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A taxonomic revision of *Parachela* with descriptions of two new species (Cypriniformes: Xenocyprididae)

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Abstract

The taxonomy of the *Parachela–Oxygaster–Macrochirichthys* clade of Xenocyprididae has been confused since the original descriptions of *Parachela oxygastroides* and *Parachela hypophthalmus* in the mid-19th century. The confusion seems attributable to the substantial intraspecific variation in color and other morphological characteristics of species of *Oxygaster* and *Parachela*. Morphological data on 401 specimens from throughout the range of *Parachela* and molecular phylogenetic analyses indicate that six available species names for *Parachela* are valid: *Parachela cyanea*, *P. hypophthalmus*, *Parachela ingerkongi*, *Parachela johorensis* (removed from the synonymy of *P. oxygastroides*), *P. oxygastroides*, and *Parachela williaminae*. In addition, two new species of *Parachela*, *Parachela melanosticta* and *Parachela microlepis*, are described. *Chela pointoni* is a synonym of *P. oxygastroides*, not a valid species of *Oxygaster* as previously hypothesized, and *Parachela maculicauda* is a synonym of *Parachela johorensis*. Considerable morphological and genetic variation is present in all well-sampled species of *Parachela*.

KEYWORDS
Macrochirichthys, *Oxygaster*, Phylogenetics, Southeast Asia, Systematics

1 | INTRODUCTION

Parachela, *Oxygaster*, and *Macrochirichthys* form a clade characterized by a highly compressed body, a ventral keel from the head to the anus, cranial intermuscular bones, and long pectoral fins (Figures 1 and 2) capable of rotating out from the body. The keel is formed anteriorly by enlarged coracoids that are juxtaposed ventrally and strongly concave posteriorly (Figure 2). The coracoids are followed posteriorly and along the venter by overlapping or juxtaposed scales and tendinous tissue that extend the keel to the anus (Howes, 1979). The mechanics of the elevated cranium and forward rotation of the pectoral girdle and fins (the rotation is common in preserved specimens) are discussed by Howes (1979). All three genera are found in the Mekong, Chao Phraya, Mae Klong, and smaller river basins in mainland Southeast Asia, the Malay Peninsula, Borneo, and Sumatra. *Parachela* is found in Java, and *Macrochirichthys* is found in the Yunnan Province of China (Wu, 1964).

The hypothesis based on osteological data by Howes (1979) that these three genera form a monophyletic group was supported with molecular data by Tang, Lumbantobing, and Mayden (2013) and Tang, Agnew, et al. (2013). All three studies found *Oxygaster* to be sister to *Macrochirichthys* + *Parachela*. *Macrochirichthys* is monotypic and easily distinguished from *Parachela* and *Oxygaster* by having the dorsal- and anal-fin origins on the posterior one-third of the body, a much larger size, to 80 (vs. <20) cm SL, more than 100 (vs. <65) lateral-line scales, 50–51 (vs. 35–43) vertebrae, and a large black spot at the base of the caudal fin (Figure 1). The cranial intermuscular bones, articulating with the epioccipital and horizontally aligned with the vertebral column (Figure 2), are much longer in *Macrochirichthys* than in *Parachela* or *Oxygaster*, extending over one-half of the body length.

FIGURE 1 Lateral views of *Macrochirichthys*, *Oxygaster*, and *Parachela*. (a) *Macrochirichthys macropterus*, UF 188048, 92.0 mm SL, Mahakam River basin, East Kalimantan Province, Indonesia. (b) *Oxygaster anomalura*, UF 243498, 124.0 mm SL, Vajiralongkorn Reservoir, Kanchanaburi Province, Thailand. (c) *Parachela melanosticta*, UF 248183, 58.9 mm SL, Mae Klong River, Kanchanaburi Province, Thailand.

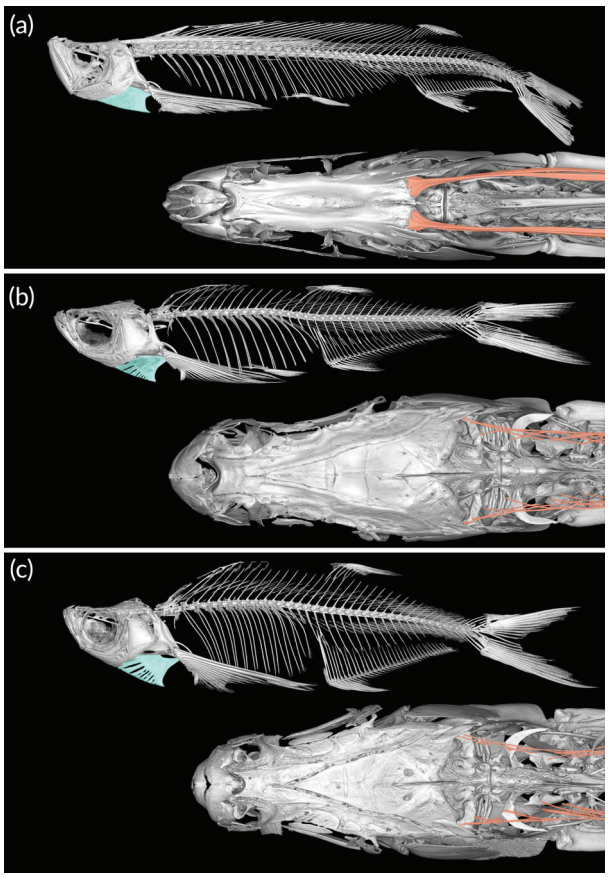

FIGURE 2 Lateral body and dorsal skull computed tomography (CT) scans of the following species: (a) *Macrochirichthys macropterus*, UMMZ 155564, 255.0 mm SL, Musi River basin, South Sumatra Province, Indonesia; (b) *Oxygaster anomalura*, UF 237316, 52.7 mm SL, Songkhram River, Sakon Nakhon Province, Thailand; and (c) *Parachela williaminae*, UF 245409, 63.9 mm SL, Chi River, Ubon Ratchathani Province, Thailand. Cranial intermuscular bones in orange and coracoids in blue.

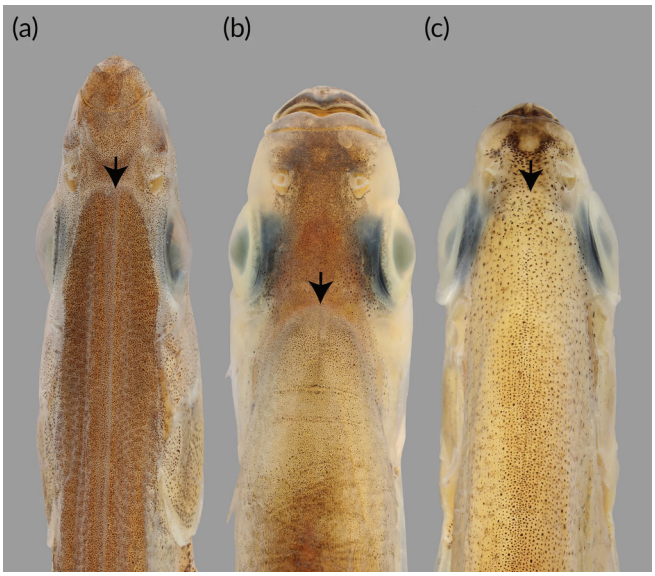

FIGURE 3 Dorsal views of nape and head of *Macrochirichthys*, *Oxygaster*, and *Parachela*. Arrows indicate anterior extent of epaxial musculature in (a) *Macrochirichthys macropterus*, UF 188048, 92.0 mm standard length (SL), Mahakam River basin, East Kalimantan Province, Indonesia; (b) *Oxygaster anomalura*, UF 243498, 124.0 mm SL, Vajiralongkorn Reservoir, Sangkhla Buri Province, Thailand; and (c) *Parachela williaminae*, UF 245409, 63.9 mm SL, Chi River, Ubon Ratchathani Province, Thailand.

In contrast to the distinctiveness of *Macrochirichthys*, *Oxygaster*, and *Parachela* can be difficult to distinguish, and the taxonomy of these two genera has been confused. In *Oxygaster*, the epaxial musculature extends anteriorly only to the posterior margin of the eye (Figure 3), and there are 14–15 pectoral-fin rays, 8 pelvic-fin rays, and 43 vertebrae. In *Parachela*, the epaxial musculature extends at least to the middle and usually past the anterior margin of the eye, and there are usually 11–13 pectoral-fin rays, 6–7 pelvic-fin rays, and 35–41 vertebrae. The epaxial musculature also extends to the front of the eye in *Macrochirichthys*.

Two species of *Oxygaster* typically are recognized (e.g., Taki et al., 2021): one as *Oxygaster anomalura*, described from the island of Java by van Hasselt (1823), and the other as *Oxygaster pointoni*, described as *Chela pointoni* from Chiang Mai, Thailand by Fowler (1934). *O. anomalura* is a valid name for a species of *Oxygaster*, but *C. pointoni* is a synonym of *Parachela oxygastroides* (Bleeker, 1852), as discussed below. Karmakar (2000) also recognized *Chela argentea*, described from the Bowany River, India, by Day (1867), as a species of *Oxygaster* occurring in the Himalayas. However, Bănărescu (1971) examined the syntypes of *C. argentea* and synonymized the name with *Salmostoma acinaces* (Valenciennes *in* Cuvier & Valenciennes, 1844). *Oxygaster* does not occur west of the Chao Phraya and Mae Klong basins of Thailand.

Seven species-group names of *Parachela* are listed as valid by Fricke, et al. (2023): *P. oxygastroides* (Bleeker, 1852), originally described from Indonesia; *Parachela hypophthalmus* (Bleeker, 1860) from Sumatra; *Parachela siamensis* (Günther, 1868) from the Chao Phraya River basin in central Thailand; *Parachela maculicauda*

(Smith, 1934) from Songkla Province in peninsular Thailand; *Parachela williaminae* Fowler, 1934 from the Mekong River in northern Thailand; *Parachela ingerkongi* (Bănărescu, 1969) from the Tawau River in Sabah, Malaysia; and *Parachela cyanea* Kottelat, 1995 from the Kapuas River basin of West Kalimantan, Indonesia. However, *Parachela* has received little attention, and diversity within *Parachela* is not adequately conveyed by the current taxonomy or descriptions of distributions. The objective of this paper is to improve the taxonomy and information on the distributions of *Parachela*, including by description of two scientifically undescribed species.

2 | MATERIALS AND METHODS

Fishes were collected with nets and hook-and-line fishing, fixed in 10% formalin and stored in 70% ethanol. Fin clips were taken from freshly captured fishes and preserved in 95% ethanol for DNA extraction. Photographs of live and preserved specimens were taken with Canon EOS 7D and R cameras. All images of live specimens were taken soon after capture. Images were edited using Adobe Photoshop CC 2021 (Adobe, San Jose, CA, USA). X-rays and computed tomography (CT) scans were generated using a Phoenix v|tome|x M scanner (GE Measurement & Control, Boston, MA, USA) at the University of Florida's Nanoscale Research Facility. CT projections were processed using datos|x software v. 2.3 (Baker Hughes, Jacksonville, FL, USA), and anatomy was segmented and visualized using VG StudioMax v. 4.2 (Volume Graphics, Heidelberg, Germany). CT scans can be downloaded from MorphoSource (https://www.morphosource.org) (Table 1). Maps were produced using ArcMap 10.8.1 in ArcGIS (Esri, Redlands, CA, USA). Photos are by the authors unless otherwise noted.

Morphological data were taken on 401 specimens (see Material Examined). Measurements were taken to the nearest 0.1 mm using digital calipers following Hubbs et al. (2004) except for body depth and width, which were measured at the dorsal-fin origin, and predorsal, pre-pectoral, and pre-anal lengths, which were taken from the tip of the snout to the origin of the relevant fin. Lateral-line scale counts exclude those on the caudal fin. Total ray counts are given for paired fins and branched ray counts for unpaired fins. The last ray of the dorsal and anal fins, sharing a pterygiophore with the last branched 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 included the Weberian complex ($N = 4$ vertebrae), and counts of caudal vertebrae began at the vertebra with the hemal spine just anterior to or in contact with the anterior anal-fin pterygiophore and included the urostyle complex ($N = 1$ vertebra).

Abbreviations for institutional collections follow Sabaj (2023): ANSP—Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA; AUM—Auburn University Museum of Natural History, Auburn, AL, USA; BMNH—Natural History Museum, London, England; LSUMZ—Louisiana State University Museum of Natural Science, Baton Rouge, LA, USA; MZB—Bogor Zoological Museum, Cibinong, West Java, Indonesia; NIFI—National Inland Fisheries Institute, Bangkok, Thailand; THNHM—Thailand Natural History Museum, National Science Museum, Pathum Thani, Thailand; RMNH—Naturalis–National Natural History Museum, Leiden, The Netherlands; ROM—Royal Ontario Museum, Toronto, Canada; UF—University of Florida, Florida Museum of Natural History, Gainesville, FL, USA; UMMZ—University of Michigan Museum of Zoology, Ann Arbor, MI, USA; USNM—National Museum of Natural History, Washington D.C., USA; ZRC—Zoological Research Collection, Lee Kong Chian Natural History Museum, Singapore.

TABLE 1 Micro-computed tomography (μCT) scans included in this study and available for download from mophosource.org.

Species	Catalog number	Country/ province or state	Morpho source media ID
Macrochirichthys macropterus	UMMZ 155564	IN, South Sumatra	000458944 000458945
Oxygaster anomalura	UF 161918	IN, Lampung	000474382 000474388
	UF 237316	TH, Sakon Nakhon	000473635 000473639
Parachela hypophthalmus	ROM 38603	IN, West Kalimantan	000458919 000458920
Parachela ingerkingi	CAS-SU 33584	MA, Sabah	000568314 000568315
Parachela johorensis	UF 161726	IN, Lampung	000049142 000049141
Parachela melanostica	UF 243504	TH, Kanchanaburi	000438508 000438523
Parachela microlepis	UF 188502	TH, Udon Thani	000568261 000568265
	UF 247795	TH, Kanchanaburi	000567505 000567509
Parachela oxygastroides	UF 162175	IN, Lampung	000077620 000077604
	UF 167207	IN, South Sumatra	000438516 000438524
	UF 237316	TH, Sakon Nakhon	000473635 000473639
Parachela williaminae	UF 245409	TH, Ubon Ratchathani	000438515 000438531

Note: Sampling locations are available at http://specifyportal.flmnh.ufl.edu/fishes and iDigBio.org. IN, Indonesia; MA, Malaysia; TH, Thailand.

A sheared principal component analysis was conducted in accordance with the protocol in Bookstein et al. (1985) adapted for R (R Core Team, 2023). Nineteen measurements taken from 230 specimens were analysed. Following species identification by morphological examination and molecular analyses, a log-transformed covariance matrix was generated from morphometric data that were centered intraspecifically and regressed on a within-group size factor. The sheared second and third principal components were plotted in R to visualize variation in shape independent of size (Humphries et al., 1981). Individuals could not be sexed using only external characteristics, and sexes were not analysed separately.

Total genomic DNA was extracted using AutoGenPrep 965 (Autogen, Holliston, MA, USA). Mitochondrial cytochrome *c* oxidase subunit 1 (*COI*) and nuclear recombination-activating gene 1 (*RAG1*) were amplified using PCR and sequenced using the following primers: FISH-BCL 5′–TCAACYAATCAYAAAGATATYGGCAC–3′, FISH-BCH 5′– ACTTCYGGGGTGRCCRAARAATCA–3′ (Baldwin et al., 2009), RAG1-F 5′–AGCTGTAGTCAGTAYCACAARATG–3′ (Perdices et al., 2005), and RAG-RV1 5'–TCCTGRAAGATYTTGTAGAA–3′ (Šlechtová et al., 2007). PCR was performed in 10-μL reactions using the following reagents and volumes: H_2O (3.2 μL), genomic DNA (1 μL), Bulk Segregant Analysis (BSA) (0.1 μL), Dimethyl Sulphoxide (DMSO) (0.1 μL), forward and reverse primers 10 nM (0.3 μL each), and GoTaq Hot Start Master Mix (Promega, Madison, WI, USA; 5.0 μL). Bidirectional Sanger sequencing was performed at the National Museum of Natural History's Laboratories of Analytical Biology using an ABI 3730xl Genetic Analyzer (Thermo Fisher, Waltham, MA). Chromatograms were assembled into bidirectional consensus sequences and edited using Geneious v. 6.1.2 (Kearse et al., 2012).

Phylogenetic analysis included our newly generated sequences and previously published data from GenBank (Table 2). No tissues or sequence data were available for *P. cyanea*, *P. hypophthalmus*, or *P. ingerkongi*. Sequences on GenBank labeled *P. hypophthalmus* were misidentifications of *P. johorensis*. Species of *Aphyocypris* were included as out-group taxa based on the phylogenetic

TABLE 2 Voucher specimen and tissue data for sequences included in the molecular phylogeny.

Species	Voucher	Tissue ID	Drainage/ region	GenSeq	GenBank *COI*	GenBank *RAG1*	Source
Aphyocypris chinensis	–	–	?		AB218688	EU292692	Saitoh et al., 2006; Conway et al., 2008
Aphyocypris moltrechti	ASIZP_0801320	–	Taiwan	genseq-4	KU942918	–	Chang et al., 2016
Aphyocypris normalis	CBM ZF 11304; CTOL01619	–	Aquarium	genseq-4	AP011396	EU711123	Tang et al., 2010; Mayden et al., 2008
Macrochirichthys macrochirus	IRKT_039901	–	Mekong	genseq-4	KF410685	–	Direct submission
M. macrochirus	IRKT_039902	–	Mekong	genseq-4	KF410686	–	Direct submission
Oxygaster anomalura	UF 160958	2005_0503	Malay Peninsula	genseq-4	PP856443	PP861072	This study
O. anomalura	UF 243498	ICH_03660	Mae Klong	genseq-4	PP856463	PP861082	This study
O. anomalura	UF 243498	ICH_03671	Mae Klong	genseq-4	PP856465	PP861084	This study
O. anomalura	UF 241493	ICH-04226	Mekong	genseq-4	PP856468	–	This study
O. anomalura	USNM_394000	IM33	Borneo	genseq-4	HQ009869	HQ009863	Tang, Lumbantobing, & Mayden, 2013
O. anomalura	USNM _394000	IM36	Borneo	genseq-4	HQ009870	HQ009864	Tang, Lumbantobing, & Mayden, 2013
O. anomalura	UF 236080	2014_0232	Malay Peninsula	genseq-4	PP856454	PP861079	This study
Parachela johorensis	UF 235881	2006_0577	Sumatra	genseq-4	PP856451	PP861076	This study
P. johorensis	BIF_3646	–	Sumatra	genseq-4	KU692736	–	Dahruddin et al., 2017
P. johorensis	BIF_3647	–	Sumatra	genseq-4	KU692734	–	Dahruddin et al., 2017
P. johorensis	BIF_3648	–	Sumatra	genseq-4	KU692737	–	Dahruddin et al., 2017
P. johorensis	BIF_3753	–	Sumatra	genseq-4	KU692733	–	Dahruddin et al., 2017
P. johorensis	BIF_3754	–	Sumatra	genseq-4	KU692738	–	Dahruddin et al., 2017
P. johorensis	BIF_3755	–	Sumatra	genseq-4	KU692735	–	Dahruddin et al., 2017
P. johorensis	UF 161726	2005–0938	Sumatra	genseq-4	PP856446	–	This study
P. johorensis	UF 161729	2005–0996	Sumatra	genseq-4	PP856447	–	This study
P. johorensis	UF 161729	2005–0997	Sumatra	genseq-4	PP856448	–	This study
P. johorensis	UF 161725	2005–1020	Sumatra	genseq-4	PP856450	–	This study
P. johorensis	UF 185034	SN1	Sumatra	genseq-4	PP856474	–	This study
P. johorensis	UF 185034	SN2	Sumatra	genseq-4	PP856475	–	This study
P. johorensis	UF 160958	2005_0505	Malay Peninsula	genseq-3	PP856444	PP861073	This study
P. johorensis	UF 161733	2005_0842	Sumatra	genseq-4	PP856445	PP861074	This study

TABLE 2 (Continued)

Species	Voucher	Tissue ID	Drainage/ region	GenSeq	GenBank *COI*	GenBank *RAG1*	Source
P. johorensis	UF 161728	2005_1002	Sumatra	genseq-4	PP856449	PP861075	This study
P. johorensis	CBM_ZF_11326	–	Sumatra	genseq-4	HM224181	HM224061	Tang et al., 2010
P. johorensis	Wk3_42	–	Sumatra	genseq-4	MN243487	–	Direct submission
Parachela melanosticta	UF 248183	ICH-03458	Mae Klong	genseq-2	PP856458	–	This study
P. melanosticta	UF 247796	ICH-03502	Mae Klong	genseq-2	PP856461	–	This study
P. melanosticta	UF 235931	2014_0105	Trat	genseq-4	PP856453	PP861078	This study
P. melanosticta	UF 243504	ICH_03663	Mae Klong	genseq-4	PP856464	PP861083	This study
P. melanosticta	UAIC_14167.21	–	Aquarium	genseq-4	HM224180	HM224060	Tang et al., 2010
Parachela microlepis	UF 247795	ICH_03485	Mae Klong	genseq-2	PP856459	–	This study
P. microlepis	UF 248101	ICH_03491	Mae Klong	genseq-2	PP856460	PP861080	This study
P. microlepis	UF 247913	ICH_03503	Mae Klong	genseq-2	PP856462	PP861081	This study
P. microlepis	UF 248209	ICH_03729	Mae Klong	genseq-2	PP856466	PP861085	This study
P. microlepis	UAIC_14269.08	–	Mekong	genseq-4	HM224183	HM224063	Tang et al., 2010
P. microlepis	UF 188502	ICH-00155	Mekong	genseq-4	PP856455	–	This study
P. microlepis	UF 188502	ICH-00156	Mekong	genseq-4	PP856456	–	This study
P. microlepis	UF 248743	ICH-05267	Mekong	genseq-4	PP856470	–	This study
P. microlepis	UF 248743	ICH-05272	Mekong	genseq-4	PP856471	–	This study
P. microlepis	UF 173082	2008_0443	Mekong	genseq-4	PP856452	PP861077	This study
P. microlepis	UF 190644	ICH_01390	Mekong	genseq-4	PP856457	–	This study
P. microlepis	FNP_085	-	?	genseq-4	MK448139	–	Direct submission
Parachela oxygastroides	UF 248531	ICH-03899	Chao Phraya	genseq-4	PP856467	–	This study
P. oxygastroides	UF 248764	ICH-05301	Mekong	genseq-4	PP856472	–	This study
P. oxygastroides	UF 248776	ICH-05327	Chao Phraya	genseq-4	PP856473	–	This study
P. oxygastroides	KP_066802	–	Mekong	genseq-4	MK049435	–	Direct submission
P. oxygastroides	KP_066803	–	Mekong	genseq-4	MK049436	–	Direct submission
P. oxygastroides	UAIC_14175.06	–	Mekong	genseq-4	HM224182	HM224062	Tang et al., 2010
Parachela williaminae	UF 245409	ICH_04367	Mekong	genseq-4	PP856469	PP861086	This study
P. williaminae	IRUM_77041211	–	Mekong	genseq-4	MW343540	–	Direct submission

Note: Locality data in material examined. GenSeq designations follow Chakrabarty et al. (2013), with genseq-3 sequences representing topotypic material.

relationships recovered in Tang, Agnew, et al. (2013). GenSeq designations were assigned following Chakrabarty et al. (2013). Individual loci were aligned in AliView v. 1.28 (Larsson, 2014) using Muscle v. 3.8.31 (Edgar, 2004), and loci were concatenated using FASconCAT-G v. 1.05.1 (Kück & Longo, 2014). A partitioned maximum likelihood (ML) tree was generated using IQ-TREE v. 2.0.3 (Nguyen et al., 2015), with model testing and partitioning scheme determined using the MFP + MERGE option (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017), 1000 ultrafast bootstrap replicates (UFboot; Hoang et al., 2018), and a minimum bootstrap support threshold of 0.5. Mean uncorrected *COI* p-distances between *Parachela* species were calculated using MEGA v. 11.0.13 (Kumar et al., 2018).

2.1 | ETHICAL STATEMENT

Fishes were collected by the authors in Cambodia with permission from the Ministry of the Environment, Cambodia, to Mr. Phanara Thach, in Indonesia with permission from the Research Center, LIPI, Bogor to Dr. Renny Hadiaty, in Malaysia with permission from the Department of Wildlife and National Parks in Peninsular Malaysia to Dr. Siti Azizah Mohd Nor, Universiti Sains Malaysia, Penang, and in Thailand with permission from the Thailand Department of Fisheries and the National Research Council of Thailand to the first author. Methods were approved by the University of Florida Animal Care and Use Committee.

3 | RESULTS

We generated 33 new *COI* sequences and 15 new *RAG1* sequences (Table 2). Our alignment included 55 terminals and had a total length (TL) of 2139 nucleotide positions, 295 of which were parsimony informative. Our concatenated ML phylogeny (−ln L = −6583.603) recovered *Parachela* as monophyletic and *Macrochirichthys* as sister to *Oxygaster* + *Parachela* (Figure 4).

Within *Parachela*, five species-level lineages are recognized (Figure 4) with *P. williaminae* sister to a poorly supported clade containing the other four species. *P. johorensis* and its sister taxon, *P. melanosticta*, n. sp., are separated from one another by a mean *COI* p-distance of 3.9%, and *P. oxygastroides* and its sister species, *P. microlepis*, n. sp., are separated by a mean *COI* p-distance of 11.1% (Table 3).

Two divergent clades of *P. microlepis* are separated from one another by a mean *COI* p-distance of 3.7%. One clade included only samples from the Mekong River basin and a sample from an aquarium; the other included samples from the Mae Klong River basin and from Tonle Sap, Cambodia, which drains into the Mekong River. The two most divergent clades of *P. oxygastroides*, one in the Chao Phraya River basin and the other in the Mekong basin, differed from one another on average by 2.3% (Table 3). These differences and those within *P. melanosticta* are discussed in species accounts.

All species-level lineages identified genetically are diagnosable morphologically (Tables 4 and 5). Meristic data are presented in Tables 6–9, and morphometric data are presented in Tables 10–13. The most significant geographic variation within each species is discussed in species accounts.

In the principal component (PC) analysis of morphometric data for all species of *Parachela* (Figure 5), size accounted for 95.9% of observed variance (on PC1, not plotted). The sheared second and third principal components (PC2 and PC3) accounted for 1.6% and 0.7% of observed variance, respectively. Snout length (−0.47), anal fin-base length (0.47), and anal-fin length (0.44) had the highest loadings on PC2. PC3 was predominantly influenced by body width at dorsal-fin origin (0.88) and to a lesser extent by eye length (−0.25) and snout length (−0.18). *P. microlepis* displayed the highest degree of shape variation compared to other species of *Parachela* along PC2, and *P. ingerkongi*, *P. oxygastroides*, and *P. cyanea* were nonoverlapping with one another. *P. williaminae* overlapped only slightly with the space occupied by *P. ingerkongi* and not at all with *P. cyanea*. Other species broadly overlapped on PC2. No species were separated along PC3, suggesting that body width is highly variable within all species and largely uninformative for distinguishing species.

3.1 | *Parachela* Steindachner, 1881

Parachela Steindachner, 1881a: 100. Type species: *Parachela breitensteinii* Steindachner, 1881a: 100, by monotypy. See also Steindachner, 1881b: 404–405.

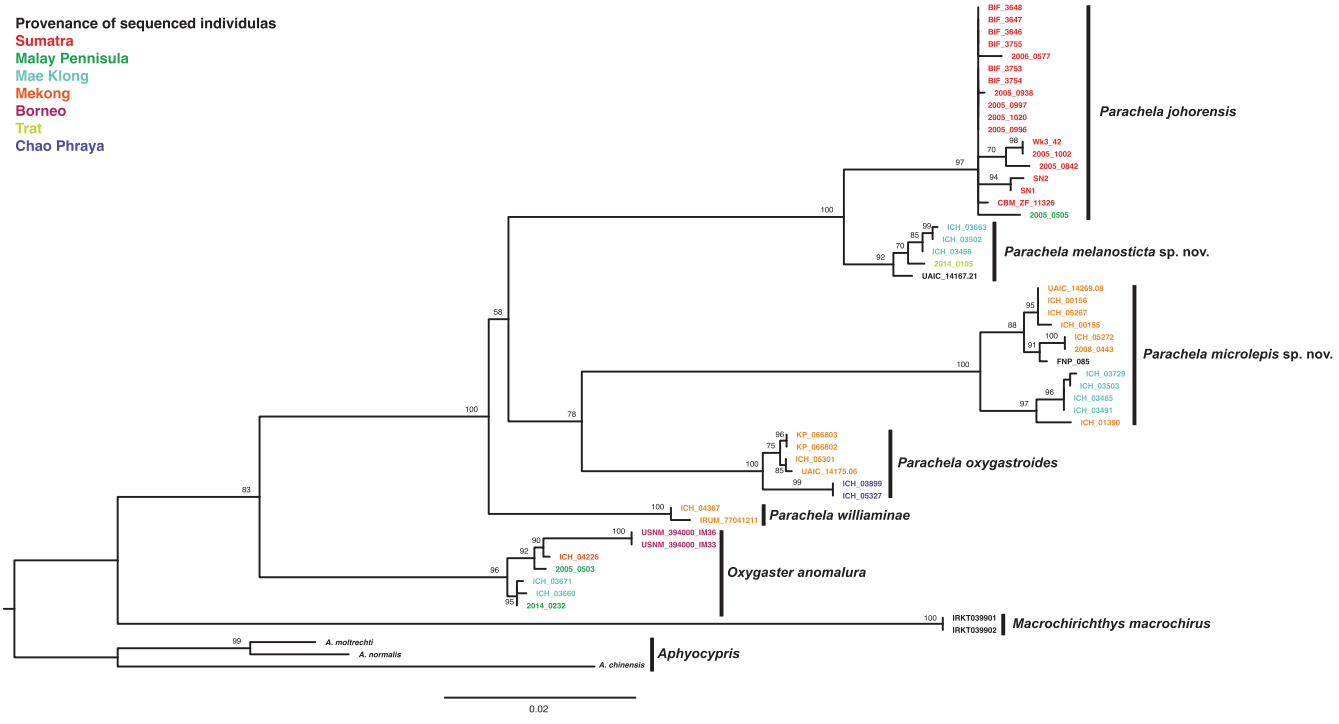

FIGURE 4 Combined (*CO1* + *RAG1*) maximum likelihood phylogenetic reconstruction (−ln L = −6583.603) of *Parachela*, *Oxygastroides*, and *Macrochirichthys*, with *Aphyocypris* as the out-group. Maximum likelihood with branch lengths in numbers of substitutions per site, ultrafast bootstrap values shown on branches, and terminals color coded based on their provenance.

TABLE 3 Mean interspecific cytochrome *c* oxidase subunit 1 (*COI*) p-distances among all analysed species of *Parachela*, with mean intraspecific p-distances in bold on diagonal.

Species	*P. johorensis*	*P. microlepis*	*P. melanosticta*	*P. oxygastroides*	*P. williaminae*
Parachela johorensis	**0.3%**	–	–	–	–
Parachela microlepis	13.5%	**2.3%**	–	–	–
Parachela melanosticta	3.9%	14.1%	**0.9%**	–	–
Parachela oxygastroides	13.2%	11.1%	12.9%	**1.4%**	–
Parachela williaminae	11.8%	12.3%	11.9%	9.8%	**0.5%**

TABLE 4 Distinguishing characteristics of species of *Parachela* in Indochina.

Characteristic	*Parachela oxygastroides* (75)	*Parachela williaminae* (17)	*Parachela johorensis* (58)	*Parachela melanosticta* (53)	*Parachela microlepis* (62)
Black pattern on caudal fin	Dusky black stripes	None	Large black spots	Large black spots	None
Pectoral fin reaches anal fin	No	Yes	Yes	Yes	No
Predorsal profile	Straight or slightly arched	Slightly arched	Strongly arched	Strongly arched	Slightly arched
Dorsal-fin origin to anal-fin origin	Slightly anterior	Distinctly posterior	Over or slightly anterior	Over or slightly anterior	Distinctly posterior
Lateral-line scales	34–45	35–42	38–43	35–44	50–63
Branched anal-fin rays	23–33	30–37	22–29 Usually 24–26	25–32 Usually 27–29	28–38
Pectoral-fin rays	12–14 Usually 13	12–14 Usually 13	11–14 Usually 13	11–13 Usually 12	11–13
Pelvic-fin rays	7	7	7	7	6
Vertebrae	37–39 ($N = 8$)	38–39 ($N = 10$)	36–37 ($N = 6$)	37 ($N = 3$)	38 ($N = 3$)
Maximum SL, mm	163	120	47	59	49

Note: Number of specimens examined in parentheses below name.
Abbreviation: SL, standard length.

TABLE 5 Distinguishing characteristics of species of *Parachela* in Borneo, Java, and Sumatra.

Characteristic	*Parachela oxygastroides* (75)	*Parachela hypophthalmus* (5)	*Parachela johorensis* (58)	*Parachela ingerkongi* (10)	*Parachela cyanea* (8)
Black pattern on caudal fin	Dusky black stripes	Dusky black stripes	Large black spots (variable)	Dusky black stripes	Black blotch at base
Pectoral fin reaches anal fin	No	Yes	Yes	No	Yes
Predorsal profile	Straight or slightly arched	Straight or slightly arched	Strongly arched	Straight or slightly arched	Straight or slightly arched
Dorsal-fin origin to anal-fin origin	Slightly anterior	Over or slightly posterior	Over or slightly anterior	Over or slightly posterior	Over or slightly anterior
Lateral-line scales	34–44	45–59	38–45	40–42	36–39
Branched anal-fin rays	25–31	23–32	24–30 Usually 25–27	29–33	23–26
Pectoral-fin rays	12–14 Usually 13	12–14	12–14 Usually 13	14–15	14
Pelvic-fin rays	7	7	7	7	7
Vertebrae	37–39 ($N = 8$)	37–38 ($N = 4$)	36–37 ($N = 6$)	40–41 ($N = 6$)	35–36 ($N = 5$)
Maximum SL, mm	163	130	47	95	50

Note: Number of specimens examined in parentheses below name. Bold indicates total values.
Abbreviation: SL, standard length.

TABLE 6 Numbers of branched anal-fin rays in *Parachela*.

Species	Basin/region	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	*N*	Mean	SD
Parachela microlepis																					
	Mae Klong											2	1		5	1	1		10	34.5	1.6
	Chao Phraya											2	3	1	5			1	12	34.2	1.7
	Mekong							4	2	3	8	5	4	1		1			28	31.1	1.9
	TS, ST[a]							1	1	4		3	3						12	31.0	1.7
	Total							**5**	**3**	**7**	**8**	**12**	**12**	**2**	**10**	**2**	**1**	**1**	**62**	**32.2**	**2.4**
Parachela hypophthalmus	Borneo		**1**	**1**	**1**	**6**	**8**	**11**	**3**	**3**	**1**	**1**							**36**	**27.6**	**1.8**
Parachela williaminae	Chao Phraya											1	2	2	2		1		8	34.1	1.6
	Mekong									1			4	1	3				9	33.4	1.6
	Total									**1**		**1**	**6**	**3**	**5**		**1**		**17**	**33.8**	**1.6**
Parachela oxygastroides	Indonesia		1			1	3	6	1	3	9	2	2						28	29.6	2.3
	Chao Phraya				4	4	7	7	2	3									27	27.3	1.5
	Mekong			1	2	4	7	12	2	1									29	27.3	1.3
	Malay Pen.				3	2	6	3			1								15	26.9	1.5
	Total		**1**	**1**	**9**	**11**	**23**	**28**	**5**	**7**	**10**	**2**	**2**						**99**	**27.9**	**2.0**
Parachela ingerkongi	Borneo								**1**		**1**	**4**	**4**						**10**	**32.0**	**1.2**
Parachela johorensis	Malay Pen.	1	2	3	6	3	1		2										18	25.2	1.9
	Indonesia			1	7	12	9	3	3	1									36	26.4	1.2
	Total	**1**	**2**	**4**	**13**	**15**	**10**	**3**	**5**	**1**									**54**	**26.1**	**1.7**
Parachela melanosticta	Mae Klong					3	7	12	10	2	1								35	28.1	1.2
	Mekong				3	2	7	1				1							14	26.9	1.7
	Bangpag., Trat				1	2		1											4	26.3	1.3
	Total				**4**	**7**	**14**	**14**	**10**	**2**	**1**	**1**							**53**	**27.6**	**1.5**
Parachela cyanea	Borneo		**4**	**5**	**12**	**8**													**29**	**24.8**	**1.0**

Note: Bold indicates total values.

[a]Tonle Sap and Stung Treng.

TABLE 7 Numbers of pectoral-fin rays in *Parachela*.

Species	River basin/region	11	12	13	14	15	*N*	Mean	SD
Parachela microlepis	Mae Klong	4	5	1			10	11.7	0.7
	Chao Phraya	5	3	1			9	11.6	0.7
	Mekong	4	20	4			28	12.0	0.5
	TS, ST[a]	2	10				12	11.8	0.4
	Total	**15**	**38**	**6**			**59**	**11.8**	**0.6**
Parachela hypophthalmus	Borneo		**15**	**15**	**5**		**35**	**12.7**	**0.7**
Parachela williaminae	Chao Phraya		1	7			8	12.9	0.4
	Mekong		1	5	1		7	13.0	0.6
	Total		**2**	**12**	**1**		**15**	**12.9**	**0.5**
Parachela oxygastroides	Indonesia		7	17	3		27	12.7	0.6
	Chao Phraya		7	10	1		18	12.7	0.6
	Mekong		3	19	2		24	13.0	0.4
	Malay Peninsula		1	12			13	12.9	0.3
	Total		**18**	**58**	**6**		**82**	**12.9**	**0.5**
Parachela ingerkongi	Borneo				**7**	**3**	**10**	**14.3**	**0.5**
Parachela johorensis	Malay Peninsula	1	4	21	1		27	12.8	0.6
	Indonesia		13	26	2		41	12.7	0.5
	Total	**1**	**17**	**47**	**3**		**68**	**12.8**	**0.5**
Parachela melanosticta	Mae Klong	3	25	7			35	12.1	0.5
	Mekong	1	4	9			14	12.6	0.6
	Bangpakong, Trat		4				4	12.0	0.0
	Total	**4**	**33**	**16**			**53**	**12.2**	**0.6**
Parachela cyanea	Borneo				**8**		**8**	**14.0**	**0.0**

Note: Bold indicates total values.
[a]Tonle Sap and Stung Treng.

Grandisquamachela Fowler, 1934: 111 (as a subgenus of *Parachela* Steindachner, 1881a, 1881b). Type species: *P. williaminae* Fowler, 1934: 111, by original designation.

3.1.1 | Diagnosis

Parachela is distinguished from *Macrochirichthys* by having dorsal- and anal-fin origins not on posterior one-third of body, 34–63 lateral-line scales (vs. >100), 35–41 (vs. 50–51) vertebrae, 6–7 (vs. 8) pelvic rays, and—except for *P. cyanea*—no large black spot on caudal-fin base. *Parachela* is distinguished from *Oxygaster* by having epaxial musculature extending forward at least to middle of eye (vs. extending forward at most to posterior margin of eye, 11–15, usually 12–13, (vs. 14–15) pectoral-fin rays; 6–7, rarely 8, (vs. 8) pelvic-fin rays; and 35–41 (vs. 43) vertebrae.

3.1.2 | Description

Meristic data in Tables 6–9, morphometric data in Tables 10–13, shape and color in Figures 1–3, 6, 8, 10–15. Body strongly compressed (mean width/SL = 5.1%–7.6%) and moderately deep (mean depth/SL = 22.0%–27.4%); mouth strongly oblique (~70–90 degrees to longitudinal axis of body); anterior tips of jaws at level of or above dorsal margin of eye; predorsal profile straight, slightly or strongly arched; ventral profile curved downward from tip of lower jaw and along ventral keel, then rising to caudal peduncle. Sharp ventral keel from head to anus. Almost all individuals of all species have 7½ branched dorsal-fin rays and 17 (9 upper, 8 lower) branched caudal-fin rays. Caudal fin forked. Anal fin extending from anus to caudal peduncle; second unbranched and first three branched rays longest, branched rays gradually decreasing in length posteriorly, 22–38 rays. Pelvic fin short (mean length/SL = 10.4%–13.2%), 6–7 rays. Pectoral fin long (mean lengths = 28.4%–35.8% SL), 11–15 rays. Lateral line curved downward on anterior half of body, then straight along third or fourth scale row above anal fin and up to center of caudal peduncle; 34–63 pored lateral-line scales on body, 0–4 on caudal fin. No sexual dimorphism was evident in external characteristics. Maximum SL = 163.3 mm.

3.1.3 | Remarks

Fowler (1934) described the subgenus *Grandisquamachela* based on the large scales and high number of anal-fin rays in *P. williaminae*.

TABLE 8 Numbers of lateral-line scales in species of *Parachela* with 45 or more pored scales.

Species	Basin/region	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	N	Mean	SD
Parachela microlepis	Mae Klong												1	2	1	1	3	1		1	10	59.1	2.1
	Chao Phraya								1	2	2	1	1	2		1					10	55.0	2.2
	Mekong												2		7	10	1	2	4	1	27	59.3	1.8
	TS, ST[a]						2	2	5		3										12	52.0	1.4
	Total						**2**	**2**	**6**	**2**	**5**	**1**	**4**	**4**	**8**	**12**	**4**	**3**	**4**	**2**	**59**	**57.1**	**3.5**
Parachela hypophthalmus	Borneo	**1**	**3**	**5**	**3**	**2**	**7**	**6**	**2**	**3**	**1**		**1**		**1**	**1**					**36**	**50.2**	**3.2**

Note: Chao Phraya includes Bang Pakong River drainage. Bold indicates total values.
[a]Tonle Sap and Stung Treng.

However, interspecific variation in lateral-line scale and anal-fin ray counts (Tables 6, 8, and 9) do not support recognizing this genus-group name.

Species of *Parachela* vary interspecifically in color pattern, position of dorsal-fin origin in relation to anal-fin origin, degree of arch in predorsal profile, whether pectoral fin reaches anal fin, and numbers of lateral-line scales, branched anal-fin rays, pectoral-fin rays, and pelvic-fin rays (Tables 4 and 5). Diagnoses and descriptions are presented after a key to identification in order of morphological similarities and with the first species described, *P. oxygastroides*, followed by the morphologically similar *P. ingerkongi*, then by the second species described, *P. hypophthalmus*, then *P. williaminae*, followed by *P. johorensis* and the morphologically similar *P. melanosticta* n. sp. and *P. cyanea*, and ending with *P. microlepis* n. sp.

3.2 | Key to species of *Parachela*

1a. Pectoral fin not reaching anal fin ... .2.

1b. Pectoral fin reaching anal fin ....4.

2a. More than 49 scales in lateral line; dorsal-fin origin distinctly posterior to anal-fin origin; no black longitudinal band in each caudal-fin lobe; 6 pelvic-fin rays; to 50 mm SL .... ***P. microlepis*** (Indochina).

2b. Fewer than 45 scales in lateral line, dorsal-fin origin slightly anterior, over, or slightly posterior to anal-fin origin; dusky black longitudinal band in each caudal-fin lobe; 7 pelvic-fin rays; to >80 mm SL ....3.

3a. 12–13, rarely 14, pectoral-fin rays; usually 27–28 branched anal-fin rays; to 165 mm SL .... ***P. oxygastroides*** (Mainland Southeast Asia, Borneo, Java, and Sumatra).

3b. 14–15 pectoral-fin rays; 29–33 branched anal-fin rays; to 80 mm SL .... ***P. ingerkongi*** (Borneo).

4a. Black blotch at base of caudal fin; 14 pectoral-fin rays .... ***P. cyanea*** (Borneo, Sumatra).

4b. No black blotch at base of caudal fin; usually 12–13 pectoral-fin rays .... 5.

5a. More than 44 scales in lateral line; dusky black longitudinal band in each caudal-fin lobe. ....***P. hypophthalmus*** (Borneo, Sumatra).

5b. Fewer than 46 scales in lateral line; no black longitudinal band in each caudal-fin lobe ....6.

6a. Dorsal-fin origin distinctly posterior to anal-fin origin; 30–37 branched anal-fin rays .... ***P. williaminae*** (Indochina).

6b. Dorsal-fin origin over or slightly anterior to anal-fin origin; 22–32 (usually <30) branched anal-fin rays. .... 7.

7a. 22–30, usually 25–27, branched anal-fin rays; 11–14, usually 13, pectoral-fin rays; black spots on caudal-fin lobes in Malay Peninsula, usually no black spots in Sumatra and Borneo .... ***P. johorensis*** (Malay Peninsula, Borneo, and Sumatra).

7b. 25–32, usually 27–29, branched anal-fin rays; 11–13, usually 12, pectoral-fin rays; black spots on caudal-fin lobes .... ***P. melanosticta*** (Indochina).

TABLE 9 Numbers of lateral-line scales in species of *Parachela* with 45 or fewer pored scales.

Species	Basin/region	34	35	36	37	38	39	40	41	42	43	44	45	N	Mean	SD
Parachela williaminae	Chao Phraya		1	1		2	1		1	1				7	38.4	2.5
	Mekong						2	4	2					8	40.0	0.8
	Total		**1**	**1**		**2**	**3**	**4**	**3**	**1**				**15**	**39.3**	**1.9**
Parachela oxygastroides	Indonesia		1			2	4	7	3	2		2	1	22	40.3	2.0
	Chao Phraya	1	2	2	5	5	1	3	3	3	1			26	38.5	2.5
	Mekong	1	1	4	9	12	2	1	3	1				34	37.8	1.7
	Malay Pen.		1	1	1		5	6	1					15	38.9	1.7
	Total	**2**	**5**	**7**	**15**	**19**	**12**	**17**	**10**	**8**	**1**	**2**	**1**	**99**	**38.7**	**2.2**
Parachela ingerkongi	Borneo							**3**	**4**	**3**				**10**	**41.0**	**0.8**
Parachela johorensis	Malay Pen.					1	5	6	1		2			15	40.0	1.4
	Indonesia					2		11	4	5	9	3	2	36	41.6	1.8
	Total					**3**	**5**	**17**	**5**	**5**	**11**	**3**	**2**	**51**	**41.2**	**1.8**
Parachela melanostica	Mae Klong					1	5	8	8	10	2	1		35	40.9	1.4
	Mekong			1	2	1	6	1	2	1				14	38.8	1.5
	Bangpakong, Trat		1		2			1						4	37.3	2.1
	Total		**1**	**1**	**4**	**2**	**11**	**10**	**10**	**11**	**2**	**1**		**53**	**40.1**	**1.9**
Parachela cyanea	Borneo				**4**	**1**	**3**							**8**	**37.9**	**1.0**

Note: Bold indicates total values.

TABLE 10 Proportional data for *Parachela oxygastroides* and *Parachela ingerkongi*.

	***Parachela oxygastroides* Indonesia (8)**			***P. oxygastroides* Indochina (29)**			***Parachela ingerkongi* (10)**		
Characteristic	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length (SL)	61.9–79.1	72.4	5.7	45.5–163.0	92.7	31.1	59.0–94.8	76.6	10.9
Relative to SL									
Predorsal fin length	62.4–64.4	63.2	0.8	61.4–65.1	63.4	1.1	58.9–64.0	61.5	1.5
Pre-pectoral fin length	26.6–30.3	27.9	1.2	24.5–28.5	26.1	1.0	24.3–26.4	25.2	0.6
Pre-anal fin length	63.0–69.8	65.8	2.1	63.6–70.6	66.1	1.5	58.5–63.4	61.6	1.5
Head length (HL)	23.2–25.0	24.3	0.6	21.0–24.4	22.8	0.8	21.8–23.8	22.6	0.6
Head width	9.0–11.3	10.5	0.7	9.9–12.0	10.7	0.5	10.1–11.2	10.5	0.4
Snout length	6.4–7.1	6.7	0.2	6.0–8.1	6.5	0.4	6.1–7.0	6.5	0.3
Eye length	7.8–8.8	8.4	0.3	6.6–8.4	7.5	0.4	7.8–8.2	7.9	0.1
Interorbital width	6.6–7.5	7.1	0.3	6.7–7.7	7.2	0.3	6.1–7.7	6.8	0.5
Depth at dorsal-fin origin	20.2–25.3	22.0	1.5	22.3–30.1	26.1	2.0	22.2–25.6	23.7	1.1
Width at dorsal-fin origin	4.1–6.4	5.5	0.6	5.1–8.9	6.9	1.1	6.0–8.2	6.8	0.7
Caudal peduncle depth	8.9–10.6	9.9	0.5	9.0–11.6	10.4	0.6	9.1–10.1	9.6	0.3
Caudal peduncle length	9.7–11.4	10.5	0.5	8.9–12.0	10.2	0.9	9.8–12.1	10.9	0.8
Pectoral-fin length	30.1–37.4	33.0	2.1	29.7–36.2	33.2	1.5	24.6–30.5	27.9	2.0
Pelvic-fin length	11.6–14.0	13.2	0.8	10.5–15.0	12.7	1.2	10.5–12.4	11.7	0.7
Anal-fin length	30.2–33.1	31.7	1.1	28.6–35.2	32.4	1.8	34.6–36.8	35.8	0.7
Dorsal-fin base length	5.1–6.6	5.8	0.5	5.2–6.8	6.2	0.3	5.6–6.6	6.1	0.3
Dorsal-fin length	14.4–15.8	15.0	0.5	13.9–16.7	15.3	0.6	13.9–15.2	14.6	0.4
Anal-fin base length	26.5–30.2	27.9	1.2	24.3–30.7	28.3	1.6	30.3–33.1	31.7	0.8
Relative to HL									
Head width	39.0–45.9	43.3	2.3	43.2–52.0	46.8	2.1	43.2–50.0	46.5	2.3
Snout length	26.4–28.7	27.6	0.9	25.9–33.1	28.5	1.5	26.8–31.1	28.9	1.3
Eye length	33.5–36.6	34.4	1.0	30.8–34.9	33.0	1.3	33.5–37.2	35.1	1.1
Interorbital width	27.7–30.5	29.3	0.9	29.4–36.4	31.8	1.5	26.9–34.7	30.2	2.7

Note: Numbers of specimens in parentheses.

TABLE 11 Proportional data for *Parachela hypophthalmus*, *Parachela williaminae*, and *Parachela cyanea*.

	Parachela hypophthalmus (26)			*Parachela williaminae* Indochina (7)			*Parachela cyanea* (8)		
Characteristic	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length (SL)	28.3–102.7	44.0	14.9	50.9–63.9	55.5	4.5	25.2–34.5	28.3	3.2
Relative to SL									
Predorsal fin length	61.0–67.4	64.2	1.5	65.2–67.4	66.4	0.8	62.3–64.1	63.3	0.7
Pre-pectoral fin length	24.5–32.0	29.6	1.7	27.7–28.8	28.1	0.5	32.3–34.8	33.8	0.8
Pre-anal fin length	62.3–85.4	64.9	1.9	61.2–65.2	63.3	1.4	62.3–65.8	64.2	1.2
Head length (HL)	22.7–26.3	24.7	0.9	23.1–25.3	24.1	0.7	26.9–28.7	28.0	0.6
Head width	8.9–12.0	10.9	0.8	10.0–11.0	10.4	0.3	11.5–13.0	12.5	0.4
Snout length	4.2–7.8	6.5	0.8	6.1–7.1	6.5	0.4	7.7–9.0	8.3	0.4
Eye length	5.2–9.8	8.4	1.2	7.3–8.2	7.9	0.3	10.3–11.3	11.0	0.4
Interorbital width	5.2–8.6	7.3	0.7	6.4–6.9	6.7	0.3	6.6–7.5	7.1	0.4
Depth at dorsal-fin origin	23.9–32.6	27.4	2.2	25.8–28.5	26.6	1.0	23.8–27.1	25.5	1.1
Width at dorsal-fin origin	4.7–9.8	6.3	1.1	4.5–6.8	6.2	0.8	4.5–6.7	5.5	0.7
Caudal peduncle depth	8.5–11.9	10.7	0.7	10.0–10.8	10.4	0.3	10.8–12.3	11.5	0.5
Caudal peduncle length	7.3–12.1	9.7	1.1	8.4–10.5	9.3	0.9	8.9–11.1	10.2	0.7
Pectoral-fin length	31.1–39.5	36.0	2.3	33.9–36.8	35.8	1.0	33.7–36.8	35.0	1.2
Pelvic-fin length	9.9–16.9	12.9	1.8	12.6–13.8	13.1	0.5	11.9–13.9	12.6	0.7
Anal-fin length	16.9–35.7	32.9	2.0	33.6–36.3	35.2	0.9	29.3–33.6	31.9	1.5
Dorsal-fin base length	4.4–6.5	5.9	0.5	5.1–6.3	5.7	0.4	5.5–7.5	6.5	0.6
Dorsal-fin length	15.1–20.7	17.2	1.4	15.9–17.2	16.5	0.5	16.3–17.8	17.0	0.5
Anal-fin base length	23.9–31.4	29.1	1.7	30.4–32.8	31.5	0.8	27.2–30.1	28.8	1.0
Relative to HL									
Head width	37.5–49.0	44.1	2.8	39.4–45.9	43.0	2.3	42.9–46.9	44.5	1.5
Snout length	17.3–31.0	26.4	3.2	25.4–28.4	27.0	1.1	28.6–32.3	29.7	1.3
Eye length	22.9–38.7	34.1	4.3	30.3–34.6	33.0	1.4	36.1–41.0	39.3	1.5
Interorbital width	22.7–35.5	29.4	2.7	26.2–29.1	27.6	1.2	23.3–27.1	25.3	1.4

Note: Numbers of specimens in parentheses.

3.3 | *Parachela oxygastroides* (Bleeker, 1852)

Leuciscus oxygastroides Bleeker, 1852: 431. Type localities: Indonesia: Kalimantan Selatan: Kusan River at Prabukarta; Sumatra: Musi River in Palembang; and Java: Batavia (Jakarta). Lectotype: BMNH 1866.5.2.216, designated by Alfred (1963: 129); geographic origin of lectotype uncertain.

Chela siamensis Günther, 1868: 336. Type locality: Thailand: Pachebon (Phetchabun Province). Holotype: BMNH 1861.10.8.17.

Chela megalolepis Günther, 1868: 337. Unnecessary replacement name for *L. oxygastroides* Bleeker, 1852.

Chela pointoni Fowler, 1934: 108, fig. 60. Type locality: Thailand: Chiang Mai. Holotype: ANSP 57456.

Oxygaster brachysoma Bănărescu, 1971: 18. Name in synonymy only, unavailable.

3.3.1 | Diagnosis

Parachela oxygastroides is distinguished from all other species of *Parachela* except *P. hypophthalmus* and *P. ingerkongi* by usually having dusky black longitudinal band (often most evident anteriorly) on each caudal-fin lobe. It is distinguished from *P. hypophthalmus* by having pectoral fin not reaching anal fin, dorsal-fin origin slightly anterior (vs. slightly posterior) to anal-fin origin, and 34–45 (vs. 45–59) lateral-line scales; from *P. ingerkongi* by having dorsal-fin origin slightly anterior (vs. over or slightly posterior) to anal-fin origin, 12–14, usually 13 (vs. 14–15) pectoral-fin rays, and 37–39 (vs. 40–41) vertebrae. *P. oxygastroides* is further distinguished from *P. microlepis* by having dorsal-fin origin slightly anterior (vs. distinctly posterior) anal-fin origin, 34–45 (vs. 50–63) lateral-line scales, and 7 (vs. 6) pelvic-fin rays; from *P. williaminae* by having dorsal-fin origin slightly anterior (vs. distinctly posterior) to anal-fin origin and often fewer branched anal-fin rays (23–33 vs. 30–37, see Table 6); from *P. johorensis* and *P. melanosticta* by having pectoral fin not reaching anal fin and lacking large black spot near tip of each caudal-fin lobe; from *P. cyanea* by having pectoral fin not reaching anal fin and lacking black blotch at base of caudal-fin. *P. oxygastroides* reaches much larger size than *P. cyanea*, *P. johorensis*, *P. melanosticta*, or *P. microlepis* (163 vs. 47–59 mm SL).

TABLE 12 Proportional data for *Parachela johorensis* and *Parachela melanosticta*.

	Parachela johorensis Malay Peninsula (14)			*P. johorensis* Indonesia (33)			*Parachela melanosticta* (48)		
Characteristic	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length (SL)	22.1–46.7	34.0	7.3	27.0–47.2	37.4	5.3	25.2–58.9	38.6	7.1
Relative to SL									
Predorsal fin length	63.2–68.0	65.2	1.4	61.6–65.6	63.8	0.9	60.8–67.6	64.0	1.4
Pre-pectoral fin length	30.9–33.7	31.9	0.9	28.9–32.3	30.5	0.9	24.1–32.3	30.1	1.2
Pre-anal fin length	62.1–67.6	65.6	1.4	61.6–67.1	64.4	1.4	60.3–66.5	64.1	1.3
Head length (HL)	25.6–28.1	26.6	0.8	24.1–27.0	25.5	0.8	22.2–26.5	24.3	1.0
Head width	11.0–13.1	12.4	0.5	11.1–12.8	12.0	0.4	10.3–12.7	11.4	0.5
Snout length	6.9–8.1	7.6	0.4	6.2–7.8	7.1	0.4	6.4–8.0	7.0	0.3
Eye length	9.1–11.3	10.0	0.7	8.4–11.1	9.1	0.7	7.3–9.8	8.7	0.5
Interorbital width	7.3–9.5	8.2	0.7	6.8–8.6	7.8	0.4	6.5–8.5	7.6	0.4
Depth at dorsal-fin origin	22.2–28.3	25.4	1.6	24.6–29.5	27.1	1.2	19.3–31.0	27.0	2.6
Width at dorsal-fin origin	4.3–7.8	6.3	1.3	3.6–6.9	5.5	1.0	4.2–7.4	6.2	0.6
Caudal peduncle depth	10.7–12.4	11.7	0.4	10.6–13.6	12.0	0.8	10.6–13.5	11.9	0.7
Caudal peduncle length	9.1–11.9	10.1	0.9	8.8–11.5	10.2	0.7	8.4–11.6	9.7	0.7
Pectoral-fin length	30.7–37.3	34.7	1.9	31.0–38.8	35.1	1.7	32.4–39.4	35.7	1.7
Pelvic-fin length	9.0–13.5	11.8	1.3	10.6–14.1	12.6	0.7	10.6–13.5	12.4	0.7
Anal-fin length	28.7–33.9	31.0	1.7	29.9–34.8	32.3	1.1	29.2–35.6	32.6	1.5
Dorsal-fin base length	4.9–7.7	5.9	0.7	5.1–8.1	6.3	0.7	4.9–7.4	6.2	0.5
Dorsal-fin length	13.5–18.6	16.3	1.4	15.3–20.4	16.7	1.0	14.3–18.3	16.5	1.0
Anal-fin base length	25.5–29.2	27.5	1.3	26.5–31.1	29.1	1.0	27.5–32.2	29.6	1.0
Relative to HL									
Head width	42.0–50.5	46.7	2.3	42.5–50.0	47.0	1.9	42.6–51.5	46.9	2.0
Snout length	25.9–31.2	28.7	1.4	24.1–31.9	27.9	1.7	26.3–31.8	28.9	1.4
Eye length	33.9–41.2	37.6	2.5	32.6–41.2	35.7	2.1	30.7–41.0	36.0	2.4
Interorbital width	26.8–35.3	30.7	2.5	25.3–34.5	30.6	1.9	25.3–36.1	31.2	2.1

Note: Numbers of specimens in parentheses.

3.3.2 | Description

Meristic data in Tables 6–9, morphometric data in Table 10, shape and color in Figure 6. Body strongly compressed (mean width/SL = 6.6%) and moderately deep (mean depth/SL = 25.2%). Dorsal profile nearly straight or only moderately arched upward from above eye to dorsal fin, then descending to caudal peduncle. Dorsal-fin origin slightly anterior to anal-fin origin. Anal fin with 23–33 (usually 25–31) rays. Pelvic fin short (mean = 12.8% SL), 7 rays. Pectoral fin long (mean = 33.1% SL), extending to pelvic fin, never to anal fin; 12–14, usually 13, rays. Lateral line with 34–45 pored scales on body, 1–3 on caudal fin. Vertebrae: 17–19 abdominal + 19–22 caudal = 37–39 total ($N = 8$). Largest specimen 163.0 mm SL (CAS 66241).

3.3.3 | Color

In life, *P. oxygastroides* is silvery and slightly translucent, yellow-green on upper body and silver-white on lower body, has a dusky black midlateral stripe, a yellow-gold stipe above the dusky stripe, and melanophores on the fin rays and in a line above the anal fin (Figure 6d). A dusky black longitudinal band is typically present in each caudal-fin lobe, usually best developed anteriorly. Individuals from tannin-stained water are much more darkly pigmented, some with a black midlateral stripe and blackish pectoral fins.

3.3.4 | Distribution

Parachela oxygastroides has the largest range of any species of *Parachela* (Figure 7). It is found in the Mekong River basin of Cambodia, Laos, Thailand, and Vietnam, the Chao Phraya and Tachin River basins of Thailand, the Malay Peninsula, and in Borneo, Java, and Sumatra. Most specimens are from flowing water in moderate-to-large rivers.

3.3.5 | Remarks

No molecular data are available for populations in Indonesia or Malaysia, but some genetic structure was present in Indochina, with

TABLE 13 Proportional data for *Parachela microlepis*.

Characteristic	Mae Klong River basin (10)			Mekong River basin (40)		
	Range	Mean	SD	Range	Mean	SD
Standard length (SL)	41.3–46.6	44.3	2.3	27.6–47.7	35.4	5.1
Relative to SL						
Predorsal fin length	59.8–66.5	64.5	2.0	62.3–66.8	64.3	1.2
Pre-pectoral fin length	24.3–26.2	25.5	0.5	24.6–27.3	25.6	0.7
Pre-anal fin length	56.8–61.2	58.9	1.9	49.2–63.1	59.0	2.2
Head length (HL)	21.2–23.1	22.0	0.6	19.2–23.0	21.5	0.9
Head width	9.2–11.5	10.8	0.5	9.3–10.9	10.1	0.4
Snout length	5.0–5.6	5.3	0.2	4.4–5.8	5.2	0.3
Eye length	6.7–7.7	7.1	0.3	6.7–8.7	7.8	0.5
Interorbital width	6.1–7.7	7.3	0.5	6.3–8.7	6.9	0.3
Depth at dorsal-fin origin	21.9–27.4	25.2	1.5	19.7–27.1	23.3	1.9
Width at dorsal-fin origin	5.1–6.7	5.8	0.5	4.0–6.6	5.1	0.7
Caudal peduncle depth	10.4–12.2	11.4	0.6	9.6–12.8	11.1	0.7
Caudal peduncle length	8.5–12.5	9.5	1.3	7.9–13.4	10.2	1.2
Pectoral-fin length	26.1–30.2	28.4	1.4	26.2–34.3	29.9	2.4
Pelvic-fin length	10.3–11.6	10.8	0.8	9.4–12.4	10.4	0.8
Anal-fin length	34.6–40.1	38.7	2.2	33.2–41.5	36.9	2.1
Dorsal-fin base length	5.8–7.4	6.7	0.5	5.7–8.0	6.6	0.6
Dorsal-fin length	14.6–16.6	15.9	0.7	13.4–17.3	15.6	1.0
Anal-fin base length	32.6–36.8	35.5	1.6	29.9–37.0	33.6	1.8
Relative to HL						
Head width	41.9–53.2	49.2	2.5	42.1–51.5	46.9	2.9
Snout length	21.9–25.3	24.1	0.9	21.0–27.0	24.2	1.3
Eye length	30.3–33.7	32.1	1.3	30.8–43.5	36.4	2.8
Interorbital width	28.0–35.8	33.1	2.3	28.7–43.5	32.0	1.9

Note: Numbers of specimens in parentheses.

the population in the Chao Phraya River separated from the population in the Mekong River basin by a genetic difference of 1.4%. No morphological variation corresponded to the genetic structure, but specimens from Indonesia averaged more branched anal-fin rays (29.6) than those from river basins in Indochina (26.9–27.3) (Table 6), and those from Indonesia averaged more lateral-line scales (40.3) than those from river basins in Indochina (37.8–38.9) (Table 9).

Bleeker's (1852) original description of *L. oxygastroides* was based on nine specimens 50–149 mm in TL from Borneo, Java, and Sumatra. They were described as having 7 branched dorsal-fin rays, 14–16 pectoral-fin rays, 7 pelvic-fin rays, and 29–32 branched anal-fin rays. Bleeker (1860) redescribed the species (as *Chela oxygastroides*) and gave counts of 40–45 lateral-line scales, 7–8 branched dorsal-fin rays, 12–14 pectoral-fin rays, 8 pelvic-fin rays, 22–32 branched anal-fin rays, and 17 branched caudal-fin rays. Both accounts described the body as greenish above and silver below, and each caudal-fin lobe as having a diffuse dark band in the middle. The longitudinal bands on the caudal fin still can be seen on the lectotype (Figure 6a). Alfred (1963) examined three of these specimens, then 45–143 mm in TL (lectotype 123.0 mm TL) and found them to have 7 branched dorsal-fin rays, 23–29 branched anal-fin rays, 12–14 pectoral-fin rays, and 7 pelvic-fin rays. He noted scales could be counted on only one of the specimens, which had 39 lateral-line scales.

Although Bleeker (1860) described *P. oxygastroides* as having a diffuse dark band in each caudal-fin lobe, an identification key to species accompanying the description incorrectly indicated that it does not have a black band in each caudal-fin lobe. Likewise, a plate in Bleeker (1864: pl. 143) incorrectly shows no black bands in the caudal fin of *P. oxygastroides* but does show the bands in *P. hypophthalmus* and *O. anomalura*. To add additional confusion, in van Oijen and Loots' (2012) translation of Bleeker (1860) with illustrations from Bleeker (1864), the figure from Bleeker (1864) for *Chela hypophthalmus* (*P. hypophthalmus*) was correctly reprinted, but that for *C. oxygastroides* (*P. oxygastroides*) was mistakenly used for *C. anomalurus* (*O. anomalura*) and correctly used for *C. oxygastroides*. The dusky black longitudinal bands in the caudal fin are characteristic of all three species but absent or poorly developed in some individuals.

Chela siamensis was described by Günther (1868) from one specimen (Figure 6), 4 inches (102 mm) long from the Chao Phraya River basin in Phetchabun Province, Thailand, as having a sharp edge on the

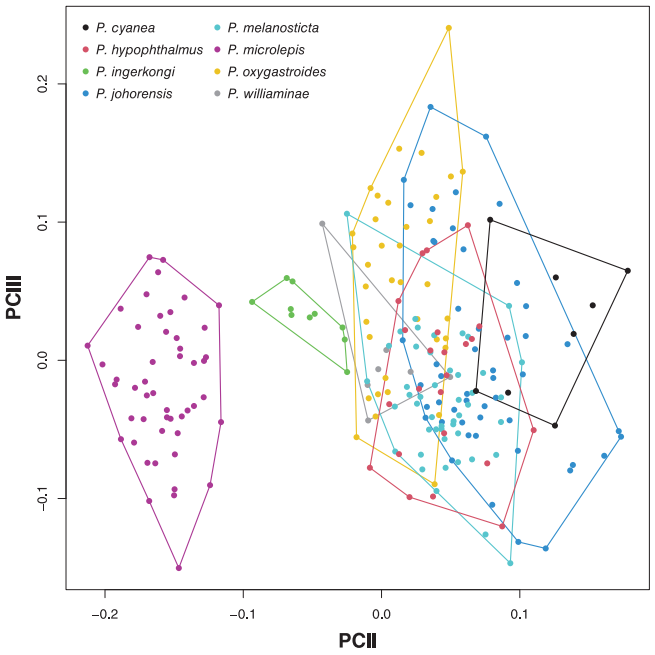

FIGURE 5 Sheared principal component (PC) analysis of morphometric data. Size accounted for 95.9% of the observed variance on PC1 (not plotted). Sheared PC2 and PC3 accounted for 1.6% and 0.7% of observed variance, respectively.

thorax, pectoral fin one-third of SL and extending to between the pelvic and anal fins, 9 dorsal-fin rays, 30 anal-fin rays, 7 pelvic-fin rays, 43 lateral-line scales, scales on the nape advancing to above the anterior margin of the orbit, dorsal-fin origin a little in advance of the anal-fin origin, and being uniformly silvery. Bănărescu (1971) examined the holotype and found it to have 26 branched anal-fin rays, 40 lateral-line scales, and an SL of 83.0 mm. These descriptions and data from other specimens from the Chao Phraya basin fall within the range of variation of *P. oxygastroides*, and we follow Bănărescu (1969, 1971) in recognizing *C. siamensis* as a synonym of *P. oxygastroides*.

Chela pointoni was described by Fowler (1934) from one specimen, 75 mm TL, from Chiang Mai, Thailand, as having 7 branched dorsal-fin rays, 33 lateral-line scales, 12 pectoral-fin rays, and 27 branched anal-fin rays. Bănărescu (1969) recognized *C. pointoni* as a species of *Oxygaster* and gave a count of 36 lateral-line scales for the type. We also found the type, which now measures 58.3 mm SL, to have 36 lateral-line scales but otherwise to agree with Fowler's description. Although Howes (1979) opined that *C. pointoni* belonged in *Parachela* based primarily on the forward extension of the epaxial musculature, he did not examine the type, and subsequent authors have continued to follow Bănărescu (1969) and treat *C. pointoni* as a species of *Oxygaster* separate from *O. anomalura*. For example, Rainboth (1996) distinguished *O. anomalura* from *O. pointoni* as having a black longitudinal band versus no band in each lobe of the caudal fin and 49–57 versus 43–47 lateral-line scales even though Fowler (1934) gave the lateral-line scale count for *pointoni* as 33 and Bănărescu (1969) as 36. Other publications (e.g., Kottelat, 2001) have suggested that *O. pointoni* can be distinguished from *O. anomalura* by having a black band only in the upper lobe of the caudal fin (vs. both lobes), but the amount of black pigment

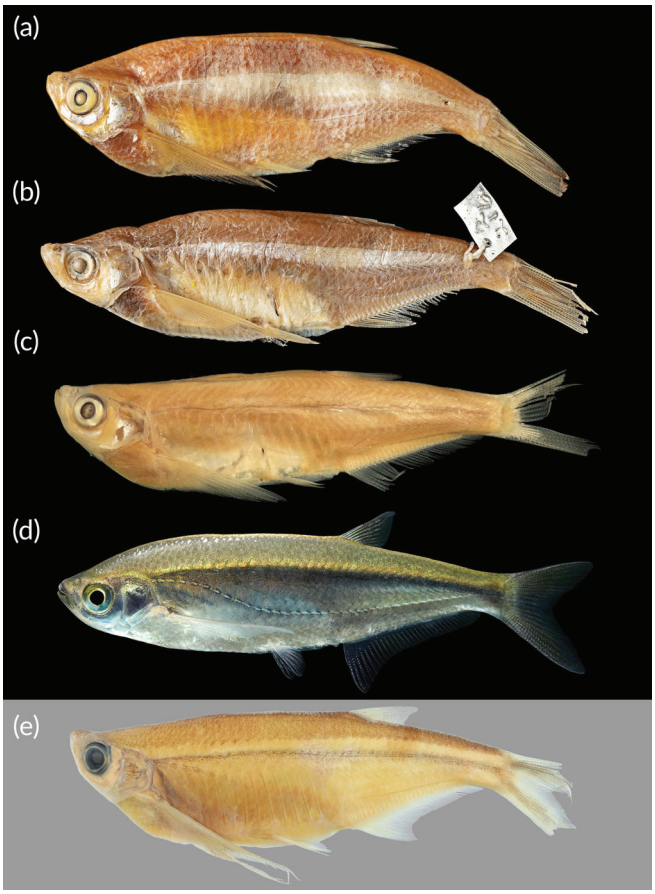

FIGURE 6 *Parachela oxygastroides*. (a) Lectotype of *Leuciscus oxygastroides*, BMNH 1866.5.2.216, 123 mm total length (TL), Indonesia, photo by Lucie Goodayle. (b) Holotype of *Chela siamensis*, BMNH 1861.10.8.17, 102 mm TL, Phetchabun Province, Thailand, photo by Lucie Goodayle. (c) Holotype of *Chela pointoni*, ANSP 57456, 58.3 mm standard length (SL), Ping River, Chiang Mai Province, Thailand, photo by Kyle Luckenbill. (d) Live individual, 120 mm SL, from aquarium dealer, Phitsanulok Province, Thailand, photo by Nonn Panitvong. (e) UF 249500, 99.8 mm SL, Ping River, Kamphaeng Phet Province, Thailand.

in the caudal fin of *O. anomalura* varies and descriptions alleging distinctions between two species are based on misinterpretations of variation within *O. anomalura*.

The type of *C. pointoni* has the epaxial musculature extending to the middle of the eye, is clearly a species of *Parachela*, and is indistinguishable from *P. oxygastroides*. Fins were described by Fowler as uniformly pale, grayish, or whitish with no mention of black longitudinal bands in the caudal fin. However, *P. oxygastroides*, like *O. anomalura*, often lacks the black bands in the caudal fin. *C. pointoni* is a synonym of *P. oxygastroides*, as noted by Howes (1979).

3.4 | *Parachela ingerkongi* (Bănărescu, 1969)

Oxygaster oxygastroides ingerkongi Bănărescu, 1969: 196. Type locality: Malaysia: Sabah State: Tawao on Tawao River (Tawau), 4°15′ N 118° E. Holotype: USNM 135946 (see Bănărescu, 1971: 18).

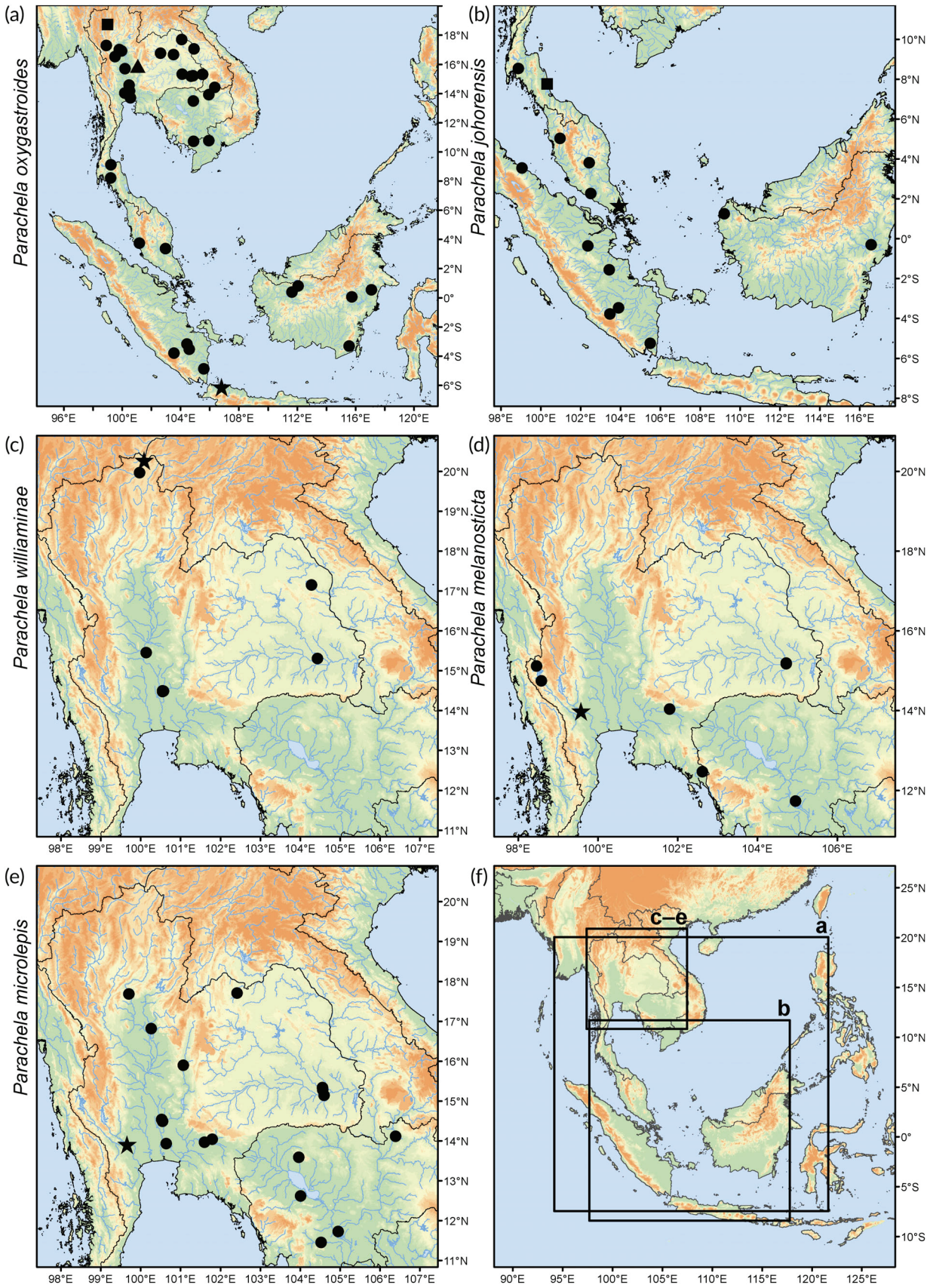

FIGURE 7 Distributions of species of *Parachela*. (a) *Parachela oxygastroides*, ★type locality, ▲type locality of *Chela siamensis*, ■type locality of *Chela pointoni*. (b) *Parachela johorensis*, ★type locality, ■type locality of *Chela maculicauda*. (c) *Parachela williaminae*, ★type locality. (d) *Parachela melanosticta*, ★type locality. (e) *Parachela microlepis*, ★type locality. (f) Areas shown in maps. Localities include specimens examined and literature records cited in text.

3.4.1 | Diagnosis

Parachela ingerkongi is distinguished from all other species of *Parachela* except *P. hypophthalmus* and *P. oxygastroides* by having a dusky black longitudinal band in each caudal-fin lobe. It is distinguished from *P. hypophthalmus* by having pectoral fin not reaching anal fin, 40–42 (vs. 45–59) lateral-line scales, and 40–41 (vs. 37–38) vertebrae, and from *P. oxygastroides* by having dorsal-fin origin over or slightly posterior (vs. slightly anterior) to anal-fin origin, 14–15 (vs. usually 12–13) pectoral-fin rays, and 40–41 (vs. 37–39) vertebrae. *P. ingerkongi* is further distinguished from *P. microlepis* by having dorsal-fin origin over or slightly posterior (vs. distinctly posterior) to anal-fin origin, 40–42 (vs. 50–63) lateral-line scales, and 7 (vs. 6) pelvic-fin rays; from *P. williaminae* by having pectoral fin not reaching anal fin, dorsal-fin origin over or slightly posterior (vs. distinctly posterior) to anal-fin origin, and 14–15 (vs. usually 13) pectoral-fin rays; from *P. johorensis* and *P. melanosticta* by having pectoral fin not reaching anal fin, 40–41 (vs. 36–37) vertebrae, and lacking black spot near tip of each caudal-fin lobe (variable in Indonesian *P. johorensis*); and from *P. cyanea* by having pectoral fin not reaching anal fin and 29–33 (vs. 23–26) branched anal-fin rays, and lacking black blotch at base of caudal fin.

3.4.2 | Description

Meristic data in Tables 6–9, morphometric data in Table 10, shape in Figure 8. Body strongly compressed (mean width/SL = 6.8%) and moderately deep (mean depth/SL = 23.7%). Dorsal profile gently arched upward from above eye to dorsal fin, then descending to caudal peduncle. Dorsal-fin origin over to slightly posterior to anal-fin origin. Anal fin with 29–33 rays. Pelvic fin short (mean = 11.7% SL), 7 rays. Pectoral fin long (mean = 27.9% SL), extending to pelvic fin, never to anal fin; 14–15 rays. Lateral line with 40–42 pored scales on body, 1–2 on caudal fin. Vertebrae: 17 abdominal + 23–24 caudal = 40–41 total ($N = 6$). Largest specimen 94.8 mm SL (CAS 33584).

3.4.3 | Color

No information on life color is available. Preserved specimens ($N = 4$) have melanophores on the fin rays, along the lateral line, and in a line above the anal fin, a black midlateral stripe subtended by a silvery stripe, and a dusky black longitudinal band in each caudal-fin lobe, partially visible in Figure 8.

3.4.4 | Distribution

Parachela ingerkongi is known only from the Tawau River basin in Sabah State, Malaysia, in northeastern Borneo (Figure 9). Inger and Kong (1962) noted the presence of insect fragments in the stomachs of *P. oxygastroides* from the Tawau District in Sabah; the fish are probably *P. ingerkongi*.

3.4.5 | Remarks

Bănărescu (1969) described *P. ingerkongi* as a subspecies of *P. oxygastroides* from the Tawao (Tawau) River in Sabah, Malaysia, and from the Mahakkan (Mahakam) River in East Kalimatan, Indonesia. However, specimens from the Mahakam River, UMMZ 70665—originally designated as paratypes of *ingerkongi*—and ROM 51764 are *P. oxygastroides*. Meristic data for *P. ingerkongi* from Bănărescu (1969) are not included in our tables because no distinction was made between specimens from Tawau and Mahakkan rivers. In Bănărescu (1969) the catalog number of the holotype was incorrectly printed as USNM 135, but this was corrected to USNM 135946 by Bănărescu (1971). Paratypes from the type locality were not given a separate catalog number in the original description but were listed as USNM 202860 in Bănărescu (1971); however, the correct catalog number for paratypes is USNM 202680.

3.5 | *Parachela hypophthalmus* (Bleeker, 1860)

Chela hypophthalmus Bleeker, 1860: 471. Type locality: Indonesia: Sumatra: Palembang (possible locality, see Bleeker, 1864: 135; Kottelat, 1995: 57). Lectotype: RMNH 4985, designated by Alfred (1963: 128).

Parachela breitensteinii Steindachner, 1881a: 100. Type locality: Indonesia: Borneo, Teweh (Steindachner, 1881b: 404–405). Holotype: NMW P 3000 (see Howes, 1979: 189).

3.5.1 | Diagnosis

Parachela hypophthalmus is distinguished from all other species of *Parachela* except *P. microlepis* by having >44 lateral-line scales, and from all other species of *Parachela* except *P. oxygastroides* and *P. ingerkongi* by usually having dusky black longitudinal band in each caudal-fin lobe. *P. hypophthalmus* is further distinguished from *P. microlepis* by having pectoral fin reaching anal fin, 7 (vs. 6) pelvic rays, and larger size (130 vs. 50 mm SL); from *P. oxygastroides* by having pectoral fin reaching anal fin and dorsal-fin origin slightly posterior (vs. slightly anterior) to anal-fin origin; from *P. ingerkongi* by having pectoral fin reaching anal fin and usually 12–13 (vs. 14–15) pectoral-fin rays; from *P. williaminae* by having 23–32 (vs. 30–37) branched anal-fin rays; from *P. johorensis* and *P. melanosticta* by having dorsal-fin origin slightly posterior (vs. over or slightly anterior) to anal-fin origin, straight or slightly arched (vs. strongly arched) predorsal profile, and no large black spot on each caudal-fin lobe (variable in Indonesian *P. johorensis*); and from *P. cyanea* by having dorsal-fin origin slightly posterior (vs. over or slightly anterior) to anal-fin origin and lacking black blotch at base of caudal fin. *P. hypophthalmus* reaches much larger size than *P. cyanea*, *P. johorensis*, *P. melanosticta*, or *P. microlepis* (130 vs. 47–59 mm SL).

3.5.2 | Description

Meristic data in Tables 6–9, morphometric data in Table 11, shape in Figure 10. Body strongly compressed (mean width/SL = 6.3%) and moderately deep (mean depth/SL = 27.4%). Dorsal profile arched anteriorly, flat to dorsal fin, then descending to caudal peduncle. Dorsal-fin origin slightly posterior to anal-fin origin. Anal fin with 23–32 branched rays. Pelvic fin short (mean = 12.9% SL), 7–8 rays. Pectoral fin long (mean = 36.0% SL), extending to or almost to anal-fin origin; 12–14, usually 12–13, rays. Lateral line with 45–59 pored scales on body, 1–2 on caudal fin. Vertebrae: 16–17 abdominal + 21–22 caudal = 37–38 total ($N = 4$). Largest specimen = BMNH 1866.5.2.218, 130 mm SL, paralectotype of *C. hypophthalmus* (Alfred, 1963).

FIGURE 8 *Parachela ingerkongi*. (a) Holotype of *Oxygaster oxygastroides ingerkongi*, USNM 135946, 75.0 mm standard length (SL), Tawao River, Sabah, Malaysia, photo by Sandra Raredon. (b) *P. ingerkongi*. CAS 33584, 94.8 mm SL, Tawau River, Sabah State, Malaysia.

3.5.3 | Color

See Remarks.

3.5.4 | Distribution

P. hypophthalmus is known from Borneo and Sumatra (Figure 9). Ng et al. (2019) listed *P. hypophthalmus* for peninsular Malaysia but noted confusion over the identification. No molecular data are available; all samples listed as *P. hypophthalmus* on GenBank are misidentified *P. johorensis*.

3.5.5 | Remarks

Bleeker (1860) described *C. hypophthalmus* as having a keel along the strongly compressed belly, strongly decurved lateral line, long pectoral fins nearly reaching the anal fin, 7–8 branched dorsal-fin rays, 12–13

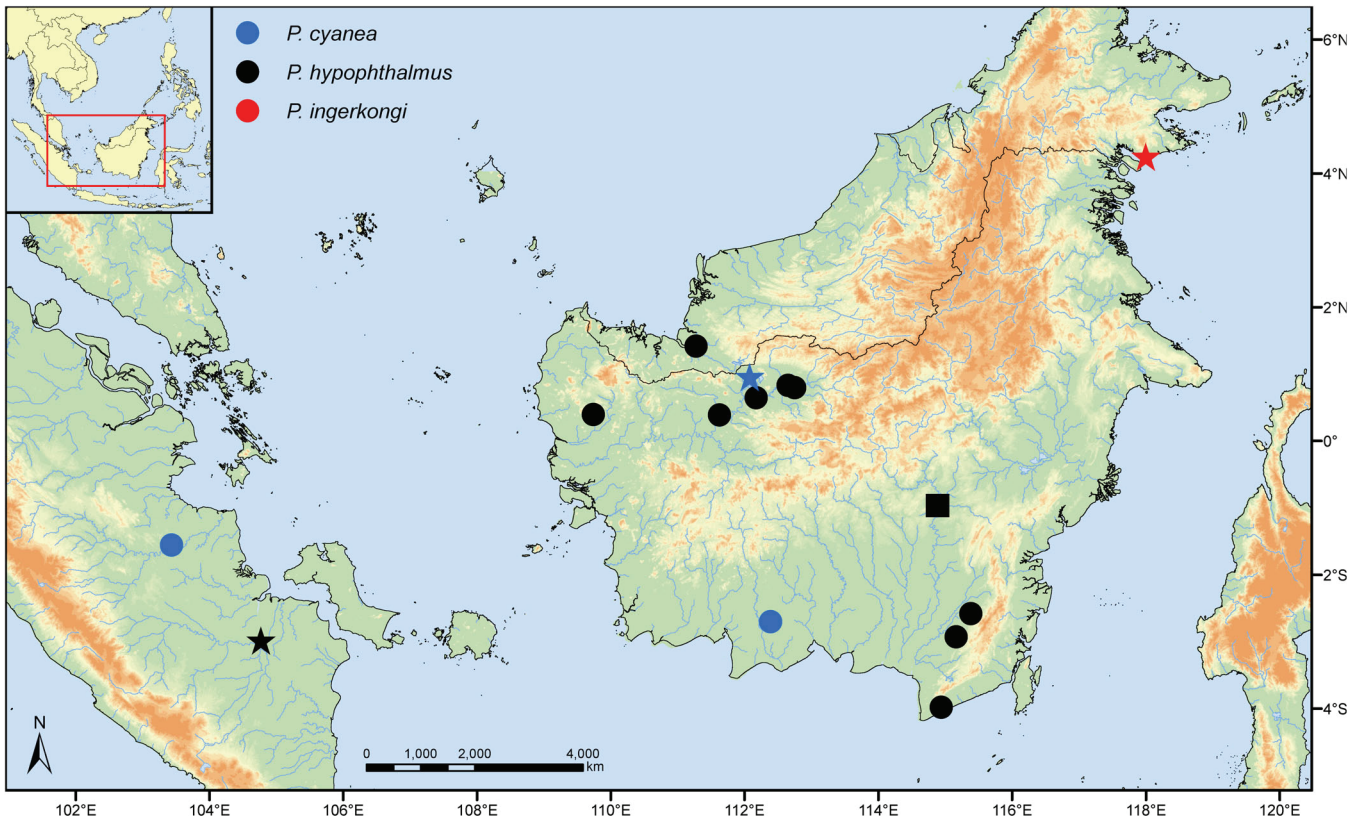

FIGURE 9 Distributions of species of *Parachela* restricted to Borneo and Sumatra. ★Type localities for valid species, ■type locality for *Parachela breitensteinii*. Localities include specimens examined and literature records cited in text.

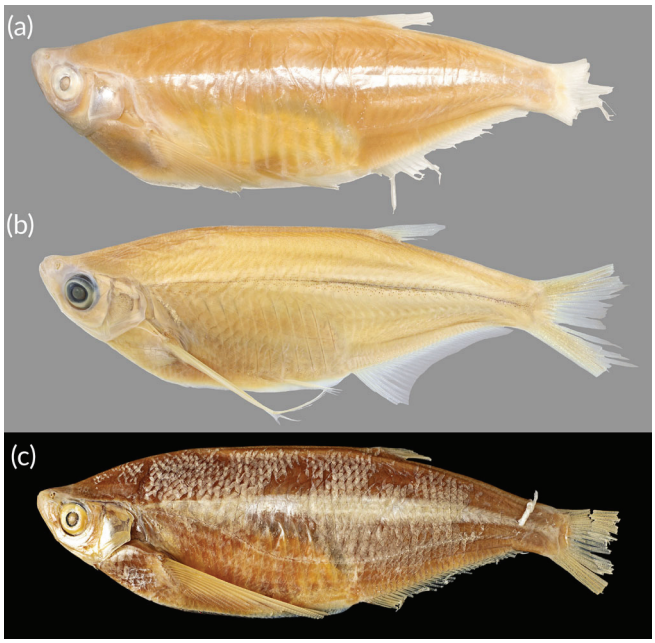

FIGURE 10 *Parachela hypophthalmus*. (a) Lectotype of *Chela hypophthalmus*, RMNH 4985, 118.5 mm standard length (SL), Musi River basin, South Sumatra, Indonesia. (b) ROM 38603, 102.7 mm SL, oxbow at Nangaembaluh, West Kalimantan Province, Indonesia. (c) Paralectotype, BMNH 1866.5.2.218, 130 mm SL, Musi River basin, South Sumatra, Indonesia, photo by James Maclaine. Pectoral and caudal fins of all images are damaged and shorter than in life.

pectoral-fin rays, 8 pelvic-fin rays, 29–30 branched anal-fin rays, 60–63 scales along the lateral line, and 17 branched caudal-fin rays. The body was described as green dorsally and silver-hyaline or pearly ventrally and with a midlateral silver stripe. Fins were described as yellowish-hyaline, and the caudal fin darkish on the basal half. Although no mention is made of a dusky black band in each caudal-fin lobe, a key to species accompanying the description correctly indicates that the caudal fin has a "blackish longitudinal band" on each lobe (and erroneously indicates that *P. oxygastroides* does not). A plate in Bleeker (1864: pl. 143) shows the black bands in the caudal fin of *P. hypophthalmus* and incorrectly, again, indicates their absence in *P. oxygastroides*. The bands on the caudal fin of both *P. oxygastroides* and *P. hypophthalmus* can be seen in Figures 6e and 10b, and in Roberts (1989: fig. 40).

Alfred (1963) examined Bleeker's two specimens of *C. hypophthalmus* and selected RMNH 4985 as the lectotype. He recorded lateral-line scale counts of 56 and 59, pelvic-fin ray counts of 7 and 8, and indicated that both specimens had 29 branched anal-fin rays and 13 pectoral-fin rays. Bleeker (1860) recorded the total lengths as 155 and 165 mm, and Alfred gave the standard lengths as 118.5 and 130 mm. The lectotype (RMNH 4985) and paralectotype (BMNH 1866.5.2.218) of *C. hypophthalmus* (Figure 10) are both missing much of the caudal fin and now too poorly preserved to have retained black pigment in the fin.

Bănărescu (1969) treated *hypophthalmus* as a species of *Oxygaster*, but Howes (1979) transferred the species to *Parachela*, where it has remained in subsequent publications. Howes (1979) examined the holotype of *P. breitensteinii* Steindachner, 1881 and concluded it was a synonym of *P. hypophthalmus*. Given the holotype has 60 lateral-line scales and a pectoral fin reaching the anal fin (Steindachner, 1881a), 30 branched anal-fin rays, the dorsal-fin origin slightly posterior to the anal-fin origin, and each caudal lobe with a dark longitudinal band (Steindachner, 1881b), Howes' decision is followed here.

3.6 | *Parachela williaminae* Fowler, 1934

Parachela williaminae Fowler, 1934: 111, fig. 63. Type locality: Thailand: Chiang Rai Province: Mekong River at Chiang Sen. Holotype: ANSP 57457.

3.6.1 | Diagnosis

Parachela williaminae is distinguished from all other species of *Parachela* except *P. microlepis* by having dorsal-fin origin distinctly posterior to anal-fin origin, and from *P. microlepis* by having pectoral fin reaching anal fin, 35–42 (vs. 50–63) lateral-line scales, and 7–8 (vs. 6) pelvic rays. *P. williaminae* is further distinguished from *P. oxygastroides* by having pectoral fin reaching anal fin, 30–37 (vs. 23–33) branched anal-fin rays, and no black longitudinal band in each caudal-fin lobe; from *P. ingerkongi* by having pectoral fin reaching anal fin, usually 13 (vs. 14–15) pectoral-fin rays, and no black longitudinal band in each caudal-fin lobe; from *P. hypophthalmus* by having 35–42 (vs. 45–59) lateral-line scales and no black longitudinal band in each caudal-fin lobe; from *P. johorensis* by having 30–37 (vs. 22–30) branched anal-fin rays and no black spots near tips of caudal-fin lobes (variable in Indonesian *P. johorensis*); from *P. melanosticta* by having 30–37 (vs. 25–32) branched anal-fin rays and no black spot near tip of each caudal-fin lobe; and from *P. cyanea* by having 30–37 (vs. 23–26) branched anal-fin rays, usually 13 (vs. 14) pectoral-fin rays, and no black blotch at base of caudal fin. *P. williaminae* reaches much larger size than *P. cyanea*, *P. johorensis*, *P. melanosticta*, and *P. microlepis* (120 vs. 47–59 mm SL).

3.6.2 | Description

Meristic data in Tables 6–9, morphometric data in Table 11, shape and color in Figure 11. Body strongly compressed (mean width/SL = 6.2%) and moderately deep (mean depth/SL = 26.6%). Dorsal profile arched anteriorly, flat to dorsal fin, then descending to caudal peduncle. Dorsal-fin origin distinctly posterior to anal-fin origin. Anal fin with 30–37 branched rays. Pelvic fin short (mean = 13.1% SL), 7 (rarely 8) rays. Pectoral fin long (mean = 35.8% SL), extending to anal-fin origin, 12–14, usually 13, rays. Lateral line with 35–42 pored scales on body, 1–2 on caudal fin. Vertebrae: 16–17 abdominal + 22–23 caudal = 38–39 total ($N = 10$). To 120 mm SL (Panitvong, 2022).

3.6.3 | Color

In life, *P. wiliaminae* is silvery and slightly translucent, yellow-green on the upper body and silver-white on the lower body, has a dusky black midlateral stripe, a yellow stipe above the black stripe, and melanophores on the fin rays, along the posterior margin of the caudal fin, and in a line above the anal fin (Figure 11).

3.6.4 | Distribution

P. williaminae, described from the Mekong River in extreme northern Thailand, is the most northerly occurring species of *Parachela* (Figure 7). It appears to be widespread in the Mekong and Chao Phraya River basins of Thailand but is rare in institutional collections.

3.6.5 | Remarks

Fowler's (1934) original description of *P. williaminae* was based on one specimen, 108 mm TL, from the Mekong River at Chiang Saen. It was described as having 7 branched dorsal-fin rays, 12 pectoral-fin rays, 35 branched anal-fin rays, and 35 lateral-line scales. The body was described as light brown, paler below, and the caudal fin as gray and pale olive at the base with the upper caudal lobe much shorter than the lower. The pectoral fin reached past the front of the anal fin. Pelvic fins were missing on the type, but as noted by Bănărescu (1971), this was likely an abnormality of this one individual. In describing the anal fin as being "inserted little before dorsal origin," Fowler was referring to the origin of the anal fin. Bănărescu (1971) found the holotype to have 40 or 41 lateral-line scales and an SL of 83.0 mm.

Molecular data are available for only two populations of *P. williaminae* (Figure 4). Morphological data (for 17 individuals) showed no geographic structure.

3.7 | *Parachela johorensis* Steindachner, 1870

Chela johorensis Steindachner, 1870: 638. Type locality: Malaysia: Johor River. Syntypes (10): possibly NMW 51458 (Fricke et al. 2023).

Chela maculicauda Smith, 1934: 301. Type locality: Thailand: Klong Ranode, tributary of Tale Sap (Thale Sap) in peninsular Thailand. Holotype: USNM 103372 (see Smith, 1945; Vilasri et al., 2018, Fig. 4).

3.7.1 | Diagnosis

Parachela johorensis is distinguished from all other species of *Parachela* in Indochina except *P. melanosticta* by having large black spot near tip of each caudal-fin lobe (Figure 12). It is distinguished from *P. melanosticta* genetically (Figure 4) and by having 22–30, usually 24–26 (vs. 25–32, usually 27–29) branched anal-fin rays and usually 13 (69% of specimens examined) (vs. usually 12, 62%) pectoral-fin rays. It is further distinguished from *P. williaminae* by having dorsal-fin origin over or slightly anterior (vs. distinctly posterior) to anal-fin origin and 22–29 (vs. 30–37) branched anal-fin rays, and from *P. microlepis* by having dorsal-fin origin over or slightly anterior (vs. distinctly posterior) to anal-fin origin, 38–43 (vs. 50–63) lateral-line scales, 22–29 (vs. 28–38) branched anal-fin rays, and usually 7 (vs. 6) pelvic-fin rays.

In Indonesian populations that lack distinctive large black spot near tip of each caudal-fin lobe, *P. johorensis* is distinguished from *P. oxygastroides* and *P. ingerkongi* by having pectoral fin reaching anal fin and usually having strongly arched (vs. straight or slightly arched) predorsal profile and lacking black longitudinal band in each caudal-fin lobe. It is distinguished from *P. hypophthalmus* by having 38–45 (vs. 45–59) lateral-line scales and lacking black longitudinal band in each caudal-fin lobe; and from *P. cyanea* by lacking black spot on caudal-fin base and having 38–45 (vs. 37–39) lateral-line scales and usually 13 (vs. 14) pectoral-fin rays.

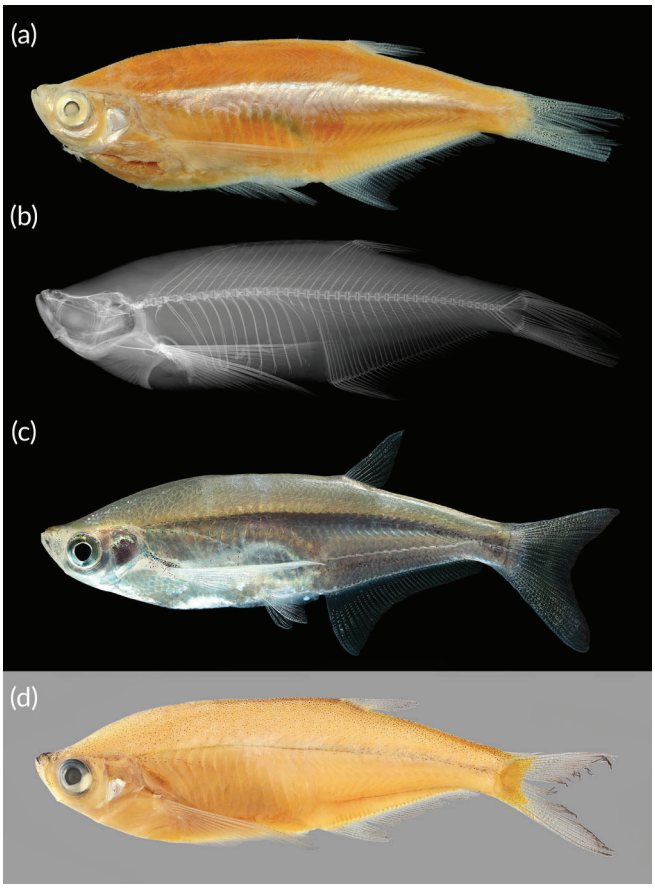

FIGURE 11 *Parachela williaminae*. (a, b) Holotype, ANSP 57457, 83.0 mm standard length (SL), Mekong River, Chiang Rai Province, Thailand, photo and X-ray by Kyle Luckenbill. (c) Live individual, 120 mm SL, from aquarium dealer, Phitsanulok Province, Thailand, photo by Nonn Panitvong. (d) UF 245409, 63.9 mm SL, Chi River, Ubon Ratchathani Province, Thailand.

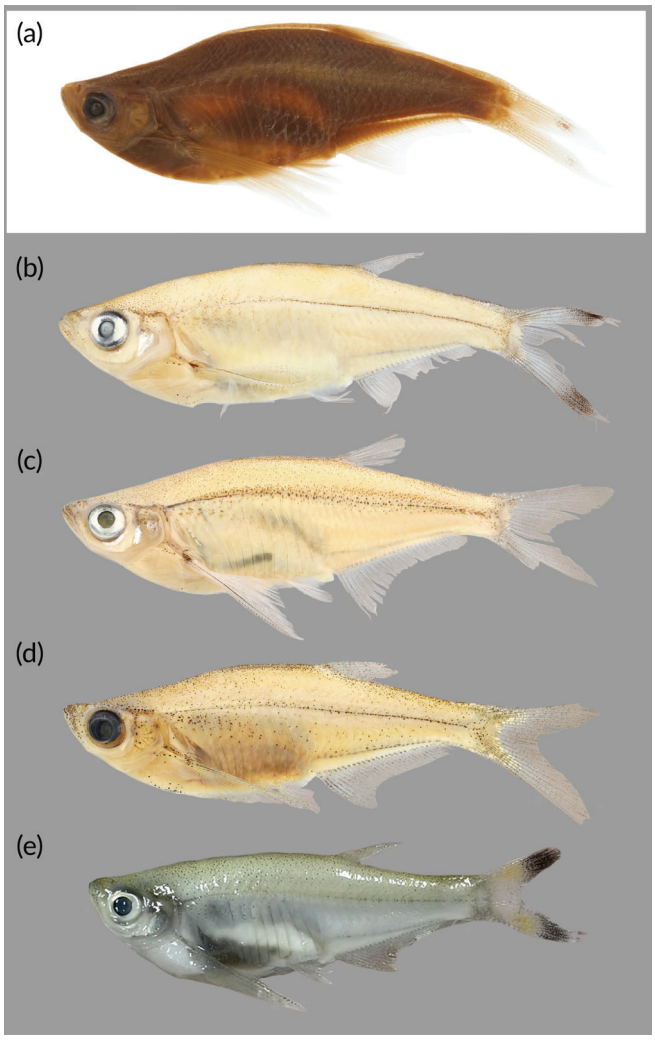

FIGURE 12 *Parachela johorensis*. (a) Holotype of *Chela maculicauda*, USNM 103372, 42.8 mm standard length (SL), Klong Ranode, Songkhla Province, Thailand, photo by Sandra Raredon. (b) UF 160958, 46.7 mm SL, South Ulu Sedili River basin, Johor State, Malaysia. (c) UF 167203, 45.1, Air Lematang basin, South Sumatra Province, Indonesia. (d) UF 190670, 34.0 mm SL, Mahakam River basin, East Kalimantan Province, Indonesia. (e) Uncatalogued, Nakhon Si Thammarat Province, Thailand, photo by Vatthanachai Phanklam.

3.7.2 | Description

Meristic data in Tables 6–9, morphometric data in Table 12, shape and color in Figure 12. Body strongly compressed (mean width/SL = 6.2%) and moderately deep (mean depth/SL = 26.6%). Dorsal profile usually strongly arched upward from eye to dorsal-fin origin, then descending to caudal peduncle. Dorsal-fin origin over or slightly anterior to anal-fin origin. Anal fin with 22–30 (usually 25–27) rays. Pelvic fin short (mean = 12.3% SL), 7 (rarely 6) rays. Pectoral fin long (mean = 35.0% SL), extending past pelvic fin, usually to anal-fin origin; 12–13 (rarely 11 or 14) rays. Vertebrae: 15 abdominal + 22 caudal = 36–37 total ($N = 6$). Lateral line with 38–45 pored scales on body, 0–3 on caudal fin. Largest specimen 47.2 mm SL (UF 167203).

3.7.3 | Color

In life, *P. johorensis* is somewhat translucent with a silvery sheen and has a dusky black midlateral stripe, and melanophores on the fin rays, along the anal-fin base, and in a line just above and parallel with the anal-fin base (Figure 12). In Indochinese populations, a large black spot is present near the tip of each caudal-fin lobe, sometimes preceded by a yellow or orange spot. In Indonesia, the large black spot and yellow or orange spot on the caudal fin usually are absent, and there often is a black posterior margin on the caudal fin and clusters of melanophores on the body. More black pigment on the body and fins is especially characteristic of populations in Borneo (Figure 12).

3.7.4 | Distribution

P. johorensis is found in the Malay Peninsula as far north as the Tapi River basin and in Sumatra and Borneo (Figure 7).

3.7.5 | Life history

Small YOY (12.1–25.7 mm SL) were collected in the Jorong River in South Kalimantan on August 7, 2007 (CAS 393659), suggesting that spawning occurred in July during the dry season.

3.7.6 | Remarks

Steindachner's (1870) original description of *C. johorensis* was based on 10 specimens from the Johor River in peninsular Malaysia. The description mentions a black oblique bar near the posterior edge of each caudal-fin lobe. Without mentioning the black bars on the caudal fin, Bănărescu (1969) synonymized *C. johorensis* with *Oxygaster* (now *Parachela*) *oxygastroides*, a species that does not have black bars or large black spots on the caudal fin. This synonymization was incorrect, and *P. johorensis* is removed from the synonymy of *P. oxygastroides*.

Populations on the Malay Peninsula and in Sumatra and Borneo form a clade (Figure 4), assignable to *P. johorensis*, and populations in Indochina north of the Malay Peninsula form a sister clade that is taxonomically described below as *P. melanosticta*.

Chela maculicauda, recently treated as *P. maculicauda* (e.g., So et al., 2018; Taki et al., 2021) was described by Smith (1934) from a tributary of Thale Sap, a lake in Songkhla Province in the southern part of peninsular Thailand. Smith mentioned a small, sharply defined black spot on each caudal-fin lobe and provided counts of "about 42" lateral-line scales and 25 branched anal-fin rays for the three specimens on which the description was based. Bănărescu (1971) examined the holotype (incorrectly giving USNM 103373 instead of 103372 as the catalog number) and gave counts of 39 or 40 lateral-line scales and 24 branched anal-fin rays. Vilasri et al. (2018) gave counts of 36 lateral-line scales and 25 branched anal-fin rays for the holotype and an SL of 42.8 mm. Our counts were 39 lateral-line scales

and 25 branched anal-fin rays. Morphological characteristics do not distinguish *C. maculicauda* from *P. johorensis*, and *C. maculicauda* is recognized here as a synonym of *P. johorensis*.

Although no molecular data are available for the population in Thale Sap, the type locality for *C. maculicauda* in the southern part of peninsular Thailand lies within a biogeographic zone that further supports recognition of *C. maculicauda* as a synonym of *P. johorensis* rather than a name available for its sister species, described below as *P. melanosticta*, and which occurs only north of the Malay Peninsula. The type locality of *C. maculicauda* lies far south of the Isthmus of Kra and the Surat Thani—Krabi Line, both of which have been recognized as major biotic transition zones (e.g., Li & Li, 2018). The relevance of these transition zones to diversification in freshwater fishes has been demonstrated by Bohlen et al. (2020a, 2020b). In both studies by Bohlen et al., populations north of the Malay Peninsula were genetically distinct and treated as taxonomically distinct from those to the south. Also, specimens from the Tapi River basin (ANSP 179972), which is north of the *C. maculidauda* type locality, are assignable morphologically to *P. johorensis* rather than to *P. melanosticta*. They have 13 (vs. usually 12) pectoral-fin rays and 22–26 branched anal-fin rays compared to usually 27–28 for *P. melanosticta*.

Most of the 34 individuals of *P. johorensis* from the Malay Peninsula examined had a large black spot (sometimes faded in preserved specimens) on each lobe of the caudal fin. In contrast, few of the 41 specimens examined from Sumatra and Borneo had large black spots on the caudal fin; most had a black posterior edge on the fin or lacked any concentration of black pigment. Although this geographic distinction suggests the presence or absence of black spots is a genetic and not an environmentally induced difference, other differences in morphology are minor, and the genetic data showed no significant distinction (Figure 4). Populations of *P. johorensis* in Indonesia have consistently been misidentified, including in GenBank, as *P. oxygastroides* or *P. hypophthalmus*, presumably because they lack black spots on the caudal-fin lobes.

3.8 | *Parachela melanosticta*, n. sp.

urn:lsid:zoobank.org:pub:
C5433ED1-6 EB8-4090-AAC2-9F835FABEC31.

3.8.1 | Holotype

NIFI 5120, 47.3 mm SL, Thailand, Kanchanaburi Province, Mae Klong River, north bank in Tha Lo (subdistrict), Tha Muang (district), 13.98272, 99.57335, Limpichat, J., Tangjitjaroen, W., Page, L., July 26, 2021.

3.8.2 | Paratypes

All from Mae Klong River basin. UF 248183 (6, 44.2–58.9), ZRC 65078 (2, 45.4–47.6), all same locality and date as holotype. UF 193003 (5, 22.2–44.9), same locality as holotype, September 14, 2021; LSUMZ 22403 (2, 36.2–40.0), same locality and date as UF 193003. UF 247796 (5, 38.6–48.4), canal, 13.90704, 99.65862, Tangjitjaroen, W., Limpichat, J., Page, L., August 13, 2021. UF 248093 (3, 40.67–41.6), tributary oxbow of Mae Klong River, 13.90699, 99.66615, Limpichat, J., Tangjitjaroen, W., Page, L., August 15, 2021. Non-paratypes in Material Examined.

3.8.3 | Diagnosis

Parachela melanosticta is distinguished from all other species of *Parachela* except *P. johorensis* by having a large black spot (vs. no spot) near the tip of each caudal-fin lobe (Figure 13). It is distinguished from *P. johorensis* genetically (Figure 4) and by having 25–32, usually 27–29 (vs. 22–29, usually 24–26) branched anal-fin rays and usually 12 (vs. usually 13) pectoral-fin rays. *P. melanosticta* is further distinguished from *P. cyanea* by lacking black spot on caudal-fin base and by having usually 12 (vs. usually 14) pectoral-fin rays; from *P. williaminae* by having dorsal-fin origin over or slightly anterior (vs. distinctly posterior) to anal-fin origin and 25–32 (vs. 30–37) branched anal-fin rays; from *P. microlepis* by having pectoral fin reaching anal fin, dorsal-fin origin over or slightly anterior (vs. distinctly posterior) to anal-fin origin, 35–44 (vs. 50–63) lateral-line scales, 25–32 (vs. 28–38) branched anal-fin rays, and usually 7 (vs. 6) pelvic rays; from *P. hypophthalmus* by having 35–44 (vs. 45–59) lateral-line scales and lacking black longitudinal band in each caudal-fin lobe; and from *P. oxygastroides* and *P. ingerkongi* by having pectoral fin reaching anal fin and usually having strongly arched (vs. straight or slightly arched) predorsal profile and lacking black longitudinal band in each caudal-fin lobe.

3.8.4 | Description

Meristic data in Tables 6–9, morphometric data in Table 12, shape and color in Figure 13. Body strongly compressed (mean width/SL = 6.2%) and moderately deep (mean depth/SL = 27.0%). Dorsal profile strongly arched upward from eye to dorsal-fin origin, then descending to caudal peduncle. Dorsal-fin origin over or slightly anterior to anal-fin origin. Anal fin with 25–32 (usually 27–29) rays. Pelvic fin short (mean = 12.4% SL), 7 (rarely 6) rays. Pectoral fin long (mean = 35.7% SL), extending well past pelvic fin, usually to anal-fin origin; 11–13 (usually 12) rays. Vertebrae: 15–16 abdominal + 21–22 caudal = 37 total ($N = 3$). Lateral line with 35–44 pored scales on body, 0–3 on caudal fin. Largest specimen 58.9 mm SL (UF 248183).

3.8.5 | Color

In life, *P. melanosticta* is translucent with a silvery sheen and silver-white on the lower body, has a dusky black midlateral stripe, and melanophores on the fin rays, along the anal-fin base, and in a line just

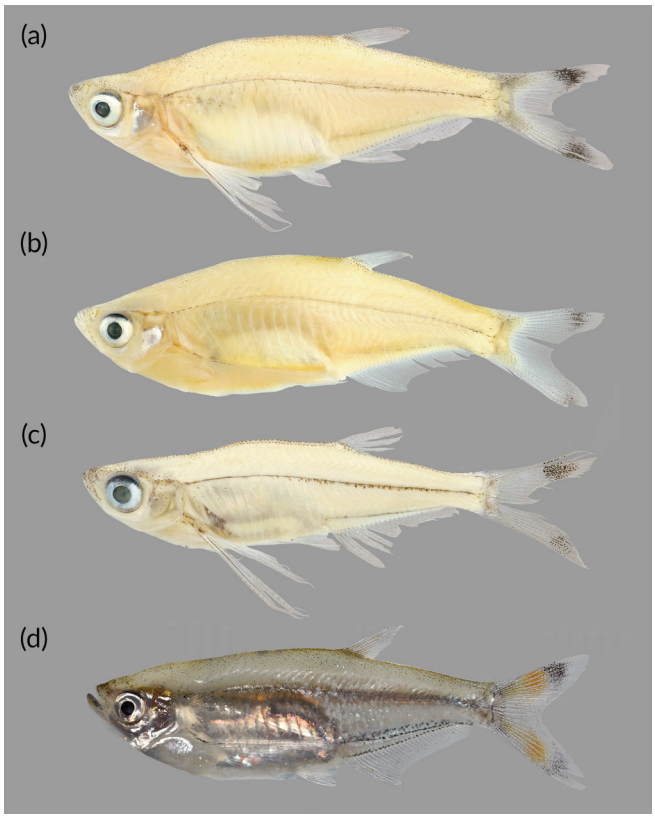

FIGURE 13 *Parachela melanosticta*. (a) Holotype, NIFI 5120, 47.3 mm standard length (SL), Mae Klong River, Kanchanaburi Province, Thailand. (b) UF 243504, 42.4 mm SL, Vajiralongkorn Reservoir, Kanchanaburi Province, Thailand. (c) UF 235931, 27.6 mm SL, Klong Sung, Trat Province, Thailand. (d) Paratype, UF 248183, 58.9 mm SL, Mae Klong River, Kanchanaburi Province, Thailand.

above and parallel with the anal-fin base (Figure 13). A large black spot is present near the tip of each caudal-fin lobe, sometimes preceded by a yellow or orange spot.

3.8.6 | Etymology

Melanosticta, meaning black spotted, is in reference to the large black spots near the tips of the caudal-fin lobes; from Greek, adjective.

3.8.7 | Distribution

P. melanosticta is found in the Mae Klong, Bang Pakong, and Trat River basins in Thailand and in the Mekong River basin in Cambodia and Thailand (Figure 7). Some of these populations previously were referred to as *P. maculicauda* (e.g., Panitvong, 2022; Taki et al., 2021), but *P. maculicauda* is a synonym of *P. johorensis* as discussed earlier. *P. melanosticta* lives in backwaters, reservoirs, and flowing pools of creeks and rivers in lowland areas.

3.8.8 | Remarks

Considerable variation occurs within *P. melanosticta* in lateral-line scale counts with the highest counts in the Mae Klong River basin and the lowest in the Trat River basin (Table 9).

3.9 | *Parachela cyanea* Kottelat, 1995

Parachela cyanea Kottelat, 1995: 55, fig. 2. Type locality: Indonesia: Borneo: Kalimantan Barat: Kapuas River basin: Sungai Tangit at Radai Tangit, 0°57′26″ N 112°04′39″ E. Holotype: MZB 5911.

3.9.1 | Diagnosis

Parachela cyanea is distinguished from all other species of *Parachela* by having a black spot at base of caudal fin, and from all species except *P. ingerkongi* by having modally 14 (vs. usually 12–13) pectoral-fin rays. It is further distinguished from *P. ingerkongi* by having pectoral fin reaching anal fin and 23–26 (vs. 29–33) branched anal-fin rays and lacking black longitudinal band in each caudal-fin lobe; from *P. oxygastroides* by having pectoral fin reaching anal fin, and lacking black longitudinal band in each caudal-fin lobe; from *P. hypophthalmus* by having 37–39 (vs. 45–59) lateral-line scales; from *P. williaminae* by having dorsal-fin origin over or slightly anterior (vs. distinctly posterior) to anal-fin origin and 23–26 (vs. 30–37) branched anal-fin rays; from *P. microlepis* by having pectoral fin reaching anal fin, dorsal-fin origin over or slightly anterior (vs. distinctly posterior) to anal-fin origin, 7 (vs. 6) pelvic-fin rays, 37–39 (vs. 50–63) lateral-line scales, and 23–26 (vs. 28–38) branched anal-fin rays; from *P. johorensis* by having 37–39 (vs. 38–45) lateral-line scales; and from *P. melanosticta* by having 23–26 (vs. 25–32) branched anal-fin rays and by lacking large black spot near tip of each caudal-fin lobe.

3.9.2 | Description

Meristic data in Tables 6–9, morphometric data in Table 11, shape in Figure 14. Body strongly compressed (mean width/SL = 5.5%) and moderately deep (mean depth/SL = 25.5%). Dorsal profile straight or slightly arched upward from nape to dorsal-fin origin, then descending to caudal peduncle. Dorsal-fin origin over or slightly anterior to anal-fin origin. Anal fin with 23–26 branched rays. Pelvic fin short (mean = 12.6% SL), 7 rays. Pectoral fin long (mean = 35.0% SL), extending usually to anal-fin origin; 14 rays. Vertebrae: 15–17 abdominal + 19–21 caudal = 35–36 total ($N = 5$). Lateral line with 37–39 pored scales on body, 1–2 on caudal fin. Largest specimen 50 mm SL (MZB 5911; Kottelat, 1995).

3.9.3 | Color

Live individuals have a bluish translucent body and a black vertical blotch or spot at the caudal-fin base; fins hyaline but pectoral and

caudal fins sometimes blackish (Kottelat, 1995). Preserved specimens have a bold black spot at the base of the caudal fin, a thin black mid-lateral stripe, and melanophores on the fin rays, along the lateral line, along the anal-fin base, and in a line just above and parallel with the anal-fin base (Figure 14).

3.9.4 | Distribution

P. cyanea is known from two river basins in western Borneo, the Kapuas River basin in West Kalimantan and the Seruyan River basin in Central Kalimantan (Figure 9). Tan and Kottelat (2009:17, table 1) listed *P. cyanea* as occurring in the Batang Hari basin in eastern Sumatra, although no specific locality or reference to specimens were provided, and the references cited in the table do not mention the species. Known localities for *P. cyanea* are in lowland areas, and the dot on Batang Hari in Figure 9 was placed in the middle of the lowland portion of the drainage. *P. cyanea* lives in streams and shallow lakes (Kottelat, 1995).

3.10 | *Parachela microlepis*, n. sp.

urn:lsid:zoobank.org:pub:4570A13F-7536-4C55-950E-8FE924073204.

3.10.1 | Holotype

THNHM-F023465, 44.1 mm SL, Thailand, Kanchanaburi Province, tributary of Mae Klong River, 13.90704, 99.65862, Limpichat, J., Tangjitjaroen, W., Page, L. M., September 14, 2021.

3.10.2 | Paratypes

All from Mae Klong River basin. LSUMZ 22294 (10, 22.2–25.4 mm SL), UF 248209 (43, 18.4–44.1 mm SL), ZRC 64380 (5, 22.7–46.6 mm SL), all same locality and date as holotype. UF 247795 (5, 41.3–48.7), same locality as holotype, August 13, 2021. UF 248101 (2, 43.5–44.8), tributary of oxbow lake of Mae Klong, 13.90699, 99.66615, Limpichat, J., Tangjitjaroen, W., Page, L. M., August 15, 2021. UF 247913, 6, 18.4–27.5, same locality as UF 248101, September 16, 2021. Non-paratypes in Material Examined.

FIGURE 14 *Parachela cyanea*. CAS 226182, 25.2 mm standard length (SL), reservoir at Bangkal, Central Kalimantan Province, Indonesia.

3.10.3 | Diagnosis

Parachela microlepis is distinguished from all other species of *Parachela* by having six versus seven pelvic rays, from all other species of *Parachela* except *P. hypophthalmus* by having >49 lateral-line scales, and from all other species of *Parachela* except *P. williaminae* by having dorsal-fin origin distinctly posterior (vs. over, slightly anterior, or slightly posterior) to anal-fin origin. *P. microlepis* is further distinguished from *P. hypophthalmus*, *P. ingerkongi*, and *P. oxygastroides* by lacking a black longitudinal band in each caudal-fin lobe; from *P. cyanea*, *P. hypophthalmus*, *P. johorensis*, *P. melanosticta*, and *P. williaminae* by having pectoral fin not reaching anal fin; from *P. johorensis* and *P. melanosticta* by having no large black spot near the tip of each caudal-fin lobe; and from *P. cyanea* by having 28–38 (vs. 23–26) branched anal-fin rays and no black blotch at caudal-fin base. *P. microlepis*, *P. cyanea*, and *P. johorensis* are smallest species in genus, reaching maximum SL of only ~50 mm (Tables 4 and 5).

3.10.4 | Description

Meristic data in Tables 6–9, morphometric data in Table 13, shape and color in Figure 15. Body strongly compressed (mean width/SL = 5.2%) and moderately deep (mean depth/SL = 23.7%). Dorsal profile arched upward above eye, flat to dorsal fin, then descending to caudal peduncle. Dorsal-fin origin distinctly posterior to anal-fin origin. Anal fin with 28–38 branched rays (see Remarks). Pelvic fin short (mean = 10.5% SL), six (rarely seven) rays. Pectoral fin long (mean = 29.6% SL), extending to pelvic fin, 11–13 (usually 12) rays. Vertebrae: 16 abdominal + 22 caudal = 38 total ($N = 3$). Lateral line with 50–63 pored scales on body, 1–2 on caudal fin. Largest specimen 48.7 mm SL (UF 247795).

3.10.5 | Color

In life, *P. microlepis* is transparent with the eyes, gills, viscera, and a dusky stripe along the spine appearing dark or silvery. There is a yellow-gold stripe along the spine and scattered melanophores in the fins and over the body, along the dorsal midline, along the anal-fin base, and in a line parallel with the anal-fin base (Figure 15). Upon capture, the body quickly becomes opaque with silver highlights on the scales (Figure 15).

3.10.6 | Etymology

Microlepis, meaning small scale, in reference to the much smaller scales on *P. microlepis* in comparison to other species of *Parachela* in Indochina; from Greek, noun.

3.10.7 | Distribution

P. microlepis is known from the Mekong River basin of Cambodia and Thailand, and the Bang Pakong, Chao Phraya, and Mae Klong River basins of Thailand (Figure 7). *P. microlepis* lives in backwaters and flowing pools of creeks and rivers in lowland areas.

3.10.8 | Life history

Small YOY (18.4–27.5 mm SL) were collected in an oxbow lake in Kanchanaburi Province, Thailand, on September 16, 2021 (UF 247913), suggesting that spawning occurred in August during the rainy season.

3.10.9 | Remarks

In several aspects, *P. microlepis* is the most distinctive species of *Parachela*. It has only six pelvic-fin rays and many more lateral-line scales than other species (except for *P. hypophthalmus*) and has the most distinctive shape with a shorter snout, longer anal fin, and longer anal-fin base (Figure 5).

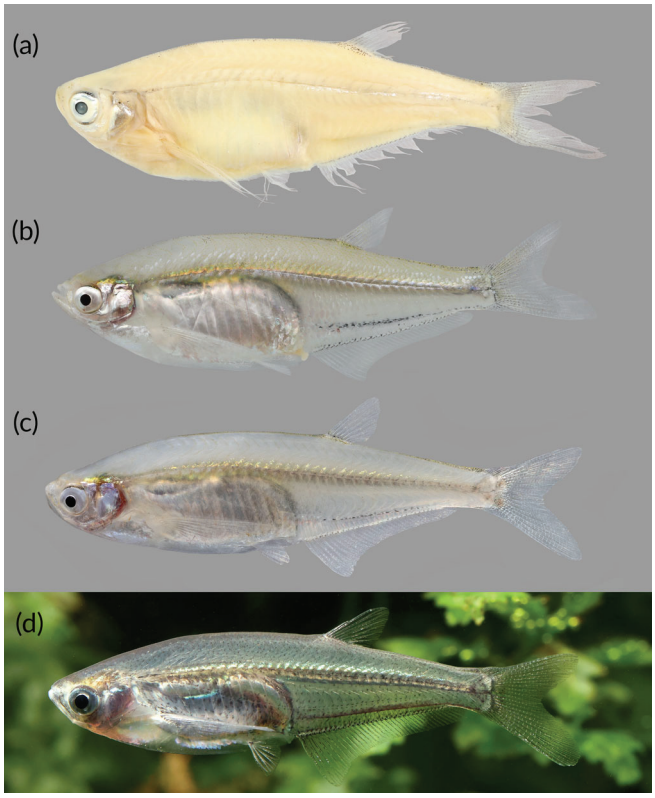

FIGURE 15 *Parachela microlepis*. (a) Holotype, THNHM-F023465, 44.1 mm standard length (SL), Mae Klong River, Kanchanaburi Province, Thailand. (b) Paratype, UF 248209, 44.1 mm SL, same collection data as holotype. (c) UF 248743, 43.8 mm SL, Mun River basin, Ubon Ratchathani Province, Thailand. (d) Live individual, 50 mm SL, Nan River, Phitsanulok Province, Thailand, photo by Nonn Panitvong.

The molecular phylogenetic analysis recovered two well-supported clades within *P. microlepis* (Figure 4). The Mae Klong River population was separated from the Mekong River population with an average between-group mean *COI* p-distance of 2.3%. Interestingly, the sample from Tonle Sap, Cambodia (ICH_01390), which now drains into the Mekong River, clustered with the Mae Klong clade rather than with other Mekong samples, perhaps reflecting the earlier westward flow of the lower Mekong River (Carbonnel, 1972; Rainboth et al., 2012) and connections with river drainages to the west. No molecular data are available for the Chao Phraya River basin.

Geographic structure also was found in the number of branched anal-fin rays (Table 6), with Mekong River specimens having fewer rays (28–36; mean = 31.1) than those in the Mae Klong (32–37; mean = 34.5) and Chao Phraya (32–38; mean 34.2); and in the number of lateral-line scales (Table 8) with specimens from Tonle Sap and Stung Treng (both part of Mekong River drainage) in Cambodia having especially low counts, those from the Mekong and Mae Klong rivers having the highest counts, and those from the Chao Phraya River having intermediate counts. Although this geographic differentiation within *P. microlepis* suggests separate evolutionary trajectories among the river basins, additional data—in particular molecular data from the Chao Phraya and rivers in Cambodia—are needed.

4 | DISCUSSION

In previous studies, *Oxygaster* was hypothesized to be sister to *Parachela* + *Macrochirichthys* (Howes, 1979; Tang, Lumbantobing, & Mayden, 2013). Our results, suggesting *Macrochirichthys* to be sister to *Oxygaster* + *Parachela*, were surprising in that the condition of epaxial musculature extending forward at least to the middle of the eye in *Macrochirichthys* and *Parachela* was a putative synapomorphy; in *Oxygaster*, as in other xenocyprinids, the musculature stops at the posterior margin of the eye or more posteriorly. However, our analysis included no *RAG1* data for *Macrochirichthys*, and additional phylogenetic studies with greater taxon and character sampling are needed to better understand the supraspecific relationships of this clade. Likewise, relationships among species of *Parachela* are based on molecular data for only five of the eight species and would benefit from additional taxon and character sampling.

The taxonomy of *Parachela* has been confused since the original descriptions of *P. oxygastroides* and *P. hypophthalmus* by Bleeker in the mid-19th century. A large part of the confusion seems attributable to the substantial intraspecific variation in color and other morphological characteristics, including meristic counts (Tables 6–9) and body shape (Tables 10–13, Figure 5).

Color is variable within at least some species, presumably in relation to environmental variables—possibly including during ontogenetic development. The transparency of the body and fins in life is extreme in some species, as observed in *P. cyanea* (Kottelat, 1995) and *P. microlepis* (Panitvong, 2022—as "*Parachela* sp. Clear"), and less

extreme in others, for example, *P. williaminae* has a more translucent appearance. Transparency and translucency are most evident in clear water. Likewise, concentrations of black pigment, including the large black spots on the caudal fin of *P. melanosticta* and some populations of *P. johorensis*, are affected by habitat. Individuals from turbid water show less black, and those from less turbid water—including "black water" found in forested swamps and wetlands—have more pigment. The usual absence of black spots on the caudal fin of *P. johorensis* in Indonesia has resulted in a lack of recognition of that species in Indonesia—at least in publications—even though it is widespread in Sumatra and found in Borneo. Dusky black longitudinal bands in the caudal fin, one in each lobe, occur in some but not all individuals of *P. oxygastroides*, *P. hypophthalmus*, and *P. ingerkongi*, as well as in the morphologically similar and often syntopic *O. anomalura*, further confounding taxonomy. The caudal-fin bands are most evident on live or recently preserved specimens (e.g., Roberts, 1989, fig. 40) but are often faint or absent in preserved specimens.

Species of *Parachela* vary interspecifically and intraspecifically in the degree to which the predorsum is arched. Most individuals of *P. johorensis* have a strongly arched predorsum, whereas most *P. oxygastroides* and *P. ingerkongi* have a nearly straight or only slightly arched predorsum. Other species fall in between. The typical state for each species is evident when examining large numbers of specimens, and that state is used in the diagnoses and descriptions. However, this character, like color, is best used in combination with other traits when making identifications.

Of the seven species names of *Parachela* listed as valid by Fricke et al. (2023), the molecular and morphological data analysed herein indicate that *P. cyanea*, *P. ingerkongi*, *P. hypophthalmus*, *P. oxygastroides*, and *P. williaminae* are valid, and *P. siamensis* and *P. maculicauda* are synonyms. *P. johorensis* is removed from the synonymy of *P. oxygastroides*, and two previously unrecognized species are described: *P. melanosticta* and *P. microlepis*. These eight species of *Parachela*, five in mainland Southeast Asia, and five in Borneo, Java, and Sumatra, with *P. oxygastroides* and *P. johorensis* in both areas, are described following a revised diagnosis of the genus *Parachela*.

AUTHOR CONTRIBUTIONS

Lawrence M. Page and Jirasin Limpichat conceived the study. Data were generated by Weerapongse Tangjitjaroen, Jirasin Limpichat, Lawrence M. Page, John M. Pfeiffer, Zachary S. Randall, and Sampan Tongnunui. Data analyses were done by Lawrence M. Page, Weerapongse Tangjitjaroen, John M. Pfeiffer, David A. Boyd, and Zachary S. Randall. Permits were obtained by Sampan Tongnunui and Lawrence M. Page. Manuscript was prepared by all the authors. Funding was generated by Lawrence M. Page and Zachary S. Randall.

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APPENDIX A: MATERIAL EXAMINED

Scientific name is followed by country (with Borneo, Java, or Sumatra added for Indonesia), river basin, province or state, institutional catalog number, number of specimens examined (and "of" if morphological data taken on subset of sample), standard length in mm of specimens examined, water body (or market), geocoordinates ("est." if estimated herein), collectors, and date of collection. Hwy = highway, P. = Province, photo = photo only examined, R. = River, St. = State.

Macrochirichthys macropterus: **Indonesia:** Borneo: Mahakam R. basin: East Kalimantan P.: UF 188048, 2, 72.7–92.0, Loa Ensihan, oxbow near Kotabangun, -0.29132, 116.56362, Lumbantobing, D., et al., 27 Jan. 2013. Sumatra: Musi R. basin: South Sumatra P.: UMMZ 155564, 3, 146.0–255.0, Palembang, -2.9917, 104.76338, Thienemann, A., no date.

Oxygaster anomalura: **Malaysia:** Baram R. basin: Sarawak St.: ROM 54052, 3 of 19, 146.2–177.2, Tabaau R., near confluence with Silat R., 2.88056, 114.92556, Ang, M., et al., 5 Oct. 1980. **Indonesia**: Sumatra: Way Seputih basin: Lampung P.: UF 161918, 1, 97.9, trib., Way Batang Hari, -4.88373, 105.57865, Page, L. M., et al., 28 Oct.

2005. Coastal basin: Lampung P.: UF 167213, 1, 90.2–94.2, Way Talangbawang at Menggala, -4.46667, 105.28333, Page, L. M., et al., 9 Aug. 2006. **Thailand**: Huay Yang basin: Prachuap Khiri Khan P.: ANSP 87865, 2, 114.1–121.1, Huay Yang, 11.61431, 99.67634, Deschauensee, R., 18 Sep. 1936. Mae Klong R. basin: Kanchanaburi P.: UF 243498, 5, 99.6–124.0, Vajiralongkorn Reservoir, Sangkhla Buri, 15.12401, 98.45347, Page, L. M., et al., 1 Jul. 2019. **Vietnam:** Dak Krong R. basin: Dak Lak P.: UF 241493, 2, 125.0–133.8, stream joining Dak Ken & Dak Tol, Yok Don National Park, 12.78803, 107.63875, Thai, T., 9 Aug. 2013.

Parachela cyanea: **Indonesia**: Borneo: Seruyan R. basin: Central Kalimantan P.: CAS 226182, 8 of 21, 25.2–34.5, reservoir at Bangkal, -2.70172, 112.38852, Roberts, T. R., 12 Jun. 1992.

Parachela hypophthalmus: **Indonesia**: Borneo: Barito R. basin: South Kalimantan P.: USNM 393974, 10 of 90, 41.5–51.9, Barabai fish market, -2.5817, 115.382, Lumbantobing, D. N., 24 Aug. 2007. Jorong R. basin: South Kalimantan P.: USNM 393659, 5 of 20, 12.1–38.9, Jorong R., Kabupaten Tanah Laut, -3.98, 114.94, Lumbantobing, D. N., 7 Aug. 2007. Kapuas R. basin: West Kalimantan P.: MZB 3237, photo, 57.0, Danau Piam near Ketungau, 0.39189, 111.6250, Roberts, T. R., et al., 5–6 Aug. 1976; MZB 3243 (photo), 117.0, oxbow at Nangaembaluh, 0.83341, 112.65, Roberts, T. R., et al. 12 Aug. 1976; ROM 38603, 1, 102.7, oxbow at Nangaembaluh, 0.83333, 112.65, Roberts, T. R., 12 Aug. 1976; UMMZ 209886, 5 of 5, 40.5–64.1, Kapuas River, Danau Mawan near Kampong Nibung, 0.65, 112.175, Roberts, T. R., et al., 5 Jul. 1976; USNM 230200, 7, 44.1–65.5, Kapuas R., 23 km W/SW Putussibau, 0.8, 112.75, Roberts, T. R., 8 Aug. 1976. Landak R. basin: West Kalimantan P.: CAS 49244, 4, 40.5–49.7, trib., Landakca R., 27 km west of Ngabang, 0.4, 109.74, Roberts, T. R. & Woejoatmodjo, S., 14 Jul. 1976. Tapin R. basin: South Kalimantan P.: USNM 393939, 5 of 20, 25.8–34.2, paddy fields, -2.9289, 115.163, Lumbantobing, D. N., 24 Aug. 2007. Sumatra: Musi R. basin: South Sumatra P.: RMNH 4985, lectotype, 118.5, Palembang, -2.98668, 104.77155 (est.); BMNH 1866.5.2.218, paralectotype, 130.0 (photo). **Malaysia**: Sarawak: BMNH 1895.2.28.66, 1, 1.42161, 111.27454 (est.). Tabulated Data for *P. hypophthalmus* includes counts for lectotype and paralectotype from Alfred (1963) and for type of *Parachela Breitensteinii* from Steindachner (1881a).

***Parachela ingerkongi*: Malaysia**: Tawau R. basin: Sabah St.: USNM 135946, holotype, 73.4 mm, Tawao [Tawau] R., at Tawau, 4.25, 118.0, Sep. 1909; USNM 202680, 6 paratypes, 59.0–75.0 mm, same as holotype; CAS 33584, 3, 85.2–94.8, Tawau R., 4.26423, 117.90334, Herre, A. W., 19 Jan. 1937.

Parachela johorensis: **Malaysia**: Sekudai R. basin: Johor St.: CAS 39347, 5, 22.1–31.7, Sekudai R., Kulai, 1.6561, 103.6032, Herre, A. W., 17 Oct. 1940. Kesang R. basin: Malacca St.: USNM 101264, 1 of 2, 31.9, 40.6–41.6, Lake Chinchin outlet, 2.26931, 102.49712, Herre, A. W., 26 Mar. 1934. Pahang River basin: Pahang St.: ZRC 3179, 7 (photo), Tasek Bera, 3.81941, 102.41907 (est.), Lindsey, C. C., 29 March 1963. Perak River basin: Perak St.: ZRC 1420, 8 (photo), Kota Tampan, 5.04036, 100.95496 (est.), Tweedie, M., 1938. South Ulu Sedili R. basin: Johor St.: UF 160958, 5, 31.9–46.7, on Hwy from Mersing to Kota Tinggi, 2.07083, 103.86533, Robins, R. H. & Page, L. M., 15 Apr. 2004. **Indonesia**: Sumatra: Air Lematang basin: South Sumatra P.: UF 167201, 5 of 11, 33.4–42.1, Air Lekukam, -3.46025, 103.8929, Page, L. M., et al., 5 Aug. 2006; UF 167203, 10 of 11, 35.5–46.2, Air Kikim Kecil, -3.76387, 103.45947, Hadiaty, R., et al., 3 Aug. 2006. Batang Hari basin: Jambi P.: ZRC 42244, 1 (photo), Pijoan, Danau Saut Padang, -1.55568, 103.43252 (est.), Tan, H. H., et al., 8 June 1996. Buluh R. basin: North Sumatra P.: UF 185034, 8 of 20, 27.0–30.8, Buluh River, 3.5505, 99.05345, Lumbantobing, D., 9 Aug. 2012. Indragiri basin: Riau P.: ZRC 41949, 7 (photo), upper Indragiri R., Riau, -0.35887, 102.35257, Tan, H. H., et al., Nov. 1996. Way Sekampung basin: Lampung P.: UF 161728, 8 of 24, 32.8–43.8, Way Gedongwani, -5.24165, 105.48433, Robins, R. H., et al., 1 Nov. 2005. Borneo: Coastal basin: West Kalimantan P.: ZRC 49968, 40 (photo), Kabupaten Sambas, 1.25800, 109.19179, Tan, H. H., et al., 17 April 1998. Mahakam R. basin: East Kalimantan P.: UF 190670, 5 of 118, 32.2–38.9, Loa Ensihan, oxbow near Kotabangun, -0.29132, 116.56362, Lumbantobing, D., et al., 27 Jan. 2013. **Thailand**: Gulf of Thailand basin: Songkhla P.: USNM 103372, holotype of *Chela maculicauda*, 42.8, Klong Ranode [Ranot], Thale Sap, 7.77167, 100.30438, Smith, H. M., 9 Oct. 1923. Tapi R. basin: Krabi/Surathani P.: ANSP 179972, 6, 26.0–40.8, Tapi R., at Hwy 4035 bridge, 8.54478, 98.86985, Sabaj, M. H. & Hardman, M., 22 Feb. 2001.

Parachela melanosticta: **Cambodia**: Mekong R. basin: Kandal P.: UMMZ 234475 (2 of 37), 33.0–35.5, floodplain lake, 11.73333, 104.95, Rainboth W. J. and fishery officers, 25 Jan. 1996. **Thailand**: Bang Pakong basin: Prachinburi P.: CAS 92533, 1, 28.8, Klong Kamong, Kabinburi, 14.04553, 101.789136, Roberts, T. R., 22 Mar. 1989. Mae Klong R. basin: Kanchanaburi P.: UF 248093, 3 paratypes, 40.67–41.6, trib. oxbow of Mae Klong R., 13.90699, 99.66615, Limpichat, J., et al., 15 Aug. 2021; NIFI 5120, holotype, 47.3, Mae Klong River, north bank in Tha Lo [subdistrict], Tha Muang [district], 13.98272, 99.57335, Limpichat, J., et al., 26 Jul. 2021; UF 248183, 6 paratypes, 44.2–58.9, same data as NIFI 5120; ZRC 65078, 2 paratypes, 45.4–47.6, same data as NIFI 5120; UF 192936, 3, 40.6–47.4, same locality & collectors as UF 248183, 12 Aug. 2021; UF 193003, 5 paratypes, 22.2–44.9, same locality as holotype, 14 Sep. 2021; LSUMZ 22403, 2 paratypes, 36.2–40.0 mm SL, same data as UF 193003. Vajiralongkorn Reservoir: UF 243504, 9 of 28, 36.1–42.4, Sangkhla Buri, 15.12401, 98.45347, Boyd, D. A., et al., 1 Jul. 2019; UF 248256, 4, 41.4–49.0, Sangkhla Buri, 14.7519, 98.57685, Page, L. M., et al., 1 Jul. 2021. Mae Klong River: UF 247796, 5 paratypes, 38.6–48.4, canal, 13.90704, 99.65862, Tangjitjaroen, W., et al., 13 Aug. 2021. Mekong R. basin: Ubon Ratchathani P.: AUM 55973, 4, 25.2–26.5, Mun R. at mouth of Chi R., 15.18126, 104.71472, Armbruster, J., et al., 8 Jan. 2012. AUM 56015, 8, 31.8–37.3, Chi R., 2 km above mouth, 15.19512, 104.71336, Grudpan, C., et al., 8 Jan. 2012. Trat R. basin: Trat P.: UF 235931, 3, 27.2–30.7, Klong Sung, Ban Kraduk Chang at Hwy 3157 bridge, 12.46943, 102.61595, Thailand Expedition 2014, 29 Jan. 2014.

Parachela microlepis: **Cambodia**: Mekong R. basin: Kandal P.: UMMZ 234477, 5 of 46, 38.7–47.7, floodplain lake near Mekong R., 11.73333, 104.95, Rainboth, W. J. & fishery officers, 26 Jan. 1996. Kompong Speu P: UMMZ 234507, 5 of 6, 38.8–42.2, Prek Thnot at

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Parachela oxygastroides: **Cambodia**: Mekong R. basin: Kandal P.: UMMZ 232368, 6, 59.7–70.2, Prek Ta Pov, 13.5, 104.86667, Rainboth, W. J., 2 Feb. 1995. Stung Treng P.: TCWC 16137.17, 1, 84.5, Sekong [Tonle Srepok] R. at Koh Chan, 14.43039, 106.33331 (est.), Ou, C., et al., 9 Jan. 2010. Takeo P.: UMMZ 235627, 5, 51–72, Tasek, 10.733, 104.8833, Rainboth, W. J., et al., 24 Feb. 1996. **Indonesia**: Sumatra: Air Lematang basin: South Sumatra P.: UF 167207, 5 of 9, 61.9–79.1, Air Belido, local fishers, -3.16432, 104.42723, Page, L. M., et al., 6 Aug. 2006; UF 167211, 1, 70.8, Air Lematang, fish market in Lahat, -3.79315, 103.53595, Hadiaty, R., et al., 5 Aug. 2006. Air Musi basin: South Sumatra P.: UF 167202, 1, 77.4, Air Rambang, market in Prabumlih, -3.51667, 104.58333, Page, L. M., et al., 7 Aug. 2006. Way Seputih basin: Lampung P.: UF 162175, 1, 70.3, Way Batang Hari at Lampung, -4.86478, 105.5961, Lopez, J., et al., 4 Nov. 2005. Borneo: Kapuas R. basin: West Kalimantan P.: CAS 49427 (photo), 63.2, Danau Piam near Ketungau, 0.39189, 111.6250, Roberts, T. R., et al., 5–6 Aug. 1976; UMMZ 209916, 1, 102.7, Sungai Tawang near Danau Pengembung, 0.81667, 112.05, Roberts, T. R. & fishers, 14 Aug. 1976; USNM 230201, 2, 114.6–128.8, same data as UMMZ 209916. Kusan R. basin: South Kalimantan P.: USNM 409797, 1, 115 mm, Aib R., Kampung Aib, -3.3000, 115.544, Lumbantobing, D., 12 Aug. 2007. Mahakam R. basin: East Kalimantan P.: ROM 51764, 10 of 14, 61.9–85.9, upstream of Muyub Ilir, 0.065, 115.74167, Christensen, M., et al., 13 Aug. 1982; UMMZ 70665, 2, 59.8–74.2, Bata Bangal [Batoe Pangal], 0.55138, 117.08463, Siboga Expedition.: no date. Java: Jakarta P.: BMNH 1866.5.2.216, lectotype of *Leuciscus oxygastroides*, 123.0 TL, Jakarta, -6.13667, 106.82778 (est.), no date. **Laos**: Mekong R. basin: Champasak P.: UMMZ 235310, 1, 77.9, Ban Hang Khone, 13.933, 105.933, Baird, I., no date. Savannakhet P.: UMMZ 241583, 2, 67.6–71.9, Xe Bangfai, Ban Hatkhamhiang, 17.0667, 104.91667, Rainboth, W. J., 27 March 1998. **Malaysia**: Andaman Sea basin: Selangor St.: CAS 66241, 10, 114.2–163.0, Bernam R., 3.75, 101.167, Zakaria–Ismail, M., 11 Feb. 1985. Pahang R. basin: Pahang St.: CAS 31122, 1, 122.1, Mentiga R., 3.37013, 102.97065, Birtwistle, W., 14 Jul. 1927. **Thailand**: Chao Phraya R. basin: Ayutthaya P.: NIFI 1159, 2, 58.9–84.8 mm SL, Chao Phraya R., 14.59123, 100.46204 (est.), 1 Dec. 1966; UF 248531, 8 of 9, 79.8–98.8, Chao Phraya R., 14.17823, 100.5019, Tangjitjaroen, W., 21 June 2022. Bangkok P.: ANSP 89515, 3 of 103, 67.8–101.0, 66.9–68.9, Bangkok, 13.70562, 100.56187 (est.), Deschauensee, R. M., 1936; ANSP 61300, 1, 60.1, Chao Phraya R., 13.70562, 100.56187, Deschauensee, R. M., no date; ANSP 89515, 3 of 103, Chao Phraya R., 13.70562, 100.56187, Deschauensee, R. M., no date; ANSP 61283, 2 of 16, 75.6–81.5, Chao Phraya R., 13.70562, 100.56187, Deschauensee, R. M., no date. Chiang Mai P.: ANSP 57456, type of *Chela pointoni*, 58.3, Ping R., 18.7458, 98.9848 (est.), Deschauensee, R. M., 5 Jan. 1933; UMMZ 236933, 1, 40.4, Ping R. above Bhumibol Reservoir, 18.42306, 98.69782, 2 Dec. 1963. Kamphaeng Phet P.: UF 249500, 2, 92.0–99.8, Ping R., Ruen Thai Ban Rim Nam Muang, 16.53063, 99.49418, Tangjitjaroen, W., 6 Feb. 2023. Nakhon Sawan P.: UF 248776, 1, 98.3, Nakhon Sawan Inland Fisheries, 15.71355, 100.18791, Randall, Z. S., et al., 8 June 2022. Phetchabun P. BMNH 1861.10.8.17, type of *Chela siamensis*, 102 mm TL, 15.90111, 101.06541 (est.), no date. Sukothai P.: NIFI 4782, 4, 35.0–55.8 mm SL, Bankong Dam, Yom River, 16.92835, 99.95091, 22 Oct. 2010; NIFI 4716, 2, 57.4–59.2 mm SL, Klong Samphung, Yom River, 17.0157, 99.8012 (est.), no date. Tak P.: UF 30230, 1, 76.1, Bhumiphol Reservoir, 17.30391, 98.90293, Haller, W., 15 Apr. 1977. Mekong R. basin: Kalasin P.: UMMZ 235152, 1, 83, Lam Pao Reservoir, 16.68194, 103.515, Rainboth, W. J. & Tucker, A., 29 Oct. 1975. Khon Kaen P.: UMMZ 236952, 1, 48.0, trib., Pong R., 16.7738, 102.62127, Witt, et al., no date. Sisaket P.: UF 248764, 2, 75.2–77.5, Mun R. at Rasi Salai Dam, 15.34318, 104.09898, Randall, Z. S., et al., 6 June 2022. Sakon Nakhon P.: UF 237316, 1, 52.7, Songkhram River at confluence with Yam River, 17.70906, 104.07671, Boyd,

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