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Resurrection of the genus *Homalopteroides* (Teleostei: Balitoridae) with a redescription of *H. modestus* (Vinciguerra 1890)

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Abstract

The genus *Homalopteroides* Fowler 1905 is resurrected and distinguished from the genus *Homaloptera* van Hasselt 1823 based on a combination of characters including a unique mouth morphology, dorsal-fin origin over pelvic fin, ≤ 60 lateral-line scales, and ≤ 30 predorsal scales. Species included in *Homalopteroides* are *H. 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 possibly *H. manipurensis* (Arunkumar 1999). *Homalopteroides modestus* (Vinciguerra 1890) is a poorly known species that was originally described from the Meekalan and Meetan rivers of southern Myanmar. It occurs in the Salween, Mae Khlong, and Tenasserim basins, and can be distinguished from all other species of *Homalopteroides* by the combination of caudal-fin pattern (black proximal and distal bars, median blotch), 15 pectoral-fin rays, pectoral-fin length greater than head length, 5½–6½ scales above and 5–6 scales below the lateral line (to the pelvic fin), 39–44 total lateral-line pores, no axillary pelvic-fin lobe, pelvic fin not reaching anus, orbital length less than interorbital width in adult, and maxillary barbel reaching to or slightly past the anterior orbital rim.

Key words: *Homaloptera*, *Balitoropsis*, *Homalopterula*, *Chopraia*, loaches

Introduction

Homaloptera van Hasselt 1823 is the most species-rich genus of the subfamily Balitorinae, comprising 35 valid species (Eschmeyer & Fricke 2012). It has been distinguished from other genera of the subfamily Balitorinae in having smooth lips vs. lips with papillae (*Balitora* Gray 1830, *Hemimyzon* Regan 1911, *Annamia* Hora 1932, *Sinogastromyzon* Fang 1930, *Metahomaloptera* Chang 1944, *Jinshaia* Kottelat & Chu 1988), a single barbel at each corner of the mouth vs. more than one barbel (*Lepturichthys* Regan 1911, *Neohomaloptera* Herre 1944, *Cryptotora* Kottelat 1998), the gill opening extending to the ventral surface of the body vs. not reaching the ventral surface (*Bhavania* Hora 1920), and absence vs. presence of two papillae between the lateral portions of the lower lip (*Travancoria* Hora 1941). Species of *Homaloptera* occur in India, Myanmar, China, Thailand, Laos, Cambodia, Vietnam, and south to Sumatra, Java, and Borneo. The species have a diverse range in body size, with the smallest species, *Homaloptera tweediei* Herre 1940, reaching 26 mm SL (Herre 1940), and the largest, *Homaloptera parclitella* Tan and Ng 2005, reaching 102 mm SL (Tan & Ng 2005).

Comparisons of specimens from the Mae Khlong basin previously identified as *Homaloptera smithi* Hora 1932 with specimens of all other species of *Homaloptera* available (26 of 35 valid species) led to the redescription of the poorly known and often misidentified *Homaloptera modesta* (Vinciguerra 1890) and to the resurrection of the genus *Homalopteroides*. Fowler (1905) removed *Homaloptera wassinkii* Bleeker 1953 from *Homaloptera* and placed it in a new genus *Homalopteroides*, which was distinguished from *Homaloptera* by having the origin of the dorsal fin posterior, rather than anterior, to the origin of the pelvic fin (Fowler 1905). This new genus, based on a single character, was given subgeneric rank by later authors (Weber & de Beaufort 1916; Fowler 1940; Silas 1953; Alfred 1969; Menon 1987). More recently, *Homalopteroides* was recognized as being possibly a distinct genus

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based on having "a short and broad body, a short caudal peduncle, relatively long paired fins with the pectorals reaching and usually overlapping the pelvics, and a dark body with a series of saddles along the back" (Kottelat 1998). Kottelat's description was treated by Tan and Ng (2005) as warranting recognition of *Homalopteroides* as a subgenus of *Homaloptera*.

FIGURE 1. Lateral views of: (A) *Homaloptera* (*Homaloptera*) *ocellata*, UF 161718, 64.1 mm SL; (B) *Homalopteroides wassinkii*, UMMZ 155660, 46.2 mm SL; (C) *Homaloptera* (*Balitoropsis*) *zollingeri*, UF 166094, 52.1 mm SL; (D) *Homaloptera* (*Homalopterula*) *ripleyi*, ANSP 188908, 43.1 mm SL. Scale bars represents 30mm; A, B, and C share a scale bar.

None of the characters provided by Kottelat (1998) for *Homalopteroides* are apomorphic given that the three other potentially valid genera that he proposed (recognized as subgenera of *Homaloptera* by Tan & Ng 2005), *Homaloptera* (*sensu stricto*) van Hasselt 1823, *Balitoropsis* Smith 1945, and *Homalopterula* Fowler 1940, include species that share one or more of these characters. Lateral and ventral views of the type species of the genera proposed by Kottelat (1998) are shown in Figures 1 & 2.

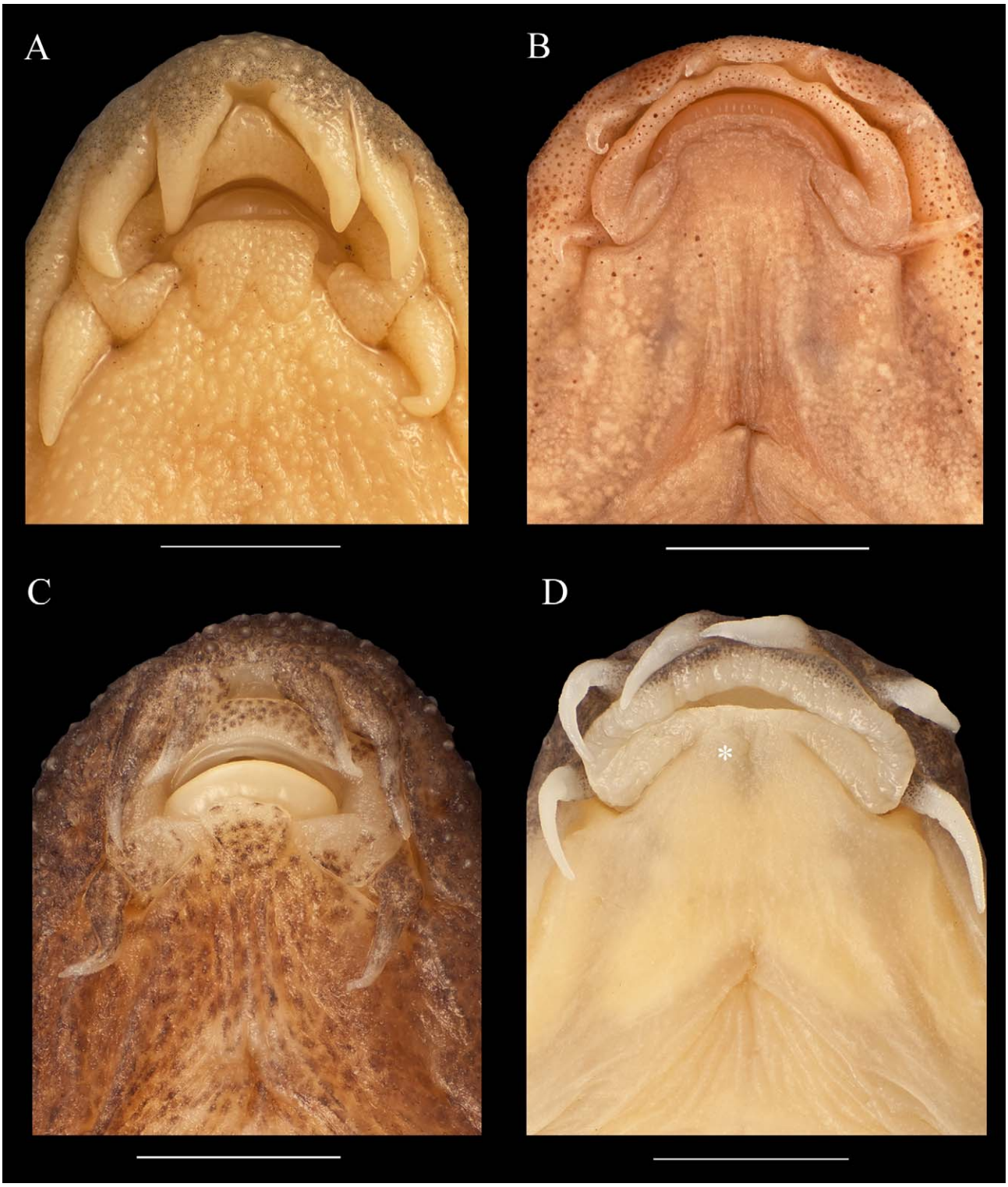

FIGURE 2. Mouths of: (A) *Homaloptera* (*Homaloptera*) *ocellata*, UF 161718, 64.1 mm SL; (B) *Homalopteroides wassinkii*, UMMZ 155660, 46.2 mm SL; (C) *Homaloptera* (*Balitoropsis*) *zollingeri*, UF 166094, 52.1 mm SL; (D) *Homaloptera* (*Homalopterula*) *ripleyi*, ANSP 188908, 43.1 mm SL, asterisk represents the mental lobes. Scale bars equal 3mm.

Fowler's character state distinguishing *Homalopteroides*, the origin of the dorsal fin in relation to the origin of the pelvic fin, also is not unique. All of the species belonging to *Homalopterula* and a related group of Indian species (see Discussion) also have the origin of the dorsal fin posterior to the origin of the pelvic fin. Based on a review of specimens and published species descriptions, *Homalopteroides* Fowler 1905 is resurrected as a genus based on a unique mouth morphology that distinguishes it from the genus *Homaloptera*.

Materials and methods

Lengths were measured to the nearest 0.1 mm using digital calipers and taken on the left side when possible. To reduce the effect of ontogenetic variation in morphometric values, only individuals classified as adults were compared interspecifically. Individuals having the orbital length shorter than the interorbital width were categorized as adults, and those with the orbital length greater than or equal to the interorbital width were categorized as juveniles. Measurements and counts (Table 1) follow Hubbs and Lagler (2004: A, B, C, D, E, H, N, O, P, Q, R, S, T, U, W, X, BB, GG; letters correspond to measurements in Table 1) and Kottelat (1984: G, J, K, L, V, DD, EE) with the exception of the following measurements. Body depth at anus (F) is the greatest body dimension at the anus. Prepectoral length (I) is from tip of the snout to the base of the first pectoral ray. Distance between anus and anal fin (M) is from the anal opening to the base of the first anal ray. Snout to nostril distance (Y) is from the tip of the snout to the anterior part of the nostril. Nostril to operculum distance (Z) is from the most posterior margin of the nostril to the hindmost part of the opercle. Internostril width (AA) is measured at the narrowest distance between the nostrils. Interorbital width (CC) is the least distance between the orbits including the orbital rim. Interrostral width (FF) is measured at the narrowest distance between the rostral barbels. Inter-lower lip width (HH) is measured at the narrowest distance between the lateral portions of the lower lips. All ray counts are given as follows: simple rays in Roman numerals followed by branched rays in Arabic numerals where dorsal- and anal-ray counts include the last ray split at the base represented by ½. The caudal-fin ray count is the total number of branched rays. Total lateral-line pore count includes the pores on the caudal fin. Small scales are counted as ½. Institutional abbreviations follow Eschmeyer and Fricke (2012), and the abbreviation for alcoholic specimens is ALC. A single specimen was cleared and double-stained for bone and cartilage using the technique of Taylor and van Dyke (1985). Photographs were taken of preserved specimens using Visionary Digital (Palmyra, Virginia) with Canon 40D and 5D cameras at UF.

TABLE 1. Morphometric measurements and meristic counts for adult (N = 58) and juvenile (N = 10) *Homalopteroides modestus*. All measurements are expressed in mm. The number of individuals associated with a value are shown in parentheses. Letters represent measurement sources, see Methods.

MORPHOMETRICS	Range (Juvenile)	Range (Adult)	Mean ± % SD (Juvenile)	Mean ± % SD (Adult)
Standard Length (A)	18.6–27.0	23.1–44.2		
% Standard Length				
Head length (B)	25.4–30.6	24.1–28.7	27.3±1.55	26.5±1.10
Head width (C)	16.7–19.4	16.8–21.0	18.3±1.04	18.5±0.98
Head depth (D)	11.1–13.1	11.7–14.8	12.0±0.67	12.9±0.66
Body depth (E)	13.5–15.1	14.6–20.0	14.3±0.60	17.0±1.19
Body depth at anus (F)	12.0–13.4	11.5–15.0	12.7±0.47	12.1±1.94
Body width (G)	11.2–13.9	11.6–17.9	12.2±0.83	14.7±1.14
Predorsal length (H)	52.6–57.7	52.4–57.4	54.0±1.56	54.8±1.21
Prepectoral length (I)	20.0–22.7	19.2–25.6	21.5±0.84	21.8±1.14
Prepelvic length (J)	45.9–48.8	43.5–51.4	47.1±0.88	46.6±1.64
Preanal length (K)	77.1–79.8	73.0–87.9	78.4±0.78	77.9±2.38
Preanus length (L)	71.1–74.4	70.0–79.7	73.3±1.03	73.2±1.93
Distance between anus and anal fin (M)	3.8–6.0	3.0–5.4	4.8±0.83	4.1±0.64
Dorsal-fin base length (N)	9.1–11.5	9.0–13.8	10.4±0.68	11.5±1.10

.....continued on the next page

TABLE 1. (Continued)

MORPHOMETRICS	Range (Juvenile)	Range (Adult)	Mean ± % SD (Juvenile)	Mean ± % SD (Adult)
Dorsal-fin length (O)	20.5–23.6	19.5–23.7	21.9±0.88	21.5±1.00
Pectoral-fin base length (P: adapted from N)	10.4–13.2	10.3–14.6	12.1±1.16	12.6±0.96
Pectoral-fin length (Q)	28.2–31.6	26.6–32.5	30.0±1.17	29.6±1.28
Pelvic-fin base length (R: adapted from N)	6.3–8.5	5.8–8.6	7.7±0.80	7.4±0.67
Pelvic-fin length (S)	19.4–22.2	19.1–23.8	21.2±0.92	21.5±1.26
Anal-fin base length (T)	6.3–8.4	4.8–9.1	7.2±0.65	6.7±1.28
Anal-fin length (U)	14.5–17.2	14.0–18.8	15.8±0.77	16.3±0.92
Caudal-peduncle length (V)	13.5–16.8	12.1–17.4	15.0±1.30	14.3±2.97
Caudal-peduncle depth (W)	9.1–10.4	9.2–11.5	9.7±0.42	10.5±0.52
% Head Length				
Head width	57.2–74.0	61.3–76.5	67.4±6.08	69.8±3.58
Head depth	39.7–48.3	42.7–54.1	44.0±2.33	48.7±2.95
Snout length (X)	32.1–45.7	37.0–50.5	41.2±3.92	44.7±2.29
Snout to nostril distance (Y)	26.8–35.4	27.3–37.4	32.8±2.45	32.4±2.06
Nostril to operculum distance (Z)	60.5–71.5	58.0–69.6	66.3±3.10	64.5±2.60
Internostril width (AA)	15.7–21.8	13.5–23.4	18.6±2.10	17.4±2.4
Length of orbit (BB)	28.0–31.4	19.1–29.6	29.4±1.25	24.5±2.04
Interorbital width (CC)	25.8–31.4	26.1–34.2	28.8±1.70	29.8±1.71
Length of maxillary barbel (DD)	12.7–16.0	10.6–19.7	14.4±1.05	14.5±2.13
Length of lateral rostral barbel (EE)	6.6–14.3	9.0–15.5	10.9±2.17	11.5±1.45
Interrostral width (FF)	6.0–8.7	4.7–9.98	7.0±0.84	7.0±1.18
Width of gape (GG)	20.2–26.3	20.0–28.4	23.8±2.19	24.3±1.84
Inter-lower lip width (HH)	13.9–17.2	11.9–19.9	15.9±1.09	15.3±1.75
% Interorbital Width				
Length of orbit	100–113.6	70.1–95.9	102.3±4.27	82.9±7.08
MERISTICS				
Dorsal-fin ray count	iii, 7, ½ (62); iii, 7 (5); iii, 8, ½ (1)			
Pectoral-fin ray count	v, 9, i (45); v, 10, i (5); iv, 9, i (1); v, 9, ii (1); v, 10 (1); vi, 9, i (1); iv, 9, i & iv, 10 (1); v, 9, i & iv, 10 (1); v, 9, i & iv, 11 (1); v, 9 & v, 8, i (1);v, 9, i & v, 9 (2); v, 9, i & v, 10 (1); v, 9, i & v, 10, i (2); v, 9, i & vi, 8, i (1); v, 9, i & vi, 10 (1); vi, 9 & v, 9, i (1); vi, 9 & v, 10 (1); vi, 9, i & v, 10 (1)			
Pelvic-fin ray count	ii, 7 (61); ii, 6, i (5); ii, 5, ii (1); ii, 7, i & ii, 6, i (1)			
Anal-fin ray count	i, 5, ½ (55); ii, 5, ½ (11); N/A (2)			
Caudal-fin ray count	17 (59); 15 (5); 16 (1); N/A (2)			
Lateral-line pore count	38–42 + 1–2 on caudal fin			
Lateral-line pore at pelvic-fin origin	14–17			
Lateral-line pore at dorsal-fin origin	16–20			
Lateral-line pore at anal-fin origin	29–33			
Caudal-peduncle scale count	17–20			
No. scale rows above/below lateral line	5–6 ½ / 4–6			
No. scale rows below lateral line to pelvic-fin origin	5–6			
Predorsal scale count	17–22			

Sequences of the nuclear Recombination Activating Gene 1 (Rag1) for phylogenetic analysis were compiled from Genbank, representing 6 genera and 10 species of Balitoridae (Table 2). Rag1 is the most species-diverse gene for *Homaloptera* on Genbank. Outgroup taxa were the loaches *Pangio elongata* (Cobitidae) and *Barbatula barbatula* (Nemacheilidae). A multiple sequence alignment was assembled in Seaview 4 (Gouy *et al.* 2010) using a muscle algorithm (Edgar 2004). In assessing the systematic position of the genera of Balitoridae, a Bayesian analysis was conducted using MrBayes 3.1 (Huelsenbeck & Ronquist 2001) with posterior probabilities estimated

with a Markov chain Monte Carlo analysis. In order to determine the best-fit model of nucleotide evolution for the dataset, likelihood scores were compared in PAUP* ver. 4.b10 (Swofford 2002) and when scores were comparable, a Likelihood Ratio Test (LRT) was performed (Felsenstein 1981). Four Markov chain Monte Carlo reactions were run simultaneously for 1,000,000 generations under the GTR+I+G model. The trees and likelihood scores were sampled at every 100 generations. The standard deviation for split frequencies was 0.003, and the overlay plot and trace files of both runs were analyzed in the program Tracer v1.5 (Rambaut & Drummond 2007). The MCMC runs reached convergence after 100,000 generations. One thousand trees were discarded as burn-in, and the remaining trees were used to construct a 50% majority consensus tree in Figtree v1.3.1 (Rambaut & Drummond 2010).

TABLE 2. Genbank accession numbers and sources for analyzed samples.

Species	Genbank No.	Source
Balitora annamitica	EF056359.1	Ŝlechtová *et al*. 2007
Barbatula barbatula	EU711107.1	Mayden *et al*. 2008
Barbucca diabolica	EF056391.1	Ŝlechtová *et al*. 2007
Beaufortia kweichowensis	EF056362.1	Ŝlechtová *et al*. 2007
Homaloptera leonardi	EU711130.1	Mayden *et al*. 2008
Homaloptera parclitella	EF056358.1	Ŝlechtová *et al*. 2007
Homaloptera smithi	EF056356.1	Ŝlechtová *et al*. 2007
Homaloptera zollingeri	EF056388.1	Ŝlechtová *et al*. 2007
Pangio oblonga	EF056346.1	Ŝlechtová *et al*. 2007
Pseudogastromyzon cheni	EF056357.1	Ŝlechtová *et al*. 2007
Pseudogastromyzon fasciatus	EF056376.1	Ŝlechtová *et al*. 2007
Sewellia lineolata	EU409609.1	Chen *et al*. 2008

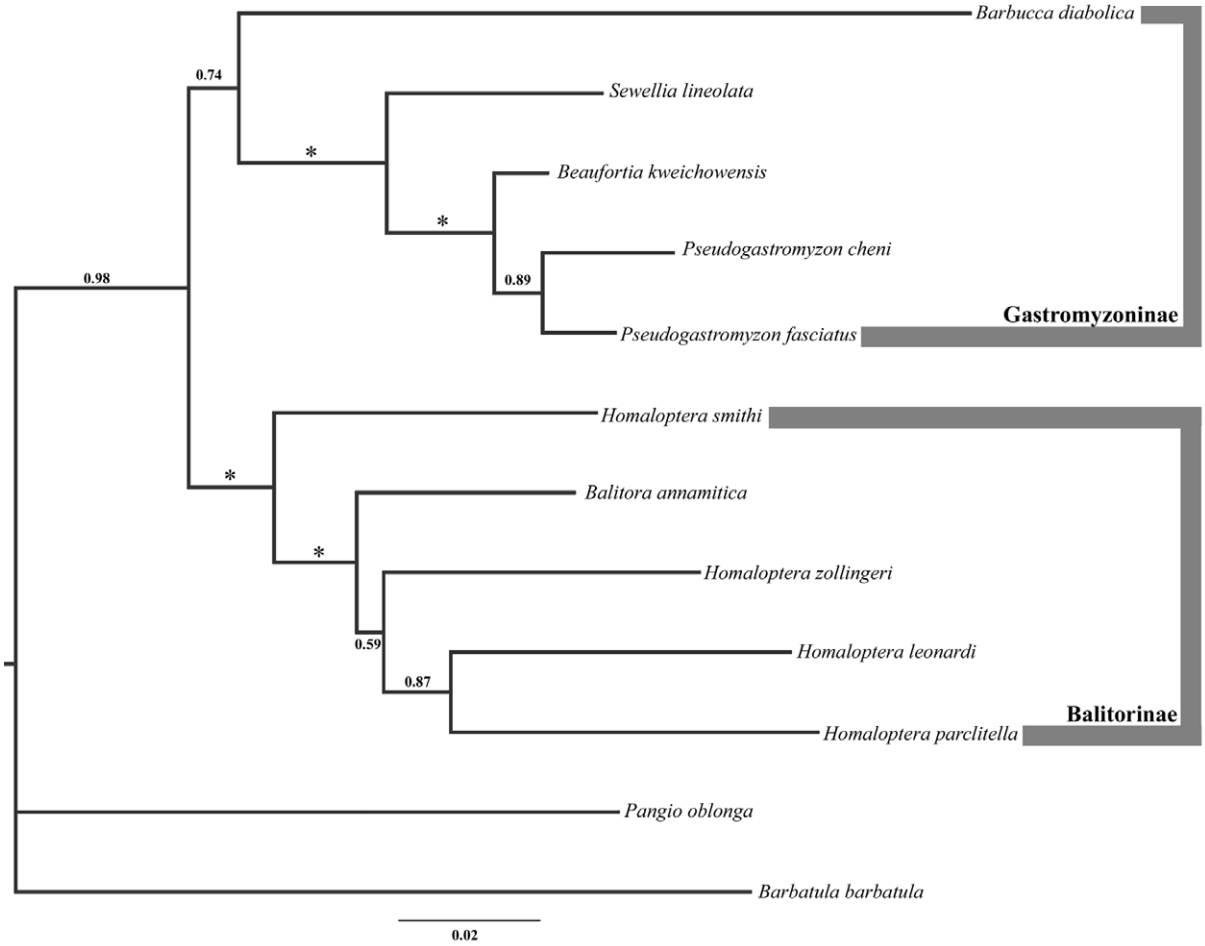

FIGURE 3. Phylogenetic relationships of the family Balitoridae from a Bayesian analysis of the Rag1 gene. An asterisk indicates a posterior probability of 100%.

Phylogenetic results

The Rag1 tree (Fig. 3) shows 98% posterior probability (pp) support for the family Balitoridae, weak support of 74% pp for Gastromyzoninae, and 100% pp for the Balitorinae. The low pp value for the Gastromyzoninae is due to the inclusion of the enigmatic genus *Barbucca* Roberts 1989, whose systematic position is questionable (Ŝlechtová *et al*. 2007). In Balitorinae, *Homaloptera* is paraphyletic, with a 100% pp that *Homaloptera smithi* Hora 1932 is sister to a clade including *Balitora annamitica* Kottelat 1998, *Homaloptera zollingeri* Bleeker 1853, *H. leonardi* Hora 1941, and *H. parclitella* Tan and Ng 2005. *Balitora annamitica* is sister to these three species of *Homaloptera* with 100% pp. Ŝlechtová *et al*. (2007) found similar results with *H. smithi* sister to a clade containing *Balitora* and *Homaloptera*. Based on these results and its morphological diagnosability, described below, *Homalopteroides*, in the phylogeny represented by *H. smithi*, is removed from the synonymy of *Homaloptera*.

Homalopteroides Fowler 1905

(Figs. 1B, 2B, 4, 5, & 6)

Homalopteroides Fowler, 1905: 476. (Type species: *Homaloptera wassinkii* Bleeker 1853, by original designation [the type species was misidentified, see below.]). Gender masculine.

Chopraia Prashad & Mukerji, 1929: 188 (Type species: *Chopraia rupicola* Prashad & Mukerji, 1929, by original designation). Gender feminine.

Fowler (1905) designated *Homaloptera wassinkii* Bleeker 1853 as the type species of *Homalopteroides*. The description given by Fowler for *H. wassinkii* was inaccurate and has caused confusion for authors, including Weber and de Beaufort (1916). The specimens (ANSP 68718) examined by Fowler are identifiable as *Homaloptera weberi* Hora 1932 when compared to the seven syntypes of *H. weberi* (BMNH 1895.7.2.81). They all have an orbital length greater than or equal to the interorbital width, and a pelvic fin that extends past the anus. Fowler inaccurately gave a total pectoral-fin ray count of 14 (v, 9) and an inaccurate count of 38 lateral-line scales from the gill opening to the base of the caudal fin. Correct counts are 16 (v, 10, i) rays and 45–47 scales.

Art. 70.3 of the International Code of Zoological Nomenclature (ICZN 1999) addresses misidentified type species. According to the provisions of the article, the species that will best serve stability and universality can either be the nominal species cited and misidentified (Art. 70.3.1, *H. wassinkii* Bleeker 1853) or the taxonomic species examined (Art. 70.3.2, *H. weberi* Hora 1932). The genus *Homalopteroides* is valid, and both of these species are members. We choose to retain the type species as *H. wassinkii* Bleeker 1853 (Art. 70.3.1).

Diagnosis. *Homalopteroides* is distinguished from *Homaloptera* by the following combination of characters: dorsal-fin origin over pelvic fin, ≤ 60 lateral-line scales, ≤ 30 predorsal scales, and a mouth morphology consisting of two thin and widely separated rostral barbels on each side of the mouth, thin crescent-shaped lips, the absence of any structure such as a mental pad or lobes (Fig. 2 D) between the lateral portions of the lower lip, and a chin that extends anterior to the lateral portions of the lower lip. Based on these characters, the following species are removed from *Homaloptera* and placed in *Homalopteroides*: *Homaloptera wassinkii* Bleeker 1853, *H. modesta* (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. nebulosa* Alfred 1969, *H. yuwonoi* Kottelat 1998, and possibly (see Discussion) *H. manipurensis* Arunkumar 1999.

Even with the transfer of species to *Homalopteroides*, *Homaloptera* remains a highly variable genus with species assigned to three subgenera: *Homaloptera* (*Homaloptera*), *H.* (*Balitoropsis*), and *H.* (*Homalopterula*). Due to this large morphological variation, *Homalopteriodes* can be distinguished from *Homaloptera* only by a combination of characters. All characters used to distinguish *Homalopteroides* from the subgenera of *Homaloptera* are described below.

Homalopteroides is distinguished from *Homaloptera* (*Homaloptera*) (Figs. 1A & 2A) by having the origin of the dorsal fin posterior, rather than anterior, to the origin of the pelvic fin, ≤ 60 total lateral-line pored scales vs. 60–67 for *H. ocellata* van der Hoeven 1833, 66–73 for *H. bilineata* Blyth 1860, 65 for *H. orthogoniata* Vaillant 1902, 60–63 for *H. ogilviei* Alfred 1967, 63 for *H. confuzona* Kottelat 2000, and 75–77 (Tan & Ng 2005) for *H. parclitella* Tan and Ng 2005, thin barbels with the medial- and lateral-rostral barbels widely separated from one

another at the base versus barbels thick and in close proximity to one another, crescent rather than triangular-shaped lips, and the absence versus presence of a mental pad.

Homalopteroides is distinguished from *Homaloptera* (*Balitoropsis*) (Figs. 1C & 2C) by having the origin of the dorsal fin posterior, rather than at or anterior to, the origin of the pelvic fin. The same mouth characters listed above for distinguishing *Homalopteroides* from *H.* (*Homaloptera*) distinguish *Homalopteroides* from *H.* (*Balitoropsis*) except lip shape, which can be crescent-shaped as in *H.* (*Balitoropsis*) *zollingeri* Bleeker 1853 (Fig 2C).

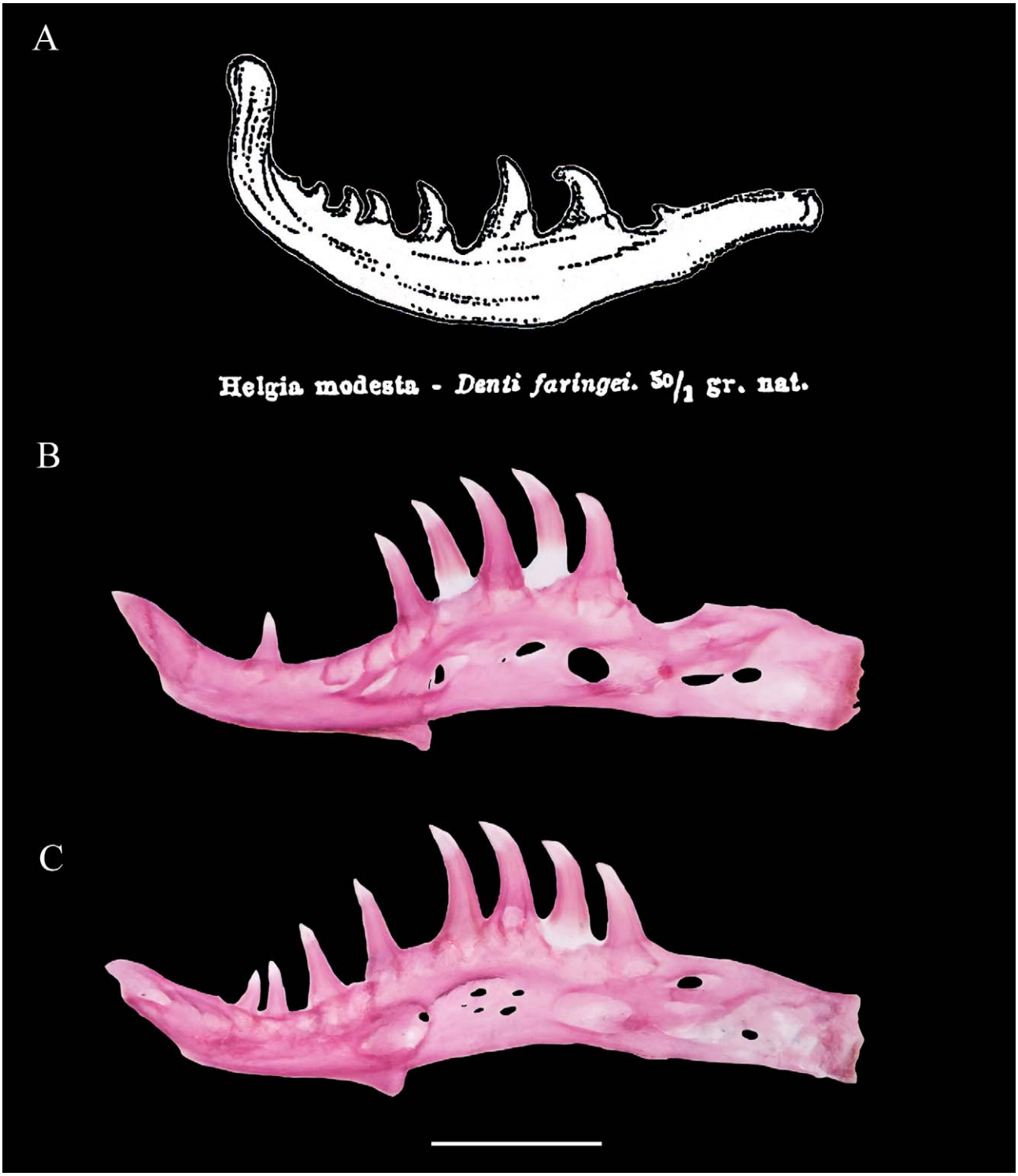

FIGURE 4. Fifth ceratobranchial of *Homalopteroides modestus*: *(*A) adapted from Vinciguerra (1890), p. 331; (B) UF 176454, 31.48 mm SL, left side, ventral view; (C) UF 176454, 31.48 mm SL, right side, dorsal view. B and C scale bar equals 0.5 mm.

Homalopteorides is distinguished from *Homaloptera* (*Homalopterula*) (Figs. 1D & 2D) by having ≤ 60 total lateral-line pored scales vs. 64–66 for *H.* (*Homalopterula*) *gymnogaster* Bleeker 1853, 63–70 (Weber & de Beaufort 1916) for *H.* (*Homalopterula*) *heterolepis* Weber and de Beaufort 1916, 70–74 for *H.* (*Homalopterula*) *ripleyi* (Fowler 1940), and 75 for *H.* (*Homalopterula*) *vanderbilti* Fowler 1940, ≤ 30 predorsal scales vs. 49–50 for *H. gymnogaster*, more than 50 (Weber & de Beaufort 1916) for *H. heterolepis*, 43–47 for *H. ripleyi*, and 56 for *H. vanderbilti*, thin vs. thick lips, the absence versus presence of mental lobes between the lateral portions of the lower lip, and a chin that extends anterior to, rather than up to, the lateral portions of the lower lip.

Redescription of *Homalopteroides modestus* (Vinciguerra 1890)

(Figs. 4, 5, & 6)

Helgia modesta Vinciguerra 1890: 330, Pl. 11 (fig. 12); Annali del Museo Civico di Storia Naturale di Genova (Serie 2) v. 9.
Lectotype. MSNG 15173A; Myanmar, Meekalan, Tenasserim; L. Fea, 1887. Designated by Tortonese 1961: 188; Catalogo del tipi de pesci del Museo Civico di Storia Naturale di Genova. (Parte I). Annali del Museo Civico di Storia Naturale `Giacomo Doria' v. 72: 179–191.
Paralectotypes. BMNH 1893.2.16.50, 1 ALC; Myanmar, Meetan, Tenasserim; L. Fea, 1887.—MSNG 15173B, 1 ALC (1, now 3); same collection data as BMNH 1893.2.16.50—ZMA 100982, 2 ALC; same collection data as BMNH 1893.2.16.50.
Homaloptera modesta: Hora 1932: 288; Memoirs of the Indian Museum, v. 12 (2).

Homalopteroides modestus was placed in the genus *Helgia* along with *Homaloptera* (*Homaloptera) bilineata* Blyth 1860 by Vinciguerra (1890). Jordan (1920) subsequently designated *H.* (*Homaloptera) bilineata* as the type species of *Helgia*, making *Helgia* Vinciguerra 1890 a synonym of *Homaloptera* van Hasselt 1823. Fowler (1905) designated *Homaloptera wassinkii* Bleeker 1853 as the type species for *Homalopteroides* to which *H. modestus* belongs.

Homalopteroides modestus originally was described from the Meekalan and Meetan rivers, Tenasserim Division (now known as the Tanintharyi Region, Mon State and southern Kayin State) of southern Myanmar, and type specimens subsequently were designated by Tortonese (1961). The only type specimen examined in this study (due to availability) was a paralectotype, BMNH 1893.2.16.50. This specimen is in extremely poor condition and only pectoral fin and pelvic-fin ray counts could be made. Vinciguerra (1890) gave a total pectoral-fin ray count of 13 (v, 8) and a total pelvic-fin ray count of 8 (ii, 6). However, the paralectotype examined has a total pectoral-fin ray count of 15–16 (v, 10–11) (only one side could be counted) and a total pelvic-fin ray count of 9 (ii, 7). Since its original description, *H. modestus* has been redescribed by Silas (1953), Menon (1987), and Selim and Vishwanath (1998). Silas (1953) gave a total pectoral-fin ray count of 13–14 (v–vi, 8) and the same pelvic-fin ray count given by Vinciguerra (1890). Menon (1987) gave the same counts as Silas (1953), whereas Selim and Vishwanath (1998) followed the original description. Based on all material examined in the present study, *H. modestus* has a total pectoral-fin ray count of 14–16 (iv–vi, 8–10, i) with a modal number of 15 (v, 9, i). Silas (1953), Menon (1987), and Selim and Vishwanath (1998) gave a lateral-line scale count of 47 although Vinciguerra (1890) states “11 numero delle squame della linea laterale non si può precisare con esattezza: esse sono circa 47” (11 Number of the scales of the lateral line cannot be precise: there are about 47). The 68 individuals sampled in this study had a lateral-line pore count of 38–42 +1–2. Vinciguerra (1890) gave a pharyngeal tooth count of 8 and described the 2nd to 4th teeth as being well developed, and the other five as rudimentary. In one of the specimens examined in this study, the pharyngeal tooth count was 8, the first six teeth being large and the last two small (Fig. 4).

Diagnosis. *Homalopteroides modestus* is distinguished from all other members of *Homalopteroides* (Table 3) by the combination of its caudal-fin color pattern that consists of a black proximal bar, a black distal bar and a black median blotch, 15 pectoral-fin rays (v, 9, i), a pectoral-fin length greater than the head length, 5–6½ scales above and 5–6 scales below the lateral line (to the pelvic fin), a total lateral-line pore count of 39–44, absence of an axillary pelvic lobe, pelvic fin not extending to the anus, orbital length less than the interorbital width (an adult character, see Discussion), and a maxillary barbel that reaches to or slightly past the anterior orbital rim.

TABLE 3. Characters distinguishing *Homalopteroides modestus* from all other species belonging to the genus. Species that may have a fully pigmented lower lobe of the caudal fin are represented by *.

Species	Number of bands on caudal fin	Total pectoral-ray count	Pectoral-fin length, >, = to, or < than head length	Scale count above and below lateral line to pelvic fin	Total lateral-line pore count	Axillary lobe present (Yes/No)	Pelvic fin extending to or past anus (Yes/No)	Orbital length >, = to, or < than interorbital width	Maxillary barbel reaches vertically to
H. modestus	2 1/3	15	>	5–6½/5–5½	39–44	No	No	< (Adult)	At or slightly past orbital rim
H. indochinensis	2–3	17	>	?	43–44	Yes	Yes	=	Posterior nostril edge
H. nebulosus	1–2*	13–14	<	5–6½/5–6½	38–42	No	No	≥	Midorbit
H. rupicola	2*	16	>	5–6/5–6	42–44	No	No	≥	Orbital rim
H. smithi	3*–4*	17–18	>	5–6½/5–6	39–42	Yes	No	<	Orbital rim
H. stephensoni	2–3	16–17	>	6–7½/7–8½	45–52	Yes	Yes	≤, ≥	Midnostril
H. tweediei	2–3*	13	<	4–5/3–4½	34–37	No	No	≥	Midorbit
H. wassinkii	3	18	>	7/6	47	Yes	No	<	Posterior nostril edge
H. weberi	2	16	>	6–7½/7–8½	46–48	Yes	Yes	≥	Midnostril
H. yuwonoi	2	16	<	6/5	41	No	Yes	=	Midnostril

Homalopteroides modestus is morphologically most similar to *H. nebulosus*, *H. rupicola*, and *H. tweediei.* It is distinguished by having 15 pectoral-fin rays vs. 13–14 in *H. nebulosus*, 16 in *H. rupicola*, and 13 in *H. tweediei*. It can be distinguished further from *H. nebulosus* and *H. tweediei* by a pectoral-fin length greater than head length vs. pectoral-fin length less than head length, and from *H. rupicola* by an interorbital width greater than the orbital length vs. interorbital width less than or equal to the orbital length. *Homalopteroides smithi* and *H. wassinkii* are distinguished from *H. modestus* by the presence vs. absence of an axillary pelvic lobe. *Homalopteroides indochinensis*, *H. stephensoni*, *H. weberi*, and *H. yuwonoi* are distinguished from *H. modestus* by a pelvic fin that extends to or past the anus.

FIGURE 5. *Homalopteroides modestus*,Thailand, Kanchanaburi, Mae Khlong basin: (A) dorsal, lateral, and ventral views of an adult, UF 181080, 37.2 mm SL, scale bar equals 30 mm; (B) lateral view of a juvenile, UF 176377, 24.8 mm SL, scale bar equals 10 mm.

Description. Dorsal, lateral, and ventral views of an adult are shown in Figures 5A and 6. Measurements and meristic counts are given in Table 1. *Homalopteroides modestus* is a moderate-sized species reaching 44 mm SL. The body has a flattened ventral surface, is arched predorsally and tapers posteriorly to the caudal base. The head is conical when viewed dorsally and covered with tubercles. The orbits are small, ovoid, positioned dorsolaterally, and smaller in length than the interorbital width. The nostrils and orbital rim are in close proximity but are not in contact.

The mouth (Fig. 6) is inferior with both upper and lower jaws slightly visible. The lips are thin, smooth, crescent-shaped, and continuous around the corners of the mouth. The lateral portion of the lower lip is broad and the medial portion is thin. The chin extends anterior to the lateral portion of the lower lip. Posterior to the lower lip is a series of large tubercles that extend onto the operculum. Rostral and postlabial grooves are present. Two pairs of rostral barbels and a pair of maxillary barbels are present at each corner of the mouth. The medial-rostral barbels are separated from one another by a large lobe. The rostral barbels are separated by a small lobe with a distance about equal to the length of the medial-rostral barbel. The lateral-rostral barbel reaches the base of the maxillary barbel, and the maxillary barbel reaches horizontally to a vertical at or slightly posterior to the anterior orbital rim. The gill opening extends to the ventral surface of the body, and the gill membrane is united to the isthmus with a large central furrow where the gills meet. The opercle reaches to or past the 2nd pectoral-fin ray.

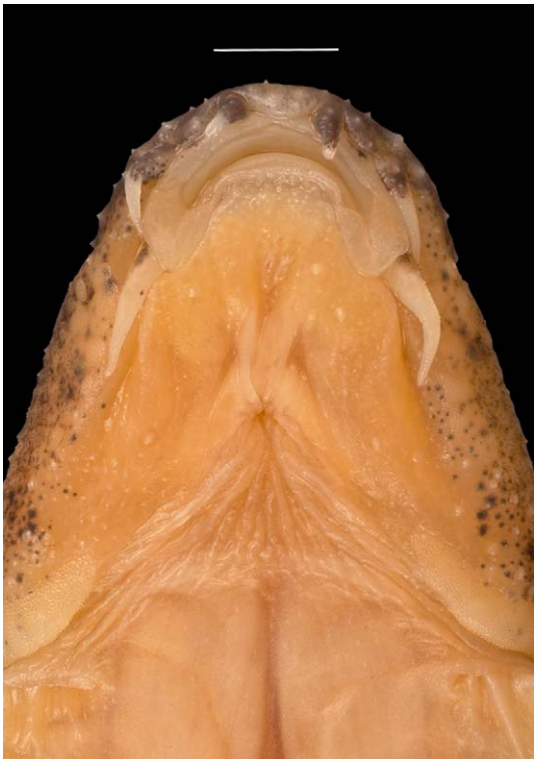

FIGURE 6. Mouth of *Homalopteroides modestus*, UF 181080, 37.2 mm SL. Scale bar equals 2 mm.

Body scaled except for the ventral surface anterior to pelvic-fin; scales between the anal-fin origin and pelvic insertion are deeply embedded. In the cleared and stained specimen a medial row of scales from the pelvic fins reached to a small patch of scales between the pectoral fins. Most scales, especially above the lateral line and at the dorsal-fin origin, have a small nipple at their posterior extremity; up to six nipples are present on a scale. The total lateral-line pore count is 39–44.

Variations in fin counts are given in Table 1; modal numbers are given here. Dorsal fin has 3 simple and 7 branched rays (iii, 7 ½) and originates over the pelvic fin, closer to the caudal-fin base than to the snout. Pectoral fin has 6 simple and 9 branched rays (v, 9, i), is longer than the head length and reaches past the pelvic-fin origin. Pelvic fin has 2 simple and 7 branched rays (ii, 7), lacks an axillary pelvic lobe, and does not reach the anus which is located closer to the anal-fin origin than to the pelvic-fin insertion. Anal fin has 1 simple and 5 branched rays (i, 5 ½). The caudal fin is forked with rounded lobes and has a total of 17 branched rays; the lower lobe slightly longer than the upper. Total number of vertebrae is 31, comprising 15 abdominal and 16 caudal. The fifth

ceratobranchial (Fig. 4) bears a large transverse ventralis process and has a single row of 8 teeth. Positioning of the teeth varies in the left and right ceratobranchials in the cleared and stained specimen examined.

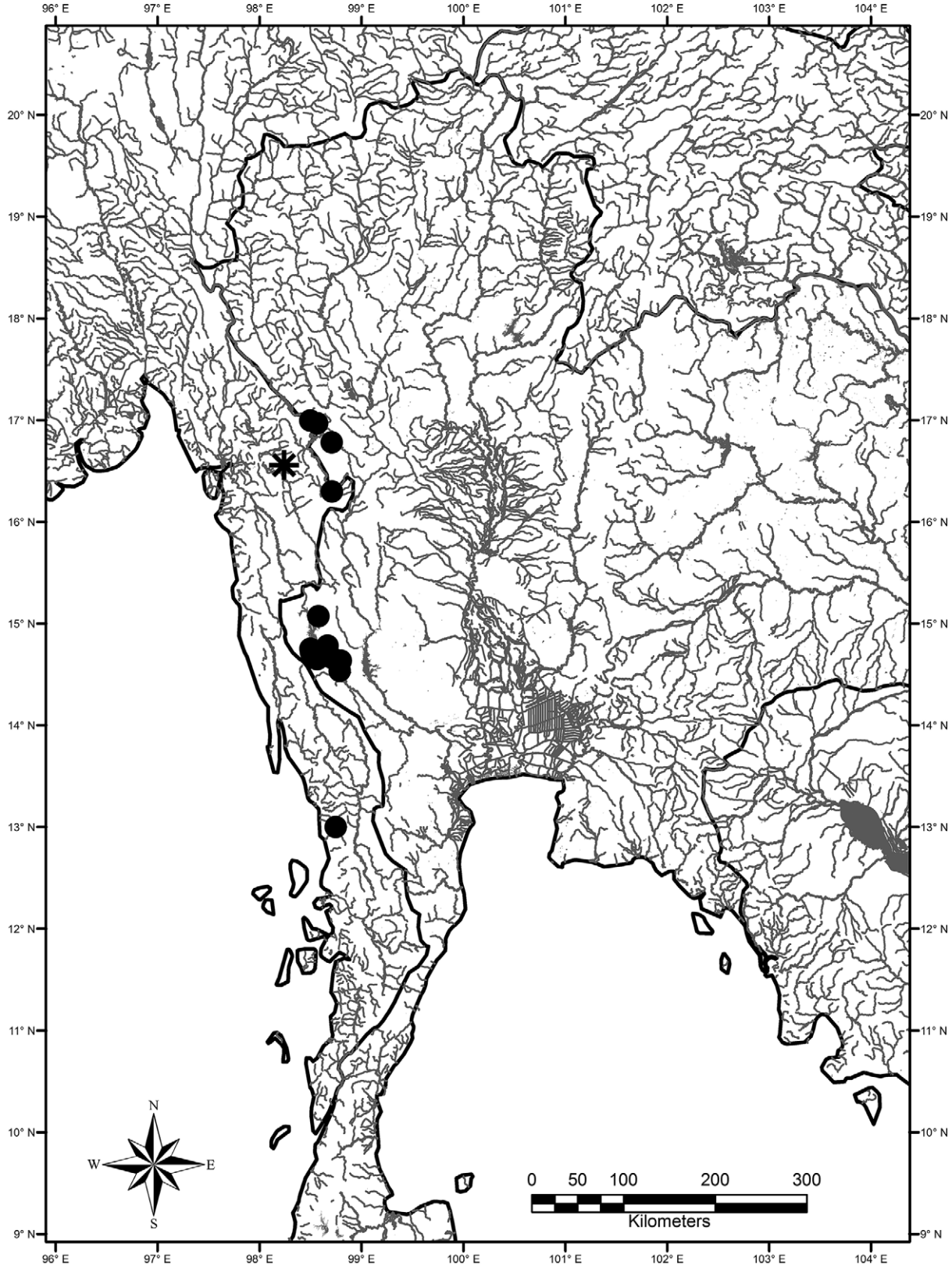

FIGURE 7. Distribution of *Homalopteroides modestus*. Black dots represent localities for specimens examined; asterisk represents type locality.

Lateral view of a juvenile is shown in Figure 5B. Measurements and meristics for juveniles (individuals with an orbital length greater than or equal to the interorbital width) are given in Table 1. The maximum size is 27 mm. Characters not shared with adults are discussed. The body lacks a well-defined predorsal arch and lobes between the barbels. Few tubercles may be present by and between the nares. Nipples on the scales are not prominently found. The pectoral fin reaches the pelvic fin, but does not always reach past it.

Coloration. In 70% Ethanol: The general color is shown in Figures 5 and 6. The color pattern varies slightly between adults and juveniles. In dorsal view, the base color is cream with small mottled brown spots. There are five black dorsal saddles. The 1st saddle may have smaller, incomplete saddles surrounding it and is between the supraoccipital and dorsal-fin origin; 2nd is located at the dorsal-fin origin; 3rd is located at the dorsal-fin insertion between the dorsal-fin and anal-fin origins; 4th is dorsal to the anal fin; and 5th wraps the caudal-fin base. The saddles often are faint and hard to distinguish in juveniles. A black bar extends from the lateral-rostral barbel base through the orbit and to the supraoccipital, which is outlined in black.

The lateral view shares the same base color pattern as the dorsal view. A black bar extends from the medial-rostral barbel base to or just before the nares. Another black bar extends from the orbit to the posterior edge of the opercle just below the origin of the lateral line. The lateral line is marked by a solid black stripe that may contain circular blotches. One–4 large pigmented blotches may be present below the black stripe between the pectoral-fin origin and the anterior edge of the orbit. The 3rd and 4th saddles usually commence at the lateral line. Mottled brown spots sometimes coalesce to form distinct lines above and below the lateral line and may form large spots between the pelvic and anal fins.

In ventral view, the base is cream and, when mottled spots are present, they are restricted to a band at the anal-fin origin. The barbel bases are black, and the lips are occasionally pigmented between the rostral barbels and at the maxillary barbels.

FIGURE 8. Habitat of *Homalopteroides modestus*. Thailand, Kanchanaburi, Mae Khlong basin, Mae Nam Kwae, Khayeng River, 30 Dec. 2011, 14.65° N, 98.566667° E.

All of the fins have black bands; the dorsal fin has 3–4 in adults and 2–3 in juveniles. The pectoral fin has 2–3 bands, the pelvic fin has 1–2, and the anal fin has 1–2 in adults and 1 in juveniles. The caudal fin has 2 bars, a proximal bar and a distal bar, and a median blotch that may fuse to the distal bar. The lower lobe of the caudal fin is pigmented only at the caudal bars. The paired fins are black at their bases, and the unpaired fins have a black spot at their origins. All fins have hyaline tips.

Distribution. *Homalopteroides modestus* occurs in the Salween, Mae Khlong, and Tenasserim basins (Fig. 7). The latter two basins drain the Tenasserim Range, a large mountain chain between Thailand and Myanmar. The eastern part of the Tenasserim Range is crossed by the Mae Nam Kwae Noi River (Mae Khlong basin) and the southwestern part gives rise to the Tenasserim River. The Salween River flows north of the Tenasserim Range. Other species that have a distribution in both the Mae Khlong and Salween basins are *Schistura mahnerti* (Kottelat 1990; Plongsesthee *et al*. 2011), and *Acanthocobitis pictilis* (Kottelat 2012). Most individuals of *H. modestus* have been collected in mountain streams in rubble and gravel riffles (Fig. 8).

Homalopteroides modestus has been reported from Borneo by Boulenger (1894) and Popta (1906); however, these populations were subsequently described as *H. weberi* and *H. stephensoni* by Hora (1932). The description given for *H. modestus* from Manipur, India (Selim and Vishwanath 1998), does not agree with the data from this study and probably refers to a different species.

Discussion

Many authors have noted the possible paraphyly of the genus *Homaloptera* (Fang 1930; Hora 1932; Kottelat 1998; Tan & Ng 2005; Tan 2009), and several genera have been created for species previously in *Homaloptera* (*Hemimyzon* Regan 1911, *Lepturichthys* Regan 1911, *Protomyzon* Hora 1932, and *Cryptotora* Kottelat 1998) or elevated from use as a subgenus (*Neohomaloptera* Herre 1944). Phylogenetic analysis of the Rag1 gene (Fig. 3) demonstrated the paraphyly of the genus *Homaloptera*. *Homalopteroides smithi* (Hora 1932) is sister to a clade including *Balitora annamitica*, *Homaloptera zollingeri*, *Homaloptera leonardi*, and *Homaloptera parclitella*. The phylogenetic analysis also showed that the subgenera *Homaloptera* (*Homaloptera*) and *H.* (*Balitoropsis*), proposed by Kottelat (1998) as possible genera, are not well defined. *Homaloptera* (*Balitoropsis*) *leonardi* is sister to *H.* (*Homaloptera*) *parclitella* (87% pp), and both of them are sister to *H.* (*Balitoropsis) zollingeri* with a weak support of 59% pp. A more comprehensive analysis is needed to understand the relationships within and between these two subgenera.

Five species of *Homaloptera* are known from the Western Ghats of India: *H. montana* Herre 1945, *H. pillaii* Indra and Rema Devi 1981, *H. menoni* Shaji and Easa 1995, *H. santhamparaiensis* Arunachalam *et al*. 2002, and *H. silasi* Madhusoodana Kurup and Radhakrishnan 2011. These species have been recognized as possibly constituting a group requiring a separate genus (Pethiyagoda & Kottelat 1994 [first two species]; Kottelat 1998 [first three species]) or subgenus (Tan & Ng 2005). The only Indian species examined in this study (due to the restricted access to specimens) was *H. montana*. *Homaloptera montana* is distinguished from all other taxa examined in this study by having the origin of the dorsal fin posterior to the insertion of the pelvic fin. It has a mouth morphology more similar to that of *Homaloptera* (*Homalopterula)* than to that of *H.* (*Homaloptera*) and *H.* (*Balitoropsis*). Based on the combination of mouth morphology, dorsal-fin origin over pelvic fin, ≥ 60 lateral-line scales, and ≥ 30 predorsal scales, *H.* (*Homalopterula*) currently includes only the endemic Sumatran species, *H. gymnogaster*, *H. heterolepis*, *H. ripleyi*, and *H. vanderbilti*. The Indian group is similar in morphology to *H.* (*Homalopterula*) in having a chin that extends up to the lateral portions of the lower lip and a larger total lateral-line pore count: 70–72 in *H. montana* and 59–62 in *H. menoni* (Madhusoodana Kurup & Radhakrishnan 2011).

Homaloptera manipurensis Arunkumar 1998 is known only from the state of Manipur in northeastern India. Based on its original description, *H. manipurensis* seems to belong to *Homalopteroides.* It is distinguished from *H. modestus* in having a total dorsal-fin ray count of 8 (ii, 6) vs. 10 (iii, 7½), a scale count above/below the lateral line to the pelvic fin of 8/4 vs. 5–6½/5–6, and a caudal-fin color pattern consisting of three well-defined black bars vs. black proximal and distal bars, and a black median blotch.

Some species of *Homalopteroides* have been described from small specimens: 24–27 mm SL (Prashad and Mukerji 1929) for *H. rupicola*, 23–26 mm SL (Herre 1940) for *H. tweediei*, and 22.3–24.5 mm SL (Alfred 1969) for *H. nebulosus*. Based on the material examined in this study all of these species have an orbital length greater

than or equal to the interorbital width. The use of this character as diagnostic for these species is problematic and may be incorrect given that orbit size may vary between juveniles and adults as in *H. modestus*.

Comparative material examined

Homaloptera batek*:** Borneo: Central Kalimantan: Katingan basin: MZB 10990 (holotype), 1 ALC.—ZRC 51743 (paratypes), 5 (of 28) ALC.—Homaloptera bilineata*:** Myanmar: Sagaing Division: Irrawaddy River: CAS 231723, 4 ALC.—***Homaloptera confuzona*:** Thailand: Changwat prov.: Trat River: UF 169906, 1 ALC.—***Homaloptera gymnogaster*:** Indonesia: Sumatra: Lake Meninju: BMNH 1866.5.2.49 (holotype), 1 ALC.—***Homaloptera leonardi*:—**Malaysia: Pahang: Kuala Tahan: ZRC 1753 (paratype) , 1 ALC.—***Homaloptera maxinae*:** Thailand: Tachin: ANSP 68004 (holotype), 1 ALC.—***Homaloptera montana*:** India: Anamallai Hills: SU 39871 (holotype), 1 ALC.—***Homaloptera ocellata*:** Indonesia: Sumatra: Tulang bawang: UF 161605, 1 ALC.—UF 166104, 3 ALC.—UF 166107, 3 ALC. Indonesia: Sumatra: Seputhi: UF 161718, 2 ALC. Indonesia: Sumatra: Lematang: UF 166096, 6 ALC.—***Homaloptera ogilviei*:** Malaysia: Negri Sembilan: Telai [Jelai] River: BMNH 1966.9.26.1 (paratype), 1 ALC.—ZRC 1553 (paratype), 2 ALC.—Malaysia: Terengganu: Sg. Tok Dor: ZRC 1555 (Holotype), 1 ALC.—Malaysia: Perak: Perak River: ZRC 1554 (paratype), 2 ALC.—***Homaloptera ophiolepis*:** Indonesia: Java: Bandong: BMNH 1866.5.2.48 (paralectotype), 1 ALC.—Indonesia: Sumatra: Musi: UF 166101, 1 ALC.—UF 166103, 1 ALC.—Indonesia: Sumatra: Tulang bawang: UF 166109, 4 ALC.—***Homaloptera orthogoniata*:** Indonesia: Kalimantan Barat: Kapuas Basin: CAS 49326, 1 ALC.—***Homaloptera parclitella*:** Malaysia: Terengganu basin: ZRC 49257 (holotype), 1 ALC.—ZRC 47167 (paratype), 1 ALC.—***Homaloptera ripleyi*:** Indonesia: Sumatra: Atjeh Prov.: Goempang River: ANSP 68713 (holotype), 1 ALC—Indonesia: Sumatra: Sumatera Utara: Kampung Bassam: ANSP 188908: 4 ALC.—***Homaloptera sexmaculata*:** Thailand: Chiang Mai: Me Nam Ping: ANSP 56374 (holotype), 1 ALC.—ANSP 56375 (paratypes), 5 ALC.—***Homaloptera vanderbilti*:** Indonesia: Sumatra: Tripa River: ANSP 68688 (holotype), 1 ALC.—***Homaloptera zollingeri*:** Indonesia: Java: Bandong: BMNH 1866.5.2.53 (syntype). Malaysia: Negri Sembilan: Jelai river: SU 66420, 2 ALC. Indonesia: Sumatra: Musi: UF 166094, 2 ALC.—UF166095, 2 ALC. Indonesia: Sumatra: Tulang bawang: UF 166102, 1 ALC.—UF 161715, 4 ALC.—***Homalopteroides indochinensis*:** Vietnam: BMNH 1933-8-19-50 (holotype, unique), 1 ALC.—***Homalopteroides modestus*:** Thailand: Kanchanaburi Prov.: Mae Khlong basin, Kwae Noi River system: ANSP 179826, 5 of 6 ALC, Ulong River at route 323 bridge, approximately 5–10 km NE of Thong Pha Phum; 14.7825° N, 98.669167° E.—NIFI 4508, 1 ALC, Huay Ka Yeng, Hauy Ban Rai; 14.719444° N, 98.505833° E.—NIFI 4517, 1 ALC, Huay Ka Yeng at highway 3272 bridge; 14.659722° N, 98.533611° E.—UF 172926, 1 ALC, Stream at km 110 on Rt. 323; 14.661944° N, 98.7125° E.—UF 173067, 1 ALC, Lichia River at 323 bridge; 15.070556° N, 98.580556° E.—UF 176377, 10 of 35 ALC, Huay Ka Yeng, Kring Ta Ko; 14.752778° N, 98.500556° E.—UF 176408, 2 ALC, same collection data as NIFI 4517.—UF 176438, 8 ALC, same collection data as NIFI 4508.—UF 176454, 4 of 6 ALC, Huay Lin Tin, 95 km on highway 323, 14.534444° N, 98.787778° E.—UF 176544, 1 ALC, Huay Ka Yeng, Huay Pok Kok, Thong Pa Pume; 14.680278° N, 98.527222° E.—UF 176557, 8 of 11 ALC, Huay Ka Yeng, Huay Ban Rai; 14.689444° N, 98.513611° E.—UF 181080, 5 ALC, Khayeng River, Station 5; 14.65° N, 98.566667° E.—UF 181160, 9 of 12 ALC, Ban Huay Paousa (Paousa River); 14.633333° N, 98.8° E.—UF 181141, 1 of 10 ALC, Ban Huay Pakkok, 14.633333° N, 98.8° E.—ZRC 53385, 1 ALC, same collection data as UF 176557.—ZRC 53386, 1 ALC, same collection data as UF 181160. Thailand: Tak Prov.: Salween Basin, Salween River system: NIFI 3786, 1 ALC; 16.994614° N, 98.499494° E (coordinates estimated).—NIFI 4514, 1 ALC, Mae Sot, Mae Ramao, Mae Ramao Stream; 16.779344° N, 98.710069° E (coordinates estimated).—ROM 51147, 2 ALC, Unknown Creek, Huai Mae Charno, 4 km S of Amphoe Mae Ramat on Road 1085; 16.9666667° N, 98.5666667° E.—ZRC 41272, 4 of 6 ALC, Mae Nam Moei; 16.296417° N, 98.712472° E. Myanmar: Tanintharyi Region: Tenasserim Basin, Tenasserim River system: ZRC 22889, 1 ALC, Tuler Khoh mountain stream (about 2/3 distance from Kita to Baowashung); 13° N, 98.75° E (coordinates estimated). Myanmar: Kayin State (?): Salween basin (?): BMNH 1893.2.16.50 (paralectotype of *Helgia modesta*), 1 ALC, Meetan; 16.555556° N, 98.24° E (coordinates estimated).—***Homalopteroides nebulosus*:** Malaysia: Kelantan: Sok River: BMNH 1967.11.15.15 (paratype of *Homaloptera nebulosa*), 1 ALC.—SU 66428 (paratype of *Homaloptera nebulosa*), 1 ALC.—ZRC 2020 (holotype of *Homaloptera nebulosa*), 1 ALC.—ZRC 1759 (paratype

of *Homaloptera nebulosa*), 1 ALC. Thailand: Narathiwat: Sungai Kolok Basin: NIFI 3613, 5 ALC.—***Homalopteroides rupicola*:** Myanmar: Myitkyna District: Sankha River: SU 28726 (paratype of *Chopraia rupicola*), 1 ALC. Myanmar: Nan-Kwe Chaung: USNM 378433, 6 ALC.—***Homalopteroides smithi*:** Thailand: Nakhon Srithammarat: Ban Kiriwong: BMNH 1934.12.18.34, 1 ALC.—USNM 109821(paratype of *Homaloptera smithi*), 5 ALC.—***Homalopteroides stephensoni*:** Indonesia: Borneo: Nangapinoh: Sungai Pinoh: USNM 230254, 5 ALC. Indonesia: Borneo: Kalimantan Selatan: Aib River: USNM 393671, 6 ALC. Indonesia: Borneo: Kalimantan Selatan: Kusan Hulu River: USNM 393729, 10 ALC.—***Homalopteroides tweediei*:** Malaysia: Johore: Mawai: BMNH 1938.12.1.132 (paratype of *Homaloptera tweediei*), 1 ALC.—SU 33012 (holotype of *Homaloptera tweediei*), 1 ALC.—SU 33013 (Paratypes of *Homaloptera tweediei*), 2 ALC. Thailand: Pattani: Saiburi River Basin: NIFI 3604, 14 ALC.—***Homalopteroides wassinkii*:** Indonesia: Java: Buitenzorg: Tjampea: BMNH 1866.5.2.52 (lectotype of *Homaloptera wassinkii*), 1 ALC. Indonesia: Java: Lab. Binnenvisscherij (fishery): UMMZ 155660, 1 ALC.—***Homalopteroides weberi*:** Borneo: Baram: ANSP 68718 (misidentified as *Homaloptera wassinkii*), 11 of 16 ALC. East Malaysia: Sarawak: Akar River: BMNH 1895.7.2.81 (syntype of *Homaloptera weberi*), 7 ALC.—***Homalopteroides yuwonoi*:** Borneo: Kalimantan Barat: Kuapas basin: MZB 5938 (holotype of *Homaloptera yuwonoi*), 1 ALC.

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References

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

Arunkumar, L. (1998) *Homaloptera manipurensis*, a new homalopterid fish from Manipur, India. *Uttar Pradesh Journal of Zoology*, 18, 175–179.

Boulenger, G.A. (1894) Descriptions of new freshwater fishes from Borneo. *Annals and Magazine of Natural History*, 13, 245–251.

Chen, W.-J., Miya, M., Saitoh, K. & Mayden, R.L. (2008) Phylogenetic utility of two existing and four novel nuclear gene loci in reconstructing Tree of Life of ray-finned fishes: The order Cypriniformes (Ostariophysi) as a case study. *Gene*, 423, 125–134.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.

Eschmeyer, W.N. & Fricke, R. (Eds) Catalog of Fishes electronic version. Available from http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 30 January 2012).

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.

Felsenstein, J. (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution*, 17, 368–376.

Fowler, H.W. (1905) Some fishes from Borneo. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 57, 455–523.

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.

Gouy, M., Guindon, S. & Gascuel, O. (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution*, 27, 221–224.

Herre, A.W.C.T. (1940) New species of fishes from the Malay Peninsula and Borneo. *Bulletin of the Raffles Museum*, 16, 5–26.

Hora, S.L. (1932) Classification, bionomics and evolution of homalopterid fishes. *Memoirs of the Indian Museum*, 12, 263–330, Pls. 10–12

Hubbs, C.L. & Lagler, K.F. (2004) *Fishes of the Great Lakes region, with a new preface*. University of Michigan Press, Ann Arbor, Michigan, 276 pp.
Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
ICZN (1999) *International code of zoological nomenclature [the Code]*. Fourth edition. The International Trust for Zoological Nomenclature, Natural History Museum, London, 306 pp.
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.
Kottelat, M. (1984) Revision of the Indonesian and Malaysian loaches of the subfamily Noemacheilinae. *Japanese Journal of Ichthyology*, 31, 225–260.
Kottelat, M. (1988) Indian and Indochinese species of *Balitora* (Osteichthyes: Cypriniformes) with descriptions of two new species and comments on the family-group names Balitoridae and Homalopteridae. *Revue Suisse de Zoologie*, 95, 487–504.
Kottelat, M. (1990) Indochinese nemacheilines. *A revision of nemacheiline loaches (Pisces: Cypriniformes) of Thailand, Burma, Laos, Cambodia and southern Viet Nam*. Verlag Dr. Friedrich Pfeil, München, 262 pp.
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) *Acanthocobitis pictilis*, a new species of loach from Myanmar and Thailand (Teleostei: Nemacheilidae). *Zootaxa*, 3327, 45–52.
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., 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.
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.
Plongsesthee, R., Page L.M. & Beamish, W. (2011) *Schistura aurantiaca*, a new species from the Mae Khlong basin, Thailand (Teleostei: Nemacheilidae). *Ichthyological Exploration of Freshwaters*, 22, 169–178.
Popta, C.M.L. (1906) Résultats ichthyologiques des voyages scientifiques de Monsieur le Professeur Dr. A. W. Nieuwenhuis dans le centre de Bornéo (1898 et 1900). *Notes from the Leyden Museum*, 27, 1–304.
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.
Rambaut, A. & Drummond, A. (2010) *FigTree v1.3.1*. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, United Kingdom.
Rambaut, A. & Drummond, A.J. (2007) *Tracer v1.4*. Available from http://beast.bio.ed.ac.uk/Tracer.
Selim, K. & Vishwanath, W. (1998) A new record of *Homaloptera modesta* (Vinciguerra): Cyprinidae from Manipur. *Journal of the Bombay Natural History Society*, 95, 352–354.
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.
Ŝlechtová, 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.
Swofford, D.L. (2002) PAUP*. *Phylogenetic Analysis Using Parsimony* (*and Other Methods). 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.
Taylor, W.R. & van Dyke, G.C. (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119
Tortonese, E. (1961) Catalogo del tipi de pesci del Museo Civico di Storia Naturale di Genova. (Parte I). *Annali del Museo Civico di Storia Naturale `Giacomo Doria'*, 72, 179–191.
Vinciguerra, D. (1890) Viaggio di Leonardo Fea in Birmania e regioni vicine. XXIV. Pesci. *Annali del Museo Civico di Storia Naturale di Genova*, 9, 129–362.
Weber, M. & de Beaufort, L.F. (1916) The fishes of the Indo-Australian Archipelago. III. Ostariophysi: II Cyprinoidea, Apodes, Synbranchi. E. J. Brill, Leiden. *The Fishes of the Indo-Australian Archipelago*, 3, 1–455.