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A review of the Cypriniform tribe Yunnanilini Prokofiev, 2010 from China, with an emphasis on five genera based on morphologies and complete mitochondrial genomes of some species

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ABSTRACT

The loach tribe Yunnanilini from China is reviewed here using morphological characters and complete mitochondrial genomes of select species. Molecular data suggest that the tribe Yunnanilini is not monophyletic and can be divided into three clades. Species of the *Yunnanilus nigromaculatus* group form an independent genus and are placed in *Eonemachilus*. In the phylogenetic tree, *Y. jinxiensis* clusters with *Paranemachilus genilepis*, and *Y. pulcherrimus* clusters with *Micronemacheilus cruciatus*, indicating that *Y. jinxiensis* and *Y. pulcherrimus* belong to *Paranemachilus* and *Micronemacheilus*, respectively. Based on

morphological data, *Y. bailianensis* and *Y. longibarbatus* are placed in *Heminoemacheilus*,

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while *Y. jinxiensis* and *Y. pulcherrimus*, are placed in *Paranemachilus* and *Micronemacheilus*, respectively. *Yunnanilus niulanensis* and *Y. qujinensis* are treated as junior synonyms of *Eonemachilus caohaiensis*. *Eonemachilus*, *Micronemacheilus*, and *Yunnanilus* are show short separation between anterior and posterior nostrils. The genera can be distinguished from each other by mouth structure, lateral line and cephalic lateral-line canals, and papillae on median part of both lips. The anterior and posterior nostrils of *Heminoemacheilus* and *Paranemachilus* are closely set. *Paranemachilus* and *Micronemacheilus* are distinguished by cheeks covered with scales and lips with papillae, respectively. Our phylogenetic tree and morphological characters support *Traccatichthys* as a valid genus, which can be distinguished from *Micronemacheilus* by anterior and posterior nostrils closely set (vs. clearly separated). Four species are placed in *Traccatichthys*.

Keywords: *Eonemachilus*; *Heminoemacheilus*; *Micronemacheilus*, *Paranemachilus*, *Yunnanilus*;
Taxonomy

INTRODUCTION

Loaches belonging to Nemacheilidae are an ecologically important and taxonomically challenging family of freshwater fish distributed in mainland Asia and adjacent islands, as well as in Europe and northeast Africa (e.g., Eschmeyer et al., 2020; Kottelat, 2012; Prokofiev, 2010; Zhang & Zhao, 2016). Nemacheilidae contains 756 species belonging to 47 genera, including 269 species belonging to 22 genera in China (Appendix I, Chen, 2013; Eagderi et al., 2019; Eschmeyer et al., 2020; Gransee et al., 2019; Jiang et al., 2021; Kaya et al., 2020a, 2020b; Kottelat, 2012; ; Prokofiev, 2010; Yoğurtçuoğlu et al., 2020; Zhang & Zhao, 2016). Morphological variation in nemacheilids is often inconsistent with molecular evidence (Chen et al., 2019; Sgouros et al., 2019). For example, based on molecular analyses, *Homatula*, *Nemacheilus*, *Schistura*, *Triplophysa*, and *Yunnanilus* exhibit polyphyly (Chen et al., 2019; Liu et al., 2012; Min et al., 2012; Sgouros et al., 2019; Tang et al., 2006).

Prokofiev (2010) studied the systematics and phylogenetic relationships of the family Nemacheilidae, and recognized five tribes (Vaillantellini Nalbant & Bănărescu 1977, Lefuini Prokofiev 2010, Yunnanilini Prokofiev 2010, Triplophysini Prokofiev 2010, and Nemacheilini Regan 1911) based on 40 morphological characters. Vaillantellini contains a sole genus, *Vaillantella* Fowler 1904; Lefuini includes two genera (*Lefua* Herzensterin 1888 and *Oreonectes* Günther 1868) from East Asia and one genus (*Aborichthys* Chaudhuri 1913) from India and Myanmar; Yunnanilini contains eight genera, including *Eonemachilus* Berg 1938, *Heminoemacheilus* Zhu & Cao 1987, *Micronemacheilus* Rendahl 1944, *Paranemachilus* Zhu

1983, *Petruichthys* Menon 1987, *Protonemacheilus* Yang & Chu 1990, *Traccatichthys* Freyhof & Serov 2001, and *Yunnanilus* Nichols 1925; Triplophysini includes three genera, namely, *Hedinichthys* Rendahl 1933, *Orthrias* Jordan & Fowler 1903, and *Triplophysa* Rendahl 1933; and Nemacheilini, the largest tribe, contains all remaining loaches (Prokofiev, 2010). Additionally, from the phylogenetic relationships among these tribes, Vaillantellini is the most primitive group, forming sister group to the remaining four tribes; Lefuini and Yunnanilini share several primitive features. Yunnanilini originated slightly later than Lefuini; and Triplophysini and Nemacheilini form a sister group, and together into Yunnanilini (Prokofiev, 2010).

In addition to those primitive features, such as posterior of bony capsule of the swim bladder open, open part of the swim bladder and preethmoid-l present. Yunnanilini possesses several diagnostic characters, including head and body laterally compressed; anterior and posterior nostrils slightly separated (distance greater than 1/5 of eye diameter) or closely set, anterior nostril not barbel-like; abdominal axillary lobe absent; capsule of swim bladder developed; and vertebrae 32–40 (Prokofiev, 2010). Among the eight genera placed in Yunnanilini, Prokofiev (2010) considered *Eonemachilus*, *Micronemacheilus*, *Paranemachilus*, and *Yunnanilus* to be valid, and that *Petruichthys* is synonym to *Yunnanilus*. Subsequently, Kottelat (2012) placed *Y. brevis* (Boulenger 1893) and an unnamed *Yunnanilus* species from Myanmar in *Petruichthys*, and treated *Heminoemacheilus*, *Protonemacheilus*, and *Traccatichthys* as valid. Hence, the validity of *Heminoemacheilus*, *Petruichthys*, *Protonemacheilus* and *Traccatichthys* need further systematic research.

Berg (1938) named the genus *Eonemachilus* but did not discuss its relationship with *Yunnanilus*. In subsequent studies, several ichthyologists treated *Eonemachilus* as a synonym of *Yunnanilus* (e.g., Kottelat & Chu, 1988; Yang, 1991; Zhu, 1989). Kottelat (2012) treated *Eonemachilus* as a valid genus, in which *E. nigromaculatus* (Regan 1904), *E. yangzonghaiensis* (Cao & Zhu 1989), and *E. longidorsalis* (Li, Tao & Lu 2000) were placed based on their deep body, terminal mouth, and shared color pattern. However, *Eonemachilus* was not generally accepted in subsequent studies because Kottelat (2012) did not provide persuasive arguments to support the decisions (Du et al., 2015, 2018). Hence, the validity of *Eonemachilus* is remains unclear.

Freyhof & Serov (2001) described the genus *Traccatichthys*, and referred two species from *Micronemacheilus* to this genus, i.e., *T. pulcher* (Nichols & Pope 1927) and *T. taeniatus* (Pellegrin & Chevey 1936). However, Prokofiev (2004) did not concur, naming the species from Hainan Island a *Micronemacheilus zispi* Prokofiev 2004. Although Du et al. (2012) discussed the research history of *Traccatichthys* and mentioned that the validity of *Traccatichthys* is doubtful, they still treated *Traccatichthys* as valid and named *T. tuberculum* Du, Zhang & Chan 2012 from Guangdong Province, and placed *M. zispi* in *Traccatichthys*. However, Zhang & Zhao (2016), without providing an explanation, retained *T. pulcher* and *T. zispi* in *Micronemacheilus* and *T. tuberculum* in *Traccatichthys*. Although *Traccatichthys* is an available name,

the phylogenetic relationships and diagnostic characters between *Traccatichthys* and *Micronemacheilus* remain vague (Du et al., 2012; Prokofiev, 2004, 2010).

One species is recorded within the genus *Protonemacheilus*, i.e., *P. longipectoralis* Yang & Chu 1990 (Zhang & Zhao, 2016). Furthermore, only two species are recorded with the genus *Paranemachilus*, *P. genilepis* Zhu 1983 and *P. pingguoensis* Gan 2013 (Lan et al., 2013; Zhang & Zhao, 2016).

Three species are recorded within of *Heminoemacheilus*, i.e., *H. hyalinus* Lan, Yang & Chen 1996, *H. parva* Zhu & Zhu 2014, and *H. zhengbaoshani* Zhu & Cao 1987 (Lan et al., 2013; Zhang & Zhao, 2016; Zhu & Zhu, 2014).

In contrast, the genus *Yunnanilus* Nichols 1925, which mainly occurs in southern China and parts of Vietnam, is a taxonomically complicated genus (Du et al., 2015, 2018; Kottelat & Chu, 1988; Kottelat, 2012; Lan et al., 2013). Diagnostic characters of the genus *Yunnanilus* include mouth inferior, anterior and posterior nostrils slightly separated, without elongated barbel-like structure (Kottelat & Chu, 1988). To date, 35 species of *Yunnanilus* have been named; however, their taxonomic status remains unclear. Initially, although Kottelat & Chu (1988) stated that species with 14 branched caudal-fin rays and without a lateral line or cephalic pores belong to the subgenus *Eonemachilus*, they also acknowledged that these characters could be of a degenerative nature and therefore treated *Eonemachilus* as a junior synonym to *Yunnanilus*. Subsequently, Yang & Chen (1995) divided the species of *Yunnanilus* into the *nigromaculatus* and *pleurotaenia* species groups, according to the absence or presence of lateral line and cephalic lateral-line canals, respectively. Kottelat (2012) further proposed that *Yunnanilus* is not a monophyletic group and that *Y. longidorsalis*, *Y. nigromaculatus*, and *Y. yangzonghaiensis* should be placed in *Eonemachilus* based on their terminal mouth (vs. inferior) and special color pattern. However, for the taxonomical status of other species, Kottelat (2012) did not provide persuasive evidence, but suggested that *Y. altus* Kottelat & Chu 1988, *Y. analis* Yang 1990, *Y. caohaiensis* Ding 1992, *Y. niger* Kottelat & Chu 1988, and *Y. obtusirostris* Yang 1995 could be placed in *Heminoemacheilus*, and *Y. pulcherrimus* Yang, Chen & Lan 2004 and *Y. chui* Yang 1991 could be placed in *Micronemacheilus*. Additionally, *Y. brevis* and *Y. cruciatus* (Rendahl 1944) were reclassified into *Petruichthys* and *Micronemacheilus*, respectively (Kottelat, 2012, 2013).

From 2017 to 2020, the first author of this paper re-checked 2 494 nemacheilid specimens. The aim of this study was to undertake a comprehensive review of the Chinese species of five genera (i.e., *Eonemachilus*, *Heminoemacheilus*, *Micronemacheilus*, *Paranemachilus*, and *Yunnanilus*) based on type specimens, original descriptions, and complete mitochondrial genome sequences. We used the complete mitochondrial genomes of Nemacheilidae species to discuss taxonomic issues within the tribe Yunnanilini.

MATERIALS AND METHODS

All care and use of experimental animals complied with the

relevant laws of the Chinese Laboratory of Animal Welfare and Ethics. We examined 2 494 specimens of *Eonemachilus* (680), *Heminoemacheilus* (91), *Micronemacheilus* (19), *Oreonectes* (64), *Paranemachilus* (15), *Protonemacheilus* (1), *Traccatichthys* (569), *Troglonectes* (35), and *Yunnanilus* (1 020) belonging to collections from the Kunming Natural History Museum of Zoology, Kunming Institute of Zoology (KIZ), Chinese Academy of Science (CAS), Guangxi Normal University, China (GXNU), Qujing Municipal Bureau of Agriculture and Rural Affairs, Fishery Administration Center, China (FACQR), Heilongtan Reservoir Administration, Shilin, China (HRAS), and Nanning Normal University, China (NNUU). Specimens of *E. bajiangensis* Li 2004 (nine specimens), *E. longidorsalis* (eight specimens), *Y. beipanjiangensis* Li, Mao & Sun 1994 (11 specimens), *Y. macrolepis* Li, Tao & Mao 2000 (five specimens), and *Y. nanpanjiangensis* Li, Tao & Lu 1994 (six specimens), and *Y. spanisbripes* Li, Mao & Yan 2009 (nine specimens) were provided by W.X. Li (Appendix II). Data for *Y. elakatis* Cao & Zhu 1989, *Y. forkicaudalis* Li 1999, *Y. ganheensis* Li, Lu & Lu 2009, and *Y. macrositanus* Li 1999 were obtained from the original descriptions. The fin tissues of *Y. jiuchiensis* and *E. nigromaculatus* were provided by the Kunming Natural History Museum, Kunming Institute of Zoology, Chinese Academy of Science, China. Five specimens of *P. genilepis* were collected by F.G. Luo and were euthanized rapidly by an overdose of anesthetic. The right-side pectoral fin was cut and preserved in ethanol for molecular analyses.

Measurements were taken point-to-point with digital calipers to the nearest 0.1 mm. Counts and measurements were made on the left side of the specimens. Methods of counts and measurements followed Kottelat (1990). Eye diameter was measured horizontally. Abbreviations used include: A: Number of anal-fin rays; BD: Body depth at dorsal-fin origin; C: Number of branched caudal-fin rays; CPD: Caudal-peduncle depth; CPL: Caudal-peduncle length; D: Number of dorsal-fin rays; ED: Eye diameter; HL: Lateral head length; P: Number of pectoral-fin rays; PDL: Predorsal length; PPL: Pre-pelvic length; PAL: Pre-anal length; SL: Standard length; TL: Total length; V: Number of pelvic-fin rays. Visual inspection of lips, nostrils, lateral lines, cephalic lateral-line canals, and scales was performed under a binocular microscope (Leica S6D, 6.3-40x). Species identifications were based on Zhu (1989), Kottelat & Chu (1988), Kottelat (1990), Freyhof & Serov (2001), and original descriptions.

Eonemachilus nigromaculatus, *P. genilepis* and *Y. jiuchiensis* were sequenced in this research. Total genomic DNA was extracted from fin clips using traditional phenol chloroform extraction (Taggart et al., 1992). Complete mitochondrial genomes were then sequenced by the Tsingke Biological Technology Company, Beijing, China following Illumina's protocols, including sample quality testing, library construction, library quality testing, and library sequencing. The genomic sequence data were submitted to GenBank and assigned accession Nos. MW532080–MW532082. To test the phylogenetic position of *Yunnanilus*, complete mitochondrial genomes of 19 nemacheilid species and two botiid species, *Parabotia fasciata* Dabry de Thiersant 1872 and *Leptobotia*

elongata (Bleeker 1870) as outgroup, were obtained from GenBank. Bayesian inference was performed using MRBAYES v3.2.6 (Ronquist et al., 2012). Two runs were performed simultaneously with four Markov chains starting from a random tree. The chains were run for three million generations and sampled every 100 generations. The first 25% of sampled trees were discarded as burn-in and the remaining trees were used to create a consensus tree and estimate Bayesian posterior probabilities (BPPs).

RESULTS

Genome organization

The complete mitochondrial genomes of *E. nigromaculatus* (GenBank accession No. MW532081), *P. genilepis* (GenBank accession No. MW532082), and *Y. jiuchiensis* (GenBank accession NO. MW532080) were 16 594 bp, 16 562 bp, and 16 571 bp long, respectively. They contained two ribosomal RNA (rRNA) genes (12S and 16S), 22 transfer RNA (tRNA) genes, and 15 messenger RNA (mRNA) genes (16 in *P. genilepis*). Like in many teleost fish, most were encoded on the heavy strand (H-strand), except for NADH dehydrogenase subunit 6 (ND6) and seven tRNA genes for Gln, Ala, Asn, Cys, Tyr, Ser, Glu and Pro, which were encoded on the light strand (L-strand). The GC gene content varied from 43.59% to 43.79%.

Phylogenetic relationships

The tribe Yunnanilini, which encompasses *Eonemachilus*, *Petruichthys*, *Micronemacheilus*, *Paranemachilus*, *Yunnanilus*, and *Traccatichthys*, was not monophyletic as its members were grouped into different clades with other tribes (Figure 1). Specifically, *Petruichthys* was closely related to *Schistura*, a genus of the tribe Nemacheilini; *Micronemacheilus*, *Paranemachilus*, and *Y. jiuchiensis* formed a clade with three genera of the tribe Lefuini; and *Eonemachilus* was the sister to

the clade consisting of the tribes Lefuini, Nemacheilini, Triplophysini, and other members of Yunnanilini.

In addition, monophyly of the genus *Yunnanilus* was not supported. *Yunnanilus brevis*, *Y. pulcherrimus*, and *Y. jinxiensis* (presented as *Petruichthys brevis*, *Micronemacheilus pulcherrimus*, and *Paranemachilus jinxiensis* in Figure 1, respectively) did not cluster together with the true *Yunnanilus*, i.e., *Y. jiuchiensis*, but were closely related to *Schistura*, *M. cruciatus*, and *P. genilepis*, respectively. Additionally, *Y. nigromaculatus* (*E. nigromaculatus* in Figure 1) represented the most basal clade of the four tribes (Figure 1). *Yunnanilus sichuanensis* was grouped with *Claea dabryi* with short branches.

Systematics

In Nemacheilidae, 10 genera, including *Eonemachilus*, *Heminoemacheilus*, *Lefua*, *Micronemacheilus*, *Oreonectes*, *Paranemachilus*, *Protonemacheilus*, *Traccatichthys*, *Troglonectes*, and *Yunnanilus*, have an anterior nostril pierced at the end of a short tube. The lips of *Micronemacheilus* and *Traccatichthys* possess papillae (vs. lips smooth with furrows in other genera, Figure 2A–D). In *Lefua*, *Oreonectes*, and *Troglonectes*, the anterior nostril extremity is barbel-like (vs. no barbel-like elongation in other genera). Furthermore, the anterior and posterior nostrils of *Heminoemacheilus*, *Micronemacheilus*, *Paranemachilus*, *Protonemacheilus*, and *Traccatichthys* are closely set (vs. separated in other genera, Figure 2G (separated) and Figure 2H (closely set)).

Key to genera of Nemacheilidae with tube-like anterior nostrils

- 1) Lips with large papillae.....2
- Lips with furrows but no papillae.....3
- 2) Anterior and posterior nostrils slightly separated.....
.....*Micronemacheilus*

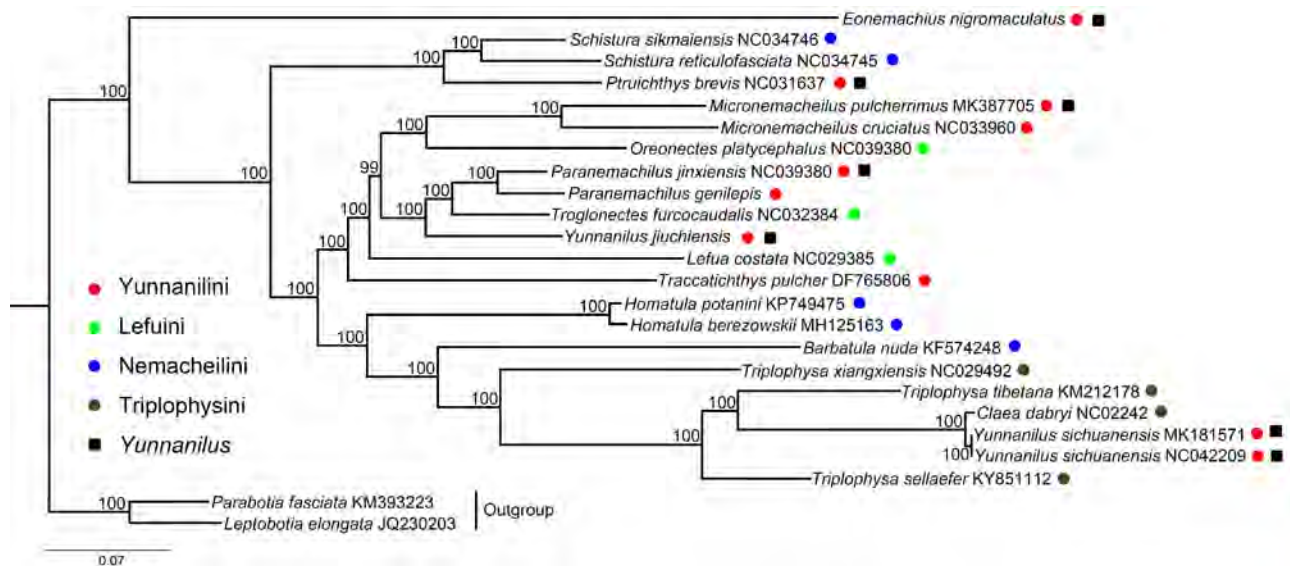


Figure 1 Bayesian phylogram of Yunnanilini based on mitochondrial genomes of 22 nemacheilid and two botiid species (outgroups). Round represents four tribes: Red, Yunnanilini; Blue, Nemacheilini; Green, Lefuini; Brown, Triplophysini. Black square is currently recognized *Yunnanilus* species.

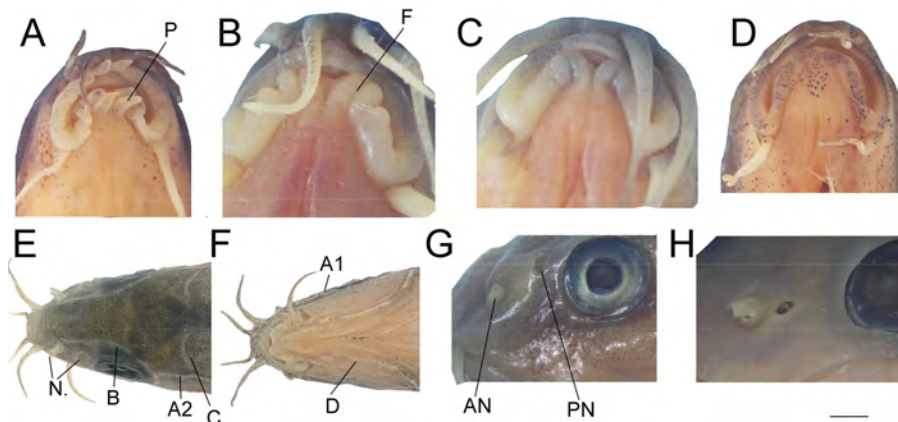


Figure 2 The types of lower lip, cephalic lateral-line pores and nostrils in *Yunnanilini*

A–D: Lower lip. A: *Micronemacheilus pulcherrimus*, with papillae; B: *Yunnanilus pleurotaenia*; C: *Paranemachilus jinxiensis*, with two strong furrows on each side; D: *Y. chui*, with slight furrows. E, F: *Y. jiuchiensis*, cephalic lateral-line pores. G: *Eonemachilus caohaiensis*, anterior and posterior nostrils well separated. H: *Heminoemacheilus zhengbaoshani*, anterior and posterior nostrils closely set. Abbreviations: A1+A2: Infraorbital canal; AN: Anterior nostril; B: Supraorbital canal; C: Supratemporal canal; D: Preoperculomandibular canal; F: Furrow; N: Nostril; P: Papillae; PN: Posterior nostril. Scale bar: 1 mm.

- Anterior and posterior nostrils closely set.....*Traccatichthys*
- 3) Tip of anterior nostril elongated and barbel-like.....4
- Tip of anterior nostril not elongated and barbel-like.....6
- 4) Longitudinal stripe as wide as eye diameter from snout to base of caudal fin.....*Lefua*
- Without longitudinal stripe.....5
- 5) Dorsal fin with 6–7 branched rays, caudal fin rounded.....*Oreonectes*
- Dorsal fin with 8–10 branched rays, caudal fin forked.....*Troglonectes*
- 6) Anterior and posterior nostrils closely set.....7
- Anterior and posterior nostrils slightly separated.....8
- 7) Cheeks scaled.....*Paranemachilus*
- Cheek scaleless.....9
- 8) Bony capsule of swim bladder open posteriorly.....*Heminoemacheilus*
- Bony capsule of swim bladder closed posteriorly.....*Protonemacheilus*
- 9) Lateral line and cephalic lateral-line canals present.....*Yunnanilus*
- Lateral line and cephalic lateral-line canals absent.....*Eonemachilus*

Based on the 35 species currently assigned to *Yunnanilus*, morphological monophyly of *Yunnanilus* was not supported. Firstly, the lips can be of two types, with large papillae or with furrows. The lips of *Y. pulcherrimus* have large papillae and the anterior and posterior nostrils slightly separated, distance nearly 1/4 of eye diameter, hence this species is transferred to *Micronemacheilus* and the valid species name is *M. pulcherrimus* (Yang, Chen & Lan 2004). Secondly, the anterior and posterior nostrils position occurs as two types, i.e., slightly separated or closely set. The nostrils of *Y. bailianensis*, *Y. longibarbatu*s, and *Y. jinxiensis* are closely set, but are clearly separated in other species of *Yunnanilus*. Furthermore, *Y. jinxiensis* has scaled cheeks. The typical character of

Yunnanilus, i.e., well-separated anterior and posterior nostrils suggests that *Y. bailianensis*, *Y. longibarbatu*s, and *Y. jinxiensis* should not be placed within this genus. Here, *Y. bailianensis* and *Y. longibarbatu*s are placed in *Heminoemacheilus*, and *Y. jinxiensis* is placed in *Paranemachilus* based on their closely set anterior and posterior nostrils and tube-like anterior nostril, with cheek scales in *Y. jinxiensis*. Thus, the valid species names are *H. bailianensis* (Yang 2013), *H. longibarbatu*s (Gan, Chen & Yang 2007), and *P. jinxiensis* (Zhu, Du & Chen 2009), respectively. Thirdly, lateral line and cephalic lateral-line canals are absent in the *Y. nigromaculatus* species group, but present in the *Y. pleurotaenia* species group.

In the phylogenetic tree (Figure 1), *Y. nigromaculatus* (*E. nigromaculatus* in Figure 1) did not cluster with *Yunnanilus* but was basal and formed as sister group with all other genera. Additionally, *Y. brevis*, *Y. pulcherrimus*, and *Y. jinxiensis* (*P. brevis*, *M. pulcherrimus*, and *P. jinxiensis*, respectively, in Figure 1) are closely related to *Schistura*, *M. cruciatus*, and *P. genilepis*, respectively. Hence, the species currently assigned to *Yunnanilus* can be divided into five genera, i.e., *Eonemachilus*, *Heminoemacheilus*, *Micronemacheilus*, *Paranemachilus*, and *Yunnanilus*, based on morphological characters and molecular analyses (Figures 1, 2). Species of the *nigromaculatus* species group, except for *Y. bailianensis* (moved to *Heminoemacheilus*), *Y. longibarbatu*s (moved to *Heminoemacheilus*), and *Y. jinxiensis* (moved to *Paranemachilus*) are placed in *Eonemachilus* based on anterior and posterior nostrils slightly separated (distance larger than 1/2 of eye diameter) and lateral line and cephalic lateral-line canals absent. *Yunnanilus pulcherrimus* is placed in *Micronemacheilus* due to large papillae on lips and anterior and posterior nostrils slightly separated (distance nearly 1/4 of eye diameter), and species of the *pleurotaenia* species group are retained in *Yunnanilus*.

The common character among *Eonemachilus*, *Micronemacheilus*, and *Yunnanilus* is the well separated

anterior and posterior nostrils. This group can be distinguished from each other by lateral line and cephalic lateral-line canals absent in *Eonemachilus* (vs. present in *Micronemacheilus* and *Yunnanilus*) and papillae on lips present in *Micronemacheilus* (vs. absent in *Eonemachilus* and *Yunnanilus*). *Heminoemacheilus* and *Paranemachilus* share closely set nostrils but can be separated from each other by cheek scales present in *Paranemachilus* vs. absent in *Heminoemacheilus* (Figure 2).

***Eonemachilus* Berg, 1938**

Eonemachilus Berg, 1938: 314 (type species: *Nemacheilus nigromaculatus* Regan, 1904: 192). Kottelat, 2012: 82.

Diagnosis: Head and body deep, laterally compressed. Anterior and posterior nostrils well-separated (distance larger than 1/2 of eye diameter), posterior nostril closer to eye than to anterior nostril. Lateral line and cephalic lateral-line canals absent.

Remarks: Although some ichthyologists treated *Eonemachilus* as a synonym to *Yunnanilus* (e.g., Kottelat & Chu, 1988; Yang, 1991; Zhu, 1989), Kottelat (2012) treated *Eonemachilus* as a valid genus, with *E. nigromaculatus*, *E. yangzonghaiensis*, and *E. longidorsalis* placed in this genus based on deep body, terminal mouth, and special color pattern. In this study, species of the *nigromaculatus* species group are placed in *Eonemachilus* based on anterior and posterior nostrils well-separated (distance larger than 1/2 of eye diameter), lateral line and cephalic lateral-line canals absent, and mouth terminal or inferior. This result was supported by molecular data for *E. nigromaculatus* (Figure 1).

Key to species of *Eonemachilus*

- 1) Caudal fin with 14 branched rays.....2
 - Caudal fin with 15–16 branched rays.....*E. obtusirostris*
- 2) Outer gill rakers on first gill arch absent.....3
 - Outer gill rakers on first gill arch present.....6
- 3) Only caudal peduncle covered with scales.....
 - *E. yangzonghaiensis*
 - Whole body covered with scales.....4
- 4) Dorsal fin with 11 or 12 branched rays.....*E. longidorsalis*
 - Dorsal fin with nine branched rays.....5
- 5) Maximum head width more than 15.2%–20.8% SL, pectoral fin with 9 branched rays.....*E. caohaiensis*
 - Maximum head width less than 12.6%–14.6% SL, pectoral fin with 12 branched rays.....*E. pachycephalus*
- 6) Mouth terminal, 3–5 outer gill rakers on first gill arch....
 - *E. nigromaculatus*
 - Mouth inferior, 1–2 outer gill rakers on first gill arch.....7
- 7) Pectoral fin with nine branched rays..... *E. bajiangensis*
 - Pectoral fin with 11–12 branched rays.....8
- 8) Head depth 56.4% HL, eye diameter 14.5% HL.....*E. niger*
 - Head depth more than 58% HL, eye diameter more than 15% HL..... *E. altus*

***Eonemachilus altus* (Kottelat & Chu, 1988)**

Yunnanilus altus, Kottelat & Chu, 1988a: 72, fig. 6 (type locality: Xiaoshuiho at Haijiashao, Zhanyi County, Yunnan, China); Chu & Chen, 1990: 17–19, fig. 12.

(Figure 3E1; Supplementary Figure S1A)

Material examined: Twelve specimens. Paratypes

KIZ1977001324, 1329, 1340–341, 1343, 1346–1347, 1349, 1374, 1376, 1378, 1396, 43.5–56.1 mm SL; Xiaoshuiho at Haijiashao, Zhanyi County, Yunnan, China, N25.6603°, E103.9647°, Nanpanjiang River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; pectoral fin with 11–12 branched rays; caudal fin with 14 branched rays; 2 outer and 12 inner gill rakers on first gill arch; processus dentiformis present; eye diameter 16%–22% HL; body depth 25%–31% SL; caudal-peduncle length 90%–116% of its depth.

Description: Body deep, compressed laterally, dorsal and ventral profiles strongly convex. Dorsal fin with 4 simple and 9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11–12 branched rays; pelvic fin with 8 branched rays; caudal fin with 14 branched rays. 2 outer and 12 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated (distance larger than 1/2 of eye diameter), posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin base, predorsal length 53%–57% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal fin emarginate.

Body covered with embedded scales, except between pectoral fins. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank dark brown, belly and lower part of flank brownish, covered with minute, dark brown, irregular blotches above level of pectoral fins. Fins hyaline.

Distribution: Known only from the Nanpanjiang River, a Pearl River tributary.

Remarks: *Eonemachilus altus* can be distinguished from other congeneric species by body covered with scales, outer gill raker on first gill arch present, caudal fin with 14 branched rays, and eye diameter 16%–22% of lateral head length.

***Eonemachilus bajiangensis* (Li, 2004)**

Yunnanilus bajiangensis Li, 2004: 94 (type locality: Heilongtan Reservoir, Shilin County, Yunnan, China).

(Figure 3E2; Supplementary Figure S1B)

Material examined: Nine specimens. Paratype HRAS9504004 and 8 uncat., 34.8–56.6 mm SL; Heilongtan Reservoir, Shilin County, Yunnan, China, N24.7635°, E103.3057°, Bajiang drainage, Nanpanjiang River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; 1–2 outer and 11–12 inner gill rakers on first gill arch; pectoral fin with 9 branched rays; caudal-peduncle length 9%–13% SL; head width 51%–66% HL; caudal-peduncle length 78%–99% of its depth.

Description: Body deep, compressed laterally, dorsal and ventral profiles strongly convex. Dorsal fin with 3 simple and 9

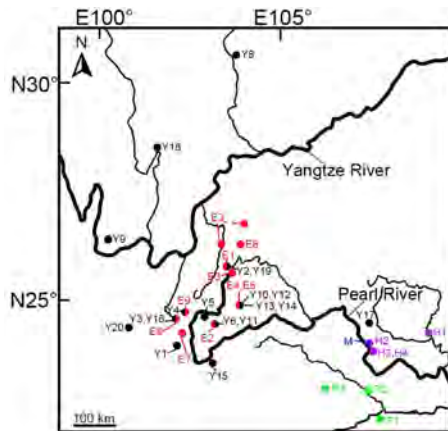


Figure 3 Map showing distribution of species of *Eonemachilus*, *Heminoemacheilus*, *Paranemacheilus*, *Micronemacheilus*, and *Yunnanilus*

Red represents *Eonemachilus*: E1: *E. altus*; E2: *E. baijiangensis*; E3: *E. caohaiensis*; E4: *E. longidorsalis*; E5: *E. niger*; E6: *E. nigromaculatus*; E7: *E. obtusirostris*; E8: *E. pachycephalus*; E9: *E. yangzonghaiensis*. Purple represents *Heminoemacheilus*: H1: *H. baillianensis*; H2: *H. longibarbatus*; H3: *H. zhengbaoshani*; H4: *H. hyalinus*. Blue represents *Micronemacheilus*: M: *M. pulcherrimus*. Green represents *Paranemacheilus*: P1: *P. genilepis*; P2: *P. jinxiensis*; P3: *P. pingguoensis*. Black represents *Yunnanilus*: Y1: *Y. analis*; Y2: *Y. beipanjiangensis*; Y3: *Y. chui*; Y4: *Y. discoloris*; Y5: *Y. elakatis*; Y6: *Y. forkicaudalis*; Y8: *Y. jiuchiensis*; Y9: *Y. longibulla*; Y10: *Y. macrogaster*; Y11: *Y. macrositanus*; Y12: *Y. macrolepis*; Y13: *Y. nanpanjiangensis*; Y14: *Y. paludosus*; Y15: *Y. parvus*; Y16: *Y. pleurotaenia*; Y17: *Y. retrodorsalis*; Y18: *Y. sichuanensis*; Y19: *Y. spanisbripes*; Y20: *Y. chuanheensis*.

branched rays; anal fin with 3 simple and 5–6 branched rays; pectoral fin with 9 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 14 branched rays. 1–2 outer and 11–12 inner gill rakers on first gill arch. Mouth terminal; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin base, predorsal length 52%–56% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length less than its depth. Caudal fin straight.

Body covered with embedded scales, except between pectoral fins. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank yellow-brown, belly and lower part of flank yellowish. Back of body with 15–18 large, dark brown spots, lateral body with irregular short bars above level of pectoral fins. Fins hyaline.

Distribution: Known from only Baijiang drainage, Nanpanjiang River, a Pearl River tributary.

Remarks: In the genus *Eonemachilus*, *E. baijiangensis*, *E. altus*, *E. niger* and *E. nigromaculatus* share 1–2 outer gill rakers on first gill arch. However, *E. baijiangensis* can be separated from these species by possessing pectoral fin with 9 branched rays (vs. 11–12).

***Eonemachilus caohaiensis* (Ding, 1992)**

Yunnanilus caohaiensis Ding, 1992: 489–491 (type locality: Lake Caohai, Weining County, Guizhou, China).

Yunnanilus niulanensis Chen, Yang & Yang, 2012: 58 (type locality: Yanglinhe River, Songming County, Yunnan, China) (new synonym).

Yunnanilus qujinensis Du, Lu & Chen, 2015: 249–254 (type locality: spring near Hujiafen Reservoir, Qujin City, Yunnan, China) (new synonym).

(Figure 3E3; Supplementary Figure S1C–E)

Material examined: Thirty-seven specimens, KIZ1990004187–4188, 4190, 1996003121–3122, 3124–3125, 3127, 46.7–67.8 mm SL; Lake Caohai, Weining County, Guizhou, China, N26.8506°, E104.2344°, a Yangtze River tributary. KIZ20060281, 287, 291–293, 45.5–55.2 mm SL; Yanglinhe River, Songming County, Yunnan, China, N25.2428°, E103.0648°. KIZ2013000636–659, 54.0–58.6 mm SL; spring near Hujiafen Reservoir, Qujin City, Yunnan, China, N25.4189°, E103.9511°.

Diagnosis: Whole body covered with scales; pectoral fin with 10–11 branched rays; caudal fin with 14 branched rays; outer gill rakers on first gill arch absent, 9–13 inner gill rakers on first gill arch; processus dentiformis present; body depth 22.1%–29.9% SL.

Description: Body deep and compressed laterally, dorsal and ventral profiles strongly convex. Dorsal fin with 4 simple and 9–10 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 10–11 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 14 branched rays. Outer gill rakers on first gill arch absent, 9–13 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin base, predorsal length 52%–60% SL. Anal fin straight, tip reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 66%–105% of its depth. Caudal fin emarginate.

Body covered with embedded scales, except between pectoral fins. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper 2/3 of flank dark brown, covered with large brown spots, belly and lower part of flank brownish. Fins hyaline or rays brown.

Distribution: Known from Jinsha and Nanpanjiang rivers.

Remarks: Although *Y. caohaiensis*, *Y. niulanensis* and *Y. qujinensis* were described as separate species in earlier

researches (Chen et al., 2012; Ding, 1992; Du et al., 2015), it is difficult to identify these species based on morphological characters alone. Chen et al. (2012) stated that *Y. niulanensis* can be distinguished from *Y. caohaiensis* by caudal-peduncle length less than its depth (vs. larger than or equal to its depth), and fins hyaline (vs. fins brown or black-brown). However, the CPL 73%–91% of its depth in *Y. niulanensis* (vs. 84%–105% in *Y. caohaiensis*) and fins obviously not hyaline in *Y. niulanensis* (Supplementary Figure S1E). Additionally, Du et al. (2015) stated that *Y. qujinensis* can be distinguished from *Y. caohaiensis* and *Y. niulanensis* by dorsal fin with 10 branched rays (vs. 11). However, a difference of only one in the number of dorsal fin branched rays is not a reliable species diagnosis, as most branched rays among species could be within that range. Hence, *Y. niulanensis* and *Y. qujinensis* are treated as synonyms to *Y. caohaiensis*, under the valid species name *E. caohaiensis*. *Eonemachilus caohaiensis* can be distinguished from other congeneric species by mouth inferior, body scaled, outer gill rakers on first gill arch absent, caudal fin with 14 branched rays and eye diameter 16%–26% HL. Kottelat (2012) considered that *Y. caohaiensis* could be a species of *Heminoemacheilus*. However, *Y. caohaiensis* is placed in *Eonemachilus* due to anterior and posterior nostrils well-separated and lateral line and cephalic lateral-line pores absent.

***Eonemachilus longidorsalis* (Li, Tao & Lu, 2000)**

Yunnanilus longidorsalis Li, Tao & Lu, in Li, Tao, Mao & Lu, 2000: 350, figs. 4–6 (type locality: Agang Longtan pool, Luoping County, Yunnan, China).

Eonemachilus longidorsalis, Kottelat, 2012: 82.

(Figure 3E4; Supplementary Figure S1F)

Material examined: Eight specimens. HRAS9506001–3, 5 uncat., 25.0–40.0 mm SL; Agang Longtan pool, Luoping County, Yunnan, China, N25.0765°, E104.1091°, Nanpanjiang River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; dorsal fin with 11–12 branched rays; anal fin with 7 branched rays; pectoral fin with 10 branched rays; caudal fin with 14 branched rays; outer gill rakers absent, 12 inner gill rakers on first gill arch; caudal-peduncle length 141%–190% of its depth.

Description: Body deep, compressed laterally, dorsal and ventral profiles strongly convex. Dorsal fin with 4 simple and 11–12 branched rays; anal fin with 3 simple and 7 branched rays; pectoral fin with 9–10 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 14 branched rays. Outer gill rakers absent, 12 inner gill rakers on first gill arch. Mouth terminal; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin close to middle of snout tip and caudal-fin base, predorsal length 47%–52% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin straight.

Body covered with embedded scales, except between pectoral fins. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestine straight.

Color pattern in formalin: Body and head brownish, covered with minute, dark brown, irregular blotches above level of pectoral fins, except lateral body, from body capsules to vertical half of pectoral fin. Dorsal fin, anal fin, and caudal fin with two lines of brown spots, other fins hyaline.

Distribution: Known from Nanpanjiang River, a Pearl River tributary.

Remarks: In the genus *Eonemachilus*, *E. longidorsalis* and *E. yangzonghaiensis* share outer gill rakers on first gill arch absent and mouth terminal. However, *E. longidorsalis* can be separated from *E. yangzonghaiensis* by whole body covered with scales (vs. only caudal peduncle scaled).

***Eonemachilus niger* (Kottelat & Chu, 1988)**

Yunnanilus niger, Kottelat & Chu, 1988: 73, fig. 8 (type locality: Tatantze, Luoping County, Yunnan, China); Chu & Chen, 1990: 16, fig. 10.

(Figure 3E5; Supplementary Figure S1G)

Material examined: Holotype KIZ1980001275, 60.5 mm SL; Tatantze, Luoping County, Yunnan, China, N24.6563°, E104.3663°, Nanpanjiang River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; pectoral fin with 12 branched rays; caudal fin with 14 branched rays; two outer and 11 inner gill rakers on first gill arch; processus dentiformis present; eye diameter 15% HL.

Description: Body deep, compressed laterally, dorsal and ventral profiles strongly convex. Dorsal fin with 4 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11 branched rays; pelvic fin with 8 branched rays; caudal fin with 14 branched rays. Two outer and 11 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin base, predorsal length 55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth larger than its length. Caudal fin emarginate.

Body covered with embedded scales, except between pectoral fins and on dorsal midline in front of and behind dorsal fin. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and fins black, without clear color pattern.

Distribution: Known from the Nanpanjiang River, a Pearl River tributary.

Remarks: Kottelat (2012) considered that this may be a species of *Heminoemacheilus*, but it is placed in *Eonemachilus* based on anterior and posterior nostrils well-separated and lateral line and cephalic lateral-line canals

absent. *Eonemachilus niger* can be distinguished from other congeneric species by mouth terminal, two outer gill rakers on first gill arch, and eye diameter 15% HL.

***Eonemachilus nigromaculatus* (Regan, 1904)**

Nemachilus nigromaculatus Regan, 1904: 192 (type locality: Yunnan fu = Lake Dianchi in Kunming, Yunnan, China).

Yunnanilus nigromaculatus, Kottelat & Chu, 1988: 68, fig. 2; Chu & Chen, 1990:14, fig. 8.

Eonemachilus nigromaculatus, Kottelat, 2012: 82, fig. 10.8.2. (Figure 3E6; Supplementary Figure S1H)

Material examined: Two specimens. KIZ0000001695–1696, 56.8–72.5 mm SL; Yunnan fu = Lake Dianchi in Kunming, Yunnan, China, N24.9525°, E102.6515°. KIZ2015003550 was sequenced in Luquan County, Kunming, Yunnan, China, N25.5615°, E102.4735°, collected by S. W. Liu, October 2015.

Diagnosis: Whole body covered with scales; pectoral fin with 11–12 branched rays; 3–5 outer and 11–12 inner gill rakers on first gill arch; processus dentiformis present; head width 20%–22% SL; caudal-peduncle length 78%–80% of its depth.

Description: Body deep, compressed laterally, dorsal and ventral profiles strongly convex. Dorsal fin with 4 simple and 8–9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11–12 branched rays; pelvic fin with 7 branched rays; caudal fin with 14 branched rays. 3–5 outer and 11–12 inner gill rakers on first gill arch. Mouth terminal; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 56%–58% SL. Anal fin straight, tip reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth larger than its length. Caudal fin straight.

Body covered with embedded scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and head brownish, covered with minute, dark brown, irregular blotches above level of pectoral fins, belly and lower part of flank yellowish. Fins hyaline.

Distribution: Known from Dianchi basin.

Remarks: In the genus *Eonemachilus*, *E. nigromaculatus*, *E. altus*, *E. bajiangensis* and *E. niger* share gill rakers on first gill arch present. However, *E. nigromaculatus* can be separated from these species by mouth terminal (vs. inferior), 3–5 outer gill rakers on first gill arch (vs. 1–2), and head width 20%–22% SL (vs. less than 20% SL).

***Eonemachilus obtusirostris* (Yang, 1995)**

Yunnanilus obtusirostris, Yang, in Yang & Chen, 1995: 21, fig. 6 (type locality: West Dragon Spring, Chengjiang County, Yunnan, China).

(Figure 3E7; Supplementary Figure S1I)

Material examined: Three specimens. Paratypes KIZ1987005735, 1987004002–4003, 24.5–37.8 mm SL; West Dragon Spring, Chengjiang County, Yunnan, China, N24.6930°, E102.8856°, Nanpanjiang River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; pectoral fin with 9–10 branched rays; caudal fin with 15–16 branched rays; outer gill rakers absent, 10 inner gill rakers on first gill arch; processus dentiformis absent.

Description: Body compressed laterally. Dorsal fin with 4 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 9–10 branched rays; pelvic fin with 6 branched rays; caudal fin with 15–16 branched rays. Outer gill rakers absent, 10 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin base, predorsal length 53%–55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth larger than its length. Caudal fin emarginate.

Body covered with embedded scales, except between pectoral fins. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank dark brown, belly and lower part of flank brownish, without clear color pattern. Fins hyaline.

Distribution: Known from Nanpanjiang River, a Pearl River tributary.

Remarks: *Eonemachilus obtusirostris* can be distinguished from other congeneric species by caudal fin with 15 or 16 branched rays and processus dentiformis absent. Furthermore, *E. obtusirostris* can be distinguished from *E. altus*, *E. bajiangensis*, *E. nigromaculatus*, and *E. niger* by outer gill raker on first gill arch absent (vs. present), from *E. yangzonghaiensis* and *E. longidorsalis* by inferior mouth (vs. terminal), and from *E. pachycephalus* by pectoral fin with 9–10 branched rays (vs. 12).

***Eonemachilus pachycephalus* (Kottelat et Chu, 1988)**

Yunnanilus pachycephalus, Kottelat & Chu, 1988: 74, fig. 10 (type locality: Weizhangho at Yangliu, Xuanwei County, Yunnan, China); Chu & Chen, 1990: 16–17, fig. 11.

(Figure 3E8; Supplementary Figure S1J)

Material examined: Nine specimens. Paratypes KIZ1982002829, 2831, 2834, 2849, 2863, 2872, 2890, 2893, 2897, 42.2–59.5 mm SL; Weizhangho at Yangliu, Xuanwei County, Yunnan, China, N26.6191°, E104.2753°, Nanpanjiang River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; pectoral fin with 12 branched rays; caudal fin with 14 branched rays; outer gill rakers absent, 11 inner gill rakers on first gill arch; processus dentiformis present; maximum head width 13%–15% SL.

Description: Body compressed laterally. Dorsal fin with 4 simple and 9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 12 branched rays; pelvic fin with 8 branched rays; caudal fin with 14 branched rays. Outer gill rakers absent, 11 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin base, predorsal length 54%–56% SL. Anal fin straight, tip reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin reaching anus. Caudal-peduncle length 93%–133% of its depth. Caudal fin emarginate.

Body covered with embedded scales, except belly in front of pelvic fins. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestine straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish, back with dark brown pigment forming irregular larger spots. Fins hyaline.

Distribution: Known from the Nanpanjiang River, a Pearl River tributary.

Remarks: In the genus *Eonemachilus*, *E. pachycephalus*, *E. caohaiensis*, *E. longidorsalis*, and *E. obtusirostris* share whole body covered with scales and outer gill rakers on first gill arch absent. However, *E. pachycephalus* can be separated from congeneric species by the following combination of characters: processus dentiformis on upper jaw present (vs. absent in *E. obtusirostris*), inferior mouth (vs. terminal in *E. longidorsalis*), pectoral fin with 12 branched rays (vs. 9–11 in *E. caohaiensis*, *E. longidorsalis* and *E. obtusirostris*), lateral head length 27%–29% SL (vs. 25%–26% in *E. obtusirostris*, 30%–32% in *E. caohaiensis*), head height 47%–55% HL (vs. greater than 57% in *E. obtusirostris* and *E. longidorsalis*).

***Eonemachilus yangzonghaiensis* (Cao & Zhu, 1989)**

Yunnanilus sp., Kottelat & Chu, 1988: 85, fig. 20.

Yunnanilus nigromaculatus yangzonghaiensis Cao & Zhu, in Zheng, 1989: 45, fig. 23 (type locality: Lake Yangzonghai, Yiliang County, Yunnan, China).

Yunnanilus yangzonghaiensis, Zhu, 1989: 19–20, fig. 10.

Without specimens, from description by Zhu (1989).

(Figure 3E9)

Diagnosis: Only caudal peduncle scaled; pectoral fin with 9–10 branched rays; caudal fin with 12–14 branched rays (mostly 14); outer gill rakers absent, 11–14 inner gill rakers on first gill arch; mouth terminal, processus dentiformis present; caudal-peduncle length 120%–160% of its depth.

Description: Body deep, compressed laterally, dorsal and ventral profiles strongly convex. Dorsal fin with 3 simple and 9–11 branched rays (mostly 10); anal fin with 3 simple and 5 branched rays; pectoral fin with 9–10 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 12–14 branched rays (mostly 14). Outer gill rakers absent, 11–14 inner gill rakers on

first gill arch. Mouth terminal; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils well-separated, posterior nostril closer to eye than to anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Predorsal length 50%–54% SL. Anal fin straight, tip not reaching base of caudal fin base. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body scaleless, except caudal peduncle. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and head brownish, covered with minute, dark brown, irregular blotches above level of pectoral fins. Dorsal and caudal fins with brown spots, other fins hyaline.

Distribution: Known from Lake Yangzonghai, N24.9412°, E103.0119°, Nanpanjiang River, a Pearl River tributary.

Remarks: *Eonemachilus yangzonghaiensis* can be separated from other congeneric species by body scaleless, except caudal peduncle (vs. whole body scaled).

***Heminoemacheilus* Zhu & Cao, 1987**

Heminoemacheilus Zhu & Cao, 1987: 324 (type species: *Heminoemacheilus zhengbaoshani* Zhu & Cao, 1987: 324).

Diagnosis: Lateral line incomplete, not reaching end of pectoral fin when folded backward or absent. Anterior and posterior nostrils closely set, anterior one tube-like. Mouth inferior. Check scaleless. Papillae on lips absent.

Remarks: *Heminoemacheilus parva* is placed in *Troglonectes* based on the anterior and posterior nostrils slightly separated, anterior nostril barbel-like. Additionally, two species of *Yunnanilus*, i.e., *Y. bailianensis* and *Y. longibarbatus*, are here referred to *Heminoemacheilus* due to anterior and posterior nostrils closely set, cheeks scaleless, and lips smooth, without papillae.

Key to species of *Heminoemacheilus*

- 1) Eyes absent *H. hyalinus*
- Eyes normal 2
- 2) Lateral line and cephalic lateral-line pores present.....
- *H. zhengbaoshani*
- Lateral line and cephalic lateral-line pores absent3
- 3) Outer gill rakers present on first gill arch.....*H. bailianensis*
- Outer gill rakers absent on first gill arch.....
- *H. longibarbatus*

***Heminoemacheilus bailianensis* (Yang, 2013)**

Yunnanilus bailianensis, Yang, in Lan et al., 2013: 51–55, figs. 36, 37 (type locality: Bailian Cave, Liuzhou City, Guangxi, China).

(Figure 3H1; Supplementary Figure S2A, E)

Material examined: Four specimens, GXNU201801–4, 26.3–33.4 mm SL; Bailian Cave, Liuzhou City, Guangxi, China, N24.2116°, E109.4338°, Hongshui River, a Pearl River tributary.

Diagnosis: Processus dentiformis absent; lateral line and cephalic lateral-line pore absent. One outer gill raker and 12–13 inner gill rakers on first gill arch. Lateral head length 29%–30% SL; head depth 49%–51% HL. Caudal fin forked.

Description: Body compressed laterally. Dorsal fin with 3 simple and 8–9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 12–13 branched rays; pelvic fin with 7 branched rays; caudal fin with 16 branched rays. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw. Anterior and posterior nostrils closely set, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 53%–58% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin reaching anus. Caudal-peduncle depth less than its length. Caudal fin forked. Body almost scaleless.

Color pattern in formalin: Back and upper part of flank yellow, belly and lower part of flank yellowish. Vertical black stripe along lateral line wider than pupil from posterior operculum to base of caudal fin. Fins hyaline.

Distribution: Known from Bailian Cave, Hongshui River, a Pearl River tributary.

Remarks: Lan et al. (2013) described *Y. bailianensis* as scaleless, but a few scales were observed in specimens from the type locality. *Yunnanilus bailianensis* possesses typical *Heminoemacheilus* characters, i.e., anterior and posterior nostrils closely set, anterior one tube-like, cheeks scaleless, and lips without papillae. Hence, *Y. bailianensis* is placed in *Heminoemacheilus* in this study. The species can be distinguished from other congeneric species by lateral line and cephalic lateral-line absent and caudal fin forked.

***Heminoemacheilus hyalinus* Lan, Yang & Chen, 1996**

Heminoemacheilus hyalinus Lan, Yang & Chen, 1996: 109 (type locality: subterranean water outlet near Bao'an Town, Du'an County, Guangxi, China).

(Figure 3H4; Supplementary Figure S2C)

Material examined: Six specimens. Holotype, KIZ1994000011, paratypes, KIZ1994000012–16, 37.5–42.2 mm SL; subterranean water outlet near Bao'an Town, Du'an County, Guangxi, China, N24.1008°, E107.8631°, Hongshui River, a Pearl River tributary.

Diagnosis: No pigmentation and no eyes; caudal fin with 14 or 15 branched rays; body colorless.

Description: Body compressed laterally. Dorsal fin with 3 simple and 7–8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11–12 branched rays; pelvic fin with 5 branched rays; caudal fin with 14–15 branched rays. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw. Anterior and posterior nostrils closely set, anterior nostril tube-like. Eyes absent. Lateral line and cephalic lateral-line pores present.

Dorsal-fin origin farther from snout tip than from caudal-fin origin. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin anterior to dorsal-fin origin, tip of pelvic fin not

reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body covered with embedded scales, except between pectoral fins and head. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and head yellow, without color pattern. Fins hyaline.

Distribution: Known from Hongshui River, a tributary of the Pearl River.

Remarks: *Heminoemacheilus hyalinus* can be distinguished from other congeneric species by eyes absent and caudal fin with 14 or 15 branched rays.

***Heminoemacheilus longibarbatu*s (Gan, Chen & Yang, 2007)**

*Yunnanilus longibarbatu*s, Gan, Chen & Yang, 2007: 322, fig. 1 (type locality: Gaoling Township, Du'an County, Guangxi, China).

(Figure 3H2; Supplementary Figure S2B, F)

Material examined: Seven specimens. Paratypes KIZ2003050248, 250, 252–254, 256–257, 42.1–58.2 mm SL; Gaoling Township, Du'an County, Guangxi, China, N24.0639°, E108.0533°, Hongshui River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; outer gill rakers absent and 12–13 inner gill rakers on first gill arch; processus dentiformis absent; lateral line and cephalic lateral-line pores absent.

Description: Body compressed laterally. Dorsal fin with 3 simple and 8–9 branched rays; anal fin with 3 simple and 5–6 branched rays; pectoral fin with 10–11 branched rays; pelvic fin with 6 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 12–13 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw. Anterior and posterior nostrils closely set, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores absent.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 51%–55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body covered with embedded scales, except between pectoral fins. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank yellow, belly and lower part of flank yellowish. Dark brown spots form a vertical stripe along lateral line from posterior of eye to base of caudal fin, upper part of lateral line with minute, dark brown, irregular spots. Fins hyaline.

Distribution: Known from Hongshui River, a Pearl River tributary.

Remarks: *Yunnanilus longibarbatu*s possesses typical characters of *Heminoemacheilus*, i.e., anterior and posterior nostrils closely set, anterior one tube-like, check scaleless, and lips without papillae. The species can be distinguished from other congeneric species by lateral line and cephalic

lateral-lines absent and outer gill rakers on first gill arch absent.

***Heminoemacheilus zhengbaoshani* Zhu & Cao, 1987**

Heminoemacheilus zhengbaoshani Zhu & Cao, 1987: 324, figs. 1–4 (type locality: subterranean water outlet near Du'an County, Guangxi, China).

(Figure 3H3; Supplementary Figure S2D, G)

Material examined: Three specimens. GXNU10060163, 166, 175, 71.6–81.6 mm SL; subterranean water outlet near Du'an County, Guangxi, China, N23.9192°, E108.1056°, Hongshui River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; one outer gill raker and 15–16 inner gill rakers on first gill arch; processus dentiformis present; lateral line and cephalic lateral-line pores present.

Description: Body compressed laterally. Dorsal fin with 3 simple and 7–9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11–12 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 16–17 branched rays. One outer and 12–13 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw. Anterior and posterior nostrils closely set, anterior nostril tube-like. Eyes medium sized, eye diameter less than interorbital distance. Lateral line and cephalic lateral-line pores present. Cephalic lateral-line canals with 9–10 supraorbital, 3+9–10 infraorbital, 2+2 or 3+3 supratemporal, and 11–12 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 53%–55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body covered with embedded scales, except between pectoral fins. Air bladder with two chambers, anterior chamber in bony capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and head dark brownish, without color pattern. Fins hyaline.

Distribution: Known from Hongshui River, a Pearl River tributary.

Remarks: *Heminoemacheilus zhengbaoshani* can be distinguished from other congeneric species by the lateral line and cephalic lateral-line pores present.

***Micronemacheilus* Rendahl, 1944**

Micronemacheilus Rendahl, 1944: 45 (type species: *Nemacheilus cruciatus* Rendahl, 1944: 37).

Diagnosis: Lateral line incomplete. Anterior and posterior nostrils slightly separated (distance 1/5 of eye diameter), posterior nostril closer to anterior nostril than to eye. Mouth inferior. Cheeks scaleless. Median parts of upper and lower lips with one and two pairs of delicate papillae, respectively. Lower posterior margin of inter-opercular with 3–4 indentations. Body with 14–18 black bars from operculum to caudal peduncle.

Remarks: Rendahl (1944) established *Micronemacheilus* for *Nemacheilus cruciatus* from Central Vietnam. However, re-

examination of *M. cruciatus* by Freyhof & Serov (2001) showed that it belonged to *Yunnanilus*. Freyhof & Serov (2001) erected *Traccatichthys* for *Nemacheilus taeniatus* Pellegrin & Chevey 1936 and included *M. pulcher* (Nichols & Pope 1927) in this genus. Kottelat (2012, 2013) considered *Micronemacheilus* to be valid. Zhang & Zhao (2016) also placed *T. pulcher* (Nichols & Pope 1927) and *T. zispi* (Prokofiev, 2004) in *Micronemacheilus*, but without providing additional reasoning. In this study, we follow Kottelat (2012, 2013) and consider *Micronemacheilus* to be valid based on several characters, including large papillae in median portion of both lips, indentations along posterior margin of operculum, and color pattern. *Micronemacheilus* can be distinguished from *Traccatichthys* by anterior and posterior nostrils slightly separated (vs. closely set) and molecular analyses (Figure 1).

***Micronemacheilus pulcherrimus* (Yang, Chen & Lan, 2004)**

Yunnanilus pulcherrimus Yang, Chen & Lan, 2004: 112 (type locality: Du'an County, Guangxi, China, Hongshuihe River, a Pearl River tributary).

(Figure 3M; Supplementary Figure S3)

Material examined: Six specimens, paratypes, KIZ1999001786–1787, 2002003720, 3723, 5673–5674, 38.5–47.8 mm SL; Du'an County, Guangxi, China, N23.9192°, E108.1056°, Hongshuihe River, a Pearl River tributary.

Diagnosis: Whole body covered with scales; pectoral fin with 8–10 branched rays; caudal fin with 16 branched rays; outer gill rakers absent, 11–12 inner gill rakers on first gill arch; processus dentiformis present; lateral line incomplete, not reaching end of pectoral fin when folded backwards. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye. Mouth inferior. One pair of papillae on median part of upper lip, two pairs of papillae on median part of lower lip. Lower posterior margin of operculum with four prominent indentations. Cheeks scaleless. Body with 14–18 black vertical bars from operculum to caudal peduncle.

Description: Body compressed laterally. Dorsal fin with 4 simple and 8–9 branched rays; anal fin with 3 simple and 5–6 branched rays; pectoral fin with 8–10 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 11–12 inner gill rakers on first gill arch. Mouth inferior. Median part of upper lip with one pair of papillae, lower lip with two pairs of papillae. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter greater than interorbital distance. Lateral line and cephalic lateral-line pores present. Cephalic lateral-line canals with 3–5 supraorbital, 3+8 infraorbital, 2+2 supratemporal, and 5 mandibular pores.

Predorsal length 50%–55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body covered with embedded scales. Cheeks scaleless. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish. Flank with 14–18 black vertical bars, 1–9 bars thin, 10–18 bars twice as wide as former bars. Spaces between bars wider than bars. Vertical black stripe along lateral line wider than pupil from eye to base of caudal fin. Fins hyaline.

Distribution: Guangxi, China, and Vietnam.

Remarks: *Yunnanilus pulcherrimus* is moved to *Micronemacheilus* based on the following characters: lips with papillae, lower posterior margin of opercula with four prominent indentations, cheeks scaleless, and body with 14–18 black vertical bars from operculum to caudal peduncle. Unfortunately, no specimens of *M. cruciatus* were available for this study, so we compared *M. pulcherrimus* with the description of *M. cruciatus* by Freyhof & Serov (2001). *Micronemacheilus pulcherrimus* and *M. cruciatus* are difficult to distinguish from each other based on morphological characters alone, but their validity is supported by molecular data (Luo et al., 2019).

***Paranemachilus* Zhu, 1983**

Paranemachilus Zhu, 1983: 311 (type species: *Paranemachilus genilepis* Zhu, 1983: 311).

Diagnosis: Lateral line incomplete. Anterior and posterior nostrils closely set, anterior one tube-like. Mouth inferior. Lips smooth. Cheeks scaled.

Remarks: *Heminoemacheilus* and *Paranemachilus* share similar body shape, anterior and posterior nostrils closely set, and incomplete lateral line. However, *Paranemachilus* can be distinguished from *Heminoemacheilus* by cheeks covered with scales (vs. scaleless). *Yunnanilus jinxiensis* Zhu, Du, Chen & Yang 2009 is referred to *Paranemachilus* based on cheeks scaled and anterior and posterior nostrils closely set.

Key to species of *Paranemachilus*

- 1) Outer gill rakers on first gill arch present.....*P. pingguoensis*
– Outer gill rakers on first gill arch absent.....2
- 2) Caudal-peduncle length less than its depth.....*P. genilepis*
– Caudal-peduncle length larger than its depth *P. jinxiensis*

***Paranemachilus genilepis* Zhu, 1983**

Paranemachilus genilepis Zhu, 1983: 311, figs. 1–4 (type locality: Fusui County, Guangxi, China).

(Figure 3P1; Supplementary Figure S4C)

Material examined: Five specimens, GXNU201908001–5, 68.4–91.3 mm SL; Fusui County, Guangxi, China, N22.6353°, E107.9041°, Hongshuihe River, a Pearl River tributary.

Diagnosis: Outer gill rakers absent, 18 inner gill rakers on first gill arch. Pectoral fin with 11–13 branched rays; pre-anal fin length 79%–82% SL; caudal-peduncle length less than its depth.

Description: Body compressed laterally. Dorsal fin with 3 simple and 7–9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11–13 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 16–18 branched rays. Outer gill rakers absent, 18 inner gill rakers on first gill arch. Mouth inferior. Lips smooth. Anterior and posterior nostrils closely set, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital distance. Lateral line and cephalic lateral-line pores present. Cephalic lateral-

line canals with 11–12 supraorbital, 3+9–12 infraorbital, 3+3 supratemporal, and 10–11 mandibular pores.

Predorsal length 55%–58% SL. Anal fin straight, tip not reaching base of caudal-fin origin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length less than its depth. Caudal fin emarginate.

Body, including cheeks, covered with embedded scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank dark brown, belly and lower part of flank yellow brown. Many small, irregular, dark brown spots on back. Many irregular, dark brown spots forming longitudinal stripe on both sides from head to caudal-peduncle base. Fins hyaline.

Distribution: Known from Pearl River basin.

Remarks: *Paranemachilus genilepis* can be distinguished from other congeneric species by a combination of the following features: outer gill rakers on first gill arch absent (vs. present in *P. pingguoensis*), 18 inner gill rakers on first gill arch (vs. 14 in *P. jinxiensis*), pre-anal fin length 79%–82% SL (vs. 71%–77% in *P. jinxiensis*), and caudal-peduncle length 88%–98% of its depth (vs. 99%–113% in *P. pingguoensis* and 100%–130% in *P. jinxiensis*).

***Paranemachilus jinxiensis* (Zhu, Du & Chen, 2009)**

Yunnanilus jinxiensis Zhu, Du & Chen, in Zhu, Du, Chen & Yang, 2009: 196, fig. 1 (type locality: Ludong Village, Jinxi County, Guangxi, China).

(Figure 3P2; Supplementary Figure S4A)

Material examined: Holotype, KIZ2008008627, 61.6 mm SL, paratypes, KIZ2008008628, 8629, 8630, 8631, 49.9–59.2 mm SL; Ludong Village, Jinxi County, Guangxi, China, N23.1345°, E106.3041°, May 2008.

Diagnosis: Pectoral fin with 13–14 branched rays. Outer gill rakers absent, 14 inner gill rakers on first gill arch; pre-anal fin length 71%–77% SL; caudal-peduncle length larger than its depth.

Description: Body compressed laterally. Dorsal fin with 3 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 13–14 branched rays; pelvic fin with 7–8 branched rays; caudal fin with 17 branched rays. Outer gill rakers absent, 14 inner gill rakers on first gill arch. Mouth inferior. Lips smooth, with strong furrows. Anterior and posterior nostrils closely set, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital distance. Lateral line and cephalic lateral-line pores present. Cephalic lateral-line canals with 9 supraorbital, 3+9 infraorbital, 2+2 supratemporal, and 10 mandibular pores.

Predorsal length 53%–59% SL. Anal fin straight, tip not reaching base of caudal-fin origin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 100%–130% of its depth. Caudal fin emarginate.

Body, including cheeks, covered with embedded scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank dark brown, belly and lower part of flank brownish. Spots forming irregular, short bars along lateral line, flank and head with many short, dark brown bars. Fins hyaline.

Distribution: Known from Pearl River.

Remarks: *Yunnanilus jinxiensis* possesses typical characters of *Paranemachilus*, including anterior and posterior nostrils closely set and cheeks scaled. Hence, the species is moved to *Paranemachilus* in this study. It can be distinguished from other congeneric species by the following combination of characters: outer gill rakers on first gill arch absent (vs. present in *P. pingguoensis*), 14 inner gill rakers on first gill arch (vs. 18 in *P. genilepis*), and pre-anal length 71%–77% of SL (vs. larger than 78% in *P. pingguoensis* and *P. genilepis*).

***Paranemachilus pingguoensis* Gan, 2013**

Paranemachilus pingguoensis, Gan, 2013: 28–32, figs. 18, 19 (type locality: Guohua Township, Pingguo County, Guangxi, China).

(Figure 3P3; Supplementary Figure S4B)

Material examined: Five specimens, GXNU20111001–5, 55.1–65.0 mm SL; Guohua Township, Pingguo County, Guangxi, China, N23.3202°, E107.6037°, collected by J.H. Lan October 2011.

Diagnosis: Pectoral fin with 12–13 branched rays. Outer gill rakers present, 17 inner gill rakers on first gill arch; pre-anal fin length 78%–82% SL; caudal-peduncle length 99%–113% of its depth.

Description: Body compressed laterally. Dorsal fin with 3 simple and 8–9 branched rays; anal fin with 3 simple and 5–6 branched rays; pectoral fin with 12–13 branched rays; pelvic fin with 6 branched rays; caudal fin with 17–18 branched rays. One or two outer and 17 inner gill rakers on first gill arch. Mouth inferior. Lips smooth, with strong furrows. Anterior and posterior nostrils closely set, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital distance. Lateral line and cephalic lateral-line pores present. Cephalic lateral-line canals with 9–10 supraorbital, 3+11–12 infraorbital, 3+3 supratemporal, and 11–12 mandibular pores.

Predorsal length 53%–58% SL. Anal fin straight, tip not reaching base of caudal-fin origin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 99%–113% of its depth. Caudal fin emarginate.

Body covered with embedded scales, cheeks scaleless. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank yellow brown, belly and lower part of flank yellow. Many small, irregular, dark brown spots on back. Many irregular spots forming bars along lateral line on both sides from head to base of caudal fin. Fins hyaline.

Distribution: Known from the Pearl River.

Remarks: *Paranemachilus pingguoensis* can be distinguished from other congeneric species by outer gill rakers on first gill arch present.

Genus *Yunnanilus* Nichols, 1925

Yunnanilus Nichols, 1925: 1 (type species: *Nemacheilus*

pleurotaenia Regan).

Diagnosis: *Yunnanilus* is easily distinguished from other nemacheilid loaches by inferior mouth, anterior and posterior nostrils slightly separated (distance greater than 2/5 of eye diameter), anterior nostril tube-like, without elongated barbel-like structure. Cheek scaleless, lips smooth with furrows. Lateral line and cephalic lateral-line pores present.

Remarks: The genus *Yunnanilus* is heterogenous. Yang & Chen (1995) divided the genus into a *nigromaculatus* species group and *pleurotaenia* species group. Subsequently, Kottelat (2012) considered that some species of the *nigromaculatus* species group belong to *Eonemachilus*, and some species of the *pleurotaenia* species group may belong to *Heminoemacheilus*. In this study, some species of the *nigromaculatus* species group are relocated to *Eonemachilus*. Species formerly of the *pleurotaenia* species group from Guangxi are relocated to *Heminoemacheilus* (*Y. baillianensis* and *Y. longibarbatus*), *Paranemachilus* (*Y. jinxiensis*), and *Micronemacheilus* (*Y. pulcherrimus*), see above. The remaining species of this group are retained in *Yunnanilus*.

Key to species of *Yunnanilus*

- 1) Whole body scaled.....2
 - Body scaleless or only caudal peduncle scaled.....10
- 2) Eye diameter greater than interorbital width.....3
 - Eye diameter smaller than interorbital width.....4
- 3) Eight inner gill rakers on first gill arch, processus dentiformis absent.....*Y. jiuchiensis*
 - 10– 12 inner gill rakers on first gill arch, processus dentiformis present.....*Y. longibulla*
- 4) Outer gill rakers on first gill arch present.....5
 - Outer gill rakers on first gill arch absent.....6
- 5) 11–12 inner gill rakers on first gill arch.....*Y. spanisbripes*
 - 14– 15 inner gill rakers on first gill arch....*Y. macrolepis*
- 6) Eye diameter less than 12% HL.....*Y. macrogaster*
 - Eye diameter more than 17% HL.....7
- 7) Caudal peduncle depth less than 10% SL.....*Y. retrodorsalis*
 - Caudal peduncle depth more than 10% SL.....8
- 8) Less than 10 inner gill rakers on first gill arch.....*Y. parvus*
 - More than 11 inner gill rakers on first gill arch.....9
- 9) Processus dentiformis present.....*Y. pleurotaenia*
 - Processus dentiformis absent.....*Y. chuanheensis*
- 10) Body scaleless.....11
 - Posterior body or caudal peduncle scaled.....16
- 11) Caudal fin forked.....12
 - Caudal fin emarginate.....13
- 12) Branched caudal-fin rays 14.....*Y. discoloris*
 - Branched caudal-fin rays 16.....*Y. forkicaudalis*
- 13) Eye diameter smaller than interorbital width .. *Y. paludosus*
 - Eye diameter greater than interorbital width 14
- 14) 12–14 inner gill rakers on first gill arch, cephalic lateral-line degenerated *Y. chui*
 - Less than 10 inner gill rakers on first gill arch, cephalic lateral-line normal 15
- 15) Eight inner gill rakers on first gill arch, snout length 26%–29% HL *Y. analis*
 - Ten inner gill rakers on first gill arch, snout length 32%–39% HL *Y. beipanjiangensis*
- 16) Caudal fin forked, outer gill rakers on first gill arch present

- *Y. macrositanus*
 – Caudal fin emarginate, outer gill rakers on first gill arch absent 17
 17) Caudal-peduncle length greater than its depth.....
 *Y. nanpanjiangensis*
 – Caudal-peduncle length smaller than its depth 18
 18) 12 branched pectoral-fin rays, processus dentiformis absent *Y. sichuanensis*
 – 10– 11 branched pectoral-fin rays, processus dentiformis present *Y. elakatis*

***Yunnanilus analis* Yang, 1990**

Yunnanilus analis Yang, in Chu & Chen, 1990: 19, fig. 14 (type locality: Lake Xingyun, Jiangchuan County, Yunnan, China).

(Figure 3Y1; Supplementary Figure S5A)

Material examined: Two specimens. Holotype, KIZ1960000625, 37.7 mm SL, paratype, KIZ1960000626, 50.2 mm SL; Lake Xingyun, Jiangchuan County, Yunnan, China, N24.3378°, E102.7833°, April 1961.

Diagnosis: Body scaleless; eye diameter greater than interorbital width; outer gill raker absent and 8 inner gill rakers on first gill arch; processus dentiformis present. Snout length 26%–29% HL; caudal-peduncle length 162%–180% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 3 simple and 9 branched rays; anal fin with 3 simple and 6 branched rays; pectoral fin with 12 branched rays; pelvic fin with 7 branched rays; caudal fin with 15 branched rays. Outer gill rakers absent, 8 inner gill rakers on first gill arch. Mouth inferior. Lips smooth, lower lip with median incision, furrows on each side. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior of eye than anterior nostril, anterior nostril tube-like. Eyes medium sized, eye diameter larger than interorbital width. Lateral line and cephalic lateral-line pores present. Cephalic lateral-line canals with 6 supraorbital, 3+6 infraorbital, 0 supratemporal, and 5 mandibular pores.

Predorsal length 56.7%–56.8% SL. Anal fin straight, tip not reaching base of caudal-fin origin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin close to anus. Caudal-peduncle length 162%–180% of its depth. Caudal fin emarginate.

Body scaleless. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Many small, irregular, dark brown spots on back and lateral body. Fins hyaline.

Distribution: Known from the Nanpanjiang River, a Pearl River tributary.

Remarks: Zheng (1989) recorded *Y. pleurotaenia* in Xingyun Lake, while Yang (1990) described it as a different species, *Y. analis*. Kottelat (2012) suggested that *Y. analis* could belong to *Heminoemacheilus*. However, the anterior and posterior nostrils are closely set in the genus *Heminoemacheilus*, whereas the anterior and posterior nostrils are slightly separated in *Y. analis*. Therefore, we treat *Y. analis* as a valid species in the genus *Yunnanilus*.

***Yunnanilus beipanjiangensis* Li, Mao & Sun 1994**

Yunnanilus beipanjiangensis Li, Mao & Sun, in Li, Mao, Sun &

Lu, 1994: 370, fig. 1 (type locality: Xintun Village, Zhanyi County, Yunnan, China).

(Figure 3Y2; Supplementary Figure S5B)

Material examined: Holotype, FACQR9107016, 47.7 mm SL, paratype, FACQR9107017, 9 uncat, 48.0–84.9 mm SL; Xintun Village, Zhanyi County, Yunnan, China, N25.9314°, E103.9943°, July 1991.

Diagnosis: Body scaleless; eye diameter greater than interorbital width; outer gill rakers absent, 10 inner gill rakers on first gill arch; processus dentiformis present. Snout length 32%–39% HL; caudal-peduncle length 130%–197% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 3 simple and 8–9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11 branched rays; pelvic fin with 7 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 10 inner gill rakers on first gill arch. Mouth inferior. Lips smooth, lower lip with median incision, furrows on each side. Processus dentiformis present on upper jaw. Anterior and posterior nostrils slightly separated, anterior nostril tube-like. Eyes medium sized, eye diameter greater than interorbital width. Lateral line and cephalic lateral-line pores present. Cephalic lateral-line canals with 6 supraorbital, 3+10 infraorbital, 2+2 supratemporal, and 9–10 mandibular pores.

Predorsal length 50%–55% SL. Anal fin straight, tip not reaching base of caudal-fin origin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 130%–197% of its depth. Caudal fin emarginate.

Body scaleless. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank yellow, belly and lower part of flank yellowish. Many small, twisting, dark brown bars on back and flank. Fins hyaline.

Distribution: Known from the Beipanjiang River, a Pearl River tributary.

Remarks: *Yunnanilus beipanjiangensis* is the only species recorded in the Beipanjiang River basin. In *Yunnanilus*, *Y. beipanjiangensis* shares similar characters with *Y. analis*, including whole body scaleless, eye diameter greater than interorbital width, less than 10 inner gill rakers on first gill arch but can be distinguished from *Y. analis* by snout length 32%–39% HL (vs. 26%–29%) and caudal peduncle depth 7%–9% SL (vs. 6.9%–7.0%).

***Yunnanilus chuanheensis* Jiang, Zhao, Du & Wang, 2021**

Yunnanilus chuanheensis Jiang, Zhao, Du & Wang, 2021: 1–5 (type locality: Nanjian County, Yunnan, China).

(Figure 3Y20)

Material examined: Holotype KIZ 2016007379, 46.8 mm SL; Paratype KIZ2016007380–90, 35.4–49.4 mm SL; Nanjian County, Yunnan, China, N24.8687°, E102.4693°, Lixianjiang River, a Red River tributary.

Diagnosis: Body covered with scales; caudal fin with 16 branched rays; 12 inner gill rakers on first gill arch; processus dentiformis absent; eye diameter smaller than interorbital width; lateral line incomplete; caudal peduncle depth

17.8%–22.8% SL.

Description: Body elongated. Dorsal fin with 3 simple and 8–9 branched rays; anal fin with 3 simple and 5–6 branched rays; pectoral fin with 11–12 branched rays; pelvic fin with 7–8 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 10–11 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital distance. Lateral line incomplete. Cephalic lateral-line canals with 8–9 supraorbital, 3+11–12 infraorbital, 3+3 supratemporal, and 9–10 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 52.1%–59.4% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth larger than its length. Caudal fin emarginate.

Body covered with scales, except on ventral area between pectoral and pelvic fins. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish, large brown blotches irregularly distributed on dorsal and lateral body, connected to longitudinal black stripe on lateral line. Fins hyaline.

Distribution: Known from Chuanhe in the upper reaches of the Lixianjiang River, a Pearl River tributary.

Remarks: *Yunnanilus chuanheensis* is the first species of *Yunnanilus* recorded in Red River. It can be distinguished from other congeneric species by body scaled (vs. scaleless or only caudal peduncle scaled in *Y. analis*, *Y. beipanjiangensis*, *Y. chui*, *Y. discoloris*, *Y. elakatis*, *Y. macrositanus*, *Y. nanpanjiangensis*, *Y. paludosus* and *Y. sichuanensis*), eye diameter smaller than interorbital distance (vs. larger in *Y. jiuchiensis* and *Y. longibulla*), 10–11 inner gill rakers on first gill arch (vs. 8–9 in *Y. parvus*), and processus dentiformis absent (vs. present in *Y. pleurotaenia*).

***Yunnanilus chui* Yang, 1991**

Yunnanilus chui Yang, 1991: 199, fig. 3 (type locality: Lake Fuxian, Chengjiang County, Yunnan, China).

(Figure 3Y3; Supplementary Figure S5C)

Material examined: Paratype KIZ1989001596, 36.2 mm SL; Lake Fuxian, Chengjiang County, Yunnan, China, N24.5201°, E102.9378°, Nanpanjiang River, a Pearl River tributary.

Diagnosis: Body scaleless; pectoral fin with 11 branched rays; caudal fin with 16 branched rays; 12 inner gill rakers on first gill arch; processus dentiformis present; lateral line incomplete, with 4 pores.

Description: Body elongated. Dorsal fin with 4 simple and 9 branched rays; anal fin with 3 simple and 6 branched rays; pectoral fin with 11 branched rays; pelvic fin with 7 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 15 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows.

Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter greater than interorbital distance. Lateral line incomplete, with 4 pores, cephalic lateral-line pores degenerated, only 2–3 infraorbital pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 53% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body scaleless. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish, vertical twisted bars on flank along lateral line, especially posterior 2/3 of flank, space between bars wider than bars. Fins hyaline.

Distribution: Known from Lake Fuxian, the Nanpanjiang River, a Pearl River tributary.

Remarks: Kottelat (2012) suggested that *Y. chui* may belong to *Eonemachilus*. However, *Y. chui* has a short lateral line and degenerated cephalic lateral-line pores, which are not typical characters of *Eonemachilus*. *Yunnanilus chui* can be separated from other congeneric species by scaleless body and eye diameter greater than interorbital distance, 12 inner gill rakers on first gill arch, cephalic lateral-line degenerated.

***Yunnanilus discoloris* Zhou & He, 1989**

Yunnanilus discoloris Zhou & He, 1989: 381, fig. 1 (type locality: White Dragon Spring, Chenggong County, Yunnan, China).

(Figure 3Y4; Supplementary Figure S5D–E)

Material examined: Six specimens, paratypes, KIZ1983000938, 939, 940, 941, 942, 943, 21.6–31.4 mm SL; White Dragon Spring, Chenggong County, Yunnan, China, N24.8709°, E102.8559°, October 1983.

Diagnosis: Body scaleless; eye diameter equal to interorbital width; processus dentiformis absent; upper lip smooth, lower lip with median incision, furrows on each side. Eye diameter 27%–31% HL; interorbital width 18%–25% HL; caudal-peduncle length 154%–189% of its depth. Caudal fin forked, with 14 branched rays.

Description: Body elongated. Dorsal fin with 4 simple and 8–9 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11–12 branched rays; pelvic fin with 7 branched rays; caudal fin with 14 branched rays. Outer gill rakers absent, 8–10 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter equal with interorbital width. Lateral line incomplete, with 4–10 pores. Cephalic lateral-line canals with 9 supraorbital, 3+13 infraorbital, 2+2 supratemporal, and 12 mandibular pores.

Dorsal-fin origin close to middle of snout tip and caudal-fin

origin, predorsal length 48%–54% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 154%–189% of its depth. Caudal fin forked.

Body scaleless. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish. Black longitudinal stripe along lateral line wider than pupil from posterior operculum to base of caudal fin on both sides in males, black blotches along lateral line on both sides in females. Fins hyaline.

Distribution: Known from the White Dragon Spring, Jinsha River basin.

Remarks: In *Yunnanilus*, *Y. discoloris*, *Y. analis*, *Y. beipanjiangensis*, *Y. chui*, *Y. paludosus* share scaleless body. However, *Y. discoloris* can be separated from these congeneric species by caudal fin forked (vs. emarginate) and processus dentiformis absent (vs. present).

***Yunnanilus elakatis* Cao & Zhu, 1989**

Yunnanilus elakatis Cao & Zhu, in Zheng, 1989: 43, fig. 21 (type locality: Yiliang County, Yunnan, China).

(Figure 3Y5)

Material examined: No specimens. Data from original description.

Diagnosis: Body scaleless, except caudal peduncle; eye diameter smaller than interorbital width; 10–12 inner gill rakers on first gill arch; processus dentiformis present. Eye diameter 20%–26% HL; interorbital width 26%–35% HL; caudal-peduncle length 90%–100% of its depth.

Description: Body elongated. Dorsal fin with 3 simple and 9–10 branched rays; anal fin with 2 simple and 5–6 branched rays; pectoral fin with 10–11 branched rays; pelvic fin with 7–8 branched rays; caudal fin with 16 branched rays. Outer gill rakers unknown, 10–12 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital distance. Lateral line incomplete.

Dorsal-fin origin located in middle between snout tip and caudal-fin origin. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 90%–100% of its depth. Caudal fin emarginate. Body scaleless, except caudal peduncle.

Color pattern in formalin: Body and head brownish, 5–7 and 5–6 dark brown bars before and after dorsal fin, respectively. Lateral body covered with minute, dark brown, irregular blotches. Fins hyaline.

Distribution. Known from the Nanpanjiang River, N24.9209°, E103.1419°, a Pearl River tributary.

Remarks: In *Yunnanilus*, *Y. elakatis*, *Y. macrositanus*, *Y. nanpanjiangensis*, and *Y. sichuanensis* share body scaleless, except on caudal peduncle. However, *Y. elakatis* can be distinguished from *Y. macrositanus* and *Y. nanpanjiangensis*

by caudal-peduncle length 90%–100% of its depth (vs. larger than 130%) and from *Y. sichuanensis* by processus dentiformis present (vs. absent).

***Yunnanilus forkicaudalis* Li, 1999**

Yunnanilus forkicaudalis Li, in Li, Wu, Xu, Gao, Chen, Wu & Wang, 1999: 4, fig. 2 (type locality: Heilongtan reservoir, Shilin County, Yunnan, China).

(Figure 3Y6)

Material examined: No specimens. Data from original description.

Diagnosis: Body scaleless; eye diameter smaller than interorbital width; one outer and 12 inner gill rakers on first gill arch. Lateral head length 22%–26% SL; caudal peduncle depth 8%–10% SL; snout length 37%–44% HL; eye diameter 13%–17% HL; interorbital width 25%–28% HL; caudal-peduncle length 120%–180% of its depth. Caudal fin forked.

Description: Body elongated. Dorsal fin with 3 simple and 7 branched rays; anal fin with 2 simple and 5 branched rays; pectoral fin with 9–11 branched rays; pelvic fin with 8 branched rays; caudal fin with 16 branched rays. One outer and 8 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital distance. Lateral line incomplete.

Dorsal-fin origin closer to snout tip than caudal-fin base. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 120%–180% of its depth. Caudal fin forked.

Body scaleless, except caudal peduncle. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Eight dark brown blotches extending from dorsal to midline body, eight dark brown blotches on lower midline body. Fins hyaline.

Distribution: Known from Heilongtan reservoir, N24.7651°, E103.3046°, Nanpanjiang River, a Pearl River tributary.

Remarks: Kottelat (2012) treated *Y. forkicaudalis* as a junior synonym of *Y. macrositanus*, but Du et al. (2018) compared the original descriptions and treated *Y. forkicaudalis* as a valid species. *Yunnanilus forkicaudalis* can be distinguished from *Y. macrositanus* by whole body scaleless (vs. caudal-peduncle scaled), 12 inner gill rakers on first gill arch (vs. 8), and interorbital width 25%–28% HL (vs. 30%–36%).

***Yunnanilus jiuchiensis* Du, Hou, Chen & Yang, 2018**

Yunnanilus jiuchiensis Du, Hou, Chen & Yang, 2018: 137–144, fig. 1 (type locality: Jiuchi County, Penzhou City, Sichuan, China).

(Figure 3Y8; Supplementary Figure S5F–G)

Material examined: Holotype, KIZ2018000002, 35.3 mm SL, paratype, KIZ2018000001, 0003–9, 29.6–37.4 mm SL; Jiuchi County, Penzhou City, Sichuan, China, N30.9876°, E104.0484°, March 2018.

Diagnosis: Whole body covered with scales; eye diameter

greater than interorbital width; processus dentiformis absent; pectoral fin with 11 branched rays. Outer gill rakers absent, 8 inner gill rakers on first gill arch; upper lip smooth, lower lip with median incision, furrows on each side. Body depth 17%–21% SL; lateral head length 25%–28% SL; eye diameter 22%–28% HL; interorbital width 20%–24% HL; caudal-peduncle length 78%–99% of its depth. Caudal fin emarginate.

Description: Body slender. Dorsal fin with 3 simple and 8 branched rays; anal fin with 3 simple and 6 branched rays; pectoral fin with 11 branched rays; pelvic fin with 6 branched rays; caudal fin with 15–16 branched rays. Outer gill rakers absent, 8 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter greater than interorbital distance. Lateral line incomplete. Cephalic lateral-line canals with 6–7 supraorbital, 3+12 infraorbital, 2+2 supratemporal, and 6–10 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 52%–57% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle length 78%–99% of its depth. Caudal fin emarginate.

Whole body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Upper 2/3 of body and head covered with brown blotches in females, longitudinal stripe along lateral line in males. Fins hyaline.

Distribution: Known from Tuojiang River, Yangtze River basin.

Remarks: *Yunnanilus jiuchiensis* and *Y. sichuanensis* are recorded in Sichuan Province. *Yunnanensis jiuchiensis* can be distinguished from *Y. sichuanensis* by whole body covered with scales (vs. posterior body), eye diameter greater than interorbital width (vs. smaller), and interorbital width 20%–24% HL (vs. 36%–46%).

***Yunnanilus longibulla* Yang, 1990**

Yunnanilus longibulla Yang, 1990: 21, fig. 16 (type locality: Lake Chenghai, Yongsheng County, Yunnan, China).

(Figure 3Y9; Supplementary Figure S5P)

Material examined: Holotype, KIZ1981002383, 41.0 mm SL, paratype, KIZ1981002384–2386, 2388–2393, 28.6–37.0 mm SL; Lake Chenghai, Yongsheng County, Yunnan, China, N26.5466°, E100.6647°, August 1981.

Diagnosis: Whole body covered with scales; eye diameter greater than interorbital width; processus dentiformis present; pectoral fin with 11 branched rays. Outer gill raker absent, 8 inner gill rakers on first gill arch; upper lip smooth, lower lip with median incision, furrows on each side. Cephalic lateral-line canals with 7 supraorbital, 4+9 infraorbital, 3+3 supratemporal, and 8–9 mandibular pores. Body depth 17%–21% SL; lateral head length 25%–28% SL; eye diameter 24%–32% HL; interorbital width 17%–23% HL; caudal-peduncle length 111%–166% of its depth. Caudal fin

emarginate.

Description: Body elongated. Dorsal fin with 4 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 11 branched rays; pelvic fin with 7 branched rays; caudal fin with 17 branched rays. Outer gill rakers absent, 10–12 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter greater than interorbital distance. Lateral line incomplete, with 11–17 pores. Cephalic lateral-line canals with 7 supraorbital, 4+9 infraorbital, 3+3 supratemporal, and 8–9 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 50%–55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish. Ten to twelve round, dark brown spots along lateral line in females, longitudinal stripe along lateral line in males. Back and head covered with brown blotches. Fins hyaline

Distribution: Known from Lake Chenghai, Yangtze River basin.

Remarks: In *Yunnanilus*, *Y. longibulla*, *Y. jiuchiensis*, *Y. macrogaster*, *Y. macrolepis*, *Y. parvus*, *Y. pleurotaenia*, and *Y. spanisbripes* share whole body covered with scales. However, *Y. longibulla* can be distinguished from these species by eye diameter greater than interorbital width (vs. smaller in *Y. macrogaster*, *Y. macrolepis*, *Y. parvus*, *Y. pleurotaenia*, and *Y. spanisbripes*), 17 branched caudal fins (vs. 15–16 in others), outer gill rakers absent (vs. present in *Y. macrolepis* and *Y. spanisbripes*), and 10–12 inner gill rakers on first gill arch (vs. 8–9 in *Y. parvus* and *Y. jiuchiensis*).

***Yunnanilus macrogaster* Kottelat & Chu, 1988**

Yunnanilus macrogaster Kottelat & Chu, 1988: 81, fig. 17 (type locality: Datangzi Village, Luoping County, Yunnan, China).

(Figure 3Y10; Supplementary Figure S5H)

Material examined: Holotype, KIZ1980004273, 70.1 mm SL, paratype, KIZ1980004274, 70.1 mm SL; Datangzi Village, Luoping County, Yunnan, China, N24.6563°, E104.3663°, June 1980.

Diagnosis: Whole body covered with scales; eye diameter smaller than interorbital width; processus dentiformis present; pectoral fin with 12–13 branched rays. Outer gill rakers absent, 13 inner gill rakers on first gill arch; upper lip smooth, lower lip with median incision, furrows on each side. Cephalic lateral-line canals with 9 supraorbital, 4+10 infraorbital, 3+3 supratemporal, and 11 mandibular pores. Body depth 22%–23% SL; lateral head length 25%–26% SL; eye diameter 11.9%–12.0% HL; interorbital width 26%–27% HL; caudal-

peduncle length 121%–137% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 4 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 12–13 branched rays; pelvic fin with 7 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 13 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital width. Lateral line incomplete, with 12–13 pores. Cephalic lateral-line canals with 9 supraorbital, 4+10 infraorbital, 3+3 supratemporal, and 11 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 55%–56% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and head yellowish brown with irregularly distributed dark brown spots on upper two-thirds. Fins hyaline.

Distribution: Known from the Nanpanjiang River.

Remarks: In *Yunnanilus*, *Y. macrogaster*, *Y. macrolepis*, *Y. pleurotaenia* and *Y. spanisbripes* share whole body covered with scales and eye diameter smaller than interorbital width. However, *Y. macrogaster* can be separated from other species by pectoral fin with 12–13 branched rays (vs. 10–11 in others), body depth 22%–23% SL (vs. 17%–22% in *Y. pleurotaenia*, 16%–22% in *Y. spanisbripes*), caudal-peduncle length 12.7%–12.8 SL (vs. 11%–12% in *Y. macrolepis*), eye diameter 11.9%–12.0% HL (vs. 13%–18% in *Y. macrolepis*, 18%–21% in *Y. pleurotaenia*, 17%–22% in *Y. spanisbripes*).

***Yunnanilus macrolepis* Li, Tao & Mao, 2000**

Yunnanilus macrolepis Li, Tao & Mao, in Li, Tao, Mao & Lu, 2000: 349, fig. 1 (type locality: Xuetian Dragon Spring, Luoping County, Yunnan, China).

(Figure 3Y12; Supplementary Figure S51)

Material examined: Five specimens, HRAS9509001, 9509003, 9506997 and 2 uncat., Xuetian Dragon Spring, Luoping County, Yunnan, China, N24.8843°, E104.3461°, September 1995.

Diagnosis: Whole body covered with scales; eye diameter smaller than interorbital width; processus dentiformis present; pectoral fin with 10–11 branched rays. One or two rakers and 14–15 inner gill rakers on first gill arch; upper lip smooth, lower lip with median incision, furrows on each side. Cephalic lateral-line canals with 9–10 supraorbital, 3+15 infraorbital, 4+2 supratemporal, and 10–14 mandibular pores. Body depth 19%–25% SL; lateral head length 23%–26% SL; eye diameter 13%–18% HL; interorbital width 21%–28% HL; caudal-peduncle length 106%–119% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 4 simple and 8–9 branched rays; anal fin with 3 simple and 6 branched rays; pectoral fin with 10–11 branched rays; pelvic fin with 6 branched rays; caudal fin with 15–16 branched rays. One or two outer and 14–15 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital. Lateral line incomplete, with 9–17 pores. Cephalic lateral-line canals with 9–10 supraorbital, 3+15 infraorbital, 4+2 supratemporal, and 10–14 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 55%–58% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank yellow brown, belly and lower part of flank yellow. Two lines longitudinal stripes formed by round dark brown spots along lateral line. Back and head covered with irregularly distributed dark brown spots. Dorsal fin with brown spots, other fins hyaline.

Distribution: Known from Xuetian Dragon Spring, Nanpanjiang River basin.

Remarks: Kottelat (2012) treated *Y. macrolepis* as a junior synonym of *Y. paludosus*. Du et al. (2018) treated *Y. macrolepis* as a valid species based on body covered with scales (vs. scaleless). In addition, *Y. macrolepis* can be distinguished from *Y. paludosus* by 1–2 outer gill rakers on first gill arch (vs. absent), 14–15 inner gill rakers on first gill arch (vs. 12), body depth 19%–25% SL (vs. 16%–17%), lateral head length 23%–26% SL (vs. 20%–21%), caudal-peduncle length 11%–12% SL (vs. 14%–16%), and caudal peduncle depth 10%–12% SL (vs. 7%–8%).

***Yunnanilus macrositanus* Li, 1999**

Yunnanilus macrositanus Li, in Li, Wu, Xu, Gao, Chen, Wu & Wang, 1999: 4, fig. 1 (type locality: Heilongtan reservoir, Shilin County, Yunnan, China).

(Figure 3Y11)

Material examined: No specimen. Data from original description.

Diagnosis: Posterior body covered with scales; eye diameter smaller than interorbital width; pectoral fin with 11 branched rays. One outer and 8 inner gill rakers on first gill arch. Body depth 20%–21% SL; eye diameter 15%–18% HL; interorbital width 30%–36% HL; caudal-peduncle length 140% of its depth. Caudal fin forked.

Description: Body elongated. Dorsal fin with 3 simple and 7 branched rays; anal fin with 2 simple and 5 branched rays; pectoral fin with 11 branched rays; pelvic fin with 8 branched rays; caudal fin with 16–17 branched rays. One outer gill raker and eight inner gill rakers on first gill arch. Mouth inferior;

upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital width. Lateral line incomplete, cephalic lateral-line pores unknown.

Dorsal-fin origin closer to snout tip than from caudal-fin origin. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin slightly forked.

Posterior body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and head yellowish brown. Eight dark brown blotches extending from dorsal to midline body, eight dark brown blotches on lower midline. Fins hyaline.

Distribution: Known from Heilongtan reservoir, N24.7651°, E103.3046°, Nanpanjiang River basin.

Remarks: Li et al. (1999) used three different species spellings in the original description, i.e., *macrositanus*, *macroistainus*, and *macroistanus*. Kottelat (2012) treated *macrositanus* as the correct original spelling, and further treated *Y. forkicaudalis* as a junior synonym to *Y. macrositanus*. Here, however, we treat *Y. forkicaudalis* as a valid species, as discussed above.

***Yunnanilus nanpanjiangensis* Li, Tao & Lu, 1994**

Yunnanilus nanpanjiangensis Li, Mao & Lu, in Li, Mao, Sun & Lu, 1994: 371, fig. 2 (type locality: Agang Township, Luoping County, Yunnan, China).

(Figure 3Y13; Supplementary Figure S5J)

Material examined: Six specimens, FACQR9191108, 13–14, 22, 29, 34, 50.5–67.4 mm SL; Agang Township, Luoping County, Yunnan, China, N25.0765°, E104.1091°, September 1991.

Diagnosis: Body scaleless, except caudal peduncle; eye diameter smaller than interorbital width; outer gill rakers absent, 10 inner gill rakers on first gill arch; upper lip smooth, lower lip with median incision, furrows on each side; processus dentiformis present; pectoral fin with 10 branched rays. Body depth 23%–25% SL; eye diameter 17%–20% HL; interorbital width 19%–24% HL; caudal-peduncle length 133%–171% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 4 simple and 8–9 branched rays; anal fin with 3 simple and 6 branched rays; pectoral fin with 10 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 10 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital width. Lateral line incomplete, with 6–10 pores. Cephalic lateral-line canals with

8–9 supraorbital, 3+12 infraorbital, 3+3 supratemporal, and 10 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 51%–55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body scaleless, except for caudal peduncle. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank yellow brown. Body and head covered with irregularly distributed dark brown pigments on upper 2/3 of body. Fins hyaline.

Distribution: Known from the Nanpanjiang River basin.

Remarks: *Yunnanilus nanpanjiangensis*, *Y. elakatis*, and *Y. macrositanus* share scaleless body, except for caudal peduncle. However, *Y. nanpanjiangensis* can be separated from *Y. elakatis* and *Y. macrositanus* by interorbital 19%–24% HL (vs. greater than 25% in *Y. elakatis* and *Y. macrositanus*). Furthermore, *Y. nanpanjiangensis* can be separated from *Y. macrositanus* by outer gill rakers on first gill arch absent (vs. present) and from *Y. elakatis* by caudal-peduncle length 133%–171% of its depth (vs. 90%–100%).

***Yunnanilus paludosus* Kottelat & Chu, 1988**

Yunnanilus paludosus Kottelat & Chu, 1988: 76, fig. 12 (type locality: Luoping County, Yunnan, China).

(Figure 3Y14; Supplementary Figure S5K)

Material examined: Five specimens, paratypes, KIZ1980001277–1281, 56.8–74.3 mm SL; Luoping County, Yunnan, China, N24.9142°, E104.2835°, June 1980.

Diagnosis: Eye diameter smaller than interorbital width; outer gill rakers absent, 12 inner gill rakers on first gill arch; processus dentiformis present. Lateral head length 20%–21% SL; caudal peduncle depth 7%–8% SL; snout length 32%–42% HL; eye diameter 15%–18% HL; interorbital width 17%–22% HL; caudal-peduncle length 182%–222% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 4 simple and 8 branched rays; anal fin with 3 simple and 5–6 branched rays; pectoral fin with 9–11 branched rays; pelvic fin with 6–7 branched rays; caudal fin with 14–16 branched rays. Outer gill rakers absent, 12 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital width. Lateral line incomplete, with 19–21 pores. Cephalic lateral-line canals with 6–7 supraorbital, 3+8 infraorbital, 3+3 supratemporal, and 6–11 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 50%–54% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Body scaleless. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brownish, belly and lower part of flank gray, back and flank covered with irregular, round, brown spots. Fins hyaline.

Distribution: Known from the Nanpanjiang River basin.

Remarks: In *Yunnanilus*, *Y. paludosus*, *Y. analis*, *Y. beipanjiangensis*, *Y. discoloris*, and *Y. forkicaudalis* share scaleless body, but *Y. paludosus* can be distinguished from these species by caudal fin emarginate (vs. forked in *Y. discoloris* and *Y. forkicaudalis*), 12 inner gill rakers on first gill arch (vs. 8–10 in *Y. analis* and *Y. beipanjiangensis*), and lateral head length 20%–21% SL (vs. 27% in *Y. chui*).

***Yunnanilus parvus* Kottelat & Chu, 1988**

Yunnanilus parvus Kottelat & Chu, 1988: 77, fig. 13 (type locality: Nantong cave, Kaiyuan County, Yunnan, China).

(Figure 3Y15; Supplementary Figure S5L)

Material examined: Holotype, KIZ1984001244, 25.1 mm SL, paratypes, KIZ1984001246, 1248, 1251, 1252, 1253, 1257, 26.7–33.5 mm SL; Nantong cave, Kaiyuan County, Yunnan, China, N23.6482°, E103.2875°, July 1984.

Diagnosis: Whole body covered with scales; eye diameter smaller than interorbital width; processus dentiformis present; pectoral fin with 10–11 branched rays. Outer gill rakers absent, 8–9 inner gill rakers on first gill arch; upper lip smooth, lower lip with median incision, furrows on each side. Body depth 21%–23% SL; lateral head length 25%–28% SL; eye diameter 21%–27% HL; interorbital width 24%–28% HL; caudal-peduncle length 97%–113% of its depth. Caudal fin emarginate.

Description: Body slender. Dorsal fin with 4 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 10–11 branched rays; pelvic fin with 7 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 8–9 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital width. Lateral line incomplete, with 7–16 pores. Cephalic lateral-line canals with 5–7 supraorbital, 3+8 infraorbital, 3+3 supratemporal, and 5 mandibular pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 52%–54% SL. Anal fin straight, tip reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin reaching anus. Caudal-peduncle length 97%–113% of its depth. Caudal fin emarginate.

Body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish. Nine or ten round spots along lateral line on each side. Fins hyaline.

Distribution: Known from the Nanpanjiang River basin.

Remarks: In *Yunnanilus*, *Y. parvus*, *Y. macrogaster*, *Y. macrolepis*, *Y. pleurotaenia*, *Y. spanisbripes*, *Y. longibulla*, and *Y. jiuchiensis* share whole body covered with scales. However, *Y. parvus* can be distinguished from congeneric species by outer gill rakers on first gill arch absent (vs. present in *Y. macrolepis*, and *Y. spanisbripes*), 8–9 inner gill rakers on first gill arch (vs. more than 10 in *Y. macrogaster*, *Y. pleurotaenia*, and *Y. longibulla*), predorsal length 52%–54% SL (vs. 55%–58% in *Y. macrolepis*), eye diameter 21%–27% HL (vs. smaller than 20% in *Y. macrogaster* and *Y. macrolepis*).

***Yunnanilus pleurotaenia* (Regan, 1904)**

Nemachilus pleurotaenia Regan, 1904: 192 (type locality: Lake Dianchi, Kunming City, Yunnan, China)

Yunnanilus pleurotaenia, Zheng, 1989: 42 (lakes Xingyun, Fuxian, Dianchi and Chenghai); Zhu, 1989: 15–17, fig. 7 (Lakes Xingyun, Fuxian, Dianchi, Er'hai and Chenghai).

Yunnanilus tigerivinus Li & Duan, 1999: 254, fig. 1 (type locality: suburbs of Kunming, Yunnan, China). Kottelat, 2012: 136.

(Figure 3Y16; Supplementary Figure S5M, N)

Material examined: Lectotype, BMNH1904.1.26.36 Yunnan fu = Lake Dianchi. KIZ 20004050, 4053, 4054, 4061, 4063, 4069, 4071, 4072, 4074, 41.8–63.4 mm SL; Green Dragon Spring, Kunming City, Yunnan, N25.3012°, E102.8894°, April 1999. KIZ2016007357–7386, 46.9–59.1 mm SL; Yousuo Village, Eryuan County, Dali City, Yunnan, N26.0201°, E100.0621°, December 2016. KIZ1988003256–3259, Lake Fuxian, Chengjiang County, Yuxi City, Yunnan, N24.5201°, E102.9378°, November 1988.

Diagnosis: Whole body covered with scales; eye diameter smaller than interorbital width; processus dentiformis present; pectoral fin with 10 branched rays. Outer gill rakers absent, 10–13 inner gill rakers on first gill arch; upper lip smooth, lower lip with median incision, furrows on each side. Body depth 17%–22% SL; lateral head length 23%–26% SL; eye diameter 18%–21% HL; interorbital width 25%–33% HL; caudal-peduncle length 104%–132% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 4 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 10 branched rays; pelvic fin with 6 branched rays; caudal fin with 15–16 branched rays. Outer gill rakers absent, 10–13 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital width. Lateral line incomplete, with 16–25 pores. Cephalic lateral-line canals with 7–8 supraorbital, 4+9–10 infraorbital, 3+3 supratemporal, and 6–9 mandibular pores.

Predorsal length 48%–55% SL. Anal fin straight, tip not reaching base of caudal-fin origin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin close to anus. Caudal-peduncle length 104%–132% of its depth. Caudal fin emarginate.

Whole body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank dark brown, belly and lower part of flank brown. Longitudinal stripe along lateral line wider than eye diameter from posterior of operculum to base of caudal fin in males, many bars or spots along lateral line in females. Back covered with large, irregular, dark brown blotches. Fins hyaline.

Distribution: Known from the Jinsha and Lancang Rivers basin.

Remarks: Species of *Yunnanilus*, except *Y. pleurotaenia*, are limited to small water bodies. *Yunnanilus pleurotaenia* was first recorded in Lake Dianchi, Yunnan (Jinsha River basin) by Regan (1904). Chaudhuri (1911) recorded the species in Dali City, Yunnan (Lancang River basin). Zheng (1989) recorded *Y. pleurotaenia* in the Nanpanjiang River basin (lakes Xingyun and Fuxian) and Jinsha River basin (lakes Dianchi and Chenghai). In later studies, specimens determined as *Y. pleurotaenia* from Lake Xingyun and Lake Chenghai were described as *Y. analis* and *Y. longibulla*, respectively (Yang, 1990). The specimens from Dali and Lake Fuxian are difficult to distinguish from *Y. pleurotaenia* as they share a similar body shape, number of branched rays, and most meristic characters. Hence, the specimens from Dali and Lake Fuxian are identified here as *Y. pleurotaenia*.

***Yunnanilus retrodorsalis* (Lan, Yang et Chen, 1995)**

Oreonectes retrodorsalis Lan, Yang et Chen, 1995: 366 (type locality: Liuzai Township, Nandan County, Guangxi, China); Du et al., 2008: 32.

Yunnanilus retrodorsalis, Lan et al., 2013: 40–44; Zhang et al., 2016: 150.

(Figure 3Y17; Supplementary Figure S5Q)

Material examined: Seven specimens. Holotype, KIZ1991003951, paratypes, KIZ1991003952–3956, 26.0–38.4 mm SL; Liuzai Township, Nandan County, Guangxi, China, N25.2961°, E107.4044°.

Diagnosis: Whole body covered with scales, except head; eye diameter greater than interorbital width. Outer gill rakers absent, 10–13 inner gill rakers on first gill arch. Cephalic lateral-line pores reduced, with only 2+4 infraorbital pores.

Description: Body compressed laterally. Dorsal fin with 4 simple and 7 branched rays; anal fin with 4 simple and 5 branched rays; pectoral fin with 10 branched rays; pelvic fin with 7 branched rays; caudal fin with 14 branched rays. Outer gill rakers absent, 10–13 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter greater than interorbital width. Lateral line incomplete, with 3–4 pores. Cephalic lateral-line pores reduced, with only 2+4 infraorbital pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin. Anal fin straight, tip not reaching base of caudal-fin origin. Pelvic-fin origin slightly anterior to dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less

than its length. Caudal fin emarginate.

Body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank brownish. Without clear color pattern. Fins hyaline.

Distribution: Known from the Pearl River basin.

Remarks: *Yunnanilus parvus*, *Y. macrogaster*, *Y. macrolepis*, *Y. pleurotaenia*, *Y. spanisbripes*, and *Y. retrodorsalis* share entire body scaled and eye diameter greater than interorbital width. However, *Y. retrodorsalis* can be distinguished from these congeneric species by caudal fin with 14 branched rays (vs. 15–16 in other species) and cephalic lateral line pores reduced (vs. developed). Other distinguishing characters: outer gill rakers on first gill arch absent (vs. present in *Y. macrolepis* and *Y. spanisbripes*), inner gill rakers more than 10 (vs. 8–9 in *Y. parvus*), body depth 15%–19% SL (vs. 22%–23% in *Y. macrogaster*), caudal peduncle depth 7%–9% SL (vs. 9.7%–11.4% in *Y. pleurotaenia*).

***Yunnanilus sichuanensis* Ding, 1995**

Yunnanilus sichuanensis Ding, 1995: 253, fig. 1 (type locality: Anning River, Mianning County, Sichuan, China).

(Figure 3Y18)

Material examined: No specimens. Data from original description.

Diagnosis: Posterior body covered with scales; eye diameter smaller than interorbital width; processus dentiformis absent; pectoral fin with 12 branched rays. Outer gill rakers absent, 9–10 inner gill rakers on first gill arch. Body depth 20%–22% SL; eye diameter 25%–30% HL; interorbital width 36%–46% HL; caudal-peduncle length 90%–100% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 3 simple and 8 branched rays; anal fin with 3 simple and 5 branched rays; pectoral fin with 12 branched rays; pelvic fin with 7 branched rays; caudal fin with 16 branched rays. Outer gill rakers absent, 9–10 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis absent on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital. Lateral line incomplete, with 16–17 pores.

Dorsal-fin origin farther from snout tip than from caudal-fin origin, predorsal length 56%–63% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Posterior body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Body and head yellowish, covered with irregular dark brown blotches. Black longitudinal stripe from gill aperture to base of caudal peduncle, 16–19 and 20–26 dark brown blotches on upper and lower longitudinal

bars, respectively. Base of dorsal fin with small, black spot, other fins hyaline.

Distribution: Known from the Anning River, N28.5513°, E102.1810°, Yangtze River basin.

Remarks: *Yunnanilus sichuanensis* can be distinguished from other congeneric species by posterior part of body covered with scales. Furthermore, *Y. sichuanensis* can be distinguished from *Y. macrositanus*, *Y. forkicaudalis*, and *Y. discoloris* by emarginate caudal fin (vs. forked), from *Y. macrolepis* and *Y. spanisbripes* by outer gill rakers on first gill arch absent (vs. present), from *Y. elakatis*, *Y. paludosus*, *Y. macrogaster*, *Y. chui*, *Y. pleurotaenia*, and *Y. longibulla* by 9–10 inner gill rakers on first gill arch (vs. more than 10), from *Y. analis*, *Y. parvus*, *Y. beipanjiangensis*, *Y. nanpanjiangensis*, and *Y. macrogaster* by caudal-peduncle length equal or less than its depth (vs. more than its depth), and from *Y. jiuchiensis* by interorbital width of 36%–46% HL (vs. 20%–24%).

***Yunnanilus spanisbripes* An, Liu & Li, 2009**

Yunnanilus spanisbripes An, Liu & Li, 2009: 631, fig. 1 (type locality: Zhanyi County, Yunnan, China).

Yunnanilus ganheensis An, Liu & Li, 2009: 635, fig. 11 (type locality: Ganhe, Xundian County, Yunnan, China). (**new synonym**)

(Figure 3Y19; Supplementary Figure S50)

Material examined: Nine specimens, HRAS199504007, 9309023, 920703001–7, 200306011, 51.2–71.9 mm SL; Deze Township, Zhanyi County, Yunnan, China, N25.9889°, E103.6064°.

Diagnosis: Whole body covered with scales; eye diameter smaller than interorbital width; processus dentiformis present; pectoral fin with 11 branched rays. One outer and 11–12 inner gill rakers on first gill arch. Body depth 16%–22% SL; lateral head length of 23%–25% SL; eye diameter 17%–22% HL; interorbital width 22%–27% HL; caudal-peduncle length 101%–139% of its depth. Caudal fin emarginate.

Description: Body elongated. Dorsal fin with 4 simple and 9 branched rays; anal fin with 3 simple and 6 branched rays; pectoral fin with 11 branched rays; pelvic fin with 7 branched rays; caudal fin with 16 branched rays. One outer and 11–12 inner gill rakers on first gill arch. Mouth inferior; upper lip smooth, lower lip thick, with strong furrows. Processus dentiformis present on upper jaw, shallow median notch on lower jaw. Anterior and posterior nostrils slightly separated, posterior nostril closer to anterior nostril than to eye, anterior nostril tube-like. Eyes medium sized, eye diameter smaller than interorbital. Lateral line incomplete, with 15–24 pores. Cephalic lateral-line canals with 7–9 supraorbital, 3+12 infraorbital, supratemporals unclear, and 6–10 mandibular pores.

Dorsal-fin origin in middle or farther from snout tip than from caudal-fin, predorsal length 51%–55% SL. Anal fin straight, tip not reaching base of caudal fin. Pelvic-fin origin slightly behind dorsal-fin origin, tip of pelvic fin not reaching anus. Caudal-peduncle depth less than its length. Caudal fin emarginate.

Whole body covered with scales. Air bladder with two chambers, anterior chamber in capsule, large posterior chamber free, filling body cavity to dorsal-fin origin. Intestines straight.

Color pattern in formalin: Back and upper part of flank brown, belly and lower part of flank yellow. Fifteen vertical, twisted, dark brown bars on flank along lateral line, space between bars three times as wide as bars. Back of body and head covered with irregular, dark brown spots. Fins hyaline.

Distribution: Known from Jinsha River basin.

Remarks: An et al. (2009) described *Y. ganheensis* and *Y. spanisbripes* in the same publication, with these species distinguished from one another by size of body blotches. Additionally, more than 20 specimens of *Y. spanisbripes* were collected in Huizhe County, Niulanjiang River by Y. P. Zhao (KIZ), which differed greatly in size of blotches on lateral body. Prokofiev (2010) stated that color pattern is not a reliable interspecies diagnostic character in this group of fishes, so we treat *Y. ganheensis* as a junior synonym of *Y. spanisbripes* in this study.

DISCUSSION

Our results indicate that the current division of five tribes (Prokofiev, 2010) is problematic because they are not monophyletic. *Micronemacheilus*, *Paranemachilus*, *Traccatichthys* and *Yunnanilus*, four genera of the tribe Yunnanilini, are nested within the tribe Lefuini. This is consistent with the results of Chen et al. (2019b), which placed *Troglonectes furcocaudalis* in the genus *Oreonectes*. Additionally, *Barbatula* and *Homatula*, two genera of the tribe Nemacheilini, are paraphyletic with respect to *Triplophysa*, a genus of the tribe Triplophysini. Prokofiev (2010) placed *P. brevis*, the type species of the genus *Petruichthys*, in *Yunnanilus*. However, we find that this species is closer to the genus *Schistura* than *Y. jiuchiensis*, which represents true *Yunnanilus* and forms a clade with *Paranemachilus* and *Troglonectes*, indicating that *Petruichthys* is not a synonym of *Yunnanilus*. According to Sgouros et al. (2019), the genus *Schistura* is polyphyletic, and Chen et al. (2019b) revealed that *P. brevis* is nested within the *Schistura* clade. Therefore, more morphological and molecular studies are needed to resolve the taxonomic problems of *Petruichthys* and *Schistura* as well as the complex relationships between these nemacheilid tribes.

In the family of Nemacheilidae, the genera of *Eonemachilus*, *Heminoemacheilus*, *Micronemacheilus*, *Paranemachilus*, *Protonemacheilus*, *Traccatichthys*, and *Yunnanilus* are characterized by a tube-like anterior nostril with tip not elongated to barbel-like structure and lateral line and cephalic lateral-line pores present or absent. These genera can be easily diagnosed by the relative position of anterior and posterior nostrils, lips with papillae or furrows, and cheeks scaled or scaleless. The anterior and posterior nostrils are closely set in *Heminoemacheilus*, *Paranemachilus*, *Protonemacheilus*, and *Traccatichthys*, but slightly separated (distance greater than 1/5 of eye diameter) in *Eonemachilus*, *Micronemacheilus* and *Yunnanilus*. Furthermore, the cheeks of *Paranemachilus* are covered with scales (vs. scaleless in other genera). *Micronemacheilus* and *Traccatichthys* share lips with large papillae but can be distinguished from each other by closely set anterior and posterior nostrils in *Traccatichthys* (vs. clearly separated in *Micronemacheilus*).

Our phylogenetic analysis did not group *M. pulcher* (*Traccatichthys pulcher* in Figure 1) together with *Micronemacheilus* clade. Thus, we refer *M. pulcher* and *M. zispi* to *Traccatichthys* based on molecular evidence and their closely set anterior and posterior nostrils.

The currently recognized *Yunnanilus* genus is not monophyletic (Figure 1). Freyhof & Serov (2001) treated the type species of *Micronemacheilus* as a member of *Yunnanilus* based on examination of type material. However, the large papillae in the median part of both lips are a useful diagnostic character to distinguish *Micronemacheilus* from *Yunnanilus*. Hence, we agree with Kottelat (2012, 2013) in terms of the inclusion of *Nemacheilus cruciatus* in *Micronemacheilus* based on several morphological characters, i.e., anterior and posterior nostrils slightly separated and large papillae in median part of both lips.

To date, 269 species of Nemacheilidae have been recorded from China, with 161 species recorded from the karst region of southern China, including Guangxi, Guizhou, Chongqing and Yunnan. Most species of nemacheilid loaches are limited to small water bodies and are very vulnerable to changes in their environment (Kottelat & Chu, 1988; Kottelat, 2012; Yang, 1991). Agricultural siltation, organic pollution, pesticides, heavy metals, habitat degradation, and severe drought have profoundly affected these endemic species (Du et al., 2017; Shu et al., 2013). Currently, four species of *Yunnanilus*, three species of *Eonemachilus*, two species of *Traccatichthys*, and one species of *Micronemacheilus* and *Paranemachilus*, respectively are listed on the IUCN Red List of Threatened Species (<http://www.iucnredlist.org>) (IUCN, 2018). Among these species, *Y. discoloris* is Critically Endangered (CR), *E. nigromaculatus* is Endangered (EN), *E. niger* and *Y. pleurotaenia* are Vulnerable (VU), *E. pachycephalus*, *M. cruciatus*, *T. pulcher* and *T. taeniatus* were Least Concern (LC), and *P. genilepis*, *Y. macrogaster* and *Y. parvus* are Data Deficient (DD). As species of *Yunnanilini* are valuable and rare, it is difficult to acquire fresh tissue. Hence, research regarding the phylogenetic relationships among *Yunnanilini* species remains limited due to a lack of appropriate tissue material.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

L.N.D. measured specimens, analyzed data, and prepared the manuscript. J.Y. collected specimens. R.M. examined specimens in KIZ. X.Y.C. and J.X.Y. contributed to funding of research and organization of the manuscript. All authors read and approved the final version of the manuscript.

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REFERENCES

- An L, Liu BS, Li WX. 2009. Two new loaches of the genus *Yunnanilus* (Balitoridae) from Yunnan, China. *Acta Zootaxonomica Sinica*, **34**(3): 630–638. (in Chinese)
- Berg LS. 1938. On some South China loaches (Cobitidae, Pisces). *Bulletin de la Société impériale des Naturalistes de Moscou*, **47**: 314–318.
- Chaudhuri BL. 1911. Contributions to the fauna of Yunnan based on collections made by J. Coggin Brown, B. Sc. 1909–1910. Part II – Fishes. *Records of the Indian Museum*, **6**(1): 13–24.
- Chen WT, Yang JP, Li YF, Li XH. 2019. Exploring taxonomic diversity and biogeography of the family Nemacheilinae (Cypriniformes). *Ecology and Evolution*, **9**(18): 10343–10353.
- Chen XY. 2013. Checklist of fishes of Yunnan. *Zoological Research*, **34**(4): 281–343. (in Chinese)
- Chen ZM, Yang J, Yang JX. 2012. Description of a new species of the genus *Yunnanilus* Nichols, 1925 (Teleostei: Nemacheilidae) from Yunnan, China. *Zootaxa*, **3269**(1): 57–64.
- Ding RH. 1992. A new species of the *Yunnanilus* from Guizhou, China (Cypriniformes: Cobitidae). *Acta Zootaxonomica Sinica*, **17**(4): 489–491. (in Chinese)
- Ding RH. 1995. A new species of the genus *Yunnanilus* from western Sichuan, China (Cypriniformes: Cobitidae). *Acta Zootaxonomica Sinica*, **20**(8): 253–256. (in Chinese)
- Du CX, Zhang E, Chan BP. 2012. *Traccatichthys tuberculum*, a new species of nemacheiline loach from Guangdong Province, South China (Pisces: Balitoridae). *Zootaxa*, **3586**(1): 304–312.
- Du LN, Hou M, Chen XY, Yang JX. 2018. A new species of *Yunnanilus* (Cypriniformes: Nemacheilidae) from Sichuan, southwest China. *Zootaxa*, **4532**(1): 137–144.
- Du LN, Jiang YE, Chen XY, Yang JX, Aldridge D. 2017. A family-level macroinvertebrate biotic index for ecological assessment of lakes in Yunnan, China. *Water Resources*, **44**(6): 864–874.
- Du LN, Lu YF, Chen XY. 2015. *Yunnanilus qujinensis*, a new species of loach from Yunnan, southwest China (Teleostei: Nemacheilidae). *Ichthyological Exploration of Freshwaters*, **26**(3): 249–254.
- Eagderi S, Mousavi-Sabet H, Freyhof J. 2019. *Paraschistura makranensis*, a new loach from the Jegin River drainage in southern Iran with comments on *P. ilamensis* and *P. pasatigris* (Teleostei: Nemacheilidae). *Zootaxa*, **4668**(2): 258–270.
- Eschmeyer WN. 2020. Catalog of fishes. Updated database version of April 2020. Catalog databases as made available to FishBase in April 2020.
- Freyhof J, Serov DV. 2001. Nemacheiline loaches from Central Vietnam with descriptions of a new genus and 14 new species (Cypriniformes: Balitoridae). *Ichthyological Exploration of Freshwaters*, **12**(2): 133–191.
- Granse A, Kaus A, Freyhof J, Borchardt D. 2019. New insights into the morphological and molecular variability of the genus *Barbatula* from across Mongolia. In: *Frontiers in Marine Science 6 Conference Abstract: XVI European Congress of Ichthyology*.
- IUCN. 2018[2018-07-05]. The IUCN Red List of Threatened Species. Version 2018–1. <http://www.iucnredlist.org>.

- Jiang WS, Zhao YP, Du LN, Wang M. 2021. *Yunnanilus chuanheensis*, a new loach species (Cypriniformes: Nemacheilidae) from the upper Lixianjiang River in Yunnan, China. *Zoological Research*, **42**(2): 241–245.
- Kaya C, Turan D, Bayçelebi E, Kalayci G, Freyhof J. 2020a. *Oxynoemacheilus cilicicus*, a new nemacheilid loach from the Goksu River in southern Anatolia (Teleostei: Nemacheilidae). *Zootaxa*, **4808**(2): 284–300.
- Kaya C, Turan D, Kalayci G, Bayçelebi E, Freyhof J. 2020b. The westernmost known population of *Paracobitis* (Teleostei, Nemacheilidae), with the description of a new species from the Euphrates River in southern Anatolia. *Zootaxa*, **4838**(4): 525–534.
- Kottelat M. 1990. Indochinese Nemacheilines: A Revision of Nemacheiline Loaches (Pisces: Cypriniformes) of Thailand, Burma, Laos, Cambodia and Southern Viet Nam. *München*: 262
- Kottelat M. 2012. Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidei). *The Raffles Bulletin of Zoology*, (S26): 1–199.
- Kottelat M. 2013. The fishes of the inland waters of southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, Mangroves and Estuaries. *The Raffles Bulletin of Zoology Supplement*, (S27): 1–663.
- Kottelat M, Chu XL. 1988. Revision of *Yunnanilus* with descriptions of a miniature species flock and six new species from China (Cypriniformes: Homalopteridae). *Environmental Biology of Fishes*, **23**(1-2): 65–94.
- Lan JH, Gan X, Wu TJ, Yang J. 2013. Cave Fishes of Guangxi, China. Beijing: Science Press, 104–139. (in Chinese)
- Li WX, Wu DF, Xu K, Gao XM, Chen AL, Wu QL, et al. 1999. Fishes in the Heilongtan reservoir and its drainage. *Sichuan Journal of Zoology*, **18**(1): 3–7. (in Chinese)
- Liu SQ, Mayden RL, Zhang JB, Yu D, Tang QY, Deng X, et al. 2012. Phylogenetic relationships of the Cobitoidea (Teleostei: Cypriniformes) inferred from mitochondrial and nuclear genes with analyses of gene evolution. *Gene*, **508**(1): 60–72.
- Luo FG, Huang J, Luo T, Yang J, Zhou HJ, Wen YH. 2019. Complete mitochondrial genome and phylogenetic analysis of *Yunnanilus pulcherrimus* (Cypriniformes, Nemacheilidae). *Mitochondrial DNA Part B*, **4**(1): 1269–1270.
- Min R, Chen XY, Yang JX, Winterbottom R, Mayden RL. 2012a. Phylogenetic relationships of the genus *Homatula* (Cypriniformes: Nemacheilidae), with special reference to the biogeographic history around the Yunnan-Guizhou Plateau. *Zootaxa*, **3586**(1): 78–94.
- Prokofiev AM. 2004. A new species of the genus *Micronoemacheilus* Rendahl, 1944 (Balitoridae: Nemacheilinae) from Hainan (China) with notes on its status. *Journal of Ichthyology*, **44**(3): 191–198.
- Prokofiev AM. 2010. Morphological classification of loaches (Nemacheilinae). *Journal of Ichthyology*, **50**(10): 827–913.
- Regan CT. 1904. On a collection of fishes made by Mr. John Graham at Yunnan fu. *Annals and Magazine of Natural History*, Ser. 7, **13**(75): 190–194.
- Rendahl H. 1944. Einige Cobitiden von Annam und Tonkin. *Göteborgs Kungliga Vetenskaps och Vitterhets Samhällets Handlingar, Series B, Matematiska och Naturvetenskapliga Skrifter*, **3**(3): 37.
- Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**(3): 539–542.
- Sgourou K, Page LM, Orlofske SA, Jadin RC. 2019. A revised molecular phylogeny reveals polyphyly in *Schistura* (Teleostei: Cypriniformes: Nemacheilidae). *Zootaxa*, **4559**(2): 349–362.
- Shu SS, Jiang WS, Whitten T, Yang JX, Chen XY. 2013. Drought and China's cave species. *Science*, **340**(6130): 272.
- Taggart JB, Hynes RA, Prodöuhl PA, Ferguson A. 1992. A simplified protocol for routine total DNA isolation from salmonid fishes. *Journal of Fish Biology*, **40**(6): 963–965.
- Tang QY, Liu HZ, Mayden R, Xiong BX. 2006. Comparison of evolutionary rates in the mitochondrial DNA cytochrome *b* gene and control region and their implications for phylogeny of the Cobitoidea (Teleostei: Cypriniformes). *Molecular Phylogenetics and Evolution*, **39**(2): 347–357.
- Yang JX. 1990. The Fishes of Yunnan, China Part II Cyprinidae. Beijing, China: Science Press. (in Chinese)
- Yang JX. 1991. The fishes of Fuxian Lake, Yunnan, China, with description of two new species. *Ichthyological Exploration of Freshwaters*, **2**(3): 193–202.
- Yang JX, Chen YR. 1995. The Biology and Resource Utilization of the Fishes of Fuxian Lake, Yunnan. Kunming, China: Yunnan Science and Technology Press, 224. (in Chinese)
- Yoğurtçuoğlu B, Kaya C, Geiger MF, Freyhof J. 2020. Revision of the genus *Seminemacheilus*, with the description of three new species (Teleostei: Nemacheilidae). *Zootaxa*, **4802**(3): 477–501.
- Zhang CG, Zhao YH. 2016. Species Diversity and Distribution of Inland Fishes in China. Beijing: Science Press, 127–151. (in Chinese)
- Zheng CY. 1989. The Fishes of the Pearl River. Beijing: Science Press, 46–47. (in Chinese)
- Zhu SQ. 1989. The Loaches of the Subfamily Nemacheilinae in China. Nanjing, China: Jiangsu Science and Technology Publishing House, 14–20. (in Chinese)
- Zhu Y, Zhu DG. 2014. Description of a new species of the genus *Heminoemachilus* (Teleostei: Balitoridae) in Guangxi, China. *Journal of Guangdong Ocean University*, **34**(6): 18–21. (in Chinese)