



A Middle Triassic stem-neopterygian fish from China shows remarkable secondary sexual characteristics

Guang-Hui Xu · Li-Jun Zhao

Received: 23 November 2015 / Revised: 31 December 2015 / Accepted: 8 January 2016 / Published online: 23 January 2016
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Abstract Secondary sexual characteristics are features that appear at sexual maturity and distinguish the two sexes of a species. They are readily observed and studied in living animals, but the phenomenon is rather more difficult to identify in fossil taxa. Here we report a new sexually dimorphic stem-neopterygian fish, *Venusichthys comptus* gen. et sp. nov., based on 30 exceptionally well-preserved specimens from the Middle Triassic (Pelsonian, Anisian) Luoping Lagerstätte of eastern Yunnan, China. The discovery represents the oldest known secondary sexual characteristics in Neopterygii. These characteristics, including pointed tubercles on cranial bones, scales and fins, and hook-like contact organ anterior to the anal fin, have three inferred primary functions: maintenance of body contact between the sexes during prespawning behavior or spawning; stimulation of the females during breeding; and defense of nests and territories. Lacking a specialized anal fin in the presumed males, *Venusichthys* would likely have a different reproductive strategy from peltopleurids and other potentially viviparous stem-neopterygians. Moreover, *Venusichthys* shows a unique character combination distinguished from any other stem-neopterygian families and consequently represents a new family of this clade. As

such, the new finding provides an important addition for understanding the behavior, reproduction, and early diversification of Neopterygii.

Keywords Sexual dimorphism · Breeding tubercles · Venusichthyidae · Neopterygii · Actinopterygii

1 Introduction

Secondary sexual characteristics, which are observed in every major group of vertebrates, are phenotypic traits that distinguish the two sexes of a species, but that are not directly related to the reproductive system (different from primary sexual characteristics). These characteristics, including defensive structures, contact organs, breeding tubercles, color variations, voice and size differences, give an individual an advantage over its rivals during courtship and aggressive interactions and have been hypothesized to be the product of sexual selection [1–3]. Studies of secondary sexual characteristics in a species are vital for fully understanding its behavior, reproduction, and evolution. Secondary sexual characteristics are easily observed and studied in living animals, but the situation is rather more complicated in extinct animals, primarily due to inadequacies of sample size or the fragmentary nature of fossil remains.

Neopterygii are the most diverse clade of extant ray-finned fishes [4], which underwent a rapid radiation in the aftermath of end-Permian mass extinction [5]. Here, we report on a new stem-neopterygian on the basis of 30 specimens collected during the last six field seasons from

Electronic supplementary material The online version of this article (doi:10.1007/s11434-016-1007-0) contains supplementary material, which is available to authorized users.

G.-H. Xu (✉)
Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
e-mail: xuguanghui@ivpp.ac.cn

L.-J. Zhao
Zhejiang Museum of Natural History, Hangzhou 310014, China

the early Middle Triassic Luoping Lagerstätte [6, 7] in eastern Yunnan, China. The superb preservation of skeletal details demonstrates a differentiation of phenotypic traits between presumed males and females. Among 30 cataloged specimens, one-third of the individuals bear pointed tubercles on cranial bones, scales and fins, and a hook-like contact organ anterior to the anal fin and are interpreted as being males. Due to the fact that the tubercles and contact organ are likely to distinguish the two sexes, but are not directly related to the reproductive system, they are reasonably interpreted as secondary sexual characteristics. Breeding tubercles and contact organs observed in several families of extant cypriniform fishes, as well as a few gonorynchiform and salmonoid fishes [8], represent a modern analogue for the secondary sexual characteristics present in this ancient taxon. Similar secondary sexual characteristics (pointed tubercles on the skull and dorsal fin) are known from presumed males of the stem-neopterygian *Peltopleurus nuptialis* from the late Ladinian (latest Middle Triassic) of Europe [9]. As the age of the Luoping fossil beds has been well constrained by conodont biostratigraphy (Pelsonian, Anisian, Middle Triassic, ~244 Ma) [6], these new specimens represent the oldest known secondary sexual characteristics in the Neopterygii. The Luoping Lagerstätte fossil beds are composed of thinly laminated micritic limestone alternating with silty limestone, indicating a semi-enclosed intraplatform depositional environment [5, 7].

2 Systematic paleontology

Neopterygii Regan, 1923

Venusichthyidae fam. nov.

Venusichthys comptus gen. et sp. nov.

Etymology The genus epithet is from Latin *venus*, meaning goddess of love, and *ichthys*, meaning fish. The species epithet is from Latin *comptus*, meaning ornamental.

Holotype A nearly complete skeleton of presumed female deposited at the collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. V20010. Standard length is 31 mm.

Referred specimens IVPP V20011–20034, 20055–20058; ZMNH (Zhejiang Museum of Natural History, Hangzhou, China) M1695.

Type locality and horizon Luoping, Yunnan, China; second (upper) member of Guanling Formation, Pelsonian, Anisian, Middle Triassic [6].

Diagnosis A new stem-neopterygian diagnosed by the following combination of features: presence of pointed

anterior process of rostral; absence of supraorbitals; quadratomandibular articulation slightly anterior to middle line of orbit; maxilla notably longer than lower jaw; presence of tubercles and contact organ in presumed males; two preopercular elements on each side; two pairs of branchiostegal rays; anterior lateral line scales six times deeper than wide; dorsal fin larger than anal fin; 24 principal caudal fin rays; and squamation formula of D14/P7, A13, C31/T37.

3 Description and comparison

Venusichthys has a blunt snout, an elongate and fusiform body, and an almost homocercal caudal fin with a forked profile (Figs. 1, 2). All 30 topotypic specimens represent a small-sized stem-neopterygian with a standard length ranging from 25 to 38 mm.

The median rostral is curved, with a pointed anterior process at its mid-portion (Fig. 3). The deep nasal, together with the dorsoventrally narrower antorbital, contributes to the anterior border of orbit. The paired premaxillae are small and elongate; each premaxilla meets its counterpart medially. The frontal is large and elongate, 3.5 times longer than the rectangular parietal, which is slightly wider than long. There are four infraorbitals between antorbital and dermosphenotic. Supraorbitals are absent, as in some stem-neopterygians (e.g., *Australosomus* [10], *Platysiagum* and *Habroichthys* [11, 12]). By contrast, other stem-neopterygians (e.g., Perleididae, Peltopleuridae, Thoracopteridae, and Luganoiidae) generally have at least one supraorbital [13]. In the cheek region, four or five suborbitals are present. The maxilla has an elongate infraorbital portion and a slightly expanded check portion that posteriorly contacts the ventral preopercle. Notably, the preopercle is composed of two elements, a large and deep dorsal one, and a small and elongate ventral one, with the preopercular sensory canal running through both elements. Two or more preopercular elements are otherwise known in a few deep-bodied stem-neopterygians [14–16], but other neopterygians generally have a single preopercle on each side. The operculogular series include a large trapezoidal opercle, a smaller sub-triangular subopercle, two branchiostegal rays on each side, and a median gular. A dermohyal is absent, resembling Thoracopteridae and more crownward neopterygians [16]. *Venusichthys* shows distinct sexual dimorphism in the skull, with presumed males bearing pointed tubercles on many of the cranial bones, including nasals, frontals, parietals, infraorbitals, suborbitals, maxillae, opercular and branchiostegal series (Fig. 3b). By contrast, presumed females lack pointed tubercles on the skull (Fig. 3a).

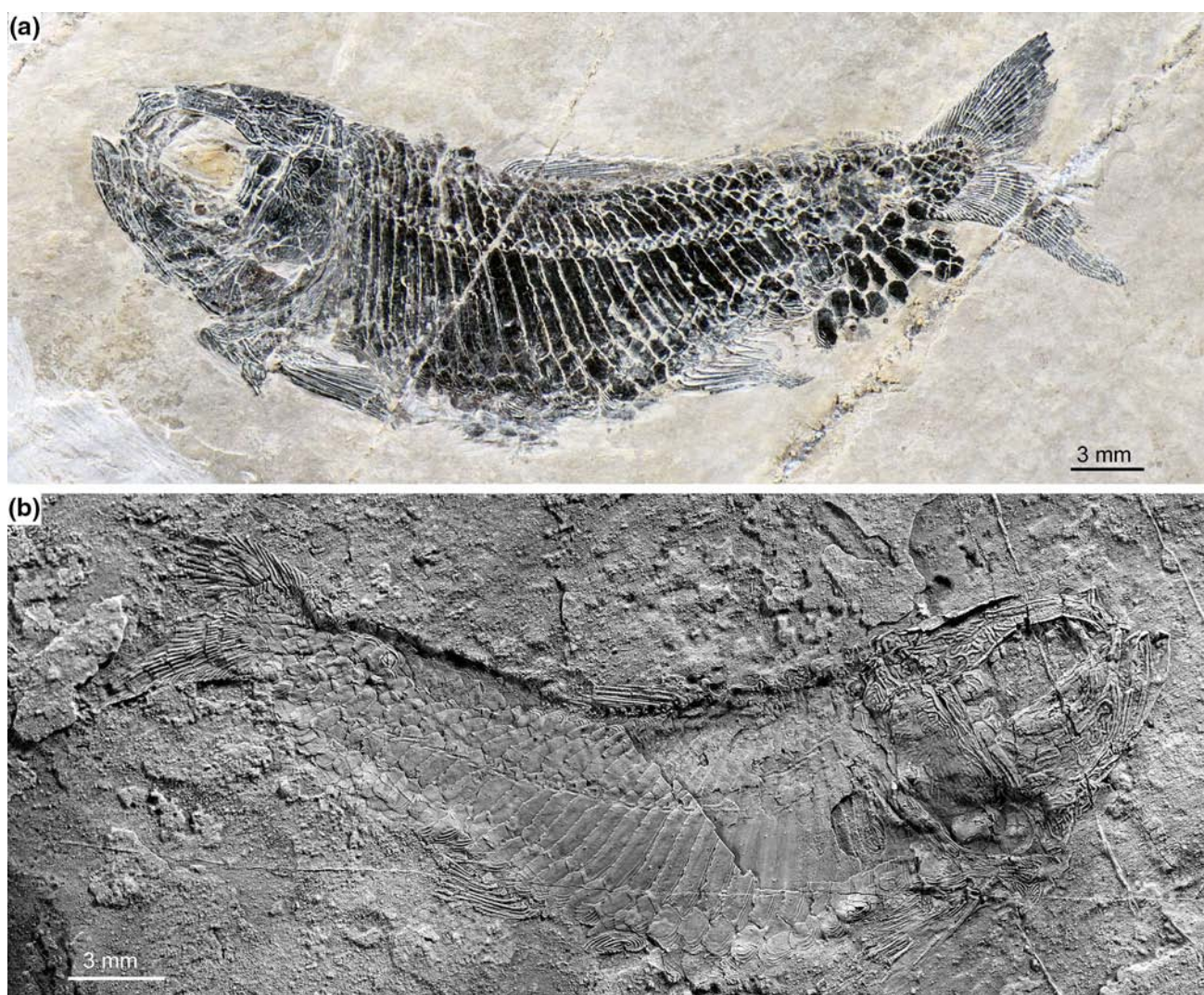


Fig. 1 Complete skeletons of *Venusichthys comptus* gen. et sp. nov. **a** IVPP V20010 (holotype), female; **b** IVPP V20011, coated with ammonium chloride, female

The lower jaw is strong and notably shorter than the maxilla, bearing a laterally protruding ridge that extends longitudinally along almost the full length of this bone. A line of tubercles is present both on this ridge and near the ventral margin of the lower jaw in presumed males (Fig. 3b), but is absent in presumed females. No distinct sutures can be discerned between the dentary and other elements of the lower jaw. The quadratomandibular articulation is located slightly anterior to the midline of orbit. A deep coronoid process is present (Fig. 2e), sharing a derived condition with *Luganoia* and more crownward neopterygians. The teeth at oral margins of jaws are small and conical; they are present along the full length of premaxilla, and only short anterior lengths of maxilla and lower jaw.

The pectoral girdle includes a sub-triangular posttemporal, a deep, anteriorly inclined supracleithrum, a much

deep postcleithrum, a large, sickle-shaped cleithrum, and a small, sub-circular clavicle (Fig. 3). The pectoral fins are large; each has about ten distally segmented and branched rays. Pelvic girdles are not exposed. Each pelvic fin has five or six rays. The dorsal fin has 17–18 principal rays, preceded by four basal fulcra. The anal fin is smaller than dorsal fin and has 10–12 principal rays. The dorsal and anal fin rays are segmented only within their distal regions. The partly exposed endoskeletal radials of dorsal fin show a 1:1 ratio to the rays (IVPP V20055), as in *Perleides* and more crownward neopterygians [13]. The caudal fin has 24 principal rays with a deeply forked profile. Additionally, eight rudimentary rays are present in the ventral lobe and a single rudimentary ray in the dorsal lobe. Fringing fulcra are present in all fins. Pointed tubercles are present on the leading rays of pectoral, dorsal and anal fins of presumed



Fig. 2 *Venusichthys comptus* gen. et sp. nov. **a–d** ZMNH M1695, male; complete skeleton before **(a)** and after coated with ammonium chloride **(b)**, close-up of dorsal fin **(c)** with arrows indicating pointed tubercles along its leading ray, and anal fin **(d)** with arrow indicating hook-like contact organ anterior to anal fin, photographed with fossil submerged in clear water; **e** IVPP V20028, lower jaw with arrow indicating coronoid process, female, photographed with fossil submerged in clear water. Scale bars, 3 mm

males (Fig. 2a–d), but are absent in presumed females. In further contrast to presumed females, presumed males bear a median, hook-like organ anterior to the anal fin (Fig. 2d). This organ is much shorter than the leading anal fin ray and was probably immobile, as its anterior portion is located between a pair of elongate, ventral margin scales.

The body is fully covered by rhomboidal, and presumably ganoid, scales. There are total 37 scales along the lateral line. Among them, scales at anterior region are about six times deeper than wide, and each has a gently serrated posterior margin, a dorsal peg and an anterodorsal process. Dorsal and ventral to the lateral line, there are,

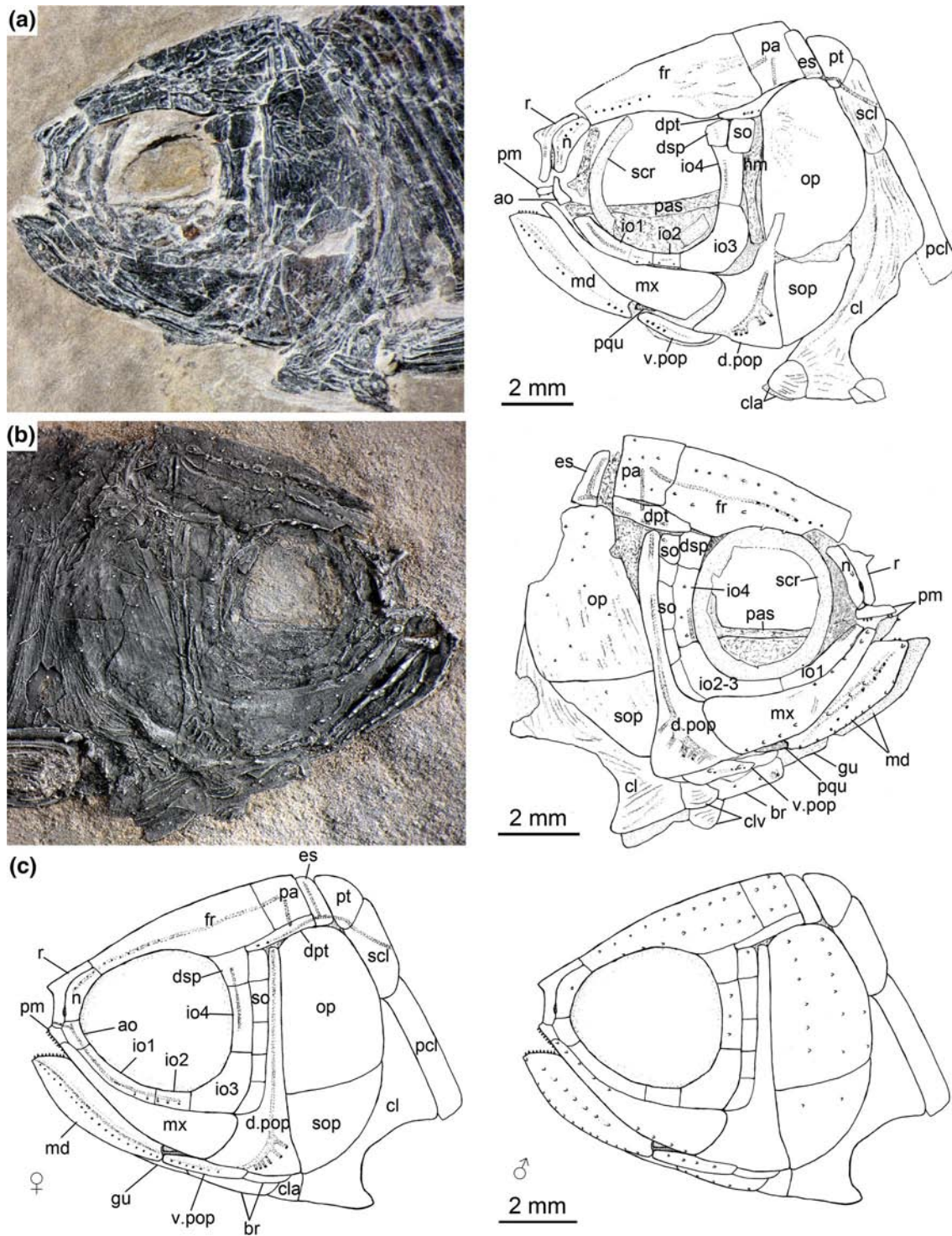


Fig. 3 Skull and pectoral girdle of *Venusichthys comptus* gen. et sp. nov. **a** IVPP V20010, female; **b** ZMNH M1695, male; **c** reconstructions, female (left) and male (right). ao, antorbital; br, branchiostegal ray; cl, cleithrum; cla, clavicle; dpt, dermopterotic; dsp, dermosphenotic; es, extracapsular; fr, frontal; io, infraorbital; md, mandible; gu, gular; mx, maxilla; n, nasal; op, opercle; pa, parietal; pas, parasphenoid; pcl, postcleithrum; pm, premaxilla; pop, preopercle; pqu, palatoquadrate; pt, posttemporal; r, rostral; scl, supracleithrum; scr, sclerotic ring; so, suborbital; sop, subopercle

respectively, two horizontal rows of scales. Scales on the middle flank region are ornamented with dense tubercles in presumed males, but are largely smooth in presumed females. Scales near dorsal and ventral margins of the body are ornamented with oblique ridges in all individuals.

4 Phylogenetic position

Traditionally, most Triassic stem-neopterygians with greatly deepened lateral line scales were grouped into the broadly inclusive ‘Peltopleuriformes’. However, recent phylogenetic analyses indicate that this grade may be paraphyletic, including several independently evolved groups of stem-neopterygians [13]. We performed a phylogenetic analysis based on a data matrix of 80 characters coded across 23 actinopteran taxa with *Pteronisculus* and *Acipenser* selected for out-group comparison (electronic supplementary material). The phylogenetic analysis yields two most parsimonious trees, the strict consensus of which (Fig. 4) recovers *Venusichthys* as the sister taxon to the clade comprising *Luganoia* and more crownward Neopterygii. This grouping is supported by the presence of a coronoid process and a quadratomandibular articulation anterior to posterior border of orbit. However, *Venusichthys* lack two derived features that *Luganoia* shares with more crownward neopterygians: presence of a mobile maxilla and a reduced rostral.

5 Discussion

These new fossil specimens represent an important addition to our understanding of early diversification of neopterygians. Prior to being formally described here, *Venusichthys* material was placed as an indeterminate species within the peltopleurid genus *Placopleurus* in the published album of the Luoping Biota [17]. This was likely due to its resemblance to *Placopleurus* in having deepened lateral line scales and an anteriorly located dorsal fin. However, *Venusichthys* is strikingly different from the type species of *Placopleurus* (*P. primus*) from the late Ladinian (latest Middle Triassic) of Besano, Italy [18], as well as other known peltopleurids [9, 11] in having an anteriorly located quadratomandibular articulation, two preopercular elements, a notably shorter lower jaw relative to maxilla, a deep coronoid process, and a larger dorsal fin relative to anal fin. In addition, *Venusichthys* lacks diagnostic features of any fish classified among other known stem-neopterygian families. Consequently, we erect a new family, *Venusichthyidae*, for *Venusichthys*.

Venusichthys shows an interesting convergent evolution with peltopleurids, basal thoracopterids, habroichthyids,

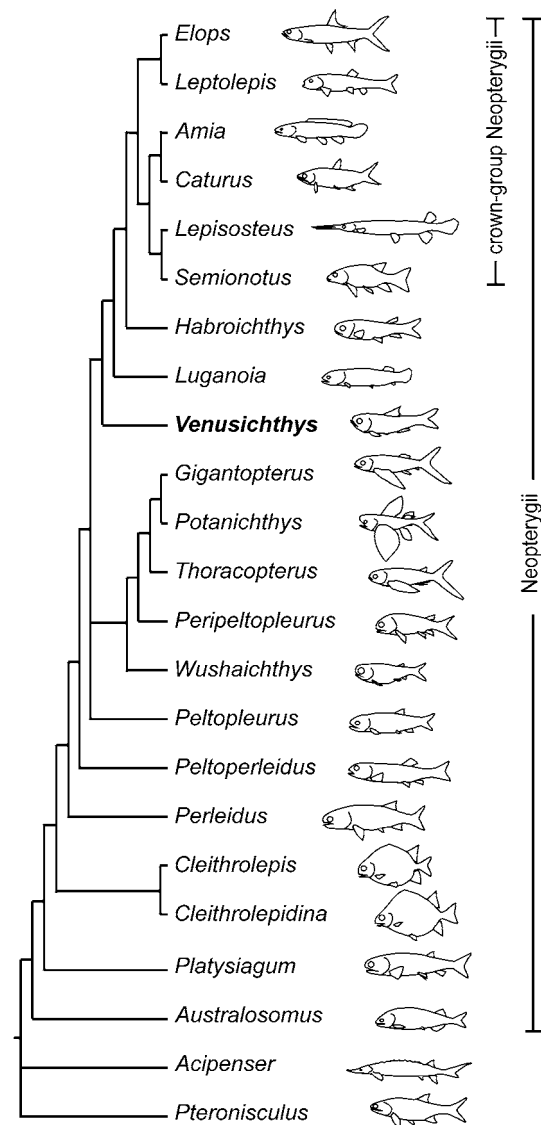


Fig. 4 Strict consensus of two most parsimonious trees, illustrating phylogenetic position of *Venusichthys*. For character description and coding of the characters for sampled taxa, see the electronic supplementary material

luganoiids, and some ‘perleidiforms’ in having greatly deepened lateral line scales. Mutter and Herzog [19] noticed that this homoplastic feature was almost entirely confined to small-sized stem-neopterygians, which is further supported by *Venusichthys*. Notably, many Triassic small-sized stem-neopterygians with conspicuously deepened flank scales, including peltopleurids, basal thoracopterids, and habroichthyids [9, 11, 12, 20], are potentially viviparous because they have hooklets (claws) on specialized anal fin in presumed males. Similar to those in modern viviparous teleosts [21], these hooklets may have played an important role in sperm transfer. However, *Venusichthys* differs from peltopleurids, thoracopterids, and habroichthyids in lacking a specialized anal fin in the

presumed male specimens, possibly indicating that *Venusichthys* have a different reproductive strategy than peltopleurids and other potentially viviparous stem-neopterygians.

Studies of secondary sexual characteristics in modern ray-finned fishes provide a comparative basis for understanding the function of similar characteristics in *Venusichthys*. The living sexually dimorphic ray-finned fishes, including several families of cypriniform fishes and a few gonorynchiform and salmonoid fishes, bear breeding tubercles and contact organs on the head, scales and fins of the male that come in direct contact with the female during prespawning behavior or during the spawning, or that come into contact with other males during fights and defense of territories. Therefore, these traits are inferred to have three primary functions: maintenance of body contact between the sexes during prespawning/spawning; stimulation of the females during breeding; and defense of nests/territories [8]. The secondary sexual characteristics of *Venusichthys* are similar in shape and distribution, to the breeding tubercles and contact organs of living sexually dimorphic ray-finned fishes, and consequently, they may have had similar functions.

Acknowledgments We thank M.M. Chang for constructive suggestions, H. Furrer and M. Richter for access to comparative fossil material in the Paläontologisches Institut and Museum, Universität Zürich (Zürich), and the Natural History Museum (London), respectively, and J.A. Finarelli for stylistic improvement. The research was supported by the National Natural Science Foundation of China (41272002) and the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; 143114).

Conflict of interest The authors declare no conflict of interest on this manuscript.

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