

Research Article

Generic Revision of the Southeast and East Asian Torrent Carp Subfamily Acrossocheilinae (Pisces: Teleostei) With Description of Three New Genera and a New Species From Vietnam

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Molecular data from 35 of the 50 Acrossocheilinae species suggest that the species-level diversity in the subfamily has been overestimated, likely due to inadequate taxon and geographic sampling and reliance on morphological characters that vary intraspecifically. Three new genera, one resurrected genus, two resurrected species, and one new species are diagnosed and described herein. Nine synonyms of three valid species of Acrossocheilinae are recognized from the Yangtze, Xijiang, Song Hong, Annamite, and Mekong ecoregions in East and Southeast Asia. Thirty-two valid and six putative new species are indicated by molecular data and a key to the genera is provided. As more molecular and morphological data become available, additional taxonomic changes in this widespread and generally poorly known subfamily are likely.

Keywords: *Angustistoma* gen. nov; Cyprinidae; *Hongiastoma* gen. nov; molecular and morphological systematics; *Scaphostoma annamense* sp. nov; *Scaphostoma* gen. nov

1. Introduction

Using mitochondrial and nuclear sequence data, Yang et al. [1] recognized 11 major clades of Cyprininae (Cypriniformes) as tribes, one of which, Acrossocheilini, included *Acrossocheilus*, *Onychostoma*, and *Folifer*. Acrossocheilini was elevated by Tan and Armbruster [2] to a subfamily, Acrossocheilinae, a classification followed here. Acrossocheilinae is a subfamily of bottom-feeding fishes inhabiting streams throughout much of Indochina and southern and eastern China. The subfamily as

currently recognized includes three genera and 48 species, including the light-lipped carps, *Acrossocheilus* (23 species); the shovel-jaw carps, *Onychostoma* (22 species); and the lobe-lipped carps, *Folifer* (three species) [3, 4]. Some of the species are threatened with extinction, including the endangered *O. alticarpus* [5].

Relationships within and among *Acrossocheilus* and *Onychostoma* have long been confused, and some species in these genera have been assumed to be more closely related to other cyprinids [6–9]. Assignment of species to genera has been based

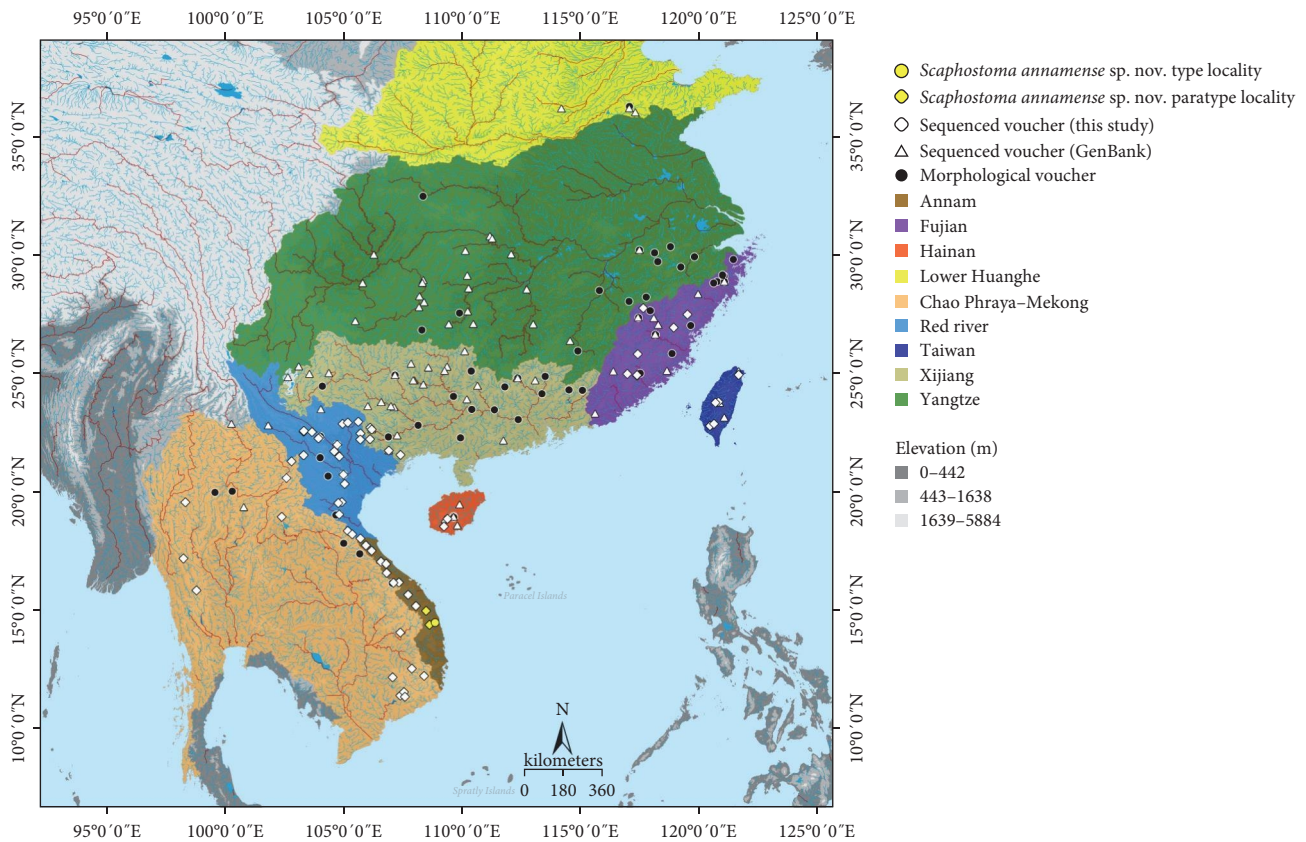


FIGURE 1: Sampling sites of Acrossocheilinae species in nine freshwater ecoregions shown in various colors. Red lines are mainstems of river drainages.

primarily on morphology [9, 10], and recent studies using molecular data have found *Acrossocheilus* and *Onychostoma* to be paraphyletic. In studies examining relationships within Cyprininae, Li et al. [11] used 16S rRNA and included two species of *Acrossocheilus* and four of *Onychostoma*; Wang, Li, and He [12] used RAG2 sequence data and included three species of *Acrossocheilus* and seven of *Onychostoma*; Yang et al. [1] used mitochondrial and nuclear genes and included eight species of *Acrossocheilus* and 10 of *Onychostoma*; and Li and Guo [13] used 13 mitochondrial protein-coding genes to examine relationships in Cyprinidae and included 14 species of *Acrossocheilus* and 10 of *Onychostoma*. In more targeted studies, Zheng, Yang, and Chen [14] used mitochondrial genes to examine relations in Barbinae and included eight species of *Acrossocheilus* and six of *Onychostoma*; Wang et al. [15] used mitogenomes to examine relations within Acrossocheilinae and included 16 species of *Acrossocheilus* and 12 of *Onychostoma*; Yuan, Liu, and Zhang [16] used the mitochondrial control region to examine relationships within *Acrossocheilus* and included two species of *Onychostoma*. All these studies except Li et al. [11] found *Acrossocheilus* and *Onychostoma* to be paraphyletic, and *Folifer* was embedded within the *Acrossocheilus*–*Onychostoma* clade in Wang et al. [15], Yang et al. [1], and Zheng, Yang, and Chen [14].

In addition to a poor understanding of relationships, an informed estimate of species diversity in Acrossocheilinae is lacking, especially in *Onychostoma* [17]. Species descriptions have sometimes failed to distinguish similar populations, as

noted by Nagao Natural Environment Foundation [18], and molecular studies have shown populations of some species to be highly structured [4, 17] suggesting taxonomically unrecognized diversity. Recent fieldwork throughout much of the distribution of the subfamily Acrossocheilinae, especially in species-rich Vietnam, have provided the material necessary for a broader study of molecular variation in the subfamily. Our study is the first to include data from Indochina as well as southern and eastern China, thereby, allowing a greater understanding of the diversity within Acrossocheilinae. Results of our study suggest that several currently recognized names of species and one genus are synonyms. In addition, three new genera, one genus resurrected from synonymy, and a newly discovered species from Vietnam are diagnosed and described herein, using morphological and molecular characteristics.

2. Materials and Methods

2.1. Field Sampling. Tissues were taken from selected specimens collected in the field or purchased in local markets in the tested localities (Figure 1) and stored in 95% ethanol for molecular analysis. Specimens were then fixed in 10% formalin, subsequently transferred to 70% ethanol and deposited at the University of Science, Ho Chi Minh City, Vietnam (UNS), Florida Museum of Natural History, Florida, USA (UF), and National Museum of Natural Science, Taichung, Taiwan (NMNS). Samples newly obtained for this study

included those from type localities for all nominal species in the molecular analysis except *O. lini*, *O. fangi*, *O. fusiforme*, *O. gerlachi*, *O. ovale*, *O. virgulatum*, and *Acrossocheilus malacopterus*; for these species, samples were from near the type localities in the Xijiang and lower Lancang drainages (Table S1). Multiple samples and localities were included when possible for widespread species. Sampling sites were assigned to freshwater ecoregions following Abell et al. [19] and Hoang et al. [20, 21] and modified herein based on newly understood distributions of Acrossocheilinae (Figure 1). We group the middle Yangtze + lower Yangtze as the Yangtze ecoregion; the Song Hong + Northern Annam as the Red River (Song Hong) ecoregion, the Southern Annam as the Annam ecoregion; the lower and middle Salween + Mae Klong + Chao Phraya + Khorat Plateau + lower Lancang + Kratie—Stung Treng + Mekong Delta as the Chao Phraya—Mekong ecoregion.

2.2. Molecular Analysis

2.2.1. DNA Extraction and Amplification. DNA was extracted from fin clips stored in 95%–99% ethanol using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA) and following the protocol suggested by the manufacturer. The mitochondrial gene, cytochrome c oxidase subunit I (*COI*), was amplified using polymerase chain reaction (PCR). Primers FishF1, FishF2, and FishR1 were used for PCR with conditions followed Ward et al. [22] for *COI*. PCR products were visualized on 1%–2% agarose gels, and the most intense products were selected for sequencing by 1st BASE (<https://base-asia.com/>).

2.2.2. Phylogenetic Analyses. Molecular sequence data were newly generated or taken from GenBank for currently recognized species of *Onychostoma* [3] (Table S1), and *Folifer*, and for species of *Acrossocheilus* considered to be closely related to *Onychostoma* and for which taxonomic ambiguity exists; that is, *Acrossocheilus lamus* (Mai, 1978), *A. laocaiensis* (Nguyễn and Đoàn, 1969), and *A. malacopterus* [23] (Table S1). *Scaphiodonichthys acanthopterus* and *Spinibarichthys denticulatus* were used as outgroup species based on recent studies of cyprinid higher-level relationships [1, 24, 25]. No *COI* data are available for *Folifer yunnanensis* (Wang, Zhuang and Gao, 1982), *Onychostoma angustistomatum* (Fang, 1940), and *O. breve* (Wu and Chen, 1977), and no opinions are offered on their validity.

Chromas 2.6.6 (<http://technelysium.com.au/>) was used to inspect the sequence chromatograms and assemble them into contigs, and MUSCLE in MEGA 7 [26, 27] was used to align the consensus sequences for each gene. Alignments were inspected by eye for accuracy, and sequences were trimmed at the 3' and 5' ends to minimize missing characters. The final data matrix consisted of 568 bp for *COI* used in the concatenated analyses. All sequences generated for this study were deposited in GenBank (Table S1). For the dataset of *COI* (568 bp), phylogenetic inferences based on maximum likelihood (ML) was made using IQ-TREE (Nguyen et al. 2015) through the IQ-TREE web server [28]. Optimal partitioning models (Chernomor et al. 2016) for the ML inference were selected by ModelFinder [29] in IQ-TREE, using the minimum Bayesian information criterion (BIC) score. Partition

analysis suggested best fit models for ML inference: TN + F + I + G4 (BIC = 6531.319, ln L = −2650.474) for *COI*. Ultrafast bootstrap (BS) analysis for 1000 iterations [30] was carried out to determine statistical support for the nodes in ML. The trees obtained from ML were visualized using Figtree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree>). Uncorrected pairwise sequence divergence was estimated using the substitution model of Kimura two-parameters, BSs 1000 implemented in MEGA 7 [27].

2.3. Morphological Analysis. Morphological data were taken on 260 specimens (Table S2) including fixed specimens from museums used for morphological description and fresh specimens for morphometric measurement and morphological description. Due to the potential synonyms and undiagnosed diversity within *Onychostoma*, we relied on examination of topotypic material and/or original species descriptions. Methods of measurements, counts, and terminology of the mouth structure following Kottelat and Freyhof [31]. Morphometric data were taken to the nearest 0.1 mm with digital calipers.

A principal component analysis (PCA) was conducted with R version 4.3.0 (R Core Team 2023) on the correlation matrix of data from 24 morphometric variables after being log transformed for 107 specimens of seven *Scaphostoma* species for comparison with the newly discovered species. The second (PC2) and third (PC3) principal components of the morphometric data representing shape factors independent of size were plotted.

3. Results

3.1. Molecular Data. The ML trees for the *COI* sequences are shown in Figure 2. The *COI* topology is consistent with recognition of 38 species, all with ≥63% BS support. Seven of the species are undescribed taxonomically, including six represented by specimens previously assigned to other species; the other is newly discovered and is described herein. Descriptions of the other undescribed species await the collection of additional material.

Hongiastoma argentatum is sister to the rest of the Acrossocheilinae (Figure 2A) and represented in the tree by specimens collected from the type locality of *Varicorhinus argentatus* in northern Vietnam in the Song Hong ecoregion. This clade received 98% BS support and has a *COI* sequence similarity of 89% with *O. ovale* (Table S3), also from northern Vietnam in the Song Hong ecoregion.

The *Scaphostoma erythrogenys* clade (Figure 2A) is based on six newly collected specimens from the type locality of *Varicorhinus erythrogenys* in northern Vietnam in the Song Hong ecoregion. This clade received 99% BS support and has a *COI* sequence similarity of 97% with specimens of *S. gerlachi* and 93% with *S. meridionale* from the Song Hong ecoregion (Table S3).

Seven of the 38 species recognized with *COI* data (Figure 2) include representatives with species names now to be recognized as synonyms based on the molecular results and lack of distinguishing morphological characteristics.

The *Scaphostoma lepturum* clade, with 76% BS support (Figure 2A), includes 23 specimens from populations currently



(A)

FIGURE 2: Continued.

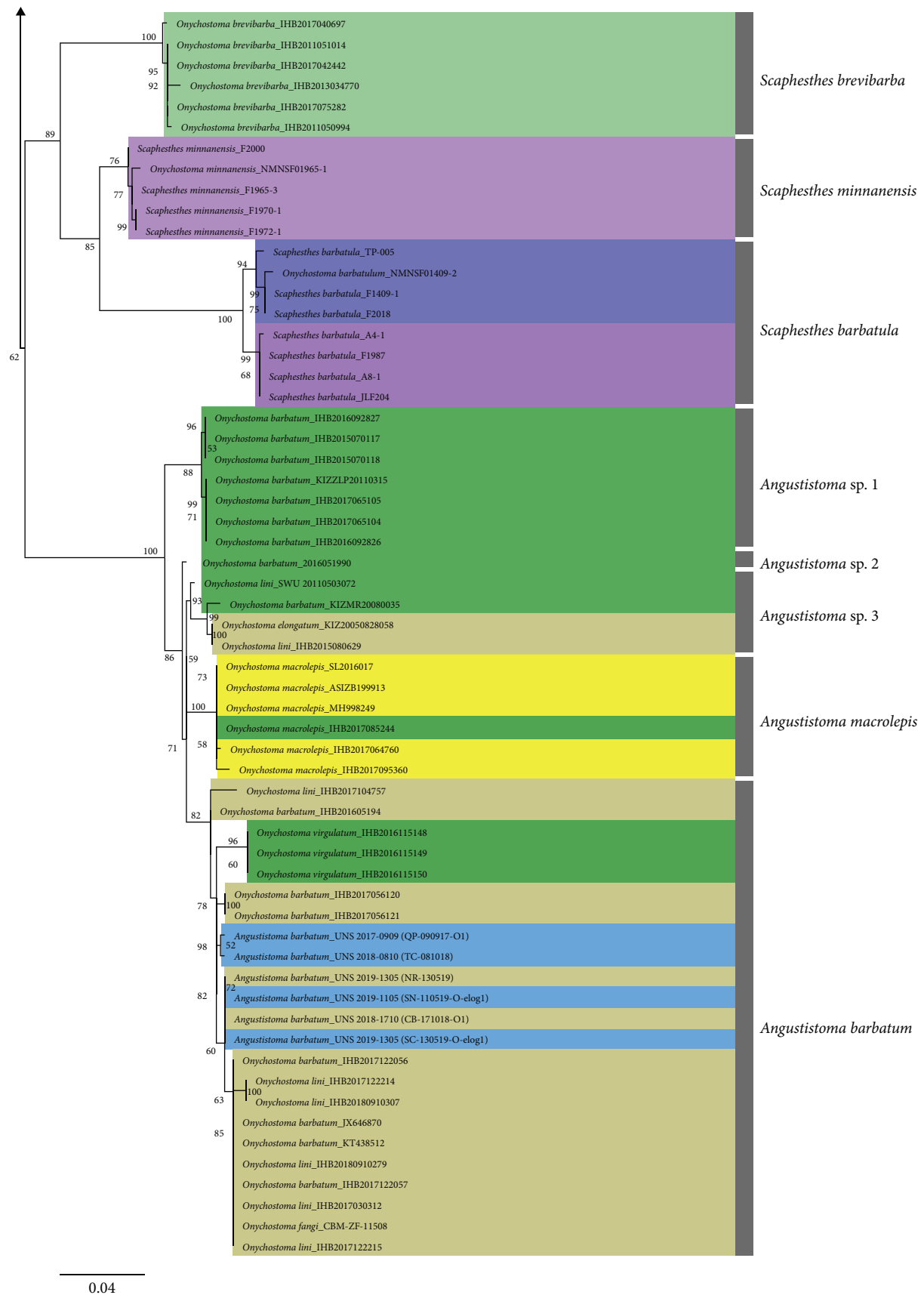


FIGURE 2: Maximum likelihood (ML) tree based on COI mitochondrial gene sequences for Acrossocheilinae (A–B). Values on branches are ML bootstrap (BS) support (values >50% shown). Bold sample labels are sequences from type localities. Colors of clades correspond to the freshwater ecoregions in Figure 1.

TABLE 1: Distinguishing characteristics in type species of Acrossocheilinae genera, *A. microstomus*, and *A. barbatum* (with new synonyms).

Species (n: specimen number)	Mouth width	Lateral line scales	Barbels	Position of the dorsal fin	Last simple dorsal ray	Caudal peduncle depth in SL
<i>Hongiastoma argentatum</i> (n = 4)	Wide horny sheath on lower jaw	46	Absent in adult	Behind/opposite of pelvic-fin insertion	Slender and smooth	11.1–11.8
<i>Folifer brevifilis</i> (n = 6)	Thick fleshy lips, lobe on lower jaw	45	2 pr	In front of pelvic-fin insertion	Strong and serrated	11.2–13.3
<i>Onychostoma simum</i> (n = 14)	Moderate, horny sheath on lower jaw	46–48	Absent	In front of pelvic-fin insertion	Strong and serrated	9.1–9.3
<i>Acrossocheilus paradoxus</i> (n = 8)	Fleshy lips, medially disrupted lower lip	40–41	2 pr	Opposite of pelvic-fin insertion	Slender and smooth	8.6–8.8
<i>Acrossocheilus microstomus</i> (n = 8)	Fleshy lips, medially disrupted lower lip	41–42	2 pr	Opposite of pelvic-fin insertion	Strong and serrated	7.9–8.1
<i>Scaphesthes barbatula</i> (n = 22)	Wide, horny sheath on lower jaw	45–48	2 pr	In front of pelvic-fin insertion	Slender and smooth	9.7–10.7
<i>Angustistoma barbatum</i> (n = 42)	Narrow, horny sheath on lower jaw	47–50	2 pr	In front of pelvic-fin insertion	Slender/strong and smooth/serrated	10–13.5
<i>Scaphostoma lepturum</i> (n = 49)	Wide, horny sheath on lower jaw	45–48	Absent	In front of pelvic-fin insertion	Slender/strong and smooth/serrated	8–11.6

Note: Data from original descriptions, Song et al. [4], Jang-Liaw and Chen (2013), Wu et al. (1977), Banareescu (1971), and this study. N = number of specimens examined.

recognized as *Onychostoma lepturus* and *O. babeense*. Specimens collected from the type localities in the Hainan and Song Hong ecoregions embedded with other specimens from the Hainan, Song Hong, and Annam ecoregions with a mean similarity of $97.6\% \pm 0.005$. *Onychostoma babeense* (Nguyễn and Nguyễn, 2001) is herein recognized as a synonym of *S. lepturum* (Boulenger, 1900). The *S. lepturum* clade has a COI sequence similarity of 93% with specimens of *S. erythrogenys* and *S. gerlachi* from the Song Hong ecoregion (Table S3).

The *Scaphostoma meridionale* clade, with 99% BS support (Figure 2A), includes 10 specimens from populations currently recognized as *Onychostoma meridionale* and *O. dongnaiense*. Specimens collected from the type localities in the Lower Mekong ecoregion and the Đồng Nai river are embedded with other specimens from the Lower Mekong with a mean similarity of $99.6\% \pm 0.003$. *Onychostoma dongnaiense* (Hoàng, Phạm and Trần, 2015) is herein recognized as a synonym of *S. meridionale* [32]. The *S. meridionale* lineage has a COI sequence similarity of 98% with *S. krongnoense* and 97% with *S. fusiforme* from the lower Mekong ecoregion (Table S3).

The *Scaphesthes* and *Angustistoma* clades are sisters, with 62% BS support (Figure 2B). The *Scaphesthes* group consists of specimens currently assigned to *O. brevibarba*, *O. minnansensis*, and *O. barbatulum*. The *Angustistoma* group consists of specimens currently assigned to *O. macrolepis* and *O. barbatum*.

The *Angustistoma barbatum* clade, with 82% BS support (Figure 2B), consists of specimens currently assigned to

O. barbatum, *O. elongatum*, *O. lini*, *O. fangi*, *O. uniforme*, *O. virgulatum*, and *A. malacopterus*. Sequences from newly collected specimens from the type localities in the Xijiang (Xi Yang), Yangtze, and Song Hong ecoregions and from GenBank are embedded with *A. barbatum* sequences from the Xijiang and show a mean similarity of $99.2\% \pm 0.002\%$. Thus, we conclude that *O. elongatum* (Pellegrin and Chevey, 1934), *O. lini* (Wu, 1939), *O. uniforme* (Mai, 1978), *O. fangi* Kottelat, 2000, *O. virgulatum* [33] and *A. malacopterus* [23] are synonyms of *A. barbatum* (Lin, 1931). The *A. barbatum* lineage from the Xijiang and Song Hong ecoregions has a COI sequence similarity of 97.8% with *Angustistoma* species 3 in the Xijiang (Table S3).

The *Acrossocheilus microstomus* clade, with 100% BS support (Figure 2A), includes specimens currently assigned to *A. lamus*, *A. laocaiensis*, and *A. microstomus*. Sequences from newly collected specimens of all three taxa from their type localities in the Song Hong ecoregion have a mean similarity of $99.8\% \pm 0.001\%$. *Acrossocheilus lamus* (Mai, 1978) and *A. laocaiensis* (Nguyễn and Đoàn, 1969) are synonyms of *A. microstomus* (Pellegrin and Chevey, 1936). The *A. microstomus* lineage has a COI sequence similarity of 97.6% with *A. longipinnis* in the Xijiang and 96.4% with *A. iridescens* in the Hainan (Table S3).

3.2. Morphological Data. Data were taken on species shown in our molecular analysis to belong in *Onychostoma* are *O. alticorpus* (Oshima, 1920), *O. monticola* (Günther, 1888) n. comb., *O. ovale* Pellegrin and Chevey, 1936, *O. rarum* (Lin, 1933),

TABLE 2: Important morphometric measurements contributed to principal component analysis (PCA) analysis for seven *Scaphostoma* species with data from 107 specimens examined by this study.

Variables	<i>Scaphostoma lepturum</i> (n = 25)	<i>Scaphostoma erythrogenys</i> (n = 10)	<i>Scaphostoma gertlachi</i> (n = 8)	<i>Scaphostoma annamense</i> (n = 31)	<i>Scaphostoma fusiforme</i> (n = 11)	<i>Scaphostoma krongnoense</i> (n = 12)	<i>Scaphostoma meridionale</i> (n = 10)
Standard length	170.97 ± 32.11 (92.62–229)	141.7 ± 17.06 (110.62–162)	183.5 ± 32.08 (131–241)	154.46 ± 24.35 (117.5–197)	145.53 ± 16.51 (123.12–181)	170.83 ± 34.36 (116–214)	153.8 ± 33.55 (86–196)
Total length	212.69 ± 38.86 (115.62–284)	173.94 ± 21.48 (134.92–197)	230.25 ± 40.85 (163–304)	188.44 ± 30.65 (141–243)	178.28 ± 20.64 (154.12–217)	208.25 ± 43.2 (141–264)	191.8 ± 39.3 (107–241)
Fork length	184.26 ± 32.67 (102.42–244)	152.15 ± 16.95 (123–171)	197 ± 33.47 (142–256)	164.58 ± 26 (124–208)	158.13 ± 18.5 (136.18–196)	180.33 ± 36.09 (124–225)	165.21 ± 33.96 (93–206)
Depth of Body	49.12 ± 10.81 (24.82–67.82)	35.73 ± 4.83 (29.12–41.98)	55.11 ± 11.5 (37.52–75.12)	45.57 ± 8.96 (31–63.72)	39.68 ± 4.79 (30.62–46.92)	41.08 ± 9.41 (27–54)	47.04 ± 11.91 (23.5–64)
Body width	22.37 ± 5.04 (10.82–31.92)	18.51 ± 1.94 (16.22–21.08)	22.56 ± 3.19 (17.62–26.32)	22.17 ± 4.32 (15–30.42)	21.9 ± 3.95 (14.62–30.21)	24.08 ± 3.77 (19–29)	22.61 ± 4.9 (13–30)
Head length	32.69 ± 5.12 (20.82–41.42)	27.45 ± 3.76 (19.9–32.08)	33.14 ± 5.28 (25.42–42)	28.87 ± 3.61 (24–35.82)	27.67 ± 1.93 (25.02–30.82)	32.88 ± 5.7 (24–40)	32.93 ± 5.1 (21–38)
Dorsal-fin base length	28.1 ± 6.65 (14.52–39.32)	21.67 ± 3.25 (16.82–28.42)	31.49 ± 6.76 (20.82–42.76)	25.3 ± 4.61 (18–33.32)	24.14 ± 2.89 (19.74–30.32)	26.92 ± 6.01 (18–35)	25.67 ± 5.12 (14–31.62)
Dorsal-fin length	37.08 ± 8.2 (20.12–56.82)	27.81 ± 3.92 (21.12–33.02)	45.52 ± 12.68 (28.94–68.12)	33.36 ± 6.03 (21–48.42)	29.98 ± 3.87 (25.32–37.62)	37.75 ± 8.28 (25–49)	37.39 ± 7.12 (22–47.46)
Pectoral fin length	30.69 ± 5.49 (17.78–42.18)	24.44 ± 2.47 (20.32–28.54)	33.77 ± 6.66 (25–45.32)	27.52 ± 4.82 (20–36.82)	25.48 ± 3.02 (19.72–28.86)	29.42 ± 6.57 (20–38)	28.7 ± 5.81 (16–35)
Pelvic-fin length	30.64 ± 5.79 (17.02–42.82)	24.34 ± 2.5 (20.54–29.28)	33.39 ± 7.89 (20.56–45.4)	28.12 ± 5.24 (20–39.62)	25.05 ± 2.64 (20.42–28.92)	29.75 ± 6.98 (19–38)	28.43 ± 6.24 (16.8–37)
Anal fin length	29.05 ± 7.45 (12.82–42.88)	24.2 ± 3.86 (17.18–29.72)	35.3 ± 8.75 (24.74–53)	25.5 ± 5.03 (18.5–35.52)	26.08 ± 4.4 (19.62–34.52)	28.92 ± 7.48 (19–40)	30.68 ± 8.33 (16–42)
Anal fin base	15.61 ± 3.59 (7.28–23.42)	11.84 ± 1.38 (9.12–13.34)	16.69 ± 2.97 (12.68–22.08)	12.95 ± 2.39 (10–17.14)	13.33 ± 1.9 (10.12–16)	13.33 ± 3.68 (7–18)	14.5 ± 4.26 (7–20)
Caudal peduncle length	26.12 ± 6.53 (13.62–41.9)	23.22 ± 3.48 (16.82–27.2)	28.4 ± 4.39 (21.74–34.42)	25.38 ± 3.38 (17.02–32.72)	23.41 ± 3.34 (18.32–30.62)	44 ± 8.9 (30–55)	31.58 ± 9.32 (18.08–46)
Caudal peduncle depth	16.79 ± 3.24 (9.04–22.62)	12.45 ± 1.51 (10.1–14.42)	17.88 ± 2.79 (12.56–21.14)	15.48 ± 3.32 (10–23)	13.9 ± 1.71 (11.92–17.72)	13.96 ± 3.54 (9–21)	15.09 ± 3.17 (8–18.94)
Distance pectoral and pelvic-fin	44.33 ± 7.96 (25.2–62.12)	37.45 ± 7 (23.22–45.02)	48.99 ± 11.35 (30.22–69.44)	39.94 ± 7.05 (27.4–50.82)	37.17 ± 7.48 (29.18–56.22)	42 ± 3.93 (38–48)	39.64 ± 10.3 (17–54)
Distance pelvic and anal fin	35.92 ± 7.77 (17.86–50.62)	28.39 ± 3.73 (22.95–34.42)	38.22 ± 7.63 (24.82–47.72)	31.87 ± 5.96 (21.6–44)	29.59 ± 4.36 (25.34–40.82)	37.42 ± 3.55 (32–43)	30.47 ± 8.31 (14.44)
Predorsal length	66.72 ± 11.61 (39.42–87.92)	54.74 ± 5.19 (45.72–60.72)	67.85 ± 11.68 (48.26–88.1)	61.33 ± 7.29 (50–74.34)	57.69 ± 5.73 (51.82–69.62)	69.96 ± 13.55 (48–88)	64.84 ± 12.54 (40–80)
Prepectoral length	32.04 ± 5.87 (19.32–43.34)	27.89 ± 4.03 (21.5–32.56)	35.54 ± 5.76 (27.32–46.18)	28.74 ± 3.45 (24–36)	27.33 ± 2.04 (24.52–31.72)	33 ± 5.56 (25–40)	31.71 ± 5.91 (21–39.4)
Prepelvic length	78.5 ± 13.78 (46.12–106.72)	63.6 ± 7.69 (53.1–72.22)	83.06 ± 13.29 (62.78–108.62)	71.49 ± 9.33 (57–89)	66.99 ± 7.48 (58.84–83.24)	77.08 ± 14.64 (53–94)	74.39 ± 15.36 (41–95)

TABLE 2: Continued.

Variables	<i>Scaphostoma lepturum</i> (n = 25)	<i>Scaphostoma erythrogenys</i> (n = 10)	<i>Scaphostoma gerlachi</i> (n = 8)	<i>Scaphostoma annamense</i> (n = 31)	<i>Scaphostoma fusiforme</i> (n = 11)	<i>Scaphostoma kronoense</i> (n = 12)	<i>Scaphostoma meridionale</i> (n = 10)
Preannal length	120.65 ± 21.6 (67.52–167)	97.11 ± 10.58 (81.3–109.12)	128.91 ± 24.18 (91.16–171)	108.46 ± 16.17 (85–136.82)	100.72 ± 11.47 (87.42–126.52)	116.5 ± 22.82 (79–145)	109.06 ± 23.1 (59–139)
Snout length	11.07 ± 3.48 (5.1–22.62)	9.33 ± 1.76 (7.05–12.72)	10.78 ± 2.27 (7.22–14.2)	9.59 ± 1.54 (7.18–13.04)	8.85 ± 0.82 (7.52–9.72)	11.21 ± 2.48 (7–14)	10.78 ± 2 (7–14)
Interorbital width	15.93 ± 3.4 (8.02–21.66)	12.3 ± 1.39 (9.88–14.18)	17.24 ± 3.57 (11–23.42)	14.57 ± 2.48 (10.3–19.22)	12.59 ± 1.6 (10.22–14.72)	16.44 ± 1.75 (14–19)	15.3 ± 3.43 (8.5–21)
Eye diameter	8.13 ± 1.52 (5.02–11.72)	6.97 ± 0.88 (5.22–8.02)	8.71 ± 1.64 (6.46–11.49)	7.04 ± 0.86 (5.58–8.82)	7.57 ± 0.43 (6.82–8.12)	7.08 ± 0.93 (6–8.5)	6.95 ± 1.06 (5–9)
Mouth width	14.88 ± 2.85 (7.38–19.32)	11.44 ± 1.1 (9.18–12.66)	16.41 ± 3.33 (12–22.76)	14.18 ± 2.59 (11–18.82)	10.72 ± 0.93 (9.34–12.04)	14.79 ± 3.11 (10–18)	13.05 ± 2.93 (7–17)

TABLE 3: Loadings on PC2 and PC3 for 107 samples of seven species of *Scaphostoma*.

Variables	PC2	PC3
Standard length	−0.003	0.057
Total length	0.034	0.004
Fork length	0.047	0.039
Body depth	0.239	−0.018
Body width	−0.022	0.380
Head length	−0.121	−0.291
Dorsal-fin base length	0.092	0.080
Dorsal-fin length	−0.006	−0.112
Pectoral-fin length	0.075	−0.056
Pelvic-fin length	0.065	−0.121
Anal-fin length	−0.043	−0.058
Anal-fin base length	0.183	−0.278
Caudal peduncle length	−0.767	0.132
Caudal peduncle depth	0.322	0.045
Pectoral-fin base to pelvic-fin base	0.112	0.417
Pelvic-fin base to anal-fin base	−0.013	0.454
Predorsal length	−0.175	−0.038
Prepectoral length	−0.169	−0.227
Prepelvic length	−0.013	−0.079
Preanal length	0.041	0.020
Snout length	−0.226	−0.354
Interorbital width	−0.095	0.186
Eye diameter	0.210	−0.164
Mouth width	−0.022	0.035

Abbreviation: PC, principal component.

O. simum (Sauvage and Dabry de Thiersant, 1874), and *O. yunnanense* (Regan, 1904) n. comb. Other valid species previously in *Onychostoma* belong to a previously described genus, *Scaphesthes*, three new genera, one new species of a new genus, and six new tentative species. *Acrossocheilus lamus* (Mai, 1978) and *A. laocaiensis* (Nguyễn and Đoàn, 1969) are synonyms of *A. microstomus* (Pellegrin and Chevey, 1936), and *A. malacopterus* [23] is a synonym of *Angustistoma barbatum* (Lin, 1931).

Morphological characteristics and morphometrics of the seven genera of Acrossocheilinae, one species of the new genus *Hongiastoma*, one valid species of *Acrossocheilus*, one valid species of the newly resurrected genus *Scaphesthes*, one valid species of the new genus *Angustistoma*, and seven species of the new genus *Scaphostoma*, identified in the molecular analysis (Figure 2), are presented in Tables 1–4 and Figures 3–8. The 32 nominal species and six putative new species in the molecular analysis of Acrossocheilinae are distributed across nine freshwater ecoregions (Figure 1).

In the PCA of seven species of *Scaphostoma*, PC1 can be defined as a size axis and contributed 84.4% of the total variation. PC2 and PC3 represented 3.8% and 2.1% of the variation, respectively (Table 3). The fourth, fifth, and sixth components contributed 1.5%, 1.1%, and 1.1%, respectively, and did not improve the separation of the samples. PC2 and PC3 separated the samples into two groups: *S. krongnoense* and the remaining species (Figure 5). *Scaphostoma krongnoense* was characterized by an elongated caudal peduncle and slender

body, whereas individuals of other species were characterized by a deep caudal peduncle and deep body (Table 3). Other species of *Scaphostoma* formed a large cluster, although *S. gerlachi* and *S. meridionale* did not overlap one another.

3.3. Taxonomic Conclusions. Based on molecular and morphological data, six of 17 species names currently in *Onychostoma* are considered valid names of *Onychostoma*. The other 11 names and *A. malacopterus* are transferred to *Scaphostoma*, *Scaphesthes*, and *Angustistoma*, as valid names or synonyms, as listed below. Also, *A. lamus* and *A. laocaiensis* are recognized as synonyms of *A. microstomus*. A key to the genera of Acrossocheilinae is provided based on data in Table 1.

Morphological and molecular data also provide evidence that newly collected specimens in Figure 2A from the Song Hong ecoregion represent a new genus *Hongiastoma* with one resurrected species; specimens from the Song Hong, Xijiang, Hainan, Annam, and lower Mekong represent a new genus *Scaphostoma*, and specimens from the Song Hong and Annam ecoregions represent a resurrected species and a new species *Scaphostoma annamense*, respectively; and specimens in Figure 2B from the Yangtze, Fujian, Taiwan, Xijiang, and Song Hong represent the previously described genus *Scaphesthes* and the new genus *Angustistoma*, those diagnosed and described below. Valid species and synonyms listed are only those addressed in this study.

TAXONOMIC ACCOUNT

Order: Cypriniformes

Family: Cyprinidae Rafinesque, 1815

Subfamily: Acrossocheilinae Yang [1]

Hongiastoma Hoàng and Nguyễn, new genus

Type species: *Varicorhinus argentatus* Nguyễn and Đoàn, 1969. Lectotype RIAH 67, 147 mm, Suối Rút, Hòa Bình, Vietnam.

Etymology: The name is from the Vietnamese prefix *hong-* meaning the Song Hong or Red River where the type species occurs, and the Greek suffix *-stoma* meaning mouth and referring especially to the horny sharp sheath on the lower lip. Gender neuter.

Diagnosis: *Hongiastoma* (Figure 3A,B) is distinguished from all other genera of Acrossocheilinae except *Scaphostoma* by having no barbels (at least in adult) and from *Scaphostoma* by having dorsal-fin origin behind or over (vs. in front of) pelvic-fin origin. It is further distinguished from *Folifer* by having horny sheath on lower jaw and lacking median lobe on lower lip, from *Onychostoma* by lacking distinct groove from snout to angle of mouth, and from *Acrossocheilus* by having sheath on lower jaw and lacking median interruption on fleshy lower lip.

Hongiastoma argentatum (Nguyễn and Đoàn, 1969), n. comb.

Varicorhinus argentatus Nguyễn and Đoàn, 1969:13. Type locality: Vietnam: Hòa Bình Province: Đà Bắc, Suối Rút. Lectotype: NCNTTSI “67”, designated by Roberts and Catania, 2007: 93 [syntypes, from NCNTTSI H.01.73.04.02 and H.01.73.04.01].

Genus *Folifer* Wu, 1977

Type species: *Barbus brevifilis* Peters, 1881b: 1033. Syntypes [2]: ZMB 11326 [1], 22290 [1] Pearl basin, China.

TABLE 4: Morphometric and meristic characters of *Scaphostoma annamense* sp. nov.

	<i>Scaphostoma annamense</i>		
	Holotype UNS00758	Range	Mean $\pm$ SD/ mode
SL (mm)	174.0	117.5–197	155.6 $\pm$ 24.7
Morphometrics			
% SL			
Total length	125.9	117.4–131.1	121.8 $\pm$ 2.8
Fork length	105.7	104–116.2	106.5 $\pm$ 2.2
Body depth	32.9	25.4–32.9	29.4 $\pm$ 2.3
Body width	15.1	12–15.9	14.3 $\pm$ 1.1
Head length	18.5	16.9–21.7	18.8 $\pm$ 1.3
Caudal peduncle length	21.5	19.5–23.4	21.6 $\pm$ 1.1
Caudal peduncle depth	11.3	8.2–11.7	10.0 $\pm$ 1.0
Dorsal-fin base length	16.7	14.8–17.8	16.3 $\pm$ 0.7
Dorsal-fin length	23.2	17.2–25.9	21.5 $\pm$ 1.8
Anal-fin base length	9.9	6.8–9.9	8.4 $\pm$ 0.6
Anal-fin length	16.9	13.3–20.9	16.5 $\pm$ 1.5
Pectoral-fin length	18.6	15.7–19.3	17.7 $\pm$ 0.9
Pelvic-fin length	18.5	15.9–21.5	18.1 $\pm$ 1.3
Predorsal length	39.4	36.2–44.7	40 $\pm$ 2.4
Prepectoral length	19	15.7–21.3	18.7 $\pm$ 1.5
Preanal length	66.4	65.6–73.3	70.3 $\pm$ 1.9
Prepelvic length	46.6	43.5–51.2	46.7 $\pm$ 2.2
Pelvic-fin base to anal-fin base	18.8	17.6–24.7	20.8 $\pm$ 1.6
Pectoral-fin base to pelvic-fin base	25.7	23.3–28.5	25.8 $\pm$ 1.3
% HL			
Head depth at nape	95.2	72–107.6	92.8 $\pm$ 9.9
Head width	79.7	58.9–84.6	73.3 $\pm$ 7.7
Snout length	33.2	27.6–38.8	33.2 $\pm$ 3.1
Interorbital width	48.5	44.4–56.1	51.2 $\pm$ 3.1
Eye diameter	23.8	20.1–28.8	24.4 $\pm$ 1.9
Mouth width	48.5	43.1–55	48.5 $\pm$ 3.8
Counts			
Dorsal-fin spines and rays	iv,8.5	iv,8.5	—
Anal-fin spines and rays	iii,5.5	iii,5.5	—
Pectoral-fin spines and rays	i,14	i,14–18	Mode = i,16
Pelvic-fin spines and rays	i,9	i,9	—
Branched caudal-fin rays	9 + 8	9 + 8	—
Lateral-line scales	48	46–49	Mode = 47
Transverse scales between lateral line and origin of dorsal fin	6.5	6.5–7.5	Mode = 7.5
Transverse scales between lateral line and middle of belly	5	4–5	Mode = 5
Transverse scales between lateral line and origin of anal fin	5.5	4.5–6.5	Mode = 5.5
Circumferential scale rows	28	26–30	Mode = 28
Circumpeduncular scale rows	16	16	—
Predorsal scales	13	12–14	Mode = 14
Scales from end of anal-fin base to caudal-fin origin	11	9–13	Mode = 10
Serrae on last simple dorsal-fin ray	26	20–34	Mode = 29

Note: N = 31 including holotype.

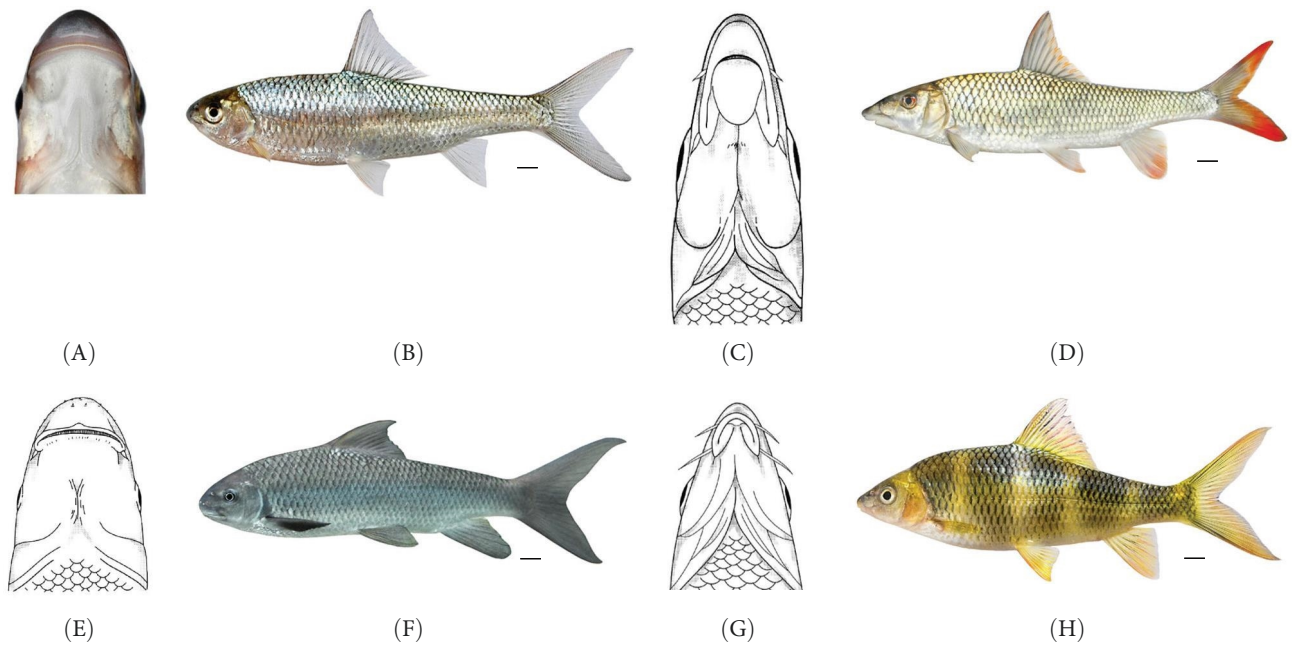


FIGURE 3: *Hongiastoma argentatum* from Song Hong ecoregion, University of Science (UNS) 2018-1210: (A) mouth and (B) lateral. *Folifer brevifilis* from the Xijiang, UNS 2019-1305: (C) mouth and (D) lateral. *Onychostoma simum* from the Xijiang: (E) mouth, re-drawn from Chen [10] and (F) lateral view from Ocean Park Hongkong, photograph by Pierre De Chabannes. *Acrossocheilus microstomus* from the Song Hong, UNS 2018-0511: (G) mouth and (H) lateral. All photographed in life. Scale: 10 mm.

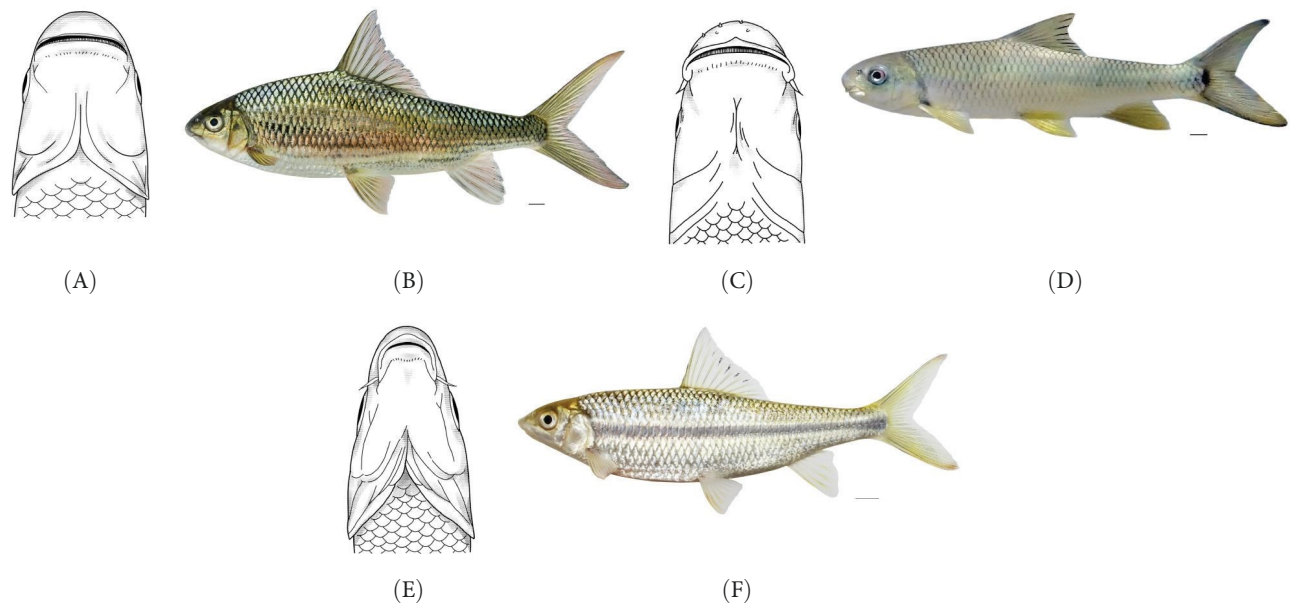


FIGURE 4: *Scaphostoma lepturum* from Song Hong ecoregion, Cà drainage, University of Science (UNS) 2018-0712: (A) mouth and (B) lateral. *Scaphesthes barbatula* from the Western Taiwan: (C) mouth, re-drawn from Chen [10] and (D) lateral view from Pingtung, Taiwan. *Angustistoma barbatum* from Song Hong ecoregion, UNS 2019-1105: (E) mouth and (F) lateral. All photographed in life. Scale: 10 mm.

Diagnosis: *Folifer* (Figure 3C,D) is distinguished from all other genera of *Acrossocheilinae* by having thick fleshy lips and large median lobe on lower lip (vs. thin lips—moderately thick in *Acrossocheilus*—and no lobe on lower lip), and from all genera except *Acrossocheilus* in lacking horny sheath on lower jaw. It is further distinguished from *Hongiastoma* and *Scaphostoma* in having two pairs of barbels (vs. no barbels

and from *Onychostoma* in having two pairs of barbels (vs. 1 pair).

Folifer brevifilis (Peters, 1881)

Barbus brevifilis Peters, 1881b: 1033. Type locality: China: sent from Hong Kong. Syntypes [2]: ZMB 11326 [1], 22290 [1].

Genus *Onychostoma* Günther, 1896

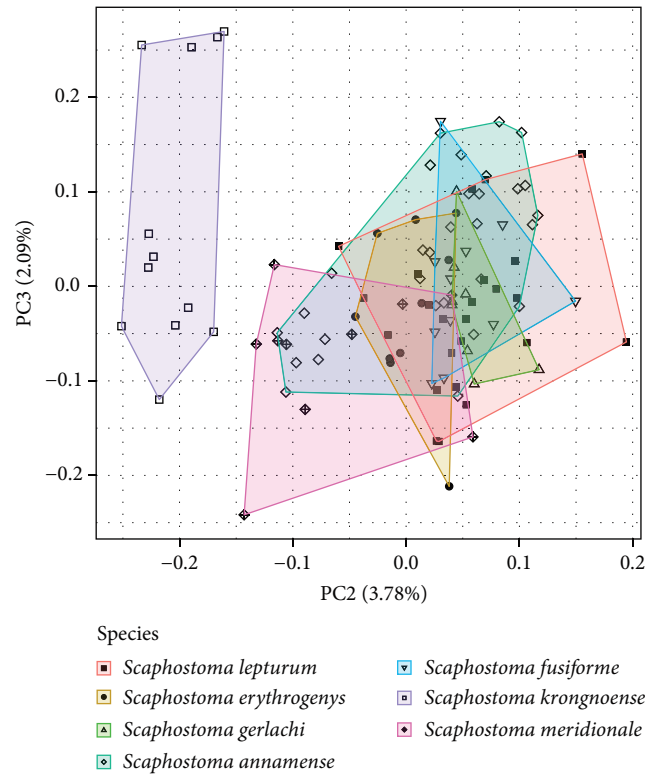


FIGURE 5: Plot of the second (PC2) and third (PC3) principal components of morphometric data from seven species of *Scaphostoma*.

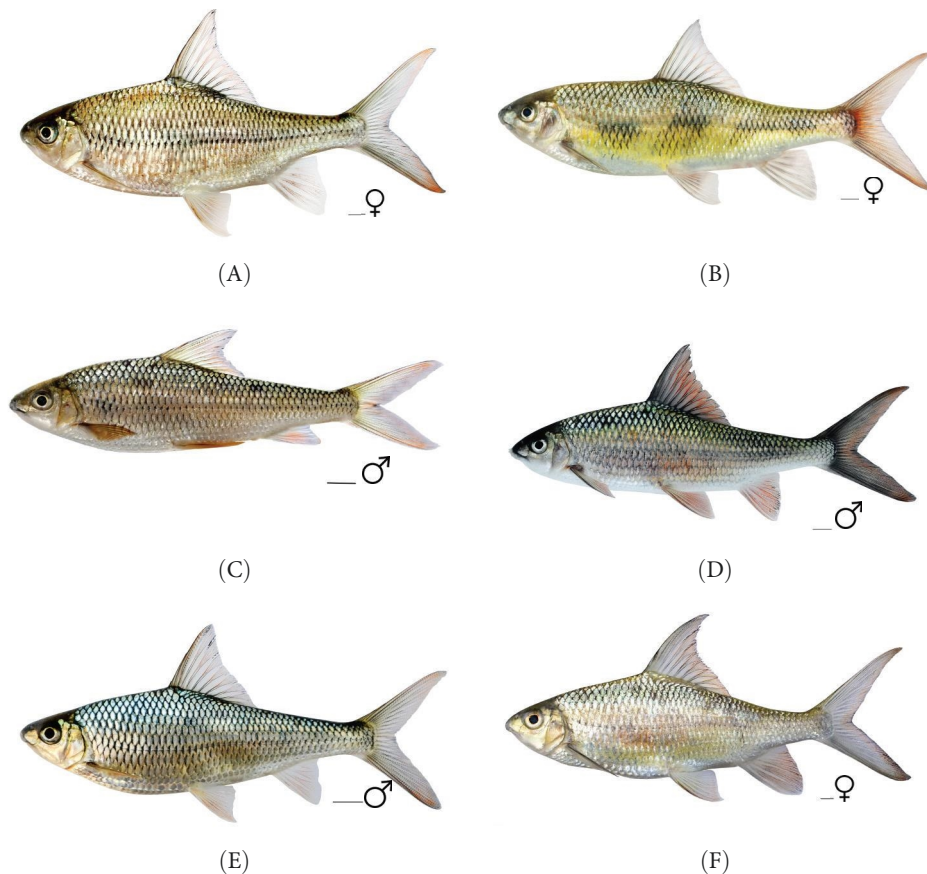


FIGURE 6: *Scaphostoma lepturum* from (A) Ba Bể Lake, University of Science (UNS) 2019-1205; (B) Red River tributaries, UNS 2018-0810; (C) Hainan, Tiên Yên drainage, UNS 2023-2002; (D) Annam, Boung drainage, UNS 2018-0503; (E) Thượng Lộ drainage, UNS 2017-0210; (F) *S. gerlachi* from Xijiang ecoregion, Bắc Giang drainage, UNS 2019-1305. All photographed in life. Scale: 10 mm.

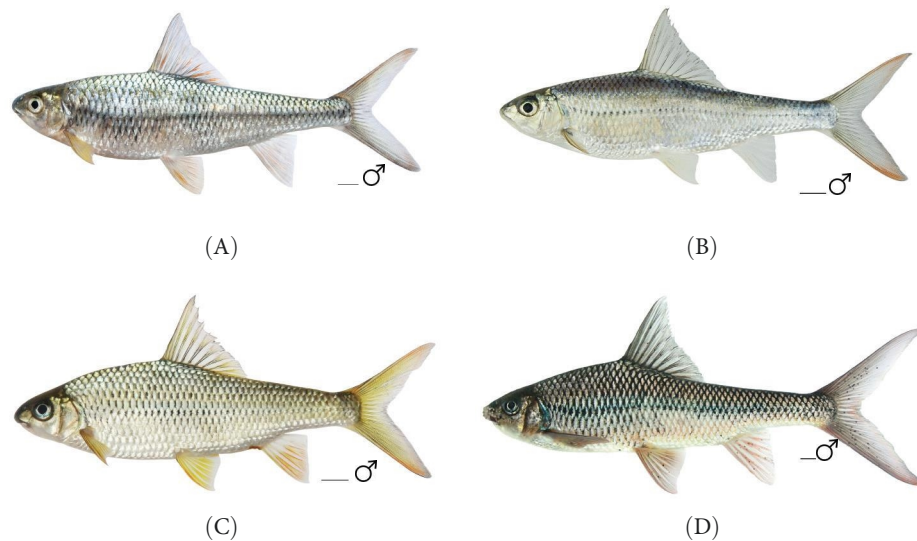


FIGURE 7: *Scaphostoma erythrogyens* from (A) Song Hong ecoregion, Lô drainage, University of Science (UNS) 2018-1210; (B) *S. fusiforme* from Chao Phraya—Mekong ecoregion, Nam Ou drainage, UNS 2018-0911; (C) *S. meridionale* from Chao Phraya—Mekong ecoregion, Đồng Nai drainage, UNS 2019-0801; (D) *S. krongnoense* from Chao Phraya—Mekong ecoregions, Krong No drainage, UNS 00805. All photographed in life. Scale: 10 mm.

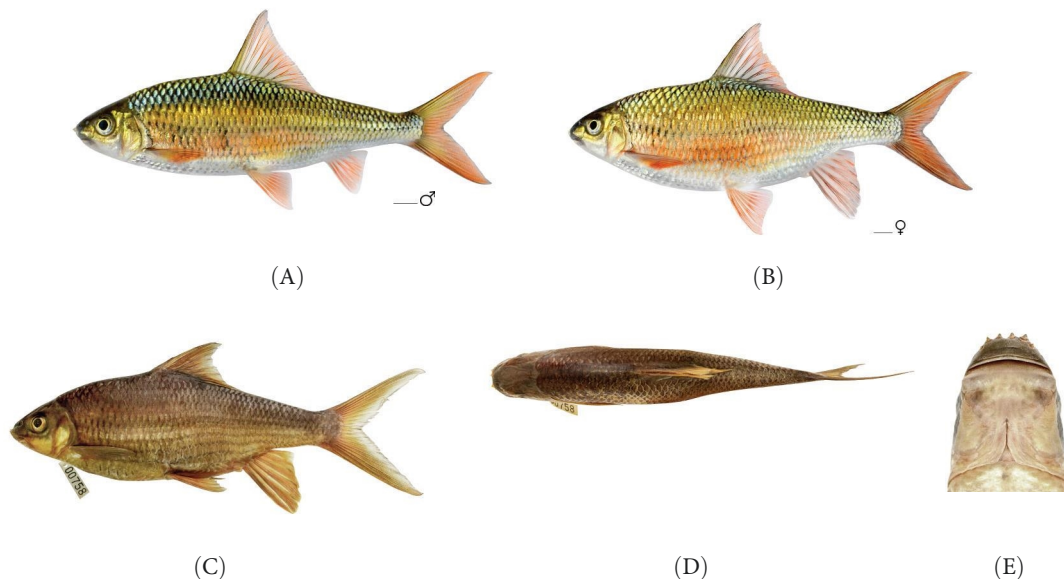


FIGURE 8: *Scaphostoma annamense*: (A) paratype (UNS00759, 147 mm SL, male) in life; (B) adult holotype (UNS00758, 174 mm SL, female) in life; (C) in preservative, lateral view; (D) dorsal view; (E) ventral view of head. Scale 10 mm.

Type species: *Onychostoma laticeps* Günther, 1896, a junior synonym of *O. simum* (Sauvage and Dabry de Thiersant, 1874): 8. Holotype: MNHN 7952, 142 mm, Yangtze basin, China.

Diagnosis: *Onychostoma* (Figure 3E,F) is distinguished from all other genera of Acrossocheilinae by having distinct groove from snout to angle of mouth and one pair of barbels (vs. no barbels or two pairs), at least in adult. It is further distinguished from *Folifer* and *Acrossocheilus* by having no horny sheath on lower jaw and from *Folifer* by lacking median lobe on lower lip.

Included species: In this study, six species of *Onychostoma*: *O. alticorpus* (Oshima, 1920); *O. monticola* (Günther, 1888),

n. comb.; *O. ovale* (Pellegrin and Chevey, 1936); *O. rarum* (Lin, 1933); *O. simum* (Sauvage and Dabry de Thiersant, 1874); and *O. yunnanense* (Regan, 1904), n. comb.

Genus *Acrossocheilus* Oshima, 1919

Type species: *Acrossocheilus formosanus* (Regan, 1908c): 149, junior synonym of *Acrossocheilus paradoxus* (Günther 1868). Syntypes: (8) BMNH 1908.5.27.6-10 (5), SMNS 4372 (3), 115 mm, Lake Candidus, Taiwan.

Diagnosis: *Acrossocheilus* (Figure 3G,H) is distinguished from all other genera of Acrossocheilinae except *Angustistoma* by having median interruption on fleshy lower lip and from *Angustistoma* by having lateral scales <47 (vs. >47). It

is further distinguished from *Onychostoma* by lacking a distinct groove from snout to angle of mouth and from *Folifer* by lacking median lobe on lower lip.

Acrossocheilus microstomus (Pellegrin and Chevey, 1936)

Cyclocheilichthys microstoma (Pellegrin and Chevey, 1936): 227. Type locality: Vietnam, Tonkin, Bân Mun, Nậm So—the tributary of Black River [Lai Châu, Phong Thổ, Sông Đà]. Holotype: MNHN 1935-0340.

Lissochilus laocaiensis Nguyễn and Đoàn, 1969:12. Type locality: Vietnam, Lào Cai Province, Trịnh Quyền stream. Lectotype: RIAH 173.

Acrossocheilus lamus (Mai, 1978): 101. Type locality: Vietnam, Lam River. Holotype: DVZUT.

Other included species: In this study, 12 species of *Acrossocheilus*: *A. beijiangensis* (Wu and Lin, 1977), *A. fasciatus* (Steindachner 1892), *A. hemispinus* (Nichols 1925), *A. iridescens* (Nichols and Pope 1927), *A. jishouensis* (Zhao, Chen, and Li 1997), *A. kreyenbergii* (Regan 1908), *A. longipinnis* (Wu 1939), *A. microstomus* (Pellegrin and Chevey 1936), *A. paradoxus* (Günther 1868), *A. parallens* (Nichols 1931), *A. spinifer* (Yuan, Wu, and Zhang 2006), *A. wenchowensis* (Wang 1935). These 12 species are widely distributed in the Yangtze, Fujian-Zhejiang, Taiwan, Xijiang, Song Hong, and Hainan ecoregions in Southeast and East Asia.

Genus *Scaphesthes* Oshima, 1919

Type species: *Scaphesthes tamusuiensis* (Oshima, 1919): 208, junior synonym of *Scaphesthes barbatula* (Pellegrin, 1908): 263. Lectotype: 230 mm, Tamsui River near Shinten, Taiwan. Gender feminine.

Etymology: The name is formed on the classical Greek prefix *σκαφ* (scaph) meaning bow-shaped and the Greek suffix *-esthes* referring to horny sharp sheath on the lower lip. Gender feminine.

Diagnosis: *Scaphesthes* (Figure 4C,D) is distinguished from all other genera of *Acrossocheilinae* except *Folifer*, *Acrossocheilus*, and *Angustistoma* by having two pairs of barbels (vs. no or one pair), from *Folifer* by having sheath on lower jaw and lacking median lobe on lower lip, from *Acrossocheilus* by having sheath on lower jaw and lacking median interruption on fleshy lower lip, and from *Angustistoma* by having a snout of head blunt, an almost transverse mouth opening, and lateral scales <47. It is further distinguished from *Onychostoma* by lacking a distinct groove from snout to angle of mouth.

Scaphesthes brevibarba Song, Cao, and Zhang [4], n. comb.

Onychostoma brevibarba Song, Cao, and Zhang [4]: 154. Type locality: China, Hunan, Hengdong County, Tributary on southern bank of Mi Shui discharging into Xiang Jiang of the middle Chang Jiang basin. Holotype: IHB 2011062587.

Scaphesthes minnanensis (Jang-Liaw and Chen, 2013), n. comb.

Onychostoma minnanense (Jang-Liaw and Chen, 2013): 64. Type locality: China, Fujian Province, Jua-an County, Yuafeng River near Guangya Mountain, in the Jukong River basin. Holotype: NMNSF 01970.

Scaphesthes barbatula (Pellegrin, 1908)

Gymnostomus barbatulus (Pellegrin, 1908): 263. Type locality: Taiwan, Lake Candidius. Holotype: MNHN 1908-0169.

Angustistoma Hoàng, new genus

Type species: *Onychostoma elongatum* (Pellegrin and Chevey, 1934): 340. Holotype: MNHN 1934-026, 142 mm, Ngòi-Thia—tributary of Red River, Nghĩa-Lộ, Yên-Bái, Vietnam.

Etymology: The name is from the classical Latin prefix *angusti-* meaning narrow, and the Greek suffix *-stoma* meaning mouth and referring especially to the horny sharp sheath on the lower lip. Gender neuter.

Diagnosis. *Angustistoma* (Figure 4E,F) is distinguished from all other genera of *Acrossocheilinae* except *Scaphesthes* by having mouth width narrow to moderate and slender body and from *Scaphesthes* by having a snout of head protruding, an arched mouth opening, and lateral scales >47. It is further distinguished from *Folifer* by having horny sheath on lower jaw and lacking median lobe on lower lip, from *Hongiastoma*, *Onychostoma*, and *Scaphostoma* by having two pairs of barbels, and from *Acrossocheilus* by having sheath on lower jaw and lacking median interruption on fleshy lower lip.

Angustistoma macrolepis (Bleeker, 1871), n. comb.

Gymnostomus macrolepis (Bleeker, 1871): 32. Type locality: China, Chang Jiang [Yangtze River]. Holotype: MNHN 0000-5064.

Angustistoma barbatum (Lin, 1931), n. comb.

Gymnostomus barbatus (Lin, 1931): 113. Type locality: China, Kwangsi [Guangxi] and southern Hunan, Yaoshan [Guilin, Yaoshan]. Lectotype: LU [118 mm SL] by Lin 1933: 201.

Onychostoma elongatum (Pellegrin and Chevey, 1934): 340. Type locality: Vietnam, Yên Bái, Nghĩa Lộ, Ngòi-Thia—tributary of Red River. Holotype: MNHN 1934-026.

Onychostoma lini (Wu, 1939): 103. Type locality: China, Guangxi, Guilin, Yangso [Yangshuo], Li Kiang [Lijiang]. Syntypes: 121 (1), 137-138 (2).

Onychostoma uniforme (Mai, 1978): 105. Type locality: Vietnam, Bắc Kạn, Nà Rì River. Syntypes: DVZUT.

Onychostoma fangi (Kottelat, 2000d): 84. Type locality: China, Kouang-Si Province: San-Fan, Lo-Chien-Hsien [Guangxi, Hechi, Luocheng County, Liujiang]. Holotype: NRIBAS M.258.

Acrossocheilus malacopterus Zhang [23]: 254. Type locality: China, Guangdong, Yangshan, Zhu Jiang drainage: Lian Jiang, a tributary of Bei Jiang. Holotype: IHB 660286. Paratypes: IHB 6440303-4.

Onychostoma virgulatum Xin, Zhang, and Cao [33]: 236. Type locality: China, Anhui Province, Shitai County, Qiupu River—the tributary of the lower Chang Jiang [Yangtze River]. Holotype: IHASW 83IX2146.

Scaphostoma Hoàng and Phạm, new genus

Type species: *Gymnostomus lepturus* (Boulenger, 1900): 961. Holotype: BMNH 1899.11.30.21, 159.2 mm, Five-fingers Mountains, Hainan Island, China.

Etymology: The name is from the classical Greek prefix *σκαφ* (scapho) meaning bow-shaped, and the Greek suffix *-stoma* meaning mouth and referring especially to the horny sharp sheath on the lower lip. Gender neuter.

Diagnosis: *Scaphostoma* (Figures 4A,B, 6–8) is distinguished from all other genera of *Acrossocheilinae* except *Hongiastoma* by having no barbels (at least in adult) and from *Hongiastoma* by having dorsal-fin origin in front of (vs. behind or over) pelvic-fin origin. It is further distinguished

from *Folifer* by having sheath on lower jaw and lacking median lobe on lower lip, from *Onychostoma* by lacking distinct groove from snout to angle of mouth, and from *Acrossocheilus* by having sheath on lower jaw and lacking median interruption on fleshy lower lip.

Scaphostoma lepturum (Boulenger, 1900), n. comb.

Gymnostomus lepturus (Boulenger, 1900a): 961. Type locality: China, Hainan, Five-Fingers Mt.. Holotype: BMNH 1899.11.30.21.

Scaphostoma erythrogyens (Nguyễn and Đoàn, 1969), n. comb.

Varicorhinus erythrogyens (Nguyễn and Đoàn, 1969): 13. Type locality: Vietnam, Hòa Bình Province, Đà Bắc, Suối Rút. Lectotype: NCNTTSI "1068", designated by Roberts and Catania, 2007:93 [possibly NCNTTSI H.01.73.02.01].

Scaphostoma gerlachi (Peters, 1881), n. comb.

Barbus gerlachi (Peters, 1881): 1034. Type locality: China, sent from Hong Kong. Holotype: ZMB 11327.

Scaphostoma fusiforme Kottelat [32], n. comb.

Onychostoma fusiforme Kottelat [32]: 40. Type locality: Laos, Nam Theun, from Ban Signo to about 6 km upriver. Holotype: ZRC 41782.

Scaphostoma krongnoense (Hoàng, Phạm and Trần, 2015), n. comb.

Onychostoma krongnoense (Hoàng, Phạm, and Trần, 2015): 42. Type locality: Vietnam, Sre Pok River's tributary—Ea Krongno. Holotype: UNS 00805.

Scaphostoma meridionale Kottelat, n. comb. [32]

O. meridionale Kottelat [32]: 42. Type locality: Laos, Upper Xe Bangfai, about 1 km upriver of confluence with (unnamed) stream descending from Phou Taloun; 17°09' 42"N 10°12'33"E. Holotype: ZRC 41783.

Onychostoma dongnaiense (Hoàng, Phạm, and Trần, 2015): 130. Type locality: Vietnam, Đồng Nai River's tributary - Dạ Tềh. Holotype: UNS 00851.

Scaphostoma annamense (Hoàng, Phạm, and Trần), sp. nov.

Holotype: UNS00758, 174 mm SL, female; An Lão drainage, Bình Định Province, Vietnam (14°40'30.6" N 108°54'13.4" E, 547 m), 19 January 2013, Hoàng Đức Huy, Phạm Mạnh Hùng and Trần Trọng Ngân (Figure 7).

Paratypes: An Lão drainage, Bình Định Province, Vietnam (14°40'30.6" N 108°54'13.4" E): UNS 2013-19-01, 5 specimens, 118–189 mm SL, 19 January 2013; Re River, Sơn Hà, Quảng Ngãi Province, Vietnam (15°01'03.9"N 108°31'55.0"E): UF 249745, 5 specimens, 132–193 mm SL, 24 February 2018.

Diagnosis: *Scaphostoma annamense* is most closely related (Figure 2) and similar to *S. fusiforme*, *S. krongnoense*, and *S. meridionale* but differs genetically and morphologically. It differs from *S. fusiforme* and *S. meridionale* in being deeper bodied (25%–33% vs. 21%–24% SL) and having a narrower mouth (1.3–1.7 vs. 2.0–2.3 times in head width), and from *S. krongnoense* in having 12–14 (vs. 14–17) predorsal scales. It further differs from *S. fusiforme* in having 12–14 (vs. 15–16) predorsal scales and a narrower caudal peduncle (1.8–2.6 vs. 3.0–3.6 times in its length) and from *S. meridionale* in having 46–49 (vs. 43–45) lateral-line scales. Data on *S. fusiforme* and *S. meridionale* are from [32] and on *S. krongnoense* from Hoang et al. [34].

Description. General appearance in Figure 8; meristic and morphometric data of 31 adult type specimens in Table 4. Head length about equal to depth; dorsal profile convex. Snout short and rounded, longer than eye diameter in adult. Interorbital area slightly convex. Mouth inferior, width about 1.3–1.7 times in maximum HW; no barbels (Figure 8E). Maxillary reaching nearly to vertical of anterior margin of orbit. Upper lip thin, covered by rostral fold medially, exposed at corners; horny sheath on lower jaw. Small to medium-sized tubercles on snout on all adult specimens. Body deep, moderately compressed; caudal peduncle slender, about 1.8–2.6 times longer than deep. Dorsal body profile convex; ventral profile rounded. Lateral line complete, 46–49 scales; 12–14 predorsal scales; 6–7/1/4–5 scales in transverse row immediately anterior to pelvic-fin insertion. Dorsal fin high with four simple and eight branched rays; first simple ray a tiny process, vestigial in a few specimens; last simple ray serrated; dorsal-fin origin inserted far in front of vertical with pelvic-fin origin; distal margin concave. Pectoral fin pointed with one simple and 14–17 branched rays. Pelvic fin pointed, with one simple and nine branched rays; axillary scale present. Anus immediately in front of anal fin. Anal fin with three simple and five branched rays; shorter in male than in female (13% vs. 20.0% SL; Figure 8A–C). Caudal fin deeply forked with 10 + 9 principal rays and 9 + 8 branched.

Color in life: Head dark greenish golden above, light gold around orbit on operculum, and on side and white on lower jaw. Body greenish gold on back, blurring to orange on lateroventral surface, belly snowy white; faint longitudinal black stripe along lateral line, three faint black stripes below lateral line. Fins orange to reddish.

Color in preservative: Brown with faded black stripes along and below lateral line (Figure 8C–E).

Etymology: Specific epithet is in reference to the eastern slope of the Annamite Cordillera, where this species occurs.

Suggested common name. Cá niên An Nam (Vietnamese), Annam shovel-jaw carp (English).

Key to genera of *Acrossocheilinae*

1a. Thick fleshy lips and large median lobe on lower lip—*Folifer*

1b. Thin lips (moderately thick in *Acrossocheilus*) and no lobe on lower lip: 2

2a. Median interruption on fleshy lower lip—*Acrossocheilus*

2a. No median interruption on lower lip: 3

3a. Two pairs of barbels: 4

3b. No or one pair of barbels: 5

4a. Almost transverse mouth opening, its width equal to or wider than the corresponding head width and lateral scales <47—*Scaphesthes*

4b. Arched mouth opening, its width is less than the corresponding head width and lateral scales >47—*Anguististoma*

5a. Distinct groove from snout to angle of mouth, one pair of barbels—*Onychostoma*

5b. No distinct groove from snout to angle of mouth, no barbels: 6

6a. Dorsal-fin origin behind or over (vs. in front of) pelvic-fin origin—*Hongiastoma*

6b. Dorsal-fin origin in front of pelvic-fin origin—*Scaphostoma*.

4. Discussion

Earlier taxonomic opinions on species names assigned to *Onychostoma* and *Acrossocheilus* were based on inadequate geographic sampling and a reliance on morphological characters that vary intraspecifically. Additional samples from unsampled or poorly sampled geographic regions have revealed more morphological variation than had been realized and allowed the use of molecular data to test previous species hypotheses.

During a decade of field work on Southeast Asian freshwater fishes, the first author and colleagues have collected numerous samples of *Scaphostoma lepturum*, *S. gerlachi*, and *Angustistoma barbatum*. These samples include specimens from river basins in which few or no fish collections have been made or reported upon previously and reveal considerable intraspecific variation in phenotype. As noted in previous studies [10, 23, 33, 35], pronounced variation among adults can be observed in body depth, ossification, serration of the last simple dorsal-fin ray, body color pattern, and fin color. For example, *Scaphostoma lepturum*, *S. erythrogyne*, and *S. gerlachi* typically share a live color pattern of a silvery to light gold-green body with a thin mid-lateral black stripe, light orange on the ventral half of the body, and a reddish caudal fin (Figures 6A,F and 7A). However, in some watersheds, they share a color pattern characterized by three dusky patches and yellow on the ventral half of the body, and red fins (Figure 6B). Color in the widespread *S. lepturum* is more subtle with the body uniformly silvery turquoise to dusky and dusky reddish fins (Figures 4A and 6C–E). *Scaphostoma lepturum* is widely distributed in the Song Hong, Hainan, and Northern Annam drainages; *S. gerlachi* is mostly distributed in the southern tributaries of the Xijiang and the northern tributaries of the Song Hong; and *S. erythrogyne* is restricted to tributaries of the Song Hong.

Further complicating taxonomy, intraspecific ecomorphological variation occurs in at least some species in *Acrossocheilinae*, including *S. lepturum*, *S. gerlachi*, *Angustistoma barbatum*, and *Acrossocheilus hemispinus*. In large rivers, the last simple dorsal-fin ray typically is ossified and serrated, but in the small upper reaches of these same rivers, the last simple dorsal-fin ray is thin and lacks serrations (Figure 6A, B). This variation is seen in *S. lepturum*, *S. gerlachi*, *A. barbatum*, and *A. hemispinus* (this study; [33]). Also, specimens of *S. lepturum* from flowing water habitats are characterized by a slender body, while those from pools have a deeper body and larger unpaired fins (Figure 6A–E). Similar patterns have been described in *Rasbora paviana*, *Lobocheilos rhabdoura*, and *Poropuntius deauratus* with populations inhabiting fast-flowing streams having more slender bodies than those inhabiting slower-flowing habitats [36–38].

Nomenclature

BIC: Bayesian information criterion
BS: bootstrap
COI: cytochrome c oxidase subunit 1
DNA: deoxyribonucleic acid
ML: maximum likelihood

PCR: polymerase chain reaction
SL: standard length.

Data Availability Statement

Voucher specimens are available as described in the text and sequence data are posted on GenBank.

Ethics Statement

The authors have nothing to report.

Consent

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Huy Duc Hoang and Hung Manh Pham worked on conceptualization and wrote the manuscript. Huy Duc Hoang, Jean-Dominique Durand, Nian-Hong Jang-Liaw, John Pfeiffer, and Lawrence M. Page obtained funds for this research. Hung Manh Pham, Jean-Dominique Durand, Nian-Hong Jang-Liaw, and John Pfeiffer worked on molecular analysis. Huy Duc Hoang, Ngan Trong Tran, Hung Manh Pham, Lawrence M. Page, Tao Dinh Nguyen, and Nian-Hong Jang-Liaw collected specimens. Jean-Dominique Durand, Lawrence M. Page, and John Pfeiffer revised the manuscript.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. (*Supporting Information*) Table S1. Samples included in the molecular analysis, with GenBank accession numbers for cytochrome oxidase c subunit 1 (COI) sequence data. Table S2. Morphological material examined. Table S3. COI genetic distances between species in the phylogenetic analysis with outgroup species

using the Kimura 2-parameter model, standard error estimates shown above the diagonal with bootstraps 1000.

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