Redescription of *Wushaichthys exquisitus* and phylogenetic revision of Thoracopteridae

By

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B.S. Capital Normal University, 2010

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Date Defended: 3 September 2019

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ABSTRACT

Wushaichthys exquisitus, a small fish from the Middle Triassic of Guizhou Province, China, was named and studied by Xu et al. (2015), and Xu et al. interpreted it as the most primitive species in the family Thoracopteridae because of the presence of the following features: the skull roof is formed by the frontal bone, which is laterally expanded whereas the dermopterotic is expanded posteriorly; the parietal bone is fused with the dermopterotic; the supraorbital sensory canal ends in the frontal; presence of a triangular extrascapular, which is separated from its counterpart medially by the posttemporals; and presence of a narrow and vertical preopercle with an anterior process contacting the maxilla. However, this hypothesis was questioned because *W. exquisitus* also shares some features with Peltopleuridae, such as the deepened-flank scales, which means *W. exquisitus* should be a peltopleurid fish.

A redescription of *Wushaichthys exquisitus* is conducted here based on five new specimens. Several new characters are described here, including the vertical preopercle sensory canal, which extends from ventral to dorsal margin of preopercle with a branch to the maxillary process; a small hyomandibular process on the antero-dorsal margin of opercle; and the presence of two lateral lines.

A phylogenetic analysis based on 101 characters and 23 taxa was conducted. The results of the phylogenetic analysis suggest that *W. exquisitus* is the most basal taxon of the extinct family Thoracopteridae, confirming previous studies. The new results also indicate that Thoracopteridae is the sister group of Peltopleuridae, and these two families form the order Peltopleuriformes. This conclusion also agrees with several previous studies.

Based on the detailed redescription, the diagnosis of the genus *Wushaichthys* is emended as well as the diagnoses of *Wushaichthy exquisitus* and of the family Thoracopteridae.

NOMENCLATURAL DISCLAIMER

The taxonomic information presented herein, including new taxa, are disclaimed as nomenclatural acts and are not available, in accordance with Article 8.3 of the International Code of Zoological Nomenclature.

ACKNOWLEDGEMENTS

There were plenty of people helping me with my thesis and the field of vertebrate paleontology before and now on. I would like to give my best appreciate to them. First, I thank my Master's Thesis Committee, Chris Beard, Gloria Arratia, Bruce Lieberman, Hans-Peter Schultze, and Leo Smith, for their support on the study of my thesis.

I give my sincere gratitude to my committee chair, Chris Beard. Although I'm not in his field of study, he is still happy to help me and guide me in every aspect.

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There are many other experts who provide me great support and help on my career. I thank Meeman Chang and Guanghui Xu from the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP). When I asked them about my interest about paleontology five years ago, they opened the gate of palaeoichthyology to me without any question. I thank to the Division of Vertebrate Paleontology. David Burnham, who gave me great support on methods and tools of fossil preparation. Desui Miao helped me a lot, not only in academic, but also in aspects of life. I acknowledge the assistance of Richard van der Laan (Utrech, The Netherlands) for his assistance and explanations concerning taxonomic nomenclature rules.

I thank to the institutions allowing me to use their specimens for my study: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP), Museum of Comparative Zoology, Harvard University (MCZ), University of Kansas (KU), Virginia Institute of Marine Science (VIMS), and Zhejiang Museum of Natural History (ZMNH).

Lastly, I extend special thanks to my family. My parents Jian Wang and Ning Shen always have supported me while I'm tracing my dream. My wife Jia Li, who suggested me to study the field of paleontology during the time of my life that I was confused about my future.

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INTRODUCTION

Thoracopteridae is an actinopterygian family that evolved a gliding adaptation, which is one of its diagnostic characters: “pectoral fins enormously developed” (Griffith, 1977: p. 37). Thoracopterids share a similar morphology with modern “flying fish” Exocoetidae with their remarkably enlarged pectoral fins. The first known member, *Thoracopterus niederristi*, from Raibl of the Upper Triassic of northern Italy (former Austria), was published in 1858 (Bronn, 1858). *Gigantopterus telleri* is the second member, which was named by Abel in 1906 (Abel, 1906). The family Thoracopteridae was erected by Griffith in 1977, based on two species, *Thoracopterus niederristi* and *Gigantopterus telleri* (Griffith, 1977). In the late 20th century, Tintori named two new species and included them in the genus *Thoracopterus*—*T. magnificus* and *T. martinisi* (Tintori and Sassi, 1987; Tintori and Sassi, 1992). All four species are from Austria and Italy and their age is Carnian and Norian, Late Triassic. In the new millennium, two new members were published from the Xingyi fauna. The first member, *Thoracopterus wushaensis* was published in 2012 (Tintori et al., 2012) (= *Potanichthys xingyiensi* [Xu et al., 2013]), and *Wushaichthys exquisitus* was discovered two years later (Xu et al., 2015). Although the new discoveries enrich the family diversity, their systematic position remains unclear. For some, Thoracopteridae belongs within the subholostean order Peltopleuriformes (Nelson et al., 2016), where it is interpreted as a neopterygian, as the sister taxon of Peltopleuridae (Xu and Ma, 2016; Xu and Zhao, 2016; Xu et al., 2015). *Wushaichthys* was interpreted as the most basal member of this group (Xu et al., 2015). This result was questioned because of the set of primitive characters of *Wushaichthys exquisitus* and the shared morphological similarities with *Peltopleurus* (Tintori, 2015; Xu and Zhao, 2015). It should be noted that *Wushaichthys* has the phenomenon of sexual dimorphism, which is represented by certain morphological difference of the anal fin (Xu et al., 2015). This is a character shared with other thoracopterifds and peltopleuriformes . In this study, my goal is to reexamine the phylogenetic systematics of *W. exquisitus*. A new morphological description is provided based on several new specimens and a phylogenetic analysis including a variety of taxa is performed to test the phylogenetic position of the fish.

CHAPTER 1. OVERVIEW OF THE XINGYI FAUNA IN GUIZHOU PROVINCE, CHINA

The Triassic is when both marine and terrestrial ecosystems recovered and established the "modern fauna" from the aftermath of the Permo-Triassic Mass Extinction during a time when only 10% of the species survived this devastating event (Vermeij, 1977). The point of view that ecosystems recovered around the Middle Triassic (Sahney and Benton, 2008) has been supported by new excavations in different parts of the world. One of the most persuasive new lines of evidence is from southwestern China, where the fossil Lagerstätten (Guanling, Panxian, Xingyi, Luoping, etc.) in Yunnan and Guizhou provinces provide an unmatched example of marine biotic recovery following the PTME (Benton et al., 2013). See Figure 1.

The Middle and Upper Triassic deposits in Yunnan and Guizhou provinces can be divided into four units based on the difference assemblage of vertebrate fossils (Sun et al., 2016) (Figure 2).

The bottom unit is the Guanling Formation dated as Anisian in the Middle Triassic, which includes two members. The lower member is identified by its yellow-green sandstones and dolomite. The upper member of the Guanling Formation contains light to dark gray limestones with dolomites. Two vertebrate fossil Lagerstätten — Luoping fauna and Panxian fauna are bedded within the upper member of Guanling Formation.

The Yangliujing Formation, which sits on the top of the Guanling Formation, is poorly fossiliferous. It comprises massive grey dolomites with gypsum and breccia. The age of Yangliujing Formation is between late Anisian to middle Ladinian of Middle Triassic (Chen and Wang, 2009).

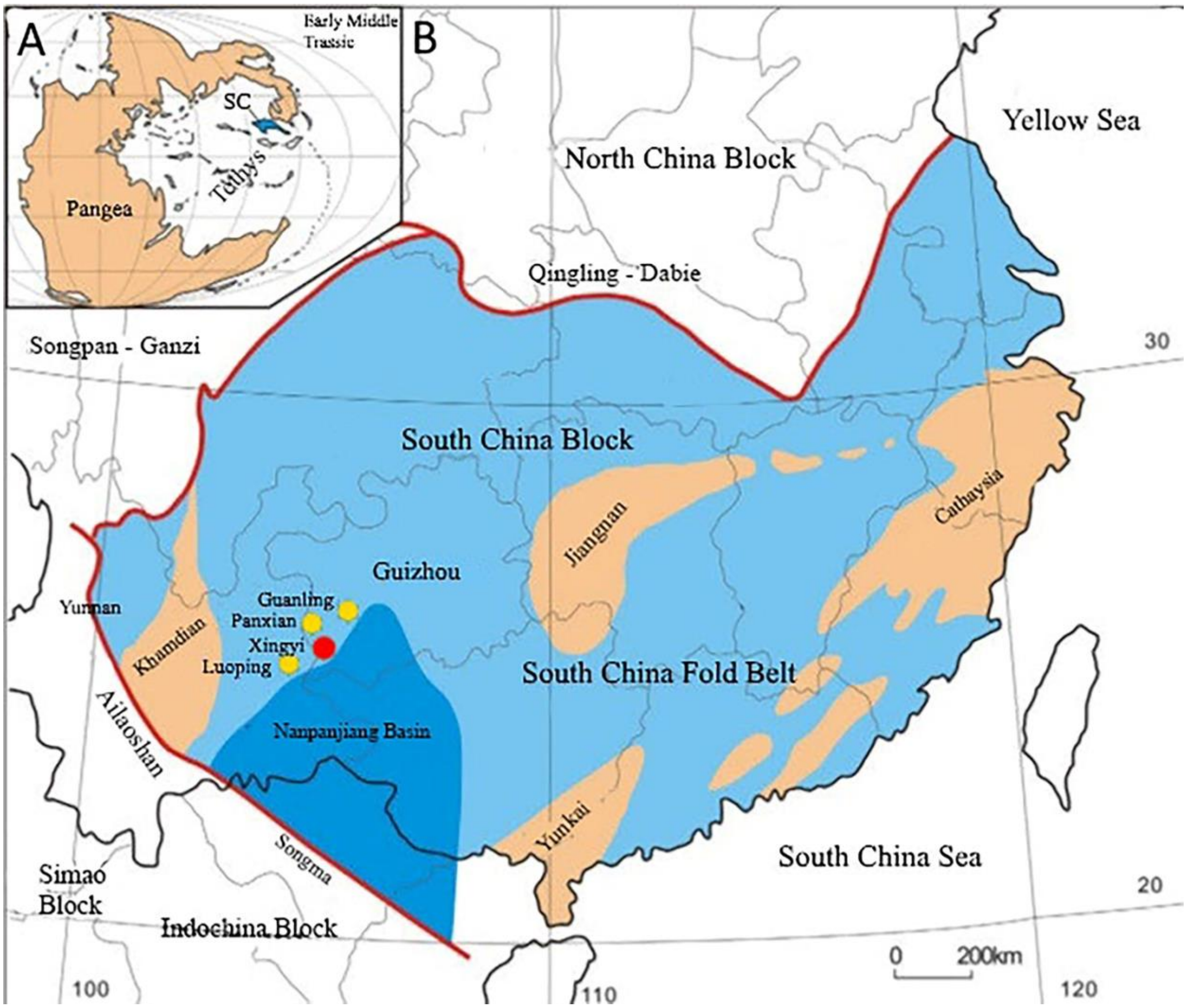

Figure 1. A. The geological reconstruction of South China during the Triassic. **B**. Fossil Lagerstätten in Guizhou and Yunnan Provinces (Benton et al., 2013). A red dot shows the location of Xingyi fauna, where the fossil material of *Wushaichthys* was found. Yellow dots show the location of other fossil Lagerstätten − Luoping fauna, Panxian fauna and Guanling fauna in Guizhou and Yunnan province.

The Zhuganpo Formation, middle to late Ladinian, was previously defined as the Zhuganpo Member of the Falang Formation (Wang et al., 2008) and has three subdivisions. The lower member is identified by its grey dolomitic limestones. The middle member includes grey chert and limestones with the bioclastic materials. The upper member consists of grey limestones with nodulation. The position of Xingyi fauna vary from the lower member (Wang et al., 2009) to the upper member (Benton et al., 2013) of the Zhuganpo Formation. However, a recent study suggests that the Xingyi fauna bearing is associated with the middle member of the Zhuganpo Formation (Sun et al., 2016).

The Xiaowa Formation (Shu, 2002), also named as Wayao Member of Falang Formation (Bureau, 1987) and Wayao Formation (Shouren et al., 1995), is famous for its black-silty shales, siltstones and micrites, along with mudstones and marlstones (Sun et al., 2016). The age of Xiaowa Formation is Carnian, Late Triassic. The marine reptile and crinoid rich fossil Lagerstätte Guanling fauna is bedded within the lower layers of the Xiaowa Formation.

The Xingyi fauna was first found and studied in 1958 (Young, 1958) through the excavation of the famous marine reptile *Keichousaurus hui*. It was followed by Su's study (Su, 1959), who excavated and named three species of actinopterygians—*Peltopleurus orientalis*, *Sinoeugnathus kueichowensis* and *Asialepidotus shingyiensis*. After a few decades of silence, a new wave of great discoveries started by the end of 20th century. So far, among the discovery of Xingyi fauna, a variety of marine reptiles, fishes and invertebrates (Lu et al., 2018) were excavated and studied. Fish species belonging to the following families have been discovered: Palaeoniscidae: *Guizhouniscus microlepidus* (Liu et al., 2003); Peltopleuridae: *Peltopleurus orientalis* (Su, 1959), *Peltopleurus tyrannos* (Xu et al., 2018b); Thoracopteridae: *Thoracopterus wushaensis* (Tintori et al., 2012) (= *Potanichthys xingyiensis* (Xu et al., 2013)), *Wushaichthys exquisitus*; Luganoidae:

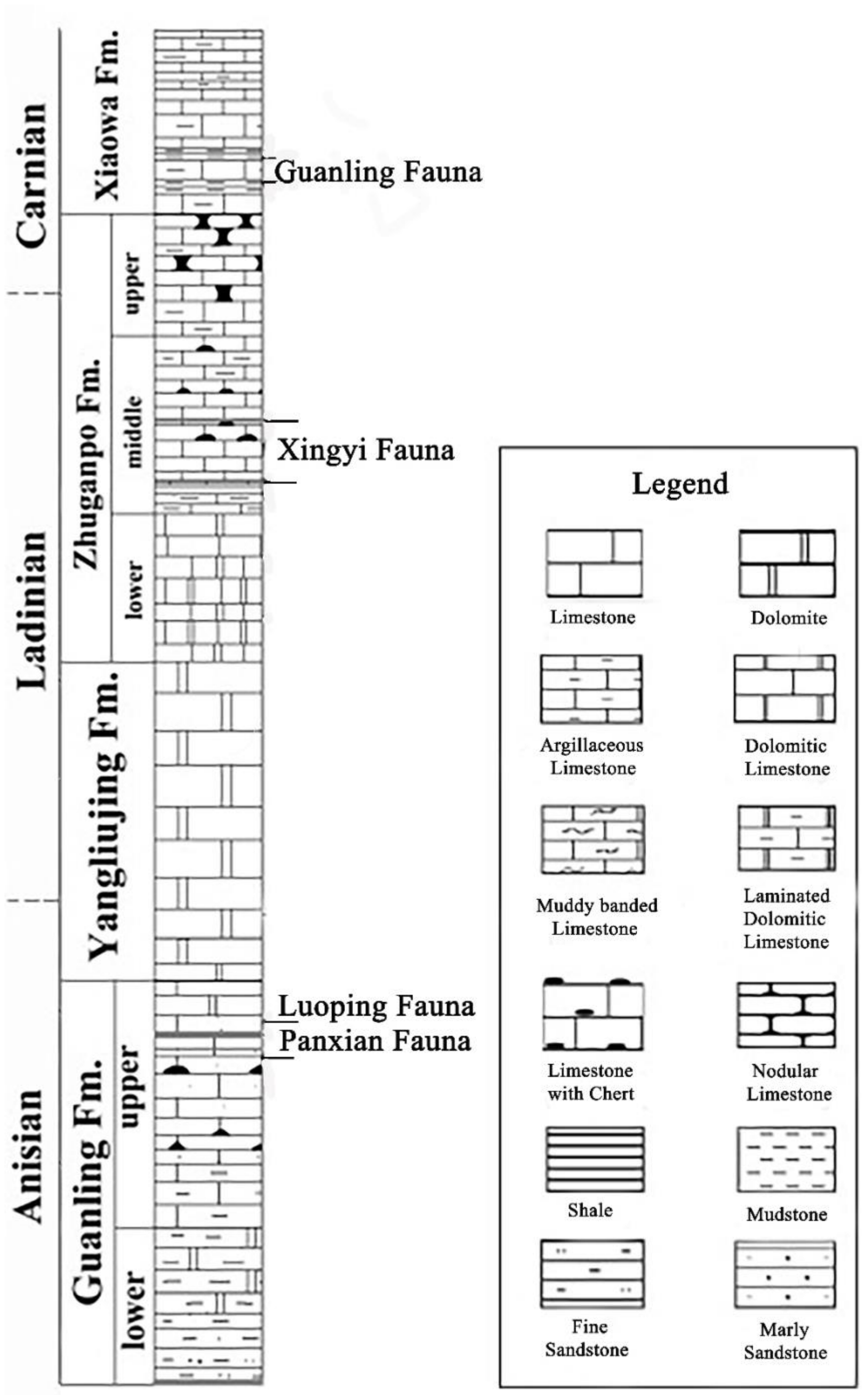

Figure 2. Stratigraphy of Middle and Upper Triassic in Guizhou and Yunnan province of China. Modified from Sun et al. (2016)

Guizhoubrachysomus minor (Liu, 2004); Eugnathidae: *Sinoeugnathus kueichowensis* (Su, 1959), *Xingyia gracilis* (Liu et al., 2003); Ionoscopiformes: *Asialepidotus shingyiensis* (Su, 1959; Xu and Ma, 2018); Amiidae: *Guizhouamia bellula* (Liu et al., 2002); and Ginglymodi: *Fuyuanichthys wangi* (Xu et al., 2018a) (Figure 3).

In addition to the fishes, marine reptiles such as *Glyphoderma kangi* (Zhao et al., 2008), *Qianxisaurus chajiangensis* (Cheng et al., 2012), *Anshunsaurus wushaensis* (Rieppel et al., 2006), *Macrocnemus fuyuanensis* (Li et al., 2007) have been recovered.

Several recent analyses using isotope dating and ammonoid biostatigraphic correlation (Zou et al., 2015; Sun et al., 2016) suggested that the age of Xingyi fauna is late Ladinian, Middle Triassic. A recent geochronological study using LA ICP MSU Pb analysis provided a more accurate age of Xingyi fauna, which is 240.8±1.8 Ma (Li et al., 2016).

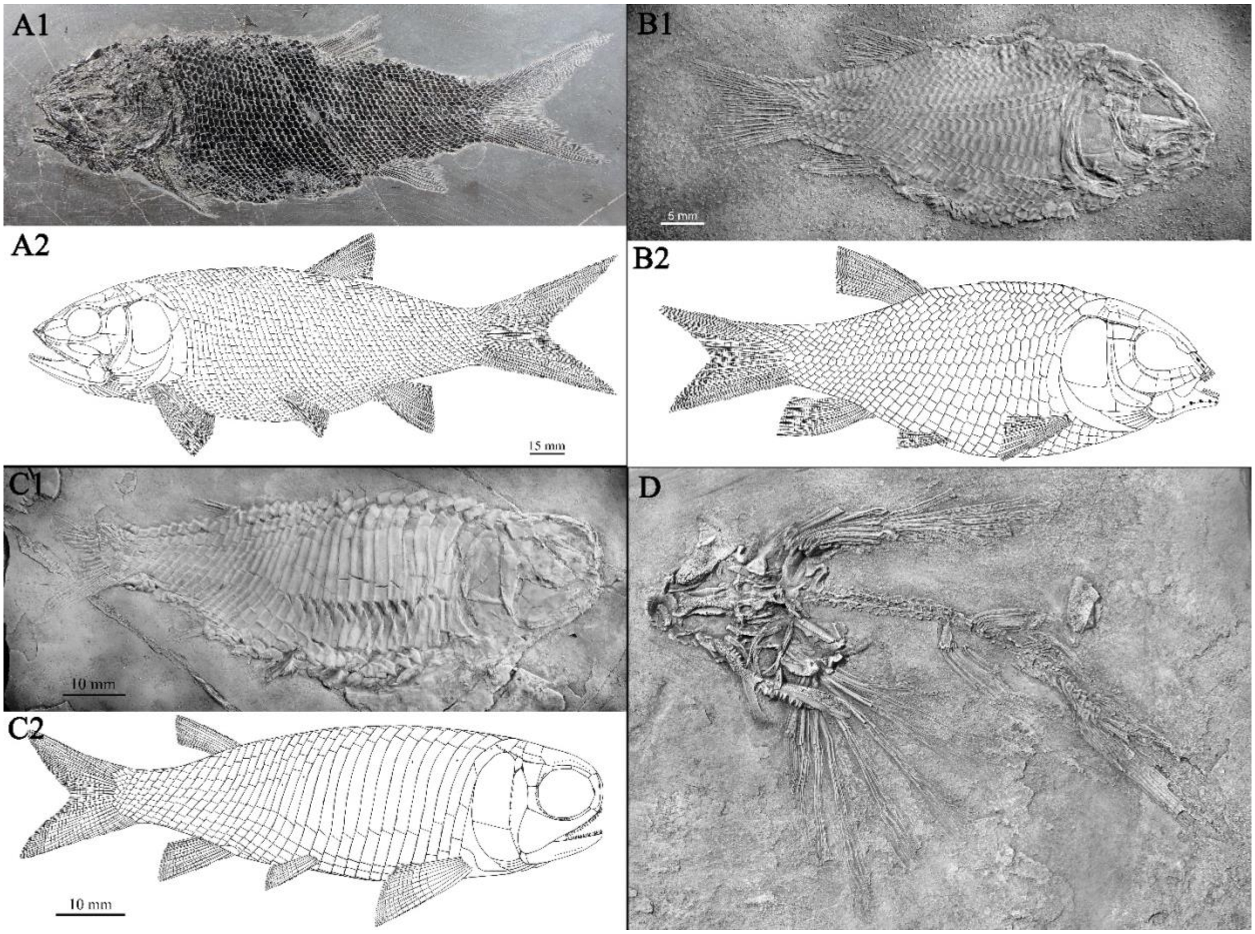

Figure 3. Fishes from the Xingyi fauna. **A1**. Photo of *Asialepidotus shingyiensis*; **A2**. Reconstruction of *Asialepidotus shingyiensis*; **B1**. Photo of *Fuyuanichthys wangi*; **B2**. Reconstruction of *Fuyuanichthys wangi*; **C1**. Photo of *Peltopleurus tyrannos*; **C2**. Reconstruction of *Peltopleurus tyrannos*; **D**. Photo of *Thoracopterus wushaensis* (= *Potanichthys xingyiensis*). All photographs and drawings were conducted and provided by Guanghui Xu.

CHAPTER 2. DESCRIPTION OF *WUSHAICHTHYS EXQUISITUS* FROM MIDDLE TRIASSIC ZHUGANPO MEMBER IN XINGYI, GUIZHOU PROVINCE OF CHINA, BASED ON NEW SPECIMENS

Material and Methods

Institutional Abbreviations— **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. **KU**, University of Kansas, Lawrence, Kansas, U.S.A. **VIMS**, Virginia Institute of Marine Science, Gloucester Point, Virginia, U.S.A. **ZMNH**, Zhejiang Museum of Natural History, Hangzhou, Zhejiang province, China.

Materials Studied— The studied material of *Wushaichthys* is housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing, China under the following numbers: IVPP V19962, V19963, V19964, V19965, V19966. Along with previously studied specimens including the holotype IVPP V19959 and other referred specimens: V19960, V19961, ZMNH M1693, M1696, M1699. Among these specimens, IVPP V19960, V19963, V19964 and V19966 are female examples; IVPP V19959, V19962, V19965 and M1696 are male individuals.

The studied material of *Acipenser* includes KU 27324 (one dry skeleton) and VIMS 12086, 12091 and 22076 (cleared and double stained specimens for both cartilage and bone).

The studied material of *Polypterus* includes MCZ 48572 and MCZ 85766 (dried skeletons).

Preparation— Specimens were mechanically prepared under a stereomicroscope using fine steel needles due to their delicate preservation. Drawings were made under ZEISS 47 50 52 microscope with camera lucida attachment, and final figures were prepared with Adobe Photoshop CC 2018. Photographs were taken with a Sony A-73 camera under natural light/lantern.

Terminology— The traditional terminology concerning the skull roof names has been followed here to facilitate comparisons with the studies of Xu et al. (Xu et al., 2015).

Phylogenetic Method— The phylogenetic analysis was conducted using PAUP* 4 (version 3.99.165.0). The character matrix was constructed using Mesquite and run in PAUP*. All characters are unordered and unweighted. The analysis used the list of characters of Xu et al. (2015) with modifications (see phylogenetic analysis and results) in the presentation of some characters and with the addition of new characters. The outgroup taxa used to polarize characters are *Acipenser*, *Australosomus* and *Polypterus*. The coding of characters was based on direct observation of the specimens and the following literature:

Acipenser brevirostrum: (Hilton et al., 2011).

Amia calva: (Grande and Bemis, 1998)

Australosomus kochi: (Nielsen, 1949; Gardiner and Schaeffer, 1989)

Boreosomus gillioti: (Nielsen, 1942; Lehman, 1952)

Dapedium pholidotum: (Thies and Waschkewitz, 2016)

Dorsetichthys bechei: (Patterson, 1975; Arratia, 2013)

Gigantopterus telleri: (Griffith, 1977)

Lepisosteus osseus: (Grande, 2010)

Leptolepis coryphaenoides: (Nybelin, 1974; Arratia, 2013)

Luganoia lepidosteoides: (Bürgin, 1992)

Peltopleurus nuptialis: (Lombardo, 1999)

Peltopleurus rugosus: (Bürgin, 1992)

Peripeltopleurus vexillipinnis: (Bürgin, 1992)

Perleidus: (Lehman, 1952; Patterson, 1975; Gardiner and Schaeffer, 1989)

Polypterus bichir: (Allis Jr, 1922; Patterson, 1982; Gardiner and Schaeffer, 1989).

Thoracopterus wushaensis (= *Potanichthys xingyiensis*) (Tintori et al., 2012; Xu et al., 2013)

Redifieldius: (Schaeffer, 1967, 1984) (Gibson, 2018)

Semionotus elegans: (Olsen and McCune, 1991)

Thoracopterus niederristi: (Griffith, 1977) (Lehman, 1978)

Thoracopterus magnificus: (Tintori and Sassi, 1992)

Thoracopterus martinisi: (Tintori and Sassi, 1992)

Watsonulus eugnathoides: (Lehman, 1952; Olsen, 1984; Grande and Bemis, 1998)

Wushaichthys exquisitus: (Xu et al., 2015) IVPP 19959, 19962-19966.

Systematic Paleontology

Subclass NEOPTERYGII Regan, 1923

Order PELTOPLEURIFORMES Gardiner, 1967

Family THORACOPTERIDAE Griffith, 1977

Diagnosis (emended from Tintori et al. 2012) — Small to medium-sized fishes. Frontal bones are paired and broad. Dermopterotics are large and broad; sometimes are fused together. No distinct parietals. No postrostral. Nasal bones are separated by a large rostral. One or a few supraorbitals. One suborbital. Suspensorium vertically oriented. Preopercle narrow and deep; it sutures with the rear edge of the maxilla with the infraorbital process. Opercular region is formed by opercle, subopercle and several branchiostegal rays. Median and lateral gulars present. Elongate maxilla extending beyond the posterior margin of the orbit. Coronoid process presents in lower jaw. Spiracular bones present. Sensory canal system reduced. Highly enlarged pectoral fins. Pelvic fin well developed. Rays of anal fin and dorsal fin reduced in length. Homocercal tail, deeply forked, with its hypaxial lobe larger than the epaxial lobe.

Content— To date this family includes seven species, *Wushaichthys exquisitus*, *Peripeltopleurus vexillipinnis*, *Gigantopterus telleri*, *Thoracopterus wushaensis* (= *Potanichthys xingyiensis*), *Thoracopterus niederristi*, *Thoracopterus magnificus* and *Thoracopterus martinisi*.

Geographical distribution— Members of Thoracopteridae are known from Austria, Italy and southwestern of China.

WUSHAICHTHYS Xu, Zhao and Shen, 2015

Diagnosis (emended from Xu et al. 2015)— Rostral bone deep and narrow, contacting frontal bones posteriorly. Nasal and antorbital form the antero-dorsal border of the orbit. Five pairs of branchiostegal rays. Short paired fins compared to other thoracopterids. Dorsal fin includes 10 principal fin rays. Squamation formula: D25–26/P14,A20–21, C28–29/T32–34.

WUSHAICHTHYS EXQUISITUS Xu, Zhao and Shen, 2015

Diagnosis— See below. Section of Discussion, p. 47.

Locality and Age— Fossil excavated from Wusha, Xingyi of Guizhou province, China. The age is Ladinian, Middle Triassic, about 240 Ma (Figure 4).

Figure 4. **A**. modern map of China with Guizhou province marked on red. **B**. position of Wusha and Xingyi in Guizhou province. **C**. photograph of Zhuganpo member, Falang formation in Wusha, where *Wushaichthys* was excavated. (Photograph was taken and provided by Guanghui Xu.)

Description

General Morphology and Size— *Wushaichthys exquisitus* is a small fish with a maximum length of about 57 mm. The standard length of the holotype (IVPP 19959) is 44 mm (Xu et al., 2015). Average standard length of new specimens is 45.39 mm. Measured data of new specimens are gathered in Table 1. The fish has a fusiform body, with a relatively large head, a blunt snout, and a large eye, about 36% of head length. The fish presents moderately short pectoral fins, about 20% of standard length, a forked and homocercal caudal fin, and a body covered with ganoid-type scales (Figure 5).

Snout—The rostral bone in *Wushaichthys* is narrow and deep, contacting the frontal bone with its posterior margin, and the two nasal bones laterally. No postrostral bones are present. The anterior nostril is formed by a notch at the antero-medial margin of the nasal and another at the antero-lateral margin of the rostral. The posterior nostril has not been observed. The nasal bone is slightly shallower than the rostral, and unlike other thoracopterids, it does not contact its antimere medially. Its latero-posterior edge forms the anterior section of the orbital rim. The nasal connects with the antorbital ventrally and with the frontal dorsally. The trajectory of the supraorbital canal has been observed in the nasal bone of the holotype (Xu et al., 2015: fig. 1), but it is not visible in the new specimens. The antorbital is a trapezoidal bone with a "T"-shaped sensory branch of the infraorbital canal, meaning that the antorbital branch of the infraorbital canal extends in the bone. The posterior margin of the antorbital also forms the anterior section of the orbital rim. All three bones, the rostral, nasals and antorbitals are strongly ornamented by short ganoine ridges and circular tubercles.

Measurements (mm)/Specimens number	IVPP19962	IVPP19963	IVPP19964	IVPP19965	IVPP19966	Mean
Standard length	42.43	46.77	42.59	46.86	48.28	45.39
Head length	14.73	13.33	15.47	13.28	14.58	14.28
Preorbital length	2.44	N/A	2.28	1.93	N/A	2.22
Predorsal length	25.62	33.51	30.72	33.04	31.38	30.85
Prepelpivc length	28.16	30.2	28.93	30.59	26.13	28.80
Preanal length	31.27	36.81	35.59	37.74	35.22	35.33
Pectoral fin length	8.73	7.65	9.34	6.83	N/A	8.138
Pelvic fin length	4.78	3.69	4.76	4.13	4.04	4.28
Anal fin base length	1.91	1.85	1.78	2.2	1.82	1.91
Head depth	11.56	N/A	12.63	11.47	16.44	13.03
Maximum body depth	14.37	15.25	18.42	16.17	N/A	16.05
Peduncle depth	5.06	4.67	5.55	6.64	5.31	5.45
Dorsal fin depth	4.22	3.8	5.13	5.1	4.54	4.56
Anal fin depth	2.76	2.35	2.22	2.17	2.63	2.43
Orbital diameter	4.25	N/A	6.23	5.24	5.57	5.32
Maximum scale depth	6.43	8.31	8.01	7.51	7.85	7.62
Minimum scale depth	1.1	1.04	1.12	1.04	1.1	1.08
Head length/Standard length	34.71%	28.50%	36.32%	23.34%	30.20%	30.61%
Predorsal length/Standard length	60.38%	71.65%	72.13%	70.51%	65%	67.93%
Prepelpivc length/Standard length	66.37%	64.57%	67.93%	65.28%	54.12%	63.65%
Preanal length/Standard length	73.70%	78.70%	83.56%	80.54%	72.95%	77.89%
Orbital diameter/Head length	28.85%		40.27%	39.46%	38.20%	36.70%

Preorbital length/Head length	16.56%		14.74%	14.53%		15.28%
Pectoral fin length/Standard length	20.58%	16.36%	21.93%	14.58%		18.36%
Pectoral fin length/Predorsal length	34.07%	22.83%	30.40%	20.67%		26.99%
Pectoral fin length/Prepelvic length	31%	25.33%	32.28%	22.33%		28%
Pectoral fin length/Preanal length	28%	21%	26%	18%		23.25%
Pelvic fin length/Preanal length	15%	10%	13%	11%	11%	12.00%
Pelvic fin length/Standard length	11.26%	7.89%	11.18%	8.81%	8.37%	9.50%

Table 1. Body measurements and ratios of new specimens of *Wushaichthys exquisitus.*

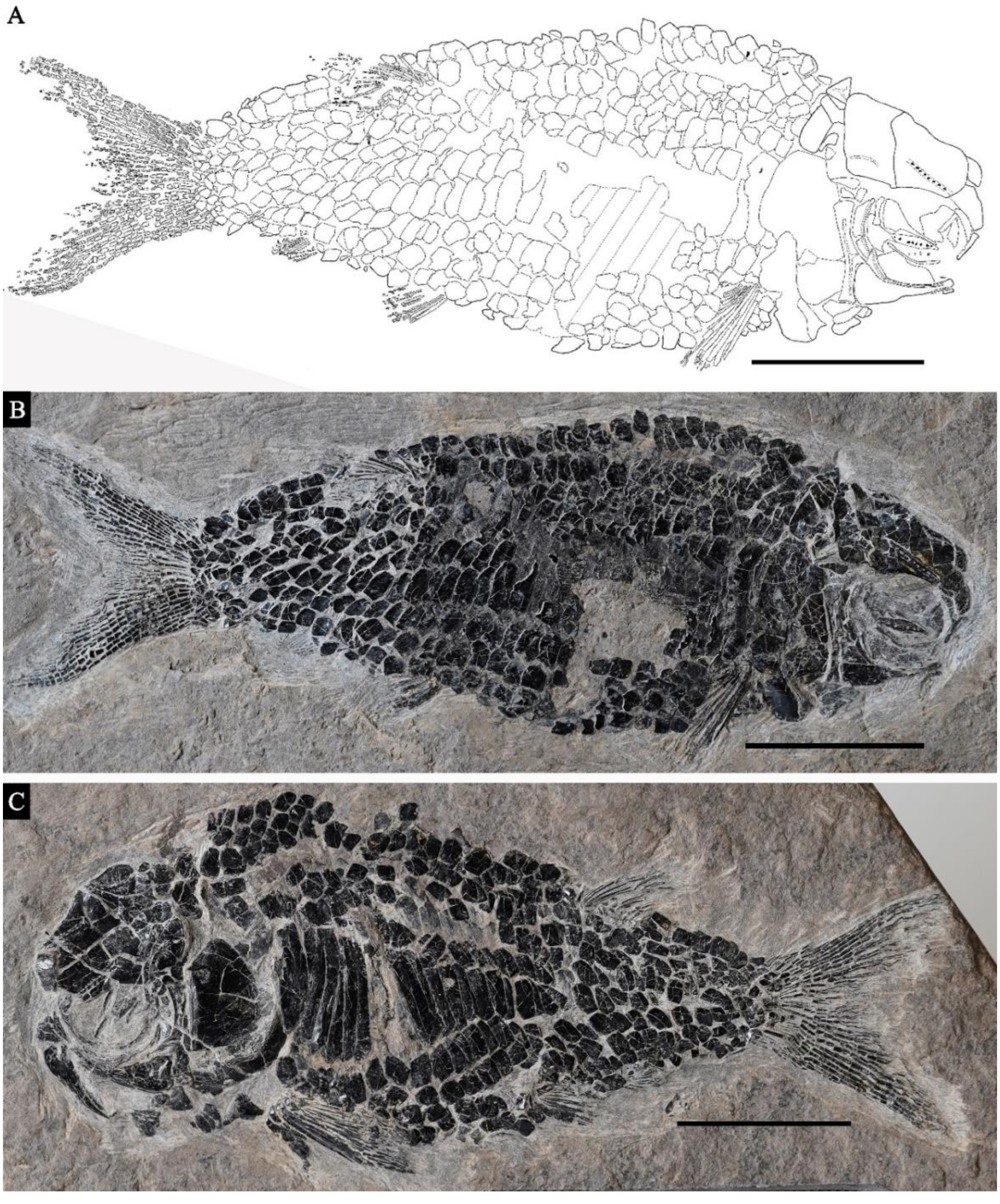

Figure 5. *Wushaichthys exquisitus* in lateral view. **A**. Drawing of IVPP V19965 based on specimens under normal light. **B**. Photograph of IVPP V19965 under normal light. **C**. Photo of IVPP V19964 under normal light. Scale bar, 10mm.

Skull Roof—The skull roof (Figures 6, 7) is expanded and relatively large for the size of the fish. The frontal bone is trapezoidal, with the posterior edge about two times broader than its anterior edge. The supraorbital sensory canal is short, placed in the anterior half of the frontal bone, so that a parietal branch is absent. No independent parietal bones are preserved in the specimens. Instead, a large bone occupies the position of the dermopterotic and parietal in other fishes, so that it is assumed here that both bones are fused forming a parieto-dermopterotic. This bone sutures with the frontal directly. The transverse and bent otic canal appears at the latero-ventral region of the parieto-dermopterotic. There is one extrascapular bone on each side of the skull (Figure 8). The triangle-shaped extrascapular is located posterior to the parieto-dermopterotic and anterior to the posttemporal. The lateral post-otic canal and the supratemporal sensory canal joins in the extrascapular. The supratemporal canal has not been observed in the extrascapular because of incomplete preservation.

Circumorbital Bones—The large orbit (Figures 6, 7) is surrounded by a nasal, an antorbital, a lachrymal, a jugal, a dermosphenotic, and supraorbitals. The lachrymal and jugal form the ventral margin of the orbital rim. The lachrymal is elongated, narrow and bent and is mainly a canal bearing bone. The infraorbital sensory canal goes through the entire bone and enters the jugal at the posterior margin of the lachrymal. The jugal is half of the length of the lachrymal. Its middle region is expanded to twice the width of both the anterior and posterior edges. The dorso-posterior margin of the orbital rim is formed by the dermosphenotic, which is similar to the jugal in shape, but it is relatively larger and deeper. The infraorbital sensory canal extends from the jugal through the entire dermosphenotic. There is no connection between the supra- and infraorbital canals. The holotype does not preserve any supraorbitals, but the paratype V19962 preserved two fragmented supraorbitals. The number of trapezoidal suborbitals located between the posterior margin of the dermosphenotic and the anterior margin of the preopercle varies among specimens from zero to five due to preservation conditions.

Upper Jaw—This jaw (Figures 6, 7) is formed by the premaxilla and the maxilla; a supramaxilla has not been observed. The premaxilla is relatively small, with generally less than 10 teeth attached to its oral margin. The maxilla is triangular-shaped and large, with a slender anterior portion and significantly expanded posterior part. This bone sutures with the lachrymal and jugal dorsally and with the preopercle at its dorso-posterior margin. Small conical teeth are only present on the first third of the ventral margin of the maxilla.

Lower Jaw—The lower jaw (Figures 6, 7) of *Wushaichthys* is only known from its lateral view and includes two bones, the dentary and angular. The dentary is elongated and slightly expanded at its posterior edge, whereas the angular is significantly smaller than the dentary. The mandibular canal is slightly bent. It starts at one third from the anterior margin of the dentary and ends at the posterior margin of this bone.

Opercular Bones, Branchiostegal Rays, and Gular Plates—The preopercle (Figures 6, 7) is a flat, column-like bone with an almost vertical position placed in front of the opercle and subopercle. There is a conspicuous maxillary process at the anterior margin of the middle region of the preopercle. The process articulates with the dorso-posterior margin of the maxilla. The preopercular sensory canal is straight, extending from the ventral to dorsal margin of preopercle. A short preopercular branch starts at the middle of the preopercular canal and runs toward the anterior maxillary process.

The opercle (Figures 6, 7) is large and trapezoidal. Its depth is twice its width. A small hyomandibular process is positioned at the antero-dorsal margin of the opercle. Ventrally, the

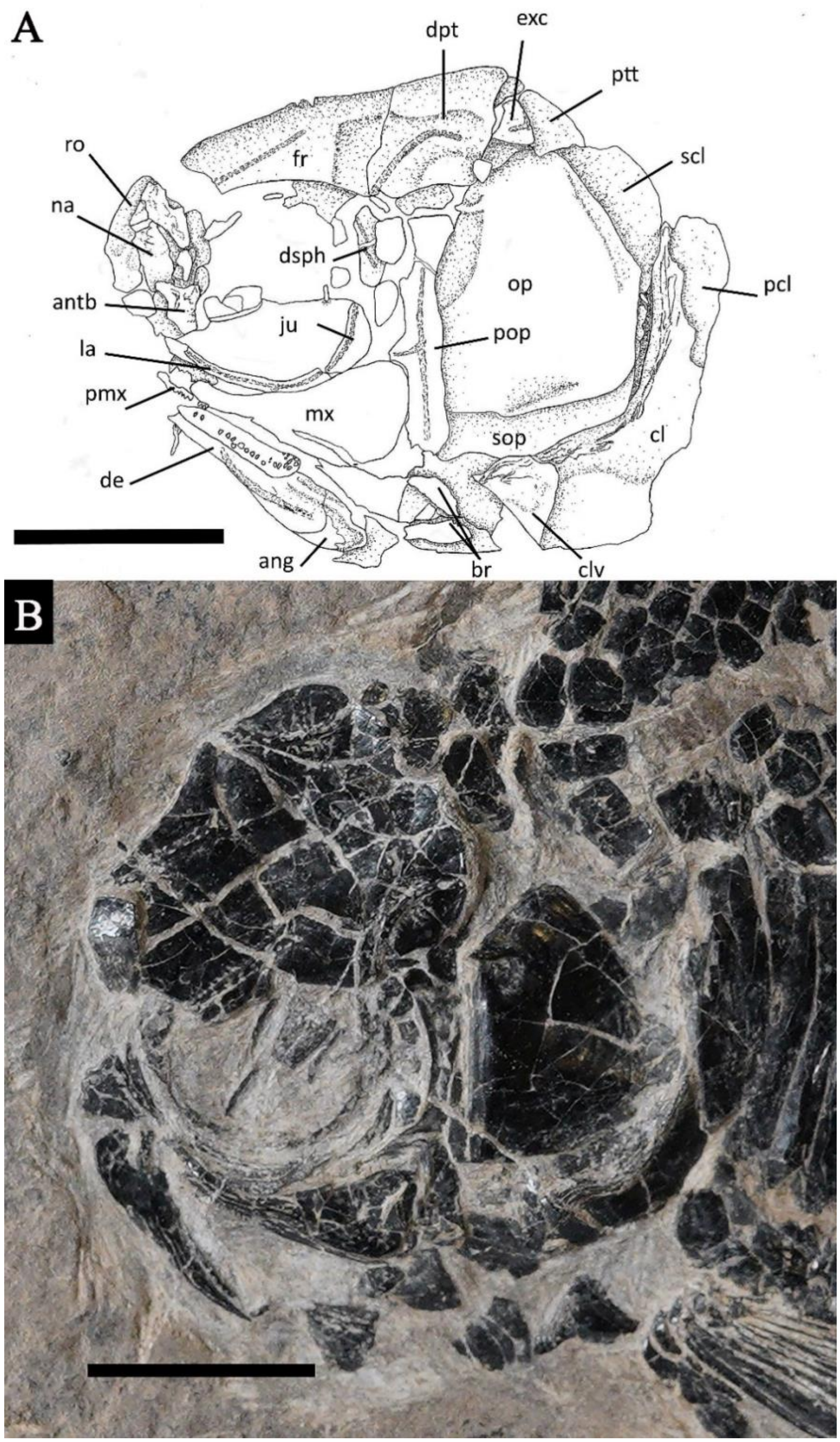
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Figure 6. Skull of *Wushaichthys exquisitus* in lateral view. **A**. Drawing of IVPP V19962 under normal light. **B**. Photo of IVPP V19964 under normal light. Scale bar = 5mm. Anatomical abbreviations— **ang**, angular; **antb**, antorbital; **br**, branchiostegal rays; **cl**, cleithrum; **clv**, clavicle; **de**, dentary; **dpt**, parieto-dermopterotic; **dsph**, dermosphenotic; **exc**, extrascapular; **fr**, frontal bone; **ju**, jugal; **la**, lachrymal; **mx**, maxilla; **na**, nasal bone; **op**, opercle; **pcl**, postcleithrum; **pmx**, premaxilla; **pop**, preopercle; **ptt**, posttemporal; **ro**, rostral bone; **scl**, supracleithrum; **sob**, suborbital; **sop**, subopercle.

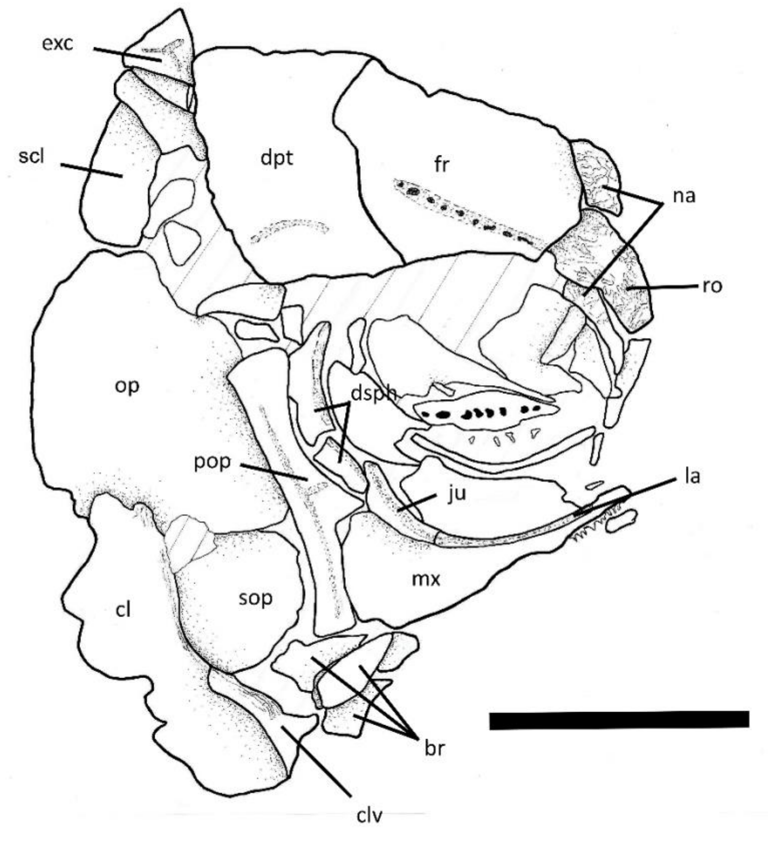

Figure 7. Skull of *Wushaichthys exquisitus* in lateral view, drawing of IVPP V19965 under normal light. Scale bar = 5 mm. Anatomical abbreviations—**br**, branchiostegal rays; **cl**, cleithrum; **clv**, clavicle; **de**, dentary; **dpt**, parieto-dermopterotic; **dsph**, dermosphenotic; **exc**, extrascapular; **fr**, frontal bone; ju, jugal; **la**, lachrymal; **mx**, maxilla; **na**, nasal bone; **op**, opercle; **pop**, preopercle; **ro**, rostral bone; **scl**, supracleithrum; **sop**, subopercle.

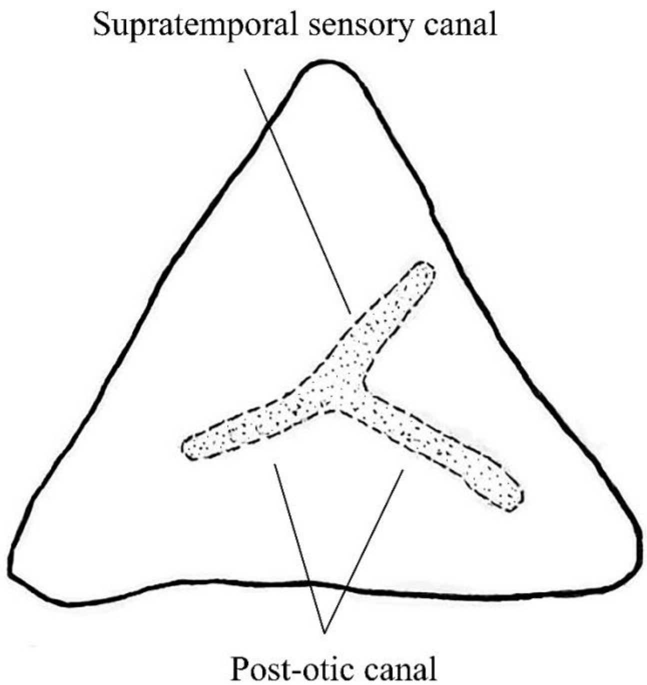

Figure 8. *Wushaichthys exquisitus*. Drawing of the extrascapular in the specimen IVPP V19965.

Note the lateral post-otic canal and the vertical supratemporal sensory canal.

opercle and subopercle are joined by an almost straight suture. The width of the subopercle is about the same as that of the opercle, but the depth is nearly six times narrower. No remnants of the hyoid arch are preserved. There are five branchiostegal rays on the holotype. However, the number of branchiostegal rays in the new specimens varies from two to four due to preservation conditions. There is a pair of rectangular lateral gulars preserved in the holotype, which can be observed in paratype V19962. The holotype also has one triangular median gular plate, but no such feature can be seen in the new specimens due to preservation (Xu et al., 2015: fig. 1f).

Pectoral Girdle and Fins—The pectoral girdle (Figures 6, 7) includes the posttemporal, the supracleithrum, the cleithrum, the clavicle and the postcleithrum on each side. The posttemporal, the bony link between the cranium and the pectoral girdle, is triangular-shaped and 1.5 times larger than the extrascapular. It connects the extrascapular antero-dorsally and supracleithrum ventrally. The supracleithrum is elongated and partially covered by the opercle. The lateral line canal has not been observed on both posttemporal and supracleithrum. The cleithrum is elongated and expanded ventrally. There is a relatively large notch located ventro-posteriorly on the cleithrum. A series of ridge-like structures forming a serrated appendage is positioned along the anterior surface of the cleithrum, close to its margin. The clavicle is nearly equilateral triangular-shaped, and it sutures with the cleithrum posteriorly. The postcleithrum is narrow, deep and scale like; it is placed postero-ventral to the supracleithrum and posterior to the cleithrum anteriorly.

The pectoral fins (Figure 9) are located near the ventral margin of the body. There are approximate nine branched fin rays on each side of the pectoral fin. Each fin ray consists of a long and broad base and short, branched distal segments. The approximate pectoral fin length is 18% of the standard length.

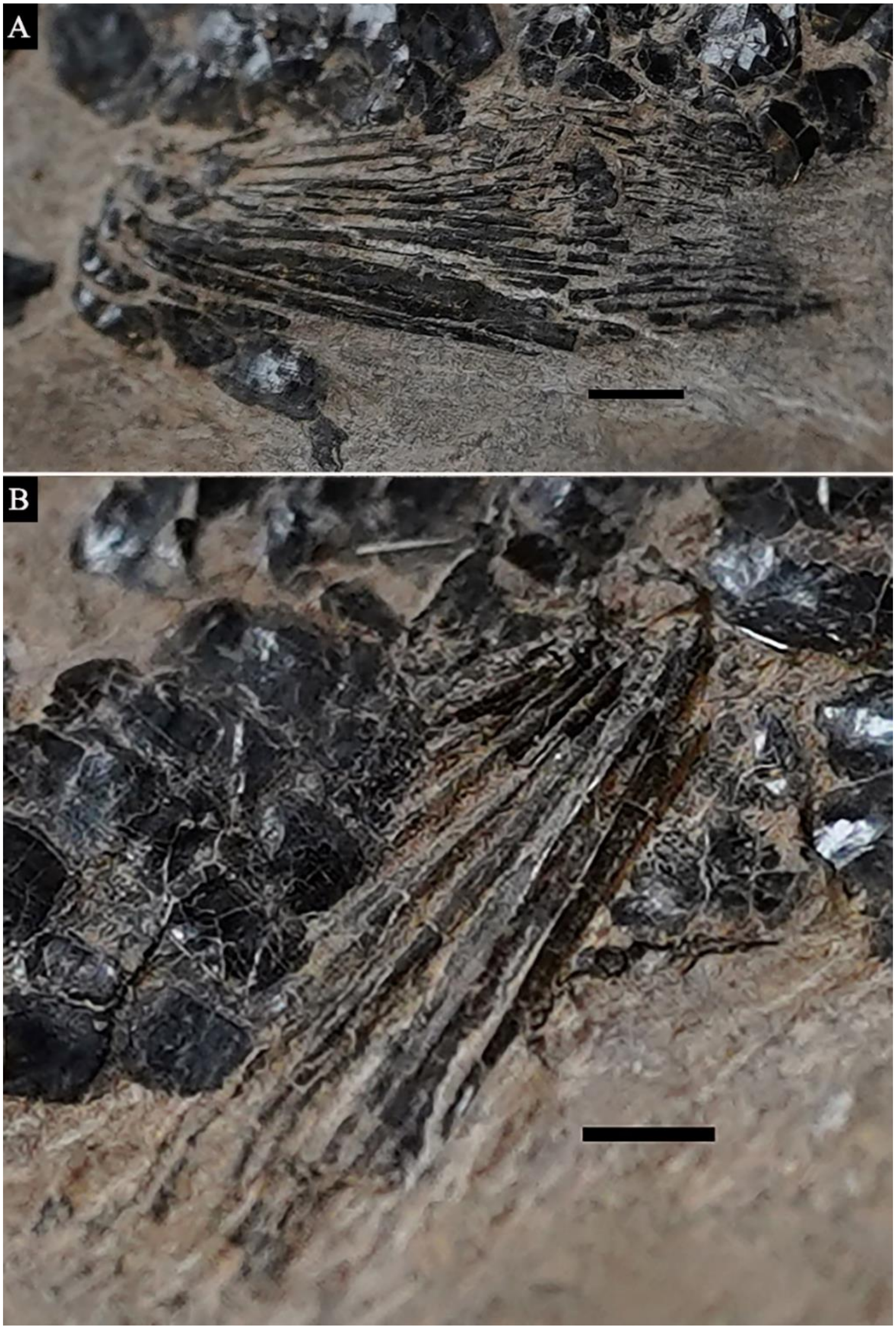

Figure 9. *Wushaichthys exquisitus*. Photos of the pectoral fins under normal light. **A**. specimen IVPP V19964. **B**. specimen IVPP V19965. Scale bar, 1mm.

Pelvic Girdle and Fins— The pelvic girdles of *Wushaichthys* cannot been observed because of the coverage of scales. The pelvic fins are short and originated at the 12th to 15th vertical scale row among specimens. Each side of pelvic fin has six to eight branched and segmented fin rays.

Median Fins—The dorsal fin is almost as short as the pelvic fins. The origin of the dorsal fin is located at the 18th to 20th vertical scale rows. It includes two or three basal fulcra anteriorly, followed by eight to 10 segmented and branched principal fin rays. The first principal fin rays are apparently much longer than the posterior principal rays, giving the fin a triangular profile. The length ratio between the first and the last ray cannot be measured due to preservation.

The anal fin (Figure 10) in *Wushaichthys* originates at about the 20th to 22nd vertical scale rows. The morphology of the anal fin has two patterns. The first pattern, which is interpreted as female examples, includes eight to ten segmented and branched principle fin rays. The other anal fin pattern, which is interpreted as a male character, has four segmented and branched principal fin rays anteriorly, and approximately 14 unsegmented and slender fin rays with backwards facing hooklets at their tip. A large triangular scute covers the base of principal fin rays of the male specimens.

The caudal fin (Figure 11) is deeply forked with two sets of rays of similar size and the extension of the body scales not projecting into the dorsal lobe of the fin. Its endoskeleton has not been observed because of the coverage of scales, so that it is not possible to establish the trajectory of the notochord in the dorsal lobe of the fin. The epaxial lobe of the caudal fin includes two basal fulcra and four to five procurrent rays. The first principal fin ray, which is segmented but not branched, is covered by fringing fulcra on its dorsal margin. The hypaxial lobe of the caudal fin

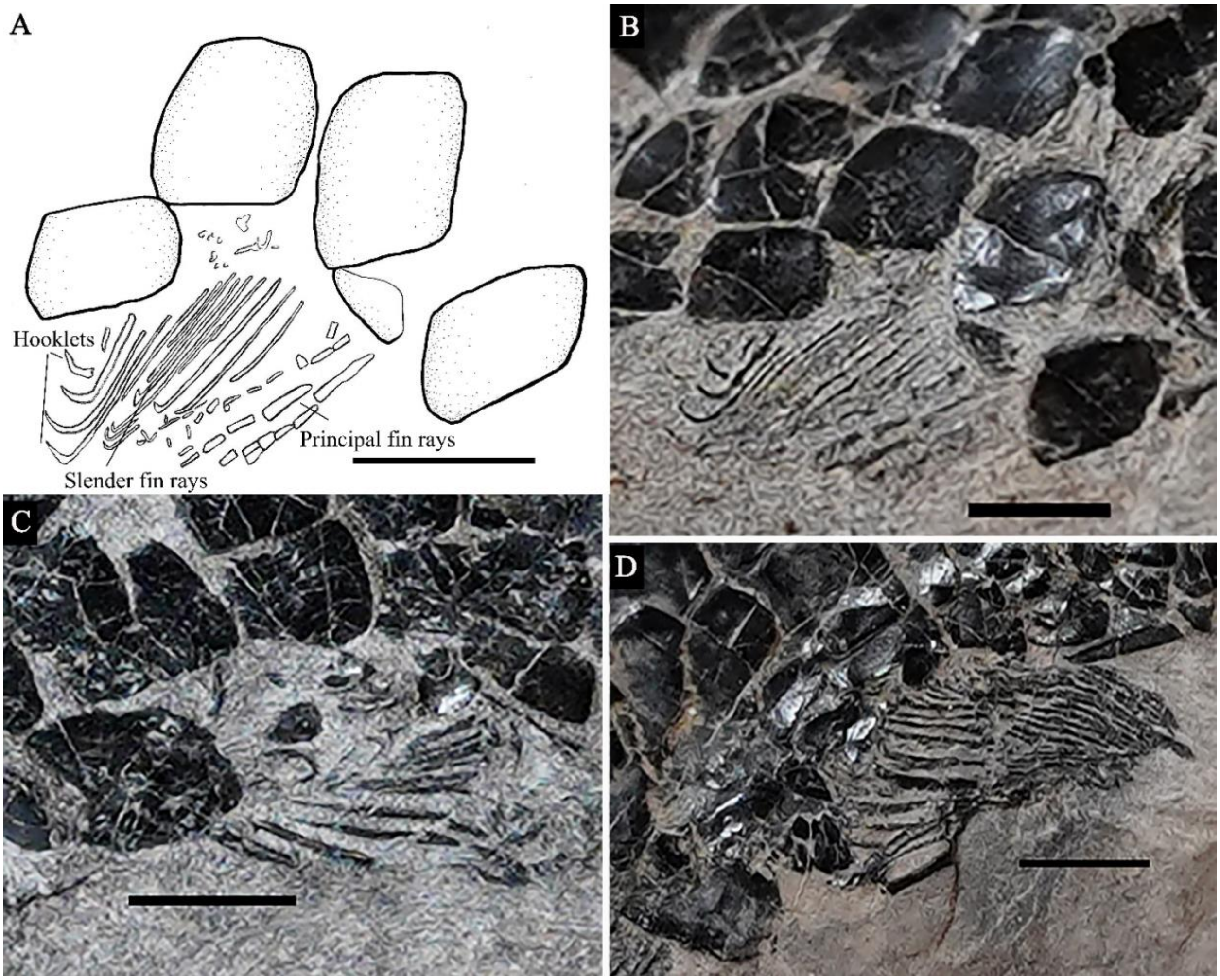

Figure 10. *Wushaichthys exquisitus*. The details of anal fins, both drawing and photos were taken under normal light. **A**. Drawing of IVPP V19965. **B**. Photograph of IVPP V19965. **C**. Photograph of IVPP V19966. **D**. Photograph of IVPP V19962. Note the morphological difference between male (A, B, D) and female (C) examples. Scale bar, 1mm.

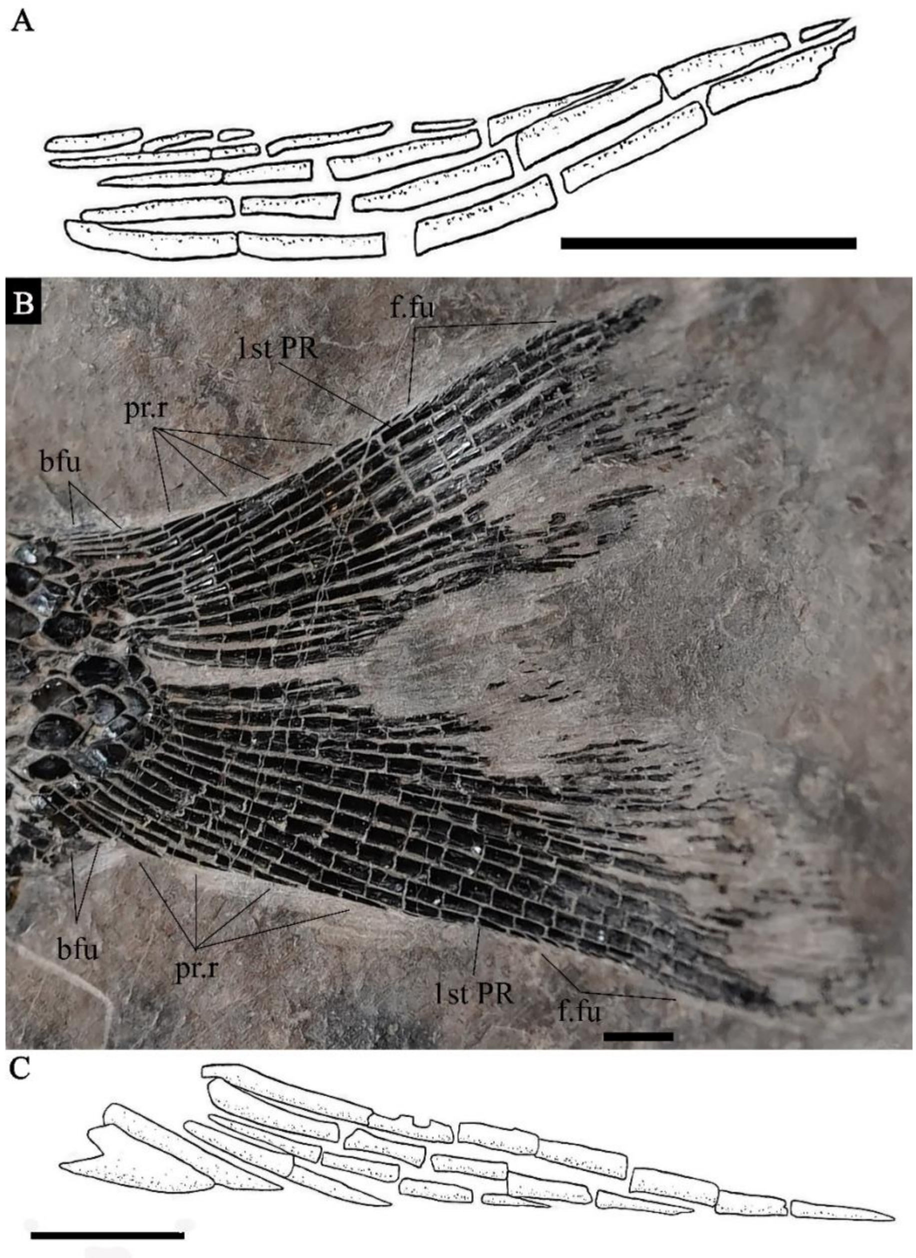

Figure 11. *Wushaichthys exquisitus*. Lateral view of the caudal fin on specimen IVPP V19962. **A**. drawings of the basal fulcra and procurrent rays in epaxial lobe. **B**. photo of the lateral view of the complete caudal fin. **C**. drawings of the basal fulcra and procurrent rays in hypaxial lobe. Scale bar, 1mm. Anatomical abbreviations—**bfu**, basal fulcra; **f.fu**, fringing fulcra; **pr.r**, procurrent-fin rays; **1st PR**, first principal caudal fin ray.

includes two basal fulcra and four procurrent rays. The last principal fin ray on the hypaxial lobe is also segmented and unbranched, and covered by fringing fulcra on its ventral margin. The basal fulcra on both epaxial and hypaxial lobes are elongate, sharp and cover the next element partially. The number of principal fin rays varies from 18 to 23 among specimens.

Scales and lateral line— Thick and ganoid scales of lepisosteid-type are preserved on all specimens of *Wushaichthys* and cover the whole body. The squamation consists of 30 to 34 vertical scale rows. There is one single row of deepened flank scales. The deepest scales (Figure 12) appear at the anterior ten vertical scale rows, with the depth-width ratio of nearly 3.6:1. At the 11th vertical scale row, the depth of the deepened flank scales starts to decrease, until about the 20th to 23rd vertical row, where the shape and size of the deepened flank scales are the same as the surrounding scales. In general, the size of the scales decreases from anterior to posterior. The shape of the scales is irregular only in the caudal peduncle area. No ornamentation can be observed on the scales.

Two lateral lines are present in *Wushaichthys*. One is in the middle region of the flank, associated with the deepened flank scales. The openings of pit organs are preserved by small vertical slits and located on the first dorsal third of the deepened flank scales. The last deepened scale with pit organ opening is located at the 12th vertical scale row. The approximate number of openings of pit organs is three. Another lateral line is located near the dorsal margin of the body. The shape and size of the lateral line scales are similar to their surrounding scales. Due to the preservation, the position of the last lateral line scale with pore is unclear, possibly before the 10th vertical row. The number of lateral line scales with pores is fewer than four.

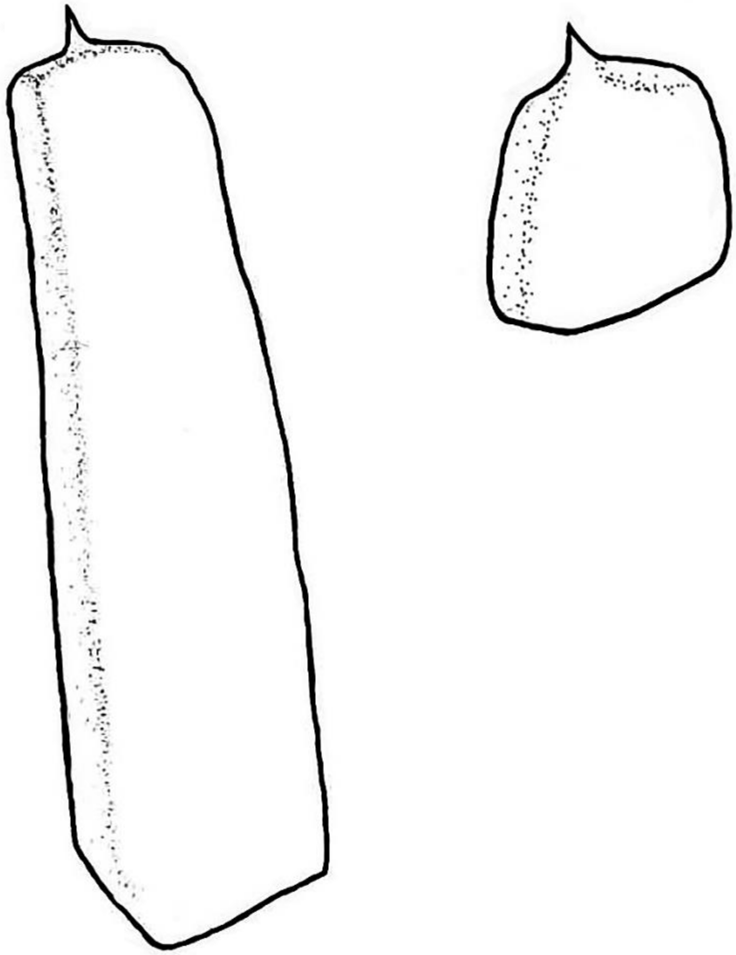

Figure 12. *Wushaichthys exquisitus*. Drawings of scales of specimen IVPP V19962 under normal light. Left, a deepened flank scale without pit organ opening. Right, a normal shaped scale above of the deepened scale.

CHAPTER 3. PHYLOGENETIC ANALYSIS AND RESULTS

Phylogenetic Analysis

The cladistic analysis was conducted using 23 taxa scored for 101 characters. The list of characters was modified from Xu et al. (2015) and the modifications (1–8) are identified below:

1. Two characters (Character 53 and 54 in Xu et al.) from the original matrix were removed from the present study because they only appear in the crown group teleost. Those characters are: presence of uncinate process on epibranchials, and number of hypobranchials.
2. Character 16, presence or absence of extrascapular, was replaced by the number of extrascapular bones (character 16 herein).
3. Character 55, concerning a comparison of sizes between opercle and subopercle, was replaced with accurate ratios based on actual measurements (character 63, herein).
4. Character 57, the position of the hinge position of lower jaw relative to the orbit, was replaced by the position of the quadrate-mandibular articulation relative to the orbit (character 60, herein).
5. Characters 67 and 71, the presence of wing-like pectoral fin and the presence of wing-like pelvic fin, were expanded to five ratios between either pectoral fin length or pelvic fin length to body lengths (character 75, 76, 77, 80 and 81, herein).
6. Character 66, presence or absence of fringing fulcra, was expanded to six characters, concerning the presence of fringing fulcra on pectoral fin, pelvic fin, dorsal fin, anal fin,

hypaxial lobe of caudal fin and epaxial lobe of caudal fin separately (character 73, 74, 79, 82 and 85, herein).

7. Four characters from Xu and Ma (2016) were added to the matrix: the dermopterotic/preopercle contact; presence or absence of the postspiracle; presence or absence of the dense brush-like rays proximally articulating several stout segments at the posterior portion of the male anal fin; and the condition of the lateral scutes associated with the anal fin (character 12, 41, 90 and 90, herein).
8. Six new characters from other publications were added to the matrix:
    - One or multiple bones in rostral region. This character is modified from Gardiner (1996) (character 2, herein).
    - The composition of coronoid process. This character is from Arratia (2013) (character 53, herein).
    - The presence of coronoid bones. This character is from Nelson (1973) (character 54, herein).
    - Shape of postcleithra. This character is modified from Arratia (1977) (character 69, herein).
    - Number of postcleithra. This character is from Arratia (1997) (character 70, herein).
    - Type of scales. This character is from Schultze (1966) (character 97, herein).

The characters and their character states used in the phylogenetic analysis are listed below. Note that the number in bracket at the beginning of some characters represents the numbering in the data matrix of Xu et al (2015).

1. (1) Skull: no more than one-fourth of total length [0]; roughly one-third of total length [1].

2. Rostral region: formed by several rostral bones [0]; one element [1].

3. (18) Only one median rostral bone: present [0]; absent [1].

4. (19) Shape of rostral bone: as a deep cap on snout apex [0]; reduced to a narrow tube [1]; non applicable [-].

5. (20) Rostral/frontal contact: absent [0]; present [1]; non applicable [-].

6. (25) Nasal involvement in antero-dorsal border of orbit: present [0]; absent [1].

7. (33) Frontal bone: elongated posteriorly [0]; expanded posteriorly [1].

8. (28) Parietal as individual bone: present [0]; fused with other bones [1].

9. (17) Sphenotic with small dermal component: absent [0]; present [1].

10. (14) Pterotic: present [0]; absent [1].

11. (34) Supraorbital sensory canal: ending at frontal bone [0]; ending at parietal bone [1].

12. Dermopterotic/preopercle contact: present [0]; absent [1]; non applicable [-].

13. (2) Post-temporal fossa: rudimentary [0]; well-developed [1]; lost [2].

14. (3) Sub-temporal fossa: present [0]; absent [1].

15. (27) Posttemporal: contacts extrascapular anteriorly [0]; contacts the extrascapular antero-laterally and separates this bone from contact with its counterpart [1].

16. Number of extrascapulars: two pairs or more [0]; three [1]; one pair [2].

17. (32) Vomers in adults: paired [0]; fused [1].

18. (4) Dilatator fossa above hyomandibular facet: absent [0]; present [1].

19. (5) Lateral cranial canal: absent [0]; present [1].

20. (6) Posterior myodome: present [0]; absent [1].

21. (7) Posterior myodome: paired [0]; enlarged into a median cavity [1]; non applicable [-].

22. (8) Anterior myodome: present [0]; absent [1].

23. (9) Number of anterior myodome: paired [0]; a median single [1]; non applicable [-].

24. (10) Parasphenoid/basioccipital contact: absent [0]; present [1].

25. (11) Basipterygoid process: present [0]; absent [1].

26. (12) Internal carotid foramen on parasphenoid: absent [0]; present [1].

27. (13) Efferent pseudobranchial foramen on parasphenoid: absent [0]; present [1].

28. (15) Intercalar: present [0]; absent [1].

29. (21) Anterior most lachrymal: as part of orbital ring [0]; anterior to orbital ring [1].

30. (31) Number of lachrymal bones: single [0]; two or more [1].

31. (22) Tube-like canal bearing anterior arm of antorbital: absent [0]; present [1].

32. (23) Foramen for olfactory nerves on premaxilla: absent [0]; present [1].

33. (24) Peg-like anterior process of maxilla: absent [0]; present [1].

34. (26) Antorbital involvement in anterior border of orbit: present [0]; absent [1]; non applicable [-].

35. (35) Number of infraorbitals: two or three elements [0]; four or more elements [1].

36. (36) Supraorbitals (including adnasal): absent [0]; present [1].

37. (37) Number of supraorbitals: one [0]; two or more [1]; non-applicable, e.g., adnasal absent [-].

38. (38) Suborbitals: present [0]; absent [1].

39. (39) Number of suborbitals: one [0]; two or more [1]; non applicable [-].

40. (40) Dermohyal: present [0]; absent [1].

41. Postspiracle: absent [0]; present [1].

42. (29) Nasal process of premaxilla that tightly sutured to frontals: absent [0]; present [1].

43. (58) Suborbital/maxilla contact: absent [0]; present [1]; non applicable [-].

44. (41) Mobile premaxilla: absent [0]; present [1].

45. (30) Premaxillae: paired [0]; fused [1]; non applicable [-].

46. (42) Maxilla free from preopercle: absent [0]; present [1]; non applicable [-].

47. (43) Mobile maxilla in cheek: absent [0]; present [1].

48. (63) Posterior margin of maxilla: straight or slightly convex [0]; concave with a posterior maxillary notch [1].

49. (44) Supramaxilla: absent [0]; present [1].

50. (45) Number of supramaxilla: one [0]; two [1]; non applicable [-].

51. (46) Surangular: present [0]; absent [1].

52. (47) Coronoid process on the lower jaw: absent [0]; present [1].

53. Coronoid process of lower jaw formed by: surangular and dentary [0]; surangular [1]; dentary and angular [2]; only dentary [3]; non applicable [-].

54. Coronoid bones: present [0]; absent [1].

55. (48) Suspensorium angle: oblique [0], nearly vertical [1].

56. (49) Symplectic: absent [0]; present [1].

57. (50) Symplectic involment in the jaw joint: absent [0]; present [1]; non applicable [-].

58. (51) Quadratojugal: present [0]; absent [1].

59. (52) Shape of quadratojugal: plate-like [0]; splint-like [1]. Non applicable [-]

60. Quadrate-mandibular articulation: posterior to orbit [0]; below the posterior half of orbit [1]; below anterior half of orbit [2]; anterior to orbit [3].

61. (60) Median gular: present [0]; absent [1].

62. (61) Lateral gular: present [0]; absent [1].

63. Size of opercle: more than 2.5 times as large as subopercle [0]; about two times as large as subopercle [1]; about 1.5 times as large as subopercle [2]; roughly equal to ro smaller than subopercle [3].

64. (56) Shape of preopercle: boomerang-shaped [0]; narrow and vertical, bearing a tapering anterior process [1]; oval-shaped [2]; crescent-shaped [3]; L-shaped [4].

65. (59) Interopercle: absent [0]; present [1].

66. (84) Ossified vertebral centra: absent [0]; present [1].

67. (79) Median caudal neural spines: absent [0]; present [1].

68. (62) Presupracleithrum: present [0]; absent [1].

69. Postcleithra/um: scale-like, superficial structure [0]; internal bone [1]; non applicable [-].

70. Number of postcleithra: none [0]; one or two [1]; three [2]

71. (64) Clavicle: present [0]; absent [1].

72. (65) Clavicle: large, cap anterior end of cleithrum [0]; reduced into small plates on postbranchial lamina of cleithrum [1]; non applicable [-].

73. Fringing fulcra on epaxial lobe of caudal fin: absent [0]; present [1].

74. Fringing fulcra on hypaxial lobe of caudal fin: absent [0]; present [1].

75. Pectoral fin enlarged as equal or more than 40% of the standard length: absent [0]; present [1].

76. Pectoral fin in prepelvic length: lower than 50% [0]; equal or larger than 50% [1].

77. Pectoral fin in preanal length: lower than 40% [0], equal or larger than 40% [1].

78. (72) Dense pectoral lepidotrichial segments between innermost principal pectoral fin rays: absent [0]; present [1].

79. Fringing fulcra on the leading marging of pectoral fin: absent [0]; present [1].

80. Pelvic fin enlarged as equal or more than 20% of the standard length: absent [0]; present [1].

81. Pelvic fin length in preanal length: lower than 30% [0]; equal or larger than 30% [1].

82. Fringing fulcra on leading margin of pelvic fin: absent [0]; present [1].

83. (70) Dorsal fin: rays more numerous than radials [0]; rays and radials equal [1].

84. (75) Dorsal fin rays: segmented throughout length [0]; segmented distally [1].

85. Fringing fulcra on leading margin of dorsal fin: absent [0]; present [1].

86. (73) Anal fin: larger than or equal to dorsal fin [0]; smaller than dorsal fin [1].

87. Anal fin: rays more numerous than radials [0]; rays and radials equal [1].

88. Anal fin rays: segmented throughout length [0]; segmented distally [1].

89. Fringing fulcra on leading margin of anal fin: absent [0]; present [1].

90. Dense brush-like rays proximally articulating several stout segments at posterior portion of male anal fin: absent (0); present (1).

91. Enlarged and posteriorly extended lateral scutes associate with anal fin: absent [0]; present [1].

92. (68) Diural caudal skeleton: absent [0]; present [1].

93. (69) Division of hypurals into dorsal and ventral groups (a gap between hypurals 2 and 3): absent [0]; present [1].

94. (78) Modified ural neural arches or uroneurals: absent [0]; present [1].

95. (76) Caudal fin: forked [0]; unforked [1].

96. (77) Caudal fin: lower lobe slightly shorter than or equal to upper lobe [0]; lower lobe longer than upper lobe present [1]; non applicable [-].

97. Type of scales: ganoid type [0]; elasmoid of amioid type [1]; elasmoid of cycloid type [2]; non applicable, e.g. absent of scales [-].

98. (80) Body squamation: body fully covered with scales [0]; reduced to a few (no more than four) rows of scales in caudal region [1]; entirely lost [2].

99. (81) Scale shape on the antero-dorsal region: rhomboid [0]; circular [1]; non applicable [-].

100. (82) Dorsal ridge scales (with posteriorly directed spines): absent [0]; present [1].

101. (83) Horizontal row of scales along lateral line: slightly deeper than those scales above or below lateral line [0]; much deeper than those scales above and below lateral line [1]; lost [2].

Results

The parsimony phylogenetic analysis was performed using PAUP* 4 (version 3.99.165.0). It includes 20 ingroup taxa and 101 characters.

The topology of the strict consensus is shown in Figure 13 and it is based on four most parsimonious trees. A description of the support of each node follow. Uniquely derived characters are identified with an asterisk [*].

Node A. This node, which includes all the taxa except the three outgroups, is supported by one uniquely derived character and one homoplastic feature: the presence of the median caudal neural spines (Ch. 67[1]*); and the antorbital is involved in the anterior border of orbit (Ch. 34[0]).

Node B. This node, which includes *Redfieldius, Perleidus* and more advanced actinopterygians, is supported by two uniquely derived characters and three homoplastic features: the suspensorium angle is nearly verticle (Ch. 55[1]*); the symplectic is present (Ch. 56[1]*); the

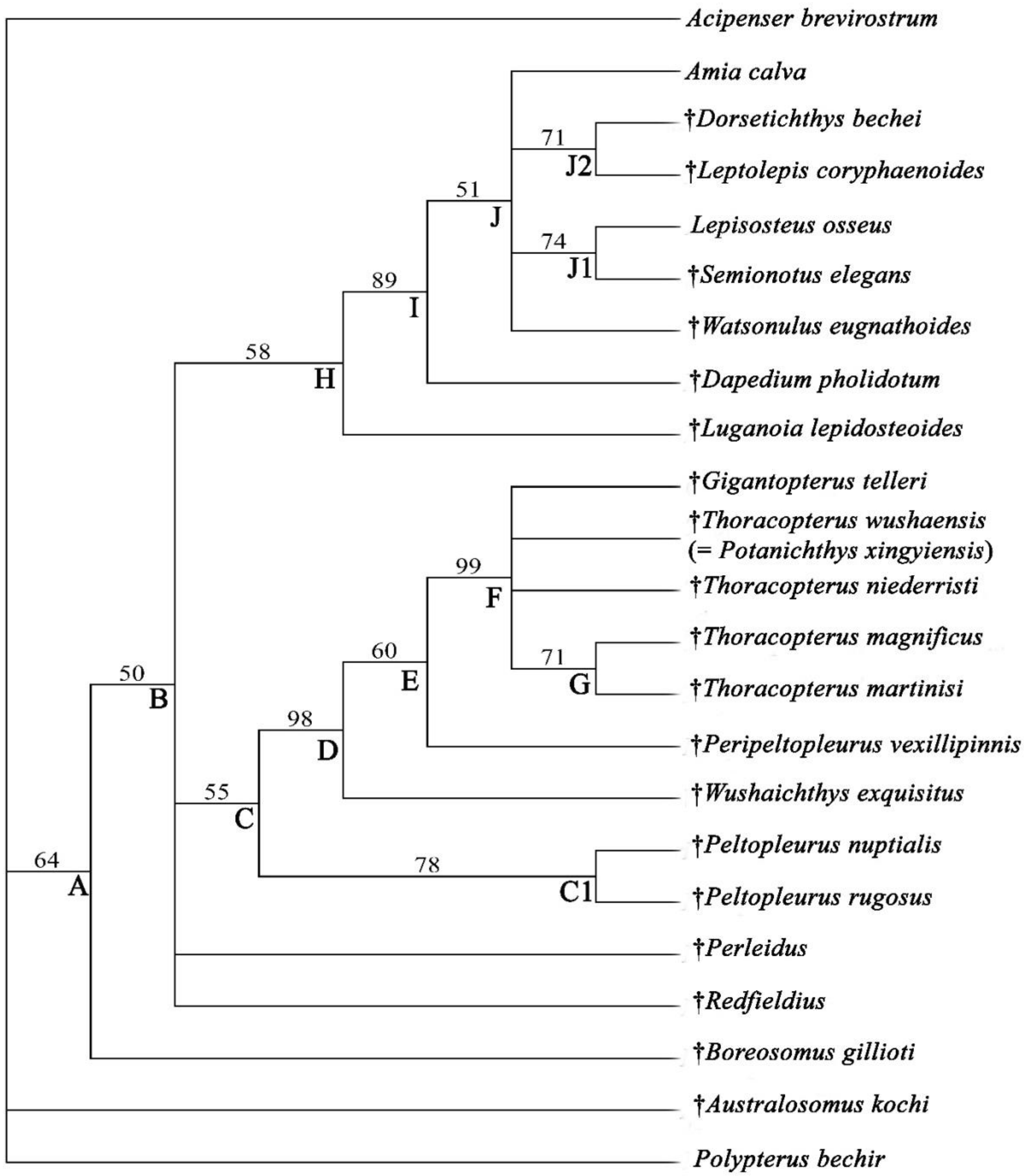
Acipenser brevirostrum
Amia calva
†Dorsetichthys bechei
†Leptolepis coryphaenoides
Lepisosteus osseus
†Semionotus elegans
†Watsonulus eugnathoides
†Dapedium pholidotum
†Luganoia lepidosteoides
†Gigantopterus telleri
†Thoracopterus wushaensis
(= Potanichthys xingyiensis)
†Thoracopterus niederristi
†Thoracopterus magnificus
†Thoracopterus martinisi
†Peripeltopleurus vexillipinnis
†Wushaichthys exquisitus
†Peltopleurus nuptialis
†Peltopleurus rugosus
†Perleidus
†Redfieldius
†Boreosomus gillioti
†Australosomus kochi
Polypterus bechir
64
A
50
B
58
H
89
I
51
J
71
J2
74
J1
55
C
98
D
60
E
99
F
71
G
78
C1

Figure 13. Hypothesis of phylogenetic relationships of *Wushaichthys* and its relatives based on 101 characters and three taxa as outgroups. Tree length is 262. Consistency index (CI) = 0.4313; homoplasy index (HI) = 0.5889; retention index (RI) = 0.6199; rescaled consistency index (RC) = 0.2674. Numbers before nodes are bootstrap values (larger than 50%). Uniquely derived characters are marked with asterisk (*). **Node A**: 5[1], 11[1], 19[1], 34[0], 37[1], 58[1], 67[1]*, 73[1], 74[1], 79[1], 82[1], 85[1], 86[1], 89[1]. **Node B**: 6[1], 12[1], 18[1], 25[1], 36[1], 55[1]*, 56[1]*, 63[3], 83[1], 84[1], 87[1], 88[1]. **Node C**: 11[0], 16[1], 41[1], 63[0], 90[1]*, 91[1]*, 101[1]. **Node C1**: 6[0]. **Node D**: 5[0], 7[1], 8[1], 15[1]*, 16[2], 45[1], 64[1], 79[0], 82[0], 85[0], 89[0]. **Node E**: 96[1]*. **Node F**: 73[0], 74[0], 75[1], 76[1]*, 77[1]*, 78[1]*, 80[1]*, 98[1], 101[2]. **Node G**: 16[1], 39[0], 70[0], 98[2]. **Node H**: 9[1], 10[1], 13[1]*, 42[1]*, 47[1], 52[1], 54[0], 58[0], 60[1], 62[1], 72[1], 95[1]. **Node I**: 33[1]*, 40[1], 46[1]*, 49[1], 59[1]*, 63[0], 64[4], 65[1]. Node J: 4[1]*, 5[0], 12[0], 16[2], 31[1], 32[1], 35[1]*, 53[1], 70[2], 95[0]. **Node J1**: 20[1], 22[1]*, 28[1]*, 29[1], 30[1]*, 34[1], 61[1], 100[1]. **Node J2**: 9[0], 10[0], 17[1]*, 23[1], 26[1], 27[1], 32[0], 39[0], 44[1]*, 50[1]*, 54[1], 71[1]*, 93[1]*, 94[1]*.

dilatator fossa above the hyomandibular facet is present (Ch. 18[1]); the rays and radials in dorsal fin are equal (Ch. 83[1]); and the dorsal fin rays are segmented distally (Ch. 84[1]).

Node C, Peltopleuriformes. This node is supported by three uniquely derived features: the postspiracle is present (Ch. 41[1]*); the anal fin in male individuals has dense brush-like rays proximally articulating with several stout segments at its posterior portion (Ch. 90[1]*); and there are enlarged and posteriorly extended lateral scutes associate with the anal fin (Ch. 91[1]*).

Node C1, Peltopleuridae. This node is weakly supported by only one homoplastic feature: the nasal bone is involved in the antero-dorsal border of orbit (Ch. 6[0]).

Node D. This node includes all the members of Thoracopteridae proposed by Xu et al. (Xu et al., 2015). It is supported by two uniquely derived features and one homoplastic feature: the posttemporal contacts the extrascapular antero-laterally and separates this bone from contact with its counterpart (Ch. 15[1]*); the preopercle is narrow and vertical, bearing a tapering anterior process (Ch, 64[1]*); and the frontal bone is expanded posteriorly (Ch. 7[1]).

Node E. This node includes *Peripeltopleurus* and the “traditionally” accepted thoracopterid members (Griffith, 1977; Tintori and Sassi, 1992). It is supported by one uniquely derived feature: the lower lobe of caudal fin is longer than the upper lobe of caudal fin (Ch. 96[1]*).

Node F, Thoracopteridae. This node is supported by four uniquely derived and one homoplastic feature: the ratio of pectoral-fin length in prepelvic length is equal or larger than 50% (Ch. 76[1]*); the ratio of pectoral-fin length in preanal length is equal or larger than 40% (Ch. 77[1]*); the presence of dense pectoral lepidotrichial segments between the innermost principal pectoral-fin rays (Ch. 78[1]*); the ratio of pelvic fin length in standard length is equal or larger than 20% (Ch. 80[1]*); and the ratio of pectoral fin length in standard length is equal or larger than 40% (Ch. 75[1]).

Node G, *Thoracopterus magnificus* and *Thoracopterus martinisi*. This node is supported by one homoplastic feature: the entirely loss of scales on the body (Ch. 98[2]).

Node H. This node, which includes *Luganoia* and members of the crown group Neopterygii, is supported by two uniquely derived characters and seven homoplastic characters: the post-temporal fossa is well developed (Ch. 13[1]*); the nasal process of the premaxilla is tightly sutured to frontals (Ch. 42 [1]*); the sphenotic has a small dermal component (Ch. 9[1]); the pterotic is lost (Ch. 10[1]); the premaxilla is mobile in cheek (Ch. 47[1]); the coronoid bones are present (Ch. 54[0]); the quadrate-mandibular articulation is located below the posterior half of the orbit (Ch. 60[1]); the lateral gular is lost (Ch. 62[1]); and the clavicle is reduced into small plates on the cleithrum (Ch. 72[1]).

Node I, Crown group Neopterygii. This node is supported by four uniquely derived and two homoplastic features: a peg-like anterior process of maxilla (Ch. 33[1]*); the maxilla is free from the preopercle (Ch. 46[1]*); the quadratojugal is splint-like (Ch. 59[1]*); the preopercle is “L”-shaped (Ch. 64[4]*); the supramaxilla is present (Ch. 49[1]); and the interopercle is present (Ch. 65[1]).

Node J. This node includes all the Neopterygii members except for *Dapedium*. It is supported by two uniquely derived features and three homoplastic treats: the rostral bone is reduced to a narrow tube (Ch. 4[1]*); four or more infraorbitals present (Ch. 35[1]*); a tube-like canal bearing the anterior arm of antorbital (Ch. 31[1]); the premaxilla has foramen for the olfactory nerves (Ch. 32[1]); and the coronoid process of the lower jaw is formed by surangular only (Ch. 53[1]).

Node J1, Ginglymodi. This node is supported by three uniquely derived and four homoplastic features: the anterior myodome is lost (Ch. 22[1]*); the intercalar is absent (Ch. 28[1]*); two or more lachrymal bones present (Ch. 30[1]*); the anteriormost lachrymal is located anterior to orbital ring (Ch. 29[1]); the antorbital is not involved in the anterior border the of orbit (Ch. 34[1]); the median gular is absent (Ch. 61[1]); and the presence of the dorsal ridge scales (Ch. 100[1]).

Node J2, **Teleostei.** This node is supported by six uniquely derived and six homoplastic features: the vomers in adults are fused into one bone (Ch. 17[1]*); the premaxilla is mobile (Ch. 44[1]*); two supramaxillae (Ch. 50[1]*); the clavicle is lost (Ch. 71[1]*); a gap presents between hypurals 2 and 3 (Ch. 93[1]*); moodified ural neural arches or uroneurals are present (Ch. 94[1] *); a small dermal component associated with sphenotic is absent (Ch. 9[0]), the pterotic is present (Ch. 10[0]); one median single anterior myodome is present (Ch. 23[1]); the presence of the efferent pseudobranchial foramen on parasphenoid (Ch. 27[1]); the foramen for olfactory nerves on premaxilla is lost (Ch. 32[0]); and the coronoid bones are absent (Ch. 54[1]).

Discussion

The results of the phylogenetic analysis (Figure 13) indicate that *Wushaichthys* is the most basal taxon within the family Thoracopteridae, which now includes *Gigantopterus*, *Thoracopterus wushaensis* (= *Potanichthys xingyiensis*), *T. niederristi*, *T. magnificus*, *T. martinisi*, *Peripeltopleurus* and *Wushaichthys*. This result is the same as that in Xu et al. (2015). However, there are several differences concerning the synapomorphies supporting nodes. For the node at the branching of the Thoracopteridae (Figure 14: Node 1), Xu et al. (2015) proposed that five synapomorphies supporting it: 1. extrascapulars separated medially by posttemporals; 2. preopercle nearly vertical and bearing an anterior process; 3. presence of laterally expanded frontals; 4. supraorbital sensory canal ending in frontal bone; 5. parietal and dermopterotic are fused into one bone. In contrast, in the current analysis (Figure 13: Node D), only the first three features are synapomorphies supporting this node. The other two features, which are also interpreted as synapomorphies by the parsimony analysis, are homoplastic features because a dermopterotic fused with the parietal is a character also present in *Luganoia* and in one of the outgroups, *Polypterus*; and the other character, the supraorbital sensory canal ending in the frontal, is also present in the genera *Peltopleurus* and *Redfieldius*, outside of the Thoracopteridae.

The results suggest that node C includes *Peripeltopleurus* and the more advanced members of the family Thoracopteridae (Figure 13, Node E). This node is supported by one synapomorphy: hypaxial lobe of the caudal fin longer than the epaxial, which matches the phylogenetic hypothesis of Xu et al. (2015; figure 14, node 2).

The present results indicate that *Gigantopterus*, *Thoracopterus wushaensis* (= *Potanichthys xingyiensis*), *T. niederristi*, *T. magnificus* and *T. martinisi* are advanced members of Thoracopteridae (Figure 13: Node F), in agreement with Xu et al. (2015: fig. 14, node 3). However, Xu et al. (2015) proposed four synapomorphies supporting this clade: 1. the pectoral fin is expanded, wing-like; 2. the pelvic fin is expanded, wing-like; 3. fringing fulcra are absent; and 4. dense lepidochrichial segments are present in pectoral fin rays. Of these, the first two features are ambiguous and need quantification; the third one is a broadly generalized feature, and consequently a homoplastic one. For instance, *Amia, Leptolepis* and *Luganoia* lack fringing

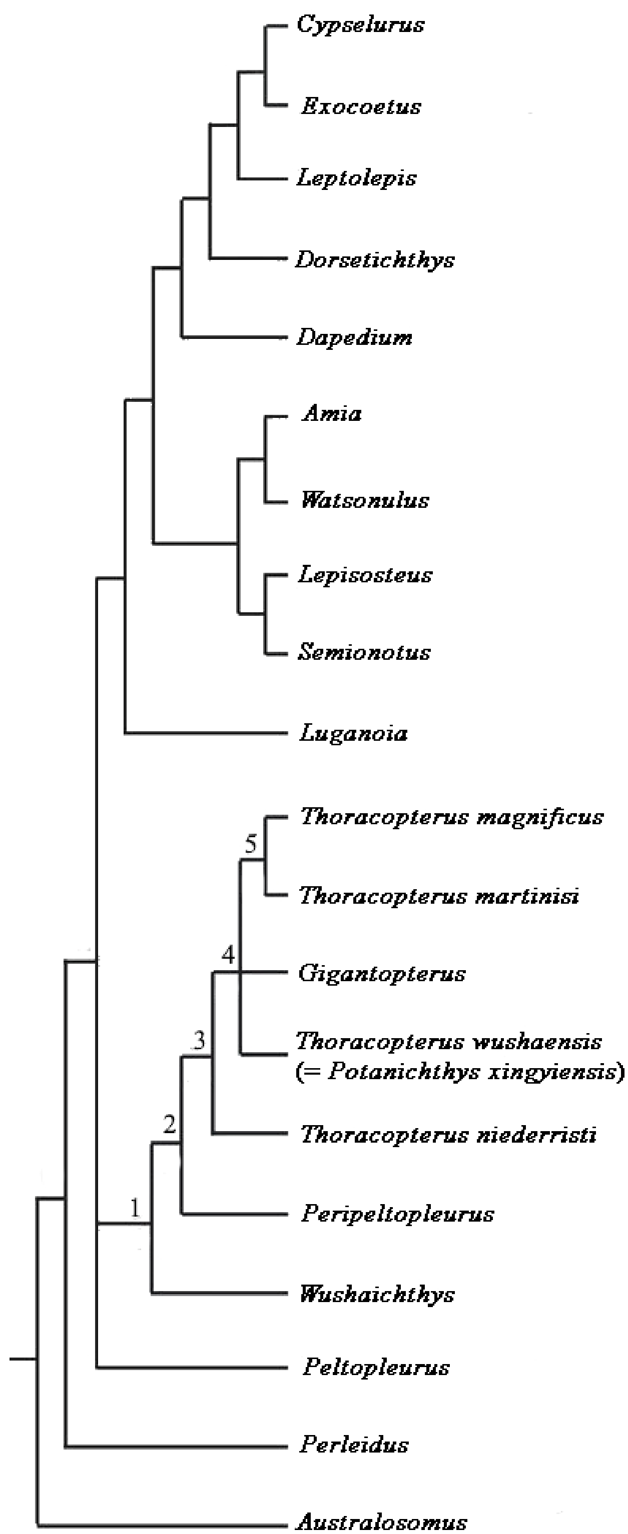

Figure 14. Phylogenetic hypothesis of *Wushaichthys* proposed by Xu et al. (2015: fig. 2c). Modified from (Xu et al., 2015).

fulcra in all fins, whereas *Wushaichthys* lacks fringing fulcra in the pectoral, pelvic and anal fins. Here, six new snynapomorphies are provided for this node: the pectoral fin length is equal or larger than 40% of the standard length; the pectoral-fin length is equal or larger than 50% of the prepelvic length; the pectoral-fin length is equal or larger than 40% of the preanal length; the pelvic fin length is equal or larger than 20% of the standard length; the presence of dense pectoral lepidotrichial segments between the innermost principal pectoral-fin rays; and the body squamation is reduced to a few row of scales in the caudal region.

Some recent studies (Xu and Ma, 2016; Xu et al., 2018b; Xu and Zhao, 2016; Xu et al., 2013; Xu et al., 2015) have suggested that *Thoracopterus niederristi*, which is the earliest discovered species of the genus *Thoracopterus* (Bronn, 1858; Tintori and Sassi, 1992), is more primitive than other two species *T. magnificus* and *T. martinisi*. *T. niederristi* is positioned as the sister taxon of the clade including *Gigantopterus, Thoracopterus wushaensis* (= *Potanichthys xingyiensis*), *T. magnificus* and *T. martinisi* (Figure 14) because of some primitive characters such as the body fully covered by scales. However, in the phylogenetic hypothesis proposed here, the position of *T. niederristi* remains unclear. More anatomical and osteological studies are needed to clarify the taxonomy and phylogenetic position of *T. niederristi*.

The order Peltopleuriformes was named by Gardiner (1967) and included two families: Peltopleuridae and Habroichthidae based in the presence of deepened flank scales. However, recent studies have removed Habroichthidae from the Peltopleuriformes due to the presence of some advanced features such as four or more infraorbitals; the quadrate-mandibular articulation positioned below the posterior half of the orbit; the presence of a coronoid process in the lower jaw; and the loss of the dermohyal (Xu and Ma, 2016; Xu et al., 2018b). These latest studies also include Thoracopteridae within the Peltopleuriformes, which previously was considered as the sister taxon of Luganoidae within the order Luganoiformes (Griffith, 1977). The current results (Figure 13) agree with the hypothesis of Xu and Ma (2016) that the Thoracopteridae is the sister group of the Peltopleuridae, and these two families form the Peltopleuriformes. Xu and Ma (2016) provided five synapomorphies to support the order Peltopleuriformes: a postpiracle present; the anal fin in male individuals has dense brush-like rays proximally articulating with several tubercle shaped segments at its base; the presence of enlarged and posteriorly extended lateral scutes associate with the anal fin; the upper margin of the preopercle in contact with the dermopterotic; and the supraorbital sensory canal ending in the frontal bone. The results herein treat the last two as homoplastic features because the preopercle is in contact with the dermopterotic also in *Polypterus, Watsonulus* and *Dorsetichthys*. The last feature, as mentioned above, is also present in *Redfieldius*.

Observation of new specimens provides new anatomical information on *Wushaichtys exquisitus*. Consequently, an emended diagnosis of *Wushaichthys exquisitus* is presented below.

Relatively small fish with fusiform body and standard length about 50 mm; large head, the head length is nearly one third of the standard length; a single narrow and deep rostral, which contacts the frontal bones; frontal expanded posteriorly; parietal fused with dermopterotic; orbit large, its diameter reaches one third of head length; the anterior margin of orbit is formed by the nasal and antorbital; nearly vertical preopercle with an anterior process like other thoracopterids; large opercle, with a small process at its antero-dorsal margin; five pairs of branchiostegal rays; small pectoral fin, about one fifth of standard length; nine principal pectoral fin rays; 10 principal dorsal fin rays; anal fin smaller than dorsal fin; 10 principal anal fin rays in female, four principal anal fin rays in male; caudal fin forked; body fully covered with ganoid scales; one horizontal row of deepened-flank scales; two lateral lines, one along the deepened-flank scales, the other near to the dorsal margin of body.

CHAPTER 4. CONCLUSION

A detailed redescription, based on newly collected specimens, provides new anatomical features of *Wushaichthys exquisitus*. The results of the phylogenentic analysis including more taxa and characters strengthened the hypothesis that *Wushaichthys* is the most basal taxon of the family Thoracopteridae and Thoracopteridae is the sister taxa of Peltopleuridae. However, the relationships within the advanced members of Thoracopteridae remain unclear. Future studies may clarify the phylogenetic position of some of the advanced flying fishes.

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APPENDIX

Character taxon matrix for 101 morphological characters and 23 taxa. Three outgroups including *Acipenser*, *Australosomus* and *Polypterus*.

Taxa	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
Acipenser	0	0	1	-	1	0	0	0	0	?	1	-	0	1	0	1	0	0	1	1
Amia	0	1	0	1	0	1	0	0	1	1	1	0	1	1	0	2	0	1	0	0
Australosomus	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	2	?	1	0	0
Boreosomus	0	1	0	0	1	0	0	0	0	?	1	0	0	1	0	0	?	0	1	0
Dapedium	0	1	0	0	1	1	0	0	?	?	1	1	1	0	0	0	0	1	1	0
Dorsetichthys	0	1	0	1	0	1	1	0	0	0	1	1	1	0	0	2	1	1	1	1
Gigantopterus	0	1	0	0	?	1	1	1	?	?	0	?	?	?	?	2	?	1	?	?
Lepisosteus	0	1	0	1	0	1	0	0	1	1	0	0	2	1	0	2	0	1	1	1
Leptolepis	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	2	1	1	1	0
Luganoia	0	0	1	-	-	1	0	1	?	?	1	1	?	?	0	0	?	1	?	?
Peltopleurus nuptialis	0	1	0	0	1	0	0	0	0	?	0	1	?	?	0	1	?	1	?	?
Peltopleurus rugosus	0	1	0	0	1	0	0	0	0	?	0	1	?	?	0	1	?	1	?	?
Peripeltopleurus	0	1	0	0	0	1	1	1	0	?	0	1	?	?	1	2	?	?	?	?
Perleidus	0	1	0	0	0	0	0	0	?	0	1	0	0	0	0	2	?	1	1	0
Polypterus	0	1	0	0	0	1	0	1	0	?	0	1	0	0	0	0	?	0	0	1
Thoracopterus wushaensis (= *Potanichthys xingyiensis*)	1	1	0	0	0	1	1	1	?	?	0	1	?	?	?	2	?	?	?	?
Redifieldius	0	0	1	-	1	1	0	0	0	?	0	1	?	?	0	0	0	?	?	?
Semionotus	0	1	0	1	1	1	0	0	1	1	1	0	1	0	0	2	0	1	?	?
Thoracopterus niederristi	0	1	0	0	1	1	1	1	?	?	0	1	?	?	1	2	?	?	?	?
Thoracopterus magnificus	0	1	0	0	0	1	1	1	?	?	0	1	?	?	1	?	?	?	?	?
Thoracopterus martinisi	0	1	0	0	0	1	1	1	?	?	0	1	?	?	1	1	?	?	?	?
Watsonulus	0	1	0	1	1	1	0	0	1	?	1	1	1	0	0	2	0	1	1	0
Wushaichthys	0	1	0	0	0	1	1	1	?	?	0	1	?	?	1	2	?	?	?	?

Taxa	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Acipenser	-	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	-	1
Amia	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	-	1	-	1
Australosomus	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	-	0	0	0
Boreosomus	1	0	1	0	0	1	0	?	0	0	0	0	0	0	0	0	-	0	1	0
Dapedium	1	0	0	1	1	1	1	0	0	0	0	0	?	0	0	1	0	0	1	1
Dorsetichthys	1	0	1	1	1	1	1	0	0	0	1	0	1	0	1	1	1	0	0	1
Gigantopterus	1	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	1	?	?	?
Lepisosteus	-	1	-	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0
Leptolepis	1	0	1	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	1
Luganoia	1	?	?	?	?	?	?	?	0	0	0	0	0	-	0	1	1	0	1	0
Peltopleurus nuptialis	1	?	?	?	?	?	?	?	0	0	0	0	0	-	0	?	?	0	1	0
Peltopleurus rugosus	1	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	1	0	1	0
Peripeltopleurus	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	1	0	1	?
Perleidus	1	?	?	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Polypterus	-	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	-	0	1	0
Thoracopterus wushaensis (= *Potanichthys xingyiensis*)	?	?	?	1	?	0	0	?	0	0	0	0	0	0	0	1	1	0	1	?
Redifieldius	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	0	0	1	0
Semionotus	?	?	?	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1
Thoracopterus niederristi	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	0	?	?	?
Thoracopterus magnificus	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	?	?	0	0	?
Thoracopterus martinisi	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	?	?	0	0	?
Watsonulus	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	1	1
Wushaichthys	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	0	0	1	?

Taxa	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Acipenser	0	0	-	0	-	-	0	0	0	-	1	0	-	1	0	0	-	0	0	0
Amia	0	1	-	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	-	1
Australosomus	0	0	0	0	?	0	0	0	0	-	0	0	-	1	0	0	-	0	0	0
Boreosomus	0	0	1	0	-	0	0	0	0	-	0	0	-	1	0	0	-	1	-	0
Dapedium	0	1	0	0	0	1	1	0	1	0	?	1	3	0	1	1	0	?	?	1
Dorsetichthys	0	1	0	1	0	1	1	0	1	1	0	1	1	1	1	1	0	0	1	1
Gigantopterus	?	0	?	0	?	0	?	0	0	-	?	?	?	?	1	?	?	?	?	0
Lepisosteus	0	1	0	0	0	1	0	0	0	-	0	1	1	0	1	1	0	0	1	3
Leptolepis	0	1	0	1	0	1	1	0	1	1	0	1	2	1	1	1	0	1	-	1
Luganoia	0	1	0	0	1	0	1	0	0	-	?	1	?	0	1	?	?	0	0	1
Peltopleurus nuptialis	?	0	0	0	0	0	0	0	0	-	?	0	-	1	1	?	?	1	-	0
Peltopleurus rugosus	?	0	0	0	0	0	0	0	0	-	?	0	-	1	1	?	?	1	-	0
Peripeltopleurus	1	0	?	0	1	0	0	0	0	-	?	0	-	1	1	?	?	1	-	0
Perleidus	0	0	0	0	0	0	0	0	0	-	0	0	-	?	1	?	?	?	?	0
Polypterus	0	0	0	0	0	0	0	0	0	-	1	1	3	1	0	0	-	0	0	0
Thoracopterus wushaensis (= *Potanichthys xingyiensis*)	1	0	0	0	1	0	0	0	0	-	?	0	-	?	1	?	?	?	?	0
Redifieldius	0	0	0	0	1	0	0	0	0	-	?	1	2	?	1	1	?	1	-	0
Semionotus	0	1	0	0	0	1	1	0	1	0	0	1	1	0	1	1	0	0	1	1
Thoracopterus niederristi	?	0	?	0	?	0	0	0	0	-	?	0	-	?	1	?	?	?	?	0
Thoracopterus magnificus	?	0	0	0	1	0	0	0	0	-	?	0	-	?	1	?	?	?	?	0
Thoracopterus martinisi	1	0	0	0	1	0	0	0	0	-	?	0	-	?	1	?	?	?	?	0
Watsonulus	0	1	0	0	0	1	1	1	1	0	0	1	3	0	1	1	1	?	?	0
Wushaichthys	1	0	0	0	1	0	0	0	0	-	?	0	-	?	1	?	?	1	-	0

Taxa	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Acipenser	1	1	-	-	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Amia	0	1	0	3	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0
Australosomus	0	0	2	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
Boreosomus	0	0	2	0	0	0	?	0	0	2	0	0	1	1	0	0	0	0	1	0
Dapedium	0	1	2	4	1	0	?	0	0	1	?	?	1	1	0	0	0	0	1	0
Dorsetichthys	0	1	3	4	1	0	1	0	0	1	?	?	1	1	0	0	0	0	1	0
Gigantopterus	?	?	0	1	0	0	?	?	0	1	?	?	0	0	1	1	1	1	0	1
Lepisosteus	1	1	0	4	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0
Leptolepis	0	1	0	4	1	1	1	1	0	2	1	-	0	0	0	0	0	0	0	0
Luganoia	0	1	3	0	0	0	?	?	-	0	?	?	0	0	0	0	0	0	0	0
Peltopleurus nuptialis	?	?	0	0	0	0	?	?	0	1	?	?	1	1	0	0	0	0	1	0
Peltopleurus rugosus	?	?	0	0	0	0	?	?	0	1	?	?	1	1	0	0	0	0	1	0
Peripeltopleurus	0	0	0	1	0	0	?	0	0	1	?	?	1	1	0	0	0	0	0	0
Perleidus	0	0	3	0	0	0	?	0	0	2	?	?	1	1	0	0	0	0	1	0
Polypterus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thoracopterus wushaensis (= *Potanichthys xingyiensis*)	?	?	0	1	0	0	1	?	0	1	?	?	0	0	1	1	1	1	0	1
Redifieldius	0	0	3	0	0	0	?	0	0	1	0	0	1	1	0	0	0	0	1	0
Semionotus	1	1	0	3	1	0	1	0	0	2	0	1	1	1	0	0	0	0	1	0
Thoracopterus niederristi	?	?	0	1	0	0	?	?	-	0	?	?	0	0	1	1	1	1	0	1
Thoracopterus magnificus	0	?	0	1	0	0	1	0	-	0	?	?	0	0	1	1	1	1	0	1
Thoracopterus martinisi	0	?	0	1	0	0	1	0	-	0	?	?	0	0	0	1	1	1	0	1
Watsonulus	0	1	3	2	1	0	?	0	0	2	0	0	1	1	0	0	0	0	1	0
Wushaichthys	0	0	0	1	0	0	?	0	0	1	0	0	1	1	0	0	0	0	0	0

Taxa	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101
Acipenser	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	2	-	0	2
Amia	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	-	1	0	1	0	0
Australosomus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Boreosomus	0	1	0	0	1	1	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0
Dapedium	0	1	1	1	1	1	1	0	1	0	0	0	0	0	1	-	0	0	0	1	0
Dorsetichthys	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Gigantopterus	0	0	1	1	0	1	1	1	0	?	?	0	0	0	0	1	0	1	-	0	2
Lepisosteus	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	-	0	0	0	1	0
Leptolepis	0	0	1	1	0	1	1	1	0	0	0	1	1	1	0	0	2	0	1	0	0
Luganoia	0	0	1	1	0	1	1	1	0	0	0	?	0	0	1	-	0	0	0	0	1
Peltopleurus nuptialis	0	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0	0	1
Peltopleurus rugosus	0	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0	0	1
Peripeltopleurus	0	0	1	1	0	1	1	1	0	1	1	?	0	0	0	1	0	0	0	0	1
Perleidus	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Polypterus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	0	0	0	0	0
Thoracopterus wushaensis (= *Potanichthys xingyiensis*)	1	0	1	1	0	1	1	1	0	1	1	0	0	0	0	1	0	1	-	0	2
Redifieldius	0	1	0	0	1	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0
Semionotus	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Thoracopterus niederristi	1	0	1	1	0	1	1	1	0	?	?	?	0	0	0	1	0	0	0	0	1
Thoracopterus magnificus	0	0	1	1	0	1	1	1	0	?	?	0	0	0	0	1	-	2	-	0	2
Thoracopterus martinisi	0	0	1	1	0	1	1	1	0	?	?	0	0	0	0	1	-	2	-	0	2
Watsonulus	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Wushaichthys	0	0	1	1	0	1	1	1	0	1	1	?	0	0	0	0	0	0	0	0	1