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PRELIMINARY DESCRIPTION AND PHYLOGENETIC POSITION OF A NEW PLESIOSAUR (REPTILIA: SAUROPTERYGIA) FROM THE TOARCIAN OF HOLZMADEN, GERMANY

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ABSTRACT—This paper offers a preliminary description of a plesiosaur (Reptilia: Sauropterygia) from the Lower Toarcian Posidonienschiefer near the village of Holzmaden in Baden-Württemberg, Germany, and discusses its phylogenetic relevance. This new taxon, *Plesiopterys wildi* new genus and species, is remarkable in its retention of several plesiomorphic features. A phylogenetic analysis places *Plesiopterys* as the sister group of the Plesiosauroidea, and as such the taxon is the most basal taxon yet known on the branch leading to this major clade. *Plesiopterys* possesses a high count of cervical vertebrae and a relatively small head, yet the limbs and limb girdles are plesiomorphic in proportion. The skull displays a mosaic of features, reminiscent of both *Thalassiodracon* and the rhomaleosaurids in some characters, yet similar to *Plesiosaurus* in others. The basicranium is plesiomorphic and resembles that of nothosaur-grade sauropterygians in several respects. A faunal comparison between Holzmaden and the Lower Toarcian deposits on the Yorkshire coast of England concludes that the Holzmaden fauna is more plesiomorphic than the roughly coeval Yorkshire fauna in two of three plesiosaur subclades.

INTRODUCTION

THE PLESIOSAURIA is a monophyletic clade of sauropterygians that arose from more basal, 'nothosaur'-grade progenitors very near the Triassic-Jurassic boundary (Storrs, 1993; for earliest occurence see Taylor and Cruickshank, 1993). The early evolution of the group is documented abundantly in the classic Lias sequences of England and Germany, and plesiosaurs were in fact some of the first extinct reptiles recognized as such at the inception of vertebrate paleontology in the nineteenth century (Taylor, 1997). The systematics of these early forms is still in flux, although much recent work has clarified the taxonomy and morphology of several taxa (''*Eurycleidus*,'' Cruickshank, 1994a; *Thalassiodracon* Storrs and Taylor, 1996; *Plesiosaurus dolichodeirus* Storrs, 1997; and *Plesiosaurus brachypterygius* Maisch and Rücklin, 2000). Recent research effort has begun to clarify the phylogeny of the group as a whole (Carpenter, 1997; Bardet et al., 1999; O'Keefe, 2001a). This paper describes a new genus and species of plesiosaur from the Posidonienschiefer (Toarcian) near Holzmaden, Germany, that displays an interesting combination of primitive and derived features.

The material described here was provisionally referred to ''*Eurycleidus*'' by O'Keefe (2001a) based on general proportional similarities in the postcranium and on similarities in the basicranium. Upon closer examination the material proves not to be referable to ''*Eurycleidus*'' and instead represents a novel taxon (see *Discussion*, herein). This new genus is the fifth valid plesiosaur genus described from the Posidonienschiefer around the village of Holzmaden in southern Germany. The Posidonienschiefer is comprised of bituminous shales interspersed with some thin limestone beds and contains abundant ammonites, used to date the deposits biostratigraphically to the *Dactylioceras tenuicostatum*, *Harpoceras falciferum*, and *Hildoceras bifrons* ammonite zones of the Early Toarcian (for dating see Crux, 1984; Harland et al., 1989; Urlichs et al., 1994). The Posidonienschiefer is famous for whole-body preservation of a wide variety of reptiles, including ichthyosaurs, marine crocodiles, and pterosaurs, as well as isolated dinosaur elements (for a review of the Posidonienschiefer and its fossils see Urlichs et al., 1994). An extensive plesiosaur fauna is also present (Fraas, 1910; Urlichs et al., 1994) and is beginning to receive research attention (Maisch and Rücklin, 2000; O'Keefe, 2001a, p. 7–9). The Holzmaden plesiosaur fauna is significant because it consists of taxa from relatively early in the radiation of the clade. Repositories and abbreviations for material discussed in this paper are: Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS); The Natural History Museum, London, England (BMNH); and the Oxford University Museum of Natural History, Oxford, England (OUM).

SYSTEMATIC PALEONTOLOGY

Supraorder SAUROPTERYGIA Owen, 1860
Suborder PLESIOSAURIA de Blainville, 1835
Family INDETERMINATE
Genus PLESIOPTERYS new genus

Type species.—*Plesiopterys wildi* n. sp., by monotypy.

Diagnosis.—As for species.

Etymology.—*Plesio*-, Gr. near, close, old; -*pterys*, Gr. wing. The latter also refers to the pterygoid bone, which is an important feature of this taxon.

PLESIOPTERYS WILDI new species
Figures 1–7

Diagnosis.—A small plesiosaur possessing 39 cervical vertebrae, a relatively small skull (17 percent of neck length, compared to 28 percent of neck length in *Thalassiodracon*; data from Table 1), and plesiomorphic proportions of the limbs and limb girdles. The skull is unique among plesiosaurs in the retention of grooves for the internal carotid artery on the dorsal surface of the pterygoid. The mandible possesses a short symphysis (number of tooth positions not determinable) without participation of the splenial, but retains a ventral mandibular ridge. Autapomorphies include: quadrate flange of the pterygoid is straight and narrow, and expands into a wide boss at its terminus; possession of flanges of the pterygoid dorsal to the plane of the palate in the anterior of the posterior interpterygoid vacuities; exposure of the cultriform process of the parasphenoid almost to margin of anterior pterygoid vacuity; large anterior interpterygoid vacuity with round posterior margin and pointed anterior margin.

Description.—See below.

Etymology.—Named for R. Wild, in recognition of his many contributions to the vertebrate paleobiology of the German Mesozoic.

Type.—SMNS 16812, a complete skeleton on display in the Staatliches Museum für Naturkunde, Stuttgart, Germany.

Other material examined.—None. Casts of the pectoral and pelvic girdles of SMNS 16812 are in the collections of The Natural History Museum, London (BMNH R5584).

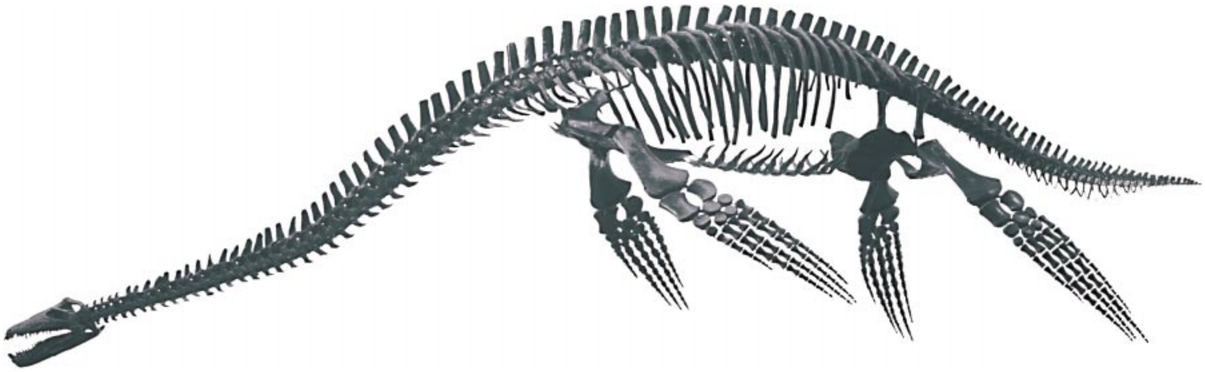

FIGURE *1*—Complete skeleton of *Plesiopterys wildi* new genus and species, SMNS 16812, as currently displayed in the Staatliches Museum für Naturkunde, Stuttgart. Glenoid-acetabulum length of the skeleton as mounted is 50.5 cm; length of skeleton, 2.2 m. The skull is a plaster reconstruction based on measurements taken from the holotype skull. For other dimensions see Table 1.

Occurrence.—Posidonienschiefer, near the village of Holzmaden, Baden-Württemberg, Germany. Lower Toarcian, Lias, Epsilon II 4 (Unterer Schiefer), *Harpoceras falciferum* zone; for locality see Urlichs et al. (1994).

DESCRIPTION

The skeleton (SMNS 16812) was found preserved on a single shale bedding plane and is essentially complete. The skeleton was originally found and prepared in the nineteenth century and little precise information concerning its discovery or preparation is available. All bones save those of the skull have been completely removed from the matrix, and the skeleton is currently mounted and hung from the ceiling of the exhibit hall of the Staatliches Museum für Naturkunde, Stuttgart (Fig. 1). The skull on the mount is a plaster reconstruction based on measurements taken from the original skull (R. Wild, personal commun.). The original skull is crushed and disarticulated (Figs. 2–4), and resides in the collections of the SMNS.

General body proportions.—Measurements and character data were taken from the mounted skeleton after the museum staff kindly arranged access into the glass enclosure surrounding the specimen (Table 1). The glenoid-acetabulum length of the specimen is 50.5 cm and the (average) femur length is 15.5 cm; both measures are quite short for a plesiosaur (O'Keefe, 2002; for comparative data see Table 1). The complete length of the skeleton as currently mounted is 220 cm. The taxon is comparable in overall size to *Thalassiodracon hawkinsi* (Storrs and Taylor, 1996) (Table 1; see also O'Keefe, 2002), the oldest plesiosaur known from adequate material (Storrs and Taylor, 1996; O'Keefe, 2001a). In plesiosaurs and other reptiles the fusion of the neural arches to the bodies of the cervical vertebrae is thought to be indicative of adult age (Vaughn, 1955; Brown, 1981). The neural arches are sutured to the centra in *Plesiopterys*, so the specimen is probably an adult; however, the sutures between centra and neural arch are still clearly visible, so the specimen may be a young adult (Storrs, 1997). The girdle elements, propodials, epipodials, and other limb elements are well ossified and display well-defined margins, also a feature of adult plesiosaurs.

Plesiopterys has generalized body proportions. O'Keefe (2002) performed a morphometric study of plesiosaur body proportion, and found that this specimen plotted in the center of the morphospace, between the plesiomorphic taxa *Plesiosaurus* (Conybeare, 1822) and *Thalassiodracon*. This position reflects the following comparisons in body proportion (comparisons from Table 1): in *Thalassiodracon*, *Plesiosaurus* (O'Keefe, 2002), and *Plesiopterys* the coracoid is much longer than the scapula, while pubis and ischium lengths are subequal in *Thalassiodracon* and *Plesiopterys*. However the pubis is usually longer than the ischium in *Plesiosaurus*, a condition which is also found in most later plesiosauroids. The lengths of the humerus and femur are subequal in both *Thalassiodracon* and *Plesiopterys* while the humerus is somewhat longer than the femur in *Plesiosaurus*, the later genus again foreshadowing the general condition in more derived plesiosauroids.

Plesiopterys has a large number of cervical vertebrae (39), while *Plesiosaurus* has about 37 and *Thalassiodracon* about 31 (plesiosaurs, like other reptiles, display intraspecific variation in the number of cervical vertebrae; Brown, 1981; Sander, 1989; O'Keefe et al., 1999). The count of approximately 31 in *Thalassiodracon* is thought to be plesiomorphic for plesiosaurs (Brown, 1981). In terms of the length of the neck, however, that of *Plesiopterys* is relatively shorter than that of *Plesiosaurus* even though it contains more vertebrae. This counterintuitive finding arises from the fact that individual vertebral centra are much longer in *Plesiosaurus*, so that that this taxon's longer neck contains fewer, longer vertebrae. The intermediate position of *Plesiopterys* in the morphospace of O'Keefe (2002) is therefore attributable to neck morphology; in body size and limb proportions *Plesiopterys* is very similar to *Thalassiodracon*, while in neck length and number of cervical vertebrae *Plesiopterys* resembles *Plesiosaurus*. Regarding the rest of the axial skeleton, *Plesiopterys* possesses 23 dorsal vertebrae, four of which may be considered pectoral vertebrae as the rib articulation is shared between the centrum and the transverse process of the neural arch (Brown, 1981). Three sacral vertebrae are present, and the tail is comprised of 41 caudal vertebrae, the last five of which are tiny spools. For further discussion of the postcranial skeleton, see below.

Skull roof.—The skull of SMNS 16812 (Figs. 2–4) is crushed and partially disarticulated but the bone is well preserved, as is typical of plesiosaur skulls from Holzmaden (Maisch and Rücklin, 2000; personal observation). The posterior portion of the skull and the skull roof, including the suspensoria, parietals, and frontals, are broken from the preorbital region of the skull and palate and rotated to the right; the posterior and anterior regions of the skull are visible, but the areas around the break—the orbit margins and the region between the orbits and external nares—are obliterated. Neither external naris can be identified with certainty. The suture between the left premaxilla and maxilla is visible, extending dorsomedially toward the orbit as is the case in all

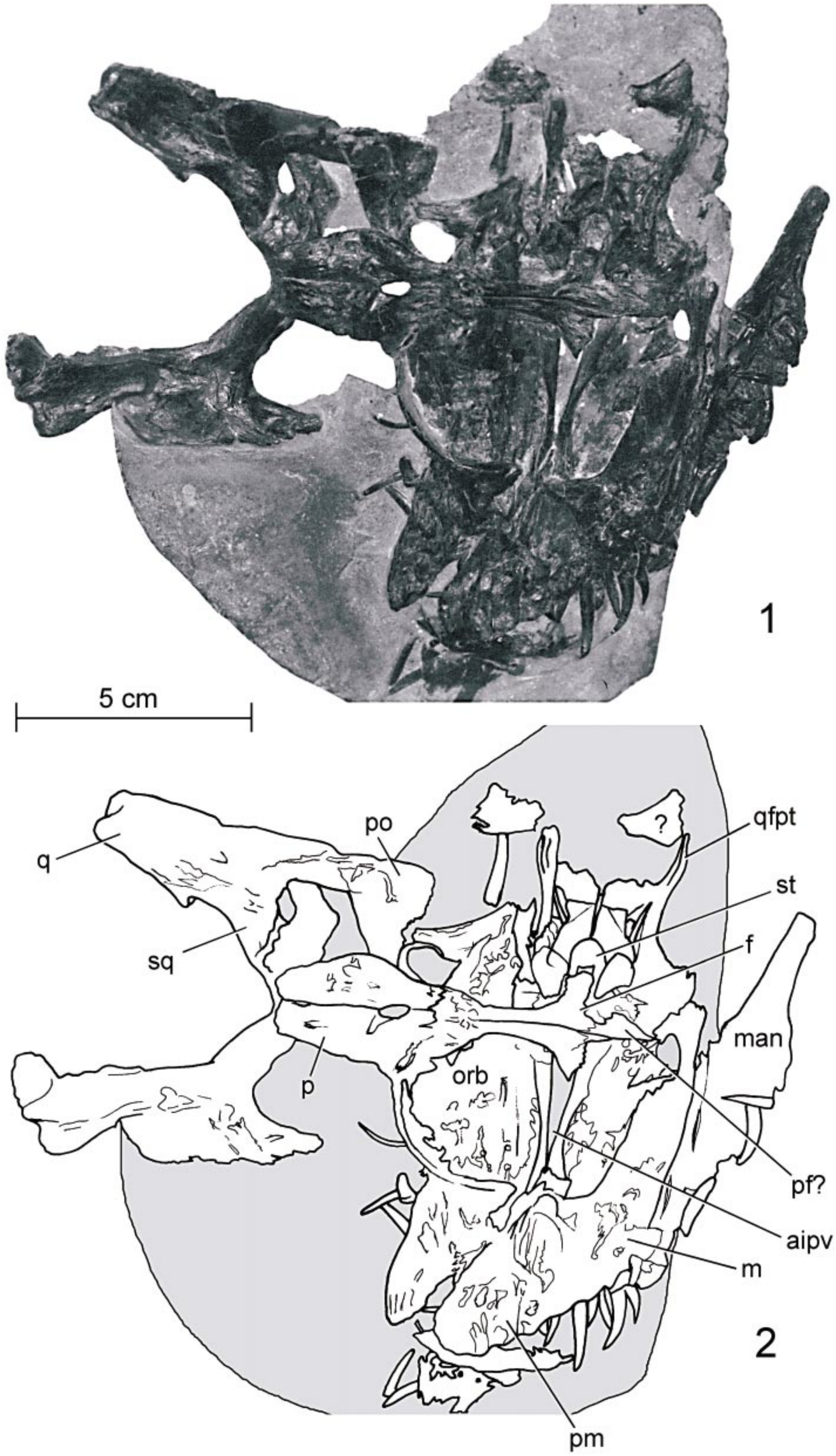

FIGURE 2—Skull of *Plesiopterys wildi* n. gen. and sp., SMNS 16812, dorsal view; *1*, photograph; *2*, interpretation. Abbreviations are: aipv, anterior interpterygoid vacuity; f, frontal; m, maxilla; man, mandible; orb, orbit; p, parietal; pf, prefrontal; pm, premax; po, postorbital; q, quadrate; qfpt, quadrate flange of pterygoid; sq, squamosal; st, sella turcica.

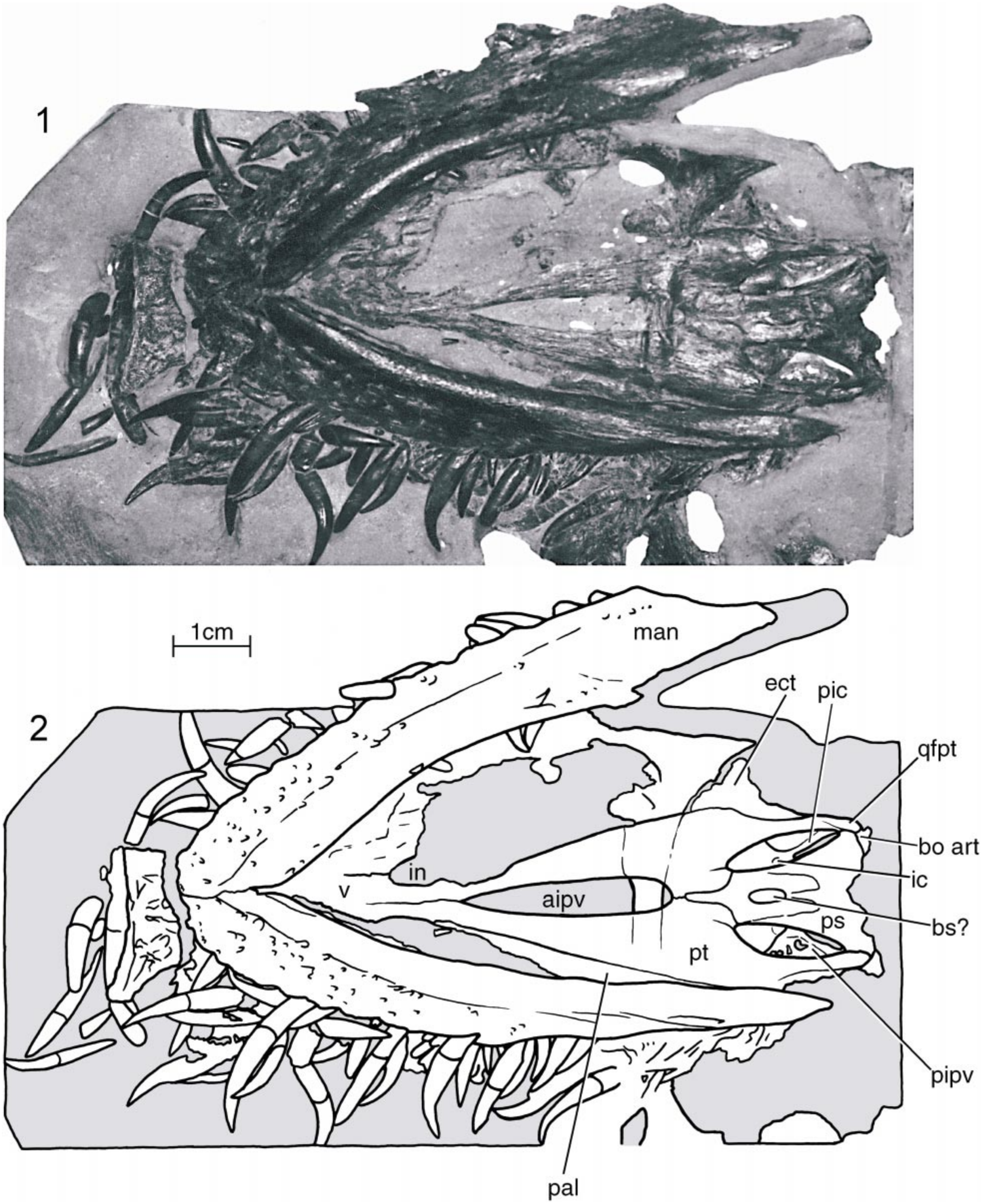

FIGURE 3—Skull of *Plesiopterys wildi* n. gen. and sp., SMNS 16812, ventral view; *1*, photograph; *2*, interpretation. Abbreviations are: aipv, anterior interpterygoid vacuity; bo art, basiocciptial articulation; bs, basisphenoid; ect, ectopterygoid; ic, internal carotid; in, internal naris; man, mandible; pipv, posterior interpterygoid vacuity; ps, parasphenoid; pal, palantine; pic, passage of internal carotid; pt, pterygoid; qfpt, quadrate flange of pterygoid; v, vomer.

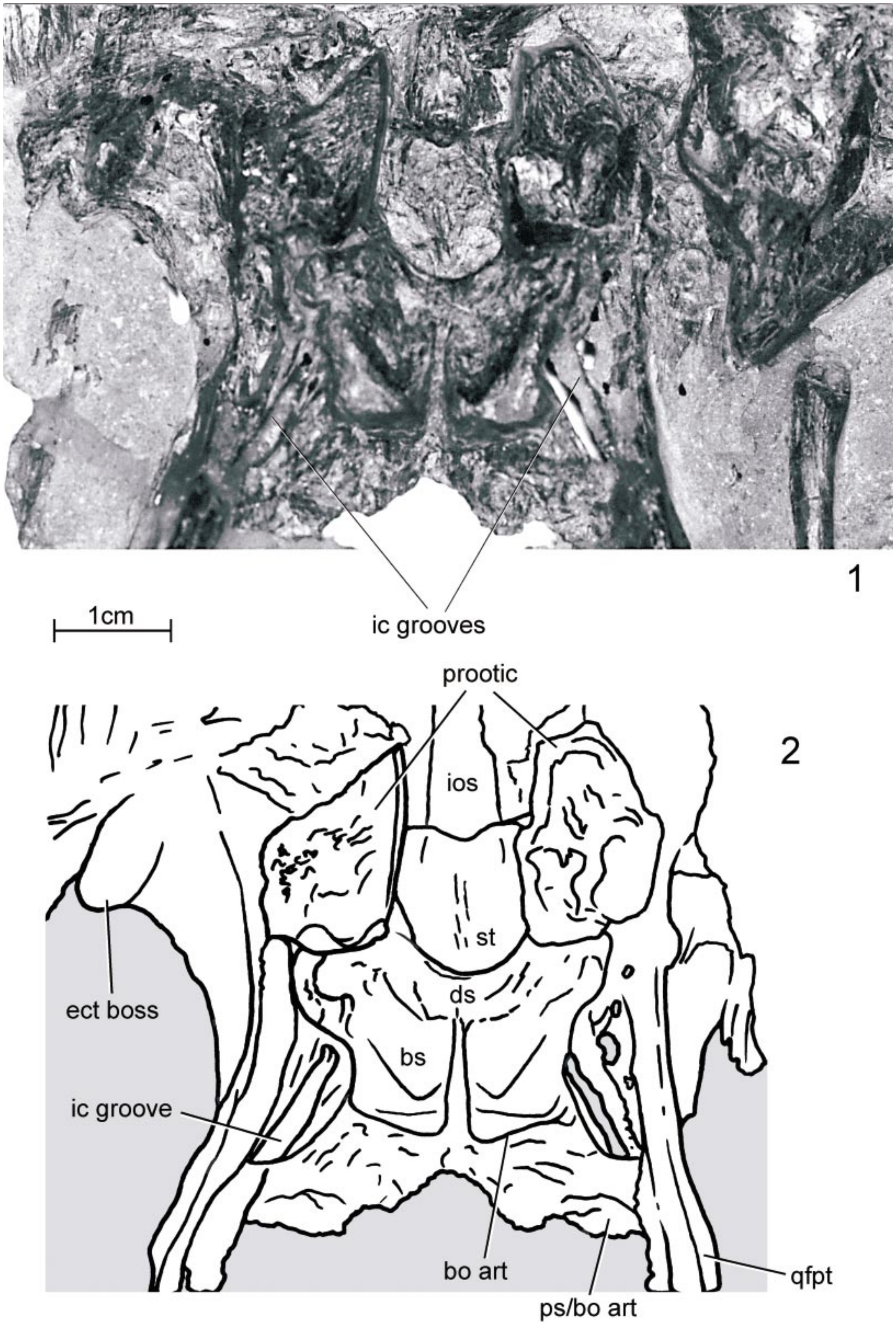

FIGURE 4—Skull of *Plesiopterys wildi* n. gen. and sp., SMNS 16812, basicranium in dorsal view; *1*, photograph; *2*, interpretation. Abbreviations are: bo art, basioccipital articulation; bs, basisphenoid; ect boss, ectopterygoid boss; ic groove, groove for internal carotid artery; ios, interorbital septum; ps/bo art, parasphenoid/basioccipital articulation; qfpt, quadrate flange of the pterygoid; st/ds, sella turcica/dorsum sellae.

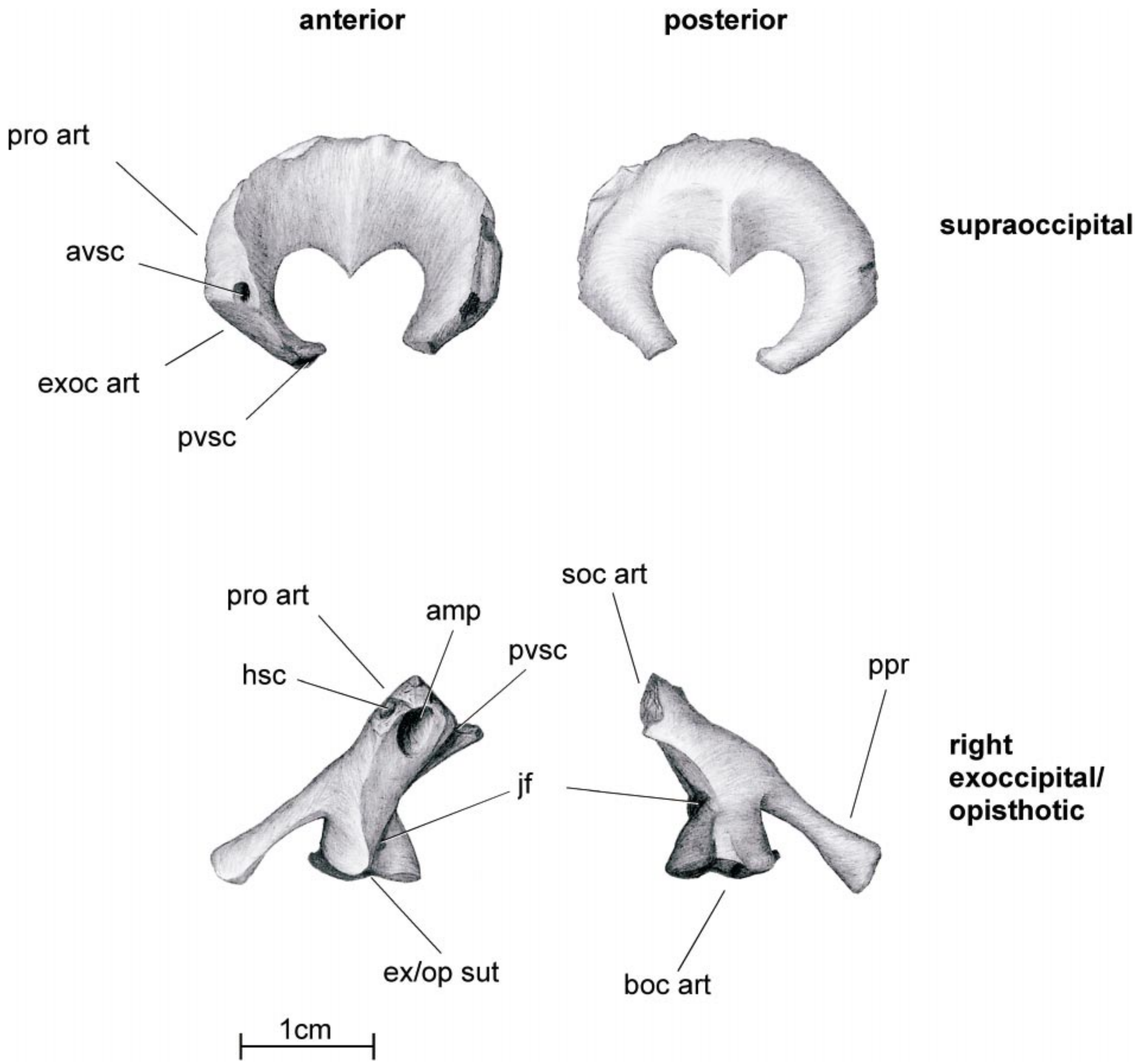

FIGURE 5—Braincase elements of *Plesiopterys wildi* n. gen. and sp., SMNS 16812. *Top*, supraoccipital in anterior and posterior views. *Bottom*, right exoccipital/opisthotic in anterior and posterior views. Abbreviations are: amp, ampulla; avsc, anterior vertical semicircular canal; boc art, basioccipital articulation; exoc art, exoccipital articulation; ex/op sut, exoccipital/opisthotic suture; hsc, horizontal semicircular canal; jf, jugular foramen; ppr, paraoccipital process; pro art, prootic articulation; pvsc, posterior vertical semicircular canal; soc art, supraoccipital articulation.

plesiosaurs (see, for example, Storrs, 1997). The premaxilla contains four or possibly five alveoli; the presence of five premaxillary teeth is plesiomorphic for plesiosaurs (Cruickshank, 1994a; Storrs and Taylor, 1996; Storrs, 1997; O'Keefe, 2001a) and was probably the condition here as well. Both maxillae are distorted, the alveoli are not visible, and the number of maxillary teeth is impossible to determine. The teeth crowns are long, narrow, and curved inward, and bear fine, longitudinal striations. The roots are long and expand to a diameter slightly greater than that of the crown.

The jugal and nasal (if present) could not be identified with confidence in SMNS 16812. This is unfortunate, as the relations of these bones are important indicators of relationship in plesiosaurs. A small flange of bone attached to the skull roof near the frontal/premaxillary suture may be a fragment of the prefrontal and, if so, the morphology of this region would resemble that in *Plesiosaurus* rather than the reduced prefrontals present in ‘‘*Eurycleidus*’’ and *Thalassiodracon* (Cruickshank, 1994a; Storrs, 1997); *Plesiopterys* is coded as similar to *Plesiosaurus* in the data matrix. The frontal clearly contacts the orbit margin for much of its length, and the prefrontal and postfrontal therefore must lack a contact above the orbit. The left postorbital is preserved and displays an oblique edge on its anterior margin for contact with the postfrontal. This suture would have been very similar to the oblique suture seen in most early plesiosaurs (Andrews, 1896; Storrs and Taylor, 1996; Storrs, 1997).

The posterior skull roof is well preserved. The frontals are unfused along the midline. The parietals are also paired, and meet the frontals in an interdigitating suture just anterior to the pineal foramen. The parietals are rather short anteroposteriorly, and

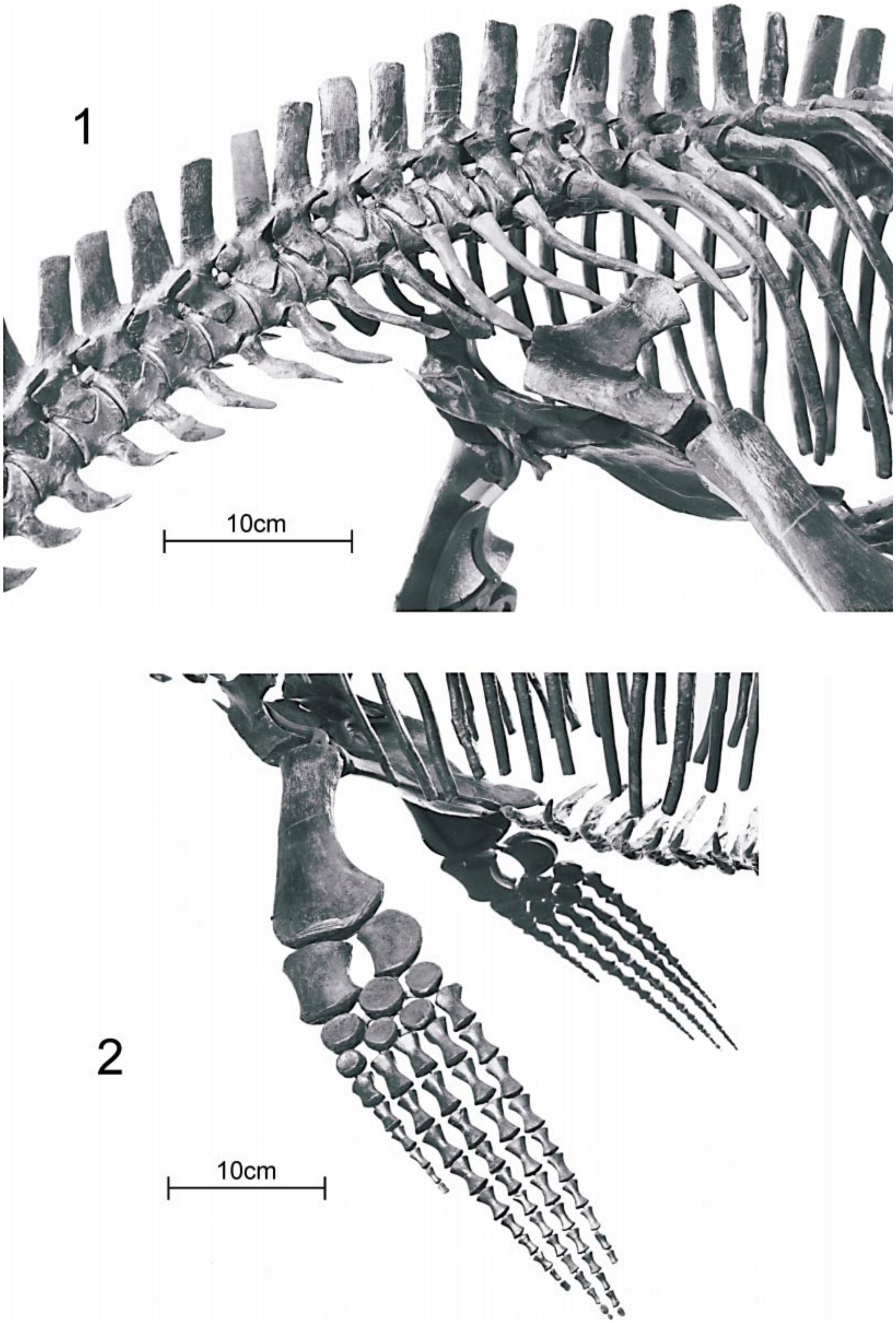

FIGURE 6—Detail views of the postcranium of *Plesiopterys wildi* n. gen. and sp., SMNS 16812. *1*, Posterior cervical, pectoral, and dorsal vertebrae and pectoral girdle. *2*, Right forelimb; note that both forelimbs are mounted ventral side dorsal and on the wrong sides of the pectoral girdle. Limb in the foreground is therefore the right forelimb in ventral view.

FIGURE 7—Detail view of the postcranium of *Plesiopterys wildi* new gen. and sp., SMNS 16812. Complete pelvic girdle in left oblique view.

apparently lack a well-developed sagittal crest; this is possibly the result of postmortem crushing, although a similar, poorly developed sagittal crest is also displayed by *Thalassiodracon* and *Plesiosaurus* among Lias taxa. The temporal fenestrae are correspondingly small and the right and left halves of the squamosal arch form a relatively acute angle at the midline. This configuration more closely resembles that found in pistosauroids rather than more derived plesiosaurs (Rieppel and Werneberg, 1998; Rieppel, 2000) and is a common feature of many Early Jurassic plesiosaurs (*Thalassiodracon*: Storrs and Taylor, 1996; *Plesiosaurus*: Storrs, 1997, Maisch and Rücklin, 2000). The sutures between the squamosals and quadrates could not be identified on either side of the suspensorium, although the mandibular condyle is preserved on the left quadrate and partially on the right quadrate.

Palate and pterygoids.—The mandible is crushed into the palate and obscures the lateral relations of the palatal bones with the maxilla and premaxilla (Fig. 3). The right palatine is fragmentary

TABLE *1*—Measurements of the holotype of *Plesiopterys wildi* new genus and species, SMNS 16812, as compared to selected Lias plesiosaur taxa. Some data also reported in O'Keefe, 2002. BMNH specimen numbers refer to The Natural History Museum, London, England. All measurements in cm.

	Plesiopterys wildi SMNS 16812	*Plesiosaurus dolichodeirus* BMNH 22656	*Plesiosaurus brachypterygius* SMNS 51143	*Thalassiodracon hawkinsi* BMNH 2020
Skull length	14.8	19.5	18.0	17.0
Neck length	86.5	115.0	132.0	61.5
Number of cervical vertebrae	39	37	36	31
Scapula length	7.9	10.0	14.5	9.5
Coracoid length	14.6	20.5	20.8	13.0
Glenoid-acetabulum length	50.5	68.0	60.5	43.0
Pubis length	10.6	13.5	13.5	12.0
Ischium length	9.8	11.5	11.5	12.0
Humerus length	15.4	18.5	22.8	15.0
Length of distal forelimb	34.0	38.0	39.5	27.0
Femur length	15.5	18.5	22.5	15.0
Distal hindlimb length	33.5	42.0	43.5	30.0

and the left is entirely absent, although the medial margins of both internal nares are preserved, and it is probable that the palatines contributed their posterior margins. The maxilla forms at least the anterior half of the lateral wall of the internal naris. The vomer is a large bone, dividing the internal nares; the suture between vomer and pterygoid could not be identified. O'Keefe (2001a) and Storrs (1997) differed in their interpretations of the location of this suture in *Plesiosaurus*; however, the condition in *Rhomaleosaurus victor* (O'Keefe, 2001a) is very similar to the condition illustrated by Storrs (1997) rather than O'Keefe (2001a), and the former author is probably correct for *Plesiosaurus* as well. In *Plesiopterys* the vomer-pterygoid suture was probably located very near the anterior border of the anterior interpterygoid vacuity.

A large anterior interpterygoid vacuity is present on the midline and has a pointed anterior margin; this feature is much larger than the anterior interpterygoid vacuity in *Thalassiodracon* (O'Keefe, in press), *Rhomaleosaurus* (Cruickshank, 1994b), or *Leptocleidus* (Cruickshank, 1997). Like *Thalassiodracon*, the pterygoids in *Plesiopterys* do meet along the midline between the anterior inpterygoid vacuity and the anterior (cultriform) process of the parasphenoid. The cultriform process extends anterior to the posterior interpterygoid vacuity, dividing the pterygoids along the midline. The cultriform process extends almost to the posterior border of the anterior interpterygoid vacuities on the midline and meets the pterygoids laterally in the plane of the palate as in *Thalassiodracon*. However, the exposed portion of the cultriform process in *Plesiopterys* is more narrow.

The prominent posterior interpterygoid vacuities flank the basicranium and are bordered laterally by the quadrate flanges of the pterygoids. The posterior interpterygoid vacuities are separated on the midline by the parasphenoid. The parasphenoid is a triangular element flooring the braincase anteriorly, then extending posterolaterally to articulate with the quadrate flanges of the pterygoids and the basioccipital tubers. A small rugosity in the center of the parasphenoid seems to represent the ventro-posterior process of the basisphenoid, exposed on the palate surface as in *Thalassiodracon* and ''*Eurycleidus*'' (O'Keefe, in press), although the sutures here are not clear. The apparent extent of the parasphenoid behind the small exposure of the basisphenoid on the palate surface is a unique feature of this taxon.

Plesiopterys differs from all other known plesiosaurs in the configuration of the pterygoids (Figs. 3, 4). These produce thin flanges that extend into the area lateral to the parasphenoid, into the anterior portion of the posterior interpterygoid vacuities. These flanges of the pterygoid are very thin, dorsal to the plane of the rest of the palate, and are closely applied to the ventral surface of the body of the basisphenoid so that the outlines of that bone are visible as contours in the pterygoid (Fig. 3). There is no apparent suture between these flanges and the quadrate rami of the pterygoids on the palate surface, and foramina for the passage of the internal carotid arteries are not visible, although two dimples just lateral to the parasphenoid may indicate their position piercing the basisphenoid dorsal to the pterygoids. The dorsal surfaces of the pterygoids (Fig. 4) are remarkable in showing paired, shallow grooves, running from posterolateral to anteromedial, terminating just behind the body of the parasphenoid. The pterygoid here is very thin, and is exposed in dorsal and ventral views. These grooves are in a similar position and configuration as the grooves for the internal carotid arteries in the pterygoids of the pistosauroid *Cymatosaurus* (Rieppel and Werneburg, 1998) and are hypothesized to be homologous with these structures.

The posterior end (as preserved) of the quadrate ramus of the pterygoid produces a short medial process that contacts the posterolateral corner of the basisphenoid beneath the area of articulation with the basioccipital tubers. There is no process or facet evident for articulation with the quadrate, although in other early plesiosaurs the quadrate ramus continues posterolaterally for a significant distance before contacting the suspensorium. It seems probable that the distal portions of both quadrate flanges have been broken away in the skull of *Plesiopterys*, although this is not certain.

Mandible.—The mandible of *Plesiopterys* is preserved in ventral view (Fig. 3). The mandible retains a prominent mandibular ridge, a feature characteristic of *Thalassiodracon* and most rhomaleosaurs (e.g., *Rhomaleosaurus victor*), but lost in all plesiosauroids (O'Keefe, 2001a). This feature does not appear to be an artifact of crushing. The lower jaw symphysis is not reinforced, and resembles the simple symphysis seen in *Plesiosaurus* and related taxa rather than the reinforced symphysis displayed by *Thalassiodracon* (Storrs and Taylor, 1996; O'Keefe, 2001a). The splenial does not participate in the lower jaw symphysis, again resembling *Plesiosaurus* and related taxa, but unlike *Thalassiodracon* and most pliosauroids (O'Keefe, 2001a). The lingual surfaces of both mandibular rami are still obscured by shale and the posterior portions of both are crushed. No bones posterior to the dentary could be identified.

Braincase.—Several elements of the braincase are disarticulated from the rest of the skull, including both exoccipital/opisthotics, the basioccipital, and the supraoccipital. These elements are quite similar to those found in *Thalassiodracon*, are figured and described below, and discussed in more detail in O'Keefe (in press). Figure 3 illustrates the ventral elements of the braincase and their relations with the palate; the basisphenoid is prominent and bears a deep notch in its posterior margin. The dorsum sellae is a poorly developed shelf just posterior to the sella turcica. The latter structure possesses a flat floor and is open anteriorly. Foramina for the passage of the internal carotid arteries through the floor of the sella turcica could not be identified. Both prootics are preserved close to their articulations with the anterior aspect of the basisphenoid, although both are crushed down onto the palate and little detailed morphology is visible on either (Fig. 4). The right basal articulation between the basisphenoid and pterygoid is just visible posterior to the right prootic. A low ridge of bone runs anteriorly from the sella turcica, and is probably the root of the interorbital septum.

Figure 5 portrays the supraoccipital and right exoccipital/opisthotic. The supraoccipital is shallow anteroposteriorly and possesses a sharp process on the midline projecting ventrally into the foramen magnum. *Plesiopterys* shares these plesiomorphic characters with *Thalassiodracon* (O'Keefe, in press) and *Plesiosaurus* (O'Keefe, 2001a) among Lias plesiosaurs. A foramen for the passage of the anterior vertical semicircular canal is present in the articulation for the right prootic, while a groove for the posterior vertical semicircular canal is identifiable in the articulation for the right opisthotic. The exoccipital/opisthotic is a complex bone, consisting of a stout column forming the lateral wall of the foramen magnum and a slender paraoccipital process. The wall of the foramen magnum possesses a distinct groove on its medial surface, interpretable as the suture between exoccipital and opisthotic; this suture is usually invisible in plesiosaurs but has been identified in *Peloneustes* (Lydekker, 1889b) by Andrews (1913). The jugular foramen rests in this groove, reflecting its developmental origin as the metotic fissure (Romer, 1956). The jugular foramen exits the lateral surface of the exoccipital/opisthotic ventral and posterior to the paraoccipital process. The paraoccipital process is gracile and extends laterally to effect an articulation with the suspensorium. A foramen for the passage of the hypoglossal nerve pierces the exoccipital near the posteroventral margin of the foramen magnum wall.

Postcranium.—Elements of the postcranium of *Plesiopterys* *wildi* n. gen. and sp. are illustrated in Figures 6 and 7. The cervical vertebrae of *Plesiopterys* are of typical plesiosaurian type; i.e., the neural arches lack zygosphene/zygantrum articulations and are not as tall as the height of the vertebral centra. As in all other plesiosaurs, (Brown, 1981) the cervical centra of *Plesiopterys* possess well-defined foramina subcentralia on their ventral surfaces. The cervical ribs retain two heads that are not elongate and the more cranial ribs possess a distinct anterior process. The cervical neural spines are high and bladelike as in *Plesiosaurus*, but are angled backward as in *Thalassiodracon* (O'Keefe, 2001a, char. 125). All centra are about as wide as they are long. As mentioned above, however, the number of cervicals is increased to 39 from the plesiomorphic 30–32. This condition contrasts with that displayed by *Rhomaleosaurus victor*; in this taxon, the number of cervicals is plesiomorphic but each centrum is compressed anteroposteriorly. As a general rule, plesiosaur neck length changes both by increasing or decreasing the number of cervicals and by changes in the dimensions of each centrum (O'Keefe, 2002). This rule does not hold for *Plesiopterys* and *Rhomaleosaurus victor*, however, and both taxa may be transitional in neck morphology. This variability highlights the high plasticity in plesiosaur cervical dimensions.

The forelimb of *Plesiopterys wildi* is very similar to that of *Plesiosaurus* (see Storrs, 1997). The humerus is of generalized plesiosaurian type; the proximal end holds a spherical glenohumeral condyle of poorly finished bone, the midshaft is roughly circular, and the distal end is broad and flattened with a teardrop cross section. The proximal shaft is surmounted on its anterodorsal aspect by a low tuberosity, a typical feature of Lias plesiosaur humeri (e.g., *Plesiosaurus* Storrs, 1997). *Plesiopterys* lacks a channel of finished bone between this tuberosity and the articular face of the glenohumeral condyle, although this condition is thought to vary ontogenetically (Brown, 1981) and is not always present even in adults. The shaft of the humerus curves backward, yielding the angled humerus that is characteristic of nothosaur-grade sauropterygians and primitive plesiosaurs (Storrs, 1993, 1997). The distal end of the humerus possesses an anterior and a posterior facet, the former for articulation with the radius, the latter for the ulna. These facets are well developed in *Plesiopterys* and this is thought to indicate an adult ontogenetic stage (Storrs, 1997). The epipodials of *Plesiopterys* are primitive, being longer than broad; the radius also retains an hourglass outline and resembles a foreshortened long bone, while the ulna is lunate. The epipodials closely resemble those of both *Plesiosaurus* (Storrs, 1997) and *Thalassiodracon* (personal observation). *Plesiopterys* possesses a proximally shifted fifth metacarpal, as do all plesiosaurs known to this author (O'Keefe, 2001a, char. 163). The remainder of the forelimb is hydrofoil-shaped and of relatively high aspect ratio, as is plesiomorphic for plesiosaurs (O'Keefe, 2001b; also noted by Storrs [1997] for *Plesiosaurus*).

PHYLOGENETIC ANALYSIS

In order to develop a hypothesis of relationship for *Plesiopterys wildi* n. gen. and sp., a cladistic analysis was performed using a revised version of the data matrix in O'Keefe (2001a). This matrix has been modified by the recoding of ''*Eurycleidus*'' to reflect the exclusion of the *Plesiopterys* type material and the coding of *Plesiopterys*. Various minor errors have also been corrected relative to the matrix presented in O'Keefe (2001a). Four new characters have also been added, and are listed and described below; the balance of characters are defined and discussed in O'Keefe (2001a). The full data matrix can be found in the Appendix.

Novel characters.—167. Possession of a marked groove around the margins of the articular surfaces of cervical and dorsal vertebral centra, as noted by Brown (1984). This character is present in most cryptocleidoids. Absent (0), present (1).

168. Possession of a posterior process of the postorbital forming part of the ventral margin of the temporal fenestra. This process is found in all known pistosauroids (Rieppel, 2000) and in some basal plesiosaurs (O'Keefe, 2001a). Absent (0), present (1).

169. Possession of a deep notch in the posterior margin of the clivus (basisphenoid body). Possession of this notch is a feature common to *Cymatosaurus* (Rieppel and Werneburg, 1998) and some plesiosaurs (O'Keefe, 2001a; Fig. 4, above). Absent (0), present (1).

170. Possession of grooves in the dorsal surface of the pterygoid for the carriage of the internal carotid artery. These grooves are found in *Nothosaurus* (Rieppel, 1994), *Cymatosaurus* (Rieppel and Werneburg, 1998), and *Plesiopterys* (Fig. 4). Absent (0), present (1).

Analysis.—A total of 170 characters and 35 taxa were included in the cladistic analysis. Three taxa [*Simosaurus* (Meyer, 1842), *Cymatosaurus*, and Pistosauridae; for discussion of outgroup choice see O'Keefe, 2001a] were specified as the outgroup, and were constrained to be paraphyletic with respect to the ingroup to reflect the topology of Rieppel (2000, p. 5). Primitive states of characters are scored as zero for convenience, and polarity was determined via comparison with the outgroup. All characters were scored as unordered except those where a second state is logically dependent on the first. Data was analyzed using PAUP* v.4.0b10 (Swofford, 2002). A heuristic search was performed on the data matrix using tree-bisection-reconnection (TBR) branch swapping. The search returned three most parsimonious trees (MPTs), the strict consensus of which is shown in Figure 8. The MPTs had a tree length of 443, a consistency index excluding uninformative characters of CI = 0.43, a rescaled consistency index of RC = 0.33, and a retention index of RI = 0.72. A bootstrap analysis was performed (1,000 replicates), and bootstrap percentages are reported for well-supported nodes in the strict consensus tree in Figure 8, along with the decay index for each node.

DISCUSSION

Comparison of Plesiopterys *and* ''Eurycleidus.''—Comparison of SMNS 16812 with *Eurycleidus* is necessary given its previous assignment to that taxon by O'Keefe (2001a). This author made this assignment without adequate examination of the *Eurycleidus* material; subsequent analysis proves the assignment was erroneous, being based on general body proportions and basicranial characters that are, in retrospect, plesiomorphic. The *Eurycleidus* type material is a single cervical vertebra (BMNH R.1318) figured and described by Owen (1840a); the specimen may also include a partial lower jaw (BMNH 2030), purchased by the (British) Natural History Museum as part of the Hawkins Collection in 1834 and described briefly by Owen (1840b). Lydekker (1889a) lists additional elements that apparently come from the same (type) skeleton (for discussion of the taxonomic history of *Eurycleidus* see Cruickshank, 1994a). The present comparison rests on personal examination of the Oxford material (disarticulated partial skull and skeleton, OUM J.28585) tentatively referred to *Eurycleidus* by Cruickshank, and on that author's revision of the generic diagnosis (Cruickshank, 1994a). However, the status of *Eurycleidus* is currently under active review, and the Oxford specimen referred to that taxon by Cruickshank (1994a) may in fact represent a new genus (Cruickshank, personal commun., 2003). Comments about this taxon should therefore be taken as provisional; throughout this paper the genus name ''*Eurycleidus*'' is placed in quotes to indicate that the comparisons being made involve the disputed Oxford material rather than the *Eurycleidus* type material.

Regardless of the true identity of the Oxford material, the German material is demonstrably different from it and is certainly a new taxon. O'Keefe (2001a) cited similarities in the basicranium

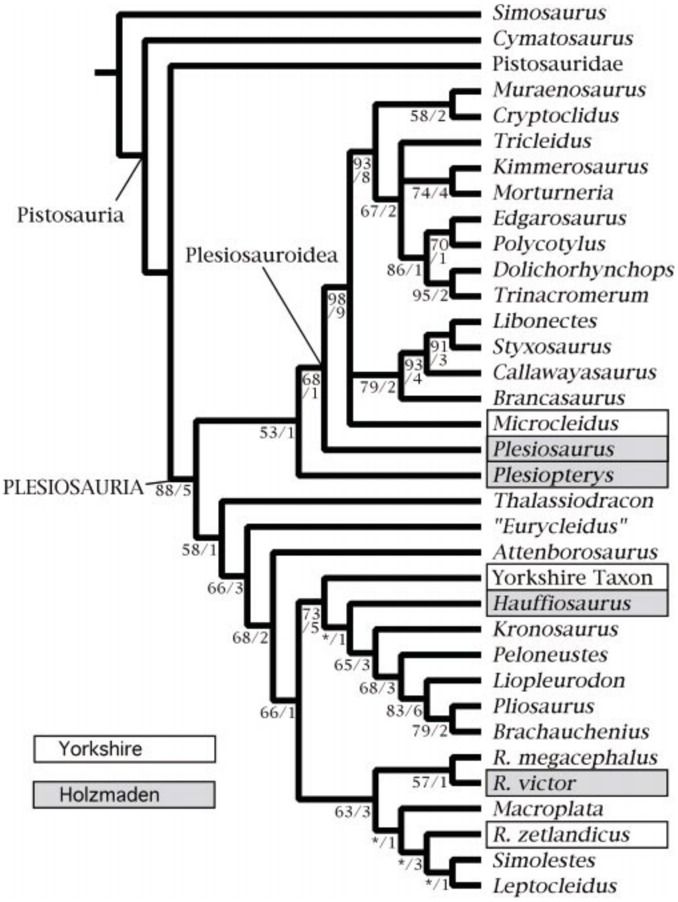

FIGURE *8*—Hypothesis of relationships for the Plesiosauria; for tree statistics and methodology, see text. Numbers below each node are bootstrap percentages/decay indices. Bootstrap percentages are based on 1,000 replicates, with an asterisk indicating less than 50 percent bootstrap support. Gray-and-white boxed taxa occur in Holzmaden and Yorkshire, respectively. Taxonomy from O'Keefe (2001a).

between the German material and that of ''*Eurycleidus*''; however, these similarities are plesiomorphic rather than apomorphic. The basicranium of ''*Eurycleidus*'' (figured in O'Keefe, 2001a, in press) differs from that of *Plesiopterys* by having a parasphenoid that is smaller and less elaborated. The basisphenoid is similar in the two taxa, although that of ''*Eurycleidus*'' is poorly ossified. Large differences are apparent in the mandibular symphysis, where *Plesiopterys* possesses several synapomorphies of the Plesiosauroidea (lack of participation of splenial in symphysis; simple, unreinforced jaw symphysis; and lack of caniniform teeth on symphysis). ''*Eurycleidus*'' possesses the reinforced jaw symphysis, splenial participation, and caniniform teeth common to most rhomaleosaurs. ''*Eurycleidus*'' also appears to have had a narrower snout and broader postorbital region than *Plesiopterys* (Cruickshank, 1994a). *Plesiopterys* is demonstrably different from ''*Eurycleidus*,'' especially based on characters of the lower jaw and other regions of the skull, and should be considered a new genus.

Faunal comparison.—The earliest fragmentary plesiosaurs known come from a glacial erratic block in northern Scotland believed to be of Rhaetian age (Taylor and Cruickshank, 1993; Storrs and Taylor, 1996), while a more complete fauna is known from the Lias of Street (Rhaetian-Hettangian) and Dorset (Hettangian-Pliensbachian). The English Toarcian fauna is best represented by deposits on the Yorkshire coast (Benton and Spencer, 1995). The Yorkshire coast fauna comes from formations coeval with the Posidonienschiefer (Jet Rock and Alum Shale formations, *falciferum* and *bifrons* ammonite zones, respectively; Benton and Taylor, 1984; Harland et al., 1989) and contains an indeterminate number of plesiosaur taxa, but there are at least three valid taxa and possibly more (Benton and Taylor, 1984). These taxa are the rhomaleosaurids *Rhomaleosaurus zetlandicus* Phillips *in* Anon., 1854; *Rhomaleosaurus cramptoni* Carte and Baily, 1863 (probably synonymous with *R. zetlandicus*, see discussion in Cruickshank, 1996); a currently unnamed basal pliosaurid (named '*Plesiosaurus*' *longirostris* by Blake, 1876, and erroneously referred to *Macroplata* Swinton, 1930 by White, 1940 and O'Keefe, 2001a); and the basal plesiosauroid *Microcleidus homalospondylus* Owen, 1865 (Benton and Taylor, 1984; taxonomy from O'Keefe, 2001a). Both *Microcleidus* and the unnamed pliosaurid possess few autapomorphies and their phylogenetic positions are poorly resolved relative to more derived members of their respective clades. The rhomaleosaurid species from Yorkshire is a relatively derived member of that clade.

The Posidonienschiefer plesiosaur fauna is comparable to that of Yorkshire in general terms, although there are interesting differences. The rhomaleosaurids are represented in Holzmaden by *Rhomaleosaurus victor* (Fraas, 1910), a relatively plesiomorphic taxon more similar to *Rhomaleosaurus megacephalus* (earliest Hettangian, Cruickshank, 1994b) than either is to the coeval Yorkshire rhomaleosaurid (O'Keefe, 2001a; Fig. 9). The genus *Plesiosaurus* is represented by several individuals of *Plesiosaurus brachypterygius*, as well as *Plesiosaurus guilelmiimperatoris* Dames, 1895. *Plesiosaurus* does not occur in Yorkshire; the plesiosauroids are represented here by the more derived taxon *Microcleidus*. Rhomaleosaurid and plesiosauroid taxa from Yorkshire are therefore more derived than their relatives from Holzmaden. However, this pattern does not hold in the pliosaurids, where the unnamed Yorkshire pliosaurid is more plesiomorphic than the Holzmaden genus *Hauffiosaurus* O'Keefe, 2001a (although bootstrap and decay index support for this node is very weak). The plesiosaur faunas from Holzmaden and Yorkshire are similar and both contain taxa retaining primitive features. There is some indication that Holzmaden might retain the more primitive fauna. This observation is significant given the morphology and phylogenetic position of *Plesiopterys* (Fig. 8).

Phylogenetic position of Plesiopterys.—The phylogenetic position of *Plesiopterys* is significant because this taxon is the sister group to the Plesiosauroidea and helps to document the early evolution of this clade. *Plesiopterys* possesses a remarkable mosaic of characters, some of which have heretofore been associated only with *Thalassiodracon*, while others are advanced features of the Plesiosauroidea. In terms of general body form, the small body size and proportions of the limb girdles are quite similar between *Thalassiodracon* and *Plesiopterys*. However, *Plesiopterys* has a relatively large number of cervical vertebrae and a relatively small head, similar to the situation in *Plesiosaurus*. This intermediate condition is also reflected in the detailed morphology of the skull. Because *Plesiopterys* is intermediate in many respects, I have chosen not to include it in the Plesiosauroidea; such a taxonomic redefinition would result in a clade lacking many of the features that have been associated with plesiosauroids for over a century. The position of *Plesiopterys* as a primitive stem taxon basal to more traditional plesiosauroids is an accurate reflection of its morphology.

The morphology of the anterior interpterygoid vacuity and parasphenoid on the palate of *Plesiopterys* is intermediate between *Thalassiodracon* and *Plesiosaurus*. The anterior interpterygoid vacuity is large, comparable to that in *Plesiosaurus* (Storrs, 1997), but the pterygoids retain a contact posteriorly covering the anterior of the parasphenoid as in *Thalassiodracon*. The lower jaw of *Plesiopterys* is also morphologically intermediate, as it retains the

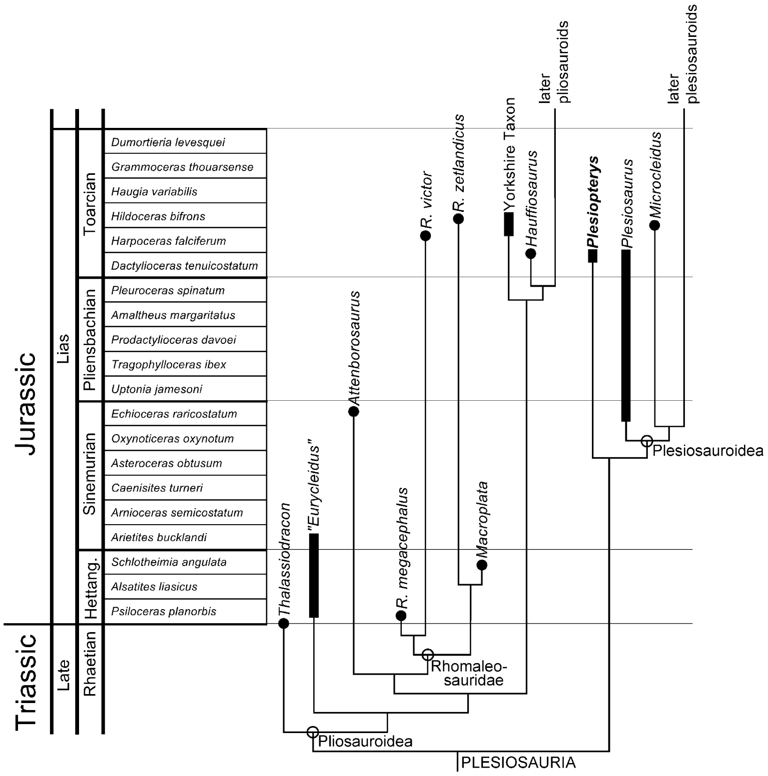

FIGURE 9—Phylogeny of Lias Plesiosauria. Topology is from Figure 7 and taxon sampling is not exhaustive. Ranges of taxa are taken from Benton and Taylor, 1984; Urlichs et al., 1994; Benton and Spencer, 1995; Storrs and Taylor, 1996; and Storrs, 1997.

ventral mandibular ridge common to *Thalassiodracon* and the rhomaleosaurids, but has lost the reinforced symphysis, caniniform teeth, and splenial participation in the symphysis found in these taxa. Instead these features resemble *Plesiosaurus* and other plesiosauroids. The cranial morphology of *Plesiopterys* may be characterized as intermediate between *Thalassiodracon* and *Plesiosaurus* in many respects.

The pterygoids are the most remarkable feature of *Plesiopterys*. They display a condition similar in some ways to that seen in more basal pistosauroids, outside of the clade Plesiosauria entirely. The presence of grooves in the dorsal surface of the pterygoid is a character found previously in nothosaur-grade sauropterygians only (Rieppel and Werneburg, 1998; O'Keefe, in press). The extensions of the pterygoids within the posterior interpterygoid vacuities and the pterygoid covering of the ventral surface of the basisphenoid likewise recall the closed palate found in nothosaur-grade sauropterygians, rather than the open palate common to all plesiosaurs (for interpretation see O'Keefe, in press). *Plesiopterys* is therefore a very primitive taxon, and its mosaic of primitive and derived characters in the skull and postcranium document a very early stage in the evolution of the Plesiosauroidea.

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APPENDIX

Cladistic data matrix for cladogram presented in Figure 7. Inapplicable characters are scored with an ‘x’, while unknowns are scored with a ‘?’. For further discussion see text.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Attenborosaurus	1	0	1	1	0	0	0	1	1	0	0	?	?	0	0	?	0	?	?	1	0	0	0	0	2	0	1	0	1	1	0	0	0	?	1	0	?	0	?	0	0	?	?	1	?	0	?	?
Brachauchenius	1	2	?	?	?	1	?	2	1	0	1	1	0	x	x	0	0	0	0	1	0	0	0	0	2	0	1	1	1	0	0	1	0	1	1	1	0	0	1	0	0	?	?	1	?	1	?	0
Brancasaurus	2	1	2	1	0	0	0	0	0	0	0	0	0	1	x	0	0	1	?	1	1	0	0	0	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	1	0	0	1	?	0	?	0
Callawayasaurus	2	1	2	0	2	0	0	0	0	0	0	0	0	0	x	0	1	1	?	1	1	0	0	0	2	1	1	1	1	2	0	0	0	1	2	x	0	x	1	1	1	0	0	1	1	0	2	0
Cryptoclidus	2	0	0	1	2	0	1	0	0	0	0	0	0	0	x	0	0	0	1	1	1	0	0	0	2	1	1	0	1	2	0	0	1	1	2	x	0	x	1	1	0	1	1	1	?	0	1	0
Cymatosaurus	0	?	?	?	?	2	x	0	1	0	0	?	0	0	1&2	1	0	1	?	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0&1	0	0	0	?	?	1	1	?	?	?
Dolichorhynchops	1	2	1	1	0	1	1	2	0	0	1	0	0	x	x	0	0	0	?	1	0	0	0	1	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	2	0	0	1	1	0	1	1
Edgarosaurus	0	2	?	?	?	0	1	1	0	0	0	1	0	0	x	0	0	0	1	1	0	0	0	0	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	2	0	0	1	1	1	?	?
"Eurycleidus"	0	?	0	?	?	0	?	1	1	0	0	?	0	0	0	1	0	0	?	1	0	0	0	0	1	0	?	?	1	?	?	?	0	1	?	?	0	?	0	1	?	0	1	1	1	0	0	?
Hauffiosaurus	1	0	2	1	0	1	0	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0	1	?	?	?	?	?	?	0	?	1	?	?	?	?	?
Kimmerosaurus	?	?	?	?	?	2	?	3	0	0	0	?	?	0	x	0	?	0	?	1	1	?	0	0	2	1	1	?	1	?	?	?	1	1	?	x	?	?	?	1	?	1	1	1	1	0	0	0
Kronosaurus	1	2	2	1	?	1	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	1	?	?	1	?	1	?	?	?	?	?	?	?	?	1	1	1	0	2	0
Leptocleidus	?	2	?	1	?	0	1	1	1	0	1	0	1	x	x	0	0	0	?	1	0	0	0	0	2	0	1	0	1	0	0	?	0	1	?	?	?	?	0	?	1	0	?	1	?	?	?	?
Libonectes	2	1	?	0	?	0	0	0	0	0	2	0	0	x	x	?	1	?	?	1	1	0	0	?	2	1	?	1	1	2	0	0	0	1	2	x	0	x	1	1	?	0	0	1	1	0	2	0
Liopleurodon	1	2	1	1	1	1	1	2	2	0	1	1	0	x	x	0	0	0	1	1	0	0	0	0	2	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0
Macroplata	1	0	1	1	1	0	1	1	1	0	?	0	1	0	?	?	0	0	1	1	?	0	0	0	2	?	1	?	1	0	0	?	0	?	1	0	1	?	0	0	?	0	1	1	?	1	?	0
Microcleidus	2	1	0	1	0	0	0	0	0	0	0	0	0	?	?	0	?	1	?	1	1	?	0	0	2	1	1	?	1	?	0	?	0	1	2	x	0	x	?	1	1	?	?	?	?	?	?	?
Morturneria	?	?	?	?	?	2	1	3	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	?	?	?	1	?	x	?	?	?	x	?	0	0	?	1	1	0	?
Muraenosaurus	2	1	0	1	2	0	1	0	0	0	0	0	0	0	x	0	0	0	0	1	1	?	0	0	2	1	1	0	1	2	0	0	?	?	?	x	0	?	?	1	?	0	1	1	?	0	?	0
Peloneustes	1	2	1	1	1	1	1	2	1	0	1	1	0	x	x	0	0	0	1	1	0	0	0	0	2	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0
Pistosauridae	0	0	?	1	?	0	x	1	0	0	0	?	0	0	1	1	0	1	?	1	0	0	0	0	1	0	1	0	1	1	0	0	0	?	1	0	0	1	0	1	0	?	?	1	?	?	?	?
Plesiopterys	2	1	0	1	0	0	0	0	1	?	0	?	?	0	0	1	0	0	?	1	0	0	0	0	1	?	1	0	?	?	?	?	?	1	?	?	?	?	1	1	?	0	1	1	?	0	0	0
Plesiosaurus	0	0	2	1	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	2	0	0	x	1	1	1	?	0	1	?	0	?	?
Pliosaurus	1	2	?	?	?	1	?	2	2	0	1	1	0	x	x	0	0	0	?	1	0	0	0	0	2	?	1	1	1	0	0	1	0	1	1	1	0	?	?	0	0	0	1	1	?	1	?	?
Polycotylus	?	2	1	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	x	?	?	?	?	?	?	?	?	?	?	?	?
R. megacephalus	0	0	0	1	0	0	0	1	1	0	0	1	0	0	x	1	0	0	1	1	0	0	0	0	2	0	1	?	1	0	0	?	0	1	1	0	1	0	0	?	1	?	1	1	1	1	?	0
R. victor	1	0	0	1	2	0	0	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
R. zetlandicus	0	2	?	?	0	1	?	1	1	0	1	0	1	x	?	0	0	0	1	1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	1	0	0	0	?	?	1	1	?	1	1	1
Simolestes	1	2	1	1	1	0	1	1	1	0	1	0	?	x	x	0	?	?	?	1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	?	0	?	?	?	0	1	1	?	1	0	0
Simosaurus	0	0	0	0	2	2	x	0	0	0	0	?	0	1	2	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	x	0	x
Styxosaurus	2	1	?	?	?	0	0	0	0	0	2	0	?	x	?	0	1	0	?	?	?	0	0	0	2	1	1	1	1	2	0	0	0	1	2	x	0	x	1	1	1	?	?	1	?	?	?	?
Thalassiodracon	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0
Tricleidus	2	0	?	1	0	2	1	0	0	0	0	0	0	0	x	?	?	0	?	1	0	0	0	0	2	1	1	?	1	2	0	0	1	1	2	x	0	x	?	1	0	0	0	1	1	0	1	1
Trinacromerum	1	2	1	1	1	1	1	2	0	0	1	0	0	x	x	0	?	0	?	1	?	0	0	1	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	2	?	0	1	?	0	1	1
Yorkshire Taxon	1	0	2	1	0	1	0	2	0	0	?	1	0	x	0	0	?	?	0	1	0	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	1	0	0	?	?	0	1	1	1	0	0	0

Taxon	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
Attenborosaurus	?	?	?	?	?	1	1	?	?	2	0	?	1	0	1	x	0	0	0	0	1	0	0	2	0	0	0	0	1	?	?	?	?	1	?	0	x	0	0	1	2	1	?	0	0
Brachauchenius	?	?	?	1	1	1	1	?	?	1	0	0	1	1	1	0	0	0	0	0	3	0	2	2	x	0	?	0	?	0	?	1	?	1	1	1	0	0	0	?	2	1	?	1	?
Brancasaurus	?	?	?	?	?	0	0	1	1	1	?	0	1	?	?	0	?	?	0	0	?	0	?	?	1	0	?	0	0	?	0	0	1	?	1	?	?	0	?	0	?	?	?	?	?
Callawayasaurus	1	1	1	?	?	0	0	1	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	2	1	?	0	0	0	0	0	0	1	0	1	0	x	1	1	0	1	0	0	0	0
Cryptoclidus	0	?	0	?	?	1	0	1	1	1	0	2	1	0	0	x	0	1	0	0	0	1	0	2	1	0	0	0	0	0	0	0	?	0	0	0	x	0	1	0	0	0	0	0	0
Cymatosaurus	?	?	?	?	?	0	x	?	?	2	0	0	0	x	x	x	0	0	?	x	x	?	x	x	x	x	?	x	0	0	0	0	1	0	1	1	0	0	?	?	2	?	?	?	?
Dolichorhynchops	1	0	0	0	0	1	0	1	1	1	0	2	1	2	0	0	0	1	1	1	0	1	0	2	1	1	0	1	0	0	0	0	1	1	0	0	x	0	x	0	3	2	0	0	0
Edgarosaurus	?	?	0	?	?	?	0	?	1	1	0	2	1	1	0	0	0	1	1	1	0	1	?	2	1	?	?	?	0	?	?	?	?	0	?	0	x	0	x	0	2	1	0	0	0
"Eurycleidus"	?	?	?	?	?	1	1	?	0	?	?	?	1	0	1	x	?	?	?	?	?	?	0	2	0	0	?	0	?	?	?	?	?	?	?	?	?	0	1	1	2	1	?	?	0
Hauffiosaurus	?	0	0	?	?	1	?	?	?	2	0	0	1	1	1	0	1	0	0	0	2	0	2	2	x	0	?	0	0	0	0	0	1	0	1	1	1	0	?	0	3	1	0	?	?
Kimmerosaurus	0	?	0	?	?	1	0	1	1	1	0	2	1	0	0	x	0	?	0	1	0	?	0	2	1	1	?	0&1	?	?	?	0	?	?	?	0	x	?	?	0	0	0	?	0	1
Kronosaurus	1	0	0	?	?	?	1	?	?	2	0	0	1	1	?	0	?	?	?	0	2	?	?	?	x	0	?	0	0	?	?	?	?	?	?	1	?	?	?	0	3	?	?	?	?
Leptocleidus	1	0	?	0	0	1	1	?	?	1	1	2	1	1	1	1	0	0	0	0	0	0	1	2	x	0	0	0	1	?	?	0	1	1	0	1	0	1	?	?	2	?	0	1	0
Liponectes	1	1	1	1	?	0	0	1	1	1	1	0	1	2	0	0	0	1	0	0	0	0	1	2	1	?	0	0	0	?	0	0	1	0	1	0	x	?	1	0	1	0	1	0	0
Liopleurodon	1	1	0	0	1	1	1	?	0	2	0	1	1	1	1	0	0	0	0	0	3	0	2	2	x	0	?	0	0	1	1	1	1	1	1	1	1	0	1	0	2	1	0	1	0
Macroplata	?	?	?	0	0	?	1	1	0	1	?	?	1	1	1	?	0	0	0	0	0	0	0	2	x	0	?	0	?	?	?	?	?	?	?	?	?	1	?	1	2	1	?	?	?
Microcleidus	?	?	?	?	?	?	0	?	?	?	1	0	1	0	1	0	0	?	0	0	0	0	?	2	1	0	0	?	?	0	?	?	?	0	?	0	x	0	1	0	1	0	?	0	?
Morturneria	1	?	?	?	?	1	?	?	1	?	?	?	1	?	0	x	?	?	0	?	?	1	?	2	?	1	0	1	?	?	0	?	1	?	?	?	?	0	1	0	?	?	?	?	?
Muraenosaurus	?	?	?	?	?	1	0	?	1	1	0	2	1	0	0	x	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	x	0	1	0	0	0	0	0	0
Peloneustes	1	1	0	0	1	1	1	1	0	2	0	0	1	1	1	0	1	0	0	0	2	0	2	2	x	0	0	0	1	0	0	0	1	1	1	1	2	0	0	0	3	1	0	1	0
Pistosauridae	?	?	?	1	?	0	0	?	?	?	0	0	1	0	x	x	0	?	0	0	0	?	1	0	?	0	?	?	0	0	0	0	0	0	0	1	?	0	?	?	1	?	?	?	?
Plesiopterys	0	?	0	?	?	1	0	1	0	1	0	1	1	0	1	x	0	0	0	0	0	0	0	2	0	0	0	0	?	0	0	0	1	?	?	0	x	0	?	1	0	0	0	?	?
Plesiosaurus	?	?	1	1	1	1	0	1	0	1	0	1	1	0	0	x	0	0	0	0	0	0	?	1	?	0	0	0	0	?	0	0	0	0	0	0	x	0	?	0	0	?	?	?	?
Pliosaurus	1	?	?	0	0	1	1	?	?	2	0	?	1	1	?	0	?	?	0	?	3	?	?	?	x	?	?	0	?	?	1	?	1	?	1	1	?	0	0	0	2	1	0	1	0
Polycotylus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	x	0	?	?	0	?	0
R. megacephalus	1	0	1	0	0	?	1	?	?	1	1	2	1	1	1	1	0	0	0	0	0	0	1	2	x	0	0	0	?	1	0	0	1	1	?	1	1	1	0	1	2	1	1	?	?
R. victor	?	?	?	?	?	?	?	?	?	1	1	2	1	1	1	1	0	?	0	0	?	?	1	1	x	?	?	0	?	1	1	0	1	0	0	1	?	?	0	1	2	1	1	?	?
R. zetlandicus	1	0	1	0	0	1	1	?	?	1	1	2	1	?	1	?	0	?	0	0	0	0	?	2	x	0	?	?	?	?	?	?	?	?	?	?	?	1	0	1	2	1	?	?	0
Simolestes	1	?	?	0	0	1	1	?	0	1	?	?	1	1	1	?	0	0	0	0	0	0	?	2	x	0	?	0	?	1	?	?	?	?	?	1	?	?	0	1	2	1	?	1	0
Simosaurus	x	0	0	0	x	0	x	0	0	0	0	0	0	x	x	x	0	0	0	x	x	?	x	x	x	x	0	x	0	0	0	0	0	0	0	0	x	0	0	0	0	0	0	0	0
Styxosaurus	?	?	1	1	0	0	0	1	1	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	1	?	0	1	?	?	0	?
Thalassiodracon	0	0	1	1	?	1	0	1	0	1	0	2	1	0	1	x	0	0	0	0	0	0	2	2	0	0	0	0	0	?	?	0	1	?	1	0	x	0	?	0	2	1	?	?	?
Tricleidus	0	0	0	?	?	1	0	?	?	1	0	2	1	0	0	x	0	1	0	1	0	1	0	2	1	1	0	1	?	?	?	0	0	?	0	0	x	0	1	0	0	0	0	0	0
Trinacromerum	?	0	?	0	0	1	0	?	?	1	1	2	1	2	0	0	0	?	1	1	0	1	0	2	1	1	?	1	0	0	?	?	?	1	?	0	x	0	?	0	3	2	?	0	?
Yorkshire Taxon	0	0	0	?	0	?	1	?	?	1	0	0	1	0	1	x	?	?	0	0	0	0	2	2	0	0	?	0	?	?	0	0	1	?	1	0	x	0	0	0	3	1	?	1	?

Taxon	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128
Attenborosaurus	?	?	0	0	0	1	?	0	0	1	0	0	0	0	?	?	?	0	0	0	?	0	0	0	1	?	2	?	0	0	0	0	1	1	1
Brachauchenius	?	0	?	0	0	1	?	0	0	1	0	?	?	?	?	?	?	2	2	?	?	0	0	1	1	1	2	?	0	?	0	1	1	1	1
Brancasaurus	?	?	?	?	?	0	x	0	0	0	0	?	0	?	?	1	0	1	1	?	?	0	0	1	1	0	2	1	0	?	0	0	1	1	1
Callawayasaurus	?	0	0	0	1	0	x	0	1	0	0	?	0	0	?	?	?	3	1	1	?	0	1	1	1	0	2	1	0	?	0	1	1	1	1
Cryptoclidus	0	1	0	1	0	0	x	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	2	0	1	1	1	1	1	1	1
Cymatosaurus	?	?	?	?	?	1	?	1	1	0	0	?	0	0	?	?	?	?	?	?	0	0	?	?	?	x	?	?	?	?	?	?	0	?	?
Dolichorhynchops	0	1	0	1	1	0	x	0	0	0	0	?	0	0	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1	1	1	1	1
Edgarosaurus	?	1	0	1	1	0	x	0	1	1	0	?	1	0	1	1	2	2	2	?	1	0	0	1	1	0	?	?	0	?	?	?	?	1	1
"Eurycleidus"	0	0	0	0	0	1	1	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hauffiosaurus	?	?	?	0	0	1	1	0	0	0	0	?	2	1	?	?	?	0	0	0	?	0	0	0	?	0	2	?	0	?	?	?	?	1	1
Kimmerosaurus	0	1	?	1	1	?	?	0	0	2	0	?	3	2	1	?	?	?	2	?	0	0	0	1	1	0	2	?	1	1	?	1	?	?	1
Kronosaurus	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	1	?	2	2	?	?	?	?	1	1	?	2	?	0	?	0	0	?	1	1
Leptocleidus	1	0	0	0	0	1	1	1	0	1	0	0	0	0	?	?	?	2	2	0	1	0	0	1	1	0	2	0	0	?	0	0	1	1	1
Libonectes	0	0	0	0	1	0	x	0	1	0	0	?	0	0	1	?	0	3	1	1	?	1	1	1	1	0	2	1	1	?	0	1	?	1	1
Liopleurodon	1	0	0	0	0	1	1	0	0	1	0	1	0	1	?	?	?	2	2	0	0	0	0	0	1	1	2	1	0	1	0	0	1	1	1
Macroplata	?	?	?	?	0	1	?	?	0	1	0	0	1	?	0	1	0	0	2	0	1	0	0	0	1	0	1	?	0	?	0	0	1	1	1
Microcleidus	0	0	?	0	1	0	x	0	?	0	0	0	?	?	0	?	?	1	1	1	0	1	1	0	1	0	2	?	1	0	0	1	1	1	1
Morturneria	0	?	?	0	1	0	x	0	0	2	0	?	2	2	0	0	2	?	2	?	?	0	1	1	1	0	2	?	0	?	?	?	?	1	1
Muraenosaurus	0	1	0	1	0	0	x	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	?	1	1	0	2	1	1	1	1	1	1	1	1
Peloneustes	1	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	2	2	0	1	0	0	0	1	0	2	0	0	1	0	0	1	1	1
Pistosauridae	?	?	?	?	?	0	x	1	0	?	0	?	0	0	?	?	?	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0&1	1	0	0
Plesiopterys	?	?	?	0	0	?	?	0	0	0	0	0	0	?	?	?	?	1	0	?	?	0	0	0	1	0	2	0	0	0	0	0	1	1	1
Plesiosaurus	0	0	?	0	0	0	x	0	0	0	0	0	0	?	?	?	0	1	0	?	0	0	0	0	1	0	2	1	0	0	0	1	1	1	1
Pliosaurus	1	1	0	0	0	1	1	0	0	1	1	1	1	1	?	?	?	?	2	?	0	0	0	0	1	1	2	?	0	?	0	0	1	1	1
Polycotylus	0	1	0	1	1	?	?	?	?	1	0	?	?	?	1	1	2	2	2	0	?	0	0	1	1	0	1	1	0	?	1	1	1	1	1
R. megacephalus	?	?	?	0	0	1	?	1	0	1	0	0	0	?	?	?	?	0	2	?	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1
R. victor	?	?	0	0	0	?	?	1	0	1	0	?	?	?	?	?	?	0	2	0	?	0	0	?	?	0	?	?	0	0	?	?	?	?	1
R. zetlandicus	?	0	0	0	0	1	?	1	0	1	0	0	?	?	?	?	?	2	2	0	1	0	0	0	1	0	1	?	0	?	0	?	1	1	1
Simolestes	1	0	0	0	0	?	?	1	0	1	0	0	0	?	?	?	0	2	2	?	0	0	0	0	1	0	1	1	0	1	0	?	1	1	1
Simosaurus	?	0	0	0	0	0	x	0	0	0	0	?	0	0	?	?	?	0	0	0	0	0	0	0	0	x	0	0	0	?	0	0	0	0	0
Styxosaurus	?	0	?	?	1	0	x	0	1	0	0	?	0	?	?	?	?	3	1	?	?	1	1	1	1	0	2	1	1	?	0	1	?	1	1
Thalassiodracon	?	0	?	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0	0	1	1	1
Tricleidus	0	?	0	1	1	0	x	0	0	0	0	0	0	?	1	?	1	0	0	1	0	0	0	1	1	0	2	1	0	1	1	1	1	1	1
Trinacromerum	0	1	0	1	1	0	x	0	0	0	0	?	0	1	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1	1	1	1	1
Yorkshire Taxon	?	?	0	0	0	?	?	0	0	0	0	0	?	1	0	?	0	0	0	?	1	0	0	0	1	0	2	0	0	?	0	0	?	1	1

Taxon	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161
Attenborosaurus	2	0	?	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0
Brachauchenius	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	0	1	?	?	0	?	?	1
Brancasaurus	2	1	1	0	0	0	1	?	2	1	1	0	1	1	1	0	1	1	1	1	1	1	1	?	?	0	0	1	?	0	1	2	1
Callawayasaurus	2	1	?	0	0	0	1	0	0&1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0	1	2	1
Cryptoclidus	2	1	?	0	0	0	1	1	2	1	1	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2	1
Cymatosaurus	?	?	?	?	?	?	?	?	?	?	?	x	?	?	?	1	?	?	1	?	?	0	0	x	?	x	x	?	?	?	0	1	?
Dolichorhynchops	2	0	x	0	0	2	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2	1
Edgarosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	0	0	1	1	0	1	2	1
"Eurycleidus"	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	1	1	?	1	?	?	?	?	?	?	?	?	?	?
Hauffiosaurus	?	0	?	0	?	?	0	0	?	1	1	0	0	1	1	1	1	?	1	1	?	1	1	0	0	0	0	1	1	1	1	2	0
Kimmerosaurus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kronosaurus	2	0	?	?	?	?	0	?	0	1	1	?	0	?	?	1	1	1	1	1	?	?	1	?	?	0	0	?	?	0	1	2	1
Leptocleidus	?	0	0	0	0	0	0	0	1	1	1	0	0	1	?	?	?	?	?	?	?	1	1	0	0	?	0	1	?	?	?	?	?
Libonectes	?	1	?	0	0	0	2	0	2	1	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Liopleurodon	2	0	?	0	?	?	0	?	?	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	2	1
Macroplata	?	0	?	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	0	1	?	0	0	0	1	1	1	1	2	0
Microcleidus	2	1	?	0	?	?	1	?	2	?	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	2	0
Morturneria	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	1
Muraenosaurus	2	1	?	0	0	1	1	1	2	1	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	1	2	1
Peloneustes	2	0	0	0	?	?	0	0	0	1	1	0	0	1	1	1	1	0	1	1	1	1	1	0	0	0	0	1	1	0	1	2	1
Pistosauridae	1&2	0	?	1	0	?	0	0	0	1	1	x	0	0	0	?	1	x	?	1	1	0	0	x	0	x	x	1	1	0	1	?	0
Plesiopterys	2	1	?	?	?	?	0	0	?	1	1	0	0	?	1	1	1	?	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0
Plesiosaurus	2	1	?	0	1	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0
Pliosaurus	?	0	?	?	?	?	?	?	?	?	?	0	?	?	1	1	1	0	1	1	?	1	1	0	0	0	1	1	1	0	1	2	1
Polycotylus	2	0	x	0	0	2	0	1	1	1	1	1	?	?	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	1	2	1
R. megacephalus	2	0	?	0	?	?	?	?	?	?	1	?	0	?	1	1	1	?	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0
R. victor	2	?	?	?	0	?	0	0	1	1	1	0	0	1	?	1	1	1	1	1	?	0	1	0	0	0	0	1	1	1	1	2	0
R. zetlandicus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	0	1	0	0	0	0	1	1	1	1	2	0
Simolestes	?	0	?	0	?	?	0	?	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	2	0
Simosaurus	0	0	0	0	0	0	0	0	0	0	0	x	x	x	0	0	0	x	0	0	0	0	0	x	0	x	x	0	0	0	1	2	0
Styxosaurus	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?
Thalassiodracon	0	0	?	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	2	0
Tricleidus	2	0	0	0	0	2	1	0	2	1	1	0	0	1	1	1	1	0	1	1	?	1	1	1	1	0	0	1	1	0	1	2	1
Trinacromerum	2	0	x	0	0	2	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	2	1
Yorkshire Taxon	2	0	?	?	?	?	?	?	?	?	1	?	?	?	1	1	1	1	1	1	?	1	1	0	0	0	0	1	1	?	1	2	0

Taxon	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**
Attenborosaurus	0	1	1	0	0	0	?	?	?
Brachauchenius	?	1	1	?	?	0	0	?	?
Brancasaurus	?	1	1	?	0	0	0	?	0
Callawayasaurus	0	1	1	1	?	0	0	?	0
Cryptoclidus	1	1	1	0	0	1	0	0	0
Cymatosaurus	?	?	?	?	0	0	1	1	1
Dolichorhynchops	3	1	1	1	?	1	0	0	0
Edgarosaurus	?	1	1	1	?	?	0	?	0
"Eurycleidus"	?	?	?	?	?	?	?	1	0
Hauffiosaurus	2	1	1	0	0	0	?	?	?
Kimmerosaurus	?	?	?	?	?	1	0	?	0
Kronosaurus	?	?	1	?	?	?	?	?	?
Leptocleidus	?	?	1	?	?	0	0	?	?
Libonectes	?	?	?	?	?	0	0	0	0
Liopleurodon	0	1	1	0	0	0	0	?	0
Macroplata	?	?	1	?	0	0	?	?	?
Microcleidus	1	1	1	0	0	0	?	?	?
Morturneria	?	?	1	?	?	1	?	?	0
Muraenosaurus	1	1	1	0	0	1	?	0	0
Peloneustes	0	1	1	0	0	0	0	?	0
Pistosauridae	0	0	?	?	0	0	1	?	?
Plesiopterys	0	1	1	0	0	0	1	1	1
Plesiosaurus	1	1	1	0	0	0	1	1	0
Pliosaurus	?	?	1	?	0	0	?	?	?
Polycotylus	3	1	1	?	0	1	?	?	?
R. megacephalus	?	?	1	?	0	0	1	?	?
R. victor	3	1	1	0	0	0	?	?	?
R. zetlandicus	?	?	1	?	?	0	?	?	?
Simolestes	0	?	1	?	?	0	?	?	?
Simosaurus	0	0	0	0	1	0	0	0	1
Styxosaurus	?	?	?	?	?	0	0	?	?
Thalassiodracon	0	1	1	0	0	0	1	1	0
Tricleidus	2	1	1	?	0	1	0	0	0
Trinacromerum	3	1	1	1	0	1	0	0	?
Yorkshire Taxon	?	?	1	?	?	0	?	1	?