High Diversity, Low Disparity and Small Body Size in Plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic Boundary

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Abstract

Invasion of the open ocean by tetrapods represents a major evolutionary transition that occurred independently in cetaceans, mosasauroïds, chelonioïds (sea turtles), ichthyosaurïs and plesiozaurïs. Plesiozaurïan reptiles invaded pelagic ocean environments immediately following the Late Triassic extinctions. This diversification is recorded by three intensively-sampled European fossil faunas, spanning 20 million years (Ma). These provide an unparalleled opportunity to document changes in key macroevolutionary parameters associated with secondary adaptation to pelagic life in tetrapods. A comprehensive assessment focuses on the oldest fauna, from the Blue Lias Formation of Street, and nearby localities, in Somerset, UK (Earliest Jurassic: 200 Ma), identifying three new species representing two small-bodied rhomaleosaurïds (Stratesaurus taylori gen et sp. nov.; Avalonnectes arturi gen et sp. nov) and the most basal plesiozaurïd, Eoplesiosaurus antiquior gen. et sp. nov. The initial radiation of plesiozaurïs was characterised by high, but short-lived, diversity of an archaic clade, Rhomaleosaurïidae. Representatives of this initial radiation were replaced by derived, neoplesiozaurïan plesiozaurïs at small-medium body sizes during a more gradual accumulation of morphological disparity. This gradualistic modality suggests that adaptive radiations within tetrapod subclades are not always characterised by the initially high levels of disparity observed in the Paleozoic origins of major metazoan body plans, or in the origin of tetrapods. High rhomaleosaurïan diversity immediately following the Triassic-Jurassic boundary supports the gradual model of Late Triassic extinctions, mostly predating the boundary itself. Increase in both maximum and minimum body length early in plesiozaurïan history suggests a driven evolutionary trend. However, Maximum-likelihood models suggest only passive expansion into higher body size categories.

Introduction

The origin of Plesiosauria 200 million years ago (Ma) was a landmark event in tetrapod evolution. Spanning 155 Ma, plesiozaurïs represent one of only three long-lived radiations of secondarily marine, non-mammalian tetrapods (alongside ichthyosaurïs and marine turtles; duration >100 Ma). Plesiozaurïs possess an unusual body plan not seen in other marine vertebrates [1]. All four limbs are enlarged and modified as propulsive flippers, the trunk is short and stiff, and proportional head size seems to vary inversely with neck length, resulting in a gradation of forms between ‘plesiozaurïomorph’ (long neck, small head) and ‘plesiozaurïomorph’ (short neck, large head) extremes [2–3]. Despite its oddity, this body plan was an extraordinarily successful adaptation to life in the open ocean [1,4]. It secured plesiozaurïan survival for the entire Mesozoïc, in spite of the emergence of possibly competing marine tetrapod clades [5], and recurrent regression events, which decimated shallow marine tetrapod lineages [6], including basal representatives of Sauropterygia, the wider clade that includes Plesiosauria.

Despite its significance for understanding the macroevolutionary dynamics of adaptive radiations, the fossil record of the oldest plesiozaurïs has been relatively understudied. This contrasts with early records of other pelagic tetrapod clades, the ichthyosaurïs [7–10] and cetaceans [11–14]. Lower Jurassic (200–175 Ma) European deposits yield the earliest plesiozaurïan fossils, possessing their full complement of pelagic adaptations. Abundant specimens provide snapshots of the emergence of Plesiosauria in the earliest Hettangian of Somerset and Leicestershire, UK (~200 million years ago [Ma]) [15–16]), the Sinemurian of Dorset and Leicestershire UK (~197–190 Ma) [17–18]) and the lower Toarcian of Yorkshire and Northamptonshire, UK, and Baden-Württemberg, Germany (~183–180 Ma) [19–20]). The occurrence of multiple intensively-sampled horizons provides unique data on key biotic and ecological parameters associated with invasion of the open ocean, including body size, species richness, and morphological disparity. Furthermore, global ecosystems were in decline for much of the Late Triassic, resulting in a progressive diminution of diversity in many invertebrate clades reviewed by [21], and possibly culminating in Late Triassic extinctions, or a
Triassic-Jurassic boundary extinction event (e.g. [22]). The exact cause and modality of these extinctions is uncertain [21–22]. However, the Lower Jurassic rise of plesiosaurians is one aspect of global recovery from this episode.

We present the results of a comprehensive review of the little-studied earliest Jurassic plesiosaurian fauna from Street, Somerset, UK (and an adjacent, contemporaneous locality at Watchet, Somerset), and a new phylogenetic dataset focused on Lower Jurassic taxa. These are used as tools to study the earliest stage of plesiosaurian evolution.

**Plesiosaurian faunal composition at Street**

The Blue Lias Formation at Street, Somerset, UK was extensively quarried for building stone in the 19th century [16,29-25], resulting in the discovery of 25 extant plesiosaur fossils [16-17,26-30]. Most specimens likely originate from the Pre-plumbeus beds, which occur below the first occurrence of the ammonite *Palaeoceras plumbeus*. Thus, they probably fall within the earliest Hettangian *P. tilmanii* Chronozome, immediately following the Triassic-Jurassic boundary [31], although some specimens may be from slightly younger horizons [16]. These specimens are usually considered to represent three taxa [16]: one individual of the large-bodied rhomaleosaurid *Eurypleurosaurus aceratus* (Owen, 1840) [32] and ‘Rhomaleosaurus’ *megacephalus* (Stutchbury, 1846) [33], plus 23 specimens of smaller-bodied individuals (trunk length <1 metre) that are typically referred to the basal pliosaurid *Thalassiodracon haukinsi* (Owen, 1838) [34]. However, Benson et al. [35] listed a number of morphologically distinct specimens and suggested that ‘*Plesiosaurus*’ *cliduchus* Seeley, 1865a [29] also represented a distinct, valid taxon.

Our taxonomic revision of the plesiosaurian fauna from Street indicates the presence of six species, including two new taxa identified here for the first time (below, Systematic Palaeontology). In total 16 plesiosaur specimens from Street are taxonomically determinate (Table 1; nine additional specimens are indeterminate). Penecontemporaneous strata at Watchet, Somerset yield an additional new taxon (below; Systematic Palaeontology). Other localities of similar age at ‘Street-on-the-Fosse’ (Pylle), Somerset and Barrow-on-Soar, Leicestershire have yielded additional specimens of ‘*Rhomaleosaurus*’ *megacephalus* [15–16], a specimen of *T. haukinsi* is also known from Walton, Somerset [35].

The presence of seven species in the lowermost Hettangian indicates high taxic diversity at a single locality immediately following the Triassic-Jurassic boundary. This is higher than the number of species known from the Late Hettangian-Sinemurian of Lyme Regis and Charmouth, Dorset and the lower Toarcian of Holzmaden, Germany and vicinity (both localities have yielded five species; Appendix S1); it is lower than the number of species known from the lower Toarcian of the UK (eight species; Appendix S1), and from the lower Toarcian of Europe (Germany and the UK combined: 13 species; Appendix S1). However, Toarcian plesiosaur faunas contain multisppecific genera that inflate species counts, and the number of genera known from the lower Toarcian of Europe is in fact comparable to that from Street (seven genera).

**Nomenclatural Acts**

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**Systematic Palaeontology**

**Pistosaurus Baur 1887–1890 [36]**

**Plesiosauria Baur of Blainville, 1835 [37]**

**Rhomaleosauridae Nopcsa, 1928 [38]**

**Stratesaurus n. gen.**

Type and only species. *Stratesaurus taylori* Diagnosis. As the type and only species. *Stratesaurus taylori* n. gen. et sp. [39] urn:lsid:zoobank.org:act:2C62769B-239B-4436-81E5-E6FA5173F618

1822 *Plesiosaurus* sp. de la Beche and Conybeare; Conybeare 1822[39]:pl. 19

1996 *Thalassiodracon haukinsi* Owen; Storr and Taylor 1996[16]:404

2001 *Thalassiodracon haukinsi* Owen; O’Keefe 2001[40]:fig. 4

**Holotype.** OUMNH (Oxford University Museum of Natural History, Oxford, UK) J.10337, a skull and partial postcranial skeleton including anterior cervical and pectoral vertebrae, a partial hindlimb and ilium (Fig. 1) from Street, Somerset, UK (likely lowermost Hettangian; see above; *Plesiosaurian faunal composition at Street*).

**Etymology.** Genus name from ‘Strate’, the name for Street recorded in the Doomsday Book and *sauros*, Greek meaning lizard. Specific epithet after Michael A. Taylor, who carried out acid preparation of OUMNH J.10337 during an earlier study of Street plesiosaurians [16].

**Referred specimens.** AGT (Alfred Gillett Trust, Street, UK) 11, a skull, and GSM 26035 [39], pl. 19, a skull with anterior cervical vertebrae. GSM 26035 possesses prominent posterior processes on the posteroconal surfaces of the prezygophosphes, an autapomorphy of *S. taylori* (below; Diagnosis). AGT 11 is difficult to distinguish from *Avallonectes arturi* (below), for which only the postorbital skull is known. However, in AGT 11, GSM 26035, and probably OUMNH J.10337, the premaxilla terminates posteriorly at approximately orbital midlength, whereas it extends further posteriorly in *A. arturi*. Furthermore, in AGT 11 and OUMNH J.10337 the squamosals contact each other dorsal to the parietals, unlike in *A. arturi*, in which this contact is more posterior. AGT 11 is otherwise indistinguishable from OUMNH J.10337 and GSM 26035 and is thus referred to *S. taylori*.

**Diagnosis.** Small-bodied basal plesiosaurian (skull of holotype 180 mm long) with five premaxillary and 16 maxillary alveoli, lacking rostral constriction. Possesses two autapomorphies: prominent posterior processes on posteroconal surfaces of anterior cervical prezygophosphes; pectoral centra proportionally short (length:anterior height ratio = 0.7).
Short description of holotype. The skull is crushed dorsoventrally, but has been prepared using acid and is almost free of matrix (Fig. 1A, B). It shows many details that are only briefly described here. The snout tapers anteriorly and lacks a rostral constriction. Thus, the premaxilla is not transversely expanded, unlike many robust Lower Jurassic taxa, including 'Rhomaleosaurus' megacephalus [15]. The premaxilla contains five teeth of subequal size, as in many basal plesiosaurs, but unlike T. hawkinsii, which has four premaxillary teeth [35]. The maxilla contains 16 weakly heterodont alveoli that terminate ventral to the postorbital bar. A superficial flange of the maxilla extends dorsally posterior to the external naris (Fig. 1A, B). This was figured as a distinct ossification contacting the naris, and identified as a nasal, by O’Keefe ([40], fig. 4). However, it does not contact the external naris, and we interpret the suture at the base of the ‘nasal’ (of O’Keefe [40]) as a crack. The parietal bears a low sagittal crest posterior to the suboval pineal foramen. The posterior part of the parietal is abruptly expanded laterally, forming the ‘lateral angle’ of Smith & Dyke [41] that is present in rhomaleosaurids and more basal pistosaurians (e.g. [42]). A dorsoventrally thin, sheet-like anterior extension of the squamosals overlaps the posterior surface of the parietals. A rounded squamosal bulb is present and the squamosals contact one another dorsal to the parietals. The posteroventral process of the postorbital extends far posteriorly, forming the dorsal margin of the temporal bar for most of its length (Fig. 1A–B). This also occurs in basal sauropterygians [42–43] and rhomaleosaurids (e.g. R. thorntoni: Natural History Museum, London, UK [NHMUK] R4853). Contrastingly, in

Table 1 Revised taxonomy of plesiosaurian specimens from the earliest Jurassic of Street, Somerset, UK, and Watchet (TTNCM 8348) (modified from [35], table 1). Abbreviation: NMING, National Museum of Ireland, Dublin, Ireland.

| Specimen                        | References and notes                                                                 |
|---------------------------------|--------------------------------------------------------------------------------------|
| *Thalassiodracon hawkinsii*     | Lectotype: skull and skeleton                                                        |
| NHMUK 2018*                     |                                                                                      |
| NHMUK 2020*[14551]              | Skull with partial postcranial skeleton                                              |
| NHMUK 2022*[14549]              | Skull and skeleton                                                                   |
| ANSP 15767                      | Skull and skeleton                                                                   |
| CAMSM J.35181                   | Partial postcranial skeleton                                                         |
| CAMSM J.46986                   | Skull, anterior cervical vertebrae and fragments                                      |
| GSM 51235                       | Skull and skeleton                                                                   |
| *Eurycleidus arcuatus*          | Lectotype: partial mandible. Disarticulated postcranial remains (NHMUK R1317–9, 2027*–2030*, 2047*, 2061*) probably represent the same individual as the lectotype (Cruickshank 1994) |
| NHMUK 2030*                     |                                                                                      |
| *Rhomaleosaurus megacephalus*   | Partial postcranial skeleton                                                         |
| NMING FI0194                    |                                                                                      |
| 'Plesiosaurus' cliduchus         | Holotype: partial postcranial skeleton                                               |
| CAMSM J.35180                   |                                                                                      |
| Stratesaurus taylori n. gen. et sp. |                                                                                          |
| OUMNH J.110337                  | Skull, and partial postcranial skeleton                                              |
| AGT 11                          | Skull                                                                                 |
| GSM 26035                       | Skull and anterior cervical vertebrae                                                |
| *Avalonnectes arturi* n. gen. et sp. |                                                                                       |
| NHMUK 14550                     | Partial skull and postcranial skeleton                                               |
| AGT uncatalogued                | Partial postcranial skeleton                                                         |
| *Eoplesiosaurus antiquior* n. gen. et sp. | Postcranial skeleton – cannot be compared to ‘Plesiosaurus’ cliduchus. |
| TTNCM 8348                      |                                                                                      |
| Not determined                  |                                                                                      |
| MANCH MM L.9767                 | Fragmentary postcranium                                                              |
| NHMUK R45                       | Not determined                                                                        |
| NHMUK R1331                     | Limb                                                                                 |
| NHMUK 2039*                     | Mandible                                                                             |
| OUMNH J.10327                   | Partial postcranial skeleton.                                                        |
| RM 4110                         | Postcranial and cranial fragments                                                     |
| SWM uncatalogued                | Not examined                                                                          |
| TTNCM 8345                      | Not examined                                                                          |
| TTNCM 9291                      | Skull without mandible; tentatively referred to new taxon B.                          |
| UCD uncat.                      | Not examined                                                                          |

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pliosaurids and plesiosaurids the length of the posteroventral process is reduced [35,44].

Eighteen anterior-middle cervical vertebrae are preserved, including most of the atlas-axis complex. The neurocentral sutures are convex, as in E. antiquior n. sp. (below), but unlike the other taxa present at Street. The cervical centra have double-headed rib facets and concave anterior and posterior surfaces that are approximately 1.2 times as broad mediolaterally as high dorso-ventrally (Fig. 1C, D, E). A small ‘lip’ projects ventrally from the anterior surface (Fig. 1E). This has been considered to be a unique synapomorphy of derived pliosaurids, known from the Middle Jurassic onwards [45–46]. However, during the present study it was also observed in a specimen referred to ‘Plesiosaurus’ macrocephalus Owen, 1840 from the Lower Lias Group of Lyme Regis, Dorset (NHMUK 49202 [47]), which also has transversely broad cervical centra. Uniquely in S. taylori, prominent processes project posteriorly from the posterolateral surfaces of the anterior cervical prezygapophyses (Fig. 1C). These are confirmed as absent in most plesiosaurian taxa represented at Street: ‘R.’ megacephalus (LEICS G221.1851), E. arcuatus (NHMUK 2047*), T. hawkinsii [16], Avalonnectes arturi and Eplesiosaurus antiquior (see below). The condition cannot be determined in ‘Plesosaurus’ clydechus, for which only posterior cervical vertebrae are preserved. However, S. taylori has proportionally short pectoral centra (Fig. 1G), unlike all other plesiosaurians from Street, including ‘P.’ clydechus (Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, UK [CAMSM] J.35180).

The ilium of S. taylori is approximately straight in lateral view and has a broadly expanded dorsal end that is rotated approximately 20 degrees relative to the proximal end (Fig. 1F). A rugose, proximodistally oriented ridge is present on the posterolateral surface of the distal expansion (Fig. 1H–I). This is also present in ‘R. megacephalus’ (LEICS G221.1851). A complete description of all material referred to S. taylori is beyond the scope of the present study but will form the basis of future work.

Avalonnectes n. gen.

urn:lsid:zoobank.org:act:027222CA-DA5A-4F63-B59F-63A47567CD93

Type and only species. Avalonnectes arturi

Diagnosis. As for the type and only species. Avalonnectes arturi n. gen. et sp.

urn:lsid:zoobank.org:act:27A8C3C1-5F02-461E-9778-2DB9E2645061

Holotype. NHMUK 14550, the posterior portion of the skull, and a partial postcranial skeleton (Fig. 2).

Etymology. Genus name from Avalon, an island from the legend of King Arthur, often identified with Glastonbury, near Street, and nectes, Greek meaning ‘swimmer’. Species epithet after Arthur Cruickshank [1932–2011], who with M. A. Taylor initiated the restudy of British Lower Jurassic plesiosaurians in the 1990s,
Figure 2. Holotype of Avalonnectes arturi (NHMUK 14550). A–B, skull in dorsal view; C–E, postcranial skeleton; in left dorsolateral (C) and left lateral (D–E) views. In line drawings (B, E) dark grey tone indicates damage and light grey tone indicates the palate. Abbreviations: ca, caudal vertebra [number following indicates order in preserved series]; ce, cervical vertebra; d, dorsal vertebra; depr, depression; ecto, ectopterygoid; epip, epipterygoid; exp, expanded neural spine apex; fr, frontal; jug, jugal; l., left [followed by name of element]; mx, maxilla; p, ‘pectoral’ vertebra; par, parietal; pmx, premaxilla; po, postorbital; pofr, postfrontal; prfr, prefrontal; qua, quadrate; r., right [followed by name of element]; s, sacral vertebra; sq, squamosal; unexp, unexpanded neural spine apex. Scale bars equal 50 mm (A–B), 20 mm (C), and 200 mm (D–E).

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and also as a reference to the legendary King Arthur of British folklore.

**Referred specimen.** AGT uncatalogued, a partial postcranial skeleton from Street, Somerset, UK (likely lowermost Hettangian; see above; *Plesiosaurian faunal composition at Street*).

**Diagnosis.** Small-bodied basal rhomaleosaurid (trunk length = 735 mm) with 18–19 dorsal vertebrae, a low, autapomorphic number.

**Short description of holotype.** The posttoral portion of the skull is preserved. It has been embedded in wax so the dorsal surface is exposed (Fig. 2A–B). The tapering posterior processes of the premaxillae extend far posteriorly compared to those of *S. taylori* (Fig. 1A–B), almost to the level of the posttoral bar. However, they do not contact the parietal. The lateral surface of the maxilla is visible on the right side (Fig. 2A–B). It underlaps the jugal and has been displaced posteriorly by crushing. The jugal is penetrated by numerous small foramina and contacts the squamosal just posterior to the posttoral bar. As in *S. taylori* and other basal plesiosaurs, the postventral process of the posttoral is long, extending more than two-thirds the length of the temporal bar. The postfrontal-posttoral suture is oriented anteroventrally, allowing only a small exposure of the posttoral in the posterior rim of the orbit. The parietal bears a low sagittal crest, which is penetrated anteriorly by a suboval pineal foramen. The posterior part of the parietal is abruptly expanded laterally (Fig. 2 A–B), forming the ‘lateral angle’ that is present in *S. taylori* and other basal plesiosaurs. A low squamosal bulb is present.

Twenty-three cervical vertebrae are preserved (Fig. 2D–E). These do not include the axis-axis complex, so *A. arturi* possessed at least 25 cervical vertebrae. Because of the very small size of the anteriormost preserved centrum (13 mm long anteroposteriorly), it is unlikely that more than one or two additional cervical vertebrae were originally present. Thus, *A. arturi* has an estimated cervical count of 26–28, fewer than in *T. hawkinsii* (31 cervicals [35], table 2), but similar to the number in the larger-bodied *R.* *megacephalus* (28 cervicals, trunk length = 1820 mm; New Walk Museum and Art Gallery, Leicester, UK [LEICT] G221.1851). The cervical rib facets have two articular surfaces separated by a narrow horizontal groove. The neurocentral sutures are V-shaped in lateral aspect (Fig. 2D–E), as in *E. arcuatus* (NHMUK R1317) and *T. hawkinsii* (GSM 26035). It lacks the ventral projection at the distal end of the scapular blade of *P.* *cidichus* ([51], fig. 14). The ilium is approximately straight in lateral view, and has an anteroposteriorly expanded distal end similar to *S. taylori* and many basal plesiosaurs. However, unlike in *S. taylori*, a deep fossa bounded anteriorly by a prominent proximodistally oriented ridge is present on the medial surface (Fig. 2D–E). The femur is approximately straight and slightly more expanded posteroventrally than anterodistally (the left femur has a symmetrical distal expansion). The tibia is slightly longer than the fibula.

A. *arturi* possesses four sacral vertebrae, with short, robust ribs that converge laterally (Fig. 2D–E). Sixteen proximal-middle caudal vertebrae are preserved. They have flat ventral surfaces, widely-spaced chevron facets, and the dorsal portion of the caudal rib facet is formed by the neural arch. The scapular blade expands dorsally (Fig. 2D–E). It lacks a prominent postosdorsal kink in the outline in lateral view, unlike in *E. arcuatus* (NHMUK R1317) and *T. hawkinsii* (GSM 26035). It lacks the ventral projection at the distal end of the scapular blade of *P.* *cidichus* ([51], fig. 14). The ilium is approximately straight in lateral view, and has an anteroposteriorly expanded distal end similar to *S. taylori* and many basal plesiosaurs. However, unlike in *S. taylori*, a deep fossa bounded anteriorly by a prominent proximodistally oriented ridge is present on the medial surface (Fig. 2D–E). The femur is approximately straight and slightly more expanded posteroventrally than anterodistally (the left femur has a symmetrical distal expansion). The tibia is slightly longer than the fibula.

Plesiosauridea Welles, 1943 [52]  
*Eoelpesaurus* n. gen.  
urn:lsid:zoobank.org:act:381ACFCA-ECE1-4450-BE6D-76DABB0FE69

**Type and only species.** *Eoelpesaurus antiquior*  
**Diagnosis.** As for the type and only species.  
*Eoelpesaurus antiquior* n. gen. et sp.  
urn:lsid:zoobank.org:act:3F5E6E6-6BCF-453C-B224-51375E656134

**Holotype and only specimen.** Somerset County Museum, Taunton, UK [TTNCM] 8348, a postcranial skeleton (Fig. 3) from Watchet, Somerset UK (likely lowermost Hettangian; see above; *Plesiosaurian faunal composition at Street*).

**Etymology.** Genus name from *Eo*, Greek meaning ‘dawn’, and *Plesiosaurus*, referring to a proportionally long neck, which is also present in *Plesiosaurus*. The species epithet is Latin meaning ‘more ancient’, in reference to the old geologic age of the specimen and *Duria antiquior* (‘a more ancient Dorset’; 1830), a watercolour depiction of Lower Jurassic fauna, including plesiosaurs and ichthyosaurs, by Henry De la Beche.

**Diagnosis.** Proportionally long-necked plesiosaurian (ratio of necktrunk length > 1.2) with at least 38 cervical vertebrae and one autapomorphy: small, conical lateral projections on the bases of the anterior cervical prezygapophyses.

**Short description of holotype.** TTNCM 8348 is an almost complete postcranial skeleton, although many features are obscured by matrix (Fig. 3). Thirty-six cervical vertebrae are preserved. These do not include the axis-axis complex, so at least 38 were present originally, more than in *A. arturi* (estimated 26–28 cervicals), *R.* *megacephalus* (28 cervicals; LEICT G221.1851) or *S. taylori* (31 cervicals [35]). The cervical rib facets are divided by a narrow horizontal groove. A small, conical eminence projects from the base of the prezygapophyses of anterior cervical vertebrae of *E. antiquior* (Fig. 3B). This differs from the posterior projection of the prezygapophyses of *S. taylori* (Fig. 1C) and is an autapomorphy of *E. antiquior*. Unlike in *A. arturi*, *E. arcuatus*, *P.* *cidichus* (CAMSM J.35180), *S. taylori* and *T. hawkinsii*, only the anteriormost 12 preserved cervical neural spines curve posteroventrally. More posterior neural spines are inclined straight posteroventrally (Fig. 3). The dorsal vertebrae are enclosed in matrix. Thirty-three possible caudal vertebrae are preserved, although a few distal elements may be missing, and it is possible that the anterior few possible caudals are sacral vertebrae; this is difficult to determine due to incomplete preparation. The ventral surfaces of the middle caudal centra are exposed. They bear prominent chevron facets posteriorly.
The pectoral girdle is preserved, although the clavicle-interclavicle complex is incompletely prepared and difficult to observe, and the coracoids are covered by the humeri (Fig. 3). The right scapula is partly visible. It lacks the ventral projection of the distal blade that is present in ‘P.’ cliduchus ([51], fig. 14). The humerus curves posterodistally. A prominent longitudinal ridge is present on its anterior surface (Fig. 3), as observed in E. arcuatus and ‘R.’ megacephalus by Smith & Dyke ([41], character 92). A possible ilium is covered by the right ischium. The left pubis is approximately as long anteroposteriorly as it is wide mediolaterally. Fore- and hindflippers are well-preserved and partly articulated (Fig. 3). A small postaxial ossicle is present between the right ulna and ulnare.

Microcleididae n. fam.

Type genus. Microcleidus Watson, 1909 [53]

Phylogenetic definition. Microcleidus homalospondylus and all taxa more closely related to it than to Plesiosaurus dolichodeirus, Cryptoclidus eurymerus, Elasmosaurus platyrurus, Leptocleidus superstes, Pliosaurus brachydeirus or Polycotylus latipinnis.

Table 2 Results of maximum likelihood model fitting of Lower Jurassic plesiosaurian trunk length evolution.

| Model                          | Parameters | AICc  | AICc weight | Parameter estimates                  |
|--------------------------------|------------|-------|-------------|-------------------------------------|
| Trunk length/mm                | 2          | 2932  | <0.001      | Trait mean = 1381; trait variance = 100 |
| Brownian motion (BM)           | 2          | 2363  | <0.001      | Step variance = 20.0                |
| Brownian motion+trend          | 3          | 2081  | ~1.000      | Step mean = 16.1; step variance = 20.0|
| ln(Trunk Length)/logmm         | 2          | 26.35 | 0.297       | Trait mean = 7.15; trait variance = 0.149|
| Brownian motion (BM)           | 2          | 26.27 | 0.358       | Step variance = 0.011               |
| Brownian motion+trend          | 3          | 26.65 | 0.344       | Step mean = 0.0096; step variance = 0.010|

Figure 3. Holotype of Eoplesiosaurus antiquior (TTNCM 8348) in right lateral view. Image in A is a composite made from four photographs (divisions are indicated by black and white lines), with enlargement of anterior cervical vertebrae (B; magnified portion is enlarged x2.0 times). Gastralia are not shown in line drawing (C). Abbreviations: ca, caudal vertebra; ce, cervical vertebra [number following indicates order in preserved series]; chv, chevron; l., left [followed by name of element]; pro, lateral projection; prz, prezygapophysis; r., right [followed by name of element]; trp, transverse process. Scale bars equal 200 mm (A, C) and 50 mm (B).

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Diagnosis. Platypterygioids possessing: widely separated posterior cervical rib facets (character 123.1 in the Phylogenetic analysis; below); posteriormost dorsal rib facets split between centrum and neural arch (sacralised), but bearing a dorsal rib (146.1); medial surface of the iliac blade anteroposteriorly concave (170.8; also present in some rhomaleosaurids); and a prominent flange extends anteriorly from the proximal half of the radius (197.1; also present in Hauffiosaurus and some rhomaleosaurids). This diagnosis focuses on unambiguous postcranial synapomorphies because cranial material of basal microcleids is unknown.

Included taxa. Microcleidus homalospondylus, M. (Hydrodon) brachypterygius (von Huene, 1923) comb. nov., M. (Occianosaurus) tournemienensis (nov. comb.), Seeleyosaurus guillemantoperatoris, Eetzmosaurus rugosus and Westphaliaosaurus simonsensi.

Remarks. Großmann [20], p. 556 referred informally to ‘microcleid elasmosaurs’, a clade containing the three taxa referred to Microcleidus herein. However, the family has not formally been erected until now. In the present study we recover very strong branch support for a clade uniting Microcleidus spp. and Seeleyosaurus guillemantoperatoris (below: Phylogenetic analysis). This forms the nucleus of a new, formally-defined plesiosaurian family Microcleidae.

Microcleidus Watson, 1909 [53].

Type species. Microcleidus homalospondylus (Owen, 1865–1881) [17].

Additional included species. Microcleidus (Hydrodon) brachypterygius (von Huene, 1923) comb. nov. [54]; Microcleidus (Occianosaurus) tournemienensis (Sciulli et al., 1990 [55]) comb. nov.

Diagnosis. Microcleidid plesiosaurs with (selected unambiguous synapomorphies); jugal excluded from orbit margin by maxilla-postorbital contact (character 32.1 in the Phylogenetic analysis; below); jugal short, terminates around posterior orbital margin (33.1); cervical centra longer anteroposteriorly than high dorsoventrally (118.1); anteroposterior constriction at base of dorsal neural spines (142.1); also present in Hauffiosaurus and some rhomaleosaurids); and a prominent vacuity forming diamond-shaped ventral platform (64.0), surangular transversely narrow and ‘blade-like’, lacking a prominent medial crest and dorsomedial fossa (99.2), distal anteroposterior width of scapular blade subequal to width at midlength (161.0; not expanded), humeral shaft has pronounced dorsodistal curvature (183.0). Strong character support for Neoplesiosauria contrasts with a previously-hypothesised ‘Pliosauridea’, comprising Pliosauria and Rhomaleosaurs, most proposed synapomorphies of which are actually plesiomorphies [35]. NHMUK 49202 was found basal to Rhomaleosauridae on the phylogenetic ‘stem’ leading to Neoplesiosauria as in Ketchum & Benson (2010 [56]). It possesses several plesiomorphies not found in more derived plesiosaurs, including: the premaxilla does not divide the anterior processes of the frontal (14.0); the occipital condyle lacks a constricting groove around its base, even ventrally (49.2); and the paraoccipital process is inclined dorsolaterally relative to the ventral surface of the exoccipital-opisthotic, resulting in a narrow cranioquadrate passage (54.1).

Specimens from Street and other earliest Jurassic localities include basal plesiosaurs (Eophleosaurus) and pliosaurs (Thalassiodracon), but most represent rhomaleosaurs (Statariosaurus, Asllonnetes, Eucylochelis, ‘Rhomaleosaurus’ megacephalus). Branch support for nodes within Rhomaleosauridae is low, but Pliosauridae, Microcleidae, and nodes within both families, are generally well-supported (a monophyletic Microcleidus comprising M. homalospondylus).
M. brachypterygius, and M. tournemirensis received exceptionally strong support (decay index = 6). This is part of a temporal pattern in the distribution of branch support. Older nodes are generally less well-supported, probably reflecting poor knowledge of Triassic pistosaurians: 12 nodes within Plesiosauria occur prior to the Triassic–Jurassic boundary (i.e. probably within the Triassic) and have an (mean) average decay index of 1.33; six younger nodes occur within or prior to the Sinemurian and have an average decay index of 1.67; and seven younger nodes occur prior to or within the Toarcian and have an average decay index of 2.86. Most nodes within Rhomaleosauridae split in the Triassic, whereas most pliosaurid and plesiosauroid nodes split in the Jurassic.

Phylogenetic diversity estimates

‘Phylogenetic diversity estimates’ were calculated for the lower Hettangian, Sinemurian and Toarcian (Fig. 5A), counting both taxon occurrences and ‘ghost lineages’ implied by the phylogeny [63]. All Hettangian–Sinemurian operational taxonomic units (OTUs) are monotypic genera (or single specimens) whereas Toarcian OTUs include multiple species within Hauffiosaurus, Microcleidus and Rhomaleosaurus. Thus, genus- and species-level phylogenetic diversity estimates are identical until the Toarcian. ‘P. cliduchus’ (lower Hettangian) and Sthenarosaurus dawkinsi (Toarcian) were not included in our phylogeny but were added to the phylogenetic diversity estimate. This resulted in phylogenetic diversity estimates of 13 in the lower Hettangian; 12 in the Sinemurian and 10 (genera) or 16 (species) in the lower Toarcian. We prefer the genus-level estimate because German and British representatives of Hauffiosaurus (other than H. longirostris) and Microcleidus are not contemporaneous and may represent chronospecies that did not exist contemporaneously [48]. The lower Toarcian diversity estimate may be underestimated due to the absence of well-sampled horizons in the immediately following stages (few early Middle Jurassic plesiosaurians are known). However, unlike older taxa, lower Toarcian plesiosaurians are known from multiple, intensely sampled horizons in both Germany and the UK, likely compensating for this effect. These
results confirm that plesiosaurian diversity immediately following the Triassic–Jurassic boundary was comparable to that later in the Lower Jurassic, including up to 20 million years later in the early Toarcian.

**Character disparity**

Faunal disparity was estimated using our cladistic data matrix, following the protocol described by Wills et al. (1994 [64]) and employed by several recent studies of tetrapod disparity (e.g. [65–67]). Pairwise dissimilarity between all Lower Jurassic taxa was calculated as the proportion of comparable cells (those cells not scored as '?' for either taxon) that differed between the taxa. Taxa known only from postcranial material such as Eoplesiosaurus, Eretmosaurus and Westphaliasaurus could not be compared with Hauffiosaurus longirostris, which has 100% postcranial missing data (a postcranial skeleton probably belonging to the holotype [68] was not scored). Thus, H. longirostris was deleted from the matrix before further analyses to eliminate problems of missing entries in the resulting symmetric dissimilarity matrix. This matrix formed the basis of a principal co-ordinates analysis (PCo) in Ginkgo (Universitat de Barcelona, http://biodiver.bio.ub.es/ginkgo/) using a negative eigenvalue correction (Cailliez method). Two disparity metrics were calculated for three narrow Lower Jurassic stratigraphic intervals (earliest Hettangian; Sinemurian; lower Toarcian): the mean pairwise dissimilarity (as used by e.g. Wagner 1997 [69]), and the sum of variance of scores on all 24 principal coordinate axes. The sum of variances was chosen instead of product- or range-based metrics, because it is robust to variation in sample size [66,70]. It was computed using the freeware program RARE (M. Wills, pers. comm.), which also allows 95% confidence intervals to be computed using rarefaction. Both character-based disparity measures show monotonic increase through the Lower Jurassic (Fig. 5B).

The scree plot exhibits a break in slope between the third and fourth PCo axes, following which, each axis describes 5.73% or less of the Gower-transformed dissimilarity. The first three principal coordinate axes encompass 38.1% of the Gower-transformed dissimilarity and are plotted in Figure 6. Earliest Jurassic taxa (unfilled shapes) have mostly negative values of PCo1, and plot in the centre of PCos 2 and 3. Later rhomaleosaurids (triangles) occupy a similar region of character-distance space, likely due to their plesiomorphic anatomy. They have negative values of PCo1, but have higher positive values of PCo2. They are well-separated from later pliosaurids (squares), which plot in the centre of PCo1, have high negative values of PCo2, and high positive values of PCo3. Later plesiosauroids (circles) have high positive values of PCo1. Thus, PCo1 differentiates Toarcian (black symbols) rhomaleosaurids (negative values) from pliosaurids (values close to zero) and plesiosauroids (positive values).

**Body size evolution**

Trunk length was used as a proxy for overall body size (Fig. 5C), defined as the distance between the anterior surface of the anteriormost vertebra with an elongate, ‘dorsalised’ rib and the

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Figure 5. Early evolution of Plesiosauria. Plots of A, phylogenetic diversity [62]; B, disparity (main pairwise dissimilarity and sum of variances of PCo axes with 95% confidence intervals [64]); C, body size, based on the proxy trunk length (in metres); D, body proportions, based on the proxy neck/trunk length ratio. In C–D, triangles represent non-neoplesiosaurian plesiosaurians (mainly rhomaleosaurids), squares represent pliosaurids and circles represent plesiosauroids; unfilled shapes represent earliest Hettangian taxa, grey-filled shapes indicate late Hettangian–Pliensbachian taxa, and black shapes indicated Toarcian taxa.

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posterior surface of the posteriormost sacral vertebra. The appearance of ribs with a ‘dorsal’ morphology (long, curving, rod-like ribs) was used because these ribs define the trunk directly, forming its lateral wall. Other criteria for identifying the neck-trunk boundary rely only on indirect proxies such as rib facet morphology. Only measurements from the largest individuals of each taxon were counted, and taxa only known from juveniles were not included in our analysis (Plesiopterys, Rhomaleosaurus zelandicus; indicated by rounded, incompletely ossified margins of slowly-ossifying bones such as the limb girdles [Plesiopterys], ulna and tarsals [Plesiopterys and R. zelandicus; compare with figures in [71]), and dorsal neural spines in R. zelandicus; SMNS 16812; The Yorkshire Museum, York, UK [YORYM] G503). Minimum body size in the Triassic–Jurassic boundary fauna, as indicated by the proxy trunk length (680 mm, Thalassiodracon) is comparable to that among Triassic pistosaurians (680 mm, Yunguisaurus [61]) and low compared to later intervals (Plesiosaurus [Sinemurian], 1100 mm; Eoplesiosaurus [Toarcian], 900 mm). Maximum body size also increases through time. The largest individual of 'Rhomaleosaurus' megacephalus from the earliest Hettangian fauna has a trunk 1820 mm long compared to 1500 mm for the Triassic pistosaurian Bobosaurus [72] and 3400 mm for the Toarcian Rhomaleosaurus thorntoni (or 2460 mm for R. cromptoni). Sinemurian representatives of the large-bodied rhomleosaurid lineage are not currently known. Increase in the maximum and minimum values through time is suggestive of a driven trend [73].

We tested the hypothesis of a driven trend by fitting maximum likelihood models of trunk length evolution representing stasis, Brownian motion (BM), and BM+trend, to our phylogenetic tree with temporal branch lengths estimated using stratigraphic age. This analysis was conducted in R version 2.10.1 [74], using both untransformed, and ln-transformed data. Taxa for which trunk was not known, and taxa occurring after the Lower Jurassic, were not analysed. Branch lengths were calibrated following the protocol of Brusatte et al. [63] using code available from http://www.graemelloyd.com/pubdata/functions_2.r (accessed 23 December 2011). Evolutionary models were fitted using the ‘fitContinuous’ function of the Geiger package [75] as described by Hunt & Carrano [76], specifying a trait standard deviation of 55 mm, based on four individuals of Thalassiodracon hacknisi. The results indicate overwhelming support for the BM+trend model when untransformed trunk length is analysed (Table 2). However, ln-transformed trunk length fits all tested models subequally well (Table 2). Thus, the appearance of driven trend in the untransformed data may arise from overweighting of extreme large sizes in taxa like Rhomaleosaurus thorntoni, and the true signal cannot be distinguished from white noise or Brownian motion.

Body proportions
Neck length excluding the skull was measured for the same individuals measured for trunk length (above). The ratio of neck length:trunk length was used as a proxy for overall body proportions (Fig. 5D). Other studies have used larger sets of measurements to quantify body plans [2–3]. The approach employed here was selected to maximize taxonomic coverage as it can be applied to some relatively incomplete specimens (e.g. those missing limbs and skulls).

Body proportions, as indicated by the proxy neck length/trunk length, occupy a narrow range in the earliest Hettangian fauna (0.72 in ‘R.’ megacephalus – 1.25 in Eoplesiosaurus [although this represents a slight underestimate because a small number of anterior cervical vertebrae are not preserved]). Sinemurian (0.71 in Archauonectrus – 1.57 in Attenborosaurus) and Toarcian (0.57 in Meyerasaurus – 1.90 in Microcleidus turnemirensis) show small decreases in the minimum ratio and larger increases in the maximum ratio, demonstrating an increase in the range of plesiosaurian body plans though the Lower Jurassic.

Discussion
Early evolution of Plesiosauria – evolutionary responses to pelagic adaptation
During the Mesozoic, at least 12 tetrapod lineages independently became adapted to marine life (e.g. [5]). Of these, most
remained restricted to nearshore, shallow water environments. Many of these possessed ‘plesiopedal’ (i.e. terrestrial proportioned) limbs (e.g. placodont sauropterygians [4]; thalattosaurs [77–78]; basal mosasauroids and related squamate groups [79]). Others possessed long, slender bodies (e.g. basal ichthyosaurs [7,10]; some basal sauropterygians [1,4,80] indicating low cruising efficiency [81] and locomotion by axial undulation, resulting in low stamina [82]). Thus these plesiomorphic body forms conferred only limited ability to survive in the open ocean, where food resources may be distributed patchily and locomotor efficiency is required. Derived ichthyosaurs [10], plesiosaurs [1], marine turtles, and possibly the mosasauroid *Plotosaurus* [83] became adapted for life in the open ocean by shortening and stiffening the trunk, and relying on caudal oscillation (ichthyosaurs and *Plotosaurus* or limb-driven locomotion (plesiosaurs and turtles; the stiff trunk is primitive for turtles). Most of these clades also show evidence of viviparity [10,64–86], freeing them altogether from the constraint of terrestrial locomotion in an otherwise aquatically-adapted animal, and inherent restriction of body size and proportions. *Archelon*, the largest marine turtle, provides evidence that oviparity, and the necessity of terrestrial locomotion constrains maximum body size in pelagic tetrapods. *Archelon* attained a maximum length of approximately four metres ([87], citing [88]: “3–5 m”). This is small compared to the largest ichthyosaurs (e.g. *Shonisaurus*; 20 metres long [89]), plesiosaurs (*Stretosaurus* (= *Pliosaurus* macronerum) and *Kronosaurus*; >10 metres [90–91]), and cetaceans (e.g. *Balaenoptera musculus*; commonly 25–27 metres, but up to 33.58 metres [92]).

Earliest Jurassic plesiosaurs possess their full suite of adaptations for specialised marine locomotion: reduction of intralimb flexibility, hyperplhalangy, interlocking phalanges, and the appearance of supernumary ossifications in the limbs resulting in the formation of a flipper; increased thoracic rigidity by modification of the limb girdles to form large ventral plates, and enlargement of the gastric basket; and shortening of the tail [1]. More basal, Triassic sauroptherygians, including basal plesiosaurs, possessed only a subset of these adaptations, demonstrated different swimming dynamics, and were restricted to shallower water facies [1,61,93].

Our data allow an assessment of the evolutionary response of plesiosaurs to full pelagic adaptation in the Lower Jurassic. They show that the advent of plesiosaurian locomotion was followed by a gradual increase in body size spanning approximately 17 million years between the Triassic-Jurassic boundary and the lower Toarcian. Thus, the largest lower Toarcian plesiosaurian, *Rhomaleosaurus thorntoni*, has a trunk almost twice as long as *Rhomaleosaurus megacephalus* from the lower Jurassic fauna (Fig. 5C). If linear dimensions scale isometrically in rhomaleosaurids, this implies an eight-fold increase in body mass (this is inexact, but provides an estimate of the order of magnitude of the change). This trend of increasing maximum body size continued in later plesiosaurian evolution; the largest plesiosaurs, known from fragmentary Late Jurassic remains, were substantially larger than *R. thorntoni*. For example, *Stretosaurus* (= *Pliosaurus* macronerum) has a humeral length of 840 mm and femoral length of 960 mm [90], compared to 720 mm and 680 mm in *R. thorntoni* (NHMUK R4853). Minimum body size also increased through the Lower Jurassic, though less prominently (Fig. 5C). *Seleosaurus*, the smallest Toarcian plesiosaurian, has a trunk length 1.32 times that of *Thalassiodracon*, the smallest plesiosaurian from the lowermost Jurassic. It is noteworthy that small-bodied individuals and taxa (*Thalassiodracon*, *Acanthosaurus*, *Stratiosaurus*) are abundant in the earliest Jurassic fauna, but rarer in the Toarcian (Fig. 5C). However, analyses of in-transformed trunk length data suggest that the pattern of body size increase in early plesiosaurian evolution cannot be distinguished from a Brownian motion, or ‘passive expansion’ model (Table 2). This is similar to the pattern observed in Mesozoic birds [94], and during early dinosaur evolution [95], suggesting that driven trends of body size change (‘Cope’s Rule’) do not always occur during Mesozoic ecological radiations.

The range of plesiosaurian body plans also increased through the Lower Jurassic (Fig. 5D). Although more basal plesiosaurs exhibit high variation in cervical vertebral counts (e.g. 20 in *Beloosaurus* [72], 44 anterior to the pectoral girdle in *Tungusaurus* [61]), this is not reflected in their overall body proportions, as even *Tungusaurus* has an ‘intermediate’ neck length that is subequal to that of the trunk [61]. The earliest plesiosaurians include taxa with intermediate and short neck lengths, as well as *Epipleiosaurus*, with a neck at least 1.2 times the trunk in length (Fig 3, 5D). The range of body proportions increased progressively through the Lower Jurassic, and Toarcian plesiosaurs include long-necked taxa such as *Microcleithrum tournemirensis*, in which the neck is 1.9 times the trunk in length [96]. These body proportions are similar to those of some Late Jurassic plesiosaurs, such as the cryptocleidid *Macronosaurus* [40,97], but Cretaceous cladosaurids exhibited substantially longer necks (e.g. ratio = 2.75 in *Alzadasaurus pembertonii* (= *Styosaurus snowii*) [98]).

**Diversity dynamics in Lower Jurassic plesiosaurian evolution**

The first appearance of plesiosaurs in the earliest Jurassic is characterised by a high diversity of rhomaleosaurids (five taxa). Despite the absence of derived plesiosaurs in older deposits, rhomaleosaurids from the earliest Jurassic are widely spread across morphospace (Fig. 6), and represent nodes deeply nested within Rhomaleosauridae. Thus, most rhomaleosaurid divergence likely occurred in the Late Triassic. In contrast, although the basal neoplesiosaurian split between Pliosauridae and Plesiosauridea probably occurred in the Triassic, most nodes within these clades occur in the Jurassic, and both clades make their earliest Jurassic first appearance at low diversity (one taxon each). Plesiosauridea became increasingly diverse and disparate through the Early Jurassic, especially at small–medium body sizes (Fig. 5C). This diversification may have been at the expense of rhomaleosaurids and represents a clear example of a candidate clade replacement event [99]; although the earliest rhomaleosaurids occupy the entire range of contemporaneous body sizes and are widely spread across morphospace, later (Toarcian) rhomaleosaurids are exclusively large-bodied (trunk length > 1.5 metres) and are restricted to a local area of morphospace (Fig. 6). Although all rhomaleosaurids have proportionally short necks (Fig. 3D), the youngest rhomaleosaurids have the shortest necks, and thus the most extreme ‘plesioauranomph’ body plans. This may be associated with a restriction of rhomaleosaurids to a macropredaceous niche prior to their final demise after the Middle Jurassic (last occurrences: *Maresaurus*, Bajocian [100]; *Borealosaurus*, Callovian [101]).

**Disparity dynamics in Lower Jurassic plesiosaurian evolution**

Despite their high diversity (Fig. 5A), the earliest Jurassic plesiosaurs are characterised by low disparity (Fig. 5B). In fact, mean pairwise dissimilarity (the number of character differences among comparable cells) is approximately half that 17 million years later in the lower Toarcian. Plesiosaurian disparity based on character data and the range of body proportions represented (see above) both increase monotonically through the Lower Jurassic. This mode of disparity accumulation, coupled with more or less
constant species diversity, differs from that shown in the origins of major groups such as the Cambrian ‘explosion’ of metazoan disparity (e.g. [102]) and the rapid evolution of early tetrapod disparity in the early Carboniferous [103]. Although further analyses of plesiosaurian disparity over a longer time interval are required to confirm this pattern, the results obtained here suggest that invasion of morphospace by plesiosauromorphs following invasion of pelagic habitats was gradual, not explosive, and comparable to that in other tetrapod subclades such as dinosaurian and crurotarsan archosauromorphs [65].

Late Triassic marine tetrapod extinctions

The observation of high taxic diversity in earliest Jurassic plesiosaurians, especially among rhomaleosaurids, suggests that an extinction event was rare or insignificant (e.g. [21]) prior to the Triassic–Jurassic boundary. It is impossible to date these rhomaleosaurid extinctions accurately, but generally low pairwise dissimilarity exhibited by earliest Jurassic plesiosaurians suggests relatively recent divergence, and may represent the influence of earlier Late Triassic extinctions, which are concentrated at the end of the Norian [21]. Our understanding of the effect of Late Triassic extinctions on plesiosaur evolution will remain incomplete until the discovery of more complete Late Triassic plesiosaurian fossils.

Thorne et al. [67] attributed a monotypic decimation of ichthyosaur disparity between Late Triassic and Lower Jurassic time bins to a Triassic–Jurassic boundary extinction event. However, the ‘Late Triassic’ time bin of their analysis includes six taxa from the Carnian, 23.4 million million years before the end of the Triassic (235–228 Ma [104]). Only four taxa represent the younger Norian stage (228–204 Ma), and zero represent the latest Triassic Rhaetian (2.4 Ma; 204–210.6 Ma). Clearly, this coarse level of temporal and taxonomic resolution is too poor to attribute a Late Triassic decline in ichthyosaur disparity to a sudden extinction event at the Triassic–Jurassic boundary. Indeed, a progressive, not precipitous, decline is suggested by the staggered last appearances of other marine reptile clades including thalattosaurs (Carnian, early Late Triassic) and basal sauropod-such as nososaurids (Ladinian, Middle Triassic) and pachypleurosaurs (Carnian) [105]. This decline occurred concur-ently with lowering sea levels and a reduction in shallow marine area [4,6,106]. A gradualistic or stepwise pattern of extinction is also exhibited by well-sampled marine invertebrate clades, including bivalves, conodonts, and ammonoids, which show intervals of concentrated extinction prior to the end of the Triassic, most notably at the end of the Norian (e.g. [21,107–111]) and throughout the Rhaetian [112].

Supporting Information

Appendix S1 Measurements, age, provenance data and lists of specimens examined for taxa included in the phylogenetic analysis.

[XLs]

Appendix S2 Character list for the phylogenetic analysis.

[DOC]

Appendix S3 Phylogenetic data matrix.

[PDF]

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Author Contributions

Analyzed the data: RBJB ME PSD. Wrote the paper: RBJB ME PSD.
Plesiosaurus macropterus

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