Revision of the substrate brooding "*Tilapia*" (*Tilapia* Smith, 1840 and related taxa), (Teleostei: Perciformes: Cichlidae)

Tilapia sparrmanii from the Eye of Kuruman, South Africa.

Dissertation

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Erklärung:

Diese Dissertation wurde im Sinne von § 12 der Promotionsordnung von Prof. Dr. Gerhard Haszprunar betreut. Ich erkläre hiermit, dass die Dissertation nicht einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

München, den 12.10.2012

Andreas R. Dunz

Ehrenwörtliche Versicherung:

Ich versichere hiermit ehrenwörtlich, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt wurde.

München, den 12.10.2012

Andreas R. Dunz

Πάντα χωρεῖ καὶ οὐδὲν μένει

(„Pánta chorei kaì oudèn ménei“, „Alles bewegt sich fort und nichts bleibt.“)

Cratylus dialogue by Platon (427-347 BC)

The work presented in this dissertation was performed in the laboratory of Prof. Dr. G. Haszprunar, Director of Bavarian State Collection of Zoology, Munich, Germany.

The work was performed under the supervision of Prof. Dr. G. Haszprunar and Dr. U. K. Schliewen.

Disclaimer: This thesis is not to be considered as published in the sense of the International Code of Zoological Nomenclature, and statements made herein are not made available for nomenclatural purposes from this document.

List of publications

Dunz AR, Schliewen UK (2010a) Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana. Zootaxa 2548, 1–21.

Dunz AR, Schliewen UK (2010b) Description of a *Tilapia* (*Coptodon*) species flock of Lake Ejagham (Cameroon), including a redescription of *Tilapia deckerti* Thys van den Audenaerde, 1967. Spixiana 33, 251–280.

Dunz AR, Schliewen UK (2012) Description of a rheophilic *Tilapia* species Smith, 1840 (Teleostei: Cichlidae) from Guinea with comments on *Tilapia rheophila* Daget, 1962. Zootaxa 3314, 17–30.

Dunz AR, Vreven E, Schliewen UK (2012) *Congolapia*, a new cichlid genus from the central Congo basin (Perciformes: Cichlidae). Ichthyological Explorations of Freshwaters. Accepted.

Dunz AR, Schliewen UK Molecular phylogeny and revised classification of the haplotilapiine cichlid fishes formerly referred to as “*Tilapia*” Molecular Phylogenetics and Evolution. (Interim Decision: acceptable for publication provided minor revisions).

Declaration of author’s contribution

In this dissertation, I present my thesis on the revision of the substrate brooding “*Tilapia*”.

For all publications listed above Andreas R. Dunz and PhD supervisor Ulrich K. Schliewen designed the projects. Andreas R. Dunz accomplished the data collection, performed all analyses and designed all figures and tables. Andreas R. Dunz led the manuscript writing under the guidance of Ulrich K. Schliewen.

For the publication in cooperation with Emmanuel Vreven (Royal Museum for Central Africa), he provided parts of the studied specimen and supported manuscript writing.

München, den 12.10.2012 ____________________________

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Zusammenfassung

Die Gattung „*Tilapia*“, Teil der Familie der Buntbarsche (Teleostei: Perciformes: Cichlidae), ist sowohl von wirtschaftlicher als auch wissenschaftlicher Bedeutung: Für die afrikanische Binnenfischerei, die weltweite Aquakultur, den Natur- und Artenschutz und im besonderem Maße für die Evolutionsbiologie (Evolution im Zeitraffer). Trotz der enormen Bedeutung der Gattung „*Tilapia*“, herrschte sowohl in der Systematik als auch in der Taxonomie große Unklarheit. Mit der vorliegenden Gattungsrevision der substratbrütenden Tilapien (*Tilapia* Smith, 1840 und verwandte Arten) wurde auf der Basis molekularer und neu etablierter morphologischer und morphometrischer Merkmale ein Beitrag zur Systematik und Taxonomie der bis dahin paraphyletischen Gruppe geleistet. Die Gattungsrevision bezieht die nahe verwandten Gattungen *Chilochromis*, *Gobiocichla* und *Steatocranus* mit ein und behandelt exemplarisch die extrem artenreiche ostafrikanische Radiation mit weit über 1000 Arten, die phylogenetisch einen Teil der Tilapien darstellt.

Als Basis zur Untersuchung einzelner Individuen wurden im Vorfeld 25 morphologische und elf morphometrische Merkmale definiert und etabliert. Im Rahmen der Dissertation wurden mit diesen neuen Merkmalen 1173 Individuen vermessen. Diese stammten von mehreren Sammelreisen (Demokratische Republik Kongo, Ägypten und Südafrika) und Museumsaufenthalten (Musée Royal de l'Afrique Centrale, Tervuren, Belgien (MRAC), Natural History Museum, London (BMNH) und Muséum National d’Histoire Naturelle, Paris (MNHN)). Durch die große Anzahl vermessener Individuen und dem taxonomisch vollständig verfügbar gewordenen Datensatz wurde es möglich, „*Tilapia*“ umfassend neu zu bearbeiten. Während den laufenden Arbeiten hat sich gezeigt, dass ganze Artkomplexe und unbeschriebene Arten im Museumsmaterial enthalten waren. Deswegen wurde damit begonnen die neuen Arten zu beschreiben bzw. einzuordnen. Diese alpha-taxonomischen Arbeiten dienten dazu, die methodische Vielfalt und die Menge des erfassten Vergleichsmaterials zu dokumentieren, um in anschließenden Untersuchungen darauf Bezug nehmen zu können und resultierte sowohl in der Neubeschreibung von sechs Arten und drei Gattungen, als auch der Revision von drei Arten und drei Gattungen.

Des Weiteren wurde auf molekularer Ebene eine Detailausarbeitung der Phylogenie von Schwarzer *et al.* 2009 durch Einbeziehen möglichst aller tilapiinen Arttaxa durchgeführt. Die überarbeitete phylogenetische Hypothese, basierend auf vier mitochondrialen und fünf nukleären Loci von 94 Taxa, stellt die erste umfassende Phylogenie der basalen Haplotilapiines dar. Anhand dieser wurden 22 diskrete Linien (Tribus) identifiziert, welche mit einer weitaus artenreicheren phylogenetischen Hypothese (784 Taxa), basierend auf dem mitochondrialen Locus ND2, bestätigt wurden und in allen weiteren phylogenetischen Untersuchungen gut unterstützt wurden. Von diesen 22 diskreten Linien waren neun

unbeschrieben und wurden auf Basis eindeutiger diagnostischer, molekularer und morphologischer Merkmale definiert.

Die Kombination der alpha-taxonomischen Arbeiten und der umfassenden phylogenetischen Hypothese stellt die Basis für eine neue Klassifikation der substratbrütenden Tilapien (*Tilapia* Smith, 1840 und verwandte Arten) dar.

Summary

The genus “*Tilapia*”, which is part of the Cichlidae family (Teleostei: Perciformes: Cichlidae), is an important genus in African freshwater fishing and worldwide aquaculture. Knowledge on its correct classification and its taxonomy are vital for the nature and species conservation and for the clarification of evolutionary processes. However, the former classification of the genus is doubtful. The present genus level revision of the substrate brooding “*Tilapia*” (*Tilapia* Smith, 1840 and related taxa) based on molecular, morphological and morphometric characteristics contributes to the current classification and taxonomy of this formerly paraphyletic genus. The genus level revision involves the closely related genera *Chilochromis*, *Gobiocichla* and *Steatocranus*. It also includes the extremely species-rich East African radiation, which is only exemplified with selected taxa (e.g. *Boulengerochromis*), due to the fact that the radiation is nested within the “*Tilapia*” phylogeny.

In the beginning a set of 25 morphological and eleven meristical characteristics were defined and established. In the context of this thesis, 1173 specimen (including all available types) were measured with the previously mentioned set of established characteristics. Examined specimen were either deposited in museum collections (e.g. Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC), the Natural History Museum, London (BMNH) or the Muséum National d’Histoire Naturelle, Paris (MNHN)) or collected in the field (Democratic Republic of the Congo, South Africa, Egypt). The comprehensive processing of “*Tilapia*” was possible due to the large number of specimen and the taxonomical completeness of the dataset. Even during the initial steps it became obvious that many undescribed species and species complexes were contained in the museum material. Prior species descriptions and species flock descriptions were therefore necessary. This alpha-taxonomic approach also conduced to document the methodical diversity and the quantity of examined specimen, with respect to subsequent studies. It resulted in the description of six species and three genera as well as the revision of three species and three genera.

Furthermore a detailed revision of the phylogenetic hypothesis of Schwarzer *et al.* (2009) with a further extended multilocus dataset, (four mtDNA and five ncDNA loci) comprising almost all previously missing haplotilapiine cichlid tribes, was conducted. This comprehensive phylogenetic hypothesis identified 22 discrete lineages and consistently recovered haplotilapiine phylogenetic lineages (tribus) which are recovered or at least do not contradict the analyses. We restrict the re-classification to non East African radiation haplotilapiine clades, although all tribus definitions (Trewavas 1983; Poll 1986; Takahashi 2003) previously proposed were considered when defining new tribes. All nine novel discrete phylogenetic haplotilapiine lineages are supported by molecular and morphological autapomorphies.

The combination of the alpha-taxonomic approaches and the comprehensive phylogenetic hypothesis represents the basis for the new classification of substrate brooding "*Tilapia*" (*Tilapia* Smith, 1840 and related species).

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1. General introduction

1.1. The family Cichlidae

The family Cichlidae (cichlids) represents the most species-rich family of vertebrates (Kocher 2004). This family belongs to the order Perciformes in the infraclass Teleostei (bony fishes) in the class Actinopterygii (ray-finned fishes) (Nelson 2006). Latest findings of Wainwright *et al.* (2012) strongly support the hypothesis of a sister group relationship of Cichlidae and the strict marine Pholidichthyidae (convict blennies). Cichlidae contain brackish as well as freshwater perciform fishes. They currently hold 1627 valid species (Eschmeyer & Fong 2012), but may count up to 3000 species (Kocher 2004), distributed throughout the Neotropics, Africa, the Middle East, Madagascar, as well as Southern India, and Sri Lanka (Snoeks 2000; Turner *et al.* 2001; Sparks 2001) (Fig. 1).

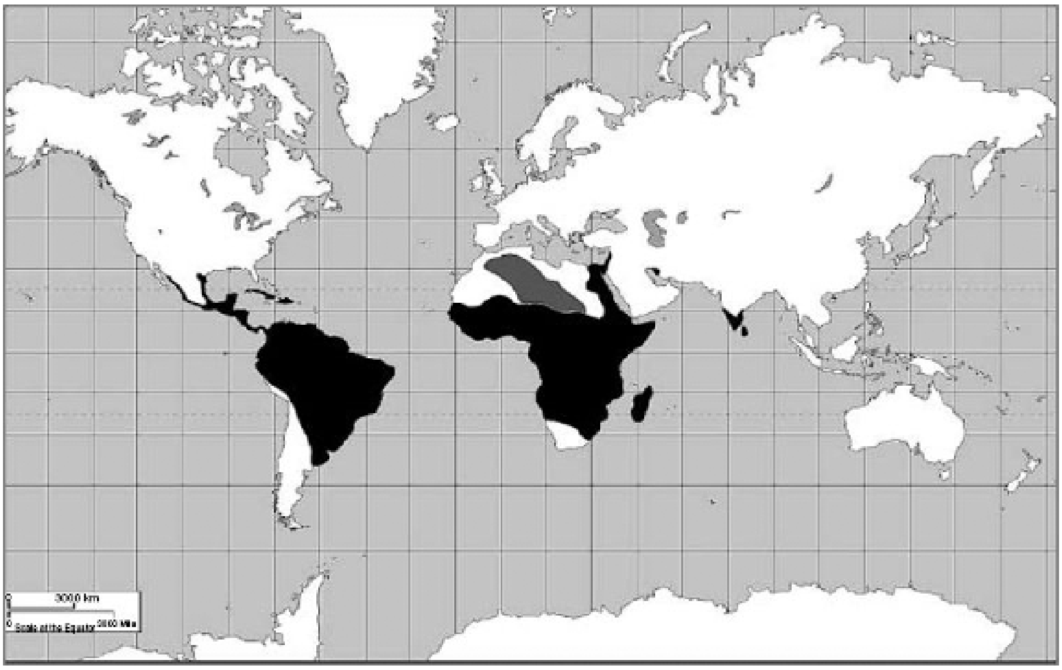

Fig. 1. Worldwide distribution of cichlids, from Sparks (2001).

This distribution pattern led to numerous hypotheses about the historical biogeography and the age of Cichlidae. Two most widely discussed hypotheses are shortly presented here. The first hypothesis of drift vicariance favours a Gondwanian distribution. The second hypothesis deals with dispersal across marine environments. The drift vicariance hypothesis is supported by the tolerance of some cichlids (e.g. *Oreochromis salinicola* (Poll, 1948)) to salty water (Murray 2001a), by the fact that the sister group of Cichlidae is strictly marine (Wainwright *et al.* 2012) and by the oldest cichlid fossil record (*Mahengechromis*), which dates from the Eocene (54-38 Ma; Murray 2000a; Murray 2000b). This finding indicates a minimum age of 45 million years for the Cichlidae (Murray 2001b), which is much younger than the break-up of Gondwana (starting 120 million years ago (Hay *et al.* 1999)). The drift vicariance hypothesis for the Gondwanan distribution is supported by monophyletic clades on all former Gondwanan landmasses shown in numerous cichlid phylogenies (Streelman *et al.* 1998; Farias *et al.* 2000; Schliewen & Stiassny 2003; Sparks & Smith 2004). The latter hypothesis remains more likely, because so far not a single case of cichlids is known, crossing a marine environment. Furthermore other non-cichlid fishes (e.g. aplocheiloid killifish) show also monophyletic clades on all former Gondwanan landmasses (Chakrabarty 2004). In addition there are doubts about the minimum age of cichlids, since derived species such as members of the *Mahengechromis* species flock indicate that cichlids are likely a much older group than what the fossil record implies (Sparks 2003).

1.2 The subfamily Pseudocrenilabrinae

The Pseudocrenilabrinae are the largest subfamily in the family Cichlidae with currently 1078 valid species (Eschmeyer & Fong 2012). The subfamily includes all the Middle Eastern and African cichlids with the exception of *Heterochromis multidens* (Pellegrin, 1900) and all Malagasy cichlid species (*Ptychochromis* Steindachner, 1880; *Paretroplus* Bleeker, 1868; *Paratilapia* Bleeker, 1868; *Ptychochromoides*, Kiener & Mauge 1966; *Oxylapia*, Kiener & Mauge 1966; *Katria* Stiassny & Sparks 2006) (Sparks & Smith 2004). *Heterochromis multidens* is basal to all members of the Pseudocrenilabrinae (Stiassny 1990; Lippitsch 1995; Salzburger *et al.* 2002; Schwarzer *et al.* 2009).

Their morphological, behavioural, and ecological diversity has fascinated biologists ever since the enormous diversity of cichlids in the East African cichlid radiation endemic to Lakes Tanganyika, Malawi and the Lake Victoria (Fig. 2) region became apparent (Fryer & Iles 1972; Kornfield & Smith 2000). The evolutionary success of the East African cichlids is amongst others based on a combination of ecological opportunities (colonization of large lakes) as well as morphological (egg-spots, colour polymorphisms, pronounced sexual dichromatism) and behavioural key-innovations (maternal mouthbrooding) (Salzburger *et al.* 2005). Another important innovation of all cichlids is the highly integrated pharyngeal jaw apparatus, giving them an advantage during subsequent colonization of new environments (Liem 1973). Over the last decades, cichlids have become a prime model system in evolutionary biology; especially in speciation research (Kocher 2004; Salzburger & Meyer 2004; Seehausen 2006). In the past ten million years almost 2000 unique species have evolved in the East African lakes (Takahashi *et al.* 2001; Kocher 2004).

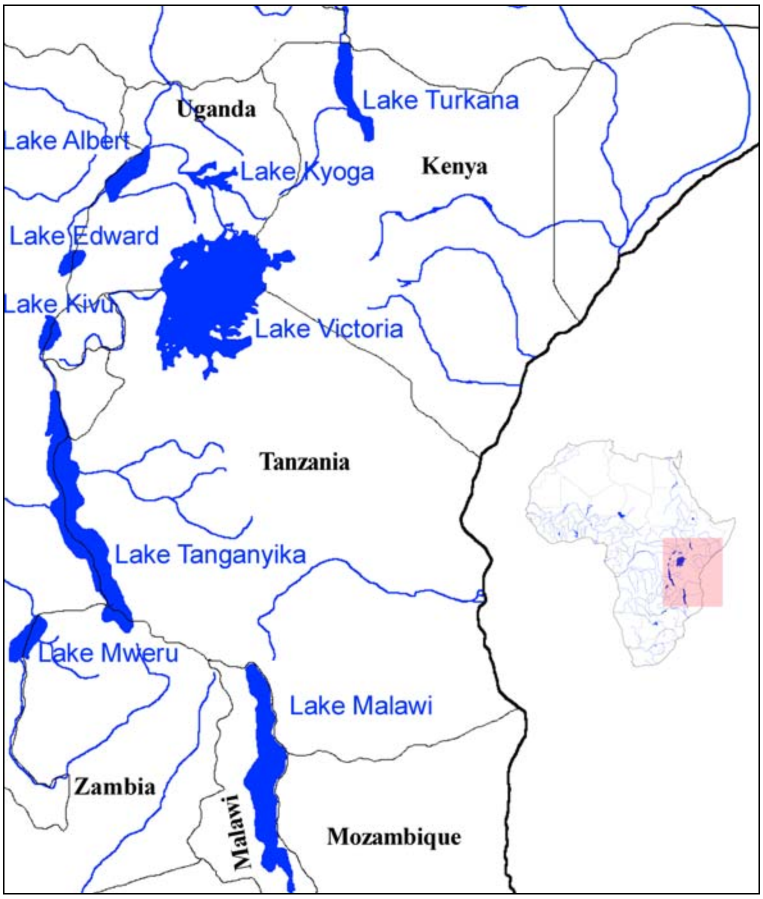

Fig. 2. Overview of the East African Lakes.

Lake Tanganyika is the oldest of the Great Lakes with deepwater conditions since about 5-6 Ma (Tiercelin & Mondeguer 1991). It harbours 197 endemic species in 49 endemic genera (Poll 1986) and was probably seeded by eight riverine ancestral lineages (Salzburger *et al.* 2002). The estimated age of these lineages corresponds to the estimated age of deepwater conditions (Nishida 1991). Further, it is assumed that the haplochromine ancestor of the species flock of Lake Malawi and Victoria originated from Lake Tanganyika (Salzburger *et al.* 2005).

The age of Lake Malawi has been estimated to two to four millions years, but the invasion occurred approximately 700,000 years ago (Meyer *et al.* 1990). The Lake Malawi flock contains more than 800 species (Konings 2007) and appears to be of non monophyletic origin (Joyce *et al.* 2011; Genner *et al.* 2012).

The youngest one, Lake Victoria with an estimated age of 250,000-750,000 years, (Temple 1969) contains more than 500 species (Turner *et al.* 2001) and originating from two separate lineages (Verheyen *et al.* 2003). Molecular phylogenetic studies of the Lake Victoria’s cichlid fauna support the young age of Lake Victoria (Meyer *et al.* 1990; Nagl *et al.* 2001; Salzburger & Meyer 2004). Usually the Lake Victoria species flock is referred to as a “superflock”, because it is closely associated with the species occurring in the surrounding lakes (Lakes Albert, Edward, Kyoga, and Kivu (Fig. 2)) (Greenwood 1973; Greenwood 1979; Greenwood 1980; Verheyen *et al.* 2003; Salzburger & Meyer 2004).

The extreme high biodiversity and the fact that the three Great Lakes rank among the top ten of the largest fresh-water lakes on earth, indicate the constraints of these model systems. Clearly arranged biotopes as the small Cameroonian crater lakes represent an alternative model system to study speciation processes, e.g. sympatric speciation.

Sympatric speciation explains the emergence of new species from a single local species without geographic isolation. Although theoretical models have now demonstrated that speciation with gene flow is possible under numerous assumptions, sympatric speciation is considered uncommon in nature (Gavrilets 2004; Bolnick & Fitzpatrick 2007). However, the debate has shifted on the question how frequent sympatric speciation occurs. There are only a few plausible examples for sympatric speciation in nature, e.g. Cameroonian crater lake cichlids (Stiassny *et al.* 1992; Schliewen *et al.* 1994; Schliewen *et al.* 2001, Schliewen & Klee 2004) or palms (*Howea*) on Lord Howe Island (Savolainen *et al.* 2006), because such cases must demonstrate species sympatry, sister relationships, reproductive isolation, and that an earlier allopatric phase is highly unlikely (Coyne & Orr 2004).

Well known systems are Lake Barombi Mbo with an endemic radiation of eleven cichlid species (Trewavas *et al.* 1972; Schliewen & Klee 2004) and Lake Bermin with an endemic radiation of nine substrate brooding tilapiine cichlids (Stiassny *et al.* 1992). A third example is Lake Ejagham, which provides the rare opportunity to study incipient species and an endemic radiation of six cichlid species (Schliewen *et al.* 2001; Dunz & Schliewen 2010b). Aquacultural research as well as evolutionary biologists caught attention of "*Tilapia*", i.e. members of the so called tilapiine cichlid assemblage (sensu Trewavas 1983 – details see below) member of the Pseudocrenilabrinae, as not only one of its members, the Nile Tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is of globally important aquacultural significance (Ridha 2006) as a food resource, but also were giving rise to small species radiations (Schliewen & Klee 2004). Further, molecular phylogenetic analyses suggest that the root of the East African cichlid radiation is nested within a paraphyletic tilapiine assemblage containing among other tilapiine genera, members of the genus *Tilapia* Smith, 1840 (Klett & Meyer 2002; Schwarzer *et al.* 2009).

1.3 The genus *Tilapia* Smith, 1840 and related taxa

Tilapia Smith, 1840 is a large genus comprising exclusively substrate brooding cichlid fishes (Perciformes: Cichlidae) that inhabit African rivers and lakes, and the Jordan valley (Middle East) (Fig. 3).

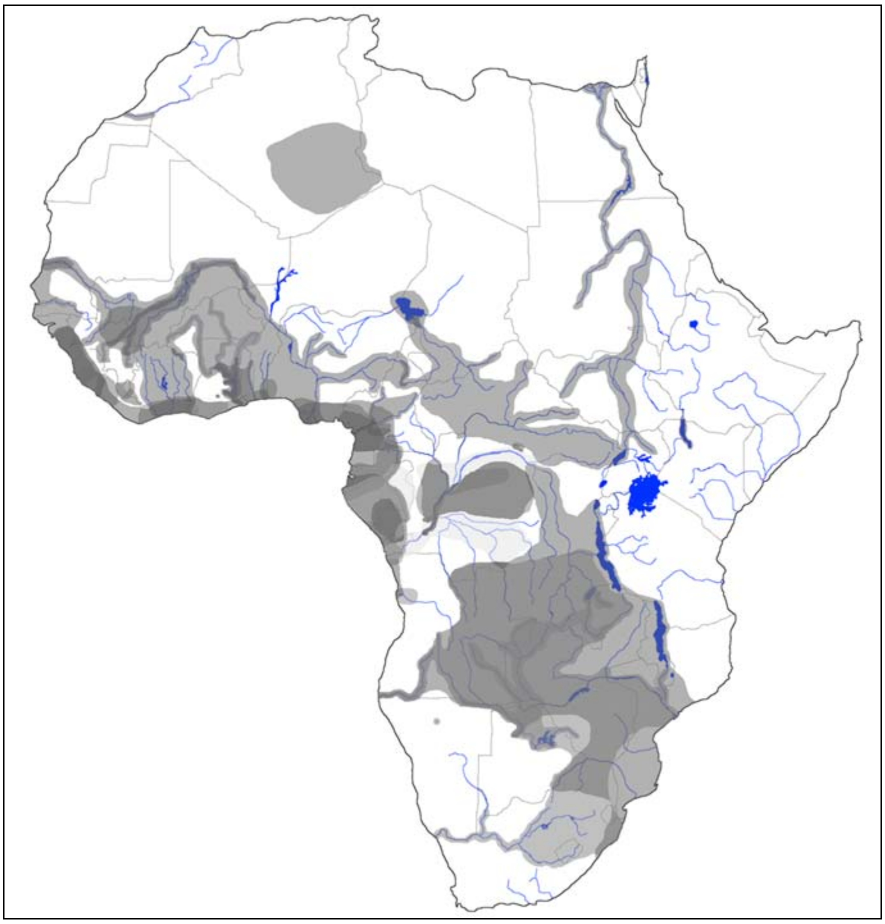

Fig. 3. Distribution of the genus *Tilapia* (shaded in grey). Areas shaded in dark grey indicate overlapping species distribution.

To facilitate the discussion about tilapiine phylogeny and classification, I provide a short overview of the previous attempts to classify *Tilapia* related taxa based on morphological, ethological and molecular data here. The genus *Tilapia* was introduced by Smith, 1840, as a new "division" of the Labyrinthiformes Cuvier 1831, with *T. sparrmanii* Smith, 1840 as type *species*. 75 years later Boulenger (1915) already listed 94 species in the genus *Tilapia*. His classification was based mainly on dentition and squamation characteristics and fin meristics. However, he stated that "the classification of the very numerous African members of the family Cichlidae presents the greatest difficulties, and the division into genera, as here followed, is unsatisfactory and open to criticism, the dentition in certain species being subject to variation, according to age, or even of a purely individual nature." Inspired by this uncertainty, Regan (1920, 1922) subsequently provided a suprageneric reclassification of African cichlid genera based on additional characteristics, mainly the structure of the pharyngeal apophysis, which supports the upper pharyngeal bones at the base of the skull. In his view, the occurrence of a "*Tilapia*" type apophysis, i.e. the pharyngeal apophysis formed by the parasphenoid (a bone located in the cranium) alone, restricted the genus *Tilapia* to those species, which Boulenger (1915) had attributed to his *Tilapia* Section I (about 50 species). Additional closely related genera with the apophysis formed by the parasphenoid alone or by the parasphenoid and the prootics (an endochondral bone of the brainpan) were, among others, *Chilochromis* Boulenger, 1902 and *Neotilapia* (Regan, 1920) (parasphenoid and prootics), but not, for example, *Steatocranus* Boulenger, 1899. Supported by additional dentition and squamation characteristics, Regan therefore redefined the genus *Tilapia* and recognized four *Tilapia* subgenera (*Coptodon* (Gervais, 1853), *Tilapia*, *Heterotilapia* (Regan, 1920) and *Sarotherodon* Rüppell, 1852), as well as a closely related separate genus, *Neotilapia*. He suggested that “a complete revision will be necessary before a final decision can be reached as to whether it should be split up”. Nevertheless, Hoedeman & De Jong (1947) taxonomically formalized Regan´s informal split of African cichlids into two major groups by introducing the subfamily Tilapiinae Hoedeman, 1947 for all African cichlids with a *Tilapia* type apophysis and the Haplochrominae[1] Hoedeman, 1947 for the rest.

Almost 50 years (after Boulenger) ago, Thys van den Audenaerde (1969) published a first comprehensive species level classification of African species of what he considered to belong to the genus *Tilapia*. In his definition, *Neotilapia* and *Pelmatochromis* sensu stricto Steindachner, 1895 were included only as subgenera of *Tilapia*, which now comprised approximately 90 described and undescribed species. He further divided the genus into three “sections”, each including several diagnosed and taxonomically available subgenera, some of them new (Tab. 1). His classification was not accompanied by a critical discussion of previous classifications and diagnostic characteristics, but was presented in the form of a key, annotated with a revised diagnosis for *Tilapia* and the subgroups. Although he referred to Regan (1920), he did not take into account the osteological characteristics described by this author, hereby indirectly accounting for Wickler´s (1963) criticism of Regan´s and Hoedeman & De Jong´s classification as being inconsistent with the distribution of ethological characteristics. Trewavas (1973) contested the inclusion of *Pelmatochromis* sensu stricto as a subgenus into *Tilapia* and proposed full generic rank for it, as well as a new genus, *Pterochromis* Trewavas, 1973. Further, she retained *Tilapia busumana* (Günther, 1903) in *Tilapia* and amalgamated all remaining species of Thys van den Audenaerde´s (1969) Section I and Section II (comprising exclusively substrate brooding genera) in a newly diagnosed genus *Tilapia* without any further subgeneric division. In addition and, mainly based on osteological characteristics and breeding behaviour, Trewavas elevated Thys van den Audenaerde´s Section III (comprising exclusively mouthbrooding genera) members to full generic rank, i.e. *Sarotherodon*. Greenwood (1978) conducted a representative review of

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[1] Fowler (1934) introduced the taxonomically available subfamily name Pseudocrenilabrinae. Apparently unaware of Fowler´s action, Hoedeman (1947) introduced Tilapinae and Haplochrominae as new subfamilies for African and Middle Eastern Cichlidae. At the moment, it remains unclear to which subfamily Hoedeman attached the type name bearing genus *Pseudocrenilabrus* Fowler, 1934, although it is very likely that he attached it to the Haplochrominae. If so, the Haplochrominae Hoedeman, 1947 is a synonym of Pseudocrenilabrinae Fowler, 1934. Then also the tribus name Haplochromini must be changed. However, since the focus of this work is not on the haplochromine cichlids, and since the issue is not finally analysed, I retain the familiar tribus name Haplochromini throughout the study.

the structure and distribution of Regan’s apophyseal character in cichlids. He confirmed Wickler´s critic and concluded that the pharyngeal apophysis must be rejected as a character useful for subfamilial classification in cichlids.

Nevertheless, Trewavas (1983) in her book “Tilapiine Fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*”, introduced a new tribe name, Tilapiini, which she distinguished from her new tribe Haplochromini on the basis Regan´s pharyngeal apophysis character states. Surprisingly, she neither referred to Greenwood´s arguments nor to Hoedeman & De Jong´s formal subfamily rank Tilapiinae. Based on cursory exploration of morphological, ethological and ecological characteristics her tribe Tilapiini still included the substrate brooding genera *Pelmatochromis*, *Pterochromis*, *Tilapia*, (tentatively) *Steatocranus* and, *Gobiochromis* (Poll, 1939), as well as the mouthbrooding genera *Sarotherodon, Oreochromis* Günther, 1889*, Danakilia* Thys van den Audenaerde, 1969*, Iranocichla* Coad, 1982, *Tristramella* Trewavas, 1942, and all endemic cichlid genera of crater lake Barombi Mbo. In addition, she suggested an extension of Thys van den Audenaerde´s (1969) subgeneric classification of *Oreochromis* by proposing an additional subgenus.

section	**section name**	**included subgenera**
I	*Tilapia* sensu lato	*Tilapia* Smith, 1840
		Trewavasia subgen. nov.
		Pelmatolapia subgen. nov.
		Pelmatochromis Steindachner, 1895
II	*Heterotilapia* and *Coptodon* sensu lato	*Heterotilapia* Regan, 1920
		Dagetia subgen. nov.
		Coptodon Gervais, 1853
III	*Sarotherodon* sensu lato	*Danakilia* subgen. nov.
		Neotilapia Regan, 1920
		Alcolapia subgen. nov.
		Nyasalapia subgen. nov.
		Loruwiala subgen. nov.
		Oreochromis Günther, 1894
		Sarotherodon Rüppell, 1854

Table 1. Thys van den Audenaerde´s (1969) subdivision of the genus *Tilapia* into three sections

Poll (1986) adopted the definition of Trewavas 1983 for Tilapiini, added additional diagnostic characteristics, but treated explicitly only the few Tilapiini taxa from Lake Tanganyika. He included the Lake Tanganyika endemic *Boulengerochromis* Pellegrin, 1904 with *Tilapia* and *Oreochromis* in his Tilapiini*.* Greenwood (1987) compared the osteology of taxa previously referred to as *Pelmatochromis* sensu lato. He concluded that neither *Pelmatochromis* nor *Pterochromis* can be considered as being phylogenetically close to *Tilapia* or tilapiines, and that the monophyly of the tilapiines (even without these two genera) remains to be demonstrated despite the fact that he identified two additional characteristics possibly supporting their monophyly. Eventually, Stiassny (1991) provided a first cladistic analysis of cichlids based on predominantly morphological cichlid characteristics. She identified two additional character states of the lower pharyngeal jaw, which she regarded as preliminary evidence for a monophyletic tilapiine lineage including *Danakilia*, *Iranocichla*, *Konia* Trewavas, 1972, *Myaka* Trewavas, 1972, *Oreochromis*, *Pungu* Trewavas, 1972, *Sarotherodon*, *Stomatepia* Trewavas, 1962, *Tristramella* and *Tilapia,* excluding *Pelmatochromis*, *Pterochromis*, *Steatocranus* and *Gobiocichla* Kanazawa, 1951 though. Pending further investigations, she preferred the ending –ine(s) for any suprageneric African cichlids groups including tilapiines.

Cichlid systematics are plagued with a paucity of phylogenetically informative morphological characteristics (Stiassny 1991). First allozyme studies tried to overcome this limitation by testing for biochemical differentiation of tilapiines using multiple markers. These studies supported a basal distinction between substrate brooding and mouthbrooding tilapiines, but were not able to assess phylogenetic relationships in more detail (McAndrew & Majumdar 1984; Sodsuk & McAndrew 1991; Pouyaud & Agnese 1995; B-Rao & Majumdar 1998). First DNA based studies incorporating a few tilapiines into a greater cichlid phylogenetic framework yielded statistically well supported evidence for tilapiines and the East African cichlid radiation representing a monophyletic lineage, and for tilapiines being paraphyletic (Sültmann *et al.* 1995; Mayer *et al.* 1998; Streelman *et al.* 1998). This unexpected and novel result has been supported or at least not contradicted by all subsequent molecular analyses which included more tilapiine taxa (Nagl *et al.* 2001; Klett & Meyer 2002). The new clade, comprising the majority of all African cichlids including tilapiines and haplochromines, is supported by one putative synapomorphy, i.e. a tricuspid inner row dentition (Schliewen & Stiassny 2003). The clade was named haplotilapiines in order to point out that a phylogenetically based classification of tilapiines is not possible without incorporating representative members of haplochromines and members of the East African cichlid radiation.

Nagl *et al.* (2001) and Klett & Meyer (2002) were the first to analyse mitochondrial DNA of more than 30 tilapiine taxa. While the first study focused on *Oreochromis*, the latter included a pan-African assemblage of 39 tilapiine as well as 19 non tilapiine, mostly species of the East African cichlid radiation in their analysis. Albeit with low statistical support for basal nodes, mouthbrooders (*Oreochromis*, *Sarotherodon*, *Stomatepia*, *Iranocichla* and *Tristramella*) and members of the East African cichlid radiation each formed a comparatively well supported clade as opposed to substrate brooding tilapiines, which split into seven clades consisting of different members of the genera *Tilapia* and *Steatocranus*, and of *Etia nguti* Schliewen & Stiassny, 2003. Interestingly, the type species of *Tilapia, T. sparrmanii* appeared more closely related to *Boulengerochromis microlepis* than to all other included "*Tilapia*" species. However, Schliewen *et al.* (1994) had previously shown that all endemic mouthbrooding tilapiine genera of crater lake Barombi Mbo (*Stomatepia*, *Pungu*, *Konia*, *Myaka*) are closely related to *Sarotherodon*.

Recently, first resolved phylogenetic hypotheses (Schwarzer et al. 2009) based on mitochondrial as well as nuclear markers representatively including all major African cichlid lineages were established. These studies conclude that all previously recognized tilapiine taxa belong to a monophyletic lineage, the haplotilapiines, encompassing not only the paraphyletic assemblage of tilapiines, but also members of the East African cichlid radiation, as well as the Cameroonian endemic *Etia nguti* (Schliewen & Stiassny 2003; Schwarzer *et al.* 2009). Both a fully representative sample of almost all haplotilapiine cichlid lineages as well as a formal and taxonomically available classification of haplotilapiines including the phylogenetically apt assignment of the type genus *Tilapia* is still missing yet.

1.4 Starting point: scientific research of "*Tilapia*"

After some unsatisfying attempts of Boulenger (1915) and Regan (1920, 1922) to classify "*Tilapia*", Thys van den Audenaerde (1969) published a first comprehensive infrageneric classification, but without a critical discussion. According to his studies, major morphologic "*Tilapia*" groups were believed to be natural groups and hence given subgeneric rank. He divided "*Tilapia*" in three sections (Tab. 1). Subsequent morphological studies (Greenwood 1978; Poll 1986; Stiassny 1991) did not consider the infrageneric level or considered only tilapiine mouthbrooders (Trewavas 1983).

In summary, African cichlids formerly referred to as "Tilapias" represent a paraphyletic species assemblage before results of this study were available (Klett & Meyer 2002; Schwarzer *et al.* 2009). Hence a revision of the genus is overdue not only for academic purposes, but also for aquaculture and fisheries which need correct names, and in conservation, since "*Tilapia*" are known as neozoan species. Furthermore, one of the subgroups of *Tilapia* apparently represents the sister group to the East African cichlid radiations (Schwarzer *et al.* 2009), which serve as an important model group for evolutionary biology and cichlid genomics (Kocher et al. 1998; Kornfield & Smith 2000).

1.5 Starting point: scientific research of Tilapiini

Most of the phylogenetic studies analysing East African cichlids have focused on lacustrine cichlids of the three Great Lakes, Tanganyika, Malawi and Victoria (Nishida 1991; Meyer 1993; Takahashi *et al.* 2001; Salzburger *et al.* 2002; Salzburger & Meyer 2004; Koblmüller *et al.* 2005; Koblmüller *et al.* 2008; Sturmbauer *et al.* 2010). However, little was known about the relationships within the original tribe Tilapiini Trewavas, 1983, containing mainly riverine cichlids, until Schwarzer *et al.* 2009 established a first well supported phylogeny as basis for further research. Several past classifications included a vaguely diagnosed tribus Tilapiini, but the composition had remained unchanged (Takahashi 2003; Koblmüller *et al.* 2008; Takahashi & Koblmüller 2011). Further, only minor changes on the tribus level were established within haplotilapiines by Poll (1986) (eleven tribes stated (including Trematocarini)) and Takahashi & Koblmüller (2011) (13 tribes stated). From 1986 until 2011 only the three tribes Boulengerochromini, Cyphotilapiini and Benthochromini have been postulated by Takahashi (2003) based on morphological characteristics. In addition Takahashi & Koblmüller (2011) stated *Orthochromis* as differentiated clade on molecular level, but without any tribus indications.

In conclusion, the starting point of my studies assumed Tilapiini as broad vaguely diagnosed tribus containing substrate and mouth brooding genera.

1.6 Boreotilapiines and austrotilapiines

Schwarzer *et al.* (2009) made the first attempt to combine an extended multilocus DNA dataset with a representative taxon sampling. Their phylogenetic analysis identified *Etia* with strong node support as the sister group ("etiines") to the remaining haplotilapiines, which were further separated into a mouthbrooding tilapiine lineage ("oreochromines") and an unnamed large clade (Fig. 4). This large clade contained all remaining species, which split into five subclades, of which two (Fig. 4: BI and BII) predominantly West African ones formed a monophyletic group ("boreotilapiines"), and two (Fig. 4: AII and AIII) predominantly South Central African clades and the East African cichlid radiation (Fig. 4: AI) formed another moderately supported one ("austrotilapiines")[2]. Due to a strongly discordant phylogenetic signal in the multilocus dataset, the sixth lineage, *T. mariae* Boulenger, 1899, could not be placed unambiguously in one of the two large clades. This result was discussed as preliminary evidence for an ancient hybrid origin of *T. mariae*.

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[2] Group names introduced by Schwarzer et al. (2009) were inappropriately ending with the suffix –ini for Etiini, Oreochromini, Austrotilapiini, Boreotilapiini. These tribus-like names are neither taxonomically available according to the ICZN, nor were they meant to be available (see disclaimer in Schwarzer et al. (2009)). As already previously suggested (Dunz & Schliewen 2010a), I refer to these groups as used in Schwarzer et al. (2009) as etiines, oreochomines, austrotilapiines and boreotilapiines in order to avoid confusion with formal tribe names ending with "-ini".

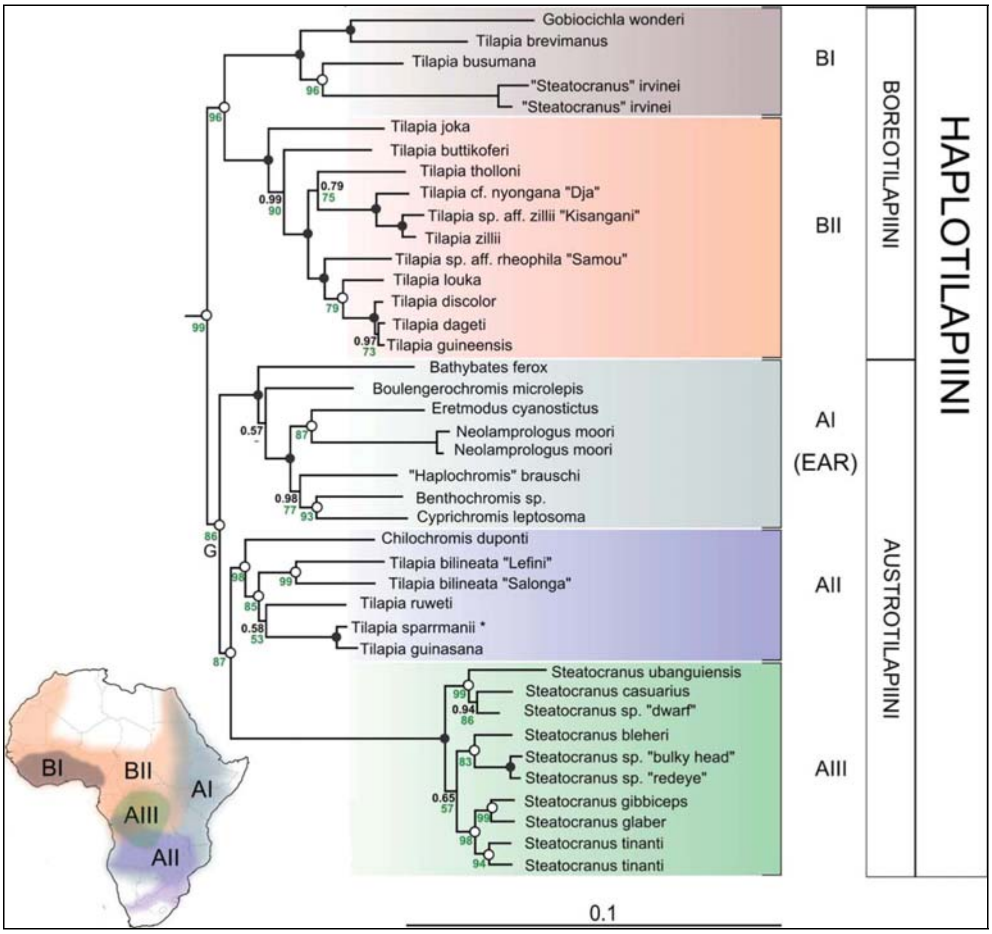

Fig. 4. Detail of the consensus tree of the African cichlid phylogeny based on a multilocus approach (modified from Schwarzer *et al.* 2009)

1.7 Speciation and Theory

1.7.1 Biodiversity

Wilson (1988) introduced the term "biodiversity" in literature. Today this term has become of major interest in the scientific community and in public policy (Roberts 1990; Lubchenco *et al.* 1991). The most commonly used definition of biodiversity is "the variety and variability among living organisms and the ecological complexes in which they occur" (OTA 1987). Other definitions are for example "the degree of nature's variety" (McNeely 1988) or "the variety of life and its processes" (Hughes & Noss 1992). A biological hierarchy can contain biodiversity at four levels, (1) genetic diversity, (2) species diversity, (3) ecosystem diversity, (4) landscape diversity (Noss 1983; Norse *et al.* 1986; OTA 1987). Because of the commercial and ecological importance of biodiversity, large efforts are made on its preservation (Cairns & Lackey 1992). Species richness is disappearing worldwide and protection is largely administered to biological entities that are referred to as species (Mayden 2002).

1.7.2 Species and species concepts

Even in the 21st century the question “what is a species actually” remains open. An overwhelming amount of literature is available on this topic. The present thesis deals exclusively with sexually reproducing species. Thus the following will mainly focus on these.

“It all comes, I believe, from trying to define the undefinable” Darwin wrote to Joseph D. Hooker on 24 December 1856 (Burkhardt & Smith 1990). More than hundred years later Coyne (1994) stated that species are real entities, not subjective human divisions, but if species represents hypotheses in the scientific process, they can never be proven (Mayden 2002).

Traditionally species are defined as "…groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Biological Species Concept, Mayr 1942). The existence of discrete groups constitutes evidence for isolating mechanisms (Coyne 1994). These mechanisms could be divided into two major groups: (1) prezygotic (acting before fertilization, e.g. gametic incompatibility) and (2) postcygotic (acting after fertilization, e.g. hybrid inviability) mechanisms (Coyne & Orr 1998).

The operational issues of the recognition of real entities are of primary importance for all species concepts, except the Evolutionary Species Concept (Wiley 1978; Wiley & Mayden 2000a; Wiley & Mayden 2000b; Wiley & Mayden 2000c). Thus a hierarchical division into primary (theoretical) and secondary (operational) concepts is useful. The following describes the Evolutionary Species Concept as primary and the Phylogenetic Species Concept (Rosen 1978; Rosen 1979; Cracraft 1983) as secondary concept.

The Evolutionary Species Concept characterizes a species as follows: “An evolutionary species is an entity composed of organisms that maintains its identity from other such entities through time and over space and that has its own independent evolutionary fate and historical tendencies” (Wiley & Mayden 2002a). As a nonoperational concept it is difficult to find anything to fit the concept without prior knowledge. However, such General Lineage Concepts do not sufficiently distinguish species from higher taxa (Ereshefsky 2010). Thus the Phylogenetic Species Concept (operational concept) was considered as surrogate concept to the Evolutionary Species Concept (Mayden 2002).

The Phylogenetic Species Concept characterizes a species as follows: “A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent” (Cracraft 1989). To put it another way species possess autapomorphic traits or can be identified on the basis of at least one shared derived character inherited from a unique common ancestor. This criterion for recognition of species is widely accepted (Mayden 2002).

2. Aims of the thesis

The main aim of this thesis was a genus level revision of all substrate brooding "*Tilapia*" and related taxa (*Chilochromis*, *Gobiocichla* and *Steatocranus*) using molecular and morphological data. It also includes the extremely species-rich East African radiation, which is only exemplified with selected taxa (e.g. *Boulengerochromis*), due to the fact that the radiation is nested within the "*Tilapia*" phylogeny.

Secondary aims on morphological level are first of all the definition and establishment of a set of 25 morphological and eleven meristical characteristics for alpha-taxonomy and secondly the reconsideration of several alpha-taxonomy problems involving all available type and comparative material (total 1173 specimen) of the genus *Tilapia*.

Revised alpha-taxonomy approaches are the description of *Tilapia pra* Dunz & Schliewen, 2010a. This species is sister group to *Tilapia busumana* (Günther, 1903) and both are located in an unresolved ancient tribe (Gobiocichlini). Further the Lake Ejagham species flock (four species) is described. All these species belong to the former subgenus *Coptodon* (Gervais, 1853). With the description of *Tilapia konkourensis* Dunz & Schliewen, 2012 the monotypic subgenus *Dagetia* Thys van den Audenaerde, 1969 was synonymized with *Coptodon*. Finally the revision of the *Tilapia bilineata* complex resulted in the description of a new genus (*Congolapia* Dunz & Schliewen, 2012), which is sister group to *Tilapia* sensu stricto.

Secondary aims on molecular level are a detailed revision of the phylogenetic hypothesis of Schwarzer *et al.* 2009 with a further extended multilocus dataset (four mtDNA and five ncDNA loci) comprising almost all previously missing haplotilapiine cichlid tribes (94 taxa). In addition an enlarged mtDNA (ND2) dataset (784 taxa) comprising about 60% of all described Pseudocrenilabrinae genera is presented. Even in a seven times larger taxaset (ND2), the resulting topology is largely congruent with the multilocus approach (four mtDNA and five ncDNA loci).

All these secondary results provide the basis for a novel classification of *Tilapia* and related lineages defined by putative molecular synapomorphies (unambiguously diagnostic character states), but critically incorporating a selected set of morphological data.

3. Paper I

Dunz AR, Schliewen UK (2010a) Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana. Zootaxa 2548, 1–21.

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Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana

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Abstract

A new species of the genus *Tilapia* Smith, 1840 is described from the Pra River drainage in Ghana. *Tilapia pra* **sp. nov.** is distinguished from all *Tilapia* species except *T. sparrmanii, T. ruweti, T. guinasana, T. baloni, T. brevimanus, T. mariae, T. cabrae* and *T. busumana* in having bicuspid posterior pharyngeal teeth on the lower pharyngeal jaw. It differs from *T. baloni* and *T. ruweti* in having more gill rakers on the first ceratobranchial (lower) gill-arch (10–12 vs. 6–9), from *T. guinasana* in having a higher number of upper lateral line scales (18–22 vs. 14–17) and from *T. sparrmanii* in a combination of a higher number of upper lateral line scales (18–22 vs. 14–19), a shorter anal fin base (15.0–18.6% vs. 18.0–23.8% of SL) and a lower number of vertical stripes (6–7 vs. 8–9). It differs from *T. mariae, T. cabrae* and *T. brevimanus* in having robust, non-spatulate outer row jaw teeth (vs. gracile spatulate teeth) and from *T. busumana* in having a longer last dorsal-fin spine (16.2–21.3% vs. 11.6–14.9% of SL), and a smaller lower lip length (8.0–10.7% vs. 9.6–13.9% of SL) and lower jaw length (9.9–13.6% vs. 10.5–15.2% of SL). In addition, *T. pra* **sp. nov.** differs from *T. busumana* in ground coloration. *T. pra* **sp. nov.** possesses a light brown to greyish dorsum and a beige to yellow ventral area vs. a bluish-purple to blackish dorsum and darker on underside of head and body of *T. busumana*.

Key words: Ichthyofauna, freshwater, Kwahu plateau, Ashanti ecoregion

Introduction

Members of the large African cichlid genus *Tilapia* Smith, 1840 (type species, *Tilapia sparrmanii*) inhabit most African rivers and lakes as well as the Jordan River drainage. Thys (1968) divided *Tilapia* into three "sections": Section I (*Tilapia* sensu lato) with the four subgenera *Tilapia* Smith, 1840, *Trewavasia* Thys, 1969, *Pelmatolapia* Thys, 1969 and *Pelmatochromis* Steindachner, 1894; Section II including the subgenera *Heterotilapia* Regan, 1920, *Coptodon* Gervais, 1853 and *Dagetia* Thys, 1969; and Section III (*Sarotherodon* group sensu lato) with the seven subgenera (and three "groups" related to one of the subgenera) *Danakilia* Thys, 1969, *Neotilapia* Regan, 1920, *Alcolapia* Thys, 1969, *Nyasalapia* Thys, 1969, *Loruwiala* Thys, 1969, *Oreochromis* Günther, 1889 and *Sarotherodon* Rüppell, 1854, all mouth-brooders. Later, Trewavas (1983) removed all mouth-brooding species from *Tilapia*, and placed them into the genera *Sarotherodon* Rüppell, 1852 or *Oreochromis* Günther, 1889. It has long been known that morphological evidence for the monophyly of the substrate-spawning tilapias is lacking (Stiassny *et al.* 1992), and this was later substantiated by molecular analyses recovering *Tilapia* as paraphyletic (Klett & Meyer 2002; Schliewen & Stiassny 2003). Recently, in a comprehensive molecular analysis of the interrelationships of haplotilapiine cichlids (sensu Schliewen & Stiassny, 2003), Schwarzer *et al.* (2009) identified a novel clade of tilapias (austrotilapiines[1])

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[1] Schwarzer *et al.* (2009) have introduced informally family group names using inappropriately the suffix –ini for Etiini, Oreochromini, Austrotilapiini, Boreotilapiini. These names were neither meant to be available (see disclaimer in Schwarzer *et al.* (2009), nor are they taxonomically available according to the ICZN. We hereby suggest to refer to these groups as etiines, oreochomines, austrotilapiines and boreotilapiines in order to avoid confusion with formal tribe names ending with "-ini".

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comprising the type species, *T. sparrmanii*, *T. ruweti* Poll & Thys, *T. guinasana* Trewavas (and very likely *T. baloni* Trewavas & Stewart), *T. bilineata* Pellegrin, *Chilochromis* Boulenger, *Steatocranus* Boulenger, (excluding "*Steatocranus*" *irvinei* (Trewavas)) and all members of the East African cichlid radiations (EAR). The sister group to this clade, the boreotilapiines[1], contains all remaining *Tilapia, Gobiocichla* Kanazawa, and "*Steatocranus*" *irvinei*. One member of Thys′ subgenus *Pelmatolapia*, *T. mariae* Boulenger, could not be placed unambiguously, but certainly is not an austrotilapiine (Schwarzer *et al.* 2009). A comprehensive revision of *Tilapia* identified a monophyletic subgroup of australotilapiines containing the type species of *Tilapia*, *T. sparrmanii* as *Tilapia* (i.e., *T. sparrmanii*, *T. ruweti*, and *T. guinasana*).

Currently, *Tilapia* contains 40 species. All are substrate-brooders recognized by the following combination of plesiomorphic cichlid features; lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel shorter than (or just as long as) the toothed area of the jaw, bicuspid or tricuspid (rarely quadricuspid) posterior pharyngeal teeth, the lower limb of first gill arch bearing at most 17 rakers, two lateral lines, cycloid scales, and 21–30 scales in the longitudinal scale row (Teugels 2003).

Currently sixteen valid *Tilapia* species are known from western central Africa: *T. brevimanus* Boulenger; *T. busumana* (Günther); *T. buttikoferi* (Hubrecht); *T. cabrae* Boulenger; *T. cessiana* Thys; *T. coffea* Thys; *T. dageti* Thys; *T. deckerti* Thys, *T. discolor* (Günther); *T. guineensis* (Bleeker in Günther); *T. joka* Thys; *T. louka* Thys; *T. mariae* Boulenger; *T. rheophila* Daget; *T. walteri* Thys and *T. zillii* (Gervais). In addition to these, there are several undescribed species from western Cameroon including *T.* sp. aff. *guineensis* "Cross" (Thys 1971) and undescribed members of the Lake Ejagham species flock, such as *T.* cf. *deckerti* "little-black", *T.* cf. *deckerti* "large-black", *T.* sp. "jewel", *T.* sp. "dark jewel" and *T.* sp. "predator" (Schliewen *et al.* 2001).

Tilapia busumana has been recorded from its type locality, Lake Bosumtwi, an impact crater lake, as well as from the Tano, Bia and Ankobra river drainages (Teugels *et al.* 2003), all located in the Ashanti ecoregion (sensu Thieme *et al.* 2005). It has repeatedly been noted that *Tilapia* sp. aff. *busumana* "Birim" (Pra drainage) differ in coloration and body shape from *T. busumana* (Lake Bosumtwi) (Linke & Staeck 1993; Freyhof 1989; Martin & Lamboj 1994). A preliminary review of ZSM specimens from the Ankobra (Draw) drainage and Lake Bosumtwi confirmed this impression and prompted an investigation of *Tilapia* cf. *busumana* complex (containing *T. busumana*, *T. pra* **sp. nov.**, *T.* sp. aff. *busumana* "Birim" and *T.* sp. aff. *busumana* "Tano") material including the types of *T. busumana* from Lake Bosumtwi. We compared members of the *Tilapia* cf. *busumana* complex with available type specimens of almost all *Tilapia* sensu lato taxa. Here we report the results of these comparisons and describe the morphometrically fully diagnosable populations as a new *Tilapia* species.

Material and methods

We examined *Tilapia* sensu lato specimens (n=610) from the following institutions (see Appendix 1): the Royal Museum for Central Africa, Tervuren, Belgium (MRAC), the Natural History Museum, London, United Kingdom (BMNH), the Muséum nationale d'Histoire naturelle (MNHN), the Naturhistorisches Museum Wien (NMW), the Zoologische Museum Berlin (ZMB) and the Bavarian State Collection of Zoology, München, Germany (ZSM). Focus was placed on material from the Ashanti biogeographic region. Comparative material of each valid *Tilapia* sensu lato species was included except for type material of *T. buttikoferi*, *T. camerunensis* Lönnberg, *T. guineensis*, *T. jallae* (Boulenger), *T. margaritacea* Boulenger and *T. zillii*, due to material being unavailable or, in the case of *T. zillii* and *T. jallae*, lost.

Twenty-five morphometric measurements and eleven meristic counts were taken. Morphometric measurements represent a composite of Barel *et al.* (1977), Thys (1964) and Dunz & Schliewen (2009). Here, we provide precise definitions for all of our measurements as a baseline for forthcoming *Tilapia* studies, because definitions were sometimes ambiguous in Barel *et al.* (1977) and Thys (1964). Measurements (the left side of specimens) were taken point-to-point under a binocular microscope using a digital caliper with an accuracy of 0.01 mm, and rounded to the nearest 0.1 mm. Measurements are given as percentage of SL.

Morphometric measurements include: total length (TL), distance between rostral tip of snout and an imaginary line drawn between the two lobe tips of caudal fin (bilobular length); SL, distance between rostral tip of snout and caudal-fin base at articulation (flexion point of hypurals at end of hypural plate); head length (HL), distance from the rostral tip of snout to the caudal end of the membranous border of opercle; interorbital width, minimal distance between orbits (membranous); preorbital width (POW), width between the left and right preorbital process; horizontal eye length (EyL), distance (excluding ligamentous ring) from the rostral point of the orbit (at lateroethmoid to lacrymal bone) to the ventral point (at sphenotic-circumorbitals) of the postorbital process of the neurocranium; snout length (SnL), distance from the rostral tip of upper lip to the rostral point of the membranous border of the orbit (as in EyL, but including the ligamentous ring); internostril distance (IND), minimum distance between the bases of the tubular nostrils; cheek depth (ChD), vertical distance from the rearmost point on the lower rim of the preopercle to the membranous margin of the orbit; upper lip length (ULL), distance from anterior tip of upper lip (at symphysis of upper jaw) to posteriormost point of upper lip; lower lip length (LLL), distance from anterior point of upper lip (at symphysis of lower jaw) to posteriormost point of lower lip; lower lip width (LLW), horizontal distance from left to right distal corner of lower lip; lower jaw length (LJL), distance from the rostral to the caudal tip of the retroarticular process marked by the insertion of the well-developed interopercular-mandibular ligament; predorsal distance (PDD), horizontal length from anterior tip of upper lip (at symphysis of the upper jaw) to the insertion of the first dorsal-fin spine; length of dorsal-fin base (DFL), distance between rostral and caudal base; length of last dorsal-fin spine (DSL), from the insertion to its distal end; length of anal-fin base (AFL), distance between the rostral and caudal base; length of third anal-fin spine (ASL), from the insertion to its distal end; pelvic-fin length (PFL), distance between insertion of pelvic-fin spine and distal end of longest pelvic-fin ray; pectoral-fin length (PecFL), distance from insertion of uppermost pectoral-fin ray to distal end of longest ray; caudal peduncle depth (CPD), minimum vertical depth of the caudal peduncle; caudal peduncle length (CPL), horizontal distance between the vertical line through the caudalmost point of the anal-fin base to the end of hypural plate; body depth at the pelvic-fin base (BD), distance between the insertion of the pelvic-fin spine to the insertion of the first dorsal-fin spine; preanal length (PAL), distance between the rostral tip of symphysis of lower jaws and the articulation of first anal-fin spine; distance from anus to base of anal fin (DAAF), distance between caudal border of anus and the articulation of first anal-fin spine.

Meristic counts include the number of dorsal-fin spines (DFSp) and dorsal-fin rays (DFBr); number of anal-fin rays (AFBr); number of pectoral-fin rays (PecBr); number of teeth in upper jaw (UJT) and lower jaw (LJT); number of scales along the horizontal line of scales including the lower lateral line from the edge of the opercle to the base of caudal fin (excluding scales on the caudal fin) (ScHL); number of scales on the upper (ScULL- Upper Lateral Line) and lower lateral line (only pored scales counted) (ScLLL); number of gill rakers on first ceratobranchial (lower) gill-arch (excluding gill rakers on cartilaginous plug) (GrC); number of gill rakers on first epibranchial (upper) gill-arch (including gill rakers on cartilaginous plug) (GrE); number of cusps on pharyngeal teeth in the posterior two transverse tooth rows on lower pharyngeal jaw (counted for the holotype and ten paratypes).

Morphometric and meristics data for the *T.* cf. *busumana* species complex were subjected to Principal Component Analyses (PCA) based on log-transformed data using the statistical program PAST 1.95 (Hammer *et al.*, 2001). Differences between the new species and other members of the *T.* cf. *busumana* complex were illustrated by plotting scores of Principal Component (PC) II versus PC III of log-transformed morphometric data. PCA were performed in two steps, first with all members of the *T. busumana* species complex, and second without the new species and *T.* sp. aff. *busumana* "Tano" (more details see Results). Meristic PC plots were based on data excluding tooth count values, because some specimens obviously lack several teeth and the tooth number appears correlated with size.

The authors suggest referring only to the monophyletic subgroup of australotilapiines containing the type species of *Tilapia*, *T. sparrmanii* as *Tilapia* (i.e., *T. sparrmanii*, *T. ruweti*, and *T. guinasana*) while the remaining species should be referred to as "*Tilapia*". The new species is described within *Tilapia* in the results, diagnosis and description to follow ICZN Article 5.3, but will appear elsewhere from now as "*Tilapia*" *pra* **sp. nov.**, because it is not closely related to the type species.

Applied species concept. We use the Phylogenetic species concept as a surrogate concept for the Evolutionary Species Concept; see Mayden (2002) for a discussion and hierarchy of Species Concepts.

Results

Members of the "*Tilapia*" cf. *busumana* complex can be distinguished from all other "*Tilapia*" in a combination of morphological and meristic characters. Number of cusps on the posterior pharyngeal teeth on lower pharyngeal jaw serves to divide *Tilapia* sensu lato into two subgroups: The first group with two cusps in the posterior two row contains *T. sparrmanii*, *T. ruweti*, *T. guinasana*, *T. baloni*, "*T.*" *brevimanus*, "*T.*" *mariae*, "*T.*" *cabrae* and all members of the "*T.*" cf. *busumana* complex. The second group with three to four cusps includes all other "*Tilapia*" species (containing the austrotilapiine "*T.*" *bilineata*) except for "*T.*" *gutturosa* of the "*Tilapia*" species flock of Lake Bermin (Stiassny *et al.* 1992). Further comparisons are restricted to the first group. Number of upper lateral line scales separates the monophyletic clade *Tilapia* sensu stricto (14–19) from "*T.*" *brevimanus* (19–23), *Pelmatolapia* ("*T.*" *mariae* and "*T.*" *cabrae*) (18–21), and from members of the "*T.*" cf. *busumana* complex (17–21). The character number of gill rakers on ceratobranchial gill-arch separates "*T.*" *brevimanus* (12–16) from "*T.*" mariae and "*T.*" *cabrae* (8–15 (mean 12)) and members of the "*T.*" cf. *busumana* complex (9–12). "*T.*" mariae and "*T.*" *cabrae* further differ in shape of outer jaw-teeth (spatulate vs. slender) from "*T.*" cf. *busumana* complex members.

A plot of morphometric PC II vs. morphometric PC III (Fig. 1) indicates two distinct and non-overlapping clusters: a *T. pra* **sp. nov.** cluster and a cluster comprised of "*T.*" *busumana* from Lake Bosumtwi and two specimens from the Birim River ("*T.*" sp. aff. *busumana* "Birim"). Separated from both clusters is "*T.*" sp. aff. *busumana* "Tano". When using the 95% confidence interval as criterion, the 95% confidence interval overlap is minimal and contains no specimen data. PC I explained 90.99% of variance, PC II 4.31% and PC III 0.76%. The highest loadings were identified for the character "length of last dorsal-fin spine" (Tab. 1). In a second PCA step, the *T. pra* **sp. nov.** specimens and the "*T.*" sp. aff. *busumana* "Tano" were removed from the analysis to reduce the total variance to detect more detailed differences between "*T.*" sp. aff. *busumana* "Birim" and "*T.*" *busumana*. The plot of PC II vs. PC III (Fig. 2) shows that values for "*T.*" *busumana* are separated from "*T.*" sp. aff. *busumana* "Birim" when using the 95% confidence interval as criterion. Values for loadings are shown in Table 2. In summary, *T. pra* **sp. nov.** is diagnosably distinct from "*T.*" *busumana*, "*T.*" sp. aff. *busumana* "Birim" and "*T.*" sp. aff. *busumana* "Tano". Therefore we here describe it as a new species.

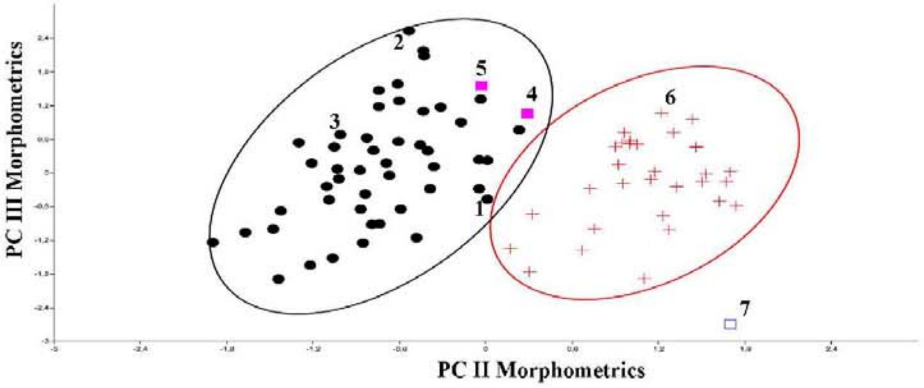


FIGURE 1. Scatter plot of scores of Principal Component II vs. Principal Component III; 95% confidence intervals outlined as ellipses. Dots = "*T.*" *busumana*; crosses = *T. pra* **sp. nov.**; squares = "*T.*" sp. Numbered specimens are: 1-3 (dots) = BMNH 1903.4.24.36-41 (syntypes *Chromis busumanus* Günther, 1903); 4-5 (squares) = MRAC 78-15-P-1-2 ("*T.*" sp. aff. *busumana* "Birim"), 6 (cross) = ZSM 36123 (holotype *Tilapia pra* **sp. nov.**) and 7 (square) = ZSM 39002 ("*T.*" sp. aff. *busumana* "Tano"). The specimen of "*T.*" sp. aff. *busumana* "Tano" has a very short caudal peduncle (9.3% of SL) and differs in mouth shape compared to all other specimens.

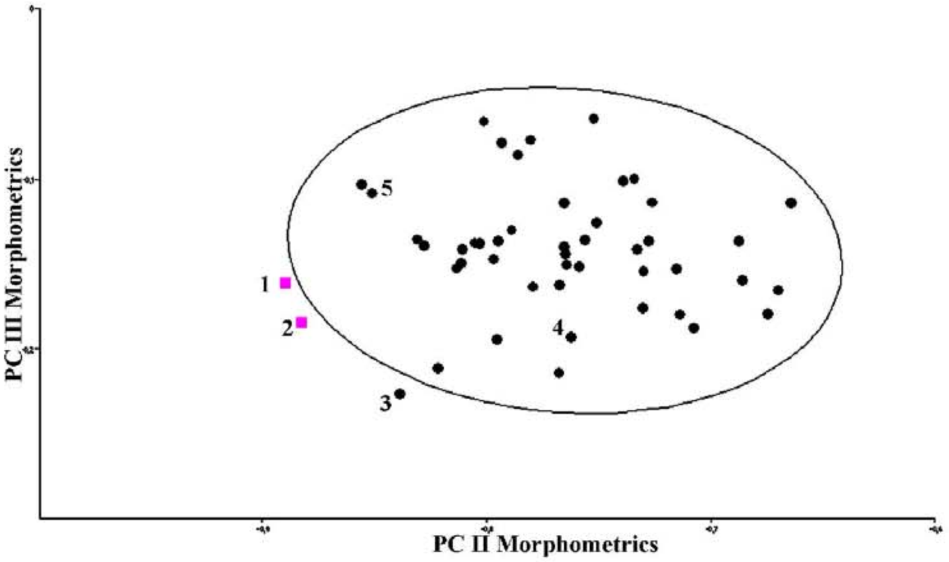


FIGURE 2. Scatter plot of scores of Principal Component II vs. Principal Component III, 95% confidence interval visualized as ellipses. Dots = "*T.*" *busumana*; squares = "*T.*" sp.; 1-2 (squares) = MRAC 78-15-P-1-2 ("*T.*" sp. aff. *busumana* "Birim"), 3-5 (dots) = BMNH 1903.4.24.36-41 (syntypes *Chromis busumanus* Günther, 1903). The specimen (marked with the number 3) outside the 95% confidence interval is one of the syntypes, which is in poor condition.

***Tilapia pra*, new species**
(Fig. 3; Tab. 3)

Holotype: ZSM 36123 (1, 83.5 mm SL), Ghana, Ashanti Region, Anum River, tributary to Pra, at Anumso village (6° 25' 44"N, 1° 17' 59" W), D. Neumann & G. Baffur E, 29 Oct. 2002.

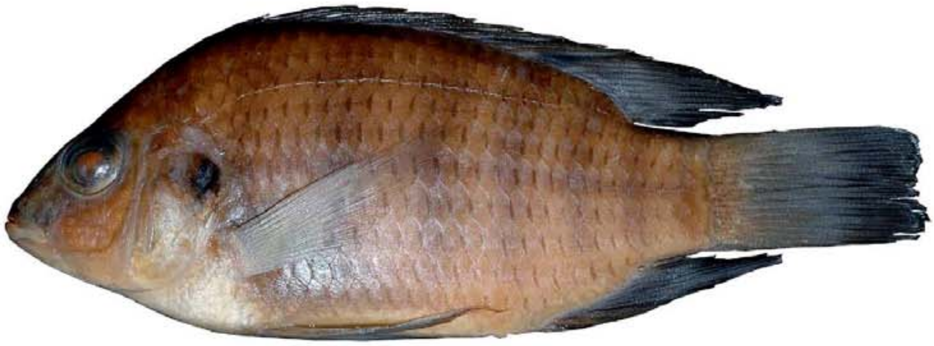
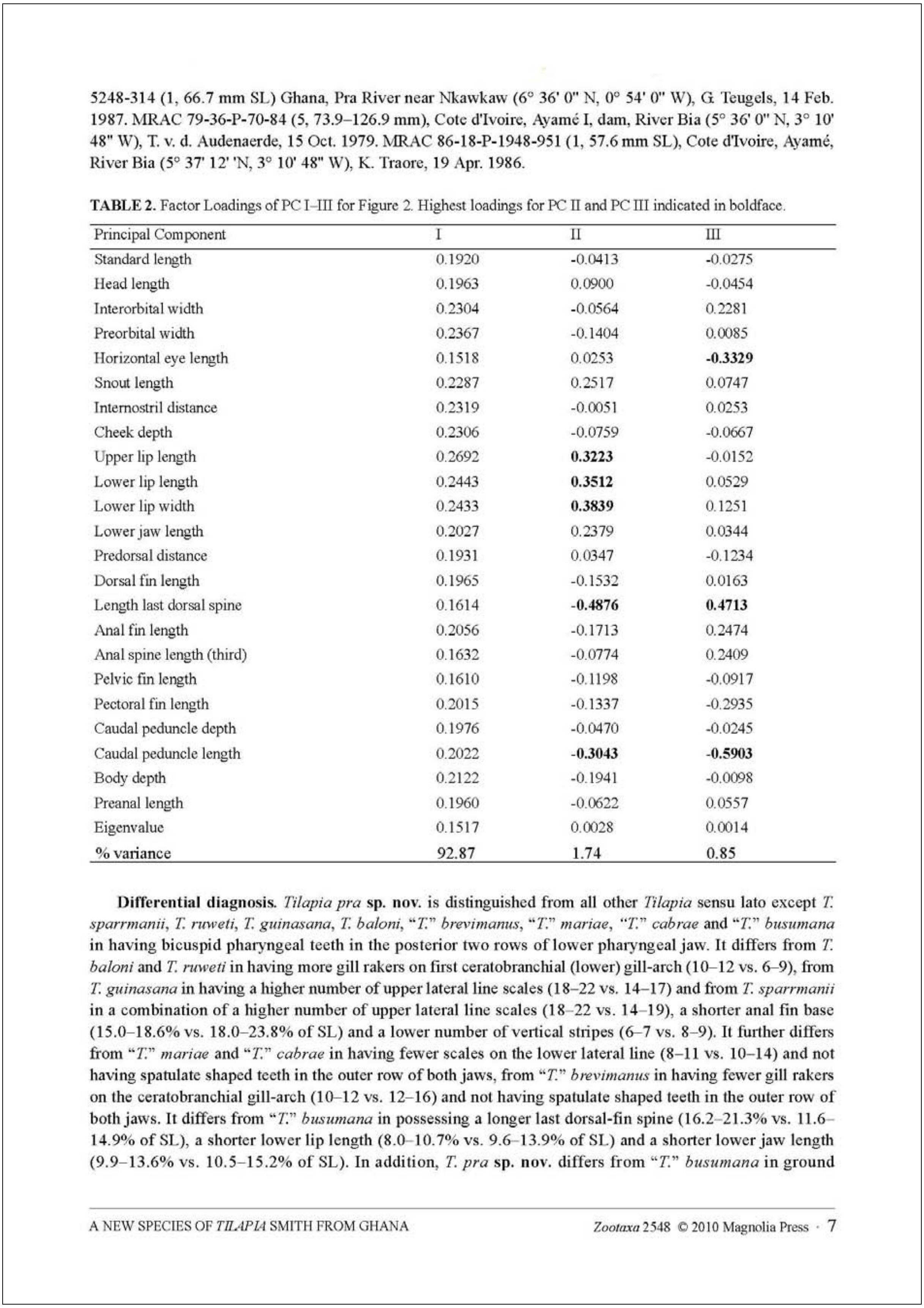


FIGURE 3. Preserved holotype of *Tilapia pra* **sp. nov.** (ZSM 36123), 83.5 mm SL; Ghana: Anum River, tributary to Pra, at Anumso village.

TABLE 1. Factor Loadings of PC I–III for Figure 1. Highest loadings for PC II and PC III indicated in boldface.

Principal Component	I	II	III
Standard length	0.1863	-0.0086	0.0055
Head length	0.1902	-0.0344	-0.0559
Interorbital width	0.2108	0.1294	-0.1381
Preorbital width	0.2185	0.0275	-0.0122
Horizontal eye length	0.1329	0.0439	-0.0621
Snout length	0.2136	-0.0758	**-0.3096**
Internostril distance	0.2187	-0.0670	0.0336
Cheek depth	0.2321	-0.0140	-0.0028
Upper lip length	0.2539	**-0.3633**	-0.0341
Lower lip length	0.2303	**-0.3828**	-0.0316
Lower lip width	0.2332	**-0.3902**	-0.1579
Lower jaw length	0.2052	-0.2170	0.0531
Predorsal distance	0.1870	0.0543	-0.1022
Dorsal fin length	0.1968	0.1102	-0.0275
Length last dorsal spine	0.1870	**0.4852**	0.1793
Anal fin length	0.1947	0.0940	-0.1588
Anal spine length (third)	0.1657	0.2609	-0.1034
Pelvic fin length	0.1925	0.1312	0.0886
Pectoral fin length	0.1988	0.2640	-0.1991
Caudal peduncle depth	0.1944	0.0776	-0.0961
Caudal peduncle length	0.2087	-0.0541	**0.4174**
Body depth	0.2098	0.2587	-0.1108
Preanal length	0.1878	0.0186	0.0600
Distance anus - anal fin	0.2162	-0.0205	**0.7217**
Eigenvalue	0.2329	0.0110	0.0020
% variance	90.99	4.31	0.76

Paratypes: ZSM 36116 (1, 84.2 mm SL), ZSM 36117 (1, 110.1 mm SL), ZSM 36118 (1, 73.1 mm SL), ZSM 36119 (1, 76.6 mm SL), ZSM 36120 (1, 77.7 mm SL), ZSM 36121 (1, 73.7 mm SL), ZSM 36122 (1, 76.1 mm SL), ZSM 36124 (1, 81.1 mm SL), ZSM 36125 (1, 79.1 mm SL); all collected with holotype. ZSM 36149 (2 now 1, 62.6 mm SL), Ghana, Ashanti Region, Oda River, tributary to Pra, floodplain and small affluent left to road entrance at bridge on road Bekwai-Awiankwata (6° 27' N, 1° 37' W), D. Neumann & K. Mensa, 2 Nov. 2002. AMNH 250601 (1 ex ZSM 36149, 57.7 mm SL), Ghana, Ashanti Region, Oda River, tributary to Pra, floodplain and small affluent left to road entrance at bridge on road Bekwai-Awiankwata (6° 27' N, 1° 37' W), D. Neumann & K. Mensa, 2 Nov. 2002. ZSM 39005 (3 now 2, 40.3–58.8 mm SL), Ghana, Nyelei, tributary to Ankobra, near Akropong at the new bridge (5° 5' 6" N, 2° 17' 13" W), U. Schliewen, 10 Mar.–30 Apr. 1998. AMNH 250602 (1 ex ZSM 39005, 54.7 mm SL), Ghana, Nyelei, tributary to Ankobra, near Akropong at the new bridge (5° 5' 6" N, 2° 17' 13" W), U. Schliewen, 10 Mar. – 30 Apr. 1998. ZSM 39000 (3, 48.7–58.4 mm SL), Ghana, Draw River at new bridge (5° 10' 04" N, 2° 15' 20" W), U. Schliewen, 10 Mar. – 30 Apr. 1998. ZSM 39001 (1, 108.2 mm SL), Ghana, Tano at Mempansem (5° 22' 12" N, 2° 39' 36" W), U. Schliewen, 10 Mar. – 30 Apr. 1998. MRAC 87-18-P-5204-240 (3, 95.7–103.4 mm SL), Ghana, Birim River at Anyinam (6° 22' 48" N, 0° 33' 0" W), G. Teugels, 14 Feb. 1987. MRAC 87-18-P-5189-203 (1, 91.0 mm SL), Ghana, Pra River at Prasu (5° 55' 48" N, 1° 22' 12" W), G. Teugels, 13 Feb. 1987. MRAC 87-18-P-

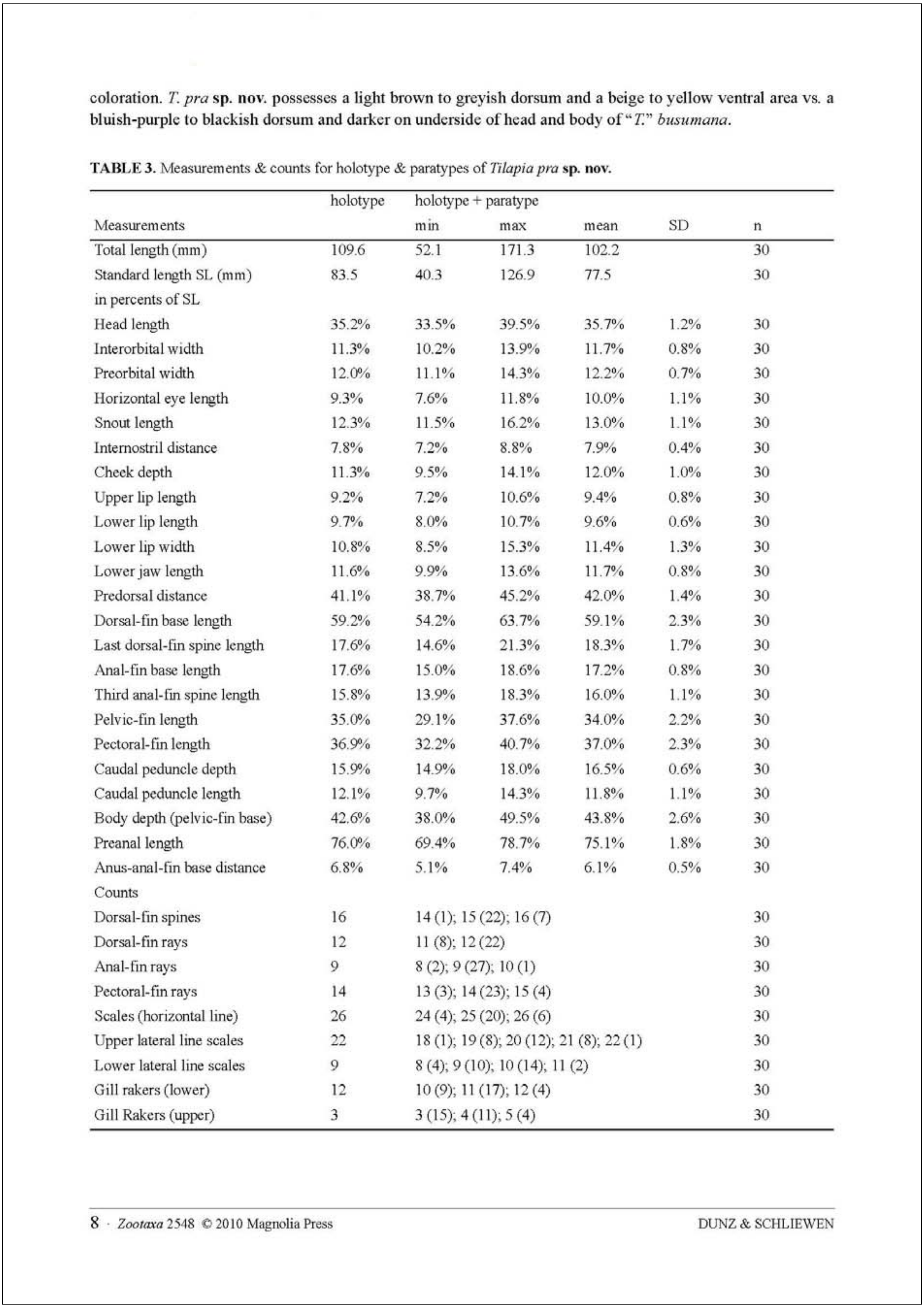


5248-314 (1, 66.7 mm SL) Ghana, Pra River near Nkawkaw (6° 36' 0" N, 0° 54' 0" W), G. Teugels, 14 Feb. 1987. MRAC 79-36-P-70-84 (5, 73.9–126.9 mm), Cote d'Ivoire, Ayamé I, dam, River Bia (5° 36' 0" N, 3° 10' 48" W), T. v. d. Audenaerde, 15 Oct. 1979. MRAC 86-18-P-1948-951 (1, 57.6 mm SL), Cote d'Ivoire, Ayamé, River Bia (5° 37' 12' 'N, 3° 10' 48" W), K. Traore, 19 Apr. 1986.

TABLE 2. Factor Loadings of PC I–III for Figure 2. Highest loadings for PC II and PC III indicated in boldface.

Principal Component	I	II	III
Standard length	0.1920	-0.0413	-0.0275
Head length	0.1963	0.0900	-0.0454
Interorbital width	0.2304	-0.0564	0.2281
Preorbital width	0.2367	-0.1404	0.0085
Horizontal eye length	0.1518	0.0253	**-0.3329**
Snout length	0.2287	0.2517	0.0747
Internostril distance	0.2319	-0.0051	0.0253
Cheek depth	0.2306	-0.0759	-0.0667
Upper lip length	0.2692	**0.3223**	-0.0152
Lower lip length	0.2443	**0.3512**	0.0529
Lower lip width	0.2433	**0.3839**	0.1251
Lower jaw length	0.2027	0.2379	0.0344
Predorsal distance	0.1931	0.0347	-0.1234
Dorsal fin length	0.1965	-0.1532	0.0163
Length last dorsal spine	0.1614	**-0.4876**	**0.4713**
Anal fin length	0.2056	-0.1713	0.2474
Anal spine length (third)	0.1632	-0.0774	0.2409
Pelvic fin length	0.1610	-0.1198	-0.0917
Pectoral fin length	0.2015	-0.1337	-0.2935
Caudal peduncle depth	0.1976	-0.0470	-0.0245
Caudal peduncle length	0.2022	**-0.3043**	**-0.5903**
Body depth	0.2122	-0.1941	-0.0098
Preanal length	0.1960	-0.0622	0.0557
Eigenvalue	0.1517	0.0028	0.0014
% variance	92.87	1.74	0.85

Differential diagnosis. *Tilapia pra* **sp. nov.** is distinguished from all other *Tilapia* sensu lato except *T. sparrmanii*, *T. ruweti*, *T. guinasana*, *T. baloni*, "*T.*" *brevimanus*, "*T.*" *mariae*, "*T.*" *cabrae* and "*T.*" *busumana* in having bicuspid pharyngeal teeth in the posterior two rows of lower pharyngeal jaw. It differs from *T. baloni* and *T. ruweti* in having more gill rakers on first ceratobranchial (lower) gill-arch (10–12 vs. 6–9), from *T. guinasana* in having a higher number of upper lateral line scales (18–22 vs. 14–17) and from *T. sparrmanii* in a combination of a higher number of upper lateral line scales (18–22 vs. 14–19), a shorter anal fin base (15.0–18.6% vs. 18.0–23.8% of SL) and a lower number of vertical stripes (6–7 vs. 8–9). It further differs from "*T.*" *mariae* and "*T.*" *cabrae* in having fewer scales on the lower lateral line (8–11 vs. 10–14) and not having spatulate shaped teeth in the outer row of both jaws, from "*T.*" *brevimanus* in having fewer gill rakers on the ceratobranchial gill-arch (10–12 vs. 12–16) and not having spatulate shaped teeth in the outer row of both jaws. It differs from "*T.*" *busumana* in possessing a longer last dorsal-fin spine (16.2–21.3% vs. 11.6–14.9% of SL), a shorter lower lip length (8.0–10.7% vs. 9.6–13.9% of SL) and a shorter lower jaw length (9.9–13.6% vs. 10.5–15.2% of SL). In addition, *T. pra* **sp. nov.** differs from "*T.*" *busumana* in ground



coloration. *T. pra* **sp. nov. possesses a light brown to greyish dorsum and a beige to yellow ventral area vs. a bluish-purple to blackish dorsum and darker on underside of head and body of "*T.*"** ***busumana*****.**

TABLE 3. Measurements & counts for holotype & paratypes of *Tilapia pra* **sp. nov.**

	holotype	holotype + paratype				
Measurements		min	max	mean	SD	n
Total length (mm)	109.6	52.1	171.3	102.2		30
Standard length SL (mm)	83.5	40.3	126.9	77.5		30
in percents of SL						
Head length	35.2%	33.5%	39.5%	35.7%	1.2%	30
Interorbital width	11.3%	10.2%	13.9%	11.7%	0.8%	30
Preorbital width	12.0%	11.1%	14.3%	12.2%	0.7%	30
Horizontal eye length	9.3%	7.6%	11.8%	10.0%	1.1%	30
Snout length	12.3%	11.5%	16.2%	13.0%	1.1%	30
Internostril distance	7.8%	7.2%	8.8%	7.9%	0.4%	30
Cheek depth	11.3%	9.5%	14.1%	12.0%	1.0%	30
Upper lip length	9.2%	7.2%	10.6%	9.4%	0.8%	30
Lower lip length	9.7%	8.0%	10.7%	9.6%	0.6%	30
Lower lip width	10.8%	8.5%	15.3%	11.4%	1.3%	30
Lower jaw length	11.6%	9.9%	13.6%	11.7%	0.8%	30
Predorsal distance	41.1%	38.7%	45.2%	42.0%	1.4%	30
Dorsal-fin base length	59.2%	54.2%	63.7%	59.1%	2.3%	30
Last dorsal-fin spine length	17.6%	14.6%	21.3%	18.3%	1.7%	30
Anal-fin base length	17.6%	15.0%	18.6%	17.2%	0.8%	30
Third anal-fin spine length	15.8%	13.9%	18.3%	16.0%	1.1%	30
Pelvic-fin length	35.0%	29.1%	37.6%	34.0%	2.2%	30
Pectoral-fin length	36.9%	32.2%	40.7%	37.0%	2.3%	30
Caudal peduncle depth	15.9%	14.9%	18.0%	16.5%	0.6%	30
Caudal peduncle length	12.1%	9.7%	14.3%	11.8%	1.1%	30
Body depth (pelvic-fin base)	42.6%	38.0%	49.5%	43.8%	2.6%	30
Preanal length	76.0%	69.4%	78.7%	75.1%	1.8%	30
Anus-anal-fin base distance	6.8%	5.1%	7.4%	6.1%	0.5%	30
Counts						
Dorsal-fin spines	16	14 (1); 15 (22); 16 (7)				30
Dorsal-fin rays	12	11 (8); 12 (22)				30
Anal-fin rays	9	8 (2); 9 (27); 10 (1)				30
Pectoral-fin rays	14	13 (3); 14 (23); 15 (4)				30
Scales (horizontal line)	26	24 (4); 25 (20); 26 (6)				30
Upper lateral line scales	22	18 (1); 19 (8); 20 (12); 21 (8); 22 (1)				30
Lower lateral line scales	9	8 (4); 9 (10); 10 (14); 11 (2)				30
Gill rakers (lower)	12	10 (9); 11 (17); 12 (4)				30
Gill Rakers (upper)	3	3 (15); 4 (11); 5 (4)				30

Description. Morphometric and meristic data for the holotype and 29 paratypes are presented in Table 3 (for comparison with "*T.*" *busumana* see Table 4). See Figure 3 for general appearance. *Tilapia pra* **sp. nov.** is a medium-sized "*Tilapia*" (maximum observed size 126.9 mm SL). Body laterally compressed. Head dorsal and ventral profile straight, head length 33.5–39.5% of SL. Head pointed. Snout outline obtuse, jaws equal anteriorly. Eye moderately large, 7.6–11.8% of SL. Interorbital width greater than eye diameter. Greatest body depth at level of first dorsal spine. Dorsal line slightly posteroventrally curved. Caudal peduncle always deeper than long; on average being 1.4 times deeper than long.

FIGURE 4. Bicuspid tooth of outer row in upper jaw of *Tilapia pra* **sp. nov.** ZSM 36125.

Squamation. Body covered with cycloid scales. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal ray. Two scale rows with or without a small scale at the basis of dorsal fin separate the upper lateral line from the last dorsal spine. 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 lines.

Gill rakers. First lower gill-arch with 10–12 gill rakers and first upper gill-arch with 3–5 gill rakers.

TABLE 4. Measurements & counts for syntypes & additional material of "*T.*" *busumana*.

	syntypes (5)		syntypes + additional material			
Measurements	min	max	min	max	SD	n
Total length (mm)	102.1	134.7	67.5	194.6		51
Standard length SL (mm)	82.1	104.4	52.9	147.5		51
in percents of SL						
Head length	34.6%	36.7%	33.5%	37.6%	1.1%	51
Interorbital width	11.0%	12.5%	9.5%	12.6%	0.7%	51
Preorbital width	13.4%	14.8%	10.8%	14.8%	0.9%	51
Horizontal eye length	8.3%	9.7%	7.8%	10.6%	0.6%	51
Snout length	12.7%	13.8%	11.4%	16.4%	1.0%	51
Internostril distance	8.4%	9.0%	7.3%	9.2%	0.4%	51
Cheek depth	11.9%	13.7%	9.4%	15.8%	1.0%	51
Upper lip length	10.3%	13.1%	8.9%	14.1%	1.1%	51
Lower lip length	9.9%	13.4%	9.6%	13.9%	1.1%	51
Lower lip width	12.7%	13.8%	9.4%	16.0%	1.3%	51
Lower jaw length	10.5%	13.4%	10.5%	15.2%	0.9%	51
Predorsal distance	39.2%	41.3%	38.8%	42.8%	1.1%	51
Dorsal-fin base length	53.9%	60.4%	52.7%	61.6%	1.8%	51
Last dorsal-fin spine length	13.1%	16.1%	11.5%	21.4%	1.7%	51
Anal-fin base length	16.3%	19.3%	14.5%	19.3%	1.0%	51
Third anal-fin spine length	12.6%	13.5%	11.6%	17.6%	1.2%	51
Pelvic-fin length	28.1%	33.6%	26.3%	36.4%	2.4%	51
Pectoral-fin length	33.3%	38.0%	27.0%	38.0%	2.5%	51
Caudal peduncle depth	15.2%	16.8%	14.4%	16.8%	0.5%	51
Caudal peduncle length	11.8%	16.2%	8.3%	16.2%	1.2%	51
Body depth (pelvic-fin base)	41.4%	43.1%	35.2%	43.1%	1.7%	51
Preanal length	70.2%	76.6%	66.9%	77.4%	2.0%	51
Anus-anal-fin base distance	4.3%	7.3%	4.3%	7.7%	0.7%	51
Counts						
Dorsal-fin spines	15 (5)		14 (5); 15 (45); 16 (1)			51
Dorsal-fin rays	11 (3); 12 (2)		11 (15); 12(36)			51
Anal-fin rays	8 (2); 9 (3)		8 (18); 9 (32); 10 (1)			51
Pectoral-fin rays	14 (4); 15 (1)		13 (10); 14 (37); 15 (4)			51
Scales (horizontal line)	24 (1); 25 (4)		24 (2); 25 (40); 26 (8); 27 (1)			51
Upper lateral line scales	18 (1); 19 (2); 20 (2)		17 (2); 18 (3); 19 (14); 20 (25); 21 (7)			51
Lower lateral line scales	9 (1); 10 (4)		9 (22); 10 (23); 11 (5); 12 (1)			51
Gill rakers (lower)	10 (5)		9 (1); 10 (20); 11(25); 12 (5)			51
Gill Rakers (upper)	4 (3); 5 (2)		3 (25); 4 (23); 5 (2); 6 (1)			51

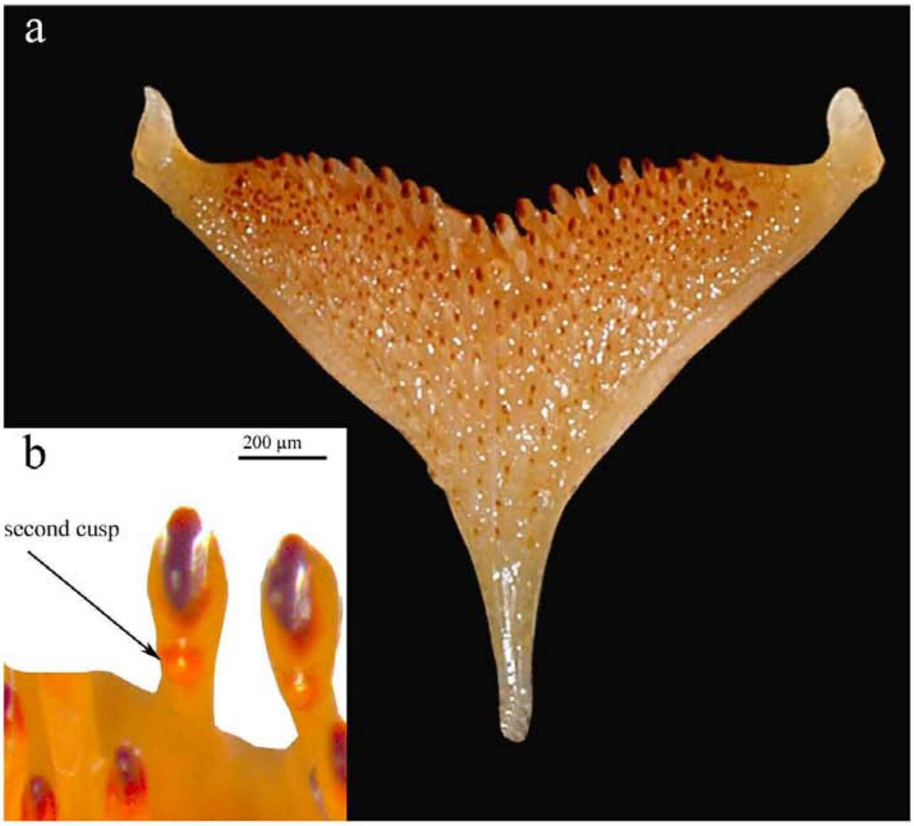


FIGURE 5. a. Lower pharyngeal jaw of *Tilapia pra* **sp. nov.** (ZSM 36125, paratype). **b.** Bicuspid tooth of outer row of lower pharyngeal jaw of *T. pra* **sp. nov.** (ZSM 36125, paratype).

Fins. Origin of dorsal fin at level of origin of pelvic fin. Dorsal-fin base 59.2% of SL in holotype and 54.2–63.7% of SL in paratypes. Dorsal spines 16 in holotype, 14–16 in paratypes. Dorsal rays 12 in holotype and 11 or 12 in paratypes. First dorsal spine always shortest, last dorsal spine always longest. Spines always shorter than rays. Last dorsal ray most deeply branched. Caudal fin outline emarginate. Anal-fin base 17.6% of SL in holotype and 15.0–18.6% of SL in paratypes. Anal spines in holotype and paratypes three. Anal rays 9 in holotype and 8–10 in paratypes. Third anal spine always longest. Last dorsal ray most deeply branched. Pelvic fin length 35.0% of SL in holotype and 29.1–37.6% of SL in paratypes. Tip of longest pelvic-fin ray mostly crossing anus, rarely reaching first anal spine Pectoral-fin length 36.9% of SL in holotype and 32.2–40.7% of SL in paratypes. Pectoral-fin rays 14 in holotype and 13–15 in paratypes.

Jaws and dentition. Upper and lower outer row in both jaws bicuspid, but some teeth appear unicuspid due to wear. Neck of anterior jaw teeth slender (i.e. about half the height of the tooth), crown expanded and cusps truncated (Fig. 4). Three 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. 5a). Posterior pharyngeal teeth bicuspid (Fig. 5b), stout, slightly hooked and regularly arranged, especially over the posterior third of the toothed area. Most of the teeth in the anterior two thirds of the toothed area approach the "kukri" tooth shape (sensu Greenwood, 1987).

FIGURE 6. *Tilapia pra* **sp. nov.** from the Draw River (ZSM 39000).

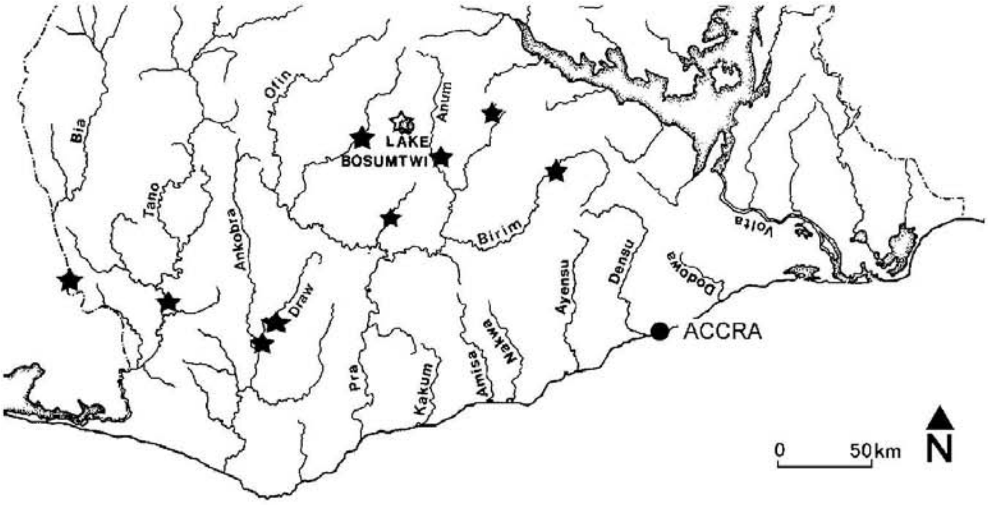
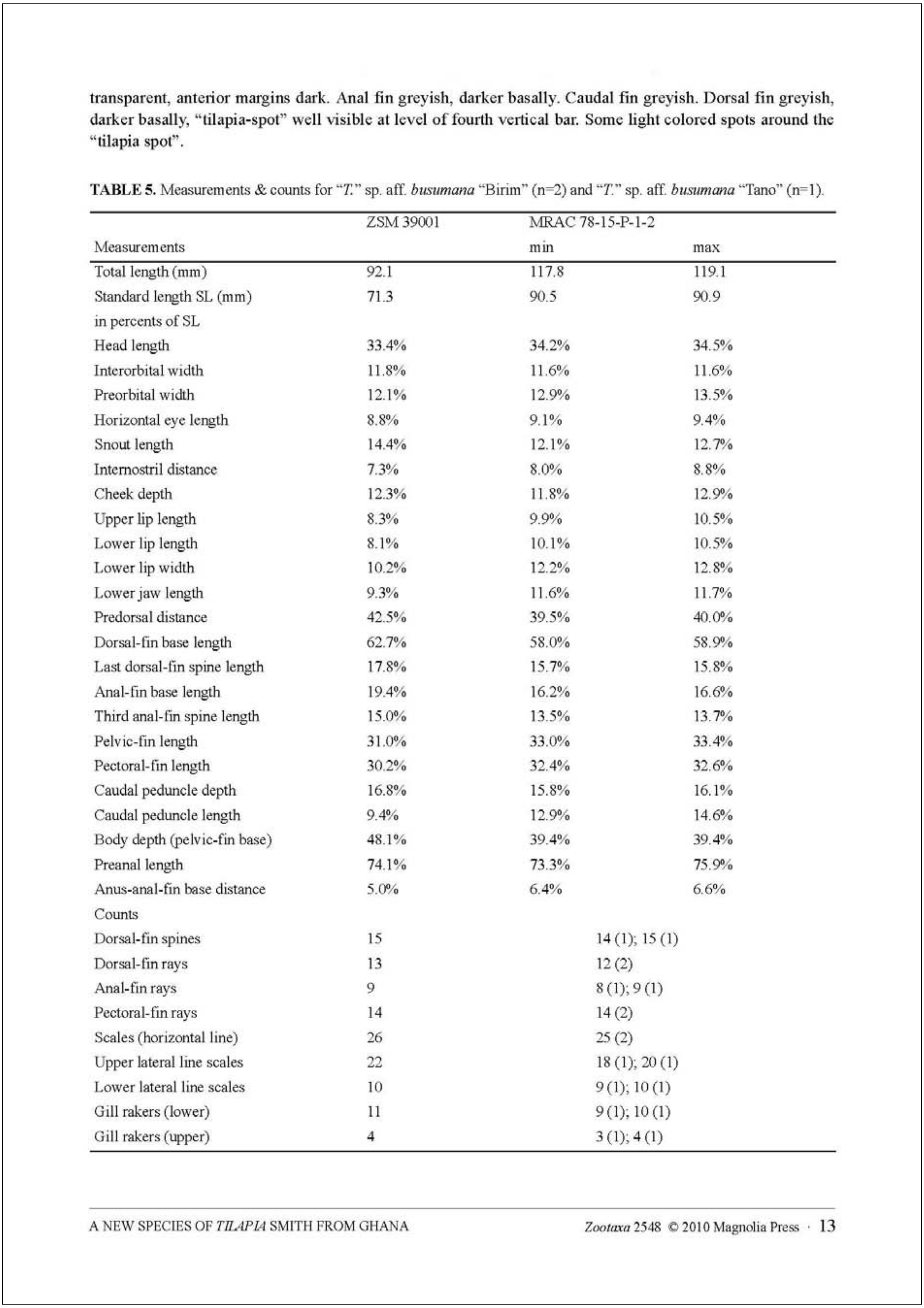


FIGURE 7. Distribution of *Tilapia pra* **sp. nov.** (filled stars) and "*T.*" ***busamana*** (Lake Bosumtwi) (open star) marked. (Map modified from Dankwa *et al.*, 1999).

Coloration in alcohol. Ground coloration light brownish with dark spots at base of each flank scale. Chest whitish, upper side of head dark brown. **Markings on body:** Six to seven dark vertical bars on dorsum and sides (the first bar at level of first dorsal spine, the last two on caudal peduncle) and a nape band. Vertical bars never bifurcate. In some specimens a longitudinal mid-lateral band is visible. Dark preorbital band extending from lachrymal to jaw angle; dark opercular spot. **Fins:** Pectoral fins transparent. Pelvic fins



transparent, anterior margins dark. Anal fin greyish, darker basally. Caudal fin greyish. Dorsal fin greyish, darker basally, "tilapia-spot" well visible at level of fourth vertical bar. Some light colored spots around the "tilapia spot".

TABLE 5. Measurements & counts for "*T.*" sp. aff. ***busumana*** "Birim" (n=2) and "*T.*" sp. aff. ***busumana*** "Tano" (n=1).

	ZSM 39001	MRAC 78-15-P-1-2	
Measurements		min	max
Total length (mm)	92.1	117.8	119.1
Standard length SL (mm)	71.3	90.5	90.9
in percents of SL			
Head length	33.4%	34.2%	34.5%
Interorbital width	11.8%	11.6%	11.6%
Preorbital width	12.1%	12.9%	13.5%
Horizontal eye length	8.8%	9.1%	9.4%
Snout length	14.4%	12.1%	12.7%
Internostril distance	7.3%	8.0%	8.8%
Cheek depth	12.3%	11.8%	12.9%
Upper lip length	8.3%	9.9%	10.5%
Lower lip length	8.1%	10.1%	10.5%
Lower lip width	10.2%	12.2%	12.8%
Lower jaw length	9.3%	11.6%	11.7%
Predorsal distance	42.5%	39.5%	40.0%
Dorsal-fin base length	62.7%	58.0%	58.9%
Last dorsal-fin spine length	17.8%	15.7%	15.8%
Anal-fin base length	19.4%	16.2%	16.6%
Third anal-fin spine length	15.0%	13.5%	13.7%
Pelvic-fin length	31.0%	33.0%	33.4%
Pectoral-fin length	30.2%	32.4%	32.6%
Caudal peduncle depth	16.8%	15.8%	16.1%
Caudal peduncle length	9.4%	12.9%	14.6%
Body depth (pelvic-fin base)	48.1%	39.4%	39.4%
Preanal length	74.1%	73.3%	75.9%
Anus-anal-fin base distance	5.0%	6.4%	6.6%
Counts			
Dorsal-fin spines	15	14 (1); 15 (1)	
Dorsal-fin rays	13	12 (2)	
Anal-fin rays	9	8 (1); 9 (1)	
Pectoral-fin rays	14	14 (2)	
Scales (horizontal line)	26	25 (2)	
Upper lateral line scales	22	18 (1); 20 (1)	
Lower lateral line scales	10	9 (1); 10 (1)	
Gill rakers (lower)	11	9 (1); 10 (1)	
Gill rakers (upper)	4	3 (1); 4 (1)	

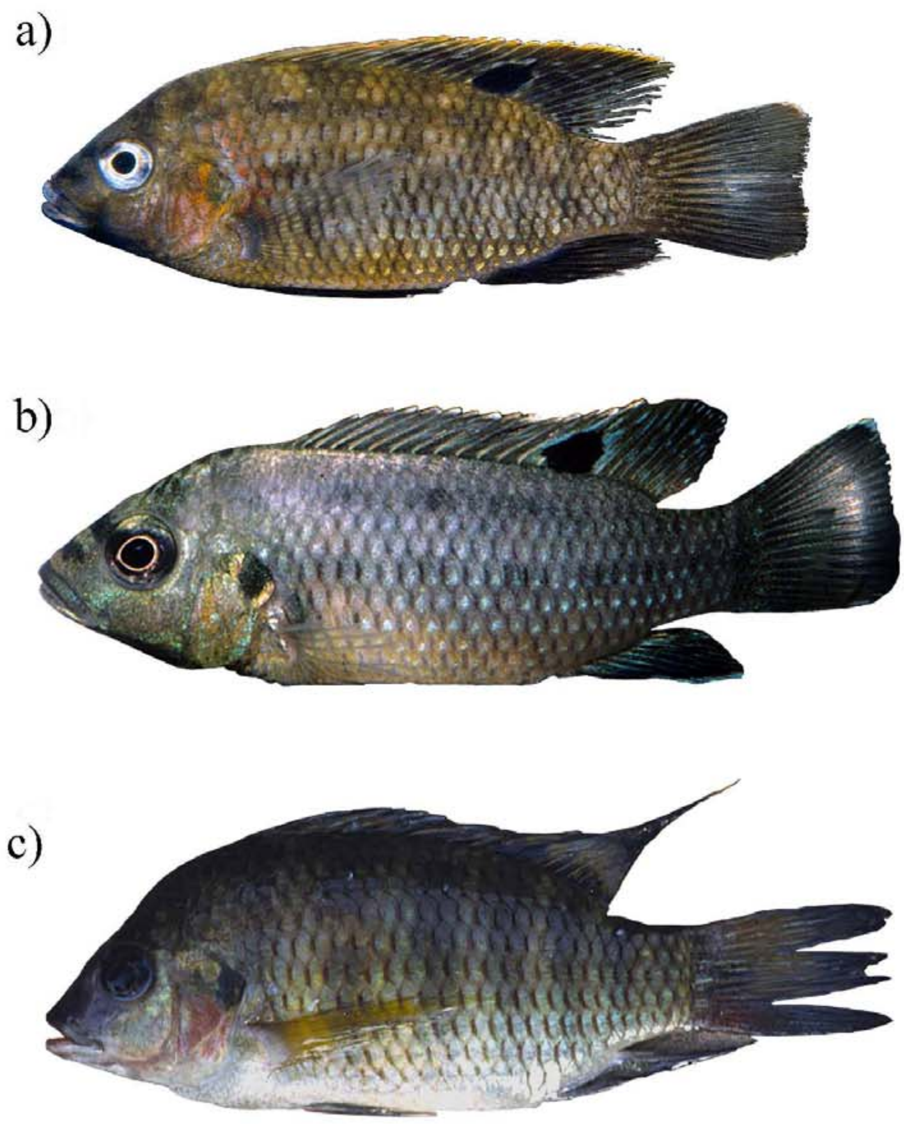


FIGURE 8. a) "*Tilapia*" sp. aff. *busumana* "Birim" (Foto: Horst Linke); b) "*Tilapia*" *busumana* (Foto: Anton Lamboj); c) "*Tilapia*" sp. aff. *busumana* "Tano" ZSM 39002.

Coloration in life. (Fig. 6) Description based on a photograph of *T. pra* **sp. nov.** from the Draw River drainage, i.e. the same location as the paratypes ZSM 39000. Ground coloration on dorsum light brown to greyish and on ventral area beige-yellow to golden, chest and belly pale. Lips bluish and upper part of opercular blotch yellowish. Light yellow colored spots around "tilapia spot". Tips of dorsal, caudal and pelvic fin white. Body with seven indistinct dark vertical stripes and a nape band. All stripes approximately as wide as the area between stripes.

Distribution. (Fig. 7) This species is known from the Pra, Ankobra, Tano and Bia Rivers in southwestern Ghana and southeastern Cote d'Ivoire.

Etymology. The species name *pra* refers both to the Akan word "pra" (river) of the Kwa language family spoken in Ghana and to the River Pra, from which drainage the holotype was collected. It refers to the riverine distribution as compared to the lacustrine distribution of its apparent sister taxon "*T.*" *busumana*. A noun in apposition.

Ecological notes. The holotype and most paratypes were collected over sandy/muddy substrate in the Anum River near Anumso village. At the collection site the Anum is 5–20 m broad and about 1–2 m deep. Specimens from the Ankobra (Draw) drainage were collected in moderately turbid water in deeper places (approx. 1–2 m depth) of medium sized rivers. No further ecological data are available.

Discussion

"*T.*" *pra* **sp. nov.** is most similar to "*T.*" *busumana*, known only from Lake Bosumtwi, and to "*T.*" sp. aff. *busumana* "Birim", which is also known from tributaries of the River Pra. All three species are endemic to the Ashanti ecoregion, which harbours a distinctive ichthyofauna characterised by several endemics, e.g., *Chrysichthys walkeri*, *Malapterurus tanoensis*, *Notoglanidium walkeri*, *Barbus subinensis*, *Barbus walkeri*, *Epiplatys chaperi schreiberi*, *Chromidotilapia bosumtwensis*, *Limbochromis robertsi* and "*Tilapia*" *busumana* (Paugy *et al.* 2003). Several of these are known only from a few individuals collected from Upper Reaches of the Pra drainage. This river system comprises three subdrainages on the so-called Kwahu plateau: In the west the Ofin, in the central area the Anum and in the east the Birim. An approximately 50 km stretch of Pra River cataracts downstream near Beposo forms a potential barrier to fish migration isolating the plateau ichthyofauna from the coastal lowlands. The fact that several of the endemics are known only from very few individuals and few locations suggests that this region remains ichthyologically underexplored. This is highlighted by the fact that population samples from within the region are almost non-existent for most of the species, which is the reason that the species status of "*Tilapia*" sp. aff. *busumana* from the Tano or from the Birim cannot be evaluated on the basis of more material.

Undoubtedly, "*Tilapia*" sp. aff. *busumana* from the Birim River is morphologically very close but distinct from "*T.*" *busumana*. Therefore it is not surprising that doubts were raised on the status of "*Tilapia*" sp. aff. *busumana* populations from the Birim River (Martin & Lamboj 1994, Freyhof 1989, Linke & Staeck 1993). Our results in combination with observations in aquaria indeed suggest that the "*Tilapia*" sp. aff. *busumana* from River Birim is another new species and not only a color variety of "*T.*" *busumana*. In contrast to the latter it exhibits a greenish yellow ground coloration with yellow tips on caudal and dorsal fin (Fig. 8). In addition, all males of "*T.*" *busumana* but none of the few preserved or photographed specimens of "*Tilapia*" sp. aff. *busumana* "Birim" and "Tano" exhibit a characteristic head gibbosity (Freyhof 1989, pers. obs.). Their morphological similarity suggests that these rather than "*T.*" *pra* **sp. nov.** gave rise to "*T.*" *busumana*, as the latter is endemic to the today (overflow 5000 y B.P.) endorheic Lake Bosumtwi drainage that is centered in a conical basin formed by a meteorite impact crater 1.07 mya ago (Reimold *et al.* 1997). Therefore the speciation process leading to "*T.*" busumana most likely is not older than the age of Lake Bosumtwi.

Unfortunately, the species status of "*T.*" sp. aff. *busumana* "Tano" remains in question due to the limited material available. A detailed ichthyological survey of the Ashanti ecoregion appears necessary.

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Literature cited

Barel, C.D.N., van Oijen, M.J.P., Witte, F. & Witte-Maas, Els L.M. (1977) An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria. *Netherlands Journal of Zoology*, 27 (4), 333–389.

Dunz, A.R. & Schliewen, U.K. (2009) Description of two new species of *Nannocharax* Günther, 1867 (Teleostei: Characiformes: Distichodontidae) from the Cross River, Cameroon. *Zootaxa*, 2028, 1–19.

Freyhof, J. (1989) Was sind *Tilapia*? Bemerkungen zu westafrikanischen Großcichliden. *Die Aquarien und Terrarienzeitschrift*, 42(8), 462–464.

Greenwood, P.H. (1987) The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. *Bulletin of the British Museum (Natural History) Zoology*, v. 53 (no. 3), 139–203.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4, 9.

Klett, V. & Meyer, A. (2002) What, if Anything, is a *Tilapia*?—Mitochondrial ND2 Phylogeny of Tilapiines and the Evolution of Parental Care Systems in the African Cichlid Fishes. *Molecular Biology and Evolution*, 19, 865–883.

Linke, H. & Staeck, W. (1993) *Afrikanische Cichliden. I. Buntbarsche aus Westafrika.* Tetra Verlag, Melle, Germany, 142 pp.

Mayden, R.L. (2002) On biological species, species concepts and individuation in the natural world. *Fish and Fisheries*, 3, 171–196.

Martin, E. & Lamboj, A. (1994) Freilandbeobachtungen zur Aufgabenteileung in der Brut- und Jungfischpflege bei *Tilapia* spec. aff. *busumana* (Teleostei, Cichlidae). *Zeitschrift für Fischkunde*, 2, 203–216.

Paugy, D., Lévêque, C. & Teugels, G.G. (2003) Poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest Tome II. Collection Faune et flore tropicale no. 40. MRAC (Tervuren)/ORSTOM (Paris). *Poissons d'eaux douces et saumâtre Afrique Ouest*, 1, 815 pp.

Reimold, W.U., Brandt, D. & Koeberl, C. (1998) Detailed structural analysis of the rim of a large, complex impact crater: Bosumtwi Crater, Ghana. *Geology*, 26, 543–546.

Schliewen, U.K., Rassmann, K., Markmann, M., Markert, J., Kocher, T.D. & Tautz, D. (2001) Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. *Molecular Ecology*, 10, 1471–1488.

Schwarzer, J., Misof, B., Tautz, D. & Schliewen, U.K. (2009) The root of the East African cichlid radiations. *BMC Evolutionary Biology*, 3 (186), 1–11.

Smith, A. (1840) Pisces. *In*: Smith, A., *Illustrations of the zoology of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa in 1834–36.*, 4: 77 pp, accompanying Pls. 1–31.

Stiassny, M.L.J., Schliewen, U.K. & Dominey, W.J. (1992) A new species flock of cichlid fishes from Lake Bermin, Cameroon with a description of eight new species of *Tilapia* (Labroidei: Cichlidae). *Ichthyological Exploration of Freshwaters*, 3 (no. 4), 311–346.

Stiassny, M.L.J. & Schliewen, U.K. (2003) *Etia nguti*, a new genus and species of cichlid fish from the River Mamfue, Upper Cross River basin in Cameroon, West-Central Africa. *Ichthyological Exploration of Freshwaters*, 14 (1), 61–71.

Stiassny, M.L.J., Lamboj, A., De Weirdt, D. & Teugels, G.G. (2007) Cichlidae. *In:*. Stiassny M.L.J., Lamboj, A., De Weirdt, D. & Teugels, G.G., *Poissons d'eaux douces et saumâtres de basse Guinée, ouest de l'Afrique centrale*

Volume 2. Co-edition RMCA (Tervuren)/IRD (Paris)/MHN (Paris)/AMNH (New York), pp. 269–278.

Teugels, G.G. (2003) Genus *Tilapia* Smith 1840. *In*: Paugy D., Lévêque, C., & Teugels, G.G., *Poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest* Tome II. Collection Faune et flore tropicale no. 40. MRAC (Tervuren)/ORSTOM (Paris). Poissons d'eaux douces et saumâtre Afrique Ouest 1, 815 pp.

Thieme, M.L., Abell, R., Stiassny, M.L.J., Skelton, P., Lehner, B., Dinerstein, E., Kamdem Toham, A., Burgess, N. & Olson, D. (2005) *Freshwater ecoregions of Africa and Madagascar. A conservation assessment.* Island Press, Washington, Covelo, London, 431 pp.

Thys, D.F.E. (1964) Révision systématique des espèces congolaises du genre *Tilapia* (Pisces, Cichlidae). *Annales Museé Royal de L'Afrique Centrale, Série IN-8°, Sciences Zoologiques*, 124, 155 pp.

Thys, D.F.E. (1968) An Annotated Bibliography of *Tilapia* (Pisces, Cichlidae). *Annales Museé Royal de L'Afrique Centrale, Série N-14°, Documentation Zoologique*, XL pp. and 406 pp.

Thys, D.F.E. (1971) Some new data concerning the *Tilapia*-species of the subgenus *Coptodon* (Pisces, Cichlidae). *Revue de Zoologie et de Botanique Africaines*, 84 (12), 160–168.

Trewavas, E. (1983) *Tilapiine Fishes of the genera Sarotherodon, Oreochromis and Danakilia.* Trustees of the British Museum (Natural History), London, 583 pp.

Turner, B.F., Gardner, L.R., Sharp, W.E. & Blood, E.R. (1996) The geochemistry of Lake Bosumtwi, a hydrologically closed basin in the humid zone of tropical Ghana. *Limnology and Oceanography* 41 (7), 1415–1424.

APPENDIX 1. Comparative material examined

"***Tilapia*" *bakossiorum*** Stiassny, Schliewen & Dominey, 1992: ZSM 27636 (1, holotype, 58.7 mm SL), Cameroon, western Lake Bermin (5° 9' N, 9° 38' E). ZSM 27637 (3, paratypes, 36.8–44.7 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ***Tilapia baloni*** Trewavas & Stewart, 1975: BMNH 1974.4.23.1-4 (4, paratypes, 84.8–134.0 mm SL), Zambia, above Musonde Falls, Luongo River. MRAC 98-007-P-0040-41 (1, 118.8 mm SL), Zambia, Kalungwishi River, pontoon Mporokoso-Kawambwa road. MRAC 98-007-P-0042-43 (2, 98.9–114.0 mm SL), Zambia, Kalungwishi River, Chipembe-Lumangwe pontoon. MRAC 98-007-P-100-102 (2, 87.0–90.9 mm SL), Zambia, Kalungwishi River, Chipembe. "***Tilapia*" *bemini*** Thys, 1972: MRAC 174739 (1, holotype, 66.2 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). MRAC 174740 (1, Paratypes, 51.0 mm SL), Cameroon, Lake Bermin (5° 9' N, 9° 38' E). MRAC 174741 (1, paratype, 47.2 mm SL), Cameroon, Lake Bermin (5° 09' N, 9° 38' E). 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). ZSM 27680 (1, 66.1 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ZSM 27632 (5, 47.8–98.1 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). "***Tilapia*" *bilineata*** Pellegrin, 1900: MNHN 1886-0445 (1, holotype, 150.4 mm SL), Central African Republic, Ndele, Alima River, upper Congo. MNHN 1886-0446 (1, paratype, 90.8 mm SL), Central Africa, Ndele, Alima River, upper Congo. MRAC A8-020-P-0971-0972 (2, 57.6–68.5 mm SL), Republic of the Congo, River Louna, affluent of Lefini, about 500 m 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 2.4 km 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 3 km to Mount Epope. MRAC A8-020-P-0962 (1, 54.6 mm SL), Republic of the Congo, River Lefini, about 600 m to camp Oteni. MRAC A8-020-P-0963 (1, 107.1 mm SL), Republic of the Congo, River Lefini, about 600 m to camp Oteni. "***Tilapia*" *brevimanus*** Boulenger, 1911: BMNH 1912.4.1.154-159 (6, syntypes, 47.5–97.4 mm SL), Guinea-Bissau, Geba River, at Bafata. MRAC 7057 (1, paratype, 94.6 mm SL), Guinea-Bissau, Portugal Guinea (10° 55' N, 13° 40' W). MNHN 1986-0700-702 (2, 88.8–121.9 mm SL), Guinea, Kolente. MNHN 1991-0181 (1, 56.6 mm SL), Guinea, Konkoure. "***Tilapia*" *busumana*** (Günther, 1903): BMNH 1903.4.24.36-41 (5, syntypes, 82.1–104.4 mm SL), Ghana, Lake Bosumtwi. ZSM 36114 (1, 147.5 mm SL), Ghana, Ashanti Region: Lake Bosumtwi, littoral zone in front of new hotel at village Abono (6° 31' 50" N, 1° 25' 47" W). ZSM 36129 (1, 98.0 mm SL), Ghana, Ashanti Region: Lake Bosumtwi, littoral zone in front of new hotel at village Abono (6° 31' 50" N, 1° 25' 47" W). ZSM 36130 (1, 82.8 mm SL), Ghana, Ashanti Region: Lake Bosumtwi, littoral zone in front of new hotel at village Abono (6° 31' 50" N, 1° 25' 47" W). ZSM 36188 (1, 84.3 mm SL), Ghana, Ashanti Region: Lake Bosumtwi, littoral zone in front of new hotel at village Abono (6° 31' 50" N, 1° 25' 47" W). ZSM 36139 (1, 53.2 mm SL), Ghana, Ashanti Region: Lake Bosumtwi, in front of *Typhia* standings between villages Abono and Obo (6° 31' 35" N, 1° 24' 45" W). ZSM 25013 (12, 54.5–86.5 mm SL), Ghana, Lake Bosumtwi, Abonu Village. ZSM 24993 (8, 70.4–91.2 mm SL), Ghana, Lake Bosumtwi. ZSM 25011 (18, 52.9–89.1 mm SL), Ghana, Lake Bosumtwi. "***Tilapia*" sp. aff. *busumana***: ZSM 39002 (1, 71.3 mm SL), Ghana, Tano at Mempansem (5° 22' 12" N, 2° 39' 36" W). MRAC 78-15-P-1-2 (2, 90.5–90.9 mm SL), Ghana, Birim River between Kibi and Asiakwa (6° 12' 0" N, 0° 31' 12" W). "***Tilapia*" *buttikoferi*** (Hubrecht, 1881): MRAC 171575-87 (4, 87.1–134.2 mm SL), Liberia, Mount Coffee, lake on St. Paul River, above dam (6° 32' N, 10° 35' W). MRAC 156032 (1, 91.0 mm

SL), Guinea, Conakry: Gaoual, River Tomine (11° 45' N, 13° 12' W). MRAC 156033 (1, 84.6 mm SL), Guinea, Conakry: Fria, River Konkoure (10° 27' N, 13° 32' W). MNHN 1992-0993 (1, 92.6 mm SL), Sierra Leone, Pampana, matotoka. MNHN 1991-0007 (1, 75.2 mm SL), Sierra Leone, Moa, Kenema. “***Tilapia***” ***bythobates*** Stiassny, Schliewen & Dominey, 1992: ZSM 27638 (6, paratypes, 78.8–115.9 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). “***Tilapia***” ***cabrae*** Boulenger, 1899: BMNH 1899.2.20.11 (1, syntype, 203.3 mm SL), Congo Rep., Kaika N'zobe, Loango. MRAC 170 (1, syntype, 264.9 mm SL), Congo Rep., Kaika Zobe (5° 3' S, 12° 34 'E). MRAC 171 (1, syntype, 223.2 mm SL), Congo Rep., Kaika Zobe (5° 3' S, 12° 34' E). MRAC A1-088-P-2818-21 (3, 128.4–159.6 mm SL), Gabon, River Dibotsa by Mbengui (2° 2' S, 11° 8' E). MRAC A1-088-P-2822-25 (2, 74.4–77.5 mm SL), Gabon, River Dola by Ndende (2° 24' S, 11° 22' E). MNHN 1911-0195 (1, 142.0 mm SL), Angola, Bengo. MNHN 1911-0196 (1, 114.0 mm SL), Angola, Bengo. MNHN 1967-0352 (1, 99.3 mm SL), Congo Rep., Noumbi, Yangala, station 22. MNHN 1967-0350 (2, 67.8–85.8 mm SL), Congo Rep., Kouilou dam by Sounda, station 14, A. Stauch. “***Tilapia***” ***cameronensis*** Holly, 1927: NMW-7645 (1, holotype, 249.4 mm SL), Cameroon, River Mbam. 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). MRAC P-93015.0101 (1, 153.2 mm SL), Cameroon, River Mbam, before river mouth of the Mape (5° 58' N, 11° 16' E). 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). MNHN 1929-0110 (1, 86.5 mm SL), Cameroon, River Mbam, Sanaga, Bankin. MNHN 1983-0615 (1, 171.2 mm SL), Cameroon, Sanaga, Edea. “***Tilapia***” ***camerunensis*** Lönnberg, 1903: BMNH 1982.17.7.1-2 (1, 64.1 mm SL), Cameroon, River Ndian (4° 45' N, 8° 44' E). BMNH 1979.7.18.454 (1, 95.6 mm SL), Cameroon, River Meme. MNHN 1988-1799 (2, 82.3–188.9 mm SL), Cameroon, Mungo. “***Tilapia***” ***cessiana*** Thys, 1968: MRAC 156025 (1, holotype, 102.1 mm SL), Cote d'Ivoire, Toyebli, River Nipoue (6° 38' N, 8° 29' W). MRAC 156030-31 (1, paratype, 74.5 mm SL), Cote d'Ivoire, Toyebli, River Nipoue (6° 38' N, 8° 29' W). MRAC 156026-29 (1, paratype, 45.8 mm SL), Cote d'Ivoire, Toyebli, basin Nipoue or Nuon (6° 38' N, 8° 29' W). MRAC 171592-014 (5, 91.9–138.8 mm SL), Cote d'Ivoire, Toyebli, River Cess (6° 38' N, 8° 29' W). MNHN 1987-0510 (1, 81.6 mm SL), Cote d'Ivoire, Toyebli, River Nipoue. MNHN 1986-0489 (2, 82.7–104.7 mm SL), Cote d'Ivoire, Binhouye, River Nipoue. “***Tilapia***” ***coffea*** Thys, 1970: MRAC 171956 (1, holotype, 115.7 mm SL), Liberia, Mount Coffee, lake on St. Paul River, near Harrisburg village, above dam (6° 32' N, 10° 35' W). 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). 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). “***Tilapia***” ***congica*** Poll & Thys, 1960: MRAC 67159 (1, holotype, 210.1 mm SL), Dem. Rep. Congo, Region of Mushie: River Kasai (3° 2' S, 16° 55' E). MRAC 66878-79 (2, paratypes, 176.7–181.3 mm SL), Dem. Rep. Congo, Region of Mushie: River Kasai (3° 2' S, 16° 55' E). MRAC 67158-60 (2, paratypes, 205.6–215.7 mm SL), Dem. Rep. Congo, Region of Mushie: River Kasai (3° 2' S, 16° 55' E). MRAC 67056-057 (2, paratypes, 114.4–122.3 mm SL), Dem. Rep. Congo, Region of Mushie: River Fimi (3° 2' S, 16° 55' E). MRAC 67162 (1, paratype 163.4 mm SL), Dem. Rep. Congo, Region of Mushie: River Fimi (3° 2' S, 16° 55' E). MRAC 67161 (1, paratype, 174.8 mm SL), Dem. Rep. Congo, Region of Mushie: Sinte Nzokele (2° 59' S, 17° 4' E). MRAC 69394 (1, paratype, 175.6 mm SL), Dem. Rep. Congo, Region of Mushie (3° 2' S, 16° 55' E). MRAC 68849 (1, paratype, 160.9 mm SL), Dem. Rep. Congo, Region of Mushie (3° 2' S, 16° 55' E). MRAC 68850-52 (3, paratypes, 159.1–163.2 mm SL), Dem. Rep. Congo, Region of Mushie (3° 2' S, 16° 55' E). MRAC 100804-11 (8, paratypes, 56.0–141.7 mm SL), Dem. Rep. Congo, Lake Tumba (0° 37' S, 17° 49' E/1° 0' S, 18° 9' E). MRAC 100802-803 (2, paratypes, 107.5–192.9 mm SL), Dem. Rep. Congo, Lake Tumba (0° 37' S, 17° 49' E/1° 0' S, 18° 9' E). MRAC 46175 (1, 204.7 mm SL), Dem. Rep. Congo, Eala (0° 4' N, 18° 20' E). MRAC 14927 (1, 168.6 mm SL), Dem. Rep. Congo, Eala, River Ruki (0° 4'N, 18° 20' E). “***Tilapia***” ***dageti*** Thys, 1971: MRAC 155731 (1, holotype, 127.6 mm SL), Ghana, Volta River below Akosombo (6° 18 'N, 0° 3' E). MRAC 155732-33 (2, paratypes, 80.3–82.3 mm SL), Ghana, Volta River below Akosombo (6° 18' N, 0° 3' E). MRAC 171871-75 (2, paratypes, 60.4–84.9 mm SL), Ghana, small stream below Akosombo (6° 18' N, 0° 3' E). MRAC 171870 (1, paratype, 120.8 mm SL), Ghana, Lake Volta at Agbogyesekwa. BMNH 1981.2.17547-548 (2, 56.9–64.4 mm SL), Ghana River Pra. MRAC 155644 (1, paratype, 88.9 mm SL), Cote d'Ivoire, Ferke basin, sur River Comoe (9° 35' N, 4° 18' W). MRAC 144591 (1, paratype, 77.0 mm SL), Burkina-Faso, River Mou, affluent of Bougouriba, 55 km from Bobo-Dioulasso (11° 11' N, 3° 49' W). MNHN 1961-0771 (6, paratypes, 92.4–131.8 mm SL), Mali, Niger by Diafarabe (Soudan). MNHN 1965-702 (4, paratypes, 104.8–137.0 mm SL), Chad, Chad basin, Aouk, Golongosso. “***Tilapia***” ***deckerti*** Thys, 1967: MRAC 157495 (1, paratype, 153.2 mm SL), Cameroon, “Lake of ancestors” by Ossidinge [Lake Ejagham]. “***Tilapia***” ***discolor*** (Günther, 1903): BMNH 1903.4.24.33-35 (3, syntypes, 75.9–92.2 mm SL), Ghana, Lake Bosumtwi. MRAC 156011-20 (9, 105.2–146.4 mm SL), Ghana, Abono, Lake Bosumtwi (6° 32' N, 1° 26' W). MNHN 1981-0948 (1, 139.7 mm SL), Ghana, Kumasi, Lake Bosumtwi. MRAC 86-18-P-1968-69 (2, 61.8–63.9 mm SL), Cote d'Ivoire, Koui (= Koun) by Yaou, River Bia (7° 30' N, 7° 16' W). MRAC 86-18-P-1965-67 (3, 68.8–97.2 mm SL), Cote d'Ivoire, Ayame, River Bia (5° 37' N, 3° 11' W). “***Tilapia***” ***flava*** Stiassny, Schliewen & Dominey, 1992: ZSM 27635 (8, paratypes, 51.6–71.6 mm SL), Cameroon, western Lake Bemin (5° 9' N, 9° 38' E). ***Tilapia guinasana*** Trewavas, 1936: MRAC 154849 (1, syntype, 87.5 mm SL), Namibia, Lake Guinas, west of Tsumeb (19° 13' 48" S, 17° 43' 12" E). MRAC 154850 (1, syntype, 70.5 mm SL), Namibia, Lake Guinas, west of

Tsumeb (19° 13' 48" S, 17° 43' 12" E). MRAC 154851 (1, syntype, 72.5 mm SL), Namibia, Lake Guinas, west of Tsumeb (19° 13' 48" S, 17° 43' 12" E). BMNH 1935.3.20.32 (1, holotype, 102.0 mm SL), Namibia, Lake Guinas, South West Africa, west of Lake Otjikoto and Tsumeb. BMNH 1935.3.20.197-208 (6, paralectotypes, 66.8–86.8 mm SL), Namibia, Lake Guinas. "***Tilapia***" ***guineensis*** (Bleeker, 1862): MNHN 1988-0315 (3, 122.4–132.5 mm SL), Senegal, Fadiout, lagoon. MNHN 1968-0066 (1, 98.0 mm SL), Senegal, Forest of Bandia Somone. MNHN 1983-0617 (1, 95.7 mm SL), Guinea, River Nunez. MNHN 1987-1497 (2, 104.2–107.2 mm SL), Guinea, Khoriba: Soumpa, Korera. MRAC 81-20-P-49 (1, 119.4 mm SL), Guinea, Soukya, River Konkoure (10° 25' N, 13° 12' W). MRAC 81-20-P-45-48 (2, 56.1–62.3 mm SL), Guinea, route Korela-Kondoya, River Konkoure (10° 32' N, 12° 52' W). MNHN 1992-0995 (2, 110.3–123.1 mm SL), Sierra Leone, River Sewa by Wjaiama-sewae. ZSM 27954 (3, 118.7–149.9 mm SL), Cote d'Ivoire, Cocody by Abidjan, Lagoon Ebrie. ZSM 23386 (1, 86.8 mm SL), Ghana, Keta-Lagoon, S. Endrödy-Younga. "***Tilapia***" ***gutturosa*** Stiassny, Schliewen & Dominey, 1992: ZSM 28200 (6, paratypes, 50.0–62.1 mm SL), Cameroon, Lake Bemin western (5° 9' N, 9° 38' E). "***Tilapia***" ***imbriferna*** Stiassny, Schliewen & Dominey, 1992: ZSM 27651 (6, paratypes, 55.3–109.1 mm SL), Cameroon, Lake Bemin western (5° 9' N, 9° 38' E). "***Tilapia***" ***ismailiaensis*** Mekkawy, 1995: BMNH 1993.9.23.6 (1, holotype, 94.2 mm SL), Egypt, Ismailia canal, Ismailia. BMNH 1993.9.23.7-8 (2, paratypes, 84.0–89.6 mm SL), Egypt, Ismailia canal, Ismailia. "***Tilapia***" ***joka*** Thys, 1969: MRAC 183585 (1, holotype, 67.5 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7° 21' N, 11° 42' W). MRAC 183596-97 (2, paratypes, 65.4–69.6 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7° 21' N, 11° 42' W). MRAC 183586 (1, paratype, 75.2 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7° 21' N, 11° 42' W). MRAC 183587-94 (8, paratypes, 56.5–72.2 mm SL), Sierra Leone, Pujehun-Gobaru, River Waanje (7° 21' N, 11° 42'W). MRAC 92-092-P-0019 (1, 68.8 mm SL), Sierra Leone, Njala, Jong River basin (8° 7' N, 12° 5' W). MNHN 1991-0610 (2, 58.6–66.7 mm SL), Sierra Leone, Pampana, Jong River basin, Matotaka. "***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. MRAC 156045-56 (3, 63.2–74.1 mm SL), Cameroon, Lake Barombi-kotto (4° 28' N, 9° 15' E). MRAC 156034-44 (3, 74.1–82.2 mm SL), Cameroon, Lake Barombi-kotto (4° 28' N, 9° 15' E). MRAC 156057-116 (3, 72.4–102.0 mm SL), Cameroon, Lake Barombi-kotto (4° 28' N, 9° 15'E). "***Tilapia***" ***louka*** Thys, 1969: MRAC 164492 (1, holotype, 74.4 mm SL), Sierra Leone, Kenema (7° 52' N, 11° 11' W). MRAC 154493 (1, paratype, 60.3 mm SL), Sierra Leone, Kenema (7° 52' N, 11° 11' W). MRAC 164494-96 (3, paratypes, 40.2–55.3 mm SL), Sierra Leone, Kenema (7° 52' N, 11° 11' W). MRAC 164497-99 (3, paratypes, 54.9–64.2 mm SL), Sierra Leone, Kenema (7° 52' N, 11° 11' W). MNHN 1991-0602 (1, 86.5 mm SL), Sierra Leone, Moa, Kenema. MNHN 1961-1104 (2, paratypes, 80.4–107.4 mm SL), Guinea, Kolente. "***Tilapia***" ***margaritacea*** Boulenger, 1916: MRAC 94-028-P-003 (1, 68.1 mm SL), Cameroon, River Lobo, vers Sangmelima. MRAC 89-32-P-65 (1, 75.9 mm SL), Cameroon, Ebogo, River Nyong (3° 23 'N, 11° 28' E). BMNH 1959.8.12.10-13 (4, 86.6–91.7 mm SL), Cameroon, River Nyong. MNHN 1983-0619 (1, 138.3 mm SL), Cameroon, Akomolinga, Nyong River. "***Tilapia***" ***mariae*** Boulenger, 1899: BMNH 1896.5.5.49-50 (2, syntypes, 51.9–64.6 mm SL), Gabon, Azuminie Creek, Opobo River, Niger Delta. MRAC 93-039-P-0170-171 (2, 60.5–64.9 mm SL), Nigeria, Ibedu stream (Ekpe Atai), Kwa Ibo River (4° 44' N, 8° 02' E). MRAC 93-039-P-0172 (1, 67.7 mm SL), Nigeria, Abak, Kwa Ibo River (4° 59' N, 7° 47' E). MRAC 93-039-P-0173 (1, 70.9 mm SL), Nigeria, Ndiya, Kwa Ibo River (4° 47' N, 7° 53' E). MRAC 92-078-P-0318-19 (2, 76.7–89.7 mm SL), Nigeria, Imo River downstream of Otamiri confluence (4° 54' N, 7° 8' E). MRAC 92-078-P-0320-24 (2, 63.3–82.4 mm SL), Nigeria, Orashi River at Odieke (5° 1' N, 6° 27' E). ZSM 39003 (55.6 mm SL), Ghana, Nyelei near Akropong at the new bridge (5° 5' 6" N, 2° 17' 13" W). "***Tilapia***" ***nyongana*** Thys, 1971: MRAC 152789 (1, holotype, 163.8 mm SL), Cameroon, Akonolinga, pond of planting Mangan, emanate from River Nyong (3° 46' N, 12° 15' E). 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). MRAC 152800-02 (3, paratypes, 45.2–59.6 mm SL), Cameroon, Ebogo, River Nyong (3° 23' N, 11° 28' E). MRAC 152794-99 (6, paratypes, 133.1–189.7 mm SL), Cameroon, Akonolinga, River Nyong (3° 46' N, 12° 15' E). MNHN 1929-118-119 (2, paratypes, 169.5–225.2 mm SL), Cameroon, locality unknown. MRAC 93-083-P-0030 (1, 71.8 mm SL), Cameroon, locality unknown. MRAC 152933-52 (1, 57.3 mm SL), Gabon, Lambarene (0° 42' S, 10° 13' E). "***Tilapia***" ***rendalli*** (Boulenger, 1897): BMNH 1896.10.5.9-11 (3, syntypes, 113.1–180.0 mm SL), Malawi, Upper Shire River. 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). 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). BMNH 1976.10.12.283-285 (3, 94.6–132.0 mm SL), Dem. Rep. Congo, Lake Kalamba at Mulongo. BMNH 1976.10.12.252 (1, 112.7 mm SL), Dem. Rep. Congo, Papyrus Islands, Lake Mulende. BMNH 1975.6.20.670 (1, 137.5 mm SL), Dem. Rep. Congo, Lake Kinsale. BMNH 1976.12.20.87 (1, 133.5 mm SL), Dem. Rep. Congo, Upembu region: Lake Kisabe. MRAC 126277-292 (3, 71.7–85.1 mm SL), Dem. Rep. Congo, Lake Mukambo (Kasai), import from Katanga (5° 45' 0" S, 23° 4' 12" E). MRAC 34340-34342 (3, 73.1–87.3 mm SL), Dem. Rep. Congo, Lukonzolwa, Lake Moero (8° 46' 48" S, 28° 38' 60"E). MRAC 33945-33947 (3, 80.2–98.5 mm SL), Dem. Rep. Congo, Lukonzolwa, Lake Moero (8° 46' 48" S, 28° 38' 60" E). MRAC 84911-915 (1, 129.7 mm SL), Dem. Rep. Congo, Manono, pond nr. 7 (7° 17' 60" S, 27° 25' 12" E). MRAC 139564-676 (6, 66.5–85.4 mm SL), Dem. Rep. Congo, Pond upstream of River Kulungu (Bambesa) (3° 22' 12" S, 25° 43' 48" E). BMNH 1976.10.12.249-250

(2, 76.9–79.3 mm SL), Dem. Rep. Congo, Lukuga River, 1 km above confluence with Zaire River. MRAC 105566 (1, 100.2 mm SL), Dem. Rep. Congo, Region of Albertville: River Lukuga, village Amisi (5° 55' 12" S, 29° 19' 12" E). BMNH 1976.10.12.236-237 (2, 54.1–63.8 mm SL), Dem. Rep. Congo, Luvua River at Ankoro. MRAC 36353-355 (2, 63.9–74.8 mm SL), Dem. Rep. Congo, Kiambi, River Luvua (7° 19' 48" S, 28° 1' 12" E). BMNH 1975.6.20.671-672 (2, 53.6–56.9 mm SL), Dem. Rep. Congo, Lualaba River at Lukuge junction. BMNH 1976.10.12.260 (1, 65.9 mm SL), Dem. Rep. Congo, Lualaba River, 20 km S of Nyangwe (4° 0' 0" S, 26° 0' 0" E). MRAC 69735 (1, 130.0 mm SL), Dem. Rep. Congo, Maka, River Lualaba (8° 55' 48" S, 26° 4' 12" E). MRAC 69955-956 (2, 52.5–59.5 mm SL), Dem. Rep. Congo, Kabalo, River Lualaba (6° 2' 60" S, 26° 31' 48" E). MRAC 78165-172 (2, 74.7 mm SL), Dem. Rep. Congo, Kindu, River Lualaba (2° 57' 0" S, 25° 55' 48' 'E). MRAC 44844 (1, 121.8 mm SL), Dem. Rep. Congo, Kasenga, River Luapula (10° 22' 12" S, 28° 37' 48" E). MRAC 4628-636 (4, 61.1–71.7 mm SL), Dem. Rep. Congo, Kasenga, River Luapula (10° 19' 48" S, 28° 37' 48" E). MRAC 33529 (1, 86.5 mm SL), Dem. Rep. Congo, confluence of Luapula and Luombwa (12° 13' 12" S, 29° 33' 0" E). BMNH 1980.7.1.67 (1, 59.4 mm SL), Dem. Rep. Congo, rapids below Stanley Pool. MRAC 135501 (1, 132.0 mm SL), Dem. Rep. Congo, River Bohonde (0° 46' 12" N, 24° 22' 48" E). MRAC 51638-639 (2, 81.7–85.2 mm SL), Dem. Rep. Congo, Inkongo, River Sankuru (4° 52' 48" S, 23° 16' 12" E). MRAC 50083-85 (1, 102.3 mm SL), Dem. Rep. Congo, affluent of River Luembe. MRAC 22510-11 (1, 73.4 mm SL), Dem. Rep. Congo, Nyonga (8° 37' 48" S, 26° 18' 0" E). ZSM 36108 (2, 125.1–169.1 mm SL), Namibia, Okavango River at Kapago, approx. 30 km W of Rundu. “***Tilapia***” ***rheophila*** Daget, 1962: MNHN 1959-106 (5, syntypes, 55.0–77.7 mm SL), Guinea, River Konkoure. MNHN 1960-0488 (1, syntype, 76.6 mm SL), Guinea, Grand chutes, Konkoure, Samou. MRAC 89-34-P-20-26 (4, 58.9–86.2 mm SL), Guinea, Konkoure, River Konkoure (10° 27' N, 13° 0' W). MRAC 92-059-P-3815-16 (1, 51.5 mm SL), Guinea, Konkoure, River Konkoure (10° 27' N, 13° 0' W). MRAC 81-20-P-51-54 (4, 66.8-85.1 mm SL), Guinea, route Korela-Kondoya, River Konkoure (10° 32' N, 12° 52' W). MRAC 89-14-P-27-31 (2, 63.0–84.2 mm SL), Guinea, Konkoure, River Konkoure, bridge on the road Telimele-Kindia (10° 27' N, 13° 13' W). MNHN 1992-0798 (2, 64.6–87.4 mm SL), Guinea, River Konkoure, on the road Telimele-Kindia (10° 27' N, 13° 13' W). MRAC 92-059-P-3817-20 (3, 76.6–90.9 mm SL), Guinea, Siraya, River Kakrima (Konkoure basin) (10° 36' N, 13° 0' W). MNHN 1987-1502 (1, 77.0 mm SL), Guinea, River Kakrima by Koussi. ***Tilapia ruweti*** Poll & Thys, 1965: MRAC 152634 (1, holotype, 78.9 mm SL), Dem. Rep. Congo, approximately at dam of the Lufira by Mwadingusha (10° 45' S, 27° 15' E). MRAC 163668-69 (2, paratypes, 55.1–64.9 mm SL), Angola, Cameia (11° 50' S, 21° 0' E), E. Luna de Carvalho. BMNH 1969.3.28.10-13 (4, 40.6–51.0 mm SL), Zambia, Lake Namutwe 64 km E of Mongu, upper Zambezi (15° 30' S, 23° 9' E). MRAC 142074-77 (4, 56.9–70.2 mm SL), Zambia, Lake Mweru at Nchelenge (9° 14' S, 28° 48' E). BMNH 1972.10.9.52-56 (2, 41.2–50.4 mm SL), Zambia, Kafue flats on Lochinvar, Game Reserve at Chunga. BMNH 1969.3.28.7-9 (3, 49.0–56.4 mm SL), Dem. Rep. Congo, Lushiba lagoon, Lake Mweru. “***Tilapia***” ***snyderae*** Stiassny, Schliewen & Dominey, 1992: ZSM 27630 (3, paratypes, 36.5–44.4 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ZSM 27652 (2, paratypes, 32.3–37.4 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ZSM 27630 (1, paratype, 42.0 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ***Tilapia sparrmanii*** Smith, 1840: BMNH 59.5.7.85 (1, syntype, 70.5 mm SL), South Africa, near Orange River. BMNH 51.10.26.84 (1, syntype, 86.9 mm SL), South Africa: near Orange River. MRAC 89-12-P-805-809 (5, 87.9–104.5 mm SL), Botswana, Thamalakane River, Okavango delta above Matlapaneng bridge (20° 8' S, 23° 23' E). MRAC 89-12-P-795-804 (5, 72.8–85.3 mm SL), Botswana, Okavango delta: Tokatsebee, Boro River (19°55'S 23°30'E). MRAC 187454-64 (3, 94.7–130.7 mm SL), Zimbabwe, Kafue River, rail bridge. BMNH 1969.9.25.39-42 (4, 107.2–114.6 mm SL), Zambia, Voissia edge, Chiansi Lagoon and River Kafue. ZSM A-0365 (4, 98.2–123.9 mm SL), Zambia, Lake Bangwelo. MRAC 97-001-P-0144-0154 (2, 54.0–93.4 mm SL), Zambia, Ngoma River, below Ntumbatushi Falls (9° 51' S, 28° 57' E). MRAC 97-035-P-0081-82 (2, 59.2–68.3 mm SL), Zambia, Ngona River, below Ntumba Chushi Falls, Luapula Province. MRAC 78-6-P-1154-163 (1, 77.8 mm SL), Angola, Cacanda, basin River Kasai (7° 23' S, 20° 45' E). MRAC 154772 (1, 63.9 mm SL), Angola, River Cubango, Vila da Ponte (14° 28' S, 16° 20' E). MRAC 154773-777 (5, 72.9–81.7 mm SL), Angola, River Cuebe, Vila Serpa Pinto (14° 36' S, 17° 48' E). ZSM A-0464 (1, 83.8 mm SL), Dem. Rep. Congo, Kando, District Lualaba. ZSM A-0468 (1, 78.2 mm SL), Dem. Rep. Congo, Kando, District Lualaba. ZSM A-0485 (1, 84.0 mm SL), Dem. Rep. Congo, Kando, District Lualaba, backwater. ZSM 38227 (4, 92.9–97.7 mm SL), Dem. Rep. Congo, Prov. Katanga: Luapula River at Port de Kasenga (10° 22' 2" S, 28° 37' 2" W). “***Tilapia***” ***spongotroktis*** Stiassny, Schliewen & Dominey, 1992: ZSM 27682 (3, paratypes, 82.1–135.0 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ZSM 27629 (3, 53.1–113.7 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). “***Tilapia***” ***tholloni*** (Sauvage, 1884): MNHN 1884-0294 (1, syntype, 137.9 mm SL), Gabon, upper Ogooue River, Passa, Franceville. MNHN 1884-0295 (1, syntype, 125.6 mm SL), Gabon, Upper Ogooue River, Passa, Franceville. MRAC 93-134-P-0782-0786 (2, 51.9–57.2 mm SL), Gabon, ± 15km from Mpere village, Ogooue River, upstream of Port-Gentil, by Ndougou. MRAC 93-134-P-0781 (1, 83.6 mm SL), Gabon, ± 15km from Mpere village, Ogooue River, upstream of Port-Gentil, by Ndougou. MRAC 20231-239 (1, 127.0 mm SL), Gabon, Passa, upper Ogooue River (1° 36' S, 13° 31' E). MRAC 20240-43 (1, 68.1 mm SL), Gabon, Leceni, Ogooue. ZSM 18789 (1, 85.9 mm SL), Dem. Rep. Congo, Archipel Mbamu, passe Limbili (4° 14' S, 15° 22' E). ZSM 37843 (2, 117.2–122.4 mm SL), Dem. Rep. Congo, Province Kinshasa: Congo

River, Malebo Pool at Kinkole, purchased in local fishmarket (4° 19' 15" S, 15° 30' 12" E). ZSM 37717 (3, 104.7–139.9 mm SL), Dem. Rep. Congo, Prov. Kinshasa: Congo River, obtained from local fishermen at Kinsuka rapids, exact collecting location unclear. ZSM 37723 (6, 81.8–143.4 mm SL), Dem. Rep. Congo, Province Kinshasa: Congo River, Malebo Pool at Kinkole, purchased in local fishmarket (4° 19' 15" S, 15° 30' 12" E). ZSM 37711 (2, 131.5–150.6 mm SL), Dem. Rep. Congo, Province Kinshasa: Congo River, Malebo Pool at Kinkole, purchased on local fishmarket (4° 19' 15" S, 15° 30' 12" E). MNHN 1962-0412 (1, 52.6 mm SL), Dem. Rep. Congo, Likouala by Ndole. MNHN 1962-0411 (2, 60.7–69.3 mm SL), Dem. Rep. Congo, Likouala, Bakouango. "***Tilapia***" ***thysi*** Stiassny, Schliewen & Dominey, 1992: ZSM 28390 (1, holotype, 62.9 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ZSM 27633 (1, paratype 50.9 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ZSM 27628 (4, paratypes, 39.3–53.8 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). ZSM 28202 (2, 119.9–124.1 mm SL), Cameroon, Lake Bermin western (5° 9' N, 9° 38' E). "***Tilapia***" ***walteri*** Thys, 1968: MRAC 155632 (1, holotype, 206.2 mm SL), Cote d'Ivoire, Sahibly, Cavally River (6° 33' N, 8° 20' W). MRAC 155630-31 (2, paratypes, 73.1–101.1 mm SL), Cote d'Ivoire, Sahibly, River Cavally (6° 33' N, 8° 20' W). MRAC 155633-35 (3, paratypes, 89.1–93.6 mm SL), Cote d'Ivoire, Tai, River Nse and Cavally (5° 52' N, 7° 27' W). MRAC 155636-40 (5, paratypes, 52.3–73.7 mm SL), Cote d'Ivoire, Tai, River Nse and Cavally (5° 52' N, 7°27'W). MRAC 85-29-P-628 (1, 104.6 mm SL), Cote d'Ivoire, Tai, Cavally River (5° 52' N, 7° 27' W). MHNH 1980-1282 (1, 119.4 mm SL), Cote d'Ivoire, Cavally River by Danane (7° 20' 60" N, 8° 10 '01" W). MHNH 1987-0509 (1, 120.4 mm SL), Cote d'Ivoire, Binhouye, River Nipoue. "***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). 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). 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). MNHN 1890-0187 (1, 103.7 mm SL), Algeria, Touggourt. MNHN 1890-0188 (1, 96.2 mm SL), Algeria, Touggourt. MRAC 96-082-P-0004-0005 (2, 50.6–51.9 mm SL), Sudan, Tamboura town, visvijvers.

4. Paper II

Dunz AR, Schliewen UK (2010b) Description of a *Tilapia* (*Coptodon*) species flock of Lake Ejagham (Cameroon), including a redescription of *Tilapia deckerti* Thys van den Audenaerde, 1967. Spixiana 33, 251–280.

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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)

Andreas R. Dunz & Ulrich K. Schliewen

Dunz, A. R. & Schliewen, U. K. 2010. Description of a *Tilapia (Coptodon)* species flock of Lake Ejagham (Cameroon), including a redescription of *Tilapia deckerti* Thys van den Audenaerde, 1967 (Perciformes, Cichlidae). Spixiana 33(2): 251-280.

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^2. 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. tholloni* (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. imbriferna*, *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.

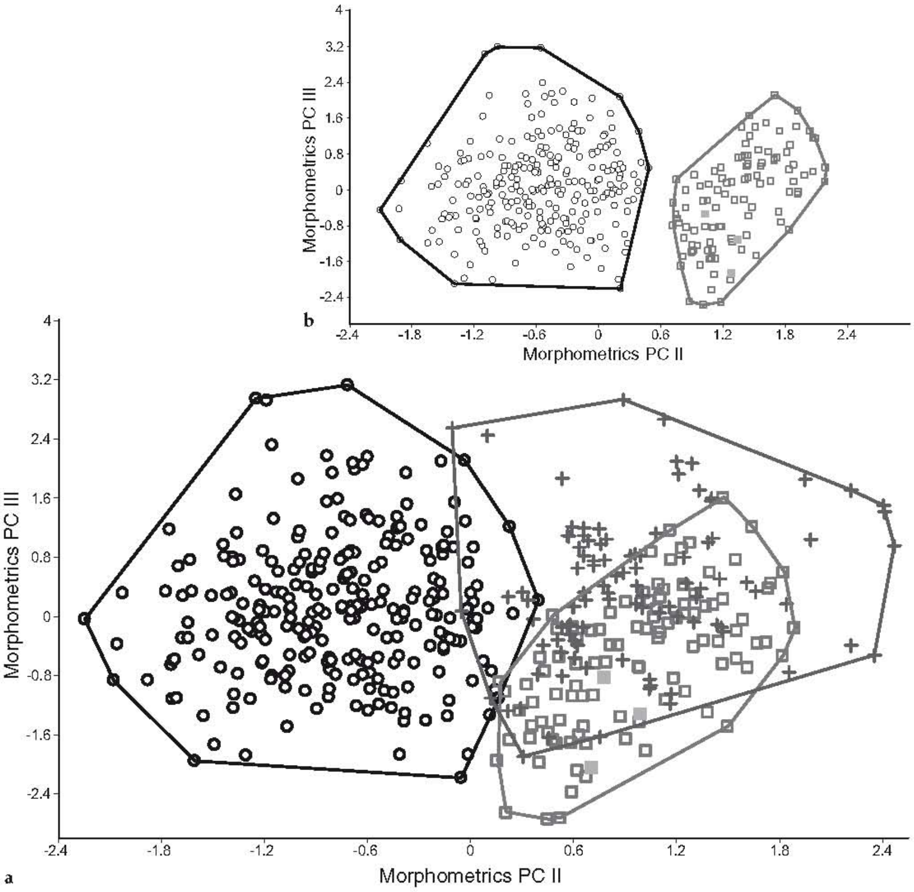

Fig. 1. a. Scatter plot of scores of Principal Component II vs. Principal Component III visualized as convex hulls. **○**, *T. cameronensis*, *T. camerunensis*, *T. coffea*, *T. congica*, *T. dageti*, *T. discolor*, *T. guineensis*, *T. louka*, *T. margaritacea*, *T. nyongana*, *T. rendalli*, *T. tholloni*, *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. imbriferna*, *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.

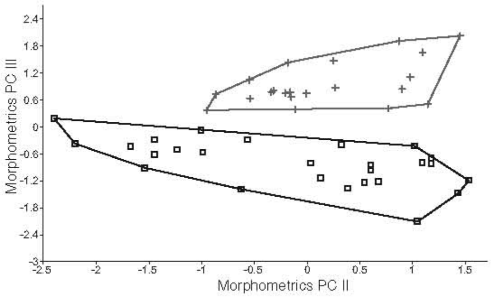

Fig. 2. Scatter plot of scores of Principal Component II vs. Principal Component III; visualized as convex hulls. **□**, *T. ejagham* spec. nov. (n=26); +, *T. zillii* (n=22).

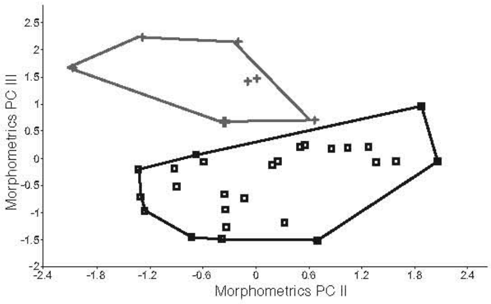

Fig. 3. Scatter plot of scores of Principal Component II vs. Principal Component III; visualized as convex hulls. **□**, *T. ejagham* spec. nov. (n=26); +, *T. spongotroktis* (n=7), **+**, holotype of *T. spongotroktis* (AMNH 98258).

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. 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

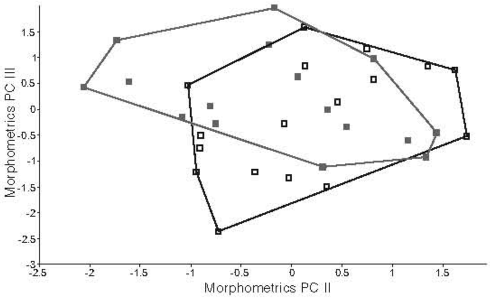

Fig. 4. Scatter plot of scores of Principal Component II vs. Principal Component III; visualized as convex hulls. **□**, *T. fusiforme* spec. nov. form "large-black" (n=17); ■, *T. fusiforme* spec. nov. form "little-black" (n=16).

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
Internostril distance	−0.204	0.094	0.075
Cheek depth	−0.240	0.040	0.195
Upper lip length	−0.213	**0.299**	0.082
Lower lip length	−0.212	**0.301**	0.077
Lower lip width	−0.238	0.166	**0.443**
Lower jaw length	−0.191	**0.378**	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	**−0.324**	−0.067
Anal fin length	−0.208	−0.182	−0.173
Anal spine length (third)	−0.192	−0.109	**−0.379**
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	**0.391**	**−0.647**
Body depth	−0.215	**−0.250**	0.119
Preanal length	−0.199	−0.001	−0.037
Eigenvalue	0.618	0.018	0.004
% variance	94.53	2.68	0.57

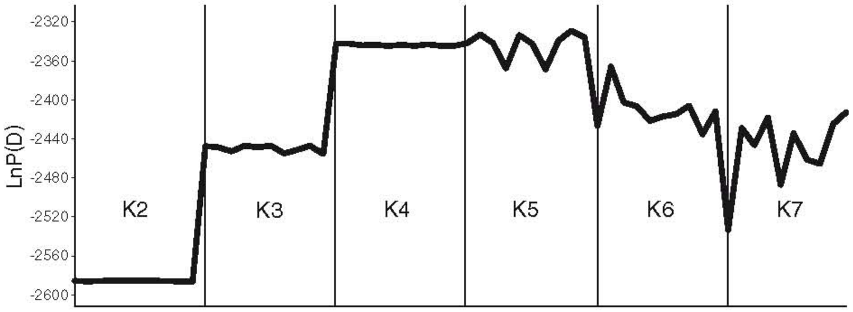

Fig. 5. XY-graph of the log probability of the data (LnP(D)) (Y) and the number of cluster K (X). The estimation for K reaches a plateau at K4.

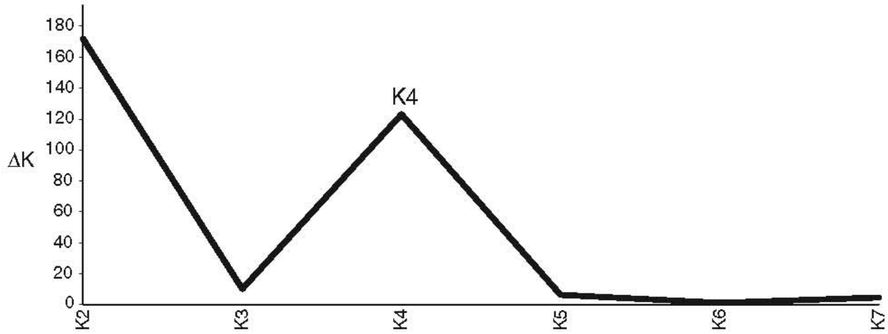

Fig. 6. XY-graph of ΔK vs. K. Calculated with the evaluated formula $\Delta K = m(|L''K|) / s[L(K)]$, the modal value of this distribution is the true K or the uppermost hierarchic level of genetic structure. ΔK (Evanno et al. 2005) peaks at K4.

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 Schliewen 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).

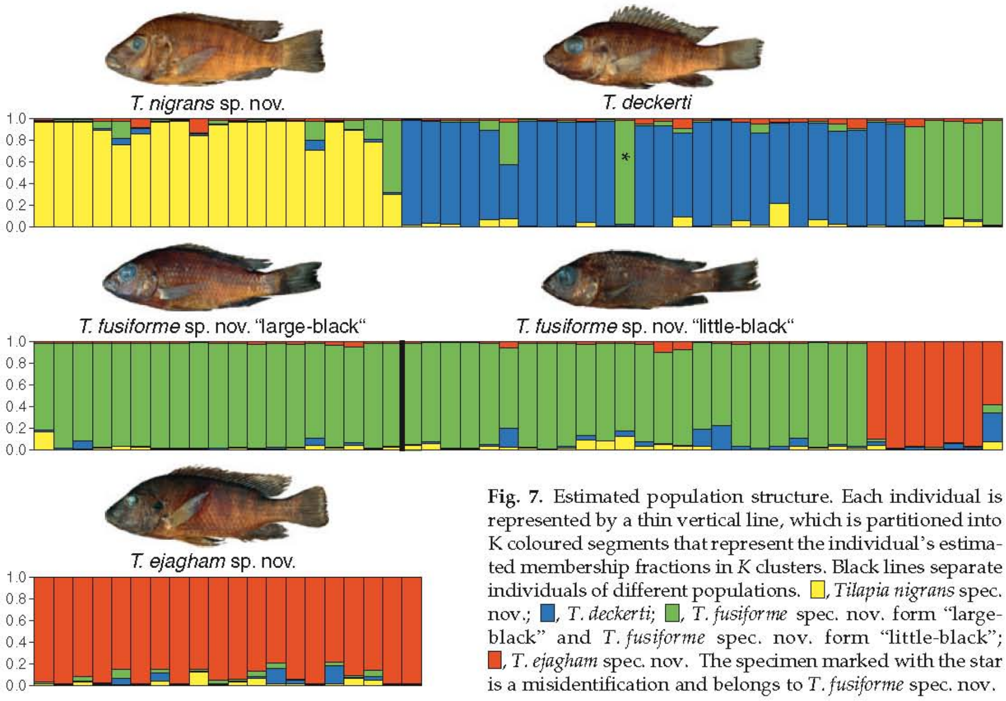

Fig. 7. Estimated population structure. Each individual is represented by a thin vertical line, which is partitioned into K coloured segments that represent the individual's estimated membership fractions in *K* clusters. Black lines separate individuals of different populations. 🟨, *Tilapia nigrans* 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.

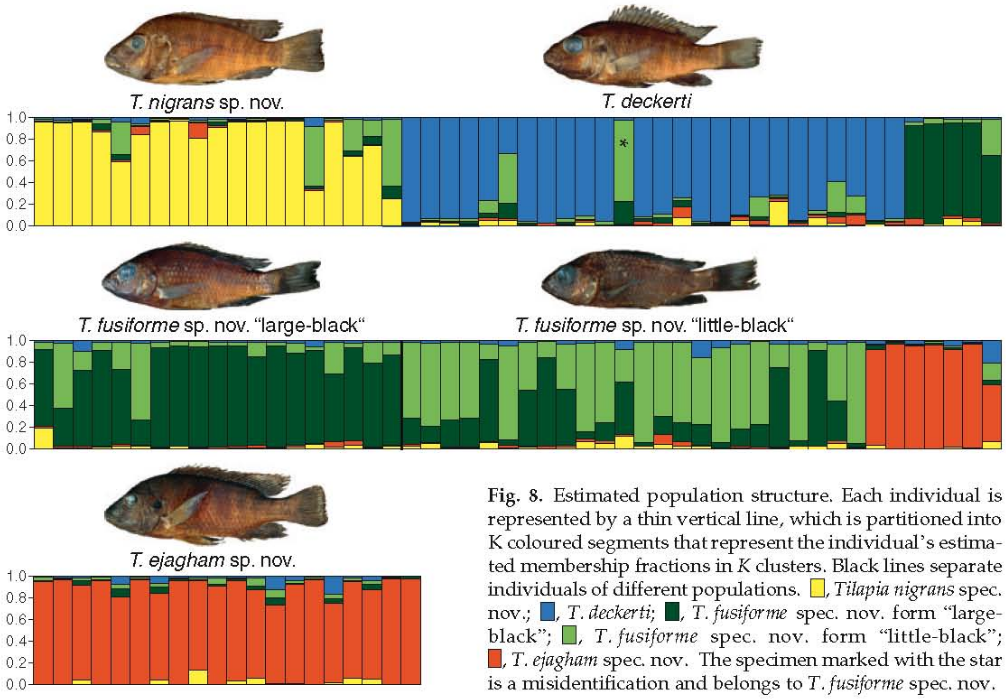

Fig. 8. Estimated population structure. Each individual is represented by a thin vertical line, which is partitioned into K coloured segments that represent the individual's estimated membership fractions in *K* clusters. Black lines separate individuals of different populations. 🟨, *Tilapia nigrans* 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. cameronensis* 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. 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 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. gutturosa* 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. ejagham* 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. ejagham* spec. nov. is

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

	holotype	holotype + paratypes				
		min	max	mean	SD	n
Measurements						
Total length (mm)	210.8	95.3	241.6	147.9		
Standard length SL (mm)	174.7	76.3	199.5	120.9		
in percents of SL						
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
Counts						
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.

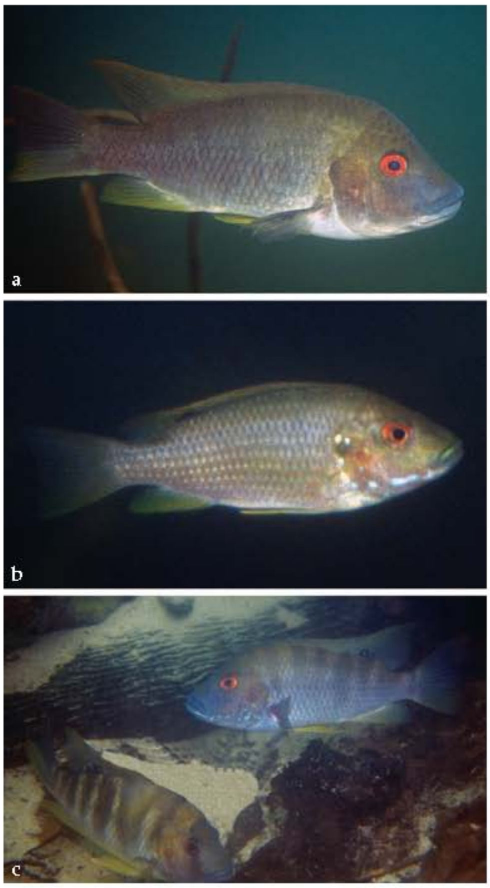

Fig. 10. *T. ejagham* spec. nov. **a.** Non breeding male of, large specimen. **b.** Non breeding small specimen. **c.** Breeding pair in shallow water.

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

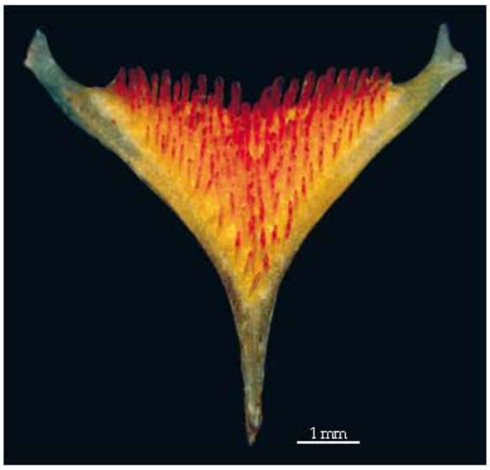

Fig. 11. Outer shape and shape of the dentigerous plate of *T. ejagham* spec. nov.

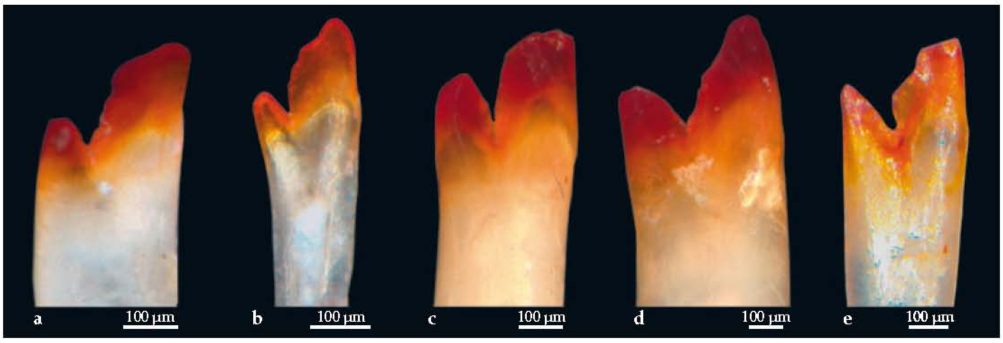

Fig. 12. Outer shape of lower jaw teeth of **a,** *T. fusiforme* spec. nov. form "large-black"; **b,** *T. fusiforme* spec. nov. form "little-black"; **c,** *Tilapia nigrans* spec. nov.; **d,** *T. deckerti*; **e,** *T. ejagham* spec. nov.

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.

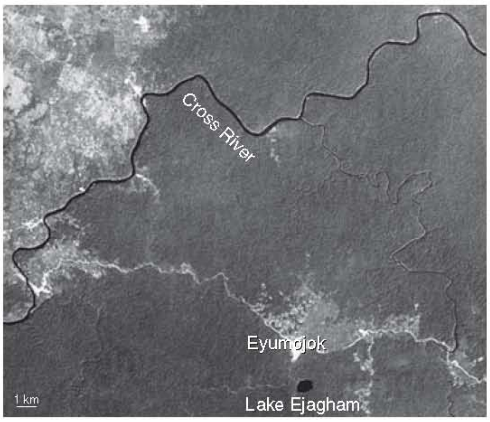

Fig. 14. Map of the area surrounding Lake Ejagham, named Eyumojok, the next village to the lake; the Cross River is the neighbouring river-system.

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 then 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				
		min	max	mean	SD	n
Measurements						
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
in percents of SL						
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
Counts						
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.

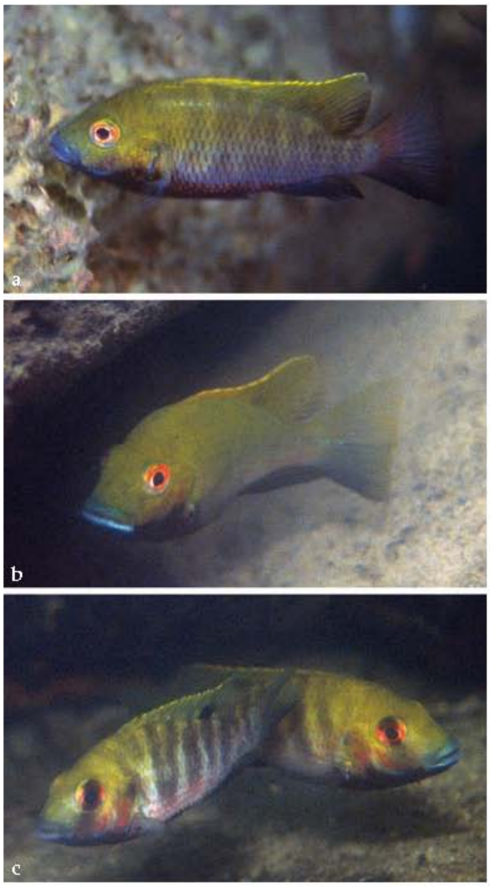

Fig. 16. *T. deckerti.* **a.** Non breeding specimen. **b.** Male without vertical bars. **c.** Breeding pair in shallow water.

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 character shared only with *T. tholloni*, *T. cameronensis*, *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. cameronensis* 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* specimen 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 depth at level of first dorsal spine. Dorsal line slightly posteroventrally curved. Caudal peduncle about as long as deep or slightly longer.

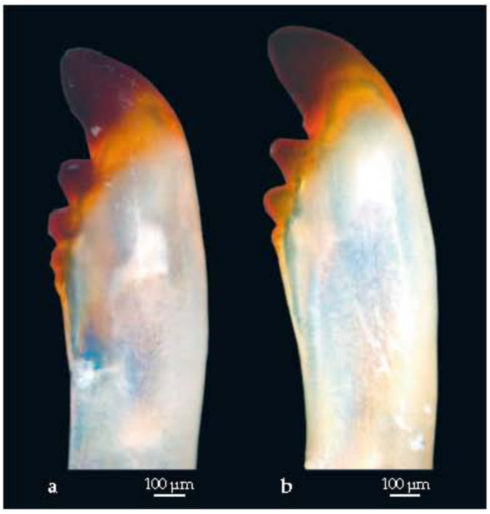

Fig. 17. Outer shape and number of cusps of posterior pharyngeal teeth of lower pharyngeal jaw of **a,** *T. deckerti*; **b,** *T. nigrans* spec. nov.

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 midlateral 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. cameronensis*, *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				
		min	max	mean	SD	n
Measurements						
Total length (mm)	146.4	131.3	185.4	159.9		
Standard length SL (mm)	117.5	105.5	151.0	129.2		
in percents of SL						
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
Counts						
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

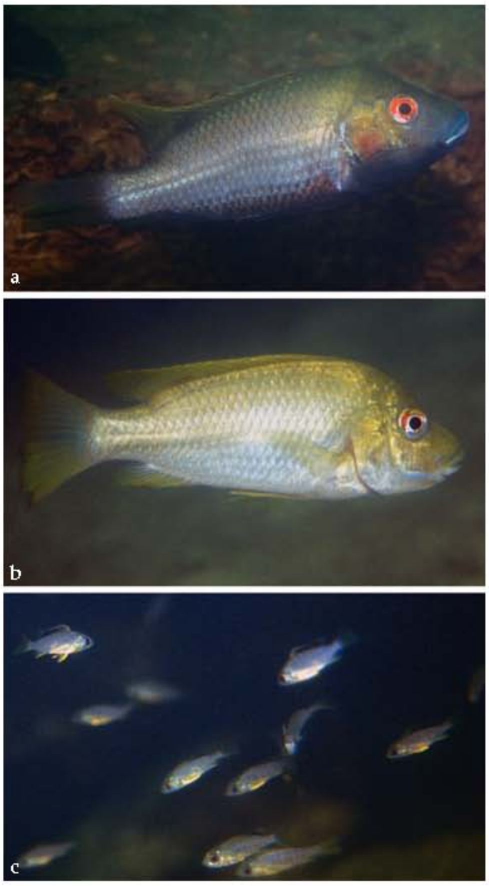

Fig. 20. *T. nigrans* spec. nov. **a.** Breeding specimen; **b.** Non breeding specimen; **c.** Juveniles, showing the extended "tilapia spot".

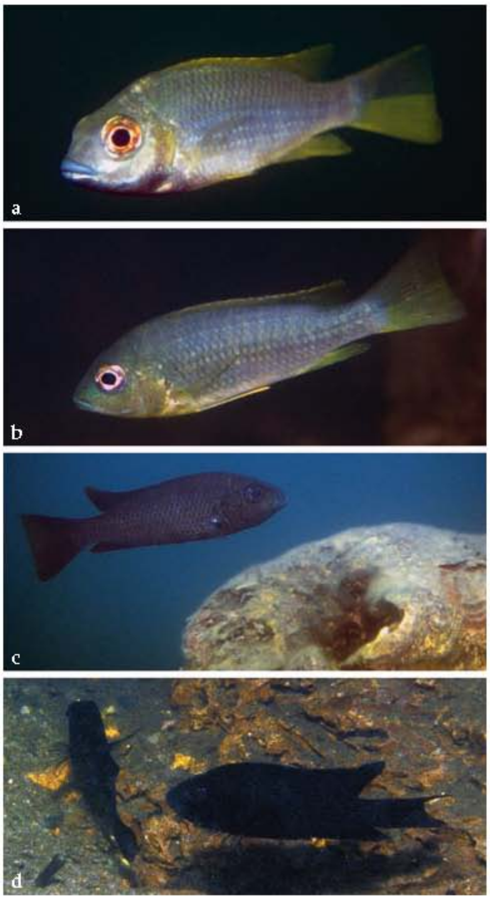

Fig. 21. *T. fusiforme* spec. nov. **a.** Non breeding specimen of "little-black" with large eyes, offshore. **b.** Non breeding specimen of "large-black" with small eyes, shallow water. **c.** Breeding specimen of "large-black" in front of a log hole. **d.** Breeding specimen of "little-black".

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 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 (Schliewen et al. 2001). It further differs from other *Tilapia* sensu lato except *T. joka*, *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. joka* 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				
		min	max	mean	SD	n
Measurements						
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
in percents of SL						
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
Counts						
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.

	T. fusiforme spec. nov. "little black"			*T. fusiforme* spec. nov. "large black"		
	min	max	n	min	max	n
Measurements						
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
in percents of SL						
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
Counts						
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 allochtonous 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)* interrelationships 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 are 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 initiave" 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 500 m 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 3 km to Mount Epope. MRAC A8-020-P-0962 (1, 54.6 mm SL), Republic of the Congo, River Lefini, about 600 m to camp Oteni. MRAC A8-020-P-0963 (1, 107.1 mm SL), Republic of the Congo, River Lefini, about 600 m 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 cessiana 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. Loiselle, 1 Oct 1970. MRAC 171870 (1, paratype, 120.8 mm SL), Ghana, Lake Volta at Agbogyesekwa, P. Loiselle, 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, Koui (= 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 Bemin western (5°9'N 9°38'E), U. Schliewen, Jan 1990. ZSM 27635 (8, paratypes, 51.6-71.6 mm SL), Cameroon, Lake Bemin 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 S4-F19, U.A. Kohler, Nov 1993. ZSM 25740 (1, 142.6 mm SL), Senegal, Street from Bathurst to Dionloulon 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 Bemin 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 Bemin western (5°9'N 9°38'E), U. Schliewen, Jan 1990.

Tilapia imbriferna Stiassny, Schliewen & Dominey, 1992: AMNH 98247 (holotype, 101.7 mm SL), Cameroon, Lake Bemin 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 Bemin 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. Mekkaway, 1983. BMNH 1993.9.23.7-8 (2, paratypes, 84.0-89.6 mm SL), Egypt, Ismailia canal, Ismailia, Imam. A.A. Mekkaway, 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., Upembu 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, Luanginga 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, 1km 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 ES 06 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. 30km 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, Schwébisch & Thollon. MNHN 1884-0295 (1, syntype, 125.6 mm SL), Gabon, Upper Ogooué, Passa, Franceville, Schwébisch & Thollon. MRAC 93-134-P-0782-0786 (2, 51.9-57.2 mm SL), Gabon, ±15km from Mpere village, River Ogooué, upstream Port-Gentil, by Ndougou, M. Levy, 1 Sep 1993. MRAC 93-134-P-0781 (1, 83.6 mm SL), Gabon, ±15km from Mpere 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 Mbamu, 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), Algeria, 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.

References

Dominey, W. J. & Snyder, A. M. 1988. Kleptoparasitism of freshwater crabs by cichlid fishes endemic to Lake Barombi Mbo, Cameroon, West Africa. Environmental Biology of Fishes 22 (2): 155-160.

Dunz, A. R. & Schliewen, U. K. 2010. Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana. Submitted.

Evanno, G., Regnaut, S. & Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14: 2611-2620.

Falush, D., Stephens, M. & Pritchard, J. K. 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164: 1567-1587.

Greenwood, P. H. 1987. The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. Bulletin of the British Museum (Natural History) Zoology 53 (3): 139-203.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2001. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4: 9.

Huber, R., van Staden, M., Kaufman, L. S. & Liem, K. F. 1997. Microhabitat use, trophic patterns, and the evolution of brain structure in african cichlids. Brain Behavior Evolution 50: 167-182.

Mansfeld, A. (Dr.) 1908. Der Totensee bei Nssakpé (Ekeu-land). Mitteilungen an die Deutschen Schutzgebiete 21: 12-14.

Neumann, D., Stiassny, M. L. J. & Schliewen, U. K. 2010. Two new sympatric *Sarotherodon* species (Pisces: Cichlidae) endemic to Lake Ejagham, Cameroon, west-central Africa, with comments on the *Sarotherodon galilaeus* species complex. Submitted.

Pritchard, J. K., Stephens, P. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics 155: 945-959.

Rassmann, K., Schlötterer, C. & Tautz, D. 1991. Isolation of simple-sequence loci for use in polymerase chain reaction based DNA fingerprinting. Electrophoresis 12: 112-118.

Schliewen, U. K. 1999. Sympatrische Artbildung bei Cichliden (Pisces: Perciformes) im Ejagham-See (Kamerun). PhD thesis, 162 pp., Ludwig-Maximilians-Universität München

– – & Klee, B. 2004. Reticulate sympatric speciation in Cameroonian crater lakes. BMC Frontiers in Zoology: 5.

-- , Rassmann, K., Markmann, M., Markert, J., Kocher, T. D. & Tautz, D. 2001. Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. Molecular Ecology 10: 1471-1488.

-- , Tautz, D. & Pääbo, S. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368: 629-632.

Stiassny, M. L. J., Schliewen, U. K. & Dominey, W. J. 1992. A new species flock of cichlid fishes from Lake Bermin, Cameroon with a description of eight new species of *Tilapia* (Labroidei: Cichlidae). Ichthyological Exploration of Freshwaters 3(4): 311-346.

Tautz, D. 1989. Hypervaribility of simple sequences as a general source for polymorphic DNA markers. Nucleic Acids Resarch 17: 6493-6471.

Trewavas, E., Green, J. & Corbet, S. A. 1972. Ecological studies on crater lakes in West Cameroon fishes of Barombi Mbo. Journal of Zoology (London) 167: 41-95.

Thieme, M. L., Abell, R., Stiassny, M. L. J., Skelton, P., Lehner, B., Dinerstein, E., Kamdem Toham, A., Burgess, N. & Olson, D. 2005. Freshwater ecoregions of Africa and Madagascar. A conservation assessment. 431 pp., Washington, Covelo, London (Island Press).

Thys van den Audenaerde, D. F. E. 1967. Description of *Tilapia deckerti* sp. nov. from Lake Ejagham, West Cameroon. Revue de Zoologie et de Botanique Africaines 76(3-4): 349-355.

-- 1968. An Annotated Bibliography of *Tilapia* (Pisces, Cichlidae). Annales Musée Royal de l'Afrique Centrale, Série N, Documentation Zoologique 14: I-XL + 1-406 pp.

-- 1971. Some new data concerning the *Tilapia*-species of the subgenus *Coptodon* (Pisces, Cichlidae). Revue de Zoologie et de Botanique Africaines 84(1-2): 160-168.

-- 1972. Description of small new *Tilapia* (Pisces, Cichlidae) from West-Cameroon. Revue de Zoologie et de Botanique Africaines 85(1-2): 93-98.

5. Paper III

Dunz AR, Schliewen UK (2012) Description of a rheophilic *Tilapia* species Smith, 1840 (Teleostei: Cichlidae) from Guinea with comments on *Tilapia rheophila* Daget, 1962. Zootaxa 3314, 17–30.

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Description of a rheophilic *Tilapia* species Smith, 1840 (Teleostei: Cichlidae) from Guinea with comments on *Tilapia rheophila* Daget, 1962

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Abstract

Tilapia konkourensis, new species, is described on the basis of three specimens from the upper Konkouré River and its tributary Kakrima. The rheophilic species differs from all other *Tilapia* sensu lato except *T. fusiforme* Dunz & Schliewen, 2010 in a shallower body 30.0–31.5% vs. 32.9–52.5% SL and from *T. fusiforme* in having eight instead of nine to twelve lower lateral-line scales. It is most similar to *Tilapia rheophila* Daget, 1962, type species of the monotypic subgenus *Tilapia* (*Dagetia*) Thys van den Audenaerde, 1969. An evaluation of the putative autapomorphies diagnosing *Dagetia* revealed that all are shared with members of the subgenus *Coptodon* Gervais, 1853 sensu Thys van den Audenaerde, 1969; hence, *Tilapia* (*Dagetia*) is placed in the synonymy of *Tilapia* (*Coptodon*).

Key words: ichthyofauna, freshwater, Fouta Djalon, West Africa

Introduction

In the course of an ongoing revision of the genus *Tilapia* Smith, 1840 we investigated all specimens identified as *Tilapia rheophila* Daget, 1962 and almost all *T. louka* in the MRAC and MNHN collections. Among the material collected in the 1980s in the Konkouré basin we discovered three very elongate and small specimens of an apparently new species, which is superficially similar to *T. rheophila*. For the description of these specimens as a new species, we examined and analysed the morphometry and taxonomic identity of all specimens previously identified as *Tilapia rheophila* Daget, 1962 and almost all *T. louka* in the MRAC and MNHN collections, as well as the only available and phenotypically similar *Tilapia* specimen from the Samou river, to which we refer here as *Tilapia* sp. aff. *louka* "Samou".

Tilapia rheophila is an endemic rheophilic cichlid, described from the Konkouré drainage on the Fouta Djalon plateau, Republic of Guinea. Unfortunately, the taxonomic identity of the few known specimens of *Tilapia rheophila* has always been problematic. Five specimens were collected by Daget in 1958 in middle Konkouré River near the bridge on the road from Kindia to Telimélé (Thys van den Audenaerde 1969). Daget (1962) referred in the original description only to these five specimens as syntypes, but he based the description of the species on additional adults, subadults and juveniles collected in a small Konkouré tributary, the Samou, near Koliagbé and around the waterfalls near Kindia ("Grand Chutes"). Although he mentioned differences between specimens from the Konkouré and the Samou, i.e. only the Samou specimens having a black mark in the soft part of the dorsal fin ("tilapia spot") and differing slightly in fin-formula and gill raker counts, he nevertheless regarded them as *T. rheophila*. It is not clear why Blanc (1962), listed in his MNHN cichlid type catalogue not only the five specimens of the Konkouré lot 59–106 as syntypes, but also three specimens of a "Grandes Chutes" lot 60–488 and one of the Koliagbé lot 60–489 as syntypes. Later, Thys van den Audenaerde (1969) based on a letter from Daget, tried to resolve this contradiction when accepting Daget´s explanations about correct publication dates and priority of Daget (1962) over Blanc (1962) by writing: "This makes that only the sample 59–106 can be considered as syntypes for *T. rheophila*, and that the largest specimen must be considered as holotype, because [it is] figured in the

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original description.” Despite Thys van den Audenaerdes´s consideration of a lectotype, and despite a subsequent listing of a “holotype” and “paratypes” in Teugels & Thys van den Audenaerde (1991:499), there is no contraindication to the fact that Daget had designated only five syntypes. Although Thys van den Audenaerde´s subsequent action could be interpreted as a lectotype designation (as suggested in litteris by Daget in Thys van den Audenaerde 1969), this runs counter to ICZN Article 74.5, which states that, for lectotype designations made before 2000, either the term “lectotype” or “the type” must be used. The article further states “when the original work reveals that the taxon had been based on more than one specimen, a subsequent use of the term “holotype” does not constitute a valid lectotype designation …”.

Therefore the recent listing in Eschmeyer and Fricke (2011) of only five syntypes from the Konkouré is correct, but nevertheless the question about the correct species assignation of *Tilapia* sp. aff. *louka*“ Samou” remains. When Thys van den Audenaerde (1969) described *Tilapia louka* Thys van den Audenaerde, 1969, he reassigned the specimens of the two Samou lots to his new species, but he also stated, that: “Because of their dubious status we do not designate them as paratypes of *T. louka*.” Meanwhile, the whereabouts of the Koliagbé specimen (MNHN 1960–0489) are unknown (P. Pruvost (MNHN), pers. comm.).

Material and methods

For morphological comparisons, we examined *Tilapia* sensu lato specimens (n=926) from Royal Museum for Central Africa, Tervuren, Belgium (RMCA), Natural History Museum, London, United Kingdom (BMNH), Muséum National 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), Royal Ontario Museum (ROM), Ontario, Canada and Bavarian State Collection of Zoology, Munich, Germany (ZSM). Focus was placed on specimens from West Africa. All *Tilapia* sensu lato species were included with type specimens except for *T. buttikoferi* (Hubrecht, 1881), *T. camerunensis* Lönnberg, 1903 and *T. zillii* (Gervais, 1848), because specimens were unavailable or, in the case of *T. zillii*, lost; in which case, topotypical specimens were included instead. For a full list of investigated specimens see Dunz and Schliewen (2010) and “additional material” below (Appendix 1). When referring to the subgenus *Coptodon* Gervais, 1853 we refer to the type species *Tilapia zillii* (Gervais, 1848) and the following species *T. bakossiorum* Stiassny, Schliewen & Dominey, 1992; *T. bemini* Thys van den Audenaerde, 1972; *T. bythobates* Stiassny, Schliewen & Dominey, 1992; *T. cameronensis* Holly, 1927; *T. camerunensis* Lönnberg, 1903; *T. coffea* Thys van den Audenaerde, 1970; *T. dageti* Thys van den Audenaerde 1971; *T. discolor* (Günther, 1902); *T. deckerti* Thys van den Audenaerde, 1967; *T. ejagham* Dunz & Schliewen 2010; *T. flava* Stiassny, Schliewen & Dominey, 1992; *T. fusiforme* Dunz & Schliewen 2010; *T. guineensis* (Bleeker, 1862); *T. gutturosa* Stiassny, Schliewen & Dominey, 1992; *T. imbriferna* Stiassny, Schliewen & Dominey, 1992; *T. ismailiaensis* Mekkawy 1995; *T. kottae* Lönnberg, 1904; *T. louka* Thys van den Audenaerde, 1969; *T. margaritacea* Boulenger, 1916; *T. nigrans* Dunz & Schliewen 2010; *T. nyongana* Thys van den Audenaerde, 1960; *T. rendalli* (Boulenger, 1896); *T. rheophila* Daget, 1962; *T. snyderae* Stiassny, Schliewen & Dominey, 1992; *T. spongotroktis* Stiassny, Schliewen & Dominey, 1992; *T. thysi* Stiassny, Schliewen & Dominey, 1992; *T. walteri* Thys van den Audenaerde, 1968, *Tilapia* sp. aff. *guineensis* “Cross”; *Tilapia* sp. aff. *zillii* “Kisangani” and *Tilapia* sp. aff. *louka* “Samou”. Measurements, meristics, application of morphological characters and statistical analysis follow Dunz and 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. For a first step a principal component analysis (PCA) of log-transformed morphometric data (24 measurements) using the statistical program PAST 2.12 (Hammer *et al.*, 2001) was conducted. This PCA contains specimens of all *Tilapia* (*Coptodon*) (see above) species including three yet undescribed species (*T.* sp. aff. *guineensis* “Cross” (closely related to the Lake Ejagham species flock, see Schliewen et al. 2001), *T.* sp. aff. *zillii* “Kisangani” as well as *T.* sp. aff. *louka* “Samou”), *Tilapia rheophila* and the new species described herein. *Tilapia tholloni* (Sauvage, 1884) and *T. congica* (Poll & Thys van den Audenaerde, 1960) were excluded a priori, because both are easily separated using the densely scaled caudal fin as an unambiguous character. In this PCA the first principal component (PC I) integrates most size-related variation, whereas the PC II, PC III and following components are theoretically size-free. A separate PCA was performed for the meristic dataset (nine counts) alone; meristics are size free in *Tilapia* sensu lato and thus PC I is the most informative component. Scores of both PCAs were combined in a single bivariate plot for most informative visualization. A second step PCA was performed using a limited taxon sampling, i.e., for all specimens of species overlapping in Fig. 1 with the new species. The second step PCA served to remove potential noise due to variance in the total dataset potentially affecting subtle differentiation patterns between similar target taxa. The second PCA was performed in the same way as the first step PCA.

Results

The first PCA with all *Tilapia* (*Coptodon*) (see Material and methods) based on 24 morphometric measurements and nine meristic counts revealed no distinct clusters but differentiate the new species from all included *Tilapia* (*Coptodon*), except *T. rheophila* (Fig. 1). The two highest factor loadings on PC III (morphometrics) are for distance between the anus and the anal fin base and caudal peduncle length, and on PC I (meristics) for number of dorsal fin rays and number of scales on the lower lateral line (Table 1). A second PCA based on the same measurements and counts as the first PCA revealed each one non-overlapping cluster for the new species and *T. rheophila* (Fig. 2). Here, the highest factor loadings on PC II (morphometrics) are for the two characters length of the anal-fin base and caudal peduncle depth and for PC I (meristics) number of scales in horizontal line and number of scales on the lower lateral line (Table 2). Although the character body depth does not contribute most strongly to the variance in the morphometric data set, the three specimens of the new species differ from all other *Tilapia* sensu lato except *T. fusiforme* in body depth 30.0–31.5% vs. 32.9–52.5% SL. It nevertheless is differentiated from *T. fusiforme*, an endemic lacustrine species from Lake Ejagham (Cameroon) in having eight instead nine–twelve lower lateral line scales. Furthermore *T. rheophila* differs from the new species in an additional four diagnostic characters (see Diagnosis).

Morphological comparisons with all non-*Coptodon Tilapia* Smith, 1840 (sensu lato) species, as well as with members of genera being closely related to *Tilapia (Chilochromis* Pellegrin, 1900, *Steatocranus* Boulenger, 1899 (incl. "*Steatocranus*" *irvinei* Trewavas & Irvine, 1943) support the morphological distinction of the three new specimens using single characters (see Diagnosis). Thus, the new species is diagnosably distinct from all other currently valid *Tilapia*, closely related cichlids as well as from three undescribed *Tilapia* (*Coptodon*) species and we therefore describe it as new.

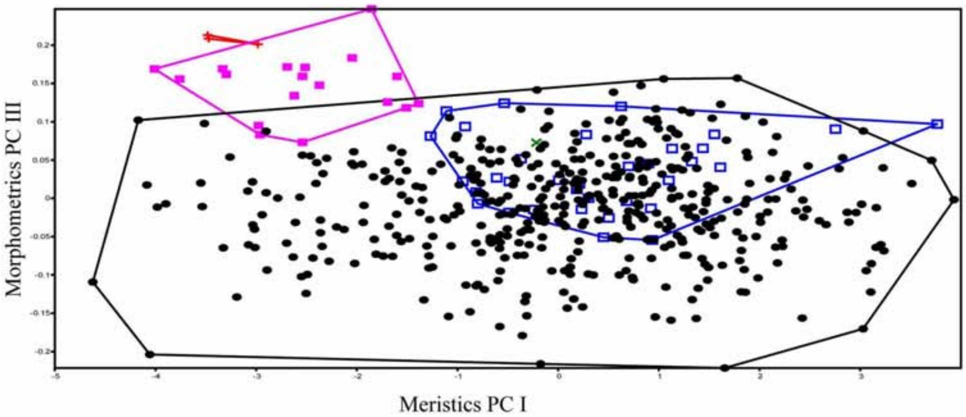

FIGURE 1. Bivariate plot of Principal Component III (morphometrics) vs. Principal Component I (meristics); visualized as convex hulls. Red crosses = *T. konkourensis* **sp. nov.** (n=3); pink filled squares = *T. rheophila* (n=18); blue open suares = *T. louka* (n=34); green cross = *T.* sp. aff. *louka* "Samou" (n=1) and black dots = all remaining *Tilapia* (*Coptodon*) (n=444). Total number of specimens in the plot (n=500).

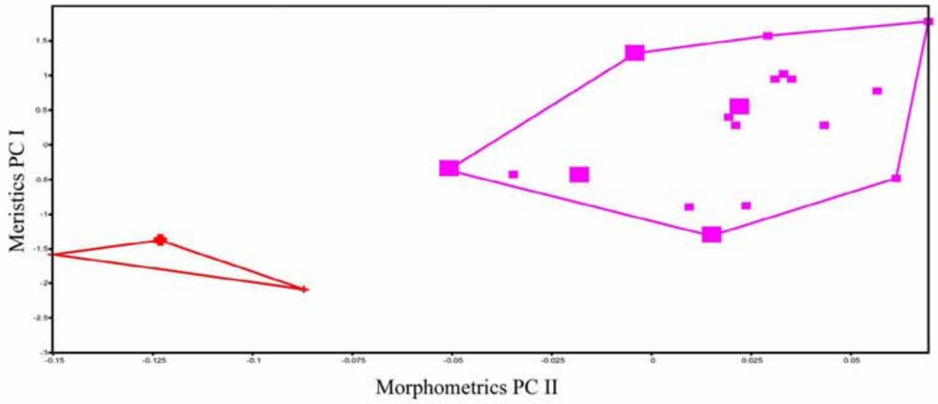

FIGURE 2. Bivariate plot of Principal Component II (morphometrics) vs. Principal Component I (meristics); visualized as convex hulls. Red crosses = *T. konkourensis* **sp. nov.** (n=3); pink filled squares = *T. rheophila* (n=18); Bold symbols refer to type specimens.

TABLE 1. Factor Loadings of PC II-III (morphometrics) and PC I-II (meristics) for Figure 1. PCA (morphometrics) based on 24 log transformed measurements and PCA (meristics) on nine not log transformed meristics. In each case highest loadings indicated in boldface. The total number of specimens in this plot is 500.

Morphometrics	PC II	PC III	Meristics	PC I	PC II
Standard length	0.009	0.131	Dorsal fin spines	-0.051	0.349
Head length	0.134	-0.026	Dorsal fin rays	**0.484**	**-0.557**
Interorbital width	-0.059	-0.200	Anal fin rays	0.254	-0.179
Preorbital width	0.005	-0.120	Pectoral fin rays	0.076	-0.091
Horizontal eye length	0.030	-0.029	Scales (horizontal line)	0.240	0.288
Snout length	0.132	0.042	Upper lateral line scales	0.310	**0.402**
Internostril distance	0.109	-0.041	Lower lateral line scales	**0.686**	0.361
Cheek depth	0.075	-0.121	Gill rakers ceratobranchial	0.249	-0.384
Upper lip length	0.319	-0.099	Gill rakers epibranchial	0.082	-0.071
Lower lip length	0.321	-0.088			
Lower lip width	0.246	-0.254			
Lower jaw length	**0.329**	0.014			
Predorsal distance	0.050	-0.054			
Dorsal-fin base length	-0.174	0.133			
Last dorsal-fin spine length	-0.316	-0.128			
Anal-fin base length	-0.275	0.135			
Third anal-fin spine length	-0.119	0.011			
Pelvic-fin length	-0.292	0.057			
Pectoral-fin length	-0.198	-0.245			
Caudal peduncle depth	-0.250	0.005			
Caudal peduncle length	**0.334**	**0.351**			
Body depth (pelvic-fin base)	-0.211	-0.193			
Preanal length	-0.012	0.078			
Anus-anal-fin base distance	-0.063	**0.736**			
Eigenvalue	0.018	0.005	Eigenvalue	2.544	1.631
% variance	2.762	0.810	% variance	31.545	20.224

TABLE 2. Factor Loadings of PC II-III (morphometrics) and PC I-II (meristics) for Figure 2. PCA (morphometrics) based on 24 log transformed measurements and PCA (meristics) on nine not log transformed meristics. In each case highest loadings indicated in boldface. The total number of specimens in this plot is 21.

Morphometrics	PC II	PC III	Meristics	PC I	PC II
Standard length	0.094	0.023	Dorsal fin spines	-0.022	0.059
Head length	0.376	-0.170	Dorsal fin rays	0.004	0.145
Interorbital width	-0.157	0.177	Anal fin rays	0.074	0.137
Preorbital width	0.262	-0.018	Pectoral fin rays	0.281	-0.176
Horizontal eye length	-0.061	0.152	Scales (horizontal line)	**0.612**	0.294
Snout length	-0.022	0.119	Upper lateral line scales	-0.206	**0.839**
Internostril distance	-0.115	0.016	Lower lateral line scales	**0.664**	-0.040
Cheek depth	0.007	-0.236	Gill rakers ceratobranchial	-0.103	**-0.349**
Upper lip length	-0.019	-0.093	Gill rakers epibranchial	-0.218	-0.108
Lower lip length	-0.237	**0.408**			
Lower lip width	-0.019	-0.230			
Lower jaw length	0.145	-0.014			
Predorsal distance	-0.290	0.099			
Dorsal-fin base length	0.138	-0.072			
Last dorsal-fin spine length	-0.064	0.217			
Anal-fin base length	**0.439**	0.067			
Third anal-fin spine length	0.253	0.136			
Pelvic-fin length	0.170	0.050			
Pectoral-fin length	-0.124	0.185			
Caudal peduncle depth	**-0.396**	-0.063			
Caudal peduncle length	0.104	0.035			
Body depth (pelvic-fin base)	-0.155	-0.022			
Preanal length	-0.248	**-0.700**			
Anus-anal-fin base distance	0.094	0.023			
Eigenvalue	0.003	0.002	Eigenvalue	1.208	0.694
% variance	2.158	1.468	% variance	38.956	22.389

***Tilapia konkourensis*, new species**

(Fig. 3A–C, Table 3)

Holotype: MRAC 81-20-P-51 (85.1 mm SL), Guinea, route Korela-Kondoya, River Konkouré (10° 32' N, 12° 52' W), P. De Kimpe, 10 Mar. 1981.

Paratypes: MRAC 81-20-P-52 (1, 68.7 mm SL), same data as holotype. MNHN 1987-1502 (1, 77.0 mm SL), Guinea, River Kakrima by Koussi, C. Lévêque, 15 Feb. 1982.

Differential diagnosis. *Tilapia konkourensis* **sp. nov.** differs from all other *Tilapia* sensu lato except *T. fusiforme* in a shallower body 30.0–31.5% vs. 32.9–52.5% SL and from *T. fusiforme* in having eight instead nine–twelve lower lateral line scales. It differs from all *Tilapia* sensu lato except *T. rheophila* by additional morphological and meristic characters: stout teeth in oral jaw vs. spatulate teeth in *T. mariae* (Boulenger, 1899) and *T. cabrae* Boulenger, 1899; median pharyngeal teeth of lower pharyngeal jaw never broadened with crest-like cusps as in *T. cessiana* Thys van den Audenaerde, 1968 and *T. buttikoferi*; posterior pharyngeal teeth of lower pharyngeal jaw never clearly bicuspid as in *T. busumana* (Günther, 1903), *T. pra* Dunz & Schliewen 2010, *T. brevimanus* Boulenger, 1911, *T. sparrmanii* Smith, 1840, *T. baloni* Trewavas & Stewart, 1975, *T. ruweti* (Poll & Thys van den Audenaerde, 1965) and *T. guinasana* Trewavas, 1936; vertical bars broader not than lighter interspaces; possessing slender to spatulate teeth in oral jaws as in *T. joka* Thys van den Audenaerde, 1969; no densely scaled caudal fin. Compared to *T. congica, T. tholloni* and *T. bilineata*, it further differs from all *Tilapia* (*Coptodon*) (excluding *T. rheophila*) by a combination of the meristic characters: number of dorsal-fin spines (16 vs. 13–17) and rays (11 vs. 10–13), number of scales on the upper (21 vs. 17–23) and lower later line (8 vs. 7–14), and number of gill rakers (7–9 vs. 7–12) on first ceratobranchial (excluding gill rakers on cartilaginous plague). It differs from *T. rheophila* by a smaller eye diameter (7.5–7.6% vs. 8.0–10.7% SL), a shorter predorsal distance (31.1–33.6% vs. 34.2–38.2% SL), a longer length of the base of dorsal fin (61.4–62.3% vs. 56.9–60.9% SL) and a shorter pectoral fin length (22.2–24.0% vs. 25.1–28.3% SL).

It differs from the *Tilapia* related species *Chilochromis duponti* Boulenger, 1902 (for haplotilapiine intrarelationships see Schwarzer *et al*. 2009) in no densely scaled caudal fin or comb-like, spatulate teeth (Stiassny 2009); from *Gobiocichla* Kanazawa, 1951 in having two unconnected lateral lines vs. one continuous lateral line, and from *Steatocranus* Boulenger, 1899 (currently including the unrelated "*Steatocranus*" *irvinei* (Trewavas, 1943)) in not developing a hump on forehead, and in fewer dorsal spines 16 vs. 19–22 (Roberts & Stewart 1976).

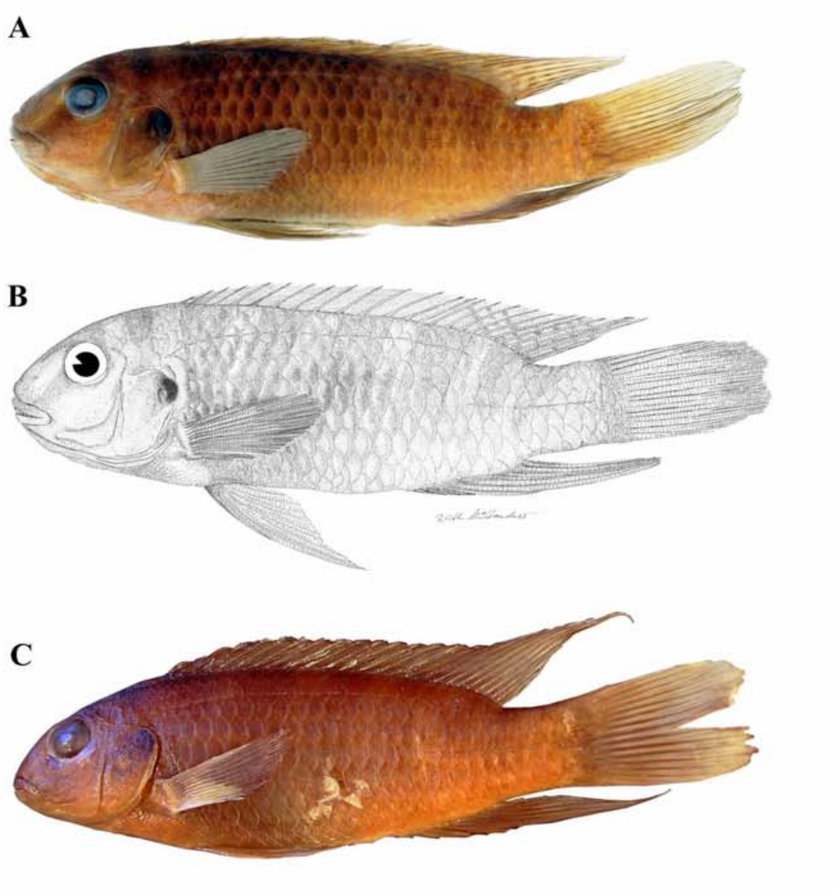

FIGURE 3. A. Preserved holotype of *Tilapia konkourensis* **sp. nov.** (MRAC 81-20-P-51), 85.1 mm SL; Guinea: route Korela-Kondoya, River Konkouré. B. Drawing (by R. Kühbandner) of holotype of *Tilapia konkourensis* **sp. nov.** (MRAC 81-20-P-51), 85.1 mm SL; Guinea: route Korela-Kondoya, River Konkouré. C. Preserved paratype of *Tilapia konkourensis* **sp. nov.** (MRAC 81-20-P-52), 68.7 mm SL; Guinea: route Korela-Kondoya, River Konkouré.

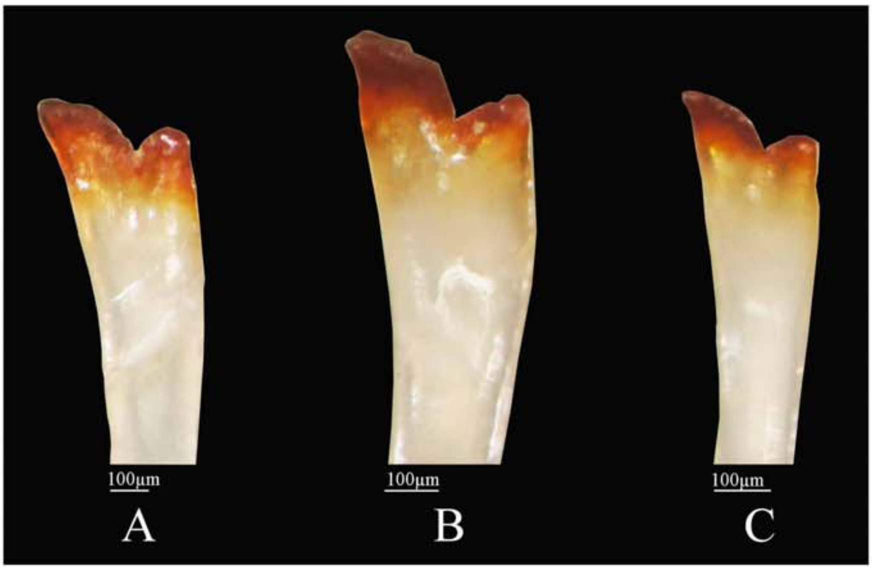

FIGURE 4. Outer shape of lower jaw teeth. A = *T. louka* (MRAC 92-59-P-3337-403), B = *T. konkourensis* **sp. nov.** (MRAC 81-20-P-51) and C = *T. rheophila* (MRAC 81-20-P-53-54).

The new species shares all typical *Tilapia* (*Coptodon*) characters, which are: lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with anterior keel shorter than or just as long as toothed area of jaw; posterior pharyngeal teeth more or less clearly tricuspid, but sometimes quadricuspid or pentacuspid, median pharyngeal teeth never broadened with crest-like cusps; first outer gill arch bearing 10–17 rakers; two unconnected lateral lines; only cycloid scales present; 22–30 scales in the longitudinal scale row; upper and lower outer teeth rows bicuspid in both jaws, inner rows with smaller tricuspid teeth in both jaws; isognathous or retrognathous jaws; stout teeth; caudal fin not densely scaled (except for *T. nyongana*, which possesses only in adults a rather densely scaled caudal fin); 13–17 dorsal spines; vertical bars (not visible in all specimens, due to conditions of preservation and/or condition of specimens before preservation), never oblique and mostly branched; pointed pelvic fin; no hump on forehead; no visor like hanging pad in pharynx (as in chromidotilapiines); only one supraneural associated with first neural spine (Takahashi 2003; Thys van den Audenaerde 1969; Stiassny 1991; pers. observ.).

Description. Morphometric and meristic data for holotype and paratype specimens presented in Table 3. See Figures 3a–c for general appearance. The new species appears to be a dwarf species with a maximum observed size of 85.1 mm SL. Body extremely elongated and laterally compressed. Dorsal head profile slightly convex from insertion of first dorsal spine to tip of upper lip. Head length about one-third SL, snout outline obtuse. Eye moderately large and interorbital width always larger than eye length. Greatest body depth at level of first dorsal spine. Dorsal profile, towards caudal, slightly posteroventrally curved (not straight). Caudal peduncle always longer than deep. Two unconnected lateral lines.

Squamation. All scales cycloid. Upper lateral line extending from posterior margin of gill cover to approximately center of dorsal fin. One complete row of large and one row of smaller, dorso-ventrally compressed scales separating upper lateral line from the last dorsal spine. Lower lateral line originating at level of first branched dorsal-fin rays, terminating midlaterally on caudal peduncle. One scale row between upper and lower lateral line. Preoperculum scaled with three to four regular rows; no scales on dark opercular spot. Chest scales smaller, slightly embedded scales. Base of caudal fin with minute scales.

Gill rakers. First lower gill-arch (ceratobranchial) with seven–nine gill rakers and first upper gill-arch (epibranchial) with four gill rakers with a single gill raker on cartilaginous plug included in the latter number. Total number of gill rakers on first gill-arch 11–13. Ceratobranchial rakers slender, broader on base, pointed. Gill rakers situated most ventrally on ceratobranchial gill-arch smaller than all other gill rakers.

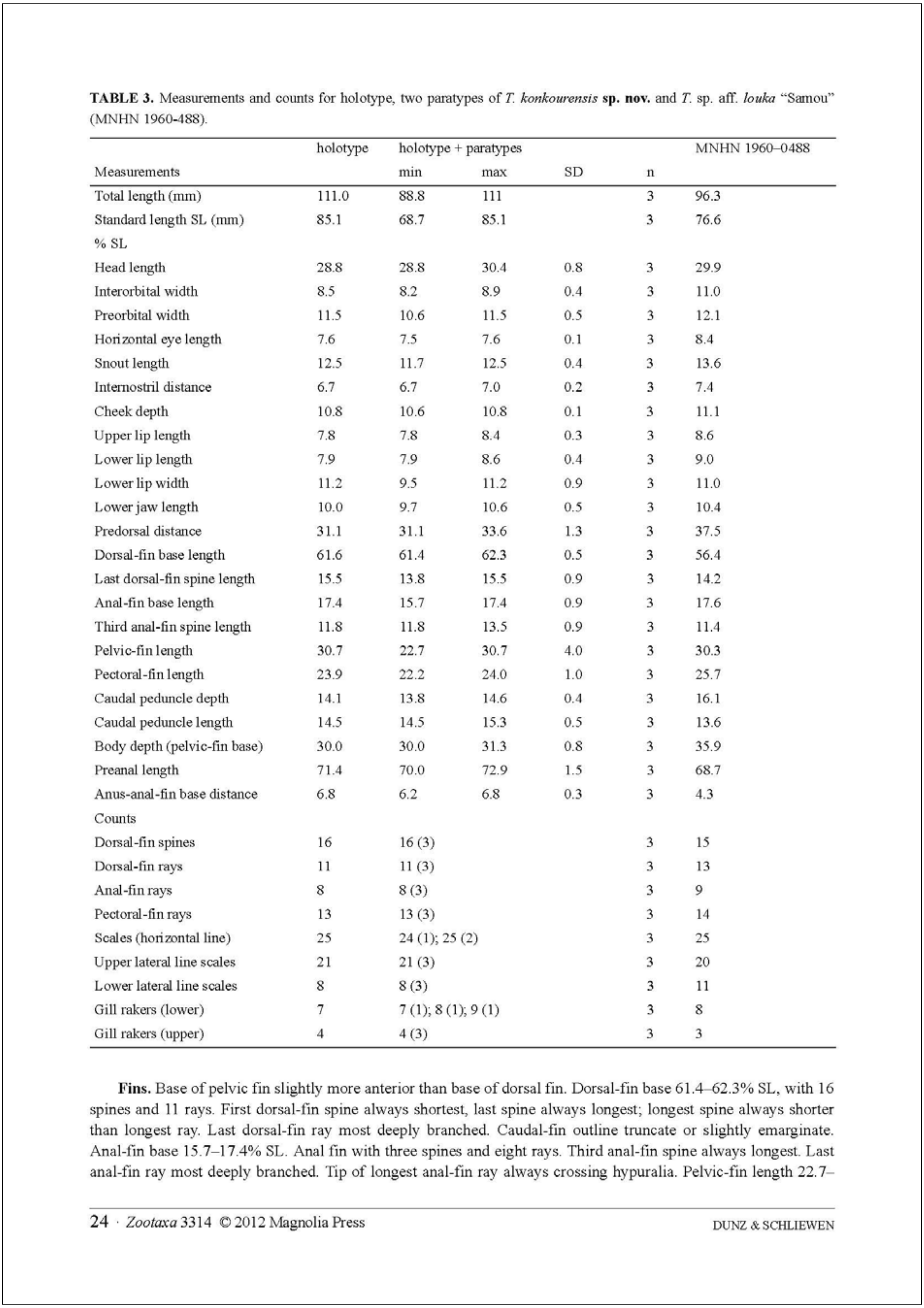

TABLE 3. Measurements and counts for holotype, two paratypes of *T. konkourensis* **sp. nov.** and *T.* sp. aff. *louka* "Samou" (MNHN 1960-488).

	holotype	holotype + paratypes				MNHN 1960–0488
Measurements		min	max	SD	n	
Total length (mm)	111.0	88.8	111		3	96.3
Standard length SL (mm)	85.1	68.7	85.1		3	76.6
% SL						
Head length	28.8	28.8	30.4	0.8	3	29.9
Interorbital width	8.5	8.2	8.9	0.4	3	11.0
Preorbital width	11.5	10.6	11.5	0.5	3	12.1
Horizontal eye length	7.6	7.5	7.6	0.1	3	8.4
Snout length	12.5	11.7	12.5	0.4	3	13.6
Internostril distance	6.7	6.7	7.0	0.2	3	7.4
Cheek depth	10.8	10.6	10.8	0.1	3	11.1
Upper lip length	7.8	7.8	8.4	0.3	3	8.6
Lower lip length	7.9	7.9	8.6	0.4	3	9.0
Lower lip width	11.2	9.5	11.2	0.9	3	11.0
Lower jaw length	10.0	9.7	10.6	0.5	3	10.4
Predorsal distance	31.1	31.1	33.6	1.3	3	37.5
Dorsal-fin base length	61.6	61.4	62.3	0.5	3	56.4
Last dorsal-fin spine length	15.5	13.8	15.5	0.9	3	14.2
Anal-fin base length	17.4	15.7	17.4	0.9	3	17.6
Third anal-fin spine length	11.8	11.8	13.5	0.9	3	11.4
Pelvic-fin length	30.7	22.7	30.7	4.0	3	30.3
Pectoral-fin length	23.9	22.2	24.0	1.0	3	25.7
Caudal peduncle depth	14.1	13.8	14.6	0.4	3	16.1
Caudal peduncle length	14.5	14.5	15.3	0.5	3	13.6
Body depth (pelvic-fin base)	30.0	30.0	31.3	0.8	3	35.9
Preanal length	71.4	70.0	72.9	1.5	3	68.7
Anus-anal-fin base distance	6.8	6.2	6.8	0.3	3	4.3
Counts						
Dorsal-fin spines	16	16 (3)			3	15
Dorsal-fin rays	11	11 (3)			3	13
Anal-fin rays	8	8 (3)			3	9
Pectoral-fin rays	13	13 (3)			3	14
Scales (horizontal line)	25	24 (1); 25 (2)			3	25
Upper lateral line scales	21	21 (3)			3	20
Lower lateral line scales	8	8 (3)			3	11
Gill rakers (lower)	7	7 (1); 8 (1); 9 (1)			3	8
Gill rakers (upper)	4	4 (3)			3	3

Fins. Base of pelvic fin slightly more anterior than base of dorsal fin. Dorsal-fin base 61.4–62.3% SL, with 16 spines and 11 rays. First dorsal-fin spine always shortest, last spine always longest; longest spine always shorter than longest ray. Last dorsal-fin ray most deeply branched. Caudal-fin outline truncate or slightly emarginate. Anal-fin base 15.7–17.4% SL. Anal fin with three spines and eight rays. Third anal-fin spine always longest. Last anal-fin ray most deeply branched. Tip of longest anal-fin ray always crossing hypuralia. Pelvic-fin length 22.7–

30.7% SL. Tip of longest pelvic-fin ray not crossing anus. Pectoral-fin length 22.2–24.0% SL. Pectoral-fin rays 13. Dorsal and anal fin elongated and pointed, pectoral fin rounded.

Jaws and dentition. Jaws slightly retrognathous. Upper and lower outer teeth rows in both jaws bicuspid. Neck of anterior jaw teeth stout, crown brownish, expanded and cusps truncated with a wide cusp gap (Fig. 4). Two to three incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad or somewhat broader, anterior keel shorter than toothed area (Fig. 5). Most posterior pharyngeal teeth tricuspid (few bicuspid), stout, slightly hooked and regularly arranged, especially at the last two–three rows of toothed area (Fig. 6). These posterior bicuspid teeth are derived from a tricuspid type, and are different than a well-marked bicuspid type (Thys van den Audenaerde, 1969). Dentigerous plate triangular. Most teeth in anterior two thirds of toothed area approach the "kukri" tooth shape (sensu Greenwood 1987) with three cusps.

FIGURE 5. Outer shape of lower pharyngeal bone of the holotype of *T. konkourensis* **sp. nov.** (MRAC 81-20-P-51).

Coloration in alcohol (adult specimen) (Figs. 3a–c). Basic color brownish. Head and dorsal side dark brownish, ventral side light brownish to whitish. Chest and belly whitish with a few darker areas. Two lines of flank scales with light scale margins and a dark centre above a horizontal line at level of the lower later line. Lower lip light brownish to whitish and upper lip darker colored. Markings on body: Five or six dark vertical bars on dorsum and sides (first bar at level of first dorsal spine and last two on caudal peduncle) not reaching belly, a nape band, a supraorbital stripe and a lachrymal stripe. Vertical bars often not present. Dark opercular spot. Fins: Pectoral and pelvic fin transparent. Anal fin and caudal fin light brownish. Dorsal fin without a "tilapia spot". Life color unknown.

Distribution and ecology. Only known from the middle Konkouré River and its tributary, the Kakrima in Guinea (Fig. 7). Occurs sympatrically with *T. rheophila* and *T. louka*. *T. rheophila* is also endemic to the Fouta

Djalon whereas *T. louka* is widespread in Guinea, Liberia and Sierra Leone. The very slender body of *T. konkourensis* **sp. nov.** in combination with a rounded head shape and slightly retrognathous jaws is unique among *Tilapia* and suggests that it is a benthic-rheophilic species, as the combination of characters is shared with other rheophilic haplotilapiine cichlid genera, e.g., *Steatocranus* (Roberts & Stewart 1976). Many rapids cichlids are exceptionally elongate for members of their family, and this is evidently a modification for life in rapids. Such rapid habitats are very common in the Fouta Djalon region of Guinea.

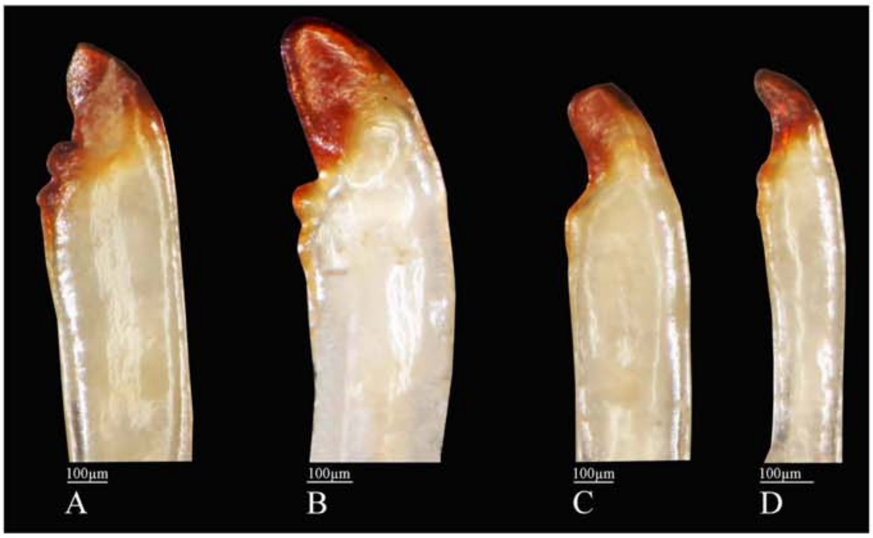

FIGURE 6. Outer shape and number of cusps of posterior pharyngeal teeth of lower pharyngeal jaw of A = *T. louka* (MRAC 92-59-P-3337-403), B = *T. konkourensis* **sp. nov.** (MRAC 81-20-P-52), C and D = *T. rheophila* (MRAC 81-20-P-53-54).

Etymology. The species name *konkourensis* refers to the Konkouré River, the drainage to which the new species appears to be endemic. Used as a noun in apposition.

Status of *Tilapia* sp. aff. *louka* "Samou". With the description of the new species a second rheophilic *Tilapia* species from the Fouta Djalon is recognized, but the status of apparently closely related *Tilapia* sp. aff. *louka* "Samou" still remains dubious. Unfortunately this species is only represented by a single adult museum specimen (MNHN 1960–0488). According to our preliminary data (Table 3), *Tilapia* sp. aff. *louka* "Samou", differs from the new species and from *T. rheophila* in several morphological, meristic and color characters, i.e., in a shorter anal spine length, a deeper caudal peduncle depth, a shorter distance from anus to base of anal-fin, posterior teeth of lower pharyngeal jaw are uniform tricuspid, higher number of dorsal rays, and a well marked "tilapia spot" in the soft part of dorsal-fin. Differences to *T. louka* are a shorter head length, a shorter pectoral fin length, a shallower body, a lower preanal length, fewer gill rakers on ceratobranchial as well as on epibranchial, a more rounded snout, and the presence of a dark spot in the centre of each scale on the flanks above a horizontal line at level of the lower lateral-line. The body is more elongate as in *T. louka*. Due to the lack of additional specimens, the final status of *Tilapia* sp. aff. *louka* "Samou" remains unresolved.

Discussion

Thys van den Audenaerde erected for *T. rheophila* a separate subgenus, *Dagetia* Thys van den Audenaerde, 1969, based on the four characters: "12 to 14 scale rows round caudal peduncle, snout rounded, mouth subterminal and posterior pharyngeal teeth often with a reduced lower cusp, becoming apparently bicuspid" (Thys van den Audenaerde, 1969). In contrast, he placed *T. louka* in *Coptodon* Gervais, 1853 sensu Thys van den Audenaerde 1969 (i.e., as a subgenus), based of the higher number of scale rows (16) around the caudal peduncle. Recently, we showed that this count is a highly variable character in *Tilapia* (*Coptodon*) (Dunz & Schliewen 2010, pers. observ.). Further he stated, that: "The bicuspid shape of the posterior pharyngeal teeth in *T. rheophila* does not constitute an objection for considering both species *T. louka* and *T. rheophila* as strongly related, as these posterior bicuspid teeth are clearly derived of a tricuspid type…". The two remaining characters defining "*Dagetia*", i.e. "snout rounded" and "mouth subterminal" are also common in *T. louka*. Thus, the subgenus *Dagetia* is not supported by any diagnostic character or character combination, and we hereby place it in the synonymy of *Tilapia* (*Coptodon*).

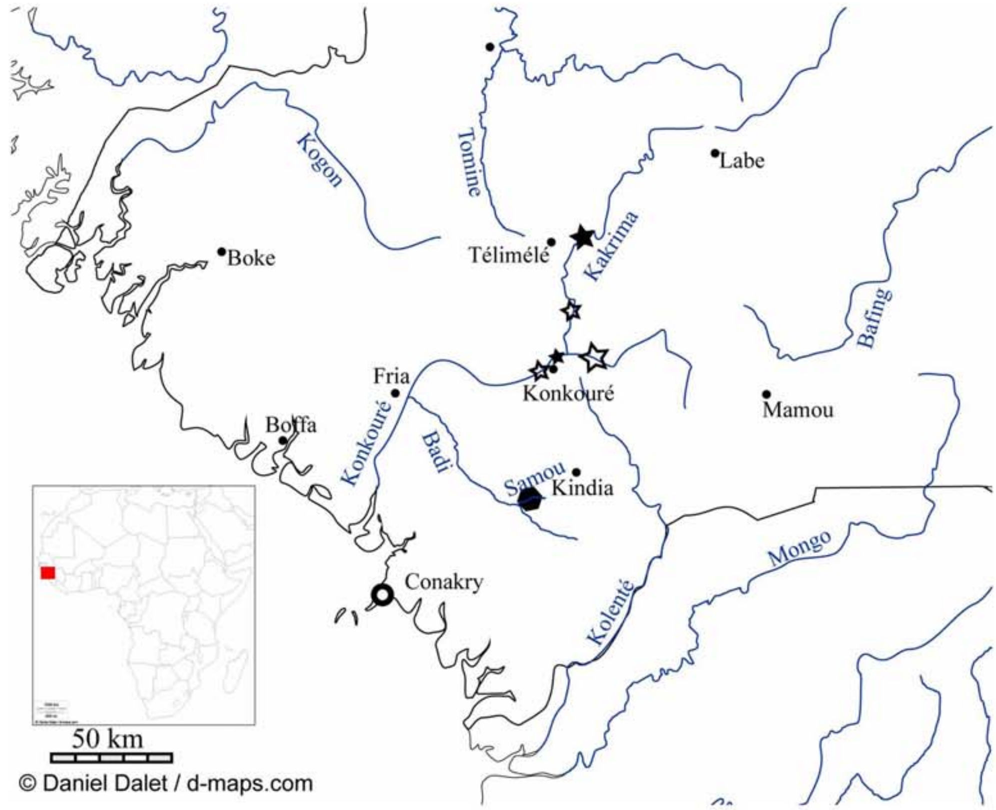

FIGURE 7. Map of western region of Guinea. Large black stars marking the two type locations of *T. konkourensis* **sp. nov.**; large open black star is type location as well as location of *T. rheophila*; small stars are locations of *T. rheophila*, filled star is type location of *T. rheophila*; filled polygon marks the location of *T.* sp. aff. *louka* "Samou". Map based on a free download from http://www.dmaps.com/carte.php?lib=guinea_Lankarte&num_car=3419&lang=de.

Endemicity in Fouta Djalon ecoregion. *T. konkourensis* **sp. nov.**, *T. rheophila* as well as *T.* sp. aff. *louka* " Samou" are endemic to the Fouta Djalon (sometimes also spelled Futa or Fouta Djallon or Dschalon). About one-quarter of the sixty described fish species in the Fouta Djalon are endemic (Thieme 2005). In West Africa two major ichthyofaunal regions are recognized, the Upper Guinea and Nilo-Sudan region (Roberts 1975); these are separated by the Guinean range, which includes the Fouta Djalon (Thieme 2005). Only a few fish species are known from both slopes of the Fouta Djalon, e.g., *Amphilius rheophilus* Daget, 1959 (Leveque 1997; Teugels *et al.* 1987). This has led to the recognition of a distinct aquatic ecoregion, the "Fouta Djalon" in a conservation assessment of freshwater ecoregions of Africa and Madagascar (Thieme *et al.* 2005). The description of a new apparently endemic cichlid species as well as the occurrence of another potentially endemic species, *T.* sp. aff. *louka* " Samou", supports this notion. Uplifting of the Fouta Djalon commenced in the late Jurrasic, and again in the Miocene (Thieme 2005). Since that time, the plateau has remained stable and has spawned the headwaters of several major West African rivers, i.e., the Niger, the Gambia, the Senegal and the Konkouré. It is therefore sometimes referred to as the *chateau d'eau* (water castle) of West Africa (Andre 2002; Nelson 1975). Only a few larger ichthyological collections were realized in this area, e.g., by Daget in 1958 (Daget 1962) or by Leveque in 1987, and many major river stretches as well as complete smaller subdrainages ichthyologically remain unsampled or poorly known (Teugels *et al.* 1987). According to the ecoregion summary in Thieme (2005) multiple headwaters and subdrainages isolated from downstream stretches through waterfalls and rapids may have served as refugial zones for ancient faunal elements. This in combination with the fact that several of the endemics are known only from few individuals and single or few locations suggests that this region holds substantially more endemic species than currently known.

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Literature cited

Abell, R., Olson, D.M., Dinerstein, E., Hurley, P., Diggs, J.T., Eichbaum, W., Walters, S., Wettengel, W., Allnutt, T., Loucks, C., & Hedao, P. (2000) *Freshwater ecoregions of North America: a conservation assessment.* Island Press, Washington, DC, 319 pp.

Andre, V. (2002) Environnement dégradé au territaire gére : *le Fouta Djalon (République de Guinée).* Bordeaux, 512 pp.

Blanc, M. (1962) Catalogue des types de Poissons de la famille des Cichlidae en collection au Muséum national d'Histoire naturelle. *Bulletin du Muséum National d'Histoire Naturelle* (Série 2) 34, 3, 252–226.

Daget, J. (1962) Les poissons du Fouta Dialon et de la basse Guinée. *Mémoires de l'Institut français d'Afrique Noire*, 65, 1–210, pls. 1–13.

Dinerstein, E., Wikramanayake, E., Graham, D.J., Webster, A.L., Primm, S.A., Bookbinder, M.P. & Ledec, G. (1995) *A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean.* The World Bank, Washington, DC, 129 pp.

Dunz, A.R. & Schliewen, U.K. (2010) Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana. *Zootaxa*, 2548, 1–21.

Eschmeyer, W.N. & Fricke, R. (eds.) Catalog of Fishes electronic version (updated 11 Sep. 2011). http://research.calacademy.org/ichthyology/catalog/fishcatsearch.html

Greenwood, P.H. (1987) The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. *Bulletin of the British Museum (Natural History) Zoology*, 53, 3, 139–203.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4, 9.

Lévêque, C. (1997) *Biodiversity dynamics and conservation: the freshwater fish of tropical Africa.* XIII, Cambridge University Press, 438 pp.

Nelson, Harold D., Dobert, M., McLaughlin, J., Marvin, B. & Whitaker D.P. (1975) *Area Handbook for Guinea.* Foreign Area Studies. American University, Washington, DC, 386 pp.

Roberts, T.R. (1975) Geographical distribution of African freshwater fishes. *Zoological Journal of the Linnaean Society*, 57, 249–319.

Roberts, T.R. & Stewart, D.J. (1976) An ecological and systematic survey of fishes in the rapids of the lower Zaire or Congo River. *Bulletin of the Museum of Comparative Zoology*, 147, 6, 239–317, pls. 1–14.

Schliewen, U.K., Rassmann, K., Markmann, M., Markert, J., Kocher, T.D. & Tautz, D. (2001) Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham, Cameroon. *Molecular Ecology*, 10, 1471–1488.

Schwarzer, J., Misof, B., Tautz, D. & Schliewen, U.K. (2009) The root of the East African cichlid radiations. *BMC Evolutionary Biology*, 3, 186, 1–11.

Stiassny, M.L.J. (1991) Phylogenetic intrarelationships of the family Cichlidae: an overview. *In:* M.H.A. Keenleyside (ed.), *Cichlid Fishes: Behaviour, Ecology and Evolution*. Chapman and Hall, London, pp. 1–35.

Stiassny, M.L.J., Lamboj, A., De Weirdt, D. & Teugels, G.G. (2008) Cichlidae. *In:* Stiassny, M.L.J., Teugels, G.G & Hopkins C.D. (eds.) *The fresh and brackish water fishes of Lower Guinea, West-Central Africa* Volume 2. Coll. faune et flore tropicales 42. Institut de recherche de développement, Paris, France, Muséum national d'histoire naturelle, Paris, France and Musée royal de l'Afrique Central, Tervuren, Belgium, pp. 269–403.

Takahashi, T. (2003) Systematics of Tanganyikan cichlid fishes (Teleostei: Perciformes). *Ichthyological Research*, 50, 4, 367–382.

Teugels, G.G., Skelton, P.H., & Lévêque, C. (1987) A new species of *Amphilius* (Pisces, Amphiliidae) from the Konkouré Basin, Guinea, West Africa. *Cybium*, 11, 1, 93–101.

Teugels, G.G. & Thys van den Audenaerde, D.F.E. (1991) *Tilapia*. *In*: Daget et al. 1991. Check-list of the freshwater fishes of Africa. CLOFFA. Vol. 4, pp. 482–508.

Thieme, M.L. (2005) Ecoregion: Fouta Djalon *In*: Thieme, M.L., Abell, R., Stiassny, M.L.J., Skelton, P., Lehner, B., Dinerstein, E., Kamdem Toham, A., Burgess, N. & Olson, D. *Freshwater ecoregions of Africa and Madagascar. A conservation assessment.* Island Press, Washington, Covelo, London, pp. 255–156.

Thys van den Audenaerde, D.F.E. (1969a) An Annotated Bibliography of *Tilapia* (Pisces, Cichlidae). *Annales Museé Royal de L'Afrique Centrale, Documentation Zoologique*, 14, 406 pp.

Thys van den Audenaerde, D.F.E. (1969b) Description of *Tilapia louka* sp. nov. from Sierra Leone and some remarks on *Tilapia rheophila* Daget 1962 (Pisces, Cichlidae). *Revue de Zoologie et de Botanique Africaines*, 79, 1– 2, 82–96.

APPENDIX 1. Comparative material examined.

Tilapia baloni Trewavas & Stewart, 1975: ROM 28120 (3, paratypes, 105.0–107.5 mm SL), Zambia, Isenga Steam, Luongo River. ROM 28071 (3, paratypes, 100.4–112.8 mm SL), Zambia, Congo River. NRM 12331 (1, 34.4 mm SL), Zambia, Zaire River drainage, Kalungwishi River, Kundabwika Falls just above cataracts (09° 12′ 60″ S, 29° 18′ 00″ E). ***Tilapia bythobates*** Stiassny, Schliewen & Dominey, 1992: AMNH 98242 (holotype, 87.5 mm SL), Cameroon, Lake Bermin western (05°09′N 09°38′E). ***Tilapia deckerti*** Thys van den Audenaerde, 1967: ZMB 32754 (1, holotype, 102.2 mm SL), Cameroon, "Toter See b. Ossidinge" [Lake Ejagham]. ZSM 40077 (18, 60.0–88.9 mm SL), Cameroon, Lake Ejagham (05° 45′ 4.37 "N, 08° 59′ 0.92″ E). ZSM 40088 (1, 71.5 mm SL), collected with ZSM 40077. ZSM 40078 (6, 64.6–77.9 mm SL), collected with ZSM 40077. ***Tilapia ejagham*** Dunz & Schliewen, 2010: ZSM 40074 (1, holotype, 174.7 mm SL), Cameroon, Lake Ejagham (05° 45′ 4.37″ N, 08° 59′ 0.92″ E). ZSM 40075 (25, paratypes, 76.0–199.5 mm SL), collected with holotype. ZSM 40076 (23, 46.6–186.6 mm SL), collected with holotype. ***Tilapia flava*** Stiassny, Schliewen & Dominey, 1992: AMNH 98264 (1, holotype, 75.9 mm SL), Cameroon, Lake Bemin western (05° 09 ′N, 09° 38′ E). ***Tilapia fusiforme*** Dunz & Schliewen, 2010: ZSM 40082 (1, holotype, 44.9 mm SL), Cameroon, Lake Ejagham (05° 45′ 4.37″ N, 08° 59′ 0.92″ E). ZSM 40083 (15, paratypes, 44.9–59.5 mm SL), collected with holotype. ZSM 40086 (10, 41.4–52.7 mm SL), collected with holotype. 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]. ZSM 40085 (14, 41.6–60.8 mm SL), (non breeding "little-black"), collected with holotype. ZSM 40087 (15, 57.9–80.0 mm SL), (non breeding/breeding "large-black"), collected with holotype. ***Tilapia guinasana*** Trewavas, 1936: SAIAB 27334 (2, 69.0–79.6 mm SL), Namibia, Lake Guinas, Guinas Farm, Tsumeb district. SAIAB 35865 (1, 76.7 mm SL), Namibia, Lake Guinas. SAIAB 39126 (1, 101.4 mm SL), Namibia, Lake Guinas. SAIAB 35865 (1, 76.7 mm SL), Namibia, Lake Guinas. SAIAB 35863 (1, 73.7 mm SL), Namibia, Lake Guinas. SAIAB 41949 (2, 68.6–73.8 mm SL), Namibia, Lake Guinas. SAIAB 35864 (1, 84.2 mm SL) Namibia Lake Guinas. SAIAB 35859 (1, 136.0 mm SL), Namibia, Lake Guinas. SAIAB 27250 (1, 59.8 mm SL), Namibia, Lake Othikoto. SAIAB 45741 (1, 76.0 mm SL), Namibia, Lake Othikoto. SAIAB 25485 (1, 83.3 mm SL), Namibia, Lake Othikoto, NHF-151. SAIAB 25486 (1, 76.2 mm SL), Namibia, Lake Othikoto, NHF-153. ***Tilapia guineensis*** (Bleeker, 1862): BMNH 1849.10.9.15 (1, holotype, 149.7 mm SL), Ghana, Ashantee. SAIAB 44334 (1, 127.5 mm SL), Senegal, Geba System, Anambe Dam S2-F8. SAIAB 44326 (1, 109.5 mm SL), Senegal, Geba System, Anambe River Bridge S4-F19. ZSM 25740 (1, 142.6 mm SL), Senegal, Street from Bathurst to Dionloulon by Selety) Caramance Region. ZSM 23002 (1, 74.4 mm SL), Ghana, Busua, 25km W of Takoradi. ***Tilapia* sp. 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. ***Tilapia gutturosa*** Stiassny, Schliewen & Dominey, 1992: AMNH 98269 (1, holotype, 61.2 mm SL), Cameroon, Lake Bemin western (05° 09′ N, 09° 38′ E). ***Tilapia imbriferna*** Stiassny, Schliewen & Dominey, 1992: AMNH 98247 (1, holotype, 101.7 mm SL), Cameroon, Lake Bemin western (05° 09′ N, 09° 38′ E). ***Tilapia louka*** Thys, 1969: MRAC 92-59-P-3337-403 (3, 69.6–88.4 mm SL), Guinea, River Kola, affluent of the Kakrima (Konkouré basin) ± 2 km to Kaba (10° 57′ N, 12° 59′ W). MRAC 92-59-P-3404 (1, 91.0 mm SL), Guinea, Senanguiri, River Kokoulo, affluent of the Kakrima (Konkouré basin), at ferry near Niasso (10° 41′ N, 12° 30′ W). MRAC 92-59-P-3302-322 (4, 70.5–78.8 mm SL), Guinea, Siraya, River Kakrima (Konkouré basin) (10° 36′ N, 13° 00′ W). MRAC 92-59-P-3296-3301 (3, 68.6–140.4 mm SL), Guinea, Siraya, River Kakrima (Konkouré basin) (10° 36′ N, 13° 00′ W). MRAC 92-59-P-3455-632 (3, 96.2–110.4 mm SL), Guinea, Kogon, River Kogon (11° 22′ N, 13° 55′ W). MRAC 77-66-P-41-48 (3, 89.0–124.5 mm SL), Guinea, barrage at Kale next to River Samou, near Kindia (10° 05′ N, 12° 48′ W). MRAC 92-59-P-3323-3336 (2, 93.7–131.0 mm SL), Guinea, Djata, River Tondon, affluent of the Kakrima (Konkouré basin) (10° 38' N, 13° 00' W). MRAC 77-10-P-1 (1, 155.7 mm SL), Guinea, River Bandi, Kolenté basin, route Kankasili-Sougeta (10° 11' N, 12° 28' W). MRAC 171083-84 1 (1, 141.5 mm SL), Liberia, Mano, River Mano (07° 30' N, 10° 57' W). MRAC 170873-76 (3, 81.9–94.9 mm SL), Sierra Leone, Pendehun, River Moa, 3 km upstream of bridge (07° 51' N, 11° 09' W). ***Tilapia margaritacea*** Boulenger, 1916: BMNH 1914.5.27.12-15 (4, syntypes, 62.9–128.3 mm SL), Cameroon, Nyong River at Akonolinga. BMNH 1959.8.12.10-13 (4, 86.6–92.3 mm SL), Cameroon, Nyong River. ***Tilapia nigrans*** Dunz & Schliewen, 2010: ZSM 40079 (1, holotype, 117.5 mm SL), Cameroon, Lake Ejagham (05° 45' 4.37' 'N, 08° 59' 0.92" E). ZSM 40080 (17, paratypes, 105.5–151.0 mm SL), collected with holotype. 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]. ***Tilapia pra*** Dunz & Schliewen 2010: ZSM 36123 (1, holotype, 83.5 mm SL), Ghana, Ashanti Region, Anum River, tributary to Pra, at Anumso village (06° 25' 44" N, 01° 17' 59" W). ZSM 36116 (1, paratype, 84.2 mm SL). ZSM 36117 (1, paratype, 110.1 mm SL). ZSM 36118 (1, paratype, 73.1 mm SL). ZSM 36119 (1, paratype, 76.6 mm SL). ZSM 36120 (1, paratype, 77.7 mm SL). ZSM 36121 (1, paratype, 73.7 mm SL). ZSM 36122 (1, paratype, 76.1 mm SL). ZSM 36124 (1, paratype, 81.1 mm SL). ZSM 36125 (1, paratype, 79.1 mm SL), all collected with holotype. ZSM 36149 (2 (now 1), paratype, 62.6 mm SL), Ghana, Ashanti Region, Oda River, tributary to Pra, floodplain and small affluent left to road entrance at bridge on road Bekwai-Awiankwata (06° 27' N, 01° 37' W). AMNH 250601 (1 ex ZSM 36149, paratype, 57.7 mm SL), Ghana, Ashanti Region, Oda River, tributary to Pra, floodplain and small affluent left to road entrance at bridge on road Bekwai-Awiankwata (06° 27' N, 01° 37' W). ZSM 39005 (3 (now 2), paratypes, 40.3–58.8 mm SL), Ghana, Nyelei, tributary to Ankobra, near Akropong at the new bridge (05° 05' 06" N, 02° 17' 13" W). AMNH 250602 (1 ex ZSM 39005, paratype, 54.7 mm SL), Ghana, Nyelei, tributary to Ankobra, near Akropong at the new bridge (05° 05' 06" N, 02° 17' 13" W). ZSM 39000 (3, paratypes, 48.7–58.4 mm SL), Ghana, Draw River at new bridge (05° 10' 04" N, 02° 15' 20" W). ZSM 39001 (1, paratype, 108.2 mm SL), Ghana, Tano at Mempansem (05° 22' 12" N, 02° 39' 36" W). MRAC 87-18-P-5204-240 (3, paratypes, 95.7–103.4 mm SL), Ghana, Birim River at Anyinam (06° 22' 48" N, 00° 33' 00" W). MRAC 87-18-P-5189-203 (1, paratype, 91.0 mm SL), Ghana, Pra River at Prasu (05° 55' 48" N, 01° 22' 12" W). MRAC 87-18-P-5248-314 (1, paratype, 66.7 mm SL), Ghana, Pra River near Nkawkaw (06° 36 '00" N, 00° 54' 00" W). MRAC 79-36-P-70-84 (5, paratypes, 73.9–126.9 mm SL), Cote d'Ivoire, Ayamé I, dam, River Bia (05° 36' 00" N, 03° 10' 48" W). MRAC 86-18-P-1948-951 (1, paratype, 57.6 mm SL), Cote d'Ivoire, Ayamé, River Bia (05° 37' 12" N, 03° 10' 48" W). ***Tilapia rendalli*** (Boulenger, 1897): SAIAB 71029 (1, 60.9 mm SL), Zambia, Chirumba River (13° 24' 47" S, 24° 22' 15" E). SAIAB 71789 (1, 73.5 mm SL), Zambia, Matondo Lagoon, upper Zambezi, Branch Zambezi UZB 34 (15° 20' 32" S, 22° 56' 49" E). SAIAB 71905 (1, 84.9 mm SL), Zambia, Kataba River main road, upper Zambezi UZB 42 (15° 34' 02" S, 23° 17' 00' 'E). SAIAB 72574 (1, 74.3 mm SL), Zambia, Mutemwa, upper Zambezi UZC 05 (17° 12' 00" S, 24° 04' 00" E). SAIAB 72710 (1, 68.9 mm SL), Zambia, Simvula Lagoon, Zambezi River UZC 18 (16° 07' 25' 'S, 23° 17' 17' 'E). SAIAB 72668 (1, 70.8 mm SL), Zambia, Sioma Falls, River Zambezi UZC 13 (16° 39' 27" S, 23° 34' 20" E). SAIAB 71784 (1, 74.4 mm SL), Zambia, Luanginga River bank, UZB 33 (15° 11' 44 "S, 22° 54' 21" E). SAIAB 71341 (1, 68.5 mm SL), Zambia, side channel upstream from Kalabo Ferry UZA 32 (15° 11' 00" S, 22° 56' 23" E). SAIAB 73146 (1, 77.0 mm SL), Zambia, Near Lealui, Kanokana River UZC 47 (15° 11' 31" S, 22° 27' 14" E). SAIAB 67718 (1, 98.6 mm SL), Mozambique, Manica, Buzi River, Revue River at main road bridge (19° 45' 54" S, 39° 56' 50" E). SAIAB 59501 (1, 60.8 mm SL), Namibia, Kunene River, 1km above Epopa Falls K 16 (16° 59' S, 13° 15' E). SAIAB 78750 (1, 74.6 mm SL), Namibia, Kunene River, Hippo pool below Ruacana Waterfall ES 06 A 49 (17° 24' 24" S, 14° 13' 01" E). SAIAB 63168 (1, 59.0 mm SL), Namibia, Oshana, Ogongo hole near canal near Ogongo (17°40'S 15°18'E). SAIAB 45760 (1, 91.3 mm SL), South Africa, Barberton, Hectorspruit TM 9325. SAIAB 85512 (2, 75.4-96.1 mm SL), Angola, Malanje, Russian Fishing Camp, Kwanza) Posto 5 ES 07 D22 (09° 48' 23" S, 15° 24' 30" E). ***Tilapia ruweti*** Poll & Thys van den Audenaerde, 1965: SAIAB 81505 (1, 62.8 mm SL), Democratic Republic of the Congo, Katanga, River Bona near Lenge Village RBDRC 08-13, (10° 36' 34" S, 25° 49 '15" E). SAIAB 77224 (1, 67.5 mm SL), Zambia, Luapula, Kalungwishi, above Lumangwe Falls on Kalungwishi River JPF 05-039 (09° 32' 34" S, 29° 23' 15" E). SAIAB 71712 (1, 48.1 mm SL), Zambia, Kasima swamp Lagoon, upper Zambezi, UZB 25b (15°14'40"S 23°11'48"E). SAIAB 68652 (1, 65.7 mm SL), Botswana, Ngamiland, Moremi Wildlife Park, River Maunachira, Paradise Lagoon, Hippo pool, Makoro channel Xa 23 E (19° 11' 57" S, 23° 27' 36" E). SAIAB 68650 (1, 58.8 mm SL), Botswana, Ngamiland, Moremi Wildlife Park, River Maunachira, Paradise Lagoon, Hippo pool, Makoro channel Xa 23 (19° 12' 09" S, 23° 27' 39" E). SAIAB 18838 (1, 71.6 mm SL), Botswana, Nxamaseri "cow dung" Molopo pool OK 83-47. SAIAB 28705 (1, 59.3 mm SL), Botswana, Matlapaneng Bridge, Thamalakane River, Okavango Delta OK 85-23. SAIAB 29567 (1, 69.4 mm SL), Botswana, Kwai Floodplain, isolated Lagoon, Moremi Game Reserve, Okavango Delta OK 86-45. SAIAB 63202 (1, 60.1 mm SL), Botswana, Thamalakane River, Bridge of Maun (19° 59' 27" S, 23° 25' 30" E). SAIAB 29474 (1, 65.6 mm SL), Botswana, Kwai Floodplain, isolated Lagoon, Moremi Game Reserve, Okavango Delta OK 86-7. SAIAB 29675 (1, 68.0 mm SL), Botswana, Maxegana Floodplain, Moremi Game Reserve Okavango Delta OK 86-73. ROM 28034 (1, 61.4 mm SL), Zambia, Luongo River. ***Tilapia snyderae*** Stiassny, Schliewen & Dominey, 1992: AMNH 98259 (1, holotype, 38.8 mm SL), Cameroon, Lake Bermin western (05° 09' N, 09° 38' E). ***Tilapia spongotroktis*** Stiassny, Schliewen & Dominey, 1992: AMNH 98258 (1, holotype, 122.0 mm SL), Cameroon, Lake Bermin western (05° 09' N, 09° 38' E). ***Tilapia zillii*** (Gervais, 1848): SAIAB 26020 (1, 42.2 mm SL), Algeria, Chouca Village (53° 26' N, 05° 57' E). ***Tilapia* indet.**: MRAC A8-020-P-0963 (1, 107.1 mm SL), Republic of the Congo, River Lefini, about 600m to camp Oteni (02° 49' 29" S, 15° 47' 31" E). MRAC A1-034-P-0001 (1, 98.8 mm SL), Algeria, Tassili, Sahara. ZSM 35146 (2, 118.9–128.0 mm SL), Sudan, White Nile River at Kosti, purchased at boat landing site, White Nile Province (13° 10' 17.2" N, 32° 40' 07.0" E).

6. Paper IV

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Congolapia, a new cichlid genus from the central Congo basin (Perciformes: Cichlidae)

Andreas R. Dunz*, Emmanuel Vreven,*** and Ulrich K. Schliewen***

Congolapia, new genus, is described, with *Tilapia bilineata* as type species. The new genus contains three species, two of which were hitherto included in the genus *Tilapia (C. bilineata, C. crassa)* and *C. louna*, new species. *Congolapia* is diagnosed by morphological, colouration and molecular characters. Diagnostically important is the combination of a densely scaled caudal fin and spatulate teeth in upper and lower jaw. *Congolapia louna* is known only from five specimens from River Louna, a tributary of River Lefini, an affluent of the Congo River, whereas the other two species are widely distributed in the central Congo basin. *Congolapia bilineata* differs from *C. crassa* and *C. louna* in the number of scale rows separating the upper lateral line from the last dorsal spine, i. e. by one complete scale row and one scale row with smaller dorso-ventrally compressed scales vs. two complete scales rows. *Congolapia louna* differs from *C. crassa* and *C. bilineata* by a higher number of gill rakers on the first ceratobranchial (13 vs. 8-11 in *C. crassa* and 8-10 in *C. bilineata*).

Un nouveau genre de cichlidé, *Congolapia*, est décrit, avec *Tilapia bilineata* comme espèce type. Le nouveau genre contient trois espèces. Deux d'entre elles *(C. bilineata, C. crassa)* étaient jusqu'à présent inclues dans le genre *Tilapia*, la troisième *C. louna* est une espèce nouvelle. *Congolapia* est diagnostiqué tant par des caractères moléculaires que, morphologiques et de coloration. La combinaison nageoire caudale densément écaillée et dents spatulées aux mâchoires supérieure et inférieure est importante pour le diagnostique. *Congolapia louna* n'est connue que de cinq spécimens de la Louna, affluent de la Léfini, elle-même affluent du fleuve Congo alors que les deux autres espèces sont largement distribuées dans le bassin central du Congo. *Congolapia bilineata* diffère de *C. crassa* et *C. louna* par le nombre de rangées d'écailles séparant la ligne latérale supérieure de la dernière épine dorsale, soit une rangée complète d'écailles et une rangée d'écailles plus petites compressées dorso-ventralement vs. deux rangées complètes d'écailles. *Congolapia louna* diffère de *C. crassa* et *C. bilineata* par un nombre plus élevé de branchiospines sur la partie inférieure (cératobranchial) du 1^er^ arc branchial (13 vs. 8-11 chez *C. crassa* et 8-10 chez *C. bilineata*).

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Introduction

Tilapia Smith, 1840 is a large genus comprised of substrate-brooding cichlid fishes (Perciformes: Cichlidae) inhabiting African rivers and lakes, and the Jordan valley. After partial revisions by Thys van den Audenaerde (summarized in Thys van den Audenaerde 1969) morphological and molecular evidence for the monophyly of *Tilapia* is still lacking (Stiassny 1992). Indeed, recent molecular phylogenetic work strongly suggests that *Tilapia* is paraphyletic (Klett & Meyer 2002, Schliewen & Stiassny 2003, Schwarzer et al. 2009), and that several subgenera described by Regan (1920) and Thys van den Audenaerde (1969) should probably be raised to generic rank.

The description of *T. bilineata* Pellegrin, 1900 was based on two syntypes, whereas the description of *T. crassa* Pellegrin, 1903 was based on the holotype only, all three specimens collected during the expedition of Savorgnan de Brazza, 1886. Both were described from "Diélé [Ndélé], Congo Français", a locality situated on the upper Alima River, a right bank tributary of the central Congo, draining the Batéké Plateau in the Republic of Congo. Pellegrin (1903) differentiated *T. crassa* from *T. bilineata* on the basis of its stockier body, the shorter snout, the larger width of the interorbital space, longer dorsal spines and a different colouration. In his revision of *Tilapia* of the Congo basin, Thys van den Audenaerde (1964) concluded that *T. crassa* is most likely a synonym of *T. bilineata*, but wrote that a larger number of specimens would be needed to finally determine the status of *T. crassa* (Thys van den Audenaerde, 1964: 37). Indeed, when discussing the nominal *Tilapia* taxa, Thys van den Audenaerde (1964: 37) stated that he had investigated altogether only six adult specimens (all adult *T. bilineata* and *T. crassa* specimens available at that time). These were both syntypes of *T. bilineata* and [according to Thys van den Audenaerde's (1964: 79–81) species account] two additional specimens from Befori at the Maringa River, DRC (MRAC 87937–938), one (all other are juveniles) from Bokuma at the Ruki River, DRC (MRAC 96726–736), and the holotype of *T. crassa*. However, in the *T. bilineata* account Thys van den Audenaerde (1964: 79) placed *T. crassa* formally but without further comments in the synonymy of *T. bilineata*. Later, Thys van den Audenaerde (1969) included *T. bilineata* in a new subgenus, *Pelmatolapia* (type species: *Tilapia mariae* Boulenger, 1899). Additional members of the subgenus were *T. eisentrauti*, *T. cabrae* and *T. brevimanus*. Thys van den Audenaerde based this subgeneric grouping primarily on a shared dentition character: outer teeth bicuspid and spatulate (with slender shafts broadening gradually near the cusps). The other three subgenera in his Section I are *Tilapia* Smith, 1840 (type species *T. sparrmanii* Smith, 1840); the new subgenus *Trewavasia* (type species *T. guinasana* Trewavas, 1936; preoccupied, now *Neotrewavasia* Ufermann, 2001) and *Pelmatochromis* Steindachner, 1895 (type species *T. buettikoferi* Steindachner, 1895). No member of those three subgenera share the character "outer teeth bicuspid and spatulate."

Recently, new specimens that resemble *T. bilineata* were collected in the central Congo basin, in the Lefini, Sangha and Luilaka drainages and in Pool Malebo. Two of these were used in a molecular phylogenetic study (Schwarzer et al., 2009), which revealed: (1) a deep split between the two specimens, one from the Lefini and one from the Luilaka; and (2) a phylogenetic placement conflicting with Thys van den Audenaerde's (1969) subgeneric placement in *Pelmatolapia*. This analysis placed the specimens of the *T. bilineata*-complex as sister-group to *Tilapia* sensu stricto, comprising *T. sparrmanii*, *T. ruweti*, and *T. guinasana*.

These results in combination with additional new specimens that resemble *T. bilineata* available at the MRAC and AMNH prompted a reassessment of the species level diversity within *T. bilineata*, as well as a critical comparison with all nominal *Tilapia* taxa and a set of phylogenetically closely related riverine taxa of the genera *Steatocranus* Boulenger, 1899 and *Chilochromis* Boulenger, 1902, currently placed in a monophyletic clade referred to as "austrotilapiines" (Schwarzer et al. 2009, Dunz & Schliewen 2010). The morphological and molecular comparisons resulted in the identification of three different species within what was formerly referred to as *T. bilineata*, here placed in the new genus *Congolapia* (and referred to as such hereafter) with a redescription of *C. bilineata*, resurrection and redescription of *C. crassa*, and description of a new species.

Material and methods

Material. Examined specimens (n = 822) are deposited in MNHN, Muséum National d'Histoire Naturelle, Paris; NHM, Natural History Museum, London; NMW, Naturhistorisches Museum, Wien; MRAC, Musée Royal de l'Afrique Centrale, Tervuren; ROM, Royal Ontario Museum, Ontario; SAIAB/RUSI, South African Institute for Aquatic Biodiversity, Grahamstown; ZMB, Zoologisches Museum, Berlin; and ZSM, Zoologische Staatssammlung, München. Specimens of all *Tilapia* sensu lato species were studied including type specimens of all taxa except for *T. buttikoferi* (Hubrecht, 1881), *T. camerunensis* Lönnberg, 1903 and *T. zillii* (Gervais, 1848), because type specimens were unavailable or, in the case of *T. zillii* lost; however, topotypical specimens were included instead. For a full list of examined specimens see Dunz & Schliewen (2010) and Appendix 1 below.

Details for some of the localities where *C. bilineata* and *C. crassa* were caught are based on those obtained in 12 ecological gill-net sampling stations selected on the Léfini River basin within the PhD. research of Armel Ibala Zamba (see Ibala Zamba, 2010). In addition all locality data of the examined specimens have been translated to English.

Morphometry and Principal Component Analysis. Measurements, meristics, application of morphological characters, and statistical analysis follow 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. 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 available *T. bilineata* specimens except the holotype of *T. crassa*, which is partially damaged and could not be scored for several diagnostic characters separating *C. louna* from *T. crassa* and *T. bilineata*. In a second step the characters, which were affected by the damaged specimen were excluded from the analysis allowing for the inclusion of the holotype of *T. crassa*. All morphometric measurements used in PCAs as well as the number of gill rakers on the first gill-arch, were tested for significant differences between species using the non-parametric Mann-Whitney-U-Test in PAST 1.98 (Hammer et al., 2001). The chosen significance levels ($p < 0.05$) were Bonferroni-corrected for multiple pairwise comparisons.

Laboratory methods and DNA based phylogenetics. Genomic DNA was extracted from fin samples or muscle tissue using the NucleoSpin® Tissue kit (Macherey-Nagel) following the standard protocol provided by the manufacturer. A region spanning the complete mitochondrial ND2 gene was amplified using primers ND2Met 5'-CATACCCCAAACATGTTGGT-3' and ND2Trp 5'-GTSGSTTTTCACTCCCGCTTA-3' (Kocher et al. 1995). Amplifications were performed following Schwarzer et al. 2009. For problematic samples, two internal primers were designed 10-ND2B" 5'-TGGYYTARYCCGCCTCA-3', and 4-ND2.2A 5'-CTGACAAAARCTYGCYCCCTT-3'.

To establish a phylogenetic hypothesis for the three species in focus and to test for species specificity of mtDNA haplotypes, mitochondrial DNA-sequence data were edited and aligned using BioEdit v.7.05.3 (Hall, 1999) with the implemented algorithm ClustalW (default settings) for a preliminary alignment and afterwards realigned with Muscle v.3.6 (Edgar, 2004). In addition, as a final quality control, sequences with missing nucleotides were checked by eye. All parameters (Γ-model of rate heterogeneity, ML estimate of α-parameter) were estimated individually for the partitioned dataset in 1st, 2nd and 3rd codon positions. A Maximum Likelihood (ML) approach was used to infer a phylogenetic hypothesis using RAxML v.7.0.3, which first performed a ML search with the GTR+Γ model (Stamatakis, 2006). The model was chosen with the Bayes Factor Test conducted in the program MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001). Node support was identified using 200 bootstrap replicates. The required number of bootstrap replicates was calculated with the autoFC function of raxmlGUI 0.93 (Silvestro & Michalak, 2010). Bayesian inference analyses were performed using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) with four parallel runs each over 10^6 generations starting with random trees and sampling of trees every 1000 generations. To ensure convergence the first 10 % generations of each run were treated as burn-in and excluded. The remaining trees from all Bayesian analyses were used to build a 50 % majority rule consensus tree.

Based on the results of Schwarzer et al. (2009) *T. brevimanus* was used as a distant outgroup, and *Steatocranus tinanti*, *S. gibbiceps*, *T. sparrmanii*, *T. ruweti*, *T. guinasana* and *Chilochromis duponti* as closely related outgroups. See Appendix 2 for list

Table 1. Nucleotide mutations of *Congolapia louna* leading to an amino acid change on mitochondrial locus ND2, using dataset as in Figure 1. Sequenced species refers to all other sequenced species in this analysis.

position at ND2	nucleotid		triplet		aminoacid	
	C. louna	sequenced species	*C. louna*	sequenced species	*C. louna*	sequenced species
427	A	C	**A**TT	**C**TT	Isoleucine	Leucine
448	C	T	**C**CG	**T**CA(**T**CG)	Proline	Threonine
487	T	C or A	CT**T**	CT**C**, CT**A**	Leucine	Isoleucine (CTC), Valine (CTA)
616	G	A	**G**CC	**A**CC, **A**TT	Alanine	Threonine (ACC), Isoleucine (ATT)
635	C	T	T**C**C	T**T**C, C**T**C	Serine	Phenylalanine (TTC), Leucine (CTC)
706	A	G	**A**CC	**G**CC (**G**CT)	Threonine	Alanine
993	G	A	AT**G**	AT**A**, TT**A**, GC**A**	Methionine	Isoleucine (ATA), Leucine (TTA), Alanine (GCA)

Table 2. Factor Loadings of PC I–III for Fig. 2a and b. PCA based on 24 log transformed measurements. Highest loadings for PC II and PC III indicated in boldface. The total number of *Congolapia* specimens in this plot is 63 (a) or 64 (b).

	2a			2b		
	PC I	PC II	PC III	PC I	PC II	PC III
Standard length	–0.180	0.098	–0.006	–0.192	0.076	–0.009
Head length	–0.192	0.002	0.028	–0.203	–0.043	0.040
Interorbital width	–0.239	–0.228	–0.018	–0.253	**–0.337**	–0.042
Preorbital width	–0.225	–0.076	0.000	–0.239	–0.148	0.035
Horizontal eye length	–0.139	–0.117	–0.083	–0.149	–0.174	–0.074
Snout length	–0.217	0.082	0.137	–0.229	0.002	0.156
Internostril distance	–0.215	0.069	0.165	–0.229	0.018	0.184
Cheek depth	–0.239	0.038	–0.118	–0.254	–0.006	–0.081
Upper lip length	–0.224	**0.321**	0.100	–0.239	**0.364**	0.130
Lower lip length	–0.227	**0.305**	0.083	–0.243	**0.346**	0.121
Lower lip width	–0.249	0.200	0.233	–0.265	0.152	**0.293**
Lower jaw length	–0.205	0.213	0.063	–0.219	0.224	0.105
Predorsal distance	–0.187	0.010	0.049	–0.198	–0.044	0.053
Dorsal-fin length	–0.186	0.007	–0.057	–0.198	–0.022	–0.051
Anal-fin length	–0.193	–0.047	0.107	–0.203	–0.103	0.136
Anal spine length (third)	–0.180	**–0.346**	0.035	–0.191	**–0.444**	–0.026
Caudal peduncle depth	–0.197	–0.082	–0.073	–0.208	–0.138	–0.033
Caudal peduncle length	–0.167	0.268	–0.045	–0.179	0.306	–0.056
Body depth	–0.218	**–0.274**	–0.075	–0.231	**–0.365**	–0.051
Preanal length	–0.188	0.065	–0.050	–0.200	0.037	–0.044
Distance anus–anal fin	–0.212	0.236	**–0.672**	–0.225	0.208	**–0.874**
Length last dorsal spine	–0.202	**–0.319**	**0.442**			
Pectoral-fin length	–0.184	–0.118	0.104			
Pelvic-fin length	–0.200	**–0.416**	**–0.407**			
Eigenvalue	0.407	0.006	0.003	0.364	0.005	0.003
% variance	95.57	1.49	0.80	96.35	1.20	0.69

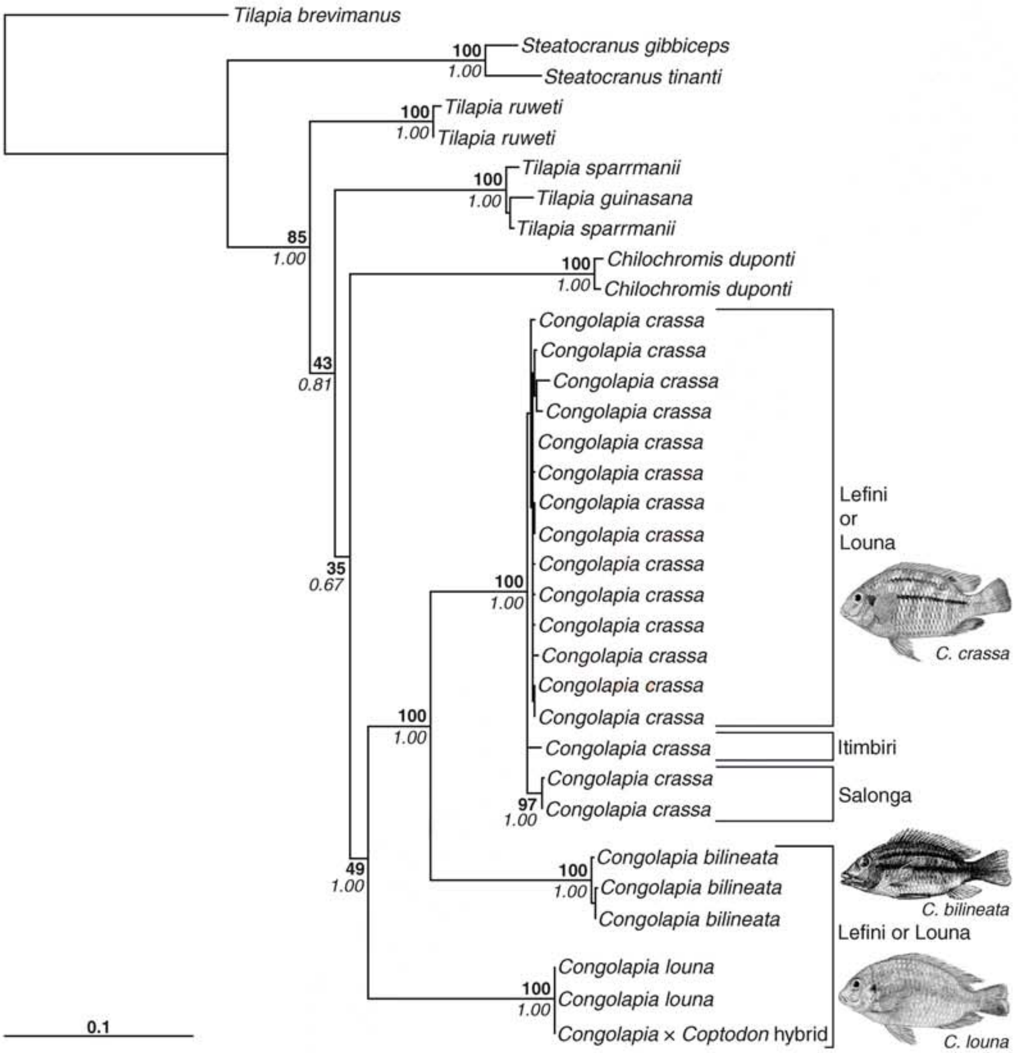

Fig. 1. Consensus tree of *Congolapia* and related genera based on 1008 bp of mitochondrial ND2 locus. Bold regular numbers at nodes refer to bootstrap values (200 replicates) of the ML run, italic numbers refer to Bayesian posterior probabilities (BPP). Different shadings of grey show the different sample location. Figures of *Congolapia crassa* and *C. louna* by R. Kühbandner and of *C. bilineata* from Boulenger (1915: 205, fig. 130).

of GenBank numbers and DNA voucher information.

Results

DNA based phylogenetic results. Preliminary results of Schwarzer et al. 2009 showed *T. bilineata* as sister-group to *Tilapia* sensu stricto and with a deep split between both *T. bilineata* specimens included, one from the Lefini River and the other from the Luilaka River. Here, additional analyses were conducted using a dataset of 33 specimens, i.e. 23 specimens representing the three species of *T. bilineata*-complex, and six species represented by nine specimens of closely related outgroup taxa as well as one specimen/species of a distant outgroup. For each taxon 1008 bp DNA of the mitochondrial ND2 locus were sequenced. Empirical base frequencies for each codon position are: 1st codon position, A = 0.290, C = 0.345, G = 0.198, T = 0.165; 2nd codon position, A = 0.154, C = 0.357, G = 0.114, T = 0.373; 3rd codon position, A = 0.303, C = 0.380, G = 0.052, T = 0.263. The Bayes factor test identified the GTR+Γ model as the best model for all partitions. All seven terminal groups of the ML tree (Fig. 1), obtained from RAxML are highly supported with a bootstrap value of 100. The best supported topology was *T. brevimanus* as outgroup, *Steatocranus* represented by *S. gibbiceps* and *S. tinanti* sister-group to all remaining taxa, *Tilapia* sensu stricto sister-group to *Chilochromis* and *Congolapia*, *Chilochromis* is the sister-group to *Congolapia*. *Congolapia louna* is the genetically distant sister-taxon to the *T. bilineata* and *T. crassa* clade. *Congolapia louna* possesses seven autapomorphic mutations on the ND2 gene, one of which causes an amino acid change (see Table 1). *Congolapia bilineata* differs from *C. crassa* genetically in 95 single mutations at mitochondrial locus ND2 (data not shown).

Table 3. Pairwise Mann-Whitney-U-Test comparisons, Bonferroni-corrected, significant values ($p < 0.05$) indicated in boldface (*Congolapia louna*, n = 5; *C. bilineata*, n = 19; *C. crassa*, n = 41).

	C. crassa / C. bilineata	*C. crassa / C. louna*	*C. bilineata / C. louna*
Standard Length	0.982	1	1
Head length	0.478	1	1
Interorbital width	0.169	1	1
Preorbital width	0.331	1	1
Horizontal eye length	0.320	1	1
Snout length	0.911	1	1
Internostril distance	0.642	1	1
Cheek depth	0.876	0.944	1
Upper lip length	1	1	1
Lower lip length	1	1	1
Lower lip width	0.922	1	1
Lower jaw length	1	1	1
Predorsal distance	0.606	1	1
Dorsal-fin length	0.564	1	1
Length last dorsal spine	**0.047**	1	0.504
Anal-fin length	0.435	1	0.615
Anal spine length (third)	0.108	0.490	1
Pelvic-fin length	**0.020**	0.170	1
Pectoral-fin length	0.284	1	1
Caudal peduncle depth	0.384	1	1
Caudal peduncle length	1	1	1
Body depth	0.126	0.995	1
Preanal length	0.821	1	1
Distance anus–anal fin	1	0.822	1
Number of gill rakers on lower part of first gill-arch	0.589	**0.001**	**0.003**

Morphology and morphometric results. Since *C. louna* is separable from *T. crassa* by a higher number of gill rakers on the first ceratobranchial 13 vs. 8–11, this second ordination was used only to assess which specimens cluster with the holotype of *T. crassa*. The smaller paralectotype of *T. bilineata* (MNHN 1886-0446) was excluded from all PCA analyses because its very poor condition did not allow all measurements and counts to be taken. A first PCA based on 24 morphometric measurements in all *T. bilineata* examined revealed three non-overlapping clusters (Fig. 2a). The highest factor loadings on PC II are for the following characters: pelvic-fin length and length of last dorsal spine (Table 2a). Both character distributions are overlapping for *T. bilineata* and *T. crassa* (Tables 4–5) but are significantly different after Bonferroni-corrected pairwise Mann-Whitney-U-test comparisons (Table 3). The characters snout length and anal-fin base length separate *C. louna* from both *C. bilineata* as well as *C. crassa* on PC III with minimal overlap. The highest loadings on PC III, are: distance from anus to anal-fin base and length of last dorsal spine. Therefore, a second PCA (Fig. 2b) was conducted without the following measurements that could not be obtained on the holotype of *T. crassa*: pelvic-fin length, pectoral-fin length and length of last dorsal spine. Even with this reduced morphometric character set, *T. bilineata*, on the positive side of PC II values, and *T. crassa*, situated on the negative side of PC II, are fully separated, but *C. louna* is not fully separated from *T. crassa* anymore. The highest factor loadings on PC II are: anal spine length and body depth (Table 2b). In combination with PC II, PC III provides a further separation between the three species. Indeed, *T. bilineata* and *T. crassa* exhibit almost completely separate values for the length of the last anal spine (10.5–14.9 % SL vs. 13.4–17.6) and body depth (32.2–40.5 % SL vs. 40.4–48.4). The body depth of *C. louna* is 37.4–42.1 % SL, which is intermediate between the two other species. Comparability of size classes was tested with a pairwise Mann-Whitney-U-Test (Table 3).

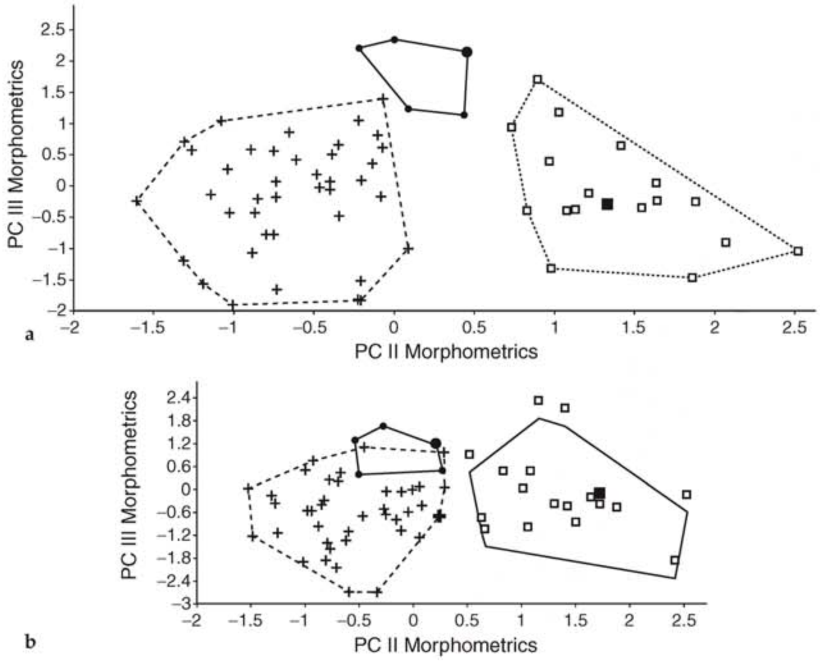

Fig. 2. Scatterplot of PCA scores of Principal Component II vs. Principal Component III of measurements of *Congolapia*; visualized as convex hulls. +: *C. crassa* (n = 40); ◻: *C. bilineata* (n = 18); •: *C. louna* (n = 5). Bold symbols refer to type specimens. Without (**a**) and with (**b**) holotype of *C. crassa*.

Congolapia, new genus

Type species. *Tilapia bilineata*, Pellgrin, 1900.

Diagnosis. *Congolapia* differs by the following characters: lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel shorter than (or just as long as) the toothed area of the jaw; bicuspid or tricuspid (rarely quadricuspid) posterior pharyngeal teeth; the first gill arch bears 11–17 rakers; two lateral lines; cycloid scales; 21–30 scales in the longitudinal row; upper and lower outer teeth rows bicuspid in both jaws, inner rows with smaller tricuspid teeth in both jaws; isognathous jaws; spatulate teeth; a densely scaled caudal fin; 16–17 dorsal spines; backward slanted, unbranched (not Y-shaped) vertical bars on flanks (when distinct); pointed pelvic fin; no hump on forehead, no expanded tissue on the roof of the pharynx ("visor-like hanging pad" sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine.

Species of *Congolapia* are further distinguished from all valid species of *Tilapia* by the densely scaled caudal fin and spatulate teeth. The presence of a densely scaled caudal fin is only shared with *T. tholloni*, *T. congica* and *T. nyongana* (only in adults), but they have stout, non-spatulate teeth.

Etymology. *Congolapia* is a contraction of the words Congo and *Tilapia*. All species of *Congolapia* are only known from the central Congo basin. Gender Feminine (as *Tilapia*).

Included species. *Congolapia bilineata* (Pellegrin, 1900); *C. crassa* (Pellegrin, 1903) and *C. louna*.

Congolapia bilineata (Pellegrin, 1900)
(Figs. 3–6)

Specimens examined. MNHN 1886-0445, lectotype, 150.4 mm SL; MNHN 1886-0446, 1 paralectotype, 90.8 mm SL; "Diélé, Mission de l'Ouest africain (M. de Brazza)" [Central African Republic: Ndele, Alima River, upper Congo; P. Savorgnan de Brazza, date not available].

Fig. 3. *Congolapia bilineata*, MNHN 1886-0445, holotype, 150.4 mm SL; Central African Republic: Alima River.

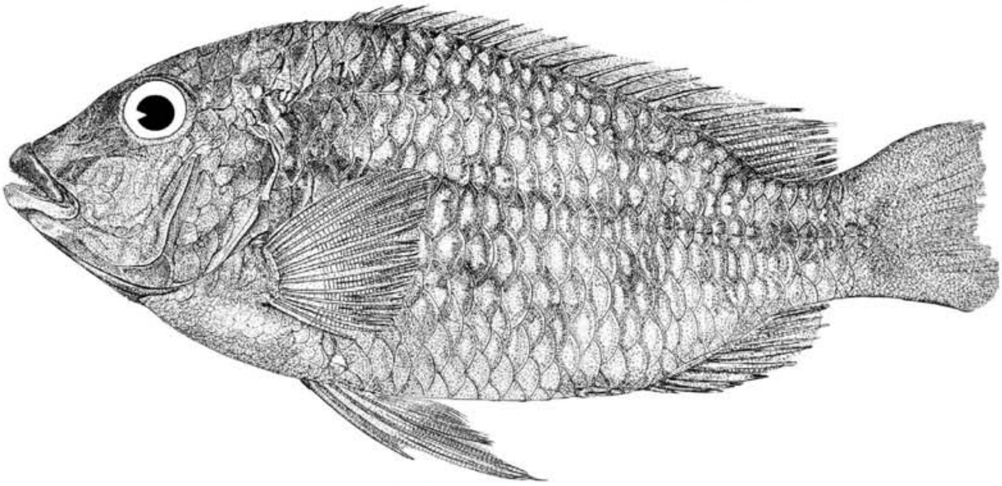

Fig. 4. *Congolapia bilineata*, MRAC A7-031-P-1922–1923, 175.4 mm SL; Republic of the Congo: Lefini River (drawing by R. Kühbandner).

Republic of the Congo: MRAC A7-31-P-57, 1, 167.1 mm SL; River Lefini, about 600m to camp Oteni, 2°54'11"S 15°59'07"E; E. Vreven & A. Ibala Zamba, 20 May 2007. – MRAC A7-31-P-58, 1, 139.3 mm SL; Lefini River, confluent Lefini-Nambouli, left bank, 2°53' 46"S 15°06'51"E; A. Ibala Zamba & A. Ngoma Moutsinga, 22 Apr 2007. – MRAC A7-31-P-61, 1, 99.1 mm SL; Lefini River, confluent Lefini-Nambouli, left bank, 2°53'46"S 15°06'51"E; A. Ibala Zamba, E. Vreven & A. Ngoma Moutsinga, 28 Sep 2007. – MRAC A7-31-P-71, 1, 119.2 mm SL; Lefini River, confluent Lefini-Nambouli, 2°53'46"S 15°06'51"E; A. Ibala Zamba, A. Ngoma Moutsinga & E. Vreven, 29 Sep 2007. – MRAC A7-031-P-1922–1923, 2, 70.0–175.4 mm SL; Lefini River, confluent Lefini-Nambouli, left bank, 2°53'46"S 15°06'51"E; A. Ibala Zamba, E. Vreven & A. Ngoma Moutsinga, 12 Aug 2008. – MRAC A8-020-P-0943, 1, 58.1 mm SL; Lefini River, about 3 km upstream of confluent Lefini-Loubilika, right bank, 3°01'11"S 15°14'25"E; A. Ibala Zamba, 30 Jul 2008. – MRAC A8-020-P-0944, 1, 68.6 mm SL; Lefini River, about 3 km upstream of Mount Epope, 3°01'58"S 15°23'42"E; E. Vreven & A. Ibala Zamba, 28 Aug 2008. – MRAC A8-020-P-0945–0949, 5, 21.5–157.3 mm SL; Louna River, affluent of Lefini River, backwater, downstream of the rapids, right bank, 3°14'57"S 15°24'55"E; E. Vreven & A. Ibala Zamba, 1 Sep 2008. – MRAC A8-020-P-0958, 1, 73.4 mm SL; Lefini River, about 700 m to camp Malina, right bank, 2°53'03"S 15°10'47"E; E. Vreven & A. Ibala Zamba, 23 Aug 2008. – MRAC A8-020-P-0961, 1, 102.5 mm SL; Louna River, affluent of Lefini River, ±321 m downstream of inlet of islet Abio 2, right bank, 2, 3°07'58"S 15°31'21"E; E. Vreven & A. Ibala Zamba, 5 Sep 2008. – MRAC A8-020-P-0962, 1, 54.6 mm SL; Lefini River, about 600 m upstream of camp Oteni, left bank, 2°49'29"S 15°47'30"E; A. Ibala Zamba, 11 Jul 2008. – MRAC A8-

Fig. 5. *Congolapia bilineata*, not preserved; collected with MRAC A7-31-P-0581; Republic of the Congo: Lefini River (photograph by A. I. Zamba).

020-P-0971-0972, 2, 57.6-68.5 mm SL; Louna River, affluent of Lefini River, about 500m to camp PPG Abio 2, left bank, 3°07'40"S 15°31'23"E; E. Vreven & A. Ibala Zamba, 6 Sep 2008. – MRAC A8-020-P-0973-0975, 3, 46.6-52.1 mm SL; Louna River, affluent of Lefini River, upstream of first rapids, 3°15'13"S 15°23'44"E; E. Vreven & A. Ibala Zamba, 2 Sep 2008. – MRAC A8-020-P-0983-0984, 2, 54.7-93.8 mm SL; Louna River, affluent of Lefini River, backwater, downstream of rapids, 3°14' 57"S 15°24'55"E; E. Vreven & A. Ibala Zamba, 1 Sep 2008. – MRAC A8-020-P-0985-0986, 2, 58.9-65.5 mm SL; Louna River, affluent of Lefini River, backwater, downstream of rapids, 3°14'57"S 15°24'55"E; E. Vreven & A. Ibala Zamba, 2 Sep 2008.

Democratic Republic of the Congo: MRAC P-96726-96736, 1 out of 11, i.e. the largest specimen of 59.4 mm SL; Bokuma, ±0°06'00"S 18°40'48"E; P. Lootens, 1954. – MRAC P-87937-87938, 2, 78.5-122.5 mm SL; Maringa River, at Befori, ±0°06'00"N 22°16'48"E; H. Bertels, 1952.

Fig. 6. *Congolapia bilineata*, female in front, male behind; aquarium specimens from unknown locality in Cuvette Centrale (photograph by O. Lucanus).

Diagnosis. *Congolapia bilineata* differs from *C. crassa* and *C. louna* by having one complete scale row and one additional scale row with smaller dorso-ventrally compressed scales between the upper lateral line and the base of the last dorsal spine (vs. two complete scale rows and one additional row of very small scales in-between).

Further, *C. bilineata* differs from *C. crassa* by a shallower body with only a minimal overlap (32.2-40.5 % SL vs. 40.4-48.4) and from *C. louna* by a shorter last dorsal spine (9.4-12.2 % SL vs. 12.9-15.0).

At the molecular level *C. bilineata* differs from *C. crassa* by 95 single mutations and from *C. louna* by seven single mutations at mitochondrial locus ND2 (data not shown, for *C. crassa* vs. *C. bilineata*; see Table 1).

Description. Morphometric and meristic data for lectotype, paralectotype and additional specimens in Table 4; see figures 3-6 for general appearance. Maximum observed size 175.4 mm SL. Body elongate and laterally compressed. Dorsal head profile slightly concave from insertion of first dorsal spine to upper margin of eye. From this point to tip of upper lip head profile changing to a weakly convex outline. Compact head with obtuse snout outline. Eye moderately large and interorbital width always larger than eye length. Greatest body depth at level of first dorsal spine. Dorsal profile, towards caudal, slightly postero-ventrally curved and not straight. Caudal peduncle as long as deep or somewhat longer. Two unconnected lateral lines.

Squamation. All scales cycloid. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal-fin ray. One complete scale row of large and one scale row of smaller, dorso-ventrally compressed scales separating upper lateral line from last dorsal spine. Lower lateral line originating at level of first dorsal branched fin rays and terminating midlaterally on caudal peduncle. Two scale rows between upper and lower lateral lines. Preoperculum scaled with three to four regular rows. Chest with smaller slightly embedded scales. Minute scales covering approx. 80 % of caudal fin, scales on rays arranged in rows, all other unordered.

Gill rakers. First ceratobranchial with 8–10 gill rakers and first epibranchial with 3–4 gill rakers, a single gill raker on cartilaginous plug in the angle of arch included in latter number. Total number of gill rakers on first gill-arch 12–14. Ceratobranchial rakers slender, broader on base, pointed and unbranched. Gill rakers situated most ventrally on ceratobranchial smaller than all others.

Table 4. Measurements and counts of lectotype and 18 additional specimens of *Congolapia bilineata*. Range includes values of lectotype.

	lectotype	range			
		min	max	mean	SD
Measurements					
Total length (mm)	180.0	73.0	210.9	124.0	
Standard length SL (mm)	150.4	58.1	175.4	101.5	
In percents of standard length					
Head length	32.9	29.6	32.9	31.2	1.0
Interorbital width	10.2	9.2	12.9	10.5	1.1
Preorbital width	13.5	11.4	14.2	12.6	0.9
Horizontal eye length	7.1	6.9	9.5	8.2	0.7
Snout length	15.6	12.8	16.6	14.6	1.2
Internostril distance	8.8	7.0	10.0	8.7	0.7
Cheek depth	13.0	9.1	13.9	11.4	1.4
Upper lip length	11.4	8.6	12.2	9.8	1.0
Lower lip length	10.9	7.7	12.3	9.7	1.1
Lower lip width	11.4	8.6	13.9	10.8	1.7
Lower jaw length	12.6	9.5	13.6	11.1	0.9
Predorsal distance	37.5	35.6	40.1	38.3	1.2
Dorsal-fin base length	56.8	53.4	57.1	55.6	1.0
Last dorsal-fin spine length	11.8	9.4	13.2	11.2	0.8
Anal-fin base length	15.2	14.7	16.7	15.6	0.6
Third anal-fin spine length	14.2	10.5	14.9	13.2	1.3
Pelvic-fin length	29.3	23.9	29.4	26.2	1.6
Pectoral-fin length	24.1	20.5	25.1	23.7	1.2
Caudal peduncle depth	14.0	12.7	14.5	13.6	0.5
Caudal peduncle length	15.5	14.0	17.2	15.6	0.9
Body depth (pelvic-fin base)	38.6	32.2	40.5	36.6	2.5
Preanal length	75.5	69.8	76.6	72.9	2.1
Anus-anal-fin base distance	5.7	3.9	6.5	5.4	0.7
Counts					
Dorsal-fin spines	17	16 (3), 17 (16)			
Dorsal-fin rays	10	9 (3), 10 (14), 11 (2)			
Anal-fin rays	8	8 (17), 9 (2)			
Pectoral-fin rays	14	13 (2), 14 (17)			
Scales (horizontal line)	27	26 (3), 27 (16)			
Upper lateral line scales	21	17 (1), 20 (4), 21 (11), 22 (3)			
Lower lateral line scales	9	8 (1), 9 (9), 10 (7), 11 (2)			
Gill rakers (lower)	10	8 (2), 9 (8), 10 (9)			
Gill Rakers (upper)	3	3 (8), 4 (11)			

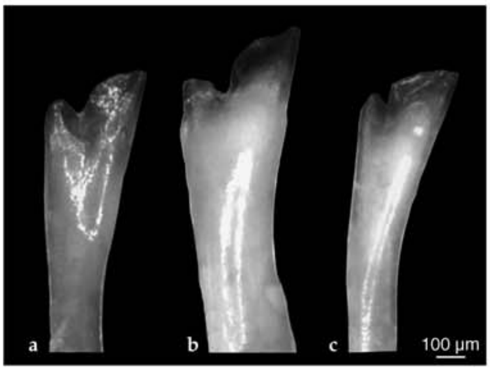

Fig. 7. Lower jaw teeth in species of *Congolapia*: **a,** *C. crassa*, AMNH 247003, 69.2 mm SL; **b,** *C. bilineata*, MRAC A8-020-P-0961, 102.5 mm SL; and **c,** *C. louna*, MRAC A8-020-P-0969, 85.3 mm SL.

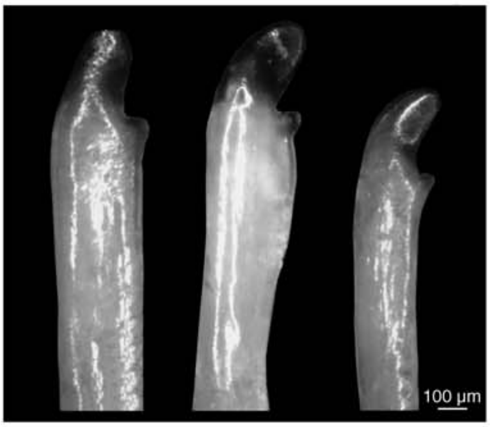

Fig. 9. Posterior pharyngeal teeth of lower pharyngeal jaw in species of *Congolapia*: **a,** *C. crassa*, AMNH 247003, 69.2 mm SL; **b,** *C. bilineata*, MRAC A8-020-P-0958, 73.4 mm SL; and **c,** *C. louna*, MRAC A8-020-P-0969, 85.3 mm SL.

Fins. Base of pelvic fin slightly in front of dorsal-fin origin. Dorsal spines 16–17. Dorsal rays 9–11. First dorsal spine always shortest and last dorsal spine always longest. Longest spines always shorter than longest rays. Last dorsal ray most deeply branched. Caudal fin truncate or slightly emarginate. Three anal spines and 8–9 anal rays. Third anal spine always longest. Last anal ray most deeply branched. Tip of longest anal-fin ray rarely crossing hypuralia. Tip of longest pelvic-fin ray not reaching anus. Pectoral-fin rays 13–14.

Jaws and dentition. Jaws isognathous. Upper and lower outer teeth rows in both jaws bicuspid. Neck of anterior jaw teeth spatulate, crown brownish, expanded and cusps truncated (Fig. 7). Two to seven incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad, anterior keel shorter than toothed area (Fig. 8). Most posterior pharyngeal

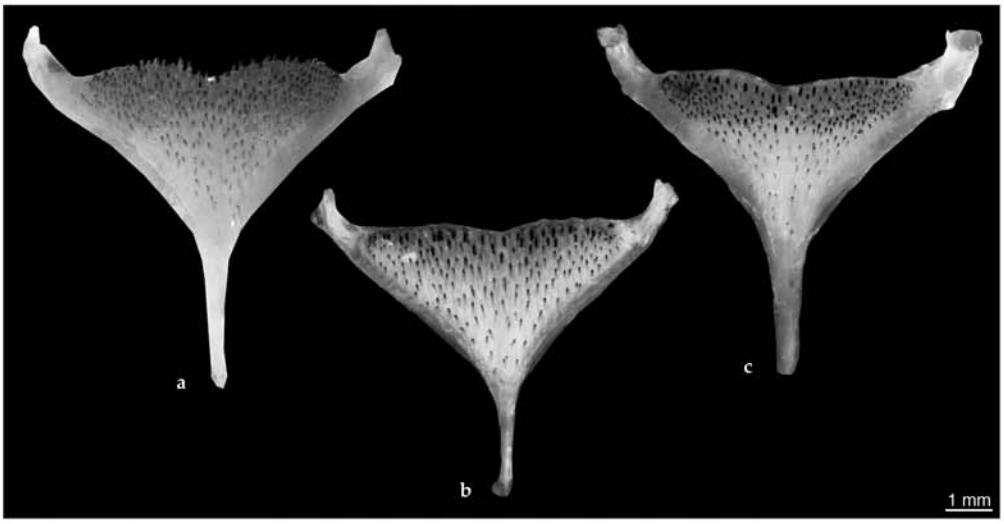

Fig. 8. Lower pharyngeal jaw in species of *Congolapia*: **a,** *C. crassa*, AMNH 247003, 69.2 mm SL; **b,** *C. bilineata*, MRAC A8-020-P-0958, 73.4 mm SL; and **c,** *C. louna*, MRAC A8-020-P-0969, 85.3 mm SL.

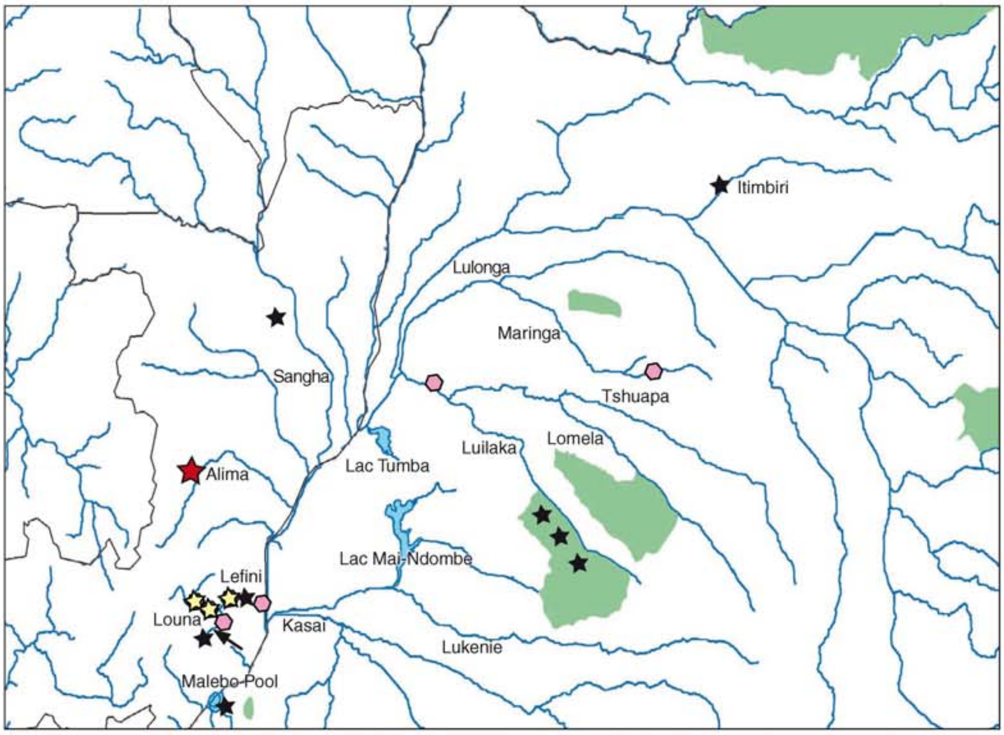

Fig. 10. Congo basin. ★: type locality of *Congolapia crassa* and *C. bilineata*. ↗: type locality of *C. louna*; ⬡: *C. bilineata*; ★: *C. crassa*; ☆: localities where *C. bilineata* and *C. crassa* were found together.

teeth bicuspid (few tricuspid), stout, slightly hooked and regularly arranged, especially on last 2–3 rows of toothed area (Fig. 9). Dentigerous plate triangular. Most of teeth in anterior two thirds of toothed area approaching "kukri" shape (sensu Greenwood, 1987), i. e. upper part of teeth angled posteriorly, and vertical through tip well behind body of tooth.

Coloration in alcohol (Fig. 3)**.** Background colour brownish. Head and dorsal side dark brownish, ventral side light brownish to whitish. Chest whitish with a few black pigments and belly sometimes slightly reddish. Flank scales with dark margin and light centre. Lower lip light brownish to whitish and upper lip darker than lower. Markings on body: six or seven black backward slanted, unbranched (not Y-shaped) bars on dorsum and sides (first bar at level of first dorsal spine and last two on caudal peduncle) and a nape band. Bars often absent, apparently depending on motivational state. A well defined longitudinal mid-lateral and dorso-lateral black stripe. Mid-lateral stripe extending onto base of caudal fin. Black opercular spot, sometimes faded. Fins: pectoral fin hyaline. Pelvic, anal and caudal fins light brownish. Dorsal fin light brownish, no well-defined "tilapia spot" except in juveniles less than 40 mm SL.

Life coloration (Figs. 5–6)**.** Description based on subadult specimens photographed in aquarium, from an unknown locality in the Cuvette Centrale (O. Lucanus, pers. comm.) and photographs of adult specimens from the Lefini taken in the field. Background colour light olive-green to yellowish, chest and belly light yellow to whitish with small reddish dots. Lower half of head yellowish olive, especially on cheek, and upper half of head olive-green. Upper lip bluish and lower lip whitish. A horizontal iridescent blue line above antero-rostral margin of preopercle. Iris dark brown. Apparently depending on motivational state, body with six or seven black backward slanted, unbranched (not Y-shaped) bars and a nape band or two black stripes along the lateral lines. A yellow line between these two lines. Black thin lachrymal stripe extending from lachrymal to jaw angle; black opercular spot, extended into a sloping stripe. Pectoral fin light greenish to hyaline with a yellow base, pelvic fin and anal fin greenish yellow. Dorsal fin greenish, yellow edged, no clear "tilapia spot" (except juveniles). Caudal fin greenish yellow.

Distribution and habitat. *Congolapia bilineata* is known from the central Congo basin in the western Cuvette Centrale (Alima, Lefini) and central Cuvette Centrale (Tshuapa, Luilaka) (Fig. 10).

Within the Lefini River basin, *C. bilineata* has been collected at, at least, four of the 12 ecological gill-net sampling stations selected. The species was collected in grass-bank (stations 1, 5 and 11) as well as forest-bank habitats (station 3) and this during the dry as well as wet season for at least one of the four stations (station 11). The detailed physico-chemical and habitat parameters for these stations are given in Table 6.

Congolapia bilineata and *C. crassa* do not only seem to occur sympatric in the Lefini River basin but seem to be syntopic at least on the locality level as both were caught together on 22 April 2007 at the confluent Lefini-Nambouli (Station 2: MRAC A7-31-P-0058 and MRAC A7-31-P-0059 -0060 respectively) and on 2 Sept 2008 on the Louna River, downstream of the rapids (MRAC A8-020-P-0973-0975 and MRAC A8-20-P-0976 -0979 respectively). In addition, also *C. louna* was caught at the latter locality although available data do not enable us to confirm syntopic presence of the tree species in the same net at the latter locality. However, for the former locality both, *C. bilineata* and *C. crassa*, are syntopic as both where caught together on the same day in the same 15 mm mesh size net of 30 m long.

Remarks. A single specimen from Bokuma (0°06'00.02"S 18°40'48"E) (MRAC 96726-736, 59.4 mm SL) belongs to *Congolapia* because it shares all characters of the genus, but cannot be referred to a species. This specimen possesses 13 ceratobranchial and 3 epibranchial gill rakers. This character state is typical for *C. louna* and unknown in *C. bilineata*, which possesses 8–10 ceratobranchial and 3–4 epibranchial gill rakers. In contrast, the specimen has the same number of scale rows separating upper lateral line from last dorsal spine as *C. bilineata*, which possesses one complete scale row and one scale row with smaller dorso-ventrally compressed scales. More material is needed to assess the identity of this specimen.

Tilapia bilineata was described based on two specimens. Pellegrin (1900) did not designate a holotype and therefore they are syntypes. The largest syntype (MNHN 1886-0445, 150.4 mm SL) was illustrated by Pellegrin (1904) and is here designated as lectotype.

Congolapia crassa (Pellegrin, 1903)

(Figs. 11–14)

Specimens examined. MNHN 1886-0448, holotype, 138.7 mm SL; "Diélé, Mission de l'Ouest africain (M. de Brazza)" [Central African Republic: Ndele, Alima River, upper Congo; P. Savorgnan de Brazza, date not available].

Republic of the Congo: AMNH 242008, 2 (3), 98.5–106.8 mm SL; Salonga, National Park, Yenge River, R. C. Schelly & R. Monsembula, 28 Jul 2006. – AMNH 244529, 2, 101.9–146.5 mm SL; region of the Sangha, Lengoue River upstream of Liouesso, V. Mamonekene, 4 Sep 2007. – AMNH 244530, 1, 141.8 mm SL; region of the Sangha, Lengoue River upstream of Liouesso, V. Mamonekene, 5 Sep 2007. – AMNH 244531, 2 (3), 91.3–101.1 mm SL; region of the Sangha, Lengoue River upstream of Liouesso, V. Mamonekene, 6 Sep 2007. – AMNH 247003, 3 (6), 69.2–111.3 mm SL; region of the Sangha, Lengoue River upstream of Liouesso, V. Mamonekene, 1 Sep 2007. – MRAC A7-31-P-0059–0060, 2, 86.1–102.1 mm SL; Lefini River, confluent Lefini-Nambouli, left bank, 2°53'46"S 15°06'51"E; A. Ibala Zamba & A. Ngoma Moutsinga, 22 Apr 2007. – MRAC A7-31-P-62–64, 3, 73.2–81.9 mm SL; Lefini River, confluent Lefini-Nambouli, left bank, 2°53'46"S 15°06'51"E; A. Ibala Zamba & A. Ngoma Moutsinga, 23 Apr 2007. – MRAC A7-31-P-65, 1, 118.7 mm SL; Lefini River, about 2.4 km downstream of camp Malina, left bank, 2°59'14"S 15°11'45"E; A. Ibala Zamba & A. Ngoma Moutsinga, 27 Sep 2007. – MRAC A7-31-P-66–69, 4, 103.3–116.6 mm SL; Lefini River, confluent Léfini-Nambouli, left bank, 2°53'46"S 15°06'51"E; E. A. Ibala Zamba & A. Ngoma Moutsinga, 22 Sep 2007. – MRAC A7-31-P-70, 1, 87.1 mm SL; Lefini River, about 2.4 km downstream of camp Malina, 2°59'14"S 15°11'45"E; E. Vreven & A. Ibala Zamba, 25 Apr 2007. – MRAC A7-31-P-72, 1, 106.6 mm SL; Ntiene River, affluent of Lessio River, Lefini River basin, 3°15'53"S 15°28'33"E; A. Ibala Zamba, A. Ngoma Moutsinga & E. Vreven, 20 Apr 2007. – MRAC A7-31-P-73–74, 2, 86.1–93.2 mm SL; Lefini River, about 2.4 km downstream of camp Malina, left bank, 2°59'14"S 15°11'45"E; A. Ibala Zamba & A. Ngoma Moutsinga, 26 Sep 2007. – MRAC A7-13-97–99, 3, 49.1–79.9 mm SL;

Lefini River, confluent Louna-Lefini, oppossite to camp PPG, 2°59'35"S 15°29'42"E; A. Ibala Zamba & A. Ngoma Moutsinga, 10 Sep 2006. – MRAC A8-020-P-0954–0955, 2, 84.3–104.0 mm SL; Lefini River, confluent Lefini-Nambouli, left bank, 2°53'46"S 15°06'51"E; A. Ibala Zamba, 5 Aug 2008. – MRAC A8-020-P-0957, 1, 86.2 mm SL; Lefini River at camp Oteni, 2°50'15"S 15°47'26"E; A. Ibala Zamba, 1 Aug 2008. – MRAC A8-020-P-0959-0960, 2, 83.0–83.6 mm SL; Lefini River, about 4 km downstream of camp Malina, 2°59'27"S 15°11'59"E; A. Ibala Zamba, 22 Mar 2008. – MRAC A8-020-P-0964, 1, 129.0 mm SL; Lefini River, about 2.4 km downstream of camp Malina, left bank, 2°59'14"S 15°11'45"E; A. Ibala Zamba, 1 Aug 2008. – MRAC A8-020-P-0966–0968, 3, 54.7–135.9 mm SL; Louna River, affluent of Lefini River, upstream of the rapids, right bank, 3°15'07"S 15°25'21"E; E. Vreven & A. Ibala Zamba, 30 Aug 2008. – MRAC A8-020-P-0976–0979, 4, 80.7–26.4 mm SL; Louna River, affluent of Lefini River, downstream of first rapids, right bank, 3°15'13"S 15°23'44"E; E. Vreven & A. Ibala Zamba, 2 Sep 2008. – Democratic Republic of the Congo: AMNH 242002, 2, 96.3–100.4 mm SL; Salonga National Park, Luilaka River, Mbokomboko, small estuary protected by sand bar from main channel, 2°30'36"S 21°22'12"E; R.C. Schelly & R. Monsembula, 11 Jul 2006. – AMNH 242004, 5 (8), 109.1–143.5 mm SL;

Table 5. Measurements and counts of holotype and 40 additional specimens of *Congolapia crassa*. Range includes values of holotype.

	holotype	range			
		min	max	mean	SD
Measurements					
Total length (mm)	164.0	85.3	180.3	126.9	
Standard length SL (mm)	138.7	69.2	146.5	104.6	
In percents of standard length					
Head length	32.7	31.0	34.6	32.9	0.8
Interorbital width	13.0	10.8	15.0	12.6	1.0
Preorbital width	15.2	12.0	16.4	14.1	0.9
Horizontal eye length	8.6	7.5	9.8	8.7	0.7
Snout length	14.0	13.0	16.7	15.0	1.0
Internostril distance	9.9	8.1	10.3	9.1	0.5
Cheek depth	13.7	10.3	14.1	12.1	0.9
Upper lip length	10.2	8.0	10.9	9.5	0.8
Lower lip length	10.5	7.8	11.1	9.5	0.9
Lower lip width	11.8	8.5	13.5	11.1	1.3
Lower jaw length	12.3	10.0	12.6	11.0	0.6
Predorsal distance	37.9	37.9	43.1	40.0	1.1
Dorsal-fin base length	59.7	54.6	60.4	57.9	1.6
Last dorsal-fin spine length	10.3	10.3	16.1	13.2	1.3
Anal-fin base length	14.9	14.9	18.4	16.7	0.9
Third anal-fin spine length	14.5	13.4	17.6	15.4	1.0
Pelvic-fin length	28.1	25.7	41.8	32.2	3.0
Pectoral-fin length	22.9	22.2	28.8	25.9	1.4
Caudal peduncle depth	13.8	13.4	15.8	14.7	0.6
Caudal peduncle length	16.4	12.6	16.9	14.5	0.9
Body depth (pelvic-fin base)	44.8	38.0	48.4	43.7	2.1
Preanal length	74.8	71.5	77.2	74.4	1.2
Anus-anal-fin base distance	5.5	4.4	7.1	5.5	0.6
Counts					
Dorsal-fin spines	16	16 (7), 17 (34)			
Dorsal-fin rays	10	8 (3), 9 (20), 10 (18)			
Anal-fin rays	7	7 (2), 8 (36), 9 (3)			
Pectoral-fin rays	13	12 (5), 13 (31), 14 (5)			
Scales (horizontal line)	25	25 (10), 26 (26), 27 (5)			
Upper lateral line scales	19	18 (2), 19 (6), 20 (23), 21 (10)			
Lower lateral line scales	10	8 (9), 9 (19), 10 (10), 11 (3)			
Gill rakers (lower)	10	8 (5), 9 (9), 10 (19), 11 (8)			
Gill Rakers (upper)	3	3 (8), 4 (25), 5 (8)			

Salonga National Park, Nkema Asondzi, small forest stream at confluence with Luilaka River, shallows of the river and along sandy bank, 2°13'12" S 21°10'48" E; R. C. Schelly & R. Monsembula, 16 Jul 2006. – AMNH 242005, 4, 34.5–133.2 mm SL; Salonga, National Park, Luilaka River, Monkoto, 1°45'0" S 20°40'48" E; R.C. Schelly et al., 18–19 Jul 2006. – MRAC A5-012-P-0044-0045, 2, 47.0–67.9 mm SL; Congo River, Molondo Island, Pool Malebo, 4°17'24" S 15°29'24" E; Pigneur et al., 2005. – ZSM 39312, 1, 33.0 mm SL; Tshimbi River, tributary to Itimbiri River, below bridge on old road Bumba-Aketi, 2°40'44" N 23°23'46" E; U. K. Schliewen et al., 24 Jul 2009.

Diagnosis. *Congolapia crassa* differs from *C. bilineata* by having two complete scale rows between the upper lateral line and the base of the last dorsal spine and one additional row of very small scales in-between (vs. one complete scale row and one additional scale row with smaller dorsoventrally compressed scales between the upper lateral line and the base of the last dorsal spine). *Congolapia crassa* is distinguished from *C. louna* by a lower number of gill rakers on first ceratobranchial (8–11 vs. 13).

Further, *C. crassa* differs from *C. bilineata* and *C. louna* by a greater body depth with only a minimal overlap (40.4–48.4 % SL vs. 32.2–40.5) and (40.4–48.4 % SL vs. 37.4–42.1).

At the molecular level *C. crassa* differs from *C. bilineata* by 95 single mutations and from *C. louna* by seven single mutations at mitochondrial locus ND2 (data not shown, for *C. crassa* vs. *C. bilineata*; see Table 1).

Description. Morphometric and meristic data for holotype and additional specimens in Table 5; see Figures 11–14 for general appearance. Maximum observed size 146.5 mm SL. Body laterally compressed. Dorsal head profile slightly concave. Head compact, snout obtuse. Eye moderately large and interorbital width always larger than eye length. Deeper bodied than *C. bilineata*. Greatest body depth at level of first dorsal spine. Dorsal profile slightly posteroventrally curved and not straight. Caudal peduncle as long as deep or somewhat longer. Two unconnected lateral lines.

Squamation. All scales cycloid. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal ray. Two scale rows with or without a small scale at base of last dorsal spine, separating upper lateral line from last dorsal spine. Lower lateral line originating at level of first dorsal branched rays and terminates midlaterally on caudal peduncle. Two scale rows between upper and lower lateral line. Preoperculum scaled with three to four regular rows. Chest with smaller mostly deeply embedded scales. Minute scales covering approx. 80 % of caudal fin, scales on rays arranged in rows, all other unordered.

Gill rakers. First ceratobranchial with 8–11 gill rakers and first epibranchial with 3–5 gill rakers, a single gill raker on cartilaginous plug in angle of arch included in latter number. Total number of gill rakers on first gill-arch 11–16. Ceratobranchial rakers slender, broader on base, pointed and unbranched. Gill rakers situated most ventrally on ceratobranchial smaller than others.

Fins. Base of pelvic fin slightly in front of dorsal-fin origin. Dorsal spines 16–17. Dorsal rays 8–10. First dorsal spine always shortest, last dorsal spine always longest. Longest spines always shorter than longest rays. Last dorsal ray most deeply branched. Caudal fin truncate or slightly emarginate. Three anal spines and 7–9 anal rays. Third anal spine always longest. Last anal ray most deeply branched. Tip of longest anal-fin ray always overlapping hypuralia. Tip of longest pelvic-fin ray reaching anus. Pectoral-fin rays 12–14.

Jaws and dentition. Jaws isognathous. Upper and lower outer teeth rows bicuspid in both jaws. Neck of anterior jaw teeth spatulate, crown brownish, expanded and cusps truncated (Fig. 7). Two to six incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad, anterior keel shorter than toothed area (Fig. 8). Most posterior pharyngeal teeth tricuspid (few bicuspid), stout, slightly hooked and regularly arranged, especially on last 2–3 rows of toothed area (Fig. 9). Dentigerous plate triangular. Most of teeth in anterior two thirds of toothed area approaching "kukri" shape (sensu Greenwood, 1987), i.e. upper part of teeth angled posteriorly, and vertical through tip well behind body of tooth.

Coloration in alcohol (Figs. 11–12)**.** Background colour brownish. Head and dorsal side dark brownish, ventral side light brownish to whitish. Flank scales with dark margin. Chest slightly pigmented and belly sometimes slightly reddish. Lower lip light brownish to whitish and upper

Fig. 11. *Congolapia crassa*, MNHN 1886-0448, holotype, 138.7 mm SL; Central African Republic: Alima River.

Fig. 12. *Congolapia crassa*, AMNH 242004, 143.5 mm SL; Democratic Republic of the Congo: Luilaka River.

lip darker than lower. Markings on body: five to seven black, broad, backward slanted, unbranched (not Y-shaped) bars on dorsum and sides (the first bar at level of first dorsal spine, the last two on caudal peduncle) and a nape band. Bars often absent, apparently depending on motivational state. A clearly longitudinal mid-lateral and dorso-lateral black stripe is present. Black extended opercular spot. Fins: pectoral fin hyaline. Pelvic, anal and caudal fins light brownish. Dorsal fin light brownish, black "tilapia spot" always present.

Life coloration (Fig. 14)**.** Based on photographs of an adult *C. crassa* from Salonga National Park. Background colour reddish-brown to bluish, chest and belly light brown to whitish with small reddish elements and dorsum darker brown, especially in range of backward slanted, unbranched (not Y-shaped) bars. Flank below lower lateral line more bluish. Lower half of head light brown to reddish and upper half of head dark olive-brown. Upper lip turquoise and lower lip whitish. A horizontal iridescent turquoise line above antero-rostral margin of preopercle. Base of pectoral fin whitish edged. Iris reddish brown. Apparently depending on motivational state, body with five or six black, broad, backward slanted, unbranched (not Y-shaped) bars and a nape band. Bluish thin lachrymal stripe extending from

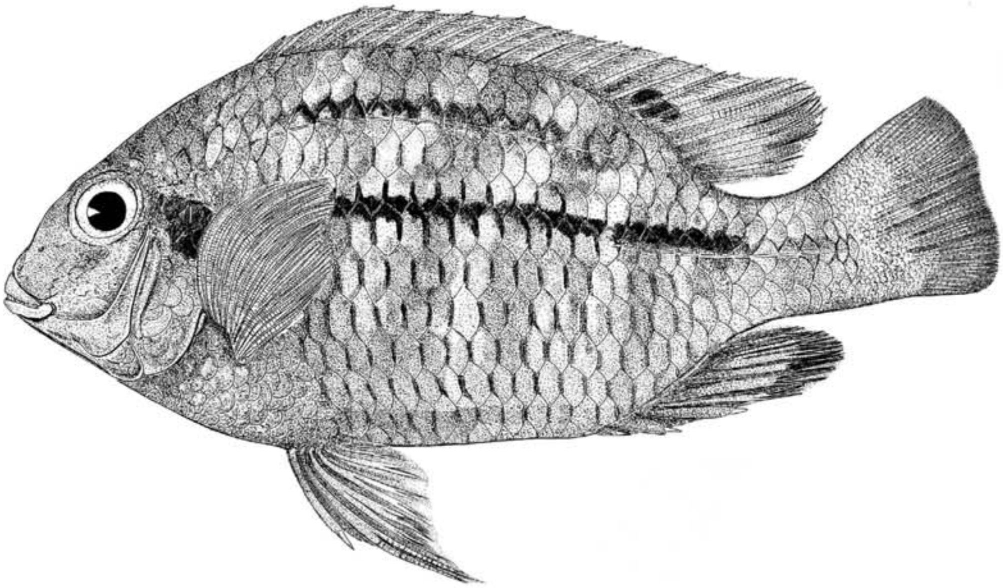

Fig. 13. *Congolapia crassa*, AMNH 242004, 143.5 mm SL; Democratic Republic of the Congo: Luilaka River (drawing by R. Kühbandner).

Fig. 14. *Congolapia crassa*, AMNH 242004, 137.0 mm SL; Democratic Republic of the Congo: Salonga National Park (photograph by Robert Schelly).

lachrymal to jaw angle; black opercular spot, extended into sloping stripe. Pectoral fin light yellowish to hyaline, pelvic and anal fin greenish yellow. Dorsal fin reddish-brown to yellow whitish edged, black "tilapia spot" present. Caudal fin reddish-brown to yellow, whitish edged.

Distribution and habitat (Fig. 10). *Congolapia crassa* is known from the western central Congo basin (Cuvette Centrale), from the Alima, Lefini, Sangha (Republic of the Congo), Malebo Pool, Itimbiri and from affluents of Luilaka (DRC) in the Salonga National Park, central Cuvette Centrale.

Within the Lefini River basin, *C. crassa* has been collected at, at least, four of the 12 ecological gill-net sampling stations selected. The species was collected in grass-bank (station 1 & 4) as well as forest-bank habitats (station 2 & 3) and this during the dry as well as wet season for at least two of the four stations, one with grass-bank and one with forest bank (stations 1 & 2). The detailed mean physico-chemical and habitat parameters for these stations are given in Table 6. For more details on sympatric and syntopic presence of *C. crassa* with the other two species see distribution and ecology heading of *C. bilineata*.

Congolapia louna, new species

(Figs. 15–17)

Holotype. MRAC A8-020-P-0980, 150.3 mm SL; Republic of the Congo: River Louna, affluent of Lefini, upstream of first rapids, right bank, 3°15'13"S 15°23'44"E; E. Vreven & A. Ibala Zamba, 2 Sep 2008.

Paratypes. MRAC A8-020-P-0981–0982, 2, 83.5–85.8 mm SL; collected with holotype. – MRAC A8-020-P-0969–0970, 2, 85.3–117.7 mm SL; Republic of the Congo: River Louna, affluent of Lefini, upstream of the rapids, right bank, 3°15'07"S 15° 24'05"E; E. Vreven & A. Ibala Zamba, 30 Aug 2008.

Diagnosis. *Congolapia louna* differs from *C. bilineata* and *C. crassa* by having more gill rakers on first ceratobranchial (13 vs. 8–10 in *C. bilineata* and 8–11 in *C. crassa*). It further differs from *C. bilineata* by having two complete scale rows between the upper lateral line and the base of the last dorsal spine and one additional row of very small scales in-between (vs. one complete scale row and one additional scale row with smaller dorso-ventrally compressed scales between the upper lateral line and the base of the last dorsal spine), and a longer last dorsal spine (12.9–15.0 % SL vs. 9.4–13.2).

It further differs from *C. crassa* by lower body depth with only a minimal overlap (37.4–42.1 % SL vs. 40.4–48.4).

Table 6. Mean values of physico-chemical and habitat parameters at six of 12 sampling stations were *Congolapia bilineata* and *C. crassa* have been collected in Lefini River basin. White background: grass bank stations; grey background: forest bank stations. Stations: **1,** Lefini River, confluent Lefini-Nambouli, left bank (2°53'46"S 15°06' 51"E); **2,** Lefini River at 2.4 km downstream of camp Malina, right bank (2°59'14"S 15°11'45"E); **3,** Lefini River, ±3 km upstream of confluent Léfini-Loubilika, right bank (3°01'11"S 15°14'25"E); **4,** Lefini River, ±4 km downstream of camp Malina, right bank (2°59'27"S 15°11'59"E); **5,** Lefini River, ±3 km upstream of mount Epopé, left bank (3°01'58"S 15°23'42"E); **6,** Lefini River at 600 m upstream of camp Oteni, left bank (2°54'11"S 15°59'07"E). *Congolapia bilineata* has been collected at stations 1, 3, 5 and 11, *C. crassa* at stations 1, 2, 3 and 4. (*): Mean values for 5 gill-nets, 2 days, 2 seasons and 2 years (total n=40).

Stations	1	2	3	4	5	11
Distance of source (km)	135.7	151.3	158.9	152.4	178.5	235.4
Altitude (m)	336.0	328.0	325.0	327.0	324.0	311.0
Canopy height (m)	0.0	10.2	15.0	0.0	0.0	0.0
Depth (m)*	1.0	0.8	1.4	0.9	1.0	0.6
Oxygen ($mg \cdot l^{-1}$)*	6.2	2.4	4.1	2.2	3.3	3.7
Conductivity ($\mu S \cdot cm^{-1}$)*	6.8	8.0	9.9	6.6	7.1	6.1
Transparency (m)*	1.0	0.8	1.3	0.9	1.0	0.6
Distance from river bank (m)*	1.1	3.2	14.0	15.0	1.3	3.2
pH*	5.5	5.4	5.3	6.1	5.7	5.6
Temperature (°C)*	25.8	25.4	25.3	29.8	25.5	26.0
Velocity ($m \cdot s^{-1}$)*	0.3	0.0	0.4	0.0	0.3	0.3
Substrate types and canopy closure (in %)						
Canopy closure	0.0	33.0	60.0	0.0	0.0	0.0
Sand	76.0	10.0	50.0	38.0	44.0	40.0
Mud	20.0	22.0	12.0	39.0	13.0	29.0
Dead leaves	0.0	30.0	11.0	0.0	0.0	0.0
Aquatic plants	2.0	12.0	9.0	19.0	41.0	29.0
Dead wood	0.0	18.0	5.0	0.0	0.0	0.0
Mixture of dead wood, dead leaves and mud	2.0	8.0	13.0	0.0	2.0	2.0

At the molecular level *C. louna* differs from *C. crassa* and *C. bilineata* by seven single mutations at mitochondrial locus ND2 (Table 1).

Description. Morphometric and meristic data for holotype and 4 paratypes in Table 7; see Figures 15–17 for general appearance. Maximum observed size 150.3 mm SL. Body laterally compressed. Dorsal head profile moderately concave from insertion of first dorsal spine to upper margin of eye. From this point to tip of upper lip head profile changing to a straight outline. Head compact, snout obtuse. Eye moderately large and interorbital width always larger than eye length. Greatest body depth at level of first dorsal spine. Dorsal profile slightly posteroventrally curved and not straight. Caudal peduncle as long as deep or somewhat longer. Two unconnected lateral lines.

Squamation. All scales cycloid. Upper lateral line extending from posterior margin of gill cover to approximately last dorsal ray. Two scale rows with a small scale at base of last dorsal spine separate upper lateral line from last dorsal spine. Lower lateral line originating at level of first

Table 7. Measurements and counts of holotype and 4 paratypes of *Congolapia louna*. Range includes values of holotype.

	holotype	range			
Measurements		min	max	mean	SD
Total length (mm)	184.1	103.5	184.1	128.3	
Standard length SL (mm)	150.3	83.5	150.3	104.5	
In percents of standard length					
Head length	32.9	32.1	34.3	33.0	0.8
Interorbital width	13.9	11.1	13.9	12.4	1.1
Preorbital width	15.2	13.1	15.2	14.0	0.8
Horizontal eye length	7.5	7.3	9.2	8.3	0.8
Snout length	17.4	15.4	17.5	16.4	1.0
Internostril distance	10.6	9.1	10.6	10.0	0.6
Cheek depth	12.0	10.2	12.0	10.9	0.9
Upper lip length	10.4	8.7	10.4	9.2	0.7
Lower lip length	10.1	8.4	10.1	9.0	0.7
Lower lip width	13.1	10.4	13.1	11.6	1.0
Lower jaw length	11.8	10.4	11.8	11.0	0.6
Predorsal distance	40.0	39.4	41.1	40.0	0.7
Dorsal-fin base length	57.9	52.9	57.9	55.3	2.1
Last dorsal-fin spine length	15.0	12.9	15.0	13.8	0.8
Anal-fin base length	21.1	17.8	21.1	18.8	1.4
Third anal-fin spine length	12.6	12.6	15.0	13.5	0.9
Pelvic-fin length	25.3	24.7	26.3	25.4	0.6
Pectoral-fin length	24.7	22.8	26.3	24.1	1.4
Caudal peduncle depth	14.8	13.1	14.8	13.9	0.6
Caudal peduncle length	15.2	13.5	15.3	14.7	0.7
Body depth (pelvic-fin base)	42.1	37.4	42.1	39.6	2.0
Preanal length	70.5	70.5	73.0	71.2	1.0
Anus-anal-fin base distance	5.1	4.3	5.2	4.8	0.4
Counts					
Dorsal-fin spines	16	16 (5)			
Dorsal-fin rays	10	10 (3), 11 (2)			
Anal-fin rays	9	8 (1), 9 (4)			
Pectoral-fin rays	13	13 (4), 14 (1)			
Scales (horizontal line)	26	26 (4), 27 (1)			
Upper lateral line scales	18	18 (1), 20 (2), 21 (2)			
Lower lateral line scales	10	9 (4), 10 (1)			
Gill rakers (lower)	13	13 (5)			
Gill Rakers (upper)	4	3 (1), 4 (4)			

Fig. 15. *Congolapia louna*, MRAC A8-020-P-0980, holotype, 150.3 mm SL; Republic of the Congo: Louna River.

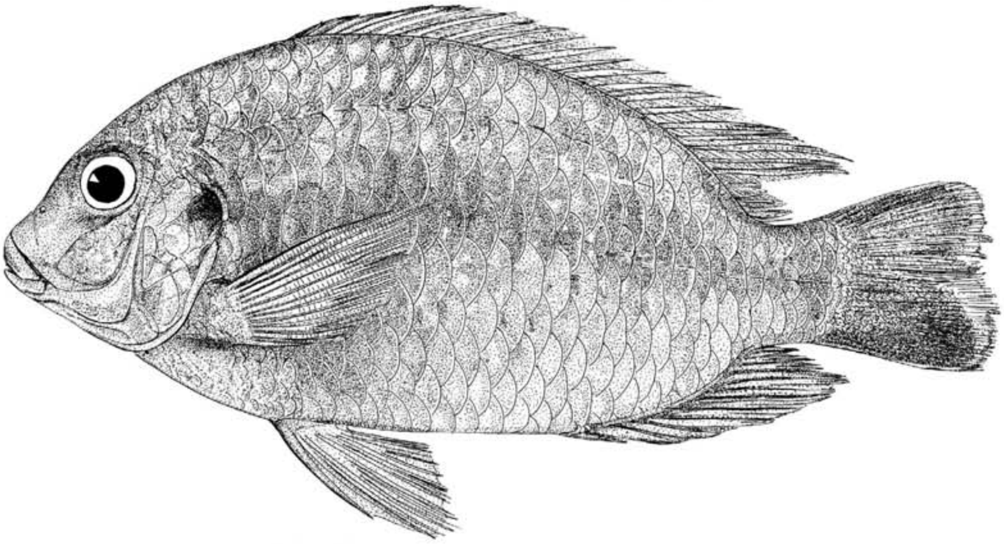

Fig. 16. *Congolapia louna*, MRAC A8-020-P-0980, holotype, 150.3 mm SL; Republic of the Congo: Louna River (drawing by R. Kühbandner).

dorsal branched rays and terminating midlaterally on caudal peduncle. Two scale rows between upper and lower lateral lines. Preoperculum scaled with three to four regular rows. Chest with smaller slightly embedded scales. Minute scales covering approx. 80 % of caudal fin, scales on rays arranged in rows, all other unordered.

Gill rakers. First ceratobranchial with 13 gill rakers and first epibranchial with 3–4 gill rakers, a single gill raker on cartilaginous plug included in angle of arch in latter number. Total number of gill rakers on first gill-arch 16–17. Ceratobranchial rakers slender, broader on base, pointed and unbranched. Gill rakers situated most ventrally on ceratobranchial smaller than others.

Fins. Pelvic-fin base at level of dorsal-fin origin. Dorsal spines 16. Dorsal rays 10–11. First dorsal spine always shortest, last dorsal spine always longest. Longest spines always shorter than longest rays. Last dorsal ray most deeply branched.

Fig. 17. *Congolapia louna*, MRAC A8-020-P-0969-0970, paratype, 117.7 mm SL; Republic of the Congo: Louna River (photograph from MRAC).

Caudal fin truncate or slightly emarginate. Three anal spines and 8–9 anal rays. Third anal spine always longest. Last anal ray most deeply branched. Tip of longest anal-fin ray overlapping hypuralia. Tip of longest pelvic-fin ray not reaching anus. Pectoral-fin rays 13–14.

Jaws and dentition. Jaws isognathous. Upper and lower outer teeth rows bicuspid in both jaws. Neck of anterior jaw teeth spatulate, crown brownish, expanded and cusps truncated (Fig. 7). Three to six incomplete inner rows of smaller tricuspid teeth in both jaws. Lower pharyngeal jaw as long as broad, anterior keel shorter than toothed area (Fig. 8). Most posterior pharyngeal teeth bicuspid (few tricuspid), stout, slightly hooked and regularly arranged, especially on last 2–3 rows of toothed area (Fig. 9). Dentigerous plate triangular. Most of teeth in anterior two thirds of toothed area approaching "kukri" shape (sensu Greenwood, 1987), i.e. upper part of teeth angled posteriorly, and vertical through tip well behind body of tooth.

Coloration in alcohol (Fig. 15)**.** Background colour brownish. Head and dorsal side dark brownish, ventral side light brownish. Chest slightly pigmented and belly sometimes reddish. Flank scales with dark scale margin and light centre. Lower lip light brownish to whitish and upper lip darker than lower. Markings on body: five to seven black, backward slanted, unbranched (not Y-shaped) bars on dorsum and sides (first bar at level of first dorsal spine, last two on caudal peduncle) and a nape band. Bars often absent, apparently depending on motivational state. Longitudinal mid-lateral and dorso-lateral stripe. Black opercular spot. Fins: pectoral fin hyaline. Pelvic, anal and caudal fins light brownish. Dorsal fin light brownish, no "tilapia spot".

Life coloration (Fig. 17)**.** Description based on photographs taken in the field of paratype from MRAC A8-020-P-0969–0970 (117.7 mm SL). The specimen was already dead, thus the colours were slightly faded. Background colour light olive-green to greyish, chest and belly whitish. Lower half of head whitish to light yellowish, and upper half of head brownish olive. Upper and lower lip whitish. Iris dark brown. Yellowish lachrymal stripe extending from lachrymal to jaw angle; black opercular spot. Pectoral fin at base light brownish, pelvic and anal fin greyish. Dorsal fin greyish, no "tilapia spot". Caudal fin greyish.

Distribution and habitat. Only known from Louna River, a right bank affluent of the Lefini River (Republic of Congo) itself also a right bank affluent of the Congo River (Fig. 10).

Congolapia louna has been collected at two neighbouring localities only, both just upstream of the first rapids on the Louna where the river makes a turn of about 90 degree to the right. No detailed environmental parameters were recorded at this locality, however the water was fast flowing and the fish were caught with gill-nets placed over the sandy bottom. For more details on sympatric and syntopic presence of *C. louna* with the other two species see under *C. bilineata*.

Etymology. The species name *louna* refers to the Louna River, type locality of this species. A noun in apposition.

Discussion

According to the molecular phylogenetic analysis of Schwarzer et al. (2009), *Congolapia* is not closely related to *T. mariae*, the type species of the subgenus *Pelmatolapia*. Thys van den Audenaerde (1969) had already placed *T. bilineata* in an isolated position. The combination of 10–11 gill rakers and the presence of a densely scaled caudal fin are not shared with any of the species of the subgenus *Pelmatolapia* sensu Thys van den Audenaerde (1969) (*T. mariae*, *T. cabrae*, *T. brevimanus*, and *T. eisentrauti*). Since, *T. eisentrauti*, a mouthbrooder endemic to crater Lake Barombi Mbo (Cameroon), has been allocated to *Konia* Trewavas, 1972, which is closely related to the oreochromine genus *Sarotherodon* (Schliewen et al., 1994). The analysis of Schwarzer et al. (2009) also shows that *T. brevimanus* is not closely related to the type species of *Pelmatolapia*, *T. mariae*. Together, these results suggest that only *T. mariae* and *T. cabrae* will eventually remain members of the subgenus *Pelmatolapia* after completion of a generic revision of *Tilapia* (Dunz & Schliewen, in prep.).

The phylogenetic analyses based on mtDNA and nuclear DNA data (Schwarzer et al., 2009; Dunz et al., unpubl.) firmly place *Congolapia* in a monophyletic clade together with *Tilapia* sensu stricto from southern Africa and *Chilochromis duponti* known from the Ogowe, Niari-Kouilou and Nyanga drainages in Gabon and the Republic of Congo (Stiassny et al., 2007). In the analysis of Schwarzer et al. (2009), *Congolapia* is sister-group of *Tilapia* sensu stricto, and *Chilochromis* is sister-group of the *Congolapia*–*Tilapia* sensu stricto clade. This *Tilapia*–*Congolapia*–*Chilochromis* clade is sister-group to the genus *Steatocranus* (*"Steatocranus" irvinei* from the Volta in Ghana excluded). In several, but not all unpublished multilocus-nuclear DNA-analyses (Dunz & Schliewen unpubl.), *Chilochromis* and *Congolapia* are sister-groups. Indeed the two taxa share several morphological characters, i.e. identical dorsal-fin spine (17) and dorsal-fin ray (10) counts, similar lateral line scale counts (lower lateral line 10 vs. 9–10; upper lateral line 22 vs. 18–21), a higher number of gill rakers on the first lower gill arch (15 vs. 13; both high in contrast to 7–10 in *Tilapia* sensu stricto), scales extending far onto the caudal fin, and finally a similar colour pattern of seven oblique vertical and/or two longitudinal stripes, which are however not visible in all specimens. The distributions of *Congolapia* and *Chilochromis* are allopatric, but directly adjacent on either watershed side of the ancient Batéké-Plateau. In summary, the sister-group of *Congolapia* is genetically not yet firmly assignable, but morphology supports *Chilochromis*. If a *Congolapia*–*Chilochromis* sister-group relationship is corroborated, the split suggests an ancient connection between the southern Lower Guinea coastal drainages and the western tributaries of the central Congo.

There is evidence that some of the *Congolapia* specimens we examined are potentially hybrids. The MRAC Lefini collection contained several specimens, which were labelled with a field-ID as *T.* cf. *congica* (e.g. MRAC A8-020-P-0963). One of these specimens was sequenced and is referred to as *Congolapia* × *Coptodon* hybrid in Figure 1. These specimens share all morphological characters with *T. congica* and *T. tholloni*, including outer jaw teeth (non-spatulate shape in contrast to spatulate) and pharyngeal bone structure (tri- to quadricuspid teeth at posterior pharyngeal jaw in contrast to bicuspid or rarely tricuspid teeth). However, genetically, the specimen MRAC A8-020-P-0963 is most similar to *Congolapia* and appears as its sister-group in analyses using both nuclear and mitochondrial loci (Dunz & Schliewen, unpubl.). It is noteworthy that the two members of *Tilapia (Coptodon)* (*T. congica* and *T. tholloni* that share the typical *Congolapia* character of a densely scaled caudal fin in juveniles and adults, turn out to be the genetic sister-group of all remaining *Coptodon* (Dunz & Schliewen, unpubl.). It is further noteworthy that *Congolapia* has an overlapping distribution with *T. tholloni* and *T. congica*-specimens in collections, but the status of these specimens must be reinvestigated.

After the recent description of *Rhabdalestes yokai* Ibala Zamba & Vreven, 2008, the description of *Congolapia louna*, apparently endemic to a subdrainage of the Lefini River, highlights both the general low level of the ichthyological exploration of the Congo basin, as well as a biogeographic importance of the western tributaries of the Congo draining the Batéké Plateau. As deduced from the node age estimates presented by Schwarzer et al. (2009), who had included two

Congolapia lineages in their analysis, the two deep divergence mitochondrial DNA branches of *Congolapia* are at least 10.13 (5.6-15.1 SD) mya years old. All these deep lineages are present in the Lefini, suggesting that either the Lefini has a long history of isolated evolution of endemic lineages, or that this drainage harbours ancient relict lineages. We know of several additional undescribed species in the Lefini, but a detailed faunistic and phylogenetic investigation of adjacent Batéké plateau rivers, i.e. the Nkeni, Alima and Koyou rivers, as well of the headwaters of the Niari and Louessé are necessary to test this hypothesis.

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This paper is dedicated to the memory of Annette Ngoma Moutsinga (†27 January 2012: Republic of the Congo). She will be remembered as a dedicated ABIC trainee 2009 at the MRAC and fieldwork collaborator of A. Ibala Zamba and Emmanuel Vreven (2007-2009), and for so much more.

Appendix 1. Comparative material listed in Dunz & Schliewen (2010). Additional material:

Tilapia baloni: ROM 28120, 3 paratypes, 105.0-107.5 mm SL; Zambia: Isenga steam, Luongo River. – ROM 28071, 3 paratypes, 100.4-112.8 mm SL; Zambia: Congo River. – NRM 12331, 1, 34.4 mm SL; Zambia: Zaire River drainage: Kalungwishi River, Kundabwika Falls just above cataracts.

T. bythobates: AMNH 98242, holotype, 87.5 mm SL; Cameroon: Lake Bermin western, 5°09' N 9°38' E.

T. deckerti: ZMB 32754, holotype, 102.2 mm SL; Cameroon: "Toter See b. Ossidinge" [Lake Ejagham]. – ZSM 40077, 18, 60.0-88.9 mm SL; ZSM 40088, 1, 71.5 mm SL; ZSM 40078, 6, 64.6-77.9 mm SL; Cameroon: Lake Ejagham.

T. ejagham: ZSM 40074, holotype, 174.7 mm SL; ZSM 40075, 25 paratypes, 76.0-199.5 mm SL; ZSM 40076, 23, 46.6-186.6 mm SL; Cameroon: Lake Ejagham.

T. flava: AMNH 98264, holotype, 75.9 mm SL; Cameroon: Lake Bemin western, 5°09' N 9°38' E.

T. fusiforme: ZSM 40082, holotype, 44.9 mm SL; ZSM 40083, 15 paratypes, 44.9-59.5 mm SL; ZSM 40086, 10, 41.4-52.7 mm SL; ZSM 40084, 17, 60.3-78.0 mm SL; ZSM 40085, 14, 41.6-60.8 mm SL; ZSM 40087, 15, 57.9-80.0 mm SL; Cameroon: Lake Ejagham.

T. guinasana: RUSI 27334, 2, 69.0-79.6 mm SL; Namibia: Lake Guinas, Guinas Farm, Tsumeb district. – RUSI 35865, 1, 76.7 mm SL; RUSI 39126, 1, 101.4 mm SL; RUSI 35865, 1, 76.7 mm SL; RUSI 35863, 1, 73.7 mm SL; RUSI 41949, 2, 68.6-73.8 mm SL; RUSI 35864, 1, 84.2 mm SL; RUSI 35859, 1, 136.0 mm SL; Namibia: Lake Guinas. – RUSI 27250, 1, 59.8 mm SL; RUSI 45741, 1, 76.0 mm SL; RUSI 25485, 1, 83.3 mm SL; RUSI 25486, 1, 76.2 mm SL; Namibia: Lake Otjikoto.

T. guineensis: BMNH 1849.10.9.15, holotype, 149.7 mm SL; Ghana: Ashantee. – RUSI 44334, 1, 127.5 mm SL; Senegal: Geba System, Anambe Dam. – RUSI 44326, 1, 109.5 mm SL; Senegal: Geba System, Anambe River Bridge. – ZSM 25740, 1, 142.6 mm SL; Senegal: road from Bathurst to Dionloulon by Selety; Caramance Region. – ZSM 23002, 1, 74.4 mm SL; Ghana: Busua, 25km W of Takoradi.

T. sp. aff. *guineensis* "Cross" (undescribed): ZSM 27618, 8, 80.8-114.7 mm SL; Cameroon: West Cameroon, Rio Munaya, Cross River Basin near Eyumojok.

T. gutturosa: AMNH 98269, holotype, 61.2 mm SL; Cameroon: Lake Bemin western.

T. imbriferna: AMNH 98247, holotype, 101.7 mm SL; Cameroon: Lake Bermin western.

T. margaritacea: BMNH 1914.5.27.12-15, 4, syntypes, 62.9-128.3 mm SL; Cameroon: Nyong River at Akonolinga. – BMNH 1959.8.12.10-13, 4, 86.6-92.3 mm SL; Cameroon: Nyong River.

T. nigrans: ZSM 40079, holotype, 117.5 mm SL; ZSM 40080, 17 paratypes, 105.5-151.0 mm SL; ZSM 40081, 5, 74.5-150.3 mm SL; Cameroon: Lake Ejagham. – MRAC 157495, 1, 153.2 mm SL; Cameroon: "Toter See bei Ossidinge" [Lake Ejagham].

T. pra: ZSM 36123, holotype, 83.5 mm SL; ZSM 36116, paratype, 84.2 mm SL; ZSM 36117, paratype, 110.1 mm SL; ZSM 36118, paratype, 73.1 mm SL; ZSM 36119, paratype, 76.6 mm SL; ZSM 36120, paratype, 77.7 mm SL; ZSM 36121, paratype, 73.7 mm SL; ZSM 36122, paratype, 76.1 mm SL; ZSM 36124, paratype, 81.1 mm SL; ZSM 36125, paratype, 79.1 mm SL; Ghana: Ashanti Region, Anum River, tributary to PraZSM 36149, 1 paratype, 62.6 mm SL; Ghana: Ashanti Region, Oda River, tributary to Pra. – AMNH 250601, paratype, 57.7 mm SL; Ghana: Ashanti Region, Oda River, tributary to Pra. – ZSM 39005, 2 paratypes, 40.3–58.8 mm SL; Ghana: Nyelei, tributary to Ankobra. – AMNH 250602, 1 paratype, 54.7 mm SL; Ghana: Nyelei, tributary to Ankobra. – ZSM 39000, 3 paratypes, 48.7–58.4 mm SL; Ghana: Draw River. – ZSM 39001, 1 paratype, 108.2 mm SL; Ghana: Tano at Mempansem. – MRAC 87-18-P-5204-240, 3 paratypes, 95.7–103.4 mm SL; Ghana, Birim River. – MRAC 87-18-P-5189-203, paratype, 91.0 mm SL; MRAC 87-18-P-5248-314, paratype, 66.7 mm SL; Ghana: Pra River. – MRAC 79-36-P-70-84, 5 paratypes, 73.9–126.9 mm SL; MRAC 86-18-P-1948-951, 1 paratype, 57.6 mm SL; Côte d'Ivoire: Ayamé, River Bia.

T. rendalli: SAIAB 71029, 1, 60.9 mm SL; Zambia: Chirumba River. – SAIAB 71789, 1, 73.5 mm SL; Zambia: Matondo Lagoon, upper Zambezi: Branch Zambezi. – SAIAB 71905, 1, 84.9 mm SL; Zambia: Kataba River main road, upper Zambezi. – SAIAB 72574, 1, 74.3 mm SL; Zambia: Mutemwa, upper Zambezi. – SAIAB 72710, 1, 68.9 mm SL; Zambia: Simvula Lagoon, Zambezi River. – SAIAB 72668, 1, 70.8 mm SL; Zambia: Sioma Falls, River Zambezi. – SAIAB 71784, 1, 74.4 mm SL; Zambia: Luanginga River. – SAIAB 71341, 1, 68.5 mm SL; Zambia: side channel upstream from Kalabo Ferry. – SAIAB 73146, 1, 77.0 mm SL; Zambia: near Lealui, Kanokana River. – RUSI 67718, 1, 98.6 mm SL; Mozambique: Manica; Buzi River; Revue River. – RUSI 59501, 1, 60.8 mm SL; SAIAB 78750, 1, 74.6 mm SL; Namibia: Kunene River. – RUSI 63168, 1, 59.0 mm SL; Namibia: Oshana, Ogongo hole. – RUSI 45760, 1, 91.3 mm SL; South Africa: Barberton, Hectorspruit. – SAIAB 85512, 2, 75.4–96.1 mm SL; Angola: Malanje, Russian Fishing Camp.

T. ruweti: SAIAB 81505, 1, 62.8 mm SL; Democratic Republic of the Congo: Katanga, River Bona. – SAIAB 77224, 1, 67.5 mm SL; Zambia: Luapula: Kalungwishi River. – RUSI 71712, 1, 48.1 mm SL; Zambia: Kasima swamp Lagoon, upper Zambezi. – SAIAB 68652, 1, 65.7 mm SL; .SAIAB 68650, 1, 58.8 mm SL; Botswana: Ngamiland, Moremi Wildlife Park, River Maunachira. – RUSI 18838, 1, 71.6 mm SL; Botswana: Nxamaseri "cow dung" Molopo pool. – RUSI 28705, 1, 59.3 mm SL; Botswana: Thamalakane River, Okavango Delta. – RUSI 29567, 1, 69.4 mm SL; Botswana: Kwai floodplain, isolated Lagoon, Moremi Game Reserve, Okavango Delta. – RUSI 63202, 1, 60.1 mm SL; Botswana: Thamalakane River. – RUSI 29474, 1, 65.6 mm SL; Botswana: Kwai Floodplain, Moremi Game Reserve, Okavango Delta. – RUSI 29675. 1, 68.0 mm SL; Botswana: Maxegana Floodplain, Moremi Game Reserve, Okavango Delta. – ROM 28034, 1, 61.4 mm SL; Zambia: Luongo River.

T. snyderae: AMNH 98259, holotype, 38.8 mm SL; Cameroon: Lake Bermin western.

T. spongotroktis: AMNH 98258, holotype, 122.0 mm SL; Cameroon: Lake Bermin western, 5°09' N 9°38' E.

T. zillii: RUSI 26020, 1, 42.2 mm SL; Algeria: Chouca Village.

T. congica × *Congolapia louna*: MRAC A8-020-P-0963, 1, 107.1 mm SL; Republic of the Congo: River Lefini, about 600 m to camp Oteni, 2°49'29" S 15°47'31" E.

Appendix 2. List of all taxa and genes (with GB accession numbers) included in dataset. *Tilapia ruweti* JQ992913, GQ167799; *Chilochromis duponti* JQ992914, GQ167776; *Congolapia crassa* JQ992915–JQ992931; *Congolapia bilineata* JQ992932, JQ992933; *Congolapia louna* JQ992934, JQ992935, *Congolapia louna* x *Paracoptodon* sp. JQ992936; *Tilapia brevimanus* GQ167828; Steatocranus tinanti GQ167795; Steatocranus gibbices GQ167791; *Tilapia sparrmanii* GQ167800, AF317260; *Tilapia guinasana* GQ167802; *Tilapia bilineata* "Lefini" GQ167775.

Literature cited

Boulenger, G. A. 1915. Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History). British Museum (Natural History), London, xii + 526 pp.

Dunz, A. R. & U. K. Schliewen. 2010. Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana. Zootaxa, 2548: 1–21.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research, 32: 1792–1797.

Greenwood, P. H. 1987. The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. Bulletin of the British Museum (Natural History), Zoology, 53: 139–203.

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium, 41: 95-98.

Hammer, Ø., D. A. T. Harper & P. D. Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica, 4: 9.

Huelsenbeck, J. P. & F. Ronquist. 2001. MrBAYES: Bayesian inference of phylogenetic trees. Bioinformatics, 17: 754–755.

Ibala Zamba, A. 2010. Faune des poissons des rivières Luki et Léfini (Bassin du Congo): diversité et écologie. Katholieke Universiteit Leuven. Arenberg Doctoral School of Science, Engineering & Technology, Faculty of Science, Department of Biology, 452 pp.

Ibala Zamba, A. & E. Vreven. 2008. *Rhabdalestes yokai* (Characiformes: Alestidae), a new species from the Léfini and Sangha River basins (Congo River basin), Africa. Ichthyological Exploration of Freshwaters, 19: 377-384.

Klett, V. & A. Meyer. 2002. What, if anything, is a *Tilapia*? – Mitochondrial ND2 phylogeny of tilapiines and the evolution of parental care systems in the African cichlid fishes. Molecular Biology and Evolution, 19: 865-883.

Kocher, T. D., J. A. Conroy, K. R. Mckaye, J. R. Stauffer & S. F. Lockwood. 1995. Evolution of NADH dehydrogenase subunit 2 in East African cichlid fish. Molecular Phylogenetics and Evolution, 4: 420-432.

Pellegrin, J. 1904. Contribution à l'étude anatomique, biologique et taxinomique des poissons de la famille des Cichlidés. Mémoires de la Société Zoologique de France, 16: 41-400.

Regan, C. T. 1920. The classification of the fishes of the family Cichlidae. – I. The Tanganyika genera. Annals and Magazine of Natural History, Ser. 9, 5: 33-53.

Schliewen, U. K., D. Tautz & S. Pääbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature, 368: 629-632.

Schwarzer, J., B. Misof, D. Tautz & U. K. Schliewen. 2009. The root of the East African cichlid radiations. BMC Evolutionary Biology, 3: 1-11.

Silvestro, D. & I. Michalak. 2010. RaxmlGUI: a graphical front-end for RAxML. Organisms Diversity and Evolution. DOI: 10.1007/s13127-011-0056-0

Smith, A. 1840. Illustrations of the zoology of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa in 1834-36. Pisces. Smith, Elder & Co., London, 4: 77 pp., pls. 1-31.

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics, 22: 2688-2690.

Stiassny, M. L. J., U. K. Schliewen & W. J. Dominey. 1992. A new species flock of cichlid fishes from Lake Bermin, Cameroon with a description of eight new species of *Tilapia* (Labroidei: Cichlidae). Ichthyological Exploration of Freshwaters, 3: 311-346.

Stiassny, M. L. J. & U. K. Schliewen. 2003. *Etia nguti*, a new genus and species of cichlid fish from the River Mamfue, Upper Cross River basin in Cameroon, West-Central Africa. Ichthyological Exploration of Freshwaters, 14: 61-71.

Stiassny, M. L. J., A. Lamboj, D. De Weirdt & G. G. Teugels. 2007. Cichlidae. Pp. 269-403 in: M. L. J. Stiassny, G. G. Teugels & C. D. Hopkins (eds.), The Fresh and brackish water fishes of Lower Guinea, West-Central Africa. Volume 2. IRD, Paris, MNHN, Paris & MRAC, Tervuren.

Thys van den Audenaerde, D. F. E. 1964. Révision systématique des espèces congolaises du genre *Tilapia* (Pisces, Cichlidae). Annales du Musée Royal de l'Afrique Centrale, Série in-8°, Sciences Zoologiques, 124: 1-155.

Thys van den Audenaerde, D. F. E. 1969. An annotated bibliography of *Tilapia* (Pisces, Cichlidae). Annales Musée Royal de l'Afrique Centrale, Série N-14, Documentation Zoologique, xl pp.

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Molecular phylogeny and revised classification of the haplotilapiine cichlid fishes formerly referred to as "*Tilapia*"

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Abstract

African cichlids formerly referred to as "Tilapias" represent a paraphyletic species assemblage belonging to the so called haplotilapiines lineage which gave rise to the spectacular East African cichlid radiations (EARs) as well as to globally important aquaculture species. We present a comprehensive molecular phylogeny of representative haplotilapiine cichlids, combining in one data set four mitochondrial and five nuclear loci for 76 species, and compare it with phylogenetic information of 378 mitochondrial ND2 haplotypes representing almost all important "*Tilapia*" or *Tilapia*-related lineages as most EAR lineages. The monophyly of haplotilapiines is supported, as is the nested sister group relationship of *Etia* and mouthbrooding tilapiines (oreochromines) with the remaining haplotilapiines. The latter are consistently placed in nine monophyletic clades over all datasets and analyses, but several dichotomous phylogenetic relationships appear compromised by ancient hybridisation events leading to cytonuclear discordant phylogenetic signal. Based on these results as well as on morphological evidence we propose a novel generic and suprageneric classification including a (re-)diagnosis of 20 basal haplotilapiine cichlid genera and ten tribus. New tribus are provided for the former subgenera *Coptodon* Gervais, 1853, *Heterotilapia* Regan, 1920 and *Pelmatolapia* Thys van den Audenaerde, 1969, in addition for "*Tilapia*" *joka*, *Tilapia* sensu stricto and *Chilochromis*, *Etia*, *Steatocranus* sensu stricto, the mouthbrooding tilapiines and for a basal clade of West African tilapiines.

Keywords

Freshwater fishes, Cichlidae, introgressive hybridisation, cytonuclear discordance, Africa

1. Introduction

Cichlids (Teleostei: Perciformes: Cichlidae) rank among the most species rich fish families. They currently hold 1627 valid species (Eschmeyer & Fong 2012), but may count up to 3000 species, distributed throughout the Neotropics, Africa, the Middle East, Madagascar, as well as Southern India, and Sri Lanka (Snoeks 2000; Turner et al. 2001). Their morphological, behavioural and ecological diversity has fascinated biologists ever since the enormous diversity of cichlids in the East African cichlid radiation (EAR) endemic to Lakes Tanganyika, Malawi and the Lake Victoria region became apparent (Fryer & Iles 1972; Kornfield & Smith 2000). Over the last decades, cichlids have become a prime model system in evolutionary biology; especially in speciation research (Kocher 2004; Salzburger & Meyer 2004; Seehausen 2006). Aquacultural research as well as evolutionary biologists caught attention of "*Tilapia*", i.e. members of the so called tilapiine cichlid assemblage (sensu Trewavas 1983 – details see below) member of the Pseudocrenilabrinae, as not only one of its members, the Nile Tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is of globally important aquacultural significance (Ridha 2006) as a food resource, but also were giving rise to small species radiations (Schliewen & Klee 2004). Further, molecular phylogenetic analyses suggest that the root of the East African cichlid radiation is nested within a paraphyletic tilapiine assemblage containing among other tilapiine genera, members of the genus *Tilapia* Smith, 1840 (Klett & Meyer 2002; Schwarzer *et al.* 2009).

To facilitate the discussion about tilapiine phylogeny and classification, we provide a short overview of the previous attempts to classify *Tilapia* related taxa based on morphological, ethological and molecular data here. The genus *Tilapia* was introduced by Smith, 1840, as a new "division" of the Labyrinthiformes Cuvier 1831, with *T. sparrmanii* Smith, 1840 as type *species*. 75 years later Boulenger (1915, 1916) already listed 94 species in the genus *Tilapia*. His classification was based mainly on dentition and squamation characters and fin meristics. However, he stated that "the classification of the very numerous African members of the family Cichlidae presents the greatest difficulties, and the division into genera, as here followed, is unsatisfactory and open to criticism, the dentition in certain species being subject to variation, according to age, or even of a purely individual nature." Inspired by this uncertainty, Regan (1920, 1922) subsequently provided a suprageneric reclassification of African cichlid genera based on additional characters, mainly the structure of the pharyngeal apophysis, which supports the upper pharyngeal bones at the base of the skull. In his view, the occurrence of a "*Tilapia*" type apophysis, i.e. the pharyngeal apophysis formed by the parasphenoid alone, restricted the genus *Tilapia* to those species, which Boulenger (1915, 1916) had attributed to his *Tilapia* Section I (about 50 species). Additional closely related genera with the apophysis formed by the parasphenoid alone or by the parasphenoid and the prootics were, among others, *Chilochromis* Boulenger, 1902 and *Neotilapia* (Regan, 1920) (parasphenoid and prootics), but not, for example, *Steatocranus* Boulenger, 1899. Supported by additional dentition and squamation characters, he therefore redefined the genus *Tilapia* and recognized four *Tilapia* subgenera (*Coptodon* (Gervais, 1853), *Tilapia*, *Heterotilapia* (Regan, 1920) and *Sarotherodon* Rüppell, 1852), as well as a closely related separate genus, *Neotilapia*. He suggested that "a complete revision will be necessary before a final decision can be reached as to whether it should be split up." Nevertheless, Hoedeman (1947) taxonomically formalized Regan´s informal split of African cichlids into two major groups by introducing the subfamily Tilapiinae Hoedeman, 1947 for all African cichlids with a *Tilapia* type apophysis and the Haplochrominae[3] Hoedeman, 1947 for the rest. Almost 50 years (after Boulenger) ago, Thys van den Audenaerde (1969) published a first comprehensive species level classification of African species of what he considered to belong to the genus *Tilapia*. In his definition, *Neotilapia* and *Pelmatochromis* sensu stricto Steindachner, 1895 were included only as subgenera of *Tilapia*, which now comprised approximately 90 described and undescribed species. He further divided the genus into three "sections", each including several diagnosed and taxonomically available subgenera, some of them new (Tab. 1). His classification was not accompanied by a critical discussion of previous classifications and diagnostic characters, but was presented in the form of a key, annotated with a revised diagnosis for *Tilapia* and the subgroups. Although he referred to Regan (1920), he did not take into account the osteological characters described by this author, hereby indirectly accounting for Wickler´s (1963) criticism of Regan´s and Hoedeman´s classification as being inconsistent with the distribution of ethological characters. Trewavas (1973) contested the inclusion of *Pelmatochromis* sensu stricto as a subgenus into *Tilapia* and proposed full generic rank for it, as well as a new genus, *Pterochromis* Trewavas, 1973. Further, she retained *T. busumana* (Günther, 1903) in *Tilapia* and amalgamated all remaining species of Thys van den Audenaerde´s (1969) Section I and Section II (comprising exclusively substrate brooding genera) in a newly diagnosed genus *Tilapia* without any further subgeneric division; and, mainly based on osteological characters and breeding behaviour, she elevated Thys van den Audenaerde´s Section III (comprising exclusively mouthbrooding genera) members to full generic rank, i.e. *Sarotherodon*.

Greenwood (1978) conducted a representative review of the structure and distribution of Regan's apophyseal character in cichlids. He confirmed Wickler´s critic, and concluded that the pharyngeal apophysis must be rejected as a character useful for subfamilial classification in cichlids. Nevertheless, Trewavas (1983) in her book "Tilapiine Fishes of the genera

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[3] Fowler (1934) introduced the taxonomically available subfamily name Pseudocrenilabrinae for all African and Middle East Cichlidae. Apparently unaware of Fowler´s action, Hoedeman (1947) introduced Tilapinae and Haplochominae as new subfamilies for African and Middle Eastern Cichlidae. At the moment, it remains unclear to which subfamily Hoedeman attached the type name bearing genus *Pseudocrenilabrus* Fowler, 1934, although it is very likely that he attached it to the Haplochrominae. If so, the Haplochrominae Hoedeman, 1947 is a synonym of Pseudocrenilabrinae Fowler, 1934. Then also the tribus name Haplochromini must be changed. However, since the focus of this work is not on the haplochromine cichlids, and since the issue is not finally analysed, we retain the familiar tribus name Haplochromini throughout the manuscript.

Sarotherodon, *Oreochromis* and *Danakilia*", introduced a new tribe name, Tilapiini, which she distinguished from her new tribe Haplochromini on the basis Regan´s pharyngeal apophysis character states. Surprisingly, she neither referred to Greenwood´s arguments nor to Hoedeman´s formal subfamily rank Tilapiinae. Based on cursory exploration of morphological, ethological and ecological characters her tribe Tilapiini still included the substrate brooding genera *Pelmatochromis*, *Pterochromis*, *Tilapia* and specialised rheophilic genera (tentatively) *Steatocranus* and *Gobiochromis* Poll, 1939, as well as the mouthbrooding genera *Sarotherodon, Oreochromis* Günther, 1889*, Danakilia* Thys van den Audenaerde, 1969*, Iranocichla* Coad, 1982, *Tristramella* Trewavas, 1942 and all endemic cichlid genera of crater lake Barombi Mbo. In addition, she suggested an extension of Thys van den Audenaerde´s (1969) subgeneric classification of *Oreochromis* by proposing an additional subgenus. Poll (1986) adopted the definition of Trewavas 1983 for Tilapiini, added additional diagnostic characters, but treated explicitly only the few Tilapiini taxa from Lake Tanganyika. He included the Lake Tanganyika endemic *Boulengerochromis* Pellegrin, 1904 with *Tilapia* and *Oreochromis* in his Tilapiini. Greenwood (1987) compared the osteology of taxa previously referred to as *Pelmatochromis* sensu lato. He concluded that neither *Pelmatochromis* nor *Pterochromis* can be considered as being phylogenetically close to *Tilapia* or tilapiines, and that the monophyly of the tilapiines (even without these two genera) remains to be demonstrated despite the fact that he identified two additional characters possibly supporting their monophyly. Eventually, Stiassny (1991) provided a first cladistic analysis of cichlids based on mainly morphological cichlid characters. She identified two additional character states of the lower pharyngeal jaw, which she regarded as preliminary evidence for a monophyletic tilapiine lineage including *Danakilia*, *Iranocichla*, *Konia* Trewavas, 1972, *Myaka* Trewavas, 1972, *Oreochromis*, *Pungu* Trewavas, 1972, *Sarotherodon*, *Stomatepia* Trewavas, 1962, *Tristramella* and *Tilapia,* however excluding *Pelmatochromis*, *Pterochromis*, *Steatocranus* and *Gobiocichla* Kanazawa, 1951. Pending further investigations, she preferred the ending –ine(s) for any suprageneric African cichlids groups including tilapiines.

Cichlid systematics are plagued with a paucity of phylogenetically informative morphological characters (Stiassny 1991). First allozyme studies tried to overcome this limitation by testing for biochemical differentiation of tilapiines using multiple markers. These studies supported a basal distinction between substrate brooding and mouthbrooding tilapiines, but were not able to assess phylogenetic relationships in more detail (McAndrew & Majumdar 1984; Sodsuk & McAndrew 1991; Pouyard & Agnese 1995; B-Rao & Majumdar 1998). First DNA based studies incorporating a few tilapiines into a greater cichlid phylogenetic framework yielded statistically well supported evidence for tilapiines and the EAR representing a monophyletic lineage, and for tilapiines being paraphyletic (Sültmann et al. 1995; Mayer et al. 1998;

Streelman et al. 1998). This unexpected and novel result has been supported or at least not contradicted by all subsequent molecular analyses which included more tilapiine taxa (Nagl et al. 2001; Klett & Meyer 2002). The new clade, comprising the majority of all African cichlids including tilapiines and haplochromines, is supported by one putative synapomorphy, i.e. a tricuspid inner row dentition (Schliewen & Stiassny 2003). The clade was named haplotilapiines in order to point out that a phylogenetically based classification of tilapiines is not possible without incorporating representative members of haplochromines and members of the EAR.

Nagl et al. (2001) and Klett & Meyer (2002) were the first to analyse mitochondrial DNA of more than 30 tilapiine taxa. While the first study focused on *Oreochromis*, the latter included a pan African sample of 39 tilapiine as well as 19 non tilapiine, mostly EAR species in their analysis. Albeit with low statistical support for basal nodes, mouthbrooders (*Oreochromis*, *Sarotherodon*, *Stomatepia*, *Iranocichla* and *Tristramella*) and members of the EAR each formed a comparatively well supported clade as opposed to substrate brooding tilapiines, which split into seven clades consisting of different members of the genera *Tilapia* and *Steatocranus*, and of *Etia nguti*, Interestingly, the type species of *Tilapia, T. sparrmanii* appeared more closely related to *Boulengerochromis microlepis* than to all other included "*Tilapia*" species. Schliewen et al. (1994) had previously shown that all endemic mouthbrooding tilapiine genera of crater lake Barombi Mbo (*Stomatepia*, *Pungu*, *Konia*, *Myaka*) are closely related to *Sarotherodon*.

Schwarzer et al. (2009) made the first attempt to combine an extended multilocus DNA dataset with a representative taxon sampling. Their phylogenetic analysis identified *Etia* with strong node support as the sister group ("etiines") to the remaining haplotilapiines, which were further bipartitioned into a mouthbreeding tilapiine lineage ("oreochromines") and an unnamed large clade. This large clade contained all remaining species, which fell into five subclades, of which two predominantly West African ones formed one monophyletic group ("boreotilapiines"), and two predominantly South Central African ones and the EAR formed another moderately supported one ("austrotilapiines")[4]. Due to a strongly discordant phylogenetic signal in the multilocus dataset, the sixth lineage, *T. mariae* Boulenger, 1899, could not be placed unambiguously in the one of the two large clades. This result was discussed as preliminary evidence for an ancient hybrid origin of *T. mariae*.

No study has yet included a fully representative taxon sampling of at least all previously suggested *Tilapia* related genera and subgenera, nor is a taxonomically valid classification

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[4] Group names introduced by Schwarzer et al. (2009) were inappropriately ending with the suffix –ini for Etiini, Oreochromini, Austrotilapiini, Boreotilapiini. These tribus-like names are neither taxonomically available according to the ICZN, nor were they meant to be (see disclaimer in Schwarzer et al. (2009)). As already previously suggested (Dunz & Schliewen 2010) we refer to these groups as used in Schwarzer et al. (2009) as etiines, oreochomines, austrotilapiines and boreotilapiines in order to avoid confusion with formal tribe names ending with "-ini".

integrating morphological and molecular data for this key group available. Using the data of Schwarzer et al. (2009) as a starting point, we present a combined phylogenetic analysis of (1) a further extended multilocus dataset (mtDNA and ncDNA loci) comprising almost all previously missing haplotilapiine cichlid tribes, and of (2) an enlarged mtDNA (ND2) dataset comprising about 60% of all described Pseudocrenilabrinae genera. This molecular analysis provides a basis for a novel classification of *Tilapia* and related lineages defined by putative molecular synapomorphies (unambiguously diagnostic character states), but critically incorporating a selected set of morphological data.

2. Material and Methods

2.1. Taxon sampling, datasets and lab protocols

This study focuses on the haplotilapiines sensu Schliewen & Stiassny 2003 (ingroup). Two datasets were established: (1) a combined nuclear and mtDNA “dataset A” representing almost all major haplotilapiine tribes and additional basal African cichlid taxa of the genera *Tylochromis* Regan, 1920, *Pelmatochromis* Steindachner, 1894 and *Pterochromis* Trewavas, 1973 consisting of 94 terminals representing 76 species. 58 terminals were adopted from Schwarzer et al. (2009) and 36 specimens are new (for Genbank IDs see Appendix A, Supplementary material 1); and (2) a “dataset B” consisting of 784 ND2 mtDNA haplotypes representing 102 haplotilapiine genera and 378 species. 707 sequences (ND2) were downloaded from GenBank and 77 are new (for Genbank IDs see Appendix A, Supplementary material 2). *Heterochromis multidens* (Pellegrin, 1900) served as outgroup in “dataset A”, because this species is basal to Pseudocrenilabrinae (Lippitsch 1995; Salzburger et al. 2002; Schwarzer et al. 2009; Stiassny 1990); *Etia nguti* served as outgroup to all remaining haplotilapiines in “dataset B”, because it was identified in the multilocus analysis as the sister group to the remaining haplotilapiines. Several Tanganyika cichlid tribes (Cyphotilapiini Takahashi, 2003, Limnochromini Poll, 1986, Ectodini Poll, 1986, Perissodini Poll, 1986) as well as *Orthochromis* Greenwood, 1954 from the Malagarazi River (Tanzania) are represented only in “dataset B”.

Genomic DNA was extracted from fin samples or muscle tissue using the NucleoSpin® Tissue kit (Macherey-Nagel) following the standard protocol provided by the manufacturer. Electropherograms and sequences of nine amplified fragments identical to the ones used in Schwarzer et al. (2009) were edited, aligned and analysed using BioEdit v.7.05.3 (Hall, 1999), after using ClustalW (default settings) for a preliminary alignment. Muscle v.3.6 (Edgar, 2004) (default settings) was used for refining the alignment. In addition, as a final quality control, sequences with missing nucleotides were checked by eye. Protein coding genes were checked for stop codons and frameshifts by translating into amino acid sequences. Saturation at each codon position was checked separately by using PAUP* 4.0 (Swofford 2003). The final “dataset A” contained five nuclear loci (ENC1: 698 bp, Ptr: 691 bp, SH3PX3: 681 bp, Tmo4c4: 425 bp, S7 intron: 508 bp) and four partial mitochondrial fragments (12S: 350 bp, 16S: 522 bp, 12S/16S: 1239 bp (originally 1295 bp, 56 bp were excluded due to alignment ambiguities), ND2: 672 bp). The third codon positions (341 bp) for ND2 were saturated in “dataset A” and excluded therein resulting 672 bp. The final “dataset A” had 6127/5786 bp (with/without third codon positions of ND2). For all loci base frequencies were not significantly different from equal (Chi-square tests, df=279; p=1.0). The final alignments are available on DRYAD (http://www.datadryad.org/).

2.2. Phylogeny reconstruction

Phylogenetic analyses were conducted applying Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. The alignment of “dataset A” was partitioned following Schwarzer et al. 2009: Partition 1 from 1-2495 bp (nuclear exons ENC1, Ptr, SH3PX3 and Tmo4c4), partition 2 from 2496-3003 (nuclear S7 intron), partition 3 from 3004-5114 bp (mtDNA:12S/16S), and partition 4 from 5115-5786 bp (mtDNA:ND2). RAxML v.7.0.3 (Stamatakis, 2006) was used for ML analysis: model parameters (Γ-model of rate heterogeneity, ML estimate of α-parameter) were estimated individually for each partition, and a ML search with the GTR+Γ model was performed as implemented in this program version. Node support values are based on 1000 non parametric bootstrap replicates (BS) of the best scoring ML tree. MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) was used for BI analyses, using the Bayes Factor Test implemented in the program for model choice, which was for partition 1: GTR+Γ, for partition 2: GTR+Γ, for partition 3: HKY, and for partition 4 GTR+Γ. BI was based on four parallel runs each over 10^6 generations starting with random trees and sampling trees every 1000 generations. To ensure convergence the first 10% generations of each run were treated as burn-in and excluded. The remaining trees from all Bayesian analyses were used to build a 50% majority rule consensus tree. BI branch supports are expressed as Bayesian posterior probabilities (BPP, BI). A ML approach was used analogously to infer a phylogenetic hypothesis of “dataset B”, with the GTR+Γ model, whereas ND2 were partitioned according to 1st and 2nd vs. 3rd codon position.

As a standard measure for the “quality” of a tree hypothesis the Rescaled Consistency Index (RC) (Farris 1989) was calculated across all 1000 bootstrap trees of the ML analysis by using the program PAUP* 4.0 (Swofford 2003). RC values range from 0-1 and are the product of the Consistency Index (CI) and Retention Index (R).

Alternative tree topologies were compared to the best supported combined nuclear loci topology (ML) or to best supported mitochondrial locus topology (ML) using the likelihood based, non parametric Shimodaira-Hasegawa Test (SH-Test) (Shimodaira & Hasegawa 1999) as implemented in CONSEL (Shimodaira & Hasegawa 2001). Single locus topologies constrained to the combined nuclear topology were compared to unconstrained ones. A value of $p<0.05$ was considered as significantly different.

2.3. Tests for alternative phylogenetic hypotheses and ancient hybrid signal

Phylogenetic hypotheses derived from "dataset A" were tested for consistency of a taxon position over 1000 bootstrap ML dichotomus trees using the leaf stability index (Thorley & Wilkinson 1999) calculated for all taxa with the program Phyutility v.2.2. (Smith & Dunn 2008). Branch attachment frequencies were calculated for taxa with low leaf stability values using all 1000 bootstrap trees of the ML analysis.

Conflicting phylogenetic signals potentially originating from loci with different ancestry in a multilocus dataset may be indicative of ancient or recent hybridisation, because the inclusion of a hybrid taxon in a dichotomous tree phylogeny is expected to produce conflicting phylogenetic signal resulting in low BS support values of affected nodes. To test for this effect we used a tree based homoplasy excess test (HET) following Seehausen (2004): 47 selected groups (single terminals 20) were successively removed from the dataset, and ML BS support values were recalculated and checked for all nodes and each removal. To assess type I error, a jackknife approach removing 100 times 16 randomly selected terminals (excluding those that produced outlier effects) was applied in order to obtain a semi random BS value distribution for all six nodes that yielded HET outliers. A removal group size of 16 was chosen because this count represents the largest removed group size in the previous 47 removal experiments that had yielded BS outliers. In some cases, if the BS for a given node was low and not directly inferable from the majority rule BS consensus tree, branch attachment frequencies for clades or single taxa were calculated in Phyutility v.2.2. Value variation (BS) of all nodes was graphically inspected for the presence of outliers in boxplots, i.e. values exceeding 1.5 (circles) or 3 (stars) times the box height (25-75 percent quartile) from the box, using the statistical program PAST 2.10 (Hammer et al. 2001).

2.4. Criteria for a novel classification

The supraspecific taxonomy of tilapiine cichlids has been instable, sometimes contradictory and often used in a mixture of taxonomically available with some unavailable names. Our analyses confirm that tilapiine cichlids as previously understood are paraphyletic and are composed of several distinct lineages. To incorporate phylogenetic results into a consistent classification for future reference in evolutionary biology and taxonomy, we discuss, introduce, revitalize and (re)define taxonomically available as well as novel genus and tribus names according to the rules of the International Commission of Nomenclature (ICZN, 1999). This is done only for *Tilapia* related lineages in the focus of this study if (1) lineages receive strong node support in the ML and BI analyses, i.e. BS (>90) and BPP (1.0), if (2) lineage specific node recovery is consistent over all analyses in “datasets A and B”, and if (3) diagnostic molecular and/or morphological characters can be used to unambiguously identify those lineages. We reason that these lineages have been cohesive over long periods and deserve taxonomic recognition, even if basal nodes remain weakly supported, sometimes possibly due to phylogenetic conflict reflecting ancient hybridisation. To establish diagnostic morphological character states for tribus diagnoses, we examined 20 easily observable character states in 1006 specimens of “*Tilapia*” and related taxa (see Appendix A, Supplementary material 3), compared these with literature data of EAR cichlids, oreochromines and outgroups (references see under 3.3. Classification) and, in addition, use our own partially unpublished data of the ongoing systematic revision of the genus *Tilapia* (Dunz & Schliewen 2010, Dunz et al. 2012 (submitted)). We point out that beyond the continued usage of established tribus names of the Lake Tanganyika tribes a critical evaluation, redefinition, and classification of haplotilapiine tribes of the EAR is beyond the explanatory power of this dataset, due to our limited taxon sampling. Only in cases in which previously established tribus names are phylogenetically nested within another one of our new tribus, we propose synonymy of the former.

3. Results

3.1. Characteristics of “datasets A and B”

The alignment of the concatenated nuclear and mitochondrial “dataset A” includes 94 taxa each with 6127 bp DNA sequence data derived from five nuclear and four mitochondrial loci. The final alignment with 5786 bp is a result from the exclusion of 341 bp due to saturation of the 3rd codon position of the mitochondrial ND2 locus and alignment ambiguities in non coding genes. The final dataset had 2497 variable sites with empirical base frequencies of A=0.281, C=0.258, G=0.221, T=0.239. These are composed of empirical base frequencies in the combined nuclear dataset: A=0.260, C=0.234, G=0.250, T=0.256, and in the mitochondrial dataset: A=0.304, C=0.285, G=0.189, T=0.221; base frequencies of the nuclear and the mitochondrial dataset are not significantly different (p>0.05, paired t-test). The Bayes factor test identified the GTR+Γ model as the best fitting model for all loci except for mitochondrial loci (12S, 12S/16S, 16S), which fitted best the HKY model.

The mitochondrial ND2 alignment of “dataset B” included 784 taxa each with 1008 bp. It contained 924 variable sites and empirical base frequencies of A=0.260, C=0.356, G=0.118, T=0.266. The Bayes factor test identified the GTR+Γ model as the best fitting model.

3.2. Phylogenetic relationships of single nuclear (Fig. 1a-f), combined nuclear and mitochondrial loci topologies of “dataset A” (Fig. 2a)

Mitochondrial genes provided good phylogenetic resolution in terminal groups whereas nuclear genes gave a better resolution in the more basal splits. Although single nuclear loci provided limited resolution, single locus phylogenetic hypotheses were largely concordant. All ML and BI consensus topologies supported the same 22 discrete phylogenetic lineages, and thus provide the basis for a new classification (see below). In order to render the reading user friendly, all new or newly defined tribes (see section 3.3.) are referred to by their novel tribus name from now on, each labelled in the text with a star and a number; this label corresponds to tribus definitions in the ***Glossary*** (Appendix). Informal clade names used in Schwarzer et al. (2009) are labelled and explained in the same way.

3.2.1. Single locus topologies (Fig. 1a-f and 2a)

The five single nuclear loci produced partially discordant phylogenetic hypotheses. The best supported ML topology (highest BS values) of all single nuclear loci is the one of S7 intron (Fig. 1a), which identifies haplotilapiines as a monophyletic clade with respect to *Tylochromis*, *Pelmatochromis* and *Pterochromis* (Pelmatochromines). Within haplotilapiines *Etia* (Etiini*[1]) is the sister group to the remaining taxa. These taxa comprise two monophyletic clades, one composed of all formerly mouthbrooding “*Tilapia*” species (Oreochromini*[2]) as the sister group to the EAR and one clade consisting of boreotilapiines*[3] (sensu Schwarzer et al. 2009), *Tilapia* sensu stricto and *Chilochromis* (Tilapiini*[4]), *Steatocranus* sensu stricto (Steatocranini*[5]) and a monophyletic clade composed of “*T.*” *cabrae* and “*T.*” *mariae* (Pelmatolapiini*[6]). With respect to the haplotilapiines, the single nuclear locus topologies of S7 intron, ENC1 and SH3PX3 (Figs. 1a, c, e) (SH-Test, $p>0.05$ for ENC1 and SH3PX3) either support this basal topology or do not contradict it significantly. The overall weakly supported single locus topologies of Tmo4c4 and Ptr (Figs. 1b, d) differ significantly (SH-Test, $p<0.05$) from the combined nuclear topology, because *Tilapia* sensu stricto (Tilapiini*[4]) (Tmo4c4) form the sister group to all other haplotilapiines or mouthbrooding tilapiines (Oreochromini*[2]) (Ptr).

All separately amplified mitochondrial data (12S, 12S/16S, 16S, ND2) were treated as a single locus in a combined mitochondrial dataset (Fig. 2a), because the vertebrate mitochondrial genome is inherited matrilinearly as an entity and without recombination (Gyllensten et al. 1985). This dataset supports a basal phylogeny that differs substantially from the combined nuclear loci topology (Fig. 2b) (SH-Test, p<0.01). In the mitochondrial dataset (Fig. 2a), the mouthbrooding tilapiines (Oreochromini*[2]) do not form the sister group to the remaining clades. Instead a clade of West African tilapiine cichlids containing *Gobiocichla* Kanazawa, 1951, "*Tilapia*." *brevimanus* (Boulenger, 1911), "*T*." *pra* (Dunz & Schliewen, 2010), "*T*." *busumana* (Günther, 1903) and "*Steatocranus*." *irvinei* (Trewavas, 1943) (Gobiocichlini*[7]) is the basal sister group to all remaining taxa (excluding the outgroup *Heterochromis*). Neither the monophyly of boreotilapiines*[3] nor that of austrotilapiines*[12] is strongly supported.

3.2.2. Concatenated nuclear loci topologies (Fig. 2b) and phylogenetic analysis of the "dataset A" (BI and ML approach)

Analysed in combination, the best supported topology of the concatenated nuclear loci set provides only little additional resolution to the single locus topologies, i.e. a well supported sister group relationship of the clade consisting of "*T*." *tholloni* (Paracoptodonini*[11]) and all other species of the former subgenus *Coptodon* (Coptodonini*[10]) with the remaining substrate brooding *Tilapia* related taxa.

For the "dataset A" the SH-Test identified twelve out of all 1000 bootstrap ML topologies as significantly or highly significantly different (p<0.05 or p<0.01) from all other 988 topologies by comparing their likelihoods. Thus the null hypothesis that all trees equally well explain the data is rejected. These twelve topologies (not shown) differ mainly in the position of "*T.*" *cabrae* and "*T.*" *mariae* (Pelmatolapiini*[6]). In addition to this the indices of the rescaled consistency index (RC) ranged from 0.246 to 0.251 for all 1000 bootstrap replicates of the ML analysis of "dataset A". Low RC values indicate a high level of "homoplasy" in the dataset, but in large datasets (here 94 taxa) the values are expected to be lower, because an increasing number of taxa increases the probability of the occurrence of homoplasy.

The SH-Test for the comparison of the mitochondrial and all single nuclear topologies indicates a highly significant (p<0.01) conflict between these tree topologies (differences see above). With this inherent phylogenetic conflict as well as the limited phylogenetic information content of single nuclear loci in mind, we analysed the combined dataset *in toto*, but accompanied this by a quantitative assessment of the distribution and kind of conflict signal.

Despite the inherent conflict, the topologies (Fig. 3) resulting from ML and BI analyses of the "dataset A" were highly congruent and nodes of all tribes, except Bathybatini and a new tribe composed of *Coptodon* (Coptodonini*[11]) were supported with high BS (>95) and BPP (1.0) values. ML and BI supported the monophyly of the haplotilapiines (100/1.0), and also the sister group relationship of this group within the remaining African cichlids was highly supported (96/1.0).

Only two minor differences appear in the best supported tree topologies of the ML and BI analyses (Fig. 3, bold faced numbers with an asterisk mark). In the ML analysis, within the *Coptodon* clade, "*T.*" *dageti* (Thys van den Audenaerde, 1971) is the sister group to "*T.*" *discolor* (Günther, 1903) (BS 54) and both are the sister group to "*T.*" *guineensis* (BS 100). In the BI analysis "*T.*" *dageti* is the sister group to "*T.*" *guineensis* (BPP 0.96) and both are the sister group to "*T.*" *discolor* (BPP 1.0). In the ML analysis, within the *Steatocranus* sensu stricto clade, the subclade of *S. bleheri* Meyer, 1993, *S*. sp. "redeye" and *S*. sp. "bulky head" is the sister group to a subclade of *S. ubanguiensis* Roberts & Stewart, 1976, *S. casuarius* Poll, 1939 and *S*. sp. "dwarf" (BS 39), both subclades are the sister group to a third subclade of *S. tinanti* (Poll, 1939), *S. glaber* Roberts & Stewart, 1976 and *S. gibbiceps* Boulenger, 1899 (BS 100). In the BI analysis the third subclade of *S. tinanti*, *S. glaber* and *S. gibbiceps* is the sister group to the subclade of *S. bleheri*, *S*. sp. "redeye" and *S*. sp. "bulky head" (BPP 0.98), both subclades are the sister group to a subclade consisting of *S. ubanguiensis*, *S. casuarius* and *S*. sp. "dwarf" (BPP 1.0). In both cases the topology of BI analysis is better supported.

3.2.3. Assessment of the inherent conflict

The assessment of the inherent phylogenetic conflict using the leaf stability index (Fig. 4) was calculated to identify the consistency of a taxon position within the combined tree of ML and BI analyses. The most inconsistently placed clade is the one combining "*T.*" *mariae* and "*T.*" *cabrae* (Pelmatolapiini^{*6}) with the lowest value of 0.71. The node support of the best supported tree topology in the combined dataset for this clade as the sister group to the boreotilapiines^{*3} is also low (BS 41 / BPP 0.5) Pelmatolapiini^{*6} is sometimes the sister group to all haplotilapiines, excluding *Etia* and mouthbrooding tilapiines (Oreochromini^{*2}) (BS 22), or the sister group to all austrotilapiines^{*12} (BS 18). When checked individually "*T." cabrae* and "*T." mariae* were positioned differently in ML tree topologies: "*T.*" *mariae* alone as the sister to the boreotilapiines^{*3} (BS 47) and "*T.*" *cabrae* alone as the sister to the austrotilapiines^{*12} (42.5%). A further detailed assessment of these two taxa follows below (see Discussion 4.6.3.). The monophyly of the EAR had a low leaf stability index of 0.81 as well as a low support at the best supported tree topology in the combined dataset (BS 47 / BPP 0.93). Percentage data given in the following is always percent of 1000 bootstrap trees of the ML analysis. The location of the EAR is quite heterogeneous and includes a sister group to all haplotilapiines excluding *Etia* and mouthbrooding tilapiines (Oreochromini*^{2}) (16.1%), to boreotilapiines*^{3} (18.6%) or to *Steatocranus* sensu stricto (12.2%). The leaf stability index of all other taxa except for the new mouthbrooding tilapiine clade (Oreochromini*^{2}) ranges from 0.85-0.90 and is moderately stable in all trees. The Oreochromini*^{2} clade was placed very consistently (0.95) in all possible topologies as the sister group to all other haplotilapiines excluding *Etia*; *Etia* had a 1.0 leaf stability index.

Based on the leaf stability index results and on the effect of single species removals ("*T.*" *cabrae* and "*T.*" *mariae*), 47 groups or single taxa (20) were successively removed from the dataset and afterwards a ML run (RAxML) with identical settings as for "dataset A" was conducted for each new resulting dataset. Six nodes (Fig. 5) of the tree topology of the concatenated data set were affected by these removals. All removal effects described in detail in Appendix A (Supplementary material 4) and potential hybrid effects within the haplotilapiines are shown in a dashed line diagram (Fig. 6). The most notable effect has the removal of a mouthbrooding tilapiine clade (Oreochromini*^{2}) that disintegrates boreotilapiines*^{3}.

Due to the differing position of the new basal West African tilapiine clade (Gobiocichlini*^{7}) (BS 73) and the clade of all tilapiine mouthbrooders (Oreochromini*^{2}) (BS 41), branch attachment frequencies of these clades were calculated. Percentage data given in the following is always percent of 1000 bootstrap trees of the ML analysis. In 3% of all 1000 bootstrap topologies, the new basal West African tilapiine clade (Gobiocichlini*^{7}) is located within the haplotilapiines (excluding *Etia*), whereas in the remaining 97% it is the sister group to all haplotilapiines (excluding *Etia*). The clade of all tilapiine mouthbrooders (Oreochromini*^{2}) is located within the former austrotilapiines*^{12} in 65%, and in 34% it is the sister group to a new monophyletic clade composed of "*T.*" *cabrae* and "*T.*" *mariae* (Pelmatolapiini*^{6}). In 0.5% it is the sister group to *Coptodon* and in 0.5% it is the sister group to *Heterochromis*.

3.2.4. Phylogenetic relationships of "dataset B"

A larger phylogenetic framework (784 taxa, "dataset B") was generated for the haplotilapiines based on the mitochondrial locus ND2 (Fig. 7). The following Lake Tanganyika and related tribes or clades are added additionally to the taxon sampling in the multilocus approach of "dataset A": Cyphotilapiini, Limnochromini, Ectodini, Perissodini and Tanzanian representatives of the genus *Orthochromis* sensu stricto. All clades, which are well supported in the multilocus approach of "dataset A", are also well supported in this ML analysis of the ND2 dataset except for the former austrotilapiines*^{12}. The monophyletic clade of "*T.*" *cabrae* and "*T.*" *mariae* (Pelmatolapiini*^{6}) is the sister group of boreotilapiines*^{3} in the multilocus approach of "dataset A", but is located as the sister group of a clade of *Tilapia* sensu stricto and *Chilochromis* (Tilapiini*[4]) in the ND2 approach of "dataset B". Thus, the austrotilapiines*[12], which contain the clade of *Tilapia* sensu stricto and *Chilochromis* (Tilapiini*[4]), are not supported as monophylum in the "dataset B", in contrast to the well supported (BS 67) monophyletic boreotilapiines*[3] in this ML analysis.

3.3. Revised classification of the haplotilapiine cichlid fishes formerly referred to as "*Tilapia*", and related taxa

Analyses presented herein identified eleven discrete and consistently recovered haplotilapiine phylogenetic lineages which are consistently recovered or at least not contradicted in all combined and single locus analyses, and if the monophyletic EAR is viewed as a single major lineage (Fig. 3 & 7). Based on these results we propose a novel genus- and tribus-level classification of haplotilapiine cichlid fishes formerly referred to as "*Tilapia"* and related lineages. We restrict this reclassification to haplotilapiine non EAR clades, although all tribus definitions (Trewavas 1983; Poll 1986; Takahashi 2003) previously proposed were considered when defining new tribes. All novel discrete phylogenetic haplotilapiine lineages are supported by molecular and morphological autapomorphies. Tilapiini Trewavas, 1983 remains unsupported by unique molecular characters which could be interpreted as autapomorphies, but the tribus members are consistently grouped in all analyses, and with strong node support in the ML and BI analyses of "dataset A". No molecular data were available for species of the subgenus *Dagetia* Thys van den Audenaerde, 1969 (recently synonymized with *Tilapia* (Dunz & Schliewen 2012) and *Danakilia* Thys van den Audenaerde, 1969, the latter therefore is conditionally assigned to a new tribus.

(1) Coelotilapiini new tribe

Type genus. *Coelotilapia*, new genus (described below).

Included genera. One monotypic genus.

Distribution. Coastal plains of Sierra Leone and western Liberia (Teugels & Thys van den Audenaerde 2003).

Diagnosis. As for generic diagnosis (see below) and additional nine (five mtDNA and four ncDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

Coelotilapia, new genus

Type species. *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.IV.1969.

Diagnosis. Lower pharyngeal jaw (united 5th ceratobranchials) as long as broad, with an anterior keel shorter than or just as long as the toothed area; bicuspid or tricuspid posterior pharyngeal teeth; first gill arch with 8–11 rakers; two lateral lines; cycloid scales; 26-27 scales in the longitudinal row; upper and lower outer teeth rows bicuspid in both jaws, inner rows with smaller tricuspid teeth in both jaws; isognathous to retrognathous jaws; slender spatulate teeth; small scales near base and upper and lower border of caudal fin; head profile rounded with a retrognathous jaw; 14–17 dorsal spines; 7–8 unbranched (not Y-shaped) vertical bars on flanks (not visible in all preserved specimens), bars broader than the light interspaces; no “tilapia spot” present in dorsal fin; pointed pelvic fins; no hump on forehead, no expanded tissue on the roof of the pharynx (“visor-like hanging pad” sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine (based on: Stiassny 1991; Takahashi 2003; Thys van den Audenaerde 1969; pers. obs.).

Etymology. The genus name *Coelotilapia* Mayland, 1995 was introduced by Mayland (1995:142) in popular aquarium book, but is not available, because “it was treated as a questionable new genus, but was described as a generic name under *Tilapia* and not used in the combination *Coelotilapia joka”* (Eschmeyer & Fong 2012). We recycle this name hereby. The name was chosen to refer to the cave-breeding habit, but Mayland refers to the Latin word *coelestis*, which mean celestial. Very likely he thought of the Greek word *koiloma* (*κοιλομα*), which means cavity.

Contained species. *Coelotilapia joka* (Thys van den Audenaerde, 1969).

(2) Paracoptodonini new tribe

Type genus. *Paracoptodon*, new genus (described below).

Included genera. *Paracoptodon*, new genus.

Distribution. Swampy central Congo area, Pool Malebo, upper and lower Ogowe, Niari-Kwilu, Shiloango and lower Congo (Stiassny et al. 2007; Daget et al. 1991).

Diagnosis. As for generic diagnosis (see below) and additional 13 (ten mtDNA and three ncDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

Paracoptodon, new genus

Type species. *Tilapia tholloni* (Sauvage, 1884), (MNHN 1884-0298, lectotype (designation below), 140.0 mm SL), Franceville, upper Ogooué River, Gabon, Schwebisch & Thollon.

Lectotype designation of *Chromis tholloni* Sauvage, 1884.

The type series of *Chromis tholloni* comprises three syntypes, but the original description of Sauvage 1884 is only based on the largest specimen MNHN 1884-0298 (140.0 mm SL). Later Blanc (1962) and Bauchot et al. (1978) inappropriately used the term "holotype" for specimen MNHN 1884-0298. The ICZN (1999) Article 74.5 clearly stipulates that for a lectotype designation made before 2000, either the term "lectotype" or "the type" must be used. Further: "when the original work reveals that the taxon had been based on more then one specimen, a subsequent use of the term "holotype" does not constitute a valid lectotype designation…".

Following recommendations 74A (Agreement with previous restrictions) and 74B (Preference for illustrated specimen) in Article 74.7 of the ICZN (1999) the largest and previously "type" designated syntype (MNHN 1884-0298: 140.0 mm SL), which is in addition illustrated by Sauvage (1884), is here designated as the lectotype of the species.

Diagnosis. Lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel shorter than or just as long as the toothed area of the jaw; tricuspid or quadricuspid posterior pharyngeal teeth; first gill arch with 13–17 rakers; two lateral lines; cycloid scales; 24–27 scales in the longitudinal row; upper and lower outer teeth rows bicuspid in both jaws, inner rows with smaller tricuspid teeth in both jaws; stout non spatulate teeth; isognathous jaws; a densely scaled caudal fin; 13–16 dorsal spines; 6–8 vertical bars on flanks (not always visible), some, or all of them are branched (Y-shaped) close to dorsal fin; pointed pelvic fins; "tilapia spot" in dorsal fin; hump on forehead in adults, no expanded tissue on the roof of the pharynx ("visor-like hanging pad" sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine. (based on: Lippitsch et al. 1998; Stiassny 1991; Takahashi 2003; pers. obs.).

Etymology. The name *Paracoptodon* is a composition of the Greek preposition para (παρα) = at, by and the genus name *Coptodon* Gervais, 1853, hereby referring to the sister group relationship of *Coptodon and Paracoptodon.*

Contained species. *Paracoptodon tholloni* (Sauvage, 1884) and *Paracoptodon congica* (Poll & Thys van den Audenaerde, 1960).

(3) Heterotilapiini new tribe

Type genus. *Heterotilapia* Regan, 1920 (formerly a subgenus, raised here to generic rank).

Included genera. *Heterotilapia* Regan, 1920.

Contained species *Heterotilapia buttikoferi* (Hubrecht, 1883), type species, and *Heterotilapia cessiana* (Thys van den Audenaerde, 1968).

Distribution. Lower reaches of coastal rivers from Guinea-Bissau to west Liberia (Saint John River) and Cess or Nipoue River (Liberia, Côte d'Ivoire) (Teugels & Thys van den Audenaerde 2003).

Diagnosis. Lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel shorter than or just as long as the toothed area; bicuspid or tricuspid posterior pharyngeal teeth; median pharyngeal teeth broadened when compared to the lateral teeth or molariform; first gill arch with 13–16 rakers; two lateral lines; cycloid scales; 25-27 scales in the longitudinal row; upper and lower outer teeth rows bicuspid in both jaws, inner rows with smaller tricuspid teeth in both jaws; stout slightly spatulate teeth; isognathous jaws; small scales near base, upper and lower border of caudal fin; 14–16 dorsal spines; 6–8 unbranched (not Y-shaped), forward slanted vertical bars on flanks (not visible in all specimens), bars broader than the light interspaces and reaching from head to caudal peduncle; "tilapia spot" in dorsal fin; pointed pelvic fins; no hump on forehead, no expanded tissue on the roof of the pharynx ("visor-like hanging pad" sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine. (based on: Stiassny 1991; Takahashi 2003; Thys van den Audenaerde 1969; pers. obs.). 14 (eleven mtDNA and three ncDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

(4) Pelmatolapiini new tribe

Type genus. *Pelmatolapia* Thys van den Audenaerde, 1969 (formerly a subgenus, raised here to generic rank).

Included genera. *Pelmatolapia* Thys van den Audenaerde, 1969.

Contained species. *Pelmatolapia mariae* (Boulenger, 1899), type species, and *Pelmatolapia cabrae* (Boulenger, 1898).

Distribution. Coastal lowlands from southern Rio Muni to mouth of the Congo River, around Cuanza (also spelled Coanza, Kwanzaa, Quanza, Kwanza, or Kuanza) delta (Angola), coastal lowlands and lagoons from the Tabou River (Côte d'Ivoire) to south-west Ghana and from south-east Benin to the Kribi and Lobe River (Cameroon) (Stiassny et al. 2007).

Diagnosis. The lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel shorter than or just as long as the toothed area; bicuspid or rarely tricuspid posterior pharyngeal teeth; first gill arch with 12–19 rakers; two lateral lines; cycloid scales;

25-27 scales in the longitudinal row; upper and lower outer teeth rows bicuspid in both jaws, inner rows with smaller tricuspid teeth in both jaws; slender spatulate teeth; isognathous jaws; small scales near base, upper and lower border of caudal fin; 15–16 dorsal spines; 7–9 unbranched (not Y-shaped), broad, vertical bars on flanks (not visible in all specimens) or 5–6 distinct mid-lateral dark blotches, more close to caudal peduncle; “tilapia spot” in dorsal fin; pointed pelvic fins; no hump on forehead, no expanded tissue on the roof of the pharynx (“visor-like hanging pad” sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine. (based on: Stiassny 1991; Takahashi 2003; Thys van den Audenaerde 1969; pers. obs.). Two (both mtDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

Note. Pelmatolapiini is the most inconsistently placed tribus across all phylogenetic analyses (see Results 3.2.3. and Schwarzer et al. 2009). Notably, each of the two species appears to harbour a different ancient hybrid signal. *P. mariae* tends to align phylogenetically with the boreotilapiines*[3] (i.e. Coelotilapiini, Heterotilapiini and Gobiocichlini), but *P. cabrae* with austrotilapiines*[12] (*Tilapia* and Steatocranini) (see Appendix A, Supplementary material 4). This is likely to cause the instability of the well supported tribe across all phylogenetic analyses; therefore we are not able to assign Pelmatolapiini with absolute certainty to either austrotilapiines*[12] or boreotilapiines*[3].We note that differential geographical distribution of *P. cabrae* and *P. mariae* agrees with their differential phylogenetic affinities. The distribution of *P. cabrae* overlaps with the distribution of austrotilapiine *Tilapia* (lower Cuanza, Angola), but the distribution of *P. mariae* overlaps with the boreotilapiine Coptodonini and Gobiocichlini (west- and west central African coastal lowlands and lagoons).

(5) Coptodonini new tribe

Type genus. *Coptodon* Gervais, 1853.

Included genera. *Coptodon* Gervais, 1853.

Contained species. Type species. *Coptodon zillii* (Gervais, 1848*),* type species; *C. bakossiorum* (Stiassny, Schliewen & Dominey, 1992); *C. bemini* (Thys van den Audenaerde, 1972); *C. bythobates* (Stiassny, Schliewen & Dominey, 1992); *C. cameronensis* (Holly, 1927); *C. camerunensis* (Lönnberg, 1903); *C. coffea* (Thys van den Audenaerde, 1970); *C. dageti* (Thys van den Audenaerde 1971); *C. discolor* (Günther, 1902); *C. deckerti* (Thys van den Audenaerde, 1967); *C. ejagham* (Dunz & Schliewen 2010); *C. flava* (Stiassny, Schliewen & Dominey, 1992); *C. fusiforme* (Dunz & Schliewen 2010); *C. guineensis* (Bleeker, 1862); *C. gutturosa* (Stiassny, Schliewen & Dominey, 1992); *C. imbriferna* (Stiassny, Schliewen & Dominey, 1992); *C. ismailiaensis* (Mekkawy 1995); *C. konkourensis* (Dunz & Schliewen

2012); *C. kottae* (Lönnberg, 1904); *C. louka* (Thys van den Audenaerde, 1969); *C. margaritacea* (Boulenger, 1916); *C. nigrans* (Dunz & Schliewen 2010); *C. nyongana* (Thys van den Audenaerde, 1960); *C. rendalli* (Boulenger, 1896); *C. rheophila* (Daget, 1962); *C. snyderae* (Stiassny, Schliewen & Dominey, 1992); *C. spongotroktis* (Stiassny, Schliewen & Dominey, 1992); *C. thysi* (Stiassny, Schliewen & Dominey, 1992); *C. walteri* (Thys van den Audenaerde, 1968); yet undescribed species: *Coptodon* sp. aff. *guineensis* "Cross"; *Coptodon* sp. aff. *zillii* "Kisangani" and *Coptodon* sp. aff. *louka* "Samou".

Distribution. Lakes: Albert (Uganda / Democratic Republic of the Congo), Barombi-ba-Kotto (Cameroon), Bermin (Cameroon), Bosumtwi (Ghana), Chad (Central Africa), Ejagham (Cameroon), Kainji (Nigeria), Malawi (Malawi / Mozambique / Tanzania), Mboandong (Cameroon), Tanganyika (Tanzania / Burundi / Zambia / Democratic Republic of the Congo), Turkana (Kenya) and Volta (Ghana). River systems: Bandama, Bia, Cavally, Comoé, Corubal River to Lofa River, Cunene, Dja, Jordan, Kasai, Konkouré, Lualaba, Meme, Mungo, Niger (upper and middle), Nile, Nipoue, Nyong, Okavango, Pra, Saint Paul, Sanaga, Sassandra (upper), Shaba, Senegal, Tano, Ubangi-Uele-Ituri, Volta (upper and lower), Zambesi, coastal waters from mouth of the Senegal River to mouth of the Cuanza River, south Morocco, Sahara (Dunz & Schliewen 2010; Stiassny et al. 2007; Teugels & Thys van den Audenaerde 2003; Daget et al. 1991).

Diagnosis. Lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel shorter than or just as long as the toothed area; bicuspid (only *C. gutturosa*) to pentacuspid (only *C. nigrans*) posterior pharyngeal teeth; first gill arch with 10–17 rakers; two lateral lines; cycloid scales; 23–29 scales in the longitudinal row; upper and lower outer teeth rows bicuspid in both jaws, inner rows with smaller tricuspid teeth in both jaws; stout non spatulate teeth; isognathous jaws; small scales near base, upper and lower border of caudal fin (only adults of *C. nyongana* with a densely scaled caudal fin); 13–17 dorsal spines; 6–8 vertical bars on flanks (when distinct), some, or all of them are branched (Y-shaped) close to dorsal fin; pointed pelvic fins; "tilapia spot" in dorsal fin; no hump on forehead, no expanded tissue on the roof of the pharynx ("visor-like hanging pad" sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine. (based on: Lippitsch et al. 1998; Stiassny 1991; Takahashi 2003; pers. obs.) and additional two (one mtDNA and one ncDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

Note. *Tilapia rheophila* is type species of the subgenus *Dagetia* Thys van den Audenaerde, 1969. *Dagetia* was part of the Section II in the Annotated Bibliography of *Tilapia* (Thys van den Audenaerde 1969). Also part of this Section II are *Coptodon* and *Pelmatolapia*. An recent evaluation of the putative autapomorphies diagnosing *Dagetia* revealed that all are shared with members of the subgenus *Coptodon* Gervais, 1853 sensu Thys van den Audenaerde, 1969; hence, *Tilapia* (*Dagetia*) was placed in the synonymy of *Tilapia*

(*Coptodon*) (Dunz & Schliewen, 2012). So far no DNA voucher of this species exists, thus a molecular support for the assignment of *Tilapia rheophila* is lacking.

(6) Gobiocichlini new tribe

Type genus. *Gobiocichla* Kanazawa, 1951.

Included genera. *Steatocranus* Boulenger, 1899; *Tilapia* Smith, 1840; *Gobiocichla* Kanazawa, 1951.

Included species. "*Steatocranus*" *irvinei* Trewavas, 1943; "*Tilapia*" *busumana* (Günther, 1903); "*Tilapia*" *brevimanus* Boulenger, 1991; "*Tilapia*" *pra* Dunz & Schliewen 2010; *Gobiocichla wonderi* Kanazawa, 1951; *Gobiocichla ethelwynnae* Roberts, 1982.

Distribution. Volta River system, coastal rivers from Guinea-Bissau to East Liberia (Cess River), Pra, Ankobra, Tano and Bia Rivers in southwestern Ghana and southeastern Cote d'Ivoire, Lake Bosumtwi, rapids in the middle and upper Niger, rapids in the mainstream of the Cross river about eight km downstream from Mamfé (Cameroon) (Dunz & Schliewen 2010; Teugels & Thys van den Audenaerde 2003).

Diagnosis. This tribe is yet only supported by three (all mtDNA) molecular autapomorphies (see Appendix A, Supplementary material 5). No diagnostic morphological characters have been identified yet. Further, the taxonomic state of "*Steatocranus*" *irvinei*, "*Tilapia*" *busumana*, "*Tilapia*" *brevimanus* and "*Tilapia*" *pra* is not resolved and needs further analysis.

Note. The Gobiocichlini is a morphologically highly heterogeneous tribus and "only" defined by molecular autapomorphies. However, all included species form a biogeographically restricted clade located in West Africa (including parts of Cameroon). All species names except those of the type genus *Gobiocichla* are maintained in quotation marks, referring to their yet unclear generic status, which needs to be revised with substantially more material.

We combine these species in a single tribus for two reasons: (1) there is no molecular support for *Gobiocichla* or "*Tilapia*", which is surprisingly at least for *Gobiocichla*, because this genus is supported by a very rare morphological character: "…a single, uninterrupted and nearly straight lateral line…" (Teugels & Thys van den Audenaerde 2003). (2) There are no identified morphological autapomorphies for the three "*Tilapia*" species. In contrast, characters, which are in other cases informative take very heterogeneous states, i.e. the shape of outer jaw teeth or the number of rakers on the first gill arch. Surprisingly, the two *Gobiocichla* species do not form a monophyletic clade in any of our DNA based analyses. Instead, *G. wonderi* is sister group to "*T.*" *brevimanus*. Thus we suggest a revision of the genus *Gobiocichla* and all other included species of this tribus with a larger dataset, focused on this basal West African tribe.

(7) Oreochromini new tribe

Type genus. *Oreochromis* Günther, 1889.

Included genera. *Oreochromis* Günther, 1889; *Alcolapia* Thys van den Audenaerde, 1969; *Tristramella* Trewavas, 1942; *Iranocichla* Coad, 1982; *Sarotherodon* Rüppell, 1852; *Pungu* Trewavas in Trewavas, Green & Corbet 1972; *Konia* Trewavas in Trewavas, Green & Corbet 1972; *Myaka* Trewavas in Trewavas, Green & Corbet 1972; *Stomatepia* Trewavas, 1962; ?*Danakilia* Thys van den Audenaerde, 1969.

Distribution. Brackish and fresh waters of West Africa from the Congo River to the Senegal; relic population in the Draa, south of the Atlas Mountains, Nile and Jordan Rivers systems, Rivers and Lakes of East and Central Africa from western Rivers in Angola to the Soudanian region (including Lake Chad). Lakes Adfera and Abaeded in Dancalia, Ethiopia and Eritrea and southern Iran (Stiassny et al. 2010; Trewavas 1983; Coad 1982).

Diagnosis. Lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel longer than the toothed area (except *Tristramella*); unicuspid, bicuspid or rarely tricuspid posterior pharyngeal teeth (molariform posterior pharyngeal teeth in *Tristramella simonis*); first gill arch with 13–32 rakers; two lateral lines; cycloid scales; 24-32 scales in the longitudinal row; upper and lower outer teeth rows unicuspid, bicuspid or tricuspid in both jaws, inner rows with smaller unicuspid, bicuspid or tricuspid teeth in both jaws; stout to slender spatulate or non spatulate teeth, sometimes spoon-shaped; isognathous, prognathous or rarely retrognathous (e.g. *Sarotherodon mvogoi*) jaws; small scales near base, upper and lower border of caudal fin; caudal fin densely scaled only in some *Oreochromis* species; 14–19 dorsal spines (except *Alcolapia* 9-11); 6–11, unbranched (not Y-shaped), thin, vertical bars on flanks (when distinct); “tilapia spot” in dorsal fin (not in all species present); pointed pelvic fins; no distinctive hump on forehead, no expanded tissue on the roof of the pharynx (“visor-like hanging pad” sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine. (based on: Stiassny 1991; Takahashi 2003; Trewavas 1983; pers. obs.).This new tribe is supported by eight (five mtDNA and three ncDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

Note. All effort to extract DNA from *Danakilia* have failed so far (Stiassny et al. 2010), thus an exact DNA-based assignment is lacking. However, Trewavas (1983) hypothesized a close relationship between *Danakilia* and *Iranocichla* and suggested a relationship between these and *Tristramella*. Schwarzer et al. (2009) as well as this study confirms a sister group relationship of *Tristramella* and *Iranocichla*. Thus *Danakilia* is assigned tentatively to the tribus Oreochromini, until an exact assignment is possible.

Tilapiini Trewavas, 1983

Type genus. *Tilapia* Smith, 1840.

Included genera. *Tilapia* Smith, 1840; *Chilochromis* Boulenger, 1902.

Distribution (Fig. 8). Chiloango basin, Kouilou basin, lower Loeme and Niari-Bouenza Rivers, Western Cuvette Centrale (Alima, Lefini) and central Cuvette Centrale (Thsuapa, Luilaka), the Sangha (Republic of the Congo), from Malebo Pool, the northern Congo tributary Itimbiri as well as from affluents of the Luilaka (DRC) in the Salonga National Park and Louna River. Kasai drainage including the Lulua and Kwango (middle Congo River basin), upper Congo River basin including the upper Lualaba, Luvua, Lake Mweru, Luapula, Lufira and Upemba region, upper Cuanza, Cunene, Okavango, Lake Ngami, Zambezi, Limpopo, Sabi, Lundi, northern tributaries of the Orange River, Lake Malawi, Bangweulu, Guinas and Otjikoto (Dunz et al. 2012 (submitted); Thys van den Audenaerde 1964).

Note. The original diagnostic character for the Tilapiini tribus sensu lato referred to "the structure of the apophysis on the base of the skull for the articulation of the upper pharyngeal bones. In Tilapiini its facets are formed from the parasphenoid alone…" (Trewavas 1983). All former substrate brooding *Tilapia* species, except *Tilapia* sensu stricto, are now assigned to new genera, except for "*T*." *brevimanus*, "*T*." *busumana* and "*T*." *pra*. Those three remain generically unassigned within Gobiocichlini and hence are referred to as "*Tilapia*" (in quotation marks) (see also 3.3. Gobiocichlini). Only the two genera *Tilapia* and *Chilochromis* remain in Tilapiini, because both form a monophyletic clade in the multilocus analysis. The genus *Tilapia* Smith 1840 contains, only *T. sparrmanii* (type species), *T. baloni*, *T. ruweti* and *T. guinasana*, as already presented in Schwarzer et al. (2009). In addition, we include the members of *T. bilineata* complex, which is a separate genus (Dunz et al. 2012, submitted). The former *Tilapia* subgenus *Dagetia* is placed in the synonymy of *Coptodon* (Dunz & Schliewen 2012).

Etiini new tribe

Type genus. *Etia* Schliewen & Stiassny, 2003.

Included genera. one monotypic genus.

Distribution. Only known from the region of Nguti in the River Mamfue and a small tributary near Mboka Village, Cameroon (Schliewen & Stiassny 2003).

Diagnosis. As for generic diagnosis: "*Etia* is readily distinguished from all remaining African cichlids by the possession of some, or all, robust tricuspid teeth in the outer row oral dentition, a characteristic upper lip crease, a spinous dorsal fin deeply excavated dorsally, a strongly marked oblique black bar anterior on the body in preserved specimens" (Schliewen & Stiassny, 2003). Additionally 27 (19 mtDNA and eight ncDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

Steatocranini new tribe

Type genus. *Steatocranus* Boulenger, 1899.

Included genera. *Steatocranus* Boulenger, 1899.

Distribution. Rapids and rocky outcrops of the middle and lower Congo River, and its affluent drainages Lefini, Sangha/Ngoko/Dja, Ubanghi/Mbomou, Kasai/Lulua, Kwango and Kwilu (Schwarzer et al. 2011).

Diagnosis. Lower pharyngeal jaw (united 5th ceratobranchials) as long as broad with an anterior keel shorter than the toothed area; bicuspid or rarely tricuspid posterior pharyngeal teeth; median pharyngeal teeth comparatively broad (if compared to the lateral teeth); first gill arch with 5–10 rakers; two lateral lines; cycloid scales; 26-36 scales in the longitudinal row; upper and lower outer teeth rows bicuspid, rarely truncate or spatulate unicuspid, in both jaws, inner rows with smaller tricuspid teeth in both jaws; slender spatulate or truncate teeth; isognathous to retrognathous jaws; 18–22 dorsal spines; 5–6 unbranched (not Y-shaped), broad, vertical bars on flanks (not visible in all specimens); "tilapia spot" in dorsal fin in some species present; rounded pelvic fins; distinctive hump on forehead (more pronounced in males), no expanded tissue on the roof of the pharynx ("visor-like hanging pad" sensu Greenwood, 1987:142); a single supraneural associated with the first neural spine. (based on: Stiassny 1991; Takahashi 2003; Roberts & Stewart 1976; pers. obs.). 21 (all mtDNA) molecular autapomorphies (see Appendix A, Supplementary material 5).

4. Discussion

This study provides a comprehensive phylogenetic hypothesis of almost all taxa formerly referred to as "*Tilapia*" and related lineages and thus provides a basis for critical reassessment of the systematics and taxonomy of this paraphyletic assemblage (Klett & Meyer 2002; Schwarzer et al. 2009).

4.1. Phylogenetic placement of haplotilapiines, Etiini, Oreochromini, boreotilapiines*[3] and austrotilapiines*[12] in analyses of the "dataset A and B" (Fig. 3 and 7) compared to Schwarzer et al. (2009)

The term haplotilapiines was introduced on the basis of the phylogenetic analysis of three nuclear loci by Schliewen & Stiassny 2003 for a monophylum comprising *Etia*, tilapiines and a selection of haplochromine-related taxa. The present findings as well as Schwarzer et al. (2009) confirm the monophyly of this clade. Consistent in all multilocus analyses *Etia nguti* is the most basal sister taxon to all remaining haplotilapiines. Oreochromini are confirmed to be the basal sister group to all haplotilapiines except *Etia*. Schwarzer et al. (2009) identified a clade of the "boreotilapiines"*[3] containing two predominantly West African subclades, named "BI" and "BII". The increased taxon sampling of the present study provided better resolution within that clade, which allowed the distinction of five tribus. Subclade "BI" corresponds to the new tribus Gobiocichlini and subclade "BII" to the new tribus Coelotilapiini, Heterotilapiini, Paracoptodonini and Coptodonini. The question arises whether it is necessary to define four separate tribus for subclade "BII" and whether, there is molecular and morphological evidence to diagnose subclade "BII" as a unit? On the molecular level there is a single molecular character state interpretable as a diagnostic autapomorphy for all four tribus, but there is no diagnostic morphological trait. In contrast, each of the four tribus is strongly supported by molecular and morphological autapomorphies in all analyses. The main argument for separating four tribus is however, that the boreotilapiines strongly compromised by apparent ancient hybrid signal (Fig. 6), and therefore appear to contain genomic partitions of non-boreotilapiine lineages i.e. it is a polyphyletic group. In contrast strongly supported by molecular and morphological autapomorphies (Schwarzer et al. 2009), the clade of the austrotilapiines*[12] identified three lineages named "AI", "AII" and "AIII"; and already in Schwarzer et al. (2009) austrotilapiines*[12] were only moderately supported (BS 86 in ML analysis). All three appear still as monophyletic lineages in the present study, with subclade "AI" corresponding to the EAR, "AII" corresponding to our Tilapiini, and "AIII" corresponding to the Steatocranini. However, the critical assessment of the ancient hybrid status of *Pelmatolapia*, both in Schwarzer et al. (2009) and in the present study with the second taxon (*P. cabrae*) compromise the monophyly support of austrotilapiines*[12], although relevant but not overwhelming support for its monophyly as well as homoplasy excess suggests that austrotilapiines*[12] evolved as a monophylum before a secondary introgression event. In summary, austrotilapiines*[12] are polyphyletic but, as for boreotilapiines, an informal clade designation remains useful to refer to their putative ancient monophyly.

Not surprisingly, single loci provided limited resolution as compared to the concatenated dataset, but single locus phylogenetic hypotheses nuclear were largely consistent. However, the monophyly of haplotilapiines is supported in all single nuclear loci analyses, but not in the mitochondrial analysis, where Gobiocichlini take a comparatively weakly supported basal position as sister group to all other African cichlids taxa except *Heterochromis*. Three alternative topologies of single loci (Tmo4c4, Ptr and the mitochondrial locus), were significantly different compared to the concatenated dataset (SH-test: $p<0.05$ (Tmo4c4 and Ptr), $p<0.01$ (mitochondrial locus); Shimodaira & Hasegawa 1999).

The single locus Tmo4c4 differs from the consensus topology of the concatenated dataset (Fig. 3) in the fact that *Tilapia* is located as sister group to all remaining haplotilapiines, which are not resolved due to a limited resolution. The single locus Ptr differs from the consensus topology of the concatenated dataset (Fig. 3) in the fact that a clade of Coptodonini and Paracoptodonini is located as sister group to all remaining haplotilapiines (excluding *Etia*), which are not resolved due to a limited resolution. The mitochondrial locus strongly supports a topology, (BS 98) which places Oreochromini in a clade of the former austrotilapiines and Pelmatolapiini. The discordant location (mitochondrial locus vs. concatenated dataset) of Oreochromini might imply cytonuclear discordance. We interpret this cytonuclear discordance as a result of introgressive hybridisation between Oreochromini and members of the former austrotilapiines (including *Pelmatolapia*) or of incomplete lineage sorting (see 4.2). Incomplete lineage sorting would suggest that Oreochromini and members of the former austrotilapiines (including *Pelmatolapia*) had a common ancestor. This ancestral species passed several speciation events in a short period of time and the ancestral polymorphism of a given gene is not fully resolved into two monophyletic lineages when the second speciation occurs (Pamilo & Nei 1988).

Although “dataset B” (Fig. 7) is about seven times larger regarding the number of taxa than “dataset A” and contains several tribus of the EAR, which are not represented in “dataset A”, the resulting topologies of both analyses (“dataset B” and “dataset A”) are largely congruent in terminal splits.

4.2. Cytonuclear discordance

Significant discordance detected by the two nuclear loci Tmo4c4 and Ptr (see above 4.1.), is mainly a result of the limited resolution of resulting topologies of these single loci and thus not useful to detect reasons for discordance. In addition the SH-Test indicated highly significant conflict ($p<0.01$) between the mitochondrial and the combined nuclear dataset (Fig. 2). The most striking disagreements are the discordant placements of Gobiocichlini and Oreochromini. Members of these two tribus are very likely involved in incomplete lineage sorting or introgressive hybridisation. The exact differentiation of incomplete lineage sorting and introgressive hybridisation is difficult, because both mechanisms generate very similar phylogenetic patterns (Holder et al. 2001). To evaluate hybridisation as the cause for cytonuclear discordance, we conducted the HET. Excluding a hybrid taxon from the dataset is expected to lead to an increase of support values (here BS) for the position of parental taxa in a bifurcating phylogenetic tree (Seehausen, 2004; Schwarzer et al. 2011a).

Interspecific conflicts among datasets are usually attributed to introgressive hybridisation or incomplete lineage sorting (Shaw 2002). A third mechanism, long-branch attraction, is able to generate artificial cytonuclear discordance by clustering most similar nodes and thus sometimes a homoplasy is erroneously interpreted as a synapomorphy (Felsenstein 1978). This is unlikely in our cases, e.g. Oreochromini, because short branches are affected by discordant placement, further the same discordances appear in ML and BI analyses takes unequal rates of branch lengths into account (Swofford et al. 2001).

Introgressive hybridisation is common and well accepted in plants (Hardig et al. 2000), but also documented in animals (Gardner 1996), and also in cichlid fishes (Rüber et al. 2001; Schliewen and Klee 2004; Koblmüller et al. 2009).

We found tentative evidence of past hybridisation, based on the HET. The inclusion of a hybrid taxon in a dichotomous tree phylogeny is expected to produce conflicting phylogenetic signal resulting in low BS support values of affected nodes. Two removal experiments increased node support strongly, will be discussed more detailed in the following. For a better understanding of these complex hybridisation events see also Figure 6.

Unless specified, all removals of specific tribus or clades mean all included members of the tribus or clade. All discussed BS values correspond to BS values of the consensus topology (Fig. 3). The first removal experiment of the four new tribus Gobiocichlini, Heterotilapiini, Coelotilapiini and Pelmatolapiini as a group increases the node support of the EAR as sister group of Tilapiini and Steatocranini from BS 47 strongly to BS 92 (see Fig. 5, E1). This indicates that Gobiocichlini, Heterotilapiini, Coelotilapiini or Pelmatolapiini affect members of the EAR or Tilapiini and/or Steatocranini. Which of the four removed tribus were involved and to what extent? This question can only be answered with the results of several previous removals.

(1) Removal of Coelotilapiini and/or Heterotilapiini shows that both tribus share a potential ancient hybrid signal with Gobiocichlini, thus for simplifying we treat the signal of Gobiocichlini, Heterotilapiini and Coelotilapiini in the following as one single signal (Gobiocichlini).

(2) Removals of Tilapiini and/or Steatocranini show only minimal effects on node support of Gobiocichlini, Heterotilapiini and Coelotilapiini.

(3) But the removal of Pelmatolapiini (especially *P. cabrae*) affects the Tilapiini and/or Steatocranini, but not the EAR (Fig. 6).

(4) Conversely, the removal of the Gobiocichlini signal affects the EAR, but not Tilapiini and/or Steatocranini.

Thus it is obvious that two different effects simultaneously caused the node support increase, because Gobiocichlini affects the EAR and Pelmatolapiini affects the Tilapiini and/or Steatocranini. By removing of these both distracting ancient hybrid effects, caused by the removed taxa, the node support increases strongly. The removal of Gobiocichlini, Heterotilapiini and Coelotilapiini without Pelmatolapiini increases the node support of the EAR as sister group of Tilapiini and Steatocranini to BS 90, this finding suggests that the effect of Pelmatolapiini in the previous removal is only minimal. The main effect comes from a Gobiocichlini-EAR interaction.

The second removal experiment of all thirteen taxa of the EAR increases the node support for the boreotilapiines Pelmatolapiini sister group relationship strongly to BS 86 (see Fig. 5, B1). This fact supports our previous findings of a Gobiocichlini-EAR interaction. By removing the distracting conflict signal (EAR) from the boreotilapiines (Gobiocichlini) the node support of boreotilapiines sister group to Pelmatolapiini increases. Notably, each of the two species of the Pelmatolapiini appears to harbour a different ancient hybrid signal. *P. mariae* tends to align phylogenetically with the boreotilapiines*[3], but *P. cabrae* with austrotilapiines*[12].

In summary there is evidence for ancient introgressive hybridisation, highlighted by the two removal experiments above. However, only effects of major lineages could be detected and interpreted, but detection of effects within these lineages is beyond the scope and also beyond the resolving power of only six loci (one mtDNA and five ncDNA) analysed of this study. We conclude that these lineages, that were involved in past hybridisation (e.g. Gobiocichlini, EAR), have been cohesive over long periods and deserve taxonomic recognition, even if basal nodes remain weakly supported, sometimes possibly due to phylogenetic conflict reflecting ancient hybridisation. To refer to such lineages adequately, a common taxonomical classification is necessary.

4.3. Classification

Most phylogenetic studies dealing with East African cichlids have focused on lacustrine cichlids of the three Great Lakes, Tanganyika, Malawi and Victoria (Koblmüller et al. 2005; Koblmüller et al. 2008; Meyer 1993; Nishida 1991 Salzburger et al. 2002; Salzburger &

Meyer 2004; Sturmbauer et al. 2010; Takahashi et al. 2001). However, little was known about the relationships within the original tribe Tilapiini Trewavas, 1983, containing mainly riverine cichlids, until Schwarzer et al. 2009 established a first well supported phylogeny as basis for further research.

Several past classifications (for a general overview see Tab. 2) included a vaguely diagnosed tribus Tilapiini, but the composition had remained unchanged (Takahashi 2003; Koblmüller et al. 2008; Takahashi & Koblmüller 2011). Further, only minor changes on the tribus level were established within haplotilapiines by Poll (1986) (11 tribes stated (including Trematocarini)) and Takahashi & Koblmüller (2011) (13 tribes stated). From 1986 until 2011 only the three tribes Boulengerochromini, Cyphotilapiini and Benthochromini have been postulated by Takahashi (2003) based on morphological characters. In addition Takahashi & Koblmüller (2011) stated *Orthochromis* as differentiated clade on molecular level, but without any tribus indications. Although we did not perform a total evidence phylogenetic analysis including morphological characters, due to the paucity of phylogenetically informative morphological characters in haplotilapiine cichlids, we nevertheless compiled and compared literature data used for previous tribus definitions (Trewavas 1983; Poll 1986; Takahashi 2003) and complemented these with our own published and unpublished data (Dunz & Schliewen 2010, Dunz et al. 2012 (submitted)) in order to work out a stable classification of *Tilapia*-related cichlids.

Due to the extensive paraphyly of *Tilapia* related taxa seven new tribes are erected in this study. Five (Gobiocichlini, Coptodonini, Paracoptodonini, Heterotilapiini and Coelotilapiini) formed the moderately supported clade of boreotilapiines*[3]. The two remaining tribes are Oreochromini and Pelmatolapiini. Oreochromini are the sister group to a clade of austrotilapiines*[12], boreotilapiines*[3] and the new tribe Pelmatolapiini. The latter remained inconsistently placed phylogenetically.

4.4. General overview of the historic situation of “*Tilapia*”

After some unsatisfactory attempts of Boulenger (1915, 1916) and Regan 1920, 1922) to classify “*Tilapia*”, Thys van den Audenaerde (1969) published a first comprehensive infrageneric classification, but without a critical discussion. In his view, major morphologic “*Tilapia*” groups were believed to be natural groups and hence given subgeneric rank. He divided “*Tilapia*” in three sections (Tab. 1). We focus here on Sections I (*Tilapia* sensu lato) and II (*Heterotilapia* and *Coptodon* sensu lato), because Section III (*Sarotherodon* sensu lato) exclusively deals with tilapiine mouthbrooders. The main difference between Thys van den Audenaerde's Section I and II is the number of cusps of teeth of the lower pharyngeal jaw, two in Section I and three to four in Section II.

In Section I, the first subgenus *Tilapia*, contains *T. sparrmanii* (type) and *T. ruweti*, but excludes *T. guinasana* (placed in the second subgenus *Trewavasia*) based on the count of scales around the caudal peduncle. Previous studies showed that this count is a highly variable character in “*Tilapia”* (Dunz & Schliewen 2010) and also in *Tilapia* sensu stricto (unpublished data). This suggests that *T. guinasana* should also be included in *Tilapia*, based on morphological characters. Thys van den Audenaerde's third subgenus *Pelmatolapia* is primarily grouped based on the dentition character outer teeth bicuspid and spatulate. It contains “*T*.” *mariae* (type), “*T*.” *cabrae*, *T. bilineata*, “*T*.” *brevimanus* and “*T.” eisentrauti* Trewavas, 1962. Thys van den Audenaerde (1969) himself mentioned an isolated position of *T. bilineata*, as the character combination of 10–11 gill rakers and the character a densely scaled caudal fin is not shared with other Thys van den Audenaerde's subgenus. Previous studies (Schwarzer et al. 2009) as well as actual findings show that “*T.” brevimanus* is not closely related to the type species of *Pelmatolapia*. Meanwhile, “*T.” eisentrauti* has been allocated to a new genus, *Konia* Trewavas, 1972, a mouthbrooder endemic to crater lake Barombi Mbo (Cameroon), which is closely related to the oreochromine genus *Sarotherodon* (Schliewen et al. 1994). In summary these findings suggest that only the two Lower Guinea taxa “*T.” mariae* and “*T.” cabrae* should remain members of the subgenus *Pelmatolapia*. The fourth subgenus *Pelmatochromis* is interesting, due to the fact that “*T*.” *busumana* was assigned to three *Pelmatochromis* species based on the dentition character: median outer teeth bicuspid, the lateral ones conical. The lateral teeth appear sometimes conical due to wear (Dunz & Schliewen 2010). Trewavas (1973) retained “*T*.” *busumana* in *Tilapia* in the course of a revision of *Pelmatochromis*. The actual status of “*T*.” *busumana* remains unclear and needs further investigation. However, “*T*.” *busumana* is surely not closely related to *Pelmatochromis* as shown here and in previous studies (Schwarzer et al. 2009).

In Section II, the first subgenus *Heterotilapia* contains “*T*.” *buttikoferi* and “*T*.” *cessiana*. The two species are primarily separated based on the molariform pharyngeal teeth, a character that is not shared with any other species in Thys van den Audenaerde's Sections I and II. Recent and previous molecular analyses confirm this restriction to a separate (sub)genus (Schwarzer et al. 2009). The second subgenus *Coptodon* contains 15 species, all sharing the dentition character: outer teeth on jaws bicuspid, not spatulate. Also included here are the two species “*T*.” *tholloni* and “*T*.” *congica*, both closely related to *Coptodon*, but different by molecular as well as morphological characters (see Classification 3.3. *Paracoptodon*) and thus allocated in a separate genus. The third subgenus *Dagetia* contains only “*T*.” *rheophila*, which is placed in the synonymy with *Coptodon* (Dunz & Schliewen, 2012).

Subsequent morphological studies (Greenwood 1978; Poll 1986; Stiassny 1991) did not consider the infrageneric level or considered only tilapiine mouthbrooders (Trewavas 1983).

5. Conclusion

After the first attempt of Schwarzer et al. (2009) to establish a well supported phylogeny based on multilocus analyses of haplotilapiines, we provide a more comprehensive phylogenetic hypothesis of basal haplotilapiines, accompanied by a revised classification of the paraphyletic tilapiine assemblage. Additional African cichlid lineages with yet informal status (chromidotilapiines, hemichromines, pelmatochromines), or with formal status (Tylochromini, Haplochromini and all Lake Tanganyika tribus) should be included into the future phylogenetic studies to provide a fully revised African cichlid classification. The detection of phylogenetic conflict in the multilocus dataset, most likely explained by ancient hybridisation events, suggests that a classification of African cichlids may have to rest on many small tribus, rather than on a few large partially polyphyletic units, i.e. whose monophyly has been compromised by too many hybridisation and introgression events.

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Appendix A. Supplementary Material (CD)

Glossary

Supplementary material 1. GenBank Accession numbers of “dataset A”.

Supplementary material 2. GenBank Accession numbers of “dataset B” and the exact composition of *Sarotherodon* I + II, Haplochromini I-IX and *Coptodon* I + II of Figure 7.

Supplementary material 3. Detailed list of all 1006 examined specimen.

Supplementary material 4. All removals of the HET in more detail.

Supplementary material 5. Molecular autapomorphies of each single tribe (total number of autapomorphies stated in brackets). Locus ND2 is boldfaced, because the results are based on the enlarged “dataset B”. Locations of nucleotide changes of all mitochondrial (12S 12S/16S 16S ND2) loci and the nuclear S7 intron locus were detected corresponding to a reference sequence of GenBank. GenBank ID: NC007231 *Oreochromis mossambicus*, complete mitochondrial genome as reference sequence for 12S, 12S/16S and 16S. GenBank ID: AF317242 *Oreochromis niloticus vulcani* NADH dehydrogenase subunit 2 (ND2) gene, complete cds as reference sequence for ND2 and GenBank ID: GQ168094 *Oreochromis niloticus* as reference sequence for S7 intron. Amino acid changes and the exchanged nucleotide within a codon were indicated in bold face.

References

B-Rao, C., Majumdar, K.C., 1998. Multivariate map representation of phylogenetic relationships: Application to tilapiine fish. J. Fish Biol. 52, 1199–1217.

Bauchot, R., Bauchot, M.L., 1978. Coefficient de condition et indice pondéral chez les téléostéens. Cybium 3, 3–16.

Blanc, M., 1962. Catalogue des types de Poissons de la famille des Cichlidae en collection au Muséum national d'Histoire naturelle. Bull. Mus. Natl. Hist. Nat. (Série 2) 34, 202–227.

Boulenger, G.A., 1915. Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History), British Museum (Natural History), London.

Boulenger, G.A., 1916. Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History), British Museum (Natural History), London.

Coad, B.W., 1982. A new genus and species of cichlid endemic to southern Iran. Copeia 1, 28-37.

Daget, J., 1991. In Daget, J., Gosse, J.-P., Teugels, G.G., Thys van den Audenaerde, D.F.E. (Eds.), Check-list of the freshwater fishes of Africa (CLOFFA). ISNB, Brussels; MRAC, Tervuren; and ORSTOM, Paris. Vol. 4.

Dunz, A.R., Schliewen, U.K., 2010. Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana. Zootaxa 2548, 1–21.

Dunz, A.R., Schliewen, U.K., 2012. Description of a rheophilic *Tilapia* species Smith, 1840 (Teleostei: Cichlidae) from Guinea with comments on *Tilapia rheophila* Daget, 1962. Zootaxa 3314, 17–30.

Dunz, A.R., Vreven, E., Schliewen, U.K., 2012. *Congolapia*, a new cichlid genus from the central Congo basin (Perciformes: Cichlidae). Ichthyol. Explor. Freshwat. Submitted.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32, 1792–1797.

Eschmeyer, W.N., Fong J.D., 2012. Species of Fishes by family/subfamily. On-line version dated 7 June 2012. http://research.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp

Farris, J.S., 1989. The retention index and the rescaled consistency index. Cladistics 5, 417–419.

Felsenstein, J., 1978. Cases in which parsimony or compatibility methods will be positively misleading. Syst Zool 27, 401-410.

Fryer, G., Iles, T.D., 1972. The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution. Oliver & Boyd, Edinburgh.

Fowler, H.W., 1934. Fishes Obtained by Mr. H. W. Bell-Marley Chiefly in Natal and Zululand in 1929 to 1932. Proc. Natl. Acad. Sci. Philadelphia 86, 405–514.

Gardner, J.P.A., 1996. The *Mytilus edulis* species complex in southwest England: effects of hybridization and introgression upon interlocus associations and morphometric variation. Mar. Biol. 125, 385–399.

Greenwood, P.H., 1978. A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. Bull. br. Mus. nat. Hist. Zool. 33, 297–323.

Greenwood, P.H., 1987. The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. Bull. br. Mus. nat. Hist. Zool. 53, 139–203.

Gyllensten, U., Warton, D., Wilson, A.C., 1985. Maternal inheritance of mitochondrial DNA during backcrossing of two species of mice. J. Hered. 76, 321–324.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl. Acids Symp. 41, 95–98.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontol. Electron. 4, 9.

Hardig, T.M., Brunsfeld, S.J., Fritz, R.S., Morgan, M., Orians, C.M. 2000. Morphological and molecular evidence for hybridization and introgression in a willow (Salix) hybrid zone. Mol. Ecol. 9, 9–24.

Hoedeman, J.J., De Jong, J.C.M., 1947. Encyclopaedie voor de Aquariumhouder. –Uitgeverij "De Regenboog", Amsterdam, Nederland.

Holder, M.T., Anderson, J.A., Holloway, A.K., 2001. Difficulties in detecting hybridization. Syst Biol 50, 978-982.

Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755.

ICZN, 1999. International Code of Zoological Nomenclature. Fourth Edition. International Trust for Zoological Nomenclature. London.

Kishino, H., Hasegawa, M. 1989. Evaluation of the Maximum Likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. J. Mol. Evol. 29, 170–179.

Klett, V., Meyer, A., 2002. What, if anything, is a *Tilapia*?—Mitochondrial ND2 phylogeny of tilapiines and the evolution of parental care systems in the African cichlid fishes. Mol. Biol. Evol. 19, 865–883.

Koblmüller, S., Duftner, N., Katongo, C., Phiri, H., Sturmbauer, C., 2005. Ancient divergence in bathypelagic Lake Tanganyika deepwater cichlids: mitochondrial phylogeny of the tribe Bathybatini. J. Mol. Evol. 60, 297–314.

Koblmüller, S., Sefc, K.M., Sturmbauer, C., 2008. The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics. Hydrobiologia 615, 5–20.

Koblmüller, S., Egger, B., Sturmbauer, C., Sefc, K.M., 2009. Rapid radiation, ancient incomplete lineage sorting and ancient hybridization in the endemic Lake Tanganyika cichlid tribe Tropheini. Mol. Phylogenet. Evol. 55, 318–334.

Kocher, T.D., 2004. Adaptive evolution and explosive speciation: the cichlid fish model. Nat. Rev. Genet. 5, 288–298.

Kornfield, I., Smith, P.F., 2000. African cichlid fishes: model systems for evolutionary biology. Annu. Rev. Ecol. Syst. 31, 163–196.

Kullander, S.O., 1998. A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes). In: Malabarba, L.R., Reis, R.E., Vari, R.P., de Lucena, Z.M.S., de Lucena, C.A.S. (Eds), Phylogeny and Classification of Neotropical Fishes. Edipucrs, Porto Alegre.

Lippitsch, E., 1995. Scale and squamation character polarity and phyletic assessment in the family Cichlidae. J. Fish Biol. 47, 91–106.

Lippitsch, E., Kawanabe, H., Hiro, M., Nagoshi, M., 1998. Phylogenetic study of cichlid fishes in Lake Tanganyika: a lepidological approach. J. Fish Biol. 53, 752–766.

Mayland, H.J., 1995. Cichliden. Landbuch-Verlag, Hannover.

McAndrew, B.J., Majumdar, K.C., 1984. Evolutionary relationships within three Tilapiine genera (Pisces: Cichlidae). Zool. J. Linn. Soc. 80, 421–435.

Mayer, W.E., Tichy, H., Klein, J., 1998. Phylogeny of African cichlid fishes as revealed by molecular markers. Heredity 80, 702–714.

Meyer, A., 1993. Phylogenetic relationships and evolutionary processes in East African cichlid fishes. Trends Ecol. Evol. 8, 279–284.

Nagl, S., Tichy, H., Mayer, W.E., Samonte, I.E., McAndrew, B.J., Klein, J., 2001. Classification and phylogenetic relationships of African Tilapiine fishes inferred from mitochondrial DNA sequences. Mol. Phylogenet. Evol. 20, 361–374.

Nishida, M., 1991. Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichlid fishes: Inferences from allozyme data. Experientia 47, 974–979.

Pamilo, P., Nei, M., 1988. Relationship between gene trees and species trees. Mol. Biol. Evol. 5, 568–583.

Poll, M., 1986. Classification des Cichlidae du lac Tanganika. Tribus, genres et espèces. Acad. R. Belg. Mém. Cl. Sci. 45, 1–163.

Pouyard, L., Agnèse, J., 1995. Phylogenetic relationships beween 21 species of three tilapiine genera *Tilapia, Sarotherodon* and *Oreochromis* using allozyme data. J. Fish. Biol. 47, 26–38.

Regan, C.T., 1920. The classification of the fishes of the family Cichlidae. –I. The Tanganyika genera. Ann. Mag. nat. Hist. (Series 9) 5, 33–53.

Regan, C.T., 1922. The classification of the fishes of the family Cichlidae. –II. On African and Syrian genera not restricted to the great lakes. Ann. Mag. nat. Hist. (Series 9) 10, 249–264.

Ridha, M.T., 2006. Evaluation of Growth Performance of Nonimproved and Improved Strains of the Nile *Tilapia* (L.), *Oreochromis niloticus*. J. World Aquacult. Soc. 37, 218–223.

Roberts, T.R., Stewart, D.J., 1976. An ecological and systematic survey of fishes in the rapids of the lower Zaire or Congo River. Bull. Mus. Comp. Zool. 147: 239-317.

Rüber, L., Meyer, A., Sturmbauer, C., Verheyen, E., 2001. Population structure in two sympatric species of the Lake Tanganyika cichlid tribe Eretmodini: evidence for introgression. Mol. Ecol. 10, 1207–1225.

Salzburger, W., Meyer, A., Baric, S., Verheyen, E., Sturmbauer, C., 2002. Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African haplochromine cichlid fish faunas. Syst. Biol. 51, 113–135.

Salzburger, W., Meyer, A., 2004. The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. Naturwissenschaften, 91, 277–290.

Schliewen, U.K., Tautz, D., Pääbo, S., 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368, 629–632.

Schliewen, U.K., Stiassny, M.L.J., 2003. *Etia nguti*, a new genus and species of cichlid fish from the River Mamfue, Upper Cross River basin in Cameroon, West-Central Africa. Ichthyol. Explor. Freshwat. 14, 61–71.

Schliewen, U.K., Klee, B., 2004. Reticulate sympatric speciation in Cameroonian crater lake cichlids. Front. Zool. 1, 5.

Schwarzer, J., Misof, B., Tautz, D., Schliewen, U.K., 2009. The root of the East African cichlid radiations. BMC Evol. Biol. 3, 1–11.

Schwarzer, J., Misof, B., Ifuta, S.N., Schliewen, U.K., 2011. Time and Origin of Cichlid Colonization of the Lower Congo Rapids. PLoS ONE 6(7): e22380. doi:10.1371/journal.pone.0022380

Schwarzer, J., Misof, B., Schliewen, U.K., 2011a. Speciation within genomic networks: A case study based on Steatocranus cichlids of the lower Congo rapids. J. Evol. Biol. 25, 138–148; doi: 10.1111/j.1420-9101.2011.02409.x.

Seehausen, O., 2004. Hybridization and adaptive radiation. Trends Ecol. Evol. 19, 198–207.

Seehausen, O., 2006. African cichlid fish: a model system in adaptive radiation research. Proc. R. Soc. Lond. B Biol. Sci. 273, 1987–1998.

Shaw, K.L., 2002. Conflict between mitochondrial and nuclear DNA phylogenies of a recent species radiation, what mitochondrial DNA reveals and conceals about modes of speciation in Hawaian crickets. Proc. Natl. Acad. Sci. USA 99, 16122–16127.

Shimodaira, H., Hasegawa, M., 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Mol. Biol. Evol. 16, 1114–1116.

Shimodaira, H., Hasegawa, M., 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. Bioinformatics 17, 1246–1247.

Smith, S.A., Dunn, C.W., 2008. Phyutility: a phyloinformatics tool for trees, alignments and molecular data. Bioinformatics 24, 715–716.

Snoeks, J., 2000. How well known is the ichthyodiversity of the large East African lakes? Adv. Ecol. Res. 31, 17–38.

Sodsuk, P., McAndrew, B.J., 1991. Molecular systematics of three tilapiine genera, *Tilapia, Sarotherodon* and *Oreochromis* using allozyme data. J. Fish Biol. 39, 301–308.

Stamatakis, A., 2006. RAxML-VI-HPC: Maximum Likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690.

Stiassny, M.L.J., 1990. *Tylochromis*, relationships and the phylogenetic status of the African Cichlidae. Am. Mus. Novit. 2993, 1–14.

Stiassny, M.LJ., 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview. In: Keenleyside, M.H.A. (Ed.), Cichlid Fishes: Behaviour, Ecology and Evolution. Chapman and Hall, London, pp. 1–35.

Stiassny, M.L.J., Lamboj, A., De Weirdt, D., Teugels, G.G., 2007. Cichlidae. In: Stiassny, M.L.J., Teugels, G.G, Hopkins, C.D. (Eds.), The fresh and brackish water fishes of Lower Guinea, West-Central Africa Volume 2. Coll. faune et flore tropicales 42. Institut de recherche de développement, Paris, France, Muséum national d'histoire naturelle, Paris, France and Musée royal de l'Afrique Central, Tervuren, Belgium, pp. 269–403.

Stiassny, M.L.J., de Marchi, G., Lamboj, A., 2010. A new species of *Danakilia* (Teleostei, Cichlidae) from Lake Abaeded in the Danakil Depression of Eritrea (East Africa). Zootaxa 2690, 43–52.

Streelman, J.T., Zardoya, R., Meyer, A., Karl, S.A., 1998. Multi-locus phylogeny of cichlid fishes: evolutionary comparison of microsatellite and single-copy nuclear loci. Mol. Biol. Evol. 15, 798–808.

Sturmbauer, C., Salzburger, W., Duftner, N., Schelly, R., Koblmüller, S., 2010. Evolutionary history of the Lake Tanganyika cichlid tribe Lamprologini (Teleostei: Perciformes) derived from mitochondrial and nuclear DNA data. Mol. Phylogenet. Evol. 57, 266–284.

Sültmann, H., Mayer, W.E., Figueroa, F., Tichy, H., Klein, J., 1995. Phylogenetic analysis of cichlid fishes using nuclear DNA markers. Mol. Biol. Evol. 12, 1033–1047.

Swofford, D.L., Waddell, P.J., Huelsenbeck, J.P., Foster, P.G., Lewis, P.O., Rogers, J.S., 2001. Bias in phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. Syst Biol 50, 525-539.

Swofford, D.L., 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4. Sinauer Associates, Sunderland, MA.

Takahashi, K., Terai, Y., Nishida, M., Okada, N., 2001. Phylogenetic relationships and ancient incomplete lineage sorting among cichlid fishes in lake Tanganyika as revealed by analysis of the insertion of retroposons. Mol. Biol. Evol. 18, 2057–2066.

Takahashi, T., 2003. Systematics of Tanganyikan cichlid fishes (Teleostei: Perciformes). Ichthyol. Res. 50, 367–382.

Takahashi, T., Koblmüller, S., 2011. The Adaptive Radiation of Cichlid Fish in Lake Tanganyika: A Morphological Perspective. Int. J. Evol. Biol. 2011, 1–14.

Teugels, G.G., Thys van den Audenaerde, D.F.E., 2003. Cichlidae. In: Paugy, D., Teugels, G.G, Leveque, C. (Eds.), The fresh and brackish water fishes of West Africa Volume 2. Coll. faune et flore tropicales 40. Institut de recherche de développement, Paris, France, Muséum national d'histoire naturelle, Paris, France and Musée royal de l'Afrique Central, Tervuren, Belgium, pp. 521–600.

Thorley, J.L., Wilkinson, M., 1999. Testing the phylogenetic stability of early tetrapods. J. Theor. Biol. 200, 343–344.

Trewavas, E., 1973: I. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. Bull. br. Mus. nat. Hist. Zool. 25, 1–26.

Trewavas, E., 1983. Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum (Natural History), London.

Thys van den Audenaerde, D.F.E., 1964. Revision systematique des especes congolaises du genre *Tilapia* (Pisces, Cichlidae). Ann. Musee Roy. Afr. Centr. Ser. 8 Sci. Zool. 124, 1–155.

Thys van den Audenaerde, D.F.E., 1969. An annotated bibliography of *Tilapia* (Pisces, Cichlidae). Ann. Musee Roy. Afr. Centr. Ser. N-14, Doc. Zool. I–XL.

Turner, G.F., Seehausen, O., Knight, M.E., Allender, C.J., Robinson, R.L., 2001. How many species of cichlid fishes are there in African lakes? Mol. Ecol. 10, 793–806.

Wickler, W., 1963. Zur Klassifikation der Cichlidae, am Beispiel der Gattungen *Tropheus*, *Petrochromis*, *Haplochromis* und *Hemihaplochromis* n. gen. (Pisces, Perciformes). Senckenb. Biol. 44, 83–96.

Figure legends

Figure 1a-f. Consensus topologies of all nuclear single loci based on a ML analysis (identical setup as for the combined ML / BI analyses).

Figure 2. Consensus topology of a combined nuclear locus dataset and a mitochondrial locus dataset based on a ML analysis (identical setup as for the combined ML / BI analyses).

Figure 3. Consensus BI / ML topology of the haplotilapiines phylogeny (94 taxa). The consensus topology (50% majority rule) of the haplotilapiines phylogeny is based on the combined "dataset A" of nine independent mitochondrial and nuclear loci. Black hexagons mark nodes of BS 100 (ML), lower values are shown in non italic numbers. All BPP values (BI) lower than 1.00 are shown in the topology as italic numbers; all other nodes have 1.00 BPP. The two bold faced numbers marked with an asterisk indicate nodes that differ in the BI and ML analyses.

Figure 4. Leaf stability indices for all taxa (N=94). OG (outgroup) outlier identified as *Tylochromis lateralis*.

Figure 5. Box plots for the results of the HET (N=147 experiments) are shown. For each node (A-F) the 25-75% quartiles are drawn, the median is shown with a horizontal line within the box, minimal and maximal values are shown with "whiskers". Values exceeding 1.5 (circles) or 3 (stars) times the box height are illustrated. For values exceeding 3 (stars) times the box height, the corresponding removal is stated.

Figure 6. Potential hybrid signals, shown with dashed straight lines, within haplotilapiines demonstrated in a consensus topology. Coptodonini and Paracoptodonini as well as Coelotilapiini and Heterotilapiini are treated each as one group, because these tribes have the same effect on other tribes and are affected in the same manner by other tribes. *Pelmatolapia* is subdivided into the two species of this genus, *P. mariae* and *P. cabrae*, because they are affected by different hybrid signals. Hybridization events of tribus indicated in blue are discussed in 4.2. Effects of tribus indicated in red are mentioned in 3.2.3. All potential hybrid signals within haplotilapiines were summarized in an arrow diagram.

Figure 7. Consensus topology (50% majority rule) of the ML analysis of the “dataset B” based on the mitochondrial locus ND2 (784 taxa). The number of used sequences of the specific taxa is stated in brackets. The exact composition of *Sarotherodon* I + II, Haplochromini I-IX and *Coptodon* I + II can be found in Appendix A, Supplementary material 2.

Figure 8. Distribution of Tilapiini. 1=*T. guinasana*; 2=*Chilochromis*; 3=*T. bilineata, T. crassa and T.* sp. *“louna”*; 4=*T. baloni* (only Luongo-system). The remaining colored area is T*. sparrmanii* and *T. ruweti* (restricted to Okavango, upper Zambezi, southern tributaries of the Congo River system, Lake Mweru and ambient rivers).

Table legends

Table 1. Division by Thys van den Audenaerde (1969) of the genus *Tilapia* into three “sections”, each including several diagnosed and taxonomically available subgenera, some of them new.

Table 2. Historical overview of the tribes within haplotilapiines.

Table 1. Division by Thys van den Audenaerde (1969) of the genus *Tilapia* into three “sections”, each including several diagnosed and taxonomically available subgenera, some of them new.

section	**section name**	**included subgenera**
I	*Tilapia* sensu lato	*Tilapia* Smith, 1840
		Trewavasia subgen. nov.
		Pelmatolapia subgen. nov.
		Pelmatochromis Steindachner, 1895
II	*Heterotilapia* and *Coptodon* sensu lato	*Heterotilapia* Regan, 1920
		Dagetia subgen. nov.
		Coptodon Gervais, 1853
III	*Sarotherodon* sensu lato	*Danakilia* subgen. nov.
		Neotilapia Regan, 1920
		Alcolapia subgen. nov.
		Nyasalapia subgen. nov.
		Loruwiala subgen. nov.
		Oreochromis Günther, 1894
		Sarotherodon Rüppell, 1854

Table 2. Historical overview of the tribes within haplotilapiines.

Poll 1986	Takahashi 2003	Koblmüller 2008	Takahashi 2011	This study
				Etiini
Tilapiini	Tilapiini	Tilapiini	Tilapiini (Oreochromis tanganicae)	Tilapiini
	Boulengerochromini	Boulengerochromini	Boulengerochromini	Boulengerochromini
				Steatocranini
				Oreochromini
				Coelotilapiini
				Coptodonini
				Paracoptodonini
				Heterotilapiini
				Pelmatolapiini
Bathybathini	Bathybathini	Bathybathini	Bathybathini	Bathybathini
		Hemibatini		
Trematocarini		Trematocarini		
Eretmodini	Eretmodini	Eretmodini	Eretmodini	Eretmodini
Lamprologini	Lamprologini	Lamprologini	Lamprologini	Lamprologini
Ectodini	Ectodini	Ectodini	Ectodini	Ectodini
Cyprichromini	Cyprichromini	Cyprichromini	Cyprichromini	Cyprichromini
Perissodini	Perissodini	Perissodini	Perissodini	Perissodini
Limnochromini	Limnochromini	Limnochromini	Limnochromini	Limnochromini
	Greenwoodochromini			
	Benthochromini	Benthochromini	Benthochromini	Benthochromini
Haplochromini	Haplochromini	Haplochromini	Haplochromini	Haplochromini
	New tribe (Ctenochromis benthicola)			
Tropheini	Tropheini	Tropheini (monophyletic sub-group within the Haplochromini)	Tropheini (monophyletic sub-group within the modern haplochromines)	Tropheini (monophyletic sub-group within the Haplochromini)
	Cyphotilapiini	Cyphotilapiini	Cyphotilapiini	Cyphotilapiini
			Orthochromis	Orthochromis sensu stricto
				Gobiocichlini

Figure 1a-f. Consensus topologies of all nuclear single loci based on a ML analysis (identical setup as for the combined ML / BI analyses).

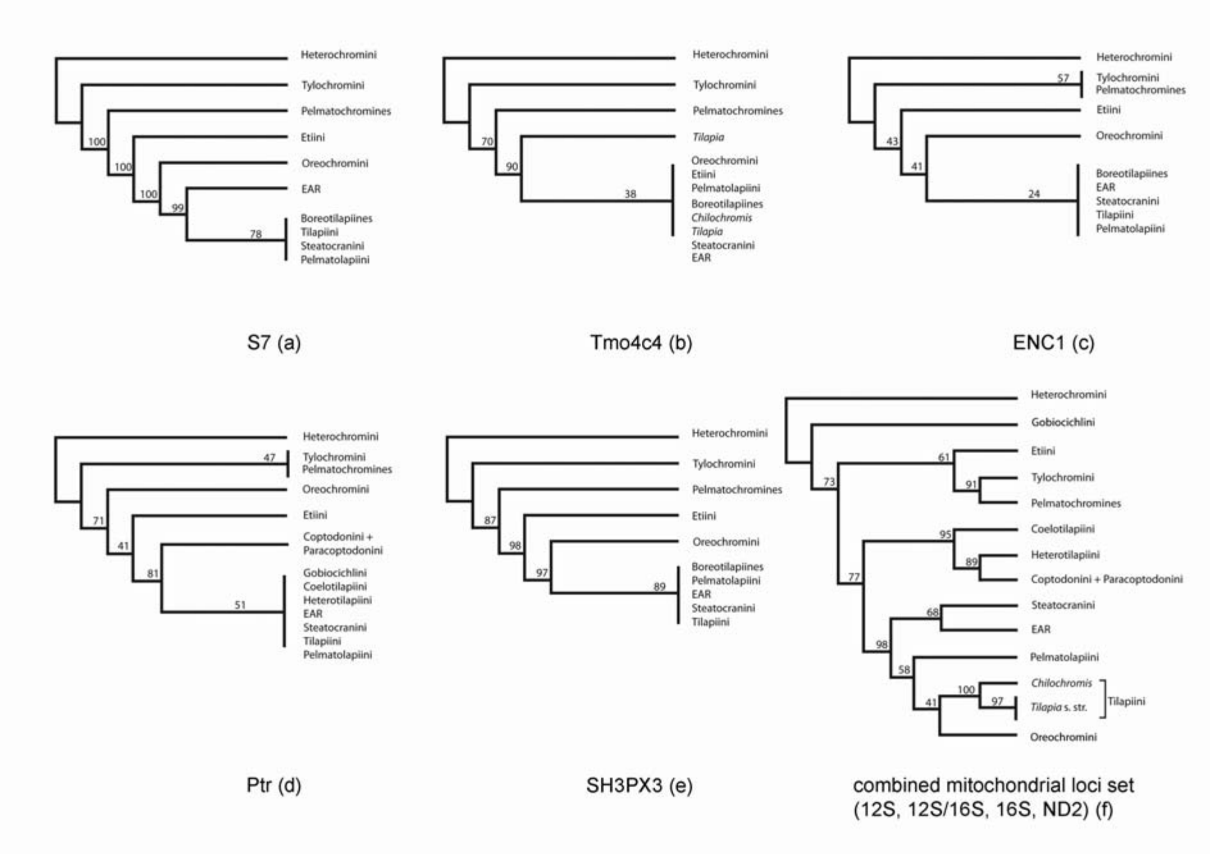
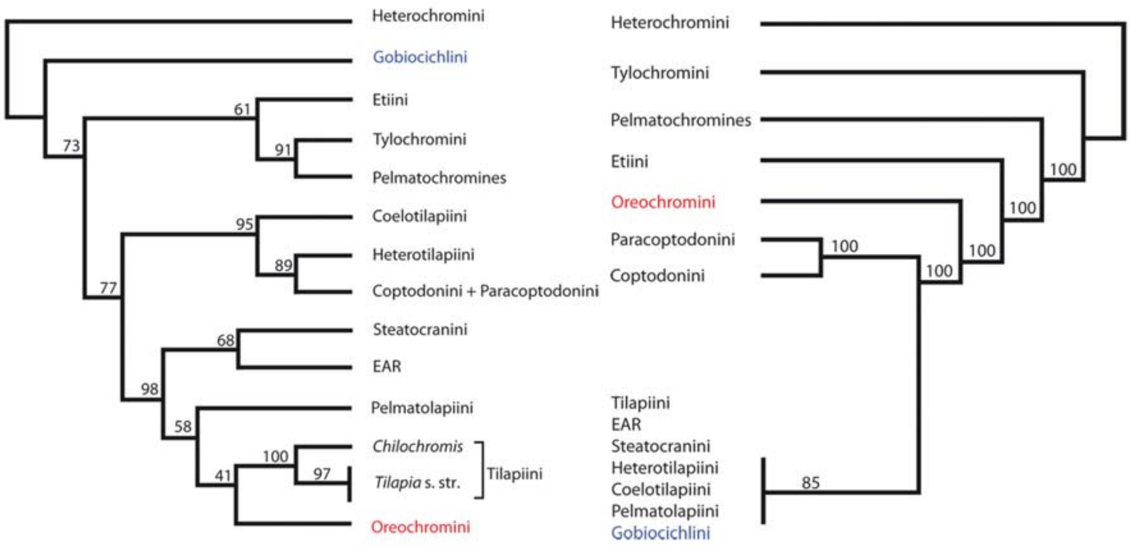


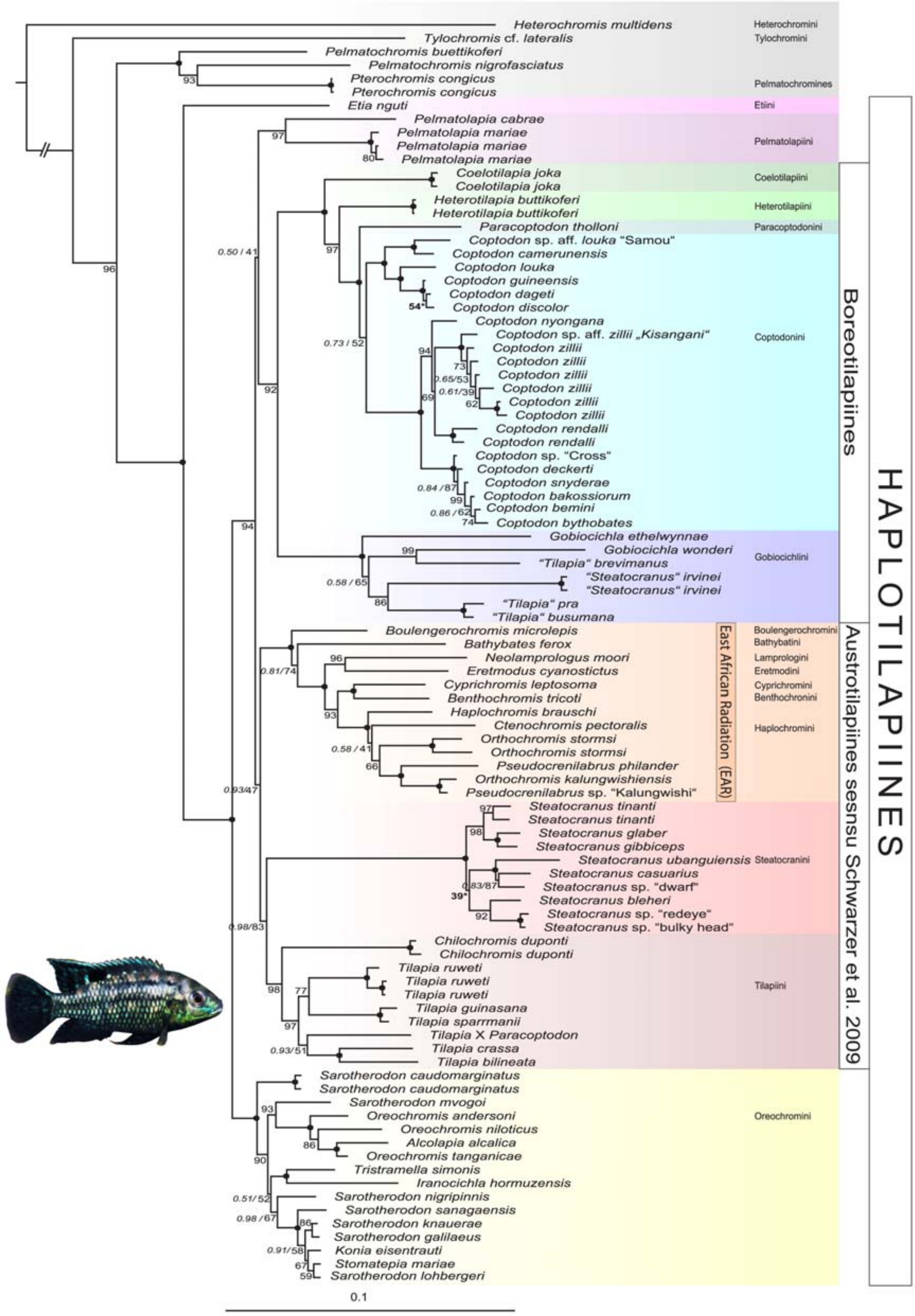
Figure 2. Consensus topology of a combined nuclear locus dataset and a mitochondrial locus dataset based on a ML analysis (identical setup as for the combined ML / BI analyses).



combined mitochondrial loci set (a)
(12S, 12S/16S, 16S, ND2)

combined nuclear data set (b)
(Tmo4c4, ENC1, SH3PX3, S7, Ptr)

Figure 3. Consensus BI / ML topology of the haplotilapiines phylogeny (94 taxa). The consensus topology (50% majority rule) of the haplotilapiines phylogeny is based on the combined “dataset A” of nine independent mitochondrial and nuclear loci. Black hexagons mark nodes of BS 100 (ML), lower values are shown in non italic numbers. All BPP values (BI) lower than 1.00 are shown in the topology as italic numbers; all other nodes have 1.00 BPP. The two bold faced numbers marked with an asterisk indicate nodes that differ in the BI and ML analyses.



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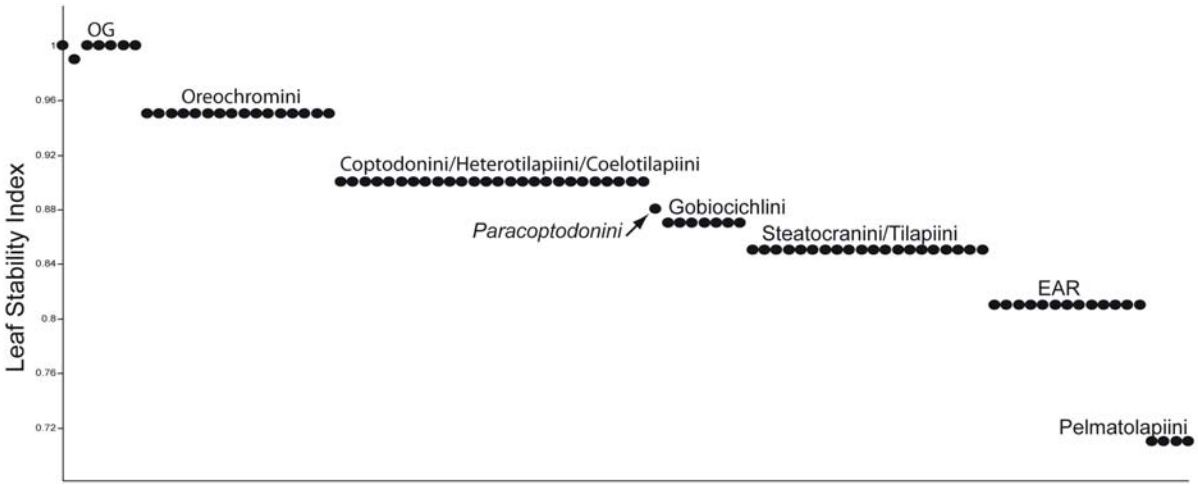

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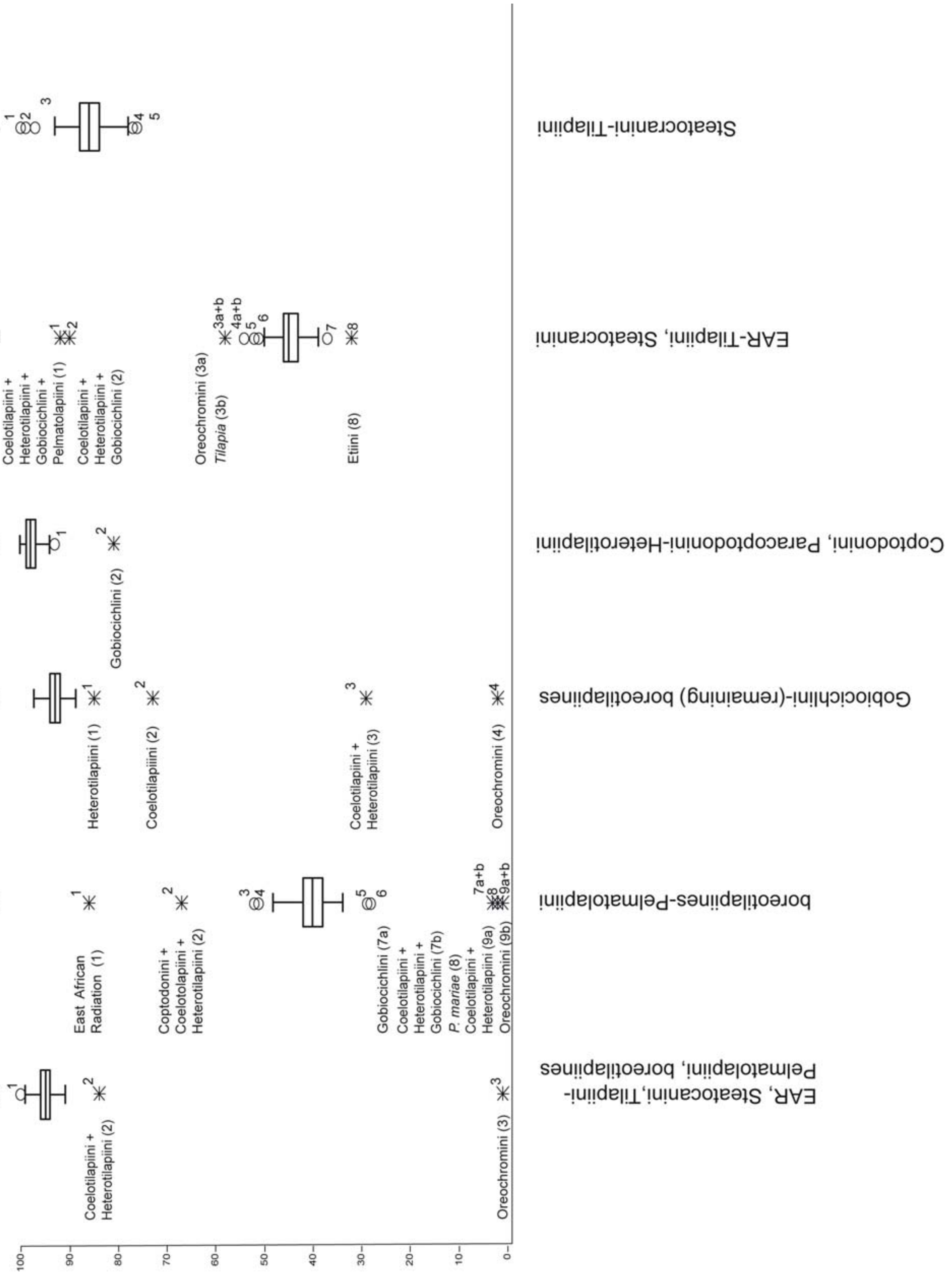

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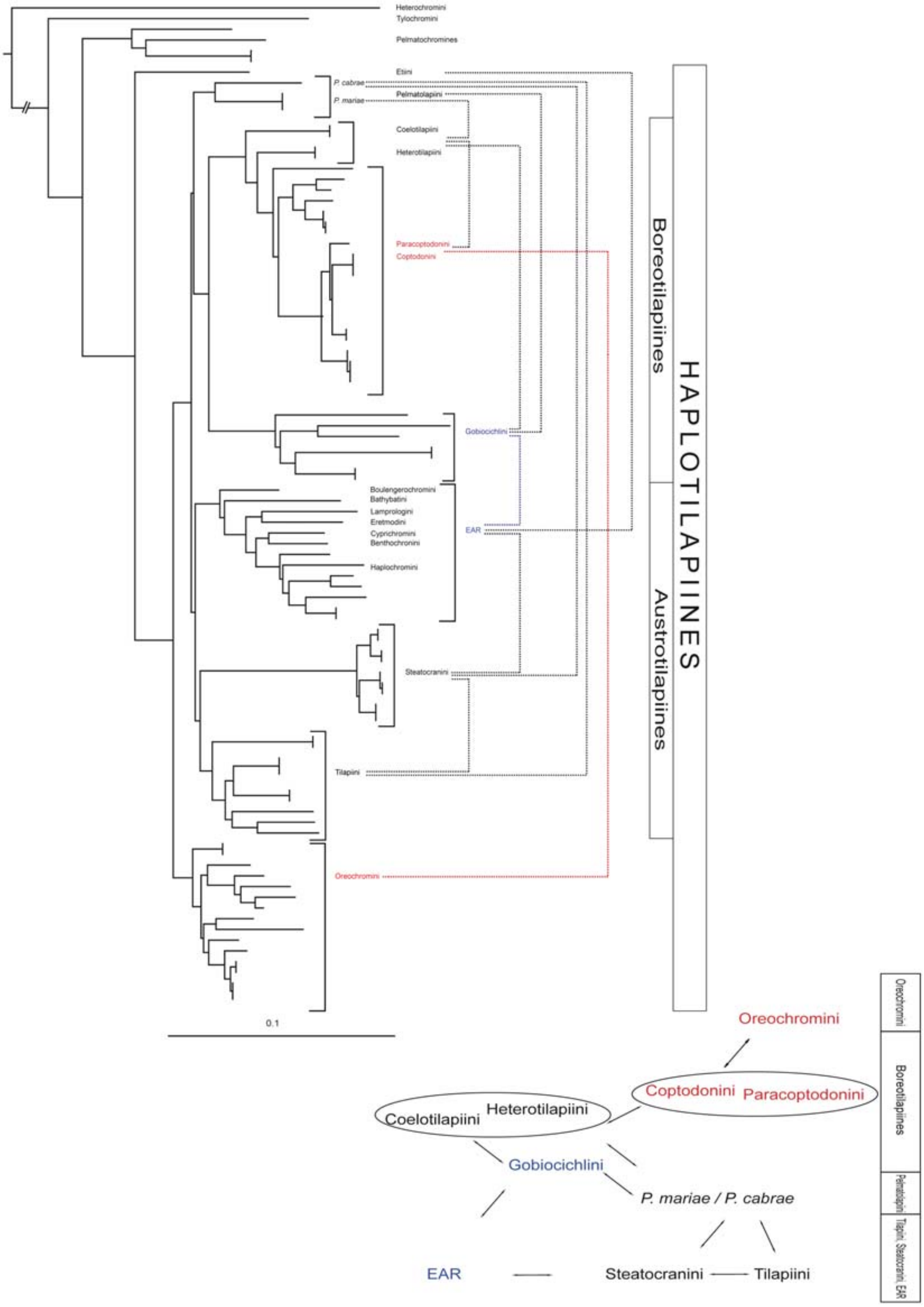
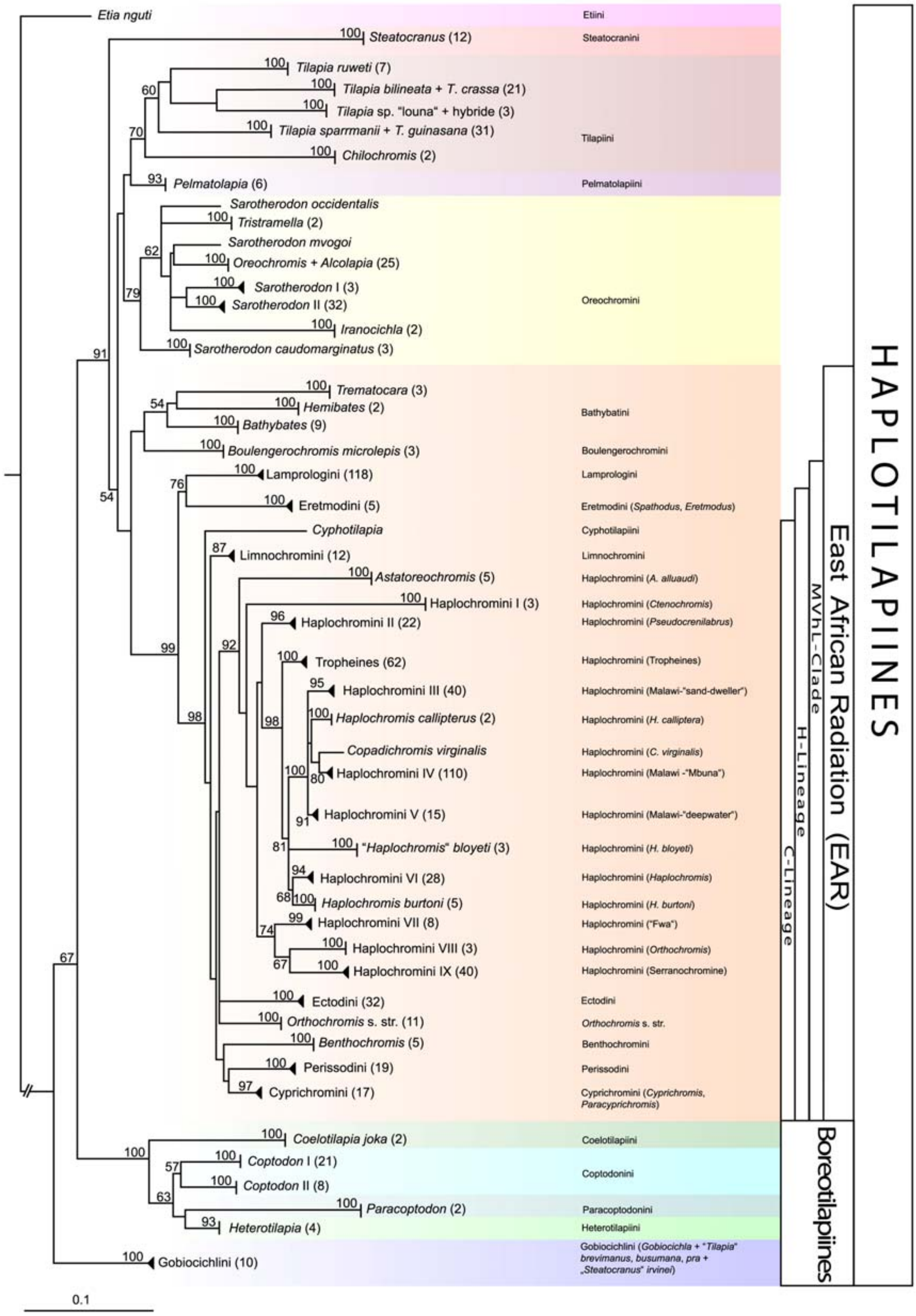


Figure 7. Consensus topology (50% majority rule) of the ML analysis of the "dataset B" based on the mitochondrial locus ND2 (784 taxa). The number of used sequences of the specific taxa is stated in brackets. The exact composition of *Sarotherodon* I + II, Haplochromini I-IX and *Coptodon* I + II can be found in Appendix A, Supplementary material 2.



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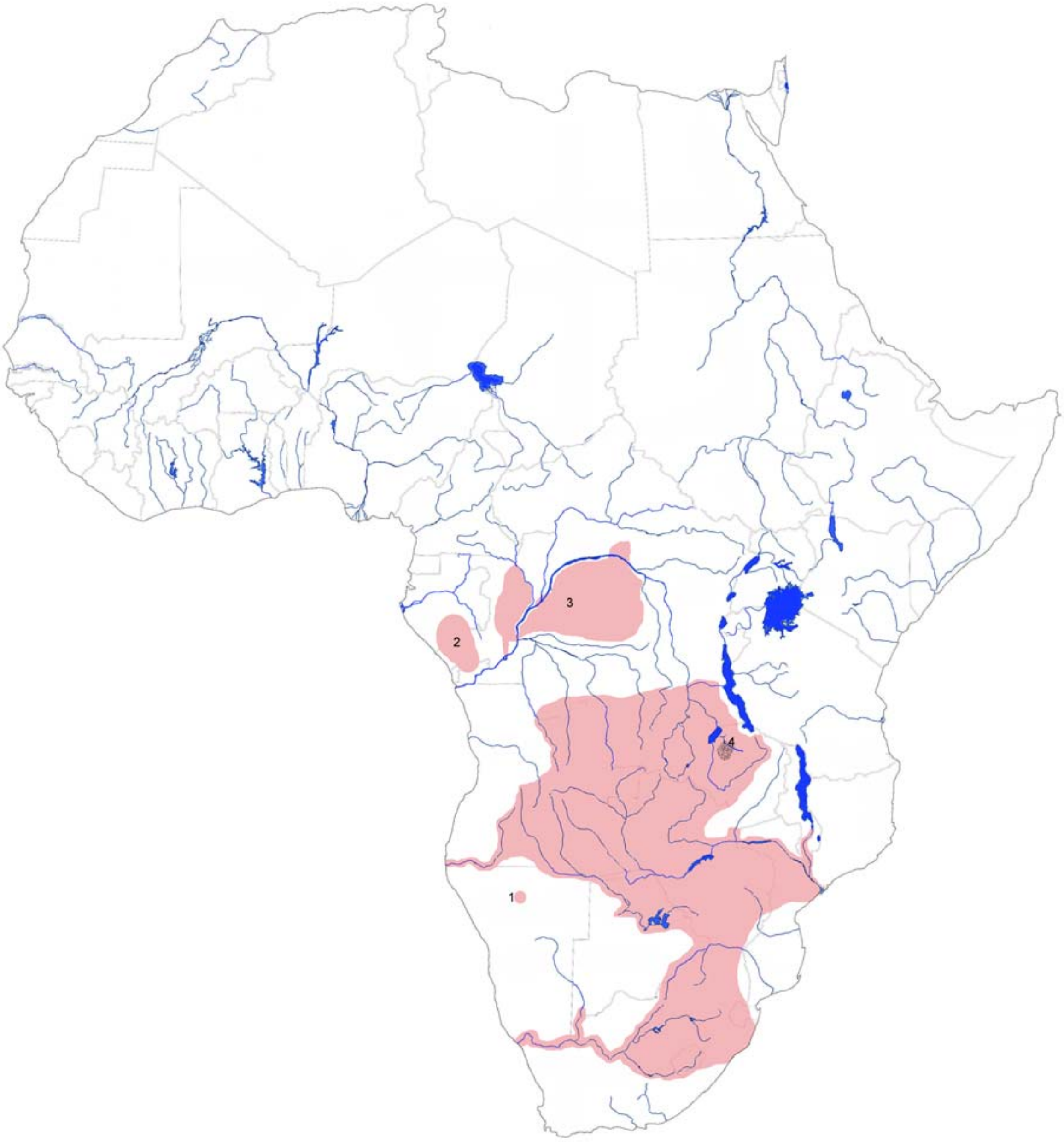

8. General discussion and results

8.1 Evaluation of the first comprehensive infrageneric classification published by Thys van den Audenaerde (1969)

Thys van den Audenaerde divided “*Tilapia*” into three sections (Tab. 1). This thesis focuses on Sections I (*Tilapia* sensu lato) and II (*Heterotilapia* and *Coptodon* sensu lato), because Section III (*Sarotherodon* sensu lato) deals with tilapiine mouthbrooders. The main difference between Thys van den Audenaerde' s Section I and II is the number of cusps of teeth of the lower pharyngeal jaw, two in Section I and three to four in Section II.

In Section I, the first subgenus *Tilapia*, contains *T. sparrmanii* (type) and *T. ruweti*, but excludes *T. guinasana* (placed in the second subgenus *Trewavasia*) based on the character “scales around the caudal peduncle”. Previous studies showed that this count is a highly variable character in “*Tilapia”* (Dunz & Schliewen 2010a) and also in *Tilapia* sensu stricto (unpublished data). This suggests that, based on morphological characteristics, *T. guinasana* should also be included in *Tilapia*. Thys van den Audenaerde' s third subgenus *Pelmatolapia* is primarily grouped based on the dentition character “outer teeth bicuspid and spatulate”. It contains “*T*.” *mariae* (type), “*T*.” *cabrae*, “*T.*” *bilineata*, “*T*.” *brevimanus* and *T. eisentrauti* Trewavas, 1962. Thys van den Audenaerde (1969) himself mentioned an isolated position of “*T.*” *bilineata*, as the character combination of 10–11 gill rakers and the character “a densely scaled caudal fin” is not shared with other Thys van den Audenaerde' s subgenus. Previous studies (Schwarzer *et al.* 2009) as well as actual findings show that “*T.” brevimanus* is not closely related to the type species of *Pelmatolapia*. Meanwhile, “*T.” eisentrauti* has been allocated to a new genus, *Konia* Trewavas, 1972, a mouthbrooder endemic to crater lake Barombi Mbo (Cameroon), which is closely related to the oreochromine genus *Sarotherodon* (Schliewen *et al.* 1994). In summary, these findings suggest that only the two Lower Guinea taxa “*T.” mariae* and “*T.” cabrae* should remain members of the subgenus *Pelmatolapia*. The fourth subgenus *Pelmatochromis* is interesting, due to the fact that “*T*.” *busumana* was assigned to three *Pelmatochromis* species based on the dentition character “median outer teeth bicuspid, the lateral ones conical”. The lateral teeth appear sometimes conical due to wear (Dunz & Schliewen 2010a). Trewavas (1973) retained “*T*.” *busumana* in *Tilapia* in the course of a revision of *Pelmatochromis*. The actual status of “*T*.” *busumana* remains unclear and needs further investigation. However, “*T*.” *busumana* is surely not closely related to *Pelmatochromis* as shown here and in previous studies (Schwarzer *et al.* 2009).

In Section II, the first subgenus *Heterotilapia* contains “*T*.” *buttikoferi* and “*T*.” *cessiana*. The two species are primarily separated based on the molariform pharyngeal teeth, a character that is not shared with any other species in Thys van den Audenaerde' s

Sections I and II. Recent and previous molecular analyses confirm this restriction to a separate (sub)genus (Schwarzer *et al.* 2009). The second subgenus *Coptodon* contains 15 species, all sharing the dentition character “outer teeth on jaws bicuspid, not spatulate”. Also included here are the two species “*T*.” *tholloni* and “*T*.” *congica*, both closely related to *Coptodon*, but different by molecular as well as morphological characteristics and thus later allocated in a separate genus (*Paracoptodon*). The third subgenus *Dagetia* contains only “*T*.” *rheophila*, which is currently placed in the synonymy with *Coptodon* (Dunz & Schliewen 2012).

8.2 Actual state of the scientific research of “*Tilapia*”

This thesis provides a comprehensive phylogenetic hypothesis (Fig. 5) of almost all taxa formerly referred to as “*Tilapia”* and related lineages and thus provides a basis for critical reassessment of the systematics and taxonomy. The supraspecific taxonomy of tilapiine cichlids has been instable, sometimes contradictory and often used in a mixture of taxonomically available with some unavailable names. Recent analyses confirm that tilapiine cichlids as previously understood are paraphyletic and are composed of several distinct lineages. To incorporate phylogenetic results into a consistent classification for future reference in evolutionary biology and taxonomy, I discussed, introduced, revitalized and (re)defined taxonomically available as well as novel genus and tribus names according to the rules of the International Commission of Nomenclature (ICZN, 1999). This is only done for *Tilapia* related lineages in the focus of this study if (1) lineages receive strong node support in the Maximum Likelihood and Bayesian Inference analyses, i.e. bootstrap support >90% and Bayesian posterior probability =1.0, (2) lineage specific node recovery is consistent over all analyses, and if (3) diagnostic molecular and/or morphological characteristics can be used to unambiguously identify those lineages. Reasoning that these lineages have been cohesive over long periods and deserve taxonomic recognition, even if basal nodes remain weakly supported, sometimes possibly due to phylogenetic conflict reflecting ancient hybridisation.

Because of the paraphyly of *Tilapia* six new tribes were erected in this study. Five (Gobiocichlini, Coptodonini, Paracoptodonini, Heterotilapiini and Coelotilapiini) formed the moderately supported clade of boreotilapiines. The tribe Pelmatolapiini remained inconsistent in phylogenetic placement. Additional tribes Etiini, Oreochromini and Steatocranini were described, but are not discussed in detail here (see 7. Paper V). All novel discrete phylogenetic haplotilapiine lineages are supported by molecular and morphological autapomorphies. Tilapiini Trewavas, 1983 remains unsupported by unique molecular characteristics which could be interpreted as autapomorphies, but the tribus members are consistently grouped in all analyses, and with strong node support in the Maximum Likelihood and Bayesian Inference analyses of the multilocus approach.

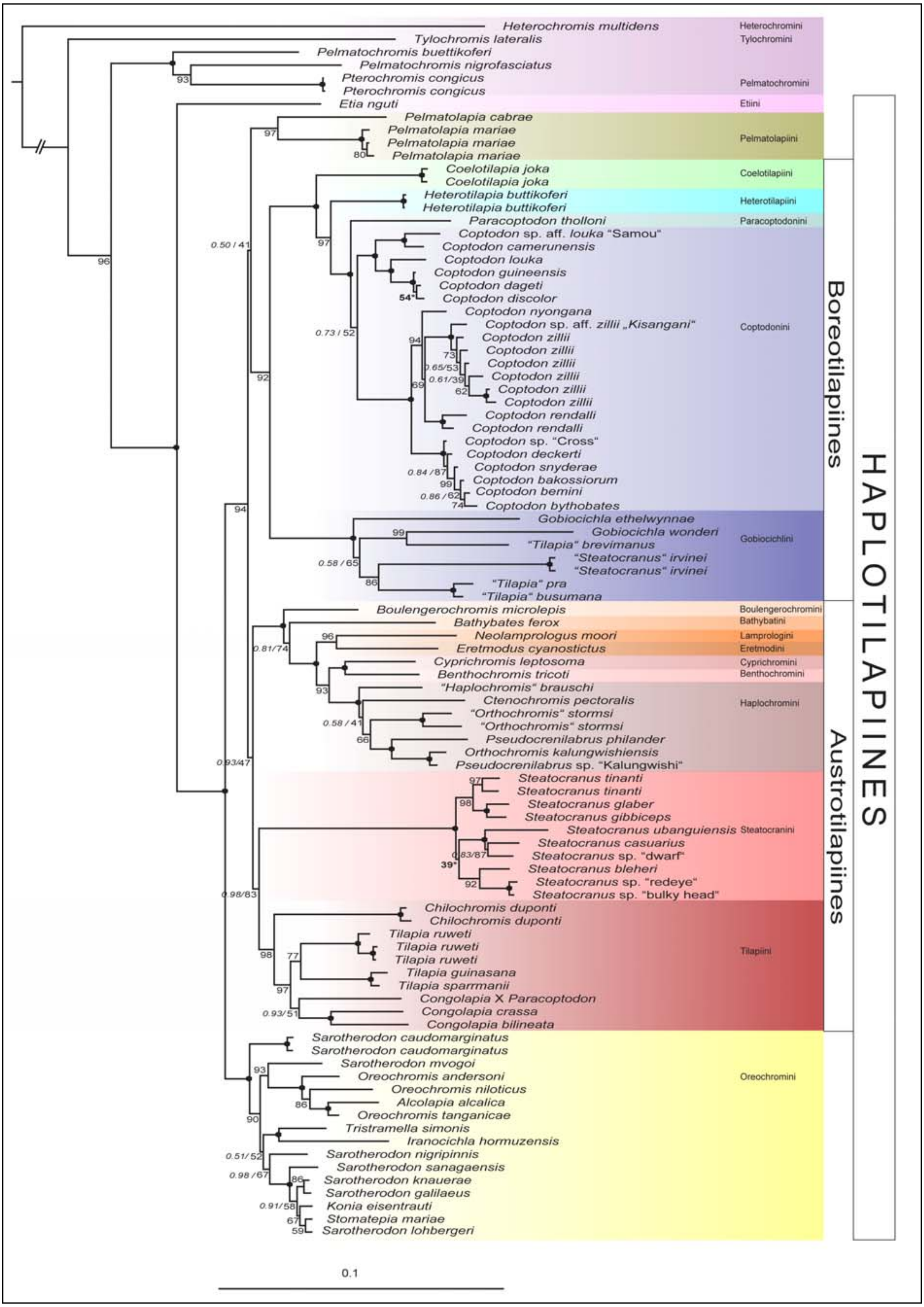

Fig. 5. Consensus of Bayesian Inference and Maximum Likelihood topologies of the haplotilapiines phylogeny (94 taxa). The consensus topology (50% majority rule) of the haplotilapiines phylogeny is based on the combined dataset of nine independent mitochondrial and nuclear loci. Black hexagons mark nodes with full bootstrap support (100%), lower values are shown in non italic numbers. All Bayesian posterior probability values < 1.00 are shown in the topology as italic numbers; all other nodes have 1.00 Bayesian posterior probabilities. The two bold faced numbers marked with an asterisk indicate nodes that differ in the Bayesian Inference and Maximum Likelihood analyses.

Three new genera (*Congolapia*, *Paracoptodon*, and *Coelotilapia*) were described and three genera (*Pelmatolapia*, *Heterotilapia* and *Coptodon*) were raised to generic rank. In addition six new species ("*Tilapia*" *pra*, *Coptodon fusiforme*, *Coptodon nigrans*, *Coptodon ejagham*, *Coptodon konkourensis*, and *Congolapia louna*) were described and three species (*Coptodon deckerti*, *Congolapia crassa*, and *Congolapia bilineata*) were revised in this thesis. With these new descriptions and revisions the number of currently valid "*Tilapia*" species was increased from 39 to 46.

8.3 A short overview of the new tribus and genera

Tribus. Coelotilapiini, new tribe.
Type genus. *Coelotilapia*, new genus.
Included genera. One monotypic genus.
Contained species. *Coelotilapia joka* (Thys van den Audenaerde, 1969).
Distribution (Fig. 6). Coastal plains of Sierra Leone and western Liberia (Teugels & Thys van den Audenaerde 2003).

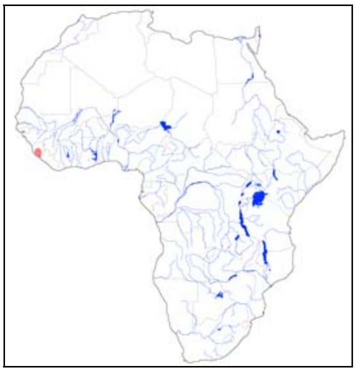

Fig. 6. Distribution (see above) of Coelotilapiini.

Fig. 7. *Coelotilapia joka*; photo: A. Lamboj.

Tribus. Paracoptodonini, new tribe.
Type genus. *Paracoptodon*, new genus.
Included genera. *Paracoptodon*, new genus.
Contained species. *Paracoptodon tholloni* (Sauvage, 1884) and *Paracoptodon congica* (Poll & Thys van den Audenaerde, 1960).
Distribution (Fig. 8). Swampy central Congo area, Pool Malebo, upper and lower Ogowe, Niari-Kwilu, Shiloango and lower Congo (Daget *et al.* 1991; Stiassny *et al.* 2007).

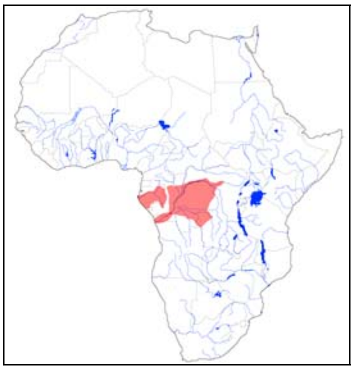

Fig. 8. Distribution (see above) of Paracoptodonini.

Fig. 9. *Paracoptodon tholloni*; photo: J. Geck.

Tribus. Heterotilapiini, new tribe.

Type genus. *Heterotilapia* Regan, 1920 (formerly a subgenus, raised to generic rank).

Included genera. *Heterotilapia* Regan, 1920.

Contained species. *Heterotilapia buttikoferi* (Hubrecht, 1883), type species, and *Heterotilapia cessiana* (Thys van den Audenaerde, 1968).

Distribution (Fig. 10). Lower reaches of coastal rivers from Guinea-Bissau to West Liberia (Saint John River) and Cess or Nipoue River (Liberia, Côte d'Ivoire) (Teugels & Thys van den Audenaerde 2003).

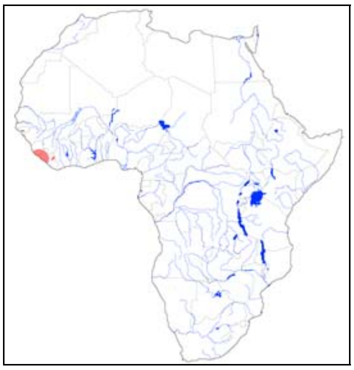

Fig. 10. Distribution (see above) of Heterotilapiini.

Fig. 11. *Heterotilapia buttikoferi.*

Tribus. Pelmatolapiini, new tribe.

Type genus. *Pelmatolapia* Thys van den Audenaerde, 1969 (formerly a subgenus, raised to generic rank).

Included genera. *Pelmatolapia* Thys van den Audenaerde, 1969.

Contained species. *Pelmatolapia mariae* (Boulenger, 1899), type species, and *Pelmatolapia cabrae* (Boulenger, 1898).

Distribution (Fig. 10). Coastal lowlands from Southern Rio Muni to mouth of the Congo River, around Cuanza (also spelled Coanza, Kwanzaa, Quanza, Kwanza, or Kuanza) delta (Angola), coastal lowlands and lagoons from the Tabou River (Côte d'Ivoire) to Southwest

Ghana and from Southeast Benin to the Kribi and Lobe River (Cameroon) (Stiassny *et al.* 2007).

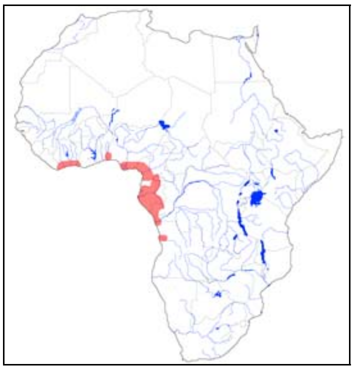

Fig. 10. Distribution (see above) of Pelmatolapiini.

Fig. 11. *Pelmatolapia mariae*; photo: A. Lamboj.

Tribus. Coptodonini, new tribe.

Type genus. *Coptodon* Gervais, 1853.

Included genera. *Coptodon* Gervais, 1853.

Included species. *Coptodon zillii* (Gervais, 1848*),* type species; *C. bakossiorum* (Stiassny, Schliewen & Dominey, 1992); *C. bemini* (Thys van den Audenaerde, 1972); *C. bythobates* (Stiassny, Schliewen & Dominey, 1992); *C. cameronensis* (Holly, 1927); *C. camerunensis* (Lönnberg, 1903); *C. coffea* (Thys van den Audenaerde, 1970); *C. dageti* (Thys van den Audenaerde 1971); *C. discolor* (Günther, 1902); *C. deckerti* (Thys van den Audenaerde, 1967); *C. ejagham* (Dunz & Schliewen 2010b); *C. flava* (Stiassny, Schliewen & Dominey, 1992); *C. fusiforme* (Dunz & Schliewen 2010b); *C. guineensis* (Bleeker, 1862); *C. gutturosa* (Stiassny, Schliewen & Dominey, 1992); *C. imbriferna* (Stiassny, Schliewen & Dominey, 1992); *C. ismailiaensis* (Mekkawy 1995); *C. konkourensis* (Dunz & Schliewen 2012); *C. kottae* (Lönnberg, 1904); *C. louka* (Thys van den Audenaerde, 1969); *C. margaritacea* (Boulenger, 1916); *C. nigrans* (Dunz & Schliewen 2010b); *C. nyongana* (Thys van den Audenaerde, 1960); *C. rendalli* (Boulenger, 1896); *C. rheophila* (Daget, 1962); *C. snyderae* (Stiassny, Schliewen & Dominey, 1992); *C. spongotroktis* (Stiassny, Schliewen & Dominey, 1992); *C. thysi* (Stiassny, Schliewen & Dominey, 1992); *C. walteri* (Thys van den Audenaerde, 1968); yet undescribed species: *Coptodon* sp. aff. *guineensis* "Cross"; *Coptodon* sp. aff. *zillii* "Kisangani" and *Coptodon* sp. aff. *louka* "Samou".

Distribution (Fig. 12). Lakes (alphabetic order): Albert (Uganda / Democratic Republic of the Congo), Barombi-ba-Kotto (Cameroon), Bermin (Cameroon), Bosumtwi (Ghana), Chad (Central Africa), Ejagham (Cameroon), Kainji (Nigeria), Malawi (Malawi / Mozambique / Tanzania), Mboandong (Cameroon), Tanganyika (Tanzania / Burundi / Zambia / Democratic Republic of the Congo), Turkana (Kenya) and Volta (Ghana). River systems (alphabetic order): Bandama, Bia, Cavally, Comoé, Corubal River to Lofa River, Cunene, Dja, Jordan, Kasai, Konkouré, Lualaba, Meme, Mungo, Niger (upper and middle), Nile, Nipoue, Nyong, Okavango, Pra, Saint Paul, Sanaga, Sassandra (upper), Shaba, Senegal, Tano, Ubangi-Uele-Ituri, Volta (upper and lower), Zambesi, coastal waters from mouth of the Senegal River to mouth of the Cuanza River, south Morocco, Sahara (Daget *et al.* 1991; Teugels & Thys van den Audenaerde 2003; Stiassny *et al.* 2007; Dunz & Schliewen 2010b).

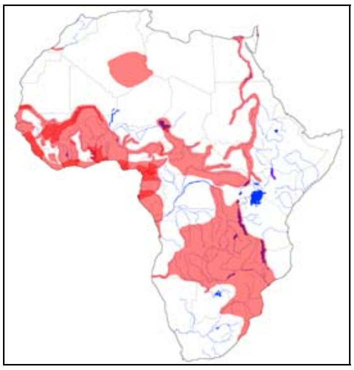

Fig. 12. Distribution (see above) of Coptodonini.

Fig. 13. *Coptodon zillii* from Lake Maryut (Egypt).

Tribus. Gobiocichlini, new tribe.

Type genus. *Gobiocichla* Kanazawa, 1951.

Included genera. *Steatocranus* Boulenger, 1899; *Tilapia* Smith, 1840; *Gobiocichla* Kanazawa, 1951.

Included species. *Steatocranus irvinei* Trewavas, 1943; *Tilapia busumana* (Günther, 1903); *Tilapia brevimanus* Boulenger, 1991; *Tilapia pra* Dunz & Schliewen 2010a; *Gobiocichla wonderi* Kanazawa, 1951; *Gobiocichla ethelwynnae* Roberts, 1982.

Distribution (Fig. 14). Volta River system, coastal rivers from Guinea-Bissau to East Liberia (Cess River), Pra, Ankobra, Tano and Bia Rivers in Southwestern Ghana and Southeastern Cote d'Ivoire, Lake Bosumtwi, rapids in the middle and upper Niger, rapids in the mainstream of the Cross River about eight kilometre downstream from Mamfé (Cameroon) (Teugels & Thys van den Audenaerde 2003; Dunz & Schliewen 2010a).

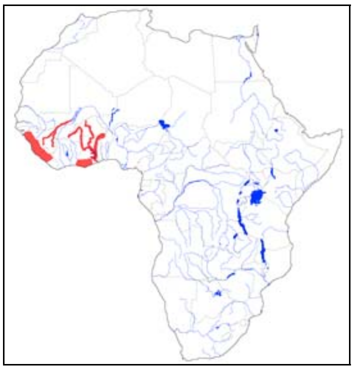

Fig. 14. Distribution (see above) of Gobiocichlini.

Fig. 15. "*Tilapia*" *brevimanus.*

Tribus. Tilapiini Trewavas, 1983

Type genus. *Tilapia* Smith, 1840.

Included genera. *Tilapia* Smith, 1840; *Chilochromis* Boulenger, 1902; *Congolapia* Dunz *et al.* 2012.

Included species. *Tilapia sparrmanii* Smith, 1840; *Tilapia ruweti* Poll & Thys van den Audenaerde, 1965; *Tilapia guinasana* Trewavas, 1963; *Tilapia baloni* Trewavas & Stewart, 1975; *Chilochromis duponti* Boulenger, 1902; *Congolapia bilineata* (Pellegrin, 1900); *Congolapia crassa* (Pellegrin, 1903); *Congolapia louna* Dunz & Schliewen, 2012.

Distribution (Fig. 16). Chiloango basin, Kouilou basin, lower Loeme and Niari-Bouenza Rivers, Western Cuvette Centrale (Alima, Lefini) and central Cuvette Centrale (Thsuapa, Luilaka), the Sangha (Republic of the Congo), from Malebo Pool, the Northern Congo tributary Itimbiri as well as from affluents of the Luilaka (Democratic Republic of the Congo) in the Salonga National Park and Louna River. Kasai drainage including the Lulua and Kwango (middle Congo River basin), upper Congo River basin including the upper Lualaba, Luvua, Lake Mweru, Luapula, Lufira and Upemba region, upper Cuanza, Cunene, Okavango, Lake Ngami, Zambezi, Limpopo, Sabi, Lundi, Northern tributaries of the Orange River, Lake Malawi, Bangweulu, Guinas and Otjikoto (Thys van den Audenaerde 1964; Dunz *et al.* 2012).

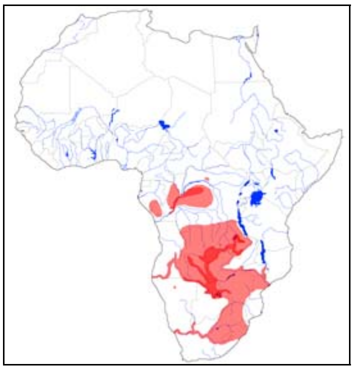

Fig. 16. Distribution (see above) of Tilapiini.

Fig. 17. *Tilapia sparrmanii* from Eye of Kuruman (South Africa).

8.4 Phylogenetic placement of haplotilapiines, Oreochromini, boreotilapiines and austrotilapiines in the multilocus approach compared to the phylogenetic hypothesis of Schwarzer *et al.* (2009)

The term haplotilapiines was introduced on the basis of the phylogenetic analysis of three nuclear loci by Schliewen & Stiassny (2003) for a monophylum comprising *Etia*, tilapiines and a selection of haplochromine-related taxa. The present findings as well as those from Schwarzer *et al.* (2009) confirm the monophyly of this clade. Consistent in all multilocus analyses *Etia nguti* is the most basal sister taxon to all remaining haplotilapiines.

Oreochromini are confirmed to be the basal sister group to all haplotilapiines except *Etia*. Schwarzer *et al.* (2009) identified a clade of the “boreotilapiines” containing two predominantly West African subclades, named “BI” and “BII” (Fig. 4). The increased taxon sampling of the present study provided better resolution within that clade, which allowed the distinction of five tribus. Subclade “BI” corresponds to the new tribus Gobiocichlini and subclade “BII” to the new tribus Coelotilapiini, Heterotilapiini, Paracoptodonini and Coptodonini. The question arises whether it is necessary to define four separate tribus for subclade “BII” and whether, there is molecular and morphological evidence to diagnose subclade “BII” as a unit? On the molecular level there is a single molecular character state interpretable as a diagnostic autapomorphy for all four tribus, but there is no diagnostic morphological criterion. In contrast, each of the four tribus is strongly supported by molecular and morphological autapomorphies in all analyses. The main argument for separating four tribus is however, that the boreotilapiines are strongly compromised by an apparent ancient hybrid signal, and therefore appear to contain genomic partitions of non-boreotilapiine lineages i.e. it is a polyphyletic group. In contrast strongly supported by molecular and morphological autapomorphies (Schwarzer *et al.* 2009), the clade of the austrotilapiines identified three lineages named “AI”, “AII” and “AIII” (Fig. 4); and already in Schwarzer *et al.* (2009) austrotilapiines were only moderately supported (bootstrap support of 86% in Maximum Likelihood analysis). All three still appear as monophyletic lineages in the present study, with subclade “AI” corresponding to the East African cichlid radiation, “AII” corresponding to the newly defined Tilapiini, and “AIII” corresponding to the Steatocranini. However, the critical assessment of the ancient hybrid status of *Pelmatolapia*, both in Schwarzer *et al.* (2009) (*P. mariae*) and in the present study with the second taxon (*P. cabrae*) compromise the monophyly support of austrotilapiines, although relevant but not overwhelming support for its monophyly as well as homoplasy excess suggests that austrotilapiines evolved as a monophylum before a secondary introgression event. In summary, austrotilapiines are polyphyletic but, as for boreotilapiines, an informal clade designation remains useful to refer to their putative ancient monophyly.

8.5 Phylogenetic placement of Oreochromini, boreotilapiines and austrotilapiines in a larger phylogenetic framework (ND2)

A larger phylogenetic framework (784 vs. 94 taxa) was generated for the haplotilapiines based on the mitochondrial locus ND2. The following Lake Tanganyika and related tribes or clades are added additionally to the taxon sampling in the multilocus approach: Cyphotilapiini, Limnochromini, Ectodini, Perissodini and Tanzanian representatives of the genus *Orthochromis* sensu stricto. All clades, which are well supported in the multilocus approach, are also well supported in this Maximum Likelihood analysis of the ND2 dataset except for the former austrotilapiines. The monophyletic clade of *P. cabrae* and *P. mariae* (Pelmatolapiini) is the sister group of boreotilapiines in the multilocus approach, but is located as the sister group of Tilapiini in the ND2 approach. Thus, the austrotilapiines, which contain the Tilapiini, are not supported as monophylum in the ND2 approach, in contrast to the moderately supported (bootstrap support 67%) monophyletic boreotilapiines in this Maximum Likelihood analysis.

Although the ND2 taxonset is about seven times larger than the multilocus set (784 vs. 94 taxa) and contains several tribus of the East African cichlid radiation, which are not represented in the multilocus approach, the resulting topologies of both analyses, ND2 and multilocus, are largely congruent in terminal splits.

8.6 Introgressive hybridisation and cytonuclear discordance

In the following section we look more closely at selected sources of genetic variation and their impact on phylogenetic hypotheses. I compared the mitochondrial and the nuclear dataset of the multilocus approach with the Shimodaira-Hasegawa test (a Likelihood-based, non-parametric test for alternative tree topologies (Shimodaira & Hasegawa 1999)). The Shimodaira-Hasegawa test indicated highly significant conflict ($p<0.01$) between the mitochondrial and the nuclear dataset. The most striking disagreements are the discordant placements of Gobiocichlini and Oreochromini. These discordant placements might imply cytonuclear discordance. This cytonuclear discordance (Oreochromini) indicates introgressive hybridisation between Oreochromini and members of the former austrotilapiines (including *Pelmatolapia*) or incomplete lineage sorting.

Incomplete lineage sorting would suggest that Oreochromini and members of the former austrotilapiines (including *Pelmatolapia*) had a common ancestor. This ancestral taxon has probably passed several speciation events in a short period of time and the ancestral polymorphism of a given gene was not fully resolved into two monophyletic lineages when the second speciation occurred (Pamilo & Nei 1988).

Introgressive hybridisation, also known as introgression, can be defined as an important source of genetic variation in natural populations, “where rare hybrids tend to backcross within populations, leading to limited gene transfer between distinct populations or species” (Baskett & Gomulkiewicz 2011). Introgressive hybridisation is common and well accepted in plants (Hardig *et al.* 2000), but also documented in animals (Gardner 1996), and also in cichlid fishes (Rüber *et al.* 2001; Schliewen & Klee 2004; Koblmüller *et al.* 2009).

The exact differentiation of incomplete lineage sorting and introgressive hybridisation is difficult, because both mechanisms generate very similar phylogenetic patterns (Holder *et* *al.* 2001). To evaluate hybridisation as the cause for cytonuclear discordance, I conducted a specific tree-based homoplasy excess test following Seehausen (2004). Excluding a hybrid taxon from the dataset is expected to lead to an increase of support values (here bootstrap support) for the position of parental taxa in a bifurcating phylogenetic tree (Seehausen 2004; Schwarzer *et al.* 2011). I found tentative evidence of past hybridisation, based on the homoplasy excess test. However, only effects of major lineages could be detected and interpreted, but detection of effects within these lineages is beyond the scope and also beyond the resolving power of only nine loci (four mtDNA and five ncDNA) analysed in this study. I conclude that these lineages (e.g. Oreochromini), that were involved in past hybridisation, have been cohesive over long periods and deserve taxonomic recognition, even if basal nodes remain weakly supported, sometimes possibly due to phylogenetic conflict reflecting ancient hybridisation.

Interspecific conflicts among datasets are usually attributed to introgressive hybridisation or incomplete lineage sorting (Shaw 2002). A third mechanism, long-branch attraction, is able to generate artificial cytonuclear discordance by clustering most similar nodes and thus sometimes a homoplasy is erroneously interpreted as a synapomorphy (Felsenstein 1978). This is unlikely in our cases, e.g. in Oreochromini, because short branches are affected by discordant placement, further the same discordances appear in Maximum Likelihood and Bayesian Inference analyses, which takes unequal rates of branch lengths into account (Swofford *et al.* 2001).

8.7 The species problem

In general there are two contrary points of view of the species category. One side claims that the species category does not exist (Mishler 2003; Fisher 2006) and the other side is in agreement that it does exist (Mayden 2002; De Queiroz 2007; Wilson *et al.* 2009).

Hey (2001) listed 24 different species concepts, but only a few are accepted by the majority of biologists and philosophers. The two most prominent species concepts are the Biological Species Concept and the Phylogenetic Species Concept. Each captures an important aspect, but neither is ubiquitous applicable. The Biological Species Concept based on interbreeding will not explain any asexual taxa. Asexual taxa are much more common than sexual taxa (Templeton 1992). The Phylogenetic Species Concept is not able to explain paraphyletic taxa, but paraphyletic taxa are no less real than monophyletic taxa (De Queiroz & Donoghue 1988).

Therefore, the question arises whether one should eliminate the term “species”? Grant (1981) suggests the term “biospecies” for interbreeding species and Ereshefsky (1992) “phylospecies” for phylogenetic species. Certainly there are several reasons to keep the term “species”. The most frequently cited reason is the pragmatic reasons. The term “species” is well entrenched in natural science and law. Such a common term is necessary to communicate scientific hypotheses and in addition there is no acuteness to eliminate the term “species”, because so far it has not impeded the scientific process (Ereshefsky 2010).

The solution of this problem is somewhere in between. We keep using the term “species” for pragmatic reasons and on condition that scientists are explicit about which species concept they are using (Ereshefsky 2010).

9. Conclusion

After the first attempt of Schwarzer *et al.* (2009) to establish a well supported phylogeny based on multilocus analyses of haplotilapiines, I provide a more comprehensive phylogenetic hypothesis of basal haplotilapiines, accompanied by a revised classification of the paraphyletic tilapiine assemblage. Additional African cichlid lineages with yet informal status (chromidotilapiines, hemichromines, pelmatochromines), or with formal status (Tylochromini, Haplochromini and all Lake Tanganyika tribus) should be included into the future phylogenetic studies to provide a fully revised African cichlid classification. The detection of phylogenetic conflict in the multilocus dataset, most likely explained by ancient hybridisation events, suggests that a classification of African cichlids may have to rest on many small tribus, rather than on a few large partially polyphyletic units, i.e. whose monophyly has been compromised by too many hybridisation and introgression events.

Furthermore, it would be necessary to resolve potential species complexes on species level. The two widespread *Coptodon* species *C. zillii* (Gervais, 1848) and *C. rendalli* (Boulenger, 1897) and the type species *Tilapia sparrmanii* Smith, 1840 are the most potential species complexes. These three species together have 27 synonyms and represent the most important substrate brooding “*Tilapia*” species in aquaculture, making it difficult and necasssary to revise. In addition, the distribution has been extended by anthropogenic influence. In order to resolve such potential species complexes, it is necessary to take extensive samples from the entire distribution area of the potential species complex.

Currently, the resolution of the *Tilapia sparrmanii* species complex is being prepared in collaboration with the South African Institute of Aquatic Biodiversity. Sampling is almost complete and the first preliminary results show that *Tilapia sparrmanii* can be split into several species based on morphologically as well as molecular findings.

10. References

B-Rao C, Majumdar KC (1998) Multivariate map representation of phylogenetic relationships: application to tilapiine fish. Journal of Fish Biology 52, 1199–1217.

Baskett ML, Gomulkiewicz R (2011) Introgressive hybridization as a mechanism for species rescue. Theoretical Ecology 4, 223–239.

Bolnick DI, Fitzpatrick BM (2007) Sympatric speciation: models and empirical evidence. Annual Review of Ecology, Evolution and Systematics 38, 459–487.

Boulenger GA (1915) Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History). British Museum (Natural History): London. 526 pp.

Burkhardt F, Smith S (1990) The correspondence of Charles Darwin. 1856-1857 (vol. 6) Cambridge: Cambridge University Press: London. 673 pp.

Cairns MA, Lackey RT (1992) Biodiversity and management of natural resources: the issues. Fisheries, Bulletin of the American Fisheries Society. 17, 6–10.

Chakrabarty P (2004) Cichlid biogeography: comment and review. Fish and Fisheries 5, 97–119.

Coyne JA (1994) Ernst Mayr and the origin of species. Evolution 51, 19–30.

Coyne JA, Orr HA (1998) The evolutionary genetics of speciation. Philosophical Transactions of the Royal Society of London Series B 353, 287–305.

Coyne JA, Orr HA (2004) Speciation. Sinauer: Sunderland, Massachusetts. 545 pp.

Cracraft J (1983) Species concepts and speciation analysis. Pp. 159–187 in Johnson RF, ed., Current Ornithology (vol. 1). Plenum Press: New York. 402 pp.

Cracraft J (1989) Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59 in Otte D, Endler J, eds., Speciation and its consequences. Sinauer: Sunderland, Massachusetts. 679 pp.

Daget J, Thys van den Audenaerde DFE (1991) *Tilapia*. Pp. 482–508 in Daget J, Gosse J-P, Teugels GG, Thys van den Audenaerde DFE, eds., Check-list of the freshwater fishes of Africa (CLOFFA): ISNB, Brussels; MRAC, Tervuren; and ORSTOM, Paris. (vol. 4). 740 pp.

De Queiroz K, Donoghue M (1988) Phylogenetic systematics and the species problem. Cladistics 4, 317–338. doi:10.1111/j.1096-0031.1988.tb00518.x.

De Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56, 879–866. doi:10.1080/10635150701701083.

Dunz AR, Schliewen UK (2010a) Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana. Zootaxa 2548, 1–21.

Dunz AR, Schliewen UK (2010b) Description of a *Tilapia* (*Coptodon*) species flock of Lake Ejagham (Cameroon), including a redescription of *Tilapia deckerti* Thys van den Audenaerde, 1967. Spixiana 33, 251–280.

Dunz AR, Schliewen UK (2012) Description of a rheophilic *Tilapia* species Smith, 1840 (Teleostei: Cichlidae) from Guinea with comments on *Tilapia rheophila* Daget, 1962. Zootaxa 3314, 17–30.

Ereshefsky M (1992) Eliminative pluralism. Philosophy of Science 59, 671–690.

Ereshefsky M (2010) Darwin's solution to the species problem. Synthese 175, 405–425.

Eschmeyer WN, Fong JD (2012) Species of fishes by family/subfamily. Online version dated 7 June 2012.
http://research.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp

Farias IP, Orti G, Meyer A (2000) Total evidence: molecules, morphology, and the phylogenetics of cichlid fishes. Journal of Experimental Zoology 288, 76–92.

Felsenstein J (1978) Cases in which parsimony or compatibility methods will be positively misleading. Systematic Zoology 27, 401–410.

Fisher K (2006) Rank-free monograph: a practical example from the moss clade *Leucophanella* (Calymperaceae). Systematic Biology 31, 13–30.

Fowler HW (1934) Fishes obtained by Mr. HW Bell-Marley chiefly in Natal and Zululand in 1929 to 1932. Proceedings of the National Academy of Sciences of Philadelphia 86, 405–514.

Fryer G, Iles TD (1972) The cichlid fishes of the Great Lakes of Africa: Their biology and evolution. Oliver & Boyd: Edinburgh. 641 pp.

Gardner JPA (1996) The *Mytilus edulis* species complex in Southwest England: effects of hybridization and introgression upon interlocus associations and morphometric variation. Marine Biology 125, 385–399.

Gavrilets S (2004) Fitness landscapes and the origin of species, Princeton University Press: Monographs in Population Biology (vol. 41). Princeton. 476 pp.

Genner MJ, Turner GF (2012) Ancient hybridization and phenotypic novelty within Lake Malawi's cichlid fish radiation. Molecular Biology and Evolution 29, 195–206.

Grant V (1981) Plant Speciation (2nd ed.) Columbia University Press: New York. 563 pp.

Greenwood PH (1973) A revision of *Haplochromis* and related species (Pisces, Cichlidae) from Lake George, Uganda. Bulletin of the British Museum (Natural History). Zoology 25, 141–242.

Greenwood PH (1978) A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. Bulletin of the British Museum (Natural History). Zoology 33, 297–323.

Greenwood PH (1979) Towards a phyletic classification of the "genus" *Haplochromis* (Pisces, Cichlidae) and related taxa. Part I. Bulletin of the British Museum (Natural History). Zoology 35, 265–322.

Greenwood PH (1980) Towards a phyletic classification of the "genus" *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II, the species from Lakes Victoria, Nabugabo, Edward, Georg and Kivu. Bulletin of the British Museum (Natural History). Zoology 39, 1–101.

Greenwood PH (1987) The genera of pelmatochromine fishes (Teleostei: Cichlidae). A phylogenetic review. Bulletin of the British Museum (Natural History). Zoology 53, 139–203.

Hardig TM, Brunsfeld SJ, Fritz RS, Morgan M, Orians CM (2000) Morphological and molecular evidence for hybridization and introgression in a willow (*Salix*) hybrid zone. Molecular Ecology 9, 9–24.

Hay WW, DeConto RM, Wold CN, Wilson KM, Voigt S, Schulz M, Wold AR, Dullo WC, Ronov AB, Balukhovsky AN, Söding E (1999) Alternative global cretaceous paleogeography. Pp. 1–47 in Barrera E, Johnson CC, eds., Evolution of the cretaceous ocean-climate system. Geological Society of America Special Paper: Boulder, Colorado. 332 pp.

Hey J (2001) The mind of the species problem. Trends in Ecology and Evolution 16, 326–329. doi:10.1016/S0169-5347(01)02145-0.

Hoedeman JJ, De Jong JCM (1947) Encyclopaedie voor de Aquariumhouder. –Uitgeverij "De Regenboog", Amsterdam, Nederland. No page numbers.

Holder MT, Anderson JA, Holloway AK (2001) Difficulties in detecting hybridization. Systematic Biology 50, 978–982.

Hughes RM, Noss RF (1992) Biological diversity and biological integrity: current concerns for lakes and streams. Fisheries (Bethesda) 17, 11–19.

ICZN (1999) International Code of Zoological Nomenclature. Fourth Edition. International Trust for Zoological Nomenclature: London. 306 pp.

Joyce DA, Lunt DH, Genner MJ, Turner GF, Bills R, Seehausen O (2011) Repeated colonization and hybridization in Lake Malawi cichlids. Current Biology 21, 108-109.

Klett V, Meyer A (2002) What, if anything, is a *Tilapia*?—Mitochondrial ND2 phylogeny of tilapiines and the evolution of parental care systems in the African cichlid fishes. Molecular Biology and Evolution 19, 865–883.

Koblmüller S, Duftner N, Katongo C, Phiri H, Sturmbauer C (2005) Ancient divergence in bathypelagic Lake Tanganyika deepwater cichlids: mitochondrial phylogeny of the tribe Bathybatini. Journal of Evolutionary Biology 60, 297–314.

Koblmüller S, Sefc KM, Sturmbauer C (2008) The Lake Tanganyika cichlid species assemblage: recent advances in molecular phylogenetics. Hydrobiologia 615, 5–20.

Koblmüller S, Egger B, Sturmbauer C, Sefc KM (2009) Rapid radiation, ancient incomplete lineage sorting and ancient hybridization in the endemic Lake Tanganyika cichlid tribe Tropheini. Molecular Phylogenetics and Evolution 55, 318–334.

Kocher TD, Lee W-J, Sobolewska H, Penman D, McAndrew B (1998) A genetic linkage map of a cichlid fish, the tilapia (*Oreochromis niloticus*). Genetics 148, 1225–1232.

Kocher TD (2004) Adaptive evolution and explosive speciation: the cichlid fish model. Nature Reviews Genetics 5, 288–298.

Kornfield I, Smith PF (2000) African cichlid fishes: model systems for evolutionary biology. Annual Review of Ecology and Systematics 31, 163–196.

Konings A (2007) Malawi cichlids in their natural habitat 4th Edition. Cichlid Press: El Paso, Texas. 424 pp.

Liem KF (1973) Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Systematic Zoology 22, 425–441.

Lippitsch E (1995) Scale and squamation character polarity and phyletic assessment in the family Cichlidae. Journal of Fish Biology 47, 91–106.

Lubchenco J, Olson A, Brubaker L, Carpenter S, Holland M, Hubbell S, Levin S, MacMahon J, Matson P, Melillo P, Mooney H, Peterson C, Pulliam H, Real L, Regal P, Risser P (1991) The sustainable biosphere initiative: An ecological research agenda. Ecology 72, 371–412.

Mayden RL (2002) On biological species, species concepts and individuation in the natural world. Fish and Fisheries 3, 171–196. doi:10.1046/j.1467-2979.2002.00086.x

Mayer WE, Tichy H, Klein J (1998) Phylogeny of African cichlid fishes as revealed by molecular markers. Heredity 80, 702–714.

Mayr E (1942) Systematics and the origin of species from the viewpoint of a zoologist. Columbia University Press: New York. 334 pp.

McAndrew BJ, Majumdar KC (1984) Evolutionary relationships within three Tilapiine genera (Pisces: Cichlidae). Zoological Journal of the Linnean Society 80, 421–435.

McNeely JA (1988) Economics and biological diversity. International Union for Conservation of Nature and Natural Resources: Gland, Switzerland. 252 pp.

Meyer A, Kocher TD, Basasibwaki P, Wilson AC (1990) Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature 347, 550–553.

Meyer A (1993) Phylogenetic relationships and evolutionary processes in East African cichid fishes. Trends in Ecology and Evolution 8, 279–284.

Mishler B (2003) The advantages of rank-free classification for teaching and research. Cladistics 19, 157.

Murray AM (2000a) Eocene cichlid fishes from Tanzania, East Africa. Journal of Vertebrate Paleontology 204, 651–664.

Murray AM (2000b) The Palaeozoic, Mesozoic and Early Cenozoic fishes of Africa. Fish and Fisheries 1, 111–145.

Murray AM (2001a) The fossil record and biogeography of the Cichlidae (Actinopterygii: Labroidei). Biological Journal of the Linnean Society 74, 517–532.

Murray AM (2001b) The oldest fossil cichlids (Teleostei: Perciformes): indication of a 45 millions-years-old species flock. Proceedings of the Royal Society of London B 268, 679–684.

Nagl S, Tichy H, Mayer WE, Klein J, Takezaki N, Takahata N (2001) The origin and age of haplochromine fishes in Lake Victoria, East Africa. Proceedings of the Royal Society 267, 1471–2954.

Nelson JS (2006) Fishes of the world. John Wiley & Sons: Hoboken, New Jersey. 601 pp.

Nishida M (1991) Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichlid fishes: Inferences from allozyme data. Experientia 47, 974–979.

Norse EA, Rosenbaum KL, Wilcove DS, Wilcox BA, Romme WH, Johnston DW, Stout ML (1986) Conserving biological diversity in our National Forests. Wilderness Society: Washington, DC. 116 pp.

Noss RF (1983) A regional landscape approach to maintain diversity. BioScience 33, 700–706.

OTA (Office of Technology Assessment) (1987) Technologies to maintain biological diversity. U.S. Government Printing Office: Washington, DC. 334 pp.

Pamilo P, Nei M (1988) Relationship between gene trees and species trees. Molecular Biology and Evolution 5, 568–583.

Poll M (1986) Classification des Cichlidae du lac Tanganika. Tribus, genres et espèces. Académie Royale de Belgique, Mémoires de la Classe des Sciences 45, 1–163.

Pouyaud L, Agnèse J (1995) Phylogenetic relationships beween 21 species of three tilapiine genera *Tilapia*, *Sarotherodon* and *Oreochromis* using allozyme data. Journal of Fish Biology 47, 26–38.

Regan CT (1920) The classification of the fishes of the family Cichlidae I. The Tanganyika genera. Annals and Magazine of Natural History (Series 9) 5, 33–53.

Regan CT (1922) The classification of the fishes of the family Cichlidae II. On African and Syrian genera not restricted to the Great Lakes. Annals and Magazine of Natural History (Series 9) 10, 249–264.

Ridha MT (2006) Evaluation of growth performance of nonimproved and improved strains of the Nile *Tilapia* (L.), *Oreochromis niloticus*. Journal of The World Aquaculture Society 37, 218–223.

Roberts L (1990) Counting on science at EPA. Science 249, 616–618.

Rosen DE (1978) Vicariant patterns and historical explanation in biogeography. Systematic Zoology 27, 159–188.

Rosen DE (1979) Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative biogeography. Bulletin of the American Museum of Natural History 162, 267–376.

Rüber L, Meyer A, Sturmbauer C, Verheyen E (2001) Population structure in two sympatric species of the Lake Tanganyika cichlid tribe Eretmodini: evidence for introgression. Molecular Ecology 10, 1207–1225.

Salzburger W, Meyer A, Baric S, Verheyen E, Sturmbauer C (2002) Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African haplochromine cichlid fish faunas. Systematic Biology 51, 113–135.

Salzburger W, Meyer A (2004) The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. Naturwissenschaften 91, 277–290.

Salzburger W, Mack T, Verheyen E, Meyer A (2005) Out of Tanganyika: genesis, explosive speciation, key-innovations and phylogeography of the haplochromine cichlid fishes. BMC Evolutionary Biology 5, 1–15.

Savolainen V, Anstett MC, Lexer C, Hutton I, Clarkson JJ, Norup MV, Powell MP, Springate D, Salamin N, Baker WJ (2006) Sympatric speciation in palms on an oceanic island. Nature 441, 210–213.

Schliewen UK, Tautz D, Pääbo S (1994) Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368, 629–632.

Schliewen UK, Rassmann K, Markmann M, Markert J, Kocher T, Tautz D (2001) Genetic and ecological divergence of a monophyletic cichlid species pair under fully sympatric conditions in Lake Ejagham. Cameroon. Molecular Ecology 10, 1471–1488.

Schliewen UK, Stiassny MLJ (2003) *Etia nguti*, a new genus and species of cichlid fish from the River Mamfue, Upper Cross River basin in Cameroon, West- Central Africa. Ichthyological Explorations of Freshwaters 14, 61–71.

Schliewen UK, Klee B (2004) Reticulate sympatric speciation in Cameroonian crater lake cichlids. Frontiers in Zoology 1, 1–12.

Schwarzer J, Misof B, Tautz D, Schliewen UK (2009) The root of the East African cichlid radiations. BMC Evolutionary Biology 3, 1–11.

Schwarzer J, Misof B, Schliewen UK (2011) Speciation within genomic networks: A case study based on *Steatocranus* cichlids of the lower Congo rapids. Journal of Evolutionary Biology 25, 138–148. doi: 10.1111/j.1420-9101.2011.02409.x.

Seehausen O (2004) Hybridization and adaptive radiation. Trends in Ecology and Evolution 19, 198–207.

Seehausen O (2006) African cichlid fish: a model system in adaptive radiation research. Proceedings of the Royal Society of London B: Biological Sciences 273, 1987–1998.

Shaw KL (2002) Conflict between mitochondrial and nuclear DNA phylogenies of a recent species radiation, what mitochondrial DNA reveals and conceals about modes of speciation in Hawaian crickets. Proceedings of the National Academy of Sciences USA 99, 16122–16127.

Shimodaira H, Hasegawa M (1999) Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 16, 1114–1116.

Snoeks J (2000) How well known is the ichthyodiversity of the large East African lakes? Advances in Ecological Research 31, 17–38.

Sodsuk P, McAndrew BJ (1991) Molecular systematics of three tilapiine genera, *Tilapia*, *Sarotherodon* and *Oreochromis* using allozyme data. Journal of Fish Biology 39, 301–308.

Sparks JS (2001) Phylogeny and biogeography of the Malagasy and South Asian cichlid fishes (Teleostei: Perciformes: Cichlidae), including a survey of the freshwater fishes of Madagascar. Unpublished doctoral dissertation, University of Michigan.

Sparks JS (2003) Molecular phylogeny of the Malagasy and South Asian cichlids (Teleostei: Perciformes: Cichlidae). Molecular Phylogenetics and Evolution 30, 599–614.

Sparks JS, Smith WL (2004) Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). Cladistics 20, 501–517.

Stiassny MLJ (1990) *Tylochromis*, relationships and the phylogenetic status of the African Cichlidae. American Museum Novitates 2993, 1–14.

Stiassny MLJ (1991) Phylogenetic intrarelationships of the family Cichlidae: an overview. Pp. 1–35 in Keenleyside MHA, ed., Cichlid fishes: behaviour, ecology and evolution. Chapman and Hall: London. 404 pp.

Stiassny MLJ, Schliewen UK, Dominey WJ (1992) A new species flock of cichlid fishes from Lake Bermin, Cameroon with a description of eight new species of *Tilapia* (Labroidei: Cichlidae). Ichthyolgical Exploration Freshwaters 3, 311–346.

Stiassny MLJ, Lamboj A, De Weirdt D, Teugels GG (2007) Cichlidae. Pp. 269–403 in Stiassny MLJ, Teugels GG, Hopkins CD, eds., The fresh and brackish water fishes of Lower Guinea, West-Central Africa (vol. 2). Collection faune et flore tropicales 42. Institut de recherche de développement, Paris, France, Muséum national d'histoire naturelle, Paris, France and Musée royal de l'Afrique Central, Tervuren, Belgium. 603 pp.

Streelman JT, Zardoya R, Meyer A, Karl SA (1998) Multilocus phylogeny of cichlid fishes (Pisces: Perciformes): evolutionary comparison of microsatellite and single copy nuclear loci. Molecular Biology and Evolution 15, 798–808.

Sturmbauer C, Salzburger W, Duftner N, Schelly R, Koblmüller S (2010) Evolutionary history of the Lake Tanganyika cichlid tribe Lamprologini (Teleostei: Perciformes) derived from mitochondrial and nuclear DNA data. Molecular Phylogenetics and Evolution 57, 266–284.

Sültmann H, Mayer WE, Figueroa F, Tichy H, Klein J (1995) Phylogenetic analysis of cichlid fishes using nuclear DNA markers. Molecular Biology and Evolution 12, 1033–1047.

Swofford DL, Waddell PJ, Huelsenbeck JP, Foster PG, Lewis PO, Rogers JS (2001) Bias in phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. Systematic Biology 50, 525–539.

Takahashi K, Terai Y, Nishida M, Okada N (2001) Phylogenetic relationships and ancient incomplete lineage sorting among cichlid fishes in Lake Tanganyika as revealed by analysis of the insertion of retrotransposons. Molecular Biology and Evolution 18, 2057–2066.

Takahashi T (2003) Systematics of Tanganyikan cichlid fishes (Teleostei: Perciformes). Ichthyological Research 50, 367–382.

Takahashi T, Koblmüller S (2011) The adaptive radiation of cichlid fish in Lake Tanganyika: a morphological perspective. International Journal of Evolutionary Biology 2011, 1–14.

Temple PH (1969) Some biological implications of a revised geological history for Lake Victoria. Biological Journal of the Linnean Society 1, 363–371.

Templeton A (1992) The meaning of species and speciation: a genetic perspective. Pp. 159–185 in M. Ereshefsky, ed., The units of evolution. MIT Press: Cambridge. 425 pp.

Teugels GG, Thys van den Audenaerde DFE (2003) Cichlidae. Pp. 521–600 in Paugy D, Teugels GG, Leveque C, eds., The fresh and brackish water fishes of West Africa (vol. 2). Collection faune et flore tropicales 40. Institut de recherche de développement, Paris, France, Muséum national d'histoire naturelle, Paris, France and Musée royal de l'Afrique Central, Tervuren, Belgium. 815 pp.

Thys van den Audenaerde DFE (1964) Révision systématique des espèces congolaises du genre *Tilapia* (Pisces, Cichlidae). Annales Musee Royal de l'Afrique Centrale Sèrie 8 Sciences Zoologiques 124, 1–155.

Thys van den Audenaerde DFE (1969) An annotated bibliography of *Tilapia* (Pisces, Cichlidae). Documentation zoologique No. 14, Musée royal d'Afrique centrale: Tervuren. I–XI; 406 pp.

Tiercelin JJ, Mondeguer A (1991) The geology of the Tanganyika trough. Pp. 7–48 in Coulter GW, ed., Lake Tanganyika and its life. Oxford University Press: New York. 354 pp.

Trewavas E, Green J, Corbet SA (1972) Ecological studies on crater lakes in West Cameroon. Fishes of Barombi Mbo. Journal of Zoology 167, 41–95.

Trewavas E (1973) I. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. Bulletin of the British Museum (Natural History). Zoology 25, 1–26.

Trewavas E (1983) Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum (Natural History): London. 583 pp.

Turner GF, Seehausen O, Knight ME, Allender CJ, Robinson RL (2001) How many species of cichlid fishes are there in African lakes? Molecular Ecology 10, 793–806.

Verheyen E, Salzburger W, Snoeks J, Meyer A (2003) Origin of the superflock of cichlid fishes from Lake Victoria East Africa. Science 300, 325–329.

Wainwright PC, Smith WL, Price SA, Tang KL, Ferry-Graham LA, Sparks JS, Near TJ (2012) The evolution of pharyngognathy: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. Systematic Biology. In press. doi: 10.1093/sysbio/sys060

Wickler W (1963) Zur Klassifikation der Cichlidae, am Beispiel der Gattungen *Tropheus*, *Petrochromis*, *Haplochromis* und *Hemihaplochromis* nov. gen. (Pisces, Perciformes). Senckenbergiana Biologica 44, 83–96.

Wiley EO (1978) The evolutionary species concept reconsidered. Systematic Zoology 27, 17–26.

Wiley EO, Mayden RL (2000a) The evolutionary species concept. Pp. 70–89 in Wheelerand QD, Meier R, eds., Species concepts and phylogenetic theory: a debate. Columbia University Press: New York. 230 pp.

Wiley EO, Mayden RL (2000b) A critique from the evolutionary species concept perspective. Pp. 146–158 in Wheelerand QD, Meier R, eds., Species concepts and phylogenetic theory: a debate. Columbia University Press: New York. 230 pp.

Wiley EO, Mayden RL (2000c) A defense of the evolutionary species concept. Pp. 198–208 in Wheelerand QD, Meier R, eds., Species concepts and phylogenetic theory: a debate. Columbia University Press: New York. 230 pp.

Wilson R, Barker M, Brigandt I (2009) When traditional essentialism fails: biological natural kinds. Philosophical Topics 35, 189–215.

Wilson EO (1988) Biodiversity. National Academy Press: Washington, DC. 521 pp.

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12. Curriculum vitae

Academic Education:

2002-2007:

Ludwig Maximilian University Munich, Germany: Biology (Systematic Biology, Ecology, Zoology)

2007:

~~Diploma Thesis, “Description of two new species of *Nannocharax* Günther 1867 (Teleostei:~~ Characiformes: Distichodontidae) from the Cross River Cameroon – with a note on *Nannocharax fasciatus* Günther, 1867” (Advisor: Prof. Dr. G. Haszprunar & Dr. U. Schliewen, Bavarian State Collection of Zoology, Munich (ZSM))

Diploma Biology (“Diplom Biologe Univ.”)

Since October 2007:

PhD, “Revision of the substrate brooding “*Tilapia*” (*Tilapia* Smith, 1840 and related taxa), (Teleostei: Perciformes: Cichlidae)” (Advisor: Prof. Dr. G. Haszprunar & Dr. U. Schliewen, ZSM)

Research Experience:

2006-2010:

Student Assistant at the LMU Munich. Supervision of the botany biodiversity course, tutor for plant determination exercises

2006:
Student Assistant at the LMU Munich. Project: African Plants Initiative founded by the Mellon Foundation

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Student Assistant at the ZSM. Project: Biodiversity of Bavarian freshwater fishes including field work and sample processing

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Student Assistant at the ZSM. Project: DFG funded “DNA Bank Network” at ZSM

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Staff member of the ZSM responsible for the DNA Bank and the molecular laboratory in cooperation with Dirk Neumann.

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June–July 2008:
SYNTHESYS Project (European Community Research Infrastructure Action): Research at the Natural History Museum, London, England.

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SYNTHESYS Project (European Community Research Infrastructure Action): Research at the Royal Museum for Central Africa, Tervuren, Belgium.

2008–2010:
Research Scholarship according to the BayEFG (Bavarian Elite Aid Act)

December 2008:
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2009:
SYNTHESYS Project (European Community Research Infrastructure Action): Research at the Muséum National d’Histoire Naturelle, Paris, France.

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Renewal of the research scholarship according to the BayEFG (Bavarian Elite Aid Act)

Poster:

March 2008:
Poster: Andreas R. Dunz & Ulrich K. Schliewen: Description of two new species of *Nannocharax* Günther 1867 (Teleostei: Characiformes: Distichodontidae) from the Cross River Cameroon – with a note on *Nannocharax fasciatus* Günther, 1867. 6. Tagung der Gesellschaft für Ichthyologie (GFI).

Peer-reviewed publications:

April 2008:
Andreas R. Dunz & Ulrich K. Schliewen: Description of two new species of *Nannocharax* Günther 1867 (Teleostei: Characiformes: Distichodontidae) from the Cross River Cameroon – with a note on *Nannocharax fasciatus* Günther, 1867. *Zootaxa* 2028: 1-19.

July 2010:
Andreas R. Dunz & Ulrich K. Schliewen: Description of a new species of *Tilapia* Smith, 1840 (Teleostei: Cichlidae) from Ghana, *Zootaxa* 2548: 1-21.

November 2010:
Andreas R. Dunz & Ulrich K. Schliewen: Description of a *Tilapia (Coptodon)* species flock of Lake Ejagham (Cameroon), including a redescription of *Tilapia deckerti* Thys van den Audenaerde, 1967, *Spixiana*, volume 33, issue 2, 251-280.

May 2012:
Andreas R. Dunz & Ulrich K. Schliewen: Description of a rheophilic *Tilapia* species Smith, 1840 (Teleostei: Cichlidae) from Guinea with comments on *Tilapia rheophila* Daget, 1962, *Zootaxa* 3314: 17-30.

September 2012 (accepted):
Andreas R. Dunz, Emmanuel Vreven & Ulrich K. Schliewen: *Congolapia*, a new cichlid genus from the central Congo basin (Perciformes: Cichlidae). *Ichthyological Explorations of Freshwaters*.

October 2012 (Interim Decision: acceptable for publication provided minor revisions):
Andreas R. Dunz & Ulrich K. Schliewen: Molecular phylogeny and revised classification of the haplotilapiine cichlid fishes formerly referred to as "*Tilapia*". *Molecular Phylogenetics and Evolution*.

Non peer-reviewed publications

March 2010:
Andreas R. Dunz und Erwin Schraml: Frisches Blut aus Ägypten - *Pseudocrenilabrus multicolor* nach Jahren wieder eingeführt, *Eggspots*, vol 3.

June 2010:
Andreas R. Dunz: Pflege und Nachzucht einer vergessenen Schönheit, *Die Aquarien- und Terrarienzeitschrift* (DATZ).

November 2010:
Andreas R. Dunz & M. Geiger: Wenig Aufwand für viel Farbe, *Die Aquarien- und Terrarienzeitschrift* (DATZ).

March 2011:
Andreas R. Dunz: Neuer haplochrominer Cichlide aus dem Kongo beschrieben, *Eggspots*, vol 5.

Skills & Interests:

- German, native language
- English, fluent in written and spoken
- Latin proficiency certificate
- Qualification in ancient Greek
- Molecular biology (DNA-extraction, PCR, sequencing)
- Phylogenetic and population genetic analyses
- EDP (Soft- & Hardware installation, Office, Photoshop, Illustrator etc.)
- driving licence
- Aikido
- fishkeeping

13. Appendix

CD including pdf files of Paper I-V.