A NEW GENUS OF PLESIOSAUR (REPTILIA: SAUROPTERYGIA)

FROM THE PLIENSBACHIAN (EARLY JURASSIC) OF ENGLAND,

AND A PHYLOGENY OF THE PLESIOSAURIA.

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by

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A new genus of plesiosaur (Reptilia: Sauropterygia) from the Pliensbachian (Early Jurassic) of England, and a phylogeny of the Plesiosauria.

Mark Evans

Two new species of plesiosaur have been recognised from the Pliensbachian (Early Jurassic) of England. They share derived characters and so are referred to the same new genus, *Raptocleidus*. *Raptocleidus blakei* is from Blockley Station Quarry, Gloucestershire (holotype specimen LEICT G1.2002) while *Raptocleidus bondi* is from the coast of Dorset (holotype specimen NHMUK R16330). The two new species share characters with different family-level groups of plesiosaur; the pliosaurids, leptocleidians and rhomaleosaurids. This makes classification of the new taxa problematic using purely comparative anatomical techniques. To further investigate their systematic position within the Plesiosauria, a phylogenetic analysis was performed. This is the largest analysis of plesiosaurian relationships ever attempted. The new species were found to be basal members of a paraphyletic assemblage which form successive sister groups to the Leptocleidia but which lie outside of this node-based taxon. The new stem-based taxon Leptocleidomorpha has been erected to encompass the new clade. The Leptocleidomorpha formed a novel sister group relationship with the Pliosauridae with the branching point situated at the very base of the Jurassic or earlier. The new clade Eupliosauria has been erected to encompass this new group. Finally two clades (Cryptoclidinae Williston, 1925 and Muraenosaurinae White, 1940) have been newly defined to describe diversity within the plesiosauroid clade Cryptoclididae. Additional specimens have been identified that may prove to be new taxa pending further work.

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Finally I would like to dedicate this thesis to the memory of Arthur Cruickshank (1932-2011), mentor, supervisor and friend.

Contents

Chapter 1 Introduction

Plesiosaurians, members of the clade Plesiosauria (Sauropterygia, Reptilia), were a successful and long-lived group of Mesozoic predatory marine reptiles, adapted to a pelagic way of life. The first plesiosaurians are known from fragmentary remains from the Westbury Formation of the British Rhaetian (Taylor and Cruickshank 1993a). By the slightly later basal Hettangian, a fauna of mainly small-bodied taxa is known from localities such as Street, Somerset, U.K. (Storrs and Taylor 1996; Benson *et al.* 2012). Plesiosaurians persisted for the duration of the Jurassic and Cretaceous, with the last taxa known from the Maastrichtian (e.g. Cruickshank and Fordyce 2002). However, marine reptile diversity declined during the terminal stages of the Cretaceous, and plesiosaurians became extinct at the Cretaceous/Palaeogene boundary (Benson *et al.* 2010). Plesiosaurian limbs were modified into two pairs of relatively long, tapering flippers, with elongation achieved through hyperphalangy of the digits (Fedak and Hall 2004). Their mode of locomotion through the water has been a subject of debate since the first complete skeletons were discovered (e.g. Conybeare 1824; Watson 1924) but is now thought to be a variation of underwater flight (Robinson 1975; Carpenter *et al.* 2010). Some plesiosaurians at least are known to have swallowed stones of various sizes (e.g. Cicimurri and Everhart 2001). While it was thought that this may have been to reduce buoyancy, food processing is now the preferred prime function, although the extra mass may have helped to improve the animal's 'trim' in the water column (Taylor 1993; Wings 2007; Henderson 2006). Recent evidence has confirmed that at least some plesiosaurians were viviparous, giving birth to single large offspring, rather than returning to land to lay eggs (O'Keefe and Chiappe 2011). Viviparity had already been achieved in Triassic non-pistosauroidean sauropterygians (Cheng *et al.* 2004) and, freed from the constraints of terrestrial life, some plesiosaurians were able to achieve lengths

of at least 15 metres (Buchy *et al.* 2003).

Bones that can now be recognised as plesiosaurian were first illustrated in the sixteenth century (Howe *et al.* 1981). These early discoveries were identified as crocodiles or whales, in themselves considered comparatively exotic and fabulous animals at the time, as there was no need to interpret them as anything different to the contemporary fauna. As theories of earth-history developed, there was a paradigm-shift in the interpretation of fossil reptiles to the functional Aristotelianism exemplified by the work of Georges Cuvier (1769-1832) (Rudwick 1976). However, the strangeness of the plesiosaur concerned even Cuvier, who described the first complete specimen as being "heteroclite" and "monstrous" (Cuvier 1825, p. 476). He even suspected it might be at the very least a composite of more than one individual, if not an outright forgery (Cuvier 1825; Torrens 1995; Taquet, 2003).

The very word 'plesiosaur' is a testament to the philosophy of the pioneer palaeontologists who first named the new fossil animal. William Daniel Conybeare (1787-1857) and Henry Thomas De la Beche (1796-1855) had been working on the recently named *Ichthyosaurus* when they encountered various bones of another fossil animal (De la Beche and Conybeare 1821; Taylor 1997). The *Ichthyosaurus* ('fish-lizard' in Greek) had been named to reflect its position between fish and reptiles in the 'Great Chain of Being', to which all created beings were thought to belong (Rupke 1983). The *Plesiosaurus* ('nearer to reptiles' in Greek) was seen by these workers as forming the link in the chain between the ichthyosaur and reptiles such as turtles (De la Beche and Conybeare 1821). The crucial evidence for its placement, and therefore the name, was the perceived anatomy of its flippers. However, this was actually based on a specimen which had been 'improved' with an unnatural arrangement of phalanges and

carpals or tarsals being glued into place (Evans 2010). This specimen, OUMNH J.50146, has been relocated during the course of this study (Fig. 1.1). When the first complete plesiosaur specimen was discovered by Mary Anning (1799–1847) (Taylor 1997), Conybeare could correct his conjectural flipper reconstruction, but he was much more surprised by the length of the neck (Conybeare, 1824). He declared that the elongated neck "deviates from the laws which were heretofore regarded as universal in quadrupedal animals and the cetacea" (Conybeare 1824, p. 382).

This thesis seeks to explore the evolutionary history of the Plesiosauria. The clade Plesiosauria Blainville, 1835 evolved from stem-group sauropterygians, the clade Sauropterygia Owen, 1860 itself most likely being a clade within the diapsid reptiles (Rieppel 2000). The first section will describe two new taxa from the Pliensbachian of the U.K., and present a detailed osteology and comparative study. The second section will present a phylogeny of the Plesiosauria, the largest to date, which will incorporate the taxa described in Chapter 2 with other new data. Reference is made in this thesis to Benson, Evans and Druckenmiller (2012). This paper is a collaboration derived from some of the work contained in this thesis, primarily the re-examination of basal Hettangian plesiosaurian specimens.
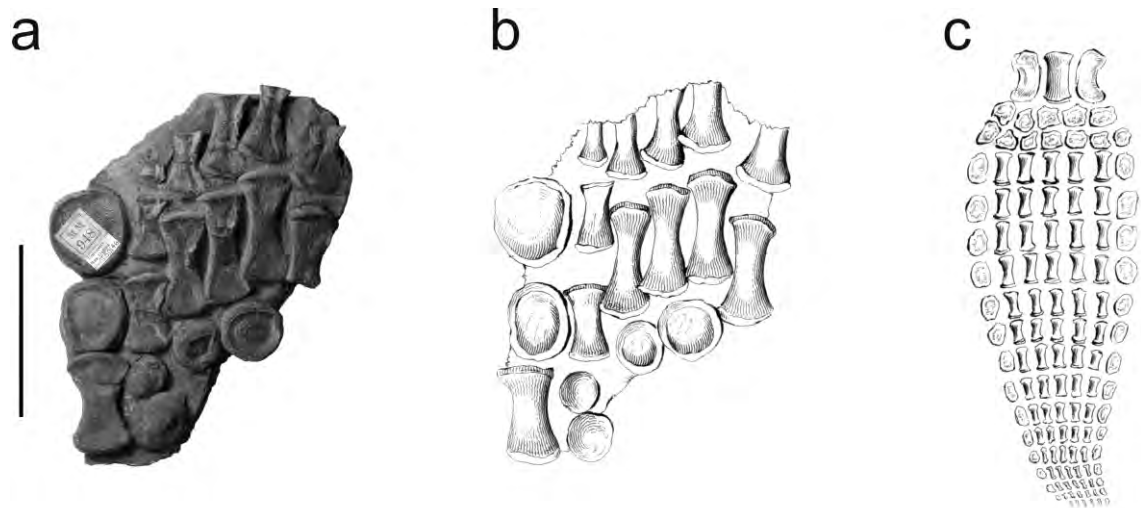
Fig. 1.1: a) OUMNH J.50146, scale bar = 50mm; b) as figured in De la Beche and Conybeare (1821); c) the reconstructed paddle from De la Beche and Conybeare (1821).

1.4

Chapter 2 A new genus of plesiosaur (Reptilia: Sauropterygia) from the Early Jurassic of England

Introduction

Plesiosaurians from the Early Jurassic were some of the first fossil reptiles to be discovered in Britain (e.g. Stukely 1719), and their initial study (De la Beche and Conybeare 1821; Conybeare 1822, 1824) can be regarded as the first competent British work in palaeontological comparative vertebrate anatomy (Taylor 1997). Since then they have been studied systematically for almost 200 years, and collecting of new specimens from coastal and inland localities continues to this day. New plesiosaur genera are still being discovered, both in the 'field' (Sciau *et al.* 1990) and in the museum drawer (Smith and Vincent 2010, Benson *et al.* 2012). Here I describe a new genus of plesiosaurian from the Pliensbachian of England comprising two species. The holotype of one was newly collected in 2000, while that of the other was collected in the late 1970's.

The stratigraphic position of the specimens is significant. Articulated material representing valid taxa from the Lyme Regis and Charmouth area of Dorset is recorded as Sinemurian, (e.g. Benton and Spencer 1995; Storrs 1997, Palmer 2001, Milner and Walsh 2010), while the similar faunas of the Yorkshire coast and Holzmaden are Lower Toarcian (Benton and Taylor 1984; Urlichs *et al.* 1994; Benton and Spencer 1995). The worldwide record of Pliensbachian plesiosaur specimens is poor (summarised by Bardet *et al.* 2008; Smith 2008), and the specimens therefore contribute towards filling what can be called the 'Pliensbachian Gap' (Evans 2003) in the occurrence of articulated plesiosaur specimens representing valid taxa. The recently described *Westphaliasaurus simonsensii* Schwermann and Sander, 2011 is the first diagnostic taxon of Pliensbachian

plesiosaur.

In this chapter I will name and diagnose the new species and provide osteological descriptions. Their osteology will then be compared with other taxa, and the comparisons evaluated to elucidate their relationships. Plesiosaur classification is in a state of flux. Since the very earliest years of plesiosaurian studies the existence of long-necked and short-necked taxa had been apparent (Conybeare 1822, 1824). These contrasting bauplans are now known as 'plesiosauromorph' and 'pliosauromorph' respectively (O'Keefe 2002). The 'traditional' classification of plesiosaurs reflected this in a fundamental dichotomy into two superfamilies: the long necked Plesiosauroidea and short necked Pliosauroidea (both Welles 1943). Since the application of cladistic analysis this has been broadly supported, but two clades, the Polycotylidae Williston, 1908 and Leptocleididae White, 1940 are of uncertain placement, having appeared on both sides of the dichotomy (e.g. O'Keefe 2001; Druckenmiller and Russell 2008; Ketchum and Benson 2010). This has implications for the classification of the new genus described below.

Systematic Palaeontology

Sauropterygia Owen, 1860

Pistosauria Baur, 1887-1890

Plesiosauria Blainville, 1835

Plesiosauria *incertae sedis*

Raptocleidus **gen. nov.**

Synonymy

1995   *?Plesiosaurus*: Storrs: 75, figs 2, 5-8.

1997   *Plesiosaurus dolichodeirus*: Storrs: 150.

2000   *Plesiosaurus dolichodeirus*: Hopley: 136, Fig. 9.

TYPE SPECIES *Raptocleidus blakei* gen. et sp. nov.

ETYMOLOGY From the Latin 'raptor', literally 'thief', but traditionally used to refer to a bird of prey, and Greek 'kleis, kleidos' (κλείς, κλειδός), literally 'key' but also 'clavicle'. The name refers to the broad clavicular arch with notable wing-like lateral expansions and a long narrow squared-off posterior interclavicle posterior process. The resulting structure is reminiscent of the silhouette of a bird of prey in flight.

DIAGNOSIS Small (2-3m) plesiosaurian possessing the following unique combination of characters (autapomorphies indicated with an asterisk): short cervical centra (vertebral length index between 0.6 and 0.8); ventral median ridge on cervical vertebrae; anterior surface of anterior cervical centra extends ventrally as a 'lip'; neurocentral suture low and arcuate; cervical ribs with two conjoined heads, small anterior processes and rounded posterior processes; parazygapophyseal processes on cervical vertebrae; large cervical prezygapophyses sub-equal to centra in width except in anterior-most vertebrae; cervical prezygapophyses transversely concave and joined dorsal to neural canal at their bases; falcate anterior and middle cervical neural spines; flattened triangular surface on anterior margin of cervical neural spines; curved posterior cervical and pectoral neural spines; high number of pectoral vertebrae; posterior cervical, pectoral and dorsal neural spines show alternating morphologies; wide and robust clavicular arch; interclavicle separates clavicles; lateral clavicular

'wings' resting on dorsal surface of ventral rami of scapulae and buttress on medial surface of dorsal rami; ventral rami of scapulae short, contact clavicular arch only; low scapula shelf present; sigmoid humerus shaft, preaxial groove on humerus leading to corner of small preaxial expansion*, prominent proximal postaxial process on humerus shaft; distinct angled epipodial facets; 'interepipodial' groove ventrally on humerus; large forelimb epipodial foramen involving the intermedium; radius with long radiale facet and short angled intermedium facet; proximal preaxial flange on radius; posterior margin of ulna convex.

Raptocleidus blakei sp. nov.

HOLOTYPE LEICT G1.2002 (Figs. 2.1-2.39)

TYPE LOCALITY Blockley Station Quarry, Gloucestershire, UK, grid reference SP 180 370.

TYPE HORIZON The top of the 'Crinoid-Belemnite Bed' (Simms 2004), Charmouth Mudstone Formation, Lias Group. This equates to the very top of the Valdani Subzone, Ibex Zone, Lower Pliensbachian, Lower Jurassic (nomenclature after Page 2003, Jurassic ammonite zones and subzones are treated as standard chronozones following Callomon 1995 and are thus written in roman script with capital initials).

ETYMOLOGY Named for Peter Blake, former resident of the town of Rugby, UK, who discovered the holotype specimen.

DIAGNOSIS Species of the genus *Raptocleidus* distinguished from *R. bondi* by: posterior cervical rib facets formed of two conjoined facets; posterior cervical and anterior pectoral rib facets face posterolaterally; asymmetrical neural spines on the posterior cervical, pectoral and dorsal vertebrae alternately expanded to the left or right;

anterior margin of radius concave. Possesses the following unique combination of characters, unknown in *R. bondi* (autapomorphies indicated with an asterisk): narrow prominent dorsomedian premaxillary ridge; splits into diverging facial ridges on premaxillae and frontals*; dorsomedial cleft; premaxillary facial processes short; circumorbital bones with surface ornamentation; postfrontal cornu projecting into orbit*; orbits larger than temporal fenestrae; posterolateral process of postorbital prominent, length unknown; parietal foramen contacts frontal anteriorly; parietal foramen large and almost circular; 'parietal table' present; parietal crest low; apex of squamosals raised significantly above skull table; squamosal bulb absent; quadrate foramen present; quadrate narrow and parallel-sided in posterior view; ventrolateral flanges of the pterygoids developed into lateral shelves and posterior lappets; ventromedial flanges of the pterygoids suture ventral to the basioccipital; ventrolateral flanges of the pterygoids end anterior to origin of quadrate rami; anterior transverse shelf on pterygoid quadrate ramus present; posterior extension of parasphenoid cultriform process short, limited to anterior third of posterior interpterygoid vacuities; paired posterior processes (cristae ventrolaterales) of the parasphenoid present; anterior process of basioccipital present; ventral basioccipital process present; exoccipital flange present; dentition heterodont; anterior teeth long and slender; small posterior 'ratchet' teeth present; 23 cervical vertebrae (estimated); 7 pectoral vertebrae; minimum of 23 dorsal vertebrae; 4 sacral vertebrae; hypophyseal ridge present on atlas-axis complex; axis intercentrum small; axis rib articulates partly with the atlas centrum; cervical rib facets single anteriorly becoming two conjoined facets posteriorly; dorsal neural spines anteroposteriorly constricted at their bases; caudal neural spines rod-like and posteriorly inclined; caudal zygapophyses abruptly disappear asymmetrically; posterior process of interclavicle present; anterior margin of dorsal ramus of scapula inflected

posterodorsally; dorsal ramus of scapula flares distally; coracoid with long dorsoventrally thin anterior process which is relatively wide transversely; anterior process of coracoid contacts clavicular arch only; cordiform coracoid embayment present; distal blade of ilium expanded, posterior expansion greater; proximal and distal ends of ilium rotated relative to one another; shaft of ilium straight, not curved; acetabular and ischial facets of ilium sub-equal in size; longitudinal rugose ridge on posterolateral surface of distal portion; median pelvic bar absent; pubis rounded anterolaterally, no cornu; femur longer than humerus; tibia lacks facet for intermedium; hindlimb epipodial foramen closed medially by tibia-fibula contact.

REFERRED SPECIMEN OUMNH J.41893-41895: posterior cervical and pectoral vertebrae, ribs and fragment of scapula; from the top of Bed 1, Blockley Station Quarry; Luridum Subzone, Ibex Zone, Lower Pliensbachian, Lower Jurassic.

REMARKS Specimen OUMNH J.41893-41895 was collected by T.J. Palmer in 1978 from just below the 'Pecten Bed', Bed 2 of Simms (2004).

Raptocleidus bondi sp. nov.

HOLOTYPE NHMUK R16330, a partial postcranial skeleton comprising: posterior cervical, pectoral and anterior dorsal vertebrae and associated ribs; incomplete pectoral girdle; humeri and other limb elements (Figs. 2.40 and 2.41).

TYPE LOCALITY The vicinity of Lyme Regis Dorset, UK.

TYPE HORIZON Bed 122 of Lang (1936), Seatown Marl Member (Page 2010, formerly the Green Ammonite Mudstone Member auct.), Charmouth Mudstone Formation, Lias Group. This equates to the Capricornus Subzone, Davoei Zone, Lower

Pliensbachian, Lower Jurassic (nomenclature after Page 2003).

ETYMOLOGY Named for Mr. T. Bond, who discovered the type specimen and presented it to the Natural History Museum, London, in February 1979.

DIAGNOSIS A species of the genus *Raptocleidus* distinguished from *R. blakei* by: posterior cervical rib facets single and face laterally; alternately wide and narrow neural spines on the anterior dorsal vertebrae. Possesses the following autapomorphy: anterior margin of radius almost entirely convex with a small notch and tubercle located mid-shaft.

REMARKS The type specimen was originally identified as a duplicate specimen of *Plesiosaurus cf. dolichodeirus* and remained unregistered at the NHMUK until 2009. It has been partially prepared both mechanically and chemically at the museum.

Raptocleidus sp.

Synonymy

1995   *?Plesiosaurus*: Storrs: 75, Figs. 2, 5-8.

1997   *Plesiosaurus dolichodeirus*: Storrs: 150.

2000   *Plesiosaurus dolichodeirus*: Hopley: 136, Fig. 9.

REFERRED SPECIMENS BRSMG Ce17972a-o, most likely from the Capricornus Subzone of the Davoei Zone, Lower Pliensbachian, Lower Jurassic on the coast between Charmouth and Seatown, Dorset, UK (Storrs, 1995); GLRCM specimen and BHI 126445, both from Blockley Station Quarry and so from the Valdani or Luridum Subzones, Ibex Zone, Lower Pliensbachian, Lower Jurassic (Simms 2004).

REMARKS Two partial juvenile specimens are referred to *Raptocleidus sp*. as they

cannot be confidently referred to either *R. blakei* or *R. bondi*. The GLRCM specimen, a partial juvenile postcranial skeleton, was collected from Blockley Station Quarry in 1990 by Messrs Steve Callaway and Terry Smith. It is mounted in plaster in the museum gallery, and access into the exhibition case is restricted, making it difficult to distinguish real bone from cast replicas within the mount. It is accompanied by a schematic indicating real bone and reconstructed elements so that, for example, 66 of the 80 vertebrae are identified as being real bone. It is referred to *Raptocleidus* due to the proportions of the cervical vertebrae, highly inclined caudal neural spines, and anterior groove on the humeri.

BRSMG Ce17972a-o, a partial juvenile postcranial skeleton, was referred to *?Plesiosaurus sp.* by Storrs (1995) and was tentatively included in the hypodigm of *P. dolichodeirus* by Storrs (1997). The specimen is here referred to *Raptocleidus* due to the proportions of the cervical vertebrae, the posteriorly curving neural spines, and coracoid with rounded median embayment(s).

Casts of the girdles, propodials and a reconstructed forelimb of BHI 126445 were figured by Carpenter *et al.* (2010). It is referred to *Raptocleidus* due to the outline of the humerus and the pectoral girdle morphology, which includes a cordiform coracoid embayment.

Description of LEICT G1.2002

LEICT G1.2002 is a moderately sized plesiosaur approximately 3 m in length. The specimen is approximately 85% complete, lacking the lower jaw, the front of the skull, and most of the right hind limb. The neural arches are fused to all vertebral centra except for the last preserved caudal vertebra, the cervical and caudal ribs are partly

fused to their respective centra, and the girdle elements are unfused. It is therefore an 'adult' specimen by the criteria of Brown (1981).

Geological setting and taphonomy

The specimen (LEICT G1.2002) was recovered from the floor of Blockley Station Quarry in May, 2000 (P. Blake pers. comm.). Blockley is a classic location, of interest to stratigraphers and palaeontologists for many years (Callomon 1968). The floor of the quarry is formed by the 'Crinoid-Belemnite Bed' (or 'Bed Z' of Dineley and Metcalf 1999), a moderately well-cemented shelly limestone (Simms 2004). As LEICT G1.2002 was excavated from mudstones, it was initially assumed to have come from Bed 1, just above the Crinoid-Belemnite Bed (Simms 2004). However, patches of shelly debris are present in several places on the dorsal vertebrae, and crinoid ossicles are not uncommon, both suggestive of the Crinoid-Belemnite Bed. Teeth referable to the neoselachian shark *Agaleus dorsetensis* Duffin and Ward, 1983, were collected with the specimen, one *in situ* on the lower surface of the nodule containing the abdominal region of the plesiosaur. This shark is only known from the Crinoid-Belemnite Bed at Blockley (Dineley and Metcalf 1999). Therefore the plesiosaur's carcass was deposited at the top of the Crinoid-Belemnite Bed, and was exposed on the surface. Following burial of the remainder of the skeleton by Bed 1 sediments, components of the top of the Crinoid-Belemnite Bed were incorporated into the calcareous nodule which grew around the abdominal region during diagenesis.

The occurrence of the specimen at the top of the Crinoid-Belemnite Bed places it at the boundary between the Valdani and Luridum Subzones of the Ibex Zone, Lower Pliensbachian (Bessa and Hesselbo 1997; Simms 2004). It is thus one of the few Lower

Jurassic plesiosaur specimens with a precisely known stratigraphic position.

The specimen was preserved with the dorsal vertebral column lying on the left side with the limbs and girdles laying dorsal side down. The specimen is shown in Figures 1 and 2 from the underside, there being some damage from the quarry machinery to the upper surface of the specimen. The exact attitude of the head, neck and tail are unknown, although the caudal vertebrae can be seen semi-articulated in photographs of the specimen taken during excavation (LEICT archives). A partial cervical neural spine crushed onto cervical vertebra G1.2002.58 indicates that at least some parts of the neck were disarticulated approximately 180º relative to each other. Similarly, although there are many limb elements preserved, many could not be placed in the taphonomic reconstruction, and were omitted from Figures 2.2 and 2.3. Encrusting epibionts, particularly oysters, serpulid worm tubes, and discinid brachiopods, are present on many bones on both upper and lower surfaces, indicating that the skeleton was exposed on the sea floor prior to burial, which would have been gradual. As is not uncommon in plesiosaur specimens preserved in mudrocks (e.g. Martill 1986, 1990), the abdominal area is encased in a nodule, while the limbs, neck and tail extend into the surrounding sediment. During preparation and study of the skeleton numerous quartzose grains have been encountered along with cephalopod hooklets, especially on the taphonomically ventral surface of the specimen. It is possible that these represent gastric contents of the animal as neither has been reported as present in the Crinoid-Belemnite Bed (Dineley and Metcalfe 1999; Simms 2004).

It can be seen from Figure 2.2 that the pectoral, dorsal, and sacral regions of the vertebral column are articulated, and that the girdles and propodials are preserved close to their original anatomical positions. It should be noted that there is a break in the

dorsal vertebral sequence, and this may be where the floating carcass burst, releasing the gases of decomposition. In contrast, the phalanges and gastralia are preserved with a much more chaotic distribution. Some gastralia are preserved in close association with one another which could be a case of imbrication due to current sorting rather than any true anatomical relationship.

Methodology

Specimen LEICT G1.2002 had been fragmented by the quarry machinery, and no plan of its disposition had been made at the time of its discovery and excavation. The specimen was reconstructed by the matching of broken surfaces and bone-on-bone contact marks. Paraloid B57 resin dissolved in acetone at a suitable concentration was used as an adhesive and consolidant, and a mixture of glass beads and paraloid resin (Larkin and Makridou, 1999) was used as a filler, along with milliput epoxy putty. In the latter case, a layer of paraloid resin was used as a separator. Matrix was removed with Chicago and Abro airscribes, and an airbrasive machine (Texas Airsonics BW'7) using calcium bicarbonate and aluminium oxide powders. Elements of the skull were briefly prepared chemically using 5% acetic acid to remove a surface dusting of matrix. The specimen was photographed with Nikon Coolpix 900 and Nikon D40x digital cameras. A large composite image (Fig. 2.2) of the specimen's layout was made using Corel Photopaint software and bone outlines were traced by hand from the composite image using CorelDraw drawing software to produce a diagrammatic plan (Fig. 2.3). CT scanning was carried out at the Royal Veterinary College, Hatfield, using a Picker PQ5000 system.

The Skull

Dermatocranium – the dermal skull roof

The dermal skull roof is incomplete, with the rostrum and lateral portions missing, but what remains is generally well preserved. The main portion (LEICT G1.2002.7-8) is shown in dorsal, ventral, lateral and posterior views, and in selected sectional views (Figs 2.4-8). The partial postorbital bars (LEICT G1.2002.9 and G1.2002.11) are shown in Fig. 2.9 and the right suspensorium (LEICT G1.2002.10) in Fig. 2.10. Although the relative length of the rostrum is unknown, the anteroposterior extent of the orbits can be reconstructed from the positions of the ventral antorbital ridge and postorbital bar. The orbits would have been larger than the temporal fenestrae.

Premaxillae

The premaxillae (pmx) are represented by the posterior-most 40 mm of the facial processes, although these are poorly preserved anteriorly. The facial processes are remarkably short and would have ended anterior to the orbit. The premaxillae are bounded by the frontals posteriorly and laterally, while damage obscures another possible lateral suture anteriorly (sut?). This could be with an anterior extension of the frontal, the maxilla, a distinct tongue of premaxillae similar to that seen in *Muraenosaurus leedsii* (pers. obs.), or even the nasal. Nasals have traditionally been thought to be absent in plesiosaurs (e.g. Romer 1956; Taylor and Cruickshank 1993b) but have recently been recognised in certain pliosauroid plesiosaurs, (Noè 2001; O'Keefe 2001). In dorsal view (Fig. 2.4) a median interpremaxillary suture is visible at the anterior of the preserved area on top of a distinct dorsomedian ridge (dmr). This ridge is triangular in section (Fig. 2.8A) and divides posteriorly into paired diverging facial ridges (dfr). The median suture becomes more distinct as this happens, but it does

not open up into a dorsomedian foramen sensu Taylor (1992), Cruickshank (1994 and 1997) and Smith (2007). The cleft formed between the diverging ridges is here referred to as the dorsomedian fossa (dmf). In lateral view (Fig 2.6) the dorsal edge of the dorsomedian ridge is gently convex anterior to the point of divergence, and gently concave posterior to it.

The posterior-most point of each premaxilla is on the medial surfaces of the diverging facial ridges. The suture rises to the crest of the ridge before running anteriorly and slightly laterally. There is some interdigitation with the frontal, especially posteriorly, and the region is ornamented with fine striations, some small foramina, and gently undulating ridges. The premaxilla/frontal suture appears to ride up over a thickened region of bone at the anterior of the underlying frontals. This thickened region is damaged on both sides, probably due to dorsoventral crushing of the skull, and is the site of the possible lateral suture referred to above.

In ventral view (Fig. 2.5) the junction between the premaxillae and frontals is V-shaped, with a triangular region formed from the premaxillae meeting a Y-shaped ridge on the frontals. The suture seems to be formed by interdigitating laminae, and these continue forward onto the preserved remainder of the premaxillae as a heavily fluted ornament. It is difficult to make out much internal detail in section (Fig. 2.8A) as the bone is cancellous and not heavily indurated so that sutures are not obvious. However, the general texture suggests that the frontals form an inverted "V" which is capped by the similarly shaped premaxillae. Ventrolaterally there appear to be interdigitating laminae of both elements, with a medial triangular spur of the premaxillae. The frontals thus appear to be 'grasped' both dorsally and ventrally by the premaxillae.

Maxillae

Two apparent fragments of maxilla from the region of the presumed premaxilla/maxilla suture are preserved. One contains a broken tooth base and fragmentary alveoli, and both have an ornament on the presumed lateral surface suggestive of a squamous suture. The texture of the broken surfaces is similar to that seen in the thickened lateral regions of the premaxillae, so it is possible that these fragments are derived from this region. However, no close fit could be made.

A fragment of the left maxilla is preserved with the palatine (see below). The preserved portion formed the palatal surface medial to the tooth row, and fragments of two primary dental alveoli are preserved. One alveolus contains a fragment of tooth. Medial to the alveoli, the ventral surface is sculpted to form a facet for the overlapping lateral edge of the palatine. The maxilla has twisted dorsally in its suture with the palatine making the detailed relationships hard to work out. The maxilla would most probably have formed the lateral border of the internal naris anterior to the preserved termination of the palatine, although this cannot be determined for certain.

Prefrontals

The prefrontals (prf) appear to be a small, but significant part of the skull roof. In ventral view (Fig. 2.5) the prefrontals contribute to the ventral antorbital ridge (vaor) anterolaterally, although their small size indicates that this structure would not have extended much beyond the preserved portion. The sutures here between the prefrontals and frontals are straight, and their form indicates that the prefrontals fill a simple cleft in the frontals. In dorsal view, the left prefrontal forms the bottom of a trough in the left frontal, which may therefore have formed a facet (mxf) for an ascending process of the maxilla. A small portion of this facet (fac) is preserved on the right side on the broken

lateral edge of the frontal. Laterally, a thin skin (0.5 mm) of prefrontal can be seen covering the frontal on the left side. Lateral to this is a notch in the edge of the frontal, identified as part of the prefrontal facet (prff). A similar notch is preserved on the right side in a more posterior position, and it seems likely that the posterolateral point of the prefrontal would have occupied it, forming the anterodorsal rim of the orbit.

Frontals

The frontals (f) are large paired bones forming the main structural element of the preserved skull roof anterior to the parietal foramen. Anteriorly, they meet the premaxillae and the prefrontals. As described above, there may have been another anterior contact, either maxilla or nasal. Posteriorly, they meet the parietals and postfrontals at approximately the level of the parietal foramen, although the internal relationships of these bones are much more complicated than they would appear from the surface. The midline suture between the frontals is visible for their whole length both dorsally and ventrally.

In dorsal view (Fig.2. 4) the frontals continue the diverging facial ridges (dfr) which arose on the premaxillae. These become lower and more rounded posteriorly, ending at approximately the level of the prefrontals. The dorsomedian fossa (dmf) deepens, as can be seen in section (Fig. 2.8B), and the interfrontal suture opens up into a slit at the bottom of the fossa. Lateral to the diverging facial ridges the frontals thin considerably, so that they are approximately 1mm thick at the edges of the preserved region. The broken edge on the right hand side reveals what may be a longitudinal facet (fac?) for a neighbouring element which could be maxilla, prefrontal or possibly nasal. An apparent natural edge running along the anterior portion of this feature would suggest that it is a

facet and not an internal channel seen in section.

As noted above, a trough on the left frontal is floored by the prefrontal, and would have formed a facet for the maxilla (mxf). The relationships of the prefrontal and frontal in this region were described above. The frontals form the dorsal margin of the orbits (the supra-orbital flanges of Noè 2001), the edges being thin and crenulated. Anteriorly the supra-orbital flanges would have been highly arched in the region of the contact with the prefrontal. The supra-orbital flanges would have been arched to a lesser degree more posteriorly. The frontals are pierced by foramina for much of their length. CT scans show internal cavities which would presumably have been confluent with these foramina (e.g. Fig. 2.8B).

The frontals and postfrontals meet in a meandering suture which runs anterolaterally from the level of the parietal foramen (pfor) to the posterodorsal corner of the orbit. A small hook-shaped extension of the orbit would have extended between the posterior end of the supraorbital flange (formed by the frontal) and the postfrontal. The frontals extend posteriorly almost to the parietal foramen. Discrete fingers of the frontal seem to have overgrown the parietals leading to an uneven suture which trends posterolaterally.

In ventral view (Fig. 2.5) the frontals form an anterior median ventral frontal ridge (mvfr). The anterior end of this splits where it meets the premaxillae as described above, and accessory ridges to either side of the median ridge die out posteriorly. Lateral to this the frontals are dorsoventrally deep at the position of the presumed suture referred to above. The relatively robust nature of this region indicates that the element here was probably either a tongue of premaxilla or the maxilla itself rather than a nasal. The frontals are smoothly curved to either side of the median ventral frontal ridge, and would have formed the roof of a cavity underlying the external nares. An apparent

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posterior foramen on the right hand side is a combination of damage from crushing and an artefact of preparation. The median ventral frontal ridge splits posteriorly and meets the ventral antorbital ridge and the frontal wings (Noè 2001). The former sweep anterolaterally and are mainly formed by the prefrontals as described above. The frontal wings (fw) are longitudinal crenulated ridges either side of a median trough which would have formed the olfactory canal (olc). The interfrontal suture is open ventrally at the apex of the olfactory canal. The frontal wings also form the medial walls of the orbits. The left frontal wing is broken, and shows what appears to be a longitudinal canal within the bone. This feature is probably a result of the intense folding of the frontals as seen in section more posteriorly (Fig. 2.8C). The contact between the postfrontal and frontal is covered ventrally by the parietal. The parietals form a triangular wedge anteriorly between the frontals, and the suture follows a zigzag path to the posterodorsal corner of the orbit.

In lateral view (Fig. 2.6) the diverging facial ridges can be seen to be slightly convex dorsally. The anterior of the supraorbital flange can be seen to be distinctly arched relative to the more posterior portion. The latter would have originally extended slightly more dorsally as there is a small amount of damage caused by crushing. The frontal wings form the medial wall of the orbit. Dorsal to the posterior end of the frontal wings there is a small isolated curved length of suture. On the right hand side (Fig. 2.6A) the underlying parietal is exposed, while on the left (Fig. 2.6B) this suture is closed, but a number of foramina surround it. These structures must be the result of incomplete fusion of thin processes of the frontals which have overgrown the parietals. The complex internal relationships of the frontals and parietals will be described below.

Postfrontals

The postfrontal (pof) is represented by fragments on both sides (Figs 2.4-6, 9), and it is possible to reconstruct it with a high degree of confidence. They contribute to both the orbits and the temporal fossae and form the dorsal portion of the postorbital bar. It is unknown whether they also contribute to the border of the temporal fenestra, as they could have been excluded by a contact between the postorbital and parietal. The suture with the parietal runs posterolaterally from the end of the suture with the frontal, so that the postfrontals are exposed close to the parietal foramen, without actually reaching it. The suture with the postorbital runs laterally across the postorbital bar, and has a tightly undulating form. Laterally there is a sharp ridge (rdg) demarcating the dorsal skull surface and the sloping wall of the temporal fossa. This ridge fades medially, and is distinct from faint ridges formed by the diverging sagittal crest (see below). The dorsal and ventral surfaces are pierced by numerous foramina.

The postfrontals have a distinctive morphology at the point where they form the posterodorsal corner of the orbit. The edge forming the orbital rim suddenly turns 90 degrees lateral to the suture with the frontals, forming small rounded "horns" projecting into the orbits. These are here termed the postfrontal cornua (pofc). A distinct notch would have been formed in the border of the orbit between the postfrontal cornua and the supraorbital flanges.

Postorbitals

The postorbital (po) is partially preserved on the left side, where it forms the lower half of the postorbital bar (Fig. 2.9). It is bordered dorsally by the postfrontals, and sutural surfaces are preserved anteriorly and posteriorly for the jugal and squamosal (sqf) respectively. The lateral and medial surfaces bear foramina in a similar way to the

2.18

postfrontals. The ridge seen on the postfrontals dividing the temporal fossa from the skull roof proper continues onto the postorbital, but fades out. The posterior-most portion of the postorbital has a sharp dorsal edge which would have formed the anterodorsal edge of the temporal bar. This sharp edge also fades out anteriorly onto the curved posterolateral surface of the postorbital. It is clear that the postorbital would have continued posteriorly to form a "footplate" (pofp) which would have overlapped the squamosal in a similar fashion to that described in *Leptocleidus capensis* by Cruickshank (1997). Only a small part of the sutural surface for the jugal is preserved, but it is enough to allow the fragment of that bone preserved to be articulated with the postorbital. The postorbital bulges laterally beyond the line of the temporal bar to a marked degree, and the orbits would have been expanded at this point. The postorbital is broken medially, where it would have formed the lateral part of the anterior wall of the temporal fossa. However, the broken surface shows that this sheet of bone would have been relatively thick, forming a robust postorbital flange (pofl). Similarly, the ventral broken surface of the postorbital shows that this element was robust at this point.

Jugals

A fragment of the left jugal (j) is preserved, and this can be articulated with the postorbital (Fig. 2.9). The preserved portion is a curved sheet of bone which continues the curve of the wall of the orbit. The junction between the two bones would have been a meandering sub-horizontal suture, with the postorbital underlying the jugal medially as the postorbital facet (porf) can be seen on the dorsomedial edge. As the most anterior edge of the preserved jugal appears to be part of the orbital rim, the anterior-most point of the suture would have been just posterior to this. The wall of the orbit would have flared laterally beyond the line of the anterior ramus of the squamosal.

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Parietals

The parietals (p) constitute the remainder of the median skull roof, and run from the anterior border of the parietal foramen posteriorly to their contact with the squamosals. Anteriorly they contact the frontals and postfrontals. The nature of the assumed contact with the absent supraoccipital is uncertain. Although the lateral edges of the parietals are damaged for much of their length, enough is preserved to be able to restore the general outline. The narrowest point is approximately halfway between the level of the anterior border of the parietal foramen and the midline contact with the squamosals. The parietals may have contacted the postorbitals laterally as in other taxa.

In dorsal view the median suture between the paired parietals can be seen for their whole length. The suture becomes enlarged into an interparietal foramen (ipf) where the dorsal rami of the squamosals overlap the parietals. The parietals form a shallow sagittal crest which splits into diverging ridges posterior to the parietal foramen. Between the ridges and the parietal foramen is a large triangular depression - the 'parietal table' (ptab) of Druckenmiller (2006). The interparietal suture is deflected into a sinuous curve as it runs over a faint median eminence within the parietal table. The parietal foramen is remarkable for both its large diameter (approximately 10mm) and sub-circular shape. The parietal foramen in plesiosaurs is usually a compressed oval in shape, and is inclined posteroventrally. In this animal it is oriented approximately vertically. The parietals form the anterior wall of the parietal foramen, where they can be seen to wrap around it, ventral to the frontals. The parietals meet the postfrontals just posterior to their junction with the frontals. The suture with the postfrontal runs approximately laterally in dorsal view, and in lateral view can be seen to descend the anterior wall of the temporal fossa. Posteriorly the parietals are overlapped by the dorsal rami of the

squamosals. The outline of this contact is best preserved on the left hand side. There is a subtle sigmoid outline to the lateral edge of the skull roof just anterior to where the squamosal and parietal meet laterally. Distortion has largely masked this in dorsal view and has accentuated it in lateral view.

In ventral view (Fig. 2.5), the median suture between the paired parietals persists for their whole length. They form an anteriorly oriented triangular wedge between the frontals. The suture runs back to the posterior corner of the frontal wings, and then turns to run dorsally up the dorsomedial wall of the orbits with some interdigitation of the bones. The ventral border of the parietal foramen is rounded, and lateral to the foramen the parietals are thickened and ornamented with rugosities and foramina. CT scans show that these foramina lead to branching channels within the body of the bone which were presumably nutritive in function. Posterior to the parietal foramen the parietals are hollowed into a deep triangular excavation (tri), which can be seen in sagittal section in Fig. 2.8F, and which would have formed the dorsal part of the cranial cavity. The triangular excavation may have housed a portion of the brain, possibly the tectum or cerebellum (Romer 1956), but may have housed the dorsal longitudinal sinus as was suggested for a similar structure in the theropod dinosaur *Majungasaurus* by Sampson and Witmer (2007). The posterior wall of the triangular excavation extends ventrally as a rugose transverse parietal ridge (tpr) which may have been the site of attachment for the supraoccipital. The transverse parietal ridge is breached by a median gap, and the lateral portion is elaborated into a small rugose boss. The interparietal suture becomes sinuous as it traverses the triangular excavation and transverse ridge. The ventral surface of the parietals is smoothly concave posterior to the ridge, except for a small fossa just anterior to the squamosal on the right hand of the midline. Damage makes it hard to be certain, but this structure may represent an interparietal foramen similar

to that seen on the dorsal surface. The suture between the parietal and squamosal is broadly sigmoid, with a finger of parietal extending along the lateral edge of the skull roof.

In lateral view (Fig. 2.6) the relatively low sagittal parietal crest (pc) is apparent. It even decreases in height between the parietal table and the contact with the squamosals. It can also be seen that the parietals contribute to the robust postorbital flanges (pofl) which are directed posteroventrally and form the anterior wall of the temporal fossae and fenestrae.

Squamosals

The squamosals (sq) conform to the typical triradiate structure seen in plesiosaurs with anterior, dorsal and ventral rami. However, they are incomplete and are represented by the partial left squamosal and dorsal ramus of the right squamosal on the main skull fragment (Figs 2.4-8) and an isolated fragment of the right suspensorium (Fig. 2.10). They can be seen to contact the parietals dorsally and the quadrate ventrally, while they would have contacted the postorbital bar anteriorly.

In dorsal view (Fig. 2.4) the dorsal rami of the squamosals (drsq) can be seen to form a gently curving squamosal arch forming the post-temporal bars. The left hand side has been distorted so that the squamosal has become rotated medially. This makes the posterior edge of the left post-temporal bar more concave, and causes the anterior ramus (arsq) to point anterolaterally; the profile of the preserved part of the right post-temporal bar is closer to the original orientation. The squamosals meet in a median suture which broadly zigzags across the midline of the skull. Anterior to this they cover the underlying parietals. It is notable that there is no posteriorly-projecting squamosal bulb

on the midline, as was reported in most pliosauroids by O'Keefe (2001). The anterior edge of the post-temporal bar is developed into an anterodorsal crest (adc) (Taylor 1992), although this is only preserved distally on the left hand side. Rugosities (rug) are present along the length of the dorsal ramus dorsally and posteriorly. The largest projects posteriorly dorsomedial of the quadrate socket (qsoc), and would probably have been attachment sites for the epaxial musculature. Smaller rugosities are present more medially, and are described below. In ventral view (Fig. 2.5) the dorsal rami can be seen to overlap the parietals, and the anterodorsal crest can be seen to project anteriorly. The ventral ramus splits into ventromedial (vmfs) and ventrolateral (vlfs) flanges (Taylor 1992), forming the edges of the quadrate socket. The quadrate socket is deep, extending 10 mm dorsally into the body of the squamosal. The dorsal margin is arched, forming one half of a large quadrate foramen (qfor).

In lateral view (Fig. 2.6) the vertex of the squamosal arch projects dorsally above the level of the parietal crest, the anterior edge sloping posterodorsally. Although damaged, enough is preserved of the anterior ramus to show that there was a significant temporal emargination ventral to the bone. In left lateral view (Fig. 2.6B), the ventral ramus appears to slope posteriorly at an angle of approximately 25° to the horizontal axis of the skull roof. This degree of slope has been slightly exaggerated by the distortion outlined above, and also by photographic parallax in the figure. It is estimated from projections derived from CT data that the true slope was approximately 19°, taking the distortion into account. The prominent rugosity noted above marks a change in angle between the ventral ramus and the dorsal ramus. A foramen (for) is visible in the lateral surface of the left squamosal ventral to the main axis of the anterior ramus. Corresponding lateral foramina can be seen on the right squamosal, and the medial surface is also perforated by foramina (Fig. 2.10G & H). The medial surface of the

left anterior ramus, (visible in Fig. 2.6A) bears a ridge (rdg) which trends anteroventrally. This was probably the site of part of the origin of the *m. adductor mandibulae externus* (Taylor 1992; Rieppel 2002). The anterior ramus would have contacted the postorbital, as part of the squamosal facet (sqf) is present on that bone (Fig. 2.9B,C). The squamosal would almost certainly have contacted the jugal, and may have reached the maxilla.

In posterior view (Fig. 2.7) the squamosal arch can be seen to be low and broad. The intersquamosal suture continues the broadly zigzagging form seen dorsally, crossing the midline. The rugosities are well displayed in posterior view; the most prominent, dorsomedial to the quadrate socket, was described above. A smoother peak of bone lateral to this on the other side of the quadrate socket may represent an attachment site for the integument, similar to those identified in '*Rhomaleosaurus' megacephalus* (Cruickshank 1994b). Medial to the position of the prominent rugosity, an indented rugose area is seen on both sides on the posterodorsal surfaces of the dorsal rami. These are most likely attachment pits for the nuchal ligament. Dorsomedially on the left hand side, a slightly rugose plateau is preserved, which may have been another integumentary attachment site. The right suspensorium fragment (Fig. 2.10) preserves an anterodorsal quadrate flange (adqf) of the squamosal which would have articulated with the anterior squamosal facet of the quadrate (asqf).

Internal relationships of dermal skull bones

The frontals, parietals and squamosals have complex internal relationships which can be seen in natural breaks, and are further illustrated by CT scans (Fig. 2.8). In broad terms, the parietals extend as a wedge within the frontals. The midline of the skull roof, which appears from the surface to consist of a simple, relatively straight suture between the

elements of the left and right sides, is strengthened by invasions of one half by the contralateral element.

In sagittal section (Fig. 2.8E), the frontals have a simple butt-joint at the level of the anterior margin of the orbits. More posteriorly the frontals interleave with anteroventrally curving lamellae. This area can be seen in transverse section (Fig. 2.8C), where the curving lamellae appear as a zigzag suture between right and left elements. This section also reveals the anterior ends of the parietals, apparently forming paired prongs piercing the frontals. CT scans show that both prongs are actually formed by the left parietal, which has invaded the right hand side of the skull, with the right parietal forming a small fillet underlying the right hand prong. This section also shows that the frontal wings are formed by flanges of the frontals folding back on themselves. In a more posterior section (Fig. 2.8D) the parietals can be seen sending dorsomedially oriented lamellae into the overlying frontals, with the left parietal in the process of invading the right hand side of the skull. An oblique section just posterior to this (Fig. 2.8F) shows the left frontal reduced to a hook-shaped process underlying the detached postfrontal and firmly anchored within the parietal. A small portion of frontal lying ventral to the hook represents the posterior end of the frontal wing, now surrounded by the parietal. Posterior to the parietal foramen (Fig. 2.8E and G) the parietals have a tightly interdigitating suture with one another. The parietals and squamosals meet in a tongue and groove contact (Fig. 2.8H). The squamosals form the majority of the skull roof at the position of the section, but the parietals send lamellae posteriorly both dorsally and ventrally, which are then covered by a thin skin of squamosal.

Dermatocranium – the palate

The palate is represented by a fragment which appears to represent the area around the

left internal naris (LEICT G1.2002.13), and portions of both pterygoids and the right ectopterygoid (LEICT G1.2002.1, 2 and 6, Figs 2.11-16). The fragment of the narial region is crushed and hard to interpret. It has been oriented according to the perceived direction of the fragmentary maxillary alveoli. In addition to this are several small fragments of thin bone which probably represent elements of the palate. The left pterygoid and posterior right pterygoid are preserved sutured to the braincase. Two additional fragments may represent the anterior ends of the pterygoids, based on their triangular cross-sections.

Palatines

The palatines are represented by the anterior portion of the left element. It forms the posterior border of the internal naris, and can be seen to have contacted the vomers medially, and the maxilla laterally. In ventral view a slightly recessed and rugose triangular area posteromedial to the internal naris probably received an overlapping posterior extension of the vomer. A sutural surface for the vomer can be seen anterior to this on the edge of the naris. Anterolaterally the maxilla would have overlapped the palatine, while the relationship between the two bones was reversed posteriorly, as noted above. In dorsal view, the palatines become thickened dorsally posterior to the naris, forming the wall of a posteriorly sloping narial channel. This thickening slopes laterally towards the suture with the maxilla, and a ridge runs from the posterolateral border of the narial channel to the anterior-most point of the palatine. Medially there is a facet for a similar thickening of the vomer, and a sharp ridge runs from the posteromedial border of the narial channel to the anteromedial end of the palatine.

Ectopterygoids.

The posterior portion of the right ectopterygoid (ect) is preserved, along with a fragment

that may represent its anterior end (LEICT G1.2002.6, Fig. 2.11). There is no connection between the two, but they share a similar curved cross section. The ectopterygoid is broad transversely with no constriction. Laterally it bears a rugose oval facet for articulation with the cheek, presumably the jugal. Anterior to this, an embayment in the lateral edge may represent part of a suborbital fenestra. Medial to the jugal facet, the bone deepens into a distinct, ventrally directed ectopterygoid boss, which then tapers to a medially oriented process. The ventral surface of the boss is rounded at its deepest point. Medially it is sharp-edged, forming the ventral edge of the medial process, while laterally it is flat, merging into the ventral surface of the cheek facet. The ectopterygoid can be fitted against the partial right pterygoid in a way that shows that the lateral ramus of the pterygoid would have dorsally overlapped the medial process. The dorsal surface at the base of the process is sculpted into a series of troughs, which would have received the distal end of the lateral ramus of the pterygoid. When the ectopterygoid is placed in approximate articulation with the pterygoid, it can be seen that the cheek facet would have been oriented dorsolaterally, rising up from the plane of the palate.

The anterior part of the ectopterygoid is dorsally dished from side to side, and the same contour is seen on the separate anterior fragment. This bears a sculpted surface, presumably for contact with the palatine. Laterally the ventral surface has a rugose border of about 3 mm from the edge. This is interrupted medially by a small projection, and comes to an end at the base of an anteriorly directed process. The dorsal surface of this bears some light ornament, and is concave, indicating that it was probably overlain by the palatine. Thus the ectopterygoid overlapped the palatine laterally, while their relationship was reversed medially. The ectopterygoid is pierced by foramina, notably

on both ventral and dorsal surface medial to the cheek facet and also at the point at which it is broken.

Pterygoids

The pterygoids (pt) evidently had the triradiate structure seen in some other plesiosaurs, with anterior, lateral and posterior/quadrate rami. However, the full extent of the anterior ramus is uncertain. They are represented by the lateral ramus of the right pterygoid (Fig. 2.11) and the lateral and quadrate rami of the left pterygoid preserved attached to the basicranium (Figs 2.12-16). A small portion of the quadrate ramus of the right pterygoid is also preserved sutured to the basicranium and the left pterygoid. Two small fragments may represent the tips of both anterior rami: they can be fitted together, forming the anterior border of what would be the anterior interpterygoid vacuity. They are triangular in section, matching the condition seen in other plesiosaurs (e.g. *'Rhomaleosaurus' megacephalus* and *Muraenosaurus leedsii*, pers. obs.), and have grooved and furrowed anterior ends where they would have contacted the vomers.

The lateral ramus (lrpt) is transversely convex ventrally. Anteriorly there is a well-defined embayment between the anterior and lateral rami, which would have formed the posterior edge of the lateral palatal fenestra (O'Keefe 2001; Druckenmiller 2006) if this feature was present. However, a small shelf on the ventral surface suggests that the palatine overlapped the pterygoid ventrally at this point, restricting the lateral palatal fenestra to a medial slit. Lateral to this on the left pterygoid is a small lappet, which would have formed a step in the contour of the bone. The right pterygoid is broken just medial to the position of this lappet (Fig. 2.11). Lateral to the lappet the pterygoid is thickened dorsoventrally marking the base of the process which would have overlapped the ectopterygoid (see above). The posterior edge of the lateral ramus is slightly

2.28

thickened and rugose distally, which would represent the beginning of the pterygoid-ectopterygoid flange, although it is not deflected ventrally below the plane of the palate. Medially the lateral ramus extends towards the parasphenoid cultriform process (pscp), but did not contact it in the preserved material. The medial-most edge is broken on both sides, and there is no evidence of a contact on the preserved cultriform process, so that any contact must have occurred more anteriorly.

The basipterygoid articulation (bpta) of the pterygoid and braincase is strongly developed. It is situated at the junction of the essentially horizontal lateral ramus and the essentially vertical posterior ramus. The pterygoid bears a large facet for the basipterygoid process (bptp) of the basisphenoid. Sculpture in this region may represent a fused suture between the pterygoid and epipterygoid (see below).

The portion of the plesiosaur pterygoid between the junction of the lateral and anterior rami and the end of the basioccipital has been referred to as the posterior ramus, with the quadrate ramus proper beginning posterior to the level of the basioccipital (Andrews 1913; Noè 2001), and this convention will be followed here. The posterior ramus of the pterygoid (prpt) forms the lateral edge of the posterior interpterygoid vacuity (pipv), and is convex in transverse section ventrally and medially, and slightly convex laterally. The posterior interpterygoid vacuity is incompletely split into two by the parasphenoid cultriform process, and despite the incomplete anterior end it would have been relatively short and wide, with a minimum ratio of length to width of approximately 0.8. The posterior interpterygoid vacuity is relatively anterior in position when compared to the front of the subtemporal fenestrae formed by the lateral pterygoid rami and the ectopterygoid. Taylor (1992) described the posterior ramus of the pterygoid of *Rhomaleosaurus zetlandicus* as possessing dorsal, ventrolateral and ventromedial

flanges, and similar features are seen in this material. The dorsal flange (dfp) is comparatively low, and bears a lateral excavation (lex) just posterior to the basipterygoid articulation. This may have been occupied by a cartilaginous epipterygoid, or may have been the site of muscle attachments. A second, more posterior, lateral excavation was probably a continuation of the same feature. The ventrolateral flange (vlfp) is drawn out into two lateral pterygoid lappets (lpl) or shelves. The first lies between the lateral ramus and the base of the quadrate ramus, while the second lies ventral to the base of the quadrate ramus. The ventromedial flanges of the pterygoids (vmfp) meet ventral to the basicranium, forming a complex structure with the parasphenoid and basioccipital. The inter-pterygoid suture is meandering, and runs off-centre from right-anterior to left-posterior. The pterygoids here are slightly rugose. Dorsally they are sutured to the vertical plate of the basioccipital, with the interdigitating suture being visible on the broken surface in right lateral view. Anteriorly the ventromedial flanges contact the anterior process of the basioccipital (see below), and the parasphenoid either side of this. The rugose facet for this contact is seen on the right hand side. On the left it can be seen that the pterygoid becomes securely sutured to the posterior process of the parasphenoid. In dorsal view, an anteromedially directed ridge separates that part of the posterior ramus forming the lateral border of the posterior interpterygoid vacuity from the area of contact with the braincase. Posterior to this complex, the medial surface of the posterior ramus becomes dished and rugose to receive the projecting basioccipital tuber. However, there is no contact between the pterygoid and basioccipital tuber.

It is at this point that the quadrate ramus (qrpt) arises from the dorsal half of the posterior ramus, and runs posterolaterally towards the position of the quadrate. Although incomplete, enough is preserved to show that the quadrate ramus was

2.30

straight rather than curved. It is inclined anterolaterally, and is convex and thick ventrally. There are several large foramina on the medial surface which appear to lead into the bone, rather than connecting up with one another. An area of sculpture at the dorsal edge of the medial surface may mark the beginning of a facet for contact with either the squamosal or the quadrate.

Parasphenoid

While the preserved contribution of the parasphenoid (ps) to the palate surface is small, being confined to the remnant of the cultriform process, it is a major component of the braincase, sheathing the basisphenoid ventrally and laterally. The two bones appear completely fused at the anterior of the basicranium, but can be distinguished more posteriorly. The conjoined parasphenoid and basisphenoid in plesiosaurians can be referred to as the parabasisphenoid ('para-basisphenoid' of Rieppel *et al.* 2002; Evans 2009; Smith *et al.* in press) as in squamates, archosaurs or testudines (e.g. Bever *et al.* 2005; Gower and Weber 1998; Sterli *et al.* 2010).

Anteriorly, the posterior-most part of the parasphenoid cultriform process (pscp) is preserved, the broken surface being sub-rectangular in section (Fig. 2.13B). The ventral surface is fluted, and is triangular in shape, with the apex pointing posteriorly, forming a short keel (Fig. 2.16B). At this point the parasphenoid forms the floor of the braincase between the basisphenoid trabeculae (tr). Although a 10 mm section is missing, the parasphenoid can be seen to widen posteriorly, cupping the basisphenoid. No suture between the two can be seen at this point, although a group of canals seen in cross-section on the anterior break surface could indicate its position (indicated on Fig. 2.13D). The ventral surface bears faint longitudinal ridges which may be a continuation

of the fluting seen on the cultriform process.

Seen in ventral view (Fig. 2.16B), the parasphenoid widens into two posterior processes (popp, equivalent to the cristae ventrolaterales of O'Keefe 2001), running to either side of the anterior process of the basioccipital (see below). These contacted both the basioccipital and pterygoids. On the right hand side, the anteroventral surface of the posterior process is slightly roughened, forming a facet for the right pterygoid (ptf). On the left hand side, this contact had started to fuse, as can be seen in a break at this position. Posterior to this, the posterior process overlaps the anteromedial ridge noted above on the pterygoid. The posterior processes then contact the anterior face of the basioccipital. On the left hand side the ventral-most half of the posterior process is sutured to the basioccipital. Dorsal to this on the basioccipital the facet for the remainder of the contact between the two bones can be seen. On the right hand side, more of the parasphenoid is preserved still attached to the basioccipital, with a small exposure of the facet (psf) visible medial to the basioccipital tuber. The posterior processes, when complete, would have formed an anterior continuation of the basal tubera seen on the basioccipital.

A natural break between the anterior and poster sections of the basicranium (Fig. 2.17) reveals a convoluted internal suture between the posterior processes of the parasphenoid and the intervening basioccipital. The parasphenoid forms the majority of the basicranium in this region, and underlies the poorly developed basisphenoid. An arc of foramina between the parasphenoid and the overlying basisphenoid ovoid bodies marks the posterior contact of the two bones (see also Fig. 2.13F). Laterally there is no clear suture between the two, but a faint line of rugosities running anteroventrally from the dorsal edge of the parasphenoid posterior processes may represent its position.

Palatoquadrate and braincase

Epipterygoids

The epipterygoid (ep) is not preserved as a distinct and separate element (Figs. 2.13-16). However, a line of rugosities on the left pterygoid anterior to the basipterygoid articulation may represent the vestige of a fused pterygoid-epipterygoid suture. This feature is similar to that seen on the line of epipterygoid-pterygoid fusion in a specimen of *Liopleurodon ferox* (LEICT G418.1956.58.1). The ridge defining the anterior border of the lateral excavation of the pterygoid may also represent the suture. If this is so, it is unclear to what extent the epipterygoid would have been involved in the basipterygoid articulation. The dorsal process or columella cranii (Romer 1956) of the epipterygoid seems to have been well developed, judging from the size of what would be its base (colc). Alternatively, the epipterygoid may have been cartilaginous, and occupied the lateral excavation of the pterygoid. In this interpretation the dermal pterygoid would have replaced much of the endochondral epipterygoid.

Quadrate

The quadrates (q) are represented by the dorsal-most 21 mm of the right element and a 15 mm long fragment of the left (Fig. 2.10). The right quadrate has been dislocated and crushed against the squamosal, while the left was in articulation with the left squamosal, to which fragments of the head are attached. The contacts with the pterygoids are not preserved.

The quadrates, at least dorsally, are narrow and rectangular, rather than the triangular shape more typical of plesiosaurs. The anterior and posterior surfaces are gently concave transversely, the anterior being more so. Grooved facets for the squamosals are

present on the lateral and medial surfaces (lsqf and msqf respectively). The anterior surface bears a dorsally located triangular facet (asqf) for an overlapping process of the squamosal. The head of the quadrate (hq) is lozenge-shaped in dorsal view, and is pierced by a number of foramina. The border of the head forms a pronounced lip with the posterior surface of the quadrate, and although there is a slight concavity to the edge, it is essentially straight. This formed the ventral edge of the large quadrate foramen.

Basisphenoid

The basisphenoid (bs) is well developed anteriorly, but is less well ossified posteriorly (Figs. 2.13-17). It rests upon the parasphenoid for the whole of its length. Anteriorly the basisphenoid is only preserved on the left side. There is a distinct left trabecula (tr), which would have been well-separated from that on the right hand side. Posterior to the trabecula a transverse shelf of bone probably marks the anterior limit of the basisphenoid on the midline. Lateral to the transverse shelf is the broken base of a dorsally projecting process. This is identified as representing the base of the pila metoptica (pm). Posterior to this is the bowl-shaped sella turcica (st) or pituitary fossa, the middle portion of which is broken. The left internal carotid foramen (icf) is present, tucked in beneath the overhanging well-developed dorsum sellae (ds); the right foramen is obliterated by crushing. A smaller foramen (for) is present just anteroventrally to the internal carotid foramen (Fig. 2.14B). In CT sections (Fig. 2.13D) this appears to communicate with a small foramen on the left side of the basisphenoid, visible in ventral view. These foramina may represent the openings of the vidian canal, which would have carried the palatine branch of the facial (VII) nerve (see, Gaffney 1972 and Bever *et al.* 2005). There is no broad low median ridge extending anteriorly from the

sella turcica as was noted by O'Keefe (2006) in *Stratesaurus* (OUMNH J.10337) and interpreted as the interorbital septum.

The dorsum sellae is a robust ridge of bone which is poorly preserved on the right hand side due to crushing. Laterally it passes into the base of the clinoid process (cp), which is broken dorsally. There is no abducens foramen such as is seen in certain other plesiosaurs such as *Muraenosaurus* (Maisch 1998 and pers. obs.). Ventrally the base of the clinoid process is confluent with the posterior half of the basipterygoid process, which extends ventrolaterally from the body of the basisphenoid. Distally the basipterygoid process fans out into a large facet for the well developed basipterygoid articulation with the pterygoid.

Posterior to the dorsum sellae, the basisphenoid has an unfinished appearance, with an open texture. There is a longitudinal median sulcus (bsms) which widens and deepens posteriorly, forming a notch in the bone's posterior margin in dorsal view. Rounded oval bodies either side of the sulcus make this region reminiscent of a pair of cerebral hemispheres. The body of the plesiosaurian basisphenoid has been referred to as the clivus by O'Keefe (2001) and Druckenmiller (2006). However, this term refers to the steeply sloping structure formed from the mammalian sphenoid bone (e.g. Gray and Carter 1858; NAV 2005), and its use in plesiosaurians is inappropriate.

Basioccipital

The basioccipital (bo) is robust and compact, and is particularly deep dorsoventrally for a plesiosaur (e.g. Fig. 2.12A). It displays the typical landmark structures of the occipital condyle (oc) and the paired basioccipital tubera (bot: Figs. 2.13-2.16). Anteriorly it contacts the basisphenoid, parasphenoid and pterygoids in a complex suture which can

be seen in section in Fig. 2.17. The basioccipital forms a shelf which extends anteriorly between the posterior processes of the parasphenoid. The latter contact the basioccipital via paired facets medial to the basioccipital tubera. Ventral to this shelf the pterygoids contact the basioccipital in convoluted lateral and ventral sutures, which can be seen in right lateral view on the broken surface of the ventromedial flange of the pterygoids (Fig. 2.15A).

The section in Fig. 2.17 also shows that the eye-shaped projection anterior to the median union of the ventromedial flanges of the pterygoids is formed by the basioccipital. This basioccipital anterior process (boap) originates from the shelf described above. The basioccipital anterior process is significant as a similar structure seen in the basicrania of other early plesiosaurs has been described as being formed by the basisphenoid (O'Keefe 2001, 2004, 2006). In this case the anterior process appears to be formed from a number of 'fingers' of bone. The anterior ovoid portion of the process at first appears to be separate from the remainder, but examination of sutures seen in natural breaks (Fig. 2.17) shows that it is all formed by the basioccipital.

Posterior to the shelf the dorsal surface of the basioccipital rises vertically, giving rise to a median ridge which reaches its highest point between the paired facets for the exoccipital-opisthotics (or otooccipitals, see below). A large median basioccipital anterior foramen (baf) pierces the basioccipital just above the shelf (Fig. 2.17), and is seen in CT section to continue posteroventrally into the body of the bone (Fig. 2.13H and I). Noè (2001) described a basioccipital anterior depression or pit in the same position in the Callovian pliosaurids *Liopleurodon* and *Simolestes*, and these structures may be homologous to that seen here. What appears to be a transverse crack runs across the median ridge. However, a cleft or foramen of some sort is often seen in this position

in plesiosaurian basioccipitals (e.g. *Muraenosaurus spp.* NHMUK R2678 pers. obs., NHMUK R2861 Andrews, 1910), and this structure may have a biological origin.

The facets for the exoccipital-opisthotics (otf) are large (Fig. 2.16A). The posterior, exoccipital, portions are well demarcated by a low ridge, while the more anterior, opisthotic, portions are rather more poorly defined, being areas of rugosities. Between the paired facets the basioccipital flattens out posteriorly, forming the floor of the neural canal (nc). Laterally the facets overhang the ventrolateral surface of the basioccipital. The basioccipital forms the major portion of the occipital condyle, which is approximately hemispherical. A notochordal pit (np) pierces the condyle just dorsal of the horizontal midline. CT sections show that this pit continues into the body of the bone as an anatomising system of smaller canals, and is unconnected with the basioccipital anterior foramen. The ventral half of the condyle is set off from the body of the basioccipital by a well-defined neck forming a ventral groove (vg). This blends into the posterior surfaces of the basal tubera anterolaterally. Ventrally, the neck of the condyle blends into the basioccipital vertical plate (bovp) (Druckenmiller, 2006), which then forms sutures with the ventromedial flanges of the pterygoids. The vertical plate and basal tubera give the basioccipital a distinctly tri-lobed appearance in posterior view (Fig. 2.14A).

Prootic

The left prootic is almost complete (Fig. 2.18), while the right element is only represented by a fragment representing the area around the lateral lamina. The left prootic is slightly crushed laterally, and a fragment of opisthotic has been forced into it posteriorly. The plesiosaurian prootic is poorly known, and is only described in detail in *Muraenosaurus* (von Koken and Linder 1913; Brown 1981; Maisch 1998; Evans 1999)

and *Peloneustes* (Andrews 1913; Ketchum and Benson 2011b).

The prootic is sub-triangular in shape in lateral view (Fig. 2.18A). The anterior edge is slightly concave, running from the anterior corner of the supraoccipital facet down to a faint point, the prootic anterior eminence (pae), which is also seen in *Muraenosaurus* (pers. obs.). A low ridge runs posteroventrally from the anterior eminence while the distal part of the prootic basal process (pbp) lies just medial and ventral to it. As the proximal portion of the basal process is broken it is unclear whether it extended as far as the basisphenoid as in *Muraenosaurus* (Maisch 1998). When the braincase is rearticulated, there is a substantial gap between the prootic basal process and the basisphenoid. Although the height of the clinoid processes is unknown, they would appear to have been too anterior in position to have bridged the gap. This would have required the missing portion of the prootic basal processes to have been disproportionately long in order to have contacted them. The basal process probably contacted the cartilaginous part of the dorsal basisphenoid surface. The basal process is short in *Peloneustes* (Andrews, 1913), and there may have been a similar cartilaginous contact to that suggested here.

Medial to the basal process is the prootic postfacial process (ppp) which has a rounded medially facing head. A longitudinal channel runs between the basal process and the postfacial process, which is identified as the facial canal (fc) for the facial nerve (VII) (Maisch 1998). A hook-like projection, the infrafenestral process, posterior to the basal process, would have described the anteroventral corner of the fenestra ovalis (fo), with the more posterior portion of the prootic forming the anterodorsal border. The posteroventral extremity of the prootic is developed into a small but distinct prootic posteroventral process (pvp), which fits into a corresponding notch on the opisthotic.

The sutural surface for the opisthotic and supraoccipital runs in an undulating curve to the dorsal extremity of the prootic. At the point where the three bones would meet, the prootic bears a small step-like ridge, the prootic lateral lamina (pll). This feature is present on both left and right elements, and is not a crack caused by crushing. The lateral surface of the bone is ornamented with small rounded tubercles.

Medially (Fig. 2.18B), the prootic is excavated into a large ampullar or utricular recess (aur). The anterior semicircular canal (asc) runs dorsally from this, piercing the supraoccipital facet (sof), while the horizontal semicircular canal (hsc) runs posteriorly, piercing the opisthotic facet (opf). The prootic is not completely ossified where it wraps around the semicircular canals. The horizontal semicircular canal is enclosed by a finger-like process, which has been displaced by crushing, while a suture is visible medial to the anterior semicircular canal. A comparatively large notch between the basal process and the anterior edge of the ampullar/utricular recess probably represents the acoustic foramen (af) for the acoustic (or vestibulocochlear) nerve (VIII) (cf. Bever *et al.* 2005). Just anterior to the suture enclosing the anterior semicircular canal is a small foramen which was probably vascular, although it may have carried a branch of the acoustic nerve. The facets for the opisthotic and supraoccipital are more or less confluent, and are only separated by a low ridge. The supraoccipital facet is pierced by a relatively large foramen (for) in addition to the semicircular canals. This was probably vascular in function, and similar to those seen in the opisthotic (below).

Exoccipital-opisthotic

The exoccipital and opisthotic are fused, as in all plesiosaurs. This unit is usually referred to as the exoccipital-opisthotic (e.g. Brown 1981). However, the equivalent fused unit is referred to as the otooccipital in squamates (e.g. Conrad and Norell 2007;

Bever at al 2005) and it is proposed that this practice should be followed when describing plesiosaurs. In fact, Maisch and Rücklin (2000) used the almost identical term "otoccipital", which is usually used for the otic and occipital region of the braincase in basal tetrapods and sarcopterygian fish (e.g. Clack, 2001). Both otooccipitals are preserved, although the paroccipital processes (pop) are broken and the right otooccipital is also broken posterodorsally. A separate fragment may represent the distal portion of the left paroccipital process. When articulated with the basioccipital, the otooccipital is inclined to the sagittal and coronal planes. The orientations used in the figure are slightly artificial (Fig. 2.19), but they show the anatomical features better than the true orientations.

Although the opisthotic and exoccipital are fused, the line of fusion can be inferred to have run obliquely from anteroventral to posterodorsal due to the trace of the suture (sut) on the dorsal and ventral surfaces. In lateral view, a ridge above the rugosities (rug) on the exoccipital flange (see below) would also appear to follow the line of fusion, running anteroventrally beneath the paroccipital process. The latter structure would therefore seem to have been formed almost exclusively by the opisthotic. When the otooccipital is articulated with the basioccipital the paroccipital process is directed posteroventrolaterally.

In medial view (Fig. 2.19B), the otooccipital is dominated by a series of foramina ventrally, and the site of the posterior portion of the vestibular system dorsally. The largest foramen is the metotic foramen (mf), situated anteroventrally (Maisch 1998; Evans 1999). It is elongated anteroventrally-posterodorsally, and a groove runs from its ventral edge, following the line of the exoccipital-opisthotic suture. The foramen straddles the suture, with the anterodorsal border being formed by the opisthotic and the

posteroventral border by the exoccipital. This foramen would have transmitted the vagus nerve (X), probably along with the glossopharyngeal (IX) and accessory (XI) nerves. As this foramen is here thought to represent an undivided metotic fissure, the perilymphatic duct would also have exited the cranial cavity through it, possibly with the posterior cerebral vein or jugular vein (Romer 1956; Rieppel 1985). Two foramina (hyf) posterior to the metotic foramen would probably have transmitted roots of the hypoglossal nerve (XII). The posterior of the two is the larger and is sub-circular, whereas the smaller anterior foramen is more oval in shape. The anteromedial part of the basioccipital facet of the otooccipital is pitted. Some of this ornament continues onto the medial face, giving the impression of extra nerve foramina.

A small crescent-shaped foramen (lvs) lies dorsal to the posterior hypoglossal foramen. The corresponding feature was identified as the endolymphatic foramen by Noè *et al.* (2003) in a Callovian pliosaurid otooccipital (although erroneously described as "eustation foramen" in the abbreviations list). This foramen in plesiosaurs has generally been identified as a vascular or nutritive foramen (Andrews 1910, 1913; Evans 1999). A foramen identical in appearance and position in the exoccipitals of many archosaurs has been identified as a diverticulum of the longitudinal venous sinus (lvs) (e.g. Hopson 1979; Averianov *et al.* 2006). It is proposed that this was also the case in plesiosaurs. Maisch (1998) also noted the similarity of this foramen in *Muraenosaurus* with those of certain dinosaurs. The break in the right otooccipital of LEICT G1.2002 occurs just dorsal to the foramen in question, and shows several small channels in section. This is more suggestive of a venous sinus as one would expect a single large channel if the foramen transmitted the endolymphatic duct. As Maisch (1998) noted in *Muraenosaurus*, this opening lies outside the otic capsule, which would also argue against it being part of the vestibular system. An apparently blind foramen anterior

to the diverticulum opening suggests that it was more extensive earlier in development, and had since closed up. A small kidney-shaped raised area lies ventral to both the lateral venous sinus and the blind foramen. This may be the site of a ligamentous attachment to the dura mater surrounding the brain.

A large excavation dorsal to the metotic foramen represents the posterior ampullar recess (par), which housed the posterior and horizontal ampullae and possibly also the utriculus of the vestibular system. This recess in plesiosaurs has been identified either as a utricular recess (e.g. Brown 1981; Cruickshank 1994a, 1994b; Evans 1999), an ampullar recess (Andrews 1910; 1913) or as a combined ampullar and utricular recess (Maisch 1998; Noè *et al.* 2003). In this case, a faint dorsoventral ridge describing the anterior border would have separated the recess from the vestibule, and this is taken as evidence that it was occupied solely by the ampullae. The posterior semicircular canal (psc) runs dorsally from the posterior ampullar recess, piercing the supraoccipital facet of the otooccipital (sof). It is entirely enclosed within the bone. The horizontal semicircular canal runs anterolaterally from the ampullar recess, and is similar to the semicircular canals in the prootic in that it is not entirely surrounded by bone. Both the supraoccipital and prootic facets (pof) are pierced by foramina, which were presumably vascular; they appear to lead into the bone rather than communicating with the interior of the bony labyrinth. The supraoccipital facet faces dorsally, and is traversed by the trace of the exoccipital opisthotic suture (sut). It is mainly formed by the opisthotic, with the exoccipital making a small triangular contribution posteriorly. The prootic facet is smaller than that for the supraoccipital, and faces mediodorsally and anteriorly.

The portion of the opisthotic extending anteroventrally of the metotic foramen can be identified as the crista interfenestralis (cif) following Maisch (1998). Anterior to the

crista interfenestralis, the opisthotic is embayed, forming the posterior edge of the fenestra ovalis (fo). The dorsomedial face of the crista interfenestralis is slightly concave, which may represent the posterior portion of a lagenar recess (lr). The ventromedial part of the crista interfenestralis is truncated, and presumably would have had a cartilaginous extension which sheathed the lagena ventrally. The crista interfenestralis continues posterodorsally, defining the posterior edge of the posterior ampullar recess. It thins considerably, and is interrupted by a posterior ampullar notch (pan). This may have been for the perilymphatic duct as it leads into the metotic foramen, but this would appear to be too dorsal in position for this. Alternatively, it may have been the route of a branch of the acoustic nerve (VIII) which innervated the cristae within the ampullae.

In lateral view (Fig. 2.19A) the otooccipital is dominated by the broken base of the paroccipital process which is sub-ovate in section. Ventral to this are the external openings of the foramina described in medial view above. The metotic foramen and the hypoglossal foramina are combined into a large common otooccipital foramen (cof). The metotic foramen and anterior hypoglossal foramen merge more medially, with the posterior hypoglossal foramen separated by a distinct wall of bone. This remains recessed by several millimetres within the common otooccipital foramen. A small foramen (for) ventral to the metotic foramen may have been vascular in nature. There is no corresponding foramen visible medially within the metotic foramen, and it does not run ventrally towards the foramina seen on the basioccipital facet. As it is situated within the line of exoccipital-opisthotic fusion, it may be a vestige of the vascular supply to the connective tissue of the suture.

In anterior view (Fig. 19C) there is no obvious facet or rugose area for attachment of the

stapes. If it was present it was free of the opisthotic, unlike the fused stapes of *Thalassiodracon* (Storrs and Taylor 1996). An opisthotic notch (opn) ventrolateral to the opening of the horizontal semicircular canal would have received the prootic posteroventral process. A small foramen lateral to the opening of the horizontal semicircular canal leads into the body of the bone, and would appear to have been vascular in function.

In posterior view (Fig. 2.19D), a small part of the occipital condyle (oc) is formed by the posteroventral edge of the exoccipital, and there is a slight depression dorsal to this. The exoccipital forms the lateral wall of the foramen magnum (fm), curving laterally and then dorsally. The lower half of this border is smoothly convex in section, but the upper half takes the form of a sharp-edged ridge which curves ventrolaterally. This is here termed the exoccipital flange (exfl), and is homologous to the "facet like a zygapophysis" described in *Peloneustes* by Andrews (1913) and the "atlas-axis articulating facet" of *Liopleurodon* described by Noè *et al.* (2003). The structure seen here clearly could not have articulated with the atlas-axis, and is less like a postzygapophysis than the structure seen in *Peloneustes*. However, all of these structures can be accommodated by the term "exoccipital flange", the differences being due to the degree of development. Rugosities on the posterior surface of the flange probably served as an attachment site for nuchal ligaments. The exoccipital flange of *Liopleurodon* is also rugose, but to a greater degree (Noè *et al.* 2003).

In ventral view (Fig. 2.19E) the basioccipital facet (bof) is large and kidney-shaped, with the exoccipital-opisthotic suture running across the anterolateral corner. Anteriorly the medial and lateral edges are pitted and cancellous, with some of the pits being blind, and some leading to foramina running into the bone. In dorsal view (Fig. 2.19F), the

semicircular canals can be seen piercing the supraoccipital and prootic facets, which also bear a number of foramina. The cleft marking the position of the exoccipital-opisthotic suture is also well displayed.

A separate fragment is thought to represent the distal portion of the paroccipital process. One broken end is a good match in general shape for the sub-ovate section of the base of the right paroccipital process. The fragment widens in one dimension and thins in the other along its length, so that the other end is broad and flattened. One side is essentially smooth and flat, while the other is gently convex and fluted. The smooth side would be the anterolateral surface, flattened for articulation with the posteromedial surface of the squamosal, quadrate, or quadrate ramus of the pterygoid. The fluting on the convex posteromedial surface may have been for the attachment of craniocervical musculature, tendons or ligaments. If this identification is correct, then the paroccipital process of *Raptocleidus* was relatively long and slender.

Supraoccipital

The supraoccipital would appear not to be preserved. However, a small fragment with sculpture complementary to the rugose transverse ridge seen on the parietal may represent part of the dorsal parietal facet. The otooccipital and prootic facets of the supraoccipital must have met at approximately 90° to each other to have matched the corresponding facets on the otic capsule.

Other skull elements

A 21 mm long fragment of one end of a columnar bone is identified as part of the hyoid apparatus. With reference to the preserved hyoid apparatus of *Meyerasaurus victor* (Fraas 1910), this would be the anterior end. The end is kite-shaped in section, with the

shorter sides concave and the longer ones convex, and is cupped. The shaft is somewhat rugose just posterior to the end, and also bears a large crush mark. The bone tapers towards the broken, posterior end, which is teardrop-shaped in section.

There is at least one sclerotic ossicle present in the preserved material of LEICT G1.2002. It is a keystone-shaped bone with undulating sutural surfaces on the radial edges. If each sclerotic ring was composed of 12 ossicles (Romer 1956), then this would result in a structure approximately 35mm in diameter with a corneal aperture of approximately 18mm. However, Ketchum (2007) describes a sclerotic ring of *Peloneustes* with at least 16 irregularly-shaped ossicles, while the sclerotic ring of *Thalassiodracon* was composed of approximately 14 ossicles (Storrs and Taylor 1996), so these estimates should be viewed with caution. Some very thin (1 mm) fragments may represent irregular sclerotic ossicles as seen in *Peloneustes*. There are several isolated fragments which are probably parts of the skull. In particular, some of these have similar surface texture and foramina to the identifiable parts of the postorbital bars, and may well represent more of these structures.

Dentition

Several fragmentary plesiosaurian teeth were collected with the specimen (Fig. 2.20.). Although only one tooth is complete (Fig. 2.20E), it can be seen that the dentition was heterodont, with large teeth with proportionately slender crowns and smaller teeth with recurved crowns ('ratchet' teeth of Taylor and Cruickshank 1993b). As only a few fragments of the dentigerous bones were recovered, there is no data on the arrangement of the teeth within the jaws. However, it seems most likely that the smaller 'ratchet' teeth were located distally in the tooth row as in other plesiosaurians in which they are present (Taylor and Cruickshank 1993b; Noè 2001). In this section I use the descriptive

terms of Noè (2001; 'concave', 'convex', 'curved', 'straight') for the different surfaces of plesiosaurian teeth. The large crowns are relatively slender, the most complete crown having a stoutness value (sensu Noè 2001; height-diameter ratio of Massare 1987) of 4.07. They are gently curved basally, becoming straighter distally, the taper of the tooth giving it the appearance of a slight sigmoid curvature. The tooth base is long, and slightly bulbous, with an open pulp cavity at its apex. The crowns are sub-circular in section, although they have a distinctive 'squared-off' appearance, with slight flattening of the 'convex' and 'concave' surfaces (sensu Noè 2001). Ornamentation is in the form of fine enamel ridges, which are most numerous on the 'concave' surface, with a few extending towards the apex of the crown. The 'convex' surface is free of enamel ridges, the transition occurring approximately half way across the 'straight' and 'curved' surfaces. Although free of enamel ridges the convex surface is not smoothly rounded but is marked into a number of flattened 'facets' which run from the base of the crown to the apex.

The 'ratchet' teeth have short crowns with a small number of short fine enamel ridges. A resorption pit on the base of one 'ratchet' tooth (Fig. 2.20F) shows that these small teeth were being replaced and thus were functional teeth occupying secondary alveoli rather than small immature replacement teeth. Crown-base wear (sensu Noè 2001) is present in some teeth, showing that the teeth tightly intermeshed and impinged on one another. The large slender teeth can be assigned to the 'pierce' guild of Massare (1987), while the 'ratchet' teeth are more similar to the 'general' guild. As with most marine reptile teeth, the teeth occupy the grasp/crush/chop area of tooth morphospace of Ciampaglio *et al.* (2005).

The Axial skeleton

The axial skeleton of plesiosaurs is divided into cervical, dorsal, sacral and caudal regions as is typical of reptiles (Romer 1956). In addition, the pectoral region has traditionally been inserted between the cervical and dorsal regions, and is characterised by vertebrae in which the rib articulation is formed from both the centrum and neural arch (Seeley 1874b). Carpenter (1999) rejected the concept of a pectoral region as it is not used when describing extant reptiles which show this morphology. I maintain the use of the term in an informal way for ease of reference. Selected measurements of the cervical and pectoral vertebrae are presented in Table 2.1.

Cervical vertebrae

The centra or neural arches of 21 cervical vertebrae are preserved, including the atlas-axis complex. There is evidence for at least two additional cervical vertebrae, resulting in a minimum total of 23. Firstly, a pair of cervical ribs which are too small for the third cervical indicate that at least one vertebra should be inserted posterior to the axis. Secondly, an analysis of vertebral proportions suggests that another vertebra is missing more posteriorly. In the congeneric NHMUK R16330 there is a linear relationship between the width of a centrum's posterior articular face and its distance along the neck. This relationship is seen anteriorly in LEICT G1.2002, but the plot deviates posteriorly (Fig. 2.21). The atlas-axis and third vertebra were omitted as their proportions are atypical. The addition of a vertebra posterior to the eighteenth centrum realigns the posterior cervicals with the regression line.

Atlas-axis complex

As in all plesiosaurs the first and second cervical vertebrae are elaborated into an atlas-

axis complex (Fig. 2.22). In LEICT G1.2002 it is relatively complete except for the atlas intercentrum and left rib which are missing. The neural arches, and right axis rib are also damaged. The complex is partially fused. The atlas and axis remain free of one another and the atlas intercentrum was also unfused, resulting in its loss. The neural arches have started to fuse to the atlas centrum with fusion being more complete on the left. The axis neural arches are fused to the centrum, although the suture is visible, and the axis intercentrum is fused to the centrum. Of the axis ribs, the right is fused to the surrounding elements, while fusion of the left had just begun.

The anterior face of the atlas is cupped to form the atlantal cotyle (atlc) for the reception of the occipital condyle. It would have been formed from the atlas centrum (atc) dorsomedially, the neural arches (atna) dorsolaterally and intercentrum ventrally. There was no contribution from the atlas centrum to the lateral edge. The atlas intercentrum would have been large, forming more than half of the cotyle.

There is a distinct notochordal pit (np) in the anterior face of the atlas centrum. The posterior face is dished and also shows a notochordal pit. The centrum is triradiate in anterior view with dorsal and paired lateral projections. The dorsal projection forms the floor of the neural canal while the lateral projections form a part of the lateral surface of atlas axis complex. These are asymmetrical, so that the lateral exposure is larger on the left hand side than on the right. There are facets for the atlas intercentrum (fatic) and neural arches anteriorly and the axis centrum and intercentrum posteriorly. Foramina are present on the floor of the neural canal, as in other vertebrae.

The right neural arch is more complete. Although broken anteromedially, no projecting prezygapophysis such as would be seen in a typical vertebra is apparent. However, a kidney-shaped facet (fac) is present which may represent the prezygapophysis. It is

possible that this may have articulated with a preatlas (Romer 1956), although none is known from any plesiosaur. The facet would not have reached either the squamosal arch or the exoccipital flange directly, although a preatlas would have bridged the gap in the latter case. The neural arch is rugose medial to the facet. This is a continuation of the rugosities on the axis neural spine, and was probably for the attachment of nuchal ligaments or musculature. A striated region posterior to the facet may be the homologue of the parazygapophyseal processes present on the other cervical vertebrae; however it is incomplete posteriorly making this identification provisional. Dorsal to this the neural arch is also broken, but must have continued posteriorly as an elongated postzygapophyseal process (pzpp) which overlapped the axis neural spine as is seen in other plesiosaurs such as *Muraenosaurus leedsii* (Andrews 1910) or *'Rhomaleosaurus' megacephalus* (pers. obs. of LEICT G229.1851). The medial surface of the base of this process is rugose, probably for ligamentous attachment to a corresponding rugose area on the axis neural spine. The neural arches remained separate, and there would have been no median neural spine.

The anterior and posterior faces of the axis centrum are deeply cupped, with small notochordal pits. Anteroventrally the axis centrum (axc) is fused to its corresponding intercentrum (axic). The ventral surface bears a triangular median hypophyseal ridge (hr) which tapers posteriorly, merging with rugosities which ring the posterior face. There is a clear subcentral foramen (scf) on the left side. That on the right is small, being largely obliterated by the development of the hypophyseal ridge. The axis intercentrum is sub-quadrate, and bears a broad hypophyseal ridge, being an anterior continuation of that on the centrum. The atlas intercentrum is better developed on the right hand side, mirroring the asymmetrical development of the atlas centrum. There is a single rib facet on each side, mostly formed by the axis centrum, but with

contributions from the atlas centrum and axis intercentrum. The bases of the axis neural arches (axna) are fused to the centrum. They closely approach the atlas neural arches anteriorly, but do not touch. Posteriorly the pedicels of the neural arches contact the rim of the articular rim of the centrum, and effectively form the dorsolateral corners. The suture between the neural arches and the centrum can be seen clearly; it is sub-horizontal for most of its length, rising up the sides of the centrum at either end.

The axis neural spine (axns) is long, rugose dorsally and lacked prezygapophyses. It projects as an anterior spinous process (asp), overhanging the front of the axis centrum. As noted above, small areas of rugosities (rug) are present to either side of the anterior spinous process, probably for connection with the postzygapophyseal processes of the atlas. The axis neural spine is slightly inclined posteriorly. Its posterior edge is formed into a sharp narrow ridge (r), which then expands to a rugose tip. The postzygapophyses are largely missing. The axis rib (axr), although incomplete, appears to have been comparatively well developed. Its large head is undivided and contacted the atlas centrum, axis centrum, and axis intercentrum. The broken shaft is triangular in cross section.

Postaxial cervical vertebrae

The cervical vertebrae posterior to the axis are comparatively short, with a mean vertebral length (see Brown 1981) index of 0.73. Their dimensions are shown in Table 2.1, while Fig. 2.23 and Fig. 2.24 show an anterior and middle cervical vertebra respectively. The first preserved postaxial centrum is proportionally slightly wider than those that follow, and the anterior and posterior articular faces are slightly heart-shaped with a slight ventral lip. In the following vertebrae the faces are approximately circular except for where they are truncated dorsally by the neural canal (nc). The centra are

amphicoelous, with dished articular faces with a rounded edge, and notochordal pits are present up to at least the eighteenth preserved vertebra. The articular surfaces are marked off from the body of the centra by concentric grooves.

As is typical of most plesiosaurs the ventral surface is pierced by paired subcentral foramina (scf). The foramina are separated from one another by a ridge (r) which has a concave profile in lateral view. In the more posterior cervical the ridge becomes more rounded and expands into a low rugose boss where it approaches the articular surfaces anteriorly and posteriorly. Each subcentral foramina lies in a shallow depression bounded by the midline ridge, rib facet and the rims of the articular surfaces. The rib facets (rf) are single rugose concavities anteriorly, and although there is some separation into diapophysis and parapophysis more posteriorly, they remain conjoined. The cervical ribs are partially fused to the centra in the middle of the neck.

The neurocentral suture (ncs) is closed in all cervical vertebrae, but its line can be traced by a series of rugosities. It is positioned comparatively low on the sides of the centra, and is horizontal or arcuate rather than V-shaped as in most plesiosaurs. The suture is particularly low posteriorly so that the pedicle of the neural arch contributes to the posterior articular surface. The suture forms distinct indentations at the dorsolateral 'corners' of the articular face.

The neural canals are ovoid, being wider ventrally. They are large anteriorly, being approximately 40% of the centrum height, becoming proportionally smaller more posteriorly. The lateral walls of the neural canal are marked by oblique ridges so that they are slightly figure-of-8 shaped. The floor of the canal is formed by the dorsal surface of the centrum and is marked by two large foramina, separated by a low median ridge which dies out at either end. In some centra there is only a single foramen. The

neural arch pedicles are indented to approximately equal amounts anteriorly and posteriorly, and are approximately 60% of centrum length at the narrowest point in anterior vertebrae.

The zygapophyses are large and ear-shaped and are situated above the roof of the neural canal. Their articular surfaces are marked by concentric ridges, presumably for cartilage attachment. The external surfaces are marked by a slight lip where they meet the articular surfaces, and radiating ridges are present ventral to this on the prezygapophyses. The postzygapophyses remain separated from one another medially by a notch which extends to the base of the neural spine. The prezygapophyses are partly separated by an anterior notch but are confluent at their bases, roofing the neural canal. Anteriorly the angle of the zygapophyses to the vertical is relatively acute at approximately 30°. They become more horizontal posteriorly, with the angle increasing to more than 50°. The result is that although in anterior vertebrae (Fig. 2.23) the zygapophyses are narrower than the centrum they become sub-equal in width with the centrum more posteriorly (Fig. 2.24). In the posterior cervicals the postzygapophyses become sigmoid in posterior view, with the ventral portion becoming sub-horizontal. This feature is here called a postzygapophyseal platform (pozp). A matching basin is present in the prezygapophyses, so that the articular surfaces are transversely concave. All the cervicals have parazygapophyseal processes (pzp), distinct posteriorly directed spurs situated lateral and just posterior to the prezygapophyses. These have rugose tips, and can be clearly seen in dorsal view. These are largest in relation to the vertebra in the anterior cervicals, and decrease in length posteriorly.

The neural spines are relatively long and falcate anteriorly, becoming more rectangular but still curved posteriorly. In anterior vertebrae the tips are rounded, becoming

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truncated and teardrop- or heart-shaped more posteriorly. This suggests that a cartilage cap was present. The anterior edge forms a narrow ridge ventrally, but widens dorsally so forming an elongated triangular surface. The posterior edge forms a sharp ridge which descends to end between the postzygapophyses. Faint ridges ascend the neural spine from the dorsal surface of the postzygapophyses. In some vertebrae shallow pits are present on base of the neural spine above the prezygapophyses.

Pectoral vertebrae

There are seven pectoral vertebrae, in which the rib facet is formed from both the centrum and the neural arch (Fig. 2.25). In the first pectoral vertebra the neural arch makes a very small contribution to the rib facet, so that the neurocentral suture (sut) can be seen adjacent to the dorsal edge of the facet. The rib facet becomes dorsoventrally elongated as its dorsal edge rises up the surface of the vertebra, and in the later pectorals it is similar in morphology to the transverse processes (tp) of the true dorsal vertebrae. Ventral to the transverse process in these later pectorals is a boss situated in a depression (boss, Fig. 2.25C) which may be a vestige of the parapophysis. The ventral surface of the anterior pectorals bears a rounded ridge (r) separating the subcentral foramina (scf) as in the more anterior cervical vertebrae. In the sixth pectoral the ridge is absent and the centrum is broad ventrally, and in the seventh the subcentral foramina are situated in a more lateral position on the centrum. Low parazygapophyseal processes (pzp) are present on the anterior pectorals, but these are absent more posteriorly and the zygapophyses are lower. They also become less expanded transversely, so that although anteriorly they are sub-equal in width with the centra as in the middle and posterior cervicals, they become narrower than the centra by the end of the series. The neural spines are still curved posterodorsally, although they become straighter in the more

posterior vertebrae. The neural spines become transversely thickened and also become anteroposteriorly expanded at around mid-height, as seen in the true dorsals. In dorsal view the apices of the neural spines develop alternating asymmetrical morphologies, so that the spine of the fourth pectoral is weakly expanded to the left (expl), while that of the fifth is weakly expanded to the right (expr). However, the morphology does not alternate in a strict left-right fashion, as the sixth pectoral spine is missing but the seventh is expanded to the left. Small circular to oval pits are excavated into the margins of the more posterior rib facets; a particularly prominent one is present on the posterior surface of the right transverse process of the sixth pectoral.

Dorsal vertebrae

There are twenty-two dorsal vertebrae preserved in articulation, although there is a dislocation after the fifteenth vertebra. A separate dorsal neural spine indicates that at least one centrum is missing at this point, and that the total number of dorsals is at least twenty-three. As the vertebrae are articulated it is not possible to take accurate measurements. The centra are approximately as long as wide and slightly waisted with foramina on their lateral surfaces (Fig. 2.26). These are homologous with the subcentral foramina of the cervical vertebrae, the change in position can be observed in the pectoral series as noted above. The rib facets are borne on short robust transverse processes, the anterior-most of which are slightly elongated dorsoventrally as in the posterior pectorals. More posteriorly the rib facets and transverse processes become approximately equidimensional in section, although they are sub-quadratic anteriorly with flattened anterior and posterior surfaces, and only become sub-circular in the more posterior half of the series. The quadratic appearance is accentuated by rugosities on the dorsal 'corners' of the transverse processes. The ventral surface of the transverse

process where it joins the centrum is marked by low rounded transverse ridges which enclose shallow depressions. This can be seen clearly where the transverse process is broken as in the fourth dorsal in Figure 2.26C. The transverse processes remain relatively low and are approximately horizontal in orientation rather than being dorsally inclined. The distal ends of the transverse processes are smoothly convex in most of the vertebrae, but in the most posterior dorsals they are elaborated with rounded excrescences which match cavities on the posterior dorsal ribs. As far as can be seen the zygapophyses are proportionally smaller than those of the cervical and pectoral vertebrae and they lack the parazygapophyseal processes.

The dorsal neural spines are proportionally short, being approximately the same height as the centra. They are mediolaterally thick and are also expanded anteroposteriorly at about mid-height by a lamina on the posterior surface, so that they are narrower ventrally. In dorsal view (Fig. 2.26B) the neural spines are asymmetrical and alternate in morphology, continuing the trend which began in the pectorals. The second, fourth and sixth dorsal neural spines are expanded to the left (expl) so that they appear D-shaped in dorsal view with a flat lateral surface on the right and a convex one on the left. The first, third, fifth and seventh neural spines show the opposite morphology in which they are expanded to the right to varying degrees (expr). This alternating morphology continues for the remainder of the series. The separate neural spine noted above is expanded to the right, but the spine of the fifteenth vertebra is also expanded to the right whereas the first immediately after the dislocation is expanded to the left. Either the asymmetrical expansion did not follow a strict left-right pattern as was seen in the pectorals, or another vertebra is missing, which would restore a strict alternation in morphologies. The apices of the neural spines are convex in their centres, but concave around the edges indicating that they were probably extended by cartilage

in life. The neural spines are oriented approximately straight dorsally but become inclined posterodorsally in the posterior-most dorsals.

Sacral vertebrae

Three sacral vertebrae are represented by centra, and a fourth is represented by its neural arch (Fig. 2.27). As this matches the number of different sacral rib morphologies, this is probably the total number. The centra are rounded ventrally, with foramina on the lateral surfaces (for). The first two centra are crushed mediolaterally, whereas the fourth is crushed dorsoventrally. The rib facets are shared between the neural arch and the centrum, and are dorsoventrally elongated relative to the sub-circular rib facets of the posterior dorsals. In the anterior sacrals they are rounded oblongs, whereas in the fourth sacral the rib facet is more semicircular in shape. The zygapophyses are relatively short with the postzygapophyses having truncated ends. Both pre- and postzygapophyses are separated by deep medial fossae (foss), the anterior one of which can be seen to extend dorsally splitting the anterior edge of the neural spine in the third vertebra (Fig. 2.27B). The neural spines are inclined posterodorsally, with a convex outline to the anterior edge at the base of the spine. The apices are weakly expanded asymmetrically (Fig. 2.27D), continuing the pattern established in the pectoral and dorsal series.

Caudal vertebrae

The caudal vertebrae are represented by twenty centra from all regions of the tail (Fig. 2.28), along with broken neural spines. The first ten seem to form a good continuous series with no obvious gaps, while it is estimated that there are in the region of 8-10 missing between the tenth centrum and the twentieth. The last preserved centrum, although much smaller than the others, is by no means the end of the tail. As plesiosaur caudal vertebrae typically reduce in size very rapidly at the end of the tail (Andrews

1910) there would probably not have been more than five terminal centra missing and the total number of caudal vertebrae was probably in the low to mid thirties. In anterior caudals the centra are similar in proportion to the posterior dorsals and sacrals in being slightly wider than high with approximately circular articular faces in anterior or posterior view (Fig. 2.28B and C). In middle caudals the centra become proportionally wider and oval in section (Fig. 2.28J and K) before becoming more circular again in posterior elements (Fig. 2.28N and O). The caudal centra are proportionally longest at the end of the preserved series.

Haemapophyses or chevron facets (cf) are present in all but the two most anterior caudals. The ventral surface of the second caudal centrum has low swellings which may be attachment sites for the small, rudimentary chevrons noted below. The more distal anterior and middle caudals (Fig. 2.28F-H) lack well-developed anterior chevron facets, although the ventrolateral corners of the centrum articular surface may be slightly expanded onto the ventral surface, and there may be slight swellings for ligamentous attachment of the chevrons. The posterior chevron facets are larger than the anterior ones where both pairs of facets are well-developed as is the case in the distal caudals (Fig. 2.28N-P). The ventral surfaces of the centra are pierced by several small foramina, and larger foramina are present on the lateral surfaces of at least some centra. The rib facet is positioned relatively high on the side of the centrum and in anterior caudals the neurocentral suture contacts the facets dorsally. However, more posteriorly this contact is lost although the rib facet is still located on the dorsal half of the centrum. The anterior-most rib facets are semicircular to triangular with the long flatter edge positioned anteriorly, but the facets become sub-circular more posteriorly. Caudal ribs are fused to the centra in more anterior vertebrae, but are unfused by the ninth preserved vertebra. Where the ribs are unfused the facets can be seen to be conical pits. The

ribs become fused with the centra again after the fifteenth caudal and are small stubby projections by the nineteenth. Rib facets or ribs are absent on the last two preserved centra.

The zygapophyses on the anterior-most caudals are short and truncated and similar to those of the sacrals. The prezygapophyses become a horizontally oriented shelf and appear conjoined for most of their length by the fourth and fifth caudals, although this area is not well preserved. In the sixth caudal there is a single postzygapophyses on the left side of the neural arch, the right postzygapophysis being absent (Fig. 2.28G-I); the single postzygapophysis has a bi-lobed articular surface. Posterior to this, zygapophyses are effectively absent, their positions marked by ridges. The lateral surface of the neural arch pedicel is marked by a longitudinal ridge. The neural spines are incomplete on the anterior caudals, with that of the sixth vertebra being the first preserved whole (Fig. 2.28A, F, G). It is inclined posteriorly and is approximately symmetrical in section having lost the asymmetrical expansion which persisted into the sacrals; however, it is slightly deflected to the right. Only two more posterior neural spines are preserved, but these are also laterally deflected, one to the right (Fig. 2.28J-M) and one to the left (caudal 15, not figured). Given the alternating asymmetry in more anterior neural spines, it is possible that the caudal neural spines may have alternated in the direction of their deflection. The two more posterior neural spines are rod-like, being about as wide mediolaterally as anteroposteriorly. They are also inclined posteriorly, the angle of inclination being greater in the more posterior spine. Their apices are truncated, suggesting that they were capped by cartilage in life. The neural arch and spine were free and unfused in the last preserved caudal. A separate fragment resembles part of a posterior neural arch, and probably represents a more distal vertebra. If this

identification is correct, the neural spine in the terminal caudals was absent or unossified, its place taken by a circular depression.

The chevrons are paired rods as in all plesiosaurs (Fig. 2.29I). As noted above, what appear to be the anterior-most elements are short and stubby and rugose with poorly-developed vertebral facets. The more distal anterior chevrons are elongate and tapering with a single well-defined vertebral facet. The middle chevrons are more blade-like, with vertebral facets that are beginning to become separated into two. Finally the most posterior preserved chevrons are short and fan-like with a constricted neck and two well-defined vertebral facets.

Ribs

Ribs were originally present on all vertebral centra except for the atlas and probably the terminal caudals (Fig. 2.29). The cervical ribs are relatively short, only becoming elongated to any degree in the posterior-most cervical region, and are oval or round in cross-section. All but the very posterior cervical ribs show evidence of being double headed, with most having separate heads, the dorsal tuberculum and ventral capitulum, separated by a groove (Fig. 2.29A). In the anterior cervical ribs the rib heads are confluent, but a foramen remains showing the position of their union (Fig. 2.23). The tuberculum is the larger of the two rib heads. Distally the ribs are flattened, more so posteriorly, and develop anterior and posterior processes. The anterior processes (arp) are very short, but form a distinct flattened flange in the anterior ribs, while the posterior processes are short and robust. In the middle cervical ribs the anterior process is more of a rounded angle (Fig. 2.24), while in more posterior ribs the distal end is flatter. The anterior process forms a spur in the posterior-most cervical ribs, while the posterior process lengthens, approaching the development seen in the anterior pectoral

ribs. The ribs are free and unfused

The pectoral ribs are intermediate in form between the cervicals and the elongate dorsal ribs. They are all single headed, and they develop a rugosity on the shaft ventrolateral to the head, as in the dorsal ribs. The anterior process of the posterior cervical ribs becomes modified into a ridge which runs down the length of the rib before disappearing in the more posterior elements. The posterior process lengthens so that the anterior pectoral ribs are curved and spatulate (Fig. 2.29B). More posterior ribs are more elongate with narrow tapering ends (Fig. 2.29C), while the posterior-most pectoral rib resembles the anterior dorsals in having a wide cupped end.

The dorsal ribs are elongate and curved (Fig. 2.29D and E). The anterior elements have dorsoventrally elongated heads, matching the elongate rib facets of the vertebrae, while the more posterior elements are more equidimensional heads. The ribs develop a rugosity on the shaft ventrolateral to the head which may be an attachment for the costal musculature or ligaments. The anterior dorsal ribs seem to be the longest, although full comparisons could not be made as many ribs are partly enclosed in matrix (see Fig. 2.3). The shaft straightens slightly and the distal ends of the anterior ribs are cupped, forming concave facets. The posterior dorsal ribs are shorter with a smaller arc of curvature and taper distally (Fig. 2.29 E). The distal ends of the posterior dorsal ribs are convex rather than concave. The transition from concave to convex rib ends occurs at the fifteenth dorsal, which is also where the vertebral column is disrupted. The heads of the posterior-most ribs are excavated to match the excrescences present on the vertebral rib facets, and when the two are articulated the ribs are directed posteriorly towards the sacrum.

Seven sacral ribs are preserved, which can be divided into four distinct sacral rib

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morphologies (Fig. 2.29F-H). As these match the four preserved sacral vertebrae this is most likely to be the total number originally present. The sacral rib heads have two facets to match the bipartite facets on the sacral vertebrae, and ribs can be matched to the vertebrae in the case of the first two and fourth sacrals. As the third sacral centrum is missing, it is possible that the ribs identified here as the third sacral ribs belong to an additional missing sacral vertebra, and that more than four sacrals were present. However, the anterior surface of the distal end of the third sacral rib is a good fit against the posterior surface of the second, and this is taken as confirmation that the sacral morphology has been correctly reconstructed. The first two sacral ribs are robust and columnar, while the third is anteroposteriorly compressed and more sheet-like. The fourth sacral rib is missing the distal end, but appears to have been more slender and has a 'step' in its dorsal surface.

The first and second caudal ribs are short and curve posteriorly, away from the sacrum (Fig. 2.28B-E). Posterior to this the ribs become straighter and longer, tapering distally. In the middle caudals the ribs become more flattened and widen distally, although they are still directed posteriorly and are also slightly inclined dorsally (Fig. 2.28J-M). The most complete posterior ribs indicate that they start to taper distally.

The Appendicular skeleton

Selected measurements of the appendicular skeleton are presented in Table 2.2.

Pectoral girdle

The pectoral girdle in sauropterygians is formed of paired lateral coracoids and scapulae of endochondral origin and an anterior clavicular arch of dermal origin (Seeley 1874a, 1892, 1894). All of these elements are preserved, although the right coracoid and

scapula are cemented to the humerus by matrix, allowing a full description of the girdle elements' morphology.

Clavicular arch

The clavicular arch is a wide and robust element (Fig. 2.30), with a wide shallow anterior embayment separating two lateral wing-like extensions and a narrow median posterior process. The shape is reminiscent of the silhouette of a bird of prey in flight, and is the reason for the derivation of the generic name *Raptocleidus*. The clavicular arch is slightly crushed which has flattened the dorsal curve of the lateral wing on the left hand side. Thus it can no longer be as closely applied to the dorsomedial surface of the scapula as it would have been in life.

The interclavicle (icl) forms the median portion of the concave anterior border, and is dorsoventrally thick and rounded anteriorly. It thins posteriorly except on the midline, where it projects posteroventrally forming a posterior process (icpp). This process is flat-topped and convex ventrally and is textured laterally where it forms facets for contact with the medial surfaces of the anterior processes of the coracoids. Although the middle part of the process is missing, its length can be confidently restored by aligning the overlapping surfaces of the girdle elements. Much of the lateral portions of the interclavicle are covered dorsally by the clavicles, but in ventral view they are exposed in a broad bar at the anterior of the arch. The clavicles (cl) form the lateral wing-like extensions of the arch and also the anterolateral corners of the anterior embayment. They are laterally concave in dorsal view and laterally convex in ventral view. The convex ventral surfaces are rugose laterally (rug) for contact with the scapulae. The posterior edge of the clavicle on each side is much thinner where it lapped onto the scapula buttress (see below). Each clavicle extends medially posterior to the lateral

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portions of the interclavicle as a thin lamina. This is rugose ventrally (rug) for contact with the dorsal surface of the anterior process of the coracoid.

Scapula

The scapula (Fig. 2.31) is triradiate with ventral, dorsal and posterior rami. The ventral ramus (vrs) is short and directed more anteromedially rather than ventrally, and the scapula has a rather 'flat bottomed' appearance, although the anteromedial edge is damaged in both the left and right elements, the broken portions are relatively thin, and it would not have extended beyond the estimated outline. It certainly did not contact the coracoid or the contralateral scapula. The dorsomedial surface is rugose, forming the contact surface for the lateral wing of the clavicular arch. Distinct cavities are present dorsally which would have accommodated the pointed posterolateral extremities of the clavicular wings. A robust convex buttress (butt) descends from the medial surface of the dorsal ramus (drs) and runs obliquely across the dorsal surface of the ventral ramus.

The dorsal ramus is oriented approximately normal to the ventral surface of the scapula and is inclined posteriorly. Its anterior edge is concave, continuing the dorsal edge of the ventral ramus, until a point near the dorsal end, where it turns posterodorsally. The edge here is crenulated, suggesting that the surface was continued in cartilage. The apex of the dorsal ramus is an unevenly concave facet, indicating that there was cartilage here too in the living animal. The dorsal ramus flares slightly dorsally in lateral view, and it is teardrop-shaped in cross-section, with the posterior margin being roundly convex and the anterior margin more acute. The posterior ramus (prs) is robust and bears two facets: a semi-oval facet which formed the scapular contribution to the glenoid (gle), and a triangular facet which contacted the coracoid (corf). The medial margin of the scapula is concave between the posterior and ventral rami, where the scapula contributed to the

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pectoral fenestra (pfen). The angle between the ventral and lateral faces of the scapula is relatively sharp, forming a low scapular shelf (scaps); this is accentuated by a number of troughs on the ventral surface just medial to the shelf itself. The lateral surface of the scapula is pierced by a number of foramina (for).

Coracoid

The left coracoid (Fig. 2.32) was originally crushed under the shaft of the humerus, but has been freed using chemical preparation. As a result, it is distorted and the distinct bowing of the postglenoid portion of the bone in medial view is an artefact. The coracoid has a long, dorsoventrally thin anterior process (apc) which contacted the interclavicle posterior process medially in a long trough-like facet (iclf) but which does not seem to have contacted the anterior process of the other coracoid medially. Anteriorly the dorsal surface of the anterior process is textured with low rugosities where it contacted the clavicle. Lateral to this the edge is excavated to form the medial and posterior margins of the pectoral fenestra. The edge for most of this margin is extremely thin (~1mm) and fragile. Posterolateral to the pectoral fenestra, the coracoid forms a triangular facet for the posterior ramus of the scapula (scaf), adjacent to which is a semi-oval facet forming the coracoid's contribution to the humeral glenoid (gle). Medial to this the coracoid is thickened into a robust bar which runs approximately directly medially to the mid-line in dorsal view. Here the coracoids meet in a symphysis (sym). The symphysis is, however, very short anteroposteriorly, as can be seen in medial view (Fig. 2.32F). The ventral surface of the coracoid is excavated into a hollow anterior to the transverse buttress, which runs a little more posteromedially compared to its course on the dorsal surface. The symphysis is therefore asymmetrical in medial view, with the ventral convexity situated posterior to the dorsal convexity.

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Posterior to the glenoid the lateral margin of the coracoid sweeps medially before returning laterally to a blunt corner known as the cornu (cor). Low rugosities (rug) are situated at the anterior and posterior ends of this embayment. With reference to the muscle reconstructions of Carpenter *et al.* (2010) these may mark the anterior and posterior origins of the *m. coracobrachialis*. From the cornu, the margin of the coracoid describes a convex arc of almost 180° before turning laterally to form the concave margin of a coracoid embayment (cem) before returning to the midline. When the two coracoid symphyseal surfaces are brought together the coracoid embayment can be seen to have a heart-like or cordiform shape. The medial 'spur' at the anterior of the embayment is preserved on the right coracoid.

Forelimb

Elements of both forelimbs were preserved. The humeri and several identifiable proximal elements from each side were either partly embedded in matrix or had crush marks which allowed them to be placed in the reconstructed plan of the skeleton's disposition (Figs. 2.2 and 2.3). Other elements however could not be placed relative to the rest of the skeleton and are omitted from these plans. The nomenclature of plesiosaur forelimb elements used here is that of Andrews (1910).

Humerus

Both humeri were preserved in close contact with their respective endochondral pectoral girdle elements. The left humerus has been freed of matrix, and forms the basis of the description (Fig. 2.33). The humerus is distinctly S-shaped due to a posterior curvature of the shaft and an anterior inclination of the capitulum (cap), or head. The anterior or preaxial margin of the shaft is marked by some low rugosities (rug) at its convex-most point. Distal to this, there is a marked groove or trough (gr: Fig. 2.33F) which blends

2.66

into the concave margin of a moderately sized preaxial expansion (prae). There is a larger postaxial expansion opposite this. Distal to the preaxial expansion the humerus forms two distinct facets for the epipodials, the anterior radius facet (radf) and posterior ulna facet (ulf) which are at a distinct angle of about 125° to one another. In distal view a distinct groove is present on the ventral surface of the humerus between the two epipodial facets (gr). Posterior to the ulna facet the humerus forms a distinct facet which seems to have articulated with a postaxial accessory ossicle (see below). The shape of the border of the postaxial expansion is taken from the right humerus. The postaxial border is relatively smooth except for a marked postaxial process (poap) just posterodistal to the capitulum which may represent the insertion of the *m. coracobrachialis* (Carpenter *et al.* 2010). In postaxial view (Fig. 2.33E) a large foramen (for) can be seen about halfway along the shaft, and a small patch of low rugosities (rug) is located near the postaxial expansion. In proximal view (Fig. 2.33D) it can be seen that the large tuberosity is displaced posteriorly relative to the capitulum and is also rotated relative to it. The capitulum is marked by numerous foramina most probably indicating that a well developed cartilaginous articular surface was originally present. Three large foramina are present between the postaxial process and the capitulum, and these seem to connect to some of the foramina on the capitulum. The surface of the capitulum is generally convex although there is a series of depressions across the centre which can be seen in proximal view. A large area of rugosities (rug) is present on the ventral surface of the humerus shaft.

Epipodials

The radius (Fig. 2.33A and Fig. 2.34) is a compact and robust bone with concave pre- and postaxial borders. The humerus facet (huf) is extensive, being anteroposteriorly

long and dorsoventrally thick. The concave portion of the preaxial border is restricted to the distal half as there is a thin convex anterior flange (rafl) more proximally. The centre of the concave portion of the border is occupied by a large foramen (for). The postaxial border is more markedly concave, although here too the more proximal part is convex, and formed the preaxial margin of a large epipodial foramen. Distally the radius has what appear to be three facets, the middle one of which is the largest and would have been the radiale facet (radef). Postaxial to this is a small but well formed oblique facet for the intermedium (intf). A larger oblique facet situated preaxially to the radiale facet may have been for a preaxial ossicle. A suitable bone is present (see below), and it this gap were purely filled with cartilage, such a large, well formed and angled facet would seem an unlikely developmental outcome.

The ulna (Fig. 2.33A and Fig. 2.34) is a polygonal bone and is not as thick and robust as the radius. There are facets proximally for the humerus (huf), and a postaxial accessory ossicle (poaof), while distally there are facets for the intermedium, ulnare (ulnef) and another accessory ossicle. When compared to the radius, the humerus facet is not as extensive whereas the intermedium facet is much larger. The preaxial margin is concave, and would have formed the postaxial border of the epipodial foramen.

Carpals, metacarpals and phalanges

Generally the more distal limb elements have been identified by shape and fit and size, as the hindlimb elements are slightly larger, and their presence in NHMUK R16330 (see Fig. 2.41) in which only an anterior section of the skeleton, including the forelimbs, was preserved or collected. The forelimb intermedium (int: Fig. 2.33A) is a relatively large bone which is instantly recognisable due to the notch in its border formed by its contribution to the epipodial foramen. The left intermedium was crushed onto the left

ulna and humerus, whereas the right element was associated with the right pectoral girdle. The ulna facet is large and slightly convex, whereas that for the radius is much smaller. There are facets for the radiale, distal carpals 2 and 3, distal carpal 4 and the ulnare.

The radiale (rade) is a dorsoventrally thick, rounded sub-oval element with small patches of finished perichondral bone on the dorsal and ventral surfaces surrounded by extensive endochondral bone. It lacks well formed facets, making its precise placement problematic. It is identified as the radiale due to its thickness, second only to the radius, and thus it would be out of place elsewhere in the forelimb. It is assigned to the forelimb as an identical bone is present in NHMUK R16330.

The ulnare (ulre) is identified on the basis of fit, size, and a narrowing in dorsoventral thickness in the proximal corner. Two different sizes of triangular accessory ossicles were preserved, associated with the forelimbs, and they are most likely postaxial elements, positioned as in Fig. 2.33A. Distal carpal 4 (dc4) is identified on the basis of shape, with a strip of perichondral bone wrapping around the postaxial edge (Caldwell 1997a, 1997b). Metacarpal V (mcV) is identified on the basis of its shape, and as it fits against distal carpal 4; it is partially situated in the distal tarsal row. The pentagonal element identified as the fused distal carpal 2 and 3 (dc2&3) is assigned to the forelimb as it is present in NHMUK R16330, and distal carpal 1 (dc1) is identified on the basis of its small size and fit. The rounded element identified as a preaxial accessory ossicle (prao) is robust, and lacks perichondral bone and so is reminiscent of the radiale.

Metacarpal I is identified due to its shortness and triangular cross-section. Identification of other metacarpals is problematic, as several elements could be either metacarpals or robust proximal phalanges. Certainly no metacarpals (or metatarsals) with angled facets

are present, and it seems likely that the metapodials were all flat ended. Several smaller elements with triangular cross-sections are identified as phalanges of digit I of either the fore- or hindlimb. Many phalanges are present (Fig. 2.34J) but it is impossible to accurately assign them to limbs. Some distal phalanges are remarkably short and wide with heavily indented margins. Small terminal phalanges are also present.

Pelvic girdle

Ilium

The ilium (Fig. 2.35) is a stout straight rod-like bone with an expanded distal end forming the iliac blade (ilb). The expansion is asymmetrical, with a larger expansion posteriorly. The posterior surface of the shaft is marked by a rugose ridge (r: Fig. 2.35D) just proximal to the blade while there is a distinct patch of rugosities (rug) on the lateral surface of the blade. The proximal end bears two facets which are sub-equal in size; a posteromedial ischium facet (iscf) and a more anterolateral facet forming the ilial contribution to the acetabulum (acet). The proximal end is rotated approximately 45 degrees relative to the iliac blade.

Pubis

The pubis (Fig. 2.36A-D) is a rounded plate of bone with a long medial symphyseal facet (sym). It bears two lateral facets; an anterior facet forming part of the acetabulum (acet) and a posterior facet for the ischium (iscf). Anterior to the acetabulum the pubis is rounded, and lacks any development of a projecting cornu. The posterior border of the pubis medial to the ischium facet is concave where it forms the anterior border of the thyroid fenestra (tfen). A posteriorly directed spur would have formed a partial pelvic bar, but it is not thought to have contacted the ischium due to its shortness and lack of a

2.70

facet. This is confirmed by the cast of the pelvic girdle of BHI 126445 figured by Carpenter *et al.* (2010, Fig. 5D).

Ischium

The ischia are both fragmentary, but most of their outline can be restored except for the anteromedial portion (Fig. 2.36E and F). The posterior portion of a median symphysis (sym) is preserved in the left ischium, while both ischia preserve the relatively short posterior extension. The ischia bear three facets anterolaterally; an anterior facet for the pubis (pubf), a lateral facet forming part of the acetabulum (acet) and a posterolateral facet for the ilium (ilf) which is directed dorsolaterally. The dorsal surface of the ischium is relatively flat, but in ventral view a rounded ridge (r) gives the shaft supporting the facets a triangular cross-section.

Hindlimb

Although the right femur and epipodials are absent, fragments of the tarsals from the right hindlimb are preserved, indicating that the whole limb was probably originally present. It may have been destroyed by the quarry machinery. The nomenclature of plesiosaur hindlimb elements used here is that of Andrews (1910).

Femur

The right femur (Fig. 2.37) is a relatively elongate bone with concave preaxial and postaxial margins which form corresponding preaxial and postaxial expansions (prae and poae). The distal end bears two well developed facets for the epipodials. The facet for the tibia (tibf) is longer than that for the fibula (fibf). There is a distinct postaxial process which gives the postaxial margin a distinct 'kink'. This was most likely the insertion for the *m. caudofemoralis* (Carpenter *et al.* 2010). In contrast to the tuberosity

of the humerus, the trochanter (tro) is situated dorsal to the capitulum and is not deflected or rotated posteriorly, as can be seen in proximal view (Fig. 2.37D). A large convex rugosity (rug) is located on the ventral surface between the capitulum and the postaxial process.

Epipodials

The tibia (Fig. 2.37A and 2.38A-D) is more elongate that the radius and lacks the anterior flange. The preaxial and postaxial borders are concave, with the latter forming the anterior border of the epipodial foramen as in the radius. Unlike the radius, however, the tibia has a proximal facet for contact with the fibula, restricting the extent of the epipodial foramen. There is no well-developed facet for the intermedium, and there is a long distal facet for the tibiale (see below). The fibula (Fig. 2.37A and 2.38E-G) is fragmentary, lacking the postaxial portion of the bone and the proximal area where the corresponding facet for the tibia was presumably located. The preaxial margin is concave, forming part of the epipodial foramen, and the intermedium facet is large and robust, as in the forelimb. A posteriorly oblique proximal facet would probably have contacted a postaxial accessory ossicle, as in the forelimb.

Tarsals and metatarsals

The hindlimb intermedium (int: Fig. 2.37A) is similar in shape to that of the forelimb, but can be distinguished due to its slightly larger size. A concave notch in the anteroproximal border contributed to the epipodial foramen. The intermedium has a small poorly-defined facet for the tibia, although a corresponding facet in absent on the latter. It contacts the fibulare and the distal tarsals and an anterior facet is reconstructed as contacting the small centrale. The fibulare (fibe) and distal tarsal 4 (dt4) are similar in shape to their serial homologues in the forelimb, although slightly larger. The fused

distal tarsal 2 and 3 (dt2&3) has been identified as such due to its robust, blocky shape and lack of a perichondrally ossified border which would suggest that it is not a marginal element. It differs in shape from the element identified as distal carpal 2 and 3. The elements identified as distal tarsal 1 and the centrale (dt1, ce) are problematic. Those illustrated in the limb reconstruction are the right hand elements, and those of the left limb are attached by matrix to the proximal end of the femur. The right hand elements have a contact scar indicating that they were preserved touching one another, while the left hand elements are partially fused in this position. It is possible that the small element is a centrale, and that it is in the process of assuming the identity of the bone traditionally identified as the plesiosaurian tibiale (e.g. Andrews 1910), as hypothesised by Caldwell (1997a). There is no large element preserved which would be a possible tibiale, unless the rounded element identified as a forelimb preaxial accessory ossicle is actually a very poorly ossified tibiale. The placement of the small element identified as the centrale follows the arrangement of what appear to be identical bones in the hindlimb of *Eretmosaurus rugosus* (NHMUK 14435).

Metatarsal V can be confidently identified due to its shape and its fit against the corresponding facet of distal tarsal 4. It is slightly larger than metacarpal V, and lies partially in the metatarsal row. Metatarsal I can be identified due to its triangular section and its larger size when compared with metacarpal I. No further elements from the collection of phalanges and possible metapodials noted above could be confidently assigned to the hindlimb.

Gastralia

Many complete and partial gastralia (Fig. 2.39) are preserved both in the main concreted mass surrounding the abdominal area (Fig. 2.2 and 2.3) and as separate elements along

with many fragments. Six gastralia can be identified as median elements (mg: Fig. 2.39A and B), and they are shallowly V- or U-shaped with a spur-like medial process (mp). The element shown in Fig. 2.39A was associated with the right humerus and is probably an anterior median gastralium, while the element in Fig. 2.39B was associated with the left femur and is probably a posterior gastralium. It has forked ends, and assuming that each 'tine' of the forked gastralium was associated with a row of lateral gastralia, at least 7 rows of gastralia would have originally been present. Several gastralia have distinct facets associated with palmate ends (Fig. 2.39C).

Description of NHMUK R16330

The specimen comprises a partial vertebral column with associated ribs, partial pectoral girdle, two humeri and limb elements which are assumed to be from the forelimbs (Figs. 2.40 and 2.41). Selected measurements are presented in Table 2.3. The only locality information recorded with the specimen is 'Lyme Regis', which could potentially refer to anywhere on the coast (presumably) between Pinhay Bay and Charmouth, and possibly beyond further to the east (Simms *et al.* 2004). A partial ammonite is preserved alongside the plesiosaur's ribs and has been identified by C. P. Palmer as *Aegoceras lataecosta* (J. de C. Sowerby), most recently referred to *Androgynoceras* by Page (2010). This ammonite is known from Bed 122g of Lang (1936) of the Seatown Mudstone Member (formerly the Green Ammonite Mudstone Member) of the Charmouth Mudstone Formation, and is the index for the Lataecosta Horizon, Capricornus Subzone, Davoie Zone, Lower Pliensbachian (Page 2010). That the specimen came from this horizon is supported by the occurrence of greenish calcite, which is characteristic of the 'Green Ammonite Beds', in an around the ammonite and plesiosaur elements. It is therefore likely that the specimen's locality was somewhere

between Charmouth and Seatown, at the base of the Seatown Mudstone Member (Simms *et al.* 2004), in close proximity to the locality of BRSMG Ce17972a-o (Storrs 1995). The specimen is eroded ventrally and on the right hand side, and it is therefore presumed that it was originally preserved lying on its dorsal side with the neck twisted towards the left anteriorly.

Axial skeleton

The specimen is an adult by the criteria of Brown (1981), and is approximately 85% the size of LEICT G1.2002 based on dimensions of the humerus. There are twenty-six vertebrae represented by centra and two partial anterior cervical neural arches, all in articulation. The first neural arch is represented by the postzygapophyses which are preserved broken and in articulation with the prezygapophyses of the second neural arch, which has an intact neural spine (Fig. 2.40B). This is preserved in articulation with the first entire vertebra. The first eight centra are preserved in articulation with one another but are free, the next four are preserved in two pairs cemented by matrix, followed by a block of four, the second of which is the first pectoral (Fig. 2.40A). Vertebrae 17 to 23 are preserved in a block of seven, and the block containing the last three vertebrae has been embedded in plaster and shellac, presumably for chemical preparation. Generally the vertebrae are 'neater' in appearance than those of LEICT G1.2002, with less rugose ornament. The neurocentral suture has closed, but its path can be traced by a line of rugosities. It was relatively ventral in position and broadly arcuate in shape, and intercepted the dorsolateral 'corners' of the posterior articular face of the centrum as in LEICT G1.2002. The vertebral centra are extended ventrally by a 'lip' in anterior view (Fig. 2.40C). The anterior cervical neural spines are more slender and all cervical neural spines curve posterodorsally to some extent. The anterior margin of the

neural spine is flattened into a ventrally pointing triangular surface from the fifth vertebra, although neural spines are absent on the third and fourth vertebrae. The anterior-most vertebrae have particularly large, almost conical, parazygapophyseal processes (pzp, Fig.2.40B). Cervical ribs are either fusing or have fused to the centra in the first ten vertebrae, and are unfused thereafter. The rib facets are single and oval-shaped. The seventh vertebra has a smooth-edge circular hole in the neural arch just posterior to the basin of the prezygapophysis.

The neurocentral suture can be seen intercepting the rib facet on the fourteenth centrum, and this is therefore taken as the first pectoral vertebra (p1). As the centra are encased in matrix on their left sides and the right sides are eroded it is difficult to tell where the dorsal series begins. A neurocentral suture is visible separating the right rib facet of the eighteenth vertebra into a ventral third (centrum) and dorsal two-thirds (neural arch). The twenty-third can be seen to be dorsal in morphology. There were therefore at least five pectoral vertebrae and the fifth is unlikely to be the last based on the position of the neurocentral suture. Neural spines are broken until the twentieth vertebra, which is probably either the last pectoral or first dorsal. The apex of the neural spine is robust, but anteroposteriorly longer than it is wide. The following neural spine is, conversely, wider than it is long (Fig. 2.40D). This pattern of alternating unexpanded (unexp) and transversely expanded (exp) neural spines continues for the remainder of the specimen, and is the main character distinguishing *R. bondi* from *R. blakei*. Dorsal and pectoral ribs (dr and pr) are preserved both in the blocks in articulation with the vertebrae and as separate fragments.

Appendicular skeleton

The clavicular arch is in three pieces: a median section adhering to the ventral surface of

the anterior pectoral vertebrae which is poorly preserved and eroded; and two lateral sections preserved in articulation with the scapulae. The left fragment fits onto the median one, and taken as a whole the clavicular arch has similar proportions to that of LEICT.G1.2002. The lateral portions represent the lateral 'wings' formed by the clavicles, but little detail can be made out. Both scapulae are present but only represented by partial ventral and dorsal rami. A convex buttress runs down the medial surface of the dorsal ramus and continues onto the dorsal surface of the ventral ramus, while a scapula shelf was evidently present but is now broken off (Fig. 2.40A). The coracoids are poorly preserved ventral to the block of seven vertebrae, and presumably continue into the block embedded in plaster. Only the lateral articular region of the left hand element is preserved, while the right is more complete, preserving the lateral margin posterior to the glenoid. A prominent rugosity is present posteromedial to the glenoid as in LEICT. G1.2002. The medial portion is eroded and the symphyseal region and any coracoid embayment is missing.

Both humeri are present, the right being the more complete (Fig. 2.41A). It is very similar to that of LEICT G1.2002 with a longitudinal groove leading to a small preaxial expansion, sigmoid shaft and angled epipodial facets. The margin leading the preaxial expansion has a slightly less concave contour. Proximally the tuberosity is posteriorly deflected and rotated and there is a prominent postaxial process. Both radii are also present (Fig. 2.41B), although due to crushing it is impossible to distinguish left from right. Compared to the radius of LEICT G1.2002 the preaxial margin is almost convex save for a small concave region. This is partly due to a small tubercle or boss (boss) which partly fills the concavity, and which is an autapomorphy of *R. bondi*. An ulna (Fig. 2.41C) missing the preaxial margin is preserved; the postaxial margin is convex and forms two facets for the ulnare and a postaxial accessory ossicle. Eight carpals

are preserved. An ulnare and radiale are identified by comparison with LEICT G1.2002 (Figs. 2.41D and E). Two examples of a pentagonal bone are preserved (Fig. 2.41F), matching the element interpreted as fused metacarpals 2 and 3 in LEICT G1.2002. The occurrence of these elements in NHMUK R16330 which is otherwise missing posterior to the anterior dorsals is the reason their homologues in LEICT G1.2002 have been assigned to the forelimb of the latter. Five robust metacarpals or proximal phalanges are present, the ends of which are approximately planar.

Discussion

Comparisons with other taxa

Raptocleidus is a relatively small-bodied and short-necked plesiosaurian, and so in general size and proportions is similar to Cretaceous leptocleidid plesiosaurs, *Nichollssaura* and *Umoonasaurus* and *Leptocleidus* although the latter genus is poorly known (Druckenmiller and Russell 2008b; Kear *et al.* 2006; Andrews 1911, 1922a). It is also similar to small-bodied short-necked taxa from the Early Jurassic such as *Meyerasaurus victor* (Fraas 1910) and the specimen from Halberstadt Germany, which was referred to *Thaumatosaurus aff. megacephalo* by Brandes (1914).

Skull

The facial processes of the premaxillae are remarkably short in comparison to the rest of the skull in *Raptocleidus*. They are usually moderately long in plesiosaurs, separating the frontals and extending to the middle of the orbit in *'Rhomaleosaurus' megacephalus* (Cruickshank, 1994b) and *Plesiosaurus* (Storrs, 1997). A convergent contact of the premaxillae and parietals occurs in several lineages (O'Keefe 2001), although in most cases this is due more to an anterior extension of the parietals rather than elongation of

the facial processes. In *Plesiopleurodon* (Carpenter, 1996) and *Edgarosaurus* (Druckenmiller, 2002) the facial processes extend to a point level with the posterior edge of the orbit, although they only contact the parietal in the former. The state of the facial processes are most similar to those of the Callovian plesiosauroids *Cryptoclidus* (Brown and Cruickshank 1994) and *Muraenosaurus* (pers. obs.) and also the Toarcian pliosaurid *Hauffiosaurus tomistomimus* (Benson e al 2011b) in ending approximately level with the anterior of the orbits and partly separating the frontals. In the Toarcian plesiosauroid *Occitanosaurus* (Bardet *et al.*, 1999) they appear to be similarly short. However, this could be an artefact of preservation as the facial processes are displaced laterally and the frontals are grooved medially between the orbits which may represent the premaxillary facet (pers. obs.). In more basal sauropterygians such as *Augustasaurus* and *Pistosaurus* the facial processes extend to a point just posterior to the anterior edge of the orbit (Rieppel *et al.*, 2002), but they do not separate the frontals (Druckenmiller, 1996: 253). *Nichollssaura* has long processes which may reach the parietal (Druckenmiller and Russell 2008b), while those of *Umoonasaurus* and *Leptocleidus capensis* extend between the orbits (Cruickshank 1997; Druckenmiller 2006; Kear *et al.* 2006).

A narrow dorsomedian ridge or crest formed by the premaxillae has been reported in several other taxa including *Leptocleidus* (Cruickshank 1997; Druckenmiller 2006), *Nichollssaura* (Druckenmiller and Russell 2008), *Umoonasaurus* (Kear *et al.*, 2006), the elasmosaurids *Libonectes*, *Terminonatator* (Druckenmiller 2006) and *Eromangasaurus* (Kear 2005). A similar ridge, triangular in section, is also partly developed posteriorly in some specimens referred to *Muraenosaurus* (pers. obs.), As Druckenmiller (2006) notes, there is a somewhat continuous range of variation in the development of this feature For example, in *Occitanosaurus* the premaxillae form a

short triangular ridge posteriorly where they overlap the frontals, but this is absent anterior to the external nares.

The splitting of the dorsomedian ridge into diverging facial ridges is unique to *Raptocleidus* among known plesiosaurs. In *Vinialesaurus* (De la Torre and Rojas, 1949) Gasparini *et al.* (2002) described the position of the premaxillary/frontal suture as being marked by two deep grooves arranged in a "V" shape. Surface preservation is poor but my own observations of MNHNCu P3008 would suggest that the facial processes of the premaxillae overlap raised ridges of the frontals in a similar fashion to NHMUK R2862 and NHMUK R2678. The deep dorsomedian fossa between the diverging facial ridges of *Raptocleidus* is also unique, but can be compared to the dorsomedian foramen reported in other taxa. The more descriptive term 'fossa' is preferred in this case, as the term 'foramen' is misleading, carrying implications of form and function. This structure is only a distinct oval opening in species of *Rhomaleosaurus* (Taylor 1992; Cruickshank 1996; Smith and Dyke 2008). As Druckenmiller (2006) observes, in *'Rhomaleosaurus' megacephalus* (LEICT G221.1851) there is only a slightly wider than average suture between the premaxillae, which is certainly not as wide as the elongated oval dorsomedian foramen reconstructed by Cruickshank (1994b). *Eurycleidus* (sensu Smith 2007) has a similarly open suture in the frontals posterior to the end of the premaxillary facial processes. A dorsally open interfrontal suture is observed in other plesiosaurs such as *Brancasaurus* (the "foramen frontale" of Wegner 1914) and *Muraenosaurus* (pers. obs.). While Cruickshank (1997) shows the dorsomedian foramen in *Leptocleidus capensis* situated between elongated premaxillary facial processes, Druckenmiller (2006) shows it between the frontals dividing the ends of shorter facial processes. The latter morphology is more similar to that seen here in *Raptocleidus*. Intriguingly Fraas (1910) illustrated a median cleft at the rear of the preserved premaxillae in

2.80

Meyerasaurus victor. This has been interpreted as a dorsomedian foramen (Taylor 1992; Smith and Dyke 2008), and the possibility arises that it may have been the anterior end of a dorsomedian fossa as in *Raptocleidus*. However, Smith and Vincent (2010) have reported that it is unclear whether a dorsomedian foramen was present or not. Although incomplete, the preserved morphology is dissimilar to that of *Raptocleidus*, suggesting that a dorsomedian fossa was absent (pers. obs. of cast AMNH 3872). Druckenmiller (2006) questioned the utility of the dorsomedian foramen for phylogenetic analysis, but included it in his analysis as it had been proposed as a synapomorphy of a clade comprising 'rhomaleosaurs' and *Leptocleidus* (Cruickshank 1997).

The extent of the prefrontal on the skull roof is unknown, but it was undoubtedly present. The distribution of prefrontals in plesiosaurians is currently controversial. It has been described as absent in the Callovian cryptoclidids *Cryptoclidus* and *Tricleidus* (Brown 1981; Brown and Cruickshank 1994) and it is also not present in the contemporaneous *Muraenosaurus* species (pers. obs., the suture identified by Andrews (1910) is a break in NHMUK R2678, the basis of his description). Druckenmiller (2006) assumed it to be present in all plesiosaurs pending confirmation of the situation in cryptoclidids, and O'Keefe (2001) coded it as being present in both *Cryptoclidus* and *Tricleidus*, but unknown in *Muraenosaurus*. Where it is present the prefrontal may extend from the orbit to the external naris as in *Plesiosaurus dolichodeirus* (Storrs 1996), *Occitanosaurus* (Bardet *et al.* 1999), *Hydrorion* (Maisch and Rücklin 2000; Grossmann 2007) and *Liopleurodon* (Noè 2001). Conversely, it may be excluded from the external naris by contact between the frontal and maxilla as in *Stratesaurus* (pers. obs. of OUMNH J.10337), *Eurycleidus* (Smith, 2007; pers. obs.), and *Simolestes* (Noè, 2001). In *Raptocleidus* the prefrontal formed at least the anterodorsal part of the

orbital rim. However, it did not extend posteriorly to exclude the frontal from contact with the orbit as is seen in *Hydrorion* (Maisch and Rücklin 2000; Grossmann 2007), *Rhomaleosaurus cramptoni* (Smith and Dyke, 2008), *Liopleurodon* (Noè, 2001) and NHMUK 49202 (Andrews, 1896; Druckenmiller, 2006).

The relatively large orbits of *Raptocleidus* are similar to those of *Cryptoclidus* (Brown 1981) but also *Thalassiodracon* and *Stratesaurus* (Storrs and Taylor 1996; O'Keefe 2001, Benson *et al*. 2012). As noted above the region of the prefrontal-frontal contact at the anterior end of the supra-orbital flange is markedly arched. Although this region is fragmentary, it appears to have been more highly arched than any other plesiosaur, and would have given the skull of *Raptocleidus* a distinctive profile. *Umoonasaurus* possesses arched frontal crests (Kear *et al.* 2006), but lacks the double arch which would have been present in *Raptocleidus*, while a raised ridge formed by the supraorbital bones is seen in some other leptocleidians (Ketchum and Benson 2010, c20). The frontals are notable for their comparatively large contribution to the skull roof, extending from far anterior to the orbits to the level of the middle of the parietal foramen. However, as the anterior extent of the rostrum and position of the external nares remain unknown, accurate comparisons with other taxa are impossible to make. Conspicuous frontal foramina have been described as a rhomaleosaurid character (Smith and Dyke 2008), but are also present in a range of pliosaurids (Ketchum and Benson 2011a). However, as Ketchum and Benson note, they are rarely described in the literature and so may be more widely distributed.

The most notable feature of the postfrontal is the distinct postfrontal cornu projecting into the orbit, which has not been described in any other plesiosaur. Other taxa do show a notch or embayment at the posterodorsal corner of the orbit, particularly

Muraenosaurus (pers. obs.) and *Liopleurodon*. However, in the latter the notch is bordered by the postorbital rather than the postfrontal (Noè, 2001). A strongly laterally curved postorbital is also seen in *Nichollssaura* (Druckenmiller and Russell, 2008) and NHMUK 49202. A slight lateral bulge is seen in several taxa including *Leptocleidus capensis* and *Libonectes* (Druckenmiller 2006). However, this region is prone to distortion or dislocation due to crushing, and accurate comparisons are hard to make. A footplate or posterior process of the postorbital overlying the squamosal and extending posteriorly on the dorsal edge of the temporal bar is seen in several early plesiosaurs – *Stratesaurus*, *'R' megacephalus* (pers. obs.), *Rhomaleosaurus* (Smith and Dyke, 2008), and NHMUK 49202. It is present in *Cymatosaurus* and pistosaurids (O'Keefe, 2004b), and also in *Nichollssaura* but not in polycotylids (Druckenmiller and Russell, 2008). This feature was originally described in *Leptocleidus capensis* by Cruickshank (1997), but could not be confidently identified by Druckenmiller (2006). The situation is unclear in *Plesiosaurus dolichodeirus*, as O'Keefe (2004b) scored it as present, but one is not shown by Storrs (1997). A comparatively robust postorbital footplate overlapping the squamosal is present in *Muraenosaurus* (pers. obs.). In *Occitanosaurus* (pers. obs.) and *Hydrorion* (Maisch and Rücklin 2000; Grossmann 2006) it is present but only has a small contact with the squamosal while in *Microcleidus* it is reduced further (Brown 1994).

The jugal would have contributed to the margin of the orbit as in most plesiosaurs, but the original extent is impossible to determine. However, the form of the jugal and postorbital indicates that the jugal would have been a relatively large part of the cheek rather than the reduced and withdrawn element seen in *Cryptoclidus eurymerus* (Brown and Cruickshank 1994). The jugal is excluded from the orbit by a contact between the maxilla and postorbital in *Microcleidus* (pers. obs.; Brown 1994), *Hydrorion*

2.83

(Maisch and Rücklin 2000; Grossmann 2006), and *Occitanosaurus* (pers. obs.; Bardet *et al.* 1999).

The parietals are unlike those of the majority of pliosauroids in that they do not extend anteriorly on the skull roof beyond the parietal foramen. The situation in *Nichollssaura* is uncertain (Druckenmiller and Russell 2008) while in *Umoonasaurus* the parietals have a large lanceolate anterior extension (Kear *et al.* 2006). The frontals form the anterior border of the parietal foramen in *Cryptoclidus* (Brown and Cruickshank 1994), but in other plesiosauroids they extend anterior to this. The large sub-circular parietal foramen is most similar to that of *Nichollssaura*, described as ovoid by Druckenmiller and Russell (2008). The parietal foramen of *Umoonasaurus* is approximately D-shaped due to a transverse ridge forming the posterior border (Kear *et al.* 2006), but is similarly wide when compared to the narrow oval foramina seen in other taxa. The triangular parietal table is a feature shared with *Nichollssaura* (Druckenmiller and Russell 2008) and *Brancasaurus* (RBJ Benson, pers. comm.). Although this would seem to be to the exclusion of all other plesiosaurs, photographs of the *Umoonasaurus* holotype taken by ARI Cruickshank and deposited in the LEICT archive seem to show a small parietal table was present in this taxon. In some taxa the anterior of the parietal crest can widen as it approaches the parietal foramen and splits into postfrontal ridges, as shown in *Muraenosaurus platyclis* by Andrews (1911, Pl. VI, Fig. 1), but this is not regarded as homologous.

A low sagittal parietal crest is seen in other early plesiosaurs, such as *Thalassiodracon* (Storrs and Taylor 1996), *'R.' megacephalus* (Cruickshank 1994b) OUMNH J.28585 (Cruickshank 1994a) and *Plesiosaurus dolichodeirus* (Storrs 1997) and is probably plesiomorphic for plesiosaurs. Stem pistosaurians such as *Augustasaurus* (Rieppel *et al.*

2002) have an incomplete parietal crest, while some derived plesiosaurs such as *Cryptoclidus* and *Dolichorhynchops* have a dorsally inflated parietal crest. An interparietal foramen is also seen in NHMUK 49202, but this feature may be more widespread amongst plesiosaurs as this area can often be obscured by matrix. Although there is a slight sigmoid outline to the lateral edge of the skull roof where the parietal meets the squamosal, it is unlike the laterally expanded plates described by Taylor (1992) in *Rhomaleosaurus zetlandicus* and seen in other rhomaleosaurids (Smith 2007) and *Augustasaurus* (Rieppel *et al.* 2002). The thickened parietals lateral to the parietal foramen and the internal cavities are similar to those described in *Nichollssaura* (Druckenmiller and Russell 2008). However, internal parietal cavities may be more widespread amongst plesiosaurs, only being detectable through CT scans or fortuitous breaks. The triangular excavation and transverse ride seen on the ventral surface of the parietals are somewhat similar to the semicircular structure and curved step described by Cruickshank (1994a) in OUMNH J. 28585, and those features may have had similar functions. The ventral surface of the parietal is frequently not visible in articulated plesiosaur skulls due to infilling matrix, so again similar structures may be more widespread.

The skull vertex formed by the squamosals differs from that of *Leptocleidus* in not being developed into a pointed "cock's comb" (Cruickshank 1997). However, it is still raised by a substantial amount above the level of the parietal crest, more so than in other early plesiosaurs such as *Thalassiodracon* (Storrs and Taylor 1996), *Plesiosaurus* (Storrs 1997), and NHMUK 49202. The skull vertex is damaged in *'R.' megacephalus*, but NMING F10194 shows that it did project dorsally in *Eurycleidus sp.* (Smith 2007). Conversely, the skull vertex is almost flat in *Nichollssaura* (Druckenmiller and Russell 2008). *Raptocleidus* lacks the posterior squamosal bulb seen in *Augustasaurus*

(Rieppel *et al.* 2002) and most pliosauromorphs, including *Dolichorhynchops* (Druckenmiller 2006). The squamosal bulb is also absent in *Leptocleidus* (Druckenmiller 2006), and in *Plesiosaurus* (Storrs 1997, although one seems to be present in NHMUK39490 this may be an artefact of crushing) and other traditional plesiosauroids although a weakly developed one is present in *Microcleidus* (pers. obs.).

A well developed ventral embayment of the anterior ramus of the squamosal is also seen in some early plesiosaurs such as *Thalassiodracon* (Storrs and Taylor 1996) NHMUK 49202 (Andrews 1896), *'R.' megacephalus* (Cruickshank 1994a), *Meyerasaurus victor* (Fraas 1910), *Hydrorion* and *Seeleyosaurus* (Grossmann 2006), but not in *Plesiosaurus* (Storrs 1997, Fig. 7). The embayment is even more pronounced in stem sauropterygians where the temporal bar is positioned more dorsally, while it is reduced in some derived plesiosaurs such as *Liopleurodon, Libonectes* and *Edgarosaurus* (Noè 2001; Druckenmiller 2006).

The contact of the palatines with the internal nares is seen in other Early Jurassic plesiosaurs and is probably plesiomorphic, also being present in *Augustasaurus* (Rieppel *et al.* 2002). However, it is not present in *Rhomaleosaurus zetlandicus* or *R. cramptoni* (Taylor 1992; Smith and Dyke 2008) or *Meyerasaurus victor* (Fraas 1910) where the vomers contact the maxillae posteriorly. There is at least some contact of the palatines with the internal nares in *Nichollssaura* (Druckenmiller and Russell 2008), while they form the majority of the narial border in *Umoonasaurus* (Kear *et al.* 2006). The palatines form the lateral margin of the nares in *Dolichorhynchops* (O'Keefe 2001), while they are excluded by the vomers and maxillae in *Leptocleidus capensis* (Druckenmiller 2006). The palatine thickening seen in *Raptocleidus* is seen in other plesiosaurs such as *Muraenosaurus* and *'Rhomaleosaurus' megacephalus* (pers. obs.),

and is probably a common feature which is rarely seen in matrix-filled skulls without the aid of CT scanning.

The ectopterygoid is similar to that of *'R.' megacephalus* (e.g. LEICT G221.1851) in being large and contacting the cheek above the plane of the palate. O'Keefe (2004a) notes that the ectopterygoids of *Dolichorhynchops* and *Trinacromerum* rise dorsally to contact the cheek, while the ectopterygoids in *Liopleurodon* remain in the palatal plane (Noè 2001). The ectopterygoid flange is reduced when compared to taxa such as *Eurycleidus* and *Rhomaleosaurus* (Smith 2007), but is still more developed than in *Nichollssaura* and polycotylids which lack an ectopterygoid flange (Druckenmiller and Russell 2008; O'Keefe 2004a). Suborbital fenestra would appear to have been present in *Raptocleidus* as is typical in large-headed plesiosaurs.

A well developed lateral ramus of the pterygoid is seen in other Early Jurassic forms such as *Thalassiodracon*, *Plesiosaurus*, *Eurycleidus* and *Rhomaleosaurus* and NHMUK 49202, while it is lost in some later forms such as *Muraenosaurus* (pers. obs.), *Nichollssaura*, and *Libonectes* (Druckenmiller 2006). The lateral rami are unusual in being convex, as the pterygoid is frequently flat or projects below the palatal plane in this region. The posterior ramus is unlike that of polycotylids in not being developed into an expanded, dished central plate as was described by O'Keefe (2004a), a feature which is also seen in *Umoonasaurus* (Kear *et al.* 2006). Druckenmiller (2006) noted that in certain other taxa this region is excavated into a trough. The paired lateral pterygoid lappets or shelves would appear to be unique to *Raptocleidus*, but a single posterior lappet is seen in some taxa. These have been recognised in *Nichollssaura*, *Edgarosaurus*, *Dolichorhynchops* and some Cretaceous long-necked taxa (Druckenmiller 2006) and *Trinacromerum* (O'Keefe 2004a), and have been cited as a

diagnostic character of the Rhomaleosauridae (O'Keefe 2001). The anterior lateral pterygoid shelf is present in *Thalassiodracon* (CAMSM J.46986, Benson *et al.* 2011a), *Stratesaurus* and *Hauffiosaurus tomistomimus* (pers. obs.). It may also have been present in *Umoonasaurus* (Kear *et al.* 2006, Fig. 1e), but this would require confirmation. The posterior ramus of the pterygoid failed to contact the prootic dorsally, as was observed in *Nichollssaura* (Druckenmiller and Russell, 2008).

Although the anterior extent of the posterior interpterygoid vacuities is unknown, they appear to be relatively wide, unlike the narrow splint-like opening noted by Smith (2007) in *Leptocleidus superstes*, *Dolichorhynchops* and *Brachauchenius*. Relatively wide posterior pterygoid vacuities with length to width ratios of 1 or below are seen in other early plesiosaurs including *'Rhomaleosaurus' megacephalus*, *Thalassiodracon*, *Plesiosaurus*, NHMUK 49202, *Plesiopterys* and *Rhomaleosaurus*. *Muraenosaurus* appears to have had the proportionally shortest and widest posterior pterygoid vacuities of all plesiosaurs (aspect ratio of 0.75), while *Trinacromerum* possessed the most elongate with an aspect ratio of 3.5. The anteriorly placed posterior pterygoid vacuities of *Raptocleidus* are seen in a number of taxa, most notably those comprising the Leptocleidoidea of Druckenmiller (2006), but also derived pliosaurids such as *Liopleurodon* and *Pliosaurus* and the rhomaleosaurids *Rhomaleosaurus cramptoni* (Smith 2007) and *'Rhomaleosaurus' megacephalus*. *Libonectes* possesses relatively elongate vacuities which nevertheless fail to reach the level of the front of the subtemporal fenestra.

The ventromedial flanges of the pterygoid extend medially on the ventral surface of the basioccipital in many taxa. They can be seen to extend towards the midline in *Stratesaurus* (OUMNH J.10337), although it is uncertain if they meet. This is in

contrast to the condition shown by Storrs and Taylor (1996) in *Thalassiodracon* (CAMSM J.46986). In common with *Raptocleidus*, the ventromedial flanges clearly meet ventral to the basioccipital in members of the Rhomaleosauridae (*sensu* Smith, 2007), *Microcleidus*, *Occitanosaurus* (pers. obs., contra Bardet *et al.* 1999) and *Hydrorion* (Maisch and Rücklin 2000), the Leptocleidoidea and the Elasmosauridae (Druckenmiller 2006). In pliosaurids such as *Liopleurodon*, and *Peloneustes* it is the ventrolateral flanges of the pterygoids which meet ventrally to the basioccipital, having apparently twisted medially. The medial surfaces of the posterior rami of the pterygoids are cupped to accommodate the basioccipital tubera in all plesiosaurs, but there is normally no sutural contact here. *Microcleidus* is unusual in having an interdigitating suture between the tubera and pterygoids (pers. obs. of NHMUK 36184). The straight, rather than curved, quadrate ramus would appear to be shared with most plesiosaurs, although as Druckenmiller (2006) noted, in taxa deemed to have a curved pterygoid-quadrate connection the curvature is subtle. In many pliosaurids the ventrolateral edge of the quadrate ramus forms an angle, which is absent in *Raptocleidus*.

The contact of the ventromedial pterygoid flange with the posterior processes of the parasphenoid is variably developed in other taxa depending on the development of both features.

The structure of the parasphenoid is broadly similar to other early plesiosaurs, although the interpretation of the extent of the parasphenoid used here differs from some other authors. In ventral view the posterior end of the plesiosaurian cultriform process is usually marked off from the rest of the parasphenoid by a change in level and associated ridges and keels. This change in level has frequently been taken to indicate the suture between the parasphenoid and basisphenoid (e.g. Storrs and Taylor 1996; Storrs 1997).

However, it merely marks the transition from the palatal surface, effectively the outside of the animal, to the deeper, supportive, structures of the bone. Once this is taken into account, the parasphenoid can be seen to sheath the braincase ventrally in many early plesiosaurs, as O'Keefe (2001) recognised in *Thalassiodracon* and *Plesiosaurus*. This can be seen on CT scans of *'R.' megacephalus* (LEICT G221.1851), where the suture between the parasphenoid and overlying basisphenoid is clear. The same can be seen in CT scans of *Nichollssaura* (Druckenmiller and Russell 2008). The parasphenoid also sheaths the braincase in pliosaurids such as *Liopleurodon* (Noè 2001) and *Peloneustes* (pers. obs.; Ketchum and Benson 2011b; *contra* O'Keefe 2001). This is also the case in the Toarcian plesiosauroids *Microcleidus* and *Occitanosaurus* (pers. obs. contra Bardet *et al.*, 1999). The parasphenoid becomes reduced in the Callovian plesiosauroids *Muraenosaurus* and *Tricleidus*, with the basisphenoid exposed laterally (Andrews 1910). However, it still extends to the posterior extent of the basisphenoid, contacting the basioccipital in *Tricleidus* (Andrews 1910) and in some specimens referred to *Muraenosaurus* (e.g. Maisch 1998: Figure 8). *Seeleyosaurus* has been reconstructed with a short parasphenoid (Grossmann 2007) based on SMNS 16812 which was erected as the holotype of *Plesiopterys wildii* by O'Keefe (2004b). However, in this specimen the notched posterior edge of the basisphenoid can be seen in dorsal view, suggesting that the ventral sheet of bone that extends posteriorly to contact the basioccipital is most probably the parasphenoid. In some taxa the posterior extension of the cultriform process forms a sharp keel on the midline of the parasphenoid between the posterior interpterygoid vacuities. In *Nichollssaura*, *Umoonasaurus* and *Libonectes* this extends for the entire length of the posterior interpterygoid vacuities (Druckenmiller 2006; Kear *et al.* 2006), while in *Leptocleidus* and *Liopleurodon* the keel only extends for part of the vacuities' length. This is also the case in *Augustasaurus* (Rieppel *et al.*, 2002) and

Stratesaurus (OUMNH J.10337). The short yet relative robust fluted parasphenoid keel of *Raptocleidus* is similar to that of *Thalassiodracon* and *Hauffiosaurus*, being shorter than that of *'Rhomaleosaurus' megacephalus* and *Rhomaleosaurus* sensu stricto (Smith, 2007). Amongst plesiosauroids, partial parasphenoid keels are seen in *Microcleidus*, *Occitanosaurus* and *Hydrorion* (pers. obs.; Bardet *et al.*, 1999; Grossmann, 2006). *Plesiosaurus* has a partial keel which is flat-bottomed (NMING F8758), while the posterior extension of the cultriform process in *Muraenosaurus* and *Tricleidus* is flat-bottomed (Andrews, 1911). The polycotylids *Dolichorhynchops* and *Trinacromerum* have relatively wide flat-bottomed keels which extend for the whole length of the posterior interpterygoid vacuities. In non-pistosaurian sauropterygians (e.g. *Cymatosaurus*: Rieppel and Werneburg 1998) the parasphenoid is entirely covered ventrally by the pterygoids.

The posterior parasphenoid processes are a typical feature of early plesiosaurs. O'Keefe (2001; 2006) referred to similar parasphenoid processes as the "cristae ventrolaterales", and identified them in *Plesiosaurus* and *Thalassiodracon* and OUM J.28585. This was by comparison with the condition seen in the basal diapsids *Araeoscelis* and *Petrolacosaurus* (Reisz 1981) where the cristae ventrolaterales of the parasphenoid run lateral to a deep median basisphenoid fossa. Similar paired structures have also been called "basioccipital processes" in lepidosaurs (Bever *et al.* 2005), although these are in a dorsal position. As these processes also contact the pterygoids in LEICT G1.2002, this term is too restrictive in this case; the more neutral term 'posterior processes' is preferred here. Posterior processes are present in *'Rhomaleosaurus' megacephalus* (LEICT G221.1851), where CT sections show that they form robust sutures with the pterygoids as in *Raptocleidus*. They would also appear to be present in *Nichollssaura*, sandwiched between the pterygoids and basioccipital (Druckenmiller and Russell

2008: Text-fig. 9E). As defined by O'Keefe (2001) the cristae ventrolaterales of early plesiosaurs enclose a disc of basisphenoid which plugs the basisphenoid fossa. This disc of bone is here indentified as the basioccipital, but the posterior processes can be present without the disc of bone. In *Occitanosaurus*, they enclose a foramen anterior to the ventromedial flanges of the pterygoids, while in *Microcleidus* the ventromedial pterygoid flanges have extended anteriorly to cover the presumed posterior processes in ventral view, although the foramen in the parasphenoid remains (pers. obs.). In derived pliosaurids such as *Liopleurodon*, the posterior processes would appear to be replaced with a single fan-shaped posterior flange of the parasphenoid, but the robust lateral sutures with the pterygoids remain (Noè 2001).

The narrow rectangular quadrates of *Raptocleidus* are also seen in *Stratesaurus*, while quadrate foramina are also known in *Rhomaleosaurus* (Taylor 1992; Smith 2007) and OUM J.28585 (Cruickshank 1994a).

The basipterygoid processes are particularly well developed when compared with other taxa in which they are known. They are also notable for their relative posterior position, approximately at the estimated midpoint of the posterior interpterygoid vacuities and level with the clinoid processes and dorsum sellae. In *'Rhomaleosaurus' megacephalus* the basipterygoid articulations can be seen in CT scans of LEICT G221.1851, and can be seen to be relatively smaller and more anterior in position. In some derived pliosauroids such as *Liopleurodon* the basipterygoid articulations may fail to ossify (O'Keefe 2001) although they have been identified in *Peloneustes* (Ketchum and Benson 2011b). The whole of the basisphenoid is poorly ossified in these taxa, while in more basal pliosauroids such as *'R.' megacephalus* it is comparatively well ossified (pers. obs.). *Raptocleidus* would appear to be intermediate in its level of basisphenoid

ossification. The internal carotid foramina are seen in all plesiosaurs which have an anteriorly ossified basisphenoid. According to O'Keefe (2001), the notch in the posterior border of the basisphenoid is seen in all plesiosaurs in which that region is ossified, as well as *Cymatosaurus* (Rieppel and Werneburg 1998). However, this feature varies ontogenetically, being less distinct in adults of, for example, *Muraenosaurus* when compared to juveniles (Maisch 1998). The basisphenoid median sulcus is most likely an extension of the posterior notch. A similar feature is seen in *'R.' megacephalus*, where a median ridge on the dorsal surface of the posterior basisphenoid is split by a median sulcus (pers. obs.).

A median ridge on the dorsal surface of the basioccipital is seen in other plesiosaurs such as *'R'. megacephalus* (CT scans of LEICT G221.1851) *Rhomaleosaurus* (Taylor 1992 Figure 2), *Muraenosaurus* and *Tricleidus* (Andrews 1910) but not in *Liopleurodon*, *Simolestes* or *Peloneustes* (Noè 2001; Ketchum 2007). However, this region of the braincase is frequently obscured in articulated skulls, so comparisons are incomplete. An anterior process of the basioccipital can be seen in certain other taxa, although as noted above the interpretation of this feature used here differs from that of certain other authors. O'Keefe (2001) recognised a disc of basisphenoid filling the space between the parasphenoid posterior processes in OUMNH J.28585, *Plesiosaurus dolichodeirus*, *'Rhomaleosaurus' megacephalus*, and *Thalassiodracon*. These structures are here interpreted as anterior processes of the basioccipital in light of the morphology of *Raptocleidus*. This interpretation is supported in the case of *'R.' megacephalus* by CT scan data of LEICT G221.1851. Smith (2007) also interpreted this feature as an anterior extension of the basioccipital in *Eurycleidus* although the posterior processes of the parasphenoid were interpreted as part of the basisphenoid. Ketchum (2007) interpreted this feature in *Thalassiodracon* as part of the basioccipital, but homologised it with

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the vertical plate of Druckenmiller (2006) and Sato (2002), using the term "ventral process".

A distinct neck and ventral groove underneath the occipital condyle as in *Raptocleidus* is seen in '*R.' megacephalus*, *Microcleidus* (pers. obs.), *Rhomaleosaurus* (Taylor 1992) and *Thalassiodracon* (Storrs and Taylor 1996). In other taxa it is less pronounced, with the occipital condyle set off from the body of the basioccipital by a lip (e.g. *Muraenosaurus*: Andrews 1910). There is no constriction in *Nichollssaura* and species of *Leptocleidus* (Druckenmiller and Russell, 2008a; 2008b) or in *Borealonectes* (Sato and Wu 2008). O'Keefe (2004a) described a pedestal in *Dolichorhynchops* and a constriction deeper ventrally than dorsally in *Trinacromerum*. Exoccipital facets which truncate the occipital condyle dorsolaterally are also found in '*R.' megacephalus*, OUMNH J.28585 (although this specimen is a juvenile; Cruickshank 1994a), *Thalassiodracon* (Storrs and Taylor 1996), *Peloneustes* (Andrews 1913), *Liopleurodon, Simolestes* (Noè 2001), *Cryptoclidus* and *Kimmerosaurus* (Brown 1981). The situation is uncertain in *Rhomaleosaurus* (pers. obs. of NMING F8785). Storrs (1997) described a slight exoccipital contribution to the occipital condyle in *Plesiosaurus*, which would imply a corresponding truncation of the condyle by the exoccipital facets. Other taxa such as *Libonectes* and *Elasmosaurus* have a 'globular' occipital condyle which is not truncated by the exoccipital facets, being approximately circular in posterior view and bounded by a lip dorsally (Carpenter 1997; Sachs 2005a). Adults of *Muraenosaurus* also show a circular morphology, although in juveniles the condyle is truncated by the exoccipital facets (Maisch 1998). Carpenter (1997) described the occipital condyle in *Dolichorhynchops* as spherical, but does not indicate the presence of a groove.

An occipital condyle situated dorsal to the plane of the posterior palate has been

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correlated with the development of a vertical plate (Druckenmiller 2006; Sato 2002) or ventral process (Ketchum 2007). The presence of a vertical plate was recovered as a pliosauroid synapomorphy by Druckenmiller and Russell (2008a), although it was noted in other taxa such as *Libonectes*. Ketchum (2007) separated the range of variation into two distinct morphologies, a rounded rugose process and a "wide, flat, relatively smooth, plate". The former state was found to be a synapomorphy of a clade comprising the majority of pliosaurids, while the latter was a synapomorphy of a clade comprising the majority of plesiosauroids (reversed in cryptoclidids). The morphology of this area in *Raptocleidus* would seem to be intermediate in that it is rounded posteriorly, but widens to fill the space between the basal tubera. *Borealonectes* lacks a ventral plate (Sato and Wu 2008) while a short one is present in *Yunguisaurus* (Sato *et al.* 2010).

The exoccipitals participate in the occipital condyle in OUMNH J.28585 (Cruickshank 1994a), *Cryptoclidus* and *Kimmerosaurus* (Brown, 1981), although Ketchum (2007) found the latter taxon to be variable. Druckenmiller and Russell (2008) found this character to be variable in *Peloneustes* and *Plesiosaurus*, although this was not reported as such in *Peloneustes* by Ketchum (2007). It is also present in *Thalassiodracon* (Storrs and Taylor, 1996) and '*R.' megacephalus* (pers. obs. of LEICT G221.1851). The occipital condyle in the pistosaurid *Yunguisaurus* would appear to be formed solely by the basioccipital (Sato *et al.*, 2010).

The general morphology of the combined otooccipital is fairly conservative among plesiosaurs, although interpretations vary. O'Keefe's (2006) discussion of plesiosaur otooccipitals is hampered by his partial back-to-front interpretation of this element in *Thalassiodracon*. The large foramen referred to in this work as the metotic foramen has also been referred to as the jugular foramen (e.g. Andrews 1910, 1913; Brown 1981;

O'Keefe 2004b, 2006; Noè *et al.* 2003; Druckenmiller and Russell 2008b) or vagus

foramen (Williston 1903; Cruickshank 1994a; Carpenter 1997). Maisch (1998) argued

that the term "metotic foramen" should be used in sauropterygians due to the absence of

a separate foramen for the perilymphatic duct, following the criteria of Rieppel (1985)

whereby the structure represents an undivided embryonic metotic fissure. Chatterjee and

Small (1989) also described this opening in *Morturneria* as the metotic foramen.

However, Druckenmiller and Russell (2008b) suggested the perilymphatic duct may

have exited the braincase via a small foramen anterior to their jugular foramen, along

with cranial nerve IX, in *Nichollssaura*. Carpenter (1997) also identified a

glossopharyngeal foramen (IX) anterior to his vagus (X) foramen in both *Libonectes*

and *Dolichorhynchops*. However, the vagus foramen in *Dolichorhynchops* is shown in a

relatively posterodorsal position in medial view (Carpenter, 1997: Figure 7E), and it is

possible that this structure actually represents the foramen for the longitudinal venous

sinus. Although there seems to be a nervous foramen on the otooccipital anterior to the

metotic foramen in these relatively derived plesiosaurs, there is none in more

plesiomorphic taxa such as *Thalassiodracon* (Benson *et al.* 2011a) or *Stratesaurus*

(OUMNH J.10337), and so the rationale for referring to the large opening as the metotic

foramen stands. O'Keefe (2006) refigured the otooccipital of *Thalassiodracon* shown

by Storrs and Taylor (1996), but labelled the large posterior hypoglossal foramen (XII)

as the vagus foramen (X) (compare with Benson *et al.* 2011a, Fig. 4H).

A common otooccipital foramen is present in *Stratesaurus*, *Thalassiodracon* (Benson *et*

al. 2011a), *Liopleurodon* (Noè *et al.* 2003), *Peloneustes* (Andrews 1913) and

'Rhomaleosaurus' megacephalus (pers. obs.), while the situation is unknown in

Pliosaurus (Taylor and Cruickshank 1993b). Williston (1903) described one in

Dolichorhynchops osborni, although Carpenter's (1997) figures of this taxon are

ambiguous. Sato (2005) described one in *D. herschelensis* while it is absent in *Edgarosaurus* (Druckenmiller 2002) and a specimen referred to *Dolichorhynchops sp.* (Sato *et al.* 2011). The anterior hypoglossal foramen opens laterally into the metotic foramen in some specimens of *Muraenosaurus* (Maisch 1998; Evans 1999) and this can also be seen in *Microcleidus* (pers. obs.) although in both taxa the posterior hypoglossal foramen remains separate from the metotic foramen and there is no common otooccipital foramen. The otooccipital nerve foramina are described as separate in *Libonectes* (Carpenter 1997) and *Nichollssaura* (Druckenmiller and Russell 2008ab), although in both of these morphology was interpreted from CT scans. They are shown to be separate in *Kimmerosaurus* (Brown 1981), *Aristonectes* (Chatterjee and Small 1989), *Tricleidus* and *Cryptoclidus* (Andrews 1910).

A fenestra ovalis is certainly present in the vast majority of plesiosaurs (Brown 1981; Carpenter 1997; Maisch 1998; Evans 1999; Druckenmiller 2006; Sato *et al.* 2011). Druckenmiller and Russell (2008b) described a thin flange of pterygoid which contacts the prootic and otooccipital in *Nichollssaura*, hiding the fenestra ovalis in lateral view. They suggested that this may be the case in taxa apparently lacking a fenestra ovalis, such as *Leptocleidus capensis*. In *Microcleidus* the fenestra ovalis is hidden by a dorsal pterygoid flange, but it also opens ventrally rather than laterally and so would not be apparent in lateral view if the pterygoid were missing (pers. obs.). The fenestra ovalis has been reported as being closed in *Dolichorhynchops osborni* (Carpenter 1997), and probably also in *D. herschelensis* (Sato 2005), but it may be that it similarly opened ventrally, there being no obvious lateral embayment between prootic and otooccipital. This would seem to be confirmed by the identification of an undoubted fenestra ovalis in *Dolichorhynchops sp.* (Sato *et al.* 2011). *Thalassiodracon* and OUMNH J.28585 both possessed a concave anterior border to the exoccipital ventral to the prootic facet

indicating a well defined fenestra ovalis was present (contra Storrs and Taylor 1996; Cruickshank 1994a).

The exoccipital flange is variably developed in other taxa. It is well developed in *Peloneustes* (Andrews 1913) and *Liopleurodon* (Noè *et al.* 2003), and is also present in OUMNH J.28585 (Cruickshank 1994a: Figure 6), *Thalassiodracon* (Benson *et al.* 2011a), *Stratesaurus* and *Leptocleidus superstes* (pers. obs.). It is absent in the plesiosauroids *Aristonectes* (Chatterjee and Small 1989), *Muraenosaurus* (pers. obs.), *Kimmerosaurus* (Brown 1981) *Microcleidus* (pers. obs.) *Plesiopterys* (Grossmann 2006) and also in the pliosauromorph *Dolichorhynchops osborni* (pers. obs. of photographs of KUVP 404 supplied by MJ Everhart).

If the morphology of the paroccipital process has been correctly interpreted, then it is similar to that of most plesiosaurs in being "paddle" or "strap-like". In contrast the Oxford Clay plesiosauroids, *Kimmerosaurus* and the elasmosaurids *Libonectes* and *Callawayasaurus* have a robust distal "footplate" for articulation with the suspensorium (Andrews 1910; Brown 1981; Maisch 1998; Carpenter 1997, Welles 1962). *Plesiopterys* also appears to have a robust footplate (Grossmann, 2006).

Dentition

Tooth robustness, curvature and ornamentation vary among plesiosaurs such that tooth morphology can frequently be diagnostic to generic or species level (e.g. Noè 2001, Ketchum 2007). The larger slender-crowned teeth of *Raptocleidus* are more similar to the teeth of small-headed, long-necked taxa such as *Cryptoclidus* or *Muraenosaurus* (Brown 1981) than to the Callovian pliosaurids described by Noè (2001) and Ketchum (2007) or *Rhomaleosaurus* (Taylor 1992; Smith 2007). The tooth of *Brancasaurus*

illustrated by Wegner (1914, Taf. VI, Fig. 10) is a particularly good match, and shares the distal straightening and slight sigmoid curvature seen in *Raptocleidus*. Conversely smaller recurved 'ratchet' teeth similar to those of *Raptocleidus* are found distally in the tooth row in the Mid and Late Jurassic pliosaurids (Taylor and Cruickshank 1993b; Noè 2001) and *Rhomaleosaurus zetlandicus* (Taylor 1992). Intriguingly Andrews (1911) illustrated a small 'ratchet' tooth in *Leptocleidus capensis*, although this tooth no longer survives (Cruickshank 1997). Both *Brancasaurus* and *Leptocleidus capensis* were recently found to be members of the Leptocleididae (Ketchum and Benson 2010, 2011a; but see Kear and Barrett 2011). The slightly squared-off cross-section and flattened areas on the tooth crown seen in *Raptocleidus* are unknown in other plesiosaurians. Most plesiosaurians have sub-circular teeth, but flattened teeth with an oval cross-section are present in *Kimmerosaurus* (Brown 1981) and some elasmosaurids such as *Hydrotherosaurus* (Welles 1943), while teeth with a trihedral section are present in *Pliosaurus* (Taylor and Cruickshank 1993b).

Axial skeleton

The form of the atlas-axis complex of *Raptocleidus* is similar to that of most plesiosaurs in that the atlas centrum is excluded from the anterior margin of the atlantal cotyle by contact between the atlas neural arches and intercentrum. This is unlike *Cryptoclidus* and *Muraenosaurus*, where the atlas centrum participates in the cotyle. *Raptocleidus* is similar to derived pliosaurids in that the axis rib facet is partly formed by the atlantal centrum, but it differs from them in the small axis intercentrum which is restricted to the ventral surface of the complex as in most plesiosaurs (Ketchum and Benson 2011a). The axis neural spine in most plesiosaurs is relatively low and does not extend far posterior to the postzygapophyses (e.g. *Thalassiodracon*, Barrett 1858). The tall and

elongate axis neural spine of *Raptocleidus* is similar to that of *Brancasaurus*, with which it also shares the characters of the axial rib facet and axis intercentrum noted above.

In its relatively short cervical vertebrae *Raptocleidus* is similar to many short-necked plesiosaurs such as *'Rhomaleosaurus' megacephalus*, but also some comparatively long-necked taxa such as *Kaiwhekea* (Cruickshank and Fordyce 2002). However, it differs from the latter and traditional elasmosaurids (e.g. *Hydrotherosaurus*, Welles 1943) in that it lacks a ventral notch in the articular faces of the cervical vertebrae. The small ventral extension of the anterior articular face is seen in pliosaurids (Ketchum and Benson 2011a) but also in *Stratesaurus* and NHMUK 49202 (Benson *et al.* 2012). However, the cervical vertebrae of *Raptocleidus* differ from these two latter taxa in that the articular faces are approximately circular rather than laterally expanded. The low, arcuate neurocentral suture is shared with *Stratesaurus* (OUMNH J.10337), while in many other plesiosaurs the suture is either V-shaped, or situated higher on the vertebrae, or both. In *Hauffiosaurus* the neural arch is deeply V-shaped so that it contacts the rib facet (Benson *et al.* 2011b). The possession of double-headed cervical ribs in at least part of the cervical series is plesiomorphic, but *Raptocleidus* differs from taxa such as *Plesiosaurus*, *Microcleidus* and *Occitanosaurus* in which the posterior cervicals have two widely spaced rib facets. The large zygapophyses are seen in other basal taxa such as *Stratesaurus* and *'Rhomaleosaurus' megacephalus* but also more derived taxa such as *Dolichorhynchops osborni* (Williston 1903), while the zygapophyses are smaller in some long-necked taxa such as *Microcleidus*. In the latter taxon the prezygapophyses straddle the neural canal, and in many plesiosaurs the prezygapophyses are similarly widely spaced with a broad notch between them. In elasmosaurids and cryptoclidids the zygapophyses are connected for much of their length dorsal to the neural canal

(e.g. Andrews 1910; Sato 2003), and some polycotylids and leptocleidids show an incipient morphology in which the prezygapophyses are partially joined (Williston 1903; Benson *et al.* in press). *Raptocleidus* also shows this second morphology, along with concave prezygapophyseal and convex postzygapophyseal facets. The distinct parazygapophyseal processes seen in *Raptocleidus* seem to be uniquely shared with *Stratesaurus* (Benson *et al.* 2012), although other basal taxa show a low rugosity on the lateral or posterolateral surface of the prezygapophysis (e.g. *Eoplesiosaurus*, pers. obs. of TTNCM 8348; *Hauffiosaurus tomistomimus*, Benson *et al.* 2011b Fig. 9K). *Raptocleidus* shares curved cervical neural spines with basal plesiosaurians such as *Thalassiodracon* (BGS GSM 51235) and *Stratesaurus* (OUMNH J.10337), but these are also found in more derived taxa such as *Brancasaurus* (Wegner 1914) and *Leptocleidus* (Andrews 1911, 1922a). In *Peloneustes* the anterior-most cervical neural spines are curved, but those of the posterior cervicals are straight and posteriorly inclined (Andrews 1913).

An elongate series of pectoral vertebrae transitional between the cervical and dorsal series is found in basal plesiosaurians such as *Thalassiodracon* (BGS GSM 51235) and *Plesiosaurus* (Storrs 1997), while many more derived plesiosaurs have a shorter pectoral region with three pectoral vertebrae at most (Andrews 1910). One of the most striking features of *Raptocleidus* is the alternating morphology of the neural spines in the pectoral and dorsal series, with spines being alternately transversely thick and narrow in *R. bondi* and alternately asymmetrically expanded in R. *blakei*. Although not as obvious as in these two species, similar morphologies have recently been recognised in other plesiosaurians. Alternately thick and thin neural spines are present in a number of basal plesiosaurians such as *'Rhomaleosaurus' megacephalus* (pers. obs.) and NHMUK 14550 (Benson *et al.* in review) and also in more derived taxa such as

Brancasaurus (Benson *et al.* in press). Alternate asymmetrically expanded neural spines are present in *Leptocleidus superstes* and MIWG 1997.302 (Benson *et al.* in press). Most plesiosaurians have dorsal neural spines which are substantially taller than the centra, sometimes substantially so as in *Occitanosaurus* (Bardet *et al.* 1999). *Raptocleidus* shares relatively short dorsal neural spines with *Macroplata* among early plesiosaurs (Ketchum and Smith 2010) and they are also present in *Leptocleidus superstes* (Andrews 1922a; Kear & Barrett, 2011), *Brancasaurus* (Wegner 1914), and also *Nichollssaura* (Druckenmiller and Russell 2008b). The latter also shares with *Raptocleidus* the lamina which projects from the posterior of the neural spine, so that it is wider at mid-height than it is at the base, although it is more marked. This is similar to the condition in *'Rhomaleosaurus' megacephalus* in which the dorsal neural spines are expanded both anteriorly and posteriorly. The short and horizontally oriented dorsal transverse processes are similar to those of other early plesiosaurs such as *Eurycleidus arcuatus*.

The robust cylindrical sacral ribs are unlike the anteroposteriorly expanded structures described for pliosaurids (Andrews 1913; Ketchum and Benson 20111a), while the anteroposteriorly thin third sacral rib is unlike that of any described plesiosaur. The 'step' on the dorsal surface of the fourth sacral rib is reminiscent of the bifurcated sacral ribs described in *Bishanopliosaurus* (Sato *et al.* 2003). The flat-bottomed middle caudal vertebrae of *Raptocleidus* are shared with other early plesiosaurians such as *Macroplata* and *Rhomaleosaurus* (Ketchum and Smith 2010, Smith 2007). The inclined rod-like caudal neural spines are most like those of *Brancasaurus* (Wegner 1914) and *Nichollssaura* (Druckenmiller and Russell 2008b), and *Raptocleidus* shares with *Brancasaurus* the sudden asymmetrical loss of postzygapophyses in the anterior half of the caudal series. In most other plesiosaurs the zygapophyses become gradually

reduced, and are vestigial by the middle of the tail (e.g. *Cryptoclidus*, Andrews 1910), while in *Dolichorhynchops* the zygapophyses are only present in the anterior-most caudal vertebrae (Sato 2005; Williston 1903) and in *Muraenosaurus beloclis* they persist into the posterior half of the tail (Andrews 1910).

Appendicular skeleton

The wide shallow embayment in the anterior margin of the clavicular arch is most similar to that of rhomaleosaurids such as *Eurycleidus* (Andrews 1922a) but also leptocleidids such as *Leptocleidus* and *Brancasaurus* (Andrews 1922a; Wegner 1914). Basal pliosaurids such as *Thalassiodracon* (e.g. NHMUK *2020) and *Hauffiosaurus* (Benson *et al.* 2011b) also have an embayed clavicular arch, but the embayment is narrower and deeper and similar to that of *Plesiosaurus* (Storrs 1997). *Thalassiodracon* also shows a narrow posterior process of the interclavicle which protrudes between the anterior processes of the coracoids. A posterior process of the interclavicle is also seen in some plesiosauroids such *Occitanosaurus* (Bardet *et al.* 1999) but is absent in *Macroplata* (Ketchum and Smith 2010). The scapula is similar to that of *Eurycleidus* in possessing a robust buttress on the dorsomedial surface of the ventral ramus, but the ventral ramus itself in *Eurycleidus* is directed more ventrally (Smith 2007). The outline of the anterior margin of the dorsal ramus with an abrupt posterodorsal turn close to the dorsal end is also similar to *Eurycleidus*. In contrast the anterior margin of the dorsal ramus in *Leptocleidus* is much straighter (Andrews 1922a). *Raptocleidus* shares with *Leptocleidus* and *Eurycleidus* the short, blunt ventral rami which only contact the clavicular arch. This is also the case in *Thalassiodracon* (NHMUK 2020*) and *Hauffiosaurus zanoni* (Vincent 2011), and it is likely that it is plesiomorphic as it is present in the plesiosauroid *Occitanosaurus* too (Bardet 1999). In more derived

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plesiosauroids the ventral rami of the scapulae contact one another and the anterior processes of the coracoids to form a stout median pectoral bar (e.g. *Cryptoclidus*, Andrews 1910). In polycotylids such as *Dolichorhynchops osborni* the ventral rami of the scapula are fairly short, and the clavicular arch forms the link between the scapula and the anterior process of the coracoid (Williston 1903) as in *Raptocleidus*. The scapula shelf is only weakly developed in *Raptocleidus blakei*, although it appears to have been a more prominent structure in *R. bondi*. It is a prominent projecting structure in many plesiosaurs including *Leptocleidus* (Andrews 1922a, Kear and Barrett 2011) and *Nichollssaura* (Druckenmiller and Russell 2008b), although it appears to be less prominent in *Dolichorhynchops osborni* (Williston 1903).

The coracoids of *Raptocleidus* are notable for the rounded cordiform embayment in their posterior margin. This is very similar to the coracoid embayment of Cretaceous elasmosaurids (Welles 1943), and its occurrence in *Raptocleidus* is unique among known Jurassic plesiosaurs. *Eurycleidus* possesses an elongated slit-like embayment posteriorly between the coracoids, while *Rhomaleosaurus thorntoni* has a slightly enclosed U-shaped embayment (Smith 2007). However, neither is cordiform as in *Raptocleidus* and elasmosaurids. *Leptocleidus superstes* has a similar, although smaller embayment (the 'intercoracoid notch' of Kear and Barrett 2011). The dorsoventrally thin anterior process of the coracoid present in *Raptocleidus* is shared with basal taxa such as *Eurycleidus* and leptocleidians such as *Leptocleidus* and *Dolichorhynchops* (Andrews 1922a; Williston 1903). In plesiosauroids such as *Microcleidus* and *Cryptoclidus* the anterior process is a dorsoventrally thickened structure. The anterior process is relatively wide transversely, and this is similar to *Eurycleidus* but unlike *Dolichorhynchops* and *Cryptoclidus* in which it is transversely narrow. However, in the polycotylid TMP 95.87.01 the anterior process is relatively wide and it is possible

that this is the plesiomorphic condition for polycotylids. In *Leptocleidus superstes* the anterior process is wider than in *Dolichorhynchops* but narrower than it is in *Raptocleidus* (Andrews 1922a). In derived pliosaurids and elasmosaurids the anterior process is reduced to a short triangular process (Andrews 1913; Welles 1943). The ventral surface of the coracoids lacks a prominent transverse keel as is seen in elasmosaurids (Sachs 2004) and as has been noted in *Brancasaurus* and MIMG 1997.302 by Benson *et al.* (in press).

The humerus is notable for the sigmoid outline to its shaft which is otherwise seen only in some polycotylids (e.g. *Dolichorhynchops*: Williston 1903), leptocleidids (*Brancasaurus*, Wegner 1914; *Leptocleidus superstes*, Kear and Barrett 2011) and elasmosaurids (e.g. Welles 1962). The small preaxial expansion with a concave proximal edge is similar to that seen in *Eurycleidus arcuatus*, whereas the humeri of other rhomaleosaurids such as *'Rhomaleosaurus' megacephalus* have convex or straight preaxial margins The humeri of *Thalassiodracon* and *Hauffiosaurus* are similar, with almost straight preaxial margins (Benson *et al.* 2011b). The humerus of the holotype of *Plesiosaurus dolichodeirus* (NHMUK 22656) has a very small preaxial expansion but a referred specimen, MNHN A.C.8592, has a larger expansion similar to that of *Raptocleidus blakei* (Vincent and Taquet 2010). This specimen is also similar to *Raptocleidus* in possessing well-formed distal epipodial facets which are set at a distinct angle and a prominent postaxial process, both of which are poorly developed in NHMUK 22656. The groove on the ventral surface of the humerus between the epipodial facets was cited as being particularly characteristic of *Plesiosaurus dolichodeirus* by Storrs (1997). However, it is present in *Raptocleidus* and many other early plesiosaurians, including *Eurycleidus*, *Meyerasaurus* and *Thalassiodracon*. The humerus of *'Cimoliasaurus' valdensis* is notable in that it combines a sigmoid

profile with an interepipodial groove, as seen in *Raptocleidus* (Ketchum 2011, Fig. 22.2M). The postaxial process is present in *Eurycleidus* and to a lesser extent in *Hauffiosaurus* (Benson *et al.* 2011b) and *Bishanopliosaurus* (Sato *et al.* 2003). A similar low process is present in *Leptocleidus superstes* (Kear and Barrett 2011) and *'Cimoliasaurus' valdensis* (Ketchum 2011). The anterior flange of the radius is also seen in rhomaleosaurids such as *Meyerasaurus*, 'microcleidids' such as *Microcleidus* and *Hydrorion* and *Hauffiosaurus* (Vincent 2011; Benson *et al.* 2011b). An extensive epipodial foramen in which the intermedium participates is seen in many early plesiosaurs such as *Thalassiodracon*, *Eretmosaurus* and *Microcleidus*. In other taxa such as *Plesiosaurus* the epipodial foramen is still extensive, extending for the length of the epipodials, but the involvement of the intermedium is minimal. In *Hauffiosaurus* the epipodial foramen is closed distally by contact between the radius and ulna (Benson *et al.* 2011b). Postaxial accessory ossicles are preserved in several early plesiosaurs, most notably *Meyerasaurus* (Smith and Vincent 2010), *Hauffiosaurus* (Vincent 2011) and *Eretmosaurus* (NHMUK 14435) and are also known from more derived taxa (e.g. *Cryptoclidus*, Caldwell 1997a; *Dolichorhynchops*, Williston 1903).

The pubis of *Raptocleidus* is plesiomorphic in lacking projecting cornua anterolateral to the glenoid facets. These are present in Callovian plesiosauroids and pliosaurids (Andrews 1910, 1913) polycotylids (e.g. Williston 1903) and elasmosaurids (Welles 1962) but are absent in *Thalassiodracon, Hauffiosaurus* (Vincent 2011) and *Occitanosaurus* (Bardet *et al.* 1999). The pubis becomes anteroposteriorly elongated in Callovian pliosaurids (Andrews 1913) and some polycotylids (Carpenter 1996). The ischia are likewise rather plesiomorphic in their proportions, lacking the expansion of Callovian pliosaurids (Andrews 1913) and polycotylids (Williston 1906). The ilium is similar in its proportions to that of *Rhomaleosaurus thorntoni* (Smith 2007), and

quite unlike the elongated morphology of *Hauffiosaurus zanoni* (Vincent 2011). It lacks the curvature seen in cryptoclidids (Andrews 1910), *Brancasaurus* (Wegner 1914), polycotylids (Albright *et al.* 2007b) and elasmosaurids (Welles 1943).

The femur of *Raptocleidus* is similar to other early plesiosaurians in its almost symmetrical concave preaxial and postaxial expansions. The effect of symmetry is distorted by the large postaxial process, which is similar to a large postaxial process on the femur of *Simolestes* (Andrews 1913, Fig. 9). *Raptocleidus* is similar to *Thalassiodracon* and *Eretmosaurus* in the lack of a well defined facet on the tibia for the intermedium. This is present in the Callovian pliosaurids (Andrews 1913) and plesiosauroids (Andrews 1910). Attention has already been drawn to the similarity between the small centrale in *Raptocleidus* and *Eretmosaurus*. A similar small ossicle which was in the process of becoming fused with a larger neighbouring one is also present in *Stratesaurus* (OUMNH J.10337). If the small element was not the tibiale, was the tibiale (sensu Andrews 1910) absent in *Raptocleidus*, *Eretmosaurus* and *Stratesaurus*? Articulated specimens of *Thalassiodracon* all seem to lack a definite tibiale (NHMUK 2018*, 2020*, 2022*; Hawkins 1834, 1840). Caldwell (1997) has proposed that delayed mesopodial ossification was occurring during plesiosaur evolution which would account for the lack of a large ossified tibiale/centrale.

Systematic Position of *Raptocleidus*

Raptocleidus possesses a mosaic of characters otherwise seen in separate grades and clades of plesiosaurian which has made classification problematic. Additionally, the absence of certain key parts of the skeleton such as the rostrum and lower jaw has hampered the understanding of what is a reasonably complete plesiosaurian specimen in LEICT G1.2002. The skeleton is plesiomorphic in its retention of characters such as a

low parietal crest and robust posterolateral process of the postorbital. In the basicranium the relatively short and wide posterior interpterygoid vacuities and posterior processes (cristae ventrolaterales of O'Keefe 2001) on the parasphenoid portion of the parabasisphenoid which contact an anterior process of the basioccipital are plesiomorphic, as is probably the common otooccipital foramen. The same is the case for the weakly double-headed cervical ribs and the arrangement of the pectoral girdle with the clavicular arch intervening between the endochondral elements in the postcranium (e.g. Andrews 1922a). *Raptocleidus* shares two features uniquely with *Stratesaurus*: prominent postzygapophyseal processes situated posterolaterally on the cervical prezygapophyses and a quadrate that is narrow with sub-parallel sides in posterior view. The two taxa also share: lateral shelves on the ventrolateral flanges of the pterygoids; an exoccipital flange; low, arcuate neurocentral sutures on the cervical vertebrae; a ventral 'lip' on the anterior articular surface of the cervical centra; and a rugose ridge on the posterolateral surface of the iliac blade. The systematic position of *Stratesaurus* itself is uncertain. The holotype (OUMNH J.10337) has been referred to *Thalassiodracon hawkinsii* (Storrs and Taylor 1996; O'Keefe 2001), but was recovered as a separate taxon at the base of Plesiosauroidea (Ketchum and Benson 2010). The taxon has more recently been recovered as a basal rhomaleosaurid (Benson *et al.* 2012).

With rhomaleosaurids such as *Eurycleidus*, '*Rhomaleosaurus' megacephalus*, *Meyerasaurus* and *Rhomaleosaurus* it shares: ventrolateral pterygoid flanges developed into posterior lappets; ventromedial pterygoid flanges that suture to the basioccipital and meet on the midline; proportionally short cervical centra; basally constricted dorsal neural spines; a wide shallow embayment in the anterior margin of the clavicular arch; and a long thin broad anterior process of the coracoid. It shares a deep and distinct dorsomedian fossa or foramen with *Rhomaleosaurus* (Smith and Dyke 2008). The

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rugose ridge on the iliac blade is also seen in *'R' megacephalus*. An anterior flange on the radius is seen in most rhomaleosaurids, although it is absent in *'Rhomaleosaurus' megacephalus* (pers. obs.). Alternating expanded and unexpanded dorsal neural spine morphologies as seen in *Raptocleidus bondi* are seen in basal rhomaleosaurids. *Raptocleidus* shares with basal pliosaurids a short posterior extension of the cultriform process into the interpterygoid vacuities, and lateral shelves on the ventrolateral pterygoid flanges. It also shares with *Hauffiosaurus tomistomimus* the anterior termination of the premaxillary facial processes (Benson *et al.* 2011b). An exoccipital flange is seen in basal and derived (i.e. Callovian and later) pliosaurids, and *Raptocleidus* also shares with the latter a ventral 'lip' on the anterior articular surface of the cervical centra, a ventral process of the basioccipital, and an axis rib that partly articulates with the atlas centrum.

The lack of a squamosal bulb is shared by most traditional plesiosauroids although this is somewhat homoplastic (e.g. *Microcleidus homalospondylus*), and basal plesiosauroids also share the short posterior extension to the cultriform process. *Raptocleidus* also shares with 'microcleidids' (sensu Grossmann 2007) pterygoid ventromedial flanges that suture and meet ventral to the basioccipital, a ventral basioccipital process, and an anterior flange on the radius. The proportionally large orbits are also seen in cryptoclidids, as is the contact between the frontals and the parietal foramen and the short facial processes of the premaxillae. With elasmosaurids *Raptocleidus* shares the cordiform coracoid embayment, a ventral basioccipital process or plate, and posterior lappets on the ventrolateral pterygoid flanges.

Raptocleidus shares several characters with leptocleidians, the clade comprising the leptocleidids and polycotylids (Ketchum and Benson 2010) although the validity of the

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Leptocleididae has recently been challenged with some of its constituent members assigned to Pliosauroidea *incertae sedis* (Kear and Barrett 2011) while *Brancasaurus* has been considered an elasmosaurid (O'Keefe 2001). *Raptocleidus* shares the 'parietal table' with *Brancasaurus* and *Nichollssaura*, taxa with which it also shares an axis rib that articulates with the atlas rib, a small axis intercentrum, a long and erect atlas neural spine, and the morphology of the caudal neural spines. Basally constricted dorsal neural spines are also seen in *Nichollssaura*, and this taxon shares with *Raptocleidus* a wide parietal foramen, as does *Umoonasaurus*. Sigmoid humeri as in *Raptocleidus* are seen in most leptocleidians except for *Nichollssaura* (Druckenmiller and Russell 2008; Benson *et al.* in press), while posterior squared lappets of the ventrolateral pterygoid flanges are present in *Umoonasaurus*, *Nichollssaura* and polycotylids (uncertain in *Leptocleidus superstes*). *Raptocleidus* shares with leptocleidids the relatively short dorsal neural spines and concave prezygapophyses that are partly joined dorsal to the neural canal, while it shares the exoccipital flange and coracoid embayment with *Leptocleidus superstes*. It is uncertain whether the arched orbits of *Raptocleidus* are homologous with the supraorbital ridges and crests of some leptocleidians.

The available evidence therefore suggests that the affinities of *Raptocleidus* lie somewhere among the pliosaurid, rhomaleosaurid or leptocleidian plesiosaurians. These are groups whose constituent members have traditionally been assigned to the Pliosauroidea (e.g. Welles 1943) and can be regarded on the whole having a pliosauromorph body plan (O'Keefe 2002). Some recent phylogenetic analyses have supported this traditional Pliosauroidea (Druckenmiller and Russell 2008; Smith and Dyke 2008; Benson *et al.* 2001b), while others have found the polycotylids (O'Keefe 2001) or both polycotylids and leptocleidids (Ketchum and Benson 2010, 2011a) to be derived plesiosauroids. Due to this uncertainty in the topology in plesiosaurian

phylogeny, *Raptocleidus* is assigned to Plesiosauria *incertae sedis* until it is included in

a global analysis of plesiosaurian relationships.

Vertebra	ventral length	dorsal length	anterior height	anterior width	posterior height	posterior width	VLI
51 (atl)		16.50		31.00	25.10	29.50	
52 (ax)	21.55	19.90	32.30	26.55	24.35	26.50	85%
	At least one missing vertebra (see text for details)						
54 (c4)	20.10	18.90	25.30	27.55	25.25	28.60	75%
55 (c5)	21.00	19.35	26.80	27.65	26.45	28.70	76%
56 (c6)	20.10	20.35	26.70	29.55	27.40	28.95	71%
57 (c7)	21.10	20.40	27.45	29.45	28.70	29.65	72%
58 (c8)	22.00	21.30	28.15	29.45	29.45	31.05	73%
59 (c9)	22.05	22.05	28.95	30.60	29.20	31.55	73%
60 (c10)	23.35	22.35	30.45	31.65	32.15	32.65	72%
61 (c11)	24.55	23.75	31.00	32.95	32.75	34.20	73%
62 (c12)	26.00	25.10	32.10	34.50	32.50	34.85	77%
63 (c13)	26.20	25.65	33.45	35.20	34.35	36.35	74%
64 (c14)	27.00	26.15	34.50	35.45	35.20	37.35	74%
65 (c15)	28.25	27.05	37.20	38.11	37.00	38.60	75%
66 (c16)	28.50	26.95	38.50	37.50	38.55	39.85	73%
67 (c17)	28.95	28.25	36.25	39.05	37.75	40.90	74%
68 (c18)	29.70	32.10	41.35	39.60	40.65	40.10	74%
69 (c19)	30.55	29.20	40.90	40.70	41.05	42.80	73%
	One missing vertebra (see text for details)						
70 (c21)	Centrum missing						
71 (c22)	31.55	31.95	43.00	44.55	42.90	47.60	70%
72 (c23)	30.20	-	44.05	46.25	-	49.80	61%
73 (p1)	33.45	-	-	47.80	47.80	52.70	67%
74 (p2)	32.65	-	45.90	48.75	-	52.80	62%
75 (p3)	33.30	-	-	52.80	48.90	55.80	64%
76 (p4)	-	-	-	57.00	-	57.00	-
77 (p5)	38.00	-	-	56.50	-	58.00	-
78 (p6)	38.30	-	50.90	58.00	-	-	-
79 (p7)	40.00	-	-	-	51.30	-	-

Table 2.1: Dimensions of cervical (c) and pectoral (p) vertebral centra of LEICT G1.2002, *Raptocleidus blakei* gen. et sp. nov.. Measurements in mm. VLI (vertebral length index) is calculated as the ventral centrum length as a percentage of the average posterior width following Brown (1981). Vertebrae are denoted by specimen number followed by estimated position in the series in parentheses.

Dimension	Value
humerus length (mean)	260.5
humerus distal width (right)	148.0
humerus capitulum width (mean)	71.0
radius length	84.0
radius minimum width	57.5
radius maximum width	85.6
ulna length	80.5
ulna width	78.2
femur length	279.0
femur distal width	144.0
femur proximal width	72.5
tibia length	83.7
tibia minimum width	65.3
tibia maximum width	81.0
coracoid, total anteroposterior length	360.0
coracoid, ventral width	189.0
coracoid, length from anterior of glenoid to posterior margin	266.0
scapula, maximum length	150.0
ilium, anteroposterior width of blade	66.7
ilium, maximum diameter of proximal end	65.8
ilium, minimum diameter of proximal end	41.3*
ilium, maximum length of acetabular facet	33.8
ilium, maximum length of ischium facet	35.1
ilium, anteroposterior width of shaft at midpoint	35.2
ilium, maximum length of shaft	145.0
ischium, length	203*
ischium, width	183.0
pubis, length	224.0
pubis, width	229.0
Ratios	
humerus length:femur length	0.94
humerus, length:distal width	1.84
radius, length:minimum width	1.46
radius, length:maximum width	0.98
radius length:ulna length	1.04
ischium, length:width	1.11
femur, length:distal width	1.94
tibia, length:minimum width	1.28
tibia, length:maximum width	1.03

Table 2.2: Selected appendicular measurements and ratios of LEICT G1.2002, *Raptocleidus blakei* gen. et sp. nov.. Values are from the left elements, unless otherwise stated. Measurements in mm; approximate values denoted by an asterisk.

2.113

Vertebral centra	Ventral length	Anterior height	Anterior width	Posterior height	Posterior height	VLI
1	17.8	25.5	27	25.7	27.7	67%
2	18.4	26.4	28.2	28.3	29.0	64%
3	18.5	28.8	30.3	27.5	30.0	64%
4	19.7	28.9	29.3	28.0	30.9	67%
5	19.8	30.2	31.6	29.5	32.5	64%
6	19.7	30.0	33.4	30.0	33.6	62%
7	20.5	30.5	33.0	31.5	34.8	62%
8	21.4	31.2	33.6	31.8	36.2	63%
9	20*	30.8	35.0	-	37.0	54%
10	20.7*	-	33.6	33.2	38.2	58%

	maximum length	distal width	length:width
right humerus	220	120	1.83

	maximum length	minimum width	length:width
radius 1	62.2	50.3	1.24
radius 2	61.9	47.3	1.31

Table 2.3: Selected measurements and indices for NHMUK R16330, *Raptocleidus bondi* gen. et sp. nov.. Measurements in mm; approximate values denoted by an asterisk. VLI (vertebral length index) is calculated as the ventral centrum length as a percentage of the average posterior width following Brown (1981).
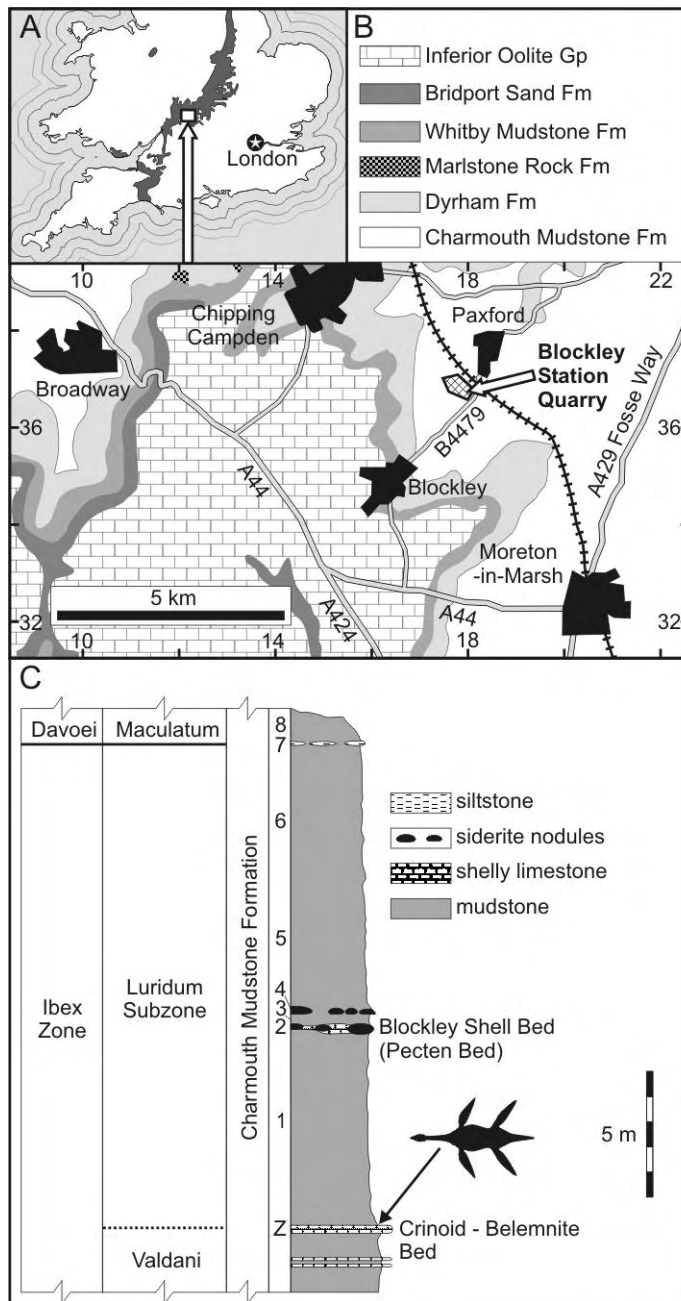
Fig. 2.1: A, geographical location of Blockley Station Quarry within Great Britain, Lower Jurassic outcrop shown in dark tone; B, regional geology; C, geological section (redrawn from Simms 2004; Jurassic ammonite zones and subzones are treated as standard chronozones following Callomon 1995 and are thus written in roman script with capital initials) and stratigraphic correlation with the position of LEICT G1.2002 indicated.

Fig. 2.2: LEICT G1.2002 as reconstructed, viewed from lower surface as preserved.

Scale bar = 1 m.

2.117
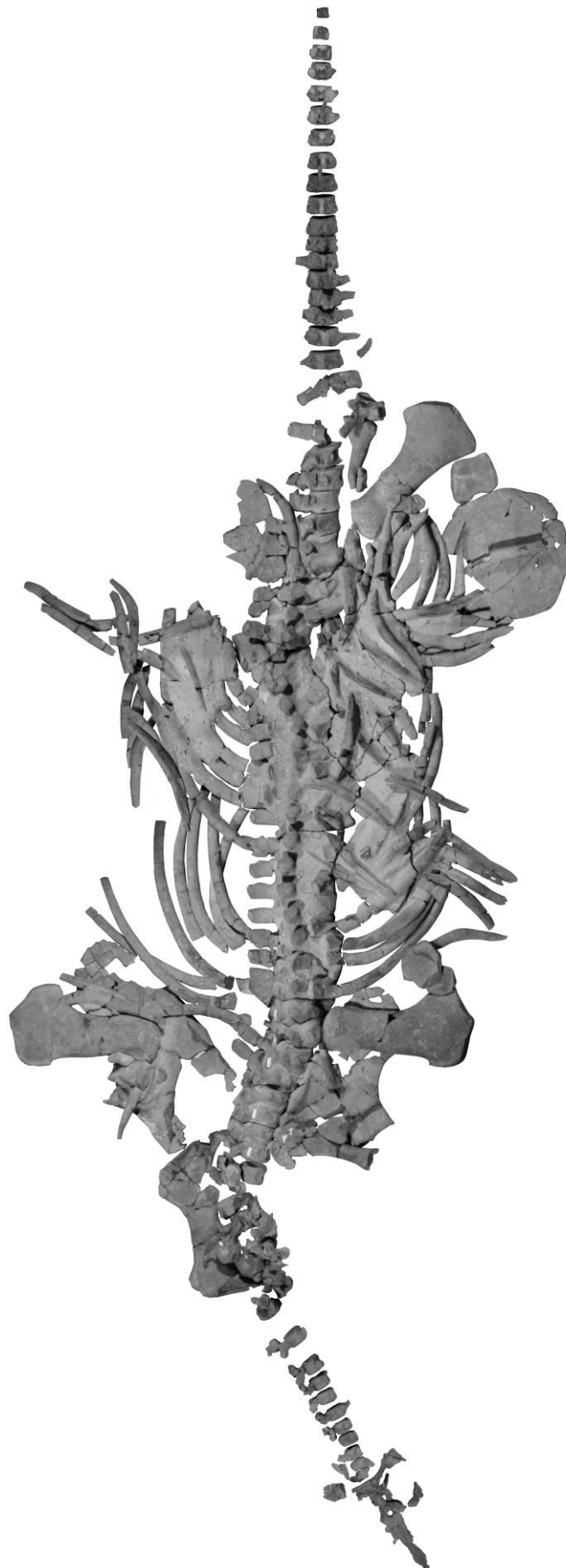
Fig. 2.3: LEICT G1.2002 as reconstructed, viewed from lower surface as preserved.

Corresponding elements from left and right side coloured identically. Scale bar = 1 m.

caudal vertebrae

sacral vertebrae

ilium (l)

femur (l)

tibia (l)

sacral ribs

dorsal vertebrae

pubis (l)

gastralia

gastralia

dorsal ribs

ulna (l)

coracoid (r)

humerus (l)

pectoral ribs

pectoral vertebrae

scapula (l)

cervical vertebrae

clavicle/interclavicle

atlas-axis complex

skull

2.119
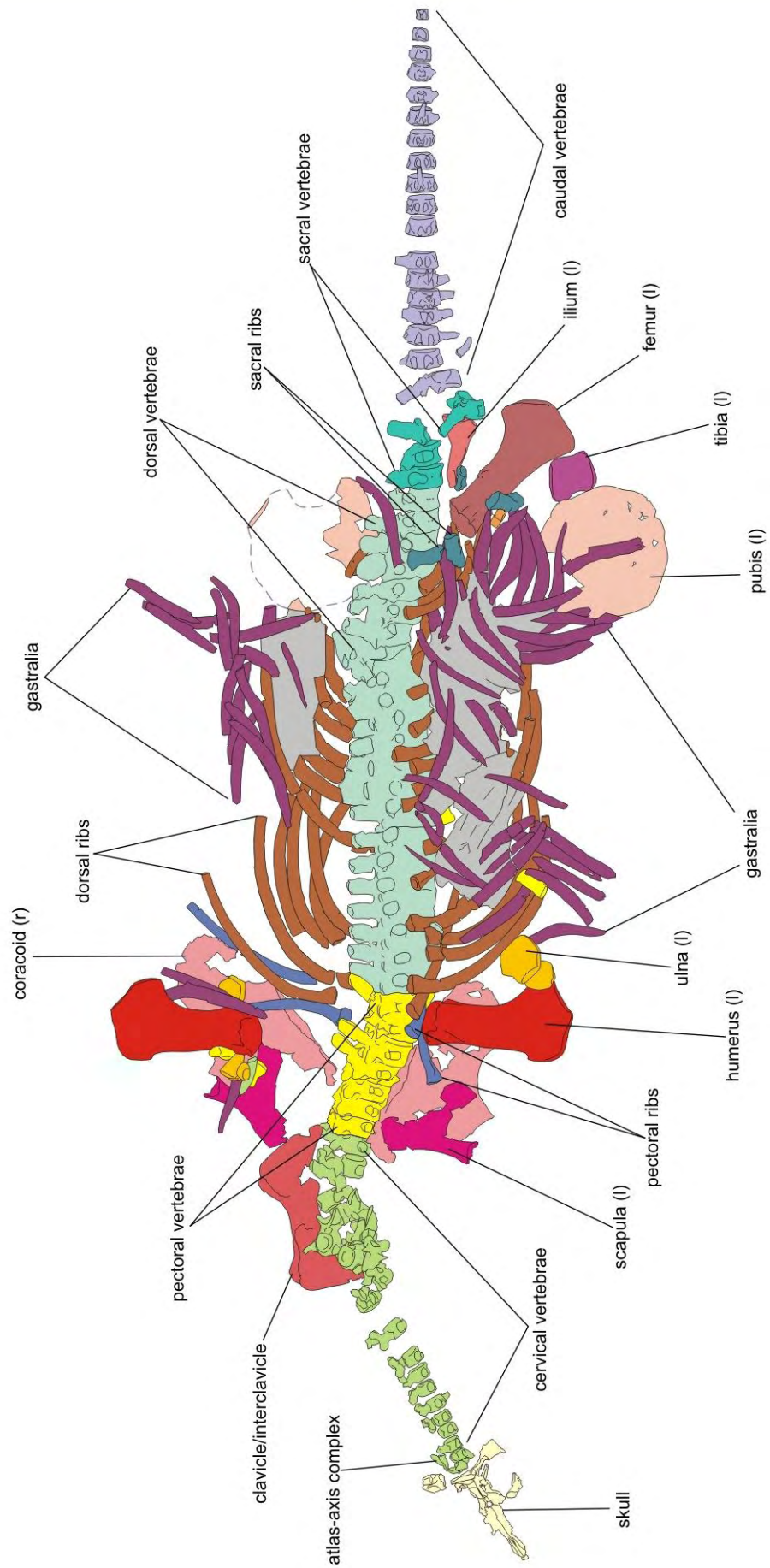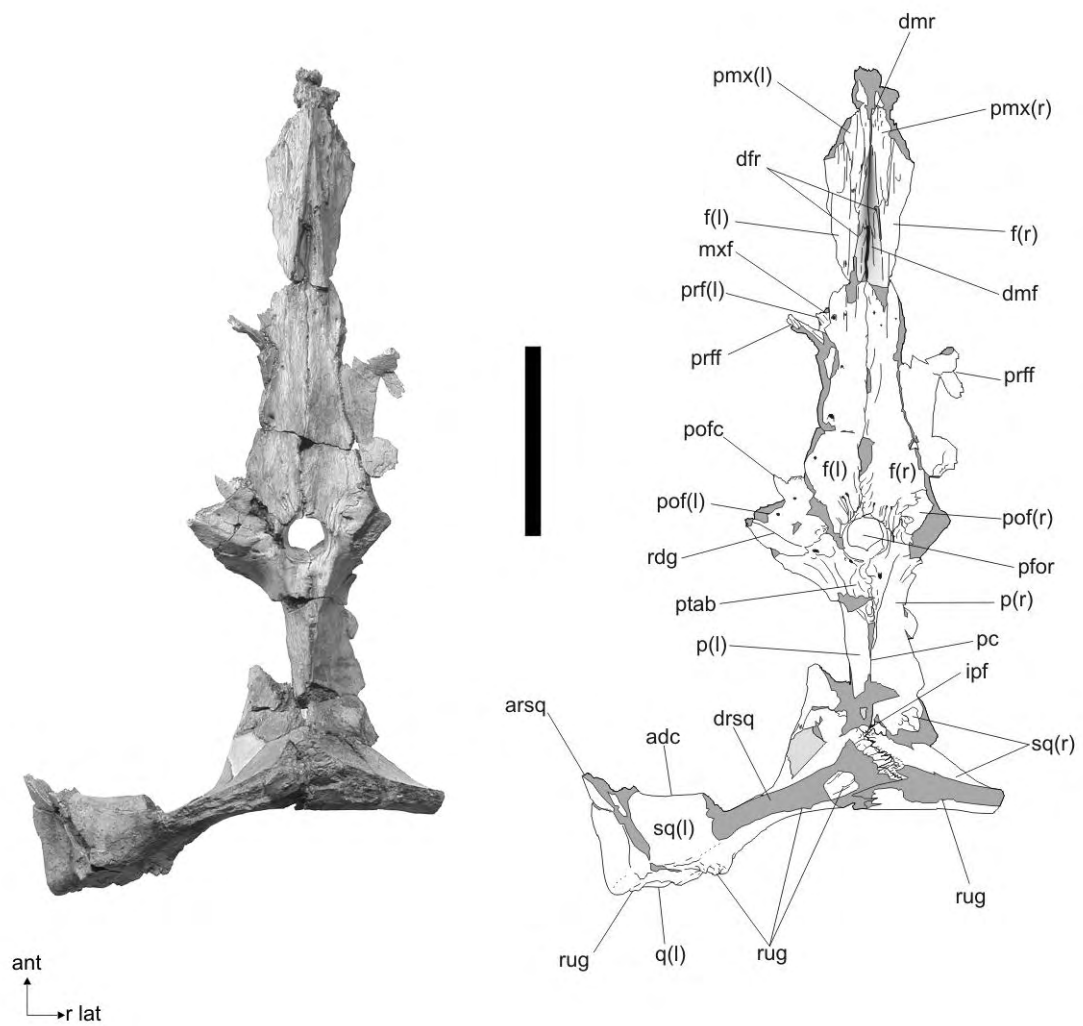
Fig. 2.4: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.7-8, skull roof in dorsal view with interpretive drawing. See text for abbreviations. Broken bone is shown in dark tone, fill in light tone. Scale bar = 50mm.

2.120
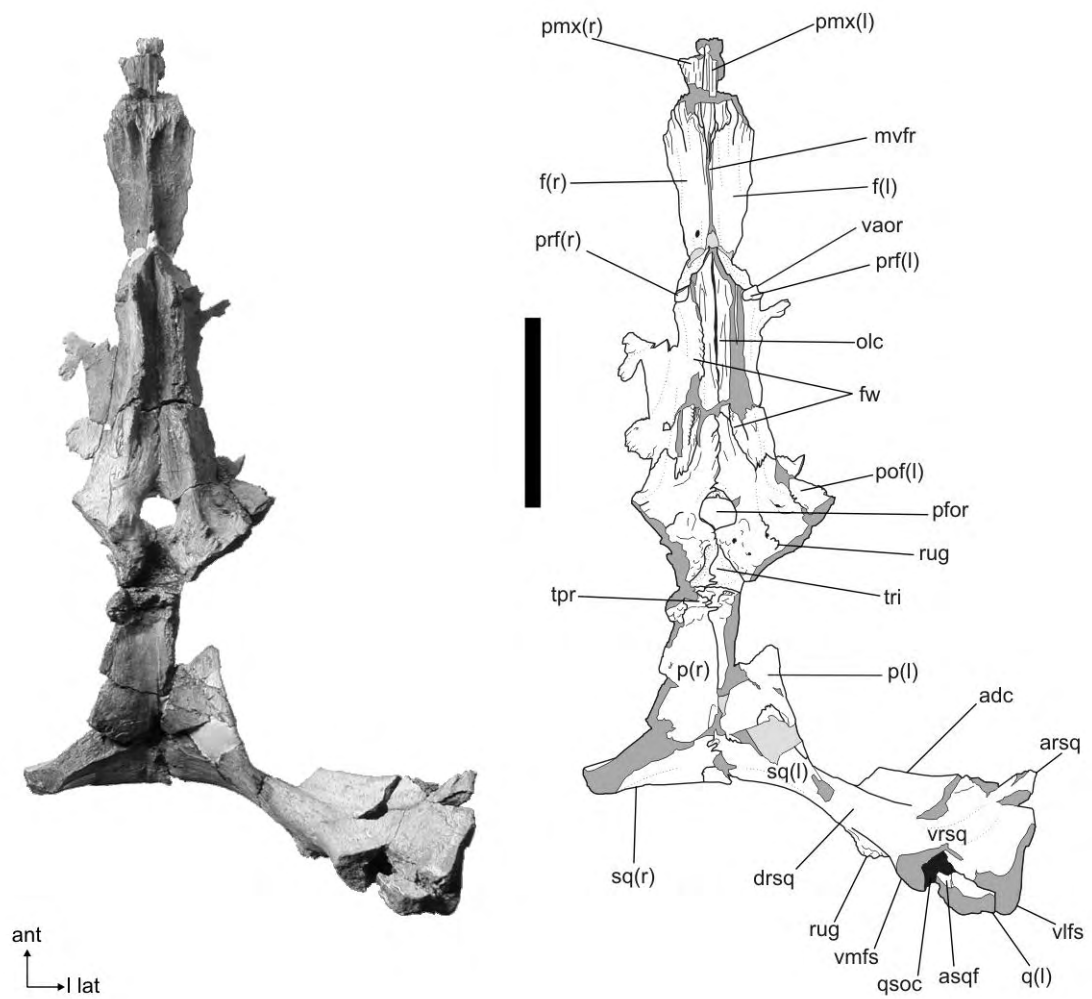
Fig. 2.5: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.7-8, skull roof in ventral view with interpretive drawing. See text for abbreviations. Broken bone is shown in dark tone, fill in light tone. Scale bar = 50mm.
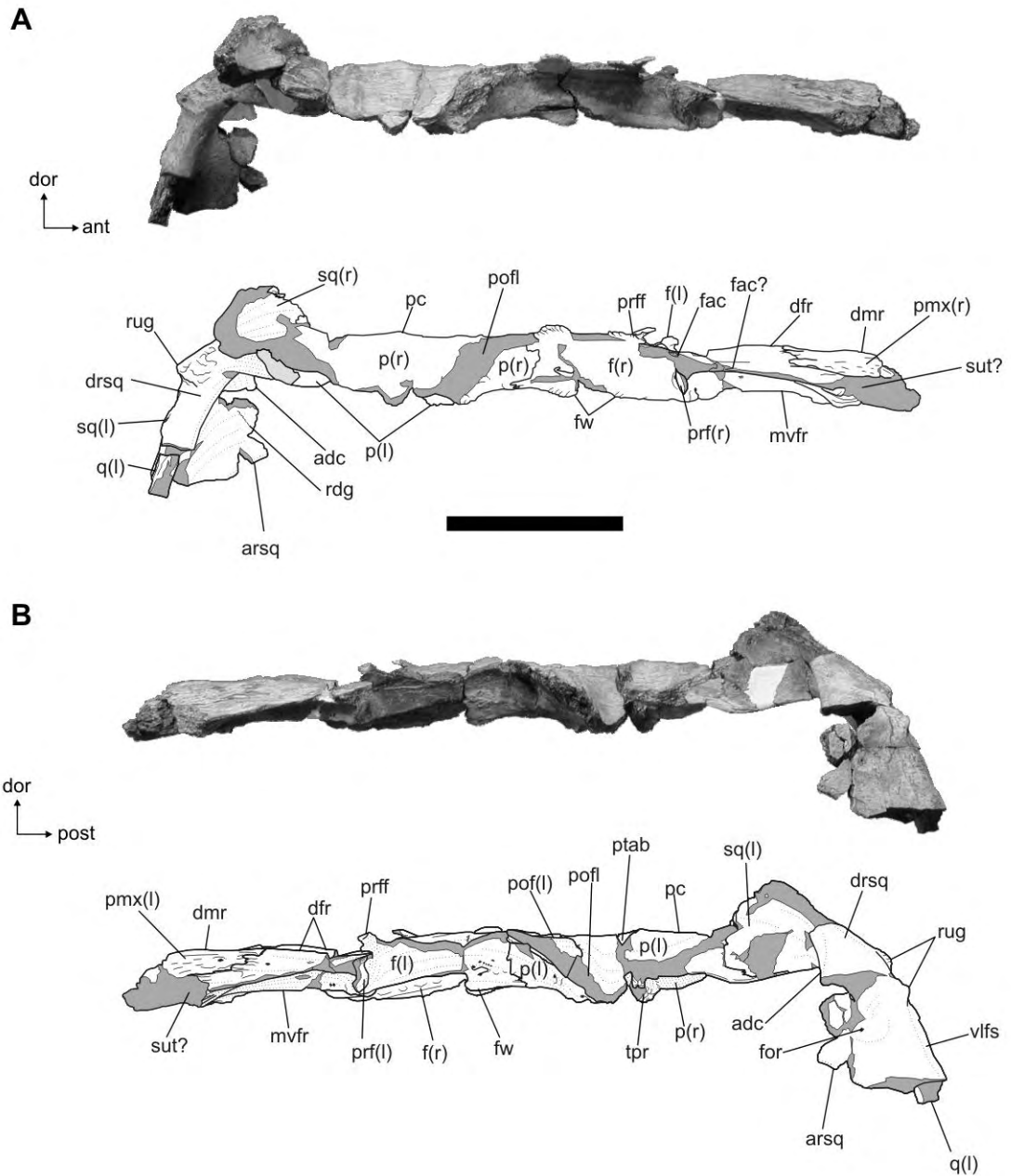
Fig. 2.6: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.7-8, skull roof in right

(A) and left (B) lateral views with interpretive drawings. See text for abbreviations.

Broken bone is shown in dark tone, fill in light tone. Scale bar = 50mm.
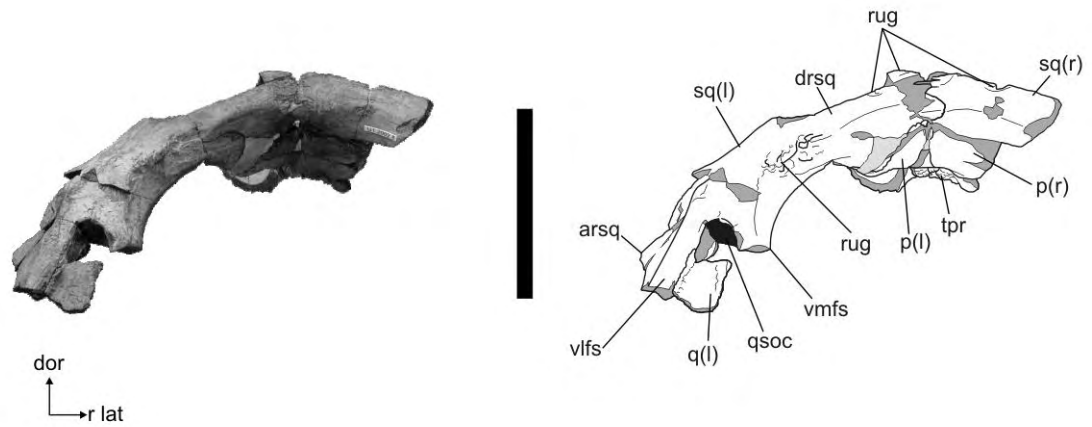
Fig. 2.7: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.7-8, skull roof in posterior view with interpretive drawing. See text for abbreviations. Broken bone is shown in dark tone, fill in light tone. Scale bar = 50mm.

Fig. 2.8: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.7-8 skull in selected sectional views: A, transverse section of premaxillae and possible frontals (camera lucida drawing, anterior view of posterior break surface, reversed); B, transverse section of frontals (reversed); C, frontals and parietals in slightly oblique transverse section (anterior view of posterior break surface, reversed); D, transverse section of parietals and frontals; E, sagittal section of right hand half of partial frontals and parietals (medial view); F, oblique section of left parietal and frontal (anterolateral view of posterior break suface); G, transverse section of parietals (posterior view of anterior break surface); H, approximately transverse section of squamosals and parietals (anterior view of posterior break surface); I, dorsal view with location of sections, sections at B and D traced from CT scans, other sections from natural breaks. See text for abbreviations. In I, broken bone is shown in dark tone and fill in light tone. In A-H, bone not shown in section is in light tone, black indicates matrix-filled sutures. Scale bar = 20mm.

2.124

2.125
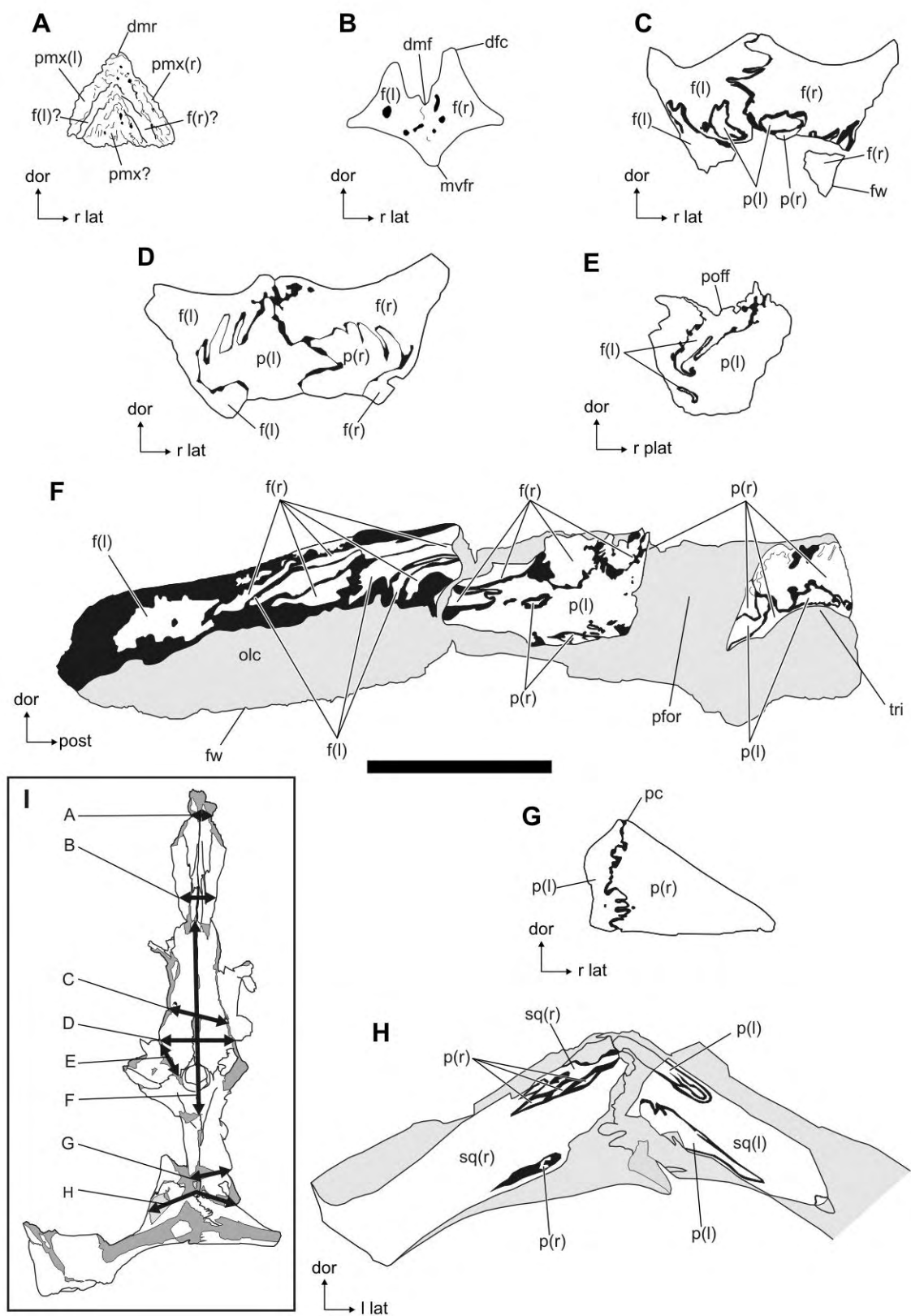
Fig. 2.9: *Raptocleidus blakei* gen. et sp. nov.: A-F, LEICT G1.2002.9, partial left postorbital bar in medial (A), lateral (B), posterior (C), anterior (D), dorsal (E) and ventral (F) views with interpretive drawings; G-H, LEICT G1.2002.11, partial right postfrontal in dorsal (G) and ventral (H) views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone. Scale bar = 20mm.

2.127
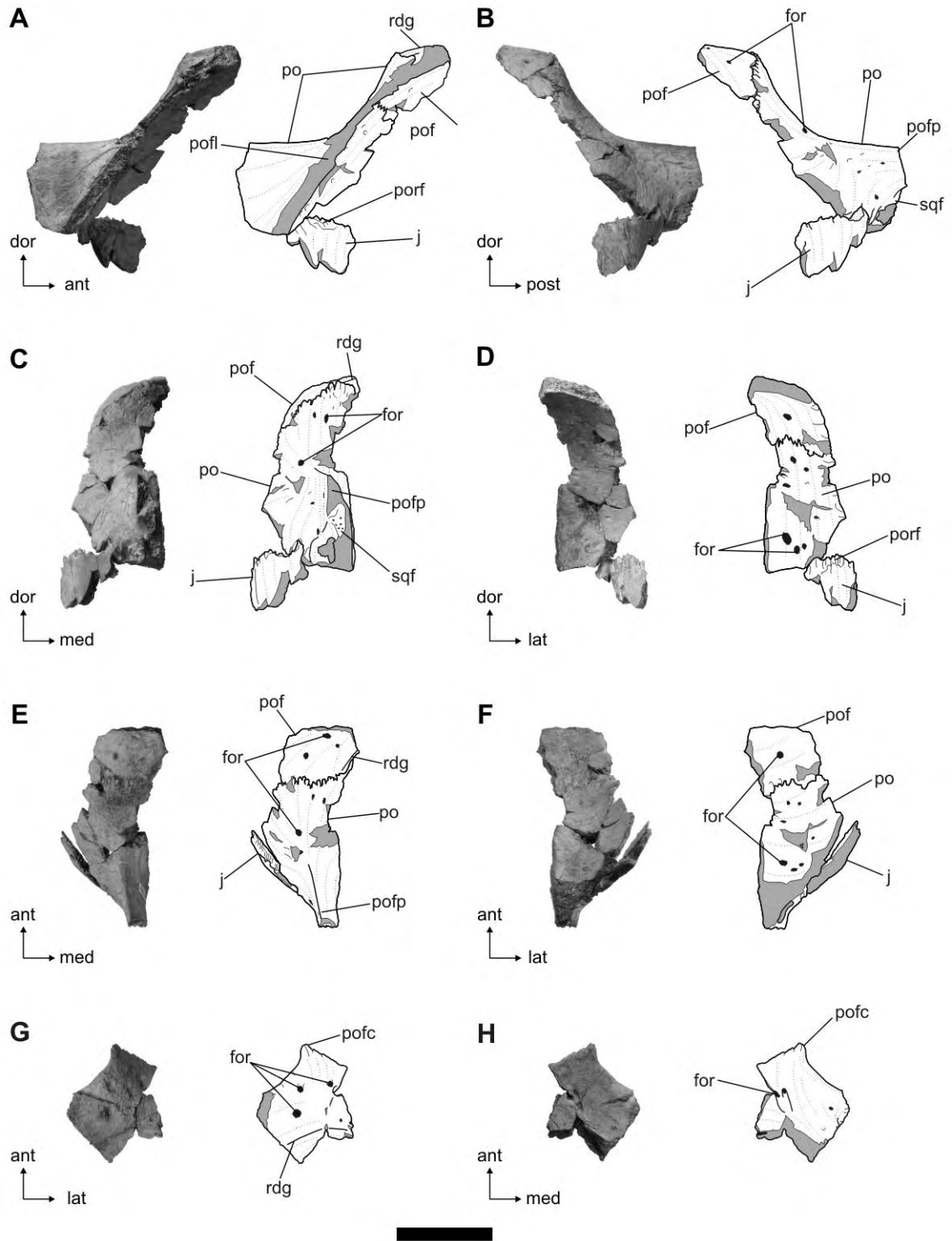
Fig. 2.10: *Raptocleidus blakei* gen. et sp. nov.: LEICT G1.2002.15, right quadrate and attached squamosal fragments, photographs and interpretive drawings in (A) lateral, (B) medial, (C) anterior, (D) posterior, (E) dorsal and (F) ventral views; LEICT G1.2002.10 partial right squamosal and LEICT G1.2002.15 right quadrate as preserved, photographs and interpretive drawings in (G) anterior and (H) posterior views. See text for abbreviations. Broken bone is shown in dark tone. Scale bars = 10 mm.

2.129
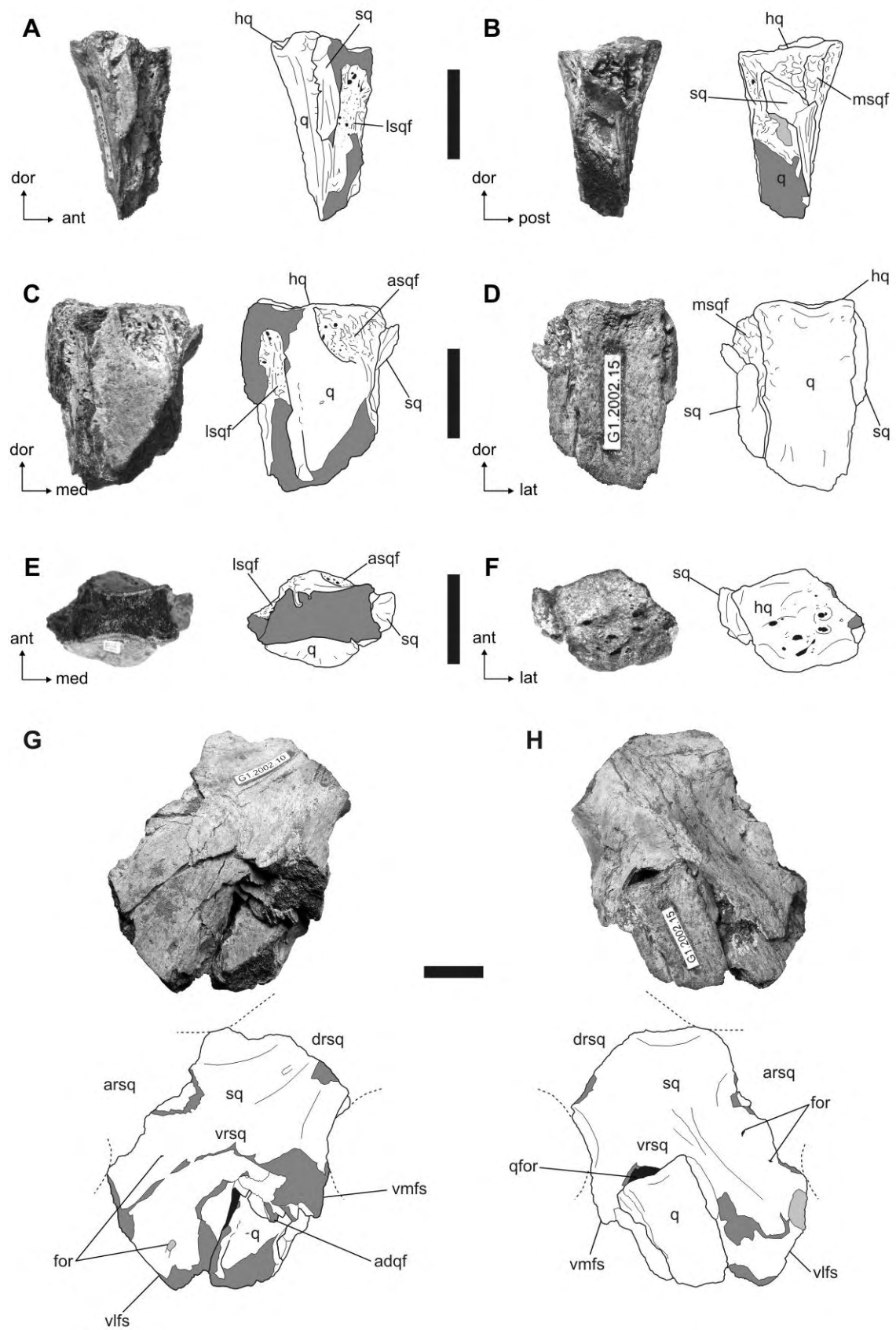
Fig. 2.11: *Raptocleidus blakei* gen. et sp. nov.: LEICT G1.2002.6, partial right ectopterygoid in ventral (A), dorsal (B), anterior (C), posterior (D), lateral (E) and medial (F) views with interpretive drawings, broken bone is shown in dark tone; LEICT G1.2002.6 articulated with LEICT G1.2002.2, partial right pterygoid, in ventral (G) and dorsal (H) views with dotted lines and light tone continuing broken edges. See text for abbreviations. Scale bar = 10mm.

2.131
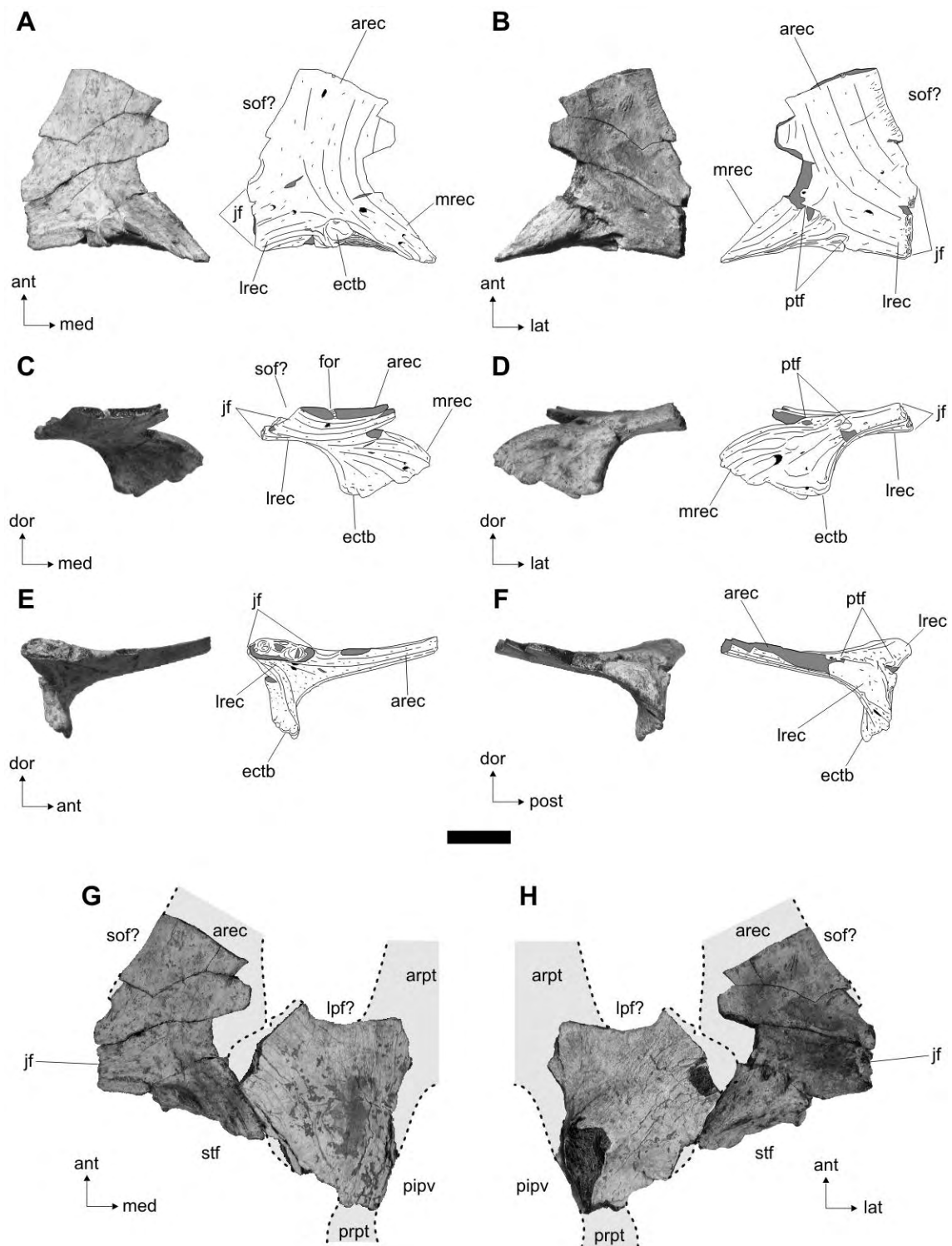
Fig. 2.12: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.1, braincase and LEICT G1.2002.3-5, otic capsule elements: stereopairs in right lateral (A), posterior (B), left lateral (C) and anterior (D) views. Scale bar = 50mm.

A

dor
→ ant

B

dor
→ r lat

C

dor
→ post

D

dor
→ l lat

2.133

Fig. 2.13: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.1, braincase and LEICT G1.2002.3-5, otic capsule elements: A, left lateral view with position of illustrated sections; B-J, CT scan sections and interpretive drawings at 18mm (B), 24mm (C), 33mm (D), 40.5mm (E), 45mm (F), 51mm (G), 58.5mm (H), 64.5mm (I) and 75mm (J) intervals. The crosshair symbol marks the midline and provides a common reference point. Scale bar = 20mm.

2.135
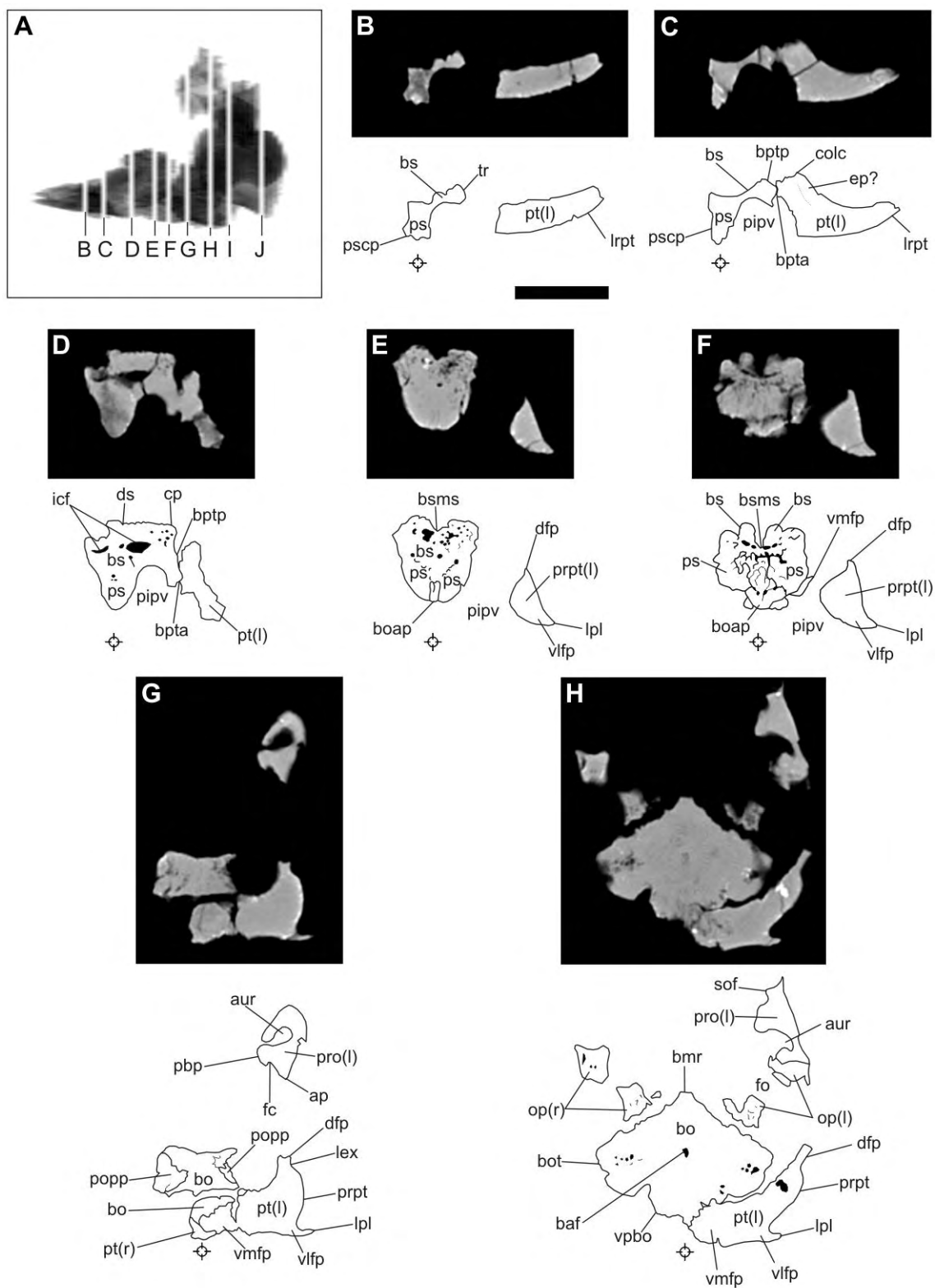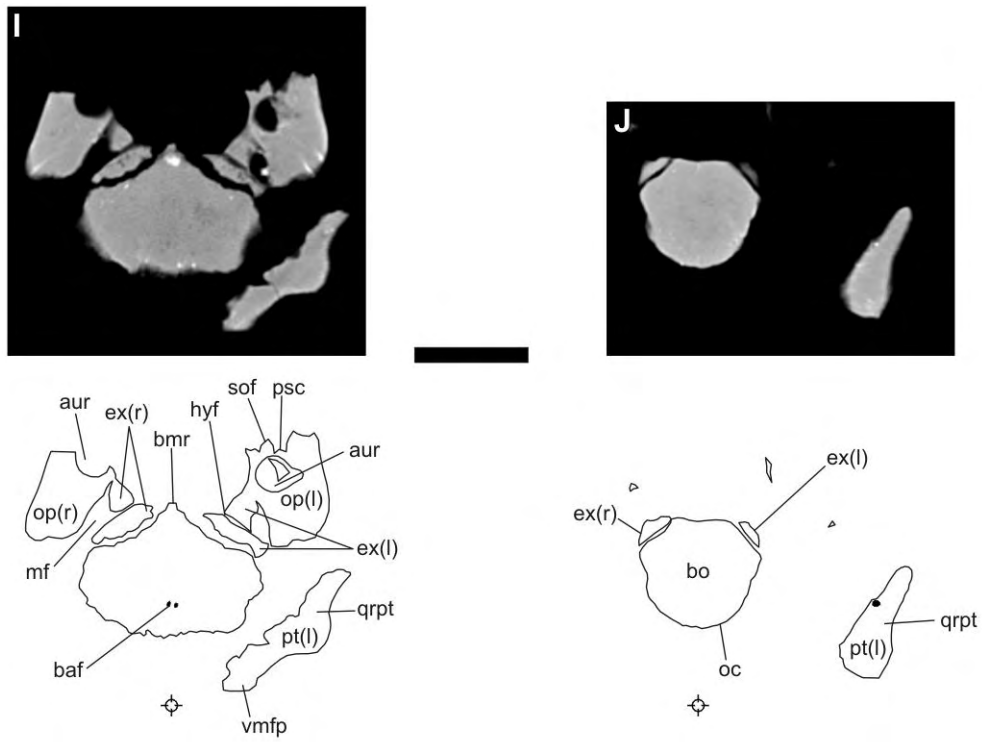
Fig. 2.13 cont.
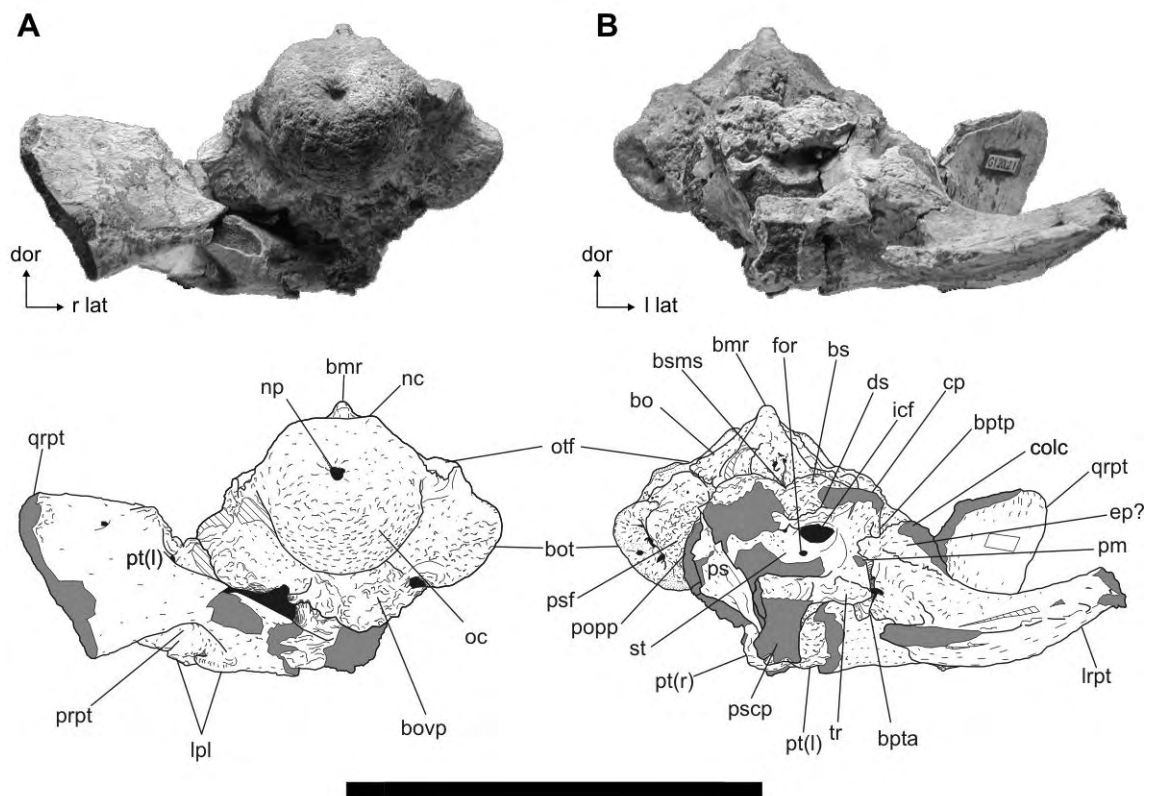
Fig. 2.14: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.1, braincase in posterior

(A) and anterior (B) views with interpretive drawings. See text for abbreviations.

Broken bone is shown in dark tone. Scale bar = 50mm.

Fig. 2.15: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.1, braincase in right (A) and left (B) lateral views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone. Scale bar = 50mm.
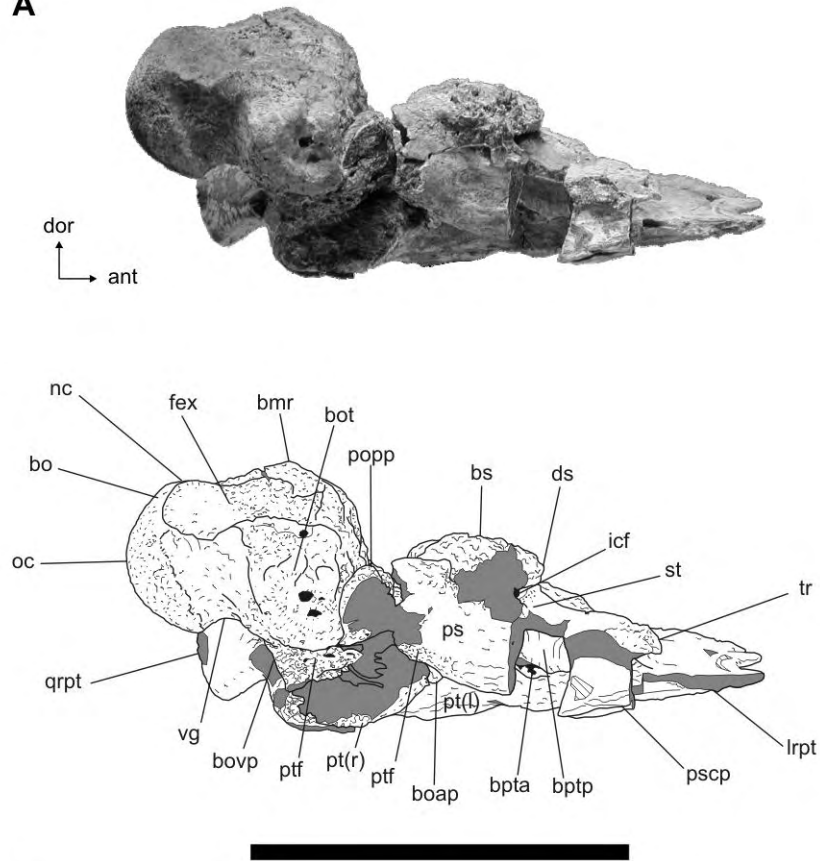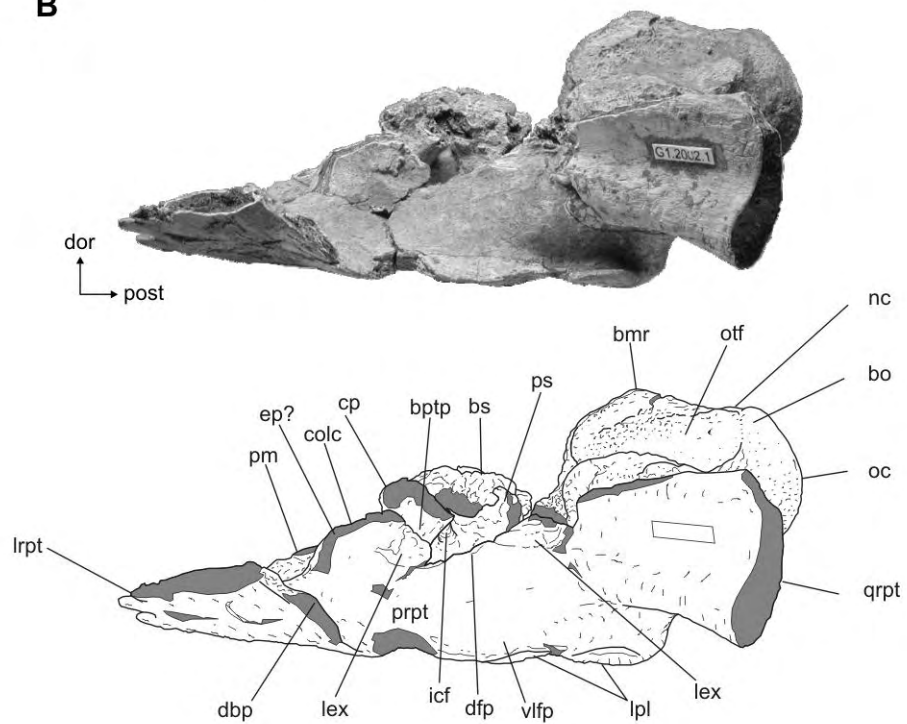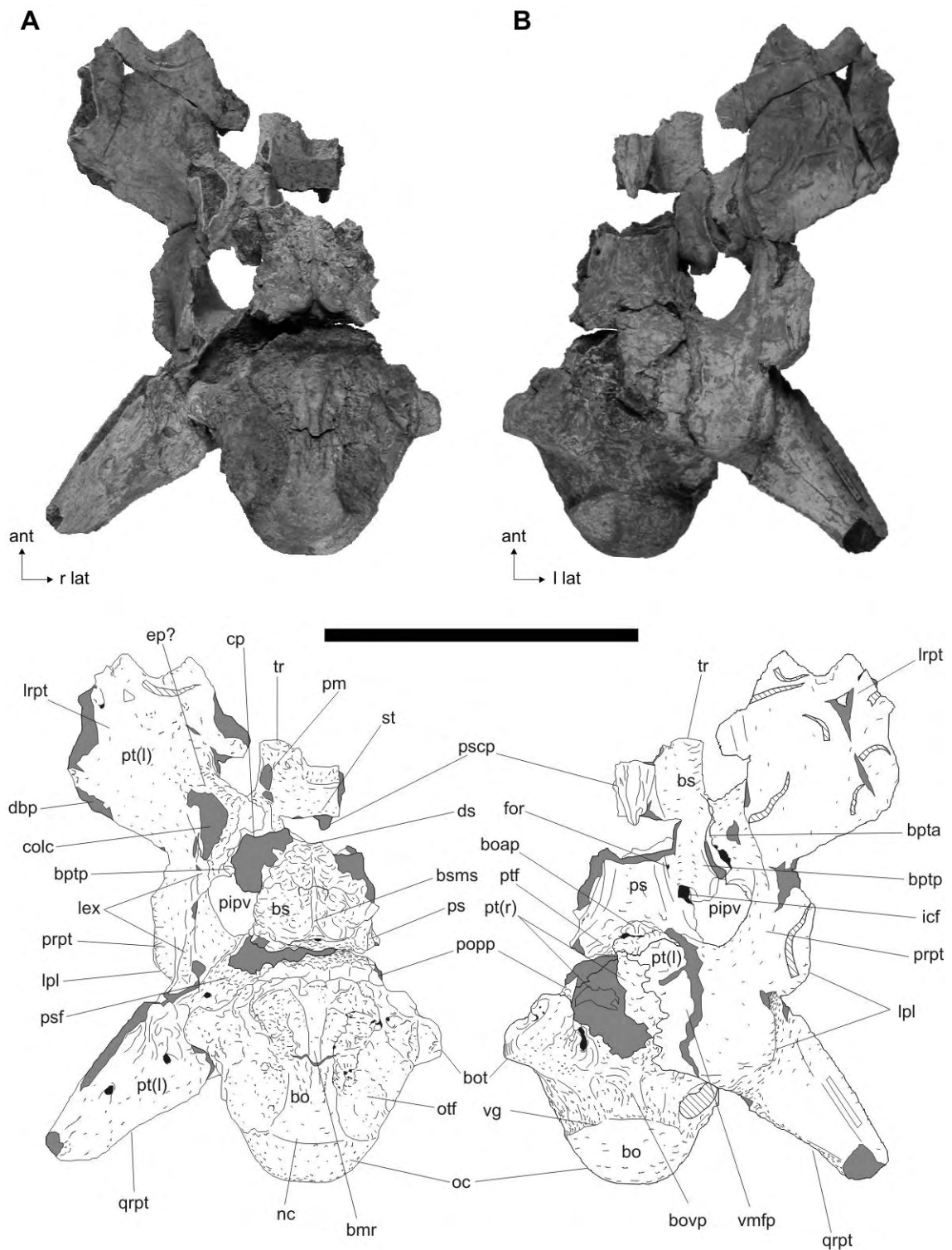
Fig. 2.16: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.1, braincase in dorsal (A) and ventral (B) views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone. Scale bar = 50mm.

2.140
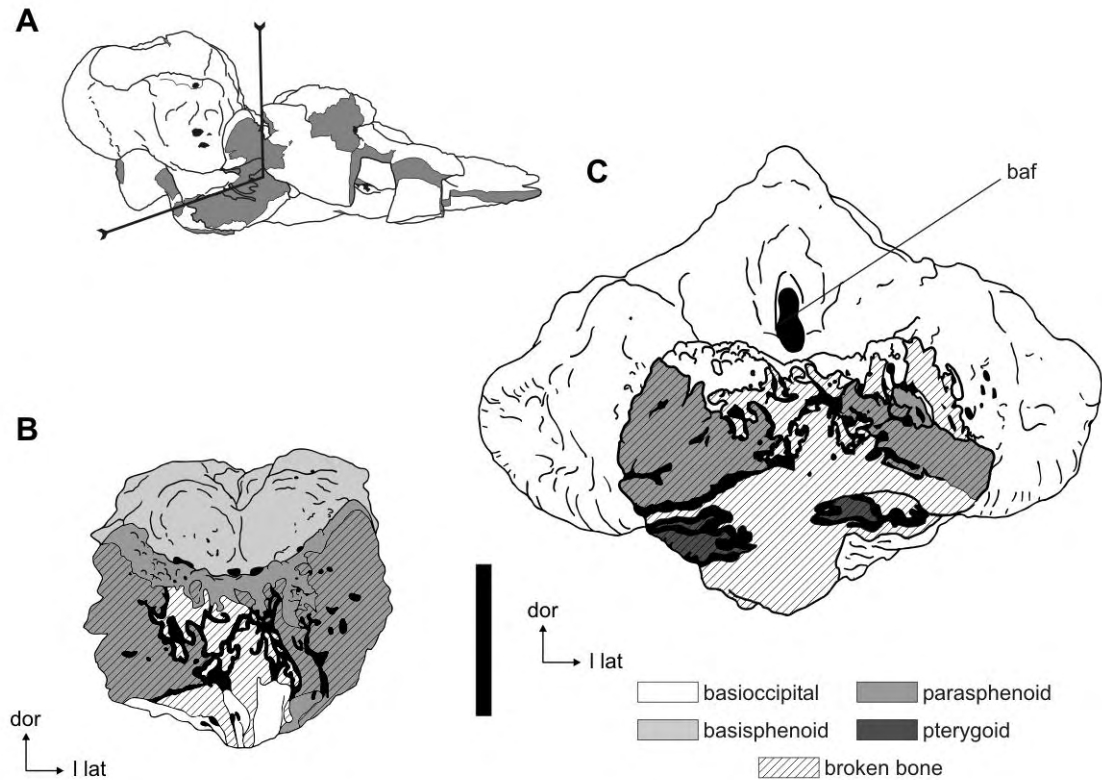
Fig. 2.17: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.1, braincase: A, sketch of right lateral view to show position of break; B, camera lucida drawing of anterior surface of break (reversed); C, camera lucida drawing of posterior surface of break. Scale bar = 10mm.
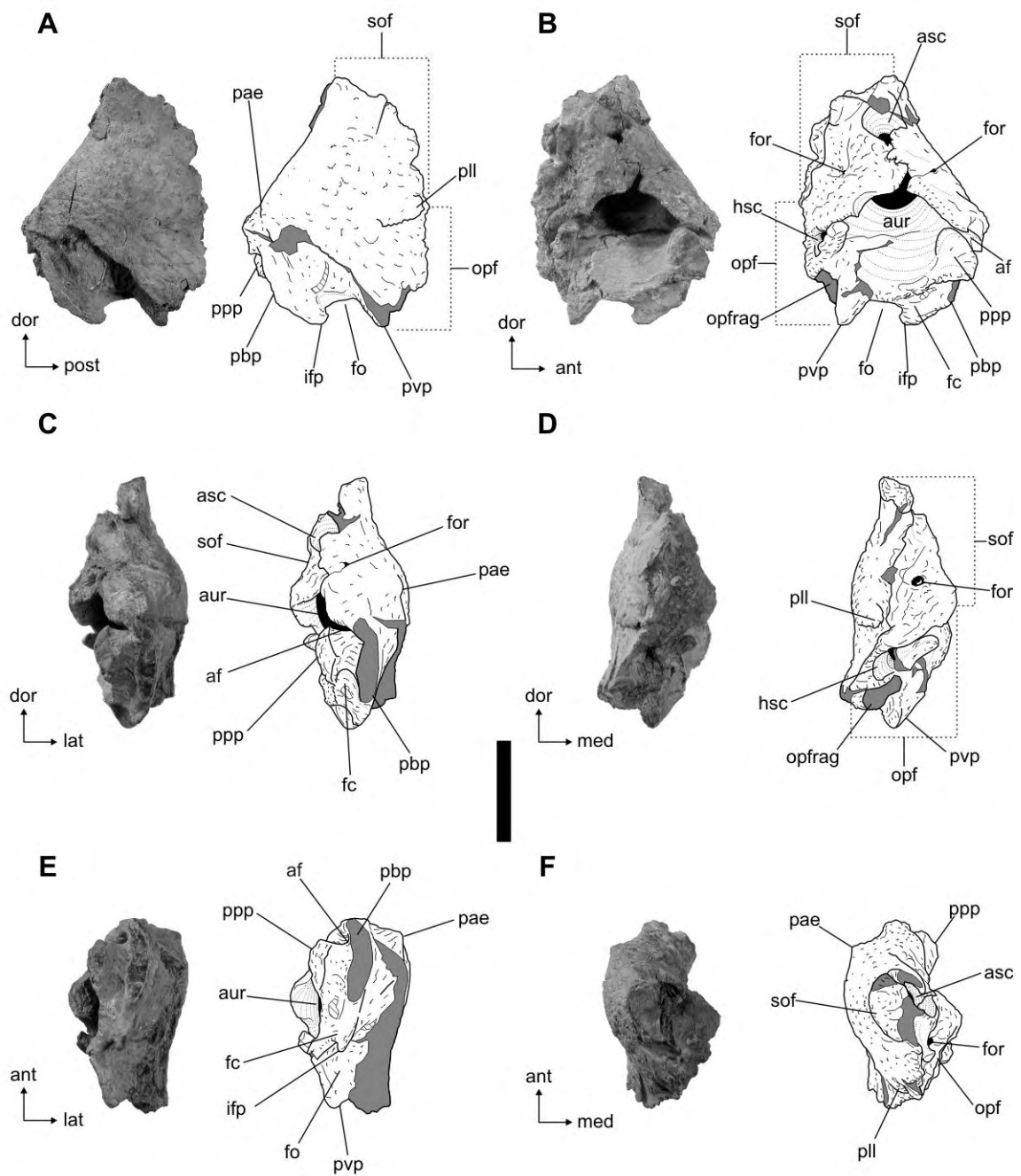
Fig. 2.18: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.5, left prootic in lateral (A), medial (B), anterior (C), posterior (D), ventral (E) and dorsal (F) views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone. Scale bar = 10mm.

2.142
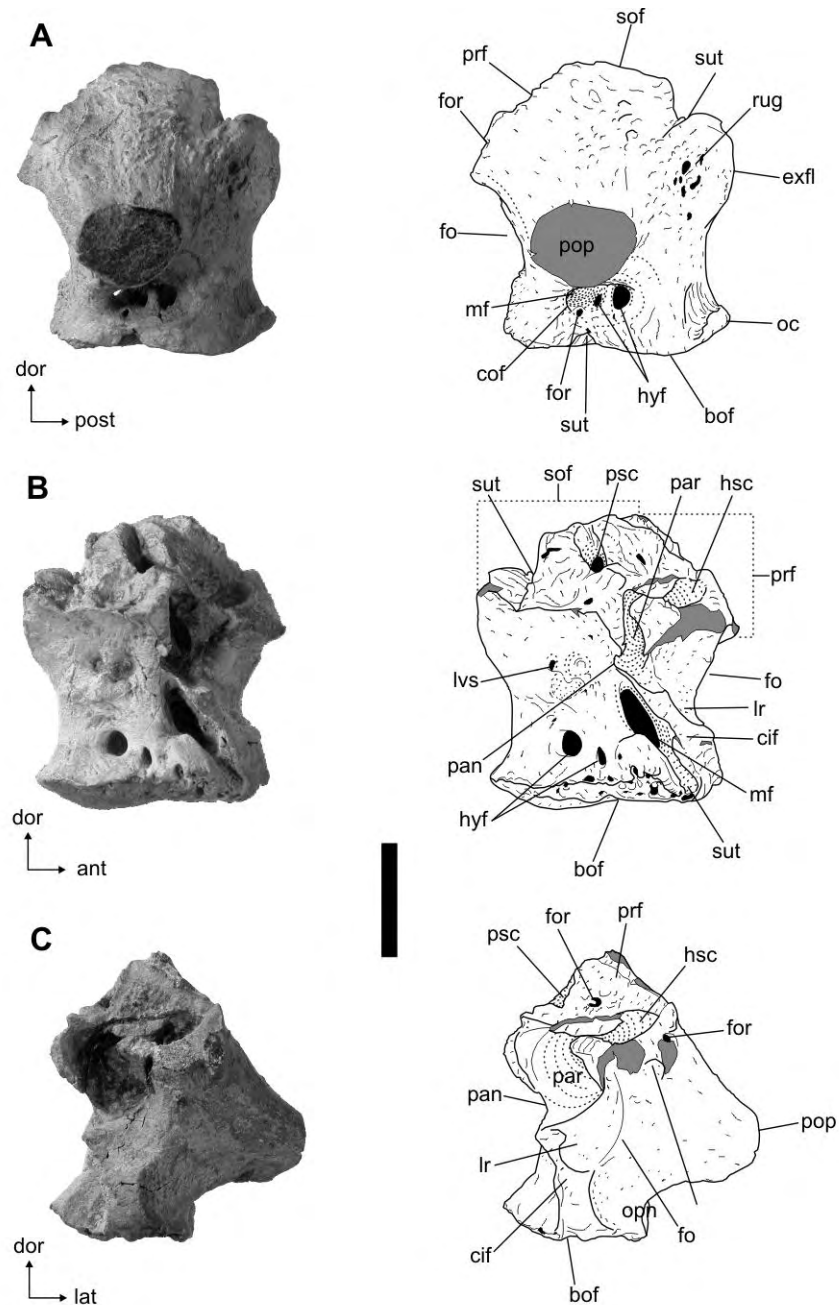
Fig. 2.19: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.3, left otooccipital in lateral (A), medial (B), anterior (C), posterior (D), ventral (E) and dorsal (F) views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone. Scale bar = 10mm.

D

dor
med

E

ant
lat

F

ant
med

Fig. 2.19 cont.

2.144
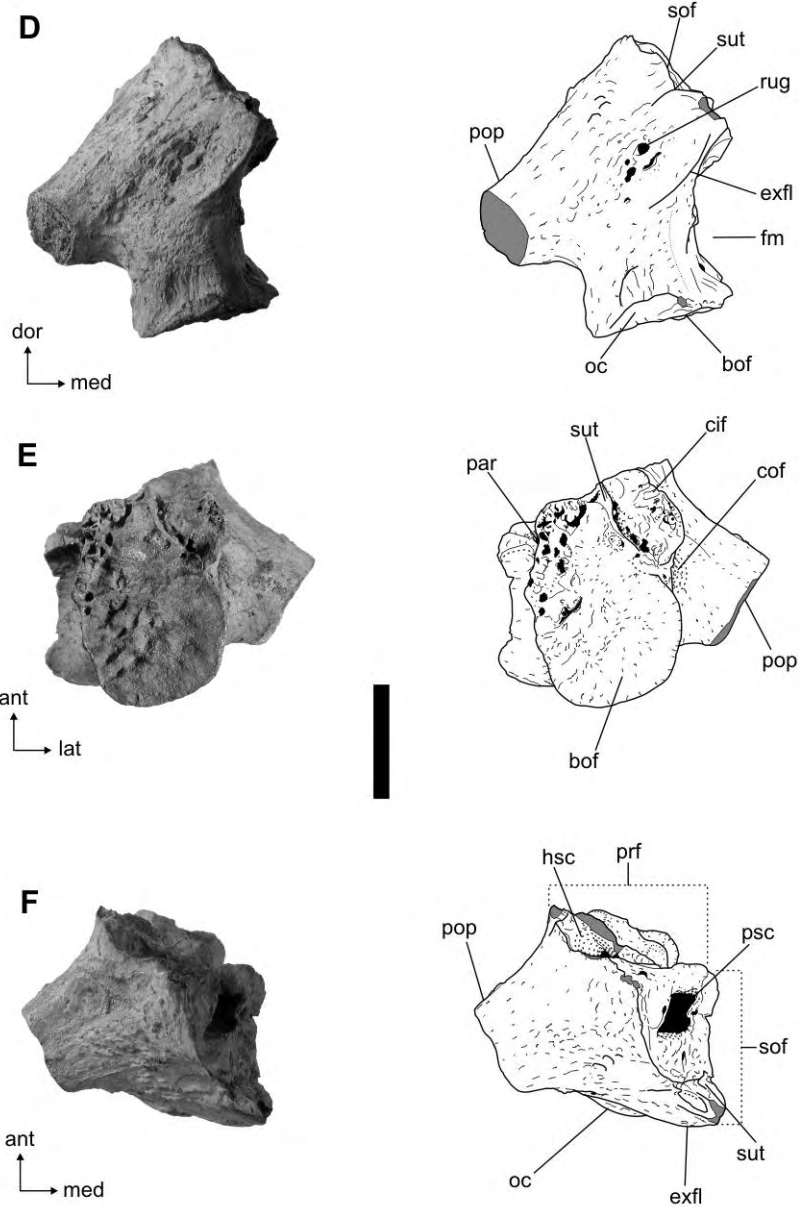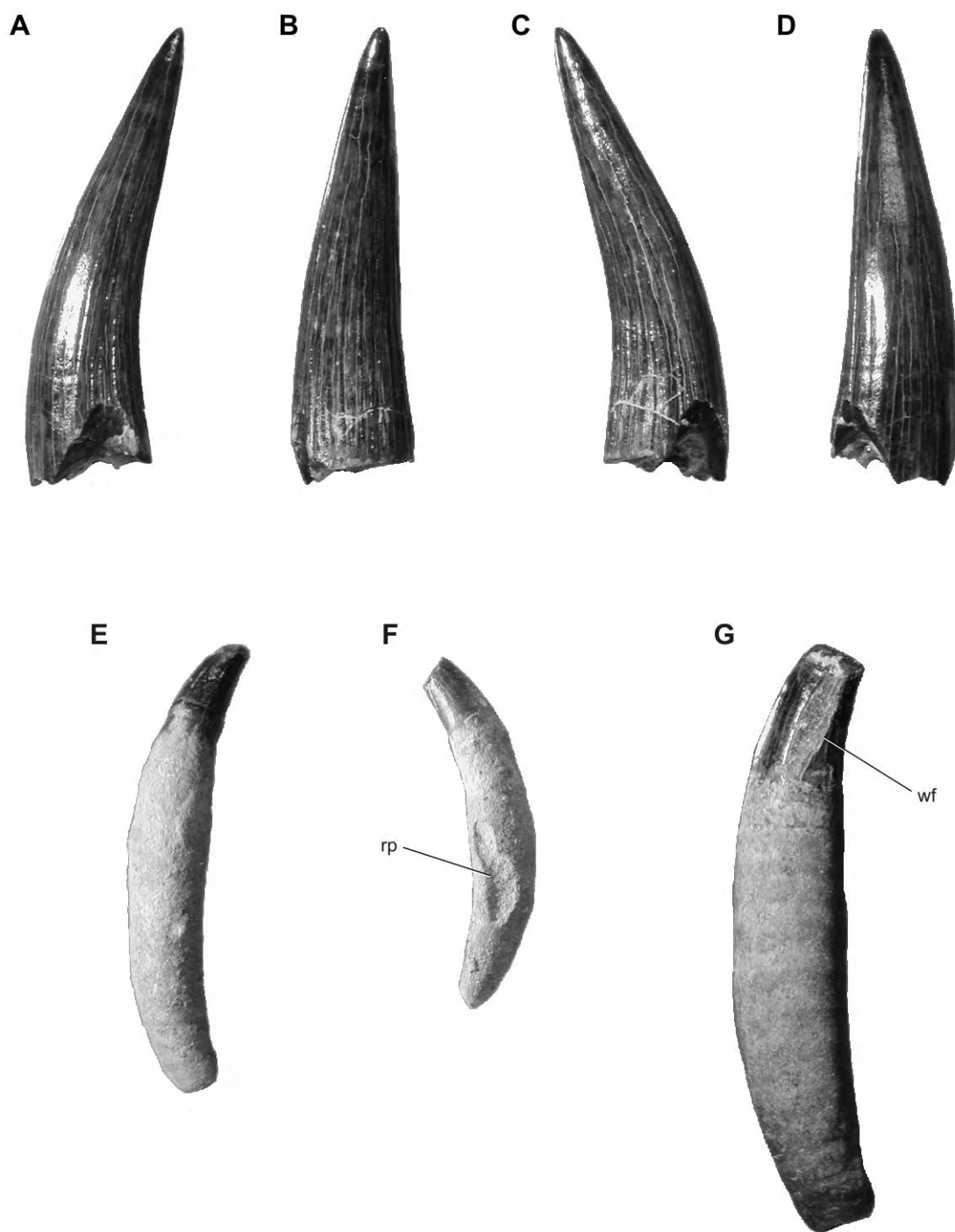
Fig. 2.20: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002: A-D, complete tooth crown in 'curved' (A), 'concave' (B), 'straight' (C) and 'convex' (D) views; E, complete 'ratchet' tooth; F, incomplete 'ratchet' tooth showing resorption pit on base (rp); G, incomplete tooth showing crown-base wear facet (wf). Scale bar = 5mm.

2.145
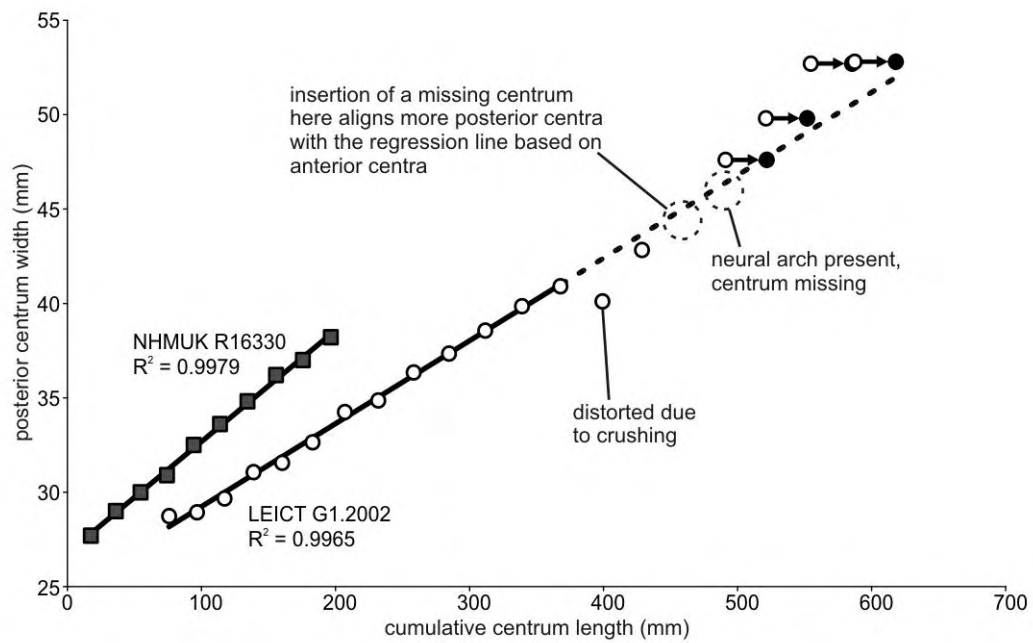
Fig. 2.21: Plot of posterior centrum width against cumulative length of the centra for the cervical vertebrae of LEICT G1.2002 and NHMUK R16330. Anterior-most centra of LEICT G1.2002 were omitted as described in the text.
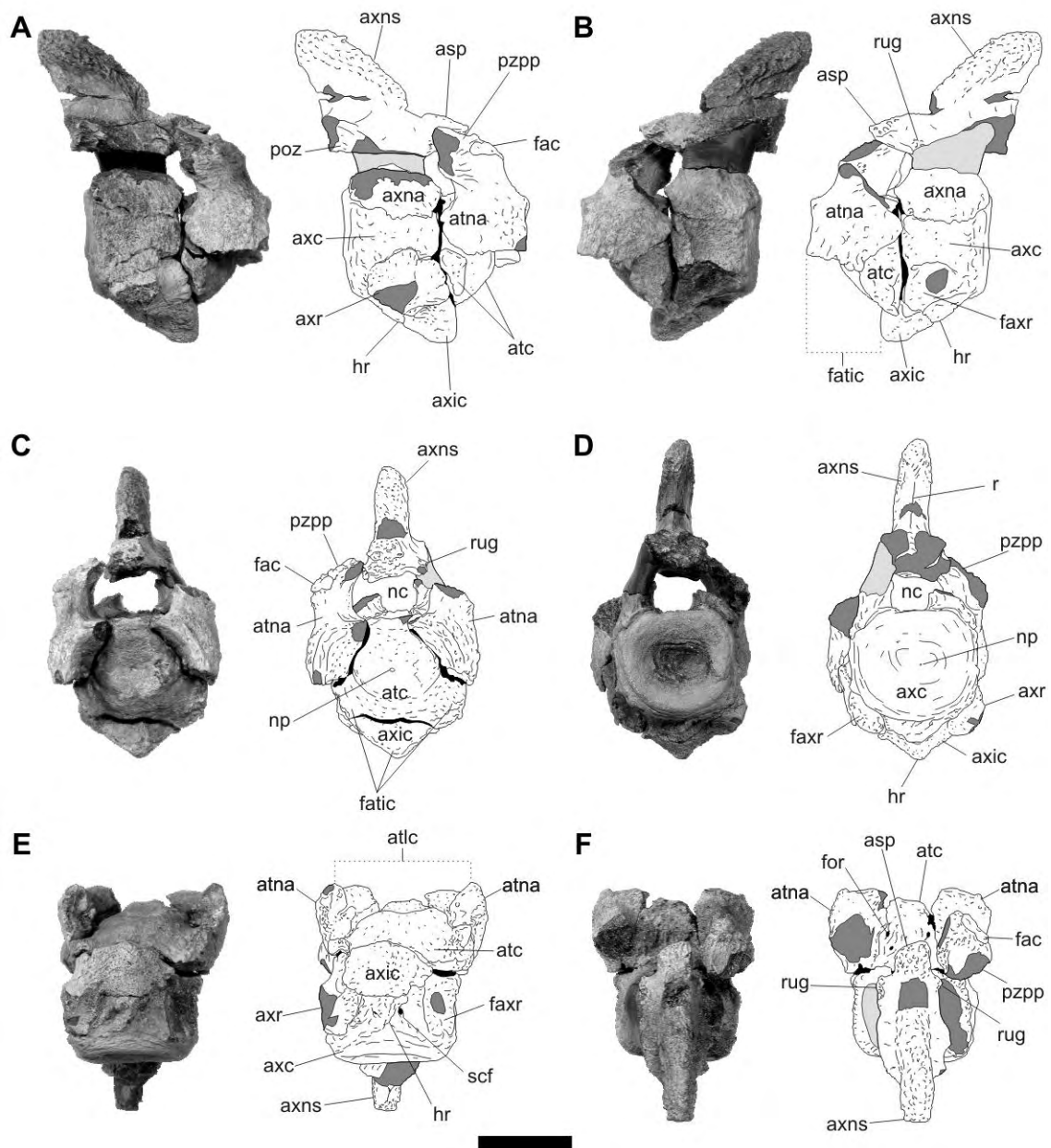
Fig. 2.22: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.51-53, atlas-axis complex in right lateral (A), left lateral (B), anterior (C), posterior (D), ventral (E), and dorsal (F) views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone; artificial fill is shown in light tone. Scale bar = 20mm.
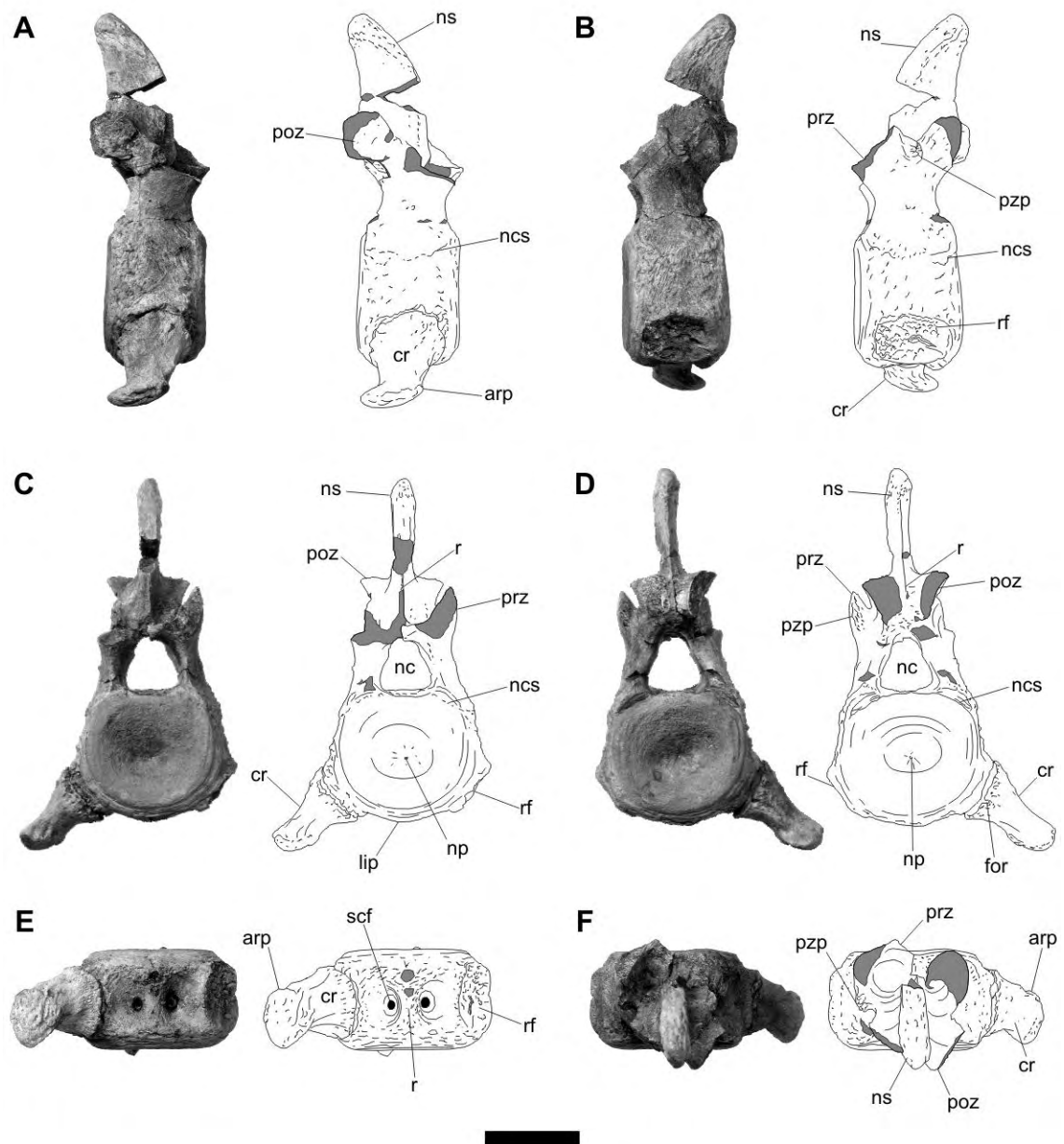
Fig. 2.23: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.57, anterior cervical vertebra in right lateral (A), left lateral (B), anterior (C), posterior (D), ventral (E), and dorsal (F) views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone. Scale bar = 20mm.

2.148
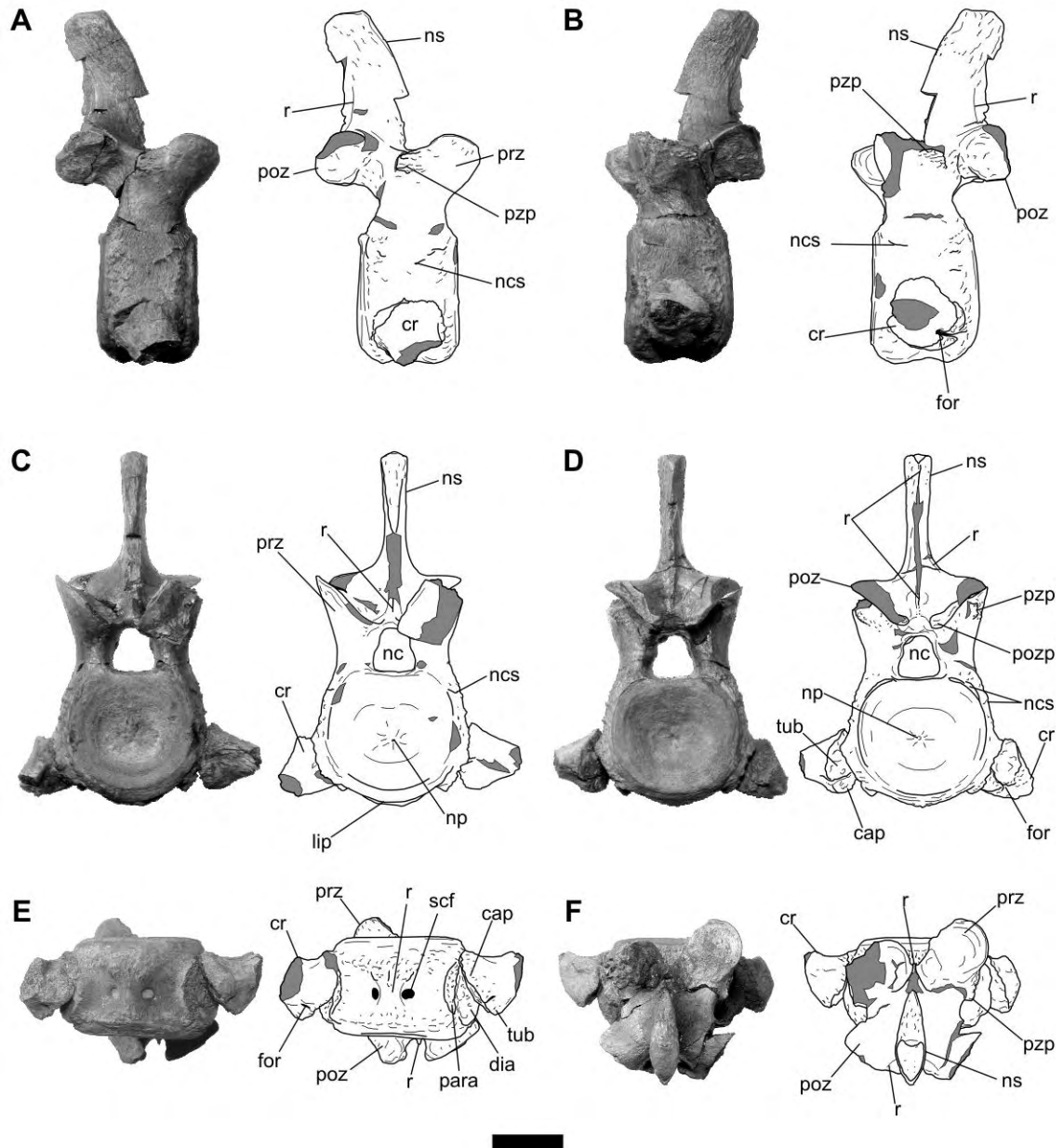
Fig. 2.24: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.65, posterior cervical vertebra in right lateral (A), left lateral (B), anterior (C), posterior (D), ventral (E), and dorsal (F) views with interpretive drawings. See text for abbreviations. Broken bone is shown in dark tone. Scale bar = 20mm.

2.149
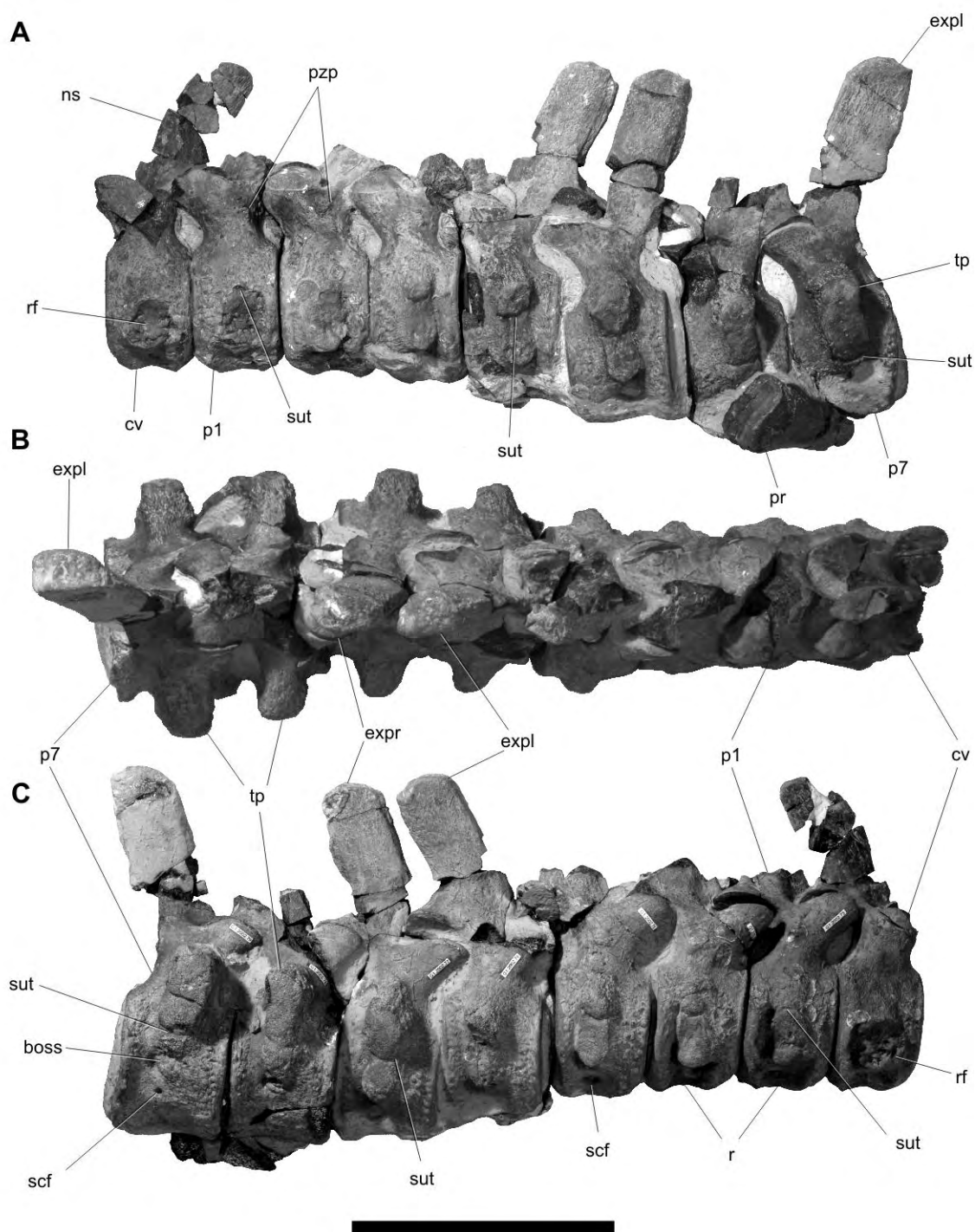
Fig. 2.25: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.72-79, last cervical and pectoral vertebrae in left lateral (A), dorsal (B) and right lateral (C) views. See text for abbreviations. Scale bar = 100mm.

2.150
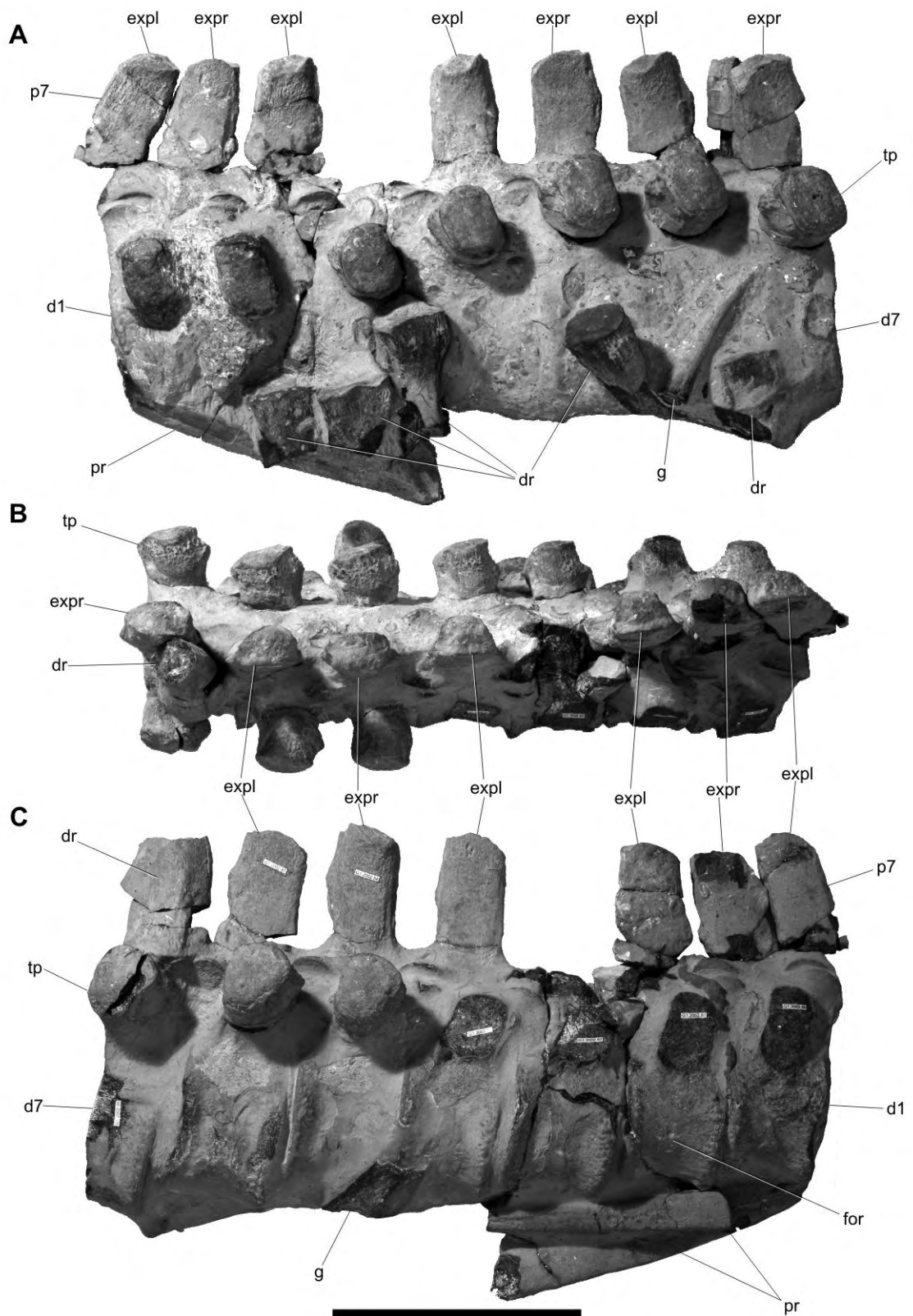
Fig. 2.26: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002.80-86, first to seventh dorsal vertebrae in left lateral (A), dorsal (B) and right lateral (C) views. See text for abbreviations. Scale bar = 100mm.

2.151
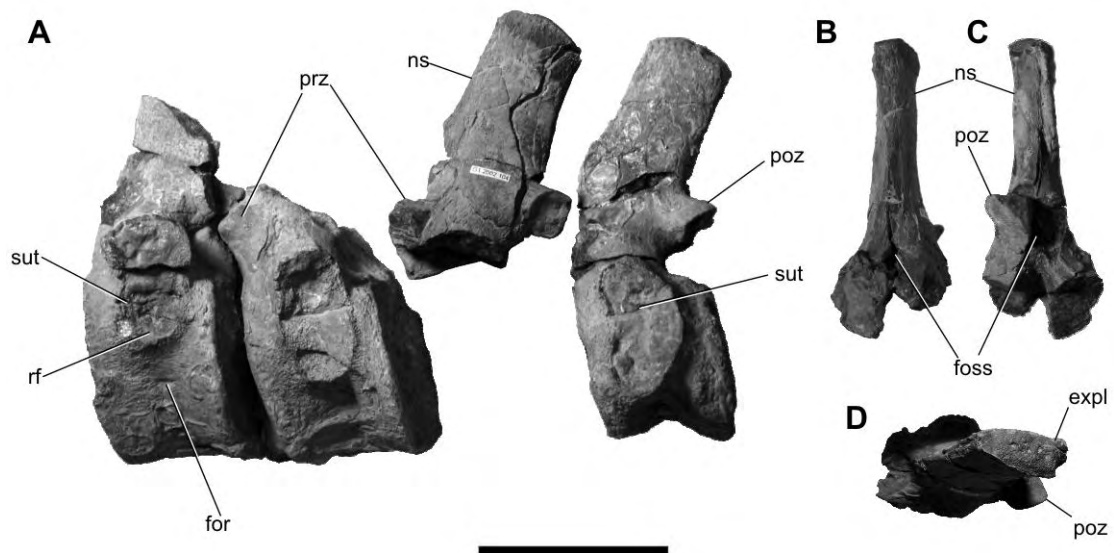
Fig. 2.27: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002, sacral vertebrae; A, sacral vertebrae in left lateral view; neural spine of third sacral vertebra (LEICT G1.2002.104) in anterior (B), posterior (C) and dorsal (D) views. See text for abbreviations. Scale bar = 50mm.

Fig. 2.28: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002, caudal vertebrae; A, selected caudal vertebrae in left lateral view; B-E, second preserved caudal vertebra (LEICT G1.2002.107); F-I, sixth preserved caudal vertebra (LEICT G1.2002.111); J-M, twelfth preserved caudal vertebra (LEICT G1.2002.117); N-Q, last preserved caudal vertebra (LEICT G1.2002.125); vertebrae are shown in anterior (B, F, J, N), posterior (C, G, K, O), ventral (D, H, L, P) and dorsal (E, I, M, Q) views. See text for abbreviations. Scale bar = 20mm.

2.154
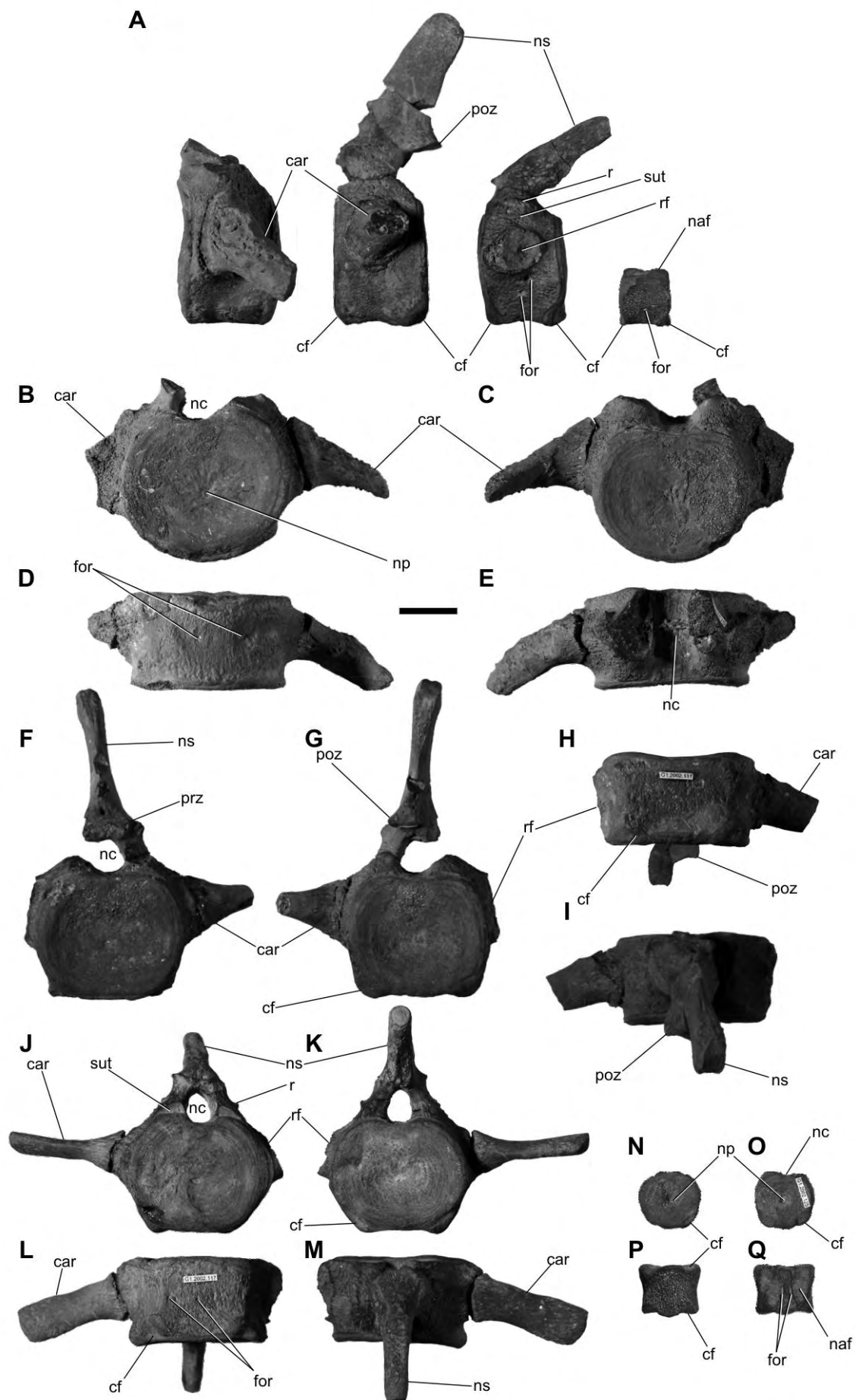
Fig. 2.29: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002, ribs and chevrons; A, cervical rib head(medial view); B, third right pectoral rib (posterior view); C, sixth right pectoral rib (posterior view); D, second left dorsal rib (posterior view); E, sixteenth right dorsal rib (anterior view); F, left sacral ribs in anterior (F), dorsal (G) and lateral (H) views; I, selected chevrons (lateral view, anterior-most elements to the left). Scale bars: A, 20mm; B-E, 100mm; F-I, 50mm.

2.156
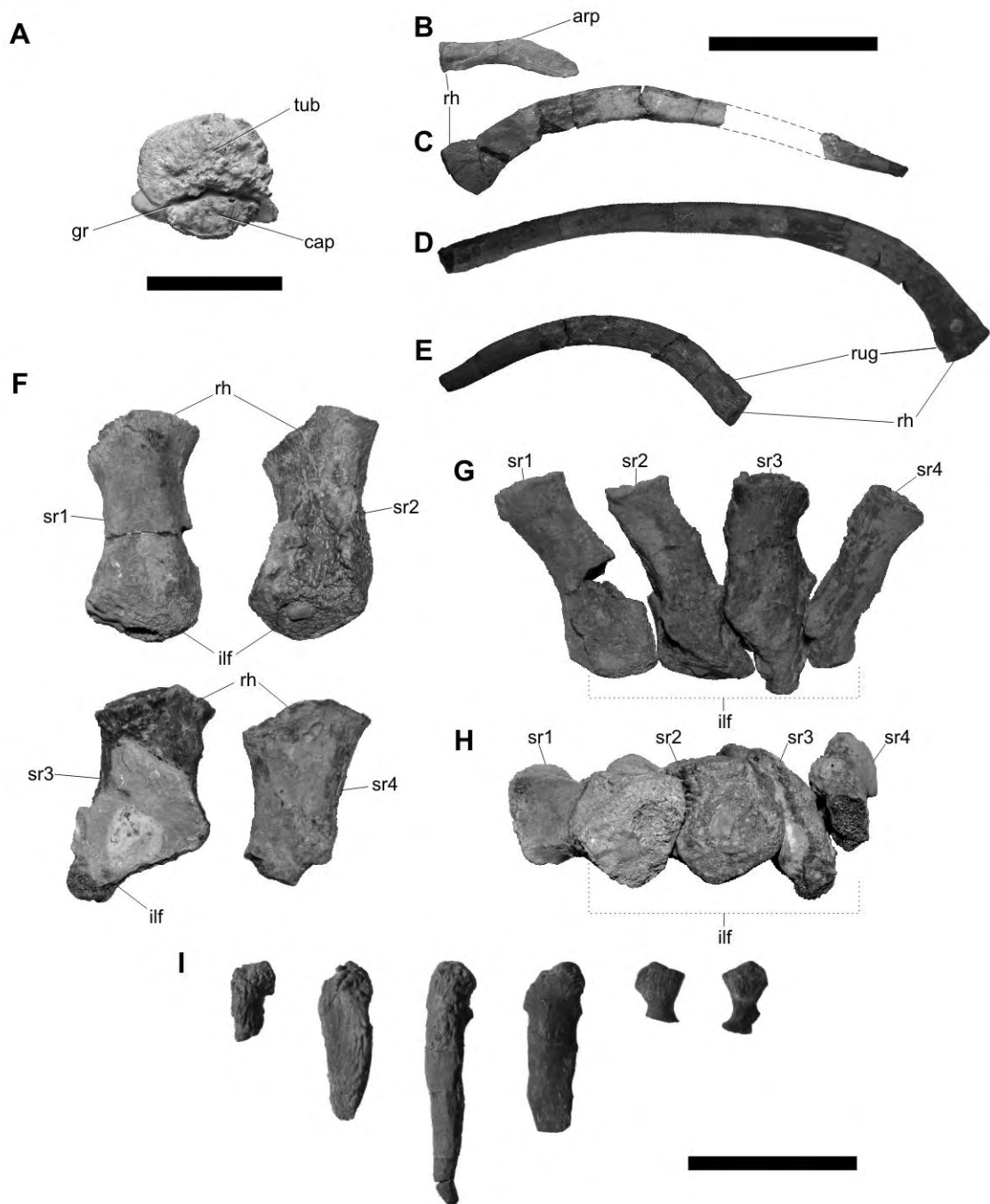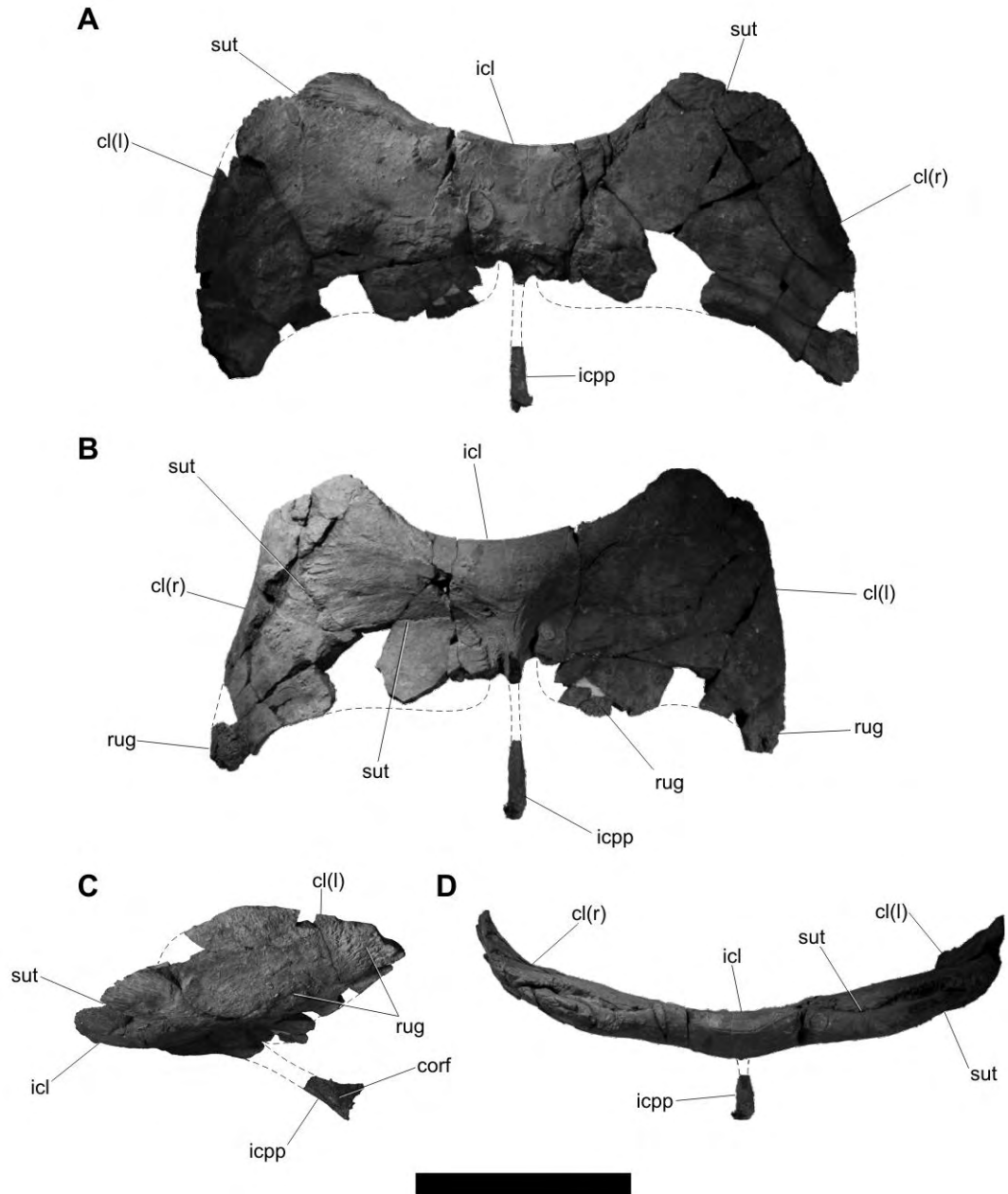
Fig. 2.30: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002, clavicular arch in dorsal (A), ventral (B), left lateral (C) and anterior (D) views. See text for abbreviations. Scale bar = 100mm.
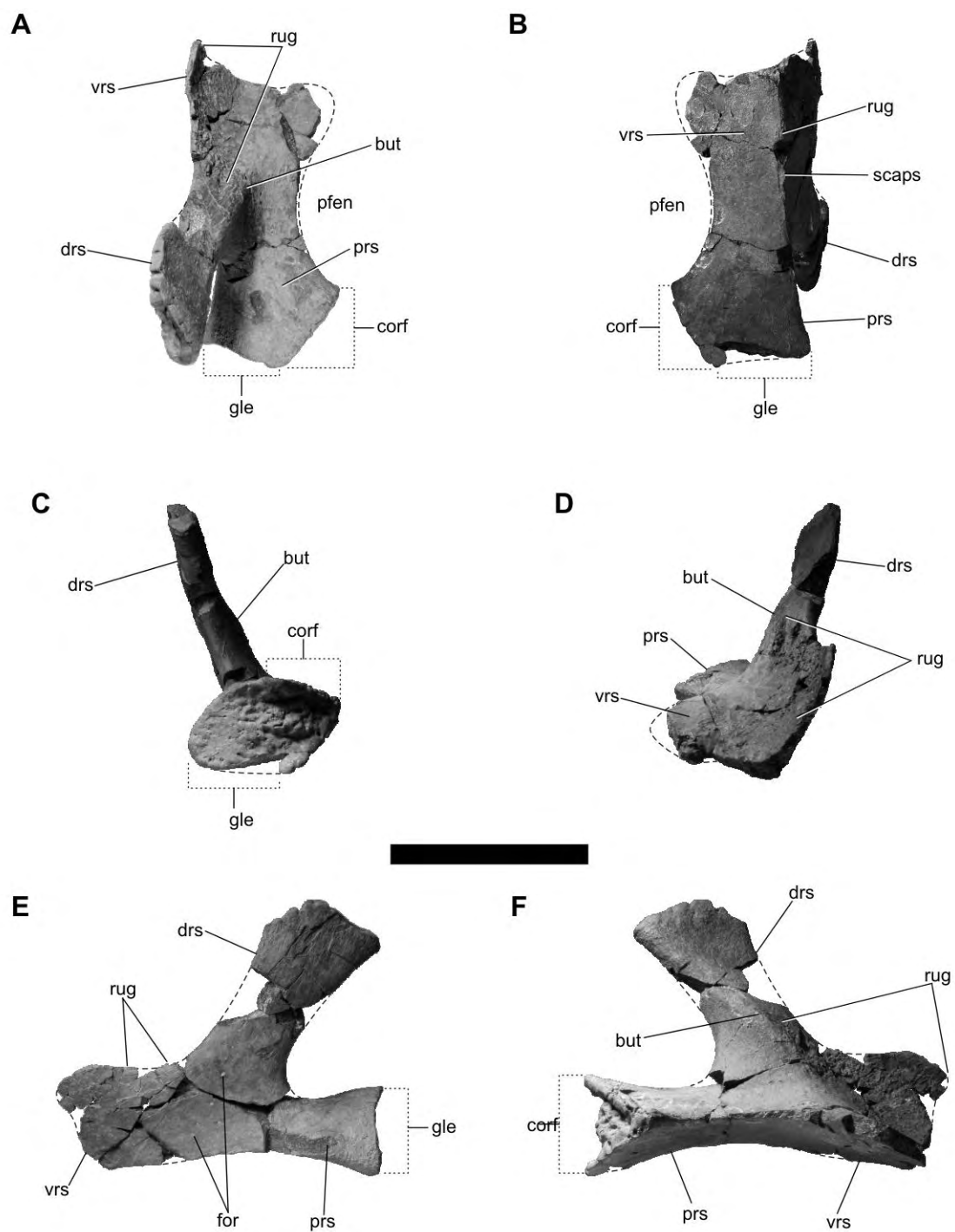
Fig. 2.31: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002, left scapula in dorsal (A), ventral (B), posterior (C), anterior (D), lateral (E) and medial (F) views. See text for abbreviations. Scale bar = 100mm.
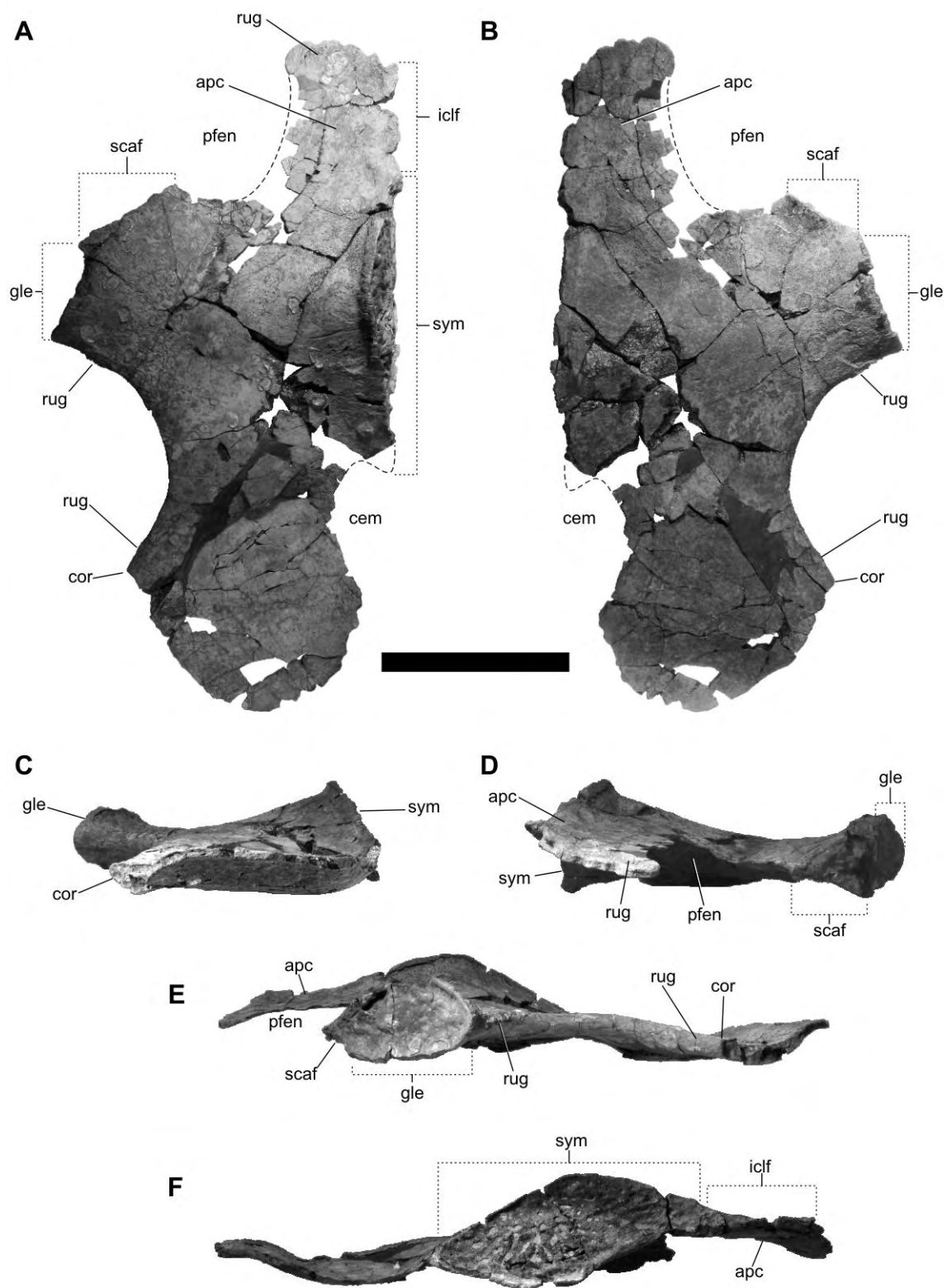
Fig. 2.32: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002, left coracoid in dorsal (A), ventral (B), posterior (C), anterior (D), lateral (E) and medial (F) views. See text for abbreviations. Scale bar = 100mm.
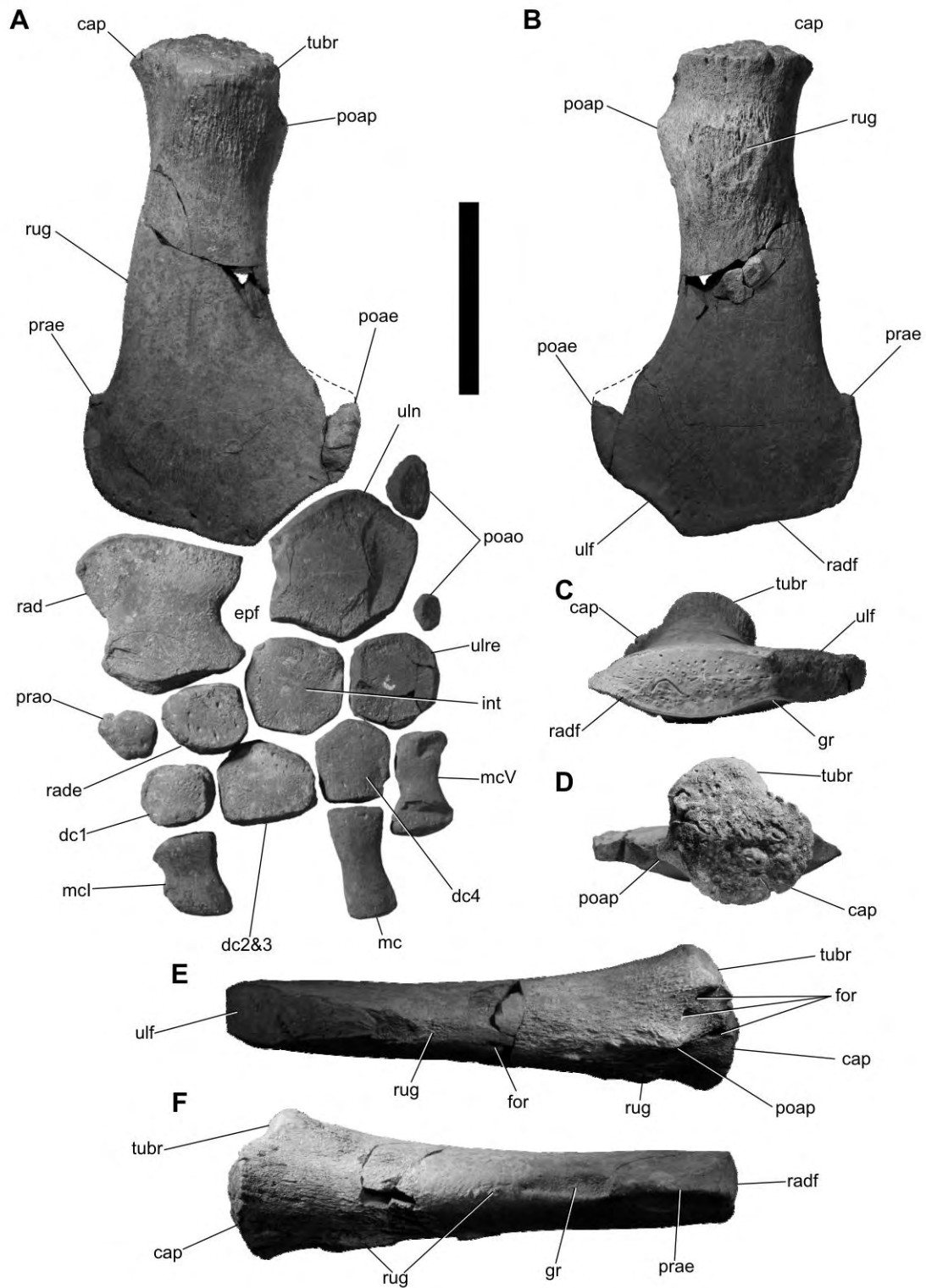
Fig. 2.33: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002; A, left humerus and proximal limb elements in dorsal view; left humerus in ventral (B), distal (C), proximal (D), posterior (E) and anterior (F) views. See text for abbreviations. Scale bar = 100mm.

2.160
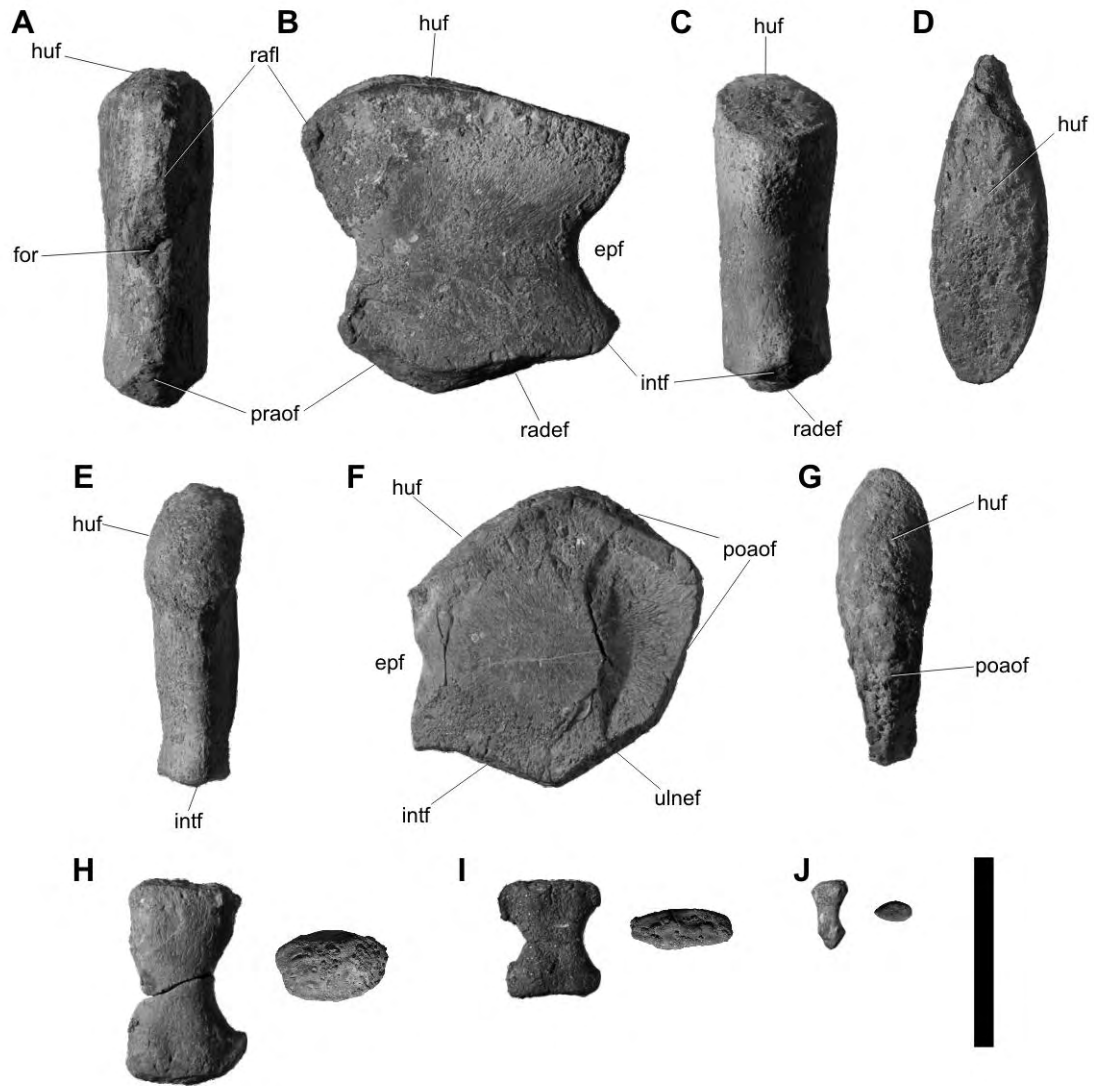
Fig. 2.34: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002; left radius in anterior (A), dorsal (B), posterior (C) and proximal (D) views; left ulna in anterior (E), dorsal (F) and proximal (G) views; proximal (H), distal (I) and terminal (J) phalanges in dorsal/ventral and proximal views. See text for abbreviations. Scale bar = 50mm.

2.161
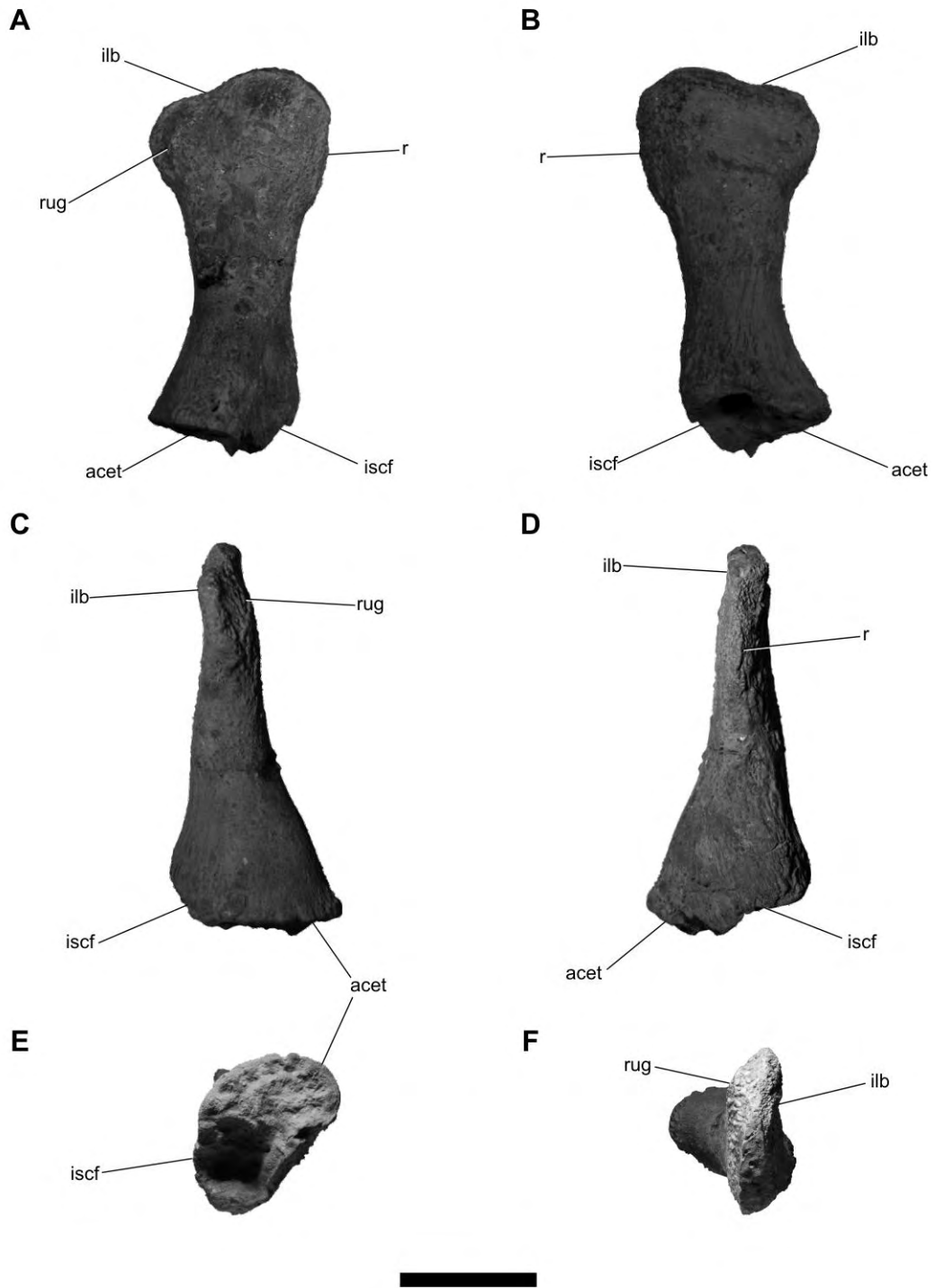
Fig. 2.35: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002; left ilium in lateral (A), medial (B), anterior (C), posterior (D), proximal (E) and distal (F) views. See text for abbreviations. Scale bar = 50mm.
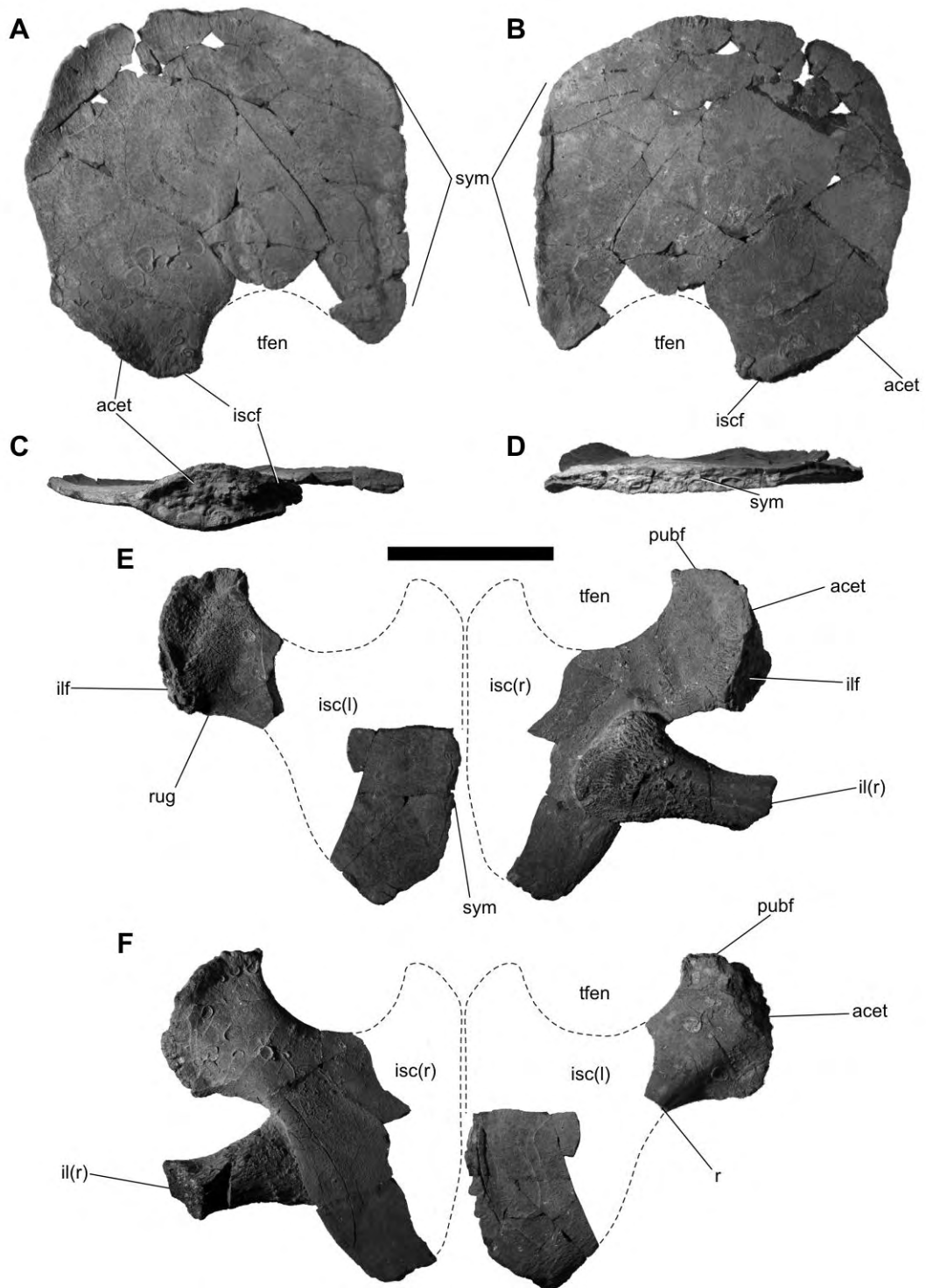
Fig. 2.36: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002; left pubis in dorsal (A), ventral (B), posterolateral (C), and medial (D) views; ischia and partial right ilium in dorsal (E) and ventral (F) views. See text for abbreviations. Scale bar = 100mm.
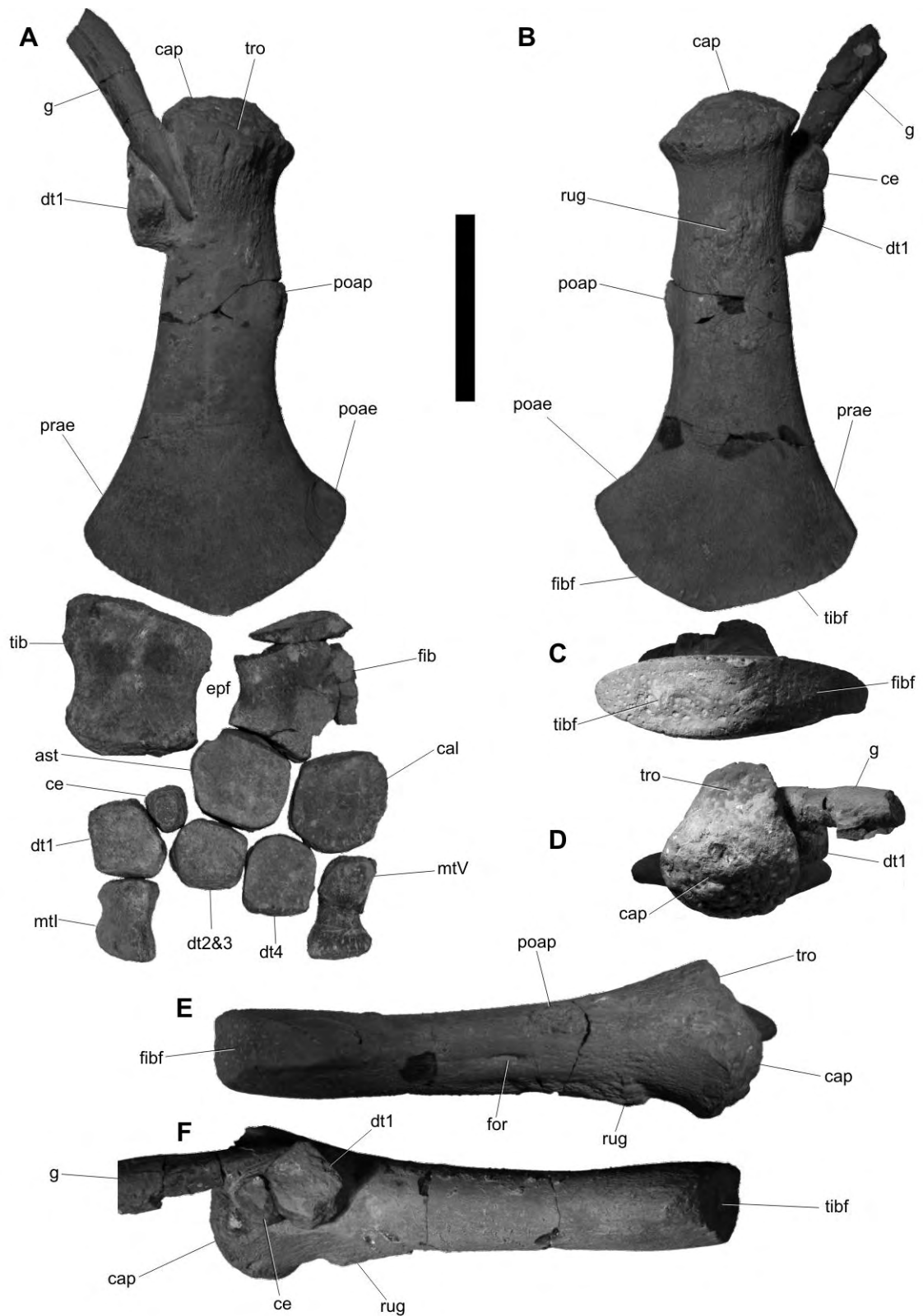
Fig. 2.37: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002; A, left femur and proximal limb elements in dorsal view; left femur in ventral (B), distal (C), proximal (D), posterior (E) and anterior (F) views. See text for abbreviations. Scale bar = 100mm.
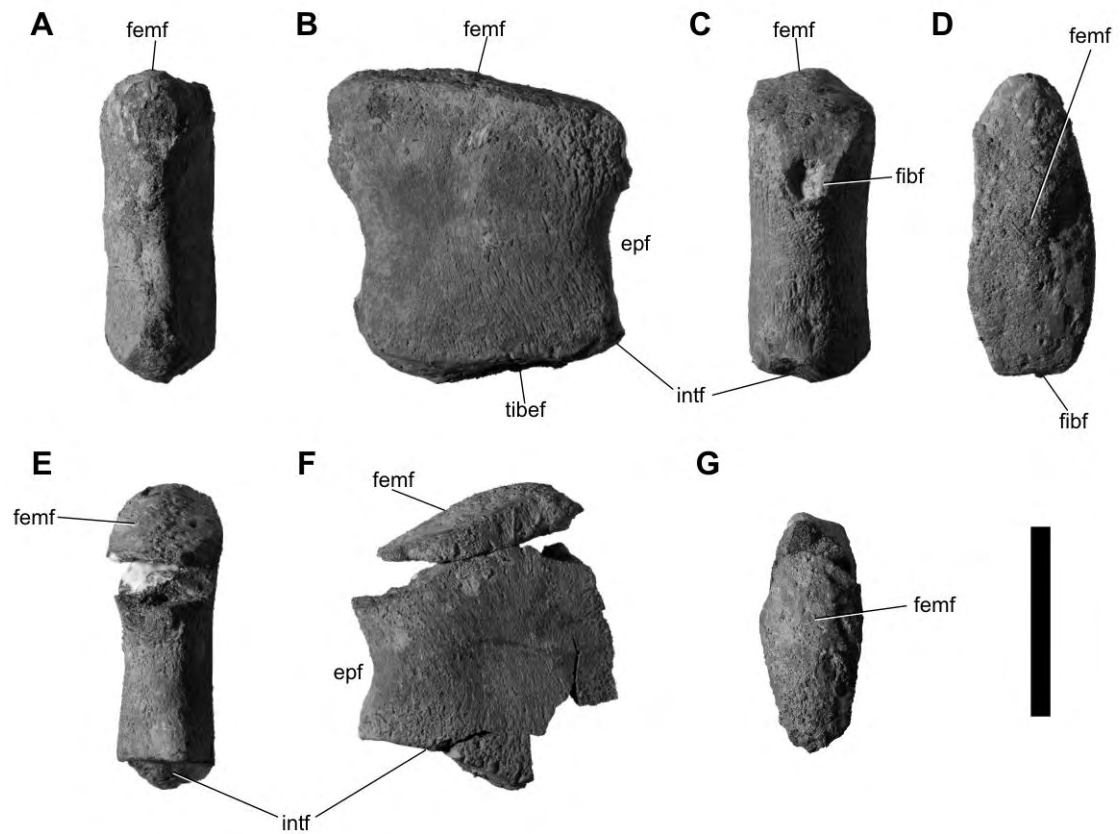
Fig. 2.38: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002; left tibia in anterior
(A), dorsal (B), posterior (C) and proximal (D) views; left fibula in anterior (E), dorsal
(F) and proximal (G) views. See text for abbreviations. Scale bar = 50mm.

2.165
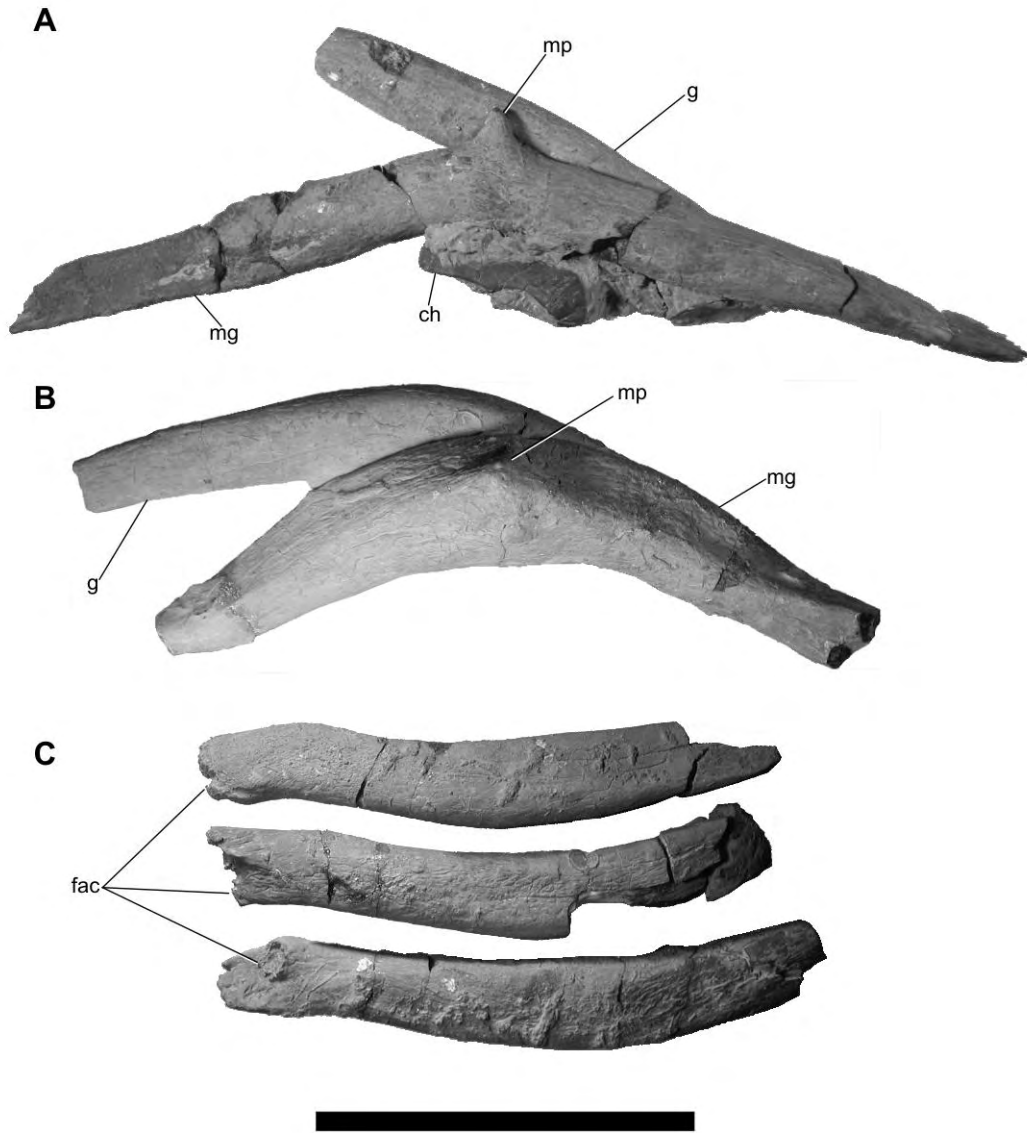
Fig. 2.39: *Raptocleidus blakei* gen. et sp. nov., LEICT G1.2002; A, anterior median gastralium in ventral view; B, posterior median gastralium in ventral view; C, gastralia with faceted ends. See text for abbreviations. Scale bar = 100mm.

Fig. 2.40: *Raptocleidus bondi* gen. et sp. nov., NHMUK R16330; A, vertebral column and pectoral girdle elements; B, anterior-most cervical vertebrae in lateral view; B, seventh cervical vertebra in anterior view; D, detail of dorsal neural spines. See text for abbreviations. Scale bars: A, 100mm, B-D, 20mm.

2.168
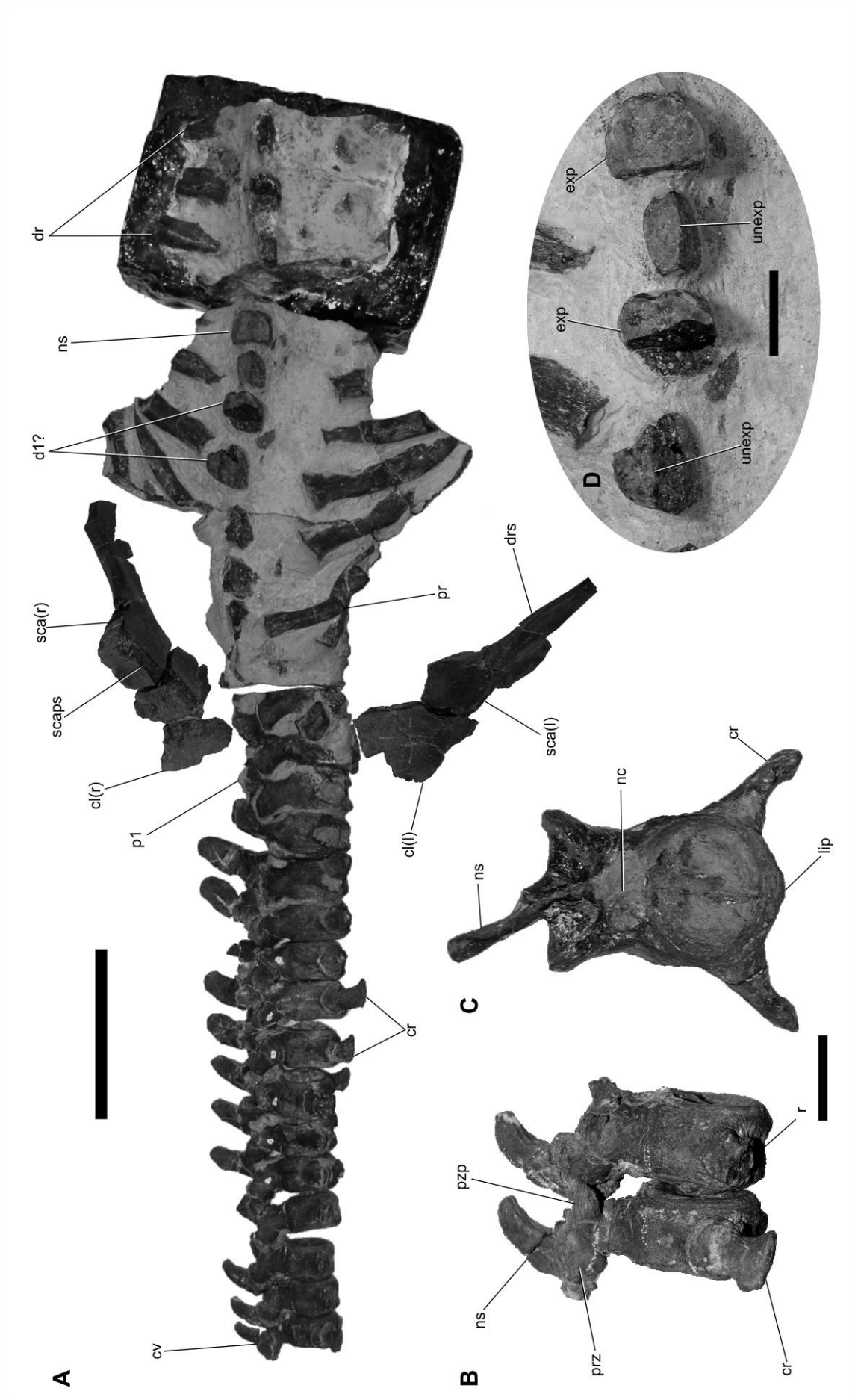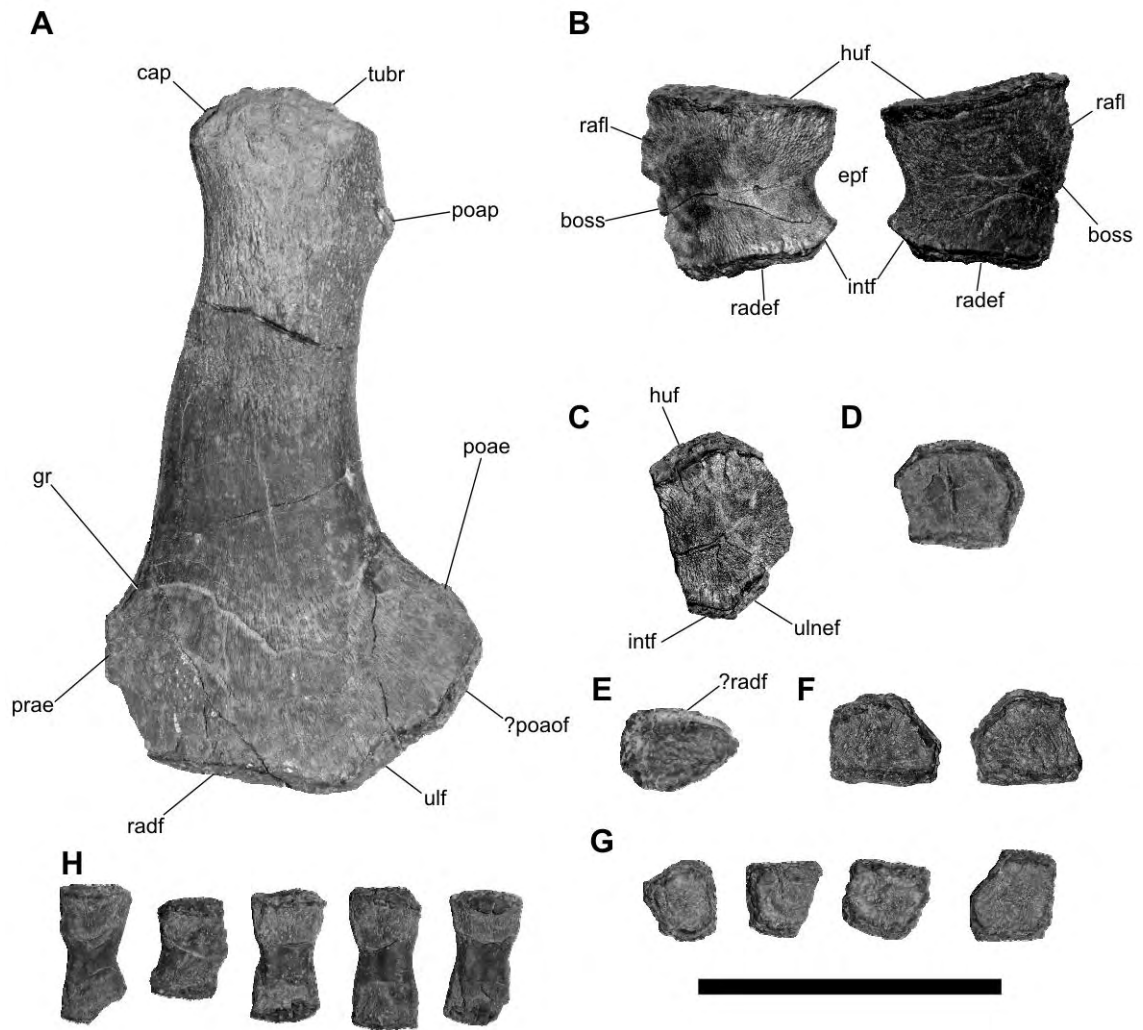
Fig. 2.41: *Raptocleidus bondi* gen. et sp. nov., NHMUK R16330; A, right humerus in ventral view; radii (B), partial ulna (C), probable ulnare (D), radiale (E), probable distal carpals 2&3 (F), additional carpals (G) and metacarpals or proximal phalanges (H) in dorsoventral view. See text for abbreviations. Scale bar = 100mm.

Chapter 3 A phylogeny of the Plesiosauria (Reptilia, Sauropterygia)

Introduction

Plesiosaurians have been the subject of phylogenetic analyses for twenty years (Hampe 1992), although it is only within the last decade that comparatively large-scale analyses have been attempted (O'Keefe 2001, 2004b; Druckenmiller and Russell 2008a). Even so, these large-scale analyses are dwarfed by some others in vertebrate palaeontology. The largest published analysis to date is that of Ketchum and Benson (2011a) which comprised 70 taxa and 201 characters. The pre-cladistic classification of plesiosaurians focussed on a small set of characters summarised by Ketchum and Benson (2010). The most influential system in the second half of the twentieth century was that of Welles (1943) who formalised a bipartite classification based, originally at least, on the "tendencies either to lengthen or shorten the neck" (Welles 1943, p200). Welles erected the superfamilies Plesiosauroidea for the long-necked plesiosaurians and Pliosauroidea for the short-necked plesiosaurians, and he attempted to identify progressive evolution with "increasingly shorter-necked forms [derived] from ancestors in which the trend is established" (Welles 1943, p201). Welles' bipartite division formed the basis of subsequent classifications, although applied differently in each case (Persson 1963; Novozhilov 1964; Romer 1966). Brown (1981) provided the most recent pre-cladistic classification of the Plesiosauria, and although maintaining Welles' two superfamilies, he critically reviewed 38 characters and rejected those that were ontogenetic, reflected grades of aquatic adaptation, or were, essentially, noise with no perceived phylogenetic signal. The resulting system featured four families in two superfamilies, with three families of plesiosauroids (Plesiosauridae Gray, 1825; Elasmosauridae Cope, 1869; Crytpoclididae Williston, 1925) and one of pliosauroids, the Pliosauridae Seeley, 1874.

The latter contained a broad diversity of plesiosaurians that are classified in at least four family-level groups in more recent classifications (e.g. Ketchum and Benson 2010), but the focus of Brown's (1981) study was the plesiosauroids of the Middle and Upper Jurassic.

The primary aim of this phylogenetic analysis is to elucidate the relationships of LEICT G1.2002 and NHMUK R16330, which were described as new species within a new genus of Pliensbachian plesiosaur in Chapter 2 of this thesis. The morphological description and subsequent comparison with other taxa did not produce a firm conclusion on the systematic placement of these new taxa due to the mosaic of characters present. This analysis will also include new data gathered in the course of this study both in the form of new morphological characters or reinterpretations of existing characters, and new Operational Taxonomic Units (OTUs). In order to best analyse the relationships of the new taxa under consideration the sampling of characters and taxa should be as comprehensive as possible and practicable, to avoid artefacts in the resulting phylogeny (Ketchum and Benson 2010).

Phylogenetic Background

The first phylogenetic analysis of members of the Plesiosauria (see Table 3.1 for phylogenetic definitions and authorities) was that of Hampe (1992) who examined a restricted set of pliosauromorph taxa (sensu O'Keefe 2002). Since this first investigation there have been over twenty published cladistic analyses of plesiosaurians, both on a 'global' scale, and a 'local' scale, focussing on a specific subset of taxa. Ketchum and Benson (2010) have thoroughly reviewed past plesiosaurian phylogenetic analyses up to the date of their study. The first global analysis was that of O'Keefe (2001: 34 taxa, 166 characters), who identified a deep dichotomy at the base of

Plesiosauria, the two clades being identified as Plesiosauroidea and Pliosauroidea, two superfamilies erected by Welles (1943). However, O'Keefe found that the Polycotylidae, which had been traditionally regarded as pliosauroids (Welles 1943; Brown 1981), were deeply nested within Plesiosauroidea. The second global analysis, that of Druckenmiller and Russell (2008a: 28 taxa, 152 characters), found that the polycotylids were deeply nested within Pliosauroidea, forming a sister-group relationship with the Leptocleididae, and they erected a new taxon, the Leptocleidoidea, for this clade. The Leptocleididae consisted of *Leptocleidus superstes* Andrews, 1922a and *L. capensis* (Andrews, 1911), a genus which had been recovered as a derived rhomaleosaurid by O'Keefe (2001). They also failed to recover a monophyletic Rhomaleosauridae, its putative members forming a paraphyletic assemblage at the base of the Pliosauroidea. These two global analyses therefore propose conflicting hypotheses of the relationships of major plesiosaurian clades. The study of plesiosaurian evolutionary history therefore lacks a consensus phylogenetic framework.

Ketchum and Benson (2010) identified a number of general principles in their review, highlighting in particular that many small 'local' scale studies did not include a sufficiently wide sample of taxa to support a particular hypothesis of relationships. This selective sampling was both morphological and temporal so that plesiosaurian diversity was not being adequately explored, and *a priori* decisions on relationships were effectively being made. Selection of outgroup taxa was also identified as a cause for concern, so that *Plesiosaurus dolichodeirus* Conybeare, 1824 was often used as the outgroup for analyses of plesiosauroids, therefore barring it from forming monophyletic clades with any of the ingroup taxa. Basal pliosauroids or non-plesiosaurians were recommended. Ketchum and Benson (2010) also sought to explore the cause of the conflicting topologies in the analyses of O'Keefe (2001) and Druckenmiller and

Russell (2008a). Their global analysis comprised 66 taxa and 178 characters, and recovered polycotylids and leptocleidids (renamed as the Leptocleidia) as a derived clade within Plesiosauroidea. This topology therefore incorporated components of that of O'Keefe (2001) and Druckenmiller and Russell (2008a). By repeating their analyses with subsamples of taxa to match these two analyses, Ketchum and Benson (2010) replicated some of the conflicting topologies with polycotylids being recovered as plesiosauroids in their 'O'Keefe simulation' and as pliosauroids in the 'Druckenmiller simulation' along with a paraphyletic 'Rhomaleosauridae'. They concluded that differences in taxon sample could explain many of the conflicts between the previous global analyses.

Five analyses have been published since that of Ketchum and Benson (2010). Druckenmiller and Russell (2009) re-ran their global analysis to include a new polycotylid specimen, TMP 95.87.01; the topology recovered was much as in their earlier analysis. This was presumably published too late to include in the review of Ketchum and Benson (2010). Benson *et al.* (2011b) repeated the analysis of Ketchum and Benson (2010) to include new data on species of *Hauffiosaurus* O'Keefe, 2001, including two new characters. This small change had a large effect, with the leptocleidians being recovered as pliosauroids, the sister group to a 'core' Pliosauridae. Rhomaleosauridae became a paraphyletic assemblage leading to this derived clade, with *Hauffiosaurus* itself forming a clade with various 'rhomaleosaurs'. Benson *et al.* (2011b, p568) stated that "relationships among Lower Jurassic plesiosaurians are far from certain".

Ketchum and Benson (2011a: 70 taxa, 201 characters) incorporated new data on *Thalassiodracon hawkinsii* (Owen, 1838) from Benson *et al.* (2011a) and

Marmornectes candrewi Ketchum and Benson, 2011a, added 21 new characters and modified 7 in addition to their earlier analysis (Ketchum and Benson 2010). Additional outgroups were also added (*Bobosaurus forojuliensis* Dalla Vecchia, 2006; the skull of *Pistosaurus longaevus* Meyer, 1839; postcranial material that was referred to *Pistosaurus* by Sues (1987); *Yunguisaurus liae* Cheng et al, 2006). The underlying structure remained unchanged, but the base of the Pliosauridae became better resolved, with *Attenborosaurus conybeari* (Sollas, 1881), *Hauffiosaurus* and *Thalassiodracon* being successive outgroups to the 'core' of Callovian and later taxa previously identified. The 'classic' pliosauromorph body plan of large head and short neck was thus independently acquired by both pliosaurids and rhomaleosaurids. Vincent *et al.* (2011: 22 taxa, 67 characters) performed a small-scale analysis to elucidate the relationships of a new Late Cretaceous plesiosauroid taxon, *Zarafasaura oceanis,* with *Serpianosaurus mirigiolensis* Rieppel, 1989 and *Simosaurus gaillardoti* Meyer, 1842 as outgroups and including *Thalassiodracon* as a non-plesiosauroid. They recovered *Zarafasaura* in a derived position within the Elasmosauridae, but also recovered the Toarcian *Microcleidus homalospondylus* (Owen, 1865) as a basal elasmosaurid and *Kaiwhekea katiki* Cruickshank and Fordyce, 2002 as a member of a clade with the polycotylids. They cited this as an alternative to the membership of *Kaiwhekea* to the clade Aristonectidae, but no other proposed aristonectid or more basal member of the larger clade Cryptoclidia (formerly Cryptocleidoidea) were included in the analysis.

Kear and Barrett (2011) focussed on the validity of Leptocleididae and nature of *Leptocleidus superstes* and after a redescription of the latter they repeated the analyses of O'Keefe (2001, 2004), Druckenmiller and Russell (2008a) and Smith and Dyke (2008) using both parsimony and Bayesian approaches. The analyses supported a pliosauroid identity of *Leptocleidus superstes*. However, they were unable to find

support for either membership of Rhomaleosauridae or a discrete 'leptocleidoid' clade, concluding that the similarities between *Leptocleidus*-like taxa were possibly a result of homoplasy in palaeobiogeographically disparate taxa. Kear and Barrett (2011) were unable to include the analysis of Ketchum and Benson (2010) in their study, but commented in notes added in proof that the characters which recovered support for Leptocleidia/Leptocleididae were mostly ambiguous or not preserved in *L. superstes*, and noted the poor bootstrap support for nodes.

Most recently Benson *et al.* (in press: 70 taxa, 216 characters) formulated characters to test the position of Leptocleididae, and found the same topology as Ketchum and Benson 2011a). Meanwhile Benson *et al.* (2012: 32 taxa, 207 characters), which includes collaborative work derived from this thesis, focussed on Lower Jurassic taxa, and the relationships of newly recognised taxa from the basal Hettangian (*Stratesaurus taylori*, *Avalonnectes arturi* and *Eoplesiosaurus antiquior*). Thus the question of the validity and placement of the Leptocleidia was outside the scope of this study. A novel topology in which pliosauroids were paraphyletic, with Pliosauridae and Plesiosauroidea forming a clade exclusive of Rhomaleosauridae, was recovered. This new development aside, the major areas of contention within the phylogeny of the Plesiosauria remain the position of the polycotylids and leptocleidids and monophyly of a widely inclusive Rhomaleosauridae.

Phylogenetic analysis

Methodology – characters and taxa selection

This analysis uses 339 characters to record the morphological variation present within the constituent taxa. Character descriptions are given in Appendix I. The skull and

dentition are described by 193 characters, the axial skeleton by 62 characters and the appendicular skeleton by 84 characters. Fifty-two characters are new to this analysis, and sixty-six have been modified from previous studies. Characters from previous analyses were examined and either included or excluded following Ketchum and Benson (2010). Where I have included a character that was previously excluded, this is indicated in the character description with justification. Characters were compiled using NEXUS Data Editor (Page 2001), which was also used for data entry to build the character-taxon matrix (see Appendix II). Three-hundred and seventeen characters encoded variation in discrete states, and are 'hierarchical' or 'conventional' (Hawkings *et al.* 1997). Twenty-two quantitative characters describe morphometric or meristic variation and were scored using the gap-weighting method of Thiele (1993) as in the analyses of Sato (2002), Druckenmiller and Russell (2008a) and those of Ketchum and colleagues (Ketchum and Benson 2010, 2011a; Benson *et al.* 2011b). Ketchum and Benson (2010) followed the advice of Wiens (2001) that the number of character states should be maximised and used 26 states, the limit imposed by their computer software. That is also the case with NEXUS Data Editor, and 26 states were used in this analysis. So that character state transitions from the quantitative characters would not be overly weighted in the final analysis, all quantitative characters were given a weight of '1', while discrete characters were given a weight of '26' (Thiele 1993). Discrete characters (1-317) were unordered, while quantitative characters (318-339) were ordered. Raw data for the quantitative characters is given in Appendix IV. This data was log-transformed before being subjected to the gap weighting procedure (Benson and Ketchum 2010). As character 322 (position of posterior interpterygoid vacuities relative to subtemporal fenestra) includes negative values, these were converted to positive values prior to log transformation.

One-hundred and seven taxa were included in this analysis. This therefore makes it the largest ever phylogenetic analysis of the Plesiosauria yet attempted. The taxon list of Ketchum and Benson (2011a) was used as a starting point, with 37 taxa included in addition. All operational taxonomic units (OTUs) are listed in Appendix III, with details of data sources. This analysis aimed to include as wide a sample of taxa as possible, to overcome artefacts in the results which could stem from a restrictive sample (Ketchum and Benson 2010). Some of these are newly published taxa (e.g. *Zarafasaura*), while others are newly discovered specimens (e.g. LEICT G1.2002, 'Golden Cap Taxon'). Others have been referred to existing taxa but during this study were found to differ from the type specimen in a number of characters (e.g. *Avalonnectes*, NHMUK R2861). Where possible taxa have been scored from personal observation; however, with a study of this magnitude this has not been possible in many cases. Thirty-four taxa have been scored by direct observation, with the remainder scored from the literature, either original descriptions or previous phylogenetic analyses. Of the new 37 taxa included in this study, 18 were scored by direct observation. The character-taxon matrix is presented in Appendix II. Following Benson *et al.* (in press), *'Plesiosaurus' macrocephalus* Owen, 1838 was deleted prior to analysis of the data matrix due to its status as a very young juvenile which can only be studied superficially.

Methodology – search strategy

The starting strategy used was based on that of Ketchum and Benson (2010). *Simosaurus gaillardoti* was chosen as the sole outgroup in order to test plesiosaurian monophyly with respect to other pistosauroids. Due to the size of the dataset, the Parsimony Ratchet of Nixon (1999) was implemented using PAUPRat (Sikes and Lewis 2001) in combination with PAUP*4.0b10 for Macintosh (Swofford 2002). The data

matrix was analysed using PAUPRat using 15% character perturbation, with weight mode set to 'multiplicative', the characters weighted and ordered and the random number seed for the starting tree set from the computer's system clock. PAUPRat generated a set of 200 permutation iterations, and these were run through PAUP* 20 times.

A most parsimonious tree (MPT) 'island' of only 3 trees of 47427 steps was found in only one of the 20 replications of the PAUPRat iterations set. This was unexpected both in the tree island's small size and its single occurrence. The principle behind the Parsimony Ratchet is that progress made in exploring tree space is not lost, and the probability of finding the shortest tree increases through a series of iterations (Sikes and Lewis 2001). Nixon (1999) reported finding the shortest trees in three out of every four replications of a set of 200 permutations. The behaviour of the Ratchet in this case seemed to be that described by Sikes and Lewis (2001) for searches with unequal starting weights; the searches do not plateau on the shortest trees. This behaviour of the Ratchet is also similar to that observed when too many characters are perturbed. The characters in this analysis had unequal starting weights due to the use of the gap weighting methodology (Thiele 1993). One of the findings of Ketchum and Benson (2010) was that their quantitative characters helped to resolve detail within clades, but that the large clades were recovered when quantitative characters were omitted. The PAUPRat strategy was therefore repeated, but only for the discrete character set (characters 1-317), with the same settings as before, but with no weights statement, and the weight mode set to 'uniform'. The shortest trees resulting from this would then be used as starting trees for the search of the full dataset under PAUP*.

Three of the 20 replicates recovered trees of 1713 steps, with 31 trees found in total.

The tree structure featured a novel grouping of leptocleidians and elamosaurids forming a sister group to cryptoclidids, a monophyletic Pistosauria, and LEICT G1.2002 was recovered at the base of Rhomaleosauridae (topology 'A'). However, in checking the results of the other replicates it was noted that two had recovered a total of 117 trees of 1714 steps with a radically different structure in which LEICT G1.2002 occupied a basal position on the branch leading to Leptocleidia with this wider clade forming the sister group to Pliosauridae, and with a paraphyletic Pistosauridae (topology 'B'). Given the similarities previously noted between LEICT G1.2002 and some leptocleidians, and that not all characters in the dataset had been included in the PAUPRat analysis, both the topology 'A' and topology 'B' trees were used as starting trees in separate analyses of the full data matrix under PAUP*. Heuristic searches were run with TBR (tree bisection and reconnection), and the "Multrees" option in effect

The topology 'A' analysis recovered 300 trees of 47271 steps, while the topology 'B' analysis recovered 3240 trees of 47255 steps. The topology B analysis was therefore regarded as the most parsimonious result of the phylogenetic analysis. Both sets of trees had an ensemble consistency index (CI) of 0.245, a retention index (RI) of 0.636, a rescaled consistency index (RC) of 0.156 and a homoplasy index (HI) of 0.755.

Results

The strict consensus tree of 3240 trees of 47255 steps is shown in Figure 3.1 and as a time-calibrated phylogeny with clade names in Fig.3.2 (see Table 3.1 for definitions of clade names). Despite the relatively high number of trees, the phylogeny of the Plesiosauria is generally well resolved. Most of the trees can be accounted for by the polytomies formed by the non-plesiosaurian pistosaurians. Pruning *Bobosaurus forojuliensis* to produce a strict reduced consensus (SRC) tree (Wilkinson 1994, 2003)

3.10

reduced the number of trees to 1080, while pruning the *Pistosaurus* postcranium further reduced the number of trees to 540. However, the full consensus tree is shown in Fig. 3.1 to best represent the full analysis. Additional polytomies are found: at the base of a derived clade of polycotylids; between *Leptocleidus superstes*, *L. capensis* and MIMG 1997.302; within the clade containing *Pliosaurus spp.*, FHSM VP321 and *Gallardosaurus iturraldei* Gasparini, 2009; at the base of the clade of elasmosaurids more derived than the Speeton taxon; and between the elasmosaurids *Callawayasaurus colombiensis* (Welles, 1962), CM Zfr 115 and *Tuarangisaurus keyesi* Wiffen and Moisley, 1986. An Adams consensus tree resolves the clade of *Manemergus anguirostris* Buchy *et al.* 2005 and *Pahasapasaurus haasi* Schumacher, 2007 as a member of the more derived clade which includes species of *Dolichorhynchops*, but *Plesiopleurodon wellesi* Carpenter, 1996 and *Thililua longicollis* Bardet et al, 2003 remain. The polytomy between the three derived leptocleidids also remains in the Adams consensus, while FHSM VP321 and *Gallardosaurus* form a clade, with the species of *Pliosaurus* remaining in a polytomy. The polytomies within the Elasmosauridae remain unresolved. A 50% majority rule tree failed to resolve the polycotylid, leptocleidid and elasmosaurid polytomies, but resolved that within the derived pliosaurids. FHSM VP321 and *Gallardosaurus* formed a clade with 60% support, with *Pliosaurus brachydeirus* Owen, 1842 as sister group to this also with 60% support. Hence *Pliosaurus* is here paraphyletic.

The consistency index of 0.245 is lower than that of Ketchum and Benson (2010: 0.328), which is itself lower than that of Druckenmiller and Russell (2008a: 0.55), and O'Keefe (2004b: 0.43). Ketchum and Benson (2010) assigned their low value to the size of the data set and proportion of missing data (Kitching *et al.,* 1998) and that would seem to be the case here too. The retention index of 0.636 is higher than that of

3.11

Ketchum and Benson (2010: 0.601) and Druckenmiller and Russell (2008a: 0.56), but lower than that of O'Keefe (2004b: 0.72). Due to the size of the dataset and computational limits, bootstrap values could not be calculated. Bremer support or decay indices were calculated using TreeRot (Sorenson and Franzosa 2007). The command file produced by TreeRot for input into PAUP* was edited so that each search on a constrained node used the topology 'B' trees as the initial tree, to replicate the conditions of the original search. However, it is possible that the support indices produced may be overestimates, as can happen with large datasets (Müller 2004, 2005). The decay indices are shown at each node in Figure 3.1. Due to the weighting protocol used, a decay index of 26 is approximately equal to an index of 1 in an un-weighted analysis, and so nodes with indices of less than 26 are poorly supported (Maidment *et al.* 2008). In theory, nodes with a decay index of less than 26 are supported by quantitative characters only, while those with an index of more than 26 will be supported by a combination of quantitative and discrete characters.

The influence of quantitative characters was investigated by repeating the analysis but only using qualitative characters, in this case all un-weighted. The topology 'B' trees were again used as the starting trees. This analysis recovered trees of length 1712, one step less than the starting trees. However, the analysis was stopped after 275673 MPTs had been found due to computational constraints. As expected, some nodes with low decay indices such as that uniting *Meyerasaurus victor* Fraas 1910 and more derived taxa (decay index 11) and the node uniting *Trinacromerum bentonianum* Cragin, 1888 and TMP 95.87.01 (decay index 12) collapsed. However the rest of the Pliosauroidea (Fig. 3.1A) remained intact. Somewhat surprisingly the basal plesiosauroids *Eretmosaurus rugosus* Owen 1865, *Eoplesiosaurus*, MNHN A.C. 8592 and *Plesiosaurus dolichodeirus* collapse into a polytomy with more derived

3.12

plesiosauroids (decay indices 26-43). The node supporting *Plesiopterys wildii* O'Keefe, 2004b with more derived cryptoclidids collapses, which is unsurprising given its decay index of 4. However, the more derived cryptoclidids collapse to a large polytomy containing just two clades: one containing *Cryptoclidus eurymerus* (Phillips, 1871) and *Colymbosaurus trochanterius* Owen, 1840; and one containing *Muraenosaurus leedsii* Seeley, 1874 and taxa more derived than it. Only one node in this series has a decay index of less than 26; that uniting the two clades each more closely related to *Cryptoclidus eurymerus* or *Muraenosaurus leedsii*. It is therefore possible that the decay indices have been overestimated for these plesiosauroid clades. The strongest node in the phylogeny with a decay index of 195 is that uniting the pliosaurids of the Callovian and later. The second strongest with a decay index of 167 is the node uniting the cryptoclidids and elasmosaurids. The third strongest node is that uniting the clade of LEICT G1.2002 and NHMUK R16330 with the clade which includes the leptocleidians.

Discussion

Tree topology and LEICT G1.2002

The phylogeny of Plesiosauria presented here contains one main novel feature: the position of the Leptocleidia. This clade is now a member of Pliosauroidea, as was recovered in the analyses of Druckenmiller and Russell (2008a; 2009) and Smith and Dyke (2008). However, in these analyses the Leptocleidia was sister group to a 'core' Pliosauridae of Callovian and later forms. Taxa which have recently been recovered as basal pliosaurids (*Thalassiodracon, Hauffiosaurus*) were either positioned more basally within Pliosauroidea, or were resolved as plesiosauroids as in the case of *Thalassiodracon* (Druckenmiller and Russell 2008a). The result of Benson *et al.* (2011b) is similar with *Hauffiosaurus* and *Attenborosaurus* arranged down the 'stem' of

the clade uniting Leptocleidia and Pliosauridae. In this analysis the most inclusive clade uniting the leptocleidids and polycotylids to the exclusion of other major clades is the sister group of a more inclusive Pliosauridae which includes *Thalassiodracon* as its basal-most taxon and the new taxon, *Stratesaurus*. This new grouping is then the sister group of Rhomaleosauridae in an enlarged Pliosauroidea. As in the phylogeny of Ketchum and Benson (2010), but not Benson and Ketchum (2011a) there is a small clade of plesiosaurians outside the Neoplesiosauria, including the somewhat aberrant NHMUK 49202. These taxa were included in Rhomaleosauridae as basal taxa in the analysis of Ketchum and Benson (2011a). The other major novel result concerning the Leptocleidia, which was defined as a node-based taxon by Druckenmiller and Russell (2008a, as Leptocleidoidea) is that there is now a paraphyletic assemblage situated basal to it.

The basal-most node of this assemblage is that uniting LEICT G1.2002 and NHMUK R16330, the Pliensbachian specimens which were described in Chapter 2. The other members of the assemblage are *Nichollssaura borealis* (Druckenmiller and Russell, 2008b) and *'Cimoliasaurus' valdensis* Lydekker, 1889. The former is early Aptian, and was originally recovered as a polycotylid (Druckenmiller and Russell 2008a, 2008b). It was recovered as a leptocleidid by Smith and Dyke (2008) Ketchum and Benson (2010, 2011a) and Benson *et al.* (in press). The latter taxon is Valanginian, and has been described by Ketchum (2011) as a valid diagnosable taxon, although it has been regarded as a *nomen vanum* (Welles 1962; Kear and Barrett 2011). It was included in the analysis of Benson *et al.* (in press) and was recovered as a pliosaurid, despite possessing some characters seen in other leptocleidids.

The Leptocleidomorpha

As the existing clade name Leptocleidia is node-based, the assemblage of successive sister taxa are currently hard to refer to other than by the informal term 'stem-leptocleidid'. It is possible that *Stratesaurus* also is a member of this assemblage, as it was recovered here in a polytomy with that grouping and the Pliosauridae. Since there is uncertainty as to the basal taxa that would be encompassed in such a grouping, a stem-based taxon is preferable to a node-based one (Sereno 1999), and as the Leptocleidia has been a node-based name since its introduction by Druckenmiller and Russell (2008a, as the Leptocleidoidea) I therefore introduce a new clade, the Leptocleidomorpha. This is defined as 'all taxa more closely related to *Leptocleidus superstes* and *Polycotylus latipinnis* than to *Cryptoclidus eurymerus*, *Pliosaurus brachydeirus* or *Rhomaleosaurus cramptoni*'. The external specifiers are included to ensure that a stem-based taxon encompassing the Leptocleidia remains valid in either the topology recovered here, that of Druckenmiller and Russell (2008a), or that of Ketchum and Benson (2010).

The clade is supported by the following 15 unambiguous discrete synapomorphies in this analysis: 'parietal table' at anterior end of parietal crest (54.2); pterygoid ventromedial flanges meet on midline ventral to basioccipital (95.1); pterygoid ventrolateral flanges form posterior squared lappets ventral to origin of quadrate rami: (98.1); pterygoid-quadrate connection transversely convex in ventral view: (105.1); quadrate ramus of the pterygoid inclined laterally (107.1); anterior cervical centra shorter than high (192.2); single rib facets of the anterior-middle cervical vertebrae (200.2); cervical zygapophyseal facets transversely concave/convex (207.1);. anterior processes of cervical ribs absent in most cervical ribs (223.2); dorsal neural spines less than or equal to the height of the centrum (228.0); mid-caudal neural spines rod-like (242.1); caudal neural spines strongly inclined posterodorsally, angle increasing

posteriorly (243.1); proximal end of humerus inclined anteriorly so shaft appears sigmoidal in dorsal view (288.1); distal end of humerus distinctly angled for articulation with the epipodials (294.1); phalanges short and robust (317.1). Under accelerated character optimisation (ACCTRAN) an additional 27 discrete synapomorphies support the clade, and an additional two under delayed character optimisation (DELTRAN). The clade is supported by 5 unambiguous quantitative synapomorphies, with an additional 6 under ACCTRAN and one under DELTRAN. The node at the base of the clade has the third strongest decay index in the analysis and is relatively well supported.

The Eupliosauria

While a clade uniting Leptocleidia and Pliosauridae has been found before, as noted above this has always been a less inclusive 'core' Pliosauridae than that recovered here and by Ketchum and Benson (2011a). In these topologies with 'core' pliosaurids the last common ancestor of pliosaurids and leptocleidians could have occurred as recently as the Mid Jurassic. The Callovian pliosaurids were relatively large-bodied, short-necked animals resembling the classic pliosauromorph body plan (O'Keefe 2002). Under the topology presented here the last common ancestor of pliosaurids and leptocleidians can have been no later than the very base of the Jurassic, as both *Thalassiodracon* and *Stratesaurus* are known from the basal Hettangian fauna of Street, Somerset, UK (Storrs and Taylor 1996; Benson *et al.* 2012). In view of the deep-seated nature of this node uniting pliosaurids and leptocleidomorphs, I introduce a new stem-based taxon, the Eupliosauria. This is defined as 'all taxa more closely related to *Pliosaurus brachydeirus* than to *Plesiosaurus dolichodeirus* or *Rhomaleosaurus cramptoni'*. In the current topology this encompasses Pliosauridae and Leptocleidomorpha. In topologies in which leptocleidians are more closely related to post-Callovian pliosaurids, taxa

3.16

situated between this node and the Rhomaleosauridae would also be encompassed. This clade is also valid if rhomaleosaurs are found not to be neoplesiosaurians (Benson *et al.* 2012). However, this clade becomes redundant in cases in which Pliosauridae and Rhomaleosauridae are sister groups within Pliosauroidea (e.g. Ketchum and Benson 2011a).

The Eupliosauria is supported by the following six unambiguous discrete synapomorphies in this analysis: no contact between premaxilla and external naris (4.2); premaxillary dorsomedian ridge elongate, extends from orbits to rostral tip (10.2); pterygoids separate vomers along the midline posteriorly (81.1); pterygoid ventrolateral flanges form lateral shelves (99.1); mandible not significantly bowed (143.1); mandibular symphysis construction involves more than two alveoli (148.2). However the only one of these which is seen in *Thalassiodracon*, *Stratesaurus* and LEICT.G1.2002 is the lateral shelves of the ventrolateral flanges of the pterygoid. In addition to the discrete unambiguous synapomorphies, the clade is supported by one unambiguous quantitative synapomorphy; the number of dorsal vertebrae increases from 21 to 23. The clade is also supported by an additional 11 discrete synapomorphies under ACCTRAN and three under DELTRAN, and by four quantitative synapomorphies under both ACCTRAN and DELTRAN.

The Plesiosauroidea

Within the Plesiosauroidea a clade of microcleidids is recovered, although support for this is relatively weak. The two new Pliensbachian specimens, the Lincoln taxon and the Golden Cap taxon, form a clade which is sister group to the late Toarcian *Occitanosaurus tournemirensis* (Sciau et al, 1990). Support is stronger for a clade comprising *Hydrorion brachypterygius* (von Huene, 1923) and *Microcleidus*

homalospondylus. MNHN A.C. 8592 was included in the analysis to test the hypothesis that it may not be conspecific with *Plesiosaurus dolichodeirus* due to the differences noted by Vincent and Taquet (2010). As it was recovered in a sister group relationship with *P. dolichodeirus*, the hypothesis cannot be disproved, but it is possible that the specimen represents ontogenetic variation or sexual dimorphism as Vincent and Taquet (2010) suggested. One reason that they favoured sexual dimorphism over ontogenetic variation was that OUMNH J.10304 does not show some of the characters seen in MNHN A.C. 8592, such as a prominent postaxial process on the humerus. However, observations made in the course of this study suggest that OUMNH J.10304 is not referable to *Plesiosaurus dolichodeirus*. The ilium shows the characteristic curved shape seen in cryptoclidids, and some elasmosaurids and polycotylids (Storrs 1997, Fig. 12), whereas the ilium of *P. dolichodeirus* is straight (pers. obs. of NHMUK 22656, holotype of *P. dolichodeirus*). The specimen may well represent a basal cryptoclidid and deserves further study. Specimen NHMUK 36183 was also omitted from the hypodigm of *Plesiosaurus dolichodeirus* used in this study as it has a large convex anterior flange on the radius which is also seen in some microcleidids, rhomaleosaurids and LEICT G1.2002, but not in NHMUK 22656. Given the robust convex skull shape and long neck, NHMUK 36183 may be a microcleidid, and deserves further study.

Specimen SMNS 16812 was described as the basal-most plesiosauroid by O'Keefe (2004b) and erected as the holotype of *Plesiopterys wildii*. The same specimen was referred to *Seeleyosaurus guilelmiimperatoris* (Dames, 1895) by Grossmann (2007). However, there are several differences between the two; not least that *Plesiopterys* has a large anterior interpterygoid vacuity, while that of *Seeleyosaurus* is either closed, or reduced to a narrow slit (Dames 1895, Taf. II). They were treated as separate OTUs in this analysis, and *Plesiopterys* was recovered as the basal-most cryptoclidid,

although support is weak, while *Seeleyosaurus* was recovered as the basal-most microcleidid. Within the more derived cryptoclidids, several specimens previously referred to *Muraenosaurus leedsii* (Brown 1981) were studied, and differences noted in the braincase, palate and lower jaws. Specimens NHMUK R2678, NHMUK R2861, NHMUK R2864 and LEICT G18.1996 were treated as separate OTUs from *M. leedsii*, which was represented by the holotype, NHMUK R2421, and NHMUK R2422. *Picrocleidus beloclis* (Seeley, 1892), which has been referred to *Muraenosaurus* (Seeley 1892; Brown 1981) was also included as a separate OTU. A monophyletic *Muraenosaurus* was not recovered. In particular, it seems that a *Muraenosaurus*-like morphology is plesiomorphic for the clade of cryptoclidids more derived than *Plesiopterys,* with *Picrocleidus*, *Pantosaurus striatus* (Marsh, 1891), and NHMUK R2861 forming successive basal taxa in a series of nested clades. Taxa above NHMUK R.2861 formed two sister clades: one containing *Muraenosaurus leedsii*, the other *'Muraenosaurus'* specimens and *Vinialesaurus caroli* (De la Torre and Rojas, 1949); the other containing *Tricleidus seeleyi* Andrews, 1909, *Kimmerosaurus langhami* Brown, 1981, *Tatenectes laramiensis* (Knight, 1900), *Colymbosaurus trochanterius* and *Cryptoclidus eurymerus*.

Although as noted above the wider clade of cryptoclidids more derived than *Plesiopterys* is unstable, a core of each of these sister clades was still recovered in the discrete characters-only analysis. I therefore introduce two new clades to describe this diversity within the cryptoclidid plesiosauroids: Cryptoclidinae and Muraenosaurinae. Cryptoclididae is defined as 'all taxa more closely related to *Cryptoclidus eurymerus* than to *Muraenosaurus leedsii*' while Muraenosaurinae is defined as 'all taxa more closely related to *Muraenosaurus leedsii* than to *C. eurymerus*'. Specimen NHMUK R2678 is the holotype of *Muraenosaurus platyclis* Seeley, 1892, and thus it appears

as this species in Figs. 3.1 and 3.2 and in Appendix II-IV. If the topology with respect to

Muraenosaurus leedsii is confirmed then this species should be referred to the genus

Tremamesacleis White, 1940 of which it is the genotype. The type specimen (NHMUK

R2428) of the other nominal species of *Muraenosaurus*, *M. durobrivensis* should be

investigated as NHMUK R2861 was referred to this species by Andrews (1910). A

wider specimen-level analysis of *Muraenosaurus* to confirm or reject the hypotheses

proposed here is recommended.

Table 3.1: Definitions of plesiosaurian higher taxa used herein. Although newly defined here, the Cryptoclidinae and Muraenosaurinae were created by Williston, (1925) and White (1940) respectively under the principle of coordination of the ICZN (Chapter 8, Article 36). Definitions that previously used *'Rhomaleosaurus' victor* as a specifier have been amended to include *R. cramptoni* following the referral of *'R' victor* to the genus *Meyerasaurus* (Smith and Vincent 2010).

Clade	Definition	Type
Plesiosauria Blainville,1835	All taxa more closely related to *Plesiosaurus dolichodeirus* and *Pliosaurus brachydeirus* than to *Pistosaurus longaevus* (amended).	stem-based
Neoplesiosauria Ketchum and Benson 2010	*Plesiosaurus dolichodeirus*, *Pliosaurus brachydeirus*, their most recent common ancestor and all of its descendants.	node-based
Plesiosauroidea Welles, 1943	All taxa more closely related to *Plesiosaurus dolichodeirus* than to *Pliosaurus brachydeirus*.	stem-based
Pliosauroidea Welles, 1943	All taxa more closely related to *Pliosaurus brachydeirus* than to *Plesiosaurus dolichodeirus*.	stem-based
Eupliosauria new clade	All taxa more closely related to *Pliosaurus brachydeirus* than to *Plesiosaurus dolichodeirus* or *Rhomaleosaurus cramptoni*.	stem-based
Leptocleidomorpha new clade	All taxa more closely related to *Leptocleidus superstes* and *Polycotylus latipinnis* than to *Cryptoclidus eurymerus*, *Pliosaurus brachydeirus* or *Rhomaleosaurus cramptoni*.	stem-based
Leptocleidia Ketchum and Benson 2010	*Leptocleidus superstes*, *Polycotylus latipinnis*, their most recent common ancestor and all of its descendants.	node-based

Cryptoclididae Williston, 1925	All taxa more closely related to *Cryptoclidus eurymerus* than to *Elasmosaurus platyurus*, *Leptocleidus superstes*, *Microcleidus homalospondylus, Ple. dolichodeirus* or *Po. latipinnis*.	stem-based
Elasmosauridae Cope, 1869	All taxa more closely related to *Elasmosaurus platyurus* than to *C. eurymerus, L. superstes, M. homalospondylus, Ple. dolichodeirus* or *Po. latipinnis*.	stem-based
Leptocleididae White, 1940	All taxa more closely related to *Leptocleidus superstes* than to *C. eurymerus, E. platyurus, M. homalospondylus, Ple. dolichodeirus, Pli. brachydeirus, Po. latipinnis* or *Rhomaleosaurus cramptoni* (amended).	stem-based
Microcleididae Benson *et al.* 2012	All taxa more closely related to *Microcleidus homalospondylus* than to *Ple. dolichodeirus, C. eurymerus, E. platyurus, L. superstes, Pli. brachydeirus* and *Po. latipinnis*.	stem-based
Plesiosauridae Gray, 1825	All taxa more closely related to *Plesiosaurus dolichodeirus* than to *C. eurymerus, E. platyurus, L. superstes M. homalospondylus* or *Po. latipinnis*.	stem-based
Pliosauridae Seeley, 1874	All taxa more closely related to *Pliosaurus brachydeirus* than to *L. superstes, Po. latipinnis* or *R. cramptoni* (amended).	stem-based
Polycotylidae Williston, 1908	All taxa more closely related to *Polycotylus latipinnis* than to *C. eurymerus, E. platyurus, L. superstes, M. homalospondylus, Ple. dolichodeirus, Pli. brachydeirus* or *R. cramptoni* (amended).	stem-based
Rhomaleosauridae Kuhn, 1961	All taxa more closely related to *Rhomaleosaurus cramptoni* than to *L. superstes, Pli. brachydeirus* or *Po. latipinnis* (amended).	stem-based
Cryptoclidinae Williston, 1925	All taxa more closely related to *Cryptoclidus eurymerus* than to *Muraenosaurus leedsii*.	stem-based
Muraenosaurinae White, 1940	All taxa more closely related to *Muraenosaurus leedsii* than to *C. eurymerus*.	stem-based

Table 3.1 cont.

Fig. 3.1: Strict consensus cladogram of 3240 most parsimonious trees of 47255 steps:

A, all taxa with the Plesiosauroidea shown as a single clade branch; B, the

Plesiosauroidea. Values adjacent to nodes give the relevant decay index.

A

Plesiosauroidea

Attenborosaurus conybeari
Marmornectes candrewi
Brachauchenius lucasi
Kronosaurus queenslandicus
FHSMVP321
Pliosaurus brachydeirus
Pliosaurus brachyspondylus
Gallardosaurus iturraldei
Liopleurodon ferox
Simolestes vorax
OUMNH J.02247
Peloneustes philarchus
Pliosaurus andrewsi
NHMUK R2439
Hauffiosaurus longirostris
Hauffiosaurus tomistomimus
Hauffiosaurus zanoni
OUMNH J.28585
Thalassiodracon hawkinsii
Brancasaurus brancai
Leptocleidus capensis
Leptocleidus superstes
MIWG 1997.302
Dolichorhynchops herschelensis
Dolichorhynchops osborni
Palmulasaurus quadratus
Trinacromerum bentonianum
TMP 95.87.01
Dolichorhynchops bonneri
Manemergus anguirostris
Pahasapasaurus haasi
Plesiopleurodon wellesi
Thililua longicollis
Edgarosaurus muddi
Leptocleidus clemai
Polycotylus latipinnis
Eopolycotylus rankini
QMF 18041
Umoonasaurus demoscyllus
'*Cimoliosaurus*' *valdensis*
Nichollssaura borealis
LEICT G1.2002
NHMUK R16330
Stratesaurus taylori
Eurycleidus arcuatus
Maresaurus coccai
Borealonectes russelli
Rhomaleosaurus zetlandicus
Rhomaleosaurus cramptoni
Rhomaleosaurus thorntoni
Rhomaleosaurus megacephalus
Meyerasaurus victor
Avalonnectes arturi
Archaeonectrus rostratus
Macroplata tenuiceps
NHMUK 49202
Pistosaurus skull
Bobosaurus forojuliensis
Yunguisaurus liae
Augustasaurus hagdorni
Pistosaurus postcranium
Cymatosaurus
Simosaurus gaillardoti

3.24

B

Fig. 3.1 cont.

Fig. 3.2: Time-calibrated strict consensus cladogram of 3240 most parsimonious trees of 47255 steps. Definitions of higher taxa are given in Table 3.1.

3.27

Chapter 4 Conclusions

1). LEICT G1.2002 and BMNH R16330 represent valid diagnosable taxa. LEICT G1.2002 has been erected the holotype of *Raptocleidus blakei* gen. et sp.nov.. BMNH R16330 has been erected the holotype of *Raptocleidus bondi* gen. et sp.nov..

2). The two new species share characters with pliosaurid, rhomaleosaurid and leptocleidian plesiosaurs, hampering their classification.

3). Following a phylogenetic analysis, the largest of the Plesiosauria to date, *Raptocleidus* was found to occupy a basal position in a clade which included the Leptocleidia. This clade formed the sister group to the Pliosauridae.

4). The new clades Leptocleidomorpha, Eupliosauria, Muraenosaurinae and Cryptoclidinae have been created and phylogenetically defined.

5). Potential new taxa in the Early and Mid Jurassic have been identified, pending further work.

Appendix I: Character Descriptions for phylogenetic analysis

Abbreviations for previous analyses

I have used abbreviations when citing the characters used in previous phylogenetic analyses, so that "S02 c151" refers to character 151 of the analysis of Sato (2002). In cases where a research group's analysis uses the same characters as an earlier study of theirs, these are not listed separately. For example, character 1 of Ketchum and Benson (2011a) is the same as character 1 of Ketchum and Benson (2010).

A+07	Albright *et al.* (2007) and O'Keefe (2008)
B+11a	Benson *et al.* (2011a)
B+11b	Benson *et al.* (2011b)
B+99	Bardet *et al.* (1999)
B+ip	Benson *et al.* (in press)
B81	Brown (1981)
BED	Benson, Evans and Druckenmiller (2012)
C99	Carpenter (1999)
D&R08	Druckenmiller & Russell (2008a)
G+02	Gasparini *et al.* (2002)
G+03	Gasparini *et al.* (2003)
G07	Großmann (2007)
H92	Hampe (1992)
K&B10	Ketchum and Benson (2010)
K&B11	Ketchum and Benson (2011a)

OK&S09   O'Keefe and Street (2009)

OK&W03   O'Keefe & Wahl (2003b)

OK01   O'Keefe (2001)

OK04   O'Keefe (2004b)

OK08   O'Keefe (2008)

R94   Rieppel (1994a)

S&D08   Smith & Dyke (2008)

S02   Sato (2002)

S91   Storrs (1991)

V+11   Vincent *et al.* (2011)

Discrete Characters

Skull roof

1. Lateral constriction of the rostrum at the premaxilla-maxilla suture: (0) absent; **(1)** present.

Previous use: V+11 c2, K&B10 c4, S&D08 c10, G07 c2, D&R08 c10, S02 c12, OK01 c9, R94 c3, S91 c33.

2. Premaxilla ornamentation: (0) relatively smooth with marked foramina; **(1)** coarsely sculptured with numerous small rugosities; **(2)** coarsely sculptured with undulating rounded ridges.

Previous use: BED c13; modified from B+ip c203, K&B10 c5, G07 c1.

3. Position of the external naris: (0) midpoint, or anterior to the midpoint of the pre-orbital region of the skull; **(1)** retracted to within the posterior half.

Previous use: K&B10 c6; modified from D&R08 c13, S02 c19, S91 c35.

4. Premaxilla and external naris: (0) broad contact; **(1)** diminutive contact on anteromedial margin; **(2)** no contact.

Previous use: B+ip c8, S&D08 c8; modified from K&B10 c8, D&R08 c7, S02 c8, OK01 c12.

5. Premaxilla, constriction of facial process at level of extenal naris: (0) absent; **(1)** present.

Previous use: BED c21.

6. Deep distinct dorsomedian cleft between premaxillary facial processes: (0) absent; **(1)** present.

Previous use: modified from K&B10 c9, S&D08 c7, D&R08 c9, S02 c9, OK01 c13.

Notes: Smith and Dyke (2008) restricted this character to an oval foramen situated between the external nares, which resolved as an autapomorphy of *Rhomaleosaurus* sensu stricto. In contrast, Druckenmiller and Russell (2008a) included the slight separation of the premaxillary suture seen in a range of taxa, and noted that this could also occur between the frontals. In this analysis this character refers to a deep cleft on

the midline of the skull at least partly bordered by the premaxillary facial processes.

7. Posterior morphology of the premaxillae: (0) contact anterior extension of frontals only; **(1)** partially split frontals along the midline; **(2)** completely split the frontals and contact the parietals.

Previous use: V+11 c5, K&B10 c10; modified from S&D08 c17, D&R08 c5, S02 c6, OK01 c11 and C99 c8.

8. Premaxilla, dorsomedian ridge: (0) absent or indistinct; **(1)** prominent.

Previous use: K&B10 c11; modified from D&R08 c6, S&D08 c5, S02 c3 andc10 partim.

9. Premaxilla, shape of dorsomedian ridge: (0) narrow and crest-like (taller than wide); **(1)** broad; **(2)** spindle-like (new state).

Previous use: modified from K&B10 c12 and OK08 c42.

Notes: I have added an extra state to the character of Ketchum and Benson (2010) to describe the "swollen" premaxillary facial processes noted in *Thililua* and *Manemergus* by O'Keefe (2008). This morphology actually appears to be due to the shape of the dorsomedian ridge, where it is 'spindle-shaped', tapering anteriorly and posteriorly but broad in-between.

10. Premaxilla, dorsomedian ridge location: (0) anterior; **(1)** posterior; **(2)** elongate,

extends from orbits to rostral tip.

Previous use: K&B10 c13; modified from S02 c3.

11. Premaxilla, dorsomedian 'bump': (0) absent; **(1)** present.

Previous use: modified from S02 c10.

Notes: Sato (2002) described a median 'bump' on the premaxillae in several Cretaceous elasmosaurs. Although these specimens are crushed I provisionally recognise a 'bump' in *Styxosaurus snowii* and *Hydralmosaurus serpentinus*. A similar structure is also present in two specimens referred to *Muraenosaurus leedsii* by Brown (1981). In both NHMUK R2861 and NHMUK R2678 a 'bump' is situated at the caudal end of the premaxillae and also includes an elevation of the underlying frontals (pers. obs.); this is absent in the holotype of *M. leedsii* (NHMUK R2421).

12. Premaxilla, posterior termination: (0) tapering; **(1)** deeply interdigitating suture with the frontal or parietal; **(2)** shallowly interdigitating suture with the frontal or parietal.

Previous use: K&B11 c14; modified from D&R08 c5 and K&B11 c14.

13. Premaxilla, posterior extent: (0) short, ends anterior to orbit; **(1)** long, extends up to orbital midlength; **(2)** very long, extends beyond orbit midlength.

New character

Notes: The nature of the posterior suture of the premaxillae is independent of which bone it contacts and of the anterior extent of the parietal (Benson *et al.* 2011a).

Similarly, the posterior extent of the premaxillae is also independent of the morphology of the bone's termination, of which bone it contacts and of the anterior extent of the parietal. It should therefore be included as a separate character. State '0' can be seen in *Hauffiosaurus tomistomimus* (Benson *et al.* 2011b), *Cryptoclidus eurymerus*, *Tricleidus seeleyi* (Brown 1981; Brown and Cruickshank 1994), FHSM VP-321 (Carpenter 1996), LEICT G1.2002, NHMUK 49202 and *Occitanosaurus* (pers. obs.). State '1' can be seen in *Rhomaleosaurus cramptoni* (Smith and Dyke 2008), *Thalassiodracon hawkinsii* (Benson *et al.* 2011a), *Macroplata tenuiceps* (Ketchum and Smith 2010), *'Rhomaleosaurus' megacephalus*, *Microcleidus homalospondylus*, and *Muraenosaurus leedsii* (pers. obs.). State '2' can be seen in *Dolichorhynchops osborni* (Carpenter 1996, contra O'Keefe 2004), *D herschelensis* (Sato, 2005), *Thalassomedon hanningtoni* (Sato 2002) and QM F18041 (Ketchum 2007).

14. Premaxilla-maxilla sutures: (0) converging gradually posteromedially for entire length; **(1)** anterior portion extends dorsomedially then abruptly curves posteriorly, resulting in a parallel-sided appearance of the facial process of the premaxilla.
Previous use: S&D08 c9, B+ip c204, BED c22.

15. Maxilla, trough anterior to the external nares: (0) absent; **(1)** present, defined laterally by a longitudinal ridge but does not extend far anteriorly; **(2)** prominent longitudinal trough extends most of the prenarial length of the maxilla.
Previous use: BED c25; modified from K&B11bc179, K&B10 c7, S&D08 c6, D&R08 c12, OK01 c37.

Notes: O'Keefe (2001; 2004b) and Druckenmiller and Russell (2008a) coded for the presence of a groove anterior to the external naris. Smith and Dyke (2008) coded for a gully both anterior and posterior to the naris, while Ketchum and Benson (2010) coded for the shape of the anterior border of the naris. The prominent trough observed in *Hauffiosaurus* by Benson *et al.* (2011b) is included as state '2'.

16. Posteromedial extension of the maxilla: (0) extends to the external naris; **(1)** extends posterior to the external naris.

Previous use: modified from K&B10 c15.

Notes: This character is inapplicable where the premaxilla contacts the external naris.

17. Ascending process of the maxilla: (0) absent; **(1)** present.

Previous use: S&D08 c13.

18. Maxilla-squamosal contact: (0) absent; **(1)** present.

Previous use: K&B10 c16, S&D08 c12, D&R08 c17, S02 c17; modified from V+11 c9, OK01 c41.

19. Nasal bone: (0) present; **(1)** absent.

Previous use: K&B10 c17, S&D08 c1, D&R08 c28, S02 c28; modified from OK01 c35, C99 c1, R94 c5, S91 c34.

20. Prefrontal present: (0) present; **(1)** absent.

Previous use: G+03 c5, G+02 c3, S02 c26, OK01 c22. Previous exclusion: K&B10X9, D&R08X175.

Notes: Druckenmiller and Russell (2008a) interpreted the apparent absence of the prefrontal as being due to fusion with the maxilla. No trace of a suture could be seen on close examination of specimens of *Muraenosaurus* sensu lato (NHMUK R.2861 and R.2678). However, in taxa where the prefrontal is clearly present it forms part of the ventral antorbital ridge (equivalent to the descending process of the prefrontal of Noè (2001) and Ketchum (2007)). If perceived loss of the prefrontal were due to complete fusion with the maxilla, then the ventral antorbital ridge would also be fused to the maxilla. However, the ventral orbital ridge is formed entirely by the frontal in taxa such as *Muraenosaurus* which appear to lack the prefrontal. It is loosely overlapped by the facial process of the maxilla. This is therefore interpreted as evidence that the prefrontal is indeed lost in some taxa such as *Muraenosaurus*, *Cryptoclidus* and *Tricleidus* as described by Brown (1981).

21. Prefrontal participates in the margin of the external naris: (0) does not participate; **(1)** participates.

Previous use: modified from V+11 c4, K&B10 c25, S&D08 c16, D&R08 c27, S02 c27, OK01 c39.

Notes: This character is scored as inapplicable for those taxa in which the prefrontal is absent.

22. Frontal participation in the border of the external naris: (0) does not participate; **(1)** participates.

Previous use: K&B10 c18, S&D08 c15, D&R08 c8, G+03 c6, S02 c25, OK01 c19, B+99 c9; modified from V+11 c6.

23. Frontal, process extending anteromedially to external naris: (0) absent or short; **(1)** extends anterior to naris and contacts maxilla in long contact.

New character

Notes: In polycotylids such as *Dolichorhynchops herschelensis*, *D. bonneri* and *Trinacromerum bentonianum* a process of the frontal extends anteriorly, contacting the maxilla and forming the dorsal and anterior margins of the external naris (Sato 2005; O'Keefe 2008; Carpenter 1996). In *D. osborni* the frontal terminates dorsomedial to the naris (Carpenter 1996). An elongate anterior process of the frontal is also present in *Brachauchenius lucasi*, although it is separated from the naris by the posteromedial process of the maxilla (Ketchum 2007). For this character to be scored as present, the frontal must run anterior of the naris lateral to the premaxilla. This character is scored as 'absent' in NHMUK 49202 in which a wide, medially situated anterior extension of the frontals separates the premaxillae on the midline anterior to the naris (contra Druckenmiller and Russell 2008a, fig. 2). This character is scored as 'inapplicable' in taxa in which the premaxilla contacts the naris.

24. Frontal participation in the orbit margin: (0) participates in the orbit margin; **(1)**

does not participate in the orbit margin.

Previous use: K&B10 c19, S&D08 c18, D&R08 c26, S02 c20, OK01 c40, R94 c8.

25. Frontal extends posterior to the anterior edge of the temporal fossa: (0) present; **(1)** absent.

Previous use: modified from V+11 c8, K&B10 c21, D&R08 c25, OK01 c16, R94 c12, S91 c30.

Notes: Previous authors have coded for the presence or absence of a distinct posterolateral process of the frontal which embraces the anterior process of the parietal. While this is distinct in *Cymatosaurus* and *Augustasaurus*, it has also been identified as present in some early plesiosaurs to varying degrees. There is inconsistency in its recognition in certain key taxa such as *Plesiosaurus dolichodeirus*, where it was coded as present by O'Keefe (2001) and absent by Druckenmiller and Russell (2008a) and Ketchum and Benson (2010). I have found this character hard to code consistently for plesiosaurs. As the parietal expands forward the frontal automatically acquires a posterolaterally directed process. I have therefore modified this character to refer to an extension of the frontal on the skull roof beyond the anterior edge of the temporal fossa. As shown by *Kaiwhekea* (Cruickshank and Fordyce, 2002) it is possible for this character to be present when the premaxilla contacts the parietal. This character is independent of contact of the frontal with the margin of the temporal fossa, as the frontal may extend beyond the edge of the fossa but not contact it, as seen in *Cymatosaurus minor* (Rieppel and Werneburg, 1998), while it can also form the border of the fossa but not extend beyond it, as in NHMUK 49202.

26. Frontal participates in the margin of the temporal fossa: (0) absent; **(1)** present.

Previous use: V+11 c7, K&B10 c 22, D&R08 c24, S02 c22, OK01 c18, R94 c13.

27. Anterior orbital margin: (0) acute in sagittal section forming sharp edge; **(1)** convex or obtuse in sagittal section.

New character

Notes: In some taxa the anterior margin of the orbit is convex or obtuse in sagittal section, the dorsal surface of the rostrum and the anterior wall of the orbit being confluent (state 1). This is seen in '*Rhomaleosaurus' megacephalus* (Smith 2007, fig 4.48) where the anterior wall of the orbit can be seen in dorsal view as a convex or posterodorsally inclined surface. In taxa in which this is absent (state 0) the anterior margin of the orbit is acute in sagittal section, forming a sharp edge so that the anterior wall of the orbit is not visible in dorsal view. This can be seen in *Peloneustes philarchus* (Ketchum and Benson 2011b, fig. 4). The presence of absence of this character is independent of the bones forming the anterior of the orbit as *Hauffiosaurus tomistomimus* shows state '1' despite having the same configuration of anterior circumorbital bones as *Peloneustes*. There may also be a raised ridge describing the anterior margin of the orbit which is covered in the following character.

28. Anterior orbital margin marked by a raised ridge: (0) absent; **(1)** present.

New character

Notes: In *Augustasaurus hagdorni* the anterior margin of the orbit is marked by a raised

ridge (state 1: Rieppel *et al.* 2002, figs. 1-3). A similar ridge, although not as extensive medially, is seen in some stratigraphically early plesiosaurs such as *Thalassiodracon hawkinsii* (Benson *et al.* 2011a, figs), OUMNH J.10337, NHMUK 14550 and TTNCM 9291 (pers. obs.). A ridge is present in *Hauffiosaurus longirostris* (White 1940) but is absent in *H. tomistomimus* (Benson *et al.* 2011b, fig. 4). A raised ridge is also seen in some later plesiosaurs such as *Umoonasaurus demoscyllus* (Druckenmiller and Russell 2008a, fig. 11).

29. Circumorbital margin dorsally: (0) not marked by a raised ridge; **(1)** marked by a raised ridge; **(2)** rounded oblique ridge running anterolaterally-posteromedially.

Previous use: modified from K&B10 c20.

Notes: I have introduced a new state to describe the curved oblique rounded ridges seen on the frontals of *Muraenosaurus leedsii* (Andrews 1910, Pl. III). These are also seen in similar Oxford Clay Formation taxa such as *Cryptoclidus eurymerus* (Brown and Cruickshank 1994, fig. 1) and also in *Vinialesaurus* (Gasparini *et al.* 2002, fig. 2). The scores for states '0' and '1' of this character in the matrices of Ketchum and Benson (2010; 2011a) appear to have become transposed.

30. Ornamentation of bone surface around the orbit margin: (0) absent; **(1)** present.

Previous use: K&B10 c34.

31. Dorsal margin of orbit with convex flanges and/or notches: (0) absent; **(1)** present.

Previous use: modified from S&D08 c19, OK01 c24.

Notes: The dorsal border of the orbit may be formed by convex flanges. In such cases an associated notch may be present at the posterodorsal corner of the orbit. Conversely the dorsal border may be smoothly concave in outline without flanges and notches. This character is separate from that coding for ornamentation of the circumorbital bones, as that morphology is at a finer scale than this.

32. Palpebral (or supraorbital) process: (0) absent; **(1)** present.

Previous use: OK08 c34.

Notes: O'Keefe (2008) discussed the homology of a rugose process of bone forming the posterodorsal margin of the orbit in *Trinacromerum* and *Dolichorhynchops bonneri*. A similar but more delicate structure was also identified by Carpenter (1996) in *Dolichorhynchops osborni*.

33. Ventral margin of orbit convex: (0) absent; **(1)** present.

Previous use: S02 c36.

Notes: The ventral outline border of the orbit may be smoothly concave, as in *Microcleidus homalospondylus* or be convex as in the taxa identified by Sato (2002). This character is separate from that coding for ornamentation of the circumorbital bones, as that morphology is at a finer scale than this.

34. Jugal, participation in orbit margin: (0) jugal participates in orbit margin; **(1)** jugal excluded from orbit margin by maxilla/postorbital contact.

Previous use: S91 c24, B+99 c3, OK01 c31, S02 c16, G07 c10, K&B10 c23, V+11 c10; modified from S&D08 c23.

35. Anterior extent of jugal ventral to orbit: (0) posterior third of the orbit; **(1)** middle third of the orbit; **(2)** anterior third of the orbit.

Previous use: R94 c20, OK01 c30, D&R08 c14, K&B10 c27.

36. Jugal morphology: (0) large, quadrilateral element with long anteroposterior axis; **(1)** narrow and vertically orientated.

Previous use: S91 c26, B+99 c1, OK01 c33, G+03 c1, G07 c11, D&R08 c15, K&B10 c28.

37. Jugal-squamosal contact: (0) absent; **(1)** present.

Previous use: OK01 c29, D&R08 c16, K&B10 c29, V+11 c11.

38. Lacrimal: (0) absent, maxilla participates in orbit margin; **(1)** present, maxilla excluded from orbit margin.

Previous use: S91 c22, R94 c7, D&R08 c18, K&B10 c30.

39. Postfrontal participation in orbit margin: (0) participates in orbit margin; **(1)** does not participate.

Previous use: OK01 c17, S02 c37, D&R08 c20, K&B10 c24, V+11 c13.

Notes: Scoring for this character follows that of Ketchum and Benson (2010).

40. Shape of postfrontal: (0) triangular; **(1)** quadrangular.

Previous use: B+99 c7, G07 c8, K&B10 c23, V+11 c12.

Notes: I have found it hard to score this character based on the shape of the postfrontal alone as a triangular postfrontal can be oriented in different ways. However, it would appear that the orientation of the postfrontal-postorbital suture is the main factor controlling this character. Where the suture runs anterolaterally to posteromedially, the anterolateral portion of the postfrontal on the postorbital bar is acutely pointed resulting in a triangular appearance (state 0). In taxa in which the suture runs more anteroposteriorly the bone's lateral portion is squared-off, resulting in the quadrangular morphology (state 1). State '0' can be seen in *Plesiosaurus dolichodeirus* (Storrs 1997), while state '1' can be seen in *Peloneustes* (Ketchum and Benson, 2011b). I differ in my scoring of this character from previous authors in taxa such as *Occitanosaurus* in which an anteroposteriorly directed crack has been mistaken for the postfrontal-postorbital suture (Bardet *et al.* 1999).

41. Postorbital, length of posterolateral process: (0) long, extending posteriorly for at least two-thirds of the temporal fenestra length; **(1)** prominent, but not elongate, extending approximately one-third of temporal fenestra length; **(2)** short or absent.

Previous use: BED c35; modified from K&B10 c33, OK&S09 c81, S&D08 c21, D&R08 c22, G07 c9, OK04 c168, G+03 c2, OK&W 03c90, S02 c38, B+99 c2, S91 c17.

42. Postorbital-parietal contact posterior to postfrontal: (0) absent; **(1)** present.

New character

Notes: In several taxa such as *'Rhomaleosaurus' megacephalus* (LEICT G221.1851) the postorbital extends medially and contacts the parietal posterior to the postfrontal. This contact can also be seen in WM 851.S which has been referred to *Rhomaleosaurus zetlandicus* (Vincent and Smith 2009). This region can be delicate, and so is frequently damaged. However, this contact can be confirmed as absent in taxa such as *Peloneustes philarchus* (Ketchum and Benson 2011b). This character may be equivalent to character 14 (postfrontal-temporal fenestra contact) of Vincent *et al.* (2011).

43. Postorbital-squamosal contact: (0) present, excluding jugal from the margin of the temporal fenestra; **(1)** absent, and jugal enters margin of the temporal fenestra.

Previous use: V+11 c15, K&B10 c31, S&D08 c21 partim, D&R08 c21, S02 c38,c15, OK01 c28, C99 c4.

44. Temporal fossae, anterior extent: (0) posterior to or approximately level with posterior orbital margin; **(1)** extend dorsomedially to orbits.

New character

Notes: In many elasmosaurids the temporal fossae extend anteromedially onto the skull roof between the orbits (e.g. *Libonectes*: Welles 1949, Pl. 5). This is also present in *Kaiwhekea* (Cruickshank and Fordyce 2002) and to a much lesser extent in *Kimmerosaurus* (Brown 1981, Fig. 31). *Augustasaurus* has been scored for the presence

of this character due to a combination of a narrow postorbital bar and posteriorly

expanded orbit (Reippel *et al.* 2002).

45. Temporal emargination: (0) deeply embayed; **(1)** moderately embayed; **(2)**

slightly embayed.

Previous use: K&B10 c32, S&D08 c32, D&R08 c23, G+03 c3, G02c4, OK01 c10.

46. Deep temporal bar: (0) absent; **(1)** present.

Previous use: modified from OK08 c40.

Notes: A particularly deep temporal bar was noted in *Manemergus* in Buchy *et al.*

(2005) and interpreted as present but dorsoventrally crushed in *Thililua* by O'Keefe

(2008). As Ketchum and Benson (2010) point out the latter is laterally crushed and so

the deep temporal bar would not appear to be present. However, it does appear to be

present in *Kaiwhekea* and *Zarafasaura* (Cruickshank and Fordyce 2002; Vincent *et al.*

2011). This character was not explicitly defined by O'Keefe (2008). Buchy et al, (2005)

observed that the height of the temporal bar is the same as that of the orbit in

Manemergus, and although this could be used to characterise a deep temporal bar, the

size of the orbits is also variable. I have scored a deep temporal bar as 'present' when

the bar's dorsal edge is at a level dorsal to the upper rim of the orbit.

47. Parietal foramen location: (0) centre of the temporal fenestrae; **(1)** between the

anterior margins of the temporal fenestrae; **(2)** closed.

Previous use: K&B10 c35; modified from S&D08 c27 and V+11 c16 andc18; modified

from OK08 c6, A+07 c6, G07 c5, D&R08 c29, G+03 c7, S02 c29, OK01 c20, B+99 c10, R94 c15, S91 c28.

Notes: Smith and Dyke (2008) introduced a modification of this character which differentiated between the parietal foramen being anterior or posterior to the posterior border of the postorbital bar. However, I have found this difficult to score objectively and consistently as it depends on being able to differentiate the postorbital bar from the anterior wall of the temporal fossa. I have therefore used Ketchum and Benson's (2010) interpretation of this character.

48. Parietal foramen proportions: (0) narrowly suboval, width/length <0.5; **(1)** anteroposteriorly elongate and slot-like; **(2)** wide, width/length >0.5.

Previous use: modified from B+ip c205.

Notes: Typically the parietal foramen in plesiosaurs is a narrow oval in shape, with its width being less than half of the length giving a ratio of 0.5 or less as can be seen in species of *Rhomaleosaurus* (state 0). Benson *et al.* (in press) noted the slot-like elongate morphology seen in several elasmosaurids in which the foramen's length is many times the width (state 1). In a third morphology (state 2) the foramen is a wide oval opening in which the width is more than half the length. This morphology can be seen in *Nichollsaura* (Druckenmiller and Russell 2008b), *Umoonasaurus* (Kear *et al.* 2006), NHMUK 49202 and LEICT G1.2002 (pers. obs.). This character is scored as 'inapplicable' in taxa in which the parietal foramen is absent.

49. Parietal foramen surrounding elements in dorsal view: (0) surrounded entirely

by the parietals; **(1)** contacted by the frontals anteriorly.

Previous use: V+11 c17, K&B10 c36, S&D08 c26, D&R08 c30, S02 c29 and OK01 c21.

Notes: This character is inapplicable for taxa in which the parietal foramen is closed, and those in which the frontals are entirely separated along the midline by contact between the premaxillae and parietals.

50. Parietal, anterior extension: (0) short or absent, parietal extends to the level of the postorbital bar; **(1)** long, parietal extends to orbital midlength or more anteriorly; **(2)** very long, parietal extends to anterior orbit margin or more anteriorly.

Previous use: BED c41; modified from K&B11 c181.

51. Parietal ornamentation anterior to the supratemporal fenestrae and/or pineal foramen: (0) ornamentation absent; **(1)** ornamented with numerous ridges that radiate from the pineal foramen, but flat or slightly concave along midline; **(2)** parietal with raised midline ridge.

Previous use: K&B10 c37; modified from S02 c32.

Notes: State '2' includes the "undivided parietal crest" of Sato (2002, c32) and the state seen in taxa such as *'Rhomaleosaurus' megacephalus* and *Thalassiodracon* where the parietal crest continues anterior to the parietal foramen. This character is scored as 'inapplicable' for taxa in which the frontals contact the parietal foramen.

52. Parietal crest: (0) absent; **(1)** present.

Previous use: K&B10 c38, modified from H92 c13, OK01 c25, D&R08 c31, OK&W03 c16.

53. Parietal, sagittal crest height: (0) low, dorsolateral surfaces at relatively high angle; **(1)** erect, transversely compressed, sides subvertical dorsally; **(2)** very high, forming convex or sigmoidal dome in lateral view rising above the skull table.

Previous use: K&B11 c182, modified from OK&W03 c94, OK08 c32, OK&S09 c85.

54. Parietal crest, apex in dorsal view: (0) narrow ridge; **(1)** triangular, widening anteriorly and flat-topped; **(2)** 'parietal table' narrow posteriorly with anterior triangular depressed region; **(3)** broad over whole length.

Previous use: Modified from BED c40 partim and B+ip c37 partim, B81 c9, R94 c16, D&R08 c31, K&B10 c39.

55. Parietal vault in dorsal view: (0) mediolaterally narrow, lateral surfaces weakly concave or slightly sinuous ; **(1)** expanded to approximately one-third the mediolateral width of the skull, lateral surfaces convex, forming abrupt 'lateral angle'; **(2)** strongly expanded, equal to at least half the transverse width of the posterior cranium, lateral surfaces concave.

Previous use: B+ip c206, BED c38, modified from S02 c33, D&R08 c32, S&D08 c29, K&B10 c40.

Notes: State '1' corresponds to the "lateral angle" of Smith and Dyke (2008,c29) and

state '2' corresponds to the "parietal wing" of Sato (2002,c33).

56. Dorsal rami of squamosals: (0) separated along the midline by the parietals; **(1)** squamosals contact along the dorsal midline.

Previous use: K&B10 c41, D&R08 c33, OK01 c27.

57. Apex of squamosal arch in lateral view: (0) low and rounded; **(1)** raised approximately a third orbit height dorsally relative to skull table; **(2)** forms anteriorly oriented vertex; **(3)** raised abruptly and substantially dorsally relative to skull table.

Previous use:BED c37, modified from B+ip c43, modified from S02 c73, D&R08 c35, S&D08 c28, K&B10 c43.

58. Inter-squamosal suture along the dorsal midline: (0) flat; **(1)** bulbous.

Previous use: K&B10 c42, S&D08 c30, D&R08 c34, S02 c72, OK01 c55.

Notes: This character is scored as 'inapplicable' for those taxa in which the squamosals do not meet at the midline.

59. Position of inter-squamosal suture: (0) posterior to parietals; **(1)** directly dorsal to parietals.

New character

Notes: In state '0', the squamosals suture to one another posterior to the parietals. This results in the squamosals forming an overhanging shelf which is visible in occipital

view. This is seen in many 'pliosauromorph' taxa such as *Peloneustes philarchus* (Ketchum and Benson 2011b, fig. 6), and is present in LEICT G1.2002. It is also present in some 'plesiosauromorph' taxa such as *Microcleidus homalospondylus* (NHMUK 36184) and was described in *Augustasaurus* and *Pistosaurus* by Rieppel *et al.* (2002). In state '1' the squamosals suture to one another directly dorsal to the parietals as in many 'plesiosauromorph' taxa such as *Muraenosaurus leedsii* (NHMUK R2421) and also OUMNH J.10337. This character is independent of the presence of a bulbous inter-squamosal suture. This character is scored as 'inapplicable' for taxa in which the squamosals do no contact one another.

60. 'Box-like' suspensorium: (0) absent; **(1)** present.

Previous use: K&B10 c44, D&R08 c37, R+02c123.

61. Inclination of the suspensorium: (0) vertical to sub-vertical; **(1)** significantly inclined.

Previous use: K&B10 c45, modified from D&R08 c36, S02 c75 and C99 c9.

62. Squamosal, outline of posterior margin in lateral view: (0) approximately straight; **(1)** dorsal portion inflected anterodorsally.

Previous use: BED c46.

63. Squamosal arch in dorsal view: (0) approximately straight or slightly

convex/concave; **(1)** squamosals angled to one another, forming a posteriorly open 'V'.

New character

Notes: In most pistosaurians the squamosal arch is either straight or gently concave or convex in dorsal view. However, in some taxa the dorsal rami of the squamosals are oriented at a high angle to one another, making a posteriorly open 'V' shape. This can be seen in *Muraenosaurus* (Andrews 1910, fig. 46) and *Cryptoclidus* (Brown and Cruickshank 1994, fig. 2), and is very marked in *Kaiwhekea* (Cruickshank and Fordyce 2002) and *Zarafasaura* (Vincent *et al.* 2011). A similar mophology is also present in *Cymatosaurus* and *Simosaurus* (the "deeply excavated"occiput of Rieppel and Werneburg 1998), although the squamosals are unfused in these taxa.

64. Elongated medial process of the ventral ramus of squamosal contacting quadrate: (0) absent; **(1)** present.

Previous use: K&B10 c46, D&R08 c38, S02 c76, OK01 c26.

65. Squamosal, anterior extent: (0) ventral to postorbital bar; **(1)** significantly posterior to postorbital bar.

Previous use: G07 c14, BED c42.

66. Quadrate foramen: (0) absent; **(1)** present.

Previous use: S&D08 c31, BED c44.

67. Shape of quadrate: (0) massive; **(1)** dished anteriorly.

Previous use: K&B10 c47, OK01 c54.

Notes: Following Ketchum and Benson (2010) this character was scored directly from the data matrix of O'Keefe (2001a).

68. Quadrate, shape in posterior view: (0) triangular/tongue-shaped; **(1)** mediolaterally narrow with sub-parallel sides.

New character

Notes: typically in plesiosaurs the quadrate in occipital view is triangular or 'tongue-shaped', being broad ventrally and tapering dorsally towards the head of the quadrate (state 0). In LEICT G1.2002 and OUMNH J.10337 the quadrate is a mediolaterally narrow bone with subparallel sides (state 1).

Palate

69. Diastema sensu Druckenmiller & Russell (2008a) at premaxillary-maxillary suture: (0) absent; **(1)** present.

Previous use: K&B10 c48, S&D08 c11, D&R08 c11, S02 c106, OK01 c99, S99c37.

70. Accessory grooves on the palatal surface of the premaxilla and vomer: (0) absent; **(1)** present.

Previous use: S&D08 c34, B+ip c207.

71. Premaxilla participation in the margin of the internal naris: (0) participates broadly; **(1)** participates minimally or just excluded; **(2)** absent, broadly excluded. Previous use: modified from V+11 c19, K&B10 c49, S&D08 c35, D&R08 c39, S02 c41, OK01 c81.

Notes: Smith and Dyke (2008) combined the characters of previous authors which coded for internal naris contact of the maxilla and premaxilla into a single multistate character. However, this is not warranted as these character states are controlled by different mechanisms. The premaxilla is frequently excluded by contact of the vomer and maxilla, while the maxilla can be narrowly or broadly excluded by an anterior expansion of the palatine as in *Hydrorion* (Grossmann 2006) or *Dolichorhynchops osborni* (O'Keefe 2004a). Theoretically it would be possible for the premaxilla to contact the internal naris while the maxilla was excluded by the palatine. State '1' describes a morphology where the premaxilla makes either a very small, point-like, contribution to the border of the naris, or is only just excluded. In these cases judging whether contact has been made with the naris is largely subjective, especially when taking into account the convex nature of the aperture rim and potential taphonomic distortion.

72. Maxilla participation in the margin of the internal naris: (0) participates broadly; **(1)** participates minimally or just excluded; **(2)** absent, well excluded. Previous use: modified from V+11 c20, K&B10 c50, S&D08 c35, D&R08 c40, G+03 c8, S02 c42, G+02 c5, B+99 c11.

Notes: As noted above, Smith and Dyke (2008) combined this character with the previous one. State '1' is similar to that described above for the premaxilla. In

Hydrorion, the maxilla has been interpreted as making a very small, almost point-like, contribution to the margin of the naris (Maisch and Rücklin 2000), and also as just failing to contact the naris (Grossmann 2006) due to differences of interpretation of the same specimen.

73. Vomer, internarial bar: (0) convex; **(1)** flat.

New character

Notes: In many taxa the bar between the internal nares formed by the vomers is transversely convex (state 0). This can be seen in *'Rhomaleosaurus' megacephalus* and *Liopleurodon* (pers. obs.; Noè 2001). A convex internarial bar is also seen in *Vinialesaurus* (Gasparini *et al.* 2002) and *Muraenosaurus leedsii* (pers. obs. of holotype specimen NHMUK R2421). However, in some taxa the internarial bar is flat ventrally (state 1). This can be seen in *Cryptoclidus* (pers. obs. of NHMUK R2860) and also in NHMUK R2861 and R2678, both of which have been referred to *Muraenosaurus leedsii* (Brown 1981).

74. Palatine participation in the margin of the internal naris: (0) participates broadly; **(1)** participates minimally or just excluded; **(2)** absent, well excluded.

Previous use: modified from K&B10 c51, S&D08 c36, D&R08 c41, S02 c43, OK01 c79.

75. Pterygoid participation in the margin of the internal naris: (0) absent; **(1)** present.

Previous use: modified from OK08 c35.

Notes: In most plesiosaurs the pterygoid is separated from the margin of the internal naris by the vomer. In *Dolichorhynchops osborni* the pterygoids extend between the internal nares, forming their posteromedial margins (O'Keefe, 2004a).

76. Palate, foramina anterior to internal naris: (0) absent; **(1)** series of foramina between maxilla and vomer; **(2)** single pair of 'vomeronasal' foramina between vomer and maxilla and/or premaxilla.

Previous use: modified from K&B11 c184, G07 c16, G+03 c10 and S02 c40.

Notes: I have added an extra state to describe the presence of a single pair of foramina anterior to the internal nares. These are situated between the vomer, maxillae and premaxillae in the holotype of *Muraenosaurus leedsii* (NHMUK R2421) and previously referred specimens (eg NHMUK R2678, R2861 and R2864). *Hydrorion* also has a single pair of foramina anterior to the internal nares, although here they are more anterior in position, situated between the vomer and premaxillae. Huene (1923) and Maisch and Rücklin (2000) described these as "foramina incisiva", while Grossmann (2006) referred to the foramen as a "fenestra vomeronasalis". Paired foramina anterior to the internal nares are also present in *Plesiosaurus dolichodeirus*, although the surrounding elements are unclear (pers. obs. of NMING F8758). I regard the large perforation anterior to the internal naris seen in *Vinialesaurus* as homologous to this foramen. In *Aristonectes*, there are two well developed openings at the front of the palate between the vomers and premaxillae (the "premaxillary fenestrae" of Gasparini *et al.* 2003 and "foramen incisivum" of Chatterjee and Small 1989), and I also regard these as homologous to the foramina seen in *Hydrorion* and *Muraenosaurus*. However,

the v-shaped opening identified in a number of elasmosaurids as the "vomer-nasal fenestra" by Carpenter (1999, c7) is probably not, and these taxa are scored for the absence of foramina here. The presence and nature of this opening was questioned by Druckenmiller and Russell (2008a) and Ketchum and Benson (2010), and they excluded this character from their analyses. A similar v-shaped cleft occurs in *Muraenosaurus* and represents a loose contact between the anterior prong of the vomer and the premaxillae. The single midline opening between the premaxillae seen in *Pistosaurus* and *Simosaurus* (Sues 1987; Rieppel 1994a) is of uncertain homology, and these taxa are not scored for the presence of 'vomeronasal' foramina.

77. Size of 'vomeronasal' foramina: (0) small; **(1)** large, subequal to internal nares.
New character
Notes: In taxa in which a single pair of foramina occur anterior to the internal nares ('vomeronasal' foramina), they can either be small (state 0) or large (state 1). *Vinialesaurus* was interpreted as having double internal nares by Gasparini *et al.* (2002) but I interpret these openings as a naris with a large foramen anterior to it and score it as state '1' here accordingly. A similar morphology is seen in NHMUK R2864 in which the notches in the vomer for the foramina are as large as those for the nares. This character is scored as 'inapplicable' for taxa that lack a pair of 'vomeronasal' foramina anterior to the internal nares.

78. Palatine midline morphology: (0) no contact along the midline; **(1)** contact of medial palatine wings.

Previous use: K&B10 c52, S&D08 c38, D&R08 c43, S02 c47, OK01 c80.

Notes: The medial palatine wings of *Liopleurodon* were described by Noè (2001).

79. Posterior extent of the vomers: (0) extend to the internal nares; **(1)** extend posterior to the internal nares.

Previous use: V+11 c21, K&B10 c53, S&D08 c37, D&R08 c42, S02 c44, OK01 c83.

80. Pterygoid, anterior termination: (0) tapering; **(1)** transversely broad.

Previous use: modified from K&B11 c185.

Notes: Ketchum and Benson (2011) stated that taxa with large anterior interpterygoid vacuities should be scored as 'indeterminate' (?) for this character. However, in some cases it is possible to determine the width of the pterygoids and score them accordingly. For example, in *Muraenosaurus leedsii* (NHMUK R2421) the pterygoids form long narrow prongs which overlap the dorsal surface of the vomers.

81. Pterygoid-vomer contact: (0) pterygoids do not separate vomers along midline; **(1)** pterygoids separate vomers along the midline posteriorly.

Previous use: K&B10 c54, V+11 c22.

82. Suborbital fenestra bordered by ectopterygoid and maxilla: (0) absent; **(1)** present.

Previous use: K&B10 c55, S&D08 c40, D&R08 c44, S02 c45, OK01 c82.

83. Lateral palatal fenestration bordered by palatine and pterygoid: (0) absent; **(1)** present.

Previous use: K&B10 c56, S&D08 c41, D&R08 c45, OK01 c78.

84. Pterygoid, lateral ramus: (0) present, pterygoid and ectopterygoid form anterior border of subtemporal fenestra; **(1)** absent or poorly developed, ectopterygoid forms anterior border of temporal fenestra.

Previous use: modified from S02 c55, D&R08 c48, V+11 c29 and BED c68. Previous exclusion: K&B10X42.

Notes: Druckenmiller and Russell (2008a) coded this character based on the elements that formed the anterior border of the subtemporal fenestra. However, this is controlled by the development of the lateral ramus of the pterygoid. In many taxa the pterygoid is a triradiate bone, with a distinct lateral ramus which forms the anteromedial margin of the subtemporal fenestra together with the ectopterygoid (state 0). In state '1' the lateral ramus of the pterygoid is absent or rudimentary so that the anterior border of the subtemporal fenestra is formed by the ectopterygoid alone. State '1' can be seen in *Libonectes*, as Druckenmiller and Russell observed, and also in *Muraenosaurus leedsii* (contra Andrews 1910), *Cryptoclidus eurymerus* (Brown and Cruickshank 1994, fig. 4) and *Tricleidus seeleyi* (Andrews 1910). This character was excluded by Ketchum and Benson (2010,X42) on the basis that it was parsimony uninformative, state '1' only being recorded for *Libonectes*.

85. Jugal contributes to the palatal surface: (0) absent; **(1)** present.

Previous use: S&D08 c22, OK01 c77.

Notes: This character was excluded by Ketchum and Benson (2010, X48) as it was not observed in their study. However, Smith (2007) has described the jugal contributing to the border of the suborbital fenestra in *Rhomaleosaurus* and *Eurycleidus*, and a similar condition was shown in *Liopleurodon* by Noè (2001). This character is therefore considered valid. However, the jugal can also be exposed in ventral view, but not form part of the palatal surface as in *Peloneustes* (Ketchum, 2007). The jugal is considered to contribute to the palatal surface when it is sutured to the maxilla, pterygoid or ectopterygoid in the same plane as the palatal components of those bones.

86. Relative positions of external and internal nares: (0) internal naris posterior to external naris; **(1)** nares overlap; **(2)** internal naris anterior to external naris.

Previous use: K&B10 c57, D&R08 c46, S02 c46.

87. Ectopterygoid/pterygoid boss: (0) absent; **(1)** present.

Previous use: K&B10 c58, D&R08 c47; modified from S02 c57, OK01 c84.

88. Anterior interpterygoid vacuity: (0) absent; **(1)** present; **(2)** present but filled by parasphenoid.

Previous use: modified from V+11 c23, K&B10 c59, S&D08 c39, G+03 c9, G+02 c6; modified from OK01 c60, B+99 c13.

Notes: Following Ketchum and Benson (2010), only a wide and distinct vacuity is

scored as representing state 1 for this character. I have added a new state to describe an anterior interpterygoid vacuity which has been filled by the parasphenoid as seen in *Rhomaleosaurus cramptoni* (Smith and Dyke 2008) and *Peloneustes* (Ketchum and Benson 2011b). I also interpret this as being the case in *Vinialesaurus* (pers. obs. of MNHNCu P3008). Whilst preservation is insufficient to allow precise location of sutures, the bone texture indicates that the pterygoids are separated for much, if not all, of their anterior extent, with the parasphenoid filling the triangular gap.

89. Anterior border of the anterior interpterygoid vacuity: (0) formed by pterygoids; **(1)** formed by palatines; **(2)** formed by vomers.

New character

Notes: The anterior border of the anterior interpterygoid vacuity, if present, may be formed by either the pterygoids, palatines, or vomers. The majority of taxa show state 0, while state 1 seems to be an autapomorphy of NHMUK 49202 and state 2 is seen in *Muraenosaurus* and *Cryptoclidus* (pers. obs.). In NHMUK 49202 there is possibly a diminutive contact of the vomers with the vacuity although distortion makes this uncertain. Nevertheless, the palatines form the majority of the anterior border. This character is scored as 'inapplicable' in taxa that lack an anterior interpterygoid vacuity.

90. Posterior border of anterior interpterygoid vacuity: (0) bordered by pterygoid; **(1)** bordered by parasphenoid.

Previous use: K&B10 c60, S02 48.

Notes: This character is scored as 'inapplicable' in taxa that lack an anterior

interpterygoid vacuity.

91. Morphology of the posterior border of the anterior interpterygoid vacuity: (0) concave; **(1)** parasphenoid projects into anterior interpterygoid vacuity.

Previous use: K&B10 c61.

Notes: This character is only applicable to taxa in which the parasphenoid forms the posterior border of the anterior interpterygoid vacuity, and it is scored as 'inapplicable' where the anterior interpterygoid vacuity is absent.

92. Posterior interpterygoid vacuities: (0) absent; **(1)** present.

Previous use: K&B10 c62, OK01 c61, S91 c11, modified from C99 c6, D&R08 c49.

93. Ventromedial flanges of the pterygoid: (0) present and robust, sutured to basicranium; **(1)** present but reduced, remains as a distinct process contacting basicranium; **(2)** absent.

New character

Notes: Taylor (1992) described the ventromedial flange in *Rhomaleosaurus zetlandicus* and showed it suturing to the basicranium on the dorsal surface. This contact is present in many plesiosaurs, the flange suturing to the posterior processes of the parabasisphenoid and sometimes also the basioccipital. In *Muraenosaurus* and *Tricleidus* the flange is reduced, but remains as a distinct process contacting the parasphenoid. The process is hook-shaped in *Muraenosaurus* (Maisch 1998, fig. 6) and more cylindrical in *Tricleidus* (identified as the pterygoid posterior medial processes by

O'Keefe, 2001). The ventromedial flanges are absent in *Kimmerosaurus*. This character is scored as 'inapplicable' in taxa in which the posterior interpterygoid vacuities are absent.

94. Pterygoid ventromedial flanges suture to basioccipital medial to the basioccipital tubera: (0) do not suture to basioccipital; **(1)** suture to basioccipital.

New character

Notes: In many taxa the ventromedial flanges of the pterygoids are sutured to the basioccipital medial to the basioccipital tubera (state 1). In most taxa in which this happens the pterygoids unite in a medial suture. However, in some taxa such as *Hauffiosaurus tomistomimus*, OUMNH J.28285 and *Thalassiodracon* the ventromedial flanges remain separate although they are sutured to the ventral surface of the basioccipital. For this reason I have coded the suturing of the ventromedial flanges to the basioccipital separately from the formation of a midline pterygoid suture. In some taxa such as *Plesiosaurus dolichodeirus* (NMING F8758) and NHMUK 49202 the ventromedial flanges are robust and sutured to the parabasisphenoid, but do not suture to the basioccipital (state 0). Taxa in which the ventromedial flanges are either reduced or absent and those without posterior interpterygoid vacuities are scored as 'inapplicable'.

95. Midline contact of pterygoid ventromedial flanges ventral to basioccipital: (0) do not meet on midline; **(1)** meet on midline.

Previous use: modified from B+99 c12, C99 c3, OK01 c62, S02 c50, G07 c19, S&D08

c44, D&R08 c50, K&B10 c63, V+11 c27.

Notes: Taxa in which the ventromedial flanges are either reduced or absent and those that lack posterior interpterygoid vacuities are scored as 'inapplicable'.

96. Anterior extent of midline contact of pterygoid ventromedial flanges: (0) incomplete, basioccipital exposed anteriorly; **(1)** basioccipital covered anteriorly.

New character

Notes: In taxa in which the ventromedial flanges of the pterygoids meet, fusion can either be incomplete anteriorly, exposing the basioccipital on the midline, (state 0) or complete anteriorly, with no exposure of the basioccipital (state 1). *'Rhomaleosaurus' megacephalus* shows state '0' and *Meyerasaurus* shows state '1'. This character is scored as 'inapplicable' in taxa in which there is no midline contact of the pterygoid ventromedial flanges, those in which the relevant area is covered by other structures or those in which the flanges are reduced or absent.

97. Pterygoid ventrolateral flanges: (0) blunt; **(1)** projecting.

New character

Notes: Taylor (1992) described the posterior ramus of the pterygoid in *Rhomaleosaurus zetlandicus*, and identified dorsal, ventromedial and ventrolateral flanges. These structures result in the posterior ramus being triangular in transverse section, and the terminology can be applied to plesiosaurs in general. The ventrolateral flanges (or edges) of the posterior rami of the pterygoids can either be bluntly angled (state 0) or be elaborated into laterally or ventrolaterally projecting structures (state 1). NHMUK

49202 shows state '0', while different morphologies of state '1' can be seen in *Liopleurodon*, *Rhomaleosaurus*, and *Microcleidus*. The different structures that a projecting ventrolateral flange can form are dealt with in the following characters.

98. Pterygoid ventrolateral flanges form posterior squared lappets ventral to origin of quadrate rami: (0) absent; **(1)** present.

Previous use: modified from K&B10 c66, S&D08 c46, D&R08 c57, OK01 c58.

Notes: this character is scored as 'inapplicable' in taxa in which the ventrolateral flanges are blunt.

99. Pterygoid ventrolateral flanges form lateral shelves: (0) absent; **(1)** present.

New character

Notes: In *Thalassiodracon* (CAMSM J.46986; Benson *et al.* 2011), OUMNH J.10337, *Hauffiosaurus tomistomimus* (MANCH LL 8004) and LEICT G1.2002 the ventrolateral flanges project as discrete 'lateral shelves'. These are situated anterior to the typical position of squared lappets and end posteriorly in a distinct corner. LEICT G1.2002 possesses both lateral shelves and squared lappets, showing the two to be separate structures. In the absence of this combination, lateral shelves could be interpreted as anteriorly placed squared lappets. A lateral shelf also seems to be preserved on the left pterygoid in *Umoonasaurus* (Kear *et al.* 2006, fig. 1e). This character is scored as 'inapplicable' in taxa in which the ventrolateral flanges are blunt.

100. Pterygoid ventrolateral flanges curve medially ventral to basioccipital: (0)

flanges do not curve medially; **(1)** flanges curve medially.

Previous use: modified from OK01 c69, S02 c54, S&D08 c45, D&R08 c51, K&B10 c64.

Notes: In derived pliosaurids and microcleidids the ventrolateral flanges curve medially across the ventral surface of the posterior rami of the pterygoids and may contact one another. The degree of curvature and contact varies, and is coded for in the following character. This character is scored as 'inapplicable' in taxa in which the ventrolateral flanges are blunt.

101. Extent of curvature and medial contact of pterygoid ventrolateral flanges: (0) curve medially becoming parallel to midline but do not meet; **(1)** curve to midline and meet in short contact; **(2)** curve to midline and meet in long contact.

Previous use: modified from OK01 c69.

Notes: State '0' is seen in *Simolestes* and *Microcleidus*, state '1' is seen in *Peloneustes* and state '2' is seen in *Liopleurodon*. This character is scored as 'inapplicable' in taxa in which the pterygoid ventrolateral flanges do not curve medially across the ventral surface of the posterior rami.

102. Posterior extent of ventrolateral flanges of the pterygoids: (0) end ventral to origin of quadrate rami; **(1)** end anterior to origin of quadrate rami; **(2)** extend posteriorly along quadrate rami.

New character

Notes: In most plesiosaurs the pterygoid ventrolateral flanges end level with the origin

of the quadrate rami (state 0). However, in *Hauffiosaurus* (MANCH LL 8004),

Peloneustes (Ketchum 2007, Plate 2.11), and *Simolestes* (Noè 2001, Fig. 154) they end

anterior to this, so that the lateral surfaces of the quadrate rami are continuous with the

ventral surfaces of the ventromedial flanges (state 1). In NHMUK 49202 the

ventrolateral flanges continue posteriorly onto the quadrate rami (state 2). This character

applies to the ventrolateral flange irrespective of whether it is blunt or projecting.

103. Ventral surface of the posterior ramus of the pterygoid lateral to the posterior interpterygoid vacuities: (0) flat; **(1)** concave laterally ; **(2)** concave laterally and medially, forming trough; **(3)** dished.

Previous use: modified from OK01 c67, S02 c53, D&R08 c56, K&B10 c65.

Notes: In addition to those states previously recognised for this character, the pterygoids may be concave laterally but not medially as was shown by Taylor (1992) in *Rhomaleosaurus zetlandicus*. This character is scored as 'inapplicable' in taxa in which the ventrolateral flanges of the pterygoid curve medially.

104. Shape of the pterygoid-quadrate connection: (0) untwisted; **(1)** twists laterally; **(2)** twists medially.

Previous use: modified from OK01 c57 partim.

Notes: The contour of the pterygoid-quadrate connection in ventral view has previously been characterised as either curved or straight (Ketchum and Benson 2010, c67; Druckenmiller and Russell 2008a, c58; Sato 2002, c60). However, differences in curvature of this structure can be subtle and subject to modification from distortion. I

have found it very difficult to confidently distinguish straight and curved morphologies, and for this reason exclude these states. O'Keefe (2001, c57) included an extra state, "sigmoid with rolled lateral margin", which other authors were unable to confidently identify. However, I believe it is present in *Rhomaleosaurus* and *Eurycleidus* (sensu Smith 2007). The sigmoid shape is due to a lateral twist to the pterygoid-quadrate connection, so that the lateral surface 'rolls' dorsally along its length, as O'Keefe (2001) observed. A sigmoid connection is also seen in *Libonectes* (eg Druckenmiller 2006, fig. 4.16), but here it is the medial surface which rotates dorsally as the connection is twisted medially. I therefore code the shape of the pterygoid-quadrate connection as untwisted as in most plesiosaurs (state 0), laterally twisted as in *Rhomaleosaurus* (state 1), or medially twisted as in *Libonectes* (state 2). This character is scored as 'inapplicable' in basal taxa possessing a massive quadrate.

105. Pterygoid-quadrate connection in ventral view: (0) longitudinally ridged; **(1)** transversely convex.

Previous use: modified from OK01 c57 partim, K&B10 c67 partim, D&R08 c58 partim, S02 c60 partim.

Notes: the presence of a ridged or angled lateral margin has been previously combined with a character describing the shape of the pterygoid-quadrate connection in ventral view (see previous character). As noted above the curved and straight morphologies of previous authors are difficult to differentiate. However, as the untwisted morphology described above can be transversely convex or bear a longitudinal ridge I have coded this as a separate character. The ridged morphology (state 0) is shown by OUMNH J.10337 and also pliosaurids such as *Peloneustes* and *Liopleurodon*. In the latter the

ridge runs along the lateral edge, resulting in the "raised lateral margin" noted by O'Keefe (2001) and Ketchum (2007). LEICT G1.2002 and *Muraenosaurus* show state 1, in which the pterygoid-quadrate connection is transversely convex. This character is scored as 'inapplicable' for taxa in which the pterygoid-quadrate connection is twisted.

106. Relative length of pterygoid-quadrate connection: (0) long; **(1)** short.

New character

Notes: In most plesiosaurs the pterygoid-quadrate connection is relatively elongate, being much longer than broad (state 0). However, in *Edgarosaurus*, *Dolichorhynchops*, *Trinacromerum* (Druckenmiller 2002; O'Keefe 2004a), *Muraenosaurus* and *Cryptoclidus* it is a relatively short structure (state 1).

107. Orientation of the quadrate ramus of the pterygoid: (0) approximately vertical; **(1)** inclined laterally.

New character

Notes: In taxa in which the pterygoid-quadrate connection is untwisted, the pterygoid quadrate rami may be either subvertical, or inclined laterally. In the latter, the lateral surface of the rami can be seen projecting laterally of the ventral surface in ventral view. Most taxa have subvertical quadrate rami, while the inclined state is seen in LEICT G1.2002 and *Leptocleidus superstes*. This character is scored as 'inapplicable' in taxa in which the pterygoid-quadrate connection is twisted.

108. Anterior transverse shelf on pterygoid quadrate ramus: (0) present; **(1)** absent.

New character

Notes: In some taxa a medial shelf is developed at the anterior end of the quadrate ramus of the pterygoid as it approaches the basicranium, so that it is approximately L-shaped in section (the "transverse shelf" of Taylor and Cruickshank 1993). This is present in basal pistosaurians such as *Augustasaurus* and *Yunguisaurus* (Rieppel *et al.* 2002; Sato *et al.* 2010) as well as *Microcleidus* and pliosaurids such as *Peloneustes*, *Simolestes* and *Liopleurodon* (Ketchum 2007; Noè 2001). It is also present in LEICT G1.2002 and *Hauffiosaurus tomistomimus*. In other taxa such as *Plesiosaurus dolichodeirus* (NMING F8758), *Muraenosaurus*, *Libonectes* and *Dolichorhynchops* the quadrate ramus lacks a medial shelf.

Braincase

109. Cultriform process of parasphenoid, ventral surface anteriorly: (0) covered by pterygoids anterior to the posterior interpterygoid vacuities; **(1)** visible through V-shaped notch in posterior pterygoid contact anterior to posterior interpterygoid vacuities.

Previous use: BED c65, V+11 c24 partim.

Notes: Vincent *et al.* (2011, c24) also coded for the length and width of the parasphenoid's anterior exposure, but this is not independent of the bone's participation in the anterior interpterygoid vacuity. This character is scored as 'inapplicable' in taxa that lack a posterior interpterygoid vacuity.

110. Cultriform process of parasphenoid, ventral surface within posterior

interpterygoid vacuity: (0) transversely narrow longitudinal keel; **(1)** convex, lacking keel; **(2)** flat; **(3)** weakly concave.

Previous use: modified from K&B11 c68, V+11 c25, D&R08 c55, OK08 c43, S&D08 c48, OK01 c71.

Notes: This character describes the morphology of the posterior extension of the cultriform process of the parasphenoid on the ventral surface of the parabasisphenoid. Ketchum (2007) regarded the structures coded for here as representing the entire posterior extent of the parasphenoid. However, I regard much of the ventral surface of the parabasisphenoid as being composed of the parasphenoid in most taxa, largely following O'Keefe's interpretation (O'Keefe 2001). This character is scored as 'inapplicable' where the pterygoids cover the basicranium as in *Simosaurus*.

111. Posterior extent of parasphenoid cultriform process: (0) short, limited to anterior third of posterior interpterygoid vacuity; **(1)** long, extends beyond anterior third of posterior interpterygoid vacuity.

Previous use: modified from D&R08 c54; K&B11 c69, B+11a c4, V+11 c28.

112. Posterior termination of parasphenoid cultriform process: (0) within posterior interpterygoid vacuity; **(1)** extends the entire length of posterior interpterygoid vacuity or more.

New character

Notes: In taxa in which the posterior extension of the parasphenoid cultriform process is long, it can end within the posterior interpterygoid vacuity as in *Microcleidus*

homalospondylus (NHMUK 36184; state 0) or extend the full length of the vacuity or more as in *Dolichorhynchops osborni* (O'Keefe 2004a; state 1). This character is scored as 'inapplicable' in taxa in which the posterior extension of the cultriform process is short and ends in the anterior third of the posterior interpterygoid vacuity.

113. Parasphenoid width ventrolaterally: (0) widens; **(1)** narrow.

Previous use: modified from OK01 c73.

Notes: The posterior ventrolateral part of the parabasisphenoid (formed by the parasphenoid) may widen posteriorly into either paired processes with an embayment or fontanelle between them as in *Thalassiodracon*, or a broad fan as in *Liopleurodon* (Storrs and Taylor 1996; Noè 2001). The presence or absence of a fontanelle is dealt with in a following character. Alternatively the posterior of the parabasisphenoid may be narrow as in *Muraenosaurus leedsii* (NHMUK R2421). In some specimens of *Muraenosaurus* the parabasisphenoid is fused to the basioccipital; however, this connection is regarded as being formed by the endochondral (basisphenoid) part of the parabasisphenoid due to a change in bone texture. This character is effectively equivalent to the cristae ventrolaterales of O'Keefe (2001, c73).

114. Parabasisphenoid contribution to the articulation surface of the basioccipital tubera for contact with the pterygoids: (0) contributes; **(1)** does not contribute.

Previous use: modified from K&B10 c71. Previous exclusion: D&R08 X159.

Notes: Ketchum and Benson (2010, c71) characterised the contribution of the basisphenoid to the basal tubera. However, the composition of the anterior portion of

the basicranium is controversial with differing interpretations (e.g. for *Thalassiodracon* see Storrs and Taylor 1996; O'Keefe 2001; Ketchum and Benson 2010). Although I consider that it is the parasphenoid which contributes to the basal tubera in all specimens where this contact is seen, I refer to this element as the conjoined parabasisphenoid. Identification of this character is therefore independent of a particular interpretation of the composition of the basicranium. State '0' is seen in taxa such as *Thalassiodracon*, LEICT G1.2002 and *Liopleurodon*, while state '1' is seen in taxa such as *Muraenosaurus* and *Tricleidus*.

115. Embayment or notch in posterior margin of parasphenoid: (0) present; **(1)** absent.

Previous use: modified from OK01 c73 partim.

Notes: The posterior margin of the parasphenoid portion of the parabasisphenoid can be marked with an embayment or notch. In some taxa such as *Thalassiodracon*, OUMNH J.10337 or LEICT G1.2002 the embayment is filled with an anterior process of the basioccipital. O'Keefe (2001) considered this process to be formed by the basisphenoid. In other taxa such as *Muraenosaurus* a notch is present even though the parasphenoid does not contact the basioccipital (NHMUK 2421). There is no notch or embayment in *Dolychorhynchops osborni* (O'Keefe 2004a). This character is scored as 'unknown' where the connection between the parabasisphenoid and basioccipital is covered by the pterygoids. It is scored as 'inapplicable' in taxa in which the whole basicranium is covered by the pterygoids.

116. Posterior contact of ventral (parasphenoid) flange of parabasispenoid and basioccipital: (0) contact; **(1)** no contact.

Previous use: modified from D&R08 c54, K&B10 c69.

Notes: In my interpretation of the plesiosaur basicranium the parasphenoid, forming the ventral portion of the parabasisphenoid, usually contacts the basioccipital, completely sheathing the endochondral basisphenoid ventrally (state 0). However, in *Muraenosaurus leedsii* (NHMUK R2421) and similar taxa (LEICT G18.1996; NHMUK R2678) the parasphenoid is shorter, exposing the basisphenoid anterior to the basioccipital (state1).

117. Parabasisphenoid-basioccipital connection in ventral view: (0) fontanelle absent; **(1)** fontanelle present.

Previous use: modified from K&B10 c70.

Notes: This character originally described a fontanelle at the junction of the basisphenoid and parasphenoid. As I consider that this can be present where the parasphenoid covers the basisphenoid I refer to the presence or absence of a fontanelle in the parabasisphenoid-basioccipital connection. This character is scored as 'unknown' where the connection between the parabasisphenoid and basioccipital is covered by the pterygoids. It is scored as 'inapplicable' in taxa in which the whole basicranium is covered by the pterygoids.

118. Deep notch in the posterior margin of the body of the basisphenoid in dorsal view: (0) absent; **(1)** present.

Previous use: OK04bc169, D&R08 c74, K&B10 c85.

Notes: The posterior border of the basisphenoid (referred to as the 'clivus' by O'Keefe, 2004b) may be interrupted by a vertical notch or groove. This would seem to be the dorsal expression of the ventral fontanelle noted above, and developmentally the cleft may represent the gap between the two trabeculae. However, the dorsal and ventral expression of this feature would seem to be independent, and so it is coded as two separate characters. As it is likely that this character is under ontogenetic control it should only be scored as present in taxa represented by adult material. It is scored as uncertain where the basisphenoid is too poorly ossified to confidently assess its absence or presence.

119. Squamosal contribution to pterygoid-quadrate connection: (0) absent; **(1)** present.

Previous use: OK01 c50, D&R08 c59, K&B10 c72, V+11 c30.

120. Epipterygoid shape in lateral view: (0) plate-like with parallel sides; **(1)** triangular; **(2)** narrow and rod-like; **(3)** reduced 'nubbin' but part of basipterygoid articulation (new state).

Previous use: modified from OK01 c52, S02 c63, D&R08 c60, K&B10 c73.

Notes: A new state describes the small reduced epipterygoid seen in *Muraenosaurus platyclis* (NHMUK R.2678) and some other cryptoclidids. The bone is a small nubbin nestling up to the medial side of a longitudinal ridge on the dorsal surface of the pterygoid. Despite its small size, the epipterygoid makes the major palatoquadrate

contribution to the basicranial articulation. This morphology may be more widely distributed especially in taxa with reduced columella cranii, as identifying it requires well preserved but disarticulated material.

121. Distinct notch or facet in suspensorium for articulation of the paroccipital process: (0) absent; **(1)** present.

Previous use: modified from OK01 c45, S02 c65, D&R08 c62, K&B10 c75.

Notes: Previous authors have coded this character for the presence or absence of a notch in the suspensorium for the distal end of the paroccipital process. I have widened this to include a distinct facet. I follow Druckenmiller (2006) in not regarding the roughened area seen in *Liopleurodon* and *Simolestes* as a notch or facet. This character is scored as 'inapplicable' in taxa which lack an open occiput with a paroccipital process.

122. Ventral basioccipital process/plate: (0) absent or weakly developed; **(1)** ventral process present; **(2)** ventral plate present.

Previous use: modified from K&B10 c80, S&D08 c51, D&R08 c70 and S02 c81.

Notes: This character refers to a process or plate of the basioccipital which projects ventrally between the basioccipital tubera. This has the effect of rendering the posteriormost point on the palatal surface ventral to the lowermost point of the edge of the occipital condyle (Druckenmiller, 2006). Ketchum and Benson (2010) separated the variation in process morphology into two states; a small, rounded rugose ventral process or a wide, flat, relatively smooth, plate. I have scored taxa as possessing a distinct process when a medial ventral projection of the basioccipital is demarcated from the

basal tubera by paired lateral troughs. Taxa are scored for the presence of a ventral plate when the ventral projection of the basioccipital is confluent with the basal tubera. Thus LEICT G1.2002 and TTNCM 9291 are scored for the presence of a ventral process, although these are larger than that of *Liopleurodon* or *Peloneustes*. Several taxa which show a transverse "step" on the ventral of the basioccipital are scored for the presence of a ventral plate including *Thalassiodracon*, and OUMNH J.28585. These taxa have previously been scored for the absence of a ventral plate or process (Ketchum and Benson 2011a; 2010).

123. Ventral basioccipital ridge: (0) absent; **(1)** present.

New character

Notes: In some taxa which lack a ventral basioccipital process or plate the ventral surface of the basioccipital is ornamented by a low, narrow ridge. This was described in NHMUK R2439 by Ketchum (2007), and is also present in NHMUK R2678 and NHMUK R2861 which were both referred to *Muraenosaurus leedsii* by Brown (1981). It is absent in NHMUK R2421, the holotype of *M. leedsii*. This character is scored as 'inapplicable' in taxa in which a ventral basioccipital process or plate is present, and also those in which the ventral surface of the basioccipital is covered by the pterygoids.

124. Shape of foramen magnum: (0) oval; **(1)** key-hole-shaped.

Previous use: S02 c82, D&R08 c67, K&B10 c78.

125. Occipital condyle constriction: (0) complete; **(1)** incomplete; **(2)** absent.

Previous use: D&R08 c69, S02 c78, modified from B81 c12, OK01 c43, K&B10 c79, V+11 c33.

126. Occipital condyle neck: (0) absent; **(1)** present.

New character

Notes: The basioccipital may be ventrally excavated just anterior to the occipital condyle, forming an occipital condyle neck sensu Noè (2001). For this character to be scored as present, there needs to be a significant excavation in addition to the occipital condyle constriction. For example, in *Thalassiodracon* the condyle is marked off from the rest of the basioccipital by a ridge and constriction, but this is no more developed ventrally than laterally. This character is scored as 'inapplicable' in taxa in which an occipital condyle constriction is absent.

127. Occipital condyle shape: (0) subcircular; **(1)** truncated dorsolaterally.

New character

Notes: In posterior view the occipital condyle can be sub-circular, or can be truncated dorsolaterally. While it could be argued that this is connected with the participation or otherwise of the otooccipital in the condyle and the relative completeness of a condylar constriction, it would appear that they are separate characters. For example, Smith (2007) reported that the condyle of NMING F8749 (referred to *Eurycleidus sp.*) is formed by the basioccipital. However, the accompanying figure (Fig. 4.39) shows that the condyle is truncated dorsolaterally which would initially suggest that the otooccipital participated in the condyle. However, my own observations of this material

confirms Smith's conclusion in that the otooccipital facets are separated from the condyle by a narrow ridge and groove. This character may be equivalent to character 34 (occipital condyle shape in occipital view) of Vincent *et al.* (2011).

128. Notochordal pit on occipital condyle: (0) absent; **(1)** present.

Previous use: S02 c79, D&R08 c66, K&B10 c81, V+11 c32.

129. Paroccipital process posterior contact: (0) squamosal only; **(1)** quadrate only; **(2)** both squamosal and quadrate.

Previous use: OK01 c47, S02 c66, D&R08 c63, K&B10 c74.

Notes: This character is scored as 'inapplicable' in taxa which lack an open occiput with a paroccipital process. .

130. Paroccipital process contact with the posterior ramus of the pterygoid: (0) absent; **(1)** present.

Previous use: K&B10 c76, modified from D&R08 c64 and OK01 c49.

Notes: The scores for this character in the matrices of Ketchum and Benson (2010; 2011a) appear to have become transposed, as it was scored as present in *Cryptoclidus* and absent in *Peloneustes*.

131. Paroccipital process proportions: (0) long and slender; **(1)** short and slender; **(2)** short and robust.

Previous use: D&R08 c61, modified from OK&W03 c24, S02 c64 and OK01 c46.

Previous exclusion: K&B10 X51.

Notes: Ketchum and Benson (2010) excluded this character citing a lack of objectivity and non-independence from skull width. However, the paroccipital process can be directed almost laterally as in *Kimmerosaurus* (Brown, 1981: Fig. 30), or more ventrally as in *Liopleurodon* (Noè 2001: Fig. 5). Therefore it would be possible for two taxa with the same skull width to possess paroccipital processes of different proportions if they were oriented differently, and I consequently accept this character as valid. Druckenmiller (2006) admitted that scoring of this character was subjective and suggested recoding it as a qualitative character. This character is scored as 'inapplicable' in taxa which lack an open occiput with a paroccipital process.

132. Paroccipital process distal morphology: (0) spatulate, distal end not expanded into distinct robust head; **(1)** distal end developed into distinct robust head; **(2)** distal end narrow and rod-like.

New character

Notes: The distal end of the paroccipital process may be expanded into a distinct and massive head with angled facets for articulation with the suspensorium as illustrated by Brown (1981) in *Cryptoclidus*, *Tricleidus* and *Kimmerosaurus* (state 1). In taxa without a distinct head, the process may either expand gradually along its whole length as in a specimen referred to *Liopleurodon* (Noè *et al.* 2003) resulting in a spatulate morphology (state 0), or end bluntly with little expansion as in *Dolichorhynchops osborni* (state 2; Williston 1903). In taxa with a distinct faceted head, the paroccipital process articulates with the suspensorium via a butt joint, while in taxa with a spatulate end it overlaps the

suspensorium posteromedially (e.g. *Microcleidus homalospondylus*, NHMUK 36184). This character is scored as 'inapplicable' in taxa which lack an open occiput with a paroccipital process.

133. Ventral extent of paroccipital process: (0) does not extend ventral to the ventral margin of the occipital condyle; **(1)** extends ventral to the occipital condyle.

Previous use: OK01 c48, D&R08 c65, K&B10 c77, modified from S02 c67, G07 c22, OK&W03 c26.

134. Otooccipital, foramina in lateral surface: (0) one; **(1)** two or more.

Previous use: K&B11 c183.

Notes: The single foramen noted by Ketchum and Benson (2011a) in the lateral surface of the exoccipital is that identified in this work as the common otooccipital foramen.

135. Lip on posterior of otooccipital pedicel: (0) absent; **(1)** present.

New character

Notes: Previous authors have used a character describing a contribution of the otooccipitals to the occipital condyle (Druckenmiller and Russell 2008a, c68; Sato 2002, c77; O'Keefe 2001a, c42; Bardet *et al.* 1999, c14; Rieppel 1994b c28; Brown, 1981:c12). While this undoubtedly occurs in *Cryptoclidus* (Brown, 1981), the distribution of this is uncertain in some other taxa. For example, Druckenmiller and Russell (2008a) coded this character as variable in *Plesiosaurus* and *Peloneustes*, and Ketchum (2007) observed variation in *Kimmerosaurus*. I prefer to code for the presence

or absence of a distinct morphological feature, a distinct lip on the ventral edge of the posterior surface of the otooccipital pedicel, rather than the more subjective recognition of an otooccipital contribution to the occipital condyle. This lip may have functioned as a 'stop' limiting movement of the condyle in the cotyle of the atlas, as appears to be the case in LEICT G1.2002.

136. Stapes fused to opisthotic: (0) not fused; **(1)** fused.

New character

Notes: Storrs and Taylor (1996) described the head of the stapes in *Thalssiodracon* as being fused to the anterolateral margin of the opisthotic where the latter forms the posterior margin of the fenestra ovalis. This morphology is also present in OUMNH J.10337, but is absent in other plesiosaurs where this area can be observed.

137. Exoccipital flange lateral to foramen magnum: (0) absent; **(1)** present.

New character

Notes: Andrews (1913) described a "facet like a zygapophysis" on the exoccipital lateral to the foramen magnum of *Peloneustes*. This was also noted as a "sharp horizontal shelf" by Ketchum and Benson (2011b). The same feature was identified as an "atlas-axis articulating facet" in the otooccipital referred to *Liopleurodon* by Noè *et al.* (2003) and is referred to in this work as the 'exoccipital flange' as its function is unclear. This is present in a number of additional taxa such as LEICT G1.2002, *Thalassiodracon* (Benson *et al.* 2011a, fig. 4), and *Leptocleidus superstes*. To be scored for the presence of this feature there must be a marked ridge or flange on the posterior

surface of the exoccipital which diverges laterally from the border of the foramen magnum. For example in OUMNH J.10337 the dorsal part of the exoccipital is ridged. However, as this ridge forms part of the edge of the foramen magnum and does not diverge laterally, the exoccipital flange is scored as absent. The "angular cavity" adjacent to the exoccipital-supraoccipital suture noted by Williston (1903) and Sato (2005) in species of *Dolichorhynchops* is not considered homologous to the exoccipital flange.

138. Otooccipital enclosure of semicircular canals: (0) fully enclosed; **(1)** partially enclosed.

New character

Notes: Where elements of the otic capsule are sufficiently well preserved the semicircular canals may be fully enclosed by bone, forming discrete foramina in the sutural surfaces, or only partially enclosed, forming broad notches in the sutural surfaces (state 0). Cases in which a foramen is almost enclosed are scored as if fully enclosed. This character codes for the state of the semicircular canals in the opisthotic. For example in NHMUK R2861, referred to *Muraenosaurus leedsii* by Brown (1981) but referred to *M. durobrivensis* by Andrews (1910, fig. 45) the semicircular canals are completely enclosed by the opisthotic (state 0). In NHMUK R2421, the holotype of *M. leedsii*, the canals are partially enclosed (state 1), as is also the case in NHMUK R2678 (nominal holotype of *M. platyclis* Seeley, 1892). As there is likely to be some ontogenetic control of the enclosure of the canals, their partial enclosure should only be scored from adult material.

139. Supraoccipital enclosure of semicircular canals: (0) fully enclosed; **(1)** partially enclosed.

New character

Notes: Where elements of the otic capsule are sufficiently well preserved the semicircular canals may be fully enclosed by bone, forming discrete foramina in the sutural surfaces, or only partially enclosed, forming broad notches in the sutural surfaces (state 0). Cases in which a foramen is almost enclosed are scored as if fully enclosed. This character codes for the state of the semicircular canals in the supraoccipital. For example in *Thalssiodracon* (CAMSM J.46986; Storrs and Taylor 1996; Benson *et al.* 2011a) the otooccipital and supraoccipital are pierced by foramina for the posterior vertical semicircular canal, while the latter also shows foramina for the anterior vertical canal and the common crus (state 0). In OUMNH J.10337, previously referred to *Thalassiodracon* by Storrs and Taylor (1996) but treated as a separate OTU by Ketchum and Benson (2010; 2011b), the foramina in the supraoccipital are confluent with one another (state 1). As there is likely to be some ontogenetic control of the enclosure of the canals, their partial enclosure should only be scored from adult material.

140. Supraoccipital morphology in lateral view: (0) wider than tall; **(1)** taller than wide.

Previous use: OK01 c59, S02 c70, D&R08 c71, K&B10 c82.

141. Posteromedian ridge of supraoccipital: (0) present; **(1)** absent.

Previous use: S02 c68, D&R08 c72 partim, K&B10 c83.

142. Posteromedian process of supraoccipital: (0) present; **(1)** absent.

Previous use: OK01 c56, S02 c69, D&R08 c72 partim, K&B10 c84.

Mandible

143. Shape of the mandible: (0) bowed; **(1)** not significantly bowed; **(2)** not significantly bowed but retroarticular process posteromedially inflected.

Previous use: modified from S02 c85, S&D08 c60, D&R08 c75, K&B10 c86, V+11 c35 and BED c95.

Notes: See Druckenmiller and Russell (2008, c75) for a description of how to distinguish whether a mandible is significantly bowed or not. The mandibles of *Augustasaurus* and *Yunguisaurus* are not significantly bowed but the retroarticular process is inflected posteromedially, the point of inflection being ventral to the glenoid (state 2; Benson *et al.* 2012, c 95). Taxa with bowed mandibles also invariably have medially inflected retroarticular processes (e.g. *'Rhomaleosaurus' megacephalus*).

144. Splenial participation in mandibular symphysis: (0) does not participate; **(1)** participates.

Previous use: S&D08 c59, K&B10 c87, V+11 c37; modified from OK01 c90, S02 c88, A+07 c9 and D&R08 c76.

145. Angular participation in mandibular symphysis: (0) does not participate; **(1)** participates.

Previous use: K&B10 c88; modified from OK01 c90, S02 c89, A+07 c9, and D&R08 c77.

146. Coronoid participation in mandibular symphysis: (0) does not participate; **(1)** participates.

Previous use: modified from OK01 c94, A+07 c10 and K&B10 c89.

Notes: This character is only applicable in taxa which possess a coronoid with a long lingual process.

147. Coronoid: (0) short, extending less than half mandibular length; **(1)** long, approaching or participating in symphysis; **(2)** small, superficial element that is often disarticulated and thus not preserved, but represented by an articular fact on the surangular.

Previous use: BED c90; modified from D&R08 c84, K&B10 c90, S02 c93 and OK01 c93.

148. Mandibular symphysis construction: (0) one alveolus; **(1)** two alveoli; **(2)** more than two alveoli.

New character

Notes: This character describes the structure of the dentary symphysis in terms of the dental alveoli involved in its construction. The symphysis includes one or more pairs of alveoli the medial borders of which participate in the fusion of the two dentaries. To score this character, a line is projected between the centres of the primary and secondary alveoli of each tooth position in the symphyseal region. These lines are then projected posteriorly so that they either intercept on the midline or exit the dentary in the same plane as the toothrow. A tooth position is judged to be involved in the construction of the symphysis if the projected line either intercepts its opposite on the midline within the symphysis or exits the dentary immediately adjacent to it. While some traditional plesiosauroids (e.g. *Muraenosaurus leedsii*) have a single pair of alveoli fused into the symphysis, other such as *Microcleidus homalospondylus* have 2, as do some traditional pliosauroids such as *Rhomaleosaurus thorntoni* and *Eurycleidus arcuatus*. Most traditional pliosauroids have 4 or more (*Liopleurodon ferox* has 6, *Peloneustes philarchus* has 10). To be able to score this character the dentary symphysis needs to be visible in dorsal view except in cases where the symphysis is obviously elongate, slender and includes many alveoli such as *Manemergus* (Buchy *et al.* 2005).

149. Dentary, subhorizontal dorsomedial symphyseal shelf: (0) shelf absent, 'posteromedial gully' present; **(1)** shelf present, no 'posteromedial gully'.

New character

Notes: In most plesiosaurs the dentaries form a subhorizontal shelf in the posterior part of the dentary symphysis (state 1). This was referred to as the "dentary raised triangle" by Noè (2001). However, some plesiosaurs such as *Rhomaleosaurus thorntoni* and *Eurycleidus arcuatus* lack a dorsomedial shelf, and the posterior part of the symphysis

is grooved and slopes ventrally (Cruickshank 1996, fig 3). This sloping groove was referred to as the "postero-dorsal gully" by Smith (2007) in a specimen of *Eurycleidus sp*. This is seen in dentaries referred to *Cymatosaurus* (Rieppel 1994a, Fig. 44). In *Simosaurus* the dentaries form a narrow shelf which slopes posteroventrally (Rieppel 1994a, Fig. 3), and this taxon is therefore scored as state '0'.

150. Dentary, posteromedially oriented grooves on dorsal surface: (0) at same level (symmetrical); **(1)** offset (asymmetrical).

Previous use: K&B11 c186.

Notes: The posteromedially oriented grooves noted on the dorsal surface of the dentary symphysis in some longirostrine plesiosaurians by Ketchum and Benson (2011a) are actually present in most, if not all, plesiosaurians. They appear to be absent in *Simosaurus* and *Cymatosaurus* (Rieppel 1994a, figs 3 and 44).

151. Shape of the mandibular symphysis in dorsal view: (0) tapers anteriorly; **(1)** laterally expanded.

Previous use: D&R08 c78, S&D08 c56, K&B10 c91.

Notes: In some taxa with a laterally expanded mandible the expansion is actually posterior to the symphysis.

152. Structure of the dentary along the ventral surface of the mandibular symphysis: (0) no ventral elaboration; **(1)** forms raised ventral platform adjacent to symphysis; **(2)** forms raised ridge adjacent and posterior to the symphysis.

Previous use: K&B10 c92; modified from OK01 c88, S&D08 c57, D&R08 c80 and V+11 c38.

153. Dentary, symphysis forms sub-vertical 'chin': (0) absent; **(1)** present.

New character

Notes: In *Kaiwhekea* and *Aristonectes* the anteroventral surface of the dentary symphysis is subvertical forming a 'chin' (Cruickshank and Fordyce 2002; Gasparini et al, 2003). In other taxa the anteroventral surface of the symphysis slopes posteroventrally.

154. Position of the mandibular glenoid fossa: (0) posterior to the occipital condyle; **(1)** coplanar with the occipital condyle.

Previous use: S02 c90, D&R08 c81, K&B10 c93.

155. Position of tooth row in lateral view: (0) level with the mandibular glenoid fossa; **(1)** considerably higher than the glenoid fossa.

Previous use: OK01 c98, S02 c91, G+03 c11, D&R08 c82, K&B10 c94, V+11 c41.

156. Mandible, prominent longitudinal trough occupies posterior half of lateral surface: (0) absent; **(1)** present.

Previous use: B+11b c180.

157. Coronoid exposure on lateral surface of lower jaw: (0) not exposed; **(1)** exposed dorsal to the dentary at the coronoid eminence.

Previous use: K&B10 c96; modified from OK01 c95.

Notes: The coronoid is exposed laterally in NHMUK R.2678. It was misidentified as the splenial by Andrews (1910).

158. Mandible, contributions to the lateral surface at the coronoid eminence: (0) mainly surangular; **(1)** mainly dentary.

Previous use: V+11 c40.

159. Longitudinal medial crest of the mandible: (0) present and well developed; **(1)** present and weakly developed; **(2)** absent.

Previous use: OK01 c97, S02 c98, D&R08 c86, K&B10 c97.

160. Surangular, dorsal/dorsomedial fossa and longitudinal crest on medial surface anterior to glenoid: (0) prominent longitudinal crest forms ventral margin of deep, dorsomedially facing surangular fossa; **(1)** prominent longitudinal crest forms medial margin of mediolaterally expanded dorsal surface of surangular bearing shallow, dorsally facing fossa; **(2)** crest and surangular fossa weak or absent, dorsal portion of surangular 'blade-like' .

Previous use: BED c99; modified from D&R08 c87, K&B10 c98.

161. Surangular foramen: (0) present; **(1)** absent.

Previous use: K&B10 c99.

162. Surangular foramen, lateral exposure: (0) visible in lateral view; **(1)** fully or partly obscured by overlapping dentary when mandible is articulated.

Previous use: BED c101.

Notes: This character is scored as 'inapplicable' in taxa which lack a surangular foramen.

163. Mandibular fenestra between surangular and angular: (0) absent; **(1)** present.

Previous use: K&B10 c100.

Notes: I refer to this opening as the mandibular fenestra to avoid confusion. It was originally described as an intermandibular foramen (Ketchum and Benson 2010) but this term was also used by Taylor (1992) to refer to the Meckelian foramen of *Rhomaleosaurus zetlandicus*.

164. Mandible, dorsal rim of Meckelian foramen: (0) formed by prearticular; **(1)** formed by splenial; **(2)** foramen at prearticular-splenial contact.

Previous use: BED c96.

Notes: Smith and Vincent (2010) refer to the large opening between the splenial, prearticular and angular in *Meyerasaurus* as both the "internal mandibular fenestra" and

the "lingual mandibular fenestra", while Taylor (1992) described a similar opening in *Rhomaleosaurus zetlandicus* as the intermandibular foramen. As it pierces the medial wall of the Meckelian canal it is best referred to as a Meckelian foramen (Romer 1956), and such a foramen can be identified in many taxa (e.g. *Peloneustes*; Ketchum and Benson 2011b). O'Keefe scored taxa for the presence or absence of a "lingual mandibular fenestra" (O'Keefe 2001, c91), a character which was excluded by Druckenmiller and Russell (2008a) as the relationship between various openings in the medial wall of the mandible was unclear. The presence or absence of a foramen seems to be more a result of poor preservation of the surrounding elements and so here I code for the morphology of the foramen in cases in which it can be identified.

165. Meckelian canal exposed ventral to splenial: (0) not exposed; **(1)** exposed in elongate slot-like opening.

Previous use: modified from OK01 c87, S02 c92 and D&R08 c83. Previous exclusion: K&B10X58.

Notes: Previous authors have included a character describing exposure of the Meckelian canal on the medial surface of the mandible. One of the primary causes cited for exposure of the canal has been loss of the splenial in taxa such as *Cryptoclidus*, *Kimmerosaurus* and *Muraenosaurus* (Druckenmiller and Russell 2008, c83; O'Keefe 2001, c87). However, portions of the splenial are preserved in many specimens referred to *Muraenosaurus* (e.g. NHMUK R2678, PETMG R.189), and in other specimens facets are preserved on the angular and dentary showing that the splenial extended posteriorly to approximately the level of the coronoid eminence. I therefore regard the apparent exposure of the Meckelian canal in these taxa as representing poor

preservation of the splenial and they are either scored '0' or '?' depending on whether there is sufficient evidence for a ventrally extensive splenial. In most other plesiosaurs the splenial forms the medial wall of the Meckelian canal for its entire length except for the occurrence of Meckelian foramina (e.g. *Peloneustes*, Ketchum and Benson 2011b). However, in *Libonectes* and *Terminonatator* there is an elongate slot-like opening into the canal ventral to the splenial (Sato 2003; O'Keefe 2001) with a well-defined posterior border which is positioned anterior to the coronoid eminence (state 1). This is also present in *Thalassomedon* (Sato 2002) and *Tuarangisaurus* (Carpenter 1999, Fig. 14). Ketchum and Benson (2010 X58) excluded this character as defined by previous authors citing crushing, disarticulation and loss of lingual mandibular elements. However, the morphology described by state '1' herein is distinctive and can be distinguished from an enclosed Meckelian canal given sufficient preservation.

166. Anterior margin of the adductor fossa: (0) not clearly defined; **(1)** clearly defined.
Previous use: S02 c97, D&R08 c88, K&B10 c101.

167. Mandible, rounded medial flange formed by articular and prearticular anterior to the glenoid fossa in dorsal view: (0) present; **(1)** absent; **(2)** absent but anterior part of outline of glenoid in ventral view appears 'squared-off'.
Previous use: BED c92; modified from K&B10 c102.

168. Prearticular: (0) present, integral part of mandible; **(1)** absent or superficial.

Previous use: modified from OK01 c96.

Notes: A character describing the presence or absence of the prearticular was excluded by Ketchum and Benson (2010, X60) who cited O'Keefe's (2001) observation that all plesiosaur specimens with adequate preservation possess a prearticular. However, a distinct prearticular has not been demonstrated in *Muraenosaurus*, *Cryptoclidus*, *Tricleidus* or *Kimmerosaurus* (Brown and Cruickshank 1994; pers. obs.), and it would seem to be absent as an integral element of the mandible. In these taxa it was either absent, or a small superficial bone which is easily lost. The latter is suggested by a semi-oval notch on the longitudinal medial crest of the angular in these taxa which may be the ventral border of a Meckelian foramen.

169. Posterior extent of prearticular: (0) extends to articular glenoid; **(1)** extends ventral to the articular glenoid.
Previous use: K&B10 c103.
Notes: This character is scored as 'inapplicable' in taxa in which the prearticular is either absent or superficial.

170. Prearticular, large dorsomedian trough or rugosity: (0) absent or weak; **(1)** present.
Previous use: B+ip c209.
Notes: This character is scored as 'inapplicable' in taxa in which the prearticular is either absent or superficial. I have scored this character as present in taxa which lack a dorsomedial crest but which have a trough lateral to the prearticular (e.g. *Libonectes*,

contra Benson *et al.* in press).

171. Articular, anterior process: (0) high, glenoid has well developed anteromedial rim; **(1)** low or absent, glenoid lacks anteromedial rim.

New character

Notes: In state '0' a sub-triangular process of the articular extends anterior to the glenoid, overlapping the angular dorsomedially (e.g. *Peloneustes*, Ketchum and Benson 2011b). This anterior process of the articular also forms the anteromedial rim of the glenoid. In state '1' the anterior process is effectively absent and there is no marked anteromedial rim to the glenoid (e.g. *Kimmerosaurus*, Brown 1981, Fig. 38). A low, lobate extension of the glenoid's articular surface may extend anteromedially, overlapping the angular for a short distance but there is no dorsoventrally tall triangular process. State '0' is found in most plesiosaurians. State '1' is found in *Cryptoclidus*, *Colymbosaurus*, *Kimmerosaurus*, *Muraenosaurus* and *Tricleidus*, and also seems to be present in *Plesiopterys* (Grossmann 2006, Fig 2.3P). *Simosaurus* is scored as showing state '0' as the glenoid has a well developed anteromedial rim (Rieppel 1994a, Fig. 11).

172. Articular, deep anteroposteriorly oriented notch or foramen posterior to glenoid: (0) absent; **(1)** present; **(2)** cleft absent, but dorsal surface is strongly concave mediolaterally.

Previous use: BED c102; modified from K&B10 c104.

Notes: Sato *et al.* (2011) identified a foramen posterior to the glenoid in *Yunguisaurus* as that for the chorda tympani nerve (Romer 1956).

173. Mandible, length of retroarticular process: (0) short; **(1)** long.

Previous use: BED c91.

174. Mandible, retroarticular process, dorsoventral orientation of long axis: (0) posterodorsal; **(1)** posteroventral or subhorizontal.

Previous use: BED c94.

Dentition

175. Regularity of premaxillary dentition: (0) homodont; **(1)** heterodont.

Previous use: D&R08 c89, K&B10 c105, V+11 c43; modified from C99 c10.

176. Premaxilla, relative size of mesial alveoli: (0) more than half the diameter of more distal alveoli; **(1)** single mesialmost alveolus less than half the diameter of second alveolus; **(2)** two mesial alveoli smaller than half the diameter of third alveolus.

Previous use: B+ip c202; modified from S02 c108.

Notes: Welles (1962) describes state '2' in *Callawayasaurus* ("Bogotá specimen").

177. Regularity of maxillary dentition: (0) homodont; **(1)** heterodont.

Previous use: OK01 c102, S02 c105, A+07 c3, D&R08 c90, K&B10 c106, V+11 c44; modified from C99 c9.

178. Maxilla, posterior extent of maxillary tooth row: (0) ventral to postorbital bar; **(1)** ventral to temporal fenestra; **(2)** around orbital midlength or more anteriorly.

Previous use: BED c23; modified from S02 c14 and G07 c12.

179. Posterior 'ratchet' teeth: (0) absent; **(1)** present.

New character

Notes: The posterior-most teeth in the jaws may be small and markedly recurved. Described as "ratchet"-like by Taylor and Cruickshank (1993) and "hook-like" by Noè (2001), this morphology is seen in *Rhomaleosaurus zetlandicus*, *Pliosaurus brachyspondylus* and the pliosaurids of the Oxford Clay Formation (Taylor 1992; Taylor and Cruickshank 1993; Noè 2001; Ketchum 2007). Small hooked teeth are preserved with *Raptocleidus* and it is therefore scored as showing state '1'.

180. Form of apicobasally extending enamel ridges: (0) coarse; **(1)** fine; **(2)** absent.

Previous use: K&B10 c107; modified from B+99 c18, G+02 c9, G+03 c16, S&D08 c53 and D&R08 c91.

181. Enamel 'striations' (grooves): (0) present; **(1)** absent.

Previous use: K&B10 c108.

Notes: The enamelled tooth crowns of *Augustasaurus hagdorni* are ornamented with apicobasally orientated striations (i.e. in negative relief) rather than ridges (Ketchum

and Benson 2010).

182. Cross-sectional shape of teeth in anterior half of tooth row: (0) round or sub-rounded; **(1)** oval; **(2)** sub-triangular.

Previous use: K&B10 c109; modified from S02 c103, D&R08 c92.

183. Dentition, number of premaxillary teeth: (0) four; **(1)** five; **(2)** six; **(3)** seven or more.

Previous use: BED c103; modified from C99 c11, B+99 c1, OK01 c106, G+02 c8, G+03 c13, A+07 c1, D&R08 c93, K&B10 c110 and V+11 c42.

184. Number of mandibular symphysial teeth relative to the number of maxillary teeth: (0) low; **(1)** high.

Previous use: K&B10 c113.

Notes: A bivariate plot of the number of teeth adjacent to the mandibular symphysis against the number of teeth per maxilla shows two distinct clusters (Ketchum 2007, Fig. A5.10).

Axial skeleton

185. Atlantal centrum morphology: (0) excluded from lateral rim of atlantal cotyle by contact between the atlantal intercentrum and neural arches; **(1)** participates in rim of atlantal cotyle.

Previous use: D&R08 c96, K&B10 c114; modified from OK01 c110, S02 c112, OK&W03 c59, OK&S09 c50.

186. Atlas-axis complex, hypophyseal ridge: (0) absent; **(1)** present.

Previous use: K&B10 c115, D&R08 c97.

187. Atlas rib/rib facet or rib-like projection: (0) absent; **(1)** rib present, contacts atlas via a distinct rib facet; **(2)** posteroventral projection resembling a fused atlantal rib, but lacking evidence of a rib facet.

Previous use: BED c113; modified from S02 c116, D&R08 c98 and K&B10 c116.

188. Axial intercentrum, size: (0) small, restricted to ventral surface of atlas-axis complex; **(1)** large, wedge-shaped element that extends dorsally; **(2)** absent.

Previous use: K&B11 c187.

189. Axial neural spine: (0) transversely narrow; **(1)** transversely broad and very low.

Previous use: modified from K&B11 c188.

190. Axis rib articulation: (0) articulates solely with the axis centrum; **(1)** articulates partially with the atlas centrum.

Previous use: K&B10 c117; modified from OK01 c109, OK&W03 c58 and OK&S09

c49.

191. Cervical vertebrae, subcentral foramina: (0) absent; **(1)** present.

Previous use: S91 c47, OK01 c118, S02 c130, D&R08 c101, K&B10 c119; modified from S&D08 c65.

192. Proportions of the anterior cervical centra: (0) approximately as long as high; **(1)** longer than high; **(2)** shorter than high.

Previous use: OK01 c112, S02 c120, D&R08 c102, K&B10 c120; modified from H92 c4, B+99 c20, OK&W03 c61, A+07 c12, G07 c28, OK08 c12 and S&D08 c61.

193. Lateral surface of anterior cervical centra: (0) longitudinal ridge absent; **(1)** longitudinal ridge present.

Previous use: B+99 c22, C99 c17, OK01 c115, S02 c123 andc124, G+03 c19, G07 c30, D&R08 c103, K&B10 c121.

194. Articular face of cervical centra in anterior view: (0) uniformly convex; **(1)** ventral notch present.

Previous use: C99 c116, S02 c121, S02 c122, D&R08 c104, K&B10 c122; modified from B+99 c23, G+03 c20, OK&W03 c64.

195. Cervical centra, median ventral surface: (0) approximately flat or convex; **(1)** bears a rounded midline ridge; **(2)** bears a sharp keel.

Previous use: D&R08 c105, BED c126; modified from OK01 c114, S02 c125 andc126, S&D08 c64 andc67, OK&W03 c63, OK&S09 c54 and K&B10 c123.

196. Cervical centra, paired lateral ridges on ventral surface: (0) absent; **(1)** present.

Previous use: BED c127; modified from K&B10 c123.

197. Cervical centra, articular surfaces: (0) strongly concave; **(1)** gently concave or nearly flat.

Previous use: B+99 c21, G+03 c18, G07 c29, D&R08 c106, BED c117; modified from S02 c128 and K&B10 c124.

198. Cervical centra, proportional width: (0) mediolateral width subequal to height or less; **(1)** at least 1.2 times as wide mediolaterally as high dorsoventrally.

Previous use: BED c133.

199. Anterior cervical centra, anterior surface extends ventrally as a 'lip': (0) absent; **(1)** present.

Previous use: K&B11 c189.

200. Rib facets of the anterior-middle cervical vertebrae: (0) rib facets broadly separated; **(1)** two co-joined rib facets; **(2)** one rib facet.

Previous use: B+ip c125, BED c122; modified from H92 c7, OK01 c117, S02 c144, D&R08 c107, S&D08 c72 and K&B10 c125.

201. Rib facets of the posterior-most cervical vertebrae: (0) rib facets broadly separated; **(1)** two co-joined rib facets; **(2)** one rib facet.

Previous use: BED c123; modified from, H92 c7, OK01 c117, S02 c144, D&R08 c107, S&D08 c72, K&B10 c125 and B+ip c210.

202. Posterior cervical rib facets: (0) face laterally; **(1)** face posterolaterally.

Previous use: BED c135.

203. Cervical vertebrae, location of neurocentral suture in anterior-middle elements: (0) dorsal; **(1)** ventral; **(2)** ventral, contacting the rib facet.

Previous use: modified from K&B10 c126 and BED c132.

Notes: In anterior and middle cervical vertebrae the neurocentral suture can be located dorsally on the centrum (state 0), more ventrally (state 1) or ventrally so that it contacts the rib facet (state 2). A dorsally located suture can be seen in *Aristonectes*, *Muraenosaurus* and *Peloneustes* (Gasparini *et al.* 2003; Andrews 1910, Fig. 51; Andrews 1913, Fig. 18). A ventrally located suture, so that the anterior and posterior limbs of the suture are located at approximately one third of the centrum height, is seen in LEICT G1.2002 and *Edgarosaurus* (Druckenmiller 2002). A ventrally located suture

that contacts the rib facet is seen in *Hauffiosaurus* (Ketchum and Benson 2010),

Thalassiodracon (Benson *et al.* 2012) and DBYMU 355-1903 (pers. obs.).

204. Cervical vertebrae, shape of neurocentral suture in anterior-middle elements:

(0) arcuate; **(1)** V-shaped.

Previous use: modified from BED c132.

Notes: The shape of the neurocentral suture appears to vary independently of its

position on the lateral surface of the cervical centrum (contra Benson *et al.* 2012). In

both *Aristonectes* and LEICT G1.2002 the suture is arcuate (state 0) even though it is

situated dorsally in the former (Gasparini *et al.* 2003) and much more ventrally in the

latter. Conversely the suture is V-shaped (state 1) in *Muraenosaurus* (e.g. Andrews

1910, Fig. 51) and *Edgarosaurus* (Druckenmiller 2002) even though it is located

dorsally in the former and ventrally in the latter. This character is scored as

'inapplicable' in taxa in which the rib facet extends ventrally to contact the rib facet as

in this case it is invariably V-shaped (e.g. *Thalassiodracon*, NHMUK 2020*).

205. Combined width of cervical zygapophyses: (0) broader than the centrum; **(1)**

subequal in width to the centrum; **(2)** distinctly narrower than the centrum.

Previous use: S91 c48, OK01 c120, S02 c134, D&R08 c108, OK&W03 c65, K&B10

c127; modified from S&D08 c63 and OK&S09 c56.

206. Cervical zygapophyses, orientation: (0) sub-horizontal; **(1)** dorsomedially facing.

Previous use: BED c128.

207. Cervical zygapophyseal facets: (0) planar; **(1)** transversely concave/convex.

Previous use: BED c130.

208. Cervical vertebrae, medial contact of the left and right prezygapophyses: (0) absent, zygapophyseal spacing subequal to width of neural canal; **(1)** contact present at bases; **(2)** contact present for entire anteroposterior length.

Previous use: B+ip c128; modified from S02 c132, D&R08 c109 and K&B10 c128.

209. Cervical prezygapophyses, rugosity or process on lateral or posterolateral surface: (0) absent; **(1)** low mound or rugosity; **(2)** posteriorly directed 'parazygapophyseal' process.

New character

Notes: In most plesiosaurians the lateral and posterolateral surface of the anterior zygapophysis is relatively smooth, although there may be some low sculpture, particularly around the rim (state 0). However, in a number of stratigraphically early plesiosaurians the lateral or posterolateral surface of the zygapophysis bears a distinct rugosity or process. In some of these taxa, this is a relatively small mound-like rugosity (state 1), the precise position of which varies. In TTNCM 8348 the rugosity is conical and situated on the lateral surface of the zygapophysis, while in *Hauffiosaurus tomistomimus* (MANCH LL 8004; Benson *et al.* 2011b, Fig. 9K) and DBYMU 355-1903 it is situated more posteriorly. This feature is also present in '*Plesiosaurus*'

cliduchus (Benson *et al.* 2011a) and a small tubercle is present in *Eretmosaurus* (pers. obs.). In state '2' the rugosity is developed into a distinct posteriorly-directed process, referred to here as the 'parazygapopyseal process'. This is seen in LEICT G1.2002, NHMUK R16330 and OUMNH J.10337.

210. Zygosphene and zygantrum articulations: (0) present; **(1)** absent.

Previous use: S91 c49, OK01 c121, S02 c141, D&R08 c110, OK&W03 c66, K&B10 c129.

211. Anterior cervical neural spines, morphology: (0) curve posterodorsally; **(1)** inclined straight posterodorsally; **(2)** inflected anterodorsally.

Previous use: BED c119; modified from S02 c135, OK01 c125, OK&W03 c70, D&R08 c111, S&D08 c70, OK&S09 c61 and V+11 c50.

Notes: This character is scored as 'inapplicable' in some pistosaurians with extremely low neural spines.

212. Shape of neural spines in anterior cervicals in dorsal view: (0) square; **(1)** transversely compressed; **(2)** transversely elongate.

Previous use: K&B10 c132; modified from OK01 c130, S02 c137 and OK&W03 c71.

213. Anterior cervical vertebrae, proportions of neural spines: (0) taller than their anteroposterior length; **(1)** longer than tall.

Previous use: modified from D&R08 c112, K&B10 c130 and BED c131.

214. Posterior cervical vertebrae, height of neural spines: (0) substantially shorter than centrum; **(1)** subequal; **(2)** substantially taller than centrum.

Previous use: BED c121; modified from D&R08 c112 and K&B10 c130.

215. Morphology of the posterior margin of cervical neural spines: (0) convex; **(1)** grooved.

Previous use: S02 c142, D&R08 c113, K&B10 c131; modified from S&D08 c68.

Notes: Following Ketchum and Benson (2010), this character was scored using data from Druckenmiller & Russell (2008a).

216. Morphology of the anterior margin of cervical neural spines: (0) convex or ridged; **(1)** flattened triangular surface.

New character

Notes: State '1' describes the distinctive morphology seen in LEICT G1.2002 and *Leptocleidus superstes* in which the anterior margin of the cervical neural spines is a flattened triangular surface with the apex directed ventrally rather than the ridged or convex morphology seen in other plesiosaurians (state 0). The triangular morphology is also present in some of the middle cervicals of *Dolichorhynchops osborni* figured by Williston (1903). In some taxa, such as *Eurycleidus arcuatus* (NHMUK R1318), the apex of the neural spine flares laterally producing a small but wide triangular surface.

However, as the majority of the spine is ridged, this morphology is scored as state '0'.

217. Cervical neural spines, morphology of middle-posterior elements: (0) curve posterodorsally; **(1)** straight and sheet-like, anteroposteriorly long compared to transverse width; **(2)** straight but anteroposteriorly short and thus rod-like; **(3)** inflected anterodorsally.

Previous use: B+ip c212; modified from S02 c136, OK01 c125, OK&W03 c70, D&R08 c111, S&D08 c70, OK&S09 c61, V+11 c50 and BED c120.

Notes: Following Benson *et al.* (2012), this character is scored as 'inapplicable' in some pistosaurians with extremely low neural spines.

218. Posterior-most cervical to dorsal neural spines: (0) show consistent morphologies; **(1)** show alternating morphologies.

Previous use: modified from B+ip c211 and BED 143.

Notes: In most pistosaurians the posterior-most cervical to dorsal neural spines are relatively consistent in morphology along the series (state 0). However, in some stratigraphically early plesiosaurians the neural spines in this region have alternating morphologies (state 1). For example, in LEICT G1.2002 the neural spines are alternately expanded to the left or the right, while in NHMUK R16330 they are alternately transversely compressed and transversely expanded. In *Rhomaleosaurus cramptoni* the neural spines are alternately inclined to the left or right with the apices sloping in the opposite direction (NMING F8785). Alternating morphologies are also seen in some leptocleidians such as *Leptocleidus superstes* (Benson *et al.* in press; pers.

obs.).

219. Posterior-most cervical to dorsal neural spines, width: (0) consistently narrow transversely; **(1)** consistently thick transversely; **(2)** apex transversely expanded into prominent 'spine table'.

Previous use: modified from B+ip c211 and BED c144.

Notes: In taxa in which the neural spines of the posterior-most cervical to dorsal vertebrae have a consistent morphology they may be either transversely narrow (state 0), transversely thickened so that they are approximately square in dorsal view as in *Rhomaleosaurus zetlandicus* (state 1) or bear prominently expanded apices (e.g. *Dolichorhynchops*, Williston 1903; the "spine table" of Benson *et al.* in press). This character is scored as 'inapplicable' in taxa in which the neural spines alternate in width.

220. Posterior-most cervical to dorsal neural spines, alternating width: (0) alternately transversely thick and narrow but symmetrical; **(1)** asymmetrical, laterally expanded to one side and so approximately 'D-shaped' in dorsal view.

Previous use: modified from B+ip c211 and BED c144.

Notes: In taxa in which the neural spines of the posterior-most cervical to dorsal vertebrae show alternating widths, there appear to be two ways in which this can occur. In state '1' the spines are alternately transversely narrow and transversely expanded but remain symmetrical. This is seen in NHMUK R16330, NHMUK 14550, some rhomaleosaurids (e.g. *'Rhomaleosaurus' megacephalus*, LEICT G221.1851) and

Brancasaurus (R.B.J. Benson pers. com.). In state '0' the spines are laterally expanded to one side, and so are asymmetrical and appear to be 'D-shaped' in dorsal view. In LEICT G1.2002 and *Leptocleidus superstes* the spines are alternately expanded to the left or the right, whereas in MIWG 1997.302 they are alternatively unexpanded and expanded to the right (pers. obs.; R.B.J. Benson pers. com.). This character is scored as 'inapplicable' in taxa in the neural spines are consistent in width.

221. Cervical ribs in taxa with two rib-heads: (0) rib-heads close together; **(1)** large foramen immediately lateral to rib-heads.

Previous use: K&B11 c190.

222. Cross-sectional shape of the cervical ribs: (0) circular to oval; **(1)** greatly depressed.

Previous use: D&R08 c114, K&B10 c133; modified from OK01 c122 and OK&W03 c67.

223. Anterior process of cervical ribs: (0) present forming a prominent elongate projection; **(1)** present but dorsoventrally thick, anteroposteriorly low, and rounded; **(2)** absent in most cervical ribs, small processes may be present in anterior cervical ribs.

Previous use: K&B11 c134; modified from OK01 c123, S02 c146, D&R08 c115, OK&W03 c68, S&D08 c71 and K&B10 c134.

224. Cervical ribs, distal end: prominent posterior process: (0) present forming a prominent elongate projection; **(1)** present but low and rounded; **(2)** absent.

Previous use: K&B11 c191.

225. Number of pectoral vertebrae: (0) 2-4; **(1)** 5-7.

Previous use: BED c139.

226. Middle-posterior dorsal transverse processes, distal articular facet: (0) dorsoventrally tall oval, perhaps composed of two weakly divided rib facets; **(1)** composed of only a single subcircular facet.

Previous use: BED c136; modified from OK01 c126, D&R08 c116, S&D08 c73, K&B10 c136, K&B11 c192 and V+11 c54.

227. Dorsal transverse processes, orientation in middle dorsal region: (0) approximately horizontal so therefore laterally directed; **(1)** inclined significantly dorsolaterally.

Previous use: BED c141.

228. Dorsal neural spines, height: (0) less than or equal to the height of the centrum; **(1)** conspicuously taller than the centrum; **(2)** more than twice as tall as the centrum.

Previous use: K&B10 c137; modified from OK01 c129, D&R08 c117 and V+11 c55.

229. Dorsal neural spines, strong anteroposterior constriction at base: (0) absent;

(1) present.

Previous use: B+ip c213.

Notes: I have scored this character for state '1' in *Nichollssaura* as there is a large

posterior constriction at the base of the neural spine (Druckenmiller and Russell 2008b).

230. Dorsal neural arch height: (0) tall, base of transverse process located dorsal to

midheight of neural canal; **(1)** short, transverse process adjacent to neural canal.

Previous use: OK01 c127, BED c140.

231. Posteriormost dorsal neural spines, orientation: (0) dorsal or posterodorsal; **(1)**

anterodorsally inclined.

Previous use: BED c145.

232. Posteriormost dorsal rib facets: (0) prominent transverse process located entirely

on neural arch; **(1)** 'sacralised' where rib facet is split between neural arch and centrum,

but bears a typical posterior dorsal rib.

Previous use: BED c146.

233. Sacral rib morphology: (0) cylindrical and slightly expanded towards distal end;

(1) transversely expanded, dorsoventrally thin and sheet-like.

Previous use: K&B11 c194.

234. Caudal vertebral count: (0) 33-35; **(1)** 36-40; **(2)** more than 40.

Previous use: BED c148.

235. Caudal vertebrae, wedge-shaped vertebra in middle part of caudal series: (0)
absent; **(1)** present.

Previous use: K&B11 c193; modified from S&D08 c74.

236. Caudal centra, outline of middle caudal centra in anterior view: (0) sub-oval;
(1) lateral surfaces converge ventrally so centrum appears to 'taper' ventrally; **(2)**
subrectangular, chevron facets widely spaced and located ventrolaterally, ventral
surface approximately flat giving 'square' appearance to centrum in anterior view.
Previous use: BED c150.

237. Caudal centra, length:height ratio of proximal elements: (0) >0.9; **(1)** 0.6-0.8;
(2) <0.55.
Previous use: BED c151.

238. Proximal caudal centra, width to height ratio: (0) width subequal to height,
ratio = 0.9-1.1; **(1)** mediolaterally broad, ratio >1.1.

Previous use: BED c153.

239. Middle and distal caudal vertebrae, chevron facets: (0) low, flush with level of ventral surface of centrum; **(1)** prominent and project ventrally.

Previous use: BED c152.

240. Caudal ribs facet location in proximal-middle caudal vertebrae: (0) located dorsally, contacting or almost contacting neural arch; **(1)** at midheight of centrum, neural arch does not form part of facet; **(2)** located ventrally.

Previous use: modified from BED c.149.

Notes: I have added an extra state (2) to describe the relatively ventral position of the caudal rib facets in elasmosaurs such as *Styxosaurus* and *Elasmosaurus* (Welles and Bump 1949; Sachs 2005).

241. Caudal zygapophyses: (0) present for majority of the tail; **(1)** absent in posterior half of tail, may reduce asymmetrically; **(2)** only present on the most anterior-most caudals.

Previous use: modified from S02 c143.

Notes: Sato (2002) scored taxa for the presence of a reduction of the zygapophyses on the sacral and caudal vertebrae, but only recorded the derived state in *Dolichorhynchops herschelensis*. Druckenmiller and Russell (2008a) and Ketchum and Benson (2010) therefore excluded this state as being parsimony uninformative. Although the extent of caudal zygapophyses can be difficult to observe due to poor preservation, it is clear that

there is variation present. In most plesiosaurians in which a representative series of caudal vertebrae is adequately preserved, the zygapophyses usually disappear at around the middle of the tail (state 1; e.g. *Cryptoclidus*, Andrews 1910, p174). In some taxa such as LEICT G1.2002 and *Brancasaurus* (Wegner 1914, pp274-275), this occurs suddenly and asymmetrically, with the zygapophysis on one side absent while that on the other side is still relatively large. In some taxa, well developed zygapophyses continue into the posterior caudals and are present for the majority of the tail's length (state 0). This is present in LEICT G18.1996 (pers. obs.), *Muraenosaurus beloclis* (Andrews 1910, p.142) and *Elasmosaurus* (Sachs 2005, Fig. 5E). In state '2' the zygapophyses are only present in the anterior-most caudal vertebrae, as in *Dolichorhynchops herschelensis* (Sato 2005), *D. osborni* (Williston 1903) and *D. bonneri* (Adams 1997, Fig. 4F).

242. Mid-caudal neural spines, shape: (0) transversely compressed and blade-like; **(1)** rod-like.

New character

Notes: In most plesiosaurians the neural spines are transversely compressed and so blade-like in the middle part of the caudal series before reducing in height more posteriorly (state 0). In LEICT G1.2002 (pers. obs.), *Brancasaurus* (Wegner 1914), *Nichollssaura* (Druckenmiller and Russell 2008b) and *Eurycleidus* (NHMUK R1318) the spines are anteroposteriorly thin and transversely thick so that they are rod-like (state 1).

243. Caudal neural spines, orientation: (0) dorsal or weakly inclined posterodorsally; **(1)** strongly inclined posterodorsally, angle increasing posteriorly; **(2)** curve posterodorsally in proximal elements.

New character

Notes: In most plesiosaurians the anterior and middle caudal neural spines are either oriented dorsally or slightly inclined posterodorsally (state 0). In LEICT G1.2002 the spines become increasingly inclined posterodorsally so that in posterior caudals they are at an angle of approximately 60 degrees to the plane of the anterior articular face of the centrum (state '1'). This is also seen in *Nichollssaura* (Druckenmiller and Russell 2008b) and *Brancasaurus* (Wegner 1914). Highly inclined neural spines are seen in a number of polycotylids (e.g. *Dolichorhynchops bonneri*, Adams 1997; *Polycotylus latipinnis* O'Keefe *et al.* 2011b) and they are scored for state '1' accordingly. In state '2' the proximal caudal neural spines curve posterodorsally at their distal ends as seen in *Seeleyosaurus* (Dames 1895), *Hydrorion* (Huene 1923) and *Microcleidus homalospondylus* (YORYM 502).

244. Gastralia, shape of median element: (0) inverted 'V' shape in dorsal view; **(1)** straight.

Previous use: S02 c148, D&R08 c118, K&B10 c138; modified from OK01 c166.

Appendicular skeleton – girdles

245. Interclavicular foramen: (0) absent; **(1)** present.

Previous use: S02 c151, modified from K&B10 c139 and D&R08 c119.

Notes: this character is scored as present when the clavicular arch is pierced by a foramen, as defined by Sato (2002). Druckenmiller and Russell (2008a) used a broader definition, including the endochondral components of the pectoral girdle in the formation of the borders of the opening. In this analysis only the dermal elements are included, as a more reliable indication of homology of the feature.

246. Posterior process of the interclavicle: (0) elongated; **(1)** not elongated; **(2)** absent.

Previous use: modified from K&B10 c140, OK01 c131, S02 c150, OK&W03 c72.

Notes: I have included separate character states to code for the presence of a short spur-like process as seen in *Tricleidus* and *Muraenosaurus* (Brown 1981) and absence of the process as seen in many elasmosaurs and polycotylids (e.g. *Dolichorhynchops*, Williston 1903).

247. Clavicle/interclavicle complex, shape of anterior margin: (0) concave, anteroposterior depth of concavity approximately 0.8 times the mediolateral width or greater; **(1)** anteriorly convex or pointed; **(2)** transversely broad and weakly concave, mediolateral width at least 4.0 times the anteroposterior depth; **(3)** transversely narrow and weakly concave.

Previous use: BED c170 and B+ip c141, modified from K&B10 c141, S02 c153, S&D08 c121.

248. Contact of the clavicles along the midline: (0) present; **(1)** absent.

Previous use: K&B10 c142, D&R08 c120, modified from OK01 c134 and OK04 c134, S02 c152, OK&W03 c74.

249. Ratio of scapula length to coracoid length: (0) low; **(1)** high.

Previous use: modified from B+99 c26, OK01 c4, S02 c160, OK04 c4, G07 c31, S&D08 c76, D&R08 c125 and K&B10 c147.

Notes: although the ratio of scapula to coracoid length actually varies continuously, most taxa in this analysis cluster around a value of 0.7. However, as outlined above, in a few taxa such as *Colymbosaurus* and *Cryptoclidus* the ratio is nearer to unity. Taxa are scored for state '0' if the ratio is less than 0.85, while they are scored for state '1' if the ratio is more than 0.85. This character is only scored for taxa known from 'adult' material.

250. Scapula morphology: (0) dorsal blade expanding ventrally to form acetabular region, lacks expanded ventral plate; **(1)** triradiate with expansive ventral plate.

Previous use: BED c157.

251. Contact of the ventral rami of the scapulae along the midline: (0) do not meet along the midline; **(1)** meet along the ventral midline.

Previous use: V+11 c56, K&B10 c145, D&R08 c123, S&D08 c80, modified from B+99 c24, C99 c19, OK01 c135, OK04 c135, S02 c156, and OK&W03 c75.

252. Shape of the anterolateral margin of the scapula where the dorsal ramus meets the ventral ramus: (0) flat or gently convex; **(1)** forms prominent ridge or shelf.

Previous use: K&B10 c146, S02 c157, D&R08 c124.

253. Scapula blade, outline of anterior margin in lateral view: (0) approximately straight, weakly concave or weakly convex; **(1)** pronounced posterodorsal inflection; **(2)** distinct concave region anterodorsally.

Previous use: BED c159, modified from K&B11 c195, OK08 c37 and S&D08 c81.

Previous exclusion: K&B10x87.

Notes: O'Keefe (2008) used this character to describe a "distinct, sharp bend of the dorsal scapular process near the body of the scapula" in certain polycotylids. Smith (2007) scored a more distal bend seen in other plesiosaurs such as *Eurycleidus*, *Peloneustes* and *Leptocleidus* as homologous with this. Ketchum and Benson (2010) considered this character to be valid, but were unable to include it in their analysis.

254. Scapular blade, anteroposterior width: (0) width at distal end subequal to that at midlength; **(1)** narrow, tapering dorsally ; **(2)** broad, distal part expanded relative to midlength.

Previous use: BED c161, modified from K&B11 c196, S02 c159, OK01 c132. Previous exclusion: K&B10X86, D&R08X171.

255. Scapula blade, medial surface: (0) smoothly convex or flat; **(1)** robust buttress oriented parallel to long axis of blade.

Previous use: BED c162.

256. Anteromedial margin of the coracoid: (0) does not contact the dermal girdle elements; **(1)** contacts dermal girdle elements.

Previous use: K&B10 c143, modified from OK01 c137 and OK04 c137, S02 c169, D&R08 c122, and OK&W03 c77.

257. Anteromedial margin of the coracoid: (0) does not contact the scapula; **(1)** contacts the scapula.

Previous use: K&B10 c144 and S&D08 c79, modified from C99 c18, A+07 and OK08 c25.

258. Coracoid, shape of anterior process: (0) anteroposteriorly long and transversely broad, approximately rectangular; **(1)** anteroposteriorly long and transversely narrow; **(2)** anteroposteriorly short and subtriangular .

Previous use: K&B11 c150, modified from S02 c161, S&D08 c78 and K&B10 c150.

259. Anterior process of coracoid: (0) thin sheet; **(1)** thick and robust bar.

Pervious use: K&B11 c197.

Notes: The anterior process of the coracoid can be a dorsoventrally thin sheet (state 0) or a thickened bar (state 1). The thin state is shown by *Leptocleidus*, while *Cryptoclidus*, in which the anterior processes form a rod-like structure, exemplifies the thick state. In

both of these taxa the anterior process is relatively narrow, demonstrating that its thickness is independent of its width.

260. Sigmoid lateral edge to anterior process of coracoid: (0) absent; **(1)** present.

New character

Notes: In some elasmosaurs such as *Wapuskanectes* and *Callawayasaurus* (Druckenmiller and Russell 2006, Welles 1962) the lateral margin of the coracoid anterior process is sigmoid in outline resulting in ear- or kidney-shaped pectoral fenestrae. A similar morphology is present in MNHN A. C. 8592.

261. Supracoracoid foramen or notch: (0) present; **(1)** absent.

Previous use: St91c64 OK01 c141, OK04 c141, D&R08 c126, K&B10 c148.

262. Ventromedial coracoid morphology: (0) unelaborated; **(1)** rounded transverse buttress present; **(2)** transverse ridge or keel, may form projection at midline.

New character

Notes: In many plesiosaurians a rounded buttress runs from the glenoid slightly posteromedially to the median symphysis across the ventral surface of the coracoid (state 0). In *Cryptoclidus* this buttress is absent (state 1), its place taken by a concavity. In most elasmosaurs a sharp transverse keel is present. This is deepest at the coracoid symphysis where it can form a blunt conical process as described in *Mauisaurus* by Hiller *et al.* (2005). Taxa listed by Sachs (2004) as possessing transverse keels can be scored for state 2. A transverse ridge and projection seen in *Brancasaurus* and MIWG

1997.302 is also scored for state 2 (Benson et al, in press). In some elasmosaurs such as *Wapuskanectes* and CM Zfr 145 (Druckenmiller and Russell 2006; Hiller and Mannering 2005) this is further developed into a "spike" or rod-like process which projects ventrally.

263. Coracoid, dorsal interglenoid buttress: (0) posteromedial; **(1)** transverse with anterior depression; **(2)** transverse and anteriorly placed, no depression.

Previous use: BED c168, modified from B+ip c214 and S02 c163.

Notes: In the coracoids, a dorsal thickened ridge extends from the glenoid to meet its counterpart at the symphysis. In stem sauropterygians and *Pistosaurus* (Sues, 1987) these ridges run posteromedially (state 0). In most plesiosaurs they run more transversely, meeting medial to the glenoids and enclosing an extensive depressed area posterior to the pectoral fenestrae (state 1). In *Cryptoclidus* they are oriented more anteriorly so that the depression is absent (state 2).

264. Posterior intercoracoid vacuity/embayment: (0) absent; **(1)** cleft; **(2)** oval or cordiform vacuity.

Previous use: modified from B+99 c27, OK01 c141, OK04 c141, S02 c164, G07 c33, D&R08 c127, Sm&D08c77, K&B10 c149.

Notes: I have distinguished two morphologies of intercoracoid embayment: an elongated cleft (state 1); and an oval or heart-shaped (cordiform) opening (state 2). In the latter the posteromedial corners of the coracoids curve medially, enclosing the embayment. This is shown by many Cretaceous long-necked taxa, but also Jurassic taxa

such as LEICT G1.2002. I also consider this to be present in *Leptocleidus superstes*, as figured by Andrews (1922, Plate XV fig1). As pointed out by Druckenmiller and Russell (2008a), a substantial portion of the coracoids has been reconstructed, but Andrews (1922) describes how this was carefully done with plaster filling in voids left by missing fragments. I therefore regard his reconstruction as valid. State '1' is shown by *Eurycleidus arcuatus* (Andrews 1922), and also seems to be present in species of *Dolichorhyncops* (Williston 1903, plate XV; Sato 2005, fig. 8).

265. Median margin of the coracoid: (0) solid; **(1)** perforated by numerous round holes.

Previous use: modified from OK01 c140, S02 c168, OK&W03 c78, OK04 c140, A+07 c27, D&R08 c129, OK08 c27 and K&B10 c152.

Notes: In cases where the coracoid is perforated by a single isolated hole, as has been documented in *Cryptoclidus* and *Wapuskanectes* by Druckenmiller and Russell (2006, 2008a), this character is scored as state (0).

266. Coracoid, posterolateral corner extent: (0) does not extend as far laterally as glenoid ; **(1)** extends lateral to glenoid ; **(2)** extends to level of glenoid .

Previous use: modified from B+99 c25, OK01 c142, S02 c166 partim, OK04 c142, G07 c32 and K&B10 c151 partim, V+11 c57.

Notes: Druckenmiller and Russell (2008a, c128) defined a well developed cornu as one which extended laterally beyond the glenoid, while other authors have scored taxa for the possession of an angled cornu which extended beyond the glenoid. It is, however,

possible for an angled cornu to end medial to the glenoid, as in *Occitanosaurus*, and for a rounded posterolateral corner to extend laterally beyond the glenoid, as in *Callawayasaurus* (Druckenmiller and Russell 2006, Fig 10B). I therefore code the morphology and lateral extent of the posterolateral coracoid margin as two separate characters.

267. Coracoid, posterolateral corner morphology: (0) absent; **(1)** gently rounded or square; **(2)** forms acute cornu.

Previous use: S&D08 c75, modified from B+99 c25, OK01 c142, S02 c166 partim, OK04 c142, G07 c32 and K&B10 c151 partim, V+11 c57.

268. Coracoid, posterior margin, outline in dorsal view: (0) oriented approximately mediolaterally, may be convex, straight or weakly concave; **(1)** anterolaterally oriented; **(2)** possesses distinct posterior process adjacent to midline; **(3)** oriented posterolaterally.

Previous use: BED c166.

269. Shape of the ilial shaft: (0) straight; **(1)** curved.

Previous use: S02 c170, A+07 c29, D&R08 c142, K&B10 c167 and V+11 c60.

270. Dorsal tip of the ilium: (0) not flared dorsally; **(1)** flared dorsally.

Previous use: modified from S02 c172, A+07 c28, S&D08 c86, K&B10 c168 and V+11 c61.

271. Dorsal flare of the ilium: (0) dorsal flare approximately symmetrical; **(1)** asymmetrical dorsal flare that is wider posteriorly.

Previous use: modified from K&B10 c168.

Notes: this character is scored as 'inapplicable' in taxa in which the ilium is not distally expanded.

272. Ilium, anteroposterior width of distal expansion: (0) less than 1.5 times the anteroposterior width of proximal end; **(1)** more than 1.5 times the anteroposterior width of proximal end.

Previous use: modified from K&B11 c201.

Notes: Ketchum and Benson (2011a) introduced this character to distinguish the marked distal expansion in the ilia of derived pliosaurids from less expanded morphologies. However, as originally formulated the distal width was compared to the minimum width of the ilium shaft. As this varies depending on the degree of constriction of the ilium, I have used the anteroposterior width of the proximal end of the ilium as the reference dimension for this character. This character is scored as 'inapplicable' in taxa in which the ilium is not distally expanded.

273. Ilium, shape of distal expansion: (0) not truncated; **(1)** truncated anteriorly and posteriorly.

New character

Notes: In contrast to most plesiosaurs, in *Occitanosaurus* the dorsal blade of the ilum is

obliquely truncated anteriorly and posteriorly, with the result that it is almost diamond-shaped (Bardet *et al.* 1999). The dorsal blades of the ilia in *Hydrorion* and *Seeleyosaurus* are similar, although the truncated surfaces do not meet so that the blade is more trapezoid in shape (Huene 1923, Taf. II, Fig. 6).

274. Ilium, relative length: (0) short (l/w<2); **(1)** long (l/w>2).

Previous use: modified from S&D08 c85. Previous exclusion: K&B10X92.

Notes: in basal sauropterygians the ilium is proportionally short, so that the ratio of dorsoventral length (measured along the axis of the ilium shaft) to anteroposterior width of the proximal articular end is less than 2 (state 0). In plesiosaurians and *Yunguisaurus* the ilium is elongated so that this ratio is greater than 2 (state 1).

275. Ilium, orientation of distal blade relative to proximal articular end: (0) slightly rotated ($< 45°$); **(1)** strongly rotated ($> 45°$).

New character

Notes: In many plesiosaurs the ilium is strongly twisted, so that the proximal and distal ends are strongly rotated relative to each other (45° or more; state 1). This results in the ilial portion of the acetabulum facing anterolaterally. However, in some basal plesiosaurs such as *Plesiosaurus dolichodeirus* and OUMNH J.10337 (Storrs, 1997; pers. obs.) the ilium is only slightly twisted (approx 25°; state 0) so that the ilial portion of the acetabulum faces more anteriorly. This character is scored as 'inapplicable' in basal taxa in which the ilium contacts the pubis.

276. Ilium, angle of junction of ischium facet and acetabulum relative to plane of ilium blade: (0) high (>45°); **(1)** low (<20°).

New character

Notes: in basal plesiosaurs the ischial and acetabular facets on the proximal end of the ilium meet at a high angle to the sagittal plane of 45° or more. In most derived taxa the angle between the facets is closer to the sagittal plane, typically less than 20°. The plane of the ilium distal blade can be used as a proxy for the sagittal plane. This character varies independently of the angle of the proximal end to the distal blade as in OUMNH J.10337 the proximal head and distal blade lie at approximately 25° to one another while the junction between the facets is oriented at a high angle of approximately 50°.

277. Ilium, size of facets on proximal end: (0) subequal; **(1)** ischial facet larger; **(2)** acetabular facet larger.

New character

Notes: the ischial facet and the ilial portion of the acetabulum may be subequal, as in LEICT G1.2002, or the ischial facet may be larger, as in *Muraenosaurus* (Andrews 1910, Pl. IV, fig. 8), or the acetabulum may be larger, as in *Palmulasaurus* (Albright *et al.* 2007, fig. 6).

278. Ilium acetabluar facet: (0) not retracted posteriorly; **(1)** retracted posteriorly.

New character

Notes: in some plesiosaurians such as *Muraenosaurus* and *Cryptoclidus* (Andrews 1910) the acetabular facet on the proximal head of the ilium is retracted posteriorly so

that its dorsal corner is posterior to its posteroventral corner. In other plesiosaurs the facet is not retracted, and its edge curves anterodorsally from the posteroventral corner. The unretracted state should only be scored for adult specimens.

279. Ilium, tubercle on posterior surface around midlength: (0) absent; **(1)** present.

Previous use: BED 176 partim, K&B11 c198.

280. Ilium, longitudinal rugose ridge on posterolateral surface of the distal portion: (0) absent; **(1)** present.

Previous use: BED 176 partim.

Notes: In *'Rhomaleosaurus' megacephalus*, OUMN J.10337 and LEICT G1.2002 the posterolateral surface of the distal portion of the ilium bears a longitudinal, rugose ridge.

281. Ilio-pubic contact: (0) present; **(1)** absent.

Previous use: S91 c68, OK01 c143, S02 c173, D&R08 c143, K&B10 c169.

282. Pubo-ischiatic plate: (0) absent; **(1)** present.

Previous use: OK01 c145, D&R08 c144 and K&B10 170.

283. Median pelvic bar: (0) present; **(1)** absent.

Previous use: C99 c20, OK01 c146, S02 c177, OK&W03 c81, D&R08 c145 and K&B10 c171.

284. Obturator foramen: (0) present; **(1)** absent.

Previous use: S91 c70, OK01 c148, D&R08 c146 and K&B10 c172.

285. Pubis, anterolateral cornu: (0) absent; **(1)** present.

Previous use: S02 c174, D&R08 c148 and K&B10 c174.

286. Pubis, ventral midline projection: (0) absent; **(1)** present.

New character

Notes: In *Brancasaurus* the pubis bears a ventrally projecting conical process on the midline just anterior to the thyroid fenestra (Wegner 1914). This is also present in SCARB 2007.51 and NHMUK R8623 which represent an undescribed plesiosaur from the Early Cretaceous Speeton Clay of North Yorkshire, UK.

Appendicular skeleton – limbs

287. Humerus, deltopectoral crest: (0) present; **(1)** absent.

Previous use: R97c93, OK01 c156, K&B10 c156.

288. Humerus, inclination of proximal end in dorsal view: (0) not inclined, extends

proximally so shaft appears straight; (**1**) inclined anteriorly so shaft appears sigmoidal;

(**2**) inclined posteriorly so that the proximal portion of the anterior margin is convex in

dorsal view (low bulge often located proximally on anterior surface).

Previous use: BED c191; modified from OK&W03 c95, A+07 c18, S&D08 c89,

OK&S09 c86.

289. Humerus, orientation of the tuberosity: (0) not tilted, tuberosity rises dorsally;

(**1**) tuberosity posterodorsally tilted.

Previous use: S02 c192, BED c191.

Notes: This character is scored as 'inapplicable' in taxa in which the humerus tuberosity

is absent.

290. Humerus, postaxial process: (0) absent; (**1**) present but low; (**2**) distinct and well-

developed.

New character

Notes: This character describes the presence of a process on the postaxial edge of the

humerus just distal to the capitulum. This is well developed in LEICT G1.2002 (state 2)

and was noted in *'Rhomaleosaurus' megacephalus* (LEICT G221.1851) and other

rhomaleosaurids by Smith (2007). It is also present and well developed in other

stratigraphically early pistosaurians such as *Thalassiodracon* (NHMUK 2018*). In

other taxa such as *Hauffiosaurus* it is a lower swelling rather than a discrete process,

and this morphology is scored as state '1' (Benson *et al.* 2011b, Fig. 14). The process is

located on the humeral shaft, and is separate from the tuberosity, and is clearly absent in

Cryptoclidus (Brown 1981, Fig. 15). This process may represent the insertion of the *m. coracobrachialis* (Carpenter *et al.* 2010), although in *Pistosaurus* it was identified as the insertion of the *m. subcoracoscapularis* (Sues 1987).

291. Humerus, outline of preaxial margin of distal half in dorsal or ventral view: **(0)** straight or convex; **(1)** concave as distal humerus expands anteriorly, but expansion relatively small, substantially less than posterior expansion; **(2)** concave, and anterior expansion is large, approaching the size of the posterior expansion.

Previous use: BED c188; modified from OK01 c150, S02 c186, OK&W03 c82, A+07 c18, D&R08 c133, S&D08 c89, OK&S09 c73, K&B10 c157 and V+11 c62.

292. Humerus, distal convex protuberance on preaxial margin: (0) absent, margin relatively smooth; **(1)** convex protuberance ("knee" sensu Sato 2002) present.

Previous use: S02 c188, D&R08 c134, K&10c158.

293. Humerus, anterior surface of shaft: (0) no ridge or groove present; **(1)** sharp longitudinal ridge present; **(2)** longitudinal groove or trough present.

Previous use: modified from S&D08 c90 and BED c189.

Notes: I have added an extra state (2) to describe the longitudinal groove present on the anterior surface of the humeral shaft in LEICT G1.2002 and NHMUK R16330.

294. Humerus, shape of the distal end: (0) uniformly convex; **(1)** humerus distinctly

angled for articulation with the epipodials.

Previous use: D&R08 c136, S&D08 c91, K&B10 c159; modified from H92 c9, OK01 c152, OK&W03 c83 and OK&S09 c74.

295. Humerus, shallow groove on ventral surface between epipodial facets (flexor groove): (0) present and prominent; **(1)** absent; **(2)** present but anteroposteriorly short and shallow.

Previous use: BED c192.

296. Humerus, shape of the posterior margin: (0) concave; **(1)** posterodistally convex (a "knee" sensu Sato 2002); **(2)** concave with long posterior extension.

Previous use: modified from S02 c189 and c187, V+11 c63.

Notes: I have added an extra state (2) to describe the posteriorly extended posterior margin of the humerus in *Hydralmosaurus serpentinus* (Carpenter 1999). This is also present in *Libonectes morgani* (Welles 1949) as was noted by Sato (2002).

297. Forelimb epipodials, ratio of maximum radius length to maximum ulna length: (0) 1.0-1.3; **(1)** 1.4-1.7; **(2)** > or equal to 2.0.

Previous use: BED c202; modified from S02 c202.

298. Radius, preaxial margin: (0) concave; **(1)** straight or convex.

Previous use: K&B10 c163; modified from S02 c204, D&R08 c139, OK&S09 c90 and

V+11 c65.

299. Radius, prominent anterior flange extends from anteroproximal surface: (0) absent; **(1)** present, radius appears 'P-shaped'.

Previous use: BED c197.

300. Radius, posterodistal facet for intermedium: (0) absent, may have small contact at posterodistal corner of radius; **(1)** present and well developed.

Previous use: BED c203.

301. Ulna, postaxial margin: (0) concave; **(1)** convex.

Previous use: K&B10 c164; modified from OK01 c157 andc158, S02 c204, D&R08 c139, S&D08 c92, OK&S09 c76 and V+11 c65.

302. Forelimb epipodial foramen, presence and distal extent: (0) present and extends the length of the epipodials or more, intermedium may form part of margin; **(1)** present but closed distally by contact between the epipodials; **(2)** absent or rudimentary.

Previous use: modified from S02 c208 andc209, A+07 c23. Previous exclusion: D&R08 c173, K&B10X98.

Notes: Previous analyses have included characters coding for the presence or absence of an epipodial foramen, antebrachial foramen or spatium interosseum. I have modified this character to describe the variation in the distal extent of the foramen. In many

stratigraphically early plesiosaurians the foramen is large and extends the length of the epipodials or more (state 0). In *Eretmosaurus rugosus* the foramen extends distally beyond the epipodials so that the intermedium forms part of its margin (NHMUK 14435), while in *Plesiosaurus dolichodeirus* it extends approximately as far as the epipodials with the intermedium making little, if any, contribution to its margin (NHMUK 22656). In many other taxa the foramen is still present, but has been closed distally by contact between the epipodials as seen in *Tricleidus seeleyi* (Andrews 1910). In state '2' the foramen is rudimentary and effectively absent, as in *Cryptoclidus eurymerus* (Andrews 1910; Brown 1981). A character describing the presence or absence of the epipodial foramina was excluded by Druckenmiller and Russell (2008a) and Ketchum and Benson (2010). The former cited that it was parsimony uninformative for their sample of taxa, while the latter that presence or absence of the foramen was linked to ontogeny, and that its size was non-independent of the length of the epipodials. However, the distal extent of the foramen is controlled by a contact between the epipodials which is independent of their length, and while the foramen is only discernable in *Cryptoclidus* in 'old adult' individuals (Brown 1981), it is still rudimentary rather than being well developed as in many other taxa. This character should be scored as '?' in young 'juvenile' specimens.

303. Forelimb epipodial foramen, proximal extent: (0) foramen proximally extensive, extends to margin of humerus; **(1)** foramen closed proximally by contact between radius and ulna.

New character

Notes: In some taxa in which the forelimb epipodial foramen is not rudimentary or

absent, it extends proximally to the margin of the humerus as in *Plesiosaurus dolichodeirus* (NHMUK 22656; state 0). In others, the foramen is closed proximally by contact between the radius and ulna as in *Tricleidus seeleyi* (Andrews 1910; state 1). This character is scored as 'inapplicable' in taxa in which the epipodial foramen is absent or rudimentary.

304. Femur, outline of preaxial margin: (0) smoothly concave or straight; **(1)** convex protuberance present.

Previous use: S02 c190. Previous exclusion: D&R08 c174, K&B10X94.

Notes: This character was excluded by previous authors as it was considered to be serially homologous to, and so not independent of, the anterior protuberance on the humerus. However, in CM Zfr 115 the femur lacks an anterior protuberance, while one is present on the humerus. I therefore include the femoral protuberance in this analysis as a separate character as it varies independently of the humeral morphology.

305. Femur, outline of postaxial margin: (0) smoothly concave; **(1)** convex protuberance present.

Previous use: S02 c191.

306. Trochanter morphology: (0) narrow; **(1)** broad.

Previous use: D&R08 c150, K&B10 c176.

307. Tibia, preaxial margin: (0) concave; **(1)** convex or straight.

Previous use: K&B10 c178; modified from S02 c205, D&R08 c152 and V+11 c67.

308. Tibia, posterodistal facet for intermedium: (0) absent; **(1)** present.

Previous use: K&B11 c200.

309. Fibula, postaxial margin: (0) concave; **(1)** convex.

Previous use: BED c200; modified from S02 c205, D&R08 c152, S&D08 c92 and V+11 c67.

310. Hind limb epipodial foramen, presence and distal extent: (0) present and extends the length of the epipodials or more, intermedium may form part of margin; **(1)** present but closed distally by contact between the epipodials; **(2)** absent or rudimentary.

311. Hind limb epipodial foramen, proximal extent: (0) foramen proximally extensive, extends to margin of femur; **(1)** foramen closed proximally by contact between tibia and fibula.

New character

Notes: In some taxa in which the hind limb epipodial foramen is not rudimentary or absent, it extends proximally to the margin of the femur as in *Plesiosaurus dolichodeirus* (NHMUK 22656; state 0). In others, the foramen is closed proximally by contact between the tibia and fibula as in *Tricleidus seeleyi* (Andrews 1910; state 1).

This character is scored as 'inapplicable' in taxa in which the epipodial foramen is absent or rudimentary.

312. Limbs, postaxial accessory ossicles: (0) absent; **(1)** present.

Previous use: BED c182; modified from H92 c17, OK01 c153 andc162, S02 c199 andc200, OK&W03 c87, A+07 c20, D&R08 c137, OK&S09 c78, K&B10 c160 andc161.

Notes: This character was scored as '?' in young juveniles.

313. Limbs, preaxial accessory ossicles: (0) absent; **(1)** present.

Previous use: BED c183; modified from OK01 c153, OK&W03 c87, A+07 c20, OK&S09 c78.

Notes: This character was scored as '?' in young juveniles.

314. Limbs, position of the fifth metapodial: (0) lies in the metapodial row; **(1)** shifted proximally so that the proximal half is in the distal mesopodial row; **(2)** shifted proximally so that the entire fifth metapodial is in the mesopodial row.

Previous use: BED c205; modified from OK01 c163, S02 c211 andc212, D&R08 c140 and K&B10 c165.

315. Metapodials, morphology of proximal ends: (0) straight, anteroposteriorly oriented butt contact with distal mesopodials; **(1)** angled facets.

Previous use: BED c206.

316. Hyperphalangy of the manus: (0) absent; **(1)** present.

Previous use: S91 c80, OK01 c164, S02 c214, D&R08 c141, K&B10 c166.

317. Phalanx proportions: (0) long and slender, approximately 2 to 3 times as long proximodistally as broad anteroposteriorly; **(1)** short and robust.

Previous use: BED c207.

Quantitative characters

318. Ratio of orbit length in dorsal view to temporal fenestra length (quantitative).

Previous use: K&B10 c1, D&R08 c4; modified from V+11 c3, S&D08 c33, G+03 c4, S02 c35, c39, B+99 c5.

319. Ratio of preorbital to total skull length (quantitative).

Previous use: K&B10 c2; modified from V+11 c1, S&D08 c3, D&R08 c2, S02 c2 and c13, OK01 c6 and c8.

320. Ratio of posterior skull width to post-orbital skull length (quantitative).

Previous use: K&B10 c3; modified from D&R08 c3, S02 c5, H92 c8.

321. Shape of the posterior interpterygoid vacuities (length/width, quantitative).

Previous use: modified from S&D08 c42.

Notes: Smith and Dyke (2008) characterised the shape of the posterior interpterygoid vacuities as either round or elongate and slit-like. However, I have observed a continuous range of variation, and so treat this character quantitatively as the ratio of vacuity length to width. The roundest vacuities are seen in *Macroplata* (0.71), while the most elongate vacuities are found in *Trinacromerum* (3.5). This character is scored as 'inapplicable' in taxa in which the posterior interpterygoid vacuities are absent.

322. Position of posterior interpterygoid vacuities relative to subtemporal fenestra (quantitative).

Previous use: modified from S&D08 c43.

Notes: Smith and Dyke (2008) divided the range of variation into two discrete states, possibly due to the restricted range of OTUs in their analysis. However, I have observed a continuous range of variation in the relative position of the posterior interpterygoid vacuities, and so treat this character as quantitative. The distance between the anterior border of the subtemporal fenestra and the anterior border of the vacuities is expressed as a percentage of the width across the vacuities (as a proxy for skull width). Vacuities which open posterior to the border of the subtemporal fenestra result in a negative score. The most posteriorly positioned vacuities are seen in *Libonectes* (-50%), while the most anterior are found in *Leptocleidus superstes* (106%). This character is scored as 'inapplicable' in taxa in which the posterior interpterygoid vacuities are absent.

323. Ratio of the height of the dentary midway along the mandible versus height of the dentary at the coronoid process (quantitative).

Previous use: D&R08 c85, K&B10 c95; modified from G+03 c12 and V+11 c39.

324. Relative length of mandibular symphysis (quantitative).

Previous use: S02 c87, D&R08 c79; modified from OK01 c8, A+07 c8 and V+11 c36.

Notes: This character was excluded by Ketchum and Benson (2010 X2), who cited logical non-independence with the number of teeth adjacent to the mandibular symphysis. However, Druckenmiller (2006) observed these characters to vary independently and he noted that the number of symphyseal teeth is partly controlled by tooth size. It is also partly controlled by tooth spacing, and for these reasons I have included this character.

325. Number of maxillary teeth (quantitative).

Previous use: OK01 c107, S02 c110, A+07 c2, D&R08 c94, K&B10 c111.

326. Number of dentary teeth adjacent to the mandibular symphysis (quantitative).

Previous use: K&B10 c112; modified from S&D08 c58, D&R08 c95.

Notes: Here this character is scored as the number of tooth positions which lie lateral to the full extent of the mandibular symphysis.

327. Number of cervical vertebrae, including 'pectoral' vertebrae (quantitative).

Previous use: S02 c118, D&R08 c9, K&B10 c118; modified from H92 c3, H92 c11, B+99 c19, C99 c12-15, G+03 c17, A+07 c13, G07 c27, OK08 c13, S&D08 c62, OK&W03 c60.

328. Number of dorsal vertebrae (quantitative).

Previous use: S02 c119, K&B10 c135.

329. Relative length of the pectoral girdle (quantitative).

Previous use: modified from B+99 c26, OK01 c4, S02 c160, OK04 c4, G07 c31, S&D08 c76, D&R08 c125 and K&B10 c147.

Notes: O'Keefe (2001) introduced a binary character comparing the length of the scapula and coracoid. Taxa were scored as state '0' where the elements were subequal in length and state '1' where the coracoid was longer. Derived elasmosaurs were the only plesiosaurs which were scored as state '0'. Druckenmiller and Russell (2008a) characterized this character further, defining the coracoid length as running parasagittally from the glenoid fossa at the scapula-coracoid suture to the posterior coracoid margin, and maximum scapular length as measured longitudinally on the bone's ventral surface. However, they followed O'Keefe's (2004b) coding and scoring in which only *Libonectes* and *Callawayasaurus* were scored as showing a scapula subequal in length to the coracoid. However, the relative lengths of the coracoid and scapula vary continuously, and the scapula is actually longest in cryptoclidids such as

Cryptoclidus and *Colymbosaurus*. The relative length of the entire endochondral pectoral girdle also varies. The proportional length of the pectoral girdle is scored as a quantitative character. The combined length of the scapula and coracoid, as defined by Druckenmiller and Russell (2008a, c125), is divided by the maximum width of the coracoid from the posterolateral edge of the glenoid to the midline on the ventral surface. The latter acts as a proxy for the width of the body. The pectoral girdle is shortest in Triassic sauropterygians such as *Simosaurus* and *Pistosaurus*, while it is longest in *Muraenosaurus leedsii*. This character is only scored for taxa known from 'adult' material.

330. Ilium, ratio of dorsoventral length (measured along the axis of the ilium shaft) to anteroposterior width of the proximal end (quantitative).

Previous use: modified from S&D08 c85. Previous exclusion: K&B10 X92.

Notes: Smith and Dyke (2008) scored the ilia in *Rhomaleosaurus cramptoni* and *R. thorntoni* as being robust in relation to the other taxa in their sample. However, they stated that the discrete binary character states they used may not be applicable to a wider sample of ilium morphology. Following Ketchum and Benson's (2010) suggestion, this character is coded quantitatively here. The lowest ratio is seen in *Rhomaleosaurus thorntoni*, while the highest is seen in species of *Muraenosaurus*. Perceptions of ilium robustness can derive partly from the relative length, coded for here, and in the degree of constriction, coded for in the following character. This character is only scored for taxa with an ilium length to width ratio of 2 or more and is inapplicable in taxa with proportionally shorter ilia.

331. Constriction of the ilium shaft, ratio of anteroposterior width of proximal end to minimum width of ilial shaft (quantitative).

New character.

Notes: Some plesiosaurians have a markedly constricted ilium, whereas in others the constriction is much less marked. *Peloneustes* and *Rhomaleosaurus cramptoni* have relatively unconstricted ilia, while the ilium is markedly constricted in *Archaeonectrus*. The degree of constriction varies independently of the proportions of the ilium or the degree of distal expansion.

332. Pubis, length to width ratio (quantitative).

Previous use: modified from S&D08 c83, K&B11 c199 and V+11 c58.

Notes: I have used a quantitative character as the proportions of the pubis vary continuously. The width was measured from the midline to the anterior corner of the acetabulum, thereby excluding any anterolateral cornu (Ketchum and Benson 2011a).

333. Ischium, length to width ratio (quantitative).

Previous use: S02 c175, D&R08 c147 and K&B10 c173, modified from H92 c2, A+07 c30, A+07 c31 and S&D08 c84.

334. Ratio of humerus to femur length (quantitative).

Previous use: S02 c182, D&R08 c131, K&B10 c153; modified from S91 c82, H92 c1,

B+99 c28 and S&D08 c88.

335. Ratio of humerus length to width (quantitative).

Previous use: S02 c184, D&R08 c131, K&B10 c154; modified from B+99 c29, OK01

c151, OK01 c154, OK01 c155, D&R08 c135 and S&D08 c87.

Notes: Following Druckenmiller and Russell (2008a, c131), the maximum

proximodistal length is divided by the maximum width at the distal end of the humerus.

336. Forefin aspect ratio (quantitative).

Previous use: D&R08 c130, K&B10 c155; modified from OK01 c7 and OK&W03 c6.

337. Ratio of radius length to width (quantitative).

Previous use: K&B10 c162; modified from H92 c10, OK01 c161, S02 c202, D&R08

c138, A+07 c21 and S&D08 c93.

Notes: Following Ketchum and Benson (2010, c162), the maximum length of the radius

is divided by the width measured midway along the shaft.

338. Femoral length versus width ratio (quantitative).

Previous use: D&R08 c149, K&B10 c175; modified from S02 c186.

339. Proportions of the tibia (quantitative).

Previous use: K&B10 c177; modified from S02 c203 and D&R08 c151.

Notes: Following Ketchum and Benson (2010, c177), the maximum length of the tibia is divided by the width measured midway along the shaft.

Appendix II: Character-taxon matrix

#	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	*Archaeonectrus rostratus*	1	0	1	?	?	1	?	1	1	1	?	?	1	0	?	?	1	?	?	?	?	?	0	?	?	?	1	?	0
2	*Aristonectes parvidens*	0	0	1	0	?	0	0	?	?	?	?	?	0	0	0	-	1	?	?	?	?	1	-	0	0	1	0	0	0
3	*Attenborosaurus conybeari*	?	0	1	?	?	?	?	1	1	2	0	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
4	*Augustasaurus hagdorni*	0	0	1	0	1	0	0	0	-	-	0	0	0	0	0	-	0	?	1	0	0	0	-	0	0	1	1	1	0
5	*Marmornectes candrewi*	0	0	?	?	?	?	0	0	-	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6	NHMUK 49202	1	0	1	?	1	0	0	1	0	0	?	2	0	0	1	0	?	0	?	0	?	0	0	1	1	1	?	?	0
7	NHMUK R2439	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8	*Brachauchenius lucasi*	?	?	1	2	0	0	2	0	-	0	1	1	0	1	0	0	1	0	1	0	1	?	1	?	1	0	0	0	0
9	*Brancasaurus brancai*	0	0	1	0	1	?	1	1	0	2	0	0	1	0	0	-	0	1	1	0	1	0	-	0	1	1	0	0	?
10	*Callawayasaurus colombiensis*	0	?	1	0	?	0	0	?	?	?	0	?	0	0	0	?	?	?	?	?	?	?	?	0	0	1	0	0	0
11	*Cymatosaurus*	1	0	0	0	1	0	0	0	-	-	0	?	0	0	0	-	1	0	0	0	0	0	-	0	0	0	1	1	0
12	*Cryptoclidus eurymerus*	?	1	?	?	1	?	1	0	-	-	0	0	0	0	0	0	1	?	1	1	-	?	0	0	1	0	0	0	2
13	*Dolichorhynchops herschelensis*	0	0	1	0	?	0	2	1	1	-	0	0	2	0	0	0	0	?	1	0	1	0	1	1	0	1	?	?	?
14	*Dolichorhynchops osborni*	0	0	1	2	1	0	2	0	-	-	0	0	2	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1
15	*Edgarosaurus muddi*	0	0	1	2	0	0	2	0	-	-	0	0	2	0	0	0	?	1	?	0	0	?	1	1	0	1	1	1	1
16	*Elasmosaurus platyurus*	?	0	?	?	?	?	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17	*Eopolycotylus rankini*	0	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	*Eromangasaurus australis*	?	?	1	0	1	?	2	?	?	?	?	1	0	0	-	1	0	?	0	?	?	?	-	0	?	0	0	0	?
19	*Eurycleidus arcuatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20	FHSMVP321	1	0	1	2	0	0	2	0	-	-	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0
21	*Hauffiosaurus longirostris*	0	2	1	?	?	?	?	1	1	2	0	1	1	0	2	0	?	1	?	1	0	?	1	0	?	?	?	1	?
22	*Hauffiosaurus tomistomimus*	0	?	1	2	0	0	1	0	-	-	0	1	0	0	2	0	0	?	1	0	0	1	0	0	1	0	1	0	0
23	*Hauffiosaurus zanoni*	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	*Hydrorion brachypterygius*	1	2	1	?	1	0	1	0	-	-	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0
25	*Hydrotherosaurus alexandrae*	0	?	1	?	1	?	2	0	-	-	0	2	1	0	0	?	?	?	0	0	?	?	?	0	1	0	?	0	0
26	*Kaiwhekea katiki*	0	?	1	0	?	0	2	?	?	?	?	2	1	0	-	1	1	?	?	1	-	0	0	1	0	0	0	?	?
27	*Kimmerosaurus langhami*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28	*Kronosaurus queenslandicus*	1	0	1	2	0	0	2	0	-	-	0	1	1	0	0	?	1	0	?	0	1	0	?	1	?	?	?	?	?
29	*Leptocleidus capensis*	1	0	1	0	?	0	1	1	0	2	0	0	{12}	0	0	-	?	1	?	?	?	?	-	0	?	?	1	1	1
30	*Leptocleidus superstes*	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31	*Libonectes morgani*	0	0	1	0	1	0	2	1	0	2	0	2	1	0	0	-	1	0	?	0	1	0	-	0	?	0	1	1	?
32	*Liopleurodon ferox*	1	0	1	2	0	0	2	0	-	-	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0
33	*Macroplata tenuiceps*	1	0	1	{01}	?	0	?	1	1	?	0	1	0	1	1	?	1	?	0	?	0	?	1	0	1	1	1	0	0
34	*Manemergus anguirostris*	0	0	1	0	0	2	1	2	2	0	0	2	0	0	0	?	0	?	0	0	1	1	?	0	?	0	?	?	?
35	*Maresaurus coccai*	1	2	1	{01}	1	0	?	1	1	2	0	?	1	0	-	?	?	?	?	0	?	1	0	?	1	0	?	1	0
36	*Microcleidus homalospondylus*	?	2	?	0	1	0	1	?	1	?	?	0	?	1	0	0	-	?	?	?	?	?	?	-	1	1	0	0	0
37	*Muraenosaurus leedsii*	0	1	1	0	1	0	1	0	-	-	0	2	1	0	0	-	1	0	1	1	-	1	-	0	1	0	0	0	2
38	*Nichollssaura borealis*	0	0	1	2	1	0	?	1	0	2	0	1	0	0	?	0	1	0	0	?	0	?	0	?	?	?	?	1	1
39	*Occitanosaurus tournemirensis*	1	2	1	0	1	0	1	0	-	-	0	0	0	0	0	0	-	0	0	1	0	1	0	-	0	1	0	0	0
40	OUMNH J.02247	1	?	1	2	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?
41	*Stratesaurus taylori*	?	0	1	{12}	1	0	1	0	-	?	0	0	1	0	0	0	1	0	?	0	0	1	0	?	?	?	1	1	?
42	OUMNH J.28585	?	0	?	?	?	?	?	?	?	?	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	*Palmulasaurus quadratus*	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	*Peloneustes philarchus*	1	0	1	2	0	0	2	0	-	-	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
45	*Plesiopleurodon wellesi*	0	0	1	2	1	0	?	1	1	2	0	?	2	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
46	*Plesiosaurus dolichodeirus*	0	0	1	0	1	0	1	0	-	-	0	0	1	0	0	-	0	0	1	0	1	0	-	0	1	0	0	?	0
47	*Plesiosaurus macrocephalus*	1	0	1	?	?	0	?	1	0	2	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48	*Pliosaurus andrewsi*	1	?	1	2	?	0	2	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	*Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	*Pliosaurus brachyspondylus*	1	0	1	2	0	0	2	0	-	-	0	1	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0
51	*Polycotylus latipinnis*	?	?	?	?	?	?	2	0	-	-	0	?	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
52	QMF 18041	0	0	1	2	0	0	2	1	2	2	?	0	2	0	0	?	?	?	?	?	?	?	?	?	?	?	1	1	1
53	*Rhomaleosaurus megacephalus*	1	2	1	1	1	0	1	1	0	2	0	0	1	0	1	-	1	1	1	0	0	1	-	?	1	0	1	0	0
54	*Meyerasaurus victor*	1	2	1	0	1	?	?	1	0	1	?	?	?	1	0	-	1	?	?	?	?	?	-	?	?	?	1	1	?
55	*Rhomaleosaurus zetlandicus*	1	0	1	1	1	2	1	0	0	0	0	1	1	0	0	-	1	?	?	0	0	1	-	?	1	0	1	0	0
56	*Seeleyosaurus guilelmiimperatoris*	0	?	1	?	?	0	?	?	?	1	?	?	1	?	0	0	-	0	1	?	?	0	?	0	?	?	?	?	?
57	*Simolestes vorax*	1	0	1	2	0	0	2	0	-	-	0	1	2	0	0	?	0	0	0	0	1	0	0	1	0	0	0	0	?
58	*Simosaurus gaillardoti*	0	0	0	0	1	0	0	0	-	-	0	2	0	0	0	-	0	0	0	0	0	0	-	0	0	0	1	1	0
59	*Styxosaurus snowii*	?	0	1	0	1	?	?	0	-	-	1	2	1	0	0	-	0	?	0	1	0	1	?	-	?	?	?	?	0
60	*Terminonatator pontiexensis*	?	?	0	?	0	0	2	1	0	2	0	?	1	0	0	-	0	1	?	0	1	0	-	0	?	0	?	?	?
61	*Thalassiodracon hawkinsii*	0	0	1	?	0	1	1	0	2	?	1	1	0	0	0	1	0	?	?	1	0	?	0	1	0	0	1	1	0
62	*Thalassomedon haningtoni*	?	0	1	0	1	?	2	?	?	?	?	2	2	0	0	-	?	0	1	0	?	1	-	?	0	?	0	0	0
63	*Thililua longicollis*	0	0	1	0	1	0	2	1	2	2	0	2	0	0	-	0	?	1	0	1	0	-	0	?	?	?	?	?	?
64	*Tricleidus seeleyi*	?	1	1	0	1	?	?	?	?	?	?	0	0	0	0	?	1	0	?	1	-	1	-	0	1	0	0	0	?
65	*Trinacromerum bentonianum*	?	0	1	2	0	?	2	1	1	2	0	2	1	0	0	0	?	0	1	?	?	1	?	1	?	1	1	1	1
66	*Umoonasaurus demoscyllus*	1	?	1	0	0	0	?	1	0	2	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
67	*Pistosaurus* skull	0	0	1	0	1	0	0	0	-	-	0	0	0	0	0	-	1	1	0	0	0	0	-	0	0	1	1	1	?
68	*Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
69	*Yunguisaurus liae*	0	0	1	0	1	0	1	0	-	-	?	0	1	0	0	-	0	?	0	0	0	0	-	0	0	1	1	1	0
70	*Bobosaurus forojuliensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
71	LEICT G1.2002	?	?	?	?	?	1	1	1	0	0	0	0	0	?	?	?	?	?	0	?	?	0	?	0	1	0	?	?	?
72	NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
73	Speeton taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
74	*Hydralmosaurus serpentinus*	?	?	1	0	?	0	2	?	?	?	1	?	1	0	0	-	0	0	?	0	1	?	-	0	?	?	0	0	0
75	*Rhomaleosaurus cramptoni*	1	0	1	1	1	1	2	1	0	0	0	1	1	0	-	1	?	1	0	0	1	-	0	1	0	1	1	0	0
76	*Rhomaleosaurus thorntoni*	1	0	?	?	1	1	?	1	0	2	?	?	{12}	1	0	-	?	?	0	0	1	-	?	1	0	1	?	0	?
77	*Avalonnectes arturi*	0	0	1	0	1	0	1	1	1	0	0	1	0	0	-	1	0	?	0	0	1	-	?	1	0	1	1	0	0
78	*Plesiopterys wildii*	0	0	1	0	1	0	1	0	-	-	0	0	1	0	0	-	0	1	0	0	0	0	-	0	1	0	0	0	0
79	Lincoln taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
80	Golden Cap taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
81	LEICT G18.1996	?	?	?	?	?	?	1	?	?	?	{02}	1	?	?	?	?	?	?	?	?	?	?	0	1	?	?	0	?	2
82	*Muraenosaurus platyclis*	0	1	1	0	1	0	1	0	-	1	0	{02}	1	0	0	-	1	0	1	1	-	?	-	0	1	0	0	0	2
83	NHMUK R.2861	0	1	1	0	?	0	1	1	0	1	1	1	2	1	0	0	-	1	0	1	1	-	1	-	0	1	0	0	2
84	NHMUK R.2864	?	?	?	?	?	?	1	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
85	*Vinialesaurus caroli*	0	1	1	0	1	0	1	0	-	-	0	2	1	0	0	-	0	?	0	0	?	1	-	0	1	0	0	0	2
86	*Gallardosaurus iturraldei*	?	?	?	2	?	?	2	0	-	-	?	1	1	?	?	1	0	0	0	0	1	0	?	1	0	0	0	0	0
87	*Pahasapasaurus haasi*	0	0	1	2	0	0	2	0	-	-	0	0	{12}	0	0	0	?	0	0	1	0	?	?	0	0	?	?	0	0
88	*Dolichorhynchops bonneri*	0	0	1	2	1	0	2	0	-	-	0	0	1	0	0	0	-	0	1	1	0	1	1	1	1	0	0	0	1
89	*Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90	TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
91	*Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
92	CM Zfr 145	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93	CM Zfr 115	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
94	*Futabasaurus suzukii*	0	0	1	?	0	{12}	1	0	1	1	?	{12}	1	0	?	?	?	0	?	0	1	0	?	?	0	?	0	0	0
95	*Tuarangisaurus keyesi*	0	0	1	0	1	0	{12}	1	0	1	0	{02}	{12}	0	0	-	0	?	0	1	0	1	0	-	0	1	?	?	0
96	*Tatenectes laramiensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
97	*Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98	MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
99	*Picrocleidus beloclis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100	*Eoplesiosaurus antiquior*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
101	*Borealonectes russeli*	1	0	1	1	1	0	2	1	1	1	0	0	2	0	0	-	0	0	1	0	1	1	0	?	1	0	1	0	0
102	*Colymbosaurus trochanterius*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
103	*Eretmosaurus rugosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
104	*Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
105	MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
106	*'Cimoliasaurus' valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
107	*Zarafasaura oceanis*	?	0	1	0	1	0	2	1	1	1	0	2	2	0	0	-	1	0	1	0	1	0	-	0	1	1	0	0	0

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
1 *Archaeonectrus rostratus*	?	0	0	0	?	?	?	?	?	?	?	0	?	?	0	?	0	?	0	?	1	?	1	1	0	?	1	0	1
2 *Aristonectes parvidens*	0	0	0	1	?	?	?	?	0	?	?	?	?	?	1	?	?	1	1	1	1	-	1	?	?	?	1	0	?
3 *Attenborosaurus conybeari*	?	?	0	0	?	?	?	?	?	?	?	?	?	0	1	0	1	?	0	?	?	1	?	?	?	?	?	?	?
4 *Augustasaurus hagdorni*	0	0	0	0	0	?	0	1	0	0	0	?	1	?	1	0	0	1	0	0	0	1	1	1	1	1	1	0	1
5 *Marmornectes candrewi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	0	0
6 NHMUK 49202	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	2	0	0	2	1	1	0	1	1	1	1
7 NHMUK R2439	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8 *Brachauchenius lucasi*	1	1	0	0	0	1	0	1	1	0	1	?	0	?	0	2	0	1	0	0	2	1	1	?	?	?	1	0	0
9 *Brancasaurus brancai*	?	?	0	?	0	?	0	1	0	1	?	1	1	0	0	2	0	1	0	1	0	-	1	1	2	2	1	3	0
10 *Callawayasaurus colombiensis*	?	0	0	?	?	?	0	?	?	?	1	?	?	0	2	0	1	0	0	?	1	?	1	2	0	0	1	0	0
11 *Cymatosaurus*	0	0	0	0	?	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	(01)	0	0	?	(03)	0	0	0	-
12 *Cryptoclidus eurymerus*	?	1	0	1	0	0	1	1	0	?	?	2	1	0	0	1	0	1	0	1	0	-	1	1	0	0	1	1	0
13 *Dolichorhynchops herschelensis*	?	?	?	?	?	?	?	?	1	0	?	?	?	?	0	?	1	2	-	-	1	?	1	2	0	2	1	3	1
14 *Dolichorhynchops osborni*	0	1	1	0	0	?	0	1	0	0	1	2	0	0	0	2	0	2	-	-	1	?	1	2	0	2	1	3	1
15 *Edgarosaurus muddi*	0	0	0	0	0	?	0	1	0	0	0	2	0	1	0	2	0	1	0	0	0	0	1	?	0	2	1	3	1
16 *Elasmosaurus platyurus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 *Eopolycotylus rankini*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18 *Eromangasaurus australis*	0	0	0	0	0	0	0	1	0	?	?	?	?	1	1	2	0	0	1	0	1	?	?	{12}	?	?	?	0	?
19 *Eurycleidus arcuatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20 FHSMVP321	1	1	0	0	0	1	0	1	1	0	1	2	0	?	0	2	0	1	0	0	2	1	1	2	0	2	1	0	0
21 *Hauffiosaurus longirostris*	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	0	0	1	0	?
22 *Hauffiosaurus tomistomimus*	0	?	0	?	0	?	?	?	1	0	0	?	?	?	0	?	?	1	0	0	1	0	1	0	0	0	1	0	?
23 *Hauffiosaurus zanoni*	0	?	0	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24 *Hydrorion brachypterygius*	0	0	0	0	1	0	0	1	0	0	0	1	?	0	0	?	0	1	0	1	0	-	1	1	0	0	1	1	0
25 *Hydrotherosaurus alexandrae*	?	0	0	1	?	?	0	1	?	1	1	0	1	0	0	?	1	?	1	?	1	1	2	?	0	?	?	?	?
26 *Kaiwhekea katiki*	?	0	0	1	?	?	?	0	0	?	0	?	1	2	1	0	1	0	1	?	1	2	0	?	0	?	0	?	?
27 *Kimmerosaurus langhami*	1	0	?	?	?	?	?	?	?	0	?	?	?	?	1	?	?	1	0	1	0	-	1	0	?	0	1	0	0
28 *Kronosaurus queenslandicus*	1	?	0	?	0	2	0	1	?	1	?	?	0	?	?	1	?	1	?	0	{12}	?	1	?	?	?	?	?	?
29 *Leptocleidus capensis*	?	1	0	0	0	1	0	1	0	?	1	0	0	0	?	0	1	0	0	0	2	1	1	0	2	1	2	0	?
30 *Leptocleidus superstes*	?	1	0	?	?	?	?	?	?	?	1	0	0	0	?	0	1	0	0	?	2	1	1	2	0	2	1	2	0
31 *Libonectes morgani*	0	?	?	0	1	0	1	0	?	?	1	?	1	2	0	2	?	-	1	?	1	{12}	?	0	?	?	?	?	?
32 *Liopleurodon ferox*	1	1	0	0	?	1	0	1	0	1	1	0	0	0	2	0	1	0	0	0	2	1	1	2	0	0	1	0	1
33 *Macroplata tenuiceps*	?	0	?	0	?	?	?	?	?	0	?	?	?	?	0	?	?	?	?	0	?	1	?	?	0	?	1	0	?
34 *Manemergus anguirostris*	0	0	0	0	0	?	?	?	0	?	?	?	?	?	1	2	1	0	0	?	2	2	1	1	0	2	1	3	1
35 *Maresaurus coccai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	1	?	1	1	1	1	1	1
36 *Microcleidus homalospondylus*	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	2	0	1	0	0	0	1	1	0	0	1	1	1	1
37 *Muraenosaurus leedsi*	1	1	0	1	0	0	?	1	0	0	?	1	1	0	0	?	?	1	0	0	0	1	2	0	0	1	1	0	0
38 *Nichollssaura borealis*	?	1	0	0	?	0	0	1	0	?	?	?	?	0	?	0	1	2	?	0	?	1	1	2	2	1	0	0	1
39 *Occitanosaurus tournemirensis*	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	0	?	?	?	0	0	1	1	0	0	1	0	1
40 OUMNH J.02247	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	1	1	2	?	?	?	?	?	?
41 *Stratesaurus taylori*	0	1	0	0	0	2	0	1	0	0	1	0	1	0	0	1	0	0	0	0	2	1	0	0	1	0	0	0	?
42 OUMNH J.28585	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	0	0	?	?	?	?	?
43 *Palmulasaurus quadratus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44 *Peloneustes philarchus*	1	1	0	0	0	?	0	1	1	0	1	2	0	0	0	2	0	1	0	0	2	1	1	2	0	0	1	0	1
45 *Plesiopleurodon wellesi*	?	1	0	0	?	?	0	1	0	0	0	2	0	0	?	2	0	?	?	0	2	?	1	?	2	1	3	1	?
46 *Plesiosaurus dolichodeirus*	0	0	0	0	1	0	1	0	0	0	{12}	1	0	0	0	2	0	1	0	0	2	1	0	0	1	0	0	1	0
47 *Plesiosaurus macrocephalus*	?	?	0	0	?	1	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	2	1	0	0	?	1	0	?
48 *Pliosaurus andrewsi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	1	?	?	?	?	0	?	?	?
49 *Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50 *Pliosaurus brachyspondylus*	1	1	0	?	0	1	0	1	1	0	1	2	0	0	0	2	0	1	0	0	1	1	1	2	0	0	1	0	1
51 *Polycotylus latipinnis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?
52 QMF 18041	0	0	0	0	?	1	0	?	0	?	?	?	0	?	2	0	2	-	-	0	2	1	1	0	2	1	3	1	?
53 *Rhomaleosaurus megacephalus*	0	1	0	0	0	2	0	0	0	0	0	1	0	0	1	0	1	0	0	0	2	1	0	0	1	1	1	0	1
54 *Meyerasaurus victor*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
55 *Rhomaleosaurus zetlandicus*	0	?	0	?	0	0	0	0	0	?	0	0	1	0	0	?	1	0	0	1	2	1	0	0	1	1	0	1	1
56 *Seeleyosaurus guilelmiimperatoris*	0	?	0	?	0	1	0	1	0	0	0	1	1	0	?	2	0	1	0	1	0	-	1	1	0	0	1	1	0
57 *Simolestes vorax*	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0	2	0	1	0	0	1	1	1	2	0	0	1	0	1
58 *Simosaurus gaillardoti*	0	0	0	0	2	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	-
59 *Styxosaurus snowii*	0	0	0	1	0	1	0	1	0	?	?	?	?	1	2	0	2	1	?	1	?	1	2	?	0	1	0	?	?
60 *Terminonatator pontiexensis*	?	?	?	1	?	?	?	?	?	?	0	?	1	?	?	2	-	-	?	1	2	0	0	?	1	0	?	?	?
61 *Thalassiodracon hawkinsii*	0	?	0	0	?	0	0	0	0	0	0	2	1	0	0	1	0	0	1	0	1	2	0	0	1	1	0	0	1
62 *Thalassomedon haningtoni*	?	0	0	1	0	?	0	1	0	0	1	1	?	1	?	1	0	2	0	1	1	1	2	0	0	1	0	1	1
63 *Thililua ongicollis*	?	?	0	?	0	0	?	1	0	?	?	?	?	?	2	2	0	2	-	-	?	1	?	?	2	1	?	?	?
64 *Tricleidus seeleyi*	?	1	?	1	?	-	1	1	0	?	?	?	?	0	1	0	1	0	1	0	0	1	2	0	0	1	?	?	?
65 *Trinacromerum bentonianum*	?	1	1	0	?	?	?	1	0	?	0	2	2	0	0	2	0	2	-	-	1	?	1	2	0	2	1	3	1
66 *Umoonasaurus demoscyllus*	?	0	0	?	?	?	?	?	?	?	?	0	?	?	?	1	2	?	1	2	1	{12}	2	?	1	0	1	?	?
67 *Pistosaurus* skull	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	1	1	0	0	?
68 *Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
69 *Yunguisaurus liae*	0	0	0	0	?	?	?	?	?	?	0	1	?	0	?	0	?	0	1	0	1	1	1	?	?	?	?	?	?
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
71 LEICT G1.2002	1	1	0	?	0	?	0	1	?	0	0	{01}	?	0	0	1	0	1	2	1	0	-	1	0	2	0	1	3	0
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
73 Speeton taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
74 *Hydralmosaurus serpentinus*	?	0	0	1	?	0	0	1	0	?	?	?	?	0	?	0	2	0	0	?	1	?	1	2	?	?	1	0	?
75 *Rhomaleosaurus cramptoni*	0	?	0	0	?	0	0	0	0	0	0	?	1	0	?	1	0	0	1	0	1	2	1	0	?	1	0	1	1
76 *Rhomaleosaurus thorntoni*	?	?	0	?	0	2	0	0	0	?	0	?	0	?	?	?	1	0	0	1	2	?	?	?	?	?	?	?	?
77 *Avalonnectes arturi*	0	1	1	0	?	0	0	1	0	0	1	0	0	0	?	1	0	0	1	0	0	2	1	0	0	1	1	0	1
78 *Plesiopterys wildii*	?	0	?	1	?	?	0	1	?	?	0	1	?	?	0	?	?	?	?	0	?	1	?	?	0	?	1	1	0
79 Lincoln taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
80 Golden Cap taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
81 LEICT G18.1996	?	1	0	?	0	?	?	?	?	?	?	?	?	0	?	?	1	0	1	0	?	1	{12}	?	0	1	1	0	?
82 *Muraenosaurus platyclis*	1	1	0	1	0	0	0	1	0	0	0	0	?	0	0	1	0	1	0	0	2	1	2	2	0	1	0	0	0
83 NHMUK R.2861	1	1	0	0	0	0	0	1	0	0	?	0	?	0	1	0	0	1	0	0	0	1	2	?	0	1	0	0	?
84 NHMUK R.2864	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
85 *Vinialesaurus caroli*	?	?	0	?	?	?	?	0	?	?	?	?	?	?	?	1	0	1	0	?	1	{12}	?	?	?	?	?	?	?
86 *Gallardosaurus iturraldei*	?	1	0	0	0	?	0	1	1	0	?	?	?	?	0	1	0	1	0	0	2	1	1	2	0	2	1	0	1
87 *Pahasapasaurus haasi*	?	?	0	0	?	?	0	1	0	?	?	?	?	0	?	1	?	2	-	?	1	?	{12}	?	0	1	0	1	?
88 *Dolichorhynchops bonneri*	?	1	1	0	0	0	0	1	0	?	?	2	0	0	?	2	0	2	-	-	1	?	1	2	0	2	1	3	1
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90 TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
91 *Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
92 CM Zfr 145	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93 CM Zfr 115	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	{12}	?	0	1	0	1
94 *Futabasaurus suzukii*	0	0	0	0	2	0	0	1	0	0	0	?	?	0	?	0	1	0	0	0	?	?	?	?	?	?	?	?	?
95 *Tuarangisaurus keyesi*	0	0	0	1	0	?	0	1	?	?	?	?	?	1	2	1	2	-	-	?	2	1	2	0	0	1	0	?	?
96 *Tatenectes laramiensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	1	?	?	?	?	?	?	?	1	{01}	?	?
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98 MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
99 *Picrocleidus beloclis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100 *Eoplesiosaurus antiquior*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
101 *Borealonectes russelli*	?	1	0	0	0	0	0	1	0	0	0	1	1	0	0	2	0	1	0	0	1	0	1	?	?	?	?	?	?
102 *Colymbosaurus trochanterius*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
103 *Eretmosaurus rugosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
104 *Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
105 MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
106 *'Cimoliosaurus' valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
107 *Zarafasaura oceanis*	0	0	0	0	0	0	0	1	0	1	0	2	0	0	1	2	1	2	-	-	0	0	1	1	1	0	1	0	0

II.2

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
1 *Archaeonectrus rostratus*	0	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2 *Aristonectes parvidens*	?	1	?	?	1	?	?	?	?	0	0	0	2	0	?	?	?	2	0	0	0	0	1	?	?	?	?	1	?
3 *Attenborosaurus conybeari*	0	?	0	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 *Augustasaurus hagdorni*	0	1	0	?	0	?	0	0	?	?	?	0	2	0	?	0	0	0	-	0	1	0	1	?	0	?	?	0	0
5 *Marmornectes candrewi*	0	?	?	0	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6 NHMUK 49202	0	1	0	0	0	1	?	0	?	0	0	0	2	0	0	0	0	0	-	0	1	?	0	?	1	0	?	2	?
7 NHMUK R2439	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8 *Brachauchenius lucasi*	0	?	0	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	1	1	1	0	?	0	0	?	?	1	1
9 *Brancasaurus brancai*	?	1	?	0	0	?	1	?	?	?	0	0	1	0	?	0	0	0	-	0	1	0	1	?	0	?	?	2	?
10 *Callawayasaurus colombiensis*	0	1	0	?	0	?	?	0	?	0	?	0	2	0	1	0	1	0	-	0	0	0	1	0	?	1	?	?	1
11 *Cymatosaurus*	0	0	0	0	1	0	1	0	0	0	1	0	2	0	0	0	0	0	-	0	1	1	0	0	0	0	0	0	1
12 *Cryptoclidus eurymerus*	1	1	0	0	1	0	0	0	1	0	0	0	2	2	1	0	0	?	?	0	1	0	1	0	0	1	?	1	1
13 *Dolichorhynchops herschelensis*	0	1	0	0	0	?	0	0	?	0	0	2	?	?	?	0	?	0	-	?	?	?	?	?	?	0	?	2	?
14 *Dolichorhynchops osborni*	0	1	0	0	0	?	0	0	1	0	0	0	2	2	?	0	1	0	-	0	0	0	1	1	1	0	0	2	?
15 *Edgarosaurus muddi*	0	1	0	0	0	1	1	?	0	?	0	?	?	?	?	0	0	?	-	?	?	?	?	?	1	0	?	?	1
16 *Elasmosaurus platyurus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 *Eopolycotylus rankini*	?	?	?	?	?	?	?	?	?	?	0	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18 *Eromangasaurus australis*	?	?	?	?	?	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 *Eurycleidus arcuatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20 FHSMVP321	?	?	?	0	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21 *Hauffiosaurus longirostris*	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22 *Hauffiosaurus tomistomimus*	0	1	0	?	0	1	?	0	1	0	1	0	2	0	0	0	0	0	-	0	1	1	0	?	?	?	?	2	?
23 *Hauffiosaurus zanoni*	?	?	?	?	?	0	?	1	?	1	0	2	0	0	?	0	0	0	-	0	1	1	0	0	1	0	?	?	1
24 *Hydrorion brachypterygius*	0	1	1	?	0	?	1	0	?	0	0	0	2	1	1	0	0	2	0	0	1	0	0	?	?	1	1	1	1
25 *Hydrotherosaurus alexandrae*	?	?	?	0	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 *Kaiwhekea katiki*	?	1	?	?	1	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27 *Kimmerosaurus langhami*	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28 *Kronosaurus queenslandicus*	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	2	?	?
29 *Leptocleidus capensis*	?	1	1	?	0	1	?	?	?	?	1	0	1	0	0	2	0	0	-	0	1	0	?	1	0	?	2	2	1
30 *Leptocleidus superstes*	?	1	1	1	0	?	?	0	?	0	?	0	2	0	?	0	0	0	-	0	1	0	?	1	0	0	?	2	?
31 *Libonectes morgani*	?	1	?	?	0	1	0	0	0	0	0	0	2	0	?	0	1	0	-	0	1	0	0	0	0	1	0	1	1
32 *Liopleurodon ferox*	0	1	0	0	0	1	1	0	1	0	1	0	2	0	0	2	0	?	1	1	1	0	1	0	0	1	2	1	?
33 *Macroplata tenuiceps*	?	1	0	?	?	0	?	?	?	0	?	0	2	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
34 *Manemergus anguirostris*	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
35 *Maresaurus coccai*	0	1	0	0	0	?	0	0	1	0	1	?	2	0	0	2	0	0	-	0	1	1	0	?	1	0	?	2	?
36 *Microcleidus homalospondylus*	0	1	1	1	0	1	1	0	?	0	0	0	1	?	0	0	0	0	-	0	0	0	0	0	0	0	0	?	1
37 *Muraenosaurus leedsi*	1	1	0	1	1	?	?	0	1	?	0	0	2	{12}	0	0	0	2	0	0	1	0	1	0	?	1	0	1	1
38 *Nichollssaura borealis*	0	1	0	1	0	1	1	?	?	0	0	0	2	0	1	{01}	0	0	-	1	?	0	?	1	0	0	?	2	0
39 *Occitanosaurus tournemirensis*	0	1	1	1	0	0	1	0	?	0	0	0	2	1	1	0	0	2	0	0	1	0	0	?	0	0	0	1	1
40 OUMNH J.02247	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41 *Stratesaurus taylori*	0	?	?	0	?	0	0	0	?	1	0	?	?	?	0	0	0	0	-	0	0	0	1	?	?	0	?	1	?
42 OUMNH J.28585	0	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43 *Palmulasaurus quadratus*	?	?	?	?	?	?	?	?	?	?	0	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44 *Peloneustes philarchus*	0	1	0	0	0	1	0	0	1	0	1	0	2	0	1	(01)	0	1	-	0	1	1	0	1	0	0	0	2	1
45 *Plesiopleurodon wellesi*	0	1	0	1	0	?	0	0	?	0	?	0	2	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?
46 *Plesiosaurus dolichodeirus*	1	1	1	0	0	1	0	0	1	0	0	0	2	{01}	1	0	0	2	0	0	1	0	1	0	?	0	0	1	1
47 *Plesiosaurus macrocephalus*	?	?	?	0	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48 *Pliosaurus andrewsi*	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49 *Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50 *Pliosaurus brachyspondylus*	0	?	?	0	0	1	1	0	1	0	0	?	?	?	1	?	1	?	-	1	?	?	?	1	1	0	?	2	0
51 *Polycotylus latipinnis*	0	?	?	0	0	1	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
52 QMF 18041	0	1	0	0	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?
53 *Rhomaleosaurus megacephalus*	0	1	1	0	0	1	1	0	?	0	1	1	2	0	0	0	0	?	0	1	1	0	1	1	0	1	2	1
54 *Meyerasaurus victor*	?	?	?	0	?	?	?	0	?	0	?	0	2	0	?	2	0	0	-	0	1	1	0	?	1	0	?	2	0
55 *Rhomaleosaurus zetlandicus*	0	1	0	0	1	1	1	0	1	0	2	0	2	0	0	2	0	?	0	1	1	0	?	0	?	2	2	1
56 *Seeleyosaurus guilelmiimperatoris*	0	1	1	1	0	?	1	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
57 *Simolestes vorax*	0	1	0	0	0	1	1	0	?	0	1	0	2	0	0	2	0	0	-	0	1	1	0	?	0	?	2	2	?
58 *Simosaurus gaillardoti*	-	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	-	0	1	0	1	0	0	0	0	1	0
59 *Styxosaurus snowii*	0	1	0	1	?	1	1	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
60 *Terminonatator pontiexensis*	?	1	0	0	?	?	?	0	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
61 *Thalassiodracon hawkinsii*	0	1	0	1	0	1	0	0	0	0	0	0	?	0	1	0	0	0	-	0	1	1	1	?	0	?	2	0
62 *Thalassomedon haningtoni*	0	1	?	1	?	1	?	0	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
63 *Thililua ongicollis*	0	1	0	0	?	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
64 *Tricleidus seeleyi*	1	1	?	0	?	0	?	0	1	0	?	?	?	?	0	?	?	?	?	0	?	0	?	?	1	?	1	?	?
65 *Trinacromerum bentonianum*	0	1	0	0	0	?	0	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0
66 *Umoonasaurus demoscyllus*	0	?	0	1	0	?	?	0	?	?	1	?	{01}	0	?	?	?	0	-	?	0	?	?	1	?	?	?	1	?
67 *Pistosaurus* skull	?	1	?	0	?	?	1	?	?	0	0	1	0	?	0	?	0	?	0	-	0	0	0	0	0	0	?	0	0
68 *Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
69 *Yunguisaurus liae*	?	?	?	?	?	?	1	?	?	?	?	{01}	{01}	?	?	0	?	0	?	?	1	0	0	?	?	0	?	?	?
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
71 LEICT G1.2002	0	1	?	?	0	1	0	1	?	1	?	?	?	{01}	?	0	0	?	?	?	?	?	?	?	?	?	?	?	1
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
73 Speeton taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
74 *Hydralmosaurus serpentinus*	0	1	0	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
75 *Rhomaleosaurus cramptoni*	0	1	1	0	0	1	1	1	0	1	1	2	0	0	0	2	0	0	-	0	1	1	0	1	1	0	2	2	1
76 *Rhomaleosaurus thorntoni*	?	?	?	?	?	?	?	?	?	?	1	1	2	0	?	?	0	2	0	?	1	?	1	?	1	?	1	1	1
77 *Avalonnectes arturi*	0	1	1	0	1	0	0	0	1	0	0	?	?	?	?	?	?	?	-	?	?	?	?	?	?	?	?	?	?
78 *Plesiopterys wildii*	1	1	?	0	1	?	?	0	1	0	?	0	?	?	?	?	?	?	?	0	?	0	?	?	1	?	?	?	?
79 Lincoln taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
80 Golden Cap taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
81 LEICT G18.1996	1	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
82 *Muraenosaurus platyclis*	1	1	0	1	1	0	0	0	?	0	0	0	2	0	0	1	2	0	0	1	0	1	0	0	1	0	0	?	1
83 NHMUK R.2861	1	1	0	0	1	0	0	0	?	0	0	0	2	2	1	0	0	2	0	0	1	0	0	?	?	?	?	0	1
84 NHMUK R.2864	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	?	0	2	1	0	1	0	1	?	1	?	?	?
85 *Vinialesaurus caroli*	?	?	?	?	?	?	?	?	?	?	0	0	?	0	?	0	?	2	1	1	0	?	?	?	?	?	1	?	?
86 *Gallardosaurus iturraldei*	0	1	0	1	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	2	1		
87 *Pahasapasaurus haasi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	-	?	?	?	?	?	0	?	2	?	?
88 *Dolichorhynchops bonneri*	0	1	0	0	0	?	0	?	0	?	0	0	2	?	?	0	?	0	-	0	?	?	?	?	?	?	{12}	?	
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90 TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
91 *Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
92 CM Zfr 145	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93 CM Zfr 115	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
94 *Futabasaurus suzukii*	?	?	?	?	?	?	?	?	?	?	0	2	0	1	1	0	0	-	0	1	0	0	?	?	?	?	1	?	
95 *Tuarangisaurus keyesi*	0	?	?	0	?	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
96 *Tatenectes laramiensis*	1	1	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98 MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
99 *Picrocleidus beloclis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100 *Eoplesiosaurus antiquior*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
101 *Borealonectes russelli*	?	1	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	2	?		
102 *Colymbosaurus trochanterius*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
103 *Eretmosaurus rugosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
104 *Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
105 MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
106 *'Cimoliosaurus' valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
107 *Zarafasaura oceanis*	?	1	?	1	1	?	0	?	?	0	?	?	2	0	?	0	0	0	-	0	1	1	0	0	?	?	?	0	0

II.3

	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116
1 *Archaeonectrus rostratus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2 *Aristonectes parvidens*	0	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3 *Attenborosaurus conybeari*	?	?	?	?	?	0	?	?	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 *Augustasaurus hagdorni*	0	-	-	-	1	0	?	0	-	1	0	0	1	0	0	?	0	0	0	0	0	0	0	1	0	?	?	?	?
5 *Marmornectes candrewi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
6 NHMUK 49202	1	1	1	0	1	0	0	0	-	0	-	-	-	-	2	0	0	0	0	0	1	1	3	1	0	0	0	0	0
7 NHMUK R2439	?	?	?	?	?	?	0	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
8 *Brachauchenius lucasi*	0	-	-	-	1	0	1	1	1	1	0	0	1	2	1	-	0	0	0	0	0	1	1	0	?	-	?	?	?
9 *Brancasaurus brancai*	?	?	?	?	1	0	1	0	-	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	0	0	1	0
10 *Callawayasaurus colombiensis*	0	-	-	-	1	0	1	1	1	1	0	0	0	-	0	1	?	?	?	0	1	1	0	1	1	?	?	?	?
11 *Cymatosaurus*	0	-	-	-	0	-	-	-	-	1	0	0	1	0	2	1	-	0	0	?	0	1	-	-	-	-	?	-	?
12 *Cryptoclidus eurymerus*	1	2	1	0	1	1	-	-	-	1	0	0	0	-	0	0	?	?	1	?	1	1	2	1	0	0	0	0	0
13 *Dolichorhynchops herschelensis*	1	?	1	1	0	1	1	?	1	1	0	0	-	0	3	?	1	?	1	2	1	1	?	?	1	?	1	?	?
14 *Dolichorhynchops osborni*	1	0	1	1	1	0	1	1	?	1	1	0	0	-	0	3	2	-	1	?	1	1	2	1	1	1	?	1	0
15 *Edgarosaurus muddi*	1	?	1	0	1	1	1	?	1	1	0	0	-	?	2	?	0	?	0	?	1	0	1	1	?	1	1	1	?
16 *Elasmosaurus platyurus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 *Eopolycotylus rankini*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18 *Eromangasaurus australis*	?	?	?	?	1	0	1	1	?	1	1	0	?	?	?	?	?	0	?	?	?	0	1	1	1	?	?	?	?
19 *Eurycleidus arcuatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20 FHSMVP321	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21 *Hauffiosaurus longirostris*	?	?	?	?	1	0	1	1	0	?	0	?	0	-	?	0	?	?	?	0	?	-	0	-	0	?	0	0	?
22 *Hauffiosaurus tomistomimus*	0	-	-	-	1	0	1	0	-	1	0	1	0	-	1	0	?	?	0	?	0	1	-	0	-	0	?	0	0
23 *Hauffiosaurus zanoni*	0	-	-	-	1	0	1	0	-	1	0	?	0	-	1	1	?	0	?	0	?	?	?	?	?	?	?	?	?
24 *Hydrorion brachypterygius*	0	-	-	-	1	1	1	1	?	1	?	?	?	?	0	0	0	0	0	0	1	1	2	1	0	?	?	?	?
25 *Hydrotherosaurus alexandrae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 *Kaiwhekea katiki*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27 *Kimmerosaurus langhami*	?	?	?	?	1	2	-	-	-	0	0	0	0	-	?	0	0	1	1	?	1	?	?	?	?	?	1	?	?
28 *Kronosaurus queenslandicus*	0	-	-	-	1	?	1	?	1	1	0	0	1	2	?	-	0	0	0	0	0	1	1	0	0	?	?	?	?
29 *Leptocleidus capensis*	1	?	0	-	1	0	1	1	?	1	?	0	?	-	2	?	?	0	?	0	?	1	0	1	0	0	?	?	?
30 *Leptocleidus superstes*	?	?	?	?	1	0	1	?	?	1	?	0	?	-	2	2	0	1	0	1	?	1	0	1	1	0	?	?	?
31 *Libonectes morgani*	0	-	-	-	1	0	1	1	1	1	0	0	0	-	0	2	2	-	0	-	1	1	0	1	1	0	?	?	0
32 *Liopleurodon ferox*	0	-	-	-	1	0	1	1	1	1	0	0	1	2	1	-	0	0	0	0	0	1	0	1	0	0	0	?	0
33 *Macroplata tenuiceps*	?	?	?	?	1	0	1	0	-	1	0	?	?	?	?	?	?	?	?	?	1	3	1	1	?	?	1	?	?
34 *Manemergus anguirostris*	?	?	?	?	?	1	1	1	?	1	?	?	0	-	?	?	?	?	?	?	?	0	1	1	0	?	?	?	?
35 *Maresaurus coccai*	0	-	-	-	1	1	1	1	?	1	0	0	-	0	1	?	0	?	0	0	1	3	1	0	?	?	?	?	?
36 *Microcleidus homalospondylus*	0	-	-	-	1	0	1	1	1	0	0	1	0	0	-	0	0	0	0	0	1	1	1	0	0	?	?	0	?
37 *Muraenosaurus leedsii*	1	2	1	0	1	1	-	-	-	0	-	-	-	-	1	0	0	1	1	?	1	1	2	1	0	1	1	0	1
38 *Nichollssaura borealis*	1	0	0	-	1	0	1	?	?	1	1	0	0	-	0	2	?	0	?	1	1	1	0	1	0	0	?	?	?
39 *Occitanosaurus tournemirensis*	?	?	?	?	1	0	1	1	1	0	0	1	0	0	-	0	0	0	0	0	1	-	0	-	0	?	0	?	0
40 OUMNH J.02247	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41 *Stratesaurus taylori*	0	-	-	-	1	0	1	0	-	1	0	1	0	-	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0
42 OUMNH J.28585	?	?	?	?	1	0	1	0	-	?	?	?	?	?	?	0	?	0	0	0	?	?	-	0	-	0	1	0	0
43 *Palmulasaurus quadratus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44 *Peloneustes philarchus*	2	-	-	-	1	0	1	1	1	1	0	0	1	1	1	-	0	0	0	0	0	1	0	1	0	0	0	?	0
45 *Plesiopleurodon wellesi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
46 *Plesiosaurus dolichodeirus*	0	-	-	-	1	0	0	0	-	0	-	-	-	-	2	?	0	0	0	0	1	1	2	1	0	0	0	?	0
47 *Plesiosaurus macrocephalus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48 *Pliosaurus andrewsi*	?	?	?	?	1	0	?	1	?	1	?	1	?	?	?	?	?	0	?	?	?	1	1	1	0	?	?	?	?
49 *Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50 *Pliosaurus brachyspondylus*	?	?	?	?	1	0	1	1	?	1	0	0	1	2	?	-	0	0	0	0	0	1	1	1	0	?	?	?	?
51 *Polycotylus latipinnis*	?	?	?	?	1	0	0	1	1	1	1	0	0	-	0	?	0	?	?	?	?	0	1	1	0	0	?	?	0
52 QMF 18041	1	?	?	?	1	?	?	0	-	1	1	0	0	-	0	2	?	0	?	1	?	0	1	1	0	0	?	?	?
53 *Rhomaleosaurus megacephalus*	1	0	0	-	1	0	1	0	1	1	1	0	0	-	1	1	?	0	0	1	3	1	0	0	0	0	0	0	0
54 *Meyerasaurus victor*	1	?	0	-	1	0	0	1	1	1	?	?	0	-	2	1	?	0	?	1	0	0	1	1	0	?	?	?	?
55 *Rhomaleosaurus zetlandicus*	0	-	-	-	1	0	1	0	-	1	0	0	0	-	0	1	?	0	0	1	0	?	?	0	?	?	0	?	?
56 *Seeleyosaurus guilelmiimperatoris*	0	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
57 *Simolestes vorax*	?	?	?	?	1	0	1	1	1	1	0	0	1	0	1	-	0	0	0	0	1	0	1	0	0	0	0	?	0
58 *Simosaurus gaillardoti*	0	-	-	-	0	-	-	-	-	1	0	0	0	-	2	1	-	0	0	1	-	?	?	?	-	?	?	?	?
59 *Styxosaurus snowii*	?	?	?	?	1	0	1	?	?	1	1	0	0	-	0	?	?	?	?	?	?	1	?	1	1	?	?	?	?
60 *Terminonatator pontiexensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
61 *Thalassiodracon hawkinsii*	0	-	-	-	1	0	1	0	-	1	0	1	0	-	1	0	0	0	0	1	1	-	0	-	0	0	0	0	0
62 *Thalassomedon haningtoni*	0	-	-	-	1	?	1	0	-	1	1	0	0	-	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
63 *Thililua longicollis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
64 *Tricleidus seeleyi*	1	2	1	0	1	1	-	-	-	0	-	-	-	-	1	0	0	1	1	1	1	1	2	1	?	1	1	0	0
65 *Trinacromerum bentonianum*	1	?	1	0	1	0	1	?	?	1	1	0	0	-	0	3	?	1	?	1	1	2	1	1	0	0	1	0	?
66 *Umoonasaurus demoscyllus*	1	?	0	-	1	0	1	1	?	1	1	1	0	-	0	3	0	1	0	1	1	1	0	1	1	0	?	?	?
67 *Pistosaurus* skull	0	-	-	-	1	{01}	0	0	-	1	0	0	0	-	2	?	0	0	0	0	1	1	0	?	?	?	?	?	?
68 *Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
69 *Yunguisaurus liae*	0	-	-	-	1	0	?	0	-	1	0	0	1	0	2	?	0	0	?	0	1	0	1	0	0	0	0	?	0
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
71 LEICT G1.2002	?	?	?	?	1	0	1	1	0	1	1	1	0	-	1	0	0	0	1	?	1	0	?	-	0	?	0	0	0
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
73 Speeton taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
74 *Hydralmosaurus serpentinus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
75 *Rhomaleosaurus cramptoni*	2	-	-	-	1	0	1	0	1	1	0	0	-	0	1	1	-	0	1	1	3	1	0	0	0	0	0	0	0
76 *Rhomaleosaurus thorntoni*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
77 *Avalonnectes arturi*	?	?	?	?	0	-	1	0	1	1	1	?	0	-	?	0	0	1	-	?	0	?	0	0	?	?	?	?	?
78 *Plesiopterys wildii*	1	0	1	0	1	1	-	-	-	0	-	-	-	-	1	0	0	?	0	1	1	2	1	0	0	0	0	0	?
79 Lincoln taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
80 Golden Cap taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
81 LEICT G18.1996	?	?	?	?	1	1	-	-	-	0	-	-	-	-	0	0	?	?	?	?	1	3	1	0	1	1	0	1	1

Wait — row 81 LEICT G18.1996 corrected: | ? | ? | ? | ? | 1 | 1 | - | - | - | 0 | - | - | - | - | 0 | 0 | ? | ? | ? | ? | ? | 1 | 3 | 1 | 0 | 1 | 1 | 0 | 1 |

82 *Muraenosaurus platyclis*	1	2	1	0	1	1	-	-	-	0	-	-	-	-	1	0	0	1	1	0	1	1	3	1	0	0	1	0	1
83 NHMUK R.2861	1	2	1	0	1	1	-	-	-	0	-	-	-	-	1	0	0	1	1	0	1	1	3	1	0	0	0	1	0
84 NHMUK R.2864	1	2	1	?	1	{12}	-	-	-	0	-	-	-	-	?	?	?	?	?	?	1	1	?	1	0	1	1	?	1
85 *Vinialesaurus caroli*	2	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
86 *Gallardosaurus iturraldei*	2	-	-	-	1	0	1	1	?	1	0	1	1	1	0	1	0	0	0	0	0	1	1	1	?	?	?	?	?
87 *Pahasapasaurus haasi*	0	-	-	-	1	0	1	1	?	?	?	?	0	?	?	?	?	?	?	?	1	0	1	?	0	0	?	?	?
88 *Dolichorhynchops bonneri*	1	0	1	0	1	0	1	1	?	1	1	0	0	-	0	3	?	1	?	1	1	2	1	1	?	?	?	?	?
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90 TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
91 *Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
92 CM Zfr 145	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93 CM Zfr 115	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	?	?	0
94 *Futabasaurus suzukii*	0	-	-	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
95 *Tuarangisaurus keyesi*	?	?	?	?	1	?	?	?	?	1	?	?	0	-	?	1	?	?	?	?	?	?	0	1	1	1	1	?	0
96 *Tatenectes laramiensis*	?	?	?	?	0	0	0	1	?	1	0	0	0	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98 MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
99 *Picrocleidus beloclis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100 *Eoplesiosaurus antiquior*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
101 *Borealonectes russelli*	0	-	-	-	1	0	1	1	?	1	1	?	0	-	?	?	?	?	?	?	1	-	0	?	?	?	?	?	?
102 *Colymbosaurus trochanterius*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
103 *Eretmosaurus rugosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
104 *Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
105 MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
106 '*Cimoliasaurus*' *valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
107 *Zarafasaura oceanis*	0	-	-	-	1	0	1	1	?	1	1	0	0	-	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?

II.4

	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145
1 *Archaeonectrus rostratus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
2 *Aristonectes parvidens*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	0	?
3 *Attenborosaurus conybeari*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 *Augustasaurus hagdorni*	0	?	?	0	1	0	0	?	{01}	1	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	2	0	0
5 *Marmornectes candrewi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
6 NHMUK 49202	0	?	0	1	1	0	?	?	1	1	1	1	0	0	2	1	0	?	?	?	?	?	0	?	?	?	1	1	0
7 NHMUK R2439	?	?	?	?	?	0	1	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0
8 *Brachauchenius lucasi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	1	1	0
9 *Brancasaurus brancai*	0	0	?	?	?	2	0	1	1	1	0	1	?	?	0	1	0	1	0	0	1	1	1	0	0	0	?	?	?
10 *Callawayasaurus colombiensis*	0	?	?	0	2	-	1	0	?	0	0	?	0	1	1	0	?	0	?	?	?	?	0	?	?	?	1	?	?
11 *Cymatosaurus*	-	1	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 *Cryptoclidus eurymerus*	0	1	?	?	1	0	?	?	1	0	1	0	0	0	2	1	0	1	1	0	1	1	1	1	?	?	0	?	0
13 *Dolichorhynchops herschelensis*	?	?	?	2	1	2	-	?	?	0	?	?	0	?	1	1	0	1	?	?	?	?	?	?	?	?	1	1	1
14 *Dolichorhynchops osborni*	?	?	0	?	?	2	-	?	?	?	?	1	?	?	0	2	?	1	1	0	0	?	?	1	?	?	1	1	1
15 *Edgarosaurus muddi*	?	0	0	1	?	2	-	?	0	?	0	0	2	?	1	1	?	1	?	0	?	0	0	1	?	?	1	1	1
16 *Elasmosaurus platyurus*	?	?	?	?	?	{12}	-	?	0	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 *Eopolycotylus rankini*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
18 *Eromangasaurus australis*	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 *Eurycleidus arcuatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
20 FHSMVP321	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21 *Hauffiosaurus longirostris*	1	1	?	?	?	2	-	?	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
22 *Hauffiosaurus tomistomimus*	1	?	1	?	?	2	-	?	?	?	1	1	?	?	?	?	?	1	?	?	?	?	0	?	?	?	1	1	0
23 *Hauffiosaurus zanoni*	1	?	?	0	?	2	-	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24 *Hydrorion brachypterygius*	?	?	?	?	?	{12}	-	?	2	1	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0
25 *Hydrotherosaurus alexandrae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 *Kaiwhekea katiki*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27 *Kimmerosaurus langhami*	0	?	0	?	?	0	1	1	1	0	1	?	0	0	2	1	0	1	1	0	0	1	?	?	0	0	?	?	0
28 *Kronosaurus queenslandicus*	?	?	?	1	?	1	-	?	?	1	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	1	0
29 *Leptocleidus capensis*	?	?	?	?	?	2	-	0	2	?	?	?	2	1	?	?	0	?	?	?	?	?	?	?	?	?	?	1	0
30 *Leptocleidus superstes*	0	?	?	?	?	2	-	?	2	2	1	0	?	?	0	?	0	0	1	?	?	?	?	?	?	?	?	1	0
31 *Libonectes morgani*	?	?	?	1	?	2	-	1	0	0	0	0	?	1	0	1	0	1	0	0	0	?	?	0	0	0	0	0	0
32 *Liopleurodon ferox*	?	?	1	0	0	1	-	1	1	1	1	1	2	1	0	0	?	0	0	0	1	?	?	?	?	?	2	1	0
33 *Macroplata tenuiceps*	?	?	?	?	?	2	-	1	?	0	1	?	0	?	?	?	?	0	?	1	?	?	0	1	0	2	?	?	?
34 *Manemergus anguirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
35 *Maresaurus coccai*	?	?	?	1	?	{12}	-	?	?	?	?	1	2	1	0	?	0	?	?	?	?	?	?	?	?	?	0	1	?
36 *Microcleidus homalospondylus*	1	?	1	0	0	2	-	1	1	1	0	1	2	0	0	0	1	1	0	0	?	?	1	0	0	0	0	0	0
37 *Muraenosaurus leedsii*	0	1	0	?	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	?	1	0	0	0	1	1	0
38 *Nichollssaura borealis*	?	0	?	1	?	2	-	?	?	?	0	0	2	1	?	0	0	0	?	?	?	?	?	0	0	0	2	1	0
39 *Occitanosaurus tournemirensis*	1	?	?	?	0	2	-	?	1	?	0	?	2	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
40 OUMNH J.02247	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
41 *Stratesaurus taylori*	0	1	0	0	1	2	-	?	1	0	1	1	0	0	1	0	?	0	1	1	0	0	1	1	0	1	1	1	?
42 OUMNH J.28585	0	1	?	1	?	2	-	?	1	0	1	1	2	?	?	?	0	1	0	1	?	0	?	?	?	?	?	?	?
43 *Palmulasaurus quadratus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
44 *Peloneustes philarchus*	0	0	1	1	1	1	-	1	1	1	1	1	?	1	0	0	0	1	0	1	0	1	0	1	0	1	1	1	0
45 *Plesiopleurodon wellesi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
46 *Plesiosaurus dolichodeirus*	0	?	?	?	?	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0	0	0
47 *Plesiosaurus macrocephalus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48 *Pliosaurus andrewsi*	?	?	?	?	?	1	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0
49 *Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
50 *Pliosaurus brachyspondylus*	0	?	?	1	?	1	?	?	?	0	2	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
51 *Polycotylus latipinnis*	0	1	?	?	?	2	-	?	1	0	?	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
52 QMF 18041	?	?	1	?	1	2	-	?	?	?	?	1	?	?	0	1	?	?	?	?	?	?	?	?	?	?	1	1	0
53 *Rhomaleosaurus megacephalus*	0	1	1	1	?	2	-	1	1	1	1	2	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
54 *Meyerasaurus victor*	?	?	?	?	?	1	-	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0
55 *Rhomaleosaurus zetlandicus*	?	?	1	1	{12}	?	-	?	?	?	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0
56 *Seeleyosaurus guilelmiimperatoris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0
57 *Simolestes vorax*	0	?	?	?	0	1	?	1	1	1	1	1	2	1	0	0	?	0	?	?	?	?	?	?	?	?	1	1	0
58 *Simosaurus gaillardoti*	-	?	0	-	-	{12}	-	0	?	2	?	0	-	-	-	-	-	0	?	?	?	?	?	1	1	0	0	0	?
59 *Styxosaurus snowii*	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
60 *Terminonatator pontiexensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	1	1	0
61 *Thalassiodracon hawkinsii*	0	1	1	?	1	2	-	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	?	1	1	0
62 *Thalassomedon haningtoni*	?	?	?	1	?	2	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	1	0
63 *Thililua ongicollis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
64 *Tricleidus seeleyi*	0	1	0	?	?	0	0	1	0	0	0	?	2	0	0	1	0	1	?	0	0	0	?	?	?	?	?	?	0
65 *Trinacromerum bentonianum*	0	1	?	?	1	2	-	?	0	1	0	?	1	0	2	?	?	?	?	?	?	?	?	?	?	?	1	1	1
66 *Umoonasaurus demoscyllus*	0	?	?	?	?	2	-	1	1	?	1	?	1	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
67 *Pistosaurus* skull	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	{12}	?	?
68 *Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
69 *Yunguisaurus liae*	0	?	?	?	?	{12}	-	?	2	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	0
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
71 LEICT G1.2002	0	1	?	?	?	1	-	1	1	1	1	?	?	?	?	?	0	1	0	1	0	?	?	?	?	?	?	?	?
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
73 Speeton taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
74 *Hydralmosaurus serpentinus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
75 *Rhomaleosaurus cramptoni*	0	?	1	1	{12}	?	-	2	0	1	1	0	1	0	0	0	?	1	?	1	?	?	?	?	?	?	0	1	0
76 *Rhomaleosaurus thorntoni*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
77 *Avalonnectes arturi*	?	1	1	1	1	1	-	?	1	1	1	1	0	?	?	0	?	?	0	?	?	?	?	?	?	?	0	0	0
78 *Plesiopterys wildii*	?	1	?	?	0	0	1	0	?	0	1	1	?	0	?	?	?	0	0	0	0	?	0	0	0	?	0	0	0
79 Lincoln taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
80 Golden Cap taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
81 LEICT G18.1996	1	0	?	3	?	0	0	?	0	0	0	0	?	?	?	?	1	0	0	0	0	1	1	?	?	?	0	0	0
82 *Muraenosaurus platyclis*	0	1	0	3	1	0	?	0	0	0	0	0	?	?	?	1	0	1	0	0	1	1	?	0	0	0	?	0	0
83 NHMUK R.2861	0	1	0	3	1	0	1	1	0	0	0	0	{02}	0	0	1	0	1	0	0	1	0	0	1	?	0	0	0	0
84 NHMUK R.2864	1	1	?	?	?	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0
85 *Vinialesaurus caroli*	?	?	?	?	?	0	?	?	{01}	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
86 *Gallardosaurus iturraldei*	?	?	?	?	?	0	1	?	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
87 *Pahasapasaurus haasi*	?	?	?	?	?	0	1	?	{01}	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	?	?
88 *Dolichorhynchops bonneri*	0	?	?	2	?	{12}	-	?	{01}	?	0	0	?	?	1	?	?	?	?	?	?	?	?	0	?	?	1	1	1
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90 TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
91 *Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
92 CM Zfr 145	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93 CM Zfr 115	0	?	?	?	?	2	-	?	0	?	0	1	?	?	?	?	1	0	0	0	0	?	?	?	?	?	?	?	0
94 *Futabasaurus suzukii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
95 *Tuarangisaurus keyesi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
96 *Tatenectes laramiensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98 MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
99 *Picrocleidus beloclis*	?	?	?	?	?	0	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100 *Eoplesiosaurus antiquior*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
101 *Borealonectes russelli*	?	?	?	0	?	0	?	?	{01}	0	?	?	?	1	0	0	0	?	?	?	?	?	?	?	?	?	2	1	0
102 *Colymbosaurus trochanterius*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
103 *Eretmosaurus rugosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
104 *Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
105 MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
106 *'Cimoliasaurus' valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
107 *Zarafasaura oceanis*	?	?	?	?	?	?	?	?	{01}	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0

II.5

	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174
1 *Archaeonectrus rostratus*	0	1	2	?	?	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
2 *Aristonectes parvidens*	?	?	{01}	1	?	0	?	1	?	0	0	?	?	?	?	?	?	?	0	?	?	1	?	?	?	0	?	1	0
3 *Attenborosaurus conybeari*	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 *Augustasaurus hagdorni*	?	?	?	?	?	0	0	0	0	?	0	?	1	?	?	?	?	?	?	?	1	?	?	?	?	0	1	0
5 *Marmornectes candrewi*	?	1	2	1	1	1	0	0	?	?	0	0	0	1	1	1	-	?	0	?	?	0	0	0	0	0	0	1	?
6 NHMUK 49202	?	0	?	?	1	2	0	0	1	0	?	?	?	?	?	?	?	0	?	?	1	?	?	?	?	0	0	1	1
7 NHMUK R2439	?	1	2	1	?	?	?	0	?	0	?	?	?	1	?	?	?	?	?	0	?	?	?	?	?	?	1	1	?
8 *Brachauchenius lucasi*	?	?	?	?	?	?	2	0	?	0	?	?	?	?	1	-	?	0	?	?	?	?	?	?	?	?	?	?	?
9 *Brancasaurus brancai*	?	?	?	?	?	?	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
10 *Callawayasaurus colombiensis*	?	0	?	?	?	0	?	0	0	1	0	?	1	?	2	?	?	0	?	1	?	?	?	?	?	?	0	?
11 *Cymatosaurus*	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 *Cryptoclidus eurymerus*	0	2	0	1	0	0	?	0	1	1	0	0	1	0	2	0	1	0	?	?	0	1	1	-	-	1	0	1	0
13 *Dolichorhynchops herschelensis*	1	1	2	1	?	0	0	0	1	0	1	0	0	?	2	1	-	0	2	?	?	1	0	0	1	0	1	0	0
14 *Dolichorhynchops osborni*	1	1	2	1	0	0	0	0	1	0	1	0	0	0	2	0	0	0	?	?	0	1	0	0	1	0	1	1	0
15 *Edgarosaurus muddi*	1	1	2	?	?	0	1	0	0	1	1	0	0	0	2	0	0	0	?	0	1	0	0	1	0	1	0	1
16 *Elasmosaurus platyurus*	0	?	1	1	?	0	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
17 *Eopolycotylus rankini*	1	1	2	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18 *Eromangasaurus australis*	?	?	?	?	?	?	2	0	?	0	0	0	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
19 *Eurycleidus arcuatus*	0	?	1	0	0	1	{12}	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
20 FHSMVP321	?	?	?	?	?	?	?	0	?	0	0	0	?	?	1	-	?	0	?	?	?	0	?	?	?	0	0	0	0
21 *Hauffiosaurus longirostris*	1	1	?	?	?	0	2	0	?	0	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	2	1	0
22 *Hauffiosaurus tomistomimus*	?	{01}	?	?	?	0	0	0	0	0	1	0	?	?	2	?	?	?	0	?	1	0	1	1	0	2	1	0
23 *Hauffiosaurus zanoni*	?	?	2	1	?	0	?	0	0	1	1	?	?	?	2	?	?	?	1	?	?	?	?	0	2	1	0
24 *Hydrorion brachypterygius*	?	?	?	?	?	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
25 *Hydrotherosaurus alexandrae*	?	?	?	?	?	0	0	0	?	0	?	?	?	?	?	?	?	1	?	?	?	?	?	0	?	1	1
26 *Kaiwhekea katiki*	?	?	{01}	?	?	0	?	1	?	0	0	0	?	?	?	?	?	?	?	1	?	?	?	0	0	1	0
27 *Kimmerosaurus langhami*	?	2	0	1	0	0	?	0	1	1	0	0	?	0	2	0	?	0	?	?	1	1	-	-	1	0	1	0
28 *Kronosaurus queenslandicus*	?	?	?	?	?	1	2	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
29 *Leptocleidus capensis*	?	1	?	?	?	?	?	0	1	1	?	1	0	2	?	?	?	0	0	1	0	1	1	0	1	1	1
30 *Leptocleidus superstes*	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31 *Libonectes morgani*	0	0	1	1	?	0	0	0	?	0	1	0	1	1	?	2	0	?	0	1	1	1	0	?	1	0	?	1	?
32 *Liopleurodon ferox*	0	1	2	1	0	1	2	0	0	1	0	0	1	1	1	1	-	0	1	0	0	0	0	0	0	0	0	0	0
33 *Macroplata tenuiceps*	?	0	?	?	1	?	0	0	0	1	?	?	?	?	?	?	?	?	2	?	2	?	?	?	?	0	0	0
34 *Manemergus anguirostris*	?	?	2	?	?	?	?	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
35 *Maresaurus coccai*	?	?	?	?	?	1	2	0	0	1	1	0	?	?	?	?	?	?	?	1	?	2	?	?	?	0	0	0
36 *Microcleidus homalospondylus*	0	?	1	1	0	0	0	0	?	0	0	1	1	0	2	0	0	0	0	0	?	0	?	?	?	?	0	0
37 *Muraenosaurus leedsii*	0	0	0	1	0	0	?	0	1	?	0	0	1	0	2	?	0	?	0	0	1	1	-	-	1	0	1	0
38 *Nichol, ssaura borealis*	0	1	?	?	?	0	2	0	1	1	0	0	0	2	0	?	0	?	0	1	?	1	?	?	1	?
39 *Occitanosaurus tournemirensis*	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
40 OUMNH J.02247	0	?	2	?	0	1	0	0	?	1	0	1	?	0	1	1	-	1	1	0	0	0	0	0	?	0	0	?
41 *Stratesaurus taylori*	?	?	?	?	?	1	?	0	?	1	0	0	0	0	0	0	?	0	1	0	0	0	0	0	1	1
42 OUMNH J.28585	?	?	1	1	0	0	?	0	?	0	?	1	2	0	?	0	0	?	0	1	0	0	0	1	1
43 *Palmulasaurus quadratus*	1	1	2	1	0	0	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?
44 *Peloneustes philarchus*	1	1	2	1	1	1	0	0	0	1	0	0	0	1	1	1	-	0	1	0	0	0	0	0	0	0	0	1	0
45 *Plesiopleurodon wellesi*	?	?	2	?	0	1	0	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	0	?
46 *Plesiosaurus dolichodeirus*	0	?	{01}	1	?	0	2	0	?	0	0	?	0	?	2	?	?	?	?	?	1	?	?	?	0	1	0
47 *Plesiosaurus macrocephalus*	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
48 *Pliosaurus andrewsi*	0	1	2	?	?	?	?	0	?	?	0	0	?	?	1	1	-	1	?	?	0	0	?	?	0	0	1	?
49 *Pliosaurus brachydeirus*	?	?	2	1	?	?	?	?	?	0	?	?	?	1	?	?	?	?	?	?	?	?	0	0	?	?
50 *Pliosaurus brachyspondylus*	?	1	2	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	0	?	?	0	0	1	0
51 *Polycotylus latipinnis*	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	0	?	1	0	?	0	1
52 QMF 18041	?	?	2	?	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
53 *Rhomaleosaurus megacephalus*	?	1	?	?	1	2	0	0	1	1	?	1	0	0	0	2	0	2	0	?	0	0	1	?
54 *Meyerasaurus victor*	?	0	?	?	?	1	2	0	1	1	0	1	?	?	0	0	?	2	0	?	2	0	?	0	0	0	0	1
55 *Rhomaleosaurus zetlandicus*	0	1	?	?	1	?	0	0	1	1	?	1	0	0	0	2	?	2	2	0	0	0	0	0
56 *Seeleyosaurus guilelmiimperatoris*	?	?	?	?	0	?	0	?	1	0	0	1	0	?	?	?	0	?	?	1	?	?	?	0	1	1
57 *Simolestes vorax*	0	1	2	1	0	1	2	0	0	1	0	0	?	1	1	1	-	0	?	0	0	0	0	0	0	1	?
58 *Simosaurus gaillardoti*	0	0	1	0	0	?	0	0	1	0	0	0	0	0	?	0	?	0	1	0	0	0	0	0	0
59 *Styxosaurus snowii*	?	?	?	?	0	?	0	1	1	0	0	1	1	2	0	?	0	1	?	1	?	?	?	?	0	?
60 *Terminonatator pontiexensis*	?	{01}	?	?	0	0	0	1	1	1	0	2	2	1	-	?	1	1	1	0	1	0	?	1	1
61 *Thalassiodracon hawkinsii*	0	1	?	?	1	0	0	0	0	0	0	0	1	2	0	0	0	0	?	1	0	?	0	1	0
62 *Thalassomedon haningtoni*	?	?	?	?	?	?	?	0	1	0	?	0	2	?	?	?	1	?	1	?	?	0	0	0
63 *Thililual ongicollis*	?	?	2	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
64 *Tricleidus seeleyi*	?	?	0	1	?	0	?	0	?	1	0	0	1	0	2	0	1	0	?	0	1	1	-	-	1	0	1	0
65 *Trinacromerum bentonianum*	?	2	2	?	0	?	0	0	1	0	?	2	0	?	0	?	?	?	?	?	?	1	0
66 *Umoonasaurus demoscyllus*	?	?	?	?	?	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
67 *Pistosaurus* skull	?	?	?	?	?	?	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
68 *Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
69 *Yunguisaurus liae*	?	?	?	?	?	0	0	0	0	?	0	1	0	{01}	?	0	0	?	0	1	?	?	?	?	1	1	0
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
71 LEICT G1.2002	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
73 Speeton taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
74 *Hydralmosaurus serpentinus*	?	?	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
75 *Rhomaleosaurus cramptoni*	0	1	?	?	?	0	2	0	0	1	1	1	0	0	0	?	0	?	2	0	?	0	0	0
76 *Rhomaleosaurus thorntoni*	0	1	1	0	0	1	2	0	?	1	?	1	?	0	0	0	?	2	1	0	?	0	0	0
77 *Avalonnectes arturi*	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
78 *Plesiopterys wildii*	?	?	0	?	?	0	2	0	?	0	?	1	0	2	0	?	?	?	?	1	?	?	0	1	0	1	0
79 Lincoln taxon	?	?	?	?	?	?	?	?	?	?	?	?	0	2	?	?	?	?	?	1	0	0	0	?	?
80 Golden Cap taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
81 LEICT G18.1996	0	2	0	1	0	0	2	0	?	1	0	?	1	0	2	?	?	0	1	1	-	-	1	0	1	0
82 *Muraenosaurus platyclis*	0	0	0	1	0	0	2	0	1	1	0	1	0	2	0	1	0	0	1	1	-	-	1	1	1	0
83 NHMUK R.2861	0	{02}	0	1	0	0	0	1	1	0	?	1	0	2	0	1	0	1	1	-	-	1	0	1	0
84 NHMUK R.2864	0	2	0	1	0	0	?	0	?	1	0	?	1	0	2	0	?	?	0	1	1	-	-	1	0	1	0
85 *Vinialesaurus caroli*	0	0	0	1	0	0	0	0	?	?	0	0	1	1	2	0	?	1	?	0	?	?	?	?	?	?
86 *Gallardosaurus iturraldei*	?	1	?	?	?	?	?	?	?	1	0	?	?	{01}	?	?	?	0	?	?	0	?	?	?	?	?
87 *Pahasapasaurus haasi*	?	2	2	1	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
88 *Dolichorhynchops bonneri*	1	1	2	1	0	0	0	0	1	?	1	0	0	0	2	?	?	0	0	1	0	?	1	0	0	0	1
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90 TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
91 *Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
92 CM Zfr 145	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93 CM Zfr 115	?	?	?	?	?	?	?	?	?	?	?	?	2	2	?	?	?	1	?	?	?	0	1	1
94 *Futabasaurus suzukii*	0	?	?	?	?	0	0	0	?	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
95 *Tuarangisaurus keyesi*	?	?	?	?	0	0	?	?	?	?	?	?	2	2	?	?	?	1	?	1	?	0	1	1
96 *Tatenectes laramiensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
98 MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
99 *Picrocleidus beloclis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
100 *Eoplesiosaurus antiquior*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
101 *Borealonectes russelli*	?	1	?	?	?	1	2	0	?	?	?	?	?	?	0	?	?	?	?	?	0	?	?	?	0	0
102 *Colymbosaurus trochanterius*	?	?	?	?	?	?	?	1	0	?	?	0	2	?	?	?	?	1	1	-	-	1	0	1	0
103 *Eretmosaurus rugosus*	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
104 *Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
105 MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
106 *'Cimoliasaurus' valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
107 *Zarafasaura oceanis*	?	0	1	1	0	0	?	0	?	1	0	?	1	2	2	1	-	0	0	1	1	1	0	0	1	0	0	1	0

II.6

	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203
1 *Archaeonectrus rostratus*	?	?	?	0	1	1	0	?	?	?	?	?	?	?	?	1	0	0	0	2	0	0	1	?	1	1	0	?	?
2 *Aristonectes parvidens*	0	2	0	{01}	?	1	1	1	3	0	0	1	2	0	0	?	1	1	1	1	?	?	1	1	0	2	2	?	0
3 *Attenborosaurus conybeari*	1	0	1	0	?	1	1	0	1	?	?	?	?	?	?	?	0	?	?	?	?	0	?	1	1	?	1	?	{01}
4 *Augustasaurus hagdorni*	?	0	?	0	?	-	0	0	1	0	0	0	2	1	?	?	1	0	?	0	2	0	?	0	0	0	0	0	0
5 *Marmornectes candrewi*	0	0	1	?	1	0	1	0	2	0	0	0	2	1	?	0	1	2	0	0	0	0	1	0	1	1	2	0	0
6 NHMUK 49202	1	0	1	?	?	1	1	0	0	0	0	0	0	?	0	0	1	0	0	0	2	0	0	1	1	2	?	?	1
7 NHMUK R2439	?	?	?	?	?	0	1	0	?	?	0	0	2	0	?	0	1	2	0	0	0	0	1	?	?	1	2	0	0
8 *Brachauchenius lucasi*	?	?	?	?	?	0	1	0	?	?	0	?	2	?	?	1	?	?	0	0	0	?	?	0	?	2	2	?	?
9 *Brancasaurus brancai*	1	2	1	?	?	1	1	?	2	?	0	0	0	0	0	1	2	0	0	2	0	0	0	0	2	2	2	0	0
10 *Callawayasaurus colombiensis*	0	2	0	2	?	1	1	1	1	?	?	?	?	?	?	?	1	?	0	?	?	1	{01}	?	2	2	2	0	?
11 *Cymatosaurus*	1	?	1	?	?	?	?	?	1	0	?	?	?	?	?	0	?	?	?	?	1	?	?	?	?	?	?	?	?
12 *Cryptoclidus eurymerus*	0	1	0	0	0	1	1	1	2	0	1	1	1	2	0	1	1	0	0	0	0	0	0	0	0	2	2	0	0
13 *Dolichorhynchops herschelensis*	0	0	0	?	1	1	1	0	1	?	?	?	?	?	?	?	0	2	0	0	0	0	2	0	0	2	2	0	?
14 *Dolichorhynchops osborni*	0	0	0	2	0	1	1	0	1	1	0	1	0	1	0	1	1	2	0	0	?	?	?	0	0	2	2	0	1
15 *Edgarosaurus muddi*	1	0	1	2	0	1	1	0	2	0	0	0	2	0	?	0	1	2	0	0	0	0	0	0	?	2	2	0	1
16 *Elasmosaurus platyurus*	?	1	?	?	?	1	?	0	?	?	?	1	{12}	?	0	?	1	1	1	1	?	?	?	{01}	0	2	2	0	?
17 *Eopolycotylus rankini*	?	0	1	?	?	0	1	0	1	?	?	?	?	?	?	1	2	0	0	?	?	?	0	?	?	2	2	?	0
18 *Eromangasaurus australis*	0	?	1	1	?	?	?	{01}	0	?	?	1	{02}	?	0	?	1	1	1	?	1	?	1	?	2	2	2	0	?
19 *Eurycleidus arcuatus*	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	1	0	0	0	2	0	0	?	?	0	1	1	0	1
20 FHSMVP321	1	0	1	?	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21 *Hauffiosaurus longirostris*	1	0	?	?	0	1	1	0	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22 *Hauffiosaurus tomistomimus*	1	?	1	2	1	0	1	0	?	?	0	?	{02}	?	1	1	1	0	0	0	0	0	0	0	0	1	1	0	2
23 *Hauffiosaurus zanoni*	1	0	1	2	?	1	1	0	3	?	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	1	0	2
24 *Hydrorion brachypterygius*	1	1	1	0	0	1	1	0	1	?	?	?	?	?	?	?	1	1	1	0	0	1	?	1	0	1	0	?	0
25 *Hydrotherosaurus alexandrae*	1	1	1	?	1	1	1	1	?	0	?	?	?	?	?	1	1	1	1	1	?	1	0	2	2	2	0	0	0
26 *Kaiwhekea katiki*	0	0	0	1	0	1	1	0	3	?	?	?	?	?	?	?	1	2	0	0	1	?	?	1	1	2	2	0	0
27 *Kimmerosaurus langhami*	?	?	?	?	?	2	1	1	3	0	?	1	{12}	?	0	?	1	2	0	0	1	0	0	1	0	2	?	?	?
28 *Kronosaurus queenslandicus*	1	0	1	?	?	0	1	0	0	0	?	?	?	2	?	?	0	2	0	0	0	0	?	?	?	?	?	?	?
29 *Leptocleidus capensis*	1	2	1	1	1	0	1	0	1	?	?	?	?	?	?	?	1	2	0	0	2	0	0	0	0	2	2	0	?
30 *Leptocleidus superstes*	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	1	2	0	0	{12}	?	0	0	?	2	2	0	?
31 *Libonectes morgani*	0	0	1	0	0	1	1	0	1	?	1	?	?	?	?	1	1	1	1	?	1	?	?	1	2	2	2	?	?
32 *Liopleurodon ferox*	1	0	1	0	1	0	1	0	1	0	0	?	2	1	1	1	1	2	0	0	0	0	1	0	1	1	?	?	0
33 *Macroplata tenuiceps*	?	0	?	0	?	1	1	0	2	0	0	0	2	1	0	1	0	2	0	0	2	0	0	?	2	1	1	0	1
34 *Manemergus anguirostris*	?	?	1	?	?	1	1	0	1	1	?	?	?	?	?	1	2	0	0	0	?	{01}	?	2	2	2	0	0	?
35 *Maresaurus coccai*	1	0	1	0	?	0	1	0	1	?	0	?	?	?	?	?	2	?	?	0	?	?	?	?	1	?	?	1	?
36 *Microcleidus homalospondylus*	1	1	1	1	?	?	?	?	1	0	?	?	?	?	?	1	1	1	0	0	1	1	1	0	1	0	1	0	0
37 *Muraenosaurus leedsii*	1	1	1	0	0	1	1	0	1	0	1	1	1	?	0	1	1	1	1	0	0	1	0	0	2	2	0	0	0
38 *Nichollssaura borealis*	0	?	0	0	0	1	1	0	2	0	0	0	0	?	0	1	2	0	0	2	0	0	0	0	2	2	2	0	1
39 *Occitanosaurus tournemirensis*	1	1	1	0	1	1	1	0	1	?	1	1	1	?	?	1	1	0	0	?	1	1	0	1	0	0	1	0	0
40 OUMNH J.02247	1	?	1	?	?	0	1	0	2	?	?	?	?	?	?	1	2	0	0	1	0	1	?	1	1	1	2	?	?
41 *Stratesaurus taylori*	0	0	1	0	0	1	1	0	1	0	0	0	2	0	0	1	0	?	0	0	2	0	0	1	1	1	?	1	1
42 OUMNH J.28585	?	?	?	?	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43 *Palmulasaurus quadratus*	0	0	0	?	?	1	?	0	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	0	2	2	0	?
44 *Peloneustes philarchus*	1	0	1	2	1	0	1	0	2	0	0	0	2	1	?	1	1	2	0	0	1	0	1	0	1	1	2	0	0
45 *Plesiopleurodon wellesi*	?	?	?	?	?	0	1	0	2	?	?	?	?	?	?	1	2	0	0	2	0	0	?	0	0	2	2	0	?
46 *Plesiosaurus dolichodeirus*	1	1	1	0	0	1	1	0	1	0	?	0	?	?	0	1	0	0	0	0	0	0	{01}	0	1	{01}	0	0	0
47 *Plesiosaurus macrocephalus*	?	?	?	?	?	2	?	1	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	1	0	?	1	1	0
48 *Pliosaurus andrewsi*	?	?	?	?	?	0	1	0	2	?	0	1	0	1	?	1	2	0	0	0	1	0	1	1	1	1	{12}	?	?
49 *Pliosaurus brachydeirus*	?	?	?	?	?	0	1	2	?	?	?	?	?	?	?	2	0	0	?	?	1	0	1	1	1	1	{12}	?	?
50 *Pliosaurus brachyspondylus*	1	?	1	0	1	0	1	2	?	?	0	1	0	?	1	1	2	0	0	1	0	0	?	1	0	2	2	0	0
51 *Polycotylus latipinnis*	?	?	?	?	?	1	1	0	?	?	1	0	?	0	?	1	2	0	0	?	0	0	?	0	0	2	2	2	0
52 QMF 18041	1	0	1	1	?	0	1	0	2	0	0	0	1	0	?	?	?	?	2	0	0	?	0	0	2	2	2	?	?
53 *Rhomaleosaurus megacephalus*	1	?	1	0	0	0	1	0	0	?	0	0	0	0	0	1	1	0	0	2	0	0	0	0	1	1	0	0	1
54 *Meyerasaurus victor*	?	?	1	?	0	0	1	0	1	?	?	0	?	?	?	?	1	2	?	0	2	0	0	?	0	?	?	0	1
55 *Rhomaleosaurus zetlandicus*	?	?	?	?	1	0	1	0	1	?	?	?	?	?	?	?	1	2	0	0	2	0	0	1	0	1	1	0	1
56 *Seeleyosaurus guilelmiimperatoris*	?	?	?	?	1	1	1	1	1	?	?	?	?	?	?	?	1	0	0	0	?	?	0	0	1	1	0	?	0
57 *Simolestes vorax*	1	0	1	{01}	1	0	1	0	1	0	?	?	?	?	?	1	2	0	0	0	1	0	1	0	?	1	?	0	?
58 *Simosaurus gaillardoti*	0	0	0	1	0	-	0	?	1	0	?	?	?	?	?	?	0	0	0	0	2	0	1	0	?	1	?	0	?
59 *Styxosaurus snowii*	?	1	1	1	0	1	1	1	1	0	?	?	?	?	?	?	1	1	1	?	?	?	1	1	?	2	2	?	?
60 *Terminonatator pontiexensis*	1	1	1	2	0	1	?	1	{01}	?	?	?	?	?	?	1	1	1	1	?	?	?	1	1	?	2	2	?	0
61 *Thalassiodracon hawkinsii*	0	0	1	0	0	1	1	0	0	0	0	0	2	0	0	0	1	0	0	2	0	0	1	0	1	1	0	0	2
62 *Thalassomedon haningtoni*	?	?	1	{01}	0	?	?	?	1	?	0	0	?	0	0	?	1	1	1	?	1	?	1	{01}	?	2	2	0	?
63 *Thililiual ongicollis*	?	0	0	2	0	1	1	0	1	1	?	?	?	?	?	0	1	2	1	0	2	0	?	1	0	2	2	2	?
64 *Tricleidus seeleyi*	1	1	1	0	?	0	1	0	1	0	?	1	{12}	0	?	1	1	0	0	2	0	0	1	0	2	2	0	?	?
65 *Trinacromerum bentonianum*	0	0	?	{01}	0	0	?	0	?	1	0	1	0	2	?	1	1	2	0	0	1	0	0	1	0	2	2	0	?
66 *Umoonasaurus demoscyllus*	1	?	1	0	?	1	1	0	1	?	?	?	?	?	?	?	0	?	?	?	1	?	1	0	0	2	2	0	?
67 *Pistosaurus* skull	0	0	1	0	0	?	0	?	?	0	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	?	0	?	?
68 *Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	1	0	0	0	0	1	?
69 *Yunguisaurus liae*	?	0	?	0	0	?	?	0	3	0	?	?	?	?	?	?	0	0	0	0	0	?	?	0	?	1	1	?	?
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	0	0	?	?	0	0	0	1	?	0	2	0	0	2	0	1	?	0	1	1	1	0	0
71 LEICT G1.2002	?	?	?	?	1	1	1	0	?	?	0	1	?	0	0	1	1	2	0	0	2	0	0	0	1	{12}	1	1	1
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	0	0	2	0	0	0	1	2	2	1	0
73 Speeton taxon	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	1	0	0	0	0	2	2	1	0
74 *Hydralmosaurus serpentinus*	?	?	1	1	0	?	?	?	1	?	?	?	?	?	?	?	1	1	1	1	0	0	1	1	0	2	2	?	?
75 *Rhomaleosaurus cramptoni*	1	1	1	0	0	0	1	0	1	0	?	?	?	?	?	1	1	2	0	0	2	0	?	1	0	1	1	0	1
76 *Rhomaleosaurus thorntoni*	1	0	1	0	?	0	1	0	1	?	?	?	?	?	?	1	1	2	0	0	1	0	0	0	?	1	1	0	1
77 *Avalonnectes arturi*	?	?	1	0	?	?	0	?	0	?	?	?	?	?	?	0	0	0	0	?	2	0	0	1	0	1	1	1	?
78 *Plesiopterys wildii*	?	?	?	0	0	1	1	0	{01}	0	?	?	?	?	0	?	1	1	1	0	0	?	?	0	1	1	1	1	0
79 Lincoln taxon	?	?	?	?	1	1	1	0	?	?	?	?	?	?	?	?	1	1	0	0	?	?	1	1	0	1	2	1	0
80 Golden Cap taxon	?	?	?	?	1	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	2	0	1	?
81 LEICT G18.1996	?	?	?	?	1	1	0	0	?	?	1	?	0	?	0	?	1	2	0	0	1	1	0	0	1	2	2	0	?
82 *Muraenosaurus platyclis*	1	1	1	0	0	1	1	0	1	0	?	?	?	?	?	1	1	1	0	0	1	1	0	0	1	1	0	2	2
83 NHMUK R.2861	1	1	1	0	0	1	1	0	1	0	?	?	?	?	?	1	1	2	0	0	1	1	0	1	1	0	2	2	?
84 NHMUK R.2864	?	?	?	?	?	1	1	0	?	?	?	?	?	?	?	1	1	2	0	0	1	1	0	1	1	0	2	2	?
85 *Vinialesaurus caroli*	?	0	1	?	0	1	1	1	1	?	1	1	{12}	?	0	?	2	?	?	?	?	?	?	?	?	2	2	?	?
86 *Gallardosaurus iturraldei*	?	?	?	?	0	?	?	2	?	?	0	0	2	1	1	0	?	2	0	0	1	?	?	?	?	1	?	?	0
87 *Pahasapasaurus haasi*	0	1	0	0	0	{01}	1	?	2	1	?	?	?	?	?	1	1	0	0	?	?	?	0	?	2	2	?	?	?
88 *Dolichorhynchops bonneri*	0	0	0	2	0	1	1	0	1	1	0	?	0	?	0	?	1	2	0	0	?	?	?	0	0	2	2	0	?
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	0	0	2	0	0	?	1	2	2	0	0
90 TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	0	0	2	?	0	0	?	?	?	?	0
91 *Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
92 CM Zfr 145	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
93 CM Zfr 115	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	0	1	1	0	2	2	2	0
94 *Futabasaurus suzukii*	0	0	1	{01}	0	1	1	0	?	?	?	?	?	?	?	?	1	2	0	0	?	1	1	?	2	2	0	?	?
95 *Tuarangisaurus keyesi*	0	?	0	1	0	1	0	{01}	1	0	?	1	{12}	?	0	?	1	1	1	?	?	?	1	1	0	2	2	?	0
96 *Tatenectes laramiensis*	?	?	?	?	?	?	?	?	?	?	?	0	1	1	?	?	1	2	0	0	0	0	0	1	0	2	2	0	0
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	0	0	?	?	0	1	1	0	2	2	0	0
98 MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	?	?	?	1	0	0	0
99 *Picrocleidus beloclis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	0	?	1	1	0	2	2	0	?	?	?	?
100 *Eopleisosaurus antiquior*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	0	2	?	?	?	1	0	1	?	?	1
101 *Borealonectes russelli*	?	?	1	{1}	?	0	1	0	{12}	0	0	0	2	0	1	0	1	2	0	0	{12}	0	0	0	0	1	?	?	1
102 *Colymbosaurus trochanterius*	?	?	?	?	?	?	?	?	?	?	1	{12}	?	?	?	1	2	0	0	0	0	0	0	0	1	2	2	0	0
103 *Eretmosaurus rugosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	2	0	0	0	1	0	1	0	1	?
104 *Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	2	0	0	0	1	0	1	?	0	1
105 MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	?	0	0	1	0	0	0	?
106 'Cimoliasaurus' *valdensis*	?	?	?	?	?	?	?	?	?	0	0	{02}	1	?	1	1	2	0	0	2	0	0	0	1	2	2	1	1	?
107 *Zarafasaura oceanis*	?	?	1	1	?	1	1	1	{01}	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

II.7

	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232
1 *Archaeonectrus rostratus*	?	0	1	?	?	0	1	0	1	0	1	?	?	0	0	1	-	?	0	0	0	0	1	1	0	1	1	0	0
2 *Aristonectes parvidens*	0	2	1	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
3 *Attenborosaurus conybeari*	0	?	1	?	?	?	?	0	?	0	1	?	1	0	0	-	?	?	?	?	0	1	1	1	0	1	1	?	?
4 *Augustasaurus hagdorni*	0	0	0	0	?	?	0	-	?	1	0	?	?	-	0	0	-	?	0	0	0	?	1	0	1	1	0	?	?
5 *Marmornectes candrewi*	0	1	1	0	0	0	1	?	0	0	1	0	0	2	0	0	-	1	0	1	0	?	0	0	1	0	1	?	?
6 NHMUK 49202	0	1	1	0	0	?	?	0	?	0	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?
7 NHMUK R2439	0	?	1	0	0	0	1	?	?	0	?	1	?	2	?	?	?	1	0	1	1	?	1	?	?	?	?	?	?
8 *Brachaucenius lucasi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	0	?	?	?	?	?	?	?
9 *Brancasaurus brancai*	1	1	1	1	1	0	1	0	1	1	1	?	0	0	1	-	0	?	0	2	0	0	1	1	0	0	1	0	?
10 *Callawayasaurus colombiensis*	?	2	1	?	?	?	0	1	1	2	1	?	3	0	0	-	?	1	?	0	1	1	1	?	1	?	1	?	?
11 *Cymatosaurus*	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	?	?
12 *Cryptoclidus eurymerus*	1	1	1	1	2	0	1	1	1	0	2	0	0	1	0	0	-	-	0	2	0	0	1	1	1	0	1	0	0
13 *Dolichorhynchops herschelensis*	?	0	1	?	0	0	1	1	1	0	2	1	?	1	0	2	-	?	0	2	0	?	1	1	1	0	1	?	?
14 *Dolichorhynchops osborni*	0	0	1	1	2	0	1	1	1	0	2	1	{01}	1	0	2	-	-	0	2	0	0	1	1	1	0	1	?	0
15 *Edgarosaurus muddi*	1	1	1	?	0	0	1	0	?	?	?	1	?	?	?	?	-	0	2	?	0	?	?	?	?	?	?	?	?
16 *Elasmosaurus platyurus*	?	2	1	1	?	?	1	{01}	1	1	2	?	3	?	?	?	?	-	1	?	0	1	1	1	?	1	?	?	?
17 *Eopolycotylus rankini*	1	?	1	?	?	0	0	?	?	?	1	?	?	0	0	0	-	-	?	?	?	?	1	1	1	?	1	?	?
18 *Eromangasaurus australis*	?	?	1	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 *Eurycleidus arcuatus*	1	0	1	0	0	0	1	0	1	0	2	0	0	0	1	-	0	0	0	0	1	?	0	1	1	1	?	?	?
20 FHSMVP321	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
21 *Hauffiosaurus longirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22 *Hauffiosaurus tomistomimus*	-	1	1	0	0	1	1	?	1	0	1	0	0	1	0	0	-	1	0	?	?	0	1	0	1	1	1	1	0
23 *Hauffiosaurus zanoni*	-	1	1	0	0	?	1	1	0	1	1	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?
24 *Hydrorion brachypterygius*	0	?	?	?	?	1	1	?	0	2	?	?	1	0	0	-	?	1	0	?	1	1	1	2	1	1	?	?	?
25 *Hydrotherosaurus alexandrae*	?	2	1	?	2	0	1	?	0	2	1	0	3	0	0	-	?	1	0	1	0	1	0	1	0	1	1	?	?
26 *Kaiwhekea katiki*	0	2	1	?	2	0	?	0	1	1	1	0	3	0	0	-	?	?	?	0	1	0	1	1	1	?	1	?	?
27 *Kimmerosaurus langhami*	?	1	1	1	2	?	1	1	0	?	0	0	?	?	?	?	?	?	2	1	?	?	?	?	?	?	?	?	?
28 *Kronosaurus queenslandicus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?
29 *Leptocleidus capensis*	?	1	1	?	?	0	1	?	?	1	?	0	?	?	?	-	0	?	0	1	?	0	1	?	?	1	?	?	?
30 *Leptocleidus superstes*	?	1	1	1	?	0	1	?	?	1	1	0	1	0	1	-	1	-	0	?	0	1	0	0	1	?	?	?	?
31 *Libonectes morgani*	?	?	?	?	?	1	?	1	?	1	1	?	3	?	?	?	?	1	0	?	?	?	?	?	?	1	?	?	?
32 *Liopleurodon ferox*	0	1	1	0	0	0	1	?	0	1	1	0	1	0	?	?	1	0	1	1	?	0	?	1	?	1	?	?	?
33 *Macroplata tenuiceps*	0	1	1	0	0	?	1	?	1	?	?	?	?	0	0	-	0	0	?	?	1	1	0	0	1	0	0	?	?
34 *Manemergus anguirostris*	1	?	1	?	?	?	?	0	?	?	?	?	?	?	?	?	-	0	0	1	?	0	0	1	?	?	?	?	?
35 *Maresaurus coccai*	0	{01}	1	?	?	?	?	0	?	0	?	?	?	1	0	0	-	?	?	?	?	?	?	?	?	?	?	?	?
36 *Microcleidus homalospondylus*	0	2	1	0	0	0	1	1	1	0	2	?	0	1	0	0	-	?	0	0	0	1	1	1	2	1	1	0	1
37 *Muraenosaurus leedsi*	1	2	1	1	2	0	1	2	1	0	2	1	0	3	0	0	-	?	1	2	0	0	1	1	1	0	1	?	0
38 *Nichollssaura borealis*	0	1	1	?	?	0	1	0	?	0	0	?	0	0	0	-	?	0	?	2	1	1	0	0	1	?	0	?	?
39 *Occitanosaurus tournemirensis*	?	2	1	0	0	0	1	1	1	0	2	?	0	1	0	0	-	?	?	0	0	1	1	2	1	1	0	1	?
40 OUMNH J.02247	?	1	?	2	0	?	1	?	1	?	?	?	1	0	0	-	1	0	0	?	1	?	0	?	1	0	?	?	?
41 *Stratesaurus taylori*	0	1	1	0	0	2	1	0	1	0	0	0	?	?	?	0	0	0	0	?	?	?	1	?	0	?	?	?	?
42 OUMNH J.28585	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43 *Palmulasaurus quadratus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
44 *Peloneustes philarchus*	0	1	1	0	0	0	1	1	1	0	2	?	0	1	0	0	-	1	0	1	1	1	0	1	1	0	1	?	?
45 *Plesiopleurodon wellesi*	?	0	?	2	?	1	1	1	1	?	?	?	?	0	0	-	?	?	?	?	?	1	1	?	?	?	0	?	?
46 *Plesiosaurus dolichodeirus*	1	1	1	1	1	0	1	0	1	0	2	?	0	1	0	0	-	0	0	0	0	1	1	1	1	0	1	0	0
47 *Plesiosaurus macrocephalus*	-	1	?	?	?	?	?	1	?	0	1	0	1	0	?	-	0	0	0	1	1	0	1	0	1	0	1	0	?
48 *Pliosaurus andrewsi*	0	1	?	?	0	?	1	?	2	0	1	0	?	2	0	0	-	1	0	0	1	?	0	1	0	?	1	?	?
49 *Pliosaurus brachydeirus*	0	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50 *Pliosaurus brachyspondylus*	0	?	?	?	0	?	1	?	0	1	?	1	?	2	0	0	-	1	0	2	2	0	0	1	?	0	?	?	?
51 *Polycotylus latipinnis*	1	1	1	?	0	0	1	0	?	1	0	?	1	0	2	-	?	0	0	1	1	0	0	1	?	0	?	?	?
52 QMF 18041	?	0	1	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	1	?	0	0	?	?	?	?	?	?
53 *Rhomaleosaurus megacephalus*	1	{01}	1	?	?	{01}	?	?	?	?	?	?	0	1	-	0	0	0	1	1	0	1	1	0	1	1	0	0	?
54 *Meyerasaurus victor*	?	?	?	?	?	?	?	?	0	?	?	?	?	1	-	0	?	0	0	0	1	1	0	1	1	0	0	?	?
55 *Rhomaleosaurus zetlandicus*	1	0	1	0	0	0	1	0	?	0	?	?	0	0	1	-	?	0	0	0	?	0	0	1	?	1	0	?	?
56 *Seeleyosaurus guilelmiimperatoris*	?	1	1	0	?	0	1	1	1	0	2	?	0	3	0	0	-	0	?	0	0	0	1	1	2	0	1	1	1
57 *Simolestes vorax*	0	1	1	0	0	0	1	?	?	0	1	0	1	0	0	-	1	0	1	1	?	0	0	0	1	?	?	?	?
58 *Simosaurus gaillardoti*	?	0	0	0	0	?	0	1	1	0	2	0	0	0	0	0	-	?	0	0	0	0	0	0	1	?	?	?	?
59 *Styxosaurus snowii*	?	?	1	?	?	?	?	0	0	1	2	?	0	3	0	0	-	?	?	?	0	1	?	1	1	1	?	?	?
60 *Terminonatator pontiexensis*	0	2	1	1	2	0	1	?	0	1	2	1	0	3	0	0	-	?	1	0	0	1	?	0	1	?	1	?	?
61 *Thalassiodracon hawkinsii*	-	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	-	0	0	0	1	1	0	1	1	0	1	0	0
62 *Thalassomedon haningtoni*	0	2	1	1	0	0	1	1	1	1	2	1	0	3	0	0	-	?	1	2	2	0	0	1	1	0	1	?	?
63 *Thililua ongicollis*	?	?	1	?	?	?	0	1	1	?	{12}	?	?	0	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?
64 *Tricleidus seeleyi*	?	1	1	1	2	0	1	1	0	2	0	0	1	0	0	-	?	1	2	0	0	1	1	1	0	1	?	?	?
65 *Trinacromerum bentonianum*	?	0	1	0	2	?	1	1	1	0	2	?	1	0	0	-	?	0	1	1	0	?	1	?	1	?	0	?	?
66 *Umoonasaurus demoscyllus*	?	1	1	?	?	0	1	?	?	1	?	?	?	?	?	?	?	0	?	1	1	1	?	0	?	?	?	?	?
67 *Pistosaurus* skull	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
68 *Pistosaurus* postcranium	?	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	-	?	0	0	0	0	0	0	1	1	0	?	?
69 *Yunguisaurus liae*	?	0	0	0	?	0	0	-	1	1	0	?	?	-	?	?	?	0	0	1	0	?	1	0	?	1	0	0	0
70 *Bobosaurus forojuliensis*	0	1	0	0	0	0	0	1	0	?	0	0	{01}	?	?	?	?	2	0	1	1	0	2	0	1	0	1		
71 LEICT G1.2002	0	1	1	1	2	1	0	1	0	1	0	1	0	1	-	1	0	2	1	1	1	0	0	1	1	0	0	?	?
72 NHMUK R16330	0	1	1	1	1	2	1	0	1	0	1	0	1	1	-	0	0	0	2	1	1	1	0	2	0	?	?	?	?
73 Speeton taxon	1	2	1	1	2	0	1	?	1	2	0	0	?	?	?	?	1	2	?	1	1	1	0	1	?	1	?	?	1
74 *Hydralmosaurus serpentinus*	?	2	1	1	2	0	1	?	1	{12}	1	?	?	?	?	?	?	2	2	?	1	0	?	1	?	1	?	1	?
75 *Rhomaleosaurus cramptoni*	1	0	1	0	0	?	?	1	0	?	2	?	0	1	-	1	1	0	0	?	1	1	0	0	0	1	0	0	?
76 *Rhomaleosaurus thorntoni*	1	0	1	0	0	0	1	0	?	2	?	?	?	?	?	?	?	0	0	1	1	0	1	1	0	?	1	1	0
77 *Avalonnectes arturi*	1	1	1	0	0	0	0	0	2	?	?	0	0	-	?	0	0	0	1	1	0	1	1	1	1	0	0	?	?
78 *Plesiopterys wildii*	1	?	1	?	?	?	1	1	1	0	2	?	?	1	0	0	-	?	1	2	0	?	1	1	1	0	1	0	0
79 Lincoln taxon	?	2	1	0	0	1	?	?	2	0	?	1	?	?	?	?	0	?	?	1	1	0	?	1	?	1	?	?	1
80 Golden Cap taxon	?	2	1	?	0	?	1	?	?	?	?	?	?	?	?	?	?	0	?	?	1	1	0	?	?	?	?	?	?
81 LEICT G18.1996	?	2	1	1	2	0	1	{12}	1	0	2	0	0	3	0	0	-	?	1	{02}	?	0	0	1	1	0	0	?	0
82 *Muraenosaurus platyclis*	?	2	1	1	2	0	1	{12}	1	0	2	0	0	3	0	0	-	?	1	2	0	?	1	?	?	?	?	?	?
83 NHMUK R.2861	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	1	?	?	?	?	?	?	?
84 NHMUK R.2864	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	{02}	?	0	?	?	?	?	?	?	?	?
85 *Vinialesaurus caroli*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
86 *Gallardosaurus iturraldei*	0	?	?	?	?	?	1	?	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
87 *Pahasapasaurus haasi*	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
88 *Dolichorhynchops bonneri*	?	?	0	0	?	?	1	1	1	0	1	?	?	1	?	?	?	?	2	2	0	1	1	1	?	1	?	?	?
89 *Leptocleidus clemai*	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90 TMP 95.87.01	1	?	?	?	?	1	0	?	0	1	?	?	1	?	?	?	?	?	2	{01}	0	?	?	0	1	1	?	?	?
91 *Wapuskanectes betsynichollsae*	?	2	?	?	?	1	0	?	?	2	?	?	3	0	0	-	?	?	?	0	1	0	1	?	1	?	?	?	?
92 CM Zfr 145	?	2	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	0	?	?	?	?
93 CM Zfr 115	?	2	1	1	2	0	1	?	1	1	2	?	0	3	0	0	-	?	1	?	2	?	?	?	{12}	?	?	?	?
94 *Futabasaurus suzukii*	?	2	1	1	2	0	1	?	?	2	1	0	3	0	0	-	?	1	2	0	?	1	0	1	0	1	0	?	?
95 *Tuarangisaurus keyesi*	?	2	1	1	2	0	1	?	1	1	?	0	3	?	?	?	1	2	?	0	1	?	?	?	?	?	?	?	?
96 *Tatenectes laramiensis*	1	2	1	1	2	0	1	1	0	?	?	0	1	0	0	-	?	0	2	0	?	1	1	1	0	1	1	0	?
97 *Pantosaurus striatus*	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	?	0	?	?	?	?
98 MNHN A. C. 8592	?	?	1	?	?	?	0	?	?	?	2	?	?	1	?	?	?	?	?	?	1	1	1	?	1	?	?	?	?
99 *Picrocleidus beloclis*	2	1	1	2	0	1	1	0	2	?	0	3	0	0	-	?	?	?	0	1	1	0	?	1	?	?	?	?	?
100 *Eoplesiosaurus antiquior*	0	1	1	?	?	1	0	0	1	?	?	0	0	-	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
101 *Borealonectes russelli*	0	?	1	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
102 *Colymbosaurus trochanterius*	?	1	1	1	{12}	?	1	?	0	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	1	0	?	?	?
103 *Eretmosaurus rugosus*	?	1	1	0	0	1	1	1	1	0	?	0	0	0	0	-	0	?	2	0	?	1	1	1	?	?	?	?	?
104 *Westphaliasaurus simonsensii*	1	{12}	1	?	0	1	?	1	1	0	2	?	0	?	0	0	-	?	2	0	?	1	1	0	1	0	1	?	?
105 MIWG 1997.302	?	1	1	1	1	?	1	1	1	0	?	1	?	0	1	-	1	W	0	?	?	1	1	0	0	?	?	?	?
106 *'Cimoliasaurus' valdensis*	1	1	1	1	{01}	?	1	0	1	0	1	0	0	{01}	?	?	?	?	0	?	?	?	?	?	?	1	?	?	?
107 *Zarafasaura oceanis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

		233	234	235	236	237	238	239	240	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261
1	*Archaeonectrus rostratus*	0	0	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	0	2	1	?	?	?	0	?	?
2	*Aristonectes parvidens*	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	*Attenborosaurus conybeari*	0	?	?	?	1	1	?	?	?	?	?	?	?	3	0	0	1	0	1	?	?	0	1	?	?	0	?	?	?
4	*Augustasaurus hagdorni*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	0	1	?	?	0	-	-	-	?
5	*Marmornectes candrewi*	1	?	0	1	1	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?	?	?
6	NHMUK 49202	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	NHMUK R2439	1	?	?	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?
8	*Brachauchenius lucasi*	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9	*Brancasaurus brancai*	0	?	0	0	1	1	0	0	1	1	1	?	1	2	2	0	?	1	?	1	0	1	?	?	?	?	0	?	1
10	*Callawayasaurus colombiensis*	?	?	?	?	1	1	?	2	?	?	?	?	0	?	1	0	0	1	0	0	0	2	?	0	0	{12}	?	1	1
11	*Cymatosaurus*	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	*Cryptoclidus eurymerus*	0	?	0	0	1	1	0	0	1	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0	1	1	1	0	1
13	*Dolichorhynchops herschelensis*	0	?	?	2	?	?	0	0	2	0	{01}	?	1	2	1	0	0	1	?	?	?	?	1	?	1	1	1	0	1
14	*Dolichorhynchops osborni*	?	0	0	?	?	?	?	?	2	0	0	?	1	2	1	0	0	1	0	0	1	0	0	1	0	1	0	0	1
15	*Edgarosaurus muddi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	*Elasmosaurus platyurus*	?	?	?	?	1	1	?	2	0	?	?	?	?	?	?	?	?	1	1	?	?	?	?	0	1	1	?	?	?
17	*Eopolycotylus rankini*	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	0	1	?	1	0	1	0	1	?	1	0	0	1
18	*Eromangasaurus australis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	*Eurycleidus arcuatus*	?	?	?	2	1	0	0	0	1	1	?	?	0	1	2	1	0	1	0	1	1	2	1	1	0	0	0	0	1
20	FHSMVP321	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21	*Hauffiosaurus longirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	*Hauffiosaurus tomistomimus*	0	0	0	?	1	?	?	?	1	0	0	?	?	?	2	?	?	1	?	1	?	?	0	?	?	?	?	?	?
23	*Hauffiosaurus zanoni*	0	?	?	2	1	0	0	0	?	{01}	0	?	?	2	?	0	1	1	?	1	1	2	1	?	1	?	2	0	0
24	*Hydrorion brachypterygius*	0	2	?	?	0	0	1	1	1	0	2	?	1	?	2	1	?	0	1	0	1	0	2	?	1	1	0	0	?
25	*Hydrotherosaurus alexandrae*	0	?	0	?	1	1	2	2	0	?	1	?	?	?	2	1	?	0	1	1	0	?	0	0	0	2	0	0	1
26	*Kaiwhekea katiki*	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27	*Kimmerosaurus langhami*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28	*Kronosaurus queenslandicus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29	*Leptocleidus capensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30	*Leptocleidus superstes*	?	?	?	?	1	?	?	?	?	?	?	1	2	2	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?
31	*Libonectes morgani*	?	?	?	?	?	?	?	?	?	?	0	?	1	0	0	1	1	?	?	0	1	?	?	0	1	{12}	?	0	1
32	*Liopleurodon ferox*	?	?	?	?	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	1
33	*Macroplata tenuiceps*	0	?	1	2	1	0	0	0	{01}	?	1	1	2	?	0	1	0	?	?	?	?	?	1	1	0	0	0	0	1
34	*Manemergus anguirostris*	?	?	?	1	?	?	?	?	2	?	0	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
35	*Maresaurus coccai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36	*Microcleidus homalospondylus*	0	?	0	0	0	1	1	1	{01}	0	2	?	0	?	?	0	1	1	1	0	0	1	0	1	1	1	1	?	1
37	*Muraenosaurus leedsii*	?	?	?	0	0	1	1	1	0	0	?	1	1	3	1	0	1	?	1	0	0	1	?	0	1	1	1	0	1
38	*Nichollssaura borealis*	0	0	0	?	0	?	?	?	0	1	1	1	?	0	?	?	?	?	0	1	?	1	0	0	0	1	?	?	?
39	*Occitanosaurus tournemirensis*	0	?	?	?	?	?	?	?	?	?	?	0	0	3	0	0	1	0	1	0	2	1	1	0	2	1	0	?	1
40	OUMNH J.02247	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
41	*Stratesaurus taylori*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
42	OUMNH J.28585	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43	*Palmulasaurus quadratus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
44	*Peloneustes philarchus*	1	?	0	1	1	1	0	0	?	?	?	?	?	?	?	0	1	0	1	1	0	0	0	0	2	0	0	?	1
45	*Plesiopleurodon wellesi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
46	*Plesiosaurus dolichodeirus*	0	0	0	0	0	{01}	0	0	?	0	0	0	?	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	1
47	*Plesiosaurus macrocephalus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
48	*Pliosaurus andrewsi*	1	?	?	?	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
49	*Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50	*Pliosaurus brachyspondylus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
51	*Polycotylus latipinnis*	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1	?	0	0	0	?	?	?	1	?	0	?	0	?
52	QMF 18041	0	?	0	?	?	?	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
53	*Rhomaleosaurus megacephalus*	0	0	1	2	?	0	?	0	0	?	0	?	?	2	?	?	0	1	?	?	1	?	?	?	?	?	?	?	?
54	*Meyerasaurus victor*	0	1	?	2	1	?	0	?	?	?	0	0	?	0	?	0	1	0	1	?	?	?	?	1	1	0	0	0	1
55	*Rhomaleosaurus zetlandicus*	?	?	1	2	2	0	0	0	{01}	?	?	?	?	2	?	?	?	?	?	?	1	?	?	?	?	0	?	?	?
56	*Seeleyosaurus guilelmiimperatoris*	0	2	?	?	0	1	1	1	1	0	2	0	?	?	3	?	0	1	0	1	0	2	?	0	1	?	0	?	1
57	*Simolestes vorax*	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	?	?	2	0	1
58	*Simosaurus gaillardoti*	0	?	?	?	?	?	?	?	0	0	0	0	0	0	2	0	-	0	0	?	1	1	1	0	0	-	?	-	0
59	*Styxosaurus snowii*	?	?	?	?	1	1	?	2	?	?	?	?	?	?	1	?	0	1	1	0	2	0	?	0	0	2	?	0	1
60	*Terminonatator pontiexensis*	?	?	?	?	1	1	1	{12}	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?
61	*Thalassiodracon hawkinsii*	0	0	0	2	1	0	0	0	1	0	0	?	0	0	{02}	?	0	1	0	1	1	0	?	1	0	0	0	0	1
62	*Thalassomedon haningtoni*	?	?	0	?	1	1	?	1	?	?	?	?	0	1	1	0	?	1	0	0	2	1	?	0	0	2	?	0	?
63	*Thililua longicollis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
64	*Tricleidus seeleyi*	?	?	?	?	?	1	?	?	?	?	?	0	1	3	1	0	1	?	0	0	0	?	0	1	1	1	0	1	?
65	*Trinacromerum bentonianum*	0	?	?	?	0	0	0	0	?	?	?	?	1	?	1	0	0	1	0	?	1	0	?	1	1	1	0	0	?
66	*Umoonasaurus demoscyllus*	?	?	?	?	?	?	1	?	0	0	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
67	*Pistosaurus* skull	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
68	*Pistosaurus* postcranium	?	?	?	2	0	0	1	0	?	?	?	?	?	?	?	?	0	0	?	?	1	2	1	?	?	-	?	-	1
69	*Yunguisaurus liae*	0	?	?	?	0	?	?	?	{01}	?	?	?	?	?	?	?	?	0	?	?	0	2	?	?	?	?	?	?	?
70	*Bobosaurus forojuliensis*	0	1	?	2	0	?	?	1	{01}	?	?	?	?	?	?	?	0	?	?	?	1	2	?	?	?	?	?	0	1
71	LEICT G1.2002	0	?	0	2	1	1	0	1	1	1	1	0	0	0	2	1	0	1	0	0	1	1	2	1	1	0	0	0	1
72	NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1	0	1	?	1	2	1	?	?	?	1	?	1
73	Speeton taxon	0	?	0	0	?	?	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?
74	*Hydralmosaurus serpentinus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1	?	?	?	?	0	0	2	?	0	1
75	*Rhomaleosaurus cramptoni*	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
76	*Rhomaleosaurus thorntoni*	0	?	?	2	1	0	0	0	?	?	?	?	?	?	2	?	?	1	0	1	0	2	1	1	0	0	0	?	?
77	*Avalonnectes arturi*	0	?	?	2	1	0	0	0	?	?	?	0	?	0	?	?	0	?	1	0	2	?	?	?	?	?	1	?	1
78	*Plesiopterys wildii*	0	2	?	0	0	?	0	0	1	?	1	1	?	1	3	0	0	1	?	0	1	2	0	?	1	1	1	0	1
79	Lincoln taxon	0	?	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	2	0	0	?
80	Golden Cap taxon	?	?	?	0	0	1	1	1	{01}	?	?	0	0	1	?	1	1	0	1	?	?	1	?	1	1	1	0	1	?
81	LEICT G18.1996	0	?	0	1	1	1	0	0	0	?	1	0	1	3	?	1	1	0	?	?	?	0	0	1	1	1	0	1	?
82	*Muraenosaurus platyclis*	?	?	0	0	1	1	?	0	1	?	?	0	?	3	1	1	?	1	?	0	?	0	0	1	1	1	1	0	1
83	NHMUK R.2861	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
84	NHMUK R.2864	?	?	0	0	1	1	0	0	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
85	*Vinialesaurus caroli*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
86	*Gallardosaurus iturraldei*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
87	*Pahasapasaurus haasi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
88	*Dolichorhynchops bonneri*	?	?	?	0	?	?	0	0	2	0	1	?	1	2	1	0	0	?	?	1	1	0	?	?	0	?	?	?	1
89	*Leptocleidus clemai*	?	?	?	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
90	TMP 95.87.01	0	?	?	?	1	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	1	?	?	?	?	0	?	?	?
91	*Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	?	2	?	0	1	1	?	1	?	1	?
92	CM Zfr 145	0	?	?	0	1	1	0	1	?	0	?	?	?	?	?	?	?	1	0	1	1	0	0	?	0	1	1	0	1
93	CM Zfr 115	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	0	?	?	2	?	0	1
94	*Futabasaurus suzukii*	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	3	?	?	?	2	?	?	?	0	?	?	?
95	*Tuarangisaurus keyesi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
96	*Tatenectes laramiensis*	0	?	?	?	?	?	?	?	?	?	{01}	?	?	1	1	0	?	?	0	1	1	1	0	1	1	1	1	0	1
97	*Pantosaurus striatus*	0	?	?	0	0	1	1	1	{01}	0	2	?	?	0	?	?	0	1	1	0	?	1	1	0	?	1	0	?	1
98	MNHN A. C. 8592	?	0	0	0	0	1	0	0	{01}	0	0	?	?	0	?	?	1	1	0	1	?	?	?	1	0	?	1	1	?
99	*Picrocleidus beloclis*	0	?	0	0	0	1	1	0	0	0	0	?	0	1	3	1	1	?	1	0	?	0	2	0	0	1	1	0	1
100	*Eoplesiosaurus antiquior*	0	0	?	?	0	0	1	0	0	?	?	?	?	?	?	?	1	0	0	1	1	0	0	0	?	1	0	0	1
101	*Borealonectes russelli*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
102	*Colymbosaurus trochanterius*	?	?	?	0	1	1	?	0	?	?	?	?	?	?	1	1	?	1	1	0	1	1	0	0	1	1	0	1	?
103	*Eretmosaurus rugosus*	?	?	?	?	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
104	*Westphaliasaurus simonsensii*	0	0	0	0	0	1	0	0	1	0	0	?	1	0	2	0	?	1	0	0	2	?	1	1	0	0	0	0	1
105	MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0	0	1
106	*'Cimoliasaurus' valdensis*	?	?	?	?	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
107	*Zarafasaura oceanis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	262	263	264	265	266	267	268	269	270	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288	289	290
1 *Archaeonectrus rostratus*	?	?	?	?	?	?	?	1	1	0	0	1	?	?	?	?	?	0	?	1	1	?	?	?	?	?	?	0	?
2 *Aristonectes parvidens*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3 *Attenborosaurus conybeari*	1	?	1	0	0	1	0	1	1	0	0	?	1	1	?	?	?	0	?	1	1	1	0	0	?	?	?	?	?
4 *Augustasaurus hagdorni*	?	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	?	?
5 *Marmornectes candrewi*	?	?	0	0	0	1	?	0	1	1	0	0	1	?	0	2	0	0	0	?	1	?	?	?	?	1	0	0	1
6 NHMUK 49202	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7 NHMUK R2439	?	?	?	?	?	?	?	0	1	1	0	0	1	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?
8 *Brachauchenius lucasi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9 *Brancasaurus brancai*	2	2	?	?	2	1	?	1	1	0	0	0	1	?	?	?	0	1	?	1	1	?	1	1	1	1	1	?	?
10 *Callawayasaurus colombiensis*	2	?	2	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	0	1	1	1	?	?
11 *Cymatosaurus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	2	?	1
12 *Cryptoclidus eurymerus*	0	2	0	0	1	2	0	1	1	0	0	0	1	1	1	1	1	1	?	1	1	1	1	1	0	1	0	1	0
13 *Dolichorhynchops herschelensis*	?	2	?	1	1	2	1	1	0	-	-	-	1	?	?	?	0	1	1	?	1	1	?	1	0	?	?	?	?
14 *Dolichorhynchops osborni*	?	2	1	1	1	2	1	1	0	-	-	-	1	?	?	1	0	?	1	1	1	1	1	1	0	1	1	1	0
15 *Edgarosaurus muddi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?
16 *Elasmosaurus platyurus*	?	2	?	?	?	?	?	1	1	0	0	0	1	1	?	?	?	?	?	1	1	0	1	?	?	?	?	?	?
17 *Eopolycotylus rankini*	?	?	0	1	1	2	1	1	0	-	-	-	1	1	?	1	0	1	?	1	1	?	1	1	0	1	1	1	1
18 *Eromangasaurus australis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 *Eurycleidus arcuatus*	1	1	1	0	0	0	1	1	1	0	?	0	1	?	?	?	?	?	?	1	?	1	0	0	1	0	0	0	2
20 FHSMVP321	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
21 *Hauffiosaurus longirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22 *Hauffiosaurus tomistomimus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	?	1	0	0	1
23 *Hauffiosaurus zanoni*	0	?	0	0	0	1	0	0	1	0	0	0	1	?	?	?	?	0	?	1	1	?	1	0	0	?	0	?	?
24 *Hydrorion brachypterygius*	0	?	0	0	1	2	3	0	1	0	0	1	1	?	?	2	?	1	1	1	1	1	1	0	?	?	2	0	0
25 *Hydrotherosaurus alexandrae*	{01}	2	2	0	2	2	0	1	1	?	0	1	?	?	?	?	?	?	?	1	1	0	1	0	?	?	1	1	?
26 *Kaiwhekea katiki*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27 *Kimmerosaurus langhami*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28 *Kronosaurus queenslandicus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29 *Leptocleidus capensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 *Leptocleidus superstes*	?	2	2	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	2
31 *Libonectes morgani*	2	?	2	0	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
32 *Liopleurodon ferox*	?	1	0	0	?	?	?	0	1	1	0	?	1	?	?	?	?	?	?	1	1	?	1	0	0	1	0	0	?
33 *Macroplata tenuiceps*	1	?	0	0	0	1	0	?	?	?	?	?	1	?	?	?	?	?	?	1	1	?	1	0	?	1	2	0	0
34 *Manemergus anguirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	?	?	?	?	?
35 *Maresaurus coccai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
36 *Microcleidus homalospondylus*	0	1	0	0	?	?	?	0	1	?	?	?	1	1	?	2	?	1	1	0	1	0	1	0	?	1	2	0	1
37 *Muraenosaurus leedsii*	0	2	0	0	1	1	2	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	0
38 *Nichollssaura borealis*	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?
39 *Occitanosaurus tournemirensis*	0	?	0	0	2	2	3	0	1	0	0	1	1	0	?	1	0	0	0	1	1	0	1	0	0	1	2	0	1
40 OUMNH J.02247	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
41 *Stratesaurus taylori*	?	?	?	?	?	?	?	0	1	0	0	0	1	0	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?
42 OUMNH J.28585	?	?	?	?	?	?	?	1	0	0	0	0	1	?	?	2	0	0	?	1	1	?	1	?	?	?	?	?	?
43 *Palmulasaurus quadratus*	?	?	?	?	?	?	1	1	?	0	0	0	1	0	?	2	0	0	?	1	1	0	1	?	?	1	0	?	0
44 *Peloneustes philarchus*	?	?	0	0	2	1	0	0	1	1	1	0	1	1	1	2	0	0	0	1	1	0	1	0	0	1	0	0	0
45 *Plesiopleurodon wellesi*	?	?	?	?	1	1	?	?	0	1	0	0	1	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
46 *Plesiosaurus dolichodeirus*	1	?	0	0	0	?	0	0	1	0	0	0	1	0	0	1	?	1	?	1	1	0	1	0	?	1	2	0	1
47 *Plesiosaurus macrocephalus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	{12}
48 *Pliosaurus andrewsi*	?	?	?	?	?	?	?	0	1	1	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?
49 *Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
50 *Pliosaurus brachyspondylus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
51 *Polycotylus latipinnis*	?	2	?	?	1	2	1	1	0	-	-	-	1	?	?	1	?	1	1	?	1	1	?	?	1	1	1	1	?
52 QMF 18041	?	?	?	?	1	?	1	0	-	-	-	1	?	?	?	?	?	1	?	?	1	0	?	?	1	1	0	?	?
53 *Rhomaleosaurus megacephalus*	?	?	?	?	?	?	?	0	1	0	0	0	1	?	?	?	?	?	?	1	?	1	0	0	1	1	0	1	2
54 *Meyerasaurus victor*	1	?	0	0	0	1	1	0	1	?	?	?	1	1	?	2	0	?	?	1	1	0	1	0	1	1	2	?	2
55 *Rhomaleosaurus zetlandicus*	?	?	0	0	?	1	0	0	1	0	0	0	1	?	?	?	?	0	?	1	1	?	1	0	0	?	1	0	1
56 *Seeleyosaurus guilelmiimperatoris*	?	?	0	0	2	2	3	0	1	0	0	1	1	?	?	2	0	0	?	1	1	?	1	0	0	?	1	2	0
57 *Simolestes vorax*	?	?	0	0	2	1	0	0	1	1	1	1	1	?	?	?	?	?	?	1	1	0	1	0	0	1	0	?	0
58 *Simosaurus gaillardoti*	-	0	-	-	0	0	0	-	1	1	0	0	0	0	?	2	?	0	?	0	0	-	0	0	0	0	2	?	0
59 *Styxosaurus snowii*	{01}	2	2	0	2	{12}	0	1	1	0	0	1	1	?	?	1	0	?	?	1	1	?	1	?	?	1	1	1	0
60 *Terminonatator pontiexensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1	?	1	?	1	1	1	2
61 *Thalassiodracon hawkinsii*	1	1	0	0	0	1	0	0	1	0	0	0	1	1	?	?	0	0	?	1	1	0	1	0	0	0	2	0	2
62 *Thalassomedon haningtoni*	2	2	?	?	?	?	?	1	1	0	0	1	1	?	?	1	0	0	1	1	1	1	1	1	1	1	1	?	2
63 *Thililua ongicollis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
64 *Tricleidus seeleyi*	?	2	0	0	1	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	2
65 *Trinacromerum bentonianum*	2	2	0	?	1	2	1	0	1	0	0	0	1	?	1	0	0	0	?	1	1	1	0	?	?	1	?	?	?
66 *Umoonasaurus demoscyllus*	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	1	1	?	?	2
67 *Pistosaurus* skull	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
68 *Pistosaurus* postcranium	0	0	0	0	0	0	0	0	1	1	0	1	0	?	?	?	?	0	0	?	0	0	?	?	?	0	2	?	2
69 *Yunguisaurus liae*	?	?	?	?	0	0	?	0	1	1	?	0	1	?	?	?	?	?	?	1	1	0	1	0	1	0	?	?	?
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	?	0	1	1	?	0	1	?	?	1	?	?	?	1	1	0	0	?	1	?	2	?	1
71 LEICT G1.2002	1	1	2	0	0	1	0	0	1	1	0	0	1	1	0	2	0	0	1	1	1	1	0	0	1	1	0	?	2
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	2
73 Speeton taxon	?	2	2	?	?	?	?	1	1	0	0	0	1	?	1	1	0	?	1	0	1	1	0	1	1	1	1	1	0
74 *Hydralmosaurus serpentinus*	2	?	2	0	0	1	0	?	?	?	?	?	1	?	?	?	?	?	?	1	1	1	1	1	0	1	1	1	2
75 *Rhomaleosaurus cramptoni*	?	1	?	0	0	0	?	0	1	0	0	0	1	?	?	?	?	0	?	1	1	0	1	1	1	0	?	?	?
76 *Rhomaleosaurus thorntoni*	1	1	?	0	0	1	?	0	1	0	0	0	1	1	?	?	?	0	0	1	1	1	0	?	?	?	2	0	1
77 *Avalonnectes arturi*	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	2	0	0
78 *Plesiopterys wildii*	0	1	0	0	?	?	?	0	0	1	?	1	1	0	1	?	0	0	1	?	1	1	1	?	1	0	1	0	0
79 Lincoln taxon	0	?	?	?	?	?	0	0	1	0	?	?	1	1	2	0	0	?	1	?	?	?	?	?	?	1	2	0	1
80 Golden Cap taxon	1	?	{01}	0	0	?	?	1	?	?	?	?	1	1	?	?	?	?	?	?	1	1	?	1	?	1	2	0	2
81 LEICT G18.1996	?	?	0	0	?	2	?	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	1	0	1	0	1	0
82 *Muraenosaurus platyclis*	?	?	?	?	?	?	?	1	1	0	0	0	1	1	1	1	1	1	0	1	?	?	?	?	?	1	0	1	?
83 NHMUK R.2861	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0
84 NHMUK R.2864	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0
85 *Vinialesaurus caroli*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
86 *Gallardosaurus iturraldei*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
87 *Pahasapasaurus haasi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
88 *Dolichorhynchops bonneri*	?	2	0	1	1	2	1	1	0	-	-	-	1	0	?	?	0	0	?	1	1	1	1	0	?	1	1	?	?
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	1	0	?	?	?	?	?	?	1	1	0	0	
90 TMP 95.87.01	?	?	0	1	?	2	1	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	?	1	0	1	?	?
91 *Wapuskanectes betsynichollsae*	2	?	2	0	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	2
92 CM Zfr 145	2	?	2	0	2	1	1	1	0	-	-	-	1	?	?	?	0	1	?	1	1	1	1	1	?	1	?	1	0
93 CM Zfr 115	2	2	0	?	1	1	0	0	1	?	?	?	1	?	?	?	?	0	?	1	1	0	1	1	1	?	?	0	?
94 *Futabasaurus suzukii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	0	1	?
95 *Tuarangisaurus keyesi*	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	0	1	0	?	?	?
96 *Tatenectes laramiensis*	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	1	0	0	1	1	1	1	1	1	0	?	?	?	?
98 MNHN A. C. 8592	1	?	0	0	0	1	3	0	1	0	0	1	1	1	?	0	?	1	1	0	1	0	1	0	?	1	2	0	2
99 *Picrocleidus beloclis*	?	2	0	0	2	2	2	?	0	?	?	?	1	1	?	?	?	1	0	1	1	0	1	?	?	1	0	1	0
100 *Eoplesiosaurus antiquior*	?	?	?	?	?	?	0	1	?	?	?	1	?	?	?	0	?	?	?	1	1	?	?	1	?	?	2	0	{12}
101 *Borealonectes russelli*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	2
102 *Colymbosaurus trochanterius*	1	2	0	0	1	2	0	0	?	?	?	1	1	0	?	?	?	?	?	1	1	0	1	?	?	1	0	1	0
103 *Eretmosaurus rugosus*	?	1	0	0	{02}	?	?	0	1	0	0	0	1	1	0	1	?	0	0	1	1	0	1	0	1	0	?	2	1
104 *Westphaliasaurus simonsensii*	1	1	0	0	0	1	0	0	1	0	1	?	1	?	?	?	1	0	1	1	0	1	?	?	1	0	0	0	{01}
105 MIWG 1997.302	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?
106 '*Cimoliosaurus*' *valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	2
107 *Zarafasaura oceanis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	291	292	293	294	295	296	297	298	299	300	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315	316	317	318	319
1 *Archaeonectrus rostratus*	0	0	?	0	?	0	0	0	0	1	0	1	0	0	0	0	?	0	1	1	0	1	0	0	1	0	1	1	L
2 *Aristonectes parvidens*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	B	A
3 *Attenborosaurus conybeari*	0	0	0	?	0	0	0	0	0	0	?	1	1	0	0	0	?	?	?	?	?	?	0	0	1	0	1	?	K
4 *Augustasaurus hagdorni*	0	0	0	0	0	0	0	1	0	0	0	0	0	?	?	?	?	?	?	0	0	0	0	?	0	2	F		
5 *Marmornectes candrewi*	0	0	0	0	1	0	?	?	?	?	1	0	?	0	0	1	1	0	1	0	0	?	?	?	1	1	1	?	?
6 NHMUK 49202	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	B	A
7 NHMUK R2439	?	?	?	0	?	0	1	1	0	1	1	{01}	0	0	?	1	1	0	1	0	0	?	?	?	1	1	?	?	?
8 *Brachauchenius lucasi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	J	N
9 *Brancasaurus brancai*	0	1	0	1	1	0	?	1	0	?	?	?	?	0	0	1	1	1	{01}	?	1	?	?	?	?	?	J	5	
10 *Callawayasaurus colombiensis*	0	1	0	1	1	0	0	0	1	0	1	?	1	1	1	0	1	1	1	1	0	?	?	2	1	?	5	B	
11 *Cymatosaurus*	1	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	1	8	G	
12 *Cryptoclidus eurymerus*	2	?	0	1	1	0	2	0	0	?	1	2	-	0	0	1	1	1	1	2	-	1	1	2	1	1	1	P	?
13 *Dolichorhynchops herschelensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	J	N
14 *Dolichorhynchops osborni*	0	0	0	1	?	0	0	1	0	1	1	2	-	0	0	1	1	1	1	2	-	1	0	1	1	1	1	J	N
15 *Edgarosaurus muddi*	0	0	0	1	?	0	0	1	0	1	1	0	?	?	1	?	?	?	?	?	0	2	1	1	1	1	D	J	
16 *Elasmosaurus platyurus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 *Eopolycotylus rankini*	0	0	0	1	1	0	?	?	?	?	?	?	?	0	0	1	1	1	1	{12}	?	1	0	1	1	1	1	?	?
18 *Eromangasaurus australis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A	C
19 *Eurycleidus arcuatus*	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	?	0	1	0	0	?	?	?	?	?	0	?	?
20 FHSMVP321	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	8	P
21 *Hauffiosaurus longirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	L
22 *Hauffiosaurus tomistomimus*	0	0	0	0	1	0	0	0	1	1	?	1	0	0	0	1	1	1	1	0	1	?	0	1	0	1	0	?	?
23 *Hauffiosaurus zanoni*	0	0	?	0	1	0	0	0	1	0	1	1	0	0	0	?	0	1	1	0	0	1	0	1	0	1	0	?	?
24 *Hydrorion brachypterygius*	1	0	?	1	?	0	0	0	1	1	0	0	1	0	0	1	0	1	1	0	0	1	0	1	0	1	1	4	B
25 *Hydrotherosaurus alexandrae*	0	1	?	1	?	0	0	1	0	1	?	0	0	1	0	1	1	1	1	{01}	?	?	1	1	1	?	?	?	
26 *Kaiwhekea katiki*	?	1	?	1	?	?	?	1	0	1	1	0	0	1	0	1	1	1	?	1	0	?	?	?	?	1	0	6	0
27 *Kimmerosaurus langhami*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28 *Kronosaurus queenslandicus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
29 *Leptocleidus capensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	1	0	?	?	?	?	?	?	C	B	
30 *Leptocleidus superstes*	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
31 *Libonectes morgani*	?	?	?	?	?	1	2	?	1	0	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	C	A
32 *Liopleurodon ferox*	?	0	?	1	1	0	0	0	1	1	1	1	0	0	1	1	1	1	1	0	?	{12}	1	1	?	C	K	
33 *Macroplata tenuiceps*	0	0	0	0	?	0	0	0	0	0	?	0	0	1	0	0	1	0	0	?	?	?	?	?	?	5	L	
34 *Manemergus anguirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	7	K	
35 *Maresaurus coccai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	F	
36 *Microcleidus homalospondylus*	0	0	?	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	1	0	0	1	?	1	0	1	1	A	C
37 *Muraenosaurus leedsii*	2	0	0	1	1	0	1	0	0	0	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	1	?	?
38 *Nichollssaura borealis*	0	0	0	?	0	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	2	1	1	1	?	F	C	
39 *Occitanosaurus tournemirensis*	0	0	?	1	?	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	1	?	?	?	1	F	C	
40 OUMNH J.02247	?	0	?	1	?	0	?	1	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	
41 *Stratesaurus taylori*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	0	?	?	?	1	?	0	K	E
42 OUMNH J.28585	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
43 *Palmulasaurus quadratus*	0	0	?	1	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	0	2	1	1	1	?	?	?	
44 *Peloneustes philarchus*	1	0	0	0	1	0	1	1	0	1	1	1	0	1	0	1	1	1	1	0	0	0	1	1	1	1	6	L	
45 *Plesiopleurodon wellesi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	6	K	
46 *Plesiosaurus dolichodeirus*	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	G	F
47 *Plesiosaurus macrocephalus*	0	0	?	0	?	0	0	0	1	1	0	0	0	?	0	?	0	1	0	1	?	1	?	1	?	A	E	
48 *Pliosaurus andrewsi*	0	0	?	1	?	0	0	1	0	1	1	0	?	0	0	1	1	1	1	1	?	2	1	?	1	?	?	
49 *Pliosaurus brachydeirus*	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	1	1	1	0	?	?	?	?	?	?	?	
50 *Pliosaurus brachyspondylus*	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	?	?	?	?	?	?	?	?	?	B	J
51 *Polycotylus latipinnis*	0	0	0	1	?	0	0	1	0	1	1	1	0	0	0	?	1	1	1	1	0	1	?	1	1	?	?	
52 QMF 18041	0	0	?	1	?	0	1	0	0	1	?	0	0	1	1	1	?	1	?	1	?	{12}	?	1	?	8	K	
53 *Rhomaleosaurus megacephalus*	0	0	1	0	?	0	?	0	0	0	0	0	0	1	0	0	1	0	1	?	0	1	?	?	?	?	0	D	F
54 *Meyerasaurus victor*	0	0	?	0	1	0	0	0	1	0	1	0	1	0	0	?	0	1	0	0	1	0	1	0	1	0	?	?
55 *Rhomaleosaurus zetlandicus*	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	?	0	1	0	1	1	0	1	0	?	?	F	
56 *Seeleyosaurus guilelmiimperatoris*	0	0	?	1	?	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	1	M	E
57 *Simolestes vorax*	1	0	0	1	?	0	0	1	0	1	1	1	0	0	1	1	1	1	0	0	?	{12}	?	1	?	9	K	
58 *Simosaurus gaillardoti*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	5	C	
59 *Styxosaurus snowii*	2	1	0	1	1	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	0	2	1	1	1	8	C
60 *Terminonatator pontiexensis*	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	?	1	1	1	1	0	2	1	1	1	H	A
61 *Thalassiodracon hawkinsii*	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	1	0	R	G
62 *Thalassomedon haningtoni*	{12}	?	?	1	1	1	0	0	1	?	?	?	?	1	1	1	?	1	1	2	-	?	?	2	?	1	?	C	
63 *Thililual ongicollis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	F	L	
64 *Tricleidus seeleyi*	1	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	?	2	1	1	?	?	
65 *Trinacromerum bentonianum*	0	0	0	1	?	0	0	1	0	1	1	0	?	?	?	?	?	?	1	1	0	2	1	1	1	?	D	P
66 *Umoonasaurus demoscyllus*	0	0	?	1	?	0	?	?	?	?	?	?	?	0	0	1	1	1	1	0	1	?	?	?	?	?	4	
67 *Pistosaurus* skull	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	6	G	
68 *Pistosaurus* postcranium	0	0	0	0	0	0	0	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	
69 *Yunguisaurus liae*	0	0	?	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	1	0	2	F	
70 *Bobosaurus forojuliensis*	0	0	?	1	?	0	?	?	?	?	?	?	0	0	?	0	0	0	0	?	?	?	?	?	F	F	
71 LEICT G1.2002	1	0	2	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0	1	1	?	1	0	1	1	P	?	
72 NHMUK R16330	1	0	2	1	0	0	0	0	1	1	1	0	0	?	?	?	?	?	?	?	?	0	1	?	P	?	
73 Speeton taxon	0	0	0	1	1	0	0	1	0	1	1	1	1	0	?	1	?	?	1	?	?	?	1	0	?	?	
74 *Hydralmosaurus serpentinus*	0	1	?	1	?	2	?	0	1	0	1	?	1	1	1	0	1	1	1	0	?	?	1	1	?	4	6	
75 *Rhomaleosaurus cramptoni*	1	0	0	0	?	0	0	0	1	0	?	0	0	1	0	1	0	1	0	0	1	?	0	0	0	H	
76 *Rhomaleosaurus thorntoni*	1	0	0	0	1	0	?	0	1	?	0	?	0	0	1	0	0	1	0	0	1	?	?	?	?	?	A	
77 *Avalonnectes arturi*	0	0	?	0	?	0	0	0	1	0	1	0	0	0	1	0	0	0	1	?	1	0	1	0	?	A	
78 *Plesiopterys wildii*	0	0	0	1	?	0	0	0	1	1	0	0	0	0	0	1	0	0	?	?	1	1	1	0	?	8	
79 Lincoln taxon	?	?	0	1	?	0	0	1	?	0	{01}	0	0	0	1	0	0	0	?	?	?	0	?	0	?	?	
80 Golden Cap taxon	1	0	0	1	2	0	0	0	1	0	1	0	0	0	?	0	1	0	0	?	?	?	1	1	0	?	
81 LEICT G18.1996	1	0	0	1	1	0	1	?	0	0	1	1	?	0	0	1	?	?	?	?	?	1	1	1	?	?	
82 *Muraenosaurus platyclis*	1	0	0	1	1	0	{01}	0	0	0	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	
83 NHMUK R.2861	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	1	1	1	?	?	?	?	?	M	C
84 NHMUK R.2864	1	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	1	0	?	?	
85 *Vinialesaurus caroli*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
86 *Gallardosaurus iturraldei*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	B	?	
87 *Pahasapasaurus haasi*	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	1	1	0	0	1	?	1	1	1	R	P
88 *Dolichorhynchops bonneri*	0	0	0	1	1	0	0	1	0	1	1	{12}	?	0	0	1	1	1	{12}	?	1	0	1	1	1	K	P
89 *Leptocleidus clemai*	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	1	0	1	?	?	?	?	?	?	?	
90 TMP 95.87.01	?	?	?	1	?	0	?	0	?	1	1	1	?	?	1	1	1	?	1	1	?	1	2	1	?	1	?	
91 *Wapuskanectes betsynichollsae*	0	1	?	1	1	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	?	?	?	?	?	
92 CM Zfr 145	0	1	?	1	1	0	?	0	?	?	?	1	0	0	1	1	?	1	?	1	?	?	?	1	?	?	
93 CM Zfr 115	1	1	1	1	?	0	0	1	0	1	1	1	0	0	0	1	?	1	0	0	1	?	?	1	1	?	
94 *Futabasaurus suzukii*	0	1	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	1	1	0	0	1	?	1	1	1	?	
95 *Tuarangisaurus keyesi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	9	B
96 *Tatenectes laramiensis*	1	0	?	1	1	0	1	0	0	1	1	1	1	?	?	?	?	?	?	1	?	?	?	1	?	?	
97 *Pantosaurus striatus*	1	0	?	1	?	0	?	2	1	0	?	1	2	-	0	0	0	0	0	?	?	?	?	1	?	F	
98 MNHN A. C. 8592	1	0	?	1	0	0	0	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	?	1	?	1	0	?	
99 *Picrocleidus beloclis*	1	0	0	1	?	0	0	0	1	0	1	1	0	0	?	1	1	1	0	0	1	1	0	1	0	?	?	
100 *Eoplesiosaurus antiquior*	0	0	1	0	?	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	0	?	?	
101 *Borealonectes russelli*	1	0	?	1	1	0	0	0	1	1	1	0	0	?	?	?	?	1	0	1	?	?	?	?	7	G	
102 *Colymbosaurus trochanterius*	1	1	1	1	?	0	1	1	0	1	?	?	1	0	0	1	1	1	1	1	1	0	?	1	P	?	
103 *Eretmosaurus rugosus*	1	0	1	1	0	0	0	0	1	0	1	0	0	?	1	0	1	0	0	1	0	0	1	0	1	0	?	
104 *Westphaliasaurus simonsensii*	1	0	0	0	2	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	?	?	?	1	?	P	
105 MIWG 1997.302	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
106 *'Cimoliosaurus' valdensis*	0	0	0	1	0	0	0	1	0	?	1	1	0	?	?	1	1	?	1	0	?	?	?	?	1	?	?	
107 *Zarafasaura oceanis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	5	

II.11

	320	321	322	323	324	325	326	327	328	329	330	331	332	333	334	335	336	337	338	339
1 *Archaeonectrus rostratus*	K	?	?	?	?	?	E	A	C	?	2	K	?	?	A	C	?	C	7	C
2 *Aristonectes parvidens*	?	?	?	?	?	R	B	?	?	?	?	?	?	?	?	?	?	?	?	?
3 *Attenborosaurus conybeari*	?	?	?	?	6	?	F	C	6	E	H	5	B	F	B	?	9	8	?	?
4 *Augustasaurus hagdorni*	B	B	G	?	H	E	7	G	C	-	?	?	?	?	9	L	?	L	?	?
5 *Marmornectes candrewi*	?	?	?	?	?	?	K	?	?	?	0	?	?	4	D	?	5	?	?	9
6 NHMUK 49202	A	4	K	?	8	0	4	?	?	?	?	?	?	?	?	?	?	?	?	?
7 NHMUK R2439	?	?	?	?	?	?	G	?	?	?	3	A	?	?	?	?	?	4	?	A
8 *Brachauchenius lucasi*	K	M	R	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
9 *Brancasaurus brancai*	0	?	?	?	?	C	?	H	8	?	5	G	3	6	C	9	?	?	7	?
10 *Callawayasaurus colombiensis*	6	E	L	C	(69)	7	4	N	G	K	?	?	9	3	L	2	?	6	2	7
11 *Cymatosaurus*	6	-	-	?	?	5	0	?	?	?	-	-	?	?	?	K	?	?	?	?
12 *Cryptoclidus eurymerus*	?	?	?	L	1	B	5	F	E	P	H	{3E}	4	6	F	0	2	7	3	5
13 *Dolichorhynchops herschelensis*	8	H	?	6	Q	B	Q	5	E	N	H	G	M	M	?	?	?	?	9	?
14 *Dolichorhynchops osborni*	B	F	L	9	N	E	R	9	?	F	A	G	N	H	9	8	7	0	9	2
15 *Edgarosaurus muddi*	?	L	P	8	J	F	H	C	?	?	?	?	?	?	?	7	?	0	0	?
16 *Elasmosaurus platyurus*	?	?	?	?	?	?	4	R	?	?	{BJ}	2	E	?	?	?	?	?	?	?
17 *Eopolycotylus rankini*	?	?	?	?	?	?	M	?	?	K	E	C	H	M	C	9	?	?	5	6
18 *Eromangasaurus australis*	?	?	?	K	?	5	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 *Eurycleidus arcuatus*	?	?	?	?	?	?	?	?	D	3	?	9	A	H	9	?	D	7	?	?
20 FHSMVP321	K	?	?	J	?	A	9	?	?	?	?	?	?	?	?	?	?	?	?	?
21 *Hauffiosaurus longirostris*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22 *Hauffiosaurus tomistomimus*	B	B	?	3	?	5	?	F	N	?	?	?	?	?	H	E	?	C	C	?
23 *Hauffiosaurus zanoni*	?	?	J	N	?	F	?	{EG}	?	?	P	8	?	0	A	F	?	C	C	E
24 *Hydrorion brachypterygius*	H	A	J	?	?	?	?	G	0	P	3	A	D	8	C	J	3	E	G	F
25 *Hydrotherosaurus alexandrae*	?	?	?	?	3	0	P	3	K	R	?	D	9	G	2	?	4	2	?	?
26 *Kaiwhekea katiki*	C	?	?	5	?	L	?	K	A	?	?	?	?	?	?	?	?	?	6	?
27 *Kimmerosaurus langhami*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28 *Kronosaurus queenslandicus*	?	M	J	?	?	?	9	2	?	?	?	?	?	?	0	9	?	?	D	?
29 *Leptocleidus capensis*	D	F	P	A	?	?	?	B	?	?	?	?	?	?	?	?	?	?	?	?
30 *Leptocleidus superstes*	?	L	R	?	?	?	?	?	C	?	?	?	?	?	?	?	?	?	?	?
31 *Libonectes morgani*	9	K	0	K	A	5	4	P	?	P	?	?	?	?	?	?	?	?	?	?
32 *Liopleurodon ferox*	C	G	Q	Q	E	D	A	9	?	?	?	?	R	J	?	?	A	?	8	9
33 *Macroplata tenuiceps*	9	0	J	?	C	D	C	C	?	?	?	5	D	?	?	?	?	?	9	C
34 *Manemergus anguirostris*	?	?	?	?	?	0	E	C	?	?	?	?	?	?	?	?	?	?	?	?
35 *Maresaurus coccai*	F	7	L	H	?	?	9	?	?	?	?	?	?	?	?	?	?	?	?	?
36 *Microcleidus homalospondylus*	0	A	K	D	9	7	4	G	0	?	?	?	C	E	8	7	H	9	5	?
37 *Muraenosaurus leedsii*	?	?	?	D	?	7	5	K	A	R	{DF}	G	C	A	H	7	A	7	5	5
38 *Nichollssaura borealis*	7	J	P	C	3	?	5	A	L	?	?	?	?	D	B	7	5	6	5	9
39 *Occitanosaurus tournemirensis*	6	G	J	?	?	4	?	K	0	L	B	G	9	9	C	B	?	D	7	E
40 OUMNH J.02247	?	?	?	N	?	E	7	?	?	7	?	?	?	?	?	7	?	5	?	?
41 *Stratesaurus taylori*	?	4	J	?	?	7	5	?	?	?	3	K	?	?	?	?	?	?	?	E
42 OUMNH J.28585	?	?	?	G	?	?	4	?	?	7	?	?	?	?	?	?	?	?	?	?
43 *Palmulasaurus quadratus*	?	?	?	?	?	?	?	?	?	?	8	8	8	G	H	7	?	4	6	8
44 *Peloneustes philarchus*	7	P	K	K	M	J	L	A	G	0	{9B}	{2C}	J	J	6	8	7	4	A	8
45 *Plesiopleurodon wellesi*	D	?	?	7	?	?	D	?	?	?	?	?	?	?	?	?	?	?	?	?
46 *Plesiosaurus dolichodeirus*	C	5	J	H	A	9	4	K	C	K	G	8	?	7	G	A	H	G	7	E
47 *Plesiosaurus macrocephalus*	?	?	?	?	?	?	?	C	A	?	7	?	8	8	E	D	7	F	?	?
48 *Pliosaurus andrewsi*	?	?	?	?	?	?	6	?	?	?	A	B	?	?	2	7	?	7	9	?
49 *Pliosaurus brachydeirus*	?	?	?	?	?	?	H	?	?	?	?	?	?	?	?	?	?	?	9	5
50 *Pliosaurus brachyspondylus*	F	J	Q	?	E	?	6	?	?	A	?	G	R	?	8	C	?	?	?	4
51 *Polycotylus latipinnis*	?	?	?	?	?	?	?	?	?	A	?	G	R	?	8	C	?	?	?	4
52 QMF 18041	K	C	M	?	N	H	G	A	A	?	?	?	?	6	G	A	H	5	8	8
53 *Rhomaleosaurus megacephalus*	D	3	J	0	B	B	7	C	{38}	?	4	D	?	K	6	?	?	5	E	?
54 *Meyerasaurus victor*	?	C	J	C	C	?	5	B	?	5	0	J	4	A	E	A	G	B	A	D
55 *Rhomaleosaurus zetlandicus*	F	6	L	?	?	?	B	N	?	?	1	M	B	?	E	4	9	B	9	C
56 *Seeleyosaurus guilelmiimperatoris*	F	?	?	L	?	?	4	H	8	?	1	M	B	?	7	9	D	9	7	C
57 *Simolestes vorax*	H	E	Q	F	D	?	7	7	?	G	D	?	N	K	A	8	?	8	7	B
58 *Simosaurus gaillardoti*	C	-	-	E	?	C	4	?	R	-	-	-	?	?	R	R	?	R	R	R
59 *Styxosaurus snowii*	?	?	?	5	?	5	4	P	?	M	9	?	E	9	D	2	M	4	0	?
60 *Terminonatator pontiexensis*	?	?	?	A	?	4	2	M	?	B	F	?	?	?	B	4	?	1	3	5
61 *Thalassiodracon hawkinsii*	?	3	K	H	A	C	4	E	E	C	{14}	{GK}	A	9	D	B	G	B	9	E
62 *Thalassomedon haningtoni*	?	?	?	?	?	?	L	6	L	?	7	D	3	?	?	4	?	?	?	?
63 *Thililua longicollis*	?	?	?	?	?	C	M	E	?	?	?	L	?	?	?	?	?	?	?	?
64 *Tricleidus seeleyi*	?	7	L	R	?	D	?	?	?	N	?	?	?	?	B	6	?	5	6	3
65 *Trinacromerum bentonianum*	?	R	P	1	?	6	J	?	?	{EH}	{FM}	P	F	?	?	?	?	?	?	?
66 *Umoonasaurus demoscyllus*	9	D	P	?	?	?	?	?	?	?	?	?	?	?	B	B	?	?	7	?
67 *Pistosaurus* skull	F	?	?	F	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
68 *Pistosaurus* postcranium	?	?	?	?	?	?	?	?	?	-	-	-	?	?	?	K	?	L	?	?
69 *Yunguisaurus liae*	F	K	K	?	H	?	?	L	G	-	6	3	0	?	0	L	?	L	D	N
70 *Bobosaurus forojuliensis*	?	?	?	?	?	?	?	?	A	5	?	-	7	7	?	?	2	?	8	?
71 LEICT G1.2002	L	2	M	?	?	?	D	G	6	7	2	B	8	A	A	?	8	7	B	?
72 NHMUK R16330	?	?	?	?	?	?	?	?	?	?	?	?	?	A	?	?	7	?	?	?
73 Speeton taxon	?	?	?	?	?	?	?	?	?	?	L	?	9	8	H	9	?	6	5	E
74 *Hydralmosaurus serpentinus*	?	?	?	H	?	4	?	P	8	?	?	B	B	7	6	?	1	5	8	?
75 *Rhomaleosaurus cramptoni*	R	5	N	K	7	E	4	D	L	?	6	2	?	?	C	D	?	B	9	A
76 *Rhomaleosaurus thorntoni*	?	?	?	?	?	?	8	?	L	?	2	6	0	7	F	C	?	9	A	?
77 *Avalonnectes arturi*	A	?	?	?	D	?	{BC}	{58}	?	?	?	9	E	?	9	E	?	A	A	F
78 *Plesiopterys wildii*	C	2	L	?	3	?	?	J	8	A	M	7	?	D	?	B	?	?	?	?
79 Lincoln taxon	?	?	?	?	?	?	?	?	?	?	D	?	?	?	?	?	?	?	7	H
80 Golden Cap taxon	?	?	?	?	?	?	?	?	8	?	?	?	?	?	D	?	E	?	?	H
81 LEICT G18.1996	?	?	K	?	?	?	?	?	?	H	D	K	8	F	A	?	?	A	?	?
82 *Muraenosaurus platyclis*	?	1	G	?	9	7	?	?	?	?	?	?	?	?	G	9	?	4	4	?
83 NHMUK R.2861	?	1	H	Q	9	9	5	?	?	?	?	?	?	G	A	A	5	?	9	B
84 NHMUK R.2864	?	?	?	?	?	?	K	8	?	?	?	?	?	?	G	A	A	5	7	5
85 *Vinialesaurus caroli*	?	?	?	R	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
86 *Gallardosaurus iturraldei*	F	L	Q	L	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
87 *Pahasapasaurus haasi*	?	?	?	?	?	A	J	?	?	?	?	?	?	?	?	9	C	6	5	9
88 *Dolichorhynchops bonneri*	?	H	K	?	R	F	Q	9	E	M	E	4	H	H	C	A	4	2	4	0
89 *Leptocleidus clemai*	?	?	?	?	?	?	?	?	?	?	A	?	?	?	?	D	?	?	9	5
90 TMP 95.87.01	?	?	?	?	?	?	?	?	?	?	?	?	L	?	?	?	?	?	?	?
91 *Wapuskanectes betsynichollsae*	?	?	?	?	?	?	?	K	?	?	?	?	?	5	?	?	?	?	?	?
92 CM Zfr 145	?	?	?	?	?	?	?	?	8	C	J	D	A	3	?	0	?	?	0	8
93 CM Zfr 115	?	?	?	?	?	?	Q	5	?	?	?	?	?	G	?	?	1	5	?	?
94 *Futabasaurus suzukii*	?	?	?	?	?	6	0	?	?	?	?	?	5	M	8	?	3	3	7	?
95 *Tuarangisaurus keyesi*	?	J	?	?	0	6	0	?	?	?	?	?	?	?	?	?	?	?	?	?
96 *Tatenectes laramiensis*	?	-	-	?	?	?	?	?	?	?	?	?	?	?	A	?	6	?	?	?
97 *Pantosaurus striatus*	?	?	?	?	?	?	?	?	?	5	R	D	8	?	D	7	5	?	?	?
98 MNHN A. C. 8592	?	?	?	?	?	?	?	?	?	?	1	G	C	?	L	E	?	G	9	H
99 *Picrocleidus beloclis*	?	?	?	?	?	?	{HK}	?	J	?	?	?	?	?	B	7	6	?	?	?
100 *Eoplesiosaurus antiquior*	?	?	?	?	?	?	G	?	?	F	2	?	?	G	J	R	F	C	H	?
101 *Borealonectes russelli*	L	H	Q	?	E	E	9	?	?	?	?	?	?	B	?	8	?	?	?	?
102 *Colymbosaurus trochanterius*	?	?	?	?	?	?	K	L	M	?	?	?	?	?	9	?	6	6	6	?
103 *Eretmosaurus rugosus*	?	?	?	?	?	G	?	?	A	B	B	A	D	D	?	F	8	H	?	?
104 *Westphaliasaurus simonsensii*	?	?	?	?	?	?	?	?	C	?	K	5	7	8	D	E	?	C	8	F
105 MIWG 1997.302	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	8	7	B
106 *'Cimoliosaurus' valdensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	F	5	?	8
107 *Zarafasaura oceanis*	2	?	?	L	8	1	4	?	?	?	?	?	?	?	?	?	?	?	?	?

II.12

Appendix III: Taxa included in phylogenetic analysis

This appendix lists operational taxonomic units (OTUs) included in the phylogenetic analysis of Chapter 3. Geological context, age and locality information are given along with data sources. Where a specimen number is given as a data source, it has been studied in person. Institutional abbreviations are listed in Appendix V.

Archaeonectrus rostratus **(Owen, 1865)**

Lower Lias Group (early Sinemurian, Early Jurassic) of Charmouth, Dorset, UK.

Data: Benson *et al.* (2012), Ketchum and Benson (2011a), Owen (1865), Smith (2007)

Aristonectes parvidens **Cabrera, 1941**

Paso del Sapo Formation (late Maastrichtian, Late Cretaceous) of Cañadón del Loro, middle Chubut River, northwest Chubut, Argentina.

Data: Chatterjee and Small (1989), Gasparini *et al.* (2003)

Attenborosaurus conybeari **(Sollas, 1881)**

Lower Lias Group (early Sinemurian, Early Jurassic) of Charmouth, Dorset, UK.

Data: Sollas (1881)

Augustasaurus hagdorni **Sander *et al.*, 1997**

Fossil Hill Member, Favret Formation, basal Rotelliformis Zone (late Anisian, Mid Triassic) of Muller Canyon, Augusta Mountains, Pershing County, Nevada,

USA.

Data: Ketchum and Benson (2011a), Sander *et al.* (1997), Rieppel *et al.* (2002)

Avalonnectes arturi **Benson *et al.*, 2012**

Pre-planorbis beds, Blue Lias Formation, Lias Group (earliest Hettangian, Early

Jurassic) of Street, Somerset, UK.

Data: NHMUK 14550, TTNCM 9291, AGT uncat., Benson *et al.* (2012)

Bobosaurus forojuliensis **Dalla Vecchia, 2006**

Lower part of the Rio del Lago Formation (early Carnian, Late Triassic) of

tributary of the Pontuz Creek, near Gran Colle, Udine, Friuli-Venezia Giulia,

Italy.

Data: Dalla Vecchia (2006)

Borealonectes russelli **Sato and Wu, 2008**

Hiccles Cove Formation (Callovian, Mid Jurassic) of Melville Island, NWT,

Canada.

Data: Sato and Wu (2008)

Brachauchenius lucasi **Williston, 1903**

Upper Greenhorn Limestone Formation or lower Fairport Chalk Member of

Carlile Shale Formation (early mid Turonian, Late Cretaceous) of Delphos,

Ottawa County, Kansas, USA.

Data: Carpenter (1996), Ketchum (2007), Ketchum and Benson (2011a),

Williston (1903, 1907)

***Brancasaurus brancai* Wegner, 1914**

Osterwald-Schichten Formation, Wealden Group (late Berriasian, Early

Cretaceous) of Gerdemann clay pit, Gronau, Nordrhein-Westfalen, Germany.

Data: R.B.J. Benson (pers. comm.), Benson *et al.* (in press), Wegner (1914)

***Callawayasaurus colombiensis* (Welles, 1962)**

'Leiva Shale' (lower Aptian, Early Cretaceous) of Loma de la Catalina, near

Leiva, Boyacá, Colombia.

Data: Druckenmiller and Russell (2008a), Welles (1962)

'*Cimoliasaurus' valdensis* Lydekker, 1889

Wadhurst Clay Formation, Hastings Group (Valanginian, Early Cretaceous) of

Hastings, East Sussex, UK.

Data: Benson *et al.* (in press), Ketchum (2011)

CM Zfr 115

Conway Formation (late Campanian, Late Cretaceous) of Ngaroma Station,

North Canterbury, South Island, New Zealand.

Data: Hiller *et al.* (2005)

Notes: Referred to *Mauisaurus haasti* by Hiller *et al.* (2005).

CM Zfr 145

Conway Formation (late Maastrichtian, Late Cretaceous) of Middle Waipara

River, North Canterbury, South Island, New Zealand.

Data: Hiller and Mannering (2005)

Colymbosaurus trochanterius **(Owen, 1840)**

Kimmeridge Clay (Kimmeridgian-Tithonian, Late Jurassic) of Oxfordshire, UK.

Data: Brown (1981), Hulke (1870)

Cryptoclidus eurymerus **(Phillips, 1871)**

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an
unspecified brick pit near Peterborough, UK.

Data: NHMUK R2860 (neotype); Benson *et al.* (2012), Brown (1981), Brown
and Cruickshank (1994), Ketchum and Benson (2011a)

Cymatosaurus **Fritsch, 1894**

Lower Muschelkalk Subgroup (late Anisian, Mid Triassic) of Halle/Sale,
Germany.

Data: Ketchum and Benson (2011a), Rieppel (1994b, 1997, 2000), Rieppel and
Hagdorn (1997), Rieppel and Werneburg (1998)

Dolichorhynchops bonneri **(Adams, 1997)**

Sharon Springs Member, Pierre Shale (early Campanian, Late Cretaceous) of
Wyoming, USA.

Data: Adams (1997), Carpenter (1996), O'Keefe (2008)

Dolichorhynchops herschelensis **Sato, 2005**

Bearpaw Formation (late Campanian-early Maastrichtian, Late Cretaceous) of
area southwest of Herschel, Saskatchewan, Canada.

Data: Sato (2005)

***Dolichorhynchops osborni* Williston, 1903**

Smoky Hill Chalk Member, Niobrara Formation, Hesperornis Zone (Santonian-

Campanian, Late Cretaceous) of Wallace, Logan County, Kansas, USA.

Data: Carpenter (1996, 1997), Ketchum and Benson (2011a), O'Keefe (2004a),

Williston (1903)

***Edgarosaurus muddi* Druckenmiller, 2002**

Shell Creek Member, 'Thermopolis Shale' within or just below the

Neogastroplites haasi zone (late Albian, Early Cretaceous) of Edgar, Montana,

USA.

Data: Druckenmiller (2002), Ketchum and Benson (2011a)

***Elasmosaurus platyurus* Cope, 1868**

Sharon Springs Shale Member, Pierre Shale (early Campanian, Late Cretaceous)

of area near McAllister, Logan County, Kansas, USA.

Data: Cope (1875), Sachs (2005a)

***Eoplesiosaurus antiquior* Benson *et al.*, 2012**

Pre-planorbis beds, Blue Lias Formation, Lias Group (earliest Hettangian, Early

Jurassic) of Watchet, Somerset, UK.

Data: TTNCM 8348, Benson *et al.* (2012)

***Eopolycotylus rankini* Albright *et al.*, 2007**

Tropic Shale Formation, middle to upper Pseudoaspidoceras flexuosum Zone

(earliest Turonian, Late Cretaceous) of Glen Canyon National Recreation Area,

Kane County, Utah, USA.

Data: Albright *et al.* (2007)

***Eretmosaurus rugosus* (Owen, 1840)**

Lias Group (Early Jurassic) of Granby, Nottinghamshire or Leicestershire, UK.

Data: NHMUK 14435 (neotype), Benson *et al.* (2012)

***Eromangasaurus australis* (Sachs, 2005b)**

Toolebuc Formation, Rolling Downs Group, P. ludbrookiae-upper C. paradoxa-

P. pannosus Zone (latest mid to late Albian, Early Cretaceous) of Yambore

Creek, near Maxwelton, Queensland, Australia.

Data: Kear (2005, 2007), Ketchum and Benson (2011a)

***Eurycleidus arcuatus* (Owen, 1840)**

Blue Lias Fiormation, Lias Group, Tilmanni Zone (earliest Hettangian, Early

Jurassic) of Marshall's Elm, near Street, Somerset, UK.

Data: R.B.J. Benson (pers. comm.), Ketchum and Benson (2011a), Smith (2007)

FHSM VP321

Middle Fairport Chalk Member of the Carlisle Shale Formation (early mid

Turonian, Late Cretaceous) of area near Fairport, Russell County, Kansas, USA.

Data: Ketchum (2007), Ketchum and Benson (2011a)

***Futabasaurus suzukii* Sato *et al.*, 2006**

Irimazawa Member, Tamayama Formation, Futaba Group (early Santonian, Late

Cretaceous) of Fukushima Prefecture, Japan.

Data: Sato *et al.* (2006)

Gallardosaurus iturraldei **Gasparini, 2009**

Jagua Formation (mid-late Oxfordian, Late Jurassic) of Viñales, Cuba.

Data: MNHNCu P3005 (holotype), Gasparini (2009)

Golden Cap taxon

Seatown Marl Member, Charmouth Mudstone Formation, Lias Group, Davoei

Zone (Pliensbachian, Early Jurassic) of coastal exposure below Golden Cap,

Dorset, UK.

Data: BRPMG specimen

Hauffiosaurus longirostris **(Blake in Tate and Blake, 1876)**

Jet Rock Member, Whitby Mudstone Formation, Serpentinum Zone (Benton and

Taylor 1984) (lower Toarcian, Early Jurassic) of Whitby, Yorkshire, UK.

Data: Ketchum and Benson (2011a), White (1940)

Hauffiosaurus tomistomimus **Benson *et al.* 2011b**

Alum Shale Member, Whitby Mudstone Formation, Bifrons Zone (Benton and

Taylor 1984) (early Toarcian, Early Jurassic) of the coast between Old Peak and

Blea Wyke Point, south-east of Robin Hood's Bay, Yorkshire, UK.

Data: MANCH LL8004, Benson *et al.* (2011b, 2012), Ketchum and Benson

(2011a)

Hauffiosaurus zanoni **O'Keefe, 2001**

Unterer Schiefer, Lias εII4, Posidonienschiefer, Serpentinum Zone (early

Toarcian, Early Jurassic) of Holzmaden, Baden-Württemberg, Germany.

Data: Benson *et al.* (2012), Ketchum and Benson (2011a), Vincent (2011)

Hydralmosaurus serpentinus **(Cope, 1877)**

Smoky Hill Chalk Member, Niobrara Formation (Santonian, Late Cretaceous) of

Cedar County, Nebraska, USA.

Data: AMNH 1495 (holotype), AMNH 5835 (holotype of *Styxosaurus browni*),

Carpenter (1999)

Hydrorion brachypterygius **Huene, 1923**

Unterer Schiefer, Lias εII4,, Posidonienschiefer, Serpentinum Zone (early

Toarcian, Early Jurassic) of Ohmden near Holzmaden, Baden-Württemberg,

Germany.

Data: Grossmann (2006), Huene (1923), Maisch and Rücklin (2000)

Hydrotherosaurus alexandrae **Welles, 1943**

Moreno Formation (Maastrichtian, Late Cretaceous) of area 22 miles west of

Mendota, Fresno County, California, USA.

Data: Druckenmiller and Russell (2008a), Sato (2002), Welles (1943)

Kaiwhekea katiki **Cruickshank and Fordyce, 2002**

Lower to Middle Katiki Formation, upper A. acutulum Zone, Palaeocystodinum

granulatum subzone (mid Maastrichtian, Late Cretaceous) of Shag Point, North

Otago, South Island, New Zealand.

Data: R.B.J. Benson (pers. comm.), Cruickshank and Fordyce (2002)

Kimmerosaurus langhami **Brown, 1981**

Kimmeridge Clay Formation, Pectinatites pectinatus Zone, P. eastlecottensis

subzone (early Tithonain, Late Jurassic) of Endcombe Bay, Dorset, UK.

Data: Brown (1981), Brown *et al.* (1986), Ketchum and Benson (2011a)

Kronosaurus queenslandicus **Longman, 1924**

Toolebuc Formation, Rolling Downs Group (Aptian-Albian, Early Cretaceous)

of Hughenden, Queensland, Australia.

Data: Ketchum and Benson (2011a), C. McHenry (pers. comm.)

LEICT G1.2002

The top of the 'Crinoid-Belemnite Bed' of Simms (2004), Charmouth Mudstone

Formation, Lias Group, uppermost Valdani Subzone, Ibex Zone (early

Pliensbachian, Early Jurassic) of Blockley, Gloucestershire, UK.

Data: LEICT G1.2002

LEICT G18.1996

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an

unspecified brick pit near Peterborough, UK.

Data: LEICT G18.1996

Notes: Referred to *Muraenosaurus leedsii* by Evans (1999).

Leptocleidus capensis Andrews, 1911

Sundays River Formation (latest Valanginian, Early Cretaceous) of Picnic Bush

Locality, Swartkops River Valley, Cape Province, South Africa.

Data: Andrews (1911), Cruickshank (1997), Druckenmiller and Russell (2008a)

Leptocleidus clemai Cruickshank and Long, 1997

Birdrong Sandstone (Barremian, Early Cretaceous) of near Kalbarri, Western

Australia, Australia.

Data: Cruickshank and Long (1997)

Leptocleidus superstes Andrews, 1922a

Upper Weald Clay Member, Weald Clay Formation (Barremian, Early

Cretaceous) of Cuckmere Brick Company Quarry, Berwick, Sussex, UK.

Data: NHMUK R4828, Andrews (1922a), Benson _et al._ (in press), Kear and

Barrett (2011)

Libonectes morgani (Welles, 1949)

Britton Formation, Eagle Ford Group (Turonian, Late Cretaceous) of area near

Cedar Hill, Dallas County, Texas, USA.

Data: Carpenter (1997), Druckenmiller and Russell (2008a), Sato (2002), Welles

(1949)

Lincoln taxon

Charmouth Mudstone Formation, Lias Group (Pliensbachian, Early Jurassic) of

Lincoln, Lincolnshire, UK.

Data: LCNCC 9766, R.A. Forrest (pers. comm.)

Liopleurodon ferox **Sauvage, 1873**

Argiles de Montaubert, Lamberti Zone (Thierry 2003; late Callovian, Mid
Jurassic) of Le Wast near Boulogne-sur-Mer, Pas-de-Calais, France.
Data: LEICT G418.1956.58.1.4, Ketchum and Benson (2011a), Noè (2001)

Macroplata tenuiceps **Swinton, 1930**

Rugby Limestone Member, Blue Lias Formation, Lias Group, Angulata Zone
(latest Hettangian, Early Jurassic) of Harbury, Warwickshire, UK..
Data: Benson *et al.* (2012), Ketchum and Benson (2011a), Ketchum and Smith
(2010)

Manemergus anguirostris **Buchy *et al.*, 2005**

Unit 4 of the Cenomanian-Turonian limestone bar (Early Turonian, Late
Cretaceous) of area near Goulmima, Er-Rachidia, Morocco.
Data: Buchy *et al.* (2005)

Maresaurus coccai **Gasparini, 1997**

upper Los Molles Formation, Emileia giebeli zone, E. multiformis subzone
(early Bajocian, Mid Jurassic) of Chacaico Sur, 70 km southwest of Zapala,
Neuquén, Argentina.
Data: Ketchum and Benson (2011a), Gasparini (1997)

Marmonectes candrewi **Ketchum and Benson, 2011a**

Peterborough Member, Oxford Clay Formation, Enodatum Subzone,

Calloviense Zone (early Callovian, Mid Jurassic) of Quest Clay Pit, Stewartby,

Bedfordshire, UK.

Data: Ketchum and Benson (2011a)

Meyerasaurus victor **(Fraas, 1910)**

Unterer Schiefer, Lias εII4, Posidonienschiefer, Serpentinum Zone (early

Toarcian, Early Jurassic) of Holzmaden, Baden-Württemberg, Germany..

Data: AMNH 3872 (cast of skull of SMNS 12478), Fraas (1910), Ketchum and

Benson (2011a), Smith and Vincent (2010)

Microcleidus homalospondylus **(Owen, 1865)**

Alum Shale Member, Whitby Mudstone Formation, probably Bifrons Zone

(Benton and Taylor 1984) (early Toarcian, Early Jurassic) of Whitby, Yorkshire,

UK.

Data: NHMUK 36184 (lectotype), Benson *et al.* (2012), Ketchum and Benson

(2011a), Owen (1865), Watson (1909, 1911)

MIWG 1997.302

Shepherd's Chine Member, Vectis Formation (late Barremian-early Aptian,

Early Cretaceous) of Shepherd's Chine, Isle of Wight, UK.

Data: Ketchum (2011), Benson *et al.* (in press)

MNHN A. C. 8592

Lias Group (Early Jurassic) of Lyme Regis, Dorset, UK.

Data: BGS GSM 118412, Vincent and Taquet (2010)

Notes: Referred to *Plesiosaurus dolichodeirus* by Storrs (1997).

Muraenosaurus leedsii Seeley, 1874b

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an
unspecified brick pit near Peterborough, UK.

Data: NHMUK R2421 (holotype), NHMUK R2422, Andrews (1910), Brown
(1981), Ketchum and Benson (2011a), Maisch (1998)

Muraenosaurus platyclis Seeley, 1892

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an
unspecified brick pit near Peterborough, UK.

Data: NHMUK R2678 (holotype), Andrews (1910)

Notes: Referred to *Muraenosaurus leedsii* by Brown (1981).

NHMUK 49202

Lower Lias Group (Hettangian-early Sinemurian, Early Jurassic) of Charmouth,
Dorset, UK.

Data: NHMUK 49202, Andrews (1896), Benson *et al.* (2012), Ketchum and
Benson (2011a)

NHMUK R16330

Bed 122 of Lang (1936), Seatown Marl Member, Charmouth Mudstone

Formation, Lias Group, Davoei Zone, Capricornus Subzone (early

Pliensbachian, Early Jurassic) of Dorset, UK.

Data: NHMUK R16330

NHMUK R2439

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an

unspecified brick pit near Peterborough, UK.

Data: Ketchum and Benson (2011a)

NHMUK R2861

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an

unspecified brick pit near Peterborough, UK.

Data: NHMUK R2861, Andrews (1910)

Notes: Referred to *Muraenosaurus durobrivensis* by Andrews (1910) and to *M.*

leedsii by Brown (1981).

NHMUK R2864

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an

unspecified brick pit near Peterborough, UK.

Data: NHMUK R2864, Andrews (1910)

Notes: Referred to *Muraenosaurus leedsii* by Andrews (1910) and Brown

(1981).

Nichollssaura borealis **(Druckenmiller and Russell, 2008b)**

Wabiskaw Member, Clearwater Formation (early Albian, Early Cretaceous) of

Syncrude Base Mine near Fort McMurray, Alberta, Canada..

Data: Druckenmiller and Russell (2008b), Ketchum and Benson (2011a)

***Occitanosaurus tournemirensis* (Sciau *et al.*, 1990)**

Marnes feuilletées, Aalensis Zone, Mactra Subzone, Celtica Zonule (late

Toarcian, Early Jurassic) of Tournemire, Aveyron, France.

Data: MMM J.T. 86-100, Bardet *et al.* (1999)

OUMNH J.02247

Pyritic nodule horizon, Peterborough Member, Oxford Clay Formation, Jason

Zone (mid Callovian, Mid Jurassic) of Yarnton Gravel Pit, Oxfordshire, UK..

Data: Ketchum and Benson (2011a)

OUMNH J.28585

Lower Lias Group (Hettangian-early Sinemurian, Early Jurassic) of Charmouth,

Dorset, UK.

Data: OUMNH J.28585, Cruickshank (1994a), Ketchum and Benson (2011a)

***Pahasapasaurus haasi* Schumacher, 2007**

Orman Lake Member, Greenhorn Formation (early late Cenomanian, Late

Cretaceous) of Butte County, South Dakota, USA.

Data: Schumacher (2007)

***Palmulasaurus quadratus* Albright *et al.*, 2007**

Tropic Shale Formation, middle-upper Pseudoaspidoceras flexuosum Zone

(earliest Turonian, Late Cretaceous) of Grand Staircase-Escalante National

Monument, Kane County, Utah, USA.

Data: Albright *et al.* (2007)

***Pantosaurus striatus* (Marsh, 1891)**

Upper Member of the Sundance Formation ('Redwater Shale' informal member)

(Oxfordian, Late Jurassic) of Carbon county, Wyoming, USA.

Data: O'Keefe and Wahl (2003a), O'Keefe *et al.* (2009), Wilhelm and O'Keefe

(2010)

***Peloneustes philarchus* (Seeley, 1869)**

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an

unspecified brick pit near Peterborough, UK.

Data: LEICT G418.1956.33, Ketchum (2007), Ketchum and Benson (2011a,

2011b)

***Picrocleidus beloclis* (Seeley, 1892)**

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an

unspecified brick pit near Peterborough, UK.

Data: Andrews (1910), Brown (1981)

***Pistosaurus* postcranium**

upper Muschelkalk (late Anisian, Mid Triassic) of Brindlacher Berg, near

Bayreuth, Bavaria, Germany.

Data: Sues (1987)

Notes: The postcranial material referred to *Pistosaurus* by Sues (1987) has been scored as a separate OTU following Ketchum and Benson (2011a).

***Pistosaurus* skull**

Lower Meissner Formation, upper Muschelkalk, mo1/mo2, *atavus-postspinosus* biozone (late Anisian, Mid Triassic) of Lainecker Höhenzug, east of Bayreuth, Bavaria, Germany.

Data: Rieppel (2000), Rieppel et al (2002), Sues (1987)

Notes: This OTU comprises the skull of *Pistosaurus longaevus* Meyer, 1839 only. The postcranial material referred to *Pistosaurus* by Sues (1987) has been scored as a separate OTU following Ketchum and Benson (2011a).

***Plesiopleurodon wellesi* Carpenter, 1996**

Belle Fourche Shale (earliest Cenomanian, Late Cretaceous) of area near Connamp Creek, Rattlesnake Hills, Natrona County, Wyoming, USA..

Data: Carpenter (1996), Ketchum and Benson (2011a)

***Plesiopterys wildii* O'Keefe, 2004b**

Unterer Schiefer, Lias εII4, Posidonienschiefer, Serpentinus Zone (early Toarcian, Early Jurassic) of Holzmaden, Baden-Württemberg, Germany.

Data: NHMUK R5884, Benson *et al.* (2012), Grossmann (2006), O'Keefe (2004b), O'Keefe (2006)

***Plesiosaurus dolichodeirus* Conybeare, 1824**

Lias Group (Hettangian-Sinemurian, Early Jurassic) of the coast below Black

Ven, Lyme Regis/Charmouth, Dorset, UK.

Data: NHMUK 22656, NMING F8758, Ketchum and Benson (2011a), Storrs (1997)

Notes: Storrs (1997) assigned the holotype to the Raricostatum Zone (uppermost Sinemurian) based on the occurrence of the ammonite *Echioceras raricostatum* in the matrix of OUMNH J.10304. However, this specimen would seem to be a separate taxon (see Chapter 3), and the matrix of the holotype is a poor match for the pyritic marls which would be expected in the Raricostatum Zone (pers. obs.; Page 2010). I therefore regard the type horizon as uncertain.

'*Plesiosaurus' macrocephalus* ?Conybeare in Owen, 1838

Lower Lias Group (Hettangian-early Sinemurian, Early Jurassic) of Charmouth, Dorset, UK.

Data: Druckenmiller and Russell (2008a), Ketchum and Benson (2011a), Owen (1838, 1840)

'*Pliosaurus' andrewsi* Tarlo, 1960

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an unspecified brick pit near Peterborough, UK.

Data: Andrews (1913), Ketchum and Benson (2011a), Tarlo (1960)

Pliosaurus brachydeirus Owen, 1841

Kimmeridge Clay Formation (Kimmeridgian-early Tithonian, Late Jurassic) of Market Rasen, Lincolnshire, UK.

Data: Ketchum and Benson (2011a), Tarlo (1960)

***Pliosaurus brachyspondylus* (Owen, 1840)**

Kimmeridge Clay Formation, Euxodus Zone (late Kimmeridgian, Late Jurassic) of Roswell Pit near Ely, Cambridgeshire, UK.

Data: Ketchum (2007), Ketchum and Benson (2011a), Tarlo (1959, 1960), Taylor and Cruickshank (1993b)

***Polycotylus latipinnis* Cope, 1869**

Smoky Hill Chalk Member, Niobrara Formation, Hesperornis zone (Santonian-Campanian, Late Cretaceous) of Smoky Hill River, 22.5 km east of Fort Wallace in Logan County, Kansas, USA.

Data: AMNH 2321 (part of holotype), Ketchum and Benson (2011a), O'Keefe (2004a), O'Keefe and Chiappe (2011)

QM F18041

Lower part of the Allaru Formation (late Albian, Early Cretaceous) of Richmond, Queensland, Australia.

Data: notes and photographs of QM F18041 taken by A.R.I. Cruickshank (LEICT archive), Ketchum (2007), Ketchum and Benson (2011a)

***Rhomaleosaurus cramptoni* (Carte and Bailey, 1863)**

Whitby Mudstone Formation, Lias Group (early Toarcian, Early Jurassic) of Kettleness, Yorkshire, UK.

Data: NMING F8785 (holotype), Smith (2007)

'*Rhomaleosaurus' megacephalus* (Stutchbury, 1846)

'Bottom Floor Limestone', Barnstone Member, Scunthorpe Mudstone

Formation, Planorbis Zone, Planorbis subzone (earliest Hettangian, Early

Jurassic) of quarry at or near Barrow-upon-Soar, Leicestershire, UK.

Data: LEICT G221.1851 (neotype), Cruickshank (1994b), Ketchum and Benson

(2011a)

***Rhomaleosaurus thorntoni* Andrews, 1922b**

Whitby Mudstone Formation, Lias Group (early Toarcian, Early Jurassic) of

Kingsthorpe, Northamptonshire, UK.

Data: R.B.J. Benson (pers. comm.), Cruickshank (1996), Smith (2007)

***Rhomaleosaurus zetlandicus* (Phillips in Anon., 1854)**

Cement Shales or upper Main Alum Shales, Alum Shale Member, Whitby

Mudstone Formation, Bifrons Zone (early Toarcian, Lower Jurassic) of Loftus

Alum Quarry, Loftus, Yorkshire, UK.

Data: R.B.J. Benson (pers. comm.), Ketchum and Benson (2011a), Smith

(2007), Taylor (1992)

***Seeleyosaurus guilelmiimperatoris* (Dames, 1895)**

Unterer Schiefer, Lias εII4, Posidonienschiefer, Serpentinum Zone (early

Toarcian, Early Jurassic) of Holzmaden, Baden-Württemberg, Germany.

Data: Benson *et al.* (2012), Dames (1895), Grossmann (2006)

Simolestes vorax **Andrews, 1909**

Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of an unspecified brick pit near Peterborough, UK.

Data: Andrews (1913), Ketchum and Benson (2011a), Noè (2001)

Simosaurus gaillardoti **Meyer, 1842**

Upper Muschelkalk Subgroup (early Ladinian, Mid Triassic) of Lunéville, France.

Data: Rieppel (1994a, b, 2000)

Speeton taxon

Bed C6, Speeton Clay Formation (mid Hauterivian, Early Cretaceous) of Filey Bay, Yorkshire, UK.

Data: SCARB 2007.51, NHMUK R8623, R.A. Forrest (pers. comm.)

Stratesaurus taylori **Benson *et al.*, 2012**

Pre-planorbis beds, Blue Lias Formation, Lias Group (earliest Hettangian, Early Jurassic) of Street, Somerset, UK.

Data: OUMNH J.10337, AGT 11, BGS GSM 26035, Benson *et al.* (2012), Ketchum and Benson (2011a)

Styxosaurus snowii **(Williston, 1890)**

Upper Smoky Hill Chalk Member, Niobrara Formation (Campanian, Late Cretaceous) of Hell Creek, Logan County, Kansas, USA.

Data: Ketchum and Benson (2011a), Welles and Bump (1949), Carpenter

(1997), Sato (2002), Storrs (1999)

Tatenectes laramiensis (Knight, 1900)

Upper Member of the Sundance Formation ('Redwater Shale' informal member)

(Oxfordian, Late Jurassic) of Natrona county, Wyoming, USA.

Data: O'Keefe and Street (2009), O'Keefe and Wahl (2003b), O'Keefe *et al.*

(2011), Street and O'Keefe (2010)

Terminonatator ponteixensis Sato, 2003

Bearpaw Formation (latest Campanian, Late Cretaceous) of Ponteix,

southwestern Saskatchewan, Canada..

Data: Sato (2002, 2003)

Thalassiodracon hawkinsii (Owen, 1838)

Blue Lias Formation, Pre-planorbis Beds (earliest Hettangian, Early Jurassic) of

Street, Somerset, UK.

Data: NHMUK 2018* (lectotype), NHMUK 2020*, Benson *et al.* (2011a),

Ketchum and Benson (2011a), Storrs and Taylor (1996)

Thalassomedon haningtoni Welles, 1943

Graneros Shales, Benton Group (late mid Cenomanian, Late Cretaceous) of

Baca County, Colorado, USA.

Data: Sato (2002), Welles (1943)

Thililua longicollis **Bardet *et al.*, 2003**

> Unit 4 of the Cenomanian-Turonian limestone bar (early Turonian, Late
>
> Cretaceous) of area near Goulmima, Er-Rachidia, Morocco.
>
> Data: Bardet *et al.* (2003)

TMP 95.87.01

> Wabiskaw Member, Clearwater Formation (early Albian, Early Cretaceous) of
>
> Syncrude North Mine, near Fort McMurray, Alberta, Canada.
>
> Data: Druckenmiller and Russell (2009)

Tricleidus seeleyi **Andrews, 1909**

> Peterborough Member, Oxford Clay Formation (Callovian, Mid Jurassic) of
>
> brick pit of Messrs Hicks and Gardner near Woodstone Lodge, Fletton,
>
> Peterborough, UK..
>
> Data: NHMUK R3539 (holotype), Andrews (1909, 1910), Brown (1981),
>
> Ketchum and Benson (2011a)

Trinacromerum bentonianum **Cragin, 1888**

> Fairport Chalk Member, Carlile Shale Formation (early mid Turonian, Late
>
> Cretaceous) of area near the fork of the Solomon River, Downs, Osborne
>
> County, Kansas, USA.
>
> Data: Carpenter (1996), Ketchum and Benson (2011a), O'Keefe (2004a)

Tuarangisaurus keyesi **Wiffen and Moisley, 1986**

> Maungataniwha Sandstone (Campanian-Maastrichtian, Late Cretaceous) of

Mangahouanga Stream, Hawke's Bay, North Island, New Zealand.

Data: R.B.J. Benson (pers. comm.), Wiffen and Moisley (1986)

Umoonasaurus demoscyllus **Kear *et al.*, 2006**

'Bulldog Shale' (Marree Subgroup), Cyclosporites hughesi, Crybelosporites

striatus Zones/Odontochitina operculata, Diconodinium davidii and Muderongia

tetracantha Zones (early Aptian-early Albian, Early Cretaceous) of the Zorba

Extension Opal Field, west of Coober Pedy, South Australia.

Data: photographs of AM F99374 (holotype) taken by A.R.I. Cruickshank

(LEICT archive), Kear *et al.* (2006), Druckenmiller and Russell (2008a)

Vinialesaurus caroli (**De la Torre and Rojas, 1949**)

Jagua Formation (mid-late Oxfordian, Late Jurassic) of Viñales, Cuba.

Data: MNHNCu P3008 (holotype), Gasparini *et al.* (2002)

Wapuskanectes betsynichollsae **Druckenmiller and Russell, 2006**

Wabiskaw Member, Clearwater Formation (lowermost Albian, Early

Cretaceous) of Syncrude Base Mine, near Fort McMurray, Alberta, Canada.

Data: Druckenmiller and Russell (2006)

Westphaliasaurus simonsensii **Schwermann and Sander, 2011**

Northrn German Lias Group, Valdani Subzone, Ibex Zone (Pliensbachian, Early

Jurassic) of Sommersell, Hoxter district, North-Rhine-Westphalia, Germany.

Data: Schwermann and Sander (2011)

***Yunguisaurus liae* Cheng *et al.*, 2006**

Lower Zhuganpo Formation (late Ladinian, Mid Triassic) of area near Chajiang,

Guizhou Province, China.

Data: Cheng *et al.* (2006), Sato *et al.* (2010)

***Zarafasaura oceanis* Vincent *et al.*, 2011**

Upper CIII level, phosphatic series (late Maastrichtian, Late Cretaceous) of Sidi

Daoui, near Oued Zem, Morocco.

Data: Vincent *et al.* (2011)

Appendix IV: Raw data for gap-weighting of morphometric characters

Taxon	318	319	320	321	322	323	324	325	326
Archaeonectrus rostratus	0.39	0.57	1.30	?	?	?	?	?	9
Aristonectes parvidens	?	?	?	?	?	?	?	50	7
Attenborosaurus conybeari	?	0.56	?	?	?	?	?	15	?
Augustasaurus hagdorni	0.41	0.47	0.94	1.40	-25	?	28.80	24	5
Marmornectes candrewi	?	?	?	?	?	0.60	?	?	13
NHMUK 49202	0.67	0.38	0.90	0.94	-5	?	15.50	10	4
NHMUK R2439	?	?	?	?	?	?	?	?	10
Brachauchenius lucasi	0.98	0.63	1.31	2.64	103	?	?	?	?
Brancasaurus brancai	0.97	0.32	0.61	?	?	?	?	21	?
Callawayasaurus colombiensis	0.49	0.40	0.78	1.73	4	0.50	17.30	13~19	3~5
Cymatosaurus	0.56	0.49	0.78	-	-	?	?	13.5	3
Cryptoclidus eurymerus	1.24	?	?	?	?	0.67	10.10	20.5	4~5
Dolichorhynchops herschelensis	?	0.53	0.83	2.16	?	0.42	47.21	20	19
Dolichorhynchops osborni	0.94	0.62	0.94	1.80	4	0.46	41.90	25	20
Edgarosaurus muddi	0.73	0.53	?	2.53	47	0.44	31.20	26	11
Elasmosaurus platyurus	?	?	?	?	?	?	?	?	4
Eopolycotylus rankini	?	?	?	?	?	?	?	?	15
Eromangasaurus australis	0.62	0.41	?	?	?	0.64	?	14	?
Eurycleidus arcuatus	?	?	?	?	?	?	?	?	5
FHSMVP321	0.57	0.65	1.28	?	?	0.62	?	19	6
Hauffiosaurus longirostris	?	0.58	?	?	?	?	?	?	?
Hauffiosaurus tomistomimus	?	?	0.96	1.42	?	0.38	?	14	?
Hauffiosaurus zanoni	?	?	?	?	-10	0.70	?	26	?
Hydrorion brachypterygius	0.45	0.40	1.20	1.42	-9	?	?	?	?
Hydrotherosaurus alexandrae	?	?	?	?	?	?	?	12.5	3
Kaiwhekea katiki	0.51	0.26	0.98	?	?	0.40	?	36	?
Kimmerosaurus langhami	?	?	?	?	?	?	?	?	?
Kronosaurus queenslandicus	?	?	?	2.80	-16	?	?	?	6
Leptocleidus capensis	0.72	0.40	1.03	1.83	47	0.48	?	?	?
Leptocleidus superstes	?	?	?	2.54	106	?	?	?	?
Libonectes morgani	0.69	0.38	0.86	2.33	-50	0.63	18.10	13.5	4
Liopleurodon ferox	0.69	0.55	1.00	2.02	89	0.76	24.20	23	6.5
Macroplata tenuiceps	0.49	0.54	0.88	0.71	-15	?	?	21	8
Manemergus anguirostris	0.54	0.54	?	?	?	?	?	10	9
Maresaurus coccai	?	0.47	1.10	1.12	12	0.59	?	?	6
Microcleidus homalospondylus	0.64	0.42	0.61	1.31	0	0.53	16.52	16	4
Muraenosaurus leedsii	?	?	?	?	?	0.52	?	16	4~5
Nichollssaura borealis	0.82	0.41	0.80	2.23	57	0.50	11.50	?	4~5
Occitanosaurus tournemirensis	0.81	0.42	0.76	1.95	-11	?	?	13	?
OUMNH J.02247	?	?	?	?	?	0.70	?	?	9
Stratesaurus taylori	1.03	0.46	?	0.91	-9	?	?	16	4.5
OUMNH J.28585	?	?	?	?	?	0.58	?	?	4
Palmulasaurus quadratus	?	?	?	?	?	?	?	?	?
Peloneustes philarchus	0.50	0.57	0.79	3.14	-6	0.63	39.30	28~37	13~15
Plesiopleurodon wellesi	0.50	0.54	1.02	?	?	0.43	?	?	8
Plesiosaurus dolichodeirus	0.85	0.47	1.00	0.96	-11	0.60	18.40	15~20	4
'Plesiosaurus' macrocephalus	0.62	0.45	?	?	?	?	?	?	?
Pliosaurus andrewsi	?	?	?	?	?	?	?	?	?
Pliosaurus brachydeirus	?	?	?	?	?	?	?	?	10~12
Pliosaurus brachyspondylus	0.65	0.53	1.12	2.22	72	?	?	25	?
Polycotylus latipinnis	?	?	?	?	?	?	?	?	?
QMF 18041	0.57	0.56	1.30	1.50	12	?	39.70	29	10
Rhomaleosaurus' megacephalus	0.73	0.47	1.04	0.85	-16	0.34	18.90	20.5	5
Meyerasaurus victor	?	?	?	1.55	-14	0.50	20.30	?	4~5

Taxon	327	328	329	330	331	332	333
Archaeonectrus rostratus	24	21	?	2.25	2.43	?	?
Aristonectes parvidens	?	?	?	?	?	?	?
Attenborosaurus conybeari	36	21	2.21	3.13	2.30	0.95	1.29
Augustasaurus hagdorni	38	21	-	?	?	?	?
Marmornectes candrewi	?	?	?	?	1.41	?	?
NHMUK 49202	?	?	?	?	?	?	?
NHMUK R2439	?	?	?	2.27	1.85	?	?
Brachauchenius lucasi	12	?	?	?	?	?	?
Brancasaurus brancai	40	19	?	2.43	2.19	0.90	1.04
Callawayasaurus colombiensis	56	23	3.04	?	?	1.04	0.92
Cymatosaurus	?	?	?	-	-	?	?
Cryptoclidus eurymerus	35	22	3.32	3.37	1.51~2.08	0.91	1.05
Dolichorhynchops herschelensis	17	22	3.27	3.35	2.18	1.4	2.00
Dolichorhynchops osborni	22	?	2.76	2.82	2.22	1.46	1.66
Edgarosaurus muddi	29	?	?	?	?	?	?
Elasmosaurus platyurus	71	?	?	2.85~3.44	1.49	1.17	?
Eopolycotylus rankini	?	?	3.03	3.07	1.97	1.27	1.98
Eromangasaurus australis	?	?	?	?	?	?	?
Eurycleidus arcuatus	?	?	2.60	2.31	?	1.07	1.24
FHSMVP321	?	?	?	?	?	?	?
Hauffiosaurus longirostris	?	?	?	?	?	?	?
Hauffiosaurus tomistomimus	35	26	?	?	?	?	?
Hauffiosaurus zanoni	32~37	?	?	3.98	1.75	?	0.79
Hydrorion brachypterygius	37	16	3.36	2.27	1.88	1.14	1.14
Hydrotherosaurus alexandrae	62	17	3.04	4.18	?	1.16	1.20
Kaiwhekea katiki	46	20	?	?	?	?	?
Kimmerosaurus langhami	?	?	?	?	?	?	?
Kronosaurus queenslandicus	14	?	?	?	?	?	?
Leptocleidus capensis	25~28	?	?	?	?	?	?
Leptocleidus superstes	?	?	2.58	?	?	?	?
Libonectes morgani	62	?	3.35	?	?	?	?
Liopleurodon ferox	22	?	?	?	?	1.56	1.76
Macroplata tenuiceps	28	21	?	?	?	0.95	1.41
Manemergus anguirostris	28	?	?	?	?	?	?
Maresaurus coccai	?	?	?	?	?	?	?
Microcleidus homalospondylus	38	16	?	?	?	1.13	1.44
Muraenosaurus leedsii	47	20	3.50	3.01~3.15	2.24	1.13	1.21
Nichollssaura borealis	24	25	?	?	?	?	1.41
Occitanosaurus tournemirensis	46	16	3.13	2.86	2.20	1.05	1.20
OUMNH J.02247	20	?	?	?	?	?	?
Stratesaurus taylori	?	?	?	2.28	2.38	?	?
OUMNH J.28585	?	?	?	?	?	?	?
Palmulasaurus quadratus	?	?	?	2.65	1.76	1.02	1.63
Peloneustes philarchus	24	23	1.93	2.73~2.89	1.49~1.97	1.31	1.73
Plesiopleurodon wellesi	?	?	?	?	?	?	?
Plesiosaurus dolichodeirus	46	21	3.03	3.29	1.74	?	1.10
'Plesiosaurus' macrocephalus	29	20	?	?	?	?	?
Pliosaurus andrewsi	18	?	?	2.77	1.93	?	?
Pliosaurus brachydeirus	?	?	?	?	?	?	?
Pliosaurus brachyspondylus	?	?	?	?	?	?	?
Polycotylus latipinnis	?	?	?	2.76	?	1.25	2.40
QMF 18041	24	20	?	?	?	?	1.03
Rhomaleosaurus' megacephalus	28	19	?	2.33	2.05	?	?
Meyerasaurus victor	27	?	2.18	2.12	2.36	0.92	1.21

IV.2

Taxon	334	335	336	337	338	339
Archaeonectrus rostratus	0.93	2.27	?	2.00	2.00	1.40
Aristonectes parvidens	?	?	?	?	?	?
Attenborosaurus conybeari	1.04	2.20	?	1.51	2.12	?
Augustasaurus hagdorni	0.91	3.40	?	4.50	?	?
Marmornectes candrewi	0.82	2.45	?	1.02	?	1.08
NHMUK 49202	?	?	?	?	?	?
NHMUK R2439	?	?	?	0.93	?	1.16
Brachauchenius lucasi	?	?	?	?	?	?
Brancasaurus brancai	0.98	1.96	?	?	2.00	?
Callawayasaurus colombiensis	1.17	1.41	?	1.15	1.52	0.92
Cymatosaurus	?	3.20	?	?	?	?
Cryptoclidus eurymerus	1.05	1.30	5.93	1.30	1.64	0.72
Dolichorhynchops herschelensis	?	?	?	?	?	?
Dolichorhynchops osborni	0.91	1.90	6.96	0.68	2.22	0.55
Edgarosaurus muddi	?	?	5.56	0.65	?	?
Elasmosaurus platyurus	?	?	?	?	?	?
Eopolycotylus rankini	0.99	2.00	?	?	1.83	0.79
Eromangasaurus australis	?	?	?	?	?	?
Eurycleidus arcuatus	1.09	1.95	?	2.36	2.00	?
FHSMVP321	?	?	?	?	?	?
Hauffiosaurus longirostris	?	?	?	?	?	?
Hauffiosaurus tomistomimus	1.1	2.48	?	2.10	2.60	?
Hauffiosaurus zanoni	0.94	2.63	?	2.10	2.63	1.81
Hydrorion brachypterygius	0.98	3.00	6.05	2.60	3.20	1.86
Hydrotherosaurus alexandrae	1.06	1.42	?	1.00	1.53	?
Kaiwhekea katiki	?	?	?	?	1.88	?
Kimmerosaurus langhami	?	?	?	?	?	?
Kronosaurus queenslandicus	0.76	2.00	?	?	2.80	?
Leptocleidus capensis	?	?	?	?	?	?
Leptocleidus superstes	?	?	?	?	?	?
Libonectes morgani	?	?	?	?	?	?
Liopleurodon ferox	?	?	7.83	?	2.08	1.14
Macroplata tenuiceps	?	?	?	?	2.24	1.42
Manemergus anguirostris	?	?	?	?	?	?
Maresaurus coccai	?	?	?	?	?	?
Microcleidus homalospondylus	0.9	1.82	9.80	1.60	1.80	2.31
Muraenosaurus leedsii	1.1	1.80	7.79	1.25	1.85	0.75
Nichollssaura borealis	0.95	1.78	6.57	1.13	1.80	1.10
Occitanosaurus tournemirensis	0.98	2.20	?	2.20	2.00	1.80
OUMNH J.02247	?	1.84	?	1.07	?	?
Stratesaurus taylori	?	?	?	?	?	1.77
OUMNH J.28585	?	?	?	?	?	?
Palmulasaurus quadratus	1.1	1.85	?	0.92	1.93	0.98
Peloneustes philarchus	0.86	1.89	6.96	0.92	2.27	0.96
Plesiopleurodon wellesi	?	?	?	?	?	?
Plesiosaurus dolichodeirus	1.06	2.10	9.85	3.00	2.00	1.80
'Plesiosaurus' macrocephalus	0.9	1.92	8.92	2.25	2.00	2.00
Pliosaurus andrewsi	0.8	1.85	?	?	1.97	1.10
Pliosaurus brachydeirus	?	?	?	?	2.20	0.72
Pliosaurus brachyspondylus	?	?	?	?	?	?
Polycotylus latipinnis	?	1.89	8.17	?	?	0.69
QMF 18041	1.06	2.10	9.63	1.10	2.10	1.00
Rhomaleosaurus' megacephalus	1.14	1.73	?	?	1.81	1.79
Meyerasaurus victor	1.02	2.10	9.51	1.80	2.29	1.60

IV.3

Taxon	318	319	320	321	322	323	324	325	326
Rhomaleosaurus zetlandicus	?	0.47	1.11	1.03	6	?	?	?	?
Seeleyosaurus guilelmiimperatoris	1.16	0.45	1.10	?	?	0.67	?	?	4
Simolestes vorax	0.60	0.54	1.21	1.72	86	0.56	22.20	?	5
Simosaurus gaillardoti	0.49	0.41	0.98	-	-	0.55	?	19~23	4
Styxosaurus snowii	0.58	0.42	?	?	?	0.40	?	14	4
Terminonatator pontiexensis	0.90	0.38	?	?	?	0.48	?	13	3~4
Thalassiodracon hawkinsii	1.40	0.49	?	0.87	0	0.59	17.60	21	4
Thalassomedon haningtoni	?	0.42	?	?	?	?	?	?	?
Thililua longicollis	0.81	0.58	?	?	?	?	?	22	15
Tricleidus seeleyi	?	?	?	1.13	4	0.78	?	23	?
Trinacromerum bentonianum	0.74	0.64	?	3.50	44	0.61	?	15	12
Umoonasaurus demoscyllus	?	0.31	0.87	1.58	52	?	?	?	?
Pistosaurus skull	0.50	0.49	1.10	?	?	?	?	?	?
Pistosaurus postcranium		?	?	?	?	?	?	?	?
Yunguisaurus liae	0.41	0.47	1.10	2.38	0	?	29.86	?	?
Bobosaurus forojuliensis		?	?	?	?	?	?	?	?
LEICT G1.2002	1.24	?	1.33	0.81	26	?	?	?	?
NHMUK R16330	?	?	?	?	?	?	?	?	?
Speeton taxon	?	?	?	?	?	?	?	?	?
Hydralmosaurus serpentinus	0.46	0.33	?	?	?	0.60	?	13	?
Rhomaleosaurus cramptoni	0.37	0.50	1.65	0.98	39	0.63	15.09	25	4
Rhomaleosaurus thorntoni	?	?	?	?	?	?	?	?	5.5
Avalonnectes arturi	?	0.39	0.92	?	?	?	?	23	?
Plesiopterys wildii	?	0.35	0.98	0.82	6	?	11.10	?	?
Lincoln taxon	?	?	?	?	?	?	?	?	?
Golden Cap taxon	?	?	?	?	?	?	?	?	?
LEICT G18.1996	?	?	?	?	0.00	?	?	?	?
Muraenosaurus platyclis	?	?	?	0.75	-24	?	?	17.5	5
NHMUK R.2861	1.15	0.42	?	0.75	-20	0.76	17.04	18	4.5
NHMUK R.2864	?	?	?	?	?	?	?	?	?
Vinialesaurus caroli	?	?	?	?	?	0.77	?	?	?
Gallardosaurus iturraldei	0.68	?	1.11	2.50	76	0.66	?	?	?
Pahasapasaurus haasi	?	0.70	?	?	?	?	?	19.5	12
Dolichorhynchops bonneri	1.01	0.66	?	2.04	0	?	49.95	27	19
Leptocleidus clemai	?	?	?	?	?	?	?	?	?
TMP 95.87.01	?	?	?	?	?	?	?	?	?
Wapuskanectes betsynichollsae	?	?	?	?	?	?	?	?	?
CM Zfr 145	?	?	?	?	?	?	?	?	?
CM Zfr 115	?	?	?	?	?	?	?	?	?
Futabasaurus suzukii	?	?	?	?	?	?	?	15	3
Tuarangisaurus keyesi	0.58	0.40	?	2.25	?	?	9.19	15	3
Tatenectes laramiensis	?	?	?	?	?	?	?	?	?
Pantosaurus striatus	?	?	?	?	?	?	?	?	?
MNHN A. C. 8592	?	?	?	?	?	?	?	?	?
Picrocleidus beloclis	?	?	?	?	?	?	?	?	?
Eoplesiosaurus antiquior	?	?	?	?	?	?	?	?	?
Borealonectes russelli	0.53	0.48	1.33	2.07	77	?	24.43	25	6
Colymbosaurus trochanterius	?	?	?	?	?	?	?	?	?
Eretmosaurus rugosus	?	?	?	?	?	?	?	?	?
Westphaliasaurus simonsensii	?	?	?	?	?	?	?	?	?
MIWG 1997.302	?	?	?	?	?	?	?	?	?
'Cimoliosaurus' valdensis	?	?	?	?	?	?	?	?	?
Zarafasaura oceanis	0.41	0.32	0.65	?	?	0.66	16.00	11	4

Taxon	327	328	329	330	331	332	333
Rhomaleosaurus zetlandicus	27	26	?	?	?	?	?
Seeleyosaurus guilelmiimperatoris	39	19	?	2.19	2.53	1.10	0.79
Simolestes vorax	20	?	2.85	3.04	?	1.44	1.80
Simosaurus gaillardoti	?	28	-	-	-	-	?
Styxosaurus snowii	61	?	3.17	2.70	?	1.17	1.17
Terminonatator pontiexensis	53	?	?	2.88	2.15	?	?
Thalassiodracon hawkinsii	?	?	2.59	2.19~2.35	2.20~2.40	0.98	1.20
Thalassomedon haningtoni	?	25	?	2.49	2.46	?	1.10
Thililua longicollis	33	?	?	?	?	?	?
Tricleidus seeleyi	?	?	3.23	?	?	?	?
Trinacromerum bentonianum	?	?	?	3.09~3.40	2.18~2.55	1.47	1.57
Umoonasaurus demoscyllus	?	?	?	?	?	?	?
Pistosaurus skull	?	?	?	?	?	?	?
Pistosaurus postcranium	?	?	-	-	?	?	?
Yunguisaurus liae	49	23	-	2.49	1.53	0.83	?
Bobosaurus forojuliensis	25	18	?	-	?	0.98	1.06
LEICT G1.2002	30	23	2.22	2.55	1.51	1.05	1.11
NHMUK R16330	?	?	?	?	?	?	?
Speeton taxon	?	?	?	3.61	?	1.01	1.13
Hydralmosaurus serpentinus	63	19	?	?	?	1.05	1.30
Rhomaleosaurus cramptoni	30	25	?	2.48	1.50	?	?
Rhomaleosaurus thorntoni	?	25	?	2.23	1.67	0.83	1.06
Avalonnectes arturi	28	19	?	?	?	?	?
Plesiopterys wildii	43	19	2.45	3.73	1.70	?	0.82
Lincoln taxon	?	?	?	?	2.03	?	?
Golden Cap taxon	?	?	2.31	?	?	?	?
LEICT G18.1996	?	?	?	3.32	2.04	1.28	1.12
Muraenosaurus platyclis	?	?	?	?	?	?	?
NHMUK R.2861	?	?	?	?	?	?	?
NHMUK R.2864	47	19	?	?	?	?	?
Vinialesaurus caroli	?	?	?	?	?	?	?
Gallardosaurus iturraldei	?	?	?	?	?	?	?
Pahasapasaurus haasi	?	?	?	?	?	?	?
Dolichorhynchops bonneri	22	22	3.19	3.10	1.59	1.22	1.67
Leptocleidus clemai	?	?	?	?	1.85	?	?
TMP 95.87.01	?	?	?	?	?	1.28	?
Wapuskanectes betsynichollsae	?	?	3.05	?	?	?	?
CM Zfr 145	?	?	?	2.60	1.95	1.24	1.40
CM Zfr 115	68	18	?	?	?	?	?
Futabasaurus suzukii	?	?	?	?	?	?	0.98
Tuarangisaurus keyesi	?	?	?	?	?	?	?
Tatenectes laramiensis	?	?	?	?	?	?	?
Pantosaurus striatus	?	?	?	2.40	2.86	1.11	1.10
MNHN A. C. 8592	?	?	1.98	3.26	1.95	?	?
Picrocleidus beloclis	47	?	2.99	?	?	?	?
Eoplesiosaurus antiquior	38	?	?	3.22	1.50	?	?
Borealonectes russelli	?	?	?	?	?	?	?
Colymbosaurus trochanterius	45	25	3.17	?	?	?	?
Eretmosaurus rugosus	38	?	?	2.75	1.90	1.09	1.24
Westphaliasaurus simonsensii	?	21	?	3.58	1.62	0.98	1.14
MIWG 1997.302	?	?	2.00	?	?	?	?
'Cimoliosaurus' valdensis	?	?	?	?	?	?	?
Zarafasaura oceanis	?	?	?	?	?	?	?

Taxon	334	335	336	337	338	339
Rhomaleosaurus zetlandicus	1.02	2.04	?	1.91	2.17	1.48
Seeleyosaurus guilelmiimperatoris	1.05	2.00	8.69	1.61	2.00	1.49
Simolestes vorax	0.93	1.91	?	1.35	1.95	1.35
Simosaurus gaillardoti	1.29	4.25	?	7.30	5.17	5.00
Styxosaurus snowii	1	1.45	11.11	0.93	1.40	?
Terminonatator pontiexensis	0.95	1.57	?	0.75	1.58	0.74
Thalassiodracon hawkinsii	1	2.22	9.59	?	?	1.80
Thalassomedon haningtoni	1	1.48	?	?	1.71	?
Thililua longicollis	?	?	?	?	?	?
Tricleidus seeleyi	0.96	1.75	?	1.06	1.91	0.64
Trinacromerum bentonianum	?	?	?	?	?	?
Umoonasaurus demoscyllus	0.96	2.17	?	?	2.03	?
Pistosaurus skull	?	?	?	?	?	?
Pistosaurus postcranium	?	3.20	?	4.50	?	?
Yunguisaurus liae	0.76	3.40	?	4.50	2.80	3.82
Bobosaurus forojuliensis	?	?	?	?	?	?
LEICT G1.2002	0.93	1.80	?	1.46	1.94	1.28
NHMUK R16330	?	1.83	?	1.24	?	?
Speeton taxon	1.09	1.70	?	1.12	1.75	1.73
Hydralmosaurus serpentinus	0.88	1.41	?	0.75	1.76	1.02
Rhomaleosaurus cramptoni	0.99	2.12	?	1.82	2.17	1.20
Rhomaleosaurus thorntoni	1.05	1.95	?	?	2.35	?
Avalonnectes arturi	0.92	2.28	?	1.76	2.33	1.97
Plesiopterys wildii	0.99	?	8.07	?	?	?
Lincoln taxon	?	?	?	?	1.94	2.33
Golden Cap taxon	?	2.09	?	2.54	?	2.31
LEICT G18.1996	1.05	1.74	?	?	2.33	?
Muraenosaurus platyclis	1.07	1.65	?	0.99	1.70	?
NHMUK R.2861	?	?	?	?	2.18	1.26
NHMUK R.2864	1.06	1.79	?	1.01	1.95	0.77
Vinialesaurus caroli	?	?	?	?	?	?
Gallardosaurus iturraldei	?	?	?	?	?	?
Pahasapasaurus haasi	0.92	1.96	6.74	1.07	2.18	0.96
Dolichorhynchops bonneri	0.98	1.80	6.41	0.77	1.66	0.46
Leptocleidus clemai		2.12	?	?	2.22	0.76
TMP 95.87.01	?	?	?	?	?	?
Wapuskanectes betsynichollsae	?	1.37	?	?	?	?
CM Zfr 145	0.93	1.22	?	?	1.37	0.95
CM Zfr 115	1.07	?	?	0.74	1.77	?
Futabasaurus suzukii	1.18	1.57	?	0.88	1.57	0.93
Tuarangisaurus keyesi	?	?	?	?	?	?
Tatenectes laramiensis	?	1.78	?	1.16	?	?
Pantosaurus striatus	?	2.12	?	1.08	?	?
MNHN A. C. 8592	1.16	2.26	?	2.96	2.23	2.26
Picrocleidus beloclis		1.85	?	1.18	1.86	?
Eoplesiosaurus antiquior	1.06	2.87	12.75	2.77	2.55	2.26
Borealonectes russelli	?	1.86	?	1.44	?	?
Colymbosaurus trochanterius	1.02	1.72	?	1.18	1.93	0.81
Eretmosaurus rugosus	1.00	2.17	?	2.73	2.05	2.29
Westphaliasaurus simonsensii	1.00	2.20	?	2.11	2.06	1.90
MIWG 1997.302	?	?	?	?	?	?
'Cimoliosaurus' valdensis	?	2.32	?	1.01	?	0.99
Zarafasaura oceanis	?	?	?	?	?	?

Appendix V: Abbreviations

Anatomical

Left and right elements are denoted by (l) and (r) suffixes respectively.

acet	acetabulum	cif	crista interfenestralis
adc	anterodorsal crest	cl	clavicle
adqf	anterodorsal quadrate flange of the squamosal	cof	common otoccipital foramen
		colc	columella cranii
af	acoustic foramen	cor	cornu
ant	anterior	corf	coracoid facet
apc	anterior process of the coracoid	cp	clinoid process
		cr	cervical rib
arp	anterior rib process	cv	cervical vertebra
arsq	anterior ramus of the squamosal		
		d1	dorsal vertebra 1
asc	anterior semicircular canal	d7	dorsal vertebra 7
asp	anterior spinous process	dbp	dorsal boss of the pterygoid
asqf	anterior squamosal facet	dc1	distal carpal 1
atc	atlas centrum	dc2&3	distal carpal 2 and 3
atlc	atlantal cup/cotyle	dc4	distal carpal 4
atna	atlas neural arch	dfc	diverging facial ridges
aur	ampullar/utricular recess	dfp	dorsal flange of the pterygoid
axc	axis centrum	dia	diapophysis
axic	axis intercentrum	dmf	dorsomedian fossa
axna	axis neural arch	dmr	dorsomedian ridge
axns	axis neural spine	dr	dorsal rib
axr	axis rib	drs	dorsal ramus of the scapula
		drsq	dorsal ramus of the squamosal
baf	basioccipital anterior foramen	ds	dorsum sellae
bmr	basioccipital median ridge	dt1	distal tarsal 1
bo	basioccipital	dt2&3	distal tarsal 2 & 3
boap	basioccipital anterior process	dt4	distal tarsal4
bof	basioccipital facet		
bot	basioccipital tuber	ep	epipterygoid
bovp	basioccipital vertical plate	epf	epipodial foramen
bpta	basipterygoid articulation	ex	exoccipital
bptp	basipterygoid process	exfl	exoccipital flange
bs	basisphenoid	expl	expanded to the left
bsms	basisphenoid median sulcus	expr	expanded to the right
but	buttress		
		f	frontal
cap	capitulum	fac	facet
car	caudal rib	fatic	facet for atlas intercentrum
ce	centrale	faxr	facet for axis rib
cem	coracoid embayment	fc	facial canal
cf	chevron facet	femf	femur facet
ch	chevron	fib	fibula

fibe	fibulare	msqf	medial squamosal facet
fibf	fibula facet	mtI	metatarsal I
fm	foramen magnum	mtV	metatarsal V
fo	fenestra ovalis	mvfr	medial ventral frontal ridge
for	foramen	mxf	maxilla facet
foss	fossa		
fw	frontal wing	naf	neural arch facet
		nc	neural canal
g	gastralium	ncs	neurocentral suture
gle	glenoid	np	notochordal pit
gr	groove	ns	neural spine
hoq	head of the quadrate	oc	occipital condyle
hq	head of the quadrate	olc	olfactory canal
hr	hypophyseal ridge	op	opisthotic
hsc	horizontal semicircular canal	opf	opisthotic facet
huf	humerus facet	opfrag	opisthotic fragment
hyf	hypoglossal foramen	opn	opisthotic notch
		otf	otooccipital facet
icf	internal carotid foramen		
icl	interclavicle	p	parietal
iclf	interclavicle facet	p1	pectoral vertebra 1
icpp	interclavicle posterior process	p7	pectoral vertebra 7
ifp	infrafenestral process	pae	prootic anterior eminence
il	ilium	pan	posterior ampullar notch
ilb	iliac blade	par	posterior ampullar recess
ilf	ilium facet	para	parapophysis
int	intermedium	pbp	prootic basal process
intf	intermedium facet	pc	parietal crest
ipf	interparietal foramen	pfen	pectoral fenestra
isc	ischium	pfor	parietal foramen
iscf	ischium facet	pipv	posterior interpterygoid vacuity
		plat	posterolateral
j	jugal	pll	prootic lateral lamina
		pm	pila metoptica
lex	lateral excavation of the pterygoid	pmx	premaxilla
		po	postorbital
lpl	lateral pterygoid lappet	poae	postaxial expansion
lr	lagenar recess	poao	postaxial ossicle
lrpt	lateral ramus of the pterygoid	poaof	postaxial ossicle facet
lsqf	lateral squamosal facet	poap	postaxial process
lvs	diverticulum of the longitudinal venous sinus	pof	postfrontal
		pofc	postfrontal cornu
		poff	postfrontal facet
mc	metacarpal	pofl	postorbital flange
mcI	metacarpal I	pofp	postorbital footplate
mcV	metacarpal V	pop	paroccipital process
mf	metotic foramen	popp	posterior process of the parasphenoid
mg	median gastralium		
mp	median process	porf	postorbital facet

post	posterior	scaf	scapula facet
poz	postzygapophysis	scaps	scapular shelf
pozp	postzygapophyseal platform	scf	subcentral foramen
ppp	prootic postfacial process	sof	supraoccipital facet
pr	pectoral rib	sq	squamosal
prae	preaxial expansion	sqf	squamosal facet
prao	preaxial ossicle	sr1/2/3/4	sacral rib 1/2/3/4
praof	preaxial ossicle facet	st	sella turcica
prf	prefrontal	sut	suture
prf	prootic facet	sut	suture
prff	prefrontal facet	sym	symphysis
prpt	posterior ramus of the pterygoid		
prs	posterior ramus of the scapula	tfen	thyroid fenestra
		tib	tibia
prz	prezygapophysis	tibef	tibiale facet
ps	parasphenoid	tibf	tibia facet
psc	posterior semicircular canal	tp	transverse process
pscp	parasphenoid cultriform process	tpr	transverse parietal ridge
		tr	trabecula
		tri	triangular excavation
psf	facet for parasphenoid	tro	trochanter
pt	pterygoid	tub	tuberculum
ptab	parietal table	tubr	tuberosity
ptf	facet for pterygoid		
pubf	pubis facet	ulf	ulna facet
pvp	prootic posteroventral process	uln	ulna
		ulnef	ulnare facet
pzp	parazygapophyseal process	ulre	ulnare
pzpp	postzygapophyseal process of the atlas		
		vaor	ventral antorbital ridge
		vg	ventral groove of the basioccipital
q	quadrate	vlfp	ventrolateral flange of the pterygoid
qfor	quadrate foramen		
qrpt	quadrate ramus of the pterygoid	vlfs	ventrolateral flange of the squamosal
qsoc	quadrate socket	vmfp	ventromedial flange of the pterygoid
r	ridge		
rad	radius	vmfs	ventromedial flange of the squamosal
rade	radiale		
radef	radiale facet	vrs	ventral ramus of the scapula
radf	radius facet	vrsq	ventral ramus of the squamosal
rafl	radius anterior flange		
rdg	ridge	wf	wear facet
rf	rib facet		
rh	rib head		
rp	resorption pit		
rug	rugosity		
sca	scapula		

Directional

ant	anterior	med	medial
dor	dorsal	plat	posterolateral
l	left	post	posterior
lat	lateral	r	right

Institutional

AGT	Alfred Gillett Trust, Street, Somerset, UK.
AM	Australian Museum, Sydney, New South Wales, Australia.
AMNH	American Museum of Natural History, New York, NY, USA.
BGS	British Geological Survey, Keyworth, Notts. UK.
BHI	Black Hills Institute of Geological Research, Hill City, South Dakota, USA.
NHMUK	The Natural History Museum, Cromwell Road, London, UK.
BRPMG	Bridport Museum, South Street, Bridport, Dorset, UK.
BRSMG	Bristol City Museum and Art Gallery, Bristol, UK.
CAMSM	Sedgwick Museum, University of Cambridge, Cambridge, UK.
CM	Canterbury Museum, Christchurch, New Zealand.
FHSM	The Sternberg Museum of Natural History, Hays, Kansas, USA.
GLRCM	Gloucester City Museum and Art Gallery, Gloucester, UK.
KUVP	The University of Kansas Natural History Museum, Lawrence, Kansas, USA.
LCNCC	The Collection, Lincolnshire Museums, Lincoln, Lincolnshire, UK.
LEICT	Leicester Museums and Galleries, New Walk Museum and Art Gallery, Leicester, UK.
MIWG	'Dinosaur Isle' Museum of Isle of Wight Geology, Sandown, Isle of Wight, UK.
MMM	Musée de Millau, Place Foch, Millau, Aveyron, France.
MANCH	The Manchester Museum, University of Manchester, Manchester, UK.
MNHN	Muséum national d'Histoire naturelle, Paris, France.
MNHNCu	Museo Nacional de Historia Natural de Cuba, Havana, Cuba.
NMING	National Museums of Ireland, Dublin, Eire.
OUMNH	Oxford University Museum of Natural History, Oxford, UK.
QM	Queensland Museum, Brisbane, Australia.
SCARB	Scarborough Museums, Scarborough, North Yorkshire, UK.
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany.
TMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.
TTNCM	Somerset County Museum, Taunton, Somerset, UK.
WM	Whitby Museum, Whitby, North Yorkshire, UK.

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