

# What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany

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Received 28 March 2008; accepted for publication 20 October 2008

The holotype and referred specimens of *Geosaurus giganteus*, a metriorhynchid crocodile from the Tithonian (Upper Jurassic) of Germany, is redescribed, along with a historical overview of the genus and species. This taxon is unique among metriorhynchids as its serrated, strongly lateromedially compressed dentition is arranged as opposing blades, suggesting it was adapted to efficiently slice through fleshy prey. A new phylogenetic analysis of Crocodylomorpha is presented, which finds *G. giganteus* to be nested within what is currently considered *Dakosaurus*, whereas the other species currently assigned to *Geosaurus* form a clade with *Enaliosuchus* and the holotype of *Cricosaurus*. The phyletic relationship of *G. giganteus* with other metriorhynchids indicates that the current definition of the genus *Geosaurus* is polyphyletic, and that the inclusion of subsequent longirostrine species to this genus is in error. The re-analysis presented herein demonstrates *Geosaurus* to be composed of three species *sensu stricto*. The appropriate taxonomic amendments to the Metriorhynchidae are also provided.

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doi: 10.1111/j.1096-3642.2009.00536.x

ADDITIONAL KEYWORDS: *Cricosaurus* – Crocodylia – *Dakosaurus* – Mörnsheim Formation – Metriorhynchidae – phylogeny – *Rhacheosaurus*.

## INTRODUCTION

Crocodylia (crocodilians and their extinct relatives) was one of the most diverse clades of amniotes during the Mesozoic, in terms of both morphology and ecology. One of the prominent departures from the typical crocodylian bauplan is the Metriorhynchidae (Fitzinger, 1843), the only group of archosaurs entirely adapted to living in the marine realm (Steel, 1973). The Metriorhynchidae appeared in the Middle Jurassic, and diversified and dispersed throughout the Jurassic, with specimens found in South and Middle America, Europe, and Russia, and eventually became extinct during the Early Cretaceous (Hua & Buffetaut, 1997; Gasparini, Vignaud & Chong, 2000; Pierce & Benton, 2006). Note that we use the term Crocodylia Gmelin, 1789 to refer to the least inclusive

clade containing *Protosuchus richardsoni* (Brown 1933) and *Crocodylus niloticus* Laurenti, 1768, which was the broad use of the term throughout the 19<sup>th</sup> and 20<sup>th</sup> centuries (see Martin & Benton, 2008) for the clade also known as Crocodyliformes Hay, 1930 (*sensu* Benton & Clark, 1988).

The evolutionary intrarelationships of the Metriorhynchidae have long been neglected, and only recently has this begun to be rectified (Mueller-Töwe, 2005; Gasparini, Pol & Spalletti, 2006; Young, 2006, 2007). However, one of the most pressing issues is that regarding *Geosaurus*. The holotype of *Geosaurus*, *Geosaurus giganteus* (Von Sömmerring, 1816), has received very little attention, even though more species have been assigned to this genus in recent years (Gasparini & Dellapé, 1976; Frey *et al.*, 2002; Buchy *et al.*, 2006). In this paper, we revise the historical changes in the conception (and misconception) of the genus *Geosaurus*, redescribe the original

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specimens of *G. giganteus*, and produce a detailed cladistic analysis of the Metriorhynchidae. We also revise the definition of the genus *Geosaurus*, introducing a new taxonomy for the family.

#### HISTORICAL BACKGROUND: *LACERTA GIGANTEA* AND THE GENESIS OF *GEOSAURUS*

The holotype and postcranial remains of *G. giganteus* was described by Von Sömmerring (1816) as *Lacerta gigantea*. These specimens were given to Von Sömmerring by Count J. A. Reisach, and were discovered in a quarry in Daiting, near Monheim, Bayern, Germany (Mörnsheim Formation, Malm Zeta 3). The quarry is the same one that *Aelodon* [= *Steneosaurus priscus* (Sömmerring, 1814)] was found in, although *Geosaurus* was located approximately at a depth of 3 m, which is at twice the depth of the *Aelodon* find. Prior to preparation, Von Sömmerring (1816) mentioned that some of the blocks from which the type material was discovered were lost. This was a result of active excavation at the quarry, and it was not until later that fossils were discovered to be within the quarry blocks. Only five or six of these blocks could later be found. Both Von Sömmerring (1816) and Von Meyer (1859) concluded the deposits were marine in nature, based upon the discovery of fish scales, ammonites and bivalves in the matrix of the quarry blocks.

Upon discovery, and for many years subsequently, *G. giganteus* was believed to be a mosasaur (Von Sömmerring, 1816; Cuvier, 1824; Holl, 1829; Bronn, 1851–52; Von Quenstedt, 1852; Lydekker, 1888a). Von Sömmerring (1816) considered *L. gigantea* to be the same ‘leviathan’ as that known from the Cretaceous of Maastricht (now called *Mosasaurus hoffmannii* Mantell, 1829), assuming that it was a young individual because of its much smaller size. He used the lack of osteoderms (now known to be a metriorhynchid apomorphy) as evidence that *L. gigantea* was not a crocodylian. By 1816, the squamate nature of the Maastricht specimen had been clearly demonstrated (Camper, 1800). Therefore, the supposition that *L. gigantea* was not a crocodylian was also a reasonable one. The Maastricht specimen was not referred to the genus *Mosasaurus* until 1822 (Conybeare 1822), whereas the epithet *Hoffmannii* [sic] was erected later by Mantell (1829: 207). Nevertheless, this did not prevent Bronn (1851–52: 404) from considering *L. gigantea* to be a junior synonym of *M. hoffmannii*.

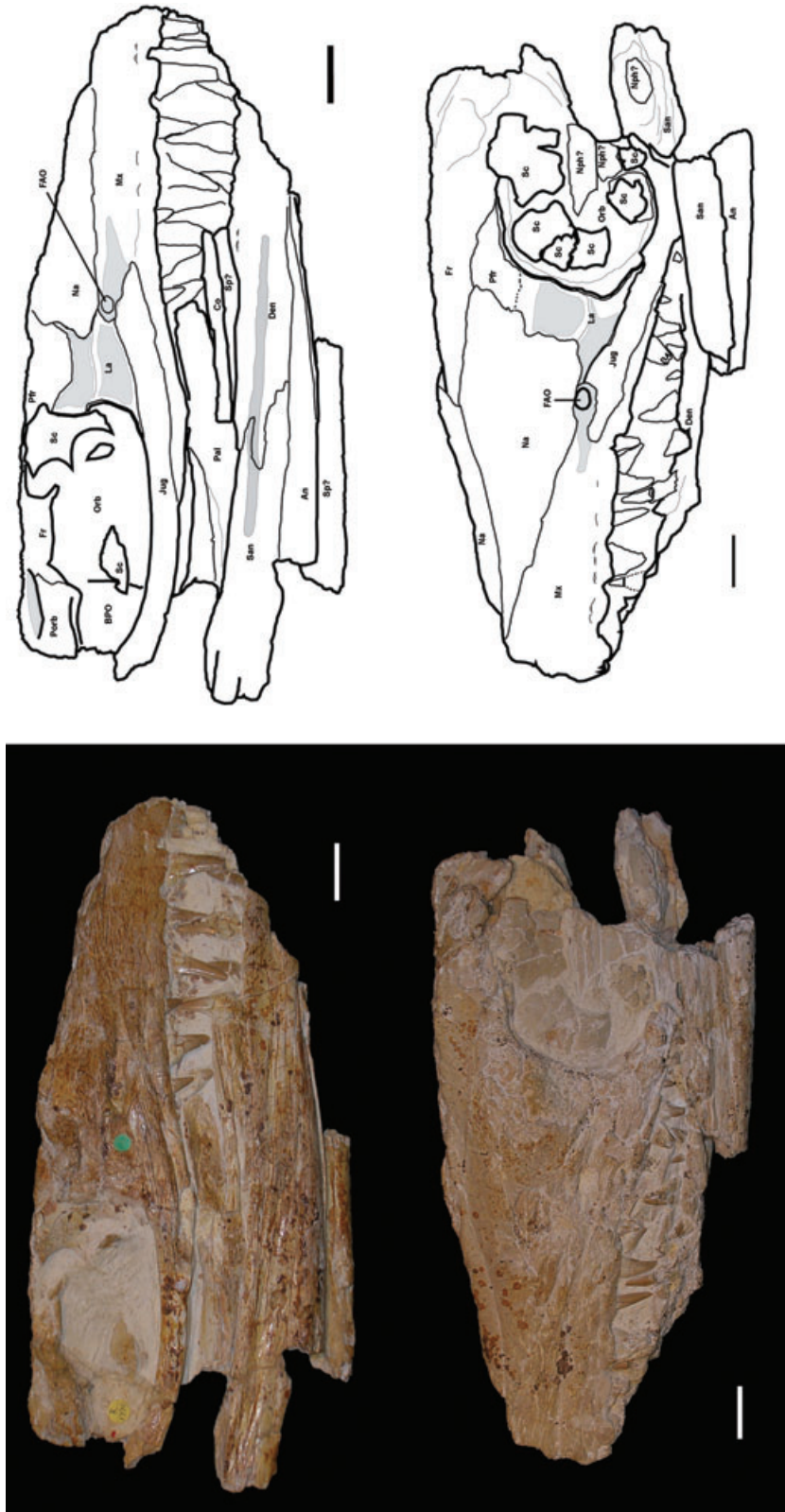
The name *Geosaurus* was first applied to *L. gigantea* when it was placed within its own subgenus by Cuvier (1824). He recognized its distinctiveness from the extant *Lacerta*, although he was of the opinion that it was ‘between the monitors and the crocodiles’, but was not a young individual of the Maastricht specimen. However, he felt he could not

retain the epithet *gigantea* for the species (‘Je ne peux lui laisser l’épithète gigantesque’) because of his inclusion of the much larger *Mosasaurus* as another subgenus of *Lacerta*. *Lacerta (Geosaurus) gigantea* (sensu Cuvier, 1824) was given a new epithet by two subsequent authors, *Mosasaurus Bavaricus* [sic] by Holl (1829) and *Geosaurus Sömmerringii* [sic] by Von Meyer (1831), although his later usage of this epithet has the genitive ending changed from *-ii* to *-i* (Von Meyer 1859).

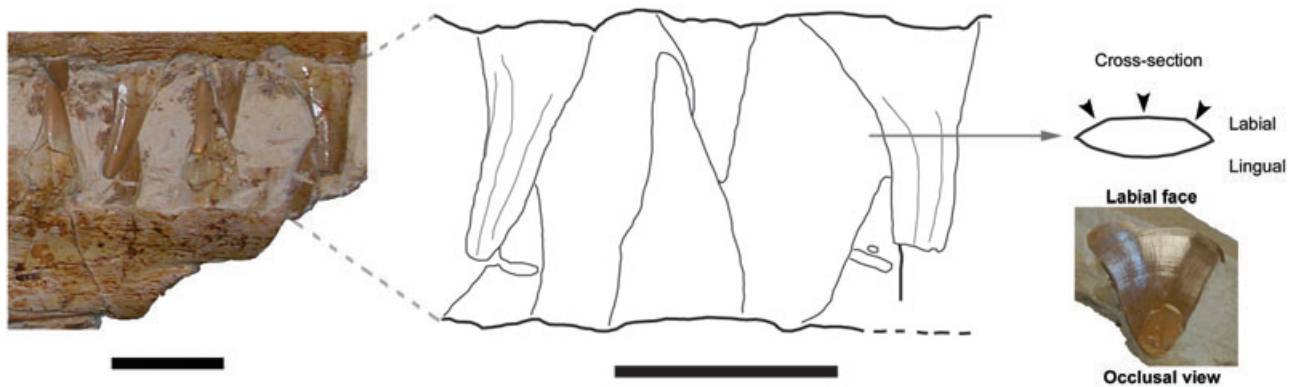
The first to dispute the lacertian affinity of *L. gigantea* was Von Meyer (1832). Following on from Cuvier’s opinion that it should be classed between the monitors and the crocodiles, Von Meyer (1832) states that it should not be classed with either, noting that the eyes are very large and similar to that of an ichthyosaur, whereas the pelvis is closest to that of the crocodylian *Rhacheosaurus gracilis* (= *Geosaurus gracilis* Fraas, 1901), although the individual bones differ in their shape. As more crocodylian material was discovered in Daiting (*Aelodon*, *Rhacheosaurus* and *Cricosaurus*), Von Meyer (1859) later considered *L. gigantea* to belong amongst them. However, Von Meyer (1859) was never able to examine the *L. gigantea* specimens, as they had been purchased, in 1827 for the British Museum (Natural History), now named the Natural History Museum (Sömmerring Collection, NHM R.1229 and R.1230; Figs 1–3).

The more familiar epithet, *giganteus*, was first explicitly mentioned by Knight (1838) in his discussion of Cuvier’s decision not to retain the epithet; however, he did not use the binomen *G. giganteus*. The earliest usage of *G. giganteus* was by Von Quenstedt (1852), who in the index to his *Hanbuch der Petrefaktenkunde* refers to *L. gigantea* as *G. giganteus*. Similarly, Cope (1869) emended the epithet using the masculine (*giganteus*) instead of the feminine form (*gigantea*), although in this case it was used for *Mosasaurus giganteus*. As Von Sömmerring (1816) had erected *L. gigantea* to be the name for both the Daiting and Maastricht specimens, Cope considered *L. gigantea* to be the senior synonym of *M. hoffmannii*. Within mosasaurid nomenclature, the use of various epithets for the Maastricht specimen (i.e. *hoffmannii*, *giganteus*, *belgicus*, and *camperi*) has historically led to confusion (see Spamer, Daeschler & Vostreys-Shapiro, 1995 for a synopsis). The binomen *M. hoffmannii* is the oldest available name for the Maastricht specimen. As such, *L. gigantea* and *M. giganteus* should not appear on synonymy lists of this taxon (e.g. as they do in Lingham-Soliar, 1995). However, the purported metriorhynchid *Capellinosuchus mutinensis* Simonelli, 1896, is a junior synonym of *M. hoffmannii* (see Sirotti, 1989).

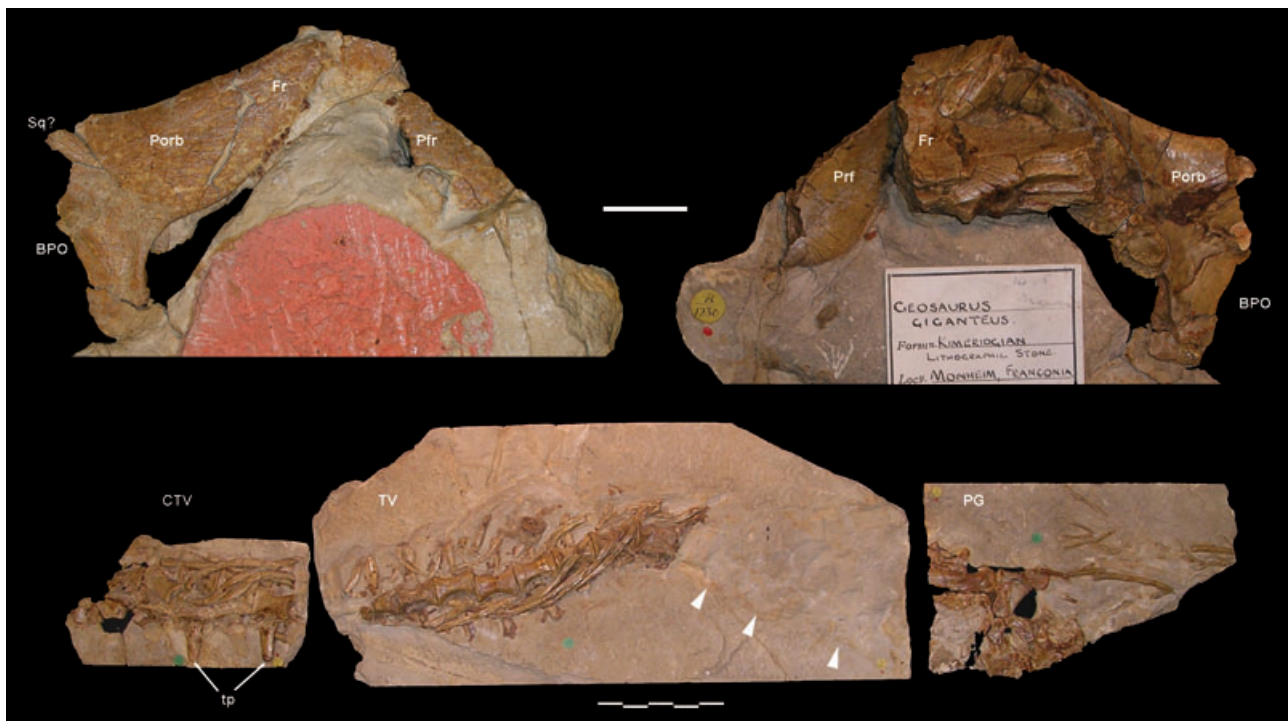
The original specimens described by Von Sömmerring (1816) were re-examined by Lydekker (1888a) as



**Figure 1.** Lateral views and line drawings of the type of *Geosaurus giganteus* (Von Sömmerring, 1816), showing the right (top) and the left (bottom) sides of the specimen (NHM R.1229). Line drawings show the interpretation of sutures and the main features of the specimen; the grey shading represents fossae. Scale bars: 20 mm.



**Figure 2.** Dental facets and their occurrence in *Geosaurus giganteus*. The close-up on the dentition of NHM R.1229 (left), and the corresponding line drawing (centre), shows the gross morphology of the teeth, with their distinctly triangular shape. On the right, a cross section of one tooth is shown, with the three labial facets indicated by arrow heads. On the lower right: an occlusal view of an isolated tooth of *Geosaurus* (SMNS 81834) displaying the facets and their limits, at the labial face of the crown. Scale bars: 20 mm.



**Figure 3.** The second specimen of *Geosaurus giganteus*, NHM R.1230, preserving remnants of the skull in dorsal (top left) and ventral (top right) views, as well as postcranial elements (bottom). The white arrows indicate the impressions of nonpreserved vertebrae on the matrix. Scale bar: 20 mm.

part for his catalogue of the fossils held within the British Museum (Natural History), and it is from here onwards that the binomen *G. giganteus* was consistently used. He initially believed it to be closely related to, or the same as, the mosasaurid *Clidastes*. However, he later changed his opinion (Lydekker, 1888b), referring it instead to the subfamily *Metriorhynchinae* within *Teleosauridae*, and considering it

to be the senior synonym of *Dacosaurus* [*sic*] and *Cricosaurus* [*in parte*], based upon his comparison with British Museum specimens of *Metriorhynchus* from the Oxford Clay near Peterborough (Leeds Collection), *Dacosaurus* from the Kimmeridge Clay of Dorset and Shotover Hill, and the description and illustrations of the three species of *Cricosaurus* by Wagner (1858). From then on, the crocodylian – and



**Figure 4.** Lateral view of the third, and forgotten, specimen of *Geosaurus giganteus*: NHM 37020. A, lateral view of the entire cranium. B, close-up of the tooth row, with the arrows highlighting the enlarged dentary tooth and the notch for its reception, whereas the box shows the occlusion of the maxillary/dentary teeth. Scale bars = 20 mm.

specifically metriorhynchid – affinity of *G. giganteus* was secure.

#### THE LOST *GEOSAURUS GIGANTEUS* SKULL OF LYDEKKER (1888A)

The metriorhynchids of the NHM Häberlein Collection (Solnhofen Formation, Malm Zeta 2b) were purchased along with the ‘London specimen’ of *Archaeopteryx* in 1862. Within his catalogue of NHM fossils, Lydekker (1888a: 271–272) referred several of these specimens to *G. giganteus*. Out of these, he provisionally referred a reasonably complete skull with mandible (NHM 37020; Fig. 4) to *G. giganteus*. It was this specimen that led Lydekker (1888a: 272) to consider *Geosaurus* to be similar, if not the same as, the mosasaurid *Clidastes*. This specimen, recently re-discovered, has never been illustrated, and has not been referred to in the literature since.

#### SUBSEQUENT ASSIGNMENT OF SPECIES TO *GEOSAURUS* AND THE ORIGIN OF A MISCONCEPTION

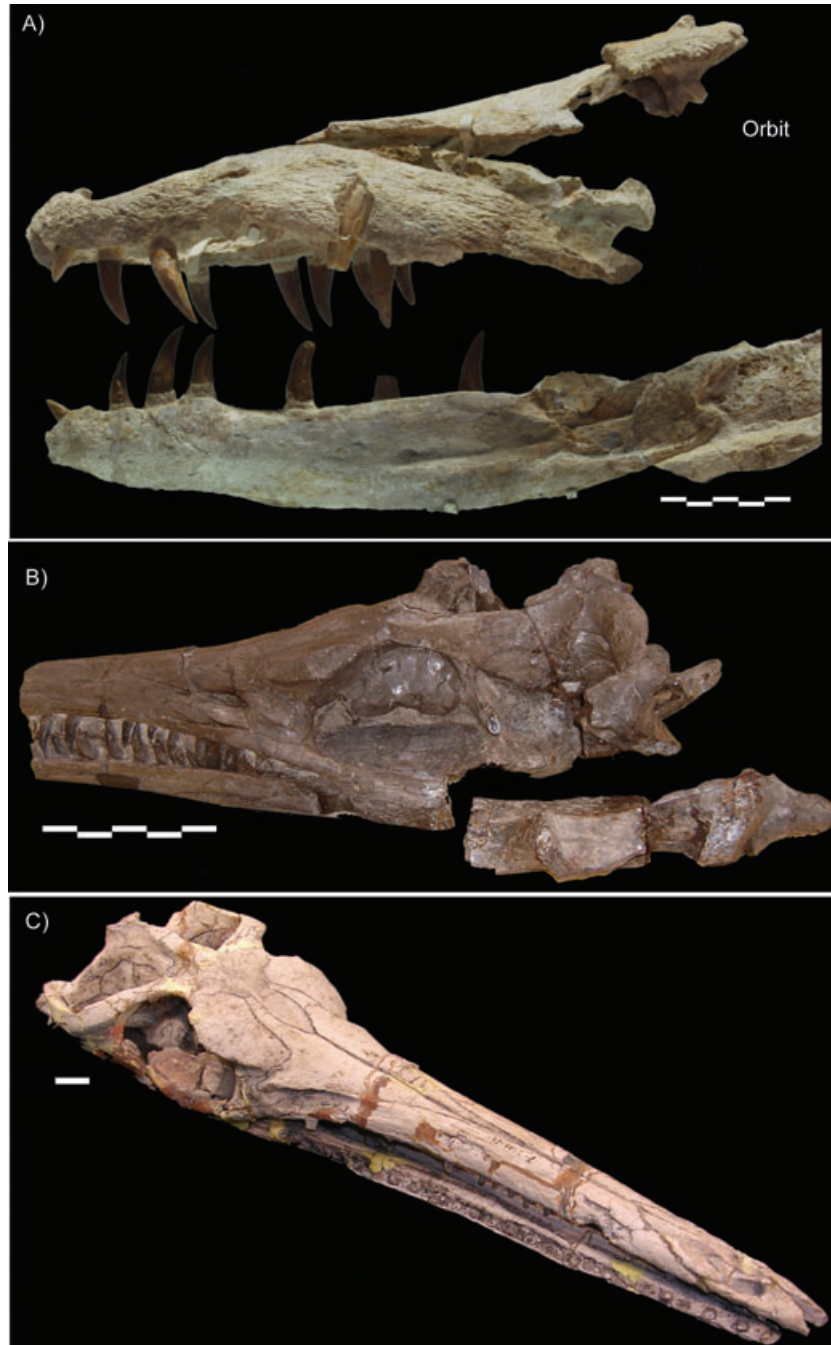
The second species assigned to *Geosaurus* was *Geosaurus bollensis* (Jäger, 1828) (= *Stenosaurus bollensis*). It was based upon isolated vertebrae from Bad

Boll, Baden-Württemberg, and was Toarcian in age. Once further specimens of this species were discovered, not only its crocodylian affinity, but also its teleosaurid status was confirmed.

*Geosaurus mitchilli* DeKay, 1830 was erected based upon a single tooth from New Jersey, USA; however, it has subsequently been reassigned to *Mosasaurus* (see Spamer *et al.*, 1995).

*Geosaurus maximus* Plieninger, 1846 (= *Dakosaurus maximus*; Fig. 5A) was erected upon a single tooth found at Schnaitheim, near Heidenheim, Baden-Württemberg. Originally believed to belong to the carnivorous theropod dinosaur *Megalosaurus* (Von Quenstedt, 1843), this specimen is apparently lost. It is also the type of the genus *Dakosaurus* (Von Quenstedt, 1856).

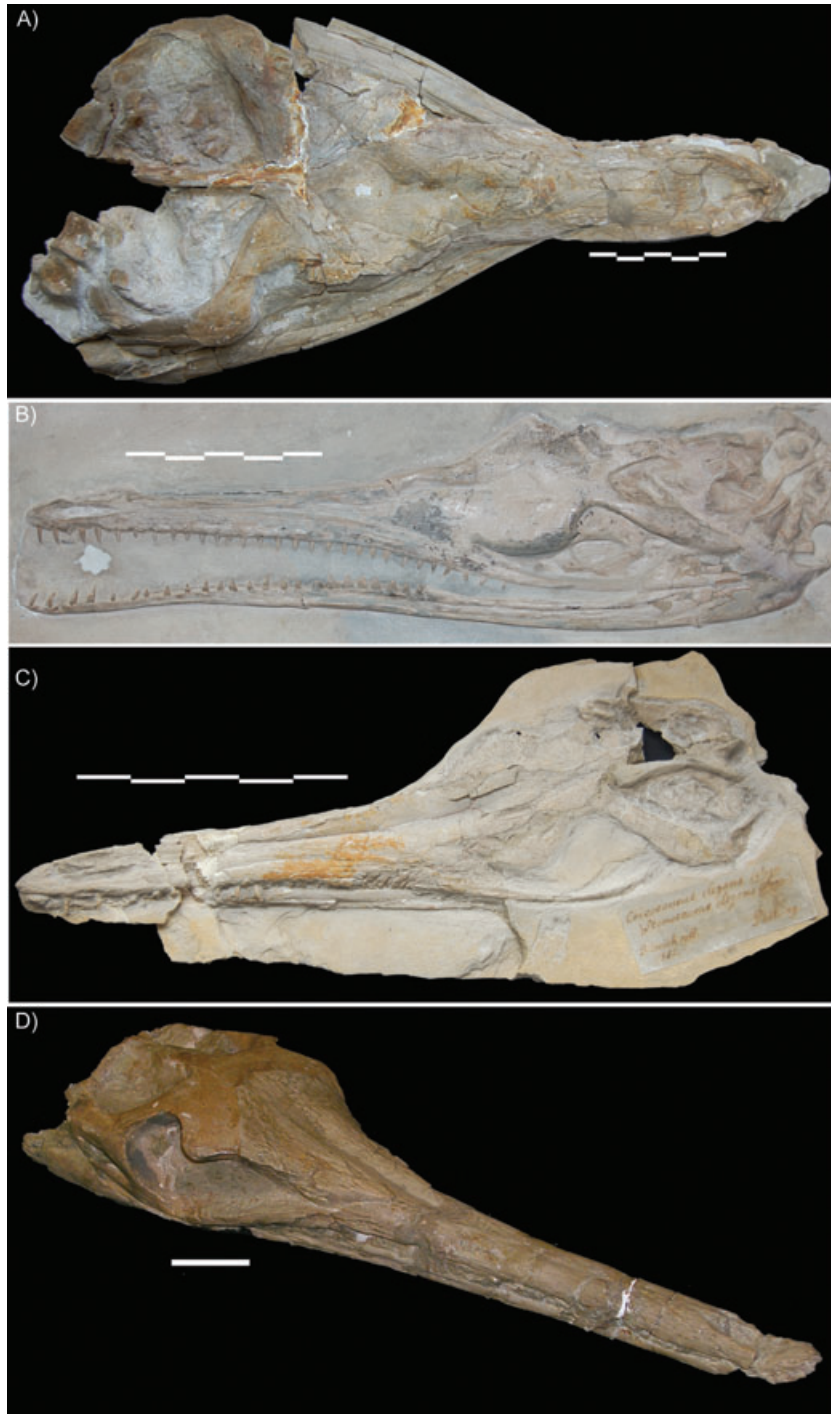
*Cricosaurus grandis* Wagner, 1858 (Fig. 6A) was the first species from another genus to be moved to *Geosaurus* (Von Zittel, 1887–1890). Wagner (1858) erected the genus *Cricosaurus* for the reception of his earlier species *Stenosaurus elegans* Wagner, 1852 [sic] (Fig. 6C), and for two new skulls: one very large and robust (*C. grandis*), and another intermediate in size between *S. elegans* and *C. grandis* (*Cricosaurus medius*). All three skulls were found in the quarries of Daiting.



**Figure 5.** Comparative cranial morphology for derived metriorhynchid species. A, *Dakosaurus maximus* neotype, SMNS 8203. B, *Enaliosuchus schroederi* holotype, MMGLV. C, *Geosaurus araucanensis* holotype, MLP 72-IV-7-1. The relative position of the orbit is indicated for *Dakosaurus*. Scale bars: 20 mm.

During the 19<sup>th</sup> century neither longirostrine nor mesorostrine taxa without serrated teeth were assigned to *Geosaurus*. *Geosaurus* was then only seen as a brevirostrine marine crocodylian with serrated teeth. In the supplement to the *Catalogue of the fossil Reptilia and Amphibia*, Lydekker (1890) even considers *Dacosaurus* [*sic*] to be a junior synonym of *Geo-*

*saurus*, as both genera possess serrated dentition. In addition, Steel (1973: 45) also states that '*Metriorhynchus* differs from *Geosaurus* in the absence of serrations on the dental carinae'. In fact, the distinction between *Dakosaurus* and *Geosaurus s.s.* teeth is problematic, and misidentification is not rare (see the material below).



**Figure 6.** Comparative cranial morphology for species previously referred to as *Geosaurus gracilis*. A, *Cricosaurus grandis* holotype, BSPG AS-VI-1. B, *Cricosaurus suevicus* lectotype, SMNS 9808. C, *Cricosaurus elegans* holotype, BSPG AS I 504. D, *Rhacheosaurus gracilis* referred specimen, NHM R.3948. Note that *R. gracilis* has a more delicate skull, when compared with all of the other specimens, in addition to a slender rostrum. Scale bars: 20 mm.

A dramatic change in the taxon concept of *Geosaurus* was introduced at the beginning of the twentieth century. Fraas (1901) was the first to attribute longirostrine taxa with uncarinated/unserrated teeth to

*Geosaurus*, namely *Cricosaurus elegans*, *Cricosaurus medius*, and *Rhacheosaurus gracilis*, at the same time as erecting *Geosaurus suevicus* (the fifth species to be erected within *Geosaurus*; Fig. 6B). Fraas (1901,

1902) successfully recognized the similarities between *Cricosaurus*, *Rhacheosaurus*, and *G. suevicus*, which later researchers have confirmed through the use of cladistics (Young, 2006, 2007; this paper). Unfortunately, Fraas (1901) erred when assigning *G. suevicus* to the genus *Geosaurus*, and in considering that these forms were similar to *G. giganteus* or *G. grandis*. With hindsight, the most appropriate approach would have been to assign *G. suevicus* to the genus *Cricosaurus*. However, the work of Fraas (1901, 1902) has become extremely popular in the field, and is cited in most thalattosuchian papers. Therefore, the idea of *Geosaurus* as a longirostrine taxon (possessing conical uncarinated teeth) became widespread, whereas the actual striking morphological features of its type species (i.e. nonlongirostrine metriorhynchid, with serrated, laterally compressed, faceted teeth) were mostly set aside and ‘forgotten’.

Since Fraas (1901, 1902), more species have been described as *Geosaurus*. *Neustosaurus gigondarum* Raspail, 1842 (Early Cretaceous of France) was assigned to *Geosaurus* based upon the similarity of the vertebrae, hindlimb, and tarsus morphology with that of *G. suevicus* (see Piveteau, 1928). Unfortunately, the lack of cranial material, with no information on the rostral and dental morphology, prevents further comparison (see the Discussion for implications). Furthermore, in the latter half of the 20<sup>th</sup> century and early 21<sup>st</sup> century, more longirostrine taxa with uncarinated uncompressed teeth, all from South and Central America, have been assigned to *Geosaurus*: *Geosaurus araucanensis* Gasparini and Dellapé 1976, *Geosaurus vignaudi* Frey *et al.*, 2002, and *Geosaurus saltillense* Buchy *et al.*, 2006. This shows that the untested nomenclatural decision of Fraas has proliferated. The detailed description of *G. suevicus* by Fraas (1901, 1902), and the completeness of these specimens, made this species an ideal candidate to build comparisons with. In effect, *G. suevicus* has been used as the hallmark of *Geosaurus* in most studies after the 19<sup>th</sup> century. This being true, both Vignaud (1995) and Buchy *et al.* (2006) noted the massive size of *G. giganteus*, and its clear distinction from all other geosaurs. Currently, the name *Geosaurus* has been applied to several longirostrine metriorhynchids with dentition characterized by uncompressed or poorly compressed teeth, lacking carinae or facets. However, there is no evidence that those species constitute a monophyletic group with *G. giganteus*.

#### ABBREVIATIONS

##### *Institutional*

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; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; CMC, Cincinnati Museum Center, Cincinnati, OH, USA; DGM, DNPM, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; FEF, Fundação Educacional de Fernandópolis, Fernandópolis, Brazil; GLAHM, Hunterian Museum, Glasgow, Scotland; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; MGHF, Museo Geológico H. Fuenzalida, Universidad Católica del Norte, Antofagasta Chile; MHNSR, Museo de Historia Natural de San Rafael, San Rafael, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMGLV, Mindener Museum für Geschichte, Landes- und Volkskunde, Minden, Germany; MPMA, Museu de Paleontologia de Monte Alto, Monte Alto, Brazil; MN-UFRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MUCPv, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; MUDE, Museo del Desierto, Saltillo, Mexico; NHM, Natural History Museum, London, UK; NMW, National Museum Wales, Cardiff, Wales, UK; OXFUM, Oxford University Museum, Oxford, UK; PETMG, Peterborough Museum & Art Gallery, Peterborough, UK; RCL, Museu de Ciências Naturais da Pontificia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; RNGHP, Réserve Naturelle Géologique de Haute Provence, Digne les Bains; RMS, Royal Museum Scotland, Edinburgh, Scotland; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; UANL, Universidad Autónoma de Nuevo León, Mexico; UJF, Université Joseph Fourier, Grenoble, France; UFRJ-DG, Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; URC, IGCE-UNESP, Museu ‘Paulo Milton Barbosa Landim’, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, Brazil; USNM, National Museum of Natural History, Washington DC, USA.

##### *Anatomical*

An, angular; BPO, postorbital bar; Co, coronoid; CTV, cervicothoracic vertebrae; Den, dentary; FAO, antorbital fenestra; Fr, frontal; Jug, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Nph, nasopharyngeal element; Orb, orbit; Pal, palatine; Pfr, prefrontal; PG, pelvic girdle elements; Porb, postorbital; San, surangular; Sc, individual ossicle of the sclerotic ring; Sp, splenial; Sq, squamosal; tp, transverse process; TV, thoracic vertebrae.



## SYSTEMATIC PALAEOLOGY

ORDER CROCODYLIA GMELIN, 1789

SUBORDER MESOEUCROCODYLIA WHETSTONE &  
WHYBROW, 1983INFRAORDER THALATTOSUCHIA FRAAS, 1901  
(*SENSU* GINSBURG, 1970)

FAMILY METRIORHYNCHIDAE FITZINGER, 1843

SUBFAMILY GEOSAURINAE LYDEKKER, 1889  
(*SENSU* THIS PAPER)*GEOSAURUS* CUVIER, 1824*Type species: Geosaurus giganteus* (Von Sömmerring,  
1816) Cuvier, 1824 *sensu* Von Quenstedt, 1852.

*Emended diagnosis:* Metriorhynchid thalattosuchian possessing brevirostrine to short mesorostrine snout; strongly lateromedially compressed teeth, with the dental carinae formed by a raised ridge (keel), finely serrated (composed of true denticles); maxillary crowns moderately enlarged; cranial bones smooth, lacking conspicuous ornamentation; prefrontal teardrop-shaped, with the inflexion point directed posteriorly approximately 70° from the anteroposterior axis of the skull; acute angle formed by the lateral and medial processes of the frontal; antorbital cavity present and much longer than higher; lacrimal–prefrontal fossa present, with a crest along the sutural contact.

*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: middle portion of cranium  
and mandible, badly deformed.*Type locality and horizon:* Daiting, near Monheim,  
Bayern, Germany. Mörsheim Formation, early  
Tithonian–uppermost *hybonotum* Tethys ammonite  
zone.

*Referred specimens:* NHM R.1230, four slabs of lithographic limestone: (1) lateral mid-portion of cranium consisting of lateral portion of the prefrontal, and frontal and postorbital portions of the beginning of the supratemporal arch; (2) anterior dorsals in ventral view with associated ribs; (3) mid-dorsals in ventral view with associated ribs; and (4) both sacrals in ventral view with gastralia, two pubis, incomplete femora proximal heads, isolated ribs, part of ischium, and iliac blade (Daiting, Mörsheim Formation). NHM 37016: tooth crown lacking apex, base, and root (Solnhofen, Solnhofen Formation). NHM 37020: skull and mandible embedded within lithographic limestone, only visible in left lateral view (Solnhofen, Solnhofen Formation).

*Emended diagnosis:* Metriorhynchid thalattosuchian with strongly lateromedially compressed teeth, with a brevirostrine snout, keeled denticulate carinae; premaxillary, maxillary, and dentary teeth tri-faceted upon their labial surface; notch at the premaxilla–maxilla contact, which an enlarged dentary tooth fits into; dentary tooth opposite to premaxillary–maxillary suture enlarged; 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.

MORPHOLOGY OF *GEOSAURUS*  
*GIGANTEUS*

## GENERAL FEATURES OF THE SKULL

The ornamentation is composed by elliptic pits, rather than the subpolygonal pits and deep grooves usually seen in neosuchians, peirosaurids, and *Araripesuchus* (Benton & Clark, 1988; Clark, 1994; Ortega *et al.*, 2000), or the irregular pattern of shallow sulci found in most notosuchians (Bonaparte, 1991; Carvalho & Bertini, 1999). The pits found in *G. giganteus* are faintly indistinct, loosely packed, and much shallower when compared with the pits of extant crocodylians. Elliptic pits can be identified in the maxilla, lacrimal, jugal, and postorbital of *G. giganteus*, but because of the poor preservation it is difficult to truly evaluate the extent of the development of this ornamentation in most elements. However, the pitted pattern is absent from the nasal and frontal, as in several metriorhynchids.

## ROSTRUM

*Nares and premaxillae*

The entire anteriormost section of the rostrum and mandible is not preserved on the holotype (Fig. 1). This contrasts with the description given by Von Sömmerring (1816), in which an isolated portion of the premaxilla is described and illustrated. However, this element is not with the rest of the material in the Sömmerring collection of the NHM, and is lost (interestingly, Cuvier, 1824 does not illustrate it either). As with other metriorhynchids, Von Sömmerring describes the premaxilla as possessing three alveoli, with its overall shape being much more reminiscent of *Dakosaurus* than the longirostrine geosaurs. The structure of the naris is highly variable in thalattosuchians: *Pelagosaurus* and *S. bollensis* have a single anterodorsally oriented naris, as with most metriorhynchids; *G. gracilis* (NHM R.3948), *G. araucanensis* (MLP 72-IV-7-1), *G. suevicus* (SMNS 9808), and *Enaliosuchus macrospodylus* Koken, 1883 (RNGHP 990201) have bifurcated nares, which are anterodorsally and laterally oriented; *Steneosaurus leedsi* Andrews, 1909 shows an undivided dorsally oriented naris (Andrews, 1913; Gasparini & Dellapé, 1976; Pierce & Benton, 2006). Although the actual morphology of the naris for the *G. giganteus* holotype is unknown, one would assume the presence of a bifurcated naris, based upon the narial morphology of the other geosaurs. However, as the phylogenetic analysis herein demonstrates, this may not be a valid prediction (as Von Sömmerring's description of the lost premaxilla suggests). This is confirmed in NHM 37020 (Fig. 4). The morphology of the premaxilla is identical to that described and illustrated by Von Sömmerring (1816), although it is more complete.

Many other elements were not preserved (or were obscured by matrix) in the holotype, making their morphology unknown, such as the parietal, quadrate, occipital surface, choanae, pterygoids, ectopterygoids, coronoid process, articular, retroarticular process, and the glenoid fossa.

*Maxilla*

Only the posterior and middle sections of both maxillae are preserved in NHM R.1229. These sections are long, low, and narrow, as in other metriorhynchids. In the specimen, the maxillae contact at least the nasals, jugals, and lacrimals. At the anteriormost section of the preserved rostrum, the maxillae meet dorsally. The alveolar margin is not differentiated from the remaining surface, and, as in *Dakosaurus manselii* (Hulke, 1870) Woodward, 1885 (NHM 40103), there are few neurovascular foramina, which are positioned distant to the alveoli (Fig. 1). In NHM 37020 almost all of the maxilla is exposed. The max-

illae meet along the midline of the skull, preventing the nasal from contacting the premaxilla, whereas the tooth row remains straight along its length, so that the anteriormost and posteriormost teeth are not displaced from one another ventrally. This contrasts with *D. maximus* (SMNS 8203) and *Dakosaurus andiniensis* Vignaud & Gasparini 1996 (see Gasparini *et al.*, 2006), where the last three maxillary alveoli (along with the maxillary posterior process) are displaced ventrally to the rest of the tooth row. At the contact between the premaxilla and maxilla in NHM 37020, there is a notch for the reception of an enlarged dentary tooth (Fig. 4).

*Nasals*

In NHM R.1229 the left nasal was completely preserved, whereas the right nasal lacks the anteriormost tip, and the medial section is broken and distorted. Nasals are paired, unfused elements. They show a triangular outline in dorsal view, as in all thalattosuchians (Andrews, 1913) and many notosuchians (Andrade, 2005). Although the specimen is badly crushed and most of the rostrum is missing, it is possible to identify the extent of the nasals over the maxilla, and to recognize that the nasals could not have any contact with the premaxillae, as in almost all thalattosuchians (Fig. 1). Furthermore, the nasals contact the maxillae, lacrimals, prefrontals, and frontal, also taking part in the antorbital fossae and fenestrae (a metriorhynchid apomorphy). In NHM 37020 the nasals are poorly preserved, but are consistent with features shown by the holotype.

*Lacrimals*

Both the left and right lacrimals are preserved in NHM R.1229. They face laterally, as in other metriorhynchids, with a concave and lightly ornamented surface. There are sutural contacts with the jugal, ventrally, and with the prefrontal, dorsally. At the contact with the prefrontal, the lacrimals form an anteroposteriorly oriented crest or ridge. This lacrimal–prefrontal crest is present on both sides of the specimen, but does not contribute to the antorbital fossae. Anteriorly, the lacrimal is isolated from the maxilla only by the antorbital fossa and the nasal, but not by a jugal–nasal contact (Fig. 1).

*Prefrontals*

In NHM R.1229 the prefrontals are badly crushed, but present on both sides. On the right side, the prefrontal is partially covered by a periocular element in its posterior section. Prefrontals contact the lacrimal ventrally, the nasals anteriorly, and the frontal medially. Only a small distal piece of the right prefrontal can be identified in NHM R.1230. However, from this fragment it is possible to identify that the

prefrontal was well-developed mediolaterally, covering the orbit (Fig. 3), as in all metriorhynchids, except for *Teleidosaurus*. The mediolateral expansion of the left prefrontal is clear in NHM 37020, with the anteriodorsal third of the orbit overhung by the prefrontal.

#### SKULL TABLE AND PERIORBITAL STRUCTURES

##### *Frontal*

The frontal is well preserved. It appears as a single element, without any signs of the interfrontal suture. The surface is smooth and unornamented, as in *Dakosaurus*, *Enaliosuchus*, other *Geosaurus*, and some species of *Metriorhynchus*; there is no indication of a frontal sagittal crest. Anteriorly, the frontal progresses in an acute angle between the nasals, extending beyond the orbits and the nasal–prefrontal contact, and reaching almost as far as the jugal. Posteriorly, the contact with the parietal is not preserved, but it is possible to identify that the element takes part in the supratemporal bar, and also in the supratemporal fossa. The frontal–postorbital contact is preserved on the right side of NHM R.1229 (Fig. 1). A small section of frontal can also be witnessed in NHM R.1230, but the frontal is poorly preserved in NHM 37020.

##### *Postorbitals*

Only the right postorbital (at the contact with the frontal and the postorbital bar) can be identified in NHM R.1229. The postorbital–frontal suture of NHM R.1230 (Fig. 3) has the characteristic posteriorly directed ‘V’-shape seen in other metriorhynchids (created by a scarf joint between the elements, with the frontal overlapping the postorbital). The postorbital descending ramus constitutes most of the postorbital bar, although it is not possible to identify clearly its contact with the jugal. The bar is subdermic, laterally flattened, and thin. It shows the same vertical disposition as other metriorhynchids (Figs 1, 4). In contrast, teleosaurids (e.g. *Steneosaurus* and *Pelagosaurus*) have a dermic bar (Andrews, 1913; Pierce & Benton, 2006), which is also found in sphenosuchians and protosuchians (Clark, 1994). Ornamentation is present in the dorsal part of the postorbital, but is completely absent from the descending ramus. The right postorbital is partially preserved in NHM R.1230, but the posterior ramus is also missing. The left postorbital is partially preserved in NHM 37020, with the descending ramus missing, and the overall shape concurs with NHM R.1229.

##### *Squamosals*

Only in NHM 37020 is there a preserved squamosal (left) (Fig. 4). It forms the posterior half of the

supratemporal arch. The morphology is very similar to that of *D. andiniensis* (Gasparini *et al.*, 2006). The suture with the prefrontal is indistinct, whereas the contact with the parietal is not preserved. In dorsal view, the squamosal is transversely wide, especially in comparison with the longirostrine geosaurs. The height of the squamosal is less than a third of its width, although the distortion of the cranium could exaggerate this.

##### *Periorbital elements*

Palpebrals are absent in *G. giganteus*, as in all thalattosuchians. Nevertheless, a sclerotic ring is clearly recognizable in NHM R.1229, with most of the preserved sclerotic ossicles preserved in their original position (Fig. 1). On the right side there is a large anterodorsal ossicle, close to the contact with the prefrontal, and a smaller ossicle can be seen in the posterior section of the orbit, partially covering the postorbital bar. On the left side, the ring shows a better preservation, including five ossicles. Four of them are in place, and constitute the anterodorsal section of the ring. The fifth ossicle is positioned in the lower part of the orbit, and, because of the deformation of the skull, it lies over an anterior section of the nasopharyngeal duct (Fig. 1). In all cases, the ossicles are flattened but thick elements, slightly variable in their morphology. The sclerotic ring is better preserved in NHM 37020 (Fig. 4). Here, the ring is laid out in its original position, with only the ossicles along the ventral margin being out of place. Twelve ossicles can be clearly distinguished, all flattened, but just as robust as those of the holotype. The sclerotic ring occupies almost all of the orbit. The ventral ossicles partially cover the aperture for the eye itself, obscuring the exact size. The annular sulcus is absent from the sclero–corneal junction, just as with *Metriorhynchus superciliosus* (Blainville, 1853) (GLAHM V983, GLAHM V985, GLAHM V987, GLAHM V1015, GLAHM V1140, NHM R.2051, and NHM R.2058), *G. suevicus* (SMNS 9808), and *Enaliosuchus schroederi* Kühn, 1936 (MMGLV unnumbered). In *D. andiniensis* (Gasparini *et al.*, 2006), the presence or absence of the annular sulcus is unknown. In nonmarine adapted species, the sclerotic ossicles are concave at the sclero–corneal junction, forming an annular sulcus that is fundamental to the process of accommodation (Walls, 1942). However, like ichthyosaurs (McGowan, 1972, 1973; Fernández *et al.*, 2005), fish (Helfman, Collette & Facey, 1997), and Magellanic penguins (Suburo & Scolaro, 1990), metriorhynchids lack a sulcus, suggesting that the cornea had lost its role in focusing, a key adaptation to aquatic vision (Walls, 1942). In *G. giganteus*, the sclerotic ring is reasonably heavy and robust (much more so than the relatively delicate sclerotic ossicles of *M. superciliosus*, and

more robust than those of *G. suevicus* and *D. andiniensis*), occupying most of the orbit, which would have offered good support for the eye, suggesting that this species was able to venture on deep dives, and/or was a faster swimmer than other metriorhynchids (Motani, Rothschild & Wahl, 1999; Humphries & Ruxton, 2002). The sclerotic ring of *E. schroederi* is the largest and most robust of any metriorhynchid.

### Jugal

Only the anterior ramus of both jugals could be identified in NHM R.1229, as the posterior ramus is not preserved on both sides, and the ascending ramus is indistinct on the right side and missing from the left side. The anterior ramus is slender, ventrally arched, and slightly compressed. As a result of lateral compression, the anterior process has a subcircular to elliptic cross section. However, this compression might be taphonomic, as the entire skull is flattened. In NHM 37020, both the anterior and posterior rami are preserved, whereas the dorsal ramus is not. The rostral extent of the jugal is unclear; however, the anterior ramus is slender, with an elliptic cross section. Once again, taphonomic compression cannot be discounted. The posterior ramus is more circular in cross section, and its suture with the quadratojugal cannot be determined. There is no neurovascular foramen on the surface of the jugal in any of the specimens examined.

### PALATE AND VENTRAL STRUCTURES OF THE SKULL

Despite the strong deformation of the skull, a few elements of the palate can be distinguished in NHM R.1229 (Fig. 1). The right palatine is partially preserved and exposed on the right side of the specimen, although it is displaced from its original position. It is slightly ornamented ventrally, although the lateral surface (inside the suborbital fossa) is absolutely smooth. The palatine is narrow throughout, extending anteriorly, and reaching at least the same relative position as the antorbital fenestra, and ending in a rounded border (Fig. 1). The anterior extension of the palatines reaches beyond the orbits and the suborbital fenestrae, between the ventral rami of the maxillae. This feature is common to all neosuchians, basal mesoeucrocodylians, and a few notosuchians; although only in neosuchians the anterior extension remains narrow throughout. In *Theriosuchus*, *Araripesuchus*, *Anatosuchus*, and *Uruguaysuchus*, palatines broaden considerably anterior to the suborbital fenestra, taking part in its anterior border (Clark & Norell, 1992; Andrade, Bertini & Pinheiro, 2006). In eusuchians, the anterior extension of the palatines only widens anterior to these fenestrae, but the palatines still do not take part in their anterior border (Buffe-

taut, 1982a; Benton & Clark, 1988; Clark & Norell, 1992; Andrade *et al.*, 2006). A few other elements of the palate were preserved on the left side of NHM R.1229. These can be seen inside the orbit, and are possibly interpreted as fragments of the dorsal part of the nasopharyngeal duct. The posteriormost elements are paired. These are quite possibly the only remaining parts of the pterygoids, suggesting that these elements were not fused, as in *S. leedsi* and *Steneosaurus durobrivensis* Andrews, 1909, which show unsutured pterygoids (Andrews, 1913; Buffetaut, 1982a).

It is impossible to verify the relationships between the palatine, ectopterygoid, and pterygoid, but it is more likely that in this species there was no palatine bar or palatine–ectopterygoid contact, as these features mostly occur in derived notosuchians (Andrade *et al.*, 2006; Andrade & Bertini, 2008).

### FENESTRAE AND FOSSAE

These structures are poorly recognizable in NHM R.1229 and NHM 37020, whereas they are mostly absent in NHM R.1230 as a result of poor preservation. On both sides of the holotype it is possible to identify the completely preserved antorbital fossae. These are typically elliptic, and are obliquely orientated in metriorhynchids, but are deformed in NHM R.1229. They are shallow, and are much longer than high. In the bottom of each fossae, close to the contact of the maxilla, jugal, lacrimal, and nasal, there is a circular antorbital fenestra. On both sides, these fenestrae are difficult to identify, as they are filled with matrix (Fig. 1).

In addition to the antorbital fossa, another depressed area is present on the rostral section of *G. giganteus*. This structure, identifiable on both sides of the type, is considered here as a fossa. The depressed area is located between the antorbital fossa and the orbit, where the shallow fossa is limited within the concave surface of the lacrimal and prefrontal. The lacrimal–prefrontal fossa is limited dorsally by a lateral expansion of the prefrontal, and ventrally by the jugal (Fig. 1). This fossa shallows anteriorly, closer to the nasal and the antorbital fossa, but without clear limits. The lacrimal–prefrontal fossae can also be identified in numerous metriorhynchids, such as *G. araucanensis* (MLP 72-IV-7-1), *Metriorhynchus brachyrhynchus* (Eudes-Deslongchamps, 1868) (NHM R.3939), and *D. andiniensis* (Gasparini *et al.*, 2006), but are absent from basal metriorhynchids such as *Teleidosaurus calvadosii* (Eudes-Deslongchamps, 1866) (NHM R.2681) and *Teleidosaurus gaudryi* Collot, 1905 (NHM R.3353), and teleosaurids such as *Pelagosaurus typus* Bronn, 1841 (NHM 19735) and *S. leedsi* (NHM R.3320). A lacrimal–prefrontal ridge develops at the contact

of these elements, almost dividing the lacrimal–prefrontal fossa into upper and lower fossae, which is well preserved in three-dimensionally complete specimens, as in *G. araucanensis* (MLP 72-IV-7-1) and *M. brachyrhynchus* (NHM R.3939). This ridge is not present in thalattosuchians without the lacrimal–prefrontal fossae.

The infratemporal (= laterotemporal) fenestra is well preserved in NHM 37020. In comparison with the orbit it is large (approximately three-quarters of the length of the orbit), far larger than that observed in the longirostrine geosaurs (e.g. in *G. araucanensis* MLP 72-IV-7-1, the fenestra is less than half of the orbit length). The shape is similar to that of *D. andiniensis*, having a tall triangular shape (with the height of the orbit and infratemporal fenestrae being subequal) with the posterior margin being the most sharply tapering (Fig. 4).

Most of the remaining fenestrae have only poor preservation. However, the anteriormost border of the supratemporal fossa can be identified on the left side of NHM R.1229, on the posterior surface of the frontal, showing an acute medial anterior angle formed by the intertemporal flange. The right suborbital fenestra is partially preserved, in its medial border, formed by the palatine, and can be identified on the right side of NHM R.1229, just below the jugal (Fig. 1). The suborbital fenestra is elongated, but apparently does not extend anterior to the orbit.

Other fenestrae are not preserved. Nevertheless, it can be stressed that: (1) maxillo–palatine fenestrae (= palatine fenestrae) are found only in notosuchids and *Eutretauranosuchus* (Woodward, 1896; Buffetaut, 1982a; Vasconcellos & Carvalho, 2005; Andrade *et al.*, 2006); (2) most thalattosuchians either lack or have a highly reduced naso–oral fenestra (= incisive foramen, *foramen incisivum*); and (3) metriorhynchids more derived than *T. calvadosii* lack an external mandibular fenestra (Andrews, 1913; Mercier, 1933).

#### MANDIBLE

The preservation of the mandible is extremely poor in the holotype, with no remnants of the symphysis, coronoid process, articular and the retroarticular process on the holotype, whereas NHM R.1230 possesses no mandibular elements. Given the section of the mandible preserved in NHM R.1229, the symphysis would not have extended as far posteriorly as the antorbital fossa (Fig. 1). The symphysis is preserved in NHM 37020, which confirms its short length (Fig. 4). This means that the symphysis of *G. giganteus* is clearly shorter than in other metriorhynchids in which the cranium and mandible are well preserved. In *Metriorhynchus cultridens* Andrews, 1913 (NHM R.3804), the symphysis reaches the same rela-

tive position as the antorbital fenestra, and the same can be observed in *G. araucanensis* and other longirostrine forms.

A lateral mandibular groove is present on the surface of the dentary and surangular, on the right side of the type (Fig. 1). It reaches the same relative position as the anterior border of the antorbital fenestra, on the dentary, and extends posteriorly as far as the posterior border of the orbit. In most other thalattosuchians bearing such a structure, the groove appears almost like a carving on the bony surface, as its limits are so abrupt and sharply defined. Although the groove can be easily recognized in the holotype, its limits are not sharply defined. In fact, the border seems to be smoother and rounder through the entire extension of the groove, like a simple depressed area in the bony surface. In the genus *Dakosaurus*, a large foramen can be observed at both ends of this groove (NHM 40103; SMNS 8203; Gasparini *et al.*, 2006). *Contra* Gasparini *et al.*, (2006), this shallow groove is present in well-preserved specimens of *Steneosaurus* and *Metriorhynchus* (e.g. NHM R.3804). Extant crocodylians exhibit a similar groove; however, it is both shorter and less deeply excavated. This groove is associated with an external cutaneous branch of the mandibular nerve (see Holliday & Witmer, 2007; S. Salisbury, pers. com. 2008, *apud* Buchy).

#### Dentary

Only small sections of the dentary are preserved on both sides of NHM R.1229 (Fig. 1). It is flattened, and its sutures with the surangular and angular can be easily identified. The posterior end of the dentary–surangular contact is located at the same relative position as the anterior border of the orbit, as in most thalattosuchians. The development of the dentary, however, varies. In most crocodylians, including extant forms and *Pelagosaurus*, the dentary is longer, reaching or surpassing the same relative position as the posterior orbital border (postorbital bar). In all longirostrine species currently assigned to *Geosaurus*, the posterior end of the dentary is positioned far in advance of the anterior border of the orbit. The dentary of NHM 37020 is largely complete, concurring with the description given for the holotype. Here, the suture with the splenial can be observed along the ventral surface of the mandible (as a result of the distortion of the skull).

#### Splenials

Only a slit of the right splenial seems to be preserved in the holotype, which can be seen below the dentary on the right side of the type specimen. It extends from the anterior border of the antorbital fossa to the anterior border of the orbit. However, because of the

state of preservation, this extension is likely to be biased, and probably represents only a minor part of the total length of the element. On NHM 37020, the splenial is much better preserved. As with other thalattosuchians, the splenial is well-developed rostrally, extending almost as far as the premaxilla, to the anterior margin of the orbit. In ventral view it significantly contributes to the symphysis (Fig. 4).

#### *Angular and surangular*

The anterior section of these elements can be seen in both sides of NHM R.1229. They are sutured alongside, by an almost horizontal contact. The anterior border of the surangular meets the dentary next to the same relative position as the anterior border of the orbit, just below the anteriormost elements of the sclerotic ring. The dentary–surangular suture is a diagonally-oriented truncated line, with the ventral border anterior relative to the dorsal border. As the medial side of the mandible is not exposed, it was not possible to verify the actual extension of the medial ramus of the surangular, but it is likely to be smaller than the lateral one. The angular is reasonably longer than the surangular (lateral ramus), and reaches at least the same relative position as the anterior border of the antorbital fossa. Although these elements are better preserved in NHM 37020, preservation at the jaw joint is poor, as it is posterior to this. There does not appear to be a deepening of the mandibular ramus along its length, in contrast with all other metriorhynchids. As seen in NHM R.1229 and NHM 37020, there is no external mandibular fenestra (Figs 1, 4).

#### *Coronoid*

On the right side of the holotype, the coronoid is positioned between the maxilla and the dentary, next to teeth and the palatine (Fig. 1). It is thin and tall, as with other metriorhynchids, and the position suggests that it is displaced from its original location, in the medial face of the right hemimandible.

#### *Hyoid*

The right hyoid can be clearly seen on NHM 37020 (Fig. 4). The element is long, with a subcircular cross section, and with a pronounced curvature dorsally.

### DENTITION

#### *Preservation*

The dentition is preserved only in the holotype and NHM 37020 (Figs 1, 4). In both specimens, all crowns show extensive nontaphonomic lateromedial compression that is identical to that observed in *M. brachyrhynchus* and *M. cultridens*. On both sides of the holotype there are 14 preserved teeth: eight in the

maxilla and six in the dentary. However, on the right side it is possible to see that the last (preserved) tooth is overlying another tooth, which was displaced from its original position, and has its root exposed (Fig. 1). On the corresponding position on the left side, no element is preserved. This displaced tooth seen on the right side is considered here as being the missing tooth from the left side, possibly resulting from the extent of the deformation and compression that the skull has undergone. On the left side, the fourth upper tooth, with only the crown preserved, also seems displaced from its original position, and might have been part of the lower dentition. Although most teeth are complete, well exposed, and in their original position, a few are only represented by the crown apex, and by the impression left by the base of the crown on the remaining matrix. This can be seen on the first and the second preserved teeth on the left dentary, as well as the first preserved maxillary and dentary teeth from the right side. Considering the elements preserved, it is most likely that the maxillary dentition extended posteriorly up to the area below the orbit, whereas the dentary dentition extended only up to the same relative position as the contact between the dentary, surangular, and angular. Furthermore, we consider that the maxillary alveoli between the anteriormost border of the nasal and the antorbital fenestra probably held six teeth. In NHM 37020, 22 teeth are preserved: three premaxillary teeth, 12 in the maxilla, and seven in the dentary (Fig. 4). As part of the rostrum is missing, and as matrix covers some dentary teeth, it is likely that both the maxillary and dentary tooth counts are underestimated. This specimen displays an enlarged dentary tooth opposite the premaxilla–maxilla suture, which is unique throughout the Metriorhynchidae.

#### *Type of dentition and occlusion*

The dentition can be considered as homodont, but not isodont, as the dentary tooth opposite the premaxilla–maxilla suture is greatly enlarged relative to the other teeth (Fig. 4). Furthermore, the posteriormost elements of the maxilla, below the lacrimal and the orbit, are smaller than the remaining teeth. The teeth are not procumbent, but the implantation of teeth in the premaxilla of NHM 37020 does appear to be procumbent. However, this may be a preservational bias. On the right side of the holotype and NHM 37020, the teeth show better preservation (Figs 1, 4). During occlusion, each maxillary tooth should have occluded laterally with a dentary tooth, with the upper element in a more lateral and mesial position relative to the lower tooth, which is settled in a more posterior and medial position. Consequently, the distal border of the upper tooth and the mesial border

of the lower one would be able to slide past each other during occlusion, acting as efficient scissors, contrasting with the common overbite pattern shown by most terrestrial or freshwater ziphodont and false-ziphodont crocodylians, and also with the interlocking arrangement found in most extant crocodylians and thalattosuchians. There is, however, no evidence of wear facets on the crowns, indicating that this dentition was not used to process food. No other thalattosuchian presents a similar feeding mechanism, as *G. araucanensis*, *Pelagosaurus*, *Steneosaurus*, and longirostrine *Metriorhynchus* species had procumbent, slightly lateromedially compressed piercing teeth. *Dakosaurus* also had serrated teeth, but the morphology of the carinae is quite distinct, and the teeth, although lateromedially compressed, are robust, and not blade-like. A somewhat similar mechanism was precluded by Price (1950) for the terrestrial notosuchian *Sphagesaurus*. Here, the middle and posterior molariform teeth were also arranged as opposing blades, acting like scissors. However, the crowns have extensive wear surfaces (Price, 1950; Pol, 2003).

#### Teeth morphology

Each tooth shows an overall caniniform morphology, and a nontaphonomic lateral compression can be recognized. Crowns are curved posteriorly, but not lingually. The crown is not curved throughout, but only at its base. Middle and apical sections of the crown are mostly straight, with a discrete bending anteriorly. In most well-preserved teeth, the surface has three basi-apical facets, which are more evident in the middle and basal sections of the crown (Fig. 2). The first facet faces mesially and laterally, the second faces laterally, and the third faces laterally and distally. There is no evident limit between the facets, and the transition from one facet to the other is smooth. These facets can be observed through close examination of the second and fourth preserved maxillary crowns of the holotype (Fig. 2), as well as the first and fourth dentary teeth, on the right side. On the left side, facets can be seen in the second and third maxillary and the second dentary preserved crowns. Other teeth are incomplete or crushed, preventing the observation of this feature. Most of the teeth on NHM 37020 display the characteristic tri-faceting, most especially the enlarged dentary tooth (Fig. 4). The facets are only visible on the labial surface of the teeth, as the lingual surface is not exposed on any tooth. However, the isolated tooth NHM 37016, although still partially encased in matrix, lacks the distinctive tri-faceting on one side. Assuming this to be the lingual surface, it suggests the faceting was only on the labial surface, but confirmation must await the discovery of new specimens. Only *C.*

*grandis* (Wagner, 1858) presents similar facets on teeth crowns. Interestingly, the exceptional lateromedial compression and triangular blade-like shape of the teeth are identical to those observed in the Oxford Clay brevirostrine species *M. brachyrhynchus* and *M. cultridens*. However, whether or not the dentition of these specimens were arranged as opposing blades is unknown, as complete upper and lower dentition on the same specimen is lacking.

#### Ornamentation, carinae, and wear

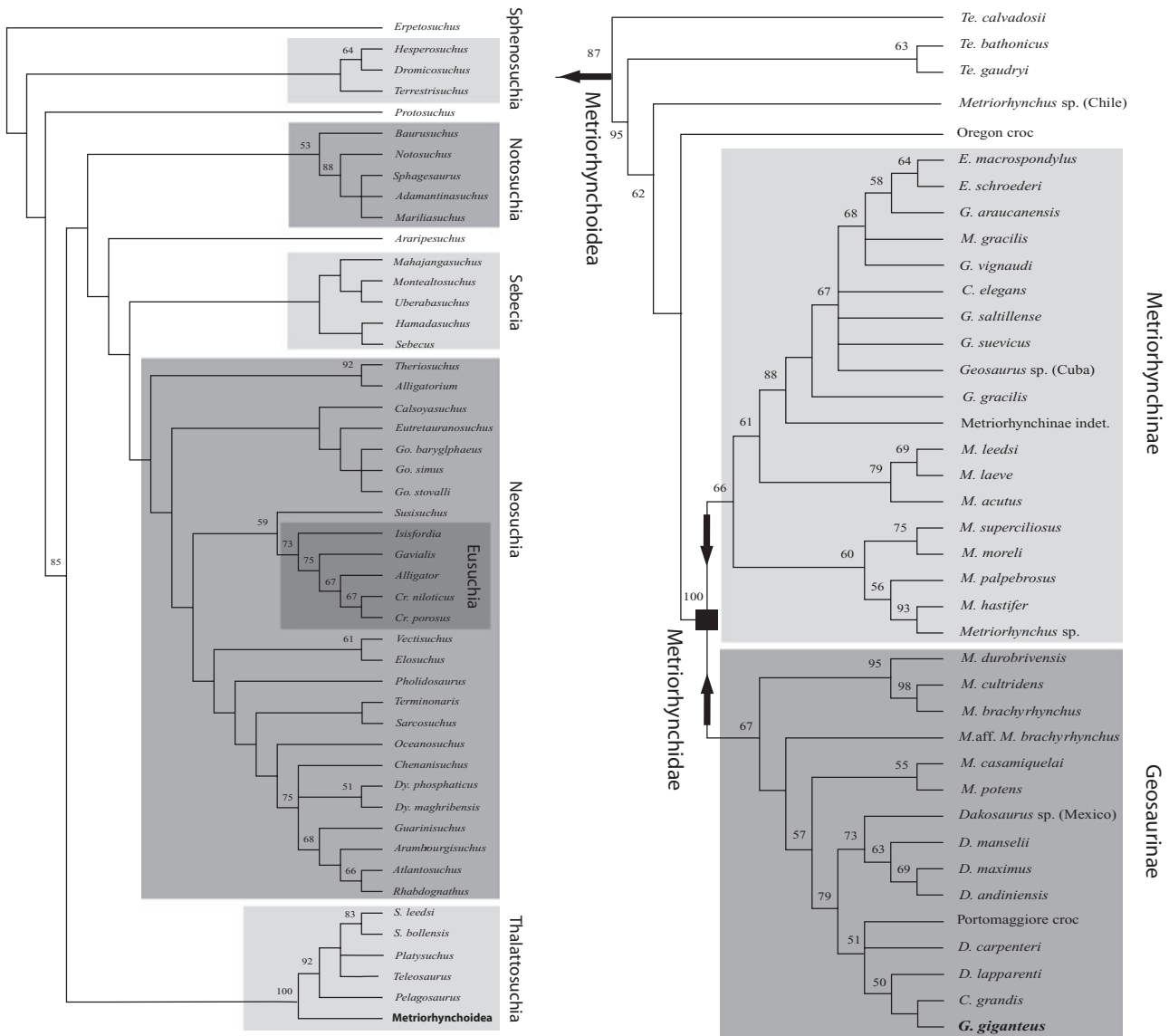
Ornamentation is light, composed of microscopic ridges in an arranged anastomosed pattern, creating a fabric of crests over the surface. Given the small size of these ridges, the overall appearance of the tooth surface is reasonably smooth. There are mesial and distal serrated carinae, with microscopic denticles. It was not possible to evaluate the teeth of the holotype with scanning electronic microscopy, thereby preventing the reliable identification of these as true denticles (as in *Dakosaurus* and *Sebecus*), or as mere extensions of the enamel ornamentation (= false-ziphodont dentition; Prasad & Broin, 2002), as in *Pristichampsus*. However, close examination of the dentition of *G. grandis* (= *C. grandis*), which is very similar in cranial and dental morphology to *G. giganteus*, confirms the presence of true denticles.

## PHYLOGENETIC RELATIONSHIPS OF *GEOSAURUS GIGANTEUS*

### METHODOLOGY

In order to assess hypotheses of evolutionary relationships within the Metriorhynchidae, and determine the phylogenetic relationship of *G. giganteus*, a global cladistic analysis was undertaken including every valid species of metriorhynchid. Although thalattosuchians, in particular metriorhynchids, were the primary focus of this analysis, several species from various other crocodylian clades were included (see Appendix S1). This analysis is an extension of Young (2006, 2007) and Wilkinson, Young & Benton (2008), in which more operational taxonomic units (OTUs) and characters were added (see Appendices S1 and S2). The matrix of this analysis includes 86 OTUs and 166 characters (Appendix S3).

The cladistic analysis was carried out with PAUP 4.0b10 (Swofford, 2003), using a heuristic search algorithm with tree bisection reconnection (TBR) branch swapping (200 replicates). All characters were treated as unordered, with equal weighting, and assuming the shortest optimization possible between accelerated and delayed transitions. These options were adopted to avoid the influence of a priori assumptions



**Figure 7.** Strict consensus of 4104 most parsimonious cladograms, with bootstrap support for each node (tree length = 578; consistency index,  $CI = 0.436$ ; retention index,  $RI = 0.861$ ; rescaled consistency index,  $RC = 0.376$ ). On the left, the position of Thalattosuchia relative to other Crocodylomorpha is shown, whereas, on the right the Metriorhynchoidea is separated to aid visualization. Arrows denote stem-based clades, whereas squares indicate node-based clades.

in the analysis. In order to provide character polarity, predefined outgroup taxa (*Erpetosuchus*) were chosen. Nodal support was evaluated using nonparametric bootstrapping (Felsenstein, 1985), with 500 replicates, each with 100 random-addition sequences.

## RESULTS

From the phylogenetic analysis, 4104 equally parsimonious cladograms (MPC) were found, with a length of 594 steps (Fig. 7). The topology of the strict consensus (consistency index,  $CI = 0.436$ ; retention index,

$RI = 0.861$ ; rescaled consistency index,  $RC = 0.376$ ) is reasonably well resolved, as only seven polytomies can be observed. The primary difference between the MPCs is in the position of taxa close to *Enaliosuchus* and *G. giganteus*. Very high bootstrap support was found for the following nodes: Thalattosuchia (100%); Teleosauridae (92%); metriorhynchoids more derived than *T. calvadosii* (95%); Metriorhynchidae, as defined below (100%); the Oxford Clay brevirostrine forms (95%); and for the sister-group relationship of *M. brachyrhynchus* and *Metriorhynchus durobrivensis* Lydekker, 1890 (98%).



The metasuchian inter-relationships are very poorly supported, with the exception of Atoposauridae (92%). However, as the majority of the characters were coded for resolving the intrarelationships of metriorhynchids, this is not surprising. What is interesting is that the large number of longirostrine metasuchians does not influence the phylogenetic position of Thalattosuchia, i.e. here they are found to be basal mesoeucrocodylians and not placed within a derived clade of longirostrine neosuchians (see Clark, 1994 for discussion). Nonetheless, further work is required to rigorously confirm the position of Thalattosuchia, such as adding more notosuchians, basal mesoeucrocodylians, and nonmesoeucrocodylian crocodyliforms.

Within Thalattosuchia, *Pelagosaurus* is found to be the basalmost teleosaurid, which is consistent with previous analyses of Thalattosuchia that include more than three taxa (e.g. Mueller-Töwe, 2005; Gasparini *et al.*, 2006). The teleosaurid *Steneosaurus* is found to be monophyletic; however, as only two species have been included in this analysis, the monophyly of *Steneosaurus* cannot be confirmed. The in-depth analysis of Teleosauridae by Mueller-Töwe (2005) strongly suggests *Steneosaurus* is paraphyletic in regards to *Teleosaurus* and *Machimosaurus*. As such, no taxonomic conclusions regarding intrarelationships of the Teleosauridae are presented here.

A sister-taxon relationship between *G. giganteus*, *C. grandis*, and *Dakosaurus lapparenti* Deblemas & Strannoloubsky, 1957 was found (bootstrap = 50%), making the genus *Dakosaurus* paraphyletic. Furthermore, a sister-taxon relationship is also supported for all other species of *Dakosaurus* (bootstrap = 73%), and for the clade containing all of the longirostrine 'geosaurs' and *Enaliosuchus* (bootstrap = 88%). The monophyly of the genera *Teleidosaurus*, *Cricosaurus*, *Metriorhynchus*, and *Geosaurus* (*sensu* Fraas, 1902) is strongly refuted. Most *Metriorhynchus* species are found to be basal members of the dictomous clades seen above a paraphyletic *Teleidosaurus* and the putative specimen of *Metriorhynchus* from the early Bajocian of Chile (Gasparini *et al.*, 2000). In addition, the species *M. gracilis* (= *Steneosaurus gracilis* in Philips, 1871) nests within the longirostrine species currently assigned to *Geosaurus*, thereby supporting the referral of this species to *Geosaurus* (as defined) by Taylor & Benton (1986). Apart from *G. giganteus*, all species of *Geosaurus* constitute a single and well-supported clade within the Metriorhynchidae, but which is paraphyletic in regards to *Enaliosuchus*.

From the resultant topology, we hereby phylogenetically define the following clade names (note that there is most likely a synonymy between *Metriorhynchus geoffroyii* Von Meyer, 1832 and *Metriorhynchus*

*palpebrosus* (Philips, 1871), MTY, pers. obs., and we herein treat them as such, but confirmation of this is beyond the scope of this paper):

- Infraorder Thalattosuchia Fraas, 1901 – the most inclusive clade consisting of *Teleosaurus cadomensis* (Lamouroux, 1820) and *Metriorhynchus geoffroyii* Von Meyer, 1832, but not *Pholidosaurus schauburgensis* Von Meyer, 1841, *Goniopholis crassidens* Owen, 1841, or *Dyrosaurus phosphaticus* (Thomas, 1893).
- Superfamily Teleosauroidea Geoffroy, 1831 – the most inclusive clade consisting of *Teleosaurus cadomensis* (Lamouroux, 1820), but not *Metriorhynchus geoffroyii* Von Meyer, 1832.
- Superfamily Metriorhynchoidea Fitzinger, 1843 – the most inclusive clade consisting of *Metriorhynchus geoffroyii* Von Meyer, 1832, but not *Teleosaurus cadomensis* (Lamouroux, 1820).
- Family Metriorhynchidae Fitzinger, 1843 – the least inclusive clade consisting of *Metriorhynchus geoffroyii* Von Meyer, 1832 and *Geosaurus giganteus* (Von Sömmerring, 1816).
- Subfamily Metriorhynchinae Fitzinger, 1843 – the most inclusive clade consisting of *Metriorhynchus geoffroyii* Von Meyer, 1832, but not *Geosaurus giganteus* (Von Sömmerring, 1816).
- Subfamily Geosaurinae Lydekker, 1889 – the most inclusive clade consisting of *Geosaurus giganteus* (Von Sömmerring, 1816), but not *Metriorhynchus geoffroyii* Von Meyer, 1832.

## DISCUSSION

The results of the cladistic analysis presented herein reject the taxonomic opinion of Fraas (1901, 1902), and support the division of *G. giganteus* from the longirostrine species currently assigned to the genus *Geosaurus*. A complete taxonomic alteration to what is currently considered *Geosaurus*, *Enaliosuchus*, and *Dakosaurus* is presented (Fig. 8; Appendix 1); along with an apomorphy list (Appendix 2). The resulting taxonomic alteration of derived metriorhynchids will be discussed herein.

### THE END OF THE FRAAS MISCONCEPTION

According to Frey *et al.* (2002: 1469; characters taken from the manual phylogeny of Vignaud, 1995), the genus *Geosaurus* can be defined by the following characteristics.

1. The postorbital process of the frontals form a closed angle of 45° with the parietal crest.
2. The angular and surangular are well developed rostrally, and extend well beyond the orbit.
3. The bones of the skull are only faintly ornamented.

Original	Fraas (1902)	Steel (1973)	This paper
<i>Enaliosuchus macrospondylus</i> Koken, 1883	-	<i>Enaliosuchus macrospondylus</i>	<i>Cricosaurus macrospondylus</i>
<i>Enaliosuchus schroederi</i> Kuhn, 1936	-	<i>Enaliosuchus schroederi</i>	<i>Cricosaurus schroederi</i>
<i>Geosaurus araucanensis</i> Gasparini & Dellape, 1976	-	-	<i>Cricosaurus araucanensis</i>
<i>Steneosaurus gracilis</i> Philips, 1871	-	<i>Metriorhynchus gracilis</i>	<i>Cricosaurus gracilis</i>
<i>Geosaurus vignaudi</i> Frey et al., 2002	-	-	<i>Cricosaurus vignaudi</i>
<i>Geosaurus saltillense</i> Buchy et al., 2006	-	-	<i>Cricosaurus saltillense</i>
<i>Geosaurus suevicus</i> Fraas, 1901	<i>Geosaurus suevicus</i>	<i>Geosaurus suevicus</i>	<i>Cricosaurus suevicus</i>
<i>Stenosaurus elegans</i> Wagner, 1852	<i>Geosaurus gracilis</i>	<i>Cricosaurus elegans</i>	<i>Cricosaurus elegans</i>
<i>Rhacheosaurus gracilis</i> von Meyer, 1831	<i>Geosaurus gracilis</i>	<i>Geosaurus gracilis</i>	<i>Rhacheosaurus gracilis</i>
<i>Steneosaurus manselii</i> Hulke, 1870	<i>Dacosaurus maximus</i>	<i>Dacosaurus maximus</i>	<i>Dacosaurus manselii</i>
<i>Geosaurus maximus</i> Plieninger, 1846	<i>Dacosaurus maximus</i>	<i>Dacosaurus maximus</i>	<i>Dacosaurus maximus</i>
<i>Dacosaurus andiniensis</i> Vignaud & Gasparini, 1996	-	-	<i>Dacosaurus andiniensis</i>
<i>Dacosaurus carpenteri</i> Wilkinson et al., 2008	-	-	<i>Geosaurus carpenteri</i>
<i>Dacosaurus lapparenti</i> Debelmas & Strannoloubsky, 1957	-	<i>Dacosaurus lapparenti</i>	<i>Geosaurus lapparenti</i>
<i>Cricosaurus grandis</i> Wagner, 1858	<i>Geosaurus giganteus</i>	<i>Cricosaurus grandis</i>	<i>Geosaurus grandis</i>
<i>Lacerta gigantea</i> von Sommerring, 1816	<i>Geosaurus giganteus</i>	<i>Geosaurus giganteus</i>	<i>Geosaurus giganteus</i>

**Figure 8.** Metriorhynchid taxonomy in historical perspective: main changes in taxon names from their original description (left column) to this paper (right column), passing through definitions by Fraas (1902) and Steel (1973). The cladogram on the right is a reduced version of the strict consensus tree in Figure 7. The grey areas indicate monophyletic genera in this taxonomic arrangement.

4. The lateral margin of the prefrontals is rounded.
5. The orbit is at least as large as the supratemporal fenestra.
6. The dorsal margin of the supratemporal arcade is lower than the parietal crest.
7. The symphyseal part of the mandible is low, only about 15-mm high.

The holotype of *G. giganteus* only possesses (1) and (3), and even then the exact angle of the lateral and medial processes of the frontal cannot be accurately determined. Neither the angular nor the surangular (2) are as well developed as that seen in the longirostrine ‘geosaurs’, as in the holotype the surangular does not extend rostrally beyond the orbit (confirmed in NHM 37020). Characteristic (6) is also absent in NHM R.1229 and NHM 37020, as the lateral and medial processes of the frontal originate on the same plane; however, the compression both crania have endured could have distorted this character. In addition, characteristics (4), (5), and (7) cannot be determined from the holotype. However, the postsymphysial part of the mandibular rami is much higher dorsoventrally than that seen in any of the longirostrine species; therefore, it is highly unlikely to have characteristic (7). Examining NHM 37020, *G. giganteus* did not possess characteristics (5) and (7). From NHM R.1230 and NHM 37020, we can also determine that *G. giganteus* did not possess a rounded lateral margin of the prefrontal (4), with the posterior shape being very reminiscent of the *Dakosaurus carpenteri* Wilkinson *et al.*, 2008 (BRSMG Ce17365) and *C. grandis* (BSPG-AS-VI-1; Wagner, 1858).

Therefore, we can only say with certainty that the type species of *Geosaurus* shares characteristics (1) and (3) with the longirostrine species assigned to that genus. Interestingly, *G. gracilis* (= *Rhacheosaurus*) also does not possess all seven characteristics, as the postorbital process of the frontals (1) does not form a closed angle with the parietal crest, but instead forms a rounded corner (NHM R.3948; Broili, 1932). However, the remaining features (2–7) are present, as considered by Frey *et al.* (2002).

These seven characteristics, as set out by Frey *et al.* (2002), do indeed define a clade of metriorhynchids, but it cannot be named *Geosaurus*. The following taxa demonstrate either all seven characteristics, or a subset of them, but without any contradictions: *M. gracilis* (OXFUM J.1431), *Geosaurus* sp. (Gasparini & Iturralde-Vinent, 2001), *G. cf. suevicus* (Rieppel, 1979), *G. suevicus* (SMNS 9808; Fig. 6B), *G. vignaudi* (Frey *et al.*, 2002), *G. saltillense* (Buchy *et al.*, 2006), *G. araucanensis* (MLP 72-IV-7-1; Fig. 5C), *C. elegans* (BSPG AS I 504; Fig. 6C), *E. macrospondylus* (RNGHP 990201; Hua *et al.*, 2000), and *E. schroederi* (MMGLV unnumbered; Fig. 5B). Within this clade,

the oldest available name is *Cricosaurus* (Wagner, 1858). We therefore propose that all species other than the type currently assigned to *Geosaurus* are transferred to *Cricosaurus*, including *Enaliosuchus*, with the exception of *G. gracilis*, which reverts back to *Rhacheosaurus* (Fig. 8).

However, no type species was designated when *Cricosaurus* was erected (see Wagner, 1858). Under Article 69 of the fourth edition of the Code of the International Commission of Zoological Nomenclature (ICZN 1999), if a nominal genus-group taxon was established prior to 1931, and no type species was fixed in the original publication, then subsequent designation of a type species can be made. Therefore, we designate *C. elegans* (holotype: BSPG AS I 504) as the type species of *Cricosaurus*. This species was chosen over *C. grandis* and *C. medius* as (1) it was the first of the Daiting metriorhynchids described by Wagner (1852); (2) the holotype and only specimen of *C. medius* is apparently lost; and (3) Wagner (1858: 433) himself noted the ‘extraordinary resemblance’ between *C. grandis* and *G. giganteus*.

The validity of *Enaliosuchus*, and the type species *E. macrospondylus* was questioned by Karl *et al.* (2006). Their restudy of the holotypes of *E. macrospondylus* and *E. schroederi*, in comparison with *M. superciliosus* and other nonmetriorhynchid mesoeucrocodylians, failed to find any autapomorphies for *Enaliosuchus* (which was based upon an atlas-axis, with cervical and dorsal vertebrae). However, the exceptionally limited metriorhynchid taxon sampling used by Karl *et al.* (2006) makes this result hardly surprising. What is unexpected is that a skull assigned to *E. macrospondylus*, with associated cervicals and the atlas-axis (RNGHP 990201; Hua *et al.*, 2000), was not included within their study. With this specimen, Hua *et al.* (2000) were able to rediagnose both the genus *Enaliosuchus* and species *E. macrospondylus*, which in our view support their validity. However, we do not propose maintaining the genus *Enaliosuchus*, as it would either render *Cricosaurus* paraphyletic or demand the creation of multiple new genera (Fig. 8).

#### CONSEQUENCES OF RESURRECTING *RHACHEOSAURUS*

The retention of *Rhacheosaurus* is further justified by several character states from the phylogenetic analysis: such as the lack of a premaxillary septum that fully bifurcates the external nares (24-2), the external nares does not extend posteriorly as far as the second maxillary alveolus (38-3), it still possesses a calcaneum tuber (74-1), and the proximal end of metatarsal I is only moderately enlarged (76-2). Interestingly, by resurrecting *Rhacheosaurus*, we invalidate the junior synonymy of *C. elegans* with ‘*Geosaurus*’ *gra-*

*cilis* (Figs 6, 8). The overall cranial architecture of *C. elegans* (BSPG AS I 504) is very similar to that observed in *G. suevicus* (SMNS 9808). The possible synonymy should be the focus of future studies. As such, *G. suevicus* is provisionally retained here as a separate species, but is included within the genus *Cricosaurus*.

The other two species originally included within *Cricosaurus* by Wagner (1858) – *C. medius* and *C. grandis* – have also been considered junior synonyms of *Rhacheosaurus* (*G. gracilis*) by several authors (e.g. Kuhn, 1936; see Fig. 6). It is worth noting that the first skeleton of *Rhacheosaurus* with a preserved cranium (NHM R.3948) was not described until 1905, by Ammon, after Fraas' (1901, 1902) referral of three *Cricosaurus* skulls to *Rhacheosaurus*. Based upon cranial morphology, we agree with the original proposition of Fraas (1902) upon the synonymy of *C. medius* with *Rhacheosaurus*, especially based on the shape of the infratemporal fenestra in lateral view (compare Wagner, 1858: plate XIV, fig. 3, with Broili, 1932: figs 1–6). However, the synonymy of *C. grandis* with *Rhacheosaurus* cannot be supported, as the former shows the same tooth morphology of *G. giganteus* (tri-faceted, strongly lateromedially compressed, and serrated and keeled carinae), rather than the more common uncompressed, noncarinated teeth. Therefore, we agree with the placement of *C. grandis* within *Geosaurus* by Von Zittel (1887–1890). A synonymy between *G. grandis* and *G. giganteus* (the holotypes of both are known from the Mörnsheim Formation of Daiting, and were contemporaneous) is rejected, as *G. grandis* lacks the enlarged dentary tooth opposite the premaxilla–maxilla contact, and the notch for its reception, and has a proportionally longer rostrum, with stronger ornamentation. It is possible these differences are the result of sexual dimorphism, or the enlarged dentary tooth of NHM 37020 could be aberrant. Nevertheless, we believe both species should be retained until further skulls are discovered that can clarify the issue.

#### IMPLICATIONS FOR *DAKOSAURUS*

With the exclusion of the longirostrine forms with nonserrated teeth from the genus *Geosaurus*, the taxa currently included within *Dakosaurus* needs to be reviewed. The genus was erected by Von Quenstedt (1856), and currently comprises large-sized brevirostrine metriorhynchids with distinctively robust skull morphology. Based upon the optimization of dental characters, the genus *Aggiosaurus* can now be conclusively referred to *Dakosaurus* (Buffetaut, 1982b, raised the possibility of a synonymy). The only specimen of *Aggiosaurus*, *Aggiosaurus nicaensis* Ambayrac, 1913, is a poorly preserved upper jaw,

within a slab of limestone, from the upper Oxfordian of south-east France (Ambayrac, 1913a, b; Buffetaut, 1982b). However, based upon the great size and robustness of the dentition (with some crowns being up to 12 cm in length), and their low number, the only genus of metriorhynchid it could possibly be is *Dakosaurus* (see Appendix 2 for the character apomorphy lists). As such, *Aggiosaurus* is here considered a junior synonym of *Dakosaurus*.

In the phylogeny obtained, *Dakosaurus* and *Geosaurus* form a monophyletic clade within Geosaurinae, in which all species could be assigned to *Geosaurus*. This is possible, as the type species of *Dakosaurus* was originally described as *G. maximus*. Despite these considerations, we believe that the species assigned within *Dakosaurus* should not be transferred to *Geosaurus* because: (1) their morphology is distinctive, especially the morphology of the teeth serrations, thereby allowing for the prompt characterization of both genera; (2) the serrations seen in both genera are likely to be nonhomologous, but are certainly of distinct morphology; (3) the prompt characterization allows for the easy identification of isolated teeth into distinct genera; (4) *Geosaurus* and *Dakosaurus*, as proposed here, are neither paraphyletic nor polyphyletic; (5) the transfer of *Dakosaurus* taxa to *Geosaurus* is unnecessary, would imply several taxonomic changes, and would introduce further confusion into the current taxonomy (Fig. 8).

However, the maintenance of *Dakosaurus* demands an additional but single modification, affecting *D. lapparenti* from the late Valanginian of south-east France. This species is based upon quite fragmentary specimens, from which the rostrum, mandible, and most of the postcrania are missing. It also possesses nonfaceted serrated teeth. However, the teeth are blade-like, and the dentition of *D. lapparenti* is keeled (a raised ridge) (E. Roberts, pers. comm., 2007). Such keels have not been reported in other species of *Dakosaurus*. In all other cases, *Dakosaurus* (*D. manselii*, *D. maximus*, and *D. andiniensis*) possess denticulate carinae with a distinct morphology from the one observed in *Geosaurus*. With effect, our phylogenetic results place this species as the sister group of *G. giganteus* + *G. grandis*, and not to other *Dakosaurus*. Therefore, this species is transferred to *Geosaurus*, and should be referred to as *G. lapparenti*.

The age for *D. lapparenti* is usually given as Hauterivian (e.g. Hua & Buffetaut, 1997), following Debelmas & Strannoloubsky (1957). However, Debelmas (1958: 43) rapidly corrected this mistake when referring to a *Dakosaurus* pelvis, assigning these remains to the Valanginian. In fact, comparison between the ammonites from the locality named by the authors

and recent ammonite zonation for the Early Cretaceous of Tethys (Wippich, 2003) clearly supports an upper Valanginian age (*peregrinus* ammonite zone) for *D. lapparenti*. As such, there are no metriorhynchid specimens known from the Hautervian.

#### THE QUESTION OF *NEUSTOSAURUS*

A final remark concerning the taxonomic validity of the genus *Neustosaurus* must be made. As mentioned above, this genus was erected upon postcrania (trunk, hindlimbs, and tail) from the early Valanginian (*pertransiens* zone) of south-east France; the zonation was determined by comparison of the ammonites mentioned in Raspail (1842) and Wippich (2003). Based upon the postcranial characteristics of *C. suevicus*, *Neustosaurus* undoubtedly nests within the *Cricosaurus* clade. However, with the exception of *C. suevicus*, no other taxon has preserved axial skeletal elements, thereby preventing appropriate comparisons. Furthermore, all subgroupings within *Cricosaurus* are defined upon cranial characters. This unfortunately means that the characteristics seen in the type of *Neustosaurus* are not diagnostic, and the precise phylogenetic position of *Neustosaurus* cannot be currently determined. As the '*Enaliosuchus*' specimens range from the *campylotoxus-furcillata* ammonite zones of the early-late Valanginian (Hua *et al.*, 2000; Karl *et al.*, 2006), the *Neustosaurus* specimen is older than any other from the *Cricosaurus* clade within the Valanginian. Nevertheless, the lack of well-preserved postcranial material for most species of *Cricosaurus*, and the resulting lack of autapomorphies for *Neustosaurus*, means that the stratigraphic position alone is not enough to consider the taxon distinct. Therefore, *N. gigondarum* should be considered a *nomen dubium* until new specimens from the Valanginian of Europe can illuminate the postcranial evolution in Early Cretaceous metriorhynchids, or until the skull morphology of *Neustosaurus* is described and an appropriate emended diagnosis is given. This therefore removes the senior synonymy of *Neustosaurus* over *Cricosaurus*.

#### FURTHER SPECIES OF *GEOSAURUS*

Other geosaurines assignable to the genus *Geosaurus*, as proposed here, include *D. carpenteri* (BRSMG Ce17365, redescribed by Wilkinson *et al.*, 2008) and the 'cocodrillo di Portomaggiore' (Leonardi, 1956). *Dakosaurus carpenteri* is now transferred to *Geosaurus* (as *G. carpenteri*), whereas the 'cocodrillo di Portomaggiore' must await proper description prior to a definitive statement on its nomenclature. In addition to these specimens, teeth identical in size and shape with those of *G. carpenteri* are known from the Cor-

alline Oolite of Malton, Yorkshire, UK (NHM 36336 and NHM 36339). This increases the range of the genus *Geosaurus* to the early Oxfordian of England [*cordatum* ammonite zone; zonation determined using BM(NH), 1983]. With these specimens included into *Geosaurus*, the genus can now be considered endemic to Europe, ranging from the Late Jurassic into the Early Cretaceous. The genus *Cricosaurus*, on the other hand, is also present in Europe, and in South and Central America, from the middle Oxfordian (*C. sp.*; Gasparini & Iturralde-Vinent, 2001) to the late Valanginian (*Enaliosuchus* holotype; Karl *et al.*, 2006; Koken, 1883), whereas *Dakosaurus* ranges from the early Oxfordian (*mariae* ammonite zone; NHM 47989) to the early Berriasian (*D. andiniensis*; Gasparini *et al.*, 2006), in Europe, and in South and Central America. This, however, is based on our current knowledge, but further discoveries may expand both the biogeographical and stratigraphical ranges for these genera.

#### CONCLUSIONS

Upon the re-examination of three long-known, but undervalued specimens of *G. giganteus*, taxonomic misconceptions could be resolved, and the morphological diversity of the Metriorhynchidae is found to be greater than previously understood. It was particularly important to rectify the problem introduced by Fraas' (1901, 1902) misconception, and to reverse its impact on the 20<sup>th</sup> century thalattosuchian literature. The phylogenetic analysis presented here clearly shows, with good support, that the type species of *Geosaurus* pertains to a lineage of highly predacious mesorostrine forms (Fig. 7). The plethora of longirostrine taxa previously assigned to *Geosaurus* constitutes a lineage of mostly piscivorous forms, not closely related to *G. giganteus* (Fig. 8). The association between *Geosaurus* and a slender, longirostrine morphology is at the heart of this long-standing misconception, quantitatively demonstrated by the present phylogenetic analysis, and the detailed redescription of the type species of *Geosaurus*.

This paper introduces taxonomic amendments (Fig. 8; Appendix 1) to *Geosaurus* and *Dakosaurus*, whereas *Cricosaurus* and *Rhacheosaurus* were resurrected, and *Enaliosuchus* was suppressed. *Geosaurus* is rediagnosed, now including three described species and two additional forms (*G. giganteus*, *G. grandis*, *G. lapparenti*, *G. carpenteri*, and the Portomaggiore geosaur). The closest lineage to *Geosaurus* is that of *Dakosaurus*, also in a less inclusive conception (*D. maximus*, *D. andiniensis*, *D. manselii*, and *Dakosaurus* sp. from Mexico). All other species previously included into *Geosaurus* are moved to either *Cricosaurus* (e.g. *C. araucanensis*, *C. vignaudi*, *C.*

*saltillense*, and *C. suevicus*) or *Rhacheosaurus* (*R. gracilis*). As no type species was proposed for *Cricosaurus*, *C. elegans* is elected here as the type. In addition, there is an overlooked similarity between *C. elegans* and *C. suevicus*, in contrast to the proposed synonymy between *C. elegans* and *R. gracilis* (e.g. Fraas, 1902; Broili, 1932). *Enaliosuchus* is here considered a junior synonym of *Cricosaurus* because: (1) the maintenance of *Enaliosuchus* would render *Cricosaurus* paraphyletic; and (2) *Cricosaurus* has priority. However, we recognize the validity of the species previously assigned to this genus (as in Hua *et al.*, 2000; *contra* Karl *et al.*, 2006).

The morphological diversity of the Metriorhynchidae is even greater than was previously realized. Not only is *G. giganteus* the first metriorhynchid known to have its dentition arranged as opposing blades, optimized for slicing and gouging flesh, but it has one of the proportionally shortest rostra among thalattosuchians. This indicates that the trend towards becoming a short-snouted hypercarnivore with serrated dentition evolved independently twice within Metriorhynchidae. Within *Dakosaurus*, the cranium and mandible became progressively deeper and more robust, with larger, stout dentition for bone-cracking and osteophagy. On the other hand, longirostrine thalattosuchians evolved slender tubular snouts into two very distinct lineages: the teleosaurid stem and the derived *Cricosaurus* branch.

The termination of Fraas' misconception represents a paradigm shift in the study of Thalattosuchia, which demands a new understanding of what exactly defines *Geosaurus*, and a new comprehension of what were the other longirostrine forms (hereby reassigned to *Cricosaurus* and *Rhacheosaurus*). However difficult it may be to overcome the traditional misconception (mainly for historical reasons), this constitutes a necessary step that will ultimately make it possible to improve our understanding on the evolution of metriorhynchids, as well as their palaeoecology, bio-chronology, and biogeography. It is important also to realize that this change in the concept of *Geosaurus* is not only a by-product of a methodological framework, but, above all, is the result of the rediscovery and reanalysis of an overlooked series of critical specimens.

#### ACKNOWLEDGEMENTS

We would like to thank A.C. Arruda-Campos (MPMA), R.J. Bertini (IGCE-UNESP), J.F. Bonaparte and A. Kramarz (MACN), M. Brett-Surman and H.-D. Sues (USNH), S. Chapman and P. Barrett (NHM), I.S. Carvalho (DG-UFRJ), R. Clark and T. Ewin (BRSMG), E. Frey (SMNK), Z.B. Gasparini, M. Reguero, and S. Bargo (MLP), O. Hampe and D. Schwarz (HMN), C.

Howells (NMW), P. Jeffrey (OXFUM), A.W.A. Kellner (MN-UFRJ), J. Liston (GLAHM), M. Lowe and S. Finney (CAMSM), C. Mehling (AMNH), C.E.M. Oliveira (FEF), O. Rauhut and D. Hone (BSPG), R. Schoch (SMNS), G. Storrs, M. Meyers, and B. Hanke (CMC), M. Taylor (RMS), and G. Wass (PETMG) for providing generous access to the specimens in their care. For assistance with translations, discussion, providing specimen photographs, etc. we would like to thank S. Brusatte and F. Marx (University of Bristol), M.-C. Buchy (MUDE), L. Cavin (MHNG), A. Clement (Université Claude-Bernard), N. Dale-Skey, C. Gillett, and S. Jackson (NHM), M. Delfino and F. Chesi (Università di Firenze), U. Menkveld (Naturhistorisches Museum Bern), N. Knötschke (Dino-Park), M. Riond (Musée géologie Lausanne), E. Robert (Université Joseph Fourier), P. Vignaud (Université de Poitiers), and E. Wilberg (University of Iowa). We would also like to thank S. Jasinowski (University of Bristol), Z.B. Gasparini (MLP), and M.-C. Buchy (MUDE), whose comments improved the quality of this paper. Credit is also due to Phil Hurst (NHM Image Resources) for the photograph of NHM 37020, and to Simon Powell (University of Bristol), for valuable directions on image treatment. MTY carried out this work during the tenure of NERC grant NER/S/M/2005/13450, and the phylogeny was in partial fulfillment of an MSc. at Imperial College London, for which N. MacLeod and A. Milner (NHM) are gratefully thanked for the opportunity to work on this group of animals. MBA receives support from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq – Proc. n° 200381/2006-9), Brazil. MBA received further support to study the specimens from the Bob Savage Memorial Fund (Department of Earth Sciences, University of Bristol; September/2007).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Species of thalattosuchians and other crocodylomorphs used in the phylogenetic analysis, including specimens examined first-hand. Holotypes are set in bold and casts are underlined.

**Appendix S2.** List of the 166 osteological characters used in the phylogenetic analysis.

**Appendix S3.** Matrix used in the analysis.

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## APPENDIX 1

## REVISED TAXONOMY OF METRIORHYNCHIDAE

*Proposed Taxonomy from this study*

Infraorder Thalattosuchia Fraas, 1901

(*sensu* Ginsburg, 1970)

Superfamily Teleosauroidea Geoffroy, 1831

Superfamily Metriorhynchoidea Fitzinger, 1843\*

*Teleidosaurus*

'*Teleidosaurus*'

Family Metriorhynchidae Fitzinger, 1843\*

Subfamily Metriorhynchinae Fitzinger, 1843\*

*Metriorhynchus*

'*Metriorhynchus*'

*Rhacheosaurus*

*Cricosaurus*

Subfamily Geosaurinae Lydekker, 1889

'*Metriorhynchus*'

*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 I.C.Z.N.); this is in accordance with Principle of Coordination, applied to the family-group names (ICZN, Article 36.1). The Principle of Coordination has been applied to family-group names (Article 36.1).

Note, the paraphyly of *Teleidosaurus* and *Metriorhynchus*, and appropriate taxonomic amendments, will be forthcoming (Young *et al.*, in press).

*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 giganteus* (Von Sömmerring, 1816) Cuvier, 1824 *sensu* Von Quenstedt, 1852.

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

*Geosaurus grandis* (Wagner, 1858) Von Zittel, 1887–1890.

Holotype: BSPG AS-VI-1, complete skull and mandible.

*Geosaurus lapparenti* (Debelmas & Strannoloubsky, 1957) comb. nov.

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

*Geosaurus carpenteri* (Wilkinson *et al.*, 2008) comb. nov.

Holotype: BRSMG Ce17365, incomplete skull.

*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, whereas *-sauros* is the Ancient Greek for lizard.

*Geological range:* From the lower Oxfordian (*cordatum* ammonite zone; NHM 36336 and NHM 36339) to the upper Valanginian (*peregrinus* ammonite zone; *G. lapparenti*).

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

*Emended diagnosis:* see above.

*DAKOSAURUS* VON QUENSTEDT, 1856

*DACOSAURUS* SAUVAGE, 1873

*PLESIOSUCHUS* OWEN, 1884

*AGGIOSAURUS* AMBAYRAC, 1913B

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

*Valid species: Dakosaurus maximus* (Plieninger, 1846) Von Quenstedt, 1856.

Holotype: lost; therefore, we designate SMNS 8203 (incomplete skull and mandible) as the neotype of the species (and the type specimen of the genus). *Dakosaurus manselii* (Hulke, 1870) Woodward, 1885.

Holotype: NHM 40103, incomplete skull and mandible.

*Dakosaurus andiniensis* Vignaud & Gasparini, 1996.

Holotype: MHNSR PV344, poorly preserved snout *Dakosaurus nicaeensis* (Ambayrac, 1913b) comb. nov.

Holotype: Muséum d'Historie Naturelle Nice unnumbered, poorly preserved upper jaw, with teeth preserved in limestone.

*Teeth taxa:* Most of the isolated teeth of *Dakosaurus* recovered in Europe have automatically been assigned to *D. maximus*. However, as the phylogeny has demonstrated, the contemporaneous species *D. maximus* and *D. manselii* have distinct cranial apomorphies. As such, only teeth from the Swabian Alb of the upper Kimmeridgian and lower Tithonian are here considered as belonging to *D. maximus*. All other isolated teeth are hereby referred to *Dakosaurus* sp. until further studies can determine if the 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 an alligatorid closely related to *Purussaurus*) for the material.

Giebel (1876) considered *Dinosuchus terror* to be a junior synonym of *Dakosaurus amazonicus*.

*Possibly valid species (1):* *Dakosaurus lissocephalus* Seeley, 1869 (CAMSM J.29419). 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 (MTY, pers. obs.), because of the shape of the supratemporal fenestra, squamosal, and parietal in *D. lissocephalus* being much more reminiscent of *D. andiniensis* and *D. maximus*, than of *D. manselii*. However, until better-preserved material is found from Ely, Cambridgeshire, the synonymy between *D. maximus* and *D. lissocephalus* must remain provisional.

*Possibly valid species (2):* Isolated *Dakosaurus* teeth have long been known from the lower Oxfordian of England (Lydekker, 1890) 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.

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

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

*Geographical range:* Cosmopolitan (Argentina, UK, France, Germany, Mexico, Poland, Russia, and Switzerland).

*Emended diagnosis:* Metriorhynchid thalattosuchian with large robust teeth, with little lateromedially compression, and the carinae formed by denticles 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; distance between the ventral margin of the antorbital fenestra and ventral margin of the tooth row is

greater than the diameter of the antorbital fenestrae; cross-sectional thickness of cranial bone generally > 1.5 mm.

#### *RHACHEOSAURUS* VON MEYER, 1831

*Type species:* *Rhacheosaurus gracilis* Von Meyer, 1831.

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

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

*Geological range:* The lower Tithonian (*hybonotum* ammonite zone).

*Geographical range:* European endemic (Germany).

*Emended diagnosis:* Metriorhynchid thalattosuchian with procumbent teeth, with no lateromedially compression, lacking carinae; cranial bones smooth, lacking conspicuous ornamentation; rounded almost 90° angle formed by the lateral and medial processes of the frontal; 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; symphyseal part of the mandible is low, only about 15-mm high; lateral margin of the prefrontals is rounded; external nares not wholly bifurcated by premaxillary septum; external nares begins just after the first premaxillary alveolus, and does not exceed the first maxillary alveolus; humerus deltopectoral crest absent; hypocercal tail possesses a fleshy upper lobe.

#### *CRICOSAURUS* WAGNER, 1858

*NEUSTOSAURUS* RASPAIL, 1842 (*NOMEN DUBIUM*)

*ENALIOSUCHUS* KOKEN (1883)

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

*Valid species:* *Cricosaurus elegans* (Wagner, 1852) Wagner, 1858.

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

*Cricosaurus suevicus* (Fraas, 1901) comb. nov.

Holotype: none designated, we therefore designate SMNS 9808 (complete skeleton) as a lectotype, as it

was one of the two skeletons upon which this species was described.

*Cricosaurus araucanensis* (Gasparini & Dellapé, 1976) comb. nov.

Holotype: MLP 72-IV-7-1, complete skull with mandible.

*Cricosaurus vignaudi* (Frey *et al.*, 2002) comb. nov.

Holotype: UANL FCT-R1, incomplete skull, mandible, atlas-axis, and two cervicals.

*Cricosaurus saltillense* (Buchy *et al.*, 2006) comb. nov.

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

*Cricosaurus gracilis* (Philips, 1871) comb. nov.

Holotype: OXFUM J.1431, skull lacking snout.

*Cricosaurus macrospodylus* (Koken, 1883) comb. nov.

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

*Cricosaurus schroederi* (Kuhn, 1936) comb. nov.

Holotype: MMGLV unnumbered, skull with mandible lacking complete snout, and atlas-axis and third cervical.

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

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

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

*Emended diagnosis*: Metriorhynchid thalattosuchian with procumbent teeth, with little to no lateromedially compression; cranial bones smooth, lacking conspicuous ornamentation; acute angle formed by the lateral and medial processes of the frontal; dorsal margin of the supratemporal arcade is lower than the medial process of the frontal; eyes as large as the supratemporal fenestra; surangular and angular well-developed, extending rostrally beyond the orbits; symphyseal part of the mandible is low, only about 15-mm high; lateral margin of the prefrontals is rounded; external nares bifurcated by premaxillary septum, and terminating at the end of the second maxillary alveoli; humerus deltopectoral crest absent; calcaneum tuber absent or vestigial; proximal end of metatarsal I greatly enlarged.

## APPENDIX 2

### APOMORPHY LIST FOR THALATTOSUCHIAN TAXA

Apomorphic characters listed that were not within the phylogenetic analysis are indicated with an asterisk.

#### Thalattosuchia

1. Premaxilla posterior to external nares: 50–65% of premaxilla total length (21-1).
2. Nasal–premaxilla contact absent (22-1).
3. Rostrum nearly tubular (25-0).
4. Supratemporal roof dorsal surface: complex (29-0).
5. Postorbital–jugal contact: postorbital lateral to jugal (35-1).
6. Relative length between squamosal and postorbital: postorbital is longer (37-1).
7. Symphysis is long, at least 40% of the mandible length (43-2).
8. Dentary and surangular possess a groove on the lateral surface that is shallow and poorly developed (46-1).
9. Splenial involvement in symphysis is extensive (49-1).
10. Coronoid projects further anteriorly than the caudalmost alveoli (51-1).
11. Dorsal part of the postorbital bar is constricted (90-1).
12. Jugal extends anteriorly in front of the prefrontals (94-1).
13. Posterior skull table nonplanar (99-0).
14. Dorsal primary head of the quadrate contacts only the squamosal (102-0).
15. Scapula anterior and posterior margins, in lateral view: symmetrically concave (105-0).
16. Fourth trochanter on femur absent (108-0).
17. Hindlimb much longer than the forelimb (109-0).
18. Dorsal and ventral rim of the squamosal groove for external earflap musculature absent (112-0).
19. Squamosal contribution to supratemporal arch less than 40% of the total length (127-0).
20. Large, pendulous basal tubera (151-1).

#### Teleosauridae

1. Basisphenoid (palatal view): projects further than quadrates by > 10% of total length (5-1).
2. Cranial XII nerve foramen above the foramen magnum (10-0).
3. External nares is oval, and dorsal width is > 10% longer than the anteroposterior length (23-1).
4. Symphysis depth is ~4% of the mandible length (44-3).
5. Angular and surangular extend rostrally beyond the orbits (47-3).

6. Surangular extends beyond the orbit along the dorsal margin of the mandible (48-1).
7. Teeth lack carinae (55-0).
8. Maxillary teeth not lateromedially compressed (57-0).
9. Orbit ventral margin: jugal makes up the medial portion, whereas the postorbital, the posterior, and the lacrimal make up the anterior portion of the margin (95-1).
10. Anterior and mid-snout maxillary crowns procumbent (123-1).

#### *Pelagosaurus*

1. More than 67% of the premaxilla total length is posterior to the external nares (21-0).
2. Jugal does not extend rostrally in front of the prefrontal (94-1).

#### *Teleosaurus* + (*Platysuchus* + *Steneosaurus*)

1. Orbit mainly dorsal (18-1).
2. More than 28 teeth per maxillae (53-3).
3. Paired ridges medially on the ventral surface of the basisphenoid (83-1).
4. Base of postorbital process of the jugal directed dorsally (85-1).
5. Squamosal does not project further caudally than the occipital condyle (125-0).

#### *Teleosaurus*

1. Lateral process of the frontal forming the beginning of the supratemporal arch: lower than the intertemporal bar (27-1).
2. Five teeth per premaxillae (52-0).

#### *Steneosaurus*

1. Orbit orientated fully dorsally (18-0).
2. Width across the frontals at the maximum intra-orbital distance subequal to the width of one supratemporal fossa (127-1).

#### Metriorhynchoidea (*Teleidosaurus calvadosii* + (('T.' *gaudryi* + 'T.' *bathonicus*) + ('Metriorhynchus' sp. + Oregon croc + Metriorhynchidae)))

1. Foramen for the internal carotid artery extremely enlarged compared with the openings for cranial nerves IX–XI (11-1).
2. Prefrontals anterior to the orbits short and broad, orientated posteriomediaally–anterolaterally (16-1).
3. Symphysis depth 4.5-6.0% of the mandible length (44-2).
4. Three teeth per premaxillae (52-2).

#### *Teleidosaurus calvadosii*

1. External nares posterior edge is straight (23-2).
2. Between 18 and 20 teeth per maxillae (53-2).
3. Antorbital fenestra absent (88-2).

4. Orbit dorsal rim composed of: lacrimal, prefrontal, frontal, and postorbital (124-1).
5. Naso–lacrimal suture length 60% or less that of the naso–prefrontal suture (136-2).

#### ('T.' *gaudryi* + 'T.' *bathonicus*) + ('Metriorhynchus' sp. + Oregon croc. + Metriorhynchidae)

1. Antorbital fossa enclosed by lacrimal, maxilla, nasal, and jugal (39-2).
2. Antorbital fossa elongated, narrow, and oriented obliquely (41-1).
3. Between 20 and 28 teeth per maxillae (53-3).
4. Orbit ellipsoid in shape (96-1).
5. Lacrimal contacts the nasal primarily along its anterior edge (97-1).
6. Orbit dorsal rim composed of: prefrontal, frontal, and postorbital (124-2).
7. Infratemporal flange present (142-1).

#### 'T.' *gaudryi* + 'T.' *bathonicus*

1. Prefrontals incipitally enlarged (12-1).
2. Prefrontal medial edge has a pronounced, rectangular convexity on the posterior half of its margin (93-1).

#### 'Metriorhynchus' sp. + Oregon croc. + Metriorhynchidae

1. Fronto–postorbital suture (dorsal view): frontal 'pushes' the postorbital in a V-shape directed posteriorly (3-1).
2. Prefrontals greatly enlarged (12-2).
3. Supratemporal fossa (dorsal view): rostral margin extends to between the anterior- and posteriormost points of the fronto–postorbital suture (28-1).
4. Caudally, the supratemporal fenestra does not exceed the parietal, but does reach the supra-occipital (31-1).
5. Lacrimal lateral and not visible in dorsal view (33-1).
6. Squamosal does not project further caudally than the occipital condyle (125-0).

#### Metriorhynchidae

1. Fronto–parietal crest (dorsal view): parietal width is < 75% of the frontal width (2-1).
2. Prefrontal teardrop-shaped, with a convex outer margin (14-1).
3. Orbit fully lateral, but the orbit shape is only clear in lateral view (18-3).
4. No conspicuous sculpture on external surface of the rostrum (84-0).

#### Equivocal synapomorphies with *T. calvadosii* + (('T.' *gaudryi* + 'T.' *bathonicus*) + ('Metriorhynchus' sp. + Oregon croc.))

1. Parasphenoid visible in palatal view, forming a ridge along the pterygoids meeting the basisphenoid posteriorly (4-1).
2. Hypocercal tail (61-1).
3. Five cervical vertebrae (63-1).
4. Humerus reduced, with the shaft contributing 35-38% of the total length (67-1).
5. Humerus subequal in length to scapula (68-1).
6. Coracoid fan-shaped, with both ends convex (69-1).
7. Metacarpal I broadly expanded (70-1).
8. Ilium dorsal border small (71-1).
9. Ischium anterior process reduced and lacking either articulation facet (72-1).
10. Tibia reduced, being 40-45% of the femur length (73-1).
11. Calcaneum tuber poorly developed (74-1).
12. Metatarsals II-IV shorter than their respective digits (75-1).
13. Metatarsal I proximal end enlarged (76-1).
14. Digit IV elongated, making it the longest digit (77-1).
15. Tail osteoderms absent (78-2).
16. Dorsal osteoderms absent (80-1).
17. Articulation for ilium on sacral rib small (81-1).
18. Sacral ribs strongly curved ventrally (82-1).
19. Proximomedially articular surface on humerus absent (107-1).
20. Ilium posterior process absent (128-1).
21. Possesses 'w'-shaped chevrons.
22. Mid to late dorsals lack a shallow fossa on the anterior margin of the diapophysis (165-1).
23. Dorsal vertebrae parapophyses orientated anteriorly (166-1).
24. Axis parapophysis is partially or wholly borne on the odontoid.\*

Equivocal synapomorphies with ('*T. gaudryi*' + '*T. bathonicus*') + ('*Metriorhynchus*' sp. + Oregon croc.)

1. External nares: a spoon-shaped elongate ellipse (23-3).
2. Infratemporal fenestra equal/subequal in length with orbit (32-1).
3. External nares terminates at the beginning of the first maxillary alveoli (38-2).
4. External mandibular fenestra absent (45-1).
5. Retroarticular process projects medially past the glenoid fossa (152-1).
6. Retroarticular process is foreshortened (153-1).
7. The surangular has a distinct coronoid process (155-1).

Equivocal synapomorphies with '*Metriorhynchus*' sp. + Oregon croc.

1. Sclerotic ossicles present (19-1).

2. Antorbital fenestra is enclosed by the lacrimal posteriorly, the nasal dorsally, and the maxilla ventrally (40-1).
3. Prefrontal-lacrimal fossae with ridge following the sutural contact between these elements (150-1).

#### Metriorhynchinae

1. Maxilla-palatine suture: forms an M-shape orientated posteriorly (6-1).
2. Lacrimal contributes less than 40% to orbit height (34-1).
3. Surangular extends rostrally beyond the orbit along the dorsal margin of the mandible (48-1).
4. Cervical centra length short (62-2).
5. Tibia more reduced, being 31-39% of femur length (73-2).
6. Atlas hypocentrum subequal to odontoid process length (122-1).
7. Anterior and mid-snout maxillary crowns procumbent (123-1).

Equivocal synapomorphies with *T. calvadosii* + ('*T. gaudryi*' + '*T. bathonicus*') + ('*Metriorhynchus*' sp. + Oregon croc.)

1. Radius greatly reduced and oval in shape (65-1).
2. Humerus-epidodium joint surface straight.\*
3. Femur-fibula joint surface straight.\*
4. Tibia and fibula-astragulus and calcaneum joint surface straight.\*
5. Loss of perichondral bone on the radius.\*
6. Loss of perichondral bone on the radiale.\*

#### *Metriorhynchus s.s.*

((*M. superciliosus* + *M. moreli*) + (*M. palpebrosus* + (*M. sp.* and *M. hastifer*)))

1. Choana V-shaped (9-1).
2. Squamosal contribution to the supratemporal arch at least 50% of the total length (127-1).

#### *Metriorhynchus superciliosus* + *M. moreli*

1. Frontals project posteriorly at least 0.5 cm after fronto-prefrontal contact (126-1).
2. Maxilla-lacrimal contact partially included in the antorbital fossa (141-0).

#### *Metriorhynchus palpebrosus* + (*M. sp.* plus *M. hastifer*)

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



*Metriorhynchus* sp. and *M. hastifer*

1. Angle between medial and lateral processes of the frontal: ~70-60° (26-2).
2. Supratemporal fossa (dorsal view): reaches at least as far anteriorly as the postorbital (28-2).
3. Convex margin on the medial surface of the supratemporal arch (91-1).

(*Metriorhynchus* 'acutus' + ('*M.*' leedsi + '*M.*' laeve) + (USNM 19640 (*Rhacheosaurus* + *Cricosaurus*))

1. Frontal smooth (1-1).
2. Choana: a broad U-shape (9-2).
3. Symphysis depth: ~4% of the mandible length (44-3).
4. Humerus smaller in length than scapula (68-2).
5. Ischium anterior process greatly reduced and lacking either articulation facet (72-2).

'*Metriorhynchus* 'acutus' + ('*M.*' leedsi + '*M.*' laeve)

1. More than 28 teeth per maxillae (53-4).
2. Squamosal projects further caudally than the occipital condyle (125-1).

'*Metriorhynchus* 'acutus

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

'*Metriorhynchus* 'leedsi + '*M.*' laeve

1. Along the dorsal border of the supratemporal arch the postorbital and squamosal curve medially inwards (120-1).

USNM 19640 + (*Rhacheosaurus* + *Cricosaurus*)

1. Frontal-postorbital suture lower than the intertemporal bar (27-1).
2. Supratemporal fossa (dorsal view): reaches at least as anteriorly as the postorbital (28-2).
3. Supratemporal fenestra subequal in length with the orbit (30-1).
4. Infratemporal fenestra shorter than the orbit (32-2).
5. Between the parietal-supraoccipital sutures the parietal is straight with an enclave for the supraoccipital (42-1).
6. Angular and surangular extend rostrally beyond the orbits (47-3).
7. Participation of the coronoid on the external face of the mandible (157-1).

*Rhacheosaurus* + *Cricosaurus*

1. Paraoccipital processes directed dorsolaterally at a 45° angle (7-1).

Equivocal synapomorphies with USNM 19640

1. Prefrontals teardrop-shaped, with a smooth convex outer margin not exceeding the jugal bar in dorsal view (14-3).
2. 28% (or less) of the premaxilla total length is posterior to the external nares (21-3).
3. Teeth lack carinae (55-0).
4. Maxillary teeth are not lateromedially compressed (57-0).
5. Increase (> eight) in caudal vertebrae count (64-1).
6. Humerus deltopectoral crest absent (66-1).
7. Humerus greatly reduced, shaft contributing <25% of the total length, and with distal head wider than proximal head (67-2).
8. Tibia highly reduced, comprising <30% of the femur length (73-3).
9. Increased (by one) presacral vertebrae count (156-1).
10. Loss of perichondral bone on the ulna.\*
11. Loss of perichondral bone on the ulnare.\*
12. Radius and ulna are subequal in size to the radiale and ulnare, respectively.\*

Equivocal synapomorphies with with *T. calvadosii* + (('T.' gaudryi + 'T.' bathonicus) + '*Metriorhynchus*' sp. + Oregon croc.)

1. Loss of the pisiform.\*

*Rhacheosaurus*

1. External nares not wholly bifurcated by premaxillary septum (24-1).
2. External nares begins just after first premaxillary alveolus, and does not exceed the first maxillary alveolus (38-3).
3. Metatarsal I proximal end moderately enlarged (76-2).
4. Infratemporal flange absent (142-0).

*Cricosaurus*

1. External nares bifurcated by premaxillary septum (24-2).
2. Angle between the medial and lateral processes of the frontal: ~45°, or more acute (26-1).
3. External nares terminates at the end of the second maxillary alveoli (38-4).
4. Calcaneum tuber absent or vestigial (74-2).
5. Metatarsal I proximal end greatly enlarged (76-3).

*Cricosaurus gracilis* + *C. vignaudi* + (*C. araucanensis* + (*C. macropondylus* + *C. schroederi*))

1. Supratemporal fossae circular, with the width across the supratemporal fenestra (including the supratemporal arches) >50% of the width across the frontals (110-1).

*Cricosaurus araucanensis* + (*C. macrospondylus* + *C. schroederi*)

1. External nares terminates at the end of the third maxillary alveoli, or further back (38-6).
2. Antorbital fenestra is enclosed by the lacrimal and nasal, excluding the maxilla (40-2).
3. Naso-frontal suture is a smooth concave curve orientated laterally (92-1).

*Cricosaurus macrospondylus* + *C. schroederi*

1. Between 18 and 20 teeth per maxillae (53-2).
2. Prefrontal anterior margin has a posteriorly directed V-shape (140-1).
3. Maxilla-lacrimal contact partially included in the antorbital fossa (141-0).

*Cricosaurus macrospondylus*

1. Unicarinate teeth (55-4).
2. Moderately enlarged maxillary teeth (56-1).
3. Teeth weakly lateromedially compressed (57-1).

Geosaurinae

1. Maxilla-palatine suture: forms a broad U-shape orientated anteriorly (6-2).
2. Choana: W-shaped (9-3).
3. Rostrum is broad (25-1).
4. Mandibular symphysis contributes to 32-38% of the mandibular length (43-1).
5. Symphysis depth ~7-8% of the mandible length (44-1).
6. Coronoid does not project as rostrally as the tooth row (51-0).
7. Between 12 and 17 teeth per maxillae (53-1).
8. Eighteen (or fewer) teeth per dentary (54-1).
9. Cervical centra length moderate (62-1).
10. Base of postorbital process of the jugal is directed dorsally (85-1).
11. Glenoid fossa is orientated dorsally (154-1).

*'Metriorhynchus' durobrivensis* + (*'M.' brachyrhynchus* + *'M.' cultridens*)

1. Prefrontals wider than the posteriorly directed 'V' of the squamosal created by the posterior margin of the supratemporal fossa (13-1).
2. Prefrontals teardrop-shaped, with the outer margin forming a 90° angle, with a distinct triangular shape (14-2).
3. Postorbital forming the supratemporal arch creates a 90° angle facing anterolaterally (118-1).

4. Squamosal overlaps the paroccipital process extensively, projecting further caudally than the paroccipital processes (119-1).

*'Metriorhynchus' brachyrhynchus* + *'M.' cultridens*

1. Mandibular symphysis makes up >40% of the mandible length (43-2).
2. Maxillary teeth strongly lateromedially compressed (57-2).
3. Tooth crowns strongly recurved (58-2).
4. Maxillary teeth have a constriction band at their base (59-1).

Geosaurinae indet. + (*'Metriorhynchus' casamiquelai* + *'M.' potens*) + (*Geosaurus s.l.* + *Dakosaurus*)

1. Paraoccipital processes starts horizontally, whereas terminal third sharply inclines dorsolaterally at a 45° angle (7-2).

(*'Metriorhynchus' casamiquelai* + *'M.' potens*) + (*Geosaurus s.l.* + *Dakosaurus*)

1. Frontal smooth (1-1).
2. Between 36 and 45% of the premaxilla total length is posterior to the external nares (21-2).
3. Supratemporal fossa in dorsal view reaches at least as anteriorly as the postorbital (28-2).

*'Metriorhynchus' casamiquelai* + *'M.' potens*

1. Teeth lack carinae (55-0).
2. Supratemporal arch in lateral view is straight (98-1).

*'Metriorhynchus' casamiquelai*

1. Symphysis depth ~4% of the mandible length (44-3).
2. Surangular extends beyond the orbit, whereas the angular does not (47-2).
3. There are 20 or more teeth per dentary (54-0).
4. Orbits are circular in shape (96-0).

*Geosaurus* + *Dakosaurus*

1. Angle between medial and lateral processes of the frontal: ~45° (26-1).
2. Supratemporal fenestra projects more posteriorly than the parietal (31-2).
3. Humerus greatly reduced, shaft contributing <25% of the total length, and the distal head is wider than the proximal head (67-2).
4. Width across the frontals at the minimum intraorbital distance is subequal to the width of one supratemporal fossa (121-1).

*Geosaurus* ('Portomaggiore croc + *G. carpenteri* + (*G. lapparenti* + (*G. giganteus* + *G. grandis*)))

1. Prefrontal teardrop-shaped, with the inflexion point directed posteriorly at  $\sim 70^\circ$  from the antero-posterior axis of the skull (14-4).
2. Maxillary crowns moderately enlarged (56-1).

*G. lapparenti* + (*G. giganteus* + *G. grandis*)

1. Maxillary teeth strongly lateromedially compressed (57-2).
2. Teeth serrations upon a raised ridge (keel) (55-3).

*Geosaurus giganteus* + *G. grandis*

1. Tri-faceted teeth (130-1).

*Geosaurus giganteus*

1. Dentary tooth opposite the premaxilla–maxilla suture enlarged (60-1).
2. Brevirostrine snout.\*

*Dakosaurus*

1. Prefrontal teardrop-shaped, with medial and lateral edges parallel, and the inflexion point directed posteriorly at a  $\sim 50^\circ$  angle from the anteroposterior axis of the skull (14-5).
2. Prefrontal length–width subequal in dorsal view (15-1).
3. Supratemporal fenestra (dorsal view): projects more rostrally than the postorbital, reaching the minimum intraorbital distance (28-3).

4. External nares begins after the first premaxillary alveolus, but does not exceed the first maxillary alveolus (38-3).
5. Pronounced groove on the lateral surface of the dentary, and surangular deep and strongly developed with a large foramen at both ends (46-2).
6. Large denticulate serration (mesio–distal width more than twice the apex–base width), creating the teeth carinae (55-2).
7. Large gap between the ventral margin of the tooth row and the ventral margin of the antorbital fenestra (134-1).
8. Basal tubera reduced (151-0).

*Dakosaurus manselii* + (*D. maximus* + *D. andiniensis*)

1. Maxillary teeth extremely enlarged (> 6-cm long) (56-2).

*Dakosaurus maximus* + *D. andiniensis*

1. Posterior three maxillary alveoli are more ventral than all other premaxillary/maxillary teeth, with the terminal third of the maxilla posteroventrally inclined (129-1).

*Dakosaurus andiniensis*

1. Rostrum is oreinirostral (25-2).
2. Symphysis depth 10% or more of mandible length (44-0).
3. Less than 11 teeth per maxillae (53-0).
4. Brevirostrine snout.\*