



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

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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

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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).

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