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ARTICLE

THE ANATOMY AND TAXONOMY OF *MACROPLATA TENUICEPS* (SAUROPTERYGIA, PLESIOSAURIA) FROM THE HETTANGIAN (LOWER JURASSIC) OF WARWICKSHIRE, UNITED KINGDOM

HILARY F. KETCHUM*,[1] and ADAM S. SMITH[2,†]
[1]Department of Palaeontology, the Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom, hilary.ketchum@cantab.net;
[2]School of Biology and Environmental Science, University College Dublin, Belfield Dublin 4, Republic of Ireland

ABSTRACT—A detailed re-description and revised diagnosis is given for *Macroplata tenuiceps* Swinton, 1930, a plesiosaurian known from a single almost complete specimen (BMNH R5488) from the Blue Lias Formation (Hettangian) of Harbury, Warwickshire, U.K. The Early Jurassic was an important time in the early evolution of the clade Plesiosauria and saw its diversification into two superfamilies, Plesiosauroidea and Pliosauroidea. As one of the earliest nearly complete, well-provenanced plesiosaurians known, *M. tenuiceps* is important for understanding early plesiosaurian evolution. Three new autapomorphies for *Macroplata tenuiceps* are presented, confirming the validity of this taxon: a triangular emargination in the posterior border of the coracoid; a triangular emargination in the posterior border of the ischium; and posterior convergence of the long axes of the posterior interpterygoid vacuities. Contrasting phylogenetic hypotheses of the position of *M. tenuiceps* and other Lower Jurassic plesiosaurians (some of which have not been treated scientifically since the 19th Century) highlights the need for revision of their anatomy and taxonomy for use in fine-grained species-level cladistic analysis.

INTRODUCTION

Plesiosauria de Blainville, 1835, is a derived clade within Sauropterygia Owen, 1860, a monophyletic group of Mesozoic reptiles secondarily adapted to life in water. The oldest plesiosaurians are known from the Rhaetian (uppermost Triassic; e.g., Taylor and Cruickshank, 1993; Storrs, 1994), and the most recent from the latest Maastrichtian (uppermost Cretaceous; e.g., Gasparini et al., 2003), a time span of approximately 135 million years. During this time, plesiosaurians achieved a cosmopolitan distribution, with their fossils found on every continent—including Antarctica (e.g., Chatterjee and Small, 1989)—and are known from both marine and freshwater deposits (e.g., Wiffen and Moisley, 1986; Cruickshank, 1997). The Early Jurassic marked the early diversification of Plesiosauria following the end-Triassic mass extinction (Cruickshank, 1994a, 1994b; Storrs and Taylor, 1996; Bardet et al., 1999; O'Keefe, 2004a; Grossmann, 2007). Early Jurassic plesiosaurians are, therefore, critical to an understanding of the early evolution of the clade, which is poorly understood at present (see the contrasting phylogenetic topologies of O'Keefe, 2001, 2004a; Druckenmiller and Russell, 2008).

The lower part of the Lias Group, the 'Lower Lias' of the U.K. (Rhaetian or Hettangian to Pliensbachian) was deposited in a shallow marine environment dominated by clays, shales, and limestones, and has yielded numerous remains of marine reptiles from at least 40 different localities extending along the length of its outcrop from Dorset to Yorkshire (Benton and Spencer, 1995). Dinosaurs and pterosaurs occur, but are much more rare (Benton and Spencer, 1995). The numerous plesiosaurian taxa are the stratigraphically earliest well-preserved members of the group known and include, in addition to *Macroplata tenuiceps*, *Attenborosaurus conybeari* (Sollas, 1881); *Archaeonectrus rostratus* (Owen, 1865); *Eurycleidus arcuatus* (Owen, 1840); *Eretmosaurus rugosus* (Owen, 1840); *Plesiosaurus dolichodeirus* Conybeare, 1824; '*Plesiosaurus*' *macrocephalus* Owen, 1838; a new genus represented by BMNH 49202 (Druckenmiller and Russell, 2008; referred to *Plesiosaurus macrocephalus* by Lydekker, 1889, and described as such by Andrews, 1896); a possible new genus represented by OUMNH J.28585 (O'Keefe, 2004a; referred to *Eurycleidus arcuatus* by Cruickshank, 1994a); '*Rhomaleosaurus*' *megacephalus* (Stutchbury, 1846); and *Thalassiodracon hawkinsi* (Owen, 1838). Many of these taxa are known from nearly complete specimens from the classic localities of Lyme Regis and Street, and represent some of the historically earliest discoveries of fossil reptiles made in the 19th Century (Storrs and Taylor, 1996). Unfortunately, because of their early discovery, stratigraphic data are often limited to the 'Lower Lias.' Given that this spans the Rhaetian or Hettangian to the Pliensbachian (Storrs and Taylor, 1996; Cox et al., 1999), it poses a problem in resolving contemporaneity of taxa (e.g., Cruickshank, 1994a). There is no modern review of lower Lias Group plesiosaurian taxonomy (Storrs and Taylor, 1996), and our understanding of their anatomy is also limited, with the most the recent descriptions of many dating to the 19th or early 20th centuries (with the notable exceptions of *Plesiosaurus dolichodeirus*, Storrs, 1997; *Thalassiodracon hawkinsi*, Storrs and Taylor, 1996; OUMNH J.28585, Cruickshank, 1994a; and '*Rhomaleosaurus*' *megacephalus*, Cruickshank, 1994b). This is problematic for attempts to incorporate 'Lower Lias' plesiosaurians into wider studies of plesiosaur origins.

Macroplata tenuiceps, the type species of the genus *Macroplata*, is known only from a single specimen from the *Schlotheimia angulata* Zone (Hettangian) of Harbury, Warwickshire (Swinton, 1930a). Sediments at Harbury were deposited in the East Midlands Shelf, and within the *S. angulata* Zone form part of the Rugby Limestone Member within the Blue Lias Formation (Cox et al., 1999; Simms, 2004). Workmen discovered the holotype specimen (BMNH R5488) in the cement quarry

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*Corresponding author. †Current address: Department of Geology, Museum Building, Trinity College Dublin, Dublin 2, Republic of Ireland.

owned by Greaves, Bull, and Lakin (Swinton 1930a, 1930b). The exact date of the discovery is uncertain, but it occurred some time in the winter of 1927–1928; a newspaper clipping outlining the discovery gives the date as November 1927 (Anonymous, 1928), whereas Swinton (1930b) gives the date as January 1928. Portland Cement Selling and Distributing Co., Ltd., presented the specimen to the Trustees of the Natural History Museum that year.

Two years after the discovery of the fossil, Swinton (1930a) published a brief preliminary description in which the novel generic and specific names were introduced. In a second publication the specimen was figured as it was mounted, accompanied by another short description (Swinton 1930b:fig. 1). However, the specimen has not received further detailed study, and most of the skeleton has never been figured.

Given the status of *Macroplata tenuiceps* as a rare taxon represented by only a single known specimen, and its significance as one of the few lowest Jurassic plesiosaurians with a well-resolved provenance, the anatomy of BMNH R5488 is critical to an understanding of the evolution of Plesiosauria at the beginning of the Early Jurassic.

Institutional Abbreviations—**BMNH**, The Natural History Museum, London, U.K.; **CAMSM**, The Sedgwick Museum of Earth Sciences, Cambridge, U.K.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **LEICT**, New Walk Museum and Art Gallery, Leicester, U.K.; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MMUM**, The Manchester Museum, Manchester, U.K.; **OUMNH**, The Oxford University Museum of Natural History, Oxford, U.K.; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TCD**, Trinity College, Dublin, Republic of Ireland; **UMH**, Urweltmuseum Hauff, Holzmaden, Germany.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
MACROPLATA TENUICEPS Swinton, 1930a
(Figs. 1–7)

Holotype—BMNH R5488, a near-complete skeleton.

Type Locality and Horizon—Blue Lias Formation of the Lias Group, Rugby Limestone Member, *Schlotheimia angulata* Zone (Hettangian), at Harbury Cement Works, Leamington Spa, Warwickshire, U.K.

Original Diagnosis—"Sauropterygian with a long skull and a long neck tapering from back to front. Cervical vertebrae moderately long, centra broader than high and narrow across the neurapophyses. Articular faces only slightly concave, and the anterior and posterior margins of the centrum rugose. Dorsals smooth and with constricted centra; articular faces not deeply concave; neural spines moderately high; transverse processes wholly supported by the arch. Sacral vertebrae with large rib-facets on the centra, and large and stout ribs. Caudals with rugose anterior and posterior margins to centra, articular faces more deeply cupped than the other vertebrae." (Swinton, 1930a:206).

Revised Diagnosis—A plesiosaurian with the following autapomorphies: posterior convergence of the long axes of the posterior interpterygoid vacuities; triangular emargination in the posterior border of the coracoid; triangular emargination in the posterior border of the ischium.

Remarks—*Macroplata tenuiceps* differs from all plesiosaurians that are temporally and geographically proximate. A unique combination of characters also diagnoses this taxon: six teeth in each premaxilla (distinguishing it from BMNH 49202, which has four teeth, and other plesiosaurians from the lower Lias Group, which have five where known); seven or eight dentary tooth pairs adjacent to the mandibular symphysis (which distinguishes it from '*R.*' *megacephalus*, which has five); lateral constriction of the snout at the premaxilla-maxilla suture in dorsal view (distinguishing it from '*Plesiosaurus*' *longirostris* in which there is no lateral constriction); raised posterior process of the premaxilla that forms a triangular-shaped ridge that tapers to a point midway between the orbits and contacts the frontals (distinguishing it from '*R.*' *megacephalus* in which the premaxillae lie flush with the surrounding elements, and distinguishing it from *Archaeonectrus rostratus* in which the premaxillary ridge is much less pronounced); basisphenoid entirely obscured by the parasphenoid in ventral view (shared only with BMNH 49202 and '*Rhomaleosaurus*' *megacephalus* among plesiosaurians where this is known); body of the basioccipital forming the posterior palatal margin (pterygoids do not meet posterior to the posterior interpterygoid vacuities; as in BMNH 49202, but unlike '*R.*' *megacephalus* and '*P.*' *longirostris* MCZ 1033); 26 cervical vertebrae (differing from all other Lower Jurassic plesiosaurians but closest in number to *Archaeonectrus rostratus*, which has 24; and we note that these counts can show intraspecific variation in plesiosaurians, e.g., *Plesiosaurus dolichodeirus*, Storrs, 1997:170); a deep sub-oval emargination on the midline of the posterior border of the clavicular arch (possibly shared with *Attenborosaurus conybeari*, Sollas, 1881, but no other Lower Jurassic plesiosaurian taxon where known); a broad sub-rectangular preglenoidal extension of the coracoid (present only in Lower Jurassic plesiosaurians); very small subcentral foramina in square-shaped depressions separated by a ventral keel in the cervical centra (distinguishing it from *Plesiosaurus dolichodeirus* and *Eretmosaurus rugosus*).

The anatomical features used by Swinton (1930a; also see above) to diagnose *Macroplata tenuiceps* are drawn almost exclusively from the postcranial axial skeleton and are not diagnostic. The present study identifies three autapomorphies relating to the girdle elements and braincase. These features confirm the validity of the taxon, in addition to 11 characters that may be used in combination to distinguish it from other plesiosaurian taxa.

The genus *Macroplata* was considered monotypic when erected by Swinton (1930a). Subsequently, White (1940:451) referred the holotype of *Plesiosaurus longirostris* Blake, 1876 (MCZ 1033), from the upper part of the Lias Group (Toarcian) of Yorkshire, U.K., to the genus forming the new combination *Macroplata longirostris*. Broadhurst and Duffy (1970:30) later referred '*M.*' *longirostris* to the genus *Rhomaleosaurus*, a decision followed by Benton and Taylor (1984:417). However, O'Keefe (2001:13) mistakenly considered '*M.*' *longirostris* as the type species of the genus *Macroplata* and referred to specimen BMNH R5488 as "Genus: unnamed ('*Macroplata tenuiceps*')." This error was amended in a later contribution (O'Keefe, 2004a), but it is worth clarifying here that the genus *Macroplata* is considered monotypic, and that the type (and only) specimen is BMNH R5488. During the present study we did not identify any potential synapomorphies uniting a clade of '*P.*' *longirostris* and *M. tenuiceps*, and a sister-taxon relationship between the two was not recovered by O'Keefe (2001, 2004a). Therefore, referral of '*P.*' *longirostris* to the genus *Macroplata* is not supported. A taxonomic revision of '*P.*' *longirostris* is beyond the scope of the present work but is currently in preparation (H.F.K., unpubl. data).

DESCRIPTION

The holotype (BMNH R5488) is a substantially complete skeleton, lacking only the posterior skull roof, suspensorium, right mandibular ramus, epipodials of the forelimb, the manus and pes, and possibly the distal end of the tail. The skull, limbs, and cervical and caudal vertebrae have been prepared so that they are free from matrix. The girdle elements and the dorsal vertebrae still remain in two large blocks of limestone and are visible in only dorsal and ventral views. A number of areas have been reconstructed in brown-painted plaster. These areas are indicated in the interpretive drawings as areas of gray shading.

Macroplata tenuiceps (BMNH R5488) is 4.65 m long from the tip of the snout to the end of the tail as preserved. The skull measures 0.56 m in length (from the tip of the snout to the end of the left retroarticular process), the neck 1.24 m (cervical and pectoral vertebrae), the trunk 1.61 m (dorsal and sacral vertebrae), and the tail 1.22 m. With a large head and short neck compared to most plesiosauroids, including the lower Lias Group taxon *Plesiosaurus dolichodeirus*, *M. tenuiceps* can therefore be considered 'pliosauromorph' (sensu O'Keefe, 2001, and O'Keefe, 2002) in overall body shape. Similarly large body size and 'pliosauromorph' body proportions are seen in some other lower Lias Group plesiosaurians: *Archaeonectrus rostratus* (BMNH 38525; 3.4 m long), although the limbs of this taxon are shorter relative to overall body length compared to *M. tenuiceps*; *Attenborosaurus conybeari* (4.3 m long; Sollas, 1881), although the neck is relatively longer than in *M. tenuiceps*; and '*Rhomaleosaurus*' *megacephalus* (LEICT G221.1851; ~5 m long), which has a similarly proportioned head and neck to *M. tenuiceps*.

Ontogenetic Stage

The holotype of *Macroplata tenuiceps* BMNH R5488 exhibits a mosaic of 'juvenile', 'adult,' and 'old adult' features (sensu Brown, 1981). Although preserved in close articulation, the individual elements of the atlas-axis complex are not fused; the neural arches and ribs of the caudal vertebrae are not fused; and the trochanter is still joined to the head of the femur and not separated from it by a groove, which is suggestive of a 'juvenile' (sensu Brown, 1981) or sub-adult individual. However, typically 'adult' features are also present, which include the fusion of the neural arches to the centra in the postaxial precaudal vertebrae, and the rugosity of the cervical centra. A 'pelvic bar' is considered to represent 'old adult' status (Brown, 1981). However, although this feature is present in BMNH R5488, the ischium and pubis are not fused as they are preserved slightly disarticulated. The specimen is therefore not considered to represent an 'old adult' sensu Brown (1981) but may be 'adult.'

Skull

The cranium and the lower jaw are preserved in close association, with the anterior end of the lower jaw displaced to the right (Fig. 1). The cranium has been crushed dorsoventrally in the area between the orbits (Fig. 1A–B), complicating intepretation of this region. The temporal fenestrae and surrounding elements (parietals and squamosals), posterior and lateral margins of the orbits, suspensorium, right mandibular ramus, and the posterior part of the mandibular symphysis have been reconstructed in plaster. The anterior portion of the palate is largely obscured by matrix and plaster, but the posterior palate surface and the braincase are exposed.

Tooth-Bearing Elements—An elongate, triangular-shaped rostrum, which is over half the length of the skull, extends anteriorly from the orbits (Fig. 1C–D). The long snout of *Macroplata tenuiceps* is similar to that seen in *Archaeonectrus rostratus* (BMNH 38525) and *Attenborosaurus conybeari* (Sollas, 1881), which have pre-orbital skull length to overall skull length ratios of 0.54, 0.57, and 0.56, respectively. Other taxa from the lower Lias Group in which this ratio can be calculated, including *Thalassiodracon hawkinsi* (0.49; Storrs and Taylor, 1996), '*Rhomaleosaurus*' *megacephalus* (0.47; LEICT G221.1851), *Plesiosaurus dolichodeirus* (0.47; Storrs, 1997), '*Plesiosaurus*' *macrocephalus* (0.45), and BMNH 49202 (0.38), have relatively shorter snouts.

The premaxillae (pmx: Fig. 1A–D) and maxillae (mx: Fig. 1A–D) bear the upper marginal dentition (see below). In dorsal view the paired premaxillae are united in a straight suture along the midline of the skull. Anteriorly they form a rounded snout tip that is pierced by numerous randomly distributed nutrient foramina and heavily ornamented with ridges and grooves (Fig. 1G). Posteriorly the fused premaxillae narrow at a constriction in the rostrum (rc: Fig. 1C–D) and form a posteriorly directed 'facial process' comprising narrow, dorsally convex rods that contact the maxilla along their lateral margins as far posteriorly as the probable location of the external nares (en: Fig. 1C–D). A transverse break in the facial process medial to the probable location of the external nares is a result of dorsoventral crushing. Posterior to the probable location of the nares, the facial process separates the frontals along the midline for part of their length. It increases in height posteriorly to form a ridge, which tapers to a point midway between the orbits. The premaxillae also form a dorsal ridge in *Archaeonectrus rostratus* (BMNH 38525) and '*Plesiosaurus*' *longirostris* (MCZ 1033); however, the ridge is taller and more pointed posteriorly in *Macroplata tenuiceps*. The premaxillary facial process partially splits the frontals along the midline in all taxa from the lower part of the Lias Group where this region of the skull is preserved, including BMNH 49202, *Plesiosaurus dolichodeirus* (Storrs, 1997), *Thalassiodracon hawkinsi* (Storrs and Taylor, 1996), '*Rhomaleosaurus*' *megacephalus* (Cruickshank, 1994b), and OUMNH J.28585 (Cruickshank, 1994a). In pliosaurids and polycotylids the premaxilla facial process splits the frontals entirely along the midline and contacts the parietal (e.g., Andrews, 1913; O'Keefe, 2004b; Druckenmiller and Russell, 2008).

The premaxilla contacts the maxilla at the rostral constriction in a straight suture that trends posteromedially to the level of the probable position of the external naris (en: Fig. 1A–D). The region surrounding the external naris is difficult to interpret due to poor preservation. Like the premaxilla, the dorsal surface of the maxilla is ornamented with numerous, randomly distributed ridges and grooves. These tend to be oriented posteroventrally (Fig. 1B, D). The maxilla contributes to the anterior margin of the orbit and probably forms the lateral and anterior margins of the external naris. Anterior to the right orbit, the maxilla bears a sharp ridge extending diagonally from the orbit to the probable position of the external naris (mr: Fig. 1C–D). This results from dorsoventral crushing in the area immediately posterior to the ridge and between the orbits and is not a natural feature.

Craniofacial Elements—The frontal is an anteroposteriorly elongate element that increases in width posteriorly. It extends from the probable location of the external naris to a position level with the anterior margin of the temporal fenestra. Each frontal is pierced by small, irregularly spaced foramina. Five foramina are preserved on the right frontal and three on the left (frf: Fig. 1C–D). More foramina may have been present but a small band of plaster extending between the orbits obscures some of the surface of the frontals. Nutrient foramina are present in the frontals of a variety of plesiosaurians (e.g., *Thalassiodracon hawkinsi*, BMNH 14550; *Peloneustes philarchus*, BMNH R8574) but their presence is not always noted in the literature (Smith and Dyke, 2008; e.g., two are present on each frontal of '*Rhomaleosaurus*' *megacephalus*, LEICT G221.1851, but they are not described or figured by Cruickshank, 1994b). The foramina are usually small and vary in number. They often vary in their precise arrangement between the left and right sides of the skull, although the presence of a single pair of large frontal foramina or fenestrae has been reported in polycotylids (e.g., Carpenter, 1996; but see O'Keefe, 2004b, 2008; Druckenmiller and Russell, 2008).

Anteriorly the frontal contributes to what seems to be the posterior margin of the external naris. However, the exact outline of the external nares and the anterior extent of the frontal element medial to them cannot be ascertained due to poor preservation. The medial margin of the frontal contacts the premaxilla in a straight suture, which extends posteriorly until the termination of the premaxillary facial process, whereupon the frontals unite

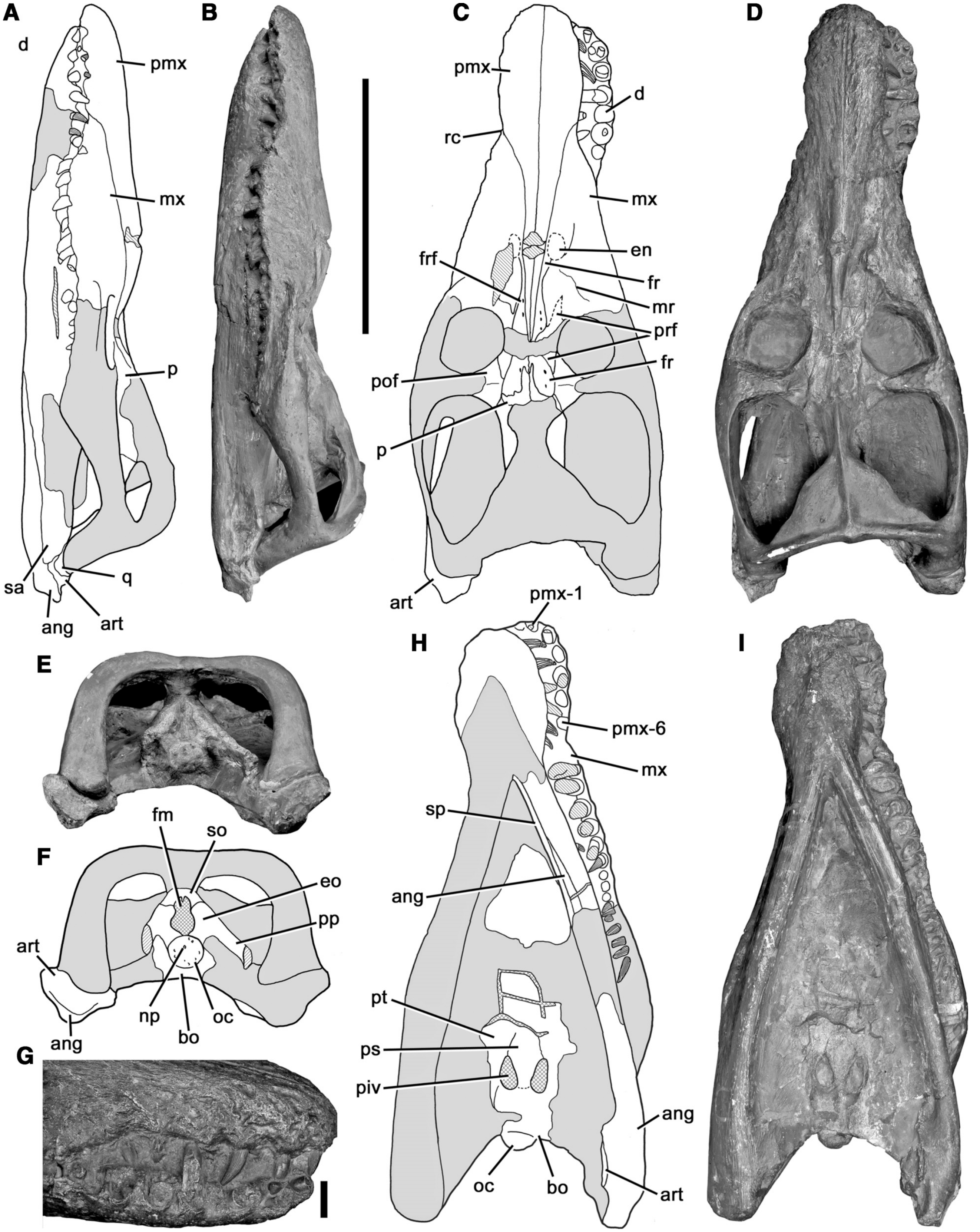

FIGURE 1. Skull of the holotype specimen of *Macroplata tenuiceps* (BMNH R5488) in left lateral (**A**–**B**), dorsal (**C**–**D**), posterior (**E**–**F**), right lateral (**G**), and ventral (**H**–**I**) views. In line drawings (**A**, **C**, **F**, **H**), grey tone indicates reconstructed areas and hatching indicates broken bone. **Abbreviations**: **ang**, angular; **art**, articular; **bo**, basioccipital; **d**, dentary; **en**, external naris; **eo**, exoccipital-opisthotic; **fm**, foramen magnum; **fr**, frontal; **frf**, frontal foramen; **mr**, maxillary ridge; **mx**, maxilla; **np**, notochordal pit; **oc**, occipital condyle; **p**, parietal; **piv**, posterior interpterygoid vacuity; **pmx**, premaxilla; **pmx-1**, premaxillary tooth 1; **pmx-6**, premaxillary tooth 6; **pof**, postfrontal; **pp**, paraoccipital process; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **rc**, rostral constriction; **sa**, surangular; **so**, supraoccipital; **sp**, splenial. Scale bars equal 20 cm (**A**–**F**, **H**, **I**) or 2 cm (**G**).

for a short distance along the midline forming an interdigitating suture. More posteriorly the frontals are separated by the anterior extension of the parietals (p: Fig. 1C–D). Lateral to this contact the dorsal surface of the frontal is gently concave forming paired lateral depressions. Anteriorly, the lateral margin of the frontal contacts the maxilla and extends to the probable position of the external naris. The lateral margin of the frontal contacts the prefrontal (prf: Fig. 1C, D) along a straight suture dorsal to the orbit, and contacts the postfrontal (pof: Fig. 1C–D) for a short distance posteriorly.

The prefrontal contacts the posterodorsal margin of the orbit, contacting the postfrontal posteriorly and the frontal dorsally. Anterior to the orbit the prefrontal contacts the maxilla. Both prefrontals are poorly preserved and largely obscured by a strip of plaster that extends between the orbits.

The postfrontal is a robust, triangular bone ornamented with a transversely oriented ridge that separates the posterior margin of the orbit from the temporal fenestra. The medial margin of the postfrontal is overlapped by the prefrontal, frontal, and parietal. Laterally the remainder of the post-orbital bar has been reconstructed in plaster.

Upon the discovery of *Macroplata* in 1927, much was made in the media concerning the pineal foramen (Swinton, 1930b), with one account claiming the specimen represented a "three-eyed plesiosaur" (Anonymous, 1928). The 'third eye' or pineal foramen is found in most plesiosaurians (although it is absent in some polycotylids and elasmosaurids; e.g., Welles, 1962; Carpenter, 1996) but it was perhaps particularly large and therefore worthy of note in *Macroplata tenuiceps*. However, Swinton (1930b:273) described the pineal foramen as merely a "small depression on the parietals." Unfortunately, this area has since been covered over in plaster. Only a small anterior portion of the parietals is visible extending between the frontals medial to the orbits.

Palate and Basicranium—The palate is largely obscured by plaster and matrix in BMNH R5488, but the region underlying the braincase is exposed (Fig. 1H–I). The parasphenoid (ps: Fig. 1H–I) is a diamond-shaped element with a short and broad cultriform process that contacts the pterygoid (pt: Fig. 1H–I) in an interdigitating suture anteriorly. The parasphenoid obscures the basisphenoid in ventral view. The ventral surface of the parasphenoid is smooth and gently concave, with raised lateral margins where it forms the medial margin of the posterior interpterygoid vacuities (piv: Fig. 1H–I). This arrangement is also seen in BMNH 49202 (Andrews, 1896) and '*Rhomaleosaurus*' *megacephalus* (Cruickshank, 1994b). It is unlike the condition in *Thalassiodracon hawkinsi* (Storrs and Taylor, 1996), OUMNH J.28585 (Cruickshank, 1994a), and *Plesiosaurus dolichodeirus* (Storrs, 1997), in which the basisphenoid is exposed along the ventral midline and contributes to the medial margins of the posterior interpterygoid vacuities.

The posterior interpterygoid vacuities are sub-oval in shape, broader posteriorly than anteriorly. The long axes of the vacuities are oriented posteromedially, which is in contrast to all other plesiosaurians, in which they are oriented posterolaterally to varying degrees; e.g., '*Rhomaleosaurus*' *megacephalus* (LEICT G122.1851), *Plesiosaurus dolichodeirus* (Storrs, 1997), *Thalassiodracon hawkinsi* (CAMSM J.46913), and BMNH 49202. This feature is therefore considered to be an autapomorphy of *Macroplata tenuiceps*.

The contact between the parasphenoid and the basioccipital is difficult to ascertain with confidence. However, a possible parasphenoid-basioccipital suture is present approximately level with the posterior margins of the posterior interpterygoid vacuities. The basioccipital would therefore form the posterior margin of the palate, as is seen in other plesiosaurians in which the pterygoids do not meet posterior to the posterior interpterygoid vacuities, including *Thalassiodracon hawkinsi* (Storrs and Taylor, 1996) and *Plesiosaurus dolichodeirus* (Storrs, 1997). This is unlike some other Lower Jurassic taxa and more derived plesiosauroids and pliosauroids more generally, such as '*Rhomaleosaurus*' *victor* (SMNS 12478), and *Microcleidus homalospondylus* (BMNH 36184), in which the pterygoids unite posteriorly. In ventral view the occipital condyle (oc: Fig. 1E–F, H–I) extends posterior to the posterior margin of the palate. In posterior view the condyle is circular with a notochordal pit situated just dorsal to the centre (np: Fig. 1E–F) that is surrounded by eight additional, smaller pits.

The posterior margin of the basicranium slopes anterodorsally. The foramen magnum has a 'figure of eight' outline in posterior view, with the constriction at the contact between the exoccipital-opisthotics ventrally and the supraoccipital dorsally. The area within the foramen magnum is filled with matrix. The supraoccipital is longer anteroposteriorly than it is tall. A narrow triangular process is present ventrally on the midline of the supraoccipital, which extends into the dorsal margin of the foramen magnum. Lateral to the triangular process the posterior margin of the supraoccipital is narrow. It increases in width ventrolaterally towards the exoccipital-opisthotics.

The exoccipital-opisthotics are preserved in articulation with the supraoccipital. The pedicles of the exoccipital-opisthotics, which articulate with the basioccipital, are located anterodorsal to the occipital condyle and do not contribute to the formation of the condyle. This condition is present in all lower Lias Group plesiosaurians in which this area of the braincase is known (BMNH 49202; *Plesiosaurus dolichodeirus*, Storrs, 1997; *Thalassiodracon hawkinsi*, Storrs and Taylor, 1996; OUMNH J.28585). In some plesiosaurians, such as *Cryptoclidus eurymerus* and *Kimmerosaurus langhami*, the pedicles of the exoccipital-opisthotic participate in the formation of the condyle (Brown, 1981), which makes them unique among Jurassic plesiosaurian taxa (Druckenmiller and Russell, 2008). In some elasmosaurids and polycotylids the facets for the exoccipital-opisthotics are located farther anterior of the occipital condyle, setting off the body of the basioccipital from the occipital condyle by a constricting groove or 'neck' (e.g., O'Keefe, 2001; Druckenmiller and Russell, 2008). The paraoccipital process of the left exoccipital-opisthotic in BMNH R5488 is broken lateral to the pedicle. The right paraoccipital process is more complete, but the distal end is also broken. The process is compressed dorsoventrally, with a broad dorsal surface approximately three times as wide as the posterior margin is high. It slopes anteroventrally at approximately 45 degrees.

Mandible—The mandibular symphysis incorporates seven or eight teeth in each dentary. The exact number is uncertain because plaster has been used to repair or reconstruct the posterior end of the symphysis and the right mandibular ramus and it is not possible to be certain whether the left and right mandibular rami originally joined in that position. However, the symphysis is elongate relative to most other lower Lias Group plesiosaurians, which have 2.5–4 (Plesiosaurus dolichodeirus; Storrs, 1997), 4 (BMNH 49202; OUMNH J.28585; and *Thalassiodracon hawkinsi*, Storrs and Taylor, 1996), or 5 (*Eurycleidus arcuatus* BMNH 2030*; and '*Rhomaleosaurus*' *megacephalus*, LEICT G122.1851) teeth adjacent to the mandibular symphysis in each dentary. *Archaeonectrus rostratus* (BMNH 38525), which has a similarly long snout as *Macroplata tenuiceps*, also has a similarly long mandibular symphysis with nine teeth incorporated in each dentary. *Attenborosaurus conybeari* (BMNH R1338) appears to have had a long mandibular symphysis, but the exact tooth count was not given by Sollas (1881) and cannot be determined from the surviving cast. A wide ventral ridge is present on the mandibular symphysis in '*Rhomaleosaurus*' *megacephalus* (LEICT G122.1851), and a similar structure appears present in *Macroplata tenuiceps*. However, as most of the ventral surface of the mandibular symphysis is covered in plaster, it is not possible to determine whether this is a true reflection of the original shape.

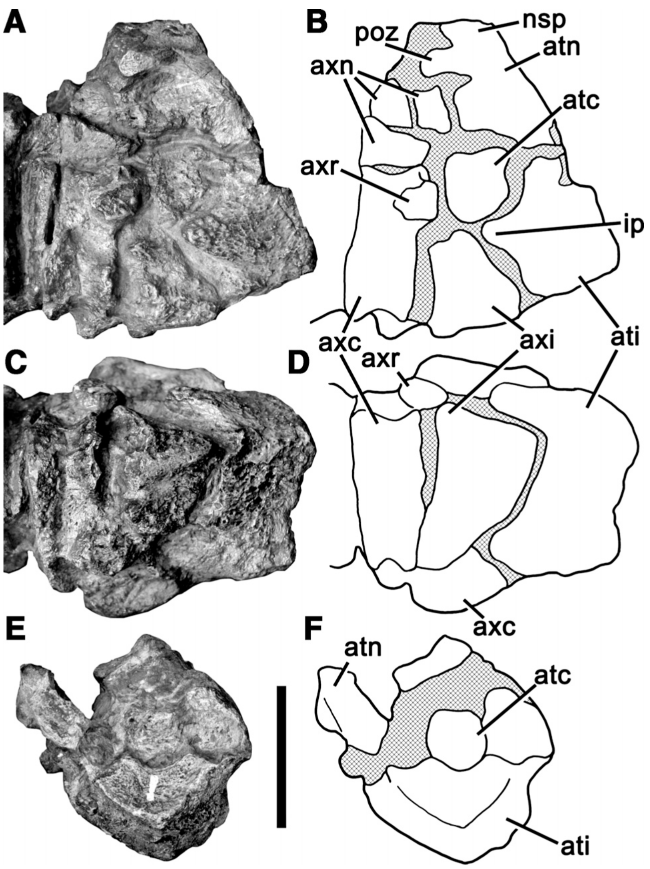

FIGURE 2. Atlas-axis complex of the holotype specimen of *Macroplata tenuiceps* (BMNH R5488) in right lateral (**A**–**B**), ventral (**C**–**D**), and anterior (**E**–**F**) views. In line drawings (**B**, **D**, **F**), hatching indicates broken bone and crossed-hatching indicates matrix. **Abbreviations**: **atc**, atlas centrum; **ati**, atlas intercentrum; **atn**, atlas neural arch; **axc**, axis centrum; **axi**, axis intercentrum; **axn**; axis neural arch; **axr**, axis rib; **ip**, posterolateral process on atlas intercentrum; **nsp**, neural spine; **poz**, postzygapophysis. Scale bar equals 5 cm.

The left mandibular ramus is nearly complete. In lateral view the dentary is pierced by numerous foramina in the region of the mandibular symphysis, as in the premaxilla and maxilla (Fig. 1B). The coronoid eminence is reconstructed in plaster and its original morphology cannot be determined. Ventral to this area a straight suture between the angular and dentary trends posterodorsally. The contact between the dentary and the surangular is not visible due to poor preservation. The articular (art: Fig. 1A) is preserved in close articulation with a narrow, broken piece of the left quadrate at the mandibular glenoid, which is the only part of either quadrate that is preserved. Posteriorly, the articular forms the dorsal surface of the retroarticular process. This process is wider than long, and slightly medially inflected.

In ventral view the splenial (sp: Fig. 1H) contacts the dentary anteriorly in a straight, anteroposteriorly oriented suture. It either closely approaches or enters the mandibular symphysis (the uncertainty is due to the presence of plaster obscuring this region, as noted above). The splenial enters the symphysis in the majority of plesiosaurian taxa, including *Archaeonectrus rostratus* (BMNH 38525), BMNH 49202, *Thalassiodracon hawkinsi* (Storrs and Taylor, 1996), '*Rhomaleosaurus*' *megacephalus* (LEICT G221.1851), and *Eurycleidus arcuatus* (BMNH 2030*). However, it does not participate in the symphysis of *Plesiosaurus dolichodeirus* (Storrs, 1997).

Posteriorly, the splenial-dentary contact is interrupted by the angular. A section of mandible approximately midway along the ramus is reconstructed in plaster, which obscures the relationships of the dentary, splenial and angular for a short distance. Posterior to this region the angular forms the entire ventral surface of the mandibular ramus. Ventral to the articular glenoid (art: Fig. 1A) the angular expands mediolaterally, and narrows posteriorly to form the ventral surface of the retroarticular process.

Dentition—Many of the teeth are broken close to their bases, but a small number in the anterior parts of the jaws are complete, with well-preserved enamel (Fig. 1G). The teeth are circular in cross-section. In both available views (lingual and labial) the tooth crown is ornamented with apicobasally oriented ridges that extend from the ventral margin of the crown. All of the ridges approach the apex, but only one or two reach the very tip of the tooth. There are approximately 6–7 ridges per 5 mm of enamel width when measured across the ventral margin of the crown.

Six alveoli for functional teeth are present in each premaxilla. In *Macroplata tenuiceps* the first (mesial-most) alveolus is the smallest of those in the premaxilla. The second through fourth premaxillary alveoli are the largest and are sub-equal in size, and the fifth and sixth alveoli are slightly smaller, but not as small as the first alveolus. The premaxillary dentition is not markedly heterodont as in some polycotylids and pliosaurids (e.g., *Edgarosaurus muddi*, Druckenmiller, 2002; *Liopleurodon ferox*, Andrews, 1913). However, the teeth are more variable in size than those in the premaxilla of *Plesiosaurus dolichodeirus* (Storrs, 1997). A diastema (sensu Druckenmiller and Russell, 2008:23) separates the premaxillary and maxillary dentition at the rostral constriction. The right maxilla contains 18 teeth, which decrease in size posteriorly. The left maxilla preserves 10 alveoli anteriorly; the remainder have been reconstructed in plaster. The total number of dentary teeth cannot be determined as the dentition is obscured by the maxilla.

Axial Skeleton

Macroplata tenuiceps possesses a series of 80 vertebrae preserved in articulation, of which 51 or 52 are presacral. The neurocentral sutures are fused in all vertebrae (see Ontogenetic Stage).

Cervical Vertebrae—Some 26 cervical vertebrae are present, including the atlas-axis complex. This is similar to *Archaeonectrus rostratus*, which has 24 cervical vertebrae (Owen, 1865). '*Rhomaleosaurus*' *megacephalus* (LEICT G221.1851) and *Thalassiodracon hawkinsi* (BMNH 2018*) both have 28 cervical vertebrae, and '*Plesiosaurus*' *macrocephalus* (BMNH R1336) has 29. *Attenborosaurus conybeari* has 36 (Sollas, 1881), and *Plesiosaurus dolichodeirus* has the most of any lower Lias Group plesiosaurian, showing intraspecific variation between 38 and 42 cervical vertebrae (Storrs, 1997). The exact count for *Eretmosaurus rugosus* is unknown because the most complete specimen (BMNH 14435) has 33–35 preserved cervical vertebrae but lacks the skull and atlas-axis complex (Owen, 1865).

The atlas-axis complex of *Macroplata tenuiceps* is preserved in articulation. However, the constituent elements are not completely fused (Fig. 2). The atlantal centrum has a small, round exposure in lateral view (Fig. 2A–B) that is surrounded by the atlantal neural arch, atlantal intercentrum, axial centrum, and axial intercentrum. The atlantal intercentrum has a short rugose process that extends posterodorsally toward the atlantal centrum (ip: Fig. 2A). A slender postzygapophysis extends from the right atlantal neural arch (poz: Fig. 2A). The axial rib (axr: Fig. 2B) articulates solely with the axial centrum. The shaft is a rounded nub of bone that is shorter than wide at the base. The anterior surface of the atlantal centrum forms a small hemispherical atlantal cotyle (Fig. 2E–F). The crescentic atlantal intercentrum and the neural arches form the ventral and lateral margins, respectively.

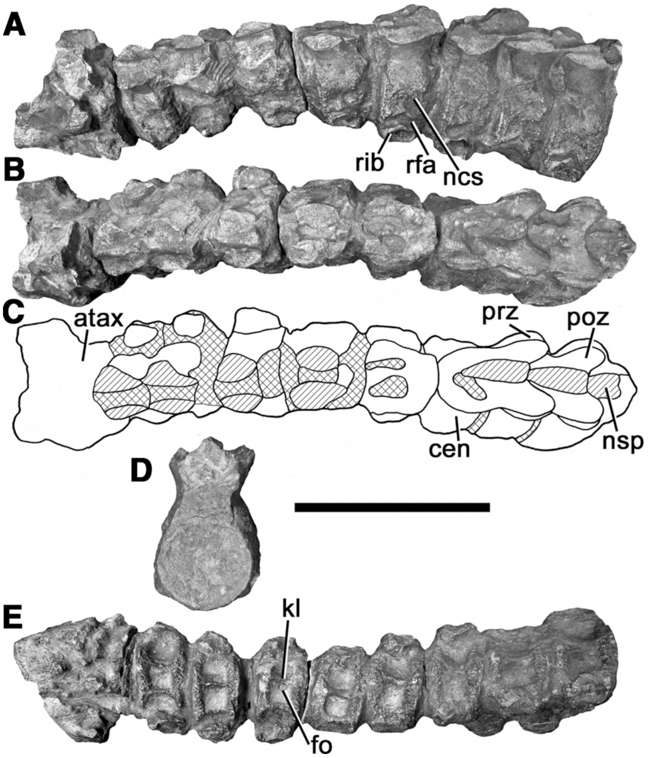

FIGURE 3. Presacral vertebrae 1–10 (cervical vertebrae) of the holotype specimen of *Macroplata tenuiceps* (BMNH R5488) in left lateral (**A**), dorsal (**B**–**C**), anterior (**D**), and ventral (**E**) views. In line drawing (**D**), hatching indicates broken bone and crossed-hatching indicates matrix. Details of atlas-axis complex (cervical vertebrae 1–2) are shown in Figure 2. **Abbreviations**: **atax**, atlas-axis complex; **cen**, vertebral centrum; **fo**, foramen; **kl**, keel; **ncs**, neurocentral suture; **nsp**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **rfa**, rib facet; **rib**, cervical rib. Scale bar equals 10 cm.

The surface of the anterior margin of the axial centrum has a gently undulating outline in ventral view. It lacks a ventral longitudinal ridge unlike the postaxial cervical vertebrae. In ventral view (Fig. 2C–D) the axial intercentrum is triangular. The apex of the triangle points anteriorly and contacts the atlantal intercentrum, thereby excluding the atlantal centrum from the ventral surface of the atlas-axis complex. It is difficult to compare the atlas-axis complex of *M. tenuiceps* with those of other Lower Jurassic plesiosaurians because they are either completely fused, obliterating all sutures (*Plesiosaurus dolichodeirus*; Storrs, 1997), not preserved (*Eretmosaurus rugosus*; BMNH 14435), or preserved but not exposed in lateral or ventral view (*Hauffiosaurus zanoni*, UMH 7; *Archaeonectrus rostratus*, BMNH 38525; *Attenborosaurus conybeari*, BMNH R1339; '*Plesiosaurus*' *macrocephalus*, BMNH R1336; MMUM LL8004). However, the basal sauropterygian *Augustasaurus hagdorni* (FMNH PR 1974), the basal plesiosauroid *Thalassiodracon hawkinsi* (lectotype: BMNH 2018*), and the pliosauroids *Liopleurodon ferox* (BMNH R3536) *Peloneustes philarchus* (CAMSM J.46913), '*Pliosaurus*' *andrewsi* (BMNH R3891), and '*Rhomaleosaurus*' *victor* (SMNS 12478) share the condition of *Macroplata tenuiceps* in which the atlantal centrum is not exposed ventrally, suggesting that this represents the plesiomorphic condition. In contrast, in BMNH R2439, a specimen from the Oxford Clay Formation referred to *P. philarchus* by Andrews (1913; but considered as a new taxon by Ketchum, 2007), the centrum is exposed in ventral view, a possible autapomorphy among Jurassic plesiosaurians.

The 3rd to 26th cervical centra (Figs. 3, 4) have subcircular articular surfaces, which are amphiceolous (Fig. 3D). The transverse width of the posterior surface of the centrum is approximately 10% greater than the height, and the anteroposterior length is approximately two-thirds of the height in all cervical centra. Progressing along the series there is a gradual size increase in all three dimensions (Table 1).

TABLE 1. Measurements (in mm) of the vertebrae of BMNH R5488, holotype of *Macroplata tenuiceps*.

Vertebral centrum	Height	Ventral length	Width
3		30.2	
4		30.2	
5	43.9	31.8	46.7
6		33.5	48.7
7		31.1	
8		31.6	
9		32.5	
10	48.4	33.0	52.5
11	47.9	36.5	53.5
12		35.4	
13		36.1	
14		36.4	
15		39.9	
16		40.0	
17		42.5	
18		40.4	
19	61.4	45.4	65.2
20	67.5	45.3	67.9
21		—	
22		44.3	
23		43.6	
24		—	
25		46.0	
26		48.8	
27		46.0	
28		48.8	
29		50.0	

The lateral surfaces of the centra are rugose (Figs. 3A; 4A, E), particularly adjacent to the pedicles of the mid-cervical neural arches. The neurocentral suture is U-shaped in anterior cervical vertebrae and becomes progressively more V-shaped towards the pectoral region. The pre- and postzygapophyseal facets are angled dorsomedially at approximately 45 degrees. The transverse width across the zygapophyses is sub-equal to the width of the centra. The bases of the neural spines are transversely compressed. Unfortunately, each of the neural arches is broken just dorsal to the zygapophyses, and neural spine morphology is hence unknown.

The ventral surfaces of the cervical centra bear a longitudinal ridge that is narrowest at its midpoint (Figs. 3E; 4D, H) as in *Archaeonectrus rostratus* (Owen, 1865), *Thalassiodracon hawkinsi* (CAMSM J.46913), and *Eurycleidus arcuatus* (BMNH R1318). This ridge is confluent with the anterior and posterior margins of the ventral surfaces of the centra, and in *M. tenuiceps* these are rugose adjacent to the articular surfaces. The ridge divides a pair of square depressions on the ventral surface of the centrum in which the subcentral foramina (fo: Fig. 3E) are located. The few subcentral foramina that are present in *Macroplata tenuiceps* are very small, which is unusual among plesiosaurians, but this could be related to ontogeny as the foramina become smaller during ontogeny and are lost in 'old adults' of *Peloneustes philarchus* (Ketchum, 2007). Compared to the condition in *M. tenuiceps*, the ventral surface of the cervical vertebrae in *Plesiosaurus dolichodeirus* (e.g., BMNH 36183) is almost uniformly convex; the subcentral foramina are not located in depressions, and only a slight bulge is present between the subcentral foramina (Storrs, 1997). A weakly developed ventral midline ridge is present in

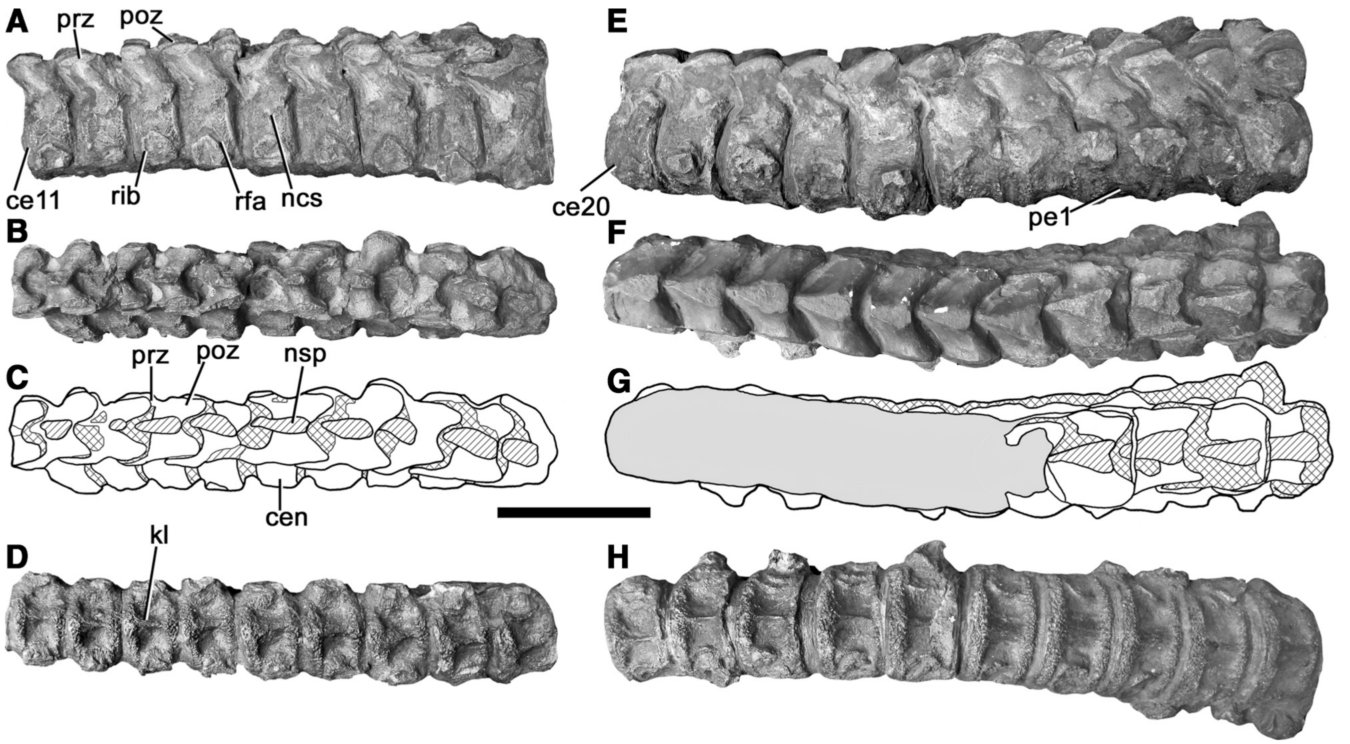

FIGURE 4. Presacral vertebrae of the holotype specimen of *Macroplata tenuiceps* (BMNH R5488). **A**–**D**, presacral vertebrae 11–19 (cervical vertebrae) in left lateral (**A**), dorsal (**B**–**C**), and ventral (**D**) views. **E**–**H**, presacral vertebrae 20–29 (including cervical vertebrae 20–26 and pectoral vertebrae 1–3) in left lateral (**E**), dorsal (**F**–**G**), and ventral (**H**) views. In line drawings (**C**, **G**), gray tone indicates reconstructed areas, hatching indicates broken bone, and crossed-hatching indicates matrix. **Abbreviations**: **ce11**, cervical vertebra 11; **ce20**, cervical vertebra 20; **cen**, vertebral centrum; **kl**, keel; **ncs**, neurocentral suture; **nsp**, vertebral neural spine; **pe1**, pectoral vertebra 1; **poz**, postzygapophysis; **prz**, prezygapophysis; **rfa**, rib facet; **rib**, cervical rib. Scale bar equals 10 cm.

Eretmosaurus rugosus, but there are no deep depressions on either side of the ridge (Owen, 1865). '*Plesiosaurus*' *rugosus* was named for the "peculiarly rugous character of the free or non-articular surfaces of the [vertebral] body" (Owen, 1840:82), which is similar to *Macroplata tenuiceps*. However, characters relating to vertebral rugosity should be treated with caution as this is variable in *Plesiosaurus dolichodeirus* (Storrs, 1997), and Brown (1981) showed that similar variation was due to ontogeny in plesiosauroids from the Oxford Clay Formation. This may arise from intraspecific variation in the degree of ossification or ontogenetic age.

The cervical ribs of BMNH R5488 have been broken along the shaft close to the rib head, so the distal ends are not preserved. The shafts have been crushed ventrally against the lateral surfaces of the centra. The rib heads are sub-circular in lateral view, with angular dorsal margins. Because the cervical rib heads are preserved in close association with the centra in the anterior and middle cervical vertebrae, the morphology of the rib facets is uncertain in this region of the neck. However, the two posterior-most centra (25th and 26th) show divided facets indicating the presence of double-headed cervical ribs (Swinton, 1930a). Double-headed ribs are present in all Lower Jurassic and some Middle–Upper Jurassic taxa, whereas single-headed ribs are known in some Middle–Upper Jurassic and all Cretaceous plesiosaurians (e.g., O'Keefe, 2001; Druckenmiller and Russell, 2008).

Pectoral Vertebrae—The pectoral vertebrae are those in which the rib facets articulate with the neural arch and the centrum (Seeley, 1874) (Fig. 4E–H). *Macroplata tenuiceps* possesses four such vertebrae. In addition to the change in the rib articulation from the cervical to pectoral vertebrae, the base of the neural spine also has a triangular rather than oval outline in dorsal view. The ventral ridge of the pectoral vertebrae is much wider than that of the cervical vertebrae.

Dorsal Vertebrae—*Macroplata tenuiceps* has 21 or 22 dorsal vertebrae (Fig. 5). The exact number cannot be determined due to the poor preservation of the 52nd presacral vertebra, which could be the first sacral vertebra or the 22nd dorsal. The number of dorsal vertebrae is relatively conservative among lower Lias Group plesiosaurians: *Archaeonectrus rostratus* (Owen, 1865), *Attenborosaurus conybeari* (Sollas, 1881), and *Plesiosaurus dolichodeirus* (Storrs, 1997) all have 21 dorsal vertebrae. By comparison, '*Plesiosaurus*' *macrocephalus* has 20 (BMNH R1336) and '*Rhomaleosaurus*' *megacephalus* (LEICT G122.1851) has only 17 dorsals.

The dorsal ribs are preserved in approximate articulation with the transverse processes, which are robust with rugose dorsal surfaces. In more posterior vertebrae the length of the transverse processes decreases, and the rounded distal end, which is flat or slightly convex in anterior dorsal vertebrae, becomes increasingly concave. The dorsal zygapophyses are smaller than the cervical and pectoral zygapophyses, but are also oriented at approximately 45 degrees. The neural spines are transversely compressed, rectangular in lateral view, and sub-equal in height to the centra. They rise vertically and are not appreciably angled. Nutritive foramina are visible where preservation allows, with one or sometimes two present on each centrum approximately one-third of the way up the lateral surface (fo; Fig. 5B).

Sacral Vertebrae—*Macroplata tenuiceps* has three or four sacral vertebrae (the uncertainty is due to poor preservation of

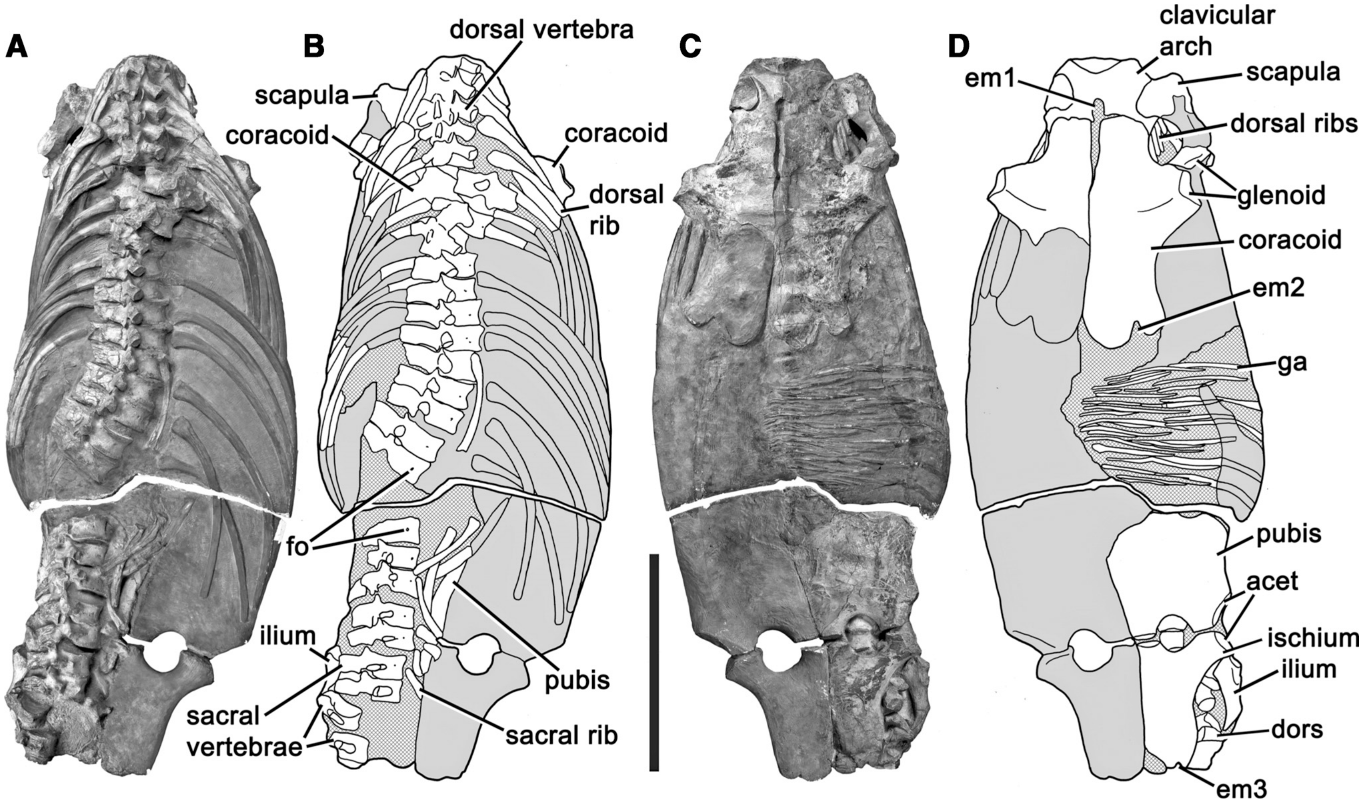

FIGURE 5. Blocks containing pectoral and pelvic girdles, and dorsal and sacral vertebrae of the holotype specimen of *Macroplata tenuiceps* (BMNH R5488) in dorsal (**A**–**B**) and ventral (**C**–**D**) views. In line drawings (**B**, **D**), gray tone indicates reconstructed areas and crossed-hatching indicates matrix. **Abbreviations**: **acet**, acetabulum; **dors**, dorsal vertebra; **em**, emargination; **fo**, foramen; **ga**, gastral rib. Scale bar equals 50 cm.

the 52nd vertebra, as mentioned above). The sacral ribs articulate with a single facet extending across the neurocentral suture (Fig. 5B). The neural spines are angled slightly more posteriorly than in the dorsal vertebrae. In contrast to the presacral vertebrae, the zygapophyseal facets face almost horizontally. The rib facets are concave. One sacral rib is identifiable, which has a shaft 75 mm long (Fig. 5A–B). The shaft is sub-triangular, with the posterior margin of the shaft forming the base of the triangle, and the apex of the triangle pointing anteriorly.

Caudal Vertebrae—Some 26 caudal vertebrae are preserved in BMNH R5488; 5 additional vertebrae within the series are constructed from plaster (Fig. 6). Swinton (1930a) noted the presence of 30 caudal vertebrae, and rather than including the plaster reconstructions, perhaps this count included 5 small vertebrae that were found associated with the type specimen, but are identified herein as ichthyosaur caudal vertebrae.

In the anterior to middle region of the tail (caudal centra 1–17) the neural arches are fused to the centra (Fig. 6A–B). The more posterior neural arches are disarticulated from the centra and not preserved. The zygapophyses are reduced in size, with vertically oriented facets that are high above their associated centra relative to the presacral vertebrae. The transverse width across the zygapophyses is approximately half that of the associated centrum. The rib facets have dorsoventrally elongate oval outlines, and raised outer margins that contact the neural arch pedicle dorsally.

The ventral surfaces of the caudal centra are flat and pierced by very small, irregularly positioned, paired subcentral foramina. Chevron facets are present ventrally on the anterior and posterior surfaces of the 4th to 26th centra; the anterior facets are smaller and more widely spaced than the posterior facets. The anterior and posterior surfaces of caudal vertebrae 17 and 18 converge ventrally so that they are 'wedge'-shaped in lateral view (Fig. 6C). This results in ventral deflection of the distal portion of the tail. This feature may also be present in some rhomaleosaurids (A. S. Smith, unpubl. data). Chevrons and/or caudal ribs (ch/r: Fig. 6A) are preserved in close association with the second to eighth caudal vertebrae, but not in articulation; consequently the identity of individual elements cannot be determined. The shafts are slightly curved posteriorly. The distal ends of some of the shafts are broken and the remainder are embedded in matrix.

Appendicular Skeleton

Pectoral Girdle—The ventral surface of the pectoral girdle is exposed in ventral view (Fig. 5C–D). It is not possible to distinguish separate clavicles or an interclavicle: they may be fused due to ontogeny (see Ontogeny), or only the interclavicle may be present. This region is therefore referred to herein as the 'clavicular arch.' It forms a large and robust plate that lies dorsal to the preglenoidal expansion of the coracoid and the ventral process of the scapula. The anterior margin of the arch is concave, with squared anterolateral 'corners,' similar to '*Rhomaleosaurus*' *megacephalus* (LEICT G122.1851). By contrast, *Plesiosaurus dolichodeirus* exhibits a much deeper, U-shaped notch along the anterior margin of the clavicular arch (Storrs, 1997:fig. 10). A deep semi-oval emargination (em1: Fig. 5C–D) is present along the midline of the posterior margin. A similarly deep, sub-oval emargination in the posterior margin of the clavicular arch was reconstructed by Sollas (1881:pl. 13, fig. 3) for *Attenborosaurus conybeari*; however, *A. conybeari* has unfused, paired clavicles (Sollas, 1881). This area of the pectoral girdle is difficult

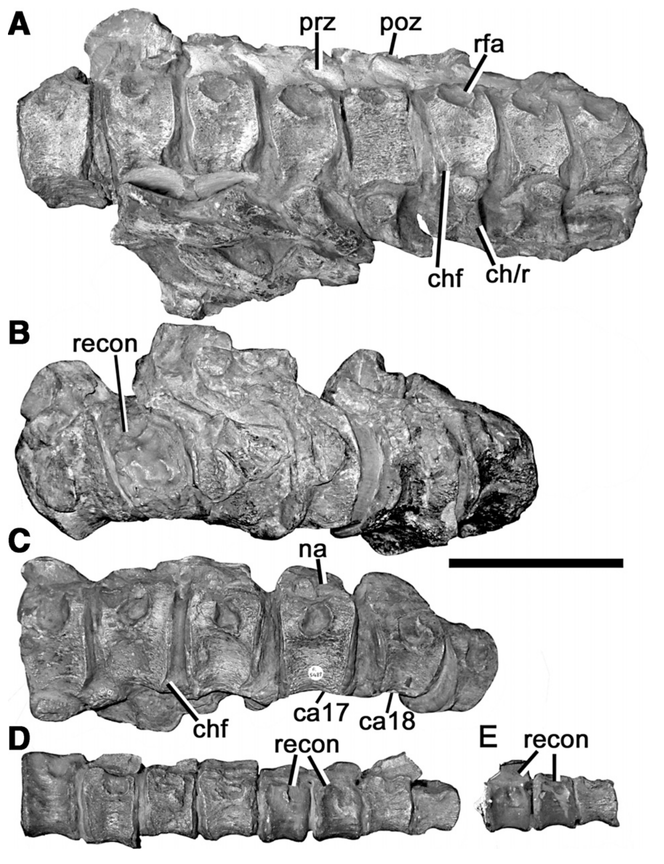

FIGURE 6. Caudal vertebrae of the holotype specimen of *Macroplata tenuiceps* (BMNH R5488) in left lateral view. **A**, caudal vertebrae 1–8; **B**, caudal vertebrae 9–13; **C**, caudal vertebrae 14–19; **D**, caudal vertebrae 20–25; **E**, caudal vertebra 26. **Abbreviations**: **ca17**, caudal vertebra 17; **ca18**, caudal vertebra 18; **ch**, chevron; **chf**, chevron facet; **ch/r**, ?chevron or rib; **na**, neural arch; **poz**, postzygapophysis; **prz**, prezygapophysis; **recon**, reconstructed vertebra; **rfa**, rib facet. Scale bar equals 10 cm.

to interpret in most lower Lias Group plesiosaurians, because it is either crushed (e.g., *T. hawkinsi*, BMNH 2018*, 2020*) or embedded in matrix (e.g., *Archaeonectrus rostratus*, BMNH 38525, and '*P.*' *macrocephalus*, BMNH R1336). The clavicular arch of *P. dolichodeirus* does not have a posterior emargination based on Storrs' reconstruction (Storrs, 1997:fig. 10).

The ventral process of the scapula closely approaches, but does not contact, the anterior margin of the coracoid; however, the two elements meet posteriorly, and contribute equally to the glenoid. The entire dorsal process of the left scapula and much of the shaft has been reconstructed in plaster.

The left coracoid is complete. It measures 490 mm long and 200 mm wide from the midline symphysis to the glenoid. The portion of the lateral margin of the coracoid anterior to the glenoid is concave, and encloses a sub-oval pectoral fenestra with the scapula. The long axis of the fenestra is oriented longitudinally, in contrast to that of *Plesiosaurus dolichodeirus* (Storrs, 1997), '*Rhomaleosaurus*' *victor* (SMNS 12478), and *Thalassiodracon hawkinsi* (BMNH 2018*), in which it is oriented posterolaterally. The preglenoidal portion is sub-rectangular and almost as wide mediolaterally as the part posterior to the glenoid. A wide preglenoidal expansion that does not narrow anteriorly is known only in Lower Jurassic plesiosaurians, including *Thalassiodracon hawkinsi* (BMNH 2018*), *Eurycleidus arcuatus* (BMNH R1317), and '*Rhomaleosaurus*' *victor* (SMNS 12478). By comparison, the preglenoid expansion of the coracoid of *Attenborosaurus conybeari* is wide but tapers anteriorly and has a convex anterior margin (Sollas 1881:pl. 13, figs. 1, 3). In *Plesiosaurus dolichodeirus* (Storrs, 1997:fig. 10) the preglenoid region is significantly narrower (less than half the width) than the region posterior to the glenoid, as in plesiosaurians from the Middle–Upper Jurassic and Cretaceous (Ketchum and Benson, 2010).

The posterior border of the left coracoid of BMNH R5488 has a single deep triangular emargination (em2: Fig. 5C–D), which is unique among plesiosaurians (e.g., Owen, 1865; Andrews, 1910, 1913) and is therefore considered here an autapomorphy of *Macroplata tenuiceps*. The right coracoid of '*Rhomaleosaurus*' *victor* (SMNS 12478) has two relatively shallow triangular emarginations along its posterior margin and is therefore distinct from *Macroplata tenuiceps*.

Forelimb—Both humeri are well preserved except for the distal ends, which have been reconstructed in plaster (Fig. 7A–F), so the reconstructed length of 320 mm may not be accurate. The capitulum of the right humerus is 80 mm wide and is distinct from the tuberosity (cap, tub: Fig. 7B). The combined dorsoventral depth of the proximal end of the humerus is 95 mm. The tuberosity is placed close to the postaxial (posterior) margin of the humerus and the proximal end faces slightly posteriorly. The shaft of the humerus has a slightly convex preaxial (anterior) margin. Humeri with convex anterior margins are known only in Lower Jurassic plesiosaurians, including *Plesiosaurus dolichodeirus* and *Thalassiodracon hawkinsi* (e.g., Druckenmiller and Russell, 2008). By contrast, taxa from the Middle–Upper Jurassic and Cretaceous, including pliosaurids, leptocleidids, cryptoclidids, polycotylids, and elasmosaurids, have humeri with concave anterior margins (e.g., Druckenmiller and Russell, 2008). The postaxial margin is of the humerus of *Macroplata tenuicep*s is concave and is pierced by a number of foramina ranging from small to large size (fo: Fig. 7D). None of the more distal elements of the forelimbs are associated with BMNH R5488.

Gastralia—Only the left side of the gastral basket is preserved in BMNH R5488. Seven bundles or rows are present (ga: Fig. 5C–D); by comparison, 10 are present in '*Rhomaleosaurus*' *victor* (SMNS 12478), and 8 in *Thalassiodracon hawkinsi* (Smith, 2007). Each row of gastralia consists of one median element and three pairs of lateral elements.

Pelvic Girdle—Only the left side of the pelvic girdle is preserved, and is visible in ventral view (Fig. 5C–D). The total anteroposterior length of the combined ischium and pubis is 630 mm, which is slightly shorter than the pectoral girdle (640 mm, maximum length from anterior margin of clavicular arch to posterior margin of coracoid). The pubis is 310 mm long and 290 mm wide. A medial pelvic bar is developed between the pubis and the ischium, although the two elements were not fused and they do not contact. The nearly circular thyroid fenestra is 80 mm in diameter.

The ischium is elongate and has a maximum width of 250 mm and length of 310 mm. As in the coracoid, the ischium has a deep triangular emargination along its posterior border (em3: Fig. 5C–D), which is not known in any other plesiosaurian (e.g., Owen, 1865; Andrews, 1910, 1913), and is considered an autapomorphy of *Macroplata tenuiceps*. The ilium is a robust, rod-shaped bone. The dorsal blade is broken and not preserved. The dorsal end of the shaft is angled at approximately 45 degrees to the ischial facet at the ventral end.

Hind Limb—Both femora are well preserved, although the postaxial distal margins are reconstructed in plaster (Fig. 7G–M). The left femur is 350 mm long with a head 100 mm wide. The combined dorsoventral depth of the head and trochanter in proximal view is 117 mm. The trochanter is located toward the preaxial margin of the femur and is angled posteriorly (Fig. 7G–H). Heavily rugose sites that may indicate regions of muscle attachment are located on the postaxial margin of the shaft and especially

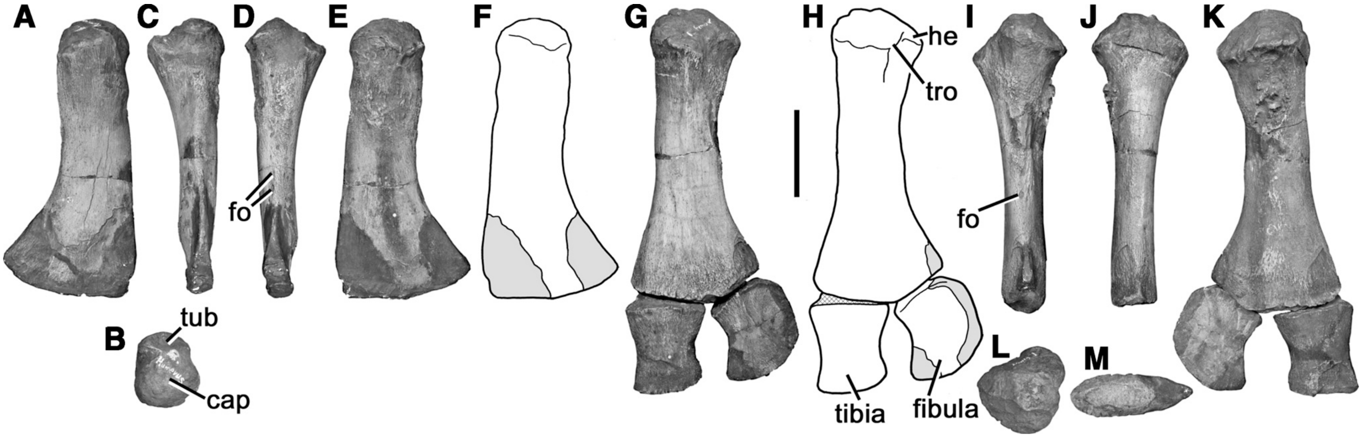

FIGURE 7. Right humerus (**A**–**F**) and left hind limb elements (**G**–**M**) of the holotype specimen of *Macroplata tenuiceps* (BMNH R5488). Right humerus in dorsal (**A**), proximal (**B**), preaxial/anterior (**C**), postaxial/posterior (**D**), and ventral (**E–F**) views. Left hind limb elements in dorsal (**G–H**), postaxial/posterior (**I**), preaxial/anterior (**J**), ventral (**K**), proximal (**L**), and distal (**M**) views. In line drawings (**F**, **H**), gray shading indicates reconstructed areas. **Abbreviations**: **cap**, capitulum; **fo**, foramen; **he**, head; **tro**, trochanter; **tub**, tuberosity. Scale bar equals 10 cm.

on the ventral surface close to the head of the femur (Fig. 7I–K). The shaft of the femur is concave along both pre- and postaxial margins, creating a nearly symmetrical distal expansion that is 150 mm wide as reconstructed. A large foramen is present two-thirds of the way along the preaxial margin (fo: Fig. 7I). The distal end is divided into two distinct, straight facets for articulation with the epipodials. The facet for the tibia is the larger of the two (110 mm wide); the facet for the fibula measures 70 mm.

The left epipodials are preserved. Of these, the tibia is the more robust and measures 110 mm long and 70 mm wide at its narrowest point. It is approximately hourglass shaped in dorsal view, narrowing distally. The tibia nearly contacts the fibula proximally but they diverge distally. The fibula is slightly crushed dorsoventrally and the convex postaxial margin has been reconstructed. The tibia and fibula are equal in length (110 mm). The length to width ratio of the tibia is 1.4, which is equal to that of *Archaeonectrus rostratus* (Owen, 1865). The tibia is longer than wide but relatively shorter than other lower Lias Group plesiosaurians: *Plesiosaurus dolichodeirus* (Storrs, 1997), *Thalassiodracon hawkinsi* (BMNH 2018*), '*Rhomaleosaurus*' *megacephalus* (LEICT G122.1851; 1.8), and '*Plesiosaurus*' *macrocephalus* (BMNH R1336; 2.0).

DISCUSSION

Systematics

Macroplata tenuiceps BMNH R5488 has been included in recent cladistic analyses by O'Keefe (2001, 2004a), Smith and Dyke (2008), and Druckenmiller and Russell (2008). All three analyses found *M. tenuiceps* as a basal member of Pliosauroidea. Both O'Keefe (2001, 2004a) and Smith and Dyke (2008) recovered *M. tenuiceps* within a monophyletic Rhomaleosauridae. Druckenmiller and Russell (2008) did not recover a monophyletic Rhomaleosauridae. In their analysis, '*Rhomaleosaurus*' *victor*, '*R.*' *megacephalus*, and *M. tenuiceps* formed successive sister taxa to a clade including Pliosauridae, Polycotylidae, and Leptocleididae.

However, the most recent cladistic analysis of plesiosaurians incorporated a larger number of taxa (Ketchum and Benson, 2010; 66 taxa, 179 characters) and codings for *Macroplata tenuiceps* were updated based on the present work. This analysis recovers *M. tenuiceps* in a novel position, as a basal plesiosaurian outside of Pliosauroidea and Plesiosauroidea (Fig. 8), as the sister taxon of *Archaeonectrus rostratus*. This relationship is based on several synapomorphies, including the presence of a broad, posteriorly located dorsomedian ridge on the premaxillae (optimized unambiguously). BMNH 49202 is the sister taxon of this clade based on the presence of a prominent dorsomedian ridge (lacking the detailed similarity shared by *Archaeonectrus* and *Macroplata*) and the exclusion of the frontal from the orbit margin.

When the data set of Ketchum and Benson (2010) is limited to include only the taxa analyzed by O'Keefe (2004a) or Druckenmiller and Russell (2008), phylogenetic analysis recovers *M. tenuiceps* in a similar position to that recovered by those authors (Ketchum and Benson, 2010). Many of the characters supporting a basal position of *M. tenuiceps* are highly homoplastic, and further investigation is required to clarify the phylogenetic

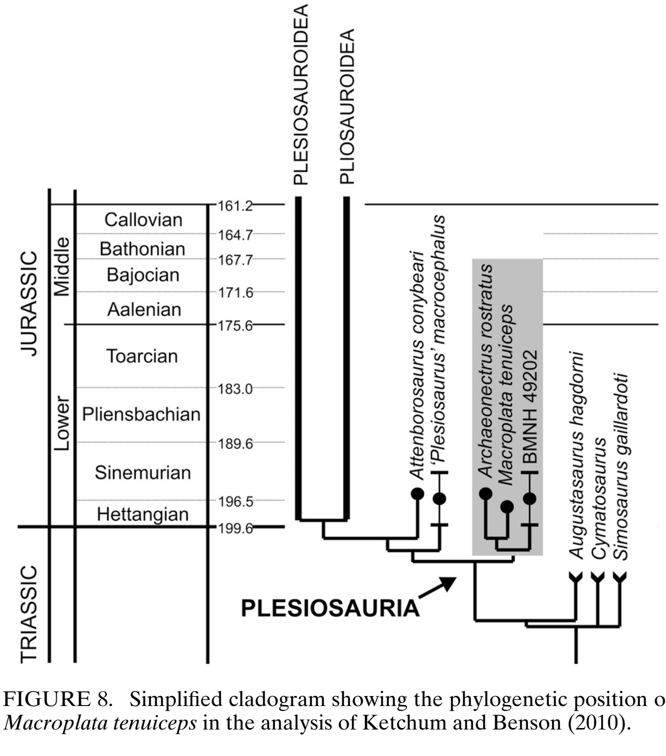

FIGURE 8. Simplified cladogram showing the phylogenetic position of *Macroplata tenuiceps* in the analysis of Ketchum and Benson (2010).

position of *M. tenuiceps* and other possibly basal plesiosaurians such as *A. rostratus*, BMNH 49202, and '*Plesiosaurus*' *macrocephalus*.

Most Lower Jurassic plesiosaurians were described early in the study of Plesiosauria (Owen, 1840, 1865; Sollas, 1881; Andrews, 1896) and these descriptions do not provide sufficient data to allow the scoring of all characters relevant to phylogenetic analysis in the 21st century. Complete descriptions of, and character exploration relevant to, these early taxa is a priority for understanding the early evolution of Plesiosauria.

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