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A new plesiosauroid from the Toarcian (Lower Jurassic) of Alhadas, Portugal

ADAM S. SMITH, RICARDO ARAÚJO, and OCTÁVIO MATEUS

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A partial plesiosauroid skull from the São Gião Formation (Toarcian, Lower Jurassic) of Alhadas, Portugal is re-evaluated and described as a new taxon, *Lusonectes sauvagei* gen. et sp. nov. It has a single autapomorphy, a broad triangular parasphenoid cultriform process that is as long as the posterior interpterygoid vacuities, and also a unique character combination, including a jugal that contacts the orbital margin, a distinct parasphenoid–basisphenoid suture exposed between the posterior interpterygoid vacuities, lack of an anterior interpterygoid vacuity, and striations on the ventral surface of the pterygoids. Phylogenetic analysis of Jurassic plesiosauroids places *Lusonectes* as outgroup to "microcleidid elasmosaurs", equivalent to the clade Plesiosauridae. *Lusonectes sauvagei* is the only diagnostic plesiosaur from Portugal, and the westernmost occurrence of any plesiosaurian in Europe.

Key words: Elasmosauridae, Plesiosauridae, Plesiosauria, *Lusonectes sauvagei*, plesiosaur, Jurassic, Toarcian, Lusitanian basin, Portugal.

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Introduction

The Lusitanian depositional basin in Portugal has yielded a rich array of Mesozoic terrestrial vertebrates, particularly dinosaurs and mammals (Antunes and Mateus 2003; Mateus 2006). In contrast, marine vertebrates are rare. Castanhinha and Mateus (2007) reviewed the known marine reptile material from Portugal and recorded a total of just 28 specimens, including 23 ichthyosaurians, four plesiosaurians, and one mosasauroid. The ichthyosaurian remains have been referred to *Ichthyosaurus intermedius* and *Stenopterygius* sp. (Antunes et al. 1981; Castanhinha and Mateus 2007), and the single mosasauroid was assigned to *Mosasaurus* sp. (Sauvage 1897–1898; Veiga Ferreira 1958). Many of these fossils were collected in Portugal during the nineteenth century and have been overlooked by modern researchers, so re-evaluation of this material is necessary.

The rare plesiosaurian fossils from Portugal range in age from Toarcian to Cenomanian (Castanhinha and Mateus 2007). The material has been referred to *Cryptoclidus* sp. and *Plesiosaurus* sp. or has been regarded as indeterminate. For example, undescribed plesiosaurian teeth are known from the Kimmeridgian- to Tithonian-aged Lourinhã Formation of Santa Cruz (Castanhinha and Mateus 2007), and an isolated vertebra assigned to *Cryptoclidus* is reported from the Cenomanian of Alcântara (Castanhinha and Mateus 2007). The most significant of these fossils is a partial plesiosaurian skull (MG33) from the São Gião Formation (Toarcian, Lower Jurassic) of Alhadas, and this forms the basis of this paper.

Other vertebrates from the Early Jurassic of Portugal include the bony fishes *Furo* cf. *arthastamus* (Amiiformes) and *Proleptolepis* sp. (Pachycormiiformes) from the Sinemurian of Água de Madeiros (Antunes et al. 1981), *Ichthyosaurus* sp. from the Sinemurian of São Pedro de Moel (Sauvage 1897–1898), the thalattosuchian crocodilian *Mystriosaurus* (= *Steneosaurus*) *bollensis* from Tomar (Antunes 1967), and the thyreophoran dinosaur *Lusitanosaurus liasicus* Lapparent and Zbyszewski, 1957, possibly also from the Sinemurian of São Pedro de Moel.

Sauvage (1897–1898: 21–22, pl. 3: 1–3) originally described and figured MG33 in the first report on plesiosaurian remains from Portugal as *Plesiosaurus* sp., but refrained from identifying it to species level. Some recent authors have also listed it as *Plesiosaurus* sp. (Bardet et al. 2008; Ruiz-Omeñaca et al. 2009). Castanhinha and Mateus (2007) allocated the skull to Plesiosauria indet., and Smith et al. (2010) provided a short description of the skull but refrained from

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identifying it. This paper provides a redescription of this rare Portuguese plesiosaurian specimen and assesses its systematic status based on detailed comparison with other Lower Jurassic plesiosauroid taxa.

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; MG, Museu Geológico, Lisbon, Portugal; MMUM, The Manchester Museum, The University of Manchester, Manchester, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SMUSMP, Southern Methodist University, Shuler Museum of Palaeontology, Dallas, USA.

Historical note

There is some confusion over the provenance of MG33 because one of the labels associated with the specimen contradicts the others. Two detailed labels are considered correct and state that MG33 originated from "600 m a N30E du pys. dans Alhadas" and "mélange du lias moyen avec q.q. fossiles du Toarcien". This is corroborated by Sauvage (1897–1898: 2) who identified the skull as "d'anciennes récoltes faites à 1500 métres O.N.O. du village d'Alhadas, et près de Murtede, présentent un mélange de Charmouthien et de Toarcien" (= collected at 1500 m WNW from the village of Alhadas, near Murtede, which yield a mix of Charmouthian [equivalent to Pliensbachian] and Toarcian fossils). A large quantity of material was collected from the extensive outcrops around Alhadas by the geologist Paul Choffat (1849–1919) and his team as they mapped the area. It is possible that MG33 was collected during those expeditions. Alhadas has yielded several other vertebrate remains including ichthyosaurs and fishes, and a new fossil fish locality was identified during a prospecting trip in November 2007. An erroneous label gives the location of MG33 as São Pedro de Moel.

Systematic palaeontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Plesiosauroidea Welles, 1943

Plesiosauridae Gray, 1825

Genus *Lusonectes* nov.

Type species: *Lusonectes sauvagei* sp. nov.; see below.

Etymology: From Latin *Luso*, Portuguese and Greek *nectes*, swimmer.

Lusonectes sauvagei sp. nov.

Figs. 1, 2.

Holotype: MG33, a partial skull and articulated mandible.

Etymology: In honour of the 19th century palaeontologist Henri Émile Sauvage (1842–1917) who made significant contributions towards vertebrate palaeontology in Portugal, and first described MG33 (Sauvage 1897–1898: pl. 3:1–3).

Type locality: 1500 m WNW of Alhadas, near Murtede, Portugal (40°11'N, 8°47'W).

Type horizon: Toarcian (Lower Jurassic) beds of the São Gião Formation, which extends from the lower Toarcian (*Dactylioceras polymorphum* Ammonite Biozone) to the mid–upper Toarcian (*Hammatoceras speciosum* Ammonite Biozone) (Kullberg et al. 2012).

Diagnosis.—*Lusonectes* possesses a single autapomorphy, a broad triangular parasphenoid cultriform process that is as long as the posterior interpterygoid vacuities. The taxon is further diagnosed by the following unique combination of characters: jugal contacts the orbital margin, a distinct parasphenoid–basisphenoid suture exposed between the posterior interpterygoid vacuities, an unkeeled ventral parabasisphenoid with a flat anterior and gently convex posterior region of the ventral surface, lack of an anterior interpterygoid vacuity, and palatal striations on the ventral surface of the pterygoids. The teeth have no ornamentation or striations, but this may be due to abrasion.

Description

MG33 is a small substantially complete cranium (127 mm long as preserved) with the mandible in articulation (Fig. 1). The anterior and posterior portions of the skull are broken off and missing. Most of the elements from the skull roof are missing and parts of the dorsal surface represent an eroded internal mould of the skull (Fig. 1C). The palatal surface is well preserved and exhibits clear sutures and surface detail.

Skull roof.—The skull roof is poorly preserved, but the overall shape can be discerned. There are large oval orbital openings and the anterior margins of the temporal fenestrae are visible (Fig. 1C). The left orbital opening is complete (42 mm long and 33 mm wide). The external nares are not apparent but must have been very small. An alveolus visible on the broken anterior surface of the cranium indicates that the total preorbital length of the skull was not much longer than the preserved portion, and the preorbital region was therefore particularly short. A short snout is also present in *Zarafasaura* from the Maastrichtian of Morocco (Vincent et al. 2011). The relative length of the preorbital region is of potential systematic significance in plesiosaurians (O'Keefe 2001; Ketchum and Benson 2010), but the postorbital region is incomplete in MG33, so meaningful comparative skull proportions cannot be obtained.

A broad and deep midline trough extends from the anterior margin of the skull and between the orbits. This trough occupies the probable position of the premaxillae and frontals and contrasts with the condition in other plesiosaurs, which possess a distinct midline prominence formed by the posterior rami of the premaxillae (e.g., *Libonectes*, SMUSMP 69120, RA personal observation, and *Nichollssaura* Druckenmiller and Russell 2008a). A complete skull from Lyme Regis referred *to Plesiosaurus macrocephalus* (BMNH 49202, AS personal observation) preserves a naturally concave surface in this region. Wegner (1914) also described a similar concavity in the skull of *Brancasaurus* from the Cretaceous of northern

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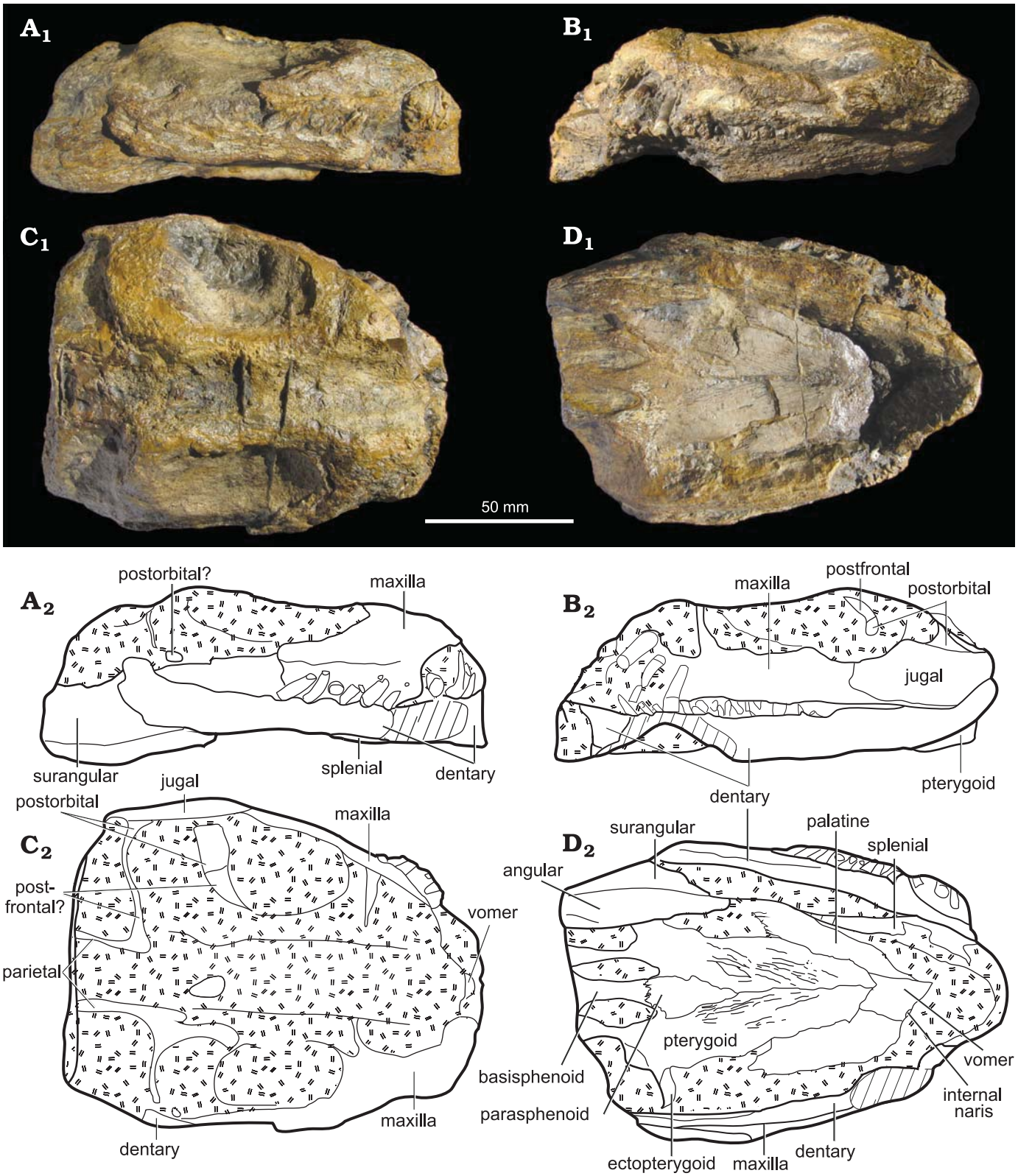


Fig. 1. Skull of the plesiosauroid *Lusonectes sauvagei* gen et sp. nov. (MG33) from the Toarcian of Portugal, in right lateral (**A**), left lateral (**B**), dorsal (**C**), and ventral (**D**) views. Photographs (A_1–D_1), explanatory drawings (A_2–D_2).

Germany. However, the highly worn surface in MG33 makes it unclear whether this trough is a natural feature, or whether the premaxillae and the frontals are missing entirely, in which case the longitudinal trough could represent a mould of the ventral surface of the skull roof.

The exact shape of the maxilla in MG33 cannot be deter-

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mined. It probably forms the anterolateral margin of the orbital opening and certainly produces a narrow posterior process on the ventro-lateral margin of the skull, below the jugal, with which it forms a long straight contact (Fig. 1B). The left jugal is almost complete and forms an anteroposteriorly elongate lozenge, although the posterior border is not preserved. The jugal is at least twice as long as it is high. It extends ventral to the orbit and contacts the maxilla anteriorly and ventrally, the postorbital dorsally, and the squamosal posteriorly (Fig. $1B_2$). The dorsal and ventral margins are sub-parallel and converge anteriorly to form an acute angle. The jugal contacts the orbital margin, as seen in *Seeleyosaurus* (Grossmann 2007), but unlike *Hydrorion* (Maisch and Rücklin 2000), *Microcleidus* (BMNH 36184, AS personal observation) and *Occitanosaurus* (Bardet et al. 1999), where the jugal is excluded from the orbital margin by a contact between the maxilla and postorbital. The jugal-postorbital suture is straight.

A small portion of the postorbital is preserved, and it contacts the jugal and the posterior rim of the orbit. It participates in the anterior margin of the supratemporal fenestra as a thin vertical wall, and probably contacts the postfrontal medially, although no suture is visible. The parietal is fragmentary and consists only of the lateral walls. Therefore its relationship to the other bones is impossible to determine. There is no indication of a pineal foramen so it may have been absent, positioned more posteriorly than the preserved portion, or removed by abrasion. Bardet et al. (1999) considered a pineal foramen to be absent in *Occitanosaurus*, but a small pineal foramen is present in the holotype (Mark Evans, personal communication 2010).

Palate.—The palate is generally well preserved and many sutures and surface details are clear (Fig. 1D). However, the occluded mandible obscures the anterior part of the palate. The vomers appear to be coossified and extend posteriorly beyond the position of the internal naris to contact the palatine and pterygoid. A small exposure of the vomer is also visible in dorsal view (Fig. $1C_2$). The internal nares appear to be small oval openings. The medial margin of the left internal naris is visible as a gently curved ridge formed entirely by the vomer, but the lateral margin (and the entire right internal naris) is covered by matrix. The vomer contacts the palatine along a serrated suture that runs postero-medially towards the pterygoid. A posteriorly directed triangular suture is formed where these three elements meet (Fig. $1D_2$). The palatines are elongate bones that extend from the vomers anteriorly and contact the pterygoids medially along a long straight suture. The lateral and posterior borders of the palatines are covered by matrix, so the relationship between each palatine and the adjacent bones, presumably the maxilla and ectopteygoid, cannot be determined. There is no evidence of a suborbital fenestra on the lateral side of the palatine, but it is possible that it is obscured by matrix or by the occluded mandible.

The pterygoids are the largest bones on the palate and extend far posteriorly (Fig. 1D). Each pterygoid has an anterior, posterior and lateral ramus. The anterior rami contact closely on the midline for their entire length so an anterior interpterygoid vacuity is absent. This condition is seen also in *Hydrorion* (Maisch and Rücklin 2000), *Microcleidus* (BMNH 36184, AS personal observation) and *Occitanosaurus* (Bardet et al. 1999), whereas *Seeleyosaurus* has a large anterior interpterygoid vacuity (Grossmann 2007). The lateral region of the ventral surface of the pterygoids is smooth, but the medial region of the ventral surface is ornamented by obliquely oriented parallel striations that extend along the length of each pterygoid (Fig. $1D_2$). This condition has been described in some specimens of *Plesiosaurus* (Storrs 1997), and similar striations are present on the pterygoids of *Tricleidus seeleyi* (Andrews 1910) and some specimens of *Seeleyosaurus* (SMNS 16812; Grossmann 2006), but the systematic utility of this character is unclear. The pterygoids contact the vomers anteriorly, but the medial part of this contact is poorly preserved. The posterior rami of the pterygoids extend below the occiput and form the lateral margins of the posterior interpterygoid vacuities, which are elongate and rounded. The posterior extent of the pterygoids is unknown because the posterior part of the skull is not preserved. The lateral rami appear quite broad but no sutures are preserved in this region. A small exposure of bone forms the concave anterior margin of the left subtemporal opening on the left side of the palate and probably represents the ectopterygoid. A pterygoid flange (also referred to as the pterygoid/ectopterygoid boss) is absent on the preserved portion of the skull, but it is possible that it is present and concealed by matrix.

The parasphenoid forms a large, 24 mm long triangular cultriform process that extends onto the surface of the palate and tapers to a sharp anterior point (Figs. 1D, 2). The length of its anterior exposure is subequal to the length of the posterior interpterygoid vacuities; the exact length of the posterior interpterygoid vacuities is uncertain because their posterior margins are damaged. The shape and size of the cultriform process varies considerably among plesiosauroids (Fig. 3) and the pliosauroid *Meyerasaurus*, from the Toarcian of Germany, has no cultriform process exposed on the palate at all (Smith and Vincent 2010). The cultriform process in *Lusonectes* differs from all other Lower Jurassic plesiosauroids and is therefore considered autapomorphic (Figs. 2, 3).

The parasphenoid–basisphenoid contact is visible between the posterior interpterygoid vacuities as a serrated suture; this contact is located far anteriorly so the basisphenoid excludes the parasphenoid almost entirely from contact with the vacuities (Fig. 2). The surface is slightly eroded so the exact path of the suture on the ventral surface is uncertain. The basisphenoid extends anteriorly along the medial wall of the interpterygoid vacuity, but the posterior extent of the basisphenoid is unknown.

The ventral surface of parasphenoid and basisphenoid between the interpterygoid vacuities is unkeeled (Fig. 2). Anteriorly, the parasphenoid is flat and the surface of the basisphenoid is gently convex. The parasphenoid–basisphenoid suture is not always visible in plesiosaurians because it is sometimes fused (Bardet et al. 1999; Sato 2005). Consequently, the posterior extent of the parasphenoid has been

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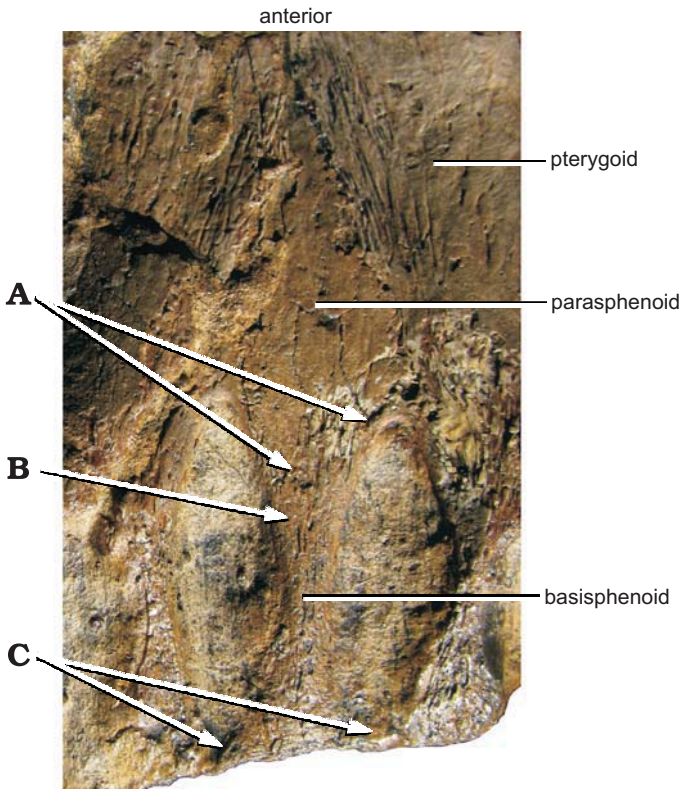


Fig. 2. Details of the rear of the palate and basicranium of the plesiosauroid *Lusonectes sauvagei* gen. et sp. nov. (MG33) from the Toarcian of Portugal. **A**. Ventral view, indicating the path of a parasphenoid–basisphenoid suture. **B**. The flat (unkeeled) surface of the parasphenoid/basisphenoid between the posterior interpterygoid vacuities. **C**. The extent of the basisphenoid to enclose the posterior margins of the posterior interpterygoid vacuities. The parasphenoid cultriform process is 24 mm long.

overestimated in some interpretations; for example, compare the interpretation of *Thalassiodracon* by O'Keefe (2006: fig. 12.2) with that of Benson et al. (2011a: fig. 4), and the interpretation of MMUM LL8004 by O'Keefe (2001: fig. 9) with that of Benson et al. (2011b: fig. 6). The appropriate term for the conjoined parasphenoid–basisphenoid is parabasisphenoid. A flat parabasisphenoid is also present in *Plesiosaurus* (Storrs 1997), *Seeleyosaurus* (Grossmann 2007), and *Hydrorion* (Maisch and Rücklin 2000), whereas it is sharply keeled in *Microcleidus* (BMNH 36184, AS personal observation), *Occitanosaurus* (Bardet et al. 1999) and in many Cretaceous elasmosaurids (Carpenter 1997; Maisch and Rücklin 2000). A keeled parabasisphenoid is also present in leptocleidids, pliosaurids, and some polycotylids (Ketchum and Benson 2010).

Mandible.—Both mandibular rami are partially preserved but are badly damaged anteriorly and the glenoid and retroarticular regions are missing. An irregular transverse cross-section through the dentaries is visible anteriorly, located in the approximate position of the posterior margin of the mandibular symphysis. Large parts of the dentary have fallen away, so the gently convex matrix exposed anteriorly (and also visible in ventral view) is a mould of the posterior margin of the mandibular symphysis and indicates that the mandibular rami may have joined posteriorly in a smooth C-shaped contact, rather than a sharp V-shaped contact (Fig. 1D).

The right ramus of the jaw preserves the posterior extent of the dentary, which forms the ascending slope of the coronoid eminence (Fig. 1A). The main body of the dentary is almost straight, although a crack at the anterior part of the right mandibular ramus, and mediolateral displacement, gives the false impression of a bowed mandible.

The angular is preserved on the medial side of the left ramus as a splinter of bone visible ventrally (Fig. 1D). On the right ramus it is visible laterally and ventrally where it contacts the surangular along a straight horizontal suture (Fig. 1A). The splenial is a sheet of bone extending anteriorly on the right side of the jaw where it is interrupted posteriorly by a crack; its anterior extension is hidden by matrix.

Dentition.— The teeth are delicate, slender, curved lingually and circular in cross section (Fig. 1A, B). An average tooth measures about 10 mm apicobasally and 2.9 mm at the base of the crown (labiolingually). The preserved dentition shows no evidence for fangs or caniniforms. The apicobasal height of the teeth increases anteriorly slightly but the dentition was essentially homodont. Plesiosaurian teeth typically have distinct apicobasally oriented enamel ridges (Brown 1981) but the tooth crowns appear entirely smooth and unornamented in MG33. This may be a preservational artefact resulting from abrasion; however, if genuine, it could represent an additional diagnostic character for this taxon. An accurate tooth count is not possible because of poor preservation; in the right lower mandible there are seven preserved teeth and six on the left (two of them displaced), in the right maxilla there are five preserved teeth and four on the left. The maxillary alveoli row appears to end below the middle of the orbits.

Comparison.—The relative size of the skull is unknown in *Lusonectes*, but it is very small in absolute terms, on a par with contemporaneous plesiosauroids (see Grossman 2007; Bardet et al. 1999). *Lusonectes* has a short preorbital region, which differentiates it from the Toarcian pliosauroids *Rhomaleosaurus* (Smith and Dyke 2008), *Hauffiosaurus* (O'Keefe 2001; Benson et al. 2011b) and *Meyerasaurus* (Smith and Vincent 2010), which have relatively longer preorbital regions. *Lusonectes* can confidently be regarded as a plesiosauroid based on its combination of an absolutely small skull, short preorbital region and delicate teeth.

Brown (1993) and Brown and Cruickshank (1994) demonstrated the importance of the cheek region in plesiosaurian systematics, especially variation in the size and morphology of the jugal. Among plesiosauroids, the jugal is a large and antero-posteriorly elongate bone in "elasmosaurids" (sensu Brown 1981), whereas it forms a narrow vertically oriented bar in cryptoclidids. *Lusonectes* has a large elongate jugal and can therefore be confidently regarded as an "elasmosaurid" sensu Brown (1981). However, recent analyses have contested the simple division of plesiosauroids into two in-

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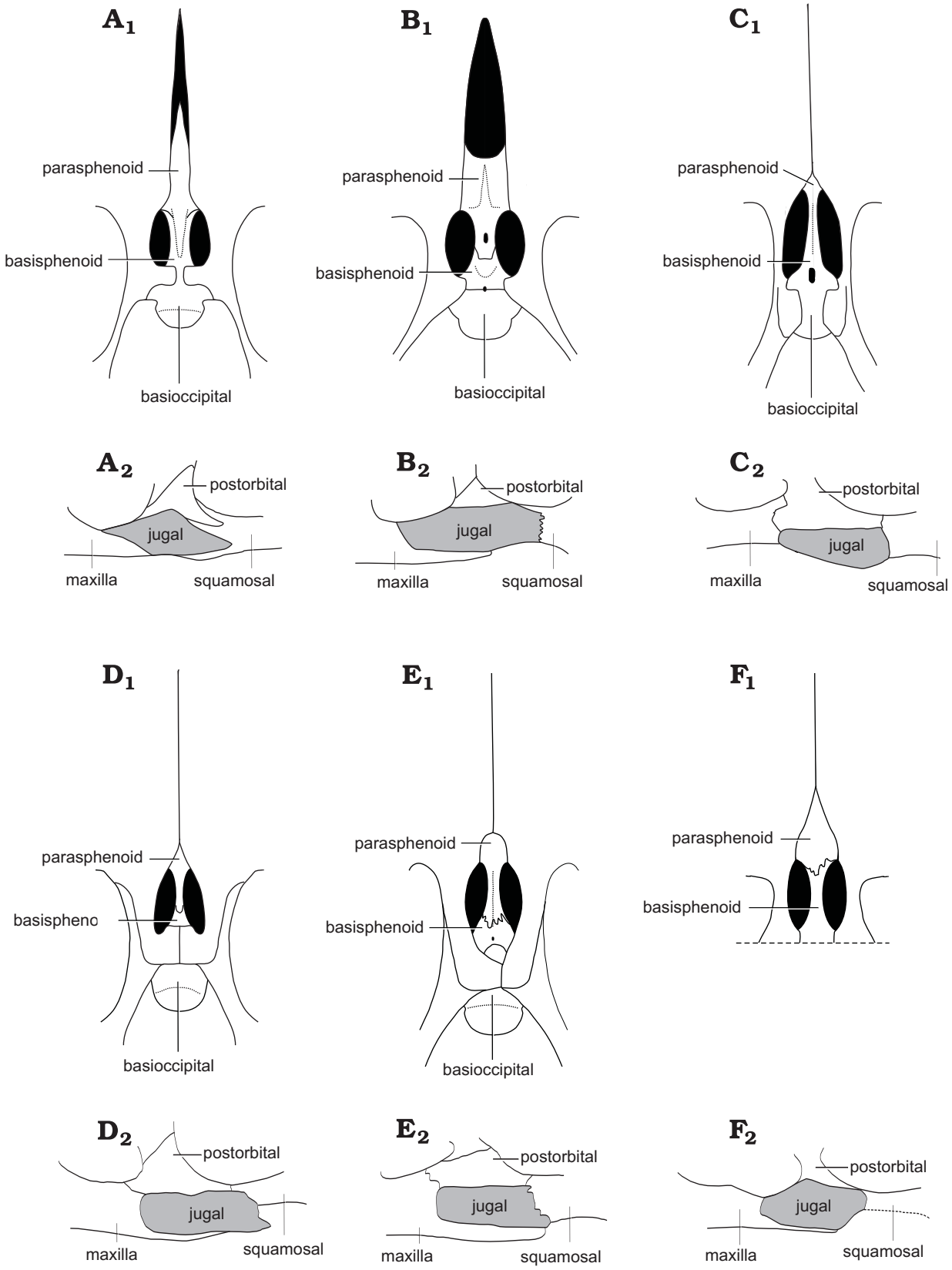


Fig. 3. Comparative illustration of key anatomical areas of the skull in several Lower Jurassic plesiosauroids. **A**. *Plesiosaurus* (redrawn from Storrs 1997). **B**. *Seeleyosaurus* (redrawn from Grossmann 2007). **C**. *Occitanosaurus* (based on Bardet et al. 1999). **D**. *Hydrorion* (based on Maisch and Rücklin 2000; Grossmann 2006). **E**. *Microcleidus* (based on BMNH 36184, AS personal observation). **F**. *Lusonectes sauvagei* gen. et sp. nov. An alternative interpretation of *Occitanosaurus* suggests that the pterygoids met on the midline behind the posterior interpterygoid vacuity (Mark Evans, personal communication 2010). A_1–F_1,ventral surface of the braincase; A_2–F_2, lateral view of the cheek region (with the jugal highlighted in grey; anterior to the left). Not to scale.

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clusive families (Ketchum and Benson 2010). Grossmann (2007) used the informal name "microcleidid elasmosaurs" to differentiate a basal clade of early Jurassic long-necked plesiosauroids (*Microcleidus*, *Occitanosaurus*, *Hydrorion*) from more derived "Cretaceous elasmosaurs". Ketchum and Benson (2010) distinguished a similar clade, which includes *Plesiosaurus*, and is only distantly related to Cretaceous elasmosaurids. They regarded this clade as Plesiosauridae and consequently use a more restrictive definition of Elasmosauridae (see below).

The jugal contacts the orbit in *Lusonectes*, which differentiates it from *Hydrorion* and *Microcleidus* where the jugal is excluded from the orbital margin (Fig. $3D_2$, E_2, F_2). Storrs (1997) reconstructed *Plesiosaurus dolichodeirus* with a diamond-shape jugal (Fig. $3A_2$), so *Lusonectes* is similar to *Plesiosaurus* in this regard. The jugal of *Hydrorion* also has a short posterior process (Fig. $3D_2$) that appears to be absent in *Lusonectes,* although the posterior part of the jugal is damaged. The relative position of the jugal also differs from *Hydrorion* where the main body of the jugal is located beneath the supratemporal fenestra (Fig. $3D_2$) (Grossmann 2006), whereas it is more anteriorly placed in *Lusonectes* (Fig. $3F_2$).

The presence of an anterior interpterygoid vacuity is variable amongst plesiosaurians. *Lusonectes* has anteriorly closed pterygoids, so lacks an anterior interpterygoid vacuity. This differentiates it from the Toarcian *Seeleyosaurus* (Fig. $3B_1$; Grossmann 2007) and *Meyerasaurus* (Smith and Vincent 2010), which have a distinct open anterior interpterygoid vacuity. Among other plesiosaurians, *Plesiosaurus* (Fig. $3A_1$; Storrs 1997) and the cryptoclidids (sensu O'Keefe 2001) *Cryptoclidus* (see Brown and Cruickshank 1994), *Tricleidus* (see O'Keefe 2001), and *Muraenosaurus* (Andrews 1910), also have an open anterior interpterygoid vacuity. The pterygoids are anteriorly closed in *Hydrorion* (Maisch and Rücklin 2000; Grossmann 2007), *Microcleidus* (BMNH 36184, AS personal observation), and Cretaceous elasmosaurids (Carpenter 1997; O'Keefe 2001; Ketchum and Benson 2010).

In *Lusonectes*, the ventral parabasisphenoid surface between the posterior interpterygoid vacuities is flat to gently convex (Fig. 2). This differentiates it from the strongly keeled parabasisphenoid in *Microcleidus* (Fig. $3E_1$; BMNH 36184, AS personal observation), *Occitanosaurus* (Fig. $3C_1$; Bardet et al. 1999), and many Cretaceous elasmosaurids (Maisch and Rücklin 2000). Among Toarcian taxa, *Lusonectes* shares a flat parabasisphenoid surface with *Hydrorion* (Fig. $3D_1$) and *Seeleyosaurus* (Fig. $3B_1$; Maisch and Rücklin 2000; Grossmann 2007).

Lusonectes has a large and distinct triangular cultriform process (Figs. 2, $3F_1$). This differs from *Microcleidus*, which has a semicircular cultriform process (Fig. $3E_1$; BMNH 36184, AS personal observation), and *Seeleyosaurus*, which has a rectangular cultriform process (Fig $3B_1$; Grossmann 2007). Note that O'Keefe (2004) interpreted the cultriform process of *Seeleyosaurus* differently from Grossmann (2007), as a short narrow process. However, even if this alternative interpretation is correct, it still differs from the condition in *Lusonectes*. *Occitanosaurus* (Fig. $3C_1$) and *Hydrorion* (Fig. $3D_1$) have a triangular cultriform process similar to *Lusonectes*, but they are much smaller and the angle of the anterior process is less acute. The length of their cultriform processes is also considerably less than the length of their posterior interpterygoid vacuities. *Plesiosaurus* has a long cultriform exposure that exceeds the length of the posterior interpterygoid vacuities (Fig. $3A_1$), but the pterygoids approach on the midline so the process is much more narrow in *Plesiosaurus* than in *Lusonectes* (Fig. 3).

MG33 is regarded as a novel taxon based on the autapomorphic morphology of the parasphenoid (Figs. 2, 3), and the validity of *Lusonectes* is supported by the unique combination of jugal, pterygoid and parabasisphenoid morphology, not seen in any other taxon.

Discussion

Diversity of Toarcian plesiosauroids.—Four valid plesiosauroid genera are known from the Toarcian stage in addition to *Lusonectes*: *Occitanosaurus*, *Microcleidus*, *Hydrorion*, and *Seeleyosaurus* (see Fig. 3). The genus *Occitanosaurus* was introduced for "*Plesiosaurus*" *tournemirensis* and is known from a single almost complete specimen including the cranium from southern France (Bardet et al. 1999). The genus *Microcleidus* is the only named plesiosauroid from the Toarcian of the UK and includes two species, *M. homalospondylus* (the type species) and *M. macropterus* (see Watson 1911). *M. homalospondylus* is known from several specimens including a complete skeleton with a skull (BMNH 36184). It was described and figured by Owen (1865), but the skull material was poorly prepared at that time. The skull of BMNH 36184 was later acid prepared by Brown. Brown (1993) presented a reconstruction of the skull in lateral view, and a full descriptive paper of the specimen is in review (David Brown, personal communication 2011). We present an interpretation of the ventral surface of the braincase of BMNH 36184 (Fig. $3E_1$). The Toarcian plesiosauroids from the Germanic basin have received recent attention (Maisch and Rücklin 2000; O'Keefe 2004; Grossmann 2006, 2007) and several genera have been erected for this material. Grossmann (2007) erected the new genus *Hydrorion* for "*Plesiosaurus*" *brachypterygius*, the skull of which was previously described in detail by Maisch and Rücklin (2000). Grossmann (2007) also reinstated the genus *Seeleyosaurus* for the plesiosaur "*Plesiosaurus*" *guilelmiimperatoris*. O'Keefe (2004) erected a new genus "*Plesiopterys*", but the specimen was later identified as a juvenile specimen of *Seeleyosaurus* (Grossmann 2007). Vincent (2010) described a possible new plesiosaurian taxon from the Toarcian of Germany, but its juvenile ontogenetic state makes diagnosis problematic. *Lusonectes sauvagei* is the first diagnostic plesiosaurian taxon from Portugal and its fossil remains represent the westernmost occurrence of any plesiosaurian in Europe.

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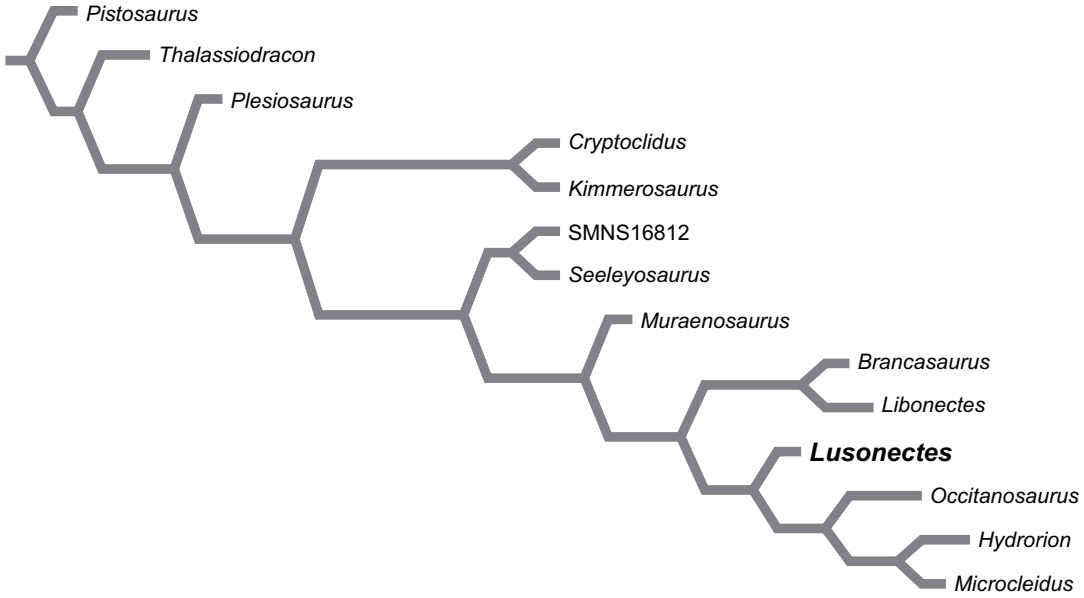


Fig. 4. Strict consensus cladogram resulting from a reanalysis of the data matrix of Grossmann (2007), with *Lusonectes* included as an additional operational taxonomic unit. See text for interpretation. SMNS16812 is the holotype of "*Plesiopterys wildii*" = *Seeleyosaurus* according to Grossman (2007).

Phylogenetic analysis and definition of Elasmosauridae.—Grossmann (2007: 555, table 3) provided a suite of key characters used to distinguish among Jurassic long-necked plesiosaurians, including all four Toarcian "elasmosaurid" plesiosaur taxa, *Microcleidus*, *Hydrorion*, *Seeleyosaurus*, and *Occitanosaurus*. These characters were incorporated into a cladistic analysis dedicated to Jurassic plesiosauroids (Grossmann 2007). To assess the phylogenetic position of *Lusonectes* we included it as an additional operational taxonomic unit in the data matrix of Grossmann (2007) (Appendix 1) and reran the cladistic analysis using PAUP* (Swofford 2002). The analysis resulted in a single most parsimonious tree (Fig. 4) with the following statistics: legth = 53, consistency index = 66, retention index = 78. In the cladogram, *Lusonectes* occupies a sister relationship with the clade informally called "microcleidid elasmosaurs" (Grossmann 2007), within the larger clade Elasmosauridae (sensu Brown 1981). The inclusion of *Lusonectes* does not alter the topology of the rest of the tree. Grossmann's (2007) "microcleidid elasmosaur" clade includes *Hydrorion*, *Occitannosaurs*, and *Microcleidus*. Ketchum and Benson (2010) also resolved these taxa in a monophyletic clade in an extensive global analysis of Plesiosauria. However, in Ketchum and Benson's (2010) analysis, *Microcleidus, Hydrorion*, and *Occitannosaurus* occupy a sister relationship with a clade consisting of *Plesiosaurus* and *Seeyleyosaurus*. Together, these taxa form a large monophyletic plesiosaurid family that is phylogenetically separate from the Elasmosauridae. Our small analysis demonstrates the close affinity of *Lusonectes* with Lower Jurassic long-necked forms (as opposed to Middle Jurassic cryptoclidids and Cretaceous elasmoaurids), and so *Lusonectes* may be regarded as a plesiosaurid sensu Ketchum and Benson (2010), although the large amount of missing data means its exact phylogenetic position should be treated as tentative. All global cladistic analyses of Plesiosauria also confirm that Jurassic plesiosauroids are phylogenetically separate from Elasmosauridae sensu stricto (O'Keefe 2001, 2004; Druckenmiller and Russell 2008b; Ketchum and Benson 2010). Use of the broad concept of Elasmosauridae (sensu Brown 1981) in recent years to include Jurassic plesiosauroids, and even Triassic forms (Sennikov and Arkhangelsky 2010), fails to account for the huge anatomical differences between Jurassic and Cretaceous forms. Moreover, it falsely represents our current understanding of plesiosauroid evolution and can therefore be misleading. For this reason, we endorse the more restrictive definition of Elasmosauridae (sensu Ketchum and Benson 2010) as opposed to the broader definition (sensu Brown 1981).

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Appendix 1

Data Matrix. See Grossmann (2007) for list of characters. SMNS16812 is the holotype of "*Plesiopterys wildii*" = *Seeleyosaurus* according to Grossman (2007).

Pistosaurus	00000000000000000000000000000000
Thalassiodracon	00010000000100??0000000?00000000
Plesiosaurus	00010110000000011000000000001000000
Cryptoclidus	00110020001001 1?0??11010110000110
Kimmerosaurus	?011002?0?1?011???01101??1?000??0
SMNS16812	00011??01001001?01000001101100110
Seeleyosaurus	000111?0100100????00??01101100110
Muraenosaurus	?00111111001011101000001101111110
Occitanosaurus	11002011110101011000000 1001111110
Hydrorion	11001111110101001010000 1001100110
Microcleidus	1100111111101?10??0100001??11011?0
Brancasaurus	00011111100111?010?00101101111101
Libonectes	0000211???011?00101001010011111?1
Lusonectes	?10?????1001??0??0???????0???????

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