



## Redescription of *Pseudotropheus livingstonii* and *Pseudotropheus elegans* from Lake Malaŵi, Africa

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### Abstract

*Pseudotropheus livingstonii* and *P. elegans* are two sand-dwelling cichlid species that belong to the so-called mbuna, a group of predominantly rock-dwelling haplochromines of Lake Malaŵi. The identity of these two species has confused taxonomists for almost a century until a recent rediscovery of representatives of *P. elegans* close to its type locality. New diagnoses for both species are provided.

**Key words:** Ethmo-vomerine bloc, mbuna, *Metriaclima lanisticola*

### Introduction

In the lakes of East Africa, fishes of the family Cichlidae have undergone an extraordinarily rapid and extensive radiation. Within Lake Malaŵi, over 450 species have been formally described, and many undescribed species have been discovered from recently explored areas. It is estimated that in Lake Malaŵi alone, there may be as many as 850 cichlid species (Konings 2007). Within this diverse assemblage of fishes the small and colorful rock-dwelling cichlids are referred to as mbuna in the local vernacular. Although not formally described, the mbuna share the following characters: 1) large number of small scales on the nape and chest region; 2) abrupt transition from large flank scales to small chest scales; 3) reduction of the left ovary which is non-functional; and 4) possession of true ocelli on the anal fin (Fryer 1959; Oliver 1984). The mbuna are mostly associated with rocky habitats, but a small group of species occurs on sandy substrates (Fryer 1959; Fryer & Iles 1972; Ribbink *et al.* 1983; Stauffer 1991), including *Pseudotropheus elegans* Trewavas and *P. livingstonii* (Boulenger).

Discrimination among cichlid species of Lake Malaŵi can be difficult, because visual differences among species may be very small (Konings 2007) and because morphological characters may be prone to convergence (Kocher *et al.* 1993) and/or are phenotypically flexible (Stauffer & Gray 2004). In conjunction with their morphological attributes, behavioral traits of these species are important diagnostic tools in distinguishing the multitude of species (Barlow 2002; Stauffer *et al.* 2002). The taxonomic history of *P. livingstonii* and *P. elegans* represents the difficulties researchers have in classifying Malaŵi cichlids.

In 1899, Boulenger described *Tilapia livingstonii* from a single specimen which was collected in Lake Malaŵi about 40 years earlier by Livingstone during his Zambesi Expedition and which was since 1863 registered as *Perca vittata* (a marine species) in the British Museum (BMNH 1863.11.12.22). In 1922, Regan synonymized *T. livingstonii* with *Pseudotropheus williamsi* Günther 1893, but it was later reinstated as *P. livingstonii* by Trewavas (1935). At the same time, Trewavas described *P. elegans* from a single specimen collected in Deep Bay (Chilumba Bay), Lake Malaŵi, by Christy. Trewavas had examined the type of *P. livingstonii* and found that it was sufficiently different from *P. elegans* to warrant the description of the latter. The type of *P. livingstonii*, even after more than 150 years of preservation, still exhibits a vague barring pattern (the drawing accompanying its description depicts

distinct bars), but no such pattern is discernable on the type of *P. elegans*. Nevertheless, Trewavas (1935) did not remark on this difference in melanin patterns, but instead distinguished *P. elegans* from *P. livingstonii* by its slightly larger eye and narrower preorbital bone. In 1983, Ribbink *et al.* (1983) found that *Pseudotropheus lanisticola* Burgess 1976, a shell-dwelling mbuna described from the southern part of the lake, was conspecific with Boulenger's *P. livingstonii* and regarded *P. lanisticola* as a junior synonym. Ribbink *et al.* (1983) further reported on the presence of large numbers of *P. elegans* in the southern portion of the lake in schools over sandy bottom. Stauffer *et al.* (1997) assigned *P. livingstonii* and *P. elegans* to *Metriaclima*, but Konings (2007) reversed this assignment.

Stauffer *et al.* (1997) diagnosed *Metriaclima*, and this diagnosis was expanded by Konings & Stauffer (2006). Condé & Géry (1999) claimed that *Metriaclima* should be regarded as a junior synonym of *Maylandia* Meyer & Foerster (1984), however, Meyer & Foerster (1984) failed to supply a character in which their subgenus *Maylandia*, defined by its type species *M. greshakei*, is distinct from *Pseudotropheus*. Characters were given for a so-called zebra complex but *M. greshakei* was not considered part of that complex. The subgenus was thus not diagnosed according to the requirements of Article 13.1.1 of the Code, and was therefore regarded a *nomen nudum* by Stauffer *et al.* (1997) and subsequent authors (Konings & Geerts 1999, Geerts 2002, Stauffer & Kellogg 2002).

In 2007, Konings also synonymized *P. elegans* with *P. livingstonii* and reinstated *P. lanisticola* as the shell-dwelling species. The purpose of this paper is to redescribe *P. livingstonii* and *P. elegans* on the basis of morphological examination of the type material and on behavioral differences obtained from field observations. Our studies show that *P. livingstonii*, *P. elegans*, and *P. lanisticola* are three species distinguishable by morphological and behavioral differences.

## Methods and materials

Fishes were collected in Lake Malaŵi by chasing them into a monofilament block net while SCUBA diving. Fishes were collected and processed under approval of the Animal Use and Care Committee at Penn State University (IACUC #24269). All fishes were anesthetized with clove oil, euthanized in 1% formalin, pinned in trays so that the bodies were flat and the fins erect, preserved in 10% formalin, and placed in permanent storage in 70% ethanol. Counts and measurements follow Stauffer (1994) and Stauffer & Konings (2006). All counts and measurements were taken from the left side of the body with the exception of gill-raker counts, which were taken on the right side.

Morphometric data were analyzed using a sheared principal component analysis, which factors the covariance matrix and restricts size variation to the first principal component (Humphries *et al.* 1981; Bookstein *et al.* 1985). Meristic data were analyzed using a principal component analysis in which the correlation matrix was factored. Differences among species were illustrated by plotting the sheared second principal components (SPC2) of the morphometric data against the first principal components (PC1) of the meristic data (Stauffer & Hert 1992).

The holotypes of *P. livingstonii* (BMNH1863.11.12.22), *P. elegans* (BMNH1935.6.14.127) and *Metriaclima lanisticola* (USNM 216266) were scanned on the high-resolution x-ray computed tomography (HRCT) system in the Center for Quantitative X-Ray Imaging (CQI) at Penn State University. Specimens were mounted vertically, the mandibles pinned together to create a standard position, and scanned with target pixel and slice resolutions of approximately 20  $\mu\text{m}$ . Scan data were reconstructed as 16-bit TIFF images with a 1024 $\times$ 1024 pixel grid. For each individual, the entire head was scanned. The volumetric image datasets for each fish were used to create a three-dimensional isosurface reconstruction (Fig. 1) in order to study bone tissue using the visualization software Avizo 6.1 (VSG, Burlington, MA). Because all of the fishes were HRCT scanned with the same energy settings and voxel resolutions, a global threshold was used for all datasets to separate bone from non-bone for the three-dimensional reconstructions.

Angles were measured on the ethmo-vomerine bloc of the parasphenoid in Avizo 8.0. The 3D reconstruction of the parasphenoid was cut along a parasagittal plane, and a line was defined along the cranio-caudal axis of this element using the ventral most extent of the juncture of the posterior parasphenoid processes and the ventral most extent of the anterior portion of the parasphenoid at the top of the ethmo-vomerine bloc. The angle was measured between this axis and the long axis of the ethmo-vomerine bloc drawn on this mid-line cross-section.

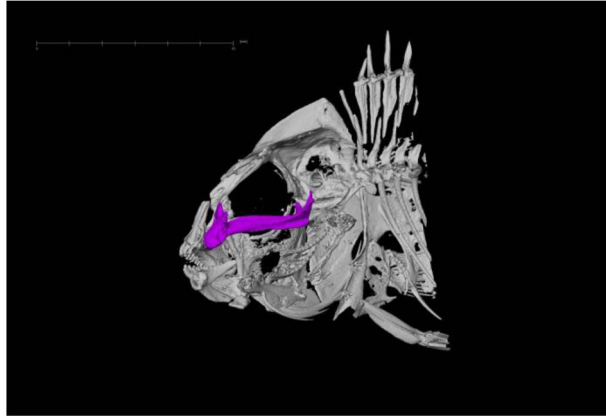


Fig. 1a

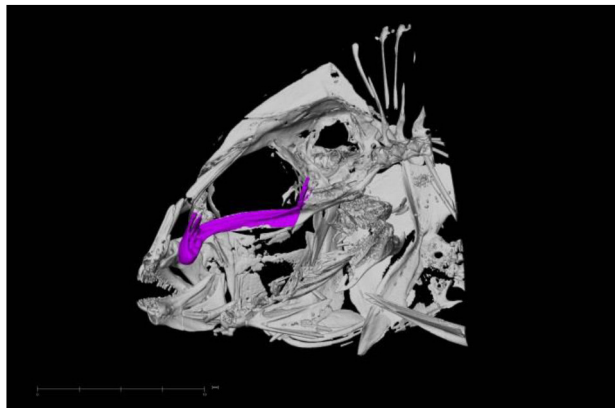


Fig. 1b

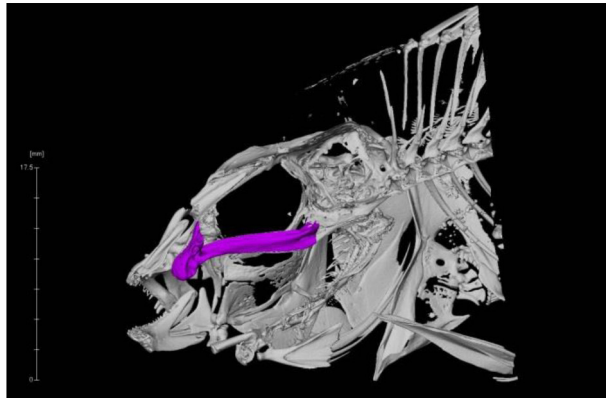


Fig. 1c

**FIGURE 1.** Three-dimensional surface reconstructions of the skulls of the three holotypes, showing the position of the parasphenoid and the angle of the ethmo-vomerine bloc. 1a, *Metriaclima lanisticola* (BMNH1976.7.29.2), angle  $48.7^\circ$ ; 1b, *Pseudotropheus livingstonii* (BMNH1863.11.12.22), angle  $57^\circ$ ; 1c, *P. elegans* (BMNH1935.6.14.127), angle  $58^\circ$ .

## Results

### *Pseudotropheus livingstonii* (Boulenger 1899)

(Fig. 2)

*Tilapia livingstonii* Boulenger 1899

*Pseudotropheus williamsi* (non-Günther).—Regan 1922

*Pseudotropheus livingstonii*, Trewavas 1935.—Konings 2007

*Pseudotropheus elegans* (non-Trewavas) .—Ribbink *et al.* 1983

*Metriaclima livingstonii*.—Stauffer *et al.* 1997

**Material examined.** *Pseudotropheus livingstonii* BMNH1863.11.12.22, holotype, 55.7 mm SL, Zambesi Expedition, Lake Malaŵi; PSU4925, 19, 64.3–114.4 mm SL, Cape Maclear, 14°05' S, 34°54'E, Lake Malaŵi .

**Diagnosis.** *Pseudotropheus livingstonii* is distinguished from all other members currently in *Pseudotropheus* (Konings 2007), except *P. crabro*, *P. demasoni*, and *P. saulosi*, by the presence of five or fewer vertical bars below the dorsal fin. Most *Pseudotropheus* species either have no bars or have greater than five below the dorsal fin. *Pseudotropheus livingstonii* is distinguished from *P. crabro*, *P. demasoni*, and *P. saulosi* by a pale yellow to hyaline dorsal fin vs. dorsal fin heavily pigmented with black.

**Description.** Principal morphometric ratios and meristics for holotype and for specimens from population at Cape Maclear in Table 1. Medium-sized to large mbuna, ovoid body (mean BD 31.4% SL) with greatest depth between fourth to sixth dorsal spine. Dorsal body profile with gradual curve downward posteriorly, more pronounced towards caudal peduncle; ventral body profile almost straight between pelvic fins and base of anal fin with upward taper to caudal peduncle. Dorsal head profile rounded, with smooth curve between interorbital and dorsal-fin origin; horizontal eye diameter (mean 32.0% HL) greater than preorbital depth (mean 19.6% HL); eye (along horizontal axis) in center of head; snout straight to slightly concave in some individuals; isognathous jaws; tooth bands with 4–5 rows in upper jaw and 3–5 rows in lower; rows continuous through symphyses; teeth in anterior outer row bicuspid with posterior lateral teeth primarily unicuspid, teeth in inner rows tricuspid.

**TABLE 1.** Morphometric and meristic values of *Pseudotropheus livingstonii*, and *P. elegans*.

Variable	<i>P. livingstonii</i> (holotype)	<i>P. livingstonii</i> (PSU4925)	<i>P. elegans</i> (holotype)	<i>P. elegans</i> (PSU11394) Chitande (n=12)		
	BMNH1863.11. 12. 22	Cape Maclear (n=19)	BMNH1935.6.1 4.127			
		Mean	Range	Mean	Range	
Standard length, mm	55.7	82.7	64.3–114.4	85.4	55.9	43.4–63.1
Head length, mm	18.4	25.0	19.7–34.7	24.8	17.5	13.5–20.0
Percent standard length						
Head length	33.0	30.3	28.2–32.5	29.3	31.3	29.4–33.1
Body depth	31.4	31.4	28–35	32.2	31.6	29–34
Snout to dorsal-fin origin	33.6	33.8	32.2–35.6	32.6	34.4	31.7–37.8
Snout to pelvic-fin origin	36.4	37.4	35.4–39.7	39.0	37.6	35.1–39.8
Dorsal-fin base length	64.0	59.2	56.9–61.8	61.1	60.7	57.6–64.9
Anterior dorsal to anterior anal	55.4	51.3	48.1–54.6	52.7	49.4	47.3–51.9
Anterior dorsal to posterior anal	63.7	62.4	58.7–65.4	64.6	61.1	57.1–64.7
Posterior dorsal to anterior anal	34.0	30.9	28.9–32.4	30.3	31.9	30.2–33.9
Posterior dorsal to posterior anal	18.2	15.2	14.3–16.2	15.4	15.8	14.5–16.9
Posterior dorsal to ventral caudal	20.6	18.0	16.0–20.0	19.5	18.4	16.8–21.1
Posterior anal to dorsal caudal	20.4	20.6	17.0–22.6	20.4	20.7	19.0–22.6
Anterior dorsal to pelvic-fin origin	33.3	33.1	30.2–36.7	34.3	32.2	29.1–35.4

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**TABLE 1.** (Continued)

Variable	<i>P. livingstonii</i> (holotype) BMNH1863.11. 12. 22	<i>P. livingstonii</i> (PSU4925) Cape Maclear (n=19)	<i>P. elegans</i> (holotype) BMNH1935.6.1 4.127	<i>P. elegans</i> (PSU11394) Chitande (n=12)		
		Mean	Range	Mean	Range	
Posterior dorsal to pelvic-fin origin	54.1	56.3	53.5–58.8	56.6	58.1	55.4–60.6
Caudal-peduncle length	17.2	16.0	14.1–17.9	15.6	15.8	14.6–17.0
Least caudal-peduncle depth	13.5	12.1	11.2–12.8	12.0	12.3	11.2–13.0
Percent head length						
Snout length	32.7	34.6	31.7–40.4	31.3	28.9	26.4–31.9
Postorbital head length	45.8	37.3	35.2–40.8	36.7	40.8	37.4–47.3
Horizontal eye diameter	32.5	32.0	29.1–35.3	36.0	36.7	34.0–39.3
Vertical eye diameter	31.7	30.5	26.3–33.7	34.7	35.1	32.5–38.0
Preorbital depth	21.5	19.6	15.4–23.8	20.5	16.3	15.1–18.3
Cheek depth	24.0	22.9	20.8–25.9	27.5	20.9	19.3–22.7
Lower-jaw length	38.1	37.5	32.6–42.0	35.6	35.9	30.6–41.0
Head depth	85.8	84.6	74.9–98.7	97.0	84.5	77.2–89.2
Counts		Mode	Range		Mode	Range
Dorsal-fin spines	17	18	17–19	17	18	17–19
Dorsal-fin rays	9	9	9–10	9	9	8–9
Anal-fin spines	3	3	3	3	3	3
Anal-fin rays	8	8	8–9	8	8	8–9
Pectoral-fin rays	5	5	5	5	5	5
Pelvic-fin rays	14	14	13–14	14	13	12–14
Lateral-line scales	31	33	32–35	31	32	32–33
Pored scales posterior to lateral line	2	3	2–4	2	2	1–2
Scale rows on cheek.	4	4	3–4	4	3	3
Gill-rakers on first ceratobranchial	10	11	9–12	11	11	10–12
Teeth on outer row of left lower jaw	11	14	12–17	11	11	11–14
Teeth rows on upper jaw	5	5	4–5	5	4	4
Teeth rows on lower jaw	5	4	3–5	5	3	3–4

**FIGURE 2.** The holotype of *Pseudotropheus livingstonii* ((BMNH1863.11.12.22).

Dorsal fin XVII–XIX (mode XVIII) and 9–10 (mode 9). Anal fin III and 8–9 (mode 8). First 4–5 dorsal-fin spines gradually longer posteriorly; fourth spine about 2 times length of first spine; last 13 spines slightly longer posteriorly; last spine longest, about 3 times length of first spine; rayed portion of dorsal fin with subacuminate

(females) to pointed (males) tip, third or fourth ray longest, to approximately  $\frac{1}{4}$  length of caudal fin in females and approximately  $\frac{3}{4}$  length of caudal fin in males. Anal-fin spines progressively longer posteriorly; third or fourth anal-fin ray longest,  $\frac{1}{2}$  length caudal fin in both sexes; 0–3 small yellow spots on posterior part of anal fin in females and 0–6 yellow spots on posterior part of anal fin in males. Caudal fin subtruncate to slightly emarginate. Pelvic fin to first or second spine of anal fin. Pectoral fin moderately long and wing-shaped with upper pointed tip, length to vertical line through base of 12th or 14th dorsal-fin spine. Flank scales ctenoid with abrupt transition to small scales on breast; 32–35 lateral-line scales; cheek with 3–4 (mode 4) rows of small scales; caudal fin with tiny scales to  $\frac{1}{4}$  length; no scales on other fins. Gill rakers on first ceratobranchial 9–12 (mode 11).

Recently captured fish with dark brown head, white gular region with gray blotches; black spot on opercle with reflected blue highlights. Laterally brown with 4 dark brown bars from dorsal fin to belly. Caudal fin with yellow rays and clear membranes. Anal fin brown anteriorly to first or second ray, hyaline posteriorly; 0–6 yellow ocelli in rayed portion. Pectoral fins with yellow rays and clear membranes. Pelvic fins black anteriorly, hyaline posteriorly. Female coloration similar to male, not as vivid.

### ***Pseudotropheus elegans* Trewavas 1935**

(Fig. 3)

*Pseudotropheus elegans* Trewavas 1935

*Metriaclima elegans*.—Stauffer *et al.* 1997

*Pseudotropheus livingstonii* (non-Boulenger).—Konings 2007

*Pseudotropheus* sp. 'acei'.—Konings 2007

**Material examined.** *Pseudotropheus elegans*, BMNH1935.6.14.127, holotype, 85.4 mm SL, Chilumba Bay, Lake Malaŵi; PSU11394, 12 specimens, 43.4–63.1 mm SL, Chitande Island, 12° 23.764'S 34° 15.275'E, Lake Malaŵi .

**Diagnosis.** *Pseudotropheus elegans* is distinguished from all other members currently in *Pseudotropheus*, except *P. williamsi*, by a pale yellow to hyaline dorsal fin and by the absence of distinct vertical bars below the dorsal fin. Most species of *Pseudotropheus* either have distinct bars below the dorsal fin or a dorsal fin with black pigment. It is distinguished from *P. williamsi* by the absence of two horizontal lines of black dots on the flank.

**Description.** Principal morphometric ratios and meristics for holotype and population from Chitande Island in Table 1. Medium-sized mbuna, ovoid body (mean BD 31.6% SL) with greatest depth at about 6–7th dorsal spine. Dorsal body profile with gradual curve downward, more acute towards caudal peduncle; ventral body profile slightly convex between pelvic fins and base of rays of anal fin with upward taper to caudal peduncle. Dorsal head profile round, with continuous curve between interorbital and dorsal-fin origin; horizontal eye diameter (mean 36.7% HL) greater than preorbital depth (mean 16.3% HL); eye (along horizontal axis) in anterior half of head; snout straight; jaws isognathus; tooth bands with 4 rows in upper jaw and 3–4 rows in lower; teeth in anterior outer row bicuspid with posterior lateral teeth primarily unicuspid, and teeth in inner rows tricuspid



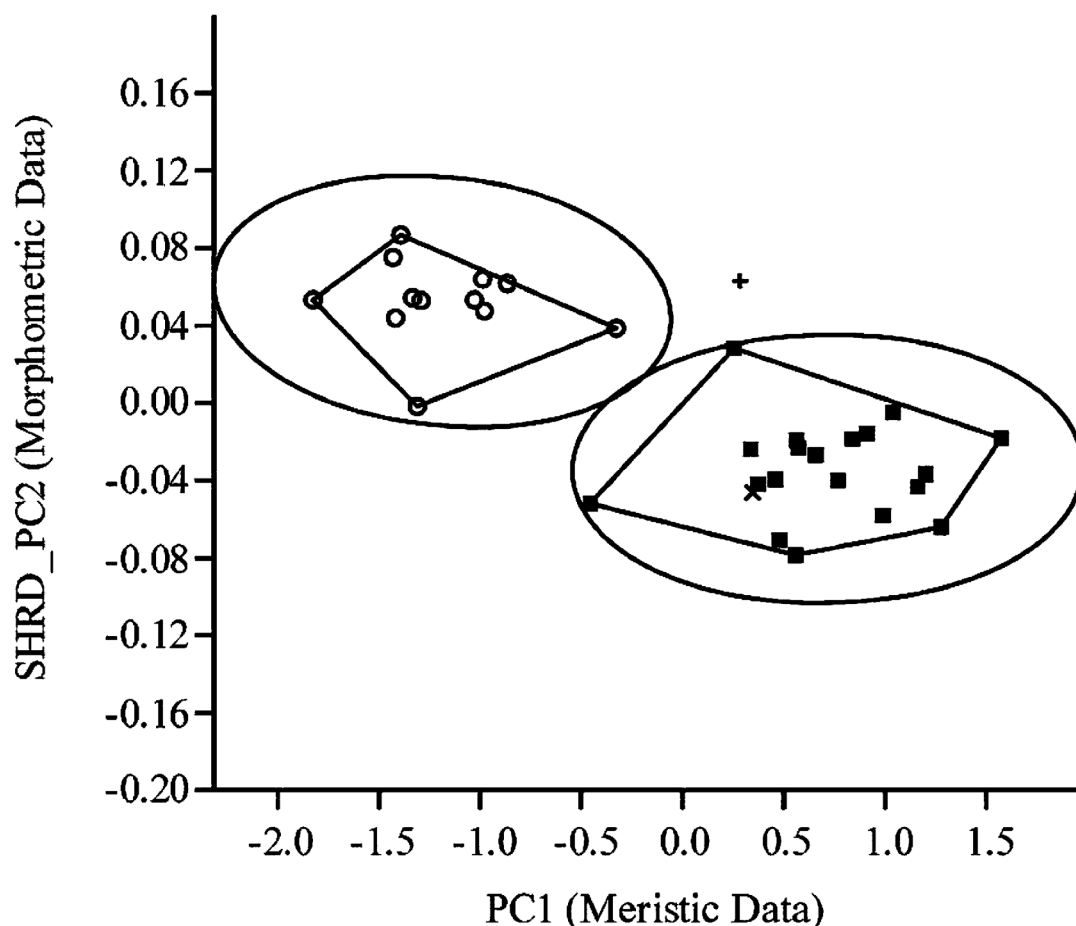
**FIGURE 3.** The holotype of *Pseudotropheus elegans* (BMNH1935.6.14.127).

Dorsal fin XVII–XIX (mode XVIII) and 8–9 (mode 9). Anal fin III and 8–9 (mode 8). First 4–5 dorsal-fin spines gradually longer posteriorly with fourth spine about  $\frac{1}{2}$  times length of first; last 13 dorsal-fin spines increasingly longer posteriorly with last spine longest, about 2 times length of first; soft dorsal fin with subacuminate tip, third or fourth ray longest, to approximately  $\frac{1}{4}$  length of caudal fin. Anal-fin spines progressively

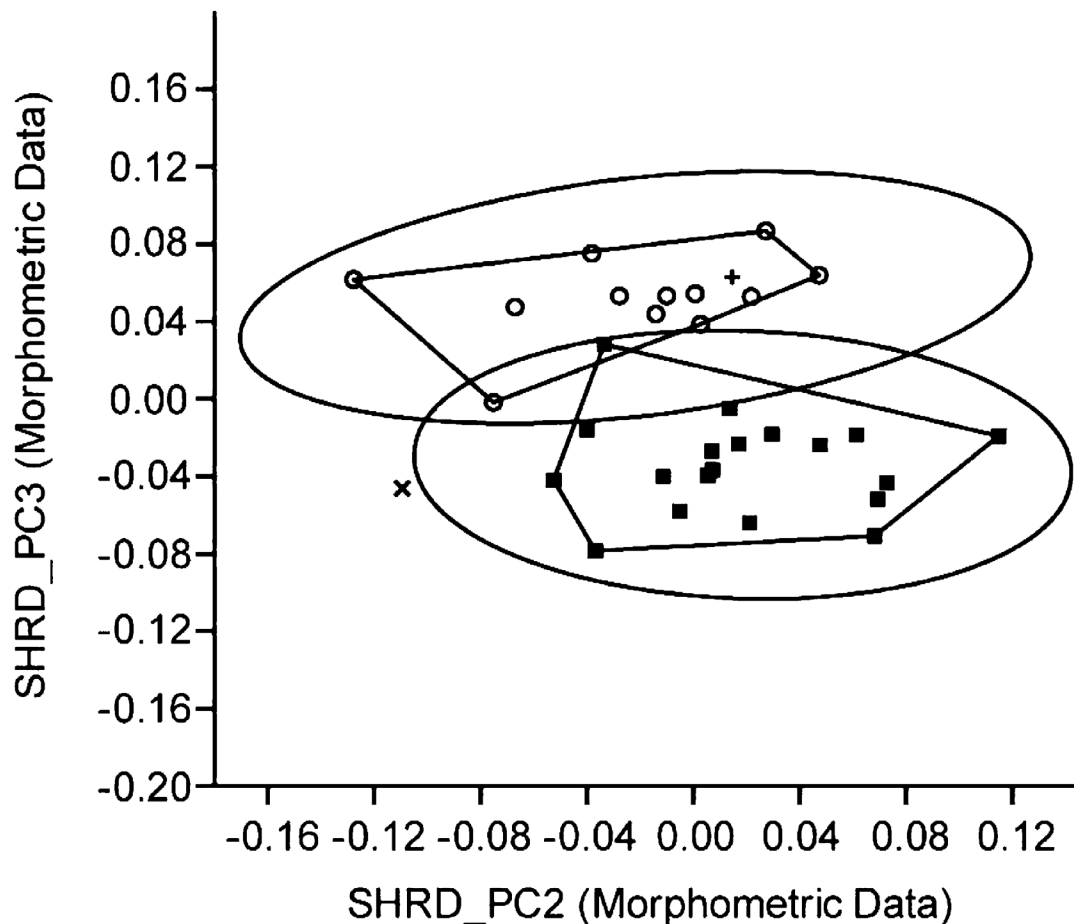
longer posteriorly; 3<sup>rd</sup> or 4<sup>th</sup> ray longest, to base of caudal fin in both sexes; 1–3 small yellow spots on posterior part of anal fin. Caudal fin subtruncate to slightly emarginate. Length of pelvic fin to first spine of anal fin. Pectoral fin short and paddle-shaped, length to vertical line through base of 10–11<sup>th</sup> dorsal-fin spine. Flank scales ctenoid with abrupt transition to small scales on breast; 32–33 lateral-line scales; cheek with 3 rows of small scales; caudal fin with tiny scales to ¼ length; no scales on other fins. Gill rakers on first ceratobranchial 10–12 (mode 11).

Recently captured fish with gray head, white gular region, and black opercular spot. Laterally gray ground coloration; scales with green outline; breast and belly gray. Dorsal fin pale yellow to hyaline. Caudal fin with two ventral rays and membranes black; remainder clear with faint white spots. Anal fin black with white marginal band; 1–3 yellow ocelli in rayed portion. Pectoral-fin rays clear; pelvic-fin rays black anteriorly, remainder clear. Coloration of female similar to male.

**Remarks.** The holotype of *P. elegans* and a population of this species collected from Chitande Island were compared morphologically to the holotype of *P. livingstonii* and a population of *P. livingstonii* collected from Cape Maclear. A plot of the sheared third principal components of the morphometric data against the first principal components of the meristic data (Fig. 4) showed that the holotype of *P. livingstonii* grouped within the minimum polygon clusters and the 95% confidence ellipses formed by the meristic and morphometric data from those individuals collected at Cape Maclear. A plot of the sheared second principal components against the sheared third principal components (Fig. 5) showed that the holotype of *P. elegans* grouped within the minimum polygon cluster and the 95% confidence ellipses formed by the morphometric data from those individuals collected at Chitande Island.



**FIGURE 4.** Sheared third principal components (morphometric data) plotted against the first principal components (meristic data) of the holotype (x) and specimens of *Pseudotropheus livingstonii* from Cape Maclear (■) and the holotype (+) and specimens of *P. elegans* from Chitande (o). The minimum polygon clusters are bounded by 95% confidence levels.



**FIGURE 5.** Sheared second principal components (morphometric data) plotted against the sheared third principal components (morphometric data) of the holotype (x) and specimens of *Pseudotropheus livingstonii* from Cape Maclear (■) and the holotype (+) and specimens of *P. elegans* from Chitande (o). The minimum polygon clusters are bounded by 95% confidence levels.

The first principal component (size variable) of the morphometric data explained 96% of the observed variance, the sheared second principal component explained 25% and the third sheared principal component explained 15% of the remaining variance. Variables that had the highest loadings on the sheared second principal components of the morphometric data were preorbital depth (-0.51), distance between the posterior insertion of the anal fin and dorsal origin of the caudal fin (0.38), and the distance between the posterior insertion of the dorsal fin and the ventral origin of the caudal fin (0.27). Variables that had the highest loadings on the sheared third principal components of the morphometric data were snout length (-0.63), vertical eye diameter (0.43), and head depth (0.31). The first principal component of the meristic data explained 39.8% of the variance. Variables with the highest loadings on the first principal components of the meristic data were tooth rows on the upper jaw (0.40), pored scales posterior to the lateral line (0.36), and anal-fin rays (0.38).

The HRCT scans permitted us to critically analyze the shape of the skull of the type specimens of *P. livingstonii*, *P. elegans*, and *M. lanisticola*, a sand-dwelling species of *Metriaclima*. We found that the angle that the ethmo-vomerine bloc makes with the parasphenoid is much more acute in *Pseudotropheus* than in *Metriaclima*. The angle in the holotype of *P. livingstonii* is 57°, and in that of *P. elegans* is 58°. The ethmo-vomerine bloc/parasphenoid angle in the holotype of *M. lanisticola* is 48°.

## Discussion

*Pseudotropheus livingstonii* and *P. elegans* belong to a small group of sand-dwelling mbuna, while almost all other members of the mbuna are found in rocky habitats. One of the characteristics that sets these sand-dwelling mbuna apart from almost all rock-dwellers is the fact that there is no, or very little, sexual dimorphism.



A third sand-dwelling mbuna, *M. lanisticola*, played a role in the taxonomic confusion as for a long time it was thought to be a junior synonym of *P. livingstonii* (Ribbink *et al.* 1983). Both of these species exhibit a distinct barring pattern, lacking in *P. elegans*, and are difficult to distinguish on the basis of external morphology. *Metriaclima lanisticola* lives in empty shells of the snail *Lanistes nyassanus* and rarely attains a total length of more than 6 cm while *P. livingstonii* can grow to a size of about 13 cm. All known populations of *M. lanisticola* are characterized by a caudal fin that has a pattern consisting of irregular yellow and blue bands. The caudal fin of *P. livingstonii*, however, is clear and usually has a white upper and lower edge. Other morphological differences between *P. livingstonii* and *M. lanisticola* include: the latter rarely has more than four rows of teeth in the oral jaws while *P. livingstonii* usually has five or six rows. The teeth of the inner rows in *M. lanisticola* are widely spaced whereas they are close-packed in *P. livingstonii*. The holotype of *P. livingstonii* has six rows of closely packed teeth.

In addition, *M. lanisticola* feeds on algae, which is raked from shells, shell fragments, or small pebbles lying on the sand. *Pseudotropheus livingstonii* and *P. elegans* feed by picking or scooping algae from the sand or from objects on the sand. Their feeding technique differs from the combing or raking technique displayed by *M. lanisticola* (Konings 2007). Since the holotype of *P. livingstonii* is a relatively small specimen (55.7 mm SL) it could be confused with a large specimen of *M. lanisticola*. Our HRCT scans, however, revealed that the vomer-parasphenoid angle in the holotype of *P. livingstonii* is 57° and that of *P. elegans* is 58°, well outside the range found in *Metriaclima* (35–50°) (Konings 2007, Konings & Stauffer 2006). The vomer-parasphenoid angle in the holotype of *M. lanisticola* is 48.7°, which is within the range found in *Metriaclima* spp.

It should be noted that we realize that *Pseudotropheus* is polyphyletic, and that *P. livingstonii* and *P. elegans* do not form a monophyletic group with *P. williamsi*, the type species of the genus. We are in effect using *Pseudotropheus* as a holding place, similar to the way in which Greenwood (1979) used *Cyrtocara* for many Lake Malaŵi species when he removed them from *Haplochromis*. We currently lack sufficient data to diagnose a new genus to accommodate these two and undoubtedly many other species that are still assigned to *Pseudotropheus*.

## Acknowledgements

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