphology of spinosaur 'crocodile-mimic' dinosaurs. *Journal of Vertebrate Paleontology* **27:** 892–901.

Rayfield EJ, Milner AC. 2008. Establishing a framework for archosaurs cranial mechanics. *Paleobiology* **34:** 494–515.

Rees J. 2005. Neoselachian shark and ray teeth from the Valanginian, Lower Cretaceous, of Wawał, central Poland. *Palaeontology* **48:** 209–221.

Reidenberg JS, Laitman JT. 2008. Sisters of the sinuses: cetacean air sacs. *The Anatomical Record* **291:** 1389–1396.

Reilly D, Burstein A. 1975. The elastic and ultimate properties of compact bone tissue. *Journal of Biomechanics* **8:** 393–405.

Richmond B, Wright B, Grosse I, Dechow P, Ross C, Spencer M, Strait D. 2005. Finite element analysis in functional morphology. *The Anatomical Record Part A* **283A:** 259–274.

Rieppel O. 1998. *Corosaurus alcovensis* Case and the phylogenetic interrelationships of Triassic stem-group Sauropterygia. *Zoological Journal of the Linnean Society* **124:** 1–41.

Rieppel O, Sander PM, Storrs GW. 2002. The skull of the pistosaur *Augustasaurus* from the Middle Triassic of northwestern. *Nevada. Journal of Vertebrate Paleontology* **22:** 577–592.

Ritgen CH. 1826. Becken der krokodilartigen Salzumpfeideche. *Nova Acta Academiae Leopoldino-Carolinae Curios* **13:** 331–358.

Robinson PL. 1975. The functions of the hooked fifth metatarsal in lepidosaurian reptiles. *Colloques Internationaux du Centre National de la Recherche Scientifique* **218:** 461–483.

Rohlf FJ. 1993. Relative warp analysis and an example of its application to mosquito wings. In: Marcus LF, Valdecasas A, Bello E, eds. *Contributions to morphometrics*. Madrid: Madrid Museum of Natural History, 131–159.

Rohlf FJ. 2003. tpsSmall v.1.20. Freeware. Available at http://life.bio.sunysb.edu/morph/

Rohlf FJ. 2005. tpsRelw v. 1.42. Freeware. Available at http://life.bio.sunysb.edu/morph/

Romer AS. 1966. *Vertebrate paleontology*, third edn. Chicago, IL: University of Chicago Press.

Rusconi C. 1948. Nuevo plesiosaurio pez y Langostas del mar Jurassico de Mendoza. *Revista del Museo de Historia Natural de Mendoza* **2:** 3–12.

Rusconi C. 1955. Acerca del plesiosaurio '*Purranisaurus*' del Jurasico de Mendoza. *Anales de la Sociedad Científica Argentina* **160:** 71–77.

Sauvage H-E. 1871. De la présence d'un reptile du type mosasaurien dans le formations Jurassique supérieures de Boulogne-sur-Mer. *Comptes rendus de l'Académie des Sciences* **10:** 141–142.

Sauvage H-E. 1873. Notes sur les reptiles, fossiles. *Bulletin de la Société Géologiques de France, série 3* **4:** 365–384.

Sauvage H-E. 1874. Mémoire sur les dinosauriens et les crocodiliens des terrains Jurassiques de Boulogne-sur-Mer. *Mémoires de la Société Géologique de France, série 2* **10:** 1–57.

Sauvage H-E. 1880. Synopsis des poissons et des reptiles des terrains Jurassiques de Boulogne-sur-Mer. *Bulletin de la Société Géologiques de France, séries 3* **8:** 524–546.

Schaeffer B, Rosen DE. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *American Zoologist* **1:** 187–204.

Schmidt WE. 1904. Uber *Metriorhynchus jaekeli* nov. sp. *Zeitschrift der Deutschen Geologischen Gesellschaft* **56:** 97–108.

Schusterman RJ, Kastak D, Levenson DH, Reichmuth CJ, Southall BL. 2000. Why pinnipeds don't echolocate. *Journal of the Acoustical Society of America* **107:** 2256–2264.

Seebacher F, Grigg GC, Beard LA. 1999. Crocodiles as dinosaurs: behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures. *Journal of Experimental Biology* **202:** 77–86.

Seeley HG. 1869. *Index to the fossl remains of Aves, Ornthosauria, and Reptilia, from the secondary system of strata, arranged in the Woodwardian Museum of the University of Cambridge*. Cambridge: Deighton, Bell, and Co., 1–143.

Seidel MR. 1979. The osteoderms of the American alligator and their functional significance. *Herpetologica* **35:** 375–380.

Sinclair AG, Alexander RM. 1987. Estimates of forces exerted by the jaw muscles of some reptiles. *Journal of Zoology* **213:** 107–115.

Smith AB. 1994. *Systematics and the fossil record. Documenting evolutionary patterns*. Oxford: Blackwell Scientific.

Smith AS, Dyke GJ. 2008. The skull of the giant predatory pliosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics. *Naturwissenschaften* **95:** 975–980.

von Sömmerring ST. 1816. Ueber die *Lacerta gigantea* der vorwelt. *Denkschriften der Königlichen Akademie der Wisseschaften zu Münch* **6:** Classe der Mathematik und Naturwissenschaften 37–59.

Spotilia JR, Terpin KM, Dobson P. 1977. Mouth gaping as an effective thermoregulatory device in alligators. *Nature* **265:** 235–236.

Stayton CT, Ruta M. 2006. Geometric morphometrics of the skull roof of stereospondyls (Amphibia: Temnospondyli). *Palaeontology* **49:** 307–337.

Steel R. 1973. *Crocodylia. Handbuch der Paläoherpetologie, Teil 16*. Stuttgart: Gustav Fischer Verlag.

Stockmeyer Lofgren A, Plotnick RE, Wagner PJ. 2003. Morphological diversity of Carboniferous arthropods and insights on disparity patterns through the Phanerozoic. *Paleobiology* **29:** 349–368.

Stricker LS, Taylor DG. 1989. A new marine crocodile (Mesosuchia: Metriorhynchidae) from the Snowshoe Formation (Jurassic), Oregon. *Journal of Vertebrate Paleontology* **9:** 40A.

Surlyk F. 1991. Sequence stratigraphy of the Jurassic – lowermost Cretaceous in East Greenland. *Bulletin of the American Association of Petroleum Geologist* **75:** 1468–1488.

Taylor MA. 1987. How tetrapods feed in water: a functional analysis by paradigm. *Zoological Journal of the Linnean Society* **91:** 171–195.

Taylor MA, Benton MJ. 1986. Reptiles from the Upper Kimmeridge Clay (Kimmeridgian, Upper Jurassic) of the vicinity of Egmont Bight, Dorset. *Proceedings of the Dorset Natural History and Archaeological Society* **107:** 121–125.

Taylor MA, Cruickshank ARI. 1993. Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Philosphocial Transactions: Biological Sciences* **341:** 399–418.

Turner AH, Buckley GA. 2008. *Mahajangasuchus insignis* (Crocodyliformes: Mesoeucrocodylia) cranial anatomy and new data on the origin of the eusuchian-style palate. *Journal of Vertebrate Paleontology* **28:** 382–408.

Underwood CJ. 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology* **32:** 215–235.

Van de Schootbrugge B, Föllmi KB, Bulot LG, Burns SJ. 2000. Paleoceanographic changes during the early Cretaceous (Valanginian-Hauterivian): evidence from oxygen and carbon stable isotopes. *Earth and Planetary Science Letters* **181:** 15–31.

Verwaijen D, Van Damme R, Herrel A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* **16:** 842–850.

Vignaud P. 1995. *Les Thalattosuchia, crocodiles marins du Mésozöique: Systématique, phylogénie, paléoécologie, biochronologie et implications paléogéographiques*. Unpublished PhD dissertation. Université de Poitiers, Poitiers, 245 pp.

Vignaud P. 1997. La morphologie dentaire des Thalattosuchia (Crocodylia, Mesosuchia). *Palaeovertebrata* **26:** 35–59.

Vignaud P, Gasparini ZB. 1996. New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) from the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences, Paris* **2:** 245–250.

Wagner A. 1852. Neu-aufgefundene saurier-veberreste aus den lithographischer Schiefern ind den obern Juralke. *Abhandlungen der Mathemat.-Physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften* **6:** 661–710.

Wagner A. 1858. Zur Kenntniss der Sauier aus den lithographischen Schiefen. *Abhandlungen der Mathemat.-Physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften* **8:** 415–528.

Wagner PJ. 1997. Patterns of morphological diversification among the Rostroconchia. *Paleobiology* **23:** 115–145.

Wahl WR, Ross M, Massare JA. 2007. Rediscovery of Wilbur Knight's *Megalnesaurus rex* site: new material from an old pit. *Paludicola* **6:** 94–104.

Wartzok D, Ketten DR. 1999. Marine mammal sensory systems. In: Reynolds JE, Rommel SA, eds. *Biology of marine mammals*. Melbourne, Australia: Melbourne University Press, 117–175.

Watanuki Y, Wanless S, Harris M, Lovvorn JR, Miyazaki M, Tanaka H, Sato K. 2006. Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. *The Journal of Experimental Biology* **209:** 1217–1230.

Wenz S. 1968. Contribution à l'étude du genre *Metriorhynchus*. Crâne et moulage endocrânien de *Metriorhynchus superciliosus*. *Annales de Paléontologie (Vertébrés)* **54:** 149–183.

Wesley-Hunt GD. 2005. The morphological diversification of carnivores in North America. *Paleobiology* **31:** 35–55.

Wilkinson LE, Young MT, Benton MJ. 2008. A new metriorhynchid crocodile (Mesoeucrocodylia: Thalattosuchia) from the Kimmeridgian (Upper Jurassic) of Wiltshire, UK. *Palaeontology* **51:** 1307–1333.

Wills MA. 1998. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biological Journal of the Linnean Society* **65:** 455–500.

Wills MA, Briggs DEG, Fortey RA. 1994. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology* **20:** 93–131.

Witmer LM. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Journal of Vertebrate Paleontology* Memoir **3:** 1–73. [Supplement to *Journal of Vertebrate Paleontology* **17** (1)].

Woodward AS. 1885. On the literature and nomenclature of British fossil Crocodilia. *Geological Magazine, Decade 3* **2:** 496–510.

Woodward AS, Sherbron CD. 1980. *A catalogue of British fossil Vertebrata*. London: Dulau & Co., 8 Volumes, xxxv + 396 pp.

Wroe S, McHenry C, Thomason J. 2005. Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Sociey B* **272:** 619–625.

Wu XC, Sues HD, Sun A. 1995. A plant-eating crocodyliform reptiles from the Cretaceous China. *Nature* **376:** 678–680.

Young MT. 2006. *Evolution and taxonomic revision of the Mesozoic marine crocodyliforms Metriorhynchidae, a phylogenetic and morphometric approach*. Unpublished MSc thesis, University of London Imperial College, London, 140 pp.

Young MT. 2007. The evolution and interrelationships of Metriorhynchidae (Crocodyliformes, Thalattosuchia). *Journal of Vertebrate Paleontology* **27:** 170A.

Young MT, Andrade MB. 2009. What is *Geosaurus*? Redescription of *G. giganteus* (Thalattosuchia, Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. *Zoological Journal of the Linnean Society* **157:** 551–585.

Zelditch M, Swiderski D, Sheets DH, Fink W. 2004. *Geometric morphometrics for biologists: a primer*. New York: Academic Press.

von Zittel KA. 1887–1890. *Handbuch der Palaeontologie, Paläozoologie Band 3. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. München und Leipzig: Oldenbourg, 667–670.

NOTE ADDED IN PROOF

After acceptance of this paper, the authors were made aware of a study conducted by S. Pierce, which also examined the evolutionary significance of skull shape variation and biomechanics in thalattosuchian crocodylomorphs (metriorhynchids and teleosaurids) using 2D finite element modelling and geometric morphometrics. The authors acknowledge that S. Pierce conducted her broader project independently and prior to our project. Our 2D FEA results are similar to those outlined by Pierce's more inclusive study (see Pierce *et al.*, 2006, 2007, 2009a, b). We have attempted to cite the relevant papers wherever possible, and our results should be considered in the context of these publications.

APPENDIX
REVISED TAXONOMY OF METRIORHYNCHIDAE

From the global phylogenetic analysis presented by Young & Andrade (2009), and the discussion regarding the correct naming of derived metriorhynchid genera, a complete taxonomic revision of Metriorhynchoidea is required. In addition to what was proposed by Young & Andrade (2009), the paraphyly of *Metriorhynchus* and *Teleidosaurus* must be considered.

Earlier incarnations of this cladistic analysis (Young, 2006, 2007; Wilkinson *et al.*, 2008) also found *Metriorhynchus* to be not only paraphyletic, but the basalmost species in both subfamilies. Within Geosaurinae, two monophyletic clades of '*Metriorhynchus*' species were recovered: one composed solely of the European brevirostrine forms, and another composed solely of the brevirostrine species from South America. Young (2007) resurrected the oldest available generic name for both clades, resulting in *Suchodus* being applied to the European brevirostrine '*Metriorhynchus*' species, and *Purranisaurus* being applied to the brevirostrine species from South America.

However, we herein erect two new generic names for Bajocio–Callovian metriorhynchoids not emended by previous taxonomic studies, namely *Eoneustes* gen.

nov. and *Gracilineustes* gen. nov. As the basal metriorhynchoid *Teleidosaurus* was found to be paraphyletic (Young, 2007; Young & Andrade, 2009), the taxa more closely related to metriorhynchids ['*Teleidosaurus*' *gaudryi* (Collot, 1905) and '*Teleidosaurus*' *bathonicus* (Mercier, 1933)] are now transferred to *Eoneustes* gen. nov.

With the paraphyly of *Metriorhynchus* (Young, 2006, 2007; Wilkinson *et al.*, 2008; Young & Andrade, 2009), and the realization that there are two clades of mesorostrine (metriorhynchine) taxa previously attributed to *Metriorhynchus* (one of which retains the generic name), a new name is required for the second clade. We give this clade the name *Gracilineustes* gen. nov.

With these final taxonomic amendments, we outline below the species currently considered valid within each genus, include a revised diagnosis for all genera, and erect a taxonomic framework for Thalattosuchia (see also Table A1). It must be noted that this review is primarily concerned with creating a taxonomic framework for assigning species to genera by establishing valid, defensible genera. As such, species diagnoses will not be presented. However, the species-level taxonomy presented herein broadly agrees with Vignaud (1995), who did established species diagnoses. However, this work is currently unpublished.

Table A1. Summary of the proposed taxonomy of Metriorhynchoidea

Genus	Type species	Other valid species
Teleidosaurus	*T. calvadosii*	–
Eoneustes gen. nov.	**E. gaudryi comb. nov.**	**E. bathonicus comb. nov.**
Metriorhynchus	*M. geoffroyii*	*M. superciliosus, M. hastifer*
Gracilineustes gen. nov.	**Gr. leedsi comb. nov.**	**Gr. acutus comb. nov.**
Rhacheosaurus	*R. gracilis*	–
Cricosaurus	*C. elegans*	*C. araucanensis, C. gracilis, C. macrospondylus, ?C. mexicanus, C. saltillense, C. schroederi, C. suevicus, C. vignaudi*
Suchodus	*S. durobrivensis*	*S. brachyrhynchus*
Purranisaurus	*P. potens*	*P. casamiquelai, P. westermanni*
Geosaurus	*Ge. giganteus*	*Ge. carpenteri, Ge. grandis, Ge. lapparenti*
Dakosaurus	*D. maximus*	*D. andiniensis, D. manselii, D. nicaeensis*

Infra-order **Thalattosuchia** Fraas, 1901
    Superfamily **Teleosauroidea** Geoffroy Saint-Hilaire, 1831
    Superfamily **Metriorhynchoidea** Fitzinger, 1843*
        Teleidosaurus
        ***Eoneustes* gen. nov.**
     Family **Metriorhynchidae** Fitzinger, 1843*
      Subfamily **Metriorhynchinae** Fitzinger, 1843*
        Metriorhynchus
        ***Gracilineustes* gen. nov.**
        Rhacheosaurus
        Cricosaurus
      Subfamily **Geosaurinae** Lydekker, 1889
        Suchodus
        Purranisaurus
        Geosaurus
        Dakosaurus

*The nominal author of a family group is the author who first erected a family-group taxon that is valid (Article 11 of the code of the International Commission on Zoological Nomenclature, ICZN), in accordance with the Code of the ICZN Principle of Coordination, applied to family-group names (Article 36.1).

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York City, NY, USA; BRSMG, Bristol City Museum & Art Gallery, Bristol, UK; BSPG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; CAMSM, Sedgwick Museum, Cambridge, UK; GLAHM, Hunterian Museum, Glasgow, UK; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; LEICT, New Walk Museum and Art Gallery, Leicester, UK; MACN, Museo Argentino de Ciências Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MDA, Museo del Desierto de Atacama, Antofagasta, Chile; MGCL, Musée Géologique Cantonal, Lausanne, Switzerland; MHNB, Musée d'Histoire Naturelle, Boulogne-sur-Mer, France; MGHF, Museo Geologico H. Fuenzalida, Universidad Catolica del Norte, Antofagasta, Chile; MHNG, Muséum d'Histoire naturelle de la Ville de Genève, Geneva, Switzerland; MHNN, Muséum d'Historie naturelle de Nice, Nice, France; MHNSR, Museo de Historia Natural de San Rafael, San Rafael, Argentina; MJCM, Museo de Ciencias Naturales y Antropológicas 'Prof. Juan C. Moyano', Mendoza, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMGLV, Mindener Museum für Geschichte, Landes- und Volkskunde, Minden, Germany; MNHN, Muséum national d'Historie naturelle, Paris, France; MNHNCu, Museo Nacional de Historia Natural de Cuba, Cuba; MUDE, Museo del Desierto, Saltillo, México; NHM, Natural History Museum, London, UK; NMING, National Museum of Ireland, Dublin, Ireland; NMW, National Museum of Wales, Cardiff, UK; OXFUM, Oxford University Museum, Oxford, UK; PETMG, Peterborough Museum & Art Gallery, Peterborough, UK; RMS, Royal Museum, Edinburgh, UK; RNGHP, Réserve Naturelle Géologique de Haute Provence, Digne les Bains, France; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; UANL, Universidad Autonoma de Nuevo Léon, México; UJF, Université Joseph Fourier, Grenoble, France.

BASAL METRIORHYNCHOIDS

TELEIDOSAURUS EUDES-DESLONGCHAMPS, 1869

Type species: Teleidosaurus calvadosii (Eudes-Deslongchamps, 1866) Eudes-Deslongchamps, 1869.

Etymology: 'Complete lizard'. *Teleidos*- is the Ancient Greek for 'to be found perfect/complete', whereas -*sauros* is the Ancient Greek for 'lizard'. This refers to the *T. calvadosii* holotype, which was a perfectly complete skull.

Geological range: Lower–Middle Bathonian (Vignaud, 1995).

Geographical range: Normandy, France.

Emended diagnosis: Metriorhynchoid thalattosuchian with between 18 and 20 carinated teeth per maxillae, with little lateromedial compression; three teeth per premaxilla; strong ornamentation on the cranial bones, including those of the rostrum; rounded angle formed by the lateral and medial processes of the frontal; the dorsal rim of the orbit is composed of the lacrimal, prefrontal, frontal, and postorbital bones (from rostral to caudal); large external mandibular fenestrae, surrounded by the dentary, surangular, and angular; the external nares are subtriangular in shape, with the posterior edge being straight; the

naso–lacrimal suture is 60% or less of the length of the naso–prefrontal suture; absence of both the antorbital fossae and fenestrae.

TELEIDOSAURUS CALVADOSII
(EUDES-DESLONGCHAMPS, 1866)
EUDES-DESLONGCHAMPS, 1869

1866 *Teleosaurus calvadosii* sp. nov.; Eudes-Deslongchamps
1869 *Teleosaurus* (*Teleidosaurus*) *calvadosii* subgen. nov.; Eudes-Deslongchamps
1867–1869 *Teleidosaurus calvadosi* unjust. emend.; Eudes-Deslongchamps
1867–1869 *Teleidosaurus joberti* sp. nov.; Eudes-Deslongchamps

Plastotype: NHM R.2681: complete skull and mandible (holotype lost during the Second World War).

Type locality: Calvados, Normandy, France (Fuller's Earth).

Etymology: 'Complete lizard from Calvados'. Named after the region in France where it was discovered.

Geological range: Lower–middle Bathonian (*zigzag–progracilis* ammonite zones; Vignaud, 1995).

Geographical range: Normandy, France.

Referred specimen: NHM 32612: plastotype of *T. joberti*, anterior fragment of right mandible.

EONEUSTES GEN. NOV.

Type species: Eoneustes gaudryi (Collot, 1905) comb. nov.

Valid species: Eoneustes bathonicus (Mercier, 1933) comb. nov.; *E. gaudryi* (Collot, 1905) comb. nov.

Etymology: 'Dawn swimmer'. *Eos-* is Ancient Greek for 'dawn', whereas *-neustes* is Ancient Greek for 'swimmer'. This refers to the basal position of this genus in the phylogeny.

Geological range: Upper Bajocian–Middle Bathonian (Hua & Atrops, 1995).

Geographical range: Normandy, Burgundy, and Castellane, France.

Diagnosis: Metriorhynchoid thalattosuchian, with over 20 teeth per maxilla; strong ornamentation on the cranial bones, including those of the rostrum; rounded angle formed by the lateral and medial processes of the frontal; the frontal forms an intertemporal flange; the dorsal rim of the orbit is composed of the prefrontal, frontal, and postorbital bones (rostral to caudal); the orbital is ellipsoid; prefrontals are incipitally enlarged over the orbits; the antorbital fossa is elongate, narrow, and oriented obliquely, and is enclosed by the lacrimal, maxilla, and jugal; the antorbital pseudofenestra is enclosed by the lacrimal and maxilla; the lacrimal contacts the nasal primarily on its anterior edge; the prefrontal–nasal suture has a pronounced, rectangular convexity on the posterior half of the suture.

EONEUSTES GAUDRYI (COLLOT, 1905) COMB. NOV.

1905 *Teleidosaurus gaudryi* sp. nov.; Collot
1933 *Metriorhynchus gaudryi* comb. nov.; Mercier

Holotype: NHM R.3353: mid-portion of skull.

Type locality: Cote d'Or, Burgundy, France.

Etymology: 'Gaudry's dawn swimmer'.

Geological range: Upper Bajocian–lower Bathonian.

Geographical range: Departments of Cote d'Or, Burgundy, and Alpes-de-Haute-Provence, France.

Referred specimen: Université Claude Bernard Lyon I, F.S.L. 330210: skull lacking occiput and tip of the rostrum (*parkinsoni* ammonite zone, upper Bajocian; 'La Clue de Chasteuil', Alpes-de-Haute-Provence, France).

EONEUSTES BATHONICUS (MERCIER, 1933) COMB. NOV.

1931 *Teleidosaurus* sp. Mercier
1933 *Metriorhynchus bathonicus* sp. nov.; Mercier
1977 *Teleidosaurus bathonicus* comb. nov.; Buffetaut & Thierry

Holotype: Lost during the Second War World.

Type locality: Calvados, Normandy, France.

Etymology: 'Dawn swimmer from the Bathonian'.

Geological range: Lower Bathonian.

Geographical range: Normandy, France.

METRIORHYNCHINAE
METRIORHYNCHUS VON MEYER, 1830

Metriorynchus Pictet, 1845 [sic]

Type species: Metriorhynchus geoffroyii von Meyer, 1832.

Valid species: Metriorhynchus geoffroyii von Meyer, 1832; *Metriorhynchus hastifer* (Eudes-Deslongchamps, 1868) Eudes-Deslongchamps, 1869; *Metriorhynchus superciliosus* (Blainville, 1853) Eudes-Deslongchamps, 1869.

Potentially valid species: Metriorhynchus littoreus Sauvage, 1874.

Etymology: 'Moderate snout'. *Metrio-* is Greek for medium/moderate, whereas *-rhynchus* is the Latinized form of the Ancient Greek *-rhynchos*, which means 'snout'.

Geological range: Lower Callovian–upper Kimmeridgian.

Geographical range: European endemic (England, France, Germany, and Switzerland).

Emended diagnosis: Metriorhynchid thalattosuchian with over 20 teeth per maxilla, and more than 20 teeth per dentary; variable ornamentation on the cranial bones, but lacking conspicuous ornamentation on the rostrum; the antorbital fossa is elongate, narrow, and oriented obliquely, and is enclosed by the lacrimal, maxilla, and jugal; the antorbital pseudofenestra is enclosed by the lacrimal, nasal, and maxilla; the internal nares opens out posteriorly into the buccal cavity, with the palatines creating a V-shape with its apex directed anteriorly; the maxilla–palatine suture forms an M-shape orientated posteriorly; the squamosal contributes at least 50% to the supratemporal arch; the length of the cervical centrum is shorter than its height; the tibia is roughly one third of the length of the femur; the atlas hypocentrum is subequal in length to the odontoid process length; the humerus is subequal in length to the scapula.

METRIORHYNCHUS GEOFFROYII VON MEYER, 1832

1824 'Deuxième gavial de Honfleur'; Cuvier [*partim*]
1825 *Steneosaurus rostro-minor* sp. nov.; Geoffroy Saint-Hilaire [*partim*]
1831 *Gavialis jurinii* sp. nov.; Gray [*partim*]
1832 *Metriorhynchus geoffroyii* sp. nov.; von Meyer [*partim*]
1871 *Steneosaurus palpebrosus* sp. nov.; Philips
1884a *Steneosaurus temporalis* sp. nov.; Owen
1885 *Metriorhynchus palpebrosus* comb. nov.; Woodward

1890 *Metriorhynchus palpebrosum* unjust. emend.; Woodward & Sherbron

Lectotype: MHNG V-2232: Anterior portion of snout.

Plastotypes: MGCL 9868, OXFUM unnumbered.

Etymology: 'Geoffroy's moderate snout'. Named in honour of Geoffroy Saint-Hilaire.

Type locality: Near Honfleur, Normandy, France.

Geological range: Lower Kimmeridgian.

Geographical range: Normandy, France; Oxfordshire, England; and Canton Jura, Switzerland.

Referred specimens: OXFUM J.29823, skull and poorly preserved mandible (holotype of *M. palpebrosus*); OXFUM J.55476-8, isolated humeri (from the type locality of *M. palpebrosus*); OXFUM J.55479, incomplete skull (from the type locality of *M. palpebrosus*).

Note: Cuvier (1824) described two species of 'gavial' based upon fragmentary remains found around Honfleur, Normandy. He illustrated the two species on the basis of snout length: long, 'tête à museau plus allongé'; and short, 'tête à museau plus court' (see Table A2). Geoffroy Saint-Hilaire (1825) erected the genus *Steneosaurus* for Cuvier's 'Gavials de Honfleur', with the short-snouted species being named *Steneosaurus rostro-minor*. However, he included some of the material from Cuvier's long-snouted species (tête à museau plus allongé) into his own short-snouted one (*S. rostro-minor*) (see Table A2). von Meyer (1830) examined Cuvier's material and erected the genus *Metriorhynchus* for the short-snouted species, but he did not establish a species epithet. It was not until 1832 that von Meyer created the binomen *M. geoffroyii*.

The issue of the type species was not revisited until the 1860s, when Eudes-Deslongchamps (1867–1869) emended the diagnosis of *Metriorhynchus*, and transferred five recently discovered species (based upon specimens found in Cambridgeshire, England, and Normandy, France) into the genus. He regarded *M. superciliosus* as fulfilling the role of type species, as he considered *M. geoffroyii* to be a composite of two species: *M. hastifer* and *M. superciliosus*. Lydekker (1888) also considered *M. superciliosus* as the type species (which today contravenes the code of the ICZN, Article 68), although he did advocate the retention of *M. geoffroyii*.

Unfortunately, like Cuvier's 'tête à museau plus court' and Geoffroy's *Steneosaurus rostro-minor*, von

Table A2. Taxonomy of cranial specimens attributed to Cuvier's 'gavials de Honfluer', showing the major taxonomic frameworks of the 19th century

Specimen and figure numbers from Cuvier (1824)	Cuvier, 1824	Geoffroy Saint-Hilaire, 1825	von Meyer, 1832	Eudes-Deslongchamps., 1867–1869	This paper
Three rostral fragments (pl. 8, figs 3–4) [MNHN 8900]	Gavial de Honfleur or Tête à museau plus allongé	*Steneosaurus rostro-major*		*S. edwardsi*	*S. edwardsi*
Skull frag. (pl. 8, fig. 8) [MNHN 8753]		*Steneosaurus rostro-minor*		*M. superciliosus*	*M. superciliosus*
Mandible (pl. 8, figs 1–2) [MNHN 8902]	Deuxième gavial de Honfleur or Tête à museau plus court		*M. geoffroyii*		
Rostrum (pl. 8, figs 5–7) [MNHN 8754]				*M. hastifer*	*M. geoffroyii*
Rostrum (pl. 10, figs 5–7) [MHNG V-2232]					

Metriorhynchus geoffroyii, the type species of *Metriorhynchus*, is today solely represented by MHNG V-2232 out of all of the specimens attributed to this species by von Meyer (1832) in the original description. Table based upon Vignaud (1995). Cuvier's 'Gavial de Guilly' is not shown; Geoffroy Saint-Hilaire (1825) included it within *Steneosaurus rostro-major* (now the type species of *Steneosaurus*, *S. megistorhynchus*).

Meyer's *M. geoffroyii* is a chimera (see Table A2). Eudes-Deslongchamps (1867–1869) was correct in his assignment of most specimens to *M. superciliosus*. This only leaves the rostrum (MHNG V-2232). It was this specimen that Eudes-Deslongchamps (1867–1869) referred to his species, *M. hastifer*.

Vignaud (1995) in his review of Thalattosuchia established the rostrum as the lectotype of *M. geoffroyii*. In addition, he considered *M. geoffroyii* to be distinct from *M. hastifer*. However, its fragmentary nature precluded him from rejecting a synonymy between *M. geoffroyii* and *M. palpebrosus*, which is herein accepted.

As *M. geoffroyii* is the type species by monotypy (under the code of the ICZN, Article 68.3), it would remain the valid type species (code of the ICZN, Article 67.1.2) even if it is considered to be a junior synonym of *Steneosaurus rostro-minor*.

METRIORHYNCHUS HASTIFER (EUDES-DESLONGCHAMPS, 1868) EUDES-DESLONGCHAMPS, 1869

1868a *Teleosaurus hastifer* sp. nov.; Eudes-Deslongchamps
1869 *Metriorhynchus hastifer* comb. nov.; Eudes-Deslongchamps
1880 *Metriorrhynchus hastifer* [sic]; Sauvage

Holotype: Destroyed/lost during the Second War World (complete skull).

Type locality: Calvados, Normandy, France.

Geological range: Lower Kimmeridgian (*cymodoce* ammonite zone).

Geographical range: Normandy, France.

METRIORHYNCHUS LITTOREUS SAUVAGE, 1874

1874 *Metriorrhynchus littoreus* sp. nov. [sic]; Sauvage

Holotype: MHNB 58, fragment of rostrum, cervical and dorsal vertebrae.

Type locality: Boulogne-sur-Mer, Nord-Pas de Calais, France (lower Kimmeridge Clay Formation).

Geological range: Upper Kimmeridgian (*austissiodorensis* ammonite zone).

Note: Although based upon a fragmentary rostrum, and cervical and dorsal vertebrae from Boulogne-sur-Mer of the upper Kimmeridgian, an occipital and posterior cranial fragment has been found from the same locality that is clearly referable to *Metriorhynchus* (SMNS 56999). However, whether this taxon is distinct from *M. geoffroyii* cannot be currently determined.

METRIORHYNCHUS SUPERCILIOSUS (BLAINVILLE, 1853) EUDES-DESLONGCHAMPS, 1869

1824 'Gavial de Honfleur'; Cuvier [*partim*]
1824 'Deuxième gavial de Honfleur'; Cuvier [*partim*]
1825 *Steneosaurus rostro-minor* sp. nov.; Geoffroy Saint-Hilaire [*partim*]

1832 *Metriorhynchus geoffroyii* sp. nov.; von Meyer [*partim*]

1853 *Crocodilus superciliosus* sp. nov.; Blainville

1868b *Teleosaurus superciliosus* comb. nov.; Eudes-Deslongchamps

1868b *Teleosaurus blainvillei* sp. nov.; Eudes-Deslongchamps

1869 *Metriorhynchus superciliosus* comb. nov.; Eudes-Deslongchamps

1869 *Metriorhynchus blainvillei* comb. nov.; Eudes-Deslongchamps

1867–1969 *Metriorhynchus moreli* sp. nov.; Eudes-Deslongchamps

1869 *Steneosaurus dasyceps* sp. nov.; Seeley

1890b *Metriorhynchus superciliosum* unjust. emend.; Lydekker

1904 *Metriorhynchus jaekeli* sp. nov.; Schmidt

Neotype: MNHN 8903, incomplete skull (chosen by Blainville, see Vignaud, 1995).

Type locality: The original holotype is believed to be from England, see Vignaud (1995) for a full discussion (Oxford Clay Formation).

Geological range: Lower Callovian–lower Oxfordian (*koenigi–mariae* ammonite zones).

Geographical range: Cambridgeshire, Huntingdon-shire, and Wiltshire, England; and Ardèche, Normandy, and Poitou, France.

Geographical range note: Metriorhynchus specimens are known from the Middle Callovian of Germany (C. Diedrich, pers. comm., 2008).

Referred specimens: AMNH FR 997, incomplete skull with mandible, and 23 assorted vertebrae (including cervicals and dorsals); CAMSM J64398, skull (holotype of *Steneosaurus dasyceps*); CAMSM J64900, mid-portion of skull; CAMSM J64918, rostrum; GLAHM V942, skull with mandible from a young individual; GLAHM V963, incomplete skull and mandible, eight dorsal vertebrae, one caudal vertebra, both coracoids, left scapula, right ilium, left ischium, and right ischium blade, distal half of the right pubis (from a baby specimen); GLAHM V964, skull, mandible, atlas axis, four cervical vertebrae, and cervical and dorsal ribs; GLAHM V965, skull with right dentary; GLAHM V971, skull in various fragments, atlas axis, five cervical vertebrae, and ten dorsal vertebrae; GLAHM V982, broken skull, mandible, cervical vertebra centrum, and atlas left rib; GLAHM V983, broken skull, mandible, sclerotic ring ossicles, and dorsal rib; GLAHM V984, broken skull and mandible fragments from two individuals; GLAHM V985, broken skull and mandible fragments, and sclerotic ring ossicles; GLAHM V987, broken skull and mandible fragments, sclerotic ring ossicles, and rib fragments; GLAHM V988, skull, mandible, atlas axis, one dorsal vertebra, left ilium, fragment of right pubis, and right femur; GLAHM V989, skull with mandible; GLAHM V996, skull with bite marks consistent with that of a metriorhynchid; GLAHM V1004, skull and mandible fragments, and atlas axis; GLAHM V1015, incomplete skull, disarticulated mandible, atlas axis, right atlas rib, both coracoids, right ischium, femora, right tibia and fibula, and two coprolites; GLAHM V1027, incomplete skull and mandible, atlas axis, four cervical vertebrae (from a young individual); GLAHM V1140, broken skull, mandible showing pathological damage, one hyoid, atlas axis, five cervical vertebrae, 14 dorsal vertebrae, scapulae, both coracoids, humeri, both radii, and femora; GLAHM V1142, skull, disarticulated mandible, one hyoid, atlas axis, right atlas rib, four cervical vertebrae, 19 dorsal vertebrae, two sacral vertebrae, four caudal vertebrae, pubes, ilia, ischia (fused), and femora; GLAHM V1143, skull broken in two, mandible, atlas ribs, five cervical vertebrae, four cervical ribs, 17 dorsal vertebrae, right scapula, right coracoid, right humerus (atlas axis and forelimb lost); LEICT G1301.1899, skull, disarticulated mandibular rami, atlas axis, two cervical vertebrae, 15 dorsal vertebrae, two sacral vertebrae, six caudal vertebrae, numerous ribs, right pubis, ilia, ischia, femora, right radius, ulnae, left astragulus and calcaneum, and fused tarsals; MGCL 9959, skull, mandible, associated dorsal and caudal vertebrae, humerus, femur; MGCL 9960, skull, mandible, associated cervical, dorsal and caudal vertebrae, isolated ribs, humerus, pubis, ischium, and femur; NHM R.1530, incomplete skull with mandible, atlas-axis, five cervical vertebrae, 16 dorsal vertebrae, two sacral vertebrae, 35 caudal vertebrae, cervical and dorsal ribs, coracoid, scapula, humeri, ilia, ischia, pubes, femora, tibiae, fibulae, isolated pes bones, and numerous chevrons; NHM R.1529, skull and mandible (from a young individual); NHM R.1666, skull and mandible; NHM R.2030, incomplete skull with mandible; NHM R.2032, incomplete skull and mandible, atlas axis, four cervical vertebrae, 17 dorsal vertebrae, two sacral vertebrae, 37 caudal vertebrae, cervical and dorsal ribs, scapula, coracoids, humerus, ilium, ischium, and femur; NHM R.2033, fragmentary skull with mandible, atlas axis, five cervical vertebrae, 17 dorsal vertebrae, two sacral vertebrae, 29 caudal vertebrae, cervical and dorsal ribs, ilia (fused), ischia (fused), pubes, one tibia, one fibula, and two metatarsals; NHM R.2036, fragments of skull and mandible, and one cervical vertebra; NHM R.2041, incomplete skull; NHM R.2044, skull and mandible; NHM R.2049, incomplete skull and mandible, two dorsal vertebrae, one sacral vertebra,

ilia, ischia, femora, tibiae, fibulae, and isolated bones of the pes; NHM R.2051, incomplete skull with mandible, atlas axis, four cervical vertebrae, 15 dorsal vertebrae, two sacral vertebrae, 32 caudal vertebrae, coracoid, scapula, ilia, ischia, pubes, femora, broken tibiae and fibulae, and isolated pes bones; NHM R.2053, incomplete skull; NHM R.2054, skull, mandible, atlas axis, four cervical vertebrae, 18 dorsal vertebrae, two sacral vertebrae, 28 caudal vertebrae, cervical and dorsal ribs, ilium, ischium, pubes, tibia, fibula, isolated pes bones, numerous chevrons; NHM R.2055, incomplete skull; NHM R.2056, fragments of skull and mandible (from a very young individual); NHM R.2058, skull with mandibular symphysis; NHM R.2065, skull fragments (from a young individual); NHM R.2069, fragments of skull and mandible, atlas axis and three cervical vertebrae (from a very young individual); NHM R.3016, incomplete skull, mandible, right coracoid, scapulae, humeri, radius, ulna; NHM R.3900, rostrum; NHM R.6859, skull with disarticulated mandible; NHM R.6860, skull with disarticulated mandible; RMS M150, incomplete skull with mandible; NMING F16892, skull with disarticulated mandible, and 16 associated vertebrae; NMING F21731, skull with disarticulated mandible, 28 associate vertebrae, and ilia; NMW 19.96 G21, skull with mandible; PETMG R8, skull lacking rostrum; PETMG R10, incomplete skull; PETMG R20, incomplete skull; PETMG R42, incomplete skull; PETMG R180, incomplete skull; SMNS 10115, skull with disarticulated mandible; SMNS 10116, skull with disarticulated mandible.

Note: The correct spelling is *M. superciliosus*, not *M. superciliosum*. Lydekker (1890b) amended the epithet based on the neuter suffix, rather than retaining the masculine suffix (i.e. *-sum* instead of *-sus*). In accordance with the code of the ICZN, Article 30.1.3, the gender of the generic and epithet name must match, and as *Metriorhynchus* is masculine (*-rhynchus* is the Latinized form of the Ancient Greek *-rhynchos*) *-sus* is the correct suffix.

GRACILINEUSTES GEN. NOV.

Type species: Gracilineustes leedsi (Andrews, 1913) comb. nov.

Valid species: Gracilineustes acutus (Lennier, 1887) comb. nov.; *Gr. leedsi* (Andrews, 1913) comb. nov.

Etymology: 'Gracile swimmer'. In reference to the slender nature of both their longirostrine crania and postcrania in comparison with other Callovian forms.

Geological range: Middle Callovian–upper Kimmeridgian.

Geographical range: European endemic (England, France, and Switzerland).

Diagnosis: Metriorhynchid thalattosuchian with over 28 teeth per maxilla, and more than 20 teeth per dentary; lacking conspicuous ornamentation on the cranial bones; the antorbital fossa is elongate, narrow, and oriented obliquely, and is enclosed by the lacrimal, maxilla, and jugal; the antorbital pseudofenestra is enclosed by the lacrimal, nasal, and maxilla; the internal nares opens out posteriorly into the buccal cavity, with the palatines creating a broad U-shape, directed anteriorly; the maxilla–palatine suture forms an M-shape, orientated posteriorly; the squamosal contributes less than 50% to the supratemporal arch; the squamosal projects further caudally than the occipital condyle; the mandibular symphysis depth is ~4% of the total mandible length; the length of the cervical centrum is shorter than its height; the tibia is roughly one third of the length of the femur; the atlas hypocentrum is subequal in length to the odontoid process length; the humerus is smaller in length than the scapula; the ischium anterior process lacks either articulation facet.

GRACILINEUSTES ACUTUS (LENNIER, 1887) COMB. NOV.

1887 *Metriorhynchus acutus* sp. nov.; Lennier

Holotype: Destroyed/lost during the Second War World (complete skull).

Type locality: Calvados, Normandy, France.

Etymology: 'Sharp-pointed gracile swimmer', because the holotype skull had a very thin snout that gave it a 'sharper' appearance.

Geological range: Lower Kimmeridgian (*cymodoce* ammonite zone).

Geographical range: Normandy, France.

GRACILINEUSTES LEEDSI (ANDREWS, 1913) COMB. NOV.

1913 *Metriorhynchus leedsi* sp. nov.; Andrews
1913 *Metriorhynchus laeve* sp. nov.; Andrews
1936 *Metriorhynchus laevis* [sic]; Kunh
1968 *Metriorhynchus loeve* [sic]; Wenz

Holotype: NHM R.3540, dorsoventrally crushed skull, with premaxilla not preserved.

Type locality: Peterborough, Cambrigeshire, England (middle Oxford Clay Formation).

Etymology: 'Leeds' gracile swimmer'. Named after Alfred Leeds, a quarry owner and amateur palaeontologist, from whose quarry a diverse assemblage of Oxford Clay marine reptiles were discovered.

Geological range: Middle–late Callovian (*calloviense–lamberti* ammonite zones).

Geographical range: Cambridgeshire and Wiltshire, England.

Referred specimens: CAMSM J64297, skull with mandible; GLAHM V973, skull with mandible; GLAHM V974, incomplete skull; GLAHM V975, incomplete skull; NHM R.2031, incomplete skull; NHM R.2042, skull, mandible, atlas axis, three cervical vertebrae, and numerous crushed vertebrae and ribs; NHM R.3014, complete skull, mandible, atlas axis, five cervical vertebrae, 16 dorsal vertebrae, two sacral vertebrae, 35 caudal vertebrae, cervical and dorsal ribs, right coracoids and scapula, humeri, right femur, tibia, fibula, and almost complete tarsus and pes, and numerous chevrons; NHM R.3015, complete skull, mandible, atlas axis, five cervical vertebrae, 16 dorsal vertebrae, cervical and dorsal ribs, coracoid, scapula, humerus, femur (holotype of *M. laeve*); NHM R.3899, incomplete skull; NHM R.5793, incomplete skull; PETMG R24, incomplete skull; PETMG R72, incomplete skull.

RHACHEOSAURUS VON MEYER, 1831

Racheosaurus Giebel, 1846 [sic]

Type species: Racheosaurus gracilis von Meyer, 1831.

Holotype: Lost; however, two plastotypes survive (of the vertebral column and hindlimbs): AMNH FR 4804 and NHM R.3961.

Etymology: 'Spine lizard'. *Rhacheos-* is Ancient Greek for 'backbone' or 'spine', in reference to the holotype, which was a vertebral column with limbs and girdles.

Geological range: Lower Tithonian (*hybonotum* ammonite zone).

Geographical range: European endemic (Germany).

Diagnosis: Metriorhynchid thalattosuchian with procumbent teeth, with no lateromedial compression, and lacking carinae; cranial bones smooth, and lacking conspicuous ornamentation; rounded, almost 90° angle formed by the lateral and medial processes of the frontal; the dorsal margin of the supratemporal arcade is lower than the medial process of the frontal; eyes as large as the supratemporal fenestra; infratemporal flange absent; surangular and angular well-developed, extending rostrally beyond the orbits; the symphysial part of the mandible is low, only about 15-mm high; the lateral margin of the prefrontals is rounded; the external nares are not wholly bifurcated by the premaxillary septum; the external nares begin just after the first premaxillary alveolus, and do not exceed the first maxillary alveolus; the humerus deltopectoral crest is absent; the hypocercal tail possesses a fleshy upper lobe.

RHACHEOSAURUS GRACILIS VON MEYER, 1831

1831 *Rhacheosaurus gracilis* gen. et sp. nov.; von Meyer
1858 *Cricosaurus medius* sp. nov.; Wagner
1901 *Geosaurus medius* comb. nov.; Fraas
1901 *Geosaurus gracilis* comb. nov.; Fraas

Holotype: Lost; however, two plastotypes survive (of the vertebral column and the hindlimbs): AMNH FR 4804 and NHM R.3961.

Type locality: Daiting, Bayern, Germany (Mörnsheim Formation).

Etymology: 'Gracile spine lizard'.

Geological range: Lower Tithonian (*hybonotum* ammonite zone).

Geographical range: Bayern, Germany.

Referred specimens: NHM R.3948, complete skeleton preserved in lithographic limestone, including impression of upper caudal tail lobe, with skull, removed from rock, and intact three-dimensionally; HMN R 3635.1–2, incomplete forelimb preserved in lithographic limestone, lacking humerus and distalmost phalanges.

CRICOSAURUS WAGNER, 1858

Neustosaurus Raspail, 1842 (*nomen dubium*)
Enaliosuchus Koken, 1883
Crikosaurus Kotsakis & Nicosia, 1980 [sic]

Type species: Cricosaurus elegans (Wagner, 1852) Wagner, 1858.

Valid species: Cricosaurus araucanensis (Gasparini & Dellapé, 1976) Young & Andrade, 2009; *C. elegans* (Wagner, 1852) Wagner, 1858; *Cricosaurus gracilis* (Philips, 1871) Young & Andrade, 2009; *Cricosaurus macrospondylus* (Koken, 1883) Young & Andrade, 2009; *C. saltillense* (Buchy *et al.*, 2006) Young & Andrade, 2009; *Cricosaurus schroederi* (Kuhn, 1936) Young & Andrade, 2009; *Cricosaurus suevicus* (Fraas, 1901) Young & Andrade, 2009; *Cricosaurus vignaudi* (Frey *et al.*, 2002) Young & Andrade, 2009.

Potentially valid species: The revaluation of *Plesiosaurus* (*Polyptychodon*) *mexicanus* Wieland, 1910 as a metriorhynchid, and not a sauropterygian, suggests that there is possibly another species of *Cricosaurus* in Mexico (see Buchy, 2008b). The dental and rostral morphology is consistent with *Cricosaurus* (procumbent, uncarinated, uncompressed crowns, with fine longitudinal ridges running from base to apex; tubular snout with the dentary and maxilla in parallel), and herein is provisionally referred to as ?*Cricosaurus mexicanus*.

Etymology: 'Ring lizard'. *Cricos-* is Ancient Greek for 'ring', referring to the large sclerotic rings preserved in the orbits of the holotype.

Geological range: Middle Oxfordian (*Cricosaurus* sp.; Gasparini & Iturralde-Vinent, 2001) to upper Valanginian (*C. macrospondylus* holotype; Koken, 1883; Karl *et al.*, 2006).

Geographical range: Cosmopolitan (Argentina, Chile, Cuba, England, France, Germany, Mexico, Russia, and Switzerland).

Diagnosis: Metriorhynchid thalattosuchian with procumbent teeth, with little to no lateromedial compression; cranial bones smooth, and lacking conspicuous ornamentation; an acute angle is formed by the lateral and medial processes of the frontal; the dorsal margin of the supratemporal arcade is lower than the medial process of the frontal; the eyes are as large as the supratemporal fenestra; the surangular and angular are well-developed, extending rostrally beyond the orbits; the symphysial part of the mandible is low, only about 15-mm high; the lateral margin of the prefrontals is rounded; the external nares are bifurcated by the premaxillary septum and terminate at the end of the second maxillary alveoli; the humerus deltopectoral crest is absent; the calca-

neum tuber is either absent or vestigial; the proximal end of metatarsal I is greatly enlarged.

CRICOSAURUS SP.

2001 *Geosaurus* sp.; Gasparini & Iturralde-Vinent
2009 *Cricosaurus* sp. comb. nov.; Young & Andrade

Specimen: MNHNCu P3009, skull and mandible articulating with deteriorated atlas axis.

Type locality: Viñales Valley, Western Cuba (Jagua Vieja Member of the Jagua Vieja Formation).

Geological range: Middle Oxfordian.

Geographical range: Western Cuba.

CRICOSAURUS ARAUCANENSIS (GASPARINI & DELLAPÉ, 1976) YOUNG & ANDRADE, 2009

1976 *Geosaurus araucanensis* sp. nov.; Gasparini & Dellapé
2009 *Cricosaurus araucanensis* comb. nov.; Young & Andrade

Holotype: MLP 72-IV-7-1, complete skull with mandible, vertebrae, ribs, and forelimb and scapula.

Type locality: Cerro Lotena, Province of Neuquén (Vaca Muerta Formation).

Geological range: Lower Tithonian.

Geographical range: Province of Neuquén, Argentina.

Referred specimens: MLP 72-IV-7-2, incomplete skull with right mandibular rami; MLP 72-IV-7-3, skull lacking occipital regions, with mandibular remains; MLP 72-IV-7-4, complete skull; MLP 86-IV-25-1, dentary fragments; MLP 86-XI-5-7, skull fragment; MACN-N 95, skull with mandible, articulated with cervicodorsal vertebrae; MACN-N 64, anterior tip of rostrum.

Note: There are more specimens referable to *Cricosaurus* from the middle and upper Tithonian, and the lower Berriasian, levels of the Vaca Muerta Formation, Argentina, and the upper Tithonian of Chile (see Pol & Gasparini, 2007, 2009, and references therein).

CRICOSAURUS ELEGANS (WAGNER, 1852) WAGNER, 1858

1852 *Stenosaurus elegans* [sic] sp. nov.; Wagner
1858 *Cricosaurus elegans* gen. et comb. nov.; Wagner

1888a *Metriorhynchus elegans* comb. nov.; Lydekker
2009 *Cricosaurus elegans* comb. nov.; Young & Andrade

Holotype: BSPG AS I 504, complete cranium preserved in lithographic limestone.

Type locality: Daiting, Bayern, Germany (Mörnsheim Formation).

Etymology: 'Slender ring lizard'.

Geological range: Lower Tithonian (*hybonotum* ammonite zone).

Geographical range: Bayern, Germany.

Referred specimen: BSPG 1977 XIX 38, skull preserved in lithographic limestone.

CRICOSAURUS GRACILIS (PHILIPS, 1871) YOUNG & ANDRADE, 2009

1871 *Steneosaurus gracilis* sp. nov.; Philips
1885 *Metriorhynchus gracile* [sic] comb. nov.; Woodward
1986 *Geosaurus* sp.; Taylor & Benton
2009 *Cricosaurus gracilis* comb. nov.; Young & Andrade

Holotype: OXFUM J.1431, skull encased in matrix, lacking snout.

Type locality: Shotover, Oxfordshire, England (upper Kimmeridge Clay Formation).

Etymology: 'Gracile ring lizard'.

Geological range: Lower Tithonian (*pectinatus* ammonite zone).

Geographical range: Oxfordshire, England.

CRICOSAURUS MACROSPONDYLUS (KOKEN, 1883) YOUNG & ANDRADE, 2009

1883 *Enaliosuchus macrospondylus* gen. et sp. nov.; Koken
2006 *Metriorhynchus* sp.; Karl *et al.*
2009 *Cricosaurus macrospondylus* comb. nov.; Young & Andrade

Holotype: HMN R3636.1–6, atlas axis, and numerous cervical and dorsal vertebrae.

Type locality: Hills near Osterwald, Lower Saxony, Germany.

Etymology: 'Ring lizard with large vertebrae'.

Geological range: Lower–upper Valanginian (*campylotoxus–furcillata* ammonite zones).

Geographical range: Hautes Alpes, France, and Lower Saxony, Germany.

Referred specimen: RNGHP 990201, dorsoventrally crushed skull, lacking occipital region.

CRICOSAURUS SALTILLENSE (BUCHY ET AL., 2006) YOUNG & ANDRADE, 2009

2006 *Geosaurus saltillense* sp. nov.; Buchy *et al.*
2009 *Cricosaurus saltillense* comb. nov.; Young & Andrade

Holotype: MUDE CEP1823, poorly preserved skull, lacking snout, and postcranium.

Type locality: Sierra de Buñuelas, near Gomez Farías, State of Coahuila, Mexico (La Caja Formation).

Etymology: 'Ring lizard from the county of Saltillo'.

Geological range: Lower Tithonian.

Geographical range: State of Coahuila, Mexico.

CRICOSAURUS SCHROEDERI (KUHN, 1936) YOUNG & ANDRADE, 2009

1936 *Enaliosuchus Schröderi* sp. nov.; Kuhn
2009 *Cricosaurus schroederi* comb. nov.; Young & Andrade

Holotype: MMGLV unnumbered, skull with mandible, lacking snout, and atlas axis and cervical three.

Type locality: Sachsenhagen, Lower Saxony, Germany ('*Platylenticeras* beds').

Etymology: 'Schröder's ring lizard'.

Geological range: Lower Valanginian.

Geographical range: Lower Saxony, Germany.

CRICOSAURUS SUEVICUS (FRAAS, 1901) YOUNG & ANDRADE, 2009

1901 *Geosaurus suevicus* sp. nov.; Fraas
2005 *Geosaurus suevecicus* [sic]; Mueller-Töwe
2009 *Cricosaurus suevicus* comb. nov.; Young & Andrade

Lectotype: SMNS 9808, complete skeleton preserved in limestone.

Type locality: Nusplingen, Baden-Württemberg, Germany (Nusplinger Plattenkalk).

Geological range: Upper Kimmeridgian (*beckeri* ammonite zone).

Geographical range: Baden-Württemberg, Germany.

Referred specimen: SMNS 90513, complete skeleton preserved in limestone.

CRICOSAURUS VIGNAUDI (FREY *ET AL.*, 2002) YOUNG & ANDRADE, 2009

1993 *Geosaurus* sp.; Stinnesbeck *et al.*
2002 *Geosaurus vignaudi* sp. nov.; Frey *et al.*
2009 *Cricosaurus vignaudi* comb. nov.; Young & Andrade

Holotype: UANL FCT-R1, incomplete skull and mandible, altas axis, and two cervical vertebrae.

Type locality: Mazatepec, State of Puebla, Mexico (La Pimienta Formation).

Etymology: 'Vignaud's ring lizard'. Named in honour of Patrick Vignaud, who has worked to greatly elucidate thalattosuchian palaeobiology and taxonomy.

Geological range: Middle Tithonian.

Geographical range: State of Puebla, Mexico.

GEOSAURINAE

SUCHODUS LYDEKKER, 1890A

Type species: Suchodus durobrivensis Lydekker, 1890a.

Valid species: Suchodus brachyrhynchus (Eudes-Deslongchamps, 1868a) comb. nov.; *S. durobrivensis* Lydekker, 1890a.

Etymology: 'Crocodile tooth'. *Suchos* is the Ancient Greek for 'Sobek' (the Ancient Egyptian crocodile god), whereas *-dus* is the Ancient Greek for 'tooth'.

Geological range: Lower Callovian–lower Oxfordian.

Geographical range: European endemic (England and France).

Emended diagnosis: Metriorhynchid thalattosuchian with less than 18 teeth per maxilla, and less than 18 teeth per dentary; variable ornamentation on the cranial bones, but lacking conspicuous ornamentation on the rostrum; the antorbital fossa is elongate, narrow, and oriented obliquely, and is enclosed by the lacrimal, maxilla, and jugal; the antorbital pseudofenestra is enclosed by the lacrimal, nasal, and maxilla; the internal nares opens out posteriorly into the buccal cavity, with the palatines creating an M-shape orientated anteriorly; the prefrontals are wider than the posteriorly orientated 'V' of the squamosal, created by the posterior margin of the supratemporal fossa; the prefrontals are greatly expanded over the orbits, with the lateral margins forming a 90° angle, giving it a distinct triangular shape; the postorbital process forming the supratemporal arch creates a 90° angle facing anterolaterally; the squamosal overlaps the parocciptial process extensively, projecting further caudally than the parocciptal process itself; the maxilla–palatine suture forms a broad U-shape, orientated anteriorly; the coronoid does not project rostrally as far as the tooth row; the mandibular symphysis depth is ~7–8% of the total mandible length; the squamosal contributes less than 50% to the supratemporal arch; the length of the cervical centrum is longer than its height; the atlas hypocentrum is longer in length than the odontoid process; the humerus is subequal in length to the scapula.

SUCHODUS BRACHYRHYNCHUS (EUDES-DESLONGCHAMPS, 1868) COMB. NOV.

1864 'Téléosaure du Mesnil de Bavent'; Eudes-Deslongchamps
1868a *Teleosaurus brachyrhynchus* sp. nov.; Eudes-Deslongchamps
1869 *Metriorhynchus brachyrhynchus* comb. nov.; Eudes-Deslongchamps
1913 *Metriorhynchus cultridens* sp. nov.; Andrews

Holotype: Lost during the Second World War (almost complete skull).

Type locality: Calvados, Normandy, France (Oxford Clay Formation).

Neotype: NHM R.3700, skull lacking the tip of the premaxilla.

Neotype locality: Peterborough, Cambridgeshire, England (middle Oxford Clay Formation).

Etymology: 'Crocodile-toothed with a short snout'. Named because it was the first 'brevirostrine' form discovered, from *brachus*, the Ancient Greek for 'short'.

Geological range: Lower Callovian–lower Oxfordian (*koenigi–mariae* ammonite zones).

Geographical range: Cambridgeshire, England, and Normandy and Poitou, France

Referred specimens: CAMSM J64267, mandibular rami from a large individual; GLAHM V978, skull with mandible; GLAHM V993, skull, four cervical vertebrae, 13 dorsal vertebrae, two sacral vertebrae, three caudal vertebrae, dorsal ribs, pubes, right ilium, ischia, and left femur; GLAHM V995, skull, mandible, three cervical vertebrae, 16 dorsal vertebrae, cervical ribs, pubes, ilia, left ischium, femora, and isolated manus bones; GLAHM V1145, left coracoid, proximal half of the right coracoid, right humerus, right ilium, left femur, and seven tooth crowns; LEICT G418.1956.13, skull fragment, ischia, femora, and numerous ribs and chevrons; NHM R.3541, incomplete skull; NHM R.3699, incomplete skull; NHM R.3804, complete skull (three-dimensionally intact), mandible, atlas-axis, four cervical vertebrae, 16 dorsal vertebrae, two sacral vertebrae, 37 caudal vertebrae, cervical and dorsal ribs, ilium, ischia, pubes, femora, and isolated pes bones (holotype of *M. cultridens*); NHM R.3939, incomplete skull, mandible, and eight distorted vertebrae; PETMG R176, skull with mandible.

SUCHODUS DUROBRIVENSIS LYDEKKER, 1890A

1890a *Suchodus durobrivensis* gen. et sp. nov.; Lydekker
1913 *Metriorhynchus durobrivense* comb. nov. et unjust. emend.; Andrews

Holotype: NHM R.1994, mandibular symphysis.

Type locality: Near Water Newton (now within Peterborough), Cambridgeshire, England (middle Oxford Clay Formation).

Etymology: 'Crocodile-toothed from Durobrivae'.

Geological range: Middle–upper Callovian (*jason–lamberti* ammonite zones).

Geographical range: Cambridgeshire, England, and Normandy, France.

Referred specimens: NHM R.2039, incomplete skull, left mandibular rami; NHM R.2618, skull with articulated mandible, atlas axis, four cervical vertebrae, 14 dorsal vertebrae, two sacral vertebrae, numerous caudal vertebrae, cervical and dorsal ribs, left ilium, pubes, femora, tibia, fibula, and isolated pes bones; NHM R.3321, incomplete skull; PETMG R19, incomplete skull lacking rostrum.

Note: The correct spelling is *S. durobrivensis* not *S. durobrivense*. Andrews (1913) amended the epithet based on the neuter suffix, rather than retaining the masculine suffix (i.e. *-se* instead of *-sis*). In accordance with the code of the ICZN, Article 30.1.3, the gender of the generic and epithet name must match, and as *Suchodus* is masculine, *-sis* is the correct suffix.

PURRANISAURUS RUSCONI, 1948

Type species: Purranisaurus potens Rusconi, 1948.

Valid species: Purranisaurus casamiquelai (Gasparini & Chong, 1977) comb. nov.; *P. potens* Rusconi, 1948; *Purranisaurus westermanni* (Gasparini, 1980) comb. nov.

Geological range: Lower Callovian–lower Tithonian.

Geographical range: South American endemic (Argentina and Chile).

Emended diagnosis: Metriorhynchid thalattosuchian with less than 18 teeth per maxilla, and more than 20 teeth per dentary; all teeth lack carinae; lacks conspicuous ornamentation on the cranial bones; the antorbital fossa is elongate, narrow, and oriented obliquely, and is enclosed by the lacrimal, maxilla, and jugal; the antorbital pseudofenestra is enclosed by the lacrimal, nasal, and maxilla; the supratemporal arch in lateral view is straight; the internal nares opens out posteriorly into the buccal cavity, with the palatines creating an M-shape orientated anteriorly; the maxilla–palatine suture forms a broad U-shape orientated anteriorly; the paroccipital process terminates with a sharp incline dorsolaterally; the squamosal contributes less than 50% to the supratemporal arch.

PURRANISAURUS CASAMIQUELAI (GASPARINI & CHONG, 1977) COMB. NOV.

1977 *Metriorhynchus casamiquelai* sp. nov.; Gasparini & Chong

Holotype: MGHF 1-08573, skull and mandible.

Type locality: Quebrada Sajasa, Región de Antofagasta, Chile.

Geological range: Middle Callovian.

Geographical range: Region of Antofagasta, Chile.

Referred specimens: MGHF 1-181097, midsection of a large skull (across the prefrontals) (from Sierra Candeleros, Región de Antofagasta).

PURRANISAURUS POTENS RUSCONI, 1948

1948 *Purranisaurus potens* gen. et sp. nov.; Rusconi
1973 ?*Metriorhynchus potens*; Gasparini
1985 *Metriorhynchus potens* comb. nov.; Gasparini
2007 *Metriorhynchus* sp.; Pol & Gasparini

Holotype: MJCM PV 2060, posterior and midportion of the skull, and a fragment of the mandible.

Type locality: Malargüe, Province of Mendoza, Argentina.

Geological range: Lower Tithonian.

Geographical range: Province of Mendoza, Argentina.

PURRANISAURUS WESTERMANNI (GASPARINI, 1980) COMB. NOV.

1980 *Metriorhynchus westermanni* sp. nov.; Gasparini

Holotype: MGHF 1-010199, skull with mandible.

Type locality: Placilla de Caracoles, Región de Antofagasta, Chile (Mina Chica Formation).

Geological range: Middle Callovian.

Geographical range: Region of Antofagasta, Chile.

Referred specimens: MDA1, posterior half of skull (Sierra del Medio, Región de Antofagasta, Chile; Vergara Formation).

Note: This species was recently revalidated (see Gasparini *et al.*, 2008).

GEOSAURUS CUVIER, 1824

Halimnosaurus Ritgen, 1826
Brachytaenius von Meyer, 1842
Ltliminosaurus [sic] Romer, 1966

Type species: Geosaurus giganteus (von Sömmerring, 1816) Cuvier, 1824 *sensu* von Quenstedt, 1852.

Valid species: Geosaurus carpenteri (Wilkinson *et al.*, 2008) Young & Andrade, 2009; *G. giganteus* (von Sömmerring, 1816) Cuvier, 1824 *sensu* von Quenstedt, 1852; *Geosaurus grandis* (Wagner, 1858) von Zittel, 1887–1890; Geosaurus *lapparenti* (Debelmas & Strannoloubsky, 1957) Young & Andrade, 2009.

Etymology: 'Earth lizard'. *Ge-* is the Ancient Greek for 'earth' (in the sense of ground), as the holotype was found within the limestones of Germany.

Geological range: Lower Oxfordian (*cordatum* ammonite zone; NHM 36336 and NHM 36339)–upper Valanginian (*peregrinus* ammonite zone; *G. lapparenti*).

Geographical range: European endemic (England, France, Germany, Italy, and Switzerland).

Diagnosis: Metriorhynchid thalattosuchian with strongly lateromedially compressed teeth, and with a keeled denticulate carinae; the premaxillary, maxillary, and dentary teeth are tri-faceted upon their labial surface; there is a notch at the premaxilla–maxilla contact that an enlarged dentary tooth fits into; upper and lower jaw dentition arranged as opposing blades; cranial bones smooth, lacking conspicuous ornamentation; acute angle formed by the lateral and medial processes of the frontal; surangular poorly developed, terminating caudal to the anterior margin of the orbit; mandibular symphysis terminating prior to the antorbital fossa; robust and well-developed sclerotic ring encompassing the entire orbit.

GEOSAURUS CARPENTERI (WILKINSON ET AL., 2008) YOUNG & ANDRADE, 2009

1996 *Metriorhynchus superciliosus*; Blainville, 1853 (*sensu* Grange & Benton)
2006 *Metriorhynchus carpenteri* manuscript name; Young
2008 *Dakosaurus carpenteri* sp. nov.; Wilkinson *et al.*
2009 *Geosaurus carpenteri* comb. nov.; Young & Andrade

Holotype: BRSMG Ce17365, incomplete skull.

Type locality: Westbury, Wiltshire, England (lower Kimmeridge Clay Formation).

Etymology: 'Carpenter's earth lizard'. Named in honour of its discoverer, Simon Carpenter.

Geological range: Upper Kimmeridgian (*mutabilis–eudoxus* ammonite zones).

Geographical range: Wiltshire, England.

Referred specimens: BRSMG Cd 7203: isolated postcranial remains (see Wilkinson *et al.*, 2008).

GEOSAURUS GIGANTEUS (VON SÖMMERRING, 1816) CUVIER, 1824 *SENSU* VON QUENSTEDT, 1852

1816 *Lacerta gigantea* sp. nov.; von Sömmerring
1824 *Lacerta* (*Geosaurus*) *gigantea* subgen. nov.; Cuvier
1826 *Halilimnosaurus crocodiloides* gen. et sp. nov.; Ritgen
1829 *Mosasaurus Bavaricus* epithet nov.; Holl
1831 *Geosaurus Sömmerringii* epithet nov.; von Meyer
1842 *Brachytaenius perennis* gen. et sp. nov.; von Meyer
1852 *Geosaurus giganteus* just. emend.; von Quenstedt
1859 *Geosaurus Sömmerringi* just. emend.; von Meyer
1869 *Mosasaurus giganteus* comb. nov.; Cope

Holotype: NHM R.1229, incomplete skull and mandible, lacking snout and occiput.

Type locality: Daiting, Bayern, Germany (Mörnsheim Formation).

Etymology: 'Giant earth lizard'.

Geological range: Lower Tithonian (*hybonotum* ammonite zone).

Geographical range: Bayern, Germany.

Referred specimens: NHM R.1230, postcranial remains preserved in limestone (found with holotype); NHM 37016, isolated tooth-crown; NHM 37020, skull preserved in limestone.

GEOSAURUS GRANDIS (WAGNER, 1858) VON ZITTEL, 1887–1890

1858 *Cricosaurus grandis* sp. nov.; Wagner
1887–90 *Geosaurus grandis* comb. nov.; von Zittel
1888 *Metriorhynchus grandis* comb. nov.; Lydekker

Holotype: BSPG AS VI 1, complete skull with mandible.

Type locality: Daiting, Bayern, Germany (Mörnsheim Formation).

Etymology: 'Large earth lizard'.

Geological range: Lower Tithonian (*hybonotum* ammonite zone).

Geographical range: Bayern, Germany.

GEOSAURUS LAPPARENTI (DEBELMAS & STRANNOLOUBSKY, 1957) YOUNG & ANDRADE, 2009

1952 *Dacosaurus maximus* var. *gracilis*; von Quenstedt (*sensu* Debelmas)
1957 *Dacosaurus lapparenti* [sic] sp. nov.; Debelmas & Strannoloubsky
2009 *Geosaurus lapparenti* comb. nov.; Young & Andrade

Holotype: UJF-ID.11847, isolated cranial remains, cervical and caudal vertebrae, and pectoral girdle elements.

Type locality: La Martre, Provence, France.

Etymology: 'Lapparent's earth lizard'.

Geological range: Upper Valanginian (*peregrinus* ammonite zone).

Geographical range: Provence, France.

'PORTOMAGGIORE CROCODILE'

1956 cocodrillo di Portomaggiore; Leonardi
1980 ?*Metriorhynchus*; Kotsakis & Nicosia
1995 *Metriorhynchus brachyrhynchus*; Eudes-Deslongchamps, 1867 (*sensu* Vignaud)
1996 *Metriorhynchus* sp.; Bizzarini

Holotype: incomplete skull with mandible, preserved in limestone; slab and counter-slab housed in the Department of Earth Sciences of Bologna University, and the Museum of Palaeontology and Prehistory of Ferrara University.

Type locality: Unknown. Possibly from Sant'Ambrogio di Valpolicella, Verona Province, Italy (Rosso Ammonitico Formation) (see Bizzarini, 1996).

Geological range: If the locality is correct, Middle or upper Oxfordian (see Bizzarini, 1996).

DAKOSAURUS VON QUENSTEDT, 1856

Dacosaurus Sauvage, 1873
Plesiosuchus Owen, 1884
Aggiosaurus Ambayrac, 1913

Type species: Dakosaurus maximus (Plieninger, 1846) von Quenstedt, 1856.

Valid species: Dakosaurus andiniensis Vignaud & Gasparini, 1996; *D. maximus* (Plieninger, 1846) von Quenstedt, 1856; *Dakosaurus manselii* (Hulke, 1870) Woodward, 1885; *Dakosaurus nicaeensis* (Ambayrac, 1913) Young & Andrade, 2009.

Potentially valid species: Dakosaurus lissocephalus Seeley, 1869.

Putative species (1): Isolated *Dakosaurus* teeth have long been known from the lower Oxfordian of England (Lydekker, 1890b) and the Middle Oxfordian of Poland (Jentzsch, 1884; Gallinek, 1895). These teeth are far smaller and less robust than those from the upper Oxfordian onwards, and possibly represent a distinct species.

Putative species (2): The incomplete *Dakosaurus* cranial specimens known from the late lower Kimmeridgian/early upper Kimmeridgian of Mexico represent at least one distinct taxon (Buchy *et al.*, 2007; Buchy, 2008a).

Putative species (3): A vertebrae and fifth metatarsal known from the upper Tithonian or lower Berriasian of Khoroshevskii Island, Volga Region, Russia, have been suggested to belong to *Dakosaurus* (Ochev, 1981).

Teeth taxa: Most of the isolated teeth of *Dakosaurus* recovered in Europe have automatically been assigned to *D. maximus* (e.g. see Steel, 1973). However, as the phylogeny in Young & Andrade (2009) has demonstrated, the contemporaneous species *D. maximus* and *D. manselii* have distinct cranial apomorphies. As such, only teeth from the Swabian Alb of the uppermost Kimmeridgian and lowermost Tithonian are here considered to belong to *D. maximus*. All other isolated teeth are hereby referred to *Dakosaurus* sp. until further studies can determine if the tooth-crowns possess species-level apomorphies.

Invalid species: Dakosaurus amazonicus was erected by Giebel (1870) for vertebrae and teeth found in the Amazon. However, Gervais (1876) erected the name *Dinosuchus terror* (currently considered to be an alligatorid closely related to *Purussaurus*) for the material. Giebel (1876) considered *Dinosuchus terror* to be a junior synonym of *Dakosaurus amazonicus*.

Etymology: 'Tearing lizard'. *Dakos-* is Ancient Greek for 'to tear', referring to the large, lateromedially compressed, and serrated teeth.

Geological range: Lower Oxfordian (*mariae* ammonite zone; NHM 47989)–lower Berriasian (Gasparini *et al.*, 2006).

Geographical range: Cosmopolitan (Argentina, England, France, Germany, Mexico, Poland, and Switzerland; and possibly Russia).

Diagnosis: Metriorhynchid thalattosuchian with large robust teeth, with little lateromedial compression, and with the carinae formed by denticles that are wider transversely than in the root–apex direction; cranial bones smooth, lacking conspicuous ornamentation; acute angle formed by the lateral and medial processes of the frontal; the supratemporal fenestrae reach the minimum intraorbital distance; the lateral mandibular groove possesses a well-developed foramen at either end; surangular poorly developed, terminating caudal to the anterior margin of the orbit; the distance between the ventral margin of the antorbital fenestra and the ventral margin of the tooth row is greater than the diameter of the antorbital fenestra; the cross-sectional thickness of the cranial bone is generally > 1.5 mm.

DAKOSAURUS ANDINIENSIS VIGNAUD & GASPARINI, 1996

1985 *Metriorhynchus* aff. *durobrivensis*; Gasparini
1995 *Dakosaurus* sp.; Vignaud
1996 *Dakosaurus andiniensis* sp. nov.; Vignaud & Gasparini

Holotype: MHNSR PV344, poorly preserved snout lacking teeth.

Type locality: Catan Lil, Province of Mendoza, Argentina (Vaca Muerta Formation).

Etymology: 'Tearing lizard from the Andes'.

Geological range: Upper Tithonian–lower Berriasian.

Geographical range: Provinces of Mendoza and Neuquén, Argentina.

Referred specimens: MOZ 6146P, skull with articulated mandible and fragmentary postcrania (upper Tithonian of Pampa Tril, Neuquén Province); MOZ 6140P, anterior mandibular fragment (lower Berriasian of Pampa Tril, Neuquén Province).

DAKOSAURUS LISSOCEPHALUS SEELEY, 1869

1869 *Dakosaurus lissocephalus* sp. nov.; Seeley

Holotype: CAMSM J29419, skull lacking the snout.

Type locality: Ely, Cambridgeshire, England (lower Kimmeridge Clay Formation).

Etymology: 'Smooth-headed tearing lizard'. Named because the holotype lacks cranial ornamentation, from *lisso*, the Ancient Greek for 'smooth', and *cephalus*, the Ancient Greek for 'head'.

Geological range: Upper Kimmeridgian (*eudoxus* ammonite zone).

Geographical range: Cambridgeshire, England.

Note: Comparison between *D. maximus* (SMNS 8203) and the holotypes of *D. manselii*, and *D. lissocephalus*, leads to the conclusion that *D. manselii* and *D. lissocephalus* are not conspecific (M.T. Young, pers. observ.), as the shape of the supratemporal fenestra, squamosal, and parietal in *D. lissocephalus* is much more reminiscent of *D. andiniensis* and *D. maximus*, than *D. manselii*. However, until better-preserved material is found from Ely, Cambridgeshire, any synonymy between *D. maximus* and *D. lissocephalus* must remain provisional.

DAKOSAURUS MANSELII (HULKE, 1870) WOODWARD, 1885

1869 *Steneosaurus rostro-minor* Geoffroy Saint-Hilaire, 1825 (*sensu* Hulke)
1870 *Steneosaurus manselii* sp. nov.; Hulke
1884b *Plesiosuchus manselii* gen. et comb. nov.; Owen
1885 *Dakosaurus manselii* comb. nov.; Woodward

Holotype: NHM 40103, incomplete skull and mandible.

Type locality: Kimmeridge Bay, Dorset, England (lower Kimmeridge Clay Formation).

Etymology: 'Mansel's tearing lizard'. Named in honour of its discoverer.

Geological range: Upper Kimmeridgian (*austissiodorensis* ammonite zone).

Geographical range: Dorset, England.

DAKOSAURUS MAXIMUS (PLIENINGER, 1846) VON QUENSTEDT, 1856

1843 *Megalosaurus* sp.; von Quenstedt
1846 *Geosaurus maximus* sp. nov.; Plieninger
1856 *Dakosaurus maximus* gen. nov.; von Quenstedt
1871 *Liodon primaevum* sp. nov.; Sauvage
1873 *Dacosaurus primaevus* [sic] just. emend.; Sauvage

Holotype: isolated tooth, of unknown location.

Type locality: Schnaitheim, Baden-Württemberg, Germany (Mergelstätten Formation).

Neotype: SMNS 8203, incomplete skull and mandible.

Neotype locality: Staufen, Baden-Württemberg, Germany (Mergelstätten Formation).

Etymology: 'Great tearing lizard'.

Geological range: Upper Kimmeridgian (*beckeri* ammonite zone)–Lower Tithonian (*hybonotum* ammonite zone).

Geographical range: Baden-Württemberg and Bayern, Germany, and Canton Jura, Switzerland.

Referred specimens: NHM 33186, NHM 35766, NHM 35835–7, SMNS 8203, and SMNS 80148: all isolated teeth.

DAKOSAURUS NICAEENSIS (AMBAYRAC, 1913) YOUNG & ANDRADE, 2009

1913 *Aggiosaurus nicaeensis* sp. nov.; Ambayrac
2009 *Dakosaurus nicaeensis* comb. nov.; Young & Andrade

Holotype: MHNN unnumbered, poorly preserved upper jaw, preserved in limestone.

Type locality: Nice, France.

Etymology: 'Tearing lizard from Nice'.

Geological range: Upper Oxfordian.