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Hemitaeniochromis brachyrhynchus, a new species of cichlid fish from Lake Malaŵi, with comments on some other supposed members of the genus (Teleostei: Cichlidae)

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Abstract

Hemitaeniochromis brachyrhynchus, an anatomically distinctive and apparently rare new cichlid, is described and illustrated from specimens collected at two widely separated localities within Lake Malaŵi. It is easily distinguished from *H. urotaenia*, type species of the genus, by its narrow lacrimal bone which is only one-third of the orbit length, a character thought to be unique not only in *Hemitaeniochromis* but among all known Lake Malaŵi cichlids. The genus *Hemitaeniochromis* Eccles & Trewavas (1989) is redefined to allow provisional inclusion of this new species. Two species placed in *Protomelas* by Eccles & Trewavas (1989) [*P. insignis* (Trewavas) and *P. spilopterus* (Trewavas)] were recently transferred to *Hemitaeniochromis* by some authors, without much evidence. The generic placement of these controversial taxa, and of several undescribed species known only from underwater photographs, is briefly reconsidered.

Key words: melanic pattern, paedophage, taxonomy, *Mylochromis, Otopharynx, Protomelas*

Introduction

Comprising fully 5% of all known vertebrate species, the perciform family Cichlidae includes close to 3,000 species counting both described forms and those that are known but undescribed. About two-thirds of cichlids are found in Africa, the large majority of them endemic to the lakes of the Great Rift Valley. Lake Malaŵi alone is home to at least one-fourth of all known cichlids—a decade ago, estimates of its cichlid fauna ranged from 700 (Turner *et al.* 2001) to 800 species (Snoeks 2001), and a more recent work (Konings 2007) mentions 843 species, of which about 400, in 58 genera, have been formally described (Oliver 2012).

In their ambitious revision of the haplochromine cichlids (other than mbuna) endemic to Lake Malawi, Eccles and Trewavas (1989) erected 23 genera distinguished chiefly by possession of different melanic color patterns and by their trophic specializations. One of these new genera was the monotypic *Hemitaeniochromis*, proposed to accommodate a distinctively marked piscivorous predator originally named *Haplochromis urotaenia* by Regan (1922). *Hemitaeniochromis* was characterized by unicuspid outer teeth in the upper and lower jaws, spaced about a tooth's width apart, and by a specific modification of the primitive haplochromine color pattern of vertical bars and two horizontal stripes. In *Hemitaeniochromis* the stripes predominate, the bars being indistinct; the supralateral horizontal stripe is reduced to a series of spots on the anterior upper flanks where it crosses the faint vertical bars, and the midlateral stripe is usually uninterrupted on the posterior half, but continues anteriorly as a row of spots, again at the intersections with bars, ending several scales behind the operculum. There is also a row of dorsal midline spots adjacent to the dorsal-fin base. Nine additional species, most known only from photographs, have been referred to *Hemitaeniochromis* by some workers (Turner 1996; Duponchelle & Ribbink 2000; Snoeks & Hanssens 2004; Konings 2007), but several of these species do not share the derived melanic pattern of interrupted stripes characteristic of *H. urotaenia* and some have dentition of unknown type.

While sorting Lake Malaŵi cichlids in the Peabody Museum of Natural History at Yale University, specimens that I had collected with colleagues in 1980, I recently came upon an adult individual with a melanin pattern resembling that of *Hemitaeniochromis*, but with the preocular part of the head strikingly modified. The fish was not a

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teratologic specimen of *H. urotaenia*, and it was immediately evident that it represented an undescribed species. Later that evening, looking through the specimen photographs of both named and undescribed Malaŵi cichlids in Snoeks & Hanssens (2004) on the chance that this book chapter might illustrate the novel species, I indeed found a photo of what appeared to be the same unusual cichlid. Their single specimen had been catalogued in the Royal Museum for Central Africa (MRAC). That fish (MRAC 99-41-P-1746), on close examination, proves to be conspecific with the one I had found.

Here, I describe and illustrate this distinctive new species, and revise the diagnosis of *Hemitaeniochromis* to provisionally accommodate the new form. I also reconsider the generic placement of two previously described and seven undescribed taxa that have been referred to *Hemitaeniochromis* by some workers, even though, at this writing, the Catalog of Fishes (Eschmeyer & Fricke 2012) accepts only *H. urotaenia* in this genus.

Material and methods

Lengths are measured on the left side of the fish when possible, to the nearest 0.1 mm using digital calipers; except for caudal peduncle length, all measurements are direct (point to point). Counts and measurements generally follow Snoeks (1994, 2004) with the following exceptions and additions. Lacrimal (preorbital) depth is measured from the middle of the orbital margin of this bone along a line continuing the radius of the eye, bisecting the bone (Trewavas 1935). Vertical eye diameter is measured, bone to bone, from the neurocranial border of the orbit vertically to the orbital margin of the infraorbitals (Barel *et al*. 1977: 359). Head angles are measured to the nearest 5° relative to the lateral midline (Oliver & Arnegard 2010) using an extension-arm protractor (General Tools no. 29, New York, NY). Gape inclination, modified from the definition of Barel *et al*. (1977: 362), is the angle between the ventral border of the upper lip and the lateral midline (see above). Counts, measurements, and terminology from Oliver (1984): Snout width is measured across the centers of the lacrimal bones. Belly length is measured from the anterior base of the pelvic-fin spine to the anterior base of the first anal-fin spine. Predorsal scales are counted just to the left side of the nuchal midline, from the first dorsal-fin spine anteriorly to the most anterior scale, usually above the eye. Prepelvic scales are counted from the left pelvic-fin spine to the most anterior scale on the isthmus (in practice, the irregularity of scale placement renders this count and the preceding one approximate). Dorsal midline spots are discrete dark spots on the dorsum on both sides of the dorsal-fin base.

All illustrations are by the author. The photographs showing anatomical details of the new species were constructed using the focus-stacking program CombineZ (Hadley 2012).

Type specimens are deposited in the Peabody Museum of Natural History, Yale University, New Haven, CT (YPM) and the Royal Museum for Central Africa, Tervuren, Belgium (MRAC). Comparison material examined, photographed, or both is in the American Museum of Natural History, New York, NY (AMNH), the Natural History Museum, London (BMNH), and the U.S. National Museum of Natural History, Washington, D.C. (USNM) and is listed at the end of this paper.

Revised diagnosis of *Hemitaeniochromis* Eccles & Trewavas

Pseudocrenilabrine cichlids of the tribe Haplochromini Poll (1986) endemic to Lake Malaŵi and the upper Shire River. Melanic color pattern modified from the plesiomorphic simple, horizontally striped and vertically barred haplochromine pattern as follows: Stripes darker than bars; midlateral stripe originating an eye length or more behind the operculum, this stripe fragmented into discontinuous spots at least on its anterior portion, more nearly continuous posteriorly, extending to end of caudal peduncle; supralateral stripe confined to anterior portion of flanks, also represented at least partly by discontinuous spots; 4 or 5 dorsal midline spots above supralateral stripe at dorsal-fin base. Jaw teeth in fishes >100 mm SL unicuspid, nearly conical, with interspaces about as wide as the tooth shafts; smaller individuals may have more closely spaced teeth with very unequally bicuspid crowns, the major cusp nearly conical. Gape inclination steep, ~50–60°. Upper lateral line bent downward at posterior end (the "Malaŵi kink"; Lippitsch 1995), separated from lower lateral line by only one untubed or unpored scale, as in many (but not all) other Lake Malaŵi haplochromines.

***Hemitaeniochromis brachyrhynchus*, new species**
Figures 1–4, Tables 1 & 2

Hemitaeniochromis sp. 'insignis big eye', Snoeks & Hanssens 2004: 284 & Fig. 52.

Holotype. YPM 25201, adult male, 123.6 mm SL. Malaŵi: Lake Malaŵi: Thumbi Island West, N side, approximately 14° 00′ 57″S, 34° 48′ 34″ E, trammel nets and experimental gillnets set in series perpendicular to shore over rocks possibly with sand in 17–38 m depth, 3–4 Jul. 1980; M.K. Oliver, K.R. McKaye, and T.D. Kocher. Field no. MKO 80–49.

Paratype. MRAC 99-41-P-1746, sex undetermined, 81.5 mm SL. Malaŵi: Lake Malaŵi: Nkhata Bay, south bay, 11° 36. 22′ S, 34° 18.16′ E, purchased from indigenous fishermen, 27 Sept. 1997; SADC/GEF. Field no. 97/20/114/7.

Diagnosis. A species of *Hemitaeniochromis* readily distinguished from its only formal congener, *H. urotaenia*, by its narrow lacrimal bone whose width, at the midpoint of the bone, is one-third (33.5–34.5%) of the orbit length (vs. nearly equal to the orbit length in *H. urotaenia*); by its snout being shorter than the orbit length (vs. longer in *H. urotaenia*); by its much larger eyes, the orbit length being about 36–38% of head length (vs. ~ 22–28% in *H. urotaenia*); by its shorter lower jaw which is about 39–41% of head length (vs. ~ 45–51% in *H. urotaenia*); and by its melanin pattern, which is composed of spots and line segments that are less well-defined than those of *H. urotaenia* (compare Figs. 1 and 5). The narrow lacrimal and large eyes also distinguish *H. brachyrhynchus* from all other species that have sometimes been placed in *Hemitaeniochromis* (see Discussion). Indeed, these two features in combination are probably unique to *H. brachyrhynchus* among all known Lake Malaŵi cichlids.

Description. Morphometric and meristic data are given in Tables 1 and 2.

Body moderately elongate, dorsal profile evenly rounded from nuchal region of head to end of spinous dorsal fin, more convex than ventral body profile (Fig. 1). Head profile concave above snout. Jaws rather short, gape steeply inclined, premaxilla nearly vertical when mouth widely opened (Fig. 2a); lower jaw apparently slightly projecting and inclined at ~50° to lateral midline when mouth is closed (in paratype; mouth of holotype cannot be fully closed due to stiffness of preservation). Lips slightly thickened but not lobate. Snout distinctly shorter than orbit, 1.28–1.33 in orbit length. Eyes large, orbit length ~36–38% HL. Lacrimal bone narrow, its width at mid-bone only about one-third orbit length, its orbital and labial margins nonparallel, converging nearer each other ventrally than at dorsal end of bone. Caudal fin emarginate.

Dental arcade of each jaw broad, semicircular in outline anteriorly (Fig. 2c). Outer jaw teeth stout, the shafts conical; those of both jaws implanted with interspaces about as wide as the teeth in holotype (upper jaw, Fig. 2c, d; lower jaw, Fig. 3d), spaced more closely with interspaces about half as wide as teeth in paratype (Fig. 3b). Paratype and holotype display what may be ontogenetic changes in crown morphology. Paratype anteriorly has 7 or 8 (upper jaw) and 9–12 (lower jaw) very unequally bicuspid teeth on each hemijaw, the cusps nearly conical and acute (Fig. 3b); and smaller, unicuspid teeth, buried to the crowns in thickened mucosa, on posterior half of dental arcade. In contrast, holotype has uniformly unicuspid teeth with nearly conical crowns, although a few have crowns with a lateral "shoulder" (Fig. 2d) in location of minor cusp of paratype's teeth. Crowns of outer upper jaw teeth are slightly incurved in both specimens, as is usual in Lake Malaŵi haplochromines. However, in both specimens, the anterior teeth of the lower jaw have the crowns angled slightly forward and outward relative to their shafts (Fig. 3b, d), an unusual condition. Inner teeth are tricuspid with acute median cusp in paratype, acutely unicuspid in holotype.

Lower pharyngeal bone (examined only in holotype; Fig. 2b) Y-shaped, delicate; all teeth laterally compressed, cuspidate, none enlarged (except those of posterior row near midline) nor submolariform. Median suture straight, not sinuous.

Gill rakers 10–12 on ceratobranchial, simple, unbranched, grading in length from longer posteriorly to short anteriorly; lightly pigmented with scattered melanophores.

Scales ctenoid. Lateral line discontinuous, the upper section kinked downward caudally so that the two sections are separated by a single scale without a canal or pore (holotype, bilaterally) or by two scales, of which the upper has a pore but no canal and is situated below and behind the last true lateral line scale (with canal) of the upper segment, and the lower has neither pore nor canal (paratype, bilaterally). Squamation extending onto caudal fin between fin rays, in paratype covering basal 60% of upper and lower lobes and basal 40% along middle rays, in holotype covering 90% of entire fin. Bases of soft dorsal and anal fins partly covered by 1–3 irregular rows of small scales.

TABLE 1. Morphometric characters of *Hemitaeniochromis brachyrhynchus*. Measurements preceded by a tilde (~) have large uncertainty because of the specimens having been fixed with the mouth open.

	Holotype	Paratype
	YPM 25201	MRAC 99-41-P-1746
Standard length (mm)	123.6	81.5
Head length (mm)	42.1	28.7
% of standard length:		
Head length	34.1	35.2
Body depth	35.4	37.5
Dorsal-fin base length	53.3	54.6
Predorsal length	35.0	37.4
Prepectoral length	37.6	36.2
Prepelvic length	49.1	46.0
Preanal length	72.4	72.9
Belly length	25.9	30.3
Anal-fin base length	19.0	19.5
Caudal peduncle length	17.1	13.6
Caudal peduncle depth	12.4	13.0
Pectoral-fin length	33.6	35.8
Pelvic-fin length	28.3	25.6
% of head length:		
Head width	49.4	46.0
Interorbital width	25.9	22.0
Snout length	28.7	28.2
Snout width	~35.6	~29.3
Lower jaw length	40.9	39.4
Lower jaw width	~38.4	~25.8
Premaxillary pedicel length	25.4	27.9
Upper jaw length	~39.0	~34.1
Cheek depth	21.1	16.7
Orbit length	38.2	36.2
Vertical eye diameter	33.3	32.8
Lacrimal (preorbital) depth	12.8	12.5
Postorbital head length	34.7	35.9
Pharyngeal bone overall length	25.9	—
Pharyngeal bone fork length	19.7	—
Pharyngeal bone width	25.4	—
Pharyngeal toothplate overall length	14.3	—
Pharyngeal toothplate fork length	11.6	—
Pharyngeal toothplate width	18.1	—
Angular measurements in degrees:		
Premaxillary pedicel	5	10
Interorbital	30	30
Nuchal region	5	15
Lower jaw underside	—	~50
Gape inclination	~60	~60

TABLE 2. Meristic characters of *Hemitaeniochromis brachyrhynchus*.

	Holotype	Paratype
	YPM 25201	MRAC 99-41-P-1746
Scales:		
Lateral line scales	33	33
Upper lateral line scales	27	22
Lower lateral line scales	17	13
Lateral line scales on caudal fin	2	1
Upper transverse line scales	5	5
Lower transverse line scales	12	11
Predorsal scales	~16	~13
Prepelvic scales	~22	~17
Belly scales	~25	~23
Cheek scale rows	3	3
Scales between pectoral- and pelvic-fin bases	7	8
Scales around caudal peduncle	16	16
Fins:		
Dorsal-fin spines, segmented rays	XVII, 10	XVII, 10
Anal-fin spines, segmented rays	III, 9	III, 9
Pectoral-fin rays	14	14
Gill rakers:		
Epibranchial/angle/ceratobranchial	3/1/12	4/1/10
Teeth:		
Outer upper jaw teeth left/right	~22/~22	19/18
Inner rows upper jaw	1	1
Outer lower jaw teeth left/right	15/13	16/15
Inner rows lower jaw	2	2
Lower pharyngeal teeth, posterior edge	28	—
Lower pharyngeal teeth, median column	8–9	—
Lower pharyngeal teeth, oblique count	6	—

Coloration in life. Unknown.

Coloration in preservative (Fig. 1). Dorsum, nuchal region, head above eye, and upper surface of snout dark brown; remainder of head and body with nearly uniform tan or light brown ground color, becoming paler on hyoid area and branchiostegal membrane and silvery tan on belly. Lacrimal brown, lacking distinct stripe; operculum with dark spot; no other distinct head markings. Seven faint vertical bars below dorsal-fin base, darkest on upper body; traces of two further bars on caudal peduncle. Four to five indistinct dorsal midline spots below dorsal-fin base. Supralateral stripe situated just above upper lateral line, extending discontinuously between subdorsal bars 1–4, darkest at bar intersections and between bars 2 and 3. Midlateral stripe just above level of lower lateral line, partly discontinuous, originating at subdorsal bar 2 and extending to end of caudal peduncle where it forms a more or less discrete small precaudal spot; this stripe darkest at bar intersections and most nearly continuous above anal fin. Dorsal fin lacking a submarginal stripe; soft dorsal marbled with darker and lighter brown markings. Caudal-fin membrane light to medium brown, without evident maculae. Anal fin nearly uniform brownish; holotype with hints of ~3 elongate paler spots with darker margins on posterior half of fin. Pectoral hyaline; pelvic brownish on anterior half, unpigmented on posterior 2 or 3 rays.

FIGURE 1. Left and right sides of *Hemitaeniochromis brachyrhynchus* specimens. Not to same scale. **a**, YPM 25201, holotype, 123.6 mm SL, Lake Malaŵi, Thumbi Island West; **b**, MRAC 99-41-P-1746, paratype, 81.5 mm SL, Lake Malaŵi, Nkhata Bay.

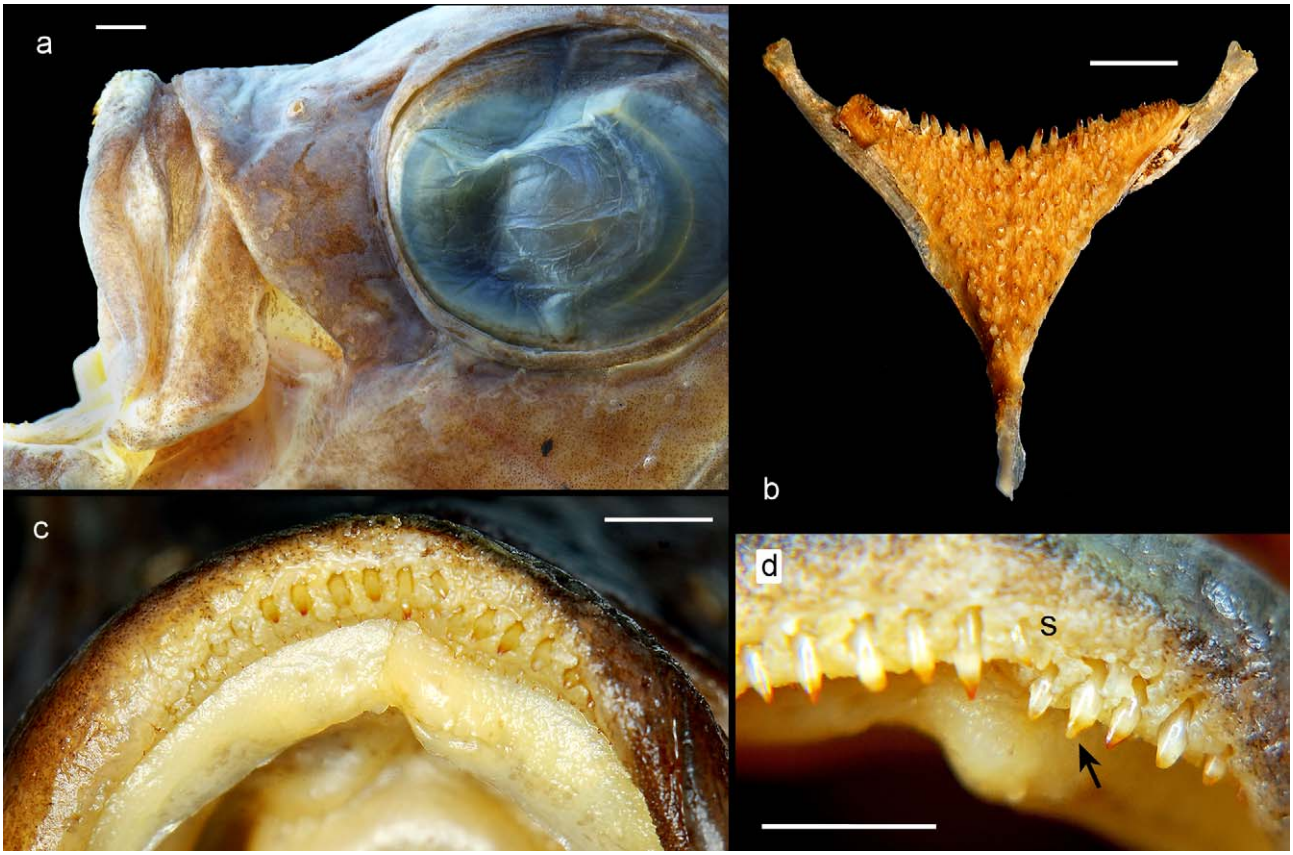

FIGURE 2. *Hemitaeniochromis brachyrhynchus*, details of YPM 25201, holotype. All scale bars = 2 mm. **a**, Snout region in left lateral view to show lacrimal and upper jaw. **b**, Lower pharyngeal bone (rostral tip at bottom of image). **c**, Anterior part of premaxillary dental arcade in occlusal view, after lip tissue has been pushed back and allowed to dry and shrink to reveal tooth shafts. **d**, Median premaxillary teeth of outer row in anterior view, after lip tissue has been pushed back and allowed to dry and shrink to reveal tooth shafts. **s**: Location of premaxillary symphysis. Arrow points to a tooth retaining a lateral shoulder, as seen more frequently in the smaller paratype.

Habitat and distribution. Almost nothing is known. Two large collecting efforts (MKO and colleagues, Jun.–Aug. 1980, 133 stations; SADC/GEF, 1990s, see Duponchelle & Ribbink 2000), each obtaining thousands of fishes from varied habitats, localities, and depths with a range of techniques, collected only a single *H. brachyrhynchus* specimen apiece. The two specimens are from localities 270 km apart (Fig. 4), indicating that *H. brachyrhynchus* is widely distributed. The depths of capture of the two specimens are uncertain. The holotype was caught in an unspecified part of a set of demersal trammel nets and experimental gillnets, of various mesh sizes, totaling 183 m in length, which had been set in series overnight on the bottom (over rocks possibly with areas of sand) where the depth extended from 17–38 m. The stomach of the holotype was everted when the specimen was brought to the surface, suggesting that it came from relatively deep water. The paratype was purchased at Nkhata Bay from artisanal fishermen; its labels do not record the method of capture, but I speculate that it might have been angled on a longline from a dugout canoe as this is a popular indigenous fishing technique at Nkhata Bay. This species does not seem to be represented in the most complete photographic atlas of Malaŵi cichlids from all habitats (Konings 2007). [An entity labeled *Hemitaeniochromis* sp. 'spilopterus blue' by Konings is, to judge by the single male and female he illustrates, reminiscent of *H. brachyrhynchus* but appears to have a distinctly wider lacrimal ~55% of orbit length (vs. 33.5–34.5% in *H. brachyrhynchus*) and has the midlateral stripe (clearly visible in the female) continuously pigmented, not broken into spots, although it is slightly darker where crossed by the vertical bars as in other striped species. I would consider it a *Protomelas*.] I am not aware of any *H. brachyrhynchus* specimens resulting from the extensive experimental trawling program in the southern lake; no specimens were illustrated or described in Turner's (1996) book on offshore cichlids. The scant available information thus suggests that *H. brachyrhynchus* is a widely distributed but rare species, apparently occurring around rocks in rather deep water. Although it has not been possible to examine stomach contents, the distinctive lower-jaw teeth, with their out-

wardly and anteriorly angled crowns, are similar to those of other haplochromine cichlids, of several lineages, that have a paedophagous diet (see Discussion).

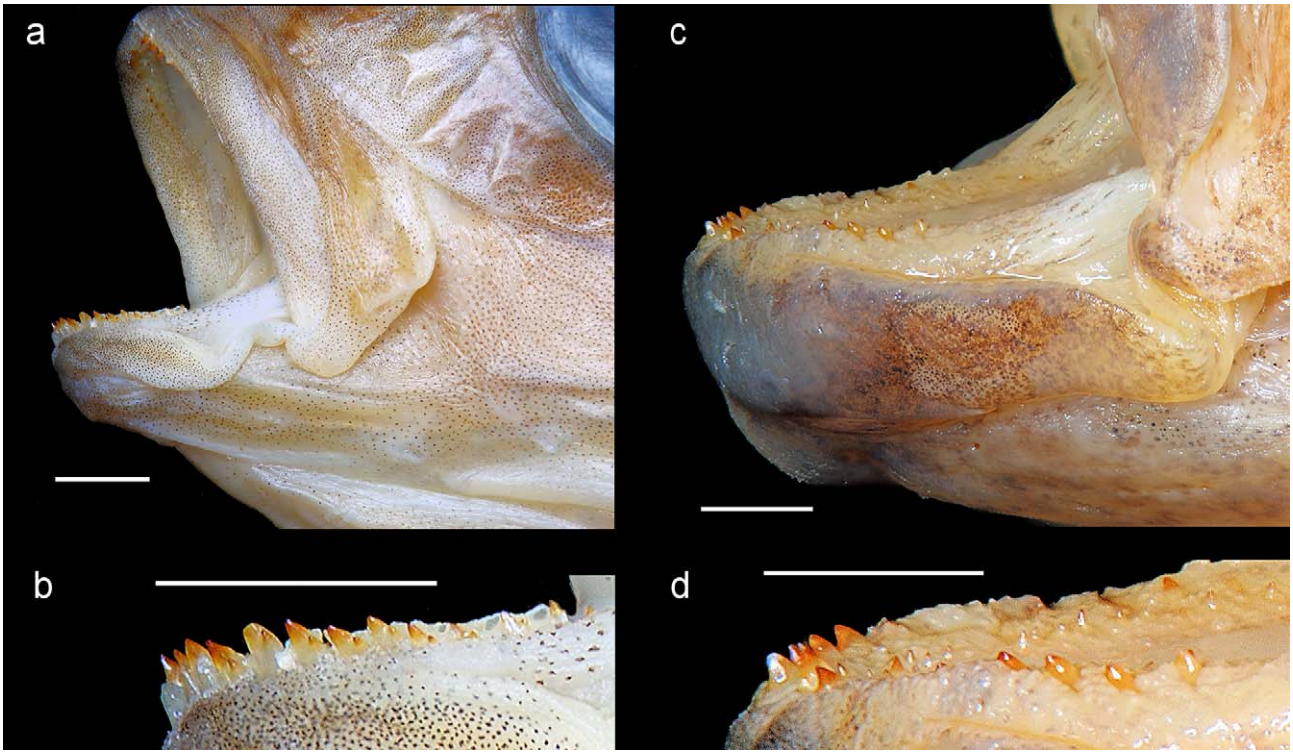

FIGURE 3. *Hemitaeniochromis brachyrhynchus*. All scale bars = 2 mm. **a**, MRAC 99-41-P-1746, paratype, 81.5 mm SL, in left and slightly anterolateral view, showing jaws, dentition, and most of lacrimal bone. **b**, Same, showing exposed crowns of unequally bicuspid anterior teeth, the nearly conical major cusps angled forward and slightly outward. **c**, YPM 25201, holotype, 123.6 mm SL, in left and slightly dorsolateral view, showing anterior part of lower jaw. **d**, Same, showing exposed tips of nearly conical crowns angled forward and slightly outward, largely buried in thickened mucosa.

Conservation status. Unknown. *Hemitaeniochromis brachyrhynchus* may normally inhabit deeper water than has generally been sampled over rocky substrates. The widely separated localities of the two type specimens at least demonstrate that the species is not restricted to a single circumscribed area.

Etymology. Latinized from the Greek adjective βραχύσ, short, and noun ρύγχοσ, snout, in reference to the abbreviated preocular region of the head; *brachyrhynchus* is a noun in apposition. No indigenous names have been recorded.

Discussion. *Hemitaeniochromis* was proposed for a single species, *H. urotaenia* (Fig. 5). The genus was diagnosed "…by having a boldly marked melanin pattern consisting of a mid-lateral band confined to the posterior half of the flank but continued forwards as a series of spots and a supralateral band broken into a series of spots. Mouth large, lower jaw 2.0 to 2.2 in head length, with well developed mental region. Outer teeth unicuspid, slightly recurved, separated by spaces approximately equal to tooth diameter" (Eccles & Trewavas 1989: 71). In couplet 57 of their key to genera, these authors noted further that *Hemitaeniochromis* (together with *Tyrannochromis*, which has a very similar melanic pattern but, because of its beaklike jaws and laterally compressed head, is not likely to be confused with *Hemitaeniochromis*) are "[l]arge-mouthed predators" with "… teeth all unicuspid in fish over 100 mm SL, sometimes very unequally bicuspid in smaller individuals." Although not mentioned in the diagnosis, it is also noteworthy that the interrupted midlateral stripe begins about 5 scales behind the operculum, instead of immediately behind it as in the plesiomorphic haplochromine pattern. However, this apomorphic condition is not unique to *Hemitaeniochromis*, being found also in some species currently assigned to *Protomelas*, in *Tyrannochromis macrostoma* (Regan, 1922), and in some individuals of *Lethrinops lethrinus* (Günther, 1894).

Hemitaeniochromis brachyrhynchus fits into this original diagnosis of *Hemitaeniochromis* well in some respects, including the apomorphic discontinuous midlateral stripe beginning well behind the operculum and the spaced, unicuspid adult jaw teeth. The exceptional characters are the smaller mouth (lower jaw 2.45–2.54 in head), the less well-defined midlateral stripe (compare Figs. 1 and 5), the outwardly curved crowns of the anterior lower

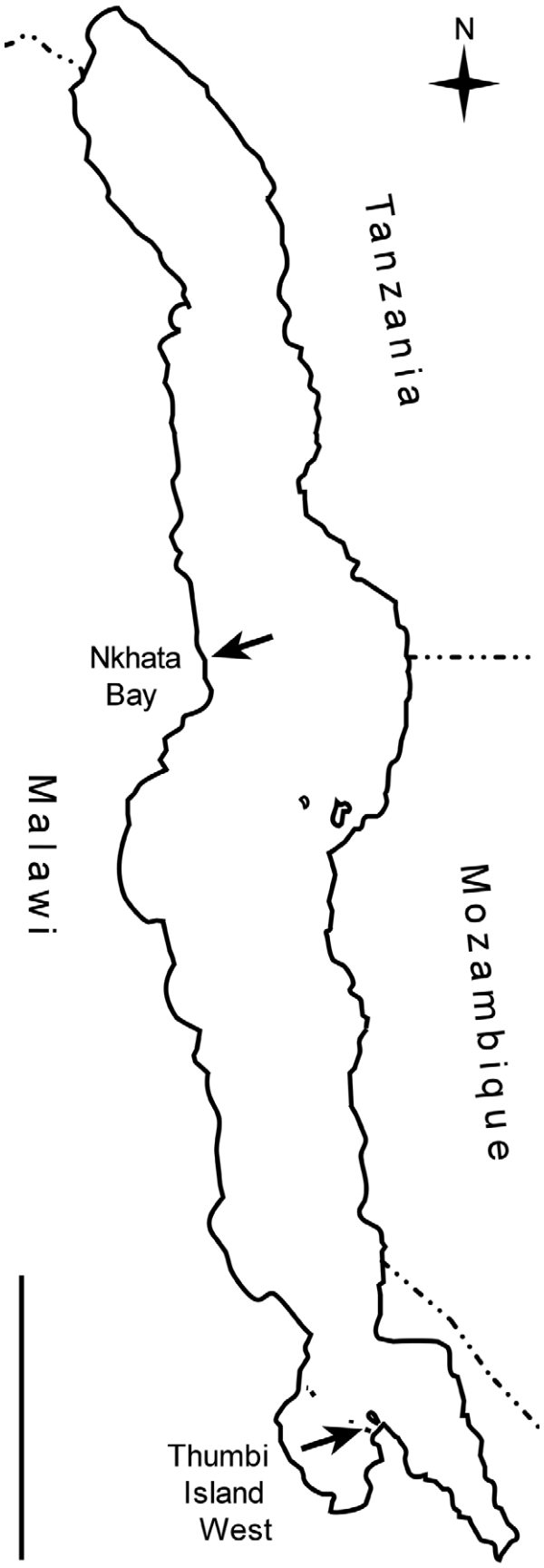

FIGURE 4. Lake Malaŵi with arrows pointing to the localities where specimens of *Hemitaeniochromis brachyrhynchus* were collected. Thumbi Island West: YPM 25201, holotype; Nkhata Bay: MRAC 99-41-P-1746, paratype. Scale bar = 100 km.

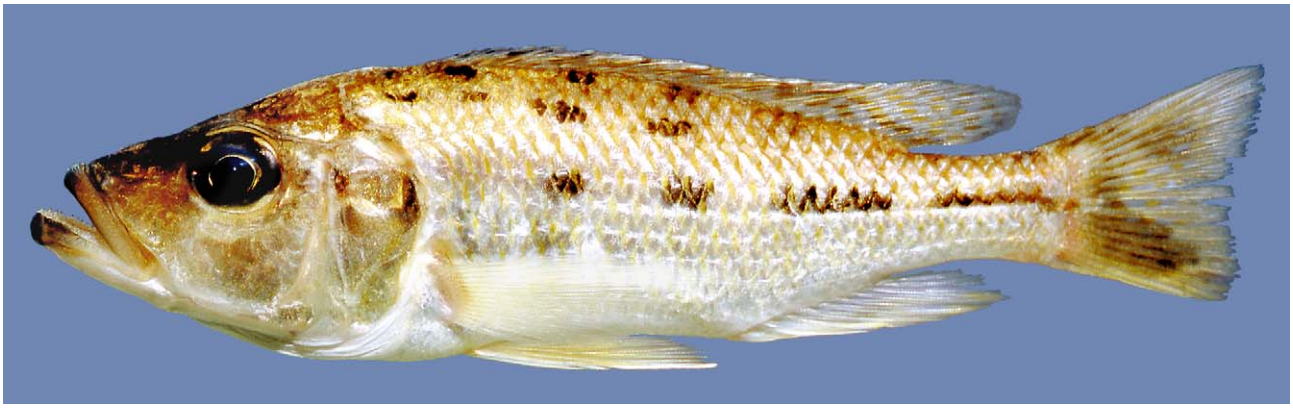

FIGURE 5. *Hemitaeniochromis urotaenia*, USNM 266842, living; Malaŵi: Lake Malaŵi: Nankumba Peninsula between Otter Island and Chembe, off sand beach, depth 9–11 m, 3 Jul. 1980; M.K. Oliver, K.R. McKaye, & T.D. Kocher. Note the wide lacrimal bone, about equal to eye length. This specimen has an atypical midlateral stripe, usually continuous on its caudal half.

FIGURE 6. *Protomelas kirkii*, type species of *Protomelas*, living adult specimens. **a**, Apparent male, YPM 14519, Malaŵi: Lake Malaŵi: Nankumba Peninsula, off beach between Otter Point and Chembe, sand with *Potamogeton* and *Vallisneria* beds, 4–5 m depth, 7 Aug. 1980; M.K. Oliver, K.R. McKaye, & T.D. Kocher. **b**, Another individual, MKO 80-126, Malaŵi: Lake Malaŵi: Nankumba Peninsula, off swamp at NE end Chembe village, sand, 3 m depth, experimental gillnets & trammel nets set in series parallel to shore, 17–18 Aug. 1980; M.K. Oliver, K.R. McKaye, & T.D. Kocher. Note midlateral stripe with origin close behind operculum, and small, narrow mouth. Note images are not to the same scale.

FIGURE 7. *Protomelas spilopterus*, living adult individuals; MKO 80-62, Malaŵi: Lake Malaŵi: Nankumba Peninsula, ~300 m S of Otter Island, trammel nets, 9–10 Jul. 1980; M.K. Oliver, K.R. McKaye, & T.D. Kocher. **a**, Breeding male; **b**, Subordinate male or female. Note images are not to the same scale.

jaw teeth, and the more closely spaced jaw teeth of the paratype (but not the holotype, a larger specimen). At present, without stronger phylogenetic evidence, *Hemitaeniochromis* appears to be the most appropriate genus for this new species, as also indicated by Snoeks & Hanssens (2004). However, except for the specialized midlateral stripe, no convincing synapomorphy shared with *H. urotaenia* is evident from external examination of the *H. brachyrhynchus* type specimens.

The unusual forward and outward curvature of the anterior tooth crowns in the lower jaw of *H. brachyrhynchus* is also seen in a few other haplochromine cichlids. Similar dentition characterizes the known paedophages (specialist feeders on eggs and larvae, usually of other cichlids) of the genus *Caprichromis* and the suspected paedophage *Protomelas spilopterus* (Trewavas, 1935) (Eccles & Trewavas 1989: 69), both endemic to Lake Malaŵi, as well as *Haplochromis obesus* (Boulenger, 1906), *H. maxillaris* Trewavas, 1928, and *H. melanopterus* Trewavas, 1928 of Lake Victoria, which are also known or suspected paedophages (Greenwood 1959). A heavily built lower jaw, and teeth partly buried in thickened mucosa are also features common to *H. brachyrhynchus* and all these fishes. It seems reasonable to hypothesize that *H. brachyrhynchus* is another convergently specialized paedophage, which may explain why its jaws, dentition, and snout anatomy differ so strikingly from those of its congener, *H. urotaenia*. Stomach contents were not examined in the two known specimens, the holotype having had its stomach everted upon capture, as noted above; the belly of the paratype remains unslit.

The nominal genus most similar to *Hemitaeniochromis* in melanin pattern and general habitus is *Protomelas*. Eccles and Trewavas (1989) provide no actual diagnostic characters in their diagnosis of the latter genus, even stating “No synapomorphies have been recognised separating *Protomelas* from the other Malaŵian genera, which are distinguished by their own synapomorphies.” Thus, *Protomelas* is a genus of convenience rather than a lineage, a

catch-all for numerous more or less similarly marked, relatively plesiomorphic Lake Malaŵi haplochromines. Included in *Protomelas* by Eccles and Trewavas were species "with moderate sized mouths" and a "[m]elanin pattern based on the plesiomorphic, with the longitudinal bands usually predominating." Some species, including the type species *P. kirkii* (Günther, 1894) (Fig. 6), have a complete midlateral stripe originating close behind the operculum. In others [e.g., *P. insignis* (Trewavas, 1935) and *P. spilonotus* (Trewavas, 1935)] this stripe begins well behind the operculum as in *Hemitaeniochromis*; some other *Protomelas* species are variable in this feature. The jaw dentition of included species is "…usually bicuspid, at least in young, but may be replaced in adults by unicuspids which, however, are not widely spaced" (Eccles & Trewavas 1989). The chief characters excluding *H. brachyrhynchus* from this broadly defined *Protomelas* and instead aligning it with *H. urotaenia* are the interrupted, spotted midlateral stripe and the widely spaced jaw teeth in the adult holotype.

Two of the species that Trewavas (1935) had originally described in *Haplochromis*, *H. spilopterus* and *H. insignis*, were among the forms assigned by Eccles and Trewavas (1989) to their new genus *Protomelas*. Both have been referred to *Hemitaeniochromis* by some recent authors.

The first of these, *P. spilopterus*, is a moderately common large-eyed cichlid of sandy shores and intermediate (sand/rock) areas, recognizable in the field by its obliquely inclined mouth, heavy lower jaw with dentary more than twice as deep as the premaxilla, and continuous midlateral stripe (exceptionally broken into separate spots) originating close behind the operculum (Fig. 7). Its jaw teeth are unequally bicuspid in young individuals, becoming mostly unicuspid in adults, the lower-jaw teeth having the crowns angled slightly forward. Although this species has not been observed to feed, it is strongly suspected of being a paedophage (Eccles & Trewavas 1989; Konings 2007). Konings (2007: 344) remarks, "…in my opinion *H. spilopterus* belongs to [*Hemitaeniochromis*] as it shares all its morphological characteristics. The only discrepancy is that the mid-lateral stripe is continuous in most individuals…."

The other species, *P. insignis*, is a rather uncommon intermediate-zone inhabitant with a midlateral stripe originating at least an eye diameter behind the operculum. This stripe is most often continuous, but may be divided into semi-discrete spots (Fig. 8a). The outer jaw teeth are predominantly unicuspid in adults, but occasional teeth with bicuspid crowns are retained. *Protomelas insignis* has been observed to feed by stealing eggs from the nests of other sandy-shore cichlids in nesting arenas, especially where multiple species are nesting (Lewis *et al*. 1986: 39). These authors, and Konings (2007), report the same unusual behavior in *Otopharynx ovatus*, a cichlid with three lateral spots (Fig. 8b). Is this mere coincidence? While re-examining one lot with five *P. insignis* specimens (YPM 14291) in preparing this paper, I was intrigued to find in it a note I had written many years ago (26 Feb. 1981): "NB—are *insignis* and *ovatus* a single sp.?—similar behavior; color pattern of latter suggested in that of former. Similar phar[yngeal]s, dentition. Do they differ in anything but color pattern?" Interestingly, Turner (1996: 196) independently developed a similar suspicion that *O. ovatus* is conspecific with what he discussed and illustrated as *Hemitaeniochromis* 'insignis', a cichlid with midlateral and supralateral stripes (although he referred to the latter species as an "oblique-striped paedophage," apparently a lapsus since both his text and his photo depict a cichlid with two horizontal stripes, not an oblique stripe). Turner remarks that "In the confusion of an attack on a spawning pair of *Copadichromis*, one [of] these fishes appeared to change between the spotted and striped pattern." Thus, if Turner's observations are correct, what were originally thought to be two separate and differently marked species, not closely related to each other, may be phases of a single species, which may even be capable of rapidly altering its melanin pattern to facilitate aggressive mimicry of various cichlid prey species with either striped or spotted melanic patterns. However, well before both my observations and Turner's, it was David Eccles who first suspected that *P. insignis* and *O. ovatus* might be the same species. This is documented by his note in the jar containing (in 1972, when I examined them) the syntypes of *Haplochromis ovatus* Trewavas, 1935, BMNH 1935.6.14.1487-1489. Eccles' note reads: "*H. insignis*, *H. ovatus*, *H. obtusus* appear to be conspecific. D.H. Eccles Oct 1969." (I had seen this notation, but did not consciously remember having read it, when I made my own note of the possible synonymy of *H. insignis* and *H. ovatus* 9 years later in 1981.) Eccles' same note was repeated in the lot of *H. insignis* types, BMNH 1935.6.14.839-843; and in that of the *H. obtusus* holotype, BMNH 1935.6.14.1453. Nevertheless, Eccles & Trewavas (1989) later treated all three as valid species, even assigning them to three different genera: *Protomelas insignis*, *Otopharynx ovatus*, and *Maravichromis obtusus* (the last of these genera synonymized with *Mylochromis* Regan, 1920 by Derijst & Snoeks 1992). The question of the possible synonymy of *P. insignis* and *O. ovatus*, species with different color patterns and currently classified in different genera, remains of considerable biological interest, but its resolution is outside the scope of this study.

FIGURE 8. a, *Protomelas insignis*, USNM 266835, large breeding male, immediately postmortem; Malaŵi: Lake Malaŵi: Thumbi Island West, off S-facing bay 200 m E of island's W end, rock/sand interface, demersal trammel and experimental gillnets, depth 41–48 m, 24–26 Jun. 1980; M.K. Oliver, K.R. McKaye, & T.D. Kocher. **b**, *Otopharynx ovatus*, MKO 80-62, adult, apparently male, immediately postmortem; Malaŵi: Lake Malaŵi: Nankumba Peninsula 300 m S of Otter Island, rock/sand interface, demersal trammel nets, depth 30–55 m, 9–10 Jul. 1980; M.K. Oliver, K.R. McKaye, & T.D. Kocher. Note images are not to the same scale.

In addition to the previously described species *Protomelas spilopterus* and *P. insignis*, several presently undescribed species are also believed by a few workers to belong to *Hemitaeniochromis*. Extensive lake-wide exploration of littoral habitats using SCUBA, notably by Adrianus Konings, has resulted in the discovery and photographic recording of at least seven additional forms that he refers to *Hemitaeniochromis* (Konings 2007). Unfortunately, no museum specimens of these species are available for study.

All eleven species that have been referred to *Hemitaeniochromis* are listed and briefly characterized in Table 3. However, there are two problems with assigning all the species in Table 3 to *Hemitaeniochromis*. First, the midlateral stripe, whose apomorphic configuration is a key feature in the definition of the genus, varies widely among these species, differing in its point of origin, width, degree of continuity, and even presence or absence. Second, nearly all of the tabulated species are either known to be, or suspected of being, paedophages, with evident adaptations in their jaw structure, dentition and, presumably, behavior for this specialized mode of predation. In contrast, the type species, *H. urotaenia*, lacks these specializations and is known to be a "standard" generalized piscivore (Eccles & Trewavas 1989). Given these two problematic character distributions, attempting to force all the varied taxa represented in Table 3 into *Hemitaeniochromis* would seem to render the genus undefinable and, very proba-

bly, polyphyletic. Perhaps some or all of the paedophagous species among them represent a single lineage (although, given their heterogeneous markings, this is open to doubt), which might even require a new genus. This, however, cannot be determined until specimens are available for detailed study. How should the various tabulated species be provisionally classified in the meantime?

TABLE 3. Species that have been referred to *Hemitaeniochromis*, with selected characteristics and authority for this generic placement. Most data were gleaned from published text and photographs in the cited sources; the author is aware of no museum specimens representing any of the undescribed species.

Species	Midlateral stripe		Diet	Authority for placement in *Hemitaeniochromis*
	Origin	Modal structure		
Hemitaeniochromis brachyrhynchus Oliver	Far behind operculum	Spotted anteriorly, more continuous posteriorly	Unknown (paedophage?)	Oliver (this paper); Snoeks & Hanssens (2004)
Hemitaeniochromis insignis (Trewavas) =*H.* sp. 'insignis'	Far behind operculum	± Continuous, wide	Steals eggs from nests (Lewis *et al.* 1986)	Turner (1996); Duponchelle & Ribbink (2000); Snoeks & Hanssens (2004)
Hemitaeniochromis sp. 'insignis mumbo'	Far behind operculum	Discontinuous, wide	Unknown; strong lower jaw as in paedophages	Konings (2007)
Hemitaeniochromis sp. 'paedophage'	Far behind operculum	Continuous, narrow	Cichlid eggs, larvae (paedophage)	Konings (2007)
Hemitaeniochromis spilopterus (Trewavas)	Close to operculum	Continuous, ± wide	Paedophage?	Konings (2007)
Hemitaeniochromis sp. 'spilopterus blue'	Far behind operculum	Continuous, wide	Cichlid & catfish eggs & larvae (paedophage or opportunistic?)	Konings (2007)
Hemitaeniochromis sp. 'spilopterus jalo'	—	None?	"Strong jaws suggest a predatory lifestyle"	Konings (2007)
Hemitaeniochromis sp. 'spilopterus kande'	Far behind operculum	Spotted anteriorly, more continuous posteriorly	Unknown	Konings (2007)
Hemitaeniochromis sp. 'spilopterus yellow'	Far behind operculum	Continuous, ± wide	Cichlid eggs, larvae (paedophage?)	Konings (2007)
Hemitaeniochromis urotaenia (Regan) (type of the genus)	Far behind operculum	Spotted anteriorly, more continuous posteriorly	Piscivore	Eccles & Trewavas (1989)
Hemitaeniochromis sp. 'urotaenia tanzania'	Far behind operculum	Discontinuous, wide, with spots like those of *Otopharynx brooksi*	Seen to hunt small fishes	Konings (2007)

Taxonomic recommendations. (1) I propose that *Protomelas insignis* and *P. spilopterus* be retained in *Protomelas*. Even though that genus is not demonstrably monophyletic, transferring the two species to *Hemitaeniochromis* would only serve to render the latter genus nonmonophyletic as well, since they share no synapomorphies with *H. urotaenia*, the type species. (2) Until voucher specimens of those species now known only from underwater photographs become available and are taxonomically studied, *Hemitaeniochromis* should be restricted to *H. urotaenia* and *H. brachyrhynchus*. These two species do share the putative synapomorphy of a midlateral stripe that originates well behind the operculum and that is discontinuous, composed both of spots and of line segments. (3) The "photo species" are, in effect, *incertae sedis* within the Lake Malaŵi non-mbuna haplochromines and should be referred to as species of '*Hemitaeniochromis*' (in single or double quotation marks) to show that they are not necessarily related closely to *H. urotaenia*; thus, '*Hemitaeniochromis*' sp. 'paedophage', '*Hemitaeniochromis*' sp. 'spilopterus yellow', etc.

Of the undescribed species in Table 3, only '*Hemitaeniochromis*' sp. 'insignis mumbo', '*H.*' sp. 'spilopterus kande', and possibly '*H.*' sp. 'urotaenia tanzania' appear to fall within *Hemitaeniochromis* as here defined (although the form of their teeth is not known). The other species in Table 3 lack the derived states of the midlateral stripe found in *H. urotaenia* and *H. brachyrhynchus* and should be excluded from *Hemitaeniochromis* proper. For example, in '*H*'. sp. 'spilopterus blue', to judge by the female depicted by Konings (2007: 167 Fig. 2), the midlateral stripe originates well behind the operculum but retains the plesiomorphic unbroken configuration seen in some *Protomelas*, as noted above, instead of being broken into spots as in *Hemitaeniochromis*.

Comparative material examined

Hemitaeniochromis urotaenia (Regan, 1922): USNM 266842 (1, not measured; Malaŵi: Lake Malaŵi: Nankumba Peninsula between Otter Island and Chembe, off sand beach, depth 9–11 m, 3 Jul. 1980).—YPM 7803 (1, 198.0 mm SL; Malaŵi: Lake Malaŵi: 4 miles SE of Monkey Bay, trawled in 11–18 m, 7 Dec. 1973).

Otopharynx ovatus (Trewavas, 1935): BMNH 1935.6.14.1487 (1, lectotype, 154.5 mm SL; Malaŵi: Lake Malaŵi: south end).—BMNH 1935.6.14.1488–1489 (2, paralectotypes, 104.5–139.0 mm SL; Malaŵi: Lake Malaŵi: south end).—AMNH 31826 (1, 143.0 mm SL, radiograph; Malaŵi: Monkey Bay, 6 Feb. 1964).—AMNH 31832 (1, 169.5 mm SL, radiograph; Malaŵi: Lake Malaŵi: reef 4 miles N of Monkey Bay, 14 Feb. 1964).—AMNH 222078 (1, 52.5 mm SL; Malaŵi: Lake Malaŵi: SE arm, W side Boadzulu Island near its S end, 15 Aug. 1971).—YPM 14292 (2, 97.5–101.0 mm SL; Malaŵi: Lake Malaŵi: Otter Point, 29 Jul. 1980).

Protomelas insignis (Trewavas 1935): USNM 266835 (7, not measured; Malaŵi: Lake Malaŵi: Thumbi Island West, off S-facing bay 200 m E of island's W end, rock/sand interface, demersal trammel and experimental gillnets, depth 41–48 m, 24–26 Jun. 1980).—YPM 14507 (1, 171 mm SL; Malaŵi: Lake Malaŵi: Nkhata Bay area: Chikale Beach, trammel nets, 22–23 Jul. 1980).—YPM 14165 (1, 115 mm SL; Malaŵi: Lake Malaŵi: Nankumba Peninsula: Otter Island, W shore, chased into gillnet, 9 Jun. 1980).—YPM 14279 (4, 83–123 mm SL; Malaŵi: Lake Malaŵi: Nankumba Peninsula: Otter Point, 29 Jul 1978 or 1979).—YPM 14291 (5, 84–101 mm SL; Malaŵi: Lake Malaŵi: Nankumba Peninsula: Otter Point, gillnet, depth 9 m, 29 Jul. 1978 or 1979).—YPM 14342 (1, 134 mm SL; Lake Malaŵi: Malaŵi: Nankumba Peninsula: 300 m S of Otter Island, trammel nets, depth 26–40 m, 10–11 Jul. 1980).

Protomelas spilopterus (Trewavas 1935): YPM 25114 (1, 118 mm SL; Malaŵi: Lake Malaŵi: Thumbi Island West, S shore, trammel & experimental gillnets, depth 41–67 m, 5–6 Aug. 1980).—YPM 14124 (1, 126 mm SL; Malaŵi: Lake Malaŵi: Thumbi Island West, N shore, trammel & experimental gillnets, depth 24–49 m, 7–8 Jul. 1980).—YPM 14288 (1, 137 mm SL: Malaŵi: Lake Malaŵi: Nankumba Peninsula: off Chembe midway between Otter Island and Ilala Gap, trammel & experimental gillnets, depth 30 m, 30 Jun–1 Jul. 1980).—YPM 14357 (1, 131 mm SL; Malaŵi: Lake Malaŵi: Thumbi Island West, S of SW corner, trammel & experimental gillnets, depth 15–65 m, 18–19 Aug. 1980).

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