

REVIEW OF THE TROPICAL ASIAN CYPRINID FISH GENUS *POROPUNTIUS*, WITH DESCRIPTIONS OF NEW SPECIES AND TROPHIC MORPHS

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ABSTRACT

Nominal species referable to the tropical Asian barbin cyprinid fish genus *Poropuntius* Smith, 1931 (excluding *Hypsibarbus* Rainboth, 1996) are reviewed, and new species described from the Salween, Tenasserim, Meklong, and Mekong basins. The cave fish *Barbus speleops* Roberts, 1991 from Tham Phu Keao in Thailand (Mekong basin) is referred to *Poropuntius*. At least two species exhibit discrete trophic polymorphism, including the riverine *P. bolovenensis* new species from streams on the Bolovens Plateau in southern Laos (Mekong basin) with four morphs. Some of the trophic morphs of *Poropuntius* have generalized mouths and other trophic structures, but others are so modified that they would be assigned to different genera if they were distinct species. Trophic polymorphism or phenotypic plasticity of the kind reported here in *Poropuntius* is extremely widespread in cyprinoids and may have contributed greatly to their speciation, adaptive radiation, and macroevolution, including in Lake Lanao (Mindanao) and Lake Tana (Ethiopia) (Mina, et al., 1996; Nagelkirke, et al., 1996) as well as over more extensive geographical areas and longer time spans.

INTRODUCTION

Poropuntius comprises numerous medium-sized species (mostly 10–20 cm in standard length as adult) living mainly in mountain streams at moderate elevations (typically less than 1,000 m) in mainland Asia, from Assam and Yunnan to the Malay peninsula. Some lacustrine and riverine species are significant ecologically and in artisanal wildcapture fisheries. A number of the species are handsomely colored, but they seldom if ever occur in the aquarium trade. The majority have relatively generalized trophic structures, with two well-developed pairs of barbels and moderately developed lips and horny jaw sheaths. The genus is very much in need of a comprehensive systematic revision but this is presently thwarted by paucity of material from many parts of the genus range, especially in Assam and Yunnan. The present paper is based mainly on specimens collected by the author in areas where little or no collecting had been done previously, but representing less than half the range of the genus. Thus no freshly collected material has been examined for some of the nominal species level taxa, especially those described by Chinese ichthyologists. Some species exhibit substantial phenotypic plasticity in the form of discrete trophic morphs, which has not been previously reported or recognized as such in the genus. The new

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species *Poropuntius bolovenensis* is described with four discrete trophic morphs having: 1) normal or generalized mouth, lips and jaws (*P. bolovenensis bolovenensis*); 2) narrow head, sharp snout, elongate jaws and thickened lips (*P. b. acuticeps*); 3) short head and laminar lower horny jaw sheath (*P. b. glaridostoma*); and 4) large, broad head and wide jaws (*P. b. laticeps*). This species and its morphs apparently is endemic to the Bolovens Plateau, and may be threatened with extinction by the Xe Nam Noi-Xe Pian hydropower project.

In this paper intraspecific trophic morphs are formally described and named as species-level trinominals. Many morphologically distinctive cyprinid fishes previously named as species are really intraspecific morphs. Others may be full species, but their status may never be resolved because they are now extinct (e.g. the so-called cyprinid "species flock" in Lake Lanao). Non-sexual intraspecific evolutionary divergence, which may prime sympatric as well as allopatric speciation, is gaining acceptance as a major factor in morphological divergence, speciation, and generation of biodiversity (see WEST-EBERHARD, 1986; 1989; MEYER, 1993; SMITH & SKULASON, 1996, and references cited therein). The sort of intraspecific trophic polymorphism reported here for *P. bolovenensis*, in many instances with even greater differences among morphs, occurs in many genera of the cyprinid subfamily Barbinae as well as in some Schizothoracinae and Leuciscinae. The genetic basis for such polymorphism probably was present in the earliest cyprinoids, or developed soon after their divergence from other Ostariophysi. It evidently has played a major role in their stunning adaptive radiation and dominance in temperate as well as tropical continental fresh waters, especially in Asia. In modern faunas this ancient assortment of genetically-determined phenotypic differences is expressed as intraspecific morphs mainly in species occupying lakes or streams on plateaus at higher elevations isolated by barriers such as waterfalls (as in *Poropuntius bolovenensis* on the Bolovens Plateau). Species not exhibiting such morphs in their phenotypes may nevertheless carry all of the information in their genome necessary to generate an array of discrete phenotypes. Ecological conditions (including biodiversity of food organisms and other fish species in the same habitat) may determine whether selection favors a phenotypically monomorphic or polymorphic species.

A laminar lower horny jaw sheath (as in *P. b. glaridostoma*) is one of the most frequently recurring and evolutionarily significant jaw structures in Cyprinidae. Its presence often involves a major dietary shift, such as from feeding on insects or higher plants to feeding on algae and associated organisms which must be scraped from filamentous or gelatinous mats. The genetic basis for shifting from an unculiferous or otherwise non-laminar lower jaw sheath to a laminar sheath probably evolved very early in cyprinid evolution, perhaps before divergence of Barbinae and Leuciscinae, and perhaps evolved only once. The laminar jaw sheath itself may be modified in shape, width, hardness and other characters to give rise to more than one intraspecific trophic morph. Distinctive morphs may evolve into full-fledged species or genera by speciation (whether allopatric or sympatric), and by subsequent linear evolution or orthogenesis into separate genera. Monomorphic cyprinid genera with laminar horny jaw sheaths which may have evolved in this fashion include but are not limited to *Capoeta*, *Cyprinion*, *Onychostoma*, *Scaphiodonichthys*, *Semiplotus*, *Varicorhinus*. Highly specialized cyprinid genera characterized by extremely broad or extremely narrow lower jaws typically have laminar lower jaw sheaths.

The systematic portion of this paper is divided into two sections. In the first section all of the nominal species known to me that are referable to *Poropuntius* (sensu Rainboth, 1996a,b), are listed in chronological order of their description beginning with *P. deauratus* (Valenciennes, 1842), the earliest described species. Some of these species are known only from their original descriptions in Chinese. Most of them are probably valid species. The Thai cavefish *Barbus speleops* Roberts 1991 is referred to *Poropuntius*. *Puntius tawarensis* Weber and de Beaufort, 1916, is retained in *Poropuntius* following KOTTELAT (1989) but probably belongs elsewhere. The second section is devoted to descriptions of new species and of trophic morphs.

Materials.—Specimens reported on in this paper are deposited in the fish collections of the following institutions: ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; KIZ, Institute of Zoology, Chinese Academy of Sciences, Kunming; MCSNG, Museo Civico di Storia Naturale, Genoa; MNHN, Museum National d' Histoire Naturelle, Paris; TISTR, Thailand Institute for Technical and Scientific Research, Bangkok; USNM, National Museum of Natural History, Washington, D.C.; and WIH, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan.

Poropuntius Smith, 1931

Poropuntius Smith, 1931: 14 (type species by monotypy *Poropuntius normani* Smith, 1931).

Comparative osteological and other anatomical studies that might provide distinguishing characters for generic placement of the two dozen or more known species of *Poropuntius* and hundreds of other species of Asian barbine cyprinids remain largely undone. At present, *Poropuntius* is definable mainly by characters present in many unrelated cyprinid species. Thus the last simple dorsal fin ray invariably is strongly serrated, and dorsal fin soft rays almost invariably are 8 (or $8\frac{1}{2}$). The main exception is the species *Poropuntius bolovenensis*, in which a few specimens have $6\frac{1}{2}$ or 7 (or $7\frac{1}{2}$). Most species have two pairs of well developed barbels, rostral and maxillary, but some species have small maxillary barbels only and one has no barbels. Mouth form tends to be generalized in species with well developed barbels, but at least two species have trophic morphs with very different oral morphology. Some species with reduced barbels have reduced lower lips, with trenchant cutting edge on a broad, horny lower jaw sheath. None of the species has a median chin "barbel" or mental lobe (mentum) like that in species of *Tor*, *Folifer*, and *Parator*. Pharyngeal teeth have only been examined or reported on in a few species; these have three rows with counts of 2,3,5. Such counts are characteristic of large numbers of barbin cyprinid species.

Most *Poropuntius* species have a longitudinal stripe extending the length of the body above the lateral line. Usually this stripe is subdued, and sometimes only the posterior half of it is evident, but in a few species the stripe is very bold. Many species have bold black or dusky submarginal stripes on the upper and lower caudal fin lobes, but in other species the stripes are absent. When present, the stripe in the lower lobe tends to be bolder than that in the upper lobe. The melanophores contributing to the stripes lie on the uppermost and lowermost (unbranched) principal caudal fin rays, or on the lowermost two principal caudal fin rays (i.e. the unbranched principal ray and the lowermost branched principal

ray). Juveniles of many or most species have a midpeduncular dark round spot, but this usually disappears at a small size or is transformed into an oval or oblong blotch often continuous with the stripe on the lower caudal fin lobe. Such stripes, however, are not unique to *Poropuntius*, but occur also in species currently assigned to *Acrossocheilus*, *Barbodes* and other genera. Sexual dimorphism is unknown in most species. In a few species males or presumed males have been observed with extensive tuberculation on the head, posterior half of body, and anal fin. *Poropuntius genyognathus* new species has striking sexual dichromatism.

Poropuntius as recognized here corresponds essentially to *Poropuntius* of RAINBOTH (1981) with removal of the species subsequently referred to his new genus *Hypsibarbus* (RAINBOTH, 1996a,b). A superficial character which may separate *Poropuntius* from other cyprinid genera is separation of the rostral cap from the first infraorbital or lacrimal bone by a deep groove. In tuberculate specimens, the rostrum anterior to this groove is most heavily (sometimes exclusively) tuberculated. Some tuberculate specimens may also have tubercles on the snout or cheek posterior to the rostro-lacrimal groove, but these are always fewer in number and usually smaller than those on the rostrum itself. In many other barbin genera, tuberculation tends to be more pronounced posterior to the rostrum. The Malaysian and Indonesian species currently referred to as *Puntius* or *Barbodes collingwoodi* (Günther, 1868) bears a strong superficial resemblance to generalized *Poropuntius*, but lacks the rostro-lacrimal groove and for that reason may be correctly identified as a species of *Barbodes* rather than of *Poropuntius*. The two genera probably are closely related.

Poropuntius has a tropical and subtropical distribution mostly in mainland Southeast Asia. A single species occurs in the Ganges-Brahmaputra basin of India. There are several species in Burma, Thailand, southern China, and Indo-China, then one or two species in the Malay peninsula and perhaps one in Sumatra. They occur mainly in high gradient foothill streams at moderate elevations (usually under 1,000 m). Species present in large lowland rivers such as the Mekong mainstream tend to occur in habitats with swift current such as rapids.

NOMINAL SPECIES OF *POROPUNTIUS*

Due mainly to the large number of nominal species described from China for which types and other material are unavailable for direct comparison with other specimens it is impossible to do a thorough systematic revision of the genus *Poropuntius* at this time. A number of early descriptions were based on specimens with vague locality data, such as "Yunnan", which could have been collected in the Irrawaddy, Salween, Mekong or Red River basins, all of which have endemic species of *Poropuntius*. For a number of the species no type material is available. Difficulties in unravelling the alpha taxonomy of *Poropuntius* increased when a large number of new species were described from China by WU & LIN (1977) without direct comparison to taxa described earlier. Many if not all of the species described by WU & LIN probably are valid, and all are reasonably well figured, but general unavailability of types or comparative material makes their identification problematic and work on closely related species difficult. These are listed here, along with

all other known nominal species referable to *Poropuntius*, in order of the date of publication. In some instances nominal species are also tentatively referred to the synonymy of earlier described species. Failure to assign a nominal species to synonymy is not an indication that it is considered a valid species. For some nominal species about all that can be said is the earlier the description, and the more isolated the type locality, the more likely that it is a valid species.

Poropuntius deauratus (Valenciennes, 1842)

Barbus deauratus Valenciennes, in Cuvier and Valenciennes, 1842: 188 (type locality "Cochinchine")

?*Poropuntius normani* Smith, 1931: 15 (type locality Pliew waterfall, Kao Sabap, near Chantabun, southeastern Siam).

?*Lissochilus smedleyi* de Beaufort, 1933: 34 (type locality Johore, southern Malay peninsula).
Poropuntius deauratus, Kottelat, 1989: 10.

Material examined.—MNHN 2727, 94.5 mm, Cochinchine, Diard (holotype *B. deauratus*); CAS 94470, 149 mm, Nakorn Phanom market, 8 May 1989, T.R. Roberts; CAS 94471, 7: 42.8–68.6 mm, rapids in Mekong mainstream about 12 km S of That Phanom, 6 April 1991, T.R. Roberts; CAS 94472, 23: 40.5–80.3 mm, rapids in lower Menam Mun at Tha Siao, 12 km N of Phibun Mangsahan, 3 April 1991, T.R. Roberts; CAS 94473, 31: 20.7–113 mm, Xe Nam Noi 26 km by road from Ban Nam Tang and 1 km downstream from bridge over Xe Nam Noi on road down escarpment valley from top of Bolovens Plateau to Attapeu town (elev. 270 m), 25 March 1995, T.R. Roberts; CAS 94474, 18: 22.8–105 mm, Xe Nam Noi about 2 km upriver from Tat Faet waterfall, 27, March 1995, T.R. Roberts; CAS 94475, 69: 17.7–105 mm, Xe Pian 1 km downstream from Se Pa waterfall and 5–6 km upstream from Ban Hin Lat, Sekong watershed, southern Laos, 8 April 1995, T.R. Roberts; CAS 94476, 130: 15.5–116 mm, small mountain stream where it flows into Se Kaman just upstream from proposed Se Kaman 1 hydropower dam site, 58 km by road from Attapeu town, 14 April 1995, T.R. Roberts; CAS 94477, 2: 71.5–73.0 mm, Se Kaman at Muang Saiseththirat, 12 km E of Attapeu town, 8 April 1995, T.R. Roberts; CAS 94478, 103 mm, Nam Hinboun, Feb. 1995, NINA; CAS 94479, 128 mm, Kinnak market, southern Laos, 7–15 Feb. 1994, T.J. Warren; CAS 94480, 76.3 mm, Mekong at Ban Hang Khone, Oct. 1993–March 1994, I.G. Baird; CAS 94481, 5: 43.0–47.5 mm, Mekong at Ban Hang Khone, March 1995, I.G. Baird; CAS 94482, 2: 138–145 mm, Stung Treng market, 2–18 Feb. 1994, T.R. Roberts; CAS 94483, 14: 21.8–52.2 mm, O Champha, 4–8 km upstream from its mouth into Tonle San near Te Veng, Ratanakiri province, Cambodia, 14–15 Feb. 1994, T.R. Roberts and K.E. Witte.

Poropuntius deauratus is distinguished from all other species of *Poropuntius* with well developed barbels, and indeed, from all other fish species in the Mekong basin, by its caudal fin coloration: bright lemon yellow, with bold submarginal black stripes on the upper and lower lobes. Some individuals, presumably male, develop extensive tuberculation on the body, but otherwise secondary sexual dimorphism and dichromatism is unknown. Almost no intraspecific variation in snout shape or mouth parts has been observed. Total gill rakers on first gill arch 11–13; lateral line scales 27–31; predorsal scales 9–11; and

circumferential scale rows 22 (RAINBOTH, 1996a: 98). The holotype has predorsal scales 10, transverse scale series 6.1.2, lateral scale series 28, circumpeduncular scales 14, and vertebrae $24+15 = 39$.

This is the species of the genus most commonly encountered in lowland parts of the Mekong basin. It occurs in the Mekong mainstream as well as in many tributaries, and is strongly migratory. Large numbers formerly migrated between the Mekong mainstream and the Mun River in Thailand, but this migration has been blocked by the Pak Mun hydroelectric dam (situated about 5 km up the Mun River from its mouth into the Mekong). It will be interesting to see whether the species survives in the Mun watershed. Although *Poropuntius* species inhabit headwaters in many places in Thailand and elsewhere where large reservoirs have resulted from hydropower projects, they apparently are unable to establish themselves in reservoirs, and often disappear downstream from them.

Examination of individual specimens listed in the material examined reveals relative constancy in morphology of the mouth parts in *P. deauratus*. This should not be taken as an indication that the species lacks inherent genetic variability for the mouth parts reported in other species of *Poropuntius*, but rather that such variability is usually not expressed in the phenotype. Thus *P. deauratus* can itself be considered as normally comprising a single trophic morph, one with generalized mouth parts and strongly migratory behavior. Such a morph is most likely to become widely dispersed without showing divergence of mouthparts in the phenotypes until it establishes isolated populations in a remote basin or watershed or lacustrine environment with less opportunity for dispersal. Several other highly migratory riverine species of *Poropuntius* also appear to conserve generalized mouth parts.

Comparison of the 84.2-mm holotype of *P. normani* Smith, 1931 (generic type species of *Poropuntius*) with the 94.5-mm holotype and other specimens of *P. deauratus* reveals that they are extremely similar and possibly conspecific. See also remarks under *P. smedleyi*.

Poropuntius clavatus (McClelland, 1845) new combination

Barbus clavatus McClelland, 1845: 280, pl. 21, fig. 2 (type locality "rivers at the foot of the Sikkim Mountains on the northern frontier of Bengal").

Barbus clavatus, Hora, 1921: 185, pl. 9, fig. 1 (Senapati stream near Kairong, Naga Hills, Assam).

Material examined.—None.

Original description evidently based on a single specimen 7 inches long. Location of type material unknown. Hora's description and much better figure, presumably based on the same species, shows a generalized *Poropuntius*, with two long barbels and apparently generalized mouth parts. Lateral line scales 40–42, transverse scale rows 7–8/1/3–4. Upper and lower caudal fin lobes with submarginal black stripes. This is the only species of *Poropuntius* reported from the Ganges basin.

Poropuntius laoensis (Günther, 1868)

Barbus laoensis Günther, 1868: 115 (type locality "Laos Mountains").

Poropuntius laoensis, Kottelat, 1989: 10.

Poropuntius laoensis, Rainboth, 1996a: 99 ("clear forested streams of Myanmar, Laos, Thailand, and Cambodia").

Material examined.—None.

Poropuntius margarianus (Anderson, 1878) new combination

Barbus margarianus Anderson, 1878: 867, pl. 79, fig. 1 (type locality "Nampoung river, Kakhyen hills", near Bhamo, Irrawaddy basin).

Barbodes (Barbodes) margarianus, Wu and Lin, 1977: 238, 242 (Yunnan).

Material examined.—CAS 94247, 118 mm, Mandalay market, April 1993, T.R. Roberts; KIZ 781056-57, 2: 128-157 mm, Yinjiang, Irrawaddy basin, Yunnan, Oct. 1978.

The 118-mm Mandalay specimen agrees very well with Anderson's description and figure of *P. margarianus* except the stripe across the middle of the dorsal fin is very faint (this color feature may have been exaggerated by the illustrator). The specimen has gill rakers on first gill arch $3+6 = 9$; lateral scale series 32; predorsal scales 12; transverse scale rows $6/1/3$; circumpeduncular scales 16. In fresh condition it was almost entirely white or silvery, with fins nearly colorless; dorsal and caudal fin with a little lack pigment distally; middle of dorsal fin with black pigment on interradiial membranes, not forming the continuous swath shown in Anderson's figure of *P. margarianus* but in the same position; caudal fin lobes without stripes.

Poropuntius hampaloides (Vinciguerra, 1890)

Barbus hampaloides Vinciguerra, 1890: 298, pl. 9 fig. 8 (type locality Meetan = a tributary of the Houngarao, lower Salween basin).

Poropuntius hampaloides, Kottelat, 1989: 10.

Material examined.—MCSNG 17326, 89.3 mm, Meetan (holotype *B. hampaloides*).

Observations. Snout truncate or obtuse, projecting only slightly beyond mouth. Horny jaw sheath of lower jaw broad and exposed, lower lip broadly interrupted. Barbels absent. Gill rakers short, $3+10 = 13$ on outer edge of first gill arch. Pharyngeal teeth in three rows, 2,3,5. Scales in lateral series 29, transverse scale rows 5.1.2-3. Lateral stripe (not shown in Vinciguerra's figure) visible under dissecting microscope as group of melanophores on posterior part of each scale in scale row above lateral line. Upper and lower caudal fin lobes with bold marginal stripes.

Comparison with other species. *Poropuntius hampaloides* is known only from the holotype. In its specialized lower jaw, with wide transverse horny jaw sheath and broadly interrupted lower lip, it resembles wide-mouthed *Poropuntius genyognathus* new species from the Tenasserim basin. Direct comparison of the holotype of *P. hampaloides* with an

80.8 mm paratype of *P. scapanognathus* new species from the middle Salween basin (MCSNG 48357) reveals different structure of the lower lip and lower horny jaw sheath. In *P. hampaloides* the lower lip is restricted to the corners of the mouth and the lower horny jaw sheath is broad; in *P. scapanognathus* the lower lip is continuous, and the lower jaw and lower horny jaw sheath are invariably narrow.

Distribution. *Poropuntius hampaloides* is known only from the Meetan, a presumably high gradient tributary of the Houngarao in the lower Salween basin of southeastern Myanmar.

Poropuntius cogginii (Chaudhuri, 1912) new combination

Barbus cogginii Chaudhuri, 1912: 16, pl. 1, fig. 2 (type locality Lake Tali Fu [Er Hai or Lake Dali], Yunnan).

?*Barbus gregorii* Norman, 1922: 562 (type locality Yunnan, no other information).

Barbus cogginii, Rendahl, 1928: 138 (Er Hai).

Barbodes daliensis Wu & Lin, 1977: 251, fig. 7-11 (type locality Xiaguan [Er Hai]).

Barbodes daliensis, Chen, 1998: 151, fig. 103.

Material examined.—WIH 122090028, 29:96.3-220 mm, Xiaguan (labelled syntypes of *B. daliensis*)

Diagnosis. *Poropuntius cogginii*, endemic to Lake Dali or Er Hai, has long barbels and well developed submarginal stripes on the caudal fin lobes. It is readily distinguished from all other *Poropuntius* except *P. exigua* by its relatively smaller fins, particularly the caudal fin. Thus in a *B. daliensis* syntype of 188 mm SL the sum of the lengths of the dorsal, one pectoral, one pelvic, the anal and the caudal fins is only 177 mm, while in 183 and 190 mm syntypes of *P. carinatus* and *P. opisthoptera* the total fin lengths are respectively 229 and 213 mm. Comparable relative differences in fin length and size are observed throughout the entire syntype series of these three nominal species. *P. cogginii* further differs from *P. carinatus* and *P. opisthoptera* in having a larger head, due mainly or entirely to a greatly expanded opercular region.

Discussion. It is unclear whether WU & LIN, 1978 intended to propose *B. daliensis* as a new species, or merely as a replacement name for *Barbus gregorii* Norman, 1922. Since their account is accompanied by a full description and figure, the specimens it is based upon have a more definite locality (Xiaguan, but almost certainly caught in Er Hai), the specimens are labelled syntypes in the WIH fish collection, and the identification with *B. gregorii* is uncertain, I tentatively recognize *B. daliensis* as a validly described species in its own right. As such, it is clearly a species of *Poropuntius*, and is here identified for the first time as a junior synonym of *B. cogginii*. Whether *B. cogginii* is also a senior synonym of *B. gregorii* Norman, 1922 requires further investigation.

The figure of a syntype of *B. daliensis* in WU & LIN, 1977 (fig.7-11), with a scale bar of 20 mm, evidently represents a specimen of about 190 mm in standard length, does not show particularly well either the smaller fins or the enlarged gill cover observed by me in all 29 syntypes. The figure of *B. daliensis* in CHEN, 1998 (fig. 103), however, with a scale

bar of 50 mm indicating a standard length of about 210 mm, shows both of these features very well (it would be most helpful if the figure legends of type and non-type specimens figured in reports by Chinese ichthyologists included the standard length, locality and sometimes also the catalog number).

***Poropuntius tawarensis* (Weber and de Beaufort, 1916)**

Punius tawarensis Weber and de Beaufort, 1916: 185 (type locality Lake Tawar, Atjeh, Sumatra).

Poropuntius tawarensis Kottelat, 1989: 42, pl. 14.

Material examined.—None.

Poropuntius tawarensis, known only from Lake Tawar in northwestern Sumatra, is a large-scaled species with long labels and apparently generalized mouth parts. Some individuals develop a gibbosity or humeral hump, a character seldom observed in other *Poropuntius*. A faint longitudinal stripe above lateral line (KOTTELAT, 1989: 42). Caudal fin without marginal stripes. Scales in lateral series 25; transverse scale rows 5.1.3; circumpeduncular scales 12. It is doubtful whether this species is correctly placed in *Poropuntius*.

***Poropuntius bantamensis* (Rendahl, 1920)**

Barbus bantamensis Rendahl, 1920: 1, fig. 1 (type locality eastern foot of Doi Chieng Dao, NW Siam).

Poropuntius bantamensis, Kottelat, 1989: 10.

Material examined.—None.

***Poropuntius gregorii* (Norman, 1923) new combination**

Barbus gregorii Norman, 1923: 562 (type locality Yunnan, no further information). Preoccupied by *Barbus gregorii* Boulenger, 1902.

Barbus yunnanensis Fowler, 1958 (unavailable substitute name for *Barbus gregorii* Norman, 1923; preoccupied by *Barbus yunnanensis* Regan, 1904.

Barbus susanae Banister, 1973 (substitute name for *B. gregorii* Norman, 1923).

Material examined.—None.

Comment. If *Barbus* or *Poropuntius gregorii* sensu Norman, 1923 is a valid species, the earliest available name is *Poropuntius susanae* (Banister, 1973).

***Poropuntius normani* Smith, 1931**

Poropuntius normani Smith, 1931: 15 (type locality Pliew waterfall, Kao Sabap, near Chantabun, southeastern Siam).

Acrossocheilus deauratus, Smith, 1945: 200 (partim).

Material examined.—USNM 90297, 84.2 mm, Pliew waterfall on Kao Sabap, near Chantabun, southeastern Siam, 9 April 1925, H.M. Smith (holotype).

See remarks under *P. deauratus* and *P. smedleyi*.

***Poropuntius smedleyi* (de Beaufort, 1933)**

Lissochilus smedleyi de Beaufort, 1933: 34 (type locality Johore, southern Malay peninsula).
Poropuntius smedleyi, Kottelat, 1989: 10.

Material examined.—CAS 63005, 8: 45.6–101 mm, Sungai Tua, Kelang drainage, 4 Feb, 1985, Mohd. Zakaria Ismail; CAS 63011, 8: 104–135 mm, Sungai Marong, 29 Sept. 1985, Mohd. Zakaria Ismail.

This is another riverine species with phenotypically conservative and generalized mouth parts. It is probably also strongly migratory. The distinction between this species and *P. normani* is unclear, as is the distinction between both of these species and *P. deauratus*. One distinction noted between *P. smedleyi* and *P. normani* by DE BEAUFORT (1933: 34) that probably will not hold up is the difference in circumpeduncular scale counts. Thus de Beaufort reported 12 in *P. smedleyi*, noting that *P. normani* has 14 according to SMITH (1931: 15). Apart from these being counts based on single specimens, there are problems with the way circumpeduncular scales are counted. Most workers report circumpeduncular scale counts only in even numbers, i.e., 12, 14, 16, indicating that they do not really complete the count all they way around caudal peduncle, but count on one side only and then double the number. This tends to exaggerate slight differences. Another problem is that it is possible to obtain different counts simply by a slight change in the starting point, or choosing to count from the starting point in one direction rather than in another. For example, in the holotype of *P. normani*, some scales on the caudal peduncle are missing. By counting where the scales are most complete, one usually gets a count of 14. But counting in a slightly different way can give a count of 12.

As in many other nominal species of *Poropuntius*, *P. smedleyi* and *P. normani* are known mainly from their original descriptions, the authors of which compared their supposed new species only with written descriptions and not with actual specimens of other nominal taxa. What is needed in such instances is examination of specimens from localities covering the combined range of the nominal forms to determine the number of species and their distribution, and then comparison with the type specimens to determine which species names should be applied. Such examination is likely to be most fruitful if examination of older museum specimens is combined with observations of coloration and so on of freshly preserved samples. In the case of *P. deauratus*, *P. normani* and *P. smedleyi* this should not be difficult, since there are many samples in museum holdings and their entire range is in areas that are relatively accessible.

***Poropuntius chondrorhynchus* (Fowler, 1934)**

Barbus chondrorhynchus Fowler, 1934: 123, fig. 81 (type locality Keng Tung, Burma).
Poropuntius chondrorhynchus, Kottelat, 1989: 10.

Material examined.—ANSP 58062, 185 mm, Keng Tung market, Southern Shan States, Burma, 17 Feb. 1933, R.M. deSchauensee (holotype); ANSP 58063, 156 mm, collected with the holotype (paratype).

This nominal species has two pairs of well-developed barbels and morphologically generalized mouth parts. It is unknown whether the type specimens originated in the Mekong or Salween basins. Keng Tung is near the drainage divide.

Poropuntius kontumensis (Chevey, 1934)

Cycocheilichthys kontumensis Chevey, 1934: 32, fig. 1 (type locality Kontum Lake near Pleiku, central Vietnam).

Poropuntius kontumensis, Rainboth, 1996a: 99 (“clear mountain brooks and streams in forested areas of Cambodia and Vietnam”).

Material examined.—CAS 94248, 4: 36.8–168 mm, Vietnam, Sai Gon river basin, large mountain stream tributary of Da Dung and Song Dong Nai S of Ban Ma Thuot at Cau Daktik 2 bridge 5.7 km on road from Gia Nghin to Dong Xoai, Dac Lac province, 7 Jan. 1994, K.E. Witte; CAS 424, 10: 77.3–171 mm, Cambodia, Mekong basin, O Changni, a small stream on road from Ann Long Mea to Ban Lung, Ratanakiri province, 12 Feb. 1994, T.R. Roberts and K.E. Witte.

A relatively generalized *Poropuntius* with two long pairs of barbels and usually generalized mouth parts, and a relatively large, thick head. Lateral line scales 35–37, predorsal scales 11–13, circumferential scale rows 24–26; total gill rakers on first gill arch 12–16 (RAINBOTH, 1996: 99).

Tuberculation. A 125-mm specimen from Saigon River is a presumed male with heavily tuberculate rostrum, body and anal fin. Large tubercles on snout, rostrum and lacrimal. Dorsum of head with widely scattered very small tubercles. Tubercles on body confined to posterior half of body, heaviest on scales above anal fin base, each with 2–6 tubercles. Scales on dorsum and sides of body with fewer and smaller tubercles. Dorsal, pectoral and pelvic fins non-tuberculate, caudal fin with a few minute tubercles on middle rays. Anal fin with large tubercles on all rays. The Cambodian samples consists of 9 presumed males, 77.3–134 mm, all with some anal fin tuberculation and several with some tubercles on the body near the anal fin base, and 171-mm ripening female, with no tubercles on the body or anal fin. All of the specimens have well-developed tubercles on the rostrum and to a less extent on the lacrimal. The tubercles tend to be slightly larger but no more numerous in the males than in the large female; the difference is not great.

Trophic polymorphism. All of the specimens in the Cambodian sample have similar mouth parts morphologically generalized for *Poropuntius*. The sample from the Sai Gon basin includes the four specimens listed here, with generalized mouth parts, and two additional specimens, representing a trophic morph with shovel-shaped lower jaw sheath described below as *P. kontumensis rasorius*.

Poropuntius krempfi (Pellegrin and Chevey, 1934) new combination

Barbus (Lissochilichthys) krempfi Pellegrin and Chevey, 1934a: 339 (type locality Nghia Lo, Tonkin).

Lissochilichthys krempfi Pellegrin and Chevey, 1934b: 467, fig. 2.

Lissochilus krempfi, Yen, 1978: 97, fig. 41.

Material examined.—None.

Poropuntius burtoni (Mukerji, 1934) new combination

Barbus clavatus burtoni Mukerji, 1934: 64, figs. 10–11 (type locality Phungkin Kha, a tributary of the Mali Kha, Irrawaddy basin; see RAINBOTH, 1981: 37).

Material examined.—None.

This nominal species, characterized by two pairs of well developed barbels and a short, broad mouth, horny jaw sheaths not described, may be a synonym of another nominal species described from the Irrawaddy or other river system. It may represent an intraspecific trophic morph of a species including a more generalized trophic morph with a narrower mouth.

Poropuntius shanensis (Hora & Mukerji, 1934)

Barbus shanensis Hora and Mukerji, 1934: 362, fig. 3 (type locality Lawksawk, southern Shan States, Irrawaddy basin).

Poropuntius shanensis, Kottelat, 1989: 10.

Material examined.—CAS 94250, 2: 175–176 mm, Inle Lake, 26 Feb.–4 March 1994, T.R. Roberts

Barbels short and thin, rostral barbel not extending posteriorly as far as anterior margin of eye, maxillary barbel reaching posteriorly to below middle or posterior 2/3 of eye. Lateral scale series 33; predorsal scales 12; transverse scale rows 6.1.3. Gill rakers on leading edge of first gill arch $2+1+5 = 8(1)$ and $3+1+6 = 10(1)$.

Poropuntius ikedai (Harada, 1943) new combination

Lissochilus ikedai Harada, 1943: 23, pl. 7, fig. 23 (type locality Hainan).

Acrossocheilus (Acrossocheilus) ikedai, Wu and Lin, 1977: 292, fig. 7–39.

Material examined.—WIH uncatalogued, 15: 99–193 mm, Chang Jiang basin, Hainan, Feb. 1960.

This species, despite its geographically isolated distribution from other species of the genus, undoubtedly belongs in *Poropuntius*. The original description, translated from Japanese by Keiichi Matsuura and Atsushi Doi, is as follows:



Figure 1. *Poropuntius deauratus*. Mekong at Nakorn Phanom, 190 mm.



Figure 2. *Poropuntius margarianus*. Mandalay, 118 mm.



Figure 3. *Poropuntius kontumensis*. Sai Gon basin, 125 mm tuberculate male.



Figure 4. *Poropuntius shanensis*. Inle, 175 mm.



Figure 5. *Poropuntius bolovenensis*. Xe Nam Noi, Mekong basin. Upper, *P. b. acuticeps*, 116 mm (holotype); middle, *P. b. bolovenensis*, 124 mm (holotype); lower, *P. b. glaridostoma*, 138 mm (holotype).



Figure 6. *Poropuntius bolovenensis*, ventral view of head. Xe Nam Noi, Mekong basin. Left *P. b. acuticeps*, 116 mm (holotype); middle, *P. b. bolovenensis*, 124 mm (holotype); right *P. b. glaridostoma*, 138 mm (holotype).



Figure 7. *Poropuntius genyognathus*. Chawa Kloh, Tenasserim basin, 112 mm (holotype).



Figure 8. *Poropuntius genyognathus*. Tuler Kloh, Tenasserim basin. Narrow and broad mouthed growth stages (both specimens about 85 mm).



Figure 9. *Poropuntius hathe*. Menam Moei, Salween basin, 61.7 mm (holotype).

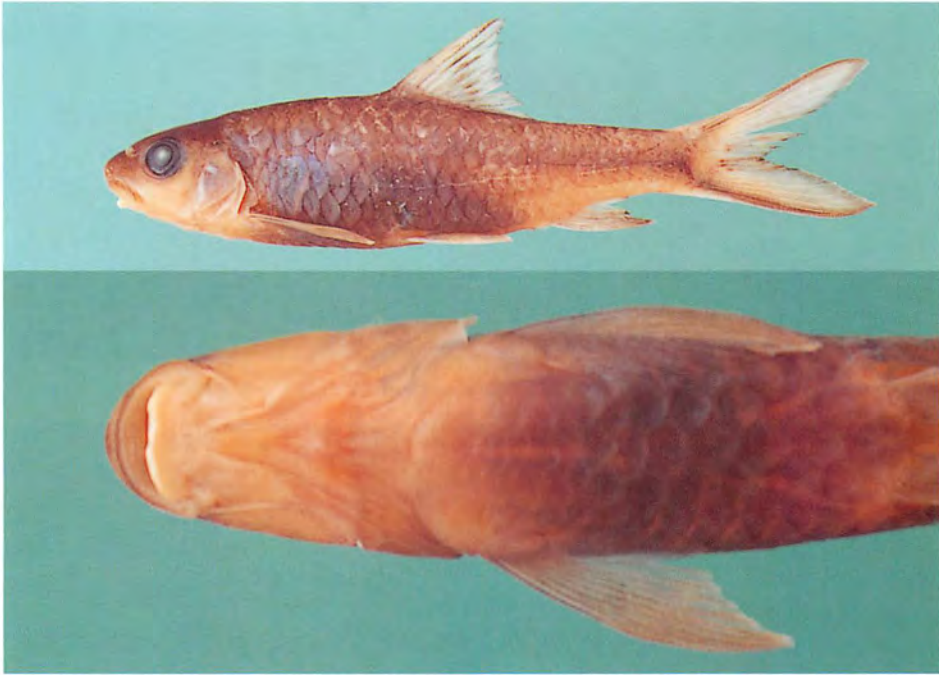


Figure 10. *Poropuntius kontumensis rasorius*. Sai Gon basin, 87.5 mm (holotype).



Figure 11. *Poropuntius melanogrammus*. Huay Sangkalia, Meklong basin, 56.3 mm (holotype).



Figure 12. *Poropuntius scapanognathus*. Huay Kong, Salween basin, 76.2 mm (holotype).

Dorsal fin rays IV/8; anal fin rays: 3/5; pectoral fin rays 1/15–16; pelvic fin rays 1/8; lateral line scales: 31–33; number of scales between dorsal fin origin and pelvic fin origin: 5/1/3; circumference scale count (around caudal peduncle) 14. Body length: head length = 4.1–4.4; body length: body depth = 3.0; predorsal length: body length = 52%; head length: caudal peduncle depth = 1.9–2.1; head length: head width = 1.5–1.7; head length: eye diameter = 4.0–4.1; head length: interorbital width = 2.4–2.6; head length: snout length = 2.6–2.8; head length: postorbital length = 2.4–2.5; pharyngeal teeth: 5, 3, 2–2, 3, 5; gill rakers: 6 + 13 (based on the specimens of 150–177 mm body length). Body laterally compressed. Snout pointed, covered with horny tubercles; rostral fold of snout extending ventrally but not covering upper lip. Mouth inferior, horseshoe shaped; lower jaw included in upper jaw when mouth closed. Upper and lower lips thin and soft, separated from each jaw by a shallow groove; both lips and chin covered with many papillae [=sensory pores?]. Surface of lower jaw horny. Two pairs of barbels; the barbel on the snout reaching below center of eye, the other barbel originating from corner of mouth extended posteriorly beyond posterior margin of eye (barbel length 1.8 times as long as eye diameter). Eye large; interorbital area distinctly convex. Dorsal fin origin slightly closer to caudal fin base than to snout tip; last simple ray of dorsal fin hardened, covered with many serrae along the posterior margin. Pectoral fin equal to head length, its tip not reaching to pelvic fin. Pelvic fin origin slightly anterior to dorsal fin origin, pelvic fin tip close to but not reaching to anal fin origin. Axillary scales long and elongated. Anal fin tip not reaching to caudal fin base. Caudal fin well developed and forked, its length 1.5 times as long as head length; lower lobe longer than upper lobe. Lateral line complete, running horizontally but slightly lowered above pelvic fin. Pharyngeal teeth arranged in three rows, their tips sharp and beak-like. Intestine long, peritoneum black. Color in life: dorsal half dark green, ventral half silver. Scales on side of body with semicircular black spots. All fins dark. Ecology: occurs in rapid streams in upper reaches of rivers. Reproductive periods probably in December–January. The smallest specimen among specimens collected in May reaching 80 mm. Systematic notes and distribution. According to Lin (1933), this genus is relatively diversified in China, represented by 8 species. Nichols (1927) described *Barbus barbodon* as a new species from Hainan Island, but it clearly differs from *L. ikedai*. *B. barbodon* has 42 scales in lateral line but my examination of many specimens of *L. ikedai* shows that the largest lateral line scale count is not larger than 33. *B. barbodon* has short barbels (the barbel on the mouth corner is 1–1.3 times as long as eye diameter) but *L. ikedai* has long barbels (the barbel on the mouth corner is 1.8 times as long as eye diameter). This species was collected only from the Chang-jiang river system on Hainan Island. This species is named in honor of Navy General Kiyoshi Ikeda. The species of *Lissochilus* found in Tokyo is *L. krempfi* and close to *L. barbodon*.

***Poropuntius faucis* (Smith, 1945)**

Puntius faucis Smith, 1945 (type locality Mechem Gorge, Meping River, Chao Phraya basin).

Poropuntius faucis, Kottelat, 1989: 10.

Material examined.—USNM 119497, 40.6 mm, Gorge of the Mechem, tributary of the Meping River, Chao Phraya basin, July 1935, Buchanan and Harrison (holotype).

Holotype has 25+15 = 40 vertebrae.

***Poropuntius susanae* (Banister, 1973) new combination**

Barbus gregorii Norman, 1923: 562 (type locality Yunnan, no further information).

Preoccupied by *Barbus gregorii* Boulenger, 1902.

Barbus yunnanensis Fowler, 1958: 12 (unavailable substitute name for *Barbus gregorii*)

Norman, 1923; preoccupied by *Barbus yunnanensis* Regan, 1904).

Barbus susanae Banister, 1973: 143 (substitute name for *B. gregorii* Norman, 1923).

Barbodes (Barbodes) daliensis Wu and Lin, 1977: 251, fig. 7–11 (substitute name for *Barbus gregorii* Norman, 1923, pre-empted by *B. susanae* Banister, 1973).

Material examined.—None.

Comments.—*Barbus yunnanensis* Fowler, 1958; *Barbus susanae* Banister, 1973; and perhaps *B. daliensis* Wu and Lin, 1977, were all proposed as substitute names for *Barbus gregorii* Norman, 1923, preoccupied in *Barbus* by *B. gregorii* Boulenger, 1902. See remarks under *P. daliensis*.

***Poropuntius carinatus* (Wu and Lin, 1977) new combination**

Barbodes (Barbodes) shanensis carinatus Wu and Lin, 1977: 240, fig. 7–3 (type locality Meng'a [Salween basin], Yunnan)

Material examined.—WIH 12209001, 2: 165–183 mm, Meng'a, Salween basin, Yunnan, 1960 (syntypes).

Poropuntius carinatus supposedly differs from other species in having a predorsal keel or carina. It also has long barbels, generalized mouth parts with elongate jaws and a pointed head, a curved stripe on body well above lateral line (possibly distinctive); caudal peduncle with a large black spot; submarginal stripes on upper and lower caudal fin lobes. The keel may be due to poorly fed condition of the syntypes or an artifact of preservation. A pronounced predorsal keel, almost as pronounced, is also present in syntypes of *P. opisthoptera*. The syntypes of *P. opisthoptera* do not exhibit a stripe above the lateral line or submarginal stripes on the caudal lobes, but do have a faint midpeduncular triangular spot.

***Poropuntius exigua* (Wu & Lin, 1977) new combination**

Barbodes exigua Wu and Lin, 1977: 249, fig. 7–9 (type locality Shi Cho, flowing into northern end of Lake Dali).

Barbodes exigua, Chen, 1998: 150, fig. 102.

Material examined.—WIH 12209007, 17: 50.4–82.8 mm, all from Shi Cho?, 1957–1964 (syntypes).

Discussion. *Poropuntius exigua* was originally distinguished from *P. daliensis* by Wu and Lin because of its much smaller size as sexually mature adults. This species, apparently endemic to Lake Dali and/or streams flowing into it, shares with that species markedly smaller fins (and particularly the caudal fin) than any other *Poropuntius*. The specimens are also sexually mature at a remarkably small size, smaller than any other species of *Poropuntius* seen by me in sexually mature condition with the likely exception of the very distinctive *P. hathe* new species from the Salween basin of Thailand. In addition, the 12 largest specimens of the syntype series, 58.5–82.8 mm, have a more or less well developed nuchal hump, a feature not observed in any other mainland *Poropuntius* including *P. cogginii* (of which *P. daliensis* is a junior synonym). The nuchal hump appears to be a normal

feature, not an artifact or preservation. The five smallest syntypes, 50.4–60.0 mm, have no or almost no hump. The smallest of these is evidently the syntype figured by WU & LIN, 1977 (fig. 7–9). In CHEN, 1998 (fig. 102) one of the larger syntypes is figured. The scale bar of 30 mm indicates a standard length of about 110 mm, much larger than the largest syntype. Be that as it may, this figure shows very well the nuchal hump characteristic of this species, reduced size of fins and especially of the caudal fin shared only with *P. cogginii*, and submarginal caudal stripes typically found in many species of *Poropuntius* including *P. cogginii*.

***Poropuntius opisthoptera* (Wu, 1977) new combination**

Barbodes (Barbodes) opisthoptera Wu in Wu and Lin, 1977: 246, fig. 7–7 (type locality Baoshan, upper Salween basin, Yunnan).

Barbodes opisthoptera Chu and Chen, 1989: 189, fig. 179.

Material examined.—WIH 12209005, 15: 121–286 mm, Huizen Cho, Baoshan, Nu Jiang basin, Yunnan, May 1958 (syntypes).

Poropuntius opisthoptera supposedly differs from *P. carinatus* in having a somewhat smaller head and smaller eye, and in lacking a stripe on body above the lateral line and submarginal stripes on caudal fin lobes. The 286-mm syntype has 4+0+6=10 gill rakers on outer edge of first gill arch.

***Poropuntius speleops* (Roberts, 1991) new combination**

Barbus speleops Roberts, 1991: 104, figs. 1–4 (type locality Tham Phu Khieo, Phu Khieo Wildlife Sanctuary [Mekong basin, Thailand]).

Material examined.—TISTR 2642, 57.9 mm, Tham Phu Khieo, 9 April 1989, P. Chapman (paratype).

Relationship to *Poropuntius* was not recognized when this species was first described. It is the only known cave fish in the genus *Poropuntius*. Young fish to 60 mm have eyes nearly normal in position although a bit smaller than in surface-dwelling species. With growth the eyes “retreat” deeper and deeper into the orbits, which remain open but become slit-like. Young fish have faint submarginal stripes on the caudal fin characteristic of *Poropuntius* (ROBERTS, 1991, fig. 1). Apart from reduction of eyes and pigmentation, *P. speleops* has not deviated greatly from riverine surface-dwelling species of the genus.

NEW SPECIES AND TROPHIC MORPHS OF *POROPUNTIUS*

During three decades of field work on Southeast Asian freshwater fishes the author has collected numerous samples of *Poropuntius*, most of which have remained unidentified and unreported until now. These include samples from a number of river basins or drainages from which few or no fish collections have been made or reported upon previously. Among the species of *Poropuntius*, several of which are undescribed, are two species exhibiting pronounced trophic polymorphism, a phenomenon not previously reported in the genus. By this is meant the occurrence, within populations of a single species, of two

or more discrete feeding morphs or phenotypes differing more or less strikingly in the morphology of the mouth, lips, and horny jaw sheaths. Such morphs, with evident potential to evolve into separate genera and species, are here formally described as trinomial species-level taxa.

Poropuntius bolovenensis new species

This species apparently is endemic to streams on the summit of the Bolovens Plateau, in the Sekong watershed of the lower Mekong basin in southern Laos. It is known from two of the largest streams on the plateau, the Xe Nam Noi and the Xe Pian. It is apparently absent from the Houai Ho, a somewhat smaller and more seasonal stream in the southeastern corner of the Bolovens Plateau. The Xe Katam, the only other stream on the plateau likely to be inhabited by this species, has not been ichthyologically surveyed. It is absent from the lower Xe Nam Noi and lower Xe Pian, which have a relatively rich fish fauna including the common Mekong lowland species of *Poropuntius*, *P. deauratus*.

Poropuntius bolovenensis is the dominant cyprinid fish in the Xe Nam Noi and Xe Pian on the Bolovens Plateau, where the two river systems have a relatively depauperate fish fauna of less than 20 known species. As the main streams have been fairly well sampled for fishes, and local villages extensively interviewed about possible additional species, it seems unlikely that this number will be much increased by further exploration, except possibly in the Xe Katam, where altogether different species might occur.

The large series of *P. bolovenensis* collected at the proposed dam site for the Xe Nam Noi-Xe Pian hydropower project comprises four distinct forms or morphs. I interpret these forms as morphs of a species with pronounced trophic polymorphism. Most of the specimens have mouth parts resembling those in many other barbin species, including most species of *Poropuntius* with well-developed barbels, such as *P. deauratus*. The species *P. bolovenensis* is based on this form. The four morphs also have slight differences in body proportions (head length, body depth, caudal peduncle length) and meristic characters (counts of dorsal fin rays, gill rakers, and scales). On the other hand, their coloration in life is virtually identical, one reason for considering that they represent a single species. Another reason is that all of the smaller individuals have mouth parts of the generalized type. That is, the smallest recognizable individuals of the three divergent morphs, if they are present in the sample, are so similar to the most generalized morph that I have been unable to distinguish them.

Coloration of all individuals at the Xe Nam Noi site was nearly identical in life: a uniformly dark greenish body and very dark or dusky fins, with almost no noticeable marks. After preservation the marginal stripe on the caudal fin lobes became more noticeable, but even then are subdued compared to the marginal caudal lobe stripes in *P. deauratus* and other species. Specimens from the upper Xe Pian locality had golden reflections not observed in other samples. Specimens from the middle Xe Pian locality were similar in coloration to those of the Xe Nam Noi.

Most of the Bolovens Plateau is many hundreds of meters above the surrounding lowlands. The Xe Nam Noi and Xe Pian, the two largest rivers on the plateau, both flow into the Sekong watershed of southern Laos and northeastern Cambodia (the Sekong flows into the Mekong mainstream at Stung Treng in Cambodia, some 70 km south of the Lao

border). The Upper Xe Nam Noi and Xe Pian where *P. bolovenensis* occurs are isolated from their lower reaches by high waterfalls. Several other species found in them also appear to be endemic. The only *Poropuntius* found in the lower Xe Nam Noi and lower Xe Pian is *P. deauratus*.

***Poropuntius bolovenensis bolovenensis* new morph**

Holotype.—CAS 94251, 124 mm, Xe Nam Noi 300 m downstream from primary dam site of Xe Nam Noi-Xe Pian hydropower scheme (elev. 730 m), Bolovens Plateau, Sekong watershed, southern Lao PDR, 24 March 1995, T.R. Roberts.

Paratypes.—CAS 94252, 110: 34.9–164 mm, collected with the holotype; CAS 94253, 134 mm, Xe Pian at secondary dam site of Xe Nam Noi-Xe Pian hydropower scheme, 8 km S of Ban Nam Tang, Bolovens Plateau, Sekong watershed, southern Lao PSR, 23 March 1995, T.R. Roberts; CAS 94254, 89: 22.1–114 mm, Xe Pian about 3 km down gorge from Ban Houay Chot (elev. about 400 m), 1 April 1995, T.R. Roberts.

Diagnosis. Snout moderately elongate, lips and horny jaw sheaths moderately developed, margin of lower horny jaw sheath rounded with no trenchant cutting edge. Two pairs of long barbels; rostral barbel reaching posteriorly to or beyond anterior margin of eye, maxillary barbel to or beyond posterior half of eye. Gill rakers on leading edge of first gill arch 2–5+7–11 = 10–16. Frequencies of these counts in 76 specimens 10(3), 11(3), 12(24), 12(23), 14(19), 15(3), and 16(1). Pharyngeal teeth 2,3,5/5,3,2 (164-mm specimen). Dorsal fin soft rays almost invariably 8 (see comments below).

Secondary sexual dimorphism. The samples of *P. bolovenensis* were collected at the end of March 1995, towards the end of the dry season. We were informed that there is often a week of early rain during the month of April, during which some fish spawn (e.g. *Garra*), but that the rain then stops and does not begin in earnest until June, when most fish spawn. Thus the specimens were not expected to be in reproductive condition. Nevertheless, the large series of *P. b. bolovenensis* includes two presumed male specimens, 88.8 and 134 mm, with pronounced tuberculation on the posterior part of the body including the anal fin. The last simple and first three branched anal fin rays each bear 3–8 small tubercles. Most of the scales on the posterior part of the body, particularly on the dorsum and on the lower part, each have a single tubercle near the middle of their exposed surface in the 88.8-mm specimen, and 1–3 tubercles in the 134-mm specimen. The entire rim of the posterior nostril (on both sides of the head) is covered with numerous small, conical structures which also seem to be tubercles, but such tubercles are present in many other specimens. Rostral tubercles are particularly large and numerous in the 134-mm specimen, but not moreso than in some other large specimens lacking tuberculation on the body. Specimens with tuberculate bodies observed only in the nominate morph or subspecies of *P. bolovenensis*.

***Poropuntius bolovenensis acuticeps* new morph**

Holotype.—CAS 94255, 116 mm, Xe Nam Noi 300 m downstream from main dam site for Xe Nam Noi-Xe Pian hydropower scheme, Bolovens Plateau, Sekong watershed, southern Lao Peoples Democratic Republic, 24 March 1995, T.R. Roberts.

Paratype.—CAS 94256, 106 mm, collected with the holotype.

Diagnosis. In this subspecies or morph, represented by only two specimens, mouth form resembles that in the nominal morph except entire head, snout and mouth are much narrower and lips are hypertrophied. The lower lip is not continuous, but interrupted near the symphysis of the lower jaw. Dorsal fin with 7 branched rays. Lateral scale series 32–33; predorsal scales 13; transverse scales 7.1.3; circumpeduncular scales 16. Gill rakers on leading edge of first gill arch $3+1+5 = 9$ (holotype) or $4+1+6 = 11$ (paratype).

The large series of *P. b. bolovenensis* includes a large number of smaller individuals some of which may be *P. b. acuticeps*. With the exception of six specimens, 37.7–79.6 mm, with only 7 (or, in one specimen, $6\frac{1}{2}$ branched dorsal fin rays) all of these specimens have 8 branched dorsal fin rays (usually 8 or $8\frac{1}{2}$, but probably also some with $7\frac{1}{2}$). There is some morphological variation in the mouth parts of these specimens but I could not discern any with clear-cut indication of *acuticeps*-like trophic structures. These specimens are catalogued separately as CAS 94286, since they might represent the otherwise unrecognized juveniles of *P. b. acuticeps*.

Tuberculation. Both specimens are almost entirely non-tuberculate on the head as well as on the body. The 106-mm paratype has no tubercles at all on the rostrum, and only a very few tiny tubercles on the side of the snout. The 116-mm holotype has only a single tiny tubercle on the left side of the rostrum and a few on the side of the snout. The nearly complete absence of rostral tuberculation is striking compared to the more or less strongly tuberculate rostrum in *P. b. bolovenensis* of comparable size.

Poropuntius bolovenensis glaridostoma new morph

Holotype.—CAS 94257, 138 mm, Xe Nam Noi 300 m downstream from main dam site for Xe Nam Noi-Xe Pian hydropower scheme, Bolovens Plateau, Sekong watershed, southern Lao Peoples Democratic Republic, 24 March 1995, T.R. Roberts.

Paratypes.—CAS 94258, 10: 48.1–128 mm, collected with the holotype; CAS 94259, 157 mm, Xe Pian at secondary dam site for Xe Nam Noi-Xe Pian hydropower scheme, Bolovens Plateau, Sekong watershed, southern Lao Peoples Democratic Republic, 23 March 1995, T.R. Roberts; CAS 94260, 2: 76.1–83.3 mm, Xe Pian about 3 km down gorge from Ban Huay Chot (elev. about 400 m), 1 April 1995, T.R. Roberts.

Diagnosis. Jaws extremely modified, especially the lower jaw. Lower lip confined to rictus (corner of mouth); lower horny jaw sheath greatly thickened and broad, with a sharp transverse cutting margin. Upper jaw with well developed lip; upper horny jaw sheath weakly developed, continuous with upper lip, and with very small transverse ridges. Head length 4 times in standard length. Body and caudal peduncle slender; standard length 4 times greatest depth; caudal peduncle twice as long as deep. Lateral scale series 35–39; predorsal scales 16–17; transverse scales 7.1.3–4; circumpeduncular scales 14–16. Gill rakers on leading edge of first gill arch $3-5+0-1+8-12 = 13-17$. Frequencies of these counts for 12 specimens are 13(1), 15(6), 16(3), 17(2). Pharyngeal teeth 2,3,5/5,3,2 (157-mm specimen).

The entire series of 13 specimens of *P. b. glaridostoma* from the single Xe Nam Noi

and two Xe Pian sampling sites exhibits little variation in trophic structures and other characters. The differences in the mouth structures between these specimens and *P. b. bolovenensis* is almost as much in the smallest specimens as in the largest, the 157-mm Xe Pian specimen. In the latter specimen the trenchant margin of the lower horny jaw sheath is 10.6 mm wide. This is disproportionately wider than in the next largest specimens, including the 138-mm holotype, in which the width of the lower horny jaw sheath is only 8.8 mm. In all but the smallest specimen the lower lip is definitely confined to the corners of the mouth. In the smallest specimen, 48.1 mm, the lips are continuous across the lower horny jaw sheath, but are no longer free from it and have withdrawn to a more posterior position. The margin of the lower lip is indicated by pigmentation. In the next smallest specimen, 52.7 mm, the lower lip is completely withdrawn from the horny jaw sheath, the ventral surface of which is therefore entirely whitish.

Specimens of *Poropuntius* with a broad lower horny jaw sheath with sharp cutting edge comparable to that of *P. b. glaridostoma* have not been reported by other authors in any species of *Poropuntius*. It is thus of interest to note that they are reported in this paper also in *P. kontumensis ratorius* new morph and *P. genyognathus* new species.

Secondary sexual dimorphism. Not observed. Tubercles relatively small, confined to rostrum in all specimens; holotype with small tubercles on lacrimal portion of cheek below nostrils.

Poropuntius bolovenensis laticeps new morph

Holotype.—CAS 94261, 132 mm, Xe Nam Noi 300 m downstream from main dam site for Xe Nam Noi-Xe Pian hydropower scheme, Bolovens Plateau, Sekong watershed, southern Lao People Democratic Republic, 24 March 1995, T.R. Roberts.

Diagnosis. The single specimen representing this morph is distinguished by a much broader head than any of the other specimens of *P. bolovenensis*. The mouth parts also are distinctive. Mouth very short (rictus of jaws far anterior to vertical line at anterior margin of eye) and nearly as broad as in *P. b. glaridostoma* but without the extreme reduction of the lower lip or development of a lower horny jaw sheath with trenchant margin. Upper and lower horny jaw sheaths well developed; upper and lower lips tightly adherent to horny jaw sheaths but complete.

Poropuntius genyognathus new species

Holotype.—CAS 94485, 112 mm, Chawa Kloh, upstream from Kita or Htee-tah, Tenasserim, 10 March 1992, T.R. Roberts.

Paratypes.—CAS 94487, 39: 73.9–119 mm, collected with the holotype; CAS 94488, 5: 40.2–58.8 mm, rapids on right bank of Tenasserim River just upstream from Htee-tah, 8 March 1992, T.R. Roberts; CAS 94489, 26: 48.4–101 mm, rapids on left bank of Tenasserim mainstream just upriver from Htee-tah, 9 March 1992, T.R. Roberts; CAS 94490, 9: 42.4–101 mm, Kayethoo Kloh, 14 March 1992; CAS 94491, 14: 47.4–128 mm, Tapoleh Kloh, 13 March 1992, T.R. Roberts; CAS 94492, 46: 37.3–65.6 mm, Tuler rapids on Tenasserim mainstream, about 2/3 of distance from Htee-tah to Baowashung, 14 March

1992, T.R. Roberts; CAS 94493, 129: 40.3149 mm, Tuler Kloh, below Tuler rapids in Tenasserim mainstream, about 2/3 of distance from Htee-tah to Baowashung, 15 March 1992, T.R. Roberts; CAS 94495, 3: 95.3–122 mm, Kaseh Kloh, 19 April 1992, T.R. Roberts.

This very distinct new species is known only from the Tenasserim River basin in the southeastern part of Myanmar, in the Indian ocean coast or western of the upper Malay peninsula, where it is one of the most abundant fish species. It differs from all other *Poropuntius* examined by me in having the last simple ray of the dorsal fin relatively thin (flexible distally) but still strongly serrated as in other *Poropuntius*. Only the maxillary barbel is present, and it is very small. The lower jaw sheath is always heavily keratinized, and large specimens always have a very broad mouth. The species exhibits marked sexual dichromatism, and there is considerable change in the morphology of the lower jaw and horny jaw sheath with growth, these parts starting out relatively narrow and becoming increasingly broader with age, but at different rates depending on the individuals. Thus at a given size it is possible to find specimens with striking difference in the width of the mouth, but all individuals start out with narrow mouths and, although some fairly large specimens have a narrow mouth, apparently change to a broad or very broad mouth if they grow to a large enough size. Thus while the feeding behavior may be quite different, these forms are not considered to be discrete trophic morphs, and are not formally described and named. Scales in lateral series 36–37; predorsal scales 10–11; transverse scale rows 7.1.3; circumpeduncular scales 16.

Coloration; sexual dichromatism. Juveniles to about 40 mm have a well defined, complete, longitudinal black stripe just above the lateral line. Juveniles at somewhat larger sizes tend to have no stripe or only a faint one. In sexually ripe or ripening adults of both sexes, but especially males, the stripe is again evident, but it is greatly thickened, especially anteriorly, and no longer confined to the body above the lateral line. Such a broadening of the lateral stripe has not been reported in other species of *Poropuntius*. In both sexes the caudal fin, especially the lower lobe, is red or reddish; the upper lobe tends to be dusky. Neither juveniles nor adults have marginal stripes on the caudal fin lobes. A red caudal fin without marginal stripes is unique in the genus; the only other species observed by the author with a red caudal fin, *P. hathe* new species, has both lobes red with well developed marginal stripes. Coloration on body and fins apparently becomes intensified as fish approach spawning condition, with the brightest and most intense colors in males. Broadening and darkening of the lateral stripe, while it also occurs in sexually mature females, is much more pronounced in males. The March samples include many mature males and females with ripe or nearly ripe gonads, and some males had flowing milt. Rostral tuberculation is much more pronounced in males than in females. Sexually dimorphic tuberculation on body (as reported here in other species) not observed. Sexual dichromatism has not been observed in other species, possibly because they were not collected in spawning or near-spawning condition.

Note on localities. The entire type series of *P. genyognathus* was collected by the author on two trips to the Tenasserim River in southeast Burma, one in March and one in April of 1992. Most of the specimens were collected in the mainstream of the Tenasserim or in the lower part of high gradient tributaries flowing into the Tenasserim mainstream

upstream from Htee-tah (sometimes spelled Kita) as far as the Tuler rapids (downstream from Baowashung). All of the tributaries are on the right side of the river (tributaries on the left side, which had been heavily logged, were mostly dry, while those on the right side, which had not been logged, were flowing well). Some of the author's notes, including a map indicating the approximate location of each of the tributaries and the distance between them, were lost in the field. The position of the streams at increasing distances upstream from Htee-tah follows the date of collection in March 1992. Kaseh Kloh, collected in April 1992, is near Mingaw (south of Htee-tah).

Etymology. The name *genyognathus* is from the Greek, genys, jaw, ax, or ax-blade; and gnathos, jaw, an allusion to the sharp cutting edge of the lower horny jaw sheath present in all *P. genyognathus*.

Poropuntius hathe new species

Holotype.—CAS 94262, 61.7 mm, rapids in Menam Moei next to highway 1035 129 km N of Mae Sot, 29 April 1991, T.R. Roberts.

Paratypes.—CAS 94263, 11: 52.1–65.5 mm, USNM 324210, 61.9 mm, collected with the holotype; CAS 94264, 3: 51.1–55.0 mm, Hathe rapids in Menam Moei next to highway 1085 132 km N of Mae Sot, 30 April 1991, T.R. Roberts.

Diagnosis. *Poropuntius hathe* is a short, deep bodied *Poropuntius* with two pairs of barbels, generalized mouth parts, and distinctive coloration. Standard length less than 3 times body depth. Caudal fin red or orangish-red with bold black submarginal stripes on upper and lower lobes. Gill rakers on first gill arch 3+1+7 = 11. Lateral line scales 34, predorsal scales 14, transverse scale rows 6.1.3. Scales on posterior third of body noticeably smaller than those lying more anteriorly.

Etymology. The name “*hathe*” is from Hathe Rapids, one of the collecting sites of this species. A large and beautiful limestone formation lies in the middle of these rapids, which extend for only a few hundred meters. Similar but less picturesque rapids occur in many other places in the Moei River.

Poropuntius heterolepidotus new species

Holotype.—CAS 94265, 138 mm, Nam Khong near Nam Tok Susa, Salween basin, Thailand, 19 April 1991, T.R. Roberts.

Paratype.—CAS 94266, 89.9 mm, Salween mainstream about 5 km upstream from mouth of Menam Moei, 18–19 March 1989, T.R. Roberts.

Diagnosis. A moderately deep-bodied *Poropuntius* with two pairs of long barbels; scales in lateral series 39–40, those on posterior half of body markedly smaller than those anteriorly; predorsal scales 15–17; transverse scale rows 7.1.3, circumpeduncular scales 17–18; dorsal fin origin elevated, its origin considerably posterior to a vertical line through pelvic fin origin; lower lip complete across lower jaw but tightly adherent to lower horny jaw sheath; caudal fin with dark distal margin but caudal fin lobes without submarginal stripes.

A similar but less striking shift in scale size occurs in *P. hathe* new species, also from the Salween basin, which has fewer scales, pelvic fin origin almost directly below dorsal fin origin, and caudal fin lobes with black marginal stripes. A similar and equally striking shift in scale size occurs in some species of the related barbin genus *Hypsibarbus*, especially the Irrawaddy endemic species *H. myitkyinae* (Prashad and Mukerji, 1929) (RAINBOTH, 1996a: 86, fig. 23). These are readily distinguished from *P. heterolepidotus* in having larger scales (therefore fewer in the lateral scale series) and lateral line tubules with secondary branches.

Etymology. The name *heterolepidotus* is from the Greek heteros, different, and lepidotus, scaly or scaled, in reference to the abrupt change in scale size on the body.

***Poropuntius kontumensis rasorius* new morph**

Holotype.—CAS 94267, 87.5 mm, Vietnam, Sai Gon river basin, large mountain stream tributary of Da Dung and Song Dong Nai S of Ban Ma Thuot at Cau Daktik 2 bridge 5.7 km on road from Gia Nghin to Dong Xoai, Dac Lac province, 7 Jan. 1994, K.E. Witte.

Paratype.—CAS 94268, 51.5 mm, collected with the holotype.

Diagnosis. *Poropuntius kontumensis rasorius* differs from *P. kontumensis kontumensis* in having a wider lower jaw with lower lip broadly interrupted rather than continuous, and a shovel-shaped, sharp-edged or laminar rather than rounded and non-laminar lower horny jaw sheath. It differs from *P. bolovenensis glaridostoma*, the only other *Poropuntius* from the Mekong basin with a laminar lower jaw sheath, in having a much larger head, broader mouth, less slender caudal peduncle, and obvious submarginal stripes on its upper and lower caudal fin lobes.

***Poropuntius melanogrammus* new species**

Holotype.—CAS 94269, 56.3 mm, Huay Sangkalia on road to Chedi Sam Ong 7 km N of Sangklaburi, 11 Feb. 1989, T.R. Robert

Paratypes.—CAS 94270, 6: 52.9–160 mm, collected with the holotype; CAS 94271, 36.3 mm, Huay Malai on road to Chedi Sam Ong 21 km WNW of Sangklaburi, 12 Feb. 1989, T.R. Roberts.

Diagnosis. A moderately elongate species, standard length more than three times greatest body depth, distinguished from all other *Poropuntius* by its distinctive coloration and (with possible exception of *P. hampaloides*) total lack of barbels (both pairs of barbels well developed, or rostral barbels absent and weakly developed maxillary barbels present in all other species of *Poropuntius*); mouth narrow, lower lip narrowly interrupted near midline, lower jaw with a very hard horny jaw sheath with strongly convex margin. *Poropuntius melanogrammus* differs from all previously described species of *Poropuntius*, with possible exception of *P. hampaloides*, in having a bold black stripe extending length of body. This stripe, persistent at all ages, does not extend beyond scaled base of caudal fin. Distal half of dorsal fin black; heavy concentration of melanophores on inter-radial

membrane connecting last simple dorsal fin ray with first branched dorsal fin ray, but almost no melanophores on last simple ray itself. Caudal fin with thin black submarginal stripes confined to upper- and lower-most simple principal caudal fin ray; distal margin of caudal fin lobes also black, caudal fin otherwise yellow (as in *P. deauratus*). Gill rakers $2+1+6-8 = 9(1), 10(2), 11(2)$. Scales in lateral series 29–31; predorsal scales 10–11; transverse scales 5,1,2; circumpeduncular scales 14.

This species is known only from swift, clearwater tributaries of the Meklong basin in Thailand.

Etymology. The name “*melanogrammus*” is from the Greek “melanos”, black or dark, and “grammus”, line, in reference to the bold midlateral stripe.

Poropuntius scapanognathus new species

Holotype.—CAS 94463, 76.2 mm, Huay Kong just below mouth of Huay Long, near km 45 on highway 1126 NW of Mae Hong Son, Salween basin, 20 Feb. 1991, T.R. Roberts.

Paratypes.—CAS 94464, 2: 74.2–74.6 mm, collected with the holotype; CAS 94465, 22: 35.1–66.2 mm, Menam Moei at Klerko village, about 100 km N of Mae Sot, 16 April 1989, T.R. Roberts; CAS 94466, 2: 52.4–67.4 mm, Tiklo Melaah, small stream flowing into Menam Moei opposite Klerko, 24 April 1989, T.R. Roberts; CAS 94467, 33.5 mm, swift flowing, sandy-botomed side channel of Menam Moei 121 km by road on highway 1085 N of Mae Sot, 27 April 1991, T.R. Roberts; CAS 94468, 56: 23.0–75.5 mm, and MCSNG 48357, 80.8 mm, rapids in Menam Moei 129 km N of Mae Sot on highway 1085, 26–30 April 1991, T.R. Roberts; CAS 94469, 10: 32.3–123 mm, Menam Moei about 0.5 km upstream from confluence with Salween mainstream, 18–19 March 1989, T.R. Roberts.

Poropuntius scapanognathus, *P. hampaloides*, and *P. melanogrammus* are the only three known species of *Poropuntius* with a narrow midlateral stripe. *Poropuntius scapanognathus* differs from *P. hampaloides*, from the lower part of the Salween basin, in the structure of the lower lip and horny jaw sheath. In *P. scapanognathus* lower jaw, lip, and horny jaw sheath invariably narrow and lower lip continuous, while in the 89.3-mm holotype (and only known specimen) of *P. hampaloides* lower jaw, lip, and jaw sheath relatively broader, and lower lip restricted to corners of mouth. Coloration of *P. hampaloides* in life unknown.

Juvenile *P. scapanognathus* are very similar in coloration to *P. melanogrammus*, a new species endemic to the Meklong basin, especially in having a continuous midlateral black stripe. However, this stripe remains bold throughout life in *P. melanogrammus*, whereas in *P. scapanognathus* it is less bold in juveniles of 70 mm and absent in specimens over 110 mm. At all sizes in *P. melanogrammus* the anterior and posterior portions of the longitudinal stripe are of nearly equal pigmented, while in *P. scapanognathus* the anterior portion is more weakly pigmented. As the stripe disappears with growth in *P. scapanognathus*, the posterior portion is the last to disappear. In *P. scapanognathus* the leading edge of the dorsal fin is darkened by melanophores concentrated along the last simple fin ray, while in *P. melanogrammus* the distal margin of the dorsal fin is darkened.

Etymology. The name "*scapanognathus*" is from the Greek, "skapane", a spade or hoe; and "gnathus", jaws.

DISCUSSION

Discrete trophic polymorphism like that found in *Poropuntius bolovenensis* is much commoner in cyprinids and other fishes than would appear from reports in the scientific literature. Most ichthyologists are unfamiliar with the phenomenon of non-sexual polymorphism and have not been looking for it. Also, much previous systematic work has been based on samples with relatively few individuals that lent themselves more readily to interpretation as different species rather than as different forms of the same species. When large samples were available, they were not adequately studied for individual variation of mouth parts. Well documented examples of trophic polymorphism are available for the neotropical characin *Saccodon wagneri* (ROBERTS, 1973) and for the cichlid *Cichlasoma minckleyi* endemic to Cuatro Ciénagas in northern Mexico (SAGE & SELANDER, 1975; KORNFIELD & TAYLOR, 1983).

Experimental evidence that the four kinds of *Poropuntius* found in the Xe Nam Noi on the Bolovens Plateau in southern Laos are intraspecific trophic morphs or subspecies of a single species is not available. No direct observations have been made on one morph changing into another, or of morphs developing from parents of a different morph. The evidence that the variants of *P. bolovenensis* are intraspecific morphs includes 1) their restricted occurrence in a limited geographical area (i.e. isolated streams on the Bolovens Plateau); 2) their similarity to intraspecific morphs in other species of *Poropuntius* and other barbin genera; 3) their great similarity in coloration and other characters to each other; 4) their distinctive features become more and more pronounced with age but small specimens are indistinguishable (as with smaller males and female individuals of most sexually dimorphic species); and 5) their apparent occurrence as part of a single population, with all of the morphs present in a single sample.

Intraspecific phenotypic variation of mouth parts has been documented in the South African cyprinid *Barbus brucii* by GROENEWALD (1958). This species has trophic morphs with greatly thickened lips and a mental lobe (a feature not observed in *Poropuntius*); with moderate lip development and no mental lobe; and with sectorial lower jaws. The greatly thickened lips and mental lobe of wild-caught specimens regress when they are confined in cement tanks.

Trophic polymorphism is a significant mechanism for phenotypic diversification of cyprinidae under certain circumstances, especially when a few species or individuals gain access to a new or isolated habitat, such as a mountain tributary above a waterfall or a newly formed crater lake. It may also play a role in seemingly sudden appearance of "evolutionary novelties". Thus several distinctive cyprinid genera—*Cyprinion*, *Onychostoma*, *Scaphestes*, *Scaphiodon*, *Scaphiodonichthys*, and *Scaphognathops* in Asia, *Varicorhinus* in Africa, *Acrocheilus* in North America—are characterized by shovel-like or otherwise modified lower horny jaw sheaths similar to those that show up in other cyprinid genera (e.g. *Poropuntius*) as intraspecific morphs. The rapid evolution of spectacular endemic "species flocks" such as those of the endemic cyprinids of Lake Lanao and endemic haplochromin cichlids in Lake Victoria may be based largely on elaboration of

the sort of intraspecific genetic and phenotypic variability documented earlier in *Barbus brucei*, *Saccodon wagneri*, *Cichlasoma minckleyi*, and now in *Poropuntius bolovenensis*. A similar conclusion has been suggested for the Victoria cichlids by MEYER (1993).

Modification of the pharyngeal jaws and teeth of cyprinoids undoubtedly has played a key role in their adaptive radiation, but the exact nature of this role needs elucidation. In large segments of cyprinids with varied feeding habits, the morphology of the pharyngeal jaws and teeth changes remarkably little. Thus in the subfamily Barbinae, species after species has the standardized or fixed count of three rows of pharyngeal teeth with 2,3,5 teeth, and the morphology of these teeth is, on the whole, remarkably conservative. The modified pharyngeal jaws and teeth of cyprinoids are no doubt linked to the divergence of cyprinoids from their jaw-toothed ancestors and the loss of jaw teeth. Cyprinoids obviously have not lost the genetic information involved in tooth development, since all or almost all of them still develop teeth on the pharyngeal jaws. Absence of teeth on cyprinoid jaws is directly linked to the variety of keratinized structures that develop on the jaws, and the evolutionary success of these structures in generating diverse oral feeding mechanisms, including unculiferous ridges, grooves, papillae, and fimbriae on the lips and horny jaw sheaths and extra-oral structures such as the rostral cap and mental disc (MINZENMAY, 1933; ROBERTS, 1982). Keratinous formations such as unculiferous horny jaw sheaths which are formed, sloughed off and replaced very rapidly may generate variation for natural selection as effectively as multicuspid teeth, and may lend themselves even more readily to trophic polymorphism.

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