First complete fossil Scleropages (Osteoglossomorpha) postprint

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Abstract

A new species of osteoglossid fish, Scleropages sinensis sp. nov., is described from the Early Eocene Xiwanpu Formation in Hunan and the Yangxi Formation in Hubei, China. The new species was attributed to Scleropages, an extant genus of Osteoglossidae, because it very closely resembles the genus in skull bones, caudal skeleton, the shape and position of fins, and reticulate scales. The new fish is very similar to extant Scleropages except: the nasals do not appear to be ornamented; the sensory pore in the antorbital is large; the posterior infraorbitals are not quite covering the dorsal limb of the preopercle; the posteroventral angle of the preopercle is produced to point; the posteroventral margin of the opercle is concave and the ventral end of the bone is produced to a point; the pectoral fin is very long and extends well behind the beginning of the pelvic fin; the vertebral count is about 46?8; the parapophyses are shorter and the upper and lower caudal rays are nearly as long as the inner rays. The new fish is closer to its Asian neighbor, S. formosus, than to its southern relative, S. leichardti. Scleropages formosus inhabits natural lakes, swamps, flooded forests, and slowly moving, deep parts of rivers with overhanging vegetative cover. It is a carnivorous fish and its food consists mainly of insects, fishes, worms, small amphibians, small mammals, and even birds. S. sinensis may live in the same natural environment and have a similar diet except for the largest items. Sexual dimorphism may exist in S. sinensis. The presumed male has a slimmer and shallower body, a relatively larger head, and a deeper mouth cleft. The discovery of Scleropages sinensis sp. nov. dates the divergence of Scleropages and Osteoglossum to no later than the Early Eocene.

Fossil scales and bone fragments of Scleropages have been reported previously, but their identification was not entirely reliable because these elements are very similar among osteoglossid fishes. Perfectly preserved Scleropages fossils are described here for the first time; specimens were collected from the Xiwanpu Formation in Xiangxiang, Hunan and the Yangxi Formation in Songzi, Hubei, and are established as a new species of the genus Scleropages in the family Osteoglossidae: Scleropages sinensis sp. nov. The new species is extremely similar to extant Scleropages in skull bones, caudal skeleton, the shape and position of fins, and reticulate scales, and is therefore assigned to this genus. However, the new species differs from extant species of Scleropages in the following characters: the nasals lack ornamentation; the sensory canal on the nasals is exposed in a groove; the sensory canal commissure does not pass through the parietal; the pterotic is laterally thickened; the sensory pore on the antorbital is large; the postorbital infraorbitals do not completely cover the dorsal limb of the preopercle, with a width-to-height ratio of 0.75 rather than 1?.2 in extant species; the posteroventral angle of the preopercle is pointed; the posteroventral margin of the opercle is concave with the ventral end pointed; the dorsal process of the cleithrum is elongated; the vertebral count is 46?8; the parapophyses are short; the pectoral fin is very elongated; and the upper and lower caudal fin rays are nearly as long as the inner rays. Extant Asian species are found in various rivers and streams, preferring still-water environments with lush aquatic vegetation, generally swimming in surface waters and feeding on fish, shrimp, insects, and other small organisms; the new species Scleropages sinensis likely had a similar habitat and diet. The new species appears to exhibit sexual dimorphism, with males having a slightly more slender body, relatively larger head, and deeper mouth cleft. The discovery of Scleropages sinensis fossils demonstrates that the genera Scleropages and Osteoglossum had already diverged before the Early Eocene, which is of great significance for explaining the transoceanic distribution of osteoglossid fishes.

Full Text

Preamble

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First Complete Fossil Scleropages (Osteoglossomorpha)

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Abstract

A new species of osteoglossid fish, *Scleropages sinensis* sp. nov., is described from the Early Eocene Xiwanpu Formation in Hunan and the Yangxi Formation in Hubei, China. The new species was attributed to *Scleropages*, an extant genus of Osteoglossidae, because it very closely resembles the genus in skull bones, caudal skeleton, the shape and position of fins, and reticulate scales. The new fish is very similar to extant *Scleropages* except: the nasals do not appear to be ornamented; the sensory pore in the antorbital is large; the posterior infraorbitals are not quite covering the dorsal limb of the preopercle; the posteroventral angle of the preopercle is produced to a point; the posteroventral margin of the opercle is concave and the ventral end of the bone is produced to a point; the pectoral fin is very long and extends well behind the beginning of the pelvic fin; the vertebral count is about 46–48; the parapophyses are shorter and the upper and lower caudal rays are nearly as long as the inner rays. The new fish is closer to its Asian neighbor, *S. formosus*, than to its southern relative, *S. leichardti*. *Scleropages formosus* inhabits natural lakes, swamps, flooded forests, and slowly moving, deep parts of rivers with overhanging vegetative cover. It is a carnivorous fish and its food consists mainly of insects, fishes, worms, small amphibians, small mammals, and even birds. *S. sinensis* may live in the same natural environment and have a similar diet except for the largest items. Sexual dimorphism may exist in *S. sinensis*. The presumed male has a slimmer and shallower body, a relatively larger head, and a deeper mouth cleft. The discovery of *Scleropages sinensis* sp. nov. dates the divergence of *Scleropages* and *Osteoglossum* to no later than the Early Eocene.

Key words: Hunan, Hubei, China; Early Eocene; Xiawanpu Formation; Yangxi Formation; Osteoglossidae

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1. Introduction

Scleropages, an extant genus of Osteoglossidae, is a freshwater fish with a transoceanic distribution in Southeast Asia and Australia. It has four species: *S. formosus* (Müller and Schlegel, 1844) and *S. inscriptus* (Roberts, 2012) distributed in Sumatra, Kalimantan, Peninsular Malaysia, Thailand, and Cambodia; and *S. jardinii* (Saville-Kent, 1892) and *S. leichardti* (Günther, 1864) in Australia and New Guinea. Pouyaud et al. (2003) described three closely related new species of *Scleropages* based on coloration, molecular data, and morphometric characters, but these new species were questioned and regarded as synonyms of *S. formosus* by Kottelat and Widjanarti (2005) and Roberts (2012). Pouyaud et al. (2003) also designated a neotype for *S. formosus* in their redescription of this species. Martien et al. (2013) considered this designation unnecessary because the types are still extant.

The Asian arowana (*Scleropages formosus*), known as the dragon fish, is one of the most prized and expensive aquarium fishes in the world. Some Asians believe that the arowana brings good luck and fortune and can even cast out evil spirits. This belief persists in Thailand, China (Taiwan and Hong Kong), and Japan, despite the fish being listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) as a highest-class protected species. At present, captive-bred dragon fish (F2 generation) may be traded.

Fossil *Scleropages* are known from the Maastrichtian of India (Hora, 1938; Rana, 1988; Kumar et al., 2005; Nolf et al., 2008), the Maastrichtian/Late Paleocene of Africa (Taverne, 2009), the Paleocene of Europe (Taverne et al., 2007), the Eocene of Sumatra (Sanders, 1934; Forey and Hilton, 2010), and the Oligocene of Australia (Hills, 1934, 1943; Unmack, 2001). All these earlier records consist of scales, otoliths, and isolated bone fragments. Here we report the first skeletons of fossil *Scleropages* from Lower Eocene strata in Xiangxiang, Hunan Province and Songzi, Hubei Province, China. Some specimens are complete and well preserved. A local farmer in Xiangxiang first collected the specimens and sent them to the IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences). Later, Li Chun from IVPP obtained a beautiful specimen (the holotype) from a farmer in Songzi. Zhang Miman of IVPP first recognized these specimens and then encouraged and advised the first author to study them (including one piece from Xiangxiang sent by Song Changqi, a senior geologist), as she often helps young researchers study specimens in her care. Thereafter, the first author and his colleagues from IVPP collected dozens of specimens of the fish along with other fishes during three field seasons, one in Xiangxiang and two in Songzi.

The specimens from Xiangxiang were found in gray-black shale of the lacustrine Xiawanpu Formation, which consists predominantly of greenish, blue-gray claystone and grey-black shale, grey-black paper shale, with marlstone lenses. The geological age of the Xiawanpu Formation was considered to be Eocene or probably somewhat later (Liu et al., 1962; Cheng, 1962), or Early Eocene to early Middle Eocene (ECSLC, 1999). In addition to osteoglossids, other fishes (Cheng, 1962) including "*Osteochilus*" *hunanensis* (originally described as a cyprinid fish by Cheng (1962) and later revised to *Amyzon hunanensis*, a catostomid, by Chang et al. in 2001), *Aoria* (a genus of bagrid catfishes), *Tungtingichthys* (Perciformes), and *Cyclurus* (Amiidae, Chang et al., 2010), as well as ostracods and plants were also found in the formation.

The Songzi specimens, including the holotype, were collected in the Yangxi Formation, which is 100–150 m in thickness and contacts conformably or disconformably with the underlying Paomagang Formation and the overlying Pailoukou Formation. The Yangxi Formation comprises shallow lacustrine deposits consisting of finely laminated mudstones and siltstones. Tons of slabs of fossil fishes (most are *Jianghanichthys*, a cypriniform fish) were unearthed by farmers and commercial collectors. Up to now, many vertebrate fossils have been found in this locality including the osteoglossid *Phareodus songziensis* (Zhang, 2003), *Jianghanichthys* (Liu et al., 2015), catfishes, perciforms, two rail-like birds *Songzia heidangkouensis* and *S. acutunguis* (Hou, 1990; Wang et al., 2012), and a pantodont mammal *Asiocoryphodon* cf. *A. conicus* (Chen and Gao, 1992). In addition, the oldest known primate was found in the same formation near this locality (Ni et al., 2013). Other fossils seen in the locality include ostracods, gastropods, charophytes, spores, and pollen. The age of the strata is Early Eocene (ECSLC, 1999).

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2. Material and Methods

The specimens studied are deposited in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. Comparative materials of extant *Scleropages* (*S. formosus*, IVPP V OP 80; *S. leichardti*, IVPP V OP 81) were purchased at a fish market in Beijing and are also deposited at IVPP. *Scleropages jardinii* and *S. inscriptus* were not found in the Beijing fish market.

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3. Systematic Paleontology

Teleostei Müller, 1846
Osteoglossomorpha Greenwood et al., 1966
Osteoglossidae Bonaparte, 1832
Scleropages Günther, 1864

***Scleropages sinensis* sp. nov.** (Figs. 1-5, 7)

Etymology: The specific name refers to China where the specimens were found.

Holotype: IVPP V 13672.2, a complete skeleton.

Referred specimens: IVPP V 12749.1-8, V 12750, V 13672.1, 3.

Locality and horizon: Specimens V 13672.1-3 and V 12750 are from Songzi County, Hubei Province, China; Yangxi Formation, Lower Eocene. Specimens V 12749.1-8 are from Xiangxiang, Hunan Province, China; Xiawanpu Formation, Eocene.

Diagnosis: A fossil species of *Scleropages* different from extant species of the genus in: nasals not appearing to be ornamented; sensory canal exposed in prominent groove on nasals; supraorbital sensory canal enclosed in bone on frontal only for middle third of its length; unornamented posterior portion of parietal is only 1/4 of length rather than 2/3; commissure in extrascapular tubes rather than passing through parietals; pterotic thicker in lateral portion; sensory pore in antorbital larger than in extant species; posterior infraorbitals not as large as in extant species and not quite covering dorsal limb of preopercle, with width-to-height ratio about 0.75 rather than 1–1.2; preopercle posteroventral angle produced to point, unlike condition in extant species; posteroventral margin of opercle concave and ventral end of bone produced to point; supracleithrum recurved; dorsal process of cleithrum long and strong; pectoral fin very long and extending well behind beginning of pelvic fin; vertebrae about 46–48; parapophyses shorter; neural spine on U1 partly doubled; upper and lower caudal rays nearly as long as inner rays.

4. Description

The body of the fish is fusiform in adults, with median fins posteriorly positioned and pelvic fins in abdominal position. Skull bones are thick and squamation is heavy. The standard length of the largest specimen is 175 mm, that of the holotype is 140 mm, and that of the smallest is 78 mm. Unless otherwise indicated, the following description is based on the holotype (Fig. 1 [Figure 1: see original paper]), which is the best-preserved example.

Cranium

The bone interpreted as the probable dermethmoid has an elongate, spear-point shape, with a pointed anterior end and a long, tapered posterior end (Fig. 4 [Figure 4: see original paper]). The nasals are large and suture in the midline along the anterior half of their length but are separated by the tapered frontals posteriorly. The nasals are not noticeably ornamented, unlike the condition in extant *Scleropages formosus* (Taverne, 1977:fig. 73 [Figure 73: see original paper]) and *S. leichardti* (IVPP dried skeleton). Also unlike the condition in the two extant species of *Scleropages* examined, the sensory canal appears to be exposed in a prominent groove in the fossil species.

The frontal is similar in shape and ornamentation to that of extant species of *Scleropages* (Taverne, 1977:fig. 73; IVPP dried skeleton of *S. leichardti*). It is long and subrectangular, with an anterior embayment for reception of the nasal and a posterior sinuous suture with its opposite member. In proportions it is slightly shorter and wider than that of *S. leichardti* and more like that of *S. formosus*. The lateral margin is embayed to conform to the medial margin of the dermosphenotic. Parallel to the lateral margin, the sensory canal is enclosed in bone for the middle third of its length, while being exposed in deep grooves for the anterior and posterior thirds of its length in the frontal. In *S. leichardti* and *S. formosus*, in contrast, the canal is enclosed in bone to or almost to its entry into the nasal.

As in other species of the genus, the parietal is subrectangular and sutures with its opposite at the midline and with the pterotic laterally. The surface of the anterior three-quarters of the bone is sculptured, while the posterior quarter lies at a lower level, beneath the canal-bearing extrascapulars, and is not sculptured.

Length-to-width proportions of the parietal are about 2:3, similar to those of *S. formosus* but unlike the 1:1 ratio seen in *S. leichardti*.

The external portion of the pterotic is a little larger and thicker than it is in extant species of *Scleropages*. The anterior half of the bone, lateral to the parietal, is sculptured and bears the temporal sensory canal in an open groove, whereas it is a simple tube in *S. formosus* (Taverne, 1977:fig. 73). The epiotic, supratemporal, and supraoccipital are not visible in the available specimens.

Scleropages sinensis appears to have its extrascapular sensory commissure carried within tubular 'extrascapulars' situated dorsal to the unsculptured area of the parietals, rather than passing directly through the parietals as seen in extant species of *Scleropages* (Taverne, 1977:fig. 71 [Figure 71: see original paper]). In both fossil and extant species, the canal is carried in paired extrascapular tubes between the previously mentioned bones and the posttemporals.

The orbital portion of the parasphenoid is toothless, moderately broad, and parallel-sided (V 12749.5). The remainder is covered by infraorbitals in available specimens.

The circumorbital series (Fig. 4) is composed of six bones: an antorbital, four infraorbitals, and a dermosphenotic. A supraorbital is absent. The antorbital, infraorbitals 1, 3, and 4, and the dermosphenotic are all prominently sculptured, while infraorbital 2 is not preserved well enough for assessment of its sculpture.

The antorbital is polygonal, making contact with the dermopterotic posterodorsally, the frontal and parietal dorsomedially, and the first infraorbital ventrally. The concave anterior and orbital margins are free. The shape is similar to that of *S. formosus* (Taverne, 1977:fig. 71). Dorsally, the circumorbital sensory canal enters the antorbital via a short, broad groove, then passes through the bone in a tube, entering the first infraorbital where a large pore communicates with the exterior. In *S. formosus* as illustrated by Taverne (1977:fig. 71), the latter pore is small and the canal is completely enclosed in bone throughout its length. The antorbital in *Osteoglossum bicirrhosum* (Taverne, 1977:fig. 42 [Figure 42: see original paper]) is more tubular and parallel-sided and unornamented; in *S. leichardti* (IVPP dried skeleton) it is also less polygonal but is ornamented.

The first and second infraorbitals are narrow and tubular. The first is slightly expanded, longer, and more ornamented than the second, but the latter is not well preserved. The two posterior infraorbitals (third and fourth) are very large but do not quite reach the size of those in extant *Scleropages* and *Osteoglossum*, in which they extend posteriorly to the articulation of the opercle, completely concealing the dorsal end of the preopercle and covering the posterior suspensorium. In *S. sinensis* there is a narrow gap through which the dorsal limb of the preopercle may be seen. The two posterior infraorbitals have a ratio of width to height of about 0.75, compared to about 1.0–1.2 in the two extant species of *Scleropages*. The two bones are nearly equal in size, like those in extant *Scleropages* but differing from those in *Osteoglossum*, in which the lower one is much larger than the upper. The infraorbital sensory canal is carried in a tube near the orbital margin of both posterior infraorbitals, with only a single small pore opening externally near the anteroventral end of the third infraorbital, as in the specimen of *S. formosus* figured by Taverne (1977:fig. 71). In *O. bicirrhosum* the pore is much larger and directed posteroventrally into a large groove (Taverne, 1977:fig. 42).

The complete or near-complete enclosure by infraorbitals of the cheek posteroventral to the orbit is considered a synapomorphy of Osteoglossidae by Li and Wilson (1996) and Hilton (2003). Among early osteoglossomorphs, this character is found only in *Paralycoptera*. Accordingly, *Paralycoptera* was considered to be closely related to or included within Osteoglossidae by different authors (Chang and Chou, 1977; Ma and Sun, 1988; Jin et al., 1995; Zhang, 2002).

The dermosphenotic is large, thick, sculptured, and approximately triangular. It bears the infraorbital canal internally near its posterior margin. The canal emerges from the posterodorsal corner of the dermosphenotic, where it enters the frontal to join with the supraorbital sensory canal near the anterior end of the posterior sensory groove of the frontal. In *S. formosus* the canal also joins within the frontal, but within a bone-enclosed tube. In V 12749.5 there is a suggestion of a branch in the infraorbital canal within the dermosphenotic, but the course of this branch cannot be detailed. Taverne (1977:fig. 71) did not show any branching within the dermosphenotic.

Jaws

The premaxilla is small, approximately triangular, and sculptured. It bears a blunt ascending process in its anterior half. There are seven teeth on the left premaxilla of the holotype, the anterior three teeth being much larger than the posterior ones. The number of teeth on the premaxilla of extant *Scleropages* has been counted differently: 4–5 by Ridewood (1905), 3–5 by Kershaw (1976), and 11 by Taverne (1977). In the four specimens of extant *Scleropages* that we examined, this number is 6–8, a condition agreeing with that of *S. sinensis*.

The maxilla is long and slender and takes an angle of about 45º with the long axis of the fish when the mouth is closed. It extends posteriorly nearly to the level of the mandibular articulation and ends well behind the posterior margin of the orbit. The posterior end is slightly expanded and downturned, especially immediately posterior to the marginal teeth. Ornament is present all along the external surface but is most prominent at the anterior and posterior ends. As in all living osteoglossomorphs, there is no supramaxilla.

The maxilla bears 40 conical teeth in an external row in the holotype, a resemblance in number with *S. formosus* and a difference from *S. leichardti*, in which the teeth number about 35 (IVPP dried skeletons). The teeth decrease in size steadily from anterior to posterior. Here and there, a few smaller teeth seen behind and between these marginal teeth might represent replacement teeth.

The mandible is also very long, makes a 45º angle with the long axis of the fish, lacks a distinct coronoid process, and consists of three bones: dentary, angulo-articular, and retroarticular. The dentary forms the great majority (3/4) of the length of the mandible. Anteriorly, the dentary curves medially to meet its opposite at a shallow symphysis. As for the premaxilla, the anterior five or six teeth of the dentary are much larger than the posterior ones. As in extant *Scleropages* (Taverne, 1977:fig. 71), the angulo-articular is relatively small, articulates with the quadrate as seen in lateral view, and the posterior tip of the retroarticular is visible laterally posterior to the quadrate articulation. Both dentary and angulo-articular bear longitudinal ridges on their lateral surfaces.

The mandibular sensory canal extends the length of the dentary and angulo-articular within a canal, with one pore located near the ventral end of the suture between the angulo-articular and dentary, as in *S. formosus* (Taverne, 1977:fig. 71), and three more pores evenly spaced and opening onto posteriorly directed grooves more anteriorly in the dentary, as in *S. formosus* and *S. leichardti* (IVPP dried skeletons).

Palato-quadrate Arch

The toothed palato-ectopterygoids are preserved in V 12749.5, in which both have a row of uniform-sized small teeth on their lateral margins. On the right one can be seen more medially an area of much smaller teeth. Both conditions are matched in extant *S. formosus* (Taverne, 1977:fig. 83 [Figure 83: see original paper]) and *S. leichardti* (IVPP dried skeleton). According to Taverne (1977:134–135), the anterior end of this bone in *S. formosus* includes the fused dermopalatine, with the autopalatine ossified only in the largest, oldest individuals. We were unable to confirm these details in *S. sinensis.*

The entopterygoid in extant species of *Scleropages* is triangular, with a single row of large conical teeth existing on the medial edge and fine denticles covering the remainder of the surface. The detailed shape is not seen in the fossils of *S. sinensis*, but part of the medial row of large teeth on the right entopterygoid is visible in the holotype. These teeth are larger posteriorly than anteriorly, and each is curved slightly ventrolaterally, as in *S. leichardti* (IVPP dried skeleton). In V 12750 the medial row and more lateral denticles are visible in cross-section. The metapterygoid, symplectic, and most of the quadrate are covered by the posterior infraorbitals in available specimens, although the quadrate and symplectic are exposed in inner view in V 12750.

Hyoid Arch and Branchiostegals

Only a very small part of the hyomandibular can be seen in the holotype. The tip of a bone protruding from beneath the anterior margin of the fourth infraorbital in the holotype might be the entopterygoid process of the hyomandibular as characteristically seen in extant osteoglossids, but it seems rather too stout. On the other hand, it is not oriented appropriately to be identified with the basipterygoid process of the parasphenoid, which might be expected to occur in the same area of the fossil.

A small triangular hypohyal, most of the anterior ceratohyal, and basihyal are seen in V 12749.5. There are nine slender, acinaciform branchiostegal rays in the holotype and at least two broad, spatulate ones. In *S. formosus*, Taverne (1977:fig. 84 [Figure 84: see original paper]) illustrates nine acinaciform and seven spatulate branchiostegals; thus we might estimate that *S. sinensis* had a similar number, perhaps 16 in total, given that only two spatulate branchiostegals are preserved.

Opercular Series

The preopercle is similar but not identical to that in extant species of *Scleropages*. The upper limb is not completely covered by posterior infraorbitals as it is in extant species of the genus (Taverne, 1977:fig. 71). The dorsal limb tapers uniformly dorsally, as far as can be seen, and is about twice as long as the ventral limb. The latter is bluntly rounded anteroventrally. The posteroventral angle of the preopercle is produced posteriorly to a point, located immediately below the ventral extremity of the opercle. This last feature is not seen in the preopercles of extant species of *Scleropages* but is met with in a more extreme form in some African osteoglossiforms such as *Chauliopareion* Murray and Wilson, 2005, and *Singida* as redescribed by Murray and Wilson (2005).

The preopercular sensory canal in *S. sinensis* has features typical for osteoglossids. The canal is open ventrally beneath a long, horizontal shelf. On the shelf, and dorsal to it, the preopercle is sculptured, but ventral to it the surface of the preopercle is smooth. From the posterior end of this shelf to the dorsal end of the vertical limb, the preopercular canal is enclosed in bone beneath the anterior edge of the exposed portion of the bone, except for a single, large pore at about half the height of the preopercle. This pore opens posteriorly from the main canal into a prominent groove directed posteroventrally. In other osteoglossids the relative height of this single pore varies, but essentially the same feature is seen, where preservation permits, in many genera of Osteoglossidae and Notopteridae including extant species of *Scleropages* and fossil taxa such as *Phareodus* and *Musperia* (e.g., Taverne, 1977, 1978). *Arapaima* and *Heterotis* do not exhibit the shelf and single large pore, showing instead a bone-enclosed canal opening via pores, while the condition in *Pantodon* is perhaps somewhat intermediate (Taverne, 1978).

The opercle in *S. sinensis* is large and nearly semicircular in shape but differs from that in extant species of *Scleropages* and *Osteoglossum* in having its ventral end produced to a point and its posteroventral margin concave. The opercle is also prominently sculptured except for its anterior margin and dorsal extremity. The opercle in the holotype has a height of 24 mm and a maximum width, at right angles to the anterior edge, of 13 mm. The hyomandibular facet is located at a height of 19 mm from the ventral end, judging by the arrangement of ornamental ridges on the external surface. The subopercle and the interopercle are not visible.

Appendicular Skeleton

The pectoral girdle is partially seen in the holotype and in V 12749.8. The posttemporal is a forked bone with the dorsal limb longer than the ventral one. The lateral line runs near the ventral margin of the bone and probably goes into the trunk scales directly, without passing through the supracleithrum, as in living osteoglossids.

The supracleithrum is strap-like dorsally and broadens ventrally; it is recurved rather than following a uniform curve as seen in extant species of *Scleropages*. In *Osteoglossum* the bone broadens ventrally but is not recurved (Taverne, 1977). A small postcleithrum is present and lies medial to the junction between the supracleithrum and cleithrum.

The cleithrum is best exposed in specimen V 12749.8, in which it is seen to have a long dorsal limb of uniform width, terminating dorsally in a long, rod-like process. In contrast, the cleithrum of extant species of *Scleropages* (Taverne, 1977:fig. 86 [Figure 86: see original paper]; IVPP dried skeletons) has only a smaller, acuminate dorsal extremity, much shorter and more slender than that of *S. sinensis*. The coracoid, scapula, and mesocoracoid have not been seen.

Four proximal pectoral radials that support the pectoral rays except for the first ray can be recognized in the holotype, with the first thick and stout and the others becoming small posteriorly.

The pectoral fin (Figs. 1, 3C) is very long and extends well behind the beginning of the pelvic fin, a difference from extant species of *Scleropages* where it does not reach the beginning of the pelvic fin. In the holotype the longest rays are 47 mm long, whereas the pelvic fin originates 35 mm posterior to the origin of the pectoral fin. The pectoral fin contains seven rays, resembling that of *S. formosus* rather than *S. leichardti* where the fin has eight rays (IVPP dried skeletons); all rays are branched and segmented except the first one, which is exceptionally thick and unbranched, though segmented. Adjacent to the base of the smallest ray there is a claw-shaped bone.

The pelvic girdle and fin are very small. The pelvic fin originates slightly closer to the anal fin than to the pectoral fin. The pelvic bone (seen in V 12749.8) is short and flat. There appear to be six pelvic fin rays, all branched but the first, a condition agreeing with that of *S. leichardti* and differing from *S. formosus*, which has five fin rays in specimens examined.

Dorsal and Anal Fins

Both dorsal and anal fins are rounded in outline and located posteriorly. The dorsal fin is small and originates posterior to the origin of the anal fin, opposite the middle of the anal fin. In the holotype there are two short procurrent dorsal rays, the second one segmented, followed by one full-length unbranched ray and 11 branched rays, the last one apparently double, for a total of 12 principal rays. Fourteen short dorsal pterygiophores can be counted, matching the fin rays one-to-one. Other specimens (V 12749.1,2) may have slightly more principal rays, 12–15 in available specimens, with 14–17 pterygiophores.

The anal fin is much larger than the dorsal fin, with three very small, unsegmented procurrent rays and 22 principal rays, supported by 23 anal pterygiophores in the holotype and 21–24 anal pterygiophores in other specimens (V 12749.1,4). This resembles the condition in *S. formosus* and differs from that in *S. leichardti*, in which 28 principal fin rays are present.

Vertebral Column and Caudal Fin

There are 46–48 vertebrae in available specimens, of which in the holotype about 22 are abdominals and 24 are caudals including the two ural centra. This number is much less than in extant osteoglossids and agrees more with that of early osteoglossomorphs such as *Kuntulunia* and *Xixiaichthys* (Zhang, 1998, 2004). The first three centra are covered by the opercle. The centra are slightly deeper than long.

The first four neural spines are paired and the remainder anterior to the dorsal fin are fused into a single element. In extant *Scleropages* and *Osteoglossum*, this condition varies, with neural spines being fused beginning with the third in *S. formosus* and with the eighth in *O. bicirrhosum* (e.g., Taverne, 1977:108, 147). Parapophyses are difficult to see but appear (V 12749.8) to be much shorter than in extant *Scleropages*, *Osteoglossum*, and *Phareodus* (Li et al., 1997) and even shorter than in most early osteoglossomorphs (Zhang and Jin, 1999; Zhang, 1998, 2004).

There are 22 pairs of pleural ribs, which extend to the ventral margin of the trunk, except for the last pair, which is only about half the length of the more anterior ones. Long, slender epineurals are present, their proximal ends not fused with the neural arches. The last epineural is related to the second vertebra following the last abdominal vertebra.

Some 22 long, slender supraneurals are seen in specimen V 12749.8, anterior to the dorsal fin and lying at a shallow angle to the long axis of the body so that each one overlaps the dorsal end of one or two neural spines.

The caudal skeleton (Figs. 3D, 5) is very similar to that of extant species of *Scleropages* with a couple of exceptions. Unfortunately, these details can only be seen in a single specimen of *S. sinensis* (V 12749.8). The caudal skeletons in the two examined extant species of *Scleropages* (Fig. 6 [Figure 6: see original paper]) display important differences, each resembling that of *S. sinensis* in some ways but not in others.

Three neural and haemal spines in *S. sinensis* are lengthened to support the caudal fin rays; these haemal spines gradually thicken posteriorly. The first preural centrum bears a complete neural spine, while in some specimens of *S. leichardti* the centrum bears two. The first ural centrum (U1) appears to have two incompletely fused neural spines, with the first complete and the second one shorter. The second ural centrum (U2) is fused with the proximal ends of hypurals 3-5. There are six hypurals. Hypural 1 is very deep and does not reach U1 proximally. Hypural 2 is less than half the width of the first and either articulates with or is fused to the centrum as in extant species of *Scleropages*. Hypurals 3 through 5 are fused proximally and fit tightly together distally. A rod-like bone dorsal to hypurals 3-5 is probably the sixth hypural. Just above this bone, a similarly shaped bone is interpreted here as fused uroneurals (see Hilton, 2003, for discussion of this unusual feature of osteoglossiforms).

In *S. leichardti*, centrum U1 supports three hypurals in every specimen available to us, a very unusual situation for a teleostean fish. The first two of these hypurals are fused to each other proximally but separated distally, and the combined first two hypurals do not reach U1. In contrast, both *S. formosus* and *O. bicirrhosum* have the more usual situation of two lower hypurals, the first not reaching U1 and the second joining it.

The greatly enlarged first hypural in *S. sinensis* seems deep enough to correspond to the two partially fused hypurals of extant *S. leichardti* specimens. This hypural is as deep as the first two (of three lower) hypurals in *S. leichardti*. However, we do not see any evidence of a division into two hypurals in this specimen. The occurrence in *S. sinensis* of two incompletely separated neural spines on U1 might suggest an origin by fusion of centra. However, the neural spine of *S. leichardti* specimens examined by us is not doubled, whereas they have an extra lower hypural. Additional specimens showing the caudal skeleton of *S. sinensis* and a study of the development of the caudal skeleton in *S. leichardti* could be very informative in light of these findings.

The caudal fin is rounded. There are 16 principal caudal rays, the first and last being unbranched and almost as long as the remaining rays, whereas in living species of *Scleropages* and *Osteoglossum*, the upper and lower rays are only half the length of the innermost ones. One or two procurrent rays are present anterior to the principal rays.

Squamation

The scales are large (Figs. 2, 7), cycloid, oval, and exhibit the reticulate pattern, involving small units called squamules, typical of osteoglossids (Fig. 8 [Figure 8: see original paper]). The external surface of the scale shows circuli in the basal portion and granular ornamentation in the apical area. The squamules (Gayet and Meunier, 1983) are rhombic, polygonal, or irregular in shape. The mesial surface of each squamule may be smooth or bear 1-25 rounded, raised tubercles, each of which has a minute transversal pore (Jolly and Bajpai, 1988) at its center.

The lateral line (Fig. 2) runs just below the vertebral column and the scales along the lateral line number about 24, a similar number to that in *S. formosus* and 10 scales fewer than is seen in *S. leichardti* (IVPP specimens).

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5. Discussion

The new fish found in Hubei and Hunan provinces of China very much resembles *Scleropages* in skull bones, caudal skeleton, the shape and position of fins, and reticulate scales (Fig. 9 [Figure 9: see original paper]). Therefore, it must belong to the genus. *Scleropages* has four species: two in Australia and New Guinea (*S. jardinii* and *S. leichardti*) and the other two in Asia (*S. formosus* and *S. inscriptus*). *S. jardinii* and *S. leichardti* are very similar to each other, while *S. formosus* and *S. inscriptus* are nearly identical except the latter has complex maze-like markings on circumorbitals, opercular series, and scales. For this reason and because specimens of the other two species were not available to us, only *S. leichardti* and *S. formosus* were used as representatives of extant *Scleropages* for comparative study.

The new fish is very similar to *S. leichardti* and *S. formosus*, except: the nasals do not appear to be ornamented; the sensory canal is exposed in a prominent groove on the nasals (unless a preservational artifact); the supraorbital sensory canal is enclosed in bone on the frontal only for the middle third of its length; the unornamented posterior portion of the parietal is only 1/4 of its length rather than 2/3; the commissure is in extrascapular tubes rather than passing through the parietals; the pterotic is thicker in its lateral portion; the sensory pore in the antorbital is larger than in extant species; the two posterior infraorbitals are not as large as in extant species of *Scleropages*, not quite covering the dorsal limb of the preopercle, and their width-to-height ratio is about 0.75 rather than 1-1.2; the posteroventral angle of the preopercle is produced to a point, unlike the condition in extant species; the posteroventral margin of the opercle is concave and the ventral end of the bone is produced to a point (in extant species the ventral end of the opercle is not as produced and the posteroventral margin is not concave); the supracleithrum is recurved versus uniformly curved; the dorsal process of the cleithrum is long, strong, and rod-shaped versus shorter and acuminate in extant species; the pectoral fin is very long and extends well behind the beginning of the pelvic fin; vertebrae number about 46–48 versus ~60 in extant species and other Recent osteoglossids; the parapophyses are shorter; the neural spine on U1 is partly doubled; the upper and lower caudal rays are nearly as long as the inner rays (versus much shorter). Based on these differences, a new species is established: *Scleropages sinensis* sp. nov.

Scleropages sinensis is similar to *S. formosus* but different from *S. leichardti* in that: proportions of length to width of parietal are 2:3 versus 1:1; the antorbital proportions are similar to those in *S. formosus* but in *S. leichardti* the antorbital is not as polygonal; maxillary teeth number about 40 versus about 35 in *S. leichardti*; principal anal rays are 21–24 versus 28 in *S. leichardti*; there are two lower hypurals versus three in *S. leichardti*; there are 24 scales along the lateral line versus ~34 in *S. leichardti*.

Scleropages sinensis also shares some similarities with *S. leichardti* but differs from *S. formosus*. These characters include six pelvic rays versus five in *S. formosus*, and the first hypural very deep (as deep as the first two in *S. leichardti*, and unlike the slender first hypural in *S. formosus*). Pelvic fin rays are seven in Hiodontidae, six principal plus one short in *Kuntulunia* and *Xixiaichthys*, and six in *Lycoptera* and *Asiatolepis* (Zhang, 2010: five in original description, but clearly six in V 11982.28a). Therefore, having more pelvic rays is likely a primitive condition in osteoglossomorphs. Centrum U1 supporting three hypurals in *S. leichardti* is a very unusual situation in teleosts. The same condition was noticed by Hilton (2003) in *S. jardinii* (152 mm SL) and by Xu and Chang (2009) in *S. jardinii* and *S. leichardti*. Hilton thought that study of more specimens was needed to confirm if this is due to ontogeny (i.e., if hypural 1 typically is composed of two elements) or is individual variation. Although the first hypural in *S. sinensis* seems deep enough to correspond to the first two hypurals in *S. leichardti*, no evidence of a possible division into two hypurals can be seen. The caudal skeleton is usually covered by scales in *S. sinensis* that make it difficult to know if there is any variation in the hypural pattern.

According to the above comparison between *S. sinensis* sp. nov. and extant *Scleropages*, it is clear that the new fish is closer to its Asian neighbor, *S. formosus*, than to its southern relative, *S. leichardti*.

The Asian arowana *S. formosus* is distributed in the Mekong Basin in Vietnam and Cambodia, southeastern Thailand, Tenassarim (Myanmar), the Malay Peninsula from Sungai Golok southwards, Borneo, and Sumatra. It inhabits natural lakes, swamps, flooded forests, and slowly moving, deep parts of rivers with overhanging vegetative cover. The Asian arowana is a carnivorous fish and its food consists mainly of insects, fishes, worms, small amphibians, small mammals, and even birds. It can jump very high in the wild to get food hanging on trees. *S. sinensis* may have lived in the same natural environment and could have had a similar diet except for the largest items, considering the smaller body size of the new fish.

Arowanas are paternal mouthbrooders. The Asian arowana is not easy to sex. Scott and Fuller (1976) found no obvious external sexual differences in 170 specimens (32 were fry) they obtained in Malaya. However, Suleiman (2003) argued that the differences become apparent after maturity is reached at about 3-4 years of age. The determination of sex is based on body shape and the size of the mouth cavity. Males have a slimmer and shallower body depth (while females have a more rounded body), a bigger mouth, and more intense color than females. A larger mouth and a deeper lower jaw in males are beneficial for holding more eggs and fry. These sexual differences can also be seen in *S. sinensis*. The holotype (Fig. 1) and another fish (Fig. 3A) have a slimmer and shallower body, a relatively larger head, and a deeper mouth cleft. In contrast, some other individuals (Fig. 2) have a more rounded body and a smaller head.

This suggests possible sexual dimorphism in *S. sinensis*. The deeper mouth cleft in the holotype and V 12749.4 (Fig. 3A) also suggests the possibility of paternal mouthbrooding in *S. sinensis*. Unfortunately, no direct evidence such as eggs and fry can be found in the fossils.

Except for *Hiodon*, which lives only in North America, all other extant osteoglossomorphs are distributed in the tropical or subtropical fresh waters of southern continents. Fossil osteoglossomorphs have been found in freshwater deposits (some forms, such as *Brychaetus*, may have lived in brackish water and even marine environments) on all continents except Antarctica. The explanation for such a transoceanic distribution of freshwater fishes is a challenge for paleogeography and historical biogeography. Nelson (1969) argued that Africa was probably the center of the ancestral distribution of osteoglossomorphs. Greenwood (1970) and Chang and Chou (1976) supposed that East Asia might be the ancestral home of osteoglossomorphs. Gayet (1987) explained the present distribution of osteoglossomorphs by a hypothetical "lost Pacifica." All these hypotheses failed to resolve the transoceanic distribution of the superorder Osteoglossomorpha satisfactorily. Li (1997) and Xu and Chang (2009), in contrast, suggested that the early evolution of Osteoglossomorpha occurred in Pangaea.

The earliest fossil record of Osteoglossomorpha is *Lycoptera* (Barremian) (Swisher et al., 2002). Early osteoglossomorphs have mostly been recovered from China but have also been found in other parts of the world, such as *Chandlerichthys* from North America (Cenomanian), *Laeliichthys* from South America (Aptian), and *Kipalaichthys* from Africa (Cenomanian). Since Osteoglossomorpha were already widely distributed on both northern and southern continents in the Early and mid-Cretaceous, it is reasonable to suggest that the superorder originated in Pangaea.

Li (1997) believed that the earliest members of the main lineages of Osteoglossomorpha had already extended their distribution to most parts of Pangaea before its final breakup and that the recent relict distribution of the superorder resulted from extinction. Li conceived that the transoceanic dispersal and vicariance of Osteoglossomorpha did not happen after the final split of Pangaea. *Phareodus*, a very common genus of fossil osteoglossid also seen in the same formation with *S. sinensis*, has been found in Pakistan, India, Sumatra (Musperia), North America, and Australia. If transmarine migration never happened, a Pangaean origin would be the most likely model to interpret the transoceanic distribution of *Phareodus*. Based on their study of molecular phylogeny of osteoglossoids, Kumazawa and Nishida (2000) concluded that the divergence time between Asian arowana (*Scleropages formosus*) and Australian arowana (*S. leichardti* and *S. jardinii*) is about 138 million years, which is close to or slightly older than the probable time of the India-Madagascan separation from Gondwanaland (120–130 Ma, Smith et al., 1994). They consequently argued that the Asian arowana originated on a part of Gondwanaland and was carried to Eurasia by the Indian subcontinent. Therefore, the transoceanic migration of Osteoglossomorpha might have occurred after the split of Pangaea.

The Eocene collision of the Indian subcontinent with Asia has been accepted for a long time (Besse et al., 1984; Metcalfe, 1999), but recent data support the view that terrestrial continuity between India and mainland Asia was already established by the time of the K/T boundary, 65 Ma ago, or probably slightly earlier (Beck et al., 1995; Jaeger et al., 1989; Prasad et al., 1994; Rage et al., 1995). The discovery of *Scleropages* and *Phareodus* from mainland Asia suggests the possibility that the genus originated in Gondwana and dispersed to Asia through the Indian subcontinent, and then *Phareodus* to North America via the Bering Strait. The Eocene fish fauna along the coast of the Bohai Gulf, eastern China, shows striking similarity in composition to those of the same age along the west coast of North America, demonstrating a "transpacific" distributional pattern (Chang and Chen, 2000). The Arctic connection of the northern continents and the broad connection between Asia and North America in the Bering Strait area may have served as a passage for fishes from both sides of the Pacific (Chang and Chen, 2000). With those connections between the two places, *Phareodus* could have dispersed from Asia to North America. *Scleropages* has been found in the Maastrichtian, Paleocene, Eocene, and Oligocene, and *Phareodus* was cosmopolitan in the Eocene, but their Late Cretaceous representatives were only found in southern continents. The fossil records thus seem to support the view of a Gondwanian origin of osteoglossids.

However, a recent work (Lavoué, 2015) rejected the Gondwanian origin of *Scleropages*. Lavoué reported an age CI of *Scleropages* ranging from 79.9 to 101.4 Ma, which is significantly younger than the (138 ± 18) Ma age inferred by Kumazawa and Nishida (2000). Recent paleogeographical reconstructions (Gibbons et al., 2013; Scotese, 2014) give a latest possible age (115.0 Ma) for a direct connection of the Indian subcontinent to Australia-Antarctica. Lavoué' s result suggests that the divergence between the Sundaland-Indochina *Scleropages* and the Australia-New Guinea *Scleropages* is younger than 115.0 Ma. The early divergence of *Scleropages* therefore occurred after the final separation between India and Antarctica-Australia. Consequently, his study rejects the Gondwanian origin hypothesis to explain the distribution of *Scleropages*.

More recently, Lavoué (2016) used newly reconstructed time-calibrated phylogenetic trees based on a large dataset combining extant and fossil taxa and molecular and morphological characters to test whether the divergence of Osteoglossiformes was compatible with the breakup of Gondwana. He thought that the most convincing evidence that some osteoglossomorphs may have achieved their current transmarine distribution through marine dispersal is from the genus *Scleropages*. Marine dispersal in *Scleropages* was also mentioned by Cracraft (1974), Briggs (1979), and Wilson and Murray (2008). Taverne et al. (2007) argued that Recent freshwater Osteoglossiformes generally tolerate brackish waters and sometimes enter marine waters near estuaries. In contrast, Lavoué (2015) suggested that *Scleropages* species are highly intolerant of salt water according to the investigations of Gehrke et al. (2011) and Roberts (1978).

The distribution of osteoglossids remains a zoogeographical enigma. Marine fossils of *Scleropages* or an unknown vicariance event are needed to explain the intercontinental distribution of the genus. In such a situation, the discovery of *Scleropages sinensis* dates the divergence of *Scleropages* and *Osteoglossum* as at least as old as the Early Eocene, which is a significant step toward solving this zoogeographical puzzle.

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Chinese Title and Abstract Translation

First Discovery of *Scleropages* (Osteoglossomorpha) Fossils

Abstract: Scales and bone fragments of *Scleropages* fossils have been reported in the past, but their identification is not entirely reliable because these scales and bones are very similar among osteoglossid fishes. Here we describe perfectly preserved *Scleropages* fossils from the Xiwanpu Formation in Xiangxiang, Hunan and the Yangxi Formation in Songzi, Hubei, establishing a new species of the osteoglossid genus *Scleropages*: *Scleropages sinensis* sp. nov. The new species is extremely similar to extant *Scleropages* in skull bones, caudal skeleton, fin shape and position, and reticulate scales, and is therefore assigned to this genus. However, the new species differs from extant *Scleropages* in the following characters: nasals lack ornamentation; sensory canal exposed in a prominent groove on nasals; sensory canal commissure does not pass through parietals; pterotic thickened laterally; sensory pore in antorbital large; posterior infraorbitals do not completely cover the dorsal limb of the preopercle, with width-to-height ratio of 0.75 versus 1-1.2 in extant species; posteroventral angle of preopercle pointed; posteroventral margin of opercle concave with ventral end pointed; dorsal process of cleithrum long and robust; vertebrae 46-48; parapophyses short; pectoral fin very long; upper and lower caudal rays as long as inner rays. Extant Asian species are found in various rivers and streams, preferring still-water environments with abundant aquatic vegetation, generally swimming in surface waters and feeding on fish, shrimp, insects, etc. The new species *Scleropages sinensis* likely had a similar habitat and diet. The new species appears to exhibit sexual dimorphism, with males having a slightly more slender body, relatively larger head, and deeper mouth cleft. The discovery of *Scleropages sinensis* fossils demonstrates that the genera *Scleropages* and *Osteoglossum* had already diverged before the Early Eocene, which is of great significance for explaining the transoceanic distribution of osteoglossid fishes.

Keywords: Hunan, Hubei, Early Eocene, Xiwanpu Formation, Yangxi Formation, Osteoglossidae