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Description of *Neolamprologus timidus*, new species, and review of *N. furcifer* from Lake Tanganyika (Teleostei: Cichlidae)

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Neolamprologus timidus, new species, is described from Ulwile Island and adjacent localities on the Tanzanian coast of Lake Tanganyika. The species was observed or collected along about 100 km of coastline from Kolwe Point, Cape Mpimbwe, south to Kisi Island. It is distinguished from the most similar species, *N. furcifer*, by presence of scales on most of the cheek, long pectoral fin and pelvic fin with the second ray longer than the first. *Neolamprologus timidus* is sympatric with *N. furcifer* at Kolwe Point and south to Kampempa Point, and at Lupita and Ulwile Islands south to Kisi Island, but *N. furcifer* is otherwise absent from the range of *N. timidus*. Two morphologically distinct forms are recognized in *N. furcifer*. Samples of *N. furcifer* from Ulwile Island and slightly more southern localities possess a caudal fin with rounded lobes and long middle rays, appearing only slightly emarginate. Samples of *N. furcifer* from Udachi and nearby localities possess pointed caudal-fin lobes with greatly elongated streamers, similar to *N. timidus* and to *N. furcifer* from other parts of Lake Tanganyika, including the type specimens from the southern part of the lake. The variation in caudal-fin shape may be an expression of character displacement as it occurs in the area of sympatry between *N. timidus* and *N. furcifer*. Mitochondrial DNA sequences are nearly identical in samples of *N. furcifer* with pointed or rounded caudal fin. A molecular phylogenetic analysis of a large set of lamprologin cichlids using two mitochondrial genes corroborates earlier analyses and places *N. furcifer* and *N. timidus* in different clades with different species of *Neolamprologus*, *Julidochromis*, *Chalinochromis*, and *Telmatochromis* despite sharing a unique combination of fin and body shape, and colour pattern. A 4648 base-pair multiloci analysis of a smaller number of species using fragments of three mitochondrial and two nuclear genes resolves *N. furcifer* and *N. timidus* in sister clades, but the *N. timidus* clade also includes *Telmatochromis brachygnathus*, and *N. furcifer* is sister species of *Chalinochromis brichardi*.

Introduction

The cichlid tribe Lamprologini forms a major component of the endemic fish fauna of Lake Tanganyika, with about 80 species distributed in seven (Poll, 1986), eight, or possibly nine (Stiassny, 1997) genera. An additional eight species are known only from the Congo River, and one species only from the Malagarasi River (Schelly & Stiassny, 2004; Schelly et al., 2003). Several of the endemic lacustrine lamprologin species are known from very few specimens and/or few localities. *Neolamprologus furcifer* (Boulenger, 1898a) is a little studied species with wide distribution in rocky habitats throughout the coast of the lake (Konings, 1998), but so far reported only from

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scattered localities and relatively few specimens. It is distinguished by its dark, blackish colour, slender shape, nuchal protuberance, large eyes, and prolonged marginal caudal-fin rays, and is usually seen swimming upside down in crevices. In molecular analyses it does not group with other species of *Neolamprologus* Colombé & Allgayer (1985) but is sister to a clade composed of species of *Julidochromis* Boulenger (1898a) and *Chalinochromis* Poll (1974) (Day et al., 2007; Sturmbauer et al., 1994, 2010).

While two of us (MK, MK) surveyed the underwater habitat in Lake Tanganyika near Maenga at Mvuna Island off the coast of Kipili, Tanzania, in April, 2008, we noticed a shy fish in a crevice at 18 m depth, in a dark habitat with huge boulders. It appeared very similar to *N. furcifer*. Its body colouration was dark brown with two darker horizontal stripes and it had elongated fins. The fish seemed more slender and had a pointed head, but we assumed that these were features of a juvenile fish, since the individual we observed was only about 6 cm. While approaching the fish it quickly disappeared among the rocks. Diving near Musi Point at Ulwile Island, located just 5 km southeast of Mvuna Island, we observed more individuals which had two horizontal stripes on the body and elongated fins, similar to the fish we had seen at Mvuna Island but here also with orange iris. In the same place there were also individuals that had no stripes at all or just blurry patches, yellow iris, short paddle-like caudal fin, and elevated occiput. A large sample was preserved and analysed with the result that the form with two horizontal stripes represent a new species, and the syntopic species represents *N. furcifer*. The objective of this paper is to provide a formal description of the new species, and to redescribe the little known *N. furcifer*.

Material and methods

Specimens were collected by means of SCUBA gear with a fine meshed net and hand nets. The specimens were fixed in 10 % formalin and later preserved in 70 % ethanol. Fin clips for DNA analyses were preserved in 95 % ethanol.

Measurements and counts were recorded as described by Roberts & Kullander (1994). The length of the caudal peduncle is measured from the base of the last ray of the anal fin to the middle of the base of the caudal fin. Caudal-fin concavity was calculated as the percentage of the length of the middle relative the length of the longest lobe; the smaller the figure, the deeper the concavity. Scales in a longitudinal row are counted as described by Trewavas (1946) and include the scales of the upper lateral line followed by those of the horizontal row containing the lower lateral line starting with the first scale in the oblique row (sloping rostrad and ventrad) next behind that containing the last scale of the upper lateral line. Lateral line scales on the caudal fin are not counted. Counts of lateral line scales include all scales up to the posteriormost canal-bearing scales in the upper lateral line, and to the anteriormost canal-bearing scale in the lower lateral line. That means that, especially in the lower lateral line, the count may include several scales from which neuromasts or bone canals are absent. Vertebral counts and counts of fin rays in unpaired fins were taken from X-radiographs. Vertebral counts include the last half-centrum. Teeth were counted in the outer row on one side (predominantly the left side) of the upper and lower jaw. Counts of caudal-fin rays include unsegmented procurrent rays, the marginal unbranched segmented ray, and the branched rays

Table 1. Specimens used for genetic analysis, with collecting site, NRM catalog and tissue bank numbers, and GenBank accession numbers.

species	locality	NRM catalog number
Boulengerochromis microlepis	Udachi	51561
Chalinochromis brichardi	Cape Chaitika	61034
Chalinochromis brichardi	Cape Kabogo	61562
Neolamprologus furcifer	Mtosi	51509
Neolamprologus furcifer	Kampemba	51517
Neolamprologus furcifer	Udachi	59576
Neolamprologus furcifer	Ulwile Island	59621
Neolamprologus furcifer	Katondo	61007
Neolamprologus sp.	Tanzania	59791
Neolamprologus timidus	Mtosi	51456
Neolamprologus timidus	Kampemba	51458
Neolamprologus timidus	Namansi	51512
Neolamprologus timidus	Ulwile Island	59622
Neolamprologus ventralis	Ulwile Island	59623
Paleolamprologus toae	Kansombo	51539
Telmatochromis brachygnathus	Katondo	59783
Tropheus duboisi	Maswa	61561

separated by periods, counts of upper and lower lobe separated by a plus sign. X-radiographs were made on Kodak X-omat V film using a Philips MG-105 low voltage X-ray unit.

Abbreviations: NLF0 = neurocranial lateral line foramen 0; SL = Standard length.

Morphometric data were managed and analysed using IBM Statistics 20 (IBM, 2011), except that the principal component analysis (PCA) of measurements was made using a separate procedure for component shearing, partialling out multivariate size residues from the second and further components as described by Humphries et al. (1981). The PCA analysis was made with log-transformed measurement data to tenth of a millimetre in a covariance matrix, and without rotation.

Five gene fragments were used for a phylogenetic analysis of DNA. Three of the fragments are mitochondrial: Cytochrome *c* Oxidase Subunit I (COI) (685 base pairs); Cytochrome *b* (CYTB) (948 bp), and NADH-Ubiquinone Oxidoreductase chain 2 (ND2) (1047 bp). Two of the fragments are nuclear fragments of the Recombination Activating Gene 1 (RAG1), representing Exon 3 (1050 bp) and Intron 2 (918 bp), respectively.

DNA was extracted using a GeneMole (Mole Genetics) fully automated liquid-handling instrument, with the MoleStrips (Mole Genetics) kit and recommended protocol. PCR reactions were performed with the puReTaq Ready-To-Go PCR kit (Amersham biosciences).

Primers used to amplify the respective fragments: COI: FishF1 (5'-tcaaccaaccacaaagacattggcac-3') and FishR1 (5'-tagacttctgggtggccaaagaatca-3') (Ward et al., 2005); CYTB: L_CYTB (5'-actaatgacttgaaaaaccacc-3') and H_CYTB (5'-caggtgaggatggcgacg-3') (Nevado et al., 2009); ND2: MET (5'-catacccaaacatgttggt-3') and TRP (5'-gagattttcactcccgctta-3') (Kocher et al., 1995) ; RAG1 exon 3: CF1 (5'-gccgccagatcttccagccct-3') and CR5 (5'-tgcgggcgtagtttccattca-3') and RAG1 intron 2: KaliF1 (5'-aagggtttatgttcaatcaa-3') and CR1 (5'-aggctggaatatctggcgg-3') (Clabaut et al., 2005).

PCR products were checked on minigel, and purified using the FastAP Thermosensitive Alkaline Phosphatase (Fermentas International) purification kit. Sequencing of both strands of all fragments was carried out by Macrogen Europe (Amstelveen, Holland) using the same primers as for PCR amplification. All sequences were proof-read and assembled using the software Geneious v. 6.1.2 (Drummond et al., 2012). Sequences used in this study are summarized in Table 1. The sequences were aligned using the MUSCLE (Edgar, 2004) plug-in for Geneious. Only one species of Tanganyika cichlid, *Tropheus duboisi* Marlier (1959), had all five corresponding fragments available in GenBank, and was included in the analysis. The combined alignment

NRM tissue number	GenBank accession number COI	GenBank accession number CYTB	GenBank accession number ND 2	GenBank accession number RAG 1 Exon 3	GenBank accession number RAG 1 Intron 2
7845	KJ187209	KJ187226	KJ187243	KJ399571	KJ399588
7804	KJ187203	KJ187220	KJ187237	KJ399565	KJ399582
8266	KJ187210	KJ187227	KJ187244	KJ399572	KJ399589
7814	KJ187207	KJ187224	KJ187241	KJ399569	KJ399586
7815	KJ187208	KJ187225	KJ187242	KJ399570	KJ399587
6699	KJ187197	KJ187214	KJ187231	KJ399559	KJ399576
6700	KJ187198	KJ187215	KJ187232	KJ399560	KJ399577
7751	KJ187201	KJ187218	KJ187235	KJ399563	KJ399580
6697	KJ187196	KJ187213	KJ187230	KJ399558	KJ399575
7812	KJ187205	KJ187222	KJ187239	KJ399567	KJ399584
7813	KJ187206	KJ187223	KJ187240	KJ399568	KJ399585
7776	KJ187202	KJ187219	KJ187236	KJ399564	KJ399581
6701	KJ187199	KJ187216	KJ187233	KJ399561	KJ399578
6702	KJ187200	KJ187217	KJ187234	KJ399562	KJ399579
7806	KJ187204	KJ187221	KJ187238	KJ399566	KJ399583
6655	KJ187195	KJ187212	KJ187229	KJ399557	KJ399574
8270	KJ187211	KJ187228	KJ187245	KJ399573	KJ399590

Fig. 1. Preserved specimens, all from Tanzania: Lake Tanganyika; **a,** *Neolamprologus timidus*, NRM 11897, holotype, 89.8 mm SL, adult male: Ulwile Island; **b,** *N. furcifer* (Udachi), NRM 65412, 108.6 mm SL, adult male: Udachi; **c,** *N. furcifer* (Ulwile), NRM 65413, 116.5 mm SL, adult male: Ulwile Island.

comprises sequences representing 18 specimens of nine species and is 4648 bp. In all analyses *Boulengerochromis microlepis* (Boulenger, 1899b) (Boulengerochromini) and *Tropheus duboisi* (Tropheini) were designated outgroup.

The phylogenetic analysis was performed using the software MrBayes v. 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist et al., 2012). Data was partitioned according to gene, protein-coding fragments was further partitioned according to codon position (first, second, third), and parameters estimated separately for each partition. The GTR + Γ + I model was used. The analysis was run for two million generations, at which time average standard deviation of split frequencies reported by MrBayes was ≤ 0.01. Samples were taken every 1000 generations, and the first 25 % of samples were discarded as "burn-in".

We also performed an analysis of all ND2 and CYTB sequences in GenBank, mostly provided in the analyses of Day et al. (2007) and Sturmbauer et al. (2010), with the addition of our own data. This analysis came out similar to already published results, and was not further elaborated.

Specimens studied are deposited in the Swedish Museum of Natural History, Stockholm (NRM) and the Natural History Museum, London (BMNH). Specimens included in the DNA analyses are listed in Table 1.

In addressing distinct samples referable to *Neolamprologus furcifer*, we designate as *N. furcifer* (Udachi) specimens conforming to the phenotype collected at Udachi, *N. furcifer* (Ulwile) for the phenotype collected at Ulwile, and simply *N. furcifer* for remaining specimens of that species.

Neolamprologus timidus, new species
(Figs. 1a, 2a, 3a–b, 4a,c,e, 5)

Holotype. NRM 11897, adult male, 89.8 mm SL; Tanzania: Lake Tanganyika at Ulwile Island; 7°28'49"S 30°34'34"E; M. Karlsson & M. Karlsson, 25 May 2008.

Paratypes. All from Tanzania: Lake Tanganyika. BMNH 1906.9.6.52, 1, adult male, 94.1 mm SL; Msambu [= Msamba]; J. E. S. Moore, 1899–1900. – NRM 51456, 1, adult female, 78.1 mm SL; Mtosi North; 7°35'35"S 30°38'22"E; M. Karlsson & M. Karlsson, 25 Oct 2008. – NRM 51458, 1, adult female, 82.0 mm SL; Kampemba Point; 7°10'49"S 30°31'02"E; M. Karlsson & M. Karlsson, 3 Dec 2008. – NRM 51512, 1, adult male, 100.0 mm SL; Namansi South; 7°37'15"S 30°39'24"E; M. Karlsson & M. Karlsson, 25 Oct 2008. – NRM 59617, 4 adult males, 83.9–94.1 mm SL, 4 adult females, 62.7–81.1 mm SL; NRM 59622, 1, adult male, 94.1 mm SL; same data as holotype.

Diagnosis. *Neolamprologus timidus* is distinguished from the most similar species, *Neolamprologus furcifer*, in scaled cheek (vs. naked), first soft ray of pelvic fin longer than second (vs. second ray longer than first), pectoral fin reaching beyond base of first anal-fin spine (vs. shorter), absence of dark spot at caudal-fin base in adults (vs. presence); longer head (34.2–35.5 % SL vs. 31.2–33.8), longer pectoral fin (29.3–35.7 % SL vs. 23.4–31.3); pectoral fin in life light yellow or transparent (vs. orange). It is distinguished from all other lamprologin species except *Lepidiolamprologus profundicola* (Poll, 1949), *Neolamprologus ventralis* Büscher (1995), and *N. leloupi* (Poll, 1948) in fully scaled cheek (vs. scales absent from cheek or present only posterodorsally). Distinguished from *N. leloupi* by the shape of the caudal fin (deeply emarginate, with long streamers vs. posterior margin concave, streamers absent), colour (overall dark, with indistinct darker horizontal stripes vs. overall light, with faint brown zigzag lines along side), and meristics (49–62 scales in a longitudinal row vs. about 30; dorsal-fin rays XIX–XXI.7–8, vs. XVII.9; gill rakers 11–13 vs. 6). Distinguished from *N. ventralis* by caudal-fin shape (deeply emarginate, with long streamers, vs. rounded, subtruncate or slightly emarginate with rounded lobes), colour pattern (overall dark with indistinct darker horizontal stripes, vs. overall light, scales with light brown margins; unpaired fins dark, with few, indistinct spots vs. numerous light spots all over unpaired fins), and meristics (49–62 scales in a longitudinal row vs. 34–37). Distinguished from *L. profundicola* by caudal-fin shape (deeply emarginate with long streamers vs. truncate or slightly emarginate), longer pectoral fin (beyond base of first anal-fin spine vs. not reaching vent), single NLF0 (versus double), dermosphenotic absent (vs. present), labial cartilage not ossified (vs. ossified.)

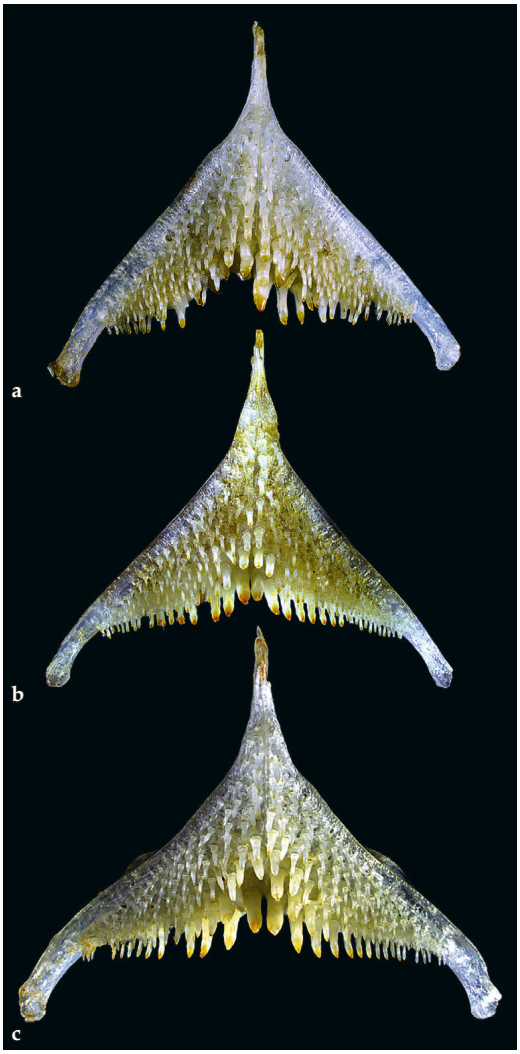

Fig. 2. Lower pharyngeal jaw in occlusal aspect; **a,** *Neolamprologus timidus*, NRM 59617, paratype, 83.9 mm SL; **b,** *N. furcifer* (Udachi), NRM 59526, 95.9 mm SL; **c,** *N. furcifer* (Ulwile), NRM 59619, 92.0 mm SL.

Description. Proportional measurements and meristics are provided in Tables 2–6. General shape features illustrated in Figures 1–5. Holotype data marked with an asterisk (*).

Body elongate; laterally compressed, more so caudally. Predorsal contour straight ascending to minor soft protuberance on top of head, present in both males and females. Dorsal contour gently sloping. Abdominal contour almost straight, slightly ascending at anal-fin base. Caudal peduncle dorsal and ventral margins slightly concave. Orbit large, positioned approximately on middle of head length.

Mouth moderately large, slightly wider than interorbital space, in low position, lower jaw in line with chest contour; upper jaw slightly projecting; upper lip thick, lower lip widely interrupted anteriorly. Maxilla reaching posteriorly to slightly behind vertical from anterior margin of orbit. Premaxillary ascending processes reaching to vertical from anterior margin of orbit. Lower jaw on each side with two long, stout, strongly recurved caniniform teeth slightly lateral to symphysis, lateral tooth slightly longer than medial tooth, commonly also one much smaller tooth of similar shape closer to symphysis; on each side of symphysis, inner transverse patch of very small teeth, in about 3–4 rows; posterior to large canines, an outer lateral row of much smaller caniniform teeth, and an inner band of much smaller teeth, in about three rows anteriorly, narrower posteriorly. Upper jaw on each side with three long, stout, strongly recurved caniniform teeth anteriorly, increasing in size from symphysial to lateral; laterally along entire dentigerous arm of premaxilla a dense row of smaller caniniform teeth; inner teeth very small, in a band if about five rows symphysially, narrowing down to one row posteriorly. Teeth in upper jaw outer hemiseries (enlarged + normal) 3+25 (2), 3+26 (2), 3+27 (2), 3+28* (3), 3+29 (3), 4+27 (1); in lower jaw outer hemiseries 2+27 (1), 2+30 (1), 2+31 (1), 2+32 (2), 2+33 (2), 2+38* (1), 3+27 (1), 33+33 (1), 3+34 (1), 3+38 (1). All teeth firmly fixed. Gill rakers slender, relatively close-set, simple; 4+1+11 (2), 5+1+11 (3), 5+1+12* (3), 6+1+11 (2), 6+1+12 (3), 6+1+13 (1). Microbranchiospines present externally on second to fourth gill arches.

Single coronalis pore (NLF0). Lachrymal present, with four lateralis openings, infraorbitals and dermosphenotic absent; free neuromasts in a pitline along orbital margin from lachrymal to sphenotic. Preoperculomandibular series corresponding to five dentary, two anguloarticular, and seven preopercular canal openings. Distinct vertical pitline posteriorly on cheek.

Trunk scales weakly ctenoid. Top of head posterior to median coronalis pore with small

Table 2. Standard length (in millimetres) and proportional measurements in percents of standard length of *Neolamprologus timidus*. SD = standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimetres. Caudal fin concavity is calculated as length of shortest ray as % of longest ray in dorsal lobe.

	N	holotype	min	max	mean	SD	a	b	r
SL (mm)	14	89.8	62.7	100.0	83.8	10.3			
Head length (% SL)	14	35.5	34.2	35.5	34.8	0.5	−0.207	0.350	0.995
Snout length (% SL)	14	12.8	11.3	13.5	12.2	0.6	−2.299	0.150	0.961
Preorbital depth (% SL)	14	6.0	4.4	6.3	5.5	0.6	−3.480	0.098	0.971
Body depth (% SL)	14	25.6	22.8	26.2	24.6	0.8	−3.384	0.287	0.986
Orbital diameter (% SL)	14	11.0	10.9	12.4	11.4	0.5	2.567	0.083	0.981
Interorbital width (% SL)	14	6.6	5.3	6.7	6.0	0.4	−2.048	0.085	0.965
Pectoral-fin length (% SL)	14	32.4	29.3	35.7	32.2	2.1	−0.470	0.327	0.891
Upper jaw length (% SL)	14	14.3	12.9	14.4	13.7	0.5	−0.997	0.149	0.972
Lower jaw length (% SL)	14	15.6	14.3	15.6	14.9	0.4	0.661	0.141	0.972
Caudal peduncle depth (% SL)	14	9.2	8.3	9.3	8.7	0.3	−0.492	0.093	0.956
Caudal peduncle length (% SL)	14	17.4	16.5	19.2	18.0	0.8	−0.266	0.093	0.938
Last dorsal-fin spine length (% SL)	14	15.8	14.3	17.1	15.7	0.7	0.066	0.156	0.932
Dorsal caudal-fin lobe length (% SL)	11	52.0	35.1	55.7	45.7	5.7	−4.606	0.515	0.705
Caudal-fin length at middle (% SL)	12	23.6	21.6	24.8	22.8	1.0	6.118	0.335	0.950
Ventral caudal-fin lobe length (% SL)	10	52.5	35.7	52.4	43.9	4.7	−6.138	0.517	0.785
Caudal-fin concavity	11	45.4	44.5	61.7	50.6	5.1	6.118	0.335	0.847

cycloid, posteriorly weakly ctenoid scales, anterior scales with margins embedded in skin, posterior scales with free margin. Cheek with about 6*–10 rows of scales, leaving only narrow naked area close to lower limb of preopercle; scales cycloid, embedded in skin. Chest and prepelvic area completely covered with very small cycloid scales. Abdominal midline with ctenoid scales similar to flank scales. Upper lateral line long, reaching onto caudal peduncle; lower lateral line long, extending far forward on side, often by several pored scales continuing series of tubed scales. Lateral line counts 44/20, 44/25, 45/21, 46/16, 46/21*, 48/16, 49/22, 50/17, 50/41, 51/14,

Table 3. Frequency of gill-raker counts in *Neolamprologus timidus*, *N. furcifer* (syntypes BMNH 1898.9.9:17–18), *N. furcifer* (Udachi) and *N. furcifer* (Ulwile). Modal values in bold. Data from type specimens marked with asterisk.

	N	11	12	13	14
N. furcifer syntypes	2				**2***
N. timidus	14	**7**	**6***	1	
N. furcifer (Udachi)	14	1	**6**	**6**	1
N. furcifer (Ulwile)	15	1	2	**7**	5

Table 4. Frequency of scales in a longitudinal row in *Neolamprologus timidus*, *N. furcifer* (syntypes BMNH 1898.9.9:17–18), *N. furcifer* (Udachi) and *N. furcifer* (Ulwile). Modal values in bold. Value of type specimens marked with asterisk.

	N	43	44	45	46	47	48	49	50	51	52	53	54	55	57	58	60	62
N. timidus	14							1	1			**3**	1	2	**3**	1		2
N. furcifer syntypes	2	1*	1*															
N. furcifer (Udachi)	14		1	1	2	**4**		2	2*	2								
N. furcifer (Ulwile)	15							2	**3**	**3**	1	1	2	2			1	

Table 5. Frequency of scales in upper lateral line in *Neolamprologus timidus*, *N. furcifer* (syntypes BMNH 1898.9.9:17–18), *N. furcifer* (Udachi) and *N. furcifer* (Ulwile). Data from type specimens marked with asterisk.

	N	35	36	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	60
N. timidus	14									2	1	2*		1	1	2	1	1	1	2
N. furcifer syntypes	2	1*	1*																	
N. furcifer (Udachi)	14			2	2	2	1	2	3	1		1								
N. furcifer (Ulwile)	15			1				1		1	5	1	2	2	1				1	

Table 6. Frequency of dorsal-fin ray, anal-fin ray, pectoral-fin ray, and vertebral counts in *Neolamprologus timidus*, *N. furcifer* (syntypes BMNH 1898.9.9:17–18), *N. furcifer* (Udachi) and *N. furcifer* (Ulwile). Modal values in bold. Data from type specimens marked with asterisk.

		dorsal-fin rays									anal-fin rays					
		XVIII	XIX			XX			XXI		V	VI	VI	VII	VII	
	N	10	8	9	10	7	8	9	8	N	6	5	6	6	7	
N. timidus	14		1			1	**9***		3	14			**10***		4	
N. furcifer syntypes	2								2*	2			1*	1*		
N. furcifer (Udachi)	14	2	1	**9**	2					14	1		**13**			
N. furcifer (Ulwile)	15			**10**	3		1	1		15	1	1	**13**			

		pectoral-fin rays			vertebrae				
	N	12	13	N	14/19	14/20	15/18	15/19	15/20
N. timidus	14	**14***		13	3		2*	**8**	
N. furcifer syntypes	2	2*		2		1*		1*	
N. furcifer (Udachi)	14	2	**12**	14	2	4	1	**7**	
N. furcifer (Ulwile)	15	3	**12**	15		4	1	**9**	1

a
b
c
d

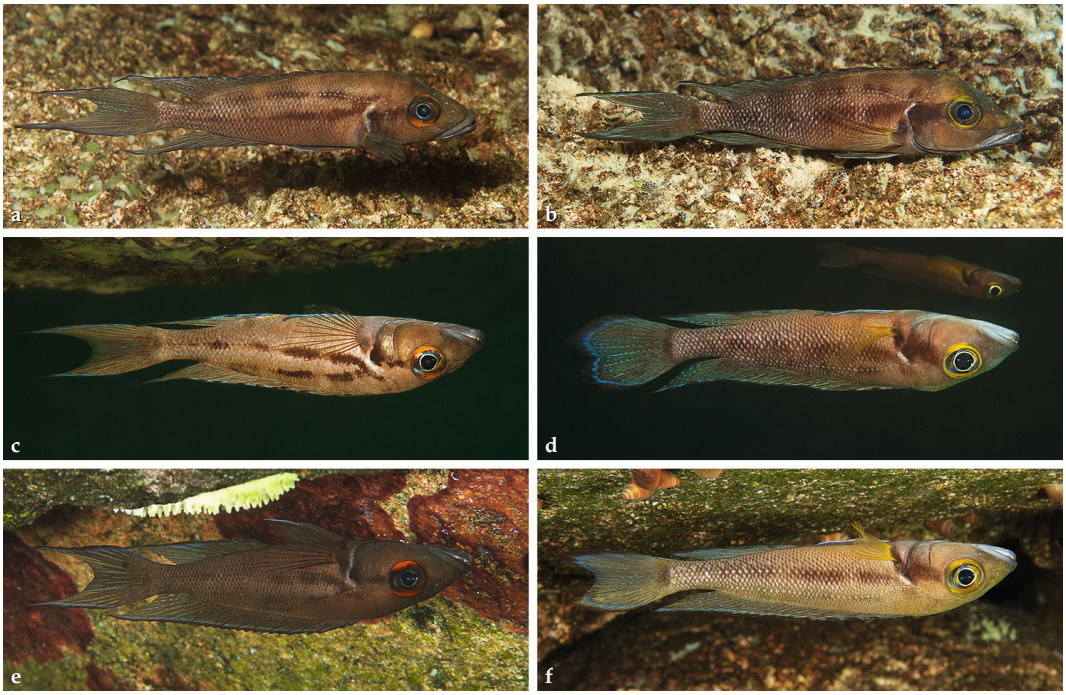

Fig. 4. Underwater photographs in natural habitats; **a**, *Neolamprologus timidus* at Kolwe Point, 20 m depth; **b,** *N. furcifer* (Udachi) at Kolwe Point, 20 m depth; **c,** *N. timidus* at Musi Point, 6 m depth; **d,** *N. furcifer* (Ulwile) at Musi Point, 6 m depth; **e,** *N. timidus* at Mtosi, 5 m depth; **f,** *N. furcifer* (Ulwile) at Mtosi, 5 m depth.

Fig. 5. *Neolamprologus timidus*; juvenile, about 20 mm total length, from Ulwile Island, photographed alive in aquarium. Not preserved.

◁ **Fig. 3.** Living specimens, all from Tanzania: Lake Tanganyika: Ulwile Island; **a,** *Neolamprologus timidus*, NRM 59617, paratype, adult male, 83.9 mm SL; **b,** *N. timidus*, NRM 59617, paratype, adult female, 75.0 mm SL; **c,** *N. furcifer* (Ulwile), NRM 59619, adult male, 116.5 mm SL; **d,** *N. furcifer* (Ulwile), NRM 59619, adult female, 96.6 mm SL.

52/19, 53/22, 60/23, 60/47, each count individual. Circumpeduncular scales 18 (4), 19* (5), 20 (4). Dorsal, anal and caudal fins scaled basally; fin scales minute, rounded, ctenoid. Scales on dorsal fin in one or several short interradial rows, from about fifth spine to penultimate soft ray, extending at most to ¾ of spinous fin height. Anal fin with 1–4 interradial rows of scales, from behind second spine extending at most to ¾ of spinous fin height. Caudal fin densely scaled, medially leaving a narrow naked margin, dorsally and ventrally squamation extending onto ⅓ of corner extensions.

Dorsal-fin origin at vertical from gill-cleft/lateral line origin; first spine about ¼ length of last, spines increasing in length to about sixth or seventh, from which gradually only slightly longer, last longest; soft dorsal fin terminating in long, slender point, tipped by fifth soft ray, reaching almost to vertical from median caudal-fin margin. Anal-fin spines increasing in length from first to last; soft fin similar to soft dorsal fin; third soft ray longest, reaching almost to vertical from median caudal-fin margin. Caudal fin emarginate with median rounded concave margin, and pointed dorsal and ventral tips, rays D3–D4 and V3–V4 longest; lobes beyond median margin slightly longer than rest of fin. Caudal-fin rays vii.8.8.vii (1), viii.8+8.vi (2), viii.8+8.ix (2), ix.8+8.vii (2), ix.8+8.viii* (4), ix.8+8.ix (1). Pectoral-fin rays i.9.ii* (8), i.8.iii (6). Pectoral fin pointed, fourth ray longest, reaching to vertical from fifth anal-fin spine. Pelvic fin pointed, first ray longest, with two branches of equal length, or the outer slightly the longer; reaching to base of first anal-fin spine.

Lower pharyngeal tooth-plate examined in one specimen (Fig. 2a). Width 95 % of length; dentigerous area width 104 % of dentigerous area length. Teeth slender, posterior median teeth slightly enlarged. Anterior teeth bevelled, with retrorse cusp, shorter toward lateral and posterolateral margins; posteriorly some median teeth with flat top, otherwise with erect or almost erect posterior cusp. Teeth 11–12 on each side along midline, 29 along posterior margin.
Single supraneural. Hypurals 3 and 4 co-ossified into a single plate, hypurals 1 and 2 co-ossified into a single plate.

No juveniles preserved, but living juveniles observed similar to adults, but with shorter caudal fin (Fig. 5).

Colour pattern in preservative (Fig. 1a)**.** Head, lips, lower jaw and gill cover grey except pale brownish yellowish cheek, indistinct dark grey band across nape posteriorly, dark grey opercle and subopercle, and greyish brown blotch immediately posterior to orbit; exposed branchiostegal membrane blackish except greyish white margin. Chest and abdomen whitish. Scales on sides brown with pale yellowish base; brown portion darker on caudal peduncle forming indistinct pattern of horizontal rows of dark spots. Blackish brown wide stripe from origin of lateral line obliquely caudoventrad to midline where becoming horizontal, followed by one, occasionally two short elongate blotches of same colour. Three indistinct broad brownish vertical bars from dorsal-fin base ventrad, at most to middle of side; caudal peduncle dorsally brown. Three narrow horizontally extended brown blotches on upper lateral line. Pectoral-fin base blackish brown externally and internally. Dorsal fin dark grey to blackish; distinct white submarginal stripe and black lappets and margin of soft dorsal fin; interradial membranes of soft dorsal fin semihyaline, in some specimens with minute whitish spots. Anal fin dark grey. Caudal fin dorsally with white submarginal and black marginal stripes continuing pattern from dorsal fin; rest of fin blackish with minute white spots in up to six longitudinal rows in upper lobe, tips of marginal rays black. Pectoral fin hyaline. Pelvic fin blackish with white leading margin. No obvious sex differences in colour pattern.

Live colouration (Figs. 3a–b, 4a,c,e)**.** Overall medium to dark brown with two dark longitudinal stripes on body just above middle of side. Eye in dominant males with red to orange marginal ring, in females orange to yellow. Iris blue. Orange colour and faint small bluish spots on caudal fin and posterior part of dorsal fin. Dorsal fin brown with a dark orange margin followed by a blue trim, both extended onto caudal fin. Pelvic fin and anal fin with the same margin and trim but less intense. Pectoral fin light yellow or transparent. At two localities (Kamamba and Ulwile Islands) solitary juveniles were observed together with adults. Their colour pattern was similar to the adults, but in the field they appeared darker; in aquarium (Fig. 5), paler with distinctive dark horizontal markings and blotch at caudal-fin base.

Geographical distribution and habitat. Preserved material is available from Kampemba Point, Ulwile Island, Mtosi, and Namansi, where observations were also made (Figs. 6–7). A preserved specimen is also available from much further south, at Msamba (Fig. 6). Observations were made at all the islands in the Kipili area (Kamamba, Kasisi, Kerenge, Lupita, Mvuna, Mwila, Nkondwe, Ulwile) and along the rocky coast from Mswa Point north to Kampemba Point, Korongwe, Mwaka, Katondo and Kolwe Point, the latter two at Cape Mpimbwe. The southernmost observation was made at Kisi Island off the rocky coast south of Ninde. The coastline extent of the distribution approximates 100 km. *Neolamprologus timidus* is sympatric with *N. furcifer* at Kolwe Point south to Kampemba Point, and at Lupita and Ulwile Islands south to Kisi Island. The type locality is the rocky shore at Musi Point, at the south-eastern side of Ulwile Island (Fig. 8). Specimens were observed at depths varying from 2 to 40 m in the dark rocky biotope (Fig. 4a,c,e), and encountered in pairs defending a territory over a dark cave difficult of access. The territory was often located to a large rock or boulder, which, if large enough was inhabited also by other species, like *N. furcifer* and *Julidochromis regani* Poll (1942) within the territory of *N. timidus*. Observed individuals were almost always found upside down in the cave with the belly close to the substrate or on a vertical substrate with the head pointing downwards.

Etymology. The species name is a Latin adjective meaning shy, with reference to the elusive or shy behavior of this species in the natural habitat.

Neolamprologus furcifer (Boulenger, 1898a)
(Figs. 1b–c, 2b–c, 3c–d, 4b,d,f)

Material examined. All from Lake Tanganyika; collectors M. Karlsson & M. Karlsson unless otherwise stated. BMNH 1898.9.9:17–18, 2 syntypes, adult male 99.4 mm SL, adult female 66.6 mm SL; Zambia: Northern Province: Kinyamkolo [= southern end of Lake Tanganyika (Konings, 2013)]; J. E. S. Moore, 1895–1896.

Referred specimens, not included in morphometric analysis: BMNH 1961.11.22.1064, 1, adult female, 88.0 mm SL; DR Congo: Katanga District: M'Toto [= Mtoto] Bay, 2–3 m depth; Exploration hydrobiologique du lac Tanganika, 15 Mar 1947. – NRM 17620, 1, adult male, 104.4 mm SL; Tanzania: Kigoma Region: Kigoma; G. Berglund, 7 Oct 1976.

Udachi form: NRM 51517, 1, adult female, 109.0 mm SL; Kampemba Point; 7°10'49"S 30°31'02"E; 3 Dec 2008. – NRM 59526, 5 adult males, 93.3–114.6 mm SL, 6 adult females, 66.2–95.9 mm SL; NRM 59576, 1, adult female, 81.9 mm SL; NRM 65412, 1, adult male, 108.6 mm SL; Udachi; 7°03'30"S 30°33'10"E; 24 Apr 2008 – NRM 61007, 1, adult female, 93.5 mm SL; Cape Mpimbwe, Katondo; 7°08'09"S 30°30'8"E; 10 Nov 2008 (Poor condition, not included in counts and measurements.)

Ulwile form: NRM 59619, 5 adult males, 94.8–110.1 mm SL, 5 adult females, 92.0–103.5 mm SL, 1 young female, 64.1 mm SL, 1 male, 85.4 mm SL with deformed head ("Mopskopf"); NRM 59621, 1, adult female, 106.2 mm SL; NRM 65413, 1 adult male, 116.5 mm SL; Ulwile Island; 7°28'49"S 30°34'34"E; 25 May 2008. – NRM 51509, 1, adult male, 113.2 mm SL; NRM 51519, 1, adult female, 95.2 mm SL; Mtosi North; 7°35'35"S 30°38'22"E; 25 Oct 2008.

Description. Full description given of Udachi form, followed by notes on syntypes and Ulwile form when different. Specimens from Kigoma and Mtoto, with long caudal-fin streamers like the syntypes and the Udachi form, are included in morphometric analyses and meristic tables only. Measurements and counts are given in Tables 3–8.

Udachi form. Body elongate; laterally compressed, more so caudally. Predorsal contour straight ascending to soft protuberance on top of head, present in both males and females, prominent in large specimens, gradually less so with smaller body size, inconspicuous in smallest specimen. Dorsal contour gently sloping. Abdominal contour almost straight, slightly ascending at anal-fin base. Caudal peduncle dorsal and ventral margins slightly concave. Orbit large, positioned approximately on middle of head length.

Mouth moderately large, slightly wider than interorbital space, in low position, lower jaw in line with chest contour; upper jaw slightly projecting; upper lip thick, lower lip widely interrupted anteriorly. Maxilla reaching posteriorly to vertical from anterior margin of orbit. Premaxillary ascending processes reaching to vertical from anterior margin of orbit. Lower jaw on each side with two long, stout, strongly recurved caniniform teeth slightly lateral to symphysis, lateral tooth slightly longer than medial tooth, commonly also one much smaller tooth of similar shape closer to symphysis; on each side of symphysis, inner transverse patch of very small teeth, in about 3–5 rows; posterior to large canines, an outer lateral

row of much smaller caniniform teeth, and an inner band of much smaller teeth, in about three rows anteriorly, narrower posteriorly. Upper jaw on each side with three long, stout, strongly recurved caniniform teeth anteriorly, increasing in size from symphysial to lateral; laterally along entire dentigerous arm of premaxilla a dense row of smaller caniniform teeth; inner teeth very small, in a band of about five rows symphysially, narrowing down to one row posteriorly. Teeth in upper jaw outer hemiseries (enlarged + normal) 3+21 (2), 3+22 (3), 3+23 (2), 3+24 (1), 3+25 (3),

Table 7. Standard length (in millimetres) and proportional measurements in percents of standard length of *Neolamprologus furcifer* (Udachi), and syntypes of *N. furcifer* (BMNH 1898.9.9:17–18). SD = standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimetres.

	N. furcifer (Udachi)								*N. furcifer*	
	N	min	max	mean	SD	a	b	r	syntypes	
SL (mm)	14	66.2	114.6	94.1	14.1				66.6	99.4
Head length (% SL)	14	31.2	33.6	32.7	0.7	0.999	0.317	0.986	33.8	31.7
Snout length (% SL)	14	10.4	12.5	11.4	0.5	−1.157	0.126	0.974	9.8	10.9
Preorbital depth (% SL)	14	4.4	5.9	5.2	0.4	−2.367	0.077	0.986	5.0	5.0
Body depth (% SL)	14	24.3	26.9	25.6	0.8	−3.713	0.296	0.992	25.2	25.6
Orbital diameter (% SL)	14	9.9	12.0	10.8	0.6	3.069	0.075	0.941	12.0	11.3
Interorbital width (% SL)	14	5.1	7.2	6.2	0.6	−3.034	0.095	0.978	5.7	6.0
Pectoral-fin length (% SL)	14	25.0	28.1	26.3	0.8	−0.791	0.272	0.981	25.5	26.0
Upper jaw length (% SL)	14	12.4	13.6	13.1	0.4	−1.048	0.142	0.987	12.8	14.0
Lower jaw length (% SL)	14	13.9	15.3	14.5	0.4	1.041	0.133	0.986	14.0	14.6
Caudal peduncle depth (% SL)	14	8.0	9.1	8.6	0.3	−0.111	0.087	0.973	9.0	8.5
Caudal peduncle length (% SL)	14	18.5	21.1	19.5	0.7	−0.366	0.199	0.968	16.5	18.0
Last dorsal-fin spine length (% SL)	14	14.4	15.3	14.8	0.3	0.461	0.143	0.992	15.2	15.1
Dorsal caudal-fin lobe length (% SL)	13	31.2	50.3	40.9	4.9	−2.243	0.435	0.788	34.2	29.8
Caudal-fin length at middle (% SL)	13	20.0	22.4	21.4	0.7	0.637	0.208	0.980	18.9	18.5
Ventral caudal-fin lobe (% SL)	12	31.0	52.0	44.7	5.6	11.054	0.325	0.640	32.1	28.8
Caudal-fin concavity	13	43.5	68.7	53.1	6.4	8.020	0.314	0.821	55.3	62.2

Table 8. Standard length (in millimetres) and proportional measurements in percents of standard length of *Neolamprologus furcifer* (Ulwile). SD = standard deviation. Regression line parameters, a (intercept), b (slope), and r (Pearson's correlation coefficient) are calculated from measurements expressed in millimetres.

	N	min	max	mean	SD	a	b	r
SL (mm)	15	64.1	116.5	100.4	12.4			
Head length (% SL)	15	31.9	33.2	32.4	0.4	1.270	0.312	0.995
Snout length (% SL)	15	10.5	11.9	11.1	0.5	−1.460	0.126	0.966
Preorbital depth (% SL)	15	4.2	5.7	5.0	0.4	−2.143	0.720	0.959
Body depth (% SL)	15	21.2	23.7	22.7	0.6	−2.343	0.251	0.988
Orbital diameter (% SL)	15	10.6	13.1	11.5	0.7	3.641	0.078	0.929
Interorbital width (% SL)	15	3.7	6.0	5.3	0.5	−2.670	0.081	0.958
Pectoral-fin length (% SL)	15	23.4	28.3	25.7	1.5	1.967	0.238	0.900
Upper jaw length (% SL)	15	11.8	12.9	12.1	0.3	0.176	0.120	0.983
Lower jaw length (% SL)	14	13.3	14.6	13.8	0.4	1.179	0.126	0.977
Caudal peduncle depth (% SL)	15	7.5	8.3	7.9	0.2	−0.600	0.085	0.984
Caudal peduncle length (% SL)	15	19.6	21.6	20.5	0.6	0.569	0.200	0.971
Last dorsal-fin spine length (% SL)	15	13.0	15.8	14.1	0.7	0.610	0.135	0.927
Dorsal caudal-fin lobe length (% SL)	15	28.3	35.8	30.9	1.8	−2.818	0.337	0.926
Caudal-fin length at middle (% SL)	15	22.8	31.8	25.7	2.7	−12.954	0.288	0.909
Ventral caudal-fin lobe length (% SL)	15	27.0	38.2	31.1	2.6	0.368	0.307	0.828
Caudal-fin concavity	15	63.6	103.7	83.3	9.2	−4.114	0.968	0.827

3+26 (1), 3+27 (2); in lower jaw outer hemiseries 2+20 (1), 2+26 (1), 2+27 (1), 2+28 (3), 2+30 (3), 2+31 (1), 2+32 (1), 3+27 (1), 3+30 (1). All teeth firmly fixed. Gill rakers slender, relatively close-set, simple; 5+1+11 (1), 5+1+12 (5), 5+1+13 (3), 5+1+14 (1), 6+1+12 (1), 6+1+13 (2), 7+1+13 (1). Microbranchiospines present externally on second to fourth gill arches.

Single coronalis pore (NLF0). Lachrymal present, with four lateralis openings, infraorbitals and dermosphenotic absent; free neuromasts in a pitline along orbital margin from lacrimal to sphenotic. Preoperculomandibular series corresponding to five dentary, two anguloarticular, and seven preopercular canal openings. Distinct vertical pitline posteriorly on cheek.

Trunk scales weakly ctenoid. Top of head with small cycloid, posteriorly weakly ctenoid scales, anterior scales with margins embedded in skin, posterior scales with free margin; scales absent from nuchal hump in one specimen, variably present anterior to extrascapular pit-line, from a few to a larger patch medially, absent from sides of hump. Cheek with patch of 3–4 short rows of cycloid, embedded scales posterodorsally, leaving most of cheek naked. Chest and prepelvic area covered with very small cycloid scales, except absent from small elongate anterolateral field on each side of chest. Abdominal midline with ctenoid scales similar to flank scales, but only about half size. Upper lateral line long, reaching onto caudal peduncle; lower lateral line long, extending far forward on side, often by several pored scales continuing series of tubed scales. Lateral line counts 38/21, 38/26, 39/20, 39/26, 40/20, 40/28, 41/14, 41/30, 42/23, 43/21, 43/22, 43/25, 44/33, 46/21, each count individual. Circumpeduncular scale counts 17 (2), 18 (5), 19 (6), 20 (1). Dorsal, anal and caudal fins scaled basally; fin scales minute, rounded, ctenoid. Scales on dorsal fin in one or several short interradial rows, from about fifth spine to penultimate soft ray, extending at most to ⅘ of spinous fin height. Anal fin with 1–4 interradial rows of scales, from behind second spine extending at most to ½ of spinous fin height. Caudal fin densely scaled, medially leaving a narrow naked margin, dorsally and ventrally squamation extending onto ⅔ of corner extensions.

Dorsal-fin origin at vertical from gill-cleft/lateral line origin; first spine about ⅓–½ length of last, spines increasing in length to about sixth or seventh, from which gradually only slightly longer, last longest; soft dorsal fin terminating in long, slender point, tipped by fifth or sixth soft ray, reaching to middle of median part of caudal fin. Anal-fin spines increasing in length from first to last; soft fin similar to soft dorsal fin; third soft ray longest, reaching little behind caudal-fin base or to vertical midway to median caudal-fin margin. Caudal fin emarginate with median rounded concave margin, and pointed dorsal and ventral tips, rays D3–D4 and V3–V4 longest; lobes beyond median margin equal or slightly longer than rest of fin. In three specimens lower lobe of caudal fin short, due to damage. Caudal-fin rays viii.8+8.vi (1), viii.8+8.vii (6), viii.8+8.viii (3), ix.8+8.vii (1), ix.8+8.viii (3). Pectoral fin pointed, fourth ray longest, reaching to vertical from first anal-fin spine or shorter. Pelvic fin pointed, outer branch or of second ray longest, reaching to base of first anal-fin spine.

Lower pharyngeal tooth-plate examined in one specimen (Fig. 2b). Width 108 % of length; dentigerous area width 119 % of dentigerous area length. Teeth slender, a few posterior median teeth slightly enlarged. Anterior median teeth erect, unicuspid posteriorly grading to bevelled with retrose cusp, posteriorly with erect posterior cusp; laterally teeth shorter, bevelled, with retrorse cusp; teeth along posterior margin increasing in length from lateral to median, with erect posterior cusp. Teeth 11 on each side along midline, 33 along posterior margin.

Single supraneural. Hypurals 3 and 4 co-ossified into a single plate, hypurals 1 and 2 co-ossified into a single plate.

Ulwile form. Predorsal contour in juvenile, 64.1 mm SL, gently curved; in adults straight ascending to soft protuberance on top of head, minor in females, prominent in males (which also larger).

Maxilla reaching posteriorly to slightly behind vertical from anterior margin of orbit. Inner teeth in upper jaw in a band of about 3–4 rows symphysially. Teeth in upper jaw outer hemiseries (enlarged + normal) 3+21 (1), 3+24 (1), 3+25 (2), 3+26 (4), 3+28 (2), 3+29 (1), 3+30 (1), 3+31 (1); in lower jaw outer hemiseries 2+25 (1), 2+26 (2), 2+28 (1), 2+29 (2), 2+30 (4), 2+31 (1), 3+26 (2), 3+27 (1), 3+33 (1). Gill rakers 4+1+13 (1), 4+1+14 (1), 5+1+12 (1), 5+1+13 (2), 5+1+14 (1), 6+1+11 (1), 6+1+13 (4), 6+1+14 (3), 7+1+12 (1).

Top of head posterior to median coronalis pore with small cycloid, posteriorly weakly cte-

noid scales, anterior scales with margins embedded in skin, posterior scales with free margin. Minute predorsal scales posterior to extrascapular pitline; absent anteriorly and from hump portion except a few scales medially. Lateral line counts 38/23 (1), 42/18 (1), 44/21 (1), 45/19 (1), 45/20 (1), 45/21 (1), 45/25 (2), 46/18 (1), 47/20 (1), 47/31 (1), 48/17 (1), 48/41 (1), 49/18 (1), 53/36 (1). Circumpeduncular scales 17 (1), 18 (5), 19 (6), 20 (3). Scales on dorsal fin extending at most to ¾ of spinous fin height. Anal fin with 1–3 interradial rows of scales, from behind second spine extending at most to ½ of spinous fin height.

Dorsal-fin first spine about ⅖ to ½ length of last, spines increasing in length to about eighth or tenth, from which equal or gradually only slightly longer, last a little longer; soft dorsal fin terminating in short point, tipped by seventh soft ray, reaching beyond caudal-fin base, at most to ¼ of caudal-fin length. Anal-fin fifth soft ray longest, not reaching to vertical from caudal-fin base, or reaching only slightly posterior to vertical from caudal-fin base. Caudal fin general outline elongately rounded, with shallow median concave margin and rounded dorsal and ventral tips. Caudal-fin rays viii.8+8.vii (1), viii.8+8.viii (2), ix.8+8.vi (1), ix.8+8.vii (3), ix.8+8.viii (6), ix.8+8.ix (2). Ray D1 shortest, ray D2 or D3 longest in dorsal lobe, ray V2 or V3 longest in lower lobe; in one specimen rays D1 and D2 longer than other rays. One specimen (NRM 51519) with short pointed lobes. Pectoral fin with rounded or subacuminate tip, fifth ray longest, not quite reaching to vertical from first anal-fin spine. Pelvic fin pointed, second ray longest, with two branches of equal length, or the outer slightly the longer; reaching beyond genital papilla, but not to base of first anal-fin spine.

Lower pharyngeal tooth-plate examined in one specimen (Fig. 2c). Width 112 % of length; dentigerous area width 111 % of dentigerous area length. Teeth slender, a few posterior median teeth slightly enlarged. Anterior median teeth erect, unicuspid posteriorly grading to bevelled with retrose cusp, posteriorly with erect posterior cusp; laterally teeth shorter, bevelled, with retrorse cusp; teeth along posterior margin increasing in length from lateral to median, with erect posterior cusp. Teeth 10 on each side along midline, 39 along posterior margin.

Syntypes. Notes from larger syntype, with information on smaller syntype in brackets when different. Predorsal contour straight ascending to minor soft protuberance on top of head [hump absent]. Abdominal contour somewhat deflated, almost straight, slightly ascending at anal-fin base.

Jaws about equal in anterior extension, Maxilla reaching posteriorly to below middle of orbit. Teeth in upper jaw outer hemiseries (enlarged + normal) 3(+1)+33 [3+24]; in lower jaw outer hemiseries 2+29 [3+24].

Scales absent from cheek; minute scales present posterodorsally between orbit and preopercular margin. Upper lateral line long, reaching to base of caudal peduncle; lower lateral line long, extending far forward on side, by several pored scales continuing series of tubed scales. Lateral line counts 36/32 [35/26].

Soft dorsal fin terminating in short slender point, reaching slightly beyond caudal-fin base. Soft anal fin similar to soft dorsal fin. Caudal fin emarginate with median rounded concave margin, and pointed dorsal and ventral tips, rays D3 and V3 longest, but tips probably broken; lobes beyond median margin slightly longer than rest of fin. Pectoral fin pointed, reaching beyond genital papilla but not to anal-fin origin. Pelvic fin pointed, tips of longest branches of first and second rays of equal extension [outer branch of second ray slightly longer]; reaching beyond genital papilla but not to base of first anal-fin spine.

Colour pattern in preservative. Udachi form (Fig. 1b): Head, lips, lower jaw and gill cover grey except pale brownish cheek, indistinct dark grey band across nape posteriorly, dark brown or grey opercle and subopercle, and dark brown wide band from orbit to posterior margin of opercle; exposed branchiostegal membrane blackish except greyish white margin. Nuchal hump light grey. Chest and abdomen pale brown. Scales on side proximally light, distally dark brown. Dark brown wide stripe from origin of lateral line obliquely caudoventrad to midline where becoming horizontal, followed or not by one or two indistinct elongate dark blotches. Three indistinct broad brownish vertical bars from dorsal fin base ventrad, at most to middle of side; caudal peduncle dorsally brown. Two or three narrow horizontally extended brown blotches on upper lateral line, indistinct, or absent. Pectoral fin base blackish brown externally and internally. Dorsal fin dark grey to blackish; distinct white submar-

ginal stripe and black lappets and margin of soft dorsal fin; lappets of spinous portion also with thin white distal margin; soft dorsal fin semihyaline or dark brown, with numerous minute whitish spots. Anal fin blackish brown, margin narrowly darker; a few white spots on soft part posteriorly. Caudal fin dorsally with white submarginal and black marginal stripes continuing pattern from dorsal fin; rest of fin blackish with numerous minute white spots, more prominent in dorsal lobe; tips of lobes black. Indistinct round dark blotch at middle of caudal fin base. Pectoral fin hyaline. Pelvic fin blackish with white leading margin. No obvious sex differences in colour pattern.

Ulwile form (Fig. 1c): As described for *N. furcifer* (Udachi), but small white spots on anal fin absent or present. NRM 51519 and 51509 lighter than remaining specimens, and 3–4 dark blotches along middle of side, and two dark blotches on upper lateral line are more distinct.

Syntypes: Colour overall light brown on body and fins. Black stripe along margin of gill cover. Pectoral-fin base blackish on medial side. Dorsal-fin lappets black at least from seventh spine caudad. Caudal fin with faint dark spots basally.

Live colours. Udachi form (Fig. 4b): Ground colour of body brownish-beige to brown with dark brown indistinct patches forming broken stripe behind eye extending posteriorly along lower lateral line, fading on caudal peduncle. Similar line of brown patches though more indistinct on dorsal side just above upper lateral line. Nape yellowish. Large specimens tending to become overall dark brown. Unpaired fins beige, covered with turquoise and yellow dots. All unpaired fins with blue margin and black trim. Pelvic fin light beige with bluish leading edge. Pectoral fin bright yellow to orange. Lips and throat light beige to grey. Eye with blue and yellow iris and bright yellow marginal ring. No sexual colour dimorphism.

Ulwile form (Figs. 3c–d, 4d,f): As described for *N. furcifer* (Udachi), but with lighter overall body colouration.

Geographical distribution. *Neolamprologus furcifer* is reported to have a lakewide distribution (Poll, 1956; Konings, 1998), associated with rocky littoral habitats. The type locality, Kinyamkolo, is imprecise, referring to the southern part of Lake Tanganyika, and the specimens were probably collected on the southwestern coast (Konings, 2013). Tanzanian specimens reported here are from Udachi and nearby localities, and from Ulwile Island and coastal localities slightly more south (Figs. 6–7).

Comparative morphometrics

The principal component analysis (Fig. 9a–c; Table 9), including *N. timidus*, *N. furcifer* (Udachi), *N. furcifer* (Ulwile), and two syntypes of *N. furcifer*, distinguishes three clusters based on pectoral-fin length (separating *N. timidus* from the rest), caudal peduncle length, and body depth, the latter two distances reflecting the more slender shape of *N. furcifer* (Ulwile). The very small measurement of the interorbital width, preorbital depth, and caudal peduncle depth apparently do not contribute much to the first few principal vectors, and have lower loadings on the first component than the eye, which normally has the lowest loading in fish PCA. Otherwise, the clusters represent the three morphological groups recognized on the form of the caudal fin and the presence or absence of scales on the cheek.

Proportional measurements (compiled in Table 10; Figs. 9d–f, 10; Tables 2, 7–8) distinguish *N. timidus* having a longer head and pectoral fin than *N. furcifer* (Udachi), *N. furcifer* (Ulwile) and the *N. furcifer* syntypes. *Neolamprologus furcifer* (Ulwile) has more slender body than *N. furcifer* (Udachi) and *N. furcifer*, but overlapping the lower range of *N. timidus*; shorter upper jaw and less deep caudal peduncle than *N. timidus* but overlapping the lower range of *N. furcifer* (Udachi) and the *N. furcifer* syntypes; and longer caudal peduncle than *N. timidus* and the *N. furcifer* syntypes but overlapping the upper range of *N. furcifer* (Udachi). The middle to marginal caudal-fin ratio is greater in *N. furcifer* (Ulwile) than in *N. timidus* and the syntypes of *N. furcifer*, but overlapping in the lower range with *N. furcifer* (Udachi); the middle of the caudal fin is longer in *N. furcifer* (Ulwile) than in *N. furcifer* (Udachi), but overlapping in the lower range with *N. timidus* and the syntypes.

The total length of the caudal fin (the length of the streamers) is slightly greater in *N. timidus* and *N. furcifer* (Udachi) than in *N. furcifer* (Ulwile), but still comparable, suggesting that the shape of the caudal fin in the latter is mostly due to extended growth of middle rays, but also shortening

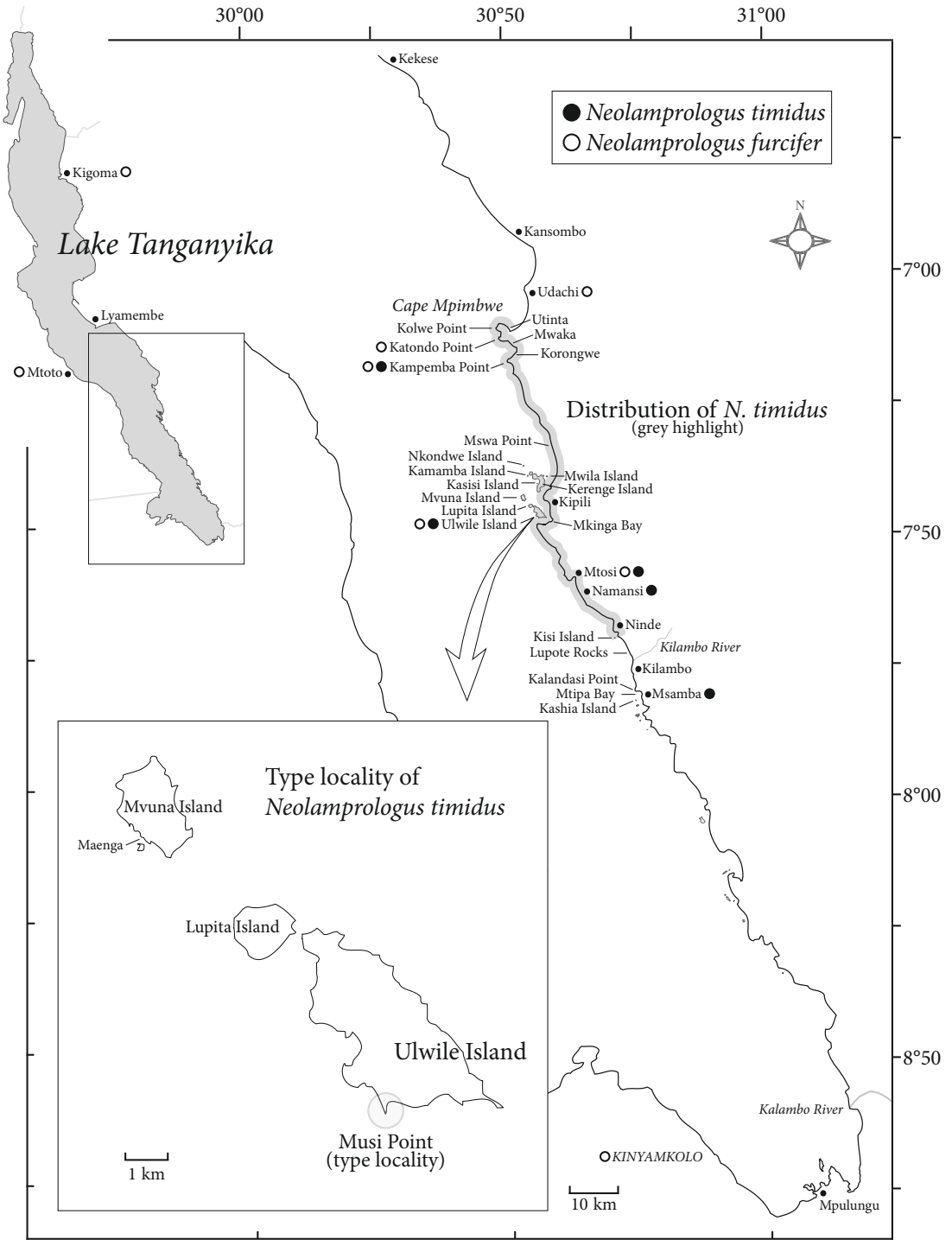

Fig. 6. Map of Lake Tanganyika showing collecting sites of *Neolamprologus timidus* and examined *N. furcifer*, and range of combined observations of *N. timidus* (grey).

of the lobe rays (Fig. 10d–e; Tables 2, 7–8, 10).

In meristics (Tables 3–6), vertebral (modally 15+19) and anal-fin (modally A. VI.6) counts are similar, with only little variation. The range of scales in the lower lateral line is similar, but without clear modal value, 13–47, mostly about 20. *Neolamprologus timidus* averages more dorsal-fin rays, more scales in a longitudinal series, more scales in the upper lateral line, and one less pectoral-fin ray (Tables 4–6). In the syntypes, the lateral line reaches only to the base of the caudal peduncle, whereas in the other material, it extends with several scales onto the caudal peduncle, as is common in lamprologins. Modal gill-rakers show a gradual shift from 11 to 14 in *N. timidus*, *N. furcifer* (Udachi) and *N. furcifer* (Ulwile) (Table 3).

Phylogenetic analysis (Fig. 11)

The Bayesian phylogenetic analysis of the combined gene fragments CYTB, ND2, COI, RAG1 Exon 3, RAG1 Intron 2) resulted in a monophyletic group of lamprologins (Bayesian posterior probability, Bpp 1.00), with *Neolamprologus ventralis* and *Paleolamprologus toae* (Poll, 1949) forming a trichotomy with a clade comprising all other Lamprologini (Fig. 11). That clade is further divided into two strongly supported (Bpp 1.00) clades, one comprising *Telmatochromis brachygnathus* Hanssens & Snoeks (2003), *Neolamprologus* sp., and *N. timidus*, the second comprising *Chalinochromis brichardi* Poll (1974) and *N. furcifer*. The

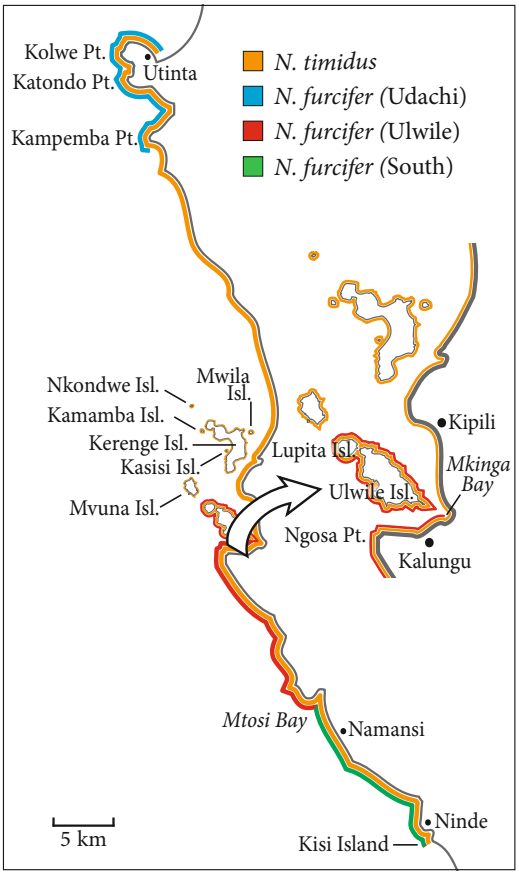

Fig. 7. Map of part of Tanzanian coast of Lake Tanganyika showing relative sympatry pattern of *Neolamprologus timidus* and *N. furcifer*, based on field observations.

Fig. 8. Type locality of *Neolamprologus timidus*, Musi Point at Ulwile Island, Lake Tanganyika, seen from the east.

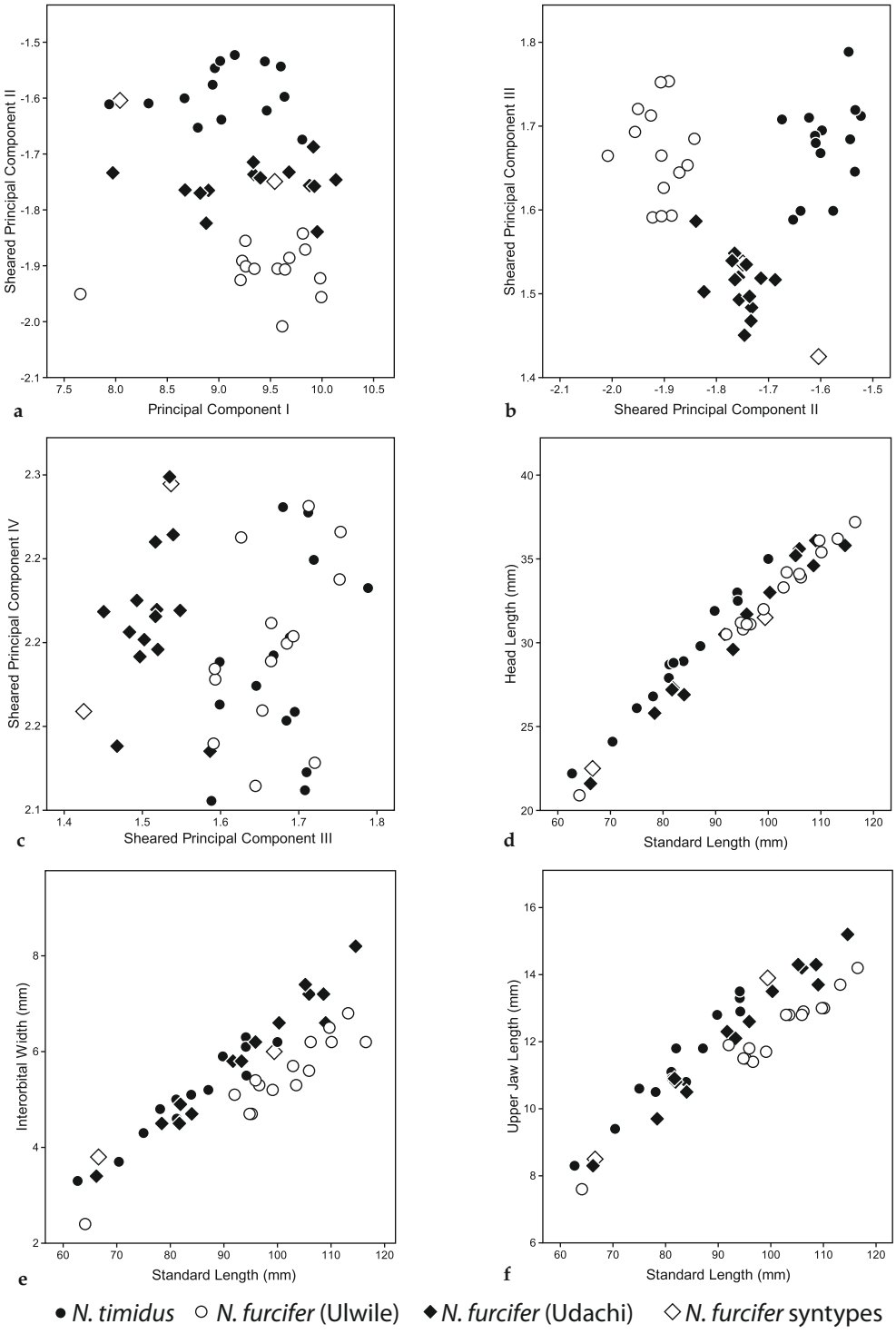

Fig. 9. Morphometry of *Neolamprologus timidus*, *N. furcifer* (Udachi), *N. furcifer* (Ulwile), and syntypes of *N. furcifer* (BMNH 1898.9.9:17–18).

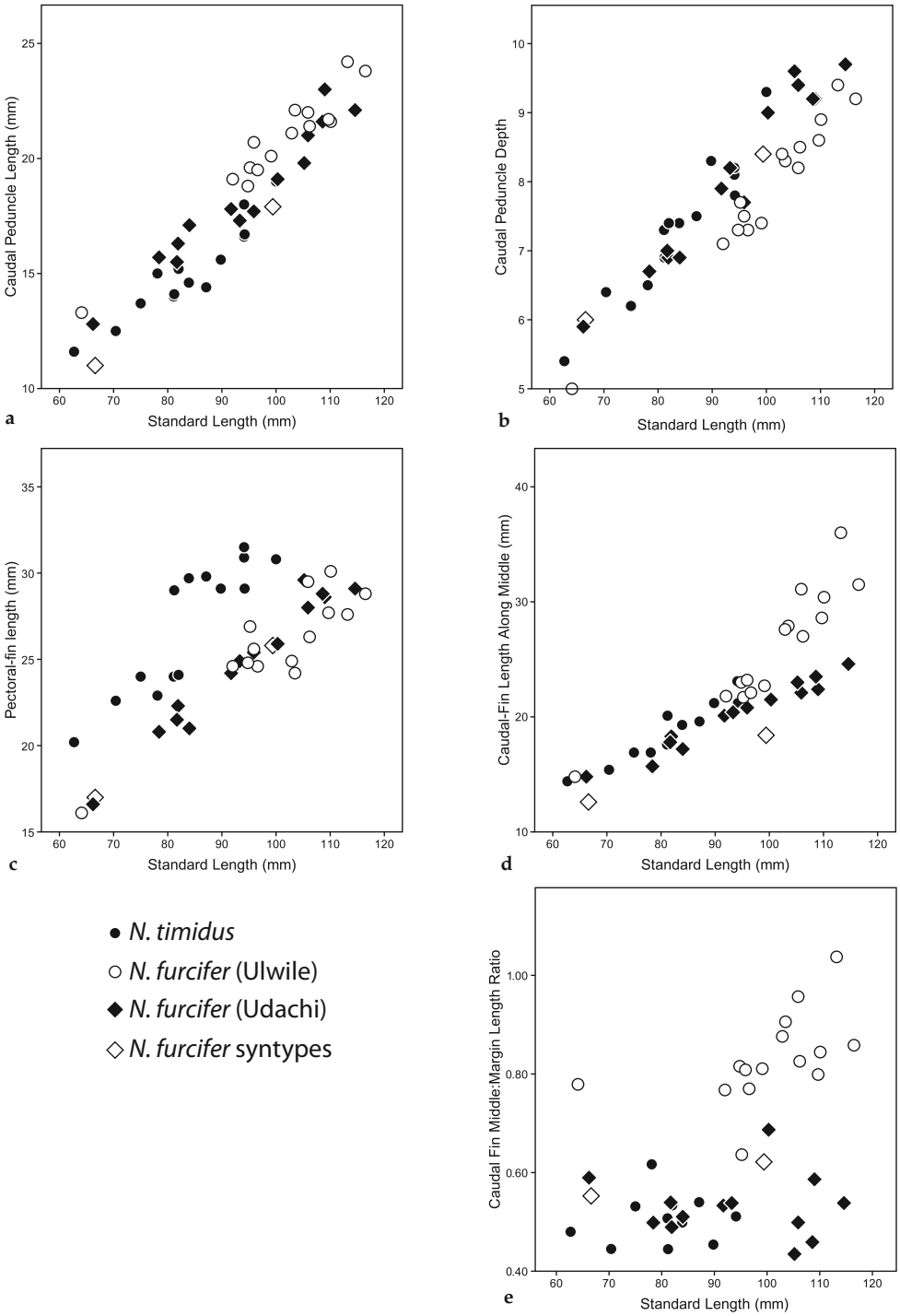

Fig. 10. Morphometry of *Neolamprologus timidus*, *N. furcifer* (Udachi), *N. furcifer* (Ulwile), and syntypes of *N. furcifer* (BMNH 1898.9.9:17–18).

monophyly of all species represented by more than one individual (*T. duboisi*, 2 specimens; *N. timidus*, 4 specimens; *C. brichardi*, 2 specimens; *N. furcifer*, 5 specimens) are strongly supported (Bpp 1.00). Analyzing the mitochondrial genes separately resulted in trees (not shown) compatible with the combined tree (Fig. 11).

Analysing the nuclear genes separately resulted in trees (not shown) broadly similar to the combined tree, but poorly resolved. The monophyly of *N. furcifer* and *N. timidus* is not supported by Bayesian analysis of the nuclear fragments: in the RAG1 intron 2 analysis they form an unresolved polytomy with *C. brichardi* and *T. brachygnathus*, while in the RAG1 exon 3 analysis *N. timidus* forms a polytomy which includes a clade comprising all Lamprologini except *C. brichardi*, and within that clade *N. furcifer* form a separate polytomy which includes a clade comprising *P. toae*, *N.* sp., and *T. brachygnathus*. This appear to be caused by the low information content of the nuclear genes: all included nuclear sequences (except the RAG1 intron 2 *T. duboisi* sequence from GenBank (DQ12180), which contains several apparent sequencing errors), are less than 2 % dissimilar (uncorrected *p*-distance) from all corresponding sequences. For comparison, the mitochondrial sequences are up to 15 % dissimilar (uncorrected p-distance) to corresponding sequences.

For the COI fragments, the uncorrected *p*-distance within *N. furcifer* and *N. timidus* was ≤0.5 %, whereas uncorrected p-distance between these putative species was 5.3–5.8 %.

Table 9. Variable loadings on principal components I–II and sheared components II–IIV from pooled morphological dataset of *Neolamprologus timidus* (N = 14), *N. furcifer* (Udachi) (N = 14), *N. furcifer* (Ulwile) (N = 14) and syntypes of *N. furcifer* (N = 2; BMNH 1898.9.9:17–18). Highest loadings in bold.

	I	II	sheared II	III	sheared III IV		Sheared IV
SL (mm)	0.264	−0.239	−0.254	0.015	0.014	0.130	0.131
Head length	0.245	−0.050	−0.065	0.151	0.150	−0.002	−0.002
Snout length	0.288	0.048	0.031	0.186	0.185	−0.263	−0.263
Preorbital depth	0.370	0.163	0.140	0.104	0.103	−0.785	−0.784
Body depth	0.287	0.040	0.023	−0.356	−0.357	0.141	0.142
Orbital diameter	0.195	−0.354	−0.364	0.284	0.284	0.246	0.247
Interorbital width	0.373	0.312	0.289	**-0.509**	**-0.510**	0.146	0.147
Pectoral-fin length	0.230	**0.439**	**0.424**	**0.649**	**0.648**	0.295	0.295
Upper jaw length	0.263	0.124	0.108	−0.057	−0.058	0.139	0.139
Lower jaw length	0.242	−0.042	−0.056	−0.029	−0.029	0.174	0.175
Caudal peduncle depth	0.253	0.065	0.050	−0.183	−0.183	0.058	0.058
Caudal peduncle length	0.297	**-0.687**	**-0.702**	0.015	0.014	−0.085	−0.084
Last dorsal-fin spine length	0.242	0.027	0.013	0.077	0.077	0.220	0.221
Eigenvalue	0.3659	0.0176	N/A	0.0088	N/A	0.0027	N/A
Cumulative Variance %	90.6	95.0	N/A	97.10	N/A	98.0	N/A

Table 10. Comparison of diagnostic proportional measurements in *Neolamprologus timidus*, *N. furcifer* (Udachi), *N. furcifer* (Ulwile) and *N. furcifer* syntypes (BMNH 1898.9.9:17–18). Distinctive values highlighted in bold.

	N. timidus	*N. furcifer* (Udachi)	*N. furcifer* (Ulwile)	*N. furcifer* syntypes
Head length (% SL)	**34.2–35.5**	31.2–33.6	31.9–33.2	31.7–33.8
Body depth (% SL)	22.8–26.2	24.3–26.9	**21.2–23.7**	25.2–25.6
Pectoral-fin length (% SL)	**29.3–35.7**	25.0–28.1	23.4–28.3	25.5–26.0
Upper jaw length (% SL)	12.9–14.4	12.4–13.6	**11.8–12.9**	12.8–14.0
Caudal peduncle depth (% SL)	8.3–9.3	8.0–9.1	**7.5–8.3**	8.5–9.0
Caudal peduncle length (% SL)	16.5–19.2	18.5–21.1	**19.6–21.6**	16.5–18.0
Caudal-fin concavity	44.5–61.7	43.5–68.7	**63.6–103.7**	55.3–62.2
Caudal-fin length at middle (% SL)	21.6–24.8	20.0–22.4	**22.8–31.8**	18.5–18.9
Dorsal caudal-fin lobe length (% SL)	**35.1–55.7**	**31.2–50.3**	28.3–35.8	29.8–34.2
Ventral caudal-fin lobe length (% SL)	**35.7–54.2**	**31.0–52.0**	27.0–38.2	28.8–32.1

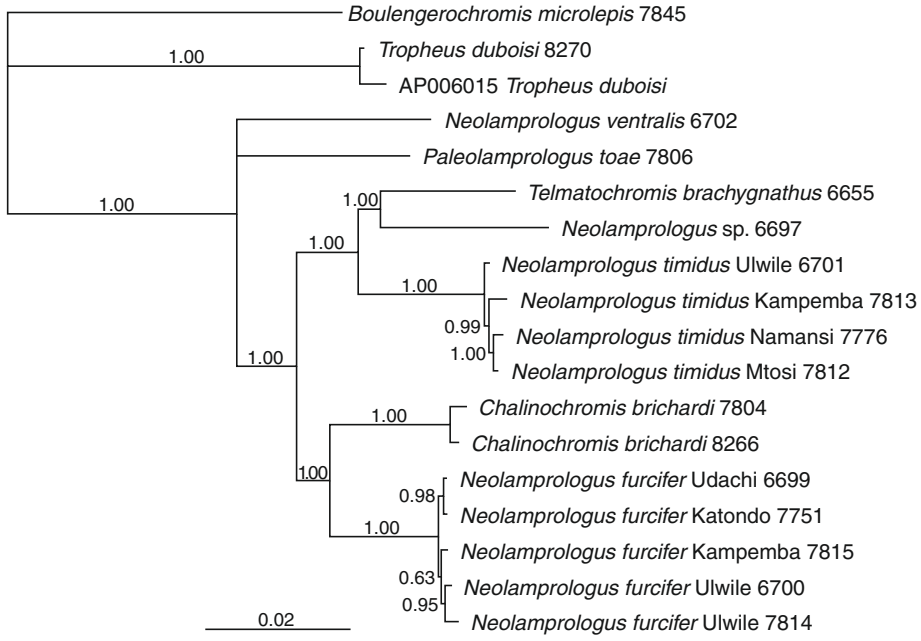

Fig. 11. Bayesian majority-rule bootstrap tree from analysis of fragments of three mitochondrial (CYTB, COI, ND2) and two nuclear genes (RAG1 Exon 1, RAG1 Intron 2). Values at nodes indicate Bayesian posterior probability estimates. Branch lengths proportional to number of expected substitutions per site. Capture locality and NRM tissue collection number are indicated after the scientific name.

Discussion

Neolamprologus furcifer was first described briefly in a key, without mention of particular specimens (Boulenger, 1898a), and then more fully and with a figure, with reference to three specimens from Kinyamkolo, and one from Mbity Rocks (Boulenger, 1898b). Boulenger (1915) listed two specimens from Kinyamkolo specifically as Types (BMNH 1898.9.9:17–18). The latter are in reasonably good condition but very soft. Scales are absent from the cheek, and the first and second pelvic-fin rays are about equal in length, or the latter slightly longer. The caudal fin is emarginate with pointed marginal tips. They thus agree with the form here described from Udachi, and with specimens available from Kigoma and Mtoto on the western coast of the lake. We thus refer those samples to *N. furcifer*, but note that the variable preservation state and wide variation in counts and proportional measurements suggest that larger series of specimens from different parts of the lake may show this concept of *N. furcifer* to be a composite, and our characterization of *N. furcifer* should be tested on a larger sample from the type locality area at the southern end of Lake Tanganyika. Kinyamkolo is often equated with the present town of Mpulungu in Zambia, but should be understood as a wider region at the southern end of Lake Tanganyika (Konings, 2013: 21).

In the Tanzanian coast material reported here and referable to *N. furcifer* of authors there are three morphologically distinct groups, identified by PCA clusters, the shape of the caudal, pectoral, and pelvic fins, and presence/absence of cheek scales. They represent six localities which span over 60 km in a straight line, 100 km coastline, from Namansi north to Udachi. Large series are available from Ulwile Island and Udachi. Specimens from Ulwile Island represent two distinct morphologies. One, here recognized as *N. timidus,* is characterized by long pointed caudal-fin streamers, scales covering the cheek, and the first pelvic-fin ray the longest. The second form has short, rounded caudal-fin lobes, naked cheek, and the second pelvic-fin ray the longest. Specimens from Udachi have long streamers like *N. timidus*, but naked cheek and the second pelvic-fin ray is the longest. Specimens from other localities were

identified as pertaining to one or another of these forms. Only two specimens proved difficult. NRM 51517, from Kampemba Point, has shorter caudal-fin streamers than other *N. furcifer* (Udachi), but the caudal-fin lobes are not broad and rounded as in *N. furcifer* (Ulwile). The specimen NRM 51519, from Mtosi, has only short caudal-fin lobes, but more pointed than in other *N. furcifer* (Ulwile), and potentially represents the more southern *N. furcifer* with long caudal-fin streamers. NRM 51509, from the same locality, however, has the typical caudal-fin shape of *N. furcifer* (Ulwile).

Molecular analysis. Day et al. (2007) published ND2 and control region sequences of a specimen from Kigoma identified as *N. furcifer*. Sturmbauer et al. (2010) reported an ND2 sequence of *N. furcifer*, without locality data. The two ND2 sequences differ only in 6 positions (99.4 % identity), and presumably represent the same species. In both analyses, *N. furcifer* is recovered as sister to mixed species of *Chalinochromis* and *Julidochromis*, and this clade makes *Neolamprologus* as well as *Julidochromis* and *Chalinochromis* paraphyletic.

An analysis using all available CYTB and ND2 sequences in GenBank resulted in about the same tree as provided by Day et al. (2007) and Sturmbauer et al. (2010), showing two major lineages (A and B+C in Day, 2007: fig. 3), and *N. furcifer* and *N. timidus* in the same lineage (B+C). Like in that tree *N. furcifer* is in the sister clade to that containing species of *Chalinochromis* and *Julidochromis*, and species of *Neolamprologus* are scattered in the tree. It is then not surprising that *N. timidus* makes up the sister clade to a group dominated by species of *Telmatochromis* Boulenger (1898a) and *Julidochromis*, and *Neolamprologus brichardi*, a grouping also obtained by Day et al. (2007).

Neolamprologus does not come out monophyletic in our analysis (Fig. 10), and the same may be said for other genera of lamprologins. Non-monophyly of *Neolamprologus* and unexpected positions of various specimens and species may better be analyzed in a context of lamprologin phylogeny. The analysis is very clear with regard to the position of *N. furcifer* and *N. timidus*, however. In all trees, specimens of *N. timidus* and *N. furcifer* form monophyletic clusters, with almost no differentiation within the clades. They are not sister groups, or even closely related. In the individual genes, *N. furcifer* tends to group with *Chalinochromis*, and *N. timidus* with *Telmatochromis* along with various other taxa. In the multilocus tree (Fig. 10), with limited taxon sampling, *Chalinochromis brichardi* is the sister group of *N. furcifer*, whereas *N. timidus* forms a clade with an unidentified species of *Neolamprologus* somewhat similar to *N. christyi* (Trewavas & Poll, 1952) and with *Telmatochromis brachygnathus*. All genes and the combined tree show unambiguously that *N. furcifer* (Ulwile) and *N. furcifer* (Udachi) form a monophyletic clade, with almost identical individual sequences, and no geographic substructure.

Taxonomic analysis. Although *N. timidus* is clearly diagnosed by the scales on the cheek and the shape of the pelvic fin as distinct from the type series of *N. furcifer* and the material here referred to *N. furcifer* (Udachi) and *N. furcifer* (Ulwile), no trenchant proportional measurements or counts were detected. In several meristic characters *N. timidus* represents an extreme in the pooled variation, overlapping with *N. furcifer* (Ulwile), and more distinct from *N. furcifer* (Udachi).

The sample from Ulwile Island with rounded caudal-fin lobes and only slightly indented caudal-fin margin are similar to *N. furcifer* (Udachi) in most respects. Counts overlap both with it and with *N. timidus*. DNA sequences agree with those from Udachi, and GenBank sequences of *N. furcifer*. It has a relatively shorter head, pectoral fin and upper jaw, and less deep caudal peduncle than the syntopic *N. timidus*, but only more slender body distinguish from *N. furcifer* (Udachi). Subjectively, there seems to be more variation in the caudal-fin shape in *N. furcifer* (Ulwile) than in *N. furcifer* (Udachi), the syntypes of *N. furcifer*, or *N. timidus*, but then mainly in the extent of median indentation, whereas the lobes are rounded, with only one exceptional specimen with short pointed tips. Because of this variability, and the absence of other morphological autapomorphies, and only minimal genetic differentiation, the taxonomic status of this form remains unresolved. Under the diagnosability criterion of the phylogenetic species concept (Kullander, 1999), it may qualify as a distinct species from *N. furcifer*, representing a very recent speciation event. As alternative to species status, we have considered that the Ulwile form may reflect character displacement in the presence of *N. timidus*. This option is not testable at this time, although a single speci-

men each of *N. furcifer* (Udachi) and *N. timidus* are present from Kampemba and those represent typical specimens of each form. Character displacement occurs where similar species or demes are syntopic, and is believed to be favoured by selection to optimize food or habitat utilization in habitats where food or other resources are scarce but represented by distinct classes (Dayan & Simberloff, 2005). At this time it is not obvious what selective advantage the broader caudal fin in *N. furcifer* (Ulwile) would have over the more common lyreate shape in other *N. furcifer* and *N. timidus*.

We are not convinced that the Tanzanian material of *N. furcifer* represents the same species as the syntypes of *N. furcifer* from the southern end of the lake. They clearly differ from *N. timidus*, and the main reason for including them in the present paper was to investigate potential conspecificity with *N. timidus*. They tend to cluster with *N. furcifer* (Udachi) in measurements, but have fewer scales in the longitudinal row (Table 4), overlapping only with an extreme *N. furcifer* (Udachi), and a shorter upper lateral line (Table 5), and extend the range of dorsal-fin ray counts (Table 6).

Geographical distribution. *Neolamprologus timidus* was observed at all islands in the vicinity of Kipili, i.e., Kamamba, Kasisi, Kerenge, Lupita, Mvuna, Mwila, Nkondwe (Fig. 5), and Ulwile (Figs. 5, 7), and along the rocky coast from Mswa Point north to Kampemba Point. We observed the species as far south as to Kisi Island off the rocky coast south of Ninde. We assume that the Kilambo River located 6 km south of Kisi Island and the subsequent 2 km sandy beaches would represent the southern border of distribution. The area of distribution then includes Lupote Rocks located barely 5 km south of Kisi Island and just 1.4 km north of the Kilambo River. The species has, however, not been observed at this locality. Since Lupote Rocks is a rocky outpost located in the most southern part of the assumed area of distribution and quite isolated from the nearby rocky coast by very deep water, it is likely that *N. timidus* is not present among the huge boulders forming this habitat. *Neolamprologus furcifer* was, however, observed at Lupote Rocks. The specimen of *N. timidus* collected at Msamba by Moore (BMNH 1906.9.6.52) suggests a much more southern distribution (Fig. 6). We made several dives at Msamba and nearby (Kalandasi Point, Mtipa Bay, Kashia Island). *Neolamprologus furcifer* is present at these localities, but we did not find *N. timidus*. Possibly the *N. timidus* were obtained more to the north, within the known range of *N. timidus* but Msamba was used as a convenient label for specimens obtained over a larger area. The northernmost observation of *N. timidus* was made at Kolwe Point, Cape Mpimbwe. We found the species at several locations from Kisi Island and Kampemba Point, located 7.5 km south of Cape Mpimbwe. We also observed it at Katondo, Mwaka, and Korongwe, all three localities south of Kolwe Point. Since there are no obvious barriers north of Kolwe Point, it is likely that *N. timidus* occurs further along the rocky coast to Utinta, which represents the last rocky habitat at Cape Mpimbwe. North of Utinta a 7 km long sandy beach is found which is most likely the northern barrier for the species. Further north, at the rocky coast of Udachi, Kansombo and Kekese we have not been able to find *N. timidus*. The confirmed coastal area of distribution is thus between Kolwe Point at Cape Mpimbwe and Kisi Island, a distance of 100 km. The distribution also includes the islands of Kamamba, Kasisi, Kerenge, Lupita, Mvuna, Mwila, Nkondwe, Ulwile and Kisi with an additional total stretch of 35 km.

In areas of sympatry, *N. timidus* and *N. furcifer* are syntopic (at Kolwe Point south to Kampemba Point; at Mtosi south to Kisi Island), forming a cryptic species pair, with about the same behaviour and with the same size, and distinctive colour, body shape, and fin shape except for the caudal fin. Figure 4 shows syntopic individuals of *N. timidus* and *N. furcifer* at three localities.

Neolamprologus furcifer is absent from a large part of the distribution of *N. timidus* (Fig. 6). No observations of *N. furcifer* have been made along the coast from south of Kampemba Point to Mkinga Bay (about 4 km south of Kipili), an area inhabited by *N. timidus* alone (Figs. 6–7). At the islands, both species are present at Lupita and Ulwile Island, but at the remaining six islands (Kamamba, Kasisi, Kerenge, Mvuna, Mwila, and Nkondwe) only *N. timidus* was present (Fig. 6). *Neolamprologus furcifer* (Ulwile) was observed southward to Mtosi; south of there, only *N. furcifer* with long, pointed caudal-fin lobes were observed.

Ecology. We found *N. timidus* and *N. furcifer* in the dark rocky biotope, where both are quite

common and equally abundant, and similar in behaviour. The former prefers the more inaccessible parts of the biotope. The feeding behaviour has not been observed, neither of *N. timidus* nor of *N. furcifer*. Both species might be nocturnal and feed at night when small shrimps and other invertebrates are abundant. The relatively large eyes on both species may be an adaption for enhanced night vision. Neither of the species is found in direct daylight but they are both always observed in the shady parts of the rocks.

Characters of *Neolamprologus*. The endemic Lake Tanganyika cichlid genus *Neolamprologus* Colombé & Allgayer (1985) represents a heterogeneous group not recovered as monophyletic in molecular phylogenetic analyses (Schelly et al., 2006; Day et al., 2007; Sturmbauer et al., 2010; present study). In their original proposal, Colombé & Allgayer (1985) provided a brief summary of characters for each of the lamprologin genera that they recognized (*Lamprologus* Schilthuis (1891); *Neolamprologus*, *Variabilichromis* Colombé & Allgayer, *Lepidiolamprologus* Pellegrin (1904), and *Paleolamprologus* Colombé & Allgayer) but did not provide any clear diagnostic character for any of the genera. Instead it appears from their discussion and figure that they consider as generic diagnostics various reductions in the number of infraorbital ossicles. In *Neolamprologus* infraorbital ossicles are absent, like in two other lamprologin genera, *Julidochromis*, and *Telmatochromis*. They are also absent in *Chalinochromis*, a genus not examined by Colombé & Allgayer, and in *Altolamprologus* Poll (1986), species of which were included in *Neolamprologus* by Colombé & Allgayer. In the remaining genera at least the dermosphenotic or other infraorbital ossicles are present (Stiassny, 1997; Schelly, 2007). The type species of *Neolamprologus* is *N. tetracanthus* (Boulenger, 1899a).

Poll (1986) rejected the value of infraorbital ossicles as diagnostic for genera of lamprologins. He diagnosed *Neolamprologus* by having the first pelvic-fin ray longer than the rest, presence of occipital, thoracic and abdominal scales, infraorbital ossicles usually absent, and not more than 60 scales in a longitudinal row. Poll (1986) synonymized the monotypic *Variabilichromis* and *Paleolamprologus*, in which infraorbitals are present. Stiassny (1997) resurrected *Variabilichromis* with reference to the presence of infraorbital ossicles and basal position in the tree of Sturmbauer et al. (1994). *Paleolamprologus* has remained in synonymy of *Neolamprologus*, but Stiassny (1997) pointed out that in the only species, *P. toae*, there are six or seven infraorbital ossicles, contrasting with the other African cichlids, in which there are typically five when not reduced or co-ossified. In the most recent molecular phylogenies (Day et al., 2007; Sturmbauer et al., 2010) lamprologins fall into two major groups, one in which the labial cartilage usually is ossified, and one in which it remains cartilaginous. *Paleolamprologus toae* and *Variabilichromis moorii* (Boulenger, 1898a) are successively basal in the "non-ossified" clade, justifying the validity of *Paleolamprologus* if *Variabilichromis* is recognized. This clade also includes the type species of *Neolamprologus*, *N. tetracanthus*, and a mix of *Julidochromis*, *Chalinochromis*, *Neolamprologus*, and fluviatile *Lamprologus*.

The dermosphenotic and other infraorbitals are absent in *N. timidus* and *N. furcifer*, and the labial cartilage is not ossified. In distinction from *Lepidiolamprologus* and a few other species of the "ossified" group, the coronalis pore is simple instead of represented by two separate openings.

Neolamprologus timidus also conforms to Poll's diagnosis of the genus in having the first pelvic-fin ray longer than the second, as is the case in most other species of the genus examined. In all specimens here reported as *N. furcifer*, but also in *N. leleupi* (Poll, 1956), either the first and second rays are of about the same length or the second slightly longer. Poll's (1986) diagnosis of *Neolamprologus* served mainly to distinguish it from *Lamprologus* in which the second and third pelvic-fin rays are the longest. The type species of *Lamprologus* is *L. congoensis* Schilthuis (1891) from the Congo River. Poll's *Lamprologus* included all lamprologin species from the Congo River and a number of species from the lake. Among the lake species with the second pelvic-fin ray the longest, referred by Poll to *Lamprologus*, the majority are small-sized bottom-oriented shell breeders like *'L.' ocellatus* (Steindachner, 1909), *'L.' stappersi* (Pellegrin, 1927), *'L.' ornatipinnis* Poll (1949), or mud-tunnel breeders like *'L.' signatus* Poll (1952) and *'L.' kungweensis* Poll (1956) with rounded pelvic fin, for which the habit of staying directly on the bottom with the broad pelvic fin as support provides an alternative, adaptive, explanation for the pelvic-fin shape. *'Lamprologus' finalimus* Nichols & La Monte (1931) is a little known species, similar to *Neolamprologus caudopunctatus* (Poll,

1978) (Konings, 1998). *'Lamprologus' callipterus* Boulenger (1906) is also a shell spawner, but with strong sexual size dimorphism, females similar to other small shell spawners, males up to 15 cm long. As far as studied, these species share the absence of infraorbitals with *Neolamprologus*, but pertain to the clade containing *Altolamprologus* and *Lepidiolamprologus* in molecular analyses (Day 2007; present study). The Congo River *Lamprologus* are a morphologically relatively homogeneous group, diagnosed by having two or three infraorbital ossicles following the lachrymal. Although molecular support is lacking, the Congo River *Lamprologus* are most likely a monophyletic group (Schelly & Stiassny, 2004; Schelly, 2007). Unless referable to some other genus, lake species included in *Lamprologus* by Poll (1986) or conforming to his diagnosis of the genus may thus conveniently be distinguished as *'Lamprologus'*, with the generic name in quotes pending a comprehensive revision of the Lamprologini, as proposed by Konings (1998). One more species with broad pelvic fin and substrate-resting, *Lamprologus lemairii* Boulenger (1899b), was also placed by Poll in *Lamprologus*. It shares with *Lepidiolamprologus* paired NLF0 pore and presence of a dermosphenotic (Schelly, 2007), and may be more conveniently classified with that group. Conclusively, the pelvic-fin shape may be more indicative of behaviour than of phylogeny. *Neolamprologus furcifer* is not known to rest on the bottom, and unlike in the benthic *'Lamprologus'*, the pelvic fin is elongate rather than rounded. Consequently, and in agreement with molecular trees, the unossified labial cartilage and the absence of infraorbitals, *N. furcifer* is referred to *Neolamprologus*.

Cheek squamation. *Neolamprologus timidus* has a fully scaled cheek. A scaled cheek is a rare character state among lamprologins (Stiassny, 1997). Usually, in lamprologins, scales are completely absent from the cheek, and rarely there is a group of scales posterodorsally between the orbit and the preopercle, as in some *N. furcifer*. The only other species of lamprologins with fully scaled cheek are *N. ventralis*, *N. leloupi*, and *Lepidiolamprologus profundicola*. According to Poll (1956: 594) the posterior half of the cheek is scaled in *N. niger* (Poll, 1956). According to Büscher (1995), scales are absent on the cheek in *N. ventralis*, but in our specimens, from Ulwile Island, the cheek is covered with embedded, minute, transparent cycloid scales, easy to overlook. Poll (1948) reported 4–5 rows of scales in the holotype of *N. leloupi*, and three rows are shown on his figure. In our material from Lyamembe tentatively identified as *N. leloupi* the cheek is deeper than shown in Poll's figure, and the embedded, minute, thin and translucent scales are difficult to observe without scraping away the skin, but the scaled area is either restricted to the posterodorsal corner or extending to the middle of the cheek only.

Absence of scales on the cheek is a rare character state in cichlids. All neotropical cichlids have scaled cheek, although the anterior portion may be naked in some geophagines (Kullander, 1998). Non-lamprologin African and Asian cichlids have scaled cheek with few exceptions, especially among rheophilic, benthic, or otherwise highly specialized taxa, e.g., Eretmodini, *Trematocara* Boulenger (1899b), *Steatocranus* Boulenger (1899c), *Gobiocichla* Kanazawa (1951).

Caudal-fin shape. Although no comparative measurement data are available, it seems that the marginal streamers in the caudal fin of *N. timidus* and *N. furcifer* are exceptionally long for lamprologin cichlids. The majority of lamprologins possess a rounded, subtruncate or slightly emarginate caudal fin. Within *Neolamprologus*, however, several species have a deeply concave caudal-fin margin, often with elongated marginal rays. The least extreme is seen in *N. mondabu* (Boulenger, 1906) in which the caudal-fin margin is concave and the marginal rays only slightly projecting. The other lamprologin species with marginal elongations are *Neolamprologus brevis* (Boulenger, 1899a), *N. brichardi* (Poll, 1974), *N. buescheri* (Staeck, 1983), *N. chitamwebwai* Verburg & Bills (2007), *N. christyi*, *N. crassus* (Brichard, 1989), *N. falcicula* (Brichard, 1989), *N. gracilis* (Brichard, 1989), *N. helianthus* (Büscher, 1997), *N. longicaudatus* (Nakaya & Gashagaza, 1995), *N. marunguensis* (Büscher, 1989), *N. pulcher* (Trewavas & Poll, 1952), *N. splendens* (Brichard, 1989), *N. savoryi* (Poll, 1949), *N. walteri* Verburg & Bills (2007), and *Chalinochromis popelini* (Brichard, 1989).

Variation in caudal-fin shape has not been reported for any of those species, and thus the variability here observed in *N. furcifer* is unusual in the genus, and the shape of the fin in *N. furcifer* (Ulwile) is unique in the genus. The caudal fin of *N. christyi* is also rather deeply concave with elongated marginal rays, but not quite as long as in *N. timidus* or *N. furcifer*. In *N. ventralis* the cau-

dal fin may be rounded or elongately rounded, or resemble that of *N. furcifer* (Ulwile) in having somewhat rounded lobes and a minor median indentation, but is much shorter than in *N. furcifer* (Ulwile); in *N. mondabu* it varies from slightly rounded to slightly emarginate. Caudal-fin shape is otherwise invariable in cichlid species and a dependable species character, although it may vary between sexes, e. g., in *Apistogramma* Regan (1913) (Koslowski, 2002). The majority of cichlid species have a rounded or subtruncate caudal fin. In the Neotropics a few taxa only present a concave margin and produced marginal rays, viz. *Dicrossus filamentosus* (Ladiges, 1958), and species of *Apistogramma*, *Geophagus* Heckel (1840), and *Pterophyllum* Heckel (1840). Lake Tanganyika is remarkable for a very large proportion of cichlid species with emarginate or forked caudal fin in several genera, and most notable in *Benthochromis*, Poll (1986), *Cyathopharynx* Regan (1920), *Ophthalmotilapia* Pellegrin (1904), and *Paracyprichromis* Poll (1986). Caudal-fin shape is likely a strong synapomorphy of species of *Neolamprologus*, but because of variation in shape, and apparent difference between the species with simply prolonged marginal rays, and those with long, broad streamers, this character needs more study to establish homologies.

Two overall dark, elongate species of *Neolamprologus* have been described from the western shore of Lake Tanganyika, opposite the localities of *N. timidus*, viz. *N. pectoralis* (Büscher, 1991b) and *N. nigriventris* Büscher (1992). Although we consider it relevant to include these species in a future revision of *N. furcifer*, we have not examined specimens. Both *N. pectoralis* and *N. nigriventris* are characterized by a rounded caudal fin (Büscher, 1991b, 1992). *Neolamprologus pectoralis* has a long (27.7–32.6 % SL; Büscher, 1991b), but rounded pectoral fin (Büscher, 1991b). *Neolamprologus nigriventris* has a unique shaded colour pattern with blackish abdomen and lower part of the head, and light flanks, dorsum and upper part of the head (Büscher, 1992). Both species have a deeper caudal peduncle, more than 10 % SL (Büscher, 1991b, 1992), vs. less than 10 % in *N. timidus* and *N. furcifer*, and apparently do not develop a nuchal protuberance (cf. Büscher, 1991b, 1992).

Comparative material: *Altolamprologus compressiceps*, NRM 17450; *Altolamprologus fasciatus*, NRM 12786; *'Lamprologus' ornatipinnis*, NRM 51501, 51494; *Lepidiolamprologus lemairii*, NRM 12650; *Neolamprologus brevis*, NRM 60260; *N. buescheri*, NRM 51502; *N. bifasciatus*, NRM 51495; *N. caudopunctatus*, NRM 60202; *N. chitamwebwai*, NRM 61911; *N. christyi*, NRM 51513; *N.* cf. *falcicula*, NRM 59646; *N. gracilis*, NRM 59637; *N. leleupi*, NRM 13289; *N. leloupi*, NRM 11895; *N. petricola*, NRM 33670; *N. modestus*, NRM 48382; *N. mondabu*, NRM, 17452, 59564; *N. pleuromaculatus*, NRM 17437; *N. savoryi*, NRM 62052; *N. tetracanthus*, NRM 59553, 59599; *N. tretocephalus*, NRM 17445; *N. ventralis*, NRM 59618, 59623; *N. walteri*, NRM 61571; *Paleolamprologus toae*, NRM 17443; *Variabilichromis moorii*, NRM 12681.

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