

A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians

XU GuangHui* & WU FeiXiang

Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

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The Ginglymodi are a group of ray-finned fishes that make up one of three major subdivisions of the infraclass Neopterygii. Extant ginglymodians are represented by gars, which inhabit freshwater environments of North and Central America and Cuba. Here, we report the discovery of well-preserved fossils of a new ginglymodian, *Kyphosichthys grandei* gen. et sp. nov., from the Middle Triassic (Anisian) marine deposits (Guanling Formation) in Luoping, eastern Yunnan Province, China. The discovery documents the first known fossil record of highly deep-bodied ginglymodians, adding new information on the early morphological diversity of this group. The studies of functional morphology of extant deep-bodied fishes indicate that *Kyphosichthys* is not a fast swimmer but has a good performance in precise maneuvering, representing a morphological adaptation to structurally complex habitats (e.g. thick macrophyte beds, rocky areas, or coral reefs), which differs from the other members of this group. A cladistic analysis with the new fish taxon included supports the hypothesis that the Ginglymodi are more closely related to the Halecomorphi than to the Teleostei. Represented by *Felberia*, *Kyphosichthys*, and *Dapedium*, a highly deep and short fish body type has independently evolved at least three times in the stem-group neopterygians, ginglymodians, and basal teleosts within the lower neopterygians of the Triassic.

deep-bodied fish, Osteology, Semionotidae, Ginglymodi, Holostei

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The Neopterygii, sister to the Chondrostei, are taxonomically the most diverse group of the subclass Actinopterygii [1]. They include three main subdivisions, the Ginglymodi, Halecomorphi, and Teleostei, and their closely related fossil taxa [2,3]. The Early Triassic (Olenekian, 245–249 Ma) parasemionotids of the stem-group Halecomorphi represent the earliest known crown-group neopterygians [4–6]. Greater diversification of the crown-group Neopterygii occurred in the Middle Triassic, and the Teleostei were first recorded in the Late Triassic [2]. Thus, the Triassic is a period of particular interest to the study of the neopterygian evolution.

The fossil record of neopterygians is rich in the Triassic

deposits of China [7,8]. Many new neopterygians have been reported in recent years [6,9–12]. Here, we report the discovery of well-preserved fossils of a new neopterygian ginglymodian from the Middle Triassic (Anisian) Guanling Formation in Luoping, eastern Yunnan Province, China. Along with this new fish is a taxonomically rich fossil assemblage, including plants, invertebrates, marine reptiles, and other kinds of fishes [13,14]. Besides the fossil material of the three named neopterygians from Luoping described in recent publications [9,11,12], there remains a large quantity of fish specimens representing a dozen of unnamed new neopterygians. Fish fossils from this assemblage provide good evidence in investigating the early diversification of the Neopterygii. The fossil beds at this locality are com-

*Corresponding author (email: xuguanghui@ivpp.ac.cn)

posed by thin lime mudstone interlaid with dark shale, siliceous concretion, and zebra limestone of apparent marine origin. The lithofacies indicate a platform margin or platform margin slope environment of this fossil site [14]. The age of the fossil beds has been determined as the Anisian, Middle Triassic, based on the conodont analysis [14].

In the past decades, most ichthyologists agreed with Gardiner [15] and Patterson [2] that within the Neopterygii, the Halecomorphi were more closely related to the Teleostei than to the Ginglymodi, and the Halecomorphi and the Teleostei formed a monophyletic clade, Halecostomi. However, a few others [16,17] insisted that the clade Holostei (Ginglymodi plus Halecomorphi) was sister to the Teleostei. In recent years, the phylogeny of the Neopterygii has been an interesting topic of molecular analyses [18–20], and most of them support that *Amia* (Halecomorphi) is more closely related to *Lepisosteus* (Ginglymodi) than to teleosts. Grande [3], based on morphological analysis, also supports the hypothesis that the Holostei are a monophyletic group, sister to the Teleostei. Here, we provide a new cladistic analysis, which includes the new fish taxon and representative taxa of major lineages of the Neopterygii, to reassess the interrelationships of this group.

1 Materials and methods

The material is deposited at the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. The specimens were prepared manually. They were dusted with ammonium chloride (NH₄Cl) when photographed for revelation of anatomical details. Illustrations were drawn manually, and then prepared with the help of Adobe Photoshop and Illustrator software packages (CS4). Cladistic analysis was executed using PAUP 4.0b10 [21]. The relative position of fins and scale count were expressed in a pterygial formula following Westoll [22].

2 Systematic palaeontology

Subclass Actinopterygii [23]

 Infraclass Neopterygii [24]

 Division Holostei [25] (*senus* Grande [3])

 Ginglymodi incertae sedis

Kyphosichthys grandei gen. et sp. nov

 (Figures 1 and 2)

Etymology: The generic name is derived from *kyphos* (Greek), meaning bent and referring to its lumped back, and *ichthys* (Greek), meaning fish. The species name honors Lance Grande for his recent, valued contribution [3] to the study of the Ginglymodi.

Holotype: IVPP V10108, a complete specimen.

Paratype: IVPP V10109.

Type locality and horizon: Luoping, Yunnan Province, China. Anisian, Middle Triassic, Guanling Formation.

Diagnosis: A deep-bodied ginglymodian with a strongly arched hump between head and dorsal fin; body depth about 70% of standard length; pelvic fins reduced; anal fin about 50% of dorsal fin in length; two lacrimal bones; two suborbital bones, an elongated, small, upper one and a deep, large, ventral one; and pterygial formula of D21/P9, A16, C25/T29.

3 Description

(i) **Shape and size.** The fish has a strikingly deep body with a strongly arched hump between head and dorsal fin (Figure 1). The holotype has a total length of 96 mm (91 mm in fork length, and 76 mm in standard length). The head is extensively ornamented by small tubercles and ridges; it has a length of 28 mm from the tip of the premaxilla to the end of the opercle in the holotype, and a length of 33 mm in the paratype (Figure 2(a)). The great body depth lies at the level of the posterior margin of the opercle, with the body height (55 mm) equaling 72.3% of the standard length in the holotype.

(ii) **Skull roof.** The median rostral is reduced, and tube-like, as commonly seen in crown-group neopterygians. The paired nasals are small, slightly deep bones, lying on the deep nasal process of the premaxilla, as in other ginglymodians (Figure 2). The frontal is significantly elongated, three times longer than the square parietal. The supraorbital sensory canal enters the frontal from the nasal, runs longitudinally through the frontal, and terminates near the posterior margin of this bone. The dermopterotic is large, nearly as deep as the parietal. The temporal sensory canal runs longitudinally through the dermopterotic, with a series of sensory pores along the ventral margin of this bone. Two extrascapulars are present on each side; they are trapezoid, and the upper one is slightly narrower than the lower.

(iii) **Circumorbital series.** The antorbital is a curved bone, having a tube-like anteroventral portion, as in other holosteans. There are seven infraorbitals. Of these, the anterior two are located anterior to the orbital ring and are termed lacrimal bones, following Grande [3]. The lacrimals are deep bones with the dorsal portion partly missing. The sensory pores of the infraorbital canal are exposed at their ventral portions (Figure 2). Three subinfraorbitals are present between the lacrimals and the postinfraorbitals; the anterior two are relatively narrow, and the posterior one is well expanded. Two small postinfraorbitals are present; the lower is slightly larger than the upper. The dermosphenotic is located at the posterodorsal corner of the orbit. It is deep and slightly curved backwards, contacting the dermopterotic posteriorly and the frontal dorsally. No supraorbital bones are preserved in the holotype, and a possible right supraorbital bone is preserved disarticulated near the frontal in the paratype. It is an elongated bone without any sensory pores.

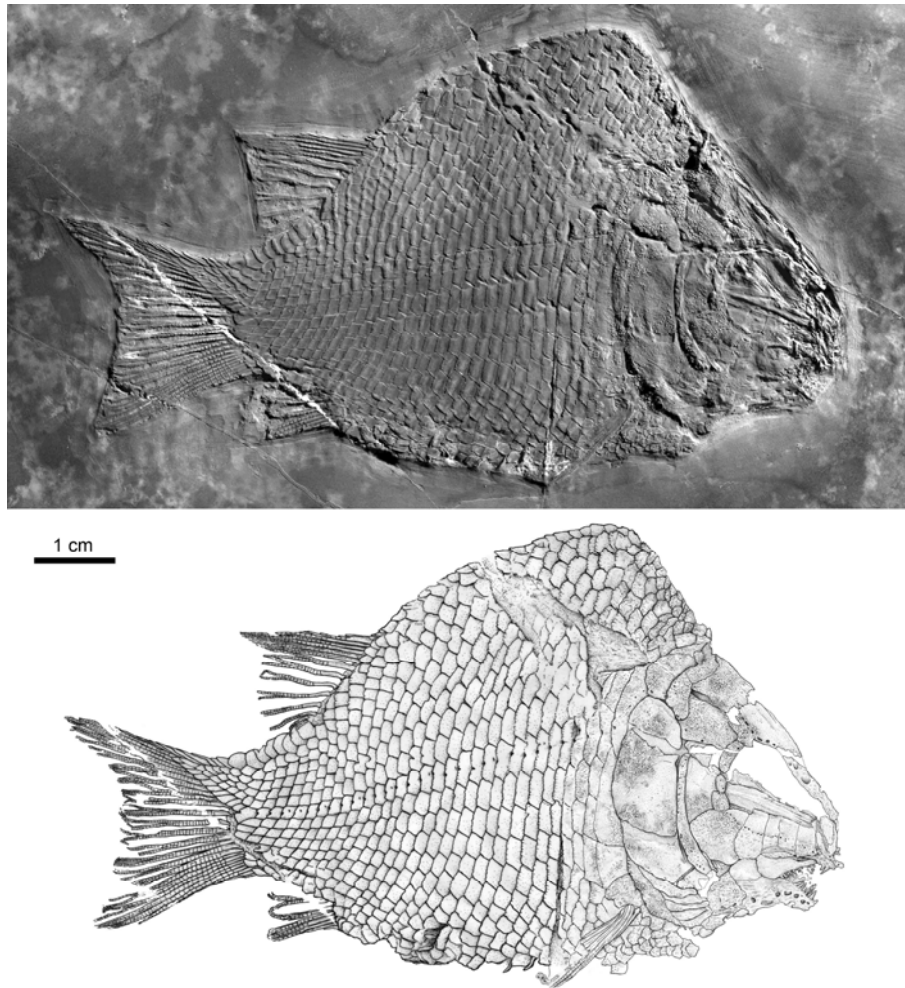


Figure 1 Holotype of *Kyphosichthys grandei* gen. et sp. nov. (IVPP V10108).

Two suborbital bones are present; the upper is low and relatively small, and the lower is deep and three times as the size of the upper.

(iv) Palate, hyoid arch, and gill arches. The palatal elements can only be observed through the orbit (Figure 2). An elongate orbital portion of the parasphenoid is discerned, while the pterygoid bones are hard to identify due to poor preservation. A triangular quadrate is partly exposed. The quadratojugal is narrow, contacting the preopercle posteriorly. A sub-trapezoid bone preserved below the dentary in the paratype is tentatively interpreted as the posterior ceratohyal according to its shape and position. The gular plate, unexposed in the holotype and paratype is probably absent as in other ginglymodians. Little can be seen of the gill arches in the available specimens.

(v) Upper jaw. As a characteristic feature of the Holo-stei, the premaxilla has a deep nasal process that contacts the frontal dorsally. At least two stout, pointed teeth are present along the oral margin of the premaxilla. The maxilla is elongated and low with a series of conical teeth along its oral margin. It bears a robust process at the anterior part that

articulates with the premaxilla and a dorsal supramaxillary process at the middle part of this bone (Figure 2(a)). Posterior to this dorsal process, the maxilla slightly expands posteriorly, having a concave dorsal margin. A low, elongated supramaxillary bone is located just posterior to the dorsal supramaxillary process and above the concave dorsal margin of the maxilla. The presence of a supramaxillary bone was previously interpreted as a halecostome synapomorphy by Patterson and Rosen [26], but as a halecomorph synapomorphy by Grande and Bemis [5]. However, a single supramaxilla is also present in some non-halecomorph neopterygians, such as semionotiforms [17,27], and osteoglossiform teleosts [28]. The presence of supramaxillar bones is recently identified as a synapomorphy of the crown-group Neopterygii by Grande [3].

(vi) Lower jaw. The lower jaw is strong, relatively short and deep, bearing a high coronoid process as commonly seen in crown-group neopterygians. Three elements can be identified in the lower jaw, including a large dentary, an angular, and a relatively small supra-angular. The anterior sensory pores of the mandibular canal on the dentary are

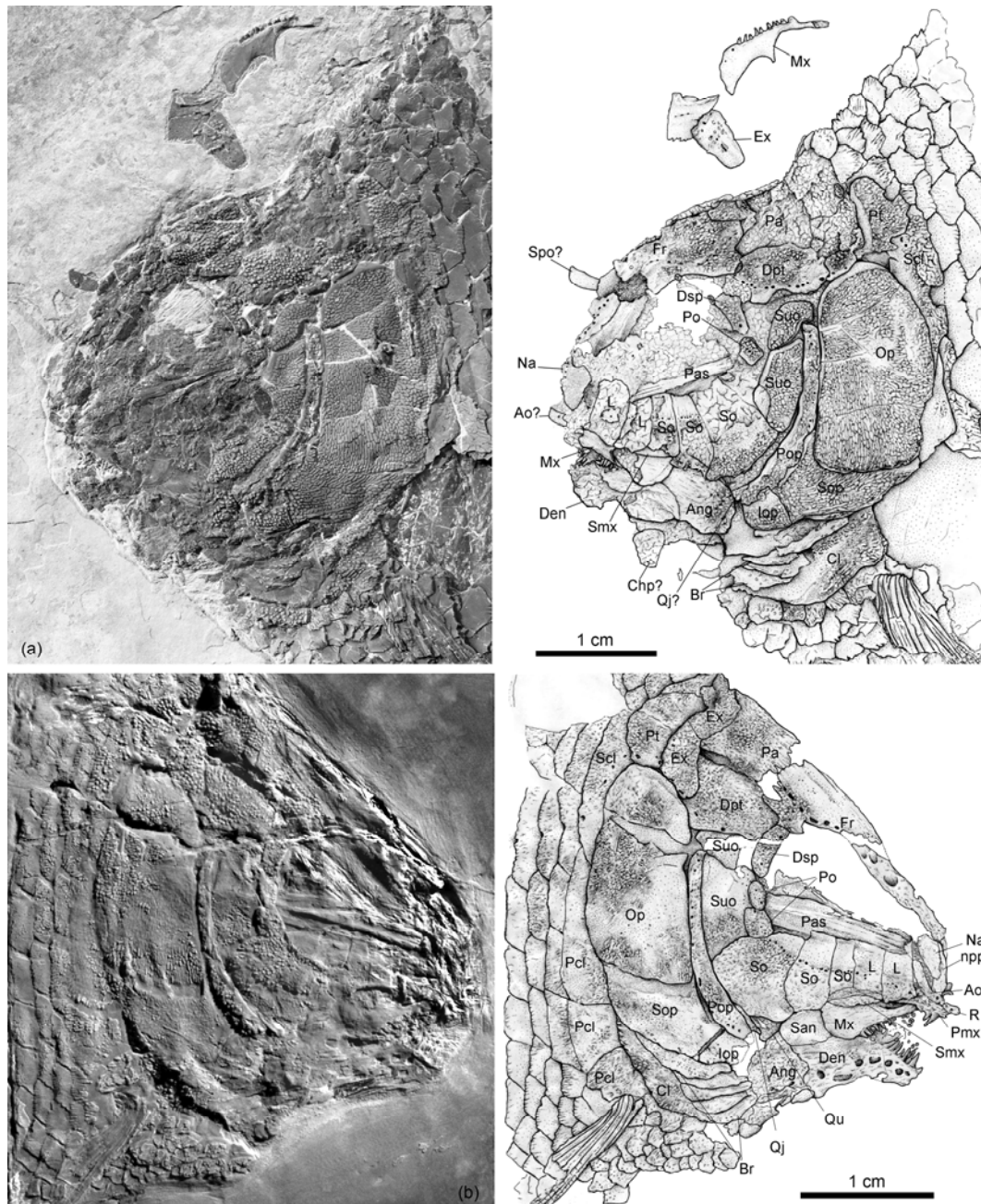


Figure 2 Close-up of cranial skeleton and pectoral girdle of *Kyphosichthys grandei* gen. et sp. nov. (a) Anterior part of paratype (IVPP V10109), anterior facing left; (b) anterior part of holotype (IVPP V10108), anterior facing right. Abbreviation: Ang, angular; Ao, antorbital; Br, branchiostegal rays; Chp, posterior ceratohyal; Cl, cleithrum; Den, dentary; Dpt, dermopterotic; Dsp, dermosphenotic; Ex, extrascapular; Fr, frontal; Iop, interopercle; Mx, maxilla; Na, nasal; npp, nasal process of premaxilla; Op, opercle; Pa, parietal; Pas, parasphenoid; Pcl, postcleithrum; Pmx, premaxilla; Po, postinfraorbital; Pop, preopercle; Pt, posttemporal; Qj, quadratojugal; Qu, quadrate; R, rostral; San, supra-angular; Scl, supracleithrium; Smx, supramaxilla; So, subinfraorbital; Sop, subopercle; Spo, supraorbital; Suo, suborbital.

significantly larger than those posterior exposed on the angular. A row of ten pointed teeth are present along the oral margin of the dentary.

(vii) Opercular and branchiostegal series. The preopercle is deep and narrow, without a distinct horizontal arm. The large opercle is suboval, and is as deep as the preopercle. The relatively small subopercle is low, having a pronounced anterodorsal process that fits between the opercle

and the preopercle. Five branchiostegal rays are preserved in the holotype; they are elongated and low, and become gradually longer backwards.

(viii) Pectoral girdle. The posttemporal is subtriangular, slightly curved backward. The supracleithrum is slightly deeper than the posttemporal; it is inclined anteriorly and partly overlapped by the opercle. The lateral line runs through the posttemporal and supracleithrum, marked by an

anteriorly inclined row of sensory pores on these bones. Three postcleithrae are present. Among them, the upper and the middle are trapezoid, the upper is the largest, twice as deep as the middle, and the lower is the smallest, being triangular in shape (Figure 2(b)). The cleithrum is partly overlapped anteriorly by the subopercle and branchiostegal series. It is large, stickle-shaped.

(ix) Paired fins. Each pectoral fin has eight distally segmented and branched fin rays, preceded by a row of fringing fulcra. The pelvic fins originate below the 9th vertical scale row, and are much shorter than the pectoral fins. Each has six distally segmented and branched fin rays.

(x) Median fins. The dorsal fin originates above the 21st vertical scale row. It has 13 distally segmented fin rays. The first fin ray is unbranched, and is preceded by three basal fulcra and a row of fringing fulcra. The remaining fin rays branch distally.

The anal fin is 50% of the dorsal fin, having six distally segmented fin rays. It originates below the 16th vertical scale row. The first fin ray is unbranched, is preceded by two basal fulcra and a row of fringing fulcra, and the remaining fin rays branch distally.

The caudal fin is hemi-heterocercal, with a scaly lobe extending slightly more than the third length of the dorsal lobe. The caudal fin has a moderately forked posterior margin; the dorsal lobe is almost symmetrical to the ventral lobe. The caudal fin has 23 segmented fin rays, among which 10 rays are in the dorsal lobe. Fringing and basal fulcra are present preceding the upper- and lowermost segmented fin ray in dorsal and ventral lobes.

(xi) Scales. The body is covered by ganoid scales. A series of ridge scales with short spines are present along the dorsal margin. Beside the ridge scales, each side has at most eight and nine horizontal rows of flank scales, respectively, above and below the lateral line. There are a total of 29 anteriorly inclined columns of scales along the lateral line (Figure 1). The anterior lateral line scales are the largest, being twice as deep as they are wide. The scales gradually decrease dorsal-, ventral-, and caudally in size. The articular pegs and anterodorsal extensions are present in the scales. The anterior flank scales are ornamented by small tubercles and ridges, but those in the caudal region are largely smooth. The posterior margins of the scales are serrated.

4 Phylogeny analysis

A cladistic analysis consisting of 15 taxa and 60 characters was conducted to assess the phylogenetic relationships of the new fish taxon *Kyphosichthys* with other taxa of the Neopterygii. Besides the new taxon, the selected taxa include 10 taxa of Triassic-Jurassic neopterygians, including *Australosomus* (Pholidopleuridae), *Dapedium* (Dapediidae), *Felberia* (Polzbergiidae), *Leptolepis* (Leptolepidae), *Luganoia* (Luganoiidae), *Macrosemius* (Macrosemidae), *Per-*

leidus (Perleididae), *Pholidophorus* (Pholidophoridae), *Semionotus* (Semionotidae), and *Watsonulus* (Parasemionotidae) and two taxa of living neopterygians, *Amia* (Amiidae), and *Lepisosteus* (Lepisosteidae). Because the Chondrostei were widely regarded as the sister-group of the Neopterygii [29], two chondrosteian taxa were selected as the out-group, including the Triassic *Birgeria* and the living *Acipenser*. Sixty characters were adopted from previous publications [3,5,6,17,19,30–37] on the phylogenetic relationships of lower actinopterygians (Appendix 1). The data matrix of taxa and characters are given in Appendix 2.

Parsimony analysis was conducted using the branch-and-bound algorithm of PAUP 4.0b10 [21]. All characters were equally weighted and unordered. The phylogenetic analysis resulted in three most parsimonious trees (TL=112 steps, CI=0.6696, RI=0.7431, RC=0.4976). The strict consensus of these three equally parsimonious trees with characters that support the nodes is shown in Figure 3. The character followed by an asterisk (*) has a CI of 1.0.

Our analysis supports the hypothesis that the Ginglymodi are more closely related to the Halecomorphi than to the Teleostei. Given these phylogenetic relationships, we agree with Grande [3] in the resurrection of the term Holostei to include the Ginglymodi and Halecomorphi within the crown-group Neopterygii. *Kyphosichthys* was identified as a ginglymodian in the Holostei.

The new fish taxon *Kyphosichthys* shares the following derived characters of the crown-group Neopterygii, including the presence of a peg-like anterior articular process of the maxilla 21(1)*, four or more infraorbitals 26(2), maxilla free from preopercular 31(1)*, one supramaxilla 32(1), interopercle 44 (1), and absence of dermohyal 29 (0-reversal). The derived characters it shares with the Holostei include presence of tube-like rostral 17(1) and tube-like canal-bearing anterior arm on antorbital 19(1)*. Furthermore, it shares the derived characters of the Ginglymodi in possession of anteriormost lacrimal anterior to orbital ring 18(1)*, three or more lacrimal bones 24(2)*, and absence of gular 45(2). The derived features that are commonly shared by other ginglymodians but, because of incomplete preservation, are unknown in *Kyphosichthys* include the presence of a reduced clavicle with a single row of denticles 47(2)* and the absence of post-temporal fossa 1(1)*, posterior myodome 5(0-reversal), anterior myodome 6(1), and intercalar 14(1).

Within the Ginglymodi, *Kyphosichthys* is more closely related to *Semionotus* and *Lepisosteus* than to *Macrosemius* by possessing a series of ridge scales along dorsal margin 58(1). However, the relationships among *Kyphosichthys*, *Semionotus*, or *Lepisosteus* are unresolved; the three taxa form a polytomy (clade I) in our analysis. In addition to the presence of ridge scales, clade I is supported by the following derived characters: presence of symplectic that is separated from quadrate by quadratojugal 40(2)* and absence of pterotic 13(1).

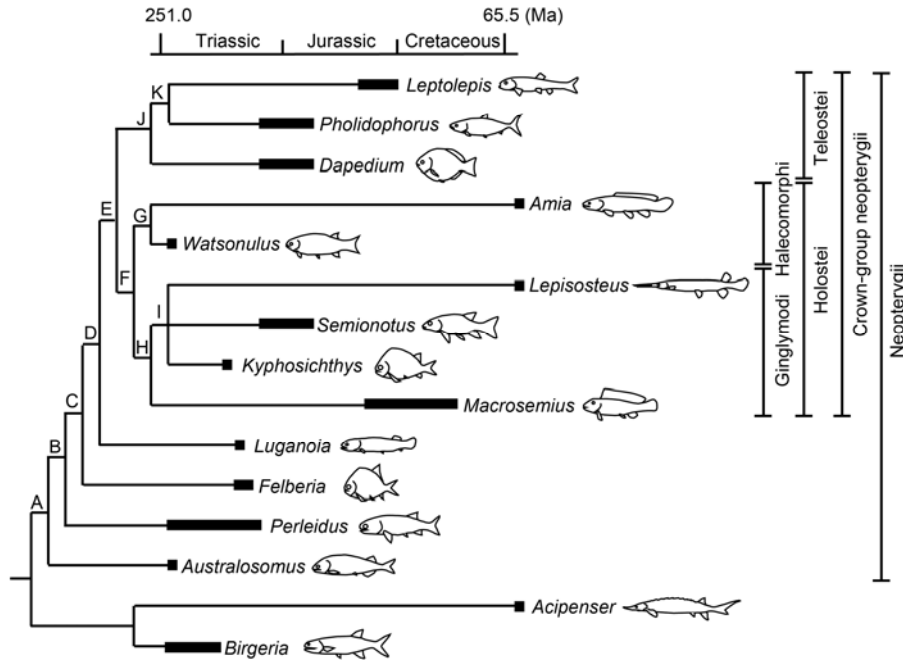


Figure 3 Calibrated strict consensus of three most parsimonious trees, illustrating the phylogenetic relationships and stratigraphic ranges of lower neopterygians. Character states supporting the clades include: A, 2(1), 3(1)*, 5(2), 8(1)*, 9(1)*, 29(1), 55(1)*, 57(1), 59(1), 60(1); B, 4(1), 25(1), 26(0), 38(1)*, 39(1)*, 41(1)*, 45(1), 53(1)*, 54(1)*; C, 36(1)*, 40(1)*; D, 22(1)*, 23(1)*, 33(1), 35(1)*; E, 21(1)*, 26(2), 29(0), 31(1)*, 32(1), 44(1), 60(0); F, 2(0), 16(1), 17(1), 19(1)*, 20(1), 42(1)*; G, 37(1)*, 39(2)*, 46(1)*; H, 1(1)*, 5(0), 6(1), 14(1), 18(1)*, 24(2)*, 45(2), 47(2)*; I, 13(1), 40(2)*, 58(1); J, 11(1)*, 12(1)*, 47(4)*; K, 25(2), 30(1)*, 32(2), 34(1), 48(0), 52(1)*, 56(1)*.

5 Discussion

(i) Convergent evolution. Having a short, deep body with a strongly arched hump between head and dorsal fin, and very deep flank scales, the new ginglymodian fish *Kyphosichthys* exhibits a striking resemblance to the stem-group neopterygian *Felberia*, and shares some resemblance to the basal teleostean *Dapedium* (which differs slightly from *Kyphosichthys* and *Felberia* in the absence of a strongly arched hump between head and dorsal fin). However, our analysis indicates convergent acquisition of these character states among them. An extremely deep and short fish body has independently evolved at least three times in the stem-group neopterygians (e.g. *Felberia*), ginglymodians (e.g. *Kyphosichthys*), and basal teleosteans (e.g. *Dapedium*) within the lower neopterygians.

The deep-bodied *Felberia* is recognized as a stem-group neopterygian that is more basal than the clade *Luganoia* plus crown-group neopterygians because it lacks the following derived features of *Luganoia* plus crown-group neopterygians: the presence of a nasal not forming the anterior margin of the orbit 22(1)*, developed nasal process of premaxilla 23(1)*, maxilla free from preopercle 31(1)*, mobile maxilla in cheek 33(1), and coronoid process 35(1)*.

Traditionally, *Dapedium* and its closely related taxa (e.g. *Tetragonolepis*, *Hemicalypterus*, and *Sargodon*) were assigned to the Semionotidae by Schaeffer [38], Jain [39], and Tinotori [40], or to the Dapedidae (Semionotiformes) by

Lehman [41], and Thies and Herzog [42]. However, our analysis agrees with Olsen [17], Gardiner et al. [32], and Hurley et al. [19] in supporting that *Dapedium* is more closely related to *Pholidophorus* and other teleosts than to the semionotiformes (Ginglymodi). *Dapedium* shares a series of derived features of the Teleostei, including the presence of internal carotid foramen on parasphenoid 11(1)*, efferent pseudobranchial foramen on parasphenoid 12(1)*, and absence of clavicle 47(4)*. To keep the Semionotiformes as a monophyletic group, the Dapedidae should be removed from the Semionotiformes (Ginglymodi). The new fossil fish *Kyphosichthys* represents the first known highly deep-bodied ginglymodian at present.

(ii) Mode of life. Among the extant deep-bodied fishes, *Kyphosichthys* is similar to the boarfish (*Antigonia*, Caproidae) and teardrop butterflyfish (*Chaetodon*, Chaetodontidae) in general shape, though with certain differences in relative size between dorsal and anal fin. All these deep-bodied fishes have a deep and short body. This kind of body has a larger surface area that causes larger drags during swimming relative to fish that have a streamlined body, so they are not fast swimmers. The position of each pectoral fin of the new fish, although still lower than that of extant deep-bodied fishes, is substantially higher in the flank than that of other ginglymodians. This relatively higher positioning of pectoral fins could enhance yaw maneuvering relative to fish with lower pectoral fins [43]. Another similarity among the deep-bodied fishes is that the distance be-

tween the trailing edge of the dorsal fin and the leading edge of the caudal fin is smaller relative to fishes with elongated bodies, like trout. This kind of dorsal fin generates relatively large lateral forces, which provides an advantage for the overall force balance during swimming [44]. Thus, *Kyphosichthys* was unlikely a fast swimmer but had good performance in precise maneuvering, based on studies of functional morphology of extant fishes [43,44]. It was likely adapted for structurally complex habitats (e.g. thick macrophyte beds, rocky areas, or coral reefs) requiring good maneuvering, similar to those of *Felberia* [45] and extant deep bodied fishes [46]. In comparison, other early ginglymodians (e.g. *Semionotus*) with a subterminal snout, typically elongated fusiform body, and relatively long caudal peduncle could be faster swimmers than *Kyphosichthys* and were likely adapted to simple habitats, implicated by the ecological study on extant fishes of Ruehl et al. [46]. The discovery of the new deep-bodied ginglymodian indicates that the earliest ecological diversification of the Ginglymodi occurred at least in the Middle Triassic. Its occurrence adds significantly to the ecological diversity of the already known vertebrate fauna from the Middle Triassic marine ecosystem of the eastern Yangtze Sea that once sustained taxonomically and functionally diverse marine reptiles and other fishes [14].

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Supporting Information

Appendix 1 Characters used in analysis

Appendix 2 Data matrix of taxa and characters

The supporting information is available online at csb.scichina.com and www.springerlink.com. The supporting materials are published as submitted, without typesetting or editing. The responsibility for scientific accuracy and content remains entirely with the authors.