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A NEW ELASMOSAURID PLESIOSAUR FROM THE LOWER CRETACEOUS OF QUEENSLAND, AUSTRALIA

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ABSTRACT—A nearly complete but badly crushed elasmosaurid plesiosaur skull is described from the Upper Albian Toolebuc Formation of northern Queensland, Australia. The specimen has a long history, being previously referred to the Australian Aptian genus '*Woolungasaurus*' (considered a nomen dubium), as well as provisionally to Elasmosauridae gen. et sp. nov., and most recently to *Tuarangisaurus* (Campanian-Maastrichtian, New Zealand and potentially Patagonia). The present assessment alternatively proposes assignment to a new taxon, *Eromangasaurus carinognathus*, gen. et sp. nov., uniquely characterized by the presence of seven premaxillary teeth (three lateral pairs, one midline), an elongate mandibular symphysis with prominent ventral midline keel, and a combination of osteological features variably developed in other elasmosaurids. Cladistic analysis using 43 discrete cranio-dental and vertebral characters coded for 16 ingroup and one outgroup taxon supports this conclusion, indicating that *E. carinognathus* is a crown-group elasmosaurid of more derived grade than *Occitanosaurus* (Lower Jurassic, Toarcian, France). Affinities with other Cretaceous elasmosaurids are poorly resolved. Nevertheless, a close relationship with *Tuarangisaurus* is not substantiated; instead, *E. carinognathus* forms a discrete clade with *Terminonatator* (Campanian, Canada).

INTRODUCTION

The Lower Cretaceous (Aptian-Albian) epicontinental marine rocks of the Eromanga Basin in central and northeastern Australia have long been known as a productive source of well-preserved plesiosaur fossils. Synopses (including maps) of these and other current Australian plesiosaur discoveries have been given by Molnar (1991), Thulborn and Turner (1993), Long (1998), Cruickshank et al. (1999), and Kear (2003, 2004).

Numerous recent studies have documented aspects of cranial osteology in plesiosaurs from the Northern Hemisphere, particularly those from the European Jurassic (e.g., Taylor, 1992; Taylor and Cruickshank, 1993; Cruickshank, 1994a, 1994b; Brown and Cruickshank, 1994; Storrs and Taylor, 1996; Storrs, 1997; Maisch, 1998; Bardet et al., 1999; Maisch and Rucklin, 2000; O'Keefe, 2001, 2004a; Noè et al., 2003) and the North American Cretaceous (e.g., Carpenter, 1996, 1997, 1999; O'Keefe, 2001, 2004b; Druckenmiller, 2002; Sato, 2003). In contrast, knowledge of taxa from the Southern Hemisphere is sparse, with only a handful of described specimens recorded from the Middle Jurassic (Bajocian) of western Argentina (Gasparini, 1997), Early Cretaceous (Valanginian) of South Africa (Andrews, 1911; Cruickshank, 1997), and Late Cretaceous (Campanian-Maastrichtian) of Patagonia (Cabrera, 1941; Gasparini et al., 2003a), Antarctica (Chatterjee and Small, 1989) and New Zealand (Wiffen and Moisley, 1986; Cruickshank and Fordyce, 2002). Well-preserved cranial remains representing both pliosauroids and polycotylids have been recovered from Lower Cretaceous deposits in Australia (see Kear, 2003 for review). Elasmosaurids, however, have proven more elusive.

At present, aside from isolated basicranial elements (Kear, 2001), the only documented Australian elasmosaurid craniomandibular material comprises an articulated although badly crushed skull (QM F11050), collected along with several anterior cervical vertebrae from the Upper Albian Toolebuc Formation of Yambore Creek, north of Maxwelton in central northern Queensland (Fig. 1). This specimen has an interesting history, being initially recovered in two separate parts by independent field parties from the Geological Survey of Queensland, Brisbane (in 1980) and Australian Museum, Sydney (in 1981). The two pieces (comprising the snout and anterior mandibular symphysis, and posterior cranium, lower jaw, attached atlas-axis complex, and three associated anterior cervical vertebrae) were later recognized as belonging to a single individual and reunited for preparation and study at the Queensland Museum (see Thulborn and Turner, 1993, for a full account of circumstances surrounding the discovery). Persson (1982) provided a brief initial description of QM F11050, tentatively assigning it to the Australian Aptian elasmosaurid '*Woolungasaurus* cf. *glendowerensis*' Persson, 1960. However, this taxon was designated a nomen dubium by Welles (1962), and the non-diagnostic holotype (a fragmentary postcranial skeleton, QM F3567) was referred to Elasmosauridae gen. et sp. indet. by Kear (2003). Similarly, Thulborn and Turner (1993) in an examination of pathologies (see below) on QM F11050 stated that there was no sound taxonomic basis for assignment of the specimen to '*Woolungasaurus*.' Consequently they suggested attribution (pending a more thorough description and reappraisal) to a possible new unnamed genus and species of elasmosaurid closely resembling *Libonectes morgani* (Welles, 1949) from the Turonian (Upper Cretaceous) Britton Formation of Texas, U.S.A. (see Carpenter, 1997). Surprisingly, a recent study by Sachs (2004) resurrected '*W. glendowerensis*' but changed the generic-level assignment (based on similarities in the postcranial skeleton) to *Styxosaurus*, a taxon known elsewhere from the Late Cretaceous (Campanian) Niobrara Formation of western North America. In addition, a short remark in the same publication suggested potential referral of QM F11050 to a new species of *Tuarangisaurus* (Sachs, 2004: 713). Notably however, these placements were not established using a cladistic framework, and no unambiguous cranial synapomorphies were presented to support the claims.

In light of the taxonomic uncertainty surrounding QM F11050, this paper aims to redescribe the specimen and determine its potential phylogenetic relationships with other elasmosaurid taxa using cladistic methods.

TERMINOLOGY

Lithostratigraphic nomenclature for the Lower Cretaceous deposits of central-northern Queensland follows Vine et al. (1967). Systematic terminology for Plesiosauria follows O'Keefe (2001) except for the ranking of Sauropterygia and Plesiosauria, which adheres to the more conventional system of Carroll (1988), Benton (1997), and Rieppel (2000). All measurements were made using calipers and are in millimeters (mm).

Institutional Abbreviations—**AM**, Australian Museum, Sydney, Australia; **KUVP**, Kansas Museum of Natural History, Lawrence, Kansas; **NZGS**, New Zealand Geological Survey, Lower Hutt, New Zealand; **QM**, Queensland Museum, Brisbane, Australia.

GEOLOGICAL SETTING

The plesiosaur skull (QM F11050) was excavated from the Lower Cretaceous Toolebuc Formation of Yambore Creek, north of Maxwelton in central-northern Queensland (Fig. 1). This unit comprises finely laminated bituminous and calcareous shales with abundant limestone concretions and corresponds to a major shallow marine transgression into the Eromanga Basin (McMinn and Burger, 1986). It has been extensively studied using sequence stratigraphy (Vine et al., 1967), invertebrate biostratigraphy (Day, 1969) and palynological analyses (McMinn and Burger, 1986; Moore et al., 1986; Helby et al., 1987). Examinations of the marine vertebrate fauna have identified a diverse assemblage of chondrichthyans (Lees, 1986; Kemp, 1991), osteichthyan fishes (Lees and Bartholomai, 1987; Lees, 1990; Long, 1991; Bartholomai, 2004), ichthyosaurs (Wade, 1984, 1990; Kear, 2003, 2004), chelonioid turtles (Owen, 1882; Longman, 1915; Gaffney, 1981, 1991; Hirayama, 1997; Kear, 2003, 2004) and plesiosaurs (Longman, 1924; Persson, 1960, 1982; Molnar, 1991; Thulborn and Turner, 1993; Cruickshank et al., 1999; Kear, 2001, 2003, 2004).

Assignment of QMF11050 to a specific stratigraphic horizon is problematic (owing to limited sediment/invertebrate macrofossil sampling at the type locality), although a broad age range (derived primarily from palynological data) can be established based upon the rock unit of origin. For example, the Toolebuc Formation is placed within the latest mid to late Albian *Pseudoceratium ludbrookiae* dinoflagellate zone, and the upper *Coptospora paradoxa* spore-pollen zone in the southern Eromanga Basin (Moore et al., 1986; Alexander and Sansome, 1996), and diachronously in the late Albian *Phimopollenites pannosus* spore-pollen zone farther north (McMinn and Burger, 1986). Considering that the Maxwelton area falls within the northern extremity of the Toolebuc Formation, a probable Late Albian age for QM F11050 seems likely.

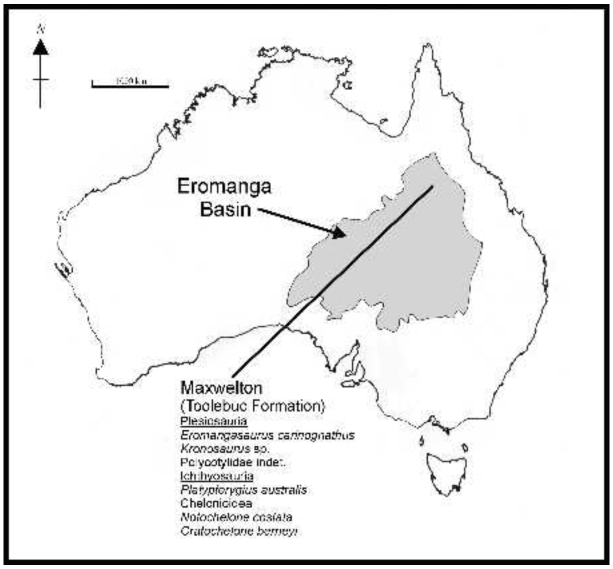

FIGURE 1. Geographical position of type locality (Maxwelton, Queensland) with a list of representative marine reptile taxa from the Toolebuc Formation. Shaded area shows extent of Eromanga Basin.

Preservation of QM F11050 is unusual. The isolated skull was found in association with five anterior cervical vertebrae (including the atlas-axis complex); however, the remainder of the postcranial skeleton was missing. A series of regular depression fractures along the back and top of the skull, in conjunction with a severe unhealed break in the lower jaw, led Thulborn and Turner (1993) to speculate that the skull may have been severely damaged by a lethal bite from a large predatory pliosaurid. This action was also thought to have potentially severed the head and anterior part of the neck. Although this dramatic scenario cannot be confirmed or denied by the present analysis the various pathologies recorded by Thulborn and Turner (1993) certainly appear to be evident on the specimen.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
ELASMOSAURIDAE Cope, 1869
EROMANGASAURUS CARINOGNATHUS, gen. et sp. nov.
(Figs. 2–7)

Woolungasaurus cf. *W. glendowerensis*: Persson, 1982.
Elasmosauridae gen. et sp. nov.: Thulborn and Turner, 1993.
Elasmosauridae gen. et sp. nov.: Kear, 2003.
Tuarangisaurus sp. nov.: Sachs, 2004.

Holotype and Only Specimen—QM F11050; nearly complete, badly crushed skull and mandible; five anterior cervical vertebrae including atlas-axis complex.

Locality and Horizon—Yambore Creek, near Maxwelton in central northern Queensland, Australia (see Persson, 1982). The only known specimen is thought to be from the Toolebuc Formation (Rolling Downs Group), Eromanga Basin, latest mid to late Albian *P. ludbrookiae* zone/upper *C. paradoxa*-*P. pannosus* zone (Moore et al., 1986; McMinn and Burger, 1986).

Etymology—*Eromanga*, referring to the Eromanga Basin, the most productive region in Australian for Cretaceous marine reptile fossils, and *-saurus* (Greek), reptile; *carin-* (Greek), keel; and *-gnathus* (Greek), jaw, referring to the prominent midline keel on the posteroventral portion of the mandibular symphysis. Gender masculine.

Diagnosis—Elasmosaurid plesiosaur uniquely distinguished by presence of seven premaxillary teeth (three lateral pairs, one midline) and elongate (enforced sensu O'Keefe, 2001) mandibular symphysis bearing prominent keel along posteroventral midline. In addition, the taxon displays a combination of characters variably developed in other elasmosaurids. These include: dorsomedial process of premaxilla contacting anterior extension of parietal; margin of temporal fenestra lacking obvious contribution from frontal; pineal foramen probably present but not bordered by frontal; contact between squamosal and postorbital absent; jugal lacking obvious contribution to narrow bar between orbit and temporal emargination; quadrate flange of pterygoid contacting both quadrate and squamosal; pterygoids in contact posterior to posterior interpterygoid vacuity but covered by posterior parasphenoid process; parasphenoid narrow and keeled along exposed posterior length; anterior portion of Meckelian canal closed over; mandibular symphysis formed by dentaries only; coronoid lacking obvious exposure on lateral surface of mandible; caniniform teeth present on maxilla; and single-headed axial rib with base confined to axis centrum.

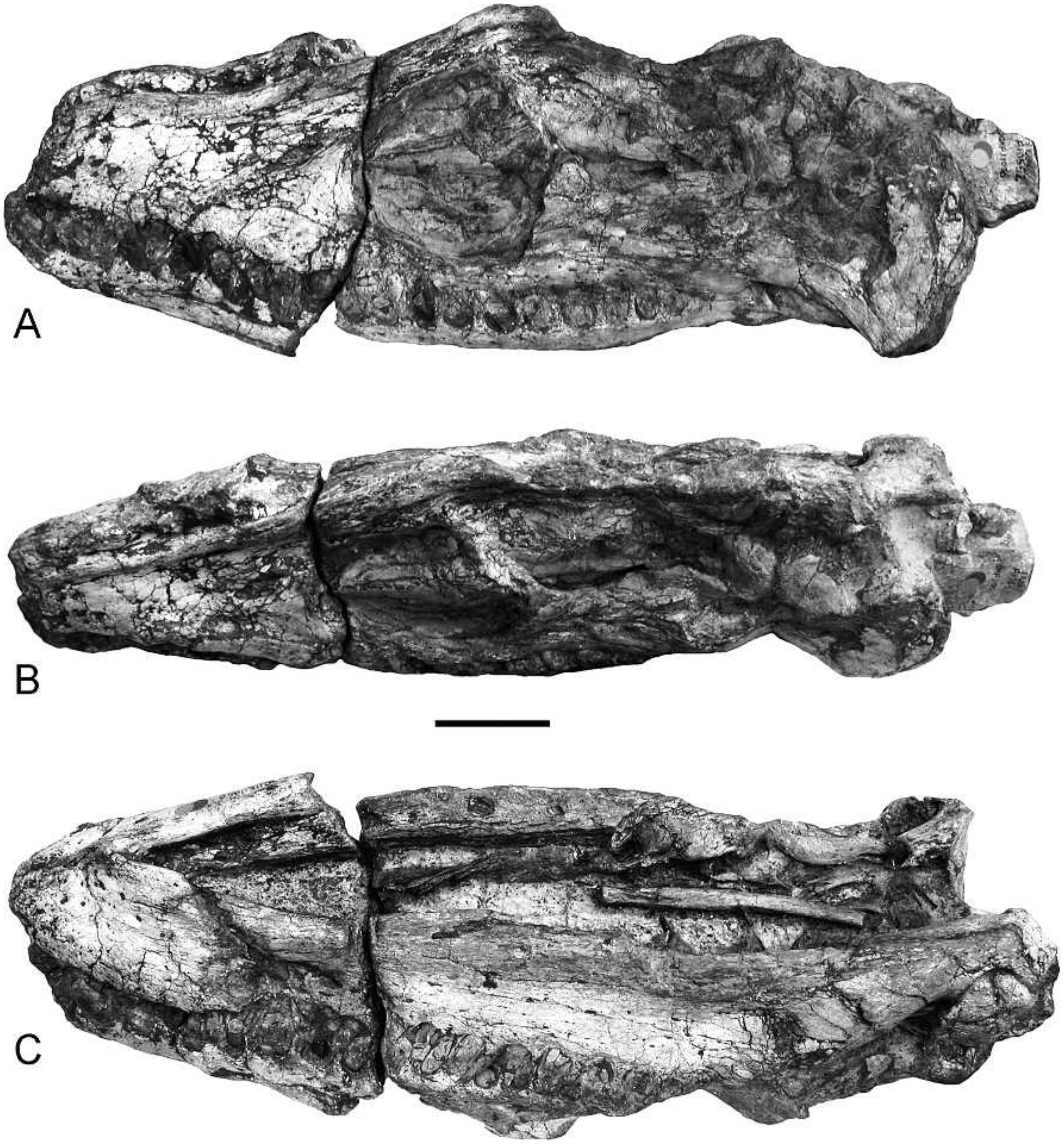

FIGURE 2. *Eromangasaurus carinognathus*, gen et sp. nov., holotype, QM F11050, from the upper Albian (Lower Cretaceous) of Queensland, Australia. Skull in **A**, lateral, **B**, dorsal, and **C**, ventral views. Scale bar equals 50 mm.

Description

The cranium of QM F11050 (Figs. 2–6) is severely crushed, restricting the amount of preparation that could be safely undertaken on the specimen. Limited removal of limestone matrix with dilute acetic acid has exposed many structures; however, much of the internal morphology of the skull remains obscured. Attempts at revealing the form and articulation of the unexposed cranial elements using high-resolution X-ray computed tomographic (CT) scans were unsuccessful.

Extreme crushing of the skull bones in QM F11050 has led to competing interpretations of the basic orientation of the cranium. Persson (1982) considered the specimen as having been flattened dorsoventrally (see Thulborn and Turner, 1993:fig. 2A), with the skull roof collapsing inwards towards the mid-line and the orbits coming to lie side-by-side in a dorsal orientation. Alternatively, Thulborn and Turner (1993) suggested that the skull had collapsed laterally (see Thulborn and Turner, 1993:fig. 2B), the left-hand side folding over onto the right (when viewed from the posterior), crushing both the skull roof and right orbit. The latter interpretation is confirmed by the present study, which indicates that the left-hand side of the skull is lying in a near horizontal plane with the skull roof mediolaterally compressed; in accordance the basicranium and squamosal arch are slightly posteriorly displaced.

Fusion of the neural arch bases and cervical ribs to the associated cervical centra (sensu Brown, 1981) indicates that QM F11050 was osteologically mature at the time of death. Indeed,

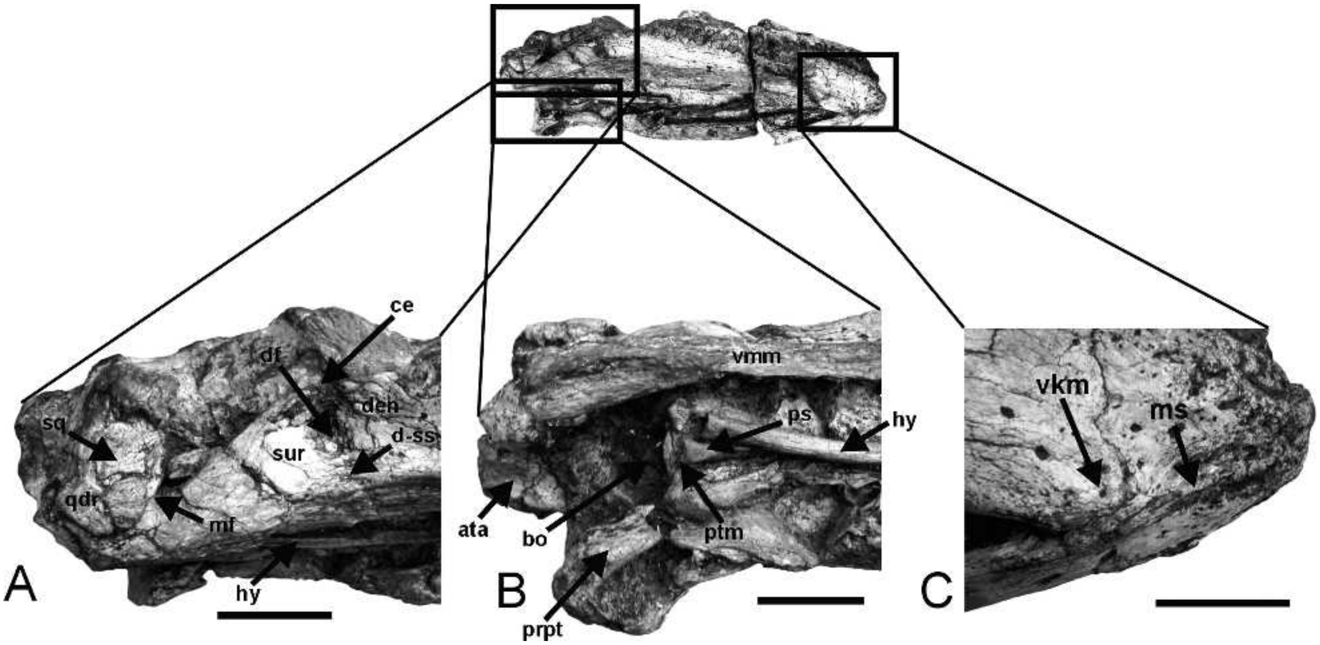

FIGURE 3. Diagrams of *Eromangasaurus carinognathus*, gen. et sp. nov., holotype skull (QM F11050) in left lateral (top) and ventral (bottom) views. Scale bar equals 50 mm. **Anatomical abbreviations**: **ata**, atlas-axis; **bo**, basioccipital; **ce**, coronoid eminence; **den**, dentary; **df**, depression fracture; **d-ss**, dentary-surangular suture; **en**, external naris; **ex**, exoccipital; **fr**, frontal; **hy**, hyoid; **j-ss**, jugal-squamosal suture; **jug**, jugal; **lpt**, lateral premaxillary teeth; **max**, maxilla; **mf**, mandibular fossa; **ms**, mandibular symphysis; **or**, orbit; **par**, parietal; **?pf**, possible parietal foramen; **pmr**, premaxillary ridge; **p-ms**, premaxillary-maxillary suture; **pmx**, premaxilla; **por**, postorbital; **p-ps**, premaxillary-parietal suture; **prpt**, posterior ramus of pterygoid; **ps**, parasphenoid; **pt**, pterygoid; **qdr**, quadrate; **rap**, retroarticular process; **?soc**, possible supraoccipital fragment; **sp**, sclerotic plates; **sq**, squamosal; **sur**, surangular; **vkm**, ventral keel on mandible.

Persson (1982) suggested that retention of a faint suture line between the atlas-axis centra might indicate that the individual was a young adult.

Cranium—The skull of QM F11050 measures 331 mm from the tip of the snout to the posterior margin of the parietals. With the displaced left squamosal, the total length of the cranium increases to 382 mm. The skull width is only 46.2 mm in the preorbital region because of the severe crushing. The preorbital length is 135 mm, thus giving a beak index (sensu Welles, 1952) of 40.8; this is consistent with those of other elasmosaurs (see Welles, 1952; Sato, 2003). The following description of individual cranial elements is based largely on observations from the better-preserved left-hand side of the skull.

The premaxillae are tapered anteriorly forming a short muzzle. Their contribution to the palate is unknown. Dorsally they unite in a closed median suture that extends to about the posterior margin of the orbit and contacts the anterior extension of the parietals in a broad suture. The median suture of the premaxillae is raised into a prominent dorsomedian ridge along the snout (Fig. 4A). This bulges slightly in the area of the external naris, although it is unclear as to whether this is an artifact of lateral crushing or a potential homologue of the premaxillary bump reported in *Styxosaurus*, *Thalassomedon*, and *Terminonatator* from the Late Cretaceous of North America (Sato, 2003). The external surface of the premaxilla is ornamented by weak ridges and a series of prominent foramina that extend along the ventral margin of the bone above the premaxillary tooth sockets. There are dental alveoli for seven premaxillary teeth, three lateral pairs (see Fig. 4A) and an additional anterior midline tooth on the left premaxilla. The number of premaxillary teeth is variable in Cretaceous elasmosaurs, ranging from the typical five pairs in *Callawayasaurus*, *Hydrotherosaurus*, *Libonectes*, and probably *Tuarangisaurus*, down to four lateral pairs and a small midline tooth in *Terminonatator* (Welles, 1943, 1949, 1952, 1962; Welles and Bump, 1949; Wiffen and Moisley, 1986; Carpenter 1997; Sato, 2003).

The suture between the premaxilla and maxilla extends posterodorsally from behind the third lateral premaxillary tooth up to the anteroventral edge of the elliptical external naris (Fig. 4A, B). Identification of other sutures around the external naris and anterior orbit is problematic because of extensive surface cracking in this region of the skull. Interestingly however, there is no evidence of a prefrontal. At present it is unclear as to whether this element has completely fused (without traceable suture), has been lost prior to burial or was absent altogether. Nevertheless, its contribution to the bony nasal aperture (and participation in the orbital margin) appears to have been negligible, the dorsal margin of the external naris being formed almost entirely by the premaxilla. The ventral and posterior margins of the external naris are formed by the maxilla, which also contributes to the anteroventral portion of the orbit. The tooth-bearing section of the maxilla is elongate, extending past the posterior edge of the orbit and underlapping the jugal for some distance (it does not contact the squamosal). A circular depression fracture is present on the left-hand side of the skull just posterior to the premaxilla–maxilla suture. This is situated in near direct opposition to the severe break in the right mandibular ramus, perhaps lending support to the bite-mark scenario of Thulborn and Turner (1993).

Both the left and right maxillae bear 14 dental alveoli. The second, third, and fourth (just posterior to the maxillary–premaxillary suture) bear large caniniform teeth; the remaining alveoli decrease progressively in size towards the back of the jaw.

The ventral margin of the orbit in QM F11050 was probably formed by the jugal as in Late Cretaceous taxa such as *Libonectes*, *Styxosaurus*, and *Thalassomedon* (see Carpenter, 1997). This, however, is speculative as the anterior extremity of the bone is partly displaced into the orbit and largely broken away

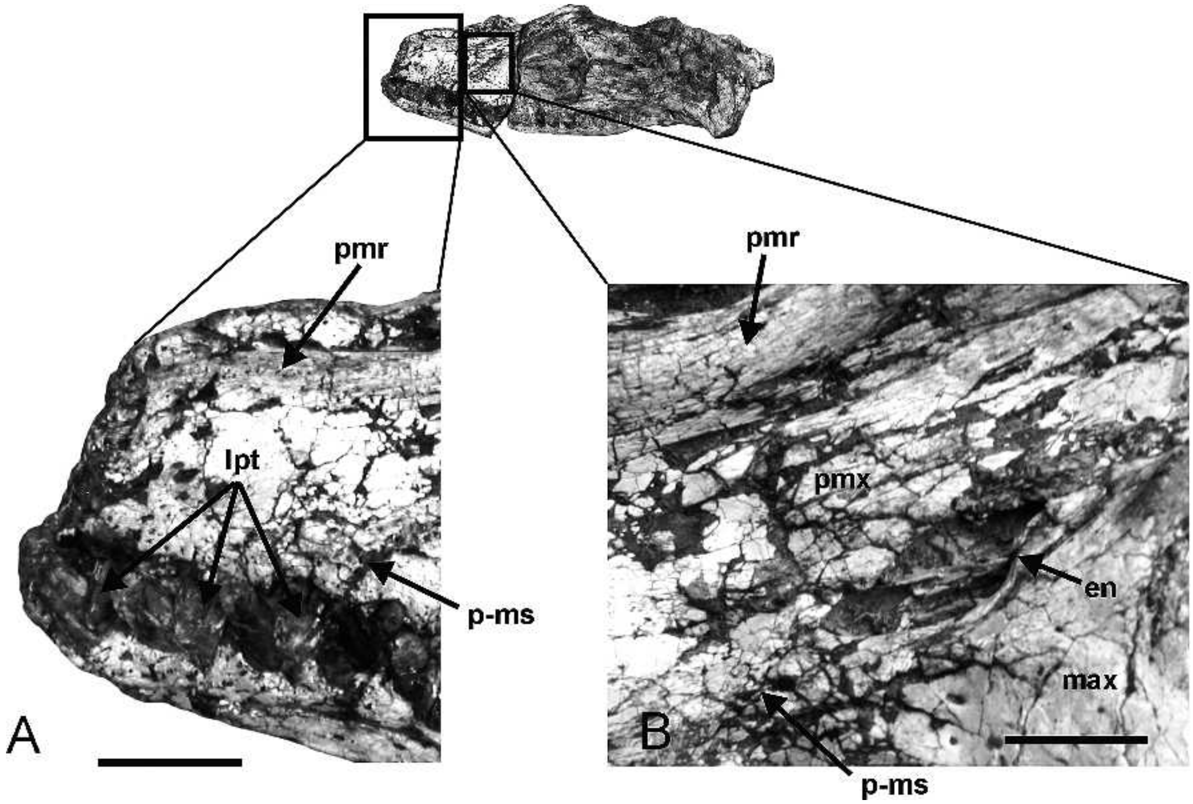

FIGURE 4. Detailed images of *Eromangasaurus carinognathus*, gen. et sp. nov., holotype skull (QM F11050). **A**, anterior snout; **B**, left external naris. Scale bar equals 30 mm. **Anatomical abbreviations**: **en**, external naris; **lpt**, lateral premaxillary teeth; **max**, maxilla; **pmr**, premaxillary ridge; **p-ms**, premaxillary-maxillary suture; **pmx**, premaxilla. Scale bars equal 30 mm.

(see Thulborn and Turner, 1993, for discussion). The posterior section of the jugal is badly crushed and its original shape is difficult to discern. Even so, a well-defined interlocking suture is evident between the jugal and squamosal on the left-hand side of the skull (see Fig. 5A-F). The contribution of the jugal to the postorbital bar is severely damaged but appears to have been limited. A large portion of what may be the postorbital lies beneath the jugal (Fig. 5A, B). If this is correct, it composed the bulk of the postorbital bar and rear wall of the orbit, as well as the anterior margin of the temporal fenestra. The dorsal portion of the postorbital bar is almost totally eroded making disposition of elements unclear. Despite this, a well-defined connection between the postorbital bar and parietal is evident.

The dorsal rim of the orbit is delineated by the frontal (Fig. 5A, B). This bone has suffered considerable damage from surface erosion (the right frontal has been obliterated by crushing), but apparently contacted the parietal dorsally and the premaxillary–maxillary region anteriorly (which it underlaps, probably extending into the olfactory cavity). The frontals are separated along the midline by the posterior extension of the premaxillae and parietals posteriorly. This resembles the derived condition in some Late Cretaceous elasmosaurids (Carpenter, 1997, 1999; Sato, 2003) but differs from Jurassic taxa (see Andrews, 1910; Maisch, 1998; Bardet et al., 1999) and the Lower Cretaceous *Brancasaurus*, in which the frontals meet along the mid-line (see Wegner, 1914; Carpenter, 1997).

The parietal region of QM F11050 (Fig. 5C, D) has been pushed in behind the orbit and displaced posteriorly. There has also been considerable transverse compaction such that little more than the dorsal mid-lines of the parietals are visible. Only the narrow base of the parietal crest is preserved, making its exact height unknown. A distorted elliptical opening (with sediment infill) in the displaced mid-section of the parietals might represent a pineal foramen. If correct, this differs from the condition in many derived elasmosaurids where the pineal foramen is notably absent (e.g. Wiffen and Moisley, 1986; Carpenter, 1997; Bardet et al., 1999; Sato, 2003). Posteriorly the fused parietals have broken away from the squamosals. The crushed remnants of the left lateral parietal wall are visible within the temporal fenestra (Fig. 5C). The temporal fenestra itself appears to have been large (over 40% of total skull length), although its complete shape is difficult to discern.

Although badly damaged, the squamosals were clearly triradiate, forming an anteriorly sloping suspensorium (Figs. 2, 3). This is corroborated by the broken remnants of the distal right squamosal and quadrate (Fig. 6A, B), which (together with the posteriorly placed lower jaw) indicate a slope angle of about 70°. The left squamosal contributes to the posterolateral margin of the temporal fenestra and contacts the jugal anteriorly (thus it is excluded from contact with the postorbital). Ventrally, the squamosal is firmly sutured to the quadrate; its descending process extends down to the level of the articular condyle (Fig. 6A). The lateral surface of the left squamosal bears a circular depression fracture near its contact with the dorsal portion of the quadrate; this corresponds to the tooth mark identified by Thulborn and Turner (1993).

Both the left and right quadrates are preserved in articulation. The distal portion of the left quadrate has been damaged by erosion but the right is nearly complete and still in place within the mandibular fossa. The quadrate itself is a massive element sandwiched between the lateral descending process of the squamosal and medial quadrate flange of the pterygoid (it contacts the latter via a distinct process). Distally the quadrate bears an expanded articular condyle that is broader than long. Both the

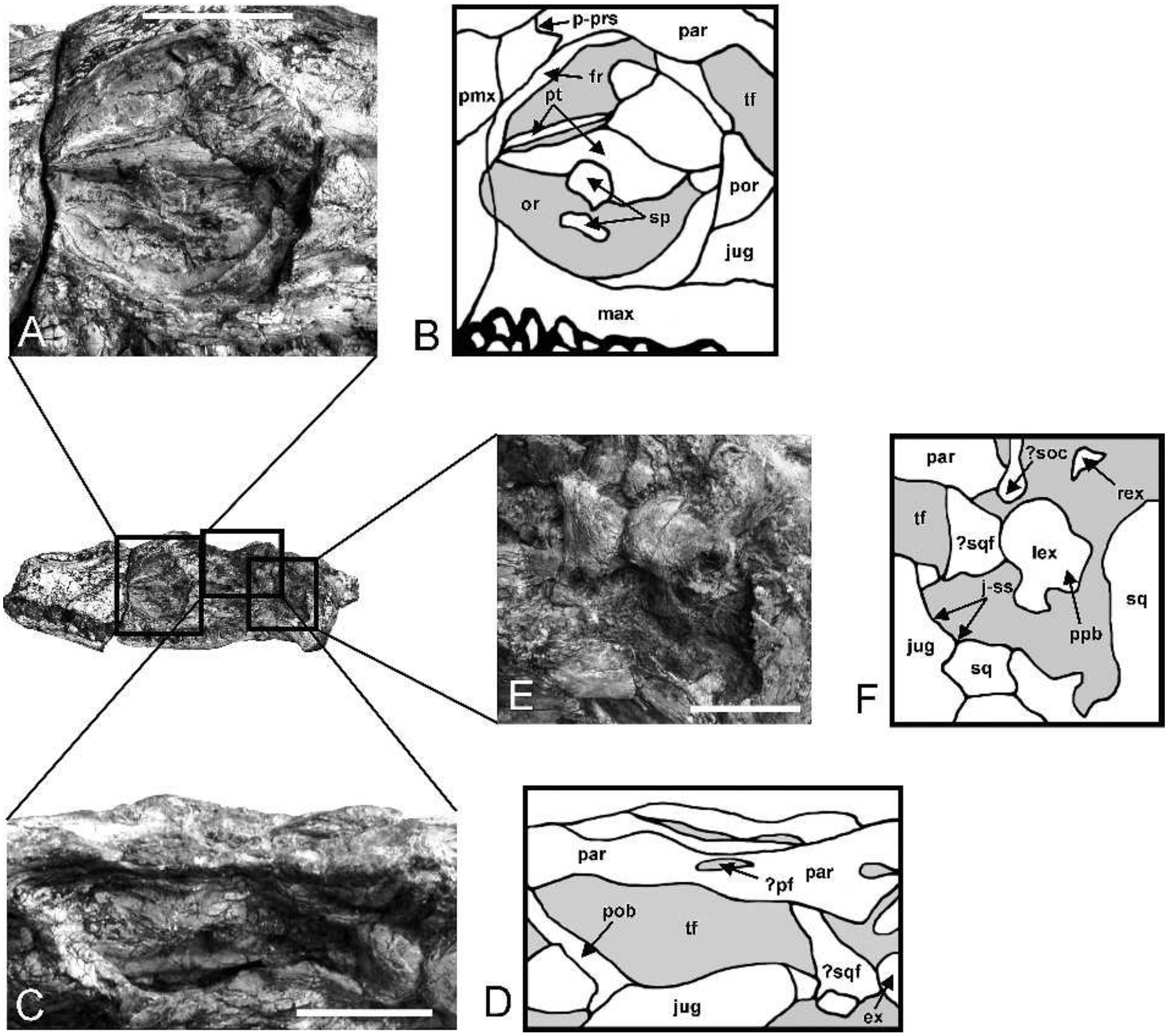

FIGURE 5. Holotype skull of *Eromangasaurus carinognathus*, gen et sp. nov. (QM F11050) in left lateral view. **A**, **B**, orbital region; **C**, **D**, temporal fenestra and parietal region; **E**, **F**, exoccipital-opisthotic and squamosal region. **Anatomical abbreviations**: **ex**, exoccipital; **fr**, frontal; **j-js**, jugal-squamosal suture; **jug**, jugal; **lex**, left exoccipital-opisthotic; **max**, maxilla; **or**, orbit; **par**, parietal; **?pf**, possible parietal foramen; **pmx**, premaxilla; **pob**, postorbital bar; **por**, postorbital; **ppb**, paroccipital process base; **p-prs**, premaxillary-parietal suture; **pt**, pterygoid; **rex**, right exoccipital-opisthotic; **?soc**, possible supraoccipital fragment; **sp**, sclerotic plates; **sq**, squamosal; **?sqf**, possible squamosal fragment; **tf**, temporal fenestra. Scale bars equal 30 mm.

lateral and medial condyles are large and posteriorly projecting; their posterodorsal margin is deeply scalloped possibly for insertion of slips from the mandibular depressor musculature.

The palatal region is obscured by matrix making arrangement of the various elements uncertain. Nevertheless, portions of the pterygoids are visible through the left orbit and between the posterior mandibular rami. Possible fragments of the palatal shelf of the left maxilla and palatine are also present around the anterior end of the mandible.

The anterior section of the pterygoids (observable through the left orbit; Fig. 5A, B) has a well-developed interdigitating interpterygoid suture. Several small sclerotic plates overlie the anterior part of the left pterygoid. These appear to have been rectangular in shape and are distinguished by their deeply crenate margins. Similar sclerotic plates have been reported in the holotype of *Styxosaurus snowii* (KUVP 1301, see Williston, 1903). Posteriorly the pterygoids are ventrally convex and extend beneath the basicranium to meet in a midline suture ventral to the basioccipital (this conforms to the typical elasmosaurid condition, see Carpenter, 1997; O'Keefe, 2001). Medially they enclose the narrow posterior interpterygoid vacuities. The posterior ramus of the left pterygoid is still preserved in articulation with the quadrate (Fig. 6B); its quadrate flange is extensive, projecting dorsally to contact the squamosal.

The basicranium is almost totally hidden by limestone. A small portion of the basioccipital (probably the occipital condyle) is visible embedded in matrix behind the pterygoids. The narrow rod-like parasphenoid covers the pterygoid midline suture (as in other elasmosaurids; O'Keefe, 2001), and is distinctly keeled long its exposed length. The anterior portion of the parasphenoid is overlain by the left hyoid bone (Fig. 6B) and thus its relationship with the anterior interpterygoid vacuity (also covered by matrix) is impossible to discern. The hyoid itself however is well exposed, being gently curved and rod-like with blunt, concave ends. Its large size relative to the overall length of the skull (total length 96mm, 28% of total skull length) could indicate considerable development of the tongue musculature.

Other recognizable basicranial elements include the exoccipital-opisthotic and possibly parts of the supraoccipital (Fig. 5E, F). The latter is severely crushed and largely covered by matrix. The left exoccipital-opisthotic, however, is clearly visible in lateral view (only part of the basioccipital facet of the right exoccipital-opisthotic is exposed), and is complete except for the robust paroccipital process; this has broken off near its base, probably during surface exposure. Identifiable parts of the left exoccipital-opisthotic include the edge of the basioccipital facet and the elongate convex edge of the supraoccipital contact.

Mandible—The mandible is well preserved but lacks its posterior left-hand end (Figs. 2, 3). Both the left and right posteroventral margins have suffered considerable damage from surface erosion; in comparison, the anterior symphysial portion is relatively unweathered. The right mandibular ramus has been displaced inwards towards the midline by a severe break just posterior to the mandibular symphysis. This is associated with a depression fracture, a second one of which is also present near the dentary-surangular suture (Fig. 6A). These traumatic injuries correspond to the potential tooth marks observed by Thulborn and Turner (1993).

In general form the mandible is narrow and anteriorly tapered with an elongate (74.7 mm) symphysis apparently formed entirely by the dentaries (there is no obvious contribution of other bones to the exposed inner surface). Notably, the posterior section of the symphysis is produced ventrally into a prominent mid-line keel that extends as a low ridge for a short distance down the ventral margin of each mandibular ramus (Fig. 6C). This feature has not been reported in other elasmosaurs, and together with the marked elongation of the symphysis, appears to be diagnostic for *E. carinognathus*.

The dentary forms over two-thirds of the total mandible length and carries alveoli for 18 teeth (on both left and right sides; Fig. 2A). It is deep in the area of the mandibular symphysis (51 mm high), but narrows slightly around the 6–8th tooth positions (approximately 37 mm high) before deepening again towards the coronoid eminence (approximately 58 mm high). The inner surface of the dentary is mostly masked by matrix, although some exposure of bone on the left-hand side suggests that the Meckelian canal was closed off anteriorly. The condition of the splenial is uncertain.

Bones of the posterior mandible are fused together, with little evidence of sutures. The coronoid eminence is low and the suture between the dentary and surangular is long and posteriorly inclined (Fig. 6A). There appears to be no exposure of the coro-

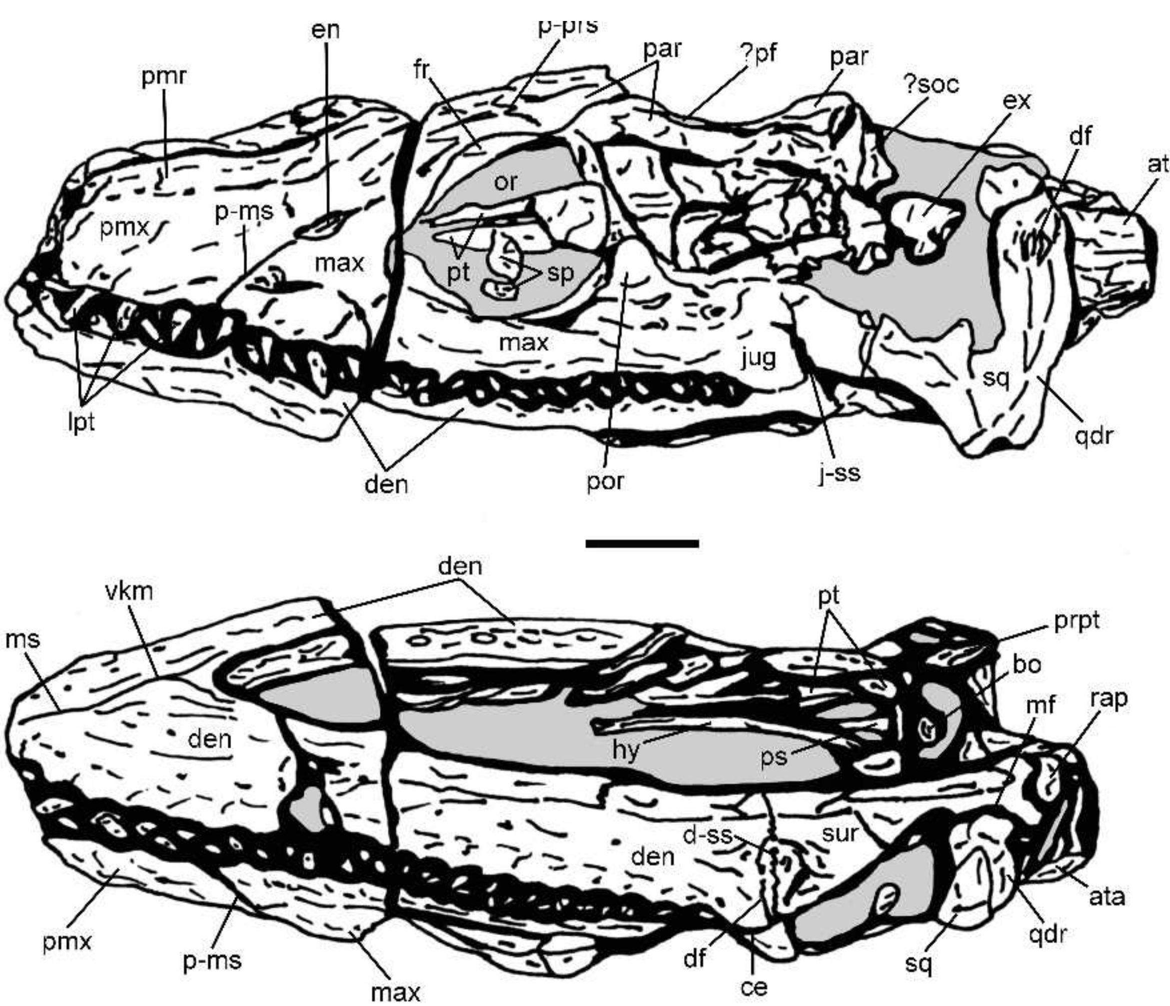

FIGURE 6. Detailed images of *Eromangasaurus carinognathus*, gen. et sp. nov., holotype skull (QM F11050). **A**, posterior end of right mandible; **B**, posterior pterygoid region; **C**, external view of mandibular symphysis. **Anatomical abbreviations**: **ata**, atlas-axis; **bo**, basioccipital; **ce**, coronoid eminence; **den**, dentary; **df**, depression fracture; **d-ss**, dentary-surangular suture; **hy**, hyoid; **mf**, mandibular fossa; **ms**, mandibular symphysis; **prpt**, posterior ramus of pterygoid; **ps**, parasphenoid; **ptm**, pterygoid midline suture; **qdr**, quadrate; **sq**, squamosal; **sur**, surangular; **vkm**, ventral keel on mandible; **vmm**, ventral margin of mandible. Scale bars equal 30 mm.

noid on the lateral surface of the jaw. The articular, angular and surangular are firmly fused in the region of the mandibular fossa. The fossa itself is positioned below the level of the tooth row, and is deeply concave with markedly elevated rims. Only the base of the retroarticular process is preserved, although this seems to have been robust (24.46 mm high and 32.9 mm wide).

Dentition—Most of the teeth preserved with the specimen are damaged. In general, however, their original shape appears to have been that of a slender, elongate cone with distinctly circular cross section. The crown surfaces are finely striated on the lingual side but smooth on the labial side. Where complete the apices taper to a rounded point and show no evidence of faceting by wear.

Teeth of both the upper and lower jaws intermesh along the entire jaw length. They are large and widely spaced in the premaxilla and anterior portion of the dentary. Posteriorly, however, the teeth become more closely packed and show a corresponding reduction in size.

Axial Elements—Only five anterior cervical vertebrae (comprising centra and basal portions of the neural arches and cervical ribs) including the fused atlas-axis complex (Fig. 7) are preserved. Persson (1982) gave a brief account of the vertebral centra, noting several key elasmosaurid synapomorphies; this description is supplemented below.

The fused atlas-axis complex is short (52.53 mm in maximum exposed length), deep, and cylindrical (similar to those reported for *Libonectes* and *Tuarangisaurus*; Carpenter, 1997). Its anterior articular and right lateral surfaces are covered by limestone; however, most of the dorsal, ventral, and left lateral surfaces are exposed (Figs. 7A–C). The incomplete posterior articular surface (32.68 mm maximum width, 31.01 mm high) is shallowly concave and ovoid in outline with a poorly defined central notocordal pit. The left lateral surfaces of the atlas and axis centra are flat and separated by a weakly discerned vertical suture line (Fig. 7A). The ventral surface of the atlas-axis complex is dominated by a prominent mid-line keel; this increases in height and width anteriorly but narrows and tapers posteriorly, terminating in a blunt rounded ridge just short of the posterior margin of the articular surface. The ventrolateral portions of the axis centrum bear fully fused elliptical bases of the single-headed axial ribs. These do not extend onto the atlas centrum but rather are covered by the brief posterolateral projection of the atlas rib (Fig. 7C). The visible dorsal surface of the axis centrum is shallowly concave where it accommodated the neural canal. Both the neural arch and spine are crushed and almost totally missing. Nevertheless, portions of the neural arch bases are still preserved. These are fully fused, with only a weak trace of suture on the left lateral surface of the axis centrum.

The cervical centra posterior to the axis (see Persson 1982:table 1 for measurements) are typical of elasmosaurids, being cylindrical and somewhat dorsoventrally compressed with centrum length exceeding height. The articular surfaces are platycoelous and ovoid in outline. The lateral sides of the centra are concave and bear prominent longitudinal ridges. The ventral surface of each centrum is pierced by paired nutrient foramina separated by a median-ventral keel.

DISCUSSION

Taxonomy of Australian Elasmosaurs

No currently described Australian elasmosaurid taxon can be unequivocally regarded as valid. Kear (2003) summarised the existing genera and species, indicating that all were probable nomina dubia (following Welles, 1962). Recently, Sachs (2004) suggested that QM F11050 was a new species of *Tuarangisaurus* (a genus known elsewhere from the Maastrichtian Maungataniwha Sandstone of New Zealand and possibly the upper Maas-

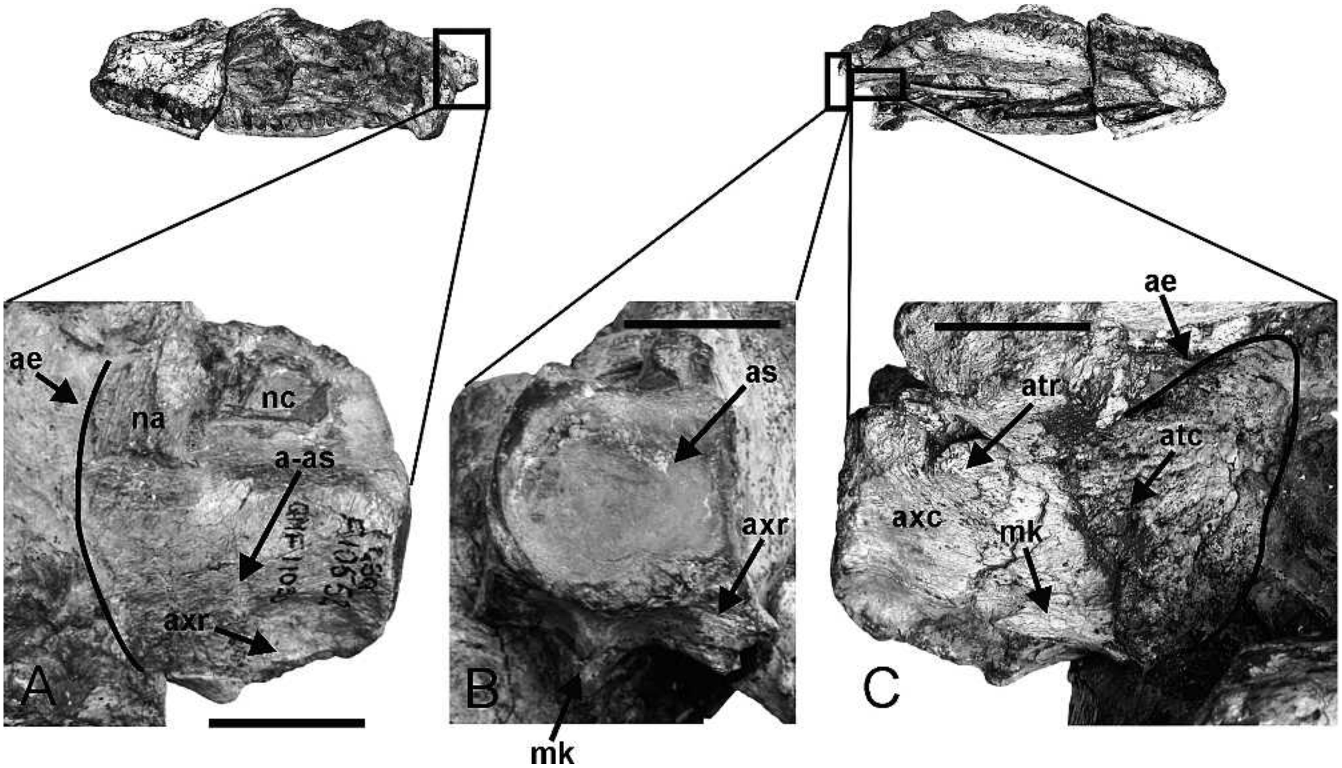

FIGURE 7. Atlas-axis complex of *Eromangasaurus carinognathus*, gen. et sp. nov., holotype (QM F11050). **A**, dorsolateral; **B**, posterior; and **C**, ventrolateral views. **Anatomical abbreviations**: **a-as**, atlas-axis suture; **ae**, anterior edge; **as**, articular surface; **atc**, atlas centrum; **atr**, atlas rib; **axc**, axis centrum; **axr**, axis rib; **mk**, mid-ventral keel; **na**, neural arch; **nc**, neural canal. Scale bars equal 30 mm.

trichtian Jagüel Formation of Patagonia; Wiffen and Moisley, 1986; Gasparini et al., 2003b). Notably, however, the holotype skull of this taxon (NZGS CD425) differs markedly from QM F11050, particularly in its plesiomorphic retention of five pairs of premaxillary teeth, relatively short mandibular symphysis, measuring only 34 mm (Wiffen and Moisley, 1986:210), compared to 74.4 mm in QM F11050, and in the apparent loss of the parietal foramen. Moreover, the presence of several discrete autapomorphies in QM F11050 (namely the presence of seven premaxillary teeth [three lateral pairs and one midline], and an elongate mandibular symphysis that bears a prominent keel along its ventral midline) clearly supports its alternative assignment as the separate taxon *Eromangasaurus carinognathus*. This conclusion is further reinforced by the present phylogenetic results, which fail to place QM F11050 and *Tuarangisaurus* in a distinct sister-taxon relationship (Fig 8A).

Persson (1982) previously attributed QM F11050 (with reservation) to '*Woolungasaurus*' cf. '*W. glendowerensis*' on the basis of its proportionally elongate anterior cervical centra (with length>height). However, this characteristic (on its own) is non-diagnostic at generic and specific levels (Brown, 1981), and thus provides insufficient evidence to warrant unequivocal association of QM F11050 with the '*Woolungasaurus*' holotype postcranial remains. Indeed, the plesiomorphic, short, deep atlas-axis complex of QM F11050 is substantially different from the derived, elongate atlas-axis centrum of the holotype of '*W. glendowerensis*' (see Sachs, 2004:715), suggesting that the two specimens may represent separate taxa.

'*Woolungasaurus glendowerensis*' was initially established by Persson (1960) on the basis of a fragmentary postcranial skeleton (QM F3567) from the Aptian Wallumbilla Formation of northwestern Queensland. Unfortunately, the taxon has subsequently become a 'waste-basket' for many non-diagnostic Australian elasmosaurid remains. The characters used by Persson (1960) to define '*W. glendowerensis*' include (1) presence of elongate anterior cervical centra (with length>breadth or height becoming broader than long posteriorly) with well-developed lateral longitudinal ridges on lateral centrum body, (2) presence of three pectoral and ?three sacral vertebrae, (3) scapula with narrowest portion in line with midline of dorsal scapular process, (4) coracoids not separated posteriorly (intercoracoid foramen absent), (5) coracoids with prominent anteromedian process, (6) midventral keel present along intercoracoid contact, (7) humerus larger than femur, and (8) humerus with confluent capitulum/tuberculum and femur with confluent capitulum/trochanter. Of these, (1) is uninformative beyond the family level, being widely regarded as a potential synapomorphy for Elasmosauridae (e.g., Brown, 1981, 1993; Bardet et al., 1999); Brown (1981) and O'Keefe (2002), however, noted that this feature is influenced by body proportions. Characters (2), (3), and (6) are variable amongst plesiosauroids and of questionable phylogenetic significance at lower taxonomic levels; (5) and (7) are ontogenetically related (Brown, 1981), and (4) is not applicable, being based on a misinterpretation of the extremely fragmentary holotype pectoral girdle (which does appear to possess an intercoracoid foramen; Sachs, 2004:719-720). Thus, '*Woolungasaurus*' (sic '*W. glendowerensis*') cannot be characterized on the basis of the type material and is a nomen dubium (sensu Welles, 1962).

Interestingly, despite the lack of adequate diagnostic characters, Sachs (2004) recently reinstated the species designation of '*W. glendowerensis*,' but suggested that the genus was a junior synonym of *Styxosaurus*. This placement was based solely on broad similarities in the postcranium, including primarily an elongate atlas-axis complex (a feature also shared with *Styxosaurus*, *Elasmosaurus*, and *Hydralmosaurus*, but notably different from other taxa including *Eromangasaurus*, *Libonectes*, and *Tuarangisaurus*, in which the atlas-axis is short and deep; Carpenter, 1997), shape of the posterior coracoid and intercoracoid foramen (reputedly resembling those of *Styxosaurus*, *Thalassamedon*, and *Hydralmosaurus*; Sachs, 2004:720), quadratic shape of the ulna (present in a range of elasmosaurids; Sachs, 2004: 723), femoral shaft with anterior and posterior sides equally slightly concave (listed as present in *Styxosaurus*, *Callawayasaurus*, and *Terminonatator*; Sachs, 2004:725), and 'general shape' of the pubis and ischium (reputedly most similar to that of *Styxosaurus*; Sachs, 2004:725-730). Importantly, none of the features listed by Sachs (2004) constituted unequivocal synapomorphies specifically uniting '*W. glendowerensis*' and *Styxosaurus* to the

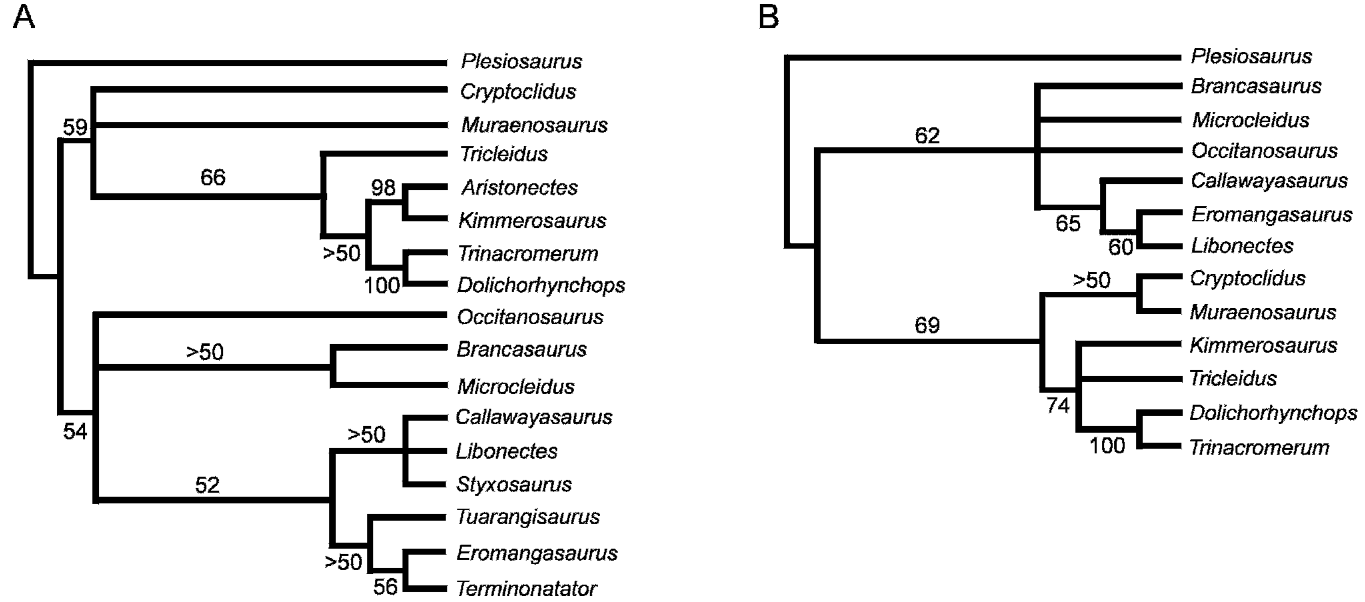

FIGURE 8. Cladograms showing phylogenetic relationships of *Eromangasaurus carinognathus*, gen. et sp. nov. **A**, consensus of 473 most-parsimonious trees; all taxa included. **B**, consensus of 16 most-parsimonious trees generated after deletion of taxa with >35% missing data (*Aristonectes*, *Styxosaurus*, *Terminonatator*, *Tuarangisaurus*). Bootstrap percentages are indicated at each node. For character list and taxa/character matrix see Appendices 1 and 2, respectively.

exclusion of all other elasmosaurids. In addition, no unambiguous characters were provided to adequately justify '*Styxosaurus glendowerensis*' as a distinct species. Consequently, remains attributed to the taxon are here provisionally referred to Elasmosauridae indet. (sensu Kear, 2003) pending discovery of more diagnostic (preferably cranial) material.

Phylogenetic Analysis

Forty-three craniodental and vertebral characters (Appendix 1) were used to assess the preliminary phylogenetic relationships of *E. carinognathus* within Plesiosauroidea. A matrix (Appendix 2) was compiled in MacClade 4 and run in PAUP, version 4.0b10 (Swofford, 2002). Forty-one of the forty-three characters were taken from O'Keefe (2001) with modifications made to 7, 10, 26–28, 32–35, and 39 for this analysis. Characters 1, 2, 6, 12, 19, 25, 29, 35, and 37 have been scored in accordance with the revised matrix of O'Keefe (2004a). Character 40 was derived from Bardet et al. (1999) and has been used elsewhere by Gasparini et al. (2003a). Following O'Keefe (2001, 2004a), characters 1, 18, 28, 34, and 35 were treated as ordered. Seventeen representative plesiosauroid taxa were selected for the analysis with *Plesiosaurus* used as an outgroup. Character scoring for taxa other than *E. carinognathus* was derived mainly from O'Keefe (2004a), except in the case of *Tuarangisaurus*, scored from Wiffen and Moisley (1986), *Terminonatator*, taken from Sato (2003), and *Aristonectes*, scored from both O'Keefe (2001, 2004a) and Gasparini et al. (2003a) to accommodate synonymy with *Morturneria* (see Gasparini et al., 2003a for discussion). An initial Branch-and-Bound search utilizing Deltran optimization and incorporating all taxa produced 473 most-parsimonious trees, each of 85 steps (see Fig. 8A for consensus cladogram), and with CI of 0.6235, RI of 0.7519, and RCI of 0.4689. Tree resolution decreased with additional steps, beyond which Elasmosauridae collapsed into a polytomy. Relationships between cryptocleidoid (sensu O'Keefe, 2001, 2004a) taxa showed a similar loss of resolution, although some individual clades including *Aristonectes*/*Kimmerosaurus* and *Dolichorhynchops*/*Trinacromerum* remained unaffected. To further test tree robustness, a second Branch-and-Bound analysis was run excluding taxa (*Aristonectes*, *Styxosaurus*, *Terminonatator*, *Tuarangisaurus*) represented by large amounts of missing data (>35%). This yielded 16 most-parsimonious trees (consensus given in Fig. 8B) each of 74 steps, with CI of 0.7162, RI of 0.7667, and RCI of 0.5491. Bootstrap percentages (based on 1000 replicates) were calculated for both trees; these are recorded next to the principal nodes in Figure 8A, B.

The results generated by this analysis compare well with those of O'Keefe (2001, 2004a). Cryptocleidoidea (sensu O'Keefe, 2001) form a monophyletic clade, with polycotylids placed in a close sister-taxon relationship with 'cimoliasaurids' (united by the presence of a derived elongate rostrum, and cervical vertebrae with centrum length less than height), and more distantly with *Tricleidus* (which shares the unambiguously synapomorphic presence of a posterior pterygoid-parasphenoid contact, parasphenoid-basioccipital contact along the ventral mid-line, and a jaw articulation that is situated below the tooth row). The position of *Tricleidus* was unresolved in the analysis of O'Keefe (2001, 2004a), although O'Keefe (2004b) placed it outside of a polycotylid/'cimoliasaurid' grouping. The traditional Cryptoclididae (including taxa such as *Cryptoclidus*, *Kimmerosaurus*, and *Aristonectes*, sensu Brown, 1981, 1993) are not substantiated in the present phylogeny and may be paraphyletic (sensu Bardet et al., 1999; O'Keefe, 2001, 2004b; Gasparini et al., 2003a; O'Keefe and Wahl, 2003). *Kimmerosaurus* and *Aristonectes* here form a robust clade supported by several unambiguous synapomorphies including an elongate, hoop-like skull rostrum, presence of very small needle-like teeth, and an increase in the number of premaxillary teeth to eight or more and maxillary teeth to in excess of thirty. Notably, this relationship contradicts previous assertions of elasmosaurid affinity for *Aristonectes*, a concept most recently championed by Gasparini et al. (2003a).

Cryptoclidus is a basal taxon within Cryptocleidoidea, and also represents a sister taxon to *Muraenosaurus* in some trees (Fig. 8B). This relationship, however, is poorly substantiated, being based on symplesiomorphic character states including positioning of the broad axis rib articulation across both the atlas centrum and other elements.

Elasmosauridae (to the exclusion of *Muraenosaurus*, contra Brown, 1981, 1993; Bardet et al., 1999; Gasparini et al., 2003a) constitute a monophyletic clade in all trees produced. Placement of individual taxa, however, is poorly resolved. *Callawayasaurus*, *Eromangasaurus*, and *Libonectes* consistently fall within a monophyletic crown group (united in Fig. 8B by the unambiguous synapomorphic absence of a squamosal-postorbital contact, presence of a posterior pterygoid contact behind the posterior interpterygoid vacuity, and caniniform teeth on the maxilla). However, with the inclusion of additional taxa (Fig. 8A), *Callawayasaurus*, *Styxosaurus*, and *Libonectes* form a discrete polytomy (united at a common node by their shared-derived mandibular bowing [with accompanying maxillary expansion], and binocular-shaped articular surfaces on the anterior cervical vertebrae) relative to a poorly supported lineage comprising *Tuarangisaurus*, *Eromangasaurus*, and *Terminonatator* (constituted solely on ambiguous states including the possession of a posterior pterygoid contact covered by the parasphenoid; this feature is not preserved in the current specimens of *Terminonatator*).

Relationships among more basal elasmosaurids are similarly poorly resolved. *Brancasaurus* is variably placed in either a basal polytomy with *Microcleidus* and *Occitanosaurus* (Fig. 8B) or in a discrete clade with *Microcleidus* (Fig. 8A). The latter relationship is established on a single apomorphic character state (presence of a narrow contribution of the frontal to the temporal fenestra), whose significance is as yet uncertain. O'Keefe (2004a) retained *Microcleidus* in an unresolved position relative to both elasmosaurids and cryptocleidoids unlike Brown (1981, 1993), Bardet et al. (1999), and Gasparini et al. (2003a), who indicated a basal sister-taxon relationship to Elasmosauridae only.

Eromangasaurus is an elasmosaurid of more derived grade than *Occitanosaurus*. It is consistently united with crown-group Cretaceous elasmosaurs (excluding *Brancasaurus*) in the present analysis, on the basis of variably developed features including absence of a squamosal-postorbital contact and presence of caniniform teeth on the maxilla. Recognition of *Eromangasaurus* as a species of *Tuarangisaurus* (sensu Sachs, 2004) cannot be substantiated. Rather *Tuarangisaurus* (represented by 42.9% missing data in this matrix) is placed outside of a monophyletic clade containing *Eromangasaurus* and *Terminonatator* (Fig. 11A). This latter grouping is supported by the unambiguous reduction in the number of lateral premaxillary teeth to between three and four primary pairs (there are seven in *Eromangasaurus* and nine in *Terminonatator* including the single small midline teeth). Ideally however, more complete cranial remains of both taxa are required before a conclusive relationship can be established.

CONCLUSIONS

Australian elasmosaurid fossils are common but sparsely documented. To date several taxa have been erected, although most are based on equivocal postcranial remains. The only currently diagnostic cranial material consists of an isolated skull from the Upper Albian Toolebuc Formation of central northern Queensland. This specimen has complex taxonomic history being variously assigned to the nomen dubium '*Woolungasaurus*' (Persson, 1982), an undescribed genus and species (Thulborn and Turner, 1993; Kear, 2003), and most recently, a possible new species of *Tuarangisaurus* (Sachs, 2004). The present assessment indicates that there is no sound basis for attribution to *Tuarangisaurus* and proposes an alternative assignment to the new taxon *Eromangasaurus carinognathus*; this is uniquely characterized by the presence of seven premaxillary teeth (three lateral pairs and one midline), an elongate mandibular symphysis that bears a prominent keel along its ventral midline, and a combination of diagnostic morphological characteristics variably developed in other elasmosaurids.

Preliminary phylogenetic analyses incorporating *E. carinognathus* indicate that it represents an elasmosaurid of more derived grade than basal forms such as *Occitanosaurus*. Notably, some significant cranial character states are shared with the Late Cretaceous *Terminonatator*. Affinities with other Cretaceous elasmosaurids are poorly resolved at present, a number of taxa being represented by large amounts of missing data. Consequently, re-evaluation of many key forms (e.g., *Tuarangisaurus*) is required before a stable framework for determining inter-generic relationships can be established.

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APPENDIX 1

List of characters used in phylogenetic analysis. Forty-one of the forty-three characters presented below are taken from O'Keefe (2001), with modifications made to 1, 7, 10, 26–28, and 32–35 for this analysis. Characters 1, 2, 6, 12, 19, 25, 29, 35, and 37 have been scored in accordance with the revised matrix of O'Keefe (2004a). Character 40 is derived from Bardet et al. (1999) and was also utilized by Gasparini et al. (2003a). Following O'Keefe (2001), characters 1, 18, 28, 34, and 35 are treated as ordered.

(1) Form of skull rostrum: not elongate (0); elongate with maxilla included (1); elongate and hoop-like/unconstricted (2) (O'Keefe, 2001, 2004a:char. 8).
(2) Dorsomedial process of premaxilla: contacting frontal (0); contacting parietal at pineal foramen (1); contacting anterior extension of parietal (2) (O'Keefe, 2001, 2004a:char.11; Bardet et al., 1989:char. 8).
(3) Posterolateral process of frontal: absent (0); present (1) (O'Keefe, 2001:char. 16).
(4) Postorbital bar: with both postorbital and postfrontal contributing to orbit margin (0); with frontal-postorbital suture excluding postfrontal from orbit margin (1) (O'Keefe, 2001:char. 17).
(5) Contribution of frontal to temporal fenestra: contribution absent (0); narrow contribution present (1) (O'Keefe, 2001:char. 18).
(6) Frontal-external naris contact: present (0); absent (1) (O'Keefe, 2001, 2004a:char.19; Bardet et al., 1999:char. 9).
(7) Pineal foramen: present and not bordered by frontals (0); present and bordered anteriorly by frontals (1); absent (2) (O'Keefe, 2001:char.21; Bardet et al., 1999:char. 10).
(8) Descending process on squamosal laterally covering quadrate: absent (0); present with squamosal becoming socket-like (1) (O'Keefe, 2001:char. 26).
(9) Squamosal-postorbital contact: present (0); absent (1) (O'Keefe, 2001:char. 28).
(10) Extension of jugal beneath orbit: anterior margin (0); restricted to posterior margin (1) (O'Keefe, 2001:char. 30).
(11) Extension of jugal forming narrow bar between orbit and temporal emargination: absent (0); present (1) (O'Keefe, 2001:char.33; Bardet et al., 1999:char. 1).
(12) Maxilla-squamosal contact: absent (0); present (1); present and expanded into stout posterior flange (2) (O'Keefe, 2001, 2004a:char. 41).
(13) Paroccipital process articulation: squamosal exclusively (0); quadrate exclusively (1); contacting both quadrate and squamosal (2) (O'Keefe, 2001:char. 47).
(14) Ventral extent of paroccipital process: not extending past condyle (0); extending ventral to occipital condyle (1) (O'Keefe, 2001:char. 48).
(15) Quadrate flange of pterygoid: contacting quadrate only (0); forming contact with both quadrate and squamosal (1) (O'Keefe, 2001:char. 50).
(16) Distinct process on quadrate for articulation with pterygoid: absent (0); present (1) (O'Keefe, 2001:char. 51).
(17) Anterodistal margin of quadrate: not embayed, (quadrate massive, 0); embayed (1) (O'Keefe, 2001:char. 54).
(18) Pterygoids posterior to posterior interpterygoid vacuity: pterygoids not meeting posteriorly (0); pterygoids in contact with distinct suture (not covered by parasphenoid process, 1); pterygoids in contact but covered by posterior parasphenoid process (2) (O'Keefe, 2001:char. 62; Bardet et al., 1999:char. 12).
(19) Dished pterygoids: absent (0); present (1) (O'Keefe, 2001:char. 67).
(20) Posterior pterygoid-parasphenoid contact: absent (0); present (1) (O'Keefe, 2001:char. 68).
(21) Parasphenoid shape: long, tapering (0); short and blunt (1) (O'Keefe, 2001:char. 70).
(22) Ventral surface of parasphenoid: not keeled (0); keeled along length (1); keeled anteriorly (2) (O'Keefe, 2001:char. 71).
(23) Parasphenoid-basioccipital contact on midline: absent (0); present (1) (O'Keefe, 2001:char. 74).
(24) Mandibular bowing (maxillary expansion sensu O'Keefe, 2001): absent (0); present (1) (O'Keefe, 2001:char. 86).
(25) Condition of anterior Meckelian canal: not open (0); open anteriorly (1) (O'Keefe, 2001, 2004a:char. 87).
(26) Ventral ridge or keel at mandibular symphysis: absent (0); present (1) (O'Keefe, 2001:char. 88).
(27) Mandibular symphysis: short (0); enforced (1); long (2) (O'Keefe, 2001:char. 89).
(28) Splenial participation in symphysis: splenials not involved in symphysis (0); splenials extending past symphysis (1) (O'Keefe, 2001:char. 90).
(29) Coronoid exposure on lateral jaw surface: absent (0); present (1) (O'Keefe, 2001:char. 95).
(30) Jaw articulation in relation to tooth row: above or collinear with tooth row (0); lower than tooth row (1) (O'Keefe, 2001:char. 98).
(31) Caniniform teeth on maxilla: absent (0); present (1) (O'Keefe, 2001:char. 102; Bardet et al., 1999:char. 17).
(32) Tooth form: gracile with small root, narrow crown and limited wear (0); very small and needle like (1) (O'Keefe, 2001:char. 103).
(33) Tooth ornament: present (0); reduced or absent (1) (O'Keefe, 2001:char. 105; Bardet et al., 1999:char. 18).
(34) Number of lateral pairs of premaxillary teeth: between five and seven (0); less than five (1); eight or more (2) (O'Keefe, 2001:char. 106; Bardet et al., 1999:char. 15; Gasparini et al., 2003a:char. 13).
(35) Number of maxillary teeth: less than thirty (0); more than thirty (1) (O'Keefe, 2001, 2004a:char. 107).
(36) Number of axial rib heads: two (0); one (1) (O'Keefe, 2001:char. 108).
(37) Articulation of axis rib: broad, extending onto atlas centrum and other elements (0); confined to axis centrum (1) (O'Keefe, 2001, 2004a:char. 109).
(38) Proportions of cervical centra: length equal to height (0); length greater than height (1); length less than height (2) (O'Keefe, 2001:char. 112; Bardet et al., 1999:char. 20).
(39) Lateral ridge on anterior cervicals: absent (0); present (1) (O'Keefe, 2001:char. 115; Bardet et al., 1999:char. 22).
(40) Articular surfaces of cervical vertebrae: amphicoelous (0); platycoelous (1) (Bardet et al., 1999:char. 21).
(41) Binocular-shaped articular faces on anterior cervical vertebrae: absent (0); present (1) (O'Keefe, 2001:char. 116; Bardet et al., 1999:char. 23).
(42) Marked groove around articular surfaces of cervical vertebral centra: absent (0); present (1) (O'Keefe, 2004a:char. 167).
(43) Number of cervical rib heads: two (0); one (1) (O'Keefe, 2001:char. 117).

APPENDIX 2

Matrix of character states for 17 taxa used in phylogenetic analysis

	Character								
Taxa	5	10	15	20	25	30	35	40	
Plesiosaurus	0 0 1 0 0	0 0 0 0 0	0 1 ? ? ?	1 1 0 0 0	0 ? 0 0 ?	0 0 ? 0 0	0 0 0 0 0	? ? 0 0 0	0 0 0
Aristonectes	2 ? ? ? ?	? ? ? 1 ?	? ? 0 ? ?	? 1 ? 0 ?	1 ? 1 0 1	0 0 ? ? 1	0 1 1 2 2	0 0 2 1 1	1 1 1
Brancasaurus	0 0 0 0 1	? 1 1 0 1	0 1 ? 0 ?	? 0 ? 0 0	0 ? 0 0 ?	0 ? ? ? ?	0 0 0 0 ?	? 1 1 1 1	0 0 1
Callawayasaurus	0 0 0 1 1	? 1 1 1 1	0 1 2 0 1	1 0 1 0 0	0 1 ? 1 1	0 1 0 0 1	1 0 0 0 0	? ? 1 1 1	1 0 1
Cryptoclidus	0 0 0 0 0	1 1 1 0 1	1 0 1 0 ?	0 1 0 0 0	1 0 0 0 1	0 0 0 1 0	0 0 1 0 0	1 0 0 0 0	0 1 1
Dolichorhynchops	1 1 0 0 0	0 0 1 0 1	0 2 1 1 0	0 1 2 1 1	1 0 1 0 0	0 2 1 1 1	0 0 0 0 0	1 1 2 0 0	0 1 1
Eromangasaurus	0 2 ? ? 0	? 0 1 1 1	0 0 ? ? 1	1 0 2 0 0	0 1 0 0 0	1 1 0 0 1	1 0 0 1 0	1 1 1 1 1	0 0 1
Kimmerosaurus	2 0 0 ? 0	? 1 1 ? ?	1 ? 0 0 ?	0 1 0 0 1	? 0 1 ? ?	0 0 0 1 1	0 1 1 2 2	1 ? 2 0 0	0 1 1
Libonectes	0 2 ? 1 ?	? 1 1 1 1	0 ? 2 0 1	1 0 2 0 0	0 1 ? ? 1	0 1 0 0 1	1 0 0 0 0	1 ? 1 1 1	1 0 1
Microcleidus	0 0 0 ? 1	? 1 1 ? ?	0 1 ? ? ?	? ? 0 0 0	0 ? 0 0 1	0 1 0 0 1	0 0 0 ? ?	0 ? 1 0 1	0 0 0
Muraenosaurus	0 0 0 0 0	0 1 1 0 1	? ? ? 0 ?	? 1 0 0 0	1 0 0 0 1	0 0 0 1 0	0 0 0 0 0	1 0 1 1 1	0 1 1
Occitanosaurus	0 0 ? 0 0	1 2 1 0 1	0 0 ? ? 1	? 0 0 0 0	0 1 0 0 ?	? ? ? ? ?	0 0 0 0 0	1 1 1 1 1	0 0 1
Styxosaurus	0 2 0 1 0	? ? 1 1 1	0 1 ? ? ?	1 0 ? ? 0	? ? ? 1 ?	0 1 1 0 1	1 0 0 0 ?	? ? 1 1 1	1 0 1
Terminonatator	0 2 0 ? ?	? 2 1 ? ?	? 1 ? ? ?	1 0 ? ? ?	? ? ? 0 1	0 1 0 1 1	1 0 0 1 0	? ? 1 1 1	0 0 1
Tricleidus	0 0 ? ? 0	0 0 1 ? 1	1 0 1 1 0	0 1 0 0 1	1 0 1 0 1	0 0 0 ? 1	0 0 0 0 ?	1 ? 0 0 0	0 1 1
Trinacromerum	1 1 0 0 0	0 ? 1 0 1	0 2 1 1 0	? 1 2 1 1	1 0 1 0 ?	0 2 1 1 1	0 0 0 0 0	1 1 2 0 0	0 1 1
Tuarangisaurus	0 ? ? ? ?	? 2 1 ? 1	? ? ? ? ?	? 0 2 0 0	? 1 0 0 ?	0 0 ? ? ?	? 0 0 0 0	1 1 1 1 1	0 0 1

Characters are listed in Appendix 1.