



## A NEW SPECIMEN OF THE TRIASSIC PISTOSAUROID *YUNGUISAURUS*, WITH IMPLICATIONS FOR THE ORIGIN OF PLESIOSAURIA (REPTILIA, SAUROPTERYGIA)

by TAMAKI SATO<sup>1,2\*</sup>, LI-JUN ZHAO<sup>3</sup>, XIAO-CHUN WU<sup>2</sup> and CHUN LI<sup>4</sup>

<sup>1</sup>Tokyo Gakugei University, 4-1-1 Nukui-Kita-Machi, Koganei City, Tokyo 184-8501, Japan; e-mail: tsato@uakugei.ac.jp

<sup>2</sup>Canadian Museum of Nature, PO Box 3443 STN 'D', Ottawa, ON Canada, K1P 6P4; e-mail: XWu@mus-nature.ca

<sup>3</sup>Zhejiang Museum of Natural History, 6 Westlake Cultural Plaza, Hangzhou 310014, China; e-mail: zlj881@126.com

<sup>4</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing, 10004, China; e-mail: lichun@pa.ivpp.ac.cn

\*Corresponding author.

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**Abstract:** An adult skeleton of the pistosauroid sauropterygian *Yunguisaurus liae* reveals a number of morphological features not observed in the holotype, such as the complete morphology of the skull roof, stapes, atlas and axis, ventral view of the postcranium, and nearly complete limbs and tail. Size and morphological differences between the two specimens are mostly regarded as ontogenetic variation, and newly added data did not affect the phylogenetic relationships with other pistosauroids significantly. The number of mesopodia (11 carpals and 8 tarsals) exceeds that known in any other Triassic

marine reptiles and does not serve as a precursor of the plesiosaurian pattern with fewer mesopodia of different topology; it demonstrates variability of the limb morphology among the Triassic pistosauroids. The pectoral girdles of *Corosaurus*, *Augustasaurus* and *Yunguisaurus* may indicate early stages of the adaptation towards the plesiosaurian style of paraxial limb movements with ventroposterior power stroke.

**Key words:** pistosauroids, origin of Plesiosauria, *Yunguisaurus liae*, Triassic.

*YUNGUISAURUS LIAE* Cheng *et al.*, 2006 is a pistosauroid sauropterygian recently discovered in the Middle Triassic of China. The holotype specimen is a nearly complete juvenile skeleton, and a full description with a phylogenetic analysis (Sato *et al.* 2010) demonstrated a mosaic of primitive (i.e. shared with basal sauropterygians) and derived (i.e. more plesiosaurian) features, as well as its relationship with other pistosauroid taxa and relevance to the origin of plesiosaurian body plan. Despite its superficial similarity to the plesiosaurian body plan, it was demonstrated that other pistosauroids such as *Pistosaurus* and *Augustasaurus* are more closely related to the Plesiosauria. Meanwhile, possible phylogenetic effects of ontogenetic changes to the juvenile skeleton remained unknown, and interpretation of certain characteristics, such as those of posterior portion of skull roof, coracoid and limb bones, requires additional specimen(s) for morphological clarification (Sato *et al.* 2010).

Another, mostly complete but much larger pistosauroid skeleton was briefly reported by Zhao *et al.* (2008a) and tentatively referred to *Yunguisaurus cf. liae*. Further preparation and subsequent studies confirm this referral and reveal a number of features wanting in the holotype skeleton, including a complete skull roof, tail, limb extremities

and the ventral structure of the girdles. In this study, we describe Zhao's specimen on characteristics not available in the holotype, assess the differences between the two specimens, re-evaluate the phylogeny and discuss the morphological and functional evolution of the girdle and limbs of Triassic pistosauroids and the accumulation of the features towards the unique mode of locomotion in the Plesiosauria.

*Institutional abbreviations.* NMNS: National Museum of Natural Science, Taichung, Taiwan, China; ZMNH: Zhejiang Museum of Natural History, Hangzhou, Zhejiang, China.

### SYSTEMATIC PALAEOLOGY

SAUROPTERYGIA Owen, 1860

PISTOSAUROIDEA Baur, 1890

*YUNGUISAURUS* Cheng, Sato, Wu and Li, 2006

*Yunguisaurus liae* Cheng, Sato, Wu and Li, 2006

Figures 1–9

2008 *Yunguisaurus cf. liae* Zhao, Sato, Wu and Li,  
pp. 283–286, figs 1–2.

*Holotype.* NMNS 004529/F003862; articulated specimen in dorsal view, missing most of the tail and tips of the limbs.

*Referred material.* ZMNH M8738; a nearly complete and articulated skeleton in ventral view, with its skull prepared on both sides.

*Locality and horizon.* Zhuganpo Member of Falang Formation (Ladinian, upper Middle Triassic) in Fuyuan County, Yunnan Province, China (Wang *et al.* 2008; Zhao *et al.* 2008a, b).

*Revised diagnosis.* Differing from known pistosauroids in the combination of the following characters: single interpterygoid vacuity with a narrow anterior extension, anterior extension of parasphenoid, at least six premaxillary teeth, elongate snout with slender teeth, pineal foramen reaching frontal/parietal suture, nasal present, longitudinal ridge on temporal bar, sharp parietal crest, lack of squamosal bulb at posterior end of skull table, long mandibular symphysis, prominent coronoid process, constriction of snout and mandible (in adult individuals), about 50 cervical vertebrae with short neural arch and accessory articulation (zygosphenes/zygantrum), rod-shaped chevrons not united medially, sickle-shaped clavicle, small scapula without ventral plate, dorsal process of scapula slightly widen, absence of interglenoidal thickening of coracoids, semicircular pubis, long shaft of ilium, slender humerus and epipodials, hourglass-shaped ulna, at least 11 carpals and 8 tarsals (in adult individuals), hyperphalangy in manus (1-5-8/9-7-4; revised from Cheng *et al.* 2006).

### Description

The following description focuses on the morphological differences between the holotype (NMNS 004529/F003862; Cheng *et al.* 2006, Sato *et al.* 2010) and the referred specimen ZMNH M8738, as well as the parts missing in the former (for skeletal measurements, see Table 1).

Total length of ZMNH M8738, including estimated length for the missing distal end of the tail (10 cm), is about 4.2 m (Fig. 1). The juvenile holotype is missing the tail after the 91st vertebra (= the 16th caudal) and measures about 1.7 m long from the tip of the premaxilla to the end of preserved tail; the corresponding length (the tip of the premaxilla to the 91st vertebra) in the ZMNH specimen is just over 3 m and thus 1.8 times longer than the holotype. The ZMNH skull is 1.7 times longer than that of the holotype.

*Skull.* The skull, mandible and a few attached vertebrae were removed from the slab and prepared separately. As in the holotype, the skull was compressed dorsoventrally. An obvious difference between the two specimens is the outline of the snout (Fig. 2); there is a notch at the premaxilla–maxilla suture in the ZMNH skull just anterior to the external naris and above the

sixth dentary tooth (Fig. 2B), but not in the holotype. The snout length (anterior tip of the skull to the anterior edge of the orbit) is <45 per cent of the skull length (anterior tip of the skull to the posterior end of the occipital condyle), and this proportion is approximately same as in the holotype (46 per cent).

The premaxilla–maxillary sutures are not exactly symmetrical but clearly marked on both sides, and there are six premaxillary teeth on both sides (uncertain but estimated to be up to seven in the holotype: Sato *et al.* 2010). The frontals are mostly fused, and the midline suture is closed and raised, indicating an advanced stage of ossification. A short suture and an obvious change in the texture mark the postfrontal/postorbital contact at the junction of the postorbital bar and the temporal arch (Fig. 4). The postorbital reaches nearly the posterior end of the temporal arch, and it laterally overlies the squamosal at the ventral edge of the supratemporal fenestra as in *Pistosaurus*; the posterior extension is not so long in *Augustasaurus* (Rieppel *et al.* 2002) and basal plesiosaurs such as *Stratesaurus* and *Avalonnectes* (Benson *et al.* 2012), in which the extension remains anterior one- to two-thirds. The longitudinal ridge on the lateral surface of the temporal arch is present but less pronounced in the referred specimen than in the holotype. The jugal–postorbital suture is traceable on both sides of the skull but unclear in places.

ZMNH M8738 reveals the complete morphology of the skull roof for the first time (Fig. 4). The anterior ends of the parietals are separated by the pineal foramen, and the midline suture is traceable along the entire parietal crest, which is widest behind the pineal foramen and gradually thins posteriorly. The anterolateral portion of the parietal forms much of the anterior wall of the temporal fossa. The paired parietals roof the braincase; the roof narrows posteriorly and is constricted in the posterior one-third and then gradually widens again to meet the squamosals at the posterior edge of the temporal fossa. Such a posterior expansion is likely plesiomorphic for the Pistosauroidea, because it variably develops among the Triassic forms (e.g. *Cymatosaurus*, *Augustasaurus*) and plesiosaurs such as rhomaleosaurids (*sensu* Benson *et al.* 2012), which later develops into the large ‘parietal wing’ consisting of the parietal and squamosal in some Cretaceous plesiosaurs (e.g. *Nichollssaura* and *Dolichorhynchops*: Sato 2002, 2005; Druckenmiller and Russell 2008), whereas such a structure is absent in most Jurassic plesiosaurs such as *Plesiosaurus* and Cretaceous elasmosaurids (Storrs 1997; Sato 2003). The squamosals meet at the midline and form the posterior edge of the skull roof, and the midline union has a short anterior process that wedges between the parietals. On the posterior edge of the skull roof, the united squamosals form a shallow V-shaped embayment; they lack the squamosal bulb, contrasting with the situation in *Augustasaurus* and many short-necked plesiosaurs (O’Keefe 2001; Benson *et al.* 2012). The suspensorium is dorsoventrally compressed postdepositionally, but it appears that the quadrate would have reached at least to the height of the lower edge of temporal opening in life.

Incomplete epipterygoids are preserved on both sides. The left exoccipital–opisthotic (Fig. 2C) is in or near life position, as the long and flat paroccipital process maintains contact with the suspensorium. Its supraoccipital facet exposes an opening for the horizontal semicircular canal. Identity of other components of the otic capsule is unclear. The possible prootic (?pr) is so iden-

**TABLE 1.** Skeletal measurements of *Yunguisaurus liae* ZMNH M8738 (referred specimen).

Dimension	Length (mm)
Total length, tip of premaxilla to broken end of tail	4016
Total length, including missing distal end of tail	4200 (est)
Skull, tip of premaxilla to occipital condyle	218
Skull, tip of dentary to retroarticular process	267 (l)
Skull, maximum width (squamosal at condyle, deformed)	132
Skull and neck, tip of premaxilla to 48th vertebra	1582
Trunk, 49th vertebra to last sacral (73rd vertebra)	928
Tail, 74th vertebra to broken end of tail (130th vertebra)	1509
Scapula, maximum length in ventral view	75
Scapula, maximum width in ventral view	55
Coracoid, maximum length	185 (l), 183 (r)
Coracoid, maximum width	109 (l), 130 (r)
Ilium, maximum length (acetabulum to sacral end)	110 (l), 109 (r)
Ilium, maximum width at sacral end	83 (l)
Ilium, maximum width at acetabular end	65 (l, est), 65 (r)
Pubis, maximum width	147 (l), 153 (r)
Pubis, length at ischial facet (perpendicular to max. width)	143 (r)
Ischium, maximum width	122 (r)
Ischium, maximum length	125 (l), 126 (r, est)
Humerus, maximum length	210 (l), 189+ (r)
Humerus, width at distal end	64 (l), 60+ (r)
Radius, maximum length	113 (l), 112 (r)
Radius, width at proximal end	50 (l), 49 (r)
Radius, width at distal end	34 (l), 37 (r)
Ulna, maximum length	120 (l)
Ulna, width at proximal end	60 (l)
Ulna, width at distal end	63 (l)
Femur, maximum length	183 (l), 186 (r)
Femur, width at distal end	63 (l), 60 (r)
Tibia, maximum length	108 (l), 109 (r)
Tibia, width at proximal end	52 (l), 54 (r)
Tibia, width at distal end	42+ (l), 47 (r)
Fibula, maximum length	125 (l), 126 (r)
Fibula, width at proximal end	37 (l), 37 (r)
Fibula, width at distal end	62 (l), 61 (r)

Abbreviations: est, estimated; l, left; max, maximum; r, right; +, actual length of damaged element.

tified because of location. Unidentified element X (Fig. 2C) may be either the right exoccipital-opisthotic or the supraoccipital; it is unclear whether another unidentified element Y represents a separate bone. The element overlying the left exoccipital-opisthotic may be the left atlantal neural arch ('?atna').

Sato *et al.* (2010) noted the presence of a groove on the dorsal surface of the quadrate ramus of the pterygoid in the holotype, and there is a corresponding structure in ZMNH M8738 ('gr' in Fig. 2C) as well. We believe that the thin element overlying the left quadrate ramus of the pterygoid represents the collapsed lateral wall of this groove; the right ramus retains the posteromost portion of this wall. This specimen also clarifies the nature of the 'medial wall' of this groove (Sato *et al.* 2010, p. 183); it is a part of the pterygoid as shown in the right quadrate ramus ('qrpt-mw') and not the stapes adhering to the ramus with residual matrix.

In ventral view (Figs 3, 4), the left pterygoid bears a prominent projection or boss ('ptb' in Fig. 3C) on the anteromedial

edge of the subtemporal fenestra; its right counterpart is obviously damaged due to crack. Such a boss does not exist in the holotype, in which the thin pterygoid is folded in the corresponding area. The anterior processes of the pterygoids do not unite at the midline until the middle of the palate, and the parasphenoid is exposed between them. There is no anterior interpterygoid vacuity, however. The ectopterygoid is partly fused with the pterygoid.

ZMNH M8738 supplements the previous interpretation of the parasphenoid morphology within the interpterygoid vacuity (Fig. 3C). At the level of the palate, the parasphenoid takes a narrow diamond shape and wedges anteriorly between the pterygoids, with a blunt midline ridge on the exposed part. This condition is shared with many basal plesiosaurs (Benson *et al.* 2012, character 65), but most of them only have a much shorter wedge; *Plesiosaurus* also has a similarly long but much wider anterior exposure of the parasphenoid (Storrs 1997). The poster-

ior end of the parasphenoid continues as a narrow midline ridge in the interpterygoid vacuity. The parasphenoid occupies much of the roof of the interpterygoid vacuity, limiting the ventral exposure of the basisphenoid to a narrow area including the basiptyergoid process ('bpt') and a narrow gap on the left side of the skull. Therefore, the parasphenoid covers much of the ventral surface of the braincase exposed between the pterygoids; what was identified as the parasphenoid in previous studies of the holotype (Sato *et al.* 2010) is actually the narrow midline ridge only. Such a wide coverage of the parasphenoid is a common feature among the members of the rhomaleosaurids (Benson *et al.* 2012, character 64). The ZMNH skull does not clearly show the internal carotid foramen, but we suspect that the matrix-filled gap medial to the basiptyergoid process likely includes this foramen ('ic').

The basioccipital in the holotype bears a ventral midline ridge that continues from the occipital condyle to the body of the bone, but the ridge is limited to the body and does not continue on the condyle in the new specimen. We suspect the basioccipital and basisphenoid are slightly dislocated in ZMNH M8738, as indicated by the small exposure of the contact facet on the basioccipital posterior to the parasphenoid.

Zhao *et al.* (2008a, b) identified a pair of narrow bones preserved on the anterior edge of the subtemporal fenestra as hyoids. They are slenderer and located more anteriorly than the hyoids in the holotype (Cheng *et al.* 2006), but may represent different portion(s) of the hyoid apparatus that consists of multiple pairs of ossified horns (cornua). Alternatively, these bones in ZMNH M8738 may represent a pair of stapes, because they are very thin and both are partially located on the dorsal surface of the pterygoid. Note that little is known about the stapes and hyoid of the Triassic sauropterygians (Carroll and Gaskill 1985; Rieppel 1989; Wu *et al.* 2011), challenging a confident identification of these elements in *Yunguisaurus*. Plesiosaurian stapes have only slightly better record than those of the Triassic sauropterygians but a considerable morphological variability has been suggested (Taylor 1992; Storrs and Taylor 1996). Known plesiosaurian hyoids are relatively thick (e.g. *Meyerasaurus* in Smith and Vincent 2010) but information is limited to a small number of taxa.

**Mandible.** The mandible is nearly complete except for the posterior portion of the right ramus, but it is flattened so that most of the lateral surface posterior to the symphysis and anterior to the mandibular fossa is shown in ventral view (Fig. 3). It is constricted posterior to the mandibular symphysis, accommodating the eighth and ninth upper teeth (= third and fourth maxillary teeth), which are larger than adjacent teeth. The constriction gives a slightly expanded mandibular symphysis as in the basal plesiosaurs such as *Thalassiodracon* (Storrs and Taylor 1996; Benson *et al.* 2011) and rhomaleosaurids (*sensu* Benson *et al.* 2012). This part in the holotype is not constricted but the upper jaw is slightly wider than the mandible. The symphyseal suture fuses and disappears in the anterior half. Fusion and fractures obscure postdentary sutures; the sutures between articular, surangular and angular are clearly marked in the retroarticular pro-

cess of the holotype but none can be traced with confidence in ZMNH skull. There is a shallow concavity on the lateral surface of the pregenoid portion except for the angular, but it is not clear whether it is original or a result of deformation (Fig. 3). The coronoid process is prominent and projects above the temporal arch (Figs 2, 4). On the medial side, the Meckelian canal is mostly covered with the possible prearticular or splenial (Fig. 4D); it contrasts with the open groove in the holotype. The mandibular fossa bulges out medially to support the quadrate condyle (Fig. 3). The retroarticular process is proportionally wider and stouter than that of the holotype; it projects slightly mediolaterally, following the gentle curvature of the mandibular ramus.

**Dentition.** Due to the occlusion, the exact numbers of maxillary and dentary teeth are unavailable, and their posterior ends cannot be observed. The maxillary teeth, however, reach at least to the middle of postorbital bar. Well-preserved teeth retain fine ridges on the surface.

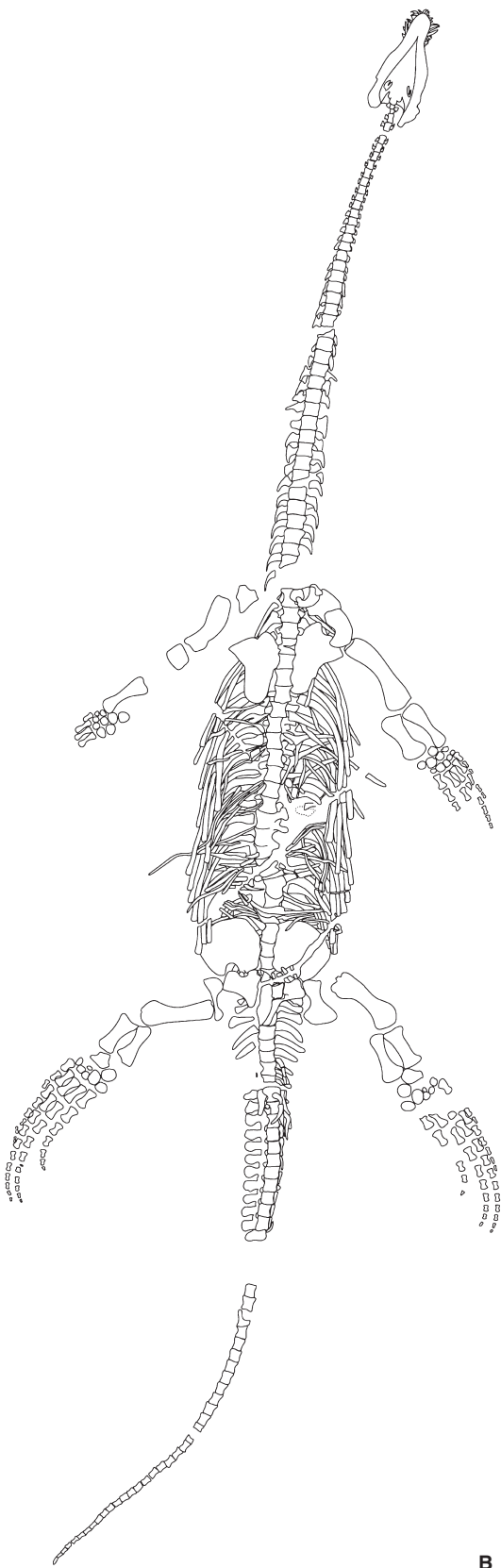
**Vertebrae and ribs.** The vertebral column is nearly complete, and we estimate about 10 vertebrae are missing at the end of the tail (Fig. 1). All presacral vertebrae are exposed in ventral or ventrolateral view (Figs 5, 6, 8). The ventral edge of the rib facet is located on the centrum until the 50th vertebra, but unclear in the 51st, and entire facet is located on neural arch from the 52nd and after. Therefore, the number of cervical, including 'pectorals' *sensu* Seeley (1874) and Welles (1943), that is, the rib facet on both centrum and neural arch, would be 50 or 51; similar total cervical counts (49 cervicals) are estimated in the holotype, in which only the atlas and axis are assumed to be missing (Sato *et al.* 2010). Meanwhile, the length of the cervical rib varies anteroposteriorly. The 45th rib is approximately twice as long as the centrum. The 46th vertebra is mostly missing due to the crack anterior to the pectoral girdle, but the remaining distal tip of the right rib indicates that it was about the same length as the 45th. The rib becomes noticeably longer in the 47th and again longer and also stouter in the 48th after which the rib length is nearly constant to the 51st. The interclavicle is located on the 46th and the missing 45th vertebrae.

Components of the atlas and axis are disarticulated, and their identification remains tentative (Fig. 3). We identify the element articulated with the occipital condyle as the atlantal centrum, consisting of the atlantal intercentrum (= 'wedge bone' of Andrews 1910, 1913) and atlantal centrum proper; the first two cervical vertebrae do not fuse to form the atlas-axis complex as in adult plesiosaurs (Andrews 1913). The atlantal centrum is in articulation with the occipital condyle, and its ventral surface is smooth and round. The posterior surface for the contact with the axis is shallowly concave. Two elements adjacent to the occipital condyle may be the atlantal neural arches ('?atna'). In dorsal view (Fig. 2), the floor of neural canal on the atlantal centrum is exposed; there is a pair of narrow groove similar to a pair of pits in the antermost cervicals of the holotype (Sato *et al.* 2010, fig. 4). In the axis (Fig. 4A), the tip of the neural

**FIG. 1.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), skeleton in ventral view. A, photograph; B, interpretation. Scale bar represents 1 m.



A



B

spine ('ns') peeks out beneath the right postzygapophysis ('ns'), indicating that the spine projects posteriorly. A small bump on the lateral surface near the anterior end ('axrf') must represent an axial rib facet, but the rib is not present.

From the third cervical, there is a pair of shallow, longitudinal concavities divided by a midline ridge on the ventral surface of the centrum (Fig. 5B), but no obvious foramina subcentralia exist in any of the cervicals except for several dubious ones. There are paired foramina on the bottom of the neural canal in the holotype (Sato *et al.* 2010), but not on the ventral side of the centrum either. The presence of foramina subcentralia is a characteristic feature of plesiosaurs, as well as in certain pistosauroids (e.g. *Augustasaurus* and *Pistosaurus*); their absence in *Yunguisaurus* is certainly notable and likely indicates a primitive nature of this taxon within the pistosauroid lineage. The zygapophyses are wider than the centra throughout the cervical series; the zygapophyseal facets appear to face dorsally. The centrum of the 20th vertebra is at a slab joint, and it is amphicoelous and wider than tall. The rib takes a hatchet shape from the third cervical; the anterior process is longer than the posterior process until 15th vertebra, after which the posterior process is longer. The rib facet consists of an oval head and a small dorsal projection, and it is located near the anterior edge of the centrum on the third vertebra (Fig. 3A). Rib facets are mostly buried in the slab in more posterior cervical and reappear in 30th to 39th vertebrae in which a horizontal neurocentral suture (variably present) divides each facet into two.

The dorsal centra are moderately constricted. It is difficult to determine the exact location of the first sacral, because the ischia cover the sacrals and there is a major break. We consider the 71st to 73rd vertebrae are sacrals based on the change in the rib morphology; the distal ends of these ribs are wide, and the combined width of the three ends on the left side is only slightly narrower than the sacral end of the ilium. In this case, the number of presacral vertebrae is at least 70 as in the holotype.

The long tail consists of about 70 vertebrae, including the estimated 10 terminals, and occupies about 40 per cent of the total body length. The vertebral counts outnumber those of Early Jurassic plesiosaurs (e.g. 28 in *Plesiosaurus*, 34 in *Rhomaelosaurus*, 33 and a few more in *Eoplesiosaurus*; Carte and Baily 1863; Storrs 1997; Benson *et al.* 2012) and some basal sauropterygians for which (nearly) complete caudal series are known (e.g. 40 to 60 in *Neusticosaurus*, 33 in *Nothosaurus giganteus*, 37 or 38 in *Lariosaurus*; Peyer 1939; Sander 1989; Rieppel 2000a). The right side is exposed for most of the caudal series. The cen-

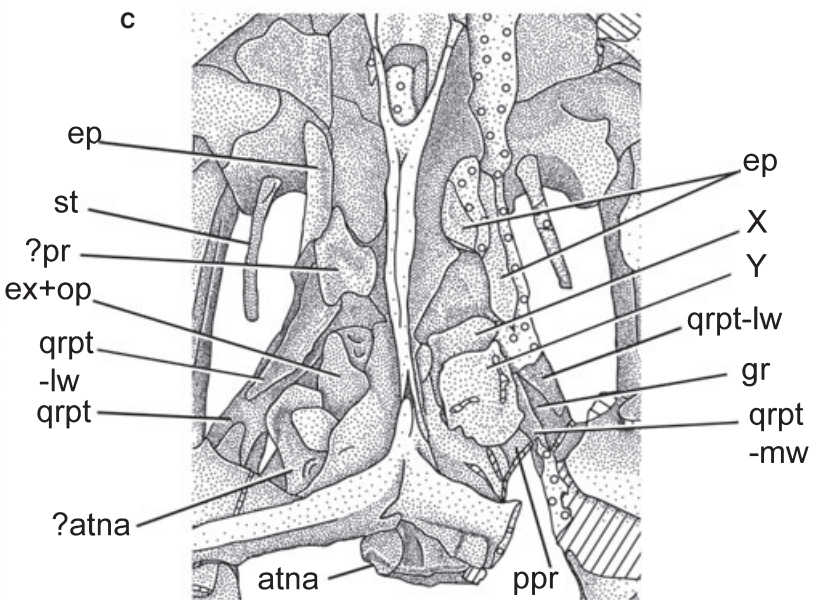
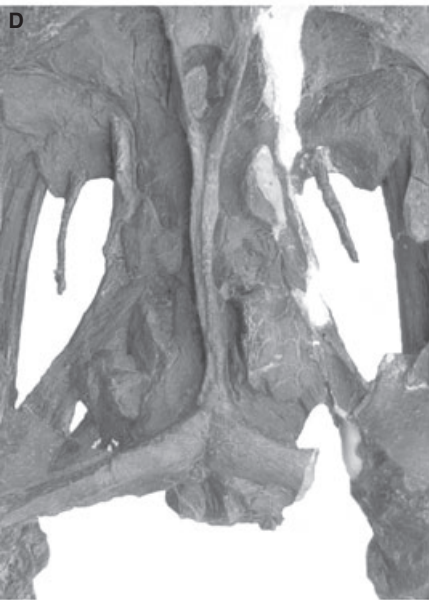
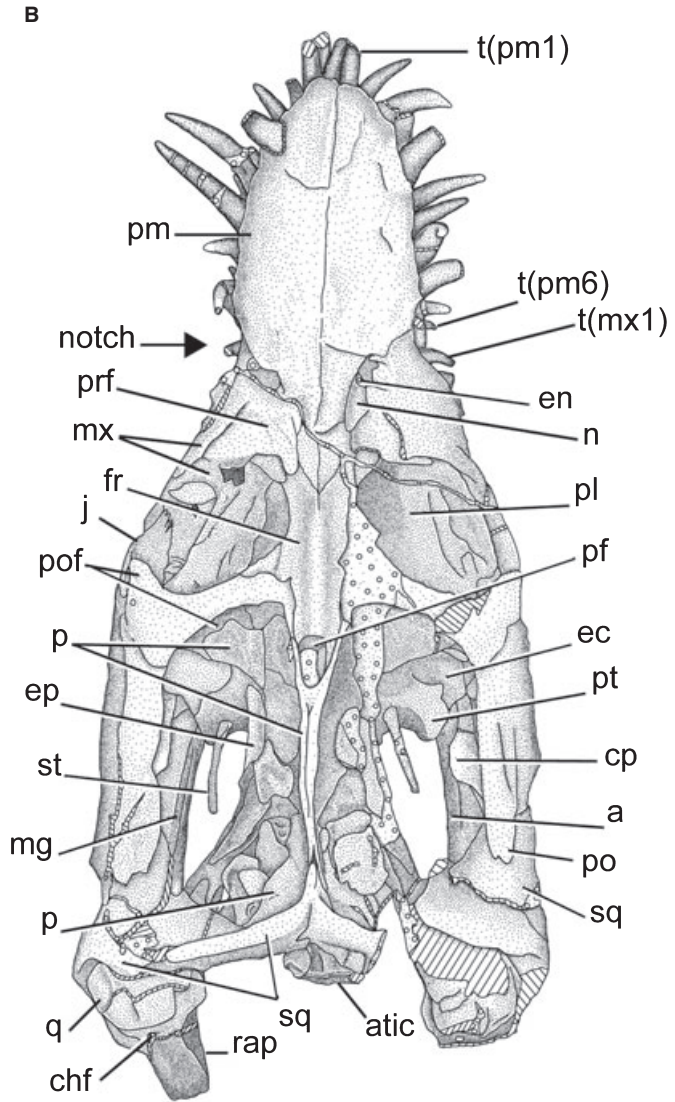
trum is approximately as tall as long in anterior caudals, but gradually becomes longer than tall posteriorly. Unlike plesiosaurs, the caudal centrum becomes relatively longer posteriorly until the preserved end of the tail. The 75th vertebra is the first caudal and distinguished from the sacrals by the narrow and posteriorly pointing caudal ribs that are fused to the centrum. The ribs are more straight and shorter in more posterior caudals and often disarticulated from the centrum (Fig. 6A, B). The transverse process is very short, and it gradually decreases in the size posteriorly and finally disappears in the 91st vertebra. Haemapophyseal facets appears from the 77th vertebra (= 3rd caudal); each facet is shared by two neighbouring vertebrae. ZMNH M8738 confirms that the left and right haemapophyses are not united along the midline in this species, as inferred in the holotype (Sato *et al.* 2010); each haemapophysis has a spherical head, and the shaft narrows gradually as in plesiosaurs (Owen 1865; Andrews 1910). Distribution of the haemapophyses and their facets are irregular and sparse after the 100th vertebra; the 121st vertebra has the last haemapophysis, which is very short and fused to the centrum. The caudal neural spine is slightly taller than or as tall as the centrum in anterior caudals, but the height decreases rapidly at anterior one-third of the tail. Morphology of the spine varies considerably; development of anterior and posterior flanges is irregular in anterior caudals, whereas the outline differs drastically even among neighbouring vertebrae more posteriorly (Fig. 6A–D). Large zygapophyses are present in the anterior and middle portion of the tail, but they become smaller posteriorly.

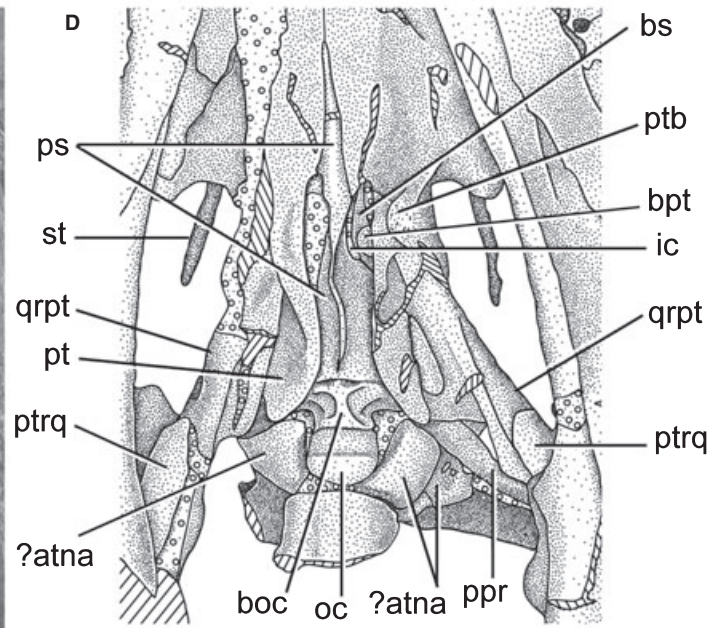
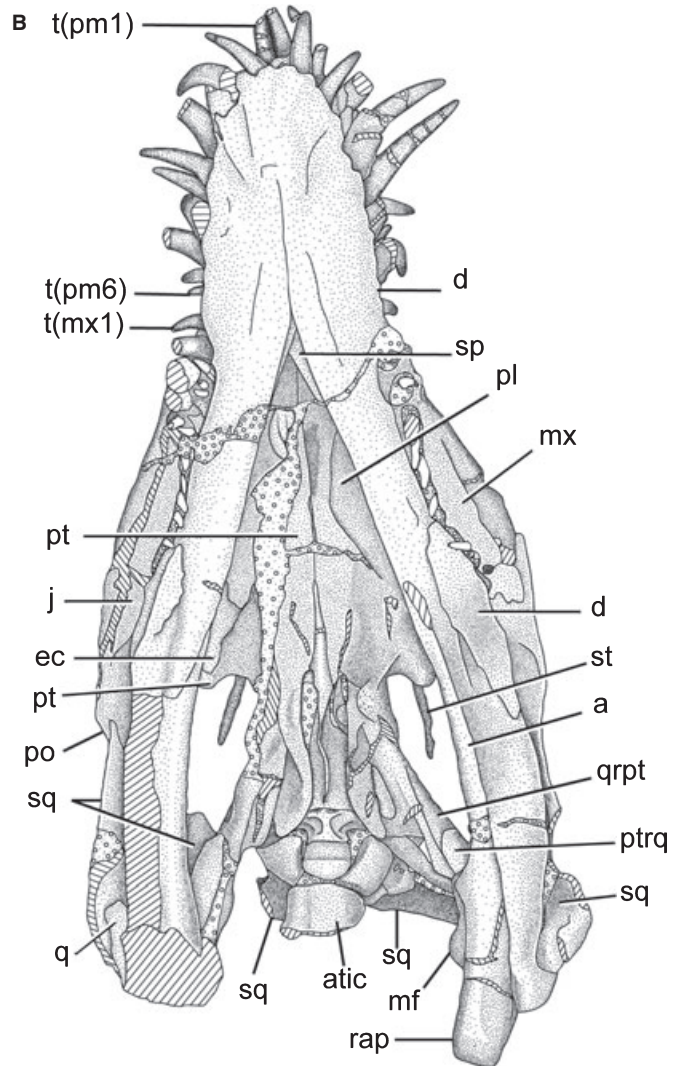
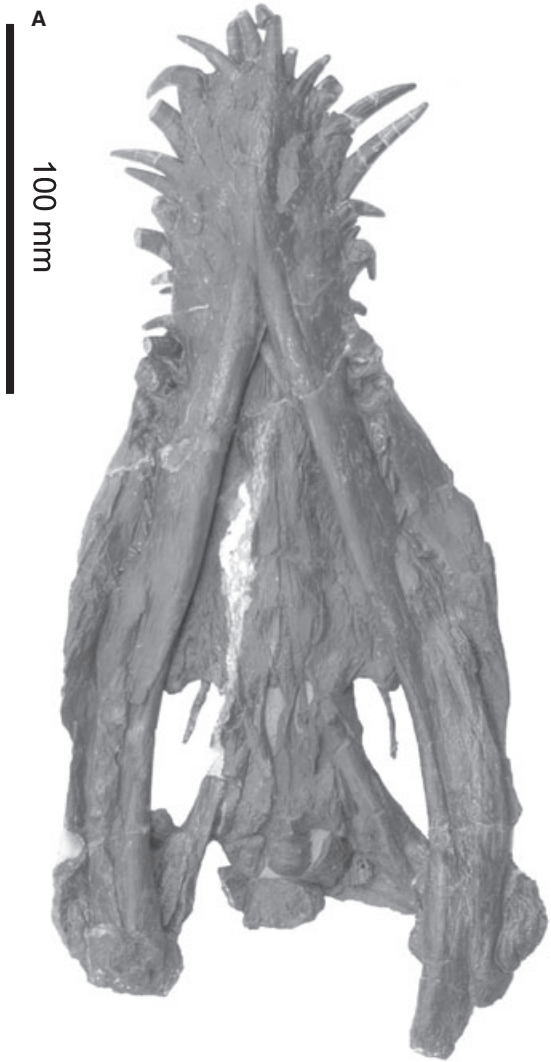
*Gastralia.* A total of 48 gastralia are exposed in the trunk region between the coracoids and pubes, but all are disarticulated (Fig. 7); orientation of the boomerang-shaped medial elements indicates some were displaced and/or inverted before burial.

*Pectoral girdle.* The right clavicle and scapula are severely damaged by a large crack, but the rest of the pectoral girdle is well-preserved and exposed in ventral view (Fig. 8A, B). The left half of the girdle is mostly complete and in articulation with the forelimb, whereas the right coracoids is displaced posteriorly and the right humerus is disarticulated and inverted.

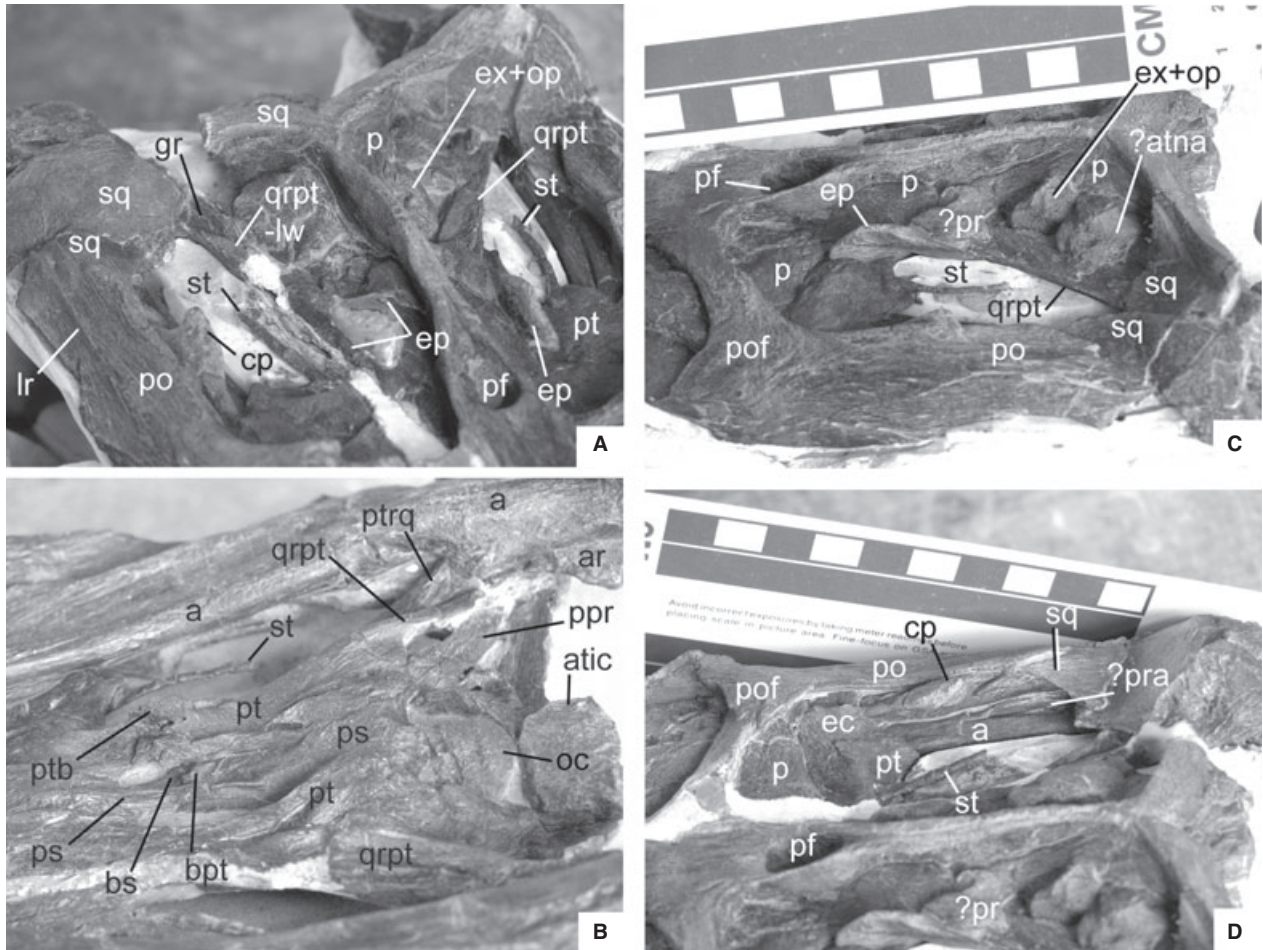
Only the left half of the interclavicles is preserved. The concave anterior edge is slightly weathered but appears to approximate the original edge. The interclavicle covers the ventral side of the anteromedial portion of the clavicle, but their dorsal/ven-

**FIG. 2.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), dorsal view of the skull. A, photograph; B, interpretation of the skull; C, photograph; and D, interpretation of the close-up of the braincase region. Abbreviations for Figures 2–4: a, angular; ar, articular; atic, intercentrum of atlas; atna, atlantal neural arch; boc, basioccipital; bpt, basipterygoid process; bs, basisphenoid; chf, foramen for chorda tympani; co, coronoid; cp, coronoid process; d, dentary; ec, ectopterygoid; en, external naris; ep, epipterygoid; ex + op, exoccipital–opisthotic; f, frontal; gr, groove; ic, internal carotid foramen; j, jugal; lr, lateral ridge on temporal arch; lw, lateral wall; m, maxilla; mg, Meckelian groove; mw, medial wall; n, nasal; oc, occipital condyle; p, parietal; pf, pineal foramen; pl, palate; pm, premaxilla; po, postorbital; pof, postfrontal; pr, prootic; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; ptb, pterygoid boss; ptrq, pterygoid ramus of quadrate; q, quadrate; qrpt, quadrate ramus of pterygoid; r, ridge; rap, retroarticular process; sa, surangular; soc, supraoccipital; sp, splenial; sq, squamosal; st, stapes; t, tooth (position in parentheses); v, vomer; and X and Y, unknown. Hatched areas in illustrations indicate damaged surface, and circle-and-dot pattern the remaining matrix or reconstruction in this and subsequent figures. Scale bar represents 100 mm.









**FIG. 4.** Close-up photographs of the skull of *Yunguisaurus liae* ZMNH M8738 (referred specimen). A, skull roof and braincase region in dorsal view; B, basicranium in ventrolateral view from the right side; C, lateral (from left side) view of braincase; and D, medial view of the right mandible. See Figure 2 for abbreviations.

tral relationship becomes less clear posteriorly. Sato *et al.* (2010) suggested the interclavicle wraps the clavicle posteriorly in the holotype; this cannot be confirmed in ZMNH M8738 because of the loss of the posteromedian portion.

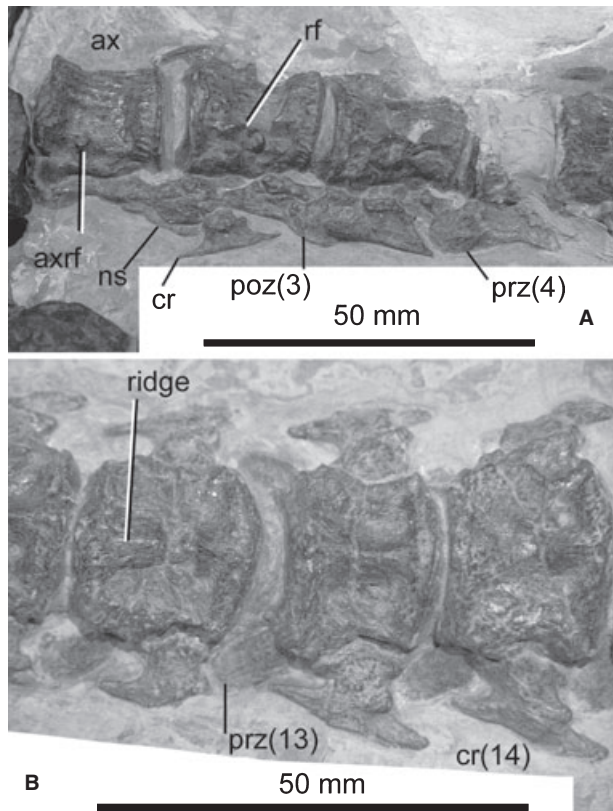
The posterolateral portion of the clavicle in ventral view is largely covered with the scapula but appears sickle-shaped as in the holotype; the bone is relatively short anteroposteriorly when compared with those in *Corosaurus* and *Augustasaurus* (Storrs 1991; Sander *et al.* 1997; Rieppel *et al.* 2002). The anterior edge projects anterior to the interclavicle. We suspect the left clavicle and scapula are slightly displaced from life position; if the left clavicle is rotated counterclockwise (in ventral view) relative to the scapula, the medial edges of the two bones will make a more smooth curve for the pectoral fenestra, and the lateral tip of the clavicle hidden. Only the posterior most portion is preserved of the left clavicle; its ventral surface is exposed because much of the scapula is lost.

The scapular morphology differs considerably between the holotype and the ZMNH specimen. In contrast to the small, *Corosaurus*-like scapula of the former in which the ventral plate does not develop (Storrs 1991), this bone in ZMNH M8738 is much more plesiosaurian in having a wide ventral surface with a concave medial edge that forms the lateral edge of the pectoral fenestra ('pcf'), and the facets for the coracoid and glenoid are thick and clearly defined. The cross section of the right scapula suggests the presence of a dorsal blade.

The coracoid in ZMNH M8738 also approaches plesiosaurian condition in several respects. There is an anterior process medial to the pectoral fenestra, and the element is much longer than wide. It reaches anterior to the level of the glenoid and may have contacted the clavicle and/or interclavicle. The left and right processes are separated by a V-shaped gap, and there was apparently a relatively small pectoral fenestra in life, as in *Plesio-*

**FIG. 3.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), ventral view of the skull. A, photograph; B, interpretation of the skull; C, photograph; and D, interpretation of the close-up of the braincase region. For abbreviations, see Figure 2. Scale bar represents 100 mm.

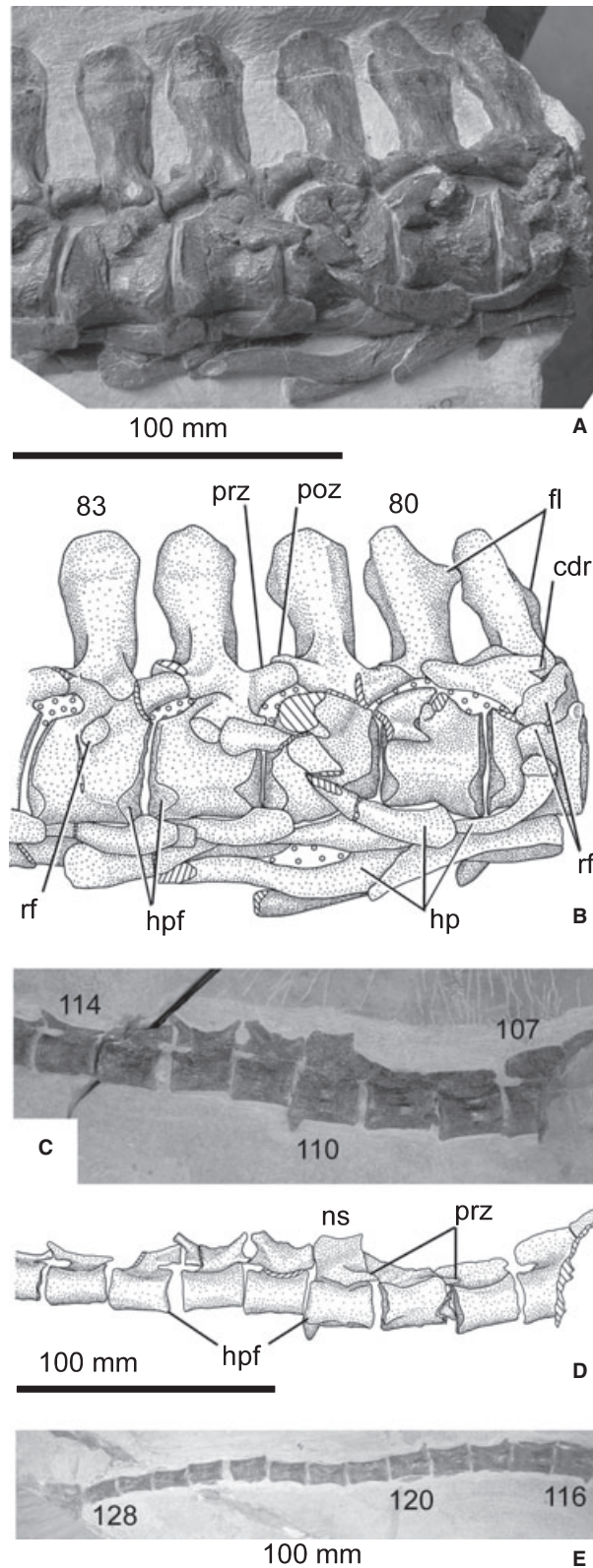
*saurus*, *Westphaliasaurus* and *Meyerasaurus* (Storrs 1997; Smith and Vincent 2010; Schwermann and Sander 2011). However, the coracoid does not widen posteriorly as in most plesiosaurs. The two coracoids probably contacted each other only in the posterior two-thirds in life; a small portion of the median symphyseal facet is exposed on each side. Except for the glenoid, the bone appears to be thin because underlying ribs show clearly in relief; the longitudinal relief of the long ribs is not interrupted, suggesting there is no transverse thickening of the coracoids between the glenoids.

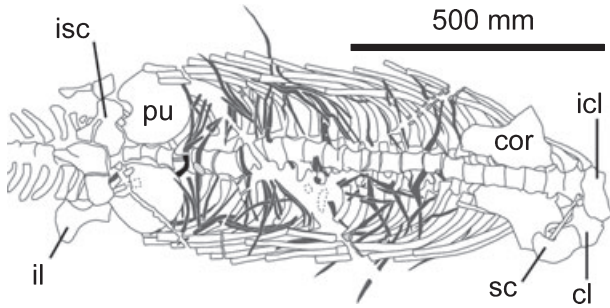


**FIG. 5.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), cervical vertebrae. A, axis to 4th in ventrolateral view (left side shown); B, 12th to 14th vertebrae in ventral view. Arabic number in parentheses indicates serial vertebral number. Abbreviations: ax, axis; axrf, axial rib facet; cr, cervical rib; ct, centrum; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; rf, rib facet. Scale bar represents 50 mm.

**FIG. 6.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), caudal vertebrae. A, photograph of anterior caudals; B, interpretation of anterior caudals; C, photograph of posterior caudals; D, interpretation of posterior caudals; and E, end of the tail. Arabic number indicates serial vertebral number. Abbreviations: cdr, caudal rib; hp, haemapophysis (= chevron); hpf, facet for haemapophysis; na, neural arch; prz, prezygapophysis; rf, rib facet. Scale bar represents 100 mm.

*Pelvic girdle.* The pelvis of ZMNH M8738 differs little from that of the holotype and, consequently, from those in early plesiosaurs (Fig. 8C, D). It is exposed in ventral view, and more





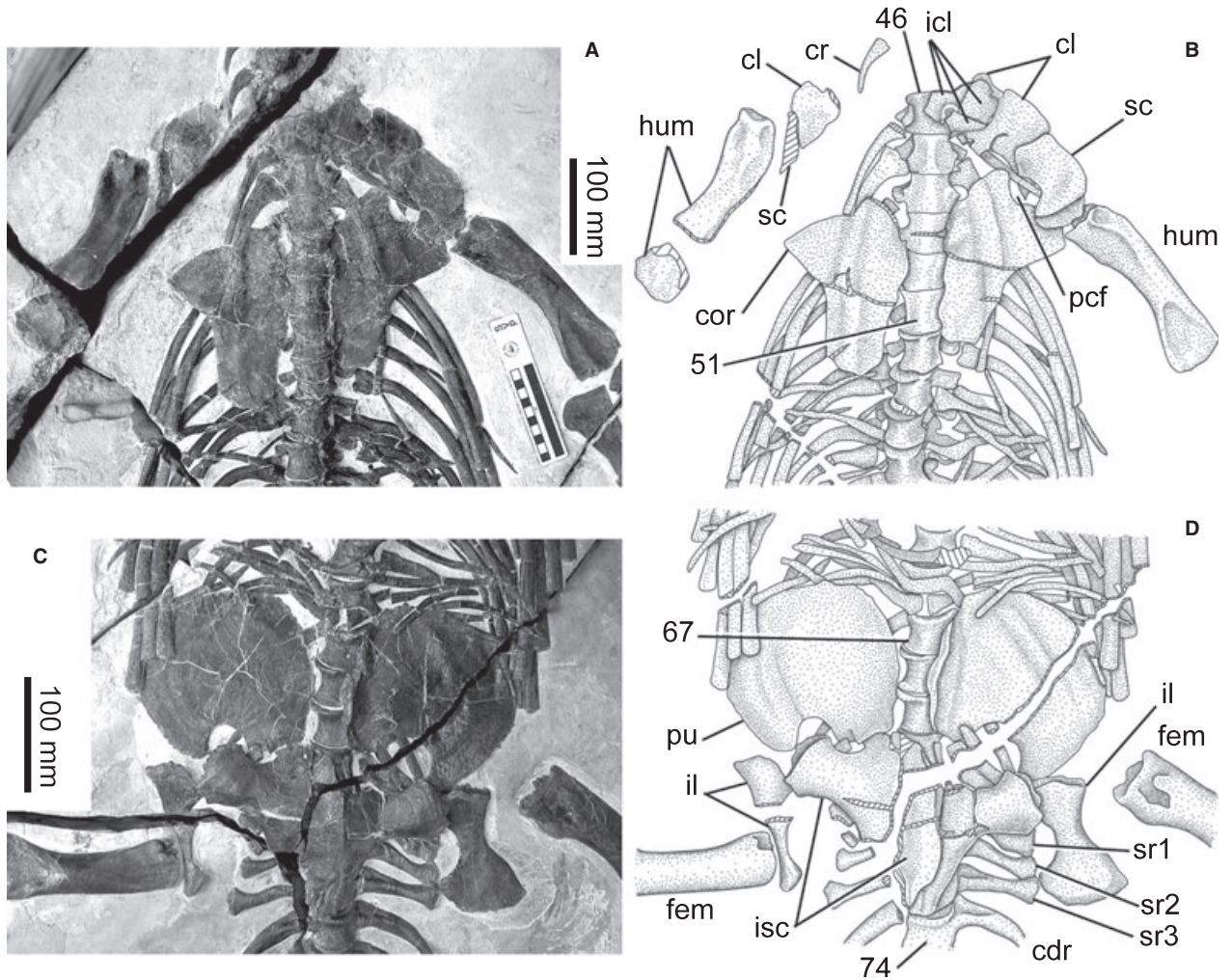
**FIG. 7.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), distribution of gastralia (in black) in ventral view. Abbreviations: cl, clavicle; cor, coracoids; icl, interclavicle; il, ilium; isc, ischium; pu, pubis; sc, scapula. Scale bar represents 500 mm.

complete outlines of each element are presented compared with the holotype. There are minor differences between the two specimens, such as the length of the pubis relative to the width,

but they can be attributed to more advanced ossification in the ZMNH specimen. The right hind limb was dislocated before burial, as indicated by the asymmetrical orientations of the ilia and inverted femur.

The left ilium is exposed in lateral view and the right in posteroventral view. In lateral view, the sacral (dorsal) end is slightly wider in ZMNH M8738 than in the holotype. The posteroventral view of the right ilium indicates that the sacral end is flat and thinner than the acetabular portion. The orientation and length of the acetabular facets in pelvic elements suggest a lack of contact between the ilium and pubis, another plesiosaurian feature.

The pubis is only slightly wider than long, giving a more circular outline compared with the short, semicircular pubis in the holotype. The pelvic fenestrae are small but clearly defined, and they are separated by a wide pelvic bar formed by the connection of the pubis and ischium along the midline; these characteristics are shared with Jurassic plesiosaurs and the Triassic pistosauroid *Bobosaurus* (e.g. Storrs 1997; Dalla Vecchia 2006).



**FIG. 8.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), girdle elements in ventral view. A, photograph of the pectoral girdle; B, interpretation of the pectoral girdle; C, photograph of the pelvic girdle; D, interpretation of the pelvic girdle. Abbreviations in addition to those in Figures 6 and 7: fem, femur; hum, humerus; pcf, pectoral fenestra; sr, sacral rib. Arabic number indicates serial vertebral number. Scale bar represents 100 mm.

The median symphyseal facet of the left pubis measures more than a half of its total length.

Neither ischium is complete nor entirely exposed due to a major crack and postmortem dislocation and overlap, but they together give a nearly complete profile of the bone in ventral view. It is slightly longer than wide and has an anterior projection along the midline to form the posterior half of the pelvic fenestra. Again, it is very similar to the ischia of plesiosaurs and *Bobosaurus* due to the presence of a pelvic fenestra and the elongation of the ischial plate along the midline.

*Limbs.* All four limbs are in or near life position, but the right humerus and femur are dislocated and exposed in dorsal view (Fig. 9). Most of the flipper elements are preserved except for the right forelimb where most of the ulna and phalanges are missing. Sato *et al.* (2010) attributed the concavity at the ends of propodial bones in the holotype to the lack of the epiphysis and young age; however, the proximal ends in ZMNH M8738 are still concave, suggesting the concavity was retained in adulthood.

The morphology of individual propodial and epipodial bones is essentially same as in the holotype, but the outline of each element is more uneven due to the development of articular facets and ridges. The distal ends of the humerus and femur are convex, and the separation of two epipodial facets is subtle but recognizable. The distal end of the radius is narrower than the proximal end, whereas the ulna is equipped with clearly marked facets for humerus and intermedium and is not a simple hour-glass-shaped bone as in the holotype. The femora of ZMNH M8738 have a rough, projected area on the posteroventral surface near the proximal ends, a feature not observed (due to orientation) in the holotype. Constriction of the shaft and distal widening of fibula are more prominent than in the holotype. The loss of perichondral ossification in the epipodial elements is a characteristic feature of the Plesiosauria (Caldwell 1997), but the loss did not occur in the four limbs of *Yunguisaurus*.

ZMNH M8738 has at least nine carpals in the right manus and 11 in the left, and eight tarsals in each pes; there is one tarsal-like bone found in a block next to the right hind limb, possibly indicating even higher count. They outnumber those of the holotype specimen, as well as other Triassic sauropterygians for which exact counts of the mesopodia are available, or even most plesiosaurs in which six carpals and six tarsals plus a few supernumerary bones are the norm in adult individuals (see discussion) although some may remain unossified in juveniles as Caldwell (1997) documented. Individual mesopodia of our specimen are identified based on the topology of those in early diapsids such as *Thadeosaurus* and modern lepidosaurs (Carroll 1988), in which comparable mesopodial counts are retained.

All carpals are circular to round polygonal in shape. The intermedium is located between the distal ends of the radius and ulna. The radiale, lateral centrale, ulnare and a pisiform form

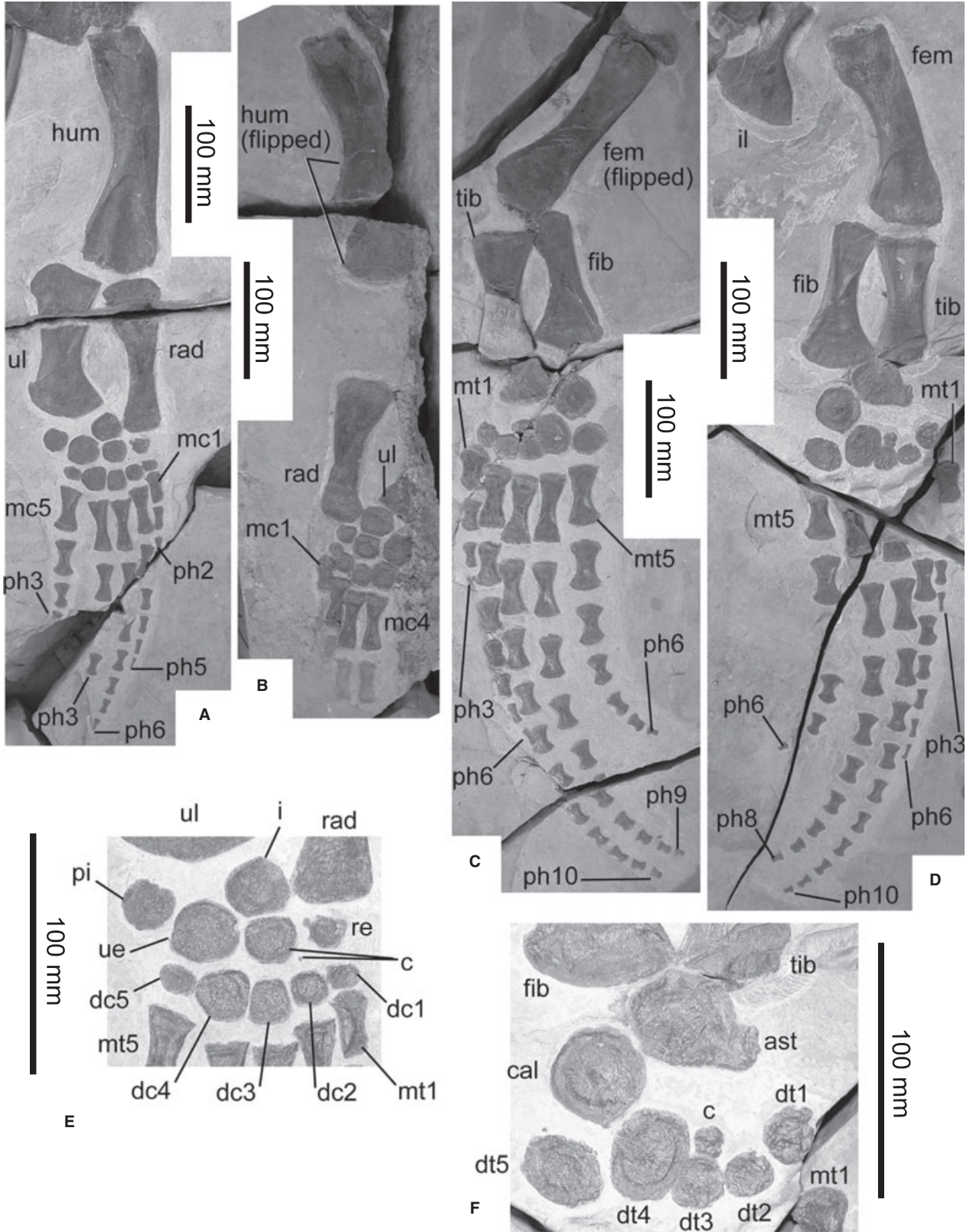
the proximal row, and five distal carpals form the distal row. A small element between the lateral centrale and the second distal carpal may represent the medial centrale. In the pes, the astragalus, calcaneum, one centrale and distal tarsals one to five are preserved. In contrast to the carpals, all tarsals but the astragalus are round and lack articular facets, suggesting the ossification of the tarsals is delayed relative to that of the carpals. Distal tarsals two to four and the centrale are in contact without developing articular facets, and further growth may result in the fusion of those elements. We also note a wide space between the distal tarsal row and the astragalus.

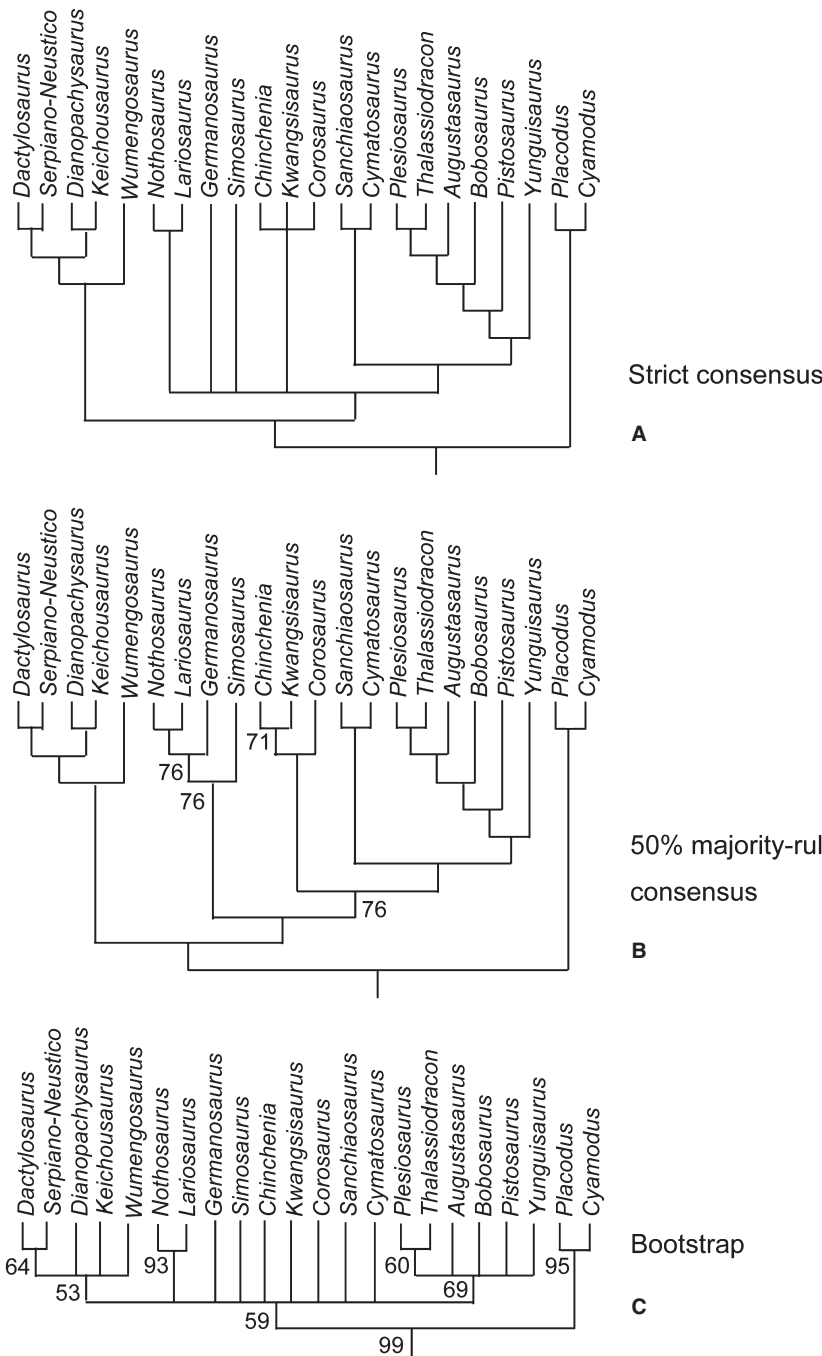
The proximal ends of metacarpals and metatarsals are not in line; in both fore and hind limbs, the first metapodium is most retracted proximally and touches the distal mesopodium, and the second and fifth metapodia are less retracted relative to the third and fourth. The holotype retains fewer carpals/tarsals, but it shares the same pattern of different levels of proximal retraction of the metapodia. The phalangeal formulae of ZMNH M8738 are 2-5-6+?-3+ in the forelimb (1-5-8[9?]-7-4 in the holotype) and 3-6-10-9-6 in the hind limb (unknown in the holotype). The nearly complete fourth digit of the left manus suggests the forelimb was shorter than the hind limb, although the humerus is more than 10 per cent longer than the femur in the ZMNH specimen; the humerus and femur are of comparable length in the holotype. In general, phalanges have broader ends and more waisted shafts in comparison with those of the holotype, and each phalanx tends to be more constricted or slender in forelimb than in hind limb as in the holotype. Proximal phalanges are relatively long and resemble the metapodials in *Yunguisaurus*, whereas the mesopodials are much longer than proximal phalanges in more basal sauropterygian limbs.

## REVISED PHYLOGENETIC ANALYSIS

To check the effect of morphological differences observed between the juvenile holotype and adult ZMNH M8738 and to include most recent studies on sauropterygian phylogeny, we reran a phylogenetic analysis using PAUP 4.0 beta 10 for Windows (Swofford 2002). See Appendices S1 and S2 in Supporting Information for data matrix and character list; the following modifications were given to the data matrix in Sato *et al.* (2010): scoring of *Yunguisaurus* was revised, three taxa (*Odontochelys*, *Dianopachysaurus* and *Wumengosaurus*) were added, and a few characters are redefined and/or added following recent studies (Wu *et al.* 2011; Liu *et al.* 2011). Various settings for the analysis, including those for the bootstrap analysis, are same as in Sato *et al.* (2010): heuristic search, all characters are unordered, addition sequence is random, 100 addition-

**FIG. 9.** *Yunguisaurus liae* ZMNH M8738 (referred specimen), limbs in ventral view. A, left forelimb; B, right forelimb; C, right hind limb; D, left hind limb; E, close-up of left carpals; and F, close-up of left tarsals. Abbreviations: ast, astragalus; c, centrale; cal, calcaneum; dc, distal carpal (with digit number); dt, distal tarsal (with digit number); fem, femur; fib, fibula; hum, humerus; mc, metacarpal (with digit number); mt, metatarsal (with digit number); ph, phalanx (with serial number in each digit); rad, radius; re, radiale; sc, scapula; sr, sacral rib; tib, tibia; ue, ulnare; ul, ulna. Scale bar represents 100 mm.





**FIG. 10.** Phylogenetic relationship between *Yunguisaurus* and other sauropterygians. A, strict consensus of 90 MPTs; B, bootstrap analysis (numbers at node indicate bootstrap support percentages); C, majority consensus; and D, Adams consensus. See text for details.

sequence replicates, 1000 trees held at each step during stepwise addition, TBR for branch-swapping algorithm.

The heuristic search yielded 58 MPTs (CI = 0.4103, RI = 0.7065). In the strict consensus (Fig. 10A), the relationship between *Yunguisaurus* and more derived pistosauroids including Plesiosauria (i.e., *Pistosaurus*, *Bobosaurus*, *Augustasaurus*, *Plesiosaurus* and *Thalassiodracon*) remained the same as those seen in the strict consensus of Sato *et al.* (2010). Of the nine synapomorphies of ‘*Yunguisaurus* and Pistosauria/Pistosauridae’ of Sato *et al.*

(2010, Table 1), reduction in the internal trochanter (character 105, character state 1) was not recovered in the revised analysis. In addition to the remaining eight synapomorphies, the following five synapomorphies also support this clade: coracoid with expanded medial symphysis (character 88, character state 3), absence of coracoid foramen (character 89, state 2), a rudimentary or absent intertrochanteric fossa (character 106, state 2), anteromedial corner of upper temporal fossa floored by descensus from the postorbital (character 122, state 2) and the

braincase deeply recessed below parietal skull roof (character 124, state 1). This clade survived the bootstrap analysis with 69 per cent support (Fig. 10C), although the relationship among Triassic genera dissolved.

*Cymatosaurus* and *Sanchiaosaurus* formed a clade sister to the clade containing *Yunguisaurus* and Plesiosauria in the strict consensus. *Corosaurus*, *Chinchenia* and *Kwangsisaurus* formed a clade, but its sister taxon relationship with other pistosauroids was recovered only in 76 per cent of the MPTs (see majority consensus in Fig. 10B). The clade containing *Corosaurus* and *Cymatosaurus* in the majority consensus includes all genera of the Triassic Pistosauroidea *sensu* Rieppel (2000a), but this clade did not survive the bootstrap analysis.

Members of the Nothosauroidea *sensu* Rieppel (2000a) (i.e. *Nothosaurus*, *Lariosaurus*, *Germanosaurus*, *Simosaurus*) formed a clade only in the majority consensus with 76 per cent support; in the strict consensus, they are involved in a polytomy with pistosauroid clades. The pachypleurosaurs formed a clade which is the sister taxon of the clade containing pistosauroids and nothosauroids in the strict consensus. In the bootstrap analysis, the pachypleurosaur clade was weakly supported with 53 per cent support.

## DISCUSSION

### *Ontogenetic variation*

The holotype and ZMNH M8738 share overwhelming similarities in the skull and postcranial skeleton (see 'Revised diagnosis' above) and a common stratigraphic origin. Unfortunately, all other pistosauroid taxa are represented by incomplete to fragmentary specimens, and it is impossible to demonstrate which of the characteristics in the revised diagnosis are truly unique to *Yunguisaurus*. Still, the completeness of the two *Yunguisaurus* skeletons gives a set of a large number of diagnostic characters, which distinguish them from other pistosauroid taxa. Therefore, we conclude that the two specimens are conspecific, and the observed differences between the two are primarily ontogenetic. The much larger and more robust ZMNH specimen must represent an older individual. As mentioned below, however, there are a few differences for which a simple ontogenetic change does not seem sufficient to explain. Needless to say, further investigations on multiple specimens are necessary to test other possibilities such as sexual dimorphism (documented in other sauropterygian taxa, Sander 1989).

Besides the sheer size difference, ZMNH M8738 shows signs of advanced ossification in various parts of the skeleton. The suture between the frontals is almost completely closed, and the neurocentral suture is closed in the

caudals and at least partially closed in the posterior cervicals (not confirmed in the rest of vertebral column due to the enclosing matrix). The pelvic fenestra is more clearly defined because of the well-developed pelvic bar. The contour of long limb bones is more complex due to the emphasized constriction of the shaft and the development of articular facets and ridges. The numbers of carpals and tarsals are higher, filling much of the space between the epipodials and metapodials.

Comparison of the two specimens also supplements information in previous studies. The right pterygoid of the holotype is medially displaced and interrupts the ventral exposure of the parasphenoid, suggesting those bones were loosely connected to each other. ZMNH M8738 also confirms that the exposure of the parasphenoid continues anterior to the interpterygoid vacuity, as well as the absence of the anterior interpterygoid vacuity seen in some Early Jurassic plesiosaurs (e.g. *Plesiosaurus* in Storrs 1997; '*Rhomaleosaurus*' *megacephalus* in Cruickshank 1994; Smith and Dyke 2008). The large number of tarsals in the holotype despite its inferred young age puzzled Sato *et al.* (2010), but it obviously reflects the even larger number in the adult.

The humerus of ZMNH M8738 is more than twice as long as that of the holotype, indicating positive allometry relative to the increase in skull length (1.7 times longer than the holotype) or to body length (1.8 times longer than the holotype, based on a length from the snout to the 91st vertebra). In addition, the humerus is longer than the femur in the ZMNH specimen, whereas they are of comparable lengths in the holotype. Sander (1989) noted the sexual dimorphism and positive allometry of the length of the humerus in a growth series of the pachypleurosaur *Neusticosaurus*, and the positively allometric growth of the humerus observed in *Yunguisaurus* may be attributed to ontogeny and/or sexual dimorphism.

Presence of a prominent pterygoid boss in ZMNH M8738 contrasts with its complete absence in the holotype, possibly representing a case in which a prominent structure does not appear until late in ontogeny. Our interpretation is admittedly tentative because such a change had not been documented among sauropterygians, but significant postnatal ontogenetic changes in the skull, including the late appearance of pterygoid teeth and/or development of the tuberosity for muscle attachment, have been documented in modern squamates and turtles (Dalrymple 1977; Barahona and Barbadillo 1998; Bever 2008).

Meanwhile, there are a few morphological variations not readily attributable to ontogeny. The drastic change in the scapular morphology is most remarkable; in fact, if the scapulae were found isolated, the juvenile scapula could be referred to a more primitive form such as *Corosaurus*, in which no obvious ontogenetic variation was

reported (Storrs 1991). The basal position of *Corosaurus* relative to *Yunguisaurus* in our majority consensus suggests that the scapula of *Yunguisaurus* is peramorphic, that is, an adult feature of an ancestor appears as an earlier developmental stage in the descendant (Gould 1977; Alberch *et al.* 1979). The plesiosaur *Cryptoclidus* also demonstrates a peramorphic change in the pectoral girdle (Andrews 1910; Storrs 1993).

The proportionally smaller size of the skull relative to the skeleton in the larger individual is predictable, because negative allometry of the skull is a common phenomenon among tetrapods, including sauropterygians (Sander 1989; Lin and Rieppel 1998). On the other hand, variation in the relative length of the snout of *Yunguisaurus* does not meet our expectation. The snout length (measured from the anterior edge of the orbit to the anterior end of the premaxilla) relative to the skull (from the posterior end of occipital condyle to the anterior end of the skull) is 44–45 per cent in ZMNH M8738 and 46 per cent in the holotype. However, the snout is generally shorter in younger individuals in many reptilian taxa. Obviously we need more than two specimens to verify the possible ontogenetic stability and range of individual variations or sexual dimorphism of the skull proportion.

### Mesopodia

There are 11 carpals (interpreted as radiale, intermedium, ulnare, pisiform, two centrales and five distal carpals) and eight tarsals (astragalus, calcaneum, centrale and five distal tarsals) in ZMNH M8738. They outnumber most other sauropterygian taxa, including Jurassic plesiosaurs, and other major clades of Triassic marine reptiles, in which numbers of mesopodia are reasonably known (Table 2). *Largocephalosaurus* Cheng *et al.* (2012) is the only other taxon in which 11 carpals are known, but the hind limb remains unknown; note that this taxon was described as a sauropterygian in Cheng *et al.* (2012), but it is more likely a saurosphargid (Table 2; Li *et al.* in press).

Identification of mesopodial ossifications in fossil marine reptiles is a challenge for a number of reasons. Most ossifications lack defined articular facets, and identification of each element is usually based on size and position. Postmortem dislocation and additional ossifications (supernumeraries) can further complicate positional homology. In ZMNH M8738, however, one-to-one correlation of each distal mesopodial element to the corresponding metapodial element is unquestionable in the manus and pes. There is room for further growth in the smaller centrale in the hand, but limited space between other elements and the presence of articular facets suggest their number, relative size and topological relationships

would not change considerably through further growth. Distal tarsals two to four and the pedal centrale are in contact and may indicate a later fusion, but all are clearly recognized as distinct elements.

Ossified fifth distal carpal and tarsal are found in primitive diapsids such as Permian younginiforms (Currie 1981; Carroll and Gaskill 1985; Bickelmann *et al.* 2009), and their presence is obviously a primitive feature for reptiles. The fifth distal carpal is often retained in turtles and lepidosaurs, but tends to be lost among the archosauromorphs and various lineages of marine reptiles. A number of taxa (*Claudiosaurus*, *Helveticosaurus*, Hupehsuchia, Ichthyopterygia, Saurosphargidae, Testudines, Thalattosauria) have been hypothesized to be closely related to the Sauropterygia (Carroll 1981; Merck 1997; Rieppel and Reisz 1999; Li *et al.* 2011). Among them, presence of the fifth distal carpal is confirmed only in *Claudiosaurus*, saurosphargid *Largocephalosaurus* and the Testudines. Presence of the fifth distal tarsal in *Yunguisaurus* is even more unusual because only the aforementioned primitive diapsids and *Claudiosaurus* are known to possess it. A close relationship between *Claudiosaurus* and the Sauropterygia proposed by Carroll (1981) was not supported in later phylogenetic studies, however, suggesting an apomorphic nature of the presence of the ossified fifth distal tarsal within the Sauropterygia.

Within the Sauropterygia, limited information is available for the Placodontia and poses a challenge in assessing the primitive condition. Although the placochelyid *Glyphoderma* has four carpals and six tarsals, and smaller numbers are known for the placodontoid *Paraplacodus*, little is known about their ontogenetic variation. Multiple specimens of different sizes are known for a few non-pistosauroid eosauroptrygians (e.g. *Keichousaurus*, *Lariosaurus*, *Wumengosaurus*; Lin and Rieppel 1998; Rieppel 1998b; Wu *et al.* 2011), but only up to six mesopodia have been reported. If the conditions in placodont taxa mentioned above are taken as fully ossified, the relationships between those non-pistosauroid taxa and *Yunguisaurus* suggest that the neomorphic nature or reversal of the fifth distal mesopodia in the lineage leads to *Yunguisaurus*.

Due to the paucity of adequate material of other Triassic pistosauroids, it remains unclear whether the mesopodia of *Yunguisaurus* represents an autapomorphy of this genus. *Augustasaurus*, *Pistosaurus* and *Kwangisaurus* are the only other Triassic pistosauroids for which carpals have been described, but they are incomplete and/or there is no guarantee that the specimens represent an ontogenetic stage comparable to ZMNH M8738 (Sues 1987; Rieppel 1999; Rieppel *et al.* 2002). Note that Sato *et al.* (2010) considered *Dingxiaosaurus luyinensis* Liu *et al.* 2002 a nomen dubium, and we maintain this view here. Its holotype and only specimen are represented by two hind limbs distal to



**TABLE 2.** Comparison of numbers of mesopodial elements of *Yunguisaurus liae* ZMNH M8738 (referred specimen) with other reptiles.

Taxa	Carpals	Tarsals	Sources
<i>Yunguisaurus</i> (Pistosauroidae)	11 (re, in, ue, pi, two c, dc 1 to 5)	8 (ast, cal, c, dt 1 to 5)	This study
<i>Corosaurus</i> (Pistosauroidae)	At least 4 (ue or in, three dc)	At least 3 (in, fe, dt)	Storrs (1991) and Rieppel (1998a)
<i>Augustasaurus</i> (Pistosauroidae)	At least 3 (in, ue, dc 4)	N/A	Rieppel <i>et al.</i> (2002)
<i>Kwangsisaurus</i> (Pistosauroidae?)	At least 3 (in, ue, dc 4)	N/A	Rieppel (1999)
<i>Pistosaurus</i> (Pistosauroidae)	3 or 4 (in, ue, dc 4, ?dc 3)	N/A	Rieppel <i>et al.</i> (2002)
<i>Plesiosaurus</i> (Plesiosauria)	7 (re, in, ue, dc 2 to 4, 1 sn)	6 (te, in, fe, three dt)	Storrs (1997)
<i>Archaeonectrus</i> (Plesiosauria)	6 (three proximal carpals, three dc)	6 (three proximal tarsals, three dt)	Owen (1865)
<i>Wumengosaurus</i> ( <i>Pachypleurosauria</i> )	3 (in, ue, dc 4)	2 (ast, cal)	Wu <i>et al.</i> (2011)
<i>Keichosaurus</i> ( <i>Nothosauroidae</i> )	5 (in, ue, dc 2 to 4)	3 (ast, cal, dt 4)	Lin and Rieppel (1998)
<i>Lariosaurus</i> ( <i>Nothosauroidae</i> )	6 (in, ue, dc 2 to 5)	4 (ast, cal, dt 3 and 4)	Rieppel (1998b)
<i>Paraplocodus</i> (Placodontia)	3 or 4 (in, ue, dc 3, ?dc 4)	3 (ast, cal, dt 4)	Rieppel (2000a,b)
<i>Glyphoderma</i> (Placodontia)	5 (individual element not ID'd)	6 (ast, cal, dt 1 to 4)	Zhao <i>et al.</i> (2008a, b)
<i>Claudiosaurus</i> (early Diapsida)	11 (re, in, ue, pi, two c, dc 1 to 5)	8 (ast, cal, c, dt 1 to 5)	Carroll (1981)
<i>Helveticosaurus</i> (Diapsida)	3 (in, ue, dt4?)	1 (in)	Rieppel (1989)
<i>Hupesuchus</i> (Hupesuchia)	8 (re, in, ue, dc 1 to 4, one sn)	7 (ast, cal, c, dt 1 to 4)	Carroll and Dong (1991)
'Second genus' of Carroll and Dong (1991) (Hupesuchia)	11 (re, in, c, ue, dt 1 to 4, three sn)	9 (ast, cal, c, dt 1 to 4, two sn)	Carroll and Dong (1991)
<i>Utatusaurus</i> (Ichthyopterygia)	8 (re, in, ue, pi, dc 1 to 4)	6 (ast, cal, dt 1 to 4)	McGowan and Motani (2002)
<i>Parvinator</i> (Ichthyopterygia)	8 (re, in, ue, pi, dc 1 to 4)	7 (ast, cal, c, dt 1 to 4)	Brinkman <i>et al.</i> (1992) and McGowan and Motani (2002)
<i>Sinosaurophargis</i> (Saurosphargidae)	7 (re, in, ue, dc 1 to 4)	N/A	Li <i>et al.</i> (2011)
<i>Largocephalosaurus</i> (Saurosphargidae)	11 (re, in, ue, two c, dc 1 to 5, pi)	N/A	Cheng <i>et al.</i> (2012) and Li <i>et al.</i> (in press)
<i>Odontochelys</i> (Testudines)	10 (re+in, ue, pi, two c, dc 1 to 5)	5 (ast+cal, dt 1 to 4)	Li <i>et al.</i> (2008)
<i>Proganochelys</i> (Testudines)	9 (in, ue, two c, dc 1 to 5) and pi?	5 (ast+cal, dt 1 to 4)	Gaffney (1990)
<i>Endennasaurus</i> (Thalattosauria)	7 (in, ue, c, dt 1 to 4)	6 (ast, cal, c, dt 1, 2 + 3, 4)	Renesto (1992)
<i>Xinpusaurus</i> (Thalattosauria)	'Two large and several small ossifications'	At least 6 (two large, four small dt)	Jiang <i>et al.</i> (2004)
'Polydactylous amniote' in Wu <i>et al.</i> (2003)	10 (re, in, ue, two c, dt 1, dt 2, dt 3 + 4, two sn)	9 (ast, cal, two c, dt 1 to 4, one sn)	Wu <i>et al.</i> (2003)

Anatomical abbreviations, see Figure 8.

Additional abbreviations: fe, fibulare; N/A, no available data; sn, supernumerary; te, tibiale.

epipodials, partial vertebrae and ribs from the Ladinian but a slightly older stratum (Yangliujing Formation) underlying the Zhuganpo Formation, which yielded *Yunguisaurus*. Although the limbs are similar to those of *Yunguisaurus*, ‘*Dingxiaosaurus*’ cannot be distinguished from many other pistosauroid taxa including Chinese ones such as *Chinchenia*, *Kwangsisaurus* and *Sanchiaosaurus* (Rieppel 1999), simply because comparable elements are not preserved to synonymize or distinguish them.

Among the primitive plesiosaurs (Owen 1865; Storrs 1997; Smith and Vincent 2010; Benson *et al.* 2012), the number, relative size and arrangement of carpals and tarsals excluding supernumeraries are nearly identical in the fore and hind limbs: three proximal and three distal elements. Fusion of the fifth mesopodial with the fifth metapodial may explain the retracted fifth digit in plesiosaurian limbs (synapomorphy of the Plesiosauria; O’Keefe 2001), but the rest of the mesopodial elements of *Yunguisaurus* and the Plesiosauria do not match in their number and topological relationships with neighbouring bones. Transformation of the mesopodia of *Yunguisaurus* into those of characteristic of the Plesiosauria requires considerable and unlikely restructuring, such as the fusion/reshaping of proximal carpals and splitting of the astragalus. Therefore, the mesopodia of *Yunguisaurus* do not represent an ancestral condition to those of the Plesiosauria.

ZMNH M8738 demonstrates the variability of mesopodial configuration among the Triassic sauropterygians. In contrast, the configuration of plesiosaurian mesopodia is relatively stable with three proximal and three distal carpals/tarsals. Derived plesiosaurs have relatively short and more angular elements, often accompanied with variable numbers of supernumeraries (Andrews 1910; Adams 1997; Caldwell 1997), but the number of carpals and tarsals remains nearly constant throughout the Jurassic and Cretaceous. The Plesiosauria are the only sauropterygians surviving the Late Triassic extinction and have limbs completely adapted for a pelagic environment, and their basic limb configuration must have been one of the key features that allowed their prosperity later in the Mesozoic (Storrs 1993; Bardet 1994; Rieppel 2000a; Benson and Butler 2011; Benson *et al.* 2012). Clearly, further discoveries and ontogenetic study of the pistosauroids are necessary to understand the origin of plesiosaurian limbs.

#### *Phylogenetic and functional inferences*

In our earlier study (Sato *et al.* 2010), *Yunguisaurus* was regarded as not suited for swimming with body undulation, and the tail anatomy of ZMNH M8738 provides further support. Although the tail is long, it does not have a skeletal support for a laterally compressed surface for effective thrusting, because the left and right haemap-

ophyses are not united to form a Y-shaped chevron, and the caudal neural arch shortens rapidly at the anterior one-third of the tail. As Storrs (1993) pointed out for nothosaurs, the long tail of *Yunguisaurus* likely represents the retention of ancestral condition and does not necessarily indicate functional adaptation.

Sato *et al.* (2010) also noted the different degrees of the ‘plesiosaur-likeness’ of the pectoral and pelvic girdles of the *Yunguisaurus* holotype; the pelvic girdle essentially achieved a plesiosaurian condition represented in Early Jurassic taxa such as *Plesiosaurus*, whereas the pectoral girdle lacks a number of plesiosaurian features. ZMNH M8738 adds more ‘plesiosaur-likeness’ to the *Yunguisaurus* pectoral girdle; the scapula is equipped with a ventral plate, the coracoid is longer than wide because of the presence of an anterior process, and there is a well-defined but incomplete pectoral fenestra. Remaining differences of the *Yunguisaurus* pectoral girdle morphology from those of typical Jurassic plesiosaurs include (1) the anterior ends of the scapulae do not reach or approach the midline, (2) the coracoid narrows posteriorly, (3) the ventral surface of the scapula is anteroposteriorly short (at least twice as long as wide in most plesiosaurs) and (4) the interglenoidal thickening of the coracoids is absent. Of those, first two states (either one or both) are actually shared with a few plesiosaurian taxa/specimens from the lowermost Jurassic (Hettangian), such as the lost holotype of ‘*Rhomaleosaurus*’ *megacephalus* (illustrated in Stutchbury 1846) and BMNH R1315 (*in* White 1940; *P. (Archaeonectrus) rostratus* *in* Andrews 1910; *P. dolicho-deirus* *in* Watson 1924, and *in* Storrs 1997), as well as the Pliensbachian *Wesphaliasaurus* (*in* Schwermann and Sander 2011), suggesting transitional nature of these characters in earliest part of the plesiosaurian history.

*Corosaurus* and *Augustasaurus* are the only other Triassic pistosauroids for which pectoral girdle elements were found associated with other parts of skeleton (Storrs 1991; Sander *et al.* 1997; Rieppel *et al.* 2002). These two taxa and *Yunguisaurus* share the ossification of the coronoids between the glenoids. Their condition contrasts with those of nothosauroids, pachypleurosaurs and *Wumengosaurus* in which the coracoid has a characteristic constriction behind the glenoid and meets its counterpart only posterior to the glenoid, with the thickening along the outer edge stretching posteromedially. Assuming the monophyly of the pistosauroid taxa (*sensu* Rieppel 2000a) in our majority consensus tree, the coracoids of *Corosaurus*, *Augustasaurus* and *Yunguisaurus* may represent an early stage of adaptation to resist the medial compression between the glenoids due to the paraxial downward movement of forelimbs, which later results in the development of the transverse thickening between the glenoids characteristic to the Plesiosauria.

The anterolateral corner of the clavicle is pronounced in *Corosaurus*, but is reduced in *Augustasaurus* and *Yunguisaurus*. Storrs (1991), who hypothesized a limb-dominated locomotion in *Corosaurus* analogous to that of plesiosaurs (i.e. combination of posteroventral power stroke with a recovery stroke in the horizontal plane; Godfrey 1984), considered the scapulohumeralis muscle probably reached to the clavicle in *Corosaurus*. Reduction in the corner results in less mechanical advantage for the craniad pull of the humerus, and the reduced corners in later pistosauroids and plesiosaurs likely indicate less muscular power to pull the humerus forward. The pectoral girdle of *Yunguisaurus* is less plesiosaur-like than the pelvic girdle, and it appears halfway to the plesiosaurian condition. Although the humerus of the adult *Yunguisaurus* specimen is longer and more massive than the femur, unlike those in the young holotype, the forelimb as a whole is still smaller than the hind limb. The larger surface of the hind limbs in *Yunguisaurus* suggests their importance in locomotion before the development of the plesiosaur-like pectoral girdle for more sophisticated posteroventral movement of the forelimbs.

In the meantime, the morphological transition of the limbs towards a typical plesiosaurian flipper was obviously not simple within the Triassic pistosauroids. The large number of mesopodia and hyperphalangy in *Yunguisaurus* (this study) and more primitive manus with possibly smaller number of mesopodia and shorter phalanges in the more derived *Augustasaurus* (Sander *et al.* 1997; Rieppel *et al.* 2002) imply considerable variation among the Triassic Pistosauroidea, in contrast with the nearly constant mesopodial counts in the Plesiosauria. Further discoveries of pistosauroid specimens with articulated limbs and their detailed anatomical studies are necessary to improve the level of confidence in the phylogeny (Fig. 10C) and then to document the evolution of limb morphology towards the Plesiosauria.

Most Triassic sauropterygians are known from the Middle Triassic, but the basal pistosauroids *Corosaurus* and *Cymatosaurus* are known from the uppermost Lower Triassic or lowermost Middle Triassic (Storrs 1991; Rieppel and Hagdorn 1997; Hagdorn and Rieppel 1999). The earliest placodonts and pachypleurosaurs are known from the lowermost Middle Triassic (Diedrich 2011; Liu *et al.* 2011), whereas the earliest nothosauroid appears slightly later (*Nothosaurus* from lower Muschelkalk; Rieppel and Hagdorn 1997). Our interpretation indicates that animals with pistosauroid coracoid appeared by the latest Early Triassic (*Corosaurus*) before various pachypleurosaurs and nothosauroids with different girdle morphology prospered in the Middle Triassic. In fact, the confidence level of the sister taxon relationship between Pistosauroidea and Nothosauroidea is

<50 per cent in our analysis (Fig. 10C), and we consider that the nothosauroid origin of the Pistosauroidea should not be taken for granted.

Fossil records of non-pistosauroid sauropterygians are primarily limited to the Tethys (Europe, Middle East, China), whereas the pistosauroids such as *Corosaurus* and *Augustasaurus* are known from western North America. The occurrence of *Augustasaurus* in Nevada could be explained by the accretion of exotic terrane from Panthalassa (Rieppel *et al.* 2002), but the Alcova Limestone that yielded *Corosaurus* is considered to be deposited at the western margin of the North American craton (Storrs 1991; see map of exotic terranes in Coney *et al.* 1980). In addition, fragmentary plesiosaurian remains have been reported from the Middle to Upper Triassic of Svalbard (Cox and Smith 1973), suggesting the presence of pistosauroids in northern high latitude regions outside the Tethys. Non-pistosauroid sauropterygians are far more diverse and common than pistosauroids in the Tethys by the Middle Triassic (Rieppel 2000a), but they have not been reported from high latitude regions and western North America, despite the occurrences of pistosauroids and other Triassic marine reptiles (ichthyosaurs and thalattosaurs; Nicholls 1999; McGowan and Motani 2003). Absence in the fossil record should not be taken literally (Sander *et al.* 1997), and further searches for non-Tethyan sauropterygians are necessary to confirm this pattern, but these lines of evidence imply that the pistosauroid lineage split early from other sauropterygians and took a unique locomotory strategy, which led the later forms to achieve a wider geographical distribution and survive the Late Triassic extinction.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Characters for phylogenetic analysis.

**Appendix S2.** Data matrix for phylogenetic analysis.

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