



REGULAR PAPERS

A revised synonymy of *Telmatochromis temporalis* (Teleostei, Cichlidae) from Lake Tanganyika (East Africa)

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The taxonomic status of the nominal species *Telmatochromis temporalis*, *T. lestradei*, *T. burgeoni* and *Julidochromis macrolepis* has been reviewed. The synonymy of *T. lestradei* with *T. temporalis* is confirmed. A comparison of *Telmatochromis burgeoni* with *Telmatochromis temporalis* revealed no significant differences either. Hence *T. burgeoni* is considered synonymous with *T. temporalis*. Examination of the type of *Julidochromis macrolepis* showed it to be conspecific with *Telmatochromis dhonti* and not with *T. temporalis*, as had been suggested.

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Key words: *Telmatochromis*; Lake Tanganyika; cichlids; synonymy; taxonomy.

INTRODUCTION

The systematics of the cichlids of the East African Lakes are very complicated and at present taxonomic knowledge is still poor (Fryer & Iles, 1972; Coulter *et al.*, 1986; Greenwood, 1991; Rossiter, 1995; Snoeks, 2000). Even for the relatively well-known Lake Tanganyika, taxa with a supposedly stable taxonomy turn out to be problematic when a revision is made (Verheyen *et al.*, 1996; Hanssens *et al.*, 1999; Rüber *et al.*, 1999). As a result of an ongoing study on the taxonomy and distribution patterns of the lamprologine cichlids from Lake Tanganyika (Snoeks *et al.*, 1994) several problems were encountered within the genus *Telmatochromis* Boulenger, 1898. This contribution tries to clear the confused status of the nominal species *Telmatochromis burgeoni* Poll, 1942 and *Julidochromis macrolepis* Borodin, 1931 and examine the proposed synonymy of *Telmatochromis lestradei* Poll, 1942 with *Telmatochromis temporalis*.

Boulenger (1898a) described the genus *Telmatochromis* including two new species, *Telmatochromis vittatus* and *T. temporalis*, from Lake Tanganyika. First he published a synopsis (Boulenger, 1898a), followed by a more elaborate description (Boulenger, 1898b). He regarded the genus as closely related to *Lamprologus* Schilthuis, 1891, but different by the presence of tricuspid instead of conical teeth in the inner oral tooth rows. *Telmatochromis temporalis* was described from four specimens, three of which originated from Kinyamkolo (=Niamkolo, a village close to Mpulungu) and one from Mbitiy Rocks

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(=Mbete), both localities in the extreme south of Lake Tanganyika, in Zambia. The first short description of *T. temporalis* (Boulenger, 1898a) was not illustrated. An illustration of this species, its skeleton and oral dentition was given with the elaborate description (Boulenger, 1898b). Later *Telmatochromis temporalis* was designated type species of the genus *Telmatochromis* by Regan (1920).

Boulenger (1919) described *Lamprologus dhonti* which he placed between *Lamprologus mocquardi* Pellegrin, 1903 and *Lamprologus tretocephalus* (Boulenger, 1899) thereby ignoring the partial tricuspid dentition in the inner rows, which would have made the species a possible candidate for inclusion in the genus *Telmatochromis*.

Borodin (1931) described *J. macrolepis* from one specimen from Ujiji, Lake Tanganyika. Regan (1932) included this species in the genus *Lamprologus*. It was later synonymized with *T. temporalis* by Trewavas (1946).

Poll (1942) described three new species within the genus *Telmatochromis*, *T. caninus*, *T. lestradei* and *T. burgeoni*. The type locality of all three new species is 'Nyanza, lac Tanganika' (=Nyanza-Lac), on the north-eastern shore of the lake in Burundi. Poll (1942) differentiated *T. caninus* from *T. temporalis* by the morphology of the posterior inner oral teeth (unicuspid v. tricuspid in *T. temporalis*), the number of external teeth in the upper jaw (40–48 v. 32–38) and the number of gill-rakers on the first branchial arch (5–6 v. 3–4). *Telmatochromis lestradei* was described from 13 specimens, varying from 53 to 92 mm L_T . Poll included nine of these 13 specimens in the type series. He considered *T. lestradei* to be closely related to *T. temporalis*, but distinguished by the higher number of teeth in the outer row of the upper jaw (42–56 v. 32–38 in *T. temporalis*), and the number of gill rakers (3–6, generally 4 v. 3, exceptionally 4). Poll (1956) synonymized *T. lestradei* with *T. temporalis*, since he found the former nominal species to be insufficiently defined. Poll's third new species (Poll, 1942), *T. burgeoni*, was described on the basis of a single specimen of 51.0 mm L_T (42.0 mm L_S) and had been identified formerly as *T. temporalis* (David, 1936; David & Poll, 1937). Poll (1942) mentioned two features characterizing this species, namely the low number of enlarged teeth in the outer row on the oral jaws (6/6), and the presence of two small dark lateral bands, similar to those found in *T. vittatus*. In 1946, Poll added a drawing of the specimen and its lower pharyngeal jaw to the description. In his key, Poll (1946) recognized two groups within the genus *Telmatochromis*: one without black longitudinal bands, containing *T. caninus*, *T. temporalis* and *T. lestradei*, the other characterized by the presence of two dark longitudinal dark bands, including *T. vittatus*, *Telmatochromis bifrenatus* Myers, 1936 and *T. burgeoni*. *Telmatochromis burgeoni* was distinguished from both species by a deeper body, by the low number of enlarged teeth in the oral jaws (6/6 in *T. burgeoni* v. 8–10/8–10 in *T. bifrenatus* and 12–16/12–16 in *T. vittatus*) and by the number of dorsal spines (20 in *T. burgeoni*, 21–22 in *T. bifrenatus* and *T. vittatus*). Later, Poll (1956) grouped *T. vittatus* and *T. bifrenatus* together based on their elongate body shape and relatively short head. *Telmatochromis temporalis* and *T. burgeoni* were grouped together as relatively deep-bodied species with all teeth in the inner rows tricuspid. *T. burgeoni* was differentiated from *T. temporalis* by its small standard length, by the presence of two longitudinal dark bands and by

the difference in the number of canines in the anterior part of the outer row of the oral jaws (6/6 in the sole specimen of *T. burgeoni* v. 7–20/7–21 in *T. temporalis*). However, it should be noted that in the same publication (Poll, 1956) the lowest value observed for the number of canines in the upper jaw in *T. temporalis* is six. This number is not mentioned in the key, nor in the main text.

In his review of the classification of Tanganyika cichlids, Poll (1986) again compared *T. burgeoni* with *T. vittatus*, *T. bifrenatus* and *T. temporalis*, distinguishing it by its deeper body and the place and the shape of the dorsalmost lateral band. He also synonymized *T. caninus* with *T. dhonti*.

Louisy (1989) recognized two groups within *Telmatochromis*. The first was formed by deep-bodied species (body depth 3.0–3.8 times in L_S) and a uniform colour pattern except for the presence of a postocular dark band. This group contained *T. temporalis*, *T. dhonti* and *T. burgeoni*. The second group comprised three species, all with an elongate body (body depth 4.2–5.7 times L_S) and possessing dark longitudinal bands which are prolonged between the eyes and on top of the head. The species in this group are *T. vittatus*, *T. bifrenatus* and *Telmatochromis brichardi* Louisy, 1989. In contrast to Poll (1986), Louisy did not consider *T. burgeoni* as a striped species, but its body proportions and colour pattern related it to *T. temporalis* and *T. dhonti*. Neither lateral bands on the type specimen was marked clearly and could be visible only temporarily on live specimens (a pattern comparable to *T. temporalis*) and there was no pigmentation between the eyes or on top of the head (Louisy, 1989).

Sturmbauer *et al.* (1994) established the mitochondrial phylogeny of the Lamprologini. Their results show two distinct lineages within the genus *Telmatochromis*. The final strict consensus tree (based on parsimony and neighbour-joining analyses) show that *T. bifrenatus* and *T. vittatus* cluster together and are found on a major branch together with some *Lamprologus* and *Julidochromis* species, while *T. burgeoni* is found on a separate branch together with *Neolamprologus christyi* (Trewavas & Poll, 1952). These results appear to confirm the split between the elongated striped and the deeper-bodied groups made by Poll (1956) and Louisy (1989).

Tawil (1988) mentioned two undescribed species within the genus *Telmatochromis*. He described one of them as a species closely related to *T. temporalis*, but smaller and deeper bodied. Seen from the front, this species has a larger head and its mouth opens more widely. It seeks empty shells for shelter and as nesting sites, as some *Neolamprologus* do. According to Tawil (1988), this behaviour seems to be related to its smaller size. He stated that this species is commonly named *T. burgeoni*, but is not conspecific. Poll (1942) described *T. burgeoni* as an elongate, light coloured species with clear horizontal stripes, while this shell-dwelling species is more deep bodied and dark coloured and the longitudinal bands show a reticulate pattern, similar to *T. temporalis* (Tawil, 1988).

Also, in the other aquarium literature the confusion around *T. burgeoni* is considerable. Konings (1988) reported *T. burgeoni* from the southern part of the lake, but stated that this species may have formed populations elsewhere. This is remarkable in view that the only preserved specimen was caught at Nyanza-Lac (type locality) in the north-eastern part of the lake.

Brichard (1989) claimed to have caught *T. burgeoni* only once, and in contrast to Konings (1988), he found this species to be the most colourful of the three dwarf species (*T. bifrenatus*, *T. vittatus* and *T. burgeoni*). According to him, from a distance it looks much like *Julidochromis ornatus* Boulenger 1898. These statements cast some doubts as to whether he really observed *T. burgeoni*. He reported that this species was absent from the northern and southern shores and indicated for the distribution of *T. burgeoni* 'Central West'. Since he claimed to have caught this species only once, it is not clear from what data he reported the distribution. This species was found at depths up to 20 m, usually at 5–10 m. His key for *Telmatochromis* followed that of Poll (1956). Hermann (1990) reported *T. burgeoni* as a species closely related to *T. temporalis* and *T. caninus*. Following his description, *T. burgeoni* bears seven to eight vertical dark lines on its flanks (which are also mentioned in the original description by Poll, 1942). This author does not add any data on ecology or behaviour, and suggested a possible synonymy between *T. burgeoni* and *Lamprologus dhonti*.

Konings (1998) reported that a small form of *T. temporalis* was very common on shell beds. This species is exported for the aquarium trade as *T. burgeoni*, but Konings stated that it is not yet clear if *T. burgeoni* should be regarded as a different species or just as a variant of *T. temporalis*. Temporarily, he regarded *T. burgeoni* as a synonym of *T. temporalis*, and the smaller shell-dwelling *T. temporalis* as a dwarf form of *T. temporalis*.

MATERIALS AND METHODS

For this study, the following specimens were examined fully: three of the four syntypes and 50 other specimens of *T. temporalis*, the holotype of *T. burgeoni*, the holotype and four paratypes ('cotypes' in Poll, 1942) of *T. lestradei* and the *J. macrolepis* holotype. In addition, meristics were taken on one of the remaining paratypes of *T. lestradei*. For comparative purposes meristics were taken on the types and 18 additional specimens of *T. dhonti* as well. Only three of the original four syntypes were examined. It is suspected that the skeleton illustrated by Boulenger (1898b) corresponds to the fourth type reported by Boulenger in the original description. The skeleton is currently registered in the Natural History Museum, London with catalogue number BMNH 1898.9.9:62 (J. Maclaine, pers. comm.).

To avoid confusion in further studies, the largest specimen of the four syntypes (BMNH 1898.9.9:22, 70.0 mm L_S) is designated as the lectotype of *T. temporalis*, the other three [BMNH 1898.9.9:23 (49.0 mm L_S), BMNH 1898.9.9:21 (64.5 mm L_S) and BMNH 1898.9.9:62 (67.0 mm L_S)] as paralectotypes. This follows recommendation 74B in the international code of zoological nomenclature (International Commission on Zoological Nomenclature, 1999). The lectotype corresponds to the specimen illustrated by Boulenger (1898b).

For the analyses 24 metric and 14 meristic characters were used, all as defined by Snoeks (1994), except for the upper jaw length and the number of enlarged outer teeth in the oral jaws. The upper jaw length is here defined as the distance between the most rostral point of the premaxilla to the posterior border of the maxilla. The enlarged outer teeth are defined as the anterior series of enlarged outer teeth in the oral jaws. They comprise an anterior series of large, unicuspid or shouldered teeth, different from the smaller posterior teeth, which are clearly tricuspid. In most cases a clear transition between both types of teeth can be observed. The following measurements were taken: standard length (L_S), body depth, head length (L_H) head width, interorbital width, snout length, lower jaw length, upper jaw length, premaxillary pedicel length, cheek depth, eye diameter, lachrymal depth, lower pharyngeal length (L_{LP}), lower pharyngeal width,

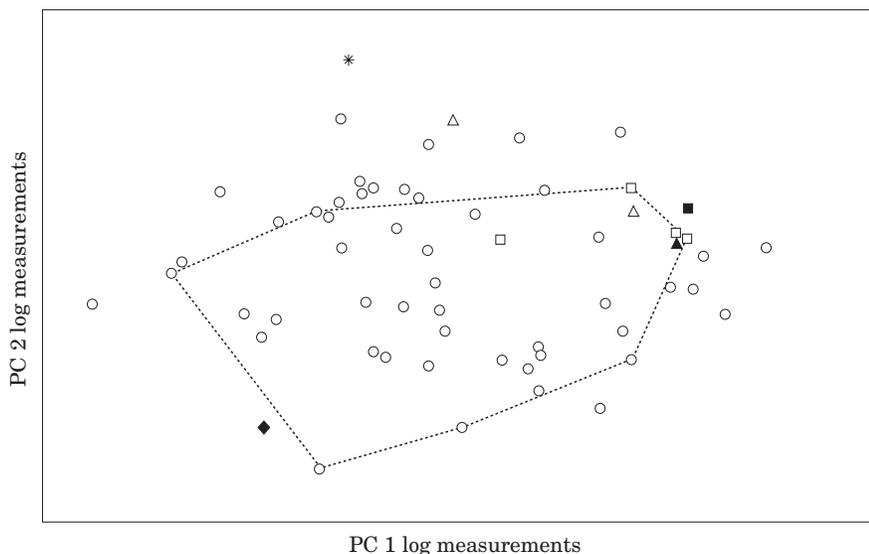


FIG. 1. Plot of the individual scores on PC 1 and PC 2 (log-transformed measurements of all specimens examined). ▲, *T. temporalis* lectotype; △, *T. temporalis* paralectotype; ○, *T. temporalis*; ■, *T. lestradei* holotype; □, *T. lestradei* paratype; ◆, *T. burgeoni* holotype; *, *J. macrolepis* holotype. The *T. temporalis* specimens from the north-eastern population are marked with a polygon.

dentigerous area length, dentigerous area width, dorsal fin base length, anal fin base length, predorsal distance, preanal distance, prepectoral distance, prepelvic distance, caudal peduncle length and caudal peduncle depth. Meristics included: outer teeth in upper and lower oral jaw, enlarged outer teeth in upper and lower oral jaw, inner tooth rows in upper and lower oral jaw, gill rakers, dorsal fin formula, anal fin formula, pectoral fin formula, longitudinal line scales, upper lateral line scales, transversal line scales and scales around the caudal peduncle.

Data were explored using principal components analysis (PCA) on the log-transformed measurements and the raw meristics. All fully examined specimens (see above) were included in the data analyses. To analyse the log-transformed measurements the covariance matrix was used to calculate the factor loadings and scores. This method allows a size-free comparison of the specimens, when the first factor, which accounts mainly for size, is discarded (Humphries *et al.*, 1981; Bookstein *et al.*, 1985).

RESULTS

First the data were explored using principal components analysis (PCA) on the log-transformed measurements and the scores were plotted on the first and second principal components (Fig. 1). As stated above, the first principal component (PC 1) from the analysis of the log-transformed measurements was strongly correlated with standard length and accounted for size. This plot shows that therefore the differences noted on the second principal component were not correlated with size or due to allometry. The second component was defined mainly by the dentigerous area length of the lower pharyngeal bone followed by (in order of importance) the caudal peduncle depth, the lower jaw length, the dentigerous area width and the dorsal fin base length (Table 1). The holotype of *J. macrolepis* was outside the range of the cluster containing the *T. temporalis* specimens, the types of *T. lestradei* and the *T. burgeoni* holotype (Fig. 1).

TABLE I. Loadings of the log-transformed measurements on the first three principal components

Log character	PC 1	PC 2	PC 3
Standard length	0.2148	-0.0187	0.0104
Body depth	0.2355	-0.0138	-0.0058
Head length	0.2101	0.0008	0.0044
Head width	0.2143	-0.0065	0.0032
Interorbital width	0.2929	-0.0135	- 0.0222
Snout length	0.2724	-0.0048	-0.0053
Lower jaw length	0.2272	0.0328	0.0071
Upper jaw length	0.2599	0.0288	0.0142
Premaxillary pedicel length	0.2420	-0.0131	0.0076
Cheek depth	0.2986	-0.0222	- 0.0265
Eye diameter	0.1604	0.0173	0.0200
Lachrymal depth	0.2899	0.0007	- 0.0636
Pharyngeal jaw length	0.2258	0.0278	0.0020
Pharyngeal jaw width	0.1985	0.0048	0.0057
Dentigerous area length	0.2120	0.0615	0.0043
Dentigerous area width	0.1841	0.0311	0.0128
Dorsal fin base length	0.2213	- 0.0301	0.0051
Anal fin base length	0.2168	0.0006	-0.0042
Predorsal distance	0.2119	-0.0115	0.0125
Preanal distance	0.2132	-0.0205	0.0068
Prepectoral distance	0.2120	0.0121	0.0077
Preventral distance	0.2010	0.0194	0.0113
Caudal peduncle length	0.2341	- 0.0468	0.0543
Caudal peduncle depth	0.2025	-0.0135	-0.0138

Analysis of *T. temporalis* ($n=53$, including three of the four types), the holotype of *T. burgeoni*, the holotype and four paratypes of *T. lestradei* and the holotype of *J. macrolepis*. The most important loadings are in bold.

Telmatochromis burgeoni was situated in the lower region of the negative part of the second axis, but inside the range of *T. temporalis*. Further confirmation was obtained by comparing the position of the *T. burgeoni* type (from Nyanza Lac) with all other specimens of the north-western part of the lake, north of the Malagarasi (Fig. 1, dotted polygon) and its score on the second axis fell within the range of the north-western region. Conversely, the separation of the *J. macrolepis* holotype, which was collected at Ujiji within the same geographic area, became even more obvious than in a comparison with all specimens.

A second principal component analysis was performed on all meristics except those for which only a limited number of observations was available (the number of outer teeth in lower oral jaw, upper lateral line scales and transversal line scales). For the number of scales around the caudal peduncle no variation was found. The first principal component was correlated strongly with size and did not allow any differentiation of the specimens (Fig. 2). The highest loadings on this axis were by the meristics of the dentition (Table II). Indeed, these characters proved to be highly allometric (results not shown, but see e.g. Figs 4 and 5). Therefore, the scores were plotted on the second principal component

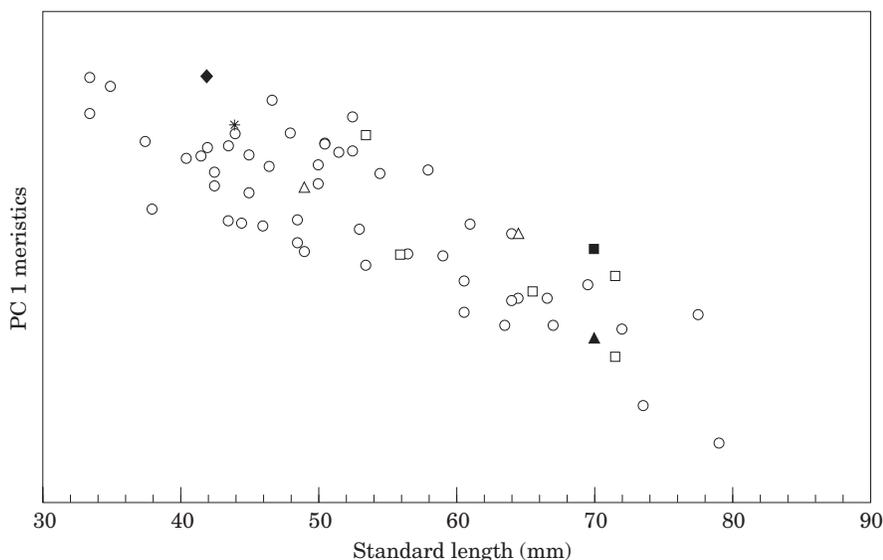


Fig. 2. Plot of the individual scores on PC 1 (meristics of all examined specimens) v. standard length. ▲, *T. temporalis* lectotype; △, *T. temporalis* paralectotype; ○, *T. temporalis*; ■, *T. lestradei* holotype; □, *T. lestradei* paratype; ◆, *T. burgeoni* holotype; *, *J. macrolepis* holotype.

TABLE II. Loadings of the meristics on the first three principal components

	PC 1	PC 2	PC 3
Enlarged teeth in upper oral jaw	− 0.8741	−0.2515	−0.1360
Enlarged teeth in lower oral jaw	− 0.8705	−0.1986	−0.1686
Teeth in upper oral jaw	− 0.7664	0.2314	−0.2015
Inner teeth rows in upper jaw	− 0.7006	−0.2189	0.4636
Inner tooth rows in lower jaw	− 0.6758	−0.1936	0.5090
Gill rakers on ceratobranchial	−0.3632	0.6085	0.0429
Gill rakers on epibranchial	−0.0808	0.7959	0.7566
Dorsal fin spines	−0.3699	−0.4292	−0.2223
Dorsal fin soft rays	−0.3224	0.6261	0.2253
Anal fin spines	0.0664	0.3354	0.3346
Anal fin soft rays	−0.2616	0.3897	−0.4901
Pectoral fin rays	0.0119	−0.0519	0.6915
Scales in longitudinal line	−0.5642	0.1608	−0.1811

Analysis of *T. temporalis* ($n=53$, including three of the four types), the holotype of *T. burgeoni*, the holotype and four paratypes of *T. lestradei* and the holotype of *J. macrolepis*. The most important loadings are in bold.

versus standard length (Fig. 3). This second component was defined mainly by (in order of importance) the number of gill rakers on the epibranchial, the number of soft rays in the dorsal fin and the number of gill rakers on the ceratobranchial (Table II). Again, the holotype of *J. macrolepis* was well outside the range of the cluster containing the *T. temporalis* specimens (Fig. 3), while the types of all other nominal species were within the range of *T. temporalis*.

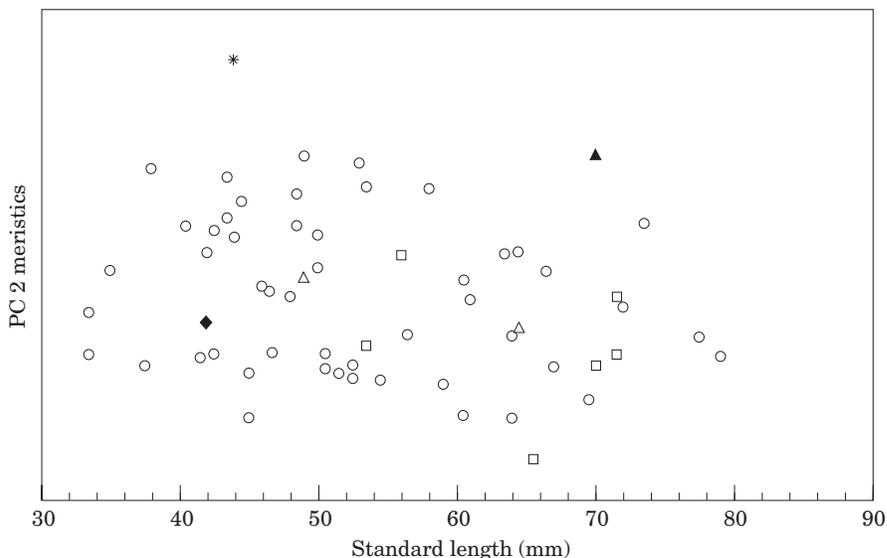


FIG. 3. Plot of the individual scores on PC 2 (meristics of all examined specimens) v. standard length. ▲, *T. temporalis* lectotype; △, *T. temporalis* paralectotype; ○, *T. temporalis*; ◆, *T. lestradei* holotype; □, *T. lestradei* paratype; ◆, *T. burgeoni* holotype; *, *J. macrolepis* holotype.

Secondly, the data and ranges of the various measurements (percentages) and meristics were compared. The holotype of *T. lestradei* fitted entirely in the range of measurements and meristics of *T. temporalis* (Tables III and IV), except for the anal fin spine count, which was five in *T. lestradei* versus six to seven in *T. temporalis*. Except for a very small difference in prepectoral distance (29.8 v. 30.0–35.8% L_S) *T. burgeoni* also fell within the range of the measurements for *T. temporalis* (Table III). To avoid possible allometric inferences in the analysis, by comparing one small specimen with a range of small to large specimens, the *T. burgeoni* type (42.0 mm L_S) was compared with a series of similar-sized specimens of *T. temporalis* (33.5–49.0 mm L_S , $n=23$) (Table V). Again, the same small difference was found between the holotype of *T. burgeoni* and *T. temporalis* for the prepectoral distance. For all other measurements *T. burgeoni* fitted the range of similar-sized *T. temporalis*. Since several meristics were also correlated strongly with size, *T. burgeoni* was compared with the same selection of similar-sized *T. temporalis* specimens (Table VI), but no difference was found between the two. Further examination of the *J. macrolepis* holotype confirmed it to be different from *T. temporalis*. Because of its small size (44 mm L_S), the relative measurements and meristics for *J. macrolepis* were compared with a selection of similar-sized *T. temporalis* specimens (Table V and VI). *Julidochromis macrolepis* had a larger mouth (upper jaw length 37.8 v. 28.6–36.1% L_H), a more elongate lower pharyngeal jaw (lower pharyngeal length 27.3 v. 22.0–25.4% L_H ; lower pharyngeal width 105.1 v. 114.7–130.8% L_{LP}) and a shorter dorsal fin (dorsal fin base 58.0 v. 59.6–66.7% L_S) than did *T. temporalis*. Although the PCA on the meristics resulted in a complete separation of *J. macrolepis* from the *T. temporalis* cluster, the meristics fitted entirely in the range of observations for *T. temporalis* (Table VI). In addition to the separation of *J. macrolepis* on morphometrics, further evidence was found in the tooth

TABLE III. Synopsis of the measurements of *T. temporalis* ($n=53$, including three of the four types), the holotype of *T. burgeoni* and the holotype of *T. lestradei*

	<i>Telmatochromis temporalis</i>		<i>T. burgeoni</i>	<i>T. lestradei</i>
	Mean \pm S.D.	Range		
Standard length (L_S) (mm)	52.9 \pm 11.9	33.5–78.5	42.0	70.0
Body depth (% L_S)	29.1 \pm 1.5	25.3–32.3	27.1	31.4
Head length (L_H) (% L_S)	31.8 \pm 1.0	29.2–34.3	30.7	32.0
Head width (W_H) (% L_H)	42.1 \pm 1.7	38.5–47.5	42.6	42.9
Interorbital width (% L_H)	22.8 \pm 2.4	17.5–29.3	21.7	26.0
Interorbital width (% W_H)	54.2 \pm 5.7	42.6–68.4	50.9	60.4
Snout length (% L_H)	33.0 \pm 2.5	27.9–39.7	31.0	35.7
Lower jaw length (% L_H)	36.7 \pm 2.1	31.4–41.6	31.8	38.4
Upper jaw length (% L_H)	34.2 \pm 2.4	28.6–40.4	32.6	35.7
Premaxillary pedicel length (% L_H)	29.2 \pm 1.8	25.8–33.1	27.9	33.0
Cheek depth (% L_H)	29.6 \pm 3.2	21.2–35.9	27.9	33.0
Eye diameter (% L_H)	26.5 \pm 1.7	23.4–29.8	25.6	24.6
Lachrymal depth (% L_H)	17.7 \pm 2.0	12.5–22.0	14.0	19.6
Lower pharyngeal length (L_{LP}) (% L_H)	24.0 \pm 1.0	22.0–27.4	22.5	—
Lower pharyngeal width (W_{LP}) (% L_{LP})	118.9 \pm 5.9	106.1–131.6	120.7	—
Dentigerous area length (% L_{LP})	59.4 \pm 4.0	50.0–66.7	58.6	—
Dentigerous area width (% W_{LP})	74.0 \pm 3.1	63.6–80.0	71.4	72.1
Dentigerous area length (% width)	67.5 \pm 4.6	55.9–77.1	68.0	72.2
Dorsal fin base length (% L_S)	62.8 \pm 1.9	59.0–66.7	63.1	64.3
Anal fin base length (% L_S)	22.7 \pm 1.1	20.7–25.0	22.6	21.4
Predorsal distance (% L_S)	29.7 \pm 1.1	27.5–32.7	29.8	29.3
Preanal distance (% L_S)	65.1 \pm 2.2	61.0–70.1	67.9	65.7
Prepectoral distance (% L_S)	31.9 \pm 1.4	30.0–35.8	29.8	32.1
Prepelvic distance (% L_S)	35.6 \pm 2.1	31.4–42.0	33.3	37.9
Caudal peduncle length (L_{CP}) (% L_S)	14.4 \pm 1.1	12.1–16.6	14.3	14.3
Caudal peduncle depth (% L_{CP})	91.5 \pm 9.8	66.7–114.3	91.7	90.0

morphology. The shape of the enlarged outer teeth did not resemble the shape in *T. temporalis*, but corresponded well to the tooth shape found in *T. dhonti*. In *T. dhonti* the outer teeth were more rounded in cross-section, and the tip of the teeth was curved inwards, while in *T. temporalis* the teeth were more flattened in cross-section, and not curved.

DISCUSSION

T. LESTRADEI

The comparison of the holotype and the paratypes of *T. lestradei* with *T. temporalis* showed no significant difference between the samples and confirmed the synonymy established already by Poll (1946). For the total number of teeth in the upper and lower jaw, high values were found for the types of *T. lestradei*. This character was used by Poll (1942) to distinguish *T. lestradei* from *T. temporalis*. The difference can now be explained by the fact that, in *T. temporalis*, this number increases with increasing size (Figs 2 and 3). Since *T. lestradei* was described on the basis of relatively large specimens, a high

TABLE IV. Synopsis of the meristics of *T. temporalis* ($n=53$, including three of the four types), the holotypes of *T. burgeoni* and the holotype of *T. lestradei*

Character	<i>Telmatochromis temporalis</i>	<i>T. burgeoni</i>	<i>T. lestradei</i>
Upper jaw teeth	28–63 (median 42, $n=53$)	33	49
Enlarged teeth upper jaw	6–17 (median 8, $n=53$)	6	10
Lower jaw teeth	26–53 (median 37, $n=22$)	—	44
Enlarged teeth lower jaw	6–18 (median 9, $n=53$)	7	11
Inner tooth rows	4/4 (f1), 5/5 (f15), 5/6 (f3), 6/5 (f7), 6/6 (f17), 6/7 (f1), 7/6 (f6), 7/7 (f3)	5/5	6/6
Gill rakers	3/1/2 (f3), 3/1/3 (f6), 3/1/4 (f2), 3/1/5 (f1), 3/1/6 (f1), 4/1/2 (f1), 4/1/3 (f3), 4/1/4 (f7), 4/1/5 (f6), 4/1/6 (f2), 5/1/2 (f2), 5/1/3 (f1), 5/1/4 (f5), 5/1/5 (f3), 5/1/6 (f4), 6/1/5 (f3), 7/1/5 (f2)	3/1/4	3/1/3
Dorsal fin formula	XIX 7 (f1), XIX 8 (f1), XX 6 (f1), XX 7 (f22), XX 8 (f11), XXI 6 (f1), XXI 7 (f15), XXI 8 (f2)	XX 7	XX 7
Anal fin formula	VI 6 (f29), VI 7 (f9), VII 5 (f1), VII 6 (f12), VII 7 (f2)	VI 6	V 7
Pectoral fin formula	13 (f4), 14 (f38), 15 (f10)	14	14
Longitudinal line scales	33 (f9), 34 (f29), 35 (f11), 36 (f2)	33	34
Upper lateral line scales	20 (f1), 21 (f1), 22 (f1), 23 (f1), 24 (f2), 25 (f10), 26 (f18), 27 (f12), 28 (f5)	27	27
Transversal line scales	—/9 (f17), —/10 (f12), 9/10 (f1), 10/9 (f1), 10/10 (f5), 10/11 (f2), 11/9 (f2), 11/10 (f3), —/11 (f2), 11/11 (f1), 11/12 (f1), 12/10 (f1)	—/10	11/11

number of outer oral teeth was to be expected. However, this number is fully within the range of *T. temporalis*. Five anal fin spines were counted in the holotype of *T. lestradei*, while Poll (1942) mentioned six to seven anal fin spines in the type series of *T. lestradei*. In all other types of *T. lestradei* and specimens of *T. temporalis* six to seven anal fin spines were counted. Hence, this difference is considered insufficient to distinguish both species.

T. BURGEONI

Two thin longitudinal bands were observed on the flanks of *T. burgeoni*, as reported by Poll (1942). Examination of the entire *T. temporalis* collection for this character showed the presence of a very faint and thin dorsal band in several

TABLE V. Synopsis of the measurements of a selection of small-sized *T. temporalis* ($n=23$), the holotypes of *T. burgeoni* and of *J. macrolepis*

	<i>Telmatochromis temporalis</i>		<i>T. burgeoni</i>	<i>J. macrolepis</i>
	mean \pm S.D.	Range		
Standard length (L_S) (mm)	42.8 \pm 4.7	33.5–49.0	42.0	44.0
Body depth (% L_S)	28.8 \pm 1.8	25.3–31.5	27.1	26.1
Head length (L_H) (% L_S)	32.1 \pm 0.9	30.4–34.0	30.7	32.5
Head width (W_H) (% L_H)	41.9 \pm 1.9	38.5–47.5	42.6	40.6
Interorbital width (% L_H)	21.0 \pm 4.6	17.5–23.0	21.7	21.0
Interorbital width (% W_H)	50.1 \pm 4.4	42.6–57.4	50.9	51.7
Snout length (% L_H)	31.2 \pm 1.8	27.9–34.3	31.0	32.9
Lower jaw length (% L_H)	36.5 \pm 2.4	31.4–41.6	31.8	37.1
Upper jaw length (% L_H)	32.8 \pm 1.8	28.6–36.1	32.6	37.8
Premaxillary pedicel length (% L_H)	28.3 \pm 1.5	25.8–31.4	27.9	29.4
Cheek depth (% L_H)	27.3 \pm 2.4	21.2–30.0	27.9	25.2
Eye diameter (% L_H)	27.8 \pm 1.4	24.7–29.8	25.6	28.7
Lachrymal depth (% L_H)	16.6 \pm 1.9	12.5–21.3	14.0	16.8
Lower pharyngeal length (L_{LP}) (% L_H)	23.7 \pm 0.9	22.0–25.4	22.5	27.3
Lower pharyngeal width (W_{LP}) (% L_{LP})	121.5 \pm 5.1	114.7–130.8	120.7	105.1
Dentigerous area length (% L_{LP})	60.6 \pm 3.6	54.3–66.7	58.6	59.0
Dentigerous area width (% W_{LP})	75.6 \pm 2.5	70.7–80.0	71.4	78.0
Dentigerous area length (% width)	66.1 \pm 4.0	55.9–73.3	68.0	71.9
Dorsal fin base length (% L_S)	62.4 \pm 2.0	59.6–66.7	63.1	58.0
Anal fin base length (% L_S)	22.8 \pm 1.3	20.9–25.0	22.6	23.9
Predorsal distance (% L_S)	29.8 \pm 0.9	27.6–32.0	29.8	29.5
Preanal distance (% L_S)	64.8 \pm 2.2	61.3–70.1	67.9	65.9
Prepectoral distance (% L_S)	32.1 \pm 1.4	30.0–35.8	29.8	35.2
Prepelvic distance (% L_S)	36.0 \pm 2.4	32.2–40.2	33.3	38.69
Caudal peduncle length (L_{CP}) (% L_S)	14.2 \pm 1.0	12.2–15.7	14.3	13.0
Caudal peduncle depth (% L_{CP})	93.9 \pm 9.8	76.9–110.0	91.7	100.0

other specimens. Two *T. temporalis* specimens that were collected in Nyanza Lac together with the *T. burgeoni* holotype, equally show two very faint and thin longitudinal bands, that seem to disappear with increasing size. These fine longitudinal bands are of a different nature than those observed in the elongated *Telmatochromis* species with clear longitudinal bands (*Telmatochromis vittatus*, *T. bifrenatus* and *T. brichardi*). The latter species were grouped together also by Poll (1956) and Louisy (1989) and are characterized by the presence of two broad black longitudinal bands, a mid-lateral band, from the tip of the snout to the base of the caudal fin, and a dorsal band, from the snout to the end of the dorsal fin base, extending into the dorsal fin base. In *T. bifrenatus* a third band can be observed, running about midway between the two other lateral bands.

In contrast to Poll (1942, 1946, 1956), there was no difference in the number of enlarged outer oral teeth in the oral jaws between *T. burgeoni* and *T. temporalis*. Although the number of enlarged outer oral teeth in *T. burgeoni* is indeed amongst the lowest values observed for *T. temporalis*, it is a normal value for its small size (Figs 4 and 5). It is, therefore, incorrect to distinguish *T. burgeoni* from *T. temporalis* on the basis of this character. These plots show equally that

TABLE VI. Synopsis of the meristics of a selection of small-sized *T. temporalis* ($n=23$, average 42.8 mm L_S), the holotypes of *T. burgeoni* and of *J. macrolepis*

	<i>T. temporalis</i>	<i>T. burgeoni</i>	<i>J. macrolepis</i>
Upper jaw teeth	29–48 (median 39, $n=23$)	33	45
Enlarged teeth upper jaw	6–10 (median 8, $n=23$)	6	6
Lower jaw teeth	30–37 (median 34, $n=9$)	—	—
Enlarged teeth lower jaw	6–11 (median 8, $n=23$)	7	6
Inner tooth rows	4/4 (f1), 5/5 (f11), 6/5 (f1), 6/6 (f10)	5/5	4/4
Gill rakers	3/1/2 (f1), 3/1/3 (f3), 3/1/4 (f2), 3/1/5 (f1), 4/1/3 (f1), 4/1/4 (f2), 4/1/5 (f1), 4/1/6 (f3), 5/1/3 (f1), 5/1/4 (f1), 5/1/5 (f2), 5/1/6 (f2), 6/1/5 (f2), 7/1/5 (f1)	3/1/4	6/1/5
Dorsal fin formula	XIX 7 (f1), XX 6 (f1), XX 7 (f9), XX 8 (f5), XXI 6 (f1), XXI 7 (f5), XXI 8 (f1)	XX 7	XIX 8
Anal fin formula	VI 6 (f11), VI 7 (f3), VII 5 (f1), VII 6 (f7), VII 7 (f1)	VI 6	VI 7
Pectoral fin formula	14 (f19), 15 (f4)	14	14
Longitudinal line scales	33 (f5), 34 (f16), 35 (f2)	33	35
Upper lateral line scales	20 (f1), 21 (f1), 24 (f2), 25 (f6), 26 (f7), 27 (f3), 28 (f2)	27	28
Transversal line scales	—/9 (f7), —/10 (f7), 10/10 (f3), 11/9 (f1), 11/10 (f2), —/11 (f2), 11/11 (f1)	—/10	—/9

the number of enlarged outer teeth in the oral jaws increased with increasing size. Interestingly, the number of enlarged teeth in both oral jaws for *T. dhonti* (equally plotted in Figs 4 and 5) appeared to be independent of size.

Sato & Gashagaza (1997) discussed the spawning and brooding behaviour of several lamprologine cichlids from Lake Tanganyika. They found that *T. temporalis* is a facultative shell brooder. They also reported the presence of a second *Telmatochromis* species, also a facultative shell-brooder, which in their opinion is either *T. temporalis* or *T. burgeoni*. Since there was no ground on which to differentiate *T. burgeoni* from *T. temporalis*, the 'undescribed' *Telmatochromis* species reported by Sato & Gashagaza (1997) is regarded as *T. temporalis*. *Telmatochromis burgeoni* sensu Konings (1988) is a shell dweller, but its behaviour differs from that of other shell dwellers. Males and females hide in their own shells but form strong pair bonds. The maximum size is 7 cm, and it is characterized by the presence of two thin lines on the flanks, which appear after preservation, and are barely recognized on live specimens. Pending a revision, Konings (1998) temporarily regarded *T. burgeoni* as a synonym of *T. temporalis*. We agree with Konings (1998) who considered the smaller

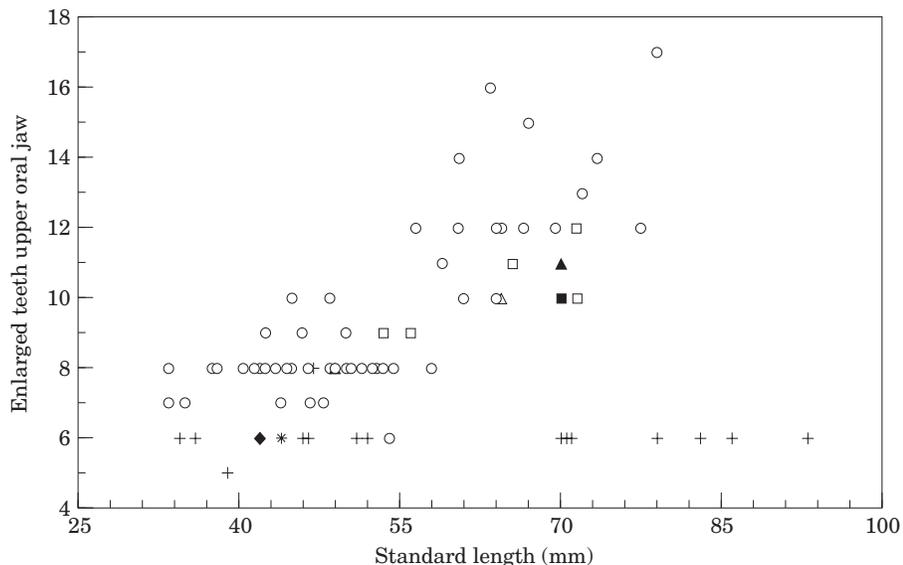


FIG. 4. Plot of the enlarged outer teeth in the upper oral jaw v. standard length. ▲, *T. temporalis* lectotype; △, *T. temporalis* paralectotype; ○, *T. temporalis*; ■, *T. lestradei* holotype; □, *T. lestradei* paratype; ◆, *T. burgeoni* holotype; *, *J. macrolepis* holotype; +, *T. dhonti*.

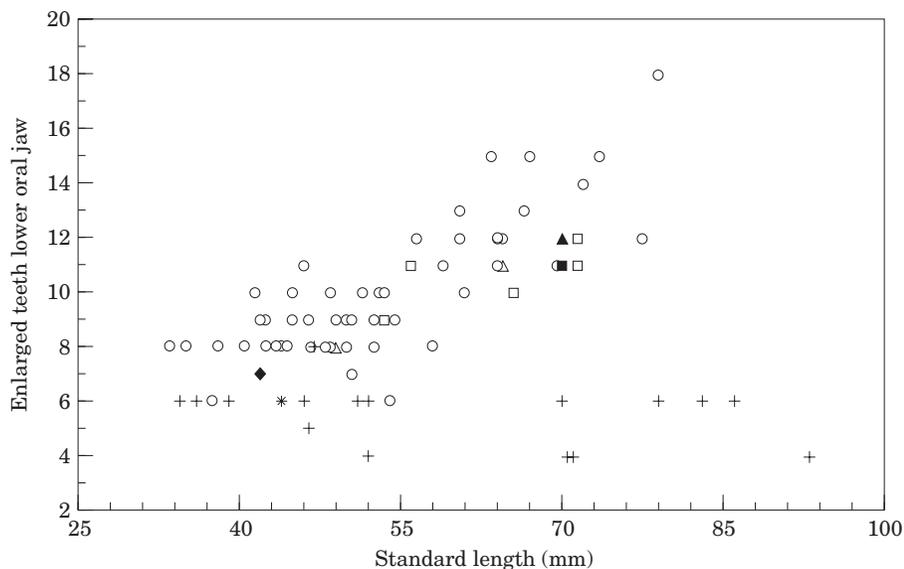


FIG. 5. Plot of the enlarged outer teeth in the lower oral jaw v. standard length. ▲, *T. temporalis* lectotype; △, *T. temporalis* paralectotype; ○, *T. temporalis*; ■, *T. lestradei* holotype; □, *T. lestradei* paratype; ◆, *T. burgeoni* holotype; *, *J. macrolepis* holotype; +, *T. dhonti*.

shell-dwelling *T. temporalis* as a dwarf form of *T. temporalis*. Dwarf forms have been reported in other facultative shell-brooders as well (Sato & Gashagaza, 1997; Konings, 1998); their smaller size seems to be an adaptation which allows them to use empty shells for brooding.

Mboko & Kohda (1995) reported on the pale and dark dichromatism found in *T. temporalis*. According to their results, this dichromatism may function as antipredator camouflage. Pale specimens defend territories on top of the rocks, in well-illuminated areas while dark specimens are found in territories in shaded areas on lateral sides of the rocks. This dichromatism is not determined genetically since specimens can change colour over a few weeks when transferred to contrasting light conditions. Pale and dark *T. temporalis* specimens were also present in the collection, often in the same sample. This dichromatism appeared to be independent of size.

J. MACROLEPIS

Examination of the *J. macrolepis* type showed it to be conspecific with *T. dhonti* and not with *T. temporalis*, as was stated by Trewavas (1946). Although the specimen was small (46 mm L_S) and the number of enlarged outer teeth in the upper and lower oral jaws (6/6) is not a sufficient character to attribute this specimen to either of both species (Figs 2 and 3), other features have enabled identification of this specimen as *T. dhonti* (see above). In addition, the morphology of the outer oral teeth in *J. macrolepis* is similar to *T. dhonti* and clearly distinct from *T. temporalis*. Examination of several small-sized *T. dhonti* for this character has shown that, in contrast to the number of enlarged outer oral teeth, the shape of the enlarged outer oral teeth is an unambiguous character to distinguish small-sized *T. dhonti* from similar-sized *T. temporalis*. Hence *J. macrolepis* should be regarded as a synonym of *T. dhonti* and not of *T. temporalis*.

List of specimens examined (all from Lake Tanganyika; DRC, Democratic Republic of Congo).

Telmatochromis temporalis

BMNH [British Museum (Natural History)] 1898.9.9:22–23; Kinyamkolo, Zambia; J. E. S. Moore; lectotype and paralectotype of *T. temporalis*; BMNH 1898.9.9:21; Mbity Rocks, Zambia; J. E. S. Moore; paralectotype of *T. temporalis*; MRAC (Musée Royale de l'Afrique Centrale) 38882; Nyanza Burundi; L. Burgeon; 31 Dec. 1932; holotype of *T. burgeoni*; MRAC 38994–995 (2 specimens); same data; 03 Jan. 1933; MRAC 45840; Rumonge, Burundi; A. Lestrade; 1935; MRAC 54656; 54686–54692 (7 specimens); Nyanza, Burundi; A. Lestrade; 1937; paratypes of *T. lestradei*; MRAC 54660; same data; holotype of *T. lestradei*; MRAC 54634–630 (3 specimens); 54673–685 (7 specimens); same data; MRAC 112748; Stat. 10, Au large de la baie de Kungwe, à 500 m de la côte; Explor. Hydrobiol. L. Tang; 10 Nov. 1946; MRAC 112755–759 (1 specimen); Stat. 108, Mtoto, dans la baie, Democratic Republic of Congo (DRC); Explor. Hydrobiol. L. Tang; 05 Feb. 1947; MRAC 112762; Stat. 176, Baie de Mtoto, rochers au Nord, DRC; Explor. Hydrobiol. L. Tang; 15 Mar. 1947; MRAC 112766–769 (2 specimens); Stat. 202, Mpulungu; Explor. Hydrobiol. L. Tang; 27 Mar. 1947; MRAC 112770–774 (2 specimens), Stat. 217, Moliro; Explor. Hydrobiol. L. Tang; 1 Apr. 1947; MRAC 112781–784 (3 specimens); Stat. 319, Mwerazi; Explor. Hydrobiol. L. Tang; 28 May 1947; MRAC 178963–964 (2 specimens); 25 km de Bujumbura vers Rumonge, Burundi; A. Schreyen; Feb. 1972; MRAC 189751–778 (6 specimens); Mpulungu,

Jetty, Zambia; H. Matthes; 18 Feb. 1966; MRAC 189779–793 (2 specimens); same data; 14 Feb. 1966; MRAC 125738–125740 (3 specimens); Route Nyanza lac, Burundi; H. Matthes, I.R.S.A.C.; 18/12/1958; MRAC 74-4-P-325–326; Cap Kabeyeye, Zambia; P. Brichard; 17 Jan. 1976; MRAC 76-4-P-180; Cap Nundo, Zambia; P. Brichard; 06 Jan. 1976; MRAC 76-4-P-517–523 (2 specimens); same data; MRAC 76-28-P-129–145 (3 specimens); Sumbu (Kamba Bay), Zambia; P. Brichard; 11 May 1976; MRAC 92-81-P-16; Locality 1, Mwamungongo, just north of Gombe National Park, Tanzania; coll. Tanganyika Expedition 1992; 24 May 1992; MRAC 92-81-P-1078–1079, 1082, 1116, 1120; Locality 40, South of Mkuyu Point, Tanzania; coll. Tanganyika Expedition 1992; 01 Jun. 1992; MRAC 92-81-P-1140, 1141; Locality 41, Segunga, south of Segunga Bay, Tanzania; coll. Tanganyika Expedition 1992; 01 Jun. 1992; MRAC 92-81-P-1186; Locality 43, Kalela, Tanzania; coll. Tanganyika Expedition 1992; 02 Jun. 1992; MRAC 92-81-P-1388–1390; Locality 4b, Ulwile Island, northern shore, Tanzania; coll. Tanganyika Expedition 1992; 27 May 1992.

Telmatochromis dhonti

BMNH 1919.1.16:132; Albertville, DRC; M. G. Dhont De Bie; type of *L. dhonti*; BMNH 1919.2.5.39; Albertville, DRC; M. G. Dhont De Bie; type of *L. dhonti*; MRAC 7018; Albertville, DRC; M. G. Dhont De Bie; type of *L. dhonti*; MCZ (Museum of Comparative Zoology) 32619; Ujiji, Tanzania; A. Loveridge; 22 May 1930; holotype of *J. macrolepis*; MRAC 112810–820 (1 specimen); Stat. 60, Kigoma, Tanzania; Explor. Hydrobiol. L. Tang; 10 Jan. 1947; MRAC 112878–879 (1 specimen); Stat. 154, Pala, DRC; Explor. Hydrobiol. L. Tang; 06 Mar. 1947; MRAC 112912–916 (1 specimen); Stat. 307, Riv. au sud de la Malagarasi, près de la baie Karago, Tanzania; 21 May 1947; MRAC 81-29-P-169–248 (3 specimens); Kalemie, DRC; P. Brichard; 10 Apr. 1981; MRAC 92-81-P-696; Locality 22, A few km south of Karema, Tanzania; coll. Tanganyika Expedition 1992; 29 May 1992; MRAC 92-81-P-749; Locality 23, Just south of Karema, Tanzania; coll. Tanganyika Expedition 1992; 29 May 1992; MRAC 92-81-P-863–864; Locality 27, Just south of Mkangasi, Tanzania; coll. Tanganyika Expedition 1992; 30 May 1992; MRAC 92-81-P-914; Locality 29, Kalia, bay at mouth Lugonesi River, Tanzania; coll. Tanganyika Expedition 1992; 30 May 1992; MRAC 92-81-P-990; Locality 35, Bulu Point, Tanzania; coll. Tanganyika Expedition 1992; 31 May 1992; MRAC 92-81-P-993, 1050; Locality 36, One third distance Bulu Point–Lualaga Point, Tanzania; coll. Tanganyika Expedition 1992; 31 May 1992; MRAC 92-81-P-1136; Locality 41, Segunga, south of Segunga Bay, Tanzania; coll. Tanganyika Expedition 1992; 01 Jun. 1992.

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