

# Article

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## A new species of *Lethrinops* (Cichliformes: Cichlidae) from a Lake Malawi satellite lake, believed to be extinct in the wild.

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### Abstract

A new species of cichlid fish, *Lethrinops chilingali* is described from specimens collected from Lake Chilingali, near Nkhotakota, Malawi. It is assigned to the genus *Lethrinops* based on the form of the lower jaw dental arcade and by the absence of traits diagnostic of the phenotypically similar *Ctenopharynx*, *Taeniolethrinops* and *Tramitichromis*. It also lacks the enlarged cephalic lateral line canal pores found in species of *Alticorpus* and *Aulonocara*. The presence of a broken horizontal stripe on the flanks of females and immature/non-territorial males of *Lethrinops chilingali* distinguishes them from all congeners, including *Lethrinops lethrinus*, in which the stripe is typically continuous. *Lethrinops chilingali* also has a relatively shorter snout, shorter lachrymal bone and less ventrally positioned mouth than *Lethrinops lethrinus*. It appears likely that *Lethrinops chilingali* is now extinct in the wild, as this narrow endemic species has not been positively recorded in the natural environment since 2009. Breeding populations remain in captivity.

**Keywords:** African cichlid, haplochromine, Lake Chilingali, morphology.

## 39 Introduction

40 Satellite lakes are small lakes lying in the catchment of much larger lakes, formerly or  
41 sometimes intermittently connected (Kaufman & Ochumba 1993; Mwanja et al. 2001; Genner  
42 et al. 2007). Their presence has been proposed to enhance the generation of biodiversity by  
43 isolating populations and facilitating allopatric speciation. Their role in the generation of  
44 African cichlid fish diversity was highlighted by the discovery of unique haplochromine cichlid  
45 fishes in Lake Nabugabo in the Lake Victoria catchment (Greenwood, 1965). Subsequently,  
46 several satellite lakes around Lake Malawi have also been shown to be inhabited by unique  
47 haplochromine cichlid fish populations (Turner *et al.*, 2019). These satellite water bodies  
48 include Lake Chilingali, from which a phenotypically distinct haplochromine species  
49 informally referred to as *Lethrinops* sp. “chilingali” (Tyers et al. 2014; Turner et al. 2019) has  
50 been sampled.

51 The genus *Lethrinops* Regan 1922 is currently used for haplochromine cichlids endemic to the  
52 Lake Malawi catchment distinguished by the semicircular shape of the dental arcade of the  
53 outer series of lower jaw teeth, which curves round to end abruptly behind the inner row(s), if  
54 present (Trewavas 1931, Turner 1996, Ngatunga & Snoeks 2004). This character is also found  
55 in the genera *Taeniolethrinops* and *Tramitichromis* which were split off from *Lethrinops* by  
56 Eccles & Trewavas (1989). The character is also known in a single species of the genus  
57 *Ctenopharynx* [*Ctenopharynx pictus* (Trewavas 1935)]. All of these taxa have ventrally  
58 positioned mouths, and relatively flat lower jaws with thin mandibular bones and small teeth.  
59 This jaw structure is believed to be associated with their feeding behaviour, which, where  
60 known, largely consists of ‘sediment-sifting’ or ‘winnowing’ (Weller *et al.* 2022), whereby  
61 loose sand or mud is picked up in the mouth, tumbled briefly and then ejected through the  
62 mouth and / or operculum, presumably with prey retained and swallowed (Fryer 1959; Fryer  
63 & Iles 1972; Konings 2016). Species in the genus *Lethrinops* are largely distinguished from  
64 *Taeniolethrinops*, *Tramitichromis* and *Ctenopharynx* by their lack of traits that distinguish  
65 those genera (Eccles & Trewavas 1989, Turner 2022). Not surprisingly, *Lethrinops* is currently  
66 believed to be polyphyletic (Ngatunga & Snoeks 2004). Currently, the genus is ‘operational’,  
67 in the sense that it is possible to determine whether newly discovered taxa fall within its  
68 definition.

69 The purpose of the current work is to describe the Lake Chilingali species previously referred  
70 to as *Lethrinops* sp. ‘chilingali’ (Tyers et al. 2014; Turner et al. 2019) as *Lethrinops chilingali*,  
71 and to compare it with its presumed sister species from the main body of Lake Malawi, the  
72 morphologically similar *Lethrinops lethrinus* (Günther, 1893). The distributions of both  
73 species are discussed, and the current conservation status of *L. chilingali* is reviewed.

## 74 Materials and methods

75 Specimens of the new species were obtained from fishermen on the shores of Lake Chilingali  
76 from 22-24 June 2009, euthanised with MS-222 (if still alive) and fixed in 10% formalin before  
77 being transferred to 70% alcohol (Industrial Methylated Spirit, IMS) for long term  
78 preservation. Additional specimens obtained from a captive strain kept at Bangor University  
79 euthanised in 2020 were preserved directly in IMS. These were used to investigate allometric  
80 comparisons between the two species, as they had grown to larger sizes than field-collected

81 material. These captive bred fishes were excluded from the type series, but were included in  
82 statistical tests.

83 Comparative material of *L. lethrinus* included the holotype, and material from collections that  
84 were made in 1991-1992. These specimens were fixed in formalin and preserved in alcohol,  
85 along with some specimens collected in 2017 that were preserved directly in alcohol.  
86 Information on other congeneric species was obtained from literature, notably Trewavas  
87 (1931), Eccles & Lewis (1978), Eccles & Trewavas (1989), Turner (1996) and Ngatunga &  
88 Snoeks (2004). Counts and linear measurements were carried out following the methods of  
89 Snoeks (2004), and analysed using SPSS v27 (IBM, NY).

90 Geometric morphometric analyses were carried out on preserved specimens, photographed  
91 against a standard grey background with a scale for calibration. An initial tps file was  
92 constructed using image file names with tpsUtil v1.82 (Rohlf, 2015). A total of 15 landmarks  
93 (Figure 1) were then placed using tpsDig2 v2.32 (Rohlf, 2015): 1 anterior tip of upper jaw; 2  
94 posterior tip of upper jaw; 3-6 anterior, posterior, lower and upper point of eye; 7-8 beginning  
95 and end of dorsal fin; 9-10 beginning and end of anal fin; 11 anterior origin of pelvic fin; 12-  
96 13 lower and upper insertion of pectoral fin, 14 most posterior part of operculum, 15 base of  
97 isthmus. The posterior of the caudal peduncle was not landmarked due to the upward flexion  
98 of the peduncle in several *L. lethrinus* specimens. Landmark data from the tps file were  
99 imported to MorphoJ v1.07 (Klingenberg 2011), where a Procrustes analysis was used to  
100 transpose, rotate and scale them into comparable Procrustes coordinates. These were analysed  
101 using SPSS v27 (IBM, NY).

102 Observations of live fish were collected from stocks descended from wild-caught fish obtained  
103 from Lake Chilingali between 2004 and 2009. Information on diets was taken from previous  
104 publications (Tyers et al. 2014; Turner et al. 2019), and an additional three specimens of the  
105 new species were dissected to inspect stomach contents.

## 106 **Results**

### 107 *Quantitative comparisons*

108 Geometric morphometric data were ordinated using a Principal Component Analysis, with the  
109 primary axis (PC1) and secondary axis (PC2) capturing 34.2 and 19.6% of the variation,  
110 respectively. Overall, there was highly significant differentiation between *L. chilingali* and *L.*  
111 *lethrinus* on PC1 (General Linear Model;  $F_{1,47} = 44.09$ ,  $P < 0.001$ ), but not PC2 ( $F_{1,47} = 0.46$ ,  
112  $P = 0.83$ ). The respective type specimens were among the most clearly differentiated  
113 individuals (Figure 1). The wireframe plots showed that the *L. lethrinus* specimens have a  
114 relatively more ventrally positioned mouth than *L. chilingali*, leading to a longer snout, and a  
115 deeper body at the anterior insertion of the dorsal fin.

116 Comparisons of linear morphometric measurements revealed significant differences in slopes  
117 of head length, anal fin base length and caudal peduncle length when regressed on standard  
118 length (Table 1). Assuming equal slopes, and using standard length as a covariable, *L. lethrinus*  
119 had significantly relatively greater body depth, interorbital width, snout length, lower jaw  
120 length, lachrymal bone depth, pre-pelvic length and caudal peduncle depth than *L. chilingali*  
121 (Table 1). The clearest differences were in snout length and lachrymal bone depth, followed by  
122 interorbital width.

123 Comparisons of meristic counts showed that *L. lethrinus* had a significantly more cheek scale  
 124 rows than *L. chilingali* (K-S test,  $Z = 2.001$ ,  $P = 0.001$ ). Meanwhile *L. chilingali* had  
 125 significantly more dorsal rays (K-S test,  $Z = 1.805$ ,  $P = 0.003$ ), upper gillrakers (K-S test,  $Z =$   
 126  $1.682$ ,  $P = 0.007$ ) and lower gillrakers (K-S test,  $Z = 2.903$ ,  $P < 0.001$ ) than *L. lethrinus* (Table  
 127 1). There were no differences between the species in dorsal spines (K-S test,  $Z = 1.05$ ,  $P =$   
 128  $0.221$ ), anal spines (always 3), anal rays (K-S test,  $Z = 0.265$ ,  $P \sim 1.00$ ) or lateral line scales  
 129 (K-S test,  $Z = 0.98$ ,  $P = 0.292$ ) (Table 1).

130

131 **TABLE 1.** Comparison of linear morphometric measurements between *Lethrinops chilingali*  
 132 (including captive-bred specimens) and *Lethrinops lethrinus* using General Linear Models and  
 133  $\log_{10}$  transformed data. Bold indicates statistically significant differences between the species.  
 134 \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

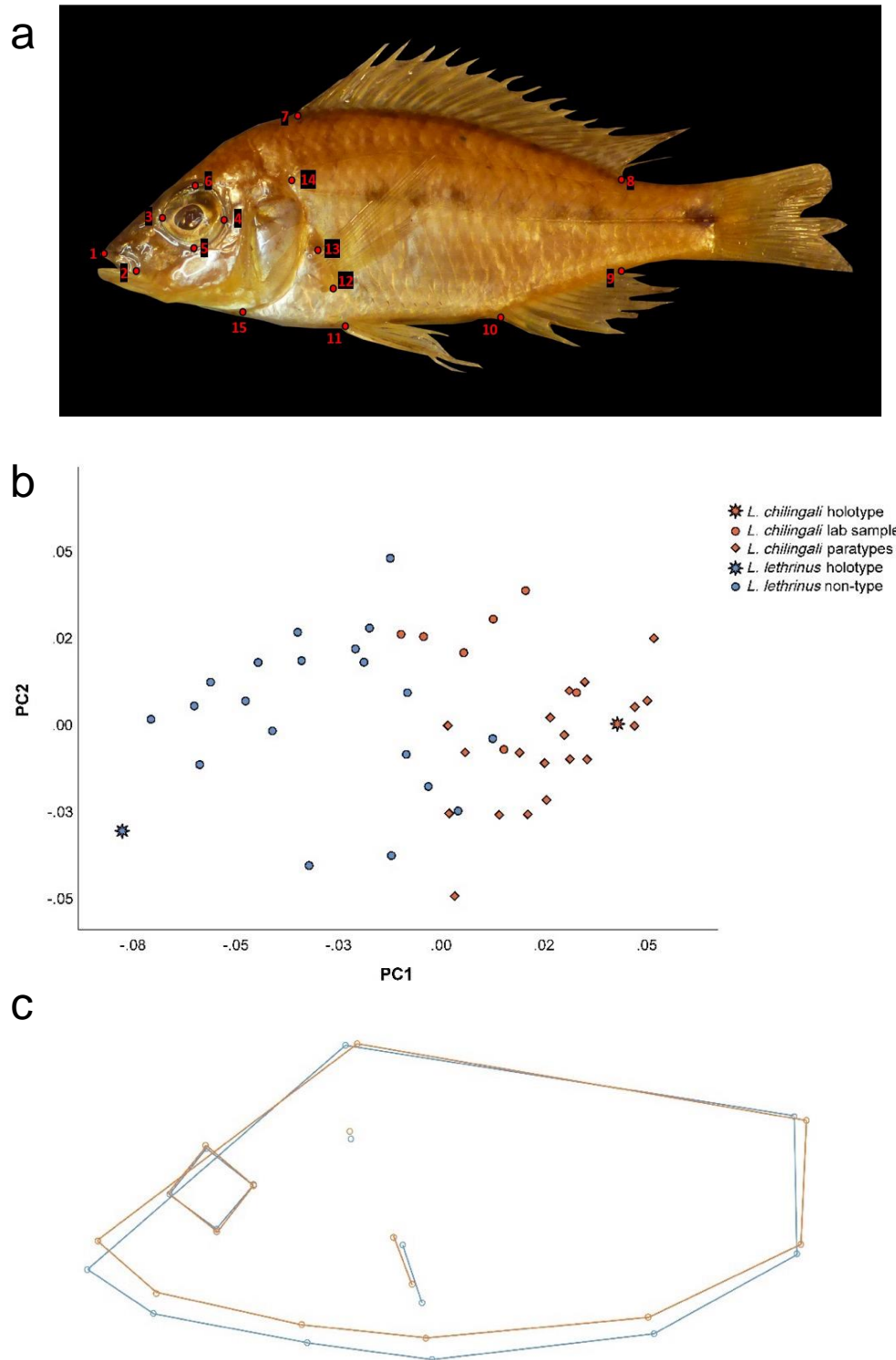
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| Measurement                 | Slope       |               | Elevation    |                      |
|-----------------------------|-------------|---------------|--------------|----------------------|
|                             | $F_{1,51}$  | $P$           | $F_{1,52}$   | $P$                  |
| Maximum body depth          | 0.07        | 0.794         | <b>4.08</b>  | <b>0.049*</b>        |
| Head length                 | <b>4.55</b> | <b>0.038*</b> | 0.62         | 0.435                |
| Head width                  | 2.09        | 0.155         | 1.41         | 0.240                |
| Interorbital width          | 1.73        | 0.198         | <b>10.80</b> | <b>0.002**</b>       |
| Snout length                | 0.72        | 0.401         | <b>15.11</b> | <b>&lt; 0.001***</b> |
| Lower jaw length            | 0.93        | 0.340         | 4.21         | 0.045                |
| Premaxillary pedicel length | 1.09        | 0.301         | 1.56         | 0.218                |
| Eye diameter                | 1.02        | 0.317         | 1.79         | 0.187                |
| Lachrymal depth             | 0.27        | 0.614         | <b>17.69</b> | <b>&lt; 0.001***</b> |
| Dorsal fin base length      | 0.00        | 0.995         | 2.09         | 0.155                |
| Anal fin base length        | <b>5.87</b> | <b>0.019*</b> | 0.87         | 0.354                |
| Predorsal length            | 3.42        | 0.070         | 0.17         | 0.686                |
| Preanal length              | 1.20        | 0.279         | 0.06         | 0.815                |
| Prepectoral length          | 0.06        | 0.808         | <b>5.41</b>  | <b>0.024*</b>        |
| Prepelvic length            | 1.08        | 0.303         | 2.51         | 0.119                |
| Caudal peduncle length      | <b>4.96</b> | <b>0.030*</b> | 0.92         | 0.341                |
| Caudal peduncle depth       | 2.48        | 0.122         | <b>4.40</b>  | <b>0.041*</b>        |

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140 **FIGURE 1.** Geometric morphometric analyses of *Lethrinus lethrinus* and *Lethrinus chilingali*  
141 **a.** Landmarks used to quantify shape variation of preserved specimen (see Materials and  
142 methods for details). **b.** Principal Component Analysis indicates strong separation of *L.*  
143 *lethrinus* and *L. chilingali* on PC1, with clear differentiation of the respective holotypes. **c.**  
144 Wireframe plots summarising shape differences between *L. lethrinus* (blue) and *L. chilingali*  
145 (orange), including the more ventrally placed mouth, longer snout, and higher back in  
146 specimens of *L. lethrinus* relative to *L. chilingali*



147 ***Lethrinops chilingali* new species.**

148 **Holotype:** BMNH 2023.1.11.1, female, 70.9 mm SL, collected from seine catches, Lake  
149 Chilingali (12.94°S, 34.21°E), 22-24 June 2009.

150 **Paratypes:** BMNH 2023.1.11.2-21, twenty specimens 59.3-81.2 mm SL, collected with  
151 holotype.

152 **Other material (excluded from the type series):** BMNH 2023.1.11.22-28; seven specimens  
153 56.8-98.7mm SL, laboratory bred from specimens collected at Lake Chilingali

154 **Etymology:** ‘chilingali’ from Lake Chilingali, the type locality, used as a noun in apposition.

155 **Diagnosis:** The outer tooth row of the lower jaw curves smoothly to end just behind the inner  
156 tooth rows (*Lethrinops*-type dentition), distinguishing the species from other Lake Malawi  
157 haplochromines apart from species of the genera *Ctenopharynx*, *Lethrinops*, *Taeniolethrinops*  
158 or *Tramitichromis*. *Lethrinops chilingali* can be distinguished from other species in the genera  
159 *Ctenopharynx*, *Lethrinops*, *Taeniolethrinops* and *Tramitichromis* by the presence of a  
160 conspicuous horizontal series of dark grey to black spots along the middle of the flanks behind  
161 the head, linked to form one or two longer dashes, in total comprising 3-6 separate elements.  
162 *Lethrinops lethrinus* has a similar horizontal dark midlateral band, but it is typically more  
163 continuous, particularly posterior to the first anal spine, rather than broken into shorter spots  
164 and dashes. The horizontal melanic elements are generally not exhibited in dominant  
165 reproductively active males, however. *L. chilingali* also typically has a less ventrally placed  
166 mouth and shorter snout than *L. lethrinus* (snout as % of head length: 31.1-41.8 in *L. chilingali*,  
167 37.6-50.0 in *L. lethrinus*).

168 **Description.** Body measurements and counts are presented in Table 1. *L. chilingali* is a small  
169 (<85m SL in wild-caught specimens) moderately laterally compressed (maximum body depth  
170 2.0-2.4 times maximum head width) cichlid fish with a moderately long snout (31.1-41.8 %  
171 head length). Females and immature males have distinctive melanic markings in the form of a  
172 horizontal row of dark spots and dashes and also have a thin red dorsal fin margin, while mature  
173 males are brilliant metallic green with a red dorsal fin margin above broader black and white  
174 bands.

175 All specimens are relatively deep-bodied and laterally compressed, with the deepest part of the  
176 body generally well behind the first dorsal fin spine. The anterior upper lateral profile is almost  
177 straight from the tip of the snout to the plane of the posterior margin of the eye, occasionally  
178 with a slight concavity above the eye, gentle sloping at an angle of about 40-degrees to the  
179 horizontal plane. There is no inflection to the angle of the profile above the eye (in contrast to  
180 *Tramitichromis* and *Tropheops*) and the premaxillary pedicel makes little or no interruption to  
181 the profile. The tip of the snout lies at about the same level in a horizontal plane as the upper  
182 margin of the insertion of the pectoral fin and at or below the level of the lowermost margin of  
183 the eye. The lower anterior lateral profile is also almost straight as far as the insertion of the  
184 pelvic fins, gently angled to the horizontal plane (about 12-15-degrees) and with little inflection  
185 at the posterior angle of the lower jaw even when the mouth is fully closed. The lower profile  
186 is more or less horizontal between the pelvic and anal fins. The mouth is relatively small and  
187 moderately upwardly-angled (gape about 40-degrees to horizontal). The caudal peduncle is  
188 relatively slender (1.4-1.8 times longer than deep). The pectoral fins are relatively long,

189 extending past the first anal spine, but the pelvic fins are generally short of this, except in the  
190 largest mature males. The dorsal and anal fins, when folded, end well short of the caudal fin  
191 insertion, except in large mature males. The caudal fin is crescentic. The eye is large and  
192 circular and almost touches the upper lateral profile in perpendicular lateral view.

193 The flank scales are weakly ctenoid, with the cteni becoming reduced dorsally, particularly  
194 anteriorly above the upper lateral line, where they transition into a cycloid state. The scales on  
195 the chest are relatively large and there is a gradual transition in size from the larger flank scales,  
196 as is typical in non-mbuna Lake Malawi endemic haplochromines (Eccles & Trewavas 1989).  
197 A few small scales are scattered on the proximal part of the caudal fin.

198 The cephalic lateral line pores are inconspicuous and the flank lateral line shows the usual  
199 cichlid pattern of separate upper and lower portions. The lachrymal bone is about as wide as  
200 deep and the lateral line pores are heavily overgrown with skin.

201 The lower jaw is relatively small, with thin mandibular bones. The jaw teeth are small, short  
202 and erect. The outer series in both the upper and lower jaw are short, blunt, erect and largely  
203 unequally bicuspid. There is a single inner series of small, pointed tricuspid teeth.

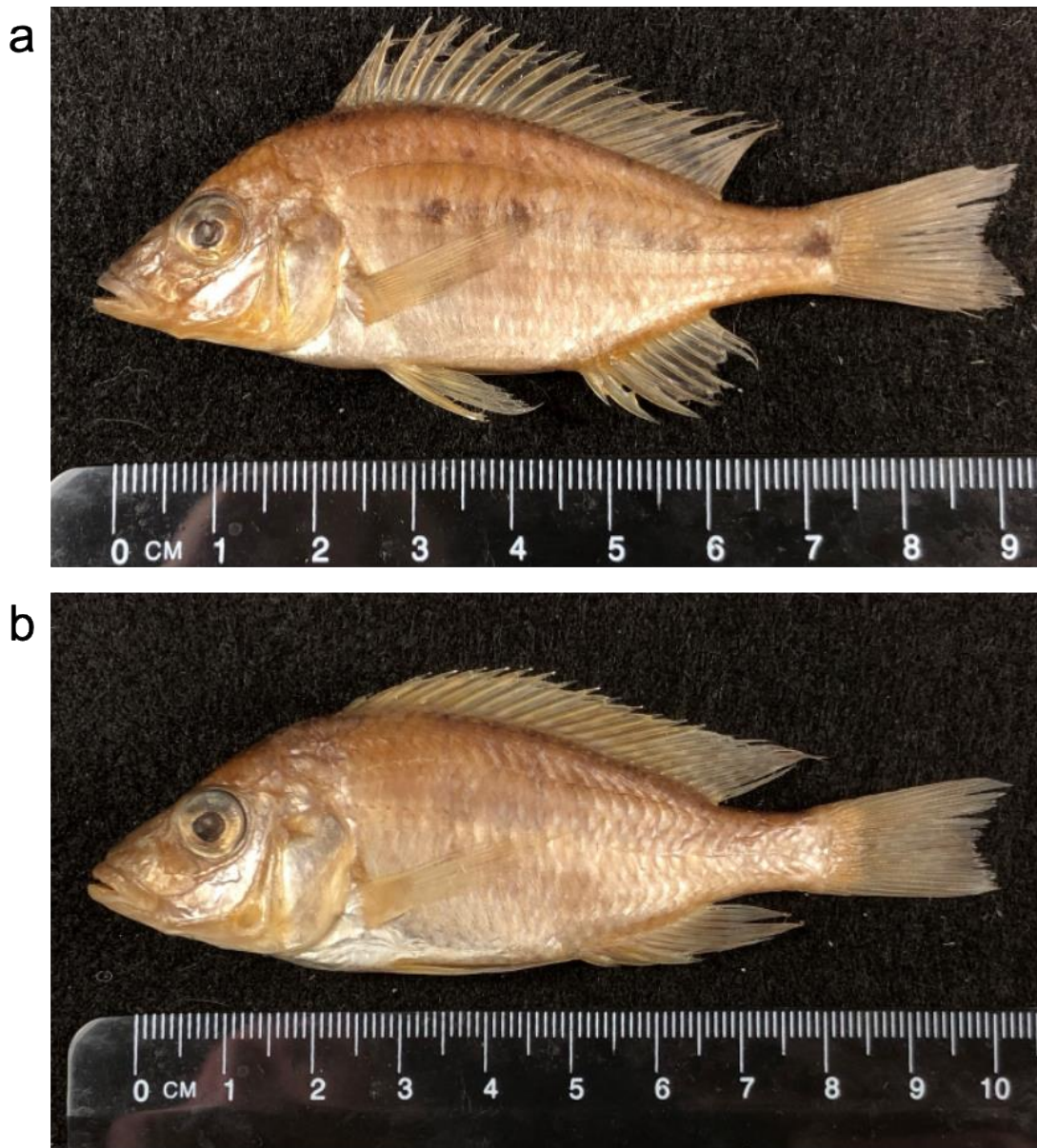
204 The lower pharyngeal bone is small, lightly built, Y-shaped, and carries small, slender, widely-  
205 spaced simple teeth. The teeth gradually increase in size from lateral to medial positions, but  
206 there are no distinctly differentiated enlarged medial teeth. There are approximately nine teeth  
207 in the midline row and 17-18 on each side on the posterior row. The gill rakers are short and  
208 blunt, generally with the most anterior rakers in the lower and upper arches reduced to small  
209 stubs.

210 Female and immature fish are countershaded, pale sandy-brown dorsally, pale silvery on the  
211 flanks and underside. The flanks are marked by a midlateral horizontal row of dark spots and  
212 stripes extending from just behind the upper part of the operculum to the caudal peduncle. This  
213 varies between individuals, but generally comprises three to six separate melanic elements. A  
214 series up to six dark blotches is sometimes visible at the base of the dorsal fin, and element of  
215 a thin longitudinal dark stripe sometimes appears about half-way between the midlateral stripe  
216 and the base of the dorsal fin, usually starting a little behind the head and ending well before  
217 the caudal peduncle. The dorsal fin has a thin red outer margin and occasionally shows some  
218 faint dark spotting on both spinous and soft portions. Occasionally there is a pale submarginal  
219 band and anteriorly a thicker dark band. The caudal fin is usually translucent, sometimes with  
220 faint spotting. The anal fin sometimes shows a few faint yellowish spots.

221 Males in breeding dress are iridescent metallic green to pale blue. The horizontal melanic  
222 markings are occasionally exhibited when individuals are caught in fishing gear, or defeated in  
223 aggressive contests (seen in aquaria). Sometimes a series of faint dark vertical bars are visible.  
224 Patches of flank scales sometimes exhibit a metallic orange section anteriorly. The dorsal fin  
225 has a broad scarlet margin, underlain with a white submarginal band: these bands are narrower  
226 on the soft dorsal area. On the spinous dorsal, the red and white bands are underlain with a  
227 broad black band which extends to the base of the dorsal fin on the first inter-radial membrane,  
228 but as the membranes become longer posteriorly, the band overlies a series of orange spots  
229 extending onto the soft dorsal area, where they can be up to 10 spots between the longest rays.  
230 The membranes between the spots are pale grey to white. The caudal fin continues this pattern  
231 of orange spots with white/grey areas between. Sometimes the white inter-spot areas are

232 missing, resulting in spots merging into stripes parallel to the fin rays. Occasionally, the white  
233 areas merge into stripes too. The upper and lower parts of the caudal fin can sometimes appear  
234 a bit darker, particularly on the basal section closer to the body, and particularly during  
235 dominant/ courting behaviour. The pelvic fins are dark grey to black with a thin white anterior  
236 edge. The anal fin is greyish to black depending on mood, with a wide pink to red lower margin.  
237 A variable number (4-18) of large pale yellow 'egg-spots' are visible in one to two rows on the  
238 membranes behind the third anal spine. The colour of the iris varies from silvery to dark gold,  
239 with a darker spot above and below the lens continuing the line of a dark lachrymal stripe from  
240 the corner of the mouth. This stripe is very variable in intensity, showing up very prominently  
241 during territorial defence and courtship phases. The lower surface of the head and chest can  
242 turn dark grey during courtship and territorial behaviour but is otherwise pale greyish.

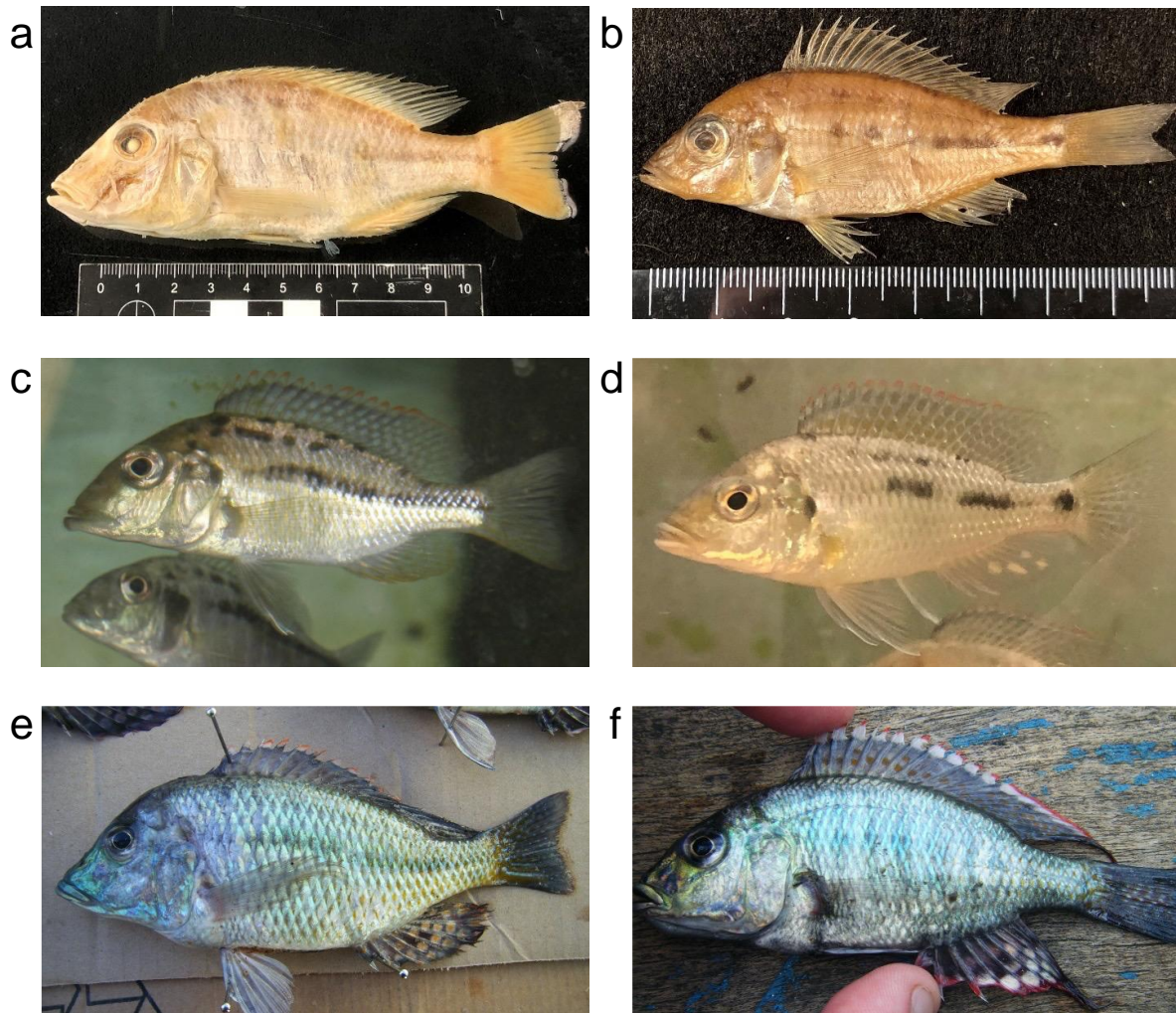
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245 **FIGURE 2.** *Lethrinops chilingali*. **a.** Holotype, BMNH 2023.1.11.1; female 70.9mm SL. **b.**  
246 Paratype, BMNH 2023.1.11.2-21; mature male, 81.2mm SL.





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248 **FIGURE 3.** Comparisons of *Lethrinops lethrinus* and *Lethrinops chilingali*. **a.** holotype of *L.*  
249 *lethrinus*, BMNH 1893.15.15., 118.5mm SL. **b.** paratype of *L. chilingali*, BMNH 2023.1.11.2-  
250 21, 60.7mm SL; **c.** *L. lethrinus* apparent female alive in aquarium. **d.** *L. chilingali* apparent  
251 immature male alive in aquarium. **e.** mature male *L. lethrinus*. **f.** mature male *L. chilingali*. The  
252 shorter snout *L. chilingali* is evident, and the more broken midlateral stripe can be seen in the  
253 live specimens.

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256 **TABLE 3.** Morphometric and meristic characters of *Lethrinops chilingali*.

|                              | <b>Holotype</b> | <b>Paratypes (n=20)<br/>mean (range)</b> | <b>Captive strain (n=7)<br/>mean (range)</b> |
|------------------------------|-----------------|--|--|
| Standard length              | 70.9            | 65.7 (59.3-81.2)                         | 80.4 (56.8-98.7)                             |
| <b>As % Standard length</b>  |                 |  |  |
| Maximum body depth           | 36.2            | 35.2 (33.1-36.8)                         | 34.1 (31.1-36.7)                             |
| Head length                  | 34.4            | 33.6 (32.1-35.9)                         | 35.9 (34.7-38.9)                             |
| Dorsal fin base length       | 53.9            | 53.0 (51.0-55.7)                         | 53.0 (50.8-56.7)                             |
| Anal fin base length         | 18.8            | 19.6 (16.9-21.5)                         | 18.0 (17.1-18.8)                             |
| Predorsal length             | 39.2            | 37.5 (35.0-39.3)                         | 39.1 (35.2-42.5)                             |
| Preanal length               | 65.3            | 64.1 (62.5-66.5)                         | 64.6 (61.1-67.8)                             |
| Prepectoral length           | 36.4            | 35.5 (33.5-38.0)                         | 36.1 (33.8-38.0)                             |
| Prepelvic length             | 40.2            | 39.9 (37.1-43.1)                         | 41.5 (38.2-44.1)                             |
| Caudal peduncle length       | 19.2            | 17.9 (16.1-20.0)                         | 17.2 (16.1-20.4)                             |
| Caudal peduncle depth        | 11.0            | 11.5 (10.4-12.4)                         | 11.4 (10.9-12.3)                             |
| <b>As % Head length</b>      |                 |  |  |
| Head width                   | 47.1            | 45.6 (40.9-50.0)                         | 43.7 (40.4-47.4)                             |
| Interorbital width           | 21.1            | 21.8 (18.8-24.5)                         | 22.7 (20.4-27.2)                             |
| Snout length                 | 33.3            | 35.2 (31.1-38.2)                         | 38.7 (34.6-41.8)                             |
| Lower jaw length             | 40.9            | 39.2 (35.3-42.9)                         | 39.2 (37.3-44.2)                             |
| Premaxillary pedicel length  | 29.8            | 29.7 (25.7-35.9)                         | 30.0 (24.9-35.4)                             |
| Eye diameter                 | 31.1            | 31.8 (28.2-37.7)                         | 29.1 (25.7-33.0)                             |
| Lachrymal depth              | 21.5            | 21.4 (18.0-25.9)                         | 23.8 (21.0-27.7)                             |
| <b>Ratios</b>                |                 |  |  |
| Body depth/Head width        | 2.25            | 2.30 (2.11-2.41)                         | 2.18 (1.99-2.34)                             |
| Caudal peduncle length/depth | 1.74            | 1.56 (1.37-1.80)                         | 1.51 (1.37-1.76)                             |
| <b>Counts</b>                |                 |  |  |
| Upper gill rakers            | 3               | 3-4                                      | 3-4  |
| Lower gill rakers            | 10              | 9-11                                     | 10-12  |
| Dorsal fin                   | XV, 10          | XIV-XVI, 9-10                            | XIV-XV, 10-11                                |
| Anal fin                     | III, 8          | III, 8-10                                | III, 8-9                                     |
| Longitudinal line scales     | 31              | 31-33                                    | 30-33  |
| Cheek scales                 | 3               | 2-4                                      | 2-4  |

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259 **Behaviour and Ecology.** The diet of *L. chilingali* specimens sampled in 2009 consisted largely  
260 of chaoborus (midge) larvae and pupae, along with cladocerans and other larger invertebrates,  
261 including odonatan nymphs and caridinid shrimps, but with little detritus, perhaps suggesting  
262 more midwater feeding than is usual in *Lethrinops* species. The behaviour of the species in the  
263 wild has not been observed, as the water of Lake Chilingali was highly turbid when visited  
264 between 2004 and 2009.

265 In captivity, *L. chilingali* females, non-territorial males and juveniles tend to aggregate in loose  
266 groups, feeding not only in the sediment, but on objects such as rocks or plants, or even at the  
267 surface. When attempts are made to catch the fish, they show a strong tendency to dive into the  
268 sand, turning sideways and completely burying themselves. This same behaviour has been  
269 reported to occur in the wild in *Fossorochromis rostratus* (Boulenger 1899), another cichlid  
270 from the Lake Malawi radiation (Fryer & Iles 1972, p. 207).

271 Dominant male *L. chilingali* are territorial and actively court females in typical haplochromine  
272 style: fins wide open, body horizontal or head-up, making rapid darts to the spawning site and  
273 back to the female, with spawning taking place amid bouts of circling and quivering, while  
274 alternating head-to-anal-fin ‘T-positions’ on the substrate. It is notable that dominant male  
275 coloration and aggression vary a lot, appearing to peak when females are approaching  
276 spawning, but are otherwise often quite subdued. During persistent bouts of courtship or  
277 aggression, the melanic elements of the male colour are emphasised, particularly the  
278 lachrymal/eye stripe, dark pelvic and anal fins, dark upper and lower margins of the caudal fin  
279 and even faint vertical barring on the flanks. Even in a large tank with a high density of fish,  
280 there is usually just a single dominant male: this is similar to *Astatotilapia*, which tend to be  
281 solitary breeders. Communal lek breeders, such as *Oreochromis* will usually divide up a tank  
282 into numerous smaller territories and engage in frequent boundary disputes. This suggests that  
283 *Lethrinops chilingali* are not communal lek breeders in the wild.

284 There is little indication of bower construction in *L. chilingali* when a sand or gravel substrate  
285 is provided: dominant males usually try to lead females to a slight depression near to an object  
286 such as a rock or piece of wood: in a bare tank, the focus would probably be the tank bottom  
287 near one of the corners or a wall near a heater or filter inlet. This is in marked contrast to reports  
288 of *L. lethrinus* where complex bowers have been recorded in the field, out over open substrate  
289 (Konings 2016, p. 369). In *L. chilingali*, the construction of the depression seems almost  
290 haphazard: males have not been observed to show consistent bouts of digging, but spend most  
291 of their time chasing, then returning to the territory focus next to the object, during which they  
292 make occasional ‘feeding movement’ of picking up a mouthful of substrate, moving forwards  
293 and ejecting it through the mouth and/or opercular openings at a slight distance away. This  
294 occurs all over the vicinity of the side of the object they are defending, but there seems to be a  
295 slight bias towards a certain point up against the object, which thereby becomes a shallow  
296 depression.

297 Female *L. lethrinus* are maternal mouthbrooders, brooding young until they are capable of  
298 independent feeding. As fry complete the absorption of the yolk, they show through the  
299 female’s buccal membrane as a dark area, but females do not develop the ‘warpaint’ typical of  
300 fry guarders, such as *Astatotilapia* or *Oreochromis*: dark eyes, lachrymal stripes and forehead  
301 stripes. There is no indication that females guard free-swimming fry or permit them to return

302 to their mouths. This non-guarding behaviour is similar to other known shallow-water  
303 *Lethrinops* species.

304

305 ***Lethrinops lethrinus* (Günther, 1893)**

306 **Holotype:** *Lethrinops lethrinus* (Günther, 1893): BMNH 1893.11.15.15, 116.1 mm SL, coll.  
307 A. Whyte, Upper Shire River at Fort Johnston (Mangochi), March 1892,

308 **Other material examined:**

309 BMNH 2023.1.11.29, 1 specimen 130.1mm SL, collected by G.F. Turner from experimental  
310 trawl at depth of 5-18m, between Namiasi and Palm Beach (approximately 14.38°S, 35.22°E),  
311 SE Arm of Lake Malawi, 30 July 1991.

312 BMNH 2023.1.11.30, 1 specimen, 120.6 mm SL, collected by G.F. Turner, trawled at 5-18m  
313 depth between Namiasi and Malindi (approximately 14.34°S, 35.22°E), SE Arm of Lake  
314 Malawi, 30<sup>th</sup> July 1991.

315 BMNH 2023.1.11.31, 1 specimen, 101.4mm SL, collected by G.F. Turner from kambuzi seine  
316 fisherman, West shore of Lake Malombe, probably at Chimwala (14.64°S, 35.18°E), 26 June  
317 1992,

318 BMNH 2023.1.11.32-36, 5 specimens, 63.2-66.6 mm SL, collected by G.F. Turner from Lake  
319 Malombe, probably at Chimwala (14.64°S, 35.18°E), 23 July 1992.

320 BMNH 2023.1.11.37, 1 specimen 90.2 mm SL, collected by G. F. Turner, Middle Shire River,  
321 probably at Liwonde Barrage (15.06°S, 35.22°E), 20<sup>th</sup> May 1992.

322 BMNH 2023.1.11.38-43, 6 specimens 129.2-152.6 mm SL, collected by G. F. Turner  
323 unspecified sites in southern Lake Malawi, 1990-1992.

324 BMNH 2023.1.11.44-46, 3 specimens 97.9-116.1 mm SL, collected by G. F. Turner, trawled  
325 at 18-21m at Ulande 1a station (14.23°S, 35.95°E), SE Arm Lake Malawi, 1991.

326 BMNH 2023.1.11.47-48, 2 specimens 106.4-130.2 mm SL, collected by David Bavin, from  
327 seine fishermen, Lake Malombe (14.64°S, 35.18°E), 6<sup>th</sup> July 2009.

328 BMNH 2023.1.11.49-50, 2 specimens 121.7-128.0 mm SL, collected by G. F. Turner, trawled  
329 at 26m depth at Michesi station (14.32°S, 35.19°E), SE Arm of Lake Malawi, 1992.

330 BMNH 2023.1.11.51-53, 3 specimens 109.4-123.2 mm SL, collected by G. F. Turner, from  
331 seine net fishermen, Palm Beach (14.41°S, 35.23°E), SE Arm of Lake Malawi, 23 Jan 2017.

332 BMNH 2023.1.11.54, 1 specimen 120.7 mm SL, collected by G. F. Turner, from seine net  
333 fishermen, Palm Beach (14.41°S, 35.23°E), SE Arm of Lake Malawi, 22 Jan 2017.

334 **Remarks:** *L. lethrinus* was selected as the type of the genus *Lethrinops* by Regan (1922). It  
335 was originally described as *Chromis lethrinus* from a single specimen, but was redescribed  
336 from additional material by Regan (1922), Trewavas (1931), Eccles & Lewis (1978) and Eccles  
337 & Trewavas (1989). It was also included in a key to the shallow-water *Lethrinops* species by  
338 Ngatunga & Snoeks (2004). The original illustration in Günther (1893) shows a specimen with  
339 a continuous horizontal midlateral stripe beginning at the eye and extending to the base of the



340 caudal fin. This is reprinted in Eccles & Trewavas (1989), where the imaged specimen is  
341 erroneously referred to as the lectotype (it is the holotype). The redescription by Eccles &  
342 Lewis (1978) includes a drawing of a non-type specimen in which the horizontal midlateral  
343 stripe is composed of a series of about 15 spots running from just behind the origin of the pelvic  
344 fin to the base of the caudal fin. Anteriorly, the first five spots are separate, but the gaps between  
345 them are much narrower than the length of the spots. Posteriorly, all of the spots overlap, to  
346 form a continuous, albeit irregular, blotchy line. Eccles & Lewis (1978) stated they examined  
347 (but did not measure) the type and there seems little doubt that the non-type material they  
348 studied (uncatalogued, Monkey Bay Fisheries Research Unit, Malawi, status unknown)  
349 corresponds to this species.

350 *Lethrinops lethrinus* is readily diagnosed based on its typical *Lethrinops*-type dentition,  
351 horizontal melanic flank markings and long snout. Mature males show a metallic blue-green  
352 breeding dress, with a prominent red and white dorsal fin margin and numerous large eggspots  
353 on the anal fin (Figure 3, see also Konings 2016). *L. lethrinus* appears to be confined to shallow  
354 waters with muddy bottoms, often river mouths with extensive beds of reeds and other  
355 macrophytes, feeding on invertebrates and other edible material obtained from the sediment  
356 (Turner 1996). Konings (2016) reports a lakewide distribution and it has been recorded from  
357 Lake Malombe and the Upper and Middle Shire Rivers (Turner 1996). Counts and  
358 measurements of the material we examined are presented on Table 3.

359

360 **TABLE 3.** Morphometric and meristic characters of *Lethrinops lethrinus*.

|                              | <b>Holotype</b> | <b>Non-types (n=26)<br/>mean (range)</b> |
|------------------------------|-----------------|--|
| Standard Length              | 118.5           | 110.7 (62.9-152.6)                       |
| <b>As % Standard length</b>  |                 |  |
| Maximum body depth           | 36.4            | 37.2 (33.0-41.0)                         |
| Head length                  | 34.5            | 35.1 (33.1-39.1)                         |
| Dorsal fin base length       | 53.9            | 53.4 (49.9-56.2)                         |
| Anal fin base length         | 17.7            | 18.7 (16.5-21.0)                         |
| Predorsal length             | 37.7            | 39.5 (37.1-42.3)                         |
| Preanal length               | 66.2            | 64.9 (61.5-68.6)                         |
| Prepectoral length           | 35.1            | 37.1 (33.9-40.1)                         |
| Prepelvic length             | 42.5            | 42.2 (35.7-46.4)                         |
| Caudal peduncle length       | 17.9            | 17.5 (14.7-20.2)                         |
| Caudal peduncle depth        | 12.5            | 12.1 (10.8-13.4)                         |
| <b>As % Head length</b>      |                 |  |
| Head width                   | 46.2            | 44.8 (41.0-50.1)                         |
| Interorbital width           | 24.2            | 22.6 (18.0-26.9)                         |
| Snout length                 | 42.5            | 44.4 (37.6-50.0)                         |
| Lower jaw length             | 40.1            | 41.0 (37.0-43.5)                         |
| Premaxillary pedicel length  | 31.1            | 31.0 (25.4-34.3)                         |
| Eye diameter                 | 29.5            | 28.4 (25.2-34.7)                         |
| Lachrymal depth              | 29.5            | 30.7 (21.6-34.8)                         |
| <b>Ratios</b>                |                 |  |
| Body depth/Head width        | 2.29            | 2.36 (2.14-2.67)                         |
| Caudal peduncle length/depth | 1.43            | 1.45 (1.17-1.66)                         |
| <b>Counts</b>                |                 |  |
| Upper gill rakers            | 3               | 2-4                                      |
| Lower gill rakers            | 9               | 8-10                                     |
| Dorsal fin                   | XV, 11          | XIV-XVI, 8-12                            |
| Anal fin                     | III, 9          | III, 8-9                                 |
| Longitudinal line scales     | 31              | 30-36                                    |
| Cheek scales                 | 3               | 3-4                                      |

361

362



363

364 **FIGURE 4.** Comparative material. **a.** Three small specimens (BMNH 1935.6.14.2077-9) from  
365 Lupembe in northern Lake Malawi match *Lethrinops lethrinus*, in melanin pattern and low  
366 position of mouth on the head. **b.** A syntype of *Lethrinops leptodon* BMNH 1921.9.6.201-207,  
367 showing two oblique stripes thickened and fused together to form a midlateral blotch. This  
368 pattern is distinguishable from those of *L. chilingali* and *L. lethrinus*, but is similar to the  
369 Nkhata Bay population reported by Eccles & Lewis (1978) and assigned by them to *L.*  
370 *lethrinus*.

371

372

## 373 4. DISCUSSION

374

### 375 Relationship of *L. chilingali* to other taxa in the Lake Malawi radiation

376 The present study has assumed that *L. lethrinus* is both the most likely sister taxon for *L.*  
377 *chilingali* and the species most likely to interbreed with it, should habitat barriers be broken  
378 down. The former proposition is based on their overall similar appearance, including very  
379 similar male breeding dress, and similar – although distinct- melanin patterns in the females  
380 and juveniles. They are the only two known *Lethrinops* species to share a largely horizontally-  
381 banded melanin pattern. Other Lake Malawi cichlids also share some of these features, notably  
382 species of *Protomelas* found in similar shallow weedy/muddy habitats, including *Protomelas*  
383 *kirkii* (Günther 1894), *Protomelas similis* (Regan 1922) and *Protomelas labridens* (Trewavas  
384 1935) (Eccles & Trewavas 1989, Konings 2016, Turner 1996). These three species also have  
385 females/immatures with a sandy/countershaded appearance, with a strong horizontal dark band  
386 running along the flank. Males are also metallic blue-green, with a red and white dorsal fin  
387 margin. These species have shorter snouts and more upwardly-angled mouths than *L. lethrinus*,  
388 but so does *L. chilingali*, which is arguably morphologically intermediate between them. The  
389 genera *Protomelas* and *Lethrinops* can be distinguished by the shape of the lower jaw dental  
390 arcade, and it presently assumed that this is a phylogenetically informative trait (Eccles &  
391 Trewavas 1989), although this requires confirmation from a phylogenetic analysis, ideally  
392 based on genome-scale sequence data. A published phylogenomic analysis places *L. lethrinus*  
393 in the middle of a clade of shallow water *Lethrinops*, *Taeniolethrinops* and *Tramitichromis*  
394 (Masonick et al. 2022), thus grouping all genera showing *Lethrinops*-type dentition (Eccles &  
395 Trewavas 1989). However, *P. kirkii*, *P. similis* and *P. labridens* were not included in that  
396 analysis (Masonick et al. 2022). Notably, however, an additional group of deep-water  
397 *Lethrinops* appears in a separate part of the phylogeny, suggesting that the *Lethrinops*-type  
398 dentition is prone to parallelism. Thus, we conclude that available evidence does not conflict  
399 with *L. chilingali* being a sister species to *L. lethrinus*, but this requires more detailed  
400 phylogenetic investigation for confirmation. If *L. lethrinus* shows relatively high levels of  
401 population structure, it could be paraphyletic (ancestral) with respect to *L. chilingali*.

402

### 403 Distributions of *L. chilingali* and *L. lethrinus*

404 *Lethrinops chilingali* has only been positively recorded from Lake Chilingali, but here we  
405 consider whether it may have a broader distribution in Lake Malawi, possibly extending to the  
406 central to northern part of the lake as an allopatric sister species to *L. lethrinus*. Although a  
407 lake-wide distribution has been claimed for *L. lethrinus* (Konings 2016), the great majority of  
408 records backed by preserved specimens or photographs come from the southern arms, Lake  
409 Malombe and the Shire River (Eccles & Lewis 1978, Turner 1996, Konings 2016). On the  
410 Global Biodiversity Information Facility website (GBIF 2023), there is a record of *Lethrinops*  
411 *lethrinus* from co-ordinates indicating a collection site off the Tanzanian shore near Ngkuyo  
412 Island, Mbamba Bay (11.334°S, 34.769°E), based on specimens at the South African Institute  
413 for Aquatic Biodiversity (SAIAB). An offshore location near a rocky headland seems an  
414 unlikely collecting site for *Lethrinops lethrinus*, which favours shallow sheltered vegetated  
415 habitats and the locality label is given as ‘Lifuwu’, which probably corresponds to the vicinity



416 of Lifuwu village (13.69°S, 34.60°E) just north of Salima, suggesting that the co-ordinates  
417 have been recorded in error. The single small specimen shows no melanic markings (faded  
418 post-preservation?), but the head shape is consistent with *Lethrinops lethrinus* rather than *L.*  
419 *chilingali*. Another GBIF record from co-ordinates 13.35°S, 33.4°E would suggest specimens  
420 were collected from the Rusa River, a tributary of the Bua River, which joins Lake Malawi  
421 near Lake Chilingali. The site is far upstream, around 97km West of the Lake Malawi shore at  
422 Benga, and might suggest specimens of *L. chilingali* could be widespread in the river  
423 catchment. However, the collection label indicates the specimens were collected from Lake  
424 Malawi at Foo, which is a trawling station in the SE Arm of Lake Malawi (also sometimes  
425 written as Fowo), which is at approximately 14.14°S, 35.18°E, again suggesting an error in the  
426 co-ordinates. Photographs of the specimens show typical *Lethrinops lethrinus*, with long snouts  
427 and strong horizontal melanic markings. The catalogue of the Natural History Museum in  
428 London contains a single accession of three specimens labelled as *L. lethrinus* from Lupembe  
429 Sand Bar, collected by Cuthbert Christy in 1925 (BMNH 1935.6.14.2077-9; Figure 4). The  
430 electronic catalogue suggests that this location is in Tanzania, perhaps following Eccles &  
431 Trewavas (1989) who suggested it might represent a site at the mouth of the ‘Kivira River’.  
432 However, the town at the mouth of the Kiwira River (as presently named) is currently known  
433 as Itungi Port. It is more likely that the 1925 collection site is Lupembe on the Malawian  
434 lakeshore, just south of Karonga (10.055°S, 33.99°E). Notably, recent satellite images show a  
435 conspicuous sandbar (Google Earth). Examination of the unpublished diary of Cuthbert Christy  
436 held at the Natural History Museum shows a single accession from Lupembe following an  
437 extensive collection of several hundred accessions from Vua / Deep Bay (Chilumba area) and  
438 immediately before another extensive collection from Mwaya in Tanzania, on the far north  
439 coast of the lake (itemising various river mouths visited). No other accessions were made from  
440 Lupembe. This suggests that the location was visited en-route from Chilumba to Tanzania,  
441 which would fit well with the location near Karonga. Unfortunately, the specimens are very  
442 small (44.8-50.9 mm SL) which makes morphological comparisons difficult with the larger  
443 specimens examined for this study, due to allometric effects. For example, they have notably  
444 relatively large eyes, making snout measurements relatively small. However, the low position  
445 of the mouth on the head and the largely continuous midlateral stripe, fit far better with *L.*  
446 *lethrinus* than with *L. chilingali*. Thus, available museum specimens strongly support the  
447 occurrence of typical *Lethrinops lethrinus* only in the southern arms of the lake, but tentatively  
448 indicate that they may also occur just north of Senga Bay and indeed almost at the northernmost  
449 extremity of the lake, but do not provide evidence for the occurrence of *L. chilingali* or any  
450 other similar form within Lake Malawi,

451 Other published records are not backed by specimens available to examine or photographic  
452 evidence. Eccles & Lewis (1978) reported that they had found *L. lethrinus* at Nkhata Bay,  
453 which is well to the north of Lake Chilingali. However, they reported an unusual melanin  
454 pattern: “the dark line along the middle of the flank curves upwards anteriorly to merge with  
455 the lower of the two rows of spots and the spots themselves may run together posteriorly to  
456 form a stripe”. The occurrence of specimens with dramatically different stripe patterns at  
457 Nkhata Bay might lend credence to the idea that *L. lethrinus* represents a complex of allopatric  
458 taxa, which might increase the probability that *L. chilingali* might persist in the main Lake  
459 Malawi. Eccles & Lewis provided no illustration of this ‘Nkhata Bay variant’. Their specimens  
460 were deposited in the collection of the Monkey Bay Fisheries Research Unit, Malawi and their  
461 present status is unknown. The pattern described is reminiscent of that seen on some of the

462 type specimens of *L. leptodon* Regan 1922. In the same 1978 paper, Eccles & Lewis  
463 redescribed that species based on a single specimen collected from Chintheche in the NW of  
464 the lake, near Nkhata Bay, but their illustration of that specimen showed a clear midlateral  
465 blotch on the upper part of the flank. They reported examining, but not measuring, three of the  
466 type specimens of *L. leptodon*, which are held at the Natural History Museum in London  
467 (BMNH 1921.9.6.201-207, collected by Wood from somewhere in ‘Lake Nyasa’). Thus, it  
468 seems unclear whether the reported Nkhata Bay populations represent *L. lethrinus* or *L.*  
469 *leptodon*, or indeed something else. In summary, the status of the northern populations of  
470 *Lethrinops* of this group is unclear but is consistent with the hypothesis that *L. lethrinus* is  
471 found in suitable habitats throughout Lake Malawi, and that *L. chilingali* is a satellite lake  
472 endemic extinct in the wild.

### 473 **Conservation status of *Lethrinops chilingali***

474 Lake Chilingali is approximately 5km in length and a maximum of 1km in width, and is  
475 characterised by two deeper basins of approximately 5m depth separated by a shallower  
476 plateau (Turner et al. 2019). It has a single outflow, the Kaombe River, which meanders for  
477 approximately 12km before reaching the main body of Lake Malawi (Genner et al. 2007). The  
478 lake is a natural water body, and the two basins of the modern lake are represented on early  
479 European exploration maps, as two separate bodies of water, Lake Chikukutu to the south,  
480 and Lake Chilingali to the north (Turner et al. 2019). The lake level was raised when a dam  
481 was constructed across the single outflow for irrigation purposes (Genner et al. 2007), which  
482 took place around 1992 according to information from the Malawi Government Department  
483 of Surveys (Genner et al. 2007). The dam collapsed between June and September 2014, and  
484 the single lake disappeared, reforming the two separate smaller shallow basins. In 2016 these  
485 basins were estimated to be only ~1m deep and fringed with macrophytes. The lake was  
486 refilled to approximately its pre-collapse-level in June-July 2019 following the construction  
487 of a new dam.

488 During the period 2004 to 2011, before the collapse of the dam, *L. chilingali* was periodically  
489 and reliably sampled from the lake, alongside another apparently endemic haplochromine  
490 cichlid, the undescribed *Rhamphochromis* sp. “chilingali” (Genner et al. 2007; Turner et al.  
491 2019). To our knowledge, the last sampling event where *L. chilingali* was recorded in the  
492 wild was on 25 June 2009 (by G. Turner), while representatives of *R. sp.* “chilingali” were  
493 last collected from an artisanal fishing catch on 12 January 2011 (by M. Genner). During  
494 sampling in February 2016, neither of the species was encountered in a survey of the main  
495 northern and southern basins of Lake Chilingali (Turner et al. 2019). A survey in April 2022  
496 also failed to sample any either *L. chilingali* or *R. sp.* “chilingali” but did find that that Lake  
497 Malawi endemic *Otopharynx tetrastigma* (Günther 1894) was abundant (H. Svardal, pers  
498 comm). This species was absent between 2004 and 2016 and is likely to have been introduced  
499 during restocking after the lake was refilled in 2019 (H. Svardal, pers comm). Although  
500 further surveys of Lake Chilingali and the Kaombe river are warranted to determine if  
501 remnant populations of either *L. chilingali* or *R. sp.* “chilingali” persist, on the basis of the  
502 current evidence, we consider it most likely that both species are no longer present in the  
503 natural environment. Breeding populations of *L. chilingali* or *R. sp.* “chilingali” are, however,  
504 maintained in captivity, and may be candidates for reintroduction. On the basis of the  
505 evidence discussed above, we recommend that *L. chilingali* is attributed the status of Extinct

506 in the Wild (EW) on the International Union for Conservation of Nature (IUCN) Red List of  
507 Threatened Species.

508

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521

## 522 **REFERENCES**

523 Eccles, D. H. & Lewis, D. S. C. (1978). A taxonomic study of the genus *Lethrinops* Part 2.  
524 *Ichthyological Bulletin of Rhodes University*, 37, 1-11.

525

526 Eccles, D. H. & Trewavas, E. (1989). *Malawian cichlid fishes. The classification of some*  
527 *Haplochromine genera*. Lake Fish Movies, Herten, Germany, 335 pp.

528

529 Fryer, G. (1959). The trophic interrelationships and ecology of some littoral communities of  
530 Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group  
531 of rock-frequenting Cichlidae. *Proceedings of the Zoological Society of London*, 132, 153-281.

532

533 Fryer, G. A. & Iles, T. D. (1972). *The Cichlid Fishes of the Great Lakes of Africa*. Oliver &  
534 Boyd, Edinburgh.

535

536 GBIF (2023) Global Biodiversity Information Facility. [www.gbif.org](http://www.gbif.org) (last accessed 12 March  
537 2023)

538

539 Genner, M. J., Nichols, P., Carvalho, G. R., Robinson, R. L., Shaw, P. W., Smith, A. & Turner,  
540 G. F. (2007) Evolution of a cichlid fish in a Lake Malawi satellite lake. *Proceedings of the*  
541 *Royal Society of London, Series B*, 274, 2249-2257

542

543 Greenwood, P. H. (1965) The cichlid fishes of Lake Nabugabo, Uganda. *Bulletin of the British*  
544 *Museum (Natural History), Zoology*, 12, 315–357.

545

546 Günther, A. (1894) Second report on the reptiles, batrachians, and fishes transmitted by Mr. H.  
547 H. Johnston, C. B., from British Central Africa. *Proceedings of the Zoological Society of*  
548 *London 1894*, 616-628, Pls. 53-57

- 549  
550 Kaufman, L., & Ochumba, P. (1993) Evolutionary and conservation biology of cichlid fishes  
551 as revealed by faunal remnants in northern Lake Victoria. *Conservation Biology*, 7, 719– 730.  
552  
553 Konings, A. (2016) *Lake Malawi Cichlids in their Natural Habitat. 5<sup>th</sup> Edn.* Cichlid Press, El  
554 Paso TX.  
555  
556 Masonick, P., Meyer, A. & Hulsey, C. D. (2022) Phylogenomic analyses show repeated  
557 evolution of hypertrophied lips among Lake Malawi Cichlid Fishes. *Genome Biology &*  
558 *Evolution*, 14, evac051.  
559  
560 Mwanja, W. W., Armodlian, A. S., Wandera, S. B., Kaufman, L., Wu, L., Booton, G. C., &  
561 Fuerst, P. A. (2001) The bounty of minor lakes: the role of small water bodies in evolution and  
562 conservation of fishes in the Lake Victoria Region, East Africa. *Hydrobiologia*, 458, 55–62  
563  
564 Ngatunga, B. P. & Snoeks, J. (2004). Key to the shallow water *Lethrinops sensu lato*. In:  
565 Snoeks, J. (ed) *The Cichlid Diversity of Lake Malawi/Nyasa/Niassa: Identification,*  
566 *Distribution and Taxonomy.* Cichlid Press, El Paso, Texas, 252-260.  
567  
568 Palmer, R. 2019 <https://www.inaturalist.org/observations/22139001>  
569  
570 Regan, C. T. (1922). The cichlid fishes of Lake Nyasa. *Proceedings of the Zoological Society*  
571 *of London*, 1921, 675-727.  
572  
573 Rohlf, F. J. (2015) The tps series of software. *Hystrix - The Italian Journal of Mammalogy*, 26,  
574 9-12.  
575  
576 Snoeks, J. (2004) Materials and Methods. In Snoeks, J. (ed) *The Cichlid Diversity of Lake*  
577 *Malawi/Nyasa/Niassa: Identification, Distribution and Taxonomy.* Cichlid Press, El Paso, TX:  
578 12-19.  
579  
580 Trewavas, E. (1931). A revision of the cichlid fishes of the genus *Lethrinops*. *Annals and*  
581 *Magazine of Natural History*, (10) 7, 133-153.  
582  
583 Trewavas, E. (1935). A synopsis of the cichlid fishes of Lake Nyasa. *Annals and Magazine of*  
584 *Natural History* (10) 16, 65-118.  
585  
586 Turner, G. F. (1996). *Offshore Cichlids of Lake Malawi.* Cichlid Press, Lauenau. 240 pp.  
587  
588 Turner, G. F. (2022). A new species of deep-water *Lethrinops* (Cichlidae) from Lake Malawi.  
589 *Journal of Fish Biology*, 101, 1405-1410.  
590  
591 Turner, G. F., Ngatunga, B. P. & Genner, M. J. (2019) The natural history of the satellite lakes  
592 of Lake Malawi. *EcoevoRxiv*. <https://ecoevorxiv.org/sehdq/> 131pp.  
593  
594 Tyers, A. M., Bavin, D., Cooke, G. M., Griggs, C. & Turner, G. F. (2014). Peripheral isolate  
595 speciation of a Lake Malawi cichlid fish from shallow-muddy habitats. *Evolutionary Biology*,  
596 41, 439-451.  
597



598 Weller, H., López-Fernández, H., McMahan, C. D. & Brainerd, E. L. (2022). Relaxed feeding  
599 constraints facilitate the evolution of mouthbrooding in Neotropical cichlids. *American*  
600 *Naturalist*, 199, E197-E210.  
601  
602