Zootaxa 5757 (6): 583–599
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5757.6.7
http://zoobank.org/urn:lsid:zoobank.org:pub:99F59D32-3F8F-465C-90F9-A7B88788F19A

Magnischistura khaokrajom, a new genus and species of loach (Cypriniformes: Nemacheilidae) from the Pachi River drainage in Western Thailand

PAGE, LAWRENCE M.[1], PARINYA PAWANGKHANANT[2], WEERAPONGSE TANGJITJAROEN[3], DAVID K. CAGLE[1], BASIL R. WILLIAMS[1] & ZACHARY S. RANDALL[1]

[1]*Florida Museum of Natural History, University of Florida, Gainesville, Florida, 32611, USA.*
dcagle@floridamuseum.ufl.edu; *https://orcid.org/0009-0008-3496-287X*
williams.g@ufl.edu; *https://orcid.org/0009-0008-6133-7033*
zrandall@flmnh.ufl.edu; *https://orcid.org/0000-0001-8973-3304*
[2]*Rabbit in the Moon Foundation, Suanphueng, Ratchaburi 70180, Thailand.*
peat_swamp@hotmail.com; *https://orcid.org/ 0000-0002-0947-5729*
[3]*Faculty of Veterinary Medicine, Chiang Mai University, Chiang Mai, 50100, Thailand.*
weerapongse@yahoo.com; *https://orcid.org/0009-0007-1961-7210*
Corresponding author: *Lpage1@ufl.edu;* *https://orcid.org/0000-0002-8823-0729*

Abstract

Magnischistura khaokrajom, new genus and species, is described from a small tributary of the Pachi River in the Suan Phueng region of the Tenasserim Hills in western Thailand. *Magnischistura* shares with several recently described genera of nemacheilids a globulous suborbital flap with tubercles at its extremity and a highly modified pectoral fin on mature males, but molecular data failed to support a close relationship to any of them. Morphologically, the new genus is distinguished by the presence of a suborbital flap in the female. The highly modified pectoral fin of males is hypothesized to facilitate juxtaposition with a female during spawning.

Key words: Taxonomy, Phylogeny, Southeast Asia

Introduction

Recent fieldwork in the Mae Klong River basin in western Thailand produced specimens of a previously unknown nemacheilid with sexually dimorphic traits similar to those of species in other genera (Kottelat 2018, 2019; Kottelat & Grego, 2020). However, a close relationship of the newly discovered species with species in those genera (*Mustura* Kottelat 2018, *Kayahschistura* Kottelat & Grego 2020*, Petruichthys* Menon 1987*, Physoschistura* Banarescu & Nalbant, in Singh, Sen, Banarescu & Nalbant (1982), and *Rhyacoschistura* Kottelat 2019) was not supported with morphological or molecular data, and the species is described and assigned to a new genus. The new species is from the Pachi River system in the Suan Phueng District of Ratchaburi Province, Thailand, an area of the Tenasserim Hills with a growing number of endemic fishes. Aspects of sexual dimorphism in nemacheilids are discussed.

Materials and methods

Fieldwork and Imaging

Fishes were collected with nets, anesthetized, and fixed in 10% formalin or kept in aquaria for several weeks, anesthetized, and fixed in 10% formalin. All were transferred to 70% ethanol for long-term preservation. Photographs of live and preserved specimens were taken with a Canon EOS R camera. Images were edited using Adobe Photoshop CC 2024 (Adobe, San Jose, CA). X-rays and computed tomography (CT) scans were generated using a Phoenix v|tome|x M scanner (GE Measurement & Control, Boston, MA) at the University of Florida's Nanoscale Research

Accepted by Y.-H. Zhao: 6 Jan. 2026; published: 11 Feb. 2026

Facility. CT projections were processed using datos|x software v. 2.3 (Baker Hughes, Jacksonville, FL), and anatomy was segmented and visualized using VG StudioMax v. 2024.3 (Volume Graphics, Heidelberg, Germany). CT scans can be downloaded from MorphoSource (https://www.morphosource.org) (Table 1).

TABLE 1. μCT scans included in this study and available for download from mophosource.org. Sampling locations are available at idigbio.org.

Species	Catalog Number	Country, Province, Drainage	MorphoSource Media ID
Magnischistura khaokrajom	UF 248549	Thailand, Ratchaburi, Mae Klong	000648073 000648081
Nemacheilus fasciatus	UF 162177	Indonesia, Lampung, Way Seputhi	000051203 000082018
Nemacheilus zonatus	UF 237302	Thailand, Kalasin, Mekong	000051229 000051230
Physoschistura pseudobrunneana	UF 177823	Thailand, Chiang Rai, Chao Phraya	000037578 000051213
Schistura aurantiaca	UF 188063	Thailand, Kanchanaburi, Mae Klong	000037610 000037611
Schistura rupecula	UF 191250	Nepal, Bagmati, Sunkoshi	000051656 000082012
Mustura maepaiensis	UF 188310	Thailand, Mae Hong Son, Salween	000739683 000739687
Tuberoschistura baenzigeri	UF 247943	Thailand, Kanchanaburi, Mae Klong	000739750 000739759

Morphological

Morphological data were taken on specimens of the new species and *Mustura maepaiensis* (Kottelat 1990), a species with similar sexually dimorphic traits and found geographically close to the Mae Klong basin where the new species is found. Comparisons also were made with published data on *Mustura* Kottelat 2018, *Kayahschistura* Kottelat & Grego 2020*, Petruichthys* Menon 1987*, Physoschistura* Banarescu & Nalbant 1982, and *Rhyacoschistura* Kottelat 2019, all of which have a modified pectoral fin and suborbital flap in mature males similar to the new species.

Measurements were taken to the nearest 0.1 mm using digital calipers and followed Hubbs *et al.* (2004) except body depth and width were measured at dorsal-fin origin, prepectoral, prepelvic, and preanal lengths were from anterior tip of snout to origin of relevant fin, pelvic fin to caudal fin length was distance from pelvic-fin origin to middle of caudal-fin base, pelvic fin to anal fin was distance from pelvic-fin origin to anal-fin origin, dorsal head length was distance from tip of snout to posterior edge of supraoccipital, and internasal width was distance between posterior nares. Total ray counts were taken for paired fins, and branched ray counts for unpaired fins. The last branched ray of the dorsal and anal fins, sharing a pterygiophore with the penultimate ray, is given as ½. Proportional data are expressed as percentages of standard length (SL) or head length (HL). Vertebral counts were made from CT scans or X-rays. Counts of abdominal vertebrae include those in the Weberian complex (n=4 vertebrae). Counts of caudal vertebrae began at the vertebra with its hemal spine just posterior to the anterior anal-fin pterygiophore and include the urostyle complex (n=1 vertebra). The bony capsules of the air bladder of the new species were compared with those of other species of nemacheilids using CT scans.

Molecular

To determine the phylogenetic relationships of the new species, sequence data for mitochondrial loci cytochrome *b* (cytb) and cytochrome *c* oxidase subunit 1 (COI), and the nuclear recombination-activating gene 1 (RAG1) were generated (Table 2). These were added to sequence data from GenBank for 22 species in 17 nemacheilid genera from Indochina in the Burmese, Indochinese, Sundaic, and Southern clades recognized by Šlechtová *et al*. (2024).

Genera from the Eastern (East Asian) and Northern (Northern Eurasian) clades were excluded as were several genera from the Southern clade occurring only in Africa and the Middle East. *Syncrossus beauforti*, a botiid, and *Acantopsis rungthipae,* a cobitid, were selected as outgroups based on phylogenetic relationships in Cobitoidea recovered in Šlechtová *et al.* (2007).

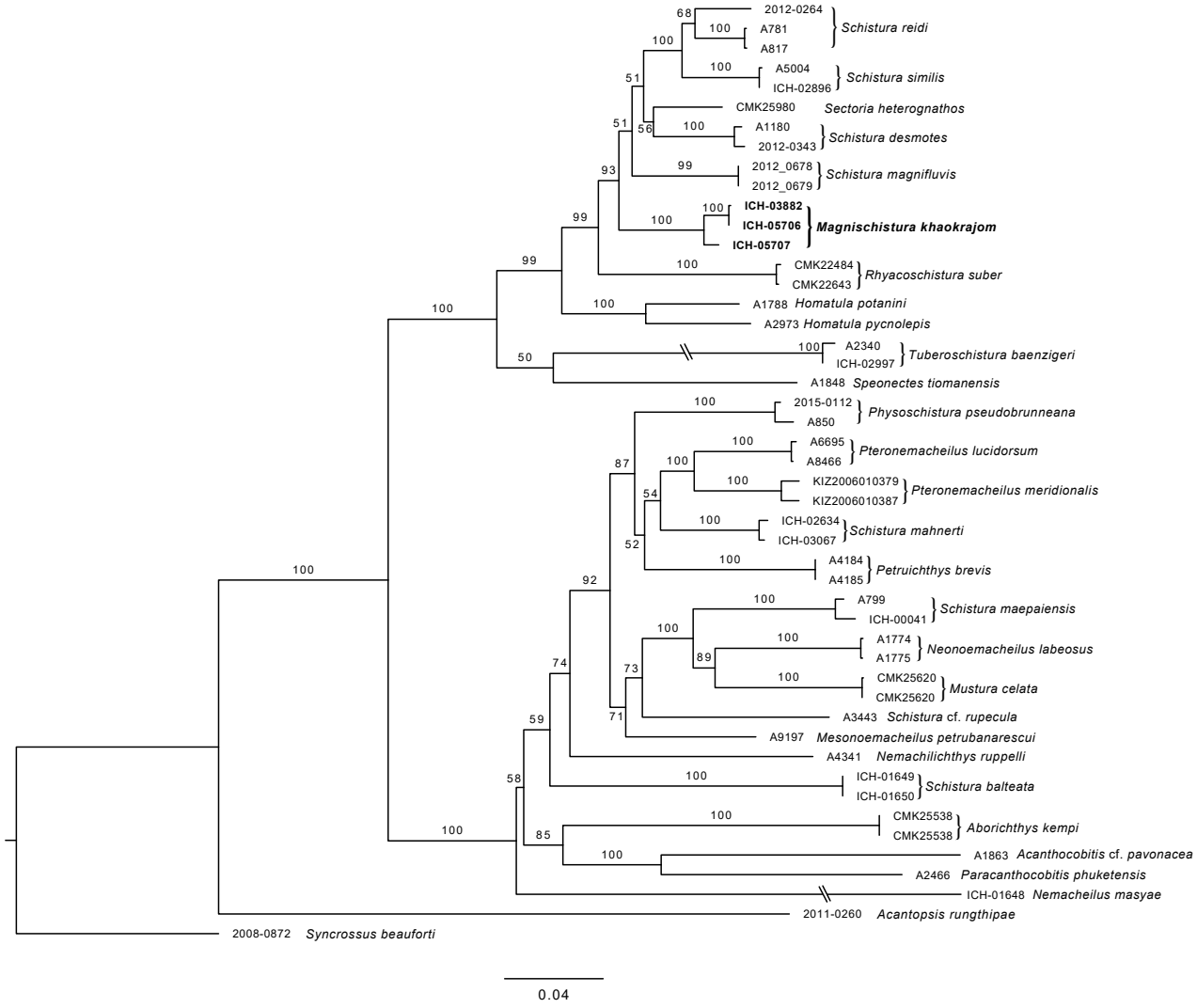

FIGURE 1. Maximum likelihood phylogenetic reconstruction for the concatenated three-locus dataset showing relationships of *Magnischistura khaokrajom.*

DNA was extracted from fin clips in 95% ethanol using the Omega Bio-Tek E.Z.N.A Tissue DNA kit (Omega Bio-Tek, Norcross, GA) following manufacturer's instructions. Polymerase chain reactions (PCR) were run in 25 µL reaction volumes with 12.5 µL GoTaq Master Mix (Promega, Madison, WI), 9.5 µL water, 0.5 µL of each primer at 10mM, and 2 µL of DNA template. Mitochondrial cytochrome *c* oxidase subunit 1 (COI) was amplified by polymerase chain reaction (PCR) and sequenced using the following primers: FishF1 5'TCAACCAACCACAAAGACATTGGCAC'3 and FishR2-5'ACTTCAGGGTGACCGAAGAATCAGAA'3 (Ward *et al.* 2005) and LCO1490-5'GGTCAACAAATCATAAAGATATTGG'3 and HCO2198-5'TAAACTTCAGGGTGACCAAAAAATCA'3 (Folmer *et al*. 1994). Mitochondrial cytochrome *b* (cytb) was amplified and sequenced using: 5'GAAGAACCACCGTTGTTATTCAA'3 and 5'ACCTCCRATCTYCGGATTACA'3 (Šlechtová *et al*. 2006), and 5'ATGGCAAGCCTACGAAAAAC3' and 5'TCGGATTACAAGACCGATGCTT3' (Yang *et al*. 2010). The nuclear recombination-activating gene 1 (RAG1) was amplified and sequenced using: 5'AGCTGTAGTCAGTAYCACAARATG'3 and 5'TCCTGRAAGATYTTGTAGAA 3' (Šlechtová *et al*. 2007). PCR cycles were completed with a MJ Research PTC-100 Thermal Cycler (GMI, Ramsey, MN) following the procedures

outlined in the primer sources. To confirm the presence of the desired amplified sequence, gel electrophoresis was run on 1.5% agarose gel with 6 µL GelRed and TBE buffer. The PCR product was purified and sequenced by Molecular Cloning Laboratories (MCLAB, San Francisco, CA).

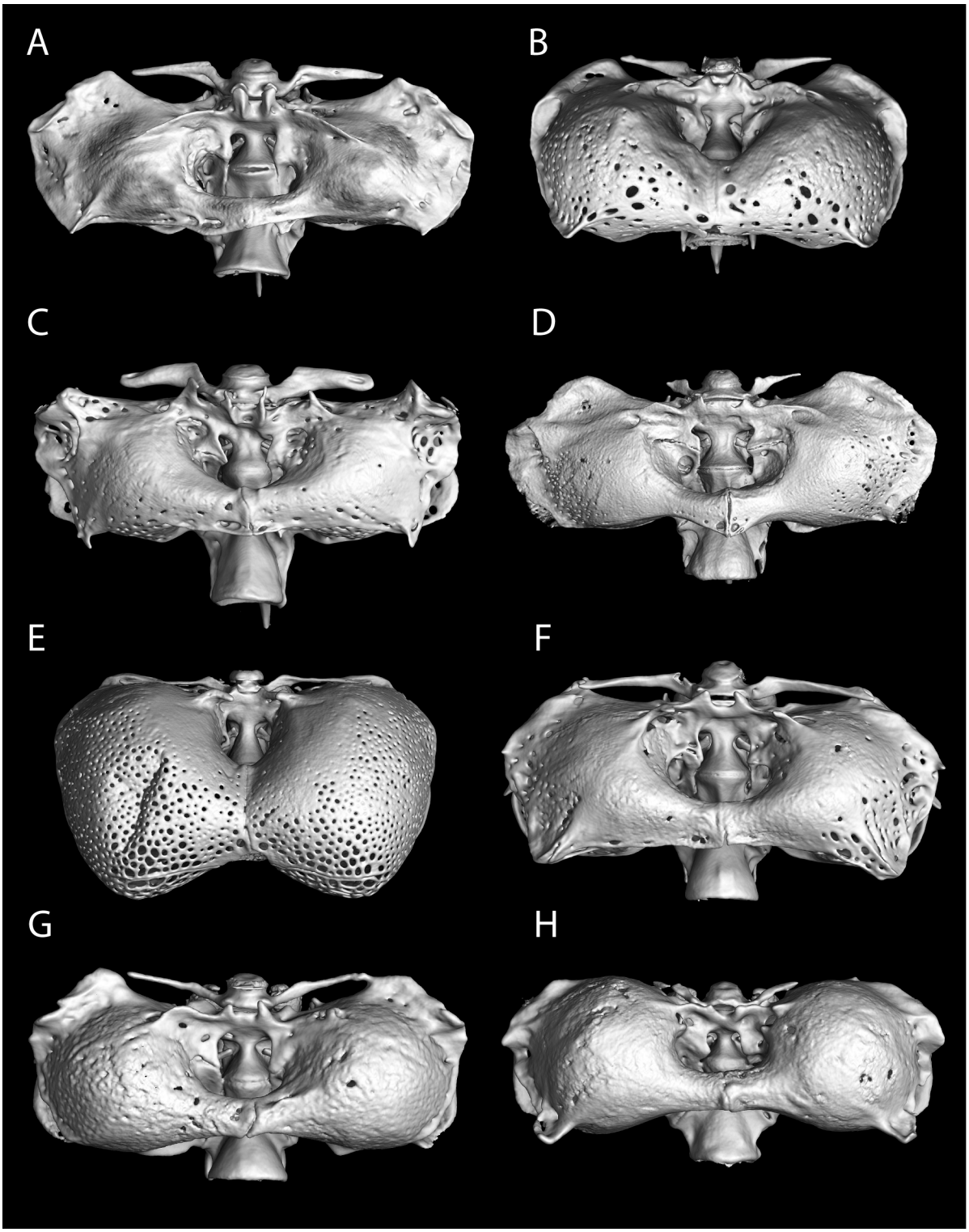

FIGURE 2. CT scans of air bladder bony capsules. (A) *Magnischistura khaokrajom,* UF 248549, 80.7 mm SL, (B) *Physoschistura pseudobrunneana,* UF 177823, 28.9 mm SL, (C) *Schistura rupecula*, UF 191250, 62.0 mm SL, (D) *S. aurantiaca*, UF 188063, 39.0 mm SL, (E) *Nemacheilus zonatus*, UF 237302, 23.2 mm SL, (F) *N. fasciatus,* UF 162177, 49.6 mm SL, (G) *Mustura maepaiensis*, UF 188310, 35.1 mm SL, (H) *Tuberoschistura baenzigeri*, UF 247943, 38.5 mm SL.

TABLE 2. Voucher specimen and tissue data for sequences included in the molecular phylogeny. All UF samples are GenSeq 4 except UF 248549 and UF 249118 are GenSeq 2 (Chakrabarty *et al*. 2013). Order after *Magnischistura khaokrajom* as in Figure 1.

Species	Voucher	Tissue ID	Country	River	Drainage	GenBank		
						COI	Cytb	Rag1
Magnischistura khaokrajom	UF 248549	ICH-03882	Thailand	Pachi	Mae Klong	PV808191	PX116065	PX127669
Magnischistura khaokrajom	UF 249118	ICH-05706	Thailand	Pachi	Mae Klong	PV808192	PX116066	PX127670
Magnischistura khaokrajom	UF 249118	ICH-05707	Thailand	Pachi	Mae Klong	PV808193	PX116067	PX127671
Schistura reidi	UF 183830	2012-0264	Thailand	Mae Nam Por	Salween	PV808190	PX116063	PX127667
Schistura reidi	GenBank	A781	Thailand	-	Salween	-	PP280032	PP315865
Schistura reidi	GenBank	A817	Thailand	-	Salween	-	PP280036	PP315871
Schistura similis	GenBank	A5004	Thailand	-	Salween	-	PP279990	PP315828
Schistura similis	UF 192118	ICH-02896	Thailand	Mae Ramat	Salween	PV808197	PX116064	PX127668
Sectoria heterognathus	GenBank	CMK25980	Laos	-	Mekong	-	PP279872	PP315705
Schistura desmotes	GenBank	A1180	Thailand	-	Chao Phraya	-	PP279892	PP315728
Schistura desmotes	UF 183066	2012-0343	Thailand	Ping	Chao Phraya	PV982133	PV983948	PV983956
Schistura magnifluvis	UF 185743	2012-0678	Laos	Huay Set	Mekong	PV808195	-	-
Schistura magnifluvis	UF 185743	2012-0679	Laos	Huay Set	Mekong	PV808196	-	-
Ryachoschistura suber	GenBank	CMK22484	Laos	-	Mekong	-	PP279856	PP315691
Ryachoschistura suber	GenBank	CMK22643	Laos	-	Mekong	-	PP279857	PP315692
Homatula potanini	GenBank	A1788	China	-	Yangtze	-	PP279908	PP315742
Homatula pycnolepis	GenBank	A2973	China	-	Mekong	-	PP279957	PP315794
Tuberoschistura baenzigeri	GenBank	A2340	Thailand	-	Tapi	-	PP315765	PP280143
Tuberoschistura baenzigeri	UF 191867	ICH-02997	Thailand	Pracham Mai	Mae Klong	PV808205	-	PX127672

.....continued on the next page

TABLE 2. (Continued)

Species	Voucher	Tissue ID	Country	River	Drainage	GenBank		
						COI	Cytb	Rag1
Speonectes tiomanensis	GenBank	A1848	Malaysia	-	Pahang	-	PP279916	PP315750
Physoschistura pseudobrunneana	GenBank	A850	Thailand	-	Chao Phraya	-	OL191155	OL191403
Physoschistura pseudobrunneana	UF 188066	2015-0112	Thailand	Sao	Mekong	PV808198	PX116068	PX127673
Pteronemacheilus lucidorsum	GenBank	A6695	Myanmar	-	Irrawaddy	-	OL191215	OL191464
Pteronemacheilus lucidorsum	GenBank	A8466	Myanmar	-	Irrawaddy	-	KP738607	KP738567
Pteronemacheilus meridionalis	GenBank	KIZ 2006010379	China	-	Mekong	MG238136.1	MG238 233.1	MG237 94.1
Pteronemacheilus meridionalis	GenBank	KIZ 2006010379	China	-	Mekong	MG238136.1		
Pteronemacheilus meridionalis	GenBank	KIZ-2006010387	China	-	Mekong	MG238 137.1	MG238 234.1	MG237942.1
Schistura mahnerti	UF 246996	ICH-02634	Thailand	Nam Khiao	Mae Klong	PV982125	PV983933	PV983950
Schistura mahnerti	UF 191983	ICH-03067	Thailand	Mae Phlu	Mae Klong	PV982121	PV983936	PV983952
Petruichthys brevis	GenBank	A4184	Myanmar	-	Salween	-	KP738571	KP738531
Petruichthys brevis	GenBank	A4185	Myanmar	-	Salween	-	KP738572	KP738532
Mustura celata	GenBank	CMK25620_1	Myanmar	-	Irrawaddy	-	PP279863	PP315699
Mustura celata	GenBank	CMK25620_2	Myanmar	-	Irrawaddy	-	PP279864	PP315700
Mustura maepaiensis	GenBank	A799	Thailand	-	Salween	-	PP280033	PP315868
Mustura maepaiensis	UF 188310	ICH-00041	Thailand	Yuam	Salween	-	PX116069	PX127674
Neonemacheilus labeosus	GenBank	A1774	Thailand	-	Salween	-	PP279905	PP315740
Neonoemacheilus labeosus	GenBank	A1775	Thailand	-	Salween	-	PP279906	PP315741

.....continued on the next page

TABLE 2. (Continued)

Species	Voucher	Tissue ID	Country	River	Drainage	GenBank		
						COI	Cytb	Rag1
Schistura cf. rupecula	GenBank	A3443	Nepal	-	Ganges	-	PP279971	PP315807
Mesonoemacheilus petrubanarescui	GenBank	A9197	India	-	Saklshpur	-	PP280055	PP315890
Nemachilichthys ruppelli	GenBank	A4341	India	-	aquarium trade	-	KP738573	KP738533
Schistura balteata	UF 191473	ICH-01649	Thailand	Pilok	Mae Klong	PV808202	PX116070	PX127675
Schistura balteata	UF 191473	ICH-01650	Thailand	Pilok	Mae Klong	PV808203	PX116071	PX127676
Aborichthys kempi	GenBank	CMK25538_1	Myanmar	-	Irrawaddy	-	PP280061	PP315697
Aborichthys kempi	GenBank	CMK25538_2	Myanmar	-	Irrawaddy	-	PP280062	PP315698
Acanthocobitis cf. pavonacea	GenBank	A1863	aquarium trade	-	-	-	MK608119	EF056379
Paracanthocobitis phuketensis	GenBank	A2466	Thailand	-	Tam Nang	-	MK608042	MK608182
Nemacheilus masyae	UF 191306	ICH-01648	Thailand	Malai	Mae Klong	PV808204	-	PX127677
Acantopsis rungthipae	UF 181114	2011-0260	Thailand	Huay Mae Park	Yom	PV808189	-	PX127666
Syncrossus beauforti	UF 173051	2008-0872	Thailand	-	aquarium trade	-	PX116072	PX127678

Chromatograms were edited, assembled using De Novo Assemble and aligned using MAFFT E-INS-l in Geneious Prime v. 2024.0.7 (Biomatters Ltd, Auckland, New Zealand; http://www.geneious.com). BIC as implemented in IQ-TREE (Nguyen *et al*. 2015) was used to determine the best partition scheme and model of nucleotide evolution (GTR+I+G). Maximum likelihood (ML) analyses were performed in IQ-TREE using the ultrafast bootstrap under a RAxML model (Stamatakis 2014) for each locus and the concatenated dataset for all three loci.

Results

In the concatenated three-locus tree, the new species, *Magnischistura khaokrajom,* was sister to a clade of *Schistura* plus *Sectoria,* then *Rhyacoschistura*, then *Homatula*, and then *Tuberoschistura* plus *Speonectes* (Figure 1). Less closely related were *Acanthocobitis, Arborichthys*, *Mustura, Mesonemacheilus, Nemachilichthys, Nemacheilus, Neonemacheilus, Paracanthocobitis, Petruichthys, Physoschistura,* and *Pteronemacheilus.*

Individual analyses of the two mitochondrial loci showed the same relationships as the three-locus tree among *M. khaokrajom*, *Schistura, Sectoria, Rhyacoschistura*, *Homatula*, and *Tuberoschistura*. The nuclear Rag1 tree showed *M. khaokrajom* to be sister to a clade composed of species of *Schistura, Sectoria,* and *Rhyacoschistura.* The clade of those four genera was most closely related to *Homatula*, and then to *Tuberoschistura*.

The two bony capsules of the air bladder were connected by a manubrium in *Magnischistura khaokrajom, Mustura maepaiensis*, *Tuberoschistura baenzigeri,* the two species of *Schistura* examined, and in one of the two species of *Nemacheilus* (*N. fasciatus*). In *Nemacheilus zonatus* and in *Physoschistura pseudobrunneana*, the bony capsules were broadly joined medially without a manubrium (Figure 2).

Magnischistura, Page, Pawangkhanant & Cagle, new genus

urn:lsid:zoobank.org:act:26DF95D6-0F3D-4318-86AC-3E55E850B28B

Type species: *Magnischistura khaokrajom*, Page, Pawangkhanant, and Cagle (Figure 3)

Diagnosis. Magnischistura is distinguished from all other genera of Nemacheilidae by the combination of: (a) in adult males, a pectoral fin that is rigid, curved upward, and has a thick tuberculated pad on the dorsal surface and epidermal flanges on the narrow membranes (Figure 4B); a large, vertically oriented, globulous suborbital flap with tubercles on its underside and distal edge (Figure 4A); (b) in adult females, a pectoral fin with a thick pad on the dorsal surface and epidermal flanges on the membranes (Figure 4D), and a small suborbital flap (Figure 4C); and (c) large size—to at least 98 mm SL.

The large suborbital flap with tubercles at its extremity, and the rigid, thickened, and curved pectoral fin with narrow membranes between the branches are traits shared with *Kayahschistura, Mustura, Petruichthys, Physoschistura*, and *Rhyacoschistura*, but not with *Schistura* or other nemacheilid genera, as noted by Kottelat (2019) and Kottelat and Grego (2020). *Magnischistura* is distinguished morphologically from *Kayahschistura, Mustura, Petruichthys, Physoschistura*, and *Rhyacoschistura* by the presence of a suborbital flap in the female. *Magnischistura* is further distinguished from *Kayahschistura* by the presence of fully developed eyes, dark pigment, and scales on the predorsum; from *Petruichthys* by having juxtaposed nares, the anterior one on the anterior side of a flap (vs. nares separated, anterior one at the end of a short tube); from *Physoschistura* by having the halves of the air bladder capsule connected medially by a manubrium (vs. broadly joined medially; Figure 2); from *Mustura* by having a finely pleated upper lip with a median notch (vs. upper lip with a finely crenulated edge and no notch; Figure 5), and from *Rhyacoschistura* by having wide, black to dark brown bars or spots on the side of the body, bars similar in size or slightly wider than the spaces between the bars (vs. with numerous, up to 16, narrow slanted bars, irregularly organised and shaped), standard length to 98 mm SL (vs. to < 70 mm SL), and 17 vs. 15–16 branched caudal rays.

Magnischistura may also be separated from all but *Rhyacoschistura* by having the pectoral-fin rays secondarily branched. However, information on secondary branching is not available for all genera. The secondary branching in *Magnischistura* is possibly related to its large size.

FIGURE 3. (A-C) *Magnischistura khaokrajom.* (A) UF 248549, paratype, 74.1 mm SL, female, live, (B) UF 248549, paratype, 68.4 mm SL male, live, (C) THNHM-F023975, holotype, 74.0 mm SL male, preserved, (D) *Mustura maepaiensis*, UF 188267, 42.3 mm SL, live.

Of the 62 species of nemacheilids from Indochina recognized by Kottelat (1990), only three were recorded as reaching >95 mm SL: *Schistura bucculenta* (Smith 1945), *S. kengtungensi* (Fowler 1936), and *S. nasifilis* (Pellegrin 1936), highlighting the large size of *Magnischistura*, to 98 mm SL. The recently described *S. titan* Kottelat 2017 also reaches 95 mm SL.

Etymology. Magni- refers to the large size of the type species relative to most species of nemacheilids in Indochina, and *Schistura* McClelland 1838 is a widespread genus of nemacheilids. Gender feminine.

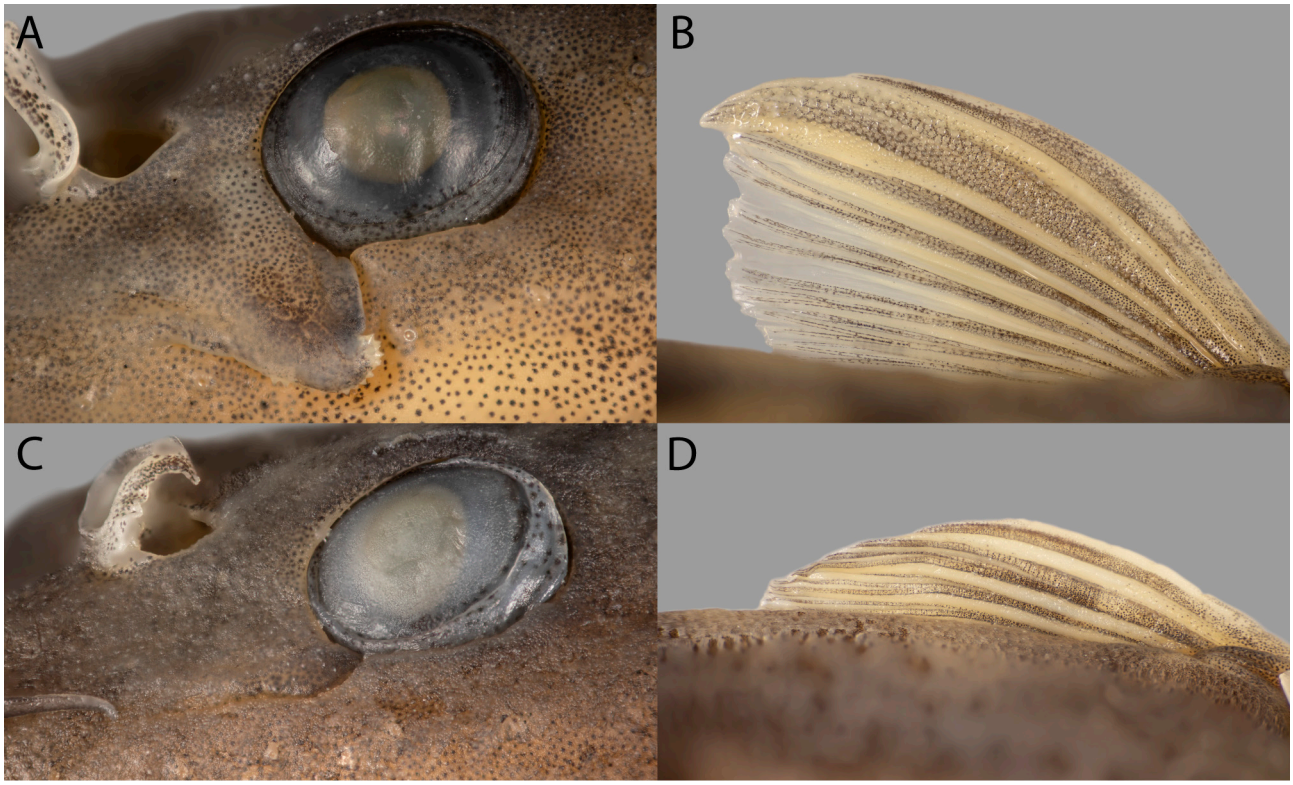

FIGURE 4. Suborbital flaps and dorsal views of pectoral fins of *Magnischistura khaokrajom.* (A-B) UF 249118, 74.5 mm SL male, (C-D) UF 248549, 80.7 mm SL female.

***Magnischistura khaokrajom*, Page, Pawangkhanant & Cagle, new species**
Krajom Mountain Stream Loach
ปลาค้อปิศาจ [Pla Kor Pi Saad]
urn:lsid:zoobank.org:act:CF5E2C4C-327E-4CFF-853B-F7D154CA3A20
(Figures 2–5)

Holotype. THNHM-F023975, male, 74.0 mm SL; Thailand, Ratchaburi Province, Suan Phueng District, Huay Thong An, Mae Klong River basin, 13.54732N, 99.20394E, 650 m above sea level, Pawangkhanant, P., Wongdee, B., and Aksorneam, A., 3 October 2022.

Paratypes. UF 248549 (6, 68.4–80.7 mm SL) same data as holotype. UF 249118 (5, 66.7–98.1 mm SL), same locality and collectors as holotype, 14 February 2023. ZRC 68439, male 72.7 mm SL, same data as holotype.

*Diagnosis***.** See diagnosis for *Magnischistura* based on *M. khaokrajom,* the only species in the genus.

*Etymology***.** *Khaokrajom,* meaning Krajom Mountain in Thai, where this species lives.

Description. General appearance as in Figure 3. Morphometric data of holotype and 12 paratypes in Table 3. Body elongate, subcylindrical anteriorly, more compressed posteriorly. Dorsal profile slightly to strongly arched to dorsal fin, then descending to caudal peduncle. Ventral profile more or less straight to pelvic fins, then ascending to caudal peduncle. Head slightly depressed; eye round, dorsolateral, not visible in ventral view. Snout rounded in dorsal view, pointed in lateral view. Caudal peduncle without adipose crests or with small dorsal crest. Dorsal fin with four simple and 8½ branched rays; origin of fin anterior to pelvic-fin origin; distal margin straight to slightly concave or slightly convex. Dorsal fin extending past pelvic fin, not to anal-fin origin. Anal fin with 3 simple and 5½ branched rays. Pectoral fin with 11 (n=1) or 12 (n=12) rays. Pelvic fin with 8 rays. Axillary pelvic-fin lobe present. Caudal fin with 17 (9 upper, 8 lower) branched rays (often secondarily branched), slightly to moderately forked. Body covered with minute scales including on belly and breast except between branchiostegal membranes; scales partially embedded on side of body anteriorly. Lateral line complete and extending onto caudal fin; 150–163 scales along lateral line, many without pores. Vertebrae: 21–22 abdominal + 13–14 caudal = 34–35 total (N=3).

Anterior naris in tube, tube with pointed flap on posterior margin. Posterior and anterior nares adjacent. Mouth arched, about twice as wide as long (Figure 5A). Lips fleshy; upper lip finely pleated and with median notch. Lower lip less fleshy than upper, with narrow medial interruption; two halves anteriorly lobed. Large processus dentiformis. Lower jaw with medial concavity opposing processus dentiformis. Inner rostral barbel reaching corner of mouth; outer rostral barbel reaching anterior margin of eye; maxillary barbel reaching past eye. Halves of air bladder capsule connected by manubrium (Figure 2A). Although the largest individual examined was a male (98.1 mm SL), the next four largest individuals were females 78.1–82.7.

FIGURE 5. Mouths of (A) *Magnischistura khaokrajom*, THNHM-F023975, holotype, 74.0 mm SL, (B) *Mustura maepaiensis*, UF 188310, 35.1 mm SL, (C) *Sectoria atriceps*, UF 191745, 25.2 mm SL, and (D) *Schistura rupecula*, AUM 38679, 68.0 mm SL.

Color. Body yellow-brown dorsally and laterally, yellow-white ventrally. Seven–13 wide black to dark brown bars or spots on side, bars extending over body to meet those on opposite side and onto underside of caudal peduncle. Bars similar in size or slightly wider than spaces between bars, sometimes anastomosing. Head, barbels, fins, and body (except breast and belly in some specimens) densely covered with melanophores. Solid black bar (darkest medially) extending from dorsal margin to ventral margin of caudal-fin base. Black along most of dorsal-fin base, interrupted by bright red spot at base of second and third branched ray. Dusky black band near center of dorsal fin; sometimes another band near edge. Specimens in ethanol similar but lack red spot.

Sexual development and dimorphism. All specimens were >70 mm SL and presumably with fully developed sexual dimorphism. The pectoral fin of the male begins curving upward about midway, is rigid, and has tubercles of various size on the dorsal surface, including on the unbranched ray. Membranes between the rays are narrow and have ridges with small tubercles (Figure 4B,D). The first branched ray, with a membrane between branches only in its distal one-fourth, is the longest and widest, expands distally, and is 3-4 times wider than other rays. Dense, longitudinal rows of conical tubercles are on all rays and ridges; tubercles are largest on the 1st branched ray and decreasing in number and size on succeeding rays.

Males have a large, ventro-posteriorly oriented suborbital flap with tubercles (spike-like in largest males) along the underside and on the distal edge (Figure 4A), flap often with a distal notch. Females have a small suborbital flap lacking tubercles (Figure 4C).

In females, the pectoral fin is rigid but not curved upward. The 1st branched ray has a membrane between its branches only in the distal one-third to one-half and is the widest ray (Figure 4D). The 3rd branched ray is the longest. Ridges are present on the membranes but with no or few small tubercles. In both sexes, the first and second branched rays (and sometimes succeeding rays) have 2–4 branches. The anterior branch of each branched ray does not branch again, while the posterior branch can be either unbranched or branched. The pelvic fin of the male reaches the anterior border of the urogenital opening, that of the females reaches about half-way between the pelvic- and anal-fin origins.

TABLE 3. Morphometric data on *Magnischistura khaokrajom* (THNHM-F023975, UF 248549, UF 249118, ZRC 68439) and *Mustura maepaiensis* (UF 183841, UF 183868, UF 188310).

	Magnischistura khaokrajom (N=13)			***Mustura maepaiensis*** (N=13)		
	Mean	SD	Range	Mean	SD	Range
Standard length	76.9	7.8	66.7–98.1	32.5	2.6	28.0–36.5
Relative to SL						
Prepectoral-fin length	23.9	1.2	22.2–25.7	25.0	1.3	23.3–28.6
Predorsal-fin length	51.0	0.6	50.3–52.1	49.8	1.4	47.7–51.9
Prepelvic-fin length	53.2	1.3	50.8–55.0	53.9	1.4	52.3–56.8
Preanal-fin length	79.1	1.1	77.8–80.8	78.7	1.7	48.9–81.8
Body depth at dorsal-fin origin	18.9	2.0	16.0–21.8	18.5	1.3	16.9–20.7
Body width at dorsal-fin origin	15.4	1.6	12.9–17.5	13.0	0.8	11.4–14.4
Dorsal-fin length	23.1	0.9	20.8–24.3	31.3	1.4	28.6–33.2
Dorsal-fin-base length	15.7	0.5	14.7–16.4	20.8	1.0	18.9–22.3
Pectoral-fin length	20.8	1.6	18.5–23.9	25.5	1.1	23.4–27.2
Pelvic-fin length	17.2	1.1	15.5–19.3	19.7	0.8	18.6–21.3
Anal-fin length	16.1	0.8	14.4–17.3	19.9	0.9	18.4–21.3
Anal-fin-base length	7.9	0.2	7.7–8.3	8.4	0.6	7.5–9.3
Pectoral fin to pelvic fin	30.7	1.6	28.6–33.3	30.2	1.1	28.6–32.3
Pelvic fin to caudal fin	48.0	1.0	45.8–49.6	48.2	0.9	46.6–49.8
Pelvic fin to anal fin	26.7	1.1	25.2–28.2	25.6	1.1	23.6–27.4
Caudal-peduncle depth	12.4	0.5	11.7–13.3	12.4	0.5	11.8–13.4
Caudal-peduncle length	14.8	0.6	14.1–15.9	14.7	0.9	13.0–15.9

.....continued on the next page

TABLE 3. (Continued)

	Magnischistura khaokrajom (N=13)			*Mustura maepaiensis* (N=13)		
	Mean	SD	Range	Mean	SD	Range
Head length	25.2	0.7	24.2–26.3	25.1	1.1	23.9–28.2
Relative to HL						
Dorsal head length	82.2	1.7	79.9–85.3	93.4	2.1	90.9–97.8
Head width	65.4	2.1	60.7–67.7	61.1	2.6	57.1–65.8
Snout length	42.0	0.6	40.7–42.9	41.3	2.4	37.2–45.6
Head depth at end of eye	46.3	2.1	42.3–50.5	54.3	2.0	51.3–58.1
Orbital length	15.3	1.0	12.8–16.6	27.9	1.6	25.3–30.6
Interorbital width	29.7	1.5	26.6–31.3	23.3	1.7	20.4–26.4
Internasal width	20.2	1.0	18.1–21.7	20.4	3.9	8.4–23.6
Inner-rostral-barbel length	20.9	2.0	16.4–24.6	27.0	2.6	22.1–29.6
Outer-rostral-barbel length	29.2	3.8	20.0–35.0	44.3	2.4	40.0–48.6
Maxillary-barbel length	32.0	2.4	28.1–35.2	35.9	2.9	30.4–41.0
Gape width	28.5	2.1	23.3–31.0	24.2	1.9	20.3–26.9

Distribution and habitat. Magnischistura khaokrajom is known only from Huay Thong An (Figure 6), a small rocky tributary of Pachi River on Khao Krajom in the Suan Phueng District of Ratchaburi Province, Thailand. This is an area of the Tenasserim Hills with steep river valleys. Huay Thong An is 1–1.5 m wide with clear, fast-flowing water over cobble and gravel. The only fishes collected with *M. khaokrajom* were *Paracanthocobitis nigrolineata* and two other undescribed nemacheilids.

FIGURE 6. Type locality of *Magnischistura khaokrajom*. Huay Thong An, Ratchaburi Province, Thailand.

Discussion

Based on our phylogenetic analysis (Figure 1), *M. khaokrajom* could be placed in *Rhyacoschistura,* but to avoid paraphyly that would require inclusion of several species of *Schistura,* at least *S. reidi* (Smith 1945), *S. similis* Kottelat 1990, *S. desmotes* (Fowler 1934), and *S. magnifluvis* Kottelat 1990, all of which lack diagnostic traits of *Rhyacoschistura*, including a curved, stiff and tuberculate pectoral fin in adult males and first branched pectoral-fin ray wider than other rays. Likewise, based on molecular data, *M. khaokrajom* could be placed in *Sectoria*, but that would require inclusion of species of *Schistura* lacking diagnostic characteristics of *Sectoria*, including a large horny sheath on each jaw and no processus dentiformis (Kottelat 1990; Figure 5). *Magnischistura khaokrajom* also lacks diagnostic characteristics of *Sectoria*. Instead, a new genus, *Magnischistura*, morphologically diagnosable from *Rhyacoschistura, Sectoria,* and *Schistura*, is created.

The creation of a genus outside a phylogenetic context leads to ambiguity about its species composition. Of the 17 species originally assigned, and tentatively assigned, to *Mustura* (Kottelat 2018), phylogenetic information now is available on six (Šlechtová *et al*. 2024), and of those six only *M. maepaiensis* is supported as being closely related to *M. celata*, type species of *Mustura.* These two species have a similar color pattern, perhaps a synapomorphy for the genus, unlike the other species originally hypothesized to be related.

More, recently described species have been added to *Mustura*, i.e., *M. taretensis* Chinglemba *et al*. 2021, *M. subhashi*, Choudhury *et al*. 2021, *M. yangi* Qin *et al*. 2022, and *M. daral* Rameshori *et al*. 2022, all without a phylogenetic context and therefore of uncertain relationship to *M. celata* and *M. maepaiensis*. These four species all had a *M. celata*-like pectoral fin and a manubrium connecting the two bony capsules of the air bladder, two character states presumably considered derived within Nemacheilidae or within a clade of species including *M. celata.* However, the pectoral fin with a tuberculated dorsal surface clearly has evolved independently in several lineages. The phylogenetic value of a manubrium connecting the two bony capsules of the air bladder versus the capsules being broadly joined medially without a manubrium seems high, as used by Kottelat (2018) to separate *Mustura* and *Physoschistura*, and herein to diagnose *Magnischistura* from *Physoschistura*. However, a survey of more taxa is needed to look for intermediate conditions that may limit its phylogenetic use. Given the assumed utility, the difference between *Nemacheilus fasciatus* and *N. zonatus*, one with and one without a manubrium (Figure 2), suggests they may belong in different genera; however, molecular data suggest a close relationship between them (Page *et al*. 2020).

The lack of a close relationship among *Magnischistura, Mustura*, *Petruichthys, Physoschistura*, and *Rhyacoschistura* (Figure 1; Slectova *et al*. 2024 with all genera included but *Magnischistura*), suggests the striking similarity of secondary sexual characteristics in these genera is due to convergence related to shared aspects of spawning behavior. The male's curved and rigid pectoral fin with a tuberculated dorsal surface may assist in clasping the female during spawning to increase the proximity during sperm release and likelihood of egg fertilization, resulting in strong positive selection. Use of paired fins and tuberculated surfaces to hold and possibly stimulate females during spawning has been observed in other fishes, e.g., in Cobitidae (Nalbant 1994), Leuciscidae (Maurakis & Woolcott 1992), and Percidae (Page 1983). Given the independent evolution of these character states in several lineages, hypothesizing close relationships among species based on these traits needs to be accompanied by independent tests of the hypotheses, e.g., with molecular or behavioral data.

The function of the suborbital flap is unknown. Species with flaps are dispersed throughout Nemacheilidae (e.g., *Acanthocobitis* in the Burmese clade, *Nemacheilus* in the Sundaic clade, and *Schistura* in the Indochinese and Southern clades) with species without flaps dispersed among them phylogenetically. Suborbital flaps are present on nemacheilids that are morphologically quite dissimilar in body shape, color pattern, and other characteristics. Some flaps are small and lack prominent tubercles on the extremities, others are large and have spike-like tubercles distally, as on *Magnischistura*.

Given its presence on males and absence on females (with rare exceptions, *M. khaokrajom* being one), the suborbital flap is assumed to have a reproductive function. Males of some species, e.g., *Schistura mahnerti*, have a well-developed flap, and females have a less conspicuous groove in place of the flap. The grooves (and smaller flap in *M. khaokrajom*) in females may have a function, or they may represent a pleiotropic effect of the gene(s) controlling development of the flap on males.

As noted by Plongsethee *et al*. (2012), the presence of suborbital flaps in species that are distantly related may indicate independent origins of the flap in separate lineages, or the flap may be an ancestral state that has been lost

in some lineages due to insufficient positive selection pressure to maintain them. Interspecific distribution of the flap in relation to behavior, habitat, or other environmental factors appears not to have been studied. As phylogenetic relationships of species of nemacheilids are better known, the evolution of sexually dimorphic features can be better understood in relation to specific behaviors or environmental factors. One possible function of the flap, proposed by Plongsethee *et al*. (2012) is the secretion of pheromones or other chemical stimuli. This potential function is supported by the fleshy globular nature of some flaps, including that on *Magnischistura*.

These shortcomings in our knowledge highlight the tremendous need for more ecological and behavioral studies as well as fieldwork to collect specimens and tissues for generating phylogenies to understand the evolutionary history of nemacheilids, one of the most spectacular clades of fishes.

Comparative Material

Mustura maepaiensis: UF 188310, 6 ex., 30.8–36.5 mm SL, Yuam River, 18.298N, 97.912E, Mae Hong Son Province, 1 Nov. 2016, D. A. Boyd, Z. S. Randall *et al*.; UF 183841, 1 ex. 28.0 mm SL, trib., Salween River, 18.015N, 97.723E, Mae Hong Son Province, Thailand, 6 Jan 2012, A. Suvarnaraksha, L. M. Page *et al*.; UF 183868, 6 ex., 29.6–35.5 mm SL, Salween River, 18.374N, 97.648E, Mae Hong Son Province, Thailand, 6 Jan 2012, A. Suvarnaraksha, L. M. Page *et al*.; UF 188267, 1 ex., 42.3 mm SL, Surin River, 18.92769N. 97.93696E, Mae Hong Son Province, Thailand, 11 Jan 2016, Z. S. Randall *et al*.

Nemacheilus fasciatus, UF 162177, 1 ex., 49.6 mm SL, Way Seputhi, 5.07183S, 104.88413E, Lampung State, Sumatra, Indonesia, 30 Oct 2005, R. H. Robins, L. M. Page *et al*.

Nemacheilus zonatus, UF 237302, 1 ex., 23.2 mm SL, Pao River, 16.30422N, 103.57584E, Kalasin Province, Thailand, 6 Jan 2015, L. M. Page, Z. S. Randall *et al*.

Physoschistura pseudobrunneana, UF 177823, 1 ex., 28.9 mm SL, montane stream, 19.83472N, 99.68250E, Chiang Rai, Province, Thailand, 16 May 2010, W. Tangjitjaroen & L. M. Page

Schistura aurantiaca, UF 188063, 1 ex., 39.0 mm SL, Parcham Mai River, 14.65983N, 98.53422E, Kanchanaburi Province, Thailand, 28 Jan 2015, D. A. Boyd, Z. S. Randall *et al*.

Schistura rupecula, AUM 38679, 1 ex., 68.0 mm SL, Seti River, Pokhara, Gandaki Province, Nepal, 8 Aug 1961, no collector; UF 191250, 1 ex., 62.0 mm SL, Indrawati River, 27.82847N, 85.57697E, Bagmati State, Nepal, 28 Oct 2008, R. L. Mayden.

Sectoria atriceps, UF 191745, 1 ex., 25.2 mm SL, Yang River, 19.09413N, 100.95252E, Nan Province, Thailand, 22 May 2017, D. A. Boyd & D. Boonwun.

Tuberoschistura baenzigeri, UF 247943, 1 ex., 38.5 mm SL, Khwae Noi, 14.19011N, 99.07561E, Kanchanaburi Province, Thailand, 28 Jun 2021, J. Limpichat *et al*.

Author contributions

Lawrence M. Page and Parinya Pawangkhanant conceived the study. Data were generated by David K. Cagle, Parinya Pawangkhanant, Zachary S. Randall, Weerapongse Tangjitjaroen, and Basil R. Williams. Data analyses were done by David K. Cagle, Lawrence M. Page, and Weerapongse Tangjitjaroen. Manuscript was prepared by all authors. Funding was generated by Lawrence M. Page.

Acknowledgements

We thank the Rabbit in the Moon Foundation, especially Mali Naiduangchan for constant support of our research, and Charnchai Bindusen and Juthamas Wangaryattawanich for organizing and supporting our fieldwork; Akkrachai Aksornneam, Pattarawhich Dawwrueng, Kawin Jiaranaisakul, Bang Ro Ta-Au, Krarok Wongde, Torn Wongde, and Jo Wongde for assistance in the field. Fishes were collected in Thailand with permission from the Thailand Department of Fisheries. Methods were approved by the National Research Council of Thailand and the University of Florida Animal Care and Use Committee to the first author.

This project was supported in part by the U.S. National Science Foundation through a Planetary Biodiversity Inventory award (NSF-DEB 0315963), a Rules of Life award (NSF 1839915), American and Thai-American Fulbright Scholar Awards (2563-64), to L.M.P., and a Research Infrastructure award (NSF-DBI 2210415).

References

Chakrabarty, P., Warren, M., Page, L.M. & Baldwin, C.C. (2013) GenSeq: an updated nomenclature and ranking for genetic sequences from type and non-type sources. *Zookeys*, 346, 29–41.
https://doi.org/10.3897/zookeys.346.5753

Chinglemba, Y., Rameshori, Y. & Vishwanath, W. (2021) A new species of stone loach of the genus *Mustura* (Teleostei: Nemacheilidae) from Chindwin River drainage, Manipur, north-eastern India. *Zootaxa*, 5081 (4), 551–565.
https://doi.org/10.11646/zootaxa.5081.4.6

Choudhury, H., Das, R., Bharali, R.C., Sarma, K., Tyagi, L.K., Lal, K.K. & Sarma, D. (2021) Description of a new species of *Mustura* Kottelat (Teleostei: Nemacheilidae) from the Brahmaputra drainage, India. *Journal of Fish Biology*, 99, 450–461.
https://doi.org/10.1111/jfb.14736

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Fowler, H.W. (1934) Zoological results of the third De Schauensee Siamese Expedition, Part I.—Fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 86, 67–163.

Fowler, H.W. (1936) Zoological results of the third De Schauensee Siamese Expedition, Part VII.—Fishes obtained in 1935. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 87, 509–513. [for 1935]

Hubbs, C.L., Lagler, K.F. & Smith, G.R. (2004) *Fishes of the Great Lakes region*. The University of Michigan Press, Ann Arbor, Michigan, 276 pp., 32 pls.
https://doi.org/10.3998/mpub.17658

Kottelat, M. (1990) *Indochinese nemacheilines. A revision of nemacheiline loaches (Pisces: Cypriniformes) of Thailand, Burma, Laos, Cambodia and southern Viet Nam*. Pfeil, München, 262 pp.

Kottelat, M. (2017) *Schistura titan*, a new species of loach from Dakchung Plateau, southern Laos (Teleostei: Nemacheilidae). *Ichthyological Exploration of Freshwaters*, 28, 65–73.

Kottelat, M. (2018) *Mustura celata*, a new genus and species of loaches from northern Myanmar, and an overview of *Physoschistura* and related taxa (Teleostei:Nemacheilidae). *Ichthyological Exploration of Freshwaters*, 28, 1–6.
https://doi.org/10.23788/IEF-1080

Kottelat, M. (2019) *Rhyacoschistura larreci*, a new genus and species of loach from Laos and redescription of *R. suber* (Teleostei: Nemacheilidae). *Zootaxa*, 4612 (2), 151–170.
https://doi.org/10.11646/zootaxa.4612.2.1

Kottelat, M. & Grego, J. (2020) *Kayahschistura lokalayensis*, a new genus and species of cave fish from Myanmar (Teleostei: Nemacheilidae). *Raffles Bulletin of Zoology Supplement*, 35, 179–185.

Maurakis, E.G. & Woolcott, W.S. (1992) Spawning in *Semotilus corporalis* (Fallfish) (Pisces: Cyprinidae). *Virginia Journal of Science*, 43, 377–380.
https://doi.org/10.2307/1446218

Menon, A.G.K. (1987) *The fauna of India and the adjacent countries. Pisces. Vol. IV. Teleostei - Cobitoidea. Part 1. Homalopteridae*. Zoological Survey of India, Calcutta, x + 259 pp., 16 pls.

Nalbant, T. (1994) Studies on loaches (Pisces: Ostariophysi; Cobitoidea). I. An evaluation of the valid genera of Cobitinae. *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'*, 34, 375–380.

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.
https://doi.org/10.1093/molbev/msu300

Page, L.M. (1983) *Handbook of Darters*. T.F.H., Inc., Neptune City, New Jersey, 271 pp.

Page, L.M., Pfeiffer, J.M., Suksri, S., Randall, Z.S. & Boyd, D.A. (2020) Variation in the Arrow Loach, *Nemacheilus masyae* (Cypriniformes: Nemacheilidae), in Mainland Southeast Asia with description of a new species. *Copeia*, 108, 392–402.
https://doi.org/10.1643/CI-19-305

Pellegrin, J. (1936) Poissons nouveaux du haut-Laos et de l'Annam. *Bulletin de la Société Zoologique de France*, 61, 243–248.

Plongsesthee, R., Beamish, F.W.H. & Page, L.M. (2012) Sexual dimorphism in species of *Schistura* (Teleostei: Nemacheilidae) from the Mae Khlong basin and peninsular Thailand. *Zootaxa*, 3586 (1), 353–358.
https://doi.org/10.11646/zootaxa.3586.1.33

Qin, T., Kottelat, M., Kyaw, Y.M.M. & Chen, X. (2022) *Mustura yangi*, a new species of loach (Teleostei: Nemacheilidae) from Putao, Irrawaddy drainage, northern Myanmar. *Ichthyological Exploration of Freshwaters*, 31, 179–189.
https://doi.org/10.23788/IEF-1181

Rameshori, Y., Chinglemba, Y., Darshan, A. & Vishwanath, W. (2022) *Mustura daral*, a new species of stone loach from Arunachal Pradesh, northeast India (Teleostei: Nemacheilidae). *Zootaxa*, 5129 (2), 285–294.
https://doi.org/10.11646/zootaxa.5129.2.8

Singh, A., Sen, N., Bănărescu, P.M. & Nalbant, T.T. (1982) New noemacheiline loaches from India (Pisces, Cobitidae). *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa"*, 23, 201–212. [for 1981]

Šlechtová, V., Bohlen, J., Freyhof, J. & Ráb, P. (2006) Molecular phylogeny of the Southeast Asian freshwater fish family Botiidae (Teleostei: Cobitoidea) and the origin of polyploidy in their evolution. *Molecular Phylogenetics and Evolution*, 39, 529–541.
https://doi.org/10.1016/j.ympev.2005.09.018

Šlechtová, V., Bohlen, J. & Tan, H.H. (2007) Families of Cobitoidea (Teleostei; Cypriniformes) as revealed from nuclear genetic data and the position of the mysterious genera *Barbucca*, *Psilorhynchus*, *Serpenticobitis* and *Vaillantella*. *Molecular Phylogenetics & Evolution*, 44, 1358–1365.
https://doi.org/10.1016/j.ympev.2007.02.019

Šlechtová, V., Dvořák, T., Freyhof, J., Kottelat, M., Levin, B., Golubtsov, A., Šlechta, V. & Bohlen, J. (2024) Reconstructing the phylogeny and evolutionary history of freshwater fishes (Nemacheilidae) across Eurasia since early Eocene. *eLife*, 13, RP101080.
https://doi.org/10.7554/eLife.101080.2.sa2

Smith, H.M. (1945) The fresh-water fishes of Siam, or Thailand. *Bulletin of the United States National Museum*, 188, i–xi + 1–622, pls. 1–9.

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033

Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R. & Hebert, P.D. (2005) DNA barcoding Australia's fish species. *Philosophical Transactions of the Royal Society of London B: Biological Science*, 360, 1847–1857.
https://doi.org/10.1098/rstb.2005.1716

Yang, L., Mayden, R.L., Sado, T., He, S., Saitoh, K. & Miya, M. (2010) Molecular phylogeny of the fishes traditionally referred to Cyprinini sensu stricto (Teleostei: Cypriniformes). *Zoologica Scripta*, 39 (6), 527–550.
https://doi.org/10.1111/j.1463-6409.2010.00443.x