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https://doi.org/10.11646/zootaxa.5311.3.3 http://zoobank.org/urn:lsid:zoobank.org:pub:9AFB80E2-7A3A-4D81-ADB9-B2DA31C24536

Species of *Garra* (Cyprinidae: Labeoninae) in the Salween River basin with description of an enigmatic new species from the Ataran River drainage of Thailand and Myanmar

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Abstract

Garra panitvongi, new species, is described from the Ataran River drainage, Salween River basin, of southeastern Myanmar and western Thailand. It is the sixth species of Garra known from the Salween River basin and is readily distinguished from all congeners by the red-orange color of the body and caudal fin, and a pointed proboscis with a blue stripe on each side from the anterior margin of the orbit to the tip of the proboscis and with the stripes forming a V-shape. Garra panitvongi is known in the aquarium trade as the Redtail Garra. Descriptive information is provided on poorly known species of Garra in the Salween River basin, and Garra nujiangensis is transferred to Ageneiogarra.

Key words: Actinopterygii, teleost, phylogenetics, Zami River

Introduction

Eschmeyer's Catalog of Fishes (Fricke et al., 2022) lists 189 species of *Garra* Hamilton 1822 making it one of the most diverse genera of fishes in the world. The distribution of *Garra* ranges from western Africa to China, north to Turkey and Afghanistan, and south to Borneo. Five species of *Garra* Hamilton 1822 have been recorded from the Salween River basin: *Garra notata* described by Blyth (1860) from the Tenasserim Provinces of Myanmar and subsequently recorded in the Salween basin by Nebeshwar & Vishwanath (2017); *G. imberbis* described by Vinciguerra (1890) from Tao in Carin country (possibly Taunggyi District, Shan State—see Likhitrakarn et al. 2017), Myanmar; *G. gravelyi* described by Annandale (1919) from Inle Lake basin near Taunggyi, Shan State, Myanmar; *G. salweenica* described by Hora & Mukerji (1934) from the Salween River at Takaw, Kengtung [Shan] State, Myanmar; and *G. nujiangensis* described by Chen & Yang (Chen et al. 2009) from the upper Salween (Nujiang) River drainage, Zhenkang County, Yunnan Province, China. Chu & Cui (1989) reported *Garra orientalis* Nichols (1925) from the Salween basin in Yunnan Province, China, but Zhang (2005) found the material to be conspecific with *G. salweenica*.

Recently collected specimens from Kasat River, a tributary of the Ataran-Salween River basin, in Kayin State in Myanmar and Kanchanaburi Province in Thailand provide type material as well as morphological and genetic data to herein name and diagnose a sixth species of the Salween River basin. This species is well known as the "Redtail Garra" in the aquarium trade but has remained scientifically undescribed.

Materials and methods

Measurements were taken to the nearest 0.1 mm using digital calipers. Morphometric data are expressed as percentages of standard length (SL) or head length (HL). Measurements follow Hubbs & Lagler (1958) except for body depth, which was measured at the dorsal-fin origin, and prepectoral, prepelvic, and preanal lengths, which were taken from the anterior tip of the snout to the origin of each fin. Total ray counts are given for paired fins and branched ray counts are given for unpaired fins. The last branched ray of the dorsal and anal fins, sharing a pterygiophore with the penultimate ray, is given as ½. Transverse scale rows are counted from the dorsal-fin origin to the lateral line and from the anal-fin origin to the lateral line; numbers are of whole scales. Measurements and counts were taken on the left side when possible. Vertebral counts were made on micro-computed tomography scans, with the first caudal vertebra with its hemal spine posterior to the anterior-most anal-fin pterygiophore (which on the *Garra* examined is nearly horizontal); counts of abdominal vertebrae include the Weberian complex (N=4 vertebrae), and counts of caudal vertebrae include the urostyle complex (N=1 vertebra). Descriptions of the snout follow Nebeshwar & Vishwanath (2017) and those of the gular disc follow Kottelat (2020). Abbreviations for institutional collections are: LSUMZ, Louisiana State University Museum of Natural Science, Baton Rouge; THNHM, Thailand Natural History Museum, National Science Museum, Pathum Thani; UF, University of Florida, Florida Museum of Natural History, Gainesville; and ZRC, Zoological Research Collection, Lee Kong Chian Natural History Museum, Singapore.

A sheared principal component analysis (PCA) in which the covariance matrix was factored (Humphries et al. 1981) was used to examine variation in morphometric data of *G. panitvongi*, n. sp., and the two most similar species of *Garra* in the Salween, *G. notata* and *G. salweenica*. The sheared second and third principal components of the data, representing shape factors independent of size, were plotted. Sheared PCA was conducted in base R (R Core Team, 2022) following the protocol in Bookstein et al. (1985) for SAS. Individuals could not be sexed reliably using only external characteristics, and therefore sexes were not analyzed separately.

Photographs of live and preserved specimens were taken with Canon 7D and R cameras. All images of live specimens were taken soon after capture. Figures were edited using Adobe Photoshop CC 2021. Computed tomography scans were generated using a Phoenix v|tome|x M scanner (GE Measurement & Control, Boston, USA) at the University of Florida's Nanoscale Research Facility. X-ray data were processed using datos|x software v. 2.3 and segmented and visualized using VG StudioMax v. 4 (Volume Graphics, Heidelberg, Germany). The scan data are freely available for download at MorphoSource (https:\\morphosource.org). A photogrammetry scan of the holotype of the new species was completed using a three-Canon RP camera system, and the model is provided for global digital access on Sketchfab (www.sketchfab.com) and can be downloaded from MorphoSource (Table 1). Maps were produced using ArcMap 10.8 in ArcGIS.

TABLE 1. μCT (CT) and photogrammetry (PT) scans included in this study. Sampling locations are available at http://specifyportal.flmnh.ufl.edu/fishes and iDigBio.org.

Species	Catalog Number	Country/Province or State/ Drainage	CT or PT	MorphoSource Media ID
Garra notata	UF 192485	Thailand, Tak, Moei	CT	000483535 000483531
Garra panitvongi	THNHM-F021641 (ex. UF 245312)	Thailand, Kanchanaburi, Zami	CT	000483563 000483567
			PT	000490270 000490267
	UF 248982	Myanmar, Kayin, Kasat	CT	000483585 000483589 000483593
	UF 245312	Thailand, Kanchanaburi, Zami	CT	000483580
Garra salweenica	UF 183853	Thailand, Mae Hong Son, Salween	CT	000483519 000483515 000483523

DNA was extracted from tissue samples using the QIAamp DNA mini kit (Qiagen). Mitochondrial cytochrome oxidase subunit I (COI) was amplified by polymerase chain reaction (PCR) and sequenced using the following primers: FISH-BCL5'-TCAACYAATCAYAAAGATATYGGCAC-3', FISH-BCH5'-ACTTCYGGGTGRCCRAARAATCA-3' (Baldwin et al., 2009). PCR was performed using 25 µL solutions containing 1 µL each primer at 10 mM; 0.25 µL MyTaq Red polymerase and 4 μL buffer (Bioline Reagents); and 2 μL DNA template. Thermocycling parameters followed Liu et al. (2012). Purification and bidirectional Sanger sequencing were performed by Eurofins Genomics. Chromatograms were assembled and edited with Geneious 8.1.9. Alignment was implemented, and uncorrected (p) distances between taxa averaged with Mesquite 3.70 (Maddison & Maddison, 2021) using Clustal W 2.1 (Larkin et al., 2007). Partitioning and phylogenetic analyses were carried out using the high-performance cluster (HiPerGator) at the University of Florida. The aligned dataset was partitioned by codon position, and a model of nucleotide substitution was selected for each subset independently in PartitionFinder 2.1.1 (Lanfear et al., 2016) using linked branch lengths, the corrected Akaike information criterion, and a greedy search algorithm (Lanfear et al., 2012). Bayesian inference (BI) analysis was conducted with MrBayes 3.2.6 (Ronquist et al., 2012) using two independent runs of four chains and 20 million generations, sampling trees every 1000 generations and discarding the first 25 % as burn-in. Maximum likelihood (ML) analysis and bootstrapping were conducted with RAxML 8.2.10 (Stamatakis, 2014) using complete random starting trees, the default rapid hill-climbing algorithm, 100 independent tree searches, and 700 bootstrap replicates, as determined by the autoMRE convergence criterion.

Initial phylogenetic analyses included all 1017 COI sequences of *Garra* available from GenBank, including those extracted from whole mitochondrial genomes, and our newly generated data for samples from the Salween River basin (Table 2). In these initial runs, closest relatives to the new species described herein were *Garra gotyla* (Gray 1830) and *G. yajiangensis* Gong, Freyhof, Wang, Liu, Liu, Lin, Jiang & Liu 2018, both from the Brahmaputra River basin, although support values were low. Because of low support values throughout the initial trees and concerns about species-level identifications of some samples on GenBank, the tree presented herein is restricted to *G. gotyla*, *G. yajiangensis*, species of *Garra* in the Salween basin, and species of *Garra* in the adjacent Mae Klong basin wherein some tributaries interdigitate with those of the Ataran River basin. Molecular data include all species known from the Salween except *G. imberbis* (Table 2). GenSeq designations were assigned following Chakrabarty et al. (2013). *Cirrhinus microlepis* Sauvage 1878 was designated as the outgroup, and *Ceratogarra cambodgiensis* (Tirant 1884) and *C. fasciacauda* (Fowler 1937) were included for topographic structure.

TABLE 2. Specimens included in the molecular phylogeny, with GenBank accession numbers for *cytochrome oxidase c subunit 1 (COI)* gene sequence data. *Sequences generated by the present study. †Sequences uploaded to GenBank by authors of reference but data unpublished within referenced study.

Taxon	GenBank no.	Drainage	Reference	Voucher	GenSeq no.
Garra fluviatilis	MK902681	Mae Klong River	Page et al. 2019	UF 181134	genseq-3
Garra fluviatilis	MK902680	Mae Klong River	Page et al. 2019	UF 176452	genseq-3
Garra fluviatilis	OP855535*	Salween River	Present study	UF 245313	genseq-4
Garra fluviatilis	OP855536*	Salween River	Present study	UF 245313	genseq-4
Garra fuliginosa	MK902686	Tapi River	Page et al. 2019	UF 191849	genseq-4
Garra fuliginosa	MK902685	Mae Klong River	Page et al. 2019	UF 191353	genseq-4
Garra fuliginosa	MK902684	Chao Phraya	Page et al. 2019	UF 188288	genseq-4
Garra fuliginosa	MK902682	Mekong River	Page et al. 2019	UF 170307	genseq-4
Garra gotyla	KF550090	Brahmaputra River	Unpublished	NBFGRGG-30	genseq-4
Garra gotyla	KF550093	Brahmaputra River	Unpublished	NBFGRGG-34	genseq-4
Garra gotyla	KF550091	Brahmaputra River	Unpublished	NBFGRGG-32	genseq-4
Garra gotyla	KF550092	Brahmaputra River	Unpublished	NBFGRGG-33	genseq-4
Garra gravelyi	KX951809	Irrawaddy River	Barman et al. 2017	MzKa-349	genseq-4
Garra notata	MK902687	Salween River	Page et al. 2019	UF 192116	genseq-4
Garra notata	OP855529*	Salween River	Present study	UF 245345	genseq-4
Garra notata	OP855530*	Salween River	Present study	UF 245345	genseq-4

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TABLE 2. (Continued)

Taxon	GenBank no.	Drainage	Reference	Voucher	GenSeq no.
Garra nujiangensis	JQ864610†	Salween River	Zheng et al. 2010	KIZ20050417001	genseq-4
Garra panitvongi	OP855532*	Salween River	Present study	THNHM-F021641	genseq-1
Garra panitvongi	OP855531*	Salween River	Present study	UF 245312	genseq-2
Garra salweenica	JQ864614†	Salween River	Zheng et al. 2010	KIZ07194	genseq-4
Garra salweenica	KX983932	Salween River	Sun et al. 2018	SWFC 1510010	genseq-4
Garra salweenica	MK902688	Salween River	Page et al. 2019	UF 183869	genseq-4
Garra surinbinnani	MK902678	Mae Klong River	Page et al. 2019	UF 192195	genseq-3
Garra surinbinnani	MK902677	Mae Klong River	Page et al. 2019	UF 192073	genseq-3
Garra surinbinnani	MK902676	Mae Klong River	Page et al. 2019	UF 191337	genseq-3
Garra yajiangensis	KY867667†	Brahmaputra River	Kaushik & Bordoloi 2016	IASST F185	genseq-4
Garra yajiangensis	OL826795	Brahmaputra River	Zhang et al. 2022	N/A	N/A
Ceratogarra cambodgiensis	MK902675	Mae Klong River	Page et al. 2019	UF 237398	genseq-4
Ceratogarra cambodgiensis	MK902674	Tapi River	Page et al. 2019	UF 183816	genseq-4
Ceratogarra cambodgiensis	MK902673	Mekong River	Page et al. 2019	UF 170343	genseq-4
Ceratogarra fasciacauda	JX074175	Mekong River	Yang et al. 2012	UAIC 14167.13	genseq-4
Ceratogarra fasciacauda	MK902679	Mekong River	Page et al. 2019	UF 185133	genseq-4
Cirrhinus microlepis	MK902690	Mekong River	Page et al. 2019	UF 190978	genseq-4

Results

Although *G. panitvongi*, *G. notata* and *G. salweenica* appear similar in body shape, they clustered with only slight overlap (Fig. 1) in the principal component analysis of morphometric data (Table 3). Size accounted for 97.9% of the observed variance (on PC1). The sheared second and third principal components (PC2 and PC3) accounted for 0.73% and 0.37% of the observed variance, respectively. Gape width (-0.55), snout length (-0.53), and body width (0.42) had the highest loadings on sheared PC2. Eye diameter (0.55), and to a lesser extent snout length (-0.37), anal-fin length (0.36), and caudal-peduncle length (-0.36), had the highest loadings on sheared PC3.

The BI and ML analyses recovered strong support for all species-level clades including *G. panitvongi* (Fig. 2), which was resolved in a polytomy with *G. yajiangensis*, and *G. gotyla*, albeit with low confidence (0.65 posterior probability and 47% bootstrap support). *Garra panitvongi* was separated from *G. yajiangensis* and *G. gotyla* by average uncorrected (p) distances of 9.0% and 9.2%, respectively. Only the clade including *G. surinbinnani* Page, Ray, Tongnunui, Boyd & Randall 2019 and *G. gravelyi* was strongly supported in the BI analysis (0.97), and no interspecific relationships were recovered with high support in the ML analysis. These low support values suggest that the closest relatives of the species of *Garra* in the Salween and Mae Klong basins occur in other basins.

Garra panitvongi, new species

Redtail Garra

(Figs. 3-9, Tables 3-4)

Holotype. THNHM-F021641, 67.8 mm SL; Thailand: Zami River drainage: Kanchanaburi Province: Kasat River, 5.5 km NE Ban Thi Rai Pa [village], 15.40366N, 98.6238E, 4 February 2020, L. Page, S. Tongnunui, Z. Randall, D. Boyd, G. Somarriba, and T. Punkumsing.

Paratypes. UF 245312, 1, 38.5 mm SL; same data as holotype. UF 248982, 15, 69.0–116.9 mm SL; LSUMZ 22058, 2, 102.6–106.8 mm SL; ZRC 63153, 2, 105.4–110.4 mm SL; all Myanmar: Kasat River drainage: Kayin State: Pha-Ton-Sai Waterfall, Pyaung Htein District, 15.39770N, 98.38644E, 1 June 2022, Kyaw Aung.

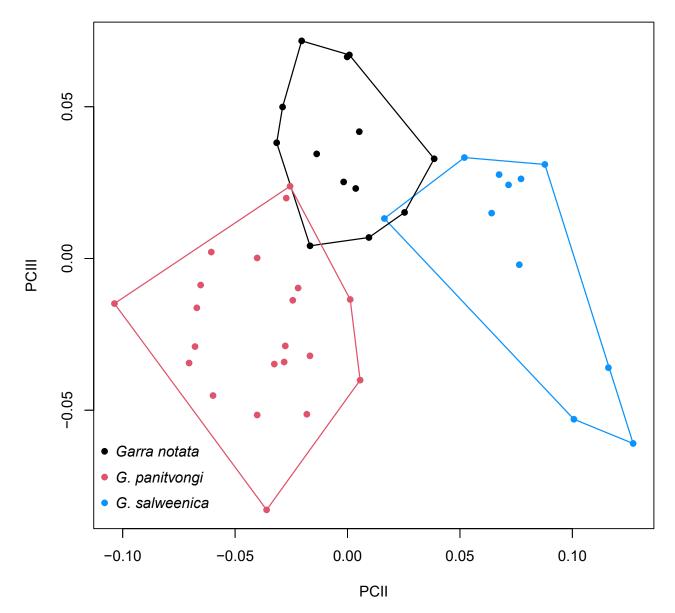


FIGURE 1. Principal component analysis. Size accounted for 97.9% of the observed variance (on PC1). The sheared second and third principal components (PC2 and PC3) accounted for 0.73% and 0.37% of the observed variance, respectively. Gape width, snout length, and body width had the highest loadings on PC2. Eye diameter, snout length, anal-fin length, and caudal-peduncle length had the highest loadings on PC3.

TABLE 3. Morphometric data for *Garra panitvongi* (THNHM-F021641, LSUMZ 22058, UF 245312, UF 248928, ZRC 63153), *G. notata* (UF 192334, 192354, and 192485), and *G. salweenica* (UF 183843, 183853, 183869, 188298).

	G. panitvongi			C	G. notata			G. salweenica		
-	n=21			n=13				n=11		
	range	mean	SD	range	mean	SD	range	mean	SD	
Standard length (mm)	38.5–116.9	91.6	18.9	36.3–97.0	63.8	20.4	34.6– 103.6	64.9	20.5	
As percent of SL										
Predorsal fin length	45.7–50.1	47	1.2	46.7-50.0	48.3	0.9	48.0-52.2	49.8	1.3	
Prepelvic fin length	49.6–55.6	52.3	1.2	49.0-52.4	50.8	1.0	50.7-55.9	53.2	1.7	
Preanal fin length	75.9–79.5	77.8	1.1	72.3–76.7	75.1	1.4	75.3–80.2	77.3	1.5	

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TABLE 3. (Continued)

	G. panitvongi			G. notata			G. salweenica			
-		n=21			n=13			n=11		
	range	mean	SD	range	mean	SD	range	mean	SD	
Body depth	21.9–25.8	23.9	0.9	22.8–26.0	24.2	1.1	21.0-24.4	22.8	1.1	
Body width	16.1–19.2	17.8	0.7	16.9–19.8	18	0.9	14.2–17.4	16.2	1.0	
Caudal-peduncle depth	12.9–14.3	13.5	0.3	12.7–14.6	13.6	0.5	12.4–14.5	13.5	0.7	
Caudal-peduncle length	14.5–18.6	16.5	1.0	13.7–19.1	16.9	1.3	11.3–18.3	15.7	1.8	
Pectoral-fin length	21.4–26.1	23.6	1.0	21.9–24.7	23.4	0.9	21.7–25.9	24	1.3	
Pelvic-fin length	20.0-23.0	21.1	0.6	19.8–23.0	21.3	0.8	21.0-23.3	22	0.7	
Anal-fin length	18.4-23.4	21	1.2	19.0-22.1	20.4	1.0	18.8-22.5	20.6	1.0	
Dorsal-fin base length	18.4–22.1	20.4	0.9	17.4–22.0	19.5	1.2	16.0–20.9	18.9	1.4	
Head length	23.0-26.8	24.6	0.9	23.7–25.8	24.9	0.6	26.1–27.7	26.7	0.6	
Head width	16.4–19.2	17.5	0.6	16.0–18.9	17.7	0.8	16.5–18.8	18.1	0.7	
Snout length	10.8-12.7	12	0.5	11.5–14.1	12.8	0.8	12.0-15.7	13.6	1.0	
Eye length	5.1-7.1	5.7	0.5	5.1-6.4	5.6	0.4	5.1-7.3	5.9	0.6	
Interorbital width	9.5–11.7	10.4	0.6	9.6–12.0	10.7	0.7	10.5-11.9	11.2	0.4	
Gape width	7.8–10.6	9.9	0.6	9.3–10.9	10.3	0.4	10.4-13.1	11.7	0.7	
As percent of HL										
Head width	67.3-76.4	71.3	2.7	66.0-75.4	71.1	3.1	63.0-71.5	67.7	2.5	
Snout length	43.7–53.9	48.8	2.6	46.0-56.8	51.6	3.6	45.0-58.9	51	4.1	
Head depth	62.7–71.9	66.9	2.6	59.1–69.5	65.9	3.1	57.6-63.9	61.4	1.8	
Eye diameter	20.5-26.7	23.3	1.6	20.7–25.7	22.6	1.4	19.2–26.3	22.2	2.0	
Interorbital width	38.3-47.5	42.5	2.3	39.4-47.0	42.9	2.6	37.8-44.6	41.8	1.9	
Gape width	34.6–45.3	40.3	2.6	37.9-44.0	41.5	1.8	38.7-44.9	42.9	1.9	
Pulvinus width	25.7–29.5	27.5	1.0	28.5-31.8	29.7	0.9	29.2–33.9	31.5	1.9	
Pulvinus length	17.8–22.3	19.8	1.1	20.5–25.2	23.2	1.5	23.2–27.3	24.4	1.1	

Diagnosis. Garra panitvongi is easily distinguished from all other species of Garra by the red-orange color of the caudal fin and posterior one-fourth of the body (Fig. 3), and a pointed proboscis with a blue stripe on each side from the anterior margin of the orbit to the tip of the proboscis and with the stripes forming a V-shape (Fig. 4). It further differs from G. notata and G. salweenica, the only other species of Garra in the Salween River basin with a proboscis, by lacking conspicuous black spots at the base of the dorsal fin and large black spots or bands on the caudal fin. It further differs from G. salweenica in having fewer pectoral rays (14–15 vs.17–18).

Description. Morphometric data in Table 3, meristic data in Table 4, shape and color in Figures 3–9. Body elongated, compressed (increasingly so posteriorly); dorsal profile arched to dorsal-fin origin, then descending to caudal peduncle. Ventral profile more-or-less straight to anal-fin origin, then rising to procurrent rays of caudal fin. Procurrent rays abruptly rising from caudal peduncle dorsally and ventrally. Head slightly convex dorsally, flat ventrally, 1.3-1.5 times longer than wide. Snout broadly rounded when viewed dorsally. Transverse lobe short, separated from rest of snout by transverse groove, 2-4 rows of unicuspid tubercles dorsally (Fig. 5). Small tubercles anterior to nostril on each side of snout; 0-1 tubercle on each side of head posterior to nostril. Central surface of snout behind transverse groove depressed, without tubercles.

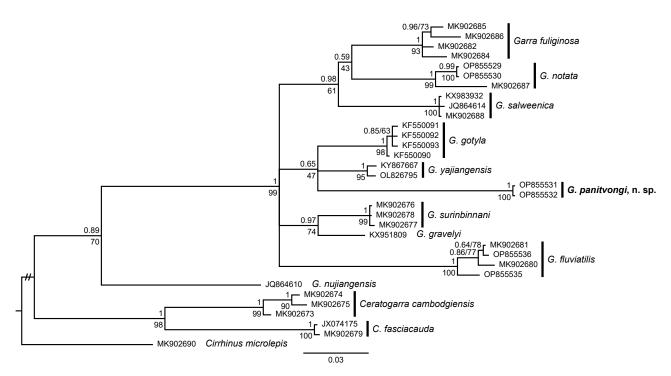


FIGURE 2. Bayesian maximum clade credibility tree inferred from COI sequence data for species of *Garra* in the Salween and Mae Klong River basins, two species of *Ceratogarra*, and the outgroup species *Cirrhinus microlepis*. BI posterior probabilities are shown above branches, ML bootstrap values below.



FIGURE 3. *Garra panitvongi*, THNHM-F021641, 67.8 mm SL, holotype; Thailand: Zami River basin: Kanchanaburi Province: Kasat River, 5.5 km NE Ban Thi Rai Pa [village], 15.40366N, 98.6238E, Kanchanaburi Province, Thailand, 4 February 2020. Upper live, lower preserved.

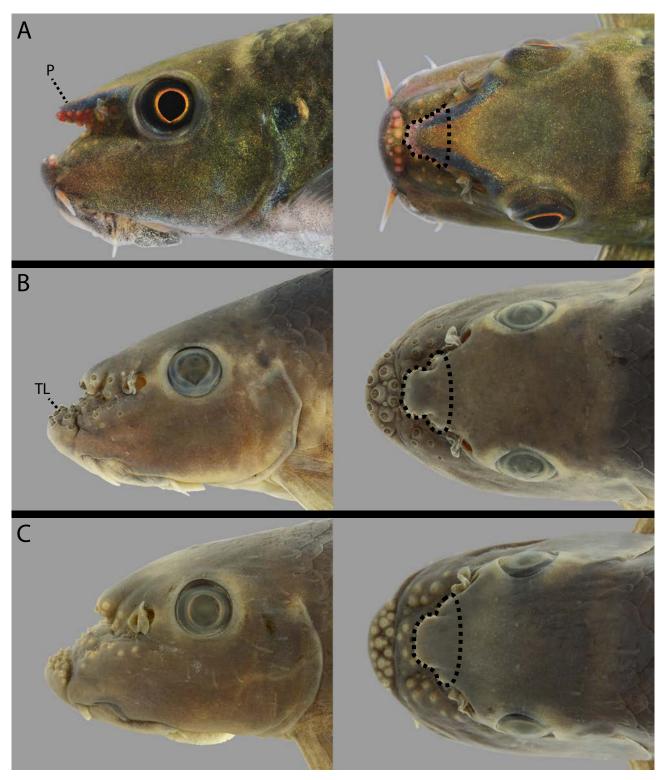


FIGURE 4. Lateral and dorsal views of the head of: (A) *Garra panitvongi* with pointed proboscis, THNHM-F021641, 67.8 mm SL, holotype; (B) *G. notata* with trilobed proboscis, UF 192485, 85.7 mm SL; (C) *G. salweenica* with trilobed proboscis, UF 183853, 101.7 mm SL. P, proboscis; TL, transverse lobe.

Proboscis (Fig. 4) triangular, pointed anteroventrally and separated from depressed rostral surface by deep cleft; 1-2 rows of small tubercles along rim, its underside with 5-6 poorly organized rows of small to medium tubercles (tubercles largest medially); no tubercles on dorsal surface. Eye large, placed dorsolaterally in middle of head; iris with small ventral notch.

TABLE 4. Meristic data for *Garra panitvongi, G. notata,* and *G. salweenica* (data from specimens as in Table 3).

	G. panitvongi n=21		G. no	otata	G. salweenica		
_			n=	13	n=11		
	range	<u>mode</u>	<u>range</u>	<u>mode</u>	range	<u>mode</u>	
Dorsal rays	81/2-91/2	81/2	81/2	81/2	81/2	81/2	
Anal rays	$4\frac{1}{2}-5\frac{1}{2}$	5½	5½	5½	5½	5½	
Pectoral rays	15–16	16	14–16	16	17–18	17	
Pelvic rays	8–9	9	8–9	9	8–9	9	
Branched caudal fin rays	16–18	17	17	17	17	17	
Procurrent caudal rays	4–5	4	3	3	3	3	
Lateral-line scales	29-31	30	31–33	33	31–32	32	
Pores on caudal fin	2–3	2	2	2	2	2	
Circumpeduncular scales	16	16	16	16	16	16	
Predorsal scales	9–10	9	10-11	11	10-11	10	
Scales lateral line to dorsal fin	4	4	4	4	4	4	
Scales lateral line to anal fin	4	4	4	4	4	4	



FIGURE 5. Tubercles on transverse lobe of: (A) *Garra panitvongi*, UF 248982, 110.8 mm SL, paratype, with one cusp on each tubercle; (B) *G. notata*, UF 192485, 99.6 mm SL, with 1–4 cusps on tubercles; (C) *G. salweenica*, UF 183853, 78.2 mm SL, with 1–2 cusps on tubercles

Rostral cap large, crenulated, with wide papillated margin, joined to labella posteriorly (Fig. 6). No upper lip. Upper jaw incompletely covered by rostral cap. Gular disc shorter than wide; torus covered by small papillae, separated from pulvinus (central pad) by deep groove; labrum a papillated flange. Two pairs of barbels; rostral barbel extending to free edge of rostral cap; maxillary barbel shorter.

Dorsal fin with 8½–9½ (usually 8½) branched rays, distal margin slightly concave, origin closer to snout tip than to caudal-fin base, far in front of pelvic-fin origin; 1st branched ray about as long as head. Anal fin with 4½–5½ (usually 5½) branched rays; origin slightly closer to caudal-fin origin than to pelvic–fin origin; distal margin straight to slightly concave; tip extending nearly to caudal-fin base when adpressed. Caudal fin shallowly forked (<50% length) with 16–18 (usually 17; 9 upper, 8 lower) branched rays; tips of caudal lobes rounded to slightly pointed, upper lobe slightly longer than lower lobe; procurrent caudal rays forming low dorsal and ventral keels. Pectoral fin with 15–16 (usually 16) rays, reaching past midway from origin to pelvic–fin origin. Pelvic fin with 8–9 (usually 9) rays, reaching past midway from origin to anal-fin origin, surpassing anus. Lateral line complete with 29–31 (usually 30) scales, 2–3 (usually 2) pored scales on caudal fin. Scales in transverse row between dorsal-fin origin and lateral line 4, between lateral line and anal-fin origin 4. Predorsal scales 9–10 (usually 9). Circumpeduncular scales 16. Scales absent or embedded on breast (Fig. 7).

Osteological features. Median ridge present on rostral surface of frontals; frontals strongly arched downward; preorbital length (vertical distance from anterior tip of premaxillae to anterior margin of orbit) shorter than orbital diameter (Fig. 8). Abdominal vertebrae 19, caudal vertebrae 12, total vertebrae 31 (N=2 specimens).

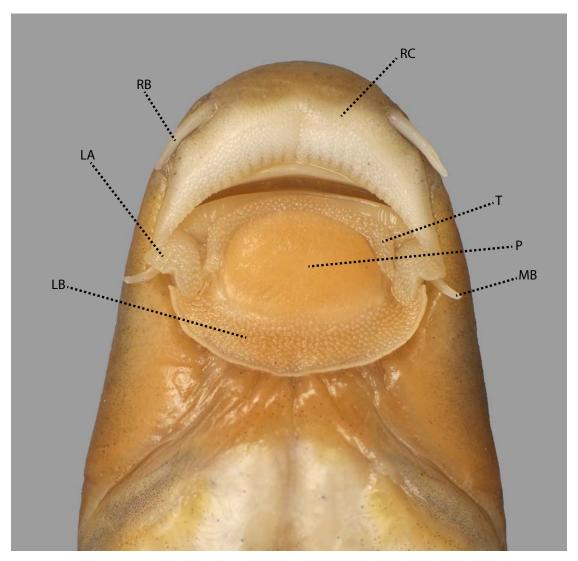


FIGURE 6. Mouth and gular disc of *Garra panitvongi*, UF 248982, 75.9 mm SL. LA, labellum; LB, labrum; MB, maxillary barbel; P, pulvinus; RB, rostral barbel; RC, rostral cap; T, torus.

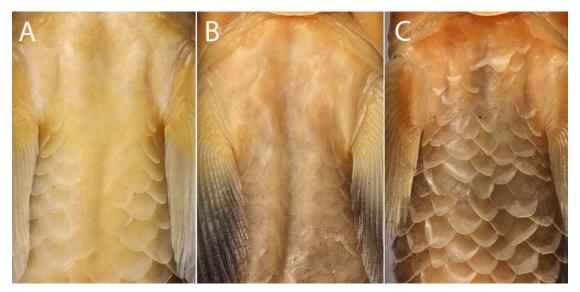


FIGURE 7. Scalation of breast of: (A) *Garra panitvongi*, UF 248982, 103.5 mm SL, paratype, exposed scales absent anteriorly on breast; (B) *G. notata*, UF 192485, 86.5 mm SL, exposed scales absent anteriorly on breast; (C) *G. salweenica*, UF 183853, 70.6 mm SL, anterior area of breast fully scaled.

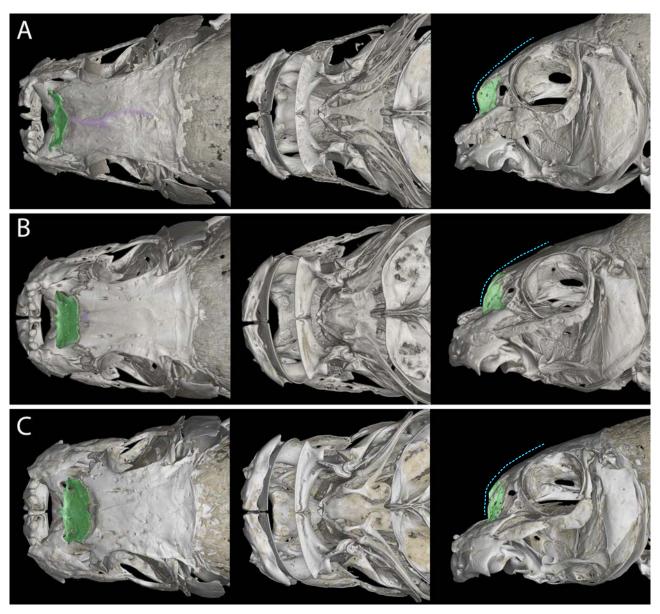


FIGURE 8. Dorsal, ventral, and lateral CT scans of (A) *Garra panitvongi*, UF 248982, 75.9 mm SL; (B) *G. notata*, UF 192485, 95.6 mm SL; (C) *G. salweenica*, UF 183853, 103.6 mm SL. Median frontal ridge highlighted in purple (absent in *G. salweenica*), ethmoid complex in green, shape of frontal slope and ethmoid complex indicated in blue in lateral view.

Color in life. Head and anterior body dark greenish brown (Fig. 3); color on body transitions to red-orange starting near level of anus; 6–7 black stripes on side, pale anteriorly, increasingly bold posteriorly; 3 middle stripes continue onto caudal fin. First lateral-line scale black; area above origin of pectoral fin dusky black in some individuals; 3–5 scales with bright yellow spots scattered on anterior half of side of body. Iris mostly black, inner rim yellow. Distinct blue stripe (blue-gray to gray on preserved specimens) from anterior margin of orbit to tip of proboscis on each side, running over dorsal surface just behind rim of proboscis; stripe tapering and paler anteriorly; stripes of two sides forming a V-shape in dorsal view. Rim and underside of proboscis red-orange. Tubercles on underside of proboscis light-red to orange, tubercles on transverse lobe and head pink to yellow. Rostral barbel orange; maxillary barbel clear to light orange. All fins except caudal clear to dusky yellow green with melanophores along rays and onto membranes. Six–7 small black spots at base of dorsal fin. Caudal fin orange to red with melanophores concentrated along rays. No black bands or large black spots on caudal fin lobes. Juvenile (N=1, 38.5 mm SL) with dusky black stripes on side of body, stripes darkest posteriorly (Fig. 9A).



FIGURE 9. Lateral views of juveniles of: (A) *Garra panitvongi*, UF 245312, 38.5 mm SL; (B) *G. notata*, UF 192354, 42.7 mm SL; (C) *G. salweenica*, UF 183853, 44.4 mm SL.

Etymology. The specific name *panitvongi*, a noun in genitive case, is applied in recognition of the tremendous contributions made by Dr. Nonn Panitvong to our knowledge of fishes of Thailand, in particular through his book, "A Photographic Guide to Freshwater Fishes of Thailand" (Panitvong 2020).

Distribution and habitat. *Garra panitvongi* appears to be restricted to the Ataran River drainage in southeastern Myanmar and western Thailand (Fig. 10). Specimens were collected in swift rocky riffles in the Zami River drainage in Kayin State in Myanmar, and in the Kasat River in Kanchanaburi Province, Thailand (Fig. 11). The Kasat River in Thailand flows west to become the Zami River in Myanmar, and the Zami River joins the Ataran River near Chaunghanakwa. The Ataran River joins the Gyaing River which joins the much larger Salween River near the city of Mawlamyine, only about 30 km from the mouth of the Salween River in the Gulf of Martaban and the Andaman Sea.

Discussion

As noted above, Fricke et al. (2022) list 189 species of *Garra* making it one of the most diverse genera of fishes in the world. Even with such high diversity, *G. panitvongi* is easily distinguished from all other species by the red-orange

color of the caudal fin and posterior one-fourth of the body, and the pointed proboscis with a bright blue stripe on each side forming a V-shape in dorsal view. The proboscis is moveable vertically, at least in large individuals and perhaps seasonally, as demonstrated in videos of aquarium-held fishes on YouTube. Although usually adpressed to the snout, the tip of the proboscis can be curled upward to display the bright red-orange color on the underside. Curling happens in the presence of other individuals, presumably as a threat.

The skull of *G. panitvongi* (N=3 specimens), compared to those of *G. notata* (N=1) and *G. salweenica* (N=2) is modified, presumably to accommodate the long and downward-sloping proboscis and perhaps its mobility. The rostral-medial area of the frontals is curved downward in *G. panitvongi*, and a mid-sagittal ridge in the rostral portion of the frontals is much higher in *G. panitvongi* than in *G. notata* and absent in *G. salweenica* (Fig. 8). The ethmoid complex is greatly reduced dorsoventrally. The preorbital length (vertical distance from the anterior tip of the premaxillae to the anterior margin of the orbit) is shorter than the diameter of the orbit in *G. panitvongi*, and longer in *G. notata* and *G. salweenica*. The ridge and adjacent concavities may accommodate musculature necessary to move the proboscis.

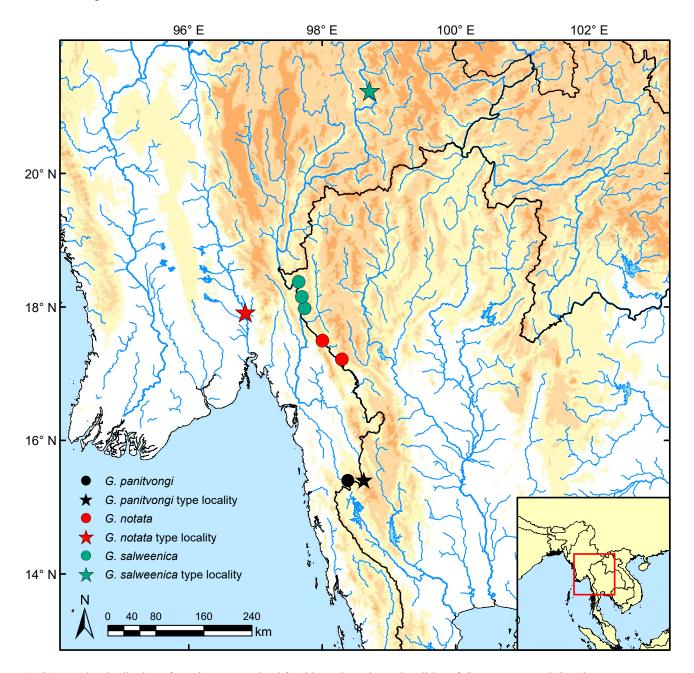


FIGURE 10. Distribution of specimens examined for this study and type localities of Garra notata and G. salweenica.

Five other species of *Garra* are known to occur in the Salween River basin: *G. notata*, *G. imberbis*, *G. gravelyi*, *G. salweenica*, and *G. nujiangensis*. Unlike *G. panitvongi*, *G. imberbis* and *G. nujiangensis* lack a proboscis on the snout, lack barbels (at least as adults), have >40 lateral-line scales, and appear to be restricted to the upper Salween basin (Menon, 1964; Talwar & Jhingran, 1991; Chen et al. 2009; Nebeshwar & Vishwanath 2017; Sun et al. 2018).

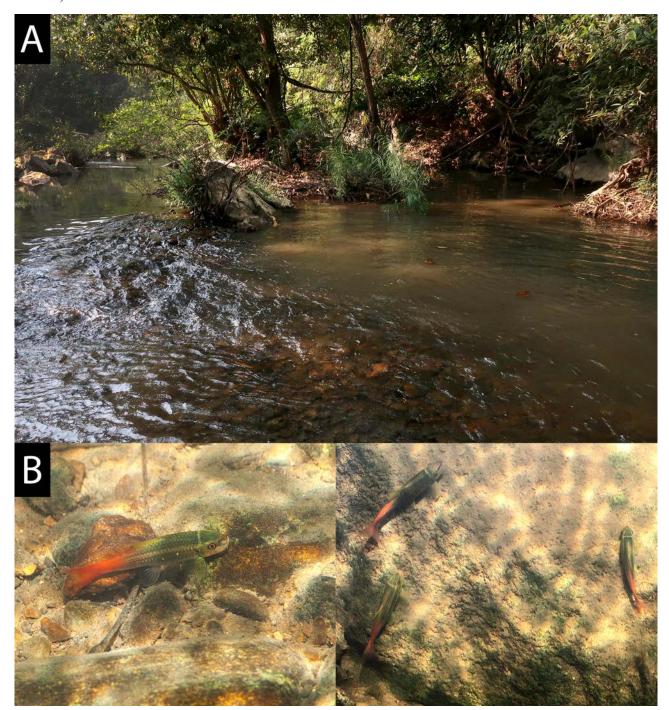


FIGURE 11. (A) Type locality of *Garra panitvongi* and (B) *G. panitvongi* in Kasat River, Kanchanaburi Province, Thailand. Photos in B by Nonn Panitvong.

The separation of *G. nujiangensis* from all other species of *Garra* in the phylogenetic analysis (Fig. 2) parallels the result of Sun et al. (2018) in which *G. nujiangensis* was found to be sister *to G. imberba* and separated from all other species of *Garra*. Given its close relationship to *G. imberba*, *G. nujiangensis* is transferred to *Ageneiogarra* Garman 1912, recognized as a valid genus by Yang et al. (2012), and which includes *A. imberba*, *A. incisorbis* (Zheng et al., 2016), *A. micropulvinus* (Zhou et al., 2005), *A. nujiangensis* and *A. theunensis* (Kottelat 1998).

Garra gravelyi was described from a single specimen by Annandale (1919) as having a transverse groove, but no mention was made of a proboscis, and no proboscis is shown on a drawing of an adult male, 112 mm in length (Annandale 1919:pl.2, fig. 3). Annandale also noted 8 branched dorsal rays, 14 pectoral rays, 8 pelvic rays, 5 branched anal rays, and 3.5 scales above the lateral line, 4 barbels, and a dark horizontal lunate mark on the caudal peduncle. In contrast, Hora (1921) examined the type and four other specimens, and described the type as having an indistinct proboscis, "a squarish area in front of nostrils." Menon (1964) examined five specimens (perhaps the same five specimens as Hora), including the type, and noted a small proboscis, and that the transverse lobe at the tip of the snout and the tip of the proboscis were "scarcely tuberculated." He also described the two pairs of barbels as shorter than the eye diameter and noted 32-34 lateral-line scales. Kullander and Fang (2004) described G. gravelyi as an elongated species with a proboscis and 12 scales around the caudal peduncle. Zhang (2006) reported G. gravelyi from the Manipur River basin as well as from Inle Lake in the Salween basin and described it as having a "poorly developed proboscis that is represented by a truncate area in front of the nostrils," 3½-4½ scales above the lateral line, 8–9 predorsal scales, a black spot above the gill opening, and black spots at the base of the dorsal fin. Nebeshwar & Vishwanath (2017) also described G. gravelyi as a species with a proboscis based on observations of Zhang (2006). Based on the information in these descriptions, G. panitvongi is distinguished from G. gravelyi, by having, in addition to color differences, a large pointed proboscis, 29–31 lateral-line scales, 15–16 pectoral rays, and 16 scales around the caudal peduncle. Garra panitvongi also lacks a lunate mark on the caudal peduncle.



FIGURE 12. Lateral views of: (A) *Garra notata* (live), UF 192334, 58.2 mm SL; (B) *G. salweenica* (preserved), UF 183853, 101.7 mm SL.

Kullander & Fang (2004) suggested that *G. salweenica* may be a junior synonym of *G. notata*, a species for which published information is available on only a few specimens (Blyth 1860, Hora 1921, Menon 1964, Page et al. 2019). Although *G. notata* and *G. salweenica* are similar and have been confused in the literature, they are easy to separate. In contrast to *G. salweenica*, *G. notata* has a black spot at/near the tip on each lobe of the caudal fin vs. a black band on each lobe, usually 6 large black spots at the base of the dorsal fin with no or little black pigment extending along the dorsal rays vs. usually 4 small black spots at the base of the dorsal fin with black pigment extending along the dorsal-fin rays (Fig. 12), scales mostly embedded between the pectoral fins vs. scales fully exposed on the breast (Fig. 7), 14–16 vs. 17–18 pectoral rays, and 21 (vs. 20) abdominal and 33 (vs. 32) total vertebrae.

Garra notata, in contrast to G. panitvongi, has a trilobed proboscis with lateral lobes evident on large individuals (Fig. 4), a black spot at/near the tip on each lobe of the caudal fin—at least in adults, usually 6 (only 4 in Fig. 12) large black spots at the base of the dorsal fin (present as early as 40 mm SL, Fig. 9), and 21 (vs. 19) abdominal and 33 (vs. 31) total vertebrae (N=1).

Garra salweenica, in contrast to G. panitvongi, has a trilobed proboscis with lateral lobes evident on large individuals (Fig. 4), a diagonal black band on each lobe of the caudal fin of most adults (Fig. 12) and in some juveniles as early as 44 mm SL (Fig. 9), scales on the breast exposed (Fig. 7), caudal fin deeply forked (>50% length), 17–18 (vs. 15–16) pectoral rays, and 20 (vs. 19) abdominal and 32 (vs. 31) total vertebrae (N=2). Juveniles have a large black spot (vs. no spot) on the caudal peduncle.

The morphology of tubercles on the transverse lobe of specimens examined varied interspecifically, with *G. panitvongi* having unicuspid tubercles, *G. salweenica* having mostly unicuspid tubercles but larger tubercles sometimes with two cusps, and *G. notata* having tubercles with 1–4 cusps and more cusps on larger tubercles (Fig. 5). Although potentially of taxonomic significance, variation in development of tubercles in relation to age, body size and season is not known.

Comparative material

Garra notata—Thailand: UF 192334, 3, Tak Province, Tha Song Yang District, Moei River at mouth of Mae Salit Noi Creek, 17.45208N, 98.03817E, 26 Dec. 2018; UF 192354, 5, Tak Province, Tha Song Yang District, Moei River at mouth of Mae Kho Creek, 17.49463N, 98.00428E, 26 Dec. 2018; UF 192485, 5, Tak Province, Tha Song Yang District, Mae Khamu Luang Creek, 17.21483N, 98.29405E, 25 Dec. 2018. Garra salweenica—Thailand: UF 183843, 3, Mae Hong Son Province, tributary Salween River, 18.015N, 97.72278E, 06 Jan. 2012; UF 183853, 5, Mae Hong Son Province, Salween River at mouth of Mae Nam Sakoep, 18.151N, 97.69467E, 05 Jan. 2012; UF 183869, 1, Mae Hong Son Province, Salween River at mouth of small tributary, 18.374N, 97.64767E, 06 Jan. 2012; UF 188298, 2, Mae Hong Son Province, Sop Moei District, Sam Laep River at Ban Mae Sam Laep, 17.97826N, 97.73903E, 12 Jan. 2016.

Acknowledgements

We thank Duangsamorn B. Boyd, John M. Pfeiffer, Gabriel A. Somarriba, Apinun Suvarnaraksha, Thanasit Punkumsing, Kyaw Aung, and Milton Tan for assistance in the field, and the Thailand Department of Fisheries (permit #6178) and the National Research Council of Thailand (permit #11880) for permission to collect fishes. The animal care and use license for scientific research was U1-07864-2561 (COA.No.MU-IACUC 2019/007) for the project "Fishes of the Mae Klong Basin, Thailand." This project was funded in part by the U.S. National Science Foundation through a Rules of Life award (uROL) (NSF 1839915), a Planetary Biodiversity Inventory award (NSF-DEB 0315963), and a Research Infrastructure award (NSF-DBI 2210415). Scans were provided by oVert (NSF-DBI 1701714). Institutional records were searched through iDigBio, funded by the NSF Advancing Digitization of Biodiversity Collections program (NSF-EF 1115210, NSF-DBI 1547229).

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