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FIRST COMPLETE PISTOSAUROID FROM THE TRIASSIC OF CHINA

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Triassic pistosauroids (Reptilia: Sauropterygia) are the closest relatives of the Plesiosauria, a group that achieved considerable taxonomic diversity and cosmopolitan distribution during the Mesozoic. Despite their importance for the understanding of the origin of the Plesiosauria, however, our knowledge on the Triassic pistosauroids (*Augustasaurus* Sander et al, 1997; *Chinchenia* Young, 1965; *Corosaurus* Case, 1936; *Cymatosaurus* Fritsch, 1894; *Kwangisaurus* Young, 1959; *Pistosaurus* Meyer, 1939; Edinger, 1935; Rieppel, 1997, 1998, 1999; Storrs, 1991) has been limited due to the lack of well-preserved specimens.

We report a new pistosauroid, *Yunguisaurus liae* gen. et sp. nov., from the Triassic of southern China. This taxon is represented by a virtually complete and articulated skeleton embedded in a limestone slab from the Falang Formation (upper Middle to lower Upper Triassic). Previously described Triassic pistosauroids are known from the upper Lower to lower Middle Triassic (Rieppel, 1999, 2000; Wang et al., 2001), and *Y. liae* is the youngest pistosauroid (excluding the Plesiosauria). Because of the rarity of pistosauroids, we are providing this preliminary report while the postcranial skeleton waits for further preparation and subsequent full description. A unique combination of primitive and derived traits is observed in this specimen, and a phylogenetic analysis confirms its close relationship with derived pistosauroids.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
PISTOSAUROIDEA Baur, 1887–90
YUNGUISAURUS LIAE gen. et sp. nov.
(Figs. 1, 2)

Holotype—National Museum of Natural Science (NMNS) 004529/F003862, a nearly complete and articulated skeleton, missing the distal tail.

Etymology—“Yungui” from the Yungui Gaoyuan (in Chinese pingying), a regional plateau named after the Yunnan and Guizhou provinces. The holotype locality is on this plateau, near the boundary between these two provinces. The species name in honor of Professor Jinling Li of the Institute of Vertebrate Paleontology and Paleoanthropology, China, for her leadership and contribution to the recent study of the Chinese Triassic marine vertebrate fauna.

Type Locality and horizon—Near Huangnihe River, Chajiang, about 10 km NW of Xingyi, Guizhou, Falang Formation. The fossil-bearing slab does not yield any microfossils for dating; the same horizon on the Yunnan side of the Huangnihe River contains conodonts belonging to the *Paragondolella naantangensis*-*P. polygnathiformis* Assemblage Zone, Carnian, early Late Triassic (Yang et al., 1995; Wang, 1996; Wang et al., 1998; 2001).

Diagnosis—Differing from known pistosauroids in the combination of the following characters: seven premaxillary teeth, single interpterygoid vacuity with a narrow anterior extension, anterior extension of parasphenoid, elongate snout with slender teeth, pineal foramen reaching frontal/parietal suture, nasal present, sharp parietal crest, long mandibular symphysis, prominent coronoid process, slender humerus and epipodials, and hour-glass-shaped ulna.

Description—The preserved skeleton measures about 1.7 m from the tip of the snout to the end of the incomplete tail. The skull (Fig. 1) is dorsoventrally compressed, with the posterodorsal portion of the skull roof and many teeth missing. It measures 126 mm from the tip of the premaxillae to the occipital condyle, and it is widest (63 mm) at the mandibular articulation.

The partially fused premaxillae and maxillae form the slender snout, and there are seven premaxillary teeth on each side. There is a separate nasal postero-medial to the external naris, between the premaxilla and prefrontal. The pineal foramen is anteriorly located, with the frontal forming its anterior edge. The postfrontal forms the postorbital bar, while the postorbital forms most of the lateral edge of the supratemporal fossa. The parietals form a narrow sagittal crest. Posteriorly they are fractured and the connection to the squamosals is missing, but the medial suture can be traced on the damaged surface. The exoccipital-opisthotic is dislocated, and the supraoccipital is missing. The pair of rods lateral to the pterygoids are likely to be hyoids rather than paroccipital processes because of the dislocation of exoccipital-opisthotic.

The right palate is slightly displaced towards the left relative to the braincase, as indicated by the asymmetry of the basisphenoid-parasphenoid seen through the interpterygoid vacuity. This displacement caused a small portion of the right pterygoid to cover a part of the interpterygoid vacuity at the level of the anterior edge of the subtemporal fenestra. The pterygoids do not meet behind the vacuity through which the basisphenoid-basioccipital contact is visible. The basisphenoid-parasphenoid suture is unclear, but the internal carotid foramen is located on the ventral surface. The internal nares are covered by the mandible. The vomer meets the pterygoid anterior to the interpterygoid vacuity.

Y. liae has an elongated, slender mandibular symphysis similar to that of *Augustasaurus*, and it is composed of the dentaries and splenials. The displaced left splenial covers the left anterior portion of the palate. The prominent coronoid process and adductor fossa are complete on both sides. The articular forms the glenoid and dorsal portion of the retroarticular process, the angular forms the ventral edge, and the surangular covers the dorsal half of the lateral side of the process.

The dorsal side of the postcranial and a small portion of the

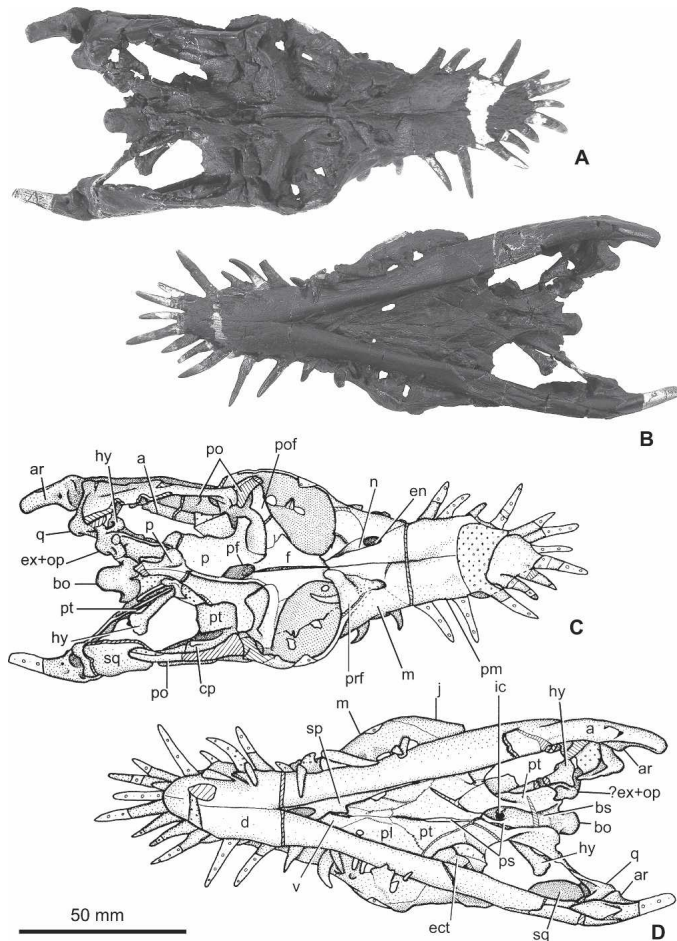


FIGURE 1. Skull of the holotype of *Yunguisaurus liae*, NMNS 004529/F003862. **A** and **B**, photograph, **C** and **D**, anatomical interpretation in dorsal (**A**, **C**) and ventral (**B**, **D**) views. **Abbreviations:** **a**, angular; **ar**, articular; **bo**, basioccipital; **cp**, coronoid process; **d**, dentary; **ect**, ectopterygoid; **en**, external naris; **ex**, exoccipital; **f**, frontal; **hy**, hyoid; **ic**, internal carotid foramen; **j**, jugal; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, parietal; **pf**, pineal foramen; **pl**, palatine; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **sp**, splenial; **sq**, squamosal; **v**, vomer.

ventral side of the pectoral region are exposed. Antermost cervicals are slightly disarticulated, showing the ventral side of a few. There are no foramina subcentralia in these cervical and pectoral centra. Proportions of the humeri and epipodials are similar to those in *Pistosaurus* (Fig. 2; Sues, 1987) and more robust than in *Kwangsisaurus*, but more slender compared with plesiosaurs. The humeral shaft is curved, and the right humerus is 91 mm long and 31 mm wide. The proximal end of the radius is notably wider than the distal end, whereas the distal end of ulna is slightly wider than the proximal end.

DISCUSSION

Chinese pistosauroids—*Chinchenia* Young, 1965 is known from the Anisian Guanling Formation and its short mandibular symphysis distinguishes it from *Y. liae* (Rieppel, 1999; Wang et al., 2001). The radius and ulna of *Kwangsisaurus* Young, 1959 from upper Lower or lower Middle Triassic of Guangxi Province are slenderer than those in *Y. liae*. Liu et al. (2002) erected *Dingxiaosaurus luyinensis* based on an incomplete specimen (represented by a pair of hind limbs missing most of the femur

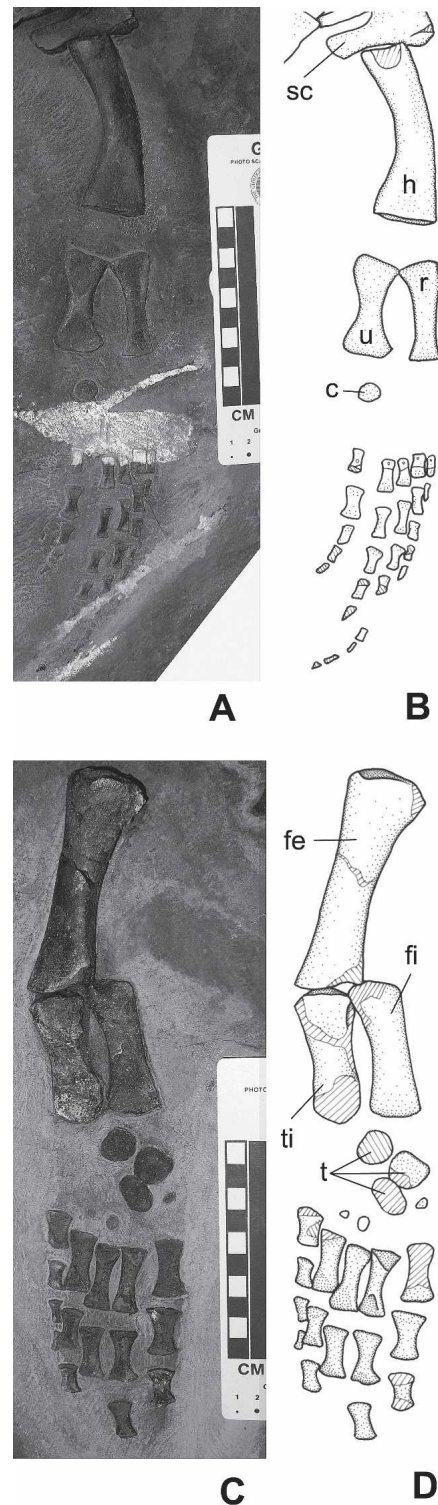


FIGURE 2. Dorsal view of the right forelimb (**A**, **B**) and left hind limb (**C**, **D**) of the holotype of *Yunguisaurus liae*, NMNS 004529/F003862. **Abbreviations:** **c**, carpus; **fe**, femur; **fi**, fibula; **h**, humerus; **r**, radius; **sc**, scapula; **t**, tarsus; **ti**, tibia; **u**, ulna. Scale bar is 100 mm.

and some fragmentary vertebrae and ribs) from the Yanjiuling Formation in Guizhou as a potential ichthyosaur with plesiosaurs-like phalanges. The slender epipodials, hyperphalangy, and seven (?) tarsals suggest it is possibly a pistosauroid, and com-

parison with *Y. liae* (Fig. 2) suggests that these might be actually forelimbs which are distinguished from those of *Y. liae* mainly on the configuration of the epipodials. The two limbs however differ from each other and from the reconstruction by Liu et al. (2000:fig. 2) in the number and/or size of tarsals (pers. obs. of a photograph provided by the Dingxiao Museum after further preparation of the specimen). Poor preservation of limbs in other pistosauroids does not allow sufficient characterization of the *D. luyinensis* limbs for taxonomic distinction. This poorly represented taxon is a *nomen dubium*.

Phylogenetic relationship of *Yunguisaurus*—The pistosauroid status (sensu Rieppel, 2000) of *Yunguisaurus* is demonstrated by diagnostic features such as the parietal sagittal crest, mandibular articulation well behind the occipital condyle, as well as by our preliminary phylogenetic analysis (Fig. 3, Appendix). *Y. liae* however has a combination of primitive and derived characters that challenges the previous hypotheses of relationship and diagnosis of subclades within the Pistosauroidea.

Major plesiomorphic characters include the presence of the nasals (condition in *Pistosaurus* and basal plesiosaurs disputed [see Appendix]; condition unknown in *Corosaurus* and previously described Chinese pistosauroids), absence of foramina subcentralia (present in *Pistosaurus*, *Augustasaurus* and plesiosaurs), and long epipodials with constricted shafts (short and lunate shape in basal plesiosaurs). The most notable derived feature is the presence of an interpterygoid vacuity, a feature only known for *Pistosaurus*, *Augustasaurus*, and plesiosaurs (condition unknown for Chinese pistosauroids and *Corosaurus*). The narrow anterior portion of the vacuity is unique to *Y. liae*, and this condition may be a precursor of the presence of an elongated vacuity in *Plesiosaurus* (Storrs, 1997) and/or two vacuities in some basal plesiosaurs such as *Rhomaleosaurus* (Cruickshank, 1994) and *Plesiopterys* (O’Keefe, 2004). The expansion at the distal end of the ulna is another derived feature shared with *Pistosaurus* and *Augustasaurus*, but the constricted shaft indicates it is not as derived as in plesiosaurs.

The strict consensus of our phylogenetic analysis (Appendix) result in the loss of resolution at the level of Eusauroptrygia, but a clade of derived pistosauroids (*Augustasaurus*, *Pistosaurus*, *Yunguisaurus*, and plesiosaurs) survive (Fig. 3A). Other Chinese pistosauroids (*Chinchenia* and *Kwangsisaurus*) are wildcards (Fig. 3B; Nixon and Wheeler, 1992), and the rest of the pistosauroids form a clade in the Adams consensus (also see Rieppel et al, 2002). *Augustasaurus*, *Yunguisaurus*, and *Pistosaurus* are successive outgroups (in this order) to the plesiosaurian clade. Monophyly of *Augustasaurus* and *Pistosaurus* is not supported, challenging the hierarchical relationship of the pistosauroid subclades Superfamily Pistosauria and Family Pistosauridae in Rieppel (2000).

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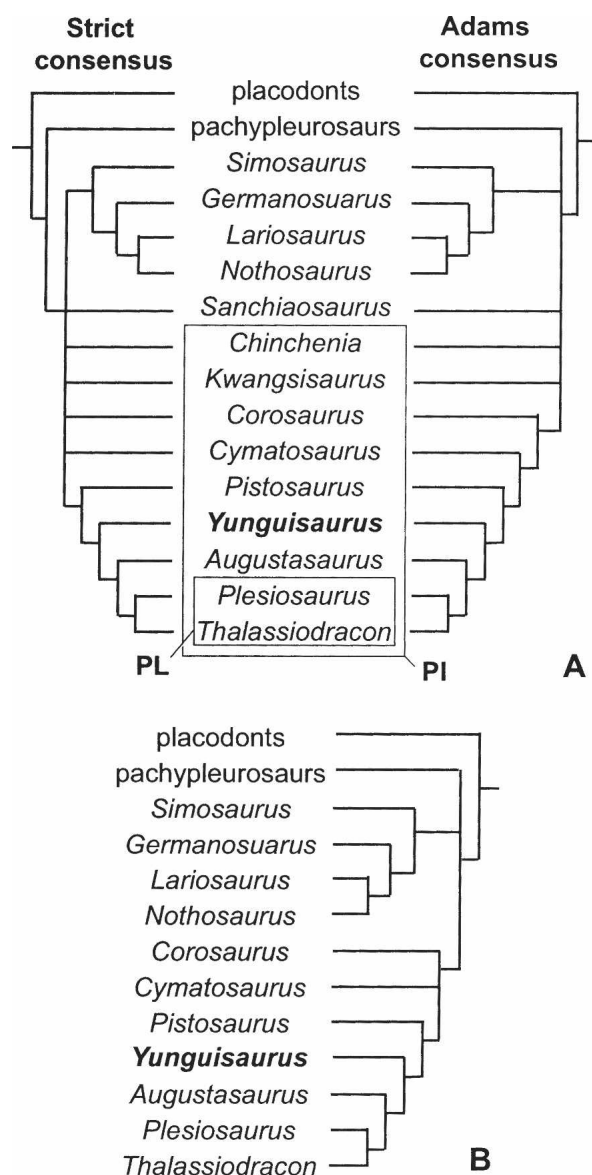


FIGURE 3. A, Strict and Adams consensus trees of 36 MPTs showing phylogenetic relationships of *Yunguisaurus liae* and other sauropterygians. B, strict consensus tree of an analysis without wildcard taxa (*Chinchenia*, *Kwangsisaurus*, *Sanchiaosaurus*). See Appendix for details.

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APPENDIX

Phylogenetic analysis is based on the based on the data matrix of Rieppel et al (2002), with the following modifications in coding. A heuristic search by PAUP 4.0b10 (Swofford and Begle, 1993) resulted in 36 MPTs (398 steps, CI=0.450, RI= 0.715).

1. Character 6 (reduced nasal) for *Cymatosaurus*, 2 to 1 (Rieppel, 2000: 99). For *Pistosaurus* (Rieppel et al., 2002; Sues, 1987) and *Plesiosaurus* (O'Keefe, 2001; Storrs, 1997), 2 to 1/2.
2. Character 38 (quadrate and squamosal) for *Augustasaurus*, *Pistosaurus* and *Plesiosaurus*, 1 to 2 (Rieppel et al, 2002: 582).
3. Additional character state “2” for character 39 (dorsal portion of epipterygoid wider than base) for *Thalassiodracon* (Storrs and Taylor, 1997:fig. 5).
4. Additional character state “3” for character 96 (ectepicondylar groove absent; coded in Rieppel et al. (2002) but state not defined) for *Augustasaurus*, *Plesiosaurus*, *Pistosaurus*, and *Yunguisaurus*.
5. Deletion of character 123 (box-like suspensorium); overlaps with character 38.
6. Additional taxa

Thalassiodracon hawkinsi (basal pliosaur, based on Storrs and Taylor, 1997; O'Keefe, 2001)

1000? 1/2??220 02101 00331 1100{01} 1201? 11112 {02}022? ??021 0?11?
10000 111?{01} 111?? ????? 1???? ????? ????? ????? ????? ????? ?????
????? ????? ????? 02111 ????? ?{12}2?? ??

Yunguisaurus liae

10{01}?0 10220 00200 {12}033? ??{12}00 1201? ???? ?0{12}?? ?20{01}?
0011? {12}00?? ?1?{01} 110?1 01?0? 1???0 ????? ????1 1???? 01111
3120? 11?01 211?? ?0??0 00??1 02??0 1?00? ?221? 0?