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Research Article

Taxonomic revision of *Asialepidotus shingyiensis* Su, 1959 (Halecomorphi, Holostei) from the Middle Triassic (Ladinian) of Guizhou and Yunnan, China

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Abstract - The holostean fish Asialepidotus shingyiensis, from the Middle Triassic (Ladinian) of Guizhou and Yunnan, China, was previously regarded as either a semionotiform ginglymodian or an amiiform halecomorph. This study provides a revision of this taxonomically controversial taxon based on a comparative study including the holotype and 50 new specimens. Newly recognized anatomical information includes the dermal component on the sphenotic, complete series of circumorbital bones, palatal bones, quadratojugal, hyomandibula, sensory canal in the maxilla, notched posterior margin of the maxilla, median gular, and many elements on the medial surface of the lower jaw. Results of a cladistic analysis incorporating these new data place Asialepidotus as an ionoscopiform halecomorph that is more derived than Subortichthys and Panxianichthys, and consists of the sister taxon of Robustichthys and all other ionoscopiforms.

Keywords: Triassic, Ionoscopiformes, osteology, phylogeny, South China

1. Introduction

The fossil taxon *Asialepidotus shingyiensis* Su, (1959) was one of the earliest known holostean fishes in China. It was originally described on the basis of a single incomplete specimen (with most of the skull and caudal fin missing) from the late Middle Triassic (Ladinian) marine deposits (Zhuganpo Member of the Falang Formation) of Xingyi, Guizhou Province. Since Su's (1959) classification of *Asialepidotus* in the Semionotidae, this taxon has long been considered as the oldest semionotid in China. Based on three nearly complete fish specimens from the same fossiliferous level, Liu *et al*. (2003) named *Guizhouella analilepida* and referred it to the family Eugnathidae (= Caturidae, Amiiformes); this genus was later renamed as *Guizhoueugnathus* because it was preoccupied by a brachiopod genus (Liu, 2004). Jin (2009) first noticed that *G. analilepida* was a junior synonym of *A. shingyiensis*, and suggested that this taxon was closely related to parasemionotiforms. Despite being included in a few recent phylogenetic analyses of neopterygian or halecomorph relationships (Benton *et al*., 2013; Sun *et al*., 2017), *A. shingyiensis* has not been redescribed, and the phylogenetic position of this taxon has remained controversial. Benton *et al*. (2013) suggested that *Asialepidotus* is the sister taxon of *Sinoeugnathus* (Su, 1959), and placed the *Sinoeugnathus–Asialepidotus* clade at the base of the Halecomorphi; contra Grande and Bemis (1998), Benton *et al*. (2013) placed the parasemionotiform *Watsonulus* at the base of the Holostei. Sun *et al*. (2017) suggested that *Asialepidotus* is the sister taxon of *Panxianichthys* (Xu and Shen, 2015) and referred it to the family Panxianichthidae (Panxianichthiformes). However, more recent studies of Ma and Xu (2017) supported that *Panxianichthys* is a basal member of the Ionoscopiformes (Xu and Shen, 2015). Here we present a redescription of *A. shingyiensis*, which provides an improvement for resolving the phylogenetic position of this taxon within the Holostei.

2. Materials and methods

The revision of *A. shingyiensis* is based on the comparative studies of 54 specimens, including the holotype (IVPP V2434; Fig. 1A), the three specimens (NIGP 136040 and 136041; MES 3603; Fig. 1B) previously studied by Liu *et al*. (2003), and 50 specimens (IVPP V19005, 19009, 19996–19999, 20673–20679, 22856–22869, 22995–23000, 23002–230018; Fig. 1C) collected in the last decade from Dingxiao, Wusha and Baiwanyao of Xingyi, western Guizhou, and Shibalianshan of Fuyuan, and Changdi, Zhongshan and Banqiao of Luoping, eastern Yunnan. Fossil specimens were prepared mechanically. In order to illuminate the phylogenetic position of *Asialepidotus*, we incorporated this taxon into the data matrix used in Ma and Xu (2017). Tree searches were accomplished by the heuristic search algorithm in

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PAUP* 4.0b10 (Swofford, 2003). All characters were unordered and equally weighted. Institutional abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China; MES, Museum of Earth Sciences, Nanjing University, Nanjing, China.

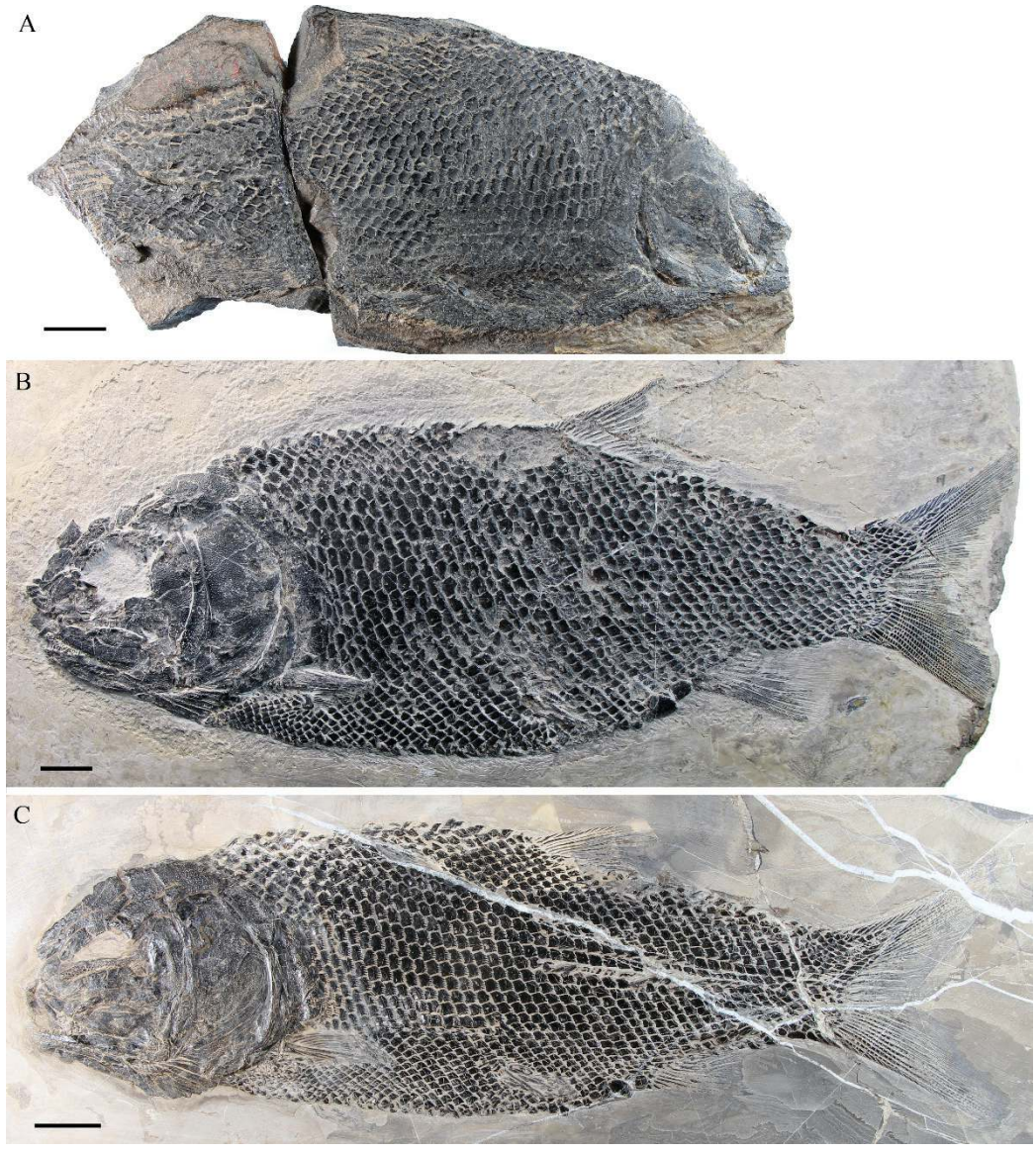

Figure 1. *Asialepidotus shingyiensis* Su, 1959. A. IVPP V2434, holotype; B. NIGP 136040; C. IVPP V19998. Scale bars =15 mm.

3. Results and discussions

Our studies have revealed new and detailed anatomical information for the skull, lower jaw and pectoral girdle of *Asialepidotus*, including the rostral, lateral ethmoids, the complete series of circumorbital bones, two suborbitals, sclerotic bones, the small fenestra for the palatine ramus of the facial nerve in ventral portion of premaxilla, the dermal component on the sphenotic, the parasphenoid, paired vomers, metapterygoids, entopterygoids, ectopterygoids, dermopalatines, quadratojugals, hyomandibulas, hypohyals, anterior and posterior ceratohyals, the sensory canal in the maxilla, the notched posterior margin of the maxilla, coronoids, prearticulars, retroarticulars and Meckelian ossifications in lower jaws, the complete series of branchiostegal rays, the gular, and the presupracleithrum and two clavicle elements in each pectoral girdle. The wealth of these new anatomical data for *Asialepidotus* has facilitated a phylogenetic analysis, the results of which recover *Asialepidotus* as an ionoscopiform that is more derived than *Subortichthys* and *Panxianichthys* and consists of the sister taxon of *Robustichthys* and all other ionoscopiforms.

Our studies support that *Asialepidotus* is an unambiguous halecomorph, as it possesses two synapomorphies of this clade: a symplectic articulating with the lower jaw, and a notched posterior margin of the maxilla. *Asialepido-*

tus is referred to the halecomorph order, Ionoscopiformes, because it possesses a synapomorphy of this order, presence of a sensory canal in the maxilla. *Asialepidotus* has relatively long parietals, showing a state more derived than that in the basal ionoscopiform *Subortichthys*. It is more derived than *Panxianichthys* and shares a derived feature with *Robustichthys* and other ionoscopiforms, presence of an innerorbital flange of the dermosphenotic bearing an infraorbital sensory canal. However, it lacks two derived features of *Robustichthys* and other ionoscopiforms, e.g., presence of a posteriorly inclined lower border of the last infraorbital, and absence of a distinct quadratojugal (Xu *et al*., 2014).

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