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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 "*Tilapia*" represent a paraphyletic species assemblage belonging to the so called haplotilapiine 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 a second data set of 378 mitochondrial ND2 haplotypes representing almost all important "*Tilapia*" or *Tilapia*-related lineages as well as most EAR lineages. The monophyly of haplotilapiines is supported, as is the nested sister group relationship of *Etia* and mouthbrooding tilapiines with the remaining haplotilapiines. The latter are consistently placed in eight monophyletic clades over all datasets and analyses, but several dichotomous phylogenetic relationships appear compromised by cytonuclear discordant phylogenetic signal. Based on these results as well as on extensive morphological evidence we propose a novel generic and suprageneric classification including a (re-)diagnosis of 20 haplotilapiine cichlid genera and nine tribes. New tribes 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 clade of West African tilapiines.

1. Introduction

Cichlids (Teleostei: Perciformes: Cichlidae) rank among the most species rich fish families. They currently hold more than 1600 valid species taxa (Eschmeyer and 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, behavioral 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 and Iles, 1972; Kornfield and Smith, 2000). Over the last decades, cichlids have become a prime model system in evolutionary biology, especially in speciation research (Kocher, 2004; Salzburger and Meyer, 2004; Seehausen, 2006). Aquaculture research as well as evolutionary biology caught attention of "*Tilapia*", i.e. members of the so called tilapiine cichlid assemblage (sensu Trewavas, 1983 – details see below) as not only one of its members, the Nile Tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is of globally important significance for aquaculture (Ridha, 2006) but also because tilapiines gave rise to small species radiations (Schliewen and Klee, 2004). Further, molecular phylogenetics revealed that the root of the East African cichlid radiation is nested within a paraphyletic assemblage containing among other tilapiine genera members of the genus *Tilapia* Smith, 1840 (Klett and Meyer, 2002; Schwarzer et al., 2009).

Despite of its importance, the phylogeny, systematics and taxonomy of tilapias have remained insufficiently treated.

To facilitate the discussion about tilapiine phylogeny and classification, we here provide a short overview of the previous attempts to classify *Tilapia* related taxa based on morphological, ethological and molecular data. 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, 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

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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 1 (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 and De Jong (1947) taxonomically formalized Regan's informal split of African cichlids into two major groups by introducing the subfamily Tilapiinae Hoedeman and De Jong, 1947 for all African cichlids with a *Tilapia* type apophysis and the Haplochrominae[1]Hoedeman and De Jong, 1947 for the rest. Almost 50 years after Boulenger, 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 (Table 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) Sections 1 and 2 (comprising exclusively substrate brooding genera) in a newly diagnosed genus *Tilapia* without any further subgeneric division; and, mainly based on osteological characters and breeding behavior, she elevated Thys van den Audenaerde's Section 3 (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 *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 (tentatively) the two specialised rheophilic genera *Steatocranus* and *Gobiochromis* Poll, 1939 (currently a synonym of *Steatocranus*), 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 one 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 mainly on morphological 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 and Majumdar, 1984; Sodsuk and McAndrew, 1991; Pouyard and Agnèse, 1995; B-Rao and Majumdar, 1998). First DNA based studies

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

[1] Fowler (1934) introduced the taxonomically available subfamily name Pseudocrenilabrinae for all African and Middle East Cichlidae. Apparently unaware of Fowler's action, Hoedeman and De Jong (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 tribe 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 tribe name Haplochromini throughout the manuscript.