Astatotilapia species (Teleostei, Cichlidae) from Malawi, Mozambique and Tanzania, excluding the basin of Lake Victoria.

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Abstract. The haplochromine cichlid fauna of the rivers and smaller lakes of Tanzania and SE Africa are of key importance in understanding the origins and inter-relationships of the great lake cichlid radiations of Malawi, Tanganyika and Victoria. Prior to formal taxonomic investigations, here we present the results of investigations of the type specimens, identification of type localities and superficial characterisation of freshly-collected material. The type locality of *Astatotilapia bloyeti* (Sauvage, 1883) is identified as the Mkondowa River, near Kilosa. This species appears to be the only haplochromine found in the Wami system. It is concluded that junior synonyms of *A. bloyeti* include *A. strigigena* (Pfeffer, 1893), *A. kilossana* (Steindachner, 1915) and *A. paludinosa* Greenwood, 1980. *Astatotilapia sparsidens* (Hilgendorf, 1905) is closely related and may constitute a junior synonym or a sister taxon. The range of *A. bloyeti* includes the Pangani system. The type locality for *Astatotilapia gigliolii* (Pfeffer, 1896) is identified as the Kingani River, or southern Ruvu, where it appears to be the only haplochromine in the river system. Junior synonyms include *Astatotilapia vollmeringi* (Steindachner, 1915) from the Great Ruaha River at Kidatu and *Astatotilapia tweddlei* Jackson, 1985 from Lakes Chilwa and Chiuta. The species is also reported from the lower part of the Rufiji system, the Ruvuma system and from other lakes and rivers in between. A few specimens were also collected in and around a fish farm at Songea, in the upper reaches of the Ruhuhu system (Lake Malawi catchment). Apart from this record, the only *Astatotilapia* species in the Lake Malawi catchment is *A. calliptera*. Four undescribed *Astatotilapia* species are identified from the Rufiji system, while other possibly undescribed taxa from the basins of Lake Tanganyika and Rukwa are discussed.

Keywords. *Astatotilapia*, haplochromine cichlid, systematics, synonymy, East Africa, Lake Malawi.

Introduction

Recent research on the African Great Lake cichlid fish radiations has indicated that the rivers have acted as conduits to the spread of haplochromine cichlids enabling their dispersal throughout much of Africa and into the Middle East, and their colonisation of Lakes Tanganyika, Malawi, Victoria, Kivu, Turkana, Albert, Edward, George, Rukwa, Kyoga etc, in which numerous endemic species have evolved (Salzburger *et al.* 2005; Meier *et al.* 2017; Malinsky *et al.* 2018, Svardal *et al.* 2020). Indeed, there is even some evidence of gene flow between lakes, carried via populations of riverine haplochromine cichlids, which, it is speculated, may have resulted in the transmission of key adaptive traits (Loh *et al.* 2012). Clarification of the identity of species and their distributions within the rivers of Tanzania may thus be of wider significance than simply their contribution to the ecology of their current habitats. Although there are a number of haplochromine genera in Tanzanian rivers, such as *Astatoreochromis*, *Ctenochromis*, *Pseudocrenilabrus* and *Orthochromis*, the species of the genus *Astatotilapia* Pellegrin 1904 are of particular relevance to the lacustrine radiations (Meier *et al.* 2017; Malinsky *et al.* 2018, Svardal *et al.* 2020). Thus, we focus on the species of *Astatotilapia* from the inland waters of Tanzania, Malawi and Mozambique, considering type specimens with particular emphasis on the clarification of type localities, and attempting to characterise the features that would enable their diagnosis in the field, making use of recently-collected material. Our survey excludes entirely the Lake Victoria basin, where numerous endemic species occur. We will also make limited comments on the faunas of the catchments of Lake Tanganyika and the Lake Rukwa basin (Seegers 1996). We will, however, cover the Lake Malawi catchment in more detail.

Methods

The overall aim is to provide a preliminary guide to the identification of *Astatotilapia* species from the inland waters of Malawi, Mozambique and Tanzania (excluding the catchment of Lake Victoria) Quantitative morphological studies are currently in progress and are expected to result in several species descriptions. Genomic analyses are also in progress and should help clarify the inter-relationships of the taxa, with preliminary results reported by Malinsky *et al.* (2018) and Svardal *et al.* (2020). In the interim, we present the results of (i) re-examination of the original species descriptions and other literature relating to the identification of type localities; (ii) a qualitative re-examination of type material; (iii) a qualitative appraisal of the results of field sampling from 2011 to the present; (iv) an examination of published and unpublished molecular phylogenetic analyses.

Figure 1: Approximate geographic coverage of the present study, incorporating Tanzania (excluding the Lake Victoria catchment, Malawi and most of Mozambique (image modified from Google Earth, 2021).

Results

Astatotilapia Pellegrin 1904

The modern concept of *Astatotilapia* dates from the revision of *Haplochromis* by Greenwood (1979). By that time, the genus *Haplochromis* had come to include over 300 species, many endemic to Lake Malawi and Lake Victoria, as well as many riverine forms. Many were highly derived, lacustrine specialists- arguably, this includes the type species of *Haplochromis*, namely *Haplochromis obliquidens* Hilgendorf 1888, from Lake Victoria, which has obliquely truncated, recurved, slender-necked, flexibly implanted outer row jaw teeth. Thus, Greenwood (1979) restricted *Haplochromis* to a few lacustrine endemics of the Lake Victoria 'superflock' and distributed the riverine species among a number of genera, including *Astatotilapia*, *Astatoreochromis, Ctenochromis, Thoracochromis, Orthochromis, Serranochromis, Chetia* and *Pharyngochromis*. Most of these genera have proved to be useful and readily diagnosable. Some even remain as putative clades, such as *Astatoreochromis* (Banyankimbona *et al.* 2013) and (a redefined) *Orthochromis* (Schedel *et al.* 2018).

However, Greenwood (1979) recognised that *Astatotilapia* lacked any defining synapomorphies and suggested that it might prove to be paraphyletic or polyphyletic. Indeed, this has been the outcome from recent molecular phylogenetic studies (Meier *et al.* 2017; Malinsky *et al.* 2018). A consequence of Greenwood's revision was the erection of a number of genera for members of the Lake Victoria Region superflock, although at that time a few endemic genera were already in use, such as *Hoplotilapia* and *Macropleurodus* (Greenwood 1980a). Subsequently, many taxonomists working on Lake Victoria haplochromines did not find Greenwood's genera easy to work with, feeling that they intergraded and lacked defining synapomorphies (Hoogerhoud 1984) these genera have largely been

adopted since (Seehausen *et al.* 1998; Meier *et al.* 2017). As an alternative to Greenwood (1980a), many Victorian cichlids have been referred to as *'Haplochromis'* (e.g. Hoogerhoud & Witte 1981), a practice which is incompatible with the International Code for Zoological Nomenclature (Schedel *et al.* 2014). In an attempt to resolve this, van Oijen (1996) suggested defining *Haplochromis* more widely in morphological terms, but restricting it to the Lake Victoria basin- basically to encompass all the Victorian haplochromines apart from *Astatoreochromis*. Van Oijen's definition would leave *Astatotilapia* and other genera as defined by Greenwood (1979) available for non-Victorian taxa. However, a number of publications have persisted in using *Haplochromis* for taxa outside the Victoria basin (e.g. Schedel *et al.* 2014; 2018; Vranken *et al.* 2019). In some studies, it seems that populations are more less allocated randomly to *Astatotilapia, Haplochromis* or '*Haplochromis*' (e.g. Meyer *et al.* 2015; Meier *et al.* 2017).

We do not intend to try to revise or redefine *Astatotilapia*, but will rather attempt to make Greenwood's (1979) definition operational for our study taxa. Greenwood's redescription is lengthy but lacks direct comparison and diagnosis, so we have found it more useful to focus on his key [pages 315-317 of Greenwood (1979)]. Here, *Astatotilapia* can be diagnosed on the basis of the following combination of traits: (i) the size of the scales on the flank grade in size gradually to the smaller chest scales; (ii) the anal fin of the males is marked by 3-9 yellow-orange spots which are 'ocellated' (surrounded by a contrasting dark or translucent area); (iii) the anal fin has 3 spines and the dorsal fin rarely more than 16 spines; (iv) the teeth in the outer row of the oral jaws are either unicuspid or unequally bicuspid with the tip lying within the major axis of the tooth (in other words, not too bent).

The oral jaw tooth trait is primarily intended to distinguish *Astatotilapia* from *Haplochromis*, which Greenwood redefined to include only species in which the outer oral jaw teeth were primarily long, slender, weakly-attached sharply recurved bicuspids with a spatulate form (i.e. a broader crown with narrow neck). In teeth of this form, the tip of the main cusp lies well outside the major axis of the tooth, because the tooth is strongly recurved. Greenwood's *Haplochromis* species were all found in lakes: Victoria, Kivu and Edward/George. Uses of *Haplochromis* or '*Haplochromis*' by many subsequent authors ignore the tooth structure as a defining feature. Indeed, none of these studies offer an alternative definition of *Haplochromis* and simply use it to encompass any haplochromine cichlid species that cannot be readily placed in another genus. For example, *Haplochromis vanheusdeni* Schedel *et al.* 2014 does not correspond to Greenwood's or van Oijen's definition of the genus, but appears to be based on a wider generic concept that would, if consistently applied, probably include thousands of species including all the endemic Lake Malawi, Edward/George, Kivu, Rukwa, Turkana and Victoria haplochromine taxa as well as numerous riverine haplochromines and a number of taxa from Lake Tanganyika.

Within our study area, Greenwood's diagnostic features serve to exclude other riverine haplochromines quite effectively: *Ctenochromis*, *Orthochromis* and *Haplochromis vanheusdeni* have an abrupt transition from large flank to tiny chest scales. *Orthochromis* lack ocellated spots on the male's anal fin. *Astatoreochromis* generally has higher anal fin spine counts. *Serranochromis* has numerous non-ocellated anal fin spots. *Pseudocrenilabrus* has no anal fin spots (or a bright spot right at the tip). The diagnosis also serves to distinguish *Astatotilapia* from the Lake Malawi endemic genera: most of these lack ocellated anal fin spots, apart from the mbuna group which have an abrupt transition to small chest scales (Eccles & Trewavas 1989).

Astatotilapia: issues of nomenclature

There are some outstanding issues of nomenclature relating to *Astatotilapia* and its type species.

Lacépède (1802) used two different spellings: *Sparus desfontainii* was used in the species description, but in a later discussion of the biology of the species largely using the French-language vernacular name 'le spare desfontaines', he added a footnote giving the scientific name as *Sparus desfontaines.* One possible explanation is that '*Sparus desfontainii*' was a printer's error (Schraml 2010). Another possible explanation is that '*Sparus desfontaines*' resulted from inadvertent copying of the vernacular form. As each form of the name is used only once, it seems unclear. The ICZN code (24.2.1) specifies that where two alternative spellings are used and there are no objective criteria to choose one over the other, "precedence is fixed by the action of the first author citing in a published work those names or acts and selecting from them; this author is termed the "First Reviser"". This was performed by Eschmeyer (1998) in the original print edition of the 'Catalog of Fishes'. Other spellings widely used in the early part of the 20th Century were deemed unjustified emendations (Eschmeyer 1998). Confusingly, Schraml (2010) also claimed to be First Reviser citing both original spellings but opting to choose a third: *Sparus desfontainesi*. This appears to be doubly invalid, both in postdating Eschmeyer's revision and in choosing a spelling not in the original description. This emended spelling appears to have been introduced by Boulenger in 1899 (who then emended it again to *Haplochromis desfontainesii* in 1915). One or the other of Boulenger's emended spellings was followed by most subsequent authorities until van Oijen *et al*. (1991) reinstated the original spelling in their widely used Checklist of Freshwater Fishes of Africa (CLOFFA) IV. Greenwood (1979) was aware of Boulenger's first emendation, and considered it justified because Lacépède intended to honour M. Desfontaines. This kind of emendation to specific epithets was frequent among ichthyologists at beginning of the 20th Century: for example, Pellegrin (1904) emended *Hemichromis livingstonii* Günther 1894 to *Astatotilapia livingstonei* while Boulenger (1915) emended *Chromis johnstoni* Günther 1893 to *Tilapia johnstonii*. In fact, such emendations are not permitted under the current ICZN code (Article 33), unless there is clear evidence that there was an inadvertent error in the original manuscript: it does not seem obvious that '*desfontainii*' would be an inappropriate derivation of 'Desfontaines'. While a case might have been made to argue for '*desfontainesi'* (Boulenger 1899, 1905; Pellegrin 1904; Greenwood 1979) or '*desfontainesii*' (Boulenger 1915; Regan 1922a, b) on the basis of 'prevailing useage' (Article 33.2.3.1), since 2010, many research papers have mentioned this species – all using '*desfontainii*' (Genner & Haesler 2010, Hermann *et al.* 2011, Genner *et al.* 2012, Schwarzer *et al.* 2012, Meyer *et al.* 2015, Meier *et al.* 2017). This is also the name accepted in major online resources, including Eschmeyer, FishBase, IUCN redlist, NCBI taxonomy browser and Wikipedia. In conclusion, it would seem that '*desfontainii*' should be preserved on the basis that it is the original spelling, the choice of the first reviser and that it is in prevailing useage.

Pellegrin (1904) erected the genus *Astatotilapia* to include the species *A. desfontainesi* (Lacépède 1802), *A. livingstonii* (Günther 1894) and *A. johnstoni* (Günther 1894). As well as using the unjustified emendation of the species name, Pellegrin also used the wrong original genus name: Lacépède (1802) originally named the species *Sparus desfontainii*, but many subsequent authors including Pellegrin (1904) followed Boulenger (1899) who erroneously listed the original name as *Labrus desfontainii*, although listing a reference to "*Sparus* (?) *desfontainii*" in Gervaise (1869).

However, the use of the wrong generic name in the citation of the original description does not invalidate *Astatotilapia*. Under the ICZN code, for a name published prior to 1931, it must have 'an indication': "in the case of a new genus-group name, the use of one or more available specific names in combination with it, or clearly included under it, or clearly referred to it by bibliographic reference, provided that the specific name or names can be unambiguously assigned to a nominal species-group taxon or taxa" (Article 12.2.5). Clearly, all three included taxa can be unambiguously assigned to particular species.

Finally, there is the issue of the authority for designation of the type species as *Astatotilapia desfontainii*. No type species was designated by Pellegrin (1904) and two of three species he included were placed by Eccles & Trewavas (1989) in Lake Malawi endemic genera: *Nimbochromis livingstonii* and *Placidochromis johnstoni*. Eschmeyer's Catalog (Fricke *et al.* 2020) gives 'Regan 1922' as the authority for the designation of *A. desfontainii* as the type species of *Astatotilapia*, although stating this was not checked and not giving a link to specific publication: Regan published several major papers on African cichlids in 1922. The correct reference appears to be Regan's monograph on the cichlid fishes of Lake Nyassa which is dated 1921 but seems to have been published early in 1922 (Regan 1922a). By the time he published his monograph on Lake Victoria cichlids later in the same year, he had once again synonymised *Astatotilapia* with *Haplochromis* (Regan 1922c: p. 158 footnote) and in his paper on the cichlid fishes of 'African and Syrian genera' excluding the great lakes (Regan 1922b), there is no mention of *Astatotilapia* at all, but he discusses *Haplochromis desfontainesii*.

In conclusion, we find that the type species of the genus *Astatotilapia* Pellegrin 1904 is *Sparus desfontainii* Lacépède 1802, originally designated by Regan (1922a).

Astatotilapia bloyeti (Sauvage 1883)

Summary: A valid species, occurring in the Wami River system, (type locality near Kilosa), the Malagarasi, the Pangani and the catchments of Lake Manyara and Eyasi and associated lakes. Junior synonyms include *A. strigigena* (Pfeffer 1893) (type localities on the Wami), *A. kilossana* (Steindachner 1915) (type locality on the Wami at Kilosa), *A. paludinosa* Greenwood 1980 (type locality in the Malagarasi) and (provisionally) *A. sparsidens* (Hilgendorf 1905) (type locality Lake Manyara).

Original Description: The original description of *Hemichromis bloyeti* (in French) is brief and contains little of use in differentiating this species from other *Astatotilapia*. It ends with the words "Kandôa (Afrique orientale) : Bloyet".

Determination of type locality: We concur with Seegers (1996) that the type locality is near Kilosa on a tributary of the Wami River system. Seegers gives no justification for this, nor did Greenwood (1979) for his statement that it was on the Great Ruaha River (repeated by Trape 2016).
These is little doubt that 'Kandoa' refers to the collecting locality and 'Bloyet' to the collector/donor, after whom the species has been named. No further details were found in the jars containing the

types or in museum records in Paris or London during our investigations in 2015 and 2017 respectively.

The nearest name currently in use in Tanzania appears to be 'Kondoa', which is a town near Dodoma in Central Tanzania. It seems plausible that a Swahili word 'Kondoa' might be written as 'Kandoa' by a Francophone collector. However, the name 'Kandoa' also appears in Ernest Hemingway's (1935) memoir of big game hunting, 'Green Hills of Africa' ("I never drink" Kandinsky said. "I will go to the lorry and fetch some butter for lunch. It is fresh from Kandoa, unsalted. Very good"). The book is believed to have been based on Hemingway's experiences in the vicinity of Lake Manyara, Tanzania in 1933 (Meyers 1985). Modern Kondoa is about 200km south of Lake Manyara. Also, the character Kandinsky is said to be Austrian and to have fought with 'von Lettöw'. This is probably a reference to General Paul von Lettow-Vorbeck, commander of the German army in German East Africa (roughly the mainland part of modern Tanzania). He engaged allied forces at the battle of Kondoa-Irangi during 1916 (Strachan 2004). So, it seems likely that Kondoa-Irangi was indeed also known as Kandoa.

However, Seegers (1996, pp. 285-286) stated 'the type locality of *H. bloyeti*, 'Kandôa', was an old Arabian village which was destroyed before the turn of the century and was situated near the Kilosa of today. It is not the Kondoa/Irangi in the Bubu district'. Seegers provided no evidence for these statements.

Bloyet (1890) stated that he was charged with founding a scientific and medical station at Kondoa near Kilassa (which may represent modern day Kilosa), by the Comité français de l'association internationale africaine. Bloyet also mentioned making collections of specimens for the Muséum d'histoire naturelle de Paris. The map from his article (Figures 2 and 3), clearly shows the 'Station de Kondoâ' on the Mkondoa River, a tributary of the Ouami (which may represent the modern day Wami river). We thus agree with Seegers that the type locality is almost certainly the Mkondoa River, on the Wami system, somewhere near Kilosa.

However, it remains possible that Bloyet's specimens were labelled with the location of his base camp, and that he may have collected the material from somewhere else on his travels between Bagamoyo and Kondoa, which would likely include not only the Wami, but also the 'southern' Ruvu system. There are two Ruvu Rivers in present day Tanzania: the 'northern' Ruvu is a tributary of the Pangani (sometimes listed as the Jipe Ruvu: Wikipedia 2021), while the 'southern' Ruvu runs close to Morogoro and enters the Indian Ocean near Bagamoyo. Bloyet's map (Figures 2 & 3) shows the 'Rouvou' in some detail.

In a footnote to the description of *A. bloyeti* by Sauvage, he also notes that Bloyet collected specimens of '*Chromis mossambicus* Ptrs, *Labeo forskalii* Rüpp., *Fundulus orthonotus* Ptrs, and *Clarias anguillaris* Lin'. It is likely that these represent *Oreochromis urolepis, Labeo congoro, Nothobranchius* spp. and *Clarias gariepinus*. All are still listed on the MNHN catalogue, although the *Oreochromis* are listed as *Tilapia mossambica* or *T. nilotica*. Unfortunately, it is unlikely that any of these widely distributed species would be diagnostic of any of the major river systems in the area. However, the relatively low species diversity suggests that Bloyet did not expend too much energy in collecting fish material on his expeditions, so making it more likely that his collection was in fact from his main base at Kondoa. Furthermore, examination of the type material indicated that the chest

scales are very small, consistent with material from Kilosa and elsewhere on the Wami system in the collections at the NHM in London, as well as in our collections. The only haplochromine species known from the Ruvu system (*Astatotilapia gigliolii*) has relatively larger chest scales. Therefore, we feel confident that the type locality of *A. bloyeti* is the Mkondoa river, on the Wami system, near Kilosa.

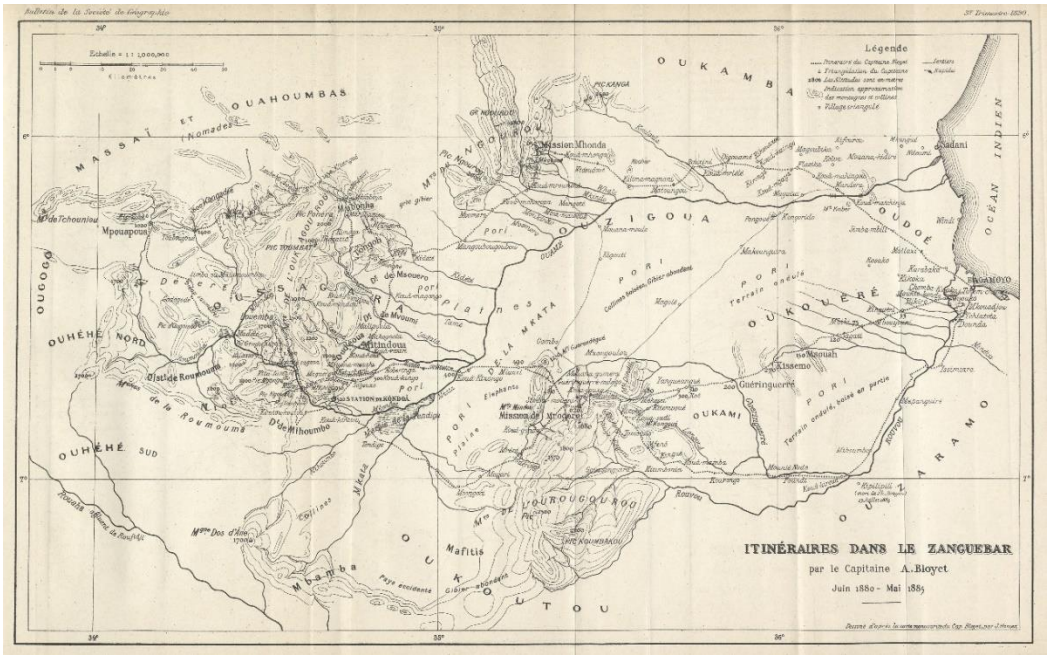

Figure 2. Map of Bloyet's (1890) report on his explorations of the area around Kondoa Station.

Figure 3a. Close-up of section of Bloyet's Map (1890), showing localities around the Kondoa Station on the Mkondoa River near present-day Kilosa. Co-ordinates shown are given as -7.00, 35.00, which is not accurate.

b. On a modern satellite map (bottom left), this location is around -6.99, 37.25. The area of river floodplain between Kilosa and Morogoro corresponds to the present day Mikumi National Park.

Examination of the types: We were able to examine a syntype in London (BMNH 1898.2.15.2 [ex MNHN], 71.2 mm SL, Kandoa, East Africa, coll. Bloyet) and four more in Paris (MNHN A-6513: 63.4-74.2 mm SL, same data as lectotype). We did not see the fifth Paris type, listed as on-loan from the museum in Paris to E. Lippitsch. The specimens were uniformly yellowish, very soft and fragile and showed considerable damage to the fins and scales (Figures 4 & 5). Nothing about their body shape or meristics was exceptional or diagnostic for a riverine haplochromine, although the chest scales did seem rather small.

Collections at the type locality: On 24th-25th July 2015, 4 localities were sampled on the Wami system in the vicinity of Kilosa. No cichlids were obtained from the main channel of the Mkondoa River, which was wide, shallow, sandy and fast-flowing. However, specimens of *Astatotilapia* were obtained from the catches of local fishermen at three sites: (i) Mwimbi Dam, a weedy floodplain pool in an extensive area of swamps about 2.5km from the Mkondoa River (-6.86, 36.979); (ii) a pool off the Miombo River among rice paddies (-6.906, 36.978); (iii) Lake Nala (or Zombo), a weedy lake on a tributary of the Mkondoa River (-6.945, 36.937). In total, 55 specimens of *Astatotilapia* were kept and many more inspected but not preserved (Figures 6-16). As far as we could tell, all were members of a single species, characterised by small chest scales and brownish-purple to reddish spots (often merging into stripes) in the soft dorsal and at least the upper half of the caudal fins. Mature males were generally dark greenish-grey, suffused with yellow on the operculum

and on the flanks behind, with a thin red margin to the soft dorsal fin and upper part of the caudal fin, and with small ocellated eggspots largely on the posterior half of the anal fin which has a broad faintly pinkish-red margin. Females were countershaded grey above, silvery on the flanks and white ventrally. The anal and caudal fins were sometimes dark yellow-orange and showed traces of spots.

On 10 Jan 2017, we sampled Hombolo Dam (-5.971, 35.943), an artificial lake on a tributary of the Wami system (Turner *et al.* 2018). No haplochromines were observed in the catches, but we hired some local fishermen to use our small-meshed monofilament net as a seine in shallow waters. This yielded numerous haplochromines (>50, of which 20 adult males were preserved), again all regarded as a single species (Figures 17-19). Although adult males were much smaller on average size and slightly more bluish, other phenotypic similarities led us to believe that these are conspecific with the Kilosa specimens. Other sampling efforts on the lower parts of the Wami in the main channel (23 Jan 2014, 2 Feb 2014) and in Mbuyuni Pool at Matipwili (23 Jan 2014, 22 Jul 2015) failed to yield any haplochromines. Thus, it appears that there is only one haplochromine species in the Wami River system, including in the vicinity of the type locality at Kilosa.

Further evidence for the presence of only one haplochromine species in the Wami basin comes from examination of specimens at the Natural History Museum in London, collected by Bailey and Trewavas in 1965 from a lake in a Sisal Plantation near the 'Mukondowa River, near Kilosa' (Figures 20-21). These too appeared to be conspecific with our Kilosa and Hombolo specimens, in overall body shape, small chest scales and characteristic spots/stripes in the soft dorsal and upper caudal fins. Additional information was obtained from examination of the types of *Paratilapia kilossana* (figures 4-5).

Figure 4: Syntype of *Hemichromis bloyeti* in Paris. MNHN A-6513

Figure 5: Syntype of *Hemichromis bloyeti* in London. NHM 1892.2.15.2

Figure 6: Adult male *Astatotilapia bloyeti* from near Kilosa, from the Miombo River, July 2015

Figure 7: Adult male *Astatotilapia bloyeti* from Lake Nala, near Kilosa, July 2015

Figure 8: Kilosa site 2, Mwimbi Dam.

Figure 9: Kilosa site 3, rice paddy near the Miombo River.

Figure 10: Kilosa site 4, Lake Nala.

Figure 11: *Astatotilapia bloyeti* adult female from Lake Nala.

Figure 12: Adult male *Astatotilapia bloyeti* from Lake Nala, near Kilosa on the Wami River system, July 2015. Note the relatively deep body and slight nuchal hump of this large (~75mm SL) specimen. Note also that the spots on the dorsal and caudal fins merge into stripes basally. In this case, the markings are largely confined to the last few dorsal rays and the upper part of the caudal fin. The 3 anal fin ocelli are relatively small and positioned close to the body and behind the 3rd anal soft ray. The genome of this specimen has been sequenced (Svardal *et al.* 2020).

Figure 13: Adult male *A. bloyeti* from Lake Nala. This smaller fish (59mm SL) shows male breeding dress, but is more slender than T7C8 (Figure 12) and lacks the nuchal hump. This individual is unusual in having the first anal fin spot quite far forwards. The caudal fin is strongly patterned in the lower half as well as the upper half.

Figure 14: Adult male *A. bloyeti*, 71mm SL, from Lake Nala. This specimen is intermediate in body shape between T7C8 and T7D2. It also illustrates much less strongly developed markings on the fins, but that the lower half of the caudal fin is reddish while the upper half is grey.

Figure 15: Adult female *A. bloyeti* from Kilosa site 2, coded T6D3. Note relatively dark flank colour and intensely orange anal and caudal fins. 2 anal fin spots are clearly visible. The dark colour and bulging throat suggests that this small fish (61mm SL) was probably mouthbrooding.

Figure 16: Adult female *A. bloyeti* from Lake Nala, coded T7C10. This fish is larger (68mm SL) than T6D3 and shows similar allometry to the males, in developing a deeper body and slightly convex profile above the eye. This individual is paler on the flanks than T6D3 and shows elements of a horizontal flank stripe also seen in the males shown above.

Figure 17: Adult male 57mm SL *A. bloyeti* from Hombolo reservoir in the Wami system. This specimen shows far less yellowish pigment than those from Kilosa, and shows hints of vertical flank barring instead of a horizontal stripe. However, it also shows well-marked spotting in the dorsal and caudal fins and a red margin to the soft dorsal and upper caudal fins, and the pinkish distal portion of the anal fin.

Figure 18: Adult male *Astatotilapia bloyeti*, 58mm SL, from Hombolo Reservoir in 2017. Although a similar overall length to G12B03 (Figure 17), this specimen has a much more prominent mouth, snout and premaxillary pedicel. However, the fin markings and lack of yellow pigment are similar.

Figure 19: Freshly collected mature male *A. bloyeti* from Hombolo Reservoir on 10th January 2017, illustrating the range of body colours in life.

Figure 20: *Astatotilapia bloyeti*, mature male collected from near the type locality (Mkondoa River near Kilosa) in 1969, from the London Natural . The dorsal and caudal fin spotting can be clearly seen, as can a row anal fin eggspots.

Figure 21: The London Natural History Museum sample of *A. bloyeti* from 1969 at the type locality is comprised of 15 rather stiff, pinned, formalin-fixed specimens.

Astatotilapia bloyeti: Synonymy of *Astatotilapia strigigena* (Pfeffer 1893)

Summary: Junior synonym of *A. bloyeti*, described from the Wami System.

Original Description: Pfeffer's description (in German) of *Ctenochromis strigigena* is reasonably detailed, but is based on small specimens, stating that the largest was only 56mm long (probably total length). Of these, 5 were collected from Mbusini on 29th August 1888 and 1 from 'Teich bei Matomondo, Ungúu', 9th September 1888. Meristics are fairly typical of riverine *Astatotilapia* in Tanzania (D: XV-XVI, 8-9; A III, 7-9). However, the illustration shows quite a lot of markings, including conspicuous spotting on the soft dorsal fin, vertical bars on the caudal fin and vague markings on the anal fin (described in the text as 2-3 spots surrounded by clear margins). There is a horizontal dark band on the flank, reported to be most conspicuous near the posterior end, and strong dark bar through the eye. These markings are consistent with those of a sexually mature male *A. bloyeti*, and the form and number of the anal fin spots fits better with *A. bloyeti* than with *A. gigliolii, Pseudocrenilabrus, Ctenochromis pectoralis* or *Astatoreochromis*. The small size of the specimens and the relatively large eye shown on the apparently mature male figured suggest precociously mature fish, which might be expected to occur in a small pool or lake, and indeed the collecting locality 'Teich bei Matomondo' indicates a pond.

Determination of type localities: Pfeffer's description of *Ctenochromis strigigena* gave the type localities as Mbusini, Matomondo, Ungúu, collected by F. Stuhlmann. Stuhlmann's map (1890) clearly shows Matomonda-qua-Súinba and Matomondo-qua-Mgalla – with a small lake illustrated-lying on the Mdjonga River, a tributary of the Wami, between Mount Kanga and the rest of the Ungúu or Angúu Mountains. We can identify this as the Mjonga River passing through the Nguru Mountains- and Mount Kanga is a term still in use. The co-ordinates for the map would suggest this lies at 5º52'S, 37º41'E (-5.87, 37.68), but this does not seem to be accurate. The Mjonga River is a tributary of the Wami River and Turiani is about 100km from Kilosa (Google Earth). However, a 'Matomondo Valley' appears on Google Earth at -6.467; 36.583, about 55km NW of Kilosa and 116km west and south from Turiani. It is possible that this is a duplication of names, or that Stuhlmann's collecting notes and map are in error. It is notable, however, that this locality, too, lies in the Wami catchment. On balance, our best estimate is that 'Matomondo' lay on the Mjonga River near Mount Kanga -6.137, 37.594.

Stuhlmann's map places Mbusini at about 6º13'S, 38º04'E (-6.22, 38.07) at the confluence of the Rukuguru (or Lukigula) and the Wami. A map by Mbilinyi *et al.* (2012) places the confluence of the Lukigula and the Wami at almost exactly the co-ordinates of Mbusini in Stuhlmann's map. Several other 19th century maps illustrate Mbusini (or Mbuzini), including Last (1882) writing about an expedition to 'Nguru country', which includes mentions of the Wami River, and Lugard (1892). However, while Mbilinyi's report lists a number of villages participating in the Wildlife Management scheme, there is no name similar to Mbusini, so it is possible that the name has fallen out of use.

On the basis of available evidence, we feel confident that both of the type localities for *Ctenochromis strigigena* lie within the Wami catchment.

Examination of the types: We have seen a photograph of a small specimen from Hamburg, listed as ZMH 404, from Matomondo. This is listed as a syntype on the online catalogue of the University of Hamburg Centre for Natural History, but Eschmeyer's catalogue (Fricke *et al.* 2019) states that it

was designated as the lectotype by Ladiges *et al.* (1958). We have not seen this publication, but the title indicates that it is not a revision, but as a curatorial exercise, and while lectotype designation in this way is not recommended, it is permissible (ICZN Recommendation 74G). We have also examined a specimen at the Natural History Museum in London (NHM 1899.2.27.2, from Mbusini), listed as a paralectotype. The whereabouts of the other four specimens from Mbusini is unclear: they are not listed in the Hamburg catalogue.

Neither specimen shows any remaining markings, except possibly a hint of stripe below the eye in the Hamburg specimen. Both are small and yellowish. The London specimen is very soft and fragile and its fins are in poor condition. They provided no particularly useful diagnostic features.

Collections at the type locality: At the time of our collections in 2015, we had not yet been able to determine the type localities in sufficient detail to sample them, but our collections from Kilosa and Hombolo suggest that there is only a single *Astatotilapia* species in the Wami catchment, and this can be referred to *A. bloyeti*.

Conclusion: *Ctenochromis strigigena* Pfeffer 1893 is a junior synonym of *Astatotilapia bloyeti* (Sauvage), as stated by Regan (1922) and listed by Eschmeyer's catalog (Fricke *et al.* 2019).

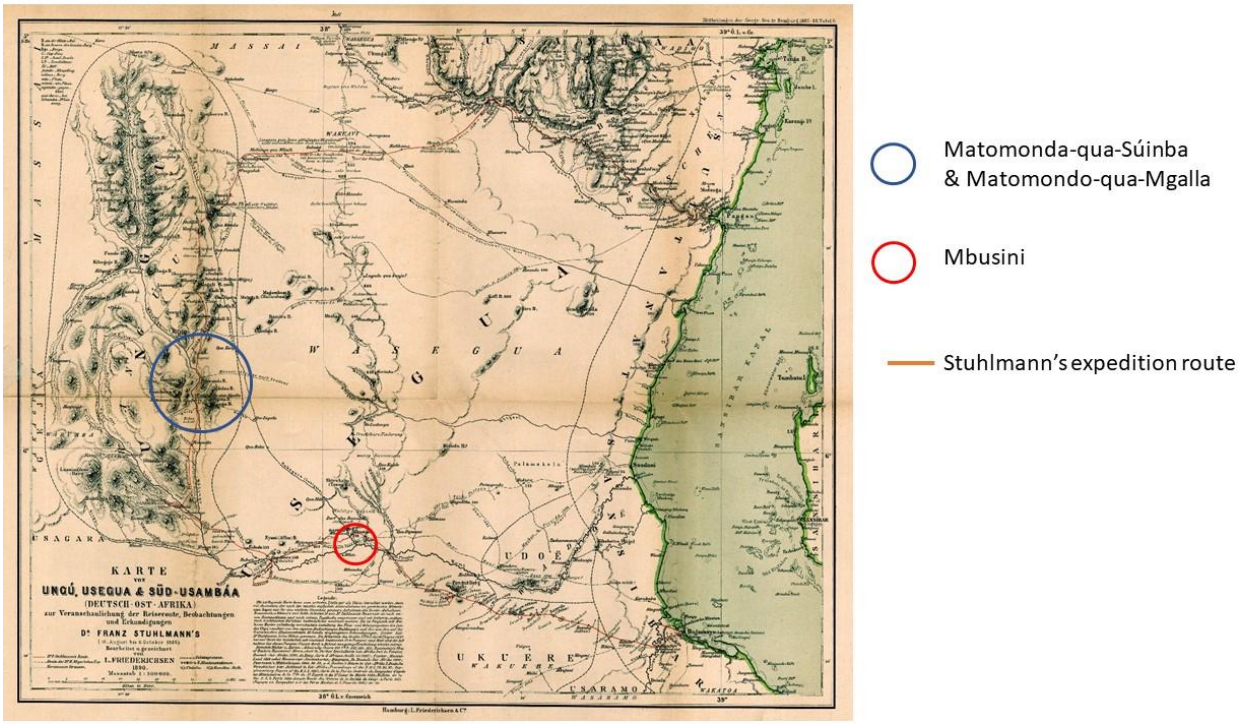

Figure 22: Stuhlmann's map, of his 1890 expedition, showing both collecting localities for *Ctenochromis strigigena*, at Mbusini and Matomondo, clearly lying within the Wami River catchment.

Figure 23: Sketch map in Last (1882), indicating that Mbuzini lay on a tributary of the Wami River, to the East of Malungu.

Figure 24a: Section of map by Bartholomew in Lugard (1892) showing Nguru, Mondo and Mbuzini situated in proximity to a river draining to the Indian Ocean at Saadani, as does the present day Wami River.

Figure 24b: Probable positions of the collecting localities for the types of *Ctenochromis strigigena*: Matomondo and Mbusini, on a current satellite image.

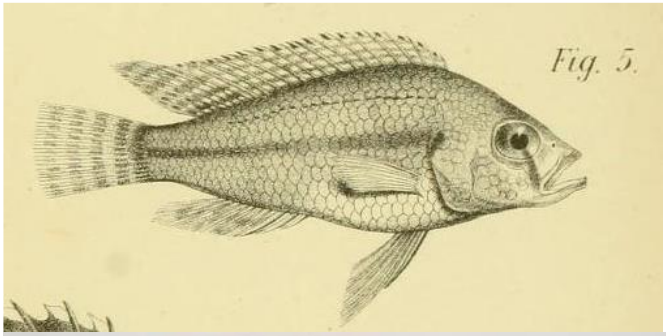

Figure 25: *Ctenochromis strigigena* original illustration in Pfeffer (1893)

Figure 26: Lectotype of *Ctenochromis strigigena* in Hamburg. ZMH 404

Figure 27: Paralectotype of *Ctenochromis strigigena* in London NHM 1899.2.27.2

Astatotilapia bloyeti: Synonymy of *Astatotilapia sparsidens* (Hilgendorf 1905)

Original description: Hilgendorf's description (in German) of *Tilapia (Ctenochromis) sparsidens* is reasonably comprehensive, but is not illustrated. Comments are made about small dark spots in the soft dorsal and caudal fins (typical for *A. bloyeti*) and the occurrence of 4-6 ocelli (anal fin eggspots, typical of male *Astatotilapia*).

Determination of type localities: Hilgendorf reports 20 specimens from Lake Manyara, 15 from a 'Graben' (ditch?) at Umbugwe, collected by Oskar Neumann, and one from Mjusi-Bach bei Jambe collected by von der Marwitz in 1897. The Manyara specimens were said to be from brackish water near river mouths, suggesting they may not have inhabited the highly saline main lake. Mbugwe is the current name of a secondary school near Manyara and a map of van Neumann's travels (1895) shows Umbugwe as the area to the south of Lake Manyara.

Examination of types: Four syntypes were examined at the Natural History Museum in London. They were in good condition and showed a strong resemblance in body shape to freshly collected *A. bloyeti* material.

Collections from the type locality: We did not find any haplochromines in catches from Lake Manyara in 2015 or 2017, despite examining many specimens of tilapiine cichlids (*Oreochromis amphimelas*). However, several specimens were collected from the nearby Lake Burungi and a few from an affluent stream of Lake Manyara at Moto wa Mtu. All of these conformed phenotypically to *A. bloyeti*, although males were generally a dark bluish olive colour with little yellow. One specimen from Lake Burungi was sequenced and included in the analysis of Svardal *et al.* (2020). This showed close affinities to other *A. bloyeti* material from the Pangani system and these formed a closely-related sister group to specimens from Kilosa and the Malagarasi.

Conclusion: *Astatotilapia sparsidens* is clearly very closely related to *A. bloyeti* and we could see no obvious phenotypic traits to justify separating these species. However, they are allopatric and show a sister group relationship in a tree based on whole genome sequences (Svardal *et al.* 2020). The 'sparsidens' group would seem to include material from the Pangani as well as the Manyara area. Pending more detailed morphological study, we feel it makes sense to retain the current status as a junior synonym of *A. bloyeti*.

Figure 28: Syntype of *Tilapia sparsidens* in London, NHM1905.7.25.32-35. Collecting locality given as Lake Manyara.

Figure 29: Young male *Astatotilapia bloyeti* from Moto wa Mbu (-3.375, 35.862), an afferent of Lake Manyara.

Figure 30: *Astatotilapia bloyeti* from Lake Burungi (-3.916, 35.861), near Manyara. Note the characteristic spots in the tail and soft dorsal and the thin red dorsal fin margin.

Figure 31: *Astatotilapia bloyeti* from Lake Kumba (-4.806, 38.622) in the Pangani system.

Astatotilapia bloyeti: Synonymy of *Paratilapia kilossana* Steindachner 1915

Summary: The name *Haplochromis (or Astatotilapia) kilossana* has recently been revived in the aquarium literature to refer to specimens collected in the Great Ruaha system (which we identify as *Astatotilapia gigliolii*). We believe that the correct type locality of *Paratilapia kilossana* is Kilosa on the Wami system and that *A. kilossana* is a junior synonym of *A. bloyeti*.

Original description: Steindachner's (1915) description of *Paratilapia kilossana* (in German) is thorough and well-illustrated, based on 2 adult male specimens. A source of confusion has stemmed from the description of the type locality, which was given as Kilosa and Kidatu on the Great Ruaha River.

Determination of the type localities: The original description uses names that are still in widespread use (Kidatu and Kilosa). Kilosa is a town on the Mkondowa River, a tributary of the Wami system and very close to the type locality of *A. bloyeti*. However, Kidatu is on the Great Ruaha River, part of the Rufiji system. Both specimens bear close resemblance to *A. bloyeti* (Figures 32-34) and this species has never been found in the Great Ruaha nor indeed anywhere else in the Rufiji system. When the types were examined in Vienna, none of the labels or catalogue entries mentioned Kidatu, only 'Mukondokwa Fluss', later misspelled as Mukondokiva (see Figures 35-36). This seems likely to refer to the Mkondowa River. It is unclear why Steindachner reported the collection locality as Kidatu. We feel the likeliest explanation is that immediately following the description of *Paratilapia kilossana* is the description of *Paratilapia vollmeringi*, which is also stated to have been collected at Kidatu. Steindachner suggests that this might be a female and that it might be conspecific with the males he had described as *P. kilossana*. It seems possible that he actually planned to describe all three specimens as types of *P. kilossana*, then changed his mind, but neglected to remove the reference to the collecting location for the *P. vollmeringi* specimen. Anyhow, it seems clear that the type locality of *P. kilossana* is Kilosa only, and this is also the type locality of *A. bloyeti.* As only a single haplochromine species has been recorded from the Wami River system, we confidently maintain the synonymy of *P. kilossana* with *A. bloyeti*.

Conclusion: *Paratilapia kilossana* is a junior synonym of *Astatotilapia bloyeti*.

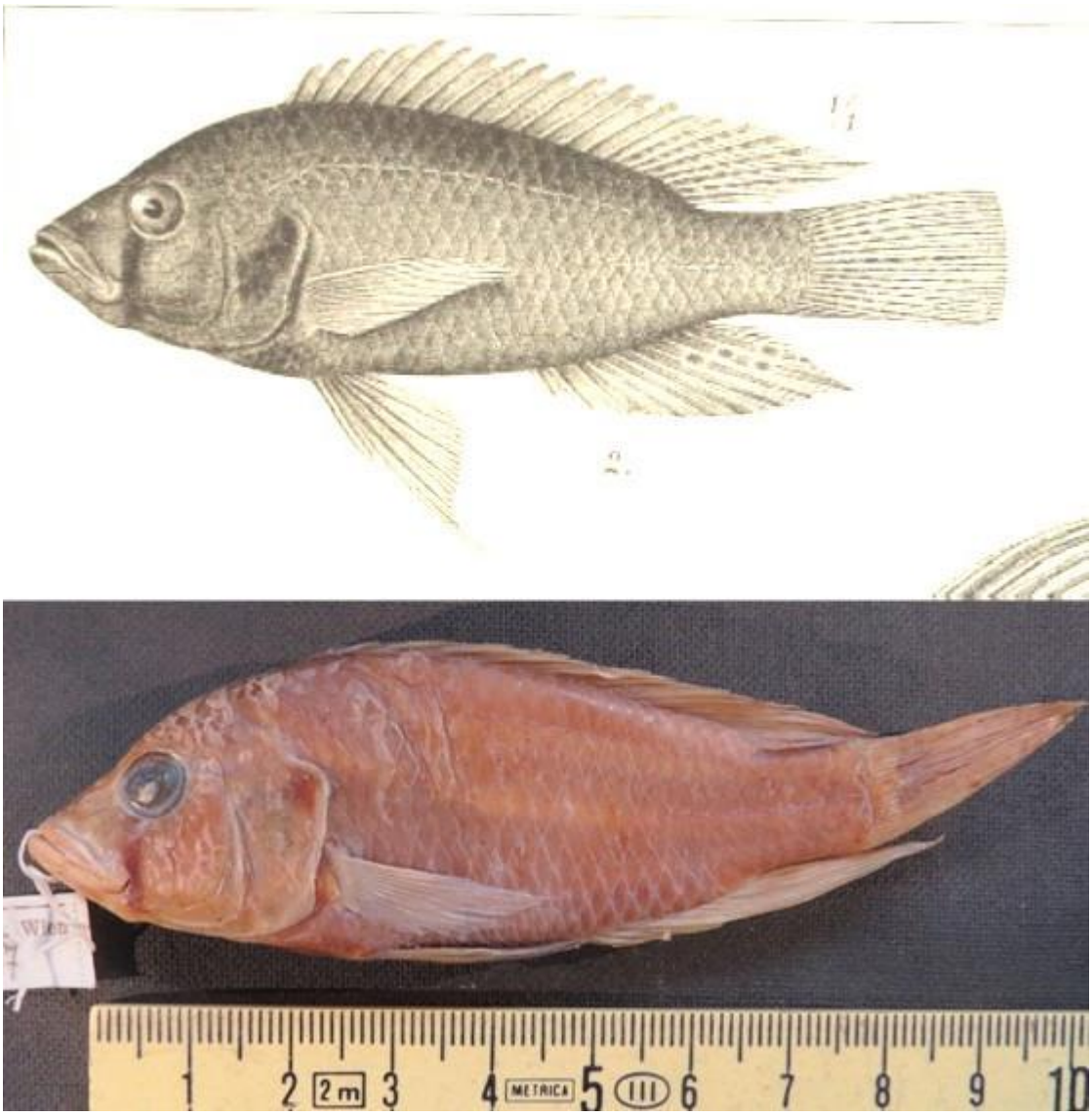

Figure 32: Original illustration of *Paratilapia kilossana* (above, from Steindachner 1915) and the same specimen (below, syntype 24567) photographed in 2017.

Figure 33: The second syntype of *Paratilapia kilossana* is very similar to the first.

Figure 34: Syntype of *Paratilapia kilossana*, showing small chest scales typical of *A. bloyeti*.

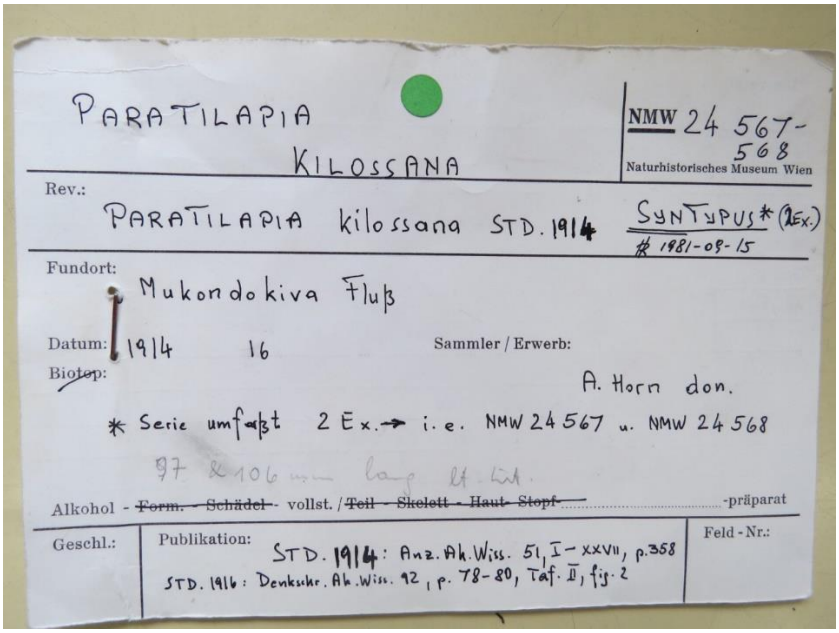

Figure 35: Card record at Vienna (Naturhistorisches Museum Wein) showing single collecting locality (Mukondokiva Fluss) for 2 type specimens (2 ex- i.e. NMW 24567 & NMW 24568). There is no mention of Ruaha or Kidatu.

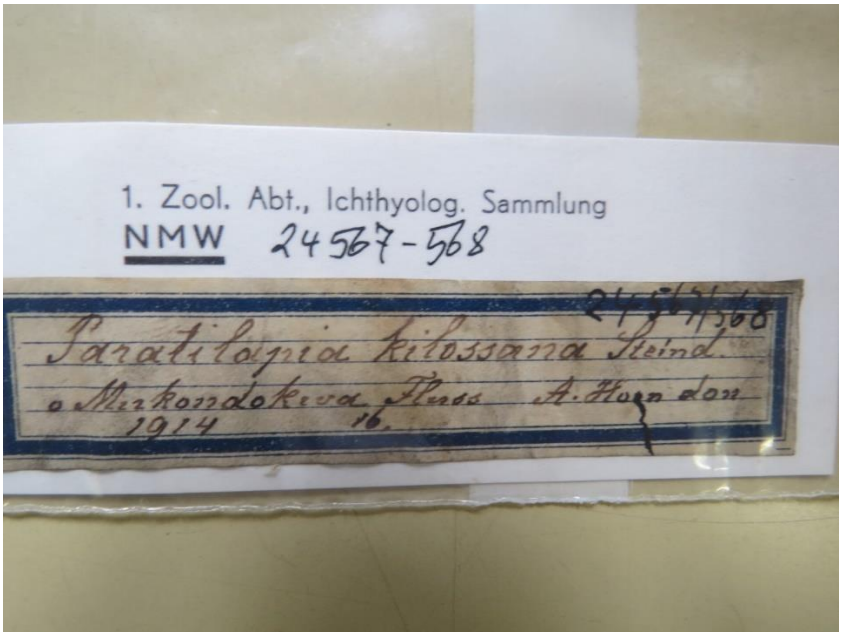

Figure 36: Original jar label preserved on rear of card record in Vienna, again clearly showing 2 catalogue numbers (24 567-568) but a single locality. It appears that the correct locality was Mukondokwa Fluss, but this was later transcribed as 'Mukondokiva', due to the tendency of the writer to miss out the middle horizontal stretch of letters (note also the 'u' after the initial 'M' and the 'n' just before the 'd'. There is no 'dot' above the supposed 'i' in '-iva', whereas it is clear in all other places in the line above. This error occurs only in the catalogue: Steindachner's description gives it as 'Mukondokwa Fluss bei Kilossa'.

Astatotilapia bloyeti: synonymy of *Astatotilapia paludinosa* Greenwood 1980

Original description: The original description is by Greenwood (in English) from 1980. It is very thorough and well-illustrated and based on a large number of specimens (56), but strangely lacks a detailed comparison of the species with the co-occurring "*Astatotilapia bloyeti"*. We now think he had the wrong species identified as *A. bloyeti*: we identify Greenwood's *A. bloyeti* as *Astatotilapia cf. stappersii* (Poll 1943) and his *A. paludinosa* as *A. bloyeti*. Greenwood's male *A. paludinosa* are described as having a yellow operculum, blue lips, dark red spots in the soft dorsal and tail fins, and a bright red margin to the dorsal fin- all consistent with *A. bloyeti* from Kilosa and elsewhere.

Type locality: Malagarasi swamps at Katare, Tanzania. Some paratypes are also from Uvinza, also on the Malagarasi in Tanzania.

Type material: We examined the holotype and several paratypes. They correspond well to *A. bloyeti*.

Collections from type locality: In 2016, we were able to collect numerous specimens from the Malagarasi, where we found phenotypes consistent with *A. bloyeti* as well those consistent with *A. stappersii*: the latter corresponded well to specimens collected by Greenwood in the 1950s and labelled as *A. bloyeti*. Whole genome sequences of both of these phenotypes was included in the study by Svardal *et al.* (2020). The '*A. paludinosa*' specimen clustered with other *A. bloyeti* material, in particular with material from Kilosa. Molecular analysis using ddRAD sequencing suggested that specimens from Lake Igombe on the upper reaches of a Malagarasi tributary as well those from Igogo and Mwamapuli dams near Lake Kitangiri all clustered with the lower Malagarasi ('paludinosus') specimens and not with the Lake Burungi ('sparsidens') specimens (Hsu, 2019).

Collecting localities: Malagarasi at Uvinza (-5.1019, 30.396) 30 July 2016; Lake Sagera (-5.189, 31.067) 31 July 2016; Upper Malagarasi (-5.094, 30.848) 1st August 2016; Lake Igombe, Malagarasi catchment (-4.854, 32.745) 2 August 2016; Igogo Dam, near Lake Kitangiri (-4.289, 33.789) 2 August 2016; Mwamapuli dam, near Lake Kitangiri (-4.356, 33.877) 2 August 2016.

Conclusion: *Astatotilapia paludinosa* Greenwood 1980 is a junior synonym of *A. bloyeti.*

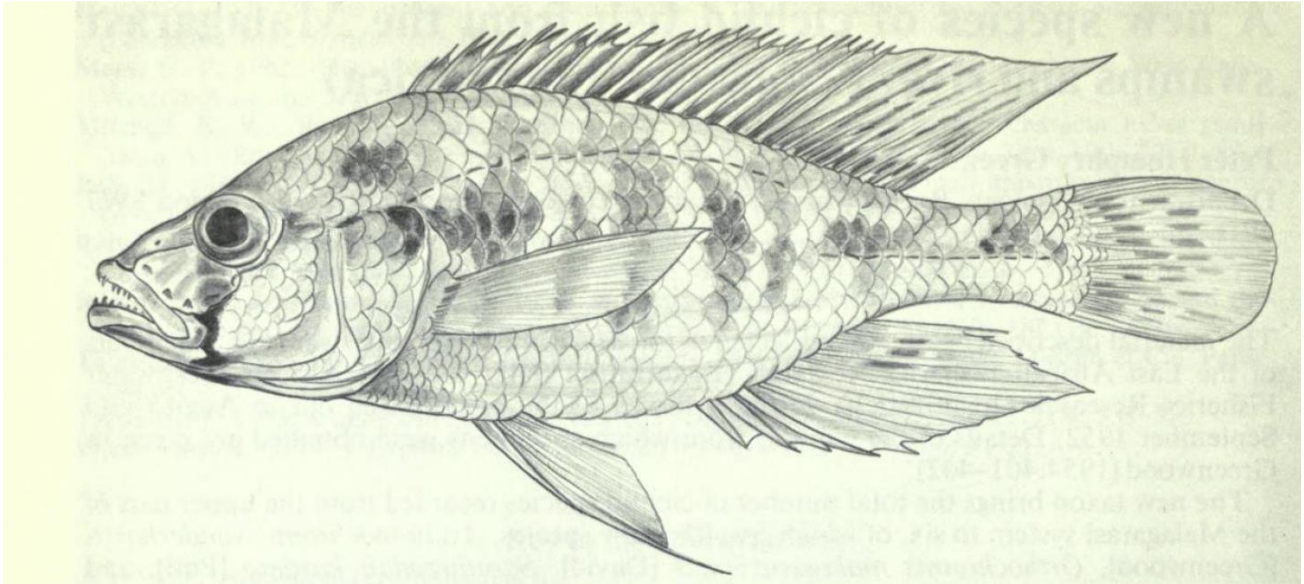

Figure 37: Original drawing of the type of *Astatotilapia paludinosa* (from Greenwood 1980b)

Figure 38: Paratypes of *A. paludinosa* (NHM 1956.7.9.266-290) correspond well to the phenotype of *A. bloyeti*.

Figure 39: *Astatotilapia bloyeti* male from the mouth of the Malagarasi River at Uvinza in July 2016.

Figure 40: *Astatotilapia bloyeti* male from Lake Sagera in July 2016.

Figure 41: This *A. bloyeti* collected from an upstream tributary of the Malagarasi about 135km east of Kigoma (-5.094, 30.848) in July 2016 shows the typical concavity above the eye of larger males, and concentration of dark orange eggspots in the posterior half of the anal fin.

Figure 42: This much smaller *A. bloyeti* from the same sample as the specimen in figure 41 shows the straight head profile typical of smaller specimens, and the yellow-tinted anal fin and lower caudal fin typical of females and immature males (e.g. figure 16).

Figure 43: *Astatotilapia bloyeti* collected in July 2016 from Lake Igombe (-4.854, 32.745), an impoundment on the Malagarasi system. This freshly collected large male is rather pale but illustrates the species-typical stripes and spots on the soft dorsal and caudal fins, the posteriorly positioned dark orange eggspots and the commonly-seen flush of yellow-orange on the operculum and lower flanks.

Figure 44: *Astatotilapia bloyeti* from the Igogo Dam (-4.289, 33.789), about 50km west of Lake Kitangiri in August 2016. This freshly collected male is very pale but again illustrates species-typical markings on the fins and body.

Figure 45: A small male *Astatotilapia bloyeti* freshly collected from Mwamapuli dam (-4.356, 33.877) near Lake Kitangiri in August 2016 shows particularly vivid yellow colour and rather large eggspots.

Figure 46: A specimen from the same catch as the specimen in figure 45, showing the colour change after euthanasia and pinning.

Astatotilapia calliptera (Günther 1894)

Summary: A valid species, found throughout Lake Malawi and its catchment, the Ruvuma system including Lakes Chilwa and Chiuta, the Shire River, the Zambezi and various Indian Ocean afferents in Mozambique. Junior synonyms include *Tilapia swynnertoni* Boulenger 1907, *Haplochromis centropristoides* Nichols and LaMonte 1931, *Neochromis simotes nyassae* Borodin 1936.

Original description: as *Chromis callipterus*. The description (in English) includes an excellent illustration (Plate LVa) of a mature male showing prominent dark stripe below the eye and a number of ocellated spots on the anal fin.

Determination of type locality: Günther (1894a) stated that most of the specimens he examined for his 1894 paper were collected by Mr Alexander Whyte in November 1892 when he visited Fort Johnston (present-day Mangochi) on the Upper Shire River. However, one of the specimens was collected by J.A. Williams from somewhere in Lake Nyasa (= Lake Malawi), and another one was labelled as being from Zomba, which is in the catchment of Lake Chilwa. Based on our designation of the Lectotype below, the type locality is fixed as southern Lake Malawi/ Upper Shire River.

Types examined: Lectotype: NHM 1893.11.15.1-4, 75.5mm SL, Lake Nyasa and Upper Shire, collected by H.H. Johnston; Paralectotypes: NHM 1893.1.17.4, 1 specimen 111.5mm SL, Lake Nyasa, collected by Mr J.A. Williams; NHM 1893.11.15.5, 1 specimen 75.3mm SL, Zomba, Nyasaland, collected by H.H. Johnston.

We exclude the following specimens: NHM 1893.11.15.1-4, 2 specimens 45.5, 49 mm SL, Lake Nyasa and Upper Shire, collected by H.H. Johnston.

We designate the 75.5mm SL specimen collected from the Johnston collection from 'Lake Nyasa and Upper Shire River' as the lectotype (Figure 48). This does not appear to be the figured specimen (Figure 47): that seems to be the specimen from Zomba (Figure 50). However, while it is recommended to designate the illustrated specimen as the lectotype where possible, it is also good practice to be confident of the type locality. In a footnote to Günther's (1894a) paper containing the description of *Chromis callipterus*, he notes that Zomba is not in the Zambezi catchment, but in the catchment of Lake Shirwa (= Lake Chilwa). This would lead us to have confidence that the specimens presented by Johnston and labelled 'Zomba' would be from the Chilwa catchment, were it not for the fact that some of the material of *Chromis tetrastigma* Günther 1894 is also labelled as coming from Zomba. This species, now known as *Otopharynx tetrastigma*, is a Lake Malawi catchment endemic and it has never been recorded from the Lake Chilwa catchment (Eccles & Trewavas 1989; Tweddle 1979). However, like *A. calliptera*, it does penetrate quite far down the Middle Shire River (Tweddle *et al.* 1979), which could conceivably have been visited from Zomba more readily than the Upper Shire at Mangochi. The catalogue of the London Natural History Museum also gives 'Zomba' as the collecting locality for specimens presented by Johnston at the same time of *Oreochromis (=Chromis) squamipinnis* and *Protomelas (=Chromis) kirkii*, again Lake Malawi species likely to penetrate into the middle Shire and not known from the Lake Chilwa catchment. Thus, we lack confidence that a recorded locality of Zomba necessarily refers to the Chilwa catchment, and so the provenance of this specimen must be treated with caution. By contrast, the specimens recorded as being collected from Whyte's expedition to Mangochi are all plausible

members of the Upper Shire River fauna, or at least the southern part of Lake Malawi, with which it shares the majority of the species.

The 111.5mm specimen collected by Williams (Figure 49; NHM 1893.1.17.4) has a more prominent nuchal hump and only showed 2 anal fin ocelli, making it unlikely to be the figured specimen. It was also in relatively poor condition at the time of examination, with a damaged caudal fin, open mouth and expanded branchiostegal (throat) membranes. The Zomba specimen (Figure 50; NHM 1893.11.15.5) was badly bent and has rather thickened lips.

We consider that the two smallest types (45.5 and 49mm SL specimens: Figures 51-52) are not conspecific with the rest of the material. These specimens have closely-packed columnar bicuspid teeth, in contrast to the lectotype and other specimens of *A. calliptera* in which the outer teeth are more widely-spaced and have markedly narrower bases, spreading widely into two divergent cusps (Figure 53). The small type specimens also have rather more rounded snouts than typical for *A. calliptera*. Finally, they have a single eggspot at the posterior margin of the anal fin. They appear to be ‘mbuna’ specimens, possibly of the genus *Tropheops* Trewavas 1984.

Collections at the type locality: *Astatotilapia calliptera* is well-known from many recent studies (e.g. Konings 2016; Nichols *et al.* 2015; Parsons *et al.* 2017; Peterson *et al.* 2017; Tyers & Turner 2013) and appears to be more or less ubiquitous in shallow weedy areas in Lake Malawi and its catchment. A striking population with blue-grey adult males is reported from Chizumulu Island (Konings 2016), but other populations seem phenotypically quite similar, with males showing a spectacular multi-coloured – largely golden yellow - breeding dress (Figure 54-58). The species is clearly distinguishable from *A. bloyeti* in body shape and male colours, and is genetically divergent, being more closely related to the endemic Lake Malawi haplochromines than to other *Astatotilapia* (Malinsky *et al.* 2018; Svardal *et al.* 2020). It has also given rise to a number of phenotypically distinctive populations in the Tanzanian crater lakes within the Lake Malawi catchment (Turner *et al.* 2019).

Conclusion: *Astatotilapia calliptera* is a valid species, with the type locality fixed through designation of the lectotype as Southern Lake Malawi/Upper Shire River.

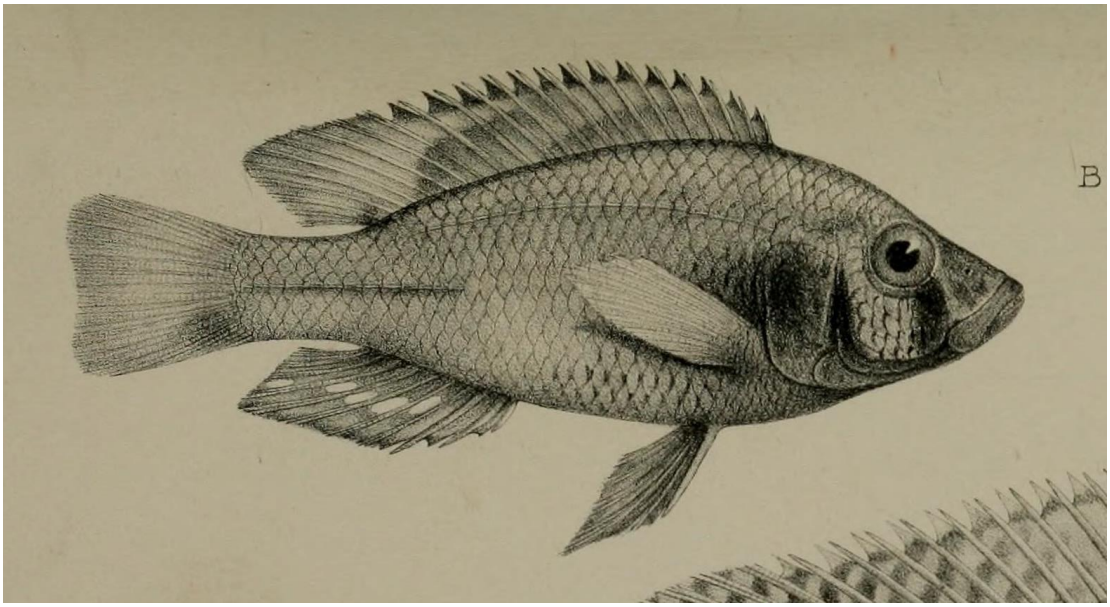

Figure 47: *Astatotilapia calliptera* from the original description by Günther (1894a). Note the acutely pointed snout and long row of eggspots.

Figure 48: Lectotype of *Astatotilapia calliptera*. NHM 1893.11.15.1-4: the largest specimen of 75.3mm SL has a row of 4 anal fin spots, but lacks the 5th spot at the fin margin seen in the figured specimen.

Figure 49: The Williams specimen, NHM 1893.1.17.4, has a more prominent nuchal hump, with only 2 anal fin ocelli visible, making it unlikely to be the figured specimen.

Figure 50: *Astatotilapia calliptera*: the type specimen from Zomba (NHM 1893.11.15) has a row of 4 anal fin spots, but an additional smaller spot near the fin margin, as shown on the illustration in Günther's (1894a) description.

Figure 51: This small (49mm SL) specimen from the type series appears to be an ‘mbuna’. NHM 1893.11.15.1-4. The upper jaw teeth are tall, closely-packed and have a broad flat major cusp, with an inconspicuous minor cusp.

Figure 52: Another specimen from the type series that appears to be an ‘mbuna’ (45mm SL), probably *Tropheops sp.* NHM 1893.11.15.1-4. The upper jaw teeth resemble those of the other small specimen, but the body is rather deeper.

Figure 53: The upper jaw teeth of the lectotype NHM 1893.11.15.1-4, 75.5 mm SL, are shorter and more widely-spaced than those of the two smaller types. The major cusp is pointed, rather than flat, and the minor cusp is relatively large and pointed. This is the more typical condition for *A. calliptera*.

Figure 54: Adult male *A. calliptera* from Kamuzu Dam, near Lilongwe, 9 April 2004.

Figure 55: *Astatotilapia calliptera* male from Lake Chilingali, Malawi, July 2004.

Figure 56: *Astatotilapia calliptera* female from Mbaka River, Tanzania, June 2011.

Figure 57: *Astatotilapia calliptera* male from the Ruvuma river catchment, Tanzania, 5th September 2012.

Figure 58: *Astatotilapia calliptera* male from Lake Chidya, Tanzania, 17th August, 2013.

Astatotilapia calliptera: synonymy of *Tilapia swynnertoni* Boulenger 1907

Original Description: by Boulenger (1907, in English) is brief and based on three specimens. There is no illustration, but the male is described as having three yellow spots on the anal fin. There is no comparison made with *A. calliptera*. An illustration of a type subsequently appeared in Boulenger's (1915) catalogue (Figure 59).

Type locality: Idunda River, flowing into Lower Buzi River, Mozambique.

Types examined: Over the last few years, all type material at the Natural History Museum in London was found to be on loan in South Africa. Jubb (1967) regarded *A. swynnertoni* as a synonym of *A. calliptera* but did not give any reasons. This was followed by Skelton (1993). Greenwood (1979) stated that he felt that *A. swynnertoni* was a distinct species, but again gave no explicit reason. However, he did state that *A. swynnertoni* has 6-8 scales on the posterior part of the upper lateral line separated from the dorsal fin base by less than 2 equal-sized scales, compared to 1-4 posteriormost scales in other species. However, he did not clearly state what material he examined, but stated that he examined all material of all taxa he discussed that was at the London Natural History Museum. At the time of writing, this collection did not list any specimens labelled as *A. swynnertoni* apart from the three types, so we may presume this was based on a relatively small sample, leaving open the possibility that this is a character that varies within or between populations. The collection of specimens labelled as *A. calliptera* is extensive but does not include any material from Mozambique that might be referrable to *A. swynnertoni*. A recent article (Morgernstern 2011) cited Greenwood in support of the distinctiveness of the species, but also suggested that *A. swynnertoni* exhibited a pattern of 6-7 relatively broad vertical bars compared to the 9-12 thinner bars shown by *A. calliptera.* This opinion does not seem to have been based on examination of the types nor on new materials, but rather on the publications by Boulenger (1907, 1915) and Greenwood (1979) and photographs appearing in Joyce *et al.* (2011). Our examination of recent photographs of specimens collected from Central to Southern Mozambique suggests that both of these traits are variable within populations and are thus not diagnostic (Figures 60-65). Male breeding colours and general morphology seem to correspond well to typical *A. calliptera* and thus we cannot justify maintaining them as distinct taxa.

Collections from the type locality: Specimens have been collected from the Buzi River by R. Bills from SAIAB. One of these was incorporated into a molecular study by Joyce *et al.* (2011). Analysis of nuclear sequence data (AFLP) placed the Buzi River specimen as closely related to specimens from the Ruvuma and Lugenda Rivers in Mozambique, but this group in turn was nested within a clade of other specimens from Lake Malawi and its catchment as well as from Lake Chilwa. Although full genome sequences are not yet available for Mozambican populations, the Ruvuma population is clustered with those from Lake Chilwa; the position of these in relation to the Lake Malawi specimens is unclear (Malinsky et al. 2018). Therefore, neither molecular nor morphological traits support a separation of *A. swynnertoni* from *A. calliptera*.

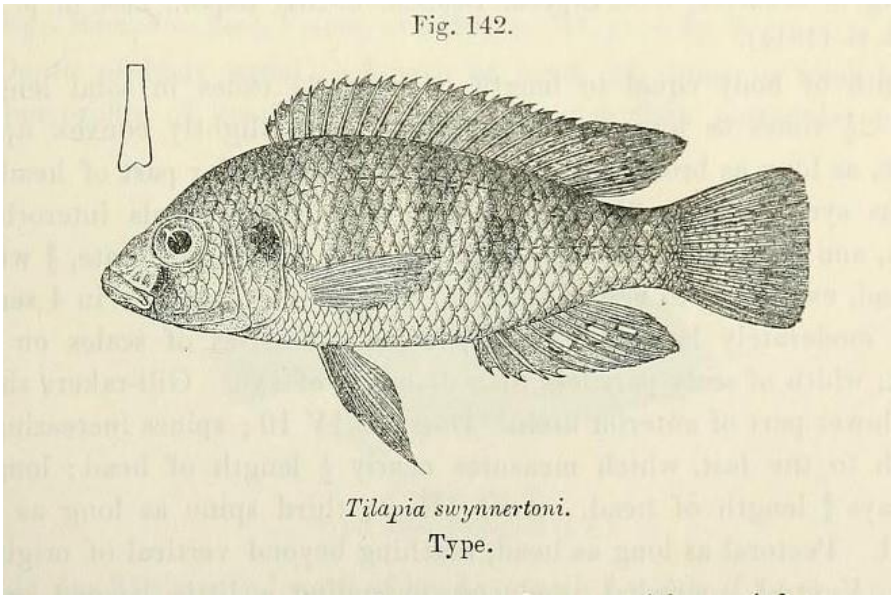

Figure 59: Type of *Tilapia swynnertoni* as depicted in Boulenger (1915). The body shape and markings are consistent with an adult male *A. calliptera*, although the barring on the flanks is unusually prominent and the bars thick.

Figure 60. Specimen of *Astatotilapia calliptera* collected by Rob Palmer 26 January 2016 from Maimelane, Inhassoro, Mozambique (-21.698, 35.163: posted on iNaturalist, some rights reserved: CC-BY-NC-SA). This site is around 200km to the south of the mouth of the Buzi River, and so would be expected to be more closely related to the population described as *A. swynnertoni* than to Malawian *A. calliptera*.

Figure 61. Specimen of *Astatotilapia calliptera* collected by Rob Palmer 18 January 2016 from Govuro, Mozambique (-21.295, 34.792: posted on iNaturalist, some rights reserved: CC-BY-NC-SA). This site is also well to the south of the Buzi River , and so would be expected to be more closely related to the population described as *A. swynnertoni* than to Malawian *A. calliptera*.

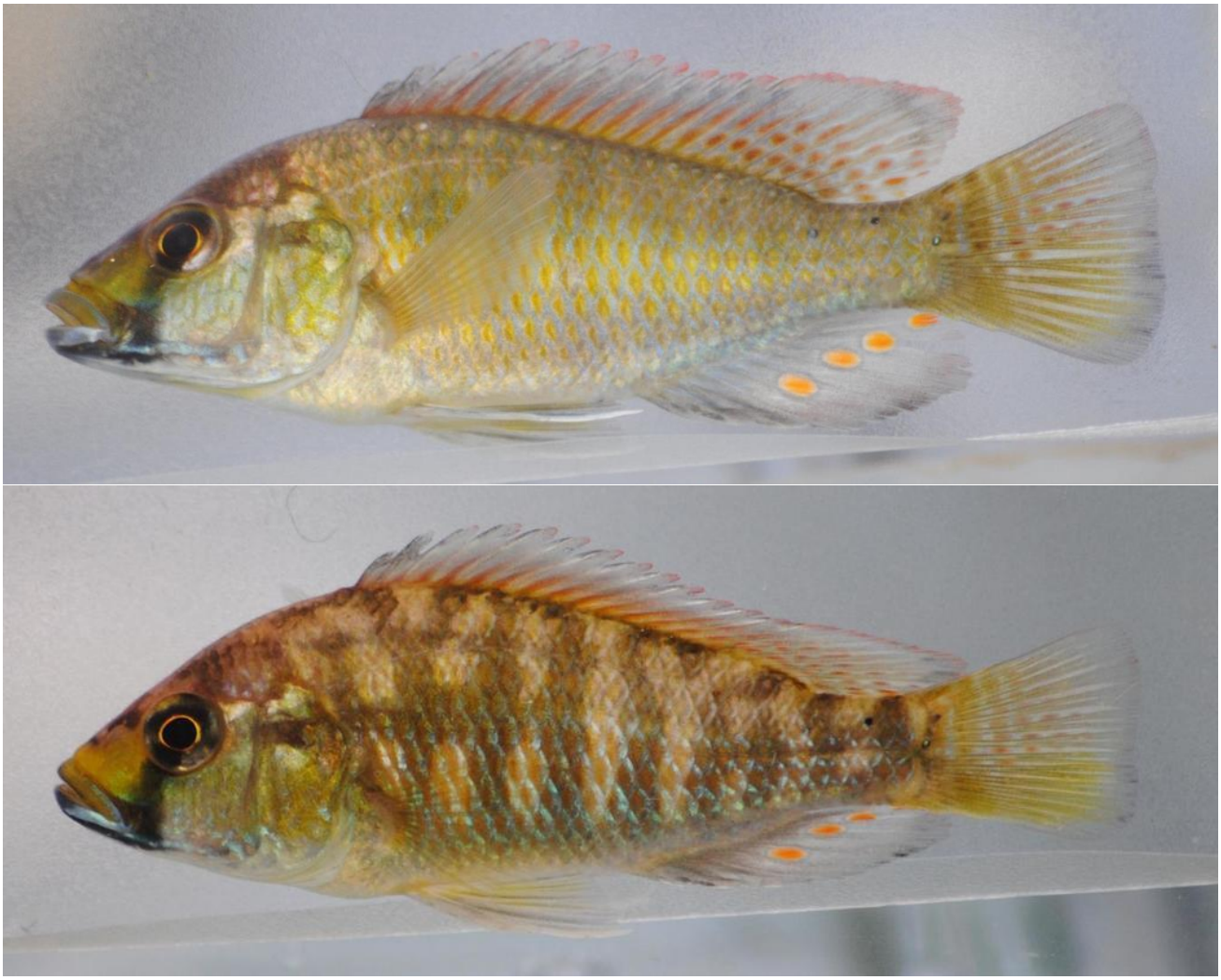

Figure 62. Specimens of *Astatotilapia* collected by Rob Palmer 4th April 2012 from Muanza District at the edge of the Gorongosa National Park, Mozambique (-18.817, 34.741: posted on iNaturalist, some rights reserved: CC-BY-NC-SA). This site is about 118km north of the mouth of the Buzi River and lies within the Pungwe catchment- the Pungwe shares an estuary with the Buzi, near the city of Beira, so these are likely to represent the population described as *A.*

swynnertoni. The lower specimen shows 9-10 dark vertical bars, not consistent with the idea of *A. swynnertoni* being distinguished from *A. calliptera* by having fewer, broader flank bars. Collecting details and morphology agree with the 2 largest specimens of specimens SAIAB 186503, which we have examined.

Figure 63. Posterior upper lateral line scales are generally closer to the dorsal fin in southern Mozambican specimens of *Astatotilapia calliptera*, as seen in this photo from a specimen collected from Muanza District at the edge of the Gorongosa National Park, Mozambique (lower specimen in figure 62). The first row of scales above the upper lateral line is numbered, starting at the posteriormost scale, with the second row of comparable-sized scales labelled 9a.

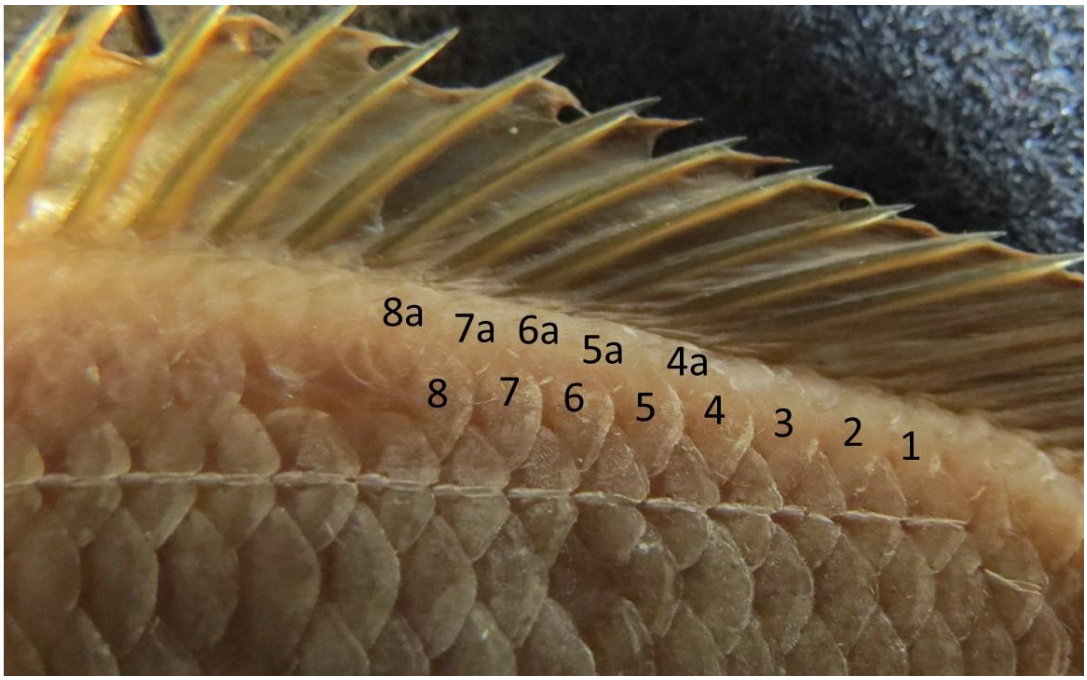

Figure 64. Posterior upper lateral line scales are generally further away from the dorsal fin in the lectotype of *Astatotilapia calliptera*, using a similar numbering system, the second row of comparable-sized scales could be scored as starting for the 3rd or 4th last scale row in the upper lateral line.

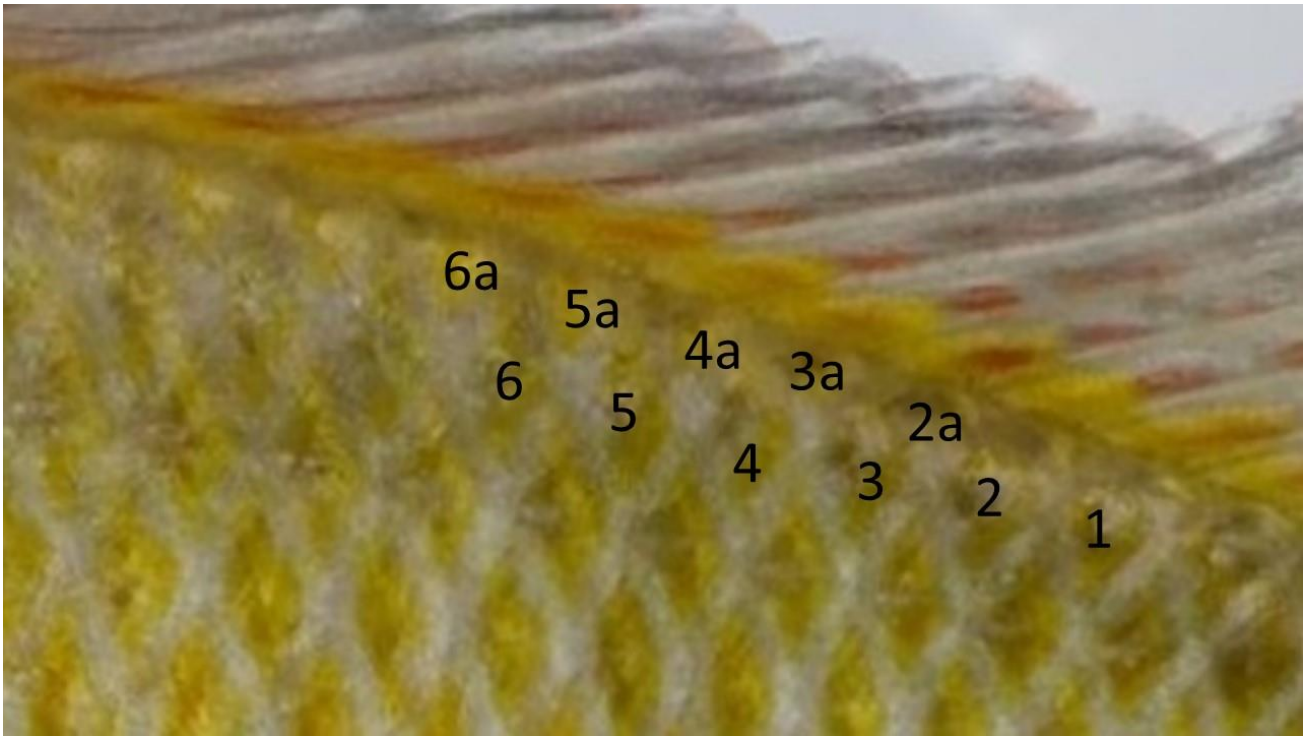

Figure 65. The Inhassoro specimen shown in Figure 60 above appears to have 2 relatively large scales between the lateral line and dorsal fin extending as far back as the 2nd last (or even the last?) pored scale, despite being from a very southern location. This suggests that the number of scale rows between the lateral line and dorsal fin is not a diagnostic trait for *A. swynnertoni*, but is likely to be variable within populations. Notably, this specimen looks like a large relatively deep-bodied male.

Astatotilapia burtoni (Günther 1894)

Summary: A well-known valid species endemic to Lake Tanganyika and its catchment.

Original Description: as *Chromis burtoni* Günther 1894. The figured specimen displays a clear row of large eggspots and strong dark markings on the head (figure 66).

Determination of type locality: Lake Tanganyika catchment. Boulenger (1915) gives the type location as Ujiji, which appears to be part of present-day Kigoma on the Tanzanian shore of Lake Tanganyika.

Type Material Examined: The single type specimen (BMNH 1889.1.35.12) was examined. It is small and lacked any melanic markings. However, the illustration in Günther's (1894b) description and associated text report pigment elements that not currently visible, presumably faded. In particular, the strong dark horizontal mark behind the eye and strong forehead stripes are characteristic of *A. burtoni* (figure 67) and not generally visible on other haplochromines with a similar body shape and dentition known from the area, such as *A. bloyeti*, *A. stappersii* and the undescribed *A.* sp.'chipwa'. The illustration also shows a single row of very large eggspots close to the body and beginning on the first anal ray. This pattern is very different from that shown by the other three species, where the eggspots are generally smaller and situated behind the 5th anal fin ray. The eggspots of the Günther illustration are, however, entirely consistent with males of the taxon presently recognised as *A. burtoni* (see figure 66).

Collections at the Type Locality: We were able to collect a number of specimens from around Kigoma in 2016 near to the type locality and exhibiting similarities with the type in key traits, such as eggspot size and distribution (figure 68).

Conclusion: *Astatotilapia burtoni* is a valid species distinct from *A. bloyeti* and *A. calliptera*, and fits with the current identification of specimens used in numerous research and aquarium fish publications (e.g. Paquet *et al.* 2018 and references therein).

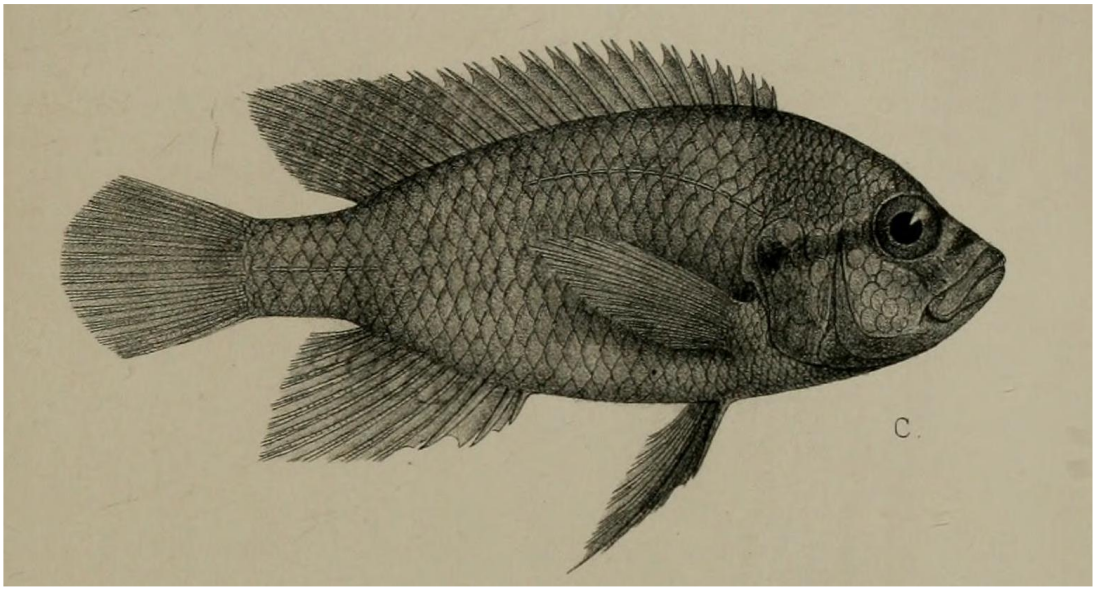

Figure 66. Original illustration of the type of *Chromis burtoni* in Günther's description (1894b), illustrating the extensive melanic head markings (fig 67), dorsal fin spotting (figs 67-68) and long row of anal fin eggspots (fig 68) seen on live fish.

Figure 67. *Astatotilapia burtoni* males in an aquarium, demonstrating the degree of colour polymorphism in this species, as well as the strongly developed melanic head markings. Photo by Russell D. Fernald and Sabrina S. Burmeister, CC-BY-2.5.

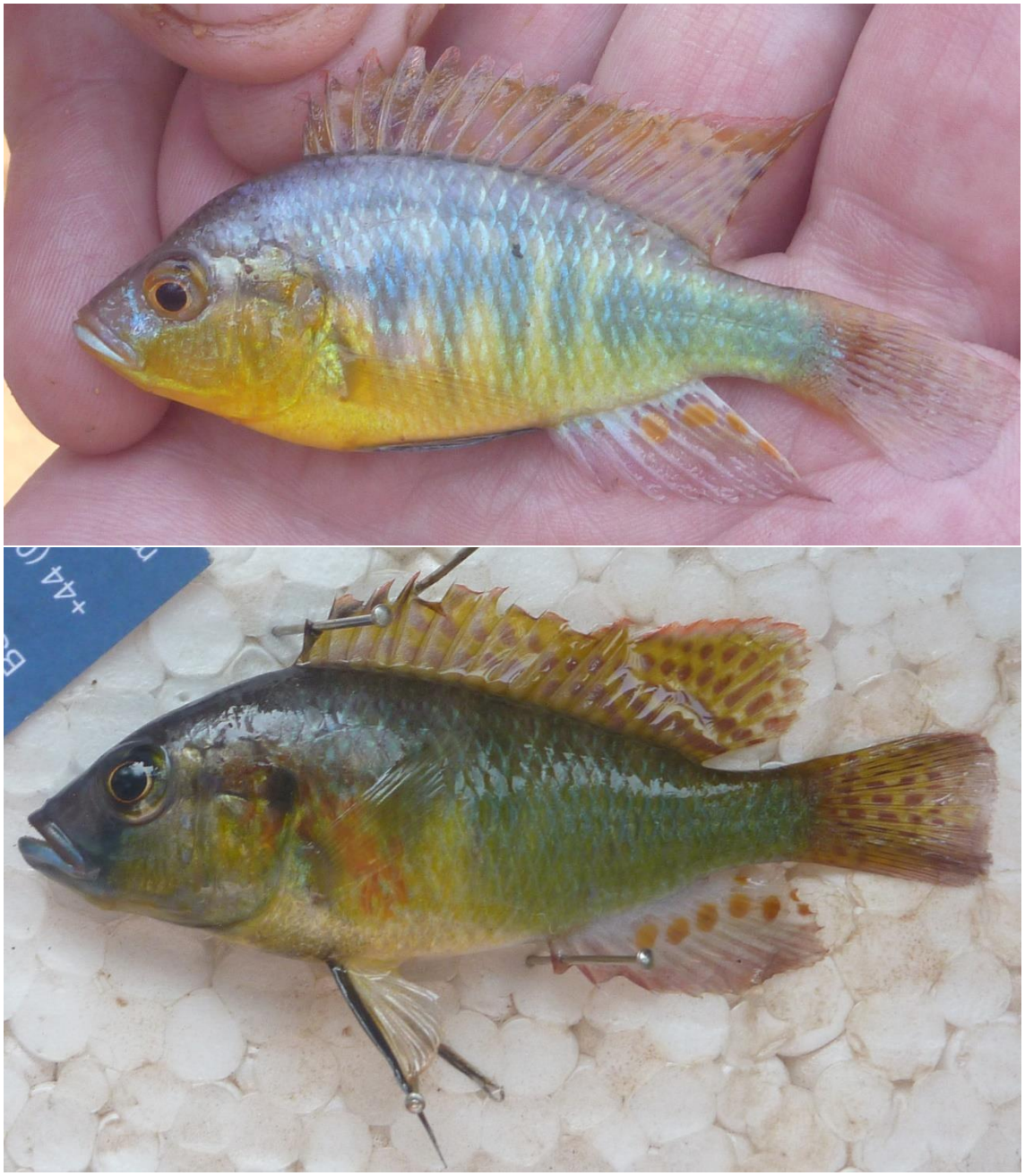

Figure 68. Adult male *Astatotilapia burtoni* from Kigoma, 29th -30th July 2016. The upper specimen is a brightly coloured yellow morph individual, but it lacks the melanic markings normally shown by live fish in aquaria. The lower specimen shows more elements of the species' typical male breeding pattern, with the dark eye stripe, orange area behind the operculum and dark red spots in the spinous as well as the soft dorsal fins.

Astatotilapia gigliolii (Pfeffer 1896)

Summary: A valid species, widely distributed. Type locality is the 'southern' Ruvu River near Bagamoyo, and it appears to be the only haplochromine in this system. Co-occurs with *Astatotilapia calliptera* in the Ruvuma system and in Lakes Chilwa & Chiuta and with other haplochromine species in the Rufiji system, but apparently never with *A. bloyeti*. *Paratilapia vollmeringi* Steindachner 1915 and *Astatotilapia tweddlei* Jackson 1985 are regarded as junior synonyms.

Original Description: As *Hemichromis gigliolii*, by Pfeffer (1896), based on a single specimen of 84mm (ZMB 13673). The catalogue in Berlin gives the name as *Chromis gigliolii* and the length as 81mm. Judging by the photograph, this is Total Length (figure 68). The description, in German, is quite detailed, but is not accompanied by an illustration. The description includes many key features, such as the dark brown spot at the base of many of the flank scales. Comments on the ocellated eggspots in the anal fin, dark pelvic fins and dark stripe beneath the eyes suggest the type was an adult male. At the time of writing, these markings were no longer visible on this type specimen (figure 68).

Determination of Type Locality: Pfeffer gave the collecting locality as 'Kingani-Fluss', collected by Stuhlmann. The Kingani is an alternative name for the (southern) Ruvu. The catalogue entry for the Berlin Natural History Museum states that it was collected at Dunde at -6.468, 38.842, on 28 January 1894. These co-ordinates place the type locality as close to present-day Mtoni, on the main highway west from Bagamoyo, on the Ruvu River (figure 69). The map accompanying Stuhlmann's (1890) report shows his expedition crossing the Kingani river at Mtoni Fort, a little downstream of 'Dunda'.

Collections from the Type Locality: Our collection from the Ruvu near to Bagamoyo (-6.443, 38.845, close to the type locality) on 19th August 2015 did not yield any haplochromines, but we obtained specimens from two further sites on the 'southern' Ruvu River: one on the lower reach of the Ruvu not far from Dar Es Salaam (December 2011), and the other in the Mindu Dam near Morogoro (January 2014). In overall body shape these are consistent with the type, although some are smaller individuals and thus predictably more slender. Adult males were generally yellowish and consistently had dark spots on the large flank scales behind the head, particularly on the lower half of the body. The dorsal fins had dark reddish spots on both spinous and rayed sections, those on the spinous dorsal forming 1 or 2 rows. Most specimens had large ocellated spots on the posterior part of the anal fin, generally continuing forwards as a single row almost to the spinous area. Melanic markings on the males were generally restricted to a near vertical dark stripe through the eye and perhaps a darkening of the anteriormost part of the dorsal fin, with no sign of a second vertical stripe on the operculum or bars across the snout or between the eyes. The head profile was generally straight, with no sign of a nuchal hump even in the largest males. The chest scales were somewhat larger than those of most other species, such as *A. bloyeti* and *A. calliptera*. In addition, field photographs and subsequent illustrations of live specimens in the aquarium have been posted illustrating what appears to be the same species collected from the Ruvu catchment near Kimbozo Forest (figure 73). The combination of body shape, eggspot form and male breeding dress are clearly distinct from all previously described species from the region (*A. bloyeti, A. calliptera, A. burtoni*), so we have no hesitation in regarding *Astatotilapia gigliolii* as a valid species. So far as we can tell, every haplochromine cichlid collected from the Southern Ruvu/Kingani system can be assigned to

this species: indeed in most samples, the only other cichlid collected was *Oreochromis urolepis*. The exception was in the Mindu dam, where we also found *Coptodon rendalli*, *Oreochromis niloticus* and *O. leucostictus* as well as a number of *Oreochromis* hybrids. These are thought to have been introduced into the reservoir (Shechonge *et al.* 2019).

Figure 68. Type of *Hemichromis gigliolii* from Berlin.

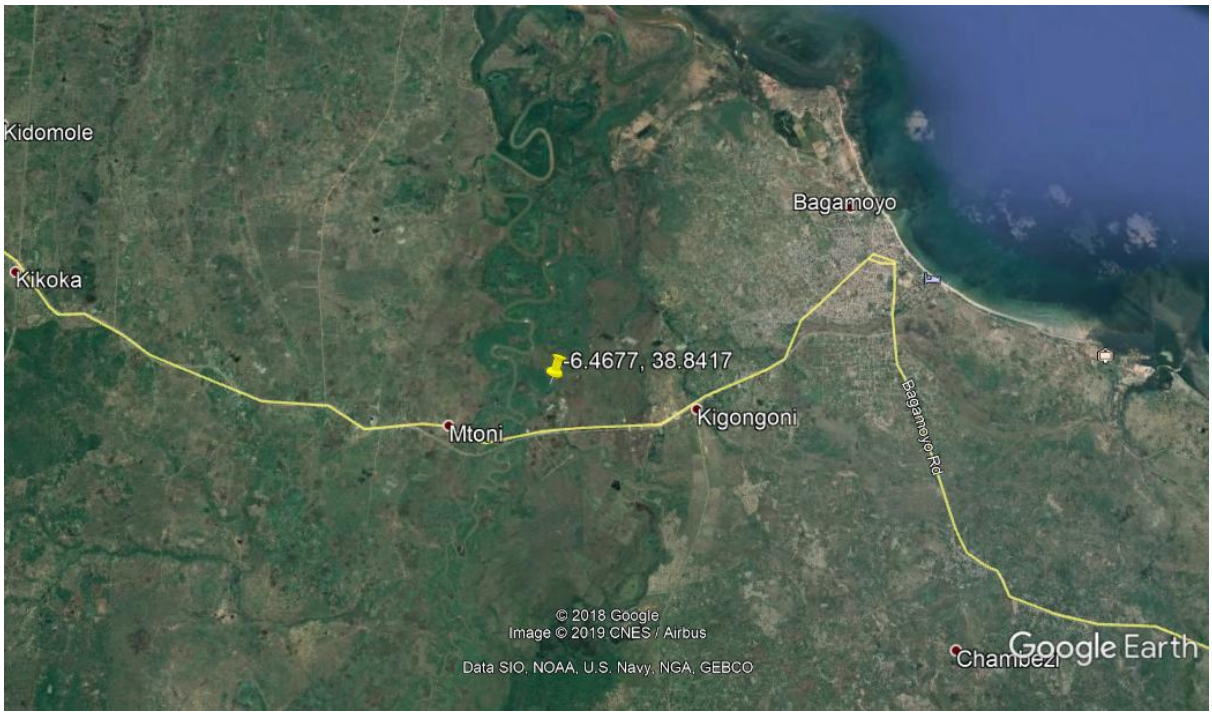

Figure 69. Co-ordinates for the type locality of *Hemichromis gigliolii*, on the 'southern' Ruvu River near Bagamoyo, indicating that the nearest present day town is Mtoni on the Bagamoyo to Msata Road.

Figure 70. This close-up of Stuhlmann's map (1890) shows the location of crossing the Kingani River. The location labelled 'Dunda' presumably corresponds to 'Dunde' on the Berlin label. Locations Mtoni Fort and Kikoko probably correspond to present-day Mtoni and Kikoka in the satellite map above. The river meanders look fairly similar. It suggests Stuhlmann's route may have been largely the same as the present main highway in the area.

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Figure 71: *Astatotilapia gigliolii* non-breeding male (left) from lower reaches of the 'southern' Ruvu River system near the A7 Dar-Morogoro Road between Kwalaza and Mlandizi, 2 December 2011. These individuals were collected from a floodplain pond (right) near the river at -6.698, 38.703, approximately 28km from the type locality at Mtoni. The river here is slow-flowing and meandering, and the elevation is only about 20m above sea level, and there seem to be no habitat barriers between the river here and at Mtoni. The relatively small anal fin eggspots suggest an immature male, but the forward extension of the dorsal fin spots into the spinous area and the dark spots on the flank scales are both typical of *A. gigliolii*.

Figure 72: *Astatotilapia gigliolii* males from Mindu Dam, Morogoro, on the 'southern' Ruvu River, January 2014. These illustrate the characteristic dark spots at the bases of the larger flank scales, and in the lower image, show the long row of anal fin eggspots on the proximal part of the fin and the prominent spotting on the spinous part of the dorsal fin.

Figure 73: *Astatotilapia gigliolii* male from near the Kimbozo forest, Morogoro District in the Ruvu catchment (-7.142, 37.679), photographed by Martin Grimm (iNaturalist, some rights reserved CC-BY-NC). Both images show the long row of large eggspots on the anal fin typical of *A. gigliolii*. The upper image also shows the characteristic golden colour, dark eye stripe, dark red dorsal fin spots in spiny as well as soft dorsal areas and dark spots on most of the flank scales of adult males of this species.

Astatotilapia gigliolii: Synonymy of *Paratilapia vollmeringi* Steindachner 1915

Summary: *Paratilapia vollmeringi* Steindachner 1915, described from the Great Ruaha River on the Rufiji system, is considered a junior synonym of *Astatotilapia gigliolii*. This species recorded from a number of sites from Kidatu downstream.

Original Description: The species was described as *Paratilapia vollmeringi* by Steindachner (1915) in the same paper as he described *P. kilossana*. The description (in German) is long and detailed and accompanied by an excellent illustration (Fig. 75). However, it is based on a single specimen of 83mm SL: Steindachner speculates that it is a female, but the elongation of the pelvic fins suggests it might be a male (Fig. 74). The abdominal cavity of the specimen had not been opened when the specimen was examined in 2017. The specimen has relatively large chest scales (Fig. 76), is slender with small head and jaws and has a short pectoral fin which ends far in front of the vent.

Determination of Type Locality: Steindachner states the collecting locality as the Ruaha at Kidatu. This is easily located, as there is a major hydro-electric dam on the Great Ruaha River just upstream from the town of Kidatu. A few kilometers downstream from the dam, the river is crossed by the main road from Mikumi to Ifakara and by a railway bridge (Fig. 77).

Collections from Type Locality: We have collected numerous haplochromines from local fish traders and fishers at the Kidatu Bridge on a number of separate sampling trips. We consider these to be comprised of four distinct species of which we consider three to be undescribed, and the other which fits well with the Ruvu material we have identified with *Astatotilapia gigliolii* and the type of *P. vollmeringi* (Figs. 78-79). The relatively large chest scales of *P. vollmeringi* are not consistent with the undescribed *A.* sp. 'longfin' and *A.* sp. 'redcheek', while the spotted dorsal and caudal fins and relatively short pectoral fin are inconsistent with *A.* sp. 'ruaha blue'. All these features are, however, consistent with the type of *A. gigliolii* and material collected from the Ruvu identified as this species. Thus, based on the type specimen and recently collected material from the type locality, we feel confident in regarding *Paratilapia vollmeringi* as a junior synonym of *Astatotilapia gigliolii*, and in extending the known range of the latter to include the Great Ruaha river, in addition to the southern Ruvu.

Figure 74: *Astatotilapia gigliolii*: type of *Paratilapia vollmeringi* Steindachner, NMW 24598.

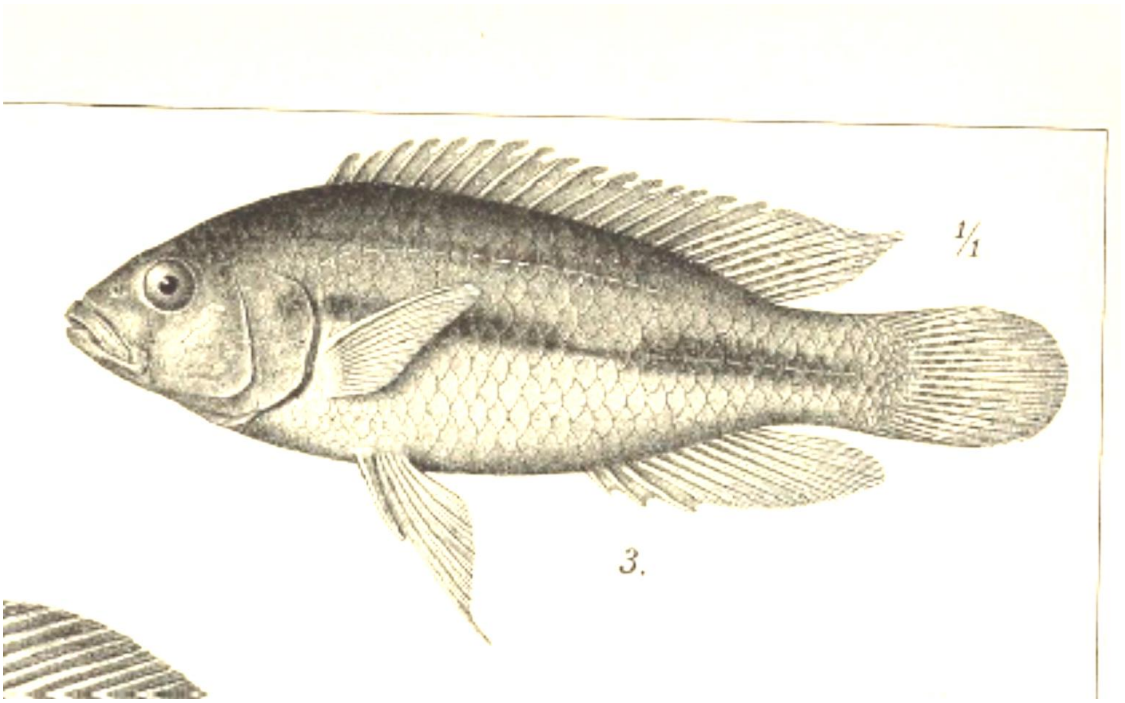

Figure 75: Original illustration of *Paratilapia vollmeringi* in Steindachner (1915). Note the spotted dorsal and caudal fins and horizontal dark midlateral stripe.

Figure 76: The type of *Paratilapia vollmeringi*, showing its relatively large chest scales.

Figure 77: The Great Ruaha river near Kidatu, showing road and rail bridges (-7.663, 36.979).

Figure 78: *Astatotilapia gigliolii* males collected from Kidatu Bridge on the Great Ruaha River, on 13 Feb 2014.

Figure 79: *Astatotilapia gigliolii* males collected at Kidatu in 2017, all showing characteristic body shape (slender with small head and jaws, lacking nuchal hump), long row of eggspots, dark red spots in spinous as well as soft dorsal fin, and generally yellow body colour with dark spots at the front end of many flank scales.

Astatotilapia gigliolii: Synonymy of *Astatotilapia tweddlei* Jackson 1985

Summary: *Astatotilapia tweddlei* Jackson 1985 is considered to be a junior synonym of *A. gigliolii*.

Original Description: *Astatotilapia tweddlei* Jackson 1985 was described based on material collected from Lakes Chilwa and Chiuta in Malawi. Jackson's paper largely compared it to *A. paludinosa* (which we now consider to be *A. bloyeti*). Key features emphasised include the slender body, large mouth, long caudal peduncle, slender rather rounded caudal fin and male breeding dress including dark maroon markings on flank scales and spots in the caudal and dorsal fins, including the spinous part. These features are all well illustrated on the drawing of the type and shared with the specimens we identify as *A. gigliolii* from the Ruvu and Rufiji catchments. The male breeding colour is given as dark brownish-green, but it seems likely that this was not based on fully sexually active fish. Jackson states that the chest scales are small compared to those of congeneric species, saying that *A. tweddlei* belongs to the group of species with 6-10 scales between the pelvic and pectoral fin based, as opposed to the group with 4-5 scales. However, he then gives the counts for *A. tweddlei* as 5-7, occasionally 8 and states that those of *A. paludinosa* are considerably smaller. In fact, based on the material we have examined, we would consider *A. tweddlei* to have rather large chest scales compared to most congeneric species. In Jackson's paper, there was no comparison made with material of *Astatotilapia gigliolii* or *A. vollmeringi*. It is possible that this is because neither of these taxa are mentioned in Greenwood's (1979) haplochromine reclassification and so they do not appear in his list of species contained in *Astatotilapia* nor indeed of any other genus. Therefore, the current study appears to be the first to make an explicit comparison of these taxa.

Examination of type material: The majority of the types are in South Africa (SAIAB) and one of the authors (GFT) was able to examine these in 2020. The holotype is in extremely poor condition, fragile, colourless and with a large black mark possibly resulting from mould infestation during a period when the specimen had dried out. We did not attempt to examine it closely. We were able to measure 14 paratypes in Grahamstown and one in London (figs. 81-83), all from Lake Chiuta. These conformed well to the description and demonstrated the relatively large size of the chest scales (fig. 82).

Collections from the type locality: At the time of visiting in 2019, the Natural History Museum in London had two well-preserved specimens from Lake Chilwa which clearly belonged to this species, although originally identified as '*Hemihaplochromis* (now *Pseudocrenilabrus*) *philander*' (figure 84). These were not part of the type series. We have also collected samples from Lake Chilwa. A freshly collected male showing a brownish body colour is shown in figure 85. Live adult male specimens held in the aquarium at the University of Hull around 2005 were bright metallic yellow with a prominent dark stripe through the eye, very similar to the Ruvu River specimen illustrated by Grimm (fig. 74). Although the types were collected in Lakes Chilwa and Chiuta, the fauna of both lakes has great affinities with that of the Ruvuma system (Tweddle 1979). Lakes Chilwa and Chiuta are currently separated by a sand bar, perhaps formed around 8500 years ago (Thomas et al. 2009) Lake Chiuta is continuous with Lake Amaramba in Mozambique, which in turn is periodically connected to a tributary of the Lugenda River which is a tributary of the Ruvuma (Tweddle 1979). Thus, it is no surprise that the fish species found in Lakes Chilwa and Chiuta are largely, if not entirely, also present in the Ruvuma system (Tweddle 1979). In addition, molecular studies have shown close affinities between the Chilwa/Chiuta and Ruvuma populations of *Astatotilapia*

calliptera (Malinsky et al. 2018). Among species shared between these systems, we can also now add *Astatotilapia gigliolii*, which we have collected from numerous sites in the Ruvuma catchment. Limited material was available to us for Chilwa and Chiuta, so we have pooled the Ruvuma/Ruhuhu material together to represent the '*A. tweddlei'* population for comparison with *A. gigliolii* from the Ruvu and Rufiji systems. Overall, we could find nothing obviously distinctive about the populations from Chilwa, Chiuta or the Ruvuma system.

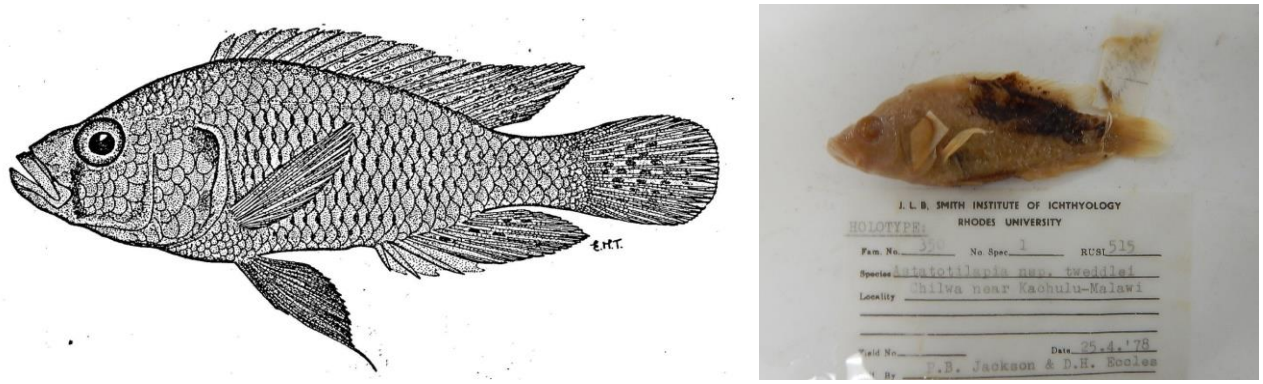

Figure 80: Holotype of *Astatotilapia tweddlei* Jackson 1985 (left: illustration from original description; right specimen photographed in 2020).

Figure 81: Paratypes of *Astatotilapia tweddlei* (left) London specimen collected from Nepiyala, Lake Chiuta (NHM 1984.11.30:4). The specimen is quite bent, hence the use of pins to attempt to straighten it out to get an overview of the body shape. (right) Grahamstown specimen RUSI 12216, also from Lake Chiuta.

Figure 82: Ventral view of *A. tweddlei* paratype NHM 1984.11.30.4, showing the relatively large chest scales, more like those of the type of *Paratilapia vollmeringi* (Figure 76) than the much smaller scales of the type of *P. kilossana* (Figure 34).

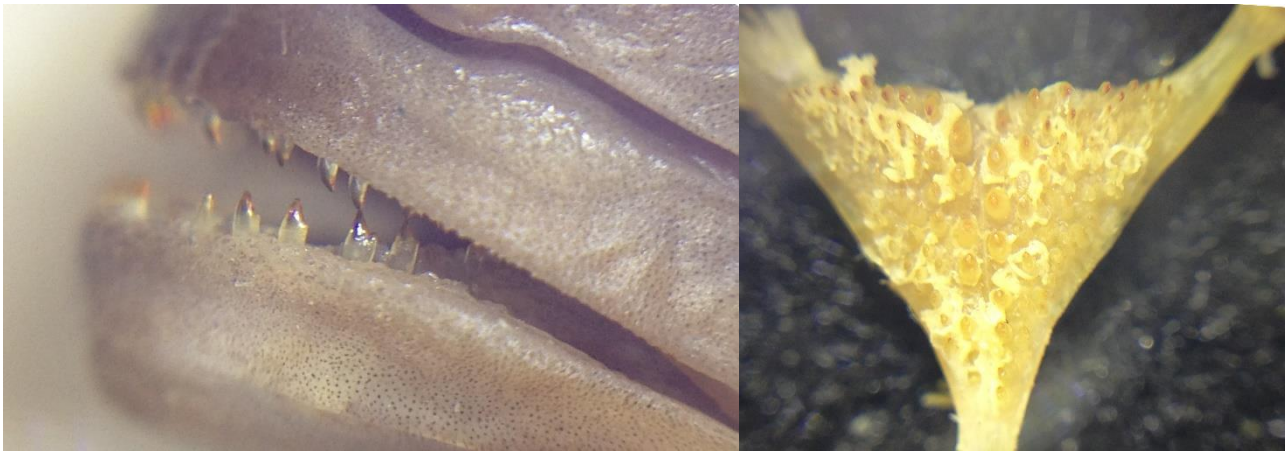

Figure 83: Outer row oral jaw teeth (left) of *A. tweddlei* paratype (NHM 1984.11.30.4) are a mixture of unicuspids to notched bicuspids, while the central teeth of the lower pharyngeal bone are slightly enlarged, but not molarised.

Figure 84: Specimens of *A. gigliolii* from Lake Chiuta originally identified as *Hemihaplochromis philander* and then *Haplochromis tweddlei*. NHM 1966.7.20.22-23.

Figure 85: *Astatotilapia gigliolii* male from Lake Chilwa.

Figure 86: *Astatotilapia gigliolii* males collected on 15th August 2013 from the Nambuti River (-10.567, 38.926), a tributary of the Ruvuma. The overall greenish body colour on the upper and posterior parts of the body are quite similar to the Mindu Dam specimens shown on figure 72, while the spotting in the spinous part of the dorsal fin, the dark marks on the flank scales and the relatively slender body are all characteristic of *A. gigliolii*.

Figure 87: *Astatotilapia gigliolii* males collected on 15th August 2013 at -10.643, 38.888 in the vicinity of Liloyo, on a tributary of the lower Ruvuma. These rather deep-bodied specimens show clearly the maroon spots on the flank scales mentioned by Jackson (1985) and shown clearly in the Kidatu specimens in figure 79. The lower illustration also demonstrates the conspicuous dark red spotting in the spinous part of the dorsal fin and the long row of anal fin spots characteristic of *A. gigliolii* males.

Figure 88: *Astatotilapia gigliolii* males collected on 6th September 2012 at the Kitai Dam (-10.71, 35.20) on a tributary of the Ruvuma near Songea. These slender males show clearly the characteristic maroon spots on the flank scales. The lower illustration also demonstrates the long row of anal fin spots characteristic of *A. gigliolii* males.

Figure 89: *Astatotilapia gigliolii* males collected on 7th September 2012 at Masimahuhu (-10.848, 35.520), a tributary of the Ruvuma near Songea. The specimens nicely demonstrate the range of body shape and colour within a single population, with the lower specimen showing the relatively squat body shape, small mouth and short snout of younger males (or females) and the upper two fish showing the progressive increase in mouth size and snout length of more mature males. Despite its larger size and stronger development of secondary sexual anatomical traits, the upper fish shows the least development of secondary sexual coloration, appearing drab with small faint anal fin eggspots- this might indicate a 'spent' male that had abandoned its breeding attempts prior to capture.

Figure 90: *Astatotilapia gigliolii* male collected on 17th August 2013 from the Muhuwesi River, a tributary of the Ruvuma near Tunduru (-10.849, 37.474). This relatively small male has weakly developed secondary sexual traits.

Figure 91: *Astatotilapia gigliolii* male collected on 7th September 2012 from Bombambili (-10.866, 35.515), a small tributary of the Ruvuma near Songea. The stream had been dammed to form a small pool, apparently as a result of road construction. This supported a very high density of the species.

Figure 92: *Astatotilapia gigliolii* males collected on 7th August 2013 from the Namiungu River (-10.869, 357.633), a tributary of the Ruvuma. The upper specimen shows that the species can sometimes have a relatively deep body and caudal peduncle, similar to the type of *Hemichromis gigliolii*.

Figure 93: *Astatotilapia gigliolii* male collected on 17th August 2013 from the Tetesi River (-11.419, 37.948), a tributary of the Ruvuma, south of Tunduru.

Astatotilapia gigliolii – additional range records

Having established the original collecting locality of *Hemichromis gigliolii* and the synonymy of *Paratilapia vollmeringi* and *Astatotilapia tweddlei*, we can conclude that *A. gigliolii* inhabits the Ruvu, Rufiji and Ruvuma Rivers, as well Lakes Chilwa and Chiuta. We now report on additional collections from other systems.

We also collected specimens of *A. gigliolii* from the upper tributaries of the Ruhuhu system, part of the Lake Malawi catchment, in the vicinity of Songea (figs 94-98). Here the tributaries of the Ruhuhu and Ruvuma lie close together, it is quite plausible that there has been movement of fish between them via tributary capture. It is also possible that fishes have been inadvertently translocated via aquaculture: we have found *A. gigliolii* in tilapia farms in the area, including one which was an entirely closed system of raised concrete ponds (fig. 97), which suggests the fish did not gain entry from feeder streams but via poor stock screening. Irrespective of its origin, *A. gigliolii* can be added to the inventory of fishes of the Lake Malawi catchment.

Additional records were made of the species in a number of lakes and streams in the coastal regions of Tanzania between the mouths of the Ruvu and the Ruvuma, including Lakes Mansi, Kitele and Rutamba. However, we have not found the species anywhere north of the mouth of the Ruvu. At present, we have little information on Mozambique. It would seem likely to be present within the catchment of the Ruvuma, but it is unclear if it occurs elsewhere.

Figure 94: *Astatotilapia gigliolii* male collected on 9th September 2013 from the Lumecha River – (10.502, 35.671), a tributary of the Ruhuhu near Songea. This individual is notably deep-bodied with a short snout and rounded head, but clearly displays the characteristic maroon markings on the flank scales.

Figure 95: *Astatotilapia gigliolii* very large male (above) and female (below) collected on 10th September 2013 from the Ruhila Fish Farm (-10.623, 36.636), on a tributary of the Ruhuhu near Songea.

Figure 96: *Astatotilapia gigliolii* male (above) and female (below) collected on a tributary of the Ruhuhu at the edge of Songea (-10.625, 35.653) on 9th September 2013.

Figure 97: *Astatotilapia gigliolii* male sampled from a tilapia farm at Songea on 28th July 2015. The farm was a closed system of concrete vats stocked largely with non-native *Oreochromis leucostictus*.

Figure 98: *Astatotilapia gigliolii* adult male sampled from Lake Mansi (-7.263, 39.158) 5th June 2015. This small coastal lake lies between Dar Es Salaam and the Rufiji delta. Specimens collected from this lake were generally quite dark, but illustrated many characteristic traits of the species, including the slender body, dark spots on flank scales, spotting in spinous as well as soft dorsal fins and long row of large anal fin spots.

Figure 99: *Astatotilapia gigliolii* male sampled from Lake Rutamba on 2nd June 2015. This lake lies between the Rufiji and Ruvuma deltas at -10.032, 39.460.

Figure 98: *Astatotilapia gigliolii* female and immature specimens collected on a tributary of the Ruhuhu (-10.624, 35.639) at the edge of Songea on 28th July 2015. This site was a short distance downstream from the Ruhila fish farm sampled in 2012 (see fig. 95).

Astatotilapia fuelleborni (Hilgendorf & Pappenheim 1903)

Summary: A valid species, but the status of different populations perhaps requires further investigation into possible cryptic species.

Original Description: The species was described as *Tilapia fuelleborni* Hilgendorf & Pappenheim in 1903. The description is fairly short and is not illustrated. It was based on three juveniles of 21-43mm (not clear whether this was standard or total length). The authors lacked confidence that the material enabled them to diagnose it as a new species, captioning the section *Tilapia (Ctenochromis) sp. nov*.? before saying in their last sentence what can be roughly translated as 'A clear judgment as to whether this represents a new species is difficult to make with such young specimens. Maybe it could be called *T. fuelleborni*'. The description contains very little information that could actually be used to diagnose it, except that it was collected in Lake Rukwa.

Determination of type locality: Lake Rukwa, although Seegers (1996) stated that Fuelleborn's material was collected from the south-eastern shores of the lake. He does not provide any evidence to back up this statement.

Type Material Examined: We examined the largest type, ZMB16305, which was designated as the lectotype by Seegers (1996). It was indeed around 43mm SL and looked like a haplochromine, perhaps *Astatotilapia*. However, no melanic markings could be discerned and there seemed little distinctive about it (Figure 99).

Collections at the Type Locality: Seegers (1996) collected extensively in Lake Rukwa, but most of his collections seem to have come from streams in the catchment. He distinguished six species of *Astatotilapia* (although he used the name *Haplochromis* for these). Diagnostic features were largely based on colour, sometimes with subtle differences in body shape. Of these, *A.* sp. 'red cap' was represented by a single specimen and it may be a colour morph of one of the more common species. *Astatotilapia* sp. 'lupa' was collected from a single site on a stream in the catchment and has not been recorded since. *Astatotilapia katavi* and *A.* sp. 'pseudopaludinosus' were also only found in (different) streams, but we believe we were able collect both in our survey and these will be mentioned later. Within the lake proper, Seegers only collected two *Astatotilapia* taxa, one of which he assigned to *A. fuelleborni* on the grounds that he collected it in the SE part of the lake, where he believed Fuelleborn had made his collections (Fig 100). The other taxon he named *Astatotilapia sp.* 'Rukwa green' (Fig 100), although closer reading of his collection data shows that it was also collected in the main lake about half way down the eastern shore at a site he called Kempi Kambuju (Seegers 1996: figure 218), which might be the village marked as Uleia on Google Earth- one of the few settlements on the eastern shore of the lake with obvious road access (-8.116, 32.619). This is only about 40km north of the main fishing beach on the SE shore: when we visited in 2012, we were told it was called Kalanda, but on Google Earth, it is marked as Bangala and Maleza; Seegers refers to Mbangala. His collection from Mbangala comprises juveniles deposited in the Africa Museum at Tervuren (nine specimens 16-40mm SL), plus some illustrations of adults grown up in the aquarium. However, he has a much more substantial collection of 'Rukwa green' from a number of sites. We believe that there are no convincing morphological or colour differences between these two forms. The 'Rukwa green' form could be the immature or subordinate male form of the blue/black form (a similar transformation takes place in *A.* sp. 'chipwa'). This interpretation is supported by comparing

his Rukwa green male in figures 100 against those in figure 101. In fact, Seegers also says that his *H. fuelleborni* males are 'greenish when young… At that stage they can hardly be distinguished from *H.* sp. 'Rukwa green'. No diagnostic colour differences are presented, and no diagnostic differences in counts or measurements are given either. His morphometric analyses of *H. fuelleborni* were based on the immature types along with three specimens of 50-53mm SL collected by Ricardo in the 1940s and deposited in the London Natural History Museum. Since nothing was known of their colour, the basis for their inclusion seems to be simply that they were collected from the southeast of the lake.

In addition, it is not unusual to find yellow and blue forms within a single population: this kind of polymorphism is well-known in *A. burtoni,* and there are hints of it in our collection of *A. bloyeti* from the Hombolo Lake (figure 19). Seegers also mentioned that some of his '*H. fuelleborni'* specimens were more green or yellowish and others more bluish.

Overall, in our opinion, Seegers does not really establish any clear differences among these two putative taxa, except that his '*Haplochromis fuelleborni'* were collected in 1987 from the SE of the lake, while his '*Haplochromis* 'Rukwa green'' were collected from 1991 to 1993 in the northern and central eastern part of the lake.

In our surveys in 2012 and 2017, we found blue and yellow-green specimens together in the SE of the lake (figures 102-103). For now, we propose to consider all of the haplochromines from the main lake body of Lake Rukwa as *A. fuelleborni*. We are satisfied that they can be distinguished from the majority of other haplochromines in the region. Features shared by putative *A. fuelleborni* specimens include eggspots positioned in the posterior half of the anal fin only (unlike the long rows of spots generally seen in male *A. gigliolii, A. burtoni* and *A. calliptera*). Males lack spots in the spinous dorsal fin, which are prominent in *A. gigliolii* and *A. burtoni*. None of the larger males showed the development of a prominent nuchal hump seen in larger male *A. bloyeti*. None of the specimens we collected showed dark maroon spots on the flank scales, characteristic of male *A. gigliolii*.

Genome-wide sequence analysis (Svardal *et al.* 2020) placed three specimens of *A fuelleborni* corresponding to the three phenotypes shown in figure 102 as forming a clade closely related to clade containing Lake Victoria and Kivu endemics, plus *Astatotilapia sp.* 'chipwa' from the Tanganyika catchment. Further work is required to investigate the diagnostic traits and relationships between *A. fuelleborni, A. stappersii* and *A.* sp. 'chipwa', to test whether there are cryptic species or ecomorphs within Lake Rukwa and to clarify the relationships with other apparently riverine taxa within the catchments, such as *A. katavi, A.* sp. 'pseudopaludinosus' and *A.* sp. 'lupa'.

Conclusion: Provisionally, we identify *A. fuelleborni* as the single haplochromine species found within the main body of Lake Rukwa. It appears to show marked variation in male breeding dress, probably encompassing the forms identified by Seegers as 'rukwa green' and 'red cap'. It is not known outside the Rukwa catchment.

Figure 99: The lectotype of *Tilapia fuelleborni* Hilgendorf & Pappenheim 1903, a juvenile of 43mm SL.

Figure 100. Illustrations from Seegers (1996) of his *Haplochromis fuelleborni* from the SE of the lake and *Haplochromis* 'rukwa green' from the north of the lake. These taxa are distinguished mainly on the basis of male breeding dress, but in our opinion, these differences could easily represent differences in motivational state of the same individual and we see no particular reason to maintain these taxa as distinct. We suggest these are both *A. fuelleborni*.

Figure 101. Further illustrations by Seegers of *Astatotilapia* 'rukwa green'. These could easily be subordinate males of the species illustrated in figure 100. *Astatotilapia* sp. 'chipwa' undergoes a similar transformation from a green-orange fish to a dominant blue-black one with red fins. Again, we suggest these are *A. fuelleborni*.

Figure 102: *Astatotilapia fuelleborni* males collected in SE Lake Rukwa in 2012, showing variation in body shape and colour from a single location. These phenotypes were labelled Blue (top left), Sunset (bottom left) and Large Yellow (right) in Svardal *et al.* (2020).

Figure 103: *Astatotilapia fuelleborni* male colour variation in a sample from the SE part of Lake Rukwa, encompassing both the 'green' and 'blue-black (=fuelleborni)' variants identified by Seegers, collected 22 January 2017 by AM Tyers.

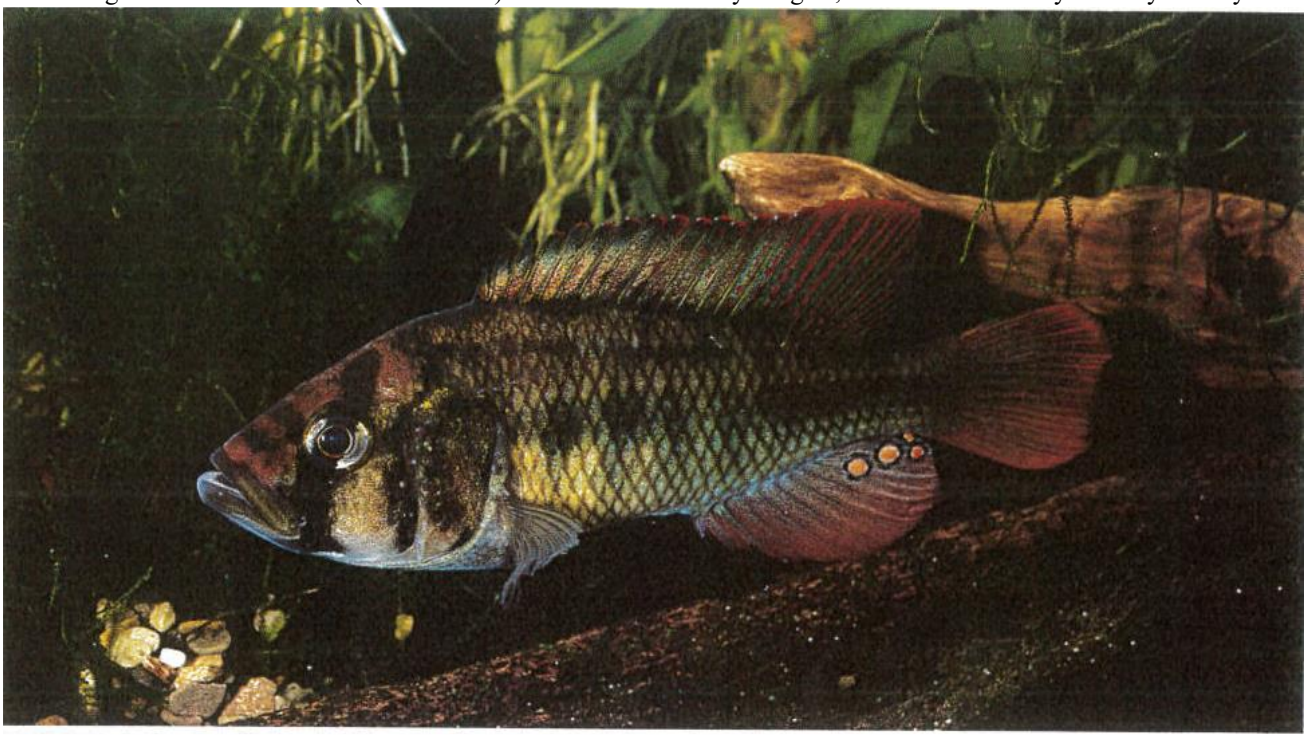

Figure 104. Male *Astatotilapia fuelleborni*? – this single specimen was labelled as *Haplochromis* 'red cap' by Seegers. It was collected from Mkamba, NE of Sumbawanga, at the NW end of Lake Rukwa. It was caught close to the main lake in the company of specimens of *Haplochromis* 'rukwa green' which we identify as *A. fuelleborni*. We suspect it is probably a colour morph of this species.

Astatotilapia stappersii (Poll 1943)

Summary: A valid species, but the status of different populations perhaps requires further investigation into possible cryptic species.

Original Description: The species was described as *Haplochromis stappersii* by Poll in 1943. Some later works refer to it as *A. stappersi* (e.g. Greenwood 1979, Salzburger *et al.* 2005, Indermaur 2011). The description (in French) is reasonably detailed and based on 57 specimens (Indermaur lists 13). No information on live coloration is given and there is no illustration. Poll stated that it could be distinguished from *A. burtoni* by its generally longer body and caudal peduncle, more conical teeth, more molariform pharyngeal dentition and by colour. Distinguishing features of the coloration are not stated, but Poll's description noted horizontal dark markings on the flanks and fins lacking spots apart from 2-4 ocelli in the posterior part of the anal fin. In *A. burtoni*, the dorsal and caudal fins are strongly spotted and the eggspots generally extend into the anterior half of the anal fin (see figure 68). If melanic elements are present on the flanks of *A. burtoni*, they tend to be vertical bars (fig. 68).

Determination of type locality: Lake Tanganyika catchment. Poll's type came from the River Lufuku at Pala, which is presumably Mpala (-6.746, 29.492) which lies on the Western shore of Lake Tanganyika in the DR Congo. The river is an afferent of Lake Tanganyika. Paratypes came from a number of locations, including Albertville (Kalemie), Lobozi River near Kirungwe (Uvira at the northern end of the lake?) and Nyanza (possibly Nyanza Lac in Southern Burundi). This suggests a relatively wide distribution in the Lake Tanganyika catchment.

Type Material Examined: We have not seen the types, which are located in the Africa Museum in Tervuren, Belgium. The type was illustrated in Poll (1946, p.246; Figure 105) and clearly shows a rather squat specimen with a distinct horizontal band on the flanks with dark vertical bands below, just behind the head.

Collections at the Type Locality: The type locality in the DRC has not been visited recently, as far as we know.

Other Collections: Specimens classed as *A. stappersii* have been collected from a variety of localities in the Lake Tanganyika catchment by the group of W. Salzburger. Adult males are generally dark blue, with dark flank markings, and deep red on the caudal and anal fins. Anal fin eggspots are generally confined to the posterior part of the fin. The body is quite deep and the mouth small (Figure 106). A molecular study by Meyer *et al.* (2015) indicated that there were two divergent mitochondrial lineages among specimens identified as *A. stappersii*: specimens from the Malagarasi system clustered with an undescribed species known as *Haplochromis sp.* 'chipwa'. Specimens from the Ruzizi River in Burundi were more distantly related. All however, were clustered in the 'Lake Victoria superflock' grouping. Preliminary genome-wide analysis of our collections also indicates two groups assigned to this species, again with Malagarasi specimens (Figure 107) from two sites over 200km apart clustering with *A. sp.* 'chipwa' (Hsu 2019). Specimens from Mwamapuli Dam near Lake Kitangiri (Figure 108) cluster more closely with material from Lake Victoria proper. We refer to these as *Astatotilapia cf. stappersii* A and B respectively (Hsu 2019). The presence of a Lake Victoria genome in Mwamapuli dam may be connected to human introductions. While it is unlikely that anyone would deliberately stock low-value, small maturing haplochromines in a dam, this

reservoir contains *Oreochromis esculentus* and *O. niloticus*, both probably introduced separately from strains originally obtained from Lake Victoria. Given the widespread accidental stocking of the small maturing *O. leucostictus* thoughout Tanzania, as well as the probable introduction of *Astatotilapia bloyeti* into Lake Chala (Moser *et al.* 2018), it seems entirely plausible that a Victorian haplochomine could have been introduced into the Mwamapuli Dam.

Finally, we have examined specimens in the London Natural History Museum collected by Greenwood (or EAFRO, standing for the East African Fisheries Research Organisation, his employer at the time) on 8th August 1952 from Katare swamp on the Malagarasi and labelled as *Astatotilapia bloyeti* (NHM 1956.7.9. 172-229). In Greenwood's (1980) description of *A. paludinosus*, he contrasts its colour and appearance with a sympatric species he regards as *A. bloyeti*. Although he does not give catalogue numbers for this material, the collector, collection dates and location make it very likely that this was his voucher material for his *A. bloyeti*. We consider *A. paludinosus* itself to be a junior synonym of *A. bloyeti*. Based on the body shape and what we can see of the markings (Figure 109), there seems little doubt that Greenwood's '*A. bloyeti*' is in fact *A. cf. stappersii* A. Thus, we have three independent collections of *A. cf. stappersii* from the Malagarasi.

Conclusion: *Astatotilapia stappersii* is a valid species distinct from *A. bloyeti* and *A. burtoni*, but molecular analysis suggests it may consist of two or more cryptic species.

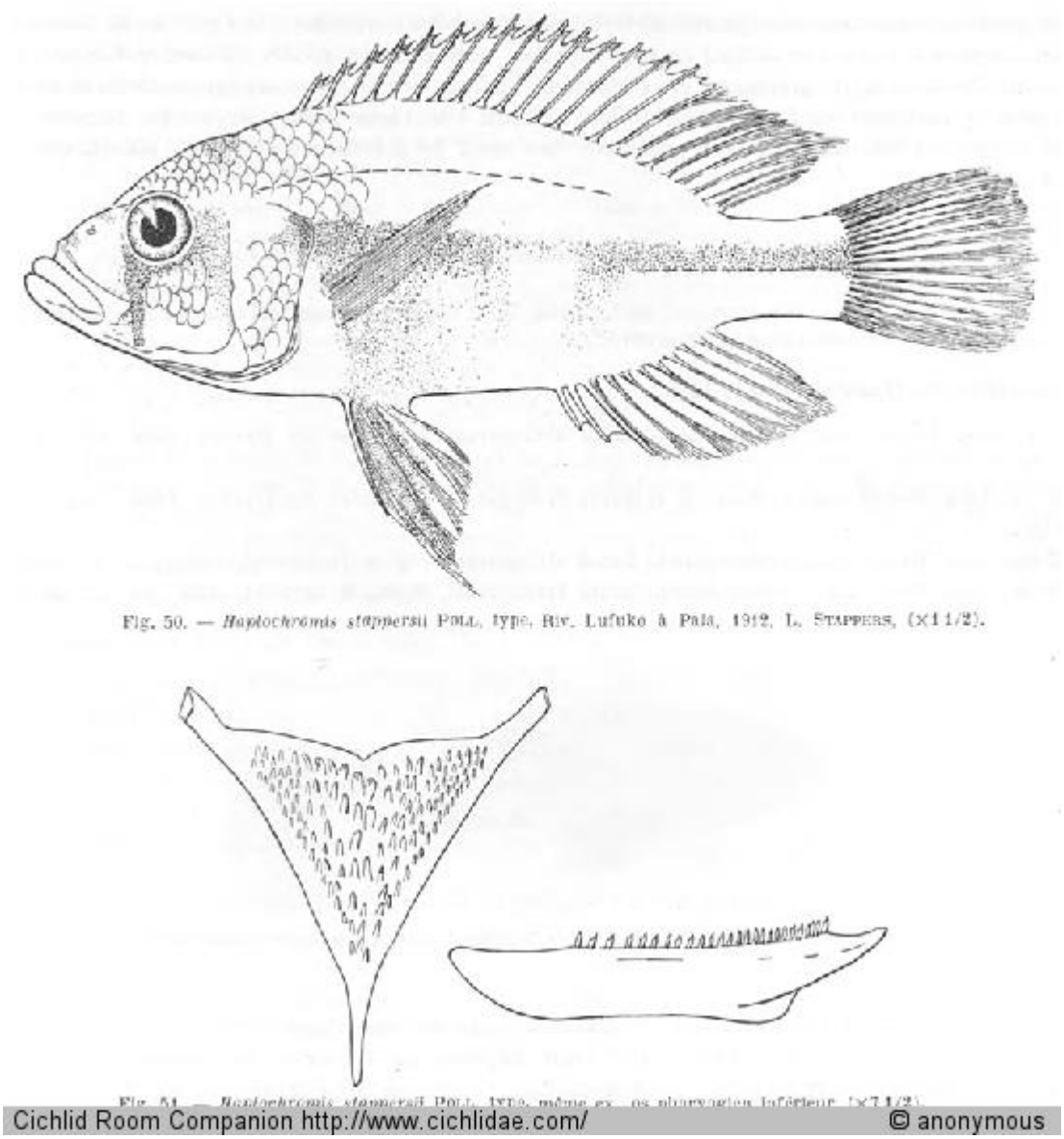

Figure 105. Illustration of the type of *Haplochromis stappersii* Poll in Poll (1946)

Figure 106: *Astatotilapia stappersii* male at Gatumba (-3.34, 29.272), Burundi, photographed by A. Indermaur (CC BY-SA 4.0) on 15th January 2015.

Figure 107. *Astatotilapia cf stappersii* A: (above) adult male from Lake Igombe, on the Malagarasi catchment about 350km East of Lake Tanganyika at (-4.854, 32.745) 2 August 2016; and (below) a female or immature from the Malagarasi (-5.094, 30.848) on 31 July 2016, around 113km East of Lake Tanganyika.

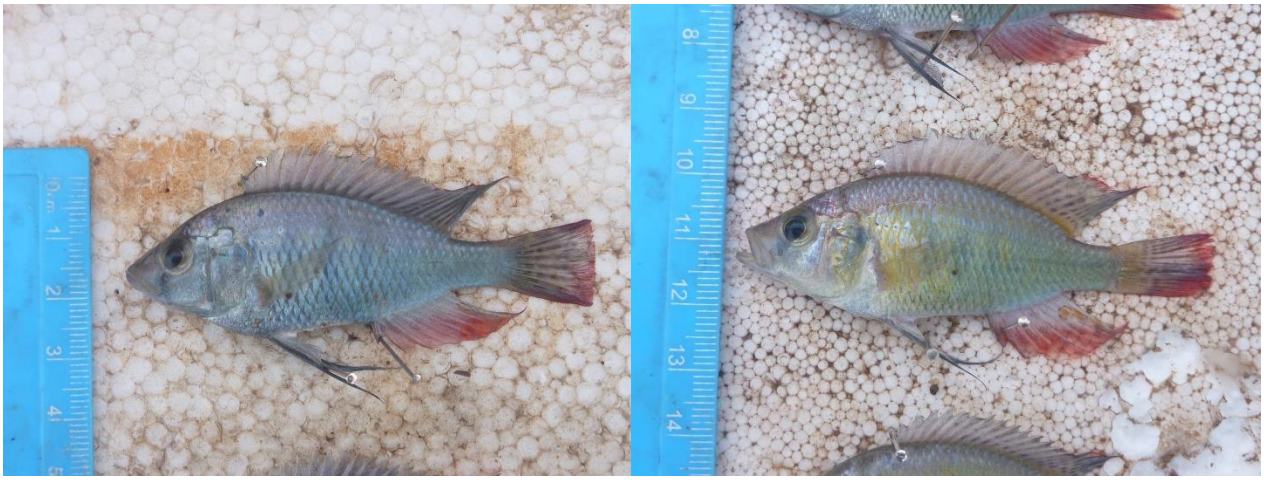

Figure 108: *Astatotilapia cf. stappersii* B, Mwamapuli dam, near Lake Kitangiri (-4.356, 33.877), collected on 2 August 2016. It is not clear whether the green & yellow colour of fish on the right represents a polymorphism or an intermediate colour of a male that is not yet fully ripe.

Figure 109: *Astatotilapia cf stappersii* A collected from Katale, on the Malagarasi River by Greenwood in 1952 (NHM 1956.7.9. 172-229). The dark markings behind the head correspond well to the illustration of the type in Poll (1946), figure 105 above.

Astatotilapia katavi (Seegers 1996)

Summary: Possibly a valid species apparently endemic to the northern part of the Lake Rukwa catchment, of perhaps a geographic variant of *A. fuelleborni*.

Original Description: The species was described as *Haplochromis katavi* by Seegers in 1996, based on 32 specimens. Seegers does not actually give a diagnosis: the section headed 'diagnosis' is merely a brief description of some of the basic characteristics of the specimens examined and gives no indication how to distinguish the species from similar species found in the area

Type locality: Lake Rukwa catchment, Katuma River (-6.65, 31.15). This is about 110km to the north and west of the northernmost extent of Lake Rukwa in 2019 (Google Earth maps).

Type Material Examined: We have not seen the holotype, which is in the Africa Museum in Tervuren, Belgium. Paratypes are in a number of institutions including the London Natural History Museum. Illustrations of living and preserved specimens are given by Seegers. The adult male illustrated is bright blue with orange areas on the lower part of the head and chest (Fig. 110). However, the description states the males to be green and red. It is not clear whether this is a flaw in the text or in the development of the photograph: many aquarium articles about cichlid fishes talk about 'red' when they really mean 'orange'. However, confusion of green and blue is rarer. The blue appearance of the illustrated male may be due to the photographic process used: Seegers' photograph was taken of a fish collected in 1989 and kept alive in the aquarium for 3 months. It would likely have been based on an image from a slide film.

Collections at the Type Locality: In July 2017, we sampled a number of locations in the Katumi river, further upstream than the actual type locality, collecting rather slender green and orange males that looked a lot like they could be *A. katavi*, if we take the colour description given by Seegers at face value. One collection was made from the Milala Dam (-6.323, 31.049) in the Rukwa catchment, but over 130km north of the main lake shoreline on 28th July 2017. Many of the live males showed blue-green flanks and little or no orange colour on the head (fig. 111), making them hard to distinguish from the blue-green phenotype of *A. fuelleborni* (fig. 102). Following euthanasia, pinning and partial drying of specimens, some continued to exhibit a prominent patch of bright orange over the head, and the lower part of the flanks just behind the head (fig 112-113). Other individuals were dark blue-grey with a red caudal fin (fig. 114). From our collections in the SE part of Lake Rukwa, we also found males with orange on the head, although perhaps not covering such an extensive area as in the most extreme 'Katavi' specimens (fig 103). So, we are not confident that there are any clear phenotypic differences between *A. katavi* and the 'main lake' *A. fuelleborni* populations.

Relationships: Genome-wide molecular analysis using ddRAD clustered specimens of *A. katavi* with those of *A.* 'pseudopaludinosus' as reciprocally monophyletic sister clades (Hsu 2019). This was based on 4 specimens of each taxon, each from a single site - the Milala Dam for the former and the Lwiche River for the latter. These sites are 189km apart and in different river catchments each flowing into Lake Rukwa, so reciprocal monophyly could easily be simply a reflection of geographic separation. As all the Milala Dam specimens selected were of the orange-chest phenotype, we can say nothing about its relationship to the dark blue phenotype. This Rukwa clade in turn, was the sister group to a clade containing the Lake Victoria endemics, along with *Astatotilapia cf stappersii*,

A. sp. 'Chipwa', and *A.* sp 'Rufiji blue'. *Astatotilapia fuelleborni* material from the main body of Lake Rukwa was not included in that analysis but a separate whole genome sequencing study placed it in the same overall clade, but as sister to the chipwa/Rufiji blue group, which is turn was sister to a clade containing Victorian and Kivu endemics.

Conclusion: At present, we have no convincing evidence from morphology, colour or molecular data to separate *A. katavi* from other Rukwa populations. For now, we will use *A. katavi* for populations for populations from the Katumi River system to the north of Lake Rukwa and *A. fuelleborni* for populations from the main body of Lake Rukwa and nearby.

Figure 110: *Astatotilapia katavi* male in aquarium, collected from type locality & photographed by Seegers (1996).

Figure 111: Probable *Astatotilapia katavi* male collected from Milala Dam (-6.323, 31.049) in 2017. This location is in the Rukwa catchment, but over 130km north of the main lake shoreline. Only a hint of a faint orange colour is visible on the operculum of this specimen photographed alive in a bag of water.

Figure 112 *Astatotilapia katavi* males collected at

(top) Misunkumilo River, -6.348, 31.057, 28th July 2017;

(middle) Milala Dam, -6.323, 31.049, 28th July 2017;

(bottom) Msaginya River, -6.365, 31.247, 29th July 2017.

All three sites were in the Katumi (or Katuma) River system some 130-145km to the north (and west) of the nearest shoreline of Lake Ruwka.

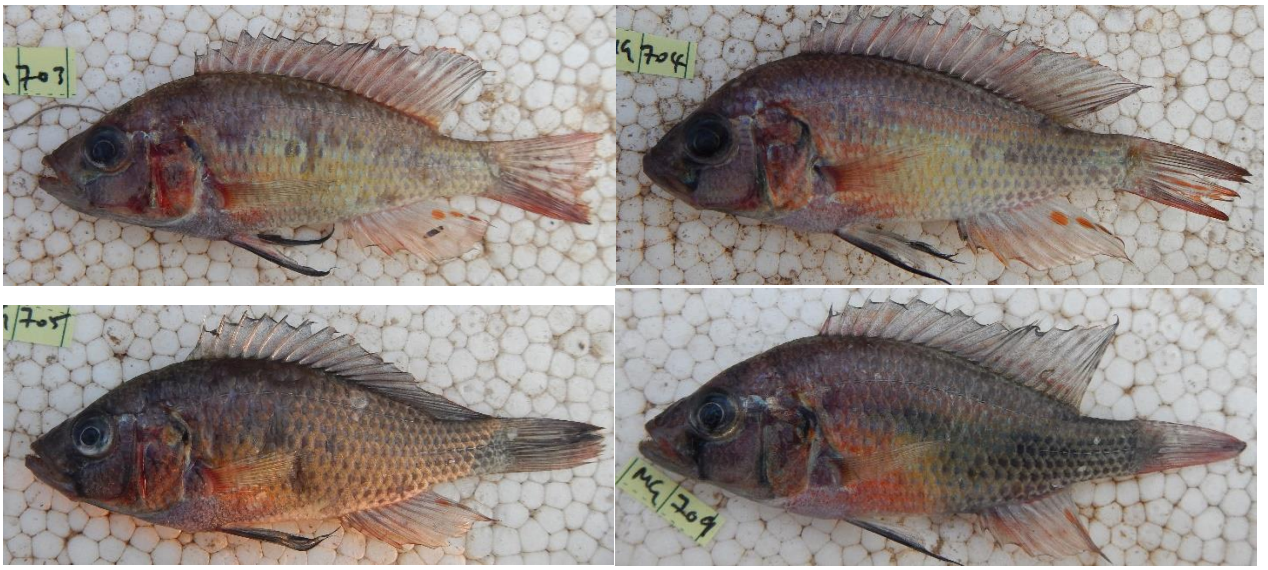

Figure 113: Male *Astatotilapia katavi* from Milala Dam (28th July 2017) all exhibited extensive areas of orange colour on the head, chest and flanks after euthanasia, pinning and partial drying.

Figure 114: These dark-coloured male *Astatotilapia cf. katavi* from Milala Dam were collected with the orange-chested specimens above (Figure 113) and treated in the same way. They may represent a different species, a colour morph or a phenotypic change relating to reproductive state.

Astatotilapia sp. 'pseudopaludinosus'

Summary: An undescribed population or species apparently endemic to the northern part of the Lake Rukwa catchment.

Original Identification: This taxon was first identified by Seegers in 1996, but it was not formally described. Seegers collected small haplochromine juveniles from a number of sites in the Rungwa River system, but was unable to find adults. He returned some live specimens to Europe and reared to them to maturity in captivity. He was uncertain whether they were specifically distinct from *Astatotilapia paludinosus*, which we regard as a junior synonym of *A. bloyeti*.

Original collecting locality: Lake Rukwa catchment, Rungwa River and Upper Lupa River.

Material Examined: Some material was deposited by Seegers in the Africa Museum at Tervuren, including 3 adult males. A few females were deposited at the Zoology Museum in Hamburg. We have not examined these, but photographs of live and preserved fish are presented by Seegers (1996).

Subsequent Collections: On 27th July 2017, we sampled a site on the Lwiche River (-7.942, 31.596) about 28.5km West of Lake Rukwa in the town of Sumbawanga. The haplochromines collected there could not be readily assigned to any of the other taxa we had collected, but the males had a consistent phenotype. The green and orange colour pattern was not dramatically different to other taxa in the Rukwa catchment, although the strongly orange operculum was quite conspicuous. The strong pattern of stripes and spots in the soft dorsal was reminiscent of *A. bloyeti* and quite different to other Rukwa species. The anal fin eggspots were largely confined to the posterior part of the fin, as is typical of Rukwa *Astatotilapia*. Overall, the phenotype fitted well with *A. sp.* 'pseudopaludinosus', although Seegers' collections of that taxon came from the North Eastern side of the lake. The closest locality where Seegers reported this species was SW of Inyonga on the Wogo River, a tributary of the Rungwa River some 122km away. However, Seegers' other collecting localities for *A.* sp. 'pseudopaludinosus' include sites on the Upper Lupa system, more than 170km away from the Wogo site. Seegers did sample the Lwiche near Sumbawanga (on 2nd July 1989) but did not find any haplochromines. For now, pending more thorough examination of the material and collections from the Rungwa, our identification of these with Seegers' 'pseudopaludinosus' should probably remain tentative.

Relationships: Genome-wide molecular analysis using ddRAD clustered specimens of *A.* 'pseudopaludinosus' with those of *A. katavi* as reciprocally monophyletic sister clades (Hsu 2019). They were not closely related to *Astatotilapia bloyeti* from the Malagarasi, formerly known as *A. paludinosus*, which Seegers speculated might be their closest relative.

Conclusion: The status of *Astatotilapia* sp. 'pseudopaludinosus' remains unresolved. The material we collected from the Lwiche may be conspecific with Seegers's taxon, although they are from widely separated localities. It is clearly distinct from, but closely related to other *Astatotilapia* from Lake Rukwa, and it cannot be referred to any other species from outside the catchment.

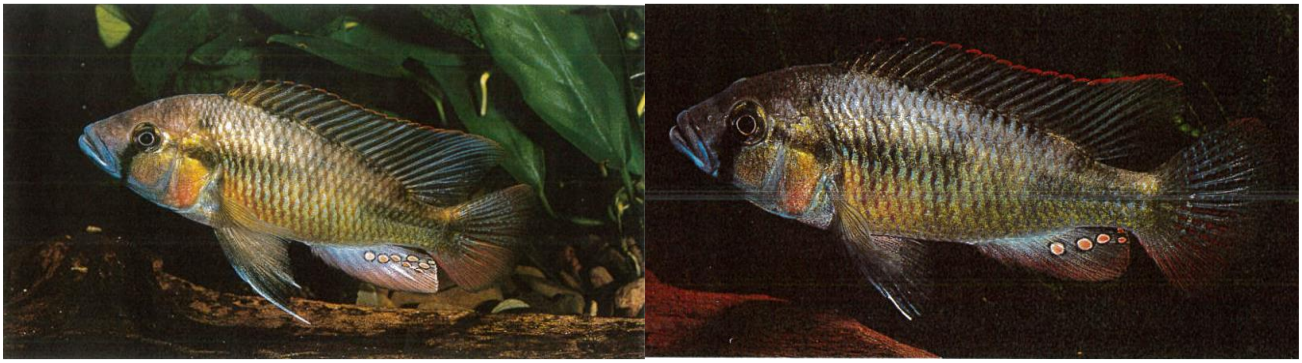

Figure 115. *Astatotilapia* sp. 'pseudopaludinosus' males collected in the Rungwa River system in the Lake Rukwa catchment and photographed in the aquarium by Seegers (1996).

Figure 116: Male *Astatotilapia* sp. 'pseudopaludinosus' ? collected from site 15, Lwiche River, (-7.942, 31.596) about 28.5km West of Rukwa on 27th July 2017.

Astatotilapia sp. 'lupa'

Summary: An undescribed potentially valid taxon known only from two sites on the Lupa River in the eastern Lake Rukwa catchment.

Original Identification: The taxon was first identified by Seegers in 1996, but it was not formally described.

Original collecting locality: Lake Rukwa catchment, recorded from a site on the Lupa River around 4km north of the village of Lupatingatinga (-7.918, 33.275). Collection of this species from a second site is mentioned in the Methods section of Seegers' paper, although not in the species account, as being on the Mkoygy River 108km south of the Rungwa River. This appears to be a tributary of the Lupa and is located at approximately -7.918, 33.311.

Material Examined: Some material was deposited by Seegers in the Africa Museum at Tervuren, including 2 adult males. We have not examined these, but photographs of live and preserved fish are presented by Seegers (1996). The adult male illustrated by Seegers seems rather distinctive with its strong melanic markings, drab background colour and relatively large head and mouth. However, the measurements of Head/SL and Snout/HL largely overlapped with the other Rukwa *Astatotilapia* species measured by Seegers, despite the relatively small sample size measured. Mouth/jaw length was not measured by Seegers.

Subsequent Collections: We have not visited Seegers' collecting site, and we have not yet found any specimens of a similar phenotype in our surveys of Lake Rukwa.

Conclusion: The status of *Astatotilapia* sp. 'lupa' remains unresolved.

Figure 117: Adult male *Astatotilapia* sp. 'lupa' collected and photographed by Seegers (1996).

Astatotilapia sp. 'Chipwa'

Summary: An undescribed species identified from the Lake Tanganyika catchment.

Original Identification: The first published identification of this species was by Meyer *et al.* (2015), but it was not formally described.

Original collecting locality: Lake Tanganyika catchment, first recorded from the village of Chipwa near the mouth of the Kalambo River on the SE Coast of the lake (-8.601, 31.188), and from the mouth of the Lufubu River in Zambia on the SW Coast (-8.573, 30.721; fig.119).

Material Examined: Voucher specimens are at the University of Basel or the Africa Museum in Tervuren. We have not examined these, but we have seen photographs of freshly collected fish (figure 118). In addition, some live specimens of the Chipwa strain have been available from aquarium fish keepers (fig. 121), and one of us (GFT) has kept and bred these (fig 122). Field collected adult males have yellowish flanks, becoming green posteriorly. The lower part of the head is bright orange, including the lips, throat membrane and the lower part of the preoperculum and operculum. The orange extends on the chest and the anterior part of the flanks. Melanin pattern is variable, but can include both horizontal stripes (midlateral and supralateral) and vertical bars on the flanks along with head markings including a vertical stripe below the eye and another on the operculum/pre-operculum, and bars across the snout and between the eyes. The anal fin has several large eggspots in the posterior part of the fin. The fins are greyish and not obviously spotted. Live males in the aquarium initially had a very similar colouration, while females were plain sandy-coloured and countershaded. However, dominant courting males ultimately adopted a very different breeding dress, with a blue/grey background colour, red fins and strong black horizontal stripes along the flanks. During spawning (fig. 122; https://www.youtube.com/watch?v=2f3pSZK-5Ro), the male has a black belly, a thick black midlateral stripe, a thinner supralateral stripe, a thin black stripe at the base of the dorsal fin. The head is black ventrally, and the black stripe though the eye extends up vertically to the nape, and the stripe though the operculum also extends to the base of the dorsal fin. There are 3 additional strong black stripes across the snout and between the eyes. The pelvic fins are black, the dorsal fin iridescent blue with red margins, the anal fin red distally, but bluish in the area around the eggspots, the caudal fin red with a bit of a dark stripe continuing from the midlateral stripe in the middle. The anal fin eggspots are bright orange. Like *A. calliptera*, the male dug a shallow depression in the sediment next to some cover, like a large rock or piece of wood.

Subsequent Collections: On 23 April 2016, we collected specimens very similar to the subordinate male colour of *A.* sp. chipwa (fig. 120) from Kasete on the Luiche River (-4.853, 29.733). If these are the same species, it considerably extends the range of the species, as our collecting site is about 450km to the north of the previous collecting localities of this species (fig. 119). This is also relevant to the discussion of the origins of the species, where Meyer *et al.* (2015) consider it more likely that the species originated in Lake Rukwa, rather than the Malagarasi system, because of the proximity of the collecting sites to the Rukwa catchment.

Relationships: A phylogeny based on mitochondrial sequences by Meyer *et al.* (2015) indicated affinities of the southern population of *A. sp.* 'chipwa' with the Lake Victoria radiation and several groups of *Astatotilapia cf. stappersii*. A tree based on whole genome sequences placed *A. sp.*

'chipwa' as sister group to a clade comprised of Victorian and Kivu species with a group of Rukwa species and/ or undescribed Rufiji species the sister group to them (Svardal *et al.* 2020). A tree using genome-wide ddRAD sequencing incorporated the northern population of *A.* sp. 'chipwa' only, again placing them in amongst *A. cf. stappersii* and Victorian, Rufiji and Rukwa species (Hsu 2019). This suggests that the northern and southern populations are likely to be closely related and possibly conspecific.

Conclusion: *Astatotilapia* sp. 'chipwa' is an undescribed species belonging to a clade that includes the Victorian, Kivu and Rukwa species, along with *A. stappersii* and some Rufiji taxa.

Figure 118: Male (above) and female (below) *Astatotilapia* sp. 'chipwa' from near the mouth of the Kalambo River. Photographed in 2011-12 by Adrian Indermaur.

Figure 119: Map of collecting localities for *Astatotilapia* sp. 'Chipwa', showing 2 sites sampled by Meyer et al. 2015 (near Chipwa village on the SE coast, and near the mouth of the Lufubu River on the SW Coast) and our collecting site in the Luiche River (-4.853, 29.733) on 23 April 2016. Map modified from Google Earth (image Landsat Copernicus). The distance between the Luiche and Chipwa sites is approximately 445km.

Figure 120: *Astatotilapia* sp. 'chipwa' collected from Kasete on the Luiche River.

Figure 121: *Astatotilapia* sp 'chipwa' (from near the Kalambo River mouth) dominant male in the aquarium displays a blue breeding dress with black horizontal stripes quite different to specimens collected from the wild. Photo by Krzysztof Haja.

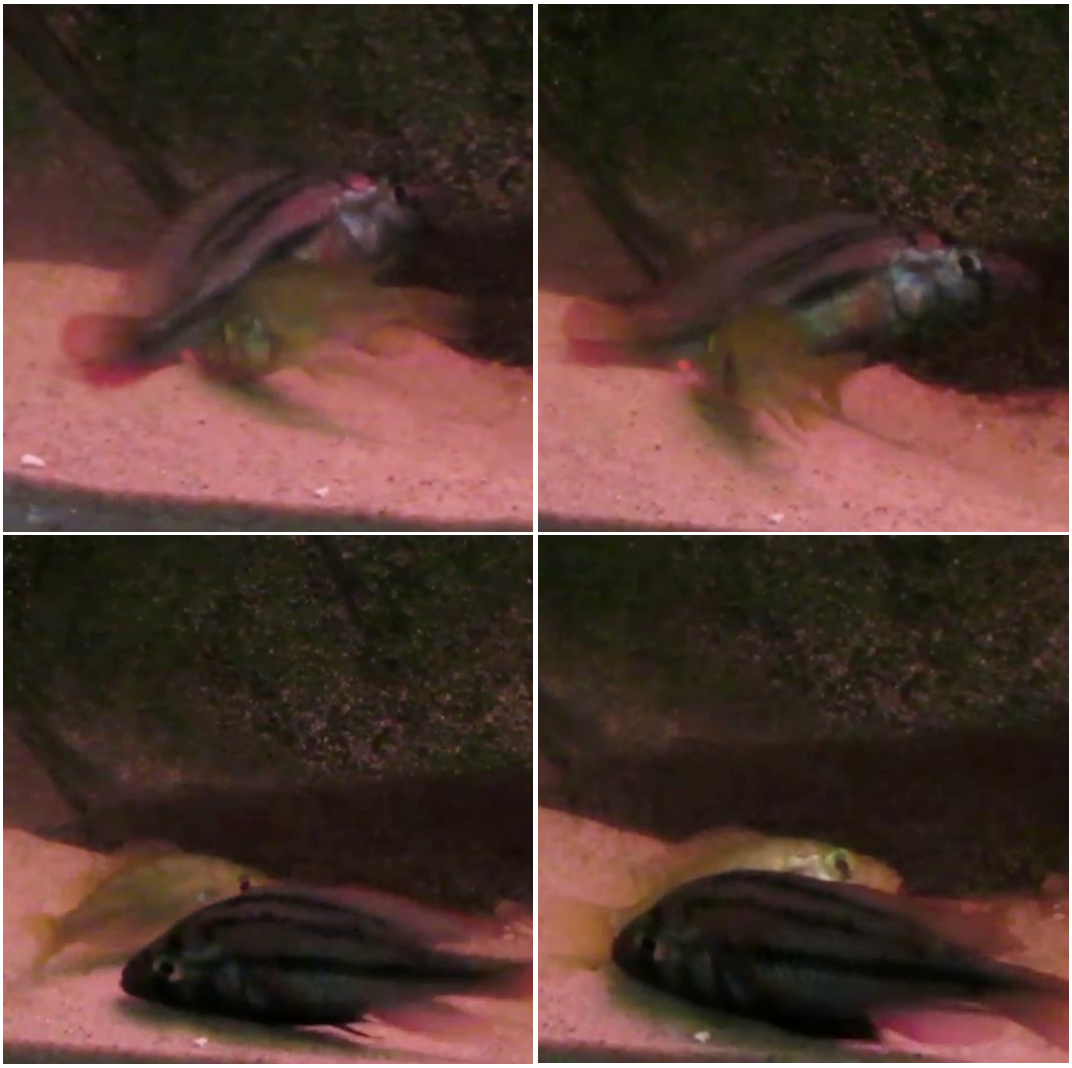

Figure 122: *Astatotilapia* sp. 'chipwa' spawning in the aquarium. Video screen grabs from https://www.youtube.com/watch?v=2f3pSZK-5Ro

Astatotilapia sp. 'ruaha blue'

Summary: An undescribed species identified from the Great Ruaha River.

Original Identification: The first published identification of this species (as *Astatotilapia* sp. ruaha') was by Genner *et al.* (2015), but it was not formally described. A sequence obtained from this this species appeared in Figure 4 of Malinsky et al. (2018, as 'ruaha 2') and again in Svardal et al. (2020) as *Astatotilapia* sp. 'ruaha blue' (figure 1, with illustration).

Original collecting locality: In 2012, this species was collected from several sites in the Great Ruaha River (fig. 123-124), as well as from a fish farm near Rujewa (fig. 125). Large numbers have since been taken from Mtera Lake and at Kidatu Bridge, both on the Great Ruaha River.

Material Examined: Numerous specimens have been collected from the wild since 2012. Adults are large, solidly built with a relatively wide elongated body and a large mouth. Mature males are blue with dark blue-grey unpaired fins and dark grey-black pelvics. The unpaired fins show little or no spotting, apart from the 2-3 (occasionally 4) very large eggspots on the posterior half of the anal fin. These are yellow-orange, surrounded by a thin white margin and a thick dark ring. Notably, there are 3-4 thin red lines between the main bodies of the scales just behind the head. Smaller maturing males often show yellowish-green colour on the flanks, and dark spots on the tailfin and soft dorsal (fig. 124). Adult females are sandy-coloured dorsally, shading to silvery on the flanks and belly (fig. 123, 125). The pelvic and anal fins and the lower part of the tailfin are often yellowish-orange. Sometimes females show around 4 wide dark bars on the flanks and the soft dorsal and upper part of the tailfin sometime have faint dark spots. A few individuals were kept in an aquarium at Bangor. Dominant males had very dark grey unpaired and pelvic fins (fig. 126). https://www.youtube.com/watch?v=uORdSlpqiYA. Preliminary examination of preserved specimens showed that they had relatively large chest scales.

Relationships: A phylogeny based on mitochondrial sequences by Genner *et al.* (2015) suggested this species was the sister group of the Lake Malawi haplochromine radiation. A tree based on full genome sequences (Malinsky *et al.* 2018, fig 4a) suggested that this species (under the name *A.* 'Ruaha 2') was the sister species of *Astatotilapia gigliolii* (under the name *A. tweddlei*) and these were the sister group of a large clade that included the Lake Malawi radiation and many other haplochromines. Later investigation of sequence data of a larger sample supported the relationship between *A.* sp. 'ruaha blue' and *A. gigliolii*, but there was a very strong signal that the Lake Malawi haplochromine species flock was descended from a lineage derived from hybridization between the ancestor of *A.* sp. 'ruaha blue' and the ancestor of a large clade of taxa including the Lake Victoria haplochromine superflock (Svardal *et al.* 2020).

Conclusion: *Astatotilapia* sp. 'ruaha blue' is an undescribed species apparently confined to the Great Ruaha River that is related to *A. gigliolii* and played a major role in the origin of the Lake Malawi haplochromine flock.

Figure 123: *Astatotilapia* sp. 'ruaha blue' adult male (above) and female (below) from Mtera Lake, collected 9 February 2014.

Figure 124: *Astatotilapia* sp. 'ruaha blue' precociously maturing male from a shallow floodplain pool off Great Ruaha River just upstream from Mtera Lake, collected 9 February 2014.

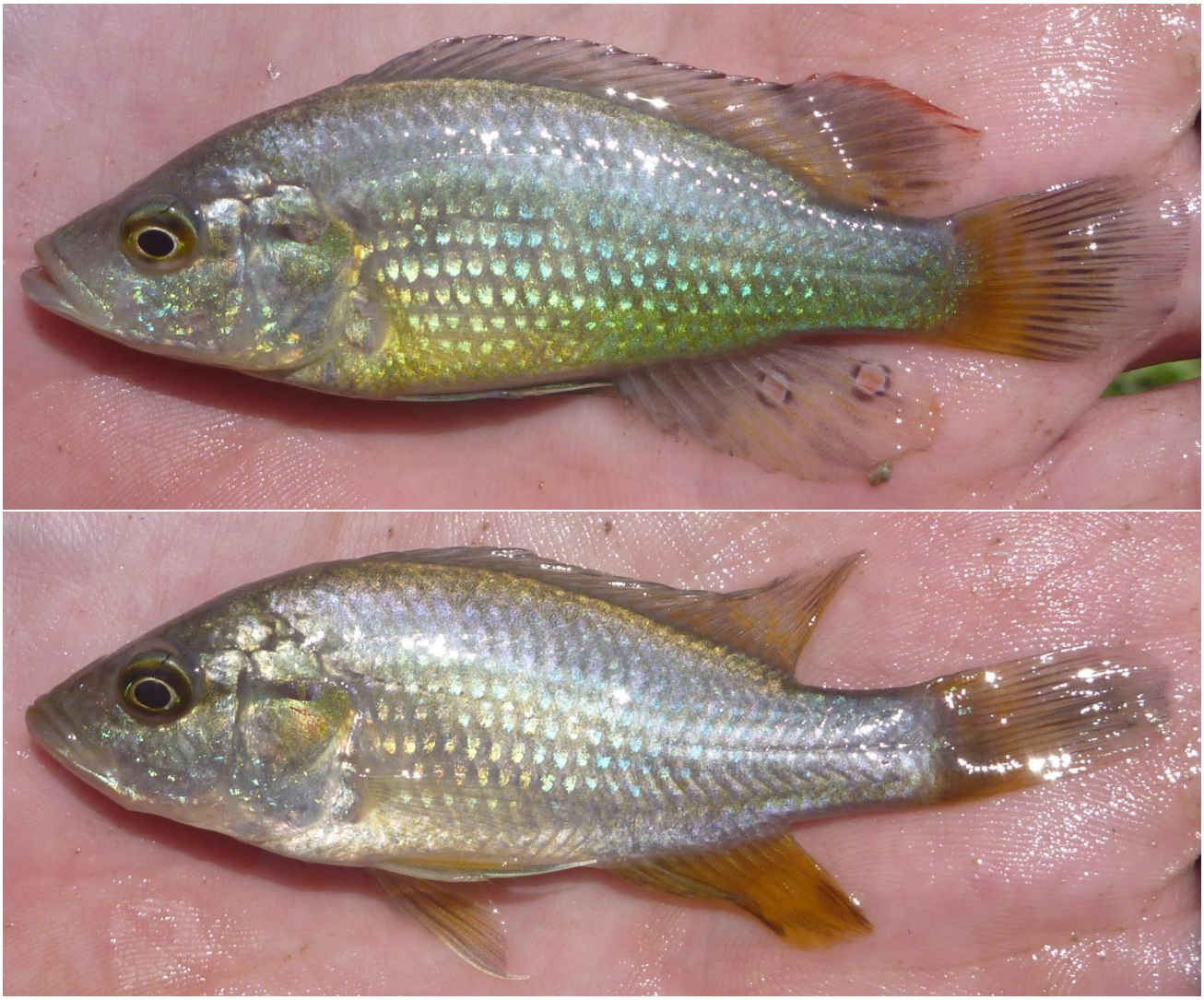

Figure 125: *Astatotilapia* 'ruaha blue' non-breeding male (above) and female from a fish farm at Rujewa, Tanzania. Note the eggspots of the male are orange, surrounded by white and dark grey rings.

Figure 126: *Astatotilapia* sp. 'Ruaha blue' from pool just upstream from Mtera Lake in the aquarium at Bangor University. Screen grabs from video https://www.youtube.com/watch?v=uORdSlpqiYA

Astatotilapia sp. 'ruaha red cheek'

Summary: An undescribed species identified from the Great Ruaha River.

Original Identification: The first published identification of this species (as *Astatotilapia* sp. 'ruaha red cheek') was by Svardal *et al.* (2020), but it was not formally described.

Original collecting locality: In 2014, this species was collected from Kidatu Bridge on the Great Ruaha River, where it was abundant. It was collected at the same site on several subsequent surveys

Material Examined: We have obtained samples the Great Ruaha River at Kidatu in several visits from 2014 onwards, purchasing fish from local traders. In most cases, samples have included male specimens with yellowish bodies and some orange-red colour on the operculum. The unspotted dorsal fin is generally the same colour as the body, but the caudal fin and the distal part of the anal are deep pinkish-red. The caudal fin usually has rows of spots and stripes running parallel to the fin rays. The eggspots are small and orange and in a jumble (not a long row) in the posterior part of the anal fin. The number of eggspots is very variable, from 2 to as many as 10, if partial spots at the fin margins are counted. Fish collected in January and February were relatively drably coloured (fig. 127-129), but those collected in July were bright and had patches of turquoise-blue iridescence and a red margin to the soft dorsal fin, with a prominent black eyestripe (fig. 130), suggesting either they had not been lying around dead for such a long time or that they were in a greater state of reproductive readiness. Smaller males were quite slender, but the larger ones quite deep-bodied, but less laterally compressed than males of *A.* 'longfin'. Mature females collected in January 2017 were generally golden brown with faint spotting in the caudal fin and small eggspots, and did not show any sign of orange/red on the operculum (fig. 131). There are two further possible records of this species. Small haplochromines were found in a sample from the Kilombero River, another tributary of the Rufiji, from 2014, but these specimens were only seen preserved and the colour was uncertain (figure 132). A photograph of a small colourful male was taken on 20th August 2013 from a sample obtained from the Luhiho River (-7.858, 38.962), a tributary of the Rufiji close to the delta. The colour of this specimen is very reminiscent of *A.* sp. 'red cheek', notably the bright orange operculum (fig. 133).

Relationships: A phylogeny based on full genome sequences by Svardal *et al.* (2020) places the species (sample from Kidatu) within the wider Lake Victoria superflock but in a rather basal position, possibly as a sister group to *A. bloyeti.*

Conclusion: *Astatotilapia* sp. 'red cheek' is an undescribed species confined to the Rufiji system, or possibly just to the Great Ruaha downstream from the Mtera Dam.

Figure 127: Male *Astatotilapia* 'ruaha red cheek' collected at Kidatu Bridge, Great Ruaha River, 12-13th February 2014. These specimens had been dead for quite a long time when purchased from traders. Key features visible include the general yellowish body colour, lack of spotting in the dorsal fin, slightly spotted pinkish caudal fin and variable number orange eggspots on the anal fin. There are hints of orange-red on the operculum.

Figure 128: Male *Astatotilapia* 'ruaha red cheek' collected at Kidatu Bridge, Great Ruaha River, 14th January 2017. This specimen has a similar body shape to the 2014 specimens but has a much more intense coloration. It retains the overall yellow body colour, pinkish caudal fin, unspotted dorsal fin and small orange anal fin eggspots, but in addition shows a clearly reddish colour on the operculum, and pink anal fin, more whitish around the eggspots.

Figure 129: Male *Astatotilapia* 'ruaha red cheek' collected at Kidatu Bridge, Great Ruaha River, 14th January 2017. These specimens both have only 2 anal fin eggspots. The smaller fish on the right shows relatively little development of male breeding dress.

Figure 130: Male *Astatotilapia* 'ruaha red cheek' collected at Kidatu Bridge, Great Ruaha River, 5th July 2017. These small slender specimens show unusually large amounts of bright turquoise-blue iridescence and red margin to the soft dorsal fin, as well as red in the posterior part of the pelvic fins.

Figure 131: Female *Astatotilapia* 'ruaha red cheek' collected at Kidatu Bridge, Great Ruaha River, 13th January 2017.

Figure 132: Possible male *Astatotilapia* 'ruaha red cheek' collected in the Kilombero catchment 8th March 2014.

Figure 133: Male *Astatotilapia* cf. sp. 'red cheek' collected from the Luhiho River (-7.858, 38.962), a tributary of the Rufiji delta 20th August 2013.

Astatotilapia sp. 'longfin'

Summary: An undescribed species identified from the Great Ruaha & Kilombero Rivers (Rufiji System), Lake Sulungali and Lake Igombe.

Original Identification: The first published identification of this species (as *Astatotilapia* sp. 'longfin yellow') was by Svardal *et al.* (2020), but it was not formally described nor illustrated.

Original collecting locality: In 2014, a few specimens of this species were collected from Kidatu Bridge on the Great Ruaha River.

Material Examined: We have sampled the Great Ruaha River (Rufiji System) at Kidatu in several visits from 2014 onwards, purchasing fish from local traders. Small numbers of this species occurred in several samples (figs. 134, 136). It also appeared in a sample from Lake Igombe in the upper Malagarasi catchment, co-occurring with *A. bloyeti* and *A. cf. stappersii* A (fig.137). In 2017, several brightly coloured specimens were collected at Lake Sulungali, a closed basin near Dodoma (fig. 138). This lake is relatively poorly known in published literature: no other haplochromines were observed in the catches of local fishermen, but we also found large numbers of *Oreochromis niloticus. O. amphimelas, Clarias* spp. and *Enteromius paludinosus*. A single large female was collected at Kilombero Ferry on the Kilombero River, another tributary of the Rufiji (fig. 135). *Astatotilapia* sp. 'longfin' attains a relatively large size (up to 96mm SL) and has a large, upwardly-angled mouth, deep cheek and a strongly laterally compressed body. The pelvic fins of mature males are particularly long, often extending well past the base of the first anal soft ray. Mature males are generally yellowish, often with a strong black stripe through the eye. The head and back are generally greyish. The dorsal fin generally appears greyish and lacks spots. The caudal fin is often pinkish with faint darker spots, but in some (ripe?) fish the caudal is dark grey basally but brilliant deep red distally. The pelvic fins are dark grey to black. The anal fin is pinkish to a brilliant deep red, but paler in the vicinity of the eggspots. The anal fin eggspots are variable in number (3-7, if partial spots on the fin margin are counted). They sometimes appear quite dull orange and inconspicuous, but in other individuals (closer to breeding condition?) they are bright with contrasting pale and dark rings around them. Females are countershaded, silvery to golden, sometimes with the pelvic, anal and lower half of the caudal fins tinted deep yellow.

Relationships: A phylogeny based on full genome sequences by Svardal *et al.* (2020) indicated close affinities with *A.* sp. 'rufiji blue' and places these within the wider Lake Victoria superflock, as a sister group to a large clade containing the Victoria, Kivu and Rukwa radiations.

Conclusion: *Astatotilapia* sp. 'longfin' is an undescribed species so far recorded in the Great Ruaha downstream from the Mtera Dam, Lake Sulungali and Lake Igombe in the upper Malagarasi catchment.

Figure 134: Male *Astatotilapia* sp. 'longfin' collected at Kidatu Bridge, Great Ruaha River, 12-13th February 2014.

Figure 135: Female *Astatotilapia* sp. 'longfin' collected at Kilombero Ferry, Rufji System, 6th July 2017.

Figure 136: Male *Astatotilapia* sp. 'longfin' collected at Kidatu Bridge, Great Ruaha River, 1st August 2018.

Figure 137: Male *Astatotilapia* sp. 'longfin' collected at Lake Igombe, in the upper Malagarasi catchment, 2nd August 2016.

Figure 138: Male (above, centre) and female (below) *Astatotilapia* sp. 'longfin' collected at Lake Sulungali, near Dodoma, 11th January 2017.

Astatotilapia sp. 'rufiji blue'

Summary: An undescribed species identified from the lower part of the Rufiji basin. Specimens from Lake Mansi are very dark and may represent an additional species.

Original Identification: The first published identification of this species was in Genner *et al.* (2015, as *A.* 'blue rufiji') then in Malinsky et al. (2018: Figure 4, as 'rufiji blue') and sequences and an illustration of this species (again as *A.* sp. 'rufiji blue') appeared in Svardal *et al.* (2020). It has not been not formally described.

Original collecting locality: In 2012, a few specimens of this species was collected from two oxbow lakes at Utete near to the Rufiji delta.

Material Examined: In 2013, the first specimens were collected from two oxbow lakes near Utete just inland from the Rufiji delta about 27-28m above sea level (fig. 139-140), but later samples were collected from Lake Mansi in 2015 (fig 141-142). This shallow swampy lake lies about 85km to the north of Utete and about 50km south of Dar Es Salaam, at about 64m above sea level. *Astatotilapia* sp. 'rufiji blue' was the only haplochromine found at Utete, but it co-occurred with *Astatotilapia gigliolii* in Lake Mansi. The Utete specimens were bluish, but the Mansi specimens were darker, with some almost black with broad red margins to the caudal and anal fins. Specimens from both populations shared an overall dark body colour, few (1-3) rather inconspicuous posteriorly placed eggspots, little or no spotting on the dorsal and caudal fins, long pelvic fins, small chest scales and a large upwardly slanted mouth and deep cheek. These traits are also shared with *A.* sp. 'longfin', but that species has a yellow male breeding colour and a deeper, more laterally compressed body. Some caveats may be appropriate here: we have seen that other haplochromines may show colour polymorphism, seasonal changes or post-mortem colour change. The photo of a long-dead specimen from Utete suggests a freshly collected blue fish might look yellow after a time (fig. 139).

Relationships: A phylogeny based on full genome sequences by Svardal *et al.* (2020) clustered the Mansi and Utete specimens together, with *A.* sp. 'longfin' from Kidatu as their sister taxon. These were placed within the wider Lake Victoria superflock, as a sister group to a large clade containing the Victoria, Kivu and Rukwa radiations.

Conclusion: *Astatotilapia* sp. 'rufiji blue' is an undescribed species so far recorded in the Rufiji catchment and perhaps also Lake Mansi. It is closely related to *A.* sp. 'longfin'.

Figure 139: *Astatotilapia* sp 'rufiji blue' males collected at Utete (-7.991, 38.749), an oxbow lake on the Rufiji River on 18th August 2013. The upper fish is shown freshly collected, the lower one photographed after it had been dead for some time, showing loss of much of the blue coloration.

Figure 140: *Astatotilapia* sp 'rufiji blue' male collected at an oxbow lake near Utete, near the 'ChemChemi' hotspring (-8.00, 38.77) on the Rufiji River 19th August 2013.

Figure 141: *Astatotilapia* sp 'rufiji blue' male collected at Lake Mansi (-7.263, 39.158), a shallow coastal lake about 50km south of Dar Es Salaam, 10th March 2015.

Figure 142: *Astatotilapia* sp 'rufiji blue' male collected at Lake Mansi, 5th June 2015.

Discussion

The major findings of our study were the clarification of the type locality, current range, field identification features and synonymies of *Astatotilapia bloyeti* and *A. gigliolii*, and the recording of four undescribed taxa from the Rufiji system and elsewhere in central Tanzania. Our investigations of the catchments of Lake Tanganyika and Rukwa were more preliminary, while the Lake Malawi catchment has already been largely covered in previous works (Malinsky *et al.* 2015, 2018; Turner *et al.* 2019).

The status of the taxon *Astatotilapia bloyeti* has been confused for many years, often being used as a catch-all for poorly-known riverine haplochromine populations from a wide geographic range. Eschmeyer (Fricke *et al.* 2019) gives a range across central Africa from Mali to East Africa. FishBase, however, following Snoeks (1994), states that the species is likely to be confined to the coastal river systems of Tanzania, and that records from Uganda, Kenya, the Nile system and Chad likely refer to other species. IUCN report the taxon as data deficient and give a confirmed range in the Upper Pangani including Lake Jipe but a possible range including much of the southern half of Kenya, and south along the coastal stretches of the Wami and Rufiji systems, as far inland as Morogoro. The southern extension of the range probably reflects confusion with *A. gigliolii*.

Recent photographic records from Kenya are lacking, at least in the public domain. *Astatotilapia bloyeti* can be assumed to be present in Kenyan parts of the Pangani catchment, including Lakes Jipe and Chala. However, the specimen illustrated in Okeyo & Ojwang (2015) and photographed by Frank Teigler appears to be an aquarium specimen of *Astatotilapia gigliolii*. No source location is given, but *A. gigliolii* is not known from Kenya, and indeed the closest record we can find is some 230km away at the type locality near Bagamoyo. Other illustrations of riverine haplochromines from Kenya are mainly of colourless preserved specimens of little value in species identification. Thus, the northernmost limit of *A. bloyeti*'s range remains uncertain. However, there is no good reason to propose that it is found in the Nile, Mali or Chad: such records must surely refer to other species, including the recently-described *Astatotilapia tchadensis* (Trape 2016) or the undescribed *Haplochromis sp.* 'Ismailia' (Schraml 2010a, b).

A slight uncertainty remains over the status of *Astatotilapia sparsidens*, originally described from the vicinity of Lake Manyara: specimens from there, along with those from the Pangani system group together and are phylogenetically resolved as closely related to, and a possible sister group to the populations from the Wami and Malagarasi. This would be consistent with them being an allopatric sister species, but at present we can see no clear morphological distinction between the two groups and so we are content to maintain the current synonymy unless further evidence becomes available to warrant specific distinction.

Our results appear to shed some light on the haplochromine phylogeny shown by Meier *et al.* (2017) in an investigation primarily focussed on the hybrid origins of the Lake Victoria cichlid radiation.

There are two clear phylogenetic clusters reported by Meier *et al.* (2017) tentatively including specimens of *Astatotilapia bloyeti* in very different parts of the tree, obtained from ddRAD sequencing, a method that is based on a genome-wide sample of DNA sequence information, but using much less data than full sequences. One cluster contains specimens labelled *A. paludinosa*

from the Malagarasi, *A. sparsidens* from Lake Manyara and *A. sp.* from the Wami. The latter is the type locality for *A. bloyeti*, which was the sole haplochromine we found in that system. All of these would make sense as *A. bloyeti*, as would their position on the tree close to the Lake Victoria radiation (see Svardal *et al.* 2020). However, a fourth taxon, resolved as the sister group of the Manyara sample, and labelled as *A. bloyeti* is reported as coming from the Mkuzi River/ Ruaha, but we did not find any *A. bloyeti* in the Ruaha nor any other part of the Rufiji system. However, the supplementary material to Meier *et al.* states that the Mkuzi is in fact a tributary of the Pangani, not the Ruaha. If so, then this indeed fits perfectly with the results of full genome sequence tree of Svardal *et al.* (2020) in which the Pangani and Manyara specimens cluster together. Thus, it seems probable that all four of these sequences represent *A. bloyeti*, although it is notable that these are actually resolved as paraphyletic with respect to another clade comprised of *'Haplochromis' gracilior* from Lake Kivu and *Thoracochromis pharyngalis* from Lake Edward, perhaps suggesting past introgression (see Meier *et al.* 2017, supplementary material).

The other cluster reported by Meier *et al.* (2017) contains *A. tweddlei* from Lake Chilwa, *A. sp.* from the Ruvuma and *Haplochromis sp.* from the Ruvu river. These, we suggest, are all *Astatotilapia gigliolii*, which we have found in all of these localities. *Astatotilapia gigliolii* co-occurs with *A. calliptera* in the Ruvuma and Lake Chilwa, but *A. calliptera* clearly nests within the Lake Malawi haplochromine clade in all recent genome-wide trees (Meier *et al.* 2017; Malinsky *et al.* 2018; Svardal *et al.* 2020). *Astatotilapia gigliolii* is the only haplochromine recorded from the 'southern Ruvu', and it is unlikely that the sample was collected from the 'northern' Ruvu, as this is a tributary of the Pangani, and would presumably have been indicated as such in the supplementary material table in Meier *et al.* Besides, the only known *Astatotilapia* from the Pangani is *A. bloyeti* of the Pangani/Manyara subclade and these we have seen appear in a different part of the tree. So we can be confident that three of the four sequences in this group represent *A. gigliolii*. More confusing is the appearance of a single taxon labelled as *Astatotilapia cf. bloyeti* Wami River/*kilossana* Sonjo river (see also Meier et al. 2017 supplementary figure 3, where these are shown as sister taxa each of two specimens). The Sonjo River is a tributary of the Rufiji, at least part of which lies within the Udzungwa National Park (van Heusden 2012), while the Wami is a quite different river entering the Indian Ocean north of Dar Es Salaam and Bagamoyo. From our experience, *A. bloyeti* is present in the Wami but absent from the Rufiji, while the reverse is true of *A. gigliolii*. It thus seems highly improbable that specimens from these two localities should have similar ddRAD sequences. However, the clustering of this sample with Chilwa, Ruvuma and Ruvu samples would be entirely consistent with these being specimen of *A. gigliolii*, perhaps with some specimens misattributed to the Wami River.

The names *Haplochromis cf. kilossana* 'Sonjo' and *Haplochromis cf. kilossana* 'Ruaha' were also used in mitochondrial DNA study by Schedel *et al.* (2019). The origin of this identification can be gleaned from a publication in an aquarium hobby magazine reporting the discovery of a new 'goby cichlid' from the Sonjo River by van Heusden (2012)- at the time reported as *Orthochromis* sp. 'sonjo' but later formally described as *Haplochromis vanheusdeni* Schedel, Friel & Schliewen 2014. In passing in van Heusden's article, an illustration of an *Astatotilapia* specimen from the Sonjo River is presented and this is identified (by U.K. Schliewen) as corresponding to *Paratilapia kilossana*, now known as *A. bloyeti*. As a result, the name *Astatotilapia (=Haplochromis) kilossana* was 'revived' from disuse (Schliewen's statement of synonymy notwithstanding) and applied to a number of specimens from the Sonjo, the Ruaha and perhaps elsewhere, both in the aquarium hobby and the

cichlid research literature. For example, illustrations labelled as *Haplochromis kilossana* alive in the aquarium can be seen on http://www.amazon-exotic-import.de/Gallerie/Cichliden/Seiten/Haplochromis%20kilossana.htm. We identify this as *A. gigliolii*.

We believe that the identification in van Heusden's paper is erroneous because (i) as discussed above, the types of *Paratilapia kilossana* were collected from Kilosa on the Wami system, not Kidatu on the Rufiji; (ii) van Heusden's illustration shows a specimen of *A. gigliolii* (abundant in our surveys from the Rufiji), not *A. bloyeti* (for which there are no records in any part of the Rufiji). Van Heusden illustrates a single adult male photographed in the field in a small glass photo-tank. The fish appears to be alive and is being held against the front glass by someone's hand. The male's colours are relatively drab, and largely obscured by a strong 'fright pattern' of horizontal and vertical dark brown bars, but the chest at least seems metallic yellowish, which could fit with either *A. bloyeti* or *A. gigliolii*. In our experience, the fishes are easier to distinguish post-mortem, in which more of the dominant male's live coloration appears to be visible. In the van Heusden photo, hints of the dark spots on the anterior portion on the flank scales are visible, but the red coloration of those of *A. gigliolii* is not evident. However, the dorsal fin is strongly spotted well forward into the spinous portion, which is consistent with *A. gigliolii*, but not *A. bloyeti*. Furthermore, the anal fin eggspots are set in a long row with the anteriormost spot far forwards, probably in the membrane behind the first anal soft ray, which is typical in *A. gigliolii* and relatively rare in *A. bloyeti*. So, overall Meier *et al.*'s second 'bloyeti' clade appears to represent *Astatotilapia gigliolii*, and its position in the tree fits well with that obtained from full genome sequences of *A. gigliolii* by Svardal *et al.* (2020).

Finally, in terms of interpreting the tree in Meier *et al.* (2017), one of the key taxa involved in the determination of hybrid ancestry to the Lake Victoria radiation is labelled as *Astatotilapia stappersi* (*sic*) from the Kalambo River, collected by W. Salzburger. The illustration of this species appears to be identical to the image (albeit reversed) used to illustrate *Astatotilapia sp.* 'chipwa' in the Meyer *et al*. (2015) paper from the Salzburger lab and cropped from the image we used in figure 118, taken by A. Indermaur, from the Salzburger lab. The Kalambo River mouth is the source of one of the populations of *A. sp.*'chipwa' discussed by Meyer *et al.* (2015). That study also included a number of specimens of *A. stappersii*, but none were sourced from the Kalambo. Therefore, we suggest that the sequence in Meier *et al.* (2017) is likely to represent *A. sp.* 'chipwa' rather than *A. stappersii*.

A mitochondrial DNA study by Hermann *et al.* (2011) focussed on a haplochromine population from the Ngare Nanyuki River in northern Tanzania (-3.189, 36.853). This river is an afferent of Lake Amboseli, a largely desiccated, occasionally highly saline, endorheic lake that lies mostly in Kenya. Mitochondrial control region sequences placed this population very close to those from Lake Chala, Babati, Manyara and the Pangani River. The closest relationship was with haplochromines from Lake Chala, which the authors interpret as indicative of a former natural connection between the two water bodies. However, subsequent authors have suggested that the haplochromines in Chala are not native (Moser *et al.* 2018; Dieleman *et al.* 2019). We would identify all these as representing the 'sparsidens' lineage of *Astatotilapia bloyeti*, which is consistent with the illustration of a freshly collected male from Ngare Nanyuki. The deeper relationships within the tree were poorly supported by Bayesian posteriors, but also included samples in distant parts of the tree that looked like they represented the Wami-Malagarasi lineage of *A. bloyeti* (Hermann *et al.* 2011). Many of the sequences used in the Hermann study were downloaded from GenBank and were originally obtained by Nagl *et al.* (2000). It seems likely that Nagl's lineages I (Malagarasi), III (Wami, Pangani), VI

(Babati, Manyara) and VII (Malagarasi) all represent *A. bloyeti*. One anomalous result on figure 1 of Nagl *et al.*'s paper is the occurrence in Lake Singida of a haplotype from a group (VC) otherwise known only from Lake Victoria proper: this does not seem to be mentioned in the text and does not appear in any of the trees in the paper. Assuming it is not a misprint, how can we explain a core Lake Victoria haplotype occurring in Lake Singida? It is notable that Singida was stocked with *Oreochromis esculentus* from Lake Victoria a long time ago (Trewavas 1983): indeed *O. esculentus* is often referred to as 'Singida Tilapia' in Tanzania (Shechonge *et al.* 2018). It is possible that the introduction of *Oreochromis esculentus* to Lake Singida could also have accidentally transferred Lake Victoria haplochromines as a 'contaminant'. This may also explain the occurrence of *A. cf. stappersii* B, which clusters closely with Lake Victoria sequences in our sample from the Mwamapuli Dam.

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References

Banyankimbona G., Vreven E.J. & Snoeks J. 2013. A revision of the genus *Astatoreochromis* (Teleostei, Cichlidae), East Africa. *European Journal of Taxonomy* 39: 1-21.

Beidelman T.O. 1962. A history of Ukaguru: 1857-1916. *Tanzania Notes and Records* 1962: 11-39.

Beidelman T.O. 2012. *The Culture of Colonialism: the cultural subjection of Ukaguru.* Indiana University Press.

Bloyet A. 1890. De Zanzibar à la station Kondoa. *Bulletin de la Société de Géographie de Paris* 7e série t. 11: 350-364. (map available from University of Illinois at Urbana-Champaign. University Library).

Borodin N.A. 1936. On a collection of freshwater fishes from lakes Nyasa, Tanganyika and Viktoria in Central Afrika. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere (Jena)* 68: 1-34, Pl. 1.

Boulenger, G. A. 1899. A revision of the African and Syrian fishes of the family Cichlidae. Part II. *Proceedings of the Zoological Society of London,* 1899 (1): 98-143, Pls. 11-12.

Boulenger G.A. 1902. List of the fishes collected by Mr. W. L. S. Loat at Gondokoro. *Annals and Magazine of Natural History* (Series 7) 10: 260-264.

Boulenger G.A. 1907. Description of a new cichlid fish from Portuguese East Africa. *Annals and Magazine of Natural History* (Series 7) 20: 50.

Boulenger G.A. 1915. *Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History).* London. v. 3: i-xii + 1-526

Dieleman J., Van Bocklaer B., Nyingi W.D., Lyaruu A. & Verschuren D. 2019. Recurrent changes in cichlid dentition linked to climate-driven lake-level fluctuations. *Ecosphere* 10: e02664

Eccles D.H. & Trewavas E. 1989. *Malawian Cichlid Fishes: A Classification of Some Haplochromine Genera.* Lake Fish Movies: Herten, Germany.

Eschmeyer W. N. (ed.) 1998. *Catalog of Fishes.* Center for Biodiversity Research and Information, Special Publication 1. California Academy of Sciences. vols. 1-3: 1-2905.

Fricke R., Eschmeyer W.N, & van der Laan R. (eds) 2020. Eschmeyer's Catalog of fishes: genera, species, references. (http://researcharchive.calacademy.org/research/ ichthyology/catalog/fishcatmain.asp). Electronic version accessed 3 January 2020.

Genner M.J.& Haesler M.P. 2010. Pliocene isolation of a north-west Saharan cichlid fish. *Journal of Fish Biology* **76:** 435–441.

Genner M.J., Ngatunga B.P., Mzighani S., Smith A. & Turner G.F. 2015. Geographic ancestry of Lake Malawi's fish diversity. *Biology Letters* 11: 20150232

Gov.UK (2019) https://www.gov.uk/foreign-travel-advice/democratic-republic-of-the-congo (accessed 6 December 2019)

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

Greenwood P.H., 1980a. Towards a phyletic classification of the 'genus' Haplochromis (Pisces, Cichlidae) and related taxa. Part II: the species from Lakes Victoria, Nabugabo, Edward. *Bulletin of the British Museum of Natural History (Zoology)* 39: 1-101.

Greenwood P.H. 1980b. A new species of cichlid fish from the Malagarasi swamps and river (Tanzania, East Africa). *Bulletin of the British Museum of Natural History (Zoology)* 38: 159-163

Günther A. 1894a. Second report on the reptiles, batrachians, and fishes transmitted by Mr. H. H. Johnston, C. B., from British Central Africa. *Proceedings of the Zoological Society of London* 1893 (pt 4): 616-628, Pls. 53-57

Günther A. 1894b. Descriptions of the reptiles and fishes collected by Mr. E. Coode-Hore on Lake Tanganyika. *Proceedings of the Zoological Society of London* 1893: 628-632.

Hassing P. & Bennett N.R. 1962. A journey across Tanganyika in 1886. *Tanzania Notes and Records* 1962: 129-148.

Hemingway E. 1935. *Green Hills of Africa*. Charles Scribner's Sons.

Hermann C.M., Sefc K.M. & Koblmüller S. 2011. Ancient origin and recent divergence of a haplochromine cichlid lineage from isolated water bodies in the East African Rift system. *Journal of Fish Biology* 79: 1356-1369.

van Heusden H. 2010. A new *Orthochromis* species from Tanzania. *CichlidNews* 21(4): 12-17.

Hilgendorf F.M. 1888. Fische aus dem Victoria-Nyanza (Ukerewe-See), gesammelt von dem verstorbenen Dr. G. A. Fischer. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1888: 75-79.

Hilgendorf F.M. 1905. Fische von Deutsch und Englisch Ost-Afrika. Gesammelt von Oscar Neumann 1893-1895. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere (Jena)* 22: 405-420.

Hilgendorf F. & Pappenheim P. 1903. Die Fischfauna des Rukwa-Sees. *Sitzungsberichte der Gesellschaft naturforschender Freunde in Berlin* 6: 259-271.

Hoogerhoud R.J.C. 1984. A taxonomic reconsideration of the haplochromine genera *Gaurochromis* Greenwood, 1980 and *Labrochromis* Regan, 1920. (Pisces, Cichlidae). *Netherlands Journal of Zoology* 34: 539-565

Hoogerhoud R.J.C. & Witte F. 1981. Revision of species from the *'Haplochromis' empodisma* group. *Netherlands Journal of Zoology* 31: 232-273

Hsu L.-L. 2019. Phylogenetic and population genetic structure of riverine *Astatotilapia* cichlid fishes of East Africa. Unpublished MSc thesis, Bristol University.

Indermaur A. 2011. *Astatotilapia stappersii* (Poll, 1943). Cichlid Room Companion. Retrieved on December 06, 2019, from: https://cichlidae.com/species.php?id=783.

IUCN 2019. IUCN Red List of Threatened Species. Red List of Threatened Species. Downloaded on December 2019.

Jackson P.B.N. 1985. *Astatotilapia tweddlei*, a new species of fluviatile haplochromine cichlid fish from Lakes Chilwa and Chiuta, Malawi, with zoogeographical notes. *J.L.B Smith Institute of Ichthyology Special Publication* No. 38: 1-10.

Joyce D.A., Lunt D.H., Genner M.J., Turner G.F., Bills R. & Seehausen O. 2011. Repeated colonization and hybridization characterize the Lake Malawi cichlids. *Current Biology* 21: R108-109.

Jubb R.A. 1967. *Freshwater Fishes of Southern Africa.* A.A. Balkema, Cape Town, RSA.

Konings A. 2016. *Lake Malawi Cichlids in their Natural Habitat, 5th Edition.* Cichlid Press, El Paso, Texas, USA.

Lacepède B.G.E. 1802. *Histoire naturelle des poissons*. v. 4: i-xliv + 1-728, Pl. 1-16.

Ladiges W., von Wahlert G. & Mohr E.1958. Die Typen und Typoide der Fischsammlung des Hamburgischen Zoologischen Staatsinstituts und Zoologischen Museums. *Mitteilungen aus dem Hamburgischen Zoologischen Institut* 56: 155-167.

Last J.T. 1882. A journey into the Nguru country from Mamboia, East Central Africa. *Proceedings of the Royal Geographical Society and Monthly Record of Geography* 4: 148-157.

Loh, Y.-H.-E., Bezault, E., Muenzel, F.M., Roberts, R.B., Loh Y.-H.-E., Bezault E., Muenzel F.M., Roberts R.B., Swofford R., Barluenga M., Kidd C.E., Howe A.E., Di Palma F., Lindblad-Toh K., Hey J., Seehausen O., Salzburger W., Kocher T.D. & Streelman J.T. 2013. Origins of shared genetic variation in African cichlids. *Molecular Biology and Evolution* 30: 906-917.

Lortet L. 1883. Études zoologiques sur la faune du lac de Tibériade, suivies d'un aperçu sur la faune des lacs d'Antioche et de Homs. I. Poissons et reptiles du lac de Tibériade et de quelques autres parties de la Syrie. *Archives du Muséum d'Histoire Naturelle de Lyon* 3: 99-189, Pls. 6-18.

Malinsky M., Challis R., Tyers A.M., Schiffels S., Terai Y., Ngatunga B.P., Miska E.A., Durbin R., Genner M.J. & Turner G.F. 2015. Genomic islands of speciation separate cichlid ecomorphs in an East African crater lake. *Science* 350: 1493-1498.

Malinsky M., Svardal H., Tyers A.M., Miska E.A., Genner M.J., Turner G.F. & Durbin R. 2018. Whole-genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow. *Nature Ecology and Evolution* 2: 1940-1955.

Mbilinyi B., Kashaigili J.J., Mwamakimbullah R. & Sohngorwa A.M. 2012. Maps of Wildlife Management Areas (WMAs) in Tanzania: Consultancy Report to WWF-TCO. Available online at: https://www.ucl.ac.uk/pima/docs/reference/06_final_mapping_report.pdf

Meier J.I., Marques D.A., Mwaiko S., Wagner C.E., Excoffier L. & Seehausen O. 2017. Ancient hybridization fuels rapid cichlid fish adaptive radiations. *Nature Communications* 8: 14363.

Meyer B.S., Indermaur A., Ehrensperger X., Egger B., Banyankimbona G., Snoeks J. & Salzburger W. 2015. Back to Tanganyika: a case of recent trans-species-flock dispersal in East African haplochromine cichlid fishes. *Royal Society Openscience* 2:140498.

Meyer H.J. 1905. *Meyers Geographischer Hand-Atlas.* Bibliographisches Institut Leipzig (https://commons.wikimedia.org/wiki/File:094_deutsch-ostafrika_(1905).png)

Meyers J. 1985. *Hemingway: A Biography*. London: Macmillan. ISBN 0-333-42126-4.

Morgenstern R. 2011. *Astatotilapia swynnertoni* (Boulenger, 1907). *Cichlid Room Companion*. Retrieved on August 03, 2019, from: https://www.cichlidae.com/species.php?id=784

Moser F.N., Van Rijssel J.C., Mwaiko S., Meier J.I. Ngatunga B. & Seehausen, O. 2018. The onset of ecological diversification 50 years after colonization of a crater lake by haplochromine cichlid fishes. *Proceedings of the Royal Society London series B* 285:20180171.

Nagl S., Tichy H., Mayer W.E., Takezaki N., Takahata N. & Klein J. 2000. The origin and age of haplochromine fishes in Lake Victoria. *Proceedings of the Royal Society London series B.* 267: 1049–1061.

Neumann O. 1895. Neumann's Journey in East Africa. *Geographical Journal* 6, 274-277.

Nichols J.T. & La Monte F.R. 1931. New cichlid fishes from Lake Nyassa. *American Museum Novitates* 451: 1-4.

Nichols P., Genner M.J., van Oosterhout C., Smith A., Parsons P., Sungani H., Swanstrom J. & Joyce D.A. 2015. Secondary contact seeds phenotypic novelty in cichlid fishes. *Proceedings of the Royal Society B Biological Sciences* 282: 20142272.

van Oijen M.J.P. 1996 The generic classification of the haplochromine cichlids of Lake Victoria, East Africa. *Zoologische Verhandelingen Leiden* 302: 57-110.

van Oijen M.J.P., Snoeks J., Skelton P.H., Maréchal C. & Teugels G.G. 1991. *Haplochromis*, pp. 100-184 in: Daget J., Grosse J.-P., Teugels G.G. & Thys van den Audenaerde D.F.E. (eds.) *Check-list of the freshwater fishes of Africa. CLOFFA.* ISBN Bruxelles, MRAC Tervuren, ORSTOM Paris. v. 4: i-xii + 1-740

Okeyo D.O. & Ojwang W.O. 2016 *A Photographic Guide to the Freshwater Fishes of Kenya.* Seriously Fish (online).

Pauquet G., Salzburger W. & Egger B. 2018. The puzzling phylogeography of the haplochromine cichlid fish *Astatotilapia burtoni*. *Ecology & Evolution* 8:5637–48.

Parsons P.J., Bridle J.R., Rüber L. & Genner M.J. 2017. Evolutionary divergence in life history traits among populations of the Lake Malawi cichlid fish *Astatotilapia calliptera*. *Ecology & Evolution* 7: 8488–506.

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, Pls. 4-7.

Peterson E.N., Cline M.E., Moore E.C., Roberts N.B, Roberts R.B. 2017. Genetic sex determination in *Astatotilapia calliptera*, a prototype species for the Lake Malawi cichlid radiation. *The Science of Nature* 104: 41.

Pfeffer G.J. 1893. Ostafrikanische Fische gesammelt von Herrn Dr. F. Stuhlmann in Jahre 1888 und 1889. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* 10: 131-177.

Pfeffer G.J. 1896. *Die Thierwelt Ost-Afrikas und der Nachbargebiete*. *Lief. v. Die Fische Ost-Afrikas.* v. 3: i-xviii + 1-72.

Poll M. 1943. Descriptions de poissons nouveaux du Lac Tanganika, appartenant aux familles des Clariidae et Cichlidae. *Revue de Zoologie et de Botanique Africaines* 37: 305-318.

Poll M. 1946. Révision de la faune ichthyologique du lac Tanganika. *Annales du Musée du Congo Belge*. Serie 1; 4: 141-364.

Regan C.T. 1922a. The cichlid fishes of Lake Nyassa. Proceedings of the Zoological Society of London 1921 (pt 4) (no. 36): 675-727, Pls. 1-6.

Regan, C.T. 1922b. 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) v. 10 (no. 57): 249-264.

Regan, C. T. 1922c. The cichlid fishes of Lake Victoria. Proceedings of the Zoological Society of London 1922 (pt 1) (no. 9): 157-191, Pls. 1-4.

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**, 17.

Sauvage H.-E. 1883. Description de quelques poissons de la collection du Muséum d'histoire naturelle. *Bulletin de la Société philomathique de Paris* 7: 156-161.

Schedel F.D.B., Friel J.P. & Schliewen U.K. 2014. *Haplochromis vanheusdeni*, a new haplochromine cichlid species from the Great Ruaha River drainage, Rufiji basin, Tanzania (Teleostei, Perciformes, Cichlidae). *Spixiana* 37: 135-149.

Schedel F.D.B., Vreven E.J.W.M.N., Manda B.K., Abwe E., Manda B.K. & Schliewen UK. 2018. Description of five new rheophilic *Orthochromis* species (Teleostei: Cichlidae) from the upper Congo drainage in Zambia and the Democratic Republic of the Congo. *Zootaxa* 4461: 301–49.

Schedel F.D.B., Muzilova, Z. & Schliewen U.K. 2019. East African cichlid lineages (Teleostei: Cichlidae) might be older than their ancient host lakes: new divergence estimates for the east African cichlid radiation. *BMC Evolutionary Biology.* 19:94.

Schraml E. 2010a. In search of haplochromines in Egypt 1- Ismailia. *Eggspots* 4: 5-11.

Schraml E 2010b. A comparison of *Haplochromis* sp. 'Ismailia' with other North African species. *Eggspots* 4: 12-24.

Schwarzer J., Swartz E.R., Vreven E., Snoeks J., Cotterill F.P., Misof B. & Schliewen U.K. 2012 Repeated transwatershed hybridization among haplochromine cichlids (Cichlidae) was triggered by Neogene landscape evolution. *Proceedings of the Royal Society of London Series B* **279:** 4389–4398.

Seegers L. 1996. The fishes of the Lake Rukwa drainage. *Annales Musée Royal de l'Afrique Centrale, Tervuren, Sciences Zoologiques* 278: 1-407.

Seehausen O. 1996. *Lake Victoria Rock Cichlids: Taxonomy, Ecology and Distribution.* Verduyn Cichlids, Zevenhuizen, 304 pp.

Shechonge A., B.P. Ngatunga, S.J. Bradbeer, J.J. Day, J.J. Freer, A.G.P. Ford, J. Kihedu, T. Richmond, S. Mzighani, A.M. Smith, E.A. Sweke, R. Tamatamah, A.M. Tyers, G.F. Turner & M.J. Genner. 2018. Widespread colonization of Tanzanian catchments by introduced *Oreochromis* tilapia fishes: the legacy from decades of deliberate introduction. *Hydrobiologia* 832: 235-253.

Skelton P.H. 1993. *A Complete Guide to the Freshwater Fishes of Southern Africa.* Southern Book Publishers, RSA.

Snoeks, J. 1994. The haplochromines (Teleostei, Cichlidae) of Lake Kivu (East Africa): a taxonomic revision with notes on their ecology. *Ann. Mus. R. Afr. Centr., Sci. Zool.* 270:1-221.

Snoeks J. 2004. Material and methods, pp. 12-19 in Snoeks J. (ed.) *The cichlid diversity of Lake Malawi/Nyasa/Niassa: identification, distribution and taxonomy.* Cichlid Press, El Paso, Texas. Pp. 1-360.

Steindachner F. 1914. Bericht über die ichthyologischen Aufsammlungen der Brüder Adolf und Albin Horn wärend einer im Sommer 1913 ausgeführten Reise nach Deutsch-Ostafrika. *Anzeiger der Akademie der Wissenschaften in Wien* 51: 536-538.

Steindachner F. 1915. Bericht über die ichthyologischen Aufsammelungen der Brüder Adolf und Albin Horn während einer im Sommer 1913 ausgeführten Reise nach Deutsch-Ostafrika. *Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse*. 92: 59-86, Pls. 1-5.

Strachan H. 2004. *The First World War in Africa.* Oxford University Press.

Stuhlmann F. 1890. Karte von Ungú, Usegua & Süd Usambáa (Deutsch-Ost-Afrika) zur Veranschaulichung der Reiseroute, Beobachtungen und Erkundigungen Dr. Franz Stuhlmann's (16. August bis 6 October 1888). *Mitteilungen der Geographischen Gesellschaft in Hamburg,* v. 8, before p. 143. (map available from University of Illinois at Urbana-Champaign. University Library)

Svardal H., Quah F.X., Malinsky M., Ngatunga B.P., Miska E.A., Salzburger W., Genner M.J., Turner G.F., Durbin R. 2020. Ancestral hybridisation facilitated species diversification in the Lake Malawi cichlid fish adaptive radiation. *Molecular Biology & Evolution* 37, 1100-1113.

Thomas D.S., Bailey R., Shaw P.A., Durcan J.A., Singarayer J.S. 2009. Late Quaternary highstands at Lake Chilwa, Malawi: frequency, timing and possible forcing mechanisms in the last 44 ka. *Quaternary Science Reviews*,28: 526-539

Tobey J. 2008. *A Profile of the Wami River Sub-Basin.* Tanzania Coastal Management Partnership.

Trape, S. 2016. A new cichlid fish in the Sahara: The Ounianga Serir lakes (Chad), a biodiversity hotspot in the desert, *Comptes Rendus Biologies* 339: 529-536.

Trewavas E. 1946. The types of African cichlid fishes described by Borodin in 1931 and 1936, and of two species described by Boulenger in 1901. *Proceedings of the Zoological Society of London* 116: 240-246.

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

Turner G.F., Ngatunga B.P. & Genner M.J. 2018. A survey of fishes of Hombolo Lake, Dodoma, Tanzania, with evidence for local extinction of a native tilapia as a consequence of stocking. *BioRxiv,* doi: https://doi.org/10.1101/452847

Turner G.F., Ngatunga B.P. & Genner M.J. 2019. The natural history of the satellite lakes of Lake Malawi. *EcoevoRxiv* 131pp.

Tweddle D. 1979. The zoogeography of the fish fauna of the Lake Chilwa basin. Pp. 177-182 in Kalk, M., McLachlan, A. J. and Howard-Williams, C. (Eds.) *Lake Chilwa: Studies of change in a tropical ecosystem,* Monographiae Biologicae 35, The Hague-Boston-London: Dr. W. Junk Publishers.

Tweddle D., Lewis D.S.C., Willoughby N.G. 1979. The nature of the barrier separating the Lake Malawi and Zambezi fish faunas. *Ichthyological Bulletin of Rhodes University* 39, 1-9.

Tyers A.M. & Turner G.F. 2013. Signal and preference divergence among populations of the non-endemic basal Lake Malawi cichlid fish *Astatotilapia calliptera* (Perciformes: Cichlidae). *Biological Journal of the Linnean Society* 110, 180-188.

Vranken N. van Steenberge M. & Snoeks J. 2019. Similar ecology, different morphology: Three new species of oral-mollusc shellers from Lake Edward. *Journal of Fish Biology*. pp. 1–16

Wikipedia 2021. https://en.wikipedia.org/wiki/List_of_rivers_of_Tanzania (checked 14 February 2021)