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Alison M. Murray[a], Lida Xing[b], Julien Divay[a], Juan Liu[ac] & Fengping Wang[d]

[a] Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada

[b] School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China

[c] Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, People's Republic of China;

[d] Qijiang District Bureau of Land and Resources, Chongqing 401420, China

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ARTICLE

A LATE JURASSIC FRESHWATER FISH (GINGLYMODI, LEPISOSTEIFORMES) FROM QIJIANG, CHONGQING, CHINA

ALISON M. MURRAY,*[,1] LIDA XING,[2] JULIEN DIVAY,[1] JUAN LIU,[1,3] and FENGPING WANG[4]
[1]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada, ammurray@ualberta.ca; divay@ualberta.ca; juan.liu@ualberta.ca;
[2]School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China, xinglida@gmail.com;
[3]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, People's Republic of China;
[4]Qijiang District Bureau of Land and Resources, Chongqing 401420, China, 455039424@qq.com

ABSTRACT—A new ginglymodian fish *Beiduyu qijiangensis*, gen. et sp. nov., is described from the freshwater Upper Jurassic Suining Formation of Chongqing, China. Although the fish is not completely preserved, it is most similar to *Lepidotes* and *Scheenstia*, which were once considered to be members of the Semionotiformes but are currently considered to be basal members of the Lepisosteiformes. The new fish lacks the strong dorsal ridge scales found in the Semionotiformes but has other features such as ganoid scales with anterodorsal and anteroventral processes but a reduced dorsal peg found in these basal lepisosteiform genera. With the description of this new taxon, there are three distinct ginglymodian fishes now known from southern China, all of them from Sichuan Province.

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INTRODUCTION

Most Asian Jurassic fish material has been collected from freshwater deposits (Chang and Miao, 2004), and these collections have produced a diversity of fishes. Reported Jurassic fishes from northern Asia (including Siberia, Mongolia, and northern China) are identified as palaeoniscids, coccolepids, chondrosteids, 'pholidophorids,' ptycholepids, galkiniids, hybodontids, ceratodontids, and an early acipenseriform (Chang and Miao, 2004).

Fewer fishes have been reported from Jurassic freshwater deposits of southern China, and the majority of these are from Sichuan (including Chongqing) and Yunnan provinces (Fig. 1; Su, 1974; Wang, 1974; Chang and Miao, 2004). From the southern area have come palaeoniscids, 'pholidophoriforms,' ptycholepids, hybodontids, and ceratodontids, with the main difference between the north and south being the addition of so-called 'semionotids' in the south (Chang and Miao, 2004).

The fishes reported as semionotids by Chang and Miao (2004) are from Sichuan, including the more recently recognized Subprovincial Municipality of Chongqing. These comprise two taxa originally referred to *Lepidotes*: *Lepidotes chungkingensis* Liu and Wang, 1961, from the Middle-Upper Jurassic near Chongqing and *Lepidotes luchowensis* Wang, 1974, from Lower-Middle Jurassic deposits near Luzhou (Chang and Miao, 2004). The latter was placed in the genus *Isanichthys* by Deesri et al. (2014), a genus erected by Cavin and Suteethorn (2006) for a fish from Thailand. There are also ganoid scales known from the Upper Jurassic of Guangyuan (Chang and Miao, 2004).

A large fish, encased in heavy ganoid scales, was recovered from Upper Jurassic deposits near Beidu (Qijiang, Chongqing District), China. Although this fish is not complete—most bones of the skull are missing—it is not conspecific with any previously reported fishes, and we here name it as a new species.

Geology

The Sichuan Basin contains seven formations with terrestrial deposits; from lowest to highest these are the Zhenzhuchong, Ziliujing, Xintiangou, Xiashaximiao, Shangshaximiao, Suining, and Penglaizhen formations (Peng et al., 2005). The uppermost three formations are all Upper Jurassic, although the majority of fossils that have been recovered from the Upper Jurassic of the Sichuan Basin are found in the lowest of the three, the Shangshaximiao Formation. The overlying Suining Formation has a single lithology predominated by red to reddish-brown calcareous mudstones, mixed with some off-white and gray-green quartz sandstone. The lithology in combination with the characteristic associations of ostracods and estherians allows a confident stratigraphic age for the Suining Formation of Late Jurassic (Gu et al., 1997; Peng et al., 2005).

The fish reported here comes from the lower to middle part of the Suining Formation of western Sichuan Province, Chongqing Municipality, from deposits laid down in a meandering fluvial/deltaic environment (Gao et al., 2006). This formation has produced many invertebrates, including ostracods, bivalves, and conchostracans (Editorial Committee of Stratigraphical Lexicon of China, 1999). It is also known for remains of dinosaurs, including *Mamenchisaurus* (Kan et al., 2005; Miyashita and Xing, 2012).

MATERIALS AND METHODS

The specimen, preserved in lateral view, lacks most of the skull bones but is otherwise an almost complete fish. The specimen is cataloged in the Qijiang National Geological Park Museum under catalog number QJGPM 1002. The specimen was prepared by Lingnian Su from the Fossil Research and Development Center of the Third Geology and Mineral Resources Exploration Academy of Gansu Province, China.

*Corresponding author.

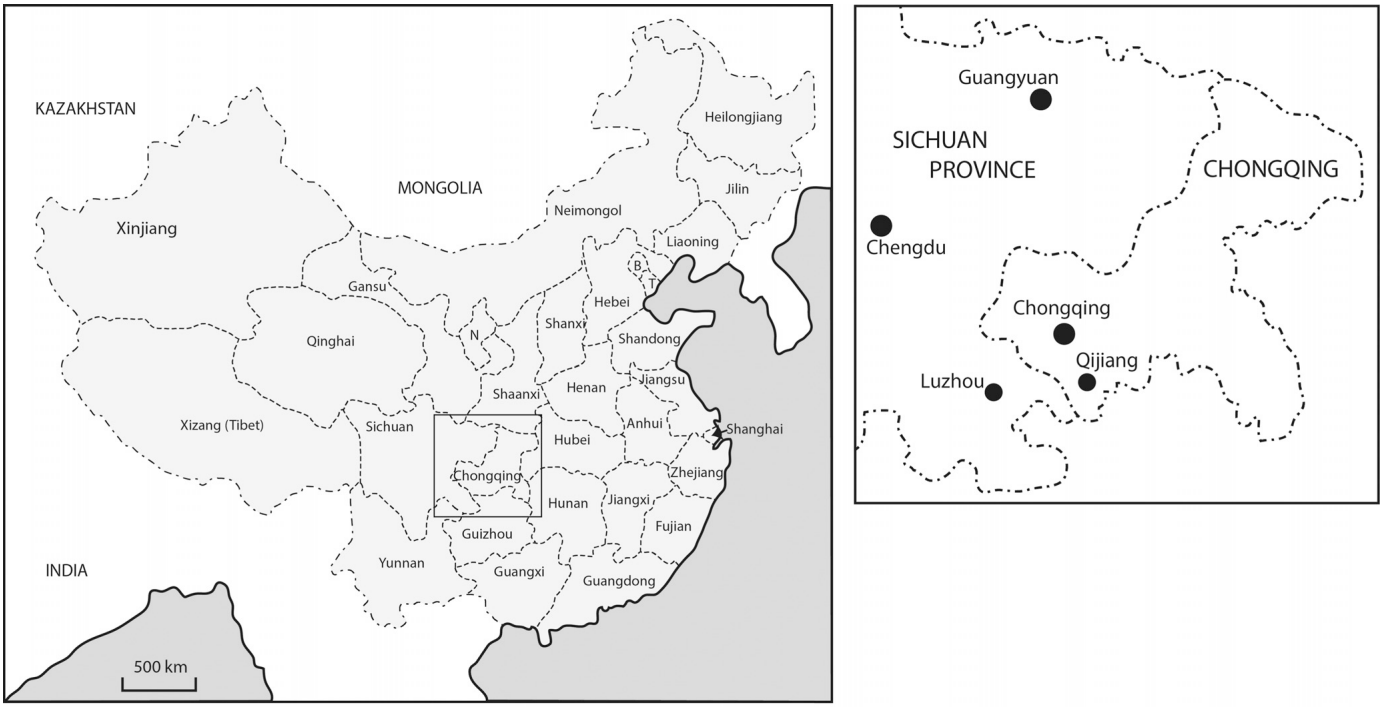

FIGURE 1. Map of locality. **A**, China (shaded), with smaller square indicating the area of map B. **B**, eastern part of Sichuan Province (small square in **A**). *Lepidotes chungkingensis* Liu and Wang, 1961, is from Middle-Upper Jurassic deposits near Chongqing; *Isanichthys luchowensis* (Wang, 1974) is from Lower-Middle Jurassic deposits near Luzhou; ganoid scales are known from the Upper Jurassic of Guangyuan; and *Beiduyu qijiangensis*, gen. et sp. nov., comes from Upper Jurassic deposits near Qijiang. **Abbreviations**: **B**, Beijing; **N**, Ningxia; and **T**, Tianjin.

SYSTEMATIC PALEONTOLOGY

We here follow the phylogeny and classification of ginglymodian fishes of López-Arbarello (2012) in attempting to determine the relationships of the new fish. In her analysis, several species originally considered to be *Lepidotes* were reassigned to new taxa. Based on her analysis, the Qijiang fish is excluded from the Semionotiformes by lacking the 1–2 rows of elongate scales at the posteroventral margin of the body lobe of the caudal fin and by lacking the scale-like ray at the dorsal margin of this fin. The new fish is instead included in the Lepisosteiformes (sensu López-Arbarello, 2012) based on the scales having a rostrocaudal articulation via anterodorsal and anteroventral processes.

Grande (2010) included within the Lepisosteiformes the living *Lepisosteus* and *Atractosteus* and the fossil genera *Cuneatus, Masillosteus, Obaichthys*, and *Dentilepisosteus*. López-Arbarello (2012) added to these *Pliodetes, Araripelepidotes, Isanichthys, Scheenstia*, and *Lepidotes* sensu stricto (represented by *L. semiserratus* and *L. gigas* in her cladogram). Essentially, the Lepisosteiformes of Grande (2010) is equivalent to the superfamily Lepisosteoidea of López-Arbarello (2012). The new fish is excluded from this group by lacking the posterior displacement of the dorsal fin to a position opposite the anal fin. The Qijiang fish is further excluded from the extinct genera *Pliodetes* and *Araripelepidotes* by lacking strong spines on the flank scales, from *Scheenstia* by being more slender and probably by having a smaller head in relation to standard length, and from *Isanichthys* based on caudal fin ray number and scale numbers (the Qijiang fish has many fewer caudal rays [11 compared with 25 in *Isanichthys*], more scales along the flank [about 60 compared with 50–53 in *Isanichthys*] and fewer in a transverse row [17 or 18 compared with 20 for *Isanichthys*]). Thus, we do not include it in any of these genera.

The remaining lepisosteiform genus (following López-Arbarello, 2012) is *Lepidotes* sensu stricto, including species from the Early Jurassic of Europe. All of the characters given by Forey et al. (2011) to distinguish *Lepidotes* relate to bones that are not visible in the Qijiang fish, but López-Arbarello (2012) further noted a reduction in the peg and socket articulation of the scales in *Lepidotes* sensu stricto: the Qijiang fish retains the peg (sockets are not visible) in the anterior flank scales where the displacement of the scales allows this feature to be seen and has scales most similar to those figured for '*L.*' *mantelli* (López-Arbarello, 2012: fig. 15E). As Forey et al. (2011) noted, the genus *Lepidotes* has been used for a great diversity of species from Lower Jurassic to Lower Cretaceous deposits worldwide. López-Arbarello (2012) retained only *L. gigas* (as she explained, this should be the type species), *L. elvensis, L. semiserratus*, and *L. bulowianus* in *Lepidotes* sensu stricto. All of these are Early Jurassic fishes from Europe and differ considerably from Late Jurassic and Cretaceous species (Forey et al., 2011). Therefore, we prefer to give the new fish from Late Jurassic deposits of China its own new genus.

López-Arbarello (2012) noted that the sister-group relationship she found between *Lepidotes* sensu stricto and *Scheenstia* (including several former species of *Lepidotes*) indicated that the Lepidotidae was probably a natural group; however, she refrained from formally using that family name because she considered that her analysis did not provide enough evidence of this relationship. We therefore use the term non-Lepisosteoidei Lepisosteiformes for these basal members following López-Arbarello's (2012) cladogram, to which we add our new species. This new fish cannot be included in any of the semionotiform taxa nor in the Lepisosteoidei as defined in the latest analyses. We consider it closest to the species of *Lepidotes* sensu stricto and *Scheenstia* (including '*L.*' *mantelli*) because it cannot be included in any of the other genera and the form of the scales is most similar to *Scheenstia mantelli*.

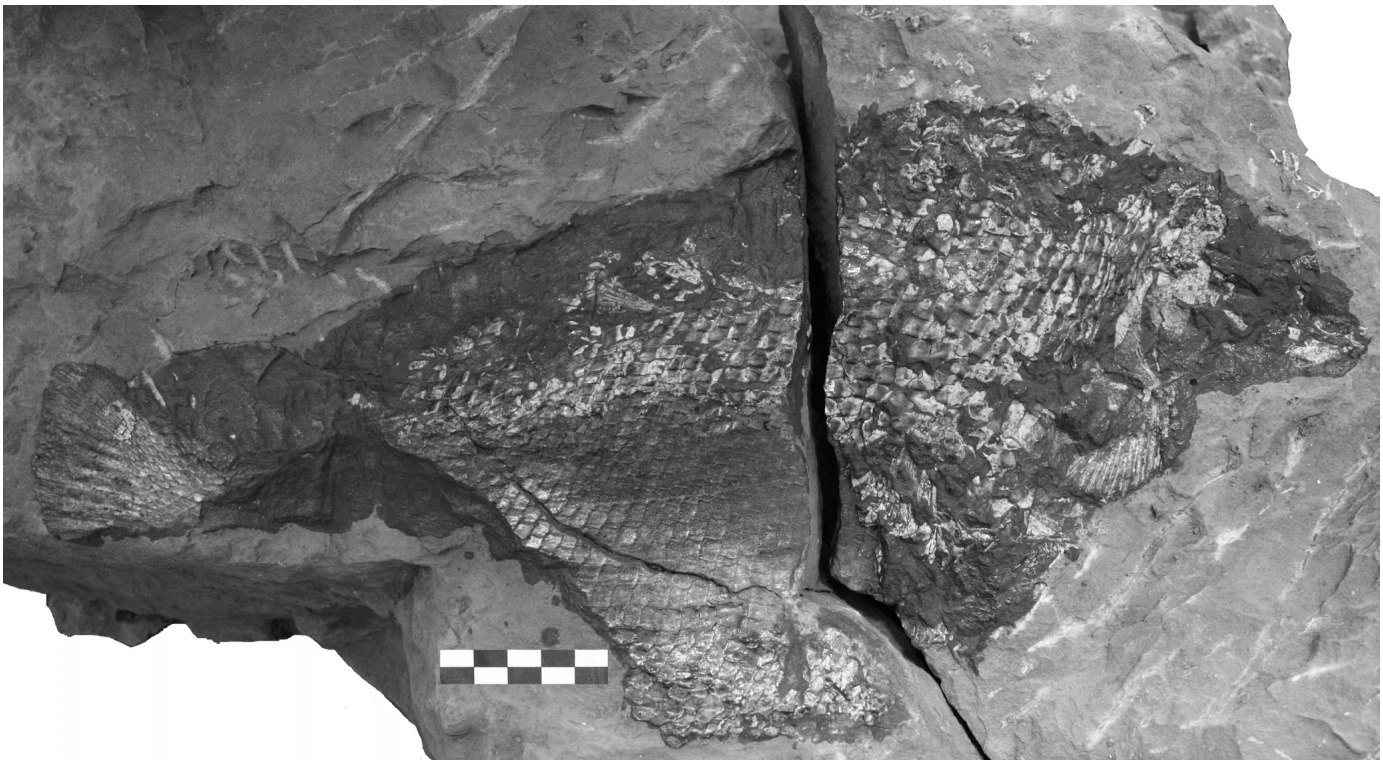

FIGURE 2. Photograph of *Beiduyu qijiangensis*, gen. et sp. nov. Holotype QJGPM 1002. The darker outline around the body is consolidant, not a body outline. Scale bar is in centimeters.

SYSTEMATIC PALEONTOLOGY

Division HOLOSTEI Müller, 1845 (sensu Grande, 2010)
Subdivision GINGLYMODI Cope, 1872 (sensu Grande, 2010)
Order LEPISOSTEIFORMES Hay, 1929 (sensu López-Arbarello, 2012)

Included Taxa—*Lepidotes* Agassiz 1832, *Scheenstia*, López-Arbarello and Sferco, 2011, and members of the Lepisosteoidei following López-Arbarello, 2012.

BEIDUYU, gen. nov.

Type Species—*Beiduyu qijiangensis*, sp. nov.

Diagnosis—As for type and only known species.

Etymology—The generic name is a combination of Beidu, the fossil locality, and 'yu,' meaning 'fish' in Chinese.

BEIDUYU QIJIANGENSIS, sp. nov.
(Figs. 2–5)

Holotype—A nearly complete fish missing part of the caudal peduncle and the anterior part of the skull. Catalog number QJGPM 1002.

Type Locality—Beidu, Qijiang, Chongqing Municipality, Sichuan Province, China.

Horizon and Age—Suining Formation, Late Jurassic age.

Diagnosis—A non-Lepisosteoidei lepisosteiform fish based on the dorsal fin positioned in middle of back, with strong anterodorsal and anteroventral processes in the scales, lacking strongly ridged dorsal scales and possibly lacking fringing fulcra in the dorsal fin, and bearing nine or 10 roughly parallel vertical furrows on the ventral third of the opercle.

Etymology—The specific epithet is for Qijiang, the area from which the fossil was recovered.

Description

General Body Form—The fish is preserved in lateral view (Fig. 2). The ventral and dorsal body walls are distorted and the scales displaced; the ventral wall displacement might be caused by bacterial action in the gut as the body decomposed that led to a bursting of the gut wall. Many of the skull bones are displaced or missing, but given the otherwise well-articulated condition of the postcranial elements, it appears likely that the fish was subjected to some scavenging before burial. If so, it is likely that the fish was not deposited in an anoxic environment.

The fish measures 33 cm in length from the anterior-most preserved part of the skull (which is probably close to the true anterior limit of the skull) to the end of the caudal plate. The preserved portion of the caudal fin (which appears complete) is another 3 cm long. The scale cover spans about 15.5 cm from dorsal to ventral limits, but the actual body depth is estimated to be about 11.5 cm (34% of standard length [SL]), from the greatest height in front of the dorsal fin to a level ventral to the pelvic fin. However, these measurements are tentative because the body is distorted so that the dorsal fin is not preserved in the midline; scales from the left side of the body are visible above the fin, and the ventral limit in the living fish is uncertain because of the displaced ventral scales. The displacement of the scales also indicates that the body was probably fairly wide, more likely cylindrical in shape rather than laterally compressed.

Skull and Pectoral Girdle—The bones of the pectoral girdle and head are not easy to interpret (Fig. 3). The most complete bone delimiting the start of the squamation at the back of the head is identified as the cleithrum. This is a large bone that is a

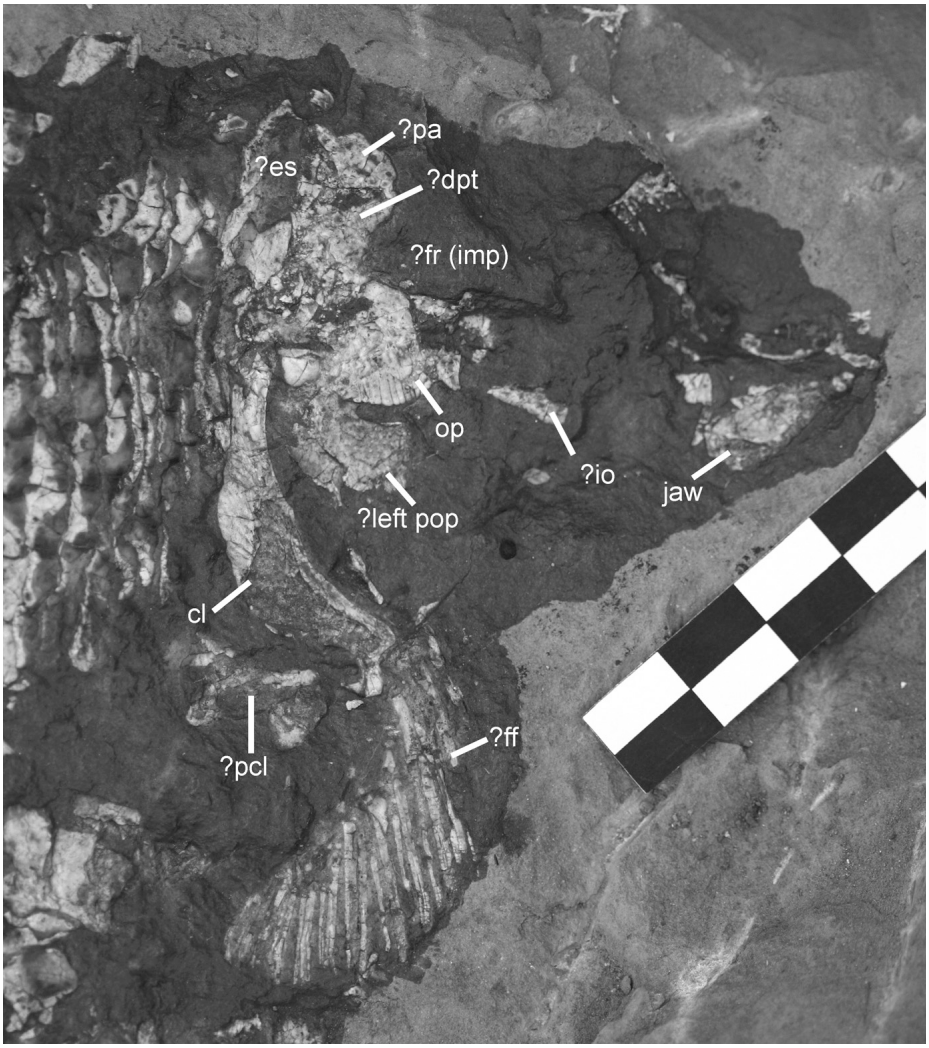

FIGURE 3. Photograph of the head of *Beiduyu qijiangensis*, gen. et sp. nov. Holotype QJGPM 1002. Identity of bones is tentative. The darker outline around the head is consolidant, not a body outline. **Abbreviations**: **cl**, cleithrum; **?dpt**, ?dermopterotic; **?es**, ?extrascapular; **?ff**, ?fringing fulcra of pectoral fin; **?fr (imp)**, impression of ?frontal; **jaw**, dentary or maxilla; **?pa**, ?parietal; **?pcl**, ?postcleithrum; **op**, opercle, **?io**, ?infraorbital. Scale bar is in centimeters.

gently curved and broader in the middle than at either dorsal or ventral end. The dorsal tip is narrower than the ventral end. The bone behind it is probably the postcleithrum.

Anterior to the cleithrum, the opercle is preserved (Fig. 3). Although the limits of the bone are obscured, it appears to be subrectangular in shape, with straight ventral and anterior edges. The ventral edge bears nine or 10 roughly parallel vertical furrows that extend over the ventral third of the bone. There are no tubercles or ridges on the external surface of the opercle. Dorsal to the opercle are bones identified as a possible dermopterotic, an extrascapular, and a parietal and impression of the frontal. However, the precise limits of these elements are not visible. The extrascapular is taller anterodorsally than wide, and larger than the parietal, which is longer in its anteroposterior dimension than its dorsoventral one. The probable dermopterotic is larger than the parietal. All of these bones are lacking in tubercles or other ornamentation.

Ventral to the opercle is a bone that appears to be preserved in medial view; it may be the broad ventral limb of the left preopercle or possibly, but less likely, the right subopercle. If it is the latter, the bone has been completely rotated into medial view. Other fragments of bone preserved are identified based on position as possible infraorbital and dentary bones, although the presumed dentary could instead be the maxilla. It is teardrop in shape, with a broadly rounded posterior end and a narrow anterior tip. No teeth are visible on any of the bones, and dermal denticles do not appear to have been present.

Fins—The dorsal fin, placed roughly equidistant between the head and tail (Fig. 2), has 5 or 6 rays (Fig. 4). The anal fin is missing. The ventrally located pectoral fin is broad-based, with probably 11 rays (the distinction between individual rays is not clear). The first few elements (not counted as part of the 11 rays) may be basal or fringing fulcra, but the poor preservation makes this unclear. Alternatively, these anterior-most elements may be a single 12th ray, in which case the fin lacks fringing fulcra (Fig. 3). In the pelvic fin, only nine elements are preserved and these may not all be rays. The truncate caudal fin (Fig. 5) has 11 rays preserved with six or seven dorsal fringing fulcra, but fringing fulcra cannot be seen on the ventral edge of the caudal fin or in the dorsal fin.

Little can be determined of the rest of the caudal skeleton. The vertebral column seems to have had a relatively short upturned portion posteriorly, because the caudal fin squamation is not greatly attenuated (Fig. 5).

Scales—The best-preserved feature of the fish is the squamation (Figs. 2, 4), which is composed of heavy ganoid scales. These scales, largest just behind the head, are distinctly taller than wide. They become progressively smaller posteriorly as their dorsoventral dimension decreases. Scales in the posterior portion of the body become distinctly anteroposteriorly elongate

FIGURE 4. Photograph of the scales and dorsal fin of *Beiduyu qijiangensis*, gen. et sp. nov. Holotype QJGPM 1002. Scale bar is in centimeters.

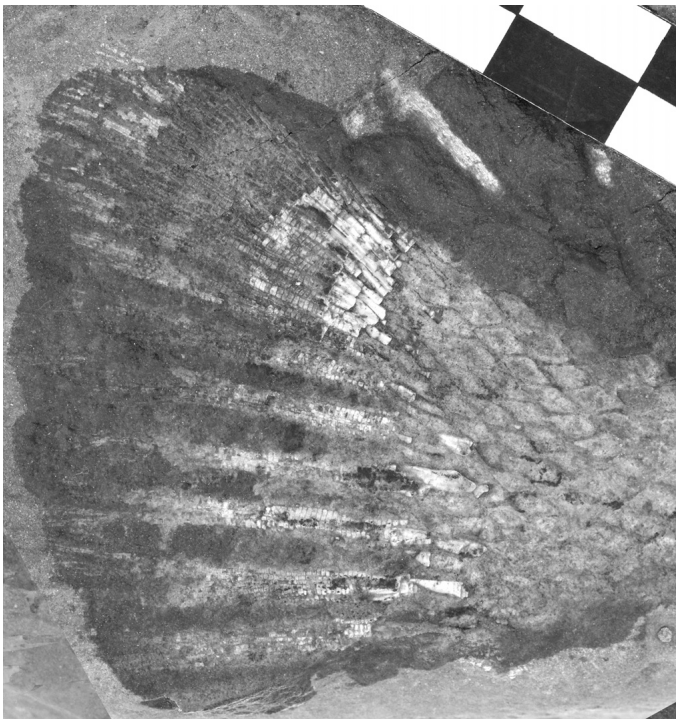

FIGURE 5. Photograph of the caudal fin of *Beiduyu qijiangensis*, gen. et sp. nov. Holotype QJGPM 1002. Scale bar is in centimeters.

relative to their height, having a more equilateral diamond shape. There are an estimated 60 scales along the length of the body, with 43 preserved anterior to a gap in preservation, eight posterior to it, and room for nine or 10 scales in the gap. Taking the distortion of the ventral body into consideration, there were likely 17 or 18 scales in a transverse row anterior to the dorsal fin, and there are 14 transverse scales preserved on the caudal peduncle.

The scales (Fig. 4) are similar to those figured for '*Lepidotes*' by López-Arbarello (2012:fig. 15) in having strong anterodorsal and anteroventral processes, with a somewhat reduced dorsal peg. They also have a distinctly extended posteroventral corner. There is no ridge or spine on the scales, but the posterior edges of some are clearly ornamented with 2–5 serrations, particularly visible in the first five anterior scale rows.

DISCUSSION

The preservation of *Beiduyu qijiangensis* prevents us from determining its relationships more precisely. An opercle with furrows is also found in the Eocene lepisosteid *Masillosteus kelleri*, but in that fish the furrows are more numerous (Micklich and Klappert, 2001: fig.2), and the fish is clearly not closely related to *B. qijiangensis* because the latter lacks the posteriorly positioned dorsal and anal fins characteristic of the Lepisosteoidea. Unfortunately, there are very few characters previously used in phylogenetic analyses (e.g., Grande, 2010; López-Arbarello, 2012) of lepisosteiforms that can be coded for *B. qijiangensis*. It is therefore left as a basal lepisosteiform.

The two articulated holostean fishes previously described from Sichuan Province were both originally described in the genus *Lepidotes*: *Lepidotes chungkingensis* Liu and Wang, 1961 (Middle-Late Jurassic), and *L. luchowensis* Wang, 1974 (Early-Middle Jurassic). Deesri et al. (in press) removed *L. luchowensis* from that genus and placed it in *Isanichthys*, a genus originally erected for material from Thailand.

The new fish *Beiduyu qijiangensis* is not included in *Isanichthys*, because the anterior scales of the Thai *Isanichthys* are not tall and narrow, or at least not to the extent seen in *B. qijiangensis*. Although the body proportions seem similar between *B. qijiangensis* and *Isanichthys lertboosi*, this is an artifact of preservation of the former and *B. qijiangensis* was much more slender than *I. lertboosi*. In *Isanichthys lertboosi*, there is no ganoin on the skull bones, whereas there appears to be ganoin on the Qijiang fish. *Isanichthys* (= *Lepidotes*) *luchowensis* also has a much larger head in proportion to body (almost 1/3 SL) than *B. qijiangensis* (estimated at about 1/5 SL), with the dorsal fin placed much closer to the tail in the former, and the anterior scales are broad as in *I. lertboosi*, rather than narrow as in *B. qijiangensis*.

Deesri et al. (2014) did not comment on whether the second Sichuan *Lepidotes, L. chungkingensis*, should be retained in that genus or removed to *Isanichthys* along with *L. luchowensis*. *Lepidotes chungkingensis* is somewhat similar to *Beiduyu qijiangensis* but represents at the least a different species (A.M.M., pers. observ.). *Lepidotes chungkingensis* is smaller and has a shallower body depth, although this latter may be related to allometric growth, with larger individuals having proportionally deeper bodies. The anterior scales of *L. chungkingensis* are taller than the posterior scales, but they are proportionally not as greatly different from the posterior scales as the anterior and posterior

scales of *B. qijiangensis*. The tail of *L. chungkingensis* is not fully preserved, and so we are unable to compare it with the caudal fin of *B. qijiangensis*; however, there are a few caudal fin rays preserved in the only known specimen that indicate that the posterior extent of the preserved fish includes all, or almost all, of the body length. The 33 scales in a lateral row preserved in *L. chungkingensis* therefore would be close to the total number that would have been present. This is much fewer than that of *B. qijiangensis*, which preserves 51 scales in a lateral row, with an estimated total in the living fish of 60 scales. Although the caudal fin is not complete in *L. chungkingensis*, there is no indication that this fish had the elongate scale at the posteroventral margin of the body lobe of the tail nor the scale-like ray at the dorsal margin of the fin as found in Semionotiformes (López-Arbarello, 2012). Neither does it have any obvious dorsal ridge scales between the nape and dorsal fin as found in Semionotidae. Unfortunately, the scale covering in the only specimen of *L. chungkingensis* is not disturbed, so the anterior fields of the scales cannot be observed and whether or not this fish had the antero-dorsal and -ventral processes of the Lepisosteiformes cannot be determined. We here leave *L. chungkingensis* in the genus *Lepidotes*, because it has fewer scales in a lateral row and fewer transverse scales (33 and 17) than reported for *Isanichthys* (50–53 and 20, respectively). However, we note that *L. chungkingensis* likely should also be removed from *Lepidotes* if that genus is better restricted to Early Jurassic European fish (e.g., Forey et al., 2011).

With the description of the new fish from Qijiang, there are now three different Jurassic ginglymodian fishes known from eastern Sichuan Province. This is the highest diversity of these fishes in Asia. Elsewhere in China, ginglymodian fishes (as 'semionotids') have been reported from Liaoning and Zhejiang provinces (*Neolepidotes*; Chang and Chou, 1977; Jin, 1987), and a younger form (Early Cretaceous) is known from Japan (*Lepidotes macropterus* Yabumoto, 1994). *Lepidotes deccanensis* Sykes, 1851 (including four other species erected by Egerton [1854, 1858] but synonomized by Jain [1983]), is from Lower Jurassic deposits of the Kota Formation, India, but this area was part of the southern Antarctic landmass at that time, and the fish is unlikely to be closely related to the Chinese or Japanese forms. All of these Asian fishes should be reanalyzed in light of the analysis by López-Arbarello (2012) and the suggested restriction of the genus *Lepidotes* to Early Jurassic species from Europe (Forey et al., 2011).

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