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TROPHIC POLYMORPHISM IN THE MALAYSIAN FISH *NEOLISSOCHILUS SOROIDES* AND OTHER OLD WORLD BARBS (TELEOSTEI, CYPRINIDAE)

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ABSTRACT

Population samples of the cyprinid species *Neolissochilus soroides* from upper Sungai Gombak (a small, high-gradient tributary of the Sungai Kelang near Kuala Lumpur in the middle of peninsular Malaysia), exhibit marked variation of oral morphology involving the lips, horny jaw sheaths, and presence or absence of a mentum (a fleshy median lobe between the lower lips). There are specimens with moderately developed lips and horny jaw sheaths without notable specializations; others with lower horny jaw sheaths thickened and with a trenchant keratinized (dark brown) cutting edge and a thin lower lip; and still others with more or less thickened upper and lower lips and a posteriorly-directed ventromedian process or mentum on the lower lip and weakly developed lower horny jaw sheath (pale or yellowish). Development of the mentum, when present, ranges from barely perceptible to so broad, thick and long as the most highly developed mentum in species of the cyprinid genus *Tor*. The variation is interpreted here as intraspecific polymorphism.

Recognition of polymorphism involving the mouth parts of *Neolissochilus soroides* contributes to a better understanding of the systematics of nominal *Neolissochilus* species in the Malay Peninsula including *N. tweediei* (HERRE & MYERS 1937) and *N. hendersoni* (HERRE 1940). Trophic morphs of *N. soroides* represent non-sexual varieties with the potential to evolve into new species and genera. Trophic polymorphism closely comparable to that of *N. soroides* also occurs in at least one population of *N. hendersoni* on Penang Island. This species, thought to be endemic to Penang but present also on Langkawi Island and on the mainland of the Malay Peninsula in Kedah, differs consistently in having fewer scales in the lateral series but otherwise is closely similar to *N. soroides*.

Malaysian and Indonesian populations of the species *Tor tambra* exhibit polymorphism of the lips and mental lobe comparable to that observed in the "normal" and "*Tor*" type morphs of *N. soroides* but apparently members of these populations do not develop a horny cutting edge on the lower horny jaw sheath as in the "*Acrossocheilus* or *Lissochilus* morph" of *N. soroides*. Trophic polymorphism similar to that reported here in *N. soroides* and *N. hendersoni* occurs in *Tor grypus* in the Tigrus-Eurphrates basin, in the South African species currently referred to as *Barbus* or *Labeobarbus brucii*, and in many other Old World barbin cyprinids not documented here.

Intraspecific variation comparable to that found in *Neolissochilus* and *Tor* also occurs in some isolated populations of the cyprinid subfamily Schizothoracinae (HORA, 1934). This suggests that such trophic polymorphism evolved before the divergence of Barbinae-Schizothoracinae and that it played an important role in the schizothoracin adaptive radiation.

Trophic polymorphism apparently represents an ancient evolutionary heritage of the "barbels" or barbin cyprinids. It evidently has played an important role in the speciation, adaptive radiation, and evolution of distinctive genera in this large fish group. This implies that in these fishes, while geographic or ecological isolation is probably necessary for speciation to occur, evolutionary divergence leading to speciation and formation of genera can occur within populations or in other words sympatrically.

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INTRODUCTION

The objectives of this paper are to 1) document the occurrence of pronounced intraspecific trophic polymorphism in the Southeast Asian cyprinid species *Neolissochilus soroides* (DUNCKER, 1904), based mainly upon intensively studied samples from Sungai Gombak in central Malaysia; 2) provide biological information relevant to this example; 3) point out a number of similar examples of intraspecific trophic polymorphism in other Old World Cyprinidae; and 4) indicate the significance of such polymorphism in the systematics and evolutionary biology of Cyprinidae.

The trophic polymorphism described here was recently recognized by the first author in a sample of *Neolissochilus soroides* obtained by researchers from the School of Biology of the Universiti Sains Malaysia in Penang from Sungai Kenyir, a high gradient stream in the Terengganu basin of eastern Peninsular Malaysia, in 1997. That sample, however, comprises relatively few specimens and does not show the full range of variation in trophic structures occurring in this species. The site is relatively remote and has not been revisited for additional sampling of its *Neolissochilus*. Here we report on *N. soroides* samples with numerous specimens exhibiting similar trophic polymorphism collected mainly in 2005–2006 near the University of Malaya Field Study Center in Ulu Gombak, Selangor. Only 40 minutes' drive from Kuala Lumpur, the site is being utilized for the second author's doctoral study on *N. soroides*. The first author visited there in December 2006.

In order to follow the ensuing account, it is necessary to appreciate the distinction between cyprinid lips and horny jaw sheaths. *Neolissochilus*, like all cyprinids at all stages of their life history, have no true teeth on the oral jaws. Cyprinidae do possess true teeth, but they are restricted to the pharyngeal jaws in their throat. The toothless bones of the upper and lower oral jaws of *Neolissochilus* and other cyprinids are covered by two discrete skin structures, the lips and the horny jaw sheaths. The latter directly cover the jaw bones where they come into contact with food items. Generally the lips and horny jaw sheaths are separated from each other by well defined furrows. The jaw bones do not extend into the lips. The superficial layer of the skin of the lips and horny jaw sheaths is often (perhaps invariably) keratinized. The superficial layer of keratinized epidermal cells often gives rise to a variety of specialized structures including ridges or plicae, papillae, unculi (unicellular projections, often hook-shaped), and sharpened cutting edges. Collectively these substitute for the teeth of other bony fishes and contribute to the stunning adaptive radiation of feeding structures of the cyprinoid fishes (including the trophic morphs of *Neolissochilus*).

The mental lobe, sometimes referred to as "mental barbel" or "mentum", is a soft, fleshy median structure located between the lower lips on the ventral surface of the lower jaw. It occurs in the Old World cyprinid subfamilies Schizothoracinae and Barbinae. In Barbinae it is best known in the Asian species of the *Tor* and in various African species usually referred to the genus *Barbus* but which may more properly belong in *Tor*. It also occurs in *Folifer*.

It is reported here in *Neolissochilus* for the first time. The mentum characteristically occurs only in species or intraspecific trophic morphs in which the lips are more or less thickened or hypertrophied. Its superficial appearance and thickness generally is comparable to that of the lips. Like the lips it is well supplied with taste buds.

Although often referred to as a "mental lobe", the mentum is really a flap. It appears to be a smooth rounded lobe because the margins of the flap fold above the structure when the mouth is closed to form a smooth cylindrical lobe with a rounded tip. Presumably the lobe expands into a flap when the mouth is fully opened in live fish when they are feeding but observations are lacking to confirm this.

Trophic polymorphism comparable to or even more complex than that reported here occurs in many other cyprinids, particularly in the Old World subfamily Barbinae. A number of examples are mentioned in the discussion section of this paper. The genetic basis of this intraspecific variation is perhaps the most important unstudied aspect of the phenomenon. This will require cross-breeding and out-crossing among the various morphs within particular species. So far as we are know such experiments have not been conducted. Since several species are widely utilized in aquaculture, the techniques for artificial spawning and rearing of Cyprinidae are well-known. Although it presently occurs only as a wild fish, *N. soroides* is a popular food fish in Malaysia, and is an excellent candidate for aquaculture, as are some other species with trophic polymorphism.

In instances of intraspecific polymorphism one would usually expect to find that the early stages up to a certain size are morphologically indistinguishable. This appears to be so in the Sungai Gombak population of *N. soroides*. All fish observed under 40 mm in standard length have mouth parts similar to the "normal" or *Neolissochilus*-like morph. The smallest specimen with *Acrossocheilus*-like mouth parts is 40.5 mm, and the smallest with *Tor*-like mouth parts 59.1 mm.

The basic kinds of oral morphology reported here as trophic morphs in species of the barbin cyprinid genera currently assigned to *Neolissochilus, Tor,* and *Labeobarbus* occur repeatedly in numerous species of Old world Barbinae referred to until now as separate species often placed in different genera. If our general hypothesis that much of this biodviserity involves genetically homologous interspecific polymorphism is basically correct, it will result in better understanding of speciation and adaptive radiation in the Cyprinidae, especially the Old World Barbinae. It will also necessitate extensive revision in the systematic status of numerous taxa.

SUNGAI GOMBAK

Sungai Gombak (Figure 1), a small, third order tributary of the Sungai Kelang (also spelled Klang), is the most thoroughly studied stream in Malaysia from the standpoint of biology and particularly limnology (BISHOP, 1973). Here we are concerned primarily with the uppermost part of the watershed. This area is in a forest reserve; the vegetation is evergreen rain forest (op. cit.: 16, fig. 5). The forest provides complete cover with exposure of only about 4–10% for the stream, the channel width of which is 4–10 m, average 6.5 m (op cit.: 82, table 29). At the University of Malaya Field Study Center and continuing on upstream the Gombak is a mountain torrent. About 1.5 km upstream from the station it is joined by a fourth order tributary, the Sungai Anak Gombak, a third as large as the Gombak (op cit.: pl. 4 is a photograph of the Anak Gombak from within the study area). Elevation of Sungai Gombak at the Field Study Center is about 290 m.

The initial study area for the second author's Ph.D. research comprises the first 1.5 km of the Gombak upstream from the field station and the first 1.5 km of the Anak Gombak. This is the same as the stretch of stream as that between field localities I on the Sungai Anak Gombak and II on the Sungai Gombak in Bishop's study (op cit.: 4, fig. 1).

All of the trophic morphs of *Neolissochilus soroides* reported here occur in this stretch. It is almost continuously rocky, with many large and more or less smooth boulders separated only by very short stretches of bottom composed of smaller rock and gravel. These conditions seemingly preclude identification of habitat preferences by the trophic morphs at this particular site: wherever an individual fish might be caught it is within a very short distance of major changes in substrate or habitat. We suspect that the substrate and/or relative availability of food resources is the main determining factor in habitat selection (if it occurs) in the trophic morphs but this is difficult to study in the Sungai Gombak.

Potential food sources of Sungai Gombak *Neolissochilus* are reported on by BISHOP (1973): accounts of the algae occupy pp. 141–186 and Appendix B, pp. 444–449; and of the invertebrates including insects, pp. 187–342 and Appendices C and D, pp. 450–463.

Bishop's account of the fishes, with an out-of-date nomenclature, occupies pp. 343–368 and Appendix F on p. 465. A total number of about 30 fish species is known now from the Sungai Gombak from its sources to the point where it joins the mainstream of the Sungai Kelang. Of these, only 10 or so species are found in the upper reaches. The names currently recognized for them are as follows:
Systomus binotatus (rare)
Neolissochilus soroides
Poropuntius smedleyi
Silurichthys hasselti (rare)
Hemibagrus nemurus (rare)
Clarias leiacanthus (rare)
Glyptothorax fuscus
Channa gachua
Betta pugnax
Macrognathus maculatus
Mastacembelus favus (rare)

Two species of Cyprinidae are dominant in terms of number of individuals and of biomass: *Poropuntius smedleyi* (reported as "*Acrossocheilus deauratus*" by Bishop) and *Neolissochilus soroides* (tentatively reported by Bishop as "*Tor soro*" and as "*Acrossocheilus* sp?"). So far as we have been able to determine no species of *Tor sensu* RAINBOTH (1985) occurs in the Sungai Gombak or in the Kelang (Klang) basin of which it is a part. Species of the South and Southeast Asian mainland cyprinid genus *Poropuntius* often exhibit more or less pronounced trophic polymorphism comparable to that reported here in *Neolissochilus soroides* except that none of the morphs in this genus develop a median mental lobe or mentum (ROBERTS, 1998). Thus far, however, trophic polymorphism has not been observed in samples of *P. smedleyi* from the Sungai Gombak or anywhere else. Based on the specimens we have examined, the Gombak population of this species is monomorphic from the standpoint of trophic structures. It is perhaps noteworthy that the most striking example of trophic polymorphism previously

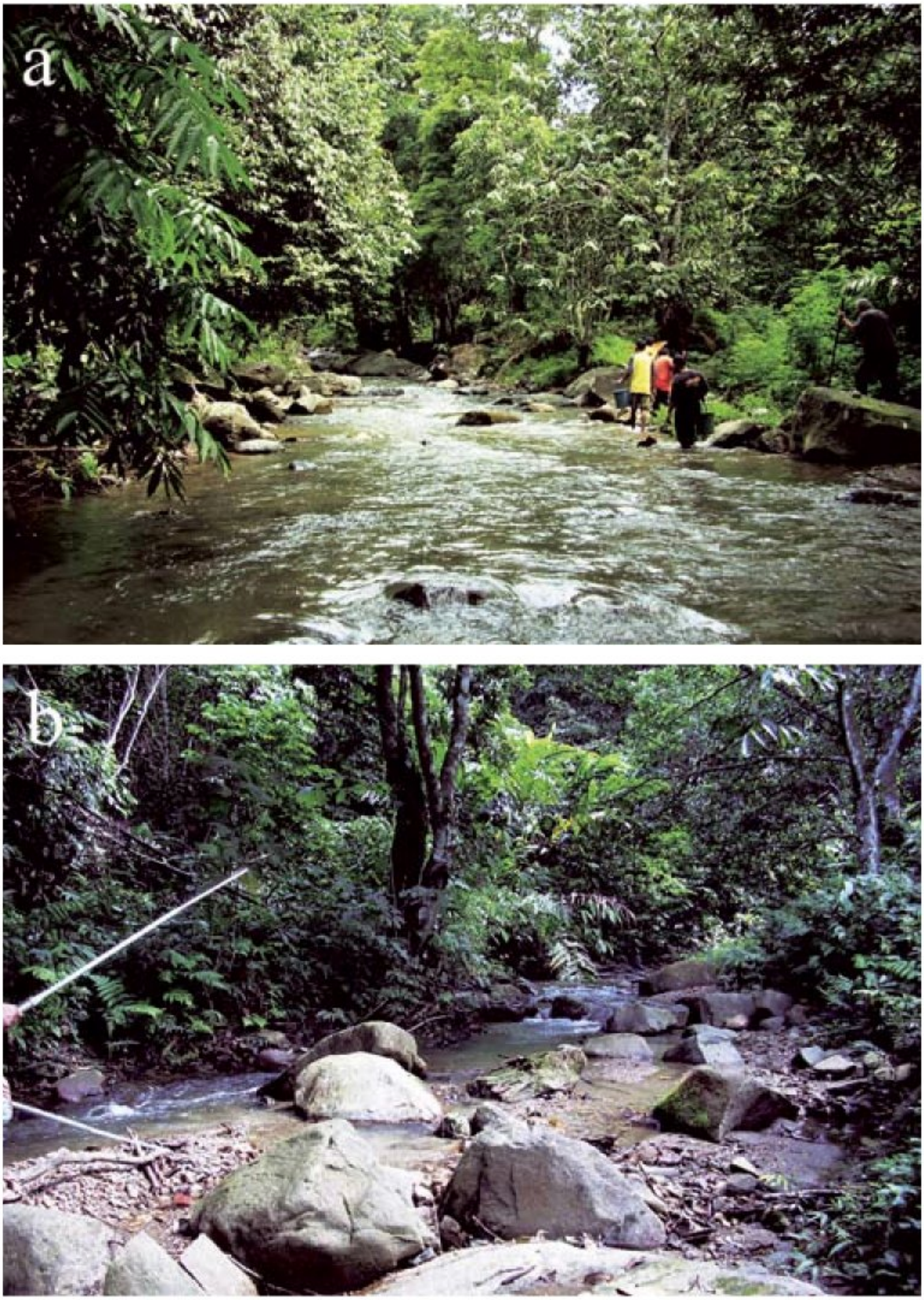

Figure 1. a, Upper Sungai Gombak less than one km upstream from the University of Malaya field station; b, Sungai Anak Gombak within the study area (photos by M. Z. Khaironizam, 14 December 2006).

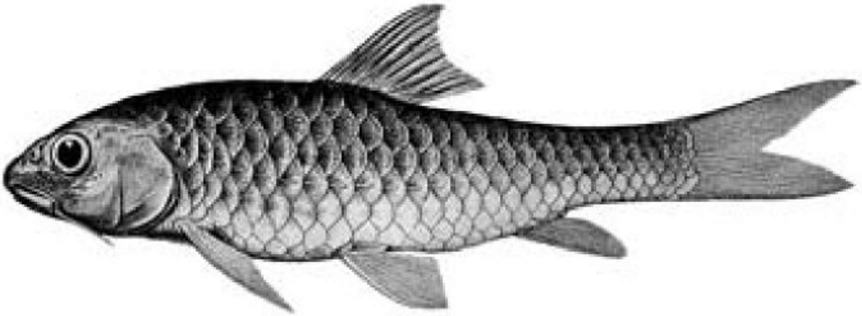

Figure 2. *Neolissochilus soroides* from the Pahang River (from DUNCKER, 1904).

Figure 3. Generalized, normal or *Neolissochilus*-like trophic morph of *Neolissochilus soroides* from Sungai Gombak, *Neolissochilus soroides soroides*, 88.8 mm? (ZRC 50996?) [standard length and catalog number to be confirmed].

Figure 4. *Lissochilus*- or *Acrossocheilus*-like trophic morph of *Neolissochilus soroides* from Sungai Gombak, 66.0 mm (ZRC 50987)

Figure 5. Extreme *Tor*-like trophic morph of *Neolissochilus soroides* from Sungai Gombak, 104 mm (ZRC 50988).

Figure 6. Intermediate *Tor*-like trophic morph of *Neolissochilus soroides* from Sungai Gombak, 68.2 mm (ZRC 50989)

reported in Asian Cyprinidae involves a species of *Poropuntius*, *P. bolovenensis*, living in isolated rocky upland streams on the Boloven Plateau in the Mekong basin of southern Laos (ROBERTS, 1998). There are no species of *Neolissochilus* or *Tor* where *P. bolovenensis* occurs.

POLYMORPHIC *NEOLISSOCHILUS* OF SUNGAI GOMBAK

Figures 3–6

Sungai Gombak near the University of Malaya Sungai Gombak Field Study Center apparently is inhabited by only a single species of cyprinid fish referable to *Neolissochilus* or *Tor*. It seems there is only this one species of *Neolissochilus* in the Kelang river basin and that no species of *Tor* (sensu RAINBOTH, 1985), as distinct from *Neolissochilus*) occurs there. We identify this species as *N. soroides* (DUNCKER 1904).

Apart from the variation in mouth parts, specimens from S. Gombak agree with Duncker's original description in most respects. The main exception is in counts of scales in the lateral line scale row, reported by Duncker as 26–29. Specimens from Sungai Gombak have 23–25 scales. Part of the difference apparently is due to Duncker including the last one or two scales posterior to the hypural fan. His figure of *N. soroides* clearly shows 25 scales to the end of the body. The actual difference, if real, involves only a scale or two, and seems insufficient to distinguish Sungai Gombak *Neolissochilus* nomenclaturally from Pahang *N. soroides*.

Given the confusion generally related to identification of *Neolissochilus* species in the Malay Pensinsula, as well as the complicating factor of their pronounced trophic polymorphism, our material has been checked carefully with the original description and figure of *N. soroides*, and also with a paratype in the ZRC collection. The characters exhibited by these specimens may be considered in the order of their appearance in the original description. All of our specimens have four long barbels. The rostral barbels extend posteriorly to a little beyond the anterior margin of the eye and the maxillary barbels almost to the posterior margin; the maxillary barbels are about 20% longer than the rostral. Barbel length is similar in the various trophic morphs. The dorsal fin has three or four simple and nine branched rays. The longest simple ray (the third or fourth) is thin but not flexible, with a smooth (non-serrated) posterior margin. The anal fin has eight or nine rays, three simple and five or six branched (last ray "divided to its base" counted as one). Lateral line scale row with 23–25 scales to base of caudal fin (Duncker's counts of 26–29 apparently include the last two or three scales on the caudal fin itself). Transverse scale rows anterior to dorsal fin origin 3½/5½, if the scales in both the dorsomedian and in the ventromedian scale rows are counted as one (Duncker's count is 3½/4½). Scale rows between lateral line and pelvic fin 2½. Predorsal scales 9, the anterior ones distinctly larger than the posterior ones (the last two scales with posterior margin deeply indented to accommodate dorsal fin origin). Dorsal fin origin distinctly anterior to a vertical line through anal fin origin. Upper lobe of caudal fin slightly shorter than lower, but lobes basically similar in shape (upper lobe more rounded according to Duncker). Many specimens, including some quite small, with well developed breeding tubercles on cheeks and sides of snout (variability in the extent and size of tubercles is comparable in the trophic morphs). Adult and subadult specimens have the upper body grey and the lower body white, not golden white; populations of *Neolissochilus* often differ in live coloration). Upper and lower caudal fin lobes with a dusky submarginal stripe; this feature is not mentioned by Duncker but is shown in his figure. The melanophores constituting the stripe are concentrated on the upper most and lowermost simple principal and first branched caudal fin rays (the melanophores do not extend onto the outermost edge of the simple rays, which are thus pale; thus the caudal lobe stripes are submarginal rather than marginal). Young up to about 35 mm have a small, round black spot at the middle of the caudal fin base.

Sungai Gombak *N. soroides* exhibit continuous variation in structures associated with feeding (i.e. continuous trophic polymorphism) but little variation in other characters. Thus, with the exception of the lips and mentum, and the difference in lateral line scale counts noted above, they all agree fairly closely with the original description and figure of *N. soroides*. Specimens with morphological differences in the lips and horny jaw sheaths, involving qualitative as well as quantifiable differences, may be conveniently grouped into three categories: "normal" or *Neolissochilus* morphotype; *Lissochilus* or *Acrossocheilus* morphotype; and *Tor* morphotype. These are characterized as follows:

Generalized, normal, or *Neolissochilus*-like trophic morphotype (Figure 3).—In this unspecialized trophic morphotype the upper and lower lips are relatively thin. The lower lip is free only laterally; near the middle it is joined closely to the lower jaw, so that its posterior margin cannot be lifted off the surface. Thus there is no development of a mentum. This corresponds to the description of the lips in the original description and figure of *N. soroides*, and for that reason is referred to here as the "generalized" morphotype. Considering a wide variety of tropical Asian barbin cyprinids, it is also morphologically the most generalized kind of mouth structure of those observed in Gombak *Neolissochilus*. In this morphotype the horny jaw sheaths are "normally" developed: they are present as always but are not notably thickened and the lower one does not have a trenchant cutting edge (such a cutting edge apparently is never developed on the upper horny jaw sheath). Duncker did not mention the condition of the horny jaw sheaths in the type specimens of *N. soroides* but it seems likely that all or most of them (including the specimen figured) were of this morphotype.

***Lissochilus*- or *Acrossocheilus*-like trophic morphotype (Figure 4).**—In this distinct morphotype, as in at least some species assigned to the genera *Lissochilus* and *Acrossocheilus*, the mouth tends to be broader than in the "normal" morphotype and the lips and horny jaw sheaths of both jaws slightly thicker. The horny jaw sheath of the lower jaw typically has a trenchant cutting edge projecting from its surface. When old, this thin sharp edge, often dark brown, is brittle and easily broken. It is periodically shed as a unit, to be replaced by a new sharp edge that is clear and not so brittle. Cyprinid species with such a trenchant cutting edge on the lower horny jaw sheath are often referred to as having "sectorial mouths." The same two kinds of relatively broad mouth with thickened lower horny jaw sheaths with deciduous trenchant cutting edges occurs in the somewhat smaller species *Neolissochilus hendersoni* in the western Malay Peninsula (Penang Island and Kedah province). The species originally described as *Lissochilus tweediei* (HERRE & MYERS, 1937: 61, type locality Malay Peninsula, Perak basin, Yum River; see photograph and radiograph of holotype posted on California Academy of Sciences website), with a trenchant cutting edge on the lower horny jaw sheath, closely resembles the Sungai Gombak *Lissochilus* morphotype and is here considered as conspecific with it. An 88-mm specimen from the Huay Yong, Prachuab Khiri Khan province, Thailand, illustrated by RAINBOTH (1985: 28, fig. 2) has a much shorter snout than the specimen illustrated by DUNCKER (1904). This, together with the ventral profile of the mouth, indicates that it also is similar to the *Lissochilus* morph of *N. soroides*.

***Tor*-like trophic morphotype (Figures 5–6).**—The middle of the lower lip has a variably developed median mental lobe or mentum. The lips tend to be thickened, the thickest generally in individuals with the mentum well developed. Many specimens have a poorly developed mentum. In these its posterior margin may be more or less tightly bound to the lower jaw, so that a needle passed along it will not cause it to rise from the surface. In other specimens, although the mentum is still very short, its posterior edge is clearly free from the lower jaw, so that a needle passes readily beneath it. The mental lobe in such specimens might be described as "incipient". This implies, however, that it is in the process of developing into a more substantial mentum. It could equally be that the structure is regressing, and then it would be more appropriate to refer to it as "rudimentary." We do not know of any criterion to determine whether a weakly developed mental lobe in a preserved specimen of *N. soroides* is incipient or regressing.

In many Sungai Gombak *Tor*-morphotype specimens of *N. soroides* the mentum is well developed. In such specimens it is generally thickened and free for most of its length from the lower jaw. Its length may be equal to one-third or one half of the lower jaw, or it may even exceed the lower jaw in length. In the most extreme specimen of *N. soroides Tor* morphotype from Gombak, the greatly thickened upper and lower lips and greatly enlarged mentum approach or equal the greatest development of the lips and mentum found in any species of the genus *Tor* (characterized mainly by possession of the mental lobe on the lower lip). As in the *Tor* specimens, the rostrum or fleshy fold overlying the upper jaw is more developed in this specimen than in any others from Sungai Gombak, but not so much as the extremely hypertrophied rostral fold present in exceptional large specimens of some *Tor* species. Also, as in *Tor* species with very long mental lobes, the mental lobe of this specimen is folded under itself anteriorly and on the sides, so that the mentum in ventral view appears to be about 90% of its actual size. In some *Tor* specimens the amount folded under (or actually over) the mentum is much greater, so that in ventral view it appears to be only about 50–70% of its actual size.

Meristic and Morphometric Characters of Sungai Gombak Trophic Morphs of *Neolissochilus soroides*

Evidence supportive of the conspecificity of the fish specimens reported here as trophic morphs of a single species is provided by counts and measurements of characters generally employed to distinguish cyprinid species (Table 1). Excluded from the table because they are identical or nearly identical for all of the specimens are the following counts of fin rays: dorsal fin simple rays (3 or 4); dorsal fin branched rays (8–9); anal fin simple rays (3); anal fin branched rays (5); pectoral fin rays (15–16); pelvic fin rays (8); and principal caudal fin rays (10/9). Excluded for the same reason are the various scale counts: scales in lateral series (23–25); predorsal scales (8–9); scales above lateral line (3½); scales below lateral line (2½); circumferential scales (16–18); circumpeduncular scales (12); scales along dorsal fin base (8–9); scales along anal fin base (5); scales from end of dorsal fin base to origin of caudal fin 12–14; scales from isthmus to pelvic fin origin 13–14; scales from end of pelvic fin to anal fin 5–; scales form end of anal fins to caudal fin 6–7.

Sexual Differentiation of the Sungai Gombak Trophic Morphs of *Neolissochilus soroides*

The question may be asked whether the trophic morphs described here are due to sexually related differences. Our overall experience with the fishes indicates that this is not the case. There are not two distinct morphs or morphic pathways, but three, so if there is a sexual relationship it cannot be a simple one, i.e. sexual dimorphism alone cannot account for it.

On 30 Jan 2007 a sample of 105 fresh *N. soroides* were collected from the Sungai Gombak just above University of Malaysia Field Center and their sex determined. All of the specimens were readily sexed. Males with testes were distinguished readily from females with ovaries all either with small clear eggs or with yolky eggs. The following data were obtained:

Neolissochilus-like morph: males 31, 76.0–133.3 mm; females 48, 77.4–166.4 mm;
Acrossocheilus or *Lissochilus*-like morph: males 17, 55.4–108.6 mm; females 6, 80.0–114.8 mm; and
Tor-type morph: males 2, 63.2–79.7 mm, females 1, 83.5 mm.

Of females with yolky eggs, there were 11, 104–166 mm in the *Neolissochilus*-type morph; 2, 98–115 mm in the *Acrossocheilus*- or *Lissochilus*-type morph; and none in the *Tor*-like morph. The smallest males of the three morphs with milky testes were 76.0, 55.4 and 63.2 mm, respectively.

The over-all sex ratio of the sample of 105 fish, 50:55, approaches the ideal fifty-fifty. Sex ratios within the morphs are more irregular. While the data on sexual differentiation and sex

Table 1. Mean, minimum and maximum of morphometric (in % of standard length) and meristic characters in trophic morphs of *Neolissochilus soroides* from upper Sungai Gombak. Methods of measurements and counts after HUBBS & LAGLER (1964).

Characteristic	*Normal* type N = 15		*Lissochilus* type N = 8		*Tor* type N=6	
	mean	min-max	mean	min-max	mean	min-max
Standard length	97.0	71.2–135.5	77.6	62.0–103.3	84.8	64.8–115.0
Body depth	30.6	27.5–34.2	31.7	27.6–35.2	30.0	26.7–33.4
Head length	30.0	28.0–32.3	30.2	28.3–32.2	31.1	29.6–32.7
Head width	21.5	19.1–23.0	18.4	16.2–21.8	18.1	13.9–20.7
Snout length	10.6	9.3–12.0	10.9	9.1–12.1	11.1	10.3–11.9
Eye length/diameter	6.9	5.6–8.4	7.6	7.0–8.7	6.5	5.8–7.3
Caudal-peduncle length	16.3	14.0–18.3	16.3	15.3–18.2	17.1	16.6–17.5
Caudal-peduncle depth	11.9	10.8–13.3	12.3	11.1–12.9	12.1	11.3–12.8
Dorsal fin base length	16.5	15.0–18.0	17.2	16.4–18.4	16.9	16.1–17.8
Dorsal fin depressed length	28.5	25.0–31.2	30.3	27.6–32.1	30.4	28.3–31.8
Dorsal fin high	24.5	21.4–27.8	25.5	23.6–28.3	26.1	21.9–36.0
Anal fin base length	8.2	7.4-9.7	8.4	7.5–9.3	7.6	7.1–7.9
Anal fin depressed length	20.4	12.3–24.0	21.3	20.3–22.1	22.1	21.0–23.2
Anal fin high	19.5	16.8–24.0	19.8	17.2–21.0	19.6	18.7–20.4
Pectoral fin length	23.8	20.7–26.1	24.3	22.5–25.8	25.1	21.9–26.4
Pelvic fin length	20.5	17.7–22.5	20.5	18.4–22.5	21.3	19.1–22.6
Pre-dorsal length	50.5	46.6–52.5	51.5	47.9–54.5	53.2	50.9–55.8
Post-dorsal length	53.8	49.9–58.8	54.1	50.2–57.4	54.1	52.9–55.6
Pre-pectoral length	30.4	26.8–33.7	29.6	27.3–33.0	29.2	28.1–31.2
Post-pectoral length	73.0	65.4–76.5	72.6	67.5–77.1	74.1	71.0–76.0
Pre-anal length	77.6	72.3–82.2	77.7	75.7–80.1	76.9	72.0–78.5
Post-anal length	24.0	22.1–26.6	24.3	22.0–26.0	23.8	22.0–25.4
Pre-pelvic length	55.4	519–65.3	53.7	49.7–56.6	54.3	53.0–55.6
Post-pelvic length	48.4	44.8–50.7	48.7	45.8–50.1	48.9	47.0–51.0
Lateral line scales	21.8	21–23	22.4	22–23	22.2	21–23
Scales beyond lateral line	2.7	2–3	2.8	2–3	3	3
Scales above lateral line	3.5	3.5	3.5	3.5	3.5	3.5
Scales below lateral line	2.5	2.5	2.5	2.5	2.5	2.5
Circumferential scales	17.4	16–18	17.6	16–18	17.7	16-18
Circumpeduncular scales	12	12	12.0	12	12	12
Predorsal scales	8.3	8–9	8.3	8–9	8.4	8-9
Scales from dorsal fin base to caudal fin	13.3	13–14	13.1	13–14	12.8	12–13
Scales at base of dorsal fin	8.1	8–9	8.3	8–9	8.2	8–9
Scales from isthmus to pelvic fin origin	13.3	13–14	13.3	13–14	13	13
Scales at base of anal fin	5	5	5	5	5	5
Scales from end of pelvic fin to anal fin	5.6	5–6	5.8	5–6	5.8	5–6
Scales form end of anal fins to caudal fin	6.5	6–7	6.6	6–7	6.8	6–7
Gill rakers on upper limb	4.3	4–5	4.5	4–5	4.2	4–5
Gill rakers on lower arm	10.7	10–11	10.5	10–11	10.3	10–11
Total gill rakers	16.1	15–17	16.1	15–17	15.5	15–17

ratio in the *Tor*-type morph is limited to only three small individuals with incipient mentums, male and female are present in all three morphs. Observations on larger samples are needed to determine whether there is any statistically significant deviation from 50:50 sex ratio within the morphs. Females apparently grow slightly larger than males.

Morphological Constancy of Morphs Maintained in Captivity

A set of four aquarium experiments was carried out from 9 January through 15 March 2007 to determine whether captivity can induce changes in the morphology of the trophic morphs of *N. soroides*. Live specimens of each of the three morphs with lengths ranging within 90 to 120 mm were placed in four glass aquarium tanks 40×60×40 cm with different substrate Conditions as follows:

(1) aquarium with clean glass bottom, 10 fish with *Neolissochilus*-like mouths (7 males 92.3–95.4 mm and 3 females 93.3–95.2 mm);

(2) aquarium with a sandy substrate, 8 fish with *Neolissochilus*-like mouths (4 males 91.5–101.2 mm and 4 females 98.6–121.4.0 mm);

(3) aquarium with a mixed stone and gravel substrate, 8 fish with *Lissochilus*-like mouths (4 males 89.6–107 mm and 4 females 96.3–111.5 mm); and

(4) aquarium with a mixed sand and mud substrate, 6 fish with *Tor*-like mouths (3 males 101–104.5 mm SL) + 3 females 99.5–105 mm).

It was intended to run the experiments for at least six months, but due to budgetary and other problems, it was terminated after only 66 days. All of the fish survived this period in captivity, and no change was observed in the structure of their mouth parts.

DISCUSSION

Trophic Polymorphism in *N. soroides* at other Localities

Neolissochilus soroides probably is monomorphic for trophic structures at many or even most localities. In such instances all individuals of this species usually have generalized or *Neolissochilus*-like morphology of the mouth parts. While they are many preserved samples comprising only one or a few specimens of one particular trophic morphotype, we do not have large samples from, nor do we know of populations of *N. soroides* composed uniquely of the *Lissochilus*-like or *Tor*-type morphologies. This is part of the strong circumstantial supporting evidence that the variation we are dealing with here is indeed intraspecific. This generalization, however, must be qualified by a caveat: nearly all populations of *N. soroides* are known from relatively small preserved samples. The instances of known trophic polymorphism is likely to increase when larger samples of individual populations are studied.

We have observed specimens of *N. soroides* with presumed trophic polymorphism with three varieties or morphs comparable to those in Sungai Gombak at only two additional localities: (1) Sungai Rengit, Pahang River basin in Pahang; and (2) Sungai Kenyir, Terengganu basin in Kwantan. At these localities the trophic morphs are essentially similar to those described at Sungai Gombak except that the extreme *Tor* morph with an exceptionally enlarged mentum is absent.

Species of *Neolissochilus* and *Tor* in the Malay Peninsula

A tentative assessment of the species of the genera *Neolissochilus* and *Tor* in the Malay peninsula may be helpful. This should not be regarded as definitive but we hope it is a step in the right direction. The following nominal taxa have been reported: *Neolissochilus soroides* (DUNCKER 1904); *N. hendersoni*; *Tor soro*; *Tor tambra*; *Tor tambroides*; *T. douronensis*; *Lissochilus* or *Acrossocheilus tweediei*; *Lissochilus* or *Neolissochilus sumatranus*; and *Acrossocheilus hexagonolepis* (McClelland). It has not been possible for us to examine the specimens that provided the basis for all of these reports. In some instances they were not reported, or were reported but not preserved, and in other instances specimens were preserved but they are no longer extant or are unavailable for examination.

Neolissochilus (formerly in *Barbus*) *hexagonolepis* has been reported by various authors from Malaysia. No evidence was found for the presence of this species in Malaysia by ZAKARIA-ISMAIL (1987) and we concur. The type locality of *Neolissochilus* (formerly *Barbus*) *hexagonolepis* McClelland 1839 is upper Assam in India, i.e. in the Ganges basin. Specimens collected and identified as this species from Chitawan Valley in Nepal (Ganges basin) by the first author in 1975, CAS 50201, 10: 41.6–115 mm, were studied by ZAKARIA-ISMAIL (1989: 100; 102). He concluded that the species probably does not occur in peninsular Malaysia, and that records of the species from there were probably based on other cyprinids such as *Tor*. He also examined type specimens of *Lissochilus tweediei* in the CAS and USNM fish collections and "did not find any evidence to suggest that it is different from *N. soroides*" (op cit.: 103, table 20).

It appears that *Tor*, in the sense of RAINBOTH (1985) (excluding *Neolissochilus*) is perhaps represented by only a single species in the Malay Peninsula: *Tor tambra* (Valenciennes in CUVIER & VALENCIENNES, 1842). This conclusion is tentative mainly because there are so few samples of preserved specimens available for examination. It is based in part on the results of the study of the material of the genus *Tor* collected by Kuhl and van Hasselt in Java in 1820–23 (ROBERTS, 1993: 22–23, 65–66, figs 21–24). This material includes the primary type specimens of two of the four nominal species of *Tor* reported from the Malay Peninsula: *T. tambra* and *T. douronensis*. There is also a drawing of one of the original specimens of *T. soro* (the holotype of which is lost). The fourth species, *Tor tambroides* (BLEEKER 1854), supposedly differs from *T. tambra* in having a longer mental lobe. Apart from the differences in presence or absence and length of the mental lobe, it seems that Java has only a single species of *Tor*, the earliest name for which is *T. tambra*. The same species occurs in Sumatra and in Borneo. *Tor tambra* from Java and Borneo include specimens with the mental lobe virtually absent, or present and ranging from extremely short to much longer than the lower jaw. Specimens from the Malay Peninsula, and the relatively few specimens examined by us from Sumatra are similar but do not exhibit mental lobes as long as those present in some specimens from Java and Borneo (this could well be the result of inadequate sampling). Apart from thickness of the lips and relative development of the mental lobe, populations of *T. tambra* vary considerably in size at sexual maturity and in coloration in life. Meristic characters including counts of gill rakers, scales, fin rays, and vertebrae are remarkably constant.

The proliferation of nominal species of *Tor* from Indonesia (and therefore recognized by various later authors writing about these fish in Malaysia) is due primarily to the work of Achille Valenciennes (in CUVIER & VALENCIENNES, 1842), who described *T. tambra*, *T. soro*, and *T. douronensis*, and of Pieter Bleeker (BLEEKER, 1854; 1863), who recognizd all of Valenciennes's species and added one more of his own, *T. tambroides*. Both of these ichthyologists were working with small samples that individually presented little variation in development of the lips and especially the mentum, the main character that led them to recognize so many species (see particularly Bleeker's account including figures (BLEEKER, 1863: pl. 121, fig 2 of *Labeobarbus soro*; pl. 122, fig. 2 of *Labeobarbus douroensis*; pl. 123, fig. 2 of *Labeobarbus. tambra*; and pl. 124 of *Labeobarbus tambroides*). These represent, in the order presented by Bleeker, specimens in which the lips are gradually thicker and in which the mental lobe is not developed at all; is just beginning to develop; is moderately developed; or is strongly developed.

Tor tambra, *Neolissochilus soroides*, and *N. hendersoni* are readily distinguished. The differences between *N. soroides* and *N. hendersoni* have been considered above.

Neolissochilus has small numbers of relatively large tubercles on the cheek at quite small sizes; *Tor tambra* of very large size (and in spawning condition?) sometimes have the cheek covered with numerous small tubercles but the small specimens are non-tuberculate. *Neolissochilus* generally have submarginal dark stripes on the upper and lower caudal fin lobes; these are absent in *Tor.*

Neolissochilus hendersoni (Herre 1940)

Neolissochilus hendersoni is superficially similar to *N. soroides* and appears to be closely related to it. *N. hendersoni* supposedly differs primarily from *N. soroides* in being monomorphic for the *Lissochilus* of *Acrossocheilus* type trophic morphology and in attaining a much smaller maximum adult size. It also differs in having fewer scales in the lateral line scale row (21–22 instead of 23–25); fewer predorsal scales (7–8 instead of 8–10); and fewer gill rakers on the first gill arch (12–14 versus 14–16) according to ZAKARIA-ISMAIL (1989: 99–103).

Most samples of this species examined by us are relatively monomorphic with regard to trophic structures. The lips are moderately developed, with no indication of a mentum. The mouth is moderately broad and the horny jaw sheath well developed. In some specimens the horny jaw sheath is smooth, in other it has a definite cutting edge. In the early stage of its development this cutting edge is translucent and soft. In the later stage it becomes brittle and dark brown. The cutting edge may be shed as a unit, immediately after which the horny jaw sheath has no cutting edge. The same occurs in the *Lissochilus*-type trophic morph of *N. soroides*. Given the reduced number of predorsal and lateral line scale counts, we expected a priori that *N. hendersoni* might have fewer vertebrae than *N. soroides* and this turns out to be so. Radiographs of two large samples of *N. hendersoni* from Penang Island (the type locality) totaling 26 specimens reveal total vertebral counts ranging from 38 to 40, with the following frequency: 38(7), 39(17), 40(2) or an average of 38.8 (the holotype of *N. hendersoni*, CAS (SU) 32632, has 25+15=40 vertebra). Long thought to be endemic to Penang Island, the species also occurs in the Langkawi islands in the Straits of Malacca (AMIRUDDIN & LIM, 2006: 109).

Neolissochilus hendersoni is a relatively small species in comparison to *N. soroides*. The largest size attained by *N. hendersoni* is about equal to largest size attained by the *Lissochilus* morph of *N. soroides*, which does not get nearly so large as the "normal" morph of *N. soroides*.

ZRC 29611-29615, 5: 30.1–44.1 mm from Langkawi Island, Kedah, has only 19–20 scales in the lateral series: 19(1), 20(4). The four smallest specimens 30.1–37.1 mm have the "normal" or "*Neolissochilus*" morphology of the lips and horny jaw sheaths, i.e., without signs of any cutting edge on the lower horny jaw sheath, but the largest (44.1 mm) specimen has a clear but well developed cutting edge. The specimens all have a highly visible large round midpeduncular spot [sample not yet radiographed so vertebral counts not available].

ZRC 49147, 10: 85.1–127 mm, Penang, Balik Palau, June 1999. This sample is monomorphic for trophic structures. None of the specimens has an obvious sharp cutting edge on horny sheath of lower jaw. They can be considered as representing the "normal" or ordinary *Neolissochilus* morph. Sales in lateral series 19(2), 20(1), 21(2), 22(3), 23(2). Total vertebrae 38(2), 39(6), 40(2). Abdominal+postabdominal vertebrae 24+14=38(2), 24+15=39(6), 25+15=40(1), and 26+14(1).

N. hendersoni: ZRC 1596, 16: 60.6–94.2 mm, Penang, Batu Feringgi, 18 Oct 1961, Eric Alfred. Except for the absence of "extreme" *Tor* morphotype, this sample shows the full range of trophic polymorphism comparable to that of *N. soroides* from the upper Sungai Gombak.

The "normal" or "*Neolissochilus*" morph is represented by 9 specimens 60.6–87.0 mm (some of these might belong with "incipient *Tor*" group (below). The "*Lissochilus*" morph with an obvious sharp dark brown cutting edge on horny jaw sheath and relatively broad mouth is represented by 3: 61.4–66.5 mm. The "*Tor*" morph, with incipient mentum is represented by 3: 74.8–89.2 mm and with well-developed mentum: by a 93.3 mm specimen with a short but thick mentum 3.8 mm wide and sides free from lower lip 2.1 mm long. This sample has scales in lateral series 19(1), 20(2), 21(3), 22(5), 23(2), too damaged to count accurately (1); total vertebrae 38(5), 39(11); and abdominal + postabdominal vertebrae 23+15=38(2), 24+14=38(3), 23+16=39(1) and 24+15=39(10)

Neolissochilus sumatranus (Weber & de Beaufort 1916)

Neolissochilus (originally *Lissochilus*) *sumatranus* (WEBER & DE BEAUFORT 1916:169, figs. 68–69) was described from Bandar Baru, Sumatra. The species is regarded as endemic to Sumatra; the lectotype and six paralectotypes are in the Zoological Museum of Amsterdam (W. N. ESCHMEYER, "Online Catalog of Fishes").

The fish collection of the Zoological reference Collection of the National University of Singapore has four fine specimens identified as *N. sumatranus* from

W. Sumatra, from "a hill stream ca 10 km before Sinicin town after passing Padangpanjang", 19 July 1997, H. H. Tan (ZRC 41952, 4: 145–164 mm). These specimens are superficially similar to *N. soroides* from the Malay Peninsula. The lower lip has a weakly developed (incipient or regressing?) mental lobe in all four specimens. The middle of the lobe is attached to the lower jaw but the sides of the lobe are free from it. Scales in lateral series 22–25; gill rakers on first gill arch 3–5+10–15=14–18 (gills damaged, making accurate counting difficult); one of the specimens has a normally developed vertebral column with 24+15=39 vertebrae (the other 3 specimens have grossly abnormal vertebral columns with multiple centric fusions or abnormally formed centra involving at least a half dozen vertebrae in each of them). We tentatively conclude that *N. sumatranus* is a junior synonym of *N. soroides*. It is unknown whether any of its Sumatran populations exhibits trophic polymorphism to the same extent as populations in the Malay Peninsula. The few Sumatran samples examined by us appear to be monomorphic for trophic structures, all of them of the *Tor* type morphology with incipient or small mental lobes.

Northern and Southern *Tor tambra*

Southern *T. tambra*, or those at least those in the Malay Peninsula and Borneo, exhibit continuous intraspecific trophic polymorphism in regard to the degree of development of the mentum. This polymorphism is comparable to that of the mental lobe in *N. soroides*. The main difference is that specimens with extreme development of the mentum are far commoner. So far as known *T. tambra*, like all of the species of *Tambra* sensu RAINBOTH (1985), never develops a horny cutting edge on the lower jaw. Malaysian *T. tambra* populations are of two kinds with regard to polymorphism of the mentum: (1) monomorphic at a given location, but with different degrees of development of the mentum in different locations; and (2) polymorphic at a given location, with mental lobe development varying continuously from barely discernible to very thick, long, and folded over at the tip and sides. The first kind of population is most frequently encountered. Populations have been examined from different locations in which the mentum is barely discernible; relatively small; intermediate in size; or uniformly relatively large and thick.

The second kind of variable population is less frequently encountered. A particularly striking example is ZRC 37713, 3: 103, 127 and 137 mm, from Lanjak Entimau Wildlife Sanctuary, Sarawak, 17–23 May 1994, coll. C. H. Diong. The mentum is present in all three specimens and cannot be described as incipient or weakly developed. In the 103-mm specimen, however, it is small, only 2.5 mm wide with free lateral margins of 1.3 mm, and flattened. In the 127-mm specimen it is somewhat wider and longer, 3.7×2.7 mm, and much thicker. The 137-mm has a spectacular mentum of 3.9×9.0 mm (extending posteriorly well beyond the end of the jaws). The lips as well as the mentum are very thick, and the upper lip is swollen dorsomedially and projects backwards to the rostrum. The sides of the mentum are folded over it and therefore are out of sight when the specimen is viewed from below. Were these folds to be expanded laterally to their full extent (it is difficult to do this with the preserved specimen without damaging the mentum) its total width equal or exceed 8 mm. In proportion to its size this specimen has by far the largest mental lobe observed by us in *T. tambra*. Gill rakers in the three specimens are 4+1+10=15, 4+0+13=17, and 4+1+11=16, respectively; scales in lateral series (many missing) about 21–23. Apart from the differences in the lips and mentum the three specimens are very similar. Samples such as this strongly support the hypothesis that the various nominal species of *Tor* distinguished primarily by the shape and size of the mentum and supposed by various authors to occur on the island of Borneo represent only a single species (ROBERTS, 1993; 1999). The nominal species with nomenclatural priority is *T. tambra* (Valenciennes in CUVIER & VALENCIENNES, 1842).

The situation in what may be conveniently called northern *T. tambra* stands in sharp contrast to that of the southern *T. tambra*. By northern *T. tambra* we refer mainly to the populations in the Mekong basin. This is because the *Tor* there are relatively well known, whereas northern *T. tambra* from the Chao Phraya and other basins are poorly known and apparently are now gone from much of their former range. Mekong basin *T. tambra* appear to represent a monomorphic species with regard to the trophic structures under discussion. The lips are moderately thickened and the mental lobe in all fish is developed to approximately the same extent. It is moderately short, as described by Valenciennes and by Bleeker for *T. tambra*. The other trophic morphs present in southern *T. tambra* are represented by *Tor* in the Mekong basin: *T. tambra* (with short mentum), *T. sinensis* (with very elongate mentum), and *Tor* sp (with very short mentum). Thus southern *T. tambra* with a constantly elongate mentum (Bleeker's concept of *T. tambroides*) is represented by the species *T. sinensis* Wu 1940. *Tor lateristriatus* Zhou and Cui 1996 has been identified as a junior synonym of *T. sinensis* (ROBERTS, 1999: 229–230). This nominal species was based upon a large specimens with adult coloration including a bold longitudinal stripe not present in juveniles and also not present in any of the southern *Tor*. Bleeker's name *T. tambroides* cannot be applied to this Mekong species, because *T. tambroides*, described from Java, represents a subspecies of *T. tambra*. *Tor sinensis*, as presently recognized, is known only from the Mekong basin. There is little doubt that it is a distinct species from Mekong *T. tambra*. The two occur sympatrically in many places including the Nam Theun and its large montane tributaries in central Laos and are always distinguishable, as juveniles and as adults, by relatively constant and marked differences in coloration (ZHOU & CUI, 1996; ROBERTS, 1998: 226–231, figs. 1–2). Notably absent are intergrades between the two species.

Malay Vernacular Names for *Neolissochilus* and *Tor*

The most important source for information about Malay names for the species of *Tor*- and *Tor*-like fishes including *Neolissochilus* and many other Malayan fishes is the "Journal of the Malayan Angling Association" issued during the period 1950–1958 (eventually issued as a single volume: VINNELL, 1962). The Malayan vernacular name of the fish referred to in the present article as *Tor tambra* is invariably "ikan kelah" (popularly known as "the Malayan mahseer", after the great Indian game fish or mahseer *Tor putitora*). Unlike Western ichthyologists, it seems the Malays knew they were dealing with a single variable and widespread species: they were not confused by differences in development of the mental lobe or in coloration. In the case of *Neolissochilus* the local name usually given is "ikan tengas". Sometimes this species is referred to as "ikan kejor". The former name was used for *N. soroides* generally, including the *Tor*-like morphotype; the latter name apparently was particularly used for the *Lissochilus* or *Acrossocheilus*-like morph. These identifications can be applied with a fair degree of confidence due to the numerous excellent photographs of large fish of both species in the pages of the journal as well as other information in the articles. Photographs of ikan kelah or *T. tambra* occur on pp. 7, 11, 103, 423, and 444; of ikan tengas or *N. soroides* on pp. 8, 12, and 443. Some of the fish caught by the members of the Malayan Angling Associations were deposited in the old Raffles Museum and are now in the Zoological Reference Collection of the Raffles Museum for Biodiversity research at the National University of Singapore.

In addition to the vernacular names of *T. tambra* and *N. soroides*, the Journal of the Malayan Anglers Association contains a great deal of information about geographical distribution, habitat, and maximum size. Tengas and kejor are repeatedly reported as occurring together. Along with the much smaller cyprinid "ikan daun" [=*Poropuntius smedleyi*] they are the only fish species in the Malay peninsula found above an altitude of 13,000 feet (TWEEDIE, 1954; reprinted in VINNELL 1962: 129).

Maximum Size and Size at Sexual Maturity

Information about maximum size attained by *Neolissochilus soroides* (ikan tengas) and *Tor tambra* (ikan kelas) in the Malay Peninsula is to be found in VINNELL (1962). Consummate anglers such as Charles S. Ogilvie, H. J. Kitchener, H. E. Ruddock, Arthur Locke, and W. D.

Tighe-Woode, in search of fishing paradise, reached ever more remote and unspoiled rivers in the Cameron Highlands and elsewhere in peninsular Malaysia. The largest kelah or *T. tambra* taken on rod and line was 8 lbs. 2 oz. and the largest *tengas* or *N. soroides* 6 lbs. 0 oz. (VINNELL, 1962: 430). Both of these record-sized fish were caught by Tighe-Woode. The kelah was caught in the upper Sungai Trengganu on a fishing trip with Locke in June 1956 (op cit: 442–444, photograph on p. 444). Both species attain larger sizes. A tengas of 7¾ lbs. is reported by KITCHENER (1955: 305). Weights of up to 10 kg or more are to be expected for species of *Neolissochilus* (RAINBOTH, 1985: 26) and much more for some species of *Tor*. A kelah or *T. tambra* caught in the Perak River in 1938 weighed 30 katis, i.e. 40 lbs. or 18 kg (OGILVIE, 1953: 10).

In most instances it is not possible to know to which of the *N. soroides* trophic morphs or subspecies the various tengas reported by the Malayan Angling Association belong. Charles Ogilvie reported a 4-lb. "ikan tengas/kejor" as *Barbus* (*Lissochilus*) *hexagonolepsis* [sic] (OGILVIE, 1953; reprinted in VINNELL, 1962: 7–13, photographs on pp. 8, 12). This specimen apparently was not preserved. As mentioned in Ogilvie's account, the photograph of the head shows a relatively small number of relatively large tubercles on the cheek, the condition characteristic of *N. soroides*. He also mentions "a horny plate on the dorsal surface of the lower lip [i.e. on the horny jaw sheath of the lower lip?]". In this instance the specimen presumably is of the *Lissochilus* trophic morph, i.e. the subspecies *N. soroides tweediei*.

As with other riverine fishes, *N. soroides* and *T. tambra* attain their largest sizes only in the largest rivers; they are most likely to occur in large rivers with deep rock-filled pools. The Sungai Gombak is a relatively small river, without deep pools, and it is safe to say that a tengas of 6 lbs. would not be found there. The largest *N. soroides* known from the Gombak are considerably smaller. It may be noted that *N. soroides* and *T. tambra* in most Malayan rivers are quite small. The large fish generally do not occur at elevations above 800 ft. or about 250 m. The elevation at Sungai Gombak, a typical *N. soroides* stream, is 290 m (BISHOP, 1973). The largest *N. soroides* ever found in the Sungai Gombak, UMKL 5428, was collected by Mohamed Zakaria-Ismail electrofishing just above the field station on 11 February 1993. It is 272 mm in standard length and weighed perhaps 2.5 kg. It is the "normal" type trophic morph. Apparently the *Lissochilus* morphotype of *N. soroides* does not attain as large a size as the normal type. Perhaps the rarer and far less often collected *Tor* morphotype also grows much larger than the *Lissochilus*

Thinking at the time that all species of *Tor* attained sizes of at least several kg, some years ago the first author was surprised to collect ripe males of *Tor* in Sumatra that were only 100–200 mm. This led to the supposition that there might be closely related species of *Tor* differing substantially in size at sexual maturity and in maximum size as adults. We have been unable, however, to make any observations that support such an hypothesis. Rather it seems that in populations of *Neolissochilus* and *Tor* generally, the males become sexually active at very small sizes. Thus in the Sungai Gombak in December 2006 we observed ripe running males of *N. soroides* as small as 60 mm. The ability for males (and females) to ripen early and at small sizes in small streams evidently is a useful adaptation.

The largest *N. soroides* attain at least 3 kg and perhaps much more but there are no preserved specimens of such large fish. The largest preserved specimen of *N. soroides*, from the Pahang basin, is 360 mm and weighs about 1.3 kg (ZRC 9255). It is of the "normal" morphotype: the lips are relatively thin and there is no mentum or any indication of one. The largest known specimen of "extreme" *Tor* morph, with a very long mentum, is only 104 mm.

Food Habits

The presence of trophic polymorphism in *N. soroides* implies corresponding differences in food selection and feeding habits (Table 2). Unaware of the trophic polymorphism, BISHOP (1973) reported that *N. soroides* in Sungai Gombak is omnivorous. Given the variety of trophic morphs in this species, it might be expected that collective food habits might indeed be omnivorous. This, however, is far from so.

Relatively undisturbed small streams in tropical evergreen rain forest such as Sungai Gombak have a single overwhelmingly important source food at the base of the food chains: leaves fallen from trees. The great biomass of leaves generally has to be broken up before it can enter the food chain, but there are also some stream specialists, especially among the insects, that feed directly upon the leaves. Apparently none of the fishes in Sungai Gombak are specialized leaf-eaters. Leaf particles are not part of the gut contents of *N. soroides*. This alone disqualifies them as truly omnivorous.

Various prawns, crabs and hard-shelled mollusks inhabit the upper Sungai Gombak (BISHOP, 1973) but, with the exception of prawns, *N. soroides* rarely if ever feeds on them. Also notably lacking from their gut contents are fishes. So far as we are aware, neither *N. soroides* nor *T. tambra* is piscivorous. This applies not only to the population of *N. soroides* attaining relatively small size as adults in Sungai Gombak, but also to much larger fish in larger rivers elsewhere in Malaysia. Members of the Anglers Society of Malaya fishing for large ikan tengas and ikan kelah baited their hooks with rice balls, insects, and earthworms (VINELL, 1962), not with fish. Charles Ogilvie mentions mole cricket, small river prawn, red centipede and the fruit "buah meris" [*Dysoxylon angustifolium*] as bait for tengas (*N. soroides*) and tapioca root, buah meris, ripe red figs known as "buah ara" [*Ficus variegata*], and small river prawn for kelah (*T. tambra*) (OGILVIE, 1953: 10, 13). *Hampala macrolepidota*, on the other hand, is specifically mentioned by Ogilvie as a fish-eater (VINELL, 1962: 85). Large tengas and kelah are particularly partial to forest fruits and their seeds. In additional to buah meris and buah ara, these include buah pendir plandok, *Aglaia saicifolia*, and buah kerayong, *Parkia javanica* (KITCHENER, 1955: 303–204). Of these plant species favored as food by ikan tengas, buah meris, red figs or buah ara, and buah kerayong are present on the banks of the Sungai Gombak.

It is generally believed that large barbin cyprinids having "sectorial" mouths (with trenchant cutting edge on the lower jaw mouths) feed on algae and aufwuchs, while those with thickened rubber-lips are adapted to grubbing between rocks and gravel and feeding mainly upon insects (e.g. SKELTON *ET AL.*, 1991: 224). Preliminary observations on gut contents of sympatric Sungai Gombak trophic morphs of *N. soroides* indicate that those with *Lissochilus* type mouths tend to feed on finely particulate plant detritus (aufwuchs?) and those with *Tor* type mouths on aquatic insects.

Preliminary data on food items present in the guts of a limited number of specimens representing the three trophic morphs of *N. soroides* present in the upper Sungai Gombak are presented in Table 2. Perhaps the most striking result is that the predominant food items in normal and *Tor* morphs are animals, while in the *Lissochilus* morph (the one with the trenchant cutting edge on the lower horny jaw sheath) the predominant items are plants. All of the morphs include substantial quantities of animals and plants in their diet. In the "normal" and *Tor* morphs the relative proportion of animal and plant food volumes is virtually identical, 58.1 and 56.7% versus 35.6 and 38.1%, while in the *Lissochilus* morph the figures are reversed,

Table 2. Gut contents of *Neolissochilus soroides* trophic morphs from Gombak River. Percentage of total volume according to methodology of HYNES (1950) and HELLAWELL & ABEL (1971).

Normal morph 5: 95.2–108.8 mm gut length: 93.3–121.7 mm (= 97.9–111.9 %SL)	*Lissochilus* morph 5: 70.2–88.9 mm SL gut length: 67.7–90.2 mm (= 96.4–101.5 %SL)	*Tor* morph 5: 64.8–91.8 mm gut length: 68.2–100.7 mm (105.2–110.1%SL)
Animal Insecta Ephemeroptera Trichoptera Diptera Crustacea Cladocera Copepoda 58.1%	Animal Insecta Ephemeroptera Trichoptera Diptera Crustacea Cladocera Copepoda Malacostraca 37.6%	Animal Insecta Ephemeroptera Trichoptera Diptera Odonata Hemiptera Crustacea prawns Cladocera Copepoda 56.7%
Plant unidentified plant material Bacillariophyceae Chlorophyta 35.6%	Plant unidentified plant material Bacillariophyceae Chlorophyta Cynophyta 52.7%	Plant unidentified plant material Bacillariophyceae Chlorophyta 38.1%
Other small lateritic particles detritus unidentified material 6.3%	Other small lateritic particles detritus unidentified material 8.7%	Other small lateritic particles detritus unidentified material 5.2%

37.6% versus 52.7%. It seems likely that the way in which the food items are obtained is equally or more important than their composition but this aspect has yet to be studied and will require careful and prolonged observation under favorable circumstances.

CONCLUSION

Is *Neolissochilus* Generically Distinct from *Tor*?

We are uncertain whether *Neolissochilus* should be retained as a separate genus representing a monophyletic group of species distinguishable from *Tor*. The kind of trophic polymorphism reported here for *N. soroides* including a *Tor* morphotype has not been found or reported in any other species of *Neolissochilus* except the closely related *N. hendersoni*. At least some populations of some other species of *Neolissochilus* apparently are relatively monomorphic with regard to trophic structures. Of particular relevance here is *N. stracheyi* (DAY, 1871), selected by Rainboth as type species of *Neolissochilus*. No information about variation of trophic structures is available for this taxon. It would be a relatively simple matter to transfer *N. soroides* and *N. hendersoni* from *Neolissochilus* to the genus *Tor*. We also refrained from this step because these species evidently are closely related to supposedly monomorphic species of *Neolissochilus* that do not (at least so far as known) have a *Tor* morphotype. In retaining *Neolissochilus* for the present despite the difficulty in providing a generic diagnosis to distinguish it from *Tor*, we essentially agree that it represents "a distinct species assemblage" as maintained by RAINBOTH (1985: 25).

The discovery that the Near Eastern species *Tor grypus*, endemic to the Euphrates-Tigris basin, exhibits infraspecific trophic polymorphism with three morphs corresponding closely to those observed in *N. soroides* and *N. hendersoni* (see below) also suggests that *Neolissochilus* can no longer be maintained as a separate genus.

Trophic Polymorphism in other Barbinae

Trophic polymorphism similar to that reported here in *N. soroides* occurs in barbin cyprinids from much of Asia, the Arabian Peninsula, and Africa. It is an important part of what might be called the "ancient bag of cyprinid evolutionary tricks." It accounts in part for the dominance of barbin cyprinids wherever they occur, for the extraordinary adaptive radiation they exhibit, and for their ability to evolve new genera and species relatively rapidly. The most spectacular displays of intraspecific trophic polymorphism occur in places where cyprinid species occur in habitats with relatively depauperate fish faunas, including isolated lakes with internal drainages and mountain streams. In some instances such habitats may be physically isolated from a richer fish fauna by a physiographical barrier, typically a waterfall or series of waterfalls. It would require a lengthy paper to review all of the known or probable instances of trophic polymorphism in Old World Cyprinidae comparable to that reported here in *N. soroides* and *N. hendersoni*. The present discussion is limited to four examples, one in the genus *Poropuntius* in the Mekong basin, two in the genus *Barbus* (=*Tor*?) in Africa, and *Barbus* or *Tor grypus* in the Near East. These examples will be treated here only briefly. The main point is that they are not isolated and rare examples but representative of a widespread phenomenon in barbin Cyprinidae wherever they occur (the group in limited to the Old World).

Two African examples are particularly relevant to the present discussion. The first example was mentioned by RAINBOTH (1985: 33) in his account of *Neolissochilus* in the following terms:

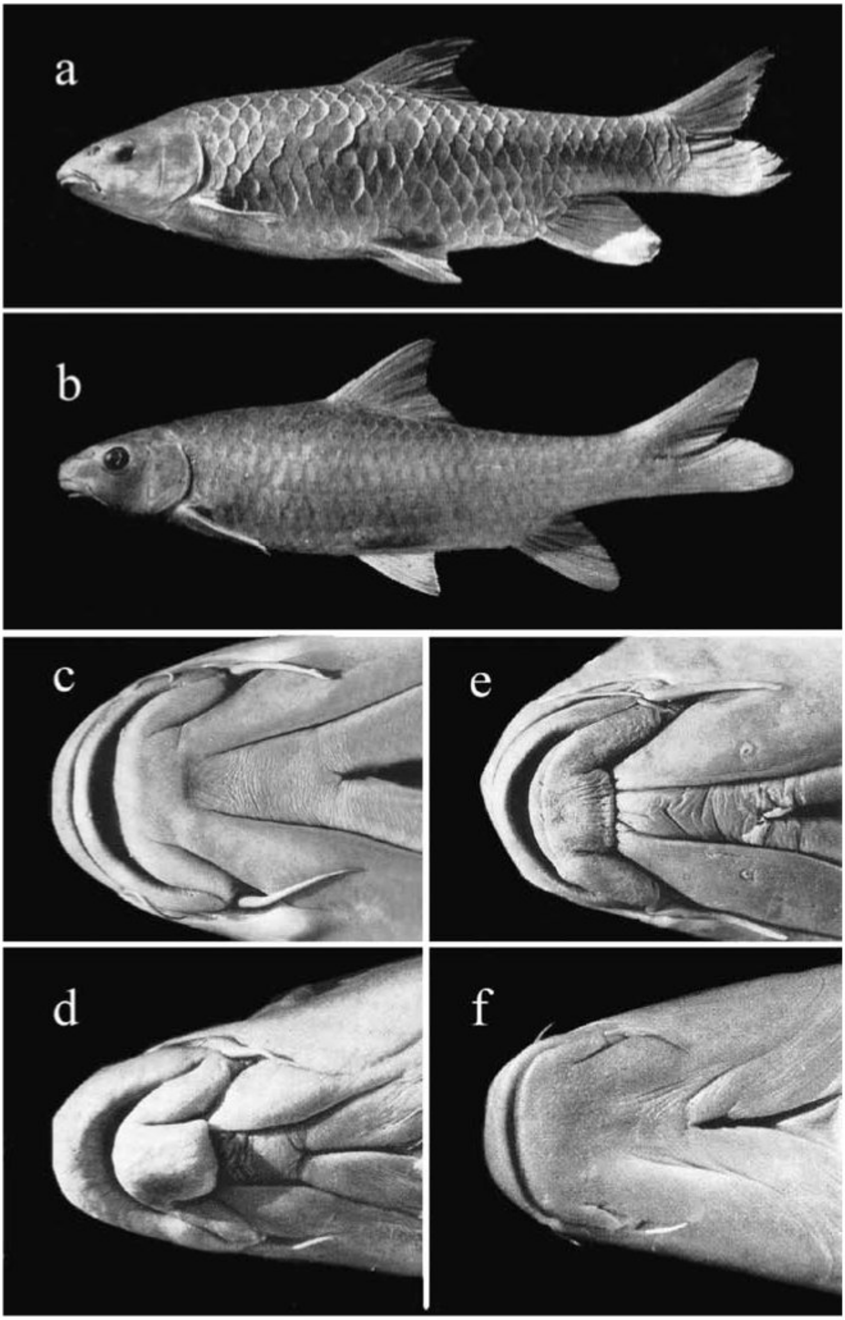

Figure 7. Probable intraspecific trophic morphs in *Labeobarbus* (formerly Barbus) brucii from Transvaal, South Africa (from GROENEWALD, 1958): a, *"Barbus brucii"*; b, *"Varicorhinus brucii"*; c, comparable to generalized *Neolissochilus* morph; d, comparable to weakly developed *Tor* morph; comparable to strongly developed *Tor* morph; e, *Varicorhinus*-like morph, with broad mouth, hypertrophied lower horny jaw sheath, and no lower lip.

> Another likely problem with our understanding of both *Tor* and *Neolissochilus* is the degree of ecophenotypic variability within species and populations. This variability could be similar to that described for the Lake Nyasa barbels (BANISTER & CLARKE, 1980), although the African situation appears extreme in comparison to all present indications from southern and southeastern Asia.

The finding of pronounced trophic polymorphism in *N. soroides* populations from Sungai Gombak and elsewhere, and of similar polymorphism in the closely related species *N. hendersoni*, as well as the polymorphism recently reported in *P. bolovenensis*, are indications that Southeast Asian barbels are subject to more ecophenotypic variation than Rainboth realized. Polymorphism in these Asian barbs is fully comparable to that previously reported in African barbs.

***Barbus* or *Tor brucei* (Fig. 7).**—A second example of trophic polymorphism in African barbs is reported in an important paper that has been overlooked (GROENEWALD, 1958) (Fig. 8). This concerns the South African species *Barbus brucii* Boulenger (1907:309, Pl. 18, fig. 1, type locality Groot Olifant R., Transvaal). Described on the basis of the "normal" or "thin-lipped morph", with neither a sharp lower cutting age or a mentum (*B. brucii* forma *typica*), this species also has a morph with a sharp-lower cutting edge (*B. brucii* forma *sector*); and a "thick-lipped" or "rubber-lipped" morph (*B. brucii* forma *gunningi*). The latter morph is provided with a *Tor*-like mentum on the lower jaw. These three morphs correspond closely to the generalized or normal, *Lissochilus* or *Acrossocheilus*, and *Tor*-type morphs of *N. soroides*. Apart from the pronounced morphological differences in feeding structures the three morphs of *B. brucii* are virtually indistinguishable. The *Tor*-like morph typically inhabits swift streams with rocky bottom. When such individuals were kept in cement tanks their thick and rubbery lips regressed until they became indistinguishable from those in the thin-lipped morph (including loss of the mentum). So far as we are aware this is the only published report of such a transformation from one morph to another, and that is one of the reasons why this particular paper is so important. The *Varicorhinus*-like morph of *B. brucii* was originally described as *Varicorhinus brucii* Boulenger (1907: 310, Pl. 19, type locality Klein Olifant R., Transvaal). In keeping with Groenewald's nomenclature, the name *B. brucii* forma *varicorhinoides*) is hereby proposed for this morph, referred to by Groenewald by the phrase "variety with a *Varicorhinus*-like cutting edge on the lower jaw." The four supposed intraspecific trophic morphs of *B. brucii* are illustrated in Fig. 7. Groenewald's paper is valuable for its experimental observations, wealth of morphological and ecological data, and comparisons to related species with similar trophic morphology, as well as for its recognition that *B. brucii* exhibits pronounced intraspecific trophic polymorphism. It is the only publication we know of in which the cyprinid trophic morphs have been reported to change with prolonged captivity (as reported above, we did not find any morphological change in *N. soroides* morphs maintained in captivity for two months).

***Tor grypus* (Fig. 8).**—The species known as *Barbus* or *T. grypus* is phylogenetically isolated in the midst of the Near Eastern cyprinid fish fauna. It is the most westerly occurring Asian member of the genus *Tor*. The species is characterized by intraspecific trophic polymorphism basically similar to that reported here for *N. soroides* except that the morph with a well developed horny jaw sheath is not known to develop a trenchant cutting edge. The type specimens of *B. grypus* have an incipient *Tor*-like mentum. Other specimens have the mentum moderately to strongly developed, and a few specimens including the holotype of *Labeobarbus kotschyi*, have the mentum extending between the lips of the lower jaw and

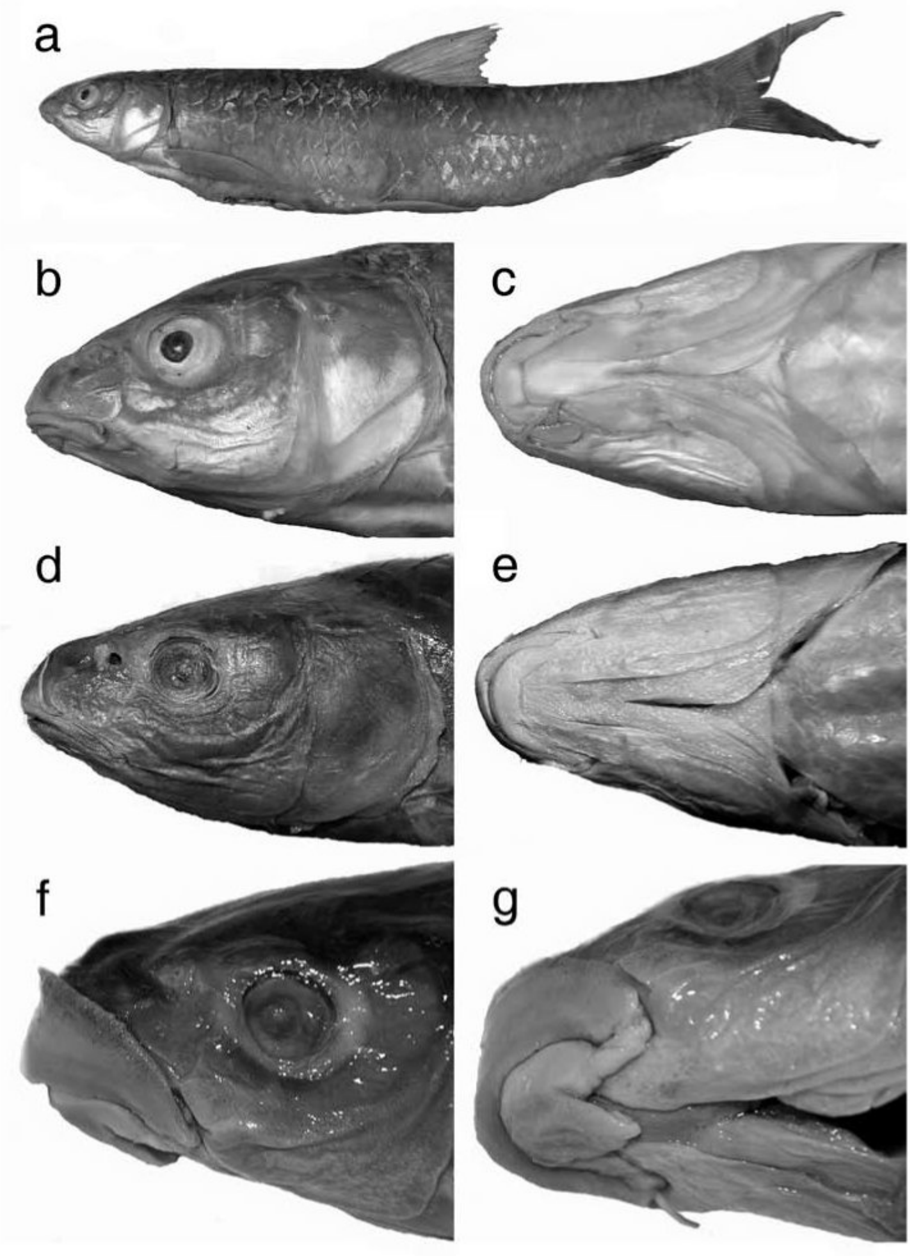

Figure 8. Intraspecific trophic morphs in *Tor grypus* from the Euphrates-Tigrus basin. a–c, NMW 81327, 200 mm, generalized or moderately developed *Tor*-like morph, Basra, (=*Tor grypus grypus*); d–e, CMNFI 1993-153, 250 mm, with well developed lower horny jaw sheath, Zohreh River, Kuzestan, Iran (horny jaw sheath barely visible because mouth is tightly closed); f–g, CMNFI 1993-164, 260 mm, extreme *Tor*-like morph (=*Tor* grypus kotschyi) (photos a–c by H. Wellendorf, d–g by B. W. Coad. Knowledge of *T. grypus* trophic polymorphism reported here is based on very few specimens. Examination of more material will reveal additional morphotypes

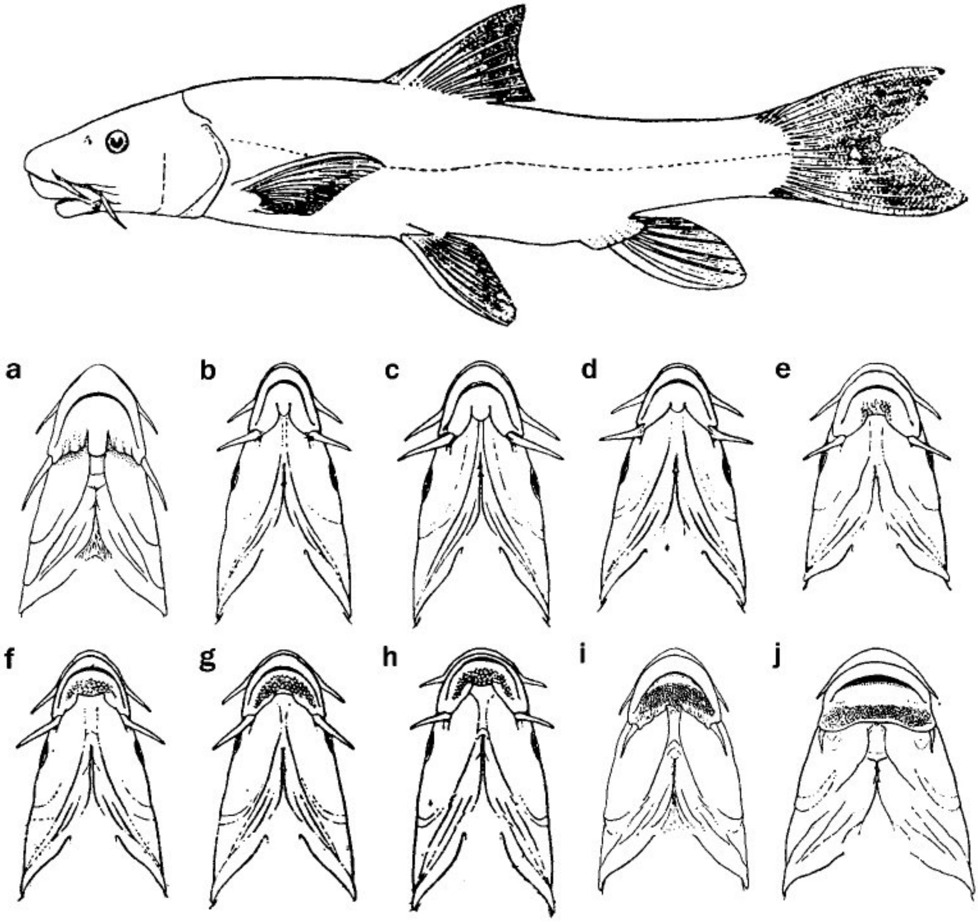

Figure 9. *Schizothorax labiatus* and *Oreinus sinuatus* var. *griffithi* intergradation in trophic structures, Chitral Region (drawings and identifications from Hora, 1934). Above adult S. labiatus with large lips and long barbels (scales omitted), Palarga stream, length not given. Below, a–j, ventral view of head showing mouth parts; precise localities not given, but all from Chital: a, "*true or typical labiatus* type", length not stated; b, "*richeana* type of *labiatus*", length not stated; c, total length 148 mm ("central lobe of lower lip much narrower otherwise similar to that of *S. labiatus*"); d, total length 131 mm, structure of lips and associated parts not very different from typical examples of *S. labiatus*; e, total length 141 mm ("the mandible somewhat shorter and broader and central lobe of posterior lip slightly reduced"); e, total length 137 mm (the head has the form of typical *Oreinus* form, though the structure of the lips and jaws are not of the *Oreinus* morphology: "the central lobe of the posterior lip has disappeared and its middle part has become papillated. The barbels are somewhat shorter"); f, total length 128 mm ("head more or less of *Schizothorax* type but lips considerably modified. Posterior lip papillated"); g. total length 145 mm ("head not so broad as in *Oreinus* but extent of papillae on lower lip considerably greater than preceding"); h, total length 141 mm ("head of *Oreinus* type and posterior lip papillated. The most remarkable feature is that the mouth is situated only slightly behind tip of snout"); j. *Oreinus sinuatus* var. *griffithii*.

the rostral flap extending from the upper lip back over the rostrum as well developed as in the extreme *Tor*-like morph of *N. soroides*. *Labeobarbus kotschyi* has been identified as a junior synonym of *Barbus grypus* by Coad (1991: 14; 1995) and we concur with this conclusion. Coad also has found a single specimen of *T. grypus* (Fig. 8, d-c) with a well-developed, sharp horny jaw sheath on the lower jaw, corresponding to the *Lissochilus*- or *Acrossocheilus*-like trophic morph in *T. soroides*.

The species *Tor grypus* often has been reported as *Barbus grypus*. *Barbus barbus*, type species of *Barbus*, differs trenchantly from *Tor grypus* in numerous respects: last unbranched ray of dorsal fin more or less strongly serrate posteriorly (versus entirely smooth), scales quite small, typically 80–90 in lateral series (vs. relatively large, 37–40 in lateral series). The soft mouth parts barbels of *Barbus* covered with fine tuberlces are differ markedly from the non-tuberculate barbels and mouthparts of *Tor*. *Barbus* has what appears at first glance to be a median lobe or mentum comparable to that in *Tor*, but the strcuture in *Barbus* is completed joined to the isthmus rather than entirely separated separated from the isthmus except for its insertion. So far as we know, *B. barbus* and its close relatives do not exhibit intraspecific trophic polymorphism of the sort reported here in *Neolissochilus*, *Tor*, African large-scaled so-called *Barbus* which may be referred to tentatively as *Labeobarbus*. Eventually *Labeobarbus* and *Neolissochilus* as well may be considered as junior synonyms of *Tor*. We have not observed trophic polymorphism in *Folifer*, the species of which have a narrow mouth, thick lips and a well developed *Tor*-like mental lobe.

Trophic Polymorphism in Himalayan Schizothoracinae

Schizothoracinae is a cyprinid subfamily restricted to elevated habitats in the mountains of Central Asia. Members of the group are characterized by very small scales (scales sometimes entirely absent) except in males, which have a row of greatly enlarged scales along the base of the anal fin. In the Himalayas the subfamily is represented by several species of *Schizothorax* and *Oreinus*. These two genera differ in the structure of their mouth parts: the mouth of *sinuatus* var. *griffithi* resembles that of *Barbus* (*sensu strict*) and of *Tor*, the mouth of *Oreinus* that of *Varicorhinus* or *Acrossocheilus*. A species of *Schizothorax* and a species of *Oreinus* often occur sympatrically, as part of a high altitude fish fauna with relatively few other species, without showing any signs intergradation. Collections of schizothoracins from Chitral reported on by Hora (1934), however, represent morphologically extreme *Tor*-like morphotypes of *Schizothorax* and *Acrossocheilus*- or *Varicorhnus*-like morphotypes of *Oreinus* with a broad range of intermediate morphotypes (Fig. 9).

The mountainous area of Chitral, in the northeastern corner of Afghanistan, is an isolated place for fish as well as for people. If a divider is placed on New Delhi and Fazaipur, some 350 km NW of New Delhi and a bit W of Lahore, and then one point is lifted from New Delhi and rotated 180° around Faizapur to a new position 350 km farther NW, it will land at Jallahabad in Chitral. Chitral "consists of an irregular series of main valleys, for the most part deep, narrower, and tortuous, into which a varying number of still deeper, narrower, and more difficult valleys, ravines, and glens pour their torrent waters. The mountain ranges which separate the main drainages from one another are all of them of considerable altitude, rugged, and toilsome" (Hora 1934: 279). The fish fauna is extremely impoverished. A zoological survey conducted by B. N. Chopra the Zoological Survey of India in 1929 obtained large numbers of fish specimens. Except for the bewildering variety of schizothoracins morphotypes, mostly identified by Hora as *Schizothorax labiatus* (McClelland 1842) and *Oreinus sinuatus* var. *griffithi* McClelland 1842, there were only three other species, *Schizothorax esocinus* Heckel 1838, *Triplophysa choprai* (Hora 1934), and *Glyptosternum reticulatum* McClelland 1842. *Schizothorax esocinus*, a large predatory species with jaws suggestive of a pike (*Esox*), was represented by only two specimens. The *Triplophysa* is a moderately specialized high altitude loach with slender a caudal peduncle and slightly expanded paired fins, while *G. reticulatum* is a highly specialized rheophilic high altitude sisorid catfish with the skin surface tuberculated overall and the ventral surfaces of the paired fins and oral disc bearing unculiferous laminae, adaptations to rheophilic conditions.

The variety of Chitral morphotypes forming a bridge between the species *Schizothorax labiatus* and *Oreinus sinuatus* var. *griffithi* appear to represent continuous trophic variation or polymorphism of the kind reported here in *Neolissochilus* and *Tor*. If these trophic morphs of Schizothoracine are homologous to those of the barbins then the trophic polymorphism reported here evolved before divergence of the barbin and schizothoracin lineages. It may also indicate that Schizothoracinae evolved from *Tor*- or *Neolissochilus*-like ancestors, and that trophic polymorphism played an important role in the differentiation of *Schizothorax* and *Oreinus* and other schizothoracins.

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