Article 1 2 (formatted for Zootaxa, BioRxiv). 3 urn:lsid:zoobank.org:pub:3DC09643-717F-45AC-9EE5-4FFB1D40BD6D 4 A new species of *Lethrinops* (Cichliformes: Cichlidae) from a 5 Lake Malawi satellite lake, believed to be extinct in the wild. 6 GEORGE F. TURNER¹, DENISE A. CRAMPTON² & MARTIN J. GENNER³ 7 8 9 ¹ School of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2UW, United Kingdom & Vertebrates Division, Natural History Museum, Cromwell Road, London SW7, 10 11 UK. Corresponding author: email bss608@bangor.ac.uk 12 ID: https://orcid.org/0000-0003-0099-7261 13 14 ² School of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2UW, United 15 Kingdom; present address: School of Biological & Environmental Sciences, Liverpool John 16 17 Moores University, Liverpool, L3 3AF, UK; email: D.Crampton@2023.ljmu.ac.uk ID: https://orcid.org/0000-0002-2877-5209 18 19 ³ School of Biological Sciences, University of Bristol, Life Sciences Building, 24 Tyndall 20 21 Avenue, Bristol, BS8 1TQ, United Kingdom. Email: m.genner@bristol.ac.uk 22 ID: https://orcid.org/0000-0003-1117-9168 23 24 25 **Abstract** 26 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 27 28 form of the lower jaw dental arcade and by the absence of traits diagnostic of the phenotypically 29 similar Ctenopharynx, Taeniolethrinops and Tramitichromis. It also lacks the enlarged cephalic 30 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* 31 chilingali distinguishes them from all congeners, including Lethrinops lethrinus, in which the 32 33 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 34 that Lethrinops chilingali is now extinct in the wild, as this narrow endemic species has not 35 been positively recorded in the natural environment since 2009. Breeding populations remain 36 37 in captivity. **Keywords:** African cichlid, haplochromine, Lake Chilingali, morphology. 38

Introduction

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Satellite lakes are small lakes lying in the catchment of much larger lakes, formerly or 40 sometimes intermittently connected (Kaufman & Ochumba 1993; Mwanja et al. 2001; Genner 41 et al. 2007). Their presence has been proposed to enhance the generation of biodiversity by 42 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 informally referred to as Lethrinops sp. "chilingali" (Tyers et al. 2014; Turner et al. 2019) has 49 50 been sampled.

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

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

Materials and methods

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

- 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
- were made in 1991-1992. These specimens were fixed in formalin and preserved in alcohol,
- 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
- onstructed 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
- 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
- transpose, rotate and scale them into comparable Procrustes coordinates. These were analysed
- using SPSS v27 (IBM, NY).
- Observations of live fish were collected from stocks descended from wild-caught fish obtained
- from Lake Chilingali between 2004 and 2009. Information on diets was taken from previous
- publications (Tyers et al. 2014; Turner et al. 2019), and an additional three specimens of the
- new species were dissected to inspect stomach contents.

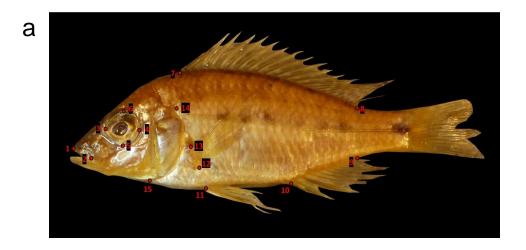
Results

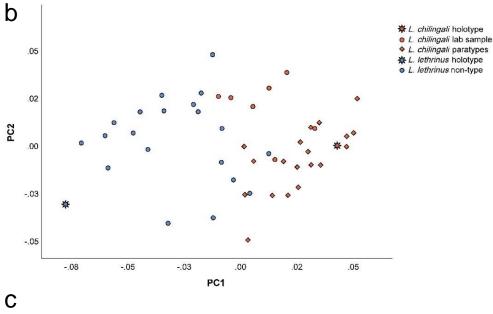
- 107 Quantitative comparisons
- 108 Geometric morphometric data were ordinated using a Principal Component Analysis, with the
- primary axis (PC1) and secondary axis (PC2) capturing 34.2 and 19.6% of the variation,
- respectively. Overall, there was highly significant differentiation between L. chilingali and L.
- lethrinus on PC1 (General Linear Model; $F_{1,47} = 44.09$, P < 0.001), but not PC2 ($F_{1,47} = 0.46$,
- P = 0.83). The respective type specimens were among the most clearly differentiated
- individuals (Figure 1). The wireframe plots showed that the L. lethrinus specimens have a
- relatively more ventrally positioned mouth than L. chilingali, leading to a longer snout, and a
- deeper body at the anterior insertion of the dorsal fin.
- 116 Comparisons of linear morphometric measurements revealed significant differences in slopes
- of head length, anal fin base length and caudal peduncle length when regressed on standard
- length (Table 1). Assuming equal slopes, and using standard length as a covariable, *L. lethrinus*
- had significantly relatively greater body depth, interorbital width, snout length, lower jaw
- 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
- interorbital width.

Comparisons of meristic counts showed that *L. lethrinus* had a significantly more cheek scale rows than *L. chilingali* (K-S test, Z=2.001, P=0.001). Meanwhile *L. chilingali* had significantly more dorsal rays (K-S test, Z=1.805, P=0.003), upper gillrakers (K-S test, Z=1.682, P=0.007) and lower gillrakers (K-S test, Z=2.903, P<0.001) than *L. lethrinus* (Table 1). There were no differences between the species in dorsal spines (K-S test, Z=1.05, P=0.221), anal spines (always 3), anal rays (K-S test, Z=0.265, $P\sim1.00$) or lateral line scales (K-S test, Z=0.98, P=0.292) (Table 1).

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

Measurement	Slope		Elevation	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*	





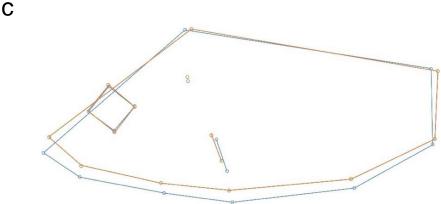


FIGURE 1. Geometric morphometric analyses of *Lethrinus lethrinus* and *Lethrinus chilingali* **a.** Landmarks used to quantify shape variation of preserved specimen (see Materials and methods for details). **b.** Principal Component Analysis indicates strong separation of *L. lethrinus* and *L. chilingali* on PC1, with clear differentiation of the respective holotypes. **c.** Wireframe plots summarising shape differences between *L. lethrinus* (blue) and *L. chilingali* (orange), including the more ventrally placed mouth, longer snout, and higher back in 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.
- Paratypes: BMNH 2023.1.11.2-21, twenty specimens 59.3-81.2 mm SL, collected with
- 151 holotype.
- Other material (excluded from the type series): BMNH 2023.1.11.22-28; seven specimens
- 56.8-98.7mm SL, laboratory bred from specimens collected at Lake Chilingali
- **Etymology:** 'chilingali' from Lake Chilingali, the type locality, used as a noun in apposition.
- Diagnosis: The outer tooth row of the lower jaw curves smoothly to end just behind the inner
- tooth rows (*Lethrinops*-type dentition), distinguishing the species from other Lake Malawi
- haplochromines apart from species of the genera *Ctenopharynx*, *Lethrinops*, *Taeniolethrinops*
- or *Tramitichromis*. *Lethrinops chilingali* can be distinguished from other species in the genera
- 159 Ctenopharynx, Lethrinops, Taeniolethrinops and Tramitichromis by the presence of a
- conspicuous horizontal series of dark grey to black spots along the middle of the flanks behind
- 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
- and dashes. The horizontal melanic elements are generally not exhibited in dominant
- reproductively active males, however. L. chilingali also typically has a less ventrally placed
- 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*).
- **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
- 2.0-2.4 times maximum head width) cichlid fish with a moderately long snout (31.1-41.8 %
- head length). Females and immature males have distinctive melanic markings in the form of a
- horizontal row of dark spots and dashes and also have a thin red dorsal fin margin, while mature
- males are brilliant metallic green with a red dorsal fin margin above broader black and white
- 174 bands.
- All specimens are relatively deep-bodied and laterally compressed, with the deepest part of the
- body generally well behind the first dorsal fin spine. The anterior upper lateral profile is almost
- straight from the tip of the snout to the plane of the posterior margin of the eye, occasionally
- with a slight concavity above the eye, gentle sloping at an angle of about 40-degrees to the
- 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
- the profile. The tip of the snout lies at about the same level in a horizontal plane as the upper
- margin of the insertion of the pectoral fin and at or below the level of the lowermost margin of
- the eye. The lower anterior lateral profile is also almost straight as far as the insertion of the
- pelvic fins, gently angled to the horizontal plane (about 12-15-degrees) and with little inflection
- at the posterior angle of the lower jaw even when the mouth is fully closed. The lower profile is more or less horizontal between the pelvic and anal fins. The mouth is relatively small and
- moderately upwardly-angled (gape about 40-degrees to horizontal). The caudal peduncle is
- relatively slender (1.4-1.8 times longer than deep). The pectoral fins are relatively long,

- extending past the first anal spine, but the pelvic fins are generally short of this, except in the
- largest mature males. The dorsal and anal fins, when folded, end well short of the caudal fin
- insertion, except in large mature males. The caudal fin is crescentic. The eye is large and
- 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
- anteriorly above the upper lateral line, where they transition into a cycloid state. The scales on
- the chest are relatively large and there is a gradual transition in size from the larger flank scales,
- 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
- deep and the lateral line pores are heavily overgrown with skin.
- The lower jaw is relatively small, with thin mandibular bones. The jaw teeth are small, short
- and erect. The outer series in both the upper and lower jaw are short, blunt, erect and largely
- unequally bicuspid. These is a single inner series of small, pointed tricuspid teeth.
- The lower pharyngeal bone is small, lightly built, Y-shaped, and carries small, slender, widely-
- spaced simple teeth. The teeth gradually increase in size from lateral to medial positions, but
- there are no distinctly differentiated enlarged medial teeth. There are approximately nine teeth
- in the midline row and 17-18 on each side on the posterior row. The gill rakers are short and
- 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
- stripes extending from just behind the upper part of the operculum to the caudal peduncle. This
- varies between individuals, but generally comprises three to six separate melanic elements. A
- series up to six dark blotches is sometimes visible at the base of the dorsal fin, and element of
- a thin longitudinal dark stripe sometimes appears about half-way between the midlateral stripe
- 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
- faint dark spotting on both spinous and soft portions. Occasionally there is a pale submarginal
- band and anteriorly a thicker dark band. The caudal fin is usually translucent, sometimes with
- faint spotting. The anal fin sometimes shows a few faint yellowish spots.
- Males in breeding dress are iridescent metallic green to pale blue. The horizontal melanic
- markings are occasionally exhibited when individuals are caught in fishing gear, or defeated in
- 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
- has a broad scarlet margin, underlain with a white submarginal band: these bands are narrower
- on the soft dorsal area. On the spinous dorsal, the red and white bands are underlain with a
- broad black band which extends to the base of the dorsal fin on the first inter-radial membrane,
- but as the membranes become longer posteriorly, the band overlies a series of orange spots
- extending onto the soft dorsal area, where they can be up to 10 spots between the longest rays.
- The membranes between the spots are pale grey to white. The caudal fin continues this pattern
- of orange spots with white/grey areas between. Sometimes the white inter-spot areas are

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

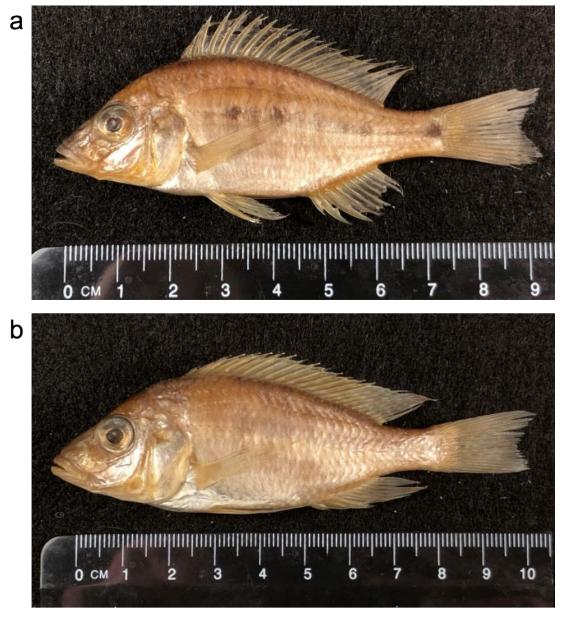


FIGURE 2. *Lethrinops chilingali.* **a.** Holotype, BMNH 2023.1.11.1; female 70.9mm SL. **b.** Paratype, BMNH 2023.1.11.2-21; mature male, 81.2mm SL.

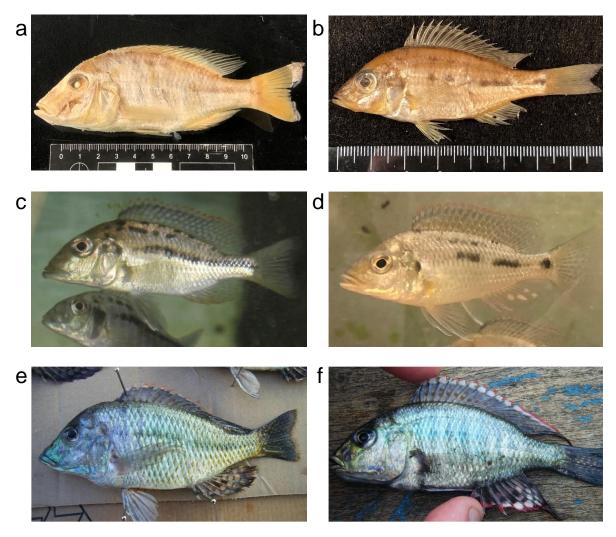


FIGURE 3. Comparisons of *Lethrinops lethrinus* and *Lethinops chilingali*. **a.** holotype of *L. lethrinus*, BMNH 1893.15.15., 118.5mm SL. **b.** paratype of *L. chilingali*, BMNH 2023.1.11.2-21, 60.7mm SL; **c.** *L. lethrinus* apparent female alive in aquarium. **d.** *L. chilingali* apparent immature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

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

Holotype	Paratypes (n=20)	Captive strain (n=7)
	mean (range)	mean (range)
70.9	65.7 (59.3-81.2)	80.4 (56.8-98.7)
36.2	35.2 (33.1-36.8)	34.1 (31.1-36.7)
34.4	33.6 (32.1-35.9)	35.9 (34.7-38.9)
53.9	53.0 (51.0-55.7)	53.0 (50.8-56.7)
18.8	19.6 (16.9-21.5)	18.0 (17.1-18.8)
39.2	37.5 (35.0-39.3)	39.1 (35.2-42.5)
65.3		64.6 (61.1-67.8)
36.4	35.5 (33.5-38.0)	36.1 (33.8-38.0)
40.2	39.9 (37.1-43.1)	41.5 (38.2-44.1)
19.2	17.9 (16.1-20.0)	17.2 (16.1-20.4)
11.0	11.5 (10.4-12.4)	11.4 (10.9-12.3)
47.1	45.6 (40.9-50.0)	43.7 (40.4-47.4)
21.1	21.8 (18.8-24.5)	22.7 (20.4-27.2)
33.3	35.2 (31.1-38.2)	38.7 (34.6-41.8)
40.9	39.2 (35.3-42.9)	39.2 (37.3-44.2)
29.8	29.7 (25.7-35.9)	30.0 (24.9-35.4)
31.1	31.8 (28.2-37.7)	29.1 (25.7-33.0)
21.5	21.4 (18.0-25.9)	23.8 (21.0-27.7)
2.25	2.30 (2.11-2.41)	2.18 (1.99-2.34)
1.74	1.56 (1.37-1.80)	1.51 (1.37-1.76)
Holotype	Paratypes	Captive strain
	(range)	(range)
3	3-4	3-4
10	9-11	10-12
XV, 10	XIV-XVI, 9-10	XIV-XV, 10-11
III, 8	III, 8-10	III, 8-9
31	31-33	30-33
3	2-4	2-4
	70.9 36.2 34.4 53.9 18.8 39.2 65.3 36.4 40.2 19.2 11.0 47.1 21.1 33.3 40.9 29.8 31.1 21.5 2.25 1.74 Holotype 3 10 XV, 10 III, 8 31	70.9 65.7 (59.3-81.2) 36.2 35.2 (33.1-36.8) 34.4 33.6 (32.1-35.9) 53.9 53.0 (51.0-55.7) 18.8 19.6 (16.9-21.5) 39.2 37.5 (35.0-39.3) 65.3 64.1 (62.5-66.5) 36.4 35.5 (33.5-38.0) 40.2 39.9 (37.1-43.1) 19.2 17.9 (16.1-20.0) 11.0 11.5 (10.4-12.4) 47.1 45.6 (40.9-50.0) 21.1 21.8 (18.8-24.5) 33.3 35.2 (31.1-38.2) 40.9 39.2 (35.3-42.9) 29.8 29.7 (25.7-35.9) 31.1 31.8 (28.2-37.7) 21.5 21.4 (18.0-25.9) 40.9 Paratypes (range) 3 3-4 10 9-11 XV, 10 XIV-XVI, 9-10 III, 8 III, 8-10 31 31-33

259 **Behaviour and Ecology.** The diet of *L. chilingali* specimens sampled in 2009 consisted largely

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
- wild has not been observed, as the water of Lake Chilingali was highly turbid when visited
- 264 between 2004 and 2009.
- 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
- surface. When attempts are made to catch the fish, they show a strong tendency to dive into the
- sand, turning sideways and completely burying themselves. This same behaviour has been
- 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
- style: fins wide open, body horizontal or head-up, making rapid darts to the spawning site and
- back to the female, with spawning taking place amid bouts of circling and quivering, while
- 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
- 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
- lachrymal/eye stripe, dark pelvic and anal fins, dark upper and lower margins of the caudal fin
- and even faint vertical barring on the flanks. Even in a large tank with a high density of fish,
- there is usually just a single dominant male: this is similar to Astatotilapia, which tend to be
- solitary breeders. Communal lek breeders, such as *Oreochromis* will usually divide up a tank
- into numerous smaller territories and engage in frequent boundary disputes. This suggests that
- 283 Lethrinops chilingali are not communal lek breeders in the wild.
- There is little indication of bower construction in *L. chilingali* when a sand or gravel substrate
- is provided: dominant males usually try to lead females to a slight depression near to an object
- such as a rock or piece of wood: in a bare tank, the focus would probably be the tank bottom
- near one of the corners or a wall near a heater or filter inlet. This is in marked contrast to reports
- 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
- of their time chasing, then returning to the territory focus next to the object, during which they
- make occasional 'feeding movement' of picking up a mouthful of substrate, moving forwards
- and ejecting it through the mouth and/or opercular openings at a slight distance away. This
- occurs all over the vicinity of the side of the object they are defending, but there seems to be a
- slight bias towards a certain point up against the object, which thereby becomes a shallow
- 296 depression.
- 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
- 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.

- 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:
- BMNH 2023.1.11.29, 1 specimen 130.1mm SL, collected by G.F. Turner from experimental
- 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
- depth between Namiasi and Malindi (approximately 14.34°S, 35.22°E), SE Arm of Lake
- 314 Malawi, 30th July 1991.
- BMNH 2023.1.11.31, 1 specimen, 101.4mm SL, collected by G.F. Turner from kambuzi seine
- 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.
- 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), 20th May 1992.
- 322 BMNH 2023.1.11.38-43, 6 specimens 129.2-152.6 mm SL, collected by G. F. Turner
- 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
- 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
- seine fishermen, Lake Malombe (14.64°S, 35.18°E), 6th July 2009.
- 328 BMNH 2023.1.11.49-50, 2 specimens 121.7-128.0 mm SL, collected by G. F. Turner, trawled
- 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
- seine net fishermen, Palm Beach (14.41°S, 35.23°E), SE Arm of Lake Malawi, 23 Jan 2017.
- BMNH 2023.1.11.54, 1 specimen 120.7 mm SL, collected by G. F. Turner, from seine net
- fishermen, Palm Beach (14.41°S, 35.23°E), SE Arm of Lake Malawi, 22 Jan 2017.
- Remarks: L. lethrinus was selected as the type of the genus Lethrinops by Regan (1922). It
- was originally described as *Chromis lethrinus* from a single specimen, but was redescribed
- from additional material by Regan (1922), Trewavas (1931), Eccles & Lewis (1978) and Eccles
- & Trewavas (1989). It was also included in a key to the shallow-water *Lethrinops* species by
- Ngatunga & Snoeks (2004). The original illustration in Günther (1893) shows a specimen with
- a continuous horizontal midlateral stripe beginning at the eye and extending to the base of the

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

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

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

	Holotype	Non-types (n=26)
	~-	mean (range)
Standard Length	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	Holotype	Non-types (range)
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





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

4. DISCUSSION

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

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

Distributions of L. chilingali and L. lethrinus

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

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

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

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

Conservation status of *Lethrinops chilingali*

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Lake Chilingali is approximately 5km in length and a maximum of 1km in width, and is characterised by two deeper basins of approximately 5m depth separated by a shallower plateau (Turner et al. 2019). It has a single outflow, the Kaombe River, which meanders for approximately12km before reaching the main body of Lake Malawi (Genner et al. 2007). The lake is a natural water body, and the two basins of the modern lake are represented on early European exploration maps, as two separate bodies of water, Lake Chikukutu to the south, and Lake Chilingali to the north (Turner et al. 2019). The lake level was raised when a dam was constructed across the single outflow for irrigation purposes (Genner et al. 2007), which took place around 1992 according to information from the Malawi Government Department of Surveys (Genner et al. 2007). The dam collapsed between June and September 2014, and the single lake disappeared, reforming the two separate smaller shallow basins. In 2016 these basins were estimated to be only ~1m deep and fringed with macrophytes. The lake was refilled to approximately its pre-collapse-level in June-July 2019 following the construction of a new dam.

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

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

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