# Anatomy and Systematics of the Rhomaleosauridae (Sauropterygia: Plesiosauria) 

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"...The pliosaurs were probably the most terrifying marine predators that ever lived...Were it not for the fossil evidence that unquestionably demonstrates their existence, they would surely be relegated to the realm of nightmares."

Richard Ellis, 2003


A Victorian restoration of the ferocious pliosaur, Rhomaleosaurus cramptoni

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## Declaration

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## Adam Stuart Smith

Thursday $1^{\text {st }}$ November 2007


#### Abstract

Specimen NMING F8785, a large pliosaur from the Toarcian of Yorkshire, is the holotype of the genus Rhomaleosaurus and the family Rhomaleosauridae. The skull of this specimen was prepared, allowing a detailed description to be presented. A strong ectopterygoid boss in Rhomaleosaurus would have been covered by a cartilaginous sheath in life, and abutted against the medial wall of the mandible. The first ever, full-body reconstruction of a rhomaleosaurid plesiosaur, Rhomaleosaurus, shows that the body of this animal is dorso-ventrally flattened and that there is very little curvature along the vertebral column, except for the pectoral and anterior dorsal regions. Many aspects of the postcranial skeleton are robust and reinforced. There is a notable change in the proportions of the terminal caudal vertebrae in Rhomaleosaurus, associated with an irregular vertebra indicating the presence of a vertical caudal fin in this taxon.

The anatomical data collected from this specimen, and a number of additional Lower Jurassic pliosaur specimens from the UK and Germany, is incorporated into the first detailed phylogenetic and morphometric analyses dedicated to pliosaurs. Based on the results of the cladistic analyses, the Pliosauroidea forms a monophyletic group in a sister relationship with Plesiosauroidea. Three groups are resolved within the Pliosauroidea: the Rhomaleosauridae, Leptocleidoidea and Pliosauridae. The genus Rhomaleosaurus contains three species, all from the Toarcian of the UK. These include NMING F8785, the holotype of the species Rhomaleosaurus cramptoni; BMNH R4853, the holotype of Rhomaleosaurus thorntoni; and YORYM G503, the holotype of Rhomaleosaurus zetlandicus. Specimen WM 852.S, the holotype of Rhomaleosaurus propinquus, is referred to Rhomaleosaurus cramptoni. ' $R$ '. megacephalus and ' $R$ '. victor do not belong to Rhomaleosaurus sensu stricto and they are removed from this genus. ' $R$ '. megacephalus is referred to Eurycleidus and ' $R$ '. victor represents a novel genus. Specimen LEICS G221.1851 was erected as the neotype of ' $R$ '. megacephalus by Cruickshank (1992b), but this neotype status is rejected because existing casts of the original holotype are valid. This specimen is here referred to Eurycleidus sp., A new species of Eurycleidus (diagnosed by an elongate mandibular symphysis) is introduced for specimen WARMS G10875 based on the cladistic analysis and morphometric analyses. The genera Macroplata and Archaeonectrus


are both valid monospecific taxa within the Rhomaleosauridae, diagnosed by a number of autapomorphies. The following pliosauroid taxa are also supported by the morphometric analysis and/or cladistic analysis: Attenborosaurus, Sthenarosaurus, Hauffiosaurus, 'P' longirostris, and an unnamed taxon represented by specimen BMNH 49202. 'Plesiosaurus’ macrocephalus represents a juvenile rhomaleosaurid plesiosaur. Simolestes resolves as a derived pliosaurid rather than a derived rhomaleosaurid, indicating that a spatulate rostrum is a convergent character amongst pliosauroids. Maresaurus resolves as a rhomaleosaurid and therefore represents the youngest member of this clade.

The descriptions and figures presented in this thesis represent the first detailed descriptions of many specimens and provide new information on the anatomy of rhomaleosaurid pliosaurs. Characters shared by many rhomaleosaurid taxa include a dorsal triangular flange of the maxilla, which extends between the orbit and the external naris; a large ectopterygoid that contacts the suborbital vacuity anteriorly; small semi-circular lateral palatine vacuities and large suborbital vacuities; plate-like developments below the basicranium incorporating squared lappets at the base of the quadrate-pterygoid flange; and a medial bump on the retroarticular process. A large dorso-median foramen situated between the external nares, is restricted to Rhomaleosaurus. The identification of gastroliths in Rhomaleosaurus confirms that this taxon ingested stones. In conclusion, this thesis provides a greater understanding of the anatomy, diversity and variation in Lower Jurassic pliosauroids and presents the first detailed systematic framework for the Rhomaleosauridae.

## Chapter 1 - Introduction and objectives

"Plesiosaurus! A fresh-water Plesiosaurus!’ cried Summerlee. 'That I should have lived to see such a sight! We are blessed, my dear Challenger, above all zoologists since the world began!'"
"The Lost World"
Arthur Conan Doyle, 1912
"...A remarkable deviation from all known recent and fossil reptiles...the Plesiosaurus might be compared to a serpent threaded through the shell of a turtle"
"The Medals of Creation"
Gideon Mantell, 1844

### 1.1. General Introduction

Plesiosaurs are a group of secondarily aquatic diapsid reptiles belonging to the clade Sauropterygia (Carroll, 1988). Diapsids (subclass Diapsida) are a monophyletic group supported by both morphological and molecular data (Lee, 2001) including lizards, snakes, crocodiles and birds, and represent a major sub-group of the amniote vertebrates, i.e. vertebrate organisms with the ability to lay eggs on land (Benton, 1997). The Sauropterygia, as a subgroup of this lineage, includes plesiosaurs, nothosaurs, pachypleurosaurs, and placodonts, taxa in which there is a single pair of temporal fenestrae at the rear of the skull, as opposed to two pairs in most other diapsids (Figure 1.1): this modified diapsid condition is known as euryapsid and is shared with ichthyosaurs. The Euryapsida is variously considered a monophyletic taxon within diapsids (e.g. Caldwell, 1996), or as a recognised (Benton, 1997) or unrecognised (Müller, 2003) polyphyletic assemblage. Plesiosaurs were predominantly marine organisms, although their fossils are not uncommon in brackish, or even freshwater deposits (Cruickshank, 1997; Sato et al. 2002). In terms of their general palaeobiology, all plesiosaurs were carnivorous, ranging in ecological strategy from piscivores and cephalopod catchers (Martill, 1992; Sato and Tanabe, 1998), to super-predators capable of subduing other large marine reptiles (Massare, 1987; Thulborn and Turner, 1993). There is also inferred and direct evidence that plesiosaurs may have occasionally ingested shelled benthic organisms (McHenry et al. 2005). Plesiosaurs vary in size from around 1.5 m long (e.g. Thalassiodracon from the Lower Lias of the UK, 205 million years ago [Ma] [Figure 3.12]) to 15m long giants (e.g. Pliosaurus from the Middle Jurassic Oxford Clay Formation of the UK, 149-159 Ma) (e.g. Buchy et al. 2003). Isolated remains, including a 3m long mandible


Figure 1.1. Diagrams of the four main types of temporal organisation in amniote skulls. A. anapsid (no temporal fenestrae), B. synapsid (single lower temporal fenestra), C. diapsid (two temporal fenestra, upper and lower), D. euryapsid (single upper temporal fenestra). Plesiosaurs possess the euryapsid condition (see text for discussion) (modified from Benton, 1997).


Figure 1.2. Cladogram showing the broad-scale interrelationships amongst basal sauropterygians indicating the derived position of Plesiosauria within the clade (arrow) (modified from Rieppel, 2000).
(Tarlo, 1959; Noè et al. 2004) indicate that these animals perhaps exceeded 17 m in length (McHenry et al. 1996; Creisler, 1998). Despite their familiarity to the public and vertebrate palaeontologists alike, many aspects of the biology and evolutionary history of these marine reptiles remain poorly understood.

Plesiosaurs have an extensive fossil record: they are known from definite but nondiagnostic material from as early as the Middle Triassic, $228-245 \mathrm{Ma}$ (see Benton, 1993 and references therein) but the oldest diagnostic specimens originate from the latest Triassic, 205 Ma (Taylor and Cruickshank 1993; Storrs, 1994). The fossil record shows that plesiosaurs radiated rapidly and reached a cosmopolitan distribution by the early Jurassic around 170 Ma . Subsequent to this radiation, they did not deviate far from a basic structural and adaptive framework (e.g O’Keefe, 2002). Their greatest diversity was achieved in the Late Jurassic (Sullivan, 1987) and as a group they persisted through a number of Mesozoic extinction events (Bakker, 1993), finally becoming victims of the Cretaceous-Paleogene (K-P) mass extinction ( 65.5 Ma ) that claimed so many other large aquatic and terrestrial vertebrate groups (Sullivan, 1987; Bardet, 1994, 1995).

Plesiosaur ancestry has been firmly placed amongst basal sauropterygians (see Rieppel, 2000 and refs therein) (Figure 1.2). In 1914, Williston wrote:
"They began their career as fully evolved plesiosaurs, so far as we know, near the close of the Triassic period".

However, there has been a recent surge in the number of taxa possessing a mosaic of basal sauropterygian and derived plesiosaurian characteristics, and this makes distinguishing and defining plesiosaurs all the more difficult. On the plus side, this aids phylogenetic analyses as more and more closely related forms are discovered and described. Traditionally, the pistosaurid Pistosaurus is regarded as the sister taxon to all plesiosaurs (Sues, 1987). The recently identified pistosauroid taxa Augustasaurus hagdorni Sander et al. 1997, Bobosaurus forojuliensis Dalla Vecchia, 2006, and Yunguisaurus liae Cheng et al. 2006, possess a number of derived characters associated with plesiosaurs, and so these taxa provide interesting information regarding the origin of plesiosaurs. In addition to providing new anatomical data, the age and location of these taxa have important implications for understanding the timing of plesiosaur origins: Yunguisaurus is from the Carnian (early Late Triassic) of China (Cheng et al. 2006), Bobosaurus is from the Carnian of

Italy (Dalla Vecchia, 2006), Augustasaurus is from the Anisian (Middle Triassic) of the USA (Sander et al. 1997), and Pistosaurus is from the Anisian of Germany (Sues, 1987) and similar remains have been described from the Rhetian/Hettangian of the UK (Cruickshank, 1996a). These plesiosaur-like semi-aquatic sauropterygians are distributed worldwide in rocks deposited millions of years before the first known diagnosic plesiosaur. Because this thesis concerns some of the oldest known diagnostic plesiosaur taxa, these pistosauroid taxa are particularly pertinent to this study.

Within Plesiosauria as currently defined (O'Keefe, 2001a), there are two generalised morphotypes: pliosauromorphs with large heads and short necks, and plesiosauromorphs with small heads and long necks (O’Keefe, 2002) (Figure 1.3). Although the gross morphology of the plesiosaurian postcrania is widely considered to have been anatomically conservative throughout the evolution of the group (Carroll, 1988; Storrs 1999), this is actually unsubstantiated and may reflect a relative lack of research on plesiosaur postcrania. There are some plesiosaur taxa, including those forming the basis of this thesis, which do not fit neatly into either of these traditional morphotypes. The large pliosaur Rhomaleosaurus (Chapters 3 and 4) for example, possesses a long neck and a large head; these early forms are therefore potentially pivotal in understanding the evolution and significance of plesiosaur morphotypes.

### 1.2 Palaeobiological review

The function of the relatively long neck in plesiosaurs, their most famous characteristic, is unresolved (Storrs, 1993; Ellis, 2003); that it was a successful adaptation is demonstrated by its duration throughout the long evolutionary history of the clade (Noè, 2006). Contrary to suggestions by early workers such as Zarnik (1925) who suggested the long neck was flexible and acted like a 'harpoon', the flexibility of the plesiosaur neck was in fact quite limited due to the close and rigid articulation between successive cervical vertebrae (Evans, pers. comm. and pers. obs.). Therefore the neck could not coil up to allow the animal to strike prey in the manner of a snake or pleurodiran turtle (Pough et al. 1996). In fact, the neck most likely served as a mechanism for approaching prey, say a school of fish, without the large body of the plesiosaur being detected (Massare, 1988; Ellis, 2003). It has also recently been suggested that the long neck may have been an adaptation for bottom feeding (Noè, 2006; Buchy, 2005).


Figure 1.3. Life restorations of plesiosaurs. A. A typical plesiosauromorph (Elasmosaurus platyurus), B. a typical pliosauromorph (Liopleurodon ferox).

A fully aquatic existence presents problems for egg-laying reptiles because they must make nests on land. Plesiosaurs, however, almost certainly overcame this problem by evolving viviparity (the ability to give birth to live young), as has been documented for other major groups of aquatic reptiles: ichthyosaurs (summarised by Benton, 1991) and mosasauroids (Caldwell and Lee, 2001). Gravid mothers and isolated embryos are known amongst basal sauropterygians (nothosaurs and pachypleurosaurs) (Cheng et al. 2004; Renesto et al. 2003) indicating viviparity in these taxa; thus by applying a behavioral 'phylogenetic bracket' (Witmer, 1995) to Sauropterygia as a whole, plesiosaurs were probably also viviparous. Unfortunately no fossil embryos have been described to empirically verify this behavior in plesiosaurs. Recently, however, Everhart (2007 p.103) points out that some undescribed plesiosaur material represents "fossils of unborn young have been found inside a mother's body cavity", providing the first solid evidence for this conjecture. Fossil plesiosaur embryos were also once identified by Seeley (1896), but they were later re-identified as nodular shrimp burrows (Thulborn, 1982).

A specialised underwater olfactory system has been suggested as a common adaptation in the Plesiosauria (Cruickshank et al. 1991, Brown and Cruickshank, 1994). The internal nostrils - or choanae - are situated anteriorly on the palate and are sometimes associated with palatal grooves, which have been interpreted as adaptations to channel water into the internal nares (Cruickshank et al. 1991). The flow of water through the nasal passage would thus have been maintained by hydrodynamic pressure over the retracted external nares during locomotion, and during its passage through the nasal ducts water would have been 'tasted' by olfactory epithelia. Consequently, under this scenario, the nares had no likely role in air intake and inhalation would have been accomplished via the mouth only. However, this long standing model was recently challenged (Buchy et al. 2006), and an alternative interpretation of the palate was proposed in which the choanae are reidentified at the rear of the palate (i.e. in this interpretation, the choanae are identified as the openings traditionally regarded as posterior interpterygoid vacuities), with the openings traditionally regarded as choanae in plesiosaurs being re-identified as vacuities associated with salt excreting glands. If this is the case, then the external nares may indeed have served a role in breathing at the water surface, as suggested by some early workers (e.g. Zarnik, 1925). More well-preserved fossil specimens will be required to resolve this debate. The traditional terminology for the internal nares is applied throughout this thesis.

Plesiosaurs are known to have intentionally swallowed stones (Taylor, 1981, 1993) gastroliths are commonly preserved in the abdominal region of both plesiosauroids (Ellis, 2003; Everhart, 2005) and pliosauroids (Martill, 1992; Taylor, 1992b). When present, these gastroliths are usually found in quite small numbers although concentrations of more than six hundred are known for some elasmosaurid specimens (Everhart, 2005). These stones may have been used for grinding food in the stomach or may have had a role in buoyancy control (Taylor, 1993), offering a less physiologically expensive way of attaining negative buoyancy than pachyostosis (the production of thickened or dense bone). Although pachyostosis is rare amongst plesiosaurs (it is common in basal sauropterygians [Rieppel, 2000]), it is present in the ribs of the genus Pachycostasaurus from the Middle Jurassic Oxford Clay Formation of England (Cruickshank et al. 1996), and in the ribs of Kronosaurus boyacensis, from the Aptian (Lower Cretaceous) of Colombia (Hampe, 1992). More recently, Henderson (2006) conducted a computational study of the effects of gastroliths in plesiosaurs and showed that rather than effecting buoyancy the presence of these stones would have increased stability and equilibrium of the body in water. Gastroliths may, of course, have had a dual or even multi-purpose in these animals.

### 1.3 Locomotion

All plesiosaurs are derived with respect to basal sauropterygians (i.e placodonts, nothosaurs and pachypleurosaurs) in the acquisition of four hydrofoil-shaped flippers, a shortened trunk, and large plate-like limb girdles (Sues, 1987) (Figure 1.4). The ventrally expanded plate-like pectoral and pelvic girdles, together with the closely packed and well-formed 'gastral basket' and tightly articulated spine provided a sturdy base for movement of the four hydrofoil-shaped flippers; these adaptations reflect a shift from an axial to a paraxial lift-based locomotory repertoire (Robinson 1975; Storrs 1993). There was only one mobile joint in the plesiosaur limb (i.e. the glenoid/ acetabulum) and the fifth digit is shifted proximally relative to the other digits, serving to reduce flexibility and maintain a stiff limb or 'wingfin' (Adams, 1997)
(Figure 1.4). The precise function of these wingfins is uncertain; because plesiosaurs are extinct they cannot be subject to experimental hydrodynamic study. Watson (1924) interpreted plesiosaurs as rowers with their limbs functioning as oars, providing a strong backstroke coupled with a feathered recovery stroke. However, this model was subsequently discounted by Robinson (1975) using a number of clear lines of evidence - particularly the construction of the glenoid and the acetabulum (the only moveable limb joints in plesiosaurs), and the 'wing-like', rather than 'oar-


Figure 1.4. Outline of Rhomaleosaurus victor, a plesiosaur from the Posidonia Shale of Germany, exposed in ventral view showing the plate-like girdles, tightly packed gastralia and wing-like limbs, typical of all plesiosaurs (length $=3.44 \mathrm{~m}$ ).
like', shape of the limbs. Rowing - moving the limbs back and forth as four flat plates - would generate little useful lift, only turbulence (Katz and Plotkin, 1991). Plesiosaur limbs are certainly efficient for underwater flying, with tapered tips for reducing drag (Storrs, 1993), and so the rowing model was replaced with an 'underwater flying' scenario. Godfrey (1984) updated the model and suggested a repertoire now known as 'rowing flight' (Riess and Frey, 1991). In this model, plesiosaurs employed a modified form of flying combining principles of both rowing and flying, in which the downstroke provides both thrust and lift, and the feathered recovery stroke is more-or-less passive. Locomotion is still a poorly understood and actively researched area of plesiosaur palaeobiology. The main area of uncertainty stems from the unique plesiosaur bauplan - they are the only known vertebrate organisms possessing two pairs of fins with a function in propulsion - this raises the question of how these limbs moved relative to each other: the so-called 'four wing problem' (Halstead, 1989). The pectoral and pelvic girdles of plesiosaurs are predominantly reinforced ventrally for muscle attachment to enable a very powerful downstroke but only a weak upstroke (Godfrey, 1984). It has been proposed that the fore and hind limbs alternated to compensate for the lack of thrust during the weak upstroke of one pair of limbs (i.e. the other pair would provide the thrust) (Frey and Riess, 1982; Riess and Frey 1991). Hypothetically, this could provide efficient and constant forward motion. LinghamSolier (2000) regards the rear limbs as being of little or no use in a flying propulsive locomotion, instead being used only for steering and stability while Sanders et al. (2004) endorse a repertoire in which all four flippers move in synchrony. Recent research into the efficiency of these different models using robots, suggests that these repertoires may have been interchangeable and depended on the specific speed and manoeuvrability desired by the animal (Long et al. 2006). Short bursts of speed would have been possible by combining the down stroke of both pairs of limbs simultaneously. Indeed, extant animal are known to change gaits in relation to speed and muscle efficiency (minimising energy output) (Rayner, 2003). Gait may have varied between taxa too, for example, pliosauromorph plesiosaurs have been interepreted as more rapid and manoeuvrable swimmers than other plesiosaurs (Robinson 1975; Massare, 1988. O'Keefe, 2001b).

The ability of plesiosaurs to move on land is another point of contention (Ellis, 2003). The mechanics of their skeletons imply a completely aquatic existence: the limb girdles are only weakly connected to the axial skeleton and this would inhibit the transfer of force from limbstrokes into movement on land. However, small plesiosaurs
may have been relatively unaffected by these constraints and might have used their powerful limb downstrokes to propel themselves forward in short 'hops'.

### 1.4 Anatomy

There is huge variation in the size and shape of plesiosaur skulls, but the general structure remains consistent throughout this clade (Figure 1.5). The parietals form a midline crest situated between the single pair of large upper temporal fenestrae and a pineal foramen is usually present at the anterior border of the parietal. In life, this foramen would have contained a light-sensitive pineal organ. The external nares are small and retracted close to a pair of large upward-facing orbits. The internal nares of the secondary bony palate are situated anteriorly and there is always a pair of posterior interpterygoid vacuities at the rear of the palate, exposing the braincase. An anterior interpterygoid vacuity between the pterygoids may, or may not, be present depending on taxa. The jaw articulation is formed by the quadrate (the quadratojugal is lost) and by the articular. All plesiosaurs possessed pointed teeth set in individual sockets, in life these were constantly replaced. Plesiosaur dentition consists of uniform long and conical teeth with longitudinal ridges (Figure 1.5A), but there is great variation within this typical situation. On one extreme some plesiosaurs had hundreds of tiny smooth pin-like teeth (Cruickshank and Fordyce, 2002) (Figure 1.5B) while on the other some had large robust coarsely ridged teeth (Tarlo, 1960) (Figure 1.5C).

A pair of nutritive foramina (or foramina subcentralia) are situated on the ventral surface of each vertebral centrum. This conspicuous character is one of the easiest to help identify isolated fossil plesiosaur vertebrae. In the cervical vertebrae, each lateral surface of each centrum bears an articulation for a cervical rib: these are double-faceted in early and most primitive plesiosaurs, but this number is reduced to a single facet in later and more derived forms (Persson, 1963). In the anterior cervical centra, the ribs are borne on the ventro-lateral surface of the centrum, but the rib facets migrate dorsally in the more posteriorly situated vertebrae. The cervical series merges into a transitional series of 'pectoral' vertebrae into the dorsal series. During this transition the rib facets migrate from the centrum onto the neural arch where they become long transverse processes in the dorsal vertebrae. These processes support long dorsal ribs. The dorsal centra are often distinctly spool shaped so that the lateral and ventral surfaces are concave. From the dorsal series we pass through the sacral and caudal series, where the rib facets return to the


Figure 1.5. Variation in plesiosaur skulls and dentition. A. Hydrorion brachypterygius, a plesiosaurid from the Toarcian of Germany (Based on Brown, 1993). B. Kaiwhekea katiki, a cryptoclidid from the Maastrichtian of New Zealand (Redrawn from Cruickshank and Fordyce, 2002). C. Liopleurodon ferox, a pliosaurid from the Callovian of Europe. Redrawn from Noè et al. (2003) (Scale bar $=10 \mathrm{~cm})$.
centrum. The caudal vertebrae also bear facets for chevrons on their ventral surfaces

The pectoral and pelvic girdles of plesiosaurs are expanded ventrally into plates (Figure 1.4). The main elements in the pectoral girdle are the coracoids and the scapulae - where these meet on their lateral surfaces they form a laterally facing glenoid facet to accommodate the forelimb. Situated between the scapulae are the clavicles and the interclavicle. In the pelvic girdle, the acetabulum is formed by the pubis situated anteriorly and the ischium posteriorly. The ilium in plesiosaurs is a small rod-like element bridging the gap between the sacral ribs and the pelvic girdle it only contacts the ischium, another diagnostic characteristic for all plesiosaurs (Sues, 1987). Between the girdles is a mesh of gastralia (the 'gastral basket' or 'plastron'); this structure consists of a central row of more-or-less symmetrical median ribs and a number of overlapping lateral ribs (Figure 1.4).

Both the fore and hind limbs of plesiosaurs are developed into wing-like flippers, which closely resemble each other. The propodials (humerus/femur) are relatively long and the epipodials (radius, ulna/ tibia, fibula) are short - they are wider than long in some derived taxa (e.g. Dolichorhynchops). The mesopodials are disk-like and the metapodials and phalanges (finger bones) are elongate and waisted (pinched). Plesiosaurs evolved hyperphalangy (i.e. an increase in the number of finger bones), and often possess accessory bones in the epipodial/mesopodial areas (Figure 1.4). The flippers are curved posteriorly and taper to a sharp tip.

### 1.5 Taxonomic diversity

The colloquial term plesiosaur is a homonym. Strictly speaking the name is reserved for the order Plesiosauria but it is also popularly applied to the Plesiosauroidea, one of two superfamilies within the Plesiosauria sensu stricto (O’Keefe, 2001a). One should be cautious not to confuse these names with the family Plesiosauridae or the genus Plesiosaurus. According to the most recent published analyses of plesiosaur systematics, there are several distinct plesiosaur families distributed between the two superfamilies (O'Keefe, 2001a). The overall taxonomy proposed in this phylogenetic study closely mirrors traditional classifications (e.g. Brown, 1981). The following list represents a current taxonomic scheme for plesiosaurs with the colloquial terminology (as used in many popular accounts and throughout this Thesis) are given in brackets:

```
Plesiosauria [= plesiosaur]
Plesiosauroidea [= plesiosauroid]
    Plesiosauridae [= plesiosaurid]
    Cryptoclididae [= cryptoclidid]
    Elasmosauridae [= elasmosaurid or 'elasmosaur']
    Polycotylidae [= polycotylid]
Pliosauroidea [= pliosauroid or 'pliosaur']
    Rhomaleosauridae [= rhomaleosaurid or 'rhomaleosaur']
    Leptocleididae [= leptocleidid]
    Pliosauridae [= pliosaurid]
    Brachauchenidae [= brachaucheniid]
```

According to the analysis of O'Keefe (2001a), and as outlined above, the first major plesiosaur division is the superfamily Plesiosauroidea, which includes the families Plesiosauridae, Cryptoclididae, Elasmosauridae and the Polycotylidae (the last lineage is sometimes regarded as a pliosauroid family, based on its pliosauromorph morphotype). In spite of this phylogenetic work, the Plesiosauridae remains a poorly supported plesiomorphic group from the Lower Jurassic. As traditionally defined, elasmosaurids span throughout the Jurassic and Cretaceous (Brown, 1993; Grossman, 2007), while cryptoclidids also appear to have had a long distribution, ranging from the Middle Jurassic to the Late Cretaceous (Cruickshank and Fordyce, 2002); however, the taxonomic status of some of the later forms, sometimes included in the clade Cimoliasauridae (Persson, 1963; O'Keefe, 2001a), is disputed (Smith, in review). Certainly, based on the fossil record, polycotylids were the most recent plesiosaur family to diverge and are restricted to the Late Cretaceous. Their position within the Plesiosauroidea (rather than the Pliosauroidea with which they were traditionally allied) has been well demonstrated (Carpenter, 1996; O’keefe, 2001a), but has recently been challenged (Druckenmiller, 2006ab). These issues will be discussed in more detail based on the analyses presented in this thesis (Chapters 5, 6 and 7)

The second recognised plesiosaur superfamily is the Pliosauroidea and forms the focus of this thesis. The group is often colloquially termed 'pliosaurs' (e.g. Ellis, 2003) and includes at least two families, the Rhomaleosauridae and the Pliosauridae (O'Keefe, 2001a). Other authors recognise a further one, or two, families within this superfamily (Ellis, 2003), further differentiating some members, otherwise positioned in the Rhomaleosauridae, into a distinct family, the Leptocleididae (White, 1940;

Kuhn 1961, Persson, 1963; Druckenmiller, 2006), and/or differentiating some derived members otherwise positioned in the Pliosauridae, into a distinct family, the Brachaucheniidae (e.g. Williston, 1925; Carpenter, 1996; Hampe, 1992, 2005). Presuming all four pliosauroid families are valid, the rhomaleosaurids and pliosaurids are restricted to the Jurassic Period; the leptocleidids and brachaucheniids are restricted to the Cretaceous Period. Again, despite the phylogenetic work of O'Keefe (2001a) the rhomaleosaurids are poorly supported.

In summary, recent phylogenetic studies recognise four plesiosauroid families, Plesiosauridae, Cryptoclididae, Elasmosauridae and Polycotylidae. Four families of pliosauroid are recognised, Rhomaleosauridae, Leptocleididae, Pliosauridae and Brachauchenidae. This thesis is primarily concerned with the Rhomaleosauridae.

### 1.7 Thesis objectives

The main aim of this thesis is to assess the diversity and determine the phylogenetic position of Rhomaleosaurus. To achieve this, I present the first cladistic analysis of morphological characters dedicated to pliosaurs, and a morphometric analysis dedicated to Lower Jurassic pliosaurs. The broad objectives of this thesis can therefore be summarised as follows:

1. To fully describe all known specimens referred to Rhomaleosaurus;
2. To assess the anatomical diversity and revise the systematics of Rhomaleosaurus;
3. To determine the validity of the family Rhomaleosauridae;
4. To determine the interrelationships within the Rhomaleosauridae (if valid) and to determine the position of this clade within Pliosauroidea and Plesiosauria

### 1.8 Thesis structure

In subsequent chapters, this thesis is structured to reflect the process through which contingent conclusions were drawn. Firstly, previous work founding the basis of this study is reviewed (Chapter 2 - Historical background). The specific history of each fossil specimen analysed during this project is then presented, along with a review of the basic palaeontological methods employed for illustrating the specimens (Chapter 3 - Material and palaeontological approaches). This is followed by an anatomical chapter, in which specimens are described and compared outside of any systematic framework (Chapter 4 - Specimen descriptions). A chapter of specimen-based
analyses is then presented (Chapter 5 - Morphometric and cladistic analyses) comprising a morphometric analysis and a cladistic analysis, the aims of which are to determine a sound systematic framework, a classification determining the taxonomic affinity of each specimen. This framework forms the basis for the subsequent chapter on systematic palaeontology, including revised diagnoses (Chapter 6 - Systematic palaeontology). Chapter 7 (Discussion) comprises a synthesis of all the results drawn from the thesis, and addresses the original aims outlined above. Finally, Chapter 8 (Conclusions) summarises the main conclusions of the thesis.

## Chapter 2 - Historical background

"There are few orders of reptiles, so long and so widely known as are the plesiosaurs, of which our knowledge is more unsatisfactory" Samuel Wendell Williston, 1903

### 2.1 History of plesiosaurs

Plesiosaurs were one of the first groups of fossil reptiles to be recognised and scientifically described. Stukely (1719) provides the oldest known published illustration of what is now known to be a plesiosaur, a partial specimen from Nottinghamshire, UK. The name Plesiosaurus was not introduced until de la Beche and Conybeare (1821) deduced a "new fossil animal" from bones in the Lias (Lower Jurassic) showing differences from Ichthyosaurus, the better understood contemporary fossil reptile of the plesiosaur. Two years later, fossil hunter Mary Anning discovered the first complete plesiosaur on the Dorset shoreline in 1823 (Cadbury, 2000). There were allegations that the specimen must be a hoax, understandably as these are mysterious animals indeed, but the specimen quickly became the subject of a descriptive paper by Conybeare (1824) who confirmed the authenticity of the fossil and produced the first full-body reconstruction of a plesiosaur (Figure 2.1).

The long scientific history of plesiosaurs therefore spans back to the early nineteenth century (Figure 2.2, Appendix 1), a time when systematic approaches differed significantly from the methodologies of today. As a consequence, plesiosaur classification is particularly confused - not least because in the 1800s the taxonomic level 'genus' was roughly equivalent to the 'ordinal' level as understood today. It is therefore unsurprising that hundreds of species of plesiosaur from strata worldwide, and ranging in age throughout the Mesozoic, were arbitrarily placed into de la Beche and Conybeare's single genus, Plesiosaurus. To some extent, the culmination of this confusion remains with us today and continues to confound our understanding of the phylogeny of plesiosaurs, and, by implication, our understanding of the palaeobiology of these unique organisms. Although many species of Plesiosaurus have now been allocated new generic names, many more remain nomina dubia (Storrs, 1996), again reflecting our changed attitude towards systematics, or simply remain unstudied. Resolving this confusion remains an important area for future research.

### 2.2 Plesiosaur systematics



Figure 2.1. The first full body reconstruction of a plesiosaur (Plesiosaurus dolichodeirus)
(From Conybeare, 1824, Plate XLIX).

Our understanding of the systematics of plesiosaurs has developed through a number of phases, reflecting changes in evolutionary thought and methodologies. The earliest classifications of plesiosaurs placed considerable weight upon the number of cervical rib facets, the length of the neck, and the number of vertebrae comprising the cervical series. Seeley (1892), for example, introduced a taxonomic dichotomy between 'single-headed' rib-forms, the Cercidopleura and 'double-headed' rib-forms, the Dicranopleura, further subdividing the Dicranopleura into the Dolichodeira and Brachydeira: long- and short-necked forms respectively. Although not widely accepted as a classification, later authors still placed much weight on these characters (e.g. Welles, 1943). Williston (1907), Persson (1963) and Brown (1981) all recognised that a change in the number of cervical rib facets actually occurs in all lineages and is thus correlated with geological age rather than evolutionary history; too much importance had been placed on this character. Similarly, doubt was also cast upon the reliability of the length of the neck as a phylogenetic indicator (Bakker, 1993, Carpenter, 1997). More holistic approaches to systematics have been proposed by White (1940), who's classification was primarily based on aspects of the pectoral girdle; Welles (1943) and Persson (1963) presented a more detailed phylogeny determined from a variety of characters, creating a classification and proposing phylogenetic links between taxa. Tarlo (1960) contributed significantly to our understanding of British Jurassic pliosaurs and Brown (1981) revised the contemporary plesiosauroids, recognising variation between individuals, ontogeny, and sexual dimorphism. Hampe (1992) created a phylogeny for seven pliosauromorph species based on 22 characters. Later Bakker (1993) devised a broad phylogeny based on cranial and atlas-axis morphology in a stratigraphic context. Brown and Cruickshank (1994) offered a family level phylogeny with nodes based on skull characters and Carpenter (1997) constructed a similarly broad phylogeny based on a suite of cranial characters. A detailed understanding of plesiosaur bone structure ontogeny (Wiffen et al. 1994), limb development and evolution (Caldwell, 1997ab, 2002), and girdle development (Andrews 1895, 1910), has also facilitated our understanding of the relative importance of characters in adult versus juvenile specimens (sensu Brown 1981).

With the advent of cladistics at the close of the $20^{\text {th }}$ Century, together with novel preparation techniques (described in Taylor, 1992ab; Taylor and Cruickshank, 1993a) and CAT-scan/X-ray technology (Cruickshank et al. 1991; Cruickshank, 1994b; Carpenter, 1997), new methods became available for elucidating the anatomy and investigating the phylogeny of sauropterygians. A comprehensive


Figure 2.2. Graph showing the actual and cumulative numbers of plesiosaur species and genera named since the first plesiosaur was introduced in 1821 (see Appendix 1). Each time interval represents two decades; the cumulative numbers of valid genera and species both increase at a steady rate for most of the history, with a noticeable exponential increase in the last two time intervals (1981-today). Data for 2008 - 2020 was estimated based on the average number of new taxa named per year between 2001 and 2007.
phylogeny of non-plesiosaurian sauropterygians has now been established through the work of Sues (1987), Rieppel (1998, 1999ab, 2000), Rieppel et al. (2002), Storrs (1991) and Cheng et al. (2006) (Figure 1.2). There has been a recent surge in the number of plesiosaurs named (Figure 2.2) and plesiosaur relationships have received recent attention with substantial cladistic works by Bardet and Godefroit (1998), Cruickshank and Fordyce (1998), O’Keefe (2001a; further modified by Smith [2003], O’Keefe [2003, 2004ab] and Kear et al. [2006]), and Druckenmiller (2006ab). Cladistic analyses dedicated to the plesiosauroid superfamily have been provided by Bardet et al. (1999), Carpenter (1999), Gasparini et al. (2003), Grossman (2007) and Sato (2002, 2003). In strong contrast to this spate of recent work, no cladistic analyses have yet been dedicated to the pliosauroid superfamily. This lack of attention is rectified in this thesis.

Of particular relevance to the work presented here, one of the major results of O'Keefe's (2001a) analysis was the corroboration of Carpenter's (1997) finding that polycotylid plesiosaurs are not pliosaurs as traditionally thought, but a clade within plesiosauroids (Figure 2.3). However, contrary to all other cladistic analyses of the Plesiosauria, Druckenmiller (2006ab) recently recognised polycotylids within the pliosauroid superfamily, again raising the question of the phylogenetic position of these derived plesiosaurs (Figure 2.3). There is also no consensus of the superfamilial affinity of Thalassiodracon (Figure 2.4). Furthermore, there is also differing opinion on the position of another family between workers; leptocleidids (i.e. Leptocleidus) are variously regarded as derived rhomaleosaurids (e.g. O'Keefe 2001a) or close relatives of polycotylids, far removed from rhomaleosaurids (Druckenmiller, 2006ab) (Figure 2.3 and 2.4). Thus, although all existing plesiosaur classifications split the order Plesiosauria into two clades, there is no consensus on the exact distribution of particular taxa between and within the two superfamilies. As outlined in Chapter 1, this thesis is concerned with the relationships amongst the Pliosauroidea, especially the interrelationships within the family Rhomaleosauridae.

### 2.4 Rhomaleosauridae - taxon history

The history of Rhomaleosauridae is complicated. Nopsca (1928) was the first to introduce a higher taxon to differentiate Rhomaleosaurus from other plesiosaurs: he erected the name Rhomaleosaurinae for forms with a large head, numerous short cervical vertebrae, and double headed-ribs, however, later workers did not adopt the name. Unusually, Nopsca (1928) regarded this taxon as a subdivision of the Elasmosauridae [=Plesiosauroidea]. The widespread use of the now defunct genus


Figure 2.3. Family-level comparison of two competing hypotheses of plesiosaur relationships. The hypotheses are broadly similar, but differ in the position of Polycotylidae. Druckenmiller (2006a) recognises a distinct clade (Leptocleididae) which form a sister relationship with Polycotylidae within Pliosauroidea. O'Keefe (2001a) resolves polycotylids within the Plesiosauroidea. N.B. The Rhomaleosauridae and Cryptoclididae are actually resolved as paraphyletic assemblages in the analysis of Druckenmiller (2006a) but they are depicted here as monophyletic in both cladograms for ease of comparison - for detailed differences between these hypotheses, see Figure 2.4.


Figure 2.4. Detailed comparison of the two competing hypotheses of relationships amongst plesiosaurs, showing the major points of variation (taxa in boxes). The top phylogeny is from Druckenmiller (2006a, modified from Figure 4.42); the bottom phylogeny is from O'Keefe (2001a, modified from Fig. 20). Both phylogenies divide plesiosaurs (labelled 'PLESIOSAURIA') into two superfamilies, Plesiosauroidea and Pliosauroidea (Pliosauroidea = Clade A in Druckenmiller's phylogeny). In particular, note the differing position of polycotylids (=Clade B in Druckenmiller's phylogeny) in a derived position in Pliosauroidea according to Druckenmiller, and in a derived position in Plesiosauroidea according to O'Keefe. There is also no consensus on the superfamilial affinity of Thalassiodracon. Within Pliosauroidea, the position of Simolestes and Leptocleidus also show significant variation between the phylogenies (see text for further discussion).

Thaumatosaurus in the early 1900s culminated in the erection of a new family by Romer (1956), Thaumatosauridae, but in accord with Tarlo's (1960) observations on Thaumatosaurus (see below), this clade was later renamed Rhomaleosauridae by Kuhn (1961) and this taxonomy ("Rhomaleosauridae Kuhn 1961") was adopted by subsequent workers who considered such a clade valid (e.g. Persson, 1963; Appleby et al. 1967; O’Keefe, 2001a). However, Nopsca (1928) takes credit for introducing a 'rhomaleosaur' clade in the first place, and so the taxon should be cited "Rhomaleosauridae (Nopsca, 1928) Kuhn 1961", because Kuhn changed the spelling from 'Rhomaleosaurinae' to the currently used Rhomaleosauridae. Other authors cite the taxon Rhomaleosauridae based on more recent revisers, for example Kear et al. (2006) cite the taxon as "Nopsca 1928 (sensu O'Keefe, 2001a)".

Persson (1963) considered the Rhomaleosauridae a valid clade, based on a combined suite of characters: the number of cervical vertebrae (20-27); a distinct notch at the premaxillary-maxillary suture; mesodeiran neck length; and a "slightly elongate" preorbital part of the skull. White (1940) also identified a clade including Rhomaleosaurus, Eurycleidus and Leptocleidus, to which he applied the new name Leptocleididae, a taxon that has only been recognised sporadically (Druckenmiller, 2006ab) and often adopted with caution -- Forrest and Oliver (2003), for example, used "the term 'Leptocleididae' to refer to small pliosauroid plesiosaurs commonly found in the Lower Cretaceous" (p.271). White (1940) also introduced another new family, Brancasauridae, to accommodate, amongst other taxa, Rhomaleosaurus victor (he referred to this species by the now defunct name Thaumatosaurus, but it is clear from his paper that he is referring to the species victor because this is the only species he refers to the genus). This taxon has not gained any acceptance; in fact, until recently, the diagnoses for all of these families were insufficient for present systematic purposes and most recent authors (e.g. Tarlo, 1960; Brown, 1981; Taylor, 1991; Cruichshank, 1994b, 1997; Benton and Spencer, 1995; Gasparini, 1997) have failed to recognise the Rhomaleosauridae, Leptocleididae, or Brancasauridae as valid taxa, instead placing all pliosauroids in a single family, the Pliosauridae. Turning the tables more recently, the first major cladistic analysis of plesiosaurs (O'Keefe, 2001a) revealed a distinct but poorly supported rhomaleosaurid clade (Figure 2.3). The Leptocleididae was rejected in this revision, with Leptocleidus being included within Rhomaleosauridae (O’Keefe, 2001a). In contrast again, Druckenmiller (2006ab) did not resolve a rhomaleosaurid clade. As the study by O'Keefe (2001a) remains the largest published phylogenetic analysis of plesiosaurs, I follow his
proposal as the null hypothesis for this Thesis: that pliosaurs may be divided into two families, pliosaurids on the one hand, and rhomaleosaurids on the other.

The eponymous rhomaleosaurid, Rhomaleosaurus, was introduced by Seeley (1874) as a new name for Plesiosaurus cramptoni, a specimen that is the holotype for the genus, and for the family Rhomaleosauridae (see Chapter 3). This taxon therefore forms the hub of any debate concerning the taxonomy and systematics of Lower Jurassic plesiosaurs (Smith, 2006a). The group remains poorly understood and the genus Rhomaleosaurus contains a high number of species, including (in alphabetical order) cramptoni, longirostris, megacephalus, propinquus, thorntoni, victor, and zetlandicus (see Chapter 3 and Appendix 2). However, there appears to be a great deal of morphological diversity between many of these specimens (Smith, 2006b). One particular problem with unravelling the systematics of the family is that "the Rhomaleosauridae is a highly conservative, plesiomorphic clade" (O'Keefe, 2001a, p.30), and they are particularly understudied. From a macroevolutionary perspective, plesiosaurs are typical in having a sudden origin and a subsequently long duration relatively morphologically unchanged (Carroll, 1997). Therefore, the position of the rhomaleosaurids at the base of the plesiosaur family tree, and the fact that they represent one of the first major plesiosaur radiations, makes this group particularly important for understanding plesiosaur origins within a phylogenetic and palaeobiological context.

Although rhomaleosaurid plesiosaurs are best known from the Lower Jurassic strata of the UK and Germany, they have also been reported from the Jurassic of China (Young, 1944; Dong, 1980; Zhang, 1985). Leptocleidids are known from the Lower Cretaceous of the UK (Andrews, 1922a), South Africa (Andrews, 1911; Cruickshank, 1997), Australia (Cruickshank and Long, 1997; Kear et al., 2006), and North America (Druckenmiller, 2006ab). Prior to the recognition of the genus Umoonasaurus from the Lower Cretaceous of Australia (Kear et al. 2006), all Cretaceous rhomaleosaurid and leptocleidid plesiosaurs were grouped under the single genus Leptocleidus making this the most geographically widespread genus of plesiosaur after Plesiosaurus (see above).

### 2.5 Rhomaleosauridae - previous work

The small body of modern research dedicated to Jurassic rhomaleosaurid plesiosaurs is predominantly restricted to reconstructions of their skulls (Taylor, 1992b, Cruickshank, 1994b, 1996b). Forrest (2000) described some large
fragmentary postcranial material referred to Rhomaleosaurus, suggesting that the animal may have reached up top 8 metres long. The holotype of Rhomaleosaurus (and of the family Rhomaleosauridae) was last described by Carte and Bailey (1963ab) (figured in 1963a), but has never been described in detail or in modern terms. The skull has only recently been prepared (see Chapter 3) allowing the first detailed analysis of this important name-bearing specimen. Due to the poor support of the clade, O'Keefe (2001a) restrained from revising the systematics of this genus: "a formal revision of Rhomaleosaurus is best left until a more detailed cladistic analysis of the Rhomaleosauridae is made" (p.23). This thesis also provides the first such detailed analysis for Lower Jurassic pliosaurs.

### 2.6 Rhomaleosaurus or Thaumatosaurus?

Historically, the genus Rhomaleosaurus has been interchangeable with 'Thaumatosaurus'. The confusion between these two taxa arose from the personal dispute and taxonomic inconsistency between Richard Lydekker and Harry G. Seeley, two prolific nineteenth century palaeontologists who both "refused steadfastly to recognise the generic and specific names proposed by one another" (Tarlo, 1960, p.148). Seeley named Rhomaleosaurus in 1874 based on a specimen already named Plesiosaurus cramptoni (Carte and Bailey, 1863a); however, Lydekker regarded Rhomaleosaurus as a synonym of Thaumatosaurus (Lydekker, 1889ab), a genus named by von Meyer (1841). The use of Thaumatosaurus (over Rhomaleosaurus) was most noticeable and influential in Lydekker's catalogues of the fossil Reptilia and Amphibia produced for the British and Irish Natural History Museums (Lydekker, 1889b, 1891). Fraas (1910) recognised both generic names, but followed Lydekker, referring a beautifully preserved specimen of a new species of plesiosaur, victor, to Thaumatosaurus. The name Thaumatosaurus, was also adopted by many other subsequent authors (e.g. Brandes, 1914; von Heune, 1921, Williston, 1925) and used in popular texts (e.g. O'Riordan, 1983), and the genus name was therefore popularised, essentially due to the exceptional preservation of the specimen described by Fraas (Tarlo, 1960). Andrews (1922a) pointed out the insufficiency of the holotype of Thaumatosaurus and created a new genus name (Eurycleidus) for Hettangian forms formerly attributed to Thaumatosaurus. However, the name Thaumatosaurus was not officially rejected, nor was any mention made by Andrews (1922a) of the genus Rhomaleosaurus. Introducing more confusion, many authors have recognised Rhomaleosaurus and Thaumatosaurus as distinct taxa (e.g. White, 1940). Tarlo (1960) finally resolved the issue and rejected the genus

Thaumatosaurus altogether, because it is based on insufficient type material, and the species victor was therefore formally referred to Rhomaleosaurus.

## Chapter 3 - Material and palaeontological approaches

## "There's bes baak-bwoone."

"An ther's hes ribs."
"Have her got a head?" A blow follows the question that breaks the head and neck - or rather the slab as the skeleton was buried in the centre of the Stone-to eleven pieces...
"What ell Measter Haakins zay?"
"Oh we can tell un that we did'nt know what 'twere and waanted to zee a bit."
"Book of the Great Sea-Dragons"
Thomas Hawkins, 1840
(Supposed colloquy between two quarry men: Hawkins later restored the fragmented
plesiosaur specimen.)

### 3.1 Institutional abbreviations

The following abbreviations are used throughout this Thesis, including the appendices:
BMNH, The Natural History Museum, London, UK (formerly British Museum of Natural History);

BRSMG, Bristol City Museum and Art Gallery, Bristol, UK;
CAMSM, Sedgwick Museum, Cambridge, UK;
CMN, Canadian Museum of Nature, Ottawa, Canada;
FMNH, Sternberg Museum of Natural History, Fort Hayes, Kansas, USA;
GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tubingen, Germany;
HALB, Halberstadt Museum, Halberstadt, Germany;
HAUFF Urwelt-Museum Hauff, Holzmaden, Germany;
LEICS, New Walk Museum, Leicester, UK;
MB, Naturkundemuseum (Humboldt Museum) Berlin, Berlin, Germany;
MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;

MM, Manchester Museum, Manchester, UK;
NMING, National Museum of Ireland (Natural History), Dublin, Ireland;
MOZ, Museo Prof. Olsacher, Zapala, Neuquén, Argentina;
NMNS, National Museum of Natural Science, Taiwan, China.
OUM, Oxford University Museum of Natural History, Oxford, UK;
PETMG, Peterborough City Museum and Art Gallery, Priestgate, Peterborough, UK;
SAM, South African Museum, Cape Town, South Africa;

SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TCD, Geological Museum, Trinity College Dublin, Dublin, Ireland; USNM, United States National Museum (Smithsonian Institution), Washington D. C., USA;

WAM, Department of Earth and Planetary Sciences, Western Australian Museum, Perth, Australia;
WARMS, Warwickshire Museum, Warwick, UK;
WM, Whitby Museum, Whitby, UK;

YORYM, Yorkshire Museum, York, UK.

### 3.2 Data collection - general

Observations (including interpretive drawings) and detailed measurements were collected from fourteen fossil plesiosaur specimens from the Lower Jurassic of Europe (Figure 3.1) (Benton and Spencer, 1995). Included in this material are four casts of pliosaur specimens, for which the original specimens are either inaccessible or destroyed (see below). Each specimen was photographed in detail and primary annotated interpretative drawings were produced. In some cases partial preparation was required to expose particular anatomical features previously compounded by matrix or other 'filler'. The final illustrations figured herein were produced in one of two ways, both methods involving a combination of the primary illustrations and photographs:

## Either,

1. Using a light box the primary illustration was redrawn on a separate sheet traced over a printed photograph,

Or 2. The same method was performed digitally using the 'layers' function in Adobe Illustrator CS10. The primary illustration was superimposed over the photograph and the photograph layer was later removed.

Where possible, these methods were also performed with the specimen present, to ensure accuracy and to double-check any areas of uncertainty. Both methods were deemed to have advantages and disadvantages, in particular the manual method is generally less time consuming (especially for detailed illustrations), but the digital method allows much more flexibility when it comes to correcting mistakes (i.e. the 'undo' button, the ability to remove and restore layers and lines). Later

Figure 3.1. Geographical map showing the discovery locations of twenty-two specimens of Lower Jurassic plesiosaurs, examined during the production of this thesis. All of the
specimens originated from the UK and Germany (highlighted in grey).
reconstructions were produced in Adobe Illustrator based on these interpretative illustrations.

The methods employed in the collection and analysis of data for the cladistic analysis and morphometric analyses are discussed in their respective chapter (see Chapter 5). The rest of this chapter outlines all of the Lower Jurassic plesiosaur material studied in detail first hand during the course of this project. A review of the history and recent preparation of each specimen is given; special detail is provided in the case of Rhomaleosaurus cramptoni.

### 3.3 NMING F8785 Rhomaleosaurus cramptoni

### 3.3.1 History

The holotype specimen of Rhomaleosaurus cramptoni was unearthed in 1848 by workers in an Alum quarry at Kettleness, near Whitby, on the Yorkshire coast, UK (Figure 3.1, 3.2). It originated from the Bifrons ammonite zone of the Whitby Mudstone Formation (Lias Group, Toarcian, Lower Jurassic) (Figure 3.3). It remains one of the largest complete pliosaurs ever discovered (Figure 3.4). However, the details of the history of this specimen are particularly complicated (O'Riordan, 1983; Benton and Taylor, 1984; Osborne, 1998). Popular media accounts (Anonymous, 1849) called the specimen Plesiosaurus macrocephalus. The magnificent fossil was secured for five years at Mulgrave Castle, the home of the Marquis of Normanby, owner of the alum quarry. The Marquis presented the fossil to his friend Sir Philip Crampton in 1853, and Sir Crampton brought the specimen to Dublin to be displayed as centrepiece at the 1853 British Association annual meeting (Anonymous, 1853). A specially constructed building was created by the Zoological Society of Ireland to accommodate the huge specimen, and the fossil found a temporary home in the Botanical Gardens (now Dublin Zoo). Despite initial optimism with the tent-like construction containing the fossil (Anonymous, 1854), it became clear that the building was insufficient for protecting the specimen from the elements (Anonymous, 1862) so in 1861 it was loaned for display in the Royal Dublin Society museum, and it was set up on the ground floor Exhibit in 1863 (O'Riordan, 1983). The fossil is visible in the foreground of a historical photograph of the ground floor of the museum taken c. 1884; it occupied a position near the entrance (photograph in the collections of the NMING, figured by O'Riordan [1983, p.43]). During the same year, the plesiosaur was scientifically described and named (Carte and Bailey, 1863ab) as Plesiosaurus cramptoni. The Royal Dublin Society museum was later merged with the National
Figure 3.2. Detailed location map of NMING F8785, the holotype of Rhomaleosaurus cramptoni (the area in grey represents the Lias Group).
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Museum of Ireland who in 1877 paid £200 to acquire the specimen permanently (Anonymous, 1878). In 1890, the fossil moved buildings again, into the museum's 'fossil hall'. But this was not to be the fossil's final resting place: in 1979 the hall was demolished, and the specimen, together with rest of the geological collection, was transferred to storage in central Ireland. The collection was then moved yet again in 1992 to the National Museum of Ireland (Natural History) reserve stores at Beggars Bush, where the giant reptile currently resides (Osborne, 1998).

As noted in Chapter 2 and in Smith (2006b), NMING F8785 is particularly important for a number of reasons, especially because it became the type species of the genus Rhomaleosaurus and family Rhomaleosauridae. The specimen was briefly described by Carte and Bailey (1863ab); however, Watson (1909) correctly pointed out that; "the description [Carte and Bailey 1863ab] is inadequate...the girdles are almost completely concealed, and the arrangement of the limbs is not natural".
Rhomaleosaurus cramptoni was also described briefly by Tate and Blake (1876). The specimen unfortunately suffered from neglect during its long history and the specimen became rather worse for wear and anatomical details became obscured by plaster, paint, and varnish (Figure 3.5). To rectify this situation, in September of 2006 the skull of NMING F8785 was transported to the Palaeontology Conservation Unit of the National History Museum, London, to undergo cleaning and preparation (Smith, 2006ab). During preparation, the wooden base to which the skull had been attached for more than a hundred years was removed, and the skull was prepared from the underside to expose the palatal surface. The project was completed in February 2007 and the prepared skull was returned to Dublin. A two-part fibreglass casing was constructed to protect NMING F8785 during transit, and to allow the specimen to be rolled over to make both the dorsal and ventral surfaces of the skull available for research, without damaging the fossil (Figure 3.6). For a full description of NMING F8785, see Chapter 4.

### 3.3.2 Iconic specimen

NMING F8785 is iconic amongst fossil reptiles because it is known from a number of casts exhibited in numerous institutions all around the world. These include the Natural History Museum, London, UK (Figure 3.7A), the Bath Royal Literary and Scientific Institution, UK (Figure 3.7B), Cornell University, New York, USA, University of Illinois, USA, and Monash University, Victoria, Australia. These casts were probably purchased from Henry A. Ward, a fossil caster who dealt in replica fossils throughout the late 1800s (Davidson, 2005). The specimen of Rhomaleosaurus

Figure 3.4. Photograph of specimen NMING F8785, the holotype of Rhomaleosaurus cramptoni, taken prior to the specimen being broken up and moved to storage. (Length of specimen from tip of skull to tip of tail, along vertebral column $=6.77 \mathrm{~m}$ )


Figure 3.5. One of ten blocks containing the postcranium of specimen NMING F8785, the holotype of Rhomaleosaurus cramptoni. As of October 2007, these still await reconstruction and preparation.


Figure 3.6. Padded fibreglass case constructed to enclose and protect specimen NMING F8785, the skull of the holotype of Rhomaleosaurus cramptoni.


Figure 3.7. Casts of the holotype of Rhomaleosaurus cramptoni on display, A. in the Natural History Museum, London, UK; B. in the Bath Royal Literary and Scientific Institute, Bath, UK. See text for discussion of the differences between these casts. C. (over page) Illustration of "Item No. 228" as figured in Ward's catalogue of Casts of Fossils (1866).

cramptoni (Item No. 228) (Figure 3.7C) was figured by Ward in his catalogue of Casts of Fossils (Ward, 1866, refigured by Davidson, 2005, Figure 1), and was available to purchase as a complete mount for US\$150 (factoring for inflation this price is equivalent to around $\$ 2000$ today). Because each cast has its own unique history, the existing specimens are not all identical. For example, the two forelimbs in the Bath cast are identical copies of each other, and they are mounted in the wrong place: the two hindlimbs in this cast are really forelimbs placed in the position of the femora (Figure 3.7). The London cast is notable for its unique limbs - all of the bones distal to the epipodials have been re-modelled. This was presumably performed by the NHM because of the unnatural arrangement of the phalanges and metapodials/mesotarsals, mesopodial/mesotarsals in the original specimen (see Chapter 4). However, no documentation can be found to verify when the cast was modified (S. Chapman, pers. comm., 2006).

### 3.4 NMING F10194

This is a partial skeleton including a complete cranium (but missing the mandibles) from Street, Somerset, UK (Figure 3.1). This specimen has not previously been described or figured, it is fully described and figured here (see Figure 3.8 and chapter 4 and figures 4.28-4.34). The skull is exposed in dorsal view and there is evidence of preparation in the form of chip marks on the matrix inside the orbits and temporal fenestrae, presumably undertaken when the specimen was first found. The majority of the palate remained obscured by matrix, most of which was removed mechanically using a range of fine chisels and a chisel-hammer. Additional preparation was performed on the girdles exposing the right scapula. There is certainly potential for further preparation of the palatal details (i.e., alveoli, internal nares), but the current state of this specimen is sufficient to describe the most important features of the skull. Lydekker (1891) referred NMING F10194 to Thaumatosaurus megacephalus, and Smith (2006b) identified this specimen as 'Rhomaleosaurus' megacephalus, noting some key features in the cranium.

### 3.5 NMING F8749

This is an almost complete specimen from Barrow-on-Soar, Leicestershire, UK (Figure 3.1) mounted in plaster and bordered by a wooden frame. NMING F8749 is preserved with its dorsal surface exposed; the vertebral column and skull are almost complete and all four propodials are present but poorly preserved (Figure 3.9). The specimen has suffered significantly from damage and pyrite decay. The skull, some anterior cervical vertebrae, and part of the left humerus were removed from the


Figure 3.8. Overview of specimen NMING F10194. This specimen is preserved in thirtyeight fragments; this figure shows a reconstruction of fourteen of the larger blocks together with the skull (inset, in dorsal view) (scale bars $=20 \mathrm{~cm}$ [for the postcranium] and 30 cm [for the skull]). For more detailed figures and interpretations of this specimen, see Chapter 4.

Figure 3.9. Specimen NMING F8749, photograph taken before parts of the specimen were excavated from the mount. The distorted appearance is natural and not an artefact of the camera angle (scale bar $=20 \mathrm{~cm}$ ).
plaster mount and partly prepared to reveal the palate and other anatomical details. Lydekker (1891) referred NMING F8749 to Thaumatosaurus arcuatus.

### 3.6 BMNH R1336, NMING F8780, TCD.22931. Plesiosaurus macrocephalus

These specimens are the holotype (BMNH R1336) and casts of Plesiosaurus macrocephalus Conybeare, in Buckland, 1837 (Figures 3.1). The original specimen (BMNH R1336) from the Sinemurian of Lyme Regis, Dorset, UK (Figure 3.10), is on display behind glass in the Marine Reptile Gallery of the Natural History Museum, London, and it is thus inaccessible. Two casts of the holotype (NMING F8780 [Figure 3.11] and TCD.22931) were therefore used as proxy specimens from which to take representative measurements and observations for this taxon. The original specimen was described and figured in detail by Owen $(1838,1840)$ (Figure 3.10). Inclusion of this specimen in cladistic analyses is problematic because it is not an adult and therefore possesses a number of characters more typical of an early ontogentic stage. Consequently this taxon was not included in the cladistic analysis. The specimen was included in two unpublished analyses which both recognised the taxon as a basal plesiosaur, situated either at the base of the pliosauroid tree (Smith and Benton, in prep) or at the base of the plesiosauroid tree (Druckenmiller, 2006ab).

### 3.7 BMNH 2018*, NMING F8771 and TCD 22932 Thalassiodracon hawkinsi

These specimens are the holotype (BMNH 2018*) and casts of Thalassiodracon hawkinsi (Owen, 1838) Storrs and Taylor, 1996, from Street, Somerset, England (Figure 3.1). The holotype specimen (BMNH 2018*) is from the Pre-Planorbis Beds, Blue Lias Formation, Lower Lias Group and again is on display behind a glass sheet in the Marine Reptile Gallery of the Natural History Museum, London, and it is thus inaccessible. NMING F8771 (Figure 3.12) and TCD 22932 were thus used as proxy specimens from which to take representative observations and measurements for this taxon. The holotype specimen was originally described and figured by Hawkins (1834) and named 'Plesiosaurus triatarsostinus' but was later changed to Plesiosaurus hawkinsi (Owen, 1838). The genus name Thalassiodracon was introduced for the existing taxon Plesiosaurus hawkinsi by Storrs and Taylor (1996). No referred material was investigated first hand during this project, but several additional specimens of this taxon were coded based on literature (CAMSM J46986, skull and vertebrae and BMNH 2039*, jaws) (Storrs and Taylor, 1996). Note that a further specimen belonging to this taxon housed in the School of Geological Sciences, University College Dublin (UCD uncatalogued), was not accessible during the course of this project (Figure 3.13).


Figure 3.10. Specimen BMNH R1336, illustration of the holotype specimen of Plesiosaurus macrocephalus, as figured by Owen (1840, Plate 43) (length of skull $=22.5 \mathrm{~cm}$ ).


Figure 3.11. Specimen NMING F8780, cast of the holotype specimen of Plesiosaurus macrocephalus (see above) (length of skull $=22.5 \mathrm{~cm}$ ).


Figure 3.12. Specimen NMING F8771, cast of the holotype of Thalassiodracon hawkinsi (BMNH 2018*) (scale bar $=20 \mathrm{~cm}$ ).


Figure 3.13. Specimen UCD 'uncatalogued', a specimen referred to Thalassiodracon hawkinsi.

### 3.8 BMNH 49202

This specimen comprises a beautifully preserved skull (and mandible) (Figure 3.14) associated with the atlas-axis and some anterior cervical vertebrae, from the Lower Lias (Sinemurian?) of Lyme Regis, UK (Figure 3.1). Lydekker (1889) referred BMNH 49202 as an adult specimen of Plesiosaurus macrocephalus, and Andrews (1896) described and figured the specimen in detail. BMNH 49202 was included as referred material for $P$. macrocephalus by Smith and Benton (in prep) but it is treated here as a separate operational taxonomic unit (OTU) for the cladistic analysis (see Chapter 5).

### 3.9 BMNH 38525 Archaeonectrus

The holotype specimen of Archaeonectrus rostratus (Owen, 1865) Novozhilov, 1964 is a completely preserved specimen exposed in dorsal view from the Sinemurian of Charmouth, Dorset, UK (Figure 3.1). No further stratigraphic details are known, but this fossil was discovered in 1863 and named two years later as Plesiosaurus rostratus (Owen, 1865). The bulk of this fossil, together with a cast of the skull, is on display as part of the Marine Reptile Gallery of the Natural History Museum, London, and is therefore not available for detailed observations or measurements (Figure 3.15). The skull, however, is separate from the postcranium and was available for investigation (see Chapter 4). BMNH 38525 was described and figured by Owen (1865); the new genus was proposed for the existing taxon Plesiosaurus rostratus by Novozhilov (1964), who also illustrated the specimen.

### 3.10 BMNH R4853 Rhomaleosaurus thorntoni

The holotype of Rhomaleosaurus thorntoni is a more or less complete specimen preserved in three dimensions (Figure 3.16), including most of the skull and mandibles, from the Toarcian of Kingsthorp, Northamptonshire, UK (Figure 3.1). The history of Rhomaleosaurus thorntoni was reviewed by Andwews (1922b) and Cruickshank (1996b); this specimen is the only well-known British Toarcian rhomaleosaurid discovered away from the Yorkshire coast. It was originally described by Andrews (1922b) and the skull was later re-described and figured by Cruickshank (1996b) who amended some of the original observations, in particular the position of the external nares. R. thorntoni was shown to be even more similar to $R$. cramptoni than Andrews (1922b) had suggested: Cruickshank (1996b) united these two species together with R. zetlandicus. The almost completely preserved and visible pectoral and pelvic regions present the only complete girdles known for any British Toarcian


Figure 3.14. Specimen BMNH 49202, the cranium (including the mandible), A. dorsal view, B. ventral view (scale bar $=20 \mathrm{~cm}$ ).


Figure 3.15. Specimen BMNH 38525, illustration of the holotype of Archaeonectrus rostratus as figured in Novozhilov (1964) (scale bar $=50 \mathrm{~cm}$ ).


Figure 3.16. Specimen BMNH R4853, the holotype of Rhomaleosaurus thorntoni (propodials not in photograph) (length of preserved vertebral column $=5.75 \mathrm{~m}$ ).


Figure 3.17. Specimen BMNH R1318, part of the type series of Eurycleidus arcuatus (length of pubis [largest element in the slab] $=25 \mathrm{~cm}$ ).
rhomaleosaurid; therefore this skeleton is very important and these elements are described and figured in Chapter 4.

### 3.11 BMNH R2028*, BMNH R2029*, BMNH R1317, BMNH R2061*, BMNH R2047*, BMNH R2027*, BMNH R1318, BMNH R1319 and BMNH R2030* Eurycleidus arcuatus

The holotype series of Eurycleidus arcuatus Andrews, 1922, consists of many separately numbered specimens belonging to a single individual (Lydekker, 1889) from the Lower Lias (Hettangian) of Street, Somerset, UK (Figure 3.1). In total, an almost complete skeleton is represented by these pieces, including a number of isolated pieces (see Chapter 4) and a large slab (BMNH R1318) (Figure 3.17) with only the cranium missing. The left coracoid (BMNH R2029*), the left femur and an associated vertebra (R2027*), the clavicles and interclavicle (R.1322), and the mandibular symphysis (R2030*) were all figured by Hawkins (1834, 1840). The mandibular symphysis was also figured by Buckland (1837) in his Bridgewater Treatise. A vertebra (part of R.1318) was figured by Owen (1840) and the clavicles and interclavicle (R.1322) were figured by Seeley (1892) and described and refigured by Andrews (1922a). Most subsequent authors follow Lydekker (1889) who lists the type material as a partial lower jaw (BMNH 2030), with the rest of the almost complete skeleton (probably belonging to the same individual) included in the type series (e.g. Andrews 1922a, Cruickshank, 1994b). The pectoral girdle of this specimen was figured by Andrews (1922a) who wrote (p.293) of the skeleton in general:

[^0]In addition to Hawkins' Book of the Great Sea Dragons (1840) (not 1834 as Andrews implies), part of the material was also figured in Hawkins' Memoires of Ichthyosauri and Plesiosauri (1834). However, the first appearance of the species name arcuatus occurs in Owen (1840, Plate XLIV Fig 5), where it is applied to a single posterior cervical vertebra in a plate, but not in the text, and without a description. The holotype material (actually a type series) of Eurycleidus (Andrews 1922a) ( $E$. arcuatus [Owen, 1840]) is a partial skeleton. According to Cruickshank (1994b), the type-material is listed as partial lower jaw (BMNH 2030), but the rest of the skeleton
probably belongs to the same individual (Andrews 1922a, Cruickshank, 1994b), and so this is also included in the type series. Although the holotype is listed by Buckland (1836) as originating from Lyme Regis, the preservation indicates otherwise and Lydekker (1889) indicated that this specimen is "probably of Street, near Glastonbury" (p.163). The history of Eurycleidus is also under investigation by Cruickshank and Noè (in prep) (L. Noè pers comm. 2007).

Cruickshank (1994b) referred a specimen from Lyme Regis (OUM J.28585; see Appendix 2) to Eurycleidus arcuatus; however, this may represent a new taxon in itself (O’Keefe, 2004b). To test this referral, OUM J. 28585 is treated as a separate OTU in the cladistic analysis presented here, albeit coded from the literature (see Appendix 2).

### 3.12 BMNH R5488 Macroplata tenuiceps

The holotype of Macroplata tenuiceps, from the Hettangian (Schlotheimia angulata zone) of Harbury, Warwickshire, UK, (Figure 3.1) is an almost complete specimen visible in both ventral and dorsal aspects and including the skull (see Chapter 4, Figure 4.43). BMNH R5488 was described by Swinton (1930a) and figured by Swinton (1930b). Contrary to the erroneous assignment of the species longirostris to the genus (White, 1940), Macroplata is actually a monospecific taxon known only from this single specimen. Due to confusion over the holotype material of Macroplata, O'Keefe (2001a) referred to BMNH R5488 as an "Unnamed genus ('Macroplata tenuiceps')" and mistakenly took the holotype specimen of Plesiosaurus longirostris (see below) as the holotype of Macroplata, a mix up that has since been resolved (see O'Keefe [2004b]). In the cladistic analysis of O'Keefe (2001a), Macroplata (BMNH R5488) was found to be a rhomaleosaurid, but the material is currently under reinvestigation (Ketchum and Smith, in preparation). Upon the discovery of Macroplata in 1927, much ado was made in the media concerning the large pineal foramen (Swinton, 1930b), some accounts spectacularly claiming the specimen represented a 'three-eyed plesiosaur' (Anonymous, 1927). The 'third eye' or pineal foramen is found in most plesiosaurs (see Chapter 1) but was presumably particularly large and worthy of note in Macroplata. Unfortunately large parts of the skull as preserved today have been subjected to reconstruction in plaster (and painted brown) including the area where the pineal foramen is usually positioned. Therefore, this interesting character of potential systematic use cannot be observed. It is baffling why this area should have been so obscured by plaster considering the interest generated by the pineal foramen at the time.

### 3.13 BMNH R1310, TCD.47762a, TCD.47762b Rhomaleosaurus megacephalus (holotype)

These specimens are casts of the holotype of 'Plesiosaurus' megacephalus (Stutchbury, 1846) (later to become Rhomaleosaurus megacephalus), itself one of a number of plesiosaurs formerly on display in the Bristol Museum and Art Gallery during the first half of the $20^{\text {th }}$ Century (Swinton, 1948). The original specimen representing this taxon (BRSMG Cb 2335) (Figure 3.18A) was from the Hettangian (angulatum? zone) of Street, Somerset, UK (Figure 3.1), but it was unfortunately destroyed in 1940 when the Bristol Museum became the victim of an air-raid during the Second World War (Swinton, 1948). All that remains of this at one time complete skeleton are photographs (Swinton, 1948), casts of the skull and the right forelimb (Wyse Jackson, 2004), and the original descriptions by Stutchbury (1846) and Sollas (1881). Unlike the holotype of Attenborosaurus conybeari, another Lower Jurassic plesiosaur destroyed in the Bristol Blitz (see below), no casts of the complete animal were ever produced. However, three casts of parts of the destroyed holotype are known, comprising the skull, associated anterior cervical vertebrae, and a right flipper (Wyse Jackson, 2004). These casts are housed in the Natural History Museum, London (BMNH R1310) (see Chapter 4), the Geology Museum, Trinity College Dublin (TCD.47762a, TCD.47762b) (see Chapter 4 Figure 4.45-4.47), and in the British Geological Survey, Keyworth, Nottingham (Wyse Jackson, 2004). The latter specimen was not examined for the purposes of this study; note that Cruickshank (1994b) did not mention the existence of these casts of the holotype when he introduced LEICS G221.1851 (see below) as the neotype of Rhomaleosaurus megacephalus.

### 3.14 YORYM G503 Rhomaleosaurus zetlandicus

The holotype specimen of Rhomaleosaurus zetlandicus Phillips, 1854, is an almost complete skull and vertebral column (Figure 3.19), associated with parts of the limbs, from the Toarcian Alum Shale of Whitby, Yorkshire, UK (Figure 3.1). The skull of YORYM G503 was thoroughly described and figured by Taylor (1992a) together with a review of its functional morphology, and the whole specimen was figured in Taylor (1992b). The history of this specimen is given in the above references; of particular note in this thesis, the associated femur may not be part of this individual (see Chapter 4).


Figure 3.18. Historical photographs of destroyed holotypes formerly in the BRSMG, A. Specimen BRSMG Cb 2335 Rhomaleosaurus megacephalus (length $=5.8 \mathrm{~m}$ ) (only casts of the skull and right forelimb of this specimen remain today, B. specimen BRSMG Cb 2479, the former holotype of Attenborosaurus conybeari, a number of casts are known of this specimen (see text) (skull $=48 \mathrm{~cm}$ ) (both images from Swinton, 1948).


Figure 3.19 Composite photograph of specimen YORYM G503, the holotype of Rhomaleosaurus zetlandicus (scale bars $=20 \mathrm{~cm}$ ) (courtesy of R. Forrest).


Figure 3.20 Specimen WM 851.S, the holotype of Rhomaleosaurus propinquus on display in the Whitby Museum (scale bar $=30 \mathrm{~cm}$ ).

### 3.15 WM 851.S Rhomaleosaurus propinquus

The holotype specimen of Rhomaleosaurus propinquus is an almost complete specimen exposed in dorsal view and wall-mounted in the Whitby Museum (Figure 3.20), from the Toarcian (A. serpentines) zone of Whitby, UK (Figure 3.1). WM 8851.S was described and figured by Tate and Blake (1876) who introduced the new species name Plesiosaurus propinquus. WM $851 . S$ was redescribed and figured in more detail by Watson (1910). The cranium is actually reasonably preserved and despite Watson's comments that "no sutures are visible" (p.1), there are in fact many visible sutures on the cranium. The tip of the snout is missing, having been broken off just posterior to the premaxilla-maxilla notch. This missing portion must have been removed some time after Watson's (1910) examination of the specimen, as he figures the specimen with the premaxillary rostrum intact. The missing portion cannot be located in the Whitby Museum (R. Osborne pers. comm., 2005), and no reference can be found mentioning when the snout was removed or where it may be. It must therefore be considered lost. The vertebral column is almost complete and all four propodials are preserved. Both ilia are present, although one is wrongly mounted in the position of the left scapula.

### 3.16 SMNS 12478 Rhomaleosaurus victor

SMNS 12478 is the holotype specimen of Rhomaleosaurus victor from the
Posidonien-Schiefer, Toarcian, of Holzmaden, Germany (Figure 3.1). It is an almost complete specimen exposed in ventral view (Figure 1.4, Figure 3.21). The specimen was described and figured in detail by Fraas (1910), and is on display in the SMNS. Unfortunately, the specimen was severely damaged during a bombing raid on the City of Stuttgart in 1944 (Figure 3.21), but the fossil was rescued from the wreckage and the missing parts were reconstructed based on the original description.

### 3.17 LEICS G221.1851 Rhomaleosaurus megacephalus (Neotype)

This specimen is the designated neotype of Rhomaleosaurus megacephalus (Figure 3.22 and see Chapter 4) (Cruickshank, 1994b) and is from the Bottom Floor Limestone, Lower Lias Group, (Planorbis sub-zone of the Psiloceras planorbis zone), Lower Hettangian, of Barrow-upon-Soar, Leicestershire, UK (Figure 3.1). Cruickshank (1994b) proposed this neotype replacement for the taxon Rhomaleosaurus megacephalus; as discussed above the original holotype was destroyed during the Second World War. However, casts of the destroyed holotype exist (see above) and were included in the analyses as a separate data entries and OTUs. The specimen history of LEICS G221.1851 is outlined by Cruickshank


Figure 3.21. Historical photograph of SMNS 12478, the holotype of Rhomaleosaurus victor, partially reconstructed after being destroyed (see text for discussion) (length of specimen $=3.44 \mathrm{~m}$ ) (photograph from the SMNS).


Figure 3.22. Specimen LEICS G221.1851, the neotype of Rhomaleosaurus megacephalus (length of specimen as mounted $=5.29 \mathrm{~m}$ ).
(1994bc). Recently the skull was excavated from its Victorian mounting (see Cruickshank [1994c] for details), separated from the body and described (Cruickshank, 1994b). Additional interpretations of LEICS G221.1851 have been provided by O'Keefe, (2001a, Fig. 8.), who reinterpreted the palatal surface of the skull, and Druckenmiller (2006a, Figure 4.20) interpreted the dorsal surface of the cranium. The fossil skull now stands on display beside the rest of the skeleton (complete with a cast of the skull) in the New Walk Museum, Leicester, UK.

### 3.18 WARMS G10875

WARMS G10875 is a complete specimen from the base of the Hettangian of Wilmcote, Warwickshire, UK (Figure 3.1), and includes the skull, exposed in ventral view and mounted in plaster on display in the Warwickshire Museum (Figure 3.23). While Wright (1860) listed the specimen as Plesiosaurus megacephalus and Cruickshank (1994b) referred WARMS G10875 to Rhomaleosaurus megacephalus, this specimen has never been described or figured. As mounted, the neck has been relocated a small distance from the body (Figure 3.23). This specimen is important because it is the only complete Hettangian rhomaleosaurid to be exposed in ventral view, preserving the girdles in association with the cranium and mandible.

### 3.19 TCD.57763, BMNH R.1338/1339 Attenborosaurus conybeari

Specimens TCD. 57763 and BMNH R.1338/1339 are casts of the holotype of Attenborosaurus conybeari. (Sollas, 1881) Bakker, 1993 (Figure 3.1). The holotype specimen of $A$. conybeari came from the Lower Lias Group (obtusus zone) (Sinemurian) of Blackven Water, $1 / 2$ a mile west of the River Char, Charmouth, Dorset, England (Figure 3.18B). This fossil material (BRSMG Cb 2479) was destroyed in World War Two, during the same event that destroyed the holotype of Rhomaleosaurus megacephalus (Swinton, 1948). BMNH R. 1339 now represents the holotype of this taxon (Bakker, 1993). The specimen is complete, including the skull, neck, axial skeleton, and the proximal portion of the limbs. The original specimen was mounted on one side, with casts of the opposite side mounted adjacent. Sollas (1881) described and figured the specimen, and Swinton (1948) briefly described and figured the specimen. Another cast, in the University Museum, Oxford, (Swinton, 1948), was not examined first hand in this study.

### 3.20 Additional material

In addition to the above fossil specimens, a number of relevant specimens of Lower Jurassic plesiosaurs and other relevant taxa from other strata, fell outside the scope

Figure 3.23. Composite photograph of specimen WARMS G10875, a full skeleton in ventral
view (scale bar $=40 \mathrm{~cm}$ ).
for detailed examination during this project and are not described or figured. Some of these specimens were studied first hand and where appropriate, data for these specimens/taxa was incorporated into the morphometric analyses and/or the phylogenetic analysis. These specimens are listed in Appendix 2.

### 3.21 Possible rhomaleosaurids excluded from this study

Three potential rhomaleosauruid taxa are known from China, they are, in fact, the only well-known Jurassic plesiosaurs from Asia. Sinpliosaurus Young, 1944 is fragmentary and seemingly non-diagnostic (Sato et al. 2003), although two species are named (Hou et al. 1975). Bishanopliosaurus youngi Dong, 1980 was originally assigned to the Rhomaleosauridae and was redescribed by Sato et al. (2003) who reviewed the phylogenetic affinity of the taxon. Familial diagnosis was not possible due to the lack of diagnostic features. Another possible Chinese rhomaleosaurid is Yuzhoupliosaurus chengjiangensis Zhang, 1985. The material was described by Zhang (1985) and regarded as being closer to Rhomaleosaurus than Bishanopliosaurus. None of these Chinese taxa are analysed or described in this thesis due to incompleteness of their remains and having not been examined first hand. Nevertheless, Bishanopliosaurus and Yuzhoupliosaurus are worthy of reanalysis.

A plesiosaur skull associated with some postcranial elements (NMC 40729) from the Callovian Hiccles Cove Formation of Melville Island in Canadian Arctic Archipelago, was originally identified as cf. Cryptoclidus richardsoni (Russell, 1993), but actually shows closer affinity with pliosauroids and was later identified as Simolestes (Sato, 2005). However, this specimen shares many similarities with rhomaleosaurids, especially Rhomaleosaurus, in its cranial proportions (pers. obs.). It is currently being described by Sato (pers comm. 2005) and is therefore omitted from this thesis.

## Chapter 4 - Descriptions and comparisons

"Rhomaleosaurus cramptoni is] the most magnificent of all the fossil reptile skeletons discovered on the Yorkshire coast"
'The Floating Egg'
Roger Osborne, 1998

### 4.1 Background

This chapter provides descriptions of key specimens with a focus on the cranial anatomy of Rhomaleosaurus cramptoni, the postcranial anatomy of Rhomaleosaurus thorntoni, and the cranial anatomy of NMING 10194. The material described here includes all of the pliosaur fossils in the NMI (NMING F8785, [R. cramptoni], NMING F10194 and NMING F8749). Some additional specimens are also described because they provide anatomical data not present in the above specimens. The postcranium of Rhomaleosaurus thorntoni (BMNH R4853) is described in detail as a surrogate for the unprepared postcranium of $R$. cramptoni (see section 4.4). Some of the key specimens have been thoroughly described in detail elsewhere (SMNS 12478 [Rhomaleosaurus victor, Fraas, 1910], and the skulls of YORYM G503 [Rhomaleosaurus zetlandicus, Taylor, 1992a), LEICS G221.1851 [Rhomaleosaurus megacephalus, Cruickshank, 1994], and BMNH R4853 [R. thorntoni, Cruickshank, 1996b]) and on this basis, redescription of this material is not necessary. However, there are some instances where my interpretations differ from the existing published descriptions and in these cases the differences are described. The detailed descriptions will then form the basis for a comparative anatomy section, which includes detailed notes on the similarities and differences present in all of the specimens analysed in this thesis (both described and undescribed). The phylogenetic placement of all these specimens is analysed in Chapters 5 and 6. See Appendix 3 for an explanation of abbreviations used in figures.

### 4.2 NMING F8785, Rhomaleosaurus cramptoni

NMING F8785 represents an almost complete skeleton preserved in dorsal aspect (Figure 3.4). The skull is almost complete and is preserved in three dimensions (Figures 4.1, 4.2 and 4.3). The skull is preserved in a block with three anterior cervical vertebrae, and part of the posterior part of the atlas-axis is exposed projecting from below the posterior margin of the cranium. The rest of the postcranium is currently preserved in eleven main blocks (Figure 3.5). The neck, tail and four limbs are each preserved in single blocks, while the main trunk region is


Figure 4.1. The skull of NMING F8785, Rhomaleosaurus cramptoni, in dorsal view, A. photograph, B. interpretation (crosshatch indicates restored areas, dotted lines indicate ridges) (scale bar $=30 \mathrm{~cm}$ ).
split into four segments, each of which can be restored along transverse breaks through the skeleton. The length of the entire restored specimen has been calculated independently for each of the casts and in the case of NMING F8785, length was calculated by combining the lengths of all the blocks, measured along the midline (in the skull), or along the vertebral column. The linear dimension of the casts (Figure 3.7) from skull tip to tail tip is 6.50 m . The total length along the vertebral column was calculated as 6.77 m for NMING F8785, and 6.69 m in the casts. Although Chapman and Smith-McNally (1997) pointed out that the plaster traditionally used in fossil casts does not "noticeably shrink or expand as it hardens" (p. 1), the observed 0.01\% difference in size between the original specimen of Rhomaleosaurus cramptoni and the casts, might indicate that a small amount of shrinkage has occurred in the casts, or in the molds from which the casts were taken. Considering that an unknown number of vertebrae are missing from the terminal end of the caudal series, it is likely that the total length of NMING F8785 reached 7m. Detailed measurements of this specimen are presented in Appendix 4.

### 4.2.1 Skull roof

Anteriorly the premaxillae form a short rounded spatulate rostrum and each premaxilla bears five tooth positions (Figure 4.1). The premaxillae send broad posterior processes along the midline extending past the large oval external nares to midway between the orbits. There is a distinct lozenge-shaped dorso-median foramen situated on the midline between the posterior margins of the external nares, and bordered by a strong raised margin. Anterior to the dorso-median foramen on the midline is a low but sharp elongate ridge formed by the juncture of the premaxillary processes. Anterior to the external nares, the width of the posterior processes of the premaxillae remain constant for most of their length so that the premaxilla/ maxilla sutures run parallel to each other (Figure 4.1). There is a minute contact between the premaxillae and the antero-medial margin of the external naris. Laterally, the premaxillae contact the maxillae at a slight restriction/notch. This restriction is coincident with a diastema between the last tooth of the premaxilla and the first tooth of the maxilla. The sutures delineating the contacts between the maxilla and the frontal/prefrontal are slightly unclear, but it appears that the maxilla contributes to the whole lateral margin of the external naris, and contacts the antero-lateral margin of the orbit. The surface of each maxilla forms four or five raised shallow ridges oriented perpendicular to the lateral margin of the skull (stippled area in Figure 4.1); these correspond to the roots of large secondary teeth in the maxilla. Each maxilla produces a short triangular flange that protrudes dorsally between the frontal and the
prefrontal. Nasals are considered absent in this specimen. At the posterior border of the external nares the maxilla meets the frontal.

The frontals are elongate bones occupying a position between the orbits; they are separated on the midline by the long posterior premaxillary process, which contacts the parietal. Each frontal sends a broad anterior process and contributes the postero-medial and medial margins of the external nares, the anterior process of the frontal almost contacts the maxilla at the antero-medial corner of the external narial margin, nearly excluding the premaxilla from the narial margin. The antero-medial border of the orbit is formed by the prefrontals: these are narrowly exposed on contact the premaxilla anteriorly and the frontal medially. The width between the orbits is equivalent to the maximum width between the external nares and it appears that a portion of the medial border of each orbit (part of the frontal bone) is missing due to damage. The premaxillae contact the fused parietals along a short suture, roughly level to the posterior margin of the orbits. The fused parietals increase in width posteriorly, the sutures meet a distinct postorbital ridge and posterior to this a short square process projects laterally, forming the antero-medial margin of the temporal fenestra. A large lozenge-shaped pineal foramen is situated on the midline between the fused parietals; the anterior margin of this foramen is level with the posterior margins of the postorbital bars (Figure 4.1). The parietal contacts the squamosals posteriorly, but the dorsal extent of the parietal crest is unknown due to damage. The postorbital bars are also obscured so sutures are difficult to identify. The postfrontals are small triangular elements and contribute to the postero-medial margins of the orbit - they contact the frontals anteriorly, the parietal medially, and the postorbital postero-laterally. Each postorbital forms the majority of the postorbital bar and unites ventrally with the jugal along a straight horizontally orientated suture (Figure 4.5). The postorbital appears to produce a posterior process, which contacts the anterior ramus of the squamosal, but the preservation is not satisfactory to be certain.

The jugal is a deep and elongate element forming the postero-lateral and lateral margin of each orbit. Again, the preservation is not perfect enough to determine with accuracy the anterior extent of the jugal; it is reconstructed here terminating approximately two-thirds along the lateral margin (Figure 4,1, 4.5). The jugal bone is ornamented by longitudinal ridges and pierced by a number of foraminae, and each jugal is bounded ventrally by the postero-lateral process of the maxilla.

The squamosals are large tri-radiate elements and form all of the posterior, and presumably most of the lateral, margins of the temporal fenestrae. However,
both post-temporal bars are missing due to damage in this region. The dorsal rami meet on the midline along a strongly inter-digitating suture at which a posterior bulb is formed, and contact the parietal anteriorly along another strongly inter-digitating suture, this one transverse. Where the squamosal and parietal meet on the medial margin of the temporal fenestra, a shallow angle or 'bulge' is formed (Figure 4.1). In cross-section through, the middle of the dorsal ramus, the anterior margin is deeply excavated and produces a pronounced, curved overhang. This rounded overhang shrinks into a shallow ridge medially, but it becomes sharp laterally where it forms the posterior margin of the temporal fenestra. Another rounded ridge runs along the dorsal surface of the dorsal ramus, dividing its surface into two flattened areas, the posterior of which becomes slightly concave as it approaches the quadrate ventrally.

Both quadrates are preserved in natural articulation with the articulars of the mandible. A dorsally tapering triangular dorsal process of the quadrate fits snugly between the lateral and medial ventral flanges of the squamosal, and there is a quadrate foramen between the squamosal and quadrate at the dorsal tip of the quadrate.

### 4.2.2 Palate

The premaxilla is obscured by the jaw symphysis of the mandibles, which are preserved in situ (Figure 4.2). It presumably forms the most anterior part of the palate surface as in all other plesiosaurs (pers. obs). The fused vomers extend posteriorly between the internal nares, and expand laterally to wrap around the posterior margin of each internal naris and contact the maxilla along a short straight suture on the postero-lateral margin. The vomer-palatine suture runs antero-posteriorly, a small raised bump is formed at the anterior part of this suture. Posteriorly the vomers contact the pterygoids on the midline along a straight transversely orientated suture. The maxilla forms the lateral margin of each internal naris, and the lateral margin of the large elongate suborbital fenestrae.

The pterygoids are large plate-like elements; there is no anterior interpterygoid vacuity between them so they contact each other for a long distance along the mid-line, between the vomer to the parasphenoid. The palatines are situated lateral to the pterygoids. The pterygoids broaden posteriorly, the pterygoidpalatine suture runs in a straight line from the posterior process of the vomer to a small but distinct lateral palatine vacuity; where it curves laterally to contact the ectopterygoid. Each pterygoid sends a wide plate-like process behind the posterior interpterygoid vacuity, and these plates meet on the midline behind the vacuities. The lateral edges of this plate run in a straight line longitudinally and are angled slightly


Figure 4.2. The skull of NMING F8785, Rhomaleosaurus cramptoni, in ventral (palatal) view, A. photograph, B. interpretation (crosshatch indicates restored areas) (scale bar $=30 \mathrm{~cm}$ ).
ventrally; the posterior edge of this plate runs transversely along a very slightly concave path. These perpendicular lateral and posterior edges meet at a rounded right angle below the base of the quadrate-pterygoid flange and form a 'squared lappet'. The cultriform process of the parasphenoid is short and the ventral surface is distinctly concave, posteriorly it forms the ventral surface of the braincase. The anterior border of the lateral palatine vacuity is formed by the palatine, the medial and posterior borders are formed by the pterygoid, which sends a lateral process to contact the palatines on the lateral margin of the vacuity, excluding the ectopterygoid. The long axis of the vacuity runs medio-laterally. The suborbital fenestrae are both present and large, each is elongate and reminiscent of a bowling pin in outline; it is widest anteriorly, slightly pinched towards the posterior, and expands slightly at the posterior border - this may be described as 'bowling pin-shape' (Figure 4.2). The posteromedial margin of the fenestra is formed by the ectopterygoid - medially this bone runs along the same horizontal plane as the majority of the palate surface, but lateral to a sharp longitudinal ridge, it slopes away in an almost vertical plane, forming a laterally facing wall (Figure 4.2).

The jugal appears to have a small contribution to the posterior margin of the suborbital fenestra but the entire lateral margin of the suborbital fenestra is formed by the maxilla. Although not visible in ventral view because of the underlying mandibular ramus, the posterior process of the maxilla and the lateral margin of the suborbital fenestrae can be seen from an oblique angle due to a natural gap between the jawline in this region. This natural gap is present in the fully occluded jaws. The ectopterygoid boss is a prominent feature formed solely by the ectopterygoid; the pterygoid contributes to the posterior part of the base, but does not extend onto the face of the boss. The flat face of this boss is directed ventro-laterally and the surface is distinctly ornamented with rugose pitting, indicating the presence of a cartilage cap - in life this boss braced the medial margin of the mandible.

### 4.2.3 Basicranium

The basicranium is preserved in three dimensions and parts are exposed in ventral and posterior view, as described above. The pterygoid plates contact on the midline below the posterior part of the neurocranium (and below the base of the quadratepterygoid flange), so the relationships between the basioccipital and basisphenoid cannot be determined (Figure 4.2). The parasphenoid forms a sharp ventral keel and merges posteriorly into the basisphenoid; however no clear suture can be seen delineating their exact relationship. The occipital condyle of the basioccipital extends beyond the posterior margin of the medial processes of the pterygoid flange and is


Figure 4.3. The skull of NMING F8785, Rhomaleosaurus cramptoni, in posterior aspect showing the basicranium, A. photograph, B. interpretation (crosshatch indicates matrix) (scale bar $=20 \mathrm{~cm}$ ).
thus partly visible in ventral view (Figure 4.2). The basicranium is also visible in posterior view.

The shape of the occipital condyle is subrounded in posterior view, being flattened on the dorsal margin where it forms the base of the foramen magnum, and very slightly keeled ventrally, so the condyle is almost heart-shaped in posterior view (Figure 4.3). A distinct dorso-ventrally orientated oval notochordal pit is present on the occipital condyle, slightly below the middle. The occipital condyle is situated higher than the level of the pterygoid plates of the quadrate-pterygoid flange. The posterior margin of the foramen magnum slopes antero-dorsally so that the dorsal parts of each exoccipital-episthotic and all of the supraoccipital are situated more anteriorly than the basioccipital; the dorsal parts of the basicranium (including all of the supraoccipital) are therefore obscured by matrix in posterior view. The paraoccipital process is an elongate splint of bone angled posteriorly and slightly ventrally. Distally it forms a flattened expanded dorso-ventrally inclined spatula, which contacts the quadrate pterygoid flange distally. The paraoccipital process and the quadrate-pterygoid flange are widely separated proximally but distally they unite for half of their length before broadly contacting the medial wall of the squamosal ventral ramus and quadrate flange (Figure 4.3).

### 4.2.4 Mandible

Most of the mandible is preserved, but parts have been artificially restored (Figure 4.2 and 4.5 C ). The long axis of each mandibular ramus is laterally compressed and angled at 24 degrees from the midline so that the mandible becomes very wide posteriorly (Figure 4.2, 4.5A). The mandibles are notably bowed so that the widest point across them is situated level with the middle of the quadrate-pterygoid flange. There is a high rounded coronoid eminence located at a level equivalent to the ectopterygoid boss of the cranium. Posteriorly, the ventro-lateral margin of the mandibular ramus expands laterally into a rounded longitudinal flange formed by the angular. The lateral margin of the mandible is consequently concave in this area, and the angular is visible on the lateral surface of the jaw in dorsal view (Figure 4.2). The ventral flange diminishes anteriorly, but there is still a distinct ventro-lateral edge to the dentary, this diminishes towards the symphysis.

The dentary forms the majority of the mandibular symphysis and extends posteriorly to meet the angular and surangular on the lateral surface of the jaw. The mandibular symphysis is slightly wider than it is long and it is not greatly expanded; there is no strong restriction posterior to the symphysis. There is a low but sharp midline ridge on the ventral surface of the symphysis. The lateral view of the
mandible is reconstructed in Figure 4.5C, at its origin on the dorsal margin of the jaw behind the coronoid process, the dentary-surangular suture runs posteriorly, but after a short distance it interdigitates, producing a narrow anterior exposure of the surangular. The surangular-angular suture is horizontal for much of its length, but posteriorly it adopts a sigmoid path, becoming dorsally concave anterior to the mandibular fossa, and dorsally convex below it (Figure 4.5C). The surangular is pierced posteriorly by two large foraminae. Due to the dorsal margins of the jaw rami being tilted medially, the dentary is visible in ventral view situated medial (as well as laterally) to the splenial (Figure 4.2). The splenial itself extends for a short distance between the mandibular symphysis. A long narrow process of the angular extends anteriorly along the ventral margin of the ramus between the splenial and dentary. The coronoid eminence is high and rounded and presumably formed by the coronoid medially, however, this region is poorly preserved in both jaw rami and the exact organisation of the bones is unclear in this region. Posterior to the coronoid process, the surangular and angular form the dorsal and ventral margins of the mandible respectively, and extend onto the medial surface. The angular also extends posteriorly underneath the glenoid and forms the base of the retroarticular process. The prearticular is an elongate element situated between the surangular and angular, forming two straight sutures in medial view. The retroarticular process is short and broad, with it long axis angled slightly medially. Distally, the ventral margin of the retroarticular process is kinked, the tip of the process is directed slightly dorsally, and it terminates in a flattened oval surface. There is a shallow bump on the medial surface of the retroarticular process, however, this area is worn down and the bump may have originally been more prominent. The articular is just visible in ventral view extending beyond the posterior margin of the angular at the tip of the retroarticular process. Both mandibular fossae are preserved with the quadrates in articulation, precluding their description.

### 4.2.5 Dentition

The teeth appear to have been large and caniniform, but all of them have been broken off or damaged. The antero-dorsal surface of the premaxilla has been worn away, exposing the deep roots of some of these teeth. There are five teeth in each premaxilla, the most anterior of which is particularly small. A diastema occurs between the last tooth in the premaxilla and the first tooth in the maxilla. In the right maxilla there are 18 preserved partial teeth or alveoli. A reconstructed region forming the lateral margin of the orbit would have accommodated an additional two teeth on the right side. In the left maxilla there are twenty-four partial teeth (broken at the


Figure 4.4. Teeth of NMING F8785, Rhomaleosaurus cramptoni, A. photograph of the last tooth in the right premaxilla (at top) with an interpretation of tooth ornamentation (bottom), B. Tooth numbers twelve, thirteen and fourteen (from right to left) in the right dentary (at top), with an interpretation of the tooth interpretation (at bottom). Tooth number thirteen is preserved in cross-section showing a recurved outline (scale bars $=10 \mathrm{~mm}$ ).
root) or alveoli, and an additional tooth position is missing where the lateral margin of the orbit has been reconstructed. There are therefore, a total of 25 observable teeth in the right upper jaw and thirty in the left. The first tooth after the diastema is very small and is followed by the largest tooth in the upper jaw. The size of the tooth alveoli gradually decreases posterior to this large caniniform tooth. Of the teeth preserved in the upper jaw, only one preserves part of the crown; the last right premaxillary tooth preserves four widely spaced ridges preserved in buccal view (Figure 4.4A). One of the ridges extends all the way to the crown apex, the others are shorter and slightly less pronounced.

The tooth count for each dentary is as follows, 29 in the right ramus and 32 in the left. The most anterior tooth in each dentary is situated lateral to the most anterior tooth in each premaxilla, as is the case in Plesiosaurus (Owen, 1865) and in all plesiosaurs (Pers. obs.). In the right dentary, teeth numbers 12 and 14 preserve parts of the crown, but they also protrude dorsally into the matrix (Figure 4.4B). The majority of the teeth are broken off at the root or otherwise badly damaged (Figure 4.4B). Tooth number 12 preserves seven buccal ridges around its base, and tooth 14 preserves six buccal ridges around its base. In the right dentary, small parts of the crowns are preserved in a number of teeth ( $1,4,8,9,10,12,15,21,32$ ), but they do not provide any further information on the tooth ornamentation.

A reconstruction of the complete skull and mandible of Rhomaleosaurus cramptoni (NMING F8785) in dorsal, ventral and lateral views, based on the above observations, is presented in Figure 4.5.

### 4.3 NMING F8785, Rhomaleosaurus cramptoni, postcranium

The postcranium of Rhomaleosaurus cramptoni has not received any preparation in recent years and the skeleton is obscured by plaster and black paint (see Chapter 3). It is therefore difficult to interpret the postcranium of NMING F8785 and as a result the description presented here remains superficial and limited in places.

### 4.3.1 Axial skeleton

There are 28 cervical vertebrae in the neck (including the atlas and the axis), and a total of 27 pectoral and dorsal vertebrae. Their preservation does not allow the transition between pectoral and dorsal vertebrae to be clearly identified, but the total number of presacral vertebrae equals 55 (Figure 3.4). There are four or five sacral (pelvic) vertebrae and 29-30 caudal vertebrae, but the transition is again difficult to interpret; the total number of vertebrae in this specimen in therefore 90 . The posterior


Figure 4.5. Reconstruction of the skull of Rhomaleosaurus cramptoni in A. ventral, B. dorsal, and C. lateral view. Grey areas represent the mandible, dotted grey lines represent ridges, and dotted black lines represent uncertain sutures. One side of the mandible has been removed in ' $A$ ' to show the organisation of the bones on the lateral portion of the palate.


Figure 4.6. Anterior cervical vertebrae of NMING F8785, Rhomaleosaurus cramptoni, A. posterior portion of the atlas-axis (left) and the first three cervical vertebrae in lateral view, quadrangles indicate the location of $B$ and $C$ (scale bar $=50 \mathrm{~cm}$ ), B. detail of the axis rib showing the hooked anterior process, C. postero-lateral view of the first cervical rib showing the double-headed articulation (scale bars in $B$ and $C=20 \mathrm{~mm}$ ).
portion of the axis together with the three articulated succeeding cervical vertebrae, have been prepared with the skull (Figure 4.6). The lateral length of the centra in the three cervical vertebrae (C3-5) is $4.05 \mathrm{~cm}, 4.79 \mathrm{~cm}$ and 4.74 cm respectively, and the height in C 3 and C 5 is 7.15 cm and 7.05 cm . The length to width ratio is therefore 0.3 in the anterior cervical vertebrae of $R$. cramptoni. No further measurements of vertebrae are presented because of the poor state of preparation of the postcranium.

On each vertebra, the neural arch facet extends far ventrally onto the lateral surface of the centrum, almost contacting the cervical rib facet. The base of each neural spine is positioned posteriorly relative to the centrum, and the neural spines are angled backwards so that they are positioned over the following vertebral centrum. In ventral view, there are a pair of a squared excavated pits separated by a rounded midline ridge. A single large nutritive foramina is situated in each of these pits (see Section 4.4.1 below for a detailed description and figures of the cervical vertebrae in Rhomaleosaurus). The cervical ribs are preserved fused onto the centrum in the axis vertebra and in C3-5. They are as tall as wide at their articulation and are very robust. In posterolateral aspect, a longitudinal foramen can be seen piercing between the rib head and the rib facet (Figure 4.6C), separating the rib into an upper and lower facet. The distal ends of the cervical ribs are incomplete, but the axis rib is almost complete and there is a clear hooked anterior process (Figure 4.6 B ); thus it can be inferred that the cervical ribs are 'hatchet' shaped.

In the cervical series, there is a distinct expansion in the width and robustness of the neural spines midway along the column; a sudden transition from laterally compressed spines to broad rounded ones. For example, in cervical vertebrae 15 and 16 the spine is 17 mm wide distally, in vertebrae $17-19$ the spines are not preserved, but in vertebra 20 the blade is 41 mm wide distally and in vertebra 21 the spine is 43 mm wide. Posterior to vertebra 21, all of the neural spines are broad and rounded. For a detailed description of the axial column in Rhomaleosaurus, see sections 4.4.1 and 4.5 below, which deal with the vertebrae in $R$. thorntoni and $R$. zetlandicus.

### 4.3.2 Limbs

Each of the four limbs of NMING F8785 is mounted separately in plaster (Figure 4.7); the distribution of many of the bones is artificial and so caution must be taken when interpreting the limbs in this specimen. As outlined in Chapter 3, most of the distal elements of the right hind limb were destroyed during the discovery and excavation of this specimen (see Figure 3.7C) (as figured by Ward, 1866), but the missing elements have since been reconstructed (Figure 3.4).


Figure 4.7. The limbs of NMING F8785, Rhomaleosaurus cramptoni, A. left forelimb, B. right forelimb, C. left hindlimb, D. right hindlimb (scale bars $=30 \mathrm{~cm}$ ).

All of the propodials (humeri and femora) are flared postaxially and preaxially, although the preaxial flare is much more noticeable in the femora. The distal facet of the humerus, which would articulate with the radius and ulna, is almost flat, and there are no separate facets for the radius and ulna (Figure 4.7A,B). This contrasts with the condition in the femur where distinct facets are present for articulation with the tibia and fibula. The humerus and femur are almost equal in length. On the left side of the animal, for example, the humerus is 53 cm in length and the femur is 53.4 cm in length. However, there is more of a discrepancy on the right side of the animal. The femur $(53.8 \mathrm{~cm})$ is longer than the humerus $(51 \mathrm{~cm})$, but this is probably an artefact of slight distal distortion to the right humerus. The humeral tuberosity is not as clearly defined as the equivalent structure (trochanter) in the femur. The tuberosity of the humerus is situated very slightly posteriorly relative to the head; in the femur the trochanter is situated directly above the head. There is a distinct preaxial bulge midshaft in each femur (Figure 4.7C,D).

All of the epipodials (eight in total) are preserved and mounted in rough articulation with the propodials (Figure 4.7). The radii are rectangular in shape with slightly concave preaxial and postaxial borders and slightly convex proximal and distal borders (facets); each is 16 cm long, but there is variation in their relative widths indicating that parts are damaged (Figure 4.7A,B). The right radius is 10.9 cm wide proximally whereas the left is 11.4 cm . Also, the right is 13.6 cm wide distally and possesses a posteriorly directed triangular process on the postero-distal corner, whereas this process is absent in the left and the distal width is therefore much shorter $(11.3 \mathrm{~cm})$. The ulnae are roughly reniform in outline, with slightly convex preaxial margins and rounded postaxial ones, and they are slightly shorter than the radii (14.6 in the left, 15.5 in the right). The distal surface of the left radius is separated by an angle into two facets for the intermedium (preaxially) and for the ulnare (postaxially); however, these facets are indistinct in the right ulna (Figure 4.7A,B).

There is also variation in the size and shape of the epipodials in the hindlimbs. Both the tibiae and fibulae are larger and broader than the equivalent bones in the forelimb (radius and ulna); the right tibia is 18 cm long (although the left is only 16 cm long) and each fibula is 16 cm long. The proximal facets (for the femur) are both straight, but the distal facets differ, being straight in the left, but producing a distinct posterior angle and facet (for the astragalus) in the right (Figure 4.7D). As mounted, the tibiae also differ in their width. The left is 11.7 cm wide proximally and 15.5 cm distally, while the right is 15.8 cm proximally and 14.98 cm distally. It is therefore probable that the left tibia has been mounted upside down with its shorter
distal surface placed in articulation with the femur. The preaxial surface of the left tibia is straight, while the equivalent surface in the right is concave. The fibulae are each 16 cm long; the maximum width of the right is 14 cm but the left is only 12 cm . They posses separate facets on their distal surfaces for the astragalus (preaxially) and the calcaneum (postaxially) (Figures 4.7C,D). The proximal facet of each fibula is straight, but angled relative to the tibia, to articulate with the separate fibular facet on the femur. The left fibula differs from the right in possessing a proximal postaxial triangular process, which articulates with the femur (Figure 4.7C); this process is probably a fused postaxial bone, similar to the condition seen in Eretmosaurus (see Owen, 1865, Tab, XIV). Therefore, the right fibula is reniform, but the left is not.

The carpals, metacarpals and phalanges in the humeri, and the tarsals, metatarsals and phalanges in the femora are all placed in rough association, but their relationships are unreliable. As mounted, there are six mesopodials and four metapodials in each limb, and there are no additional preaxial or postaxial bones (supernumeracies or pisiforms). The metapodials and phalanges comprise four digits in each limb. This arrangement is unique to this particular specimen and was listed as a diagnostic feature of this taxon by Seeley (1874), an interpretation accepted by Tate and Blake (1876) and Fraas (1910). However, Carte and Bailey (1863a, p. 168) originally considered this feature to be un-natural and "...so anomalous, that we believe it can scarcely be relied upon as a distinguishing character" and pointed out that the missing additional digits "may have got misplaced in setting up the fossil". The limbs also differ from all other known plesiosaurs in that the metapodials and digits are lined up in neat rows, rather than being staggered in other plesiosaurs. A portion of naturally articulated phalanges situated at the tip of the left forelimb (Figure 4.7A), indicate that the phalanges were indeed staggered in this taxon in life.

Together with the fact that the bones are mounted in plaster, it is therefore concluded that the arrangement of all of these limb elements are artificial (with the exception of the propodials and most of the epipodials).

### 4.3.3 Girdles

The majority of the anatomy of the pectoral and pelvic girdles is not visible in this specimen because it is exposed in dorsal view. However, some of the lateral edges of particular elements do extend beyond the rest of the skeleton in dorsal view (Figure 3.4), and transverse cross-sections indicate that the girdles are apparently preserved in their entirety. The only completely exposed girdle element is the left ilium, which is 26 cm long and very robust (Figure 4.8). It is clear that this bone has been broken away from the rest of the specimen in two pieces at some time in its


Figure 4.8. The left ilium of NMING F8785, Rhomaleosaurus cramptoni, in medial view (scale bar $=5 \mathrm{~cm}$ ).
history; it has been crudely fixed with some artificial matrix. The shaft has a flattened lateral surface and a rounded medial surface so that a transverse cross section through the bone is roughly semi-circular. There is a shallow ridge running from the postero-medial proximal corner, diagonally along the rounded medial part of the shaft to the antero-medial distal tip of the bone. The shaft is twisted so that the long axis of the distal flare is rotated clockwise by about 45 degrees relative to the long axis of the proximal facet.

### 4.4 BMNH R4853, Rhomaleosaurus thorntoni

Specimen BMNH R4853 was first described by Andrews (1922b), and a thorough description of the cranium was later provided by Cruickshank (1996). There is thus no need to repeat a description of the skull here. Notably, Cruickshank (1996) reinterpreted the position of the external naris in this specimen and my observations confirm that the depression identified by Andrews (1922b) as the external nares is indeed a taphonomic artefact, thus the interpretation of the cranium of BMNH R4853 presented here (Figure 4.9, 4.10) agrees with Cruickshank (1996) in most aspects. However, on the palate, the vomers are interpreted here extending far posterior to the external nares (contra Cruickshank [1996]) (Figure 4.10). Also, some of the bones of the postero-lateral portion of the palate are interpreted differently. In ventral view, the bone identified as the ectopterygoid by Cruickshank (1996) is regarded as the jugal, and the pterygoid as the ectopterygoid (Figure 4.10), although the pterygoid overlaps the ectopterygoid dorsally and is thus visible in dorsal view (Figure 4.9) (N.B, the sutures are unclear and this interpretation is based on comparison with NMING F8785, NMING F10194 and LEICS G221.1851).

The postcranium of BMNH R4853 was described by Andrews (1922b), but it has not been reviewed in recent years nor figured in detail and so it is thus described here. Note that a small, smooth rounded stone, 2 cm long, was found associated with this specimen, embedded in the matrix underlying the dorsal region between fragments of the gastralia (Figure 4.11, Figure 4.17). This stone contrasts with the rest of the matrix surrounding the specimen and is thus interpreted as a gastrolith.

### 4.4.1 Axial skeleton

The vertebral column of BMNH R4853 is almost complete. Vertebrae are only missing from the anterior part of the cervical series and from the posterior part of the caudal series (Figure 4.12). For the most part, the vertebrae are free of matrix and preserved in three dimensions, making them ideal for illustration and description (Figures 4.12-4.18) The incomplete cervical column contains ten vertebrae, about a


Figure 4.9. The cranium of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, in dorsal view, A. photograph, B. interpretation (dotted lines indicate uncertain sutures) (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.10. The cranium of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, in ventral (palatal) view, A. photograph, B. interpretation (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.11. A single gastrolith (arrow) preserved in the abdominal region of BMNH R4853, the holotype of Rhomaleosaurus thorntoni (scale bar $=5 \mathrm{~cm}$ ).
third of the probable total number (based on $R$. cramptoni). The cervical vertebrae are preserved in five blocks of articulated vertebrae, the fifth block also contains the first three 'pectoral' vertebrae (the rib facet articulates with the centrum and neural arch). A sixth block of vertebrae contains the remaining three pectoral vertebrae (total six) and the first four dorsal vertebrae. The total number of dorsal vertebrae is 25 , preserved in six blocks of articulated vertebrae (including block six). Five sacral vertebrae are preserved in articulation, as figured by Andrews (1922b, PI. VII). Finally, 15 caudal vertebrae are preserved in four blocks - an unknown number of terminal caudal vertebrae are missing.

The fourth cervical vertebra in the series is one of the best preserved of the cervical vertebrae (although the neural arch and spine have been broken off), and so it is described here as a representative middle cervical vertebra (Figure 4.13). The centrum is taller than it is long (lateral length 60 mm , anterior height 104mm) and very slightly wider ( 106 mm ) than it is high, so that the articular facets are circular (Figure 4.13A). The lateral margins of the articular faces are rounded-off (in horizontal crosssection) and the faces themselves are concave: thus the cervical vertebrae are amphiocoelus. In lateral view, there are distinct areas of rugose pitting (Figure 4.13B,D); these are delineated anteriorly and posteriorly by a boundary marking the edge of the smooth vertical band on the rounded antero- and postero-lateral margins of each vertebra. The delineation between each smooth band and the rugose area persists onto the ventral surface of the centrum (Figure 4.13C,E). The facet for the neural arch is ' $V$ ' shaped and the neurapophysis extends ventrally onto the lateral surface of the centrum and tapers ventrally into a narrow passage of smooth bone. This passage just separates the two bands of rugose bone and then widens ventrally to form the dorsal rim of the cervical rib facet. The cervical rib facet is large and 'crater-like', with raised rims, and it is tall, occupying the lower one-third of the centrum. It is divided into a large rectangular lower facet and a triangular upper facet (Figure 4.13B,D). Between these facets runs a very narrow longitudinal ridge so that, although the ribs are anatomically double-headed, functionally they are singleheaded. This longitidinal ridge represents the medial wall of a channel, as seen in the cervical ribs of Rhomaleosaurus cramptoni (NMING F8785) (Figure 4.6C). The cervical rib facets are also visible in ventral view and from this aspect the raised rims of the 'crater-like' rib facets are clearly visible (Figure 4.13,C,E). The ventral surface can be divided into three bands: the smooth bands (distal bands) closest to, and rolling onto, the articular faces; a single smooth band extending between the two facets in the middle of the centrum ('middle-band'); and in between are the rugose bands described above. The middle band is divided into two square depressions,

Figure 4.12. The articulated vertebral column of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, in dorsal view, A. the complete articulated column, B. detail of the posterior part of the vertebral column, C. detail of the anterior portion of the vertebral column (scale bars $=20 \mathrm{~cm}$ ).
separated by a rounded keel on the midline. The rounded keel has a slight ridge on its midline and a pair of very large nutritive foraminae are situated close to each other on the ventral surface of the centrum, separated by the rounded keel; each foramen is situated medially within the square depression.

Within the preserved series, cervical vertebra ten is the last cervical and is described here as a representative of the posterior cervical vertebrae (Figure 4.14). It is chosen over the other posterior cervical vertebrae because it is the only one to preserve a complete neural arch and zygapophyses, together with most of the neural spine (Figure $4.14 \mathrm{~A}, \mathrm{~B}, \mathrm{C}$ ). The centrum is similar in its overall proportions to the middle-cervical vertebra described above, but it is relatively wider (ventral length, 65 mm ; lateral length, 110 mm ; anterior width 126 mm ) than the more anterior vertebral centra (Figure 4.14A). Rugose pitting is again present on the lateral surface in the regions anterior to, and posterior to, the cervical rib facet and the triangular ventral process of the neural arch. The passage of smooth bone between the neural arch and the cervical rib is wider. The neural arch is fused onto the centrum and it is as tall as the centrum. The zygapophyses are located far from the centrum and expand laterally so that the width between the lateral margins of the prezygapophyses is slightly wider than the body of the centrum (Figure 4.14A,C). On the lateral surface of the neural arch there is a buttress-like rounded ridge running diagonally from the prezygapophysis anteriorly, to the base of the arch posteriorly (Figure 4.14B). This ridge is expanded at its terminal ends and narrow along its middle: there is a notable concave depression situated antero-ventrally to this ridge near the base of the neural arch. An ornamentation of fine ridges is present on the lateral edge of each prezygapophysis and there are six ridges oriented perpendicular to the edge of the zygapophysis. The articular face of each prezygapophysis faces dorsally and in dorsal view these appear circular with convex anterior and lateral margins (Figure 4.14C). The articular surface of the prezygapophysis is large and extends backwards to occupy almost half the length of the centrum. A horizontal 'table' of bone links the posterior margin of the prezgapophysis to the anterior margin of the postzygapophysis. In dorsal view the four zygapophyses in the vertebra form a 'butterfly' shape. A distinct lateral notch is present between the pre- and postzygapophyses (this represents the 'table' described above), and there is a similar notch between each pair of zygapophyses on the midline (Figure 4.14C). The postzygapophyses are in articulation with, and are therefore obscured by, the prezygapophyses of the succeeding vertebra. However, these extend far posterior relative to the posterior margin of the centrum. Like the prezygapophyses, the postzygapophyses are broad rounded facets oriented horizontally. The neural spine

Figure 4.13. Anterior cervical vertebrae of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, A. anterior view of cervical one, B. lateral view of cervical two, C. ventral view of cervical two, D. lateral views of cervicals four, five and six, E. ventral view of cervical five (numbers refer to position in the preserved sequence) (scale bar $=5 \mathrm{~cm}$ ).

Figure 4.14. The last cervical vertebra and first three pectoral vertebrae of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, A. anterior view of cervical 10, B. lateral view of all four vertebrae, C. dorsal view of all four vertebrae, D. ventral view of all four vertebrae, C. anterior view (number '10' refers to position in the preserved sequence) (scale bar $=5 \mathrm{~cm}$ ).
is not complete in cervical vertebra ten, but its base is preserved. This is situated posterior relative to the centrum, the anterior extent of the neural arch is roughly equivalent to half-way along the length of the centrum. The entire posterior half of the base of the neural spine is situated posterior to the centrum (i.e. located over the proceeding intervertebral space and anterior portion of the following vertebra). The preserved parts of the anterior and posterior margins of the spine slope posteriorly indicating that the complete spine was angled backwards. On the ventral surface of the centrum, the square pits are smaller relative to the size of the centrum than in the anterior cervicals.

In general structure, the pectoral vertebrae are similar to the posterior cervical vertebrae. However, In the first pectoral (vertebra 11 in the preserved series), the ventral surface of the centrum preserves an additional nutritive foramina on the right side there are two foramina, one close to the midline as in the cervical vertebrae, the other is more distant (Figure 4.14D). On the left side there is a single elongate foramina stretching laterally. Four nutritive foraminae are present in the next pectoral vertebra, one pair situated close to the midline, the other pair more distant (Figure 4.14D). In the following pectoral vertebrae, the number of nutritive foraminae returns to just a single pair. There is also a transition in the position of the rib facets in the pectoral vertebrae, which become incorporated, and eventually migrate dorsally onto the neural arch (Figure 4.14B, 4.15A). The smooth passage of bone between the neural arch and the rib facet described in the cervical vertebrae expands and becomes part of the tall, biconcave facets in the anterior pectoral vertebrae (Figure 4.14B). Another large block also preserves a sequence of seven vertebrae including the posterior three pectoral vertebrae and the first four dorsal vertebrae (Figure 4.15). This articulated sequence shows that the posterior part of the pectoral series and anterior part of the dorsal series was gently curved. Each vertebra is slightly higher than the proceeding one so that in lateral view the vertebral column follows a sigmoid path in this region, and the dorsal series is slightly arched (Figure 4.15A).

The sequence of 25 dorsal vertebrae is complete. The centrum in each dorsal vertebra is a simple spool-shape with no ornamentation, and the suture with the neural arch is a shallow ' $U$ ' shape (Figure 4.16A). The articular surfaces are platycoelus and the lateral margins are very slightly rounded and raised to form a lateral rim. The articular faces of the centrum are smooth ovals taller than they are wide (Figures 4.16C, 4.17B), and the neural canal is circular. A thin horizontal plate of bone overlies the neural canal between the postzygapophyses in posterior view, separating the neural canal from a triangular cavity at the base of the neural spine.

Figure 4.15. Articulated series of pectoral and dorsal vertebrae in specimen BMNH R4853, the holotype of Rhomaleosaurus
thorntoni (the last three pectoral vertebrae and the first four dorsal vertebrae), A. lateral view, B. dorsal view (scale bar $=5 \mathrm{~cm}$ ).

Figure 4.16. Dorsal vertebrae of BMNH R4853, the holotype of Rhomaleosaurus thorntoni (dorsal vertebrae 9 and 10), A. lateral view, B. dorsal view, C. posterior view of dorsal vertebra 10 (scale bars $=5 \mathrm{~cm}$ ).
(Figure 4.16C). The smooth, slightly concave lateral surfaces of the centrum are pierced by a number of small nutritive foraminae, there are typically two on each side, one positioned higher than the other (Figure 4.16A).

In dorsal view the transverse processes are robust, short, and angled backwards. In anterior/posterior view, these processes are oriented horizontally along the entire dorsal column. As identified by Andrews (1922b, p.410), a deep pit occurs below each lateral process where it originates from the neural arch (Figure 4.16A). This excavation extends along the ventral surface of the process and is bounded anteriorly and posteriorly by a raised ridge. A cross-section through the base of the lateral process is rectangular (Figure 4.16A) but the terminal tips expand distally into very smooth, circular, convex facets, bounded by a sharp rim, and in life these would have articulated with the concave facets of the dorsal ribs (Figure 4.17B,C). A sharp longitudinal ridge runs along the postero-ventral margin of the transverse process.

The prezygapophyses are oval in dorsal view, slightly longer than wide, and the postzygapophyses are triangular in dorsal view (Figure 4.16B). The articular surfaces of the zygapophyses are inclined at about 45 degrees in the most anterior dorsal vertebrae, but they gradually become increasingly vertically orientated in posterior vertebrae, and they become more closely spaced. All of the neural spines of the dorsal vertebrae are imperfect, but a transverse cross-section through the base of the spine in dorsal vertebra fifteen reveals a number of characteristics: 1 , the base of the blade is broad and situated directly over the centrum, 2, the lateral margins of the dorsal neural spine are slightly convex, but the posterior margin is concave with sharp postero-lateral edges, 3 , the anterior margin is similarly concave, but also includes an additional raised ridge on the midline so that a transverse crosssection through the anterior margin of the base of the neural spine is therefore ' $W$ 'shaped. Dorsally this 'W' shape disappears, a cross section through the middle of a neural spine in dorsal 9 and10 shows that the anterior margin becomes convex in cross section and articulates with the preceeding neural spine (Figure 4.16B).

There are five sacral vertebrae, preserved in articulation, with the sacral ribs in place (Figure 4.18), an area well described by Andrews (1922b). The facets of the prezygapophyses and postzygapophyses are oriented vertically and they appear narrow in dorsal view. The sacral rib facets are flat distally (unlike the convex facets in the dorsal vertebrae) and angled slightly posteriorly. The sacral ribs are angled backwards (this angle is greater in the anterior ribs), and they expand distally and unite, although as pointed out by Andrews (1992b), they are not fused, to form a straight horizontal facet for the ilium.

Figure 4.17. Dorsal vertebrae of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, A. ventral view of dorsal vertebrae 11-16 (obscured by paint and fragments of gastralia), B. posterior view of dorsal vertebra 16, C. right lateral view of dorsal vertebrae 17-20 (scale bars $=5 \mathrm{~cm}$ ).


[^1]The caudal vertebrae in this sequence are incomplete and the sequence is imperfect, there are only fifteen preserved vertebrae (Figure 4.11). For a detailed description of the caudal vertebrae in Rhomaleosaurus, see section 4.52 below, describing R. zetlandicus.

### 4.4.2 Pectoral girdle

Both coracoids of BMNH R4853 are preserved, (Figure 4.19) although most of the posterior process of the left has been reconstructed based on the counterpart element, and parts of the preglenoid region of the right are missing. The following description concentrates on the more complete right coracoid.

The coracoid is a very broad element, 39 cm across its widest point (level with the posterior-most part of the glenoid) and 52.5 cm long from the posterior margin of the posterior process to the posterior border of the pectoral fenestra. There is also a very broad preglenoid extension ( 18 cm wide). The midline symphysis of the right coracoid is remarkable in the possession of distinct process halfway along the dorsal surface of the symphysis (Figure 4.19); this is associated with a notch in the counterpart, which accommodates the process when the coracoids are articulated. This region of the coracoid is therefore asymmetrical in dorsal view, but in ventral view the symphysis is straight. When articulated, the angle between the coracoids at the middle of the symphysis is shallow (approximately 25 degrees); the posterior processes of the coracoids are 'rolled', i.e., in transverse cross-section they are curved along their entire length so that they are convex ventrally and concave dorsally. The 39.4 cm long symphysis does not extend for the entire length of the coracoid but terminates posteriorly, separating the coracoids on the midline. This separation results in a discrete posterior coracoid vacuity - the medial margins of the posterior processes of the coracoids form the margins of this vacuity. Immediately posterior to the symphysis, the medial margins of the coracoids diverge for a few centimetres, but distally they expand medially so that the vacuity is oval-shaped (Figure 4.19). The terminal surface of the plate-like bone surrounding the vacuity has a longitudinal gully bordered by a dorsal and ventral longitudinal ridge, this indicates a region of articulation with cartilage in the posterior coracoid vacuity. The coracoid is also thickened anteriorly between the glenoids, and forms a laterally oriented ridge. The posterior process is very broad and almost as wide $(28 \mathrm{~cm})$ as it is long $(28.5 \mathrm{~cm}$ from the distal margin of the glenoid); this process is 26 cm wide at its narrowest point about half way between the glenoid and its posterior tip. The posterior cornua (or 'wing') of the coracoid is rounded and poorly developed.


Figure 4.19. The pectoral girdle of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, in dorsal view (scale bar $=20 \mathrm{~cm}$ ).

The posterior part of the scapula is fused onto the scapular facet of the glenoid process of the coracoid, forming the anterior part of the ' V ' shaped glenoid for the articulation of the humerus (Figure 4.19). The glenoid is a shallow oval shape in lateral view, 13.2 cm deep and 26 cm long. The right scapula has been reconstructed (a small piece is still preserved in articulation with the coracoid) but the left is quite complete, missing only the ventral (anterior) process and some of the lateral border of its main shaft. The left scapula is fused with the left coracoid. In dorsal view, the scapula-coracoid suture follows a straight path from the pectoral fenestra, posteriorly to the glenoid (about 40 degrees perpendicular to the coracoid symphysis) but in lateral view this suture slopes antero-ventrally along the glenoid facet. The dorsal process of the scapula protrudes postero-dorsally and slightly outwards (Figure 4.19). It is gently arched with a concave ventral margin and dorsal margin that is convex in lateral view. The dorsal blade of the scapula is also very robust and broad mediolaterally, a transverse cross-section through the middle of the process presents an elongate 'half-moon' shape with its flat surface facing laterally and its convex surface facing medially. This distinct cross-section is reversed at the tip of the process so that the rounded surface of the cross-section is positioned laterally. The surface of the terminal face of the dorsal process of the scapula is flat and so appears squared-off in lateral view. On the lateral surface at the base of the dorsal process is a distinctive longitudinal ridge. This ridge appears to have continued anteriorly onto the dorsal surface of the ventral process, but this area has been broken away.

The clavicles and interclavicle are fused into a broad complex, which fits in the girdle between the scapulae (Figure 4.19). Many of the margins of this complex are broken and plaster has been used to reconstruct missing areas, so the sutures are not clearly visible and it is difficult to interpret the exact organisation of the bones. The whole element is concave dorsally and the anterior margin of the interclavicle forms a shallow concavity, considered equivalent to the 'medial notch' described by Owen (1883). Fragments of the left and right clavicle flank the interclavicle and in dorsal view the clavicle-interclavicle sutures appear to converge posteriorly.

### 4.4.3 Pelvic Girdle

The pelvic girdle is represented by both ischia (complete), both pubes (incomplete) and both ilia (complete) (Figure 4.20). The pubes of BMNH R4853 are large flat plates, slightly wider $(43 \mathrm{~cm})$ than long $(48 \mathrm{~cm})$. The pubis expands slightly anteriorly and has a distinct facet for the attachment of the femur. There is no angle delineating the facet and the anterior blade of the pubis so the glenoid simply tapers out


Figure 4.20. The pelvic girdle of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, A. articulated pubes and ischia in dorsal view (scale bar $=20 \mathrm{~cm}$ ), B. Right ilium in medial view (articulation with ischium towards the left) (scale bar $=20 \mathrm{~cm}$ ).
anteriorly. The mid-line symphysis between the pubes is 25 cm long. The anterior margin of the pubis is convex, but the middle part has been reconstructed in plaster so it is not possible to determine if this is a natural feature. The postero-medial corner of the pubis forms a triangular process forming the medial margin of the pelvic fenestra and forming a pelvic bar, which extends towards, but does not actually contact, the anterior mid-line process of the ischium (Figure 4.20A). The process forming the pelvic bar in the ischium is square in dorsal and ventral views.

The ischium is also roughly equal in its length and width. The lateral process of the ischium is particularly broad and the flared distal end of this process bears three facets, one for articulation with the pubis anteriorly, and two less distinct facets for the femur and the ilium respectively. The posterior process of the ischium is truncated posteriorly so that this element is short relative to its width. The terminal tip of the posterior process is flattened and forms a sharp angle where the posterior margin meets the lateral margin at its postero-lateral tip.

Both ilia are preserved in their entirety; these are robust and relatively short elements (Figure 4.20B). The facets for the ischium and femur are poorly developed and no clear sutural relationship can be determined with the ischium. The shaft of each ilium can be divided into a flattened lateral surface and a rounded medial one so that a transverse cross section through the bone is roughly semi-circular proximally. There is also a shallow ridge running from the postero-medial proximal corner of each ilium, diagonally along the rounded medial part of the shaft to the antero-medial distal tip. This ridge results in a squared, almost ' $X$ '-shaped cross sectioned mid-shaft, but this diminishes distally as the iliac blade becomes mediolaterally compressed and slightly flared. The compressed distal end is thus wider (thicker) posteriorly, and pinched at its narrowest extent anteriorly. The pinched anterior end produces a flange on the antero-distal margin of the ilium (Figure 4.20B). The shaft of each ilium is twisted so that in the right element, the long axis of the distal flare is rotated anticlockwise by about 45 degrees relative to the long axis of the proximal facet, and the shaft is rotated by a similar amount in a clockwise direction in the left ilium.

### 4.4.4 Limbs

Portions of all four propodials are preserved although their missing parts have been reconstructed in plaster and painted to match the bone (Figure 4.21 and 4.22). No other elements of the limbs are preserved in BMNH R4853.

The left humerus is more complete in this specimen than is the right humerus. The whole posterior half of the shaft, the proximal tip, and the posterior flange on the


Figure 4.21. The humeri of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, A. left humerus in dorsal view, B. right humerus in dorsal view, $C$. left humerus in posterior view (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.22. The femora of BMNH R4853, the holotype of Rhomaleosaurus thorntoni, in dorsal view, A. left femur, B. right femur (scale bar $=20 \mathrm{~cm}$ ).
distal tip have been reconstructed on the right side, presumably based on these areas in the left humerus, and as a result this element is shorter than its more complete counterpart (Figure 4.21B). The left humerus is complete with the exception of a small area of the distal articulation for the ulna (reconstructed in plaster) and its antero-distal end has been broken off (Figure 4.21A). This area is also missing in the right humerus but neither element has been restored in this region. The anterior margin is slightly concave due to a preaxial distal flare and the shaft is oval in cross section. There is a nubbin of bone protruding from the dorsal surface of the humerus midway along the shaft. In posterior view, the head of the humerus is clearly angled ventrally relative to the long axis of the shaft (Figure 4.21C).

The femora are both almost complete in BMNH R4853, but the preaxial flare of the right has broken away, as has the postaxial distal flare of both elements (Figure 4.22). On the posterior margin there are two raised bumps in a row, presumably areas for muscle attachments.

### 4.5 YORYM G503, Rhomaleosaurus zetlandicus

The skull of YORYM G503 was described and figured in detail by Taylor (1992). An interpretation of the dorsal surface of the skull is provided here (Figure 4.23), but does not differ significantly from the earlier work of Taylor (1992). The only additional observation made here with reference to the palate of YORYM G503, is the identification of lateral palatine vacuities: the posterior edge of the right vacuity is preserved. However, this specimen provides some important postcranial characters which are absent or poorly preserved in all other Toarcian specimens of Rhomaleosaurus, in particular, its almost complete caudal series (Figure 4.24) and articulated forelimb (Figure 4.25).

### 4.5.1 Forelimb

The left forelimb of YORYM G503 is an isolated humerus. The humerus of the right forelimb is broken into two (Figure 3.19), but the distal part is preserved in natural articulation with the epipodials, mesopodials and metapodials (Figure 4.25). The limb is exposed in ventral view and has rotated anteriorly so that it runs in parallel with the long axis of the trunk (see Taylor [1992b] for a review of the taphonomy of this specimen). The distal portion of the humerus is divided into separate facets for the radius and ulna, however, these separate facets are not clear in dorsal view (as seen in the left humerus). The ventral surface is pinched between the two facets whereas the dorsal surface is not (Figure 4.25). The radius is a large roughly rectangular element with a flat proximal articulation for the humerus, and concave preaxial and


Figure 4.23. The skull of YORYM G503, the holotype of Rhomaleosaurus zetlandicus, in dorsal view, A. photograph, B. interpretation of the cranium (mandibles not included) (scale bar $=20 \mathrm{~cm}$ ).
postaxial margins. The distal facet is divided into two flat surfaces, the largest ( 9 cm long) runs parallel to the proximal facet and articulates with the radiale; a shorter facet ( 4 cm long) on the postaxial part of the radius is angled for articulation with the intermedium. The lunate ulna ( 15.1 cm long) is shorter than the radius ( 18.5 cm long). The preaxial surface is slightly concave and the postaxial surface is rounded, however, there is a slight angle representing the end of the proximal facet for the humerus (Figure 4.25). There are three widely spaced disc-like bones in each mesocarpal row, the first (proximal) row comprises the radiale, intermedium, and ulnare; the second row comprises three distal mesocarpals (one is only visible as an imprint). The radiale is a broad short element ( 7 cm wide and 4.7 cm long) whose surfaces can be divided into five separate facets/edges, but these do not articulate closely with any other elements. The intermedium is a roughly hexagonal bone divided into six flattened edges, one edge articulates closely with a special facet on the radius and another articulates with the ulna. The intermedium articulates loosely with the ulnare, which is similar in size and shape to the intermedium. However, the edges are more rounded in the ulnare. Distal metacarpal one is a small wedgeshaped bone, 4.7 cm wide. Distal metacarpal two-three is not preserved, but its outline is visible in the matrix (indicated by dotted lines in Figure 4.25); it is rounded and quite large (similar to the intermedium). Distal mesocarpal four is represented by a proximal fragment of the bone, but the distal part is preserved as an impression; it is slightly wider than it is long and the proximal surfaces are divided into facets for loose articulation with the intermedium and ulnare. The two rows of mesocarpals do not form neat rows: the intermedium and unlare are situated proximally relative to the radiale, and distal mesocarpal four is roughly in line with the radiale. Metacarpals i-iv are preserved in a row, however, only ii and iii are complete; each one is 8.7 cm long. Metacarpal $v$ is not preserved but it was likely shifted proximal relative to the other metacarpals (as in R. victor), occupying the gap situated distal to the ulnare and postaxial to distal mesocarpal four (Figure 4.25). Taylor (1992b) noted the presence of a phalanx associated with the skull, but otherwise, there are no distal limb elements and the arrangement of the phalanges in this specimen cannot therefore be determined.

### 4.5.2 Caudal vertebrae

YORYM G503 is also notable for its almost complete caudal series comprising 29 vertebrae (a small number of terminal vertebrae are probably missing) (Figure 4.24 shows the articulated series of caudal vertebrae 9-29). In lateral view, the surface of the centrum is flat and the facet for the caudal rib is situated high upon the margin; it

Figure 4.24. The posterior portion of the articulated series of caudal vertebrae (caudal vertebrae 9 to 29) in YORYM G503, the holotype of Rhomaleosaurus zetlandicus, A. left lateral view, B. ventral view, arrows indicate the position of a conspicuous vertebra near the tip of the tail (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.25. The right forelimb of YORYM G503, the holotype of Rhomaleosaurus zetlandicus, in ventral view, A. photograph, B. interpretation (scale bar $=10 \mathrm{~cm}$ ).
was presumably formed partly by the neural arch. The rib facets decrease in size posteriorly and disappear completely after vertebra 19. The ventral surface of each caudal vertebra is flat with a slightly rugose surface and widely spaced nutritive foraminae (situated slightly medially to the chevron facets). In caudal vertebra numbers one to 13 , the anterior margin of the centrum is slightly convex, whereas the posterior ventral margin bears deeply pinched facets for the chevrons. In caudal vertebra 13 to 17 , these pinched facets develop on the anterior ventral margin of the centrum too, and posterior to vertebrae 18, the facets on the anterior and posterior borders are equal in size. Therefore, anteriorly the chevrons articulate with single vertebrae, but posteriorly they articulate with two vertebrae. There are no chevron or rib facets at all in vertebrae 27 and 28; a sliver of bone belonging to vertebrae 29 is preserved at the tip of the sequence. There is a notably shortened vertebral centrum situated near the tip of the tail (number 21) (Figure 4.24) and the vertebrae succeeding this vertebra become compressed laterally (Figure 4.24).

### 4.6 Rhomaleosaurus full body reconstruction

In addition to the reconstruction of the skull of Rhomaleosaurus cramptoni (Figure 4.5), a reconstruction of the whole skeleton of Rhomaleosaurus was produced for this thesis. This is the first detailed full-body skeletal reconstruction for any Lower Jurassic pliosaur (Figure 4.26 and 4.27) and was constructed by combining data collected from Rhomaleosaurus cramptoni (NMING F8785), Rhomaleosaurus thorntoni (BMNH R4853) and Rhomaleosaurus zetlandicus (WM 851.S). This was done because preliminary cladistic and morphometric analyses supported the notion that they are congeneric (Smith, 2006b). Ideally, only data from a single specimen should be used for such a reconstruction (in this case, R. cramptoni), but it was necessary for data to be combined from different specimens here because some areas of the anatomy of $R$. cramptoni are not exposed. The skull and the general proportions of the reconstruction are therefore based upon NMING F8785, the majority of the postcranial anatomy is based upon BMNH R4853) and the terminal part of the tail is based upon (YORYM G503).

The body of the animal is dorso-ventrally flattened and there is very little curvature along the vertebral column; the entire sequence of vertebrae is almost straight, except for the pectoral and anterior dorsal regions, which are slightly ' S 'shaped in lateral view. Many aspects of the postcranial skeleton are robust and/or reinforced, i.e., the neural spines of the posterior cervical and dorsal vertebrae, the wide, buttress-like cervical zygapophyses, the asymmetrical midline tooth-and-socket joint in the coracoid, and the robust dorsal blade of the scapula and the ilium. The


Figure 4.26. Full body reconstruction of Rhomaleosaurus in dorsal view (scale bar $=1 \mathrm{~m}$ )


Figure 4.27. Full body reconstruction of Rhomaleosaurus in lateral view (scale bar $=1 \mathrm{~m}$ )
ribs are wide and swept backwards and the distance between the coracoid is notably large. It would be possible to bring the girdles slightly closer to each other by introducing more curvature into the dorsal column, however, there is no evidence for this in the vertebrae. As outlined above, the total length of NMING F8785 reached 7 m , and a similar length has been calculated for R. thorntoni (Appendix 4). Additional fragmentrary remains referred to Rhomaleosaurus have been tentatively scaled up to 8 m (Forrest, 2000), and this is certainly within the realm of possibility for this genus.

### 4.7 NMING F10194, skull

Most of the fossil bones belonging to NMING F10194 are enclosed within a number of limestone blocks and fragments (specimens NMING F10194/1 - F10194/38)
(Figure 4.28A). The larger blocks can be reconstructed along sharp breaks, but some of the elements are isolated and free of matrix. Although thirty-eight fragments are listed in the museum register, some of these have been glued together along sharp breaks (five with 22,15 with 16,19 with 23,30 with 31 ), and new blocks have been created via preparation (39, fragment of coracoid; 40, fragment of palate). Although most of the blocks can be confidently or at least roughly matched up and correlated, the relative position of some blocks remains a mystery. There is some indication that the whole animal may have been preserved lying on its right side, which is rare and unusual in plesiosaurs. In general, the articulated dorsal vertebrae have rotated to the right (so they are exposed in lateral aspect), and the majority of the ribs protrude in one direction from the vertebral column, pointing towards the girdles and the limbs (Figure 4.28B). The skull was originally exposed in dorsal and lateral views but most of the palate is now visible after preparation (Figures 4.29, 4.30 and 4.31); the position of the skull relative to the rest of the specimen is unknown.

### 4.7.1 Skull roof

The premaxillae form an elongate spatulate rostrum with crenulated lateral margins in dorsal view, i.e., broad rounded protrusions, which correlate to the positions of the secondary tooth alveoli (Figure 4.29), and each premaxilla bears five teeth. The premaxillae send back tapering posterior processes along the midline reaching midway between the orbits. There is no dorso-median foramen or cleft situated between the premaxillae on the midline, however a longitudinal midline ridge is formed between the juncture of the premaxillae. Anteriorly this ridge is sharp and narrow but posteriorly it widens gradually, becoming smooth and rounded, and by the level of the external nares it incorporates the whole of each premaxilla, and gradually disappears as the premaxillae approach the frontals. The maxillae contact the


Figure 4.28. Interpretation of the reconstructed postcranium of NMING F10194 (for original photograph see Figure 3.8), A. identification of the blocks comprising the specimen superimposed onto the original photograph, white blocks represent fragments excluded from the photograph. The numbers represent the last digits of the museum number (e.g. NMING F10194/--), (N.B. the relationship of some other blocks cannot be determined and so these are not included in this figure), B. interpretation of the skeletal elements (scale bar $=20 \mathrm{~cm}$ ).
premaxillae at a distinct lateral restriction/notch (Figure 4.29), coincident with a diastema between the last premaxillary tooth and the first maxillary tooth. Each maxilla/premaxilla suture runs from the antero-medial border of the external naris and runs in an antero-lateral direction for most of its length, curving abruptly as it approaches the outer margin of the jawline, which it joins perpendicularly. The maxilla contacts the frontal and prefrontal dorsally and contributes to the whole lateral margin of the external naris and the antero-lateral margin of the orbit. It unites with the jugal on the lateral border of the orbit. Each maxilla produces a strongly developed triangular flange that protrudes dorsally between the frontal and the prefrontal (Figure 4.29). The lack of sutures antero-lateral to this flange indicate that these flanges do not represent separate nasal bones; nasals are therefore considered absent in this specimen.

The paired frontals occupy a position between the orbits and meet on the midline. Each frontal sends a narrow anterior projection to contact the postero-medial border of the external nares, almost to the exclusion of the premaxillae, which retain a diminutive contact. The antero-medial border of the orbit is formed by the prefrontals. These are narrowly exposed on the dorsal surface and contact the premaxilla flange anteriorly and the frontal medially. The width between the orbits is notably short and it appears that a portion of the medial border of each orbit (parts of the frontal and prefrontal bones) is missing due to damage. The frontals joins the fused parietals along a strongly interdigitating suture at a level equivalent to the posterior margin of the orbits. A large lozenge shaped pineal foramen is situated on the midline between the fused parietals, immediately posterior to this suture and almost contacting the frontals. The parietal contacts the squamosals posteriorly, but the dorsal extent of the parietal crest is unknown due to damage. The postorbital bars are also obscured in parts by matrix so that sutures are difficult to identify. The postfrontals appear to be triangular elements and contribute to the postero-medial margins of the orbit, contacting the frontal anteriorly, the parietal medially, and the postorbital laterally. Each postorbital bridges the postorbital bar and unites with the jugal along a straight horizontally orientated suture spanning from the orbit margin to the squamosal (Figure 4.31). The postorbital produces a posterior process or 'footplate', which contacts the anterior ramus of the squamosal. The jugal is a very deep and elongate element forming a cup-like postero-lateral margin to the orbit (Figure 4.32), terminating approximately $2 / 3$ along the lateral margin (Figures 4.29, 4.31). The jugal is bounded ventrally by the posterior process of the maxilla (on the lateral cheek margin but not on the palate), and contacts the squamosal along an anteriorly inclined suture (Figure 4.31). The jugal has a short contact with the cheek


Figure 4.29. The skull of NMING F10194 in dorsal view, A. photograph, B. interpretation (scale bar $=30 \mathrm{~cm}$ ).
margin, but this area is slightly damaged and it is therefore possible that the maxilla contacted the squamosal in life, excluding the jugal from the cheek margin. The triradiate squamosals form the posterior and lateral margins of the temporal fenestra, and their dorsal rami meet on the midline along a strongly interdigitating suture at which a posterior bulb is formed (Figure 4.29). The right quadrate is completely preserved; it is a wide element with a posterior expansion. The dorsal process fits snugly between the lateral and medial ventral flanges of the squamosal but there is no quadrate foramen. The skull is very shallow in lateral view and there is no strong excavation of the cheek margin (Figure 4.31).

### 4.7.2 Palate

The anterior part of the palate in NMING F10194 is incompletely exposed and the posterior and right lateral parts are exposed in horizontal cross-section. The vomers form the medial margins of the internal nares and extend and expand posteriorly beyond their posterior margins to contact the pterygoids on the midline and the palatines laterally (Figure 4.30). The pterygoids contact each other anterior to an anterior interpterygoid vacuity, and unite along a broad mid-line suture posterior to the vacuity. The anterior interpterygoid vacuity is narrow with pointed anterior and posterior ends. The palatines are situated lateral to the pterygoids and contribute to the posterior margin of the internal nares. The pterygoid-palatine suture runs in a straight line from the internal naris to a palatine vacuity so that the pterygoids broaden posteriorly. The anterior border of the kidney-shaped palatine vacuity is formed by the palatine and the medial and posterior borders are formed by the pterygoid, which sends a lateral process to contact the palatine again on the lateral margin of the vacuity, excluding the ectopterygoid from the margin. In contrast to the smooth posterior border formed by the pterygoid, the anterior palatine border is irregular; the long axis of the palatine vacuity runs medio-laterally. The surface of the palatine is mostly confluent with the flat surface of the pterygoids, but laterally it slopes away (in a dorsal direction) resulting in a longitudinal ridge, which extends posteriorly and incorporates the ectopterygoid.

The maxilla contributes to the lateral margin of the internal nares and forms the lateral margin of an elongate and narrow suborbital fenestra. Both palatal fenestrae/vacuities and suborbital fenestrae/vacuities are therefore present in NMING F10194. The straight palatine-maxilla suture runs from the posterior margin of the internal naris to the anterior margin of the suborbital fenestra. The medial margin of the suborbital fenestra is formed by the palatine anteriorly, and posteriorly it is formed by an anterior extension of the large ectopterygoid (Figure 4.30). The


Figure 4.30. The skull of NMING F10194 in ventral (palatal) view, A. photograph, $B$. interpretation (grey indicates bone surface, crosshatch indicates broken surface, white indicates matrix, dotted lines indicate ridges) (scale bar $=10 \mathrm{~cm}$ ).

Figure 4.31. The skull of NMING F10194 in left lateral view, A. photograph, B. interpretation (dotted lines indicate ridges)(scale bar $=20 \mathrm{~cm}$ )..
jugal has a long narrow exposure on the palate between the ectopterygoid and the maxilla, and it extends to participate in the posterior margin of the suborbital vacuity. The posterior extent of the jugal is unclear because this region is obscured by matrix, but a cross-section through this region in the right hand side of the skull, confirms the relationship of the bones in this area and shows a clear contact of the jugal with the palatal surface (Figure 4.32). The ectopterygoid boss appears to be formed predominantly by the ectopterygoid, but the pterygoid contributes slightly to the postero-medial margin. The cultriform process of the parasphenoid is short, narrow and terminates in a very sharp tip. It is asymmetrical, with the right pterygoid sending a flange over the parasphenoid just anterior to the posterior pterygoid vacuity, and the left pterygoid is recessed at this level giving the cultriform process a sinuous path (Figure 4.30).

### 4.7.3 Basicranium

In plesiosaurs, the relationship between the basioccipital and the basisphenoid is usually obscured by the posterior processes of the pterygoids, which meet on the midline behind the posterior interpterygoid vacuities in many taxa. The preservation of NMING F10194 is fortuitous in this regard because this region has suffered damage; the rear of the basicranium is exposed in a roughly horizontal cross-section, beginning at the anterior part of the posterior interpterygoid (Figure 4.30). This section is estimated to be only a few millimetres deep for most of its length, but deepens posteriorly to about a centimetre. The pterygoid plates, which presumably underlapped the basicranium in this specimen, are therefore missing. The crosssection preserves a clear suture between the basioccipital posteriorly and the basisphenoid anteriorly. On the midline, the basioccipital plugs into a squared basisphenoid facet forming an angular suture (Figure 4.30). Laterally a slightly interdigitating suture is visible, uniting the basisphenoid with the pterygoid. This suture runs from the posterior margin of the posterior interpterygoid vacuity and postero-laterally it meets the edge of the basicranium. However, there is no evidence of a basioccipital tuber, or any contact between the basioccipital and the pteryggoid, presumably this contact was situated more ventrally relative to the preserved crosssection. There is no evidence of a suture between the basisphenoid and the parasphenoid; this is probably because of the low angle of the cross-section. In the right interpterygoid vacuity, a distinct basal articulation is preserved in cross-section protruding from the anterolateral margin.


Figure 4.32. Detail of the skull of NMING F10194, showing the anterior view of a break in the skull through the posterior margin of the right orbit, showing the cup-like posterior border of the orbit formed by the jugal (area inside dotted lines), and a clear contact of the jugal on the palatal surface, A. photograph, B. interpretation (scale bar $=5 \mathrm{~cm}$ ).

### 4.7.4 Mandible and dentition

The mandible is absent in NMING F10194, so details of the shape, structure and dentition of the mandibular symphysis are unknown; these characters are usually of taxonomic importance amongst pliosauroids (Tarlo, 1960). Another diagnostic character amongst pliosauroids is the morphology and ornamentation of their teeth. A fracture resulting from preparation conveniently exposes a horizontal longitudinal section through the maxilla revealing some un-erupted teeth and primary tooth alveoli. No surface ornamentation is preserved on the teeth. However, there is another very fragmentary tooth preserved in the associated material, and from what can be seen of the ornamentation, the pattern of ridges is identical to that described in Rhomaleosaurus megacephalus (Cruickshank, 1994b).

### 4.8 NMING F10194, postcranium

The postcranial skeleton is preserved in thirty-six blocks, the majority of which can be reconstructed to their original in situ relationships (Figure 4.28A). In the following description, numbers in brackets with an asterisk refer to the numbers of individual blocks as illustrated in Figure 4.28A.

### 4.8.1 Axial skeleton

There are a total of six cervical vertebrae and seventeen dorsal (including pectoral) vertebrae; the vertebral column is therefore incomplete. The cervical vertebral column is poorly represented, although the vertebrae are articulated in the few blocks that are preserved. The neural spines are angled backwards in the smallest (presumably anterior) cervicals and taper to a rounded apex. In contrast, the neural spines of the larger (posterior) cervicals do not taper: the posterior and anterior borders of the neural spines run parallel and the spine terminates in a flat apex; they appear to be angled very slightly anteriorly. Large portions of the dorsal vertebral column are preserved in articulation (Figure 4.28B). The first of the vertebrae in the articulated column is a posterior pectoral and the matrix anterior to this vertebra is empty, indicating that the neck was dislocated at this point in the column before burial and fossilisation. There are nine vertebrae articulated in the largest block (35*). The most posterior of these joins up with the rest of the column (posterior dorsal vertebrae) in a large block (34*) associated with the pelvic girdle. The dorsal vertebrae are simple spool-shapes and where visible, the suture between the centrum and the neural arch is straight and horizontal. The neural spines of the dorsal vertebrae are positioned directly over the centrum, so that in lateral view the anterior and posterior borders of the centrum and neural spine are almost parallel.

The transverse processes appear robust but they are enveloped in matrix and difficult to observe. The terminal facets are round in shape and convex. The articulated column is notable for its curvature in the dorso-ventral plane. The spine is bent upwards at its extremities, arching along an unnatural dorsally concave path. This has caused the tips of the neural spines to meet, and in one case, slightly overlap (Figure 4.28B). Such curvature is not frequently observed amongst plesiosaurs, although it is a common occurrence in the necks and spines of terrestrial vertebrates. Three isolated fragmentary ribs are preserved ( $15^{*}, 18^{*}, 21^{*}$ ), these are round in cross-section but do not provide any further information.

### 4.8.2 Pectoral girdle

The pectoral girdle in NMING F10194 is complete, but the elements are scattered throughout the specimen and obscured by matrix in places (Figure 4.28B). One scapula lies in close association with the interclavicle in the largest block of this specimen ( $35^{*}$ ). They are intersected by a sharp break, which can be matched up neatly $\left(36^{*}-35^{*}\right)$ with a block containing the rest of the scapula and the rest of the clavicle-interclavicle complex, together with the second scapula and the anteriormost portion of the left coracoid. Part of this coracoid is not fixed into the matrix and can be removed and examined in three dimensions (32*). Three more fragments can be matched up with this block, and with each other ( $9^{*}, 24^{*}, 36^{*}$ ). The largest contains the posterior process of the coracoid and also the majority of both humeri. Two blocks align with the medial margin of the coracoid ( $9^{*}, 29^{*}$ ), and completes the proximal part of a humerus (29*) and right scapula (9*) respectively (Figure 4.28). Figure 4.33A shows a reconstruction of the left side of the pectoral girdle with the clavicle-intercalvicle complex in the correct position. The right coracoid (Figure 4.33 B ) is preserved in a separate block ( $13^{*}$ ) but the relationship of this block with the rest of the specimen cannot be determined. According to the NMI museum register, M. Taylor regarded this coracoid "too small to be part of this animal" and noted that the bone is more like "'plesiosaurus' hawkinsi scale". However, the coracoid is actually identical in morphology, size and preservation to the left coracoid preserved with NMING F10194 (see above), confirming that both coracoids are associated with this specimen (Figure 4.33). The isolated right coracoid (13*) has apparently been treated with plaster to join two parts together. The preglenoid process of the right coracoid preserves an anterior-facing facet, presumably for the articulation of the posterior process of the interclavicle.

The coracoid is an elongate element, 22.7 cm at its widest point (level with the posterior-most part of the glenoid) and 46.5 cm long. The midline symphysis


Figure 4.33. The partially reconstructed pectoral girdle of specimen NMING F10194, A. reconstruction of the articulated left coracoid and left scapula in ventral view, together with the exposed portion of the clavicle-interclavicle complex, B. the complete right coracoid in dorsal view, note that the size and shape is identical to its counterpart (see text for discussion) (scale bar $=20 \mathrm{~cm}$ ).
terminates after 25 cm and posteriorly the coracoids separate on the midline to form a deep ' V '-shaped coracoid vacuity, 17 cm long. The medial margins of the posterior processes of the coracoids are crenulated (Figure 4.33). The coracoid is thickened anteriorly between the glenoids, and forms a laterally oriented ridge. The posterior cornua ('wing') of the coracoid is squared off and the posterior margin of the coracoid process is straight. The clavicles and interclavicle are fused into a broad complex and the anterior margin of the interclavicle forms a shallow concavity.

### 4.8.3 Pelvic girdle

In NMING F10194, the right pubis is preserved in the second largest block ( $34^{*}$ ); it is seemingly complete, but overlain and obscured by an articulated sequence of dorsal vertebrae (Figure 4.28B). A fragment of right ischium articulates with the pubis, the rest of the right ischium is represented by loose fragments ( $22^{*}$ and $5^{*}$ ). A complete left pubis is preserved in two isolated blocks ( $3^{*}$ and $11^{*}$ ), however, one of these blocks is inverted so that the dorsal surface of the pubis is exposed in block three and the ventral surface of the pubis is exposed in block 11. It should be noted, therefore, that block 11 in Figure 4.25, has been inverted. When these pieces are reunited, a large circular pelvic fenestra, 8.7 cm long and 9 cm wide, is preserved between the pubis and the ischium (Figure 4.28B). The pubis is a broad plate of bone almost as wide as it is long ( 29.8 cm long and about 26 cm wide). The overall shape of the anterior border of the pubis is shallowly convex, but there is a distinct concave notch on the antero-lateral margin. The lateral process of the left ischium is also preserved in articulation with the pubis $\left(11^{*}\right)$. The anterior processes of the pubes on the midline closely approach the anterior processes of the ischia on the midline, forming a pectoral bar between the pectoral fenestrae. There are some small planar fragments, most likely pertaining to the pelvic girdle, but they cannot be reconstructed. However, they must be pelvic elements because the pectoral girdle is complete. The ilia are not immediately apparent in NMING F10194, they are either not preserved, or they are completely obscured by matrix in one of the larger blocks.

### 4.8.4 Limbs

The forelimbs of NMING F10194 are represented by two complete humeri, preserved together in a block ( $37^{*}$ ). The proximal half of the right humerus is free of matrix ( $38^{*}$ ) and can be matched up with its counterpart along a sharp break. No epipodials, mesopodials, metapodials or phalanges of the forelimbs are preserved. The humerus has an almost straight preaxial border and strongly concave postaxial border, giving the humerus a considerable posterior flare (Figure 4.34A). The distal surface bears


Figure 4.34. Detail of the limbs of specimen NMING F10194, A. left humerus in dorsal view, B. right femur in dorsal view, with the complete tibia and partial fibula in rough articulation, also note the posterior dorsal vertebra exposed in articular view, C. distal portion of the left femur in ventral view, with part of the fibula in articulation (scale bars $=20 \mathrm{~cm}$ ).
two weakly separated facets, the larger for the radius and the smaller for ulna. There is a strong posterior flange located proximally on the shaft near to the head of the humerus and there is a sharp longitudinal ridge on the anterior (preaxial) margin of the humerus. Although the propodials of the hindlimbs are less complete than the forelimbs, they are represented by a larger number of bones. There are a number of isolated blocks containing hindlimbs; three blocks ( $4^{\star}, 8^{*}, 34^{*}$ ) comprise the right limb including a complete right femur, complete tibia and partial fibula (Figure 4.34B). Block four contains the flared distal extremity of the femur with the tibia and partial fibula is rough articulation. A break runs along the long axis of the femur between blocks $8^{*}$ and $34^{*}$. Another block ( $10^{*}$ ) contains the distal end of the left femur with a partial fibula (Figure 4.34C). Distally, the femur is flared preaxially and slightly more postaxial - the anterior border of the femur is therefore concave. The cross-section through the middle of shaft of the left femur is almost circular, it does not possess the sharp longitudinal ridge described above for the humerus. The distal surface for articulation with the tibia and fibula is gently concave. The complete right tibia is roughly rectangular, longer $(13 \mathrm{~cm})$ than it is wide ( 10.3 cm proximally). It is widest proximally, constricted in its middle to a minimum width of 7 cm (so that the preaxial and postaxial margins are concave), and expands distally to a width of 8.5 cm . The right fibula in articulation with the femur and tibia is about 11 cm long ( 2 cm shorter than the tibia). The preaxial border is concave so that there is a large interosseal space between the radius and ulna (Figure 4.34B), the distance between the posterior and anterior preaxial angles is 7.5 cm and the fibula expands postaxially: the fibula therefore appears to have been reniform, but the postaxial portion is broken off so this cannot be confirmed.

### 4.9 NMING F8749

Despite the apparent completeness of NMING F8749 (Figure 3.9), it is very poorly preserved and few details can be ascertained from the specimen as mounted, which is covered in layers of paint and suffering from pyrite decay. Therefore, after photographing and interpreting the mounted skull (Figure 4.35), the skull was removed in a number of segments from the plaster mount, revealing a number of anatomical features previously not visible in this specimen (Figure 4.36, 4.37) such as the palate, and details of the internal structure of the skull (Figure 4.38, 4.39).

### 4.9.1 Skull roof

Before being prepared, the premaxillary rostrum of NMING F8749 was reconstructed in plasticine including carved nostrils (the nostrils in this specimen [and in all


Figure 4.35. The skull of NMING F8749 in dorsal view, A. photograph, taken before the specimen was removed from the mount. Note the carved nostrils in the plasticine premaxillae, B. interpretation, horizontal lines ' $A$ '- 'F' indicate of the position of cross-sections visible after excavation of the skull, as figured in Figures 4.38A-C and 4.39A-D (scale bar = 20cm).
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Figure 4.36. Part of the skull of NMING F8749 in ventral (palatal) view showing the internal nares on the palate, A. photograph, B. interpretation (white indicates matrix, coarse dotted lines indicate uncertain sutures, fine dotted lines indicate ridges) (scale bar $=20 \mathrm{~cm}$ ).
plesiosaurs] are actually retracted close to the orbits)(Figure 4.35). Each premaxillamaxilla suture runs from the lateral constriction to the external naris and the premaxilla extends posteriorly between the external nares to half-way between the orbits. A sharp medial ridge formed by the premaxilla runs along the midline of the skull. The maxilla is a large element and contributes to the lateral margin of the external naris. A triangular process interpreted as part of the maxilla extends posteriorly between the premaxilla and prefrontal. Anterior to the left orbit, the maxilla has a distinct excavation or channel trending in the direction of the external naris. No such feature is present on the right maxilla and the lack of predation marks on the rest of the specimen precludes this interpretation. It is probable that this represents damage to the bone during diagenesis, indeed, cross-sections through the maxillae anterior to each orbit, show is a spongy maxilla cavity (Figure 4.38B,C). This represents an area of weakness in the maxilla disposed to crushing. Furthermore, there is other evidence of compaction in this skull: the premaxilla and frontals are depressed between the orbits.

The frontals appear to closely approach and maybe even contact on the midline, but the surface preservation is insufficient to determine this. A section through the frontals shows that they do contact on the midline (Figure 4.39A). A sharp lateral ridge is situated on the postero-medial portion of the postorbital bar between the orbit and the parietal. The parietal extends anteriorly between the orbits and the pineal foramen appears small on the surface but this region is covered in plaster and a cross-section through the pineal foramen shows that it is actually large ( 13.1 mm wide), almost as wide as the external nares (Figure 4.39B). Posteriorly the parietal is missing, and so are the dorsal-most elements of the basicranium, so that as preserved the dorsal surface of the basioccipital is exposed. The majority of the skull in dorsal view is reconstructed in plaster, or obscured by layers of plaster and/or paint. However, removal of the skull has allowed the description of some additional cranial and palatal elements. The jugal forms the postero-lateral corner of the orbit and is overlain by the 'footplate' of the postorbital.

### 4.9.2 Palate and dentition

Some parts of the palate of NMING F8749 are visible, but the surface of the bone is encrusted with concrete (Figure 4.36,4.37). A clear diastema can be seen at the lateral constriction: this is interpreted as the area of the premaxilla-maxilla suture, but no suture is visible on the palate in this region because of poor preservation. The first tooth after the diastema is small, and the succeeding tooth alveolus is the largest in the maxillary tooth row; all proceeding alveoli gradually decrease in size posterior to


Figure 4.37. The rear of the palate of NMING F8749 in ventral view, showing the posterior interpterygoid vacuities (scale bar $=5 \mathrm{~cm}$ ).
the large second maxillary tooth. Level with the lateral constriction between the premaxilla and maxilla, the vomer occupies the midline: the premaxilla-vomer sutures run parallel and extend posteriorly to the internal nares (Figure 4.36). The surface of the vomer is flat and smooth and it extends posteriorly between the internal nares. A transverse break runs through the middle of the internal nares; the anterior fragment and posterior fragment can be reconstructed to show that both internal nares are complete and form elongate ovals in shape. In cross-section the channel of the naris extends dorsally and trends slightly posteriorly towards the external nares (Figures 4.38B,C).

On the palatal surface, a longitudinal ridge flanks the lateral margin of each external naris and extends postero-laterally (parallel with the lateral margin of the skull (maxilla)). Lateral to this ridge there are three primary alveoli in a row, and running medially alongside this ridge is the maxilla-palatine suture. This ridge disappears 35 mm from the internal naris, but the suture continues to meet the anterior margin of the suborbital fenestra. The palatine contacts the posterior margin of the internal nares and contacts the posterior process of the vomer. The sutures between the vomer, pterygoids and palatine are not clear but the vomer appears to extend some centimetres posterior to the internal nares. There are nine tooth alveoli situated between the lateral constriction and the anterior margin of the suborbital fenestrae, but these are highly worn away. Much of the posterior part of the palate is crushed but the parts underlying the braincase are quite well preserved (Figure 4.39). The posterior interpterygoid vacuities are broad ovals inclined slightly oblique to the midline so that they converge slightly anteriorly. A rounded basal articulation protrudes into each vacuity from a position just dorsal to the antero-lateral margin. The cultriform process of the parasphenoid is wide and triangular and the parasphenoid extends posteriorly along the midline between the posterior interpterygoid vacuity. The ventral surface of the parasphenoid is flat anteriorly and slightly rounded (gently keeled) posteriorly. The relationships and identity of the bones in the area posteromedial to the vacuities is unclear on the palatal surface, with the exception of a midline suture between the medial processes of the pterygoids, no sutures are visible.

The pterygoids meet on the midline posterior to the posterior interpterygoid vacuities; their lateral and posterior margins are damaged. On the right side, the base of the ventrolateral flange of the quadrate-pterygoid process is preserved and as seen in cross-section, this area of the palatal surface is concave or 'dished' (Figure 4.39C). A transverse break through the basicranium occurs just anterior to the basioccipital process (basioccipital tuber), revealing some features of the

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A
Figure 4.38. Transverse sections through the skull of NMING F8749 (photographs on the left, interpretations on the right), A. transverse section through the premaxillary rostrum (section ' $A$ ' in Figure 4.35), B. transverse section anterior to internal nares (section 'B' in Figure 4.35), C. transverse section just anterior to the external nares (section ' C ' in Figure 4.35) (crosshatching represents plaster) (scale bar $=5 \mathrm{~cm}$ ).


A


Figure 4.39. Transverse sections through the skull of NMING F8749 (photographs on the left, interpretations on the right), A. transverse section between the orbits (section ' $D$ ' in Figure 4.35), B. transverse section through the pineal foramen (section ' $E$ ' in Figure 4.35), C. transverse section through basicranium (section 'F' in Figure 4.35), D. posterior view of the basicranium (scale bar $=5 \mathrm{~cm}$ ).
basicranium. The suture between the pterygoid and the basioccipital is visible on the right side of the break; this is slightly interdigitated and runs ventro-medially from the dorsal surface of the articulation to the ventral surface. The left side of this break is situated slightly posterior to the right side, showing a clear dorsally projecting flange on the pterygoid (Figure 4.39C): the surface of the area between the body of the basicranium and the pterygoid is therefore ' U '-shaped. On the dorsal surface of the basioccipital (representing the base of the braincase) there is a deep notch on the midline, visible in cross section (Figure 4.39C). The dorsal surface of the preserved basioccipital region represents the base of the foramen magnum and base of the braincase. The facets for the supraoccipitals are just visible; the minimum width between them is 8.8 mm (Figure 4.35) and they do not extend onto the occipital condyle. The dorsal surface of the skull in NMING F8749 is otherwise completely obscured by filler and paint. In posterior view, the occipital condyle is circular and the ventral margin is situated 10 mm above the level of the palate (Figure 4.39D).

### 4.9.3 Mandible

The mandibular symphysis and the posterior portion of the left mandible of NMING F8749 are quite well preserved (Figures 4.40). The symphysis is expanded - there is a lateral constriction between it and the main jaw ramus, corresponding with the lateral constriction in the cranium. The maximum width across the symphysis is about 12 cm and it is spatulate in outline (Figure 4.40A). There are six teeth in the expanded part of the mandibular symphysis and three and a half teeth adjacent to the visible midline symphysis. However, because the symphysis is preserved in horizontal cross-section, both its length and the actual number of teeth it contains must be estimated. As exposed in cross section, the symphysis is only 6.34 cm long, but its postero-dorsal gully is covered with matrix and so presumably it extended further posteriorly below this region.

The posterior portion of the left mandibular ramus was excavated from this specimen; as originally mounted, it was upside-down and so the lower surface is covered in black paint (Figure 4.35). The retroarticular process is complete (Figure 4.40 B ) and is 77 mm long and 50 mm wide (maximum width). The exact inclination of this fragment along its axis is uncertain, but the mandibular fossa was probably inclined medially as is the case in other complete pliosaur mandibles (e.g. Peloneustes, BMNH R8574 pers. obs.). This means that the flat dorsal surface of the retroarticular process in NMING F8749 would have been inclined about 30 degrees from the horizontal. The lateral margin of this process forms a sharp longitudinal ridge, whereas the medial margin is deep with a flat surface: a cross


Figure 4.40. Parts of the mandible of NMING F8749, A. dorsal view of a horizontal cross-section through the mandibular sympysis, B. dorsal view of the left articular region showing the complete retroarticular process with a strong medial boss (scale bars $=5 \mathrm{~cm}$ ).
section through the middle of the process is therefore triangular. A strongly developed boss is also present on the medial surface of the retroarticular process, about halfway along its length. The majority of the mandibular fossa is complete but the margins (the anterior and posterior transverse crests) are broken away, and the glenoid fossa is especially eroded on its medial surface. This 'kidney-shaped' fossa is 68 mm wide as preserved. Three centimetres anterior to the anterior transverse crest there is a cleft. Medial to this cleft is a flat (not deeply excavated) dorso-medial trough (Figure 4.40B). The area ventral to this flat area is broken off but appears to have formed a longitudinal medial crest. The ventral surface of the angular is smooth and convex.

### 4.10 Comparison of taxa

This section comprises a detailed comparison of all of the specimens described above, and all of the specimens outlined in Chapter 3. Photographs and interpretations of described specimens are presented above, detailed photographs and interpretations of undescribed specimens are presented in Figures 4.41-4.54. These figures thus serve to illustrate the following holotypes and specimens: Archaeonectrus (Figure 4.41); Macroplata (Figure 4.42); WARMS G10875 (Figure 4.43); Eurycleidus (Figure 4.44); Rhomaleosaurus megacephalus (Figures 4.45, 4.46, 4.47); LEICS G221.1851 (the neotype of Rhomaleosaurus megacephlaus) (Figure 4.48, 4.49); Rhomaleosaurus victor (Figure 4.50); and Rhomaleosaurus propinquus (Figures 4.51, 4.52, 4.53). Variation between these specimens has been quantified via morphometric analyses (see Chapter 5) and relevant analyses are referred to in this discussion. Figure 5.54 directly compares the coracoid, humerus and mandubular symphysis in six Hettangian specimens (i.e., Macroplata, Eurycleidus, R. megacephalus [holotype], LEICS 221.1851 [R. megacephalus neotype], NMING F10194 and WARMS G10875). In the following section, holotype specimens are referred to by name and all other specimens are referred to by numbers (in the case of Rhomaleosaurus megacephalus, the casts [TCD.47762a,b] are regarded as the holotype, and the neotype [LEICS G221.1851] is referred to by specimen number]. The abbreviation ' $R$ ' refers to Rhomaleosaurus.

### 4.10.1 Skull roof comparison

The premaxillary rostrum of $R$. cramptoni is shorter than in all other taxa examined in this thesis. R. zetlandicus, R. thorntoni and R. victor also have short and robust premaxillary rostra (length to width ratio $\sim 1.0$ ) and this contrasts sharply with the elongate rostrum in Macroplata (Figure 4.42), NMING F10194, BMNH 49202 (Figure


Figure 4.41. Specimen BMNH 38525, the skull of the holotype of Archaeonectrus rostratus, A. photograph, B. interpretation (dotted lines indicate uncertain sutures)(scale bar $=20 \mathrm{~cm}$ ).


Figure 4.42. BMNH R5488, the skull of the holotype of Macroplata tenuiceps, in dorsal view, A. photograph, B. interpretation (dotted lines indicate ridges, crosshatching represents reconstructed areas, stippling represents damaged areas) (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.43. The skull of WARMS G10875, in palatal view, A. photograph, B. interpretation (dotted lines indicate ridges) (scale bar $=30 \mathrm{~cm}$ ).


Figure 4.44. Parts of the holotype series of Eurycleidus arcuatus, A. photograph of BMNH R2030*, mandibular symphysis in ventral view, B. interpretation (dotted lines indicate ridges), C. the reconstructed girdles and limbs, in dorsal view (some have been inverted to ease interpretation) (scale bars $=10 \mathrm{~cm}$ ).


Figure 4.45. Specimen TCD.47762a, a cast of the skull of the destroyed holotype of Rhomaleosaurus megacephalus, in dorsal view, this piece represents a 3D removable segment of the entire specimen (see Figure 4.46), A. photograph, B. interpretation (scale bar $=30 \mathrm{~cm}$ ).


Figure 4.46. Specimen TCD.47762a, a cast of the skull of the destroyed holotype of Rhomaleosaurus megacephalus, in ventral (palatal) view.. A. photograph, B. interpretation (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.47. Specimen TCD.47762b, a cast of the right forelimb of the destroyed holotype of Rhomaleosaurus megacephalus, in ventral view, A. photograph, B. interpretation (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.48. The skull of LEICS G221.1851, the neotype of Rhomaleosaurus megacephalus, in dorsal view, A. photograph, B. interpretation (scale bar $=30 \mathrm{~cm}$ ).


Figure 4.49. The skull of LEICS G221.1851, the neotype of Rhomaleosaurus megacephalus, in ventral (palatal) view, A. photograph, B. interpretation (dotted lines indicate ridges) (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.50. The skull of SMNS 12478, the holotype of Rhomaleosaurus victor, in ventral (palatal) view, A. photograph, B. interpretation (dotted lines indicate ridges) (scale bar $=20 \mathrm{~cm}$ ).


Figure 4.51. The skull of WM 852.S, the holotype of Rhomaleosaurus propinquus, in dorsal view, A. photograph, B. interpretation (scale bar $=20 \mathrm{~cm})$.


B


Figure 4.52. WM 852.S, the holotype of Rhomaleosaurus propinquus, A. the cervical vertebrae, $B$. the left humerus (scale bars $=30 \mathrm{~cm}$ ).


Figure 4.53. The pectoral girdle of WM 852.S, the holotype of Rhomaleosaurus propinquus, in ventral view, A. photograph, B. interpretation, showing that many fragments are arranged artificially, fragments highlighted in white are certainly not in natural position and the bone in the position of the scapula is interpreted as an ilium (length of coracoid as preserved $=30 \mathrm{~cm}$ ).
3.14), and LEICS G221.1851 (Figure 4.48). The proportions of the skull of the holotype of $R$. megacephalus (Figures 4.45, 4.46) differ from all other Hettangian specimens in that they are similar to R. zetlandicus and R. thorntoni (Figure 5.5L). The rostrum morphology cannot be verified in $R$. propinquus (Figure 4.51), however, based on Watson (1910, Fig.1) this taxon appears to be unique with a particularly deep lateral notch and a triangular-shaped premaxillary rostrum. On the other hand, in Tate and Blake (1876, Plate II, fig. 1) this rostrum as reconstructed is foreshortened: it appears that the anterior border of the skull has been drawn truncated at the end of the maxilla.

A discrete character in R. cramptoni is the large dorso-median foramen with raised borders, situated on the dorsal midline of the skull between the external nares (Figure 4.1). This character is also shared with $R$. zetlandicus and $R$. propinquus. Taylor (1992 p.249) noted the presence of this feature in $R$. victor and a cleft was also figured for this taxon by Fraas (1910 Taf. X); however, this area is not well preserved in SMNS 12478 and cannot be confirmed. The dorso-median foramen is either not preserved in R. thorntoni (the specimen is broken just posterior to the external nares), or more likely, it is obscured due to the disruption of the bones. The same shift of bones was noted by Cruickshank (1996b) to explain the apparent absence of the right external narial opening in this specimen. Such a distinct dorsomedian foramen is not present in any other plesiosaur (see Chapter 5) and is certainly absent in Macroplata (Figure 4.42) and NMING F10194 (Figure 4.29). On the other hand, a narrow dorso-median foramen or 'cleft' is present in Archaeonectrus, but this is positioned on the rostrum (Figure 4.41) rather than between the external nares as in Rhomaleosaurus cramptoni, and does not have raised margins.

The premaxilla-maxilla sutures run parallel, anterior to the external nares in $R$. cramptoni (Figure 4.1) and all of the Toarcian specimens examined for this thesis. These sutures diverge anteriorly in NMING F10194 (Figure 4.29) and all Hettangian and Sinemurian specimens. The distinct lateral constriction between the premaxilla and maxilla is present in the majority of specimens but is almost absent in $R$. cramptoni and a ridge, present on each postorbital, is shared by nearly all of the taxa analysed here. On the dorsal surface of the skull between the orbits, the frontals are separated on the midline in $R$. cramptoni and in all Toarcian specimens due to the posterior processes of the premaxillae contacting an anterior extension of the parietal. The frontals in LEICS G221.1851, NMING F10194 and NMING F8749 contact on the midline; the parietal in these specimens does not extend as far anteriorly. Consequently, the relative position of the pineal foramen on the parietal
differs; it almost contacts the frontals in NMING F10194 and LEICS G221.1851 but it is positioned posterior relative to the frontal in R. cramptoni, R. propinquus and $R$. zetlandicus. Archaeonectrus is more similar to the Toarcian specimens in this regard - the parietal extends anteriorly to contact the premaxilla (Figure 4.41).
R. cramptoni and in R. thorntoni both share ornamentation of the jugal in the form of longitudinal ridges and they are pierced by numerous foramina in both. The external nares are situated in a channel in R. megacephalus (Figure 4.45), LEICS G221.1851 (Figure 4.48) and Macroplata (4.42), whereas no channel is obvious in the other specimens examined. The rounded lateral margin at the parietal-squamosal suture, as described in R. cramptoni (Section 4.2.1) is widespread amongst the specimens examined. It is present in all Toarcian taxa and NMING F10194, LEICS G221.1851 and BMNH 49202 (Figure 3.14). It is reconstructed in Macroplata (Figure 4.42). The quadrate foramen so clearly preserved in R. zetlandicus (see Taylor, 1994 Fig. 3) and present in $R$. cramptoni, is not present in any of the other observed taxa (although it is present in specimen OUM.J28585 [Cruickshank, 1994a], which is included in the cladistic analysis).

The excavation or depression in the maxilla, just anterior to the orbit, as described above for NMING F8749, is also present in R. megacephalus (in both maxillae) (Figure 4.45) and in Macroplata (in both maxillae) (Figure 4.42), in which it extends anteriorly from the orbit to the external nares. Both of these specimens have also suffered from compression, endorsing the interpretation of this feature as a taphonomic artifact. It is possible, however, that this widespread feature may actually represent a natural channel, perhaps related to salt-secreting glands. A slight excavation is present in this position on the right hand side of $R$. cramptoni.

### 4.10.2 Palate comparison

There are several discrete differences between the palatal surfaces of the skulls of the various taxa examined during this thesis. Raised (ventrally projecting) bumps situated where the vomers meet the palatines appear in R. cramptoni (Figure 4.1) and $R$. zetlandicus for example. The absence of an open anterior interpterygoid vacuity in $R$. cramptoni also contrasts with the narrow open anterior interpterygoid vacuities in R. megacephalus (Figure 4.46), LEICS G221.1851, WARMS 10875 (Figure 4.43) and NMING F10194, as well as the broad anterior interpterygoid vacuity in $R$. victor (Figure 4.50). In R. zetlandicus this region is also preserved and a small narrow anterior interpterygoid vacuity has been delineated by an earlier worker; however, the preservation of this specimen is poor and it is possible that the apparent vacuity is an artefact of unremoved matrix located between the pterygoids.

This feature was therefore included as missing data in the cladistic analysis for this taxon. Similarly, in R. thorntoni there is a notch on the midline that has been interpreted as the anterior margin of an interpterygoid vacuity (Cruickshank, 1996b), but this notch is also present in $R$. cramptoni, which does have an open anterior interpterygoid vacuity. All of the taxa examined in this study share the laterally facing surface of the palate, which is angled relative to the rest of the palate and incorporates the palatine and ectopterygoid; this is especially well developed in $R$. cramptoni.

There is no evidence for the exposure of the basioccipital on the posteriormost ventral surface of the palate between the pterygoids in R. cramptoni, as inferred for Rhomaleosaurus zetlandicus (Taylor, 1992a), and I could not confirm the presence of this character in R. zetlandicus. In R. cramptoni, R. zetlandicus, R. thorntoni and $R$. victor, the vomer meets the maxilla posterior to the internal naris, excluding the palatine from the internal narial margin. In contrast, these elements do not meet in LEICS G221.1851, NMING F10194, NMING F8749, or WARMS G10875; the palatines in these specimens do contact the internal naris. However, proportions of the suborbital fenestrae vary between species; they are wider in R. cramptoni and have broad, rounded anterior and posterior borders (Figure 4.5A), while they are narrow and elongate in LEICS G221.1851, NMING F10194 (Figure 4.30), and WARMS G10875 (Figure 4.43).

All of the taxa examined have lateral palatine vacuities (where preserved). The cultriform process is short in most taxa but it is completely absent in R. victor (Figure 4.50). This process is asymmetrical in LEICS G221.1851 and NMING F10194, while in Macroplata (pers obs.) and BMNH 49202 (Figure 3.14), the parasphenoid is very wide anteriorly, contrasting with all other taxa, where the width of the parasphenoid is roughly equal for its entire length. Consequently, the posterior interpteryoid vacuities in Macroplata differ from all of the other taxa examined in this thesis, in that they are more widely spaced anteriorly and converge posteriorly (the opposite is true in, for example, R. cramptoni, NMING F10194 and NMING F8749).

### 4.10.3 Mandible and dentition comparison

There are significant differences in the proportions of the mandibular symphyses (Figure $5.5 \mathrm{~B}, \mathrm{~J}, \mathrm{~L}, \mathrm{U}$ ) amongst the taxa examined. The shortest (relative to width of symphysis) is preserved in the Hettangian specimen BMNH 49202 (Figure 3.14), while the longest is present in WARMS G10875 (Figure 4.43). However, these specimens represent endpoints along a continuum of variation in symphysial proportions (Figure 5.2, 5.3): the symphysis is wider than it is long in all Toarcian
species and in BMNH 49202. A 'short' symphysis is present in Eurycleidus, R. megacephalus, NMING F8749 and LEICS G221.1851 (length-width ratio $=1.0-1.1$ ). The ratio in NMING F8749 is particularly short (Figure 4.40A), but this measurement is unreliable for this specimen (see Section 4.9.3). An elongate symphysis is present in Macroplata (Figure 4.54) and WARMS G10875 (Figure 4.43) but Archaeonectrus and Attenborosaurus possess the longest symphyses amongst the Hettangian/Sinemurian taxa relative to mandible length (Figure 5.5H). The symphyses in these taxa are laterally compressed, so their widths are unknown.

In Toarcian forms, the symphysis length may be short or very elongate, the very short symphysis is typical of Rhomaleosaurus cramptoni, and the other Toarcian taxa figured here, whereas a very long symphysis is present in the Toarcian forms 'p'. Iongirostris and Hauffiosaurus (White, 1940; O’Keefe, 2001a). In contrast, all of the Hettangian taxa examined here are intermediate between these Toarcian extremes. The significance of symphysis length in pliosaur taxonomy has been well demonstrated by Tarlo (1960) and Noè et al. (2004) for Middle Jurassic pliosaur faunas and it is also regarded as significant in this thesis (see Chapter 6).

The ventral ridge on the midline of the mandibilar symphysis is widespread amongst the specimens observed during this thesis, being present in R. cramptoni, R. thorntoni, R. zetlandicus, Eurycleidus, and R. megacephalus. This region is restored in plaster in Macroplata and is distorted in Attenborosaurus and Archaeonectrus. The strongly developed medial boss described on the retroarticular process of NMING F8749 (Figure 4.40), is present to a lesser degree in the Toarcian taxa R. cramptoni (Figure 4.1, 4.5B), R. zetlandicus (Figure 4.23) and R. propinquus (Figure 4.51), and was figured for ' $P$ '. Iongirostris by White (1940). This boss is not clearly present in any other Hettangian specimens and it is certainly absent in WARMS G101875 (Figure 4.43). The large foramina present on the lateral surface of the surangular of $R$. cramptoni are also present in R. zetlandicus (Taylor, 1992) and R. victor (pers. obs.). Finally, note that the mandible of NMING F10194 is unknown, and so despite its cranium being one of the best preserved of all the Hettangian specimens, the absence of this crucial character makes identifying it to species level problematic (see Chapter 6).

From what can be seen of the ornamentation of the teeth in $R$. cramptoni (Figure 4.4), the pattern of ridges is identical to those described for R. zetlandicus (Tayor, 1992) and R. thorntoni (Cruickshank, 1996). The ornamentation in all other taxa consists of more closely spaced ridges, and these are very closely spaced in Archaeonectrus (see Owen 1865, Tab IX) and Attenborosaurus (see Sollas, 1881) .

### 4.10.4 Axial skeleton comparison

The broad 'butterfly-shaped' zygapophyses described in the cervical vertebrae of $R$. thorntoni (Figure 4.14C), are also shared by most of the taxa examined for this thesis. The strongly convex distal ends of the transverse processes in R. thorntoni are shared with R. cramptoni, but contrast with the flat ends seen in NMING F10194 and LEICS G221.1851. All of the taxa examined here have double-headed ribs (but see Macroplata below) and two rib facets on the vertebral centrum, however, in $R$. thorntoni and R. zetlandicus, the lower facet is larger and the upper facet is smaller and triangular, whereas in LEICS G221.1851, the upper facet is the largest, and is round in outline. In Macroplata, the posterior cervical vertebrae are double-headed, but the anterior 24 are single headed (Swinton, 1930b).

The deeply excavated squared pits present on the ventral surface of the centrum in R. thorntoni and R. cramptoni are shared by the majority of taxa observed in this thesis, but the midline keel is, narrow, tall, and sharp in LEICS G221.1851 (Figure 3.22) and WARMS G10875 (Figure 3.23), compared with the rounded keel in R. cramptoni, R. thorntoni and R. zetlandicus. The nutritive foramina in these pits are very large in R. thorntoni (Figure 4.13), R. zetlandicus, whereas they are small in all of the Hettangian specimens examined in this thesis, and absent in some of the cervical vertebrae in Macroplata (pers. obs.). The position of the cervical vertebral neural spines is shifted backwards relative to the centrum in many specimens examined in this thesis, but not Macroplata. The very broad robust posterior neural spines in R. cramptoni and R. thorntoni, are not seen in any of the other taxa examined here, however, the distal tip of the laterally compressed neural spines in the posterior cervical vertebrae of Eurycleiuds arcuatus, are greatly expanded into a wide apex (see Owen, 1840, Plate 44). R. thorntoni and LEICS G221.1851 share the double pair of nutritive foramina in the dorsal vertebrae, one high on the lateral wall of the centrum and the other positioned lower.

The number of vertebrae in the specimens studied in this thesis can be summarised as follows, the number of presacrals are given because this figure ignores the transition between pectoral vertebrae, which can often be difficult to distinguish:

- R. cramptoni: 28 cervicals, 25 dorsals and pectorals ( 55 presacrals), 5 sacrals, 29-30 caudals (total 90).
- R. zetlandicus: 28 cervicals, 22 dorsals ( 52 presacrals), 6 sacrals, 29 caudals (total 87).
- R. thorntoni: 10 preserved cervicals, 6 pectorals, 25 dorsals, 15 preserved caudals.
- R. propinquus: 28 cervicals, 21 dorsals (49 presacrals), 5 sacrals, 30 caudals (total 84)
- R. megacephalus (as given by Stutchbury, 1846), 29 cervicals, 34 pectorals and dorsals ( 63 presacrals), 31 sacral and caudals (total 94 )
- NMING F8749: 21 visible cervicals (placed in plaster and probably many missing), about 14 dorsals, ( 35 preserved presacrals), 4 sacrals, about 24 caudals (total 63 preserved).
- NMING F10194, at least 16 dorsals.
- WARMS G10875: 24 cervicals (about four missing), 18 pectorals and dorsals (46 presacrals), 20 sacrals and caudals (total 66).
- LEICS G221.1851: 27 cervicals. 4 pectorals, 19 dorsals ( 50 presacrals), 4 sacrals, 34 caudals (total 88).
- 'P'.macrocephalus (Figures 3.10, 3.11): 29 cervical, 18 dorsal and pectoral (47 presacrals), 5 sacral, 18 caudal (total 70 ).
- Macroplata: 26 cervicals, 5 pectoral, 19 dorsals ( 50 presacrals), 4 sacrals, 24 preserved caudals (total 78).

Based on comparison with the other specimens listed here, Stutchbury (1846) appears to have overestimated the number of presacral vertebrae (63, compared with 46-45 in all other complete specimens). The total number of presacral vertebra ranges from 46 in WARMS G10875 (an small number may be missing) to 55 in $R$. cramptoni. Comparison of the total numbers of vertebrae (ranging between 70 in ' $P$ '. macrocephalus and 94 in $R$. megacephalus) is unreliable because it is not usually possible to know how many terminal caudal vertebrae are missing in these specimens.

There is also variation in the number of complete rows of gastralia, an entire set of gastralia is apparently preserved in the following taxa: Macroplata has seven, Thalassiodracon has eight, WARMS G10875 has nine, and R. victor has ten. The number is uncertain in $R$. thorntoni due to poor preservation; but based on the large distance reconstructed between the coracoid and pubis in Rhomaleosaurus, it is estimated that Rhomaleosaurus has about 11 or 12 rows of gastralia (Figure 4.26). Note that the number of gastralia also differ in other plesiosaurs; Andrews (1910) noted "eight or nine" in Cryptoclidus and Andrews (1913) reconstructed Peloneustes with just six rows of gastralia.

### 4.10.5 Girdles comparison

The pectoral girdle is currently unknown in $R$. cramptoni and is poorly preserved in $R$. zetlandicus and R. propinquus (Figure 4.53). However, the girdles of R. thorntoni are very well preserved (Figures 4.19, 4.20). They differ significantly from the girdles in Eurycleidus (Figure 4.44C), NMING F10194 (Figure 4.33), Macroplata (Figure 4.54) and WARMS 10875 (Figure 3.23, 4.54), which are all very similar to one another (see comparison in Figure 4.54). In overall proportions, the coracoids of $R$. thorntoni are much shorter and wider than all other specimens (Figures 5.4, 5.5R): the proportions of the posterior process are truncated in $R$. thorntoni, whereas they are elongate and narrow in all Hettangian species and $R$. victor (Figure 1.4). The posterior coracoid embayment is shorter and narrower in $R$. thorntoni than the deep ' $V$ '-shaped embayment seen in Eurycleidus, NMING F10194 and WARMS G10875, and there is no such embayment in R. victor and Macroplata. An unusual notch in the posterior margin of the coracoid, and an elongate foramen between the coracoids and clavicleinterclavicle complex in Macroplata, are absent in all other taxa examined in this thesis (Figure 4.54). A round accessory foramen in WARMS G10875, visible between the anterior process of the right coracoid and the posterior portion of the clavicle-interclavicle complex (Figure 3.23), is also not present in any other specimens observed during this thesis.

The midline symphysis of the coracoid is asymmetrical in dorsal view in $R$. thorntoni; this taxon has a rounded notch in its right coracoid and an accompanying embayment in the left (Figure 4.19), a feature not present in any other taxon, although this area is not visible in any other Toarcian taxa examined. In Eurycleidus, the posterior process of the coracoid narrows distally whereas in all other Hettangian taxa, the medial and lateral margins of the posterior process of the coracoid run parallel (Figure 4.54), while in $R$. thorntoni they expand distally (Figure 4.19). The dorsal process of the scapula in $R$. thorntoni is short and robust with a rounded transverse cross-section; in all other taxa this process is elongate and laterally compressed. The crenulated margins of the coracoid in the posterior coracoid vacuity described above for NMING F10194, are similar to the Cretaceous taxon Leptocleidus (pes. obs.). The facet for the interclavicle on the dorsal surface of the preglenoid process of the coracoid in NMING F10194 (Figure 4.33B) is not present in R. thorntoni (Figure 4.19) or Eurycleidus arcuatus (Figure 4.44C); this area is not exposed in any of the other specimens examined in this thesis. The scapula and coracoid meet medial to the pectoral fenestra in R. victor, but not in Macroplata, Eurycleidus or WARMS G10875, and this region is unclear in R. thorntoni. The dorsal
margin of the dorsal process of the scapula has a distinct angle in Eurycleidus: is expands distally. This contrasts with the smooth border to the scapula in R. thorntoni.

Like the coracoid, the ischium in $R$. thorntoni is short and its posterior process is truncated in comparison to the elongate processes in Eurycleidus (Figure 4.44C), Macroplata, LEICS G221.1851 and WARMS G10875 (Figure 3.23). The ischium of $R$. victor is intermediate between these forms (Figure 1.4) while there is a notch in the posterior process of the ischium in Macroplata, similar to the coracoid (pers. obs.). The ilia are particularly short and stout and identical in size and shape in $R$. thorntoni (Figure 4.20B) and R. cramptoni (Figure 4.8). This condition differs from the elongate ilia of Eurycleidus (Figure 4.44C), Macroplata, LEICS G221.1851 and WARMS G10875 (Figure 3.23). The pelvic fenestrae in the pelvic girdle are wider than they are long in Thalassiodracon, whereas they are circular in Eurycleidus and R. victor, and slightly longer than wide in R. thorntoni.

### 4.10.6 Limbs comparison

The humeri of $R$. cramptoni, R. thorntoni and R. propinquus all differ from one another: those of $R$. thorntoni are greatly flared distally (Figure 4.21), one reason for the erection of a new species by Andrews (1922b). In contrast, the humeri of $R$. propinquus are only gently flared distally (Figure 4.52B) and the condition in $R$. cramptoni is intermediate between these two ( $R$ thorntoni and $R$. propinquus) (Figure 5.5M). The humeri of Eurycleidus, R. megacephlaus, LEICS G221.1851, NMING F10194, and WARMS G10875 are compared in Figure 4.54; these elements are all very similar to one another in their proportions (Figure 5.5M). The longitudinal ridge on the anterior margin of the humerus is very clear in Eurycleidus and can be seen in NMING F10194 and NMING F8749.

The femur is longer than the humerus in Macroplata but the distal proportions are reconstructed in plaster in this specimen so this is unreliable, as are the general proportions of the humeri in this taxon (Figure 5.5M). The postaxial process on the shaft described in NMING F10194 is also particularly pronounced in LEICS G221.1851 and WARMS G10875, but is poorly developed in R. megacephalus, Eurycleidus and Macroplata (Figure 4.54). The equivalent structure in the femora are seen as roughened bumps in some specimens, there are two on the postaxial surface of the femur in R. thorntoni (Figure 4.22); similarly, there are three bumps in the same position in WARMS G10875 (Figure 3.23), but the postaxial border in this region in Eurycleidus arcuatus preserves only a single roughened surface ( 2 cm long, 14 cm from the head of the humerus), and it is smooth in R. cramptoni and Macroplata.
R. megacephalus
(Neotype)
(LEICT 221. 1851)


WARMS G10875


NMING F10194




$\sim$


Macroplata tenuiceps
(holotype)
(BMNH R.5488)


Coracoid


Humerus


Mandibular

A foramen, and notch in the postaxial margin of the fibula is seen in Eurycleidus (Figure 4.44C), but is absent in all other taxa examined in this thesis. Similarly, a notch and a short postaxial flange is present in the posterior margin of the ulna of WARMS G10875 (Figure 3.23). The ulna is longer than the fibula in Eurycleidus arcuatus, Lydekker (1889) considered this discrepancy to be diagnostic for this species. The ulna and fibula are equally sized in $R$. cramptoni, whereas the ulna is also larger than the fibula in WARMS G10875.

The organisation and shape of the meso- and metapodial rows of the forelimb are very similar in R. zetlandicus (Figure 4.25), R. megacephalus (Figure 4.47) and $R$. victor (Figure 1.4), although there are some differences. The intermedium is relatively larger in $R$. megacephalus, and the elements in this specimen are also more closely spaced (contact each other) compared with R. zetlandicus. In R. zetlandicus the distal margin of distal mesocarpal 4 is situated level with the postaxial border of distal mesocarpal 1, whereas in $R$. victor these bones are level, and in $R$. megacephalus the distal mesocarpal 4 is positioned further distally. Metapodials i-iv form a straight row in R. zetlandicus (Figure 4.25) and R. victor, whereas they are staggered in R. megacephalus (Figure 4.47) and WARMS G10875 (Figure 3.23). R. victor differs from these taxa in the possession of three additional postaxial bones in the forelimb: a large pisiform articulates closely with the postaxial margin of the ulnare and the ulna, and an equally sized supernumeracy articulates with the pisiform and the postaxial margin of the ulna (the supernumeracy and pisiform have fused in the right limb, and Frass [1910] regarded both elememts as pisiforms). A further postaxial element is located postaxial to the ulnare (Figure 1.4). None of these additional postaxial bones were observed in any of the specimens investigated for this thesis. As described above, the organisation of mesopodials in R. cramptoni differ from all other specimens, but this is not regarded as a natural feature. The organisation of these bones in LEICS G221.1851 is also artificial. Based on figures in Owen (1865) and Novizhilov (1964) (Figure 3.15), the limbs of Archaeonectrus are most similar to $R$. megacephalus in all respects.

### 4.10.7 General proportions comparison

The relative lengths of the propodials and the skull are similar in all Hettangian specimens (around 0.8), similar in $R$. cramptoni and R. zetlandicus (around 1.0) and extreme in $R$. victor (1.8). This latter taxon combines a relatively longer humerus with a relatively smaller skull (Figure 4.5W), and a smaller skull relative to the size of the body (Figure 5.5 Y ). The relative size of the skull to the length of the skeleton is similar in all of the specimens measured in this analysis, with the exception of $R$.
victor and Thalassiodracon (which has the smallest skull) (Figure 5.5Y). The skull is largest relative to the size of the body in Archaeonectrus (Figure 5.5Z) (the data point for NMING F8749 in this graph is related to the artificial preservation of the specimen, see Chapter 7).

Taken in sum, the numerous discrete and proportional differences between the skulls and the postcrania of the Hettangian specimens and the Toarcian holotype of Rhomaleosaurus, strongly suggest that the Hettangian specimens are not congeneric with Rhomaleosaurus. There is also generic variation within the Toarcian fauna, separating $R$. victor from Rhomaleosaurus. These interpretations will be further tested in the next chapter (Chapter 5) via a cladistic analysis, and the morphometric analysis incorporated into these comparisons will also be explained.

## 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 15 cm were made with callipers and these are accurate to the nearest 0.1 mm ; larger measurements were made with a tape measure and are accurate to the nearest 0.5 cm . 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 specimenbased 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 " $\mathrm{n} / \mathrm{a}$ ", 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 $5.5 \mathrm{M}-\mathrm{S}$ ), 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





Figures 5.5A-G. Morphometrics of cranial proportions.


Figures 5.5 H -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.
sauropterygians included in this analysis (Rieppel, 2000). All other basal ('nonplesiosaur') sauropterygians coded for this analysis (Augustasaurus, Pistosaurus and Yunguisaurus) were included within the ingroup to minimise assumptions of relationships between basal and derived sauropterygians. 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 pliosauroids 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 characterevolution, 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 '.

A


B


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 posteromedially 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.

See O'Keefe (2001a, character 9, p.35); Druckenmiller, (2006a, character 10, p.255).

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.

See O’Keefe (2001a, character 99, p.48); Druckenmiller, (2006a, character 11, p.256).

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).

See O'Keefe (2001a, character 41, p.40); Druckenmiller, (2006a, character 17, p.259).

+ 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 plesiosaur 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

## A



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).

See O’Keefe (2001a, characters 35, 36 and 38, p.39); Druckenmiller (2006a, character 28, p.265).

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.

See O'Keefe (2001a, character 19, p.37).

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).

See O’Keefe (2001a, character 39, p.40); Druckenmiller, (2006a, character 27, p.264).
*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], Pliosaurus Taylor and Cruickshank, 1993), the frontal is clearly excluded from the orbital margin.

See O'Keefe (2001a, character 40, p.40); Druckenmiller (2006a, character 26, p.264).
*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.

See O'Keefe (2001a, character 24, p.24).

Character 20. Frontal foramina. Absent $=0$. present $=1$.
Frontal foraminaa, '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.

See O'Keefe (2001a, character 23, p.37).
*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 nothosauroids 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 postemporal 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,

See O'Keefe (2001a, character 28, p. 38; 2004b), character 168, p.982); Druckenmiller (2006a, characters 21 and 22, p.261-262).

Character 22. Jugal exposed on palate surface. $A b s e n t=0$, 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), Rhomaeleosaurus 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 postemporal 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.
See Druckenmiller (2006a, character 35, p.269).
+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 sauropterygians where the squamosals merge gradually into the parietals (pers. obs.). This character is shared by Archaeonectrus (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 (YORYM 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 cramptoni (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 postemporal 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).

See O’Keefe (2001a, character 10, p.36); Smith, (2003, character 11) Druckenmiller (2006a, character 23, p.262).

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 nothosauroids, 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 postemporal 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 naris (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 naris 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
3.2 B], Plesiosaurus [Storrs, 1997, Fig. 7B]). 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 (Noè, 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 (Noè, 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 naris.

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 (Noè, 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 posteromedial 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 Cruichkshank, 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-pterygoid 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 vacuity (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).

See O'Keefe (2001a, character 46, p.40); Druckenmiller (2006a, character 61, p.284).
+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 Brachauchenius (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]).

See O'Keefe (2001a, character 89 p.47); Druckenmiller (2006a, character 79, p.295).
+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 cramptoni (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). Druckenmiller
(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 mandubilar 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. Porportions 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 shortnecked 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.S) (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 shortnecked 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 Brachauchenius (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 (BRSMG 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 doubleheaded 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).

See Druckenmiller (2006a, character 116, p.322).

+ 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 sauropterygians usually become progressively narrower posteriorly (state ' 0 ') (Reippel, 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), Brachauchenius (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.
A
B


Figure 5.6F. Illustration of character $81, A=$ state ' 1 ', $B$ =state ' 0 '.
A

B


Figure 5.6G. Illustration of character $89, A=$ state ' 0 ', $B$ =state ' 1 '.


B


Figure 5.6 H . Illustration of character $90, \mathrm{~A}=$ 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 Brachauchenius (Albright et al. 2007, Kronosaurus (Romer and Lewis, 1959), Liopleurodon (Andrews, 1913), Peloneustes, (Seeley, 1910), and Simolestes (Andews, 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), Simoletes (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 analyisis (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 Pliosauroidea, but the humerus is very slightly longer than the femur (ratio between 1 and 1.1, see Figures $5.5 \mathrm{M}, \mathrm{V}$ ) 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 cramptoni [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.

See Druckenmiller (2006a, character 134, p.333).
+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).

See O’Keefe (2001a, character 161, p.55); Druckenmiller (2006a, character 138, p.337).

### 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 Cl 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 5.7 B ). 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 jacknife values, and figures to the bottom right of the nodes, in bold, represent decay indices. Nodes lacking values were poorly supported, with bootstrap and jacknife values below 50 and decay indices 1 or less.


## Chapter 6 - Systematic palaeontology

> "Sea-saurians have had a sorry experience in the treatment they have received from nomenclators"

> Samuel Wendell Williston, 1914

### 6.1 Rhomaleosauridae - generic and species-level systematics

As defined in this thesis, and confirmed by cladistic analysis (see Chapter 5), the Rhomaleosauridae is a valid monophyletic clade and comprises the following generic-level taxa: Archaeonectrus; Macroplata; Euryclidus; Maresaurus; Sthenarosaurus, Rhomaleosaurus; and a new, and as yet unnamed genus ( $R$. victor); see section 6.2 for characters that support this clade. The following section represents a revised taxonomy for all those specimens included in the Rhomaleosauridae. Sthenarosaurus and Maresaurus were not examined first hand in this Thesis and so although they were included in the cladistic analysis, systematic revisions of these taxa are not provided.

### 6.1.1 Genus Rhomaleosaurus Seeley, 1874

Three Toarcian species are very closely related to R. cramptoni: Rhomaleosaurus zetlandicus was described by Taylor (1992ab); Rhomaleosaurus thorntoni was described by Andrews (1922b) and re-worked by Cruickshank (1996b); and Rhomaleosaurus propinquus was briefly described by Watson (1910).
R. zetlandicus and R. thorntoni have been suggested to be synonymous with R. cramptoni by Cruickshank (1996b). In such a case, the species R. zetlandicus takes priority, and so $R$. cramptoni and $R$. thorntoni were included under the synonym list for Rhomaleosaurus zetlandicus by Cruickshank (1996b), and minor variation was interpreted as representing size variants within the same species. Now that the skull of NMING F8785, the holotype of Rhomaleosaurus cramptoni, has been prepared and described (Chapter 4), it is possible to assess these inferences.
R. cramptoni, R. zetlandicus (YORYM G503), R. thorntoni (BMNH R4953), and R. propinquus (WM 851.S) form a monophyletic group in the cladistic analysis (Figures 5.7, 5.8) because they share a number of unique derived characters, not present in any other plesiosaurs (see below). This group is thus regarded as Rhomaleosaurus sensu stricto and so from this point on in this thesis, all species of Rhomaleosaurus outside of this clade (Rhomaleosaurus megacephalus, Rhomaleosaurus victor) are placed in inverted commas.

Monophyly of the genus Rhomaleosaurus is supported by the following unambiguous synapomorphies (i.e., $\mathrm{Cl}=1$ ) in the cladistic analysis:

1. A large dorso-median foramen situated between the external nares (character 7);
2. Ilium robust (Character 85) (not present in WM 852.S, but see below);

The following additional characters $(\mathrm{Cl}<1)$ also optimise as synapomorphies for this genus as a result of the cladistic analysis (Chapter 5) and represent a unique combination in this genus:

1. Foraminae present in the frontals (character 20, shared with Dolichorhynchops) ( $\mathrm{Cl}=0.5$ );
2. The premaxilla-maxilla sutures run parallel to each other anterior to the external nares (Character 9, shared with Maresaurus) $(\mathrm{CI}=0.5)$;
3. Palatine excluded from internal naris (character 36 , shared with R. victor, Maresaurus, and Simolestes) $(\mathrm{Cl}=0.25)$;
4. Length and width of premaxillary rostrum sub-equal (Character 54, shared with BMNH 49202, OUM J28585, and Maresaurus) (CI = 0.286);
5. Short mandibular symphysis (length/width $=0.6-0.89$ ) (character 54 , shared with Simolestes) ( $\mathrm{Cl}=0.286$ );
6. Bulb/bump on the medial margin of the retroarticular process (Character 55, shared with NMING F9749 and P. longirostris) ( $\mathrm{Cl}=0.333$ );
7. Smooth bands on the lateral margins of the cervical centra (character 66, shared with Hauffiosaurus and Dolichorhynchops) ( $\mathrm{CI}=0.333$ );
8. Length and distal width of radius equal (Character 93 , shared with ' $R$ '. victor and $L$. capensis) ( $\mathrm{CI}=0.667$ ).

As a result of the analysis presented in Chapter 5, and additional anatomical observations, the division of species within this genus is as follows:

Rhomaleosaurus cramptoni (Carte and Bailey, 1863a) Seeley, 1874

Holotype: NMING F8785

## Synonyms:

Rhomaleosaurus propinquus (Tate and Blake, 1876) Lydekker, 1889

## Diagnosis:

This taxon differs from all other species of Rhomaleosaurus in possessing the following unique suite of characters: preorbital region about $42 \%$ of skull ( $47 \%$ in $R$. zetlandicus); premaxillary rostrum length much shorter than width (length/width = 0.76 ) (Figure 5.5 L ); lateral notch between premaxilla and maxilla poorly developed (Figure 4.1); posterior interpterygoid vacuities positioned relatively anteriorly (anterior border situated around $65 \%$ of skull length, compared with $73 \%$ in $R$. zetlandicus) (Figure 5.5 K ); humerus proportions moderately flared (Figure 5.5 M ); humerus and femur equal in length (Figure 5.5M). If included in the cladistic analysis, and as listed throughout this section, these characters would optimise as autapomorphies for Rhomaleosaurus cramptoni. WM 852.S (the holotype of Rhomaleosaurus propinquus) does not possess the robust ilium typical of Rhomaleosaurus, however, this specimen is in part a composite (Taylor, 1992b) so it is probable that the ilia mounted in this skeleton are not part of the specimen and that robust ilia are actually autapomorphic for Rhomaleosaurus. WM 852.5 also possesses an additional autapomorphic character - as originally noted by Taylor (1992b p. 52): "the articular bears a strong anteriorly pointing boss along the dorsomesial side of the rear mandibular ramus, where R. zetlandicus [and R. thorntoni, pers. obs.] has a concave trough". This feature was confirmed by Cruickshank (1994b p. 257) and described as a "prominent knob in the same position as the dorso-median trough". This region is not visible in NMNG F8785, but this character is considered an autapomorphy of $R$. cramptoni based on the referred specimen WM 852.S (Figure 4.51).

## Rhomaleosaurus thorntoni Andrews, 1922b

## Holotype: BMNH R4853

## Diagnosis:

This taxon is retained because it differs from all other species of Rhomaleosaurus in possessing the following combination of characters: premaxillary rostrum length equal to width (length/width $=0.98$, compared with 0.76 in $R$. cramptoni) (Figure 5.5 L ); lateral notch between premaxilla and maxilla strongly developed; humerus greatly flared distally, greater in length relative to the skull, and longer than the femur (Figure 5.5M). Other possible autapomophies include an asymmetrical midline notch
between the coracoids (but this area is unknown in all other specimens of Rhomaleosaurus) and the possible lack of a dorso-median foramen (Figure 4.9); however, this region has suffered from taphonomic effects (see Chapter 4). Indeed, the differences in skull proportions may be due to crushing; still, the differences between the limbs are natural.

Rhomaleosaurus zetlandicus (Phillips, in Anon., 1854) Lydekker, 1889

Holotype: YORYM G503

## Diagnosis:

This taxon differs from all other species of Rhomaleosaurus in possessing the following unique combination of characters: premaxillary rostrum length equal to width (length/width $=0.96$ ) (Figure 5.5 L ); lateral notch between premaxilla and maxilla well developed; preorbital region about $47 \%$ of skull length ( $42 \%$ in $R$. cramptoni) (Figure 5.5 H ); posterior interpterygoid vacuities positioned relatively anteriorly (anterior border situated around $73 \%$ of skull length); angle at parietalsquamosal suture very strongly developed (Figure 4.23).
6.1.2 Gen. nov. (for 'Rhomaleosaurus' victor) (Fraas, 1910) Tarlo, 1960

Results of the cladistic analysis presented in Chapter 5, in combination with anatomical observations and morphometric results, suggest generic-level differentiation for specimen number SMNS 12478 (Figures 1.4, 4.50, 5.8). A new taxonomic name for this specimen will be erected in a subsequent publication (Smith, in preparation).

Holotype: SMNS 12478

## Diagnosis:

This new genus shows considerable proportional differences from Rhomaleosaurus sensu stricto; in relative terms, its skull is much smaller and its humeri are much larger (Figures $5.5 \mathrm{~W}, \mathrm{Z}$ ) while the rostrum is shorter and wider (Figure $5.5 \mathrm{H}, \mathrm{I}$ ). A number of autapomorphic characters also differentiate ' $R$ '. victor from Rhomaleosaurus sensu stricto and all the other taxa in the cladistic analysis: absence of a cultriform process; large broad anterior interpterygoid vacuity; basioccipital tubers visible and projecting beyond the posterior margin of the
pterygoid plates; and ten rows of gastralia (Figure 4.50). This genus is currently monospecific (containing just the species victor).

### 6.1.3 Genus Eurycleidus Andrews, 1922a

In the cladistic analysis, Eurycleidus forms an unresolved polytomy with ' $R$ '. megacephlaus, LEICS G221.1851, NMING F10194 and NMING F8749. WARMS G10875 forms a sister relationship with this clade (Figure 5.7, 5.8). The only part of the skull preserved in the holotype of Eurycleidus (E. arcuatus, BMNH R.2028*) is the mandibular symphysis and its length and width are equal (Figure 5.5 U ). This is almost identical to the ratio in the holotype of ' $R$ ' megacephalus (BRSMG Cb 2335), and as discussed in Chapter 4, there are only subtle differences between the postcrania of the holotypes of Eurycleidus and 'R' megacephalus. The holotype of 'Rhomaleosaurus' megacephalus together with LEICS G221.1851, NMING F10194 and NMING F8749, are therefore referred to the genus Eurycleidus (as hypothesised by the cladistic analysis). Because the postcranium and palate of WARMS G10875 are almost indistinguishable from these specimens it is also placed into the genus Eurycleidus. Note that the taxon Eurycleidus as currently understood is very plesiomorphic: it is not very derived and shares many characters with other genera of equally basal plesiosaurs. Given that the specimens listed above are hypothesised to form a monophyletic clade (Chapter 5), the genus is supported by the following synapomorphies $(\mathrm{Cl}=1.0)$, inferred to be present in all representatives (although additional fossil material will be required to test this):

1. Strongly developed triangular process of the maxilla (character 13);
2. Sharp longitudinal keel on the anterior margin of the humerus (character 90 ).

Further characters supporting the monophyly of Eurycleidus, (Shared with Dolichorhynchops and Leptocleidus) include character 81, the dorsal margin of the dorsal process of the scapula produces an angle and the entire process expands distally ( $\mathrm{Cl}=0.333$, and the ulna is larger than the fibula. In addition, and in support of this hypothesis, specimens referred here to Eurycleidus also tend to cluster in the morphometric analyses (Figures 5.5A,M,O,W,V,W.). Proportional synapomorphies include: distal flare of the humerus relative to humerus length is about 0.52 (between 0.515 in BMNH R2028*, to 0.530 LEICS G221.1851). As a result of the analysis presented in Chapter 5, and additional anatomical observations, the division of species within this genus is as follows:


Figure 6.1. Reconstruction of the skull of Eurycleidus (sp.) in A, ventral and B, dorsal view; dotted grey lines represent ridges and dotted black lines represent uncertain sutures. $A$ is based on a specimens NMING F10194 (Eurycleidus sp.), LEICS G221.1851 (Eurycleidus sp.), TCD.47762a (E. megacephalus), and NMING F8749 (Eurycleidus sp.). B is based on NMING F10194 (Eurycleidus sp.) and LEICS G221.1851 (Eurycleidus sp.).

## Eurycleidus arcuatus (Owen 1840) Andrews, 1922a

Holotype: (Type series) BMNH R2028*, BMNH R2029*, BMNH R1317, BMNH R2061*, BMNH R2047*, BMNH R2027*, BMNH R1318, BMNH R1319 and BMNH R2030*.

## Diagnosis:

This taxon differs from all other species of Eurycleidus in the possession of a narrowing posterior process of the coracoid (Figure 4.44C), and in the pronounced preaxial distal flare to its humerus (Figure 4.44C). In addition, the symphysial proportions (1.0) of this species are similar to E. megacephalus (1.0=1.1), but differ from Eurycleidus sp. nov (see below) (=1.5) (Figures 5.2, 5.3, 5.5U). The postaxial margin of the lunate fibula is unique in possessing a notch and the postaxial portion is pierced by a small foramen (Figure 4.44C); although this may have phylogenetic significance, it may also be an ontogenetic feature. This species is represented by the single holotype specimen, albeit each block bears a different number (see Chapter 3).

Eurycleidus megacephalus (Stutchbury, 1846) Andrews, 1922a

Holotype casts: BMNH R1310, TCD.47762a and TCD.47762b (all casts of destroyed specimen BRSMG Cb 2335).

## Notes:

The systematics of this taxon are complicated. Although Cruickshank (1994b) introduced a neotype specimen for this taxon (LEIC G221.1851), the available plaster casts of the original holotype are satisfactory and must remain valid. A neotype should only have been erected in the absence of the holotype, clearly not the case because of the existence of casts; the neotype status of LEIC G221.1851 is therefore unwarranted. Note also that the accepted holotype for the plesiosaur Attenborosaurus is a plaster cast (see Chapter 3 and Bakker, 1993).

## Diagnosis:

This taxon differs from all other species of Eurycleidus in the proportions of its rostrum -- this is short and robust and groups with Rhomaleosaurus sensu stricto in the morphometric analyses (Figure 5.5A,E,G). The proportions of the mandibular
symphysis are also different from Eurycleidus sp. nov (Figures 5.2, 5.3, 5.5U). The actual proportions of the symphysis and the humerus in E. megacephalus are almost identical to $E$. arcuatus, however, their absolute sizes differ considerably: the bones in the forelimbs (both radius and humerus) are much shorter in comparison to the mandibular symphysis length in $E$. megacephalus, indicating that the limbs of $E$. megacephalus are shorter relative to the skull (Figure 5.5AA). E. megacephalus also differs from $E$. arcuatus in the relative lengths of its humerus and radius, the radius is relatively shorter in E. megacephalus (Figure 5.5P).

## Eurycleidus sp. nov.

Holotype: WARMS G10194.

## Diagnosis:

This species - to be named in a later paper - differs from all other species of Eurycleidus in the relatively more elongate proportions of its mandibular symphysis (length-width ratio $=1.5$ ) (Figures 5.2,5.3). This distinction in the mandible also holds true for the length of the symphysis relative to the length of the mandible ( 0.199 , compared with 0.161 in $R$. mecacephalus 0.142 in LEIC G221.1851) (Figure 5.5B). This new species also differs from all other species of Eurycleidus in its possession of a postaxial flange on the lunate ulna, and three rounded bumps on the postaxial surface of the femur shaft (Figure 3.23). A distinct circular foramen between the coracoid and the clavicle-interclavicle complex (medial to the pectoral fenestra and lateral to the midline) may be an additional autapomorphy of this taxon (Figure 3.23), but this region is not well preserved in the other specimens of Eurycleidus.

## Eurycleidus sp.

## Referred specimens:

Three specimens are here referred to Eurycleidus sp.: LEICS G221.1851, NMING F10194, and NMING F8749. The reason for this is a combination of the incompleteness of the holotypes (as selected by earlier workers), and of the absence of key areas in the referred specimens. None of the diagnostic characters listed for the other species of Eurycleidus above are preserved on these specimens.

The specific placement of NMING F10194 is problematic because, although the specimen is very complete (Figure 3.8), it lacks a key area for systematic placement: the mandibular symphysis (Figures 5.2, 5.3). Based on the elongate
proportions of its rostrum, NMING F10194 does not belong to E. megacephalus and it clusters instead with LEICS G221.1851 and Macroplata instead (Figure 5.5A). These proportions are unknown in Eurycleidus arcuatus and Eurycleidus sp. nov. In the proportions of its humerus and coracoid, and in the relative proportions of the skull to the humerus, NMING F10194 is equally close to both Eurycleidus sp. nov. and to $E$. arcuatus (Figure $5.5 \mathrm{O}, \mathrm{M}, \mathrm{V}$ ). Therefore, without the mandibular symphysis in this specimen, and without knowledge of the cranium in E. arcuatus, or the dorsal surface of the cranium in E. sp. nov, NMING F10194 cannot be ascribed to either species and must be regarded as Eurycleidus sp..

LEICS G221.1851 is also problematic, because it lacks the coracoid and it presents a combination of characters; for example, the proportions of the mandibular symphysis in this specimen (this measurement includes a broken portion from the anterior tip) are intermediate between E. arcuatus/E. megacephalus, and Eurycleidus sp.nov. The posterior process of the humerus is also strongly developed, unlike $E$. arcuatus/E. megacephalus (Figure 4.54). LEICS G221.1851 and NMING F10194 cluster very closely in terms of skull proportions (Figure 5. A,G) although the orbits, as preserved, are larger in NMING F10194 (Figure 5.D). Note that it is possible that LEICS G221.1851 and NMING F10194 may both belong to Eurycleidus sp.nov. or to a new unnamed species; however, without any key apomorphies the most conservative course of action is to regard these specimens as Eurycleidus sp.. The same applies for NMING F8749: the skull proportions of NMING F8749 are intermediate between LEICS G221.1851 and NMING F10194; it is also missing a large proportion of the skeleton, and those parts that are present are very poorly preserved (Figure 3.9). Future discoveries may elucidate the specific identity of these specimens, and the diversity within Eurycleidus.

### 6.1.4 Genus Macroplata Swinton, 1930a

The genus Macroplata forms a sister relationship with Eurycleidus based on the cladistic analysis (Chapter 4) (Figure 5.8); in addition, the proportions of the skull of this taxon are very similar to Eurycleidus (Figure 5.5A, E), and the proportions of its symphysis are similar to Eurycleidus sp. nov. (Figure 5.2, 5.3, 5.5B).

Nevertheless, the validity of the genus Macroplata is secured by a number of unique apomorphies as given by Swinton (1930ab) and confirmed here: a distinct notch in the posterior border of the coracoid (Figure 4.54); an elongate midline foramen between the coracoids and the interclavicle; and single rib facets on the anterior cervical vertebrae. In addition, this taxon shares a broad preglenoidal extension of the coracoid with Eurycleidus (Figure 4.54) (this was listed as a
diagnostic character of Macroplata by Swinton 1930ab). A combination of further distinguishing characters diagnose this taxon, and are reported here for the first time: an elongate mandibular symphysis; a parasphenoid that widens anteriorly; a notch in the posterior border of the ischia; pubes slightly wider than they are long (the opposite is true in Eurycleidus) (Figure 5.5Q); diminutive nutritive foraminae in the cervical vertebrae; and the position of the cervical neural arches positioned directly over the centrum (rather than displaced posteriorly as in Rhomaleosaurus and Eurycleidus). The femur is significantly longer than the humerus (Figure 5.5M) but the distal portion of the humeri are partially reconstructed so the validity of this character is dubious. This genus is currently monospecific (containing just the species Macroplata tenuiceps). The holotype of the genus is BMNH R5488 (Figures $4.42,4.54$ ) and a full description of this specimen will be presented in a later paper (Smith and Ketchum in prep.)

### 6.1.5 Genus Archaeonectrus Novozhilov, 1964

Based on the results of the cladistic analysis, Archaeonectrus is the most basal (earliest diverging) member of the rhomaleosaurid clade and as such it differs from the closely related Rhomaleosaurus, Eurycleidus and Macroplata in many respects. The proportions of the rostrum are the most elongate of all the taxa measured in this thesis (Figure $5.5 \mathrm{H}, \mathrm{A}$ ). Discrete autapomorphies in the skull of Archaeonectrus include: an elongate cleft-like dorso-median foramen located between the premaxillae, halfway along the rostrum; a blunt anterior margin to the premaxillary rostrum; a sharp midline ridge extending between orbits and between the postorbital bars. This taxon also shares a unique combination of characters in the skull (Figure 4.41): circular orbits; the premaxillae contact the parietals, separating the frontals on the midline; a tiny pineal foramen and very small external nares; 8 teeth located in an elongate mandibular symphysis ( $26.6 \%$ of the length of the mandibular ramus) (Figure 5.3). It was not possible to investigate the postcranium of the holotype specimen (BMNH 38525) first hand (see Chapter 3), so it is not possible to confirm or quantify the observations made on the postcranium of this taxon by Owen (1865) and Novozhilov (1964). This genus is currently monospecific (containing just the species Archaeonectrus rostratus).

### 6.2 Revised supra-generic systematics

The following clades are supported by one or more synapomorphies as optimised by the cladistic analysis presented in Chapter 5. Character numbers (see Chapter 5) and Cl values for each character are also given for each character.

## Unnamed clade including Augustasaurus and Plesiosauria:

This clade is supported by the following synapomorphy: character 73, rounded distal facets on the transverse processes of the dorsal vertebrae ( $\mathrm{Cl}=1.0$ ).

## Plesiosauria (Attenborosaurus, Yunguisaurus, Pliosauroidea, Plesiosauroidea):

This clade is supported by the following synapomorphy: character 89, the anterior margin of the humerus is straight or concave (states 1 and 2, except Yunguisaurus, and Plesiosaurus) $(\mathrm{CI}=0.4)$.

## Plesiosauroidea/Plesiosauridae (Plesiosaurus, Seeleysaurus, Hydrorion):

This clade is supported by the following synapomorphies: character 3, postorbital region of skull greater that preorbital region ( $\mathrm{Cl}=0.286$ ); character 54 (state 3), very short mandibular symphysis (length to width ration less that 0.6$)(\mathrm{CI}=0.286)$, character 59 (state 0 ), splenial does not participate in the mandibular symphysis (shared with Augustasaurus) $(\mathrm{Cl}=0.5)$.

## Unnamed clade including Yunguisaurus, Thalassiodracon and Plesiosauroidea:

This clade is supported by the following synapomorphies: character 50 (state 0), occipital condyle visible in dorsal view ( $\mathrm{Cl}=1.0$ ); character 52, teeth delicate and needle-like (shared with Dolychorhynchops) ( $\mathrm{Cl}=0.5$ ).

## Unnamed clade including Hydrorion and Seeleysaurus:

This clade is supported by the following synapomorphy: character 24 (state 2), ‘ledge’ on postorbital ( $\mathrm{Cl}=0.5$ ).

## Pliosauroidea (OUM J.28585, BMNH 49202, ‘P’. longirostris, Hauffiosaurus,

 Rhomaleosauridae, Leptocleidoidea, Pliosauridae):This clade is supported by the following synapomorphies: character 40 (except Hauffiosaurus), suborbital fenestrae present ( $\mathrm{Cl}=0.5$ ); character 59 , splenial participates in mandibular symphysis (shared with Yunguisaurus, Thalassiodracon) ( $\mathrm{CI}=0.5$ ); character 61, length of cervical vertebrae shorter than height (except Macroplata, shared with Pistosaurus) $(\mathrm{Cl}=0.333)$.

## Rhomaleosauridae (Archaeonectrus, Macroplata, Eurycleidus, Sthenarosaurus, Maresaurus, Rhomaleosaurus, 'R’ victor):

This clade is supported by the following synapomorphies: character 8 (state 1 ), diminutive contact of premaxilla with external naris (except Archaeonectrus) (CI $=0.667$ ); character 34, accessory grooves on the palatal surface ( $\mathrm{Cl}=1.0$ ); character 60, bowed mandible (except Archaeonectrus, shared with Plesiosaurus, Simolestes) (CI =0.5); character 62 (state 1), between 27 and 29 cervical vertebrae (except Macroplata) ((Cl $=0.571)$; character 64 , nutritive foramina on cervical vertebrae sunk in deep depressions (shared with L. clemai, Dolychorhynchops) ( $\mathrm{CI}=0.5$ ); character 65 (state1), large nutritive foramina on cervical vertebrae (except Macroplata, shared with Dolychorhynchops, L. clemai) ( $\mathrm{Cl}=0.286$ ).

## Unnamed clade including Macroplata and Eurycleidus:

This clade is supported by the following synapomorphy: character 13 , triangular process of premaxilla between the external naris and orbit ( $\mathrm{Cl}=1.0$ ).

## Unnamed clade including Rhomaleosaurus and Maresaurus:

This clade is supported by the following synapomorphy: character 9, premaxillamaxilla sutures run parallel anterior to the external nares $(\mathrm{Cl}=0.5)$.

## Unnamed clade including Rhomaleosauridae, Hauffiosaurus, Leptocleidoidea and Pliosauridae:

This clade is supported by the following synapomorphy: character 44, pterygoids meet behind the posterior interpterygoid vacuities (except TMP, shared with Hydrorion) (0.333). Also note that this character is widespread amongst many plesiosauroids not included in this analysis.

## Unnamed clade including Hauffiosaurus, Leptocleidoidea and Pliosauridae:

This clade is supported by the following synapomorphies: character 42 (state 1), posterior interpterygoid vacuities elongate and splint-like ( $\mathrm{Cl}=0.667$ ); character 71, cervical ribs without hooked anterior process (except Liopleurodon and TMP) (0.250); character 88, femur longer than humerus (minus Umoonasaurus, L. clemai, and shared with Yunguisaurus) $(\mathrm{Cl}=0.2)$.

## Unnamed clade including Leptocleidoidea and Pliosauridae:

This clade is supported by the following synapomorphy: character 81, angled dorsal margin on the dorsal blade of the scapula (except Simolestes, shared with

Eurycleidus) ( $\mathrm{Cl}=0.333$ ); character 93 (state 2), radius shorter than wide (except $L$. capensis) ( $\mathrm{Cl}=0.667$ ).

## Leptocleidoidea:

This clade is supported by the following synapomorphies: character 12, maxilla contacts squamosal (shared with Peloneustes) $(\mathrm{CI}=1.0)$; character 72 , singleheaded cervical ribs (shared with Kronosaurus and Brachauchenius) ( $\mathrm{Cl}=0.5$ ). Within Leptocleidoidea, the genus Leptocleidus is supported by the following synapomorphy: character 28 , vertex with dorsal noch on the parietal $(\mathrm{CI}=1.0)$.

## Pliosauridae:

(Brachauchenius, Kronosaurus, Peloneustes, Liopleurodon, Pliosaurus, Simolestes) This clade is supported by the following synapomorphies: character 8 (state 2), premaxilla excluded from the external nares (shared with TMP) ( $\mathrm{CI}=0.667$ ); character 45 , laterally projecting flange on pterygoid (shared with Yunguisaurus and Hydrorion); character 62 (states 3 or 4), cervical vertebrae less than 34 ( $\mathrm{Cl}=0.333$ ); character 83 , pubis length greater than width $(\mathrm{Cl}=1.0)$; character 86 , distal end of ilium greatly flared (except Brachauchenius and Simolestes) $(\mathrm{CI}=0.5)$.

## Unnamed clade including Simolestes Peloneustes, Liopleurodon and

## Pliosaurus:

This clade is supported by the following synapomorphy: character 18 , frontal excluded from orbit margin (shared with BMNH 49202 and Hydrorion) ( $\mathrm{CI}=0.250$ ); character 89 (state 2), anterior margin of humerus concave (shared with Rhomaleosaurus) ( $\mathrm{Cl}=0.4$ ).

## Unnamed clade including Peloneustes, Liopleurodon and Pliosaurus:

This clade is supported by the following synapomorphies: character 23 (state 2), maxilla excluded from the orbit margin ( $\mathrm{Cl}=1.0$ ); character 80 , scapulae meet on the midline $(\mathrm{Cl}=1.0)$; character 86 , distal end of ilium greatly flared $(\mathrm{CI}=0.5)$.

## Brachauchenidae (Brachauchenius and Kronosaurus):

This clade is supported by the following synapomorphies: character 62, (state 4), less than 21 cervical vertebrae ( $\mathrm{CI}=0.571$ ); character 65 (state 2), nutritive foramina absent (reversal) ( $\mathrm{CI}=0.286$ ).

## Chapter 7 - Discussion

> "A family on every account highly deserving an attentive examination, its members being not only unknown in the recent state, but presenting many peculiarities of general structure... as if it were a transition between different races, and adds new links to the connected chain of organised beings" de la Beche and Conybeare, 1821

The plesiosaur was instrumental in understanding the history and processes of life on Earth

### 7.1 Phylogenetic analysis - discussion

Within the cladistic analysis, the majority of pliosaur taxa occur within one of three main broad monophyletic subdivisions within the pliosauroid superfamily: the Rhomaleosauridae, Leptocleidoidea and Pliosauridae (Figure 5.7). Two taxa fall outside of these clades and may be regarded as 'basal pliosaurs': OUM J. 28585 and BMNH 49202. A further two taxa (' $P$ '. longirostris and Hauffiosaurus zanoni) form an unresolved polytomy, together with the Rhomaleosauridae and a large unnamed clade including all other post-Sinemurian pliosaurs. This un-named clade consists of the Leptocleidoidea and the Pliosauridae (see Chapter 6). These broad-scale relationships correspond very well with those presented by Druckenmiller (2006ab), but differ in many aspects from those presented by O'Keefe (2001a). The main points of similarity and difference will be discussed in the following sections.

### 7.2 Plesiosauroid-pliosauroid dichotomy

O'Keefe's (2001a) analysis recognised a traditional dichotomy between plesiosaurs into pliosauroids and plesiosauroids. This distinction held true in the analysis of Druckenmiller (2006a), but a number of pliosaur taxa in the latter analysis were distributed around the base of the plesiosauroid tree (Thalassiodracon, 'Plesiosaurus' macrocephalus and BMNH 49202). The present analysis also supports a dichotomy within plesiosaurs into separate plesiosauroid and pliosauroid superfamilies, but in this analysis Attenborosaurus is excluded from both of these clades (Figure 5.7). However, there are no clear characters present in plesiosaurs and absent in Attenborosaurus, therefore Attenborosaurus is regarded as a plesiosaur (Figure 5.7). The size of the ingroup for Plesiosauroidea is small and does not include enough taxa to make informed comments on the interrelationships of families within that clade; for example, no elasmosaurids or cryptoclidids were included in the analysis. Therefore, in this analysis, the plesiosauroid clade may be considered equivalent to the clade Plesiosauridae (see Chapter 6). The lack of derived plesiosauroids in this
analysis also affects the position of Dolichorhynchops, which is either a derived plesiosauroid or pliosauroid (see Chapter 3). As hypothesised in Chapter 5, Dolichorhynchops clades within the Pliosauroidea (Figure 5.7), agreeing with the analysis of Druckenmiller (2006a), the phylogenetic significance of this finding is uncertain, because of the lack of derived plesiosauroid characters in the cladistic analysis. In the current analysis, an enforced constraint placing this taxon in a derived position within Plesiosauroidea increases tree length by 21 steps.

### 7.3 The base of the Pliosauroidea

The arrangement of taxa at the base of the strict consensus tree (Figure 5.7) approximates Druckenmiller's (2006a) consensus cladograms in some respects, i.e. the inclusion of Thalassiodracon within the Plesiosauroidea, but it differs in others, the position of BMNH 49202 for example. There is no statistical support for the position of Thalassiodracon and an enforced constraint placing Thalassiodracon within the Pliosauroidea resulted in a tree length just five steps longer than the actual MPTs. The position of Thalassiodracon is therefore liable to change in future analyses. Specimen BMNH R1336 (the holotype of $P$. macrocephalus) was not included in the cladistic analysis because it is a juvenile (see Section 7.10). In this analysis, the unnamed taxon represented by BMNH 49202 (Figure 3.14), referred to ' $P$ '. macrocephalus, is situated at the base of the pliosauroid tree and represents the most basal pliosaur. This specimen is currently under study and represents a new genus (P. Vincent pers. comm. 2007). The second most basal pliosauroid is OUM J28585; it is possible that these two specimens (BMNH 49202 and OUM J28585) represent the same taxon; both specimens are quite poorly known, but they are both from the same locality and horizon and differ in only six characters in the cladistic analysis (Appendix 5). They both share characters considered by Cruickshank (1994a) to be intermediate between pliosaurs and plesiosauroids, combining a short postorbital region (typical of plesiosaurs, see Chapter 6) and an expanded mandibular symphysis (typical of pliosaurs, see Chapter 6). The cladistic analysis also indicates that OUM J28585 does not belong to Eurycleidus (contra Cruickshank, 1994a; O'Keefe 2001a and Smith, 2003)(see below).

### 7.4 Leptocleididae, Pliosauridae and Brachauchenidae

As mentioned in Chapter 2, the Leptocleididae has been a family of historical dubiousness. This analysis places Leptocleidids in a sister relationship with pliosaurids (Figure 5.7). This is significant because Leptocleidus has typically been allied with the rhomaleosaurids (Andrews. 1922a; Persson 1963, Cruickshank, 1997;

O'Keefe 2001a, 2004b) because both share a number of plesiomorphic characteristics (including head shape and proportions) and derived characters (including the dorso-median foraminae, a similarity rejected here). Umoonasaurus has also been allied with rhomaleosaurids (Kear et al. 2006), but it resolves as a member of Leptocleididae in this thesis. The only other analysis to separate Leptocleidus and Umoonasaurus from the Rhomaleosauridae is that of Druckenmiller (2006ab).

The family Brachauchenidae has previously been proposed to include Brachauchenius and Kronosaurus. Some characters in the cladistic analysis support this clade e.g. the number of cervical vertebrae - less than 21 (Character 62, state ' 4 '); and the lack of nutritive foraminae (character 65, state ' 2 '), and the

Brachauchenidae form a sister relationship with all other pliosaurids (Figure 5.7). These results differ from O'Keefe's cladogram (2001a), in which a brachauchenid clade is not resolved. Druckenmiller (2006) did not include Brachauchenius in his analysis so no comparison can be made regarding the significance of Brachauchenidae. However, the position of Kronosaurus in Druckenmiller (2006) differs from the current analysis; it occupies a derived position within the pliosauridae, in a sister relationship with Peloneustes (Figure 2.4). It should be noted that no material for either of these taxa (Kronosaurus and Brachauchenius) was investigated first hand in this thesis, and so it is possible that more detailed investigation of specimens may reveal more codable similarities amongst Cretaceous pliosaurids.

### 7.5 Rhomaleosauridae

The finding that the Rhomaleosauridae is a valid taxon agrees with the analysis of O'Keefe (2001a) (Figure 5.7). Archaeonectrus occupies the most basal position within the Rhomaleosauridae, agreeing with the classification of Persson (1963) (Figure 5.8). The only other cladistic analysis to previously include this taxon was Smith (2005), who's coding was based on the literature, and it was identified as a basal pliosaurid in a sister relationship with ' $P$ ' longirostris, a relationship not supported here. All other rhomaleosaurids are divided into a dichotomy, one clade includes only Hettangian taxa (Macroplata and Eurycleidus), and the other includes Toarcian taxa (Sthenarosaurus, gen. nov victor, and Rhomaleosaurus) and a single member from the Bajocian (Middle Jurassic) (Maresaurus). The position of gen. nov. victor is therefore closer to R. zetlandicus than it is to R. megacephalus, the opposite was found by O'Keefe (2001a) (Figure 2.4).

The Rhomaleosauridae ranges throughout the Lower Jurassic and extends into the Lower part of the Middle Jurassic. The latter part of the Middle Jurassic sees the emergence of the first pliosaurids and it is possible that the rhomaleosaurids were out competed by these very short-necked predators during the Middle Jurassic. Similarly, Andrews (1922a) and Cruickshank (1997) speculated that conservative Cretaceous forms such as Leptocleidus may have derived from pliosauroid stock (like Rhomaleosaurus), after being forced into freshwater environments under competition from larger open marine plesiosaurs. However, the results here do not support a close relationship between Leptocleidus and Rhomaleosaurus; rhomaleosaurids became extinct in the Middle Jurassic.

### 7.6 Eurycleidus

Eurycleidus is a key taxon concerning the systematics of Hettangian plesiosaurs. This is because, despite lacking much of the skull, and having a complicated history (see chapter 3), Eurycleidus arcuatus still represents the first named diagnostic species of large-headed (indicated by the size of the jaw symphysis) Hettangian plesiosaur (Owen, 1840). Importantly, the cladistic analysis convincingly separates OUM J. 28585 from Eurycleidus (Figure 5.7). This specimen was described and identified as Eurycleidus by Cruickshank (1994a); who included data from this specimen in a revised diagnosis of the genus. In the current cladistic analysis, the specimen is placed far from Eurycleidus, at the base of the pliosaur tree.
Cruickshank's identification of this taxon as Eurycleidus and the revised diagnosis, are therefore invalid: OUM.J28585 does not belong to Eurycleidus. This is significant because O'Keefe (2001a) coded Eurycleidus arcuatus primarily based on two referred specimens, one of which was OUM J.28585. The second specimen O'Keefe referred to Eurycleidus was SMNS 16812, but O'Keefe (2004b) later recognised that this specimen certainly does not belong to Eurycleidus: he proposed a new taxon name for it, Plesiopterys, but this specimen has since been re-examined and sunk into the taxon Seeleysaurus guilelmiimperatoris (Grossman, 2007). O'Keefe also recognised that it was possible that OUM J. 28585 may represent a new taxon and so in later analyses (O'Keefe 2004b), this specimen was paces in inverted commas, thus; 'Eurycleidus'. In summary, the phylogenetic analyses presented here support the notion that Eurycleidus is a separate taxon from OUM J.28585, and agrees with the results of O'Keefe's (2004b) analysis, in also recognising SMNS 16812 (Seeleyosaurus) as a separate taxon from Eurycleidus.

The cladistic analysis presented here does not completely reflect the systematic palaeontology within the genus Eurycleidus i.e. parts of the cladogram are
unresolved (Figure 5.8). Three species are included within Eurycleidus: Eurycleidus arcuatus, Eurycleidus megacephalus and the new species Eurycleidus sp. nov. These species are so similar to $E$. arcuatus that it was deemed unnecessary to introduce a new genus or genera for either $E$. megacephalus or $E$. sp. nov. This classification follows Andrews (1922a), who placed the species megacephalus within the genus Eurycleidus. In fact, this classification was accepted by Persson (1963), and was only revised recently when Cruickshank (1994b) placed it into Rhomaleosaurus, after description of a neotype (LEICS G221.1851). Therefore, the revised classification endorsed here mirrors the traditional classification.

The genus Eurycleidus is a monophyletic taxon in the cladogram, supported by some synapomorphies (see Chapter 6), but there is very poor resolution amongst the species in the cladogram in this area. The only resolution within Eurycleidus consists of a dichotomy between the single holotype specimen of Eurycleidus sp. nov. (WARMS G10875), and all other specimens (Figure 5.8). The lack of resolution between $E$. arcuatus and $E$. megacephalus is attributed to a combination of lack of data combined with the lack of overlapping characters amongst the five specimens referred to these two species of Eurycleidus (see also Section 7.8 below). For example, the skull of the holotype of Eurycleidus arcuatus is known from only the mandibular symphysis, however, the best-preserved skull of this genus (NMING 10194) lacks this vital piece of anatomy. In another vital area, the coracoids, the holotype E. megacephalus and LEICS G221.1851 provide no data, whereas the coracoids in the holotype of Eurycleidus are complete. The coracoids of NMING F10194 are also known (Figures 4.33), and differ from E. arcuatus, in that they do not narrow posteriorly (Figure 4.54). Again, no comparison can be made with $E$. megacephalus. This makes defining and differentiating between species especially problematic, and this explains why quite complete specimens have been referred to Eurycleidus sp.. Nevertheless, the morphometric analyses support the systematic palaeontology proposed here, and hopefully future discoveries will provide more information on the anatomical variation between different species of Eurycleidus. Andrews (1922a) differentiated between $E$. arcuatus and $E$. megacephalus on the form of the clavicular arch, the interclavicle being wider and the anterior border more concave in E. arcuatus. However, the specimen of E. megacephalus (BMNH R.1322) (see also Lydekker, 1889b) is not the type specimen of this species, and in any case, both specimens are damaged, having had their antero-lateral portions broken (pers. obs). These differences were not recognised in any of the other specimens referred to Eurycleidus in this Thesis.

### 7.7 Comparison of Eurycleidus reconstructions

Cruickshank (1994b) provided a thorough description of the skull of specimen LEICS G221.1851 and provided a reconstruction of the skull (Figure 7.1A,B). However, the specimen is imperfectly preserved, especially with regard to the surface detail and preservation of sutures, and this specimen is therefore open to interpretation. It is fortuitous that supplementary data for this genus has come to light in a hitherto undescribed specimen (NMING F10194) (Figures 4.28-4.34) in the collections of the National Museum of Ireland (Natural History) (Chapters 3 and 4). Both LEICS G221.1851 and NMING F10194 are regarded as Eurycleidus sp. (see Chapter 6); enabling a new reconstruction of the cranium of Eurycleidus combining data from these specimens (Figure 6.1). This section provides a comparison of the two existing interpretatations of Eurycleidus as produced by Cruickshank (1994b) (Figure 7.1A,B), and as produced in this thesis (Figure 6.1 and 7.1 C,D) (see also Figures 4.48 and 4.49 for the interpretations of specimen LEICS G221.1851). The differences listed do not represent taxonomic differences, but are due to differing interpretations.

In NMING F10194 the premaxillary rostrum is notably more elongate and more ventrally directed than the reconstruction of LEICS G221.1851 given by Cruickshank (1994b). Each frontal sends a narrow anterior projection and contacts the postero-medial border of the external nares in the current reconstruction, this contrasts with the frontals as reconstructed by Cruickshank (1994b) in which the anterior projections are broad and contact the external nares all the way to the postero-lateral border (Figure 7.1). The posterior border of the frontals meets the parietal at a level anterior to the posterior border of the orbits in NMING F10194 and a large lozenge shaped pineal foramen is situated immediately behind the parietalfrontal suture. In Cruickshank (1994b) the pineal foramen is small and located far posterior to the parietal-frontal suture, this suture is located posterior to the posterior border of the orbit margin. The characters of the jugal differ between the two interpretations. The jugal extends to the anterior margin or the orbit, possibly even excluding the maxilla from the orbit margin in Cruickshank's interpretation (1994b), and only extends half way along the orbit margin in the current interpretation of both NMING F10194 and LEICS G221.1851 (Figure 7.1). NMING F10194 certainly lacks a dorso-median foramen between the posterior processes of the premaxillae, whereas a cleft in this region between the external nares, was interpreted as a dorso-median foramen by Cruickshank (1994b). This cleft is therefore interpreted as a taphonomic artefact in LEICS G221.1851 and NMING F8749, and is due to crushing.

On the palate, Cruickshank (1994b) reconstructed the vomers in LEICS G221.1851 terminating at the posterior margin of the internal nares (Figure 7.1B);


Figure 7.1. Two interpretations of Eurycleidus, A, B. interpretation of LEICS G221.1851 by Cruickshank (1994b) (modified from Cruickshank 1994b, figs. 1 and 4), C, D. new interpretation of Eurycleidus based on LEICS G221.1851 and supplemented with data from three additional specimens (see Figure 6.1) (scale bar $=30 \mathrm{~cm}$ ).
however, in the current reconstruction they extend far beyond the internal nares (Figure 7.1D). The ectopterygoid position, shape and size, also differs considerably between the interpretations; Cruickshank (1994b) reconstructs the bone as a broad short element forming the posterior margin of the palate. In contrast, the ectopterygoid is situated far more laterally and extends anteriorly to contact the suborbital fenestra in the current interpretation; the pterygoid also sends out a lateral process behind a lateral palatine vacuity, absent in Cruickshank's (1994b) interpretation of LEICS G221.1851, but illustrated by O'Keefe (2001a) for this specimen. A squared-lappet is also reconstructed here in Eurycleidus (Figure 7.1D); this is absent in the interpretation of Cruickshank (1994b) (Figure 7.1B).

### 7.8 Rhomaleosaurus

Three species of Rhomaleosaurus are recognised in this thesis, and so Rhomaleosaurus sensu stricto consists of Rhomaleosaurus cramptoni, Rhomaleosaurus thorntoni and Rhomaleosaurus zetlandicus. The genus is supported by numerous synapomorphies (see Chapter 6). The following species are removed from Rhomaleosaurus: ' $R$ ' megacephalus (now placed in Eurycleidus [see above]), ' $P$ '/'R' longirostris (awaits description and new genus name), ' $R$ ' victor. In resolving the systematics of rhomaleosaurid plesiosaurs, a sensible first course of action should be to reinstate rejected genera, rather than propose new genera and create even more confusion. The genus Thaumatosaurus could potentially have been reapplied to the species victor, which it is often associated in the popular literature and amongst palaeontologists (see Chapter 2). However, due to the insufficient (non-diagnostic) type material, the name Thaumatosaurus cannot be reintroduced for any of the specimens described here.

The division of specimens into species within Rhomaleosaurus, and also within Eurycleidus (as outlined in Chapter 6), was problematic. Unlike the generic separation between these taxa, which is supported by many discrete autapomorphies, the division between species within the genera are less well supported, and in some cases are recognised predominantly by proportional differences. This is partly because of the lack of overlapping characters (see Chapter 6), but also because species within a genus are, by definition, very similar, and so differences are less abundant and easily lost due to damage, lack of preservation, or lack of exposure/preparation in the specimen. This explains why some very complete specimens of Eurycleidus cannot be allocated to species level (NMING F10194, NMING F8749 and LEICS G221.1851) (see above). The possibility of uniting all specimens of Rhomaleosaurus sensu stricto under one species, and all specimens of

Eurycleidus under fewer (or even one) species, was strongly considered. Cruickshank (1996b) took such an approach for Rhomaleosaurus, allocating observable differences to intraspecific variation within a single species. Even when there are slight quantifiable differences between specimens (as is the case here) it is still possible to allocate specimens to the same species. However, the main purpose of any taxonomy is to be utilitarian (Benton, 2000); and in this context, it is considered (albeit subjectively) that it is more helpful to be able to refer to specimens by name rather than number. The retention of species was therefore favoured over sinking species.

The identification of a gastrolith in $R$ thorntoni (Figure 4.11), combined with the presence of gastroliths in R. zetlandicus (Taylor, 1992b), indicates that Rhomaleosaurus swallowed stones, at least on occasion. This is significant because gastroliths are rare in pliosaurs (very common in plesiosauroids) and the discrepancy has been suggested as being related to different functional regimes between these groups (Storrs, 1993). However, the above evidence for gastroliths in the pliosaur Rhomaleosaurus indicates that this may not be the case.

### 7.9 Simolestes and Maresaurus

Simolestes has been regarded as a pliosaurid (Andrews, 1913; Tarlo, 1960; Brown, 1981), a rhomaleosaurid (Romer, 1956; Persson, 1963; O’Keefe, 2001), and White (1940) included Simolestes in the Elasmosauridae because "the character of both the skull and shoulder girdle compare more favourably [sic] with Elasmosaurus than with Pliosaurus or Peloneustes" (p. 466). Tarlo (1960) pointed out that White's interpretation is simply incorrect, indeed, all subsequent cladistic analyses have strongly supported a pliosauroid affinity for Simolestes. The main question regarding Simolestes is where exactly does it fit within the pliosauroid tree? The uncertainly stems from the unusual suite of characters possessed by this taxon: on one hand Simolestes displays a number of pliosaurid characteristics (notably the construction of the palate surrounding the posterior interpterygoid vacuities), and on the other hand, the short rostrum and spatulate symphysis are reminiscent of Rhomaleosaurus. Gasparini (1997) demonstrated that Maresaurus, another pliosaur with a spatulate symphysis, shares characters with both Rhomaleosaurus and Simolestes. Noè (2001) regarded Maresaurus as a junior synonym of Simolestes. The main problem with using symphyseal morphology in classification was summarised by Gasparini (1997, p.144): "the spatulate symphysis...could be a convergent character of animals with similar feeding habits". The same may also apply to another character used by O'Keefe (2001) to unite Simolestes with the
rhomaleosaurid, the bowed mandibles (see Druckenmiller, 2006). To overcome this problem and potentially identify convergence, the cladistic analysis conducted here incorporated an exhaustive list of characters from the skull and postcranium. The results indicate that the spatulate pliosaur symphysis is indeed a convergent character, which developed in the rhomaleosaurids (e.g. Rhomaleosaurus) and the pliosaurids (Simolestes) independently (Figure 5.7). Simolestes is strongly supported in the Pliosauridae. This differs from O'Keefe (2001a) who recovered Simolestes in a derived Rhomaleosaurid position, but agrees with Druckenmiller (2006ab), who recovered Simolestes in a basal position within the pliosaurid family. In contrast, Maresaurus is positioned deep within the Rhomaleosauridae, and forms a sister relationship with Rhomaleosaurus supported by some convergent characters (rostrum and symphyseal morphology) but also some rhomaleosaurid synapomorphies (see Chapter 6). The most significant of these include the same construction of the rear of the palate, rounded lateral angles on the parietal, a midline ridge on the premaxilla, and parallel maxilla-premaxilla sutures anterior to the external nares. Simolestes lacks these rhomaleosaurid characters and shares the following characters with pliosaurids: the premaxilla is excluded from the margin of the external nares and the nasals are present. An enforced constraint placing Simolestes within the Rhomaleosauridae in a sister relationship with Maresaurus resulted in a twelve step increase in tree length, and a constraint placing Simolestes in a sister relationship with Rhomaleosaurus (as in O'Keefe, 2001a), increased the tree length by eighteen steps. The results of the cladistic analysis therefore show that Simolestes and Maresaurus are not synonymous (contra Noè, 2001).

### 7.10 Morphometrics analysis - discussion

The morphometric analyses have been incorporated in relevant discussions in chapter 4 , section 4.10 . However, some of the data points in the morphometric analyses stand out as anomalous, and probably reflect an underlying error related to the authenticity of the specimen and provide evidence for composites. Taylor (1992b p. 51) pointed out that the femur associated with the holotype of $R$. zetlandicus may not belong to this individual, but that "resolving this problem requires comparative study of other material pertaining to Rhomaleosaurus". The position of the data point for R. zetlandicus in Figure 5.5 V and Figure 5.5W, comparing the relative proportions of the femur with the humerus and skull respectively, plot away from other species of Rhomaleosaurus (R. cramptoni) and thus confirm that it is probably not part of this specimen. However, the actual proportions of the femur (Figure 5.5S) show that it is a likely a rhomaleosaurid.

The data point for Macroplata in Figure 5.5M, representing the relative length of the humerus and femur, plots far away from its closest relatives (Eurycleidus) and this is probably due to the fact that distal portion of the humerus has been slightly reconstructed in this specimen. In Figure 5.5Z, which compares the relative size of the skull with the postcranium, specimen NMING F8749 plots away from other specimens of Eurycleidus. The proportions of this specimen are noticeably different from other plesiosaurs, the head is especially large (Figure 3.9). The neck vertebrae are certainly artificially mounted and it is likely, based on the unusual proportions, that this specimen in a composite.

Specimen HALB 'uncatalogued' plots very closely with Rhomaleosaurus and gen. nov. victor, (Figure 5.5M,U) and is not close to R. megacephalus, the species to which this specimen was referred to by Brandes (1914). This agrees with observations by Grossman (2007), who also pointed out that the affinities of this specimen must await a detailed examination of the fossil. Attenborosaurus (see Figure $5.5 \mathrm{H}, \mathrm{Q}$ ) and Archaeonectrus (see Figure $5.5 \mathrm{~A}, \mathrm{H}, \mathrm{Z}$ ) both fail to cluster with any of the other taxa included in this analysis, confirming that, in terms of their proportions at least, they are distinctive. In the morphometric analysis, specimen BMNH R1336 (Figure 3.10, 3.11) shows a number of proportions confirming its juvenile nature (also indicated by the anatomy, i.e. small size and poorly ossified skeleton). The actual skull proportions and femur proportions in this taxon are no different from the other rhomaleosaurids (Figures 5.5C,D,Y), however, in terms of the relative size of the skull to the body (Figure $5.5 \mathrm{Y}, \mathrm{Z}$ ), BMNH R1336 plots away from the other taxa in this analysis because the head is relatively larger, as is typical for juveniles. This specimen also differs in the relative proportions of the humerus and skull (Figure 5.5 X ); again the skull is much larger, and in relative lengths of the humerus and femur, the femur is much longer in this specimen (Figure 5.5M). Amongst other Hettangian and Sinemurian rhomaleosaurids, this specimen is closest to E. megacephalus (Figure 5.5Y,Z).

### 7.11 Caudal fin in plesiosaurs

Amongst Mesozoic marine reptiles, ichthyosaurs (Buchholtz, 2001) and thalattosuchian crocodiles (Andrews, 1913), possess one or two irregular, often wedge- shaped vertebrae (Mcgowan, 1989), near the tip of the tail, associated with laterally compressed distal caudal vertebrae, and resulting in a downward kink, 'tailbend' or 'fluke' at the tail tip. It has long been inferred that this fluke supported a caudal fin in ichthyosaurs (see discussion in Rowe et al. 2001), and this was later confirmed by spectacular fossils from Holzmaden, Germany, preserving soft-tissue
outlines of caudal fins in ichthyosaurs (Bauer, 1898). Mosasaurs also have laterally compressed tail vertebrae and are inferred to have supported a caudal fin (Everhart, 2005).

Plesiosaurs have also been inferred to have had, and have sometimes been reconstructed with, a caudal fin. In 1865, Owen (p26) noted that the last ten caudal vertebrae in Archaeonectrus rostratus were laterally compressed, and that "this compression of the centrums would indicate...some development of the terminal dermal expanse". Dames (1895) is the only author to report soft-tissue evidence for a caudal fin in a plesiosaur; the holotype of Seeleysaurus guilelmiimperatoris preserves a black soft-tissue outline (see Dames, 1895, Plate 1; and reproduced by Tarlo, 1957, Plate 37, Fig. 2), and this taxon was therefore restored with a large diamondshaped caudal fin at the tip of the tail (see Dames, 1895, unnumbered illustration p.79). This specimen has since been covered with grey paint and so this feature cannot be verified (Grossman, 2006). Zarnick (1925) cited this evidence, but employed sea snakes as an analogue for interpreting the exact outline of the fin, restoring this taxon with a rounded tail fin (see Zarnick, 1925, Fig. 22). Tarlo (1957) also cited the evidence presented by Dames (1895), and on this basis suggested that a tail fin may also occur in Callovian pliosaurs (p. 199): "In pliosaurs too a tail of this sort may have played some part in their locomotion". A later reconstruction of a pliosaur, produced by Newman and Tarlo (1967), bears out this inference.

It is in this context that the unusually shortened $21^{\text {st }}$ caudal vertebra in the tail of $R$. zetlandicus is interpreted (Figure 4.24), and it is regarded as putative evidence for a tail fin in this taxon. No such feature has been documented before in any plesiosaur. The laterally compressed distal caudal vertebrae described in Archaeonectrus by Owen (1865), are also present in R. zetlandicus. As seen in ichthyosaurs and thalattosuchians, lateral compression of the vertebrae is typically related to a laterally compressed tail fin. The sudden shift in the morphology of the tail vertebrae at the position of the $21^{\text {st }}$ vertebra, coincides with a subtle kink in the tail, and possibly represents the point of origin of a caudal fin. The exact outline of this caudal fin must remain speculative, the reconstruction presented here (Figure 4.27) is based on Dames (1895) and Newman and Tarlo (1967).

## Chapter 8 - Conclusions

### 8.1 Context

The very long history associated with the study of Lower Jurassic plesiosaurs has resulted in a complicated, and, as Taylor put it in 1992b (p.51), "utterly confused taxonomy". As presented in Chapter 2, recent attempts have come some way in rectifying this detrimental situation (e.g. O'Keefe, 2001a), but in the case of Lower Jurassic pliosaurs there were simply too many insufficiently described (or completely undescribed) specimens upon which to base a sound systematic framework. In this context, the main outcomes of this thesis provide a greater understanding of the anatomy, diversity and variation in Lower Jurassic pliosauroids. In turn, this has led to a revised phylogenetic hypothesis and taxonomy of pliosaurs, and a detailed revision of the systematics of rhomaleosaurids in particular.

### 8.2 Systematics - conclusions

In light of the revised systematic framework presented in Chapter 6, the main systematic conclusions of this thesis may be subdivided as follows:

1. The genus Rhomaleosaurus contains three species, all from the Toarcian of the UK. These include:

- NMING F8785, the holotype of the species Rhomaleosaurus cramptoni, the genus Rhomaleosaurus, and the family Rhomaleosauridae.
- BMNH R4853, the holotype of Rhomaleosaurus thorntoni.
- YORYM G503, the holotype of Rhomaleosaurus zetlandicus.

2. Specimen WM 852.S, the holotype of Rhomaleosaurus propinquus, is referred to Rhomaleosaurus cramptoni. Based on the results of the morphometric and cladistic analyses, the following species, previously referred to Rhomaleosaurus, do not belong to Rhomaleosaurus sensu stricto: ' $R$ '. megacephalus, ' $R$ '. victor, and ' $R$ ' longirostris, and are removed from this genus.
3. The holotype of the genus Eurycleidus ( $E$. arcuatus) is represented by an almost complete postcranial specimen, but only the mandibular symphysis is preserved of the skull. A number of pliosaur specimens have been referred to this genus, because they do not show sufficient difference in anatomy or morphometric proportions from
the holotype series and they form a monophyletic group in the cladogram (Figure 5.7). These specimens include:

- WARMS G10875, this specimen is allocated as the holotype of a new species of Eurycleidus, supported by proportional autopomorphies of the skull, and discrete autapomorphies of the postcranium (see Chapter 6).
- BMNH R1310, TCD. 47762 a and TCD.47762b, all casts of destroyed specimen BRSMG Cb 2335, the holotype or Eurycleidus megacephalus (previously Rhomaleosaurus megacephalus). These casts are valid holotype specimens for this species, and therefore the introduction of a neotype specimen for ' $E$ '. megacephalus (LEICS G221.1851) was unnecessary (see below).
- LEICS G221.1851, this specimen was introduced as a neotype of $E$. megacephalus by Cruickshank (1992b). This assignments is rejected here because the casts of the holotype are valid. The specimen is here regarded as a referred specimen of Eurycleidus sp.
- NMING F10194, this specimen is referred to Eurycleidus sp.
- NMING F8749, this specimen is referred to Eurycleidus sp.

4. The genera Macroplata and Archaeonectrus are both valid monospecific taxa within the Rhomaleosauridae, supported by a number of autapomorphies (see Chapter 6).
5. The following pliosauroid taxa are also supported by the morphometric analysis and/or cladistic analysis; Attenborosaurus, Sthenarosaurus, Hauffiosaurus, 'P' longirostris, Thalassiodracon, and BMNH 49202. However, detailed description of these specimens was outside the scope of this thesis and so these specimens should be subjected to full description in the future.
6. According to the cladistic analysis presented in this thesis, the Pliosauroidea forms a monophyletic group in a sister relationship with Plesiosauroidea. Three groups are resolved within the Pliosauroidea: the Rhomaleosauridae, Leptocleidoidea and Pliosauridae.
7.Other significant results include: Simolestes resolves as a derived pliosaurid rather than a derived rhomaleosaurid, indicating that a spatulate rostrum is a convergent character amongst pliosauroids. Maresaurus, from the Middle Jurassic (Bajocian)
resolves as a rhomaleosaurid and therefore represents the youngest known member of this clade.

### 8.3 Anatomy - conclusions

The descriptions and figures presented in this thesis represent the first descriptions of many specimens, including all of the pliosaur material in the NMI, and provide new information on the anatomy of rhomaleosaurid pliosaurs. The main anatomical conclusions of this thesis may be subdivided as follows:

1. The strong ectopterygoid boss in Rhomaleosaurus was covered in a cartilaginous sheath in life, and abutted against the medial wall of the mandible, strengthening the skull.
2. The following characters are widely shared by rhomaleosaurid plesiosaurs, but have not always been recognised, or accessible, to earlier workers:

- A dorsal triangular flange of the maxilla extends between the orbit and the external naris.
- The vomers extend posterior to the internal nares.
- A large ectopterygoid contacts the suborbital anteriorly.
- Small semi-circular lateral palatine vacuities and large suborbital vacuities.
- Plate-like developments below the basicranium incorporating squared lappets at the base of the quadrate-pterygoid flange.
- A medial bump on the retroarticular process.

3. The first ever, full body reconstruction of a rhomaleosaurid plesiosaur (Rhomaleosaurus) provides information on the shape of the animal. Characters to note include:

- The total length of the animal is 7 m , but probably reached about 8 m in old adults.
- The body of the animal is dorso-ventrally flattened.
- There is very little curvature along the vertebral column, except for the pectoral and anterior dorsal regions.
- The ribs are wide and swept backwards.
- The distance between the coracoid and pubis is notably large.
- Many aspects of the postcranial skeleton are robust and/or reinforced i.e. the neural spines of the posterior cervical and dorsal vertebrae, the wide, buttress-like cervical zygapophyses, the asymmetrical midline tooth-and-
socket joint in the coracoid, and the robust dorsal blade of the scapula and the ilium.
- A notable change in the proportions of the terminal caudal vertebrae, associated with a conspicuous vertebrae, indicate the presence of a vertical caudal fin.


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Appendix 1. List of valid plesiosaur species with information on authors and date of publication.

| Date | Original paper | Renamer | Species | Age |
| :---: | :---: | :---: | :---: | :---: |
| 1824 | De la Beche and Conybeare 1824 |  | Plesiosaurus dolichodeirus | Sinemurian |
| 1876 | Blake in Tate and Blake 1876 |  | Plesiosaurus' longirostris | Toarcian |
| 1837 | Buckland in Conybeare 1837 |  | Plesiosaurus' macrocephalus | Sinemurian |
| 1841 | Owen 1841 |  | Pliosaurus brachydeirus | Kimmeridgian |
| 2004 | Noe et al 2004 |  | Pliosaurus portentificus | Kimmeridgian |
| 1841 | Owen 1841 |  | Pliosaurus brachyspondylus | Kimmeridgian |
| 1948 | (Novozhilov 1948) | Tarlo1960 | Pliosaurus irgisensis | Tithonian |
| 1871 | (Phillips 1871) | Noe et al. 2004 | Pliosaurus macromerus | Callovian-Tithonian |
| 1960 | Tarlo 1960 |  | Pliosaurus andrewsi | Callovian |
| 1841 | Owen 1841 |  | Polyptychodon interruptus | Turonian-Santonian |
| 1868 | Cope 1868, |  | Elasmosaurus platyurus | Campanian |
| 1869 | Cope 1869 |  | Polycotylus latipinnis | Santonian |
| 1948 | (Novozhilov 1948) | Halstead 1971 | Liopleurodon rossicus | Tithonian |
| 1869 | (Seeley 1869) | Tarlo 1960 | Liopleurodon pachydeirus | Callovian |
| 1873 | Sauvage1873 |  | Liopleurodon ferox | Callovian |
| 1874 | Hector 1874 |  | Mauisaurus haasti | Campanian |
| 1865 | (Owen 1865) | Seeley 1874 | Eretmosaurus rugosus | Sinemurian |
| 1874 | Seeley 1874 |  | Muraenosaurus leedsi | Callovian |
| 1892 | (Seeley 1892) | Brown 1981 | Muraenosaurus beloclis | Callovian |
| 1863 | (Carte and Bailey 1863) | Seeley 1874 | Rhomaleosaurus cramptoni | Toarcian |
| 1846 | (Stutchbury 1846) | Andrews 1922 | Rhomaleosaurus megacephalus | Hettangian |
| 1910 | (Fraas 1910) | Tarlo 1960 | Rhomaleosaurus victor | Toarcian |
| 1840 | (Owen 1840) | Seeley 1874 | Colymbosaurus trochanterius | Kimmeridgian-Tithonian |
| 1881 | (Sollas 1881) | Bakker 1993 | Attenborosaurus conybeari | Sinemurian |
| 1888 | Cragin 1888 |  | Trinacromerum bentonianum | Turonian |
| 1935 | Russell 1935 |  | Trinacromerum kirki | Turonian |
| 1869 | (Seeley 1869) | Lydekker 1889 | Peloneustes philarchus | Callovian |
| 1871 | Phillip(s 1871) | Seeley 1892 | Cryptoclidus eurymerus | Callovian |
| 1889 | (Lydekker 1889) | Bogolubov, 1909 | Cryptoclidus richardsoni | Callovian |
| 1898 | Knight 1898 |  | Megalneusaurus rex | Kimmeridgian-Portlandiar |
| 1902 | Williston 1902 |  | Dolychorhynchops osborni | Campanian |
| 2005 | Sato 2005 |  | Dolichorhynchops herschelensis | Campanian-Maastrichtian |
| 1903 | Williston 1903 |  | Brachauchenius lucasi | Cenomanian-Turonian |
| 1994 | Godefroit 1994 |  | Simolested keileni | Bajocian |
| 1877 | Lydekker 1877 | Bardet et al. 1991 | Simolestes indicus | Tithonian |
| 1909 | Andrews 1909 |  | Simolestes vorax | Callovian |
| 1909 | Andrews 1909 |  | Tricleidus seeleyi | Callovian |
| 1865 | (Owen, 1865) | Watson 1909 | Microcleidus homalospondylus | Toarcian |
| 1865 | Seeley, 1865? | Watson 1909 | Microcleidus macropterus | Toarcian |
| 1909 | Watson, 1909 |  | Sthenarasaurus dawkins | Toarcian |
| 1913 | Brown 1913 |  | Leurospondylus' ultimus | Maastrichtian |
| 1914 | Wegner 1914 |  | Brancasaurus brancai | Berriasian |
| 1840 | (Owen 1840) | Andrews 1922 | Eurycleidus arcuatus | Hettangian |
| 1911 | (Andrews 1911) | Cruickshank 1997 | Leptocleidus capensis | Valanginian |
| 1922 | Andrews 1922 |  | Leptocleidus superstes | Barremian |
| 1997 | Cruickshank and Long, 1997 |  | Leptocleidus clemai | Hauterivian-Barremian |
| 1924 | Longman 1924 |  | Kronosaurus queenslandicus | Aptian-Albian |
| 1992 | Hampe, 1992 |  | Kronosaurus boyacensis | Aptian-Albian |
| 1930 | Swinton 1930 |  | Macroplata tenuiceps | Hettangian |
| 1895 | (Dames 1895) | White 1940 | Seeleysaurus guilelmiimperatoris | Toarcian |
| 1941 | Cabrera 1941 |  | Aristonectes parvidens | Maastrichtian |
| 1943 | Welles 1943 |  | Aphrosaurus furlongi | Maastrichtian |
| 1890 | (Williston 1890) | Welles 1943 | Styxosaurus snowii | Santonian-Campanian |
| 1890 | Welles 1943 |  | Morenosaurus stocki | Maastrichtian |
| 1943 | Welles 1943 |  | Thalassomedon haningtoni | Cenomanian |
| 1949 | (Welles 1949) | Carpenter 1997 | Libonectes morgani | Turonian |
| 2006 | Buchy 2006 |  | Libonectes atlasense | Turonian |
| 1871 | (Cope 1871) | Welles 1943 | Hydralmosaurus serpentinus | Santonian-Campanian |
| 1943 | Welles 1943 |  | Fresnosaurus drescheri | Maastrichtian |
| 1943 | Welles 1943 |  | Hydrotherosaurus alexandrae | Maastrichtian |
| 1865 | (Owen 1865) | Novozhilov 1964 | Archaeonectrus rostratus | Sinemurian |
| 1976 | (Ochev 1976) | Ochev 1977 | Georgiasaurus penzensis | Santonian |
| 1980 | Dong 1980 |  | Bishanopliosaurus youngi | Toarcian |
| 1981 | Brown 1981 |  | Kimmerosaurus langhami | Kimmeridgian |


| 1982 | Delair 1982 |  | Bathyspondylus swindoniensis | Kimmeridgian |
| :---: | :---: | :---: | :---: | :---: |
| 1985 | Zhang 1985 |  | Yuzhoupliosaurus chengjiangensi | Bathonian |
| 1986 | Wiffen and Moisley 1986 |  | Tuarangisaurus keysei | Campanian-Maastrichtian |
| 1996 | Carpenter 1996 |  | Plesiopleurodon wellesi | Cenomanian |
| 1996 | Cruickshank et al. 1996 |  | Pachycostasaurus dawni | Callovian |
| 1840 | (Owen 1840) | Storrs and Taylor 1996 | Thalassiodracon hawkinsii | Hettangian |
| 1997 | Gasparini 1997 |  | Maresaurus coccai | Bajocian |
| 1990 | (Sciau et al. 1990) | Bardet et al. 1999 | Occitanosaurus tournemirensis | Toarcian |
| 1962 | (Welles, 1962) | Carpenter 1999 | Callawayasaurus colombiensis | Aptian |
| 2001 | O,Keefe 2001 |  | Hauffiosaurus zanoni | Toarcian |
| 2002 | Cruickshank and Fordyce 2002 |  | Kaiwhekea katiki | Maastrichtian |
| 2002 | Druckenmiller 2002 |  | Edgarosaurus muddi | Albian |
| 1949 | (de la Torre and Rojas 1949) | Gasparini et al. 2002 | Vinielasaurus caroli | Callovian |
| 2003 | Bardet et al. 2003 |  | Thililua longicollis | Maastrichtian |
| 2003 | Sato 2003 |  | Terminonatator ponteixensis | Campanian |
| 2006 | Kear 2006 |  | Umoonasaurus demoscyllus | Aptian-Albian |
| 2006 | Kear 2006 |  | Opallionectes andamookaensis | Aptian-Albian |
| 2005 | (Sachs 2005) | Kear 2006 | Eromangasaurus australis | Albian |
| 1893 | Marsh 1893 |  | Pantosaurus striatus | Oxfordian |
| 1900 | (Knight 1900) | O'Keefe and Wahl 2003 | Tatenectes laramiensis | Oxfordian |
| 1990 | Gasparini and Spalleti, 1990 |  | Sulcusuchus erraini | Maastrichtian |
| 1923 | (Huene 1923) | Grossman 2007 | Hydrorion brachypterygius | Toarcian |
| 1942 | Young 1942 |  | Sinopliosaurus weiyuanensis | Kimmeridgian? |
| 2006 | Sato et al 2006 |  | Futabasaurus suzukii | Santonian |
| 2005 | Buchy et al. 2005 |  | Manemergus anguirostris | Maastrichtian |
| 2007 | Albright et al. 2007 |  | Eopolycotylus rankini | Turonian |
| 2007 | Albright et al. 2007 |  | Palmula quadratus | Turonian |

## Appendix 2. Additional material

The following list outlines additional fossil material adopted in the cladistic analysis and/or the morphometric analysis, but not figured or described herein. The list begins with specimens of uncertain taxonomic affinity ( 1 A ) and continues with a taxon list (1B). The taxon list includes the type and referred material employed in the analyses (the lists of referred material are therefore not exhaustive), and data on the type locality and horizon. Although not figured or described in this thesis, some of this material was observed first hand (observed material is indicated by the following symbol proceeding the specimen number: ${ }^{* * *}$ ), otherwise the taxa were coded from the literature, as listed in the 'remarks' section. The taxa in Appendix 1B are listed in the order that they appear in the cladograms resulting from the cladistic analysis (Figure 5.7).

## Appendix 1A - Additional specimens of uncertain taxonomic affinity

## OUM J. 2858 'Eurycleidus’

Cruickshank (1994a) referred OUM J.28585, a specimen from Lyme Regis, to Eurycleidus arcuatus. The specimen consists of a partial skull including the mandible and some postcranial elements (from the pelvic girdle). However, this specimen may represent a new taxon in itself (O'Keefe 2004b). To test affinities of OUM J.28585, it is treated as a separate OTU in the current cladistic analysis, albeit coded from the literature.

## HALB 'Uncatalogued'

This specimen from the Toarcian of Kanonenberg, northern Germany, was described by Brandes (1914) and referred to Thaumatosaurus aff. megacephalo (= Rhomaleosaurus megacephalus). However, Grossman (2007, p. 557-558) noted that this specimen "resembles Rhomaleosaurus victor more than R. megacephalus and it is probably synonymous with the German taxon [R. victor]". The specimen was included in the morphometric analysis based on measurements given by Brandes (1914).

## Appendix 1B - Additional taxa

Type material. IGWH uncatalogued, skull.
Type locality. Halle-Nietleben, Saxony-Anhalt, Germany.
Type horizon. Myophoria beds, Upper Röt Formation (Beneckeia buchi and
Dadocrinus assemblage zone), Upper Buntsandstein (Lower Anisian, Middle Triassic).
Remarks. A review of Cymatosaurus is presented by Rieppel (2000).

## Pistosaurus longaevus Meyer, 1839

Type material. Uncatalogued, Oberfränkisches Erdgeschichliches Museum, Bayreuth, skull.

Type locality. Lainecker Hohenzug, east of Bayreuth, southern Germany.
Type horizon. Lower Meissner Formation, Upper Muschelkalk (atavus to postspinosus zones), (Upper Anisian, Middle Triassic).
Referred material. SMF R 4041, postcranial skeleton.
Remarks. Some authors have considered Pistosaurus as a member of the Plesiosauria (e.g. White, 1940, p. 459). Rieppel (2000) presents a concise summary of the unusual history of this genus. A cast of the holotype skull was investigated first hand (SMNS ‘uncatalogued') ***

## Augustasaurus hagdorni Sander, Rieppel and Bucher, 1997

Type material: Holotype: FMNH PR 1974, complete skull and mandible, post-cranial skeleton consisting of posterior neck vertebrae, pectoral girdle, majority of forelimbs, dorsal vertebrae and associated fragmentary ribs and gastralia.
Type locality: Pershing County, Nevada, USA.
Type horizon: Fossil Hill Member, Farvet Formation, Star Peak Group, Rotelliformis Zone, Late Anisian, Middle Triassic.

Remarks: The postcranium of A. hagdorni is described by Sander et al. (1997) and the cranium is described by Rieppel et al. (2002). This taxon has important implications because it is only the second non-plesiosaurian sauropterygian to be discovered in the New World; Corosaurus alcovensis was the first (Storrs, 1991).

## Yunguisaurus liae Cheng, Sato, Wu and Li, 2006

Type material: NMNS 004529/F003862, almost complete articulated specimen missing the distal portion of the tail.

Type Locality: Near Huangnihe River, Chajiang, 10km northwest of Xingyi, Guizhu. Type Horizon: Falang Formation, Carnian (early Late Triassic).

Remarks: The skull and limbs of Yunguisaurus were described by Cheng et al. (2006) but "the postcranial skeleton waits for further preparation and subsequent full description" (p.501). Consequently, some characters, presumably preserved but not described or figured for this taxon, could not be coded in this cladistic analysis; this is taken into account in the discussion (Chapter 6).

## Plesiosaurus dolichodeirus Conybeare, 1824

Type material. BMNH 22656, complete skeleton. ***
Type locality. Lyme Regis, Dorset, England.
Type horizon. Black Ven Marl Formation, Lower Lias Group, (Echioceras
raricostatum Zone), (Uppermost Sinemurian, Lower Jurassic).
Referred material. NMING F8758 ***
Remarks. This genus was described by Owen (1865) and extensively revised by Storrs (1997).

Hydrorion brachypterygius (Huene, 1923) Grossman, 2007
Type material. GPIT/477/1/1; complete skeleton including skull. Type locality. Steinbruch 29, Ohmden (near Holzmaden), Baden-Württemberg, Germany.

Type horizon. Lias epsilon II, 4 (Unterer Schiefer), Posidonienschiefer, (Harpoceras falcifer zone), (Lower Toarcian, Lower Jurassic).
Referred material. MB.R. 1991, SMNS 51143.
Remarks. The holotype skull is described by Maisch and Rucklin (2000) as
Plesiosaurus brachypterygius; Grossman $(2006,2007)$ redescribed the material pertaining to this taxon and introduced the new genus name Hydrorion.

## Seeleysaurus guilelmiimperatoris (Dames, 1895) Grossman, 2007

Type material. MB R.1992, complete skeleton.
Type locality. Holzmaden, Baden-Württemberg, Germany.
Type horizon. Lias Epsilon II, 4 (Unterer Schiefer), Posidonienschiefer, (Harpoceras falciferum zone), (Lower Toarcian, Lower Jurassic).
Referred material. SMNS 16812, more or less complete skeleton ***, SMNS 12039, (specimen figured by Fraas [1910]).
Remarks. Dames (1895) and Fraas (1910) described this taxon. This species was renamed 'Seeleysaurus' by White, (1940). Storrs (1997) modified Persson's (1963) suggestion that Plesiosaurus contains only three valid species by proposing $P$. brachypterygius as a junior synonym of $P$. guilielmiimperatoris, reducing the number
to two. However, Maisch and Rucklin (2000, p. 38) justify retention of $P$. brachypterygius. Some workers (Bakker, 1993) have retained the name
'Seeleyosaurus' for P. guilielmiimperatoris and recently, Grossman (2007) formalised this taxonomy.
O'Keefe (2004b) erected a new genus and species name for SMNS 16812
(Plesiopterys wildii), but the specimen was later regarded as a juvenile Seeleysaurus guile/miimperatoris (Grossman, 2007).

## 'Plesiosaurus’ longirostris Tate and Blake, 1876

Type material: MCZ 1033 (in the collection of fossil reptiles and amphibians), damaged skull, 85 vertebrae and 4 limbs.

Type locality: Whitby, Yorkshire, England.
Type horizon: Alum Shale, Upper Lias, serpentinus ammonite zone, Toarcian, Lower Jurassic.
Referred material: MM 8004, skull and associated skeleton.
Remarks: 'Plesiosaurus' longirostris has an extremely confusing taxonomic history, complicated by the perplexing history of the type material. White (1940) included the species 'Plesiosaurus' longirostris in the genus Macroplata (see below). Other authors have placed it in Rhomaleosaurus (Broadhurst and Duffy, 1970). However, even after superficial examination, it is clear that Plesiosaurus 'Iongirostris' is far removed morphologically from both Rhomaleosaurus and Macroplata, not least in the extreme elongation of the rostrum (pers. obs.). O'Keefe (2004b) contended the placement of the species longirostris in Macroplata (see Chapter 3). Plesiosaurus longirostris may be far more abundant than previously recognised: another contemporary taxon, Sthenarosaurus dawkinsi (see below), may also pertain to the species longirostris (R. Forrest pers. comm., 2005). Even Watson (1909), in his original description of Sthenarosaurus, suggested the possibility that the type of $S$. dawkinsi was congeneric with 'Plesiosaurus’ longirostris. This cladistic analysis will test this contention.

## Sthenarosaurus dawkinsi Watson, 1909

Type material. MM L8023, a partial postcranial skeleton including both girdles, propodials, and vertebrae.
Type locality. Saltwick, Yorkshire, UK.
Type horizon. Upper Lias (D. commune zone) (Toarcian, Lower Jurassic)
Remarks. Sthenarosaurus was described and figured by Watson (1909), no cranial material has been referred to this taxon.

## Maresaurus coccai Gasparini, 1997

Type material: MOZ 4386 V Museo Prof. Olsacher, Zapala, Neuquén, articulated skull and mandible, atlas-axis and first cervical vertebrae.
Type locality: Chacaico Sur, ( $39^{\circ} 15^{\prime} \mathrm{S}, 70^{\circ} 18^{\prime} \mathrm{W}$ ), 70 km southwest of Zapala, Neuquén Province, Argentina.
Type horizon: Upper part of the Los Molles Formation, Cuyo Group, Emileia giebeli and Emileia multiformis subzone, Lower Bajocian, Middle Jurassic.
Remarks: Diagnosed as a pliosaurid under the current limitations of poor understanding of pliosaur phylogeny. Noè (2001) suggests that this may by a junior synonym of Simolestes. The cladistic analysis presented here will test this contention.

## Hauffiosaurus zanoni O’Keefe, 2001 ***

Type material: HAUFF 'Uncatalogued', complete skeleton on display in the UrweltMuseum Hauff.
Type locality: Holzmaden, Germany.
Type horizon: Posidonien-schiefer, Toarcian, Lower Jurassic
Remarks: O'Keefe (2001a) briefly described this specimen and proposed the new taxon name.

## Brachauchenius lucasi Williston, 1903

Type material: USNM 4989, skull and mandible (palatal view) plus 37 ribs and associated vertebrae.

Type locality: Ottawa County, Kansas, USA.
Type horizon: Greenhorn Limestone, Turonian, Late Cretaceous.
Referred material: USNM 2361, skull and vertebrae; FMNH VP321, compete skull. Remarks: This taxon is described by Williston (1903) and was reviewed by Carpenter (1996).

## Kronosaurus queenslandicus Longman, 1924

Type material: Queensland Museum (unspecified)
Type locality: Army Downs, north of Richmond, Queensland, Australia.
Type horizon: Aptian-Albian
Referred material: MCZ 1284, 1285.

Remarks: The skull of Kronosaurus queenslandicus was described by White (1935) and the postcranium by Romer and Lewis (1959). The genus Kronosaurus is currently under revision (C. McHenry, pers. comm., 2003).

## Simolestes vorax Andrews, 1909

Type material: BMNH R.3319, complete skeleton. ***
Type locality: Peterborough, England.
Type horizon: Lower Oxford Clay, Callovian, Middle Jurassic Referred material: PETMG R296.
Remarks: Simolestes was described by Andrews (1913) based on the holotype. The most recent treatments of Simolestes are unpublished - Noè (2001) thoroughly described the holotype skull and also referred a second skull to this taxon (PETMG R296) originally discovered in 1990 and identified as Liopleurodon (Dawn, 1991).

## Liopleurodon ferox Sauvage, 1873

Type material: BMNH R.3536, a single tooth (but see below).
Type locality: Wast, Boulogne, France.
Type horizon: Callovian, Middle Jurassic.
Referred material: Associated skeleton (also BMNH R.3536), "the teeth of which are indistinguishable from the type" (Tarlo, 1960, p.166) and BMNH R. 2680 and GPIT 1754/2 (O'Keefe, 2001a). ***
Remarks: The skull of Liopleurodon ferox has been described by Andrews (1913). L. pachydeirus, also from the Callovian (Tarlo, 1960), has been recently recognised as a junior synonym of $L$. ferox (Noè, 2001). Noè et al. (2003) recently described the exoccipital-opisthotic bone in this taxon. According to Noè et al. (2004), the species Liopleurodon macromerus should be assigned to Pliosaurus.

## Peloneustes philarchus (Seeley, 1869) Lydekker, 1889a

Type material: CAMSM J.46913, almost complete skeleton.
Type locality: Peterborough, England.
Type horizon: Oxford Clay, Callovian, Upper Jurassic
Referred material. SMNS 10113 (***) $^{* *}$
Remarks: Peloneustes has been described by Lydekker (1889) and Andrews (1895, 1910b and 1913). According to Martill (1991), Peloneustes is often difficult to distinguish from Pliosaurus and some species may possibly be congeneric. Peloneustes is currently under revision by H. Ketchum (H. Ketchum, pers. comm., 2006).

## Pliosaurus Owen, 1841 (Owen, 1842)

Type material: P. brachydeirus OXFUM J. 9245 A.B., "teeth, lower and upper jaws, vertebral column, femur, tibia and fibula" (Tarlo, 1960, p. 152).
Type locality: Market Rasen, Lincolnshire, England.
Type horizon: Kimmeridge Clay, Kimmeridgian, Upper Jurassic.
Referred material: BRSMG Cc332 (***), P. brachyspondylus, the 'Westbury Pliosaur' (Taylor and Cruickshank, 1993). Almost complete skull and mandible, some associated cervical vertebrae, phalanges and a rib.

Remarks: I have refrained from including both Kimmeridgian species of Pliosaurus because few characters separate them, many of questionable validity (Taylor and Cruickshank, 1993). However the type specimens of $P$. brachyspondylus and $P$. brachydeirus are complementary and, combined, allow a greater degree of resolution for the genus. Accordingly, I have coded Pliosaurus to genus level only, albeit discounting characters of the Callovian species $P$. andrewsi, which is omitted from the analysis (see table 1). The coding for Pliosaurus can therefore be regarded as follows: P. brachydeirus + P. brachyspondylus $-P$. andrewsi. The genus Pliosaurus was described by Owen (e.g. 1869) and Tarlo (e.g. 1960).

## TMP 94.122.01

Type material: TMP 94.122.01, complete skeleton including the skull.
Type locality: Syncrude Canada Ltd. oil sand mine (Mildred Lake site), 30km northeast of Fort McMurray, Athebasca Oil Sands Area of northeastern Alberta, Canada.

Type horizon: Wabiskaw Member, Clearwater Formation, (Lower Albian, Lower Cretaceous).
Remarks: TMP 94.122.01 represents a distinct but as yet un-named taxon (Druckenmiller, 2006ab). A detailed unpublished description of this taxon is provided by Druckenmiller (2006a).

## Umoonasaurus demoscyllus Kear, Schroeder and Lee, 2006

Type material: AM F99374, quite complete opalised skeleton including the skull. Type locality: Zorba Extension Opal Field, west of Coober Pedy, northern South Australia.

Type horizon: Bulldog Shale (Maree Subgroup) (Lower Aptian-Lower Albian, Lower Cretaceous).

Remarks: Umoonasaurus was briefly described and named by Kear et al. (2006). This plesiosaur was formally known as 'Eric' the pliosaur.

## Leptocleidus superstes Andrews, 1922a

Type material: BMNH R. 4828 (***), incomplete skull.
Type locality: Berwick, Sussex, England.
Type horizon: Barremian, Lower Cretaceous
Remarks: The holotype of Leptocleidus superstes (also the holotype of the genus) is a partial skull and vertebral column associated with a complete pectoral girdle and partial limbs, from the Lower Cretaceous Upper Weald Clay (Barremian?) of Sussex, UK. BMNH R4828 was described and figured by Andrews (1922a). Leptocleidus superstes is omitted from the morphometric analysis because it is so far removed stratigraphically form the other taxa included, and it has already been well distinguished as a separate taxon based on discreet characteristics. Species referred to this genus are also known from South Africa and Australia (see below), making Leptocleidus one of the most widespread genera of plesiosaur.

## Leptocleidus capensis (Andrews, 1911) Cruickshank, 1997.

Type material: SAM-K5822, skull.
Type locality: Zwartkops River Valley, Algoa Basin, South Africa.
Type horizon: Sundays River Formation, (Upper Valanginian, Lower Cretaceous)
Remarks: This specimen was originally described and named 'Plesiosaurus capensis' by Andrews (1911). It was later redescribed and refigured by Cruickshank (1997) who referred it the genus Leptocleidus.

## Leptocleidus clemai Cruickshank and Long, 1997

Type Material: WAM 92.8.1-1 to 60, a partial postcranial skeleton.
Type locality: Kalbarri region, Western Australia.
Type horizon: Birdrong Sandstone (Hauterivian-Barremian, Early Cretaceous)
Remarks: Leptocleidus clemai is described by Cruickshank and Long (1997) and represents one of three species of the genus Leptocleidus.

## Dolichorhynchops osborni Williston, 1903

Type material: KUVP 1300, almost complete skeleton.
Type locality: Logan County, Kansas, USA.
Type horizon: Niobrara Formation, Cenomanian, Late Cretaceous
Referred material: MCZ 1064, FHSM VP404.

Remarks: Dolichorhynchops osborni has been thoroughly described by Williston (1903), Carpenter $(1996,1997)$ and O'Keefe $(2004 a)$. This taxon is included as a representative polycotylid taxon to test whether polycotylids are plesiosauroids (as endorsed by Carpenter, 1997 and O’Keefe, 2001a) or pliosauroids (as endorsed by Druckenmiller, 2006ab).

## Appendix 3. Anatomical abbreviations

1-4 - distal carpals 1-4
Ang - angular
Ar - articular
Bo - basioccipital
Bs - basisphenoid
C - coronoid
Cc - central cavity
Co - coracoid
D - dentary
Ect - ectopterygoid
Ep - epipterygoid
Ex - external naris
Exop - exoccipital-opisthotic
F - frontal
Fe - femur
Fi - fibula
H - humerus
Ic - interclavicle
In - intermedium
Int - internal nares
Is - ischium
i-v - metacarpals i-v
$J$ - jugal
M - maxilla
Mc - maxillary cavity
Oc - occipital condyle
Or - orbit
P - parietal
Par - parasphenoid
Pal - palatine
Pin - pineal foramen
Pm - premaxilla
Po - postorbital
Poc - paraoccipital process
Pof - postfrontal
Pre - prearticular
Prf - prefrontal
Pt - pterygoid
Pu - pubis

Q - quadrate
Qp - quadrate-pterygoid flange
R - radius
Ra - radiale
Rbs - ribs
Sa - surangular
Sc - scapula
Soc - supraoccipital
Sp - splenial
Sq - squamosal
St - stapes (hyoid)
T- tibia
Ta - tooth alveoli
Tem - temporal fenestra
U-ulna
UI - ulnare
V - vomer

## Appendix 4. Morphometric data

(all measurements in cm)

| （8LヤてI SNWS）ıOłכ！＾＇प｜ | $\|\stackrel{\mathrm{n}}{\mathrm{~m}}\|$ |  | ｜r｜r |  |  | ｜ñ |  |  |  |  | N | ｜n | $\left\|\begin{array}{c} \vec{m} \\ \dot{e} \end{array}\right\|$ | $\left\|\begin{array}{c} n \\ \infty \\ i \end{array}\right\|$ | $\stackrel{\rightharpoonup}{\text { a }}$ |  | ¢ | ¢ |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\stackrel{\infty}{+}$ | $\left\|\begin{array}{c} n \\ \underset{\sim}{n} \\ \sim \end{array}\right\|$ | $\underset{N}{n}$ | $\stackrel{m}{m}$ | $\left\|\begin{array}{l} n \\ \underset{N}{n} \end{array}\right\|$ | $\cdots$ | $\sim$ | $\sim$ | $\begin{aligned} & \hat{N} \\ & 0 \\ & 0 \end{aligned}$ | $\stackrel{\sim}{\sim}$ | 이긴 | $\|\stackrel{n}{n}\|$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\cdots$ | $\sim$ | $\underset{\sim}{n}$ | N |
| （＊8L0Z HNWの）uoכeıpo！sseןeyı | $\left\|\begin{array}{\|c\|} \hline 0 \\ 1 \end{array}\right\|$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | ～ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | ～ | $\cdots$ | $\sim$ | $\sim$ |
| pənбоןеұеวun 97＊H | $\sim$ |  |  |  | $\underset{\sim}{\sim}$ |  |  |  |  |  |  |  | $\left\|\begin{array}{c} \mathbf{9} \\ \mathbf{0} \end{array}\right\|$ | $\left\|\begin{array}{c} \mathbf{r} \\ \vec{r} \end{array}\right\|$ | $\left\|\begin{array}{c} \mathbf{N} \\ \vec{r} \end{array}\right\|$ | $\stackrel{\rightharpoonup}{\boldsymbol{r}}$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ |
| Z0Z6ヶ HNW8 | $\begin{aligned} & \stackrel{i n}{0} \\ & \underset{N}{2} \end{aligned}$ | $\left\lvert\, \begin{aligned} & \infty \\ & \dot{n} \\ & \underset{1}{2} \end{aligned}\right.$ | $\stackrel{0}{\circ}$ | $\left\|\begin{array}{c} \underset{\sim}{i} \\ \underset{\sim}{2} \end{array}\right\|$ | $\left\|\begin{array}{c} \underset{\sim}{\underset{~}{\sim}} \end{array}\right\|$ | $\left\|\begin{array}{\|c\|} \hline \stackrel{\rightharpoonup}{i} \end{array}\right\|$ | $\frac{\square}{\square}$ | $\frac{\square}{2}$ | $\hat{\dot{f}}$ | $\stackrel{\sim}{c}$ | $\left.\begin{array}{\|c\|} \infty \\ \dot{0} \end{array} \right\rvert\,$ | $\begin{gathered} N \\ 0 \\ 0 \end{gathered}$ | $\left\lvert\, \begin{gathered} \mathrm{N} \\ \underset{n}{n} \end{gathered}\right.$ | $\left\|\begin{array}{c} n \\ \underset{\sim}{2} \end{array}\right\|$ | N | $\stackrel{\sigma}{\triangle}$ | $\left\|\begin{array}{l} \infty \\ 0 \\ \underset{N}{2} \end{array}\right\|$ | $\left\lvert\, \begin{gathered} n \\ \underset{\sim}{i} \\ \underset{\sim}{2} \end{gathered}\right.$ | $\begin{gathered} N \\ \cdots \\ \sigma \end{gathered}$ | $\left.\begin{array}{\|c} n \\ \dot{0} \end{array} \right\rvert\,$ | $\stackrel{\square}{6}$ |
|  | $\begin{aligned} & \underset{\sim}{n} \\ & \underset{N}{2} \end{aligned}$ | $\begin{gathered} N \\ \underset{\sim}{N} \\ \hline \end{gathered}$ | の | $\sim$ | $\left\|\begin{array}{c} 10 \\ 0 \\ -1 \end{array}\right\|$ | 넹 | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\sim}{\square}$ | $\sim$ | $\left\|\begin{array}{c} n \\ \hat{0} \\ 0 \end{array}\right\|$ | $\sim$ | $\cdots$ | $\begin{aligned} & \infty \\ & m \\ & m \end{aligned}$ | $\left\|\begin{array}{c} \underset{\sim}{m} \\ \dot{m} \end{array}\right\|$ | $\stackrel{\square}{\text { m }}$ |
| （88ャG¢ HNWG）ełeןdoıכew | －1 | $\left\lvert\, \begin{aligned} & \stackrel{\sim}{7} \\ & \underset{\sim}{2} \end{aligned}\right.$ | $\stackrel{n}{N}$ | － | N | $\left\|\begin{array}{c} \underset{r}{\prime} \\ \dot{r} \end{array}\right\|$ | $\frac{\square}{c}$ | $\frac{\sim}{x}$ | $\sim$ | $\stackrel{\pi}{\perp}$ | $\begin{aligned} & \infty \\ & \underset{\sim}{\infty} \end{aligned}$ | $\left\|\begin{array}{c} \infty \\ -1 \end{array}\right\|$ | $\begin{aligned} & n \\ & \infty \\ & \infty \end{aligned}$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\left\|\begin{array}{c} i n \\ i n \end{array}\right\|$ | $\underset{i}{+}$ | $\stackrel{\sim}{\sim}$ | N |
|  | $\begin{aligned} & N \\ & \text { Ni } \\ & \text { in } \end{aligned}$ |  | $\underset{\sim}{\underset{\sim}{2}}$ | $\left\|\begin{array}{l} n \\ \underset{m}{n} \end{array}\right\|$ | $\mid \underset{N}{2}$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\pi}{\perp}$ | $0$ | $\sim$ | $\left\|\begin{array}{c} n \\ \vdots \end{array}\right\|$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\cdots$ | $\left\|\begin{array}{c} \varphi \\ m \end{array}\right\|$ | $\left. \right\rvert\,$ | $\stackrel{\sim}{\square}$ |
| 6ヵL8」 9 NIWN | N | $\left\|\begin{array}{l} n \\ \dot{m} \end{array}\right\|$ | m | $\mid \widehat{\gamma}$ | $\left.\begin{array}{\|l\|} \mathbf{n} \\ \mathrm{n} \\ \mathrm{~m} \end{array} \right\rvert\,$ | ＊I | $\sim$ | $\frac{\pi}{x}$ | $\sim$ | $\stackrel{c}{\sim}$ | $\stackrel{1}{\square}$ | $\left\|\begin{array}{c} n \\ \underset{N}{n} \end{array}\right\|$ | $\stackrel{\square}{1}$ | $\mid \vec{i}$ | $\begin{array}{\|c} \hline \mathrm{N} \\ \mathrm{ri} \end{array}$ | $\sim$ | ＊ | $\underset{\sim}{\circ}$ | al | $\left\|\begin{array}{c} 0 \\ \underset{\sim}{\mathrm{j}} \end{array}\right\|$ | $\sim$ |
|  | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ |
| SL80IS SWY甘M | $\mid \underset{\|c\|}{\|c\|}$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ |
| ち6L0L」 9NIWN | $\widehat{\circ}$ | $\begin{gathered} \underset{\sim}{n} \\ \stackrel{m}{2} \end{gathered}$ | へ | $\stackrel{\sim}{\gamma} \mid$ | $\left\|\begin{array}{l} n \\ \underset{m}{2} \end{array}\right\|$ | $\begin{aligned} & \hat{a} \\ & \dot{m} \end{aligned}$ | $\frac{\square}{\square}$ | $\stackrel{\pi}{c}$ | $\begin{aligned} & n \\ & m \\ & \hline \end{aligned}$ | $\stackrel{\sim}{\sim}$ | $\begin{aligned} & 0 \\ & m \\ & -1 \end{aligned}$ | $9$ | $\begin{aligned} & \infty \\ & \infty \\ & \infty \end{aligned}$ | $\begin{gathered} \mathrm{N} \\ \mathrm{~m} \end{gathered}$ | $\begin{gathered} \vec{r} \\ \overrightarrow{-i} \end{gathered}$ | $\begin{gathered} n \\ i \\ i \end{gathered}$ | － | $\begin{array}{\|c\|} \hat{m} \\ \mathbf{m} \end{array}$ | $\underset{\sim}{N}$ | $\left.\begin{array}{\|c\|} \hline n \\ m \\ \sim \end{array} \right\rvert\,$ | $\pm$ |
|  | $\underset{6}{\mathrm{n}}$ | $\left.\begin{aligned} & \mathbf{n} \\ & \dot{e} \\ & \mathbf{m} \end{aligned} \right\rvert\,$ | へ | $\left\lvert\, \begin{gathered} \operatorname{n} \\ \underset{\gamma}{n} \end{gathered}\right.$ | $\begin{aligned} & \mathrm{m} \\ & \mathrm{~m} \end{aligned}$ | $\begin{array}{\|c\|} \underset{\sim}{\sim} \\ \underset{y}{2} \end{array}$ |  |  | $\underset{\underset{N}{N}}{\substack{n}}$ |  | $\left\|\begin{array}{l} \infty \\ m \\ r \end{array}\right\|$ | $\begin{aligned} & n \\ & \underset{\sim}{n} \\ & \hline \end{aligned}$ | $\left.\begin{aligned} & \infty \\ & \infty \\ & \infty \end{aligned} \right\rvert\,$ | $\left.\begin{aligned} & \hat{o} \\ & \dot{m} \end{aligned} \right\rvert\,$ | $\begin{gathered} n \\ n \\ i \end{gathered}$ | $\stackrel{N}{N}$ | $\begin{array}{\|c\|} \hline \underset{\sim}{N} \\ \dot{\sim} \end{array}$ | $\stackrel{\sim}{*}$ | al | $\begin{array}{\|c\|} \hline \infty \\ \sigma^{\prime} \end{array}$ | N |
|  | $\left\|\begin{array}{\|c\|} \mathbf{\omega} \end{array}\right\|$ | $\|\mathrm{m}\|$ | $\stackrel{n}{n}$ | $\cdots$ | $\underset{N}{2}$ | $\left\|\begin{array}{c} \stackrel{\sim}{N} \\ \underset{m}{2} \end{array}\right\|$ | $\stackrel{\widetilde{0}}{\square}$ | $\stackrel{\pi}{\square}$ | $\sim$ | $\stackrel{\tau}{\square}$ | $\begin{aligned} & \mathrm{r} \\ & \hline \end{aligned}$ | $\left.\begin{array}{\|c\|} \hline \stackrel{n}{0} \\ \dot{1} \end{array} \right\rvert\,$ | $\overrightarrow{-}$ | $\left\|\begin{array}{l} \underset{0}{\hat{N}} \\ \mathbf{N} \end{array}\right\|$ | $\left\|\begin{array}{l} N \\ \underset{\sim}{N} \end{array}\right\|$ | $\left\lvert\, \begin{gathered} N \\ \\ -1 \end{gathered}\right.$ | $\left\|\begin{array}{l} \vec{\lambda} \\ \underset{i}{2} \end{array}\right\|$ | $\left\lvert\, \begin{gathered} \underset{\sim}{N} \\ \underset{\sim}{2} \end{gathered}\right.$ | $\sim$ | $\sim$ | $\sim$ |
| （S＇LS8 WM）snnbu！doıd＇y | \|in | m | $\begin{aligned} & \underset{\sim}{n} \\ & \underset{N}{2} \end{aligned}$ | $\left\lvert\, \begin{gathered} n \\ \stackrel{n}{m} \end{gathered}\right.$ | $\stackrel{N}{N}$ | $\left.\begin{array}{\|c\|} \hline m \\ \dot{n} \end{array} \right\rvert\,$ | $\left\|\begin{array}{l} \underset{\sim}{\sim} \\ \underset{\sim}{n} \end{array}\right\|$ | ค | $\underset{m}{9}$ |  |  |  |  | $\begin{aligned} & n \\ & m \\ & m \end{aligned}$ | $\begin{aligned} & 9 \\ & i \\ & i \end{aligned}$ | $\vec{i}$ | $\begin{array}{\|l\|} \infty \\ m \\ m \end{array}$ | $\left\|\begin{array}{l} \vec{m} \\ \dot{m} \end{array}\right\|$ | $\stackrel{r}{i}$ | $\begin{array}{\|c} \hline 0 \\ -1 \end{array}$ | $\sim$ |
|  | $\stackrel{n}{n}$ | $\mid \vec{\nabla}$ | $\stackrel{N}{N}$ | $\hat{\forall}$ | $\left.\begin{aligned} & n \\ & \stackrel{n}{\dot{m}} \end{aligned} \right\rvert\,$ | $\left\lvert\,\right.$ | $\left.\begin{aligned} & N \\ & \underset{\sim}{N} \\ & \underset{N}{2} \end{aligned} \right\rvert\,$ | $\left.\begin{array}{\|c\|} \hline n \\ m \end{array} \right\rvert\,$ | $0 \begin{aligned} & n \\ & m \\ & \hline \end{aligned}$ | $\checkmark$ | $\begin{aligned} & n \\ & \underset{r}{n} \\ & \hline \end{aligned}$ | $\stackrel{\sim}{N}$ | $\xrightarrow{\sim}$ | － | $\begin{aligned} & 9 \\ & i \\ & i \end{aligned}$ | N | $\left\lvert\, \begin{array}{\|c\|} \hline \underset{\sim}{*} \end{array}\right.$ | $$ | $\begin{aligned} & n \\ & \infty \\ & \infty \end{aligned}$ | －1 | $\cdots$ |
| （عऽ8ャ¢ HNWg）！uołua0પ7＇y | N | $\cdots$ | $\stackrel{\mathrm{n}}{\mathrm{m}}$ | $\cdots$ | $\stackrel{\sim}{\sim}$ | ＊ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\left.\begin{aligned} & n \\ & 0 \\ & 0 \\ & -1 \end{aligned} \right\rvert\,$ |  | $\begin{aligned} & \infty \\ & \dot{0} \\ & \dot{-} \end{aligned}$ | $\begin{array}{\|c\|} \hline \stackrel{n}{\dot{\sigma}} \end{array}$ | $\left.\begin{gathered} 0 \\ i \\ i \end{gathered} \right\rvert\,$ | $\sim$ | $\cdots$ | 01 | $\cdots$ | $\stackrel{\infty}{\sim}$ | n |
|  | $\infty$ | $\begin{aligned} & \underset{\sim}{n} \\ & \underset{\sim}{2} \end{aligned}$ | $\begin{aligned} & n \\ & 0 \\ & m \end{aligned}$ | $\left.\begin{aligned} & n \\ & n \\ & n \\ & n \end{aligned} \right\rvert\,$ | － | N | $\stackrel{+}{\mathrm{m}}$ | $\checkmark$ | $\underset{\sim}{\infty}$ | $\begin{gathered} N \\ r- \end{gathered}$ | $\xrightarrow{-7}$ | $\stackrel{\circ}{\sim}$ | $$ | ～ | $\begin{aligned} & 9 \\ & i \end{aligned}$ | $\stackrel{N}{\mathrm{~N}}$ | $\left.\begin{gathered} \underset{\sim}{n} \\ \dot{n} \end{gathered} \right\rvert\,$ | $\left.\begin{gathered} n \\ \dot{n} \end{gathered} \right\rvert\,$ | $\left\|\begin{array}{c} n \\ n \\ r \end{array}\right\|$ |  | $\stackrel{n}{n}$ |
|  |  |  |  |  |  |  |  |  |  |  | Snout tip to maxilla（lateral） |  |  | length of external nares |  | $\begin{aligned} & 0 \\ & \frac{0}{0} \\ & -\frac{0}{5} \end{aligned}$ |  |  | Width between orbits |  | 促 |
|  | ＜ | $\infty$ |  | $\bigcirc$ | 山 | － | $\bigcirc$ |  |  |  | V |  | $\Sigma$ | 2 | $\bigcirc$ |  |  |  | い |  | $\bigcirc$ |


| 8LヤてI SNWS |  | $\sim$ | $\left\|\begin{array}{c} \mathrm{n} \\ \stackrel{N}{\mathrm{~m}} \end{array}\right\|$ | $\left\lvert\,\right.$ | $\begin{array}{\|c\|} \hat{0} \\ \underset{i}{i} \end{array}$ | $\left.\begin{array}{\|l\|} \hline- \\ 0 \\ n \\ \cdots \end{array} \right\rvert\,$ | 1 <br> $\vdots$ <br> $\vdots$ <br> 1 | $\cdots$ |  | $\begin{array}{l\|l} \hline \Omega \\ \underset{N}{N} & \stackrel{n}{n} \\ \hline \end{array}$ | $$ |  | $\begin{array}{l\|l} \hline 0 \\ \stackrel{1}{2} \\ i & \text { c } \end{array}$ | $\begin{aligned} & \hat{O} \\ & \dot{N} \end{aligned}$ | $\begin{array}{\|l\|l} \hline \begin{array}{l} 0 \\ 0 \\ 0 \\ i \end{array} \\ i \end{array}$ | ｜ris | O |  | $\stackrel{\sim}{\square}$ | － $\begin{aligned} & n \\ & 0 \\ & \sim\end{aligned}$ | $\stackrel{\sim}{\sim}$ | $\left\lvert\, \begin{aligned} & \stackrel{\sim}{\sim} \\ & \infty \\ & \infty\end{aligned}\right.$ |  | － |  | ｜ron | $\stackrel{\sim}{m}$ | $\stackrel{\sim}{\infty}$ |  | ｜r｜rorn | $\bigcirc$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 6عદโप HNWg | $\left\|\begin{array}{c} n \\ \vdots \end{array}\right\|$ | $\left\|\begin{array}{l} 1 \\ 0 \\ 0 \end{array}\right\|$ | $\sim$ | $\cdots$ | $\sim$ | － | $\cdots$ | $\begin{aligned} & \hline \stackrel{n}{\dot{子}} \\ & \underset{\sim}{2} \end{aligned}$ |  | $\sim \cdot$ | $\sim$ | $\sim$ | $\sim$ | ～ | $\sim$ | $\sim$ | $\sim$ | $\checkmark$ | กิ｜ |  |  | $\xrightarrow{\sim}$ |  |  |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ |
| ＊8โ0Z HNWg | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim \sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ |  | $\begin{aligned} & \stackrel{1}{\infty} \\ & \infty \\ & \sim \end{aligned}$ | $\left.\begin{aligned} & -1 \\ & 0 \\ & m \end{aligned} \right\rvert\,$ | $\underset{\sim}{n}$ | $\begin{aligned} & \infty \\ & \infty \\ & m \end{aligned}$ |  | $\left.\begin{array}{\|c\|} \infty \\ \underset{\sim}{\infty} \\ \dot{-} \end{array} \right\rvert\,$ |  | － | $\stackrel{\square}{4}$ | $\left\|\begin{array}{c} n \\ \underset{N}{n} \end{array}\right\|$ | $\left.\begin{aligned} & \mathrm{n} \\ & 0 \\ & \mathrm{n} \end{aligned} \right\rvert\,$ | $\stackrel{\sim}{\sim}$ | $\stackrel{\sim}{N}$ |
| 97＊H | $\sim$ | $\sim$ | $\cdots$ | $\left\|\begin{array}{c} n \\ \omega^{\prime} \end{array}\right\|^{\sim}$ |  | $\|\mathbf{N}\|$ | $\cdots$ | $\sim$ |  | $\sim \sim$ | $\sim$ | $\sim$ |  | $\stackrel{\stackrel{n}{\boldsymbol{r}}}{ }$ | $\cdots$ | $\sim$ | $\sim$ | $\pm$ |  | $\left\|\begin{array}{l} \infty \\ \dot{\boldsymbol{f}} \end{array}\right\|$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | － |
| Z026t HNWG | $\left\|\begin{array}{r} + \\ i \\ i \end{array}\right\|$ | $\left.\begin{array}{\|c\|} \hline-r \\ i n \end{array} \right\rvert\,$ | $\left\|\begin{array}{l} n \\ \infty \\ m \end{array}\right\|$ | $\begin{array}{\|l\|l} \hline \ln \\ \underset{1}{1} \\ \stackrel{n}{n} & \infty \end{array}$ | $\begin{array}{\|c\|} \hline \\ \infty \\ \hline \end{array}$ | $\begin{array}{\|c\|} \hline \\ 0 \\ \dot{r} \end{array}$ | $\left\|\begin{array}{c} n \\ n \\ n \\ r \end{array}\right\|$ | $\left\lvert\, \begin{aligned} & \infty \\ & \stackrel{+}{\circ} \\ & \stackrel{1}{2} \end{aligned}\right.$ |  | $\sim$ | $\underset{\sim}{\mathrm{N}} \underset{\sim}{+}$ |  | $\stackrel{0}{0} \underset{\sim}{n}$ | $\begin{array}{\|c} \stackrel{N}{N} \\ \underset{i}{2} \end{array}$ | $\left\lvert\, \begin{array}{l\|l} \stackrel{n}{\Omega} \\ \stackrel{N}{N} \\ c \end{array}\right.$ | $\begin{array}{\|c\|} \hline \left.\begin{array}{l} 0 \\ m \\ \hline \end{array} \right\rvert\, \end{array}$ | $\left.\begin{array}{\|c\|} \infty \\ n \\ m \end{array} \right\rvert\,$ | $\cdots$ | $\begin{aligned} & n \\ & \infty \\ & \infty \end{aligned}$ | $\begin{aligned} & N \\ & \infty \\ & 0 \end{aligned}$ | $\mathfrak{N}$ | $\begin{aligned} & 9 \\ & 0 \end{aligned}$ | $\sim$ | $\begin{array}{\|c} \stackrel{n}{2} \\ \stackrel{\rightharpoonup}{r} \end{array}$ |  | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ |
| 9عદโप HNWg | $\sim$ | $\begin{array}{\|c} \hline \stackrel{m}{i} \\ i \end{array}$ | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ |  | $\sim \sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\infty}{\infty}$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ |
| 88ャG¢ HNWg | $\stackrel{n}{n}$ | $\stackrel{\sim}{N}$ | $\begin{aligned} & m \\ & \infty \\ & \infty \end{aligned}$ | $\stackrel{\sim}{\sim}$ | $\stackrel{\square}{\square}$ | \|잇| | $\stackrel{\sim}{N}$ | N |  | $\stackrel{\sim}{\dot{\circ}} \underset{\sim}{\sim}$ | $\cdots \cdot \left\lvert\, \begin{aligned} & \underline{m} \\ & m \end{aligned}\right.$ | $\begin{array}{l\|l} \hline 0 \\ m \end{array}$ | $\cdots$ | $\sim$ | $\begin{aligned} & m \\ & m \\ & \hline \end{aligned}$ | $\left.\begin{array}{\|c\|} \hline n \\ \dot{n} \end{array} \right\rvert\,$ | $\begin{array}{\|c} \underset{N}{N} \\ i \end{array}$ |  | $\bigcirc$ | $\begin{gathered} N \\ \sigma \end{gathered}$ | © | $\begin{aligned} & \underset{\sim}{9} \\ & \underset{-1}{ } \end{aligned}$ |  | $\left.\begin{gathered} \stackrel{N}{n} \\ \stackrel{n}{\sim} \end{gathered} \right\rvert\,$ |  | $\begin{array}{\|c} \hline m \\ 0 \\ i n \end{array}$ | $\stackrel{\sim}{4}$ | $\stackrel{\sim}{2}$ | ก |  | ก |
| ¢Z¢8E HNWG | 0 | $\left\lvert\, \begin{gathered} \underset{i}{\mid} \\ i \end{gathered}\right.$ | $\sim$ | $$ | $\begin{gathered} n \\ \underset{\sim}{n} \\ \hline \end{gathered}$ | $\cdots$ | $\left\|\begin{array}{c} n \\ \infty \\ n_{1} \end{array}\right\|$ | $\sim$ |  | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ |  | N | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | ～ |
| 6ヶL8」 9NIWN | $\because$ | $\sim$ | $\sim$ | $\bigcirc$ | $\stackrel{\infty}{\sim}$ | $\stackrel{N}{N}$ | $\stackrel{\sim}{m}$ | $\sim$ |  | $\sim_{\sim}^{\circ}{ }^{\text {n }}$ | เ | $\sim \sim \begin{aligned} & \infty \\ & M \\ & \sim\end{aligned}$ | $\begin{array}{c\|c} \infty \\ & \underset{N}{n} \\ \end{array}$ | $\begin{aligned} & \bar{m} \\ & \underset{\sim}{n} \end{aligned}$ |  | $\begin{array}{\|l\|} \hline \\ \overrightarrow{0} \\ \dot{0} \end{array}$ | $\left\|\begin{array}{c} n \\ i \end{array}\right\|$ |  | $\stackrel{+}{\sim}$ | $\left\|\begin{array}{c} \underset{\sim}{n} \\ \underset{\sim}{n} \end{array}\right\|$ | $0$ | $\underset{-}{0}$ | $\sim$ | $\begin{aligned} & \hline \left.\begin{array}{l} n \\ 0 \\ 0 \end{array} \right\rvert\, \end{aligned}$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | － |
| ＇כұə＊8ZОZप HNW马 | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ |  | $\sim \sim$ | $\cdots$ | $\cdots$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sigma$ | $\sim$ | $\begin{gathered} -r \\ 0 \\ 0 \\ -1 \end{gathered}$ | $\mathfrak{N}$ | $\left\lvert\, \begin{aligned} & \infty \\ & \underset{\sim}{\infty} \end{aligned}\right.$ | $\left\|\begin{array}{l} \stackrel{n}{N} \\ \underset{n}{n} \end{array}\right\|$ | $\underset{r}{9}$ |  | $\left\lvert\, \begin{aligned} & \mathrm{n} \\ & \mathrm{n} \\ & \underset{\gamma}{2} \end{aligned}\right.$ | $\left.\begin{array}{\|c\|} \stackrel{n}{n} \\ \mathrm{~N} \end{array} \right\rvert\,$ | $\stackrel{\sim}{2}$ | $\begin{aligned} & 9 \\ & \dot{e} \end{aligned}$ | $\stackrel{\sim}{\sim}$ | $\xrightarrow{-}$ |
| SL80โ口 SWप甘M | $\sim$ | $\sim$ | $\cdots$ | $\cdots$ | $\cdots$ | $\cdots$ | ～ | $\sim$ |  |  | － | ค 0 | $\stackrel{\sim}{i}$ | $\sim$ | $\sim$ | $\begin{array}{\|c\|} \hline N \\ \underset{n}{n} \end{array}$ | $\cdots$ | ？ | $\stackrel{\infty}{\sim}$ | $\begin{aligned} & 10 \\ & 0 \\ & 0 \\ & \hline \end{aligned}$ | の | $\stackrel{\text {－}}{\text {－}}$ |  | $\begin{aligned} & \hline \left.\begin{array}{l} n \\ 0 \\ 0 \end{array} \right\rvert\, \end{aligned}$ |  | $\mid \stackrel{\cap}{\sim}$ | N | $\stackrel{\sim}{\sim}$ | $\infty$ | $\sim$ |  |
| 七6โ0โ」 9NIWN | $\underset{i}{n}$ | $\pm$ | $\left\lvert\, \begin{gathered} n \\ 0 \\ \hline \end{gathered}\right.$ | $\begin{array}{l\|l\|} \hline 0 \\ \infty & 0 \\ \hline \end{array}$ | $\begin{aligned} & n \\ & \dot{\sim} \\ & \underset{\sim}{n} \end{aligned}$ | $\stackrel{\rightharpoonup}{N}$ | $\stackrel{\stackrel{\rightharpoonup}{N}}{ }$ | $\left.\begin{aligned} & n \\ & 0 \\ & 0 \\ & -1 \end{aligned} \right\rvert\,$ |  | $\underset{\sim}{\gamma} \underset{\infty}{\sim}$ | $\begin{array}{c\|c} \sim \\ \hline \end{array}$ | $$ | $\cdots{ }_{\sim}^{+}$ | $\stackrel{\rightharpoonup}{\underset{\sim}{i}}$ |  | $\left.\begin{array}{\|c\|} \hline n \\ \dot{n} \end{array} \right\rvert\,$ | m | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | $\left.\begin{array}{\|c} n \\ \dot{0} \\ \dot{\sigma} \end{array} \right\rvert\,$ | $\stackrel{\sim}{\sim}$ | N | $\stackrel{\sim}{n}$ | $\stackrel{\sim}{N}$ | へ |
|  | $\|\stackrel{n}{n}\|$ | －1 | $\left\lvert\, \begin{gathered} \infty \\ i \\ i \end{gathered}\right.$ | $\begin{array}{\|l\|l} \hline \underset{\sim}{-1} \\ \underset{\infty}{\infty} \\ - \\ \hline \end{array}$ | $\begin{array}{\|c} 0 \\ -1 \end{array}$ | $\stackrel{\rightharpoonup}{N}$ | $\left\|\begin{array}{l} n \\ \underset{\sim}{\sim} \\ \underset{\sim}{2} \end{array}\right\|$ | $\left\lvert\, \begin{array}{\|c} \stackrel{\rightharpoonup}{\mathrm{N}} \\ \stackrel{\rightharpoonup}{2} \end{array}\right.$ |  | $\begin{array}{l\|l} \mathrm{N} & \mathbf{o} \\ \hline \end{array}$ |  | $\stackrel{\sim}{n} \stackrel{n}{n}$ | $\sim$ | N | $\stackrel{-}{-}$ | เก｜ | $\stackrel{\infty}{+}$ |  | $\stackrel{+}{\infty}$ | $\begin{aligned} & 9 \\ & 0 \\ & -1 \end{aligned}$ | $\begin{aligned} & \infty \\ & \underset{\sim}{\infty} \\ & \sigma_{1} \end{aligned}$ | $\begin{aligned} & n \\ & 0 \\ & -1 \end{aligned}$ |  | $\left\|\begin{array}{l} N \\ \infty \\ \cdots \end{array}\right\|$ |  | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | ． |
| ૬દદて qว ЭWSપ્ | $\sim$ | $\sim$ | $\begin{array}{\|c} 9 \\ \\ i \end{array}$ | $\begin{array}{\|c\|c} \hline n \\ n \\ n & n \\ n \end{array}$ | $$ | $\stackrel{\sim}{N}$ | $\sim$ | $\sim$ |  | $\begin{array}{l\|l} \hline \sim \sim \\ \underset{寸}{f} & 6 \end{array}$ |  | $\begin{array}{c\|c} \stackrel{n}{N} & \infty \\ \mathrm{~m} & - \end{array}$ | $\begin{aligned} & \infty \\ & i \\ & i \end{aligned}$ | $\cdots$ | $\cdots$ | $\begin{array}{\|c\|} \hline N \\ \hat{n} \end{array}$ | $\sim$ | m | $\begin{aligned} & \hline 0 \\ & 0 \\ & 0 \end{aligned}$ | $\xrightarrow{\sim}$ | $\begin{aligned} & \because \\ & \underset{r}{2} \end{aligned}$ | $\stackrel{\infty}{-1}$ | $\sim$ | $\left.\begin{aligned} & n \\ & \infty \\ & \infty \\ & 1 \end{aligned} \right\rvert\,$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |
| S＇LS8 WM | 入 | $\sim$ |  |  |  |  |  |  |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | (이 | $\stackrel{\sim}{N}$ | $\left\lvert\, \begin{aligned} & n \\ & 0 \\ & \hline \end{aligned}\right.$ |  | $\sim$ | $\sim$ |
| ع0GЭ W入પO人 | $\begin{aligned} & n \\ & \infty \\ & \infty \end{aligned}$ | $\sim$ | $\left\lvert\, \begin{gathered} \mathrm{n} \\ \mathbf{0} \\ \mathrm{n} \end{gathered}\right.$ |  | ar\| | $\stackrel{\sim}{N}$ | $\sim$ | $\left.\begin{aligned} & \mathrm{N} \\ & \underset{N}{N} \end{aligned} \right\rvert\,$ |  | $\begin{aligned} & n \\ & \underset{n}{n} \\ & n \end{aligned}$ |  | $\bigcirc \mathrm{m}$ | $\cdots \sim$ | $\sim$ | $\stackrel{N}{\mathrm{~N}}$ | $\mid \vec{n}$ | $\sim$ |  | － | $\stackrel{+}{-}$ | $\begin{aligned} & \text { O } \\ & \underset{\sim}{r} \end{aligned}$ | $\begin{aligned} & n \\ & n \\ & n \\ & n \end{aligned}$ |  | $\cdots$ |  | 앤 | $\sim$ | $\sim$ | － | $\sim$ | － |
| عG8七¢ HNWG | $\cdots$ | $\sim$ | $\sim$ | $\begin{array}{\|c\|c} \underset{\sim}{n} \\ \underset{r}{n} & m \\ m \end{array}$ | $\left\|\begin{array}{c} \mathrm{m} \end{array}\right\|$ | n | $\left\|\begin{array}{c} \infty \\ \mathrm{m} \end{array}\right\|$ | $\sim$ |  | $\sim$ | $\sim$ | $\cdots$ |  | $\begin{aligned} & \mathrm{N} \\ & \mathrm{O} \\ & \dot{\gamma} \end{aligned}$ | $\cdots$ | $\sim$ | $\sim$ |  |  | 안 | $\stackrel{\infty}{\sim}$ | $\begin{aligned} & n \\ & 0 \\ & \underset{N}{2} \end{aligned}$ | $\begin{gathered} \mathrm{m} \\ \stackrel{\rightharpoonup}{n} \end{gathered}$ |  |  | $\mid \infty$ | $\left\lvert\, \begin{gathered} \underset{~}{\dot{m}} \mid \\ \underset{m}{2} \end{gathered}\right.$ | $\left.\begin{aligned} & n \\ & n \\ & n \\ & n \end{aligned} \right\rvert\,$ | $\begin{array}{\|c} \hline-1 \end{array}$ | $\stackrel{\sim}{n}$ | $\stackrel{\infty}{\square}$ |
| S8L8」 9NIWN | $\begin{aligned} & 0 \\ & 0 \\ & 0 \end{aligned}$ | $\begin{array}{\|c\|} \hline \stackrel{n}{n} \\ \underset{\sim}{n} \end{array}$ | $\stackrel{N}{n}$ |  | $\begin{aligned} & n \\ & \stackrel{n}{0} \\ & \sim \end{aligned}$ | $\left\|\begin{array}{l} n \\ \underset{m}{n} \end{array}\right\|$ | N | $\left.\begin{aligned} & n \\ & 0 \\ & 0 \\ & m \end{aligned} \right\rvert\,$ |  | $$ | $$ | $\begin{array}{l\|l} 0 \\ 0 & \\ \end{array}$ | $$ | $\begin{aligned} & \mathrm{n} \\ & \mathrm{~m} \end{aligned}$ | $\begin{gathered} m \\ \underset{N}{2} \\ \hline \end{gathered}$ | $\begin{aligned} & n \\ & 0 \\ & 0 \end{aligned}$ | $\stackrel{\sim}{\mathrm{N}}$ |  |  | $\stackrel{-}{-1}$ | $$ | $\underset{\sim}{\infty}$ | $\sim$ | $\stackrel{\text { 앙 }}{ }$ |  | $\sim$ | $\sim$ | $\sim$ | ～ | $\sim$ | $\sim$ |
|  | $\begin{aligned} & \frac{9}{4} \\ & 0 \\ & 0 \\ & 0 \\ & \frac{5}{0} \\ & 0 \\ & 3 \\ & 4 \\ & \frac{0}{0} \\ & \frac{0}{0} \end{aligned}$ | $\begin{array}{\|l} 0 \\ \frac{7}{0} \\ \frac{0}{5} \end{array}$ |  |  |  |  |  |  |  |  |  |  |  |  | maximum width of parasphenoid |  | cultriform process length |  |  | Symphysis width |  |  |  |  |  |  |  | humerus facet（ventral） |  |  |  |
|  |  |  |  |  |  | $\stackrel{*}{4}$ | $\stackrel{*}{*}$ | $\stackrel{*}{*}$ |  | $\stackrel{4}{4}$ | $\infty$ | $\bigcirc \bigcirc$ | －吅 |  | 嵓 | $\begin{array}{\|l} \hline \\ \hline 0 \\ \hline \end{array}$ | ㅍ |  | 0 － | ט | 0 | c |  | O |  | $\checkmark$ | N | m | － | ก | $\bigcirc$ |


| 8LヤてI SNWS |  | $\infty$ | 우 | N |  | $\left\lvert\,\right.$ | ｜ros | 今 | $\stackrel{+}{4}$ | $\underset{\sim}{\sim}$ | 인 | $\bigcirc$ | $\left\lvert\, \begin{aligned} & \underset{m}{n} \\ & \hline \end{aligned}\right.$ | m |  | ， | $\stackrel{ \pm}{-}$ | $\stackrel{\bullet}{6}$ | N－1 |  | $\sim$ | 안 | $\stackrel{\square}{\square}$ | $\infty$ | $\stackrel{\sim}{\sim}$ | m | m |  |  |  |  | ¢ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 6عદโप HNWg | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |
| ＊8L0Z HNWG | $\left\lvert\, \begin{array}{l\|l} \hline \underset{i}{\mid} \\ \dot{N} \end{array}\right.$ | $\underset{\sim}{\sim} \underset{\sim}{\sim}$ | $\left.\begin{array}{\|l\|} \hline \\ \infty \\ n \\ n \end{array} \right\rvert\,$ | $\begin{aligned} & \infty \\ & \underset{\sim}{n} \\ & i \end{aligned}$ | $\sim$ | $\left.\begin{aligned} & \mathbf{a} \\ & \stackrel{1}{n} \end{aligned} \right\rvert\,$ | $\begin{array}{\|c} \mathbf{r} \\ i \end{array}$ | $\begin{aligned} & 9 \\ & -子 \\ & -8 \end{aligned}$ | $\begin{array}{\|c} \stackrel{n}{r} \\ \underset{m}{2} \end{array}$ | $\sim$ | $\left.\begin{aligned} & n \\ & \stackrel{n}{i} \\ & \underset{\sim}{n} \end{aligned} \right\rvert\,$ | $\begin{gathered} n \\ \underset{m}{n} \end{gathered}$ | $\begin{aligned} & \stackrel{n}{m} \\ & \underset{\sim}{n} \end{aligned}$ | $\begin{aligned} & \hat{N} \\ & \underset{n}{n} \end{aligned}$ |  |  | $\underset{\sim}{N}$ | $\left\|\begin{array}{l} 0 \\ 0 \\ \mathrm{~N} \end{array}\right\|$ | $\left.\begin{aligned} & \infty \\ & 0 \\ & m \\ & m \end{aligned} \right\rvert\,$ | $\sim$ | $\sim$ | $\stackrel{\infty}{\sim}$ | $\begin{aligned} & n \\ & m \\ & \sim \end{aligned}$ | $\left\|\begin{array}{c} \infty \\ \underset{m}{\infty} \end{array}\right\|$ | $\begin{aligned} & \infty \\ & 0 \\ & 0 \\ & -1 \end{aligned}$ | $\left\lvert\, \begin{gathered} \underset{\sim}{n} \\ \underset{i}{2} \end{gathered}\right.$ | $\left\|\begin{array}{l} \stackrel{n}{n} \\ 0 \\ 0 \\ \cdots \end{array}\right\|$ | $\sim$ | $\sim$ | $\sim$ |  |  |
| 87\％H | $\sim$ | $\sim$ | $\left\|\begin{array}{c} \boldsymbol{\infty} \\ \mathbf{N} \end{array}\right\|$ | $\sim$ | $\cdots$ | $\sim$ | ～ | $\sim$ | $\mid \text { 잇 }$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ |  | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\rightharpoonup}{\mathbf{N}}$ | $\left\|\begin{array}{c} \mathbf{M} \\ \boldsymbol{n} \end{array}\right\|$ | $\cdots$ | $\cdots$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | N |
| Z0Z6t HNWQ | $\cdots$ | $\cdots$ | $\cdots$ | $\cdots$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ |  | $\bigcirc$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | ～ |  | $\sim$ |
| 9عદโ¢ HNWG | $\cdots$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\stackrel{+}{+}$ | $\left.\begin{aligned} & \underline{n} \\ & \dot{n} \end{aligned} \right\rvert\,$ | $\cdots$ | $\cdots$ | $\begin{array}{\|c\|} N \\ \dot{\sigma} \end{array}$ | $\begin{array}{\|c\|} \hline-i \\ \infty \end{array}$ | $\sim$ | $\sim$ | $\sim$ |  | $\stackrel{-}{+}$ |
| 88ャ¢ |  | \|O | 우 | $\stackrel{\sim}{\sim}$ | $\underset{\sim}{\sim}$ | $\left.\begin{array}{\|l\|} \hline \infty \\ 0 \\ -1 \end{array} \right\rvert\,$ |  | $\begin{array}{\|c} \underset{-}{n} \\ \underset{r}{2} \end{array}$ | $\begin{aligned} & \mathbf{r} \\ & \underset{r}{n} \end{aligned}$ | $\left\lvert\, \begin{gathered} \underset{-}{2} \\ \underset{-}{2} \end{gathered}\right.$ |  |  |  |  |  | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | m | $\underset{\sim}{0}$ |  |  |  |  | $\sim$ | $\sim$ | $\sim$ |  | $\stackrel{\sim}{n}$ |
| ऽZS8E HNW8 | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | ～ | $\sim$ | $\sim$ | $\sim$ | ～ | $\sim$ | $\cdots$ | $\sim$ |  |  | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\begin{array}{\|c\|} \hline-1 \\ \hline-1 \end{array}$ | ～． | $\cdots$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim$ |
| 6ヶL8」 9NIWN | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ |  |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\sim}{\sim}$ | N | $\infty$ | $\mid \stackrel{\rightharpoonup}{N}$ |  | $\mathrm{m}$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim$ |
| ＇วృə＊8てOZप HNW8 |  |  | $\begin{aligned} & \mathrm{r} \\ & \dot{o} \\ & \mathrm{~N} \end{aligned}$ | $\underset{\sim}{N}$ | $\left\|\begin{array}{c} n \\ m \\ r \\ n \end{array}\right\|$ |  | 0 | $\underset{\sim}{m}$ | $\left\|\begin{array}{c} N \\ i \\ i \end{array}\right\|$ | $10$ |  | $\sim$ | $\cdots$ | へ |  | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\sim}{\text { n }}$ | $\begin{gathered} m \\ \underset{r}{n} \end{gathered}$ | $\stackrel{N}{N}$ | $\left.\begin{array}{\|c} n \\ \underset{\sim}{n} \end{array} \right\rvert\,$ | Po | $\left.\begin{aligned} & \mathrm{m} \\ & \underset{\sim}{n} \end{aligned} \right\rvert\,$ |  |  | $\sim$ |  |  |
| SL80TS SWप甘M |  |  | $\begin{aligned} & m \\ & \vec{N} \\ & \stackrel{2}{2} \end{aligned}$ |  | $\underset{\sim}{\mathrm{N}}$ | $\left.\begin{array}{\|c\|} \hline 0 \\ 0 \\ 0 \\ -1 \end{array} \right\rvert\,$ | に | $\stackrel{-}{\square}$ | $\stackrel{+}{\square}$ |  | $\underset{\sim}{N}$ | $\begin{aligned} & N \\ & \sigma \end{aligned}$ | $\xrightarrow{\text { N }}$ | $\cdots$ |  | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\begin{aligned} & n \\ & \dot{0} \\ & \mathrm{~m} \end{aligned}$ | $\underset{\square}{9}$ | $\sim$ | $\cdots$ | $\cdots$ | $\sim$ | $\stackrel{\sim}{\square}$ | $\infty$ | $\cdots$ |  | $\sim$ |
| 七6L0โ」 9NIWN | $\left\lvert\, \begin{aligned} & \mid n \\ & \underset{\sim}{n} \\ & \stackrel{0}{0} \end{aligned}\right.$ |  | $\begin{gathered} N \\ \underset{\sim}{2} \\ \underset{y}{n} \\ \end{gathered}$ | $\stackrel{N}{\underset{N}{N}}$ | $\left.\begin{array}{\|c} \infty \\ \underset{\sim}{\sim} \end{array} \right\rvert\,$ | \| | $\left.\begin{aligned} & 0 \\ & 0 \\ & 0 \\ & -1 \end{aligned} \right\rvert\,$ | $\underset{\sim}{n}$ | $\left.\begin{aligned} & \underset{\sim}{n} \\ & \stackrel{n}{-} \end{aligned} \right\rvert\,$ | $\begin{array}{\|l\|} \hline n \\ \end{array}$ | m |  | N | $\begin{aligned} & n \\ & \hline \mathbf{m} \\ & \hline \end{aligned}$ |  | $\mathrm{N}_{\mathrm{N}}^{2}$ | $\begin{aligned} & 0 \\ & 0 \\ & 0 \\ & \end{aligned}$ | $\bigcirc$ | $\mid$ | $\sim$ | $\sim$ | $\begin{aligned} & n \\ & \dot{0} \\ & \mathrm{~m} \end{aligned}$ | $\underset{\square}{9}$ |  |  | $\stackrel{\square}{\text { m }}$ | 안 |  |  | $\sim$ |  | $\stackrel{n}{n}$ |
| โ¢8โ＇โててら SつIヨา | $\cdots$ | $\cdots$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | － | $\sim$ | $\sim$ | $\sim$ | － | $\sim$ | $\cdots$ | $\sim$ |  | ～ | $\sim$ | $\sim$ | $\cdots$ | $\|\underset{r}{\mid}\|$ | $\sim$ | $\begin{aligned} & \stackrel{\sim}{7} \\ & \underset{\gamma}{2} \end{aligned}$ | $\underset{N}{N}$ | $\begin{aligned} & n \\ & \infty \\ & \infty \end{aligned}$ | $\stackrel{m}{N}$ | $\begin{aligned} & \infty \\ & m \\ & \hline \end{aligned}$ | $\begin{aligned} & \mathbf{O} \\ & \hline \mathbf{m} \end{aligned}$ | $\sim$ | $\sim$ | $\sim$ |  | $\underset{\sim}{\sim}$ |
| ธعદて qว ЭWSપg | $\cdots$ | $\sim$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | － | $\cdots$ | $\sim$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\sim}{n}$ | $\begin{gathered} N \\ \infty \\ \infty \end{gathered}$ | $\infty$ | $\stackrel{\rightharpoonup}{N}$ | 앙 | $\stackrel{N}{N}$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim$ |
| S＇LS8 WM | $\cdots$ | $\sim \sim$ |  | $\underset{N}{N}$ | $\underset{\sim}{\text { m }}$ | $\cdots$ | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | － | $\sim$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{\sim}{n}$ | $\stackrel{\sim}{\mathrm{n}}$ | $\left\lvert\, \begin{aligned} & n \\ & \hat{\infty} \\ & \infty \end{aligned}\right.$ |  | $\cdots$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ |  | $\sim$ |
| عOGЭ W入પ¢O人 | $\sim$ | $\underset{r}{m}$ | $\stackrel{\sim}{\sim}$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\cdots$ | $\sim$ | $\cdots$ | $\underset{\sim}{\sim}$ | 악 | $\cdots$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\stackrel{+}{6}$ | $\stackrel{\sim}{\sim}$ | $\begin{array}{\|c} \underset{\sim}{n} \\ \underset{i}{2} \end{array}$ | $\stackrel{+}{\sim}$ | $\|\underset{q}{\varphi}\|$ | － 7 | $\stackrel{\square}{-1}$ | al | $\stackrel{\infty}{+}$ |  | $\sim$ |
| عऽ8ヵ¢ HNWG | $\left\|\begin{array}{l} \stackrel{\sim}{n} \\ \stackrel{n}{n} \\ \sim \end{array}\right\|$ |  | $\left\lvert\, \begin{aligned} & n \\ & m \\ & m \\ & m \end{aligned}\right.$ | $\underset{m}{\infty}$ | $\begin{array}{\|c\|} \hline \infty \\ \sim \end{array}$ | $\begin{array}{\|l\|} \hline \infty \\ -1 \end{array}$ | m | $\begin{aligned} & n \\ & \underset{\sim}{n} \\ & \sim \end{aligned}$ | $\left.\begin{aligned} & \underset{+}{\dot{0}} \\ & \stackrel{y}{*} \end{aligned} \right\rvert\,$ | $\begin{array}{\|c\|} \hline \infty \\ \sim \end{array}$ | $\stackrel{\text { ¢ }}{ }$ | $\left\|\begin{array}{l} m \\ \vec{n} \end{array}\right\|$ | \|ت口| | $\begin{array}{\|c} \substack{n \\ \\ \hline} \end{array}$ |  | $\sim$ | $\sim$ | － | $\left\|\begin{array}{c} n \\ \stackrel{n}{2} \\ \underset{-1}{ } \end{array}\right\|$ | の | $\stackrel{\square}{+}$ | N | $\hat{m}$ | $\stackrel{n}{1}$ | $\stackrel{\sim}{m}$ | $\left\lvert\, \begin{gathered} \mathbf{n} \\ \mathbf{0} \end{gathered}\right.$ | $\left\lvert\, \begin{array}{\|c\|} \hline 0 \\ \hline \end{array}\right.$ | $\stackrel{\pi}{\triangle}$ | $\frac{\pi}{\square}$ | $\bigcirc$ |  | $\sim$ |
| S8L8」 9NIWN | $\sim$ | $\sim$ | $\cdots$ | $\cdots$ |  | $\sim$ | $\cdots$ | $\sim$ | r． | $\cdots$ | $\cdots$ | $\cdots$ | $\cdots$ | $\sim$ |  | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | $\sim$ | ñ | $\stackrel{\sim}{\sim}$ | $\xrightarrow{\sim}$ | － | $\stackrel{m}{*}$ | $\stackrel{m}{*}$ | $\sim$ | $\sim$ | $\sim$ |  | त |
|  |  |  |  |  |  | width of preglenoid process |  | max posterior coracoid cornua（from midline） |  |  |  |  |  |  |  |  |  |  |  | पұбиәן ssəวoıd ןesıop |  | $\stackrel{C}{ \pm}$ | $\begin{aligned} & \frac{0}{2} \\ & \frac{1}{\frac{\pi}{4}} \\ & \frac{\pi}{0} \\ & \frac{n}{0} \\ & \hline \end{aligned}$ |  |  |  |  |  |  |  |  |  |
|  | N | $\infty$ |  | O | $\xrightarrow{-7}$ | $\xrightarrow{\sim}$ | $\stackrel{\sim}{\square}$ | $\stackrel{+}{\square}$ | $\stackrel{\sim}{\square}$ | $\stackrel{-}{\square}$ | $\stackrel{\text { N }}{ }$ | $\stackrel{\infty}{\square}$ | $\stackrel{\square}{7}$ | 안 |  | $\cdots$ | N | $\stackrel{\sim}{\sim}$ | $\stackrel{ \pm}{\sim}$ | $\stackrel{\stackrel{i n}{N}}{ }$ | $\stackrel{\underset{\sim}{N}}{\mathbf{N}}$ | へ | $\underset{\sim}{\infty}$ | － | 앙 | $\cdots$ | N | $\cdots$ | m | $\stackrel{1}{n}$ |  | $\stackrel{N}{N}$ |





Appendix 5. Data matrix for cladistic analysis




[^0]:    "the type-specimen of plesiosaurus arcuatus [Andrews adds in a footnote - "referred below to the new genus Eurycleidus"] [was] figured in Hawkins's 'Sea Dragons’ (1834) and described in part by Richard Owen...it is only recently that the bones of the shoulder-girdle have been developed and mounted'.

[^1]:    view (scale bar $=5 \mathrm{~cm}$ ).

