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A TAXONOMIC STUDY OF THE FISH GENUS *PETROTILAPIA* (PISCES: CICHLIDAE) FROM LAKE MALAWI

by

A.C. MARSH

ABSTRACT

Marsh, A.C. 1983. A taxonomic study of the fish genus *Petrotilapia* (Pisces: Cichlidae) from Lake Malawi. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology*, No. 48, 14 pages, 12 figures.

The type-species of the cichlid fish genus *Petrotilapia* Trewavas 1935, *P. tridentiger*, is redescribed and two new species, *P. genalutea* and *P. nigra*, are described. These three species occur sympatrically at Monkey Bay. Morphological differences between the three species are slight and of little diagnostic value. Live coloration is the most important taxonomic character and can be used reliably to identify adults of the three species. Field observations of live fishes are shown to be of paramount importance in taxonomic studies of the genus *Petrotilapia*.

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A TAXONOMIC STUDY OF THE FISH GENUS *PETROTILAPIA* (PISCES: CICHLIDAE) FROM LAKE MALAWI

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A.C. MARSH[1]

INTRODUCTION

In 1925-26 Dr C. Christy collected over 3 500 cichlid fish from Lake Malawi. In a brief report on this collection, Trewavas (1935) gave a list of all Lake Malawi cichlid species known at that time, including several new species and genera, and keys for their identification. *Petrotilapia tridentiger,* one of the new species described by Trewavas, was placed in a new genus, because of its distinctive dentition. According to Trewavas (1935), the jaw teeth are all movable, have long slender shafts and end in expanded tricuspid tips. *Petrotilapia* belongs to a closely-related group of 10 genera that are characterized by having small scales on the nape, chest and cheek, 30 — 31 vertebrae, 15 — 19 dorsal fin spines, 8 — 10 dorsal fin rays, 3 anal fin spines and 7 — 9 anal fin rays (Trewavas, 1935; Loiselle and Oliver, 1972). Members of these genera are typically rock-frequenting and are known locally by the Chitonga name Mbuna (Fryer, 1959). Two characteristics, tooth shape and mouth position, clearly distinguish the genus *Petrotilapia* from other Mbuna genera.

Recent work, based primarily on direct field observations while using SCUBA, has shown that there are numerous colour forms of *Petrotilapia* in Lake Malawi (Marsh et al., 1981). At Monkey Bay three distinct colour forms occur sympatrically on the rocky shores. No interbreeding occurs between these colour forms, and consequently they are regarded as distinct species, rather than merely morphs of one polychromatic species (Marsh et al., 1981). The three species differ from one another in terms of their ecology and behaviour (Marsh et al., 1981) and in swimbladder physiology (Marsh and Ribbink, 1981).

This paper represents a taxonomic study of the three species of *Petrotilapia* that occur at Monkey Bay; the type-species, *P. tridentiger,* is redescribed and two new species are described.

METHODS

Live coloration is the most reliable feature distinguishing the three species. Notes on live coloration were recorded in the field and from photographs taken both in the field and in aquaria. Although it is easy to recognize adults of the three species under water, it is very difficult to identify preserved specimens reliably. Consequently it was necessary to base the species descriptions on specimens that had been identified in the field, and then captured. Specimens were collected individually by SCUBA divers who herded the fish into a fine mesh net. Measurements and counts were taken of Monkey Bay specimens, and observations and limited collections were made at other sites in the lake. Measurements were taken with vernier calipers reading to 0.1 mm using the technique of Eccles and Lewis (1977). The specimen is placed on a measuring board with its head touching the head block and with its body axis at right angles to the block. The perpendicular distance from the block to the appropriate point is then measured.

The following measurements were made: Total length: measured with tail closed. Standard length: from tip of the snout to posterior edge of hypurals. Body depth: greatest depth, taken at right angles to horizontal axis of body. Body width: greatest width of fish. Caudal peduncle length: distance from posterior end of hypurals to a vertical from posterior base of dorsal fin. Caudal peduncle depth: minimum vertical depth. Head length: from tip of lower jaw to most posterior margin of bony operculum. Snout length: from anterior edge of snout to a vertical at the anterior border of orbit. Eye diameter: horizontal diameter of bony orbit. Interorbital width: least distance between dorsal bony margins of orbits. Preorbital depth: length of lachrymal bone. Premaxillary pedicel length: from dorsal tip of premaxillary pedicel to anterior margin of premaxilla. Premaxillary length: projected distance between posterior tip of premaxillary arm and anterior end of premaxillary symphysis. Premaxillary width: distance between tips of premaxillary arms. Lower jaw length: from tip of dentary arm to symphysis. Lower jaw width: distance between proximal ends of dentary arms. Length to dorsal fin end and length to anal fin end: axial distance from posterior base of dorsal and anal fins respectively to tip of snout. Dorsal spine length: measured along rear edge of last dorsal fin spine. Anal spine length: measured along rear edge of third anal fin spine. Length of pectoral fin: from upper part of axilla to tip of longest ray. Pelvic spine length and pelvic ray length: from base of pelvic fin spine to tip of spine and longest ray respectively.

The following measurements refer to the lower pharyngeal bone: Pharyngeal fork length: measured along median suture. Pharyngeal total length: from anterior end of pharyngeal bone to a line joining tips of the horns. Pharyngeal width: distance between horn tips. Pharyngeal depth: greatest depth, including the teeth. Pharyngeal blade length: from tip of blade to anterior tip of dentigerous portion. Pharyngeal blade depth: greatest depth transverse to the long axis of the blade.

The pored scales in the upper and lower lateral line are counted, excluding any pored scales which occur posterior to the hypurals. The total lateral-line count reflects the number of scales in a longitudinal series as defined by Trewavas (1935): "at the end of the upper lateral line, one proceeds to the scale of the lower lateral

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line next behind the transverse row that includes the last scale of the upper lateral line and slopes downwards and forwards from it."

All gill-rakers on the outer edge of the first gill arch were counted. Counts are given for upper-limb and lower-limb gill-rakers. Counts of lower-limb rakers include any rakers that occur on the region of articulation between the epibranchial and ceratobranchial.

Vertebrae were counted from radiographs using the technique of Barel et al. (1977) to differentiate the caudal vertebrae from the abdominal vertebrae. The first caudal vertebra is taken as the one to which the first anal pterygiophore points. The last hypural bearing vertebra was included in the caudal vertebral count.

The illustrations and text in Barel et al. (1977) were used as the standard for the description of nonquantified form characters, such as the degree of curvature of the dorsal head profile.

Abbreviations for repositories of materials examined are BMNH — British Museum (Natural History), London; RUSI — J. L. B. Smith Institute of Ichthyology, Grahamstown; USNM — United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Abbreviations for measurements are L — length, D — depth, W — width and SL — standard length.

The specific names of the species referred to by code letters in Marsh et al. (1981) and Marsh and Ribbink (1981) are: *P. tridentiger* — BB, *P. genalutea* — OC and *P. nigra* — OL.

Genus *Petrotilapia* Trewavas

Petrotilapia Trewavas, 1935: 76 (type-species: *P. tridentiger* Trewavas, 1935, by monotypy).

In general the diagnostic characters of the genus presented by Trewavas in her original key (1935: 67) distinguish this genus from all other Lake Malawi cichlids. It should be noted, however, that contrary to the definition of Trewavas (1935), the jaw teeth of *Petrotilapia* species are not all tricuspid and every specimen examined in the present study had some distinctly unicuspid teeth. There is usually a single or double lateral series of stout unicuspid teeth on both jaws posterior to the major dentigerous area, although some of these teeth may be weakly tricuspid. The broad bands of closely set teeth on the major dentigerous area are usually all tricuspid, but in some specimens the three posteriormost rows have a few unicuspid teeth. Trewavas' definition of the genus *Petrotilapia* should be modified to include those Lake Malawi cichlids with predominantly tricuspid teeth on the major dentigerous area of the jaws excluding the posterior sides of the premaxilla and dentary.

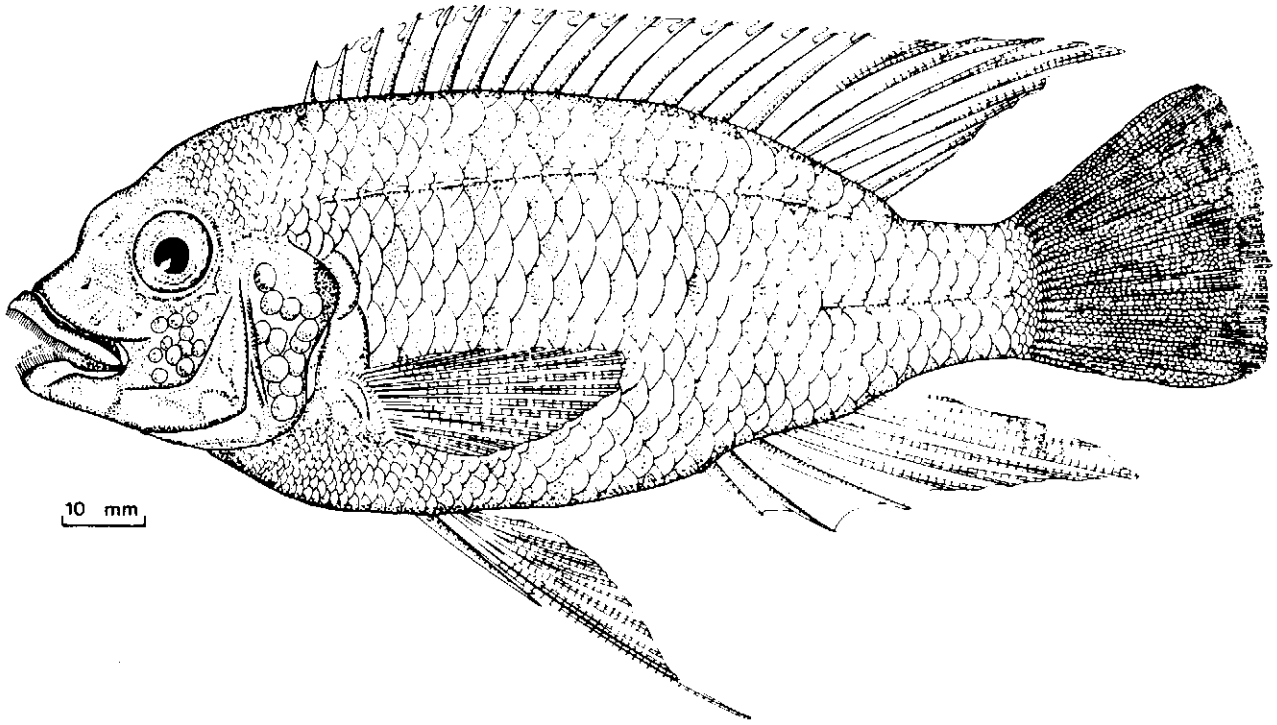

Figure 1. *Petrotilapia tridentiger*, male, 137 mm SL, RUSI 13394.

Petrotilapia tridentiger Trewavas
Figs. 1-7, 11, 12

Petrotilapia tridentiger Trewavas, 1935: 76 (type-locality: Lake Nyasa [Lake Malawi]).

DIAGNOSIS: In live and preserved specimens the dorsal fin has no submarginal stripe and lappet coloration is no different from the rest of the fin. Live adult males are normally uniform sky blue and live females and juveniles are normally uniform brown. Faint vertical bars, slightly darker than ground coloration, may be present in some specimens. Dorsal fin spines 16-18 (mode 17); head L/interorbital W 2.3-3.2 (mean 2.5); SL/caudal peduncle L 6.4-8.7 (mean 7.6).

DESCRIPTION: This is one of the largest Mbuna in Lake Malawi, attaining 141 mm SL at Nkhata Bay (n = 7), and 137 mm at Monkey Bay (n = 45). Greatest body depth between second and fourth dorsal-fin spines. Snout length subequal to eye diameter. Head profile variable, in small specimens and some adults the profile forms a smooth curve between the snout and the first dorsal fin spine, whereas other adults have an interorbital gibbosity of variable size. Figure 2 illustrates the extremes of head profile. Although there is no clear-cut correlation between size of interorbital gibbosity and standard length, large gibbosities are normally found in large males. The mouth is terminal with numerous irregular bands of closely set teeth visible in closed jaws. Proportional measurements for male and female *P. tridentiger* are given in Table 1.

In the following description, counts of the lectotype are in bold print. Dorsal-fin spines **16**-18, dorsal-fin rays 7-**8**-9; anal fin-spines **3**, anal fin rays 6-**7**-8. Spinous dorsal fin has well-developed lappets; the longest rays in males extend from one third to halfway along caudal fin, and in females from beyond base of caudal fin to one third along caudal fin. Anal fin extends posteriorly to a position slightly less than or equal to that of the dorsal-fin. Pelvic-fin rays moderately filamentous; in adult males they extend to between first anal-fin spine and first anal-fin ray. In females, the pelvic fins extend to between vent and anal fin origin. Pectoral-fin length 72-91% of head length. Caudal-fin subtruncate and densely scaled except on trailing edge. Pored scales: Upper lateral line 19-**21(22)**-24, lower lateral line 7-**10(11)**-13, total 29-**31**-33 (if left and right sides varied on the lectotype, both counts are given). Gill-rakers 2-**3**-4 + 8-**10**-12; the first one or two rakers on lower limb often reduced (see Tables 2—5 for additional counts).

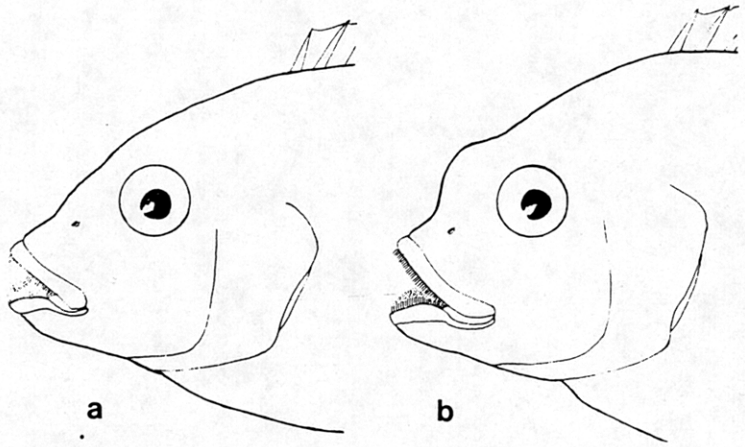

Figure 2. *Petrotilapia tridentiger*. Variation in head profile; (a) male, 132 mm SL; (b) male, 130 mm SL.

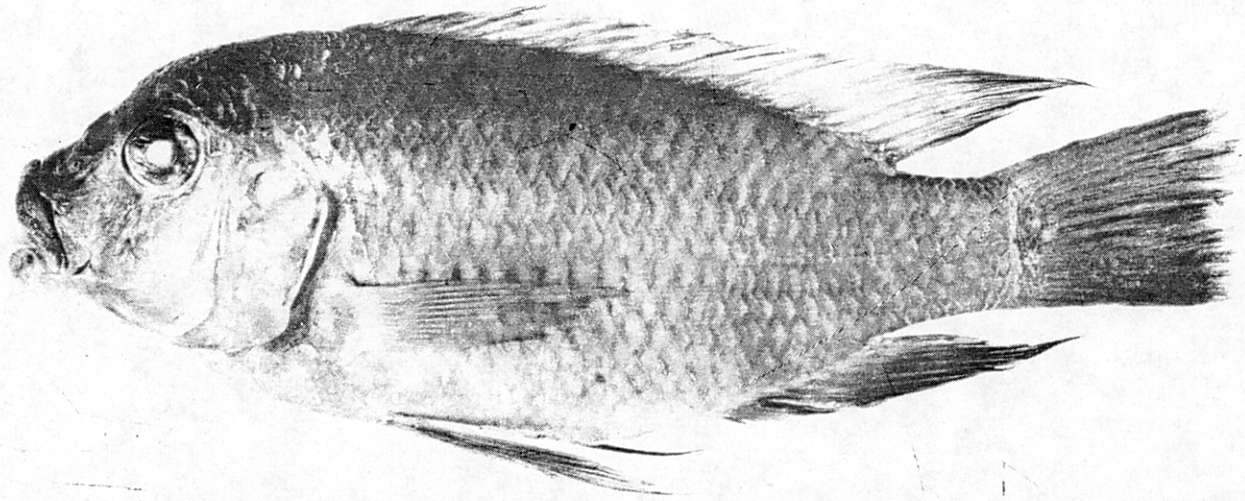

Figure 3. *Petrotilapia tridentiger*, Lectotype, male 125 mm SL, BMNH 1935-6-14: 244-248B.

Dentition (Fig. 4): Teeth closely set in numerous irregular bands; outermost rows procumbent. Most teeth comprise a long slender, slightly recurved shaft ending in a strongly recurved tricuspid tip. On the dentary and premaxilla, posterior to the major dentigerous area, the teeth are in one to three rows and are all unicuspid. Premaxillary unicuspid teeth approximately two thirds length of majority of tricuspid teeth, but considerably stouter. Dentary unicuspid teeth much smaller, being approximately one third length of tricuspid teeth and of similar shaft diameter. In some specimens unicuspid teeth occur in the three posteriormost rows of the major dentigerous areas of the premaxilla and dentary. Many teeth in these posterior rows are only weakly tricuspid, with two rudimentary cusps on either side of a major cusp.

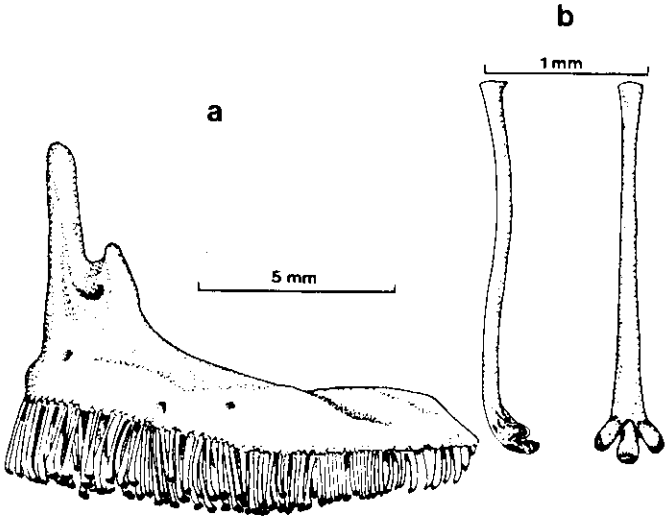

Figure 4. *Petrotilapia tridentiger*. (a) Lateral aspect of left premaxillary; (b) lateral aspect and frontal aspect of a single tricuspid tooth. Drawings from 137 mm SL territorial male.

Lower pharyngeal bone moderately indented posteriorly, with a triangular dentigerous area (Fig. 5). The anterior blade moderately long. Teeth in anterior half oval in cross section and strongly recurved towards the posterior. Teeth in posterior half rounded in cross section basally, becoming oval higher up the shaft with a slight anterior curvature. Teeth in posterior row much stouter than those of penultimate row. Tips of all teeth slightly hooked and blunt.

Colour of live territorial males: background colour pale blue with 7—9 darker blue vertical bars below dorsal fin visible in some specimens (Fig. 6a). Belly and gular regions whitish-blue. Dorsal fin pale blue with dark blue to black bars in posterior interradial membranes. Caudal fin trailing edge pale orange-brown, rays dark blue to black, and membrane between rays sky blue. Anal fin pale blue with dark blue to black stripes in posterior membranes and 1—5 bright orange to yellow ocelli on posterior angle membrane; leading and ventral edge of anal fin whitish-blue. Pelvic fins with whitish-blue leading edge and pale blue rays and membranes. Pectoral fins hyaline. Adult non-territorial males darker than territorial males; their overall colour tends towards purple. Background colour of live adult females and juveniles varies from dark

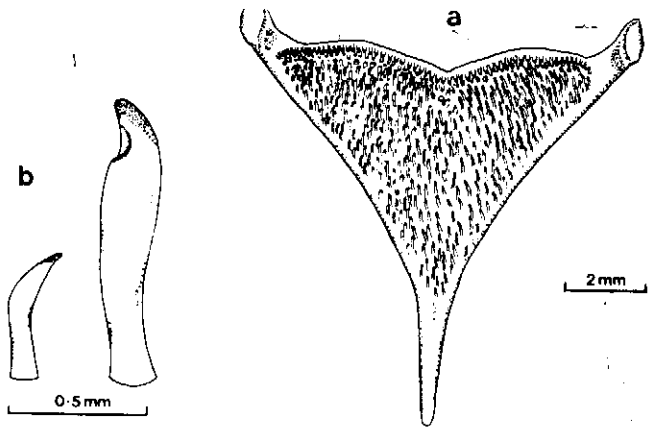

Figure 5. *Petrotilapia tridentiger*. (a) Dorsal aspect of lower pharyngeal bone; (b) lateral aspect of typical lower pharyngeal tooth (left) and tooth from posterior row (right).

brown to pale grey-brown (Fig. 7). Females and juveniles have 7—10 dark brown vertical bars below dorsal-fin, although in darker individuals these markings are partially obscured. The dorsal, caudal, anal and pelvic-fins are a semi-transparent brown and match the background colour of the fish. Pectoral fins hyaline. Preserved specimens uniform dull dark brown to grey with no dark bands on the fins.

COMPARISONS: *P. tridentiger* is readily distinguished from *P. genalutea* n.sp. and *P. nigra* n.sp. on the basis of coloration. In live and preserved specimens of *P. tridentiger* the dorsal fin has no submarginal stripe and lappet coloration is no different from the rest of the fin. Both *P. genalutea* and *P. nigra* have a dark submarginal stripe and pale lappets on their dorsal fins. Live males of *P. tridentiger* have a distinctive almost uniform sky blue colour, unlike the darker and duller coloration of the other two congeners. *P. tridentiger* usually has fewer dorsal-fin spines than the other two species (modally, 17 versus 18), a broader interorbital (head L/interorbital W mean, 2.5 versus 2.7), and longer caudal peduncle (SL/peduncle L mean 7.6 versus 8.0 and 8.2 for *P. genalutea* and *P. nigra* respectively).

ECOLOGY. *P. tridentiger* is a lithophilous species which feeds predominantly on epilithic algae and the benthic invertebrates living in the algal mat. In general it is a shallow water species being confined to the upper 8 m of water although at Boadzulu Island (14°15'S; 35°08'E) it penetrates to 20 m . *P. tridentiger* is a widespread species with a disjunct distribution (Figs. 11 & 12). It does not occur at any of the sites surveyed between Otter Point in the south and Nkhata Bay in the central region of Lake Malawi (a distance of approximately 240 km). Most of the intervening shore is sandy and therefore the species could at most be represented by small populations on scattered reefs. At the two sites where there are substantial rocky shores (Senga Point and Bandawe Point) this species did not occur, suggesting that it may not occur in this part of the lake at all. The shores of Mozambique and Tanzania were not visited and therefore the distribution between Chilumba and Makanjila is not known.

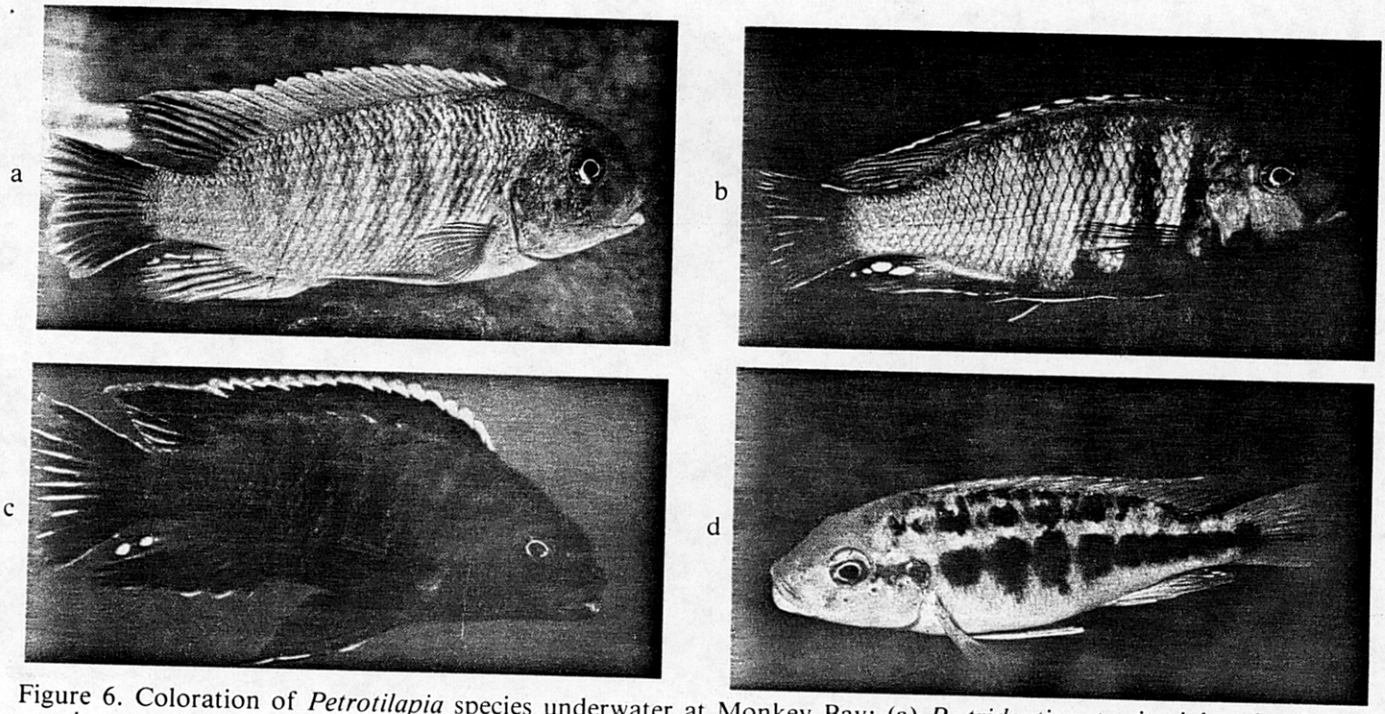

Figure 6. Coloration of *Petrotilapia* species underwater at Monkey Bay: (a) *P. tridentiger* territorial male, (b) *P. genalutea* territorial male, (c) *P. nigra* territorial male, (d) *P. genalutea* adult female.

Color photos x4

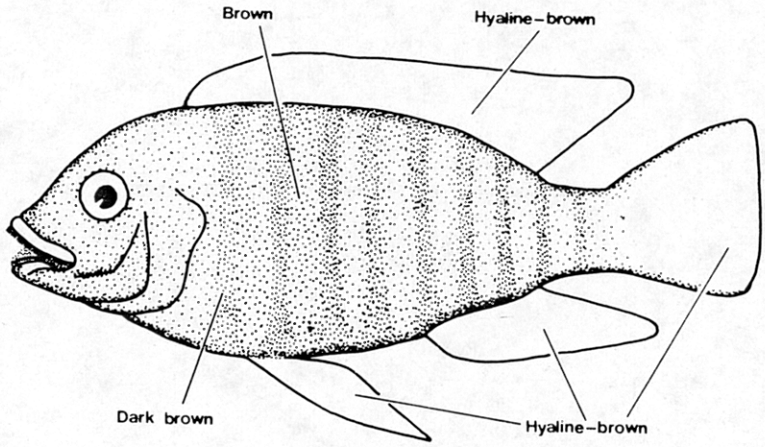

Figure 7. Typical coloration of an adult female *Petrotilapia tridentiger* from Monkey Bay.

MATERIAL EXAMINED: Lectotype: BMNH 1935-6-14: 244-248B, male, 125 mm SL, Monkey Bay, 1925-26, C. Christy. 45 specimens including 2 unsexed (97 and 99 mm SL), 31 males (99-137 mm SL), and 11 females (85-116 mm SL), captured at Monkey Bay (14°03'S; 34°55'E) in 0-4 m over rock by A.C. Marsh: RUSI 13394, male 137 mm SL, 10 September 1980; RUSI 13395-13396, two males, both 130 mm SL, 4 August 1980; RUSI 13397, male, 114 mm SL, 24 February 1980; RUSI 13398, male 137 mm SL, 10 September 1980; RUSI 13399-13400, two females, 116 and 111 mm SL, 10 September 1980; RUSI 13401-13402, two unsexed, 99 and 97 mm SL, 10 September 1980; RUSI 13403-13404, two males, 127 and 111 mm SL, 10 September 1980; BMNH 1981-2-2; 212-220, eight males, 132, 130, 128, 125, 123, 115, 113 and 99 mm SL and one female, 114 mm SL: USNM 228, 443, four males, 123, 121, 112 and 104 mm SL and two females, 107 and 102 mm SL, 10 September 1980.

The syntypes of *P. tridentiger* were examined at the British Museum (Natural History) by D. S. C. Lewis. The type-series comprises three adult specimens greater than 100 mm SL and two subadult specimens of approximately 81 mm SL from Monkey Bay; two specimens of 89 and 75 mm SL and numerous very small specimens from the extreme south of the lake from "Bar to Kudzi"; and three very small specimens of approximately 30 mm SL from Chilumba. D. S. C. Lewis compared specimens of the three species mentioned in this paper with the type-series from Monkey Bay and concluded that the type-series is polytypic. He was able to match one of the syntypes with one of the recently collected specimens from Monkey Bay. This syntype specimen (Fig. 3) has been examined by the author. Unfortunately the lower pharyngeal bone of this specimen has been lost (P.H. Greenwood, pers. comm.). Nevertheless, in view of the fact that this is the only syntype that can be confidently matched with one of the Monkey Bay species, it is here chosen as the lectotype.

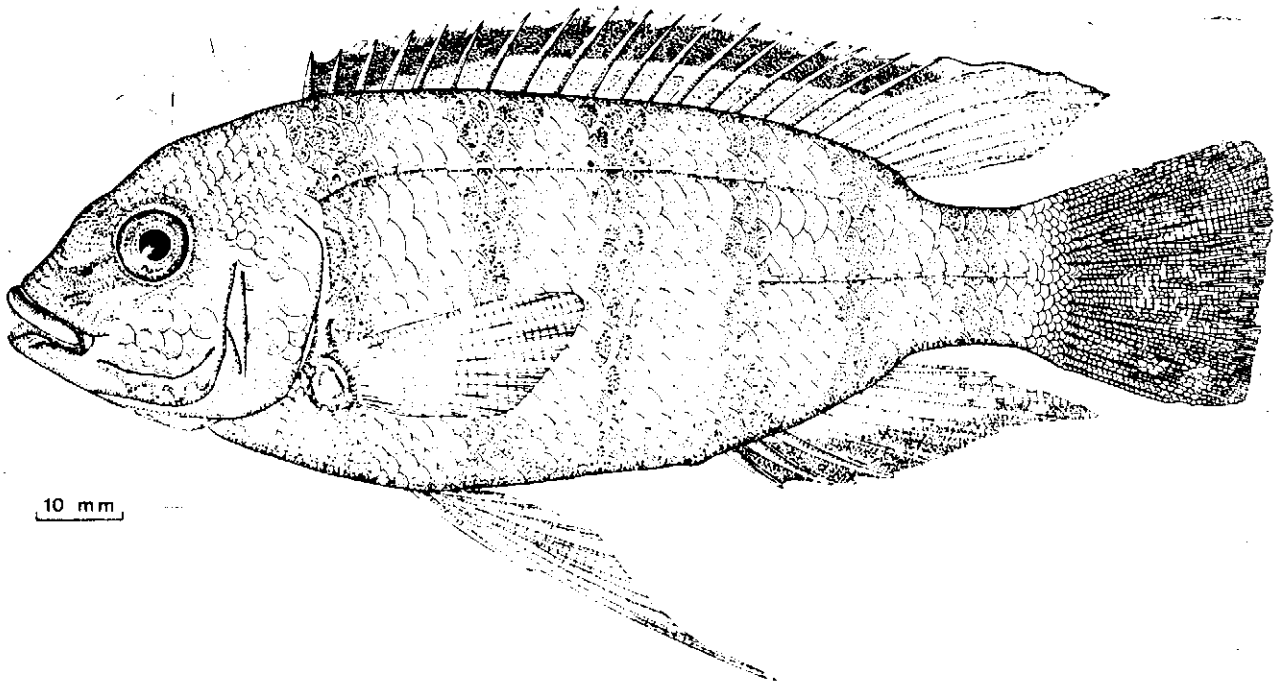

Figure 8. *Petrotilapia genalutea*, holotype, male, 121 mm SL, BMNH 1981-2-2: 221.

Petrotilapia genalutea n. sp.
Figs. 6b, 6d, 8, 11, 12

DIAGNOSIS: In live and preserved specimens the dorsal fin has a thin dark grey to black submarginal stripe. A dark submarginal stripe, (more evident in males) is also present on the pelvic and anal fins. Live territorial males: background colour bluish-grey with 4—6 dark grey vertical bars on body below dorsal fin; 'cheek' region and gular area an orange-brown rust colour. Live females and non-territorial males: background colour off-white to pale yellow-brown with white belly; dark mid-lateral blotches often fused on rear half of fish to form a thick stripe. Submarginal stripes in fins are retained in preserved specimens. Dorsal-fin spines 17-19 (mode 18); head L/interorbital W 2.5-3.2 (mean 2.7); SL/caudal peduncle L 6.9-9.3 (mean 8.0).

DESCRIPTION: A relatively large Mbuna, attaining 131 mm SL at Nkhata Bay (n = 8) and 126 mm at Monkey Bay (n = 38). Greatest body depth between second and fourth dorsal-fin spines. Snout length subequal to eye diameter. Dorsal head profile varies from weakly concave between eye and dorsal-fin origin (n = 18) to moderately and smoothly convex from snout to dorsal fin origin (n = 20). Some specimens, irrespective of sex or size, have a small interorbital gibbosity. Mouth terminal; numerous irregular bands of closely-set teeth visible in closed jaws. In a third of specimens examined, anterior tip of lower jaw projected slightly beyond tip of upper jaw. Proportional measurements for *P. genalutea* are given in Table 1.

In the following counts, data from the holotype are in bold print and, if left and right sides varied on the holotype, both counts are given. Dorsal-fin spines 17-**18**-19, dorsal-fin rays **8**-9; anal-fin spines **3**, anal-fin rays 6-7-9. Spinous dorsal fin with well-developed lappets; longest rays in males extend from one-third to halfway along caudal-fin, and in females from base of caudal-fin to one third along caudal fin. Anal-fin extends as far as dorsal fin. Pelvic rays filamentous; in adult males, they extend from just beyond first anal-fin spine to just beyond third anal-fin spine; in females, pelvic-fins extend to between vent and base of second anal spine. Pectoral-fin length 75-92% of head length, (one exceptional female with pectoral-fin length 45% of head length). Caudal-fin subtruncate and densely scaled except on trailing edge. Pored scales: Upper lateral line 19-**22(23)**-25, lower lateral line 9-**11(12)**-14, total 29-**31(32)**-35. Gill rakers 2-**3**-4 + **10(11)**-13, anterior one or two rakers on lower limb often reduced. (See Tables 2-5 for additional counts).

Dentition: Virtually indistinguishable from *P. tridentiger*. The lower pharyngeal bone similar to *P. tridentiger*, except that in *P. genalutea* the blade is not as deep (Table 6). Colour of live territorial males: background colour bluish-grey with 4—6 dark grey vertical bars below dorsal fin from first dorsal spine to base of caudal fin (Fig. 6b). Four anteriormost bars invariably distinct but posterior ones often partially faded and sometimes completely absent. Two dark grey stripes on head, one from tip of snout to orbit, the other between orbits. 'Cheek' region (below orbit from snout to posterior margin of operculum) and gular area an orange-brown rust colour. This rust area may extend beyond operculum below pectoral fins from base of pelvic fins to midway between pelvic fins and vent. Rust colour fades posteriorly; remainder of belly dark bluish-grey. Dorsal fin lappets variable in coloration; in some specimens they are pale orange-yellow, sometimes fading posteriorly and giving way to pale blue; in others, the lappets are entirely pale blue. Immediately below dorsal-fin lappets is a thin light blue stripe bordered by a black submarginal longitudinal band approximately one half of dorsal fin height and extending entire length of dorsal-fin in most specimens. Directly below this black band is another thin light blue stripe.

Below this stripe, the dorsal fin is a semi-transparent grey with orange-brown oval blotches on interradial membranes of some specimens. Posterior few membranes black. Caudal fin trailing edge orange; rays black and interradial membranes semi-transparent pale blue. Anal fin semi-transparent grey with thick black bar on distal edge extending from base of first anal spine to posterior angle; 1—4 bright yellow ocelli on rear end of fin. Pelvic fins with whitish-blue leading edge, including the spine; rays black and interradial membranes orange-brown. Pectoral fins hyaline. Background coloration of live non-territorial fish off-white to pale yellow-brown with white belly (Fig. 6d). A series of broad dark brown to black mid-lateral blotches from just posterior to operculum to base of caudal-fin; blotches normally close together and often fuse, particularly posteriorly, to form a continuous band. A series of thin, dark brown to black, dorso-lateral blotches runs above and parallel to thick blotches to end of dorsal fin base. Nine to ten pale brown vertical bars on flanks and caudal peduncle. Dorsal fin hyaline, except for orange-brown tips on lappets, a thin dark grey to black submarginal longitudinal stripe and orange-brown posterior rays. The anal-fin and pelvic-fins hyaline except for dark grey stripes on distal edges. Small pale yellow ocelli on rear end of anal-fin in some specimens. Adult non-territorial males with a yellow to orange flush on their 'cheeks' and gular region. Preserved adult males with dark grey background colour; 4-6 dark vertical flank bars in some specimens. Dorsal, pelvic and anal-fins with dark submarginal stripes. Orange-brown rust colour on cheeks of live males fades in preserved specimens. Preserved females and juveniles dark grey dorsally, becoming pale grey ventrally; dark grey to black mid-lateral blotches and submarginal stripe in dorsal fin present.

ETYMOLOGY. The trival name from the Latin *gena* = cheek and *lutea* = orange, refers to the characteristic orange 'cheeks' of adult males of this species.

COMPARISONS: *P. genalutea* is most distinguishable from *P. tridentiger* and *P. nigra* on the basis of coloration. Live adult male *P. genalutea* have distinctive orange-brown 'cheek' and gular areas, features which are not shared with the other two species. The presence of submarginal stripes in the dorsal fin distinguishes *P. genalutea* from *P. tridentiger;* this feature is reliable in live and preserved specimens of both sexes. Preserved male *P. genalutea* normally have 4-6 wide vertical flank bars and a narrow submarginal stripe in the dorsal fin, whereas, *P. nigra* territorial males are uniform black and have a broad submarginal band which occupies most of the dorsal fin. Differences between female *P. genalutea* and female *P. nigra* are subtle and there are no reliable features of morphology or colour to separate preserved specimens. In live females and juveniles *P. genalutea* generally have a paler and yellower background colour and consequently very obvious flank blotches. Furthermore, the mid-lateral blotches normally fuse posteriorly to form a wide black stripe. *P. nigra* females are normally darker in ground colour and the mid-lateral flank blotches rarely fuse together. *P. nigra* juveniles are uniform pale brown and generally lack adult body and fin markings.

ECOLOGY. Like *P. tridentiger, P. genalutea* is a lithophilous species which feeds predominantly on epilithic algae and on benthic invertebrates living in the algal mat. In general, it is a shallow water species occurring in less than 8 m of water, although at Boadzulu Island (14°15'S; 35°08'E) it penetrates to 18 m . *P. genalutea* is a widespread species (Figs. 11 & 12), occurring on most rocky shores and islands on the western side of Lake Malawi south of Ruarwe and as far north as Makanjila on the eastern side of the lake. It is not known whether it occurs north of Makanjila or between Senga Point and Bandawe Point.

MATERIAL EXAMINED: 38 specimens including 1 unsexed (106 mm SL), 18 males (95-124 mm SL) and 19 females (92-126 mm SL); all from Monkey Bay (14°03'S; 34°55'E) in 0-4 m over rock; collected during 1980 by A.C. Marsh.

HOLOTYPE: BMNH 1981-2-2:221, male, 121 mm SL, Monkey Bay, 6 August 1980.

PARATYPES: RUSI 492, male 123 mm SL, 6 August 1980; RUSI 494-495, two males, 113 and 110 mm SL, 6 August 1980; RUSI 496-498, three females, 118, 95 and 92 mm SL, 16 September 1980; RUSI 499, male, 96 mm SL, 16 September 1980; BMNH 1981-2-2:222-226, two males, 115 and 108 mm SL and three females, 115, 105 and 95 mm SL, 6 August 1980; USNM 228,444, three males, 122, 121 and 120 mm SL, 6 August 1980 and three females, 107, 101 and 99 mm SL, 16 September 1980.

Petrotilapia nigra sp. n.

Figs 6c, 9, 10, 12

DIAGNOSIS: In live and preserved specimens the dorsal, anal and pelvic fins have dark grey to black submarginal bands. In males these bands occupy most of the fins but in females they are considerably narrower. Live territorial males: dark grey-blue background colour with 7-9 wide black vertical bars below dorsal fin. These bars almost obscure the background colour in live specimens and in preserved specimens they fuse to create a uniformly black fish. Live females: pale brown background colour; superimposed on flanks are two longitudinal dark brown to black stripes, segmented by 7-9 narrow grey-brown vertical bars. Dorsal fin spines 17-19 (mode 18); head L/interorbital W 2.4-3.2 (mean 2.7); SL/caudal peduncle L 7.2-10.1 (mean 8.2).

DESCRIPTION: A relatively large Mbuna, attaining 122 mm SL at Monkey Bay (n = 45). Greatest body depth occurs between second and fourth dorsal-fin spines. Snout length generally slightly longer than eye diameter. Dorsal head profile variable; in most specimens the profile between orbit and dorsal-fin origin is a gentle smooth convex curve to an almost straight line, but some specimens have a slightly concave dorsal head profile. A small interorbital gibbosity present in some individuals, but there is no obvious relationship between this gibbosity and size or sex. Mouth terminal, and numerous irregular bands of closely set teeth are visible in the closed jaws. Proportional measurements for male and female *P. nigra* are given in Table 1.

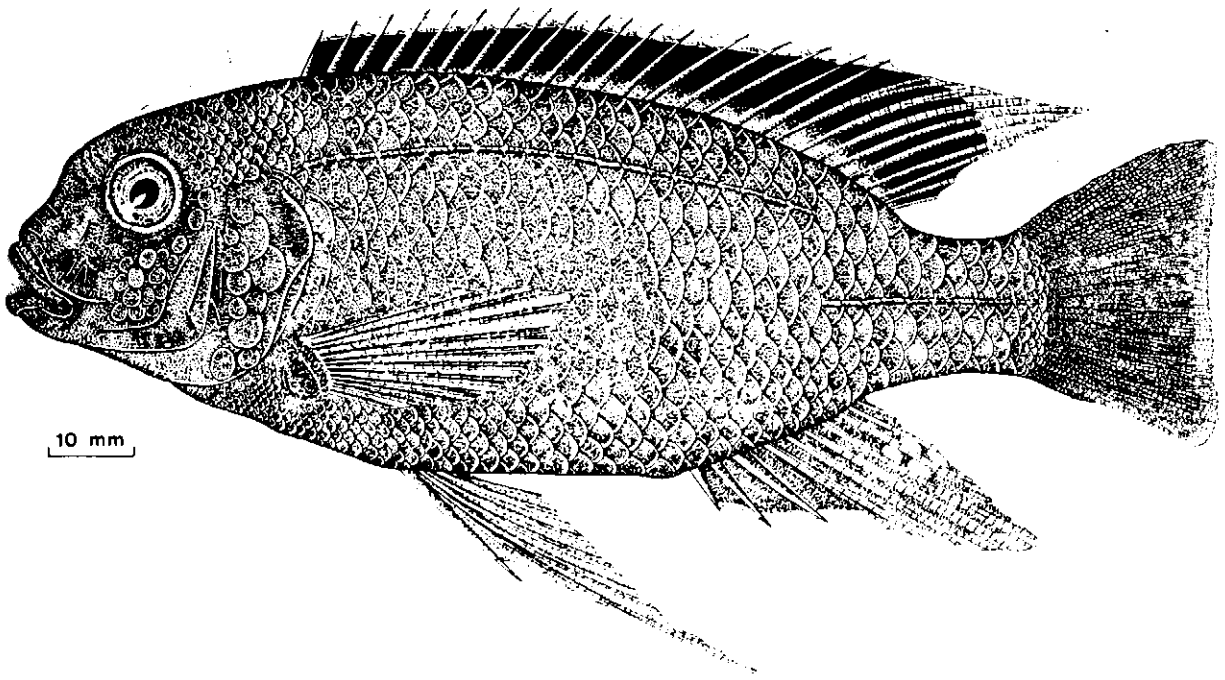

Figure 9. *Petrotilapia nigra*, holotype, male, 122 mm SL, BMNH 1981-2-2: 206.

In the description that follows, counts of the holotype are in boldface and, if left and right sides varied on the holotype, both counts are given. Dorsal fin spines **17-18-19**, dorsal-fin rays **7-9**; anal-fin spines **3**, anal-fin rays **6-7-9**. Spinous dorsal fin with well developed lappets; dorsal and anal-fins extend to approximately one-third along caudal fin. Pelvic-fin rays moderately filamentous; in adult males they extend from vent to base of third anal-fin ray. In females, the pelvic fins extend from just anterior to vent to base of second anal-fin spine.

Pectoral-fin length 70-94% of head length. Caudal fin subtruncate. Pored scales: upper lateral line 20-**23**-24, lower lateral line 8-**9**-13, total 29-**32**-33. Gill-rakers **2(3)-4 + 9-12**, anterior one or two rakers on lower limb often reduced (see Tables 2-5 for additional counts). Dentition indistinguishable from *P. tridentiger*. Lower pharyngeal bone indistinguishable from that of the other two species to the naked eye. Measurements with vernier calipers, however, indicate that the blade of *P. nigra* is not proportionally as deep as that of *P. tridentiger*, and is proportionally longer than that of *P. genalutea*. The pharyngeal bone of *P. nigra* is not proportionally as deep as that of *P. genalutea* (Table 6).

Colour of live territorial males: dark grey-blue background colour with 7-9 broad black vertical bars below dorsal fin (Fig. 6c). Head, gular region and caudal peduncle black, except for dark blue interorbital bar. Dorsal-fin lappets normally orange, but may be pale blue in some specimens. Immediately beneath the dorsal-fin lappets is a thin stripe of sky blue followed by a wide black longitudinal band that covers most of the fin; below this stripe the dorsal-fin is dark grey with orange flecks in some specimens. Caudal-fin trailing edge orange-brown, rays black and interradial membranes sky blue. Anal-fin predominantly black with pale blue distal edge and 1-4 bright yellow ocelli on rear end. Pelvic-fins with whitish-blue leading edge, black rays and dark brown interradial membranes; trailing edges often hyaline. Pectoral fins with black rays and hyaline interradial membranes. Non-territorial adult individuals: pale brown background colour; superimposed on flanks are two longitudinal dark brown to black stripes, segmented by 7-10 grey-brown vertical bars (Fig. 10). Ground colour of fins hyaline; dorsal-fin with pale orange lappets and a thin dark grey to black submarginal stripe. Anal and pelvic-fins with pale blue distal borders and thin brown to black stripes adjacent to these borders; posterior end of anal-fin sometimes with a few yellow ocelli. Juveniles uniform pale brown with hyaline fins; adult markings faintly visible in some juveniles. Preserved territorial males uniform black; preserved non-territorial fish dark brown-grey becoming light brown ventrally with a variable amount of flank markings visible. Black submarginal dorsal fin stripe always visible.

ETYMOLOGY: The trivial name is from the Latin *nigra* = black and refers to the dominant colour of territorial males.

COMPARISONS: Coloration is the most reliable feature which distinguishes *P. nigra* from other congeners. Live adult males: *P. nigra*, predominantly black body and head, wide black submarginal band in dorsal, pelvic and anal fins; *P. tridentiger*, predominently blue body and head, no submarginal bands in fins; *P. genalutea*, orange-brown 'cheek' and gular regions, blue-grey flanks with dark grey vertical bars, thin black submarginal stripes in dorsal, pelvic and anal fins. Preserved adult males: *P. nigra*, black head and body, thick black submarginal bands in dorsal, pelvic and anal fins; *P. tridentiger*, dark brown to grey head and body, no submarginal bands in fins, *P. genalutea*, dark grey head and body (may have 4-6 vertical flank bars), thin black submarginal stripes in dorsal, pelvic and anal fins.

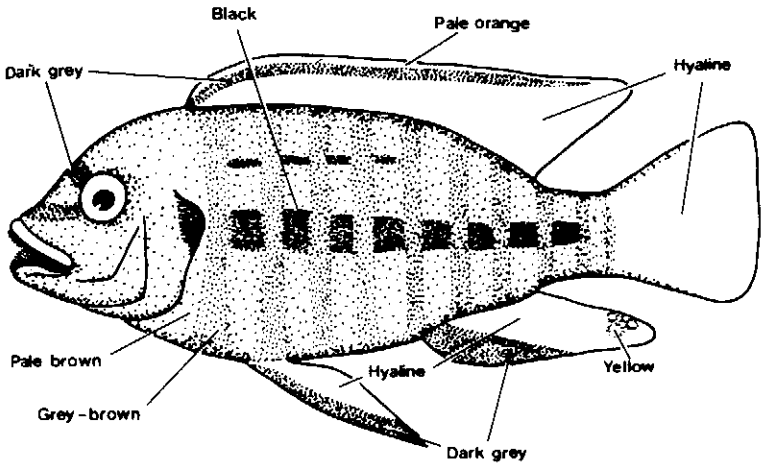

Figure 10. Typical coloration of an adult female *Petrotilapia nigra* from Monkey Bay.

Live adult females: *P. nigra,* pale brown head and body with two longitudinal dark brown to black stripes segmented by 7-10 grey-brown vertical bars, thin brown, dark grey or black submarginal stripes in dorsal, pelvic and anal fins; *P. tridentiger,* predominantly uniform brown, no submarginal stripes in fins; *P. genalutea,* off-white to pale yellow background colour with a series of thick dark brown to black mid-lateral blotches which often fuse posteriorly and a series of thin dark brown to black dorso-lateral blotches. Preserved adult females: *P. nigra* cannot be reliably separated from *P. genalutea* on morphological or colour characters; *P. tridentiger* females uniform brown-grey, including fins, whereas *P. nigra* and *P. genalutea* females have a pattern of blotches, stripes and bars on their flanks and dark submarginal stripes in their fins.

ECOLOGY: *P. nigra* is a lithophilous species which feeds predominantly on epilithic algae and benthic invertebrates living in the algal mat. It has a limited distribution in the south-east arm of Lake Malawi (Fig. 12) and a broad depth range. At Monkey Bay it occurs from the shallows down to 30 m and at Thumbi West Island (14°01'S; 34°49'E) it penetrates to 35 m .

MATERIAL EXAMINED: 45 specimens including 24 males (99-122 mm SL) and 21 females (83-114 mm SL); all from Monkey Bay (14°03'S; 34°55'E), captured in 0-10 m over rock during 1980 by A.C. Marsh.

HOLOTYPE: BMNH 1981-2-2:206, male, 122 mm SL, Monkey Bay, 11 September 1980.

PARATYPES: RUSI 500-501, two males, 118 and 115 mm SL, 27 August 1980; RUSI 502 male, 113 mm SL, 11 September 1980; RUSI 503, male, 107 mm SL, 27 August 1980; RUSI 504-508, five females, 111, 108, 106, 102 and 99 mm SL, 11 September 1980; RUSI 509, male, 102 mm SL, 11 September 1980; RUSI 510, male, 99 mm SL, 27 August 1980; BMNH 1981-2-2:207-211, two males, 120 and 111 mm SL and three females, 113, 108 and 95 mm SL, 11 September 1980; USNM 228, 442, one male, 116 mm SL, 27 August 1980, one male, 103 mm SL and two females, 107 and 105 mm SL, 11 September 1980.

DISCUSSION

The difficulty in distinguishing on morphological grounds between the three species of *Petrotilapia* treated here focuses attention on one of the major problems facing biologists working on the cichlids of the Great Lakes of Africa, namely the existence of sibling species complexes. The problems encountered when attempting to separate the species on morphological grounds alone are in part attributable to intraspecific character variation which results in large interspecific character overlaps (Tables 1-6). Of the three species, *P. tridentiger* is morphologically most distinct in usually having fewer dorsal-fin spines (Table 2), a lower number of total vertebrae (Table 3), a relatively broader head (head L/interorbital W, Table 6) and a relatively longer caudal peduncle (Table 6) than the other two congeners. As a consequence of their similar morphologies, no character was found that was completely distinctive for any one of the three species. Morphometric differences only became apparent when the data were treated statistically. Using a t-test for two means, numerous significant morphometric differences between territorial males of the three species were revealed $p < 0.05$; Table 6). Nevertheless in only four characters were all three species significantly different from one another. Although statistical tests may aid in resolving morphological differences between sibling species, proportional differences that can only be detected with the aid of statistics are not of much diagnostic value.

Similar situations exist for other cichlid species complexes in Lake Malawi as well as in Lakes Tanganyika and Victoria. Barel et al. (1977) suggest that accurate species diagnosis in Lake Victoria cichlids is normally possible only if a number of taxonomic characters are considered together. Eccles and Lewis (1977) found that for a reliable separation of the three Lake Malawi cichlids *Lethrinops stridei* Eccles and Lewis, *L. micrentodon* (Regan) and *L. microdon* Eccles and Lewis, it is necessary to use a number of characters in conjunction. In the Lake Malawi genus *Labidochromis* Trewavas, all species display considerable variation in most taxonomic characters, and owing to the degree of interspecific overlap, these taxonomic characters have little diagnostic value (Lewis, in press).

The most distinctive difference between the three species of *Petrotilapia* is live coloration particularly of territorial males. Although Barel et al. (1977) suggest that, as a rule, the diagnostic value of live coloration is of limited use in cichlid taxonomy, in the case of sibling species it is often the only reliable diagnostic character. The most important character separating the four endemic sibling species of *Sarotherodon* in Lake Malawi is the coloration of sexually active males (Trewavas, 1947; Lowe, 1952) in Lake Victoria as a rule, morphological characters separating cichlid species are slight, and male breeding colour is the most distinctive specific feature (Greenwood, 1974). Eccles and Lewis (1979) suggest that live coloration is of considerable taxonomic value in the genus *Lethrinops;* and Lewis, (in press) concludes that the most useful diagnostic character in the genus *Labidochromis* is the coloration of sexually active males.

Before the taxonomic value of live colour can be accepted, however, it is necessary to establish that the various colour forms are distinct species and not merely morphs of the same species. There are numerous examples in which the systematic status of certain fish is

in doubt due to the existence of numerous colour forms. One of the most interesting examples concerns the marine serranid genus *Hypoplectrus* (Walbaum). In this genus there are at present nine putative "species", and due to the absence of any other morphological differences the species descriptions are based almost exclusively on colour patterns (Graves and Rosenblatt, 1980). Furthermore, in addition to these nine "species" there are three distinctive unnamed colour forms (Thresher, 1978). Barlow (1975) has, however, shown that the *Hypoplectrus* "species" do not mate assortatively; and an electrophoretic analysis of their enzyme systems indicates that there is probably only one highly polymorphic *Hypoplectrus* species (Graves and Rosenblatt, 1980). The South American cichlid *Cichlasoma citrinellum* (Günther) is a polychromatic species. In Lake Jiloa, Nicaragua, the two colour morphs of *C. citrinellum* generaly mate assortatively but a certain amount of interbreeding has been reported (McKaye and Barlow, 1976). McKaye (1980) believes that the two morphs may be incipient species, but at present they share a common gene pool.

In Lake Malawi, Fryer (1959) noted that polymorphism occurs in five species of Mbuna; *Genyochromis mento* Trewavas, *Labeotropheus fuelleborni* Ahl, *L. trewavasae* Fryer, *Pseudotropheus tropheops* Regan and *P. zebra* (Boulenger). In most of these species the male is monochromatic and the female occurs in two forms, a 'normal' type and a 'blotched' type. At Nkhata Bay, however, *P. zebra* has five different colour forms, two male and three female. Using evidence of positive assortative mating amongst the colour forms of *P. zebra*, as well as other ecological differences, Holzberg (1978) suggests that *P. zebra* comprises two discrete gene pools (= species). Both species are sexually dimorphic and one of the females is also dimorphic, thus accounting for five colour forms. *P. zebra* is therefore polychromatic and polytypic. Polychromatic cichlid species have also been reported from the African Lakes Kivu, Kioga, Victoria and Tanganyika (Fryer and Iles, 1972), but no information exists on assortative mating in these populations. Evidence of positive assortative mating within the genus *Petrotilapia* (Marsh et al., 1981) provides another example in which a so-called polychromatic species is shown to be a complex of species. The *Petrotilapia* species covered in this paper are sexually dimorphic but none are polymorphic.

In the Great Lakes of Africa where 'explosive speciation' (*sensu* Greenwood, 1964) has occurred, there are likely to be numerous sibling species complexes in which coloration is the most distinctive specific feature. In a situation such as this, traditional taxonomic methods are inadequate unless they are combined with sound field observations, particularly on mate selection. Furthermore, prior to a morphological study on sibling species that differ mainly in terms of live coloration, it is imperative that collections should be made by identifying, capturing and labelling specimens in the field. If this method had not been adopted in the present study, a preserved collection representing all three species of *Petrotilapia* would probably have been assigned to one species only, or at most two if fin markings were considered.

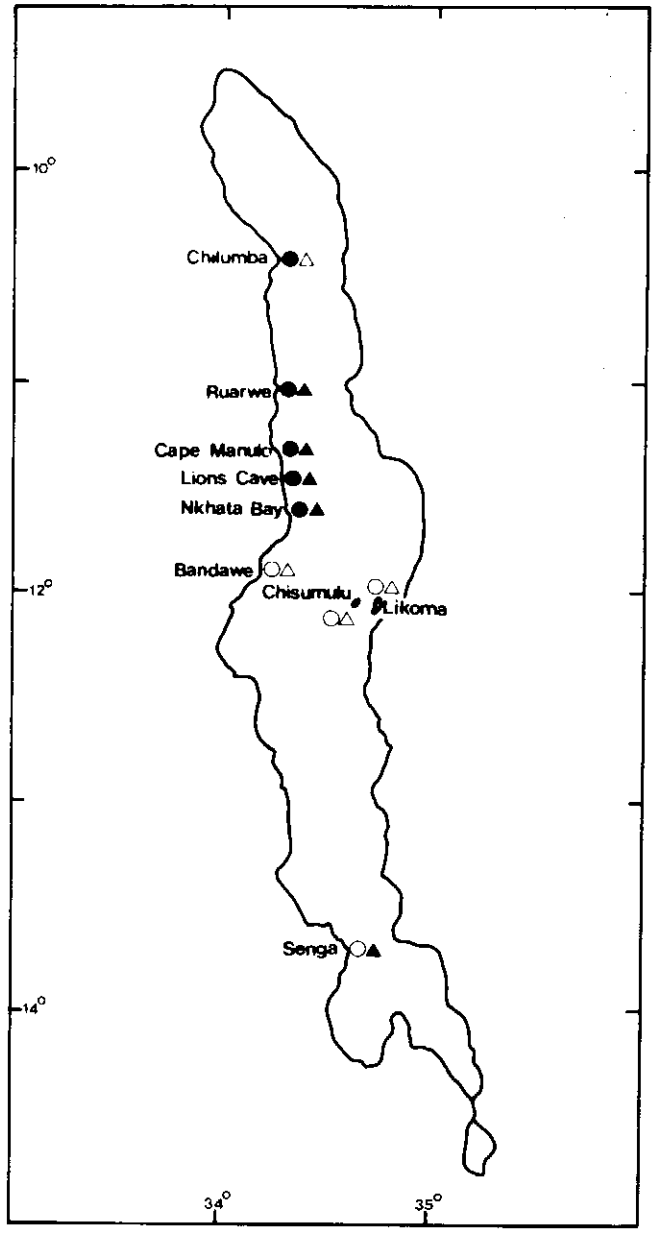

Figure 11. Map of Lake Malawi showing distribution of *P. tridentiger* and *P. genalutea* north of Senga. *P. tridentiger* present ●, absent o; *P. genalutea* present ▲, absent Δ.

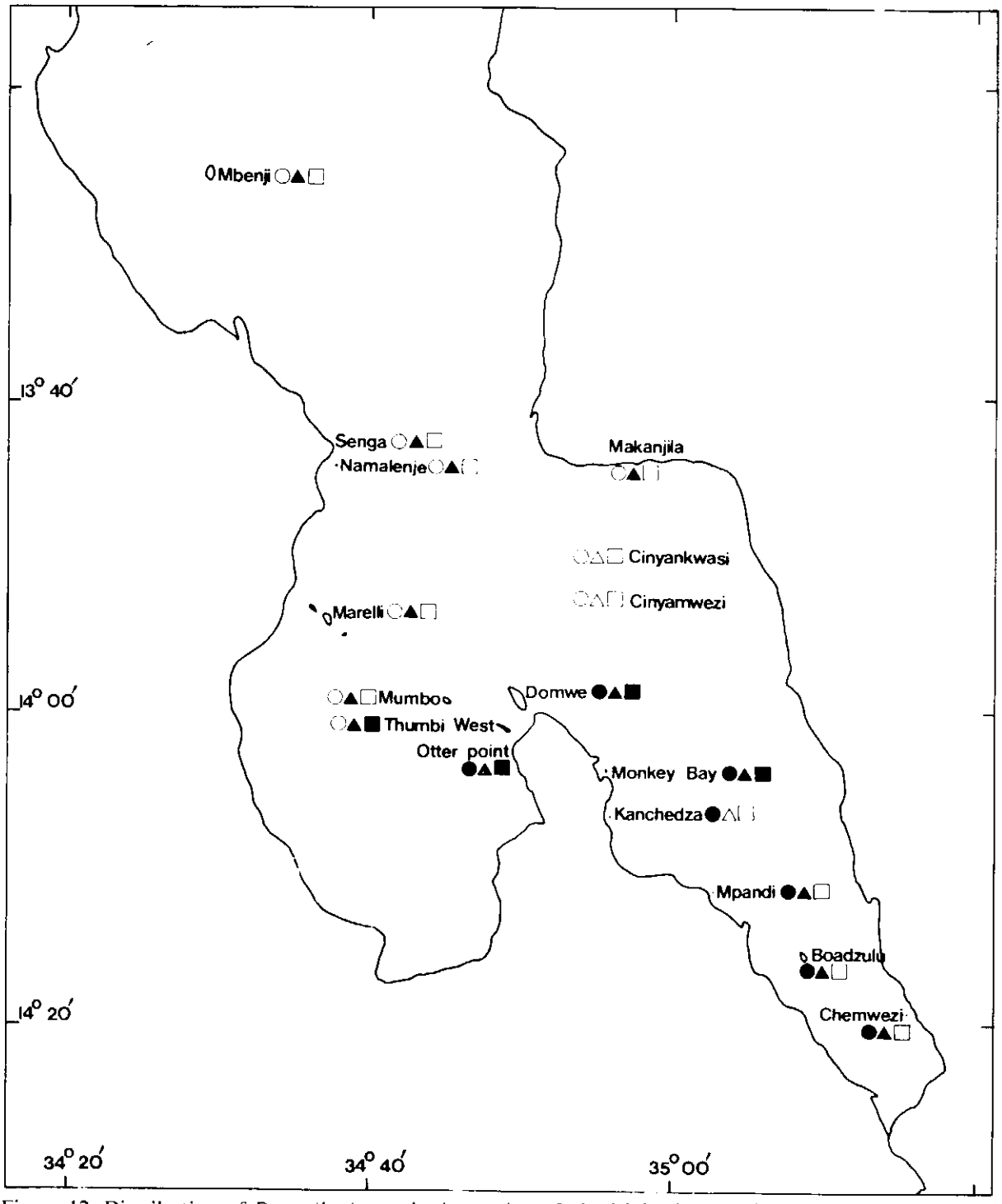

Figure 12. Distribution of *Petrotilapia* species in southern Lake Malawi. *P. tridentiger* present ●, absent o; *P. nigra* present ■, absent □; *P. genalutea* present ▲, absent △.

ACKNOWLEDGEMENTS

I would like to thank A.J. Ribbink for suggesting that the various colour forms of *Petrotilapia* may represent discrete species, D.S.C. Lewis for examining syntypes, for access to unpublished information and for many stimulating discussions, R. Brown for the excellent underwater photographs, M.M. Smith for advice on nomenclature, P.C. Heemstra for providing literature on *Hypoplectrus* and for critically reviewing the manuscript, B.A. Marsh for assistance with measuring specimens, help with statistical tests and for critically reading the manuscript, M.N. Bruton and P.B.N. Jackson for their useful comments on an early draft of this manuscript, and A. Chunga and E. Chioka for their assistance with field collections. The research was funded by the governments of Malawi and South Africa.

TABLE 1. Proportional measurements for species of *Petrotilapia*; *P. tridentiger* (n = 44, 85-137 mm SL), *P. genalutea* (n = 37, 92-126 mm SL and *P. nigra* (n = 45, 83-122 mm SL). Data for lectotype of *P. tridentiger* (pharyngeal bone missing) and holotype of *genalutea* and *nigra* in parentheses.

IN STANDARD LENGTH	*tridentiger*	*genalutea*	*nigra*
Body D	2.5-3.0(2.7)	2.6-3.0(2.8)	2.5-3.1(2.8)
Head L	2.9-3.3(3.2)	3.0-3.5(3.3)	3.0-3.5(3.4)
Caudal peduncle L	6.4-8.7(7.9)	6.9-9.3(8.5)	7.2-10.1(7.9)
Caudal fin L	3.7-5.3(4.4)	3.4-4.5(4.2)	3.5-5.1(4.4)
Pectoral fin L	3.5-4.3(3.7)	3.4-4.3(4.1)	3.4-4.5(3.7)
Pelvic fin spine L	5.7-7.2(6.2)	5.7-7.5(6.3)	5.6-6.9(6.1)
Pelvic fin ray L	2.5-3.7(2.6)	2.2-3.7(2.6)	2.2-3.7(2.5)
L to dorsal fin end	1.1-1.2(1.2)	1.1(1.1)	1.1-1.2(1.2)
L to anal fin end	1.1-1.2(1.2)	1.1-1.2(1.2)	1.1-1.2(1.2)
IN HEAD LENGTH:			
Eye diameter	3.0-3.7(3.6)	3.0-3.4(3.2)	2.9-3.7(3.3)
Snout L	2.7-4.0(2.7)	2.8-3.7(2.9)	2.6-3.8(3.2)
Preorbital D	3.5-4.9(4.2)	3.9-5.2(4.6)	2.8-5.0(3.8)
Interorbital W	2.3-3.2(2.8)	2.5-3.2(2.7)	2.4-3.2(2.6)
Lower Jaw L	3.3-4.5(3.6)	3.0-4.0(3.7)	3.1-4.7(3.5)
Premaxillary L	2.7-4.5(3.3)	2.8-4.2(4.0)	2.8-4.7(3.6)
Premaxillary pedicel L	4.0-6.5(4.8)	4.3-7.0(4.5)	4.0-5.7(4.5)
IN PHARYNGEAL BONE FORK L:			
Total L of pharyngeal	0.8-0.9	0.8-1.0(0.9)	0.8-0.9(0.9)
Pharyngeal W	0.8-1.0	0.8-1.0(0.9)	0.8-1.1(0.9)
Pharyngeal D	2.6-3.6	2.3-4.0(2.4)	2.7-3.8(2.9)
Pharyngeal blade L	2.0-4.2	2.0-3.5(3.2)	2.2-3.0(2.2)
Pharyngeal blade D	2.6-5.5	3.3-5.8(5.0)	4.1-5.7(4.5)
IN EYE DIAMETER:			
Interorbital W	0.7-1.0(0.8)	0.8-1.1(0.8)	0.8-1.0(0.8)
Preorbital D	1.0-1.6(1.4)	1.2-1.7(1.5)	0.9-1.6(1.2)
Premaxillary pedicel L	1.2-1.9(1.3)	1.4-2.4(1.4)	1.2-1.9(1.4)
MISCELLANEOUS PROPORTIONS:			
Caudal peduncle L/peduncle D	0.8-1.2(0.9)	0.8-1.1(0.9)	0.7-1.1(1.0)
Pelvic ray L/pelvic spine L	1.6-2.8(2.3)	1.6-3.3(2.4)	0.9-2.7(2.4)
Body W/premaxillary W	1.2-1.7(1.4)	1.0-1.8(1.7)	1.2-1.8(1.6)
Interorbital W/premaxillary W	0.9-1.1(1.0)	0.7-1.1(1.0)	0.8-1.1(1.0)
Premaxillary W/premaxillary D	1.1-1.7(1.2)	1.0-2.1(1.5)	1.0-1.8(1.4)
Body D/caudal peduncle D	2.6-3.0(2.8)	2.5-3.0(2.7)	2.5-3.0(2.8)

TABLE 2. Frequency distribution of dorsal-fin spine and soft-ray counts and anal-fin soft-ray counts for species of *Petrotilapia*.

Species (n)	Dorsal fin spines				Dorsal soft-rays			Anal soft-rays			
	16	17	18	19	7	8	9	6	7	8	9
tridentiger (34)	3	25	6	0	1	21	12	4	28	2	0
genalutea (36)	0	7	27	2	0	27	9	2	30	2	2
nigra (44)	0	7	36	1	1	31	12	8	31	4	1

TABLE 3. Frequency distribution of vertebral counts for species of *Petrotilapia*.

Species	Abdominal			Caudal		Total		
	14	15	16	15	16	30	31	32
tridentiger	4	5	0	3	6	7	2	0
genalutea	0	9	0	0	9	0	9	0
nigra	0	8	1	2	7	1	7	1

TABLE 4. Frequency distribution of lateral-line scale counts from left and right sides of species of *Petrotilapia*. Pored scales on caudal fin not counted.

Species (n)	Upper lateral line							Lower lateral line								Longitudinal series						
	19	20	21	22	23	24	25	7	8	9	10	11	12	13	14	29	30	31	32	33	34	35
tridentiger (33)	2	3	8	19	28	6	0	0	4	15	26	16	4	1	0	6	5	23	26	6	0	0
genalutea (35)	3	4	10	15	23	14	1	1	1	8	26	24	8	1	1	3	4	12	27	18	5	1
nigra (43)	0	4	12	25	37	8	0	0	3	12	22	35	13	1	0	1	9	21	40	15	0	0

TABLE 5. Frequency distribution of gill-raker counts from left and right sides of first gill arch for species of *Petrotilapia*.

Species (n)	Upper limb			Lower limb					
	2	3	4	8	9	10	11	12	13
tridentiger (44)	17	69	2	1	5	25	48	9	0
genalutea (36)	21	49	2	0	0	12	44	14	2
nigra (43)	25	58	3	0	2	19	50	15	0

TABLE 6: Proportional measurements of territorial male *Petrotilapia* species from Monkey Bay. Means ($\bar{X}$) in boldface are significantly different from other means. Significant differences ($P < 0.05$) determined using t-test for two means.

Proportion	*tridentiger (n = 31)*		*genalutea (n = 18)*		*nigra (n = 24)*	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Standard L (mm)	**126**	(114-137)	**122**	(108-124)	**112**	(102-122)
SL/body D	**2.7**	(2.5-2.9)	**2.8**	(2.6-3.0)	2.7	(2.5-2.9)
SL/head L	3.2	(2.9-3.3)	**3.3**	(3.1-3.4)	3.2	(3.0-3.4)
SL/caudal peduncle L	**7.6**	(6.5-8.7)	8.0	(6.9-8.8)	**8.2**	(7.6-10.1)
SL/caudal fin L	**4.3**	(3.7-4.8)	4.0	(3.6-4.5)	4.1	(3.7-4.5)
SL/pectoral fin L	3.9	(3.5-4.2)	4.0	(3.7-4.2)	**3.7**	(3.4-4.5)
SL/pelvic fin spine L	**6.3**	(5.8-7.2)	**6.6**	(5.8-7.5)	**6.0**	(5.6-6.5)
SL/pelvic fin ray L	2.7	(2.5-3.7)	2.7	(2.2-3.6)	2.6	(2.2-3.2)
SL/L to dorsal end	**1.2**	(1.1-1.2)	1.1	(1.1)	1.1	(1.1-1.2)
SL/L to anal fin end	1.2	(1.1-1.2)	1.2	(1.1-1.2)	1.2	(1.1-1.2)
Head L/eye diameter	**3.4**	(3.2-3.7)	**3.2**	(3.0-3.4)	**3.3**	(3.0-3.7)
Head L/snout L	3.2	(2.7-3.8)	3.2	(2.8-3.7)	3.1	(2.6-3.6)
Head L/preorbital D	**4.1**	(3.5-4.6)	4.4	(3.9-5.2)	4.3	(2.8-4.8)
Head L/interorbital W	**2.5**	(2.3-2.8)	2.7	(2.5-3.2)	2.7	(2.5-3.1)
Head L/lower jaw L	3.6	(3.3-4.1)	3.7	(3.4-4.0)	**3.9**	(3.2-4.7)
Head L/premaxillary L	3.2	(2.7-4.1)	3.4	(2.8-4.2)	3.3	(2.8-4.3)
Head L/premaxillary pedicel L	4.8	(4.0-6.3)	5.1	(4.3-6.6)	4.8	(4.0-5.7)
Pharyngeal fork L/pharyngeal total L	0.9	(0.8-0.9)	0.9	(0.8-1.0)	0.9	(0.8-0.9)
Pharyngeal fork L/pharyngeal W	0.9	(0.8-1.0)	0.9	(0.9-1.0)	0.9	(0.8-1.0)
Pharyngeal fork L/pharyngeal D	3.0	(2.6-3.6)	**2.9**	(2.3-4.0)	**3.2**	(2.7-3.8)
Pharyngeal fork L/pharyngeal blade L	2.5	(2.0-4.2)	**2.7**	(2.1-3.5)	**2.4**	(2.2-3.0)
Pharyngeal fork L/pharyngeal blade D	**4.2**	(2.6-5.1)	4.7	(4.1-5.8)	4.6	(4.1-5.0)
Eye diameter/interorbital W	**0.8**	(0.7-0.9)	0.9	(0.8-1.1)	0.8	(0.8-1.0)
Eye diameter/preorbital D	**1.2**	(1.0-1.6)	**1.4**	(1.3-1.7)	**1.3**	(0.9-1.6)
Eye diameter/premaxillary pedicel L	**1.4**	(1.2-1.9)	**1.6**	(1.4-1.9)	1.5	(1.2-1.9)
Caudal peduncle/L/caudal peduncle D	1.0	(0.8-1.1)	1.0	(0.8-1.1)	0.9	(0.7-1.0)
Pelvic fin ray L/pelvic fin spine L	2.3	(1.6-2.8)	2.5	(1.6-3.3)	2.4	(0.9-2.7)
Body W/premaxillary W	1.4	(1.2-1.7)	1.4	(1.2-1.7)	1.4	(1.3-1.6)
Interorbital W/premaxillary W	1.0	(0.9-1.1)	1.0	(0.9-1.0)	1.0	(0.8-1.1)
Premaxillary W/premaxillary D	1.3	(1.1-1.5)	1.3	(1.0-1.6)	1.3	(1.1-1.7)
Body D/caudal peduncle D	2.7	(2.6-3.0)	2.8	(2.5-3.0)	2.7	(2.5-3.0)

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