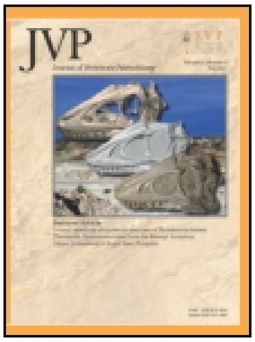

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NEW FOSSIL OSTEOGLOSSOMORPH FROM NINGXIA, CHINA

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ABSTRACT—The fish described here is from the Madongshan Formation, Liupanshan group (Early Cretaceous), Tongxin County, Ningxia Autonomous Region, China. It is assigned to Osteoglossomorpha because it has the following synapomorphies of the superorder: a full neural spine on the first preural centrum, a primary bite between parasphenoid and basihyal, and absence of a supraorbital. This fish differs from other osteoglossomorphs in having a very short premaxilla with only three teeth, of which one is exceptionally large, and an unusual caudal skeletal in which hypural 1 is fused to the first ural centrum and hypural 2 remains autogenous. A new name is proposed, *Xixiaichthys tongxinensis* gen. et sp. nov., based on the unique characters and a combination of other characters. The results of the phylogenetic analysis show that *Xixiaichthys* is the sister group of the Osteoglossiformes ([[*Notopterus* + *Osteoglossum*] + [*Huashia* + *Kuntulunia*]]). Therefore, the new genus is referred to Osteoglossiformes.

INTRODUCTION

The two specimens studied here were discovered from Wangtuan, Tongxin County, Ningxia Autonomous Region, China, in 1982. The specimens were collected by Liu Zhi-cheng, Li Guo-qing, and the author. Besides those specimens, 26 specimens of *Kuntulunia*, another osteoglossomorph fish, were also found in this locality. In 1993, Dr. Zhou Zhong-he and the author excavated the site again and collected nearly one hundred specimens, but they are all referable to *Kuntulunia* (see Zhang, 1998). The specimens were from the Madongshan Formation, Liupanshan group. The deposits of the formation are represented by interbedding of gray mudstones and marlstones, shales, limestones, oil shales, and thin layers of gypsum. The stratum contacts conformably with the underlying *Lycoptera*-bearing strata of the Liwaxia Formation. Plants, lamellibranchiata, and ostracods also have been found in this formation (Hao et al., 1986).

The age of the *Lycoptera*-bearing strata previously was considered as Late Jurassic to Early Cretaceous (Chang and Chou, 1986; Chang and Jin, 1996), but as Early Cretaceous (Barremian) according to a new $^{40}Ar/^{39}Ar$ dating of the *Lycoptera*-bearing Yixian Formation in Liaoning Province, northwestern China (Swisher et al., 2002). The strata bearing *Kuntulunia* are generally considered as Early Cretaceous (Hao et al., 1986; Liu et al., 1982; Tan, 1982).

MATERIAL AND METHODS

Specimens and Preparation

The specimens studied are deposited in the collection of Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. The comparative materials in the following list are in the collections of IVPP. *Huashia gracilis* Chang and Chou (IVPP V2995.1, 3, 33, 44, 48, 142, 204), *H. tungi* (Liu et al.) (IVPP V2323.1, 8; V8063.1B, 3, 5-7), *Jiuquanichthys liui* Ma (IVPP V6184.1-6, 8-10, 12-46, 48-51, 53-70), *Kuyangichthys microdus* Liu et al. (IVPP V5668.2, 6, 8, 11, 12, 14-22, 24, 26, 30-36, 38, 46, 48-50, 57, 59, 73), *Jiaohichthys pulchellus* Ma (IVPP V6186.1-a, 1-b), *Jinanichthys longicephalus* (Liu et al.) (IVPP V2321.1, 3, 4; V8475.1-4; V8477.1, 2; V10148.1-23; V10149.1-56), *Kuntulunia longipterus* Liu et al. (IVPP V5669.1-45, V6794.1-32, V8556.1-32), *Lycoptera davidi* (Sauvage) (IVPP V2328.1, 4, 9, 12-14, 16, 17, 19-22, 24, 27, 28, 31-33), *Osteoglossum bicirrhosum* (Vandelli) (a dried specimen, uncatalogued), *Paralycoptera wui* Chang and Chou (IVPP V2989.6, 7, 12, 20, 26, 28-31, 37, 45, 47, 58, 80, 83, 88, 106, 124, 138, 180), *Tongxinichthys microdus* Ma (IVPP V2332.1-43, V11373.1-93). The specimens were mechanically prepared. The drawings were executed under a Wild MZ8 microscope with camera lucida attachment.

Systematic Methodology

The phylogenetic analysis was conducted using PAUP software (version 3.1.1; Swofford, 1993) using DELTRAN character-state optimization. The trees obtained using the heuristic search option and tree-bisection-reconnection (TBR) was employed as the branch-swapping algorithm. All the characters were unweighted, unordered, and considered to be simple and independent of one another. Missing characters or unclear conditions owing to the quality of preservation were coded as "?".

Huashia, *Jinanichthys*, *Jiuquanichthys*, *Kuntulunia*, *Kuyangichthys*, *Lycoptera*, *Paralycoptera*, *Tongxinichthys*, *Xixiaichthys*, and *Jiaohichths* were considered in the analyses as part of the ingroup because these genera are comparatively well preserved relative to other early osteoglossomorphs (Zhang, 1998). Three extant genera (*Hiodon*, *Notopterus*, *Osteoglossum*) were included in the analyses as representatives of the major subgroups Hiodontidae (Hiodontoidea, Hiodontiformes), Notopteridae (Notopteroidei), and Osteoglossidae (Osteoglossoidei) of osteoglossomorpha (Hilton, 2003; Li and Wilson, 1996a; Patterson and Rosen, 1977). *Allothrissops*, *Anaethalion*, *Leptolepides* and *Tharsis* were chosen as a combined outgroup in analysis.

The focus of this paper is the morphology of *Xixiaichthys* and the phylogenetic position of *Xixiaichthys* in early and extant osteoglossomorphs. Only the characters that can also be found in fossils were included in the analysis. Although there are many more characters that have been considered for osteoglossomorphs available in published analyses (Li and Wilson, 1996a, 1996b; Hilton, 2003), some are not found in fossils, some not found in the taxa selected, and some even problematic (see criticisms in Hilton, 2003). Characters found in all the taxa selected (such as supraorbital bone absent) are not included in this analysis.

Characters of the ten Chinese fossil genera are mainly based on my observations supplemented by descriptions and figures in the following literature: Chang and Chou (1977), Gaudant (1965), Greenwood (1970), Liu et al. (1963, 1982), Ma (1987, 1993) and Zhang et al. (1994). Characters for *Hiodon*, *Notopterus* and *Osteoglossum* were coded from descriptions and illustrations in Arratia and Schultze (1991), Hilton (2002), Li and Wilson (1994), Ridwood (1904), Schultze and Arratia (1988) and Taverne (1977, 1978). The outgroup was coded based on Arratia (1987, 1991), Nybelin (1967, 1974), Patterson and Rosen (1977) and Taverne (1975, 1981).

SYSTEMATIC PALEONTOLOGY

Subdivision TELEOSTEI Müller, 1844
Superorder OSTEOGLOSSOMORPHA
Greenwood et al., 1966
Order OSTEOGLOSSIFORMES Berg, 1940
Family incertae sedis
Genus *XIXIAICHTHYS* gen. nov.

Type Species—*Xixiaichthys tongxinensis* gen. et sp. nov.

Etymology—*Xixia*, the ancient name of Ningxia Province; *ichthys*, Greek, means fish; *Tongxin*, Tongxin County, the fish locality.

Diagnosis—A genus differing from other genera of Osteoglossiformes in the following combination of characters: frontal narrowed anteriorly and broad posteriorly; parietal small, nearly rectangular in shape; temporal fenestra absent; supraorbital absent; mouth gape deep; articulation between quadrate and mandible behind posterior margin of orbit; premaxilla very short with only three teeth, of which one is exceptionally large; maxilla straight and long, extending to articulation between quadrate and mandible, with fine teeth on oral margin; supramaxilla absent; dentary strong, with large conical teeth on oral margin; 13 branchiostegals; posttemporal fork-like, with dorsal limb more than twice as long as ventral limb; pectoral fin low, with posterior end extending to origin of pelvic fin; pelvic fin small, located at midpoint between pectoral and anal fins; dorsal fin small, with origin slightly before that of anal fin; anal fin larger than dorsal fin; full neural spine on first preural centrum and first ural centrum present; 7 hypurals; hypural one large fused to first ural centrum at proximal end; hypural two small separated from ural centrum; epurals absent; 3 uroneurals; lateral line lying near dorsal margin of body.

XIXIAICHTHYS TONGXINENSIS sp. nov.
(Figs. 1–5)

Holotype—A complete specimen, right lateral view (Fig. 1). IVPP V13114.1.

Additional Material—A skull of the fish. IVPP V13114.2.

Horizon and Locality—Madongshan Formation, Early Cretaceous; Tongxin, Ningxia.

Diagnosis—Same as for the genus (monotypic).

Description

The body of the fish is fusiform (Fig. 1). The standard length of the holotype is 18.5 cm and the total length is 22.5 cm. The standard length of the body is 3.46 times of the depth and 4.09 times of the length of the head. The head length is 1.17 times of the head depth. The depth of the caudal peduncle is 1.17 times of the length. Specimen V13114.2 (Fig. 2) shows mainly the bones of the skull. The standard length of *Xixiaichthys* may reach 40 cm, based on comparison of the size of the skull bones preserved in V13114.2 with those in the complete specimen (V13114.1). Vertebrae 48 with 24 abdominals and 24 caudals; four proximal pectoral radials; pelvic bone rod-like; fourteen dorsal pterygiophores. Ray counts: pectoral fin, I+10; dorsal fin, I+14; pelvic fin, I+6; anal fin, 21, caudal fin, I+17+I.

Braincase—The skull roof is smooth (Fig. 3). The nasal (Fig. 3) bone is relatively large, with its posterior end only slightly narrower than the anterior end of the frontal. The two nasals are probably separated by the mesethmoid. The sensory canal on the nasal bone is relatively thick. The lateral ethmoid is small. The mesethmoid and the vomer were not shown in the specimens.

The frontal (Fig. 3) is large, with the anterior end only slightly narrower than the posterior end. The interfrontal suture is straight. The supraorbital sensory canal lies in the middle part of the frontal and extends to the nasal anteriorly and ends posteriorly within the parietal.

The parietal (Fig. 3) is relatively small and nearly rectangular in shape. The interparietal suture is straight. The pterotic (Fig. 3) is small. The temporal sensory canal passes along the lateral margin of the bone, with a branch near the posterior end of the bone through which the temporal and preopercular sensory canals joined. The suture between the pterotic and the parietal is relatively straight.

No temporal fenestra was found. The supraoccipital is only partially visible in specimen V13114.2 and the shape of the bone is unclear. One of the two bones between the pterotic and the parietal anteriorly and the posttemporal posteriorly is probably the epioccipital (V13114.1), but the shape of this bone is unclear. The bone postero-ventral to the pterotic is probably the extrascapular. The bone partially shown behind the upper head of the preopercle is possibly the exoccipital (V13114.1).

The parasphenoid (V13114.1) crosses the middle part of the orbit. Only one tooth can be seen on its ventral margin (Fig. 3). Three protuberances on the endopterygoid just behind the tooth show that three teeth of the parasphenoid are covered by the endopterygoid. It is unclear whether there are basisphenoid processes because the posterior part of the parasphenoid is covered. The basisphenoid is only partially shown. The pterosphenoid is sculptured and nearly square in shape. The anterior end of the bone is covered by the orbitosphenoid. The orbitosphenoid (V13114.1) is slightly larger than the pterosphenoid and is approximately square in shape.

Circumorbital Bones—The orbit is relatively large (Fig. 3). The circumorbital ring is likely composed of an antorbital, four infraorbitals and the dermosphenotic. The supraorbital bone is absent. The antorbital is comparatively large and strip-shaped. The first and second infraorbitals are strip-shaped, with the first longer than the second. The third infraorbital is large and quadrilateral. The fourth infraorbital is visible in V13114.1, but its shape is unclear. The dermosphenotic is not shown in the two specimens. The infraorbital canal runs along the orbital margin and has a branch pointing postero-ventrally in the midpoint of the canal on the third infraorbital.

Jaws—The mouth gape is large (Fig. 3). The joint between the jaw and quadrate is behind the orbit. The premaxilla (Fig. 4A) is relatively small, with a large ascending process at its antero-dorsal margin. There are three conical teeth on the oral margin of the bone, with one exceptionally strong and the other two small. The maxilla (Fig. 3) is long, straight, and relatively broad. The posterior end of the bone extends to the joint between the jaw and the quadrate, and the anterior end of the bone becomes pointed. Fine teeth are present on the oral margin of the bone, with 36 preserved in V13114.1; the total number is estimated to be about 45. The supramaxilla is absent. The dentary is strong, with large conical teeth (23 preserved in V13114.2) on the oral margin. The ventral margin of the bone is almost straight and the symphysis is relatively deep. The angular (Fig. 4C) is large and nearly triangular in shape. The retroarticular (Fig. 4C) lies postero-ventral to the angular and is not fused to the bone. The bone posterior to the angular, thick and covered in great measure by the angular, is probably the articular. All three of the posterior bones of the lower jaw are autogenous. The articulation facet of the mandible to the quadrate is composed of the angular and the articular; whether or not the retroarticular is included is unclear due to preservation. The mandibular sensory canal exits the preopercular, enters the angular, and then runs within the

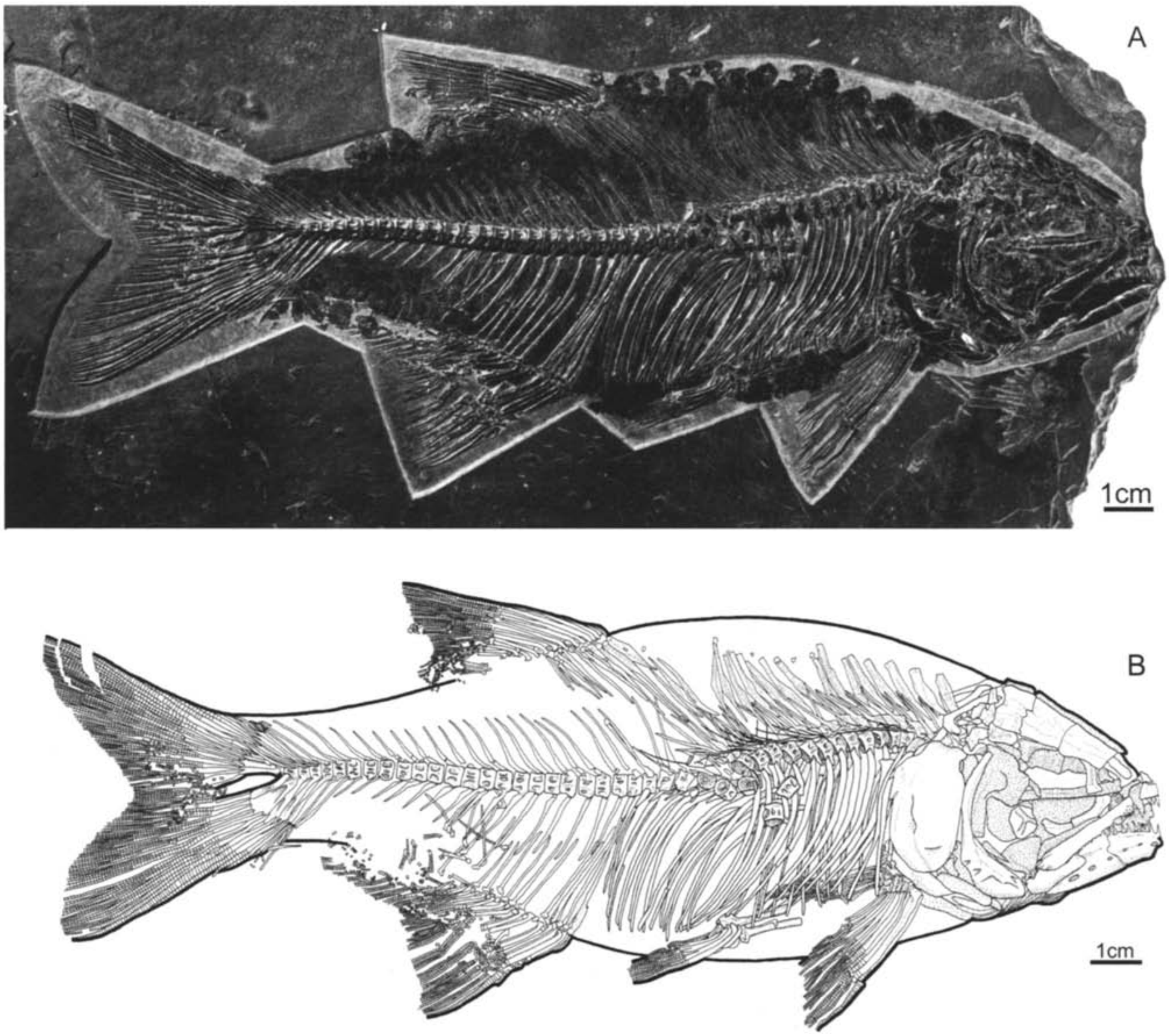

FIGURE 1. *Xixiaichthys tongxinensis* gen. et sp. nov. A complete fish (V 13114.1) in right lateral view; **A**, photograph; **B**, line drawing.

middle part of the dentary, opening through seven pores on the dentary.

Palato-quadrate Arch—Most of the dermopalatine (Fig. 3) is covered by the maxilla. Fine teeth are present on the dermopalatine. The ectopterygoid (Fig. 4D) is rod-like, with its anterior end pointed and the posterior end curved downwards. The postero-dorsal margin of the bone is grooved to receive the quadrate. The ventral margin bears 17 small teeth (Fig. 4D). The endopterygoid is nearly triangular with its anterior part smooth and posterior part sculptured. It is difficult to determine if the teeth are present on the internal surface of the bone due to the preservation. The metapterygoid is relatively large and is roughly semicircular. The dorsal margin is concave. The quadrate (Fig. 5A) is fan-shaped.

Hyoid Arch, Branchiostegals and Gill Arches—The hyomandibula (V13114.1) is slightly inclined forwards, with a thin, broad wing anteriorly and a narrow wing posteriorly. The bone articulates with the cranium by a single head. Below the head (V13114.2), there is a relatively large opening, probably for the mandibular branch of the hyomandibular nerve. The symplectic is a small rod-like bone that is narrow anteriorly. The bone articulates with the quadrate anteriorly and the hyomandibula posteriorly. The anterior ceratohyal (Fig. 4D) is nearly hour-glass shaped. The anterior part is small and sculptured and the posterior part large. The posterior ceratohyal (Fig. 4D) is semicircular and tightly sutured to the anterior ceratohyal. Two sculptured hypohyals are present and lie anterior to the posterior ceratohyal. The foramen for the afferent hyoidean artery is not visible. The urohyal was not observed. The bone with strong teeth that is preserved below the dentary in V13114.2 is possibly the basihyal. There are 13 branchiostegals (Fig. 3). The posterior three are broad while the anterior ones are thin and hair-like. No gular plate was found. The gill arch skeleton is only partially shown in V13114.2; no details can be described.

Opercular Series—The opercle is large and elliptical. The depth/width ratio of the bone is 1.8. The anterior margin of the opercle is arc-shaped in V13114.1 but relatively straight in V13114.2. The vertical limb of the preopercle (Fig. 3) is long and narrow, and is only slightly broader than its sensory canal. The horizontal limb of the bone is short and broad. The angle between the two limbs is about 120 degrees. The preopercular sensory canal runs along the dorsal margin of the horizontal limb

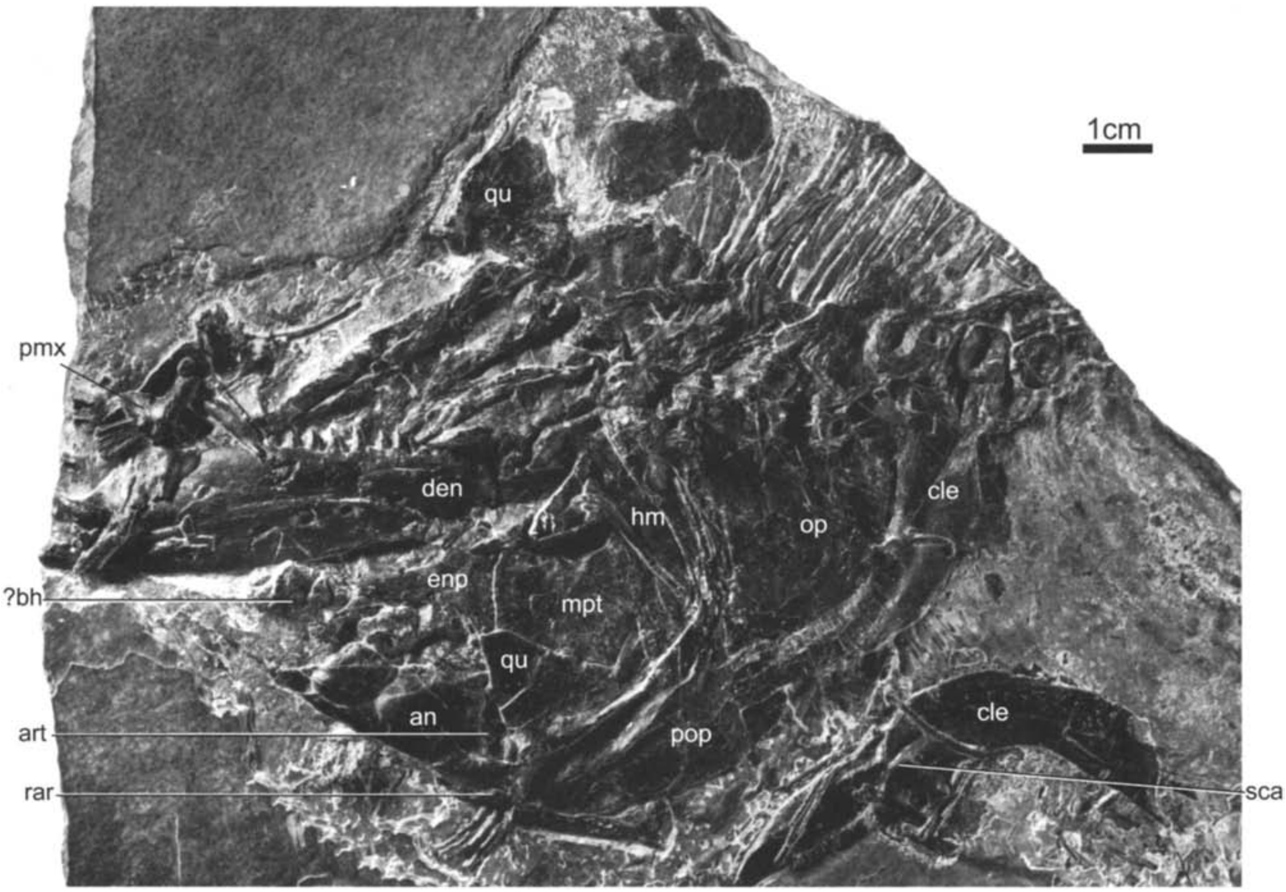

FIGURE 2. *Xixiaichthys tongxinensis* gen. et sp. nov. Skull as preserved in V 13114.2, left lateral view. **Abbreviations: an**, angular; **art**, aricular; **bh**, basihyal; **cle**, cleithrum; **den**, dentary; **enp**, endopterygoid; **hm**, hyomandibula; **mpt**, metapterygoid; **op**, opercle; **pmx**, premaxilla; **pop**, preopercle; **qu**, quadrate; **rar**, retroarticular; **sca**, scapula.

and has four branches. The subopercle is not preserved. A strip-like bone postero-ventral to the preopercle in V13114.1 is probably the interopercle.

Pectoral Girdle and Fin—The posttemporal (Fig. 3) is forked, and its dorsal limb is nearly two and a half times as long as the ventral limb. The lateral line runs on the ventral limb of the bone. The supracleithrum (Fig. 3) is rod-like. The cleithrum (Fig. 5B) is curved, with the vertical arm longer than the horizontal arm. The postcleithrum is not visible. The scapula (Fig. 5B) has a large scapular foramen, with two processes and two grooves on its posterior margin. The coracoid, partially shown in V13114.1, has a straight ventral margin.

Four proximal pectoral radials can be recognized. The first one is relatively short and broad and the others are long and thin. The pectoral fin is low and long, reaching the origin of the pelvic fin. The fin contains eleven rays, all branched except the first one which is not obviously enlarged.

Pelvic Girdle and Fin—The pelvic girdle is small (V13114.1). The origin of the pelvic fin is at the midpoint between the origin of the pectoral fin and that of the anal fin. The pelvic bone is rod-like with its posterior end enlarged. A small, rounded radial is visible. The pelvic fin rays are seven in number and are segmented and branched except the first, which is only segmented.

Dorsal and Anal Fin—The dorsal fin is small and originates slightly anterior to the origin of the anal fin. The fin is composed of about 15 principal fin rays, all branched except the first. There are five short rays anterior to the principal rays. About 14 pterygiophores support the fin rays. The first one is short, broad, and spearhead shaped. The second is the longest and the others gradually become shorter. Some distal radials are visible but their shape is unclear.

The anal fin is larger than the dorsal fin. There are approximately 22 principal rays, all of which are segmented and all but the first branched. Four short rays are present anterior to the principal rays. The 21 pterygiophores of the fin are composed of proximal, middle, and distal radials. The middle radials are short and shaft-like while the distal ones are spherical.

Vertebral Column—There are 48 vertebrae, of which 24 are caudals. Each centrum is well ossified and pierced by a small opening for the notochord. Some longitudinal ridges are present on the lateral surfaces of the centra. The parapophyses are relatively large and fused to the centra. The neural arches anterior to the dorsal fin are autogenous and paired. There are 22 pairs of ribs. The last pair is relatively short. It is unclear if the first two centra have ribs. The haemal arches are fused to the centra. The most posterior haemal spines are expanded to support the caudal fin rays. The epineurals are long and fine with their proximal ends fused to the bases of the neural arches. The 19 supraneurals are slightly broader anteriorly and narrower posteriorly.

Caudal Skeleton and Fin—Five neural and haemal spines are lengthened to support the caudal fin-rays and gradually thickened posteriorly (Fig. 5C). The first preural centrum bears a complete neural spine. The "first" ural centrum (U1+2) is slightly longer than the first preural centrum and has a complete neural spine. The "second" ural centrum is small and triangular in shape.

There are seven hypurals. Hypural 1 is large and fused to the "first" ural centrum proximally. Hypural 2 is only half the width

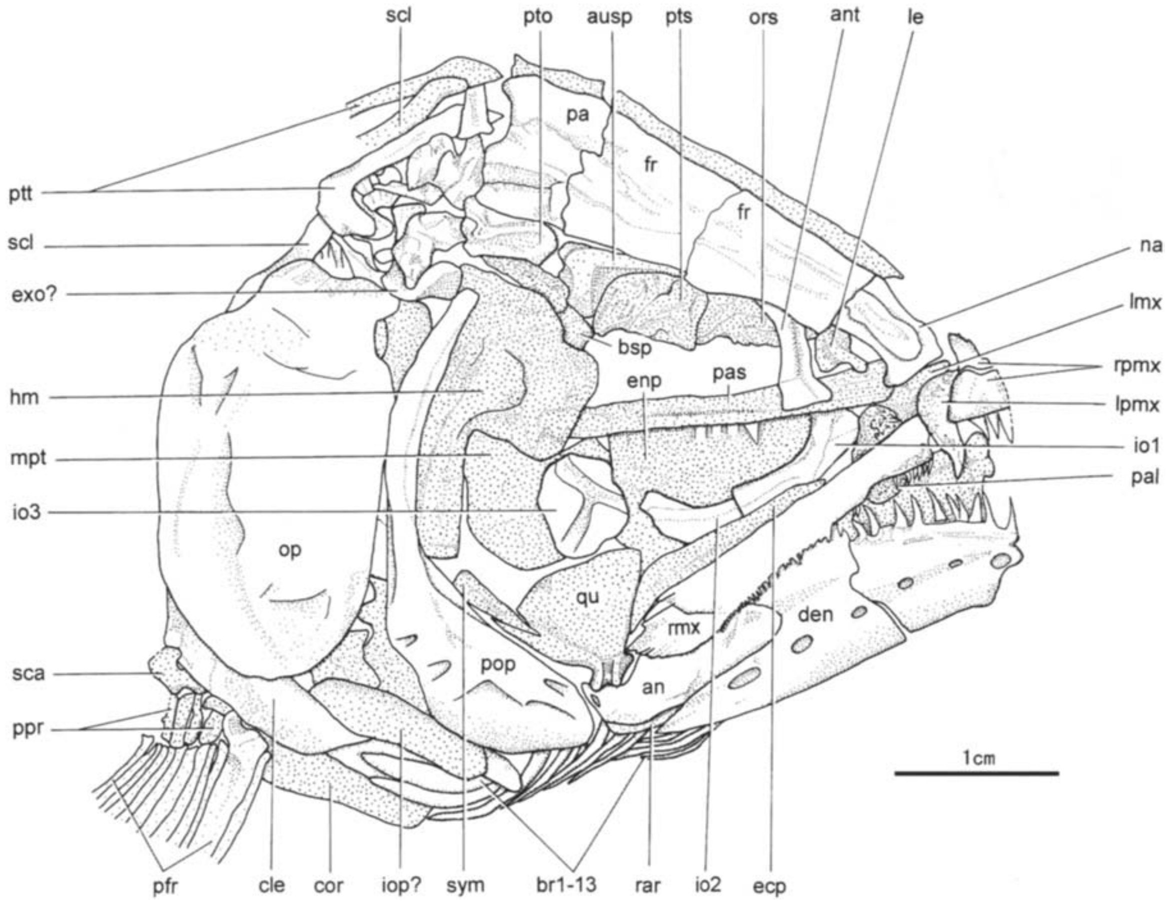

FIGURE 3. *Xixiaichthys tongxinensis* gen. et sp. nov. Skull as preserved in V 13114.1, right lateral view. **Abbreviations: an**, angular; **ant**, antorbital; **ausp**, autosphenotic; **br1-13**, branchiostegals1-13; **cle**, cleithrum; **cor**, coracoid; **den**, dentary; **ecp**, ectopterygoid; **enp**, endopterygoid; **exo**, exoccipital; **fr**, frontal; **hm**, hyomandibula; **io1-3**, first to third infraorbitals; **iop**, interopercle; **le**, lateral ethmoid; **lpmx**, left premaxilla; **mpt**, metapterygoid; **mx**, maxilla; **na**, nasal; **op**, opercle; **ors**, orbitosphenoid; **pa**, parietal; **pal**, dermopalatine; **pas**, parasphenoid; **pfr**, pectoral fin rays; **pop**, preopercle; **ppr**, proximal pectoral radials; **pto**, pterotic; **pts**, pterosphenoid; **ptt**, posttemporal; **qu**, quadrate; **rar**, retroarticular; **rpxm**, right premaxilla; **sca**, scapula; **scl**, supracleithrum; **sym**, symplectic.

of the first and is not fused to the centrum. Hypurals 3–4 articulate with the "second" ural centrum. Hypurals 5–7 are free.

The epural is absent. Uroneurals are 3 in number, with the first extending to the anterior margin of the second preural centrum and the second to the anterior margin of the first preural centrum. The anterior tip of the third uroneural is on the lateral side of the "first" ural centrum.

The caudal fin (V13114.1) is deeply forked and has 19 principal caudal rays (10 in the upper lobe, nine in the lower). There are 13 and 11 procurrent rays on the upper and lower lobes respectively, of which the longer ones are segmented distally.

Squamation—The cycloid scales are round, thin, and have circuli around the focus; 3–4 radii are present in the posterior field of some scales. No scales cover the skull or the bases of the fins.

COMPARISONS AND DISCUSSION

Xixiaichthys has a primary bite between parasphenoid and basihyal, a full neural spine on the first preural centrum, and no supraorbital. These features are supposed to be synapomorphies of Osteoglossomorpha (Greenwood et al., 1966; Patterson and Rosen, 1977; Li and Wilson, 1996a; although see Hilton, 2001). Therefore, this fish can be assigned to the superorder. Among the early osteoglossomorphs, at first sight this fish is resembles *Jiuquanichthys* and *Jiaohichthys* also from the Early Cretaceous of China in having an elongate jaw and strong oral teeth. However, *Xixiaichthys* is different from the two genera mentioned above in that it has a very short premaxilla with only three teeth, of which one is exceptionally large. Such a premaxilla is unique among the early osteoglossomorphs. Furthermore, a temporal fenestra is present in *Jiuquanichthys* and *Jiaohichthys* but absent in *Xixiaichthys*.

Xixiaichthys probably has an autogenous articular. The three posterior lower jaw bones (articular, retroarticular, and angular) of the fish are separate. This condition, seen only in *Arapaima*, *Heterotis*, and *Phareodus* (Patterson and Rosen, 1977), may pull *Xixiaichthys* further into Osteoglossiformes. Both the articular and retroarticular of *Arapaima*, *Heterotis*, and *Phareodus* contribute to the joint surface for the quadrate, but whether the retroarticular of *Xixiaichthys* is included in the joint surface is unclear due to the preservation.

The principal caudal rays are usually 18 in basal osteoglossomorphs, but 19 in *Xixiaichthys*. The number of principal caudal fays may be an important feature at a variety of taxonomic levels within teleosts. The evolutionary trend in teleosts is to reduce the number of principal caudal rays. *Pholidophorus* has 22 to 24 principal rays, while *Protoclupea* and *Luisichthys* have 20, *Anaethalion*, *Leptolepides*, *Diplomystus*, and many extant teleosts have 19 (Schultze and Arratia, 1989). That the caudal fin contains 18 principal fin rays was proposed as a synapomorphy of

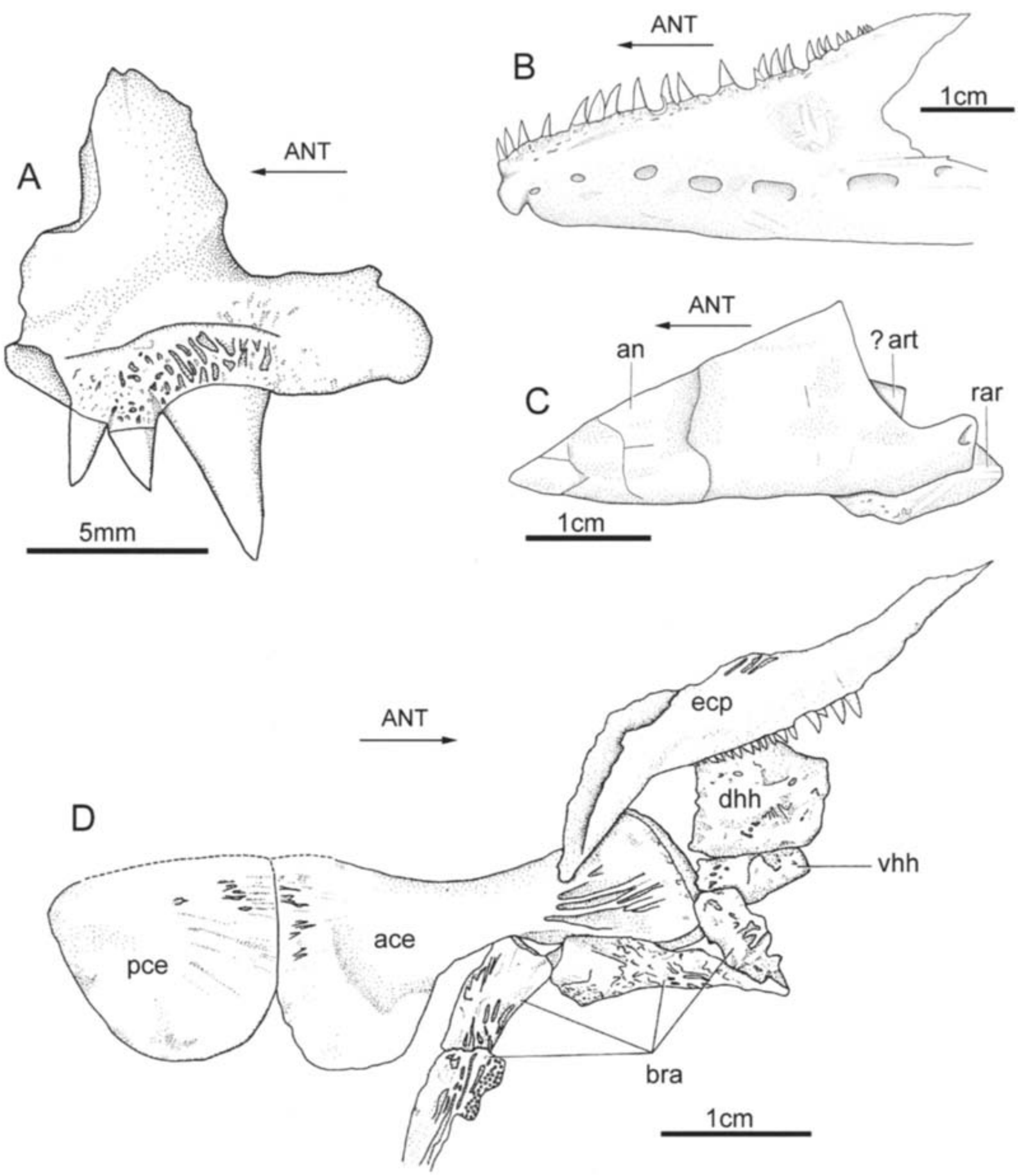

FIGURE 4. *Xixiaichthys tongxinensis* gen. et sp. nov. **Abbreviations: ANT**, anterior; **A**, premaxilla, V 13114.1, in left lateral view; **B**, dentary, V 13114.2, in left lateral view; **C**, angular (**an**), articular (**art**) and retroarticular (**rar**), V 13114.2, in left lateral view; **D**, ectopterygoid (**ecp**), anterior ceratohyal (**ace**), posterior ceratohyal (**pce**), dorsal hypohyal (**dhh**) and ventral hypohyal (**vhh**) and some segments of branchial skeleton (**bra**), V 13114.2, in right lateral view.

Osteoglossomorpha by Patterson and Rosen (1977). Schultze and Arratia (1988) argued that 18 principal rays is not useful as a feature to define the Hiodontidae or higher units of Osteoglossomorpha because they found that seven of the 16 counted *Hiodon* specimens have 18 principal caudal rays. One specimen had only 14, while two specimens had 19, and six specimens had 20 principal rays. Shen et al. (1991) found that having 18 principal caudal fin rays is not unique to osteoglossomorphs but also seen in other teleosts. Moreover, not all the osteoglossomorphs have 18 principal caudal fin rays. Therefore, Shen et al. (1991) determined that this feature could not be a defining character of Osteoglossomorpha. In some individuals of *Lycoptera*, *Jiuquanichthys*, and *Qilianichthys*, the principal caudal fin rays are 19. This fact demonstrates that having 19 principal caudal fin rays is not unusual in osteoglossomorphs and that the number of 18 principal caudal rays does not define Osteoglossomorpha.

An epural is absent in the new fish studied. "Number of epurals decreased to one or zero" was suggested as a synapomorphy of Osteoglossomorpha by Li and Wilson (1996a). One epural is present in many early osteoglossomorphs such as *Lycoptera*, *Jiuquanichthys*, *Jinanichthys*, and *Tongxinichthys*, but two in *Qilianichthys* of the Early Cretaceous of China (Kuyangichthyidae, Osteoglossomorpha; Ma, 1993). The bone is missing in some relatively derived early osteoglossomorphs such as *Huashia* and *Kuntulunia* and all extant osteoglossomorphs except *Hiodon* (Schultze and Arratia, 1988). The absence of epurals in *Xixiaichthys* indicates that the fish is derived relative to other Early Cretaceous osteoglossomorphs.

The new fish has an unusual caudal skeleton, in which hypural 1 is fused to the first ural centrum (U1+2) while hypural 2 is separated. The number of hypurals is gradually decreased in the evolution of teleosts. *Pholidophorus* has 12–13 hypurals, while *Leptolepis coryphaenoides* and *Leptolepides sprattiformis* have nine. Generally, osteoglossomorph fishes have six hypurals, but

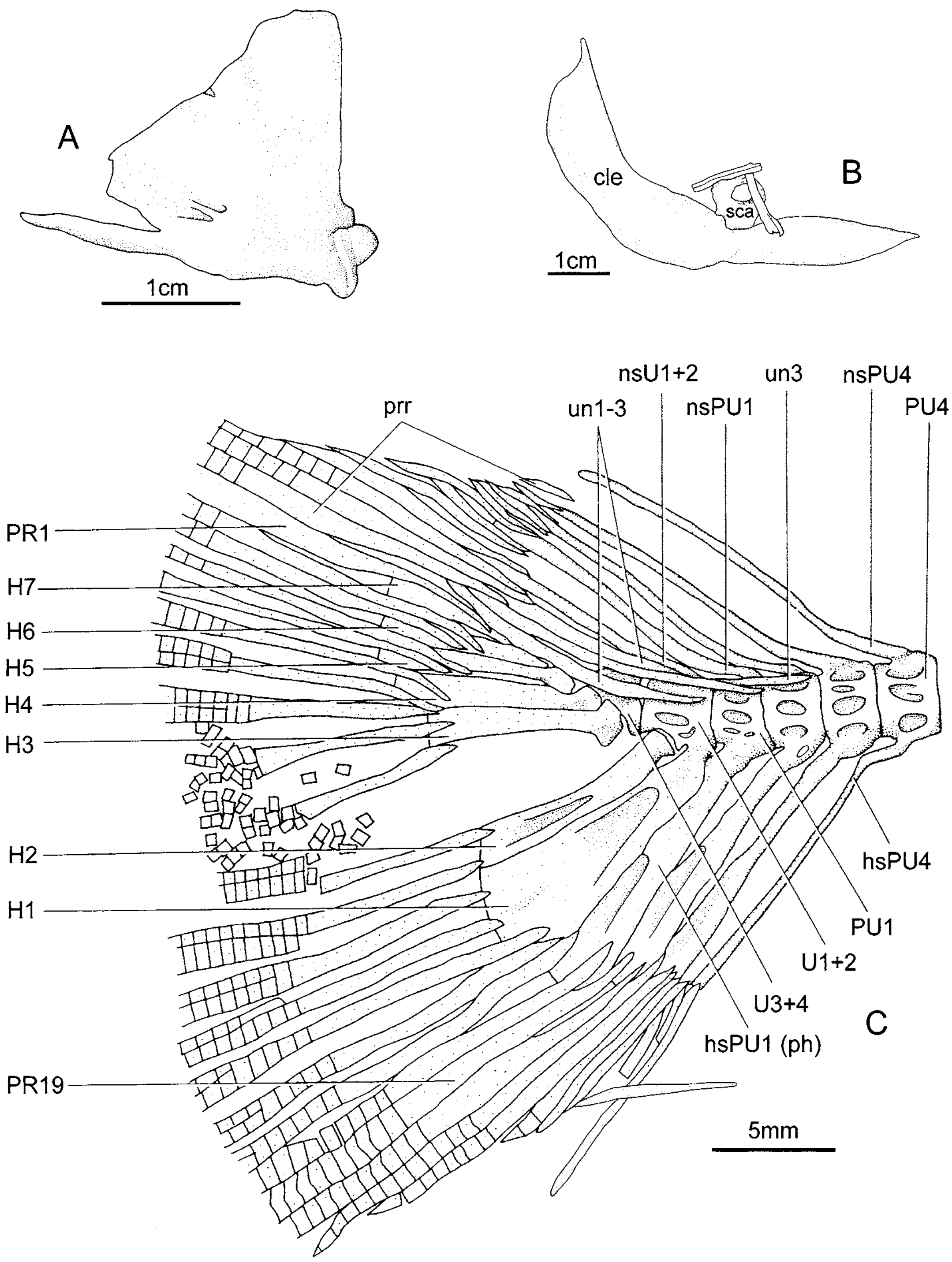

FIGURE 5. *Xixiaichthys tongxinensis* gen. et sp. nov. **A**, quadrate, V 13114.1; **B**, cleithrum (**cle**) and scapula (**sca**), V 13114.1; **C**, caudal skeleton, V 13114.1. **Abbreviations: H1–7**, hypurals1-7; **ph**, parhypural; **hsPU4**, haemal spines on PU4; **nsPU1, 4**, neural spines on PU1, 4; **nsU1+2**, neural spine on U1+2; **PR1**, first principal caudal ray; **PR19**, lowermost principal caudal ray; **prr**, procurrent rays; **PU1, 4**, preural vertebrae 1, 4; **U1+2**, ural centra 1+2; **U3+4**, ural centra 3+4; **un1-3**, uroneurals1–3.

in *Hiodon* and *Jinanichthys*, this number could be eight. Schultze and Arratia (1988) noted that eight hypurals are present in small specimens of *Hiodon*, but Hilton (2002) found only seven hupurals in both species of *Hiodon*, even in small specimens. In basal teleosts, both hypural 1 and hypural 2 may be separated from the first ural centrum, as in *Pingolepis* (Chang and Chou, 1977), *Tharsis dubius* (Arratia, 1991), *Pachythrissops*, and *Allothrissops mesogaster* (Arratia, 2000), or both hypurals are fused to the first ural centrum, as in *Domeykos profetaensis* (Arratia, 1997), *Leptolepis coryphaenoides* (Arratia, 1991), *Ascalabothrissops voelkli*, and *Elopsomolos frickhingeri* (Arratia, 2000). In a few cases, only hypural 2 is fused to the first ural centrum as in *Paraclupea chetungensis* (Chang and Grande, 1997), *Luisichthys vinalesensis* (Arratia, 1997), and *Allothrissops sp.* (Arratia, 2000). Hypural 1 and hypural 2 are not fused to the first ural centrum in most osteoglossomorphs except for perhaps the large individuals of *Hiodon* (Schultze and Arratia, 1988) and *Kuntulunia* (Zhang, 1998), in which they are both fused. That hypural

1 is fused while hypural 2 is separated from the first ural centrum in *Xixiaichthys* is probably a unique caudal skeletal pattern in Osteoglossomorpha.

Xixiaichthys tongxinensis has a large mouth gape, a strong lower jaw, and huge conical teeth on the dentary, premaxilla, and parasphenoid, indicating a possible carnivorous habit. *Kuntulunia*, a fish found in the same stratum, is probably its prey. *Xixiaichthys* may reach 40 cm in standard length, but *Kuntulunia* is only 15 cm long in the largest specimen. The two fishes are fusiform and have terminal mouths, indicating that they were possibly swimming in the middle or upper layers of water. *Kuntulunia*, with a short mouth gape and fine teeth on its oral margin, mainly ate small insects and plankton. Among the more than one hundred specimens of fishes found in the locality, only two represent *Xixiaichthys* and all others represent *Kuntulunia*. The rarity of *Xixiaichthys* in the locality is probably due to the preservation or the fact that the fish was a solitary swimmer in open water.

PHYLOGENETIC RELATIONSHIPS OF *XIXIAICHTHYS*

The cladistic analysis includes 13 fossil and Recent Osteoglossomorphs and is based on 27 morphological characters listed in Appendix 1. For character states see Appendix 2. Six shortest trees were found (45 steps; consistency index CI = 0.644). The cladogram shown in Figure 6 represents the strict consensus tree of the six equally parsimonious trees.

The consensus tree shows that the relationships among *Tongxinichthys*, *Lycoptera*, *Jiuquanichthys*, and the clade including all other osteoglossomorphs are unresolved (node A). This node is supported by two uniquely derived characters (full neural spine on preural centrum 1, i.e., close to or reaching dorsal margin of body: 20[1]; one epural: 22[1]) and five homoplasies (temporal fenestra present: 4[1]; retroarticular excluded from articular facet for quadrate: 9[1]; opercle oval or somewhat kidney-shaped: 12[1]; three or four of ural neural arches modified as uroneurals: 23[1]; and "urodermals" absent: 26[1]). *Jiuquanichthys* and *Tongxinichthys* are sister groups in three trees, as supported by two homoplasies (supraoccipital with long, narrow process on its anterior margin: 3[1] and retroarticular excluded from articular facet for quadrate: 9[1]). In the other three trees, *Jiuquanichthys*, *Tongxinichthys*, and *Lycoptera* are all stem-group osteoglossomorphs.

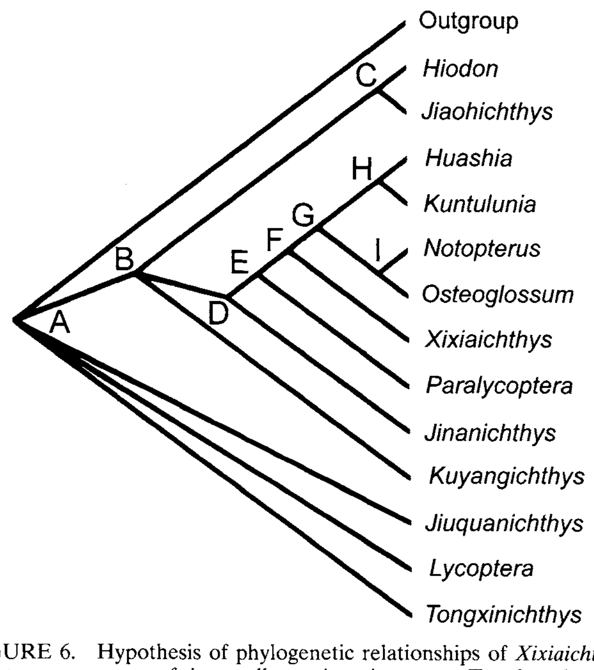

FIGURE 6. Hypothesis of phylogenetic relationships of *Xixiaichthys*. Strict consensus tree of six equally parsimonious trees. Tree length = 45. Consistency index (CI) = 0.644. For explanation of characters see Appendix 1. Data matrix provided in Appendix 2. Uniquely derived characters are indicated with an asterisk (*). Node A: 4[1], 9[1], 12[1], 20[1]*, 22[1]*, 23[1], 26[1]. Node B: 5[1], 6[1]*. Node C: 8[1], 12[0]. Node D: 9[1], 13[1]*, 17[0]. Node E: 4[0]. Node F: 8[1], 22[2]*. Node G: 11[1]*. Node H: 1[1], 10[1], 18[1]. Node I: 2[1]*, 12[0], 16[1]*, 19[1]*, 23[2], 24[1]*, 25[1].

Node B is a trichotomy among *Kuyangichthys*, the clade [*Hiodon* + *Jiaohichthys*] and the clade [*Jinanichthys* + [*Paralycoptera* + [*Xixiaichthys* + [[*Notopterus* + *Osteoglossum*] +[*Huashia* + *Kuntulunia*]]]]]. This node is supported by one uniquely derived character (five infraorbital bones: 6[1]) and one homoplasy (large posteroventral infraorbital bone representing third and fourth infraorbitals of other teleosts: 5[1]). It is the position of *Kuyangichthys* that varies in different trees. In one tree, it is the sister group of [*Jinanichthys* + [*Paralycoptera* + [*Xixiaichthys* + [[*Notopterus* + *Osteoglossum*] +[*Huashia* + *Kuntulunia*]]]]]; in the other two trees it is a sister group of [*Hiodon* + *Jiaohichthys*], while in the two remaining trees, it is a stem group of osteoglossomorphs.

Node C corresponds to the clade [*Hiodon* + *Jiaohichthys*]. This node is supported by two homoplasies (supramaxilla absent: 8[1] and opercle not oval or somewhat kidney-shaped: 12[0]).

Node D represents the branch leading to *Jinanichthys* and the clade [*Paralycoptera* + [*Xixiaichthys* + [[*Notopterus* + *Osteoglossum*] +[*Huashia* + *Kuntulunia*]]]] and is characterized by one uniquely derived character (subopercle missing or atrophied, lying below anteroventral corner of opercle: 13[1]) and two homoplasies (retroarticular excluded from articular facet for quadrate: 9[1] and dorsal arm of posttemporal less than 1½ times as long as ventral arm: 17[0]). However, this character was coded as unknown in *Xixiaichthys* because the subopercle of the fish is not preserved.

Node E represents *Paralycoptera* and the clade [*Xixiaichthys* + [[*Notopterus* + *Osteoglossum*] +[*Huashia* + *Kuntulunia*]]]. This node is supported by only one homoplasy (temporal fenestra absent: 4[0]).

Node F corresponds the sister group relationship between *Xixiaichthys* and the clade [[*Notopterus* + *Osteoglossum*] +[*Huashia* + *Kuntulunia*]]. The node is characterized by one uniquely derived character (epural absent: 22[2]) and one homoplasy (supramaxilla absent: 8[1]).

Node G represents the clades [*Notopterus* + *Osteoglossum*] and [*Huashia* + *Kuntulunia*]. This node is supported by one uniquely derived character (preopercular sensory canal on lower limb of preopercle expanded as raised area with several foramina opening ventro-laterally: 11[1]).

Node H represents the clade [*Huashia* + *Kuntulunia*] and is supported by three homoplasies (frontal short and broad, not narrowed anteriorly: 1[1]; length of lower limb of preopercle nearly as long as upper limb: 10[1]; and anterior supraneurals expanded: 18[1]).

Node I corresponds to the clade [*Notopterus* + *Osteoglossum*] and is characterized by four uniquely derived characters (nasals contacting each other: 2[1]; supratemporal commissural sensory canal passing through parietals or through parietals and supraoccipital: 16[1]; neural arches of most abdominal vertebrae with fused halves of neural arch forming median neural spine: 19[1]; and less than two uroneurals extending forward beyond "second" ural centrum: 24[1]) and three homoplasies (opercle not oval or somewhat kidney-shaped: 12[0]; two or fewer ural neural arches modified as uroneurals: 23[2]; and six or fewer hypurals in adult individuals: 25[1]).

In conclusion, the results of the phylogenetic analysis show that *Xixiaichthys* has the same position in all six trees as the sister group of Osteoglossiformes ([[*Notopterus* + *Osteoglossum*] +[*Huashia* + *Kuntulunia*]]). This sister-group relationship is characterized by one uniquely derived character and one homoplasy.

Therefore, the new genus is assigned to Osteoglossiformes. It is more derived than most osteoglossomorphs from the Early Cretaceous; only *Kuntulunia* and *Huashia* are more derived.

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APPENDIX 1

List of character transformation series.

1. Frontal: 0 = long and narrowed anteriorly; 1 = short and broad, not narrowed anteriorly.
2. Relationship between nasals (modified from Li and Wilson, 1996b): 0 = separated by mesethmoid; 1 = contacting each other; 2 = contacting posteriorly.
3. Supraoccipital with long, narrow process on its anterior margin: 0 = absent; 1 = present.
4. Temporal fenestra: 0 = absent; 1 = present.
5. Large posteroventral infraorbital bone representing third and fourth infraorbitals of other teleosts (Nelson, 1969; Patterson and Rosen, 1977): 0 = absent; 1 = present.
6. Number of infraorbital bones including first infraorbital to dermosphenotic (Nelson, 1969): 0 = six or more; 1 = five.
7. Pterygo-quadrate area behind and below orbit (Li and Wilson, 1996a): 0 = not completely covered by infraorbitals; 1 = completely covered by infraorbitals.
8. Supramaxilla: 0 = present; 1 = absent.
9. Retroarticular (Nelson 1973, Patterson and Rosen, 1977): 0 = included in articular facet for quadrate; 1 = excluded from articular facet for quadrate.
10. Length of lower limb of preopercle: 0 = shorter than upper limb; 1 = nearly as long as upper limb.
11. Preopercular sensory canal on lower limb of preopercle expanded as raised area with several foramina opening ventrolaterally. 0 = absent; 1 = present.
12. Opercle oval or somewhat kidney-shaped (modified from Li and Wilson, 1996a): 0 = absent; 1 = present.
13. Subopercle: 0 = lies below opercle; 1 = missing or atrophied, lying below anteroventral corner of opercle.
14. Orbitosphenoid (Fink and Fink, 1981): 0 = present; 1 = absent.
15. Heads of hyomandibula articulating with cranium (modified from Li and Wilson, 1994): 0 = one; 1 = two, bridged.
16. Supratemporal commissural sensory canal passing through parietals or through parietals and supraoccipital (Grande, 1985). 0 = Absent; 1 = Present.
17. Dorsal arm of posttemporal (modified from Li and Wilson, 1994): 0 = less than 1½ times as long as ventral arm; 1 = more than 1½ times as long as ventral arm.
18. Anterior supraneurals: 0 = slender; 1 = expanded.
19. Neural arches of most abdominal vertebrae (modified from Arratia, 1996): 0 = with separate halves of neural arch; 1 = with fused halves of neural arch forming median neural spine.
20. Neural spine of preural centrum 1 (Arratia, 1991): 0 = rudimentary or short; 1 = long, close to, or reaching dorsal margin of body.
21. Neural spine of first ural centrum (U1+2) (Arratia, 1991): 0 = present; 1 = absent.
22. Number of epurals (Greenwood, 1970): 0 = three or more; 1 = one; 2 = none.
23. Number of ural neural arches modified as uroneurals (modified from Arratia, 1991): 0 = five or more; 1 = four or three; 2 = two or fewer. The number of uroneurals is fewer than five in some species of *Anaethalion*, but five in *Anaethalion* cf. *A. subovatus* (Arratia, 1996), and probably more than five in *A. angustus* (Arratia, 1987). The other three taxa of the outgroup have five or more. Therefore, the presence of four or fewer uroneurals is considered apomorphic.
24. Two or more uroneurals extending forward beyond "second" ural centrum (modified from Patterson and Rosen, 1977): 0 = present; 1 = absent.
25. Number of hypurals in adult individuals (modified from Arratia, 1996): 0 = seven or more; 1 = six or less.
26. "urodermals" (modified from Arratia, 1996): 0 = present ; 1 = absent.
27. Scales: 0 = not reticulate; 1 = reticulate.

APPENDIX 2

Data matrix of 27 morphological characters for 13 genera of fossil and extant teleosts. 0, plesiomorphic character state, 1-2, apomorphic character states; ?, unclear owing to preservation of the specimens or not applicable. Outgroup consisted of *Allothrissops*, *Anaethalion*, *Leptolepides* and *Tharsis*.

		1	11111	11112	22222	22
	12345	67890	12345	67890	12345	67
Outgroup	00?00	00000	0000?	0?000	00000	00
Hiodon	00011	10100	00001	01001	01100	10
Huashia	10101	10111	?1100	00101	02100	10
Jinanichthys	00?11	10011	01100	00001	01?00	10
Jiuquanichthys	00110	00110	01000	01001	01100	00
Kuntulunia	10001	10111	11100	00101	02100	10
Kuyangichthys	00??1	?00?0	01000	01101	??100	10
Lycoptera	00010	000?0	01000	01001	01000	10
Notopterus	01000	10110	10100	10011	02211	10
Osteoglossum	01001	11110	10110	10011	02211	11
Paralycoptera	0??01	?10?0	01100	00001	??101	10
Tongxinichthys	00110	?0010	01000	01001	01100	10
Xixiaichthys	00000	10110	01?00	01001	02100	10
Jiaohichthys	10???	?01?0	0000?	01001	11100	10