A new species and geographical variation in the *Telmatochromis temporalis* complex (Teleostei, Cichlidae) from Lake Tanganyika

M. Hanssens* and J. Snoeks

Africa Museum, Vertebrate Section, Cichlid Research Unit, Leuvensesteenweg, 13, B-3080 Tervuren, Belgium

Telmatochromis brachygnathus sp.n. is described from the southern and central parts of Lake Tanganyika. It can be distinguished from the similar *T. temporalis* mainly by its smaller mouth. Morphological distinct populations were found in both species. © 2003 The Fisheries Society of the British Isles

Key words: Cichlidae; distribution; geographical variation; Lake Tanganyika; taxonomy; *Telmatochromis brachygnathus*.

INTRODUCTION

The systematics of the cichlids of the East African Lakes are complicated and taxonomic knowledge is poor (Coulter *et al.*, 1986; Greenwood, 1991; Rossiter, 1995; Snoeks, 2000). Even the relatively well-known Lake Tanganyikan ichthyofauna turns out to be problematic in view of the results of some recent morphological and molecular studies (Verheyen *et al.*, 1996; Stiassny, 1997; Rüber *et al.*, 1999; Hanssens *et al.*, 1999).

An ongoing study of the taxonomy and distribution patterns of the lamprologine cichlids from Lake Tanganyika (Snoeks *et al.*, 1994) revealed several problems within the genus *Telmatochromis* Boulenger. Hanssens & Snoeks (2001) addressed the confused status of the nominal species *Telmatochromis burgeoni* Poll and *Julidochromis macrolepis* Borodin and confirmed the proposed synonymy of *Telmatochromis lestradei* Poll with *Telmatochromis temporalis* Boulenger.

In the present study, a new *Telmatochromis* species, morphologically similar to *T. temporalis* is described; both are referred to as the *T. temporalis* complex (Hanssens & Snoeks, 2001), because of their high degree of similarity and obvious close relationships.

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*Author to whom correspondence should be addressed. Tel.: +32 2 7695628; fax: +32 2 7695642; email: mhanssens@africamuseum.be

MATERIALS AND METHODS

The following specimens were examined: the holotype and 36 paratypes of *T. brachygnathus*; the lectotype, two paralectotypes and 57 other specimens of *T. temporalis* (including the holotype and four paratypes of *T. lestradei* and the holotype of *T. burgeoni*, both junior synonyms of *T. temporalis*). A list of specimens is presented in the type list and in the Appendix. For the description and analyses, 24 morphometric and 16 meristic characters were used, all as described by Snoeks (1994), except for the upper jaw length and the number of enlarged outer row teeth in the oral jaws, which were described by Hanssens & Snoeks (2001). The measurements and meristics taken are listed in Tables I and II, respectively.

Data were explored and analysed using principal component analyses (PCA) and Mann–Whitney *U*-tests. Some of the meristics were excluded from the statistical analyses. On some specimens part of the scales were missing, so the number of upper lateral line scales could not be determined. Also the total number of outer oral teeth in the oral jaws could not be counted on all specimens. The number of scales around the caudal peduncle is invariable and was therefore also excluded from the analyses. PCA are used here as model-free and distribution-free techniques for exploring the multivariate data set (Marcus, 1990). PCA were carried out on log-transformed measurements and raw meristics. A covariance matrix was used to calculate the factor loadings and scores of the log-transformed measurements. In all analyses of measurements, the loadings of the variables

TABLE I. Measurements of the holotype and the holotype plus 36 paratypes of *T. brachygnathus*

	Holotype	Mean ± S.D.	Range
Standard length (L_S)	58·5	54·9 ± 8·3	42·0–76·0
Body depth % L_S	29·9	27·9 ± 1·9	24·8–32·8
Head length (L_H) % L_S	30·9	30·5 ± 0·8	28·8–32·3
Head width (W_H) % L_S	44·2	44·1 ± 1·3	40·5–46·1
Interorbital width % L_H	28·2	25·1 ± 2·6	18·9–29·3
Interorbital width % W_H	63·8	56·9 ± 6·0	42·9–66·7
Snout length % L_H	35·9	35·8 ± 2·1	32·4–40·2
Lower jaw length % L_H	28·2	29·3 ± 2·3	24·7–33·9
Upper jaw length % L_H	29·3	29·9 ± 1·5	26·3–32·9
Premaxillary pedicel length % L_H	30·9	30·6 ± 1·2	28·1–33·1
Cheek depth % L_H	29·3	29·9 ± 3·1	22·6–34·8
Eye diameter % L_H	26·0	26·7 ± 1·4	24·4–29·1
Lachrymal depth % L_H	23·8	20·7 ± 1·8	17·1–25·6
Lower pharyngeal jaw length (L_{LP}) % L_H	22·7	22·4 ± 0·9	20·6–24·3
Lower pharyngeal jaw width (W_{LP}) % L_{LP}	122·0	124·4 ± 4·6	113·9–134·5
Dentigerous area length % L_{LP}	58·5	60·3 ± 3·9	52·4–66·7
Dentigerous area width (W_{DeA}) % W_{LP}	70·0	74·0 ± 2·5	70·0–80·0
Dentigerous area length % W_{DeA}	68·6	65·6 ± 3·9	57·1–72·7
Dorsal fin base length % L_S	65·0	64·5 ± 1·5	61·5–67·8
Anal fin base length % L_S	25·6	22·4 ± 1·4	20·2–25·6
Predorsal distance % L_S	29·1	28·9 ± 1·0	26·4–31·2
Preanal distance % L_S	64·1	64·9 ± 1·7	62·1–67·9
Prepectoral distance % L_S	29·9	30·0 ± 1·2	27·7–33·3
Preventral distance % L_S	33·3	33·8 ± 1·7	31·1–37·8
Caudal peduncle length (L_{CP})% L_S	12·8	14·1 ± 1·1	11·8–16·9
Caudal peduncle depth % L_{CP}	106·7	91·1 ± 9·0	73·3–107·7

TABLE II. Meristics of the holotype and the holotype plus 36 paratypes of *T. brachygnathus*. Frequency indicated between parentheses

	Holotype	Number and frequency
Enlarged outer teeth upper jaw	16	8–18 (median 13)
Enlarged outer teeth lower jaw	17	10–20 (median 15)
Outer teeth upper jaw	44	29–61 (median 38)
Outer teeth lower jaw		27–44 (median 38, $n = 10$)
Inner tooth rows upper/lower jaw	5/4	5/4 (f 2), 5/5 (f 12), 6/5 (f 2), 6/6 (f 15), 6/7 (f 1), 7/6 (f 1), 7/7 (f 4)
Gill raker	3/1/4	2/1/4 (f 1), 2/1/5 (f 1), 3/1/2 (f 4), 3/1/3 (f 10), 3/1/4 (f 8), 3/1/5 (f 3), 3/1/6 (f 1), 4/1/3 (f 2), 4/1/4 (f 2), 4/1/5 (f 2), 4/1/6 (f 1), 5/1/3 (f 1), 5/1/5 (f 1)
Dorsal fin formula	XXII 7	XX 7 (f 2), XXI 6 (f 1), XXI 7 (f 9), XXI 8 (f 4), XXII 6 (f 1), XXII 7 (f 17), XXII 8 (f 1), XXIII (f 1), XXIII 6 (f 1)
Anal fin formula	VIII 6	VI 5 (f 1), VI 6 (f 9), VI 7 (f 2), VII 6 (f 17), VIII 5 (f 2), VIII (f 2)
Pectoral fin	14	13 (f 1), 14 (f 30), 15 (f 6)
Upper lateral line scales	27	22–29 (median 27)
Longitudinal line scales	34	33–36 (median 35)
Scales around caudal peduncle	16	16 (f 35)

on the first principal component (PC) were of the same sign and of a similar magnitude, indicating that this axis can be interpreted as a proxy for general size (Jolicoeur & Mosimann, 1960; Humphries *et al.*, 1981; Bookstein *et al.*, 1985). This was confirmed by plotting the first axis *v.* standard length (L_S). The correlation matrix was used for the PCA on the raw meristics. Non-parametric Mann–Whitney *U*-tests were used for univariate comparisons; they were only performed on samples of similar length class and calculated on the relative measurements (percentages) and meristics.

Abbreviations used in the text are: MRAC, Musée Royale de l'Afrique Centrale (Tervuren); BMNH, Natural History Museum [formerly British Museum (Natural History), London]; DRC, Democratic Republic of Congo; L_H, head length. Further abbreviations for the measurements are explained in Tables I and II.

RESULTS

TELMATOCHROMIS BRACHYGNATHUS SP. NOV. [FIGS. 1(A), 3 AND 4]

Etymology
From the Greek βραχνζ 'short' and γναθοζ 'jaw', used as a noun in apposition, referring to the relatively small mouth of the species.

Diagnosis
Telmatochromis brachygnathus is readily distinguished from the 'three banded' *Telmatochromis* species, *T. vittatus* Boulenger, *T. bifrenatus* Myers and *T. brichardi* Louisy, by the lack of dark longitudinal bands and a deeper body (body depth 24·8–32·8 *v.* ≤ 23·5% of L_S).

Telmatochromis brachygnathus is differentiated from *T. dhonti* by a smaller head (head length 28·8–32·3 *v.* 31·4–34·1% of L_S), smaller mouth (upper jaw length 26·3–32·9 *v.* 32·0–42·8% of L_H; lower jaw length 24·7–33·9 *v.* 35·8–43·6% of L_H), and by the enlarged outer row oral dentition [enlarged flattened, straight tipped anterior oral teeth *v.* rounded teeth with recurved tips, Fig. 1(a), (c)].

Telmatochromis brachygnathus is most similar to *T. temporalis* from which it is differentiated by a smaller mouth (upper jaw length 26·3–32·9 *v.* 29·8–40·5% of L_H; lower jaw length 24·7–33·9% of 31·8–41·6% of L_H) [Fig. 1(a), (b) and Fig. 2].

Holotype
MRAC 78–25-P-720; Cap Chaitika, Zambia; P. Brichard; January 1978; male of 58·5 mm L_S.

Paratypes
Not all paratypes were measured, the number of specimens measured is mentioned between parentheses, when relevant.

MRAC 331, Albertville, DRC, Capt. Hecq, 1899; MRAC 112746-747 (1), Baie de Kabimba, rochers, DRC, Explor. Hydrobiol. L. Tang., 10 November 1946; MRAC 113118-119 (1), Kabimba, Nord du lac Tanganyika, DRC, G. Leleup; 18 July 1961; MRAC 112755-759 (2), Stat. 108, M'Toto dans la baie et parmi les rochers au sud de l'entrée, DRC, Explor. Hydrobiol. L. Tang, 5 February 1947; MRAC 122760-761 (1), Stat. 166, Baie de Vua, plage du fond,
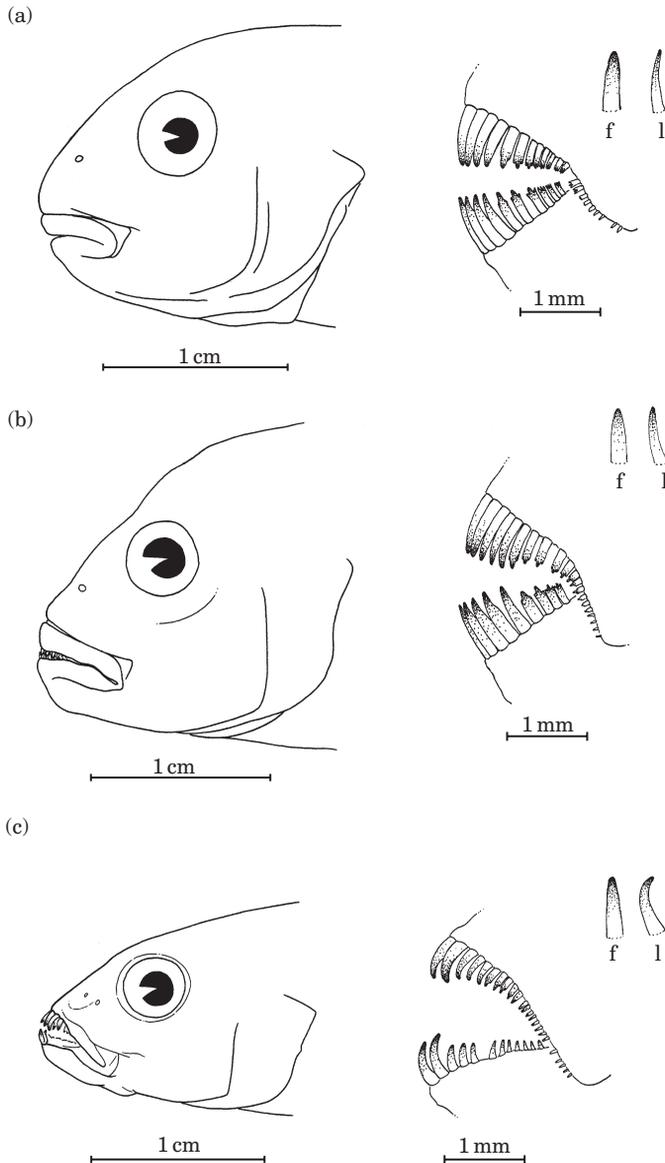
FIG. 1. Outline of the head, outer oral dentition and detail of a single anterior tooth (f, frontal; l, lateral view) of (a) *T. brachygnathus* (59·5 mm L_S, MRAC 92–81-P-1291), (b) *T. temporalis* (59·0 mm L_S, MRAC 92–81-P-1186) and (*c*) *T. dhonti* (52·0 mm L_S, MRAC 92–81-P-990).

DRC, Explor. Hydrobiol. L. Tang., 12 March 1947; MRAC 112763-765, Stat. 189, Baie de Vua, rive Nord, DRC, Explor. Hydrobiol. L. Tang., 24 March 1947; MRAC 112781-784 (2), Stat. 319, Mwerasi, le long de la rive sud, DRC, Explor. Hydrobiol. L. Tang., 28 May 1947; MRAC 74-4-P-415, 423-427 (2), 434-439 (3), Sud du lac Tanganyika, Cap Chaitika, à l'Est de la rivière Lufubu, Zambia, P. Brichard, 15 January 1976; MRAC 78-25-P-721-722, Cap Chaitika,
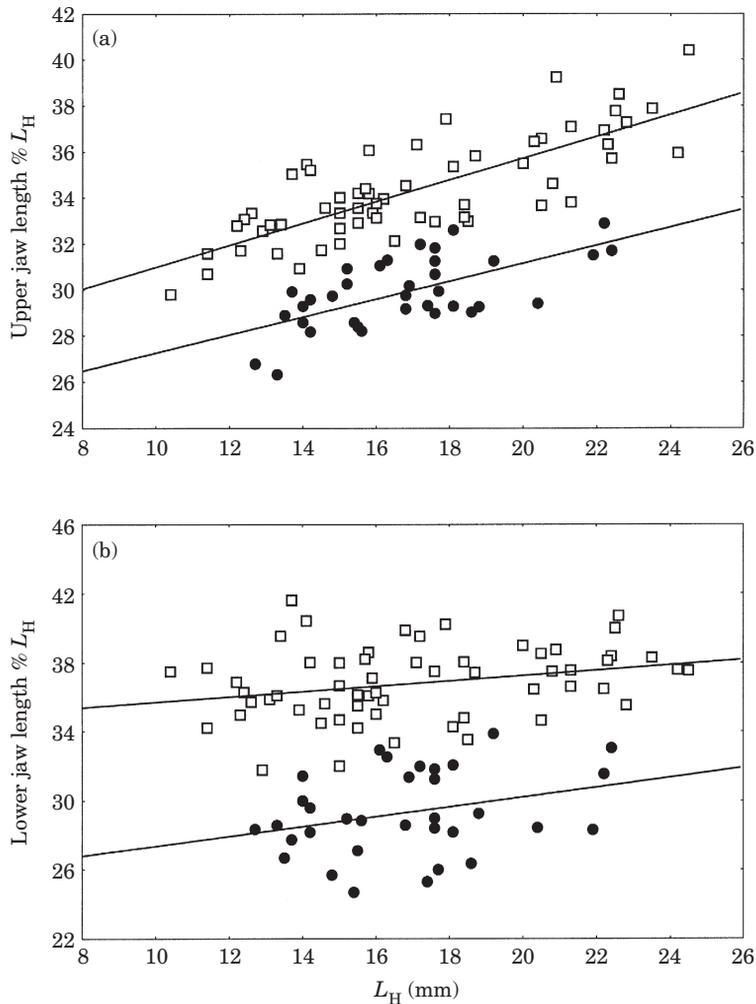
FIG. 2. Plot of the upper (a) and lower (b) jaw length as a percentage of head length and head length for *T. brachygnathus* (●, $n = 37$) and *T. temporalis* (□, $n = 60$).

Zambia, P. Brichard, January 1978; MRAC 78-25-P-723-725 (2), same data, March 1978; MRAC 84-23-P-100, Baie de Lunangwa, DRC, P. Brichard, 11 June 1984; MRAC 84-23-P-101-102, deuxième crique au Nord de Masanza, DRC, P. Brichard, 13 June 1984; MRAC 92-81-P-695, Locality 22, a few kilometres south of Karema, Tanzania, Tanganyika Expedition '92, 29 May 1992; MRAC 92-81-P-741-742, Locality 23, Just south of Karema, Tanzania, Tanganyika Expedition '92, 29 May 1992; MRAC 92-81-P-915-916, Locality 29, Kalia, bay at mouth of Lugonesi River, Tanzania, Tanganyika Expedition '92, 30 May 1992; MRAC 92-81-P-968-971, Locality 35, Bay Mahale Park, Tanzania, Tanganyika Expedition '92, 31 May 1992; MRAC 92-81-P-1291, 1298-1299, Locality 46, Kibwe Bay, Tanzania, Tanganyika Expedition '92, 03 June 1992.

Description

Description is based on the holotype and 36 paratypes. Measurements and meristic data are given in Tables I and II.

Body elongate, ventral body profile anterior to anal fin straight, dorsal body profile slightly curved. Head relatively small (L_H 28·8–32·3% of L_S); dorsal head profile strongly curved; snout obtuse [Figs 1(a) and 3(a)]. Premaxillary pedicel not prominent; mouth small, terminal and lower jaw retrognathous. Maxilla extending to just before vertical trough anterior border of eye. Gape horizontal or slightly downwards orientated.

Outer oral teeth enlarged and unicuspid anteriorly, with straight, sharp and flattened tips; teeth closely set [Fig. 1(a)]. Behind the unicuspid anterior outer oral teeth a series of smaller tricuspid teeth, the smallest of which become unicuspid posteriorly. Inner oral teeth tricuspid, closely set in several tooth rows. Inner and outer oral teeth erect.

Outer gill rakers on first branchial arch short and slender, well spaced and restricted to the upper half of ceratobranchial and on epibranchial.

Lower pharyngeal jaw triangular, wider than long (lower pharyngeal jaw width 113·9–134·5% of its length); posterior border with a wide but shallow notch. All pharyngeal teeth small and slender, laterally compressed; median teeth on posterior row sometimes enlarged [Fig. 3(b)].

Dorsal fin base long; origin of dorsal fin anterior to vertical of posterior border of operculum; posterior soft dorsal rays prolonged to just beyond caudal fin origin. Caudal fin rounded. Posterior soft anal-fin rays prolonged to about one third of caudal fin length. Pelvic fin slightly pronounced and filamentous, extending to just beyond anal fin origin.

Scales on body ctenoid. Small scales (height <0·33 of height of largest body scales) on belly and anterior part of dorsum. Chest scales and scales on nuchal region very small (height <0·25 of height largest body scales), or absent. Small scales on operculum and cheek in some specimens (height *c.* 0·5 of height of largest body scales), absent in others. Very small scales on basis of dorsal and anal fins and also covering about three quarters of surface of caudal fin (height <0·25 of height of largest body scales) [Fig. 4(a), (b) and (c)]. When present, scales on dorsal and anal fin found on the interray membrane [Fig. 4(a), (c)]. Scales on caudal fin covering both fin rays and interray membrane at fin base (where scale rows are touching), small elongate scales on posterior part fin only covering interray membrane [Fig. 4(b)].

Colouration

Dark and light coloured individuals of *T. brachygnathus* were found syntopically. The base body colouration of pale live specimens is beige yellow. Nape, snout and cheek are darker brownish yellow, sometimes blotched. A small iridescent blue line runs along the upper edge of the upper lip, continues obliquely upwards from the edge of the maxilla below the eye and ends just beyond the orbit. Some scales on the body have a dark border, forming a dark reticulate pattern on the flanks. Some specimens have dark vertical bars on the dorsum and flanks. Dorsal fin pale beige, with small yellow spots on the soft dorsal membrane. Caudal fin similar to dorsal fin, with yellow trailing edge on the upper margin. Anal fin pale beige or greyish. Pelvic fins pale. Dark live

specimens have a similar but much darker colouration pattern. Dorsal and caudal fins dark brown, anal fin with a dark trailing edge; pelvic fins with dark leading edges.

Melanin pattern of preserved specimens similar to live specimens; the blue line on the head and the yellow pigmentation on the fins are absent.

Distribution

Telmatochromis brachygnathus is found in the southern and central parts of Lake Tanganyika. The northernmost localities where *T. brachygnathus* were collected are Kabimba, DRC, and Bulu Point, Tanzania (Fig. 5).

COMPARISON OF *TELMATOCHROMIS BRACHYGNATHUS* WITH *T. TEMPORALIS*

A first PCA was performed on the log-transformed measurements of all specimens examined of *Telmatochromis brachygnathus* ($n = 37$) and *T. temporalis*
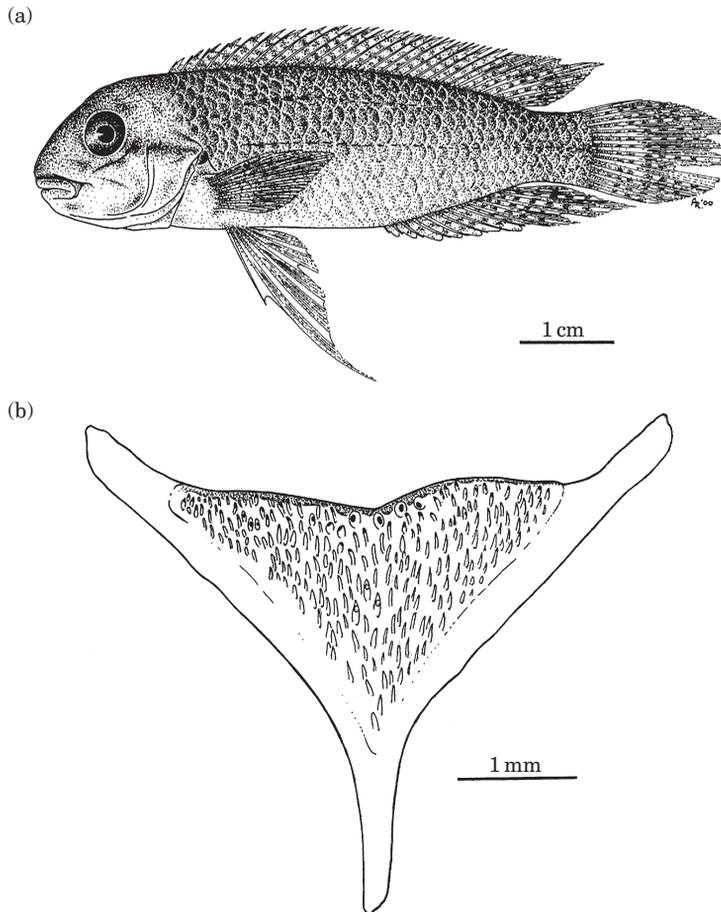
FIG. 3. *Telmatochromis brachygnathus* sp. nov. (holotype, 58·0 mm L_S, MRAC 78–25-P-720) (a) lateral view and (b) lower pharyngeal jaw.

($n = 60$). In a plot of the scores on the second and third principal component (Fig. 6) *Telmatochromis brachygnathus* and *T. temporalis* are well separated on PC 2. The loadings with the highest significance on PC 2 are (in order of significance): the lower jaw length, the lachrymal depth and the upper jaw length (Table III). PC 3 was mainly defined by (in order of importance): the caudal peduncle length and the lachrymal depth. Mann–Whitney U-tests were done on a selection of similar-sized [*T. brachygnathus* 54.9 ± 8.4 (42.0–76.0) mm L_S, $n = 37$; *T. temporalis* 55.8 ± 10.6 (40.5–78.5) mm L_S, $n = 54$; P $L_S = 1.00$] *T. brachygnathus* and *T. temporalis* and resulted in significant differences between the species for 17 out of the 25 relative measurements (percentages) (Table IV). Highly significant differences ($P < 0.001$) were found for head length percentage of L_S, head width percentage of L_H, lower jaw length percentage of L_H, upper jaw length percentage of L_H, lachrymal depth percentage of L_H, lower pharyngeal jaw length percentage of L_H, lower pharyngeal jaw width percentage of lower pharyngeal jaw length, prepectoral distance percentage of L_S, preventral distance percentage of L_S and caudal peduncle depth percentage of caudal peduncle length.

A PCA was carried out on 12 of the 16 meristics. The first principal component was defined by (in order of magnitude of loadings): the number of enlarged outer
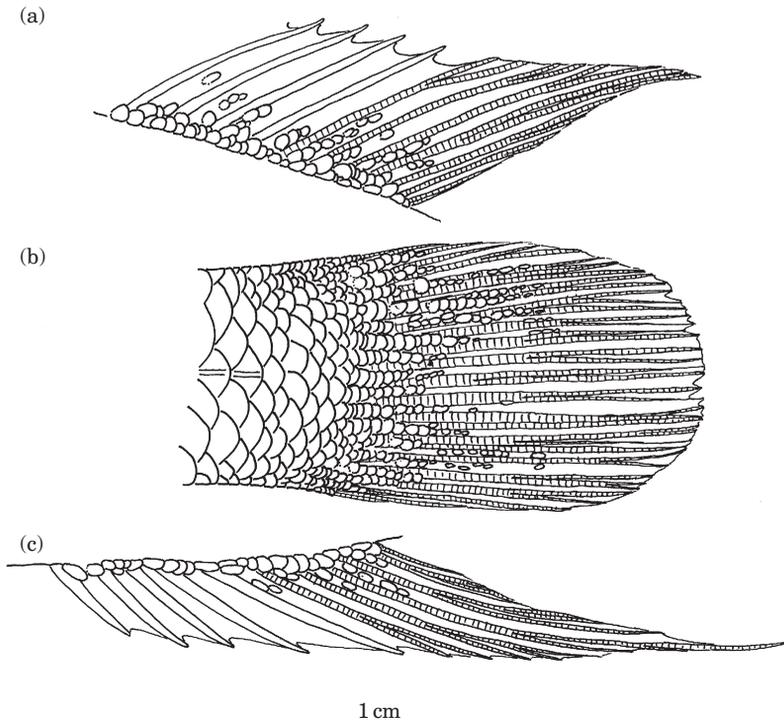
FIG. 4. *Telmatochromis brachygnathus* sp. nov. (66.5 mm L_S, from MRAC 92–81-P-968–971). Fin squamation of (a) dorsal (last four spines and soft dorsal illustrated), (b) caudal and (c) anal fins.
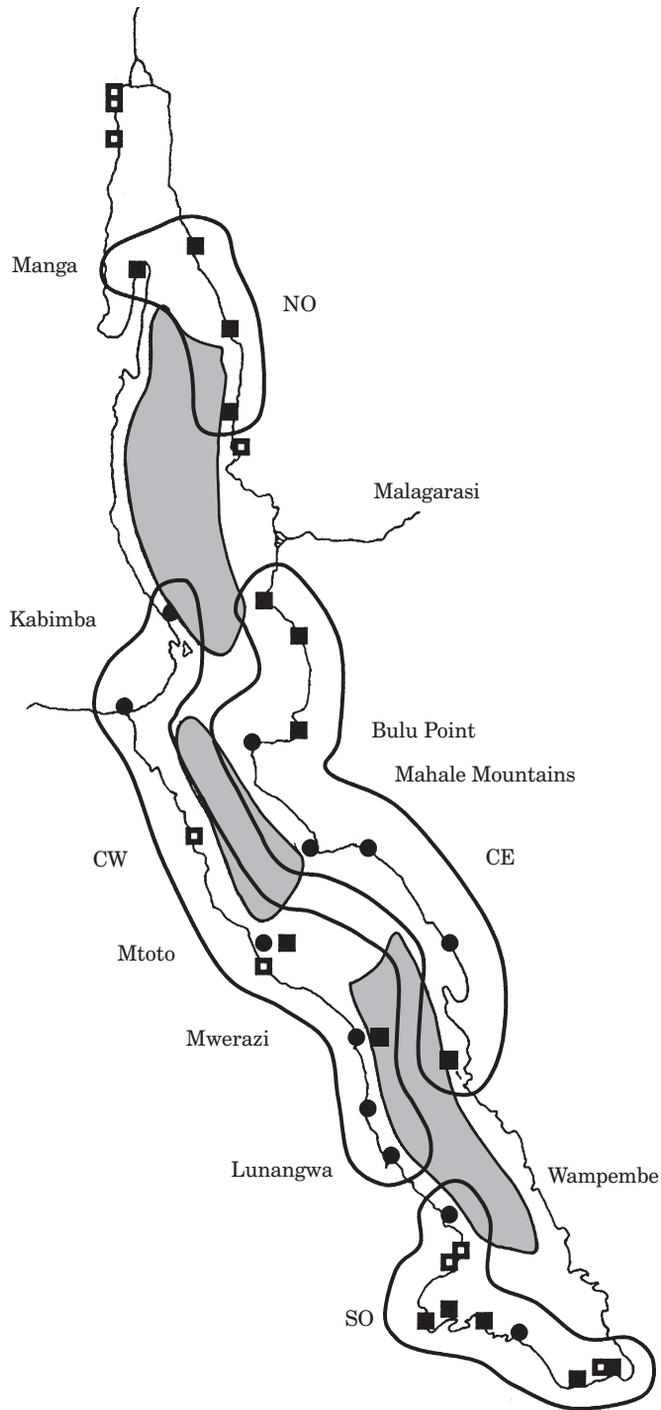
FIG. 5. Outline of Lake Tanganyika with the three former subbasins (▨) showing the distribution of *T. brachygnathus* (●) and *T. temporalis* (■, localities where specimens were measured and □, localities where specimens were identified). The four geographical regions distinguished in the geographical variation study are: NO, north; CE, central-east; CW, central-west; SO, south.
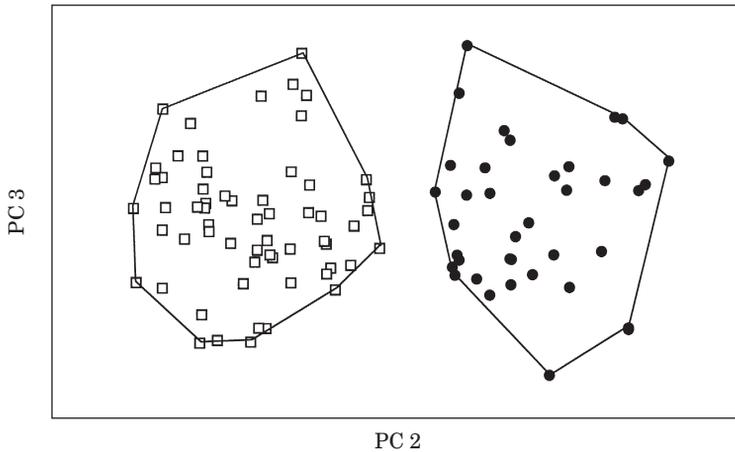
FIG. 6. Plot of the individual scores on PC 2 and PC 3 (log-transformed measurements of all specimens examined) for *T. brachygnathus* (●, $n = 37$) and *T. temporalis* (□, $n = 60$).

TABLE III. Loadings of the log-transformed measurements on the first three principal components of *T. brachygnathus* ($n = 37$) and *T. temporalis* ($n = 60$). The most significant loadings on PC 2 and PC 3 are shaded

	PC 1	PC 2	PC 3
Relative eigenvalue	0·9219	0·0342	0·0103
Standard length	0.1920	0·0187	−0·0187
Body depth	0·2112	−0·0034	0·0165
Head length	0.1886	−0·0026	−0·0042
Head width	0.1911	0·0204	−0·0078
Interorbital width	0·2708	0·0465	0·0255
Snout length	0·2477	0·0380	0·0007
Lower jaw length	0·2077	−0·1226	0·0027
Upper jaw length	0·2337	−0·0726	0·0033
Premaxillary pedicel length	0·2179	0·0176	−0·0150
Cheek depth	0·2745	−0·0008	0·0125
Eye diameter	0·1426	−0·0009	−0·0116
Lachrymal depth	0·2674	0·0830	0·0405
Pharyngeal jaw length	0.1991	−0·0427	0·0109
Pharyngeal jaw width	0.1766	−0·0159	−0·0007
Dentigerous area length	0.1884	−0·0437	0·0256
Dentigerous area width	0·1686	−0·0225	0·0033
Dorsal fin base length	0.1974	0·0317	−0·0163
Anal fin base length	0.1975	0·0143	0·0105
Predorsal distance	0.1857	0·0050	−0·0225
Preanal distance	0.1904	0·0174	−0·0155
Prepectoral distance	0.1906	−0·0148	−0·0014
Preventral distance	0.1944	−0·0109	0·0042
Caudal peduncle length	0·2062	0·0102	−0·0782
Caudal peduncle depth	0.1840	0·0069	0·0058

TABLE IV. Results (*P*-values) of the Mann–Whitney *U*-tests (measurements) on *T. brachygnathus* ($n = 37$) and *T. temporalis* ($n = 54$). NS, non significant

L_S	1·00
Body depth % L_S	<0·001
Head length (L_H) % L_S	<0·001
Head width (W_H) % L_H	<0·001
Interorbital width % L_H	<0·005
Interorbital width % W_H	NS
Snout length % L_H	<0·001
Lower jaw length % L_H	<0·001
Upper jaw length % L_H	<0·001
Premaxillary pedicel length % L_H	<0·005
Cheek depth % L_H	NS
Eye diameter % L_H	NS
Lachrymal depth % L_H	<0·001
Lower pharyngeal jaw length (L_{LP}) % L_H	<0·001
Lower pharyngeal jaw width (W_{LP}) % L_{LP}	<0·001
Dentigerous area length % L_{LP}	NS
Dentigerous area width (W_{DeA}) % W_{LP}	NS
Dentigerous area length % W_{DeA}	<0·005
Dorsal fin base length % L_S	<0·001
Anal fin base length % L_S	NS
Predorsal distance % L_S	<0·05
Preanal distance % L_S	NS
Prepectoral distance % L_S	<0·001
Preventral distance % L_S	<0·001
Caudal peduncle length (L_{CP}) % L_S	NS
Caudal peduncle depth % L_{CP}	NS

teeth in upper and lower jaw, the number of dorsal fin spines and the number of longitudinal line scales (Table V). The second principal component was mainly defined by the total number of outer teeth in the upper jaw and the number of gill rakers on the ceratobranchial. A plot of the scores of the first *v.* the second principal component showed a large overlap between the species. This overlap was mainly due to the fact that some counts such as enlarged and total outer tooth numbers in the oral jaws were correlated with size, and was greatly reduced by plotting PC 1 *v.* L_S (Fig. 7). Generally, the scores for *T. brachygnathus* on PC 1 were higher for a given L_S. Two small *T. brachygnathus* fell within the range of *T. temporalis*. This was due to their exceptional low number of enlarged outer teeth in the upper and lower oral jaw, for which they fell within the range of *T.temporalis* rather than the range of most *T. brachygnathus* (8 and 10 *v.* 12 or more enlarged teeth in upper jaw in other *T. brachygnathus*; 10 *v.* 11 or more enlarged teeth in lower jaw in other *T. brachygnathus*). In all other aspects, however, these two specimens clearly belonged to *T. brachygnathus*. Mann–Whitney *U*-tests on the meristics of the same size-selected specimens as for the analysis on the measurements resulted in highly significant differences between the species [*T. brachygnathus* $54·9 \pm 8·4$ (42·0–76·0) mm L_S, $n = 37$; *T. temporalis*

TABLE V. Loadings of the meristics on the first three principal components of *T. brachygnathus* ($n = 37$) and *T. temporalis* ($n = 60$). The most significant loadings on PC 1 and PC 2 are shaded

	PC 1	PC 2	PC 3
RelativeVariance	3·5967	2·5772	1·4327
Enlarged teeth in upper jaw	0·8897	0·2278	−0·1159
Enlarged teeth in lower jaw	0·8836	0·1359	−0·1311
Teeth in upper jaw	0·0725	0·7804	−0·1702
Inner tooth rows in upper jaw	0·2871	0·6733	0·5110
Inner tooth rows in lower jaw	0·3503	0·6425	0·5126
Gill rakers on ceratobranchial	−0·3198	0·6396	−0·3008
Gill rakers on epibranchial	−0·1612	0·2964	−0·6583
Dorsal fin spines	0·8286	−0·2937	−0·1592
Dorsal fin soft rays	−0·1728	0·4223	−0·2334
Anal fin spines	0·5498	−0·2462	−0·2622
Anal fin soft rays	−0·4391	0·4265	−0·2545
Pectoral fin rays	−0·0330	0·0894	0·2323
Scales in longitudinal line	0·6877	0·1404	−0·2409

$55 \cdot 8 \pm 10 \cdot 6$ $(40 \cdot 5 - 78 \cdot 5)$ mm L_S, $n = 54$; P $L_S = 1 \cdot 00$] for eight out of the 13 meristics examined (the same three meristics as for the PC analyses were excluded from these test as well). Highly significant differences ($P < 0 \cdot 001$) were found for the number of enlarged teeth in upper and lower oral jaw, the number of gill rakers on the ceratobranchial and the number of dorsal fin spines (Table VI).
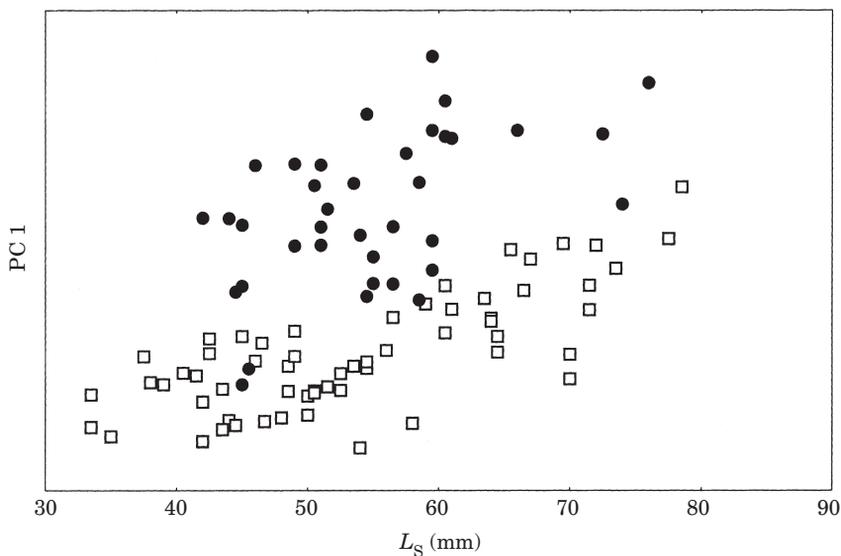
FIG. 7. Plot of the individual scores on PC 1 and standard length (meristics of all specimens examined) for *T. brachygnathus* (●, $n = 37$) and *T. temporalis* (□, $n = 60$).

TABLE VI. Results (*P*-values) of the Mann–Whitney *U*-tests (meristics) on *T. brachygnathus* ($n = 37$) and *T. temporalis* ($n = 54$). NS, non significant

L_S	1·00
Enlarged teeth in upper jaw	<0·001
Enlarged teeth in lower jaw	<0·001
Teeth in upper jaw	<0·001
Inner tooth rows in upper jaw	NS
Inner tooth rows in lower jaw	NS
Gill rakers on ceratobranchial	<0·001
Gill rakers on epibranchial	NS
Dorsal fin spines	<0·001
Dorsal fin soft rays	NS
Anal fin spines	<0·001
Anal fin soft rays	<0·05
Pectoral fin rays	NS
Scales in longitudinal line	<0·001

GEOGRAPHIC VARIATION

The analyses showed geographical variation in the morphology of both *T. brachygnathus* and *T. temporalis*. Based on preliminary analyses four geographical regions were delimited (Fig. 5). These regions were the north (NO, Burundi and the Tanzanian coast north of the Malagarasi on the north-east and Manga on the Ubwari Peninsula, Democratic Republic of Congo), the central-east (CE, Tanzanian coast south of the Malagarasi and north of Kipili), the central-west (CW, the Congolese coast from Kabimba to Lunangwa) and the south (SO, the Zambian Coast, including the extreme south of the Congolese shoreline). Since no specimens were measured from the three localities in the extreme north-east, these localities are not included in the north region. *Telmatochromis temporalis* is found in all four regions and *T. brachygnathus* is absent from the northern region.

A new plot of the scores on PC 2 and PC 3 from the PCA on the log-transformed measurements was made. In this plot, all specimens originating from one of the four geographical regions were marked with a polygon (Fig. 8). Within *T. brachygnathus* two clearly distinct groups were observed; the central populations overlapped but both were completely separated from the southern populations. In *T. temporalis* the pattern was less clear, but again both central populations were distinct from the southern population, with only a small overlap. The *T. temporalis* from the north overlapped with all other populations.

Separate PC analyses were made to further explore the geographical variation within each species, but did not reveal more detailed geographical patterns.

Intraspecific differences between the populations of both species were further examined and quantified using the Mann–Whitney *U*-tests (Tables VII and VIII). For each analysis a different subset of specimens was used with a similar average L_S. For the Mann–Whitney *U*-tests, both central populations were treated as a single population (CEW).
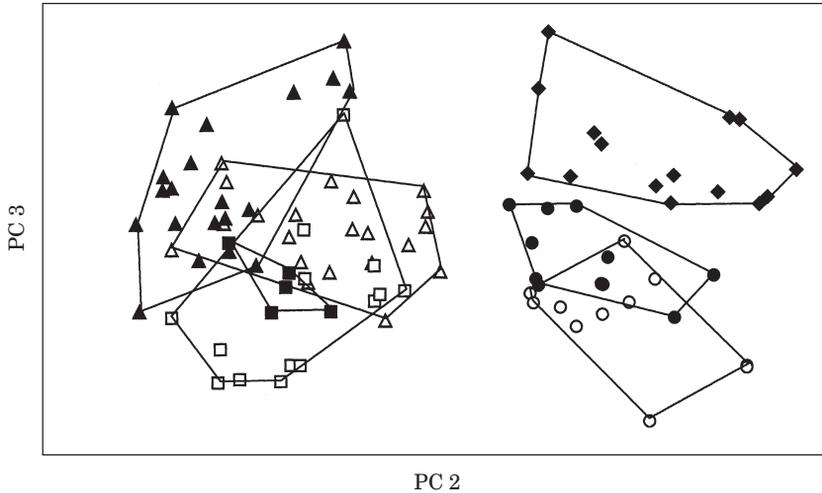
FIG. 8. Plot of the individual scores on PC 2 and PC 3 (log-transformed measurements of all specimens examined); polygons include the specimens originating from the four geographical regions: *T. brachygnathus* from the central-east ($\bigcirc$, $n = 12$), the central-west ($\bullet$, $n = 10$) and south ($\blacklozenge$, $n = 15$); *T. temporalis* from the north ($\triangle$, $n = 21$), central-east ($\square$, $n = 14$), central-west ($\blacksquare$, $n = 5$) and south ($\blacktriangle$, $n = 20$).

A comparison between the central and southern populations in *T. brachygnathus* showed significant differences for 11 relative measurements ($P < 0.05$), five of which were highly significant ($P < 0.005$), *i.e.* the anal fin base length, the caudal peduncle length, the body depth, the lachrymal depth and the preventral distance.

In *T. temporalis*, seven significant differences ($P < 0.05$) for the relative measurements were found in the comparison between populations NO and CEW. Comparison of the SO with the NO and CEW showed 10 and 11 significant differences, respectively. These results confirmed those of the PCA already discussed. For the relative measurements, the NO and CEW populations mainly differed in preanal distance and caudal peduncle depth. The SO differed from both other populations in head length, upper jaw length, anal fin base length, prepectoral distance and preventral distance.

PCA analyses on the meristics of *T. brachygnathus* and *T. temporalis* separately revealed no clear geographical patterns.

For the Mann–Whitney *U*-tests on the meristics the same subsets were used as for the analyses of the relative measurements. For the two populations of *T. brachygnathus* significant differences were found in only two of the 13 meristics analysed (Table VIII): the number of enlarged teeth in the upper oral jaw and the number of scales in longitudinal line. For *T. temporalis*, more significant differences between the populations were found in the meristics. The NO population differed from the CEW population in the number of enlarged teeth in upper and lower oral jaw, the number of gill rakers on the epibranchial and the number of dorsal fin spines. The SO population differed from the NO population in the number of gill rakers on the ceratobranchial and epibranchial ($P < 0.005$), the number of outer teeth in the upper oral jaw and the number of

TABLE VII. Results (*P*-values) of the Mann–Whitney *U*-tests (measurements) on the populations of *T. brachygnathus* and *T. temporalis*, respectively. NO, north; CEW, central-east-west; SO, south. NS, non significant

	T. brachygnathus	*T. temporalis*	*T. temporalis*	*T. temporalis*
	CEW *v.* SO $n=20$ *v.* $n=15$	NO *v.* CEW $n=20$ *v.* $n=19$	NO *v.* SO $n=15$ *v.* $n=15$	CEW *v.* SO $n=13$ *v.* $n=13$
L_S	1·00	0·89	0·80	0·76
Body depth % L_S	<0·005	<0·05	NS	<0·05
Head length (L_H)% L_S	<0·05	NS	<0·005	<0·001
Head width (W_H)% L_H	NS	NS	NS	NS
Interorbital width % L_H	<0·05	NS	NS	NS
Interorbital width % W_H	<0·05	NS	NS	NS
Snout length % L_H	NS	NS	NS	NS
Lower jaw length % L_H	NS	NS	NS	<0·005
Upper jaw length % L_H	NS	NS	<0·05	<0·05
Premaxillary pedicel length % L_H	NS	NS	NS	NS
Cheek depth % L_H	NS	NS	NS	NS
Eye diameter % L_H	NS	<0·05	<0·05	NS
Lachrymal depth % L_H	<0·05	NS	NS	NS
Lower pharyngeal jaw length (L_{LP}) % L_H	<0·05	<0·05	NS	<0·005
Lower pharyngeal jaw width (W_{LP}) % L_{LP}	NS	NS	NS	<0·05
Dentigerous area length % L_{LP}	NS	NS	NS	NS
Dentigerous area width (W_{DeA}) % W_{LP}	NS	NS	<0·05	NS
Dentigerous area length % W_{DeA}	NS	NS	NS	NS
Dorsal fin base length % L_S	<0·05	NS	<0·05	NS
Anal fin base length % L_S	<0·001	<0·05	<0·05	<0·005
Predorsal distance % L_S	<0·05	NS	<0·05	NS
Preanal distance % L_S	NS	<0·005	<0·005	NS
Prepectoral distance % L_S	NS	NS	<0·001	<0·001
Preventral distance % L_S	<0·05	NS	<0·005	<0·005
Caudal peduncle length (L_{CP})% L_S	<0·001	<0·05	NS	<0·05
Caudal peduncle depth % L_{CP}	NS	<0·005	NS	<0·05

TABLE VIII. Results (*P*-values) of the Mann–Whitney *U*-tests (meristics) on the populations of *T. brachygnathus* and *T. temporalis*, respectively. NO, north; CEW, central-east-west; SO, south. NS, non significant

	T. brachygnathus	*T. temporalis*	*T. temporalis*	*T. temporalis*
	CEW *v.* SO	NO *v.* CEW	NO *v.* SO	CEW *v.* SO
	$n=20$ *v.* $n=15$	$n=20$ *v.* $n=19$	$n=15$ *v.* $n=15$	$n=13$ *v.* $n=13$
L_S	1·00	0·89	0·80	0·76
Enlarged teeth in upper jaw	NS	<0·05	NS	<0·05
Enlarged teeth in lower jaw	<0·05	<0·05	NS	<0·05
Teeth in upper jaw	NS	NS	<0·05	NS
Inner tooth rows in upper jaw	NS	NS	NS	NS
Inner tooth rows in lower jaw	NS	NS	NS	NS
Gill rakers on ceratobranchial	NS	NS	<0·005	NS
Gill rakers on epibranchial	NS	<0·05	<0·001	<0·05
Dorsal fin spines	NS	<0·05	NS	<0·05
Dorsal fin soft rays	NS	NS	<0·05	NS
Anal fin spines	NS	NS	NS	<0·05
Anal fin soft rays	NS	NS	NS	NS
Pectoral fin rays	NS	NS	NS	NS
Scales in longitudinal line	<0·05	NS	NS	NS

soft dorsal fin rays. Comparison of the SO with the CEW population showed significant differences for the number of enlarged teeth in upper and lower oral jaw, the number of gill rakers on the epibranchial and the number of dorsal and anal fin spines.

DISCUSSION

Two major groups can be distinguished within the genus *Telmatochromis*. The first group contains very elongate species with dark longitudinal bands, and includes *T. vittatus*, *T. bifrenatus* and *T. brichardi*. The second group consists of deeper-bodied species without or with very faint longitudinal bands. Several species have been described in this group, but only three species are considered to be valid: *T. dhonti* (junior synonyms: *T. caninus* and *Julidochromis macrolepis*), *T. temporalis* (junior synonyms: *T. lestradei* and *T. burgeoni*) and *T. brachygnathus*. The latter is morphologically most similar to *T. temporalis*. Both are informally included in what is called the *T. temporalis* complex. Several *T. brachygnathus* specimens were registered in the MRAC collections as *T. temporalis*. *Telmatochromis brachygnathus* can, however, be easily distinguished

from *T. temporalis* by its smaller mouth and shorter jaws. The difference in mouth size between *T. brachygnathus* and *T. temporalis* is illustrated in Fig. 2. Both the relative (as percentage of L_H) upper and lower jaw lengths are positively allometric. As a consequence, there is a large overlap between the percentages for both species, but within any given length class overlap is very small or non-existent. A meristic character that was found to be significantly different between both species (in the PCA and Mann–Whitney *U*-test) was the number of enlarged outer teeth in both oral jaws. But for mouth size, this character varies with size. A plot of the number of enlarged outer teeth in upper and lower oral jaw showed that, on average, *T. brachygnathus* had a higher number of enlarged teeth than *T. temporalis*, but there was considerable overlap between both (unpubl. data). Due to the large overlap (overall and within any given length class), this character was not suitable in the diagnosis.

A new species reported by Tawil (1988) to be closely related to *T. temporalis*, seems not to correspond to *T. brachygnathus*. Tawil (1988) found this species to be smaller and deeper bodied and with a larger mouth than *T. temporalis*, which contrasts with the data for *T. brachygnathus*. Sato & Gashagaza (1997) reported an unidentified *Telmatochromis* species, closely related to *T. temporalis*, and also a facultative shell brooder. A specimen from Wonzye, Zambia, was illustrated, and possibly corresponds to *T. brachygnathus*. Sato & Gashagaza (1997) recorded this species also in Rumonge, Burundi. *Telmatochromis brachygnathus*, however, has not yet been found in the northern part of the lake.

Telmatochromis sp. 'temporalis tanzania' reported by Konings (1998) is most probably conspecific with *T. brachygnathus*. The distribution area he reported for this species falls within the range of *T. brachygnathus*.

No ecological data are available yet for *T. brachygnathus*, but its close morphological resemblance to *T. temporalis* indicates similarities in the ecology of these species. *Telmatochromis temporalis* is reported to be an algal feeder; the major part of its diet consists of filamentous algae, with some unicellular and microfilamentous algae as well (Hori, 1997; Konings, 1998). This feeding behaviour is remarkable within the *tribus* of the lamprologini, most species of which are reported to be carnivorous, with the exception of *T. temporalis* and *Variabilichromis moorii* (Boulenger) which feed on filamentous algae (Yamoaka, 1997).

Dark and light-coloured specimens of *T. brachygnathus* were found. This dichromatism, however, is not geographically arrayed. Both forms occurred syntopically. Such dichromatism was also found in *T. temporalis*. According to Mboko & Kohda (1995) this dichromatism may function as antipredator camouflage. Pale specimens defended territories on top of the rocks, in well-illuminated areas, while dark specimens were found in territories in shaded areas on lateral sides of the rocks. This dichromatism is not genetically determined, since specimens can change colour over a few weeks when transferred to different light conditions (Mboko & Kohda, 1995).

DISTRIBUTION

Whilst *T. temporalis* has a circumlacustrine distribution, *T. brachygnathus* seems to be confined to the southern and central parts of the lake (Fig. 5).

Konings (1998) reported *T.* sp. 'temporalis tanzania' (= *T. brachygnathus*) from a small part of the south-central Tanzanian lakeshore between Wampembe and the Mahale Mountains. *Telmatochomis brachygnathus* was also found in this region during the present study. Konings (1998) further assumed that *T. brachygnathus* had taken the place of *T. temporalis* in this area. Since *T. temporalis* and *T. brachygnathus* have been found in sympatry at two localities (Mtoto and Mwerazi, DRC), the presence of one species does not seem to exclude the presence of the other.

GEOGRAPHIC VARIATION

Geographic colour variation in the Tanganyikan cichlid fishes has been extensively documented, both in the scientific and in the aquarist literature (Kohda *et al*., 1996; Konings, 1998). Geographic colour variation occurs in most of the major lineages of the Tanganyikan cichlids (*e.g. Julidochromis, Neolamprologus, Altolamprologus, Ophthalmotilapia, Cyathopharynx, Tropheus, Cyprichromis, Petrochromis, Eretmodus* and *Tanganicodus*), and is documented for species with or without sexual dichromatism (Kohda *et al*., 1996). In contrast, geographical variability in morphology has hardly been documented. Poll (1956) reported several morphologically distinct subspecies, mostly with a complementary north *v*. south distribution. All but two of these subspecies were originally described as different species and all have gained specific status afterwards. Geographical races in *Neolamprologus savoryi* and *N. brichardi* were documented by Louage (1996). An overview of the variability of some meristic characters in several *Tropheus* species was given by Snoeks *et al*. (1994).

Based on the analyses of measurements, *T. brachygnathus* and *T. temporalis* populations from the south were clearly distinct from the central and northern populations (the latter only in *T. temporalis*). The distinctness of the southern population in *T. temporalis* was confirmed by the analysis of the meristics. Interestingly, in *T. temporalis*, the differences observed between the most distant populations (north and south) were found to be smaller than between the central and southern populations.

For the African Great Lakes, and in particular for Lake Tanganyika, several factors have been suggested to explain the isolation of populations, which eventually would lead to speciation. The most important extrinsic factors are the disjunct shoreline habitat, where substratum barriers restrict dispersal of stenotopic and philopatric species, and the subdivision of the lake during low water levels (Coulter, 1994). These low water levels at *c*. 600 m below the present level created three separate sub-basins at *c*. 200 000 years before present (Tiercelin & Mondeguer, 1991). Subsequent, more recent low lake stands have been reported (Cohen *et al*., 1997), but were not extreme enough to cause another split into three separate basins.

Though the split in sub-basins may partially explain the geographical variation found, the distributions of the populations of *T. brachygnathus* and *T. temporalis* did not appear to correspond very well with the position of these sub-basins (Fig. 5). The split in sub-basins can be considered as the foundation upon which other phenomena have acted resulting in the present-day distributions of species (Snoeks, 2000).

The distribution of the two opposite central populations in both species overlapped with the former central and southern sub-basins. The similarity between the opposite central populations probably resulted from their former presence in a single, smaller basin in which genetic exchange between populations from opposite shorelines was less restricted by geographical distance. Interestingly, the distribution of *T. brachygnathus* extended to the north only to the level of the Kalemie-Mahali shoal (Tiercelin & Mondeguer, 1991) which may have been, in times of low levels, the split between the northern and southern part of the lake. The situation was somewhat different for *T. temporalis*, for which the Malagarasi delta appears to have acted as a barrier separating the northern and central eastern populations. Both species had distinct populations in the southern part of the lake. This may well have been due to the recent colonization of that part of the lake after the lake rose to its present level. Such distinct taxa have been documented for other genera as well (Konings, 1998; pers. obs.).

Stenotopy and philopatry may be important intrinsic factors as *T. temporalis* is reported to be restricted to rocks (or shell-beds when those are present). Hence, there may be a certain degree of genetic isolation of its populations on these isolated stretches of suitable habitat.

Another intrinsic factor, female mate choice based on male colouration (Ribbink, 1994; Turner, 1994), may have enhanced isolation between populations. The data presented here do not provide evidence for further discussion of its importance. A key role for female mate choice, however, is difficult to envisage, since neither species is sexually dimorphic and no geographical colour races are known.

KEY TO THE *TELMATOCHROMIS* SPECIES

Data for *T. bifrenatus*, *T. brichardi* and *T. vittatus* from Poll (1956) and Louisy (1989).

1a Distinct dark longitudinal bands present on body·······················2
1b No dark longitudinal bands present ·······························4
2a Three longitudinal bands ·····························*T. bifrenatus*
2b Two longitudinal bands·································3
3a Body depth 19·0–22·1% of L_S, head length 26·7–30·4% of L_S, enlarged outer oral teeth 7–8/5–6·····························*T. brichardi*
3b Body depth 22·0–23·6% of L_S, head length 25·4–26·1% of L_S, enlarged outer oral teeth 10–13/10–13·····························*T. vittatus*
4a Number of enlarged outer oral teeth invariable with size, 4–6 (exceptionally 8) in both jaws, clear size transition between enlarged anterior outer teeth and lateral outer teeth, anterior outer teeth circular in cross section, with recurved tips, 18–20 dorsal fin spines·····························*T. dhonti*
4b Number of enlarged outer oral teeth increases with size, 6–18 in upper jaw, 6–20 in lower jaw, size transition between anterior outer teeth and lateral outer teeth much smaller, anterior outer teeth more flattened in cross section, with straight tips, 19–23 dorsal spines·····························5

5a Upper jaw length 29·8–40·5% of L_H, lower jaw length 31·8–41·6% of L_H· ·*T. temporalis*
5b Upper jaw length 26·3–32·9% of L_H, lower jaw length 24·7–33·9% of L_H· ·...·*T. brachygnathus*

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APPENDIX

Other specimens of *Telmatochromis temporalis* examined. (The number of specimens fully examined is given in parentheses, when relevant.)

BMNH 1898·9·9 : 21, Mbity Rocks, Zambia, J.E.S. Moore, lectotype of *T. temporalis*.; BMNH 1898·9·9 : 22-23, Kinyamkolo, Zambia, J.E.S. Moore, paralectotypes of *T. temporalis*.; MRAC 38882, Nyanza, Burundi, L. Burgeon, 31 December 1932, holotype of *T. burgeoni*.; MRAC 38994-995 (1), same data, 03 January 1933.; MRAC 45840, Rumonge, Burundi, A. Lestrade, 1935.; MRAC 54656; 54686-54692 (3), Nyanza, Burundi, A. Lestrade, 1937, paratypes of *T. lestradei*.; MRAC 54660, same data, holotype of *T. lestradei*.; MRAC 54634-640 (2); 54673-685 (7), same data.; MRAC 112748, Stat. 10, Au large de la baie de Kungwe, à 500 m de la côte, Explor. Hydrobiol. L. Tang., 10 November 1946.; MRAC 112755-759 (2), Stat. 108, Mtoto, dans la baie, DRC, Explor. Hydrobiol. L. Tang., 05 February 1947.; MRAC 112762, Stat. 176, Baie de Mtoto, rochers au Nord, DRC, Explor. Hydrobiol. L. Tang., 15 March 1947.; MRAC 112766-769 (2), Stat. 202, Mpulungu; Explor. Hydrobiol. L. Tang., 27 March 1947.; MRAC 112775, Stat. 249, Manga, plage et rive rocheuse, DRC, Explor. Hydrobiol. L. Tang., 17 April 1947.; MRAC 112781-782, Stat. 319, Mwerazi; Explor. Hydrobiol. L. Tang., 28 May 1947.; MRAC 125738-125740 (2), Route Nyanza lac, Burundi; H. Matthes, I.R.S.A.C., 18 December 1958.; MRAC 189751-778 (5), Mpulungu, Jetty, Zambia, H. Matthes, 18 February 1966.; MRAC 189779-793 (2), same data, 14 February 1966.; MRAC 74-4-P-325-326, Sud du Lac Tanganyika, Cap Kabeyeye, Zambia, P. Brichard, 17 January 1976.; MRAC 76-4-P-180, Sud du Lac Tanganyika, Cap Nundo, Zambia, P. Brichard, 06 January 1976.; MRAC 76-4-P-517-523 (2), same data.; MRAC 76-28-P-129-145 (3), Sumbu (Kamba Bay), Sud du Lac Tanganyika, Zambia, P. Brichard, 11 May 1976.; MRAC 92-81-P-16, Locality 1, Mwamungongo, just north of Gombe National Park, Tanzania, Tanganyika Expedition '92, 24 May 1992.; MRAC 92-81-P-1078-1079; 1082; 1116; 1120; Locality 40, South of Mkuyu Point, Tanzania, Tanganyika Expedition '92, 01 June 1992.; MRAC 92-81-P-1138-1141, Locality 41, Segunga, south of Segunga Bay, Tanzania, Tanganyika Expedition '92, 01 June 1992.; MRAC 92-81-P-1186, Locality 43, Kalela, Tanzania, Tanganyika Expedition '92, 02 June 1992.; MRAC 92-81-P-1388-1390, Locality 4b, Ulwile Island, northern shore, Tanzania, Tanganyika Expedition '92, 27 May 1992.