

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.

GEORGE F. TURNER¹, DENISE A. CRAMPTON² & MARTIN J. GENNER³

¹ School of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2UW, United Kingdom & Vertebrates Division, Natural History Museum, Cromwell Road, London SW7, UK.

Corresponding author: email bss608@bangor.ac.uk

ID: <https://orcid.org/0000-0003-0099-7261>

² School of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2UW, United Kingdom; present address: School of Biological & Environmental Sciences, Liverpool John Moores University, Liverpool, L3 3AF, UK; email: D.Crampton@2023.ljmu.ac.uk

ID: <https://orcid.org/0000-0002-2877-5209>

³ School of Biological Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol, BS8 1TQ, United Kingdom. Email: m.genner@bristol.ac.uk

ID: <https://orcid.org/0000-0003-1117-9168>

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, a small lake lying on the Kaombe River which flows into the middle
49 of the western shoreline of Lake Malawi near Nkhotakota, from which a phenotypically distinct
50 haplochromine species informally referred to as *Lethrinops* sp. “chilingali” (Tyers et al. 2014;
51 Turner et al. 2019) has been sampled.

52 The genus *Lethrinops* Regan 1922 is currently used for haplochromine cichlids endemic to the
53 Lake Malawi catchment distinguished by the semicircular shape of the dental arcade of the
54 outer series of lower jaw teeth, which curves round to end abruptly behind the inner row(s), if
55 present (Trewavas 1931, Turner 1996, Ngatunga & Snoeks 2004). This character is also found
56 in the genera *Taeniolethrinops* Eccles & Trewavas 1989 and *Tramitichromis* Eccles &
57 Trewavas 1989 which were split off from *Lethrinops* by Eccles & Trewavas (1989). The
58 character is also known in a single species of the genus *Ctenopharynx* Eccles & Trewavas 1989
59 [*Ctenopharynx pictus* (Trewavas 1935)]. All of these taxa have ventrally positioned mouths,
60 and relatively flat lower jaws with thin mandibular bones and small teeth. This jaw structure is
61 believed to be associated with their feeding behaviour, which, where known, largely consists
62 of ‘sediment-sifting’ or ‘winnowing’ (Weller *et al.* 2022), whereby loose sand or mud is picked
63 up in the mouth, tumbled briefly and then ejected through the mouth and / or operculum,
64 presumably with prey retained and swallowed (Fryer 1959; Fryer & Iles 1972; Konings 2016).
65 Species in the genus *Lethrinops* are largely distinguished from *Taeniolethrinops*,
66 *Tramitichromis* and *Ctenopharynx* by their lack of traits that distinguish those genera (Eccles
67 & Trewavas 1989, Turner 2022). Not surprisingly, *Lethrinops* is currently believed to be
68 polyphyletic (Ngatunga & Snoeks 2004; Malinsky et al. 2018; Masonick et al. 2022).
69 Currently, the genus is ‘operational’, in the sense that it is possible to determine whether newly
70 discovered taxa fall within its definition.

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

76 Materials and methods

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

82 comparisons between the two species, as they had grown to larger sizes than field-collected
83 material. These captive bred fishes were excluded from the type series, but were included in
84 statistical tests.

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

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

104 Observations of live fish were collected from stocks descended from wild-caught fish obtained
105 from Lake Chilingali between 2004 and 2009. Information on diets was taken from previous
106 publications (Tyers et al. 2014; Turner et al. 2019), and an additional three wild-caught
107 specimens of the new species were dissected to inspect stomach contents. Data and images
108 used in analyses are available at: <https://doi.org/10.5281/zenodo.8007304>.

109 **Results**

110 *Quantitative comparisons*

111 Geometric morphometric data were ordinated using a Principal Component Analysis, with the
112 primary axis (PC1) and secondary axis (PC2) capturing 34.2 and 19.6% of the variation,
113 respectively. Overall, there was highly significant differentiation between *L. chilingali* and *L.*
114 *lethrinus* on PC1 (General Linear Model; $F_{1,47} = 39.25$, $P < 0.001$), but not PC2 ($F_{1,47} = 0.52$,
115 $P = 0.60$). The respective type specimens were among the most clearly differentiated
116 individuals (Figure 1). The wireframe plots showed that the *L. lethrinus* specimens have a
117 relatively more ventrally positioned mouth than *L. chilingali*, leading to a longer snout, and a
118 deeper body at the anterior insertion of the dorsal fin.

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

124 (Table 1). The clearest differences were in snout length and lachrymal bone depth, followed by
 125 interorbital width.

126 Comparisons of meristic counts showed that *L. lethrinus* had significantly more cheek scale
 127 rows than *L. chilingali* (K-S test, $Z = 2.001$, $P = 0.001$). Meanwhile *L. chilingali* had
 128 significantly more dorsal rays (K-S test, $Z = 1.805$, $P = 0.003$), upper gillrakers (K-S test, $Z =$
 129 1.682 , $P = 0.007$) and lower gillrakers (K-S test, $Z = 2.903$, $P < 0.001$) than *L. lethrinus* (Tables
 130 2 & 3). There were no differences between the species in dorsal spines (K-S test, $Z = 1.05$, $P =$
 131 0.221), anal spines (always 3), anal rays (K-S test, $Z = 0.265$, $P \sim 1.00$) or lateral line scales
 132 (K-S test, $Z = 0.98$, $P = 0.292$) (Tables 2 & 3).

133

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

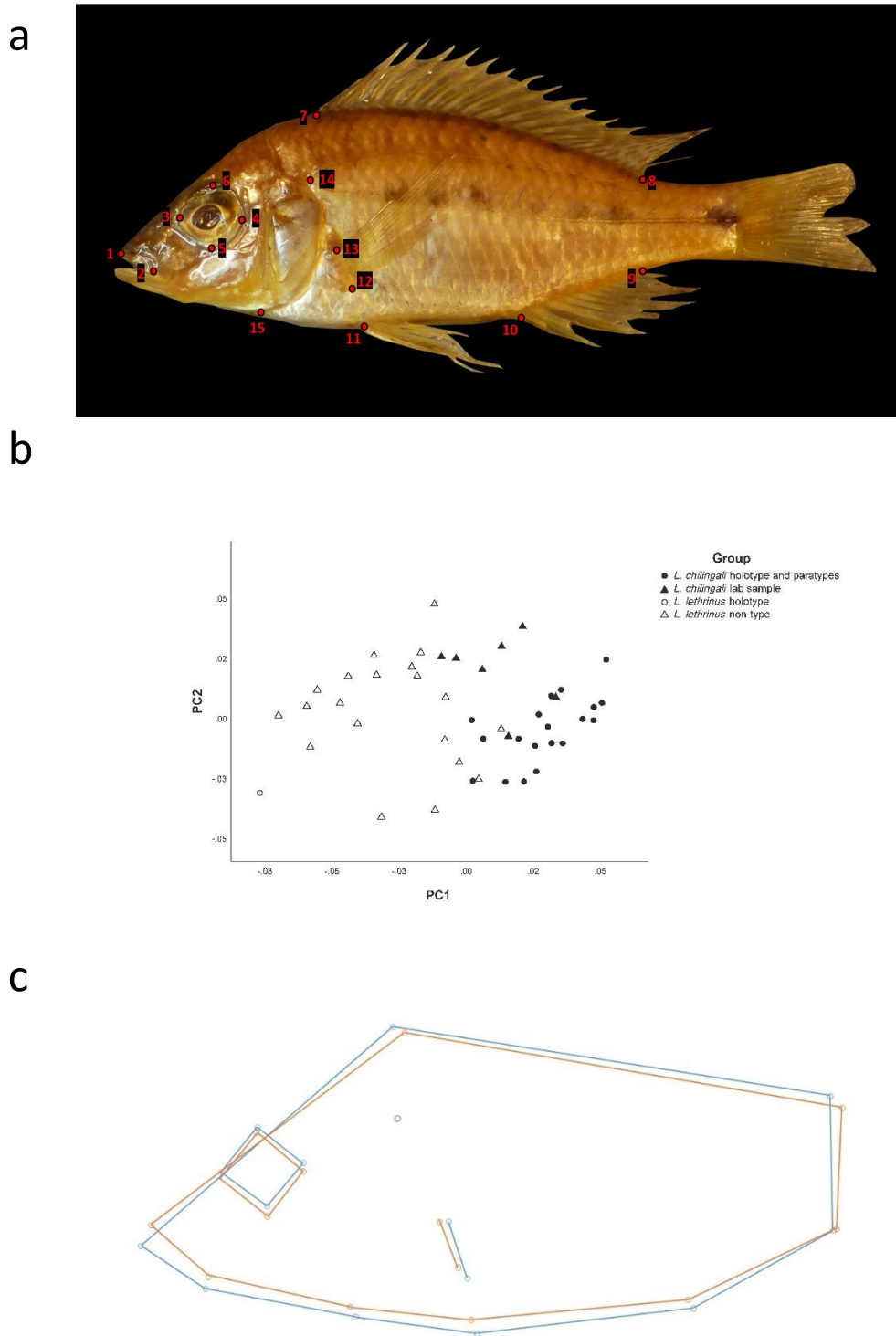
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Measurement	Slope		Elevation	
	$F_{1,51}$	P	$F_{1,52}$	P
Maximum body depth	0.07	0.794	4.08	0.049*
Head length	4.55	0.038*	0.62	0.435
Head width	2.09	0.155	1.41	0.240
Interorbital width	1.73	0.198	10.80	0.002**
Snout length	0.72	0.401	15.11	< 0.001***
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	17.69	< 0.001***
Dorsal fin base length	0.00	0.995	2.09	0.155
Anal fin base length	5.87	0.019*	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	5.41	0.024*
Prepelvic length	1.08	0.303	2.51	0.119
Caudal peduncle length	4.96	0.030*	0.92	0.341
Caudal peduncle depth	2.48	0.122	4.40	0.041*

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141



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

149 ***Lethrinops chilingali* new species.**

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

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

154 **Other material (excluded from the type series):** BMNH 2023.1.11.22-28; seven specimens
155 56.8-98.7mm SL, laboratory bred from specimens collected at Lake Chilingali

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

157 **Diagnosis:** The outer tooth row of the lower jaw curves smoothly to end just behind the inner
158 tooth rows (*Lethrinops*-type dentition), distinguishing the species from other Lake Malawi
159 haplochromines apart from species of the genera *Ctenopharynx*, *Lethrinops*, *Taeniolethrinops*
160 or *Tramitichromis*. *Lethrinops chilingali* can be distinguished from other species in the genera
161 *Ctenopharynx*, *Lethrinops*, *Taeniolethrinops* and *Tramitichromis* by the presence of a
162 conspicuous horizontal series of dark grey to black spots along the middle of the flanks behind
163 the head, linked to form one or two longer dashes, in total comprising 3-6 separate elements.
164 *Lethrinops lethrinus* has a similar horizontal dark midlateral band, but it is typically more
165 continuous, particularly posterior to the first anal spine, rather than broken into shorter spots
166 and dashes. The horizontal melanic elements are generally not exhibited in dominant
167 reproductively active males, however. *L. chilingali* also typically has a less ventrally placed
168 mouth and shorter snout than *L. lethrinus* (snout as % of head length: 31.1-41.8 in *L. chilingali*,
169 37.6-50.0 in *L. lethrinus*).

170 **Description.** Body measurements and counts are presented in Table 2. *L. chilingali* is a small
171 (<85mm SL in wild-caught specimens) moderately laterally compressed (maximum body
172 depth 2.0-2.4 times maximum head width) cichlid fish with a moderately long snout (31.1-41.8
173 % head length). Females and immature males have distinctive melanic markings in the form of
174 a horizontal row of dark spots and dashes (fig. 3b, d) and also have a thin red dorsal fin margin,
175 while mature males are brilliant metallic green with a red dorsal fin margin above broader black
176 and white bands (fig. 3f).

177 All specimens are relatively deep-bodied and laterally compressed, with the deepest part of the
178 body generally well behind the first dorsal fin spine. The anterior upper lateral profile is almost
179 straight from the tip of the snout to the plane of the posterior margin of the eye, occasionally
180 with a slight concavity above the eye, gentle sloping at an angle of about 40-degrees to the
181 horizontal plane. There is no inflection to the angle of the profile above the eye (in contrast to
182 *Tramitichromis* and *Tropheops* Trewavas 1984) and the premaxillary pedicel makes little or no
183 interruption to the profile. The tip of the snout lies at about the same level in a horizontal plane
184 as the upper margin of the insertion of the pectoral fin and at or below the level of the lowermost
185 margin of the eye. The lower anterior lateral profile is also almost straight as far as the insertion
186 of the pelvic fins, gently angled to the horizontal plane (about 12-15-degrees) and with little
187 inflection at the posterior angle of the lower jaw even when the mouth is fully closed. The
188 lower profile is more or less horizontal between the pelvic and anal fins. The mouth is relatively
189 small and moderately upwardly-angled (gape about 40-degrees to horizontal). The caudal
190 peduncle is relatively slender (1.4-1.8 times longer than deep). The pectoral fins are relatively

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

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

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

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

206 The lower pharyngeal bone (fig. 4a) is small, lightly built, Y-shaped, and carries small, slender,
207 widely-spaced simple teeth, as illustrated for *L. lethrinus* by Eccles & Lewis (1978, figure 5).
208 The teeth gradually increase in size from lateral to medial positions, but there are no distinctly
209 differentiated enlarged medial teeth. There are approximately nine teeth in the midline row and
210 17-18 on each side on the posterior row. The gill rakers are short and blunt, generally with the
211 most anterior rakers in the lower and upper arches reduced to small stubs.

212 Female and immature fish (fig. 3d) are countershaded, pale sandy-brown dorsally, pale silvery
213 on the flanks and underside. The flanks are marked by a midlateral horizontal row of dark spots
214 and stripes extending from just behind the upper part of the operculum to the caudal peduncle.
215 This varies between individuals, but generally comprises three to six separate melanic
216 elements. A series up to six dark blotches is sometimes visible at the base of the dorsal fin, and
217 element of a thin longitudinal dark stripe sometimes appears about half-way between the
218 midlateral stripe and the base of the dorsal fin, usually starting a little behind the head and
219 ending well before the caudal peduncle. The dorsal fin has a thin red outer margin and
220 occasionally shows some faint dark spotting on both spinous and soft portions. Occasionally
221 there is a pale submarginal band and anteriorly a thicker dark band. The caudal fin is usually
222 translucent, sometimes with faint spotting. The anal fin sometimes shows a few faint yellowish
223 spots.

224 Males in breeding dress (fig. 3f) are iridescent metallic green to pale blue. The horizontal
225 melanic markings are occasionally exhibited when individuals are caught in fishing gear, or
226 defeated in aggressive contests (seen in aquaria). Sometimes a series of faint dark vertical bars
227 are visible. Patches of flank scales sometimes exhibit a metallic orange section anteriorly. The
228 dorsal fin has a broad scarlet margin, underlain with a white submarginal band: these bands are
229 narrower on the soft dorsal area. On the spinous dorsal, the red and white bands are underlain
230 with a broad black band which extends to the base of the dorsal fin on the first inter-radial
231 membrane, but as the membranes become longer posteriorly, the band overlies a series of
232 orange spots extending onto the soft dorsal area, where they can be up to 10 spots between the
233 longest rays. The membranes between the spots are pale grey to white. The caudal fin continues

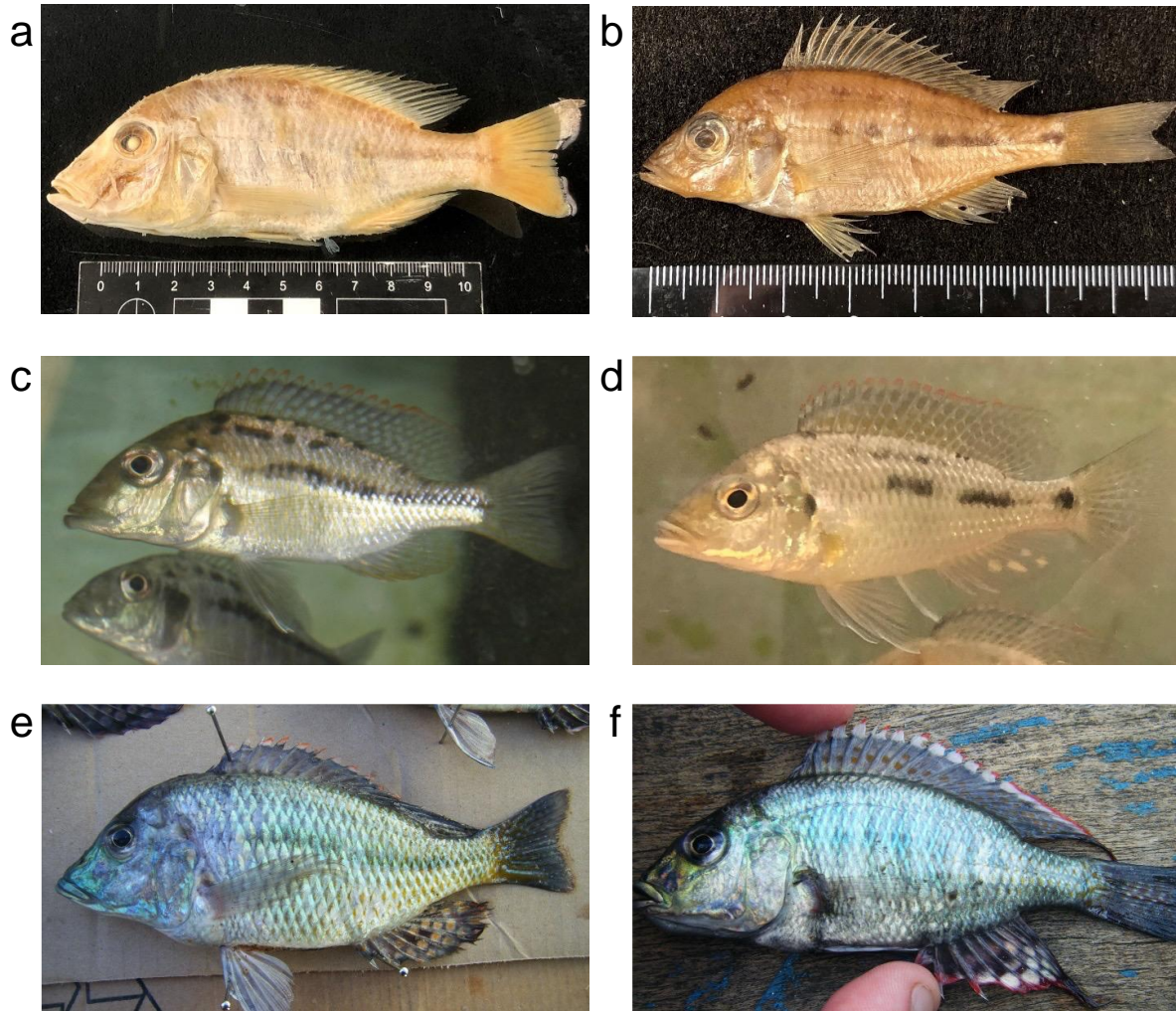
234 this pattern of orange spots with white/grey areas between. Sometimes the white inter-spot
235 areas are missing, resulting in spots merging into stripes parallel to the fin rays. Occasionally,
236 the white areas merge into stripes too. The upper and lower parts of the caudal fin can
237 sometimes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

247



248

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



251

252 **FIGURE 3.** Comparisons of *Lethrinops lethrinus* and *Lethinops chilingali*. **a.** holotype of *L.*
253 *lethrinus*, BMNH 1893.15.15., 118.5mm SL. **b.** paratype of *L. chilingali*, BMNH 2023.1.11.2-
254 21, female, 60.7mm SL; **c.** *L. lethrinus* apparent female alive in aquarium. **d.** *L. chilingali*
255 apparent immature male alive in aquarium. **e.** mature male *L. lethrinus*. **f.** mature male *L.*
256 *chilingali*. The shorter snout *L. chilingali* is evident, and the more broken midlateral stripe can
257 be seen in the live specimens.

258

259

260 **TABLE 2.** Morphometric and meristic characters of *Lethrinops chilingali*.

	Holotype	Paratypes (n=20) mean (range)	Captive strain (n=7) mean (range)
Standard length (mm)	70.9	65.7 (59.3-81.2)	80.4 (56.8-98.7)
As % Standard length			
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)
As % Head length			
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)
Ratios			
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)
Counts			
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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262

263 **Distribution.** Known only from Lake Chilingali in the Lake Malawi catchment (fig. 4b).

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

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

276 Dominant male *L. chilingali* are territorial and actively court females in typical haplochromine
277 style: fins wide open, body horizontal or head-up, making rapid darts to the spawning site and
278 back to the female, with spawning taking place amid bouts of circling and quivering, while
279 alternating head-to-anal-fin ‘T-positions’ on the substrate. It is notable that dominant male
280 coloration and aggression vary a lot, appearing to peak when females are approaching
281 spawning, but are otherwise often quite subdued. During persistent bouts of courtship or
282 aggression, the melanic elements of the male colour are emphasised, particularly the
283 lachrymal/eye stripe, dark pelvic and anal fins, dark upper and lower margins of the caudal fin
284 and even faint vertical barring on the flanks. Even in a large tank with a high density of fish,
285 there is usually just a single dominant male: this is similar to *Astatotilapia* Pellegrin 1904,
286 which tend to be solitary breeders. Communal lek breeders, such as *Oreochromis* Günther 1889
287 will usually divide up a tank into numerous smaller territories and engage in frequent boundary
288 disputes. This suggests that *Lethrinops chilingali* are not communal lek breeders in the wild.

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

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

307 to return to their mouths. This non-guarding behaviour is similar to other known shallow-water
308 *Lethrinops* species.

309

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

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

313 **Other material examined:**

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

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

320 BMNH 2023.1.11.31, 1 specimen, 101.4mm SL, collected by G.F. Turner from kambuzi seine
321 fisherman, West shore of Lake Malombe, probably at Chimwala (14.64°S, 35.18°E), 26 June
322 1992,

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

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

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

329 BMNH 2023.1.11.44-46, 3 specimens 97.9-116.1 mm SL, collected by G. F. Turner, trawled
330 at 18-21m at Ulande 1a station (14.23°S, 35.21°E), SE Arm Lake Malawi, 1991.

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

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

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

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

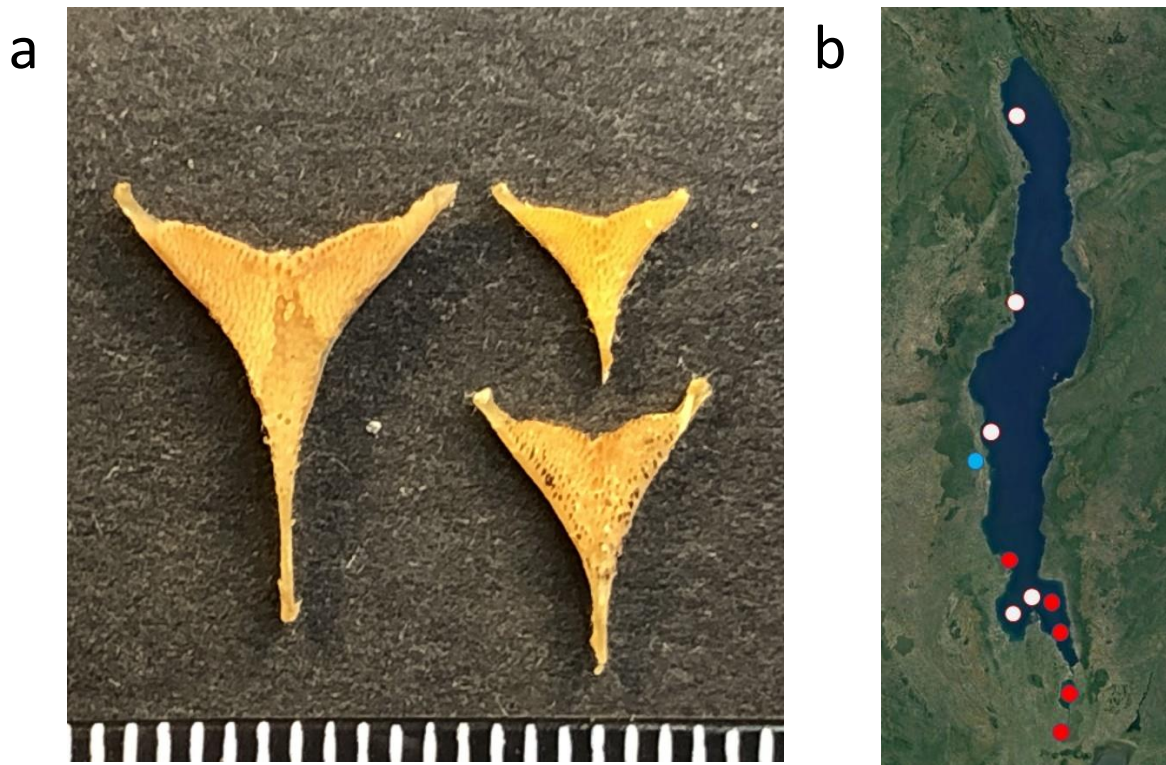
339 **Remarks:** *L. lethrinus* was selected as the type of the genus *Lethrinops* by Regan (1922). It
340 was originally described as *Chromis lethrinus* from a single specimen, but was redescribed
341 from additional material by Regan (1922), Trewavas (1931), Eccles & Lewis (1978) and Eccles
342 &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

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

355 *Lethrinops lethrinus* is readily diagnosed based on its typical *Lethrinops*-type dentition,
356 horizontal melanic flank markings and long snout. Mature males show a metallic blue-green
357 breeding dress, with a prominent red and white dorsal fin margin and numerous large eggspots
358 on the anal fin (Figure 3, see also Konings 2016). *L. lethrinus* appears to be confined to shallow
359 waters with muddy bottoms, often river mouths with extensive beds of reeds and other
360 macrophytes, feeding on invertebrates and other edible material obtained from the sediment
361 (Turner 1996). Konings (2016) reports a lakewide distribution and it has been recorded from
362 Lake Malombe and the Upper and Middle Shire Rivers (Turner 1996), but records from Domira
363 Bay northwards are based on juveniles that are hard to distinguish from *L. chilingali* or lack
364 available voucher material (fig. 4b). Counts and measurements of the material we examined
365 are presented on Table 3.

366

367



368

369 **FIGURE 4.** a. Lower pharyngeal bones of *Lethrinops lethrinus*, 128mm SL, BMNH
370 2023.1.11.49-50 (left); *Lethrinops lethrinus* 84mm SL (unregistered, bottom right); *Lethrinops*
371 *chilingali* 69mmSL (unregistered, top right); b. Distribution of *Lethrinops lethrinus* specimens
372 examined (●), unconfirmed records: juveniles or not examined (○) and *Lethrinops chilingali*
373 (●).

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

	Holotype	Non-types (n=26) mean (range)
Standard Length (mm)	118.5	110.7 (62.9-152.6)
As % Standard length		
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)
As % Head length		
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)
Ratios		
Body depth/Head width	2.29	2.36 (2.14-2.67)
Caudal peduncle length/depth	1.43	1.45 (1.17-1.66)
Counts		
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

375

376



377

378 **FIGURE 5.** Comparative material. **a.** Three small specimens (BMNH 1935.6.14.2077-9) from
379 Lupembe in northern Lake Malawi match *Lethrinops lethrinus*, in melanin pattern and low
380 position of mouth on the head. **b.** A syntype of *Lethrinops leptodon* BMNH 1921.9.6.201-207,
381 showing two oblique stripes thickened and fused together to form a midlateral blotch. This
382 pattern is distinguishable from those of *L. chilingali* and *L. lethrinus*, but is similar to the
383 Nkhata Bay population reported by Eccles & Lewis (1978) and assigned by them to *L.*
384 *lethrinus*.

385

386

387 4. DISCUSSION

388

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

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

417

418 Distributions of *L. chilingali* and *L. lethrinus*

419 *Lethrinops chilingali* has only been positively recorded from Lake Chilingali, but here we
420 consider whether it may have a broader distribution in Lake Malawi, possibly extending to the
421 central to northern part of the lake as an allopatric sister species to *L. lethrinus*. Although a
422 lake-wide distribution has been claimed for *L. lethrinus* (Konings 2016), the great majority of
423 records backed by preserved specimens or photographs come from the southern arms, Lake
424 Malombe and the Shire River (Eccles & Lewis 1978, Turner 1996, Konings 2016). On the
425 Global Biodiversity Information Facility website (GBIF 2023), there is a record of *Lethrinops*
426 *lethrinus* from co-ordinates indicating a collection site off the Tanzanian shore near Ngkuyo
427 Island, Mbamba Bay (11.334°S, 34.769°E), based on specimens at the South African Institute
428 for Aquatic Biodiversity (SAIAB). An offshore location near a rocky headland seems an
429 unlikely collecting site for *Lethrinops lethrinus*, which favours shallow sheltered vegetated

430 habitats and the locality label is given as ‘Lifuwu’, which probably corresponds to the vicinity
431 of Lifuwu village (13.69°S, 34.60°E) just north of Salima, suggesting that the co-ordinates
432 have been recorded in error. The single small specimen shows no melanic markings (faded
433 post-preservation?), but the head shape is consistent with *Lethrinops lethrinus* rather than *L.*
434 *chilingali*. Another GBIF record from co-ordinates 13.35°S, 33.4°E would suggest specimens
435 were collected from the Rusa River, a tributary of the Bua River, which joins Lake Malawi
436 near Lake Chilingali. The site is far upstream, around 97km West of the Lake Malawi shore at
437 Benga, and initially we thought this might suggest specimens of *L. chilingali* could be
438 widespread in the river catchment. However, the collection label indicates the specimens were
439 collected from Lake Malawi at Foo, which is a trawling station in the SE Arm of Lake Malawi
440 (also sometimes written as Fowo), which is at approximately 14.14°S, 35.18°E, again
441 suggesting an error in the co-ordinates. Photographs of the specimens show typical *Lethrinops*
442 *lethrinus*, with long snouts and strong horizontal melanic markings. The catalogue of the
443 Natural History Museum in London contains a single accession of three specimens labelled as
444 *L. lethrinus* from Lupembe Sand Bar, collected by Cuthbert Christy in 1925 (BMNH
445 1935.6.14.2077-9; Figure 4). The electronic catalogue suggests that this location is in Tanzania,
446 perhaps following Eccles & Trewavas (1989) who suggested it might represent a site at the
447 mouth of the ‘Kivira River’. However, the town at the mouth of the Kiwira River (as presently
448 named) is currently known as Itungi Port. It is more likely that the 1925 collection site is
449 Lupembe on the Malawian lakeshore, just south of Karonga (10.055°S, 33.99°E). Notably,
450 recent satellite images show a conspicuous sandbar (Google Earth). Examination of the
451 unpublished diary of Cuthbert Christy held at the Natural History Museum shows a single
452 accession from Lupembe following an extensive collection of several hundred accessions from
453 Vua / Deep Bay (Chilumba area) and immediately before another extensive collection from
454 Mwaya in Tanzania, on the far north coast of the lake (itemising various river mouths visited).
455 No other accessions were made from Lupembe. This suggests that the location was visited en-
456 route from Chilumba to Tanzania, which would fit well with the location near Karonga.
457 Unfortunately, the specimens (fig. 5a) are very small (44.8-50.9 mm SL) which makes
458 morphological comparisons difficult with the larger specimens examined for this study, due to
459 allometric effects. For example, they have notably relatively large eyes, making snout
460 measurements relatively small. However, the low position of the mouth on the head and the
461 largely continuous midlateral stripe, fit far better with *L. lethrinus* than with *L. chilingali*. Thus,
462 available museum specimens strongly support the occurrence of typical *Lethrinops lethrinus*
463 only in the southern arms of the lake, but tentatively indicate that they may also occur just north
464 of Senga Bay and indeed almost at the northernmost extremity of the lake, but do not provide
465 evidence for the occurrence of *L. chilingali* or any other similar form within Lake Malawi,

466 Other published records are not backed by specimens available to examine or photographic
467 evidence. Eccles & Lewis (1978) reported that they had found *L. lethrinus* at Nkhata Bay,
468 which is well to the north of Lake Chilingali. However, they reported an unusual melanin
469 pattern: “the dark line along the middle of the flank curves upwards anteriorly to merge with
470 the lower of the two rows of spots and the spots themselves may run together posteriorly to
471 form a stripe”. The occurrence of specimens with dramatically different stripe patterns at
472 Nkhata Bay might lend credence to the idea that *L. lethrinus* represents a complex of allopatric
473 taxa, which might increase the probability that *L. chilingali* might persist in the main Lake
474 Malawi. Eccles & Lewis provided no illustration of this ‘Nkhata Bay variant’. Their specimens
475 were deposited in the collection of the Monkey Bay Fisheries Research Unit, Malawi and their

476 present status is unknown. The pattern described is reminiscent of that seen on some of the
477 type specimens of *L. leptodon* Regan 1922 (fig. 5b). In the same 1978 paper, Eccles & Lewis
478 redescribed that species based on a single specimen collected from Chintheche in the NW of
479 the lake, near Nkhata Bay, but their illustration of that specimen showed a clear midlateral
480 blotch on the upper part of the flank. They reported examining, but not measuring, three of the
481 type specimens of *L. leptodon*, which are held at the Natural History Museum in London
482 (BMNH 1921.9.6.201-207, collected by Wood from somewhere in ‘Lake Nyasa’). Thus, it
483 seems unclear whether the reported Nkhata Bay populations represent *L. lethrinus* or *L.*
484 *leptodon*, or indeed something else. In summary, the status of the northern populations of
485 *Lethrinops* of this group is unclear but is consistent with the hypothesis that *L. lethrinus* is
486 found in suitable habitats throughout Lake Malawi, and that *L. chilingali* is a satellite lake
487 endemic extinct in the wild.

488 **Conservation status of *Lethrinops chilingali***

489 Lake Chilingali is approximately 5km in length and a maximum of 1km in width, and is
490 characterised by two deeper basins of approximately 5m depth separated by a shallower
491 plateau (Turner et al. 2019). It has a single outflow, the Kaombe River, which meanders for
492 approximately 12km before reaching the main body of Lake Malawi (Genner et al. 2007).
493 The lake is a natural water body, and the two basins of the modern lake are represented on
494 early European exploration maps, as two separate bodies of water, Lake Chikukutu to the
495 south, and Lake Chilingali to the north (Turner et al. 2019). The lake level was raised when a
496 dam was constructed across the single outflow for irrigation purposes, initially in the 1950s,
497 before being modified in the early 1970s (Denys et al. 2013). The dam collapsed early in
498 2012 (Denys et al. 2013), and the single lake disappeared, reforming the two separate smaller
499 shallow basins. In 2016 these basins were estimated to be only ~1m deep and fringed with
500 macrophytes. The lake was refilled to approximately its pre-collapse-level in June-July 2019
501 following the construction of a new dam.

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

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

522

523 **Acknowledgements**

524 We are grateful to the Malawi Government Department of Fisheries for collaboration and
525 permits. Sampling and specimen collection on Lake Chilingali in 2004 was funded by the
526 Natural Environment Research Council award NER/A/S/2003/00362, and in 2009 by a student
527 expedition grant from Zoological Society of London to Gavan Cooke, Dave Bavin, Lucy Ferris,
528 Cat Griggs and Bev Stubbs, to whom we are grateful for help in specimen collection. We thank
529 Rupert Collins, Oliver Crimmen, James Maclaine and Simon Loader at the Natural History
530 Museum in London for helping us with access to specimens, finding old field notes and
531 cataloguing new material. We are grateful to Jay Stauffer and Roger Bills for photos of the
532 SAIAB specimens and their labels, to Hannes Svardal for information about the 2022
533 expedition and to Alexandra Tyers and Dave Bavin for photographs of *Lethrinops lethrinus* in
534 the aquarium and field respectively.

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