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Revision of the Genus *Henicorhynchus*, with a Revised Diagnosis of *Gymnostomus* (Cyprinidae: Labeoninae)

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The Southeast Asian cyprinid genus *Henicorhynchus* has a complicated taxonomic history due to morphological similarities with other genera and among species within the genus itself. *Henicorhynchus* and its constituent species are herein revised based on morphological examinations of over 1,000 specimens with a particular emphasis on oromandibular structures. Five species are now recognized in the genus. *Henicorhynchus entmema* and *H. caudimaculatus* are senior synonyms of *H. lobatus* and *H. lineatus*, respectively. *Henicorhynchus caudiguttatus* is removed from synonymy with *H. caudimaculatus*. A revised diagnosis of the South Asian cyprinid genus *Gymnostomus*, previously considered a senior synonym of *Henicorhynchus*, is also provided.

THE Southeast Asian cyprinid genus *Henicorhynchus* was described by Smith (1945) to accommodate *H. lobatus* that was described in the same monograph. Since the original description, *Henicorhynchus* and its constituent species have had a complex taxonomic history owing in part to the morphological similarities among the species and with other labeonin taxa, in particular to species of the genus *Cirrhinus* Oken, 1817 (type species: *Cyprinus cirrhosus* Bloch, 1795). Bănărescu (1983) considered *Henicorhynchus* to be a subgenus of *Cirrhinus*, with constituent species distinct from other species in the genus (therein placed in the subgenus *Cirrhinus*) based on branched dorsal-fin ray counts (8 in *Henicorhynchus* vs. 11–15 in *Cirrhinus*). Roberts (1997) treated *Henicorhynchus* as a junior synonym of *Cirrhinus*, arguing that separating the two genera based on dorsal-fin ray counts was phylogenetically invalid when considering additional species then placed in *Cirrhinus* that had 9 or 10 branched dorsal-fin rays. Roberts (1997) further noted that even if recognized as a valid genus, *Henicorhynchus* would be a junior synonym of *Cirrhinichthys* Bleeker, 1863 (type species: *Cirrhina dussumieri* Valenciennes, 1842). Based on specimens from Southeast Asia, Kottelat (2001) recognized *Henicorhynchus* as a distinct genus from *Cirrhinus*, referencing the differences in branched dorsal-fin rays (*Henicorhynchus* with 8–9 rays and *Cirrhinus* with 10–15 rays). Kottelat (2003) later stated that if all species of *Cirrhinus sensu* Roberts (1997) with 8–9 dorsal-fin rays are to be treated as congeneric, then the genus name for the group should be *Gymnostomus* Heckel, 1843 (type species: *Cyprinus ariza* Hamilton, 1807) as *Gymnostomus* is a senior synonym of *Henicorhynchus*. This nomenclature was maintained by Kottelat (2013), who remarked that because *Cirrhinichthys dussumieri* is a junior synonym of *Cyprinus ariza* (=*Gymnostomus ariza*) according to Roberts (1997), *Gymnostomus* is the valid name of this group of species with 8–9 branched dorsal-fin rays.

In his revision of *Cirrhinus*, Roberts (1997) noted that the genus was likely a polyphyletic group. This hypothesis has since been supported with molecular phylogenetic analyses (Yang et al., 2012; Zheng et al., 2012). Notably, species of *Cirrhinus* with 8 branched dorsal-fin rays that are distributed in Southeast Asia (Cambodia, Lao PDR, Thailand, and Vietnam) are consistently resolved as a monophyletic group distinct from other species of *Cirrhinus sensu* Roberts (1997) and nested in a clade with genera endemic to Southeast Asia and China (viz., *Barbichthys* Bleeker, 1860; *Crossocheilus* Kuhl and van Hasselt in van Hasselt, 1823; *Epalzeorhynchos* Bleeker, 1855; *Labiobarbus* van Hasselt, 1823; *Lobocheilos* Bleeker, 1854; *Osteochilus* Günther, 1868; and *Thynnichthys* Bleeker, 1859; and also '*Cirrhinus*' *molitorella* [Valenciennes in Cuvier and Valenciennes, 1844]). In the phylogenetic hypothesis of Yang et al. (2012), *Gymnostomus ariza*, which is distributed in South Asia (Bangladesh, India, Nepal, and Pakistan [IUCN, 2019]) was phylogenetically distinct from this clade as well, being resolved in a clade largely containing species of the African and Asian genus *Labeo* Cuvier, 1816 and other species of *Cirrhinus*. Based on these results, Yang et al. (2012) recognized *Henicorhynchus* as a valid genus distinct from *Cirrhinus* and *Gymnostomus*.

The goals of this paper are to 1) provide revised diagnoses for *Henicorhynchus* and *Gymnostomus* and 2) examine morphological variation in *Henicorhynchus* to diagnose species. Remarks on the taxonomic status of the types of *Cirrhinus inornatus* Roberts, 1997, *C. rubirostris* Roberts, 1997, and *Tylognathus cryptopogon* Fowler, 1935 are also provided. The taxonomy of *Cirrhinus* is under study and will be addressed later.

MATERIALS AND METHODS

Measurements and counts mostly follow Kottelat (2001). Internarial width and mouth width follow Armbruster (2012). Lengths were measured to the nearest 0.1 mm on the left side, when possible, using digital calipers. Body measurements are reported as proportions of standard length (SL), and head measurements are reported as proportions of head length (HL). Mouth orientation is useful in distinguishing species of *Henicorhynchus* and described either as terminal and strongly oblique (35–45° to midline of body; Fig. 1A) or subterminal and weakly oblique (less than or equal to 20° to midline of body; Fig. 1B). The condition of the rostral cap is also useful for identifications, with the edge overhanging the upper lip and jaw either being relatively straight (Fig. 2A) or

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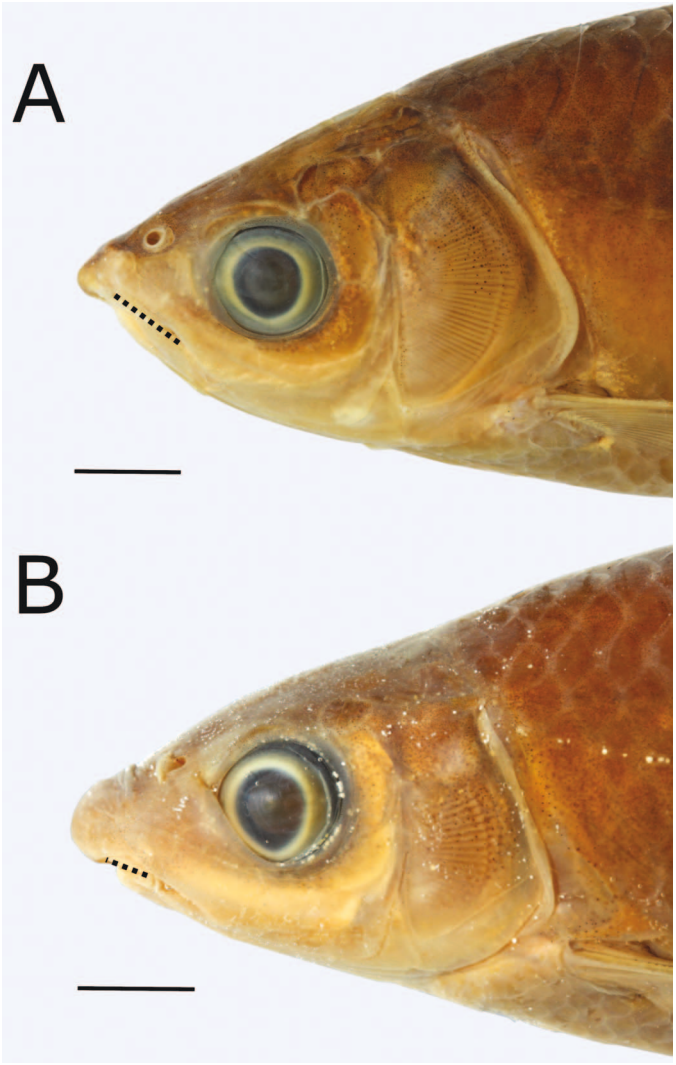

Fig. 1. Lateral views of (A) *Henicorhynchus siamensis*, CAS 93270, 81.5 mm SL, and (B) *H. entmema*, CAS 96199, 79.5 mm SL. Dashed lines indicate angle of mouth. Scale bars = 5 mm. Photos by Z. Randall (FLMNH).

possessing a medial indent (Fig. 2B). Unless otherwise stated, color descriptions are of preserved specimens. When possible, the GEOLocate web service (https://www.geo-locate.org) was used to obtain latitude and longitude based on locality descriptions for specimen lots lacking geographic coordinates. Maps were created in ArcMap 10.5 in ArcGIS (Esri, Redlands, CA). Institutional codes follow Sabaj (2019). Nomenclature issues were investigated with the aid of *Eschmeyer's Catalog of Fishes* (Fricke et al., 2019).

RESULTS

Henicorhynchus Smith, 1945

Figures 1–8

Henicorhynchus Smith, 1945:256. Type species: *Henicorhynchus lobatus* Smith, 1945, by original designation (also monotypic).
Synonym of *Cirrhinus* Oken, 1817—Roberts, 1997.
Synonym of *Gymnostomus* Heckel, 1843—Kottelat, 2003.

Diagnosis.—*Henicorhynchus* is distinguished from other labeonin genera by the following combination of characters: 1) mouth transverse, either terminal or subterminal; 2) rostral cap covering most of upper lip, in some individuals strongly overhanging medial portion; 3) edge of rostral cap smooth or with single medial indent; 4) shallow lateral groove extending obliquely anteriorly from corner of mouth to snout; 5) upper lip adnate to exposed surface of upper jaw and continuous with lower lip around corner of mouth, not covering entire upper jaw; 6) edge of upper lip smooth, without papillae; 7) maxillary barbels present or absent, but rostral barbels always absent; 8) lower lip firmly attached to lower jaw and without fleshy medial cushion or lobe; 9) 8 branched dorsal-fin rays; 10) humeral region immaculate, without distinct blotch.

Description.—Mouth terminal, strongly oblique (35–45° to midline of body), or subterminal, weakly oblique to nearly horizontal (less than or equal to 20° to midline of body). Rostral cap covering most of upper lip; edge with papillae, either straight or with distinct medial notch; tubercles infrequently present on tip of snout. Upper lip thin, fused with upper jaw; continuous with lower lip around corner of mouth; edge with papillae. Lower jaw slightly arched, cornified at edge. Lower lip thin, adnate to jaw; postlabial

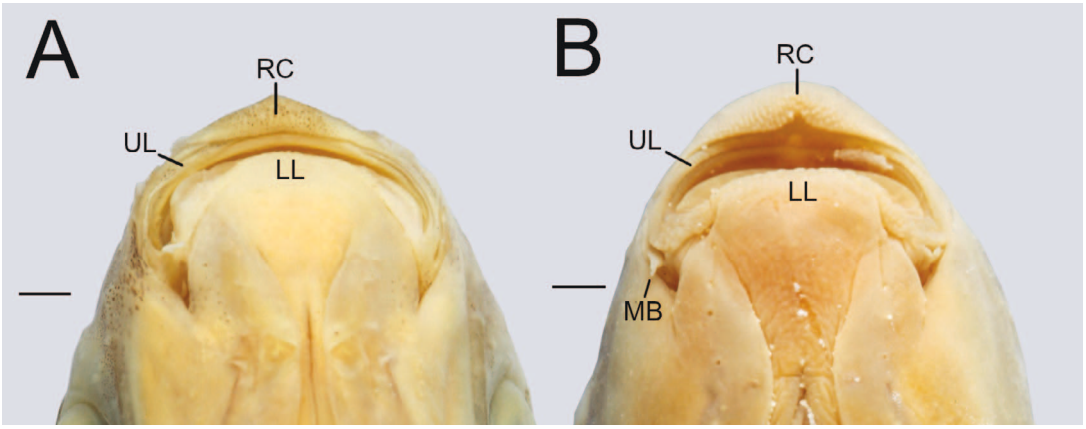

Fig. 2. Ventral views of (A) *Henicorhynchus siamensis*, CAS 93270, 81.5 mm SL, and (B) *H. entmema*, CAS 96199, 79.5 mm SL. Abbreviations: LL, lower lip; MB, maxillary barbel; RC, rostral cap; UL, upper lip. Scale bars = 1 mm. Photos by Z. Randall (FLMNH).

Fig. 3. *Henicorhynchus caudiguttatus*, ANSP 58452, holotype, 59.8 mm SL. Photo by K. Luckenbill (ANSP).

grooves separating lateral aspects from center. Maxillary barbels present or absent; if present, small and barely exposed at corner of mouth.

Dorsal profile slightly arched; deepest at dorsal-fin origin; ventral profile slightly convex. Head short, longer than wide; snout conical, rounded anteriorly; eyes lateral. Dorsal-fin origin anterior of pelvic-fin origin. Pectoral fins positioned ventrally, reaching approximately ½ to ¾ distance from origin to pelvic-fin origin when adpressed. Pelvic fins reaching ⅔ distance to just anterior to anus when adpressed. Anal fin reaching ⅔ distance or to base of caudal fin when adpressed. Axillary pelvic lobes well developed. Dorsal and anal fins slightly concave to falcate; pectoral and pelvic fins triangular. Caudal fin deeply forked with pointed lobes approximately equal in length.

Dorsal fin with 3 simple and 8½ branched rays; anal fin with 3 simple and 5½ branched rays; pelvic fin with 1 simple and 8 branched rays; pectoral fin with 1 simple and 13–16 branched rays; caudal fin with 10+9 principal rays, 9+8 branched. Body entirely scaled; scales well developed. Lateral-line scales and pored scales on caudal fin 31–35+1–4; predorsal scales 8–12; scale rows above lateral line 5½ (rarely 6½); scale rows below lateral line 4½–5½ (rarely 6½); scale rows between lateral line and pelvic-fin origin 4½ (rarely 5½); circumpeduncular scales 20.

Comparisons.—*Henicorhynchus* is most similar to *Gymnostomus* (see generic account below), several species currently placed in *Cirrhinus*, and *Lobocheilos*. *Henicorhynchus* is distinguished from *Gymnostomus* by a rostral cap with a straight edge or single medial indent (vs. rostral cap with fimbriae in *Gymnostomus*) and the absence (vs. presence) of rostral barbels. *Henicorhynchus* is distinguished from species of *Cirrhinus sensu* Kottelat (2013), including *C. cirrhosus*; *C. jullinei* Sauvage, 1878; *C. microlepis* Sauvage, 1878; *C. molitorella*; and *C. prosemion* (Fowler, 1934), by having 8 branched dorsal-fin rays (vs. 9 or more in the aforementioned species of *Cirrhinus*). *Cirrhinus cirrhosus*, *C. jullieni*, *C. molitorella*, and *C. prosemion* all have rostral barbels (vs. rostral barbels absent in *Henicorhynchus*). In both *C. cirrhosus* and *C. microlepis*, the upper lip covers the entirety of the upper jaw (vs. upper lip adnate to upper jaw). In *C. molitorella* and *C. prosemion*, the upper lip possesses distinct papillae along the edge (vs. smooth edge to upper lip in *Henicorhynchus*). *Henicorhynchus* is distinguished from *'Cirrhinus' ornatus* and '*C.*' *rubirostris* (originally described in *Cirrhinus* by Roberts [1997] and later placed in *Gymnostomus* by Kottelat [2013]; see discussion below about generic classification for these two species) by an upper lip adnate to the upper jaw and a cornified sheath on the upper jaw (vs. an upper lip that covers the entire upper jaw), the absence (vs. presence) of a post-oral groove, 8 (vs. 9) branched dorsal-fin rays, and an immaculate humeral region (vs. supracleithral blotch present). *Henicorhynchus* is distinguished from *Lobocheilos* by having the lower lip firmly attached to the lower jaw (vs. lower lip with a fleshy medial lobe that is free anteriorly and laterally).

Remarks.—*Henicorhynchus* is a member of the cyprinid subfamily Labeoninae based on the ventrally expanded rostral fold, the presence of a superficial posterior labial fold, and the presence of a vomero-palatine organ (Stiassny and Getahun, 2007). The diagnostic characters of Labeoninae reported by Reid (1982), including a terete process on the basioccipital and the direct contact between the neural complex of the Weberian apparatus and the supraoccipital region, could not be examined in specimens on loan to us, but were reported present in *H. siamensis* by Stiassny and Getahun (2007). Additionally, an incised border on the first anal-fin pterygiophore was observed in radiographs of the holotypes of *H. entmema* (Fowler, 1934; ANSP 59092) and *H. ornatipinnis* (Roberts, 1997; CAS 91756), and was observed in *H. siamensis* (Sauvage, 1881) by Stiassny and Getahun (2007), who reported this character as an additional diagnostic character of Labeoninae. Several molecular phylogenies place *Henicorhynchus* within Labeoninae (Wang et al., 2007; Yang et al., 2012; Zheng et al., 2012).

The common name "mud carp" is used for several species of *Henicorhynchus* and *C. molitorella*, which is often more specifically referred to as the Chinese Mud Carp. We retain the use of mud carp in the common names of species of *Henicorhynchus*.

Henicorhynchus caudiguttatus (Fowler, 1934)

Spotted Mud Carp
Figure 3

Crossocheilus caudiguttatus Fowler, 1934:137, fig. 103. Type locality: Thailand, Chieng Mai. Holotype: ANSP 58452.

Diagnosis.—A member of *Henicorhynchus* distinguished from other members of the genus (Table 1) by the following combination of characters: mouth terminal, strongly oblique

Table 1. Characteristics that distinguish species of *Henicorhynchus*.

	H. caudiguttatus	*H. caudimaculatus*	*H. entmema*	*H. ornatipinnis*	*H. siamensis*
Mouth position	Terminal, strongly oblique	Subterminal, weakly oblique	Subterminal, weakly oblique	Subterminal, weakly oblique	Terminal, strongly oblique
Maxillary barbels	Present	Present	Usually present	Absent	Absent
Medial indent on rostral cap	Absent	Absent	Present	Absent	Absent
Flank patterning	Immaculate	Longitudinal stripes or immaculate	Immaculate	Immaculate	Immaculate
Spot on caudal peduncle	Present	Present or absent	Present or absent	Absent	Absent
Caudal-fin patterning	Distinct brown spots or hyaline	Mostly hyaline, with scattered melanophores	Mostly hyaline, with scattered melanophores	Anterior ¾ dusky, posterior ¼ hyaline	Mostly hyaline, with scattered melanophores
Coloration of ventral fins	Hyaline	Hyaline	Hyaline	Red/orange	Hyaline

(35–45° to midline of body); maxillary barbels present; edge of rostral cap straight, without medial indent; flank immaculate, without longitudinal stripes; caudal peduncle with small brown spot at medial insertion of caudal fin; caudal fin with scattered brown spots in larger specimen (holotype, 59.8 mm SL).

Comparisons.—*Henicorhynchus caudiguttatus* is distinguished from all other species of *Henicorhynchus* by the presence of brown spots on the caudal fin in larger specimens. *Henicorhynchus caudiguttatus* is further differentiated from all other species of *Henicorhynchus* except for *H. siamensis* by the presence of a terminal, strongly oblique mouth. Unlike *H. siamensis, H. caudiguttatus* possesses maxillary barbels.

Description.—Morphometrics and meristics in Table 2. Mouth terminal, strongly oblique. Maxillary barbels present. Edge of rostral cap straight, without medial indent. Pectoral fin with 15 branched rays. Lateral-line scales and pored scales on caudal fin 32+2; predorsal scales 8–10; scale rows above lateral line 5½; scale rows below lateral line 4½–5½; scale rows between lateral line and pelvic-fin origin 4½. Maximum length = 59.8 mm SL.

Dorsum of head and body brown. Dorsal ¼ of side of head light brown; ventral ¾ cream to yellow; cheeks and opercula silver. Dorsal ⅓ of flank brown, with scattered darker brown spots on scales; ventral ⅔ silver. Faint brown spot on medial portion of caudal peduncle near caudal-fin insertion in holotype. Venter cream to yellow; breast silver. Dorsal fin with dark brown clusters of melanophores forming blotches

Fig. 4. *Henicorhynchus caudimaculatus*. (A) ANSP 58332, holotype, 41.4 mm SL, (B) USNM 107960, holotype of *Cirrhinus lineatus,* 108.8 mm SL. Images not to scale. Photo A by K. Luckenbill (ANSP); photo B by S. Raredon (USNM).

Table 2. Morphometric and meristic values of *Henicorhynchus caudiguttatus*, *H. caudimaculatus*, *H. entmema*, *H. ornatipinnis*, and *H. siamensis*.

	H. caudiguttatus ($n = 3$)		*H. caudimaculatus* ($n = 18$)		*H. entmema* ($n = 24$)		*H. ornatipinnis* ($n = 14$)		*H. siamensis* ($n = 29$)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
MORPHOMETRICS										
Standard length (mm)	41.4	30.3–59.4	63.1	26.8–108.8	79.3	46.4–109.8	75.2	53.9–93.2	83.8	32.4–142.3
% Standard length										
Predorsal length	50.0	48.5–50.9	49.1	45.5–51.1	49.1	47.2–50.9	48.3	46.5–50.7	48.9	46.1–51.8
Preanal length	75.9	72.0–78.4	77.7	76.4–80.3	77.7	74.6–80.2	78.3	75.4–82.3	76.9	74.0–80.4
Prepelvic length	52.5	50.6–55.1	53.5	50.9–57.2	53.4	50.7–55.9	51.7	49.1–53.7	52.2	48.8–57.4
Head length	26.3	24.2–28.2	26.0	22.5–29.6	24.8	22.6–27.9	21.7	20.1–23.0	28.1	25.5–32.1
Body depth at dorsal fin	24.1	23.5–24.6	27.4	24.0–29.7	28.6	21.4–35.2	28.3	26.4–30.1	29.9	25.2–34.4
Caudal-peduncle depth	11.5	10.8–12.0	12.4	11.4–13.1	12.1	11.2–13.2	14.6	14.1–15.3	12.7	11.7–13.9
Caudal-peduncle length	13.6	11.9–14.7	14.8	12.1–18.1	15.0	12.8–16.6	15.4	13.8–16.8	15.4	13.1–17.6
Dorsal-fin base length	14.5	13.3–16.2	15.3	13.3–17.8	15.5	13.9–17.6	15.1	12.5–16.8	16.1	14.1–17.5
Anal-fin base length	7.4	6.6–8.0	7.7	6.1–8.3	7.7	6.5–9.0	7.6	6.5–8.6	8.0	6.8–9.2
Pelvic-fin length	17.8	17.1–18.3	17.9	16.1–18.7	18.2	16.4–19.5	18.8	16.8–20.6	19.6	17.2–21.6
Pectoral-fin length	21.2	20.3–22.1	21.3	20.1–22.3	21.5	19.5–23.2	21.1	19.7–22.9	22.1	20.2–24.5
% Head length										
Head depth	73.9	72.0–77.8	74.0	69.3–85.7	74.9	69.0–80.7	85.9	81.1–91.7	75.9	69.8–84.9
Head width	51.9	49.1–53.5	55.9	47.4–66.1	59.8	54.1–67.2	62.3	59.1–67.3	58.3	50.1–67.6
Snout length	28.5	27.6–29.0	32.3	27.0–37.1	34.4	30.6–38.9	30.4	25.3–32.7	30.8	25.1–35.8
Orbit diameter	28.0	26.1–30.3	25.1	19.5–30.1	24.5	21.2–29.6	29.3	27.5–33.3	25.1	19.1–33.8
Interorbital width	36.4	35.0–38.6	38.6	29.7–46.5	42.9	37.4–48.4	45.0	42.1–48.2	44.5	37.0–54.0
Mouth width	26.1	25.9–26.3	27.7	23.4–32.3	26.5	23.7–30.8	28.3	25.7–32.6	27.2	24.9–30.8
Postorbital length	44.6	42.3–46.6	43.5	39.3–48.4	40.8	35.0–47.1	41.1	36.6–45.1	45.2	38.4–49.6
Internarial width	22.8	21.7–23.5	20.6	17.0–24.4	21.9	15.8–27.0	21.1	18.4–25.7	21.5	18.1–25.0
	Mode	Range	Mode	Range	Mode	Range	Mode	Range	Mode	Range
MERISTICS										
Pectoral-fin rays	15	15	14	14–16	15	14–16	14	13–14	15	14–16
Lateral-line scales	32	32	33	31–34	34	31–35	34	33–35	34	33–35
Pored scales posterior to lateral line	2	2	3	2–3	2	1–3	3	2–3	3	2–4
Predorsal scales	8,9,10	8–10	10	9–11	10	9–11	10	10–12	10	9–11
Scales between dorsal-fin origin and lateral line	5½	5½	5½	5½	5½	5½	5½	5½	5½	5½–6½
Scales between anal-fin origin and lateral line	4½	4½–5½	5½	4½–5½	5½	5½–6½	5½	5½	5½	5½
Scales between pelvic-fin origin and lateral line	4½	4½	4½	4½	4½	4½–5½	4½	4½	4½	4½

in middle portions of interradial membranes, distal edge brown; pectoral, pelvic, and anal fins hyaline; caudal fin with scattered brown spots in holotype, hyaline in other specimens.

Remarks.—Roberts (1997) recognized *H. caudiguttatus* as a junior synonym of *H. caudimaculatus* (Fowler, 1934), noting that only the spotted caudal fin of the holotype of *H. caudiguttatus* differentiated this specimen from the type of *H. caudimaculatus*. No other specimen of *Henicorhynchus* examined here possesses similar spots on the caudal fin. The mouth positions of the type specimens of these two species also vary, with *H. caudiguttatus* possessing a terminal, strongly oblique mouth vs. a subterminal, weakly oblique (less than 20° to midline of body) to nearly horizontal mouth in *H. caudimaculatus*. Based on differences in mouth position and caudal-fin coloration, we recognize *H. caudiguttatus* as a valid species. This species has only been collected once, despite more recent collections throughout Chiang Mai province.

Distribution.—*Henicorhynchus caudiguttatus* is known only from the type locality of Chiang Mai in northern Thailand (Fig. 9A).

Material examined.—Thailand: Chao Phraya basin: ANSP 58452, 1, 59.8 mm SL, Chieng Mai, on Me Nam Ping, North Siam, 5 February 1933; ANSP 59089, 2 (of 3), 30.3–34.0 mm SL, same as ANSP 58452.

***Henicorhynchus caudimaculatus* (Fowler, 1934)**

Striped Mud Carp
Figure 4

Tylognathus caudimaculatus Fowler, 1934:133, figs. 89–90. Type locality: Thailand, Chiang Mai. Holotype: ANSP 58332.

Cirrhinus lineatus Smith, 1945:163, fig. 25. Type locality: Thailand, Lam Ton Lang, a tributary of Menam Sak. Holotype: USNM 107960.

Cirrhinus caudimaculatus—Roberts, 1997.

Fig. 5. *Henicorhynchus entmema*. (A) ANSP 59092, holotype, 46.4 mm SL, (B) USNM 119490, holotype of *H. lobatus*, 96.7 mm SL. Images not to scale. Photo A by K. Luckenbill (ANSP); photo B by S. Raredon (USNM).

Cirrhinus lineatus—Roberts, 1997.
Gymnostomus caudimaculatus—Kottelat, 2013.
Gymnostomus lineatus—Kottelat, 2013.

Diagnosis.—A member of *Henicorhynchus* distinguished from other members of the genus (Table 1) by the following combination of characters: mouth subterminal, weakly oblique to nearly horizontal (less than or equal to 20° to midline of body); maxillary barbels present; edge of rostral cap straight, without medial indent; longitudinal stripes on flanks in most specimens, particularly larger individuals;

Fig. 6. *Henicorhynchus ornatipinnis*, CAS 91756, holotype, 69.4 mm SL. Photo by J. Fong (CAS).

Fig. 7. *Henicorhynchus siamensis*, ANSP 68069, holotype of *Cirrhinus marginipinnis*, 113.7 mm SL. Photo by K. Luckenbill (ANSP).

caudal peduncle with small brown spot at medial insertion of caudal fin in smaller specimens; caudal fin mostly clear, with scattered melanophores; pectoral, pelvic, and anal fins hyaline in life.

Comparisons.—*Henicorhynchus caudimaculatus* is most similar to *H. entmema* in having a subterminal mouth and maxillary barbels, but differs in having a straight edge on the rostral cap (vs. a medial indent on the rostral cap of *H. entmema*) and in usually having a series of longitudinal stripes along the flank (vs. flank always immaculate in *H. entmema*).

Description.—Morphometrics and meristics in Table 2. Mouth subterminal, weakly oblique to nearly horizontal. Maxillary barbels present. Edge of rostral cap straight, without medial indent; rostral cap occasionally with well-developed tubercles. Pectoral fin with 14–16 branched rays. Lateral-line scales and pored scales on caudal fin 31–34+2–3; predorsal scales 9–11; scale rows above lateral line 5½; scale rows below lateral line 4½–5½; scale rows between lateral line and pelvic-fin origin 4½. Maximum length = 150 mm SL (Kottelat, 2001).

Dorsum of head and body brown. Dorsal ¼ of side of head light to dark brown; ventral ¾ cream to yellow; cheeks and opercula occasionally silver. Dorsal ⅓ to ½ of flank light to dark brown, with scattered darker brown spots on scales in some specimens; ventral ½ to ⅔ cream, yellow, or light brown. Brown to black spot on medial portion of caudal peduncle near caudal-fin insertion in smaller specimens (<100 mm SL). Up to seven brown longitudinal stripes on flanks in most specimens; usually distinct in specimens greater than approximately 40 mm SL. Venter cream, yellow, or light brown. Dorsal fin with dark brown clusters of melanophores forming blotches in middle portions of interradial membranes, distal edge brown; pectoral, pelvic, and anal fins hyaline; caudal fin generally clear, with scattered melanophores.

Remarks.—In the original description of *H. caudimaculatus*, Fowler (1934) noted a "grayish axial streak" along the flank of the holotype (p. 126, fig. 90) in addition to a brown spot on the caudal peduncle near the insertion of the caudal-fin rays. In similarly sized specimens previously identified as *H. lineatus*, a similar spot on the caudal peduncle is present and the lateral stripes vary from very faint to bold (also noted by Roberts [1997]), with some small specimens also possessing one distinct stripe. The types of *Tylognathus caudimaculatus* and

Fig. 8. *Henicorhynchus siamensis*, UF 191421, live, 51.5 mm SL. Photo by Z. Randall (FLMNH).

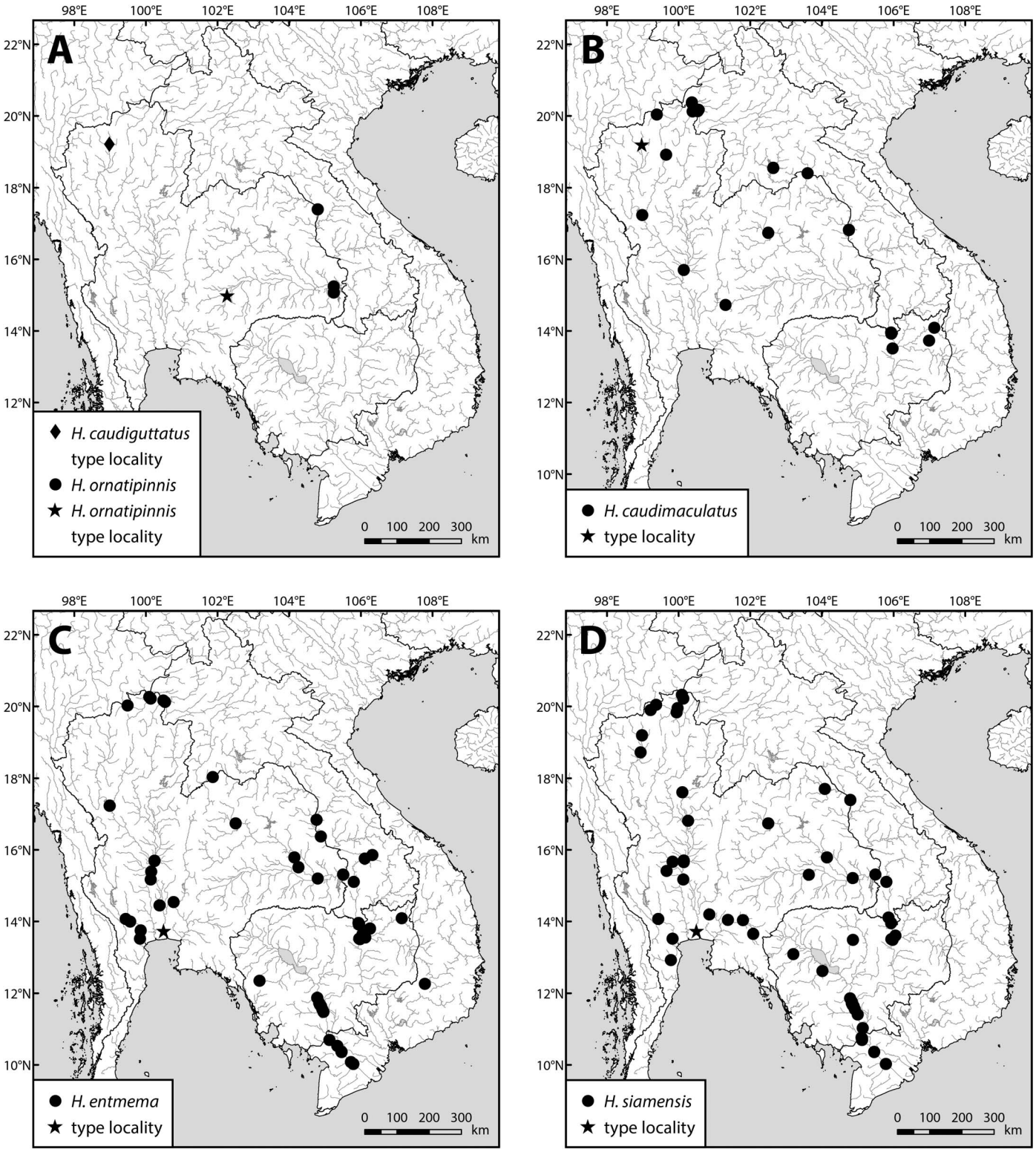

Fig. 9. Distributions of georeferenced specimens examined of: (A) *Henicorhynchus caudiguttatus* and *H. ornatipinnis*, (B) *H. caudimaculatus*, (C) *H. entmema*, and (D) *H. siamensis*.

Cirrhinus lineatus Smith, 1945 share similar oromandibular morphology, specifically a subterminal, weakly oblique mouth, maxillary barbels, and a smooth rostral cap without a medial indent. Based on similarities in oromandibular structures and color patterns when comparing specimens of variable sizes, we recognize *Cirrhinus lineatus* as a junior synonym of *H. caudimaculatus*. There is ontogenetic variation in color pattern, with small individuals possessing a brown to black spot at the base of the caudal peduncle, with longitudinal stripes developing with age and the spot eventually disappearing. A similar pattern is observed in *Lobocheilos rhabdoura* (Fowler, 1934) (Ciccotto and Page, 2016a).

Distribution.—*Henicorhynchus caudimaculatus* is distributed in the Chao Phraya basin in Thailand and the Mekong basin in Cambodia, Lao PDR, and Thailand (Fig. 9B).

Material examined.—(Identified, but not measured if no SL given). Cambodia: Mekong basin: CAS 81552, 5, O Champha, 4–8 km upstream from its mouth into Tonle San (near Te Veng, Ratanakiri prov.), 14.1006°N, 107.1352°E, 14 February 1994; CAS 91763, 4, 39.8–49.2 mm SL, Se Khone at Stung Treng, 13.5167°N, 105.9667°E, 6 February 1994; CAS 91765, 1, 100.1 mm SL, Rotanah Kiri, O Changni, small stream on road from Ann Long Mea to Bang Lung, 13.7394°N, 106.9873°E, 12 February 1994; UMMZ 234464, 2, Kandal, Mekong River at northern tip of island upstream from Phnom Penh, 25 January 1996; UMMZ 234727, 1, Kandal, Prek Muk Kandal, across Tonle Sap from Phnom Penh, 1 March 1996. Lao PDR: Mekong basin: CAS 92453, 2, 76.8–104.5 mm SL, Attapu, Houay Samong, about 1 km upstream from its mouth into Xe Pian near Ban Hin Lat, 18.4155°N, 103.6008°E, 10 April 1995; CAS 92480, 10, Sekong watershed, small mountain stream entering right side of Se Kaman just upstream from Se Kaman, 14 April 1995; CAS 94791, 8, Mekong River, at Bang Hang Khone, just below Khone Falls, 13.9675°N, 105.9298°E, June 1993; CAS 96192, 3, Nam Hinboun watershed; UMMZ 235345, 1, Champasak, Mekong River at Ban Hang Khone, just downstream from Khone Falls, 13.9333°N, 105.9333°E; UMMZ 238636, 1, Vientiane, Nam Ngao at south end of Nam Ngum Reservoir, 18.5648°N, 102.6388°E, 5 February 1997; UMMZ 238669, 1, same as UMMZ 238636; UMMZ 240585, 6, Bokeo Province, Mekong River, 5 km upstream from Houay Xai, 20.1333°N, 100.3833°E, 25 April 1997; UMMZ 241035, 1, Bokeo, Mekong River, 9 km upstream from Houay Xai, 20.3667°N, 100.3667°E, 22 April 1997; UMMZ 241136, 2, Bokeo, Nam Tin at Ban Paktin, Nam Tin, 20.1833°N, 100.55°E, 26 April 1997; UMMZ 241148, 3, Bokeo, Nam Ngam at Ban Namngion, 20.3833°N, 100.3667°E, 24 April 1997. Thailand: Chao Phraya basin: ANSP 58332, holotype of *Tylognathus caudimaculatus*, 41.4 mm SL, Chieng Mai, North Siam, 720 km N of Bangkok, 19.2112°N, 98.9708°E, 1 January 1933; ANSP 58333, 1, 26.8 mm, same as ANSP 58332; CAS 91781, 1, 53.3 mm SL, Menam Wang, 79 km by road north of Lampang and 6 km east of highway 1035, 18.9321°N, 99.6495°E, 28 February 1991; UMMZ 236742, 19, Ping River below Blaumipol Dam at guesthouse, 17.2406°N, 98.9815°E, 8 May 1965; UMMZ 236915, 1, Bung Borapet, tributary to Nau River, 4 km N. Nakhon Sawan, 15.7091°N, 100.1354°E, 11 November 1964. Mekong basin: CAS 79169, 5, mouth of Huay Ngao where it flows into Mekong, 1 km south of Ban Chaem Pong (ca. 30 km southeast of Chiang Khong), 20.142°N, 100.5269°E, 12 May 1990; CAS 91764, 5 (of 7), 48.6–59.8 mm SL, Menam Kok at Tha Ton and up to 5 km downstream, 20.049°N, 99.3846°E, 15 May 1990; CAS 91766, 9, Mekong mainstream between Pak Ing and Jom Paeng (about 4–5 km downstream), 20.1743°N, 100.4901°E, 16 January 1989; CAS 92855, 1, 77.7 mm SL, Mekong River mainstream, 14 km south of That Phanom, 16.8274°N, 104.7499°E, 6 April 1991; CAS 96196, 1, same as CAS 91766; UMMZ 251889, 1, Pong Need, trib. Pong River, 16.75°N, 102.5°E; USNM 107960, holotype of *Cirrhinus lineatus*, 108.8 mm SL, Lam Tong Lang, north of Pakjong, 14.74°N, 101.3044°E, 19 July 1925; USNM 119484, 1, 94.7 mm SL, Mefang, tributary of Mekok, 12 July 1936.

***Henicorhynchus entmema* (Fowler, 1934)**

Notched Mud Carp
Figure 5

Tylognathus entmema Fowler, 1934:134, figs. 101–102. Type locality: Thailand: Bangkok: Silom canal. Holotype: ANSP 59092.
Cirrhina sauvagei Fang, 1942:168. Type locality: Mekong, southeastern Asia. Syntypes: MNHN 8598 [8].
Crossocheilus thai Fowler, 1944: 49, 1 fig. Type locality: Thailand, Bangkok. Holotype: ANSP 71336.
Henicorhynchus lobatus Smith, 1945:257, fig. 49. Type locality: Thailand: Chiang Rai Province: Mekok River near Chiang Rai. Holotype: USNM 119490.
Cirrhinus lobatus—Roberts, 1997.
Gymnostomus lobatus—Kottelat, 2013.

Diagnosis.—A member of *Henicorhynchus* distinguished from other members of the genus (Table 1) by the following combination of characters: mouth subterminal, weakly oblique to nearly horizontal (less than or equal to 20° to midline of body); maxillary barbels almost always present (rarely absent); edge of rostral cap with distinct medial indent; flank immaculate, without longitudinal stripes; caudal peduncle immaculate or with brown to black spot at medial insertion of caudal fin; caudal fin mostly clear, with scattered melanophores; pectoral, pelvic, and anal fins hyaline in life.

Comparisons.—*Henicorhynchus entmema* is distinguished from all congeners by the presence of a distinct medial indent on the edge of the rostral cap.

Description.—Morphometrics and meristics in Table 2. Mouth subterminal, weakly oblique to nearly horizontal. Maxillary barbels usually present, rarely absent. Edge of rostral cap with medial indent; rostral cap occasionally with well-developed tubercles. Pectoral fin with 14–16 branched rays. Lateral-line scales and pored scales on caudal fin 31–35+1–3; predorsal scales 9–11; scale rows above lateral line 5½; scale rows below lateral line 5½ (rarely 6½); scale rows between lateral line and pelvic-fin origin 4½–5½. Maximum length = 109.8 mm SL.

Dorsum of head and body brown. Dorsal ¼ to ½ of side of head light to dark brown; ventral ½ to ¾ cream to yellow; cheeks and opercula occasionally silver. Dorsal ⅓ to ½ of flank light to dark brown, with scattered darker brown spots on scales in some specimens; ventral ½ to ⅔ cream, yellow, or light brown. Brown to black spot on medial portion of caudal peduncle near caudal fin occasionally present. Venter cream, yellow, or light brown. Dorsal fin with dark brown clusters of melanophores forming blotches in middle portions of interradial membranes, distal edge brown; pectoral, pelvic, and anal fins hyaline; caudal fin mostly clear, with scattered melanophores.

Distribution.—*Henicorhynchus entmema* is distributed in the Chao Phraya and Mae Klong basins in Thailand and the Mekong basin in Cambodia, Lao PDR, Thailand, and Vietnam (Fig. 9C).

Remarks.—*Tylognathus entmema* was described by Fowler (1934), who noted a "notch" on the rostral cap as well as the presence of maxillary barbels and a faint spot at the base of the caudal peduncle. These characters were confirmed in

our examination of the holotype (ANSP 59092). This "notch," herein labeled a medial indent in the rostral cap, is shared by the holotype and paratypes of *Henicorhynchus lobtatus* Smith, 1945 (except for one specimen that also lacks maxillary barbels and a black spot on the caudal peduncle that is herein identified as *H. siamensis* [USNM 119492, 1 of 3 specimens, 96.5 mm SL]). In the original description of *H. lobatus*, Smith (1945) noted that each of the paratypes possesses a black spot at the base of the caudal peduncle. The presence of the black spot on the caudal peduncle, in addition to the distribution of the paratypes solely in the Chao Phraya basin (vs. the occurrence of the holotype from the Mekong), led Roberts (1997) to identify these specimens as *Cirrhinus caudimaculatus*. We have confirmed the presence of the medial indent and maxillary barbels in all of the paratypes examined, exclusive of the one identified as *H. siamensis* (see above). This set of oromandibular characters in addition to the black spot on the caudal peduncle is shared by several specimens from the Mekong basin (i.e., CAS 79181, CAS 96200, CAS 96195). We also observed a lot (CAS 96195, $n = 3$) with specimens possessing these oromandibular characters in which there was variation in the presence of the black spot on the caudal peduncle. We consider these specimens with maxillary barbels, a black spot present or absent on the caudal peduncle, and a distinct medial indent on the rostral cap to be conspecific. The oldest available name for this species is *Tylognathus entmema* (*Tylognathus* is a junior synonym of the labeonin genus *Bangana* Hamilton, 1822; see Zhang and Chen, 2006), and we herein recognize this species as *Henicorhynchus entmema*.

The presence of the spot on the caudal peduncle is uncommon in specimens examined and not restricted to populations from a particular river basin. Smith (1945) hypothesized that the paratypes, which were smaller than the holotype, were young of the year and the spot was lost at adulthood. This trend was generally observed here as well; however, we note relatively large specimens (>100 mm SL) also may possess this spot, albeit rarely.

The types of *Cirrhina sauvagei* Fang, 1942 (MNHN 8598) and *Crossocheilus thai* Fowler, 1944 (ANSP 71336) each possess a medial indent in the rostral cap, but lack obvious maxillary barbels. Only one other specimen examined in this study that possesses the medial indent in the rostral cap characteristic of *H. entmema* similarly lacks maxillary barbels (USNM 119491); all others have maxillary barbels that are either barely exposed or hidden in the corner of the mouth. In light of overall morphological similarities with *H. entmema* and the large number of specimens examined that possess a medial indent on the rostral cap in addition to maxillary barbels (which can be tiny and hidden in the corner of the mouth), we assign *Cirrhina sauvagei* and *Crossocheilus thai* as junior synonyms of this species. The absence of maxillary barbels in these few specimens may be the result of their destruction from previous examinations or possible biological factors (i.e., mutation or hybridization).

Material examined.—(Identified, but not measured if no SL given). Cambodia: Mekong basin: CAS 91609, 9, Phnom Penh markets, 11.5625°N, 104.9160°E, 18 January 1994; CAS 94278, 40, Stung Treng market, 13.5167°N, 105.9667°E, 2 February 1994; CAS 94322, 21, rapids in Se San or Tonle San, 7 km upstream from Stung Treng, 13.8132°N, 106.25°E, 5 February 1994; CAS 96185, 2, Tonle Sap at km 12 from Phnom Penh?, 11.6448°N, 104.8805°E; CAS 96200, 2 (of 6), 81.1–82.3 mm SL, O Champha, 4–8 km upstream from its mouth into Tonle San (near Te Veng, Ratanakiri prov.), 14.1006°N, 107.1352°E, 14 April 1994; UF 190436, 1, 87.4 mm SL, Stung Treng, Tonle Kong approximately 10 km upstream of confluence with Tonle Srepok, 13.6096°N, 106.0922°E, 22 May 2016; UF 190963, 2, 96.8–101.4 mm SL, Stung Treng, morning market, 13.5306°N, 105.9710°E, 22 May 2016; UMMZ 232355, 4, Stung Treng, Mekong river rapids 7 km downstream from the mouth of the Tonle San, 13.5333°N, 105.95°E, 29 January 1995; UMMZ 232580, 3, Stung Treng, Mekong river rapids 7 km downstream from the mouth of the Tonle San, 13.5333°N, 105.95°E, 16 February 1995; UMMZ 232673, 1, Kompong Chhnang, Tonle Sap at Kompong Chhnang, fishing lot 9 in second channel east of town, 12.2667°N, 107.7833°E, 27 February 1995; UMMZ 234365, 4, Kandal, Prek Phnov at crossing under road #5 along bank of Tonle Sap, 11.8807°N, 104.7795°E, 22 January 1996; UMMZ 234682, 66, Stung Treng, Mekong River, shallow channel across the S end of Kaoh Han (Han Island), 14 km NE of Stung Treng, 13.6621°N, 106.0436°E, 14 February 1996; UMMZ 235114, 5, Kandal, Tonle Sap River 35 km upstream from Phnom Penh, day row 1, net A, 11.8807°N, 104.7795°E, 16 January 1995; UMMZ 235116, 1, Kandal, Tonle Sap at Dai fishery row 9, 25 km upstream from Phnom Penh, 11.8807°N, 104.7795°E, 22 January 1996; UMMZ 235476, 4, Kandal, Stung Kandal, 1 km upstream from its junction with Prek Thnot, 11.4847°N, 104.9484°E, 24 January 1996; UMMZ 235503, 4, Kandal, Tonle Sap at Dai fishery row 9, 15 km upstream from Phnom Penh, 11.6851°N, 104.8528°E, 27 January 1996; UMMZ 235563, 164, Stung Treng, Tonle San rapids at Kaoh Dan Man, 20 km ENE of Stung Treng, 13.5667°N, 106.1167°E, 10 February 1996; UMMZ 235583, 1, Stung Treng, Mekong River on W edge of Kaoh Han (Han Island), 16 km NE of Stung Treng, 13.6333°N, 106.05°E, 12 February 1996; UMMZ 235600, 19, Tonle San rapids at Kaoh Dam Man, 20 km ENE of Stung Treng, 13.5667°N, 106.1167°E, 15 February 1996; UMMZ 235720, 2, Kandal, Tonle Sap, fishing lot 8, 35 km upstream from Phnom Penh, 11.7333°N, 104.8333°E, 1 March 1996; UMMZ 246538, 1, Pursat, Pursat River at crocodile pool and in riffles below, 12.35°N, 103.1667°E, 23 February 2005; UMMZ 251890, 13, Kandal, Prek Muk Kandal, across Tonle Sap from Phnom Penh, 1 March 1996. Lao PDR: Mekong basin: CAS 92422, 1, Kinnak market, 7 February 1994; CAS 92516, 17, Sekong watershed, small mountain stream entering right side of Se Kaman just upstream from Se Kaman, 14 April 1995; CAS 94931, 1, Mekong at Bang Hang Khone, 13.9675°N, 105.9298°E, March 1995; CAS 94936, 11, same as CAS 94931; CAS 94942, 9, Mekong River at Ban Hang Khone, just below Khone Falls, 13.9675°N, 105.9298°E, June 1993; CAS 96194, 2, Se Khone, 15.8633°N, 106.3131°E, August 1993; CAS 96195, 3, 89.6–109.8 mm SL, Mekong River at Bang Hang Khone, just below Khone Falls, 13.9333°N, 105.9333°E, June 1993; CAS 96199, 1 (of 2), 79.5 mm SL, Champasak, Sekong watershed, Houay Khaliang near Ban Napakiap, Muang Khong, September 1995; CAS 96204, 1, 75.5 mm SL, same as CAS 96195; UF 185139, 1, 70.2 mm SL, Champasak, Pathumporn fish market in Pakse, 15.1202°N, 105.7990°E, 6 January 2013; UMMZ 235346, 3, Champasak, Mekong River at Ban Hang Khone, just downstream from Khone Falls, 13.9333°N, 105.9333°E. Thailand: Chao Phraya basin: ANSP 59092, 1, holotype of

Tylognathus entmema, 46.4 mm SL, Bangkok, Silom Canal, 13.7540°N, 100.5014°E, 18 December 1932; ANSP 71336, 1, holotype of *Crossocheilus thai*, 77.4 mm SL, Bangkok, 13.7540°N, 100.5014°E; UMMZ 231994, 5 (of 500), Nakom Sawan, creek under Hwy 1 bridge, 30 km S of Nakom Sawan, 15.4021°N, 100.1364°E, 23 October 1975; UMMZ 233686, 1, Pak Hai flood fishery, 14.4574°N, 100.3699°E; UMMZ 233688, 2, same as UMMZ 233686; UMMZ 236743, 3, Ping River below Blaumipol Dam at guesthouse, 17.2406°N, 98.9815°E, 8 May 1965; UMMZ 236835, 5, Bungboraphet Swamp, Nakhon Sawan, tributary of Nan River, 15.7061°N, 100.2321°E, 9 February 1965; UMMZ 236991, 15, same as UMMZ 236835; UMMZ 237254, 1, Bung Boraphet, trib. to Nan River, Nakhon Sawan, 15.7061°N, 100.2321°E, 11 November 1964; UMMZ 251882, 1, same as UMMZ 236743; UMMZ 251892, 2, Chai Nat, flood plain fishery, 15.1864°N, 100.1235°E; USNM 107850, 4, Mechem River, tributary of Meping, 11 July 1935; USNM 119491, 1, paratype of *H. lobatus*, 66.8 mm SL, Menam Chao Phraya, Pankmanko, 19 November 1923; USNM 119492 (in part), 2, paratypes of *H. lobatus*, 67.4–83.7 mm SL, Bung Borapet, 20 November 1923; USNM 119493, 2, paratypes of *H. lobatus*, 58.1–59.2 mm SL, Menam Chao Phraya Bangsai, 27 November 1923; USNM 119494, 1, paratype of *H. lobatus*, 72.1 mm SL, Pasak River at Dha Luang, 14.55°N, 100.7667°E, 20 August 1923. Mae Klong: UMMZ 195845, 75, Mae Nam Mae Klong at Kanchanaburi (confluence of the 2 Mae Nam Khwae rivers), 14.0032°N, 99.5501°E, 23 March 1965; UMMZ 195888, 4, Mae Nam Mae Klong at Ban Pong, 2 km downstream, 13.7572°N, 99.8474°E, 25 March 1965; UMMZ 236715, 8, Khwae Noi, 4 km from Kanchanaburi, 14 April 1965; UMMZ 251885, 1, Mae Nam Khwae Noi, ca. 20 km upstream from Kanchanaburi (purchased from fisherman), 14.0794°N, 99.4234°E, 23 March 1965; UMMZ 251897, 22, Rajburi, Mae Nam, Mae Klong River, vicinity of Rajburi (purchased in market at Rajburi), 13.5307°N, 99.8240°E, 14 November 1964. Mekong basin: CAS 79181, 13, mouth of Huay Ngao where it flows into Mekong, 1 km south of Ban Chaem Pong (ca. 30 km southeast of Chiang Khong), 20.14196°N, 100.5269°E, 12 May 1990; CAS 79182, 5, 62.5–94.7 mm SL, Menam Kok at Tha Ton and up to 20 km downstream, 20.039°N, 99.4768°E, 15 May 1990; CAS 79183, 3, Mekong mainstream rapids ca. 4 km downriver from Pak Ing (ca. 25 km downriver from Chaing Kong), 20.1833°N, 100.4816°E, 10 May 1990; CAS 79184, 2, Mekong River mainstream near Ban Ha Bia, 30–40 km NE of Chiang Khan on highway 2186, 18.0428°N, 101.8562°E, 12 March 1990; CAS 79186, 3, Khong Chiam market, 15.3218°N, 105.4942°E, 24 December 1988; CAS 91768, 9, Menam Chi at/near Maha Chana Chai, 15.5248°N, 104.2494°E, 13 March 1991; CAS 91770, 25, Yasothon market (=Menam Chi), 15.7971°N, 104.1353°E, 13 March 1991; CAS 91751, 1, Pakmenam Mun, May 1991; CAS 91771, 28, same as CAS 91770; CAS 94628, 1, mouth of Huay Ngao where it flows into Mekong 1 km south of Ban Chaem Pong (ca. 30 km southeast of Chiang Khong), 20.142°N, 100.5269°E, 12 May 1990; CAS 96186, 3, Mekong River mainstream rapids ca. 12 km south of That Phenom, 16.8483°N, 104.7587°E, 6 April 1991; CAS 96197, 1, 97.9 mm SL, Pak Menam Mun (mouth of Mun R.), 15.3162°N, 105.5055°E, 26 May 1991; CAS 96206, 1, Mekong mainstream near Chiang Saen, 20.2754°N, 100.0892°E, 1 May 1991; UF 238787, 1, Chiang Rai, Mae Kong, roadside market highway 1129 at km 46-47, 20.2383°N, 100.1256°E, 15 May 2010; UMMZ 224348, 1, Nakon Phanom, Mekong River, island off Ban Tha Kai, 20 km downstream from Mukdahan, 1 km from Thai, 5 km from Laos side, 16.3845°N, 104.8753°E, 25 June 1975; UMMZ 235124, 1, Ubon Ratchathani, Huay Mark Tai, 1 km from Mekong River, Huay Mark Tai flows into Mekong 0.5 km downstream from Mun-Mekong confluence, 15.7667°N, 106.1°E, 16 October 1975; UMMZ 236948, 3, Pong Need, trib. of Pong River, 16.75°N, 102.5°E; UMMZ 236992, 5, Khon-kaen, Pong Neeb, trib. Pong River, 16.75°N, 102.5°E, 5 October 1964; UMMZ 251886, 5, Ubon Ratchathani, Huay Thom-loe, at Ban Bung Khee-lek, 7 km E of Khemerat, 2.5 km from Mekong River, 30 September 1975; USNM 119490, 1, holotype of *H. lobatus* (photographs), 96.7 mm SL, Mekok River near Chiang Rai, Chiang Rai Prov., 2 March 1924; USNM 271291, 4, Ubon Ratchathani, market in fishing village at Ban Dan, 15.32°N, 105.5°E, 14 March 1972; USNM 331910, 1, Mun River at Bung Wai about 7 km W of Ubon, Ubon Ratchathani Prov., 15.2083°N, 104.792°E, 14 September 1971. Vietnam: Mekong basin: UMMZ 217914, 1, My Tho Prov, My Tho, Vam Ky Hon, 19 June 1974; UMMZ 218653, 1, An Giang, Bassac River, 1.3 km S of Long Xuyen, LF-4, 10.375°N, 105.451°E, 28 October 1974; UMMZ 227578, 1, Phong Dinh Prov, canal in city of Can Tho, 200 m from bridge on main stream (NR 10), 10.0864°N, 105.7174°E, 15 July 1974; UMMZ 235118, 2, Phong Dinh, Bassac River at Can Tho, CF-8, 10.0333°N, 105.7833°E, 3 November 1974; UMMZ 235119, 2, An Giang, Bassac River, 1 km S of Long Xuyen, LF-3, 10.3649°N, 105.4591°E, 28 October 1974; UMMZ 235120, 13, Phong Dinh, Bassac River at city of Can Tho, CF-4, 10.0333°N, 105.7833°E, 3 November 1974; UMMZ 245418, 1, An Giang, Bassac River, around Vam Nao town, 10.5333°N, 105.3333°E, 18 April 1999; UMMZ 251891, 13, Chau Doc, south end of Vinh Tuong Island, Bassac River, 10.7°N, 105.1167°E; UMMZ 251893, 4, Phong Dinh, Bassac River at Can Tho, CF-2, 10.0333°N, 105.7833°E, 3 November 1974; UMMZ 251894, 1, Chau Doc fish market, 10.7°N, 105.1167°E, 11 October 1974. Mainland Southeast Asia: Mekong basin: MHNH 8598, syntype of *Cirrhina sauvagei* (photographs), Mekong River, 1874.

Henicorhynchus ornatipinnis (Roberts, 1997)

Red-finned Mud Carp
Figure 6

Cirrhinus ornatipinnis Roberts, 1997:195, fig. 13. Type locality: Thailand, roadside ditch on highway 24 at km 150 marker, 179 km by road east of Nakorn Ratchasima. Holotype: CAS 91756.

Gymnostomus ornatipinnis—Kottelat, 2013.

Diagnosis.—A member of *Henicorhynchus* distinguished from other members of the genus (Table 1) by the following combination of characters: mouth subterminal, weakly oblique to nearly horizontal (less than or equal to 20° to midline of body); maxillary barbels absent; edge of rostral cap straight, without medial indent; flank immaculate, without longitudinal stripes; caudal peduncle immaculate, without spot; anterior ¾ of caudal fin dusky, posterior ¼ hyaline; pectoral, pelvic, and anal fins red or orange in life.

Comparisons.—*Henicorhynchus ornatipinnis* differs from all other species of *Henicorhynchus* in having red or orange pectoral, pelvic, and anal fins in life (vs. hyaline fins) and from all except *H. siamensis* and some specimens of *H.*

entmema (see Remarks for that species) in lacking maxillary barbels. *Henicorhynchus ornatipinnis* possesses a rostral cap with a straight edge, vs. edge with medial indent in *H. entmema*, and a subterminal, weakly oblique mouth, vs. terminal in *H. siamensis*.

Description.—Morphometrics and meristics presented in Table 2. Mouth subterminal; weakly oblique to nearly horizontal. Maxillary barbels absent. Edge of rostral cap straight, without medial indent. Pectoral fin with 13–14 branched rays. Lateral-line scales and pored scales on caudal fin 33–35+2–3; predorsal scales 10–12; scale rows above lateral line 5½; scale rows below lateral line 5½; scale rows between lateral line and pelvic-fin origin 4–4½. Maximum length = 93.2 mm SL.

Dorsum of head and body light brown. Dorsal ¼ of side of head brown; ventral ¾ cream to yellow; cheeks and opercula silver. Dorsal ⅓ of flank light brown, with scattered darker brown spot on scales; ventral ⅔ cream to yellow. Venter cream to yellow. Dorsal fin with dark brown clusters of melanophores forming blotches in middle portions of interradial membranes; pectoral, pelvic, and anal fins hyaline; anterior ¾ of caudal fin dusky, posterior ¼ hyaline.

Distribution.—*Henicorhynchus ornatipinnis* is native to temporary habitats, including roadside canals, of the middle portion of the Mekong River basin in Thailand (Roberts, 1997; Fig. 9A). It is also reported from slow-flowing lotic habitats in Lao PDR (Kottelat, 2001).

Material examined.—(Identified, but not measured if no SL given). Thailand: Mekong basin: CAS 91756, 1, holotype, 69.4 mm SL, roadside ditch on highway 24 at km 150, 17.9 km by road east of Nakorn Ratchasima, 15.0048°N, 102.2739°E, 27 May 1991; CAS 91758, 4, 84.3–93.2 mm SL, Nakorn Phanom market, 17.4019°N, 104.7913°E, 4 March 1991; CAS 91759, 15, Nakorn Phanom market, 17.4019°N, 104.7913°E, 26 May 1990; CAS 91760, 9, 53.9–87.8 mm SL, roadside canals 5–30 km south of Phibun Mangsahan, 15.0826°N, 105.2333°E, 16 September 1990; CAS 91761, 26, Phibun Mangsahan market, 15.2493°N, 105.2356°E, 15 September 1990.

Henicorhynchus siamensis (Sauvage, 1881)

Siamese Mud Carp
Figures 7–8

Morara siamensis Sauvage (ex Bleeker), 1881:164, 187, pl. 6 fig. 2. Type locality: Thailand, Bangkok. Syntypes: MNHN 0000-1839 (4).
Tylognathus siamensis de Beaufort, 1927:5. Type locality: Thailand: Chiang Rai Province, Payao Swamp. Holotype: ZMA 112.583.
Tylognathus brunneus Fowler, 1934:131, figs. 87–88. Type locality: Thailand, Chiang Mai. Holotype: ANSP 58369.
Cirrhinus marginipinnis Fowler, 1937:173, figs. 108–109. Type locality: Thailand, Pitsanulok. Holotype: ANSP 68069.
Cirrhinus siamensis—Roberts, 1997.
Gymnostomus siamensis—Kottelat, 2013.

Diagnosis.—A member of *Henicorhynchus* distinguished from other members of the genus (Table 1) by the following combination of characters: mouth terminal, strongly oblique (35–45° to midline of body); maxillary barbels absent; edge of rostral cap straight, without medial indent; flank immaculate, without longitudinal stripes; caudal peduncle immaculate, without spot; caudal fin mostly clear, with scattered melanophores; pectoral, pelvic, and anal fins hyaline in life (Fig. 9).

Comparisons.—*Henicorhynchus siamensis* differs from all other species of *Henicorhynchus*, except *H. ornatipinnis* and some specimens of *H. entmema* (see Remarks for that species) in lacking maxillary barbels. *Henicorhynchus siamensis* possesses a rostral cap with a straight edge (vs. edge with medial indent in *H. entmema*). *Henicorhynchus siamensis* possesses a terminal, strongly oblique mouth (vs. subterminal in *H. ornatipinnis*) and hyaline pectoral, pelvic, and anal fins in life (vs. red or orange fins in *H. ornatipinnis*).

Description.—Morphometrics and meristics presented in Table 2. Mouth terminal, strongly oblique. Maxillary barbels absent. Edge of rostral cap straight, without medial indent. Pectoral fin with 14–16 branched rays. Lateral-line scales and pored scales on caudal fin 33–35+2–4; predorsal scales 9–11; scale rows above lateral line 5½ (rarely 6½); scale rows below lateral line 5½; scale rows between lateral line and pelvic-fin origin 4½. Maximum length = 142.3 mm SL.

Dorsum of head and body brown. Dorsal ¼ to ½ of side of head light to dark brown; ventral ½ to ¾ cream to yellow; cheeks and opercula occasionally silver. Dorsal ⅓ to ½ of flank light to dark brown, with scattered darker brown spots on scales in some specimens; ventral ½ to ⅔ cream, yellow, or light brown. Venter cream, yellow, or light brown. Dorsal fin with dark brown clusters of melanophores forming blotches in middle portions of interradial membranes, distal edge brown; pectoral, pelvic, and anal fins hyaline; caudal fin mostly clear, with scattered melanophores.

Distribution.—*Henicorhynchus siamensis* is distributed in the Bang Pakong, Chao Phraya, Mae Klong, and Phetchaburi basins in Thailand as well as the Mekong basin in Cambodia, Lao PDR, Thailand, and Vietnam (Fig. 9D).

Material examined.—(Identified, but not measured if no SL given). Cambodia: Mekong basin: CAS 91611, 11, Phnom Penh markets, 11.5625°N, 104.916°E, 18 January 1994; CAS 94276, 13, Stung Treng market, 13.5167°N, 105.9667°E, 2 February 1994; CAS 94775, 3, 105.1–129.5 mm SL, Tonle Sap at km 13–16 north of Phnom Penh, 11.6587°N, 104.8683°E, 21 January 1994; CAS 96187, 2, Tonle Sap at km 12 from Phnom Penh?, 11.6448°N, 104.8805°E; UF 190623, 1, 104.9 mm SL, Pursat, Pursat River 13 km NE of Pursat, 12.6242°N, 104.0087°E, 25 May 2016; UMMZ 232121, 2, Kandal, Tonle Sap River 35 km upstream from Phnom Penh, day row 1, net A, 11.8667°N, 104.7833°E, 16 January 1995; UMMZ 232297, 1, Stung Treng morning market, 13.5°N, 105.9667°E, 26 January 1995; UMMZ 232364, 2, Kandal, Prek Ta Pov, 11 km S of Phnom Penh, 13.5°N, 104.8667°E, 2 February 1995; UMMZ 232532, 4, Kandal, Tonle Sap day nets series 8 & 9, 11.7333°N, 104.8333°E, 13 February 1995; UMMZ 232640, 3, Kandal, Prek Bak Nam at fishing lot 9, just upstream Phum Chong Sao, 11.0333°N, 105.1333°E, 21 February 1995; UMMZ 234378, 3, Kandal, Tonle Sap at Dai fishery row 9, 25 km upstream from Phnom Penh, 11.7754°N, 104.8273°E, 22 January 1996; UMMZ 234426, 1, Kandal, Prek Ta Pov, 13 km south of Phnom Penh, 23 January 1996; UMMZ 234465, 1, Kandal, Mekong River at northern tip of island upstream

from Phnom Penh, 25 January 1996; UMMZ 234533, 14, Kandal, Tonle Sap at Dai fishery row 9, 13 km upstream from Phnom Penh, 11.6674°N, 104.8667°E, 29 January 1996; UMMZ 234649, 4, Stung Treng, Mekong River, 2 km downstream from mouth of Tonle San on sandbars, 13.5167°N, 105.9333°E, 11 February 1996; UMMZ 234683, 6, Stung Treng, Mekong River, shallow channel across the S end of Kaoh Han (Han Island), 14 km NE of Stung Treng, 13.6167°N, 106.05°E, 14 February 1996; UMMZ 234728, 2, Kandal, Prek Muk Kandal, across Tonle Sap from Phnom Penh, 1 March 1996; UMMZ 234752, 8, Battambang, Sang Ke River at Ek Phnom district, 13.0988°N, 103.1979°E, 6 February 1996; UMMZ 235504, 12, Kandal, Tonle Sap at Dai fishery row 9, 15 km upstream from Phnom Penh, 11.6851°N, 104.8528°E, 27 January 1996; UMMZ 235505, 11, same as UMMZ 235504; UMMZ 235721, 6, Kandal, Tonle Sap, fishing lot 8, 35 km upstream from Phnom Penh, 11.7333°N, 104.8333°E, 1 March 1996; UMMZ 238586, 1, Kandal, pond E of Phnom Penh, between Bassac River and Mekong River, 11.4167°N, 105°E, 7 March 1996. Lao PDR: Mekong basin: CAS 93270, 1 (of 3), 81.5 mm SL, Mekong River near Ban Hang Khone, below Lee Pee waterfalls, October 1993; CAS 94279, 4, Mekong River at Ban Hang Khone, just below Khone Falls, 13.9675°N, 105.9298°E, June 1993; CAS 96190, 1 (of 3), 84.8 mm SL, Champasak, Houay Khaliang near Ban Napakiap, Muang Khong, 14.1173°N, 105.8532°E, September 1995; UF 185139 (in part), 1, 85.8 mm SL, Champasak, Pathumporn fish market in Pakse, 15.1202°N, 105.799°E, 6 January 2013. Thailand: Bang Pakong basin: CAS 79179, 1, Menam Bangpakong, near Prachinburi, 14.0522°N, 101.3728°E, 6 December 1990; CAS 79180, 1, 82.4 mm SL, Klong Waeh Kamong, on highway 304, 9 km by road north of junction with highway 33 at Kabinburi, 14.0455°N, 101.7891°E, 22 March 1989; CAS 91749, 4, Menam Bang Pa Kong at Ban Khao Cha-kan, on highway 317, 19 km south of Sa Kaeo, 13.668°N, 102.0757°E, 23 March 1989. Chao Phraya basin: ANSP 58369, 1, holotype of *Tylognathus brunneus* (photographs), Chieng Mai, on Me Nam Ping, North Siam, 720 km N of Bangkok, 19.2112°N, 98.9708°E, 24 December 1932; ANSP 68069, 1, holotype of *Cirrhinus marginipinnis* (photographs), 113.7 mm SL, Pitsanulok, 16.8248°N, 100.2589°E, 1936; CAS 79177, 3, Uttaradit market, 17.6181°N, 100.0999°E, September 1989; CAS 91752, 1, Nakorn Sawan market, 15.6887°N, 100.1252°E, 5 February 1989; CAS 93903, 5, 99.7–127.6 mm SL, same as CAS 91752, MNHN 0000-1839, 4, syntypes of *Morara siamensis* (photographs), Bangkok, 13.754°N, 100.5014°E, 1862; UF 176503, 1, 123.3 mm SL, Saraburi, Rapeepat Canal, from market along Highway 1, 14.2078°N, 100.8556°E, 21 November 2009; UF 176587, 1, Chiang Mai, Ping River from community market on canal road (highway 121), 18.7375°N, 98.9319°E, 25 December 2009; UF 237590, 5, 61.3–82.3 mm SL, Nakhon Sawan, Wang Ma River, trib. of Sakae Krang River at Rt. 3013 bridge, 15.6754°N, 99.8257°E, 17 January 2015; UF 237596, 1, 36.4 mm SL, Uthai Thani, Thap Salao River, trib. of Sakae Krang River, north of Rt. 3438, 15.4261°N, 99.6574°E, 17 January 2015; UMMZ 236678, 4, Chai Nat, flood plain fishery, 15.1864°N, 100.1235°E; UMMZ 236858, 5, Bung Borapet, tributary to Nau River, 4 km N. Nakhon Sawan, 15.7091°N, 100.1364°E, 11 November 1964; UMMZ 236978, 1, Bungboraphet Swamp, Nakhon Sawan, tributary of Nan River, 15.673°N, 100.1364°E, 9 February 1965; UMMZ 251895, 2, Khon-kaen, Pong Neeb, trib. Pong River, 16.75°N, 102.5°E, 5 October 1964; USNM 119492 (in part), 1, paratype of *H. lobatus*, 96.5 mm SL, Bung Borapet, 20 November 1923. Mae Klong basin: UMMZ 195257, 6, Rajburi, Mae Nam, Mae Klong River, vicinity of Rajburi (purchased in market at Rajburi), 13.5307°N, 99824°E, 14 November 1964; UMMZ 195830, 1, Mae Nam Khwae Noi, ca. 20 km upstream from Kanchanaburi (purchased from fisherman), 14.0794°N, 99.4234°E, 23 March 1965; UF 191421, 1 (of 3), 51.5 mm SL, Regional Freshwater Aquaculture Research and Development Center to Kanchanaburi (in Kanchanaburi town), 13.9643°N, 99.6274°E, 16 January 2017. Mekong basin: CAS 79185, 2, Nakorn Phanom market, 17.4019°N, 104.7913°E, 28 May 1990; CAS 79187, 4, Yasothon market (=Menam Chi), 15.7971°N, 104.1353°E, 13 March 1991; CAS 91750, 3, same as CAS 79187; CAS 96183, 2, Ubon Ratchathani market, 15.2225°N, 104.8585°E, 11 September 1990; UF 170200, 1, Chiang Rai, Reservoir, Thailand Department of Fisheries Office, 19.8504°N, 99.9372°E, 12 November 2007; UF 170201, 7, Chiang Mai, Kok River, 19.9696°N, 99.9687°E, 12 November 2007; UF 173102, 1, 88.7 mm SL, Ubon Ratchathani, commercial fisher from Mun River, 15.3253°N, 105.4899°E, 9 June 2008; UF 178156, 3, Chiang Rai, Mae Kong, roadside market highway 1129 at km 46–47, 20.2383°N, 100.1256°E, 15 May 2010; UF 178209, 1, Chiang Rai, Mekong at a roadside market in Chiang Saen, 20.3358°N, 100.0878°E, 15 May 2010; UF 185497, 3, Chiang Mai, Kok River at Thaton, 20.0603°N, 99.3639°E, 30 December 2012; UF 185549, 1, Chiang Mai, Fang River fishes from market in Ban Sri Bun Ruang on Hwy 107, 19.9183°N, 99.2136°E, 30 December 2012; UF 185552, 1, 63.9 mm SL, same as UF 185549; UF 237589, 2, 59.1–90.1 mm SL, Sakon Nakhon, Songkhram River at confluence with Yam River, 17.7091°N, 104.0767°E, 8 January 2015; UF 237599, 4, 32.4–49.4 mm SL, Surin, Mun River, 15.3153°N, 103.6299°E, 6 January 2015; UMMZ 233730, 4, Ubon Ratchathani, Huay Thom-loe, at Ban Bung Khee-lek, 7 km E of Khemerat, 2.5 km from Keong River, 30 September 1975; ZMA 112.583, 1, holotype of *Tylognathus siamensis* (photographs), Chiang Rain, Payao Swamp, 5 March 1924. Phetchaburi basin: UF 236014, 1, 58.4 mm SL, Phetchaburi, Mae Prachan at bridge on highway 3499, 12.9344°N, 99.7814°E, 1 February 2014. Vietnam: Mekong basin: UMMZ 218031, 2, Kihn Thuy Cai canal, 10 km E of Vinh Long (at mouth of canal into Mekong), 21 June 1974; UMMZ 218570, 4, Phong Dinh, Bassac River at Can Tho, CF-2, 10.0333°N, 105.7833°E, 3 November 1974; UMMZ 218584, 8, Phong Dinh, Bassac River near Can Tho (CF-3), 10.0333°E, 105.7833°E, 3 November 1974; UMMZ 218664, 12, An Giang, Bassac River, 1 km S of Long Xuyen, LF-3, 10.3649°N, 105.4591°E, 28 October 1974; UMMZ 224738, 1, Cha Doc fish market, 10.7°N, 105.1167°E, 11 October 1974; UMMZ 224818, 3, Chau Doc, south end of Vinh Tuong Island, Bassac River, 10.7°N, 105.1167°E; UMMZ 245386, 1, An Giang, Son Chau Doc 3 km upstream from Chau Doc, 10.75°N, 105.1167°E, 19 April 1999; UMMZ 245448, 1, An Giang, Song Chau Doc 5 km upstream from Chau Doc, 10.7667°N, 105.1°E, 19 April 1999.

Gymnostomus Heckel, 1843

Gymnostomus Heckel, 1843:1030. Type species: *Cyprinus ariza* Hamilton, 1807:344, by subsequent designation by Bleeker, 1863:197.

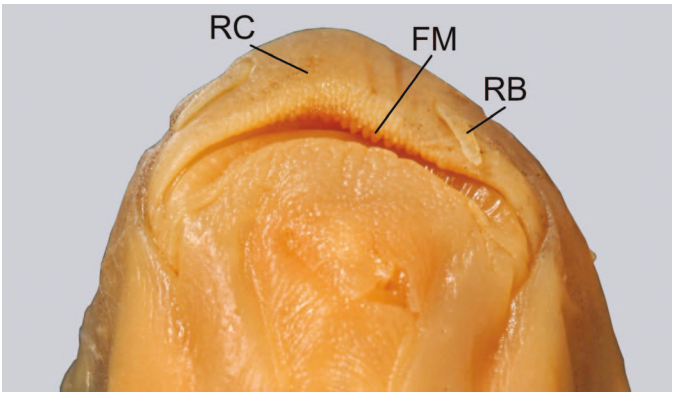

Fig. 10. Ventral view of *Gymnostomus ariza*, CAS 94081, 120.8 mm SL. Abbreviations: FM, fimbriae; RB, rostral barbel; RC, rostral cap. Photo by Z. Randall (FLMNH).

Mrigala Bleeker, 1859:259. Type species: *Cirrhina bengalensis* Bleeker, 1853:136, by monotypy; also in Bleeker, 1860:427.
Cirrhinichthys Bleeker, 1863:202. Type species, *Cirrhina dussumieri* Valenciennes, in Cuvier and Valenciennes, 1842:291, by original description.

Diagnosis.—Member of the cyprinid subfamily Labeoninae based on the ventrally expanded rostral fold, the presence of a superficial posterior labial fold, and the presence of a vomero-palatine organ (Stiassny and Getahun, 2007). A molecular phylogeny also places *Gymnostomus* within Labeoninae (Yang et al., 2012). *Gymnostomus* is distinguished from other labeonin genera by the following characters: 1) mouth subterminal; 2) upper lip adnate to exposed surface of upper jaw and continuous with lower lip around corner of mouth, not covering entire upper jaw; 3) lower lip attached to lower jaw; 4) rostral barbels present; 5) edge of rostral cap with weakly developed papillous fimbriae forming distinct fringed edge; 6) 8–9 branched dorsal-fin rays; 7) humeral region immaculate, without distinct blotch.

Comparisons.—*Gymnostomus* is morphologically most similar to *Henicorhynchus* (see above), *Crossocheilus*, *Epalzeorhynchos*, *Garra* Hamilton, 1822, *Tariqilabeo* Mirza and Saboohi, 1990, and several species currently placed in *Cirrhinus*. *Gymnostomus* is distinguished from *Henicorhynchus* and *Cirrhinus* by the presence of a rostral cap with weakly projecting fimbriae at edge (Fig. 10; vs. straight edge in *C. cirrhosus*, *C. jullieni*, *C. microlepis*, *C. molitorella*, *C. prosemion*, '*C.*' *inornatus*, and '*C.*' *rubirostris*, and either straight edge or edge with a single medial indent in *Henicorhynchus*). *Gymnostomus* possesses rostral barbels (vs. rostral barbels absent in *Henicorhynchus* and *C. microlepis*). The upper lip is adnate to the upper jaw in *Gymnostomus* (vs. completely surrounding the upper jaw in *C. cirrhosus*, *C. microlepis*, '*C.*' *inornatus*, and '*C.*' *rubirostris*). Species of *Crossocheilus*, *Epalzeorhynchos*, *Garra*, and *Tariqilabeo* possess more strongly projecting and deeply grooved fimbriae on the rostral cap compared to *Gymnostomus* (Ciccotto and Page, 2016b; Ciccotto et al., 2017).

Remarks.—*Gymnostomus* is composed of three species: *G. ariza*; *G. fulungee* Sykes, 1839; and *G. horai* Bănărescu, 1986. *Gymnostomus horai* is distinguished from *G. ariza* and *G. fulungee* by the presence of 9 (vs. 8) dorsal-fin rays and 16–18 (vs. 20–22) circumpeduncular scales. Roberts (1997) reported 8–9 branched dorsal-fin rays in *G. ariza*; however, one of the lots examined in that study (CAS 62067) contained two specimens of *Bangana* (tentatively identified as *B. devdevi* [Hora, 1936]) and one specimen of *Cirrhinus cirrhosus*, all of which possess more than 8 branched dorsal-fin rays. All other specimens examined, as well as the figure from the original description of *G. ariza*, possess 8 branched dorsal-fin rays. In his revision of *Cirrhinus*, which included all three species of *Gymnostomus* listed here, Roberts (1997) diagnosed *G. fulungee* from other species based on (among other characters) 42–52 scales in the lateral series. Specimens of *G. fulungee* re-examined here, all from the Deccan plateau of southern India, have 39–52+2–3 lateral-line scales. Most specimens of *G. ariza* re-examined here, from Bangladesh, India, Nepal, and Pakistan, possess 33–35+2–3 lateral-line scales. However, specimens identified by Roberts (1997) as *G. ariza* from the Kaveri River basin (CAS 62032) and Pune (CAS SU 34565) in the Deccan plateau possess 36–38+2–3 lateral-line scales. Based on this information, *G. fulungee* may be separated from *G. ariza* by having more lateral-line scales (39–52+2–3 vs. 33–38+2–3); however, other scale counts of *G. ariza* and *G. fulungee* exhibit some overlap, and we observed no other diagnostic characters separating these species. Additional molecular and morphological data are warranted to better diagnose *G. ariza* and *G. fulungee*, with their identities further hampered by the lack of types for both species.

Material examined.—*Gymnostomus ariza*: Bangladesh: Karnapouli basin: CAS 94081, 1 (of 4), 120.8 mm SL, Chittagong Hill Tracts, small stream about 30 km north of Khagrachari town, heavily vegetated banks, 23.3663°N, 91.9124°E, 6 June 1996. India: Bhima basin(?): CAS SU 34565, 1, Poona, April 1937. Brahmaputra basin: CAS SU 41128, 1, Assam, Tezpur fish market, 26.6298°N, 92.7971°E. Ganges basin: CAS SU 34566, 1, Ganges River delta at Pulta, 22.7872°N, 88.3445°E, 10 April 1937; USNM 165085, 1, Bihar, Chotanagpur. Hooghly basin(?): CAS SU 34564, 3, West Bengal, Calcutta, 22.5878°N, 88.3484°E, April 1937. Kaveri basin: CAS 62032, 9, Karnataka, NW/WNW of Mysore, 12.3979°N, 76.7819°E, 5–8 January 1985. Mahanadi basin: CAS 79176, 1, Orissa, Hirakud Reservoir and Sambalpur market, 21.4689°N, 83.9634°E, 22–24 February 1985; CAS SU 34568, 2, Mahanadi, Siliguri, 26.7128°N, 88.4116°E, April 1937. Nepal: Ganges basin: CAS 50369, 1, Terai, market at Kalaiya (Khailaya), 12 km east of Birganj, 1 May 1975; CAS SU 52929, 6, Biratnagar and vicinity—purchased at bazaar, 26.4617°N, 87.28°E, 27–30 November 1955. Pakistan: Indus basin: CAS 24237, 5, Sindh, Indus River, 523 km north of Karachi (i.e., 8 km north of Sukkur), 27.7675°N, 68.858°E, 1–11 November 1968. Unknown basin: CAS 29653, 1, Arabian Sea, off Karachi, 24.8048°N, 66.9744°E, 22 October 1973. *Gymnostomus fulungee*: India: Bhima basin(?): CAS SU 41123, 5, Maharashtra, Poona, Bombay Pres., 10.4953°N, 99.2552°E, 3 April 1937. Gangavali basin: CAS 61967, 2, Karnataka, North Kanara, Bedti (Gangavali) R., ca. 15 km east of Yellapur, 14.9679°N, 74.8666°E, 25 January 1985. Penna basin(?): CAS SU 34563, 2, Andhra Pradesh, Kodur, Cuddapah, 14.4717°N, 78.8209°E, April 1937. Unknown basin: CAS SU 41124, 2, Mugao Dharwar, Bombay Pres., 15.4418°N, 74.9168°E, 21 July 1937. *Gymnostomus horai*: Myanmar: Inle Lake: CAS 81548, 24, 20.5474°N, 96.9161°E, February 1994; USNM

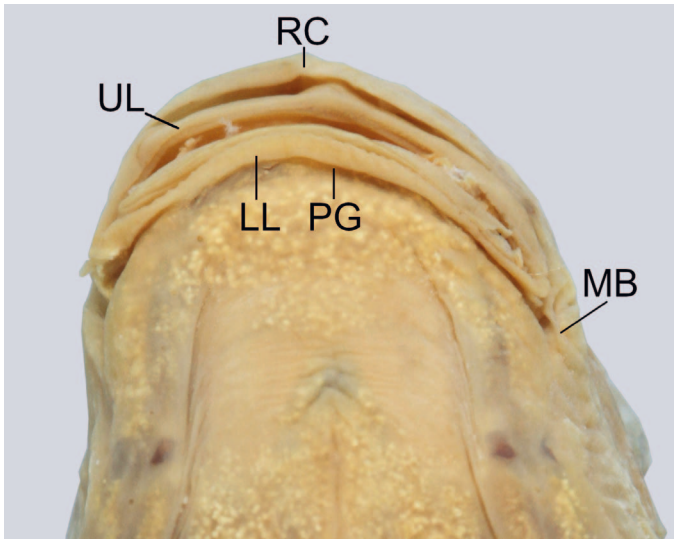

Fig. 11. Ventral view of *Labeo boga*, CAS SU 41167, 74.3 mm SL. Abbreviations: LL, lower lip; MB, maxillary barbel; PG, post-oral groove; RC, rostral cap; UL, upper lip. Photo by Z. Randall (FLMNH).

191451, 1, holotype, Shan State, 20.5474°N, 96.9161°E, 31 January 1956.

'Cirrhinus' inornatus and *'Cirrhinus' rubirostris*

Remarks.—The type specimens of '*Cirrhinus*' *inornatus,* recognized as *Gymnostomus inornatus* in Kottelat (2013), and '*C.*' *rubirostris* both possess a subterminal mouth, an upper lip that covers the entire upper jaw, a post-oral groove separating the lower lip from the lower jaw, a smooth edge to the rostral cap, maxillary barbels, 9 branched dorsal-fin rays (see below), 34–35 lateral-line scales, and a supracleithral blotch. This combination of characters is not observed in any species of *Gymnostomus* or *Henicorhynchus*, or other putative species of *Cirrhinus* (*C. cirrhosus*, *C. jullieni*, *C. microlepis*, *C. molitorella*, and *C. prosemion*). However, this combination of characters is observed in specimens of *Labeo boga* (Hamilton, 1822) examined here. Although no types are known for *L. boga*, the figure in the original description by Hamilton (1822) depicts a specimen with an inferior mouth, a post-oral groove, a smooth rostral cap, maxillary barbels, 9 branched dorsal-fin rays, and a supracleithral blotch. Based on morphological similarities with *L. boga*, particularly in regard to oromandibular structures (Fig. 11), *C. inornatus* and *C. rubirostris* are assigned to the genus *Labeo*.

In the original diagnosis of *L. inornatus*, Roberts (1997) noted "branched dorsal fin rays usually 9." Two specimens of CAS 91776 included in the description of *L. inornatus* are *Bangana devdevi* with 10 branched dorsal-fin rays. In the same publication, *L. rubirostris* was described with 10 branched dorsal-fin rays; however, all specimens examined here have 9 branched dorsal-fin rays. Roberts (1997) distinguished *L. inornatus* and *L. rubirostris* based on tuberculation (without rostral tubercles in *L. inornatus* vs. well-developed rostral tubercles in *L. rubirostris*), snout color (snout without red in *L. inornatus* vs. red snout in *L. rubirostris*), gill-raker counts (35 in *L. inornatus* vs. 43 in *L. rubirostris*), and number of pairs of tuberculate lamellae on the palatal lamellar organ (5 in *L. inornatus* vs. 6 in *L. rubirostris*).

Material examined.—*Labeo boga*: India: Adyar basin: CAS SU 41167, 1, 74.3 mm SL, Tamil Nadu, Adyar River, Madras, 4 January 1941. Myanmar: Irrawaddy basin: USNM 44756, 1, Kachin, Bhamao, Upper Burma, 29 June 1885. *Labeo inornatus* (all primary types): Myanmar: Irrawaddy basin: CAS 88903, 1, Mandalay, Nyaung-U fish market, 21.2042°N, 94.9138°E, 13 April 1996; CAS 91772, 1, Mandalay, market, 21.9697°N, 96.0874°E, 13–25 April 1993; CAS 91774, 9, Mandalay, Nyaung-U market, 21.2042°N, 94.9138°E, 8 November 1996; CAS 91775, 1, Kachin, Myitkyina market (morning), 25.3864°N, 97.3944°E, 21–22 April 1996; CAS 91776, 5 (of 7), Mandalay market, 21.9697°N, 96.0874°E, 13–25 April 1993. Sittang basin: CAS 91773, 6, Bago, Sittang River at Taungoo or Taungoo Market, 18.9437°N, 96.4473°E, 7 April 1996. *Labeo rubirostris* (all primary types): Myanmar: Tenasserim basin: CAS 91753, 1, Tenasserim River backwater (huge rocky ledge) midway between Kita or Htee-tah and Baowashung, 12 March 1992; CAS 91754, 1, Tenasserim River, upstream from Kita (Htee-tah), 8–9 March 1992; CAS 91755, 1, mainstream Tenasserim River between Kita or Htee-tah and Baowashung, March 1992; MNHN 1992.1043, 1 (photographs), Tenasserim River, 12 March 1992; MNHN 1992.1044, 2 (photographs), Tenasserim River, 12 March 1992.

Tylognathus cryptopogon

Remarks.—Rainboth (1996) placed *Tylognathus cryptopogon* in the genus *Henicorhynchus* (see also Rainboth et al. [2012]). Roberts (1997) remarked that the holotype of *T. cryptopogon* is a species of *Lobocheilos*. Kottelat (2001) recognized *T. cryptopogon* as a simultaneous subjective synonym of *T. melanotaenia* Fowler, 1935 and gave precedence to *T. melanotaenia*, but later recognized *Gymnostomus cryptopogon* (Kottelat, 2013). Examination of the holotype of *T. cryptopogon* (Fig. 12) and the original figure from the description by Fowler (1935) confirms the claim of Roberts (1997). This specimen is identified as *Lobocheilos rhabdoura* following Ciccotto and Page (2016a).

Material examined.—Thailand: Chao Phraya basin: ANSP 61273, 1, holotype of *Tylognathus cryptopogon*, 73.8 mm SL, Khao Nam Poo, October 1934.

DISCUSSION

In molecular phylogenetic analyses of Labeoninae, *Henicorhynchus* has been resolved as sister to the Southeast Asian genus *Lobocheilos* (Yang and Mayden, 2010; Yang et al., 2012; Zheng et al., 2012). Species in both genera share similar oromandibular features, differing primarily in the lower lip being a fleshy medial lobe free on the anterior and lateral sides in *Lobocheilos* vs. lower lip firmly attached to the jaw in *Henicorhynchus*. Both *Henicorhynchus* and *Lobocheilos* are nested within the tribe 'Osteochilini' following Yang et al. (2012) and Tan and Armbruster (2018), although this tribe name is not valid according to the code (van der Laan et al., 2014). Interestingly, all genera in this group except for *Henicorhynchus* (and '*Cirrhinus*' *molitorella*) are distributed in both mainland Southeast Asia and the islands of Borneo, Java, and Sumatra. *Henicorhynchus* is restricted to the Mekong, Chao Phraya, Mae Klong, and several smaller river basins in mainland Southeast Asia. Examinations of mor-

Fig. 12. Holotype of *Tylognathus cryptopogon*, ANSP 61273, 73.8 mm SL. Photo by K. Luckenbill (ANSP).

phologically similar labeonin specimens from Indonesia and Myanmar indicate species of *Henicorhynchus* are not distributed in these countries.

In a molecular phylogeny reconstructing the relationships of Labeoninae, Yang et al. (2012) included four species of *Henicorhynchus*. *Henicorhynchus lobatus* (herein *H. entmema*) was resolved as sister to *H. siamensis*, with this clade being sister to a clade containing *H. lineatus* (herein *H. caudimaculatus*) and *H. ornatipinnis*. We did not examine the specimens used in the analysis to see if they conformed to our morphological identifications.

Henicorhynchus entmema and *H. siamensis* are the most common species of *Henicorhynchus* and are among the most numerically abundant and economically important freshwater fishes in Southeast Asia, particularly in the Mekong basin (Roberts and Baird, 1995; Roberts, 1997; Baird et al., 2003). Accordingly, substantially more is known about the biology of these two species compared to *H. caudiguttatus*, *H. caudimaculatus*, and *H. ornatipinnis*, although these species are often confused with one another, and hence available biological information may be inaccurate. In general, species of *Henicorhynchus* inhabit large rivers, with high abundances found in the mainstem of the Mekong and its larger tributaries (Rainboth, 1996; Poulsen et al., 2004). A notable exception is *H. ornatipinnis*, which inhabits smaller temporary aquatic habitats, canals, and slow-flowing streams (Roberts, 1997; Kottelat, 2001). Available diet data suggest species of *Henicorhynchus* consume detritus, algae, phytoplankton, and occasionally zooplankton (Rainboth, 1996; Suvarnaraksha et al., 2011; Ou et al., 2017). Spawning in *H. entmema* and *H. siamensis* occurs during periods of high water either in river channels or surrounding floodplains in the Mekong. Larvae are dispersed into the floodplain habitats where growth occurs until the onset of the dry season when water recedes back into the main river channels and juveniles enter deeper water (Poulsen et al., 2004).

In the Mekong River at Khone Falls, *H. caudimaculatus*, *H. entmema*, and *H. siamensis* migrate upstream during high water from May to June in conjunction with reproductive periods and downstream during low water from December to March with other migratory species. *Henicorhynchus entmema* is among the first species to migrate during the drier season and is apparently an important forage species for other migratory fishes (Roberts and Baird, 1995). Similar mass migrations of *H. entmema* and *H. siamensis* occur in the Tonle Sap Lake in Cambodia, and the lunar cycle appears to play a major role in the migrations of these species throughout their distribution in the Mekong River basin (Baird et al., 2003). Otolith microchemistry suggests the migration patterns of *H. entmema* and *H. siamensis* are fixed within populations, making it unlikely that individuals will use alternative routes if original migration routes are blocked, and that these species are unlikely to utilize fish passages on existing dams (Fukushima et al., 2014). Dams and other stream blockages are likely to have a major negative impact on migratory populations of *Henicorhynchus*, particularly in the Mekong River basin where the construction of many hydroelectric dams throughout the basin are either proposed or in progress (Intralawan et al., 2019). Data presented here should allow for accurate identifications of species of *Henicorhynchus* that will contribute substantially to the management of this economically important group of fishes in light of proposed hydroelectric dams in the region as well as other anthropogenic influences on riverine ecosystems.

KEY TO SPECIES OF *HENICORHYNCHUS*

1a. Edge of rostral cap with distinct medial indent ..... ***H. entmema***

1b. Edge of rostral cap straight, without distinct medial indent 2

2a. Maxillary barbels absent 3

2b. Maxillary barbels present 4

3a. Mouth terminal, strongly oblique; ventral fins hyaline in life ..... ***H. siamensis***

3b. Mouth subterminal, weakly oblique to horizontal; ventral fins orange to red in life ..... ***H. ornatipinnis***

4a. Mouth terminal, strongly oblique; caudal fin with brown spots in larger specimens; flank immaculate, without longitudinal stripes ..... ***H. caudiguttatus***

4b. Mouth subterminal, weakly oblique to horizontal; caudal fin immaculate; flank usually with longitudinal stripes ..... ***H. caudimaculatus***

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