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 Pliosauridea (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 Plesiosauroididea increases tree length by 21 steps.

### 7.3 The base of the Pliosauridea

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 Plesiosauroididea, 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 Pliosauridea 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 pliosaurid 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 pliosaurid 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 pliosaurs (Figure 5.7). This is significant because *Leptocleidus* has typically been allied with the rhomaleosauroids (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 outcompeted 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 guilemiimperatoris* (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 placed 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 interpretations of *Eurycleidus* as produced by Cruickshank (1994b) (Figure 7.1A,B), and as produced in this thesis (Figure 6.1 and 7.1C,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 parietal-frontal 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 = 30cm).
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 5.5V 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 (*Euryleidus*) 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 *Euryleidus*. 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 5.5H,Q) and *Archaeonectrus* (see Figure 5.5A,H,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 5.5Y,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 5.5X); 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). Mosasaurus 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 guilemi imperatoris* 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 diamond-shaped 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 21st 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 21st 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).