

A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia)

Frank Robin O'Keefe

Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, New York 11568, U.S.A

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The Plesiosauria (Reptilia: Sauropterygia) is a group of Mesozoic marine reptiles known from abundant material, with specimens described from all continents. The group originated very near the Triassic–Jurassic boundary and persisted to the end-Cretaceous mass extinction. This study describes the results of a specimen-based cladistic study of the Plesiosauria, based on examination of 34 taxa scored for 166 morphological characters. The Pliosauroidae is found to be polyphyletic due to the inclusion of the Polycotylidae; this second clade is instead a member of the Plesiosauroidae, and thus more closely related to elasmosaurs than to other 'pliosaurs'. Characters of body proportion such as neck length and head size are very labile, with the 'pliosauroform' body plan evolving three times, while extremely long necks evolved in two clades. Characters from the entire skeleton support these relationships, although characters of the skull roof and palate are especially useful. Lastly, a new genus and species, *Hauffiosaurus zanoni*, is named based on German material of Toarcian age.

Introduction

The term 'plesiosaur', meaning 'near-lizard', is not an informative name from a modern perspective. However, when Conybeare (1822) coined the term to describe fossils from the English Lias little was known concerning any extinct reptile. The realization that plesiosaurs were a completely extinct group was significant at a time when the occurrence of extinction itself was uncertain (Taylor 1997). These 'near-rep-

tiles' were named at a time when there was no need, and no context, for a more specific term.

The Plesiosauria was a clade of Mesozoic marine reptiles that evolved from stem-group sauropterygians very near the Triassic–Jurassic boundary (reviewed in Rieppel 1997a, Rieppel 2000). The clade diversified during the Jurassic and Cretaceous, only to join the dinosaurs as casualties of the end-Cretaceous mass extinction (Romer 1966). Plesiosaurs were advanced over their 'nothosaur'-grade forebearers in the evolu-

tion of wing-shaped fore and hind flippers that generated thrust via lift as well as drag (Godfrey 1984, Lingham-Soliar 2000). Plesiosaurs were unusual among marine reptiles because they used no axial flexure when generating thrust (Storrs 1993); plesiosaurs are unique among aquatic tetrapods in the elaboration of both fore and hind limbs for lift-based thrust generation. The evolution of this novel locomotor apparatus, and the pelagic lifestyle it allowed, led to rapid diversification and the evolution of different morphotypes linked to prey size (Massare 1988, O'Keefe 2002).

Plesiosaur taxonomy

The taxonomy of the Infra-order Plesiosauria (de Blainville 1835) suffers from the comparative taxonomic chaos of the Victorian era. However, Andrews (1910, 1913), Welles (1943, 1952), Tarlo (1960), Persson (1963), and Brown (1981) have all revised plesiosaur taxonomy. All formalized the plesiosauromorph/pliosauromorph dichotomy in their classifications, following the lead of earlier workers such as Owen (1841), Lydekker (1889b), and Seeley (1892). Until the work of Carpenter in 1997, Williston (1925) was the only worker to break with the accepted, morphotype-based taxonomy. Plesiosaur relationships have been considered recently by Brown and Cruickshank (1994). These workers also retain the traditional dichotomy. The current taxonomy is listed below, based on Tarlo (1960), Persson (1963), Brown (1981, 1993), and Brown and Cruickshank (1994).

Diapsida Osborn, 1903

Sauropterygia Owen, 1860

 Infra-Order Plesiosauria de Blainville, 1835

 Superfamily Plesiosauroidae Welles, 1943

 Family Plesiosauridae Gray, 1825

 Family Elasmosauridae Cope, 1870

 Family Cryptoclididae Williston, 1925

 Family Cimoliasauridae Delair, 1959

 Superfamily Pliosauroidae Welles, 1943

 Family Pliosauridae Seeley, 1874

 Family Rhomaleosauridae Kuhn, 1961

 Family Polycotylidae Williston, 1908

Early taxonomies classified plesiosaurs with respect to two body proportion morphotypes (classifications reviewed in Welles 1943). These morphotypes were the long-necked, small-headed 'plesiosaurs' (here termed *plesiosauromorphs*) and the large-headed, short-necked 'pliosaurs' (here termed *pliosauromorphs*). However, as early as 1907 Williston suggested that the short neck in 'pliosaurs' might have evolved at least twice. The validity of the pliosauromorph/plesiosauromorph dichotomy was challenged more recently by Carpenter (1997), and preliminary cladistic analyses by Bardet (1998) and Druckenmiller (1998) challenged the monophyly of the Superfamily Pliosauroidae as traditionally defined. This study is a specimen-based analysis whose goal is the elucidation of the phylogeny of the Plesiosauria. The terminal taxa in this analysis are genera, as higher-level relationships are the primary goal. The principal finding is the polyphyly of the Pliosauroidae as traditionally defined, by inclusion of the Polycotylidae. Placement of this family in the Plesiosauroidae also results in some reorganization of that taxon.

Phylogenetic context

The Sauropterygia is a clade of basal diapsids, more closely related to lepidosaurs than archosaurs but near this basal dichotomy (*see* Rieppel & Reisz 1999 for a review). Some recent work has indicated that Testudines is the sister group of Sauropterygia, although this work is controversial (Rieppel & deBraga 1996, Lee 1997, de Braga & Rieppel 1997, Rieppel & Reisz 1999). The comparative anatomy and phylogeny of Triassic sauropterygians have been the subject of intense study over the last decade. Storrs (1991) published a cladogram of stem-group sauropterygians in the context of his redescription of *Corosaurus*, at that time the only Triassic sauropterygian known from the New World. Storrs also reviewed stem-group sauropterygians. This phylogeny underwent exhaustive revision by Rieppel, who engaged in a program of redescription, taxonomic revision, and biogeography of all stem-group sauropterygians (reviewed in Rieppel 1999, Rieppel 2000, Rieppel

1994a, 1998, Rieppel & Wild 1996, and especially Rieppel 2000 are good entrance points to Rieppel's literature on the group). Field work by Rieppel, Storrs, and others also yielded remains of a new sauropterygian from Nevada (Sander *et al.* 1997). This new genus (*Augustasaurus*) is a pistosaurid, and is significant because pistosaurids are thought to be the sister group to the Plesiosauria (Sues 1987). The only other known pistosaurid is *Pistosaurus* from the Triassic of Germany, described by Meyer (1839) and Edinger (1935) from two skulls, the more complete of which is now lost. Rieppel (1994a) redescribed the remaining skull, while Sues (1987) described the postcranium of *Pistosaurus* in detail.

The cladogram topologies obtained by Rieppel varied as his research program evolved. More definitive versions from later publications such as Rieppel (1998, 1999, 2000) agree on the broad outline of sauropterygian phylogeny. In Rieppel's topology, placodonts are the first branch within the clade Sauropterygia, making them the outgroup to all other 'nothosaur'-grade sauropterygians plus the Plesiosauria (clade Eosauropterygia). Three subclades are found within this group, one comprised of pachypleurosaurs such as *Dactylosaurus* and *Neusticosaurus* (clade Pachypleurosauroidea). A second clade is composed of the 'nothosaurs' *Simosaurus*, *Nothosaurus*, and related taxa (clade Nothosauria), and a third contains the Plesiosauria and plesiosaur-like 'nothosaurs' (clade Pistosauroida; nomenclature from Rieppel 1998, Rieppel 1999, 2000). Clade Pistosauroida contains the genera *Cymatosaurus*, *Corosaurus*, *Pistosaurus*, and the closely related *Augustasaurus*. In the following discussion, stem-group eosauroptrygians (i.e., eosauroptrygians minus the Plesiosauria) are referred to using the colloquial terms 'nothosaur' or 'nothosaur'-grade taxa'. When the term nothosaur appears without quotes, it refers only to the monophyletic clade Nothosauria.

Anatomical background

Some introductory comments concerning the anatomy of plesiosaurs and their sauropterygian

antecedents are necessary. This section discusses only areas of variability, especially concerning the skull and limb girdles. Specific characters and their states are discussed in Appendix 1.

Cranial anatomy

No comprehensive review of the plesiosaur skull has been attempted since the work of Andrews (1910, 1913). Brown (1981, 1993), and Brown and Cruickshank (1994) discussed the skull roof of *Cryptoclidus* and related genera, while the cranial anatomy of rhomaleosaurids has been treated recently by Cruickshank (1994a, 1994b, 1997). Carpenter (1996) reviewed the cranial anatomy of the polycotyliids. The primitive taxa *Plesiosaurus* (Storrs 1997) and *Thalassiodracon* (Storrs & Taylor 1996) have also been redescribed recently, as has the primitive *Eurycleidus* (Cruickshank 1994b).

The sauropterygian skull roof is remarkable in several ways. The first and most obvious is the pattern of temporal fenestration, where the presence of the upper temporal fenestra and the lack of a lower temporal fenestra led Williston (1925) to classify the sauropterygians within his 'Synapsosauria'. Colbert amended this name to 'Euryapsida', a term retained by Romer (1956, 1966). Like many higher-level taxon names, 'Euryapsida' has fallen into disuse due to a lack of certainty concerning its monophyly, although Merck (1997) has performed a cladistic analysis on all 'euryapsids' and believes them to be monophyletic.

The condition of the Permian plesiomorphic diapsid *Araeoscelis*, described in detail by Vaughn (1955), is an acceptable model from which to derive the sauropterygian skull roof. All sauropterygians retain only the upper temporal fenestra, as does *Araeoscelis*. The upper temporal fenestra becomes greatly enlarged in the Sauropterygia, concurrent with a narrowing of the parietal skull table, creating a large surface for attachment of the jaw adductor musculature (Rieppel 1994a). The trends of enlargement of the upper temporal fenestra and narrowing of the parietals become extreme in plesiosaurs; in all plesiosaurs, the posterior parietals

form a sharply keeled sagittal crest, and the pineal foramen moves far forward to a position near the parietal-frontal suture. Both of these characters are present in *Pistosaurus*, the most plesiosaur-like of the basal sauropterygians. Also present in *Pistosaurus* and all plesiosaurs is the 'squamosal arch', or the meeting at the postero-dorsal margin of the skull of median processes of the squamosals. This median squamosal suture excludes the parietals from the occiput. The pistosaurid genus *Cymatosaurus* is intermediate between basal 'nothosaurs' and plesiosaurs in having a very narrow exposure of the parietal on the occiput (Rieppel & Werneburg 1998).

In *Araeoscelis*, paired nasal bones contact the external nares and meet in a long midline suture, anterior to the paired frontals that also meet broadly on the midline. All three clades of sauropterygians contain members where the nasal midline suture is lost due to the formation of a midline frontal-premaxilla suture. *Pistosaurus* has this suture, and is further derived in having very small nasals that do not contact the external nares (Edinger 1935). Rieppel (1994a) could not determine whether nasals were present in the remaining skull of this taxon. The presence or absence of nasals in plesiosaurs has always been debated, with Andrews (1910) identifying them in some pliosaurs. More recently, Storrs has maintained that all plesiosaurs lack nasals (Storrs 1991), and his skull roof reconstructions of the very primitive plesiosaurs *Plesiosaurus* (Storrs 1997) and *Thalassiodracon* (Storrs & Taylor 1996) omit nasals. However, nasals are in fact present in *Thalassiodracon* as well as in all more derived members of the Pliosauroida (see below). The nasal is lost in all Plesiosauroidea, including *Plesiosaurus*. When present in plesiosaurs, the nasals are always separated by posterior processes of the premaxillae, as is the case in *Cymatosaurus*. In many plesiosaurs the premaxillary processes extend back to contact the parietals, separating the frontals on the skull surface, although the frontals may continue to have a midline suture beneath the premaxillae (Andrews 1911b).

Araeoscelis is plesiomorphic in the retention of the lacrimal, stretching from orbit to external naris. The lacrimal is lost in all sauropterygians (Rieppel 1997b), including all plesiosaurs (con-

tra Andrews 1913, and Taylor & Cruickshank 1993). The quadratojugal, also present in *Araeoscelis* and most basal sauropterygians, is also lost in the Pistosauroidea and all plesiosaurs. The position and relations of the jugal is variable in sauropterygians, but *Pistosaurus* and many plesiosaurs possess a prominent suture between the maxilla and squamosal. This suture excludes the jugal from the ventral skull margin; in *Simosaurus* and other 'nothosaur'-grade sauropterygians the jugal enters the ventral skull margin (Rieppel 1994a). The jugal is taxonomically important in plesiosaurs, and the configuration of the other circum-orbital bones in general is also diagnostic.

The posterior palate and basicranium are diagnostic in plesiosaurs, but this area is highly conserved in more basal sauropterygians, and is often obscured by other skull elements. In all 'nothosaur'-grade sauropterygians, the pterygoids meet in a median suture that extends caudally almost to the occipital condyle, forming a solid plate of bone beneath the basicranium (Storrs 1991, Rieppel 1997b). This pterygoid median suture closes off both the anterior and posterior interpterygoid vacuities, the presence of which in *Araeoscelis* exposes the dermal ossification of the parasphenoid as well as the endochondral ossifications of the braincase (i.e. basisphenoid and basioccipital). *Araeoscelis* is primitive in this regard, very similar to the Carboniferous diapsid *Petrolacosaurus* (Reisz 1981). In *Pistosaurus*, the posterior interpterygoid vacuity reappears, again exposing the ventral surface of the braincase. The morphology of the braincase is unknown in *Pistosaurus*. In primitive plesiosaurs, the palate opens further to reveal the anterior parasphenoid and the braincase. These structures show a remarkable similarity to the condition in *Araeoscelis*. The reappearance of the anterior and posterior interpterygoid vacuities in plesiosaurs is correlated with a trend of reduced ossification in the skeleton generally, a common feature of many aquatic tetrapods (Storrs 1991, Romer 1956). Ossification of the more ventral structures of the braincase is also reduced in plesiosaurs, to the point that the dorsum sellae and sella turcica are no longer identifiable in derived pliosauroids. These structures are prominent and well-ossified

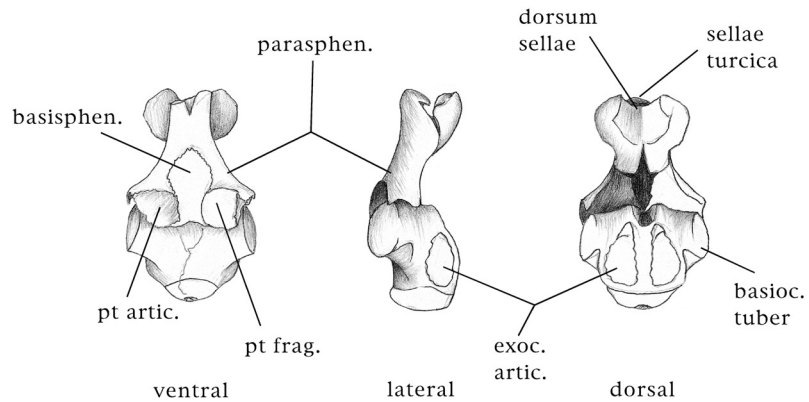


Fig. 1. *Eurycleidus arcuatus* braincase, OUM J.28585. Length of fragment 4.5 cm.

in *Nothosaurus* (Rieppel 1994b), and are present but less well-ossified in the pistosauroid *Cymatosaurus* (Rieppel & Werneburg 1998). *Cymatosaurus* also possesses a deep, narrow notch in the posterior border of the clivus, a feature it shares with all plesiosaurs in which the dorsum sellae and clivus are ossified (Fig. 1).

Postcranial anatomy

Romer's (1956: pp. 298–332) introduction to the anatomy of the reptilian limb girdles illustrates the general conditions of the pectoral and pelvic girdles in primitive amniotes. Again, *Araeoscelis* is a plesiomorphic diapsid that may be used as a model from which to derive the sauropterygian conditions. In the pelvic girdle of *Araeoscelis*, the pubis and ischium form a solid plate without a thyroid fenestra, surmounted dorsally by the ilium (Vaughn 1955). The obturator foramen is primitively present in the pubis. All sauropterygians have a large thyroid fenestra. The obturator foramen is present in all sauropterygians except plesiosaurs, the pistosauroid *Cymatosaurus*, and the true nothosaur *Lariosaurus*. Girdle ossification in plesiosaurs is slow and varies intra-specifically to some degree (Brown 1981), leading Brown to question the taxonomic utility of characters relating to girdle shape. The plesiosaur pelvic girdle is apomorphic in the great reduction of the ilium, the loss of contact between ilium and pubis, and the concomitant absence of the ilium from the acetabulum. In all plesiosaurs, the ilium is a narrow rod of bone running from the ischium to

a reduced sacrum composed of one to three sacral ribs.

The pectoral girdle is more complex and much more variable within the Sauropterygia. All sauropterygians have one coracoid ossification rather than the primitive two present in *Araeoscelis*; the cleithrum is also absent in all sauropterygians (Rieppel 1997b). Furthermore, there is a broad trend of reduction in the dorsal structures of the pectoral girdle and elaboration of them ventrally. In placodonts the shoulder girdle is still relatively plesiomorphic. The blade of the scapula is prominent laterally, and the coracoids do not meet on the ventral midline. However, the dermal elements of the shoulder girdle (clavicles and interclavicle) are large and robust, and are primarily ventral structures. In 'nothosaur'-grade sauropterygians, the clavicles remain large and, unlike placodonts, have a prominent medial suture and concomitant reduction of the interclavicle. Also in contrast to placodonts, 'nothosaur'-grade sauropterygians possess a ventral median suture of the coracoids. The coracoids are enlarged relative to those of placodonts and are distinctively narrowed or 'waisted' near their centers (Storrs 1991: p. 75). The coracoids are plate-like and not waisted in the pistosauroid *Corosaurus*. In *Augustasaurus* the coracoids are large ventral plates similar to those in plesiosaurs (Sander *et al.* 1997; author's pers. obs.). The coracoid foramen is also lost in *Corosaurus* and *Augustasaurus*, a trait these taxa share with plesiosaurs.

The pectoral girdle in plesiosaurs is characterized by reduction of the scapular blade (Romer 1956) and a great ventral elaboration of

the scapulae. The dorsal blade of the scapula is situated dorsal to the glenoid in 'nothosaur'-grade sauropterygians, but is anterior to the glenoid in all plesiosaurs (Kebang & Rieppel 1998). The ventral processes of the scapulae angle anteriorly toward the midline and meet in a midline suture in some derived taxa. This ventral elaboration of the scapulae comes at the expense of the clavicles and interclavicle, which are reduced and near the midline in plesiosaurs. The coracoids are also greatly elaborated in plesiosaurs, forming large plate-like extensions posteriorly with a long midline suture between them. The coracoids may also send processes forward to meet either the clavicles or scapulae on the midline, dividing the ventral space enclosed by the pectoral girdle into two pectoral fenestrae (for example Welles 1962, Storrs 1997). This median pectoral bar is slow to ossify (Brown 1981), as is the comparable median pelvic bar (present in *Plesiosaurus*, Storrs 1997, and some elasmosaurs, Welles 1962). The aggregate effect of changes in the pelvic and pectoral girdles is the formation of two large,

ventral plates of bone vaguely reminiscent of a turtle plastron. The short space between the anterior and posterior girdles was filled with closely spaced gastralia. The ventral plates were presumably the areas of attachment for large locomotor muscles (Williston 1914).

The limbs of plesiosaurs are highly specialized hydrofoils. The modifications of propodials and epipodials are complex in sauropterygians, especially across the pistosaurid/plesiosaur transition and within basal plesiosaurs. In general terms, the propodials tend to lose obvious processes for muscle attachment and become short and stout (Storrs 1997, Romer 1956). A pronounced bend caudad in the shaft of the humerus is characteristic of 'nothosaur'-grade taxa and some very primitive plesiosaurs, but the shaft is straight in all derived plesiosaurs (Storrs 1997). Both the ectepicondylar and entepicondylar foramina are lost in all plesiosaurs; in 'nothosaur'-grade sauropterygians the ectepicondylar foramen is often reduced to a groove or notch, and both features are variably present in basal sauropterygians. However, the pistosauroids *Corosaurus* and *Cymatosaurus* possess both open-

Table 1. Repositories and abbreviations for sauropterygian material referenced in this report.

Repository	Abbrev.	Location
1 American Museum of Natural History	AMNH	New York, New York, USA
2 The Natural History Museum	BMNH	London, UK
3 Banque de la República de Villa de Leyva	BRI	Bogota, Columbia
4 Bristol Museum and Art Gallery	BRSMG	Bristol, UK
5 Sedgwick Museum	CAMSM	Cambridge, UK
6 Sternberg Museum of Natural History	FHSM	Fort Hayes, Kansas, USA
7 Field Museum of Natural History	FMNH	Chicago, Illinois, USA
8 Institut und Museum für Geologie und Paläontologie	GPIT	Tübingen, Germany
9 Umwelt Museum Hauff	Hauff	Holzmaden, Germany
10 Kansas Museum of Natural History	KUVP	Lawrence, Kansas, USA
11 Leicester City Museum	LEICT	Leicester, UK
12 Manchester Museum	MAN UM	Manchester, UK
13 Geologisch-Paläontologisches Museum der Universität Münster	Münster	Münster, Germany
14 Museum of Comparative Zoology, Harvard University	MCZ	Cambridge, Massachusetts, USA
15 Museum of the Rockies	MOR	Bozeman, Montana, USA
16 National Museum of Wales	NMW	Cardiff, Wales
17 Oxford University Museum of Natural History	OXFUM	Oxford, UK
18 Peterborough Museum and Art Gallery	PETMG	Peterborough, UK
19 Strecker Museum, Baylor University	SM	Waco, Texas, USA
20 Staatliches Museum für Naturkunde, Stuttgart	SMNS	Stuttgart, Germany
21 Southern Methodist University Museum of Paleontology	SMUSMP	Dallas, Texas, USA
22 Texas Technical Institute	TTVP	Lubbock, Texas, USA
23 University of California Museum of Paleontology	UCMP	Berkeley, California, USA
24 Smithsonian Institution	USNM	Washington, D.C., USA
25 University of Wyoming	UW	Laramie, Wyoming, USA
26 Yorkshire Museum	YORYM	York, UK
27 Yale-Peabody Museum	YPM	New Haven, Connecticut, USA

ings, whereas the pistosaurids *Pistosaurus* and *Augustasaurus* lack both openings, another condition these taxa share with plesiosaurs. The epipodials resemble the propodials in becoming relatively short and broad in basal eosauropterygians. The manus and pes are characterized by hyperphalangy in all plesiosaurs. The phalangeal formulas in the pistosaurids are unknown. The hypophalangy hypothesized by Sander *et al.* (1997) in *Augustasaurus* is probably an artifact of preservation (O. Rieppel pers. com.).

Materials and methods

The plesiosaur material discussed here is held in 27 institutions in the United States, South America, and Europe (listed in Table 1). Material in 24 of these institutions was examined personally; material from the other three institutions (Geologisch-Paläontologisches Museum der Universität Münster, Museum of the Rockies, Banque de la República de Villa de Leyva) was scored from the literature. The three outgroup and 31 ingroup taxa considered in this report are listed below. Each genus is presented with primary and more recent references, holotype and specimen number, referred material, and other remarks. Characters used in the phylogenetic analysis are discussed in the second part of the Materials and Methods section, and listed in Appendix 1. The data matrix is listed in Appendix 2.

Description of *Hauffiosaurus* gen. n. and *Hauffiosaurus zanoni* sp. n.

Hauffiosaurus gen. n.

DIAGNOSIS: as for species.

ETYMOLOGY: The genus name refers to the Urwelt-Museum Hauff, the institution in Holzmaden, Germany where the type species is housed.

TYPE SPECIES: *Hauffiosaurus zanoni*

Hauffiosaurus zanoni sp. n.

DIAGNOSIS: A plesiomorphic member of clade Pliosauridae possessing the following autapo-

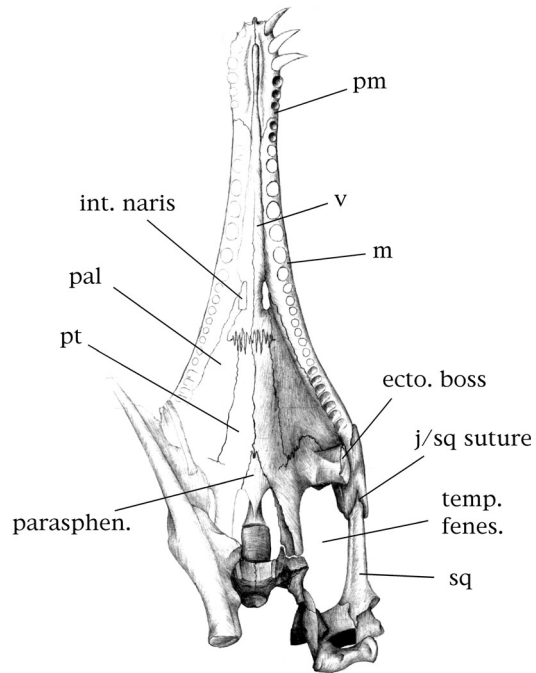


Fig. 2. *Hauffiosaurus zanoni* n.gen n.sp palate, Hauff uncat. Length of skull 43 cm.

morphies: seven premaxillary teeth; ectopterygoid boss contacts jugal exclusively; propodials very long.

TYPE MATERIAL: — Holotype: Hauff museum uncatalogued, a complete skeleton in the Hauff Museum, Holzmaden, Germany. Figs. 2 and 3.

ETYMOLOGY: The species name *zanoni* refers to the late R. T. Zanon, who first realized this specimen represented a new genus (R. T. Zanon unpubl.).

REFERRED MATERIAL: none.

TYPE LOCALITY: Posidonien-Schiefer, Holzmaden, Germany. AGE: Toarcian.

DESCRIPTION: The specimen here designated *Hauffiosaurus zanoni* (Hauff museum uncatalogued) is a complete plesiosaur skeleton preserved in ventral view, found in the Posidonien-Schiefer of Holzmaden, Germany (Toarcian). The skeleton is approximately 2.5 m long, and displays an interesting mix of plesiomorphic, derived, and apomorphic features. For a complete listing of character states in this taxon, see Appendix 2.

The skull is preserved in palatal view (Figs. 2 and 3), with the mandibles crushed and displaced to one side. The snout and mandibular

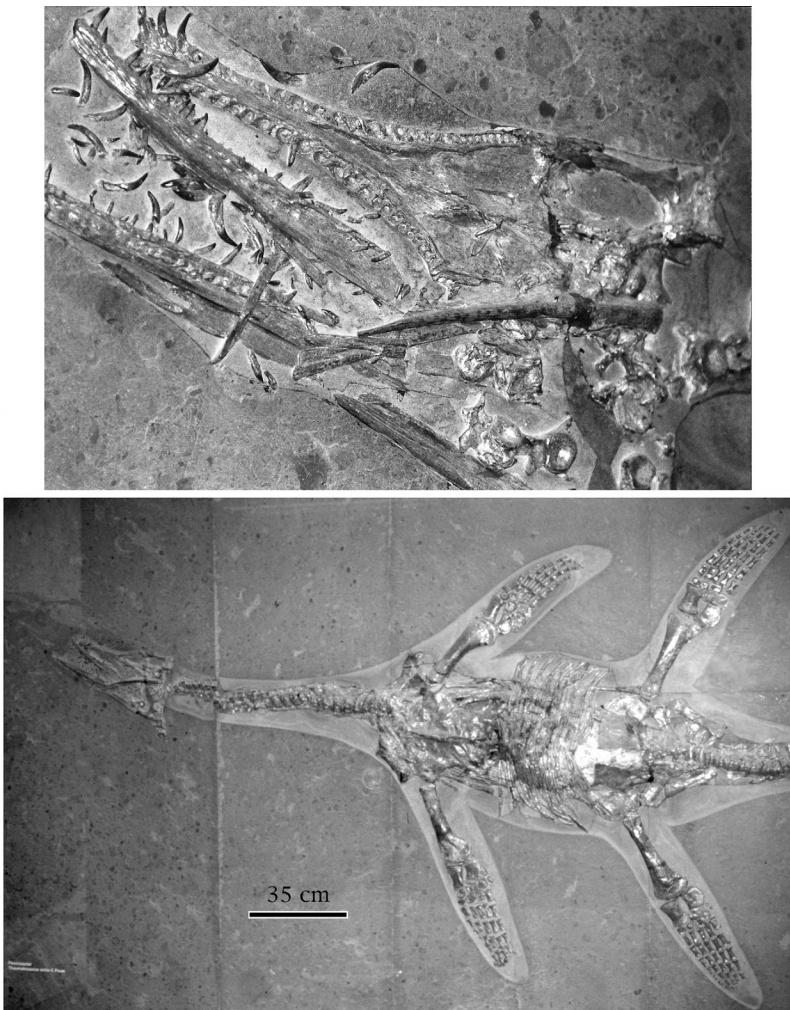


Fig. 3. Photographs of the holotype of *Hauffiosaurus zanoni*. Top, detail of skull and mandibles. Compare to Fig. 2. Length of skull 43 cm. Bottom, entire skeleton as preserved. Note that 'body outline' was carved during preparation; no soft tissue is preserved with the specimen.

symphysis are both very long, indicating that the specimen is not a rhomaleosaur, and is instead a member of the Pliosauridae. On the palate, the vomers extend beyond the posterior margin of the internal nares and meet the pterygoids in a wide, interdigitating suture very similar to that in *Peloneustes*. This suture lacks the median extension on the midline characteristic of *Macroplata*. The Hauff taxon also possess a prominent ectopterygoid boss unlike *Macroplata* but like *Peloneustes*, although the boss articulates laterally with the jugal only rather than both the jugal and squamosal as in *Peloneustes*. There is no anterior interpterygoid vacuity. The parasphenoid is exposed prominently on the palate

surface anterior to the posterior interpterygoid vacuity. The basisphenoid is poorly ossified, as in *Peloneustes* and all other pliosaurids except *Macroplata*. The pterygoids meet behind the posterior interpterygoid vacuity, and there is evidence of a lateral flange around the vacuities similar to that in *Peloneustes* and *Kronosaurus*. However, the sigmoid shape and rolled lateral margin of the quadrate flange of the pterygoid are absent in the Hauff taxon, as in *Macroplata* but unlike all more derived pliosaurids. There are seven teeth in each premaxilla, an autapomorphy (*Peloneustes* has six teeth in the premaxilla). In sum, the palate of the Hauff specimen shows a mixture of primitive and derived

features, and seems to be intermediate between the plesiomorphic *Macroplata* and more derived *Peloneustes*. The position of the Hauff taxon on the cladogram reflects this impression.

The most remarkable aspect of the postcranium is the extreme length of the propodials. The humerus is 32 cm long, while the femur is 35 cm long. Both propodials are longer than any of their associated girdle bones, a unique feature among plesiosaurs and an autapomorphy of this taxon. The postcranium in general displays relatively small girdles, high aspect-ratio fins, and a neck that is primitive in length and vertebral number. *Hauffiosaurus zaroni* is a stratigraphically early (Toarcian) and morphologically intermediate member of the Pliosauridae, and possesses several autapomorphies in the skull and postcranium.

Included taxa

Outgroup taxa

Three taxa were chosen as outgroups for this analysis. They are the nothosaur *Simosaurus*, the pistosauroid *Cymatosaurus*, and the family Pistosauridae. The family Pistosauridae comprises the genera *Pistosaurus* and *Augustasaurus*. These two taxa were scored together because they are closely related, and because the material for the two genera is complementary. The postcranium of *Augustasaurus* is articulated and well-preserved, unlike that of *Pistosaurus*, which has led to some doubt in the postcranial reconstruction of the later taxon (Sues 1987). The skull of *Augustasaurus* is extant, and a description is in press at this time (O. Rieppel pers. com.), while that of *Pistosaurus* was described in detail by Edinger (1935; skull now lost).

GENUS: *Simosaurus* Meyer, 1842

TYPE SPECIES: *Simosaurus gaillardoti* Meyer, 1842.

TYPE MATERIAL: — Holotype: lost. — Neotype: SMNS 16700 (Rieppel 1994a).

TYPE LOCALITY: Upper Muschelkalk, Lunéville, France.

AGE: Ladinian.

REFERRED MATERIAL: various, one known species.

REMARKS: Taxonomy and referred material reviewed in Rieppel 1994a.

GENUS: *Cymatosaurus* v. Fritsch, 1894

TYPE SPECIES: *Cymatosaurus fridericianus* v. Fritsch, 1894.

TYPE MATERIAL: — Holotype: Institut für Geowissenschaften, Martin-Luther Universität, Halle/Saale, uncatalogued.

TYPE LOCALITY: Lower Muschelkalk, Halle/Saale, Germany.

AGE: Ladinian.

REFERRED MATERIAL: various, at least four known species.

REMARKS: Taxonomy and referred material reviewed in Rieppel (1997b, 1998b), and Rieppel and Hagdorn (1997).

FAMILY: Pistosauridae Zittel, 1887

TYPE SPECIES: *Pistosaurus longaevus* Meyer, 1839.

TYPE MATERIAL: — Holotype: Oberfränkisches Erdgeschichtliches Museum, Bayreuth, uncatalogued.

TYPE LOCALITY: Upper Muschelkalk, Bayreuth, Germany.

AGE: Late Anisian.

REFERRED MATERIAL: various, possibly two species.

REMARKS: Taxonomy, referred material, and postcranium reviewed in Sues (1987). Cranium described by Edinger (1935), and Rieppel (1994a).

TYPE SPECIES: *Augustasaurus hagdorni* Sander, Rieppel and Bucher, 1997.

TYPE MATERIAL: — Holotype: FMNH PR 1974.

TYPE LOCALITY: Favret Formation, Pershing County, Nevada.

AGE: Late Anisian.

REFERRED MATERIAL: none.

REMARKS: *Augustasaurus* is one of two nothosaur-grade sauropterygians from North America; the other is *Corosaurus*. The skull of *Augustasaurus* is currently being described by O. Rieppel, M. Sander, and G. Storrs.

Ingroup taxa

Thirty-one plesiosaur genera were coded for inclusion in the phylogenetic data matrix. Two of these taxa are unnamed at present; these taxa are referred to by specimen number. Several of the genera included here contain more than one species. The common genus *Plesiosaurus* probably contains three valid species, while *Muraenosaurus* contains at least two valid species. Because genus-level and higher relationships are the primary goal of this analysis, polytypic genera are treated as terminal taxa here. However, species level diagnoses are given in the Systematic Paleontology section where appropriate. Another complication is that the genus *Rhomaleosaurus* is paraphyletic (see Results). The species of *Rhomaleosaurus* included here

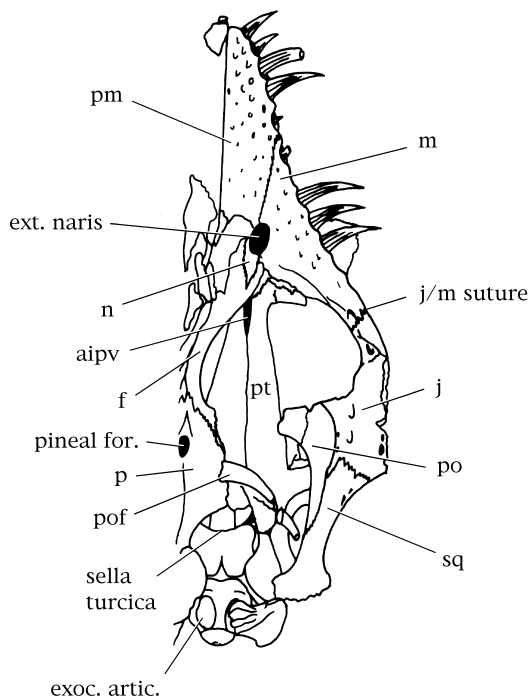


Fig. 4. *Thalassiodracon hawkinsi* skull roof, OUM J.10337. Abbreviations used in the following figures are as follows: aipv, anterior interpterygoid vacuity; ang, angular; cor, coranoid; d, dentary; ect, ectopterygoid; f, frontal; j, jugal; m, maxilla; n, nasal; p, parietal; pal, palatine; pt, prefrontal; pipv, posterior interpterygoid vacuity; pm, premaxilla; po, postorbital; pof, postfrontal; preart, prearticular; pt, pterygoid; q, quadrate; sof, suborbital fenestra; spl, splenial; sq, squamosal; surang, surangular; v, vomer. Length of skull 18 cm.

are referenced using both genus and species names. The listings of referred material below mention only material used in this study; complete lists of referred material can generally be found in references cited in the remarks for each taxon. The sampling of plesiosaur taxa in this study is not exhaustive. Several *Rhomaleosaurus* species are omitted, as are several elasmosaur genera and some other poorly-known taxa. All known clades are well-represented, however, and the omission of some ingroup taxa from some clades should not influence the results reported here. The genus *Rhomaleosaurus* and the Elasmosauridae are both in need of taxonomic revision. Lastly, exhaustive synonymies are not given for each taxon. Some remarks on

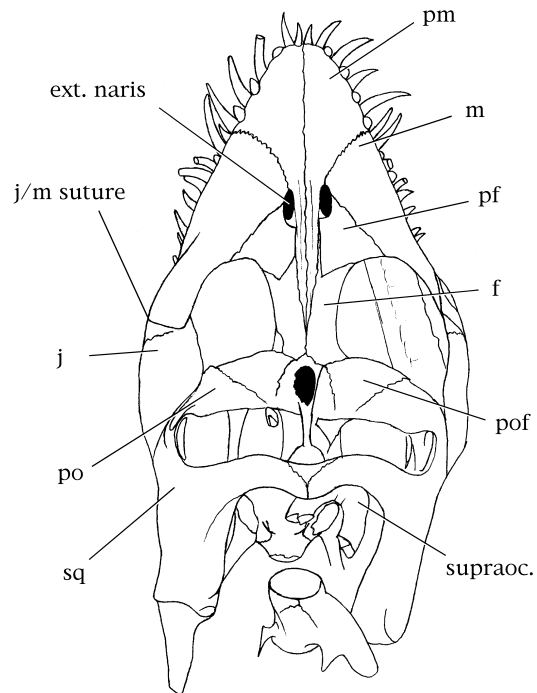


Fig. 5. *Plesiosaurus dolichodeirus* skull roof, BMNH 39490. Length of skull 23 cm.

the taxonomic history of most genera are given in the remarks section, along with references where synonymies can be found for those taxa.

GENUS: *Thalassiodracon* Storrs & Taylor, 1996

TYPE SPECIES: *Thalassiodracon hawkinsi* (Owen, 1838).

TYPE MATERIAL: — Holotype: BMNH 2018.

TYPE LOCALITY: Street, Somerset, England.

AGE: Rhaetian-Hettangian boundary.

REFERRED MATERIAL: BMNH 14550, 2020, R.1336 (juv.) CAMSM J.46986, OUM J.10337, MM L. 9767.

REMARKS: Fig. 4. Storrs and Taylor (1996) created this genus name for the taxon '*Plesiosaurus*' *hawkinsi* (Owen 1838), a stratigraphically early and morphologically primitive plesiosaur. These authors list other material referable to this taxon, and describe the skull in some detail. A redescription of the postcranium is necessary.

GENUS: *Eurycleidus* Andrews, 1922

TYPE SPECIES: *Eurycleidus arcuatus* (Owen, 1840).

TYPE MATERIAL: — Holotype: BMNH 2030 (see Cruickshank 1994b).

TYPE LOCALITY: Lyme Regis, Dorset, England.

AGE: Hettangian- Lower Sinemurian.

REFERRED MATERIAL: OUM J.28585, SMNS 16812.

REMARKS: Fig. 1. Cruickshank (1994b) redescribes this

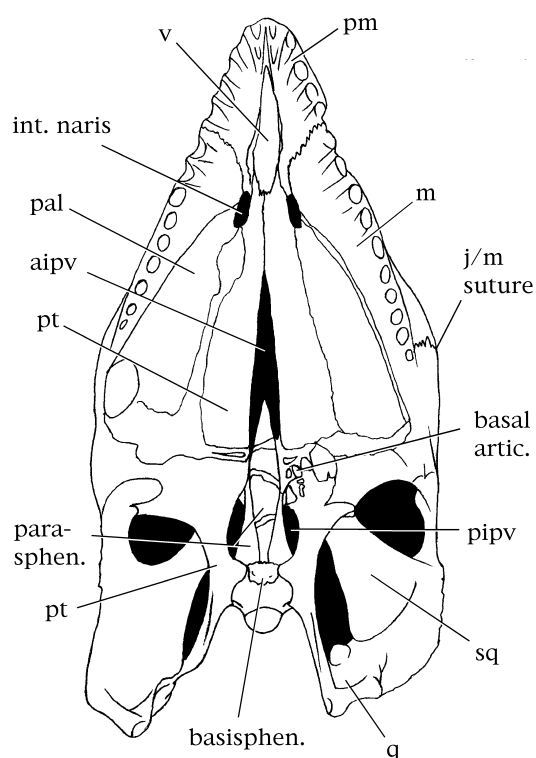


Fig. 6. *Plesiosaurus dolichodeirus* palate, BMNH 41101. Length of skull 20 cm.

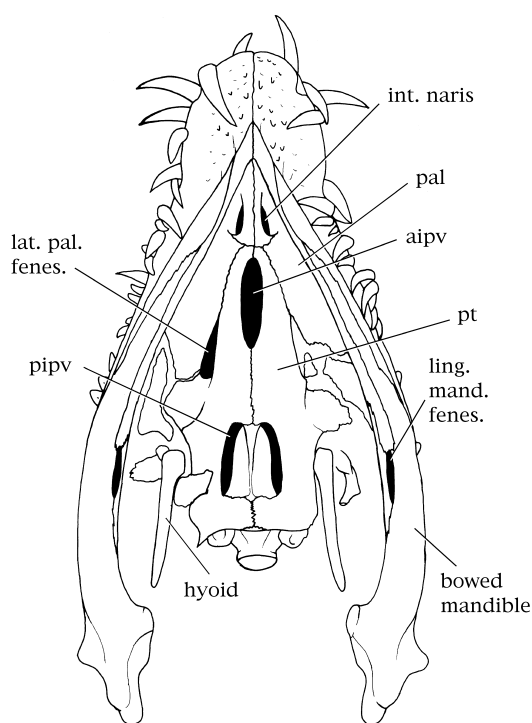


Fig. 7. *Rhomaleosaurus victor* palate, SMNS 12478. Length of mandible 40 cm.

genus and refers other material to it. I refer the German specimen to this taxon based on similarities in the basicranium; however this referral is provisional until the German material (a complete skeleton) can be described in more detail. Fig. 1.

GENUS: *Plesiosaurus* De la Beche & Conybeare, 1821

TYPE SPECIES: *Plesiosaurus dolichodeirus*, Conybeare 1824.
 TYPE MATERIAL: — Holotype: BMNH 22656.
 TYPE LOCALITY: Lyme Regis, Dorset, England.
 AGE: Uppermost Sinemurian.
 REFERRED MATERIAL: *P. dolichodeirus*: BMNH 39490, 41101, 36183, R.1756, OXFUM J.10304; *P. brachypterygius*: SMNS 51143, Hauff uncatalogued, GPIT 477/1/1; *P. guilemiimperatoris*: SMNS 51015.
 REMARKS: Figs. 5 and 6. Andrews (1896) gives the first detailed account of the structure of the palate in this taxon. The genus is reviewed exhaustively in Storrs (1997). Storrs discusses other material also referable to this taxon, and advances the hypothesis that the many nominal species in this common and widespread genus are representative of perhaps three valid species. My interpretation differs somewhat; *P. brachypterygius* lacks the lunate ulna characteristic of *P. dolichodeirus*, and may be a valid species

as well. I agree with Storrs that *P. guilemiimperatoris* is a valid species; that author also states that material from France may represent another valid species. The French material was not examined in the course of this study.

GENUS: *Rhomaleosaurus* Seeley, 1874 (Seeley 1874b)

TYPE SPECIES: *Rhomaleosaurus cramptoni* Seeley, 1874.

Rhomaleosaurus victor (Fraas, 1910)

TYPE MATERIAL: — Holotype: SMNS 12478.
 TYPE LOCALITY: Posidonien-Schiefer, Holzmaden, Germany.
 AGE: Toarcian.
 REFERRED MATERIAL: none.
 REMARKS: Fig. 7. The taxonomic history of this species is complex; this species was originally described as '*Thaumatosauros victor*' (Meyer 1841) by Fraas (1910). The genus *Rhomaleosaurus* is in need of revision (Cruikshank 1994a; see below). Lydekker (1889b) attempted to make *Rhomaleosaurus* a junior synonym of *Thaumatosauros*, based on his opinion that Seeley's type of the genus, *Rhomaleosaurus cramptoni* (Seeley 1874b), does not differ from the type material of '*Thaumatosauros*'. Tarlo (1960) rejected '*Thaumatosauros*' because the type material is not diagnostic (reviewed in Taylor 1992a).

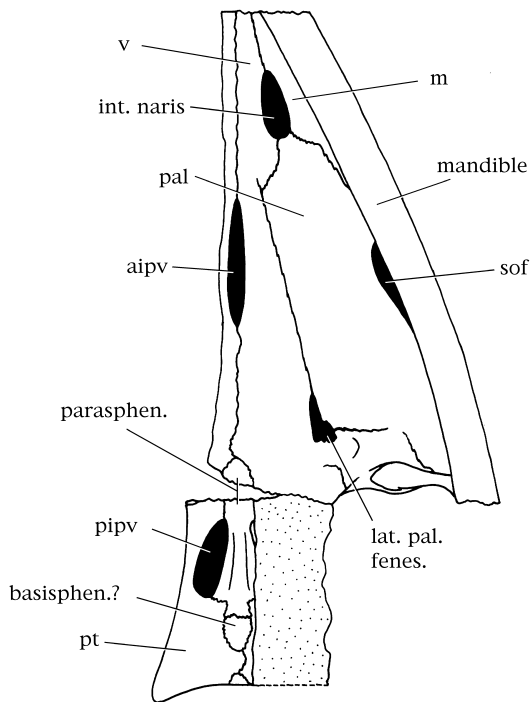


Fig. 8. *Rhomaleosaurus megacephalus* palate, LEICT G221.1851. Length of mandible 42 cm.

Tarlo (1960) also believed the complete skeleton named '*Thaumatosauros victor*' by Fraas (1910) to be congeneric with *Rhomaleosaurus*, and recommended dropping '*Thaumatosauros*' altogether. I follow his suggestion. Lydekker (1889a) also referred an isolated jaw symphysis from India to *Thaumatosauros*; the symphysis has characters diagnostic of the Rhomaleosauridae but is not diagnostic at the genus level.

Rhomaleosaurus megacephalus Stuchbury, 1846

TYPE MATERIAL: — Holotype: lost. — Neotype: LEICT G221.1851 (Cruikshank 1994a).

TYPE LOCALITY: Barrow upon Soar, Leicestershire, England.

AGE: Earliest Hettangian.

REMARKS: Fig. 8. Cruikshank (1994a) designates and describes the neotype, which is a complete skeleton superficially similar to the destroyed holotype described and figured by Stuchbury (1846) under the name '*Plesiosaurus megacephalus*'. Cruikshank (1994a) and Taylor (1992a) also discuss the taxonomic confusion surrounding the name *Rhomaleosaurus*.

Rhomaleosaurus zetlandicus Phillips, 1854 (in Anon. 1854)

TYPE MATERIAL: — Holotype: YORYM G503

TYPE LOCALITY: Alum Shale, Whitby, Yorkshire, England.

AGE: Toarcian.

REMARKS: Taylor (1992a) discusses the taxonomy of this specimen and of *Rhomaleosaurus* in general. Taylor (1992b) describes the cranial anatomy of this taxon.

GENUS: *Simolestes* Andrews, 1909

TYPE SPECIES: *Simolestes vorax* Andrews 1909.

TYPE MATERIAL: — Holotype: BMNH R.3319.

TYPE LOCALITY: Oxford Clay, Peterborough, England.

AGE: Callovian.

REFERRED MATERIAL: none.

REMARKS: Andrews (1913) and Tarlo (1960) describe this taxon thoroughly.

GENUS: *Leptocleidus* Andrews, 1922

TYPE SPECIES: *Leptocleidus capensis* (Andrews, 1911a).

TYPE MATERIAL: — Holotype: BMNH R.4828.

TYPE LOCALITY: Berwick, Sussex, England.

AGE: Barremian.

REFERRED MATERIAL: SAM-K5822 (South African Museum).

REMARKS: Cruikshank (1997) reviews the type material of this genus and refers the South African specimen to the genus. The type material was originally described by Andrews (1911a) under the genus name '*Plesiosaurus*'.

GENUS: *Macroplata* Swinton, 1930

TYPE SPECIES: *Macroplata longirostris* (Blake, 1876).

TYPE MATERIAL: — Holotype: MCZ 1033.

TYPE LOCALITY: Alum Shale, Whitby, Yorkshire, England.

AGE: Toarcian.

REFERRED MATERIAL: MAN UM 8004.

REMARKS: Fig. 9. *Macroplata longirostris* was named and described from a complete skeleton by Blake (1876) as '*Plesiosaurus longirostris*'. Swinton (1930) erected *Macroplata* for the specimen when he realized that it was not referable to *Plesiosaurus*. However, as discussed by White (1940), Blake and later workers were aware that the specimen was a composite. Blake (1876) argued that the holotype be restricted to the skull only. White (1940) felt that the associated vertebral column might also be included in the holotype. The skull was prepared poorly in Victorian times, and the serious 'pyrite disease' noted by White (1940) has continued to degrade the already battered skull. However, several diagnostic characters are still visible, such as the very long snout and the plesiomorphic, rhomaleosaur-like pattern of the posterior basicranium. Both of these characters are shared by a new skull with associated complete skeleton in the Manchester Museum (MAN UM 8004), which was found at the same locality and in the same formation as the holotype. The Manchester specimen also possesses a groove in front of the external naris, and a perforation in the dorsal surface of the basisphenoid through which the clivus is visible. Both of these characters are also present in the *Macroplata* holotype, and I therefore refer MAN UM 8004 to this taxon.

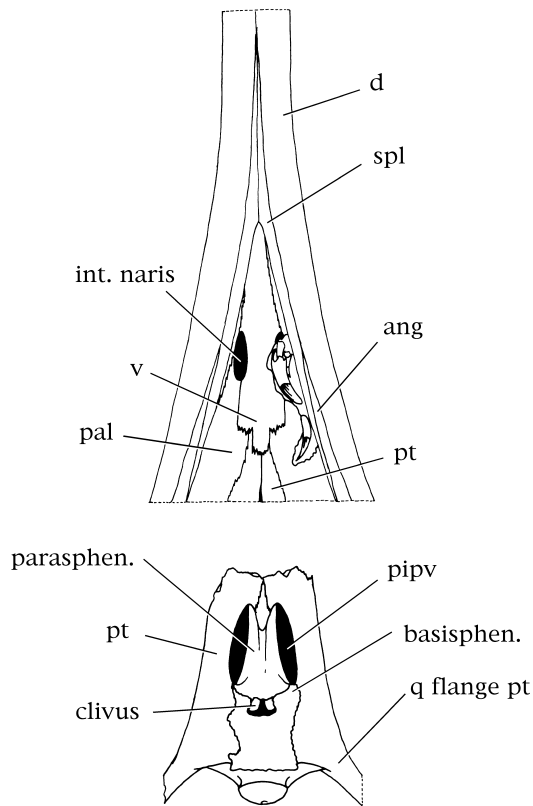


Fig. 9. *Macroplata longirostris* palate, MAN UM 8004.

GENUS: unnamed (*'Macroplata tenuiceps'*).

TYPE SPECIES: n/a.

TYPE MATERIAL: — Holotype: BMNH R.5488.

TYPE LOCALITY: Harbury, Warwickshire, England.

AGE: unknown.

REMARKS: This specimen is a complete skeleton in the collection of the Natural History Museum, London. The specimen is identified as *'Macroplata tenuiceps'* on the labels accompanying the material. The skeleton is certainly not referable to this genus based on characters noted by Cruickshank (1994a), Swinton (1930), and White (1940). The specimen is certainly a rhomaleosaurid, although the skull material is not diagnostic at the species level. The taxonomic status of this specimen awaits revision of the Rhomaleosauridae.

GENUS: *Hauffiosaurus* gen. n.

TYPE SPECIES: *Hauffiosaurus zanoni* sp. n.

HOLOTYPE: Hauff Museum, uncatalogued; see above.

TYPE LOCALITY: Posidonien-Schiefer, Holzmaden, Germany.

AGE: Toarcian.

REFERRED MATERIAL: none.

REMARKS: Figs. 2 and 3. This specimen is a complete

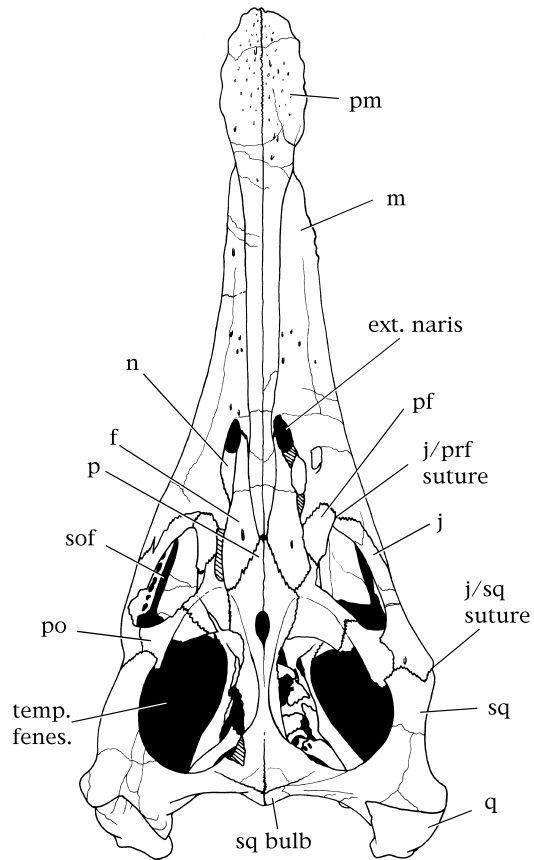


Fig. 10. *Peloneustes philarchus* skull roof, BMNH R. 8574. Length of skull 69.5 cm.

skeleton of an unnamed taxon in the collections of the Hauff Museum. The taxon is named here, and a preliminary description is given above with figures of the skull and skeleton.

GENUS: *Peloneustes* Lydekker, 1889 (Lydekker 1889b)

TYPE SPECIES: *Peloneustes philarchus* (Seeley, 1869).

TYPE MATERIAL: — Holotype: CAMSM J.46913

TYPE LOCALITY: Oxford Clay, Peterborough, England.

AGE: Callovian.

REFERRED MATERIAL: BMNH R.8574, R.3803, R.3897, R.3318.

REMARKS: Figs. 10, 11 and 12. Lydekker names and describes this taxon (1889b), and comments on its relationships to *Thaumatosauros*. Tarlo (1960) discusses this taxon, and Andrews (1913) describes it in detail. Linder (1913) describes Oxford Clay material of this taxon at the SMNS, and compares it to *Pliosaurus*. This taxon is extremely well-represented by material in the Leeds collection in the Natural History Museum

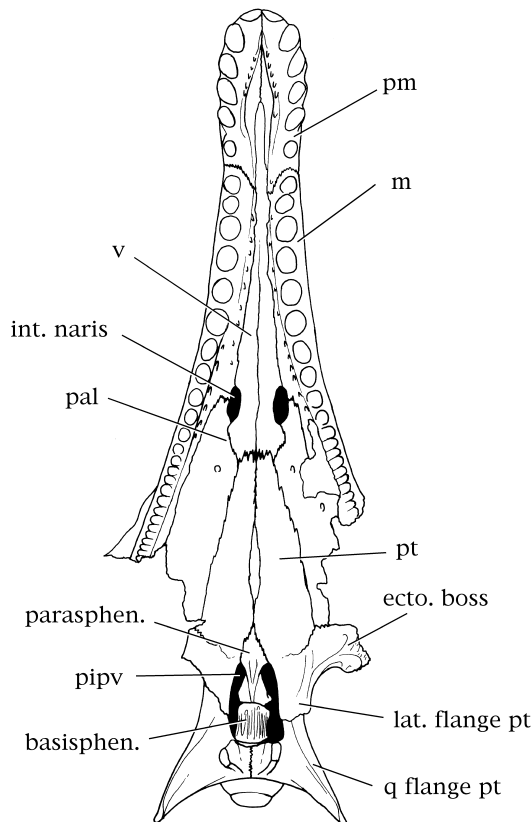


Fig. 11. *Peloneustes philarchus* palate, SMNS 10113. Length of skull 63 cm.

(BMNH), including several complete skeletons with well-preserved skulls.

GENUS: *Liopleurodon* Sauvage, 1873

TYPE SPECIES: *Liopleurodon ferox* Sauvage, 1873.

TYPE MATERIAL: — Holotype: BMNH R.3536.

TYPE LOCALITY: Oxford Clay, Peterborough, England.

AGE: Callovian.

REFERRED MATERIAL: BMNH R.2680, GPIT 1754/2.

REMARKS: Tarlo (1960) offered the latest review of Upper Jurassic pliosaurs, and reviews the complex taxonomic history of the genus name. Andrews (1913) describes this taxon in detail under the name '*Pliosaurus ferox*'. The genus *Stretosaurus* was made a junior synonym of this taxon by Halstead (1989); this poorly-defined taxon is based on enormous pliosaurid postcranial elements from the Kimmeridge Clay. Further comparison of this material with that of *Pliosaurus* is probably necessary.

GENUS: *Pliosaurus* Owen, 1841

TYPE SPECIES: *Pliosaurus brachydeirus* Owen, 1841.

TYPE MATERIAL: — Holotype: OXFUM J.9245 A,B.

TYPE LOCALITY: Oxford Clay, Peterborough, England.

AGE: Callovian.

REFERRED MATERIAL: BMNH R.3891, BRSMG Cc332, 'Westbury Pliosaur 2' (BRSMG uncatalogued.).

REMARKS: Taylor and Cruickshank (1993) discuss the taxonomic history of this genus. Tarlo (1960) also reviews this taxon. Referred specimens listed above are Kimmeridgean, from the Kimmeridge Clay in Wiltshire, UK.

GENUS: *Brachauchenius* Williston, 1903

TYPE SPECIES: *Brachauchenius lucasi* Williston, 1903.

TYPE MATERIAL: — Holotype: USNM 4989.

TYPE LOCALITY: Greenhorn Limestone, Ottawa County, Kansas, USA.

AGE: Turonian.

REFERRED MATERIAL: USNM 2361, FHSM VP321.

REMARKS: Fig. 13. This taxon was described in detail by Williston (1907). Carpenter (1996) referred the Fort Hayes skull to the genus.

GENUS: *Microcleidus* Owen, 1865

TYPE SPECIES: *Microcleidus homalospondylus* Owen, 1865.

TYPE MATERIAL: — Holotype: YORYM G.502.

TYPE LOCALITY: Alum Shale, Whitby, England.

AGE: Toarcian.

REFERRED MATERIAL: MM L. 7077.

REMARKS: This genus is in need of redescription, having last been treated by Watson (1911).

GENUS: *Brancaesaurus* Wegner, 1914

TYPE SPECIES: *Brancaesaurus brancai* Wegner 1914.

TYPE MATERIAL: — Holotype: Münster; Wegner does not give the specimen number.

TYPE LOCALITY: Münster, Westphalia, Germany.

AGE: Valangian.

REFERRED MATERIAL: none.

REMARKS: Wegner's (1914) thorough description is the only publication on this taxon.

GENUS: *Callawayasaurus* Carpenter, 1999

TYPE SPECIES: *Callawayasaurus columbiensis* (Welles, 1962).

TYPE MATERIAL: — Holotype: UCMP 38349.

TYPE LOCALITY: Columbia, South America.

AGE: Aptian.

REFERRED MATERIAL: UCMP 125328, partial skull. Same locality.

REMARKS: Fig. 14. This genus was erected by Carpenter (1999) for the holotype of '*Alzadasaurus columbiensis*' (Welles 1962), an essentially complete elasmosaur skeleton from the Aptian of Columbia. The skull shows a number of primitive features. For holotype and other information on *Alzadasaurus* proper see Welles (1962).

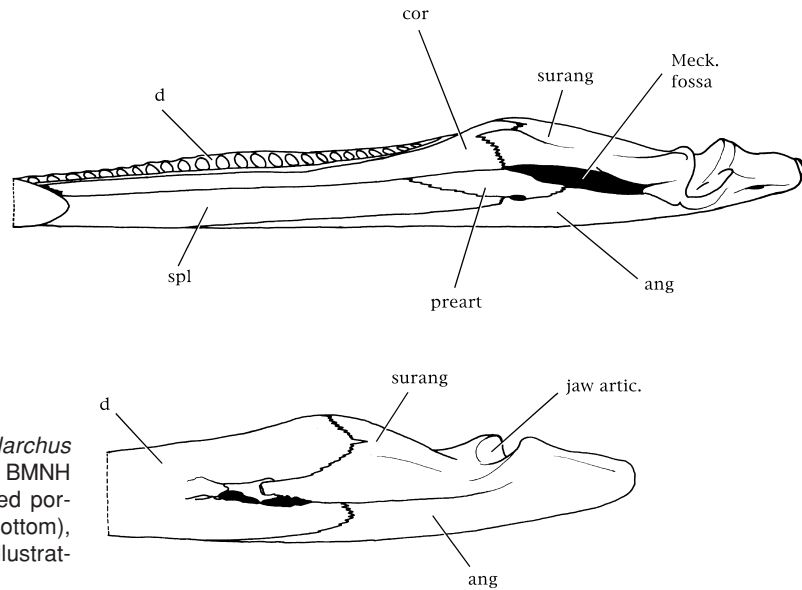


Fig. 12. *Peloneustes philarchus* mandible, lingual view (top), BMNH R. 8574, length of illustrated portion 28 cm; lateral view, (bottom), BMNH R. 2439, length of illustrated portion 18 cm.

GENUS: *Libonectes* Carpenter, 1996

TYPE SPECIES: *Libonectes morgani* (Welles, 1949).
TYPE MATERIAL: — Holotype: SMUSMP 69120.
TYPE LOCALITY: Britton Formation, near Cedar Hill, Texas, USA.
AGE: Coniacian.
REFERRED MATERIAL: none
REMARKS: Fig. 15. Carpenter (1996) describes the well-preserved skull of this taxon, and erected the new genus name for a specimen that had been referred to *Elasmosaurus* by Welles (1949).

GENUS: *Styxosaurus* Welles, 1943

TYPE SPECIES: *Styxosaurus snowii* (Williston, 1890).
TYPE MATERIAL: — Holotype: KUV 1301.
TYPE LOCALITY: Niobrara Formation, Hell Creek, Logan County, Kansas, USA.
AGE: Santonian.
REFERRED MATERIAL: AMNH 5835.
REMARKS: Reviewed in Welles (1943, 1952, 1962), and more recently in Storrs (1999).

GENUS: *Cryptoclidus* Phillips, 1871

TYPE SPECIES: *Cryptoclidus eurymerus* Phillips 1871.
TYPE MATERIAL: — Holotype: lost. — Neotype: BMNH R.2860 (Brown 1981).
TYPE LOCALITY: Oxford Clay, Peterborough, England.
AGE: Callovian.
REFERRED MATERIAL: PETMG R.283, BMNH R.2417, GPIT 1754/1.
REMARKS: Andrews (1910) describes this taxon thorough-

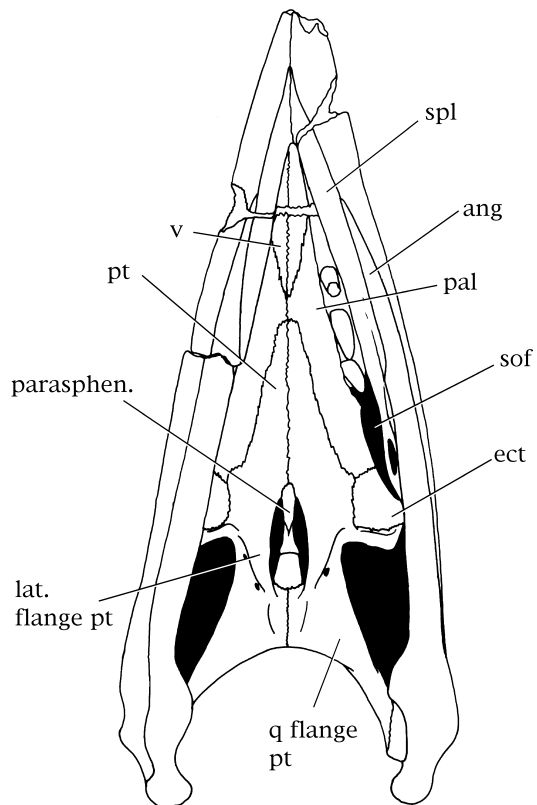


Fig. 13. *Brachauchenius lucasi* palate, USNM 4989. Length of mandible 112 cm.

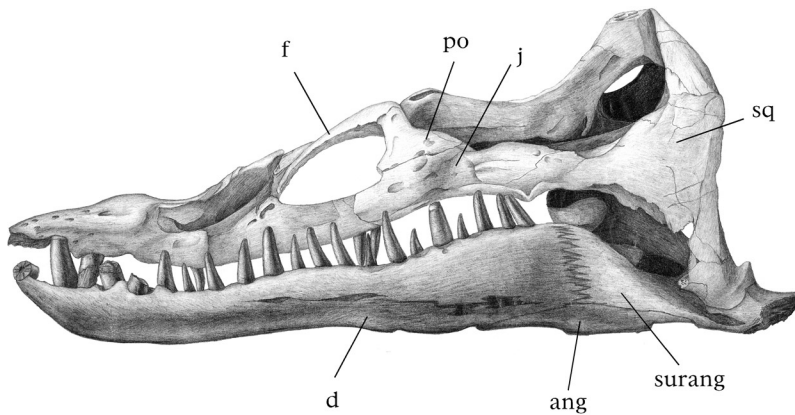


Fig. 14. *Callawayasaurus columbiensis* skull, lateral view, UCMP 38349. Length of skull 15.8 cm.

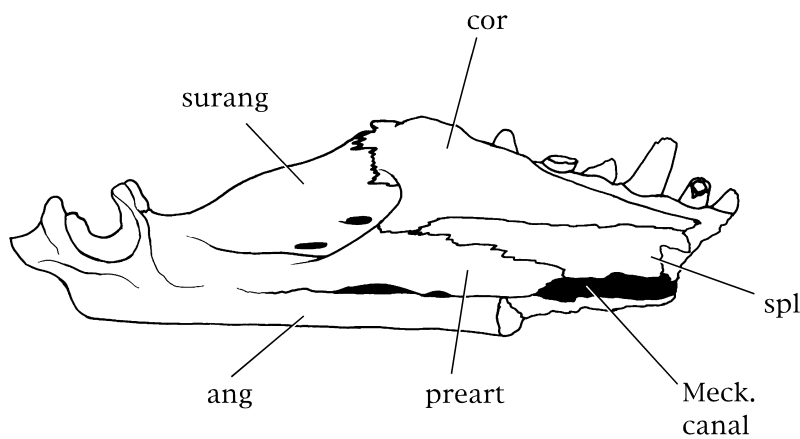


Fig. 15. *Libonectes morgani* mandible, lingual view, SMUSMP 69120. Length of fragment 28 cm.

ly. Brown (1981) redescribes this taxon and refers other material to it. Brown and Cruickshank (1994) describe the skull in some detail from referred material.

GENUS: *Muraenosaurus* Seeley, 1874 (Seeley 1874a)

TYPE SPECIES: *Muraenosaurus leedsii* Seeley, 1874 (Seeley 1874a).

TYPE MATERIAL: — Holotype: BMNH R.2421.

TYPE LOCALITY: Oxford Clay, Peterborough, England.

AGE: Callovian.

REFERRED MATERIAL: BMNH R.2678, R.2864, R.2863, R.2861, R.3704, LEICT G.18.1996.

REMARKS: Andrews (1910) describes this taxon thoroughly. Brown (1981) redescribes the skull and refers other material to it.

GENUS: *Tricleidus* Andrews, 1909

TYPE SPECIES: *Tricleidus seeleyi* Andrews, 1909.

TYPE MATERIAL: — Holotype: BMNH R.3539.

TYPE LOCALITY: Oxford Clay, Peterborough, England.

AGE: Callovian

REFERRED MATERIAL: none.

REMARKS: Fig. 16. Described in Andrews (1910). Brown (1981) redescribes this taxon. Known from one fairly complete skeleton.

GENUS: *Kimmerosaurus* Brown, 1981

TYPE SPECIES: *Kimmerosaurus langhami* Brown, 1981.

TYPE MATERIAL: — Holotype: BMNH R.8431.

TYPE LOCALITY: Kimmeridge Clay, Dorset, England.

AGE: Kimmeridgian.

REFERRED MATERIAL: BMNH R.1798, R.10042.

REMARKS: A poorly known but important taxon. Additional material described by Brown *et al.* (1986). The genus *Colymbosaurus*, also from the Kimmeridge Clay, may be related to this taxon; however, no cranial material of *Colymbosaurus* is yet known (Brown 1984), and the taxon is in need of revision. The humerus of *Colymbosaurus* is very similar to that of *Polycotylus* (Brown, 1981).

GENUS: *Morturneria* Chatterjee & Small, 1989

TYPE SPECIES: *Morturneria seymourensis* Chatterjee & Small, 1989

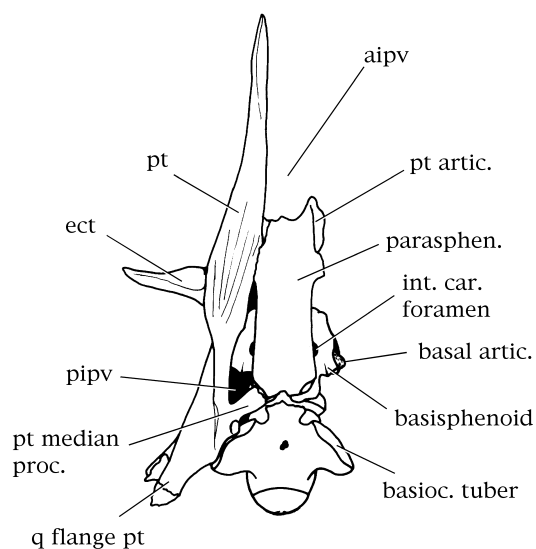


Fig. 16. *Tricleidus seeleyi* palate, BMNH R. 3539. Length of illustrated portion 14 cm.

TYPE MATERIAL: — Holotype: TT VP9219.
 TYPE LOCALITY: Lopez de Bertodana Formation, Seymour Island, Antarctica.
 AGE: Maastrichtian.
 REFERRED MATERIAL: none.
 REMARKS: This taxon is the best-known of a poorly-known group of aberrant Cretaceous cryptoclidids. This group also includes the taxon *Aristonectes parvidens* Cabrera 1941, from South America; like *Morturneria* this taxon is Maastrichtian in age.

GENUS: currently unnamed

TYPE SPECIES: n/a.
 TYPE MATERIAL: — Holotype: MOR 751.
 TYPE LOCALITY: Thermopolis Shale, Montana, USA.
 AGE: Upper Albian.
 REFERRED MATERIAL: none.
 REMARKS: This specimen is an unnamed, primitive polycotylid described in a thesis by Druckenmiller (1998). Druckenmiller has a publication naming this taxon in press (Druckenmiller pers. com.).

GENUS: *Polycotylus* Cope, 1869

TYPE SPECIES: *Polycotylus latipinnis* Cope, 1869.
 TYPE MATERIAL: — Holotype: USNM 27678.
 TYPE LOCALITY: Niobrara Formation, Fort Wallace, Kansas, USA.
 AGE: Cenomanian.
 REFERRED MATERIAL: AMNH 2321, YPM 1125.
 REMARKS: Carpenter (1996) reviewed all Cretaceous pliosauroforms from North America. *Polycotylus* is the largest of known polycotylids, and its skull is known from very fragmentary material.

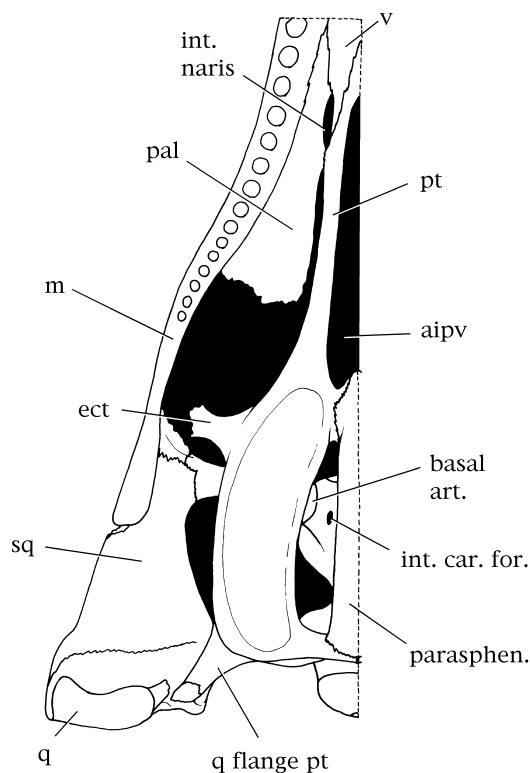


Fig. 17. *Dolichorhynchops osborni* palate, FHSM VP404. Length of illustrated portion 24 cm.

GENUS: *Dolichorhynchops* Williston, 1903

TYPE SPECIES: *Dolichorhynchops osborni* Williston 1903.
 TYPE MATERIAL: — Holotype: KUV 1300.
 TYPE LOCALITY: Niobrara Formation, Logan County, Kansas, USA.
 AGE: Cenomanian.
 REFERRED MATERIAL: MCZ 1064, FHSM VP404
 REMARKS: Figs. 17, 18 and 19. Carpenter (1996) reviewed all Cretaceous pliosauroforms from North America, including *Dolichorhynchops*.

GENUS: *Trinacromerum* Cragin, 1888

TYPE SPECIES: *Trinacromerum bentonianum* Cragin, 1888.
 TYPE MATERIAL: — Holotype: USNM 10945.
 TYPE LOCALITY: Fencepost Limestone, Osborne County, Kansas, USA.
 AGE: Turonian.
 REFERRED MATERIAL: USNM 10946, MCZ 1064, FHSM VP404, KUV 5070, SM 3025.
 REMARKS: Carpenter (1996) reviewed all Cretaceous pliosauroforms from North America, including *Trinacromerum*.

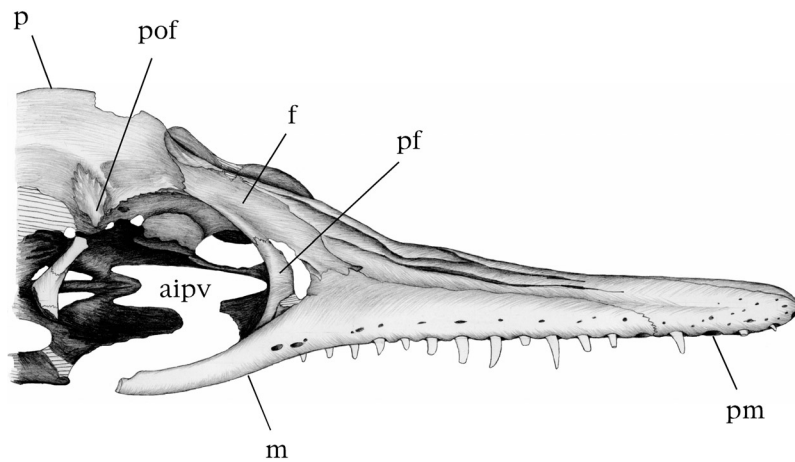


Fig. 18. *Dolichorhynchops osborni* skull roof in oblique lateral view, MCZ 1064. Length of illustrated portion 39 cm.

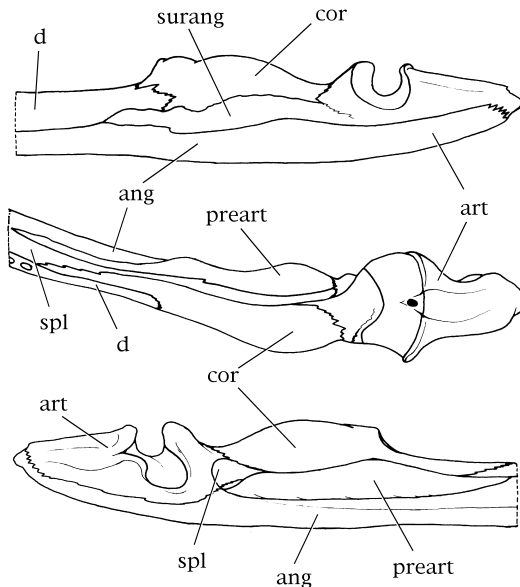


Fig. 19. *Dolichorhynchops osborni* mandible, FHSM VP404; lateral (top), dorsal (middle), lingual (bottom). Length of illustrated portion 19 cm.

GENUS: *Attenborosaurus* Bakker, 1993

TYPE SPECIES: *Attenborosaurus conybeari* (Sollas, 1881).

TYPE MATERIAL: — Holotype: lost; BMNH R.1339 (cast).

TYPE LOCALITY: Charmouth, Dorset, England.

AGE: Sinemurian (?).

REFERRED MATERIAL: BMNH 40140, BMNH R.1360, BMNH 39514.

REMARKS: Described by Owen (1865) as '*Plesiosaurus rostratus*', material referable to this taxon was renamed by Bakker (1993) to replace '*Plesiosaurus conybeari*' (Sollas 1881), after Persson (1963) remarked that the

specimen was clearly not a member of the genus *Plesiosaurus*. Persson also noted that the skull was very similar to that of *Rhomaleosaurus*, but the postcranium was plesiosauromorph; see O'Keefe (2002) for interpretation.

GENUS: *Kronosaurus* Longman, 1924

TYPE SPECIES: *Kronosaurus queenslandicus* Longman, 1924.

TYPE MATERIAL: — Holotype: Queensland Museum; Longman (1924, 1930) does not list specimen number.

TYPE LOCALITY: Army Downs, north of Richmond, Queensland, Australia.

REFERRED MATERIAL: MCZ 1284, 1285.

REMARKS: *Kronosaurus* was originally described on the basis of a fragment of mandibular symphysis and propodial fragments. The more complete Harvard material was collected in 1931–1932 and described by White (1935). The Harvard skull has been on loan to C. McHenry for some time, who is working on a redescription of this taxon based on new material (C. McHenry pers. com.). An additional complete skeleton was assigned to this genus by Hampe (1992). Hampe also furnishes 22 characters and a cladogram of seven 'pliosaur' species.

Characters and coding

The 34 taxa listed above were scored for 166 morphological characters. Of these characters, 107 concerned the skull and 59 were postcranial. About half of the characters appear in the literature in some form. Appendix 1 gives a number and name for each character, the reference (if any) for that character, a description of states, numerical codings, and any relevant remarks. The references cited in the table are the most informative and generally the most recent

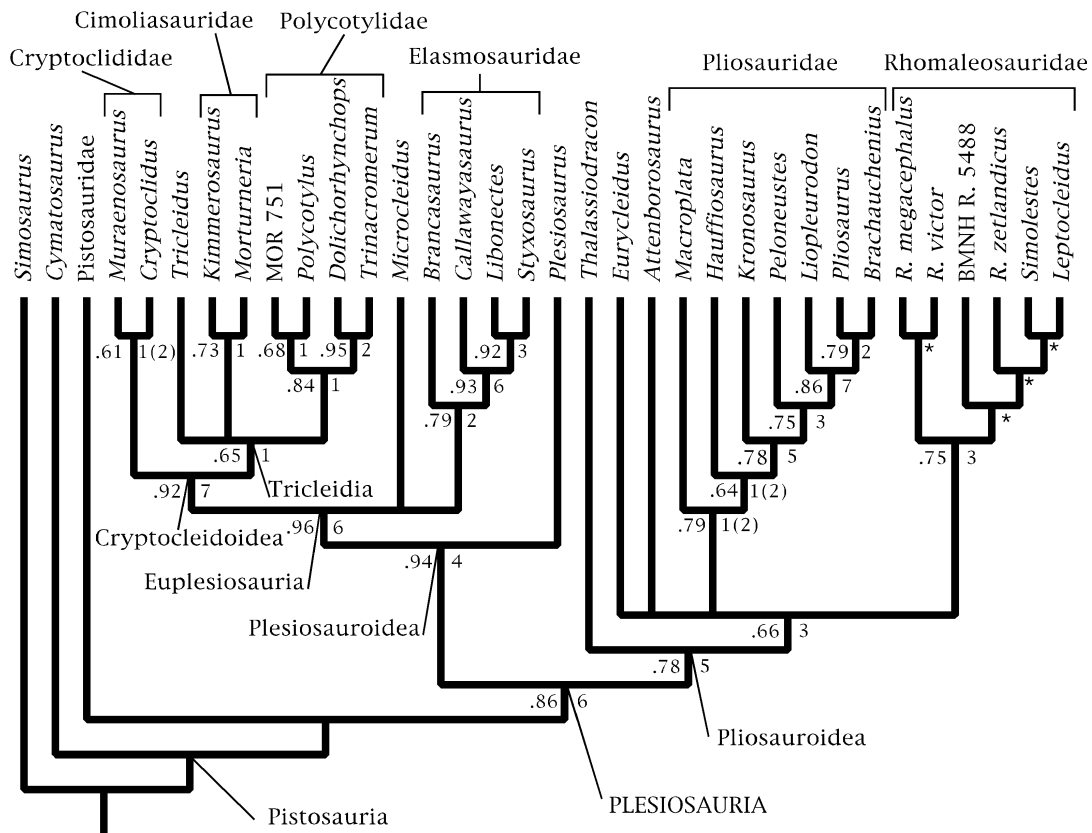


Fig. 20. Phylogenetic relationships of the Plesiosauria. Topology shown is the strict consensus of 12 MPTs, tree lengths 432. CI = 0.47, RCI = 0.34, RI = 0.72. Numbers just below and to the left of a given node are bootstrap support values; those to the right are decay indices. Indices in parentheses are the support for a given node after morphometric characters have been removed and analysis rerun. Dots represent nodes with less than 50% bootstrap support and a decay index of one. Named groups are diagnosed in the text.

source for a given character, and the listing is not exhaustive. The figures where states of a given character are illustrated are listed in the remarks section for each character. Characters are scored with the primitive state as zero for convenience, and polarity was determined by comparison with the outgroup. Most characters are unordered; those that are ordered are noted in the remarks section. Characters are only ordered if a second state is logically dependent on the presence of the first state, such as characters concerning successive neck lengths or the number of maxillary teeth. Running all characters as unordered results in identical results as running some characters as ordered. The matrix has a relatively high proportion of characters that are inapplicable to some taxa, due largely to

the profound reorganizations of the pectoral girdle and palate between the outgroup and the ingroup. Characters which code only for the outgroup were included to help establish the topology within the outgroup, which can effect character reconstruction at the basal node of the ingroup and hence the ingroup topology. Characters which code only for the ingroup will affect only the topology of the ingroup. The presence of both types of characters will not give rise to spurious effects as long as the basal ingroup node is strongly supported by other characters, and it is in this case (bootstrap value 86%, decay index 6; see Fig. 20).

The data matrix (Appendix 2) was analyzed using PAUP 3.1.1 (Swofford & Begle 1993). The non-plesiosaur taxa *Simosaurus*, *Cymato-*

saurus, and Pistosauridae were specified as the outgroup, and the outgroup was constrained to be paraphyletic with respect to the ingroup to reflect the topology of Rieppel (2000). The heuristic search strategy was used, using tree-bisection-reconnection (TBR) branch swapping. The reference taxon was random; iterations showed that using any taxon as the reference taxon yielded the same set of trees. Initial analysis was run with all characters included and weighted equally. A second analysis was performed with the 'morphometric' characters removed, based on the finding that the pliosauromorph body type may have evolved convergently (O'Keefe 2002).

Results

Parsimony analysis of the data matrix yielded twelve most-parsimonious trees (MPTs), each with a tree length of 432. The strict consensus tree computed from the twelve MPTs is shown in Fig. 20. The MPTs had a Consistency Index (CI) of 0.47, and a Rescaled Consistency Index (RCI) of 0.34 (excluding uninformative characters). The Retention Index (RI) was 0.72. I investigated the robustness of the strict consensus tree topology by bootstrapping the character list (1000 replicates), and by calculating decay indices (Bremer 1994) for each ingroup node. Bootstrap percentages and decay indices are stated beneath each node in Fig. 20. The tree is well-supported with the exception of some cryptocleidoid relationships and the ingroup relationships of the rhomaleosaurids.

The topology of clade Plesiosauria replicates many of the findings advanced by earlier workers. The basic dichotomy between the Plesiosauroidae and the Pliosauroidae is a well-supported finding. Within the Pliosauroidae two large monophyletic groups exist, the Rhomaleosauridae and the Pliosauridae, as suggested by Carpenter (1997). The base of the clade Pliosauroidae contains the plesiomorphic taxon *Thalassiodracon*, as well as the plesiomorphic and transitional *Eurycleidus*. The basal position of *Eurycleidus* was predicted by Cruickshank (1994b). The Polycotylidae is not a member of the Pliosauroidae, establishing that the pliosauromorph

body type is a polyphyletic grade. To investigate the stability of this result, parsimony analysis was performed with the constraint of pliosauroid/polycotylid monophyly in effect. This analysis resulted in two MPTs with tree lengths of 447, fifteen steps longer than the MPTs from the original analysis. This large increase in tree length indicates that polyphyly of the traditional Pliosauroidae is a well-supported finding, and that monophyly of the traditional Pliosauroidae is unlikely.

Within the Plesiosauroidae, the monophyly of the Elasmosauridae is well-supported. The Cryptocleidoidea, however, is the one group in which the cladogram departs radically from the traditional taxonomy. The placement of *Muraenosaurus* in this clade suggests that *Muraenosaurus* is not an elasmosaur (contra Andrews 1910). The elasmosaur-like long neck and small head evolved independently in *Muraenosaurus*. Also within the Cryptocleidoidea is a novel clade composed of *Tricleidus*, the Polycotylidae, and the short-necked cryptocleidoids *Kimmerosaurus* and *Morturneria*. This clade documents the derivation of the pliosauromorph polycotylids from a *Tricleidus*-like cryptocleidoid. Taxonomy of clade Plesiosauria is revised below in the systematic paleontology section of the discussion. The taxonomic revision is followed by a discussion of character transitions at various nodes.

To investigate the effect of morphometric characters on the tree topology, a PAUP analysis was run with the eight morphometric characters excluded (characters 1–7, 112). This analysis resulted in 6 MPTs, each with a tree length of 387. The CI of these trees was 0.49, and the RCI was 0.36. The RI was 0.73. The topology of the strict consensus tree computed from this set of MPTs was almost identical to the topology in the first analysis, differing only in the position of *Microcleidus*. In the first analysis *Microcleidus* formed a polytomy with two large clades, the elasmosaurs and cryptocleidoids. The second, non-morphometric analysis resolved this polytomy so that *Microcleidus* became the outgroup to a clade in which the elasmosaurs and cryptocleidoids were sister taxa. *Microcleidus* is a plesiomorphic and problematic taxon, and it is treated as a stem taxon in this report.

The one area where the removal of the morphometric characters had a significant effect was the tree length, and the RCI derived from it. The RCI increased from 0.34 to 0.36 in the second analysis. The MPTs derived from the second analysis were 47 steps shorter than those derived from the first; this is an average of almost six steps for each of the eight morphometric characters. The average number of steps per character for the rest of the data is about 2.5. The length of the neck and skull, and other characters of body proportion, are therefore more labile than the remaining characters. The observation that the number of steps per morphometric character is about three times the average for the other characters can be explained by the fact that the pliosauromorph body type evolved independently three times. Decay indices calculated on this tree showed minor improvement for several nodes, and the revised decay indices appear in Fig. 20 in parentheses next to the indices from the primary analysis.

Discussion

The first section of this discussion is a revision of the higher taxonomy of the Plesiosauria, based on the cladogram topology in Fig. 20. The taxonomic revision is followed by a short discussion of characters important in the diagnosis of various clades and a short review of morphological evolution in the Plesiosauria.

Systematic paleontology

The following is a revised taxonomy of the Plesiosauria. All diagnostic characters are described in Appendix 1, and scoring can be found in the character matrix in Appendix 2. All synapomorphies listed in the diagnoses are unambiguous. Character reconstructions that differ between ACCTRAN and DELTRAN optimizations are not listed. Only genera included in the present analysis are listed; note that the taxonomic sampling in this analysis is not exhaustive at the genus level, especially within the Elasmosauridae and Rhomaleosauridae. The definitions given here are node-based (*see* Sereno 1998, and refer-

ences therein for discussion). Taxa defined on the basis of more than two taxa refer to clades whose basal node is well-supported but whose internal relationships are obscured by polytomy.

Sauropterygia Owen, 1860

DIAGNOSIS: diagnosed in Rieppel 1998.

DEFINITION: A monophyletic taxon including the Placodontia and the Eosauropterygia.

Pistosauria Rieppel, 1998

DIAGNOSIS: diagnosed in Rieppel 1998.

DEFINITION: A monophyletic taxon including *Cymatosaurus*, *Pistosaurus*, and the Plesiosauria.

Plesiosauria de Blainville, 1835

REVISED DIAGNOSIS: Maxilla/squamosal contact present; quadrate embayed anteriorly; parasphenoid is exposed anterior to posterior interpterygoid vacuities on palate surface; cervical zygophyses narrower than centrum width; dorsal neural arches shorter than centrum height; zygosphene/zygantrum articulation absent; longitudinal pectoral bar present; lack of articulation between ilium and pubis; expanded distal propodials with dorsal trochanter/tuberosity; ulna distinctly lunate; shifted fifth metapodial present; hyperphalangy present.

REVISED DEFINITION: A taxon including the Plesiosauroidea, the Pliosauroidea, their most recent common ancestor, and all descendants.

Plesiosauroidea Welles, 1943

REVISED DEFINITION: A monophyletic taxon including *Plesiosaurus* and the Euplesiosauria, their most recent common ancestor, and all descendants.

REVISED DIAGNOSIS: Prefrontal contacts margin of external naris; nasal absent; cervical neural spines not angled backward; dorsal neural spines compressed and blade-like.

Euplesiosauria (new taxon)

DIAGNOSIS: Relative skull length short; anterior border of pineal foramen formed by frontal; long lateral and short medial posterior processes of squamosal; jugal confined to posterior orbit

margin; supraoccipital deep with sigmoid ventral sutures; ectopterygoid contacts postorbital bar out of palate plane; distinct change in angle of cervical zygopophyses; anterior processes of scapula meet in median symphysis; longitudinal pectoral bar present, formed by coracoid and scapula; humerus not angled.

DEFINITION: A taxon including the Elasmosauridae, the Cryptocleidoidea, and *Microcleidus*, their most recent common ancestor, and all descendants.

FAMILY: Elasmosauridae Cope, 1870

REVISED DIAGNOSIS: Anterior quadrate embayment absent (reversal); premaxilla excluded from border of internal naris; vomer extends posterior to internal nares; number of cervical rib heads reduced to one; coracoids long with deep median embayment; ventro-medial margin of pubis concave; ulna not lunate (reversal); epipodials wider than long.

REVISED DEFINITION: A taxon including *Branca-saurus*, *Styxosaurus*, their most recent common ancestor, and all descendants.

Cryptocleidoidea Williston, 1925

REVISED DIAGNOSIS: Fin aspect ratio low; anterior interpterygoid vacuity wide with rounded ends; anterior parasphenoid short and blunt; coronoid exposed on lateral mandible surface; groove formed by prearticular/socket in angular; atlas centrum exposed on lateral surface between intercentrum and neural arch; anterior neural flange on cervical neural spines.

REVISED DEFINITION: A taxon including the Cryptocleididae, the Tricleidia, their most recent common ancestor, and all descendants.

FAMILY: Cryptocleididae Williston, 1925

REVISED DIAGNOSIS: Humerus longer than femur, occipital condyle short with no groove, cervical rib heads elongate.

REVISED DEFINITION: A taxon including *Muraenosaurus*, *Cryptocleidus*, their most recent common ancestor, and all descendants.

Tricleidia (new taxon)

DIAGNOSIS: Pterygoid medial process for articu-

lation with parasphenoid present; parasphenoid contacts basioccipital on midline; basioccipital tubers reduced and confluent with basisphenoid articulation; cervical neural spines not compressed (reversal); clavicles meet in medial symphysis behind notch.

DEFINITION: A taxon including the Polycotylidae, the Cimoliasauridae, *Tricleidus*, their most recent common ancestor, and all descendants.

FAMILY: Cimoliasauridae Delair, 1959

REVISED DIAGNOSIS: Rostrum long, unconstricted, and hoop-like; paraoccipital process articulates with squamosal only; teeth very small and needle-like; number of premaxillary teeth seven or greater; number of maxillary teeth much greater than thirty.

REVISED DEFINITION: A taxon including *Morturneria*, *Kimmerosaurus*, their most recent common ancestor, and all descendants.

FAMILY: Polycotylidae Williston, 1908

REVISED DIAGNOSIS: Neck length short; ischium longer than pubis; maxillary/squamosal suture present and formed by posterior expansion of maxilla; pterygoids with distinct medial processes which meet behind posterior interpterygoid vacuities; pterygoids dished lateral to posterior interpterygoid vacuities; mandibular symphysis scoop-like or long; splenial included in mandibular symphysis; number of cervical vertebrae reduced; longitudinal pectoral bar present and formed by clavicle and coracoid; posterior perforations in coracoid; supernumerary ossifications in propodial and epipodial rows; interlocking phalanges anterior to fifth digit.

REVISED DEFINITION: A taxon including *Polycotylus*, *Dolichorhynchops*, their most recent common ancestor, and all descendants.

Pliosauroida Welles, 1943

REVISED DIAGNOSIS: Snout constricted at premaxilla/maxilla suture; occipital condyle short with no groove; posterior bulb formed by squamosals present; pterygoids meet anterior to posterior interpterygoid vacuity; premaxilla excluded from internal naris margin; mandibular symphysis scoop-like or long; splenial included in man-

dibular symphysis; ventral keel present on cervical vertebrae; posterior articulation for succeeding neural spine in cervical neural spines absent. REVISED DEFINITION: A taxon including *Thalassiodracon*, an unnamed clade comprised of *Eurycleidus*, *Attenborosaurus*, the Rhomaleosauridae, and the Pliosauridae, their most recent common ancestor, and all descendants.

FAMILY: Pliosauridae Seeley, 1874 (Seeley, 1874)

REVISED DIAGNOSIS: Preorbital skull length longer than postorbital skull length; rostrum elongate; no contact between premaxilla and external naris; distinct postero-lateral process of frontal absent (reversal); anterior interpterygoid vacuity absent (reversal); vomer reaches past internal nares and meets pterygoid in wide interdigitating suture; mandibular symphysis long; number of maxillary teeth between twenty and thirty; humerus not angled.

REVISED DEFINITION: A taxon including *Macroplata*, *Brachauchenius*, their most recent common ancestor, and all descendants.

FAMILY: Rhomaleosauridae (Kuhn, 1961)

REVISED DIAGNOSIS: Grooves in front of external nares present; paraoccipital process robust; squared lappet of pterygoid underlying pterygoid quadrate ramus present; lateral palatal fenestration present; bowed maxilla present; premaxillary/dentary fangs present; cervical centra lengths less than heights; cervical zygopophyses as wide as centra (reversal).

REVISED DEFINITION: A taxon including *Rhomaleosaurus victor*, *Leptocleidus*, their most recent common ancestor, and all descendants.

Comments on the classification

The above classification is based on the more conservative first parsimony analysis, in which all characters were included. The morphometric characters have high levels of homoplasy; such high levels of convergence can arise, however, in rapidly-evolving characters, and can hold phylogenetic information, especially within smaller subclades (Chippindale & Wiens 1994). It is therefore conservative to base taxonomic

conclusions on the MPTs from all data. Nodes that were not replicated in the non-morphometric tree were not used in the classification. Taxonomic conclusions are also not based on nodes which have weak decay indices and bootstrap support. A good example is the Rhomaleosauridae. The genus *Rhomaleosaurus* is paraphyletic according to the cladogram although the decay index and bootstrap values are low (decay index one, bootstrap support < 50%) for all rhomaleosaurid ingroup relationships. A formal revision of *Rhomaleosaurus* is best left until a more detailed cladistic analysis of the Rhomaleosauridae is made.

The revised classification splits the Plesiosauria into four major subclades, two within the Plesiosauroidae and two within the Pliosauroidae. Within the clade Plesiosauroidae, the Elasmosauridae remains as traditionally defined, with *Brancaesaurus* as the most basal elasmosaur. See Carpenter (1999) for a more complete list of elasmosaur taxa and a revised taxonomy of this clade. The Cryptocleidoidea is revised here to include the Polycotylidae and *Muraenosaurus*; furthermore, a new clade is recognized (the Tricleidia) comprising the Cimoliasauridae, the polycotylids, and *Tricleidus*. *Tricleidus* is a generalized form, falling out in a trichotomy with the other members of the Tricleidia. *Tricleidus* possesses several synapomorphies linking it with the short-necked plesiosauroids, including the presence of posterior medial processes of the pterygoids, reduced basioccipital tubers, a median contact between the basioccipital and parasphenoid, and the possession of a third distinct articulation on the propodials for a supernumery ossification in the epipodial row. All short-necked plesiosauroids share these traits.

A last, problematic taxon within the Plesiosauroidae is *Microcleidus*. This taxon possesses several plesiomorphic characters such as retention of a lunate ulna and retention of an angled humerus; however, the skull is elasmosaur-like in the absence of an anterior interpterygoid vacuity and in the location of the jaw articulation (below the tooth row). The coracoids are known from fragmentary material, but appear not to have the posterior extensions and embayment synapomorphic of true elasmosaurs. The neck is long and the cervical rib heads elongate,

although these characters are homoplastic. Because of this homoplasy the topology given by the morphometric-omitted cladogram is probably more accurate in this case, with *Microcleidus* forming the sister taxon to a clade consisting of the Elasmosauridae and Cryptocleidoidea. The outgroup to this clade is the very plesiomorphic *Plesiosaurus*. A thorough redescription of this taxon based on the type material as well as another complete skeleton at Manchester should shed more light on this genus.

The clade Pliosauroida includes two long-recognized clades of pliosaurs, the Rhomaleosauridae and the Pliosauridae, as well as the plesiomorphic stem taxa *Thalassiodracon*, *Eurycleidus*, and *Attenborosaurus*. Of the two major pliosauroid clades, the Pliosauridae possesses more derived characters. The rhomaleosaurids are conservative, similar to *Thalassiodracon* (and hence plesiomorphic) in the palate, skull roof, and postcranium. This conservatism is partially responsible for the lack of support for intrafamilial rhomaleosaurid relationships. Changes in relative neck and skull length and a great increase in body size are the only known trends in this clade.

In contrast to the Rhomaleosauridae, the Pliosauridae is morphologically derived, and good intermediates exist that document the derivation of the pliosaurid conditions of the skull roof, palate and braincase. The monophyly of the Pliosauridae is a correspondingly well-supported finding. The plesiomorphic taxa *Eurycleidus* and *Attenborosaurus* form a polytomy with the Pliosauridae and Rhomaleosauridae. The taxonomic status of these genera are left open, and the Pliosauridae is limited to *Macroplata* and more derived taxa.

Major patterns in plesiosaur cranial evolution

This overview describes the morphology of the four major plesiosaur subclades in variable regions of the skull. These areas are the skull roof, the palate, and the braincase. Discussion of the anatomy characteristic of each subclade is intended as an aid to future classification.

The skull roof

An important feature of the skull roof is the retention of the nasals in *Thalassiodracon* and the rest of the Pliosauroida. Nasals were thought to be absent in all plesiosaurs by Storrs (1991); however, the loss of nasals diagnoses only the Plesiosauroida, not the Plesiosauria as a whole. The nasals in all pliosauroid taxa are small but present, and usually form the posterior margin of the external nares. The pliosauroid condition is very similar to that of *Cymatosaurus*. In some very derived members of the Pliosauridae, the nasal forms the anterior rather than the posterior margin of the external naris. The nasals in all pliosaurs lack a midline suture, being separated on the midline by processes of the premaxillae.

The pattern of circumorbital bones is diagnostic within the Plesiosauria. The lacrimal is absent in all plesiosaurs due to its loss in more basal sauropterygians (Rieppel 1997b). The prefrontal and postfrontal do not exclude the frontal from the orbital margin in early plesiosaurs, and this condition is retained in all plesiosauroids, including the polycotylids. However, the frontal is excluded from the orbital margin in all more derived rhomaleosaurids and pliosaurids. The jugal is also diagnostic; in the most primitive plesiosauroids and pliosauroids the jugal reaches anteriorly to about the midpoint of the ventral orbital margin, which is plesiomorphic (Rieppel 1997b). In more derived plesiosauroids the jugal is restricted to the posterior orbital margin. This condition contrasts with that in more derived pliosauroids, where the jugal reaches far anterior to the orbit and forms its anterior border, meeting the prefrontal and excluding the maxilla completely from the orbital margin. The presence of a prominent anterior process of the jugal and its contact with the prefrontal probably account for its misidentification as a lacrimal by earlier workers (Andrews 1913, Taylor & Cruickshank 1993).

The cryptocleidooids are extreme in their specialization of the cheek region (Brown & Cruickshank 1994, Brown 1993). In *Cryptocleidus* and *Tricleidus* the contact between maxilla and squamosal is lost, and the jugal forms a

narrow bar connecting these two elements beneath the orbit. This area of the cheek is not known in *Muraenosaurus* or the Cimoliasauridae. This condition is reversed in the polycotyliids, where the maxilla again forms a suture with the squamosal. The morphology of this suture differs from the corresponding suture in true pliosaurs. In true pliosaurs the maxilla/squamosal suture is small and not significant, and the jugal is large and has a prominent lateral suture with the squamosal. In the polycotyliids the jugal is small and restricted to the posterior orbital margin, and does not form a prominent suture with the squamosal. The major suture in this region is that between the maxilla and squamosal, which is formed by an expanded posterior process of the maxilla. A possible explanation for this pattern is secondary strengthening of this area of the skull made necessary by the evolution of a long snout in taxa with a highly reduced cheek region, such as *Tricleidus*.

A feature that evolves repeatedly in long-snouted taxa is a contact between the dorsal processes of the premaxillae and the parietals. A median premaxilla/parietal suture evolves four times, once each in the three derivations of the pliosaumorph body type and once in relatively long-snouted elasmosaurs. This suture probably serves to strengthen the interorbital region of the skull in response to greater forces produced at the tip of the long snout. A long snout is also generally correlated with larger tooth size and a more robust skull in general; larger teeth probably indicate larger average prey size and a concomitant need to reinforce the skull. The robust maxilla/squamosal suture in the polycotyliids is also interpretable as a means of strengthening the skull in response to increased snout length.

The palate

The primitive plesiosaur palate is derived compared to the condition in more basal sauropterygians. The plesiomorphic condition for the plesiosaur palate is shown by *Thalassiodracon* and *Plesiosaurus*; both taxa possess anterior and posterior interpterygoid vacuities exposing the ventral surface of the braincase. The pterygoids

do not meet behind the posterior interpterygoid vacuities in either taxon. In *Plesiosaurus*, the pterygoids also fail to meet between the posterior and anterior vacuities, exposing the cultriform process of the parasphenoid (Storrs 1997). This open palate is retained (with some modification) in all members of the Cryptocleidoidea. In the Elasmosauridae and *Microcleidus*, however, the anterior interpterygoid vacuity is absent. The pterygoids also meet in a prominent midline suture behind the posterior interpterygoid vacuity in all elasmosaurs, but not in *Microcleidus*. Elasmosaurs are therefore characterized by a secondarily closed palate, and this condition is foreshadowed to some extent in *Microcleidus*.

The anterior interpterygoid vacuity is small in *Thalassiodracon*, and is separated from the posterior vacuities by a long midline suture of the pterygoids. This pattern is retained without change in the rhomaleosaurids. The rhomaleosaurids are advanced over *Thalassiodracon*, however, in possessing a contact of the pterygoids behind the posterior interpterygoid vacuity; this contact is partial in the plesiomorphic species *Rhomaleosaurus megacephalus* and complete in all later rhomaleosaurids. The anterior palate of rhomaleosaurs is like that of *Eurycleidus*, and unlike that of derived pliosaurs, in that the vomers do not extend far posterior to the internal nares. The *Thalassiodracon* material is not sufficiently well preserved to establish the presence or absence of sub-orbital fenestrae (Storrs & Taylor 1997). This feature occurs in some rhomaleosaurids and some pliosaurs. The presence or absence of sub-orbital fenestrae can be difficult to establish because the palatine is very thin and is rarely preserved intact.

In contrast to that of rhomaleosaurids, the palate in pliosaurs is highly derived compared to the plesiomorphic condition in *Thalassiodracon*. The anterior interpterygoid vacuity is closed in the intermediate form *Macroplata*. The vomers extend posterior to the internal nares and meet the pterygoids in a wide, interdigitating suture in *Macroplata*, as well as in *Hauffiosaurus* and all more derived pliosaurs. The quadrate flange of the pterygoid is wide, sigmoid in shape, and possesses a ridged lateral margin in

Kronosaurus, *Peloneustes*, *Liopleurodon*, *Pliosaurus*, and *Brachauchenius*. The pliosaurids *Macroplata* and *Hauffiosaurus* are plesiomorphic for this character; however, *Attenborosaurus* is derived, possessing the ridged lateral margin and sigmoid shape of the quadrate pterygoid flange. *Attenborosaurus* is intermediate for another synapomorphy of derived pliosaurids, namely the elaboration of lateral flanges of the pterygoid on either side of the posterior interpterygoid vacuities. These flanges are present in *Kronosaurus* and all more derived pliosaurids, although they fuse over the posterior end of the interpterygoid vacuity in *Liopleurodon* and more derived forms. The elaboration of these flanges gives the posterior palate a distinct two-tiered morphology in lateral view, with the lateral flanges, ventral braincase structures, and interpterygoid vacuity on a more ventral level and the quadrate pterygoid flanges reaching dorsally and caudally back toward the quadrates on a more dorsal level. The polycotylids show no trace of this condition; the palate in this group is very similar to the cryptocleidoid pattern, as observed by Carpenter (1997).

The mandible

The plesiosaurian mandible has been a source of confusion for many years. The presence of the coronoid and prearticular bones has been debated; Andrews illustrates both bones as absent in *Muraenosaurus* (1910) and the prearticular as absent in *Peloneustes* (1913). Cruickshank (1994b) states that absence of the coronoid is typical of plesiosauroids, and that the prearticular is usually absent as well. Storrs and Taylor (1996) illustrate a prearticular but no coronoid in *Thalassiodracon*, while Taylor (1992b) illustrates both bones as present in *Rhomaleosaurus*. I believe the prearticular is present in all taxa with adequately preserved material. The coronoid is present in all taxa but *Kimmerosaurus*. The morphology of the lower jaw in plesiosauroids is illustrated here by *Libonectes* (Fig. 15) and *Dolichorhynchops* (Fig. 19), and that of pliosauroids by *Peloneustes* (Fig. 12). The lingual surface of the lower jaw is poorly ossified in plesiosaurs and the Meckelian canal is often

open for some of its length. The bones covering the Meckelian canal (splenial, coronoid, and prearticular) are very thin and often damaged or lost in fossils, which may account for the confusion concerning the two smaller bones.

The lower jaw symphysis was taken as an important taxonomic character by Tarlo (1960) and later workers. The simple, unexpanded symphysis present in most plesiosauroids is in fact derived over the primitive condition exemplified by *Thalassiodracon* (Storrs & Taylor 1996) or the outgroup taxon *Cymatosaurus* (Rieppel 1997b). In these taxa the symphysis is reinforced and scoop-like (Rieppel 1997b, character 51), and the presence of a scoop-like symphysis in *Rhomaleosaurus* and related taxa is plesiomorphic. The snout and lower jaw symphysis becomes very elongate in the most primitive members of the Pliosauridae and remains a stereotyped feature of that family. The length of the symphysis does vary within this group, remaining very long in *Peloneustes* and reverting to scoop-like in *Liopleurodon*, *Pliosaurus*, and related taxa. A long lower jaw symphysis is also present in all members of the Polycotylidae, where a long snout evolved convergently.

The braincase

The morphology of the braincase is known to varying degrees in different plesiosaur subclades. In the elasmosaurids and rhomaleosaurids very little is known, because a broad suture of the pterygoids between the posterior and anterior interpterygoid vacuities obscures most of the anterior braincase in ventral view (although see Carpenter, 1997, for comments on the more dorsal elements of the elasmosaur braincase). More is known concerning the cryptocleidoids and pliosaurids, in which the posterior interpterygoid vacuities are larger and open farther anteriorly. In addition, the brain case is not as tightly integrated into the skull roof in the later taxon, so that the elements are more often preserved in a visible manner.

The braincases of *Plesiosaurus* and *Thalassiodracon* are similar, and are very primitive when observed in ventral view. The occipital condyle is hemispherical in *Plesiosaurus* and set

off from the body of the basioccipital by a groove, while in *Thalassiodracon* the condyle is less rounded with no groove (Storrs and Taylor 1996, Storrs 1997). These condyle morphologies are characteristic of later plesiosauroids and pliosauroids, respectively. The occipital condyle may have a notochordal pit; the pit is more obvious in material from younger animals, and there is intraspecific variation in its presence. The body of the basioccipital is a short, robust block of bone, with paired articulations on its dorsal surface for the exoccipitals (see Brown 1981; Fig. 1). The basioccipital produces two prominent basioccipital tubers projecting antero-ventrally that articulate with the pterygoids. The exoccipitals are columnar bones rising dorsally on either side of the foramen magnum, and giving rise laterally to slender paraoccipital processes that trend laterally to articulate with the squamosals. The occiput is therefore open, and the suture between exoccipital and opisthotic is seldom visible (Storrs and Taylor 1996). The medial surface of each exoccipital is pierced by the jugular foramen and by one or two foramina for the passage of the hypoglossal nerve (Storrs and Taylor 1996, Carpenter 1997).

In *Plesiosaurus* and *Thalassiodracon*, the basioccipital tubers also articulate on their anterior margins with lateral processes of the parasphenoid. These lateral parasphenoid processes are termed cristae ventrolaterales following Reisz (1981: p. 24). The possession of the cristae ventrolaterales is a plesiomorphic condition found in *Petrolacosaurus* (Reisz 1981) and *Araeoscelis* (Vaughn 1955). In these plesiomorphic taxa, the cristae ventrolaterales are two crests of bone surrounding a deep basisphenoid fossa on the midline, with the posterior margin of the basisphenoid visible in the floor of this fossa. The condition in basal plesiosaurs is similar, except the basisphenoid fossa has been filled with a disc of basisphenoid confluent with the ventral plane of the cristae ventrolaterales. In *Petrolacosaurus* and *Araeoscelis*, the body of the parasphenoid runs forward into a long, narrow cultriform process. *Plesiosaurus* has a similar cultriform process. The condition in *Thalassiodracon* is unknown due to that taxon's possession of a median pterygoid suture between the posterior and anterior interpterygoid vacuities. Ventral to the

parasphenoid in the region of origin of the cultriform process is the dorsum sellae and the body of the basisphenoid (the clivus) just posterior to it, a shelf of bone which ossifies just posterior to the sella turcica (Romer 1956). In both *Plesiosaurus* and *Thalassiodracon* the basisphenoid is well ossified, and the basal articulations arising laterally from it are prominent. Like *Araeoscelis*, *Thalassiodracon* possesses foramina in the ventral surface of the basisphenoid for the passage of the paired internal carotid arteries. The presence or absence of these foramina was impossible to establish in *Plesiosaurus*. These foramina are not ossified in *Euryycleidus*, and the basisphenoid facet of the basal articulation was impossible to identify as a distinct feature (Cruickshank 1994b). These observations probably arise from the fact that the *Euryycleidus* braincase material is from a juvenile, and so is not well-ossified. However, lack of ossification of the basisphenoid is also characteristic of later pliosauroids, so the condition in *Euryycleidus* may foreshadow this to some degree. All plesiosaurs share a lack of ossification of the lateral walls of the braincase. The area of origination of the pila antotica from the dorsal surface of the basisphenoid is therefore impossible to identify.

Two major changes to the plesiomorphic pattern of the plesiosaur braincase can be identified in more derived groups. In the cryptocleoids the palate remains open and the skull roof is gracile, while the braincase is well-ossified. The cristae ventrolaterales disappear and the parasphenoid loses the characteristic triangular shape present in *Araeoscelis* and *Plesiosaurus*. The parasphenoid becomes a massive, block-like medial structure extending caudally almost to the basioccipital in more primitive cryptocleoids, and forming a novel median suture with the basioccipital in more derived taxa (see Fig. 21). The cultriform process is also lost; the anterior margin of the parasphenoid becomes broad and blunt and develops novel articulations with the pterygoids on its antero-lateral edges. In contrast to the parasphenoid, the basisphenoid in this group is conservative. Facets for the basal articulation are well-defined, and the internal carotid foramina pierce the body of the basisphenoid ventro-laterally and run into the floor of the sella turcica.

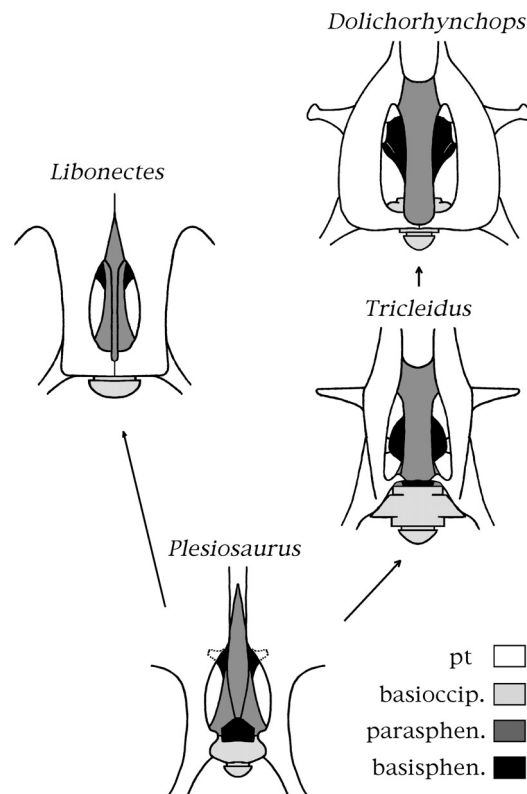


Fig. 21. Schematic transformation series of the basicranium and posterior palate, Plesiosauroidea. Homologous bones are indicated in shades of gray. The plesiomorphic condition for this clade is demonstrated by *Plesiosaurus*. The palate is broadly open, and the pterygoids lack a median suture between both the anterior and posterior interpterygoid vacuities, and beneath the basioccipital. The parasphenoid is exposed medially along its entire length, the cultriform process is wide and prominent, and is confluent with a ventral eminence or ridge running posterior to the exposed basisphenoid on the midline. The basisphenoid is visible in ventral view in two areas: anteriorly the processes comprising the basal articulation are visible in the anterior of the posterior interpterygoid vacuities, while posteriorly an island of basisphenoid is exposed between parasphenoid and basioccipital. In elasmosaurs, here represented by *Libonectes*, this pattern is modified by the formation of a median pterygoid suture over the basioccipital and basisphenoid. The anterior interpterygoid vacuity is also closed. In *Tricleidus*, however, the anterior interpterygoid vacuity stays open and the cultriform process loses its pointed anterior end, instead developing prominent later sutures with the pterygoids. The ventral eminence of the parasphenoid reaches almost to the basioccipital, and is broad along its entire length. Each pterygoid develops a novel process reaching medially to the ventral eminence of the parasphenoid. The basal articulation is well-developed, and the ectopterygoid reaches dorsally to the ventral surface of the postorbital bar. The situation in *Dolichorhynchops* is very similar, except that the medial processes of the pterygoids meet in a suture ventral to the basioccipital. Additionally, the ventral eminence of the parasphenoid reaches far to the posterior, overriding the basioccipital and the median suture of the pterygoids.

In derived pliosaurids, the skull roof and pterygoids are massive and well-ossified, whereas the braincase is poorly ossified. In pliosaurids such as *Peloneustes*, the anterior margin of the parasphenoid articulates tightly with the pterygoids at the anterior margin of the posterior

interpterygoid vacuities. From this articulation the parasphenoid runs caudally, expanding into the plesiomorphic triangular shape. However, the parasphenoid ends after a short distance, articulating with the basisphenoid on the midline. The cristae ventrolaterales are again absent.

The basisphenoid is usually preserved as a rugose and unremarkable barrel of bone between the parasphenoid and the basioccipital. In life the basisphenoid was completely encased in cartilage, and the dorsum sellae and sella turcica usually failed to ossify. One extremely well-preserved skull of *Peloneustes* (BMNH 3803) does preserve a poorly ossified basisphenoid. Enough morphology is visible on this specimen to establish that the basal articulation is present in the plesiomorphic location, and the pterygoid facet of the basal articulation is usually identifiable in skulls of *Peloneustes*. Foramina for the internal carotids were not preserved in this specimen. In conclusion, the braincase in pliosauroidea is a poorly ossified structure showing few morphological details in most specimens; well-preserved specimens seem to demonstrate that the cartilaginous elements of the braincase retained the plesiomorphic pattern seen in *Thalassiodracon*. Trends in basicranium evolution are illustrated in two summary figures (Figs. 21 and 22).

Trends in postcranial evolution

The most remarkable aspect of plesiosaur postcranial evolution is the convergent attainment of body morphotypes. The 'pliosauroform' body type, characterized by a relatively large head, short neck, relatively long coracoids and ischia, and low aspect-ratio paddles, evolves in three plesiosaur clades (Rhomaleosauridae, Pliosauridae, Polycotylidae; for analysis and discussion see O'Keefe 2002). This striking convergence is responsible for the polyphyly of the Pliosauroidae as traditionally defined, because characters of body overall body proportion were the basis of traditional taxonomy (e.g. Persson 1963). This analysis strongly rejects the traditional hypothesis that all pliosauroform taxa form a monophyletic group. In addition, the long neck thought to be characteristic of elasmosaurs exclusively also evolved in the cryptoclidid *Muraenosaurus* (contra Andrews 1910, Persson 1963).

Several specific trends in the limb girdles and limbs also deserve mention. Stratigraphically early and plesiomorphic plesiosaurs, including *Thalassiodracon* and *Plesiosaurus*, retain a distinct bend or angle in the shaft of the humerus

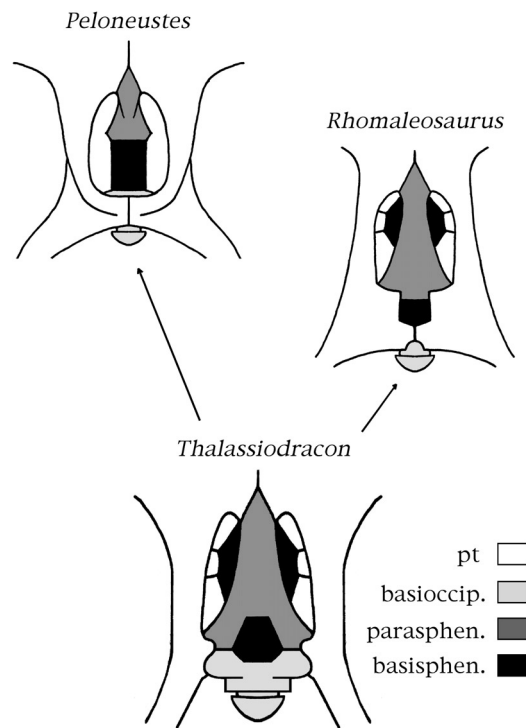


Fig. 22. Schematic transformation series of the basicranium and posterior palate, Pliosauroidae. Homologous bones are indicated in shades of gray. The plesiomorphic condition for this clade (and probably for plesiosaurs in general) is demonstrated here by *Thalassiodracon*. The pattern in this taxon is very similar to that described for *Plesiosaurus* in Fig. 21, except that the pterygoids meet in a median suture anterior to the posterior interpterygoid vacuities, and the parasphenoid is sutured to the pterygoids on the midline. The cultriform process is not visible in ventral view. The anterior interpterygoid vacuity is present but not illustrated here; it is visible in Fig. 4. The pattern in *Rhomaleosaurus* is very similar to *Thalassiodracon*, the only difference being a median suture of the pterygoids over the basioccipital and basisphenoid (partial in *R. megacephalus*, complete in most other rhomaleosaurs). By contrast the palate is very derived in true pliosaurs, here represented by *Peloneustes*. The parasphenoid is not ossified around the basisphenoid as in other plesiosaurs, although given that the parasphenoid is dermal bone it is doubtful that it persisted in cartilage. The basisphenoid is very poorly ossified, and the basal articulation was cartilaginous. The pterygoids form ventral flanges lateral to the posterior interpterygoid vacuities that curve medially and meet beneath the basioccipital. The quadrate flanges of the pterygoids are prominent, sigmoid processes which override the lateral flanges of the pterygoids.

(Storrs 1997). All 'nothosaur'-grade sauropterygians also have this bend (Rieppel 1997b), while the shaft of the humerus is straight in all more derived plesiosaurs (Storrs 1997). Correlated with this transition is the loss of the 'lunate ulna' in more derived plesiosaurs; plesiomorphic plesiosaurs have epipodials that, while short, are very similar to those in 'nothosaur'-grade sauropterygians, and recognizable as radius, ulna, tibia, and fibula (Storrs 1997). In more derived plesiosaurs these bones become unidentifiable on the basis of morphology, being simple ossified disks integrated into the other ossifications of the flipper (Storrs 1993, Caldwell 1997a, 1997b). The functional significance of these transitions has yet to be investigated. A last character of note is the presence of a median symphysis of the scapulae. All plesiosauroids were thought to have this symphysis (Persson 1963); however, the placing of the Polycotylidae within the Plesiosauroidea demonstrates that this character is reversed in the polycotylids. This placement may also explain the similarities in the humeri of *Polycotylus* and *Colymbosaurus*, although revision of the later taxon is necessary. A character of unknown significance is the scalloped margin of the vertebral centra in many cryptocleidoids; this may be a synapomorphy of this clade but further research is necessary. If present, however, the character would form another link between the Polycotylidae and the Cimoliasauridae. The Cimoliasauridae certainly deserve further research effort, both on known material and through field work.

Conclusions

1. The Plesiosauria is a monophyletic clade of sauropterygians most closely related to the Pistosauridae.
2. The Plesiosauria is composed of various stem taxa and four major derived clades. These clades are the Rhomaleosauridae and Pliosauridae within the Pliosauroida, and the Cryptocleidoidea and Elasmosauridae within the Plesiosauroidea.
3. The Polycotylidae is not a member of the Pliosauroida, and is instead a derived group of cryptocleidoids.
4. Morphometric characters relating to body proportions are very homoplastic in the Plesiosauria, and the pliosauromorph body type evolved three times.
5. Nasals are present in all members of the Pliosauroida.
6. The plesiosaur braincase is very primitive, comparable to that of primitive diapsids such as *Araeoscelis*.

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Appendix 1. Characters, state definitions, references, and comments for the cladistic characters used in this paper. For discussion see text.

Char. type	Character	States/Coding	Citation	Remarks
1 Morphometric	Relative skull length	Primitive/ 'nothosaurian' (0), large (1), small (2)	Brown 1981, char. 2	Scored from morphometric data in O'Keefe 2000: chapter 3. <i>Thalassiodracon</i> is primitive for this character, as are most rhomaleosaurids.
2 Morphometric	Relative neck length	Primitive (0), long (1), short (2)	Storrs 1991, char. 2	Scored from morphometric data in O'Keefe 2000: chapter 3.
3 Morphometric	Relative length of ischium/pubis	Subequal (0), ischium longer (1), pubis longer (2)	Brown 1981, char. 29	Scored from morphometric data in O'Keefe 2000: chapter 3.
4 Morphometric	Relative length of scapula/coracoid	Subequal (0), coracoid longer, (1)	Welles 1962	Scored from morphometric data in O'Keefe 2000: chapter 3; derived elasmosaurs are the only plesiosaurs in which this ratio is subequal.
5 Morphometric	Relative length of humerus/femur	Subequal (0), humerus longer (1), femur longer (2)	Brown 1981, char. 32	Scored from morphometric data in O'Keefe 2000: chapter 3.
6 Morphometric	Preorbital and postorbital skull length	Subequal (0), longer preorbital (1), shorter (2)	Rieppel 1994a, 1997b, chars. 9, 12	This ratio is controlled by the length of the snout relative to the temporal fenestra and suspensorium.
7 Morphometric	Fin aspect ratio	High (0), low (1)		Scored from morphometric data in O'Keefe 2000: chapter 3; the two states are based on a break in the distribution of aspect ratio data.
8 Skull shape	Elongate rostrum	Absent (0), premaxilla only (1), very long with maxilla included (2), elongate and hoop-like/unconstricted (3)	Partially modified from Tarlo 1960	State one is defined as a long snout with little or no increase in snout length posterior to premaxilla/maxilla suture. State two includes lengthening of maxilla; state three describes the large, unconstricted snouts of <i>Kimmerosaurus</i> and related taxa. This character is ordered, using the character state tree (0)(3)(1,2), Figs. 7, 2 and 11.
9 Skull shape	Constricted snout	Unconstricted (0), constricted at maxilla/premaxilla suture(1), second constriction in maxilla (2)	Rieppel 1994a, 1997b, Storrs 1991, chars. 3, 13	Constriction at the premaxilla/maxilla suture is common in long-snouted sauropterygians. State two describes the condition of <i>Lipoleurodon</i> , which has a second, more posterior constriction (Andrews 1913). This character is ordered because the second constriction never occurs in the absence of the first. Fig. 11.

Continued

Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
10	Skull shape	Temporal emargination Present (0), absent(1)	Storrs 1991, char. 6	<i>Araucoscelis</i> has a straight skull margin below the temporal fenestra; most sauropterygians have an emargination here. The condition in plesiosaurs is difficult to determine, as the variation is continuous; my criterion for the presence of emargination is an excavated ventro-lateral embayment of the squamosal. By this criterion most plesiosaurs have temporal emargination. Fig. 14.
11	Skull roof	Dorso-medial process of premaxilla Contacts frontal (0), contacts parietal at pineal foramen(2), contacts anterior extension of the parietal (1)	Andrews 1911b	The premaxillae send dorso-medial processes posteriorly across the skull roof in most plesiosauriform taxa and some elasmosaurs, and these processes may meet the parietals in various ways. While these processes separate the frontals on the dorsal midline, the frontals may retain a midline suture beneath the premaxillae (Andrews 1911b). Figs. 5 and 10.
12	Skull roof	Premaxilla/external naris contact Present (0), absent (1)		Contact of the premaxilla with the external naris is primitive, occurring in <i>Araucoscelis</i> . This contact is lost in some plesiosaurs. Fig. 10.
13	Skull roof	Dorsal median foramen Absent (0), present (1)	Cruikshank 1997	A shallow depression occurs in the dorso-medial processes of the premaxillae in some rhomaleosaurids.
14	Skull roof	Frontals paired/fused in adult Paired (0), fused (1)	Rieppel 1994a, 1997b, chars. 11, 14	Fusion of the frontals on the skull roof can only be scored for taxa in which the frontal midline suture is visible; this character is therefore inapplicable for taxa in which the dorso-medial processes of the premaxillae reach the parietals.
15	Skull roof	Parietals paired or fused in adult Paired (0), fused posteriorly (1), fused (2)	Rieppel 1997b, char. 17	Fusion of the parietals on the dorsal midline is an important character in basal 'nothosaurs'; however this character is difficult to score in taxa where the parietal skull table is a narrow sagittal crest, which is vulnerable to breakage. I have therefore scored this character as inapplicable for plesiosaurs.

16	Skull roof	Frontal with or without distinct postero-lateral process	Without processes (0), with processes (1)	Rieppel 1994a, 1997b, chrs. 12, 15; Storrs 1991 char. 30	A distinct postero-lateral process of the frontal occurs in the plesiosauids <i>Cymatosaurus</i> and <i>Pistosaurus</i> . It also occurs in very primitive plesiosaurs such as <i>Thalassiodracon</i> and <i>Plesiosaurus</i> . Fig. 4.
17	Skull roof	Postorbital bar	Both po and pof have orbital contact (0), frontal/po suture excludes pof from orbit margin (1)		In some elasmosaurs, the postfrontal is confined to the inside of the temporal fenestra and excluded from the orbit by a frontal-postorbital suture.
18	Skull roof	Frontal enters margin of temporal fenestra	Does not (0), does narrowly (1)	Rieppel 1994a, 1997b, chrs. 13, 16	
19	Skull roof	Frontal contacts external naris	Does contact (0), does not contact (1)		The frontal contacts the external naris in some plesiosaurs. Fig. 10.
20	Skull roof	Pineal foramen location	Middle of parietal (0), anterior (1)	Rieppel 1994a, 1997b, chrs. 15, 18, also Sues 1987	The movement of the pineal foramen to the anterior of the parietal skull table is a character shared by the plesiosauids and plesiosaurs. Some workers (Welles 1962, Carpenter 1996) contend that the pineal foramen is lost in some taxa; It is present in all taxa I have examined. Figs. 4 and 5.
21	Skull roof	Pineal foramen bordered anteriorly by frontals on dorsal skull surface	Not bordered by frontal (0), bordered by frontal (1)	Andrews 1911b	In <i>Peilonautes</i> (and possibly other plesiosaurs known from inferior material), the frontals form part of the anterior margin of the pineal foramen, but only beneath the premaxillae. Taxa were scored as derived for this character only if the frontal formed part of the margin on the dorsal skull roof, as is the case in some elasmosaurs and cryptoclidids, but not in plesiosaurs.
22	Skull roof	Prefrontal present or absent	Present (0), absent (1)		
23	Skull roof	Accessory fenestra above orbits	Absent (0), present (1)	Carpenter 1996	Carpenter described this feature in the polycotylids <i>Dolichorynchops</i> and <i>Trinacromerum</i> ; I was unable to confirm its presence in either taxon. The orbital region in polycotylids is delicate and liable to breakage.
24	Skull roof	Frontal process projects into orbit	Absent (0), present (1)	Carpenter 1996	Carpenter described this feature in the polycotylids <i>Dolichorynchops</i> and <i>Trinacromerum</i> ; It is present in both taxa although preservation of the feature is poor due to the delicate nature of the bones in the orbit region.

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Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
25	Skull roof Parietal skull table	Relatively broad (0), constricted (1), sagittal crest (2)	Rieppel 1994a, 1997b, chars. 16, 19; Brown 1981, char. 9	Possession of a sharply keeled sagittal crest is a feature shared by all plesiosaurs and <i>Pistosaurus</i> . The sagittal crest is the culmination of a trend of skull table narrowing in the pistosauroids. Figs. 14 and 18.
26	Skull roof Squamosal produces long, thin process covering quadrate laterally	No medial process (0), medial process and socket-like squamosal (1)		The suture of the quadrate with the squamosal is prominent and robust in all plesiosaurs. In some plesiosaurs the squamosal has descending lateral and medial processes on either side of the quadrate in occipital view, forming a socket that accepts the quadrate. In some plesiosauroids the lateral process is much longer than the medial process, the lateral process reaches almost to the jaw articulation, and the suture is less socket-like. The polycotyliids possess the second type of suture.
27	Skull roof Squamosal dorsal processes	No suture (0), meet in arch at midline (1)	Sues 1987, Rieppel 1997b, char. 36	An occipital arch formed by a median squamosal suture is characteristic of all plesiosaurs and <i>Pistosaurus</i> . <i>Cymatosaurus</i> is intermediate in having a very narrow separation of the squamosals in occipital view (see Rieppel 1998b). Figs. 5 and 10.
28	Skull roof Squamosal/postorbital contact	Contact (0), no contact (1)		The squamosal often contacts the postorbital within the temporal fenestra on the rear of the postorbital bar; however, this character concerns only the margin of the temporal fenestra in lateral view. Contact of the two bones excludes the jugal from the margin of the temporal fenestra. Fig. 14.
29	Skull roof Jugal/squamosal contact	No contact (0), contact (1)		Contact of the jugal and squamosal is characteristic of all plesiosaurs and <i>Cymatosaurus</i> . Fig. 14.
30	Skull roof Jugal extends anteriorly along ventral orbital margin	Anterior margin (0), middle of orbit (1), restricted to posterior margin (2)	Rieppel 1994a, 1997b, chars. 20, 23; Storrs 1991, char. 24; Cruickshank 1994b, char. 2	Figs. 4, 5 and 10.
31	Skull roof Jugal contacts orbit margin	Contacts orbit (0), excluded by po/m contact (1)	Modified from Storrs 1991, char. 24	

32	Skull roof	Jugal/prefrontal suture anterior to orbit	Absent (0), present (1)	Many plesiosaurs have a suture between the prefrontal and jugal anterior to the orbit, excluding the maxilla from the orbit margin. The jugal extends forward and medially around the orbit to meet the prefrontal. The presence of the jugal in this position has been interpreted as a lacrima by Andrews (1913), and Taylor and Cruickshank (1993); however the lacrima is lost in basal sauropterygians. Fig. 10.
33	Skull roof	Jugal forms narrow bar between orbit and temporal emargination	Does not (0), does (1)	As reconstructed by Brown and Cruickshank (1994), and Brown (1981), the cheek region in cryptocleidids is reduced, so that the jugal is the sole element between the temporal emargination and the orbit. This area is very fragile and generally not preserved in the cryptocleidids. The apomorphic condition of the cheek in polycolytids is very similar to this condition. Fig. 18.
34	Skull roof	Quadratojugal	Present (0), absent (1)	Cruickshank 1994b, char. 2 Rieppel 1994a, 1997b, chars. 24, 29; Storrs 1991, char. 7; Sues 1987
35	Skull roof	Nasal	Not reduced (0), reduced (1), absent (2)	Storrs (1991) believed the nasal lost in all plesiosaurs; however it is small but present in <i>Peloneustes</i> and other plesiosaurs, as well as <i>Thalassiodracon</i> . Figs. 4 and 10.
36	Skull roof	Location of nasal relative to external naris	Behind external naris (0), in front of external naris (1)	This character is applicable only to taxa in which the nasals are present. The derived state occurs in stratigraphically late plesiosaurs such as <i>Brachauchenius</i> .
37	Skull roof	Distinct grooves anterior to external naris	Absent (0), present (1)	Distinct grooves in the maxillae anterior to and leading into the external naris are present in some rhomaleosaurids and <i>Macropelta</i> .
38	Skull roof	Nasal enters margin of external naris	Do enter (0), do not enter (1)	The nasals are reduced and do not enter the external naris in <i>Pistosaurus</i> , and there is some question whether the nasals are present in this taxon at all (Rieppel 1994a). When present, the nasals do enter the margin of the external naris in plesiosaurs. Figs. 4 and 10.

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Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
39	Skull roof Prefrontal contacts margin of external naris	No contact (0), contact (1)		The prefrontal runs from the anterior margin of the orbit to the posterior margin of the external naris in <i>Plesiosaurus</i> , elasmosaurids, cryptocleidids, and the polycotylids. Figs. 5 and 18.
40	Skull roof Prefrontal and postfrontal exclude frontal from dorsal orbit margin	Frontal excluded (0), frontal enters margin (1)	Rieppel 1997b, char. 10	Fig 10.
41	Skull roof Maxilla/squamosal contact	No contact (0), contact (1), expanded posterior flange (2)	Williston 1903, p. 19	This character describes the contact, or lack of contact, between the posterior end of the maxilla and the squamosal. State two describes the condition in polycotylids, in which the maxilla forms a stout, expanded contact with the squamosal.
42	Occiput Exoccipital participates in formation of occipital condyle	Do not participate (0), do participate (1)	Brown 1981, char. 7; Cruikshank 1994b	
43	Occiput Occipital condyle morphology	Hemispherical with groove (0), short with no groove (1)	Brown 1981, char. 12	Brown (1981) stresses the presence of a groove between the occipital condyle and the body of the basioccipital in his definition of this character. The groove is variably present and probably varies ontogenetically; I have found the shape of the condyle to be more reliable in defining states. Fig. 11.
44	Occiput Paraoccipital process/ formation of posttemporal fossa margin	No process/ occiput plate-like (0), rod-shaped process (1)	Rieppel 1997b, char. 31	A plate-like occiput is present in most basal sauropterygians; however, an open occiput with a rod-shaped paraoccipital process occurs in the pistosauroids and all plesiosaurs.
45	Occiput Distinct squamosal notch for articulation of paraoccipital process	Without notch (0), with notch (1)	Rieppel 1997b, char. 32	
46	Occiput Paraoccipital process morphology	Gracile (0), robust (1)	Brown 1981, char. 11	Modified from Brown (1981). My 'gracile' is a combination of Brown's 'long' and 'thin' states, while my 'robust' is a combination of his 'short' and 'thick' states. The paraoccipital process is robust in true plesiosaurs.

47	Occiput	Paraoccipital process articulation	Squamosal exclusively (0), quadrate exclusively (1), both quadrate and squamosal (2)		<i>Libonectes</i> has state two, while the articulation of the paraoccipital process shifts to the quadrate in some cryptocyloids and all polyotyloids.
48	Occiput	Ventral extent of paraoccipital process	Does not extend ventral to occipital condyle (0), extends past condyle (1)	Andrews 1910	<i>Tricleidus</i> and the polyotyloids have long paraoccipital processes which extend ventral of the occipital condyle.
49	Occiput	Nature of paraoccipital process/quadrate pterygoid flange contact	No contact (0), contact at lateral articulation only (1), long contact along bodies of processes (2)		Taylor and Cruickshank (1993) and Taylor (1992a) illustrate the occiput of <i>Pliosaurus</i> and <i>Rhomaleosaurus</i> respectively, depicting a long contact (state two) between the paraoccipital process and the quadrate flange of the pterygoid in both taxa. I did not observe this condition; these taxa possess state one, as illustrated by Cruickshank (1994a).
50	Occiput	Quadrate flange of pterygoid/quadrate articulation	Quadrate only (0), quadrate and squamosal (1)	Modified from Brown 1981, char. 10; Cruickshank 1994b, char. 3	The squamosal shares in the quadrate articulation of the quadrate flange of the pterygoid in some elasmosaurs and some pliosaurs.
51	Occiput	Quadrate produces distinct process for articulation with pterygoid flange	Process absent (0), process present (1)		
52	Braincase	Dorsal wing of epipterygoid	Broad/columnar (0), reduced (1)	Rieppel 1997b, char. 39	
53	Braincase	Epipterygoid dorsal process contacts parietal	Contact (0), no contact (1)	Zanon unpublished	
54	Occiput	Quadrate embayed/dished-shaped anteriorly	Massive quadrate (0), dished anteriorly (1)		Most plesiosaurs have a dished or embayed anterior margin of the quadrate above the jaw articulation. This embayment is lost in some elasmosaurs.
55	Skull roof	Posterior bulb formed by squamosals	Absent (0), present (1)		The apex of the squamosal arch is elaborated into a posteriorly-directed bulb in most pliosaurs. Fig. 10.

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Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
56	Braincase Supraoccipital morphology	Round (0), median process (1)	Zanon unpublished	The supraoccipital has a median process projecting ventrally into the foramen magnum in most plesiosaurs. Some taxa lack this feature, although it is also delicate and liable to breakage. The supraoccipital in general is not bound tightly to the rest of the skull and is often lost, at least in Lower Jurassic taxa. Fig. 5.
57	Palate Shape of the quadrate pterygoid flange	Curved with raised lateral margin (0), straight and narrowing (1), sigmoid with rolled lateral margin (2)		The quadrate flange of the pterygoid is a large, sigmoid structure in many plesiosaurs. This condition is derived compared to <i>Thalassiodraco</i> . <i>Attenborosaurus</i> displays a fairly intermediate condition. Fig. 11.
58	Palate Squared lappet of pterygoid underlies quadrate pterygoid flange	No squared lappet (0), squared lappet (1)		This character describes the elaboration of a small flange or lappet from the body of the pterygoid, which underlies the quadrate flange of the pterygoid at its origination from the palatal portion of that bone.
59	Braincase Supraoccipital depth/sigmoid suture	Shallow (0), deep antero-posteriorly/sigmoid suture with exoccipital and prootic (1)		The supraoccipital in <i>Plesiosaurus</i> and other primitive taxa is shallow antero-posteriorly; the suture with the exoccipital is short and the lateral contact with the prootic is small. In other plesiosaurs the supraoccipital tends to become deeper, and the suture with the exoccipital and prootic becomes longer, more lateral, and sigmoid in shape. The space for the vertical semicircular canal is usually larger and deeper in the second type of supraoccipital. Fig. 6.
60	Palate Anterior interpterygoid vacuity	Absent (0), slit-like (1), broad with round ends (2)		The presence of an anterior interpterygoid vacuity is a reversal with respect to more basal sauropterygians, which have a closed palate. Figs. 4, 5, etc.
61	Palate Posterior interpterygoid vacuity	Absent (0), present (1)	Storrs 1991, char. 11; Sues 1987	The presence of a posterior interpterygoid vacuity is a reversal with respect to more basal sauropterygians, which have a closed palate. Present in all plesiosaurs and <i>Pistosaurus</i> . Figs. 6, 7, 8, etc.

62	Palate	Pterygoids meet posterior to posterior interpterygoid vacuity	Pterygoids do not meet (0), pterygoids meet (1), meet but are covered by posterior parasphenoid process (2)	Williston 1908 illustrates state two	In <i>Pistosaurus</i> and some Lower Jurassic plesiosaurs the pterygoids do not meet on the midline of the palate surface behind the posterior interpterygoid vacuity. Most later plesiosaurs have distinct pterygoid processes which meet on the midline behind the vacuity. This character is ordered because state two is dependent on the possession of state one. Figs. 6, 11 and 17.
63	Palate	Pterygoids meet between anterior and posterior interpterygoid vacuities	Do not meet between vacuities (0), do meet between vacuities (1)		In plesiosaurs possessing both anterior and posterior interpterygoid vacuities, the pterygoids may or may not meet between the two vacuities. In taxa in which the pterygoids do not meet, the two vacuities are separated by the cultriform process of the parasphenoid. Figs. 4, 6, 7, etc.
64	Palate	Basioccipital exposed posterior to posterior pterygoid suture	Exposed (0), not exposed (1)		This character is conditional on the presence of a derived state for character 62. The medial processes of the pterygoid forming the medial symphysis behind the posterior interpterygoid vacuity either completely cover the body of the basioccipital, or fail to cover it. Figs. 7 and 8.
65	Palate	Ectoptyergoid reaches medially to lateral margin of posterior interpterygoid vacuities	Does not (0), does (1)		In <i>Peloneustes</i> , the ectoptyergoid extends medially to near the lateral margin of the posterior interpterygoid vacuity, overlapping the pterygoid. Fig. 11.
66	Palate	Columnar ectoptyergoid contacts postorbital bar	No contact (0), contact (1)	Illustrated by Carpenter, 1997	The ectoptyergoid in many plesiosauroid taxa rises dorsally out of the plane of the palate, and contacts the ventro-medial margin of the postorbital bar. This character is shared by elasmosaurs, cryptocleidids, and polycotylids. Figs. 16 and 17.
67	palate	Dished pterygoids	Absent (0), present (1)		In polycotylids, the pterygoids antero-lateral and lateral to the posterior interpterygoid vacuities are broadly dished or depressed shallowly along their length. This character was observed in <i>Dolichorhynchops</i> , <i>Trinacromerum</i> , and MOR 751, and is not a preservational artifact. Fig. 17.

Continued

Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
68	Palate Posterior pterygoid/ parasphenoid contact	Absent (0), present (1)	Illustrated by Andrews, 1910	In <i>Tricleidus</i> and the polycolytids, the pterygoids send out distinct medial processes that contact the posterior margin of the parasphenoid. These processes meet in a median suture in the polycolytids, but I do not believe this condition is homologous to the condition in character 62. Figs. 16 and 17.
69	Palate Ectopterygoid and pterygoid form lateral flanges ventro-lateral to posterior pterygoid vacuity	Do not form flanges (0), form flanges (1), flanges meet in short, dished contact at midline (2), meet in broad contact (3)	State two figured by White 1935	The formation of accessory flanges around the posterior intern pterygoid vacuity is characteristic of almost all pliosaurs exclusive of the rhomaleosaurids. State one occurs in <i>Attenborosaurus</i> . State two occurs in <i>Peloneustes</i> and <i>Kronosaurus</i> ; state three occurs in <i>Liopleurodon</i> , <i>Pliosaurus</i> , and <i>Brachauchenius</i> . Figs. 11 and 13.
70	Braincase Parasphenoid morphology	Long, tapering anteriorly (0), short and blunt(1)	Andrews 1910 p. 81–89; Williston 1903 p.218	The anterior portion of the parasphenoid runs anteriorly in a long, tapering cultriform process in <i>Araucocelis</i> , other primitive diapsids, and <i>Plesiosaurus</i> . In the cryptoclidids and polycolytids, the anterior portion of the parasphenoid terminates in a short, blunt process with prominent lateral articulations for the pterygoids located at either side on the palate surface. Figs. 6, 16, and 17.
71	Palate Parasphenoid keel	Not keeled (0), sharp keel (1), keeled anteriorly (2)		The ventral surface of the parasphenoid, visible through the posterior interpterygoid vacuities, has a sharp keel in various taxa. Carpenter (1997) illustrates state one in Libonectes. <i>Peloneustes</i> and other pliosaurs possess state two. Figs. 7 and 11.
72	Palate Parasphenoid exposure anterior to posterior interpterygoid vacuities	Anterior parasphenoid not exposed on palate surface (0), exposed via extension of posterior interpterygoid vacuities (1) exposed with lateral pterygoid sutures (2)		The anterior portion of the parasphenoid is either exposed on the palate surface or covered by the pterygoids. State one refers to exposure of the parasphenoid below the palate surface due to enlargement of the posterior interpterygoid vacuities; state two refers to exposure on the palate surface, accompanied by lateral sutures with the pterygoids. Figs. 6, 7, 11, and 13.

73	Palate	Possession of cristae ventrolaterales	Present (0), absent (1)	Vaughn 1955, Reisz 1981	As described above, the plesiosaur braincase is primitive in the retention of cristae ventrolaterales of the parasphenoid, at least in Lower Jurassic taxa. The configuration in early plesiosaurs differs from earlier diapsids in that the basisphenoid fossa is replaced by a disc of endochondral bone (basisphenoid) confluent with the medial margins of the cristae ventrolaterales. Fig. 1.
74	Braincase	Parasphenoid/basioccipital contact on midline.	Absent (0), present (1)		Given the configuration described in character 73, the parasphenoid is separated from the basioccipital on the midline by the basisphenoid in early plesiosaurs. In some cryptoclidids and all polycotyliids, the parasphenoid extends backward over this area and contacts the ventro-anterior margin of the basioccipital on the midline. Figs. 16 and 17.
75	Palate	Possession of basal articulation	Present (0), absent (1)		Illustrated for <i>Thalassiodracon</i> in Storrs and Taylor (1994) and present in <i>Plesiosaurus</i> , the basal articulation is present and prominent in all plesiosauroids. The articulation appears absent in most pliosaurs; however, one skull of <i>Peloneustes</i> (BMNH R. 3803) preserves this feature. The basisphenoid and the basal articulation arising from it are very poorly ossified in most pliosauroids; the <i>Peloneustes</i> skull mentioned here is unusual in the preservation of an extremely delicate and poorly ossified basisphenoid in which the articulation is visible. The area of articulation with the dorsal surface of the palate is usually visible, however, in pliosaur material in which the skull roof has been removed. The fact that the character is present in all taxa makes this character uninformative; it is included due to previous confusion about the presence of the basal articulation. Figs. 6, 16, and 17.
76	Palate	Basioccipital tubers reduced	Not reduced (0), reduced/ tuber facets confluent with basisphenoid articulation (1)		Andrews (1910) illustrates the basioccipital in <i>Tricleidus</i> ; in this taxon and in the polycotyliids, the basioccipital tubers are reduced, and their pterygoid articular facets are confluent with the median basisphenoid articulation. Fig. 16.

Continued

Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
77 Palate	Jugal has small exposure on palate surface	No exposure (0), exposure (1)		In <i>Peloneustes</i> and some other pliosaurs, the jugal has a small exposure on the palate surface between the maxilla and squamosal.
78 Palate	Lateral palatal fenestration bordered by palatine and pterygoid	Absent (0), present (1)		Some pliosaurs have small fenestra in the palate, formed by the lack of a suture between the pterygoid and palatine near the posterior margin of the palatine. Figs. 7 and 8.
79 Palate	Palatine/ internal naris	Palatine enters internal naris border (0), excluded by vomer/maxilla contact (1)		The palatine is excluded from the internal naris by a suture between the vomer and maxilla in <i>Liopleurodon</i> and <i>Pliosaurus</i> .
80 Palate	Palatines approach closely or meet at midline	Do not meet (0), close approach or meet at midline (1)	Williston 1903, 1910	Fig. 13.
81 Palate	Premaxilla/ anterior border of internal naris	Premaxilla enters anterior border (0), is excluded by vomer/ maxilla contact (1)	Rieppel 1994a, 1997b, chars. 35, 45	
82 Palate	Sub-orbital fenestration	Absent (0), present (1)	Storrs 1991, char. 9	Sub-orbital fenestra are present in many pliosaurs. Figs. 8 and 13.
83 Palate	Vomers extend far posterior to internal nares on midline	Do not (0), extend posterior and meet pterygoids in wide interdigitating suture (1)		Figs. 9, 2, 11, etc.
84 Palate	Prominent 'pterygoid flange/ ectopterygoid boss	Absent (0), present (1)	Rieppel 1994a, 1997b, chars. 35, 44; Storrs 1997	As discussed by Storrs (1997), the 'pterygoid flange' present in some pliosaurs is not a true pterygoid flange, because it is comprised almost entirely by the ectopterygoid. Storrs therefore suggests the term 'ectopterygoid boss' for this feature. Figs. 11 and 13.
85 Palate	Ectopterygoid boss has wide contact with jugal/ squamosal	Contact absent (0), contacts jugal (1)		The ectopterygoid boss can either be free of the medial wall of the skull roof, or contact the jugal and/or squamosal. Fig. 16.

86	Mandible	Bowed maxilla	Absent (0), present (1)	This character refers to mandibles that expand noticeably anterior of the jaw articulations; such mandibles have a hoop-like or bowed appearance when viewed on the ventral surface. Fig. 7.
87	Mandible	Meckelian canal open anteriorly	Not open (0), open (1)	The lingual surface of the lower jaw is poorly ossified in plesiosaurs; however, in some taxa the splenial does not ossify at all, leaving the Meckelian canal open far anterior to the jaw articulation.
88	Mandible	Ventral mandibular ridge/pedestal-like symphysis	No ridge (0), ridge (1)	The rhomaleosaurid jaw symphysis has a distinct ridge or pedestal-like elaboration along its ventral margin. This ridge extends posteriorly for a short distance past the symphysis along each jaw ramus. Fig. 7.
89	Mandible	Mandibular symphysis	Short (0), somewhat enforced (1), scooplike (2), long (3)	The length of the mandibular symphysis has been historically important in classifying the plesiosaurs (Tarlo 1960). My state 'scooplike' applies to both the rhomaleosaurid and <i>Liopleurodon</i> conditions; 'long' applies to the condition in <i>Peloneustes</i> . Figs. 7 and 13.
90	Mandible	Splenial participates in symphysis	Does not participate (0), does participate (1), angulars extend past symphysis (2)	The splenial enters the mandibular symphysis in all long-snouted taxa. State two describes the polycotyliids, in which the symphysis is so long that it extends posterior to the anterior margin of the angulars. This character is ordered. Figs. 9 and 12.
91	Mandible	Lingual mandibular fenestra	Absent (0), present (1)	<i>Thaumatosaurus</i> possess a fenestra in this position, bounded by the splenial, angular, and prearticular. Fig. 7.
92	Mandible	Morphology of dentary/angular-surangular suture	Angular projects forward of surangular in lateral view (0), surangular anterior process (1)	In most plesiosaurs, the suture of the dentary with the angular and surangular on the lateral surface of the mandible is relatively straight (Storrs & Taylor 1996); however in plesiosauroids the surangular sends a process anteriorly into an embayment in the dentary. Fig. 12.
93	Mandible	Coronoid	Present (0), absent (1)	The status of the coronoid and prearticular is a long-standing problem in plesiosaurs. I believe the coronoid to be present in all taxa except <i>Kimmerosaurus</i> , contra Cruickshank (1994b). Figs. 12, 15, and 19.

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Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
94 Lower Jaw	Long lingual coronoid process	Absent (0), present (1)		The coronoid in pliosaurs runs anteriorly to the mandibular symphysis. Fig. 12.
95 Mandible	Coronoid exposed on lateral jaw surface	No exposure (0), exposure (1)		Fig. 24. Intermediate state in <i>Muraenosaurus</i> illustrated by Andrews (1910) is correct, although he identifies this bone as the splenial rather than the coronoid Fig 19.
96 Mandible	Preatticular	Present (0), absent (1)	Cruikshank 1994b, char. 9	Cruikshank (1994b) believed the prearticular to be present but small in pliosaurs; I was able to confirm its presence in all taxa with adequate preservation. Figs. 12 and 19.
97 Mandible	Preatticular shelf/groove	Absent (0), present (1)	Andrews 1910	In cryptoclidids and polycoylids, the prearticular forms a shelf below the posterior end of the Meckelian canal, which is a distinct groove. The prearticular fits into a socket in the angular. Noted in <i>Muraenosaurus</i> by Andrews (1910), Fig. 19.
98 Mandible	Jaw articulation in relation to tooth row	Above or at collinear with tooth row (0), lower than tooth row (1)		Figs. 12, 14, and 15.
99 Skull shape	Diastema at maxilla/premaxilla suture	Absent (0), present (1)	Modified from Storrs 1991, char. 37	Figs. 2 and 11.
100 Dentition	First tooth after diastema	Large (0), reduced (1)		The first maxillary tooth is generally much smaller than those caudal to it in taxa possessing a diastema. Figs. 2 and 11.
101 Dentition	Premaxilla and dentary fangs	Absent (0), present (1)	Rieppel 1994a, 1997b, chars. 44, 55; Storrs 1991, char. 39; Brown 1981, char. 8	Fig. 7.
102 Dentition	One or two caniniform teeth on maxilla	Present (1), absent (0)	Rieppel 1994a, 1997b, chars. 45, 56; Storrs 1991, char. 41	

103	Dentition	Tooth form	Gracile, small root, narrow, no wear (0) robust, large root, wear (1), very small/ needle-like (2)	Brown 1981, char. 3, Tarlo 1960	Figs. 4, 5, 11, and 14. Tooth types defined by Massare (1987) were not used because most plesiosaurs have the same type of teeth in this more general coding.
104	Tooth shape	Teeth round or with reinforced planar face	Round (0), planar face (1)	Tarlo 1960	
105	Tooth ornament	Longitudinal striations on teeth	Striations all around (0), lingual only (1), none (2)	Tarlo 1960	
106	Dentition	Number of premaxillary teeth	5(0), 6(1), 7(2), greater than 7(3)	Brown 1981, char. 7; Cruikshank 1994b, char. 1	This character is ordered. Figs. 2 and 11.
107	Dentition	Maxillary teeth	Less than twenty (0), more twenty to thirty (1), many more than thirty (2)	Cruikshank 1994b, char. 1	This character is ordered.
108	Atlas/Axis	Number of axis rib heads	2(0), 1(1)		This character is difficult to score in many taxa due to poor preservation and/or incomplete ossification.
109	Atlas/Axis	Articulation of axis rib	Broad articulation with atlas centrum and/or other elements (0), head confined to axis centrum (1)	Andrews 1910, 1913	This character is variable within <i>Peloneustes</i> , and may be ontogenetically variable. Difficult to score in adult individuals in which the atlas/axis complex is generally fused.
110	Atlas/Axis	Atlas/axis morphology	No lateral exposure of atlas centrum on cup face (0), lateral exposure (1), no lateral exposure, but atlas and axis intercentra exclude atlas centrum ventrally (2)	Andrews 1909, Williston 1910, Brown 1981, char. 13. Also Romer, 1956	
111	Vertebrae	Number of cervical vertebrae	Primitive (0), increased (1), reduced (2), greater than 50	Brown 1981, char. 14	The number of cervical vertebrae is unfortunately unknown in <i>Pistosaurus</i> (Sues 1987); however this taxon is similar to plesiosaurs in possessing 'pectoral' vertebrae, defined as vertebrae in which the rib articulation arises from a short transverse process arising from both the centrum and neural arch (illustrated in Brown, 1981). Here I define cervical vertebrae as vertebrae in which the rib articulation arises from the centrum only. Brown (1981) also believed 28–32 cervicals to be primitive in plesiosaurs; I have retained this criterion. State one is 33 cervicals or larger, while state two is fewer than 28. State three concerns necks of 50 cervicals or longer. This character is ordered using the character state tree ((2)1,3)0.

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Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
112	Morpho-metric Proportions of cervical centra	Length equal to height (0), length greater than height (1), length less than height (2)	Brown 1981, char. 15; Welles 1952	Welles (1952) identified ontogenetic variation in this character, as well as variation along the vertebral column, but also found that taxonomically relevant interspecific differences existed. I scored this character loosely; vertebrae had to be markedly compressed or elongated over most of the column to be scored as derived.
113	Vertebrae Distinct change in zygopophyseal angle along cervical column	No change in angle (0), change (1)	Noted by Welles 1962	In elasmosaurs and some other taxa, the cervical zygopophyses are oriented dorso-ventrally in the anterior part of the column. This orientation shifts gradually to medio-lateral in the posterior part of the neck.
114	Vertebrae Ventral keel on cervical vertebrae	Absent (0), present (1)	Tarlo 1960	
115	Vertebrae Lateral ridge on anterior cervical vertebrae in adults	Absent (0), present (1)	Brown 1981, char. 16; illustrated in Welles, 1943	A low, lateral ridge is present on the centrum body above the rib articulation in elasmosaurs and some other plesiosauroids.
116	Vertebrae Binocular shaped anterior cervical centra	Absent (0), present (1)	Welles 1943	The anterior cervical centra in some elasmosaurs have a distinct dorso-ventral constriction medially, yielding a centrum that has a 'binocular' outline in anterior or posterior view.
117	Vertebrae Number of cervical rib heads	Two (0), one (1)	Sander <i>et al.</i> 1997; Brown 1981, char. 21	
118	Vertebrae Ventral foramina in cervical vertebrae	Absent (0), present (1)	Sander <i>et al.</i> 1997; Storrs 1991, char. 47	Termed "foramina subcentralia" by Storrs (1991), the possession of paired foramina in the ventral surface of the cervical centra is a trait shared by plesiosauroids and all plesiosaurs.
119	Vertebrae Foramina subcentralia reduced and lateral	Medial and large (0), lateral and reduced (1)	Tarlo 1960; <i>see also</i> Williston 1907	
120	Vertebrae Width of cervical zygopophyses	Wider than centrum (0), subequal with centrum (1), more narrow than centrum (2)	Sander <i>et al.</i> 1997; Storrs 1991 char. 48	This character is ordered.

121	Vertebrae	Posterior articulation for succeeding neural spine, cervical vertebrae	Absent (0), present (1)	Noted in <i>Pistosaurus</i> by (Sues 1987) and in <i>Calawayasaurus</i> (Welles 1962), this feature is a small notch in the posterior base of the cervical neural spine which accepts the anterior edge of the succeeding neural spine. This notch may represent the zyganktrum present in more basal sauropterygians; however, no corresponding zygosphenes is ever present. Lost in many plesiosaurs.
122	Vertebrae	Cervical rib articulation greatly elongate/ cervical ribs expanded and blade-like	Circular or subcircular (0), elongate (1)	Antero-posterior elongation of the cervical ribs, and elongation of their articulation with the centrum, is common in long-necked taxa in which the centrum is longer than wide.
123	Vertebrae	Anterior process of cervical ribs	Present (0), absent (1)	A distinct anterior process is present on the cervical ribs of <i>Augustasaurus</i> , as well as <i>Thalassiodracon</i> , <i>Plesiosaurus</i> , and some other Jurassic plesiosaurs. This process is lost in later plesiosaurs.
124	Vertebrae	Anterior neural flange on cervical neural spines	Absent (0), present (1)	<i>Muraenosaurus</i> and some other plesiosauroids have a distinct flange on the anterior margin of the cervical neural spines. This character is not necessary to form the articulation described in character 121.
125	Vertebrae	Neural spines, cervical vertebrae	Angled backward (0), not angled (1)	The cervical neural spines in elasmosaurs and some other taxa are not angled, while they are angled backward in <i>Thalassiodracon</i> and the plesiosauroids.
126	Vertebrae	Distal end of transverse processes, dorsal vertebrae	No diameter increase (0), thickened (1)	Thickened transverse processes are present in all plesiosaurs, <i>Pistosaurus</i> , and <i>Augustasaurus</i> .
127	Vertebrae	Dorsal neural arch height	Subequal to centrum height (0), shorter than centrum height (1)	The neural arch tends to be small and short compared to the centrum in plesiosaurs, while it is larger in more basal sauropterygians.
128	Vertebrae	Zygosphenes/ zyganktrum articulation	Present (0), absent (1)	The pistosauroid condition is also discussed in Sues (1987).

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Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
129 Vertebrae	Height of neural spines, dorsal vertebrae	Low (0), low and rugose (1), high (2)	Sander <i>et al.</i> 1997	The dorsal neural spines of <i>Augustasaurus</i> are low with rugose tops; the spines in <i>Thalassiodracon</i> are low but not rugose; those in <i>Pistosaurus</i> are high. The dorsal neural spines are high in all plesiosaurs.
130 Vertebrae	Lateral compression of neural spines, dorsal and cervical vertebrae	Not compressed (0), compressed and blade-like (1)	Sander <i>et al.</i> 1997	The neural spines in many plesiosaurs are laterally compressed and blade-like; the neural spines of many plesiosaurs lack this feature.
131 Pectoral Girdle	Interclavicle posterior process	Present (0), absent (1)	Storrs 1991, char. 58	The interclavicle was probably present but is not known in many plesiosaurs.
132 Pectoral Girdle	Dorsal process of scapula	Tapers to blunt tip (0), ventrally expanded posteriorly (1)	Rieppel 1997b, char. 85	
133 Pectoral Girdle	Presence of clavicles and interclavicle	Present (0), interclavicle absent (1), both absent (2)	Modified from Brown 1981, chars. 22 and 23	The interclavicle and clavicles are slow to ossify and often do not preserve well; <i>Plesiosaurus</i> is the only taxon in which I could be sure of the absence of the interclavicle, based on Storrs 1997 and my own observations.
134 Pectoral Girdle	Clavicle median symphysis	Symphysis (0), separated by interclavicle (1), meet only behind notch (2)		
135 Pectoral Girdle	Scapulae meet in anterior median symphysis	Separated by clavicles/interclavicle (0), meet medially but leave notch for dermal elements (1), meet in long symphysis with no notch (2)	Modified from Brown 1981, char. 24	The scapulae meet in an anterior median symphysis in many later plesiosaurs; however, the antero-medial processes of the scapulae are usually separated by the dermal girdle elements in plesiosaurs (contra Brown 1981).
136 Pectoral Girdle	Anterior intrascapular fenestra	Absent (0), present (1)		Some cryptoclitids and some polycolytids have a small fenestra perforating the anterior girdle elements on the midline.
137 Pectoral Girdle	Longitudinal pectoral bar	Absent (0), formed by clavicle and coracoid (1), formed by scapula and coracoid (2)	Modified from Storrs 1991, char. 66; Brown 1981, char. 25	This character is certainly variable ontogenetically, as discussed by Brown (1981). I include it here because most of the taxa in this analysis are adults, and for the sake of completeness.

138	Pectoral Girdle	Supracoracoid foramen/ notch	Present (0), absent (1)	Rieppel 1997b, char. 64; Storrs 1991, char. 64	The supracoracoid foramen is absent in plesiosauids and all plesiosaurs.
139	Pectoral Girdle	Coracoid shape	Rounded contours/ not plate-like (0), expanded median symphysis (1)	Rieppel 1997b, char. 88; Storrs 1991, char. 63	
140	Pectoral Girdle	Median coracoid perforations	Absent (0), present (1)	Illustrated in Williston 1906, 1906	Most polycotyliids have one or two perforations on either side of the midline in the posterior extensions of the coracoids.
141	Pectoral Girdle	Posterior coracoid extension with deep median embayment	Absent (0), present (1)	Brown 1981, char. 27	Welles (1943, 1962) and many others have documented that the posterior extensions of the coracoids are long and surround a deep median embayment in many elasmosaurs.
142	Pectoral Girdle	Postero-lateral coracoid wings	Absent (0), present (1)	Brown 1981, char. 26	Storrs (1997) and Brown (1981) discuss the clear ontogenetic variation in this character. It is included here because most genera in this analysis are adults, and for the sake of completeness.
143	Pelvic Girdle	Contact between ilium and pubis	Present (0), absent (1)	Storrs 1991, char. 68; Sues 1987	The loss of the primitive contact between the ilium and pubis has long been used as a diagnostic character of the Plesiosauria (i.e. Romer, 1956, p. 329).
144	Pelvic Girdle	Pubis ventral (medial) margin	Convex (1), concave (0)	Rieppel 1997b, char. 100; Storrs 1991, char. 69; Brown 1981, char. 28	
145	Pelvic Girdle	Large, ventral pubo-ischiatic plate	Absent (0), present (1)	Sues 1987	A large ventral plate formed by the ischium and pubis is characteristic of plesiosaurs.
146	Pelvic Girdle	Median pelvic bar	Absent (0), present (1)	Brown 1981, char. 30	Analogous to the median pectoral bar, the median pelvic bar is slow to ossify, as discussed by Brown (1981). I include it here because most of the taxa in this analysis are adults, and for the sake of completeness. The character is also difficult to score; the presence of a suture between the median processes of the pubis and ischium can only be determined by articulating the two elements.
147	Pelvic Girdle	Thyroid fenestra closed or open in adult	Closed (0), open (1)	Rieppel 1997b, char. 102; Storrs 1991 char. 71	

Continued

Appendix 1. Continued.

Char. type	Character	States/Coding	Citation	Remarks
148 Pelvic Girdle	Obturator foramen	Present (0), absent (1)	Rieppel 1997b, char. 101; Storrs 1991, char. 70	The obturator foramen is lost in some plesiosauroids and all plesiosaurs; see discussion above.
149 Pelvic Girdle	Iliac blade	Well-developed (0), reduced (1)	Rieppel 1994a, 1997b, chars. 79, 99; Storrs 1991, char. 67; Brown 1981, char. 31; Sues 1987	
150 Humerus	Angled humerus	Absent (1), present (0)	Rieppel 1994a, 1997b, chars. 74, 92; Storrs 1991 char. 73	The angled humerus is characteristic of stem-group sauropterygians, and of early plesiosaurs. See Storrs (1997) for the condition in <i>Plesiosaurus</i> .
151 Pro-podials	Expanded distal propodials with dorsal trochanter/ tuberosity	Absent (0), present (1)		Short propodials whose distal ends are expanded antero-posteriorly and flattened dorso-ventrally are characteristic of all plesiosaurs. The possession of a dorsal trochanter or tuberosity is also characteristic of all plesiosaur propodials.
152 Humerus	Distal end of humerus has two distinct planes in adult	Absent (0), present (1)	Illustrated by Williston 1906	The humerus in many plesiosauroids has two distinct planes or facets on its distal end, with which the epipodials articulate.
153 Propodials	Distinct facet on distal humerus for supernumerary ossification	Absent (0), present (1)	Illustrated by Williston 1906	<i>Tricleidus</i> and <i>Polycotylus</i> have a third distinct facet on the postero-distal end of the humerus which articulates with a supernumerary ossification of the epipodial row.
154 Propodials	Gracile or massive	Gracile/constricted (0), massive (1)	Brown 1981, char. 32	Applicable only to plesiosaurs.
155 Propodials	Propodials relatively elongate	Not elongate (0), elongate with narrow distal head (1)		Late plesiosaurs such as <i>Brachauchenius</i> have long, narrow propodials compared to earlier plesiosaurs.
156 Humerus	Deltopectoral crest	Present (0), absent (1)	Rieppel 1997b, char. 93	

157 Ulna	Ulnar shape	Narrow (0) or broad (1) distally	Sander <i>et al</i> 1997; Storrs 1991, char. 83	A broad distal ulna is thought to be a synapomorphy of <i>Agustasaurus</i> and <i>Pistosaurus</i> (Sander <i>et al.</i> 1997); however I believe it forms part of a transformation series of decreasing perichondral ossification in plesiosauroids and plesiosaurs. I have therefore coded it as present in plesiosaurs rather than inapplicable.
158 Ulna	Distinctly lunate ulna	Absent (0), present (1)		Many early plesiosaurs have an ulna which is distinctly lunate in shape.
159 Femur	Internal trochanter	Well-developed (0), reduced (1)	Rieppel 1997b, char. 105	Both this character and character 160 are related to the progressive loss of femoral features as sauropterygians became more aquatic.
160 Femur	Inter-trochanteric fossa	Deep (0), distinct but reduced (1), rudimentary or absent (2)	Rieppel 1997b, char. 106	
161 Epi-podials	Epi-podial morphology	Longer than broad (0), equal or broader than long (1)	Brown 1981, char. 35.; Sues 1987	
162 Epi-podials	Supernumery ossifications, forelimb	None (0), epi-podial row/pisiform (1), propodial (2), both (3)	Modified from Storrs 1991, char. 84; Brown 1981, char. 34	Plesiosaurs often have a supernumery ossification in the epi-podial row and/or on a level with the distal propodial. These bones are slow to ossify and are liable to loss during collection.
163 Meta-podials	Fifth metapodial	In line with rest of metapodial row (0), shifted into distal mesopodial row	Owen 1865, Brown 1981, char. 37	Owen (1865) was the first to note that the fifth metapodial is shifted into the distal mesopodial row in all plesiosaurs. This shift results in a misalignment of the phalangeal articulations of digit five relative to the other digits.
164 Phalanges	Hyperphalangy	No increase (2-3-4-5-3) (0), hyperphalangy present (1)	Modified from Storrs 1991, char. 80	
165 Phalanges	Interlocking distal phalanges anterior to fifth phalangeal row	Absent (0), present (1)		The phalanges of <i>Trinacromerum</i> and related taxa have joints which are misaligned between digits in digits one through four. This character is difficult to score due to concerns over preservation.
166 Ribs	Median gastral rib element	Always one lateral process (0), may have two lateral processes (1)	Rieppel 1997b, char. 119	

Appendix 2. Data matrix for the cladistic analysis in this paper. The first three taxa comprise the outgroup. Inapplicable characters are coded as 'x'; unknown characters are coded as '?'. The ancestral condition is generally coded as '0'.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Simosaurus</i>	0	0	0	0	2	2	x	0	0	0	0	?	0	1	2	0	0	0	?
<i>Cymatosaurus</i>	0	?	?	?	?	2	x	0	1	0	0	?	0	0	1,2	1	0	1	?
<i>Pistosauridae</i>	0	0	?	1	?	0	x	1	0	0	0	?	0	0	1	1	0	1	?
<i>Calawayasaurus</i>	2	1	2	0	2	0	0	0	0	0	0	0	0	0	x	0	1	1	?
<i>Attenborosaurus</i>	1	0	1	1	0	0	0	1	1	0	0	?	?	0	0	?	0	?	?
BMNH R.5488	1	0	1	1	1	0	1	1	1	0	?	0	1	0	?	?	0	0	1
<i>Brachauchenius</i>	1	2	?	?	?	1	?	2	1	0	1	1	0	x	x	0	0	0	0
<i>Brancasaurus</i>	2	1	2	1	0	0	0	0	0	0	0	0	0	1	x	0	0	1	?
<i>Cryptoclidus</i>	2	0	0	1	2	0	1	0	0	0	0	0	0	0	x	0	0	0	1
<i>Dolichorhynchops</i>	1	2	1	1	0	1	1	2	0	0	1	0	0	x	x	0	0	0	?
<i>Eurycleidus</i>	0	?	0	?	?	0	0	1	1	0	0	?	0	0	0	1	0	0	?
<i>Hauffiosaurus</i>	1	0	2	1	0	1	0	2	1	0	?	?	?	?	?	?	?	?	?
<i>Kimmerosaurus</i>	?	?	?	?	?	2	?	3	0	0	0	?	?	0	x	0	?	0	?
<i>Kronosaurus</i>	1	2	2	1	?	1	?	2	?	?	?	?	?	?	?	?	?	?	?
<i>Leptocleidus</i>	?	2	?	1	?	0	1	1	1	0	1	0	1	x	x	0	0	0	?
<i>Libonectes</i>	2	1	?	0	?	0	0	0	0	2	0	0	0	x	x	?	1	?	?
<i>Liopleurodon</i>	1	2	1	1	1	1	1	2	2	0	1	1	0	x	x	0	0	0	1
<i>Macroplata</i>	1	0	2	1	0	1	0	2	0	0	?	1	0	x	0	0	?	?	0
<i>Microcleidus</i>	2	1	0	1	0	0	0	0	0	0	0	0	0	?	?	0	?	1	?
MOR 751	0	2	?	?	?	0	1	1	0	0	0	1	0	0	x	0	0	0	1
<i>Morturneria</i>	?	?	?	?	?	2	1	3	0	0	?	?	?	?	?	?	?	?	?
<i>Muraenosaurus</i>	2	1	0	1	2	0	1	0	0	0	0	0	0	0	x	0	0	0	0
<i>Peloneustes</i>	1	2	1	1	1	1	1	2	1	0	1	1	0	x	x	0	0	0	1
<i>Plesiosaurus</i>	0	0	2	1	0	0	0	0	0	0	0	0	0	?	?	1	0	0	0
<i>Pliosaurus</i>	1	2	?	?	?	1	?	2	2	0	1	1	0	x	x	0	0	0	?
<i>Polycotylus</i>	?	2	1	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>Rhomaleo. megaceph.</i>	0	0	0	1	0	0	0	1	1	0	0	1	0	0	x	1	0	0	1
<i>Rhomaleo. victor</i>	1	0	0	1	2	0	0	1	1	?	?	0	?	?	?	?	?	?	?
<i>Rhomaleo. zetland.</i>	0	2	?	?	0	1	?	1	1	0	1	0	1	x	?	0	0	0	1
<i>Simolestes</i>	1	2	1	1	1	0	1	1	1	0	1	0	?	x	x	0	?	?	?
<i>Styxosaurus</i>	2	1	?	?	?	0	0	0	0	0	2	0	?	x	?	0	1	0	?
<i>Thalassiodracon</i>	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1
<i>Tricleidus</i>	2	0	?	1	0	2	1	0	0	0	0	0	0	0	x	?	?	0	?
<i>Trinacromerum</i>	1	2	1	1	1	1	1	2	0	0	1	0	0	x	x	0	?	0	?

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0,1	0	0	0
1	0	0	0	0	2	0	1	0	1	1	0	0	0	?	1	0	0	1	0	1	0
1	1	0	0	0	2	1	1	1	1	2	0	0	0	1	2	x	0	x	1	1	1
1	0	0	0	0	2	0	1	0	1	1	0	0	0	?	1	0	?	0	?	0	0
1	?	0	0	0	2	?	1	?	1	0	0	?	0	?	1	0	1	?	0	0	?
1	0	0	0	0	2	0	1	1	1	0	0	1	0	1	1	1	0	0	1	0	0
1	1	0	0	0	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	1
1	1	0	0	0	2	1	1	0	1	2	0	0	1	1	2	x	0	x	1	1	0
1	0	0	0	1	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	2
1	0	0	0	0	2	0	1	0	1	?	0	?	0	1	?	?	0	?	0	?	?
?	?	?	?	?	?	?	?	?	1	?	?	?	0	1	?	?	?	?	?	?	0
1	1	?	0	0	2	1	1	?	1	?	?	?	1	1	?	x	?	?	?	?	?
?	?	?	?	?	?	0	1	?	1	?	?	1	?	1	?	?	?	?	?	?	?
1	0	0	0	0	2	0	1	0	1	0	0	?	0	1	?	?	?	?	0	?	1
1	1	0	0	?	2	1	?	1	1	2	0	0	0	1	2	x	0	x	1	1	?
1	0	0	0	0	2	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0
1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	1	0	0	?	?
1	1	?	0	0	2	1	1	?	1	?	0	?	0	1	2	x	0	x	?	1	1
1	0	0	0	0	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	2
?	?	?	?	?	?	?	1	1	1	?	?	?	?	1	?	x	?	?	?	x	?
1	1	?	0	0	2	1	1	0	1	2	0	0	?	?	?	x	0	?	?	1	?
1	0	0	0	0	2	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0
1	0	0	0	0	2	0	1	?	1	?	?	?	?	?	?	x	?	?	?	?	?
1	0	0	0	0	2	0	1	?	1	0	0	?	0	1	1	0	1	0	0	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	1	0	0	0	?
1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	1	0	0	?	?
1	0	0	0	0	2	1	1	?	1	2	0	0	1	1	2	x	0	x	?	1	0
1	?	0	0	1	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	2

Continued

Appendix 2. Continued.

Taxon	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Simosaurus</i>	0	0	0	0	x	0	x	x	0	0	0	x	0	x	0	0	0	0	0
<i>Cymatosaurus</i>	?	?	1	1	?	?	?	?	?	?	?	?	0	x	?	?	2	0	0
<i>Pistosauridae</i>	?	?	1	?	?	?	?	?	?	?	1	?	0	0	?	?	?	0	0
<i>Calawayasaurus</i>	0	0	1	1	0	2	0	1	1	1	?	?	0	0	1	1	1	1	0
<i>Attenborosaurus</i>	?	?	1	?	0	?	?	?	?	?	?	?	1	1	?	?	2	0	?
BMNH R.5488	0	1	1	?	1	?	0	?	?	?	0	0	?	1	1	0	1	?	?
<i>Brachauchenius</i>	?	?	1	?	1	?	0	?	?	?	?	1	1	1	1	?	?	1	0
<i>Brancaesaurus</i>	0	0	1	?	0	?	0	?	?	?	?	?	0	0	1	1	1	?	0
<i>Cryptoclidus</i>	1	1	1	?	0	1	0	0	?	0	?	?	1	0	1	1	1	0	2
<i>Dolichorhynchops</i>	0	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0	2
<i>Euryclidus</i>	0	1	1	1	0	0	?	?	0	0	?	?	1	1	1	0	1	0	2
<i>Hauffiosaurus</i>	?	1	?	?	?	?	?	?	0	0	?	?	1	?	?	?	2	0	0
<i>Kimmosaurus</i>	1	1	1	1	0	0	0	0	?	0	?	?	1	0	1	1	1	0	2
<i>Kronosaurus</i>	?	1	1	1	0	2	0	1	0	0	?	?	?	1	?	?	2	0	0
<i>Leptocleidus</i>	0	?	1	?	?	?	?	1	0	?	0	0	1	1	?	?	1	1	2
<i>Libonectes</i>	0	0	1	1	0	2	0	1	1	1	1	?	0	0	1	1	1	1	0
<i>Liopleurodon</i>	0	1	1	0	1	0	0	1	1	0	0	1	1	1	?	0	2	0	1
<i>Macroplata</i>	0	1	1	1	0	0	0	0	0	0	?	0	?	1	?	?	1	0	0
<i>Microcleidus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	0
MOR 751	0	0	1	1	1	?	?	?	?	0	?	?	?	0	?	1	1	0	2
<i>Morturneria</i>	0	0	?	1	1	0	?	1	?	?	?	?	1	?	?	1	?	?	?
<i>Muraenosaurus</i>	0	1	1	?	0	?	0	?	?	?	?	?	1	0	?	1	1	0	2
<i>Peloneustes</i>	0	1	1	0	0	0	0	1	1	0	0	1	1	1	1	0	2	0	0
<i>Plesiosaurus</i>	?	0	1	?	0	?	?	?	?	1	1	1	1	0	0	0	1	0	1
<i>Pliosaurus</i>	0	1	1	?	1	?	?	1	?	?	0	0	1	1	?	?	2	0	?
<i>Polycotylus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Rhomaleo. megaceph.</i>	?	1	1	1	1	?	0	1	0	1	0	0	?	1	?	?	1	1	2
<i>Rhomaleo. victor</i>	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	2
<i>Rhomaleo. zetland.</i>	?	1	1	?	1	1	1	1	0	1	0	0	1	1	?	?	1	1	2
<i>Simolestes</i>	0	1	1	?	1	0	0	1	?	?	0	0	1	1	?	0	1	?	?
<i>Styxosaurus</i>	?	?	1	?	?	?	?	?	?	1	1	0	0	0	1	1	?	?	?
<i>Thalassiodracon</i>	0	1	1	1	0	0	0	0	0	1	1	?	1	1	0	0	1	0	2
<i>Tricleidus</i>	0	0	1	1	0	1	1	0	0	0	?	?	1	0	?	?	1	0	2
<i>Trinacromerum</i>	?	0	1	?	0	1	1	?	0	?	0	0	1	0	?	?	1	1	2

61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
0	x	x	x	0	0	0	x	x	?	x	x	x	x	0	x	0	0	0	0	0	0
0	x	x	x	0	0	?	x	x	?	x	x	x	x	?	x	0	0	0	0	1	0
1	0	x	x	0	?	0	0	0	?	1	0	?	0	?	?	0	0	0	0	0	0
1	1	0	0	0	1	0	0	0	0	1	2	1	?	0	0	0	0	0	0	1	0
1	0	1	x	0	0	0	0	1	0	0	2	0	0	0	0	1	?	?	?	?	1
1	1	1	?	0	0	0	0	0	0	0	2	x	0	?	0	?	?	?	?	?	?
1	1	1	0	0	0	0	0	3	0	2	2	x	0	?	0	?	0	?	1	?	1
1	?	?	0	?	?	0	0	?	0	?	?	1	0	?	0	0	?	0	0	1	?
1	0	0	x	0	1	0	0	0	1	0	2	1	0	0	0	0	0	0	0	?	0
1	2	0	0	0	1	1	1	0	1	0	2	1	1	0	1	0	0	0	0	1	0
1	0	1	x	0	0	0	0	0	0	2	2	0	0	0	0	?	?	0	0	?	?
1	1	1	0	1	0	0	0	2	0	2	2	x	0	?	0	0	0	0	0	1	0
1	0	0	x	0	?	0	1	0	?	0	2	1	1	?	0,1	?	?	?	0	?	?
1	1	?	0	?	?	?	0	2	?	?	?	x	0	?	0	0	?	?	?	?	?
1	1	1	1	0	0	0	0	0	0	1	2	x	0	0	0	1	?	?	0	1	1
1	2	0	0	0	1	0	0	0	0	1	2	1	?	0	0	0	?	?	0	1	0
1	1	1	0	0	0	0	0	3	0	2	2	x	0	?	0	0	1	1	1	1	1
1	0	1	x	?	?	0	0	0	0	2	2	0	0	?	0	?	?	0	0	1	?
1	0	1	0	0	?	0	0	0	0	?	2	1	0	0	?	?	?	?	?	?	0
1	1	0	0	0	1	1	1	0	1	?	2	1	?	?	?	0	?	?	?	?	0
1	?	0	x	?	?	0	?	?	?	1	?	?	1	0	1	?	?	0	?	1	?
1	0	0	x	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
1	1	1	0	1	0	0	0	2	0	2	2	x	0	0	0	1	0	0	0	1	1
1	0	0	x	0	0	0	0	0	0	?	1	?	0	0	0	0	?	0	0	0	0
?	?	?	0	?	?	0	?	3	?	?	?	x	?	?	0	?	?	1	?	?	?
?	?	?	0	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?
1	1	1	1	0	0	0	0	0	0	1	2	x	0	0	0	?	1	0	0	1	1
1	1	1	1	0	?	0	0	?	?	1	1	x	?	?	0	?	1	1	0	1	0
1	?	1	?	0	?	0	0	0	0	?	2	x	0	?	?	?	?	?	?	?	?
1	1	1	?	0	0	0	0	0	0	?	2	x	0	?	0	?	1	?	?	?	?
?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?
1	0	1	x	0	0	0	0	0	0	2	2	0	0	0	0	?	?	?	?	0	?
1	0	0	x	0	1	0	1	0	1	0	2	1	1	0	1	?	?	?	0	0	?
1	2	0	0	0	?	1	1	0	1	0	2	1	1	?	1	0	0	?	?	?	0

Continued

Appendix 2. Continued.

Taxon	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101
<i>Simosaurus</i>	0	0	x	0	0	0	0	0	0	0	0	?	0	0	0	0	0	x	0
<i>Cymatosaurus</i>	1	1	0	0	?	?	2	?	?	?	?	?	?	?	?	?	1	?	1
<i>Pistosauridae</i>	0	1	?	0	?	?	1	?	?	?	?	?	?	?	?	?	0	x	1
<i>Calawayasaurus</i>	1	0	x	1	1	0	1	0	0	0	0	?	0	0	0	1	0	x	0
<i>Attenborosaurus</i>	?	0	x	0	0	1	2	1	?	0	0	?	?	0	0	0	1	?	0
BMNH R.5488	?	?	?	1	?	1	2	1	?	?	?	?	?	?	?	?	0	1	?
<i>Brachauchenius</i>	1	1	0	0	0	?	2	1	?	1	?	?	0	?	0	0	1	?	0
<i>Brancaesaurus</i>	1	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	0	x	0
<i>Cryptoclidus</i>	0	0	x	0	1	0	0	0	0	0	0	0	1	0	1	0	0	x	0
<i>Dolichorhynchops</i>	0	0	x	0	x	0	3	2	0	0	0	0	1	0	1	1	0	x	0
<i>Euryclidus</i>	0	0	x	0	1	1	2	1	?	?	0	?	0	0	0	0	1	1	?
<i>Hauffiosaurus</i>	1	1	1	0	?	0	3	1	0	?	?	?	?	?	0	0	1	1	0
<i>Kimmerosaurus</i>	?	0	x	?	?	0	0	0	?	0	1	0	1	?	1	1	?	?	0
<i>Kronosaurus</i>	?	1	?	?	?	0	3	?	?	?	?	?	?	?	?	?	?	?	?
<i>Leptocleidus</i>	0	1	0	1	?	?	2	?	0	1	0	1	0	0	0	0	1	1	1
<i>Libonectes</i>	1	0	x	?	1	0	1	0	1	0	0	0	0	0	0	1	0	x	0
<i>Liopleurodon</i>	1	1	1	0	1	0	2	1	0	1	0	1	0	0	0	0	1	1	0
<i>Macroplata</i>	1	0	x	0	0	0	3	1	?	1	?	?	?	0	0	0	?	?	0
<i>Microcleidus</i>	?	0	x	0	1	0	1	0	?	0	?	0	0	?	0	1	0	x	0
MOR 751	?	0	x	0	x	0	2	1	0	0	0	?	1	0	1	1	0	x	0
<i>Morturneria</i>	?	?	?	0	1	0	?	?	?	?	?	0	?	?	0	1	0	x	0
<i>Muraenosaurus</i>	1	0	x	0	1	0	0	0	0	0	0	0	1	0	1	0	0	x	0
<i>Peloneustes</i>	1	1	2	0	0	0	3	1	0	1	0	1	0	0	0	0	1	1	0
<i>Plesiosaurus</i>	0	0	x	0	?	0	0	?	?	?	?	0	0	?	0	0	0	x	0
<i>Pliosaurus</i>	1	1	?	0	0	0	2	1	0	1	0	1	1	0	0	0	1	1	0
<i>Polycotylus</i>	?	?	?	?	x	0	?	?	0	?	0	0	1	0	1	1	?	?	?
<i>Rhomaleo. megaceph.</i>	?	1	1	1	0	1	2	1	1	?	?	?	?	?	0	0	1	?	1
<i>Rhomaleo. victor</i>	0	1	?	?	0	1	2	1	1	?	?	?	?	0	0	0	?	?	1
<i>Rhomaleo. zetland.</i>	?	?	?	1	0	1	2	1	?	?	0	?	0	0	0	0	1	?	1
<i>Simolestes</i>	?	1	?	?	0	1	2	1	?	1	0	1	0	0	0	0	?	?	1
<i>Styxosaurus</i>	?	?	?	1	?	0	1	?	?	0	?	?	0	?	?	1	0	x	0
<i>Thalassiodracon</i>	1	0	x	0	?	0	2	1	?	?	?	?	0	?	0	0	0	x	0
<i>Tricleidus</i>	0	0	x	0	1	0	0	0	0	0	0	0	?	0	1	1	0	x	0
<i>Trinacromerum</i>	?	0	x	0	?	0	3	2	?	0	?	0	1	0	1	1	0	x	0

102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124
0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	0	0	x	0	0	0	?	0
1	0	0	?	0	0	?	?	?	?	?	?	?	0	0	?	?	?	x	?	?	?	?
0	?	0	?	0	0	?	?	?	0	0	0	0	0	0	0	1	0	1	1	0	0	0
1	0	0	?	0	0	?	?	?	3	1	1	?	0	1	1	1	0	2	1	0	?	0
0	1	0	0	0	0	?	?	?	0	0	0	?	0	0	0	1	?	2	?	0	0	0
0	1	0	0	1	?	0	1	0	0	2	0	1	0	0	0	1	0	1	?	0	?	0
0	1	0	?	?	?	?	?	?	2	2	?	?	0	0	1	1	1	2	?	0	?	0
0	0	0	?	0	?	?	1	0	1	1	?	?	0	0	1	1	0	2	1	0	?	0
0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	2	0	1	1	1
0	0	0	?	0	0	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1
0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	0	?	2	1	?	?	?	0	0	0	?	0	0	0	?	0	2	?	0	?	?
0	2	0	?	3	2	1	?	?	?	2	?	0	0	0	1	1	0	2	?	1	1	?
0	1	?	?	?	?	?	?	1	?	2	2	?	?	?	?	1	1	?	2	?	0	?
0	1	0	0	0	0	?	?	?	2	2	0	1	0	0	1	1	0	2	0	0	?	0
1	0	0	?	0	0	1	?	0	3	1	1	?	1	1	1	1	0	2	1	1	?	0
0	1	0	1	0	1	?	?	?	2	2	0	0	0	0	0	1	1	2	1	0	1	0
0	0	0	0	?	1	0	?	0	0	0	?	1	0	0	0	1	0	2	0	0	?	0
?	0	0	0	?	?	0	?	?	1	1	1	0	1	1	0	1	0	2	?	1	0	0
1	1	0	?	1	0	1	1	2	2	2	?	1	0	0	1	1	0	?	?	0	?	?
0	2	0	?	2	2	0	0	2	?	2	?	?	0	1	1	1	0	2	?	0	?	?
0	0	0	0	0	0	1	0	1	1	1	0	0	0	?	1	1	0	2	1	1	1	1
0	1	0	0	1	1	0	0	0	2	2	0	1	0	0	0	1	0	2	0	0	1	0
0	0	0	0	0	?	?	?	0	1	0	?	0	0	0	0	1	0	2	1	0	0	0
0	1	1	1	1	1	?	?	?	?	2	?	0	0	0	0	1	1	2	?	0	?	0
?	1	0	?	?	?	1	1	2	2	2	0	?	0	0	1	1	0	1	1	0	?	1
0	1	0	0	0	?	?	?	?	0	2	?	1	0	0	0	1	0	1	?	0	0	0
0	1	0	?	?	?	?	?	?	0	?	0	?	0	0	?	?	0	?	?	0	0	?
0	1	0	0	?	?	?	?	?	2	2	0	1	0	0	0	1	0	1	?	0	?	0
0	1	0	0	0	?	?	?	0	2	2	?	0	0	0	0	1	0	1	1	0	1	0
1	0	0	?	0	?	?	?	?	3	1	?	?	1	1	1	1	0	2	1	1	?	0
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0
0	0	0	0	0	?	1	?	1	0	0	1	0	0	0	1	1	0	2	1	0	1	1
0	0	0	?	0	1	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1

Continued

Appendix 2. Continued.

Taxon	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143
<i>Simosaurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	x	x	0
<i>Cymatosaurus</i>	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	x	?	?	?
<i>Pistosauridae</i>	0,1	1	0	0	1,2	0	?	1	0	?	0	0	0	1	1	x	0	0	0
<i>Calawayasaurus</i>	1	1	1	1	2	1	?	0	0	0	1	0	0,1	1	1	0	1	1	1
<i>Attenborosaurus</i>	0	1	1	1	0	0	?	0	0	0	0	0	0	1	1	0	0	1	1
BMNH R.5488	0	1	1	1	?	0	?	0	0	0	0	0	1	1	1	0	0	0	1
<i>Brachauchenius</i>	1	1	1	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brancaasaurus</i>	0	1	1	1	2	1	1	0	0	0	1	?	2	1	1	0	1	1	1
<i>Cryptoclidus</i>	1	1	1	1	2	1	?	0	0	0	1	1	2	1	1	0	0	1	1
<i>Dolichorhynchops</i>	1	1	1	1	2	0	x	0	0	2	0	1	1	1	1	1	0	1	1
<i>Eurycleidus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	1
<i>Hauffiosaurus</i>	?	?	1	1	?	0	?	0	?	?	0	0	?	1	1	0	0	1	1
<i>Kimmerosaurus</i>	1	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Kronosaurus</i>	0	?	1	1	2	0	?	?	?	?	0	?	0	1	1	?	0	?	?
<i>Leptocleidus</i>	0	1	1	1	?	0	0	0	0	0	0	0	1	1	1	0	0	1	?
<i>Libonectes</i>	1	?	1	1	?	1	?	0	0	0	2	0	2	1	1	?	1	1	?
<i>Liopleurodon</i>	0	1	1	1	2	0	?	0	?	?	0	?	?	1	1	0	0	1	1
<i>Macroplata</i>	0	?	1	1	0	0	?	?	?	?	?	?	?	?	1	?	?	?	1
<i>Microcleidus</i>	1	1	1	1	2	1	?	0	?	?	?	1	?	2	?	1	0	0	1
MOR 751	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Morturneria</i>	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Muraenosaurus</i>	1	1	1	1	2	1	?	0	0	1	1	1	2	1	1	0	0	1	1
<i>Peloneustes</i>	0	1	1	1	2	0	0	0	?	?	0	0	0	1	1	0	0	1	1
<i>Plesiosaurus</i>	1	1	1	1	2	1	?	0	1	0	0	0	1	1	1	0	0	1	1
<i>Pliosaurus</i>	0	1	1	1	?	0	?	?	?	?	?	?	?	?	?	0	?	?	1
<i>Polycotylus</i>	1	1	1	1	2	0	x	0	0	2	0	1	1	1	1	1	?	?	1
<i>Rhomaleo. megaceph.</i>	0	1	1	1	2	0	?	0	?	?	?	?	?	?	1	?	0	?	1
<i>Rhomaleo. victor</i>	?	?	?	1	2	?	?	?	0	?	0	0	1	1	1	0	0	1	?
<i>Rhomaleo. zetland.</i>	?	1	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Simolestes</i>	?	1	1	1	?	0	?	0	?	?	0	?	0	1	1	0	0	0	1
<i>Styxosaurus</i>	1	?	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Thalassiodracon</i>	0	1	1	1	2	0	?	0	0	0	0	0	1	1	1	0	0	1	1
<i>Tricleidus</i>	1	1	1	1	2	0	0	0	0	2	1	0	2	1	1	0	0	1	1
<i>Trinacromerum</i>	1	1	1	1	2	0	x	0	0	2	0	1	1	1	1	1	0	1	1

144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	
0	0	x	0	0	0	0	0	x	0	x	x	0	0	0	1	2	0	0	0	0	0	1	
1	?	?	1	?	?	0	0	x	?	x	x	?	?	?	0	1	?	?	?	?	?	0	
?	1	x	?	1	1	0	0	x	0	x	x	1	1	0	1	?	0	0	0	?	?	0	
0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	1	2	1	0	1	1	1	?	
1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0	0	?	1	1	0	
1	1	1	1	1	1	0	1	?	0	0	0	1	1	1	1	2	0	?	?	1	?	0	
?	?	?	?	?	?	1	1	?	?	0	1	?	?	0	?	?	1	?	1	1	?	?	
0	1	1	1	1	1	1	1	?	?	0	0	1	?	0	1	2	1	?	1	1	?	0	
1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2	1	1	1	1	0	0	
1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2	1	3	1	1	1	?	
1	1	0	1	1	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
1	1	?	1	1	?	1	1	0	0	0	0	1	1	1	1	2	0	2	1	1	0	0	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
1	1	1	1	1	?	?	1	?	?	0	0	?	?	0	1	2	1	?	?	1	?	?	
?	?	?	?	?	?	1	1	0	0	?	0	1	?	?	?	?	?	?	?	1	?	?	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	2	1	0	1	1	0	0	
1	1	1	1	1	1	1	1	0	0	0	0	1	1	?	1	2	0	?	?	1	?	?	
1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	2	0	1	1	1	0	0	
1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	2	0	1	1	1	0	0	
1	1	0	1	1	1	1	1	1	1	1	0	0	1	1	0	1	2	1	?	?	1	?	0
1	1	?	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0	?	?	1	?	0	
1	1	1	1	1	?	0	1	0	0	0	0	1	1	1	1	2	0	3	1	1	0	0	
?	1	?	?	?	?	0	1	0	0	0	0	1	1	1	1	2	0	?	?	1	?	?	
1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	2	0	0	?	1	?	?	
?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	
1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0	0	1	1	0	0	
1	1	0	1	1	?	1	1	1	1	0	0	1	1	0	1	2	1	2	1	1	?	0	
1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2	1	3	1	1	1	0	