Systematic revision of the formerly monotypic genus *Tanganikallabes* (Siluriformes: Clariidae)

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The monotypic genus *Tanganikallabes*, endemic to Lake Tanganyika, is a poorly known member of the family Clariidae. Examination of 142 specimens housed in museum collections has revealed the presence of at least two additional species in this genus. ***Tanganikallabes alboperca* sp. nov.** is distinguished from all congeners by the length of its pelvic fins, the presence of a depigmented vertical bar on the opercular margin, and a combination of additional morphometric (pectoral spine length, preanal length, body depth at anus) and meristic (dorsal and anal fin ray counts) characters. ***Tanganikallabes stewarti* sp. nov.** is distinguished from other *Tanganikallabes* species by having a relatively shorter, incomplete lateral line, and shallow body depth at the anus, as well as shorter prepelvic and preanal lengths, and a longer anal fin with a higher number of fin rays. Several morphological characters, as well as genetic data from cytochrome *b* (mitochondrial DNA) and *18S–ITS1–5.8S–ITS2–28S* (ribosomal DNA), indicate that *Tanganikallabes* constitutes a monophyletic group within the Clariidae and support the recognition of additional species diversity. The monophyly of *Tanganikallabes*, coupled with the geographical isolation of this group to a single lake satisfy the requirements for its classification as a true species flock, the latest to be described from Lake Tanganyika.

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INTRODUCTION

Fishes of the East African Rift Valley lakes have long been the subject of biological studies, with most attention having focused on their cichlid species flocks, which have become model systems for the study of rapid speciation and adaptive radiations (Kornfield & Smith, 2000; Kocher, 2004; Seehausen, 2006). The catfish species of Lake Tanganyika have, in contrast to its cichlids, received less attention from biologists studying the ichthyofauna of African Rift Valley lakes, although the endemic Tanganyikan *Synodontis* species have been the focus of increasing taxonomic

(Wright & Page, 2006) and phylogenetic (Day & Wilkinson, 2006; Koblmüller *et al.*, 2006; Day, Bills & Friel, 2009) attention as a possible comparative system for the study of these evolutionary phenomena. Studies of nearly every other group of Tanganyikan catfishes, although perhaps not as numerous or recent, have also been undertaken, including revisions of *Dinotopterus* (Greenwood, 1961), *Bathybagrus* (Bailey & Stewart, 1984) (with five other Tanganyikan claroteid species being assigned to this genus; Mo 1991) and *Lophiobagrus* (Bailey & Stewart, 1984), and descriptions of new species of *Chrysichthys* (Hardman, 2008) and *Phyllonemus* (Bailey & Stewart, 1984; Risch, 1987). The exception is the genus *Tanganikallabes* (family Clariidae), a poorly known monotypic genus that has received very little consideration since its original description.

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The genus *Tanganikallabes* and its single species, *Tanganikallabes mortiauxi*, was described in 1943 from a single specimen collected in Albertville, on the western (Democratic Republic of Congo) coast of Lake Tanganyika (Poll, 1943). Poll distinguished this specimen from other clariid genera using a combination of characters, including extensive reductions in cranial osteology, its relatively non-anguilliform body (as determined by a comparison of body depth with standard length and the presence of well-developed pectoral and pelvic fins), and dorsal and anal fins that are not confluent with the caudal fin. A later study of the suprabranchial respiratory organ used for breathing air by other clariids noted that this structure, as well as the suprabranchial chamber that accommodates it, is completely absent in *Tanganikallabes* (Greenwood, 1961). The dearth of specimens available to earlier authors [the holotype and a single additional specimen collected in 1947 are the only specimens cited in the literature prior to the year 2007; Poll, 1953) led to the speculation that *T. mortiauxi* was quite rare (Poll, 1953; Coulter, 1991; Seegers, 2008). This assumption, however, requires modification, as a search of the holdings of several museums has revealed dozens of collections of *Tanganikallabes*.

The evolutionary relationships of *Tanganikallabes* to other clariid genera are poorly known. The genus has been included in two previous studies of clariid phylogenetics: one based exclusively on nuclear genetic data (Jansen *et al*., 2006) and the other combining morphological and molecular characters (Devaere *et al*., 2007). The earlier, exclusively molecular study indicated several different (depending on the optimality criteria used) positions for *Tanganikallabes* within the African representatives of the Clariidae, although the genus was usually recovered in a sister position to all other African clariids. This relationship seems somewhat dubious, because of the youth of Lake Tanganyika (9–12 Mya; Cohen, Soreghan & Scholz, 1993), relative to the estimated age of African clariids (> 56 Mya; Jansen *et al*., 2006), and the generally low support values recovered for this relationship by Jansen *et al*. However, the possibility that the *Tanganikallabes* lineage pre-dates the formation of Lake Tanganyika cannot be completely discounted because of evidence suggesting that several other ancient lineages colonized the lake while being extirpated elsewhere (Nishida, 1991; Wilson, Glaubrecht & Meyer, 2004).

The uncertainty in the phylogenetic placement of *Tanganikallabes* was not resolved by the combined morphological and molecular data set of Devaere *et al*. (2007), which included sequence information from *18S*, *5.8S*, and partial *28S* ribosomal genes, along with *ITS1* and *ITS2* [the same markers used by Jansen *et al*. (2006)]. In this case, *Tanganikallabes* was placed in a basal position within a clade also containing *Channallabes sanghaensis* and *Clarias platycephalus*, with very high Bremer and bootstrap support values. The morphological characters used in the combined analysis, when considered by themselves, placed *Tanganikallabes* in a clade composed of *Gymnallabes* and *Platyallabes*, another monotypic genus that is found in the lower Congo basin. According to the cladogram provided by Devaere *et al*. (2007), this relationship was supported by a single synapomorphy: limited contact between the endopterygoid and quadrate. However, in their character descriptions and in their figure 8, *Gymnallabes* is clearly described and depicted as lacking any contact, leaving little morphological support for this grouping. It is therefore difficult to generate a clear idea of the relationships of *Tanganikallabes* with other clariid genera from the information provided by these papers, and it is probable that future analyses will provide alternative results.

While preparing material at the University of Michigan Museum of Zoology for a separate study, the first author examined several lots of *Tanganikallabes* collected by the second author and his then graduate student Donald J. Stewart on expeditions to Lake Tanganyika in the early 1970s. These specimens were recognized as undescribed species at the time of their collection, but until now have not been formally described. Herein, we describe this species diversity using a combination of morphometric, meristic, colour, and osteological characters. This study also granted the opportunity to provide additional descriptive details for the one previously described *Tanganikallabes* species (*T. mortiauxi*). We then used molecular data to investigate the phylogenetic relationships of *Tanganikallabes* species and to provide evidence for their common ancestry. This common ancestry, coupled with the endemism of these species to the geographically circumscribed area of the Lake Tanganyika basin, satisfies the most basic criteria for their classification as a species flock (Greenwood, 1984; Ribbink, 1984).

MATERIAL AND METHODS
MORPHOLOGICAL DESCRIPTIONS

Species diagnoses and descriptions were prepared using measurements taken from the left side of specimens with digital calipers, to the nearest 0.1 mm, as depicted by Teugels (1986; Fig 1). All fin ray and vertebral counts were made from lateral and ventral radiographs. Vertebral counts include all elements except for those contained within, and fused to, the Weberian apparatus. Notations for fin ray counts are as follows: upper case Roman numeral, fin spine;
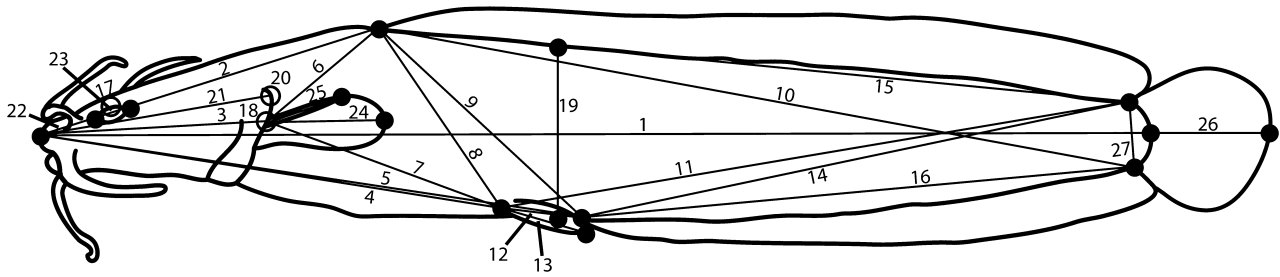
Figure 1. Morphometric measurements used in species comparisons.

Table 1. Primers used in the generation of *18S–ITS1–5.8S–ITS2–28S* sequence data. Annealing locations were determined through examination of previously published *Tanganikallabes mortiauxi* sequence data (GenBank: AJ873680)

Primer	Sequence	Annealing location
18S-F1	5′–TACCTGGTTGATCCTGCCAG–3′	Bases 1–20 of the 5′ terminus of the *18S* rDNA gene
18S-R1	5′–GCGGCGCAATACGAATGCCCCCGG–3′	Bases 931–956 of the *18S* rDNA gene
18S-F2	5′–TGAGCTAGGAATAATGGAATAGG–3′	Bases 855–877 of the *18S* rDNA gene
18S-R2	5′–ACGGGCGGTGTGTACAAAGGGCAGGG–3′	Bases 1682–1707 of the *18S* rDNA gene
18S-F3	5′–CAATTATTCCCCATGAACGAGGAATTCCCAG–3′	Bases 1618–1648 of the *18S* rDNA gene
18S-R3	5′–CACATTAGTTCTCGCAGCTGGCTGCG–3′	Bases 45–70 of the *5.8S* rDNA gene
18S-F4	5′–CAACTCTTAGCGGTGGATCACTCGG–3′	Bases 1–25 of the 5′ terminus of the *5.8S* rDNA gene
18S-R4	5′–TAAATTCAGCGGGTCGTCTC–3′	Bases 24–43 of the *28S* rDNA gene

lower case Roman numeral, unbranched rays; Arabic numeral, branched fin rays. Histological preparations of fin spines and venom glands were performed as described in Wright (2009). Institutional abbreviations follow Leviton *et al*. (1985), with the exception of the South African Institute for Aquatic Biodiversity (SAIAB). Osteological examinations were performed on specimens that had been cleared and stained following the method of Taylor (1967). Abbreviations of osteological structures used herein are as follows: ant, antorbital; apal, autopalatine; fr, frontal; hyo, hyomandibular; io-ii, -iii, -iv, infraorbitals ii, iii, iv; lac, lacrimal; leth, lateral ethmoid; meth, mesethmoid; mx = maxillary; ns, nasal; op, opercle; p-trc, transscapular process; par-soc, parieto-supraoccipital; pmx, premaxillary; pop, preopercle; pt, pterotic; pp–v$_{4,5}$, parapophyses of vertebrae 4 and 5; pt-scl, post-temporo supracleithrum; sph, sphenotic; spop, suprapreopercle.

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total genomic DNA was obtained by extraction using the Qiagen DNeasy® Blood and Tissue Kit, from approximately 25 mg of white muscle tissue, provided by SAIAB. Additional DNA extractions were performed for *Dolichallabes* and *Platyallabes* (provided by AMNH). The genes chosen to investigate the relationships of *Tanganikallabes* species and their placement within the Clariidae [cytochrome *b* (cyt *b*) mitochondrial (mt)DNA, and *18S–ITS1–5.8S–ITS2–28S* ribosomal (r)DNA] have been used in previous studies of clariid systematics (Agnese & Teugels, 2001a, 2005; Jansen *et al*., 2006; Mwita & Nkwengulila, 2008). The primers used for cyt *b* amplification were H15891 and L15267, as described by Briolay *et al*. (1998). Initial amplifications of *18S–ITS1–5.8S–ITS2–28S* rDNA were attempted using the procedures described by Jansen *et al*. (2006), but were unsuccessful. Instead, sequences from these regions were downloaded from GenBank (Table S1) and aligned using Se-Al 2.0a11 Carbon (Rambaut, 1996). Using this alignment, primers were designed to amplify four overlapping segments of the *18S–ITS1–5.8S–ITS2* sequence and a *28S* sequence fragment (Table 1). Amplifications were carried out in an MJ Research PTC 200 Thermocycler using the settings described (for cyt *b*) in Agnese & Teugels (2001a). For the overlapping segments of the *18S–ITS1–5.8S–ITS2–28S* sequence data, optimal amplification parameters were determined via gradient PCR, using annealing temperatures with a range of 45–60 °C. Segments were then amplified using the following conditions: initial denaturation at 94 °C for 3 min, followed by 30 cycles of 94 °C for 30 s, annealing at 55.5 °C (for segment 1) or 57.0 °C (for segments 2–4) for 30 s, and elongation at 72.0 °C for 1 min, with an additional 10-minute elongation at the conclusion of

the amplification procedure. PCR products were prepared for sequencing by 1 : 5 dilution with distilled water, and all sequencing was performed at the University of Michigan DNA Sequencing Core, using the cyt *b* and *18S–ITS1–5.8S–ITS2–28S* forward and reverse PCR primers.

PHYLOGENETIC ANALYSIS

Tanganikallabes sequences and chromatograms were analysed using SEQUENCHER 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). Cytochrome *b* and *18S–ITS1–5.8S–ITS2–28S* rDNA sequences for additional clariid species were downloaded from GenBank (Table S1), and were aligned with the appropriate *Tanganikallabes* sequences using Se-Al 2.0a11 Carbon (Rambaut, 1996).

As a result of differences in the taxa for which sequence data were available, the cyt *b* and *18S–ITS1–5.8S–ITS2–28S* rDNA sequences were analysed separately, rather than as a combined data set. Both data sets were analysed using maximum parsimony (MP) and Bayesian phylogenetic approaches. MP analysis was carried out using PAUP* 4.0b10 (Swofford, 2003), with full heuristic searches using TBR branch swapping with 10 000 random sequence additions. Branch support was assessed using non-parametric bootstrap analysis (Felsenstein, 1985) with 1000 replicates, and nodes with ≥ 75% bootstrap support were considered to be well supported. Bayesian analysis was conducted using MRBAYES 3.1.12 (Huelsenbeck & Ronquist, 2001), with appropriate likelihood model settings determined using MODELT-EST 3.04 (Posada & Crandall, 1998). Four independent Markov chain Monte Carlo (MCMC) analyses were run for 1×10^7 generations, with three heated (0.2 temperature) and one cold chain, and a tree sampling frequency of 1000 generations. Trees sampled before convergence (average standard deviation of split frequencies > 0.01) were discarded as burn-in. Estimates of posterior probabilities were used to measure nodal support of the Bayesian consensus tree, and nodes with ≥ 0.95 posterior probability were considered to be well supported.

RESULTS

GENUS *TANGANIKALLABES* POLL, 1943

Tanganikallabes Poll, 1943: 127. Type species: *Tanganikallabes mortiauxi* Poll, 1943. Type by monotypy. Gender: feminine.

Diagnosis: Tanganikallabes is distinguished from all African clariid genera except for *Platyallabes* Poll and possibly *Uegitglanis* Gianferrari (see additional comments below) by the complete lack of both a suprabranchial chamber and an arborescent respiratory organ. Some authors (Gianferrari, 1923; David, 1936) mentioned the presence of a vestigial suprabranchial organ in *Uegitglanis*, whereas others (Chardon, 1968; Burgess, 1989) have indicated that this genus does not possess an accessory respiratory organ. Because of the lack of well-preserved material of *Uegitglanis* available for analysis, and the low probability that new material will become available in the near future, the utility of this character in diagnosing these two genera remains questionable. Adequate material does exist, however, to indicate that these genera can easily be distinguished by the presence of well-developed swimbladder capsules in *Tanganikallabes* (versus absent in *Uegitglanis*), absence of body pigmentation in the cave-dwelling *Uegitglanis* versus extensive body pigmentation in *Tanganikallabes*, and differences in number of both dorsal fin (65–83 in *Tanganikallabes* versus 48–55 in *Uegitglanis*) and anal fin (55–69 in *Tanganikallabes* versus 36–45 in *Uegitglanis*) elements.

Tanganikallabes can additionally be distinguished from nearly all clariid genera except for *Dinotopterus* Boulenger, *Platyallabes* Poll and *Uegitglanis* Gianferrari by the absence of a well-developed, anteriorly directed process on the cleithral bone in adult specimens (Fig. 2A). This structure can sometimes (albeit rarely) be observed in juvenile *Tanganikallabes* specimens, but was never present in adults. Similarly, such a structure can be observed in juvenile *Dinotopterus* specimens only (Fig. 2C), but has never been documented in *Platyallabes* specimens of any size.

Tanganikallabes is distinguished from the anguilliform clariid genera [defined as having an abdominal body depth < 11.6% of the standard length (SL); Devaere *et al.*, 2005, 2006] *Channallabes* Günther, *Dollichallabes* Poll, *Gymnallabes* Günther, *Platyallabes* Poll, and *Platyclarias* Poll by generally having a more fusiform body shape (body depth at anus 8.7–17.2% SL), and from all but the last of these genera [as well as from *Clariallabes attemsi* (Holly, 1927), *Clariallabes brevibarbis* Pellegrin, 1913, *Clariallabes centralis* (Poll & Lambert, 1958), *Clariallabes heterocephalus* Poll, 1967, *Clariallabes melas* (Boulenger, 1887), *Clariallabes petricola* Greenwood, 1956, *Clariallabes simeonsi* Poll, 1941, *Clariallabes uelensis* (Poll, 1941), *Clariallabes variabilis* Pellegrin, 1926] in having dorsal and/or anal fins that are not fused with the caudal fin (with the exception of three abnormal specimens found in MRAC 130952-954, radiographs of which also showed numerous skeletal deformities). *Tanganikallabes* also differs from several of the aforementioned anguilliform genera in its number of dorsal fin rays (65–83 in *Tanganikallabes* versus 86–160 in *Channallabes*, 130–140 in *Platyallabes*, and 85–87 in *Platyclarias*) and anal fin rays (55–69 in
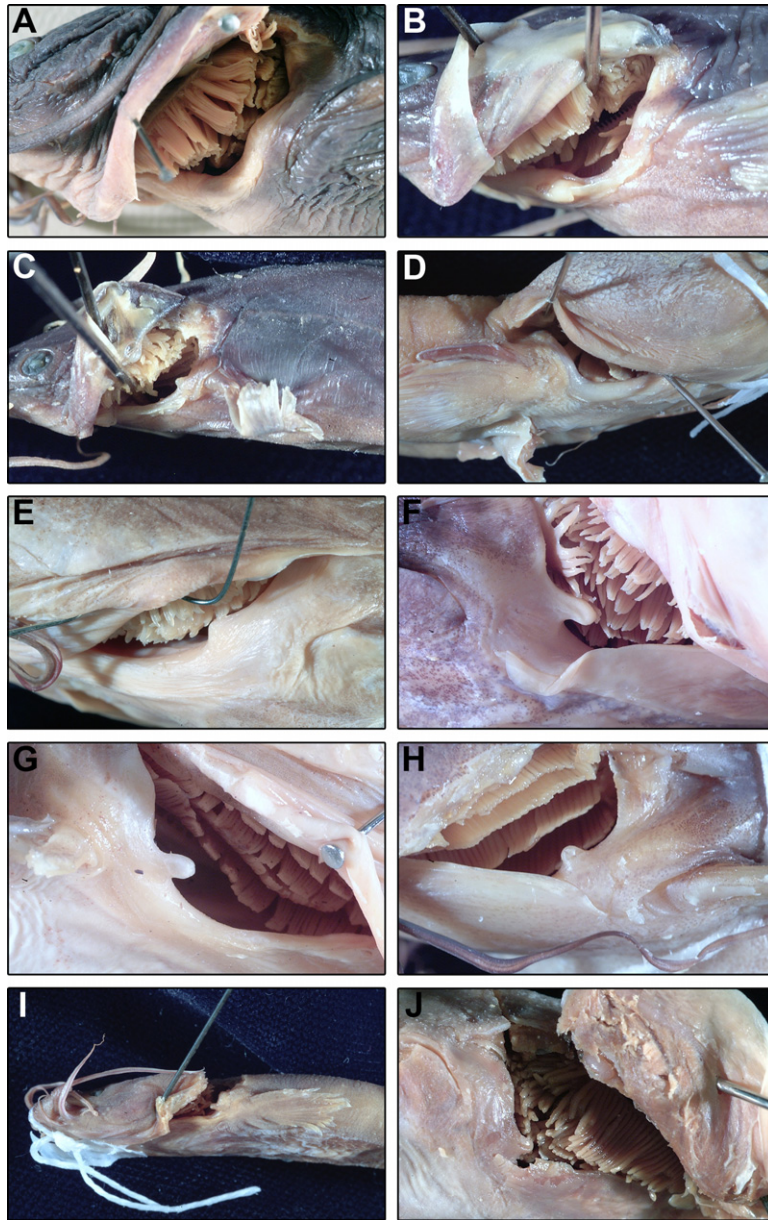
Figure 2. Condition of the anterior cleithral process in African clariid genera. A, *Tanganikallabes mortiauxi*, UMMZ 199862, in which an anterior cleithral process is absent in adult specimens. B, *Dinotopterus cunningtoni*, 78 mm standard length (SL), UMMZ 199855, showing a clear lack of anterior cleithral process. C, *Dinotopterus cunningtoni*, 51 mm SL, UMMZ 199855, showing the presence of weak anterior cleithral process in small individuals of this genus. D, *Platyallabes tihoni*, MRAC 73-22-P-3128-130, also lacks the anterior cleithral process. E, *Bathyclarias nyasensis*, AMNH 31912. F, *Clarias stappersi*, UMMZ 200355. G, *Heterobranchus longifilis*, UMMZ 189168. H, *Heteropneustes fossilis*, UMMZ 209799. I, *Platyclarias machadoi* MRAC 78-006-P-1348-1362. J, *Xenoclarias eupogon*, UMMZ 187331.

Tanganikallabes versus 75–155 in *Channallabes*, 115–125 in *Platyallabes*, and around 80 in *Platyclarias*).

Tanganikallabes is further distinguished from the fusiform genera *Dinotopterus* and *Heterobranchus* Saint-Hilaire by the absence of an adipose fin and the presence of a correspondingly longer dorsal fin, with a larger number of rays (65–83 versus 47–54 in *Dinotopterus* and 24–45 in *Heterobranchus*). *Tanganikallabes* can be further differentiated from the Lake Malawi-endemic genus *Bathyclarias* Jackson by having dorsal and anal fins that extend all the way to the origin of the caudal fin (versus fins separated by varying, but always clearly visible, distances in

Bathyclarias species), and from the Lake Victoria-endemic *Xenoclarias* Norman by having 53–61 post-Weberian vertebral elements, rather than 51 or 52.

Differences in cranial osteology further distinguish *Tanganikallabes* from *Bathyclarias*, *Heterobranchus*, and *Xenoclarias*, as well as from *Clarias* Scopoli and *Clariallabes* (for illustrations of *Bathyclarias* neurocranium, see Anseaume & Teugels, 1999; for illustrations of *Clariallabes*, see Cabuy *et al*. 1999; for *Clarias*, see Fig. 3). These differences include reductions of nearly every bone in the neurocranium, but are perhaps most evident in the infraorbital bones (particularly infraorbital iv) and the suprapreopercle, which are small and mostly tubular in *Tanganikallabes* versus large and plate-like in these other genera. Additional differences between these genera and *Tanganikallabes* can be easily observed in the size and shape of the lateral ethmoid, frontal, sphenotic, pterotic, and post-temporo supracleithrum.

Comparative material examined: Bathyclarias nyasensis, AMNH 31912; *Channallabes apus*, UMMZ 242728; *Clarias gariepinus*, UMMZ 166654; *Clarias stappersi*, UMMZ 199997; *Dinotopterus cunningtoni*, UMMZ 199855; *Dolichallabes microphthalmus*, AMNH 242552, MRAC P176123, 176124; *Gymnallabes typus*, UMMZ 243235; *Heterobranchus longifilis*, UMMZ 189155; *Heteropneustes fossilis*, UMMZ 209799; *Platyallabes tihoni*, AMNH 237540, 25022, MRAC 73-22-P-3128-130; *Platyclarias machadoi*, MRAC 78-006-P-1348-1362; *Uegitglanis zammaranoi* (radiographs and photographs only), USNM 164549, MRAC 37783, 37784; *Xenoclarias eupogon*, UMMZ 187331.

SPECIES DESCRIPTIONS

TANGANIKALLABES MORTIAUXI Poll, 1943
(FIGS 2A, 3A, 4A, 5A, 6–8; TABLES 2, 3)

Tanganikallabes mortiauxi Poll, 1943: 131, figs 1–4, diagnosis and description, Albertville, Lake Tanganyika; Poll, 1946: 234, figs 27–29, reproduction of original species description, Albertville, Lake Tanganyika; Poll, 1953: 182, description including additional collection, Albertville and M'Toto, Lake Tanganyika. Greenwood, 1961: 238, 239, comments on lack of suprabranchial chamber and organ. Coulter, 1991: 183, brief note of endemicity and low abundance, Lake Tanganyika. Devaere *et al*., 2007: 214, figs 1, 12, 14, phylogenetic position within African Clariidae. Seegers, 2008: 274, description, brief ecological notes, Lake Tanganyika.

Diagnosis: Tanganikallabes mortiauxi is distinguished from its congeners by the morphology of the vomerine toothpad, which, at its widest point anteroposteriorly, is thicker than the premaxillary toothpad (versus a

uniformly thin, broad crescent in other *Tanganikallabes* species) (Fig. 4). The presence of a complete lateral line (versus incomplete lateral line in other *Tanganikallabes* species), free lower orbital margin (versus no free margin in other *Tanganikallabes* species), well-defined, thick basal membranes on the barbels (versus thin membranes in all other *Tanganikallabes* species), and a larger eye (1.8–3.0% SL versus 0.8–1.6% SL in *Tanganikallabes alboperca* sp. nov. or 1.0–1.9% SL in *Tanganikallabes stewarti* sp. nov.) further distinguish *T. mortiauxi* from all congeners.

The cranial osteology of *T. mortiauxi* further separates this species from all congeners. In *T. mortiauxi*, io-iv consists of a single element (versus two separate elements in *T. alboperca* sp. nov. and *T. stewarti* sp. nov.) (Fig. 3). Similarly, the suprapreopercle of *T. mortiauxi* is composed of a single element, whereas that of *T. alboperca* sp. nov. and *T. stewarti* sp. nov. is composed of two, or sometimes three, elements (Fig. 5). Furthermore, the extensions of the lateral ethmoid nearly overlie io-ii when viewed from above, but are well separated in *T. alboperca* sp. nov. and *T. stewarti* sp. nov. (Fig. 3).

Tanganikallabes mortiauxi can also be distinguished from *T. alboperca* sp. nov. by having longer pelvic fins (7.4–9.3% SL versus 6.0–7.7% SL in *T. alboperca* sp. nov.) that reach beyond the origin of the anal fin when adpressed, longer pectoral fin spines (5.6–8.8% SL versus 3.6–5.3% SL in *T. alboperca* sp. nov.), a higher number of dorsal fin rays [72–81 (modally 80) versus 65–74 (modally 70) in *T. alboperca* sp. nov.], and the lack of a depigmented opercular margin. *Tanganikallabes mortiauxi* is further separated from *T. stewarti* sp. nov. by its proportionally longer prepelvic (39.7–44.4% SL versus 35.7–39.2% SL in *T. stewarti* sp. nov.) and preanal (47.1–51.7% SL versus 42.4–44.8% SL in *T. stewarti* sp. nov.) lengths, and shorter anal fin (anal fin base 47.6–54.2% SL versus 54.1–58.9% SL in *T. stewarti* sp. nov.).

Description: Morphometric data in Table 2, frequency distributions of selected meristic data in Table 3. Maximum total length (TL) 325 mm. Body elongate, moderately compressed posterior to origin of dorsal fin. Predorsal profile slightly convex, with small indentation formed by curvature and insertion of cheek muscles on skull. Prepelvic profile convex. Skin on body forming numerous vertical ridges and folds, extending onto and encasing all fins.

Head depressed and broad; skin thick; lateral cranial muscles hypertrophied, forming trough in centre of head over bones of skull. Snout short, with bluntly rounded margin when viewed dorsally; acute, narrow margin when viewed laterally. Anterior nostrils tubular; posterior nostrils poorly visible, located
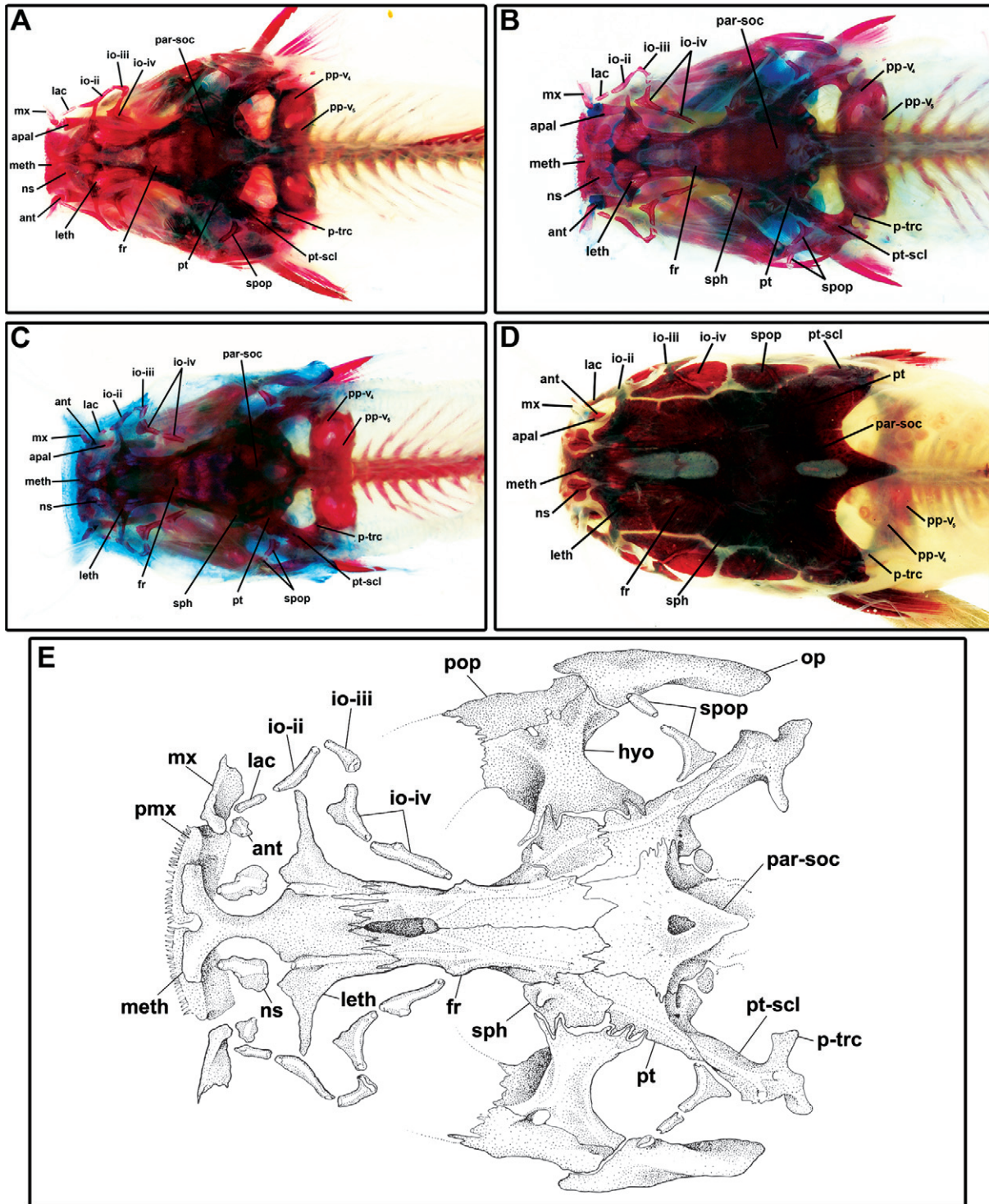
Figure 3. Cranial morphology of *Tanganikallabes* species (and *Clarias gariepinus* for comparison), showing interspecific differences in orbital and lateral ethmoid morphology, as well as overall reductions of cranial osteology. A, *Tanganikallabes mortiauxi* (UMMZ 199862), in which infraorbital iv (io-iv) is composed of a single element and the extensions of the lateral ethmoid nearly overlie io-ii. B, C, **Tanganikallabes alboperca sp. nov.** (UMMZ 199861) and **Tanganikallabes stewarti sp. nov.** (UMMZ 196154), respectively, in which io-iv consists of two elements and the extensions of the lateral ethmoid do not reach io-ii. D, *Clarias gariepinus*, UMMZ 166654. E, Drawing of **T. alboperca sp. nov.** skull (UMMZ 199861), more clearly showing delimitations of cranial elements in *Tanganikallabes*.
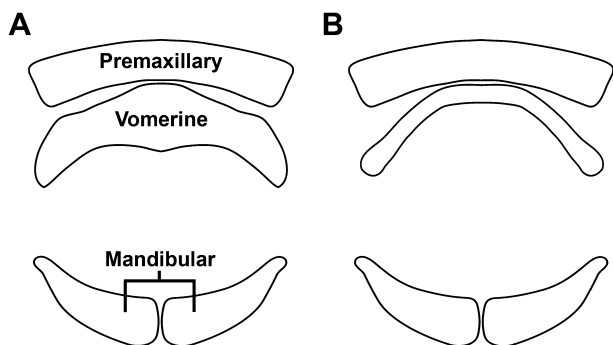
Figure 4. Toothpad morphology of *Tanganikallabes* species: A, *Tanganikallabes mortiauxi*; B, ***Tanganikallabes alboperca*** **sp. nov.** and ***Tanganikallabes stewarti*** **sp. nov.**

at posterior base of nasal barbel. Opercular flap extending over base of pectoral fin spine. Eye small, located dorsolaterally; ovoid; horizontal axis longer; lower margin free. Interorbital area broad, flat.

Mouth terminal; lips narrow and papillate; jaws equal or upper jaw slightly longer. Mandibular, premaxillary, and vomerine teeth pointed, unicuspid, arranged in multiple transverse rows. Mandibular toothpad wide, crescentic. Premaxillary toothpad broadly curved, rectangular. Vomerine toothpad located immediately posterior to premaxillary; wider than premaxillary; broadly curved; crescentic.

Nasal barbel extends approximately to upper origin of opercular flap. Maxillary barbel extends nearly to end of pectoral fin. Lateral mandibular barbel extending approximately to vertical through posterior tip of adpressed pectoral fin. Medial mandibular barbel extending slightly beyond lower opercular margin. All barbels covered with thick, tuberculate skin, with broad basal membrane; membrane becoming increasingly crenulated in larger specimens.

Dorsal fin elongate, lacking spine, with 72–83 soft rays; origin located approximately at vertical through posterior tip of adpressed pectoral fin; posterior margin not joined with caudal fin. Pectoral fin I,7–9: strong spine, well-developed venom glands present (Fig. 6); spine approximately 2/3 length of pectoral fin; posterior margin of spine with between zero and five very small, retrorse serrations. Adipose fin absent. Pelvic fin i,5: tip of adpressed fin reaches beyond origin of anal fin. Anal fin elongate, with 58–65 branched rays; posterior margin not joined with caudal fin. Caudal fin i,7,8,i: rounded.

Coloration in alcohol: Dorsum and flanks uniformly dark brown to black, with ventral surfaces slightly lighter (Fig. 7). Nasal, maxillary, and lateral mandibular barbels uniformly dark brown to black,

sometimes with slightly lighter pigmentation near tips. Medial mandibular barbels dark brown to black on proximal half, with distal half becoming noticeably lighter. All rayed fins uniformly dark brown to black.

Distribution: Lake Tanganyika, distributed lakewide (Fig. 8).

Habitat: Littoral to benthic zones over rocky bottoms. This species was originally considered to be specialized for a deep water habitat, because of the reduction of its cranial osteology (Poll, 1943; Greenwood, 1961). Subsequently, however, a specimen was collected at a depth of 2–3 m (Poll, 1953), suggesting that this species may inhabit rocky bottoms over a wide range of depths.

Diet: Tanganikallabes mortiauxi appears to be an opportunistic, generalist predator, with the stomachs of six specimens (from UMMZ 199862) containing, collectively, the eggs of indeterminate fish species, platythelphusid crabs, several species of atyid shrimps, insect larvae, and, in one specimen, a single juvenile *Synodontis* catfish.

Material examined: Holotype (photograph only): MRAC 63731, 325 mm TL, Albertville, Democratic Republic of Congo, Lake Tanganyika, 1939. Additional material: MRAC 129132 (1 alc; 127 mm SL), Uvira, Lake Tanganyika, 19.XI.1962; MRAC 84-09-P-45 (1 alc; 135 mm SL), 5th parallel, west coast of Lake Tanganyika, Democratic Republic of Congo, 14.IV.1984; MRAC 130863-872 (10 alc; 38–80 mm SL), Kigongo, Lake Tanganyika, 6.VII.1961; MRAC 131185, 131186 (2 alc; 97–132 mm SL), Uvira, Lake Tanganyika, 14.VII.1961; MRAC 130952–130958 (5 alc; 86–137 mm SL), Kalungwe, Lake Tanganyika, 11.VII.1961; MRAC 96-083-P-0781 (1 alc; 194 mm SL), Pemba, 24 km S. of Uvira, Lake Tanganyika, 18.VIII.1995; MRAC 77-11-P-235 (1 alc; 105 mm SL), Southern Lake Tanganyika, Zambia; MRAC 130826, 130827 (2 alc; 103–113 mm SL), Luhanga, Lake Tanganyika, 7.VII.1961; MRAC 187086–187088 (2 alc; 52–161 mm SL), Nkumbula Island, Lake Tanganyika, Zambia, 14.VII.1965; MRAC 129091 (1 alc; 143 mm SL), Uvira, Lake Tanganyika, 17.IX.1959; MRAC 131102–105 (4 alc; 106–214 mm SL), Kabimba, northern Lake Tanganyika, 18.VII.1961; MRAC 130971 (1 alc; 104 mm SL), Kalungwe, Lake Tanganyika, 13.VII.1961; MRAC 130768 (1 alc; 95 mm SL), Mbemba, Lake Tanganyika, 10.VII.1961; SAIAB 79967 (1 alc; 110 mm SL), Mbita Island (north bay), 08°44.82′S, 31°05.83′E, Zambia, Lake Tanganyika, 05.III.2004; SAIAB 77437 (2 alc; 97–105 mm SL), Mbita Island (south-west cliff), 08°45.59′S, 31°05.08′E, Zambia, Lake Tanganyika, 02.III.2005; SAIAB 56683
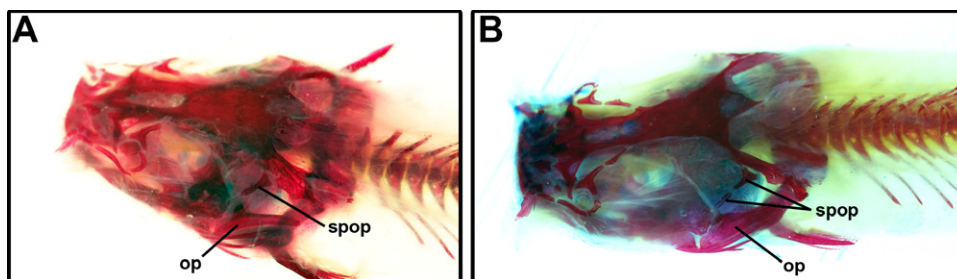
Figure 5. Condition of the suprapreopercle in *Tanganikallabes* species. A, *Tanganikallabes mortiauxi* (UMMZ 199862), in which the suprapreopercle is composed of a single element. B, ***Tanganikallabes alboperca* sp. nov.** (UMMZ 199861), in which the suprapreopercle is clearly composed of multiple elements. This condition is also found in ***Tanganikallabes stewarti* sp. nov.**
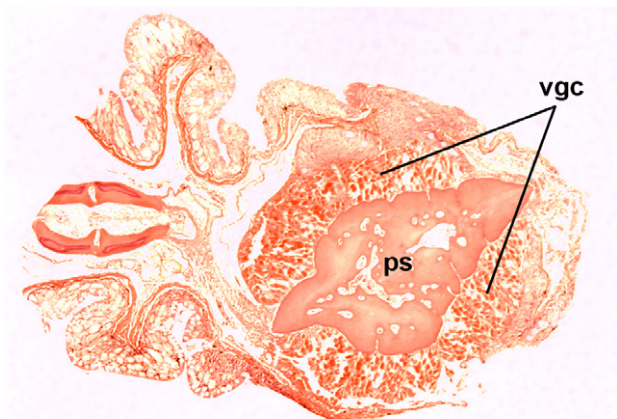

Figure 6. Cross section of the pectoral fin spine (ps) of *Tanganikallabes mortiauxi*, showing the associated venom gland (vgc). This morphology is highly similar to that seen in ***Tanganikallabes alboperca* sp. nov.** and ***Tanganikallabes stewarti* sp. nov.**

(1 alc; 115 mm SL), Muzungu beach, 04°54′53″S, 29°35′58″E, Tanzania, Lake Tanganyika, 10.X.1997; SAIAB 40178 (1 alc; 128 mm SL), Mbita Island, 8.7500°S, 31.1000°E, Zambia, Lake Tanganyika, 08.VIII.1992; SAIAB 80011 (2 alc; 160–208 mm SL), Chimba, 08°25.27′S, 30°27.44′E, Zambia, Lake Tanganyika, 07.III.2004; SAIAB 79845 (3 alc; 75–167 mm SL), Cape Kashese Harbor, 08°29.29′S, 30°28.47′E, Zambia, Lake Tanganyika, 08.III.2004; SAIAB 56074 (1 alc; 91 mm SL), Lake Tanganyika Hotel, Kigoma, 04°52′40″S, 29°37′15″E, Tanzania, Lake Tanganyika, 04.X.1997; SAIAB 39585 (1 alc; 88 mm SL), Sumbu, 8.5167°S, 30.4833°E, Zambia. Lake Tanganyika, 00.V.1983; UMMZ 199938 (2 alc; 122–126 mm SL), E. side of Nyika Bay, on N. side of Nkumbula Island, Zambia, Lake Tanganyika, 31.X.1970; UMMZ 199862 (9 alc, 1 c&s; 59–222 mm SL), N. end of Nkumbula Island, 2 km N. of Mpulungu, Zambia, Lake Tanganyika, 1.XI.1970.

TANGANIKALLABES ALBOPERCA SP. NOV.
(FIGS 3B, E, 4B, 5B, 9, 10, 11B; TABLES 3, 4)

Diagnosis: Tanganikallabes alboperca sp. nov. is distinguished from all congeners by its relatively shorter pelvic fins (6.0–7.7% SL versus 7.1–9.3% SL in other *Tanganikallabes* species), which do not reach past the origin of the anal fin when adpressed (versus reaching past the anal fin origin in all other *Tanganikallabes* species). It is also distinct from other *Tanganikallabes* species in the presence of a well-defined, depigmented border on the operculum, which extends from the upper margin of the operculum all the way to the union of the gill membranes at the isthmus (border absent in *T. mortiauxi* and *T. stewarti* sp. nov.).

Tanganikallabes alboperca sp. nov. is further distinguished from *T. mortiauxi* by its premaxillary toothpad shape (uniformly thin, broad crescent versus widest point anteroposteriorly thicker than the premaxillary toothpad in *T. mortiauxi*; Fig. 4), io-iv and the suprapreopercle consisting of multiple separate elements (versus a single element in *T. mortiauxi*; Figs 3, 5), the extensions of the lateral ethmoid not reaching io-ii when viewed from above (versus nearly or completely overlying io-ii in *T. mortiauxi*; Fig. 3), its incomplete lateral line (versus complete in *T. mortiauxi*), shorter pectoral fin spine (3.6–5.3% SL versus 5.6–8.8% SL in *T. mortiauxi*), generally lower number of dorsal fin rays [65–74 (modally 70) versus 72–81 (modally 80) in *T. mortiauxi*], smaller eye (0.8–1.6% SL versus 1.8–3.0% SL in *T. mortiauxi*), and lack of a free lower orbital margin. *Tanganikallabes alboperca* sp. nov. is further separated from *T. stewarti* sp. nov. by having a relatively deeper body (body depth at anus 11.7–14.6% SL versus 8.7–10.9% SL in *T. stewarti* sp. nov.), longer lateral line (see below description of *T. stewarti* sp. nov.), greater preanal length (45.2–49.0% SL versus 42.4–44.8% SL in *T. stewarti* sp. nov.), and by generally having a lower number of anal fin rays [55–63 (modally 59) versus 63–69 (modally 65) in *T. stewarti* sp. nov.].

Figure 7. Dorsal, lateral, and ventral views of *Tanganikallabes mortiauxi*, UMMZ 199862, 189 mm standard length. Scale bar: 1 cm.

Description: Morphometric data in Table 4, frequency distributions of selected meristic data in Table 3. Maximum TL 180 mm, SL 160 mm. Body elongate, moderately compressed posterior to origin of dorsal fin. Predorsal slightly convex, with small indentation formed by curvature and insertion of cheek muscles on skull. Prepelvic profile slightly convex. Skin on body forming numerous vertical ridges and folds; extending onto and encasing all fins.

Head depressed and broad; skin thick; lateral cranial muscles hypertrophied, forming trough in centre of head over bones of skull. Snout short, with bluntly rounded margin when viewed dorsally; acute, narrow margin when viewed laterally. Anterior nostrils tubular; posterior nostrils poorly visible, located at posterior base of nasal barbel. Opercular flap extending over base of pectoral fin spine. Eye small, located dorsolaterally; circular; lacking free margin. Interorbital area broad, flat.
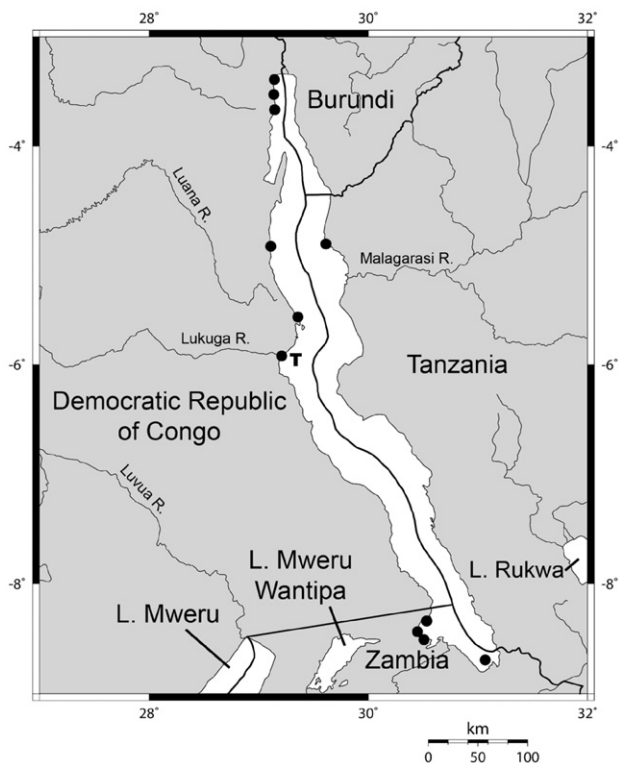
Figure 8. Known distribution of *Tanganikallabes mortiauxi*. **T** denotes the type locality.

Mouth terminal; lips narrow and papillate; jaws equal, or upper jaw slightly longer. Mandibular, premaxillary, and vomerine teeth pointed, unicuspid, arranged in multiple transverse rows. Toothpads granular in appearance because of embedding of teeth in fleshy pad for most of their length. Mandibular toothpad wide, crescentic. Premaxillary toothpad broadly curved, rectangular, noticeably wider than vomerine toothpad. Vomerine toothpad located immediately posterior to premaxillary; narrow; broadly curved; crescentic.

Nasal barbel short; not extending to any aspect of opercular flap. Maxillary barbel occasionally extends beyond margin of opercular flap, but is usually shorter. Lateral mandibular barbel extending to, or slightly beyond, lower opercular margin. Medial mandibular barbel short, slightly over half the lateral mandibular barbel length. All barbels smooth, with very narrow basal membrane.

Dorsal fin elongate, lacking spine, with 65–74 soft rays; origin located well behind vertical through posterior tip of adpressed pectoral fin; posterior margin not joined with caudal fin. Pectoral fin I,7,8; strong spine, well-developed venom glands present; spine approximately half the length of pectoral fin; posterior margin of spine with between zero and five very small, retrorse serrations. Adipose fin absent. Pelvic

fin i,5; tip of adpressed fin does not reach beyond origin of anal fin. Anal fin elongate, with 55–63 branched rays; posterior margin not joined with caudal fin. Caudal fin i,7,8,i; rounded.

Coloration in alcohol: Dorsum and flanks uniformly light to dark brown, ventral surfaces noticeably lighter (Fig. 9). All barbels pigmented as body on their proximal half, distal half lacking pigmentation. All fins with brownish bases and narrow, depigmented border; border wider in younger specimens. Operculum with wide, depigmented margin, extending onto underside of head.

Distribution: Lake Tanganyika. *Tanganikallabes alboperca* sp. nov. is apparently distributed lakewide, although existing collections come only from the extreme southern and northern areas of the lake (Fig. 10).

Habitat: Habitat details for this species are absent for the collections examined. It is likely to inhabit rocky bottoms, over a range of depths, as is the case for *T. mortiauxi*.

Diet: The stomachs of three specimens (from UMMZ 199937 and UMMZ 199861) contained, collectively, fish eggs (species indeterminate), the remains of a single platythelphusid crab, and insect larvae.

Etymology: The specific epithet, *alboperca*, is a combination of the latin adjective *alba*, meaning white, and the noun *operculum*, meaning lid or cover, a reference to the distinctive depigmented posterior margin seen in the operculum of this species. Gender: feminine.

Material examined: Holotype: UMMZ 199936 (153 mm SL), E. side of Nyika Bay, N. side of Nkumbula Island, Zambia Lake Tanganyika, 31.X.1970. Paratypes: UMMZ 199937 (7 alc, 1 c&s; 102–155 mm SL), collection data as for holotype; UMMZ 199861 (27 alc, 2 c&s; 47–152 mm SL), N. end of Nkumbula Island, 2 km N. of Mpulungu, Zambia, Lake Tanganyika, 1.XI.1970; UMMZ 196021 (2 alc; 122–146 mm SL), Zambia, Lake Tanganyika (no additional data); SAIAB 76160 (3 alc; 66–145 mm SL), Mbita Island (north-west end), 8°45.18′S, 31°05.07′E, Zambia, Lake Tanganyika, 29.II.2004; SAIAB 86974 (1 alc; 115 mm SL), Sumbu, 8.5167°S, 30.4833°E, Zambia. Lake Tanganyika, 00.V.1983; SAIAB 86968 (1 alc; 105 mm SL), Chimba, 08°25.27′S, 30°27.44′E, Zambia, Lake Tanganyika, 07.III.2004; SAIAB 80225 (1 alc; 99 mm SL), Chituta Bay, cliffs, bottom of bay on west side, 8°43.82′S, 31°9.41′E, Zambia, Lake Tanganyika, 09.III.2004; MRAC 125751 (1 alc; 104 mm SL), Luhanga,

Table 2. Morphometric data for *Tanganikallabes mortiauxi*

Measurement	Range (N = 56)	Mean ± SD
1. Standard length	37.8–221.9 mm	
% Standard length		
2. Snout to dorsal fin origin	29.1–34.8	32.6 ± 1.1
3. Snout to pectoral fin origin	19.0–22.8	21.1 ± 0.9
4. Snout to pelvic fin origin	39.7–44.4	41.6 ± 0.9
5. Snout to anal fin origin	47.1–51.7	48.8 ± 1.0
6. Pectoral fin origin to dorsal fin origin	12.8–19.4	17.1 ± 1.3
7. Pectoral fin origin to pelvic fin origin	20.0–26.4	23.4 ± 1.1
8. Dorsal fin origin to pelvic fin origin	14.5–20.2	16.9 ± 1.4
9. Dorsal fin origin to anal fin origin	18.6–24.7	22.9 ± 1.7
10. Dorsal fin origin to anal fin insertion	69.2–74.7	71.4 ± 2.0
11. Pelvic fin origin to dorsal fin insertion	58.4–64.9	61.0 ± 1.4
12. Pelvic fin origin to anal fin origin	6.5–9.0	7.9 ± 0.5
13. Pelvic fin length	7.4–9.3	8.6 ± 0.4
14. Anal fin origin to dorsal fin insertion	51.0–57.4	53.6 ± 1.3
15. Dorsal fin base length	66.6–73.4	69.9 ± 1.5
16. Anal fin base length	47.6–54.2	51.9 ± 1.3
17. Interorbital width	7.6–11.4	9.0 ± 0.6
18. Body width at pectoral fin origin	14.1–18.6	16.6 ± 0.9
19. Body depth at anus	12.3–17.2	13.9 ± 1.0
20. Head width	15.4–19.5	17.1 ± 0.9
21. Head length	21.2–24.1	22.7 ± 0.6
22. Snout length	5.7–8.2	6.6 ± 0.5
23. Eye diameter	1.8–3.0	2.2 ± 0.3
24. Pectoral fin length	8.0–14.0	12.0 ± 0.9
25. Pectoral spine length	5.6–8.8	7.3 ± 0.7
26. Caudal fin length	10.0–14.8	12.0 ± 1.2
27. Caudal peduncle depth	5.4–7.1	6.3 ± 0.4
28. Maxillary barbel length	18.7–39.9	26.9 ± 3.7
29. Nasal barbel length	11.5–27.3	18.2 ± 3.0
30. Lateral mandibular barbel length	18.0–29.3	23.7 ± 2.6
31. Medial mandibular barbel length	10.5–19.1	15.2 ± 2.1

Lake Tanganyika, 13.II.1959; MRAC 78025.0013, 78025.0014 (2 alc; 83–104 mm SL), Cape Kabeyeye, Zambia, Lake Tanganyika, I.1978; MRAC 78025. 0013, 78025.0014 (1 alc; 93 mm SL), Cape Kabeyeye, Zambia, Lake Tanganyika, I.1978; MRAC 76004.0566 (1 alc; 126 mm SL), Cape Nunda, southern Lake Tanganyika, Zambia, 6.I.1976; MRAC 130952–130970 (4 alc; 141–161 mm SL), Kalungwe, Lake Tanganyika, 11.VII.1961; MRAC 187088 (1 alc; 104 mm SL), Nkumbula Island, Lake Tanganyika, Zambia, 14.VII.1965; MRAC 81062.0001 (1 alc; 146 mm SL), Kabimba, 50 km N. Albertville, Lake Tanganyika, Democratic Republic of Congo, 7.IV.1981.

TANGANIKALLABES STEWARTI SP. NOV.
(FIGS 3C, 4B, 11–13; TABLES 3, 5)

Diagnosis: Tanganikallabes stewarti sp. nov. is distinguished from all congeners by having an incomplete lateral line, which terminates at a vertical through a point approximately two-thirds of the distance along the anal fin base (versus lateral line reaching the caudal peduncle in *T. mortiauxi* and extending much closer to the caudal peduncle in *T. alboperca* sp. nov.; Fig. 11), and by its relatively shallower body (body depth at anus 8.7–10.9% SL versus 12.3–17.2% SL in *T. mortiauxi* and 11.7–14.6% SL in *T. alboperca* sp. nov.).

Tanganikallabes stewarti sp. nov. is further separated from *T. mortiauxi* by its premaxillary toothpad shape (uniformly thin, broad crescent versus widest point anteroposteriorly thicker than the premaxillary toothpad in *T. mortiauxi*; Fig. 4), lack of a free lower orbital margin, io-iv and the suprapreopercle consisting of multiple separate elements (versus a single element in *T. mortiauxi*; Figs 3, 5), the extensions of the lateral ethmoid not reaching io-ii when viewed from above (versus nearly or completely overlaying io-ii in *T. mortiauxi*; Fig. 3), its proportionally shorter prepelvic (35.7–39.2% SL versus 39.7–44.4% SL in

Table 3. Frequency distributions of select meristic data in *Tanganikallabes* species

Post-Weberian vertebral elements

Species	53	54	55	56	57	58	59	60	61	N	$\bar{x}$
T. mortiauxi	1	2	8	12	10	12	2	1		48	56.6
T. alboperca **sp. nov.**			1	1	11	23*	11	1		48	57.9
T. stewarti **sp. nov.**						13	11*	2	1	27	58.7

Dorsal fin rays

Species	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	N	$\bar{x}$
T. mortiauxi								1	1	1	3	3	5	5	7	9	6	4	2	47	78.7
T. alboperca **sp. nov.**		1	1	13*	6	8	5	6	5	4										49	70.2
T. stewarti **sp. nov.**								1	2	3	4	7	1*	2	4					24	75.9

Anal fin rays

Species	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	N	$\bar{x}$
T. mortiauxi				4	7	12	2	7	6	4	4					46	61.2
T. alboperca **sp. nov.**	3	7	7	5	13*	5	7	1	1							49	58.5
T. stewarti **sp. nov.**									3	4	7	5*	4	1	1	25	65.4

Pectoral fin rays

Species	I,7	I,8	I,9	N
T. mortiauxi	1	13	12	26
T. alboperca **sp. nov.**		4	9	13
T. stewarti **sp. nov.**	6	7	1	14

Caudal fin rays

Species	22	23	24	25	26	N	$\bar{x}$
T. mortiauxi	4	17	16	5		42	23.5
T. alboperca **sp. nov.**	1	14*	12	2	8	37	24.0
T. stewarti **sp. nov.**	6	16*	6			28	23.0

*Value for holotype.

Figure 9. Dorsal, lateral, and ventral views of *Tanganikallabes alboperca* **sp. nov.**, Holotype, UMMZ 199862, 153 mm standard length. Scale bar: 1 cm.

T. mortiauxi) and preanal (42.4–44.8% SL versus 47.1–51.7% SL) lengths, longer anal fin (anal fin base 54.1–58.9% SL versus 47.6–54.2% SL in *T. mortiauxi*). It can additionally be distinguished from *T. alboperca* sp. nov. by its lack of a depigmented opercular margin, having longer pelvic fins (7.1–9.3% SL versus 6.0–7.7% in *T. alboperca* sp. nov.), which reach beyond the origin of the anal fin when adpressed, proportionately longer pectoral fin spines (5.0–6.8% SL versus 3.6–5.3% SL in *T. alboperca* sp. nov.), a shorter preanal length (42.4–44.8% SL versus 45.2–49.0% SL in *T. alboperca* sp.

nov.), and a (generally) higher number of dorsal fin rays [72–79 (modally 76) versus 65–74 (modally 70) in *T. alboperca* sp. nov.] and anal fin rays [63–69 (modally 65) versus 55–63 (modally 59) in *T. alboperca* sp. nov.].

Description: Morphometric data are presented in Table 5, with the frequency distributions of selected meristic data presented in Table 3. Maximum TL 170 mm, SL 155 mm. Body elongate, moderately compressed posterior to origin of dorsal fin. Predorsal
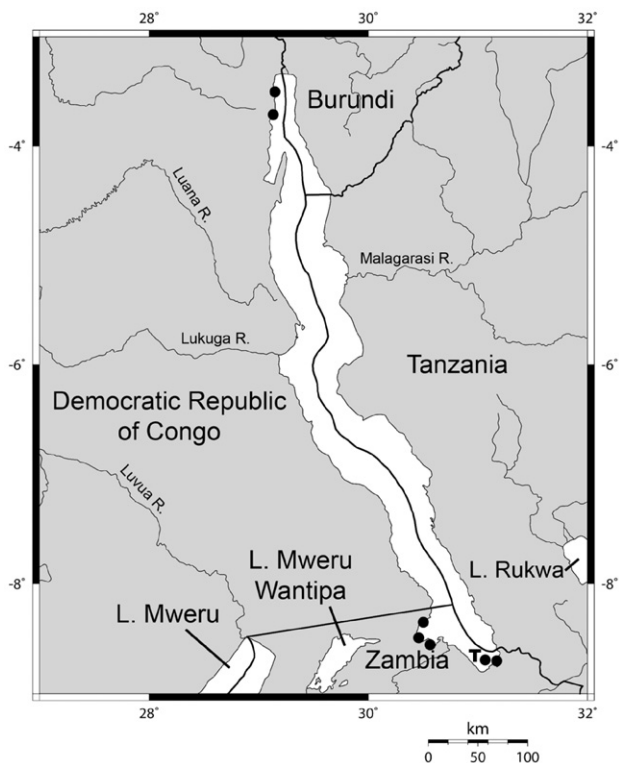
Figure 10. Known distribution of ***Tanganikallabes alboperca*** **sp. nov. T** denotes the type locality.

profile convex, with distinct hump formed between origin of dorsal fin and basioccipital; only slightly convex from basioccipital to snout. Prepelvic profile slightly convex. Skin on body forming numerous vertical ridges and folds; extending onto and encasing all fins.

Head depressed and broad; skin thick; lateral cranial muscles hypertrophied, forming trough in centre of head over bones of skull. Snout short, with bluntly rounded margin when viewed dorsally; acute, narrow margin when viewed laterally. Anterior nostrils tubular; posterior nostrils poorly visible, located at posterior base of nasal barbel. Opercular flap extending over base of pectoral fin spine. Eye small, located dorsolaterally; circular; lacking free margin. Interorbital area broad, flat.

Mouth terminal; lips narrow and papillate; jaws equal, or upper jaw slightly longer. Mandibular, premaxillary, and vomerine teeth pointed, unicuspid, arranged in multiple transverse rows. Toothpads granular in appearance because of embedding of teeth in fleshy pad for most of their length. Mandibular toothpad wide, crescentic. Premaxillary toothpad broadly curved, rectangular, noticeably wider than vomerine toothpad. Vomerine toothpad located immediately posterior to premaxillary; narrow; broadly curved; crescentic.

Nasal barbel short; not extending to any aspect of opercular flap. Maxillary and lateral mandibular barbels extending to, or slightly beyond, tip of adpressed pectoral fin spine. Medial mandibular barbel extending slightly beyond lower opercular margin. All barbels smooth, with very narrow basal membrane.

Dorsal fin elongate, lacking spine, with 72–79 soft rays; origin located well behind vertical through posterior tip of adpressed pectoral fin; posterior margin not joined with caudal fin. Pectoral fin I,7–9: strong spine, well-developed venom glands present; spine approximately two-thirds the length of pectoral fin; posterior margin of spine with between zero and five very small, retrorse serrations. Adipose fin absent. Pelvic fin i,5: tip of adpressed fin reaches beyond origin of anal fin. Anal fin elongate, with 63–69 branched rays; posterior margin not joined with caudal fin. Caudal fin i,7,8,i: rounded.

Coloration in alcohol: Dorsum and flanks brown to dark brown, with ventral surfaces slightly lighter, although less so than in other *Tanganikallabes* species. Some specimens (including holotype) show marbled appearance, with randomly arranged regions of lighter and darker coloration; other specimens uniform in dorsum and flank coloration (Fig. 12). Maxillary barbels uniformly brown, sometimes with slightly lighter pigmentation near tips. Nasal and mandibular barbels brown on proximal half, with distal portions becoming noticeably lighter. All rayed fins uniformly brown, with distinct, thin, white margin in smaller individuals.

Distribution: Most collections come from the northern part of Lake Tanganyika (Fig. 13), although a single collection from the southern Zambian coastline indicates that *T. stewarti* sp. nov., like the other two known *Tanganikallabes* species, has a lakewide distribution.

Habitat: Habitat details for this species are absent for the collections examined. It likely to inhabit rocky bottoms, over a range of depths, as is the case for *T. mortiauxi*.

Diet: The stomach of the single specimen examined (UMMZ 196154) contained only the eggs of unidentified fish species.

Etymology: The specific epithet of this species is a patronym in honour of American ichthyologist Donald J. Stewart, who collected the holotype and other material used in the description of this species, as well as assisting in the collection of much of the type series of *T. alboperca* sp. nov.
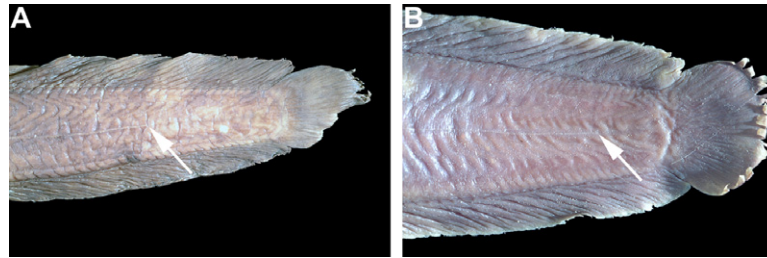
Figure 11. Differences in the extent of lateral line between (A) *Tanganikallabes stewarti* **sp. nov.** and (B) *Tanganikallabes alboperca* **sp. nov.** White arrows indicate the posterior terminus of the lateral line.

Table 4. Morphometric data for *Tanganikallabes alboperca* sp. nov.

Measurement	Holotype	Range (*N* = 52)	Mean ± SD
1. Standard length	152.9 mm	47.3–161.0 mm	
% Standard length			
2. Snout to dorsal fin origin	32.8	29.3–34.9	32.9 ± 1.1
3. Snout to pectoral fin origin	19.9	18.4–21.2	19.7 ± 0.7
4. Snout to pelvic fin origin	41.2	37.3–42.0	39.7 ± 1.1
5. Snout to anal fin origin	48.3	45.2–49.0	47.0 ± 1.0
6. Pectoral fin origin to dorsal fin origin	16.0	15.5–19.4	17.3 ± 0.9
7. Pectoral fin origin to pelvic fin origin	22.6	19.8–24.7	22.2 ± 1.1
8. Dorsal fin origin to pelvic fin origin	14.3	12.8–17.7	15.4 ± 1.2
9. Dorsal fin origin to anal fin origin	19.9	18.4–22.8	20.3 ± 1.1
10. Dorsal fin origin to anal fin insertion	70.5	66.4–72.2	69.7 ± 1.5
11. Pelvic fin origin to dorsal fin insertion	64.7	54.1–64.8	62.3 ± 1.7
12. Pelvic fin origin to anal fin origin	8.3	6.9–9.0	7.8 ± 0.4
13. Pelvic fin length	7.3	6.0–7.7	6.9 ± 0.4
14. Anal fin origin to dorsal fin insertion	57.8	52.6–62.7	55.8 ± 1.5
15. Dorsal fin base length	69.9	66.1–73.1	69.7 ± 1.5
16. Anal fin base length	55.6	51.9–56.5	54.5 ± 1.2
17. Interorbital width	8.9	8.0–9.7	8.7 ± 0.4
18. Body width at pectoral fin origin	15.6	13.2–17.3	14.8 ± 0.7
19. Body depth at anus	12.4	11.7–14.6	13.3 ± 0.8
20. Head width	17.3	14.4–17.7	16.0 ± 0.7
21. Head length	21.8	20.0–23.7	21.4 ± 0.7
22. Snout length	4.8	4.4–6.0	5.1 ± 0.4
23. Eye diameter	1.4	0.8–1.6	1.3 ± 0.1
24. Pectoral fin length	9.6	8.9–11.0	9.5 ± 0.5
25. Pectoral spine length	4.3	3.6–5.3	4.3 ± 0.4
26. Caudal fin length	11.0	9.1–13.1	10.3 ± 1.0
27. Caudal peduncle depth	6.7	5.9–7.1	6.6 ± 0.3
28. Maxillary barbel length	14.1	13.1–30.1	19.6 ± 3.9
29. Nasal barbel length	12.0	10.6–19.5	13.8 ± 1.8
30. Lateral mandibular barbel length	13.7	13.1–28.8	18.3 ± 3.3
31. Medial mandibular barbel length	10.5	8.1–16.9	12.5 ± 1.8

Material examined: Holotype: UMMZ 249379 (155 mm SL), between Mutumba and Magara among rocks, 3°40′S, 29°20′E, Burundi, Lake Tanganyika, X.1973. Paratypes: UMMZ 196154 (3 alc, 1 c&s; 48–87 mm SL), collection data as for holotype; SAIAB 86970 (1 alc; 131 mm SL), Chimba, 08°25.27′S, 30°27.44′E, Zambia, Lake Tanganyika, 07.III.2004; MRAC 130959–130970 (8 alc; 83–147 mm SL), Kalungwe, Lake Tanganyika, 11.VII.1961; MRAC 130828–130832 (5 alc; 68–113 mm SL), Luhanga, Lake Tanganyika, 7.VII.1961; MRAC 94662 (1 alc; 112 mm SL), northern Lake Tanganyika (no additional collection data); MRAC 125723–125725 (3 alc; 81–109 mm SL), Kalungwe, Lake Tanganyika, 11.II.

Figure 12. Dorsal, lateral, and ventral views of ***Tanganikallabes stewarti* sp. nov.** Holotype, UMMZ 196154, 155 mm standard length. Scale bar: 1 cm.

1959; MRAC 130972–130974 (3 alc; 103–146 mm SL), Kalungwe, Lake Tanganyika, 13.VII.1961; MRAC 130769–130771 (3 alc; 77–100 mm SL), Mbemba, Lake Tanganyika, 10.VII.1961; MRAC 94670, 94671 (2 alc; 78–131 mm SL), Luhanga, Lake Tanganyika, 29.VII.1954.

MOLECULAR PHYLOGENETIC RESULTS

New sequences obtained for inclusion in cyt *b* and *18S–ITS1–5.8S–ITS2–28S* data sets were easily alignable with sequences obtained from GenBank (Table S1), and did not differ appreciably from these sequences in terms of base composition or substitution rates, details of which can be found in the studies for which these sequences were originally generated (Agnese & Teugels, 2001a, b, 2005; Sudarto, Teugels & Pouyaud, 2003; Jansen *et al.*, 2006). The cyt *b* data set (34 taxa) consisted of 601 base positions, 160 of which were parsimony informative. The *18S–ITS1–5.8S–ITS2–28S* data set (25 taxa) consisted of 3622 characters, 503 of which were parsimony informative. Maximum parsiomony analysis of the cyt *b* data set resulted in 13 most parsimonious trees (tree
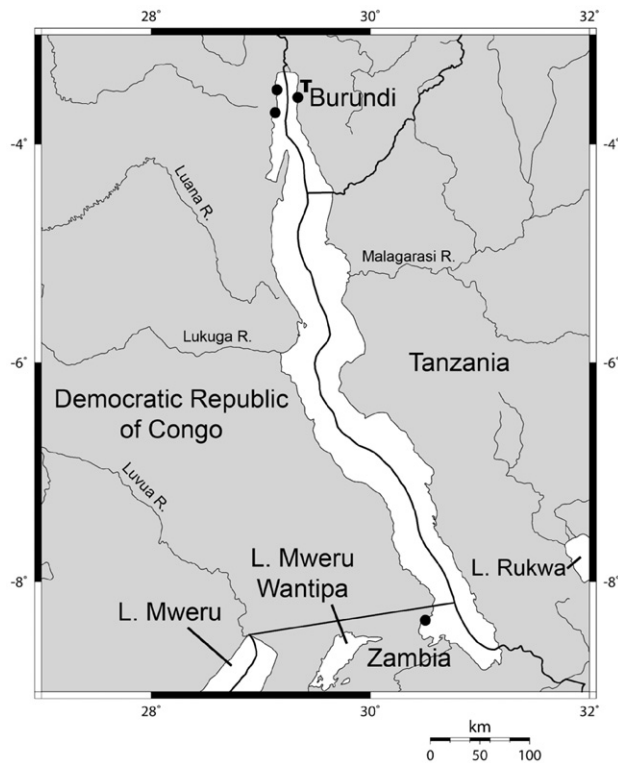
Figure 13. Known distribution of *Tanganikallabes stewarti* **sp. nov. T** denotes type locality.

length = 685 steps; consistency index, CI = 0.458; retention index, RI = 0.654), whereas MP analysis of the *18S–ITS1–5.8S–ITS2–28S* data set yielded a single optimal tree (tree length = 1888 steps; CI = 0.766; RI = 0.677). Bayesian consensus trees for both data sets were largely congruent with those obtained from MP analyses, and the results from both sets of analyses are summarized in Figure 14.

The consensus topologies obtained from cyt *b* and *18S–ITS1–5.8S–ITS2–28S* analyses are largely congruent with those of previous studies (Agnese & Teugels, 2001a, b, 2005; Jansen *et al.*, 2006; Mwita & Nkwengulila, 2008) using these genes. Several well-supported clades were evident within the Clariidae (Fig. 14), but as was the case in the aforementioned previous studies, basal relationships between these groups were very poorly supported. Among the well-supported groups is a clade consisting of all included *Tanganikallabes* samples. A sister relationship between *T. alboperca* sp. nov. and *T. stewarti* sp. nov. was recovered regardless of the genetic data set used, with *T. mortiauxi* showing a sister-group relationship to these two species. This relationship was strongly supported by both molecular data sets, using both MP and Bayesian approaches. Cyt *b* analysis suggested a possible sister relationship between *Tanganikallabes* and *Channallabes apus*, which has not

been indicated by previous analyses. However, *18S–ITS1–5.8S–ITS2–28S* indicated a strongly supported sister relationship between *Channallabes apus* and *Clarias buthupogon*, a species that was not suggested to be closely related to either *Channallabes apus* or *Tanganikallabes* by the mitochondrial genetic data. In both cases, the molecular data unambiguously supports the monophyly of *Tanganikallabes* species with respect to other members of the Clariidae, and their recognition as a new species flock within Lake Tanganyika.

DISCUSSION

The morphological and molecular analyses presented here demonstrate the presence of previously unrecognized species diversity in a formerly monotypic Tanganyikan clariid genus. Numerous characters were found to be useful to readily distinguish *Tanganikallabes* from all other clariid genera. Although no unique, unreversed morphological synampomorphies were found to support the monophyly of this genus (which can be said of several currently recognized clariid genera), both molecular data sets strongly support this hypothesis. Molecular analyses also provided insight into the relationships between *Tanganikallabes* species, indicating a sister relationship between *T. alboperca* sp. nov. and *T. stewarti* sp. nov. The fact that several morphological characters (vomerine toothpad shape, incomplete lateral line, lack of fusion of io-iv and suprapreopercular elements, and extent of lateral ethmoid projections) are found in *T. alboperca* sp. nov. and *T. stewarti* sp. nov., but not in *T. mortiauxi*, provides an even greater level of confidence in the relationships of these species.

The discovery of additional species diversity within *Tanganikallabes* is not surprising, given the frequency with which previously montypic Tanganyikan genera have been found to contain additional taxa (Bailey & Stewart, 1984; Takahashi & Nakaya, 1999, 2003), or have been placed in synonymy with previously described genera (Takahashi, 2002). The results of these studies, in conjunction with the results presented here for *Tanganikallabes*, suggest that a review of *Dinotopterus*, another monotypic clariid genus found in Lake Tanganyika, might also be fruitful in yielding additional undescribed species, as previous studies by Greenwood (1961) and Anseaume & Teugels (1999) did not address possible diagnosable variation in specimens assigned to this genus. Although the results of the present study have increased our knowledge of the species diversity of *Tanganikallabes*, much of its biology, including aspects of diet, predators, reproduction, and evolutionary history, remains unknown.

Table 5. Morphometric data for ***Tanganikallabes stewarti* sp. nov.**

Measurement	Holotype	Range ($N = 28$)	Mean ± SD
1. Standard length	155.1 mm	48.0–155.1 mm	
% Standard length			
2. Snout to dorsal fin origin	28.9	28.0–31.2	29.7 ± 0.8
3. Snout to pectoral fin origin	17.6	17.6–20.6	19.2 ± 0.7
4. Snout to pelvic fin origin	35.9	35.7–39.2	37.5 ± 0.9
5. Snout to anal fin origin	42.4	42.4–44.8	43.8 ± 0.7
6. Pectoral fin origin to dorsal fin origin	14.2	13.9–16.4	14.6 ± 0.5
7. Pectoral fin origin to pelvic fin origin	21.1	18.8–22.5	20.2 ± 0.9
8. Dorsal fin origin to pelvic fin origin	12.8	11.5–14.4	13.2 ± 0.6
9. Dorsal fin origin to anal fin origin	17.7	17.4–20.6	18.4 ± 1.5
10. Dorsal fin origin to anal fin insertion	73.0	70.9–73.8	72.4 ± 1.3
11. Pelvic fin origin to dorsal fin insertion	65.2	62.2–67.5	65.0 ± 1.3
12. Pelvic fin origin to anal fin origin	7.5	4.8–8.5	7.1 ± 0.9
13. Pelvic fin length	8.0	7.1–9.3	8.1 ± 0.5
14. Anal fin origin to dorsal fin insertion	60.5	55.7–60.5	58.2 ± 1.1
15. Dorsal fin base length	71.3	70.3–75.4	72.6 ± 1.2
16. Anal fin base length	58.9	54.1–58.9	56.7 ± 1.2
17. Interorbital width	7.2	7.2–8.9	8.0 ± 0.4
18. Body width at pectoral fin origin	13.5	12.5–15.1	13.7 ± 0.6
19. Body depth at anus	9.5	8.7–10.9	10.1 ± 0.6
20. Head width	14.1	13.5–15.9	15.0 ± 0.6
21. Head length	18.2	18.2–22.3	20.8 ± 0.7
22. Snout length	3.9	3.5–6.2	4.6 ± 0.6
23. Eye diameter	1.3	1.0–1.9	1.3 ± 0.2
24. Pectoral fin length	9.0	9.0–11.7	10.6 ± 0.6
25. Pectoral spine length	5.1	5.0–6.8	5.6 ± 0.5
26. Caudal fin length	9.5	9.4–13.1	11.7 ± 1.1
27. Caudal peduncle depth	5.5	5.3–6.6	5.8 ± 0.3
28. Maxillary barbel length	21.3	18.5–33.3	25.3 ± 3.8
29. Nasal barbel length	11.9	11.9–20.8	16.7 ± 2.0
30. Lateral mandibular barbel length	15.5	15.5–26.1	22.2 ± 2.6
31. Medial mandibular barbel length	13.8	10.6–18.6	15.7 ± 1.6

The monophyly of *Tanganikallabes* species, along with their endemism to the Lake Tanganyika basin, satisfies one set of criteria for the recognition of this genus as a species flock (Greenwood, 1984). A potential barrier to this classification arises, however, when one considers an additional requirement advocated by Ribbink (1984): that of disproportionate speciosity. To satisfy this condition, a group must contain more species than would be expected based on the levels of related species diversity in the surrounding regions. Furthermore, rates of speciation and adaptive radiation within the putative species flock must be greater than in groups arising from the same, or closely related, lineages remaining in the areas from which colonization by the group in question occurred. Without a well-resolved phylogeny of the Clariidae as a whole (also see below), it is impossible to determine precisely which clariid genera would provide the most appropriate comparisons for the evaluation of this measure. This limitation notwithstanding, the family Clariidae contains 13 currently recognized genera (and at least one undescribed genus; J.J. Wright, unpubl. data), half of which are monotypic. Four of these genera are found either within Lake Tanganyika (*Dinotopterus*) or the Congo River Basin (*Dolichallabes*, *Platyallabes*, and *Platyclarias*), with an additional genus having only a single representative in the Congo River Basin (*Gymnallabes*). It therefore appears likely that the 200% greater level of species diversity in *Tanganikallabes* relative to these other genera (especially those of the adjacent Congo River Basin, which covers a massive geographical area), further justifies its classification as a true species flock.

The inability of current molecular data to resolve the postion of *Tanganikallabes* within the Clariidae is a relatively minor issue when considered in the context of the relatively poor state of clariid systematics. Our lack of a well-resolved phylogenetic frame-
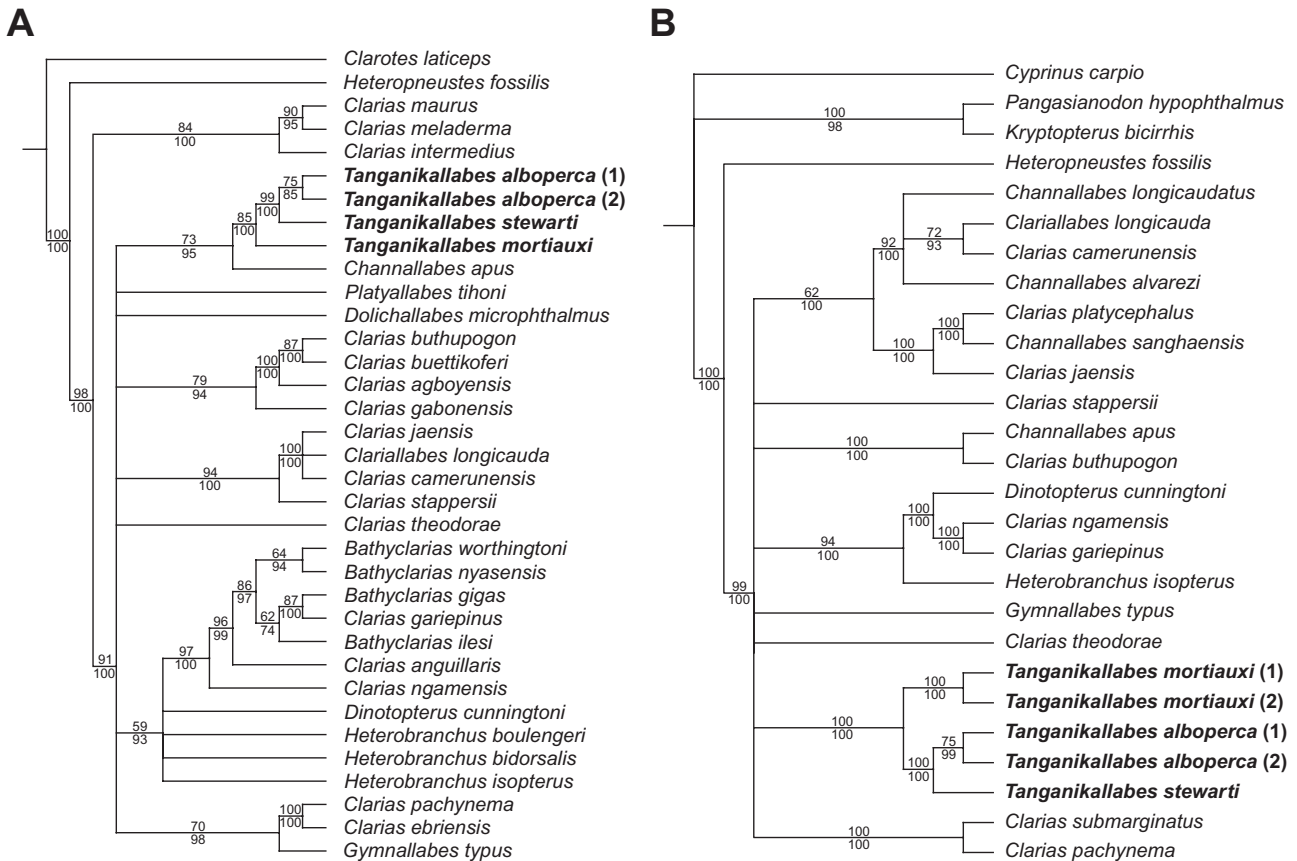
Figure 14. Consensus trees resulting from maximum parsimony and Bayesian analyses of (A) cytochrome *b* and (B) *18S–ITS1–5.8S–ITS2–28S* genetic data. Numbers above branches represent maximum parsimony bootstrap support values, numbers below are Bayesian posterior probabilities.

work and proper taxonomic revision for multiple clariid genera represents a major stumbling block for studies of the evolution of many of the interesting adaptive traits and morphological modifications that members of this family possess. The paraphyly of *Clarias*, by far the largest genus in the family, has been well established in the past (Agnese & Teugels, 2001a, 2005; Jansen *et al*., 2006; Sullivan, Lundberg & Hardman, 2006; Devaere *et al*., 2007; Mwita & Nkwengulila, 2008), and is reconfirmed here. This is to be expected given that nearly all of the sequence data analyzed came from these earlier studies. Both present and past (Jansen *et al*., 2006; Devaere *et al*., 2007) analyses of *18S–ITS1–5.8S–ITS2–28S* data indicate that *Clarias* may also be polyphyletic, owing to the well-supported positions of *C. gariepinus* and *C. ngamensis* relative to *Dinotopterus* and *Heterobranchus* (Fig. 14), although these analyses were lacking data from the *Bathyclarias* species that were found to be most closely related to *C. gariepinus* according to cyt *b* analyses (rendering *Bathyclarias* paraphyletic as well). *Channallabes* was also recovered as paraphyletic, in agreement with earlier

molecular reconstructions incorporating multiple species from this genus (Jansen *et al*., 2006; Devaere *et al*., 2007). It is highly likely that at least one additional clariid genus, *Clariallabes*, may also be paraphyletic, as has been recently implied (Seegers, 2008), although to date, no phylogenetic analysis of African clariids has included more than one species from this genus. It is evident that additional work using multiple genetic loci and a greater coverage of species diversity will be necessary to more confidently resolve the evolutionary relationships of this widespread family of catfishes, and to guide the taxonomic reassignments that will be required.

Information regarding the biology of this Tanganyikan catfish species flock (and others as well) has potential ramifications for questions relating to species formation and maintenance in the most ancient of the East African rift lakes. After cichlids, catfishes represent the greatest degree of ichthyological diversity in Lake Tanganyika at the generic level (albeit still much lower, with over 50 cichlid genera versus eight catfish genera). Levels of species diversity are generally quite low, especially when

compared with many cichlid genera, and can vary widely between groups of Tanganyikan catfishes as well. The species diversity of the *Tanganikallabes* species flock is among the lowest of any non-monotypic catfish genus in Lake Tanganyika, although it is reasonably close to that of several other Tanganyikan genera, including *Phyllonemus* (three species), *Lophiobagrus* (four species), and *Bathybagrus* (six species). The ten currently recognized endemic Tanganyikan *Synodontis* species (Wright & Page, 2006) represent by far the greatest level of species diversity in any Tanganyikan catfish genus. However, whereas studies concerning the mechanisms and rates of rift lake cichlid species diversification abound, examinations of why other groups of rift lake fishes (catfishes being the ready example) have not followed suit are comparatively sparse. Such comparative studies are necessary to uncover biotic and historical factors that may be responsible for disparate levels of diversification between cichlids and these other groups.

ACKNOWLEDGEMENTS

REFERENCES

Agnese J-F, Teugels GG. 2001a. Genetic evidence for monophyly of the genus *Heterobranchus* and paraphyly of the genus *Clarias* (Siluriformes, Clariidae). *Copeia* **2001:** 548–552.

Agnese J-F, Teugels GG. 2001b. The *Bathyclarias-Clarias* species flock. A new model to understand speciation in African Great lakes. *Conptes Rendus de l'Académie des Sciences de Paris* **324:** 683–688.

Agnese J-F, Teugels GG. 2005. Insight into the phylogeny of African Clariidae (Teleostei, Siluriformes): implications for their body shape evolution, biogeography, and taxonomy. *Molecular Phylogenetics and Evolution* **36:** 546–553.

Anseaume L, Teugels GG. 1999. On the rehabilitation of the clariid catfish genus *Bathyclarias* endemic to the East African Rift Lake Malawi. *Journal of Fish Biology* **55:** 405–419.

Bailey RM, Stewart DJ. 1984. Bagrid catfishes from Lake Tanganyika, with a key and descriptions of new taxa. *Miscellaneous Publications, Museum of Zoology, University of Michigan* **168:** 1–41.

Briolay J, Galtier N, Brito RM, Bouvet Y. 1998. Molecular phylogeny of Cyprinidae inferred from cytochrome *b* DNA sequences. *Molecular Phylogenetics and Evolution* **9:** 100–108.

Burgess W. 1989. *An atlas of freshwater and marine catfishes: a preliminary survey of the Siluriformes*. Neptune, NJ: T.F.H. Publications, Inc.

Cabuy E, Adriaens D, Verraes W, Teugels GG. 1999. Comparative study on the cranial morphology of *Gymnallabes typus* (Siluriformes: Clariidae) and their less anguilliform relatives, *Clariallabes melas* and *Clarias gariepinus*. *Journal of Morphology* **240:** 169–194.

Chardon M. 1968. Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. *Annales du Musée Royal de l'Afrique Centrale* **169:** 1–273.

Cohen AS, Soreghan MJ, Scholz CA. 1993. Estimating the age of formation of lakes – an example from Lake Tanganyika, East African rift System. *Geology* **21:** 511–514.

Coulter GW. 1991. *Lake tanganyika and its life*. New York: Oxford University Press.

David L. 1936. *Uegitglanis*, silure aveugle de la Somalie italienne, chaînon entre bagrides et clariides. *Revue de Zoologie et Botanique Africains* **28:** 369–388.

Day JJ, Bills R, Friel JP. 2009. Lacustrine radiations in African *Synodontis* catfish. *Journal of Evolutionary Biology* **22:** 805–817.

Day JJ, Wilkinson M. 2006. On the origin of the *Synodontis* catfish species flock of Lake Tanganyika. *Biology Letters* **2:** 548–552.

Devaere S, Adriaens D, Teugels GG, Verraes W. 2006. Morphology of the cranial system of *Platyclarias machadoi* Poll, 1977: interdependencies of skull flattening and suspensorial structure in Clariidae. *Zoomorphology* **125:** 69–85.

Devaere S, Adriaens D, Teugels GG, Verraes W, De Clerq N, Postnov A. 2005. Holotype skeletal morphology of *Gymnallabes nops* (Roberts and Stewart, 1976), using micro CT-scanning. *Cybium* **29:** 281–293.

Devaere S, Jansen G, Adriaens D, Weekers P. 2007. Phylogeny of the African representatives of the catfish family Clariidae (Teleostei, Siluriformes) based on a combined analysis: independent evolution towards anguilliformity. *Journal of Zoological Systematics & Evolutionary Research* **45:** 214–229.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39:** 783–791.

Gianferrari J. 1923. *Uegitglanis zammaranoi*, un nuove Siluride cieco africano. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia* **62:** 1–3.

Greenwood PH. 1961. A revision of the genus *Dinotopterus* BLGR (Pisces: Clariidae) with notes on the comparative anatomy of suprabranchial organs in the Clariidae. *Bulletin of the British Museum (Natural History). Zoology* **7:** 215–241.

Greenwood PH. 1984. What is a species flock? In: Echelle

AA, Kornfield I, eds. *Evolution of fish species flocks*. Orono: University of Maine at Orono Press, 13–19.

Hardman M. 2008. A new species of catfish genus *Chrysichthys* from Lake Tanganyika (Siluriformes: Claroteidae). *Copeia* **2008:** 43–56.

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

Jansen G, Devaere S, Weekers PHH, Adriaens D. 2006. Phylogenetic relationships and divergence time estimate of African anguilliform catfish (Siluriformes: Clariidae) inferred from ribosomal gene and spacer sequences. *Molecular Phylogenetics and Evolution* **38:** 65–78.

Koblmüller S, Sturmbauer C, Verheyen E, Meyer A, Salzburger W. 2006. Mitochondrial phylogeny and phylogeography of East African squeaker catfishes (Siluriformes: *Synodontis*). *BMC Evolutionary Biology* **6:** 49.

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.

Leviton AE, Gibbs RH Jr, Heal E, Dawson CE. 1985. Standards in ichthyology and herpetology. Part I. Standard symbolic codes for institutional resource collections in ichthyology and herpetology. *Copeia* **1985:** 802–832.

Mo T. 1991. Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei) with a hypothesis of siluroid phylogeny. *Theses zoologicae* **17:** 1–216.

Mwita CJ, Nkwengulila G. 2008. Molecular phylogeny of the clariid fishes of Lake Victoria, inferred from cytochrome *b* DNA sequences. *Journal of Fish Biology* **73:** 1139–1148.

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.

Poll M. 1943. Description du *Tanganikallabes mortiauxi*, gen. nov., sp. n. de la famille des Clariidae. *Revue de Zoologie et Botanique Africains* **37:** 126–133.

Poll M. 1946. Révision de la faune ichthyologique du Lac Tanganika. *Annales du Musée du Congo Belge, Zoologie* Series (1) **4:** 141–364.

Poll M. 1953. Poissons non-Cichlidae. Résultats scientifiques de l'exploration hydrobiologique du Lac Tanganika (1946–1947). *Institut Royal des Sciences Naturelles de Belgique* **3** (5A): 1–251.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14:** 817–818.

Rambaut A. 1996. Se-Al: sequence alignment editor [computer program]. Available at: http://evolve.zoo.ox.ac.uk/ Accessed 25 May 2005.

Ribbink AJ. 1984. Is the species flock concept tenable? In: Echelle AA, Kornfield I, eds. *Evolution of fish species flocks*. Orono: University of Maine at Orono Press, 21–25.

Risch L. 1987. Description of four new bagrid catfishes from Africa (Siluriformes: Bagridae). *Cybium* **11:** 21–38.

Seegers L. 2008. *The catfishes of Africa: a handbook for identification and maintenance*. Rodgau, Germany: Aqua Verlog A.C.S. GmbH.

Seehausen O. 2006. African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society B* **273:** 1987–1998.

Sudarto S, Teugels GG, Pouyaud L. 2003. Description of two new *Clarias* species from Borneo (Siluriformes, Clariidae). *Cybium* **27:** 153–161.

Sullivan JP, Lundberg JG, Hardman M. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag1* and *rag2* nuclear gene sequences. *Molecular Phylogenetics and Evolution* **41:** 636–662.

Swofford DL. 2003. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Sunderland, MA: Sinauer Associates.

Takahashi T. 2002. Systematics of the tribe Trematocarini (Perciformes: Cichlidae) from Lake Tanganyika, Africa. *Ichthyological Research* **49:** 253–259.

Takahashi T, Nakaya K. 1999. New species of *Haplotaxodon* (Perciformes: Cichlidae) from Lake Tanganyika, Africa. *Copeia* **1999:** 101–106.

Takahashi T, Nakaya K. 2003. New species of *Cyphotilapia* (Perciformes: Cichlidae) from Lake Tanganyika, Africa. *Copeia* **2003:** 824–832.

Taylor WR. 1967. An enzyme method of clearing and staining small vertebrates. *Proceedings of the United States National Museum* **122:** 1–17.

Teugels GG. 1986. A systematic revision of the African species of the genus *Clarias* (Pisces; Clariidae). *Annales Musée Royal de l'Afrique Centrale* **247:** 1–199.

Wilson AB, Glaubrecht M, Meyer A. 2004. Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society of London B* **271:** 529–536.

Wright JJ. 2009. Diversity, phylogenetic distribution, and origins of venomous catfishes. *BMC Evolutionary Biology* **9:** 282.

Wright JJ, Page LM. 2006. Taxonomic revision of Lake Tanganyikan *Synodontis* (Siluriformes: Mochokidae). *Bulletin of the Florida Museum of Natural History* **46:** 99–154.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Taxon sampling, GenBank accession data, and sources for genetic information used in phylogenetic analyses. *Paragenetype sequence.

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