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## Description of a *Tilapia* (*Coptodon*) species flock of Lake Ejagham (Cameroon), including a redescription of *Tilapia deckerti* Thys van den Audenaerde, 1967

(Perciformes, Cichlidae)

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Three new species of the genus *Tilapia* Smith, 1840 are described from Lake Ejagham (Cameroon) and *T. deckerti* Thys van den Audenaerde, 1967 is redescribed. *T. deckerti* differs from all other *Tilapia* sensu lato except few members of the subgenus *Coptodon* in quadricuspid posterior pharyngeal teeth on lower pharyngeal jaw, which is in addition only known from *T. tholloni*, *T. cameronensis*, *T. dageti*, *T. congica*, *T. ejagham* spec. nov., and *T. nigrans* spec. nov. From these species it can be distinguished by discrete characters. *Tilapia ejagham* spec. nov. differs from all other *Tilapia* sensu lato except *T. joka*, *T. bilineata*, *T. nigrans* spec. nov. and all members of the subgenus *Coptodon* (including *T. ismailiaensis* and *T. camerunensis*) in tricuspid (rarely quadricuspid) pharyngeal teeth in the posterior two rows of lower pharyngeal jaw. It differs from *T. joka* in a higher number of gill rakers on first ceratobranchial (9-10 vs. 6-8), from *T. bilineata* in lacking a densely scaled caudal fin, from members of the subgenus *Coptodon* in discrete characters or in a combination of characters as deduced from principal component analyses. *Tilapia nigrans* spec. nov. differs from all other *Tilapia* sensu lato except few members of the subgenus *Coptodon* in quadricuspid or pentacuspid posterior pharyngeal teeth on lower pharyngeal jaw. Quadricuspid pharyngeal teeth are otherwise only known from *T. tholloni*, *T. cameronensis*, *T. dageti*, *T. congica*, *T. ejagham* spec. nov. and *T. deckerti*. From these species it is distinguished by discrete characters. *Tilapia fusiforme* spec. nov. is characterized by a slender fusiform body, an acute mouth, a black breeding coloration and a “tilapia spot” extended to a longitudinal stripe in juveniles.

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### Introduction

Lake Ejagham (5°45'4.37" N 8°59'0.92" E) is a very small lake in Western Cameroon covering an area of only 0.49 km<sup>2</sup>. It was first mentioned by Mansfeld (1908) as “Totensee bei Nssakpé (Ekeu land)”.

Mansfeld mentioned one fish species and collected three specimens, which he deposited in the Museum für Naturkunde, Berlin (ZMB). Thys van den Audenaerde used these specimens as type material for the description of *Tilapia deckerti* Thys van den Audenaerde, 1967, up to now the single described

*Tilapia* species from Lake Ejagham (Thys van den Audenaerde 1967). Dominey (1988) and Schliewen et al. (1994) identified a small cichlid species flock in Lake Ejagham. After extensive field work Schliewen et al. (2001) suggested that five (incipient) *Tilapia* species exist in the lake, which were referred to as *Tilapia* cf. *deckerti* “little-black”, *T.* cf. *deckerti* “large-black”, *T.* spec. “jewel”, *T.* spec. “dark jewel”, and *T.* spec. “predator”. According to their molecular phylogenetic analyses (Schliewen et al. 2001), all these species are closely related to *T.* spec. aff. *guineensis* “Cross” (referred as *Tilapia* spec. “Cro” in Thys van den Audenaerde (1971)), an apparently undescribed *Tilapia* species endemic to the Cross River drainage (Thys van den Audenaerde 1971).

Members of the large African cichlid genus *Tilapia* Smith, 1840 (type species, *Tilapia sparrmanii*) naturally inhabit most African rivers and the Jordan River drainage. After splitting *Tilapia* in three sections, Thys van den Audenaerde (1968) assigned *T. deckerti* to the subgenus *Coptodon* Gervais, 1853 (type species, *Tilapia zillii* (Gervais, 1848)). *Coptodon* sensu Thys van den Audenaerde (1968) is characterized by a suite of characters including: Median pharyngeal teeth not broadened; outer teeth on jaws bicuspid, not spatulate; colour-pattern with or without vertical bars (never oblique) on sides; 16 scale rows (exceptionally 15 or 17) around caudal peduncle (Thys van den Audenaerde 1968). According to the most recently published data and keys (Thys van den Audenaerde 1971, 1972, Stiassny et al. 1992), the subgenus contains 25 described and undescribed species: *T. zillii*, *T. guineensis* (Bleeker, 1862), *T. walteri* Thys van den Audenaerde, 1968, *T. cameronensis* Holly, 1927, *T. nyongana* Thys van den Audenaerde, 1960, *T. congica* Poll & Thys van den Audenaerde, 1960, *T. rendalli* (Boulenger, 1896), *T. discolor* (Günther, 1902), *Tilapia* spec. “Cro” (see above), *T. kottae* Lönnberg, 1904, *T. deckerti*, *T. tholoni* (Sauvage, 1884), *T. margaritacea* Boulenger, 1916, *T. louka* Thys van den Audenaerde, 1969, *T. dageti* Thys van den Audenaerde, 1971, *T. coffea* Thys van den Audenaerde, 1970, *T. bemini* Thys van den Audenaerde, 1972, and additional members of the Lake Bermin species flock described by Stiassny, Schliewen & Dominey, 1992, namely *T. bakossiorum*, *T. bythobates*, *T. flava*, *T. gutturosa*, *T. imbriferina*, *T. snyderae*, *T. spongotroktis*, and *T. thysi*. Based on molecular phylogenetic analysis, *Tilapia* cf. *deckerti* “little-black” and *Tilapia* cf. *deckerti* “large-black” are members of *Coptodon*, too (Schliewen et al. 1994, 2001). This is supported by the presence of all diagnostic characters of the subgenus *Coptodon* (sensu Thys van den Audenaerde 1968), except for the number of scale rows around caudal peduncle

(a highly variable character in *Coptodon*; pers. obs.) in all Ejagham-*Tilapia*.

Since most members of the Ejagham-*Coptodon* species flock have remained undescribed since their discovery, the purpose of this paper is a critical examination of their species status, based on a morphometric examination of extensive comparative material of all described *Tilapia* (*Coptodon*) taxa and a re-examination of molecular data published by Schliewen et al. (2001). This has led to the identification of four diagnosable taxa including *Tilapia deckerti*, which are described or redescribed herein.

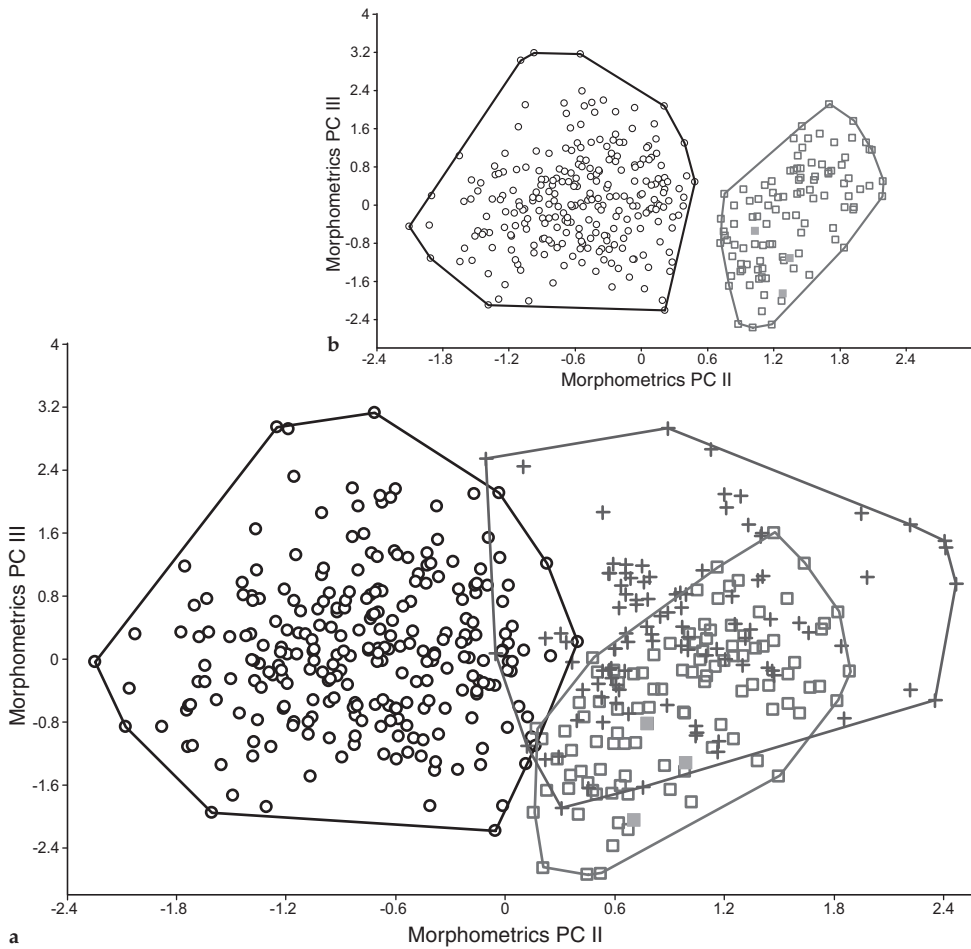
## Material and methods

### Material

Collection details for *Tilapia* specimens from Lake Ejagham are provided in the species descriptions below and collection methods for ZSM material are described in Schliewen et al. (2001). Non-Ejagham *Tilapia* sensu lato specimens (n=408) are deposited in the following collections: Africa Museum, Tervuren, Belgium (MRAC); Natural History Museum, London, United Kingdom (NHM); Muséum nationale d’Histoire naturelle, Paris, France (MNHN); Naturhistorisches Museum Wien, Vienna, Austria (NMW); Zoologisches Museum Berlin, Berlin, Germany (ZMB); South African Institute for Aquatic Biodiversity, Grahamstown, South Africa (SAIAB/RUSI); and the Bavarian State Collection of Zoology, München, Germany (ZSM). Investigated material includes type material of all described *Tilapia* (*Coptodon*) taxa except for holotype of *T. lata camerunensis* Lönnberg, 1903 and syntypes of *Acerina zillii* Gervais, 1848, which were either unavailable during the study (*T. lata camerunensis*) or lost (*A. zillii*). However, topotypical material of *Tilapia camerunensis* and *Tilapia zillii* was available for comparison. Although not formally assigned to *Coptodon* before, *T. ismailiaensis* Mekkawy, 1995 and *T. camerunensis* Lönnberg, 1903 share diagnostic *Coptodon* characters (see Introduction). We therefore consider them members of the subgenus *Coptodon* and included them in our comparative analyses. For a detailed list of comparative material see Appendix 1. Description of live specimens is based on photographs from Lake Ejagham and on observations of the second author (UKS).

### Morphology and principal component analysis

Measurements, meristic counts and application of morphological characters follows Dunz & Schliewen (2010). Measurements were taken point-to-point on the left side of specimens using a digital caliper with an accuracy of 0.01 mm and rounded to the nearest 0.1 mm. Except for total length (TL) and standard length (SL), measurements are given as percentage of SL.



**Fig. 1.** a. Scatter plot of scores of Principal Component II vs. Principal Component III visualized as convex hulls. ○, *T. cameronensis*, *T. camerunensis*, *T. coffea*, *T. congica*, *T. dageti*, *T. discolor*, *T. guineensis*, *T. louka*, *T. margaritacea*, *T. nyongana*, *T. rendalli*, *T. tholloni*, *T. walteri*, and *Tilapia* spec. aff. *guineensis* "Cross" (n=295); □, Lake Ejagham species flock (*Tilapia ejagham* spec. nov., *Tilapia nigrans* spec. nov., *Tilapia fusiforme* spec. nov., *T. deckerti* (n=99)); ■, Type material of *T. deckerti* (n=3); +, Lake Bermin species flock (*T. bakossiorum*, *T. bythobates*, *T. flava*, *T. gutturosa*, *T. imbriferina*, *T. snyderae*, *T. spongotroktis*, *T. bemini*, and *T. thysi*), *T. zillii*, *T. ismailiaensis* and *T. kottae* (n=101). b. Scatter plot of scores of Principal Component II vs. Principal Component III showed with convex hulls. ○, *T. cameronensis*, *T. camerunensis*, *T. coffea*, *T. congica*, *T. dageti*, *T. discolor*, *T. guineensis*, *T. louka*, *T. margaritacea*, *T. nyongana*, *T. rendalli*, *T. tholloni*, *T. walteri* and *Tilapia* spec. aff. *guineensis* "Cross" (n=295); □, Lake Ejagham species flock (*Tilapia ejagham* spec. nov., *Tilapia nigrans* spec. nov., *Tilapia fusiforme* spec. nov., *T. deckerti* (n=99)); ■, Type material of *T. deckerti* (n=3).

Principal component analysis (PCA) of log-transformed morphometric data were calculated using the statistical program PAST 1.98 (Hammer et al., 2001). In this analysis, the first principal component (PC I) integrates most size-related variation, whereas the PC II, PC III and following components are theoretically size-free. PCAs were performed in

a stepwise approach, first including all specimens, followed by PCAs of only selected taxa that were apparently discernable in the first step. The second step PCAs served to remove potential noise due to variance in the total dataset affecting subtle differentiation patterns between morphometrically similar taxa.



**Fig. 2.** Scatter plot of scores of Principal Component II vs. Principal Component III; visualized as convex hulls. □, *T. ejagham* spec. nov. (n=26); +, *T. zillii* (n=22).



**Fig. 4.** Scatter plot of scores of Principal Component II vs. Principal Component III; visualized as convex hulls. □, *T. fusiforme* spec. nov. form "large-black" (n=17); ■, *T. fusiforme* spec. nov. form "little-black" (n=16).



**Fig. 3.** Scatter plot of scores of Principal Component II vs. Principal Component III; visualized as convex hulls. □, *T. ejagham* spec. nov. (n=26); +, *T. spongotroktis* (n=7), +, holotype of *T. spongotroktis* (AMNH 98258).

**Laboratory methods and population genetic analysis**

Individualized microsatellite data of five loci (UNH002, UME002, 780/783, 781/84, and 753/773) were taken from the unpublished PhD thesis (Schliewen 1999), i. e. the identical data set that served for population genetic analyses published in Schliewen et al. (2001). These data have now been made available online under [http://www.zsm.mwn.de/ich/Lociset\\_of\\_Lake\\_Ejagham\\_species\\_flock.xls](http://www.zsm.mwn.de/ich/Lociset_of_Lake_Ejagham_species_flock.xls). Except for *Tilapia ejagham* spec. nov. (described below), all individuals for population genetic analysis were breeding individuals that had mated assortatively. For further sampling and molecular methods, see Schliewen et al. (2001). We reanalysed the microsatellite data with a model-based clustering method in the program *structure* version 2.2 (Pritchard et al. 2000) to investigate coherence of genotypic and morphological identification. Individual allocation to a number (K) of populations or closely related species was determined using the admixture model (Falush et

al. 2003), which is based on the assumption that each individual draws some fraction of his/her genome from each of the K populations. We followed Evanno et al. (2005) to detect the uppermost hierarchical level of genetic structure, i. e. the most likely number of

**Table 1.** Factor Loadings of PC I-III for Fig. 1b. Highest loadings for PC II and PC III indicated in boldface.

Principal Component	I	II	III
Standard length	-0.196	0.041	-0.140
Head length	-0.193	0.132	0.042
Interorbital width	-0.220	-0.188	0.024
Preorbital width	-0.226	-0.063	0.161
Horizontal eye length	-0.128	0.029	-0.168
Snout length	-0.238	0.139	0.157
Interostril distance	-0.204	0.094	0.075
Cheek depth	-0.240	0.040	0.195
Upper lip length	-0.213	<b>0.299</b>	0.082
Lower lip length	-0.212	<b>0.301</b>	0.077
Lower lip width	-0.238	0.166	<b>0.443</b>
Lower jaw length	-0.191	<b>0.378</b>	0.038
Predorsal distance	-0.195	0.045	0.074
Dorsal fin length	-0.208	-0.125	-0.139
Length last dorsal spine	-0.226	<b>-0.324</b>	-0.067
Anal fin length	-0.208	-0.182	-0.173
Anal spine length (third)	-0.192	-0.109	<b>-0.379</b>
Pelvic fin length	-0.224	-0.273	-0.039
Pectoral fin length	-0.204	-0.242	-0.065
Caudal peduncle depth	-0.212	-0.211	0.056
Caudal peduncle length	-0.188	<b>0.391</b>	<b>-0.647</b>
Body depth	-0.215	<b>-0.250</b>	0.119
Preanal length	-0.199	-0.001	-0.037
Eigenvalue	0.618	0.018	0.004
% variance	94.53	2.68	0.57



Fig. 5. XY-graph of the log probability of the data (LnP(D)) (Y) and the number of cluster K (X). The estimation for K reaches a plateau at K4.



Fig. 6. XY-graph of  $\Delta K$  vs. K. Calculated with the evaluated formula  $\Delta K = m(|L^*K|) / s[L(K)]$ , the modal value of this distribution is the true K or the uppermost hierarchic level of genetic structure.  $\Delta K$  (Evanno et al. 2005) peaks at K4.

K groups being identifiable in the dataset. The following programme settings were chosen: burnin of 30,000 generations and 100,000 MCMC generations after burnin; admixture model with default settings; allele frequencies correlated among populations; significantly different values of  $F_{ST}$  for populations assumed with a prior  $F_{ST}$  mean for populations set to 0.01 (based on results in Schlieven et al. 2001) and a prior SD of  $F_{ST}$  for populations set to 0.05; uniform lambda for all populations; initial value of Lambda: 1.0; estimation of probability of the data under the model and frequency of Metropolis update for Q: 10. All runs were replicated ten times with K ranging from one to eight at each replicate.

## Results

### Morphometric distinction of Lake Ejagham taxa and remaining species of the subgenus *Coptodon*

The morphometric analyses using PCA and the investigation of discrete characters and measurement values revealed that all members of the Lake Ejagham species flock are distinguishable from all other *Coptodon* species.

The first PCA run of morphometric data of all species of the subgenus *Coptodon* identified 14 taxa as discernable from Lake Ejagham *Coptodon*, however with marginal overlap (Fig. 1a). These 14 taxa are: *T. cameronensis*, *T. camerunensis*, *T. coffea*, *T. congica*, *T. dageti*, *T. discolor*, *T. guineensis*, *T. louka*, *T. margaritacea*, *T. nyongana*, *T. rendalli*, *T. tholloni*, *T. walteri*, and *Tilapia* spec. aff. *guineensis* "Cross". In this analysis PC I explained 93.95 % of variance, PC II 2.63 % and PC III 0.62 %. The remaining, strongly overlapping *Coptodon* are *T. zillii*, *T. ismailiaensis* and

*T. kottae*, and members of the Lake Bermin species flock. A PCA without potentially confounding variation of the specimens of *T. zillii*, *T. ismailiaensis*, *T. kottae*, and members of the Lake Bermin species flock, confirms the morphometric discreteness of all Ejagham taxa as compared to all 14 of the other *Coptodon* species analysed, i.e. the overlap between the 95 % confidence interval (not shown) of these two groups is minimal and contains no specimen data (Fig. 1b). Here, PC I explained 94.53 % of variance, PC II 2.68 % and PC III 0.57 %. The highest loadings on PC II were identified for the character caudal peduncle length (Tab. 1).

The remaining species *T. zillii*, *T. ismailiaensis* and *T. kottae*, and members of the Lake Bermin species flock, i.e. *T. bakossiorum*, *T. bemini*, *T. bythobates*, *T. flava*, *T. gutturosa*, *T. imbriferna*, and *T. snyderae* were subjected to species by species comparisons with Ejagham species. All ten species were distinguishable from any Ejagham species based on either discrete character states or a combination of characters.

The two forms referred as *T. cf. deckerti* “little-black” and *T. cf. deckerti* “large-black” in Schliewen et al. (2001) (hence *Tilapia fusiforme* spec. nov., described below) are characterized by a slender fusiform body, an acute mouth, a black breeding coloration and the “tilapia spot” being extended to a longitudinal stripe in juveniles, i.e. characters not shared by any other *Coptodon* (Schliewen et al. 2001).

*Tilapia deckerti* and *Tilapia nigrans* spec. nov. (described below) are distinguished from all remaining *Coptodon* except from *T. ejagham* spec. nov., *T. ismailiaensis*, and *T. kottae* (pharyngeal jaw not examined) by quadricuspid or pentacuspid posterior pharyngeal teeth on lower pharyngeal jaw vs. bicuspid (only *T. gutturosa*) to tricuspid posterior pharyngeal jaw teeth; however, both differ from *T. kottae* in a narrower interorbital width (9.4-12.2 % vs. 12.4-14.0 % of SL) and from *T. ismailiaensis* in longer lower jaw length (13.8-17.3 % vs. 11.8-12.0 % of SL); furthermore, *T. deckerti* differs from *T. ejagham* spec. nov. in a larger eye length (8.5-10.7 % vs. 6.2-8.4 % of SL), and *T. nigrans* spec. nov. differs from *T. ejagham* spec. nov. in having dark square-shaped blotches at the base of each flank scale (filled or with a light coloured window at centre of blotch), vs. a flank scale coloration with dark scale margins and a light centre, especially on scales below lateral line.

*T. ejagham* spec. nov. differs from *T. kottae* in narrower interorbital width (9.2-12.2 % vs. 12.4-14.0 % of SL), from *T. imbriferna* in shorter head length (32.6-39.7 % vs. 40.1-42.6 % of SL), from *T. thysi* in higher number of gill rakers on first ceratobranchial (9-10 vs. 7-8), from *T. snyderae* in longer snout length (13.5-16.9 % vs. 11.3-13.3 % of SL), from *T. bakossiorum* in

longer cheek depth (12.0-15.4 % vs. 8.7-11.2 % of SL), from *T. bythobates* in shorter caudal peduncle length (12.6-15.7 % vs. 15.9-17.5 % of SL), from *T. flava* and *T. gutturosa* in deeper caudal peduncle depth (13.0-15.1 % vs. 11.4-12.5 % of SL), from *T. ismailiaensis* in longer lower jaw length (12.4-16.2 % vs. 11.8-12.0 % of SL), from *T. bemini* in robust, non-spatulate outer row jaw teeth (vs. gracile spatulate teeth), from *T. deckerti* in smaller eye length (6.2-8.4 % vs. 8.5-10.7 % of SL) and from *T. nigrans* spec. nov. in flank scale coloration with dark scale margins and a light centre, especially on scales below lateral line vs. dark square-shaped blotches at base of each flank scale (filled or with a light coloured window at centre of blotch).

Morphometric differentiation between *T. zillii*, *T. spongotroktis*, and *T. ejagham* spec. nov. had to be assessed using PCAs with only these taxa, because no single diagnostic character was identifiable. In the *T. zillii*–*T. ejagham* spec. nov. PCA (Fig. 2), PC I explained 95.47 % of variance, PC II 1.42 % and PC III 0.95 %. The highest loadings on PC III were identified for the character snout length (data not shown). In the *T. spongotroktis*–*T. ejagham* spec. nov. PCA (Fig. 3), PC I explained 95.94 % of variance, PC II 1.69 % and PC III 0.76 %. The highest loadings on PC III were identified for the character interorbital width (data not shown). When plotting PC II vs. PC III, both analyses did not reveal any overlap with *T. ejagham* spec. nov. data, hereby supporting its morphometric distinctiveness based on a combination of characters with regard to *T. spongotroktis* and *T. zillii* (further details see Diagnosis of *Tilapia ejagham* spec. nov. below).

### Morphological distinction between Lake Ejagham species

No discrete morphometric differentiation is evident between the five Ejagham phenotypes using PCA plots of PC II vs. PC III (data not shown). However, *T. fusiforme* spec. nov. differ from all other *Tilapia* in Lake Ejagham by their black breeding coloration and “tilapia spot” extended to a longitudinal stripe in juveniles as already described in Schliewen et al. (2001). In addition, they differ from *T. nigrans* spec. nov. and *T. deckerti* in having a more slender body (body depth 30.8-34.7 % vs. 34.9-40.2 % of SL) and from *T. ejagham* spec. nov. in having a shorter snout length (10.3-13.3 % vs. 13.5-16.9 % of SL). Both forms are not morphometrically diagnosable among each other even in a pairwise comparison (Fig. 4); the only discrete difference among them is size at reproduction (Schliewen et al. 2001).



Fig. 7. Estimated population structure. Each individual is represented by a thin vertical line, which is partitioned into K coloured segments that represent the individual's estimated membership fractions in K clusters. Black lines separate individuals of different populations. ■, *Tilapia nigrans* spec. nov.; ■, *T. deckerti*; ■, *T. fusiforme* spec. nov. form "large-black" and *T. fusiforme* spec. nov. form "little-black"; ■, *T. ejagham* spec. nov. The specimen marked with the star is a misidentification and belongs to *T. fusiforme* spec. nov.

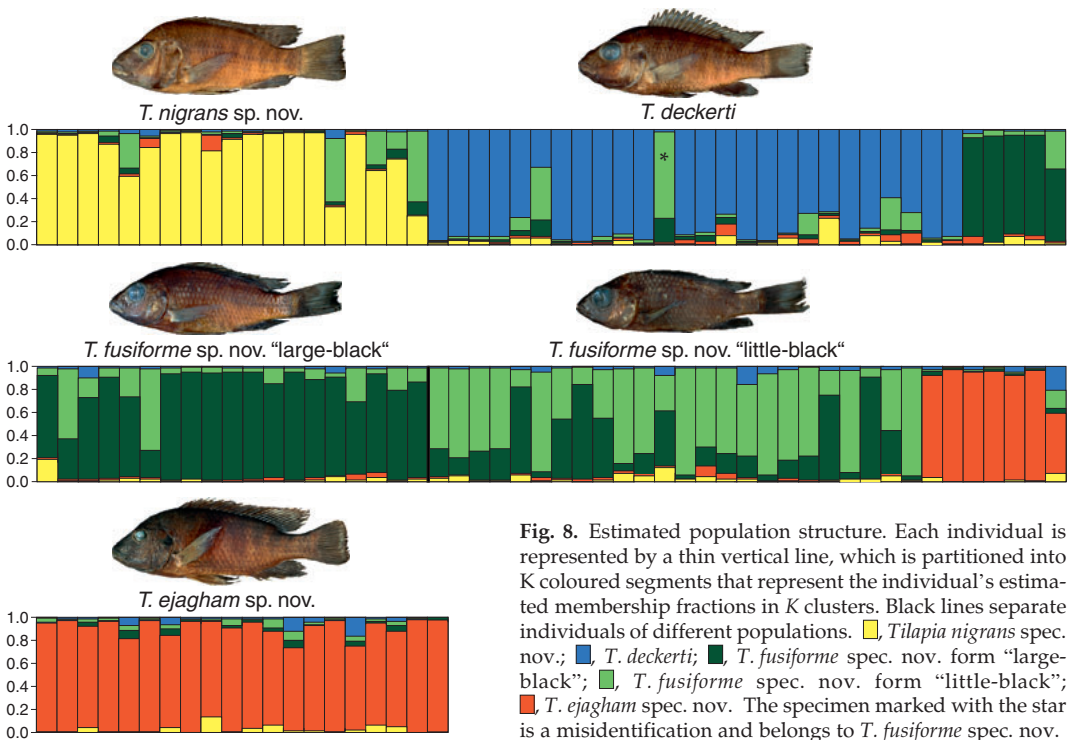


Fig. 8. Estimated population structure. Each individual is represented by a thin vertical line, which is partitioned into K coloured segments that represent the individual's estimated membership fractions in K clusters. Black lines separate individuals of different populations. ■, *Tilapia nigrans* spec. nov.; ■, *T. deckerti*; ■, *T. fusiforme* spec. nov. form "large-black"; ■, *T. fusiforme* spec. nov. form "little-black"; ■, *T. ejagham* spec. nov. The specimen marked with the star is a misidentification and belongs to *T. fusiforme* spec. nov.

*T. ejagham* spec. nov. differs from *T. deckerti* in smaller eye length (6.2-8.4 % vs. 8.5-10.7 % of SL) and from *T. nigrans* spec. nov. in flank scales with dark scale margins and a light centre, especially on scales below lateral line vs. dark square-shaped blotches at base of each flank scale (filled or with a light coloured window at the centre of the blotch). *T. deckerti* differs from *T. nigrans* spec. nov. in shorter snout length (12.7-15.6 % vs. 15.8-18.2 % of SL).

*T. deckerti* always has quadricuspid pharyngeal teeth as compared to *T. nigrans* spec. nov. (rarely quadricuspid). The largest reproductively active *T. deckerti* specimen are smaller than the smallest reproductively active specimens of *T. nigrans* spec. nov. (60.2-102.2 vs. 105.5-151.5 mm of SL).

### Population genetic differentiation

We reanalysed microsatellite data already used in Schliewen et al. (2001) (five loci, 120 specimens) using a Bayesian clustering algorithm to calculate individual assignment to a number of K groups within the Lake Ejagham species assemblage. After applying, the estimation method for K described by Evanno et al. (2005), the most likely number of groups explaining population structure within the Lake Ejagham data set was identified as K=4 populations (Figs 5, 6; without regarding the always most likely value of K=2). Using the K=4 prior and the admixture model in structure, *T. nigrans* spec. nov., *T. deckerti*, combined the two forms of *T. fusiforme* spec. nov., and *T. ejagham* spec. nov. were identified as separate populations (Fig. 7). We also analysed the data with a K=5 prior, because Schliewen et al. (2001) provided evidence for differentiation of the two forms of *T. fusiforme* spec. nov. based on small but significant differences in pairwise  $F_{ST}$  values. This result was confirmed as visualized in the bar plot of the *structure* analysis for K=5 (Fig. 8) by showing a slight but not complete differentiation of the two forms of *T. fusiforme* spec. nov. Hence, the two forms appear not yet fully reproductively isolated, i.e. they are incipient rather than fully differentiated species. In contrast, *T. nigrans* spec. nov., *T. ejagham* spec. nov., and *T. deckerti* appear well differentiated from each other and from the two forms of *T. fusiforme* spec. nov.

In summary, all Ejagham taxa are morphologically discernable from all described *Tilapia* (*Coptodon*) species, and *T. fusiforme* spec. nov., *T. nigrans* spec. nov., and *T. ejagham* spec. nov. are morphologically diagnosable. Therefore, we formally describe these three new species from Lake Ejagham and redescribe *T. deckerti*.

### Taxonomy

#### *Tilapia ejagham* spec. nov.

Figs 9, 10; Tab. 2

*Tilapia deckerti* (partim) – Thys van den Audenaerde, 1967  
(Photo Fig. 1)

*Tilapia* spec. “predator” – Schliewen et al., 2001

**Holotype.** ZSM 40074 (174.7 mm SL), Cameroon, Lake Ejagham (5°45'4.37" N 8°59'0.92" E), U. Schliewen, Mar 1993-Oct 1994.

**Paratypes.** ZSM 40075 (25, 76.0-199.5 mm SL), collected with holotype.

**Additional material.** ZSM 40076 (23, 46.6-186.6 mm SL), collected with holotype.

**Differential diagnosis.** *Tilapia ejagham* spec. nov. differs from all other *Tilapia* sensu lato except *T. joka* Thys van den Audenaerde, 1969, *T. bilineata* Pellgrin, 1900, and all members of the subgenus *Coptodon* (including *T. ismailiaensis* and *T. camerunensis*) in tricuspid (rarely quadricuspid) pharyngeal teeth in the posterior two rows of lower pharyngeal jaw. It differs from *T. joka* in more gill rakers on first ceratobranchial (9-10 vs. 6-8), from *T. bilineata* in not having a densely scaled caudal fin. *Tilapia ejagham* spec. nov. differs from *T. walteri*, *T. rendalli*, *T. congica* and *T. dageti* in lower body depth (33.8-40.6 % vs. 41.4-51.3 % of SL), from *T. camerunensis* in lesser number of dorsal rays (10-12 vs. 13-14), from *T. kottae* in narrower interorbital width (9.2-12.2 % vs. 12.4-14.0 % of SL), from *T. imbriferina* in shorter head length (32.6-39.7 % vs. 40.1-42.6 % of SL), from *T. thysi* in higher number of gill rakers on first ceratobranchial (9-10 vs. 7-8), from *T. snyderae* in longer snout length (13.5-16.9 % vs. 11.3-13.3 % of SL), from *T. bakossiorum* in higher cheek depth (12.0-15.4 % vs. 8.7-11.2 % of SL), from *T. bythobates* in shorter caudal peduncle length (12.6-15.7 % vs. 15.9-17.5 % of SL), from *T. guineensis*, *T. margaritacea*, *T. discolor*, *T. tholloni*, *T. flava*, and *T. guttuosa* in a lower caudal peduncle depth (13.0-15.1 % vs. 15.2-19.2 % of SL), from *T. ismailiaensis*, *T. camerunensis*, *T. coffea*, *T. louka*, *T. nyongana*, and *T. spec. aff. guineensis* “Cross” in greater lower jaw length (12.4-16.2 % vs. 7.8-12.2 % of SL) and from *T. bemini* in robust, non-spatulate outer row jaw teeth (vs. gracile spatulate teeth). *T. ejagham* spec. nov. differs from *T. deckerti* in shorter eye length (6.2-8.4 % vs. 8.5-10.7 % of SL), from *T. nigrans* spec. nov. in flank scales with dark scale margins and a light centre, especially on scales below the lateral line vs. dark square-shaped blotches at base of each flank scale (filled or with a light coloured window at centre of blotch) and from *T. fusiforme* spec. nov. in greater



snout length (13.5-16.9 % vs. 10.3-13.3 % of SL). *T. spongotroktis* is distinguishable by combination of characters as visualized in a PCA plot (Fig. 3); here, highest loadings of PC III are noticeable for the characters interorbital width (0.5273), lower jaw length (-0.4598) and caudal peduncle length (0.3414). *T. zillii* is distinguished by a combination of characters as visualized in a PCA plot (Fig. 2), the separation in the plot is based on a combination of PC II and PC III. Highest loadings of PC II are noticeable for the characters anal spine length (-0.5467) and length of last dorsal spine (-0.4171). The highest loadings

of PC III are the characters snout length (-0.4189), lower jaw length (-0.2311), caudal peduncle depth (0.3113) and head length (-0.2433). With a combination of only those characters *T. spongotroktis* as well as *T. zillii* are unambiguously distinguished from *T. ejaquam* spec. nov.

**Description**

**Shape.** Morphometric and meristic data for holotype and 25 paratypes in Table 2. See Figs 9 and 10 for general appearance. *T. ejaquam* spec. nov. is

**Table 2.** Measurements and counts for holotype and 25 paratypes of *Tilapia ejaquam* spec. nov.

	holotype	holotype + paratypes				n
		min	max	mean	SD	
<b>Measurements</b>						
Total length (mm)	210.8	95.3	241.6	147.9		
Standard length SL (mm)	174.7	76.3	199.5	120.9		
<b>in percents of SL</b>						
Head length	33.3	32.6	39.7	35.5	2.1	26
Interorbital width	11.8	9.2	12.2	10.7	0.9	26
Preorbital width	12.0	10.9	13.0	11.8	0.6	26
Horizontal eye length	6.2	6.2	8.4	7.5	0.7	26
Snout length	14.9	13.5	16.9	15.4	1.0	26
Internostril distance	8.1	7.3	8.6	7.8	0.3	26
Cheek depth	14.8	12.0	15.4	13.6	0.8	26
Upper lip length	11.0	9.6	12.8	10.7	0.7	26
Lower lip length	11.2	9.3	12.7	10.8	0.8	26
Lower lip width	12.7	11.2	15.2	13.1	1.0	26
Lower jaw length	13.1	12.4	16.2	14.1	1.2	26
Predorsal distance	39.4	37.5	46.2	40.5	1.9	26
Dorsal-fin base length	55.1	51.1	58.6	54.0	2.2	26
Last dorsal-fin spine length	15.5	11.3	17.8	14.5	1.8	26
Anal-fin base length	16.5	14.3	17.8	15.8	0.8	26
Third anal-fin spine length	12.8	10.0	15.8	12.7	1.6	26
Pelvic-fin length	29.1	22.9	32.2	28.3	2.3	26
Pectoral-fin length	28.2	25.1	34.0	28.6	2.5	26
Caudal peduncle depth	13.7	13.0	15.1	14.0	0.7	26
Caudal peduncle length	14.3	12.6	15.7	14.3	0.8	26
Body depth (pelvic-fin base)	37.7	33.8	40.6	37.4	1.7	26
Preanal length	71.4	70.5	75.1	72.8	1.0	26
Anus-anal-fin base distance	5.4	4.6	6.1	5.3	0.4	26
<b>Counts</b>						
Dorsal-fin spines	15		15 (20); 16 (6)			26
Dorsal-fin rays	12		10 (1); 11 (11); 12 (14)			26
Anal-fin rays	9		8 (6); 9 (17); 10 (3)			26
Pectoral-fin rays	14		13 (7); 14 (17); 15 (2)			26
Scales (horizontal line)	26		25 (1); 26 (10); 27 (15)			26
Upper lateral line scales	19		19 (11); 20 (11); 21 (4)			26
Lower lateral line scales	11		10 (2); 11 (13); 12 (10); 13 (1)			26
Gill rakers (lower)	9		9 (11); 10 (15)			26
Gill rakers (upper)	4		4 (23); 5 (3)			26



Fig. 9. Preserved holotype of *Tilapia ejagham* spec. nov. (ZSM 40074), 174.7 mm SL; Cameroon: Lake Ejagham.



Fig. 10. *T. ejagham* spec. nov. a. Non breeding male of, large specimen. b. Non breeding small specimen. c. Breeding pair in shallow water.

a large *Tilapia* (maximum observed size 199.5 mm SL) with a laterally compressed body. Dorsal head profile moderately concave from insertion of first dorsal spine to upper margin of eye henceforward the head profile changes to slightly convex. Large and compact head. Snout outline obtuse. Eye small and interorbital width always larger than eye length. Greatest body depth at level of first dorsal spine. Dorsal line slightly posteroventrally curved. Caudal peduncle as long as deep.

**Squamation.** Body scales cycloid, chest scales smaller than flank scales and slightly embedded. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal ray. Upper lateral line separated from first dorsal spine by two



Fig. 11. Outer shape and shape of the dentigerous plate of *T. ejagham* spec. nov.



Fig. 12. Outer shape of lower jaw teeth of **a**, *T. fusiforme* spec. nov. form “large-black”; **b**, *T. fusiforme* spec. nov. form “little-black”; **c**, *Tilapia nigrans* spec. nov.; **d**, *T. deckerti*; **e**, *T. ejagham* spec. nov.

to three scale rows. Lower lateral line originating at level of first dorsal branched rays and terminates midlaterally on caudal peduncle. One or two scales of lower lateral line extending onto caudal fin. Two scale rows between upper and lower lateral line. Preoperculum with three to four regular rows. Lower one third of pectoral base mostly lacking scales.

**Gill rakers.** First ceratobranchial with 9-10 gill rakers and first upper gill-arch with 4-5 gill rakers. Ceratobranchial rakers stout, broader on base, pointed. Gill raker in angle of arch and first four

epibranchial rakers more slender, decreasing in size towards last.

**Fins.** Origin of dorsal fin at level of origin of pelvic fin. First dorsal spine always shortest, last dorsal spine always longest. Longest spines always shorter than longest ray. Last dorsal ray most deeply branched. Caudal fin outline truncate. Third anal spine always longest. Tip of longest anal fin ray in most cases overlapping hypuralia. Last dorsal ray most deeply branched. Tip of longest pelvic-fin ray mostly reaching anus.



Fig. 13. Outer shape and number of cusps of posterior pharyngeal teeth of lower pharyngeal jaw of **a**, *T. fusiforme* spec. nov. form “large-black”; **b**, *T. fusiforme* spec. nov. form “little-black”; **c**, *T. ejagham* spec. nov.



**Fig. 14.** Map of the area surrounding Lake Ejagham, named Eyumojok, the next village to the lake; the Cross River is the neighbouring river-system.

**Jaws and dentition.** Jaws isognathous. Upper and lower outer teeth rows in both jaws bicuspid. Neck of anterior jaw teeth stout (i. e. width about equal over whole length of the teeth), crown expanded and cusps truncated (Fig. 12). Two to four incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad, anterior keel shorter than toothed area (Fig. 11). Posterior pharyngeal teeth tricuspid (rarely quadricuspid) (Fig. 13), stout, slightly hooked and regularly arranged, especially over the posterior third of the toothed area. Dentigerous plate triangular. Most of teeth in anterior two thirds of toothed area approach the “kukri” tooth shape (sensu Greenwood, 1987).

**Coloration in alcohol (adult specimen).** Basic coloration brownish, with head and dorsal side darker than ventral side. Flank scales with dark scale margins and light centre, especially on scales below lateral line. Lower lip light brownish to whitish and upper lip darker.

Markings on body: Six to seven dark vertical bars on dorsum and sides (first bar at level of first dorsal spine, last two on caudal peduncle) and a nape band, second vertical bar deeply bifurcated. Vertical bars sometimes not present. No longitudinal mid-lateral band. Dark and broad lachrymal stripe extending from lachrymal to jaw angle; dark opercular spot.

Fins: Pectoral fins transparent. Pelvic fins light brownish, margins transparent. Anal fin dark brownish, margins transparent. Caudal fin either dark brownish and margins transparent or completely light brownish with light dots in the upper part. Dorsal fin dark brownish, margins transparent,

“tilapia spot” mostly not visible, if visible some light dots in soft ray part of dorsal fin are also present.

**Coloration in life (adult specimen)** (Fig. 10). Non breeding coloration: Basic coloration light greyish, chest and belly pale. Upper lip dark and lower lip whitish. A horizontal iridescent blue line above antero-rostral margin of preopercle. Iris of eyes bright red. Body with six to seven black dark vertical bars and a nape band. Second bar always deeply bifurcated. Dark broad lachrymal stripe extending from lachrymal to jaw angle; dark opercular spot. All fins with yellow coloration at margins except pectoral fins. Upper part of caudal fin with yellow dots. In soft part of dorsal fin “tilapia spot” and a few yellow spots.

Breeding coloration: Basic coloration dark brown to blackish, especially on head, chest and belly pale. Upper lip dark brownish and lower lip whitish. A horizontal iridescent blue line above antero-rostral margin of preopercle. Iris of eyes bright red. No vertical bars. Pectoral and pelvic fins transparent. Anal fin dark brownish, margins bright yellow. Caudal fin dark brownish, margins bright yellow, no dots visible. Spiny part of dorsal fin transparent with bright yellow margins and soft part with “tilapia spot” and a few yellow spots, margins slightly yellow.

**Distribution and ecology** (Fig. 14). Only known from Lake Ejagham (Cameroon), where non-breeding individuals are observed both inshore and in the benthic deepwater region. *T. ejagham* spec. nov. pairs breed exclusively in the shallow inshore region above 2 m. Pairs excavate large nest-pits under large branches or logs. In life, non-breeding *T. ejagham* spec. nov. are moving solitarily and are and appear to permanently scan their environment for prey while swimming permanently without a hast, and rarely being motionless. Rare observations suggest that this species are predators of small fish, mostly juvenile cichlids. During underwater observations it is readily identifiable for the trained observer by their typical snout facies in combination with their “scan/swim” behavior.

**Etymology.** The species name *ejagham* refers both to Lake Ejagham as well as to the Ejagham people, whose major sacred site is Lake Ejagham. A noun in apposition.

**Note.** The photograph in the original description of a freshly collected specimen does not show *T. deckerti* spec. nov., but most likely a *T. ejagham* spec. nov. specimen. However, a critical examination of this specimen, which was not preserved, was not possible.

***Tilapia deckerti* Thys van den Audenaerde, 1967**  
Figs 15, 16; Tab. 3

*Tilapia* spec. "jewel" – Schliewen et al., 2001

**Holotype.** ZMB 32754 (102.2 mm SL), Cameroon, Toter See b. Ossidinge [Lake Ejagham], Dr. Mansfeld, 10-20 Sep 1907.

**Material examined.** ZSM 40077 (18, 60.0-88.9 mm SL), Cameroon, Lake Ejagham (5°45'4.37" N 8°59'0.92" E), U. Schliewen, Mar 1993-Oct 1994. ZSM 40088 (1, 71.5 mm SL), collected with ZSM 40077.

**Additional material.** ZSM 40078 (6, 64.6-77.9 mm SL), collected with ZSM 40077.

**Notes on type material of *Tilapia deckerti* Thys van den Audenaerde, 1967.** According to the description (Thys van den Audenaerde, 1967), the holotype is the medium-sized specimen of the type series (ZMB 16758, according to the description including all three type specimens). We obtained in our type material request from ZMB two lots with each one specimen, ZMB 16758 with a specimen of 74.1 mm SL (our

**Table 3.** Measurements and counts for holotype and 19 additional specimens of *Tilapia deckerti*.

	holotype	additional specimens				n
		min	max	mean	SD	
<b>Measurements</b>						
Total length (mm)	124.9	75.6	124.9	97.9		20
Standard length SL (mm)	102.2	60.2	102.2	78.3		20
<b>in percents of SL</b>						
Head length	34.5	35.3	39.0	36.9	1.2	20
Interorbital width	10.7	9.4	12.2	10.6	0.7	20
Preorbital width	11.8	11.8	13.7	12.3	0.5	20
Horizontal eye length	9.2	8.5	10.7	9.6	0.8	20
Snout length	13.8	12.7	15.6	14.8	0.7	20
Internostril distance	7.0	7.3	9.1	8.2	0.5	20
Cheek depth	12.1	11.9	14.5	13.0	0.7	20
Upper lip length	9.7	10.4	12.9	11.1	0.7	20
Lower lip length	9.6	10.6	12.9	11.2	0.7	20
Lower lip width	11.8	11.8	15.3	13.2	0.9	20
Lower jaw length	12.9	13.8	16.5	14.5	0.7	20
Predorsal distance	40.5	41.2	46.1	42.1	1.2	20
Dorsal-fin base length	54.5	50.6	54.7	52.7	1.2	20
Last dorsal-fin spine length	13.1	11.0	16.6	13.8	1.6	20
Anal-fin base length	15.0	13.7	16.1	15.2	0.6	20
Third anal-fin spine length	11.8	9.9	15.3	13.0	1.4	20
Pelvic-fin length	22.2	22.2	32.3	27.6	2.6	20
Pectoral-fin length	28.0	26.9	32.2	29.5	1.6	20
Caudal peduncle depth	14.4	13.2	14.7	14.0	0.5	20
Caudal peduncle length	15.9	13.4	15.6	14.6	0.7	20
Body depth (pelvic-fin base)	37.8	36.0	40.0	37.6	0.9	20
Preanal length	72.8	71.7	75.2	73.4	0.9	20
Anus-anal-fin base distance	5.9	4.6	6.1	5.4	0.4	20
<b>Counts</b>						
Dorsal-fin spines	15		14 (1); 15 (6); 16 (13)			20
Dorsal-fin rays	12		11 (15); 12 (5)			20
Anal-fin rays	8		8 (6); 9 (14)			20
Pectoral-fin rays	14		13 (5); 14 (15)			20
Scales (horizontal line)	26		25 (1); 26 (12); 27 (7)			20
Upper lateral line scales	19		18 (3); 19 (4); 20 (8); 21 (4); 22 (1)			20
Lower lateral line scales	10		10 (4); 11 (11); 12 (5)			20
Gill rakers (lower)	8		8 (2); 9 (14); 10 (4)			20
Gill rakers (upper)	4		3 (2); 4 (14); 5 (4)			20



Fig. 15. Preserved holotype of *Tilapia deckerti* (ZMB 32754), 102.2 mm SL; Cameroon: Lake Ejagham.

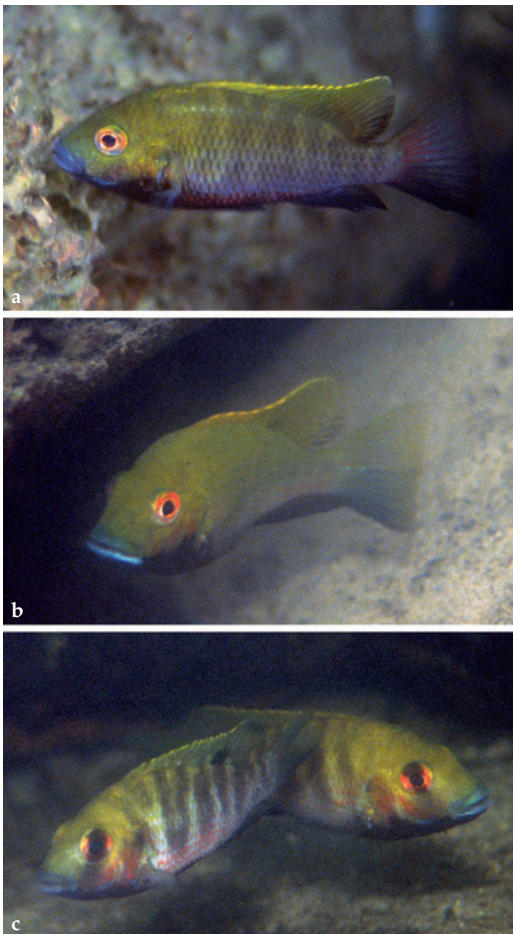


Fig. 16. *T. deckerti*. a. Non breeding specimen. b. Male without vertical bars. c. Breeding pair in shallow water.

measurement), and ZMB 32754 with a specimen of 102.2 mm (our measurement). In addition, Thys van den Audenaerde mentioned, that the largest paratype was given to Tervuren, and we obtained MRAC 157495 with 153.2 mm SL (our measurement). Apparently, the two ZMB types were later separated into two lots, with the medium-sized specimen put into ZMB 32754, the smallest to ZMB 16758. This contradicts the original description, therefore we conclude that the medium-sized specimen is the holotype and that it has to retain the original ZMB number 16758, and the smallest specimen is to be labelled with ZMB 32754.

Holotype has quadricuspid pharyngeal teeth, a character which is only shared among *T. deckerti*, *T. nigrans* spec. nov. and partially with *T. ejagham* spec. nov. We assigned the discoloured holotype to *T. deckerti*, because it differs from *T. nigrans* spec. nov. specimens in shorter snout length (13.8 % in holotype, 12.7-15.6 % vs. 15.8-18.2 % of SL) and from *T. ejagham* spec. nov. specimens in larger eye length (9.2 % in holotype, 8.5-10.7 % vs. 6.2-8.4 % of SL). Paratypes are in bad condition and do not belong to *T. deckerti*, as the larger of the two (MRAC 157495) has pentacuspid pharyngeal teeth and is therefore clearly assignable to *T. nigrans* spec. nov.; the small paratype (ZMB 16758) is assignable to *T. fusiforme* spec. nov., because it differs from *T. ejagham* spec. nov. and from *T. nigrans* spec. nov. in shorter snout length (12.2 % in paratype 10.3-12.5 % (*T. fusiforme* spec. nov.) vs. 13.5-18.2 % of SL) and from *T. deckerti* in lower body depth (34.4 % in paratype 30.8-34.7 % (*T. fusiforme* spec. nov.) vs. 36.0-40.0 % of SL).

**Differential diagnosis.** *Tilapia deckerti* differs from all other *Tilapia sensu lato* except for a few members of the subgenus *Coptodon* in quadricuspid posterior pharyngeal teeth on lower pharyngeal jaw, a char-

acter shared only with *T. tholloni*, *T. camerounensis*, *T. dageti*, *T. congica*, *T. ejagham* spec. nov., and *T. nigrans* spec. nov. (pharyngeal jaws of *T. ismailiaensis* and *T. kottae* not examined). *Tilapia deckerti* differs from *T. camerounensis* and *T. dageti* in lower length of dorsal fin base (50.6-54.7 % vs. 57.2-65.0 % of SL), from *T. tholloni* in higher predorsal distance (41.2-46.1 % vs. 35.6-40.7 % of SL), from *T. congica* in lower body depth (36.0-40.0 % vs. 41.5-49.2 % of SL), from *T. kottae* in narrower interorbital width (9.4-12.2 % vs. 12.4-14.0 % of SL), and from *T. ismailiaensis* in longer lower jaw length (13.8-16.5 % vs. 11.8-12.0 % of SL). Differences to *T. nigrans* spec. nov. are based on a combination of morphometric, life history, genetic and ecological data, i. e. a shorter snout length (12.7-15.6 % vs. 15.8-18.2 % of SL), by breeding exclusively in the shallow water above 2 m water depth (vs. excavated caves below 5 m depth); analysis of population structure using microsatellite alleles within Lake Ejagham members supports the view that *T. deckerti* is reproductively isolated from *T. nigrans* spec. nov. (see Results). Largest reproductively active *T. deckerti* specimens are smaller than smallest reproductively active specimens of *T. nigrans* spec. nov. (60.2-102.2 vs. 105.5-151.5 mm of SL). It differs from *T. ejagham* spec. nov. in larger eye length (8.5-10.7 % vs. 6.2-8.4 % of SL).

### Description

**Shape.** Morphometric and meristic data for holotype and 19 additional specimens in Table 3. See Figs 15 and 16 for general appearance. *T. deckerti* is a medium-sized *Tilapia* (maximum observed size 102.2 mm SL) with a laterally compressed body. Large and compact head, head profile slightly concave. Snout outline obtuse. Eye large and interorbital width always greater than eye length. Greatest body

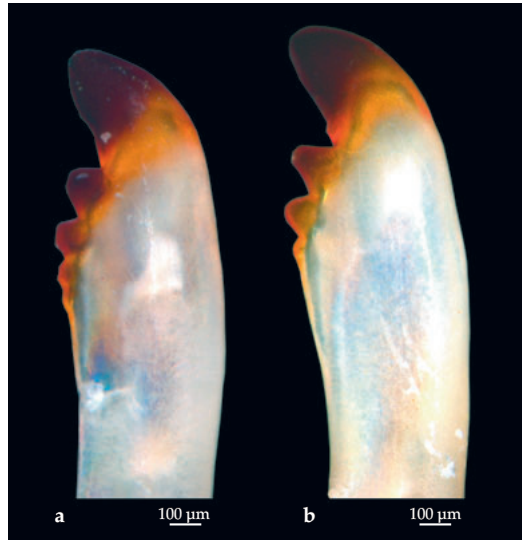


Fig. 17. Outer shape and number of cusps of posterior pharyngeal teeth of lower pharyngeal jaw of **a**, *T. deckerti*; **b**, *T. nigrans* spec. nov.

depth at level of first dorsal spine. Dorsal line slightly posteroventrally curved. Caudal peduncle about as long as deep or slightly longer.

**Squamation.** Body scales cycloid, scales on chest smaller than flank scales and deeply embedded. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal ray. Upper lateral line separated from first dorsal spine by two to three scale rows. Lower lateral line originating at level of first dorsal branched rays and terminating midlaterally on caudal peduncle. One or two scales of lower lateral line extending onto caudal fin. Two



Fig. 18. Preserved specimen of *Tilapia deckerti* (ZSM 40088), 71.5 mm SL; Cameroon: Lake Ejagham.

scale rows between upper and lower lateral line. Preoperculum with three to four regular rows. Lower one third of pectoral base mostly scaled.

**Gill rakers.** First ceratobranchial with 8-10 gill rakers and first upper gill-arch with 3-5 gill rakers. Ceratobranchial rakers stout, broader on base, pointed. Gill raker in angle of arch and first four epibranchial rakers more slender, decreasing in size towards last.

**Fins.** Origin of dorsal fin at level of origin of pelvic fin. First dorsal spine always shortest, last dorsal spine always longest. Longest spines always shorter than longest ray. Last dorsal ray most deeply branched. Caudal fin outline truncate. Third anal spine always longest. Tip of longest anal fin ray overlapping hypuralia. Last dorsal ray most deeply branched. Tip of longest pelvic-fin ray in most specimens reaching anus, in rare cases terminating slightly before anus.

**Jaws and dentition.** Jaws isognathous. Teeth in upper and lower outer row in both jaws bicuspid. Neck of anterior jaw teeth stout (i.e. width about equal over whole length of the teeth), crown expanded and cusps truncated (Fig. 12). One to three incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad, anterior keel shorter than toothed area (Fig. 11). Posterior pharyngeal teeth quadricuspid (Fig. 17), stout, slightly hooked and regularly arranged, especially over posterior third of toothed area. Dentigerous plate triangular. Most of teeth in anterior two thirds of toothed area approach the “kukri” tooth shape (sensu Greenwood, 1987).

**Coloration in alcohol.** (Fig. 18) Basic coloration brownish. Dorsal side dark brownish, ventral side light brownish. Flank scales with dark scale margins and a light centre on scales below lateral line (not always present). Lower lip light brownish to whitish, upper lip darker. Lower side of head completely black. Chest and lower side of head blackish or with blackish areas, sometimes extending onto light coloured belly.

Markings on body: Seven to eight dark vertical bars on dorsum and sides (first bar at level of first dorsal spine, last two on caudal peduncle) and a nape band. Second vertical bar deeply bifurcated. Vertical bars sometimes not present. No longitudinal mid-lateral band. Dark broad lachrymal stripe extending from lachrymal to jaw angle; dark opercular spot.

Fins: Pectoral fins transparent. Pelvic fins blackish. Anal fin dark brownish, margins transparent. Caudal fin either dark brownish and margins transparent or lower part dark brownish with light dots in the upper part. Dorsal fin dark brownish, margins

transparent, “tilapia spot” always visible, with some light dots in soft part behind “tilapia spot”.

**Coloration in life** (Fig. 16). Basic coloration silvery-bluish to brown-greyish, chest and belly blackish-red, dorsum yellow-greenish to bright yellow in courting individuals. Lower half of head completely black, upper half of head yellow-greenish. Upper lip light bluish and lower lip whitish. A horizontal iridescent blue line above antero-rostral margin of preopercle. Iris bright red. Apparently depending on motivational state, i.e. during parental care, body with seven to eight black dark vertical bars, nape band, supraorbital and interorbital stripe. Second vertical bar always deeply bifurcated. Dark broad lachrymal stripe extending from lachrymal to jaw angle; dark opercular spot. Pectoral fins transparent, pelvic fins and anal fin with black tips. Dorsal fin yellow edged, “tilapia spot” well visible, sometimes light dots in soft part of dorsal fin behind “tilapia spot”. Caudal fin either completely greyish or upper half pale with few yellow dots and lower half blackish.

**Distribution and ecology** (Fig. 14). Only known from Lake Ejagham (Cameroon). Breeds in shallow water above 2 m water depth (Schliewen et al. 2001), where pairs excavate shallow pits often close to stones, branches or similar structures. Due to difficulties in differentiation between juveniles and subadults of *T. deckerti* and *T. nigrans* spec. nov. in the field, estimates of habitat choice of non-breeding fishes are not available, although the general impression is that *T. deckerti* is restricted to more shallow areas above 4 to 6 m depth.

**Note.** ZMB 16758 and MRAC 157495 were originally part of the type series *T. deckerti*. The type series however is polytypic, i.e. ZMB 16758 is identified as *T. fusiforme* spec. nov. and MRAC 157495 is *T. nigrans* spec. nov.

#### *Tilapia nigrans* spec. nov.

Figs 19, 20a,b; Tab. 4

*Tilapia deckerti* (partim) – Thys van den Audenaerde, 1967

*Tilapia* spec. “dark jewel” – Schliewen et al., 2001

**Holotype.** ZSM 40079 (117.5 mm SL), Cameroon, Lake Ejagham (5°45'4.37" N 8°59'0.92" E), U. Schliewen, Mar 1993-Oct 1994.

**Paratypes.** ZSM 40080 (17, 105.5-151.0 mm SL), collected with holotype.

**Additional material.** ZSM 40081 (5, 74.5-150.3 mm SL), collected with holotype. MRAC 157495 (1, 153.2 mm SL), Cameroon, Toter See bei Ossidinge [Lake Ejagham], Dr. Mansfeld, 10-20 Sep 1907.



**Differential diagnosis.** *Tilapia nigrans* spec. nov. differs from all other *Tilapia* sensu lato except for a few members of the subgenus *Coptodon* in quadricuspid to pentacuspid posterior pharyngeal teeth on lower pharyngeal jaw. Quadricuspid pharyngeal teeth in *Tilapia* are only known from *T. tholloni*, *T. cameronensis*, *T. dageti*, *T. congica*, *T. deckerti*, and partially from *T. ejagham* spec. nov. (pharyngeal jaws of *T. ismailiaensis* and *T. kottae* not examined). *Tilapia nigrans* spec. nov. differs from *T. cameronen-*

*sis*, *T. ismailiaensis* and *T. dageti* in longer lower jaw (13.9-17.3 % vs. 9.6-13.2 % of SL), from *T. tholloni* in longer snout length (15.8-18.2 % vs. 11.7-14.6 % of SL), from *T. congica* in lesser body depth (34.9-40.2 % vs. 41.5-49.2 % of SL), and from *T. kottae* in narrower interorbital width (10.0-11.8 % vs. 12.4-14.0 % of SL). Differences to *T. deckerti* are based on a combination of morphometric, life history, genetic and ecological data, e. g. in longer snout length (15.8-18.2 % vs. 12.7-15.6 % of SL), by breeding exclusively in excavated

**Table 4.** Measurements and counts for holotype and 17 paratypes of *Tilapia nigrans* spec. nov.

	holotype	holotype + paratypes				n
		min	max	mean	SD	
<b>Measurements</b>						
Total length (mm)	146.4	131.3	185.4	159.9		
Standard length SL (mm)	117.5	105.5	151.0	129.2		
<b>in percents of SL</b>						
Head length	37.7	35.8	39.0	37.1	0.9	18
Interorbital width	11.2	10.0	11.8	10.7	0.6	18
Preorbital width	13.0	12.0	13.4	12.7	0.4	18
Horizontal eye length	8.0	7.0	9.1	8.0	0.6	18
Snout length	17.2	15.8	18.2	16.8	0.8	18
Internostril distance	8.9	7.8	8.9	8.3	0.3	18
Cheek depth	15.2	13.5	15.7	14.6	0.7	18
Upper lip length	11.4	10.4	13.4	11.6	0.8	18
Lower lip length	11.6	10.5	13.3	11.6	0.7	18
Lower lip width	12.6	11.3	14.5	12.9	1.0	18
Lower jaw length	15.3	13.9	17.3	15.0	0.8	18
Predorsal distance	43.9	40.6	45.5	42.7	1.2	18
Dorsal-fin base length	54.0	50.9	57.1	53.6	1.7	18
Last dorsal-fin spine length	14.2	12.7	15.6	14.3	0.8	18
Anal-fin base length	15.7	14.2	18.2	15.8	1.0	18
Third anal-fin spine length	12.3	11.1	14.7	12.7	0.9	18
Pelvic-fin length	28.0	26.6	32.3	29.7	1.6	18
Pectoral-fin length	31.0	25.4	32.4	29.2	2.0	18
Caudal peduncle depth	14.7	13.0	15.0	14.1	0.5	18
Caudal peduncle length	15.5	13.5	16.0	15.0	0.7	18
Body depth (pelvic-fin base)	39.9	34.9	40.2	37.2	1.6	18
Preanal length	72.3	68.0	75.0	71.8	1.7	18
Anus-anal-fin base distance	5.9	4.1	6.9	5.6	0.7	18
<b>Counts</b>						
Dorsal-fin spines	15		14 (7); 15 (8); 16 (3)			18
Dorsal-fin rays	12		11 (3); 12 (11); 13 (4)			18
Anal-fin rays	9		8 (7); 9 (11)			18
Pectoral-fin rays	13		13 (10); 14 (8)			18
Scales (horizontal line)	26		26 (7); 27 (11)			18
Upper lateral line scales	21		18 (1); 19 (3); 20 (7); 21 (7)			18
Lower lateral line scales	11		10 (2); 11 (9); 12 (5); 13 (2)			18
Gill rakers (lower)	9		8 (2); 9 (13); 10 (3)			18
Gill rakers (upper)	5		4 (11); 5 (7)			18



Fig. 19. Preserved holotype of *Tilapia nigrans* spec. nov. (ZSM 40079), 117.5 mm SL; Cameroon: Lake Ejagham.

caves below 5 m water depth (vs. always breeding above 2 m); analysis of population structure using microsatellite alleles within Lake Ejagham members supports that *T. nigrans* spec. nov. is reproductively isolated from *T. deckerti* spec. nov. (see Results). The smallest reproductively active specimens of *T. nigrans* spec. nov. are larger than largest reproductively active *T. deckerti* specimen (105.5-151.5 vs. 60.2-102.2 mm of SL). It differs from *T. ejagham* spec. nov. in dark square-shaped blotches at base of each flank scale (filled or with a light coloured window at centre of blotch) vs. flank scales with a dark scale margin and a light centre, especially on scales below lateral line.

### Description

**Shape.** Morphometric and meristic data for holotype and 17 paratypes in Table 4. See Figs 19 and 20a,b for general appearance. *T. nigrans* spec. nov. is a large *Tilapia* (maximum observed size 151.0 mm SL) with a laterally compressed body. Dorsal head profile moderately concave from insertion of first dorsal spine to upper margin of eye henceforward head profile changes to slightly convex. Large and compact head. Snout outline obtuse. Eye moderately large and interorbital width always greater than eye length. Greatest body depth at level of first dorsal spine. Dorsal line slightly posteroventrally curved. Caudal peduncle somewhat longer than deep.

**Squamation.** Body scales cycloid, scales on chest smaller than flank scales and deeply embedded. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal ray. Upper lateral line separated from first dorsal spine by three to four scale rows. Lower lateral line originating at level of first dorsal branched rays and terminates midlaterally on caudal peduncle. One or two scales of lower lateral line extending onto caudal fin. Two

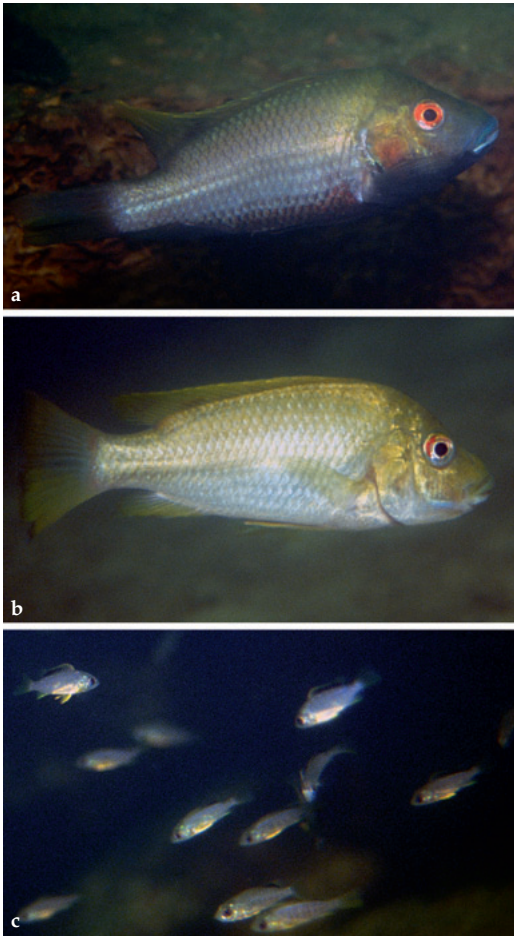
scale rows between upper and lower lateral line. Preoperculum with three to four irregular (adult) rows. Lower one third of pectoral base mostly lacking scales.

**Gill rakers.** First ceratobranchial with 8-10 gill rakers and first upper gill-arch with 4-5 gill rakers. Ceratobranchial rakers stout, broader on base, pointed. Gill raker in angle of arch and first four epibranchial rakers more slender, decreasing in size towards last.

**Fins.** Origin of dorsal fin at level of origin of pelvic fin. First dorsal spine always shortest, last dorsal spine always longest. Longest spines always shorter than longest ray. Last dorsal ray most deeply branched. Caudal fin outline truncate. Third anal spine always longest. Tip of longest anal fin ray overlapping hypuralia. Last dorsal ray most deeply branched. Tip of longest pelvic-fin ray mostly crossing anus.

**Jaws and dentition.** Jaws isognathous. Teeth in upper and lower outer row in both jaws bicuspid. Neck of anterior jaw teeth stout (i. e. width about equal over whole length of teeth), crown expanded and cusps truncated (Fig. 12). One to three incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad, anterior keel shorter than toothed area (Fig. 11). Posterior pharyngeal teeth quadricuspid to pentacuspid (Fig. 17), stout, slightly hooked and regularly arranged, especially over posterior third of toothed area. Dentigerous plate triangular. Most teeth in the anterior two thirds of toothed area approach the “kukri” tooth shape (sensu Greenwood, 1987).

**Coloration in alcohol (adult specimen).** Basic coloration brownish. Dorsal side dark brownish, ventral side light brownish. Dark square-shaped blotches at base of each flank scale (filled or with a light coloured



**Fig. 20.** *T. nigrans* spec. nov. **a.** Breeding specimen; **b.** Non breeding specimen; **c.** Juveniles, showing the extended “tilapia spot”.

window at centre of blotch) creating the impression of dark network on flanks. Lower lip light brownish to whitish, upper lip dark. Cheek pale, lower side of head and operculum completely dark. Chest blackish and belly light with blackish blotches.

Markings on body: Seven to eight dark vertical bars on dorsum and sides (first bar at level of first dorsal spine, last two on caudal peduncle) and a nape band. Second vertical bar deeply bifurcated. Vertical bars sometimes not visible, apparently depending on motivational state by collection. Sometimes entire body very dark. No longitudinal mid-lateral band.

Fins: Pectoral fins transparent. Pelvic fins blackish. Anal fin dark brownish, margins transparent. Caudal fin dark brownish and margins transparent with light dots in the upper part. Dorsal fin dark



**Fig. 21.** *T. fusiforme* spec. nov. **a.** Non breeding specimen of “little-black” with large eyes, offshore. **b.** Non breeding specimen of “large-black” with small eyes, shallow water. **c.** Breeding specimen of “large-black” in front of a log hole. **d.** Breeding specimen of “little-black”.

brownish, margins transparent; “tilapia spot” not always visible, however, if present then with two to three dark oblique lines in soft part behind “tilapia spot”.

**Coloration in life (adult specimen)** (Figs 20a,b). Description based on breeding pairs and non-breeding, large specimens (larger than breeding *T. deckerti*). Basic coloration yellow-greenish (breeding grey-greenish), ventral side whitish to reddish (breeding: completely black). Lower side of head whitish (breeding: black) and upper side of head yellow-greenish. Upper lip light bluish, lower lip whitish. A horizontal iridescent blue line above antero-rostral

margin of preopercle. Iris of eyes bright red. Body with seven to eight black dark vertical bars, nape band, supraorbital and interorbital stripe (no vertical stripes in breeding coloration). Dark opercular spot (breeding: opercular spot mostly not visible, operculum yellow-greenish). Pectoral fins transparent, pelvic fins and anal fin with black tips. Dorsal fin yellow edged, "tilapia spot" noticeable. Caudal fin completely yellow-greenish.

**Distribution and ecology** (Fig. 14). Only known from the Lake Ejagham (Cameroon). *T. nigrans* spec. nov. bred exclusively in excavated caves below 5 m depth (Schliewen et al. 2001). Unambiguously identifiable individuals were restricted to breeding pairs, which served as a basis for population genetic analysis and description. Differential ecological observations have not been possible for non-breeding individuals, as *T. nigrans* spec. nov. and *T. deckerti* could not unambiguously differentiated in the field. However, specimens larger than breeding *T. deckerti* were regularly observed digging with their mouths over open sand areas in deeper parts of the lake between the shallow inshore zone (above 2 m) and the central mud area (for a lake description see Schliewen et al. 2001).

**Etymology.** The specific epithet, *nigrans*, is a Latin adjective, meaning dark(ly) coloured.

***Tilapia fusiforme* spec. nov.**  
Figs 20c, 21, 22; Tab. 5

*Tilapia deckerti* (partim) – Thys van den Audenaerde, 1967

*Tilapia* cf. *deckerti* "little-black" and *T. cf. deckerti* "large-black" – Schliewen et al., 2001

**Holotype.** ZSM 40082 (44.9 mm SL), Cameroon, Lake Ejagham (5°45'4.37"N 8°59'0.92"E), U. Schliewen, Mar 1993-Oct 1994.

**Paratypes.** ZSM 40083 (15, 44.9-59.5 mm SL). ZSM 40086 (10, 41.4-52.7 mm SL), both collected with holotype.

**Additional material (examined).** ZSM 40084 (17, 60.3-78.0 mm SL), collected with holotype. ZMB 16758 (1, 74.1 mm SL), Cameroon, Toter See b. Ossidinge [Lake Ejagham], Dr. Mansfeld, 10-20 Sep 1907.

**Additional material.** ZSM 40085 (14, 41.6-60.8 mm SL), (non breeding "little-black"). ZSM 40087 (15, 57.9-80.0 mm SL), (non breeding/breeding "large-black") all collected with holotype.

**Differential diagnosis.** *Tilapia fusiforme* spec. nov. is distinguished from all *Tilapia* by the combination of a slender fusiform body, an acute mouth, a pitch black breeding coloration and the "tilapia spot" being extended to a longitudinal stripe in juveniles (Schlie-

wen et al. 2001). It further differs from other *Tilapia* sensu lato except *T. joko*, *T. bilineata* and all members of the subgenus *Coptodon* in tricuspid pharyngeal teeth in the posterior two rows of lower pharyngeal jaw (pharyngeal jaws of *T. ismailiaensis* and *T. kottae* not investigated). It differs from *T. joko* in more gill rakers on first ceratobranchial (10-11 vs. 6-8), from *T. bilineata* in a caudal fin not densely scaled.

**Description**

**Shape.** Morphometric and meristic data for holotype and 15 paratypes in Table 5. See Figs 20c, 21 and 22 for general appearance. *T. fusiforme* spec. nov. is a small *Tilapia* (maximum observed size 80.0 mm SL) with a laterally compressed body. Head profile straight. Moderately pointed head. Snout outline obtuse. Eye very large and interorbital width always smaller than eye length. Greatest body depth at level of first dorsal spine. Dorsal line slightly posteroventrally curved. Caudal peduncle always longer than deep.

**Squamation.** Body scales cycloid, chest scales smaller than flank scales and slightly embedded. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal ray. Upper lateral line separated from first dorsal spine by three to four scale rows. Lower lateral line originating at level of first dorsal branched rays and terminates midlaterally on caudal peduncle. One or two scales of lower lateral line extending onto caudal fin. Two scale rows between upper and lower lateral line. Preoperculum with three to four regular rows. Lower one third of pectoral base mostly lacking scales.

**Gill rakers.** First ceratobranchial with 10-11 gill rakers and first upper gill-arch with 4-5 gill rakers. Ceratobranchial rakers slender and pointed. Gill raker in angle of arch and first four epibranchial rakers more slender, decreasing in size towards last.

**Fins.** Origin of dorsal fin at level of origin of pelvic fin. First dorsal spine always shortest, last dorsal spine always longest. Longest spines always shorter than longest ray. Last dorsal ray most deeply branched. Caudal fin outline truncate. Third anal spine always longest. Tip of longest anal fin ray not overlapping hypuralia. Last dorsal ray most deeply branched. Tip of longest pelvic-fin ray mostly overlapping anus.

**Jaws and dentition.** Jaws isognathous. Teeth in upper and lower outer row in both jaws bicuspid. Neck of anterior jaw teeth stout (i.e. width about equal over whole length of teeth), crown expanded and cusps truncated (Fig. 12). One to two incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad, anterior

keel shorter than toothed area (Fig. 11). Posterior pharyngeal teeth tricuspid (Fig. 13), stout, slightly hooked and regularly arranged, especially over posterior third of toothed area. Dentigerous plate triangular. Most teeth in anterior two thirds of toothed area approach the “kukri” tooth shape (sensu Greenwood, 1987).

**Coloration in alcohol. Non breeding coloration:** Basic coloration light brown. Dorsal side brown, darker than on ventral side. Upper lip dark coloured,

lower lip pale. Cheek and operculum light brown. Belly light brown. Markings on body: Seven to eight indistinct dark vertical bars on dorsum and sides (first bar at level of first dorsal spine, the last two on caudal peduncle) Operculum spot indistinct. Fins: All fins transparent, “tilapia spot” extended to a longitudinal stripe, especially in juveniles.

**Breeding coloration:** Basic coloration dark brown to blackish. Dorsal parts brown to blackish, darker than ventral side. Lips dark. Cheek and operculum pale. Ventral parts with some pale

**Table 5.** Measurements and counts for holotype and 15 paratypes of *Tilapia fusiforme* spec. nov.

	holotype	holotype + paratypes				n
		min	max	mean	SD	
<b>Measurements</b>						
Total length (mm)	56.3	56.3	73.9	62.4		16
Standard length SL (mm)	44.9	44.9	59.5	49.6		16
<b>in percents of SL</b>						
Head length	34.5	32.5	35.8	34.3	0.9	16
Interorbital width	9.4	8.9	10.2	9.6	0.4	16
Preorbital width	9.8	9.0	10.7	9.7	0.4	16
Horizontal eye length	12.2	10.6	12.9	12.0	0.6	16
Snout length	10.7	10.3	12.5	11.1	0.6	16
Internostril distance	6.9	6.6	7.9	7.1	0.4	16
Cheek depth	9.6	8.8	10.5	9.7	0.4	16
Upper lip length	9.1	9.1	11.1	9.7	0.5	16
Lower lip length	9.6	8.9	10.7	9.8	0.6	16
Lower lip width	8.0	7.7	10.4	9.2	0.8	16
Lower jaw length	13.8	12.7	13.9	13.4	0.3	16
Predorsal distance	37.6	36.6	40.6	38.1	1.0	16
Dorsal-fin base length	53.5	51.5	54.6	53.0	0.8	16
Last dorsal-fin spine length	12.7	11.7	14.6	12.8	1.0	16
Anal-fin base length	17.6	14.5	17.7	16.4	1.0	16
Third anal-fin spine length	14.0	12.8	16.7	14.5	0.9	16
Pelvic-fin length	25.4	21.9	33.1	26.4	2.5	16
Pectoral-fin length	27.2	22.8	31.0	28.0	1.8	16
Caudal peduncle depth	12.5	11.7	13.4	12.8	0.4	16
Caudal peduncle length	14.9	13.6	16.8	15.5	0.9	16
Body depth (pelvic-fin base)	32.3	30.8	34.7	32.7	1.1	16
Preanal length	71.3	66.3	72.5	69.3	1.6	16
Anus-anal-fin base distance	5.3	4.3	6.0	5.1	0.5	16
<b>Counts</b>						
Dorsal-fin spines	15		15 (13); 16 (3)			16
Dorsal-fin rays	12		11 (3); 12 (13)			16
Anal-fin rays	10		8 (4); 9 (8); 10 (4)			16
Pectoral-fin rays	14		13 (5); 14 (11)			16
Scales (horizontal line)	27		26 (2); 27 (10); 28 (4)			16
Upper lateral line scales	21		19 (1); 20 (7); 21 (3); 22 (5)			16
Lower lateral line scales	12		10 (2); 11 (7); 12 (6); 13 (1)			16
Gill rakers (lower)	11		10 (7); 11 (9)			16
Gill rakers (upper)	4		4 (7); 5 (9)			16



**Fig. 22.** *Tilapia fusiforme* spec. nov. **a.** Preserved holotype (ZSM 40082), 44.9 mm SL; Cameroon: Lake Ejagham. **b.** Live coloration (non breeding) **c.** Preserved “large-black” (ZSM 40084), 78.0 mm SL; Cameroon: Lake Ejagham.

areas. Markings on body: Entire body dark, no vertical bars. Operculum spot indistinct. Fins: Pectoral fins transparent. Pelvic fins transparent or slightly blackish. Anal fin dark brownish to blackish, margins transparent. Caudal fin dark brownish to blackish and margins transparent. Dorsal fin dark brownish to blackish, margins transparent, “tilapia spot” not always visible. If present, then extended to a longitudinal stripe, especially in juveniles.

**Coloration in life. Non breeding coloration** (Figs 21, 22): Basic coloration chartreuse greyish, chest bright yellow and belly pale. Head slightly darker than body and more green. Upper lip bluish green and lower lip whitish. A horizontal iridescent blue line above antero-rostral margin of preopercle. Iris of eyes brown to slightly reddish. Body with indistinct slightly blackish vertical bars and a nape band. Opercular spot indistinct. All fins bright yellow. In

soft part of dorsal fin “tilapia spot” extended to a longitudinal stripe.

**Breeding coloration** (Fig. 21c,d): Basic coloration dark brown to blackish, especially on head, blackish coloration on chest and ventral side interrupted by pale areas. Lips dark brownish. Lower side of head with some pale areas. Iris of eyes slightly dark red. No vertical bars. Pectoral fins transparent. Pelvic and anal fin slightly yellow with black blotches and black base. Base of caudal fin completely dark, margins yellow with blackish blotches. Base of dorsal fin black,

margins yellow with blackish blotches. Operculum and “tilapia spot” not visible.

**Distribution and ecology** (Fig. 14). Only known from Lake Ejagham (Cameroon). A detailed analysis of habitat preferences, life history and breeding observations is given in Schliewen et al. (2001). Qualitative feeding observations suggest that the deepwater specimens primarily feed on planktonic organisms in the open water column, while inshore specimens, in addition, pick on small particles from

**Table 6.** Measurements and counts of the two phenotypes of *T. fusiforme* spec. nov. in comparison.

	<i>T. fusiforme</i> spec. nov. “little black”			<i>T. fusiforme</i> spec. nov. “large black”		
	min	max	n	min	max	n
<b>Measurements</b>						
Total length (mm)	56.3	73.9	16	74.7	96.4	17
Standard length SL (mm)	44.9	59.5	16	60.3	78.0	17
<b>in percents of SL</b>						
Head length	32.5	35.8	16	32.8	34.6	17
Interorbital width	8.9	10.2	16	9.1	10.7	17
Preorbital width	9.0	10.7	16	10.2	11.5	17
Horizontal eye length	10.6	12.9	16	9.2	11.4	17
Snout length	10.3	12.5	16	11.1	13.3	17
Internostril distance	6.6	7.9	16	6.8	8.4	17
Cheek depth	8.8	10.5	16	10.4	11.7	17
Upper lip length	9.1	11.1	16	8.3	10.7	17
Lower lip length	8.9	10.7	16	8.5	10.8	17
Lower lip width	7.7	10.4	16	8.2	11.2	17
Lower jaw length	12.7	13.9	16	11.9	13.6	17
Predorsal distance	36.6	40.6	16	36.8	39.5	17
Dorsal-fin base length	51.5	54.6	16	50.9	54.5	17
Last dorsal-fin spine length	11.7	14.6	16	10.0	14.5	17
Anal-fin base length	14.5	17.7	16	14.9	16.9	17
Third anal-fin spine length	12.8	16.7	16	10.6	13.8	17
Pelvic-fin length	21.9	33.1	16	22.8	28.0	17
Pectoral-fin length	22.8	31.0	16	25.0	30.5	17
Caudal peduncle depth	11.7	13.4	16	12.4	13.8	17
Caudal peduncle length	13.6	16.8	16	14.9	16.9	17
Body depth (pelvic-fin base)	30.8	34.7	16	32.2	34.5	17
Preanal length	66.3	72.5	16	69.3	73.0	17
Anus-anal-fin base distance	4.3	6.0	16	4.6	6.4	17
<b>Counts</b>						
Dorsal-fin spines	15 (13); 16 (3)			15 (8); 16 (9)		
Dorsal-fin rays	11 (3); 12 (13)			12 (9); 13 (8)		
Anal-fin rays	8 (4); 9 (8); 10 (4)			8 (1); 9 (16)		
Pectoral-fin rays	13 (5); 14 (11)			13 (1); 14 (16)		
Scales (horizontal line)	26 (2); 27 (10); 28 (4)			26 (3); 27 (12); 28 (2)		
Upper lateral line scales	19 (1); 20 (7); 21 (3); 22 (5);			19 (3); 20 (7); 21 (6); 22 (1)		
Lower lateral line scales	10 (2); 11 (7); 12 (6); 13 (1)			10 (3); 11 (5); 12 (9)		
Gill rakers (lower)	10 (7); 11 (9)			9 (1); 10 (9); 11 (7)		
Gill rakers (upper)	4 (7); 5 (9)			4 (8); 5 (9)		

substrate and feed on allochthonous matter from the water surface. *T. fusiforme* spec. nov. bred in all depth zones, however, only the “little-black” form in all depth zones whereas, “large-blacks” bred preferentially in log-holes of dead wood in the shallow region above 1 m (Schliewen et al. 2001).

**Etymology.** The species name *fusiforme* is derived from the Latin *fusus* – spindle and *forma* – shape. A noun in apposition.

**Differences between two phenotypes of *Tilapia fusiforme* spec. nov.** (Tab. 6). Two phenotypes of *T. fusiforme* spec. nov. had previously referred to as *T. cf. deckerti* “little-black” and *T. cf. deckerti* “large-black” (Schliewen et al. 2001). These two forms are incipient species, which are almost but not completely reproductively isolated according to observations of strong assortative with only very few “mixed” pairs (Schliewen et al. 2001 and re-analysis of microsatellite data presented under Results above). Both phenotypes are morphologically very similar, but to some extent, morphometric divergence is detectable. The “little-black” form is always smaller when breeding (Schliewen et al. 2001); head measurements of the “little-black” form (mentioned in the following numerical comparisons first) show that the head of the “little-black” form is shorter with larger eyes, i. e. preorbital width 9.0-10.7 % vs. 10.2-11.5 % of SL, eye length 10.6-12.9 % vs. 9.2-11.4 % of SL and cheek depth 8.8-10.5 % vs. 10.4-11.7 % of SL. *T. fusiforme* spec. nov. “little-black” are most likely recruited from the big-eyed deep-offshore animals, whereas *T. fusiforme* spec. nov. “large-black” come predominantly from small-eyed shallow individuals (Schliewen et al. 2001). Meristic counts of both forms are very similar, except for dorsal ray counts: 11-12 vs. 12-13. In addition, the “large-black” form appears to have lighter coloured ventral parts when breeding.

## Discussion

**Affinities.** According to Schliewen et al. (1994, 2001) members of the *Tilapia (Coptodon)* species flock are most closely related to each other and to the yet undescribed *Tilapia (Coptodon)* spec. aff. *guineensis* “Cross” from the neighboring Cross River system. Although the taxon sampling in the 1994 study was incomplete, preliminary mtDNA data presented in that publication suggest that the four Lake Ejagham *Tilapia*, *Tilapia* spec. “Cross”, all members of the Lake Bermin *Tilapia (Coptodon)* species flock and *Tilapia kottae* are closely related to each other, and that they are more distantly related to *Tilapia guineensis*. A detailed molecular phylogeny of *Tilapia* sensu lato with emphasis on clarifying *Tilapia (Coptodon)* inter-

relationships is in preparation (Dunz et al., in prep.). A discussion of the origin and sympatric speciation of the *Tilapia (Coptodon)* species flock with a focus on *T. fusiforme* spec. nov. is available in Schliewen et al. (2001).

**Conservation.** Three Western Cameroonian crater lakes are well known for their small endemic cichlid species flocks, which have arisen in sympatry (Schliewen et al. 1992, Schliewen & Klee 2004). The most famous, Lake Barombi Mbo and contains eleven endemic species which are closely related to the mouthbrooding *Sarotherodon galilaeus*, (Trewavas et al. 1972). The second lake, Bermin, is home to nine endemic substrate brooding *Tilapia (Coptodon)* species (Stiassny et al. 1992). The third lake, Ejagham, is home to an endemic sibling species pair of the genus *Sarotherodon* (Schliewen et al. 1994, Neumann et al., submitted) and the four *Tilapia* species described here. Together, these three lakes harbor 27 endemic haplotilapiine cichlid species. The unique fish diversity has led to the designation of a distinct ecoregion, the “Western Equatorial Crater Lakes”, in a conservation assessment of freshwater ecoregions of Africa and Madagascar (Thieme et al. 2005). The taxonomic description of the *Tilapia (Coptodon)* species presented here, provides the formal basis for recognizing this species diversity, supports the classification as a distinct ecoregion and highlights the importance of conservation measures to be implemented. Main threats to the biological integrity of these lakes are legal and illegal logging of the rainforest, accidental or targeted introduction of allochthonous fish species and unsustainable water extraction (Reid 1990, Schliewen, Peck & Burgess in Thieme et al. 2005). The area of endemism for the species described here are formally protected through the Ejagham Forest Reserve, which is part of the Korup National Park area in Western Cameroon. However, protection is not strictly enforced and there is no special recognition of the uniqueness and vulnerability of the Lake Ejagham ecosystem. According to a recent unpublished report by C. Martin, University of California (Davis), an allochthonous catfish of the genus *Parauchenoglanis* (Claroteidae) has been introduced from neighboring Munaya River (Cross River drainage) into the lake in large numbers and is now present in all gill net catches (C. Martin, pers. comm. Feb. 10, 2010). This poses a severe threat to the endemic species richness of Lake Ejagham and calls for immediate action. In collaboration with IUCN Cameroon, a proposal for a “Dispersed Crater Lakes National Park initiative” has been submitted to establish a monitoring and conservation programme that includes Lake Ejagham.



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## Appendix 1. Comparative material examined

*Tilapia bakossiorum* Stiassny, Schliewen & Dominey, 1992: ZSM 27636 (holotype, 58.7 mm SL), Cameroon, western Lake Bermin (5°9'N 9°38'E), U. Schliewen, Jan 1990. ZSM 27637 (3, paratypes, 36.8-44.7 mm SL), Cameroon, Lake Bermin western (5°9'N 9°38'E), U. Schliewen, Jan 1990.

*Tilapia bemini* Thys van den Audenaerde, 1972: MRAC 174739 (holotype, 66.2 mm SL), Cameroon, Lake Bermin western (5°9'N 9°38'E), J. Grimshaw, 4 Feb 1970. MRAC 174740 (1, Paratypes, 51.0 mm SL), Cameroon, Lake Bermin (5°9'N 9°38'E), J. Grimshaw, 4 Feb 1970. MRAC 174741 (1, paratype, 47.2 mm SL), Cameroon, Lake Bermin (5°09'N 9°38'E), J. Grimshaw, 4 Feb 1970. MRAC 73-40-P-715-17 (2, 66.9-84.3 mm SL), Cameroon, Lake Bermin in upper Bakossi area, known as Sidejok (5°9'N 9°38'E), J. Grimshaw, 4 Feb 1971. ZSM 27680 (1, 66.1 mm SL), Cameroon, Lake Bermin western (5°9'N 9°38'E), U. Schliewen, Jan 1990. ZSM 27632 (5, 47.8-98.1 mm SL), Cameroon, Lake Bermin western (5°9'N 9°38'E), U. Schliewen, Jan 1990.

*Tilapia bilineata* Pellegrin, 1900: MNHN 1886-0445 (holotype, 150.4 mm SL), Central African Republic, Ndele, Alima River, upper Congo, Savorgan de brazza, mission west Africa. MNHN 1886-0446 (1, paratype, 90.8 mm SL), Central African, Ndele, Alima River, upper Congo, Savorgan de brazza, mission west Africa. MRAC A8-020-P-0971-0972 (2, 57.6-68.5 mm SL), Republic of the Congo, River Louna, affluent of Lefini, about 500m to camp PPG Abio 2. MRAC A8-020-P-0964-0965 (2, 95.4-129.0 mm SL), Republic of the Congo, River Lefini, about 2,4km to camp Malina. MRAC A8-020-P-0954-0955 (2, 84.3-104.0 mm SL), Republic of the Congo, Confluent Lefini-Nambouli. MRAC A8-020-P-0944 (1, 68.6 mm SL), Republic of the Congo, River Lefini, about 3km to Mount Epope. MRAC A8-020-P-0962 (1, 54.6 mm SL), Republic of the Congo, River Lefini, about 600m to camp Oteni. MRAC A8-

020-P-0963 (1, 107.1 mm SL), Republic of the Congo, River Lefini, about 600m to camp Oteni.

*Tilapia bythobates* Stiassny, Schliewen & Dominey, 1992: AMNH 98242 (holotype, 87.5 mm SL), Cameroon, Lake Bermin western (5°9'N 9°38'E), W.J. Dominey, 15. May 1985. ZSM 27638 (6, paratypes, 78.8-115.9 mm SL), Cameroon, Lake Bermin western (5°9'N 9°38'E), U. Schliewen, Jan 1990.

*Tilapia cameronensis* Holly, 1927: NMW-7645 (holotype, 249.4 mm SL), Cameroon, River Mbam, Haberer, Mar 1908. MRAC 95-088-P-0014-0015 (2, 146.9-170.1 mm SL), Cameroon, above Nachtigale falls, middle reaches of Sanaga (4°21'N 11°38'E), E.C.v.d. Bergh et al., 28 Mar 1995. MRAC P-93015.0101 (1, 153.2 mm SL), Cameroon, River Mbam, before river mouth of the Mape (5°58'N 11°16'E), J.J. Breine & E.C.v.d. Bergh, 6 Dec 1992. MRAC 93-051-P-0186-0191 (4, 91.5-113.6 mm SL), Cameroon, Magba, River Mbam, 500 m before confluence with the Mape (5°57'N 11°13'E), J.J. Breine et al., 14 Mar 1993. MNHN 1929-0110 (1, 86.5 mm SL), Cameroon, River Mbam, Sanaga, bankin, T. Monod. MNHN 1983-0615 (1, 171.2 mm SL), Cameroon, Sanaga, Edea, T. Monod, 1926.

*Tilapia camerunensis* Lönnberg, 1903: BMNH 1982.17.7.1-2 (1, 64.1 mm SL), Cameroon, River Ndian (4°45'N 8°44'E), T. Roberts, 1982. BMNH 1979.7.18.454 (1, 95.6 mm SL), Cameroon, River Meme, H. Peters, 1977. MNHN 1988-1799 (2, 82.3-188.9 mm SL), Cameroon, Mungo, J. Lazard, 1986.

*Tilapia cessiona* Thys van den Audenaerde, 1968: MRAC 156025 (holotype, 102.1 mm SL), Côte d'Ivoire, Toyebli, River Nipoué (6°38'N 8°29'W), Thys van den Audenaerde, 3 Aug 1966. MRAC 156030-31 (1, paratype, 74.5 mm SL), Côte d'Ivoire, Toyebli, River Nipoué (6°38'N 8°29'W), Thys van den Audenaerde, 29-30 Jul 1966. MRAC 156026-29 (1, paratype, 45.8 mm SL), Côte d'Ivoire, Toyebli, basin Nipoué or Nuon (6°38'N 8°29'W) Thys van den Audenaerde, 3 Aug 1966. MRAC 171592-014 (5, 91.9-138.8 mm SL), Côte d'Ivoire, Toyebli, River Cess (6°38'N 8°29'W), Thys van den Audenaerde, 18 Mar 1969. MNHN 1987-0510 (1, 81.6 mm SL), Côte d'Ivoire, Toyebli, River Nipoué, cestos, G.G. Teugels, 29-30 Apr 1985. MNHN 1986-0489 (2, 82.7-104.7 mm SL), Côte d'Ivoire, Binhouye, River Nipoué, cestos, Apr 1977.

*Tilapia coffea* Thys van den Audenaerde, 1970: MRAC 171956 (holotype, 115.7 mm SL), Liberia, Mount Coffee, lake on St. Paul River, near Harrisburg village, above dam (6°32'N 10°35'W), Thys van den Audenaerde, 14 May 1969. MRAC 171957-66 (7, paratypes, 66.8-118.2 mm SL), Liberia, Mount Coffee, lake on St. Paul River, above dam (6°32'N 10°35'W), Thys van den Audenaerde, 13 May 1969. MRAC 171967-77 (7, paratypes, 72.1-94.1 mm SL), Liberia, Mount Coffee, lake on St. Paul River, above dam (6°32'N 10°35'W), Thys van den Audenaerde, 13 May 1969.

*Tilapia congica* Poll & Thys van den Audenaerde, 1960: MRAC 67159 (holotype, 210.1 mm SL), Congo Dem. Rep., Region of Mushie: River Kasai (3°2'S 16°55'E), C. Vleeschouwers, 1945. MRAC 66878-79 (2, paratypes, 176.7-181.3 mm SL), Congo Dem. Rep., Region of Mushie: River Kasai (3°2'S 16°55'E), C. Vleeschouwers, 1-30 Sep 1941. MRAC 67158-60 (2, paratypes, 205.6-215.7 mm SL), Congo Dem. Rep., Region of Mushie: River Kasai (3°2'S 16°55'E), C. Vleeschouwers, 1945. MRAC 67056-057 (2, paratypes, 114.4-122.3 mm SL), Congo Dem. Rep., Region of Mushie: River Fimi (3°2'S 16°55'E), C. Vleeschouwers, 1-30 Nov 1945. MRAC 67162 (1, paratype 163.4 mm SL), Congo Dem. Rep., Region of Mushie: River Fimi (3°2'S 16°55'E), C. Vleeschouwers, 1-30 Nov 1945. MRAC 67161 (1, paratype, 174.8 mm SL), Congo Dem. Rep., Region of Mushie: Sinte Nzokele (2°59'S 17°4'E), C. Vleeschouwers, 1-30 Nov 1945. MRAC 69394 (1, paratype, 175.6 mm SL), Congo Dem. Rep., Region of Mushie (3°2'S 16°55'E), C. Vleeschouwers, 1946. MRAC 68849 (1, paratype, 160.9 mm SL), Congo Dem. Rep., Region of Mushie (3°2'S 16°55'E), C. Vleeschouwers, 1946. MRAC 68850-52 (3, paratypes, 159.1-163.2 mm SL), Congo Dem. Rep., Region of Mushie (3°2'S 16°55'E), C. Vleeschouwers, 1946. MRAC 100804-11 (8, paratypes, 56.0-141.7 mm SL), Congo Dem. Rep., Lake Tumba (0°37'S 17°49'E/1°0'S 18°9'E), G. Marlier, 29-30 Sep 1955. MRAC 100802-803 (2, paratypes, 107.5-192.9 mm SL), Congo Dem. Rep., Lake Tumba (0°37'S 17°49'E/1°0'S 18°9'E), G. Marlier, 29-30 Sep 1955. MRAC 46175 (1, 204.7 mm SL), Congo Dem. Rep., Eala (0°4'N 18°20'E), J. Ghesquière, 23 Apr 1936. MRAC 14927 (1, 168.6 mm SL), Congo Dem. Rep., Eala, River Ruki (0°4'N 18°20'E), v. Oye, 26 Jan 1926.

*Tilapia dageti* Thys van den Audenaerde, 1971: MRAC 155731 (holotype, 127.6 mm SL), Ghana, Volta River below Akosombo (6°18'N 0°3'E), Thys van den Audenaerde, 28 Oct 1966. MRAC 155732-33 (2, paratypes, 80.3-82.3 mm SL), Ghana, Volta River below Akosombo (6°18'N 0°3'E), Thys van den Audenaerde, 28 Oct 1966. MRAC 171871-75 (2, paratypes, 60.4-84.9 mm SL), Ghana, small stream below Akosombo (6°18'N 0°3'E), P. Loisselle, 1 Oct 1970. MRAC 171870 (1, paratype, 120.8 mm SL), Ghana, Lake Volta at Agbogyesekwa, P. Loisselle, 1 Oct 1970. BMNH 1981.2.17547-548 (2, 56.9-64.4 mm SL), Ghana River Pra, A. Hopson, 1981. MRAC 155644 (1, paratype, 88.9 mm SL), Côte d'Ivoire, Ferké basin, sur River Comoé (9°35'N 4°18'W), Thys van den Audenaerde, 25 Aug 1966. MRAC 144591 (1, paratype, 77.0 mm SL), Burkina-Faso, River Mou, affluence of Bougouriba, 55 km of Bobo-Dioulasso (11°11'N 3°49'W), B. Roman, 1 May 1964. MNHN 1961-0771 (6, paratypes, 92.4-131.8 mm SL), Mali, Niger by Diafarabé (Soudan), J. Daget, 8 Apr 1950. MNHN 1965-702 (4, paratypes, 104.8-137.0 mm SL), Chad, Chad basin, Aouk, Golongosso, A. Strauch, Mar 1962.

*Tilapia deckerti* Thys van den Audenaerde, 1967: MRAC 157495 (1, paratype, 153.2 mm SL), Cameroon, Lake Ejagham (5°46'12"N 8°58'12"E), Mansfeld, 10-20 Sep 1907.

*Tilapia discolor* (Günther, 1903): BMNH 1903.4.24.33-35 (3, syntypes, 75.9-92.2 mm SL), Ghana, Lake Bosumtwi, R. B. N. Walker, 1903. MRAC 156011-20 (9, 105.2-146.4 mm SL), Ghana, Abono, Lake Bosumtwi (6°32'N 1°26'W), Thys van den Audenaerde, 18-19 Sep 1966. MNHN 1981-0948 (1, 139.7 mm SL), Ghana, Kumasi, Lake Bosumtwi, Bianco, 21 May 1978. MRAC 86-18-P-1968-69 (2, 61.8-63.9 mm SL), Côte d'Ivoire, Kouli (= Koun) by Yaou, River Bia (7°30'N 7°16'W), K. Traore, 18 Apr 1986. MRAC 86-18-P-1965-67 (3, 68.8-97.2 mm SL), Côte d'Ivoire, Ayamé, River Bia (5°37'N 3°11'W), K. Traore, 19 Apr 1986.

*Tilapia flava* Stiassny, Schliewen & Dominey, 1992: AMNH 98264 (holotype, 75.9 mm SL), Cameroon, Lake Bemini western (5°9'N 9°38'E), U. Schliewen, Jan 1990. ZSM 27635 (8, paratypes, 51.6-71.6 mm SL), Cameroon, Lake Bemini western (5°9'N 9°38'E), W. J. Dominey, 15. May 1985.

*Tilapia guineensis* (Bleeker, 1862): BMNH 1849.10.9.15 (holotype, 149.7 mm SL), Ghana, Ashantee, collector and year unknown. MNHN 1988-0315 (3, 122.4-132.5 mm SL), Senegal, Fadiout, lagoon, Romand, Apr 1985. MNHN 1968-0066 (1, 98.0 mm SL), Senegal, Forest of Bandia Somone, Villiers. RUSI 44334 (1, 127.5 mm SL), Senegal, Geba System, Anambe Dam S2-F8, U.A. Kohler, Nov 1993. RUSI 44326 (1, 109.5 mm SL), Senegal, Geba System, Anambe River Bridge 54-F19, U.A. Kohler, Nov 1993. ZSM 25740 (1, 142.6 mm SL), Senegal, Street from Bathurst to Dionloulou by Selety; Caramance Region, D. Vogt, Dec 1978. MNHN 1983-0617 (1, 95.7 mm SL), Guinea, River Nunez, J. Thomas, 1923. MNHN 1987-1497 (2, 104.2-107.2 mm SL), Guinea, Khoriba: Soumpa, Korera, C. Lévêque, 11 Feb 1986. MRAC 81-20-P-49 (1, 119.4 mm SL), Guinea, Soukya, River Konkouré (10°25'N 13°12'W), P. De Kimpe, 12 Mar 1983. MRAC 81-20-P-45-48 (2, 56.1-62.3 mm SL), Guinea, bac route Korela-Kondoya, River Konkouré (10°32'N 12°52'W), P. De Kimpe, 10 Mar 1983. MNHN 1992-0995 (2, 110.3-123.1 mm SL), Sierra Leone, River Sewa by Wjaiama-sewae, C. Lévêque, Mar 1991. ZSM 27954 (3, 118.7-149.9 mm SL), Côte d'Ivoire, Cocody by Abidjan, Lagoon Ebrie, Sheljieshko, 15 Oct 1952. ZSM 23386 (1, 86.8 mm SL), Ghana, Keta-Lagoon, S. Endrödy-Younga, 30 Dec 1966-2 Jan 1967. ZSM 23002 (1, 74.4 mm SL), Ghana, Busua, 25km W of Takoradi, S. Endrödy-Younga, 18. Feb 1966.

*Tilapia spec. aff. guineensis* "Cross" (undescribed): ZSM 27618 (8, 80.8-114.7 mm SL), Cameroon, West Cameroon, Rio Munaya, Cross River Basin at road bridge near Eyumojok, U. Schliewen, Feb 1990.

*Tilapia gutturosa* Stiassny, Schliewen & Dominey, 1992: AMNH 98269 (holotype, 61.2 mm SL), Cameroon, Lake Bemini western (5°9'N 9°38'E), W. J. Dominey, 15. May 1985. ZSM 28200 (6, paratypes, 50.0-62.1 mm SL), Cameroon, Lake Bemini western (5°9'N 9°38'E), U. Schliewen, Jan 1990.

*Tilapia imbriferina* Stiassny, Schliewen & Dominey, 1992: AMNH 98247 (holotype, 101.7 mm SL), Cameroon, Lake Bemini western (5°9'N 9°38'E), W. J. Dominey, 15. May 1985. ZSM 27651 (6, paratypes, 55.3-109.1 mm SL), Cameroon, Lake Bemini western (5°9'N 9°38'E), U. Schliewen, Jan 1990.

*Tilapia ismailiaensis* Mekkawy, 1995: BMNH 1993.9.23.6 (holotype, 94.2 mm SL), Egypt, Ismailia canal, Ismailia, Imam. A.A. Mekkawy, 1983. BMNH 1993.9.23.7-8 (2, paratypes, 84.0-89.6 mm SL), Egypt, Ismailia canal, Ismailia, Imam. A.A. Mekkawy, 1983.

*Tilapia joka* Thys van den Audenaerde, 1969: MRAC 183585 (holotype, 67.5 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7°21'N 11°42'W), Thys van den Audenaerde, 16 Apr 1969. MRAC 183596-97 (2, paratypes, 65.4-69.6 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7°21'N 11°42'W), Thys van den Audenaerde, 16 Apr 1969. MRAC 183586 (1, paratype, 75.2 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7°21'N 11°42'W), Thys van den Audenaerde, 16 Apr 1969. MRAC 183587-94 (8, paratypes, 56.5-72.2 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7°21'N 11°42'W), Thys van den Audenaerde, 16 Apr 1969. MRAC 92-092-P-0019 (1, 68.8 mm SL), Sierra Leone, Njala, Jong River basin (8°7'N 12°5'W), D.E. Chaytor, 1 Jan 1969. MNHN 1991-0610 (2, 58.6-66.7 mm SL), Sierra Leone, Pampana, Jong River basin, Matotaka, D. Paugy & J.F. Agnese, 29 Mar 1990.

*Tilapia kottae* Lönnberg, 1904: BMNH 1904.2.15.1-2 (2, syntypes, 98.3-109.0 mm SL), Cameroon, Lake Barombi-ba-kotta, Cameroon Mountain, G. Linnell, 1904. MRAC 156045-56 (3, 63.2-74.1 mm SL), Cameroon, Lake Barombi-kotto (4°28'N 9°15'E), Thys van den Audenaerde, 24 Oct 1966. MRAC 156034-44 (3, 74.1-82.2 mm SL), Cameroon, Lake Barombi-kotto (4°28'N 9°15'E), Thys van den Audenaerde, 24 Oct 1966. MRAC 156057-116 (3, 72.4-102.0 mm SL), Cameroon, Lake Barombi-kotto (4°28'N 9°15'E), Thys van den Audenaerde, 24 Oct 1966.

*Tilapia louka* Thys van den Audenaerde, 1969: MRAC 164492 (holotype, 74.4 mm SL), Sierra Leone, Kenema (7°52'N 11°11'W), E. Roloff. MRAC 154493 (1, paratype, 60.3 mm SL), Sierra Leone, Kenema (7°52'N 11°11'W), E. Roloff. MRAC 164494-96 (3, paratypes, 40.2-55.3 mm SL), Sierra Leone, Kenema (7°52'N 11°11'W), E. Roloff. MRAC 164497-99 (3, paratypes, 54.9-64.2 mm SL), Sierra Leone, Kenema (7°52'N 11°11'W), E. Roloff. MNHN 1991-0602 (1, 86.5 mm SL), Sierra Leone, Moa, Kenema, D. Paugy & J.F. Agnese, 31 Mar 1990. MNHN 1961-1104 (2, paratypes, 80.4-107.4 mm SL), Guinea, Kolenté, J. Daget, 16 Sep 1958.

*Tilapia margaritacea* Boulenger, 1916: BMNH 1914.5.27.12-15 (4, syntype, 62.9-128.3 mm SL), Cameroon, Nyong River at Akonolinga, G. Bates. BMNH 1959.8.12.10-13 (4, 86.6-92.3 mm SL), Cameroon, Nyong River, J. Daget. MRAC 94-028-P-003 (1, 68.1 mm SL), Cameroon, River Lobo, vers Sangmelima field nr. 94022202, C.F. Bilong Bilong, 1994. MRAC 89-32-P-65 (1, 75.9 mm

SL), Cameroon, Ebogo, River Nyong (3°23'N 11°28'E), E. Birgi, 5 Jan 1988. BMNH 1959.8.12.10-13 (4, 86.6-91.7 mm SL), Cameroon, River Nyong, J. Daget, Feb 1958. MNHN 1983-0619 (1, 138.3 mm SL), Cameroon, Akomolinga, Nyong River, Letouzey.

*Tilapia nyongana* Thys van den Audenaerde, 1971: MRAC 152789 (holotype, 163.8 mm SL), Cameroon, Akonolinga, pond of planting Mangan, emanate from River Nyong (3°46'N 12°15'E), Thys van den Audenaerde, 28 Oct 1964. MRAC 152790-93 (4, paratypes, 102.4-133.0 mm SL), Cameroon, Akonolinga, pond of planting Mangan, emanate from River Nyong (3°46'N 12°15'E), Thys van den Audenaerde, 28 Oct 1964. MRAC 152800-02 (3, paratypes, 45.2-59.6 mm SL), Cameroon, Ebogo, River Nyong (3°23'N 11°28'E), Thys van den Audenaerde, 22-24 Sep 1964. MRAC 152794-99 (6, paratypes, 133.1-189.7 mm SL), Cameroon, Akonolinga, River Nyong (3°46'N 12°15'E), L. Mvogo, 22-28 Mar 1965. MNHN 1929-118-119 (2, paratypes, 169.5-225.2 mm SL), Cameroon, unknown, T. Monod. MRAC 93-083-P-0030 (1, 71.8 mm SL), Cameroon, unknown, C.F. Bilong Bilong. MRAC 152933-52 (1, 57.3 mm SL), Gabon, Lambaréné (0°42'S 10°13'E), Thys van den Audenaerde, 11-12 Nov 1964.

*Tilapia rendalli* (Boulenger, 1897): BMNH 1896.10.5.9-11 (3, syntypes, 113.1-180.0 mm SL), Malawi, Upper Shire River, P. Rendall, 1896. RUSI 50072 (1, 59.2 mm SL), Malawi, Dwanga River; Dwanga sugar estate canal gate 1 06.04, D. Tweddle, 20. Jul 1995. MRAC 105569-71 (3, 83.5-146.4 mm SL), Tanzania, branch south of Malagarazi delta, station 146, 4 km upstream (5°14'S 29°47'E), M. Poll, 25 Feb 1947. MRAC 105575-88 (4, 68.3-96.2 mm SL), Tanzania, outside of Malagarazi delta, station 304, islet of reed (5°12'S 29°47'E), M. Poll, 20 May 1947. RUSI 18563 (1, 77.0 mm SL), Botswana, Okavango; Nxamaseri; Molapo out off pool at flood end OK 83-1, M.N. Bruton, 13. Feb 1983. SAIAB 72535 (1, 91.8 mm SL), Botswana, Kasane, upper Zambezi, Chobe River UZC 02 (17°47'13"S 25°10'13"E), D. Tweddle, B.C.W. van der Waal, Alex D. Chilala, 5. Sep 2003. RUSI 24027 (2, 82.5-92.5 mm SL), Botswana, Boro River 5 km upstream from Thamalakane confluence OK 85-18B, G. Merron, 14. May 1985. BMNH 1976.10.12.283-285 (3, 94.6-132.0 mm SL), Congo Dem. Rep., Lake Kalamba at Mulongo, K.E. Banister & Fish Team, 1976. BMNH 1976.10.12.252 (1, 112.7 mm SL), Congo Dem. Rep., Papyrus Islands, Lake Mulende, K.E. Banister, 1976. BMNH 1975.6.20.670 (1, 137.5 mm SL), Congo Dem. Rep., Lake Kinsale, K.E. Banister, 1975. BMNH 1976.12.20.87 (1, 133.5 mm SL), Congo Dem. Rep., Upemba region: Lake Kisabe, K.E. Banister, 1976. MRAC 126277-292 (3, 71.7-85.1 mm SL), Congo Dem. Rep., Lake Mukambo (Kasai), import from Katanga (5°45'0"S 23°4'12"E), G. Marlier, 3 Oct 1951. MRAC 34340-34342 (3, 73.1-87.3 mm SL), Congo Dem. Rep., Lukonzolwa, Lake Moero (8°46'48"S 28°38'60"E), G.-F. de Witte, 9 Feb 1931. MRAC 33945-33947 (3, 80.2-98.5 mm SL), Congo Dem. Rep., Lukonzolwa, Lake Moero (8°46'48"S 28°38'60"E), G.-F. de Witte, 9 Feb 1931. MRAC 84911-915 (1, 129.7 mm SL), Congo Dem.

- Rep., Manono, pond nr. 7 (7°17'60" S 27°25'12" E), Miss. Pisc. Katanga, 22 Mar 1947. MRAC 139564-676 (6, 66.5-85.4 mm SL), Congo Dem. Rep., Pond upstream of River Kulungu (Bambesa) (3°22'12" S 25°43'48" E), J.P. Gosse, 14 Oct 1954. BMNH 1976.10.12.249-250 (2, 76.9-79.3 mm SL), Congo Dem. Rep., Lukuga River, 1 km above confluence with Zaire River, K.E. Banister & Fish Team, 1976. MRAC 105566 (1, 100.2 mm SL), Congo Dem. Rep., Region of Albertville: River Lukuga, village Amisi (5°55'12" S 29°19'12" E), M. Poll, 4 Dec 1946. BMNH 1976.10.12.236-237 (2, 54.1-63.8 mm SL), Congo Dem. Rep., Luvua River at Ankoro, K.E. Banister & Fish Team, 1976. MRAC 36353-355 (2, 63.9-74.8 mm SL), Congo Dem. Rep., Kiambi, River Luvua (7°19'48" S 28°1'12" E), G.-F. de Witte, 4-20 May 1931. BMNH 1975.6.20.671-672 (2, 53.6-56.9 mm SL), Congo Dem. Rep., Lualaba River at Lukuge junction, K.E. Banister, 1975. BMNH 1976.10.12.260 (1, 65.9 mm SL), Congo Dem. Rep., Lualaba River, 20 km S of Nyangwe (4°0'0" S 26°0'0" E), K.E. Banister & Fish Team, 1976. MRAC 69735 (1, 130.0 mm SL), Congo Dem. Rep., Maka, River Lualaba (8°55'48" S 26°4'12" E), M. Poll, 27 Jun 1947. MRAC 69955-956 (2, 52.5-59.5 mm SL), Congo Dem. Rep., Kabalo, River Lualaba (6°2'60" S 26°31'48" E), M. Poll, 3 Jul 1947. MRAC 78165-172 (2, 74.7 mm SL), Congo Dem. Rep., Kindu, River Lualaba (2°57'0" S 25°55'48" E), V. Heymans, 21 Mar 1950. MRAC 44844 (1, 121.8 mm SL), Congo Dem. Rep., Kasenga, River Luapula (10°22'12" S 28°37'48" E), A. Denis, 1 Jan 1935. MRAC 4628-636 (4, 61.1-71.7 mm SL), Congo Dem. Rep., Kasenga, River Luapula (10°19'48" S 28°37'48" E), L. Stappers, 18 Jul 1911. MRAC 33529 (1, 86.5 mm SL), Congo Dem. Rep., confluence Luapula and Luombwa (12°13'12" S 29°33'0" E), G.-F. de Witte, 23-31 Oct 1930. BMNH 1980.7.1.67 (1, 59.4 mm SL), Congo Dem. Rep., Rapids below Stanley Pool, O. Clark, 1980. MRAC 135501 (1, 132.0 mm SL), Congo Dem. Rep., River Bohonde (0°46'12" N 24°22'48" E), J.P. Gosse, 12 Feb 1955. MRAC 51638-639 (2, 81.7-85.2 mm SL), Congo Dem. Rep., Inkongo, River Sankuru (4°52'48" S 23°16'12" E), H. Wilson, 1 Jan 1937. MRAC 50083-85 (1, 102.3 mm SL), Congo Dem. Rep., Affluence of River Luembe, P. Brien, 1 May 1937. MRAC 22510-11 (1, 73.4 mm SL), Congo Dem. Rep., Nyonga (8°37'48" S 26°18'0" E), G.-F. de Witte, 1925. SAIAB 71029 (1, 60.9 mm SL), Zambia, Chirumba River (13°24'47" S 24°22'15" E), D. Tweddle & B.C.W. van der Waal, 24 Oct 2002. SAIAB 71789 (1, 73.5 mm SL), Zambia, Matondo Lagoon; upper Zambezi Branch Zambezi UZB 34 (15°20'32" S 22°56'49" E), D. Tweddle & B.C.W. van der Waal, 24 Apr 2003. SAIAB 71905 (1, 84.9 mm SL), Zambia, Kataba River main road, upper Zambezi UZB 42 (15°34'02" S 23°17'00" E), D. Tweddle & B.C.W. van der Waal, 27 Apr 2003. SAIAB 72574 (1, 74.3 mm SL), Zambia, Mutemwa, upper Zambezi UZC 05 (17°12'00" S 24°04'00" E), D. Tweddle, B.C.W. van der Waal, Alex D. Chilala, 7 Sep 2003. SAIAB 72710 (1, 68.9 mm SL), Zambia, Simvula Lagoon, Zambezi River UZC 18 (16°07'25" S 23°17'17" E), D. Tweddle, B.C.W. van der Waal, Alex D. Chilala, 12 Sep 2003. SAIAB 72668 (1, 70.8 mm SL), Zambia, Sioma Falls, River Zambezi UZC 13 (16°39'27" S 23°34'20" E), D. Tweddle, B.C.W. van der Waal, Alex D. Chilala, 10 Sep 2003. SAIAB 71784 (1, 74.4 mm SL), Zambia, Luangwa River bank, UZB 33 (15°11'44" S 22°54'21" E), D. Tweddle & B.C.W. van der Waal, 24 Apr 2003. SAIAB 71341 (1, 68.5 mm SL), Zambia, side channel upstream from Kalabo Ferry UZA 32 (15°11'00" S 22°56'23" E), D. Tweddle, B.C.W. van der Waal, Alex D. Chilala, 9 Sep 2002. SAIAB 73146 (1, 77.0 mm SL), Zambia, Near Lealui, Kanokana River UZC 47 (15°11'31" S 22°27'14" E), D. Tweddle, B.C.W. van der Waal, Alex D. Chilala, 20 Sep 2003. RUSI 67718 (1, 98.6 mm SL), Mozambique, Manica; Buzi River; Revue River at main road bridge (19°45'54" S 39°56'50" E), R. Bills, Chimela, Chivindzi, 20 Sep 2002. RUSI 59501 (1, 60.8 mm SL), Namibia, Kunene River, 1 km above Epopa Falls K 16 (13°15' E 16°59' S), P.H. Skelton, 31 Oct 1997. SAIAB 78750 (1, 74.6 mm SL), Namibia, Kunene River, Hippo pool below Ruacana Waterfall ES06 A 49 (17°24'24" S 14°13'01" E), E. Swartz, B. Kramer, 20 Aug 2006. RUSI 63168 (1, 59.0 mm SL), Namibia, Oshana, Ogongo hole near canal near Ogongo (17°40' S 15°18' E), B.C.W. van der Waal. ZSM 36108 (2, 125.1-169.1 mm SL), Namibia, Okavango River at Kapago, approx. 30 km W of Rundu, J. Peters. RUSI 45760 (1, 91.3 mm SL), South Africa, Barberton, Hectorspruit TM 9325, F. Streeter, 24 Apr 1912. SAIAB 85512 (2, 75.4-96.1 mm SL), Angola, Malanje, Russian Fishing Camp: Kwanza; Posto 5 ES 07 D22 (9°48'23" S 15°24'30" E), E. Swartz, D. Neto, P. Skelton, 19 Aug 2007.
- Tilapia snyderae* Stiassny, Schliewen & Dominey, 1992: AMNH 98259 (holotype, 38.8 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990. ZSM 27630 (3, paratypes, 36.5-44.4 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), W.J. Dominey, 15 May 1985. ZSM 27652 (2, paratypes, 32.3-37.4 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990. ZSM 27630 (1, paratype, 42.0 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990.
- Tilapia spongotroktis* Stiassny, Schliewen & Dominey, 1992: AMNH 98258 (holotype, 122.0 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), W.J. Dominey, 15 May 1985. ZSM 27682 (3, paratypes, 82.1-135.0 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990. ZSM 27629 (3, 53.1-113.7 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990.
- Tilapia tholloni* (Sauvage, 1884): MNHN 1884-0294 (1, syntype, 137.9 mm SL), Gabon, Upper Ogooué, Passa, Franceville, Schwébissh & Thollon. MNHN 1884-0295 (1, syntype, 125.6 mm SL), Gabon, Upper Ogooué, Passa, Franceville, Schwébissh & Thollon. MRAC 93-134-P-0782-0786 (2, 51.9-57.2 mm SL), Gabon, ±15 km from Mperé village, River Ogooué, upstream Port-Gentil, by Ndougou, M. Levy, 1 Sep 1993. MRAC 93-134-P-0781 (1, 83.6 mm SL), Gabon, ±15 km from Mperé village, River Ogooué, upstream Port-Gentil, by Ndougou, M. Levy, 1-30 Sep 1993. MRAC 20231-239 (1, 127.0 mm SL), Gabon, Passa, upper Ogooué (1°36' S 13°31' E), A. Baudon. MRAC 20240-43 (1, 68.1 mm SL), Gabon, Lécéni,

Ogooué, A. Baudon. ZSM 18789 (1, 85.9 mm SL), Congo Dem. Rep., Archipel Mbamou, passe Limbili (4°14' S 15°22' E), P. Brien et al., 22 Jul 1957. ZSM 37843 (2, 117.2-122.4 mm SL), Congo Dem. Rep., Province Kinshasa: Congo River, Malebo Pool at Kinkole, purchased in local fish market (4°19'15" S 15°30'12" E), J. Schwarzer et al., 29 Jul 2008. ZSM 37717 (3, 104.7-139.9 mm SL), Congo Dem. Rep., Prov. Kinshasa: Congo River, obtained from local fishermen at Kinsuka rapids, exact collecting location unclear, J. Schwarzer et al., 27 Jul 2008. ZSM 37723 (6, 81.8-143.4 mm SL), Congo Dem. Rep., Province Kinshasa: Congo River, Malebo Pool at Kinkole, purchased in local fish market (4°19'15" S 15°30'12" E), J. Schwarzer et al., 29 Jul 2008. ZSM 37711 (2, 131.5-150.6 mm SL), Congo Dem. Rep., Province Kinshasa: Congo River, Malebo Pool at Kinkole, purchased on local fish market (4°19'15" S 15°30'12" E), J. Schwarzer et al., 30 Jul 2008. MNHN 1962-0412 (1, 52.6 mm SL), Congo Dem. Rep., Likouala by Ndolé, A. Stauch, 16 Feb 1961. MNHN 1962-0411 (2, 60.7-69.3 mm SL), Congo Dem. Rep., Likouala, Bakouango, A. Stauch, 27 Feb 1961.

*Tilapia thysi* Stiassny, Schliewen & Dominey, 1992: ZSM 28390 (holotype, 62.9 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990. ZSM 27633 (1, paratype 50.9 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990. ZSM 27628 (4, paratypes, 39.3-53.8 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990. ZSM 28202 (2, 119.9-124.1 mm SL), Cameroon, Lake Bermin western (5°9' N 9°38' E), U. Schliewen, Jan 1990.

*Tilapia walteri* Thys van den Audenaerde, 1968: MRAC 155632 (holotype, 206.2 mm SL), Côte d'Ivoire, Sahibly, River Cavally (6°33' N 8°20' W), Thys van den Audenaerde, 2-3 Aug 1966. MRAC 155630-31 (2, paratypes, 73.1-101.1 mm SL), Côte d'Ivoire, Sahibly, River Cavally (6°33' N 8°20' W), Thys van den Audenaerde, 29-30 Jul 1966. MRAC 155633-35 (3, paratypes, 89.1-93.6 mm SL), Côte d'Ivoire, Tai, River Nsé and Cavally (5°52' N 7°27' W), Thys van den Audenaerde, 8 Aug 1966. MRAC 155636-40 (5, paratypes, 52.3-73.7 mm SL), Côte d'Ivoire, Tai, River Nsé and Cavally (5°52' N 7°27' W), Thys van den Audenaerde, 8 Aug 1966. MRAC 85-29-P-628 (1, 104.6 mm SL), Côte d'Ivoire, Tai, River Cavally (5°52' N 7°27' W), G. Teugels, 1-2 May 1985. MHNH 1980-1282 (1, 119.4 mm SL), Côte d'Ivoire, River Cavally by Danane (7°20'60" N 8°10'01" W), C. Lévêque, Apr 1977. MHNH 1987-0509 (1, 120.4 mm SL), Côte d'Ivoire, Binhouyé, River Nipoué, G. Teugels, 28-29 Apr 1985.

*Tilapia zillii* (Gervais, 1848): MRAC 73-42-P-2267-271 (2, 154.3-170.2 mm SL), Algeria, Temacine, 6 km S of Touggourt, large pond (33°3' N 6°2' E), Thys van den Audenaerde, 31 May 1973. MRAC 73-42-P-808-856 (16, 75.4-113.4 mm SL), Algeria, Temacine, 6 km S of Touggourt, large pond (33°3' N 6°2' E), Thys van den Audenaerde, 31 May 1973. MRAC 73-42-P-857-70 (4, 93.1-140.2 mm SL), Algeria, Temacine, 6 km S of Touggourt, large pond (33°3' N 6°2' E), Thys van den Audenaerde, 31 May 1973. MNHN 1890-0187 (1, 103.7 mm SL), Al-

geria, Touggourt, Dybowski. MNHN 1890-0188 (1, 96.2 mm SL), Algeria, Touggourt, Dybowski. RUSI 26020 (1, 42.2 mm SL), Algeria, Chouca Village (53°26' N 5°57' E), G. Balma, 15. Sep 1982. MRAC 96-082-P-0004-0005 (2, 50.6-51.9 mm SL), Sudan, Tamboura town, visvijvers, K. Vanlerberg, 1 Jan-20 Nov 1996.

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