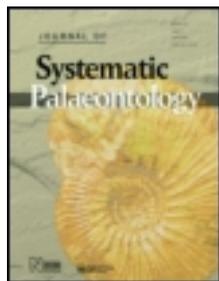


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A new leptocleidid (Sauropterygia, Plesiosauria) from the Vectis Formation (Early Barremian-early Aptian; Early Cretaceous) of the Isle of Wight and the evolution of Leptocleididae, a controversial clade

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A new leptocleidid (Sauropterygia, Plesiosauria) from the Vectis Formation (Early Barremian–early Aptian; Early Cretaceous) of the Isle of Wight and the evolution of Leptocleididae, a controversial clade

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Among the most enigmatic and controversial plesiosaurian clades is the Early Cretaceous Leptocleididae, a small group of (mostly) short-necked taxa with ‘intermediate’ or ‘pliosauromorph’ body proportions. Leptocleidids have often been interpreted as basal members of Pliosauroida, and their presence in marginal marine and even freshwater facies has led to suggestions that they might represent late-surviving relicts, perhaps related to the Lower Jurassic rhomaleosaurids. We describe a new leptocleidid, *Vectocleidus pastorum* gen. et sp. nov., from the late Barremian part of the Cowleaze Chine Member (Vectis Formation), Isle of Wight, UK, and undertake a detailed reassessment of leptocleidid anatomy and relationships. New data on the long-necked *Brancaesaurus* gives extra support to a monophyletic Leptocleididae with taxa of ‘intermediate’ body plan and robust skulls, *Leptocleidus superstes*, *Leptocleidus capensis*, *Nichollssaura* and *Vectocleidus*. Thus, leptocleidids adopted a range of body plans on the pliosauromorph–plesiosauromorph spectrum. Support for a placement of Leptocleididae within Pliosauroida is weak, and most proposed synapomorphies fail the test of similarity. However, numerous synapomorphies, including many new observations, support a derived position within Plesiosauroida. Thus, the ‘intermediate’ body plan of many leptocleidids is not plesiomorphic, and plesiosaurian body plan evolution was complex and highly plastic. We also summarize the anatomy of ‘*Cimoliasaurus*’ *valdensis*, a short-necked Early Cretaceous taxon. ‘*C.*’ *valdensis* is a valid taxon for which we erect the new monotypic genus *Hastanectes*. *Hastanectes* shows evidence of possible pliosaurid affinities. Thus, multiple plesiosaurian clades may have invaded margin and freshwater environments.

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Keywords: plesiosaurians; Leptocleidia; Wealden; body plan evolution; Early Cretaceous

Introduction

Plesiosaurians were an ecologically diverse, successful and long-lived clade of marine reptiles. They are easily recognized thanks to their distinctive body plan: a stiff barrel-shaped trunk, abbreviated tail, two pairs of large, wing-like flippers and highly variable neck length (e.g. O’Keefe 2002; O’Keefe & Carrano 2005). Although it differs from that of any extant organism, this body plan was highly successful in the Mesozoic oceans, where plesiosaurians achieved a global distribution in the Jurassic and Cretaceous (e.g. White 1940; Brown 1981). Europe has a particularly rich plesiosaurian fossil record (Persson 1963; Benton & Spencer 1995), and the majority of known Jurassic plesiosaurians are European (e.g. Owen 1865–1881; Andrews 1910, 1913; Benton & Spencer 1995; Großmann 2007). In contrast, European Cretaceous plesiosaurians are

rare (Milner 1987; Kear & Barrett 2011), and much of what is known of the later history of the group has been derived from the late Early–Late Cretaceous of North America, and the southern continents (e.g. Williston 1903; Welles 1943; White 1935; Bardet *et al.* 2003; Kear 2003; Benson *et al.* 2010, Online Supplementary Material Appendix).

Jurassic plesiosaurians (pliosaurids, rhomaleosaurids, cryptocecidids, ‘microcecidids’ and plesiosaurids; e.g. Großmann 2007; Smith & Dyke 2008; Ketchum & Benson 2010) are distinct from those of the ‘middle’–Late Cretaceous (brachaucheninine pliosaurids, polycotyliids and elasmosaurids; O’Keefe 2001; Sato 2002; Druckenmiller & Russell 2008a; Ketchum & Benson 2011). Plesiosaurians from the first few stages of the Cretaceous are poorly known. This is unfortunate as the early history of well-defined Cretaceous clades is poorly sampled, resulting in long phylogenetic ghost lineages extending approximately

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45 million years (e.g. Ketchum & Benson 2010, fig. 6). These long ghost lineages may be one cause of a lack of consensus on the interrelationships of Cretaceous families (O’Keefe 2001, 2004a; Druckenmiller & Russell 2008a; Ketchum & Benson 2010; Kear & Barrett 2011). The only way to overcome this problem is to improve phylogenetic sampling of lowest Cretaceous (Berriasian–Barremian) taxa, and of characters devised to elucidate their relationships.

The lowest Cretaceous strata of Germany (Wegner 1914), the UK (Andrews 1922; Kear & Barrett 2011), South Africa (Andrews 1911; Cruickshank 1997) and Australia (Cruickshank & Long 1997) have yielded partial plesiosaurian specimens. However, their systematics are controversial (O’Keefe 2001; Druckenmiller & Russell 2008a; Ketchum & Benson 2010; Kear & Barrett 2011). Much of the more complete material is referred to the genus *Leptocleidus*. *Leptocleidus* is often described as having intermediate or rhomaleosaurid-like body proportions, leading to a hypothesized relationship with ‘primitive’ pliosauroids (Cruickshank 1997; Cruickshank & Long 1997; Kear & Barrett 2011). However, a sister-clade relationship with the derived, longirostrine polycotyliids has also been suggested (Druckenmiller & Russell 2008a (as pliosauroids); Ketchum & Benson 2010 (as plesiosauroids)). If this is correct, then the evolution of body proportions among plesiosaurians is more complex than many classical, and even more recent assessments (e.g. O’Keefe 2002) have suggested.

The short-necked taxon ‘*Cimoliasaurus*’ *valdensis* was erected by Lydekker (1889) for several specimens from the Berriasian Wadhurst Clay Formation near Hastings. The taxon is known primarily from vertebrae and has been dismissed as a *nomen vanum* by Welles (1962). Kear & Barrett (2011) suggested that it was indistinguishable from *Leptocleidus superstes*. However, Andrews (1922, pp. 290–291) and Ketchum (2011) listed several differences between ‘*C.*’ *valdensis* and *L. superstes*, and observed distinctive anatomical features indicating that ‘*C.*’ *valdensis* is a valid taxon. The systematic position of ‘*C.*’ *valdensis* has never been determined, but if it is related to leptocleidids then the low, pliosaurid-like cervical count (*c.* 20 vertebrae) indicates further plasticity in leptocleidid neck length.

The proportionally long-necked taxon *Brancaesaurus*, from the Wealden of Germany, was first described as a member of the long-necked plesiosaurian clade Elasmosauridae (Wegner 1914). Initial phylogenetic analyses recovered *Brancaesaurus* as a basal elasmosaurid (O’Keefe 2001, 2004a). More recently however, it was recovered as a basal leptocleidid (Ketchum & Benson 2010). If *Brancaesaurus* is an earliest Cretaceous elasmosaurid then it is significant for establishing character polarity within the clade. If it is a leptocleidid then it is significant for understanding the repeated evolution of long necks, and further underlines the evolutionary plasticity of body proportions among plesiosaurians. Thus, clarifying the anatomy and

affinities of Lower Cretaceous European plesiosaurians is central to understanding the relationships of derived plesiosaurians, the youngest representatives of one of the most successful radiations of marine tetrapods that ever lived. It is also an essential first step in constraining the degree of plasticity in plesiosaurian body plan evolution, which impacts on our understanding of the evolution of developmental constraint in amniotes (Müller *et al.* 2010).

Here we report an articulated partial postcranial skeleton of a leptocleidid from the Shepherds Chine Member of the Vectis Formation (late Barremian–early Aptian; Kerth & Hailwood 1988). This specimen forms the basis for an improved phylogenetic study focused on resolving the relationships of earliest Cretaceous plesiosaurians, including a detailed discussion of the affinities of *Brancaesaurus*, ‘*Cimoliasaurus*’ *valdensis* and leptocleidids, and new characters devised specifically to resolve long-standing uncertainty on these issues.

Institutional abbreviations

CAMSM: Sedgwick Museum of Earth Sciences, Cambridge, UK; **FMNH:** Field Museum of Natural History, Chicago, USA; **GWWU:** Geomuseum der Westfaelischen Wilhelms-Universitaet, Münster, Germany; **IGNS:** Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand; **LEICS:** New Walk Museum and Art Gallery, Leicester, UK; **MIWG:** ‘Dinosaur Isle’ Museum of Isle of Wight Geology, Sandown, UK; **NHMUK:** Natural History Museum, London, UK; **NZMS:** Geology Museum, University of Otago, Dunedin, New Zealand; **OUMNH:** Oxford University Museum of Natural History, Oxford, UK; **QM:** Queensland Museum, Brisbane, Australia; **SAM:** Iziko South African Museum, Capetown, South Africa; **USNM:** Smithsonian Institution, Washington DC, USA.

Geological setting

The new leptocleidid specimen reported here was discovered in 1995 at Shepherds Chine, in Brighstone Bay on the south-west coast of the Isle of Wight. It was collected from the foreshore at the point where the stream in Shepherds Chine (OS grid reference SZ 4466 7982) discharges to the sea at high water. The specimen comprises three accessioned blocks, each of which was collected independently (a fourth block, containing six partial vertebrae, is currently in private hands). The first block was collected by Mr Warwick Fowler near the top of the beach and close to the reach of the sea. It is worn by erosion and contains only a single partial vertebra, a partial rib and an unidentifiable bone fragment. The second block (‘block one’ in the description) – the largest, and the one containing the majority of elements – was collected by one of the authors (LT) from among a jumble of blocks within the stream bed, approximately 11 m from the chine mouth and 4 m to the west. The third block, containing additional

vertebrae and dorsal ribs, was collected further down the beach by Mrs Hazel Underwood. The material in the blocks is thought to represent a single articulated specimen because all of the elements indicate an individual of the same size, no elements are repeated and the blocks and parts of the specimen approximately fit together (Fig. 1).

The Lower Cretaceous Wealden Group of the Wessex Sub-basin (incorporating the Isle of Wight and coastal Dorset) is famous for the abundant preservation of dinosaur fossils (Martill & Naish 2001). However, the Wessex and Vectis formations of the Wealden Group also yield other vertebrates, including fishes, turtles, pterosaurs, crocodyli-forms and exceptionally rare plesiosaurians (Ketchum 2011). The type section of the Vectis Formation crops out along the south-west coast of the Isle of Wight (Radley & Barker 1998). It consists primarily of clays and shales with thin sandstones, shelly limestones and lenticular mudstone nodules. At the base of the formation, shallow lacustrine and lake-margin sediments dominate the Cowleaze Chine Member. The overlying Barnes High Sandstone Member appears to represent a small lacustrine delta. At the top of the formation, the Shepherds Chine Member is mudstone-dominated: it preserves a low-salinity invertebrate assemblage and represents an exposed regime of broad mudflats and coastal lagoons (Radley 2004, 2006).

The new Vectis Formation plesiosaurian is enclosed in a fine-grained sideritic mudstone nodule. Several bands of mudstone nodules occur in the Shepherds Chine Member. One of these descends to beach level at the mouth of Shepherds Chine and crops out just a few metres from where the largest block was collected, and may have yielded the new specimen. Kerth & Hailwood (1988) showed that a reliably established reverse polarity magnetozone, dubbed by them the Vectis magnetozone, occurred within the Shepherds Chine Member, and that it corresponds either with the Lower Aptian reverse polarity Chron CM-0 or with the Lower Barremian Chron CM-1, with the former being regarded as more likely (Kerth & Hailwood 1988). The Barremian–Aptian transition thus occurs within the Shepherds Chine Member. The new specimen probably originates from the lower, late Barremian part of the unit.

Systematic palaeontology

Sauropterygia Owen, 1860
Plesiosauria de Blainville, 1835
Leptocleididae White, 1940
Vectocleidus gen. nov.

Type species. *Vectocleidus pastorum* gen. et sp. nov.

Diagnosis. As for type and only species.

Vectocleidus pastorum gen. et sp. nov.
Figs 1–3

Diagnosis. Leptocleidid plesiosaurian with autapomorphic dorsal neural spines that are anteroposteriorly short, and successive spines alternate between being transversely compressed, and being expanded to the right. *V. pastorum* additionally differs from *Leptocleidus superstes* in having more gracile clavicles and the anterior process of the coracoid is inflected anterolaterally. The posterior cervical centra are shorter anteroposteriorly than high dorsoventrally, differing from *Brancaesaurus*.

Derivation of name. *Vectocleidus*, a modified combination of *Vectis* (i.e. the Vectis Formation) and *Leptocleidus*; and *pastorum* (Latin: of the shepherds), referring to Shepherds Chine.

Material. The holotype (MIWG 1997.302), a partial postcranial skeleton.

Occurrence. MIWG 1997.302 is from the late Barremian (Lower Cretaceous) part of the Shepherds Chine Member of the Vectis Formation, recorded from Shepherds Chine, Isle of Wight, UK.

Plesiosauria de Blainville, 1835
Pliosauridae Seeley, 1874
Hastanectes gen. nov.

Type species. *Cimoliasaurus valdensis* Lydekker, 1889

Diagnosis. As for type and only species.

Remarks. A new genus is erected here for the species '*Cimoliasaurus*' *valdensis*. The holotype of this taxon was recently redescribed by Ketchum (2011, figs 2, 3) and figured by Kear & Barrett (2011, fig. 8B–H), and its affinities are assessed in the current work. The genus *Cimoliasaurus* (incorrectly spelled as '*Cimoliosaurus*' by Lydekker (1889) when erecting '*Cimoliasaurus*' *valdensis*) is based on undiagnostic remains (Welles 1962). Thus, we make '*C.*' *valdensis* the type species of a new genus *Hastanectes*, forming the new combination *Hastanectes valdensis*. The taxonomic history of the specimen is discussed in detail below (Phylogenetics of other European lowest Cretaceous plesiosaurians).

Hastanectes valdensis Kear & Barrett (2011, fig. 8B–H),
Ketchum (2011, figs 2, 3)

Diagnosis. Plesiosaurian possessing a possible autapomorphy (ventral ridge of cervical centra pierced by subcentral foramina at midlength, and expands anteriorly to form a triangular platform) and unique character combination explained below (Phylogenetics of other European lowest Cretaceous plesiosaurians): a short neck (*c.* 20 cervical vertebrae; one or two may be missing), broadly spaced cervical prezygapophyses, cervical centra with a prominent

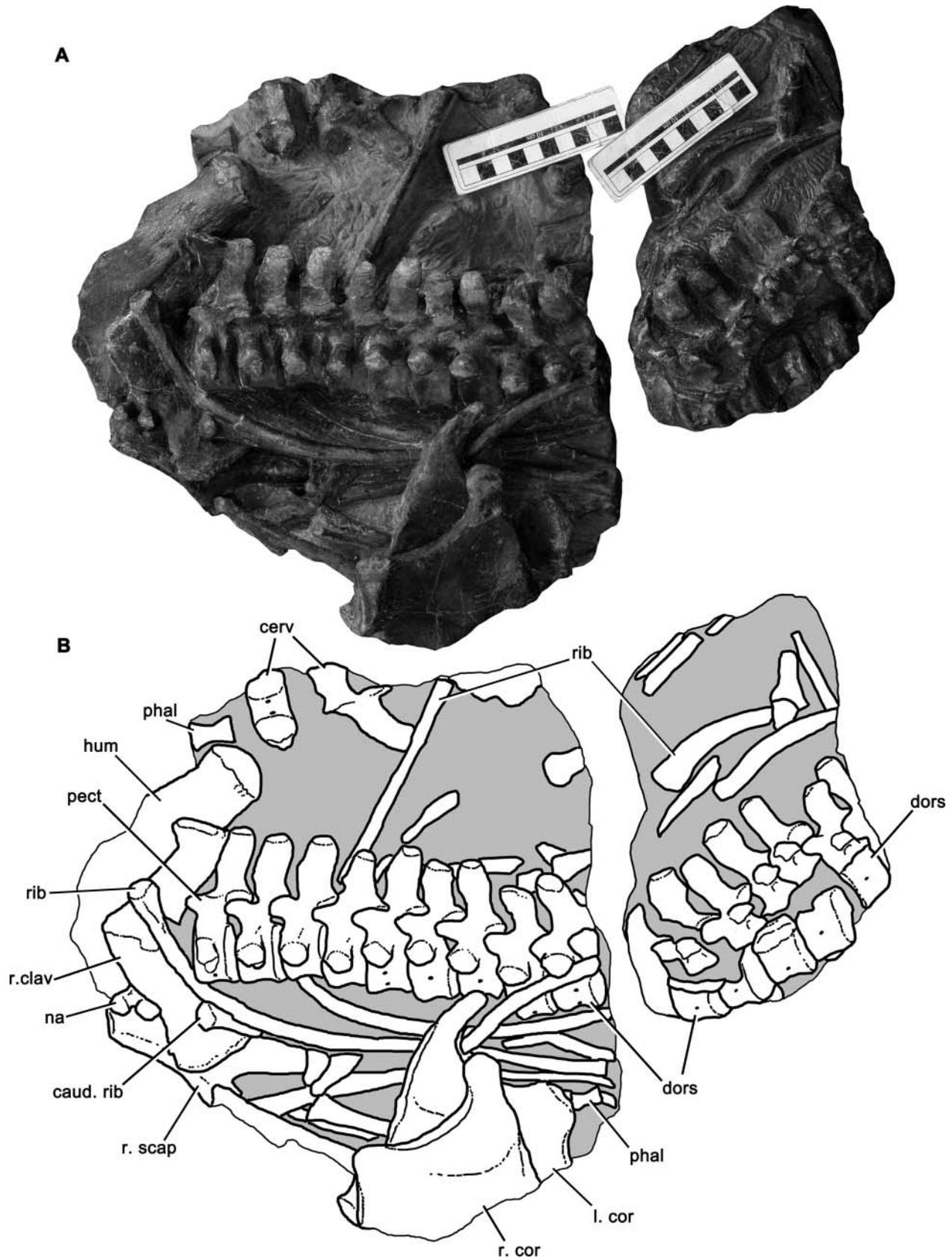


Figure 1. Holotype of *Vectocleidus pastorum* (MIWG 1997.302; blocks one and two). In line drawing (B), grey shading indicates matrix. Abbreviations: caud. rib, caudal rib; cerv, cervical vertebra; clav, clavicle; cor, coracoid; dors, dorsal vertebra; hum, humerus; l., left; na, neural arch; pect, 'pectoral' (anterior dorsal) vertebra; phal, phalanx; r., right; scap, right scapula. Scale bars (in A) 100 mm.

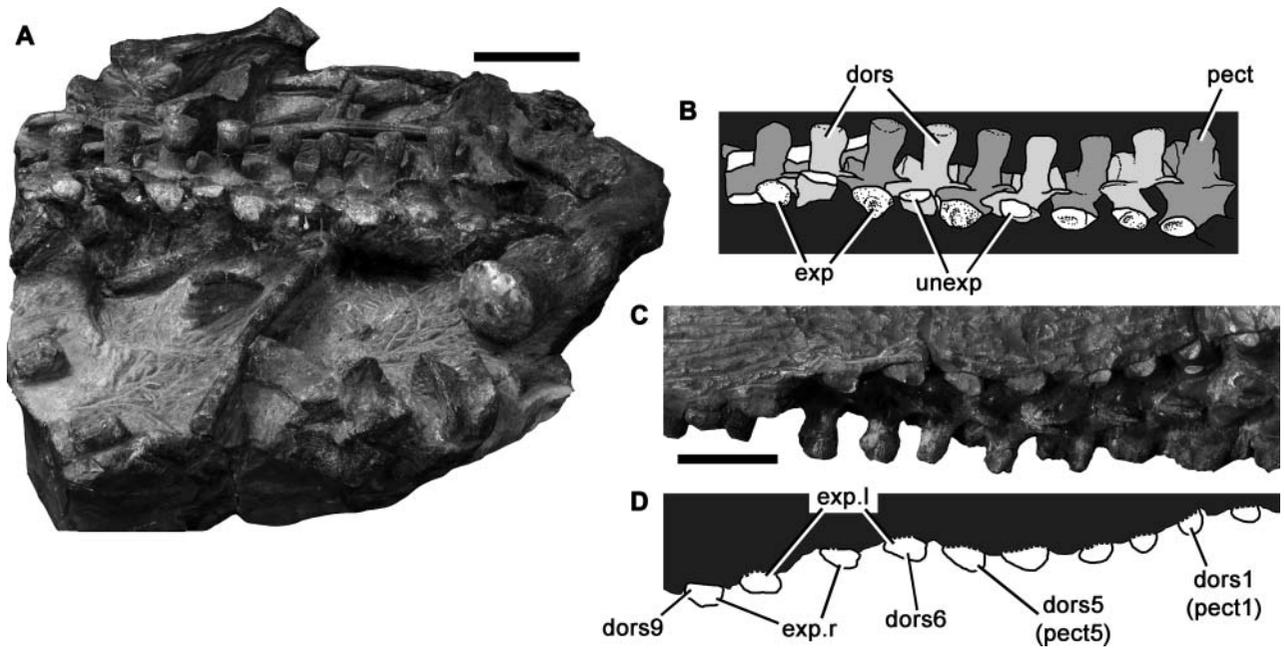


Figure 2. Leptocleidid neural spines in dorsal view showing alternating asymmetrical morphology of apices. **A, B**, holotype of *Vectocleidus pastorum* (MIWG 1997.302; block one); **C, D**, holotype of *Leptocleidus superstes* (NHMUK R4828). In the line drawings (**B, D**) dark grey shading indicates matrix and lighter shades of grey emphasize alternating vertebral morphology. Abbreviations: dors, dorsal vertebra; exp, expanded neural spine apex ('r' indicates expansion to right; 'l' indicates expansion to left); pect, pectoral vertebrae; unexp, transversely compressed neural spine apex. Scale bars 50 mm.

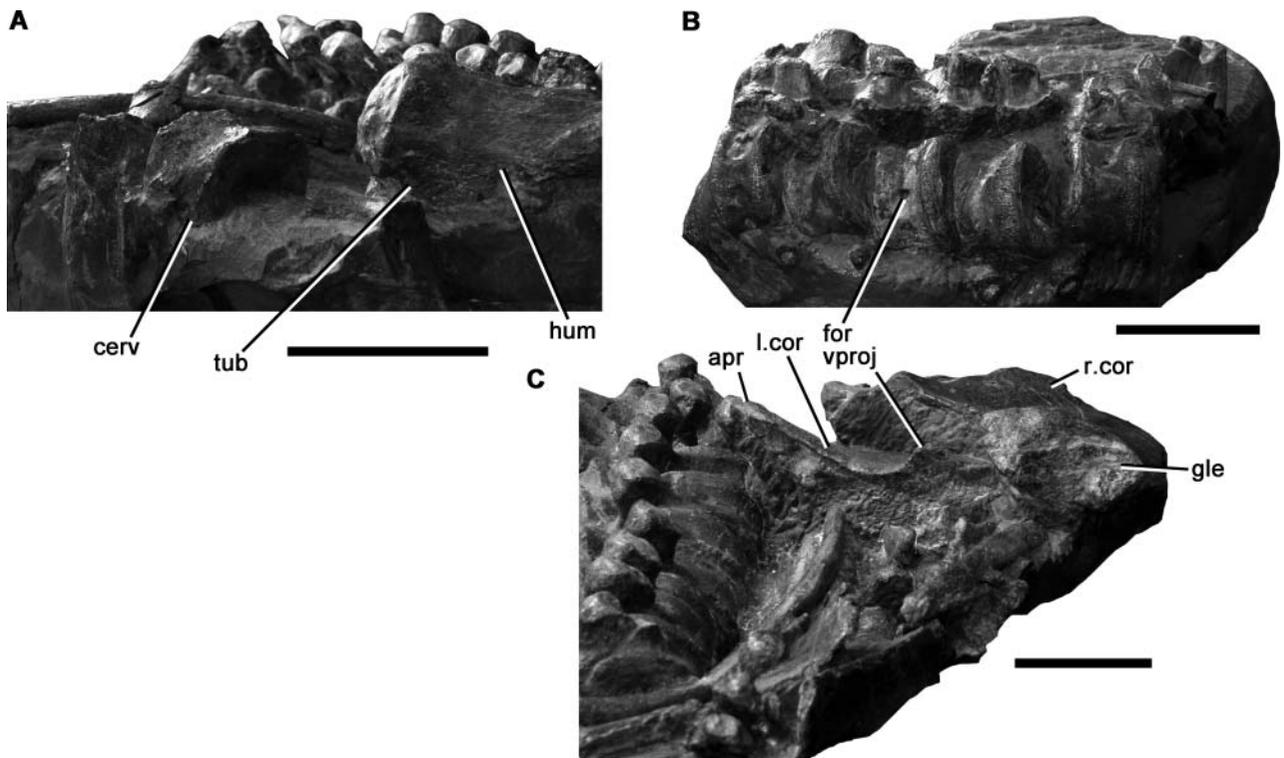


Figure 3. Details of the holotype of *Vectocleidus pastorum* (MIWG 1997.302). **A**, cervical centrum in right anterolateral view and proximal end of humerus in anterior view (block one); **B**, posterior dorsal centra in ventral view (block two); **C**, left coracoid in medial view and right coracoid in lateral view (block one). Abbreviations: apr, anterior process of the coracoid; cerv, cervical vertebra; for, foramen; gle, coracoid portion of glenoid; hum, humerus; l.cor, left coracoid; r.cor, right coracoid; tub, tuberosity of humerus; vproj, ventral projection of the coracoid symphysis. Scale bars 50 mm.

'lip' extending ventrally from the anterior articular surface, a transversely narrow ventral midline ridge on the cervical centra, single-headed rib facets in all cervical vertebrae and a sigmoidal humerus.

Derivation of name. 'Hastings swimmer', combining *Hasta*, referring to Hastings, from where the holotype and several referred specimens were collected and *nektes* (Greek: swimmer).

Material. The holotype (NHMUK R609) comprising a right humerus and 62 vertebrae (cervicals, dorsals, sacrals and caudals; a small number of these vertebrae may represent a second individual; Lydekker 1889); a partial skeleton (NHMUK R5264) including much of the axial column (including the atlas-axis complex), the acetabular portion of an ischium, and some limb bones; and numerous isolated vertebrae NHMUK unregistered, HASMG 992.1.189, 992.1.195, G388.48.

Occurrence. The Wadhurst Clay Formation (Valanginian; Radley 2006), Hastings Group (Weald Sub-basin) of Hastings, Sussex (NHMUK R609 and unregistered cervical vertebrae; Lydekker 1889) and Brenchley, Kent (NHMUK R5264). Referred specimens from Black Horse Quarry (HASMGS specimens) and Hollington, Hastings (e.g. CAMSM B.53464, B. 53480) were also likely collected from the Wadhurst Clay Formation (Benton & Spencer 1995), although collection data for these specimens are incomplete.

Description of *Vectocleidus pastorum*

MIWG 1997.302 is preserved in three blocks (a fourth is owned privately), the two largest blocks are contiguous (Fig. 1). The largest block (designated 'block one' herein; Figs 1, 2A, B, 3A, C) contains two disarticulated cervical vertebrae, nine complete, articulated dorsal vertebrae (including two 'pectoral vertebrae'; *sensu* Seeley 1874), and the anterior portion of a 10th; articulated clavicles, the right scapula, anterior portions of both coracoids, a humerus, a caudal rib, dorsal ribs and two phalanges. The smaller block ('block two'; Figs 1, 3B) contains the posterior portion of a dorsal vertebra (shared with block one), six additional articulated dorsal vertebrae and several dorsal ribs. The final accessioned block ('block three') contains a fragmentary dorsal vertebra and rib. An additional block in private ownership contains a further six vertebrae.

Cervical vertebrae. The most conspicuous cervical centrum is embedded in matrix adjacent to the humeral head so only its dorsal half is exposed (Figs 1, 2A, 3A). The neural arch is missing. The centrum is biconcave, and the anterior surface (Fig. 3A) is deeper than the poste-

rior surface as in *Leptocleidus capensis* and *L. superstes* (Andrews 1922). The centrum is shorter anteroposteriorly than high dorsoventrally, also as in *Leptocleidus* spp., but unlike the anteroposteriorly long cervical centra of *Brancaosaurus* (Wegner 1914). The portion of the neural canal impressed on the dorsal surface of the centrum has an hourglass-shaped outline in dorsal view (Fig. 1). Paired foramina on the dorsal surface of the centrum are located at midlength, immediately medial to the neural arch facets. Due to adhering matrix, it is impossible to determine whether the cervical rib facets were single, as in leptocleidids and many other derived plesiosauroids (Seeley 1892; Brown 1981; O'Keefe 2001; Druckenmiller & Russell 2008b), or divided into separate dorsal and ventral facets by a horizontal groove as in more basal pistosaurians (O'Keefe 2001; Dalla Vecchia 2006).

A second cervical vertebra consists of a disarticulated neural arch exposed in right lateral view (Figs 1, 2A). Its centrum is almost fully enclosed in matrix. The prezygapophyses contact on the midline at their bases and diverge anterolaterally. They have transversely concave facets, the medial portions of which face dorsally, and the lateral portions face dorsomedially. Their posterior midline contact bears an abraded longitudinal ridge. Transversely concave cervical prezygapophyses that contact along the midline only at their bases are also present in *Brancaosaurus* (Wegner 1914) and possibly *Leptocleidus superstes* (NHMUK R4828; the zygapophyses are concave but their medial portions are not visible). In contrast, cryptoclidids (Andrews 1910; Brown 1981), some polycotyliids (*Dolichorhynchops*: FMNH PR 187; Williston 1903) and elasmosaurids (Sato 2002, character 132; Druckenmiller & Russell 2008a, character 109) have transversely concave prezygapophyses that contact along the midline for most of their anteroposterior length. More basal pistosaurians such as *Pistosaurus* (Sues 1987), *Thalassiodracon* (CAMSM J.46986a) and pliosaurids (Andrews 1913; Ketchum & Benson 2011) have planar prezygapophyseal facets that are separated from the midline, placed lateral to the neural canal.

The neural spine is transversely compressed and curves posterodorsally along its length (Figs 1, 2A). This condition also occurs in Lower Jurassic plesiosauroids (Hawkins 1834, plate 25; Owen 1865–1881; Ketchum & Smith 2010), as well as the leptocleidids *Brancaosaurus* (Wegner 1914), *Leptocleidus* spp. (Andrews 1911, 1922) and *Nichollssaura* (Druckenmiller & Russell 2008b). In contrast, pliosaurids (e.g. Andrews 1913) and most plesiosauroids, including polycotyliids, have straight, posterodorsally inclined posterior cervical neural spines (e.g. Williston 1903; Andrews 1910; O'Keefe 2004b), and elasmosaurids and *Muraenosaurus* have anterodorsally inclined neural spines (Andrews 1910; Welles 1943; Hiller *et al.* 2005).

Dorsal vertebrae. Sixteen dorsal vertebrae are preserved in the three blocks under study (Fig. 1). The 10th dorsal vertebra is broken across the join between blocks one and two, and only the anterior portion of the 16th dorsal vertebra is preserved. The anterior 10, and the 15th and 16th dorsal vertebrae are closely articulated. The 11th–14th dorsal vertebrae are only approximately articulated, and their centra are detached from their neural arches.

The most anterior dorsal vertebra is anteroposteriorly short; the anteroposterior width of the centrum is approximately two-thirds of its height. More posterior vertebrae have proportionally longer centra. Most cannot be measured precisely due to adhering matrix and the articulated condition of the column, but the 13th dorsal centrum is approximately three-quarters as long anteroposteriorly as it is high dorsoventrally. The dorsal centra bear two foramina on their lateral surfaces, one located dorsolaterally, the other just ventrolateral to midheight (Fig. 1). The exposed ventral surfaces of the 11th–15th preserved dorsal vertebrae are evenly rounded (Fig. 3B).

The anterior two preserved dorsal vertebrae are ‘pectorals’ (*sensu* Seeley, 1874). They have robust diapophyses which do not project far laterally and are located primarily on the neural arch, but contact the centrum ventrally. In more posterior vertebrae the diapophysis projects further laterally, arches dorsolaterally, and is located solely on the neural arch (Fig. 3). Low ridges extend antero- and posteroventrally along the lateral surface of the neural arch ventral to the diapophysis, enclosing a weak depression. This is also present in *Brancaasaurus* (GWWU A3.B4). The dorsal prezygapophyses of *Vectocleidus* are transversely concave, so their lateral portions are inclined at a steep angle (approximately 60°), but their medial portions are horizontal. The zygapophyses are transversely narrow, measuring just over half the mediolateral width of the centrum (Fig. 2A, B).

The dorsal neural spines are relatively short, approximately equal to the centrum in height (Fig. 1). This is similar to the condition in *Leptocleidus superstes* (Andrews 1922; Kear & Barrett 2011), *Brancaasaurus* (Wegner 1914) and the rhomaleosaurid *Macroplata* (Ketchum & Smith 2010). The dorsal neural spines of *Nichollssaura* are also proportionally short (although the height relative to the centrum cannot be determined because the centra are not visible; Druckenmiller & Russell 2008b). In contrast, most pistosaurians have neural spines that are at least 1.5 times the height of the centrum (Brown 1981; Sander *et al.* 1997; Rieppel 2000). The dorsal neural spines of *Vectocleidus* are transversely compressed, with a slight dorsal expansion in the anterior three preserved vertebrae. However, in more posterior vertebrae this expansion is absent, or the dorsal ends of the spines are expanded to the right (Fig. 2A, B). These conditions alternate so that the fourth, sixth and eighth preserved neural spines are transversely compressed and sheet-like, whereas the fifth, seventh and

possibly also the ninth dorsal neural spines are expanded to the right. The expanded neural spines have a concave dorsal surface, as do posterior cervical and anterior dorsal neural spines of *Leptocleidus superstes* (Druckenmiller & Russell 2008b) and *Brancaasaurus* (Wegner 1914). *L. superstes* and *Brancaasaurus* also show alternating asymmetry in the outline of the anterior dorsal neural spines in dorsal view. The situation in *L. superstes* differs from that in *Vectocleidus* and *Brancaasaurus* however, as all the anterior dorsal neural spines are transversely expanded, and they alternate between being expanded to the right, with a flat left lateral surface and convex right lateral surface, and being expanded to the left (Fig. 2C, D). In *Brancaasaurus* the apices of the neural spines are anteroposteriorly long (Fig. 4E) and thus distinct from the shorter apices of *L. superstes* and *Vectocleidus*. Alternating asymmetry of the dorsal neural spines also present in some rhomaleosaurids (Benson *et al.* 2012), but the combination of morphological features shown by the neural spines of *Vectocleidus* (anteroposteriorly short apices alternately expanded to the right) is autapomorphic.

Caudal rib. A small, flat, paddle-like bone preserved under one of the dorsal ribs may be a single-headed caudal rib (Fig. 1).

Clavicle. The clavicles are dorsoventrally thin, paired elements. The left element overlaps the right anteriorly on the midline (Fig. 1). They are preserved in articulation at the anterior end of the dorsal vertebral series with their triangular posterior portion facing anteriorly. This reversed orientation is congruent with the disarticulated condition of the other pectoral elements. The lateral processes of the clavicles curve dorsolaterally and their distal extremities are slightly expanded anteroposteriorly (Fig. 1). This overall morphology is similar to that in *Leptocleidus superstes* (Andrews 1922; Kear & Barrett 2011), but the clavicles of *Vectocleidus* are more gracile, with a relatively narrower anteroposterior width.

Scapula. The right scapula is embedded in matrix, obscuring all but its medial surface (Fig. 1). The dorsal portion of the scapula blade is not visible so it is impossible to determine whether the blade was broad along its length, or tapered dorsally as in cryptocleidids (Andrews 1910), leptocleidids (Wegner 1914; Andrews 1922; Kear & Barrett 2011) and some polycotylids (Albright *et al.* 2007; Ketchum & Benson 2011). The dorsoventral height of the scapula posterior to the base of the blade is low. This is similar to the condition in cryptocleidids (Andrews 1910), *Brancaasaurus* (GWWU A3.B4) and *Leptocleidus superstes* (Andrews 1922; Kear & Barrett 2011). A prominent lateral shelf of the scapula is present in *Vectocleidus* and the leptocleidids *Brancaasaurus* (GWWU A3.B4), *Leptocleidus superstes*, *Nichollssaura* and *Umoonasaurus* (Druckenmiller & Russell 2008a, character 124). This shelf is also present in

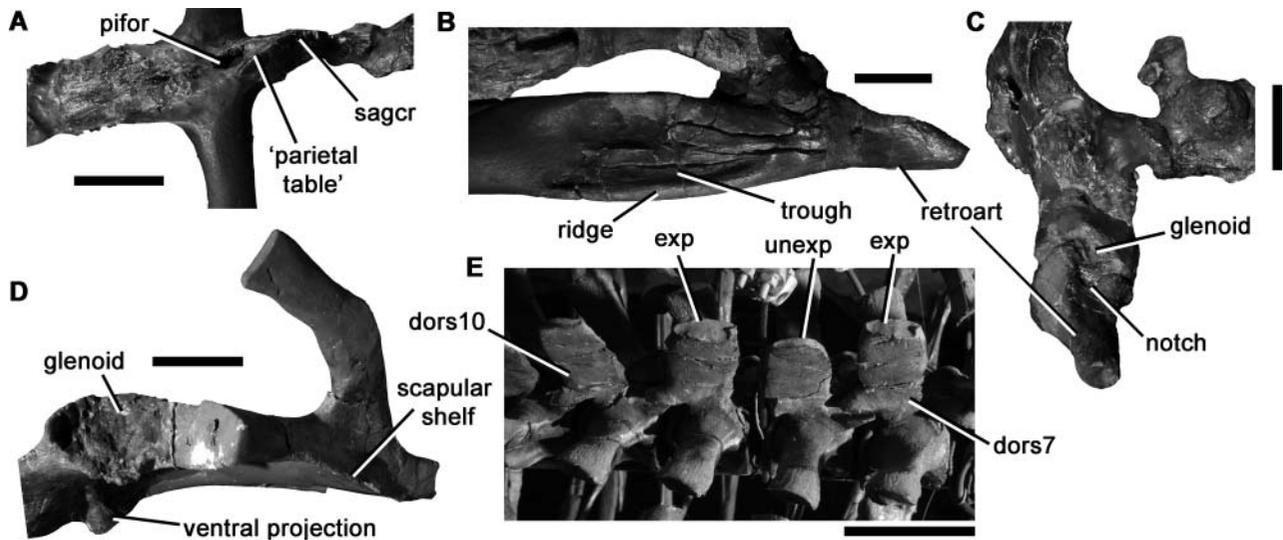


Figure 4. Previously undescribed leptocleidid features of the holotype of *Brancasaurus* (GWWU A3.B4). **A**, parietal in left dorsolateral view; **B**, posterior portion of left mandible in lateral view; **C**, posterior portion of left mandible in posterodorsal view; **D**, anterior portion of pectoral girdle in right lateral view; **E**, dorsal vertebrae 7–10 in right dorsolateral view. Abbreviations: dors, dorsal vertebra; exp, expanded neural spine apex; pifor, pineal foramen; retroart, retroarticular process; sagcr, sagittal crest; unexp, transversely compressed neural spine apex. Scale bars 20 mm (A–C) and 50 mm (D, E).

pliosauroids (Ketchum & Benson 2010, character 146) and other Lower Jurassic plesiosauroidea (e.g. *Occitanosaurus*, Bardet *et al.* 1999; *Microcleidus*, MMUM LL 7135).

Coracoid. The anterior portions of both coracoids are preserved, including the midline symphysis, anterior process and the glenoid. They are exposed in ventral view, and the right coracoid covers a large portion of the left (Fig. 1). The anterior process is transversely narrow and anteroposteriorly long, as in other derived plesiosauroidea (Williston 1903; Andrews 1910; Welles 1943; Ketchum & Benson 2010, character 150), but unlike the transversely broad condition in most plesiosauroidea (e.g. *Eurycleidus* NHMUK 2028/9, *contra* Andrews 1922; *Macroplata*, Ketchum & Smith 2010), and short, triangular morphology of most elasmosaurids (Welles 1943; Hiller *et al.* 2005) and pliosaurids (Andrews 1913). In *Vectocleidus*, the anterior portion of the anterior process is deflected anterolaterally. This is also present in the polycotyloid *Trinacromerum* (*'Ceraunosaurus brownorum'*; Thurmond 1968) and perhaps also in *Brancasaurus* (Sato 2002, character 161), although the coracoid is heavily restored (Wegner 1914). A broad, anteromedially curving, transverse ridge on the ventral surface of the coracoid of *Vectocleidus* forms the posterior margin of a shallow anterior depression. This ridge extends to the medial contact surface where it forms a distinct ventral projection (Fig. 3C). This projection is also present in *Brancasaurus* (Fig. 4D) and elasmosaurids (e.g. Welles 1943, 1962), including the basal taxon *Wapuskaneptes*, in which it is very prominent (Druck-

emiller & Russell 2006). The projection is apparently absent in *L. superstes* (NHMUK R4828), but this may be due to partial reconstruction of the damaged specimen.

Humerus. The humerus is exposed in ventral view (Fig. 1). Its distal end is strongly expanded, but a substantial anterodistal portion is broken and missing. The proximal articular surface forms a subspherical dome, delimited from the humeral shaft by a pronounced lip. The tuberosity extends into the matrix on the dorsal surface of the proximal humerus (Fig. 3A).

Discussion

Leptocleidid affinities of *Vectocleidus*

Comparative appraisal of *Vectocleidus* suggests leptocleidid affinities. Detailed comparative data and supporting citations are given in the description (above) and the list of new and modified characters for our phylogenetic analysis (Online Supplementary Material Appendix). This information is summarized here.

Several features of *Vectocleidus* suggest affinities among derived plesiosauroidea. The presence of transversely concave cervical prezygapophyses that are not widely separated on the midline is uniquely shared with elasmosaurids, cryptocleidids, and some polycotyloids and leptocleidids. These families form a derived clade within Plesiosauroidea according to Ketchum & Benson (2010) (note, however, that

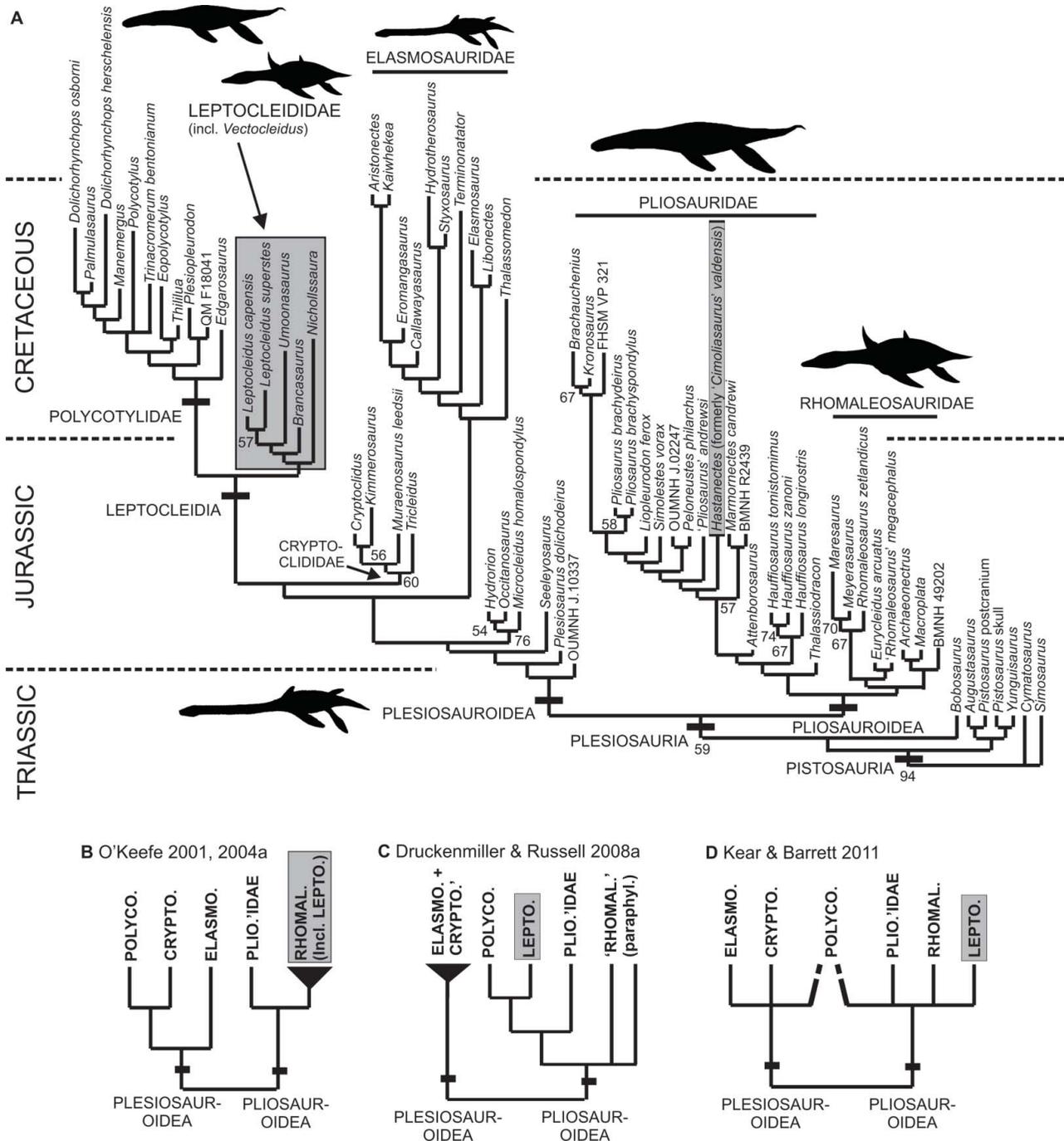


Figure 5. Phylogenetic results. **A**, time-calibrated strict reduced consensus of trees derived from analysis of the modified dataset of Ketchum & Benson (2010, 2011). *Vectocleidus* was recovered as a wildcard taxon (Wilkinson 2003), occupying multiple possible positions within Leptocleididae. *Hastanectes* was recovered as a pliosaurid. Bootstrap support values >50% are given below nodes. Silhouettes indicate common approximate body proportions within selected clades. **B–D**, summary of previous hypotheses on leptocleidid affinities showing relationships among major plesiosaurian clades recovered by: **B**, O'Keefe (2001, 2004a); **C**, Druckenmiller & Russell (2008a) and **D**, Kear & Barrett (2011). All previous authors considered leptocleidids as pliosauroids.

alternative phylogenetic analyses have not recovered a clade comprising all four of these families (Fig. 5B–D; O'Keefe 2001; Druckenmiller & Russell 2008a; Smith & Dyke 2008; Kear & Barrett 2011)). The transversely narrow anterior

processes of the coracoids of *Vectocleidus* are uniquely shared with cryptocleidids, polycotylids, leptocleidids and the basal elasmosaurid *Wapuskaneetes* (Druckenmiller & Russell 2006). In cryptocleidids the process is dorsoventrally

thick, whereas in polycotyliids, leptocleidids and *Vectocleidus* it is dorsoventrally thin.

Among derived plesiosauroids, *Vectocleidus* uniquely shares three features with leptocleidids (*sensu* Ketchum & Benson 2011): cervical prezygapophyses that only contact across the midline at their bases; posterodorsally curving posterior cervical neural spines (also present in most pliosauroids and basal plesiosaurians); short dorsal neural spines, equal to the centrum in height (also present in the rhomaleosaurid *Macroplata*). Furthermore, an alternating, asymmetrical morphology of the dorsal neural spine apices has only been reported in *Brancaasaurus*, *Leptocleidus*, *Vectocleidus* and some rhomaleosaurids (Benson *et al.* 2012).

Phylogenetic analysis

To test the phylogenetic position of *Vectocleidus* and other Lower Cretaceous plesiosaurians, we analysed a modified version of the data set of Ketchum & Benson (2011; updated from Ketchum & Benson 2010; Benson *et al.* 2011a). Four characters were modified and 15 were added, including nine new characters and five taken from previous studies (Sato 2002; Smith & Dyke 2008). A description of rescored, modified and new characters is given in the Online Supplementary Material Appendix. *Vectocleidus* and *Hastanectes* (formerly '*Cimoliosaurus*' *valdensis*) were added to the matrix. '*Plesiosaurus*' *macrocephalus* and OUMNH J.28585 were deleted from the matrix as they are represented by juvenile individuals with high proportions of missing data. These changes resulted in a matrix of 70 taxa and 216 characters. A nexus file of the matrix is found in the Online Supplementary Material.

We analysed the dataset using PAUP 4.0b10 for Macintosh (Swofford 2002), using PAUPRat (Sikes & Lewis 2001) followed by Tree Bisection and Reconnection (TBR) branch swapping as described by Ketchum & Benson (2010). Several characters were scored using gap weighting (Thiele 1993; see Ketchum & Benson 2010). The analysis recovered 14 most parsimonious trees (MPTs) of length 20120 steps. The strict consensus was well resolved, other than within Leptocleididae, in which *Nichollssaura* is the sister taxon of a polytomy comprising *Brancaasaurus*, *Leptocleidus capensis*, *Leptocleidus superstes*, *Umoonasaurus* and *Vectocleidus*. This results from the unstable position of *Vectocleidus*, which is found equally parsimoniously in multiple positions within Leptocleididae. Implementation of strict reduced consensus (Wilkinson 2003) by pruning *Vectocleidus* from the set of MPTs resulted in a reduction to two unique topologies and full resolution within Leptocleididae (Fig. 5A). Therefore, although *Vectocleidus* can be confidently identified as a leptocleidid, its affinities within the clade cannot currently be resolved.

Hastanectes was recovered within Pliosauridae as the sister taxon of the clade comprising '*Pliosaurus*' *andrewsi* and all more derived pliosauroids (Fig. 5). This basal position

relative to other Cretaceous pliosauroids (Brachaucheninae) results from the retention of plesiomorphic features such as a narrow ventral keel in the cervical centra (Ketchum 2011).

Phylogenetic position of leptocleidids

The phylogenetic position of leptocleidids has been controversial. Most authors suggest pliosauroid affinities (Andrews 1922; Persson 1963; Cruickshank 1997; Cruickshank & Long 1997; O'Keefe 2001; Smith & Dyke 2008; Druckenmiller & Russell 2008a; Kear & Barrett 2011). However, this suggestion has typically been based on comparisons with the fragmentary *Leptocleidus superstes* (Andrews 1922; Kear & Barrett 2011) and *L. capensis* (Andrews 1911; Cruickshank 1997). The phylogenetic analysis of Ketchum & Benson (2010, 2011), modified herein (above) indicates affinities with cryptoclidian plesiosauroids, in a leptocleidid clade that is larger than that obtained by other analyses, including more completely known taxa such as *Brancaasaurus* and *Nichollssaura*.

Andrews (1922) suggested that leptocleidids represented a primitive radiation of freshwater plesiosaurians. This inference was based on the supposedly primitive configuration of the pectoral girdle shared with pliosauroids such as *Eurycleidus arcuatus* ('*Plesiosaurus arcuatus*'), in which the clavicle–interclavicle complex is large and the scapulae do not contact each other anteromedially. Andrews (1922, p. 297) also noted this morphology in the polycotyliid *Dolichorhynchops* (Williston 1903, pl. 13), on which basis Andrews (1922) and Welles (1962) proposed a relationship between *Leptocleidus* and polycotyliids (which Andrews (1922) also considered as plesiomorphic relicts). Thurmond (1968) later observed additional features shared by *Leptocleidus* and the basal polycotyliid *Trinacromerum* ('*Ceraunosaurus*'). Polycotyliids have subsequently been shown to share numerous synapomorphies with derived plesiosauroids (Bakker 1993; Carpenter 1997; O'Keefe 2001; Ketchum & Benson 2010; but see Druckenmiller & Russell 2008a; Smith & Dyke 2008; Benson *et al.* 2011a). This results in conflicting hypotheses: leptocleidids are either primitive pliosauroids related to rhomaleosaurids, or derived plesiosauroids related to polycotyliids. Druckenmiller & Russell (2008a) were the first to demonstrate a relationship between leptocleidids and polycotyliids in a phylogenetic analysis, although they found both clades within Pliosauroidae (i.e. more closely related to rhomaleosaurids than to plesiosauroids). We observe that the pectoral girdle of leptocleidids is uniquely similar to rhomaleosaurids in only one respect: the anterior margin of the interclavicle is transversely broad and weakly concave (Wegner 1914; Andrews 1922; Smith 2007; Ketchum & Smith 2010; Kear & Barrett 2011). This differs from the plesiomorphic condition of a transversely narrow, deeply concave anterior margin (e.g. Storrs 1997; Smith & Vincent 2010), and from the anteriorly pointed condition of elasmosaurids and

polycotylics (Sato 2002, character 153; Druckenmiller & Russell 2008a, character 121).

Persson (1963) suggested that *Leptocleidus* represented a ‘rhomaleosaurian’, based on the similar body proportions and the presence of a rostral constriction of the snout. Cruickshank (1997, p. 221) noted three derived characters of the skull supporting this relationship:

1. A dorsomedian ‘foramen’ or cleft between the posterior processes of the premaxillae. However, this feature may in fact be absent in leptocleidids (*L. superstes*: Kear & Barrett 2011). Smith & Dyke (2008; Online Supplementary Material Appendix) thought that the well-defined foramen of derived rhomaleosaurids was distinct from the shallow cleft of *L. capensis*, a condition that is widely distributed among plesiosaurians.
2. Dorsomedian troughs on the articulators and prearticulators. However, these are shallow and weakly developed in rhomaleosaurids (Cruickshank 1994), whereas in *L. capensis* (Cruickshank 1997) and polycotylics (O’Keefe 2008) a dorsoventrally expanded portion of the prearticular bears a broad depression or rugosity. The condition in rhomaleosaurids is more similar to the condition in other basal plesiosaurians such as *Hauffiosaurus* (Benson *et al.* 2011a) and is not similar to the condition in derived leptocleidids and polycotylics.
3. Prominent posteroventral process of the postorbital. However, in *L. capensis*, *Brancaosaurus* (Wegner 1914) and *Nichollssaura* (Druckenmiller & Russell 2008b) this feature extends approximately one-third the length of the temporal fenestra posteriorly (Cruickshank 1997). It is substantially less prominent than the plesiomorphic posteroventral process of rhomaleosaurids (Andrews 1896; Smith 2007) and other basal plesiosaurians (Storrs 1991, character 17; Rieppel *et al.* 2002), that extends posteriorly for greater than half the length of the fenestra. In plesiosaurids and most derived plesiosauroids the posteroventral process is shorter, or absent (O’Keefe 2004a, character 168; Ketchum & Benson 2010, character 33). The ‘intermediate’ condition in *L. capensis*, *Nichollssaura* and possibly *Brancaosaurus*, may be a leptocleidid synapomorphy. However, even if it is lumped in with the plesiomorphic condition shown in rhomaleosaurids and more basal plesiosaurians, then it is plesiomorphic, and does not provide positive evidence for a relationship between rhomaleosaurids and leptocleidids. Other features shared by rhomaleosaurids and leptocleidids, such as the subtriangular skull outline, rostral constriction of the snout (“rosette of intermeshing teeth”) and conical tooth shape were regarded as primitive by Cruickshank (1997), and are widely distributed among robust plesiosaurians.

It is clear from the above discussion that the number of features shared between rhomaleosaurids and leptocleidids has been overstated. Global cladistic analyses of Plesiosauria have generally recovered *Leptocleidus* and potentially related Early Cretaceous taxa with similar body proportions (*Nichollssaura*, *Umoonasaurus*) as plesiosauroids (Fig. 5B–D; O’Keefe 2001; Druckenmiller & Russell 2008a; reviewed by Ketchum & Benson 2010; Kear & Barrett 2011). The case for plesiosauroid affinities has been stated several times (Cruickshank 1997; Kear & Barrett 2011), and alternatives have been neglected and strongly criticised (Kear & Barrett 2011). Here we summarize the evidence for plesiosauroid affinities of leptocleidids, including novel anatomical observations. Important components of this argument are: (1) leptocleidid monophyly, and the fact that the less fragmentary leptocleidids such as *Brancaosaurus* and *Nichollssaura* show numerous plesiosauroid synapomorphies; (2) the likely existence of a clade comprising Leptocleididae and Polycotylicidae (Leptocleidia), which shares synapomorphies with cryptocleidid plesiosauroids forming the inclusive clade Cryptocleidia; and (3) stratigraphic consistency, which is improved if leptocleidids are derived plesiosauroids on the Early Cretaceous polycotylic lineage rather than primitive plesiosauroids that survived 55 million years from the earliest appearance of Rhomaleosauridae (e.g. Cruickshank 1994) and Pliosauridae (Benson *et al.* 2011b), or 25 million years from the last appearance of Rhomaleosauridae (Gasparini 1997).

Leptocleidid monophyly, inclusion of *Brancaosaurus*.

The most recent version of the analysis of Ketchum & Benson (2011) recovered a monophyletic Leptocleididae comprising *L. capensis*, *L. superstes*, *Brancaosaurus*, *Nichollssaura* and *Umoonasaurus*. Previous analyses recovered reduced taxonomic subsets within Leptocleididae (Druckenmiller & Russell 2008a; Smith & Dyke 2008; Kear & Barrett 2011). However, the leptocleidid affinities of *Brancaosaurus* provide particularly compelling evidence for plesiosauroid relationships as it is known from an almost complete skeleton. *Brancaosaurus* has uniformly been considered as a derived plesiosauroid based on its long neck, comprising 37 cervical vertebrae, and the presence of plesiosauroid synapomorphies (Wegner 1914; O’Keefe 2001, 2004a; Ketchum & Benson 2010). Most previous authors considered *Brancaosaurus* to be an elasmosaurid (e.g. Wegner 1914; Brown 1981; O’Keefe 2004a; Kear & Barrett 2011). However, analysis of the dataset of Ketchum & Benson (2010) revealed that trees placing *Brancaosaurus* within Elasmosauridae were significantly longer than those in which it was a leptocleidid (Ketchum & Benson 2010; using Templeton’s test; Templeton 1983; Kitching *et al.*, 1998). Importantly, the large posterior intercoracoid vacuity reconstructed in plaster by Wegner (1914) and also present

in many elasmosaurids (Welles 1943) may not be present in *Brancaasaurus* (Welles 1962; Ketchum & Benson 2010).

Brancaasaurus was described in detail by Wegner (1914), and examined directly during the course of the present study (GWWU A3.B4; Fig. 4). It shares several features with other leptocleidids: the anterior two premaxillary alveoli are substantially reduced relative to more posterior alveoli (*L. capensis*, Cruickshank 1997); a long posteroventral process of the postorbital approximately one-third the length of the temporal fenestra (leptocleidids; Cruickshank 1997; Druckenmiller & Russell 2008b; Kear & Barrett 2011); posteriormost cervical neural spines with suboval, concave dorsal surfaces (Wegner 1914; *L. superstes*, NHMUK R4828; Druckenmiller & Russell 2008b); a scapular shelf (Fig. 4D); and proximodistally long epipodials (Andrews 1911). Three of these leptocleidid features are described and compared above in *Vectocleidus*: posterior cervical neural spines curve posterodorsally (also present in basal plesiosaurians); dorsal neural spine apices with alternating, asymmetrical morphology (Fig. 4E); and dorsal neural spines short, subequal to the height of the centrum (also present in the rhomaleosaurid *Macropata*; Ketchum & Smith 2010). *Brancaasaurus* also lacks any particular derived features of elasmosaurids or other plesiosaurian clades.

Our examination reveals two additional features suggesting leptocleidid affinities for *Brancaasaurus*. Firstly, a triangular fossa with a posteriorly directed apex separating the pineal foramen from the anterior end of the sagittal crest on the dorsal surface of the parietal (Fig. 4A). This was considered an autapomorphy of the leptocleidid *Nichollssaura* by Druckenmiller & Russell (2008b; 'parietal table') and is uniquely shared by the two taxa. Secondly, a deep notch on the dorsal surface of the articular immediately posterior to the glenoid (Fig. 4C). This was observed in the polycotyliids *Edgarosaurus* and *Dolichorhynchops* by Ketchum & Benson (2010, character 104), and may also be present in *Leptocleidus capensis* (based on photographs of SAM PK 5822 provided by L. Porro). The condition has not been determined in any other leptocleidids, but it is absent in all other plesiosaurians, including cryptocleidids (e.g. Andrews 1910) and elasmosaurids (*Kaiwhekea*, NZMS 260; *Turangisaurus*, IGNS CD426).

Leptocleididae as the sister clade to Polycotyliidae. Druckenmiller & Russell (2008b, 2009) described *Nichollssaura*, a short-necked (24 cervical vertebra) plesiosaurian from the Albian (Early Cretaceous) of Canada known from an almost complete skeleton. Druckenmiller & Russell (2008b) noted its similar stratigraphic age, small size (*c.* 3 metres) and body proportions shared with *Leptocleidus*, *Umoonasaurus* and polycotyliids. They also made numerous comparisons between *Nichollssaura* and these taxa, demonstrating shared features such as a dorsomedian crest on the premaxilla, prominent lateral shelf of the scapula, the proportions of the ischium (with *Lepto-*

cleidus and *Umoonasaurus*), a ventrally dished pterygoid and a squared pterygoid lappet (with polycotyliids; the squared pterygoid lappet is also present in derived rhomaleosaurids). Correspondingly, subsequent phylogenetic analyses recovered *Nichollssaura* as a representative of a new clade comprising Polycotyliidae and Leptocleididae (Leptocleidia), either as a basal polycotyliid (Druckenmiller & Russell 2008a) or leptocleidid (Smith & Dyke 2008; Ketchum & Benson 2010, 2011). This finding is significant because, despite their pliosauromorph body proportions, polycotyliids share numerous features with plesiosauroids (Bakker 1993; Carpenter 1997; primarily based on comparisons with elasmosaurids), especially cryptocleidids (O'Keefe 2001, 2004b). These have caused them to be recovered as derived plesiosauroids by several phylogenetic analyses (O'Keefe 2001; Ketchum & Benson 2010, 2011).

Kear & Barrett (2011) regarded the position of Polycotyliidae as plastic within Plesiosauria, suggesting that leptocleidids were consistently recovered as pliosauroids and may not be related to polycotyliids. However, since the work of Druckenmiller & Russell (2008a, b, 2009), all phylogenetic analyses incorporating new anatomical data have recovered a monophyletic Leptocleidia. This clade is stable, regardless of its affinities within Pliosauroidea (Druckenmiller & Russell 2008a; Smith & Dyke 2008; Benson *et al.* 2011a) or Plesiosauroidea (Ketchum & Benson 2010, 2011). During the present study we observed several new synapomorphies of Leptocleidia:

1. The parietal is transversely flared posteriorly so its contact with the squamosal arch is more than half the width of the posterior cranium (e.g. Cruickshank 1997; Druckenmiller 2002; Bardet *et al.* 2003; Sato 2005). This is unlike the narrower 'lateral angle' morphology of the posterior parietal described in rhomaleosaurids and basal pistosaurians by Smith & Dyke (2008, character 29).
2. A dorsoventrally broad longitudinal trough occupies the lateral surface of the mandible, bounded dorsally and ventrally by robust lateral ridges (Fig. 4B). Usually the ventral ridge is prominent but the dorsal ridge is less pronounced (e.g. Bardet *et al.* 2003, fig. 3; Druckenmiller & Russell 2008b, fig. 9; O'Keefe 2008, fig. 3; *Brancaasaurus*, GWWU A3.B4). This morphology is also present in derived rhomaleosaurids (Gasparini 1997; Smith & Vincent 2010) and the pliosaurid *Hauffiosaurus* (Benson *et al.* 2011a). It is absent in most pliosaurids, including the basal taxon *Thalassiodracon* (Benson *et al.* 2011b).
3. S-curved humerus. Albright *et al.* (2007, character 18) and O'Keefe (2008) described a 'sigmoidal' humerus as a polycotyliid synapomorphy. Indeed, derived polycotyliids possess a highly S-curved humerus in which the head is inclined anteroproximally (O'Keefe

2004b, 2008). However, a weakly S-curved humerus is present in many leptocleidids (Wegner 1914; Kear & Barrett 2011) and basal polycotyliids (e.g. Albright *et al.* 2007). The status of this character is difficult to assess as it is absent in *Nichollssaura* (Druckenmiller & Russell 2008b).

4. Posterior portion of skull table abruptly raised dorsally. Several previous authors have noted a ‘cockscorn’ morphology of the squamosal arch in *Leptocleidus superstes* and *L. capensis*, wherein the posterior portion of the skull table is raised dorsally and produces an anteriorly oriented spur (Cruickshank & Long 1997; Sato 2002, character 73; Druckenmiller & Russell 2008a, character 35; Ketchum & Benson 2010, character 43). Although other leptocleidians lack the anterior spur, the squamosal arch is raised dorsally (Williston 1903; Wegner 1914; Carpenter 1996, fig. 2; Sato 2005). This morphology is absent in *Nichollssaura* (Druckenmiller & Russell 2008b) and all non-leptocleidian plesiosaurians (e.g. Andrews 1910, 1913; Welles 1943; Taylor 1992) except the Lower Jurassic large-skulled specimen NHMUK 49202 (*Plesiosaurus macrocephalus*).

Plesiosauroid features of leptocleidids. Leptocleidids share several synapomorphies with derived plesiosauroid clades that have not been observed previously. Here we focus on those features known in *Leptocleidus* spp., although additional features are present in *Brancaasaurus* (Wegner 1914) and *Nichollssaura* (Druckenmiller & Russell 2008b), and features present in Polycotyliidae suggesting plesiosauroid relationships (e.g. Bakker 1993; Carpenter 1997; O’Keefe 2001) lend extra support to this relationship. Two of the plesiosauroid features known in *Leptocleidus* spp. were described above: the cervical prezygapophyses are transversely concave and close to the midline; and the anterior process of the coracoid is anteriorly long and transversely narrow. Several others can be added to this list:

1. The cervical ribs articulate with single, undivided facets (e.g. Seeley 1892; Welles 1962; Brown 1981). The posterior cervical vertebrae of pliosaurids also have this morphology (only known in *Brachauchenius*, *Marmornectes* and *Stretosaurus*; Williston 1907; Tarlo 1959; Ketchum & Benson 2011). However, the anterior–middle cervical vertebrae of most pliosaurids have double-headed ribs (e.g. Andrews 1913), or are not known (in *Brachauchenius*, USNM 2361, 4989). *Hastanectes valdensis*, recovered here as a pliosaurid (see below), is one exception as all of its cervical ribs are single-headed. However, a relationship between leptocleidids and derived pliosaurids has never been suggested.
2. The anterior margin of the scapular blade is almost straight, so the primitive posterodorsal inflection (retained by pliosauroids; Ketchum & Benson 2011) is very weak or absent. The right scapula of *L. superstes* figured by Andrews (1922, pl. 15, fig. 3) and Kear & Barrett (2011, fig. 4D, in medial view, *contra* Kear & Barrett 2011) is broken at midlength and has been poorly mended so as to give the appearance of a pronounced inflection. This inflection is very weak in the well-preserved right scapular blade. Some polycotyliids have independently derived an inflected scapular blade (O’Keefe 2008).
3. The scapula blade tapers dorsally, as in cryptocleidids (Ketchum & Benson 2011; e.g. Andrews 1910).
4. The dorsal surface of the coracoid lacks a shallow depression anteriorly. In basal pistosaurians a robust, transversely oriented buttress on the dorsal surface of the coracoid connects the glenoid to a thickened portion of the midline symphysis (e.g. pliosaurids, Andrews 1913; *Eurycleidus*, Andrews 1922; *Pistosaurus* and ?*Plesiosaurus*, Sues 1987). A broad depression marks the dorsal surface of the coracoid anterior to this buttress. In ‘microcleidids’ (Bardet *et al.* 1999); elasmosaurids (Welles 1943; Sachs 2005), cryptocleidids (Andrews 1910) and polycotyliids (Williston 1903; Sato 2005) the buttress is located further anteriorly so that the depression is absent. This morphology is also present in the leptocleidids *Brancaasaurus* (Wegner 1914) and *Leptocleidus* (NHMUK R4828). Its identification requires an accurate assessment of the orientation of the coracoid because a depression can also be present anteriorly on the ventral surface of the coracoid (e.g. Kear & Barrett 2011, fig. 4B, C (coracoids figured as ‘clavicles’)).

Kear & Barrett (2011) listed four features distinguishing *Leptocleidus* from “long-necked Plesiosauroides”: (1) a prominent ectopterygoid flange; (2) anterior cervical centra shorter than high; (3) cervical zygapophyses subequal to width of centrum; and (4) cervical neural spines lacking posterior articulations but displaying a distinct backwards slope. However, the absence of features (2–4) in extremely long-necked taxa possibly representing three independent lineages (e.g. *Microcleidus* Owen 1865–1881; elasmosaurids, Welles 1943; *Muraenosaurus*, Andrews 1910; *Occitanosaurus*, Bardet *et al.* 1999) likely relates to functional constraints, so their absence in short-necked *Leptocleidus* is not surprising. Most of these features are also present in other short-necked plesiosauroids such as *Tricleidus* and polycotyliids (e.g. Williston 1903; Andrews 1910; Storrs 1997; O’Keefe 2004b) and thus their presence in *Leptocleidus* does not preclude plesiosauroid affinities for leptocleidids. Furthermore, an ectopterygoid flange with identical morphology to that of *Leptocleidus superstes* is present in the long-necked plesiosauroid *Microcleidus*

(NHMUK 36184), and a very prominent, rugose ectopterygoid flange is present in the extremely long-necked elasmosaurid *Libonectes* (P. S. Druckenmiller, pers. comm. 2011).

Phylogenetics of other European lowest Cretaceous plesiosaurians

Other than the leptocleidids discussed above, few lowest Cretaceous (Berriasian–Barremian) plesiosaurians are known from more than isolated, fragmentary elements. All recent assessments concur that these remains represent a range of plesiosauroid and pliosauroid clades, although their precise affinities are unclear (Kear & Barrett 2011; Ketchum 2011). The only possibly valid taxon is ‘*Cimoliasaurus*’ *valdensis*, for which the new monotypic genus *Hastanectes* was erected above (Systematic palaeontology). *H. valdensis* is known from two partial skeletons, primarily comprising vertebrae, and several additional isolated vertebrae (Lydekker 1889). Although this material was considered undiagnostic by Welles (1962) and Kear & Barrett (2011), Ketchum (2011) described and figured a highly characteristic combination of characters that rendered it distinct from other plesiosaurians. Specifically, *H. valdensis* possesses a short neck comparable to those of polycotyliids and pliosaurids (*c.* 20 cervical vertebrae; the exact count is uncertain as one or two may be missing), and cervical centra with a prominent ‘lip’ extending ventrally from the anterior articular surface, a unique synapomorphy of derived pliosaurids (Tarlo 1960; Ketchum & Benson 2011, character 189). *H. valdensis* combines these features with others that are absent in most pliosaurids, such as a transversely narrow ventral midline ridge on the cervical centra, single-headed rib facets on all cervical vertebrae and a sigmoidal humerus. Also, *H. valdensis* lacks various features of derived plesiosauroids such as polycotyliids including the hypophyseal ridge of the atlas–axis complex and cervical zygapophyses that contact on the midline (they are widely spaced either side of the neural canal in *H. valdensis*). Unlike in leptocleidids, the cervical neural spines of *H. valdensis* are not curved. The morphology of the ventral ridge on the cervical centra of *H. valdensis* may be autapomorphic as it expands anteriorly to form a triangular platform and is penetrated at its midlength by the subcentral foramina, which are often more widely spaced in plesiosaurians (Ketchum 2011). On the basis of the observations summarized here, we contend that *H. valdensis* is a valid taxon (following Ketchum 2011), which is recovered as a pliosaurid in our phylogenetic analysis.

Evolution of neck length in Plesiosauria

Most previous studies have assigned either leptocleidids or polycotyliids, or both taxa, to Pliosauroida, sometimes as sister taxa (Fig. 5B–D; e.g. Cruickshank 1997;

O’Keefe 2001; Druckenmiller & Russell 2008a; Benson *et al.* 2011a; Kear & Barrett 2011). This implies that the intermediate body proportions of leptocleidids, and pliosauromorph proportions of polycotyliids, are characteristic of pliosauroids. However, detailed anatomical observations suggest that these clades instead represent derived plesiosauroids (Ketchum & Benson 2010; and herein; some previous studies suggested plesiosauroid affinities for polycotyliids only: Williston 1903; Bakker 1993; Carpenter 1997; O’Keefe 2001). We have reviewed these features in detail and described numerous characters supporting a monophyletic Leptocleidia (Polycotyliidae + Leptocleididae) within Plesiosauroida above.

Ketchum & Benson (2011) observed that robust, large-bodied pliosauroids appeared first among Lower Jurassic rhomaleosaurids with intermediate body proportions. These were succeeded in the Middle Jurassic–early Late Cretaceous by pliosauromorph pliosaurids. Surprisingly, basal pliosaurids (and, by inference, basal pliosauroids) had relatively long necks comprising 34–36 cervical vertebrae in taxa such as *Hauffiosaurus* and *Attenborosaurus*. In some respects, leptocleidian evolution parallels that among Jurassic pliosauroids; leptocleidids with ‘rhomaleosaurid-like’ proportions are abundant in the Early Cretaceous fossil record, and polycotyliids acquired their pliosauromorph body proportions only in the Late Cretaceous (e.g. O’Keefe 2002). Although some leptocleidians have relatively long necks comprising 33–37 elongate cervical vertebrae (*Brancaosaurus*, Wegner 1914; *Thililua*, Bardet *et al.* 2003), and many of the most basal representatives have already undergone reduction to 24 anteroposteriorly shortened cervical vertebrae (e.g. QM F18041; *Nichollssaura*, Druckenmiller & Russell 2008b). Thus, few clear trends are apparent in the Early Cretaceous, and leptocleidians primitively retained at least some of the evolutionary plasticity of other plesiosauroids, and basal pistosaurians (e.g. 49 elongate cervical vertebrae in *Yunguisaurus*, Sato *et al.* 2010; 38 in *Augustasaurus*, Sander *et al.* 1997; 19 short cervical vertebrae in *Bobosaurus*, Dalla Vecchia 2006). Early Cretaceous leptocleidians (primarily leptocleidids) thus included taxa with highly variable body proportions. This is somewhat comparable to the situation within Cryptocleididae, a plesiosauroid clade that was diverse in the Middle–Late Jurassic and includes both long-necked taxa such as *Muraenosaurus* (47 elongate cervical vertebrae), and shorter-necked taxa like *Tricleidus* (27 anteroposteriorly short cervical vertebrae). Given the high levels of plasticity in neck length among restricted plesiosauroid clades such as Cryptocleididae and Leptocleididae, we strongly recommend that the practice of referring most long-necked taxa to Elasmosauridae (e.g. Wegner 1914; Brown 1981; Bardet *et al.* 1999; Kear & Barrett 2011) be abandoned. Family-level assignments like this require support from global cladistic datasets with rich character samples, or detailed anatomical observations as employed here.

Plesiosaurian adaptation to marginal and freshwater environments

The hypothesis that leptocleidids represent a primitive radiation of plesiosaurians that survived extended geological time intervals by taking refuge in freshwater environments (Andrews 1922; Cruickshank & Long 1997) is appealing. However, we have demonstrated that it is not supported by the bulk of anatomical evidence. Instead, leptocleidids are a derived plesiosauroid clade that convergently reacquired 'primitive', intermediate, body proportions. If we are correct, and leptocleidids represent derived cryptocleidian plesiosauroids (known from the late Middle Jurassic onwards), then their phylogenetic placement is inconsistent with a Lower Jurassic origin implied by the hypothesis of Andrews (1922) as developed by Cruickshank & Long (1997).

Plesiosaurians are known from freshwater and marginal marine deposits for their entire history. In the Lower–Middle Jurassic they are represented by specimens from lacustrine deposits in China (Dong 1980; Zhang 1985; Sato *et al.* 2003) and Australia (Bartholomai 1966; Molnar 1991). Further fragmentary remains are known throughout the Cretaceous (e.g. Lower Cretaceous: Hou *et al.* 1975; Rich *et al.* 1989; Molnar 1991; Rich 1996; Vickers-Rich 1996; Smith 1999; Upper Cretaceous: Russell 1931; Sato *et al.* 2003; but see Brinkman & Eberth 1987). Few freshwater plesiosaurians have been incorporated into phylogenetic analyses. However, *Hastanectes* (formerly '*Cimoliasaurus*' *valdensis*) from the Wadhurst Clay Formation (representing a series of freshwater and slightly brackish, often shallow-water lacustrine environments; Radley 2004, 2006) may be a pliosaurid, indicating that multiple plesiosaurian clades were found in marginal or freshwater habitats, even during the brief earliest Cretaceous interval. Kear & Barrett (2011) suggested that plesiosaurians underwent multiple radiations into freshwater and marginal marine environments. Our phylogenetic results indicate that this is correct. However, this issue awaits resolution in the form of phylogenetic work resolving the status of other material from these facies.

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