Chapter 5 - Morphometric and cladistic analyses

“It cannot but be matter of regret, that so considerable a rarity, the like whereof has not been observ’d before…should be maim’d and imperfect, yet we may content ourselves if enough be still visible to favour a conjecture of what it has been.”

William Stukely, 1719

The first ever account of (what is now known to be) a plesiosaur.

5.1 Analyses
To resolve the systematics of Lower Jurassic plesiosaurs, and to investigate the relationships amongst pliosaurs in general, two complementary approaches were used. Morphometric analyses of the proportions of Lower Jurassic pliosaurs were performed to augment interpretation of taxonomic units and to aid in the formulation of discrete characters for phylogenetic analysis. A specimen-based cladistic analysis of relevant rhomaleosaurid specimens was also performed, combined with Operational Taxonomic Units (OTUs) representing many other pliosaur genera, and additional genera of plesiosaurs for outgroup comparisons.

5.2 Specimen-based morphometric analyses
Morphometric analyses comprise mathematical comparisons of linear distances measured from specimens, allowing size to be differentiated from shape (Reyment et al. 1984). However, analyses of this type are not always straightforward when dealing with fossils and a number of limiting factors were encountered during the collection of the morphometric data in this Thesis. These are outlined below together with a number of other caveats.

5.2.1 Taphonomy 1 - Preservation of parts. Most specimens are incomplete so that it is impossible to take measurements of missing elements. Consequently, the most useful measurements are those taken from the most frequently and completely preserved parts of the anatomy, in particular, the skull and mandible, the girdles, the propodials and the epipodials (Figure 5.1).

5.2.2 Taphonomy 2 – Exposure. Even in more-or-less complete specimens, data is typically limited because plesiosaur remains are usually preserved in a matrix horizon exposing only one view of the skeleton (dorsal or ventral). From the perspective of this analysis, specimens exposed in ventral view were the most useful because these provided data for the girdles. However, due to the typical lack of
overlap, morphometric comparisons of girdle measurements with dorsal skull measurements were generally not possible.

5.2.3 Accessibility - Some specimens are not accessible because they are ‘permanently’ displayed high off the ground and/or behind a glass screen. Other specimens have been destroyed (see Chapter 3). In many cases this problem was overcome by the existence of accessible casts (casts exist of BMNH R1336, BMNH 2018*, BRSMG Cb 2335, BRSMG Cb 2479, see Chapter 3 for details).

5.2.4 Size of data set - The number of specimens included in the analysis is low, this is an artefact of the relatively low numbers of specimens collected.

5.2.5 Data collection

Morphometric data was for compiled for 18 specimens; measurements were collected first hand for 17 specimens and from the literature for a single specimen (see below). Measurements were taken for a large number of variables in all specimens seen first hand during this project (Appendix 4). All of the linear dimensions incorporated in the analysis are represented in figure 5.1. Measurements under 15cm were made with callipers and these are accurate to the nearest 0.1mm; larger measurements were made with a tape measure and are accurate to the nearest 0.5cm. Some widely used key measurements had to be estimated for particular taxa; in most cases these estimates were only made for measurements that were almost, but not entirely, preserved, either due to slight damage or being partly obscured by matrix. These estimates are probably accurate and are indicated by underlined italics in Appendix 4. In some cases, estimates were based on their most closely related taxon, as determined post-hoc from the a preliminary specimen-based cladistic analysis (Smith 2006b); this was only done for taxa which were otherwise very complete in other aspects, for example, the length of the skull (a widely used variable in the following analyses) was estimated for Rhomaleosaurus thorntoni based on R.cramptoni so that all of the postcranial data for the former could be included. These values are indicated by bold type in Appendix 4. **Bold, underlined** values indicate figures based on a counterpart element, for example, the measurements of a right humerus may replace an empty data entry for a missing left humerus. **Bold, italicised, underlined** values indicate figures based on the literature. This includes all of the measurements for HALB ‘uncatalogued’ (see Appendix 2), which were taken from Brandes (1914). Also, some figures in the column for Rhomaleosaurus megacephalus (holotype) were based on Stutchbury
Figure 5.1. Diagram showing various linear dimensions of the plesiosaur skeleton, A. the dorsal surface of the skull, B. the palatal surface of the skull, and C. the mandible and postcranium. These measurements were taken for inclusion in morphometric analyses. Each lettered linear dimension corresponds to a line in Appendix 4.
(1846), this was necessary because only the skull and right forelimb are available for direct measurement as casts, the rest of the specimen was destroyed (see Chapter 3). Additional measurements were taken from Owen (1865) for *Archaeonectrus*. Some data entries in Appendix 4 are represented by a question mark (‘?’) indicating that the measurement is unknown (i.e., not preserved/not exposed), or by the symbol “n/a”, indicating that the measurement is not applicable in that specimen because the particular feature is known to be absent (i.e. characters not shared by all taxa). Finally, data entries represented by a ‘_’ indicate measurements that were omitted due to logistical or time constraints.

Abundant missing data resulted in a considerable lack of overlap between many specimens (Appendix 4), precluding the calculation of principal component coefficients and ruling out a principle component analysis. Instead, ratios were calculated for pairs of variables, selected based on their presence in numerous specimens, and these sets of ratios were then plotted against each other.

5.2.6 Results
The results from the morphometric analyses are presented in Figures 5.2, 5.3, 5.4 and 5.5A-AA. Figures 5.2 and 5.3 are simple charts showing variation in the proportions of the mandibular symphyses in the specimens examined, and Figure 5.4 shows similar variation in the coracoids. Each of the graphs presented in figures 5.5A-AA combines four variables and can be divided into three categories: morphometrics of cranial proportions (Figures 5.5 A-L), morphometrics of postcranial proportions (Figure 5.5M-S), and morphometrics of a combination of cranial and postcranial proportions (Figure 5.5T-Z and AA). In these graphs, black data points represent Toarcian-aged specimens and red data points represent Hettangian and Sinemurian-aged specimens. Despite containing a total of eighteen specimens, the most inclusive graph (comparing four separate variables) (Figure 5.5M), contains fourteen specimens. The most complete data is present for the limbs; this reflects the fact that limb variables can be measured from specimens exposed in both dorsal and ventral view. For a thorough discussion of these results, see Chapters 4 and 7, and for a review of their systematic significance see Chapter 6.

5.3 Specimen-based cladistic analysis
40 operational taxonomic units (OTUs) (see Chapter 3 and Appendix 2) were scored for a total of 93 characters (see below) (Appendix 5). *Cymatosaurus* was chosen as an outgroup because it has been identified as the most basal of all the
Figure 5.2. Mandibular symphysis proportions in Lower Jurassic pliosaurs (grey = Toarcian specimens, black = Hettangian specimens, white = Sinemurian specimens).
Figure 5.3: Mandibular symphysis length in Lower Jurassic pliosaurs (grey = Toarcian specimens, black = Hettangian specimens, white = Sinemurian specimens).
Figure 5.4. Coracoid proportions in Lower Jurassic pliosaurs (grey = Toarcian specimens, Black = Hettangian specimens).
Figures 5.5A-G. Morphometrics of cranial proportions.
Figures 5.5H-L. Morphometrics of cranial proportions, and 5.5AA. Morphometrics of a combination of cranial and postcranial proportions.
Figures 5.5M-S. Morphometrics of postcranial proportions.
Figures 5.5T-Z. Morphometrics of a combination of cranial and postcranial proportions.
sauropthygians included in this analysis (Rieppel, 2000). All other basal (‘non-plesiosaur’) sauropthygians coded for this analysis (Augustasaurus, Pistosaurus and Yunguisaurus) were included within the ingroup to minimise assumptions of relationships between basal and derived sauropthygians. The majority of ingroup taxa are pliosaurs, however, a number of Lower Jurassic plesiosauroid taxa were also included because they share many plesiomorphic characters with the other taxa in this analysis. No derived plesiosauroids (cryptocleidoids, elasmosaurids) were included because there is a strong consensus on the phylogenetic position of these taxa (O’Keefe, 2001a, 2004b; Druckenmiller 2006ab) and they have never been regarded as pliosaurs (Figure 2.3). In contrast, a single representative of the derived, but controversial clade Polycotylidae (see Chapter 2 and Figure 2.3) was included in the analysis (Dolichorhynchops) because there is no consensus as to whether this is a pliosaur or plesiosauroid clade. It was predicted, however, that because of the lack of derived plesiosauroids and associated plesiosauroid characters in this analysis, Dolichorhynchops would tend to group with pliosaurs rather than with plesiosauroids. There is also no current consensus on the phylogenetic position of Simolestes, Leptocleidus or Thalassiodracon (see Chapter 2), so all of these taxa were included. Note that the majority of Lower Jurassic pliosaurs in this analysis are predominantly represented by single specimens.

A heuristic search was performed by use of standard software for phylogenetic analysis (PAUP version 4.0 Swofford, 2000), using a random addition sequence (10 reps). To minimise a priori assumptions regarding the importance of character-evolution, all characters were unweighted for the analysis. Characters 8, 21, 47, 54, 62, 65 and 78 were ordered (see below), because included character states represent stages along a continuum. Tree robustness was tested with jacknife/bootstrap analyses (Efron, 1979) and decay analyses (Bremer support) (Bremer, 1988; Lee and Hugall, 2003). MacClade (Maddison and Maddison, 2000) was employed for drawing trees, tracing characters (to determine clade synapomorphies and homoplastic characters) and for determining tree statistics.

5.3.1 Character list and discussion
All ninety-three of the characters employed in the cladistic analysis presented in this Thesis are listed here and accompanied with an explanation. However, because many of these characters have been the subject of detailed discussion elsewhere (e.g. O’Keefe, 2001a; Smith, 2003; and notably Druckenmiller, 2006a), this is not repeated here. The reader is instead referred to the relevant character discussions
presented by earlier authors. However, twenty-six novel characters have been introduced into the following suite (indicated by a plus sign: ‘+’), and some have been treated to novel modifications to optimise their coding for the specific set of OTUs under investigation (indicated with an asterisk ‘*’). These characters, therefore, warrant justification and are thus accompanied with a thorough explanation and discussion. Character citations refer to existing cladistic analyses that are at least partly dedicated to investigating the relationships within pliosaurs. Other cladistic analyses of plesiosaurs have been dedicated to plesiosauroids (Bardet et al. [1999], Carpenter [1999], Gasparini et al. [2003], Grossman [2007] and Sato [2002, 2003] and they are therefore not cited below. For those characters included in the analyses of O’Keefe (2001a, 2004b) only the original cladistic analysis is cited because, with the exception four novel characters introduced by O’Keefe (2004b), the two character suites are identical.

Characters are listed based on their anatomical position, beginning anteriorly with the cranium. Characters describing the dorsal surface of the cranium are followed by characters describing the palatal (ventral) surface, the brain case and the mandible. The suite of postcranial characters begins with the axial skeleton (moving posteriorly along the vertebral column), and moves into the appendicular skeleton, beginning with the pectoral girdle, the pelvic girdle, and finally, characters of the limbs.

Cranium

+Character 1. Lateral margins of maxillae run parallel. Absent =0, present =1.
In most plesiosaurs the rostrum is triangular and gradually increases in width posteriorly towards the orbits and tapers anteriorly towards the rostrum tip. This character describes a contrasting condition where the preorbital region is compressed laterally along its entire length to form a narrow rostrum in which the lateral margins are parallel for most of their length (Figure 5.6A). In this analysis this character is always associated with a longirostrine condition, although it is potentially possible for a narrow rostrum to occur in a short-snouted species. The character is present in ‘Plesiosaurus’ longirostris (White, 1940), Hauffiosaurus (O’Keefe, 2001a), and Dolichorhynchops (Williston, 1903). This character differs from character 3, in that it differentiates between longirostrine morphologies.
Figure 5.6A. Illustration of character 1, A = state ‘0’, B = state ‘1’.

Figure 5.6B. Illustration of character 2, A = state ‘1’, B = state ‘0’.
**Character 2.** Premaxillary rostrum proportions (premaxilla width relative to premaxilla length). ‘Elongate’ (width of premaxillary rostrum greater than length) =0. ‘Short’ (width of premaxillary rostrum shorter than length) =1.

The posterior margin of the premaxillary rostrum is defined here as the lateral margin of the premaxilla-maxilla suture (where it meets the jaw line). The premaxillary rostrum may be ‘elongate’ (length greater than width) (Figure 5.6B, 4.42), or ‘short’ (width equal to, or greater than length) (Figure 4.1). This character differs from characters 1 and 3 because it is possible for a plesiosaur with a narrow rostrum and/or an elongate preorbital region, to have a ‘short’ premaxillary rostrum (e.g. *Pliosaurus* [see Taylor and Cruickshank, 1993]).

**Character 3.** Preorbital/postorbital length. Equal =0, preorbital region greater (longirostrine) =1, postorbital region greater =2.

This character describes the overall proportions of the skull (see Figure 1.5)

See O’Keefe (2001a, characters 6 and 8, p.35); Druckenmiller, (2006a, character 2, p.251).

*Character 4.** Number of premaxillary teeth. Five =0, more than five =1.

Most Jurassic plesiosaurs have five teeth in each premaxilla; this number increases in some derived forms (e.g. *Hauffiosaurus* [O’Keefe 2001a], *Peloneustes* [Andrews, 1895b], *Macroplata* [BMNH R.5488]). The presence of only five premaxillary teeth in the longirostrine taxon *Dolichorhynchops* (O’Keefe, 2004a) demonstrates that tooth number is not necessarily correlated with an increase in rostrum length. This character has been modified from O’Keefe (2001a, character 106, p.49) and Druckenmiller, (2006a, character 2, p.251) by reducing the coding to two states. The above analyses recognised multivariate states to distinguish between forms with more than five teeth.

**Character 5.** Dorsal midline ridge. Absent =0, present =1.

A sharp midline ridge extends along the premaxilla in some taxa. This feature is typically quite low as in, for example, *Rhomaleosaurus cramptoni* (NMING F8785), *Macroplata* (BMNH R.5488) and *Maresaurus* (Gasparini, 1997), but sometimes extends into a relatively high crest as in *Umoonasaurus*. (Kear et al. 2006). Both of these morphologies are considered homologous in this analysis. The ridge is visible as a triangular cross section (although eroded) in NMING F8749 (Figure 4.38).

See Druckenmiller (2006a, character 6, p. 253).
**Character 6.** Gully anterior and posterior to external nares. Absent = 0, present = 1.
In some taxa the external nares are sunk below the level of the rest of the rostral surface, and are located in an anterior-posteriorly trending gully (Figure 4.48). This character is especially noticeable in the casts of the holotype of *Rhomaleosaurus megacephalus* (BRSMG Cb 2335) (Figure 4.48) and in *Macroplata* (BMNH R.5488) (Figure 4.42).

See O’Keefe (2001a, character 37, p.39); Druckenmiller, (2006a, character 12, p.256).

*Character 7.** Dorsomedian foramen between external nares. Absent = 0, present = 1.
In some specimens a distinct oval foramen bounded by high ridges is situated between the posterior processes of the premaxilla, level with the external nares (Figures 4.1, 4.23, 4.51). An indistinct dorsomedian foramen or ‘cleft’ (Druckenmiller, 2006a) is present in some specimens (e.g. *Archaeonectrus* [BMNH R38525] [Figure 4.41], *Leptocleidus capensis* [Cruickshank, 1997], NMING F8749, LEICS G221.1851) but these differ significantly in position and morphology from the steeply walled condition described here. In some instances this cleft may represent a taphonomic artefact due to crushing (e.g. LEICS G221.1851, NMING F8749) (see Chapters 4 and 7), but the cleft in *Archaeonectrus* (BMNH R38525) appears to be distinct and natural. However the position of the cleft on the rostrum in *Archaeonectrus* is autapomorphic for this taxon and is therefore currently of no phylogenetic significance. Other workers have coded these ‘clefts’ as dorsomedian foraminae (O’Keefe, 2001a, character 13, p.36; Druckenmiller, (2006a, character 9, p.255).

*Character 8.** Premaxilla contacts external nares. Contacts whole medial margin=0, diminutive contact on anteromedial margin =1, no contact =2. Ordered.
In all plesiosaurs the premaxilla extends on the midline between the external nares. In basal sauropterygians the premaxilla forms most of the medial margin of the external nares but in some derived plesiosaurs the contact between the premaxilla and external nares becomes diminutive or absent. The diminutive contact is usually present at the antero-medial margin of the external naris and results from the anterior extension of the frontal reaching the antero-medial margin of the external nares and almost contacting the maxilla (Figure 4.1). This state (1) is novel to this analysis, and typically results in a distinct constriction in the width of the premaxilla, level with the anterior border of the external nares, as seen in *Rhomaleosaurus cramptoni* (NMING F8785), for example (Figure 4.1). This character was used in just two states by O’Keefe (2001a, character 12, p.36) and Druckenmiller, (2006a, character 7, p.254).
**Character 9.** Premaxilla-maxilla sutures diverge or run parallel anterior to the external nares. Absent =0, present =1.

Each premaxilla-maxilla suture runs from the lateral margin of the skull anteriorly (often associated with a restriction or notch, see character 10), extending postero-medially towards the external nares (Figure 4.1). In most taxa these sutures diverge anteriorly at a steady rate for much of their length, but in some they run parallel (e.g. *Rhomaleosaurus cramptoni* [NMING F8785] and *Maresaurus* [Gasparini, 1997]). This character is difficult to code in some longirostrine forms such as *Liopleurodon* and *Peloneustes* because the sutures in these particular taxa appear to run parallel for some of their length (see, for example, Andrews [1913, Plate 1, Fig. 2]) but this is interpreted as an artefact of the length and narrowness of the premaxillary processes and rostrum, and is not considered homologous.

**Character 10.** Lateral constriction/notch at premaxilla-maxilla suture. Absent =0, present =1.

This character refers to a distinct constriction, often present between the premaxilla and maxilla, most easily seen in dorsal or ventral view (Figure 4.9). This character is widely distributed amongst the taxa in this analysis.


**Character 11.** Diastema between premaxilla and maxilla. Absent =0, present =1.

In some taxa, the last premaxillary tooth and/or first maxillary tooth are positioned at a distance from the premaxilla-maxilla suture, forming a diastema or ‘gap’ in the tooth row (Figure 4.36). Following Druckenmiller (2006a), a diastema was coded as present if the gap between the last premaxillary tooth and first maxillary tooth was long enough to accommodate an additional tooth whilst maintaining equal spacing in the tooth row.


**Character 12.** Maxilla-squamosal contact. Absent =0, present =1.

In some specimens the maxilla contacts the squamosal, excluding the jugal from the ventral margin of the skull. This is the case in *Dolichorhynchops* (Williston, 1903), *Leptocleidus capensis* (Cruickshank, 1997), and TMP 94.122.01 (Druckenmiller, 2006a). In this analysis, I follow the simple binary coding of this character introduced...
by Druckenmiller (2006a). In most taxa in this analysis, the jugal contacts the ventral margin of the cheek, separating the maxilla from the squamosal (Figure 4.31).


**Character 13. Triangular process of maxilla. Absent =0, present =1.**
This character describes a process of the maxilla that protrudes postero-dorsally between the orbit and external naris in some taxa (Figure 5.6C). This is most noticeable in NMING F10194 (Figure 4.29) and *Macroplata* (BMNH R.5488) (Figure 4.42). This flange is thin and lies superficial to the frontal and prefrontal; in some specimens (e.g. LEICS G221.1851, Figure 4.48), the flange has been partly eroded away, but flakes are still visible.

**Character 14. Nasal bone. Present =0, absent =1.**
The presence or absence of a nasal bone in derived sauropterygians has been subject to much debate and difference of opinion. In most basal sauropterygians such as the Pachypleurosauria and the Nothosauroidea the nasal is a distinct and often large element situated postero-medially to the external nares (Rieppel, 2000). In contrast, the absence of a nasal has been well established for many derived plesiosaurs, e.g. cryptoclidids (O’Keefe, 2001a). However, there is much confusion regarding this character in many Lower Jurassic plesosaur taxa and basal pistosauroid taxa, and interpretations of the dorsal region of many key specimens vary considerably with respect to the nasal bone. Amongst basal pistosauroids, Sues (1987) and all previous workers recognised nasals in *Pistosaurus* but Rieppel et al. (2002) recently regarded nasals as absent in this taxon. Rieppel et al. (2002) also considered the nasal to be absent in *Augustasaurus*, whereas other workers have identified a nasal in this taxon (R. O’Keefe pers. comm., 2007). In these instances (where I have been unable to make first hand observations), I have followed the most recent published descriptions. Inconsistency in the recognition of nasals also applies to many plesiosaur taxa, with some authors regarding the nasal as absent in all plesiosaurs (e.g. Storrs, 1991; Carpenter, 1999), and others regarding the nasal absent in all plesiosauroids, but retained in pliosauroids (e.g. O’Keefe, 2001a). I follow a general consensus established by Noè (2001), O’Keefe (2001a) and Druckenmiller (2006a) in scoring a nasal as present in the following pliosaur taxa: *Liopleurodon, Simolestes, and Kronosaurus*. However, personal observation of a well-preserved pliosaur (specimen NMING F10194) indicates that nasals are certainly not present in this taxon, at least not exposed on the dorsal surface (Figure 4.29).
Chapter 5

Morphometric and cladistic analyses

Figure 5.6C. Illustration of character 13, A = state ‘1’, B = state ‘0’

Figure 5.6D. Illustration of character 29, A = state ‘1’, B = state ‘0’

Figure 5.6E. Illustration of characters 42 and 43, A = state ‘1’, B = state ‘0’
4.29). It is possible that nasals may be present in this, and other specimens, but that they are overlain by flanges of other bones. Nasal were also not identified, for example, following personal observation of Archaeonectrus (BMNH R38525) (Figure 4.41), NMING F8749 (Figure 4.35), Peloneustes (BMNH R.8574), R. cramptoni (NMING F8785) (Figure 4.1), R. propinquus (WM 851.S) (Figure 4.51), or R. zetlandicus (YORYM G503) (Figure 4.23).


**Character 15.** Frontals contact the external nares. Absent =0, present =1.
In some derived taxa the frontals extend anteriorly and participate in the posterior margin of the external nares (Figure 4.1). In most sauropterygians the frontal is excluded from the narial margin.


**Character 16.** Prefrontals contact the external nares. Absent =0, present =1.
This character describes a condition where the prefrontal contacts the posterior margin of the external nares. This character is independent from character 15, as exemplified by the fact that in some taxa the frontal contacts the external nares but the prefrontals do not (e.g. Rhomaleosaurus cramptoni [NMING F8785] [Figure 4.1], Simolestes [Noè, 2001]), while in other taxa the situation is reversed and the frontal is excluded and the prefrontal contacts the external nares (e.g. Seeleyosaurus [Grossman, 2007], Liopleurodon [Noè, 2001]). Further, these characters are not mutually exclusive (the presence of a positive state for character 15 does not preclude a negative state for 16, and vice versa: for example, Dolichorhynchops possesses a positive state for both characters 15 and 16 (O’Keefe, 2004a).


*Character 17.** Frontals separated on midline (premaxilla contacts parietal). Absent =0, present =1.
In many specimens, the posterior process of the premaxilla extends all the way to the parietals, separating the frontals on their midline (Figure 4.1). In this analysis, this character occurs only in some large-headed forms (e.g. Liopleurodon [Noè, 2001] and Rhomaleosaurus cramptoni [NMING F8785]), but has also been documented in some small-headed forms (not included in the analysis), such as in elasmosaurids (Carpenter, 1997) and in cryptoclidids (Brown and Cruickshank, 1994). The coding
for this character in this analysis differs from that of other analyses, in that only simple binary states are recognised (i.e. presence/absence). Previous workers presented multivariate states to differentiate between the relative position of the premaxilla-parietal contact. This relates primarily to the anterior extent of the parietal, and is incorporated into a novel character in this analysis (character 27).

See O’Keefe (2001a, character 11, p.36); Druckenmiller (2006a, character 5, p.253).

**Character 18.** Frontals contact orbit margin. Present =0, absent = 1.
This character describes the condition in some taxa, where the frontal is excluded from the orbital margin by a contact between the prefrontal and the postfrontal. This character is often difficult to interpret because this region frequently suffers from damage. However, in a number of taxa (e.g. BMNH 49202 [Figure 3.14], *Pliosaurs* Taylor and Cruickshank, 1993), the frontal is clearly excluded from the orbital margin.


*Character 19.** Dorsal margin of orbit convex. Absent =0, present =1.
The dorsal margin of the orbit in plesiosaurs is formed by the prefrontal, frontal, and postfrontal (Figure 4.1). In most sauropterygians the orbits are more or less circular in dorsal view and the dorsal orbital margin is concave (Figure 4.41). This condition differs in some plesiosaurs where the dorsal orbital margin is at least partly convex in dorsal view. A rounded prefrontal and/or frontal bulge forms this convexity. This character is very variable, it is coded as present in *Thalassiodracon* based on Storrs and Taylor’s (1996) figures, however this feature is subtle and contrasts significantly with the most extreme condition as seen in BMNH 49202 (Figure 3.14) where the bulge expands as a wide plate and almost entirely obscures the orbits in dorsal view. Note that this character is also prone to damage and cannot be coded for some specimens.


**Character 20.** Frontal foramina. Absent =0, present =1.
Frontal foraminae, ‘frontal fenestrae’ (Carpenter, 1996), or accessory fenestra (O’Keefe, 2001a) in the frontal bones have been described in *Dolichorhynchops* and *Trinacromerum* (Carpenter, 1996), but O’Keefe (2001) was unable to confirm their presence, presumably because of the state preservation in the specimens.

Druckenmiller (2006a) omitted this character from his analysis (his character X24)
because of “the uncertainty of this feature’s existence” in some taxa (p. 356). More recently this character has been confirmed in other polycotylids (Thililua, Bardet et al. [2003] and Manemergus, Buchy et al. [2005]), and this feature has been regarded as a synapomorphy for the Polycotylidae or a slightly less inclusive clade (Bardet et al. 2003). Distinctive but much smaller foraminae are present in the frontal bones of Rhomaleosaurus cramptoni (NMING F8785) (Figure 4.1), R. propinquus (WM 851.S) (Figure 4.51) and R. zetlandicus (YORYM G503) (Figure 4.23), these are here considered homologous with the larger foraminae seen in polycotylids.


*Character 21. Postorbital forms a ‘footplate’ contacting the squamosal. Contact present as footplate overlapping squamosal =0, contact present but not overlapping squamosal =1. Contact but no footplate =2. Contact absent = 3. Ordered.

This character describes variation in the morphology of the postorbital and the construction of the cheek region (Figure 4.31). The basal condition (state ‘0’), is typified by the nothosauruids Nothosaurus and Lariosaurus (see Rieppel, 2000) and is widespread amongst derived non-plesiosaur sauropterygians (e.g. Augustasaurus [see Rieppel et al. 2002, fig. 3A] and in many plesiosaurs. In these taxa a posterior extension or ‘footplate’ of the postorbital contacts and overlaps the squamosal, extending posteriorly along the dorso-medial surface of the temporal bar and excluding the jugal from the margin of the postorbital fenestra. State ‘1’ describes a similar condition in which a postorbital ‘footplate’ is present and contacts the squamosal, but does not overlap it (e.g. Rhomaleosaurus megacephalus [LEICS G221.1851], NMINGF10194 [Figure 4.31], Hydrorion [Grossman, 2006]). State ‘2’ describes a condition where there is contact between the postorbital and squamosal but no footplate at all (e.g. Dolichorhynchops [Williston, 1903] and Plesiosaurus [Storrs, 1997]). State ‘3’ describes a condition where the postorbital does not contact the squamosal and the jugal concacts the antero-lateral margin of the posttemporal fenestra (e.g. Pliosaurus [Taylor and Cruickshank, 1993], Seeleyosaurus [Grossman, 2007]). This character as formulated for this analysis combines data from two closely related characters used by earlier workers -- ‘postorbital-squamosal’ contact and ‘postorbital morphology’. They were combined because they are partly dependent upon each other, i.e. the footplate represents an extension contacting the squamosal,

**Character 22. Jugal exposed on palatal surface. Absent = 0, present =1.**

This character describes the degree to which the jugal contributes to the palatal surface. In some taxa including *Liopleurodon* (Noè, 2001), *Pliosaurus* (Taylor and Cruickshank, 1993) and NMING F10194 (Figure Figure 4.30), the jugal contacts the suborbital fenestrae, and is bounded laterally by the maxilla. However, this character is often difficult to code because even in skulls exposed in palatal view the position and preservation of the lower jaws frequently obscures this region (Figures 3.14, 4.43, 4.46, 4.49, 4.50).

See O'Keefe (2001a, character 77, p.46).

*Character 23. Jugal contacts orbit margin. Jugal contacts orbital margin but does not exclude maxilla from orbital margin =0, jugal excluded from orbit margin =1 jugal contacts lachrymal or prefrontal, excluding the maxilla from the orbit margin =2.*

The relationship between the jugal and the orbital margin is divided for this analysis into three character states. Most commonly in sauropterygians, the jugal forms the postero-lateral margin of the orbit (Figure 4.31); however, in some taxa, the jugal is excluded from the orbital margin due to contact between the postorbital and the maxilla (state ‘1’). O’Keefe (2001a) included a separate character (char. 31) for this state, but did not recognise a derived state for any of the taxa he coded. In the current analysis this state is also uninformative, an autapomorphy of *Hydrorion* (Grossman, 2006), although because the condition has been documented in other plesiosauroids, it will likely prove informative to later analyses (Grossman, 2007).

State ‘2’ describes a contact between the jugal and another element anteriorly, excluding the maxilla from the orbital margin (e.g. *Pliosaurus* [Taylor and Cruickshank, 1993], *Liopleurodon* [Noè, 2001] and *Peloneustes* [Andrews, 1895b]). The element that contacts the jugal in these taxa is usually interpreted as the lachrymal (Taylor and Cruickshank, 1993; Noè 2001), although O’Keefe (2001a) regarded it as a prefrontal. Irrespective of the identity of this element, this state can be coded if the maxilla is excluded from the orbit.

This character combines three dependent characters used by O’Keefe (2001a, characters. 30, 31 and 32), also note that Druckenmiller’s (2006a) character 14 is equivalent to the single character in O’Keefe’s analysis (30). See O’Keefe (2001a, characters 30, 31 and 32, p.38-39); Druckenmiller (2006a, character 14, p.257).

**+Character 24. Postfrontal ridge. Absent =0, shallow =1 forms sharp ‘ledge’, incorporating the postorbital =2.**
In many of the taxa under study, the medial portion of the postorbital bar may bear a ridge running medio-laterally (Figure 4.5B, 6.1B). State ‘1’ refers to a shallow ridge as described in *Pliosaurus* (Taylor and Cruickshank, 1993), *Rhomaleosaurus megacephalus* (Cruickshank, 1994b) and in *Rhomaleosaurus zetlandicus* (Taylor, 1992a); this ridge is a short shallow feature restricted to the postfrontal. This character is also present as state 1 in BMNH 49202 (Figure 3.14), *Macroplata* (BMNH R.5488) (Figure 4.42), *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.1, 4.5B) and *R. propinquus* (WM 851.S) (Figure 4.51). State (‘2’) is shared by *Hydrorion* (Grossman, 2006) and *Seeleyosaurus* (Grossman, 2007) in the current analysis, but is widespread amongst other plesiosaurs excluded from this analysis. When expressed as state 2 there is a ridge, but it is elongate and positioned posteriorly, extending from the parietal to the postfrontal, and functionally it may be regarded as the anterior margin or ‘ledge’ of the posttemporal fenestra, or the posterior margin of the postorbital bar.

**+Character 25. Pineal foramen size (relative size of pineal foramen/external nares).**

*Large* =0, *small* =1.

In many sauropterygians the pineal foramen is very large, equivalent in size, or exceeding the size of the external nares (Figure 4.29). However, in derived plesiosaurs the pineal foramen may be a subtle feature, much smaller than the external nares. Characters relating to the pineal foramen have been included in analyses of plesiosauroids by Bardet et al. (1999) and Gasparini et al. (2003) who noted that the pineal is lost in some derived plesiosauroids, a state incorporated into a character describing the position of the pineal foramen by Druckenmiller (2006a, character 29) (see character 27 below). However, no cladistic analysis of plesiosaurs has ever coded for difference in the size of the pineal foramen.

**Character 26. Pineal foramen contacts frontals.** *Absent* =0, *present* =1.

This character describes a condition where the anterior margin of the pineal foramen is partly formed by the frontal bones. The character differs from character 27, state ‘2’, because it is possible for the pineal foramen to contact the frontal, even when the pineal foramen is situated posterior to the postorbital bar (e.g. *Yunguisaurus* [see Cheng et al. 2006, fig 1]). This character is shared by *Dolichorhynchops* (O’Keefe 2004a), *Hydrorion* (Grossman, 2006), *Leptocleidus* (e.g. Andrews, 1922a), *Umoonasaurus* (Kear et al. 2006), and *Yunguisaurus* (Cheng et al. 2006).

See O’Keefe (2001a, character 21, p.37); Druckenmiller (2006a, character 30, p.266).
**Character 27. Pineal foramen position.** On posterior portion of parietal = 0, on anterior portion of parietal, but behind the postorbital bar = 1, anterior to posterior border of postorbital bar = 2.

In pachypleurosaurs, nothosauroids and *Pistosaurus* the pineal foramen is always situated posteriorly on the parietal (Rieppel, 2000). In all plesiosaur taxa, however, the pineal foramen is located anteriorly on the parietal (Figure 4.1). In this analysis, two states are recognised for taxa with an anteriorly positioned pineal foramen, those where the pineal foramen is situated behind the posterior margin of the postorbital bar (state ‘1’) (e.g. Figure 4.1) and those where the pineal foramen is situated between the postorbital bars (state ‘2’) (Figure 3.14). State 2 is present in BMNH 49202 (Figure 3.14), *Dolichorhynchops* (Williston, 1903), *Leptocleidus capensis* (Cruickshank, 1997), *Plesiosaurus* (Storrs, 1997), *Pliosaurus* (Taylor and Cruickshank, 1993), *Thalassiodracon* (Storrs and Taylor, 1996), TMP 94.122.01 (Druckenmiller, 2006a) and *Umoonasaurus* (Kear *et al.* 2006). All of the other plesiosaurs in this analysis possess state ‘1’.

See O’Keefe (2001a, character 20, p.37); Druckenmiller (2006a, character 29, p.266).

**Character 28. Dorsal notch on the parietal.** Absent = 0, present = 1.

A distinct notch or ‘cockscomb’ arising on the midline vertex of the posterior part of the parietal, is shared by all species of *Leptocleidus* in which this region is known (e.g Andrews, 1922a). Sato (2002 character 73) first introduced this character in a cladistic analysis dedicated to plesiosauroids, but which also included species of *Leptocleidus*.


**Character 29. Parietal-squamosal lateral angle.** Absent = 0, present = 1.

This character describes a distinct morphology at the rear of the skull, where a rounded lateral angle is formed between the temporal fenestrae at the junction between the squamosals (which are considerably wide) and the parietals (which are narrow) (The ‘squamosal-parietal plate’ [Taylor, 1992a]) (Figure 5.6D). This contrasts with the condition in most sauropod species where the squamosals merge gradually into the parietals (pers. obs.). This character is shared by *Archaenectrus* (BMNH R38525, although it is not clear in this specimen) (Figure 4.41), *Augustasaurus* (Rieppel *et al.* 2002), BMNH 49202 (Figure 3.14), *Maresaurus* (Gasparini, 1997), *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.1), *R. megacephalus* (LEICS
G221.1851) (Figure 4.48), NMING F10194 (Figure 4.29), *R. propinquus* (WM 851.S) (Figure 4.51), *R. zetlandicus* (ORYM G503) (Figure 4.23), and TMP 94.122.01 (Druckenmiller, 2006a). A very strong lateral angle has been restored for *Macroplata* (BMNH R.5488) (Figure 4.42) but this may not be based on a natural feature and is therefore coded as ‘?’. This character is considered distinct from the character ‘parietal wing’ described by Sato (2002, character 33) and Druckenmiller (2006a, character 32) for some polycotylid taxa.

**Character 30. Posterior bulb on the midline.** Absent =0, present =1.

A rounded bulb is formed in many plesiosaurs by the squamosals where their dorsal rami meet on the midline (e.g. Figures 3.14, 4.48). For specimens where the squamosals do not meet on the midline (i.e. they are separated by the parietals) the bulb can still be coded as present or absent, i.e. the presence of a bulb is not dependent on the squamosals contacting on the midline. According to Druckenmiller (2006a), the bulb is absent in *Leptocleidus capensis* (contra Cruickshank, 1997).

See O’Keefe (2001a, character 55, p.41); Druckenmiller (2006a, character 34, p.268).

**+Character 31. Squamosal-quadrate foramen.** Absent =0, present =1.

In some specimens a distinct foramen is situated on the posterior surface of the ventral ramus of the suspensorium, where the squamosal meets the dorsal-most part of the quadrate (See Taylor, 1992a, Figure. 3). This feature was identified by Taylor (1992a) for *Rhomaleosaurus zetlandicus*, and by Cruickshank (1994a) for OUMJ 28585. It is also present in *Rhomaleosaurus cramponi* (NMING F8785) (Figure 4.5B), albeit poorly preserved.

**Character 32. Temporal emargination.** Excavated temporal bar =0, temporal bar not excavated, ventral margin straight =1.

The sauropterygian cheek, the region formed by the posttemporal bar, is excavated in basal forms (Rieppel, 2000). This excavation is regarded as a remnant of a lower temporal fenestra, which would have been present in the diapsid ancestor of sauropterygians (Brown and Cruickshank, 1994). Many derived plesiosaurs however, have no excavation of the ventral cheek margin; in lateral view this region is straight (Figures 4.5C, 4.31).

**Character 33.** Relative size of post-temporal fenestrae and orbits. *Fenestrae longer than orbits* =0, *fenestrae equal to or shorter than orbits* =1.

The temporal fenestrae are typically much longer than the orbits in nothosaurians, but the condition is variable amongst plesiosaurs, with many taxa (e.g. *Dolichorhynchops* [Williston, 1903], *Plesiosaurus* [Storrs, 1997], *Seeleyosaurus* [Grossman, 2007], *Thalassiodracon* [Storrs and Taylor, 1996], TMP 94.122.01 [Druckenmiller, 2006a] and *Yunguisaurus* [Cheng et al. 2006]) possessing fenestrae that are equal in length to, or smaller than, the orbits. Most of the taxa examined in this study have larger posttemporal fenestrae than orbits (e.g. Figures 4.1, 4.48).

See Druckenmiller (2006a, character 4, p.252).

**Palate**

+**Character 34.** Accessory grooves on the palatal surface of the premaxilla and vomer. *Absent* =0, *present* =1.

This character describes an ornamentation of longitudinal grooves and ridges anterior and lateral to the internal nares on the palate surface (Figure 4.36). However, it was recognised in only a small number of specimens in this analysis -- NMING F8749 (Figure 4.36), *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.2), *R. megacephalus* (LEICS G221.1851) (Figure 4.49) and *R. thorntoni* (BMNH R4853) (Figure 4.10) -- which may explain why it has not been employed in any other cladistic analyses of plesiosaurs. The significance of this character was discussed by Cruickshank et al. (1991) who regarded it as an adaptation for channelling water into the internal nares.

**Character 35.** Premaxilla/maxilla contacts internal naris. *Premaxilla contacts margin* =0, *premaxilla excluded from margin (vomer-maxilla contact)* =1, *premaxilla and maxilla excluded from margin (lateral vomer-palatine contact)* =2.

This character describes the configuration of bones around the anterior margin of the internal nares. The premaxilla contacts the external nares in BMNH 49202 (Figure 3.14), *Cymatosaurus* (Rieppel, 2000), *Leptocleidus capensis* (Cruickshank, 1997) and in *Pistosaurus* (Sues, 1987). However, in most plesiosaurs the vomer contacts the maxilla anteriorly excluding the premaxilla from the margin of the external nares (state ‘1’) (Figures 4.43, 4.49, 4.50). A third morphology also occurs when both the premaxilla and the maxilla are excluded from the internal nares due to the vomer contacting the palatine on the lateral margin of the internal nares (e.g. *Dolichorhynchops* [Williston, 1903, Plate IV, Fig. 2.], *Hydrorion* [Grossman, 2006, Fig
This character, as formulated for this analysis, represents a combination of two characters used before: 'premaxilla contacts internal naris margin' (O'Keefe [2001a, character 81, p.46] and Druckenmiller [2006a], character 39, p.271) and 'maxilla contacts internal naris' (Druckenmiller [2006a], character 40, p.272).

See O'Keefe (2001a, character 81, p.46); Druckenmiller (2006a, characters 39 and 40, p.271-272).

**Character 36. Palatine excluded from the internal nares. Absent =0, present =1.**

This character describes the configuration of the bones around the posterior margin of the internal naris. The palatines contact the internal nares in most sauropterygians (Figures 4.30, 4.36, 4.43) but in some plesiosaurs the vomer wraps around the postero-medial margin of the internal naris to contact the maxilla, excluding the palatine from the margin of the internal naris (Figure 4.2). This morphology is shared by *Leptocleidus capensis* (Cruickshank, 1997), *Liopleurodon* (Noé, 2001), *Maresaurus* (Gasparini, 1997), *Pliosaurus* (Taylor and Cruickshank, 1993), *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.2), *R. victor* (Figure 4.50), *R. zetlandicus* (YORYM G503) and *Simolestes* (Noé, 2001). Note also that this character is not dependent on particular states in character 35, because the palatine can at least potentially be excluded by a vomer-premaxilla contact, or even by the vomer forming the entire margin of the internal nares.

See O'Keefe (2001a, character 79, p.46); Druckenmiller (2006a, character 41, p.272).

**Character 37. Vomers extend posterior to internal nares. Present =0, absent =1.**

In most plesiosaurs the vomers extend on the midline posteriorly beyond the internal nares (e.g. Figure 4.2). However, in *Dolichorhynchops* (Williston, 1903), *Hydrorion* (Grossman, 2006) and *Umoonasaurus* (Kear et al. 2006), the vomer terminates at the posterior border of the internal nares.

See O'Keefe (2001a, character 83, p.46); Druckenmiller (2006a, character 42, p.272).

**Character 38. Palatines meet on the midline. Absent =0, present =1.**

The vomers and pterygoids in plesiosaurs usually contact one another on their midline, separating the palatines on the midline (e.g. Figures 4.2, 4.43). The condition differs, however, in *Brachauchenius* (Williston, 1903) and *Liopleurodon* (Noé, 2001), where the palatines meet anteriorly on the midline, separating the
vomer from the pterygoid. O'Keefe (2001a) noted that in some taxa the palatines closely approach on the midline and he coded these as state ‘1’. This is highly subjective and therefore rejected here in favour of a presence/absence character.

See O'Keefe (2001a, character 80, p.46); Druckenmiller (2006a, character 43, p.273).

**Character 39. Open anterior interpterygoid vacuity. Absent =0, present =1.**
The midline region of the palate can be coded from two perspectives. One can code for the absence or presence of vacuities on the midline (e.g. O’Keefe, 2001a), or alternatively one can code for the absence or presence of discrete midline contacts between the paired pterygoids; the degree of fusion between the pterygoids (e.g. Druckenmiller, 2006a). Both perspectives are obviously closely related, but the latter is more useful because it deals with a greater deal of variation than does the simplified presence/absence coding. However, due to the restricted suite of taxa in this analysis, I follow the simplified coding of O’Keefe (2001a) and use a separate character (47) to describe additional variation in the amount of midline contact between the pterygoids. The current character is specified as ‘open’ because in some taxa (e.g. Peloneustes [SMNS 10113 (pers. obs) and O’Keefe, 2001a, Fig. 11.] and Rhomaleosaurus cramptoni [NMING F8785] (Figure 4.2), while the pterygoids are separated anteriorly, there is no distinct vacuity and the parasphenoid extends anteriorly to completely occupy the space between the pterygoids.

See O’Keefe (2001a, character 60, p.42); Druckenmiller (2006a, character 49, p.275).

**Character 40. Suborbital fenestrae. Absent = 0, present =1.**
Open fenestrae, or vacuities, are frequently present between the palatine and the maxilla on the lateral surface of the palate in many large-headed plesiosaurs (Figures 4.2, 4.10, 4.30, 4.49).

See O’Keefe (2001a, character 82, p.46); Druckenmiller (2006a, character 44, p.273).

**Character 41. Lateral palatine vacuities. Absent =0, present =1.**
The lateral palatine vacuities are small openings in the palate situated at the postero-medial edge of the palatine and bounded by the palatine anteriorly and the pterygoid posteriorly (Figures 4.2, 4.30, 4.43, 4.49, 4.50). Because they are small, they have not always been recognised; for example, contrary to some published interpretations lateral palatine vacuities are certainly present in Rhomaleosaurus megacephalus.
(LEICS G221.1851) (contra Cruickshank, 1994b) (Figure 4.49) and Rhomaleosaurus zetlandicus (YORYM G503) (contra Taylor, 1992a) (pers. obs).

This feature is also clearly figured (but termed the ‘palatine fenestra’) in Pliosaurus by Taylor and Cruickshank (1993), and a pair of small vacuities on the palate of Liopleurodon are also considered homologous to this fenestra by Noè (2001). Although in Liopleurodon these are situated far more anteriorly than those of other plesiosaurs, they are treated as homologous in this analysis. Lateral palatine vacuities are also described for Kronosaurus (White, 1935, p.224) (termed ‘palatine foramen’).

See O’Keefe (2001a, character 78, p.46); Druckenmiller (2006a, character 45, p.274).

**Character 42. Shape of the posterior interpterygoid vacuities.**

Round=0, elongate and splint-like=1.

In basal plesiosaurs the posterior interpterygoid vacuities are broad and oval in shape (Figure 4.46). In some derived plesiosaurs, however, these vacuities are stretched out and splint-like in shape (e.g. Leptocleidus superstes, [pers obs], Dolichorhynchops [Williston, 1903, Plate IV, Fig 2.], Brachauchenius (Williston, 1903, Plate XXIV). State ‘1’ is codeable when the anterior and posterior margins form acute angles, rather than being rounded (Figure 5.6E). This character is coded as ‘inapplicable’ for taxa with no posterior interpterygoid vacuities (e.g. Cymatosaurus [Rieppel, 2000]). An additional character state would be uninformative in the current analysis.

**Character 43. Position of vacuities relative to posterior border of ectopterygoid.**

Middle of vacuities situated posterior to margin of ectopterygoid =0, middle of vacuities situated anterior to posterior margin of ectopterygoid =1.

In many taxa the posterior interpterygoid vacuities are situated entirely posterior to the posterior border of the ectopterygoid -- Augustasaurus (Rieppel et al. 2002), BMNH 49202, Hydrorion (Grossman, 2006) -- or the anterior half of the posterior interpterygoid vacuities are roughly level with the posterior border of the ectopterygoid (state ‘0’) (Figure 5.6E) (e.g. Figures 4.2, 4.43, 4.49, 4.50). This condition contrasts with state ‘1’ where the anterior border of the posterior interpterygoid vacuities extend anteriorly so that the posterior margin of the ectopterygoids is level with the middle of the vacuities (e.g. Brachauchenius [Williston, 1903], Leptocleidus capensis [Cruickshank, 1997], L superstes, Pliosaurus [Taylor and Cruickshank, 1993], and Umoonasaurus [Kear et al. 2006]) or level with
the posterior half of the vacuities (seen in *Liopleurodon* [Noè, 2001] and *Simolestes* [Noè, 2001], for example). As in character 42, this character was coded as ‘inapplicable’ for taxa with no posterior interpterygoid vacuities (e.g. *Cymatosaurus* [Rieppel, 2000]).

**Character 44.** Pterygoids meet behind the posterior interpterygoid vacuities. Absent =0, present =1.

In some specimens the pterygoids send medial flanges underlying the basioccipital and basisphenoid and meet on the midline (e.g. Figures 4.2, 4.43, 4.49, 4.50). There is a considerable degree of variation in the structure of this contact, partly dependent on character 45.

See O’Keefe (2001a, character 62, p.43); Druckenmiller (2006a, character 50, p.278).

**Character 45.** Ventrally projecting rolled flange on the pterygoid. Absent =0, present =1.

Situated immediately postero-lateral to the posterior interpterygoid vacuity on the main quadrate-ptyerygoid flange, a ventrally projecting rolled flange occurs in some specimens, for example, *Brachauchenius* (Williston, 1903), *Kronosaurus* (White, 1940), *Liopleurodon* (Andrews, 1913), *Peloneustes* (Andrews, 1895b), *Pliosaurus* (Taylor and Cruickshank, 1993) and in *Simolestes* (Noè, 2001). In state ‘0’, the palatal surface of the pterygoids around the posterior interpterygoid vacuities a flat (Figure 4.39C). In some taxa these flanges unite posterior to the posterior interpterygoid vacuities in a raised symphysis. It is also coded as present in *Hydrorion* (Grossman, 2006) and *Yunguisaurus* (Cheng et al. 2006), and outside of this analysis it is well preserved in *Microcleidus* (BMNH R36184).

See O’Keefe (2001a, character 69, p.44); Druckenmiller (2006a, character 51, p.278).

**Character 46.** Squared lappets of the pterygoid absent =0, present =1.

The ‘squared lappet’ was introduced by O’Keefe (2001a) to describe a small flange that underlies the anterior end of the quadrate ramus of the pterygoid in some taxa (e.g. *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.2), WARMS G10875 (Figure 4.43), *Maresaurus* [Gasparini, 1997]). The lateral and posterior margins of each flange are oriented perpendicular to each other so that the posterior portion of the palate surrounding the posterior interpterygoid vacuities is squared off. However, as pointed out by Druckenmiller (2006a), the codings given by O’Keefe (2001a,
2004b) for this character seem to have been transposed with another; this has led to some confusion regarding the definition of this character. This represents a mistake in the formulation of the matrix of O'Keefe (2001a).

See O'Keefe (2001a, character 50, p.42); Druckenmiller (2006a, character 57, p.282).

Basicranium

**Character 47. Cultriform process of the parasphenoid.** Elongate narrow exposure on palate surface =0, elongate wide exposure =1, diminutive exposure or absent =2. Ordered.

This character describes variation in the amount of parasphenoid exposed on the palate surface. In states ‘0’ and ‘1’ the parasphenoid is exposed between the pterygoids and in some specimens the parasphenoid contacts the posterior margin of the anterior interpterygoid vacuity, completely separating the pterygoids on the midline posterior to the anterior interpterygoid vacuity (e.g. *Plesiosaurus* [Storrs, 1997] and *Dolichorhynchops* [O'Keefe, 2004a]), or it may extend and expand anteriorly into a closed anterior interpterygoid vacuities (e.g. *Peloneustes* [SMNS 10113], *R. cramptoni* [NMING F8785] [Figure 4.2]). Thus, in state ‘0’ the cultriform process is narrow and ‘splint-like’ and/or forms a closed anterior interpterygoid vacuity, while in state ‘1’ it is broad and expanded anterior to the posterior interpterygoid vacuities. State ‘2’ describes a diminutive cultriform process (e.g. Figures 4.30, 4.46, 4.49) or a completely absent cultriform process, as seen in *R. victor* (SMNS 12478) (Figure 4.50).

See O'Keefe (2001a, character 72, p.44); Druckenmiller (2006a, character 49, p.275).

*Character 48. Sharp keel on the parasphenoid.** Absent =0, present =1.

The ventral surface of the parasphenoid may be flat or may produce a sharp keel (Figure 4.2). O'Keefe (2001) subdivided the keel into two states but these are merged for the purpose of this analysis into a simple binary coding. All previous formulations of this character have recognised both a ‘partially keeled’ and ‘fully keeled’ morphology but I have found it difficult to distinguish between these states in the taxa studied for this thesis. The surface of the parasphenoid is completely flat in *Macroplata* (BMNH R5484) and BMNH 49202 (Figure 3.14).

See O'Keefe (2001a, character 71, p.44); Druckenmiller (2006a, character 55, p.281).
**Character 49. Paraoccipital process.** *Elongate and slender = 0, short and robust = 1.*

This character describes the morphology of the paraoccipital processes (Figures 3.14, 4.3). Druckenmiller (2006) included a third state for paraoccipital processes that have a short and slender morphology, but this is not applicable in the current analysis (none of the included taxa exhibit this state). The paraoccipital process is notably short and robust in BMNH 49202 (Figure 3.14), *Dolichorhynchops* (Williston, 1903), and *Plesiosaurus* (Storrs, 1997).


**Character 50. Occipital condyle visible in dorsal view.** *Absent = 0, present = 1.*

In many basal sauropterygians and Lower Jurassic plesiosaurs the occipital condyle, and sometimes parts of the exoccipitals and the supraoccipital, are visible in dorsal view, extending posterior to the squamosal arch (e.g. *Hydrorion* [Grossman, 2006], *Plesiosaurus* [Storrs, 1997], *Seeleyosaurus* [Grossman, 2007], *Thalassiodracon* [Storrs and Taylor, 1996] and *Yunguisaurus*; [Cheng et al. 2006]). This contrasts with the condition seen in most plesiosaurs where the braincase is shifted anteriorly relative to the squamosal arch, so that the occipital is not visible in dorsal view (e.g. Figures 3.14, 4.1, 4.23, 4.29). A median dorsal shelf has also been described in the squamosal arch of polycotylid plesiosaurs (Buchy et al. 2005a), which obscures the condyle in dorsal view; thus an additional character state may be applied in future analyses which include these taxa (*Edgarosaurus* and *Manemergus*).

**Character 51. Vertical position of the occipital condyle.** *Low, below the level of the palate = 0, high, above the level of the palate = 1.*

This character describes the vertical height of the occipital condyle in relation to the palatal surface (Figures 4.3, 4.39) (see also Druckenmiller, 2006a, Fig. 4.24). In the current analysis the only taxa to possess state ‘0’ are BMNH 49202 (Figure 3.14) and *Yunguisaurus* (Cheng et al. 2006); in all other taxa in which this character is determinable, it is situated well above the level of the palatal surface (Figure 4.3). See Druckenmiller (2006a, character 70, p.289).

**Dentition**

**Character 52. Tooth morphology.** *Robust = 0, delicate and needle-like = 1.*
There is a lot of variation in the shape and size of teeth between plesiosaur taxa and indeed within the jaws of a single specimen (Figure 4.5C). Nevertheless, most plesiosaurs can be placed into a broad category of tooth morphology: they either possess large robust caniniform teeth with broad bases (state 0) (Figures 1.5C, 4.4), or have narrow needle-like teeth (state 1) (Figure 1.5A,B). Druckenmiller (2006a) omitted this character because it is difficult to code.

See O’Keefe (2001a, character 103, p.49).

**Character 53. Tooth ornamentation. Finely spaced ridges =0, sparsely spaced ridges =1.**

Most plesiosaur teeth are ornamented by longitudinal ridges (Figure 4.4). These may be divided into two gross morphologies: those where the ridges are numerous and tightly packed, and those that are sparsely spaced (Figure 4.4).

See O’Keefe (2001a, character 105, p.49); Druckenmiller (2006a, character 91, p.304).

**Mandible**

**Character 54. Mandibular symphysis proportions (length/width). Mandibular symphysis long (1.3-2.49) =0, length and width equal (0.9-1.29)=1, short (0.6-0.89)=2, very short (below 0.6)=3, very long (greater than 2.5) =4. Ordered with the following character state tree: (2, 1)(3, 4), 0.**

Although there is a lot of variation in symphysis proportions, this character has typically been employed in pliosaur taxonomy (e.g. Tarlo, 1960). Codings here have been optimised to differentiate between the wildly variable morphologies of say, the very long symphysis in *Peloneustes* (Tarlo, 1960) compared with the short symphysis in *Plesiosaurus* (Storrs, 1997), but also to incorporate more subtle differences between Lower Jurassic pliosaur taxa as identified in the morphometric analyses (see Chapter 5; Figures 5.2, 5.3). The elongate basal condition (state ‘0’) (length/width ratio between 1.1 and 2.49) is seen in *Augustasaurus* (Rieppel et al. 2002) and is also present in many pliosaur taxa. State ‘1’ represents a symphysis where length and width are almost equal (e.g. BMNH 49202, *Eurycleidus* (BMNH R2030*)) (Figure 4.44A), the cast of *R. megacephalus* (BRSMG Cb 2335) (Figure 4.46), *Maresaurus* (Gasparini, 1997), and OUM J28585 (Figure 5.2). State ‘2’ is typified by *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.2), *R. victor* (SMNS 12478) (Figure 4.50), and *Simolestes* (Noè, 2001), their symphyses being shorter than wide (ratio between 0.6 and 0.89) (Figures 5.2). State ‘3’ (very short)
symphyses are only found in Plesiosaurus (Storrs, 1997), Seeleyosaurus (Grossman, 2007) and Hydorion in the current analysis. Peloneustes typifies state ‘4’ with a symphysis length to width ratio of 3.6, [SMNS 10113] but very elongate symphyses (ratio exceeding 2.5) are also found in Brachauenius (Albright et al. 2007) Dolichorhynchops (Williston, 1903), Hauffiosaurus (O’Keefe, 2001a), Kronosaurus (White, 1940), Pliosaurus (Tarlo, 1960) and ‘Plesiosaurus’ longirostris (White, 1940). This character differs from Druckenmiller’s (2006a) character 61, ‘relative length of mandibular symphysis’, which codes for the length of the symphysis relative to the mandible length. However, this ratio provides a similar phylogenetic signal (Figure 5.3). Also, the character employed here is more useful, because complete mandibles are not always preserved in the current suite of taxa, whereas complete mandibular symphyses are more common (e.g. Eurycleidus [BMNH R2030*] [Figure 4.44A]).


+Character 55. Distinct bulb on the medial surface of the retroarticular process. Absent =0, present =1.
This character describes a rounded bulb protruding from midway along the medial surface of the retroarticular process in some plesiosaurs (Figure 4.40B). Although this character is shared by NMING F8749 (Figure 4.40B), ‘P’ longirostris (see White, 1940, Fig. 1), Rhomaleosaurus cramponi (NMING F8785) (Figure 4.2), R. propinquus (WM 851.S) (Figure 4.51), and R. zetlandicus (YORYM G503) (Figure 4.23A), it is prone to damage and is therefore sometimes difficult to code.

Character 56. Constriction behind mandibular symphysis. Absent =0, present =1.
This character describes a constriction, or shallow notch, that is seen behind the mandibular symphysis resulting in a spatulate expanded symphysis (Figure 4.44A). This character is similar to, but independent from, character 10, which describes the spatulate premaxilla.

See O’Keefe (2001a, character 89, p.47); Druckenmiller (2006a, character 78, p.294).

Character 57. Sharp ventral keel on mandibular symphysis. Absent =0, present =1.
This character describes a sharp midline keel sometimes present on the ventral surface of the mandibular symphysis in pliosaurs (Figure 4.44A,B).
(2006a) introduced a third state for this character, differentiating between sharp and rounded keels, but this is not applicable in the current analysis.

See O’Keefe (2001a, character 88, p.47); Druckenmiller (2006a, character 80, p.296).

**Character 58. Number of teeth in the mandibular symphysis. Five to six=0, seven to fourteen=1, less than five =2.**
The number of teeth in the mandibular symphysis varies from less than five (e.g Plesiosaurus [Storrs 1997]) to as many as fourteen in some taxa (e.g. Peloneustes [Tarlo 1960]). Druckenmiller (2006a) concluded that this character is independent of symphysis length.

See Druckenmiller (2006a, character 95, p.307).

**Character 59. Splenial participates in mandibular symphysis. Absent =0, present =1.**
The splenial extends anteriorly along the medial surface of the jaw ramus and participates in the mandibular symphysis in almost all taxa included in this analysis (Figures 4.2, 4.43, 4.44, 4.46, 4.49, 4.50) with the exception of Augustasaurus (Rieppel et al. 2002), Plesiosaurus (Storrs, 1997) and Seeleyosaurus (Grossman, 2007).

See O’Keefe (2001a, character 90, p.47); Druckenmiller (2006a, character 76, p.293).

**Character 60. Bowed mandible. Absent =0, present =1.**
This character was introduced by O’Keefe (2001a), and explored and quantified by Druckenmiller (2006a) who provided an objective method for coding it, i.e. the derived state is present when the mediolateral midpoint of the jaw ramus, at the widest point across the mandible, is situated lateral to the mediolateral midpoint of the mandibular fossa. The ramus in such cases is defined as being curved or ‘bowed’ (e.g. Figures 4.2, 4.50), and contrasts with the straight jaw ramus seen in other plesiosaurs (Figure 3.14).

See O’Keefe (2001a, character 86, p.47); Druckenmiller (2006a, character 75, p.293).

**Vertebrae**

*Character 61. Proportions of anterior cervical vertebral centra. Length greater or equal to height=0, length shorter than height =1.*
The proportions of the cervical vertebrae in plesiosaurs have traditionally been used to separate pliosauroids from plesiosauroids (Brown, 1981). In this analysis, only taxa with cervical vertebrae whose length is shorter than height are coded as state ‘1’; because of the scope of this analysis, most taxa possess state ‘1’ (e.g. Figures 3.4, 4.6, 4.13, 4.14) – only *Attenborosaurus* (BMNH R.1338/1339) (Figure 3.18B), *Augustasaurus* [Sander et al. 1997], *Cymatosaurus* (Rieppel, 2000), *Hydrorion* [Grossman, 2006], *Macroplata* (BMNH R.5488), *Plesiosaurus* (Storrs, 1997), *Seeleyosaurus* (Grossman, 2007) and *Thalassiodracon* (BMNH 2018*) (Figure 3.12) possess state ‘0’. This character is simplified relative to all other cladistic analyses of plesiosaurs (see below) in that only two states are coded; previous analyses recognise equally proportioned vertebrae as a separate state, this state was dropped in this analysis because of the restricted set of OTUs.

See O’Keefe (2001a, character 112, p.50); Druckenmiller (2006a, character 102, p.314).

*Character 62. Number of cervical vertebrae. 24-26=0, 27-29=1, >29=2, 21-23=3, <21=4. Ordered with the following character state tree: (2,1)(3,4),0.*

As with character 54, this character has been optimised to code for both wide and subtle variation amongst the OTUs in the current analysis. The number of cervical vertebrae includes both the atlas and axis and state ‘0’ defines a relatively short-necked basal condition shared by *Augustasaurus* (Sander et al. 1997), *Cymatosaurus* (Rieppel, 2000), and some other plesiosaurs (e.g. *Macroplata*, BMNH R5488, *Archaeonectrus* (BMNH R38525) (Figure 3.15). State ‘1’ represents taxa with between 27 and 29 cervical vertebrae e.g. WARMS G10875 (3.23), *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 3.4), *R. megacephalus* (BRSMG Cb 2335) (Stutchbury, 1846) (Figure 3.18A), *R. megacephalus* (LEICS G221.1851) (Figure 3.22), *R. propinquus* (WM 851.5) (Figure 3.20), *R. victor* (SMNS 12478) (Figure 1.4), *R. zetlandicus* (YORYM G503) (Figure 3.19). State ‘2’ describes taxa with more than 29 cervical vertebrae, these are typically very-long-necked (e.g. *Attenborosaurus* (BMNH R.1338/1339) (Figure 3.18B), *Hauffiosaurus* (HAUFF ‘uncatalogued’), *Hydrorion* [Grossman, 2006], *Plesiosaurus* (Storrs, 1997), *Seeleyosaurus* (Grossman, 2007), *Thalassiodracon* (BMNH 2018*) (Figure 3.12). State ‘3’ represents taxa with between 21 and 24 cervical vertebrae, these are typically short-necked forms (*Peloneustes* [Seeley, 1910], *Pliosaurus* [Tarlo, 1960], *Simolestes* [Andrews, 1913]). Those taxa with the shortest necks occur in state ‘4’: *Brachauchenius* (Williston, 1903) and *Kronosaurus* (Romer and Lewis, 1959) both possess less than 21 cervical vertebrae. These states were formulated based on the
number of vertebrae traditionally recognised in different plesiosaur families (e.g. Persson, 1963).

See O’Keefe (2001a, character 111, p.49); Druckenmiller (2006a, character 99, p.311).

**Character 63.** Zygopophyses ‘butterfly-shaped in dorsal view. Absent =0, present =1.

In state ‘0’ the width between the left and right zygopophyses is shorter than the length from the anterior tip of the prezyapophysis to the posterior tip of the postzygapophysis; this contrasts with the ‘butterfly’ shaped zygapophyses characteristic of state ‘1’ (Figure 4.14C), where the width between the zygapophyses is equal or greater than the length from the anterior tip of the prezygapophysis to the posterior tip of the postzygapophysis, and a distinct lateral notch is present between the pre- and postzygapophyses in dorsal view (Figure 4.14C). This character is widely distributed amongst the plesiosaurs in the current analysis.

**Character 64.** Pair of deep squared depressions on ventral surface of cervical vertebrae. Absent =0, present =1.

This character describes a pair of roughly quadrangular sunken pits, or depressions, sometimes present on the ventral surface of the cervical centra either side of the midline (Figure 4.13C). The nutritive foramina are situated in the base of each pit. This feature is common in Lower Jurassic plesiosaurs such as *Rhomaleosaurus zetlandicus* (YORYM G503), *Macroplata* (BMNH R.5488) and *Sthenarosaurus* (Watson, 1909) and is also present in some more derived Cretaceous forms like *Dolichorhynchops* (Williston, 1903).

**Character 65.** Size of nutritive foramina in cervical vertebrae. Small =0, large =1, absent =2. Ordered with the following character state tree: (0,1),2.

Nutritive foramina in the cervical vertebrae may be very small, large, or completely absent. Within plesiosaurs, *Kronosaurus* (Romer and Lewis, 1959) and *Brachacuenius* (Albright et al. 2007) share state ‘2’. Druckenmiller (2006a) only recognised two states for this character - presence/absence – while O’Keefe (2001a) separated this morphology into two characters, one describing size and position (character 119), and the other coding for presence/absence (character 118). These characters are combined here because the character ‘size of the foramina’ is entirely dependent on a positive state for character 118.
See O'Keefe (2001a, characters 118 and 119, p.50); Druckenmiller (2006a, character 101, p.313).

**Character 66.** Distinct smooth bands on the lateral margins of the cervical centra. Absent =0, present =1.
This character describes a smooth band that runs around the lateral and ventral margin of both the anterior and posterior portions of the centrum where they meet the articular face (Figure 4.13B,D). These smooth bands are delineated from the rest of the lateral surface of the centrum by a sharp line. This character is shared by *Dolichorhynchops* (Williston, 1903), *Hauffiosaurus* (HAUFF 'uncatalogued'), *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.6), *R. propinquus* (WM 851.S), *R. thorntoni* (BMNH R4853) (4.13B,D), *R. zetlandicus* (YORYM G503) and *Sthenarosaurus* (Watson, 1909).

**Character 67.** Sharp ventral keel on cervical vertebrae. Absent =0, present =1.
This character describes a sharp longitudinal keel that is sometimes present on the ventral surface of the cervical vertebrae (Figure 3.23). Tarlo (1960) discussed the significance of this character for differentiating between Callovian pliosaurs, but this keel is widespread amongst plesiosaurs.
See O'Keefe (2001a, character 114, p.50); Druckenmiller (2006a, character 105, p.315).

**Character 68.** Deep median groove on the posterior and terminal surface of posterior cervical vertebrae neural spines. Absent =0, present =1.
A groove is situated on the posterior and terminal surface of the neural spines in some taxa, including *Liopleurodon* (Andrews, 1913), *Rhomaleosaurus cramptoni* (NMING F8785), *R. thorntoni* (BMNH R4853) and *Simolestes* (Andrews, 1913).
See O'Keefe (2001a, character 121, p.51); Druckenmiller (2006a, character 113, p.320).

**Character 69.** Position of the cervical neural spine base relative to the centrum. Situated directly above centrum =0, displaced posterior to centrum =1.
In most sauropterygians the neural spines of the cervical vertebrae are located directly above the centrum (pers. obs). However, in some plesiosaurs the base of the neural spine is shifted posteriorly beyond the posterior margin of the centrum and is positioned above the centrum of the proceeding vertebra (Figure 4.14). This character state is shared by *Eurycleidus* (BMNH R1318), *Maresaurus* (Gasparini,
1997), *Rhomaleosaurus cramptoni* (NMING F8785) (Figure 4.6), *R. megacephalus* (BRS MG Cb 2335), *R. megacephalus* (LEICS G221.1851), *R. propinquus* (WM 851.S), *R. thorntoni* (BMNH R4853), *R. zetlandicus* (YORYM G503) and *Umoonasaurus* (Kear, 2006). The posterior position of the cervical neural spine is accentuated by, but not dependent upon, Character 70.

**Character 70. Cervical neural spine angled backwards. Present =0, absent =1.**
The neural spines of the cervical vertebrae may be predominantly oriented vertically, or inclined posteriorly, relative to the centrum (Figure 3.18B, 4.14B).

See O'Keefe (2001a, character 125, p.51); Druckenmiller (2006a, character 111, p.319).

**Character 71. Cervical ribs bearing hooked anterior process. Present =0, absent =1.**
This character describes a distinct anterior process on the cervical vertebrae ribs (including the axis rib) in many sauropterygians (Figures 1.4, 3.10, 3.12, 3.15, 4.6B). The loss of this character is the derived state.

See O'Keefe (2001a, character 123, p.51); Druckenmiller (2006a, character 115, p.321).

**Character 72. Number of cervical rib facets. Double headed ('dicranopleurous') =0, single headed ('cercidopleurous') =1.**
The earliest classifications of plesiosaurs placed considerable weight upon the number of cervical rib facets -- Seeley (1892) introduced a taxonomic dichotomy between single-headed forms, the Cercidopleura and double-headed forms, the Dicranopleura. Although not widely accepted as a classification, later authors still placed much weight on this character (e.g. Welles, 1943). Williston (1907), Persson (1963) and Brown (1981) all noted that a change in the number of facets actually occurs in all lineages and is correlated with geological age; thus, perhaps too much systematic weight had been placed on this character. Note that although double-headed ribs in some taxa are functionally single-headed (Figure 4.13), both facets abut against each other; since two facets are still visible, these taxa are coded as state '0'.

See O'Keefe (2001a, character 117, p.50); Druckenmiller (2006a, character 107, p.317).

**Character 73. Rib facet on transverse process of dorsal vertebrae. Oblong =0, round =1.**
With the exception of *Cymatosaurus* (Rieppel, 2000) and *Pistosaurus* (Sues, 1987), all of the taxa coded for in this analysis possess round distal facets on the transverse processes of their dorsal vertebrae (Figure 4.16B).


**Character 74.** Irregular vertebra in caudal series. Absent =0, present =1.

This character describes a single irregular vertebra in the terminal caudal series of some plesiosaurs. Most easily seen in *Rhomaleosaurus zetlandicus* (YORYM G503) (Figure 4.24), as a single element notably shorter than all preceding and proceeding vertebrae. A similarly conspicuous (but not necessarily shortened) vertebra was noted in WARWKS G108745, *Rhomaleosaurus megacephalus* (LEICS G221.1851) and possibly in *Rhomaleosaurus cramptoni* (NMING F8785, preparation of this region is required in this specimen). Because the terminal vertebrae are rarely preserved, the distribution of this character is difficult to determine and it is not possible to determine if the vertebra is always in the same position in the caudal series. See Chapter 7 for a review of the possible biological significance of this character.

*Pectoral girdle*

**Character 75.** Postero-lateral corner of coracoid (cornua morphology). Absent =0, present and sharp =1, present and rounded =2.

The coracoids in basal sauropods usually become progressively narrower posteriorly (state ‘0’) (Rieppel, 2000). The posterior process of the coracoid in plesiosaurs is usually elongate in plesiosaurs, constricted immediately posterior to the glenoid and expanded distally to form a posterior cornua or ‘coracoid wing’ (Figures 4.19, 4.33). This lateral cornua may be sharp (state ‘1’), with the lateral and posterior margins forming a distinct angle (Figure 4.33), as in most of the specimens included in this analysis, or may be rounded with the lateral and posterior margins merging gradually into each other (state ‘2’) (Figure 4.19) (e.g. *Attenborosaurus* (BMNH R.1338/1339), *Brachiauchenius* (Albright et al. 2007), *Hauffiosaurus* (HAUFF ‘uncatalogued’), *R. thorntoni* (BMNH R4853) (Figure 4.19) and *Simolestes* (Andrews, 1913).

See O’Keefe (2001a, character 142, p.53); Druckenmiller (2006a, character 128, p.329).
+**Character 76.** Coracoid proportions (ratio of length/width at glenoid). Wide and short (over 0.5) = 0, narrow and long (below 0.5) = 1.

This character describes the proportions of the coracoid by calculating a ratio of length (measured in the parasaggital plane from the tip of the anterior process to the posterior extent of the coracoid) relative to the width (measured across the glenoid). The coracoid proportions may be wide and short (state '0': over 0.5) or narrow and long (state '1': below 0.5). Most plesiosaurs possess the derived state, but the coracoids of *Attenborosaurus* (BMNH R.1338/1339), *Rhomaleosaurus thorntoni* (BMNH R4853), *R. victor* (SMNS 12478), *R. zetlandicus* (YORYM G503) and *Sthenarosaurus* (Watson, 1909) share the short wide coracoid morphology present in all of the non-plesiosaur sauropterygians in this analysis. The codings are based upon the morphometric analysis (Figure 5.4).

**Character 77.** Posterior coracoid median embayment. Absent = 0, present = 1.

This character describes a posterior embayment between the coracoids (Figure 4.19, 4.33). This character is typically regarded as an elasmosaurid feature (e.g. Bardet *et al.* 1999; O'Keefe, 2001a), but is actually much more widespread amongst plesiosaurs. In future analyses including additional taxa with this feature, it should be possible to subdivide this character so as to further describe the shape of this embayment (see Chapter 4).

See O'Keefe (2001a, character 141, p.53); Druckenmiller (2006a, character 127, p.328).

+**Character 78.** Proportions of the anterior process of the coracoid. No process = 0, process width equal to, or greater than length = 1, length greater than width = 2. Ordered.

In most plesiosaur taxa, each coracoid sends an anterior process between the pectoral fenestrae to form a pectoral bar (Figures 4.19, 4.33). Each process may be almost square, i.e. length equal to width (state ‘1’), or the length may exceed the width (state ‘2’) as in *Dolichorhynchops* (Williston, 1903), *Eurycleidus* (BMNH R1317) (Figure 4.44C), *Leptocleidus superstes* (Andrews, 1922a), and *Thalassiodracon* (BMNH 2018*) (Figure 3.12). State ‘0’ applies to taxa with no process or a diminutive process whose width is greater than length.

**Character 79.** Scapula contacts the coracoid medial to the pectoral fenestra. Absent = 0, present = 1.
This character describes the contact between the ventral ramus of the scapula and the anterior process of the coracoid (see character 78), medial to the pectoral fenestra (Figure 1.4). The presence of this contact is seen in a small number of plesiosaurs included in the current analysis (e.g. *Liopleurodon* [see White, 1940, Fig 11c], *Plesiosaurus* [Storrs, 1997], *Peloneustes* [see White, 1940, Fig. 11b], *Rhomaleosaurus victor* (SMNS 12478), *Seeleyosaurus* (Grossman, 2007) and *Thalassiodracon* (BMNH 2018*) (Figure 3.12). See O’Keefe (2001a, character 137, p.52); Druckenmiller (2006a, character 122, p.325).

**Character 80. Scapulae meet on midline. Absent =0, present =1.**
The scapulae may, or may not, contact each other on the midline in plesiosaurs. This character has been shown to vary with ontogeny (Andrews, 1895a) but is still of phylogenetic significance in differentiating between the adult ontogenetic stages of different plesiosaur taxa (see Brown, 1981, Carpenter 1999). On this basis the character is included in the current analysis; the derived state is shared by *Liopleurodon* (White, 1940, Fig 11c) and *Peloneustes* (see White, 1940, Fig 11b).

See O’Keefe (2001a, character 135, p.52); Druckenmiller (2006a, character 123, p.326).

**+Character 81. Dorsal margin of the dorsal scapula blade. Straight =0, angled =1.**
There is a distinct angle to the margin of the dorsal blade of the scapula in some specimens, whereas this margin is straight or gently curved in other taxa (Figure 5.6F). This angle is present in *Dolichorhynchops* (see Williston, 1903, Plate XII), *Eurycleidus* (BMNH R1317) (Figure 4.44C), *Leptocleidus superstes* (Andrews, 1922a), *Peloneustes* (See Tarlo, 1960, Fig 1b), *Pliosaurus* (see Tarlo, 1960, Fig. 5b), TMP 94.122.01 (Druckenmiller, 2006a) and *Umoonasaurus* (see Kear et al. 2006, Text-Fig 5D).

**Pelvic girdle**

**Character 82. Anterior border of pubis excavated. Absent =0, present =1.**
The anterior border of the pubis may by completely convex (Figure 4.20), or it may be interrupted by one or more excavations (Figures 1.4, 3.12, 3.23, 4.44C). O’Keefe (2001a) referred to this character as occurring on the “ventral (medial) margin” (p. 53) but this should read “anterior margin” (R. O’Keefe, pers. comm. 2007). This character is widely distributed amongst plesiosaurs.
Figure 5.6F. Illustration of character 81, A = state ‘1’, B = state ‘0’.

Figure 5.6G. Illustration of character 89, A = state ‘0’, B = state ‘1’.

Figure 5.6H. Illustration of character 90, A = state ‘1’, B = state ‘0’ (A and B represent cross sections though the humerus at point x-y).
See O’Keefe (2001a, character 144, p.40).

**Character 83. Proportions of pubis.** Length equal to, or shorter than width =0, length greater than width =1.

In most plesiosaurs the length of the pubis is shorter than or equal to its width (Figure 4.44C), but in many pliosaurs this element forms an elongate plate whose length exceeds its width (See Seeley, 1910, Text-figs. 7, 10 and 24). This character is shared by *Brachyauchenius* (Albright et al. 2007, *Kronosaurus* (Romer and Lewis, 1959), *Liopleurodon* (Andrews, 1913), *Peloneustes*, (Seeley, 1910), and *Simolestes* (Andrews, 1913). (It should be noted that as figured by Albright et al. 2007 [Fig. 11] the pubis is rotated 90 degrees relative to the midline, so that it appears wider than long in their figure). This character is associated with a notable shortening in the distance between the coracoid and the pubis, and consequently a reduced number of gastralia. This character represents a subdivision of O’Keefe’s (2001a) character 3, ‘relative length of ischium/pubis’.

**Character 84. Length of posterior process of ischium.** Short =0, long =1.

The posterior process of the ischium may be short and broad (Figure 4.20) or elongate (Figure 4.44C).

See O’Keefe (2001a, character 3, p.35); Druckenmiller (2006a, character 147, p.341).

**Character 85. Ilium morphology.** Slender=0, robust =1.

The ilia in basal sauropterygians and most plesiosaurs are elongate slender rod-like elements (e.g. Figure 3.23). In *Rhomaleosaurus cramptoni* (NMING F8785) and *Rhomaleosaurus thorntoni* (BMNH R4853), however, these elements are strikingly robust and short (Figure 4.8, 4.20B). In the current analysis this character is discrete and easy to code, but it may be necessary to quantify this character in future analysis where there is greater variation in ilia morphology.

**Character 86. Distal end of ilium flared.** Absent =0, present =1.

This character describes the greatly flared medio-laterally flattened expansion present on the distal end of the ilium in some taxa (Figure 5.6G) (the distal end is here regarded as the end in contact with the sacral ribs). This flare is so extreme in some cases that ilia have sometimes been misidentified for scapulae (Halstead, 1989). The most infamous example of this mistake resulted in the erection of a new genus based on the unique scapula morphology: ‘*Stretosaurus*’ macromerus’ (Tarlo,
1959), The genus was sunk when later discoveries revealed the scapula was in fact an ilium (Halstead, 1989), but so deeply entrenched has this mistake become, it still confounds authors today (e.g. Albright et al. 2007). This character is present in Liopleurodon (Andrews, 1913), Peloneustes (Seeley, 1910), Simolestes (Andrews, 1913) and Kronosaurus (Romer and Lewis, 1959).

**Fore and hind limbs**

*Character 87. Humerus proportions (distal flare/length). Below 0.49 =0, 0.49 or over (greatly expanded distally) =1.*

This character describes the overall morphology of the humerus. It has been quantified here as a ratio of two measurements: the distal width of the humerus and its length. This character was split into two states based on the clusters resolved in the morphometric analysis (Figure 5.5M) The humeri of taxa possessing state ‘1’ are notably flared distally, whereas in taxa possessing state ‘0’, the humerus is not greatly expanded distally, and/or the humerus is very elongate.

See O’Keefe (2001a, characters 154 and 155, p.54); Druckenmiller (2006a, character 132 p.332).

**Character 88. Relative length of humerus and femur. Humerus longer than or equal to femur =0, femur longer =1.**

The humerus is usually longer than the femur, or both propodials are equal in length. In some taxa, the femora are more elongate than the humeri (e.g. Dolichorhynchops [Williston, 1903], Hauffiosaurus (HAUFF ‘uncatalogued’), Liopleurodon (Andrews, 1913), Simolestes (Andrews, 1913), Peloneustes [see Tarlo, 1960, Fig.9], TMP 94.122.01 [Druckenmiller, 2006a]). Brown (1981, p341) regarded the character “femur larger than humerus” as diagnostic for the Pliosauridea, but the humerus is very slightly longer than the femur (ratio between 1 and 1.1, see Figures 5.5M,V) in many of the pliosauroid taxa investigated in this thesis (Figures 1.4, 3.12, 3.20, 3.22, 3.23). The only Triassic sauropterygian to exhibit a derived state for this character is Yunguisaurus (see Cheng et al. 2006, fig. 2).

See O’Keefe (2001a, character 5, p.35); Druckenmiller (2006a, character 131, p.331).

**Character 89. Anterior margin of humerus. Convex=0, straight =1, anterior flange/concave =2.**
In basal sauropterygians there is often a distinct posteriorly directed kink midway along the humerus shaft (Rieppel, 2000). In taxa with this kink the preaxial margin of the humerus is convex, as seen in *Yunguisaurus* (Cheng et al. 2006) and *Plesiosaurus* (Storrs, 1997). In some taxa there is no distinct kink, but the preaxial margin is still subtly convex, such taxa are also coded as state ‘0’ (*Augustasaurus* [Sander et al. 1997], *Pistosaurus* [Sues, 1987]). State ‘1’ describes a condition where there is no kink in the humerus and the preaxial border is straight for all of its length (the humerus may still appear to be swept backwards [e.g. *R. victor*, Figure 1.4], but the anterior border is not) (Figures 3.15, 3.18B, 4.25, 4.34A, 4.44). State ‘2’ describes a concave preaxial margin. The concave preaxial margin is associated with an anterior flange of the humerus, sometimes termed a ‘knee’, although this is often very subtle (e.g. *Rhomaleosaurus cromptoni* [NMING F8785] (Figure 4.7A,B), *Liopleurodon* (Andrews, 1913), *Simolestes* (Andrews, 1913), *Peloneustes* [see Tarlo, 1960, Fig. 9b]. The preaxial margins of the femora in plesiosaurs are always concave and do not therefore exhibit the same variation as is present in the humeri.


**Character 90.** Sharp longitudinal ridge on anterior margin of humerus. Absent = 0, present = 1.

An elongate longitudinal ridge runs from the base of the humerus head and extends along the preaxial surface of the humerus in the holotype of *Eurycleidus* (BMNH R1317) (Figure 4.44C) (Figure 5.6H). This is rounded proximally but sharp distally, so that a transverse cross section taken mid-shaft is therefore teardrop shape and contrasts with the typically oval shape in other plesiosaurs. This feature was also recognised in F10194 and F8749, but it is difficult to determine in most taxa preserved in slabs because, if present, the ridge may be obscured by matrix (whether the specimen is exposed in dorsal or ventral aspect).

**Character 91.** Distinct facets on humerus for radius and ulna. Absent = 0, present = 1.

In many plesiosaur taxa the distal end of the humerus is angled into separate facets for the radius and ulna (Figure 3.23, 4.34A, 4.44C). Some plesiosaurs possess additional facets for the pisiform and additional postaxial/preaxial bones in the epipodial row (see Robinson, 1975) but most of these taxa are outside the scope of the current analysis.

See O’Keefe (2001a, character 152, p.54); Druckenmiller (2006a, character 136, p.334).
Character 92. Lunate ulna and fibula. Absent =0, present =1.

This character describes the distinctly moon-shaped ulna and fibula as seen in dorsal/ventral view in many plesiosaur taxa (Figures 3.23, 4.34A, 4.44C). The lunate morphology is derived with respect to basal sauropterygians, but amongst plesiosaurs it is restricted to Lower Jurassic forms (pers. obs). Although the ulna and fibula are discrete bones, a lunate ulna is always associated with a lunate fibula and vice-versa. In fact, the fore and hindlimbs within every plesiosaur taxon, consistently and very closely resemble each other in most osteological and proportional details (see for example figure 3 in Caldwell (1997a) and figure 3 in Lingham-Soliar (2000). This indicates that both fore limbs and hindlimbs are, to some degree, under the same genetic controls. Characters of the limbs in plesiosaurs should therefore not be duplicated for fore and hindlimbs respectively. The correlation between fore and hindlimb development in plesiosaurs noted here (also see character 93) is worthy of thorough qualification and quantification.

See O'Keefe (2001a, character 158, p.55); Druckenmiller (2006a, character 139, p.337).

Character 93. Radius: width relative to length. Radius longer than wide =0, equal =1, shorter than wide =2.

In this character, ‘width’ is standardised to represent distal width i.e. the distance from the distal-most preaxial corner to the distal-most postaxial corner of the radius. The radius in all non-plesiosaur sauropterygians is an elongate bone (Rieppel, 2000). In plesiosaurs the length of this element is much shorter and broader, however, state ‘0’ still applies to a number of plesiosaurs where the radius is notably elongate and/or not expanded distally e.g Hauffiosaurus (HAUFF ‘uncatalogued’), Plesiosaurus (Storrs, 1997), Rhomaleosaurus megacephalus (LEICS G221.1851) (Figure 3.22), WARMS G10875 (Figure 3.23), Eurycleidus (BMNH 2061*) (Figure 4.44C). In some plesiosaurs the length and distal width of the radius is equal (state ‘1’) (e.g. Rhomaleosaurus cramptoni [NMING F8785] (Figure 4.7AB) and Leptocleidus capensis (Cruickshank, 1997). In the most derived state, the distal width of the radius is greater than the length (state ‘2’) including Liopleurodon (Andrews, 1913), Leptocleidus clemai (Cruickshank and Long, 1997) and Dolichorhynchops (Williston, 1903). A similar degree of variation can be observed in the tibia of the hind limb, but this is always correlated with an associated change in the radius and so a separate character describing tibia proportions was not deemed appropriate (see character 92 above).
5.3.2 Results
The heuristic search resulted in 2114 equally most-parsimonious-trees (MPTs), each 364 steps in length (sum of minimum possible lengths = 117, sum of maximum possible lengths = 839). The MPTs are supported by the following statistics: CI, 0.321; RI, 0.658; RC, 0.211; HI 0.679; and G-fit, -55.852. Strict and 50% majority-rule consensus trees were computed (Figure 5.7) and have been annotated with the calculated bootstrap, jackknife and decay (Bremer) indices. Overall, the tree support is weak, only seven nodes have decay indices greater than one, and many nodes have bootstrap and jackknife indices lower than 50 percent (Figure 5.7). Also, only 12 characters out of the total 93 have a CI value of 1.0. Despite this, the strict consensus tree (Figure 5.7A) is very well-resolved in overall structure and most of the unresolved areas (resulting in the high number of MPTs) occur in the terminal branches. The 50% majority rule consensus tree resolves two additional nodes (Figure 5.7B). Figure 5.8 shows detail of part of the majority rule consensus tree, illustrating the relative positions of *Rhomaleosaurus* and other lower Jurassic pliosaurs within a monophyletic clade, regarded here as the Rhomaleosauridae. For a thorough discussion of the results and their systematic implications, see Chapters 6 and 7.
Figure 5.7 Consensus trees, A. Strict consensus tree, B. 50% majority rule consensus tree, resolving an additional two nodes (figures in bold). Figures to the left of the nodes represent bootstrap values, figures to the top right of the nodes represent jackknife values, and figures to the bottom right of the nodes, in bold, represent decay indices. Nodes lacking values were poorly supported, with bootstrap and jackknife values below 50 and decay indices 1 or less.
5.8. Detail of the 50% majority rule consensus tree showing the Rhomaleosauridae. Node support is identical to values in figure 5.7B (skulls not to scale).