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

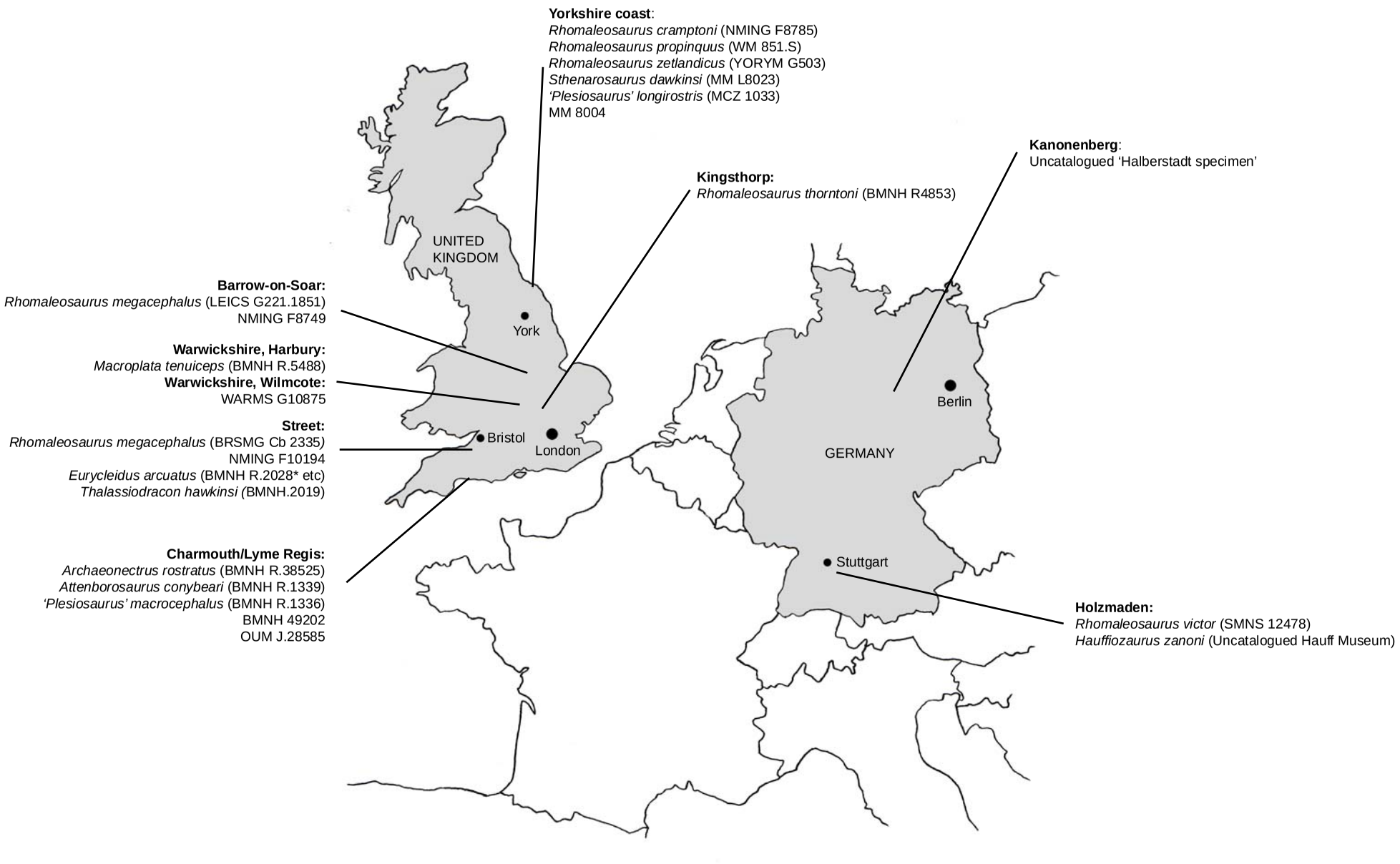

Figure 3.1. Geographical map showing the discovery locations of twenty-two specimens of Lower Jurassic plesiosaurs, examined during the production of this thesis. All of the specimens originated from the UK and Germany (highlighted in grey).

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

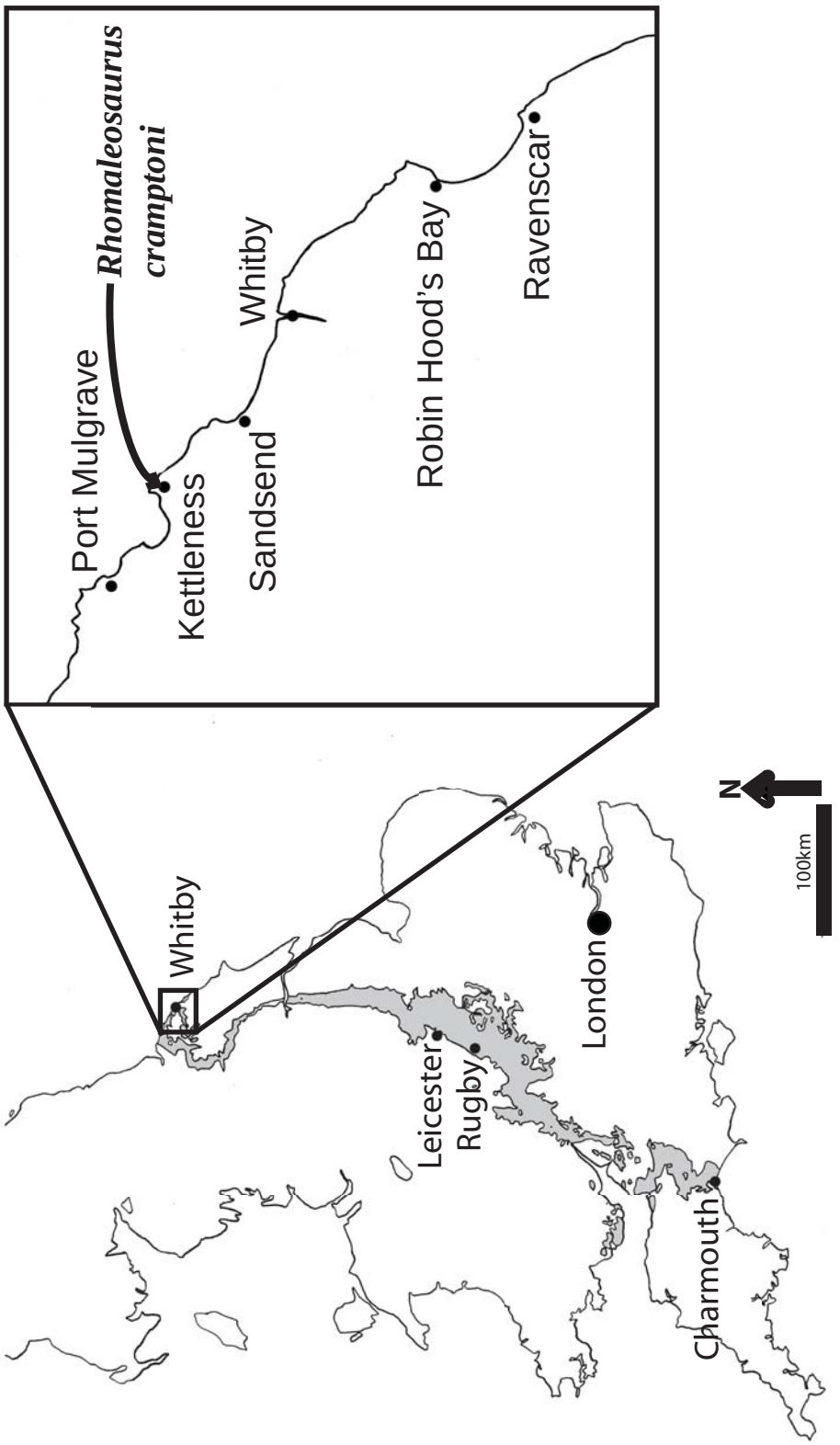

Figure 3.2. Detailed location map of NMING F8785, the holotype of *Rhomaleosaurus cramptoni* (the area in grey represents the Lias Group).

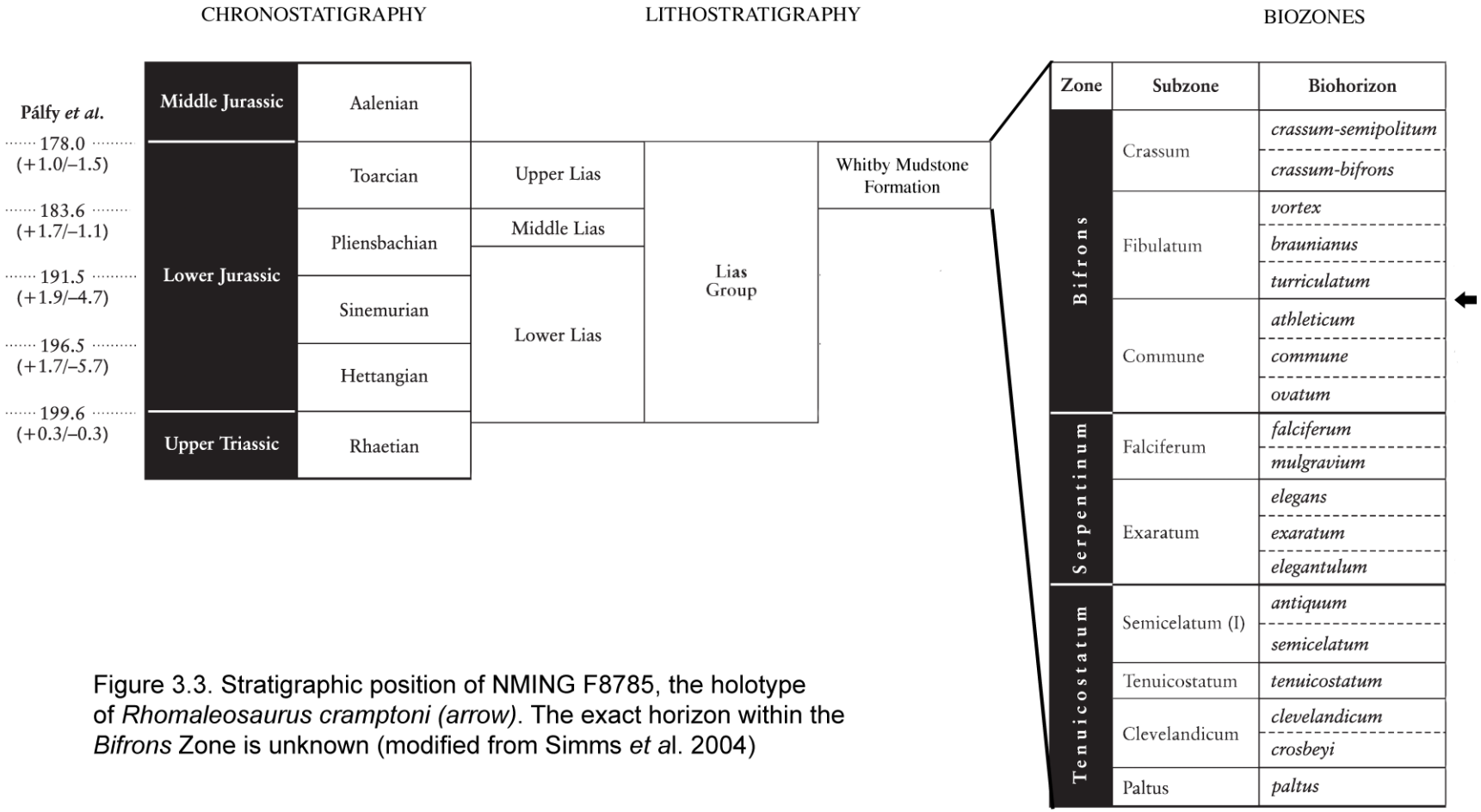

Figure 3.3. Stratigraphic position of NMING F8785, the holotype of *Rhomaleosaurus cramptoni (arrow)*. The exact horizon within the *Bifrons* Zone is unknown (modified from Simms *et a*l. 2004)

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*

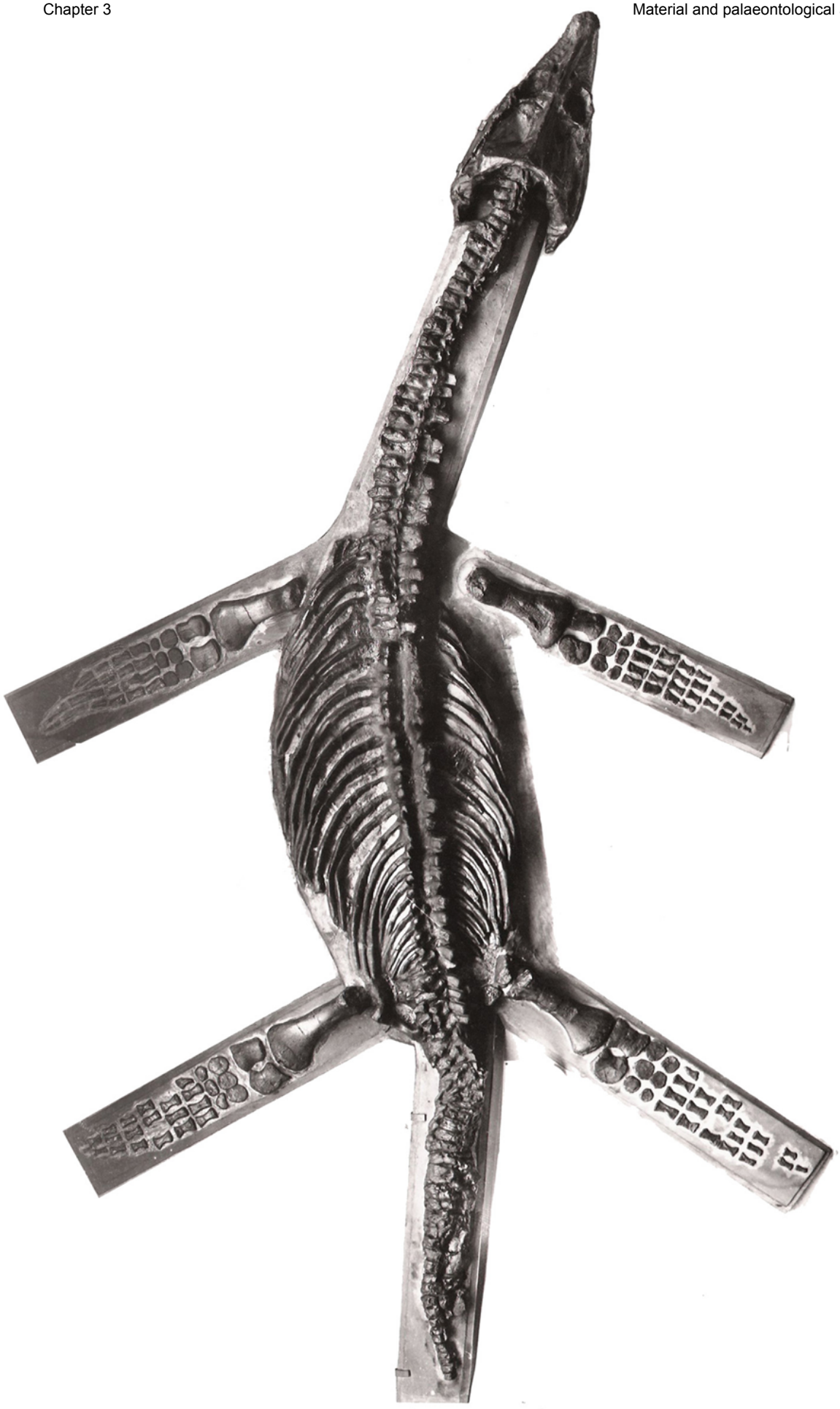

Figure 3.4. Photograph of specimen NMING F8785, the holotype of *Rhomaleosaurus cramptoni*, taken prior to the specimen being broken up and moved to storage. (Length of specimen from tip of skull to tip of tail, along vertebral column = 6.77m)

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*.

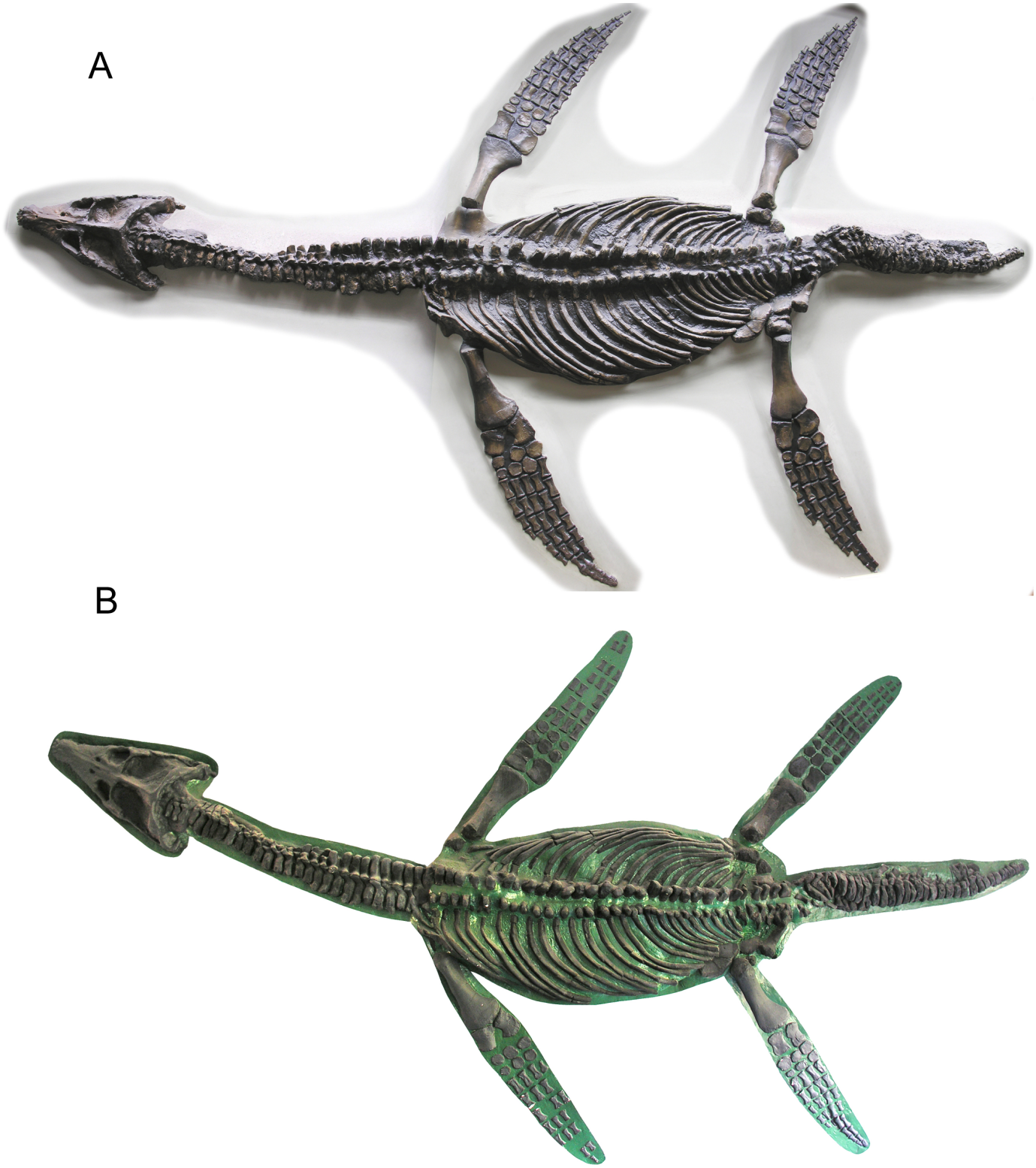

Figure 3.7. Casts of the holotype of *Rhomaleosaurus cramptoni* on display, A. in the Natural History Museum, London, UK; B. in the Bath Royal Literary and Scientific Institute, Bath, UK. See text for discussion of the differences between these casts. C. (over page) Illustration of “Item No. 228” as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

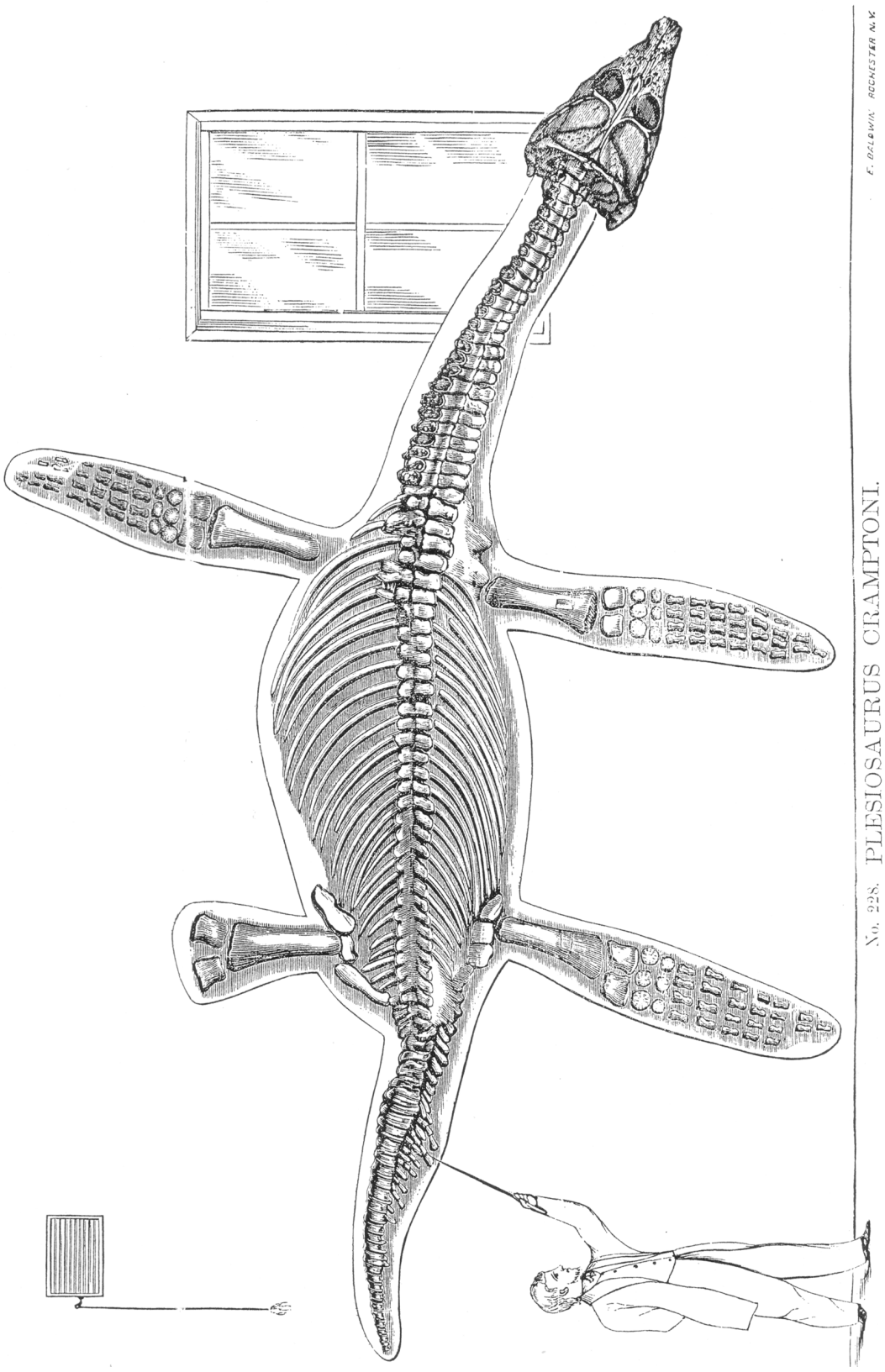

Figure 3.7C. Illustration of "Item No. 228" as figured in Ward's catalogue of *Casts of Fossils* (1866).

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

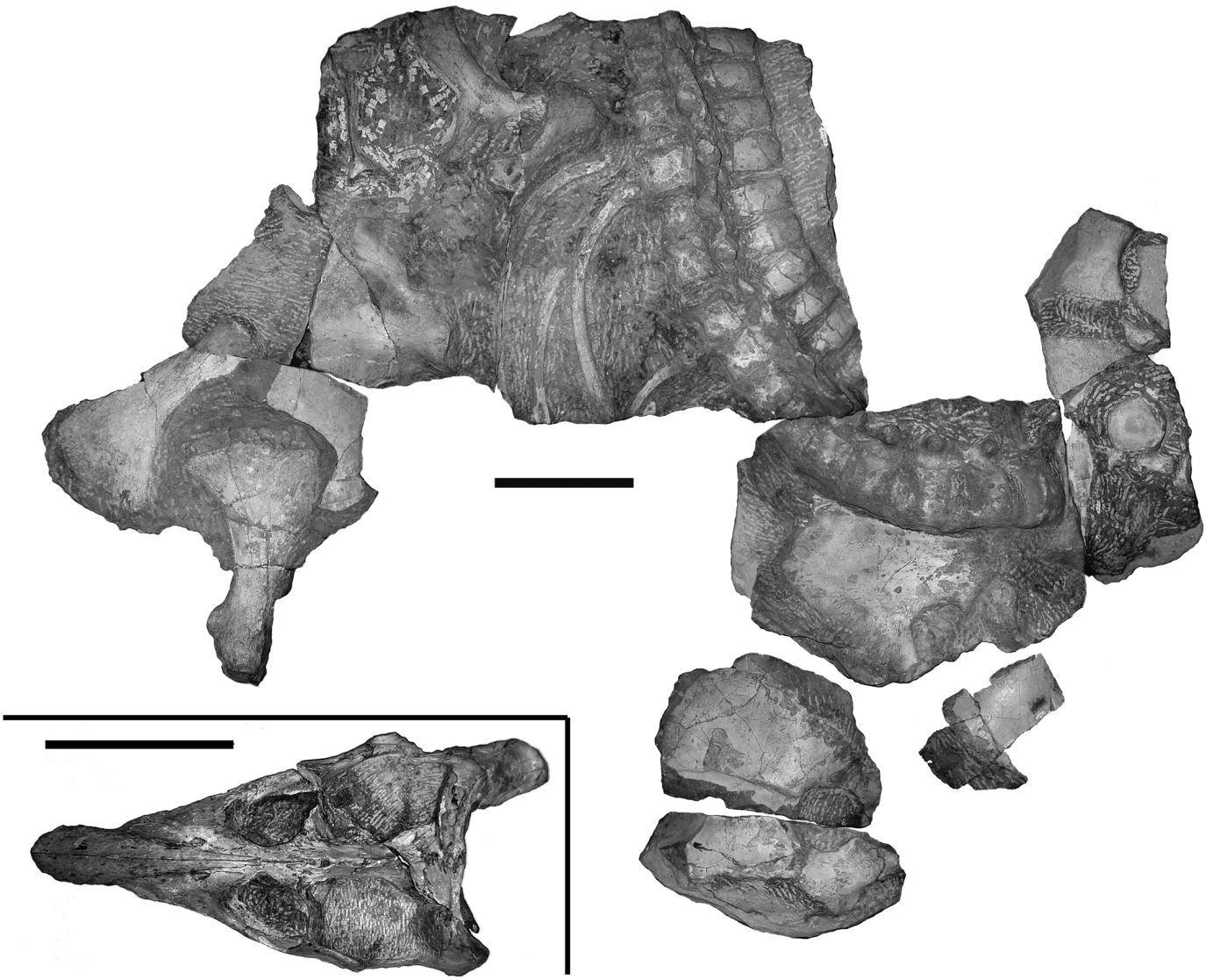

Figure 3.8. Overview of specimen NMING F10194. This specimen is preserved in thirty-eight fragments; this figure shows a reconstruction of fourteen of the larger blocks together with the skull (inset, in dorsal view) (scale bars = 20cm [for the postcranium] and 30cm [for the skull]). For more detailed 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 = 20cm).

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).

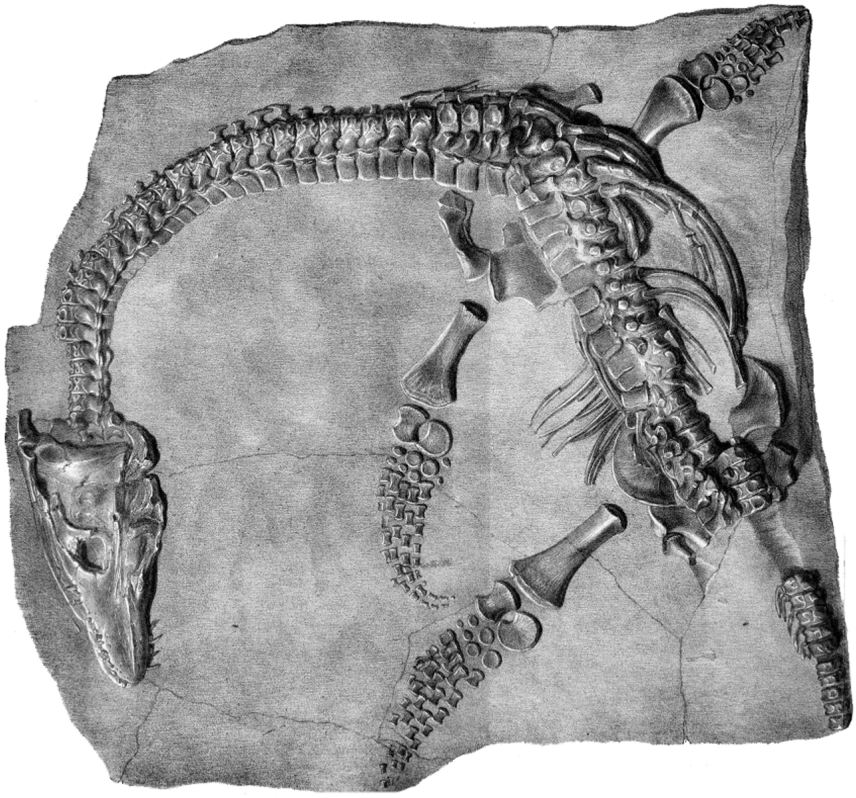

Figure 3.10. Specimen BMNH R1336, illustration of the holotype specimen of *Plesiosaurus macrocephalus*, as figured by Owen (1840, Plate 43) (length of skull = 22.5cm).

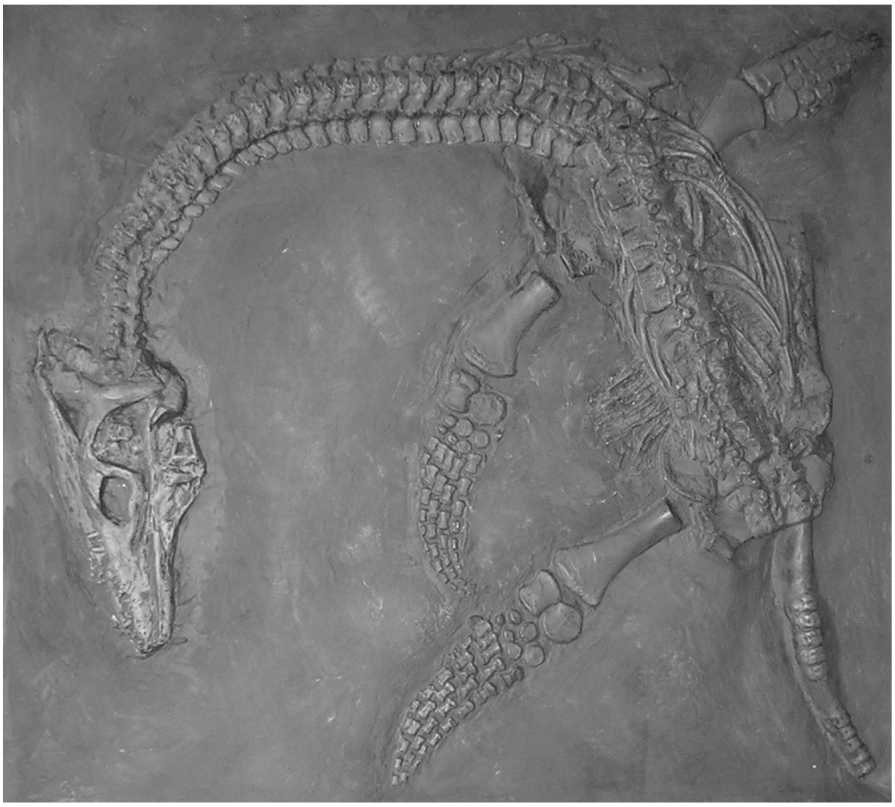

Figure 3.11. Specimen NMING F8780, cast of the holotype specimen of *Plesiosaurus macrocephalus* (see above) (length of skull = 22.5cm).

Figure 3.12. Specimen NMING F8771, cast of the holotype of *Thalassiodracon hawkinsi* (BMNH 2018*) (scale bar = 20cm).

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 = 20cm).

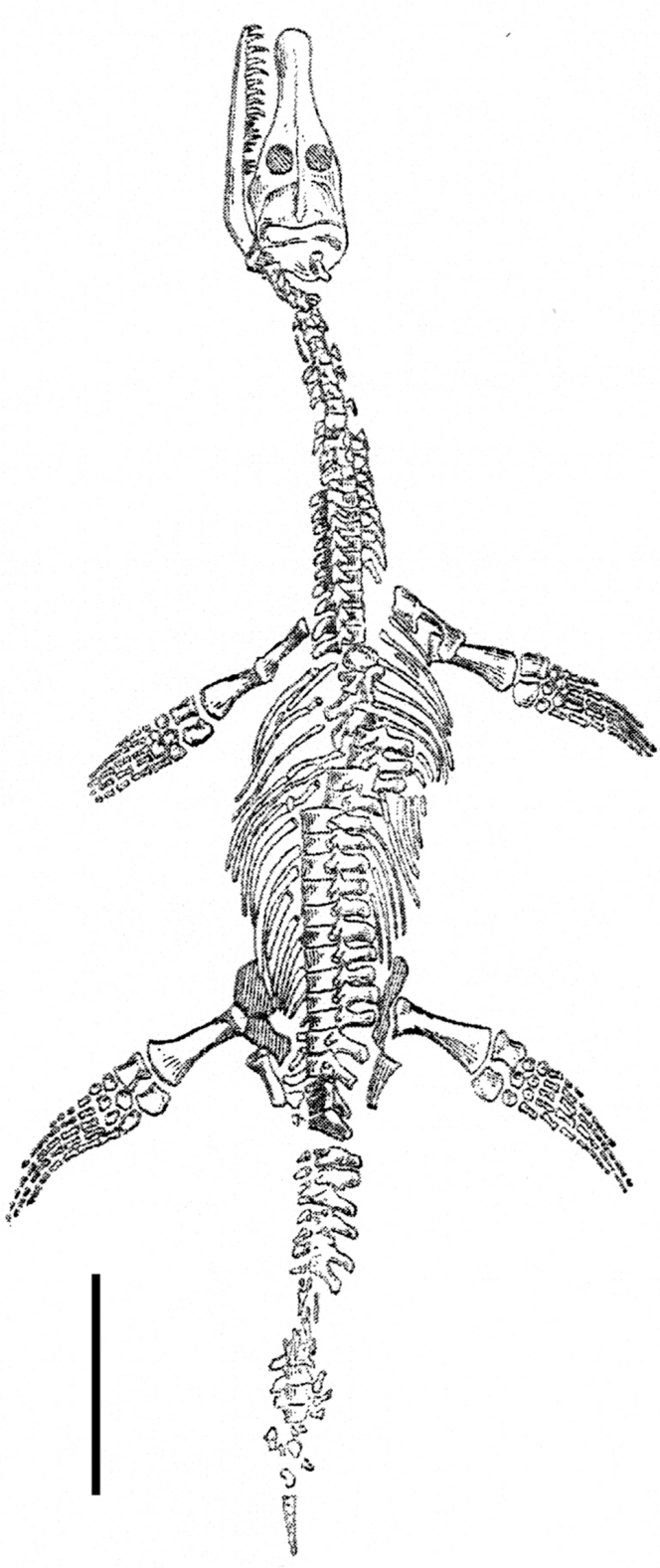

Figure 3.15. Specimen BMNH 38525, illustration of the holotype of *Archaeonectrus rostratus* as figured in Novozhilov (1964) (scale bar =50cm).

Figure 3.16. Specimen BMNH R4853, the holotype of *Rhomaleosaurus thorntoni* (propodials not in photograph) (length of preserved vertebral column = 5.75m).

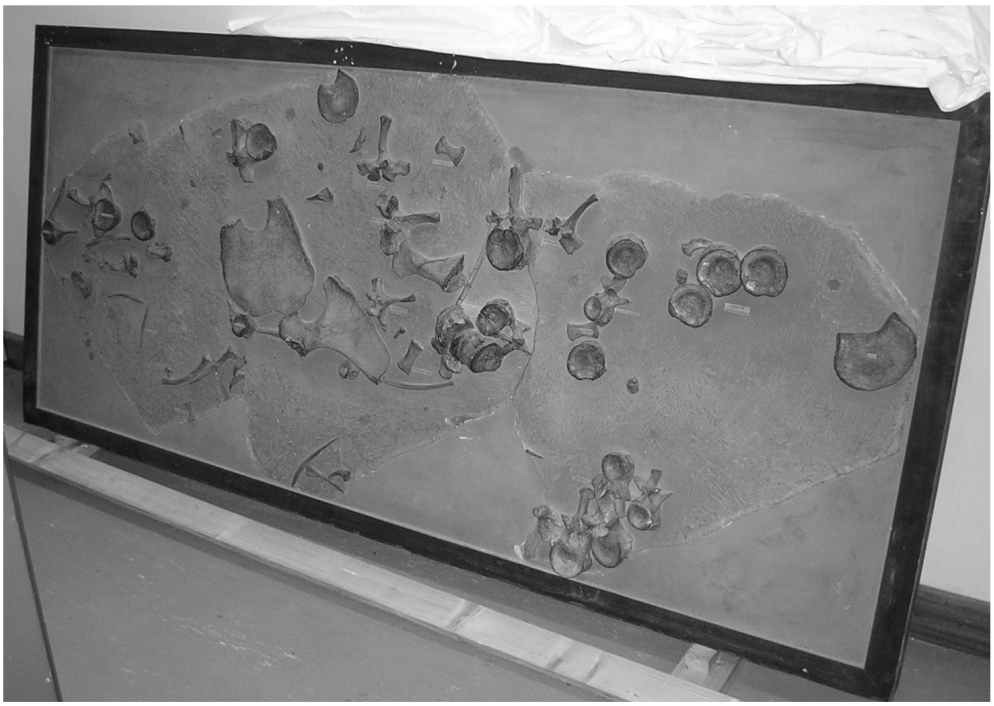

Figure 3.17. Specimen BMNH R1318, part of the type series of *Eurycleidus arcuatus* (length of pubis [largest element in the slab] = 25cm).

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:

"*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*".

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 20th 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).

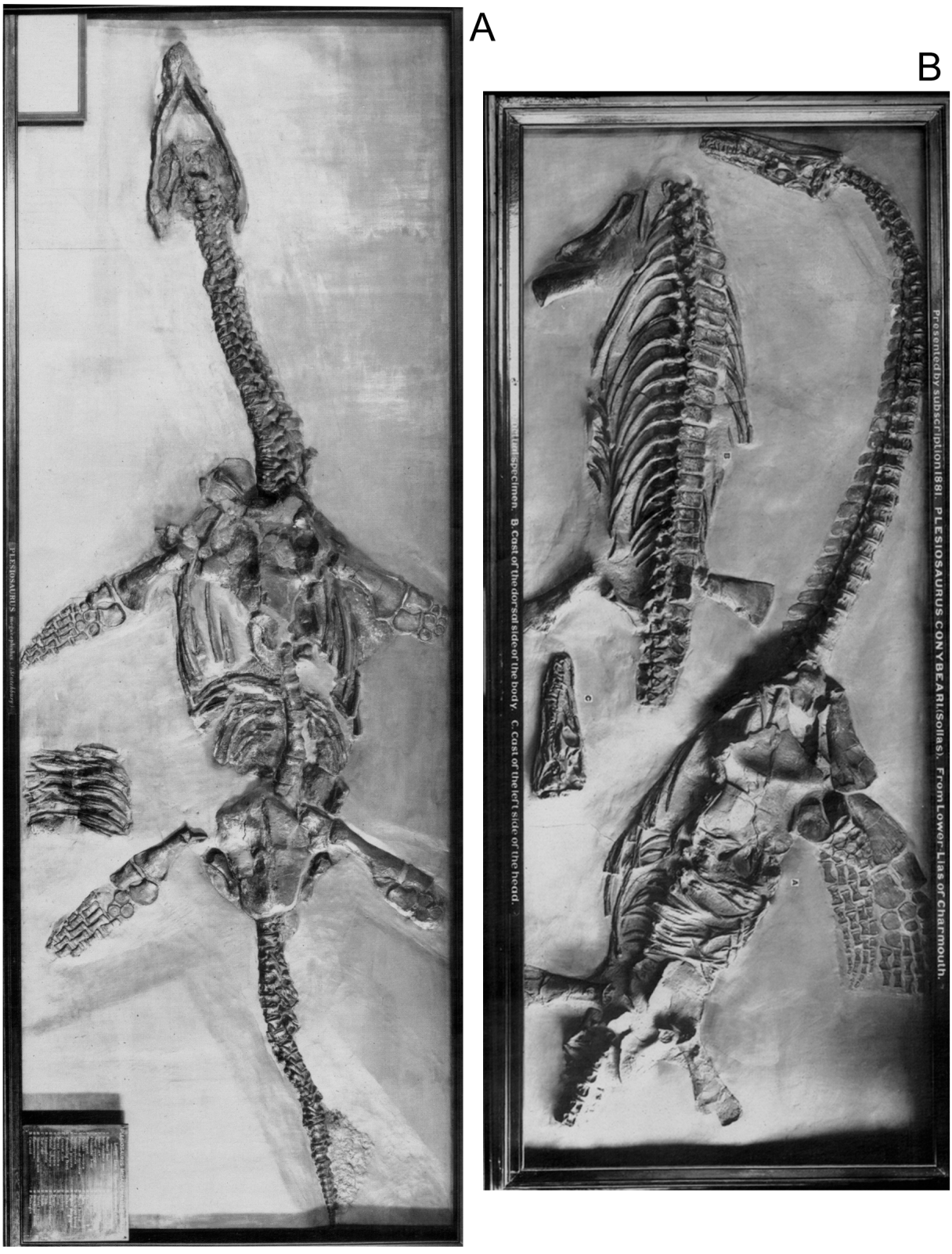

Figure 3.18. Historical photographs of destroyed holotypes formerly in the BRSMG, A. Specimen BRSMG Cb 2335 *Rhomaleosaurus megacephalus* (length =5.8m) (only casts of the skull and right forelimb of this specimen remain today, B. specimen BRSMG Cb 2479, the former holotype of *Attenborosaurus conybeari*,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

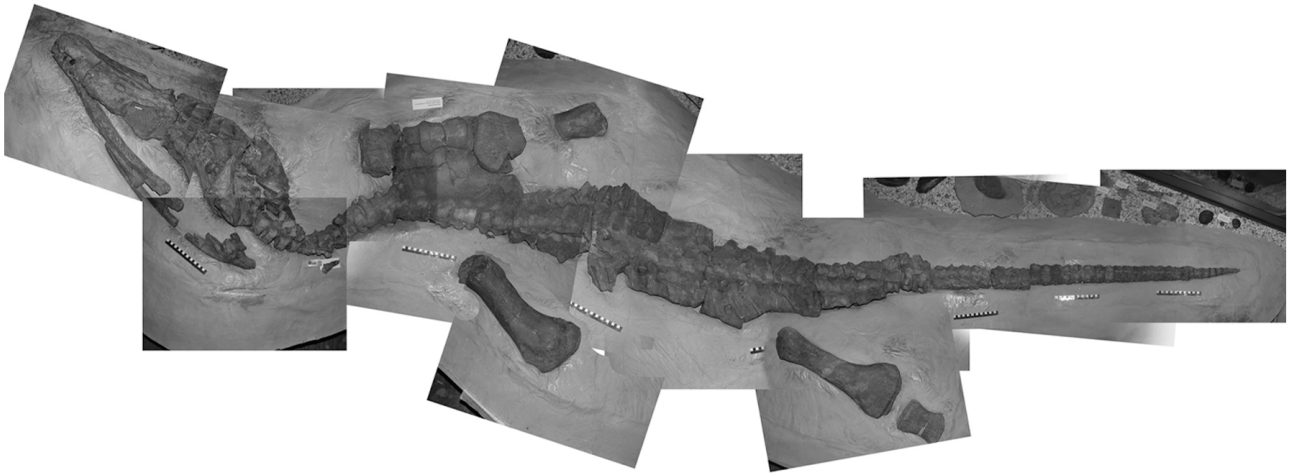

Figure 3.19 Composite photograph of specimen YORYM G503, the holotype of *Rhomaleosaurus zetlandicus* (scale bars =20cm) (courtesy of R. Forrest).

Figure 3.20 Specimen WM 851.S, the holotype of *Rhomaleosaurus propinquus* on display in the Whitby Museum (scale bar = 30cm).

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

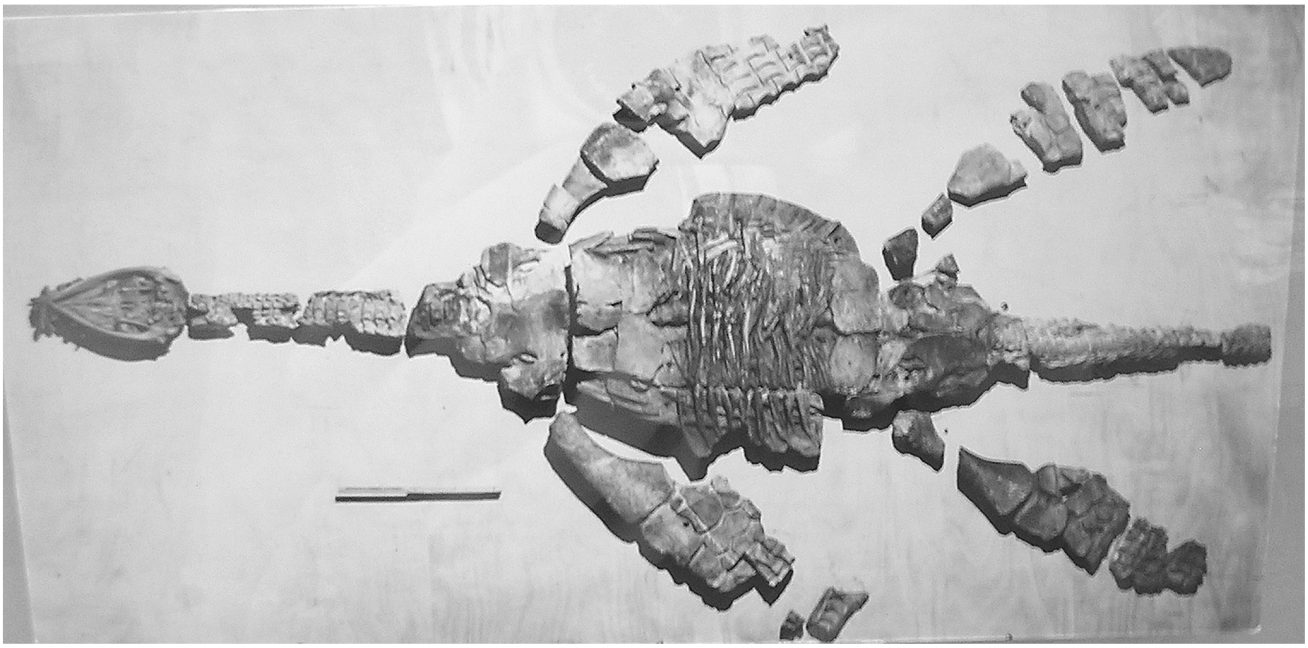

Figure 3.21. Historical photograph of SMNS 12478, the holotype of *Rhomaleosaurus victor*, partially reconstructed after being destroyed (see text for discussion) (length of specimen = 3.44m) (photograph from the SMNS).

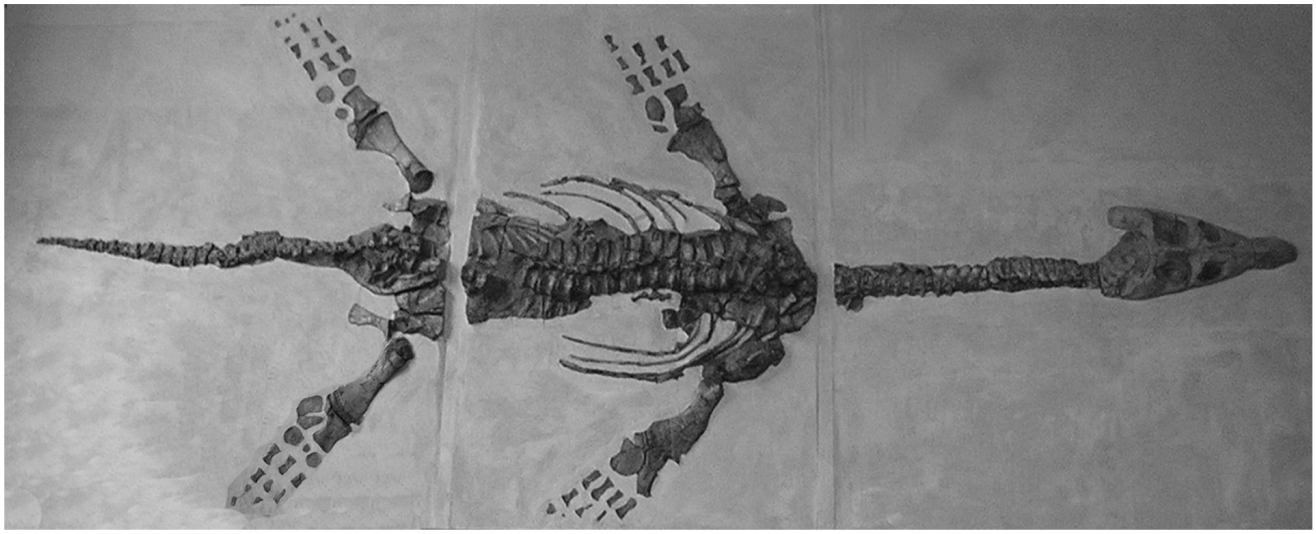

Figure 3.22. Specimen LEICS G221.1851, the neotype of *Rhomaleosaurus megacephalus* (length of specimen as mounted = 5.29m).

(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

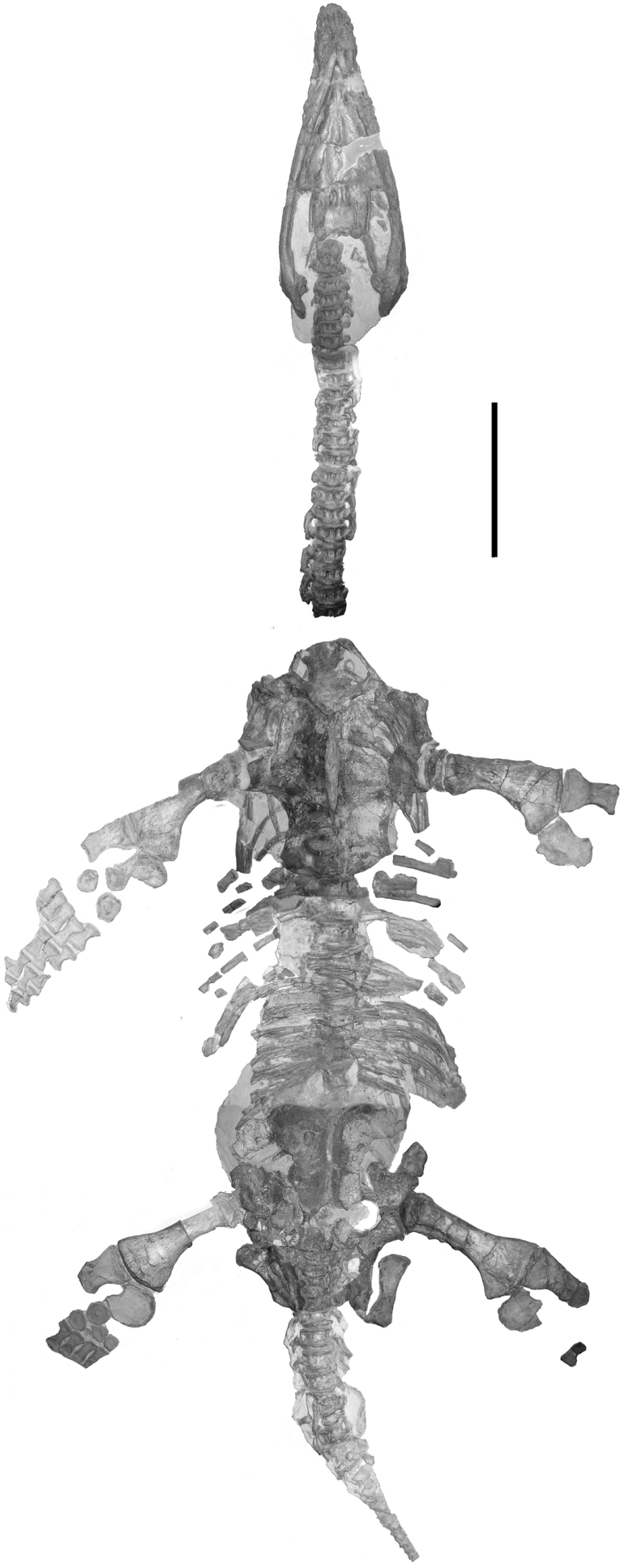

Figure 3.23. Composite photograph of specimen WARMS G10875, a full skeleton in ventral view (scale bar = 40cm).

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.