Article

ZOOTAXA

On the paraphyly of *Homaloptera* (Teleostei: Balitoridae) and description of a new genus of hillstream loaches from the Western Ghats of India

ZACHARY S. RANDALL & LAWRENCE M. PAGE

Florida Museum of Natural History, University of Florida, Dickinson Hall, Gainesville, FL 32611, USA.
E-mails: zrandall@flmnh.ufl.edu, lpage1@ufl.edu

Abstract

Homaloptera van Hasselt 1823 as treated historically exhibits substantial morphological diversity and is paraphyletic based on both morphological and molecular data. The morphological diversity and phylogenetic relationships of *Homaloptera*, *Homalopteroides* Fowler 1905, *Homalopterula* Fowler 1940, and *Balitoropsis* Smith 1945, are elucidated. *Pseudohomaloptera* Silas 1953 is removed from the synonymy of *Homaloptera*. Homalopteroidini is created for the monophyly of *Homalopteroides* and *Homalopterula*; it is the sister group to balitorini Swainson 1839. *Ghatsa* n. gen. is created for species previously assigned to *Homaloptera* from the Western Ghats of India, and a redescription of *Ghatsa montana* (Herre 1945) is provided.

Key words: *Ghatsa*, *Balitoropsis*, *Homalopterula*, *Pseudohomaloptera*, *Homalopteroides*, *Helgia*, *Chopraia*, Loaches, Southeast Asia

Introduction

The limited information on phylogenetic relationships of hillstream loaches has led to inconsistent and often transient recognition of genera. Relationships among species historically assigned to *Homaloptera* van Hasselt 1823 have been particularly problematic, as noted by Fang (1930), Hora (1932), Kottelat (1998), Tan & Ng (2005), Tan (2009), and Randall & Page (2012). Several names historically synonymized with *Homaloptera* (*Helgia* Vinciguerra 1890, *Homalopteroides* Fowler 1905, *Chopraia* Prashad & Mukerji 1929, *Homalopterula* Fowler 1940, *Balitoropsis* Smith 1945, and *Pseudohomaloptera* Silas 1953) have been recognized as genera or junior synonyms in recent years (Randall 2012; Kottelat 2012; Kottelat 2013). Some of these recent classifications are without supporting data or diagnoses, which only adds to the confusion of balitorid classification. The objectives of this study were to test the most recent classifications (Randall 2012; Kottelat 2012; Kottelat 2013) by analyzing genetic and morphological data (including type species when available) to identify clades and to diagnose well-supported clades as genera using morphological criteria.

Material and methods

Morphological. Measurements follow Hubbs & Lagler (2004) or Kottelat (1984) (see Randall & Page 2012 for measurements from each source), and counts follow Randall & Page (2014). The definition of a rostral cap follows Roberts (1982). A central furrow refers to an indentation on the ventral surface of the head at the branchiostegal membrane just anterior to the isthmus. The terms origin and insertion refer, respectively, to the anterior and posterior ends of fin bases for paired and unpaired fins. Total lateral-line scale count includes scales on the caudal fin. Counts are given as ranges where taxa are distinguished by the mode of that range (M). Lengths were measured to the nearest 0.1 mm using digital calipers and taken on the left side when possible. All measurements are given in millimeters (mm). Head length and measurements of the body are given as proportions of standard length (SL). Measurements of the head are presented as proportions of head length (HL).

Institutional abbreviations follow Sabaj Pérez (2012). A '(?)' represents a lack of data or an uncertain locality. Photographs of preserved specimens were taken using a Visionary Digital system (Palmyra, Virginia) with Canon 40D and 5D cameras at the Florida Museum of Natural History and edited using Photoshop CS3. When coordinates for localities were unavailable, they were estimated using maps and GEOlocate. Maps were constructed using ArcMap Version 9.3.1 in ArcGIS 9th edition.

Three-hundred and three individuals were examined in this study representing all but four species of *Homaloptera* (sensu lato) (as recognized by Kottelat 1998) from the Western Ghats of India. The taxonomic status of these species from the Western Ghats of India was assessed using only original descriptions, due to the inaccessibility of specimens.

Molecular. The supraspecific relationships of balitorids were reconstructed using the nuclear recombination activating gene 1 (RAG1) based on recently collected tissues (Table 1) and sequences available on Genbank (Table 2). Total genomic DNA was extracted from fin clips or muscle tissue preserved in 95% ethanol using a DNeasy Tissue Kit (Qiagen) or with a 5% Chelex solution and 3 µl of proteinase K with an overnight digestion. RAG1 was amplified and sequenced using the primers RAG-1F: 5'–AGC TGT AGT CAG TAY CAC AAR ATG–3' (Quenouille *et al.* 2004) and RAG-RV1: 5'–TCC TGR AAG ATY TTG TAG AA–3' (Ŝlechtová *et al.* 2007). Individual samples for the polymerase chain reaction (PCR) consisted of a total 25 µl reaction containing 16.5 µl of sterile water, 2 µl of genomic DNA, 4 µl of MyTaq Reaction Buffer (BioLine USA, Boston, MA), 0.5 µl of MyTaq DNA Polymerase (BioLine USA, Boston, MA), and 1 µl of 10 µm of each primer. The PCR cycling parameters for RAG1 followed Ŝlechtová *et al*. (2007). PCR cleaning with ExoSAP-IT and sequencing took place at the Interdisciplinary Center for Biotechnology Research (ICBR), University of Florida, Gainesville. Geneious version 7.1.4 (Kearse *et al.* 2012) was used to view chromatograms, assemble consensus sequences, and generate a final alignment using the Geneious global alignment tool which was corrected manually. All sequences produced from this study are available on Genbank (Accession numbers given in Table 1).

A Bayesian inference (BI) analysis using MrBayes 3.2.2 (Ronquist *et al.* 2012) and a Maximum Likelihood (ML) analysis using RAxML 7.2 (Stamatakis 2014) were performed through the Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller, Pfeiffer, & Schwartz 2010). In both analyses the cyprinid *Cyprinus carpio* was used to root the tree.

For the BI analysis, SYM+I+G was the best fit substitution model of nucleotide evolution, using the Akaike Information Criterion with JModeltest version 2.1.5 (Darriba *et al.* 2012). Two Markov chain Monte Carlo (MCMC) analyses with four simultaneous chains were run for 5 million generations sampling every 1,000 generations resulting in a 10,002 sampled trees. The standard deviation for split frequencies was 0.002942 and the average potential scale reduction factor for all parameters was 1.015, indicating clear convergence of the two runs. A total of 25% of the first sampled trees were discarded as burn-in, sampling 7,502 trees. The best tree was viewed in Figtree v 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/).

For the ML analysis, GTR+I+G was used as the substitution model of nucleotide evolution, being the best fit substitution model using the Akaike Information Criterion with JModeltest version 2.1.5 (Darriba *et al.* 2012) available for use in RAxML. The –f a option of RAxML was used to generate 1,000 bootstrap replicates (Stamatakis, Hoover, & Rougemont 2008) followed by a search of the best scoring ML tree. The best tree was viewed as in the BI analysis.

Bayes factor (BF), Shimodaira-Hasegawa (SH) and Approximately unbiased test (AU) were performed to determine if various positive and negative topological constraints were significantly different from the optimal topology (Table 3). It was not possible to implement negative constraints in the ML analysis. *Homaloptera* (sensu lato) was constrained as monophyletic to include all species of *Homaloptera*, *Homalopteroides*, *Balitoropsis*, *Pseudohomaloptera*, and *Homalopterula*. BF was used for the BI analysis while SH and AU tests for the ML analysis using Paup 4.0 (Swofford 2003). The Bayes factor (2*ln*Bfs) for competing models was evaluated using the criteria of Kass & Raftery (1995) where a 2*ln*Bfs of 0–2 is not worth more than a bare mention, a 2*ln*Bfs of 2–6 provides positive support, a 2*ln*Bfs of 6–10 provides strong support, and a 2*ln*Bfs of > 10 provides very strong support for the unconstrained best tree.

TABLE 1. Samples produced from this study included in the phylogenetic analysis,

Genus	Species	Vial #	Voucher	Origin (region, province, river)	Genbank accession #
Balitora	*meridionalis*	332	ANSP 179834	Thailand, Kanchanaburi, Ulong	KP322550
Balitoropsis	*ophiolepis*	2006-0588	UF 166109	Sumatra, Lampung, Way Besai	KP322540
	zollingeri	2005-0948	UF 161715	Sumatra, Lampung, Way Rarem	KP322535
		2005-0962	UF 161715	Sumatra, Lampung, Way Rarem	KP322537
Homaloptera	*bilineata*	DAN09-182.02	CAS 231723	Myanmar, Sagaing, Irrawaddy	KP322549
	confuzona	2007-1185	UF 169906	Thailand, Changwat, Khlong Sato	KP322543
		344	ANSP 178721	Thailand, Chanthaburi, shop	KP322551
	ocellata	2005-0955	UF 161719	Sumatra, Lampung, Way Rarem	KP322536
		2005-0980	UF 161605	Sumatra, Lampung, Way Abung	KP322539
	parclitella	336	ANSP 179982	Thailand, Surat Thani, Tapi	KP322552
Homalopteroides	*wassinkii*	2005-0975	UF 161619	Sumatra, Lampung, Way Seputhi	KP322538
	nebulosus	2012-0600	UF 235748	Malaysia, Kelantan, Kelantan	KP322548
	smithi	2012-0157	UF 182840	Thailand, Nakhon Si Thammarat, Pong	KP322546
	stephensoni	E97	USNM 393671	Borneo, S Kalimantan, Aib	KP322553
Homalopterula	*gymnogaster*	SN25	UF 185031	Sumatra, Sumatra Utara, Aek Tongguran	KP322554
Pseudohomaloptera	*leonardi*	2012-0597	UF 235746	Malaysia, Kelantan, Kelantan	KP322547
		2007-1071	UF 169909	Thailand, Chanthaburi, Khruv Wui	KP322541
		2007-1104	UF 169909	Thailand, Chanthaburi, Khruv Wui	KP322542
	sexmaculata	2010-0211	UF 177819	Thailand, Chiang Mai, Mae Tiaen	KP322544
		2011-0203	UF 181170	Thailand, Kanchanaburi, Kroeng Krawia	KP322545

**TABLE 2.** Genbank accession numbers and sources for samples included in the phylogenetic analysis.

Genus	Species	Accession #	Source
Acantopsis	*choirorhynchos*	EU711139	Mayden *et al.* 2008
Balitora	*annamitica*	EF056359	Ŝlechtová *et al.* 2007
Balitoropsis	*zollingeri*	EF056388	Ŝlechtová *et al.* 2007
Cyprinus	*carpio*	EF458304	Mayden *et al.* 2007
Formosania	*fascicauda*	JN177173	Liu *et al.* 2012
Hemimyzon	*yaotanensis*	JN177053	Tang *et al.* 2012
Homaloptera	*parclitella*	EF056358	Ŝlechtová *et al.* 2007
Homalopteroides	*smithi*	EF056356	Ŝlechtová *et al.* 2007
Jinshaia	*abbreviata*	JN177051	Tang *et al.* 2012
	sinensis	JN177052	Tang *et al.* 2012
Lepturichthys	*dolichopterus*	JN177035	Tang *et al.* 2012
	fimbriata	JN177039	Tang *et al.* 2012
Pangio	*kuhlii*	EF056331	Ŝlechtová *et al.* 2007
Sewellia	*lineolata*	HM224068	Tang *et al.* 2010
Sinogastromyzon	*sichangensis*	JN177040	Tang *et al.* 2012
	szechuanensis	JN177055	Tang *et al.* 2012
	hsiashiensis	JN177054	Tang *et al.* 2012
Metahomaloptera	*omeiensis*	JN177041	Tang *et al.* 2012
Pseudogastromyzon	*changtingensis tungpeiensis*	JN177175	Liu *et al.* 2012
	cheni	JN177176	Liu *et al.* 2012
	cheni	EF056357	Ŝlechtová *et al.* 2007
	fangi	JN177177	Liu *et al.* 2012
Vanmanenia	*pingchowensis*	JN177174	Liu *et al.* 2012

TABLE 3. Bayes factor (2lnBF), Shimodaira-Hasegawa (SH) and Approximately Unbiased (AU) tests performed on various positive (+) and negative (-) topological constraints. Bayes factor was evaluated using the criteria of Kass and Raftery (1995). A bolded value represents a significantly better optimal topology.

Constraint	BI ln score	2*ln*BF	ML ln score	SH	AU
Optimal topology	-5402.97	-	-5577.940582	-	-
Homaloptera (sensu lato) (+)	-5412.18	**18.42**	-5591.793874	**0.0449**	**0.0158**
Homalopteroidini (-)	-5417.85	**29.66**	-	-	-
Balitorini (-)	-5409.02	**12.1**	-	-	-
Homalopteroides (-)	-5411.32	**16.7**	-	-	-
Balitoropsis (-)	-5405.45	4.96	-	-	-
Homaloptera (sensu stricto) (-)	-5431.55	**57.16**	-	-	-
Pseudohomaloptera (-)	-5404.87	3.8	-	-	-
(*Balitoropsis* (*Homaloptera*, *Pseudohomaloptera*)) (-)	-5404.66	3.38	-	-	-
(*Homaloptera, Pseudohomaloptera*) (-)	-5404.00	2.06	-	-	-

Phylogenetic results

The optimal topology (i.e. the one with the greatest likelihood) was generated in the BI analysis (Table 3) and is represented in Figure 1.
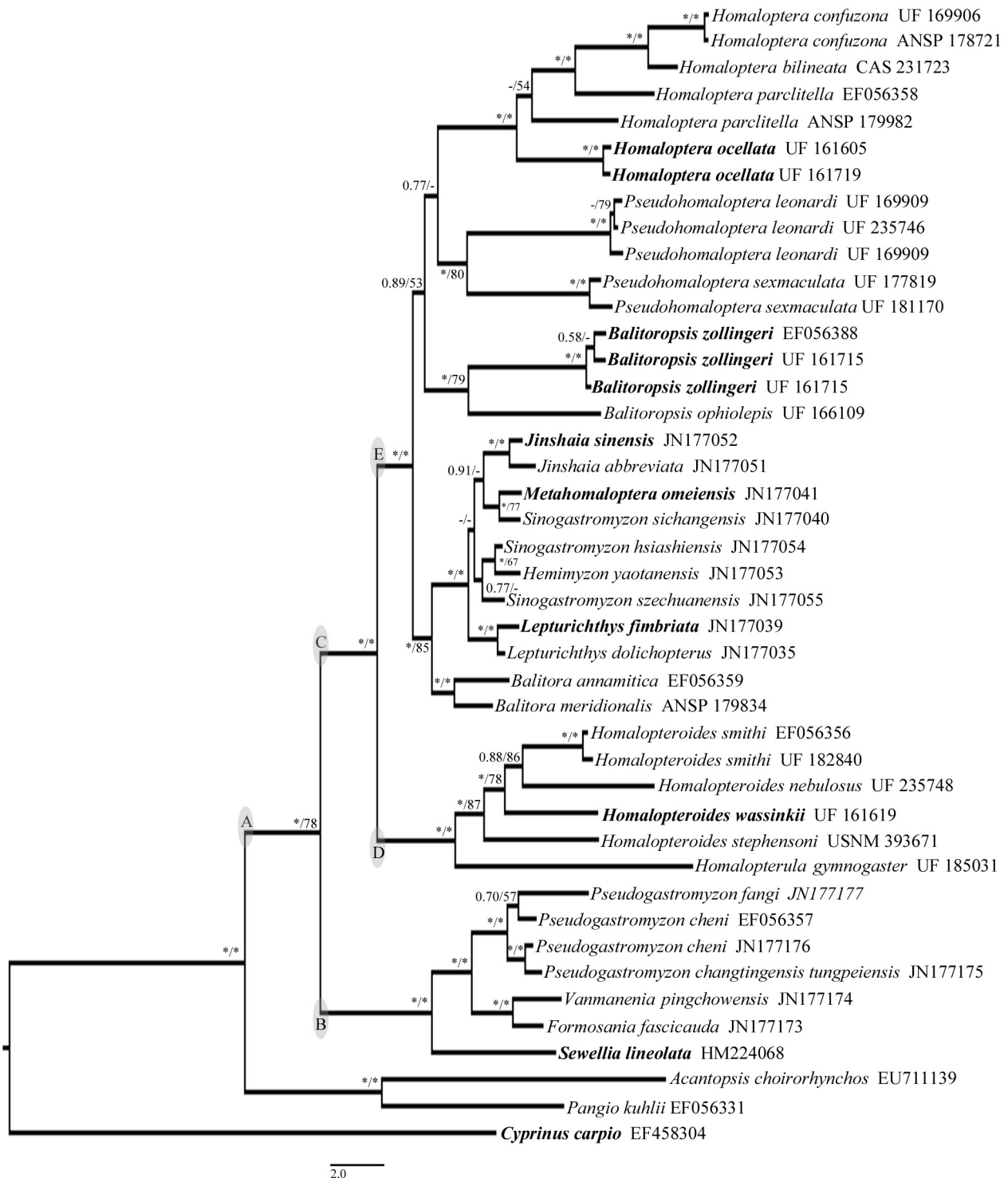
FIGURE 1. Balitorid phylogeny based on Bayesian analysis of RAG1 with support values indicated at the branch lengths (PP/BS). Posterior probability values ≥ 0.95 and bootstrap support ≥ 90 are represented by an asterisk (*). Posterior probability and bootstrap support less than 50 are represented by a hyphen (-).Type species are in bold. A) Balitoridae; B) Gastromyzontinae; C) Balitorinae; D) Homalopteroidini; E) Balitorini.

Homaloptera (sensu lato) is not resolved as monophyletic in either analysis. *Homaloptera*, *Homalopteroides*, *Balitoropsis*, and *Pseudohomaloptera* formed monophyletic groups with the same interrelationships among them and the single species of *Homalopterula* included in the analysis in both BI and ML analyses (Fig. 1). *Balitoropsis*, *Homaloptera* and *Pseudohomaloptera* are more closely related to *Balitora* and its close relatives than they are to *Homalopteriodes* and *Homalopterula*. Within Balitorinae two major clades are resolved: Homalopteroidini, newly proposed tribe name (Fig. 1, D) (*Homalopteroides*, *Homalopterula*), and Balitorini Swainson 1839 (Fig. 1, E) (*Balitora*, *Lepturichthys*, *Sinogastromyzon*, *Hemimyzon*, *Metahomaloptera*, *Jinshaia*, *Balitoropsis*, *Pseudohomaloptera*, *Homaloptera*). Within Balitorini, two major clades are resolved: a strongly-supported clade consisting of *Balitora* as the sister group to *Lepturichthys*, *Sinogastromyzon*, *Hemimyzon*, *Metahomaloptera*, *Jinshaia*; and a weakly-supported clade consisting of *Balitoropsis* as the sister group to *Homaloptera* plus *Pseudohomaloptera*. Species recognized in *Balitoropsis* by Kottelat (2012) (*B. leonardi*, *B. sexmaculata*, *B. stephensoni*) are resolved in the genera *Pseudohomaloptera* (*P. leonardi*, *P. sexmaculata*) and *Homalopteroides* (*H. stephensoni*).

Nearly all negative and positive constraints were significantly worse than the optimal topology (Table 3). The constrained *Homaloptera* (sensu lato) Bayesian best tree had a Likelihood Harmonic mean of -5412.18, a 2lnBfs of 18.42 (very strong support for a paraphyletic *Homaloptera* [s.l.]). The SH and AU tests for the likelihood analysis resulted in a constrained tree that was significantly worse (SH score: 0.0449; AU score: 0.0158). The negative constrained *Homalopteroides* best tree resulted in *Homalopterula gymnogaster* being nested within *Homalopteroides*. The Likelihood Harmonic mean was -5411.32, a 2*ln*Bfs of 16.7 (very strong support for *Homalopteroides*). The negative constrained clade containing *Homaloptera* and *Pseudohomaloptera* resulted in a best tree with *Pseudohomaloptera* as the sister group to *Balitoropsis*. The Likelihood Harmonic mean was -5404.00, a 2*ln*Bfs of 2.06 (positive support for *Homaloptera* being the sister group to *Pseudohomaloptera*).

Based on consistent monophyly, clades recognized herein as genera are *Homaloptera*, *Homalopteriodes*, *Balitoropsis*, *Pseudohomaloptera,* and *Homalopterula. Homalopterula* is represented in the phylogeny by only one individual, but based on its long branch length and morphological diagnosibilty described below, it is recognized as a genus. Although species of *Balitoropsis* and *Pseudohomaloptera* are most similar morphologically, they were not found to form a monophyletic group in any of the unconstrained analyses of genetic data and are easily separated morphologically as described below.


Homaloptera van Hasselt 1823
(Figures 2, 3A, 4D, 5A)

Homaloptera van Hasselt, 1823:133 (type species: *Homaloptera ocellata* van der Hoeven 1830, by subsequent monotypy in van der Hoeven, 1830:211). Gender feminine.
Helgia Vinciguerra, 1890:328 (type species: *Homaloptera bilineata* Blyth, 1860:172, by subsequent designation by Jordan 1920:448). Gender feminine.

Remarks. Two species names were listed in *Homaloptera* by van Hasselt (1823), *H. javanica* and *H. fasciata*. Both lacked a description or figure and are unavailable (nomina nuda) (Hora 1932; Kottelat 1987). The first species described and figured under *Homaloptera* was *H. ocellata* van der Hoeven 1830 (see Roberts 1993:24 for 1830 as publication date), making *H. ocellata* the type species of *Homaloptera*. *Homaloptera bilineata* Blyth 1860 was placed in the genus *Helgia* Vinciguerra 1890 and subsequently designated as the type species of *Helgia* by Jordan (1920). *Helgia* Vinciguerra 1890 is a synonym of *Homaloptera* van Hasselt 1823 (Hora 1932; Kottelat 1998). Kottelat (1998) recognized *Homaloptera ocellata* van der Hoeven 1830, *H. bilineata* Blyth 1860, *H. orthogoniata* Vaillant 1902, and *H. ogilviei* Alfred 1967 as possibly forming a clade (*Homaloptera* sensu stricto) based on the following characters: "unique color patterns (having in common reddish tints and similar dark markings on the head and the fins), a slightly compressed body, 56–65 lateral-line scales and the dorsal-fin origin situated in advance of the pelvic-fin origin." Based on this diagnosis and an elongated head and a lateral-line scale count of 61–77, Tan & Ng (2005) treated this same clade as a subgenus of *Homaloptera*. With the availability of more data and analyses, the only character provided by Kottelat (1998) that seems to be apomorphic for *Homaloptera* (sensu stricto) is color pattern.
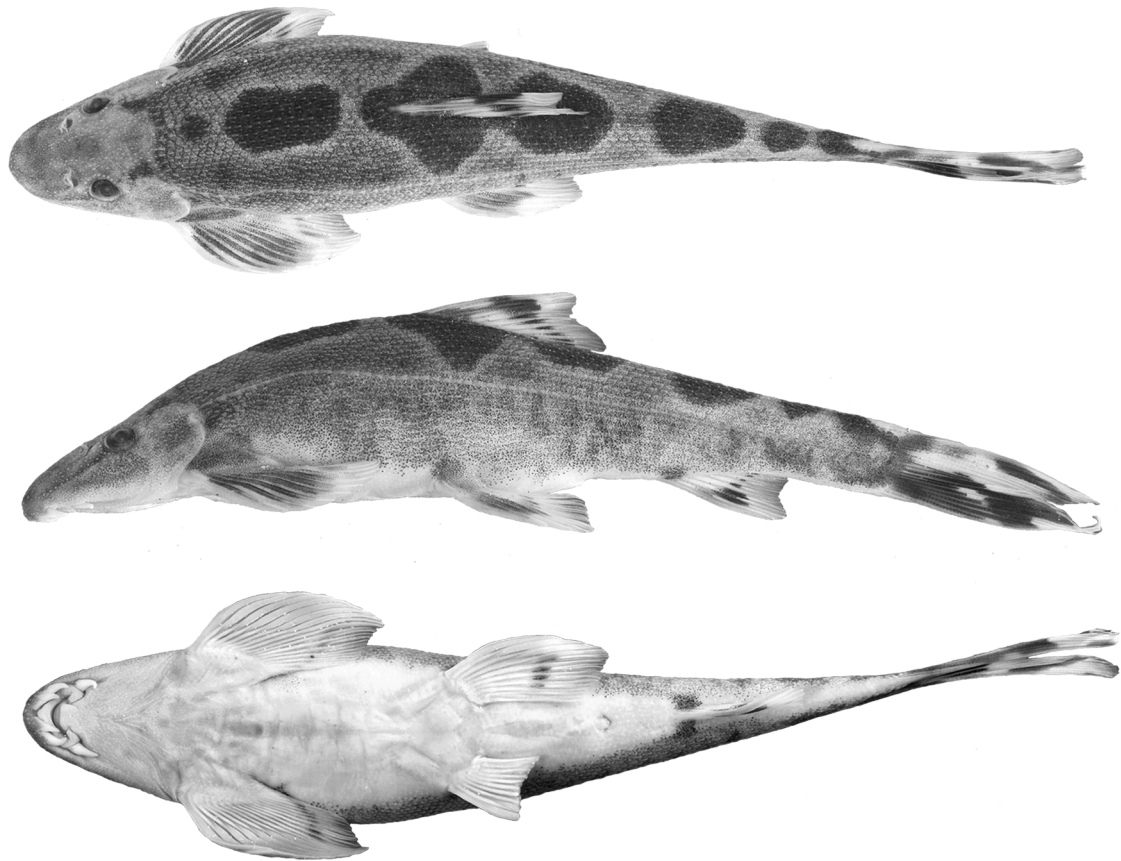
FIGURE 2. Dorsal, lateral, and ventral views of preserved *Homaloptera ocellata*, UF 161718, 64.1 mm SL, Way Seputhi, Lampung Province, Sumatra, Indonesia.

Diagnosis. Distinguishing characters are given in Table 4 and shown in Figures 2, 3A, 4D and 5A. *Homaloptera* is distinguished by the following combination of characters: reddish tints on fins in life (Fig. 3A); dorsal-fin origin anterior to pelvic-fin origin; 7–8½, 8½ (M) branched dorsal-fin rays; 7 branched pelvic-fin rays; forked caudal fin; keeled scales (Fig. 4D); 20–27 predorsal scales; 59–73 total lateral-line scales; no adipose keel on caudal peduncle; anus closer to anal-fin origin than to pelvic-fin insertion; large rostral cap; 2 thick rostral barbels in close proximity to each other; thick triangular upper lip (Fig. 5A); fleshy pad between lateral portions of lower lip (Fig. 5A); absence of central furrow at isthmus.

Species included. *Homaloptera ocellata* van der Hoeven 1830, *H. bilineata* Blyth 1860, *H. orthogoniata* Vaillant 1902, *H. ogilviei* Alfred 1967, *H. confuzona* Kottelat 2000, and *H. parclitella* Tan & Ng 2005. The type localities for species of *Homaloptera* are shown in Figure 6.

Comparison. *Homaloptera* is distinguished from *Homalopteroides* by presence vs. absence of reddish tints on fins in life, having a dorsal-fin origin anterior vs. posterior to pelvic-fin origin; 7–8½, 8½ (M) vs. 6–8½, 7½ (M) branched dorsal-fin rays; 59–73 vs. 33–52 total lateral-line scales; large vs. small rostral cap; medial- and lateral-rostral barbels in close proximity to one another vs. widely separated from one another at base; triangular vs. crescentic upper lip; thick vs. thin upper lip; presence vs. absence of pad between lateral portions of lower lip; and absence vs. presence of a central furrow at isthmus.

Homaloptera is distinguished from *Homalopterula* by presence of reddish tints on fins in life vs. without red color; dorsal-fin origin anterior vs. posterior to pelvic-fin origin; 7–8½, 8½ (M) vs. 5½ and 7½, 7½ (M) branched dorsal-fin rays; keeled vs. smooth scales; 20–27 vs. 28–56 predorsal scales; forked vs. truncated or deeply emarginated caudal fin; absence vs. presence of adipose keel on caudal peduncle; large vs. small rostral cap; medial- and lateral-rostral barbels in close proximity vs. widely separated at base; triangular vs. crescentic upper lip; presence of fleshy pad vs. lobes between lateral portions of lower lip; and absence vs. presence of a central furrow at isthmus.

TABLE 4. Characters distinguishing *Homaloptera*, *Homalopteroides*, *Homalopterula*, *Balitoropsis*, *Pseudohomaloptera* and *Ghatsa*. Values are given as ranges; numbers in parentheses represent modal values. For *Ghatsa*, data from original descriptions are included; values in parentheses are for *G. montana* (CAS-SU 39871).

Character	Homaloptera	Homalopteroides	Homalopterula	Balitoropsis	Pseudohomaloptera	Ghatsa (G. montana)
No. specimens examined	51	148	24	42	37	1
Reddish tints on fins in life	Yes	No	No	No	No	?
Dorsal-fin origin relative to pelvic-fin origin	Anterior	Posterior	Posterior	Anterior or above	Anterior or above	Posterior (Posterior)
Branched dorsal-fin rays	7–8½ (8½)	6–8½ (7½)	5½, 7½ (7½)	8½	8½	7–9½ (7½)
Branched pelvic-fin rays	7	5–8 (7–8)	7	7–9 (8)	8–9 (8)	6–9 (7–8)
Caudal-fin shape	Forked	Forked	Truncate/deeply emarginated	Forked	Forked	Slightly emarginated-emarginated (truncate)
Scales keeled	Yes	Yes/No	No	Yes	Yes	? (No)
Predorsal scales	20–27	14–25	28–56	13–15	13–19	? (ca. 53)
Total lateral-line scales	59–73	33–52	57–75	42–55	50–61	59–95 (ca. 101)
Adipose keel	No	No	Yes	No	No	? (Yes)
Anus closer to pelvic-fin base or anal fin	Anal fin	Anal fin	Anal fin	Pelvic-fin base	Anal fin	Anal fin
Rostral cap	Large	Small	Small	Large	Large	Small
Rostral barbels separated at base	No	Yes	Yes	No	No	Yes
Upper lip shape/width	Triangular/Thick	Crescent/Thin	Crescent/Thick	Crescent/Thick	Triangular and crescent/Thick	Crescent/Thin
Large central furrow at isthmus	No	Yes	Yes	Yes/No	No	?
Structure between portions of lower lip (Pad/Lobes/None)	Pad	None	Lobes	Pad	Pad	None

Homaloptera is distinguished from *Balitoropsis* and *Pseudohomaloptera* by presence vs. absence of reddish tints on fins in life; 7 vs. 8–9 branched pelvic-fin rays; 20–27 vs. 13–15 and 13–19 predorsal scales, respectively. It is further distinguished from *Balitoropsis* by having 59–73 vs. 42–55 total lateral-line scales; anus closer to anal-fin origin vs. closer to pelvic-fin insertion; triangular vs. crescentic upper lip.
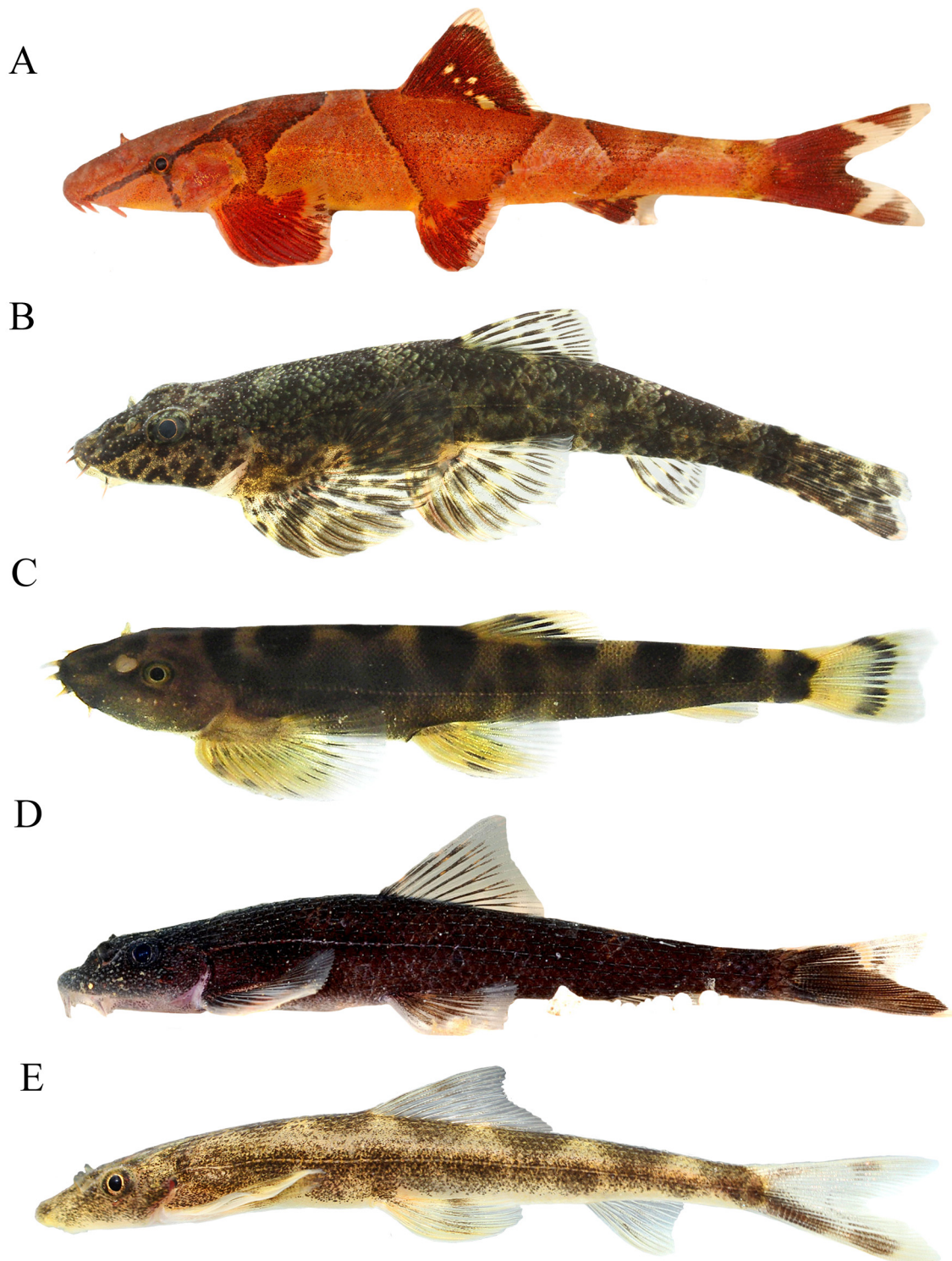
FIGURE 3. Lateral views of living (A) *Homaloptera orthogoniata*, not cataloged, Kalimantan, Borneo, Indonesia. Strong reddish tints on body likely breeding colors; (B) *Homalopteroides smithi*, UF 235740, 45.0 mm SL, Khlong Tasae, Salui Subdistrict, Chumphon, Thailand; (C) *Homalopterula* cf. *ripleyi*, not cataloged, Sumatra, Indonesia; (D) *Balitoropsis zollingeri*, not cataloged, Kalimantan, Borneo, Indonesia; (E) *Pseudohomaloptera leonardi*, UF 235735, 34.2 mm SL, Ta Pi River, Nakhon Si Thammarat, Thailand. Photos (A) & (D) by Renny Hadiaty. Photo (C) by Daniel Lumbantobing. Specimens not to scale.
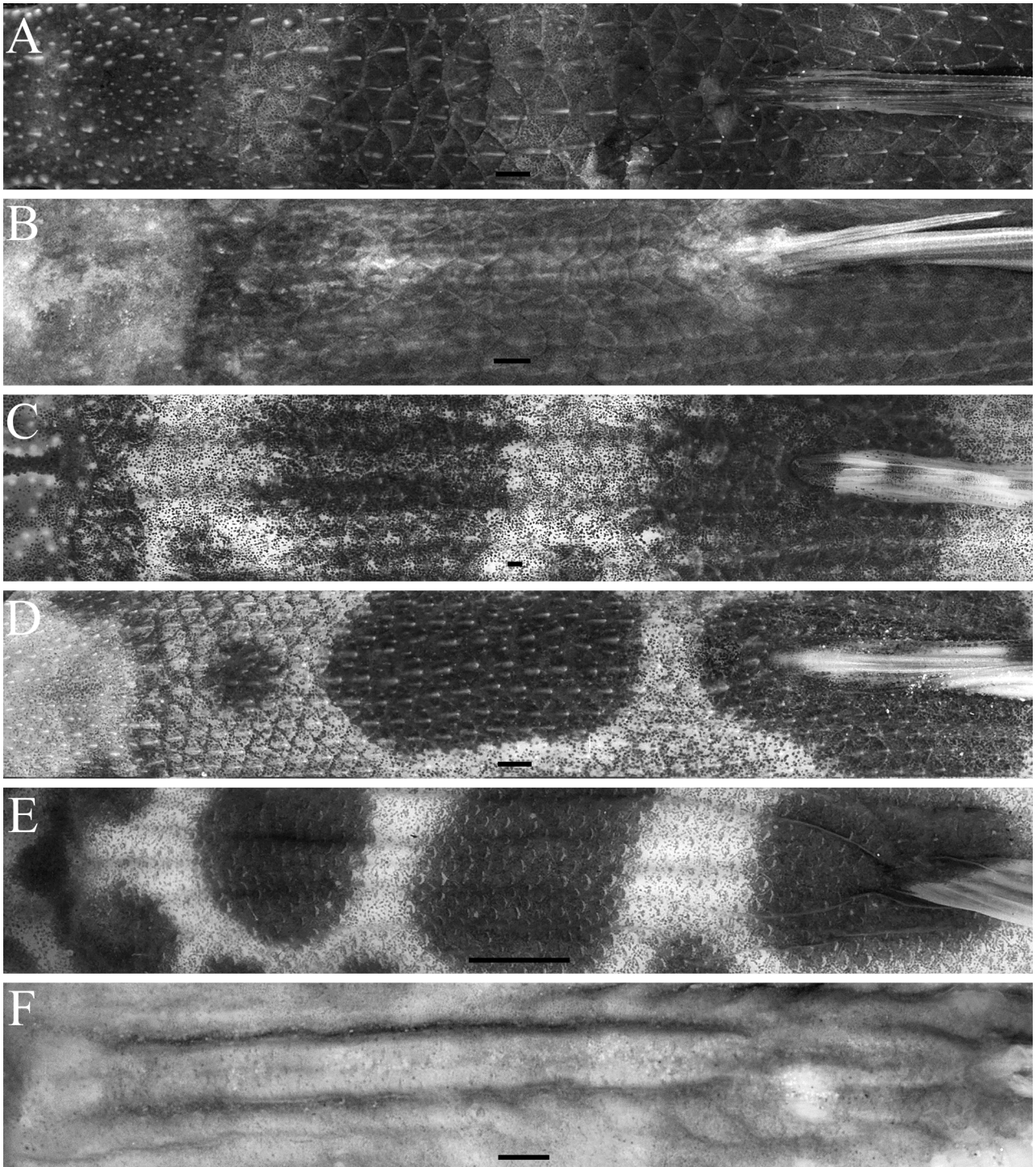
FIGURE 4. Scale sizes and keel patterns of predorsal region: Large, and keeled scales, (A) *Balitoropsis zollingeri*, UF 166094, 52.1 mm SL; (B) *Pseudohomaloptera tatereganii*, RMNH 7632 (holotype), 64.6 mm SL. Large, and wart-like/keeled scales (C) *Homalopteroides wassinkii*, UF 183330, 43.6 mm SL. Medium, and keeled scales, (D) *Homaloptera* cf. *ocellata*, UF 161718, 64.1 mm SL. Small, and smooth scales, (E) *Homalopterula ripleyi*, ANSP 188908, 43.1 mm SL; (F) *Ghatsa montana*, CAS-SU 39871 (holotype), 46.6 mm SL. Scale bar represents 1 mm. Left side of photo is anterior.

Material examined. *Homaloptera ocellata*: Java: RMNH 2723 (holotype); ZMA 100.645 (2), 103.205 (1). Sumatra: UF 161605 (1), 161719 (4), 161718 (2), 166096 (4), 166104 (2), 166106 (2), 166107 (4). *H. bilineata*: Myanmar: RMNH 10263 (1); CAS 231723 (4). *H. orthogoniata*: Borneo (Kalimantan): RMNH 7790 (lectotype); CAS 49326 (1). *H. ogilviei*: Peninsular Malaysia: ZRC 1555 (holotype); BMNH 1966.9.26.1 (paratype); RMNH 25443 (paratype); UF 235405 (1), 235408 (1). Sumatra: UF 161716 (2), 166085 (2), 166091 (2). Thailand: INHS

93605 (1). **H. confuzona**: Thailand: UF 169906 (1); INHS 93493 (5). **H. parclitella**: Peninsular Malaysia: ZRC 49257 (holotype); CAS-SU 39390 (2).
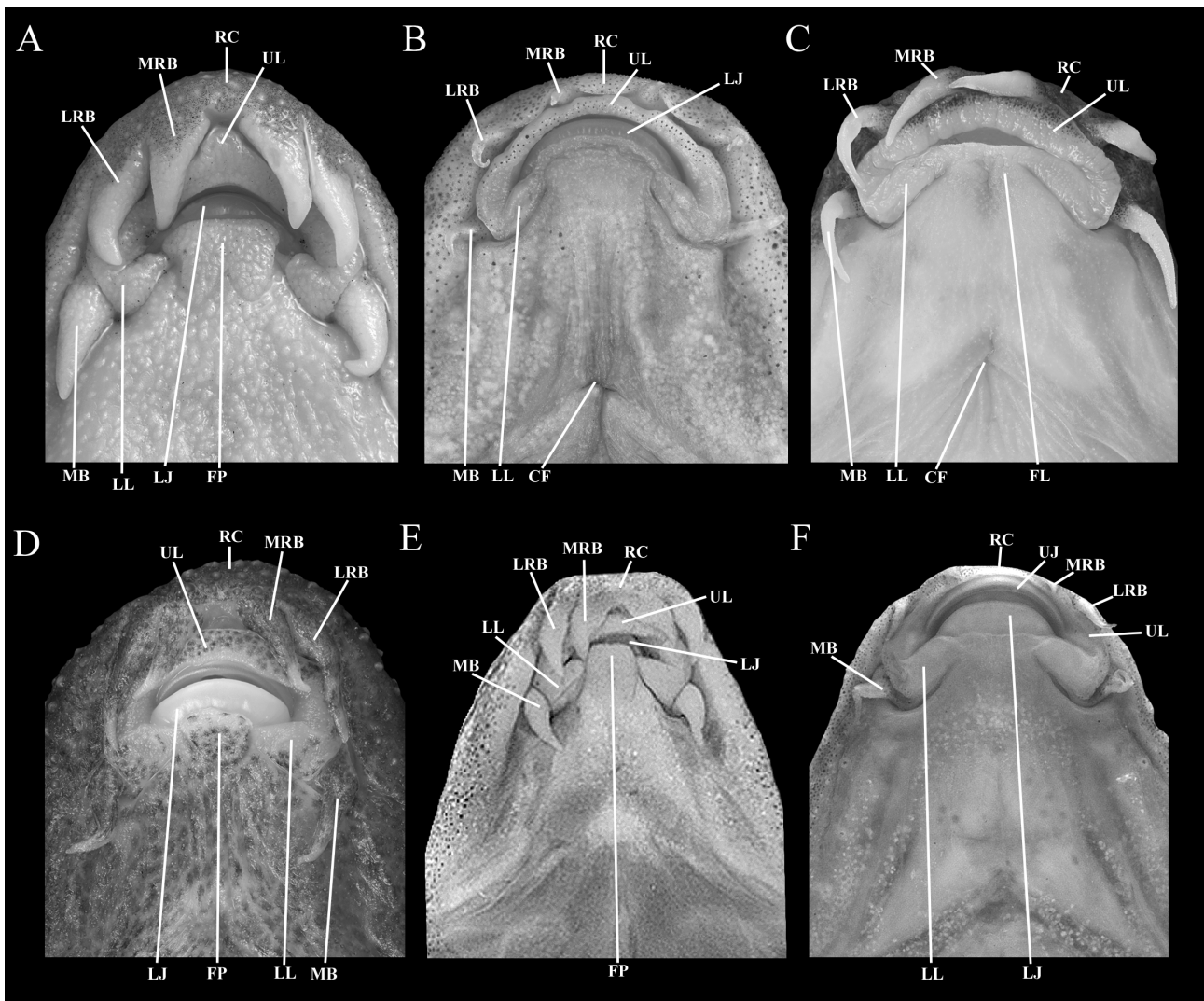
FIGURE 5. Oral morphology of (A) *Homaloptera* cf. *ocellata*, UF 161718, 64.1 mm SL; (B) *Homalopteroides wassinkii*, UMMZ 155660, 46.2 mm SL; (C) *Homalopterula ripleyi*, ANSP 188908, 43.1 mm SL; (D) *Balitoropsis zollingeri*, UF 166094, 52.1 mm SL; (E) *Pseudohomaloptera tatereganii*, RMNH 7632 (holotype), 64.6 mm SL; (F) *Ghatsa montana*, (holotype) CAS-SU 39871, 46.4 mm SL. Abbreviations: CF, central furrow; FL, fleshy lobe; FP, fleshy pad; LJ, lower jaw; LL, lower lip; LRB, lateral-rostral barbel; MB, maxillary barbel; MRB, medial-rostral barbel; RC, rostral cap; UJ, upper jaw; UL, upper lip.

Homalopteroides Fowler 1905
(Figures 3B, 4C, 5B, 7)

Homalopteroides Fowler, 1905:476. (Type species: *Homaloptera wassinkii* Bleeker 1853, by original designation; see Randall & Page, 2012:335 fixed type species as *H. wassinkii*, under Code art. 70.3.1). Gender masculine.
Chopraia Prashad & Mukerji, 1929:188 (Type species:*Chopraia rupicola* Prashad & Mukerji, 1929, by original designation). Gender feminine.

Remarks. *Homalopteroides rupicola* was originally designated as the type species of *Chopraia* (Prashad & Mukerji 1929). *Chopraia* was distinguished from other balitorines by "shape of the head, the situation and better development of the eyes, the branchial openings and the fins (Prashad & Mukerji 1929)." Since these characters are shared with species of *Homalopteroides*, we treat *Chopraia* as a junior synonym of *Homalopteroides* (Randall & Page 2012).
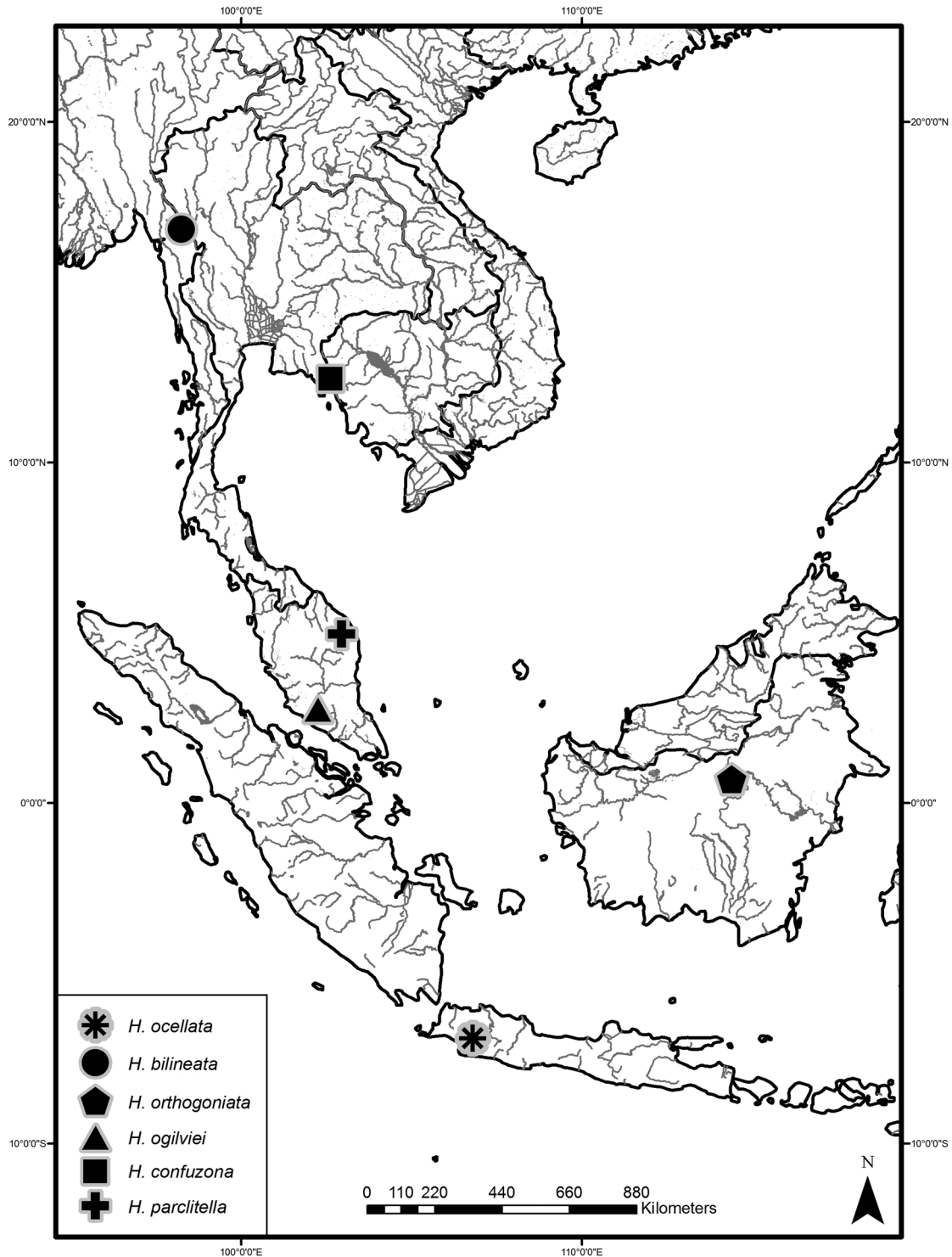
FIGURE 6. Type localities for species of *Homaloptera*. Asterisk represents the type species of the genus.

Diagnosis. Distinguishing characters are given in Table 4 and shown in Figures 3B, 4C, 5B and 7. *Homalopteroides* is distinguished by the following combination of characters: without reddish tints on fins (Fig. 3B) in life, dorsal-fin origin posterior to pelvic-fin origin; forked caudal fin; 6–8½, 7½ (M) branched dorsal-fin rays; wart-like/keeled scales (Fig. 4C), 14–25 predorsal scales; 33–52 total lateral-line scales; anus closer to anal-fin origin than to pelvic-fin insertion; no adipose keel on caudal peduncle; small rostral cap; 2 thin rostral barbels, widely separated from one another; thin crescentic upper lip; no fleshy pad or lobes between lateral portions of lower lip (Fig. 5B); and presence of a central furrow at isthmus.

FIGURE 7. Dorsal, lateral, and ventral views of preserved *Homalopteroides wassinkii*, UMMZ 155660, 46.2 mm SL, Tjisokan, Java, Indonesia.

Species included. *Homalopteroides wassinkii* (Bleeker 1853)*, H. modestus* (Vinciguerra 1890)*, H. rupicola* (Prashad & Mukerji 1929)*, H. smithi* (Hora 1932)*, H. stephensoni* (Hora 1932)*, H. weberi* (Hora 1932)*, H. tweediei* (Herre 1940)*, H. indochinensis* (Silas 1953)*, H. nebulosus* (Alfred 1969)*, H. yuwonoi* (Kottelat 1998), and *H. avii* Randall & Page 2014. The type localities for species of *Homalopteroides* are shown in Figure 8.

Comparison. *Homalopteroides* is distinguished from *Homaloptera* by absence vs. presence of reddish tints on fins in life; dorsal-fin origin posterior vs. anterior to pelvic-fin origin; 6–8½, 7½ (M) vs. 7–8½, 8½ (M) branched dorsal-fin rays; 33–52 vs. 59–73 total lateral-line scales; small vs. large rostral cap; medial- and lateral-rostral barbels widely separated from one another at base vs. barbels in close proximity to one another; crescentic rather than triangular upper lip; thin vs. thick upper lip; presence vs. absence of a central furrow at the isthmus; absence vs. presence of fleshy pad between lateral portions of lower lip.

Homalopteroides is distinguished from *Homalopterula* by having forked vs. truncated or emarginated caudal fin; wart-like/keeled vs. smooth scales; 14–25 vs. 28–56 predorsal scales; 33–52 vs. 57–75 total lateral-line scales; absence vs. presence of adipose keel on caudal peduncle; thin vs. thick upper lip; absence vs. presence of fleshy lobes between lateral portions of lower lip.

Homalopteroides is distinguished from *Balitoropsis* and *Pseudohomaloptera* by having dorsal-fin origin posterior vs. anterior to or above the pelvic-fin origin; 6–8½, 7½ (M) vs. 7–9½, 8½ (M) branched dorsal-fin rays; small vs. large rostral cap; medial- and lateral-rostral barbels widely separated from one another at base vs. barbels in close proximity to one another; thin vs. thick upper lip; absence vs. presence of pad between lateral portions of lower lip. It is further distinguished from *Balitoropsis* by having the anus closer to anal-fin origin than to pelvic-fin insertion.
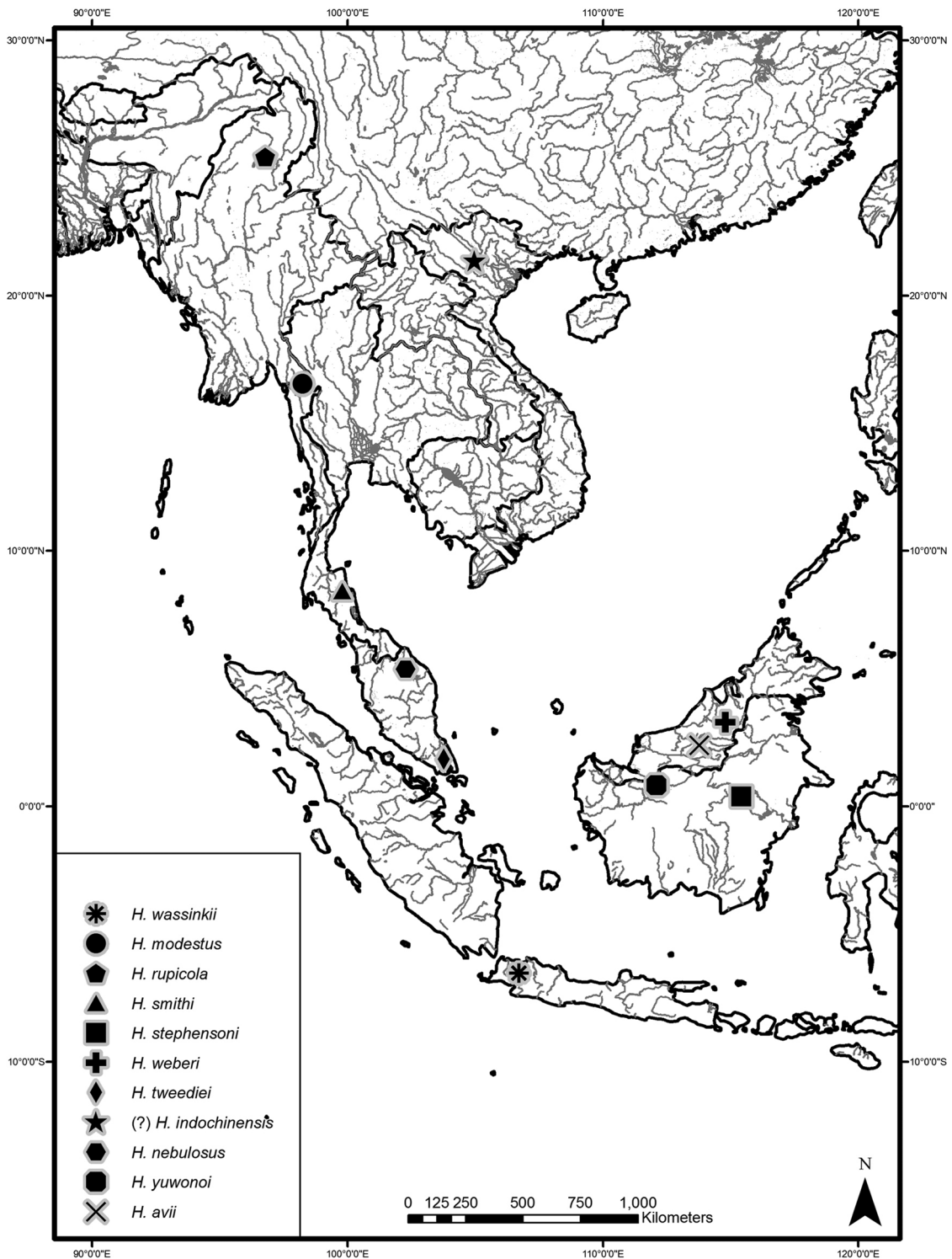
FIGURE 8. Type localities for species of *Homalopteroides*. Asterisk represents the type species of the genus.

Material examined. ***Homalopteroides wassinkii*:** Java: RMNH 4987 (lectotype of *Homaloptera wassinkii*), 1934 (paralectotypes of *Homaloptera wassinkii*) (2), 4627 (2); BMNH 1866.5.2.52 (1); ZMA 103.206 (2); UMMZ 155660 (1); MNHN 3122 (syntype of *Balitora ocellata*). Sumatra: UF 161619 (7). ***H. modestus*:** Thailand: ANSP 179826 (5); NIFI 4517 (1), 3786 (1), 4514 (1); ROM 51147 (2); UF 172926 (1), 173067 (1), 176377 (10), 176408 (2), 176438 (8), 176454 (4), 176544 (1), 176557 (8), 181080 (5), 181160 (9), 181141 (1); ZRC 53385 (1), 53386 (1), 41272 (4). Myanmar: ZRC 22889 (1); BMNH 1893.2.16.50 (paralectotype of *Helgia modesta*); ZMA 100.982 (paralectotype of *Helgia modesta*). ***H. rupicola*:** Myanmar: CAS-SU 28726 (paratype of *Chopraia rupicola*); CAS

231681 (2), 231726 (3), 231835 (1), 61338 (1); USNM 378433 (3); ZRC 43569 (2). ***H. smithi***: Thailand USNM 109821 (syntypes of *Homaloptera smithi*) (5); ANSP 76852 (1), 76851 (3); BMNH 1934.12.18.34 (1); UF 183330 (3), 183411 (2), 183915 (1). ***H. stephensoni***: Borneo: RMNH 7633 (holotype of *Homaloptera stephensoni*); USNM 393671 (3). ***H. weberi***: East Malaysia: BMNH 1895.7.2.81 (syntypes of *Homaloptera weberi*) (7); ZMA 100990 (syntype of *Homaloptera weberi*). ***H. tweediei***: Malaysia: BMNH 1938.12.1.132 (paratype of *Homaloptera tweediei*); CAS-SU 33012 (holotype of *Homaloptera tweediei*), 33013 (paratype of *Homaloptera tweediei*) (2). ***H. indochinensis***: Vietnam?: BMNH 1933.8.19.50 (holotype). ***H. nebulosus***: Malaysia: BMNH 1967.11.15.15 (paratype of *Homaloptera nebulosa*); CAS-SU 66428 (paratype of *Homaloptera nebulosa*); ZRC 1759 (paratype of *Homaloptera nebulosa*); ZRC 2020 (holotype of *Homaloptera nebulosa*); UF 235748 (6). ***H. yuwonoi***: East Malaysia: MZB 5938 (holotype of *Homaloptera yuwonoi*). ***H. avii***: East Malaysia: USNM 323875 (holotype of *Homalopteroides avii*), 323878 (paratype of *Homalopteroides avii*), USNM 323879 (paratypes of *Homalopteroides avii*) (2); UF 185293 (paratype of *Homalopteroides avii*).

Homalopterula Fowler 1940
(Figures 3C, 4E, 5C, 9)

Homalopterula Fowler, 1940:379 (type species: *Homaloptera ripleyi* Fowler 1940:379) by original designation. Gender feminine.

Remarks. *Homalopterula* was created for the new species *Homalopterula ripleyi* Fowler 1940 and distinguished from other balitorids by the "peculiar shape of its jaws, in combination with its truncated caudal and entirely naked medial under surface of the abdomen" (Fowler 1940:379). *Homalopterula* was treated as a junior synonym of *Homaloptera* based on the illustration provided in Fowler's type description and the variation that "exists regarding the nature of the caudal and presence or absence of scales on the ventral surface of the abdomen in species of *Homaloptera*" by Silas (1953). This decision was followed by Roberts (1989).

Kottelat (1998) recognized *Homaloptera gymnogaster* Bleeker 1853, *H. heterolepis* Weber & de Beaufort 1916, *H. ripleyi* (Fowler 1940), and *H. vanderbilti* Fowler 1940 as possibly forming a clade (*Homalopterula*) based on having "a more cylindrical body, a relatively wide mouth, short paired fins, and a truncated or slightly emarginated caudal fin." Based on this description, Tan & Ng (2005) and Ott (2009) treated *Homalopterula* as a subgenus of *Homaloptera*. Randall & Page (2012) recognized *Homalopterula* as a subgenus based on "mouth morphology, dorsal-fin origin over pelvic fin, $\geq$ 60 lateral-line scales, and $\geq$ 30 predorsal scales." They did not include *H. modiglianii*, then recognized as a junior synonym of *H. gymnogaster* (Kottelat 1993). Including it in this study following Kottelat (2012, 2013) changes the lateral-line and predorsal scale count range found in *Homalopterula* to 57–75 and 28–56, respectively.

Diagnosis. Distinguishing characters are given in Table 4 and shown in Figures 3C, 4E, 5C and 9. *Homalopterula* is distinguished by the following combination of characters: without reddish tints on fins in life (Fig. 3C); dorsal-fin origin posterior to pelvic-fin origin; 5½ and 7½, 7½ (M) branched dorsal-fin rays; 7 pelvic-fin rays; truncated or emarginated caudal fin; smooth scales (Fig. 4E), 57–75 total lateral-line scales, 28–56 predorsal scales; anus closer to anal-fin origin than to pelvic-fin base; adipose keel on caudal peduncle; small rostral cap; 2 thick and widely separated rostral barbels; thick crescentic upper lip; 2 fleshy lobes between lateral portions of lower lip (Fig. 5C); and presence of a central furrow at the isthmus.

Species included. *Homalopterula gymnogaster* (Bleeker 1853), *H. modiglianii* (Perugia 1893), *H. amphisquamata* (Weber & Beaufort 1916), *H. heterolepis* (Weber & de Beaufort 1916), *H. ripleyi* Fowler 1940, and *H. vanderbilti* (Fowler 1940). The type localities for species of *Homalopterula* are shown in Figure 10.

Comparison. *Homalopterula* is distinguished from *Homaloptera* by absence vs. presence of reddish tints on fins in life; dorsal-fin origin posterior vs. anterior to pelvic-fin origin; 5½ and 7½, 7½ (M) vs. 7–8½, 8½ (M) branched dorsal-fin rays; 28–56 vs. 20–27 predorsal scales; smooth vs. keeled scales; truncated or emarginated vs. forked caudal fin; presence vs. absence of adipose keel on caudal peduncle; small vs. large rostral cap; medial- and lateral-rostral barbels widely separated from one another at base vs. barbels in close proximity to one another; crescentic rather than triangular upper lip; presence vs. absence of a central furrow at the isthmus; fleshy lobes vs. pad between lateral portions of lower lip.


FIGURE 9. Dorsal, lateral, and ventral views of preserved *Homalopterula ripleyi*, ANSP 188908, 43.1 mm SL, Kampung Bassam, Sumatera Utara Province, Sumatra, Indonesia.

Homalopterula is distinguished from *Homalopteroides* by having truncated or emarginated vs. forked caudal fin; smooth vs. wart-like/keeled scales; 28–56 vs. 14–25 predorsal scales; 57–75 vs. 33–52 total lateral-line scales; presence vs. absence of adipose keel on caudal peduncle; thick vs. thin lips; presence vs. absence of fleshy lobes between lateral portions of lower lip.

Homalopterula is distinguished from *Balitoropsis* and *Pseudohomaloptera* by having dorsal-fin origin posterior vs. anterior to or above pelvic-fin origin; 5½ and 7½, 7½ (M) vs. 8½ branched dorsal-fin rays; 7 vs. 7–9, 8 (M) branched pelvic-fin rays; truncated or emarginated vs. forked caudal fin; smooth vs. keeled scales; 28–56 vs. 13–15 and 13–19 predorsal scales, respectively; presence vs. absence of adipose keel on caudal peduncle; small vs. large rostral cap; medial- and lateral-rostral barbels widely separated from one another at the base vs. barbels in close proximity to one another; presence of fleshy lobes vs. pad between lateral portions of lower lip. It is further distinguished from *Balitoropsis* by having the anus closer to anal-fin origin than to pelvic-fin insertion and 57–75 vs. 42–55 lateral-line scales.

Material examined. *Homalopterula gymnogaster*: Sumatra: BMNH 1866.5.2.49 (holotype of *Homaloptera gymnogaster*); ZMA 100256 (syntypes of *Homaloptera lepidogaster*) (3); UF 185031 (1). ***H. modiglianii*:** Sumatra: BMNH 1931.10.29.1-2 (syntypes of *Homaloptera modiglianii*) (2). ***H. amphisquamata*:** Sumatra: ZMA. 100.998 (syntype of *Homaloptera amphisquamata*), 100.994 (syntypes of *Homaloptera amphisquamata*) (2). ***H. heterolepis*:** ZMA 100.999 (syntypes of *Homaloptera heterolepis*) (3). ***H. ripleyi*:** Sumatra: ANSP 68713 (holotype), 187003 (2), 187004 (1), 188907 (1), 188908 (4). ***H. vanderbilti*:** Sumatra: ANSP 68688 (holotype of *Homaloptera vanderbilti*), 68700 (Holotype of *Homaloptera ulmeri*).
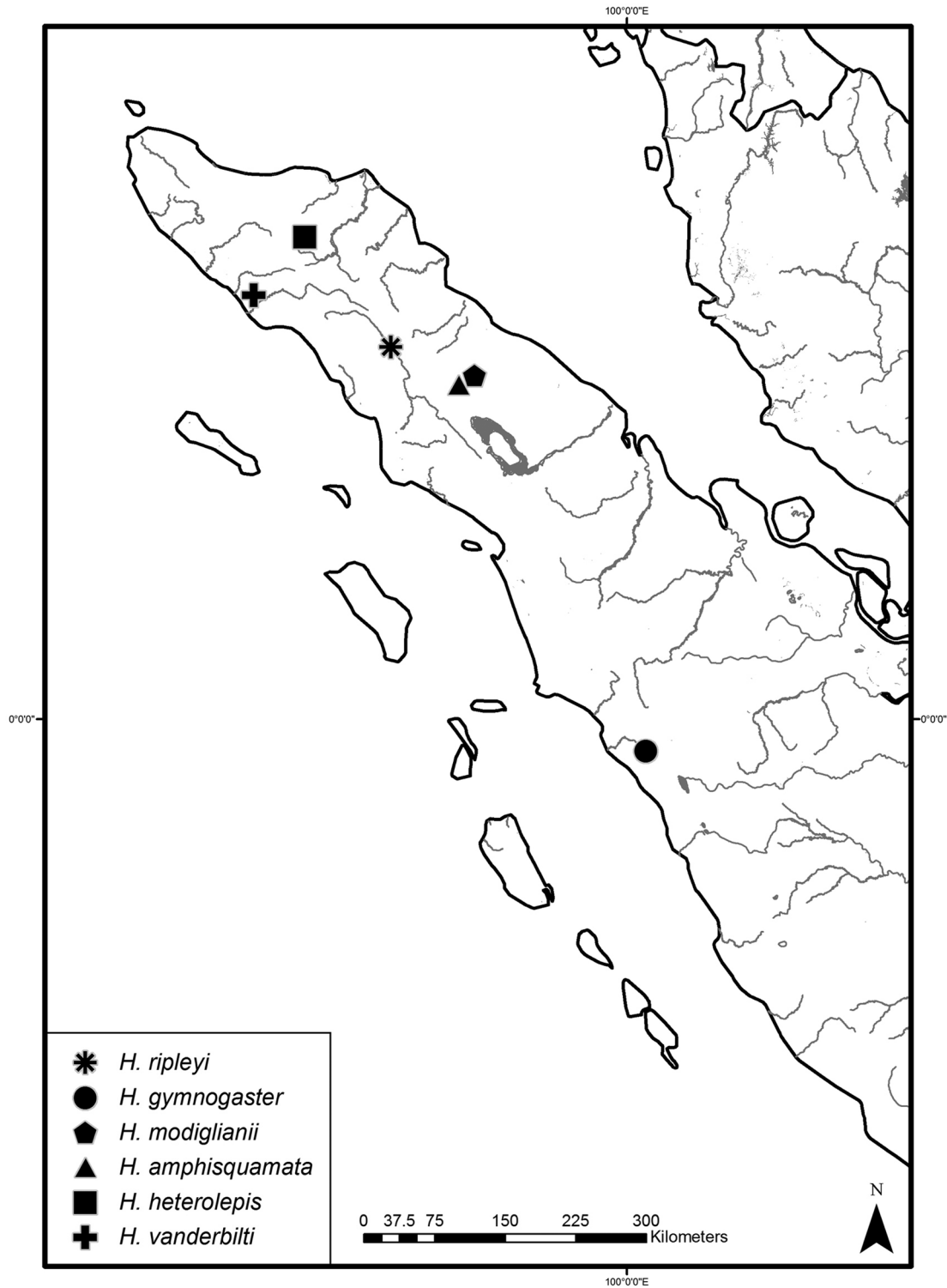
FIGURE 10. Type localities for species of *Homalopterula*. Asterisk represents the type species of the genus.

Balitoropsis **Smith 1945**
(Figures 3D, 4A, 5D, 11, and 12)

Balitoropsis Smith, 1945:278. (type species: *Balitoropsis bartschi* Smith 1945:279, by original designation). Gender feminine.

Remarks. The genus *Balitoropsis* was created for the species *B. bartschi* Smith 1945 and distinguished from

Homaloptera (sensu lato) by having a deep preoral groove extending around the corners of the mouth and papillated lips. Kottelat & Chu (1988) noted that all members of *Homaloptera* (sensu lato) have a preoral groove to a varying degree and recognized *Balitoropsis bartschi* as a junior synonym of *H. zollingeri*. The papillated lips of Smith (1945) refer to unculi found on the lips of most balitorids, not the large diagnosable papillae of some balitorid genera (e.g., *Balitora*, *Hemimyzon*, *Metahomaloptera*). The holotype of *B. bartschi* (USNM 107963) is identified as a gravid female of *Homaloptera zollingeri* Bleeker 1853, as assumed by Kottelat & Chu (1988) (Fig. 12).

Kottelat (1998) recognized *Balitoropsis* as possibly warranting recognition as a genus based on having "an elongate body, a slender caudal peduncle, carinated scales, short paired fins (pectorals usually not reaching pelvic base, pelvics not reaching anal), a dark body with a series of saddles along the back." *Balitoropsis* was recognized as a genus by Kottelat (2012, 2013) and as a subgenus by Tan & Ng (2005) and Randall & Page (2012). It is recognized herein as a genus containing two species (*B. zollingeri* and *B. ophiolepis*).

Diagnosis. Distinguishing characters are given in Table 4 and shown in Figures 3D, 4A, 5D, and 11. *Balitoropsis* is distinguished by the following combination of characters: without reddish tints on fins in life (Fig. 3D); dorsal-fin origin anterior to or above pelvic-fin origin; 8½ branched dorsal-fin rays; 7–9, 8 (M) branched pelvic-fin rays; forked caudal fin; keeled scales (Fig. 4A); 42–55 total lateral-line scales; 13–15 predorsal scales; large rostral cap; 2 thick rostral barbels in close proximity to one another; thick crescentic upper lip; fleshy pad between lateral portions of lower lip (Fig. 5D); anus closer to pelvic-fin insertion than to anal-fin origin.

Species included. *Balitoropsis zollingeri* (Bleeker 1853) and *B. ophiolepis* (Bleeker 1853). Type localities for species of *Balitoropsis* are shown in Figure 13.

FIGURE 11. Dorsal, lateral, and ventral views of preserved *Balitoropsis zollingeri*, UF 166094, 52.1 mm SL, Air Ogan, Sumatera Selatan Province, Sumatra, Indonesia.
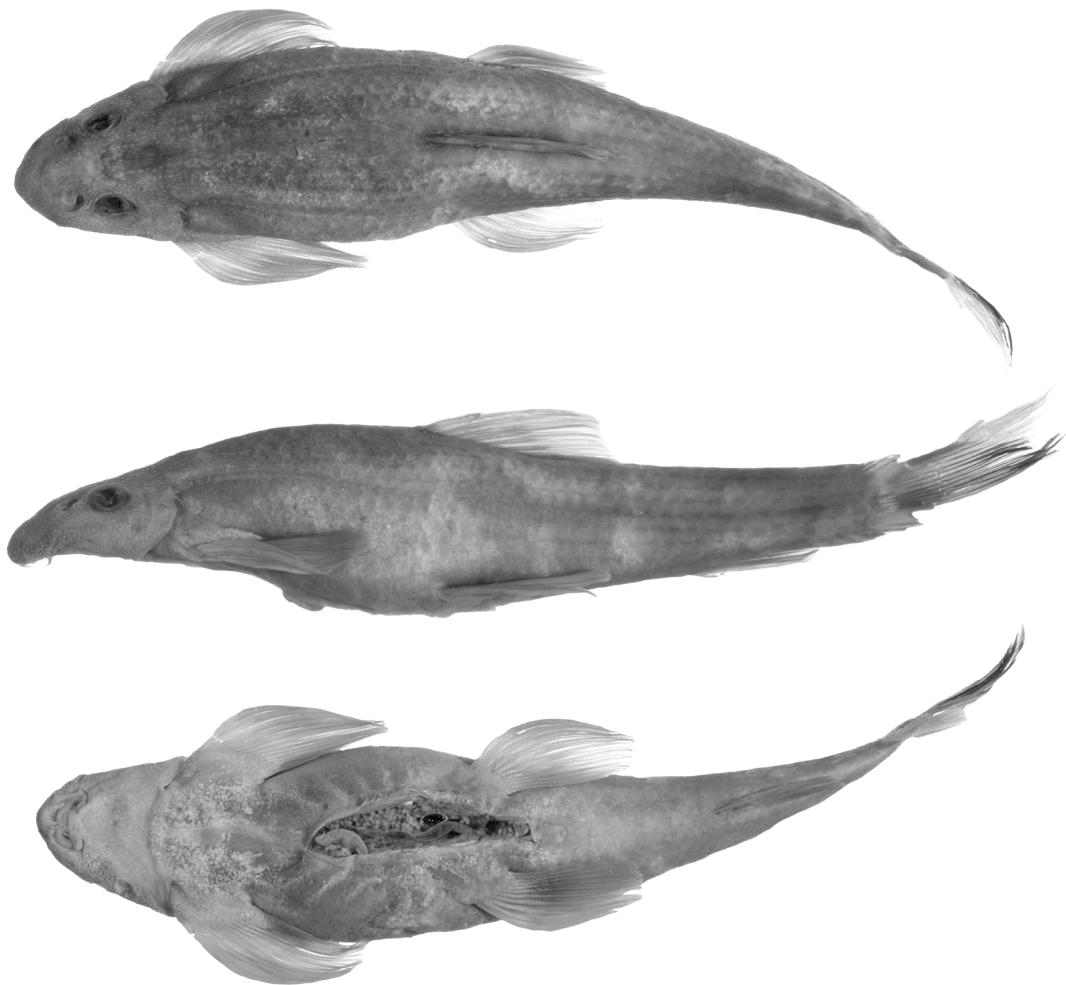
FIGURE 12. Dorsal, lateral, and ventral views of preserved *Balitoropsis bartschi*, USNM 107963 (holotype), 76.0 mm SL, Waterfall stream on Kao Chong, Trang Province, Thailand. Photos by Sandra Raredon, USNM, Ichthyology Division.

Comparison. *Balitoropsis* is distinguished from *Homaloptera* by absence vs. presence of reddish tints on fins in life; 7–9, 8 (M) vs. 7 branched pelvic fin-rays; 13–15 vs. 20–27 predorsal scales; 42–55 vs. 59–73 total lateral-line scales; crescentic vs. triangular upper lip; anus closer to pelvic-fin insertion than to anal-fin origin.

Balitoropsis is distinguished from *Homalopteroides* by having dorsal-fin origin anterior to or above the pelvic-fin origin vs. posterior to pelvic-fin origin; 8½ vs. 6–8½, 7½ (M) branched dorsal-fin rays; anus closer to pelvic-fin insertion vs. anal-fin origin; large vs. small rostral cap; medial- and lateral-rostral barbels in close proximity to one another vs. barbels widely separated at base; thick vs. thin upper lip; presence vs. absence of fleshy pad between lateral portions of lower lip.

Balitoropsis is distinguished from *Homalopterula* by having dorsal-fin origin anterior to or above the pelvic-fin origin vs. posterior to pelvic-fin origin; 8½ vs. 5½ and 7½, 7½ (M) branched dorsal-fin rays; 7–9, 8 (M) vs. 7 branched pelvic fin-rays; forked vs. truncated or emarginated caudal fin; keeled vs. smooth scales; 13–15 vs. 28–56 predorsal scales; 42–55 vs. 57–75 total lateral-line scales; anus closer to pelvic-fin insertion than to anal-fin origin; large vs. small rostral cap; medial- and lateral-rostral barbels in close proximity to one another vs. barbels widely separated at base; presence of fleshy pad vs. lobes between lateral portions of lower lip.

Balitoropsis is distinguished from *Pseudohomaloptera* by having anus closer to pelvic-fin insertion than to anal-fin origin.

Material examined. *Balitoropsis zollingeri*: Sumatra: BMNH 1866.5.2.53 (1); UF 161715 (3), 166094 (2), 166095 (1), 166102 (1), 166105 (1). Borneo: CAS 49331 (1); USNM 230253 (2). Thailand: USNM 107963 (Holotype of *B. bartschi*, examined photo); ANSP 68004 (Holotype of *Homaloptera* maxinae); UF 183727 (1), 235545 (1). Malaysia: CAS-SU 66420 (2), 66424 (Paratypes of *Homaloptera nigra*) (2); USNM 288456 (1); UF

235547 (9), 235421 (2), 235420 (1); ZRC 2009 (Holotype of *Homaloptera nigra*). **B. ophiolepis:** Java: RMNH 4986 (lectotype of *Homaloptera ophiolepis*); BMNH 1866.5.2.49 (1). Sumatra: UF 166109 (3), 166103 (1), 166101 (1). Borneo: RMNH 28866 (1); USNM 230251 (1).
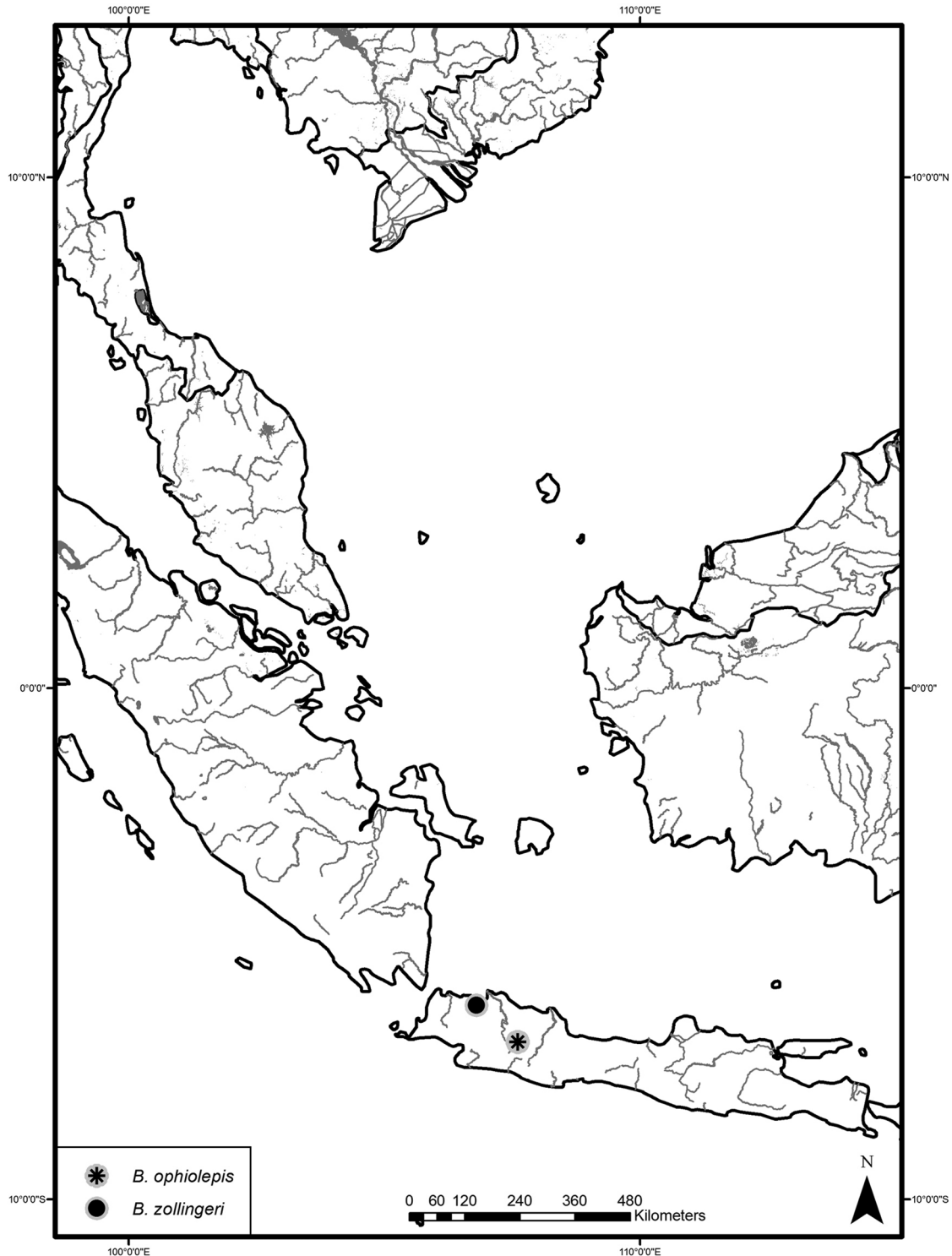
FIGURE 13. Type localities for species of *Balitoropsis*. Asterisk represents the type species of the genus. The type locality for *B. ophiolepis* shares one of the type localities for *B. zollingeri* (Bandung, Java).

Pseudohomaloptera Silas 1953
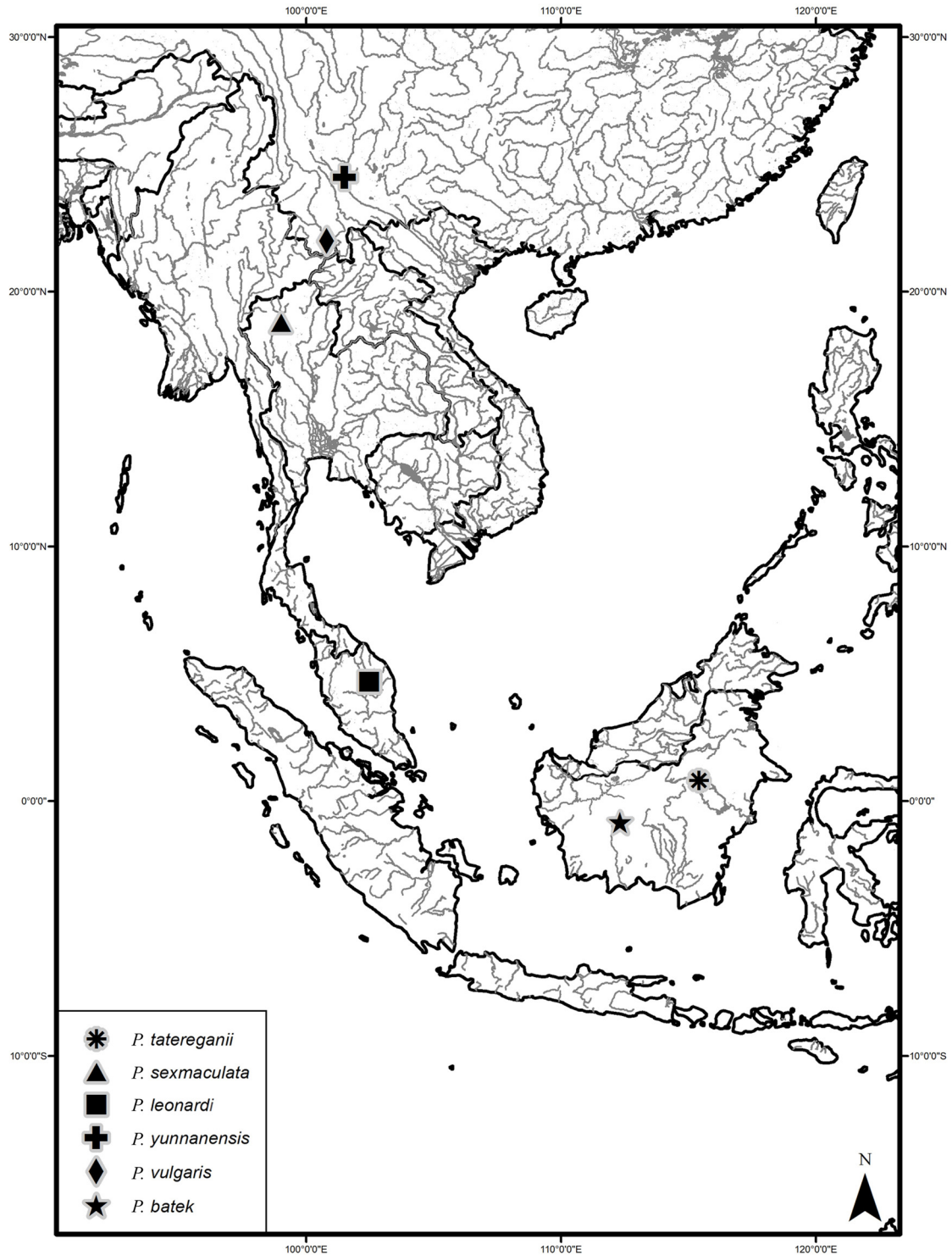(Figures 3E, 4B, 5E, 14)

Pseudohomaloptera Silas, 1953:204. (type species: *Homaloptera tatereganii* Popta 1905:180, by original designation). Gender feminine.

Remarks. *Homaloptera tatereganii* Popta 1905 was designated as the type species for the genus *Pseudohomaloptera* by Silas (1953). *Pseudohomaloptera* was distinguished from *Homaloptera* by the "presence of a rostral groove and other structures associated with the mouth" (Silas 1953:205). Tan (2009) recognized *Pseudohomaloptera* as a junior synonym of *Homaloptera*, since all species of *Homaloptera* (sensu lato) have a rostral and postoral groove to varying degrees. Kottelat (2012) recognized *H. tatereganii* as a species of *Balitoropsis* and treated *Pseudohomaloptera* as a junior synonym of *Balitoropsis*.

Pseudohomaloptera is morphologically very similar to *Balitoropsis,* and the mouth characters given by Silas (1953) cannot differentiate the two genera. Tan (2009) gave a simple pelvic-fin ray count of 3 for *H. tatereganii* to distinguish it from species of *Homaloptera* (s.l.), which have 2 simple pelvic-fin rays. However, the holotype, the only known specimen of *H. tatereganii* (RMNH 7632), has only 2 simple pelvic-fin rays (on both sides). Other counts that differ from those given by Tan (2009) are the following: iii, 8½ vs. ii, 8 dorsal-fin rays; ii, 5½ vs. ii, 5 anal-fin rays; vii, 12 vs. viii, 12 pectoral-fin rays; 18 vs. 14 circumpeduncular scale count; and 6/7 vs. 5/6 transverse scale count. The following measurements differ from Tan (2009) (owing likely to different methods): predorsal length 44.1% vs. 45.3% SL; body depth 12.5% vs. 10.4% SL; dorsal-fin base 16.7% vs. 18.8% SL; pectoral-fin length 29.4% vs. 28.5% SL; head depth 48.2% vs. 42.8% HL; head width 81.3% vs. 78.3% HL; snout length 61.9% vs. 57.2% HL; 15.1% vs. 14.5% HL; 40.3% vs. 37.7% HL.

FIGURE 14. Dorsal, lateral, and ventral views of preserved *Pseudohomaloptera tatereganii*, RMNH 7632 (holotype), 64.6 mm SL, Bo River, Upper Mahakam River basin, East Kalimantan, Borneo, Indonesia.

FIGURE 15. Type localities for species of *Pseudohomaloptera*. Asterisk represents the type species of the genus.

Diagnosis. Distinguishing characters are given in Table 4 and shown in Figures 3E, 4B, 5E, and 14. *Pseudohomaloptera* is distinguished by the following combination of characters: without reddish tints on fins in life (Fig. 3E); dorsal-fin origin anterior to or above pelvic-fin origin; 8½ branched dorsal-fin rays; 8–9 branched pelvic-fin rays; forked caudal fin; keeled scales (Fig. 4B); 50–61 total lateral-line scales; 13–19 predorsal scales; anus closer to anal-fin origin than to pelvic-fin insertion; no adipose keel on caudal peduncle; large rostral cap; 2 thick rostral barbels in close proximity to one another; thick and triangular/crescentic upper lip; fleshy pad between lateral portions of lower lip (Fig. 5E).

RANDALL & PAGE

Species included. *Pseudohomaloptera tatereganii* (Popta 1905), *P. sexmaculata* (Fowler 1934), *P. leonardi* (Hora 1941), *P. yunnanensis* (Chen 1978), *P. vulgaris* (Kottelat & Chu 1988), and *P. batek* (Tan 2009). Type localities for species of *Pseudohomaloptera* are shown in Figure 15.

Comparison. *Pseudohomaloptera* is distinguished from *Homaloptera* by absence vs. presence of reddish tints on fins in life; 8–9, 8 (M) vs. 7 branched pelvic fin-rays; 13–19 vs. 20–27 predorsal scales.

Pseudohomaloptera is distinguished from *Homalopteroides* by having dorsal-fin origin anterior to or at pelvic-fin origin vs. posterior to pelvic-fin origin; 8½ vs. 6–8½, 7½ (M) branched dorsal-fin rays; large vs. small rostral cap; medial- and lateral-rostral barbels in close proximity to one another vs. barbels widely separated at base; thick vs. thin upper lip; presence vs. absence of fleshy pad between lateral portions of lower lip.

Pseudohomaloptera is distinguished from *Homalopterula* by having dorsal-fin origin anterior to or at pelvic-fin origin vs. posterior to pelvic-fin origin; 8½ vs. 5½ and 7½, 7½ (M) branched dorsal-fin rays; 8–9 vs. 7 branched pelvic fin-rays; keeled vs. smooth scales; 13–19 vs. 28–56 predorsal scales; forked vs. truncated or emarginated caudal fin; absence vs. presence of adipose keel on caudal peduncle; large vs. small rostral cap; medial- and lateral-rostral barbels in close proximity to one another vs. widely separated at base; presence of fleshy pad vs. lobes between lateral portions of lower lip.

Pseudohomaloptera is distinguished from *Balitoropsis* by having anus closer to anal-fin origin than to pelvic-fin insertion.

Material examined. ***Pseudohomaloptera tatereganii*:** Borneo: RMNH 7632 (holotype of *Homaloptera tatereganii*). **P. sexmaculata:** Thailand: ANSP 56374 (holotype of *Homaloptera sexmaculata*), 56375 (paratypes of *Homaloptera sexmaculata*) (2), 56402 (holotype of *Homaloptera septemmaculata*), 56403 (paratype of *Homaloptera septemmaculata*); UF 183358 (2), 177819 (3), 181170 (3). **P. leonardi:** Peninsular Malaysia: ZRC 1753 (paratype of *Homaloptera leonardi*); RMNH 23264 (6), 25921 (4); UF 169909 (3), 235746 (3). **P. yunnanensis:** China: IHASW 60-VII-012 (holotype of *Balitoropsis yunnanensis*). **P. vulgaris:** China: 788229 (KIZ 1978001047) (holotype of *Homaloptera vulgaris*), 788225-788227 (KIZ 1978001048-50) (paratypes of *Homaloptera vulgaris*). **P. batek:** Borneo: MZB 10990 (holotype of *Homaloptera batek*); ZRC 51743 (paratype of *Homaloptera batek*).


Ghatsa, **new genus**
(Figures 4F, 5F, 16)

Remarks. The following five species of balitorines from the Western Ghats of India have been recognized as belonging to the genus *Homaloptera* (Randall & Page 2012; Kottelat 2012): *H. montana* Herre 1945, *H. pillaii* Indra & Rema Devi 1981, *H. menoni* Shaji & Easa 1995, *H. santhamparaiensis* Arunachalam *et al.* 2002, and *H. silasi* Madhusoodana Kurup & Radhakrishnan 2011. Due to the inaccessibility of specimens from institutions in India, this group has had an unresolved taxonomic status. It has been proposed by Pethiyagoda & Kottelat (1994) [for the first two species listed above], and by Kottelat (1998) [for the first three species listed above] that these species require a new genus or subgenus (Tan & Ng 2005). The only species examined in this study from this Indian assemblage was *H. montana* (holotype, CAS-SU 39871) (Fig. 16). *Homaloptera montana* can be distinguished from all species of *Homaloptera* (sensu lato) by the combined characters of placement of dorsal-fin origin, tiny and smooth scales, truncated caudal fin, and features of the mouth. Based on these characters, *H. montana* does not belong to any established balitorid genus and the newly created genus, *Ghatsa* is created for it. The four other species formerly recognized in *Homaloptera* from the Western Ghats that were unavailable for examination (*H. pillaii* Indra & Rema Devi 1981, *H. menoni* Shaji & Easa 1995, *H. santhamparaiensis* Arunachalam *et al*. 2002, and *H. silasi* Madhusoodana Kurup & Radhakrishnan 2011) are tentatively placed in *Ghatsa*, since they are morphologically (based on type descriptions) more similar to *H. montana* than to any other balitorine. Further examination of these species is needed.

Type species. *Homaloptera montana* Herre, 1945:400.

Diagnosis. Distinguishing characters are given in Table 4 and shown in Figures 4F, 5F, and 16. *Ghatsa* is distinguished by the combination of the following characters: dorsal-fin origin posterior to pelvic-fin origin; emarginated-truncated caudal fin; small, smooth scales (Fig. 4F) (data only available for *G. montana*); 59–ca.101 lateral-line scales, ca. 53 predorsal scales (data only available for *G. montana*); anus closer to anal-fin origin than to

pelvic-fin insertion; adipose keel on caudal peduncle (data only available for *G. montana*); small rostral cap; 2 thin, widely separated rostral barbels; thin, smooth crescentic upper lip; absence of fleshy pad or lobes between lateral portions of lower lip (Fig. 5F).
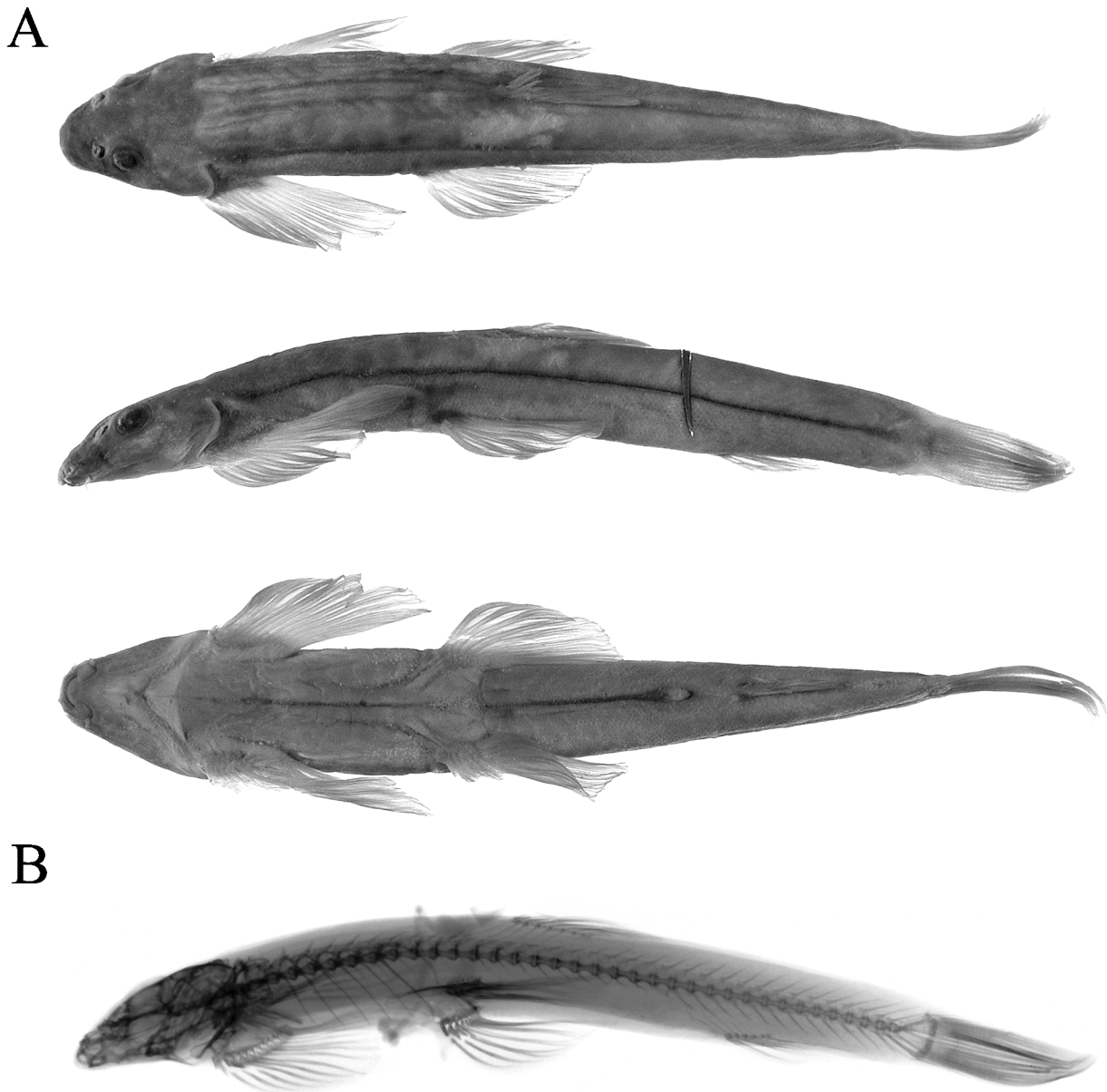
FIGURE 16. *Ghatsa montana*, CAS-SU 39871 (holotype), 46.4 mm SL. (A) Dorsal, lateral, and ventral views, Puthutotam Estate, brook in Anamallai Hills, India; (B) radiograph. Photos by CAS, Ichthyology Section.

Species. *Ghatsa montana* (Herre 1945). The following species are tentatively recognized in *Ghatsa*: *G. pillaii* (Indra & Rema Devi 1981), *G. menoni* (Shaji & Easa 1995), *G. santhamparaiensis* (Arunachalam *et al*. 2002), and *G. silasi* (Madhusoodana Kurup & Radhakrishnan 2011). Type localities for species in *Ghatsa* are shown in Figure 17.

Comparison. *Ghatsa* is distinguished from *Homaloptera* by having the dorsal-fin origin posterior vs. anterior to the pelvic-fin origin; scales small and smooth (data only available for *G. montana*) vs. medium and keeled; ca. 53 (data only available for *G. montana*) vs. 20–27 predorsal scales; truncated or slightly emarginated vs. forked caudal fin; adipose keel present (data only available for *G. montana*) vs. absent; small vs. large rostral cap; medial- and lateral-rostral barbels widely separated from one another at base vs. barbels in close proximity to one another; crescentic rather than triangular upper lip; thin vs. thick upper lip; absence vs. presence of fleshy pad between lateral portions of lower lip.

Ghatsa is distinguished from *Homalopteroides* by having small and smooth scales (data only available for *G. montana*) vs. large and wart-like/keeled scales; ca. 53 (data only available for *G. montana*) vs. 14–25 predorsal scales; 59–ca. 101 vs. 33–52 lateral-line scales; truncated or slightly emarginated vs. forked caudal fin; and adipose keel present (data only available for *G. montana*) vs. absent.

Ghatsa is distinguished from *Homalopterula* by having thin vs. thick barbels and upper lip; absence vs. presence of fleshy lobes between lateral portions of lower lip; and by 59–ca. 101 vs. 57–75 lateral-line scales.

Ghatsa is distinguished from *Balitoropsis* and *Pseudohomaloptera* by having the dorsal-fin origin posterior vs. anterior to pelvic-fin origin; smooth (data only available for *G. montana*) vs. keeled scales; ca. 53 (data only available for *G. montana*) vs. 13–15 and 13–19 predorsal scales, respectively; slightly emarginated to truncated vs. forked caudal fin; adipose keel present (data only available for *G. montana*) vs. absent; small vs. large rostral cap; medial- and lateral-rostral barbels widely separated from one another at base vs. barbels in close proximity to one another; absence vs. presence of a fleshy pad between lateral portions of the lower lip. It is further distinguished from *Balitoropsis* by having an anus closer to anal-fin origin than to pelvic-fin insertion; 59–ca. 101 vs. 42–55 lateral-line scales.

Etymology. Named for the Western Ghats of India where species of this genus appear to be endemic. Gender feminine.

Redescription of *Ghatsa montana* (Herre 1945)
(Figures 4F, 5F, 16)

Homaloptera montana Herre 1945:400 (no figure in original description); Journal of the Washington Academy of Sciences 35(12).
Type locality: brook on the Puthutotam Estate in Anamallai Hills at 3,600 feet altitude, Valparai Post Office, Madras Presidency, South India. Holotype. CAS-SU 39871, Böhlke 1953:40.

Description. Dorsal, lateral, and ventral views are shown in Figure 16. Measurements and meristic counts are given for the only specimen available to us, the holotype (CAS-SU 39871). The holotype is 46.4 mm SL, 54.8 mm TL. Body (depth: 10.1% SL, width: 13.5% SL) arched predorsally, tapers posterior of anal-fin origin to caudal base, flattened ventrally. Head (length: 21.7% SL, width: 76.2% HL, depth: 44.5% HL) triangular when viewed dorsally; tubercles absent. Snout length 47.5% HL. Orbit (length: 22.8% HL) small, ovoid, positioned dorsolaterally, shorter than interorbital width (31.7% HL).

Mouth (Fig. 5F) (width: 25.7% HL) subterminal, large portions of upper and lower jaws visible. Lips thin, smooth, crescentic, continuous around corners of mouth; widest at corners of mouth. Lower lip medially interrupted; the chin extending to most anterior portion of lip. Rostral and postlabial grooves present. Two pairs of rostral barbels, 1 pair of maxillary barbels. Medial-rostral barbels widely separated from one another, distance equal to that of medial interruption of lower lip. Medial and lateral-rostral barbels unequal in size, separated by distance about equal to length of lateral-rostral barbel. Lateral-rostral barbel not reaching base of the barbel, maxillary barbel reaching horizontally to vertical at anterior nostril. Gill opening extends to ventral surface of body. Dorsal fin (base length: 9.7% SL, length: 18.5% SL) originates posterior to pelvic-fin base and closer to caudal-fin base than to snout (predorsal length: 54.3% SL). Pectoral fin (length: 26.8% SL) longer than head, not reaching pelvic-fin origin. Pelvic fin (length: 20.8% SL) lacks axillary pelvic lobe, not reaching anus; anus closer to anal-fin origin than to pelvic-fin insertion. Anal fin length 13.5% SL. Adipose keel on caudal peduncle. Caudal peduncle length 15.9% SL, depth 9.0% SL. Caudal fin truncate.

Body scaled except for ventral surface anterior to pelvic-fin insertion. Scales small, smooth, not obvious to naked eye (Fig. 4F). Total lateral-line pores ca. 101, predorsal scales ca. 53, circumpeduncular scales ca. 60. Scales above and below lateral line ca. 18 and ca. 15, respectively. Scales below lateral line to pelvic-fin origin ca. 12. Dorsal-fin rays iii, 7½; anal-fin rays ii, 5; pectoral-fin rays vi, 9 for left side, and a total of 15 rays for the right side (right fin damaged; simple and branched rays could not be differentiated); pelvic-fin rays ii, 8 for left side and iii, 7 for right side; total caudal-fin ray count 16. Pores of cephalic lateralis system: 7 supraorbital, 5+11 infraorbital, 7 preoperculomandibular, and 3 supratemporal. Total vertebrae count 38 (Fig. 16B).

Coloration. In 70% ethanol: The specimen is faded, and the general color of the body is brown with a black stripe along the lateral-line. Herre (1945:400) gave the following description: "The color in alcohol is brown, the

underside yellowish; 10 short dark brown bars across the back, but not extending down to the lateral-line; a poorly defined dark longitudinal stripe below the lateral line from the eye to the caudal base; top of head very dark brown; a blackish-brown spot on the ventral base; caudal with a blackish blotch on its base and another near its tip; other fins all clear."

Distribution. The type locality is the Puthutotam Estate, brook in Anamallai Hills, southern India, elevation about 3,600 feet (Fig. 17). This is in the state of Tami Nadu close to the border with Kerala, Coimbatore District; estimated coordinates are 10.36° N, 76.93° E. This drainage was reported to be adjacent and northeast to the Chalakudy basin by Pethiyagoda & Kottelat (1994:110).
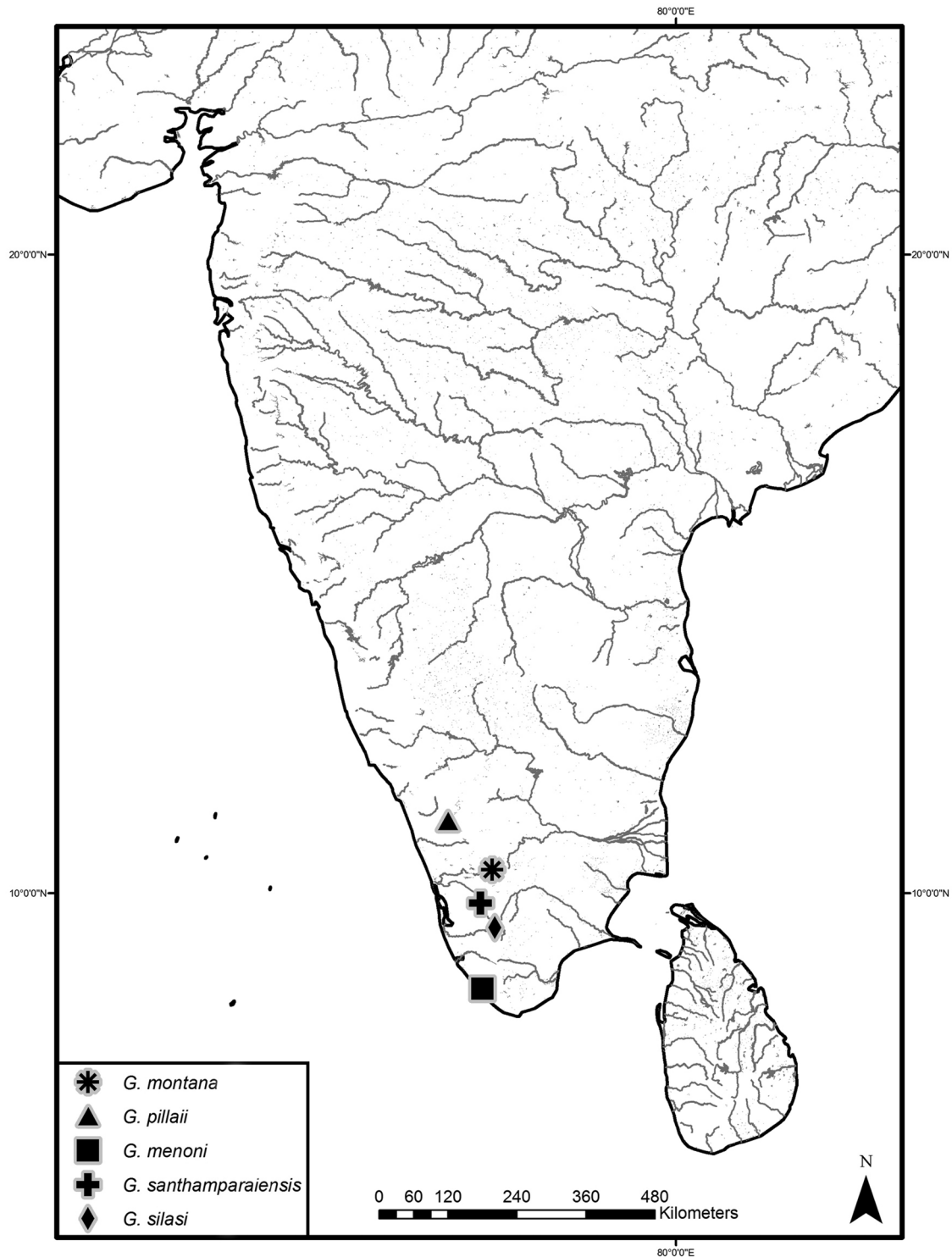
FIGURE 17. Type localities for species of *Ghatsa*. Asterisk represents the type species of the genus.

Menon (1987) reported *H. montana* from Silent Valley and New Amarambalam of the Western Ghats, but this is likely *H. pillaii* (see Remarks). Arunachalam *et al*. (2002) examined an individual from Kerala at Malakkapara, headwaters of Chalakudy River. This specimen (KFRI F. 107) was not examined in this study, and this locality for *H. montana* cannot be confirmed.

Remarks. Menon (1987) recognized *H. pillaii* (spelled *pillai*) as a junior synonym of *H. montana*. Menon (1987) examined only the type series of *H. pillaii* but gave different counts than those in the original description (also see Pethiyagoda & Kottelat 1994:109). Many authors (Indra & Rema Devi 1981; Madhusoodana Kurup & Radhakrishnan 2010; Arunachalam *et al*. 2002; Silas 1953) have given a pectoral-fin ray count of iv, 8 for *G. montana*. The pectoral-fin ray count here and in the original description (Herre 1945) is vi, 8.

Material examined. *G. montana*: India: CAS-SU 39871 (holotype of *Homaloptera montana*).

Discussion

As recognized herein, *Homaloptera* consists of six species (*Homaloptera ocellata*, *H. bilineata*, *H. orthogoniata*, *H. ogilviei*, *H. confuzona*, and *H. parclitella*) found in Myanmar, Thailand, Cambodia, Peninsular Malaysia, Sumatra, Java, and Borneo. Of these six, *H. parclitella* and *H. ogilviei* are known to occur sympatrically, in the Pahang (Alfred 1969) and Endau drainages (Ng & Tan 1999), Malaysia.

Homalopteroides, with 11 species (*Homalopteroides wassinkii, H. modestus, H. rupicola, H. smithi, H. stephensoni, H. weberi, H. tweediei , H. indochinensis, H. nebulosus, H. yuwonoi*, and *H. avii*), is the most diverse and widely distributed genus of species formerly in *Homaloptera*. It is known from northeast India, Myanmar, Thailand, Laos, Cambodia, Vietnam (? see Kottelat 2012:51), Peninsular Malaysia, Sumatra, Java, and Borneo. *Homalopterula* is only known to occur in Sumatra and consists of six species, five of which – *H. heterolepis, H. ripleyi, H. modiglianii, H. amphisquamata,* and *H. vanderbilti* – were described from Aceh Province, while *H. gymnogaster* was described from Sumatera Barat province. *Homaloptera lepidogaster* Weber & de Beaufort 1916 and *H. ulmeri* Fowler 1940 were recognized as junior synonyms of *H. gymnogaster* and *H. vanderbilti*, respectively, by Kottelat *et al*. (1993), but without supporting data. Variation and relationships within *Homalopterula* are unknown, and a taxonomic revision of the genus is needed.

Based on molecular and morphological data, *Balitoropsis* contains only two species. This differs from the classification of Kottelat (2012) and Kottelat (2013), which recognizes ten and nine species in *Balitoropsis*, respectively. Our results are consistent with the phylogenetic analysis of Randall & Page (2012, fig. 3), where *B. zollingeri* is the sister species to a clade consisting of *Pseudohomaloptera leonardi* (previously designated in *Balitoropsis*) and *Homaloptera parclitella*. *Balitoropsis zollingeri* has a wide distribution, having been reported from Java, Sumatra, Borneo, Malay Peninsula, Thailand, Laos, and Cambodia. *Balitoropsis ophiolepis* has been reported from Java, Sumatra, and Borneo.

Pseudohomaloptera, which has not been recognized as a valid genus since its original description by Silas (1953), contains six species (*Pseudohomaloptera tatereganii, P. sexmaculata, P. leonardi, P. yunnanensis, P. vulgaris,* and *P. batek*) and is known to occur in southern China, Thailand, Laos, Cambodia, Peninsular Malaysia, and Borneo. The relationships within *Pseudohomaloptera* are unknown. Based on limited access to specimens, four species are tentatively assigned to *Ghatsa* (*G. pillaii, G. menoni, G. santhamparaiensis,* and *G. silasi*). Intraspecific and interspecific variation and relationships among species of *Ghatsa* are unknown, and a revision of this genus is needed. Based on a literature review, *G. menoni* is the most unusual, with a lateral-line scale count much lower than that of other species (59–62 vs. 83–ca. 101).

Hora (1949) proposed the Satpura Hypothesis to explain the presence in peninsular India of taxa that seemed mostly closely related to taxa in the Malay Peninsula. The disjunct populations of *Homaloptera* as understood at the time in the Western Ghats and in the Malay Peninsula were used to support the hypothesis. However, based on this study, *Homaloptera* as recognized by Hora is not monophyletic. In order to further test this hypothesis (see also Karanth 2003; Dahanukar *et al*. 2013) and better understand the evolutionary history of *Ghatsa* and other endemic hill stream loaches from the Western Ghats, phylogenetic analyses including these genera and those from Indochina are required.

Key to genera diagnosed in this study

1a.	Origin of dorsal fin anterior to or above origin of pelvic fin; lateral- and medial-rostral barbels in close proximity to one another; large rostral cap; fleshy pad between lateral portions of lower lip; 8½ (M) branched dorsal-fin rays 2
1b.	Origin of dorsal fin posterior to origin of pelvic fin; rostral barbels widely separated; small rostral cap; fleshy pad between lateral portions of lower lip absent; 7½ (M) branched dorsal-fin rays 4
2a.	Reddish tints on fins in life; predorsal scales ≥ 20; medium-sized keeled scales (Fig. 4D); 7 (M) branched pelvic-fin rays . . . . *Homaloptera*
2b.	Absence of reddish tints on fins in life; predorsal scales < 20; large keeled scales (Fig. 4A & B); 8 (M) branched pelvic-fin rays 3
3a.	Anus closer to pelvic-fin base than to anal fin . . . . *Balitoropsis*
3b.	Anus closer to anal fin than to pelvic-fin base . . . . *Pseudohomaloptera*
4a.	Scales large (Fig. 4C); predorsal scales ≤ 25; total lateral-line scales ≤ 52; caudal fin forked; adipose keel absent . . . . *Homalopteroides*
4b.	Scales small (Fig. 4E & F); predorsal scales > 26; total lateral-line scales > 53; caudal fin truncated or slightly emarginated; adipose keel present 5
5a.	Thick barbels and lips; fleshy lobes between lateral portions of lower lip; endemic to Sumatra. . . . . *Homalopterula*
5b.	Thin barbels and lips; no fleshy lobes between lateral portions of lower lip; endemic to Western Ghats of India . . . . . . *Ghatsa*

Comparative material. *Balitora brucei*: India: RMNH 11924 (neotype). ***Balitora* sp:** Thailand: NIFI 02927 (3). ***Bhavania australis*:** India: MNHN 50-79 (1); CAS 62052 (2). ***Cryptotora thamicola*:** Thailand: NIFI 3046 (1). ***Hemimyzon yaotanensis*:** China: KU 21445 (1). ***Neohomaloptera johorensis*:** Peninsular Malaysia: CAS-SU 39840 (holotype), 39841 (paratype). ***Sewellia elongate*:** Laos: UF 185476 (3), 185488 (3). ***Travancoria jonesi*:** India: MNHN 1950-0080 (1).

References

Alfred, E.R. (1969) The Malayan cyprinoid fishes of the family Homalopteridae. *Zoologische Mededelingen (Leiden)*, 43, 213–237.

Arunachalam, M., Johnson, J.A. & Rema, Devi, K. (2002) *Homaloptera santhamparaiensis*, a new species of balitorid fish (Teleostei: Balitoridae) from a Western Ghats stream of Kerala, India. *Acta Zoologica Taiwanica*, 13, 31–37.

Böhlke, J.E. (1953) A catalogue of the type specimens of Recent fishes in the Natural History Museum of Stanford University. *Stanford Ichthyological Bulletin*, 5, 1–168.

Dahanukar, N., Philip, S., Krishnakumar, K., Ali, A. & Raghavan, R. (2013) The phylogenetic position of *Lepidopygopsis typus* (Teleostei: Cyprinidae), a monotypic freshwater fish endemic to the Western Ghats of India. *Zootaxa*, 3700 (1), 113–139. http://dx.doi.org/10.11646/zootaxa.3700.1.4

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9, 1–772. http://dx.doi.org/10.1038/nmeth.2109

Fang, P.-W. (1930) New and inadequately known homalopterin loaches of China, with a rearrangement and revision of the generic characters of *Gastromyzon, Sinogastromyzon* and their related genera. *Contributions from the Biological Laboratory of the Science Society of China*, 6, 25–43.

Fowler, H.W. (1940) Zoological results of the George Vanderbilt Sumatran Expedition, 1936–1939. Part II.–The fishes.

Proceedings of the Academy of Natural Sciences of Philadelphia, 91, 369–398.

Herre, A.W.C.T. (1945) Notes on fishes in the Zoological Museum of Stanford University:XX, New fishes from China and India, a new genus, and a new Indian record. *Journal of the Washington Academy of Sciences*, 35, 399–404.

Hora, S.L. (1932) Classification, bionomics and evolution of homalopterid fishes. *Memoirs of the Indian Museum*, 12, 263–330.

Hora, S.L. (1949) Satpura hypothesis of the distribution of the Malayan fauna and flora to Peninsular India. *Proceedings of the National Institutes of Science of India*, 15, 345–351.

Hubbs, C.L. & Lagler, K.F. (2004) *Fishes of the Great Lakes region, revised edition.* University of Michigan Press, Ann Arbor, Michigan, 276 pp.

Indra, T.J. & Rema, Devi, K. (1981) A new species of the genus *Homaloptera* from Silent Valley, Kerala, s. India. *Bulletin of the Zoological Survey of India*, 4, 67–70.

Jordan, D.S. (1920) The genera of fishes, part IV, from 1881 to 1920, thirty-nine years, with the accepted type of each. A contribution to the stability of scientific nomenclature. *Leland Stanford Jr. University Publications*, 43, 411–576.

Karanth, K.P. (2003) Evolution of disjunct distributions among wet-zone species of the Indian subcontinent: testing various hypotheses using a phylogenetic approach. *Current Science*, 85, 1276–1283.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28, 1647–1649. http://dx.doi.org/10.1093/bioinformatics/bts199

Kottelat, M. (1984) Revision of the Indonesian and Malaysian loaches of the subfamily Noemacheilinae. *Japanese Journal of Ichthyology*, 31, 225–260.

Kottelat, M. (1987) Nomenclatural status of the fish names created by J. C. van Hasselt (1823) and of some cobitoid genera. *Japanese Journal of Ichthyology*, 33, 368–375.

Kottelat, M. (1998) *Homaloptera yuwonoi*, a new species of hillstream loach from Borneo, with a new generic name for *H. thamicola* (Teleostei: Balitoridae). *Ichthyological Exploration of Freshwaters*, 9, 267–272.

Kottelat, M. (2012) Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidei). *The Raffles Bulletin of Zoology,* Supplement 26, 1–199.

Kottelat, M. (2013) The fishes of the inland waters of southeast Asia: a catalogue and core biography of the fishes known to occur in freshwaters, mangroves and estuaries. *The Raffles Bulletin of Zoology Supplement*, 27, 1–663.

Kottelat, M. & Chu, X.-L. (1988) The genus Homaloptera (Osteichthyes, Cypriniformes, Homalopteridae) in Yunnan, China. *Cybium*, 12, 103–106.

Kottelat, M., Whitten, A.J., Kartikasari, S.N. & Wirjoatmodjo, S. (1993) *Freshwater Fishes of Western Indonesia and Sulawesi.* Periplus Editions, Hong Kong, 259 pp.

Liu, S., Mayden, R.L., Zhang, J., Yu, D., Tang, Q., Deng, X. & Liu, H. (2012) Phylogenetic relationships of the Cobitoidea (Teleostei: Cypriniformes) inferred from mitochondrial and nuclear genes with analyses of gene evolution. *Gene*, 508, 60–72. http://dx.doi.org/10.1016/j.gene.2012.07.040

Madhusoodana Kurup, B. & Radhakrishnan, K.V. (2011) Fishes of the genus *Homaloptera* van Hasselt, 1823 in Kerala, with description of a new species *Homaloptera silasi*. *Journal of the Bombay Natural History Society*, 107, 224–226.

Mayden, R.L., Tang, K.L., Conway, K.W., Freyhof, J., Chamberlain, S., Haskins, M., Schneider, L., Sudkamp, M., Wood, R.M., Agnew, M., Bufalino, A., Sulaiman, Z., Miya, M., Saitoh, K. & He, S. (2007) Phylogenetic relationships of Danio within the order Cypriniformes: a framework for comparative and evolutionary studies of a model species. *Journal of Experimental Zoololgy Part B: Molecular and Developmental Evolution*, 308 (B), 642–654. http://dx.doi.org/10.1002/jez.b.21175

Mayden, R.L., Tang, K.L., Wood, R.M., Chen, W.-J., Agnew, M.K., Conway, K.W., Yang, L., Li, J., Wang, X., Saitoh, K., Miya, M., He, S., Liu, H., Chen, Y. & Nishida, M. (2008) Inferring the tree of life of the order Cypriniformes, the earth's most diverse clade of freshwater fishes: implications of varied taxon and character sampling. Journal of Systematic Evolution, 46, 424–438.

Menon, A.G.K. (1987) The fauna of India and the adjacent countries. Pisces. Vol. IV. Teleostei – Cobitoidea. Part 1. Homalopteridae. *Zoological Survey of India*, i–x, 1–259.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) *"Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in Proceedings of the Gateway Computing Environments Workshop (GCE),* 14 Nov. 2010, New Orleans, LA, 8 pp.

Ng, H.H., Tan, H.H. & Lim, K.K.P. (1999) The inland fishes of Pulau Tioman, Peninsular Malaysia. *Raffles Bulletin of Zoology*, Supplement 6, 169–187.

Tan, H.H. & Ng, P.K.L. (2005) *Homaloptera parclitella*, a new species of torrent loach from the Malay Peninsula, with redescription of *H. orthogoniata* (Teleostei: Balitoridae). *Ichthyological Exploration of Freshwaters*, 16, 1–12.

Ott, G. (2009) Redescription of *Homaloptera ripleyi* (Fowler, 1940) from Sumatra, Indonesia (Teleostei: Balitoridae). *Bulletin of Fish Biology*, 11, 73–86.

Parenti, L.R., Hadiaty, R.K., Lumbantobing, D.L. & Herder, F. (2013) Two new ricefishes of the genus *Oryzias* (Atherinomorpha: Beloniformes: Adriachthyidae) augment the endemic freshwater fish fauna of southeastern Sulawesi, Indonesia. *Copeia*, 2013, 403–414.

http://dx.doi.org/10.1643/CI-12-114

Pethiyagoda, R. & Kottelat, M. (1994) Three new species of fishes of the genera *Osteochilichthys* (Cyprinidae), *Travancoria* (Balitoridae) and *Horabagrus* (Bagridae) from the Chalakudy River, Kerala, India. *Journal of South Asian Natural History*, 1, 97–116.

Prashad, B. & Mukerji, D.D. (1929) The fish of the Indawgyi Lake and the streams of the Myitkyina District (Upper Burma). *Records of the Indian Museum*, 31, 161–223.

Quenouille, B., Bermingham, E. & Planes, S. (2004) Molecular systematics of the damselfishes (Teleostei: Pomacentridae): Bayesian phylogenetic analyses of mitochondrial and nuclear DNA sequences. *Mol. Phylogenet. Evol*, 31, 66–88.
http://dx.doi.org/10.1016/S1055-7903(03)00278-1

Randall, Z.S. & Page, L.M. (2012) Resurrection of the genus *Homalopteroides* (Teleostei: Balitoridae) with a redescription of *H. modestus* (Vinciguerra 1890). *Zootaxa*, 3586, 329–346.

Randall, Z.S. & Page, L.M. (2014) A New Species of *Homalopteroides* (Teleostei: Balitoridae) from Sarawak, Malaysian Borneo. *Copeia*, 1, 160–167.
http://dx.doi.org/10.1643/CI-13-055

Roberts, T.R. (1982) The Bornean gastromyzontine fish genera *Gastromyzon* and *Glaniopsis* (Cypriniformes, Homalopteridae), with descriptions of new species. *Proceedings of the California Academy of Sciences*, 42, 497–524.

Roberts, T.R. (1989) The freshwater fishes of western Borneo (Kalimantan Barat, Indonesia). *Memoirs of the California Academy of Sciences*, 14, 1–210.

Roberts, T.R. (1993) The freshwater fishes of Java, as observed by Kuhl and van Hasselt in 1820–23. *Zoologische Verhandelingen*, 285, 1–94.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
http://dx.doi.org/10.1093/sysbio/sys029

Sabaj Pérez, M.H. (2012) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 3.0. American Society of Ichthyologists and Herpetologists, Washington, DC. Electronically available from: http://www.asih.org/ (Accessed 28 Feb. 2015)

Silas, E.G. (1953) Classification, zoogeography and evolution of the fishes of the cyprinoid families Homalopteridae and Gastromyzonidae. *Records of the Indian Museum*, 50, 173–263.

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

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

Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology*, 57, 758–771.
http://dx.doi.org/10.1080/10635150802429642

Stamatakis, A. (2014) RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30 (9), 1312–1313.

Swainson, W. (1839) On the natural history and classification of fishes, amphibians, & reptiles, or monocardian animals. *Spottiswoode & Co.*, 2, 1–448. [London]

Swofford, D.L. (2003) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tan, H.H. (2009) A new species of hill stream loach (Teleostei: Balitoridae) from central Kalimantan, with redescriptions of *Homaloptera tateregani* Popta and *Homaloptera stephensoni* Hora. *Zootaxa*, 2171, 48–64.

Tan, H.H. & Ng, P.K.L. (2005) *Homaloptera parclitella*, a new species of torrent loach from the Malay Peninsula, with redescription of *H. orthogoniata* (Teleostei: Balitoridae). *Ichthyological Exploration of Freshwaters*, 16, 1–12.

Tang, Q., Liu, S., Yu, D., Liu, H. & Danley, P. (2012) Mitochondrial capture and incomplete lineage sorting in the diversification of balitorine loaches (Cypriniformes, Balitoridae) revealed by mitochondrial and nuclear genes. *Zoologica Scripta*, 41, 233–247.
http://dx.doi.org/10.1111/j.1463-6409.2011.00530.x

van Hasselt, J.C. (1823) Uittreksel uit een' brief van den Heer J. C. van Hasselt, aan den Heer C. J. Temminck, geschreven uit Tjecande, Residentie Bantam, den 29sten December 1822. *Algemeene Konst- en Letter-Bode voor het Jaar 1823*, 2, 130–133.

RANDALL & PAGE