



A morphometric revision of the genus *Ophthalmotilapia* (Teleostei, Cichlidae) from Lake Tanganyika (East Africa)

M. HANSENS* AND J. SNOEKS

Africa Museum, Vertebrate Section, Ichthyology, Leuvensesteenweg 13, B-3080 Tervuren, Belgium

E. VERHEYEN

Royal Belgian Institute of Natural Sciences, Section of Taxonomy and Biochemical Systematics, Vautierstraat 29, B-1000 Brussels, Belgium

Received August 1996; accepted for publication December 1997

A detailed morphometric study of the endemic cichlid genus *Ophthalmotilapia* Pellegrin, 1904 from Lake Tanganyika was made. At present, four species are recognized within the genus *Ophthalmotilapia*: *O. boops* (Boulenger, 1901), *O. heterodonta* (Poll & Matthes, 1962), *O. nasuta* (Poll & Matthes, 1962) and *O. ventralis* (Boulenger, 1898). The morphometric analysis included 24 measurements on 129 specimens and 17 meristics on 132 specimens, that belong to the four species. A redescription of the genus is given. The most important diagnostic features distinguishing the genus *Ophthalmotilapia* from the other genera within the tribe Ectodini are listed. The four species currently recognized are redefined on the basis of distinctive morphological characters and their within-lake distributions are discussed.

© 1999 The Linnean Society of London

ADDITIONAL KEY WORDS:—morphometry – taxonomy – distribution patterns.

CONTENTS

Introduction	488
Historical overview	488
Material and methods	491
Results	492
Morphometry	492
Species diagnoses	496
Distribution	500
Discussion	500
The genus <i>Ophthalmotilapia</i>	500
Taxonomy of the <i>Ophthalmotilapia</i> species	504
Acknowledgements	509
References	509
Appendix: specimens examined	511

* Corresponding author. Email: hanssens@africamuseum.be

INTRODUCTION

Lake Tanganyika is by far the oldest of the East African Rift lakes and harbours the morphologically and behaviourally most diversified cichlid fauna. The almost 200 endemic species described so far are contained within 49 endemic genera grouped into 12 tribes (Poll, 1986). The origin and evolution of these cichlid species swarms have been—and continue to be—the subject of intensive phylogenetic and ecological research (e.g. Meyer, 1993; Sturmbauer *et al.*, 1997; Nakai *et al.*, 1994; Kohda *et al.*, 1996). It is evident that such studies require both a sound taxonomic knowledge as well as reliable keys. However, several recent studies indicate that the taxonomical knowledge of these fauna is less advanced than often assumed (e.g. Snoeks *et al.*, 1994).

The genus *Ophthalmotilapia* is part of the cichlid tribe of the Ectodini. This tribe currently comprises 13 mouthbrooding genera which are all endemic to Lake Tanganyika (Poll, 1986). The taxonomic status and identification of the currently recognized species are still problematic. For example, *O. ventralis* and *O. heterodonta* were described as subspecies of *Ophthalmochromis ventralis* by Poll & Matthes (1962), and designated as species by Poll (1986). This designation was made without a further discussion on the morphological differences between both former subspecies and the intermediate populations as reported by Poll & Matthes (1962). The taxonomic status of both taxa therefore remained uncertain.

This study attempts to resolve the present confusion concerning the alpha taxonomy of the *Ophthalmotilapia* species that is apparent in the scientific and the aquarium literature. In order to do so, we performed a detailed morphological analysis on all known *Ophthalmotilapia* species and species complexes. Based upon these results we updated the within-lake distribution patterns. The obtained results will also serve as a basis for a future description of the different races and species (Hanssens *et al.*, in prep) within the complexes as defined in this publication and for an ongoing mitochondrial DNA (mtDNA) study on this genus and closely related Ectodini. This study forms part of a series of studies on the taxonomy, evolution, speciation and distribution patterns of several cichlid taxa from Lake Tanganyika (Snoeks *et al.*, 1994; Meyer *et al.*, 1996; Verheyen *et al.*, 1996; Sturmbauer *et al.*, 1997).

HISTORICAL OVERVIEW

In 1904, Pellegrin described the genus *Ophthalmotilapia*. He characterized it by its moderately deep body, subinferior or almost subinferior mouth with several rows of bicuspid or tricuspid teeth, large eyes, visible maxillary, short gill rakers (13–20) cycloid or ctenoid scales (there are two lateral lines, the upper complete or almost complete), 12 to 14 dorsal fin spines, and three anal fin spines. This genus included two species, *O. boops* and *O. fuae* (Vaillant, 1899), the latter currently considered a synonym of *Cyathopharynx furcifer* (Boulenger, 1898) (Poll, 1946).

O. boops was originally described as *Tilapia boops* Boulenger, 1901 based upon two specimens originating from Msambu, Tanganyika (Tanzania) (Boulenger, 1901a). According to Boulenger (1901b), within the genus *Tilapia* Smith, 1840 this species is characterized by the large size of its eyes.

In his revision of the Tanganyika cichlid genera, Regan (1920) added *Paratilapia*

ventralis Boulenger, 1898 to the genus *Ophthalmotilapia*. The original description of this species was based on eight specimens from Kinyamkolo (the former name of Mpulungu) and one from Mbity Rocks (= Mbete), Zambia. According to Boulenger (1898) this species can be distinguished from its African congeners by the low number of its dorsal spines combined with the large eyes, the crescentic caudal, the extremely prolonged ventrals and the upper lateral line extending to the caudal peduncle. Pellegrin (1904) also stressed the remarkable prolongation of the ventral fins. Regan (1920) stated that *O. ventralis* differed from *O. boops* in the loss of the lateral cusps on the oral teeth.

Poll (1946) revised the genus *Ophthalmotilapia*, which then included three species: *O. boops*, *O. ventralis* and *O. stappersii* Poll, 1943. Later on, *O. stappersii* was implicitly synonymized with *Lestradea perspicax* Poll, 1943 by Poll (1951a) and considered as a subspecies. Poll (1956) confirmed this synonymy and discussed the status and distribution of both subspecies of *Lestradea perspicax*. Poll (1946) listed the following differences between *O. boops* and *O. ventralis*. *O. boops* has 13 gill rakers on the lower part of the first branchial arch, and three rows of tricuspid teeth in the oral jaws, while in *O. ventralis* he counted 17–19 gill rakers and 2–3 rows of conical teeth.

Poll (1956) stated that the differences in oral dentition between *O. boops* and *O. ventralis* were too large to consider both as belonging to the same genus. He therefore created for *Ophthalmotilapia ventralis* a new genus—*Ophthalmochromis*. *O. boops* possessed tricuspid teeth, whilst in *O. ventralis* only conical teeth were found. Poll (1956) furthermore reported upon the differences between populations of certain localities of *Ophthalmochromis ventralis*. He specifically drew attention to the large range in the number of dorsal spines.

In 1962, Poll & Matthes described *Ophthalmochromis nasutus* based on a holotype and allotype from Kalungwe, Congo (now Democratic Republic of Congo) and 126 paratypes. They distinguished this species from *O. ventralis* on the basis of several characters. The nose of *O. nasutus* was longer and more narrow than in *O. ventralis*. It was prolonged by a fleshy appendix, which, in male specimens, grew thicker with age. The morphology of the skull and the interorbital region was also found to be different. In *O. nasutus* the interorbital region was normal, more or less convex and the interorbital width less than the snout length. In *O. ventralis*, the interorbital width was large, the interorbital region flat or slightly concave with supraorbital ridges. The mean number of outer oral teeth was also slightly lower in *O. nasutus* due to the narrower snout and mouth. The outer oral teeth were less robust and slightly compressed. The teeth in the inner rows of *O. nasutus* were spatulate while those in *O. ventralis* were conical. The implantation of the outer teeth in the lower jaw was more horizontal in *O. nasutus*. In *O. nasutus*, the posterior teeth on the lower pharyngeal jaw were smaller and more densely packed. The anterior lamella of the lower pharyngeal jaw was longer in *O. nasutus*. For the meristic characters, Poll & Matthes (1962) noted a higher number of mean dorsal spines in *O. nasutus*, and a higher mean number of gill rakers on the lower part of the first branchial arch. The mean numbers of longitudinal and lateral scales and scales around the caudal peduncle were found to be slightly different between both species. The males of *O. nasutus* were darker, while the colour of *O. ventralis* live males was bluish. Female *O. ventralis* showed 4–5 faint blotches on their flanks, while female *O. nasuta* showed distinct black vertical dorsal stripes.

Poll & Matthes (1962) furthermore described a new subspecies *O. ventralis heterodontus* and listed a holotype from Ile de Mboko, Congo, an allotype and 27 paratypes.

This subspecies was present in the northern part of the lake, with the exception of one specimen from Mtoto, Congo (see discussion), while the nominotypical subspecies was only found in the southern part of the lake. The differences reported were mainly found in the lower pharyngeal jaw dentition: the posterior median teeth in *O. v. heterodontus* had a tendency to become more molariform. The meristic characters for both subspecies were very similar. From figure 2 in Poll & Matthes (1962) it can be deduced that the mean number of dorsal spines is slightly lower in *O. v. ventralis*. In addition, *O. v. heterodontus* has a shorter and broader snout than *O. v. ventralis* and its preorbital distance is smaller. They furthermore reported the occurrence of intermediate populations, from localities in between the northern- and southernmost localities, sometimes mixed with *O. v. heterodontus* (but see Discussion). The occurrence of these intermediate populations has been invoked as proof for the subdivision of Lake Tanganyika as the result of an extreme decrease in its water level (Poll & Matthes, 1962). These authors argued that after both subspecies were separated due to the division of the lake into two separate basins, they regained contact after the lake basins were reunited.

Based on osteological and myological characters, Liem (1981) made a phylogenetic analysis of the genera *Asprotilapia* Boulenger, 1901, *Ectodus* Boulenger, 1898, *Lestradea* Poll, 1943, *Cunningtonia* Boulenger, 1906, *Ophthalmochromis* and *Ophthalmotilapia*. His phylogenetic analysis indicated a recent common ancestor for *Ophthalmochromis ventralis*, *Ophthalmochromis nasutus* and *Ophthalmotilapia boops*, which was not shared by any other taxon. He also found that *O. nasutus* showed intermediate characters between *O. ventralis* and *O. boops*. Liem (1981) therefore synonymized the genera *Ophthalmochromis* and *Ophthalmotilapia*. This synonymy was accepted by Greenwood (1983) and later confirmed by Poll (1986). According to Liem (1981) three derived characters characterize the genus *Ophthalmotilapia*: (1) the distal end of the very elongate first ray of each pelvic fin in the male is uniquely bifid and widened into spatulae; (2) all *Ophthalmotilapia* species show a trend towards enlargement of the sensory canals and pores of the head; (3) the hypertrophied retractor dorsalis is subdivided into two distinct heads.

The first and third character are confirmed by Greenwood (1983) as autapomorphies for the genus *Ophthalmotilapia* (*sensu* Liem). He did not discuss or mention the second apomorphic character listed by Liem. Liem (1981) furthermore proved that the five genera (*Asprotilapia*, *Ectodus*, *Lestradea*, *Cunningtonia* and *Ophthalmotilapia*) formed a monophyletic group, which he called the *Ophthalmotilapia* assemblage. Greenwood (1983) added the genera *Aulonocranus* Regan, 1920, *Callochromis* Regan, 1920, *Xenotilapia* Boulenger, 1899, *Grammatotria* Boulenger, 1899, *Cyathopharynx* Regan, 1920 and *Cardiopharynx* Poll, 1942 to the *Ophthalmotilapia* assemblage, as defined by Liem (1981). Greenwood (1983) listed five apomorphic characters which are shared by the genera included in the *Ophthalmotilapia* assemblage as he defined it. Poll (1986) placed all these genera, including the newly described genus *Microdontochromis* Poll, 1986 in the tribus of the Ectodini. Sturmbauer & Meyer (1993) confirmed the monophyly of the Ectodini by a phylogenetic analysis, based upon mtDNA sequences.

In 1986, Poll attributed specific status to *O. ventralis heterodontus*. He argued that real subspecies are geographical races, more or less separated by geographical barriers, which he claims is not the case in Lake Tanganyika. According to Poll, isolation between so-called subspecies is difficult to prove, or has not been confirmed. He therefore considered the subspecific status improper for these taxa and to him

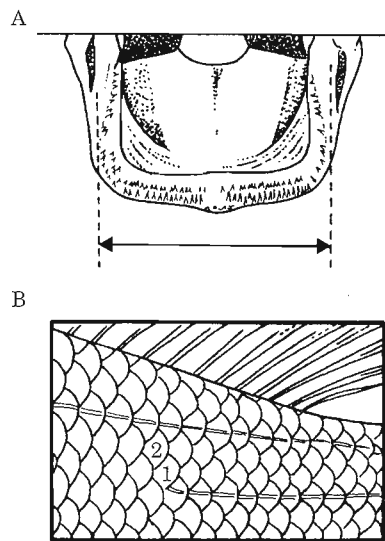


Figure 1. A, schematic representation of the measurement of the lower jaw width. B, schematic representation of the count of scales between the upper and lower lateral line.

the earlier subspecies are in reality biometrically highly similar species, showing different colour patterns. These different colour patterns assure them genetic isolation and prove that one is dealing with good species (Poll, 1986).

MATERIAL AND METHODS

The morphometric analysis included 24 measurements on 129 specimens and 17 meristics on 132 specimens that represent all four species which belong to the genus *Ophthalmotilapia* as currently defined. Specimens examined (see Appendix) included part of the type material, part of the collection from the Africa Museum, Tervuren, Belgium, including both collections from recent expeditions to Lake Tanganyika in 1992 and 1995, and material from the Royal Belgian Institute of Natural Sciences, Brussels. During the 1992 expedition, 59 *Ophthalmotilapia* specimens were collected in 29 localities over a distance of about 450 km on the Tanzanian coast between Kigoma and Kipili. During the 1995 expedition, 173 *Ophthalmotilapia* specimens were collected in 27 different localities over more than 350 km along the entire Zambian coast and the part of the Tanzanian coast south of the Kipili Islands (Fig. 7).

All measurements and meristics taken are listed in Tables 3–6. Measurements and meristics are as defined by Snoeks (1994) except for the following. The lower jaw width is defined as the maximum width of the lower jaw, measured in the anterior part of the lower jaw (Fig. 1A). The number of scales between upper and lower lateral line is counted starting from the first scale of the lower lateral line, in an oblique line up to the upper lateral line, not including the scales of the lateral lines (Fig. 1B). The scales around the caudal peduncle are counted in an oblique row on one side of the caudal peduncle; half a scale is counted for the dorsal and ventralmost scales; the total number is then multiplied by two.

TABLE 1. Factor loadings on the first three principal axes resulting from a PCA on the log transformed metric data, using the covariance matrix. PC 1 is regarded as a size factor, PC 2 and PC 3 as shape factors. The most important loadings on PC 2 and PC 3 are shaded

Log character	PC 1	PC 2	PC 3
SL	0.196567	0.019356	-0.001152
Body depth	0.217357	0.006563	-0.026983
Head length	0.208327	-0.008684	-0.001041
Head width	0.195939	0.007891	-0.001199
Interorbital width	0.248419	0.021059	-0.018749
Lower jaw width	0.292404	-0.122728	0.014440
Snout length	0.259013	-0.021956	-0.016708
Lower jaw length	0.229134	-0.019647	0.054882
Premaxillary ped length	0.213160	0.055609	-0.020968
Cheek depth	0.232844	-0.057869	-0.049474
Eye diameter	0.164695	0.001181	0.010558
Lachrymal depth	0.250360	0.009476	-0.006267
Pharyngeal jaw length	0.202342	0.025647	0.007763
Pharyngeal jaw width	0.188414	0.027506	0.007763
Dentigerous area length	0.203451	0.009437	0.047577
Dentigerous area width	0.193291	0.026309	0.020460
Dorsal fin base length	0.206292	0.036432	-0.004669
Anal fin base length	0.206257	0.008511	0.006674
Predorsal distance	0.191441	0.009924	-0.010402
Preanal distance	0.197471	0.020637	-0.010341
Prepectoral distance	0.198524	0.005577	0.005660
Preventral distance	0.205982	0.003446	-0.005566
Caudal peduncle length	0.186928	0.012539	0.019815
Caudal peduncle depth	0.188072	-0.009870	-0.014054

Data were analysed using CSS Statistica releases 3.1 and 5.4. Multivariate data analyses included principal component analyses (PCA) of the log transformed metric data, factoring the covariance matrix; the correlation matrix was factored for PCA on the raw meristic data. To allow a size-free discrimination of different populations or groups of organisms, a PCA carried out of the log transformed metric data, factoring the covariance matrix (Humphries *et al.*, 1981; Bookstein *et al.*, 1985). In this analysis the first principal component is generally interpreted as a size factor, whilst the following principal components allow a size-free discrimination of the different individuals.

The within-lake distribution of the four *Ophthalmotilapia* species as shown in Figure 7 is based on data from the type specimens, the entire *Ophthalmotilapia* collections in the Africa Museum, Tervuren, the Royal Belgian Institute of Natural Sciences in Brussels, all *Ophthalmotilapia* specimens collected during the 1992 and 1995 expeditions, literature data (Schupke, 1993; Konings, 1988; Konings & Dieckhoff, 1992), and a slide collection provided by Ad Konings. The identification of all specimens in these collections was checked.

RESULTS

Morphometry

A PCA was carried out factoring the covariance matrix of the log transformed metric data, the factor loadings of which are given in Table 1. The second axis is

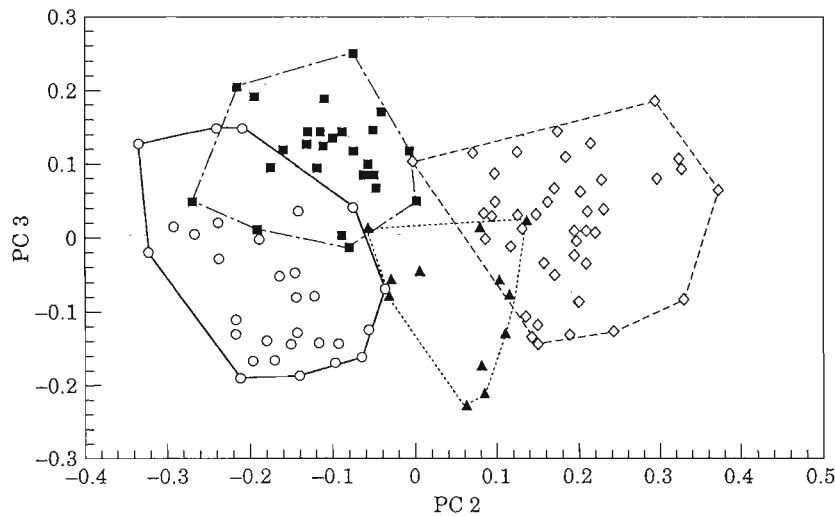


Figure 2. Plot of the factor scores for PC2 and PC3 of the log transformed metric data. (○) *O. ventralis*; (■) *O. heterodonta*; (◇) *O. nasuta* and (▲) *O. boops*.

mainly defined by measurements of head structures. In order of importance these are the lower jaw width (which is by far the most important character); cheek depth and premaxillary pedicel length. The third factor is defined by the lower jaw length, cheek depth and dental area length. When the factor scores for all individuals are plotted on the second and third principal component, we can distinguish two major groups (Fig. 2). A first group contains *O. nasuta* and *O. boops*, both with a relatively small lower jaw. *O. nasuta* is found entirely and *O. boops* mainly in the positive sector of the first axis. The second group contains *O. ventralis* and *O. heterodonta*, which are both characterized by a broad lower jaw. Both species are within the negative sector of the second factor, except for a single specimen of *O. heterodonta*. The existence of both groups is well-illustrated by a plot of the lower jaw width in % HL against the head length which shows that, although the lower jaw width increases with size, *O. ventralis* and *O. heterodonta* are characterized by a relatively broad snout. For a given length they have the highest mean lower jaw width (Fig. 3). *O. boops* and particularly *O. nasuta* possess a narrow snout and small mean lower jaw width. The third factor of the PCA does not separate the species. Although the majority of the *O. heterodonta* specimens cluster in the positive sector of the third factor, and most *O. ventralis* are found in the negative sector, there is still overlap between both. Most of the *O. boops* specimens cluster in the negative part of the third factor, *O. nasuta* clusters in both the negative and positive parts of the third factor, so both species show overlap as well.

A PCA of the meristic data was made including all raw counts, except for the number of outer teeth in the oral jaws, which appeared to vary considerably with size. The table with factor loadings shows that the first principal component is mainly defined by the number of teeth rows in the lower and upper oral jaw, the number of gill rakers on the ceratobranchial, the number of scales around the caudal peduncle and the number of soft dorsal fin rays. The second principal component is mainly defined by the number of scales between the upper and lower lateral lines

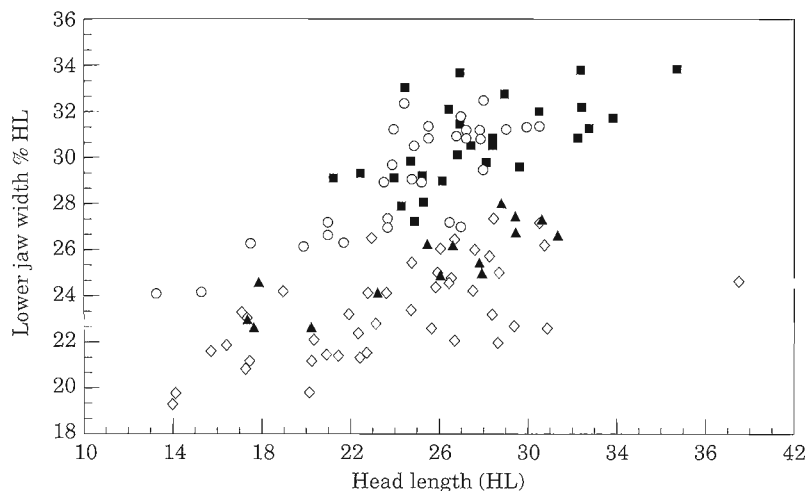


Figure 3. Plot of the lower jaw width as percentage of the head length against the head length (HL, in mm). (○) *O. ventralis*; (■) *O. heterodonta*; (◇) *O. nasuta* and (▲) *O. boops*.

TABLE 2. Factor loadings on the first two principal axes resulting from a PCA on the meristic data, using the correlation matrix. The most important loadings on PC 1 and PC 2 are shaded

Character	PC 1	PC 2
Teeth rows in upper jaw	0.695409	-0.061771
Teeth rows in lower jaw	0.737747	0.107364
Gill rakers on ceratobranchial	-0.716591	0.154282
Gill rakers on epibranchial	-0.585933	-0.286992
Dorsal fin spines	0.241118	0.692833
Soft dorsal fin rays	0.682634	-0.208554
Soft anal fin rays	-0.098060	0.465428
Pectoral fin rays	-0.014792	0.265837
Upper lateral line scales	0.613807	0.263307
Longitudinal line scales	0.581616	0.294031
Transversal scales above lateral line	0.278601	-0.456743
Transversal scales below lateral line	0.501656	-0.532363
Scales round caudal peduncle	0.687002	0.035509
Scales between upper and lower lateral line	0.059316	-0.873985
Cheek scales	-0.064723	-0.348124

and the number of dorsal fin spines. A plot of the factor scores of the first and second principal components shows that the polygons representing the four species are well separated, except for a small overlap between *O. heterodonta* and *O. nasuta* (Fig. 4). The second principal component, which is mainly defined by the number of scales between the upper and lower lateral line, completely separates *O. ventralis* and *O. boops*, both species with three scales between the lateral lines, from *O. heterodonta* and *O. nasuta*, with two scales between the lateral lines.

Although the number of outer teeth in the oral jaws has not been used in the PCA, they are also useful for species discrimination. The number of outer oral teeth in the upper jaw plotted against the standard length (Fig. 5) shows that this number

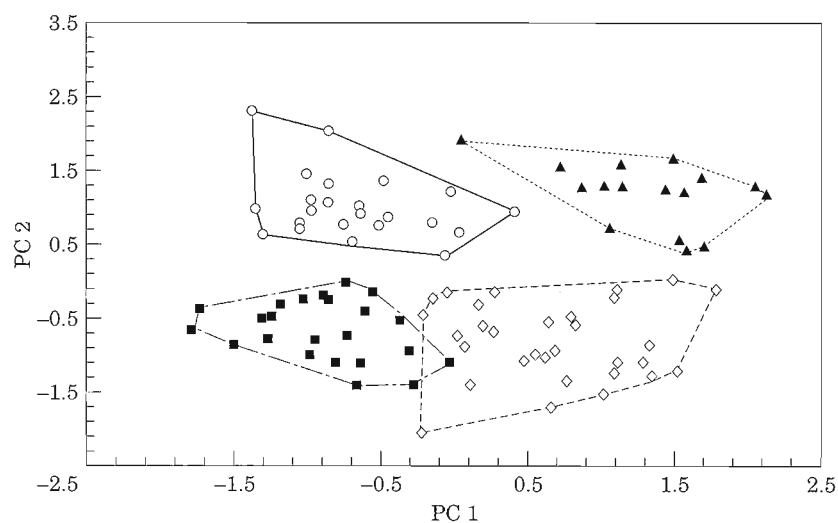


Figure 4. Plot of the factor scores for PC1 and PC2 of the meristic data. (○) *O. ventralis*; (■) *O. heterodonta*; (◇) *O. nasuta* and (▲) *O. boops*.

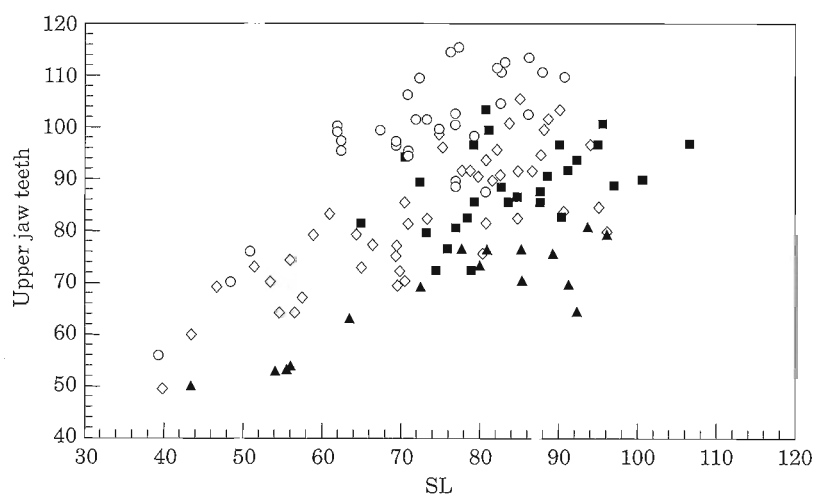


Figure 5. Plot of the number of outer teeth in the upper jaw against the standard length (SL, in mm). (○) *O. ventralis*; (■) *O. heterodonta*; (◇) *O. nasuta* and (▲) *O. boops*.

increases during growth. The highest mean number of outer teeth in the upper oral jaw is found in *O. ventralis*, followed by *O. nasuta* and *O. heterodonta*, while *O. boops* has the lowest number of outer teeth in the upper oral jaw. This plot equally shows that on the basis of this character we can distinguish between *O. ventralis* and *O. heterodonta*, both species characterized by a broad snout, and between *O. nasuta* and *O. boops*, with a narrow snout.

TABLE 3. *Ophthalmotilapia boops*. Synopsis of the morphometric and meristic characters

<i>Ophthalmotilapia boops</i> (n=15)	Mean ± SD	Range
Standard length (SL) in mm	78.4 ± 14.8	54.0–96.5
Body depth % SL	34.0 ± 1.9	30.7–36.8
Head length (HL) % SL	32.4 ± 0.6	31.5–33.5
Head width (HW) % HL	48.5 ± 1.2	46.2–50.5
Interorbital width % HL	25.8 ± 1.9	22.6–29.8
Snout length % HL	31.9 ± 2.2	28.2–37.3
Lower jaw length % HL	29.7 ± 1.6	25.4–31.8
Lower jaw width % HL	25.4 ± 1.8	22.6–28.0
Premaxillary pedicel length % HL	22.8 ± 1.1	20.7–24.2
Cheek depth % HL	16.7 ± 1.0	15.3–18.6
Eye diameter % HL	40.8 ± 2.0	38.4–44.7
Lachrymal depth % HL	18.0 ± 1.1	16.4–19.7
Lower pharyngeal length (LPL) % HL	26.2 ± 1.0	23.6–27.7
Lower pharyngeal width (LPW) % LPL	101.0 ± 3.3	96.0–106.3
Dentigerous area length % LPL	51.4 ± 2.8	45.0–55.6
Dentigerous area width % LPW	77.3 ± 2.1	74.4–80.6
Dentigerous area length % width	67.0 ± 3.4	62.1–74.6
Dorsal fin base length % SL	56.3 ± 1.6	53.8–59.0
Anal fin base length % SL	17.5 ± 0.8	15.9–19.3
Predorsal distance % SL	34.6 ± 1.2	32.2–36.0
Preanal distance % SL	65.3 ± 1.7	61.5–69.0
Prepectoral distance % SL	31.4 ± 0.7	30.6–32.7
Prepelvic distance % SL	36.7 ± 1.2	34.8–39.2
Caudal peduncle length (CPL) % SL	19.3 ± 0.7	18.1–20.7
Caudal peduncle depth % CPL	59.0 ± 3.5	54.3–65.7
Meristics (n=16)	Number and frequencies	
Upper jaw teeth	50–80 (median 70)	
Inner teeth rows	3/3 (f5), 4/4 (f6), 4/5 (f1), 5/4 (f1), 5/5 (f3)	
Gill rakers	16/1/6 (f3), 17/1/5 (f2), 17/1/6 (f5), 17/1/7 (f2), 18/1/5 (f1), 18/1/6 (f3)	
Dorsal fin formula	XII 15 (f5), XIII 14 (f2), XIII 15 (f8), XIV 14 (f1)	
Anal fin formula	III 7 (f1), III 9 (f14), III 10 (f1)	
Pectoral fin formula	13–15 (median 14)	
Longitudinal line scales	36–39 (median 38)	
Lateral line scales	32–36 (median 35)	
Transverse line scales	5/12 (f3), 5/13 (f4), 5/14 (f1), 6/12 (f1), 6/13 (f6), 6/14 (f1)	
Scales upper and lower lateral line	3 (f16)	
Scales around caudal peduncle	20–22 (median 22)	
Cheek scales	2–3 (median 2)	

Species diagnoses

A synopsis of the measurements and meristic characters of the *Ophthalmotilapia* species is given in Tables 3–6, and illustrated in Figure 6.

Ophthalmotilapia boops can easily be distinguished from all other *Ophthalmotilapia* species on the basis of its entirely tricuspid oral dentition; the outer oral teeth in all other species are unicuspid. The mean lower jaw length is smaller in *O. boops* (25.4–31.8% HL) than in the three other species (28.0–42.6% HL), the mean lower jaw width in *O. boops* (22.6–28.0% HL) is smaller than in *O. ventralis* and *O. heterodonta* (24.0–33.9% HL), but higher than in *O. nasuta* (19.3–27.4% HL). The mean anal fin base length is smallest in *O. boops* (15.9–19.3 versus 16.9–22.3% SL in the other species). The anterior border of the lower oral jaw in *O. boops* is more rounded than

TABLE 4. *Ophthalmotilapia heterodonta*. Synopsis of the morphometric and meristic characters

<i>Ophthalmotilapia heterodonta</i> (n=27)	Mean ± SD	Range
Standard length (SL) in mm	84.4 ± 10.7	64.5–107.5
Body depth % SL	34.2 ± 1.6	31.9–38.4
Head length (HL) % SL	33.1 ± 0.7	31.5–34.3
Head width (HW) % HL	47.8 ± 1.0	46.1–49.8
Interorbital width % HL	26.6 ± 1.6	23.7–29.8
Snout length % HL	32.2 ± 1.7	28.2–35.8
Lower jaw length % HL	37.0 ± 1.9	33.1–42.6
Lower jaw width % HL	30.7 ± 1.8	27.2–33.9
Premaxillary pedicel length % HL	21.2 ± 0.8	19.2–23.0
Cheek depth % HL	17.0 ± 1.0	14.7–19.0
Eye diameter % HL	39.1 ± 2.0	35.6–43.7
Lachrymal depth % HL	17.3 ± 0.8	15.9–18.7
Lower pharyngeal length (LPL) % HL	26.3 ± 1.0	24.1–28.3
Lower pharyngeal width (LPW) % LPL	97.6 ± 2.7	93.5–104.2
Dentigerous area length % LPL	56.4 ± 3.7	50.6–62.5
Dentigerous area width % LPW	81.2 ± 2.0	77.1–84.8
Dentigerous area length % width	71.2 ± 3.8	63.9–78.8
Dorsal fin base length % SL	55.3 ± 1.1	53.1–58.0
Anal fin base length % SL	20.1 ± 0.7	18.5–22.3
Predorsal distance % SL	33.4 ± 0.9	32.0–35.2
Preanal distance % SL	62.7 ± 1.6	59.6–65.9
Prepectoral distance % SL	32.2 ± 0.9	30.5–34.0
Prepelvic distance % SL	37.4 ± 1.0	35.4–39.5
Caudal peduncle length (CPL) % SL	20.0 ± 1.1	18.0–22.3
Caudal peduncle depth % CPL	58.0 ± 4.0	51.4–66.7
Meristics (n=28)	Number and frequencies	
Upper jaw teeth	72–103 (median 88)	
Inner teeth rows	2/2 (f2), 2/3 (f4), 3/3 (f18), 3/4 (f2), 4/4 (f2)	
Gill rakers	17/1/7 (f1), 18/1/6 (f1), 18/1/7 (f3), 19/1/6 (f3), 19/1/7 (f6), 19/1/8 (f3), 20/1/7 (f3), 20/1/8 (f2), 21/1/6 (f1), 21/1/7 (f1), 21/1/8 (f2), 22/1/7 (f2)	
Dorsal fin formula	XII 13 (f1), XIII 13 (f10), XIII 14 (f14), XIV 13 (f2), XIV 14 (f1)	
Anal fin formula	III 9 (f12), III 10 (f16)	
Pectoral fin formula	13–15 (median 14)	
Longitudinal line scales	36–37 (median 37)	
Lateral line scales	29–35 (median 34)	
Transverse line scales	4/10 (f4), 4/11 (f3), 5/10 (f11), 5/11 (f8), 6/10 (f1)	
Scales upper and lower lateral line	2 (f 28)	
Scales around caudal peduncle	20–22 (median 20)	
Cheek scales	1–3 (median 2)	

in *O. ventralis* or *O. heterodonta*; the outer teeth in the lower oral jaw in *O. boops* have a more horizontal inclination, while the implantation of the outer teeth in the lower oral jaw in *O. ventralis* and *O. heterodonta* is more erect. *O. boops* has three scales between upper and lower lateral line while *O. heterodonta* and *O. nasuta* have two.

The average number of outer teeth in the upper oral jaw for a given length is lower in *O. boops* than in the other species (Fig. 5). The number of teeth rows in upper and lower jaw is higher in *O. boops* (3–5 versus 2–4), the number of gill rakers on the ceratobranchial is lower in *O. boops* (16–18) than in *O. ventralis* (18–21) or in *O. heterodonta* (17–22).

The head length (29.8–34.4 versus 31.5–35.9% HL in the other species), jaw width (19.3–27.4 versus 22.6–33.9% HL) in *O. nasuta* is smaller than in the other species, while the mean premaxillary pedicel length is larger (21.3–27.5 versus

TABLE 5. *Ophthalmotilapia nasuta*. Synopsis of the morphometric and meristic characters

<i>Ophthalmotilapia nasuta</i> (n = 48)	Mean ± SD	Range
Standard length (SL) in mm	75.4 ± 15.1	43.5–124.5
Body depth % SL	34.6 ± 2.6	29.8–40.3
Head length (HL) % SL	31.9 ± 1.0	29.8–34.4
Head width (HW) % HL	49.4 ± 1.3	46.6–51.5
Interorbital width % HL	27.2 ± 2.2	22.0–32.0
Snout length % HL	31.3 ± 2.4	27.1–37.5
Lower jaw length % HL	34.5 ± 1.6	28.0–38.6
Lower jaw width % HL	23.5 ± 2.1	19.3–27.4
Premaxillary pedicel length % HL	24.0 ± 1.3	21.3–27.5
Cheek depth % HL	15.8 ± 1.2	13.7–19.0
Eye diameter % HL	40.4 ± 2.4	34.0–44.8
Lachrymal depth % HL	17.2 ± 1.1	15.1–19.6
Lower pharyngeal length (LPL) % HL	27.8 ± 0.8	26.2–29.5
Lower pharyngeal width (LPW) % LPL	100.9 ± 3.5	92.0–108.7
Dentigerous area length % LPL	52.9 ± 3.4	44.6–61.4
Dentigerous area width % LPW	80.0 ± 2.0	73.8–84.1
Dentigerous area length % width	65.5 ± 4.2	56.9–76.1
Dorsal fin base length % SL	56.6 ± 1.4	53.4–59.1
Anal fin base length % SL	19.8 ± 1.1	16.9–22.2
Predorsal distance % SL	34.0 ± 1.1	31.9–38.2
Preanal distance % SL	65.0 ± 1.6	61.0–68.4
Prepectoral distance % SL	32.2 ± 1.3	29.8–35.3
Prepelvic distance % SL	37.7 ± 1.5	34.8–42.4
Caudal peduncle length (CPL) % SL	18.4 ± 1.1	16.5–20.6
Caudal peduncle depth % CPL	60.6 ± 5.2	50.0–71.4
Meristics (n = 48)	Number and frequencies	
Upper jaw teeth	60–105 (median 83)	
Inner teeth rows	2/2 (f1), 2/3 (f1), 3/3 (f20), 3/4 (f13), 4/4 (f12) 4/5 (f1)	
Gill rakers	15/1/5 (f1), 16/1/5 (f1), 17/1/5 (f1), 17/1/6 (f2), 17/1/7 (f3), 17/1/8 (f1), 18/1/4 (f1), 18/1/5 (f1), 18/1/6 (f7), 18/1/7 (f9), 19/1/4 (f2), 19/1/6 (f4), 19/1/7 (f3), 20/1/6 (f4), 20/1/7 (f2), 21/1/7 (f1)	
Dorsal fin formula	XIII 14 (f7), XIII 15 (f10), XIV 13 (f3), XIV 14 (f6), XIV 15 (f9), XV 13 (f1), XV 14 (f1), XVI 13(f1)	
Anal fin formula	III 9 (f7), III 10 (f39), III II (f1)	
Pectoral fin formula	13–15 (median 14)	
Longitudinal line scales	37–40 (median 38)	
Lateral line scales	33–36 (median 35)	
Transverse line scales	4/11 (f1), 5/11 (f8), 5/12 (f19), 5/13 (f8), 5/14 (f1), 6/12 (f1), 6/13 (f1)	
Scales upper and lower lateral line	2 (f48)	
Scales around caudal peduncle	20–24 (median 22)	
Cheek scales	1–3 (median 2)	

17.6–24.2% HL). The morphology of the lower jaw and the implantation of the oral teeth is similar to *O. boops* and differs from *O. ventralis* and *O. heterodonta*. The inner oral teeth are weakly tricuspid in some *O. nasuta* specimens, with a shouldered appearance. In *O. heterodonta* and *O. ventralis* all oral teeth are unicuspid and cylindrical. In *O. nasuta* larger mature males and some females have a fleshy appendix on the nose.

Meristic differences between *O. nasuta* and *O. heterodonta* or *O. ventralis* are mainly found in the dorsal fin formula (13–16 dorsal spines and 13–15 soft fin rays in *O. nasuta* versus 12–14 dorsal spines and 13–14 soft fin rays in *O. heterodonta* and *O.*

TABLE 6. *Ophthalmotilapia ventralis*. Synopsis of the morphometric and meristic characters

<i>Ophthalmotilapia ventralis</i> (n=33)	Mean \pm SD	Range
Standard length (SL) in mm	72.8 \pm 11.5	39.5–91.0
Body depth % SL	36.0 \pm 2.0	31.7–39.6
Head length (HL) % SL	33.9 \pm 1.1	31.5–35.9
Head width (HW) % HL	47.8 \pm 1.4	45.1–51.0
Interorbital width % HL	26.4 \pm 2.1	21.6–30.6
Snout length % HL	32.2 \pm 2.0	29.0–36.2
Lower jaw length % HL	33.8 \pm 1.9	31.0–40.7
Lower jaw width % HL	29.4 \pm 2.5	24.1–33.7
Premaxillary pedicel length % HL	21.1 \pm 1.3	17.6–23.2
Cheek depth % HL	18.5 \pm 1.8	15.4–21.9
Eye diameter % HL	39.4 \pm 1.8	36.3–43.8
Lachrymal depth % HL	16.8 \pm 1.2	13.5–18.8
Lower pharyngeal length (LPL) % HL	25.9 \pm 1.0	24.0–29.4
Lower pharyngeal width (LPW) % LPL	100.5 \pm 3.7	92.4–108.3
Dentigerous area length % LPL	52.5 \pm 3.6	45.6–58.3
Dentigerous area width % LPW	79.4 \pm 2.6	73.0–84.6
Dentigerous area length % width	65.9 \pm 4.3	56.6–76.0
Dorsal fin base length % SL	54.4 \pm 1.6	50.3–57.6
Anal fin base length % SL	20.3 \pm 1.1	17.6–22.3
Predorsal distance % SL	35.4 \pm 0.9	33.3–37.3
Preanal distance % SL	65.0 \pm 1.4	62.0–68.6
Prepectoral distance % SL	32.9 \pm 1.5	30.6–36.6
Prepelvic distance % SL	39.1 \pm 1.5	35.2–41.6
Caudal peduncle length (CPL) % SL	18.5 \pm 0.9	16.5–20.6
Caudal peduncle depth % CPL	64.4 \pm 4.6	54.8–73.1
Meristics (n=34)	Number and frequencies	
Upper jaw teeth	56–115 (median 100)	
Inner teeth rows	2/2 (f4), 2/3 (f4), 3/3 (f23), 3/4 (f3)	
Gill rakers	18/1/7 (f1), 19/1/6 (f3), 19/1/7 (f4), 19/1/8 (f5), 19/1/9 (f4), 20/1/7 (f4), 20/1/8 (f6), 20/1/9 (f5), 21/1/8 (f1)	
Dorsal fin formula	XII 13 (f1), XII 14 (f2), XIII 13 (f10), XIII 14 (f19), XIV 13 (f2)	
Anal fin formula	III 8 (f1), III 9 (f10), III 10 (f23)	
Pectoral fin formula	13–15 (median 14)	
Longitudinal line scales	35–39 (median 37)	
Lateral line scales	29–35 (median 33)	
Transverse line scales	5/11 (f1), 5/12 (f1), 5/13 (f1), 5/14 (f1), 6/12 (f4), 6/13 (f2), 6/14 (f1)	
Scales upper and lower lateral line	3 (f34)	
Scales around caudal peduncle	20–22 (median 20)	
Cheek scales	2–3 (median 2)	

ventralis), the number of transversal line scales (11–14 below the lateral versus 10–11 in *O. heterodonta*), and the number of longitudinal line scales (37–40 versus 36–37 in *O. heterodonta*).

At first, it was difficult to distinguish between *O. heterodonta* and *O. ventralis* as we found no trenchant characters. A closer examination of the *O. heterodonta* types and *O. ventralis* from the southern part of the lake showed differences in scale numbers. In *O. heterodonta* two scales were found between both lateral lines, and three in *O. ventralis*. All other specimens belonging to the 'ventralis-heterodonta' complex were identified on the basis of this character. The number of transverse line scales below the lateral line proved also to be different, between 11 and 14 in *O. ventralis*, and 10 and 11 in *O. heterodonta*.

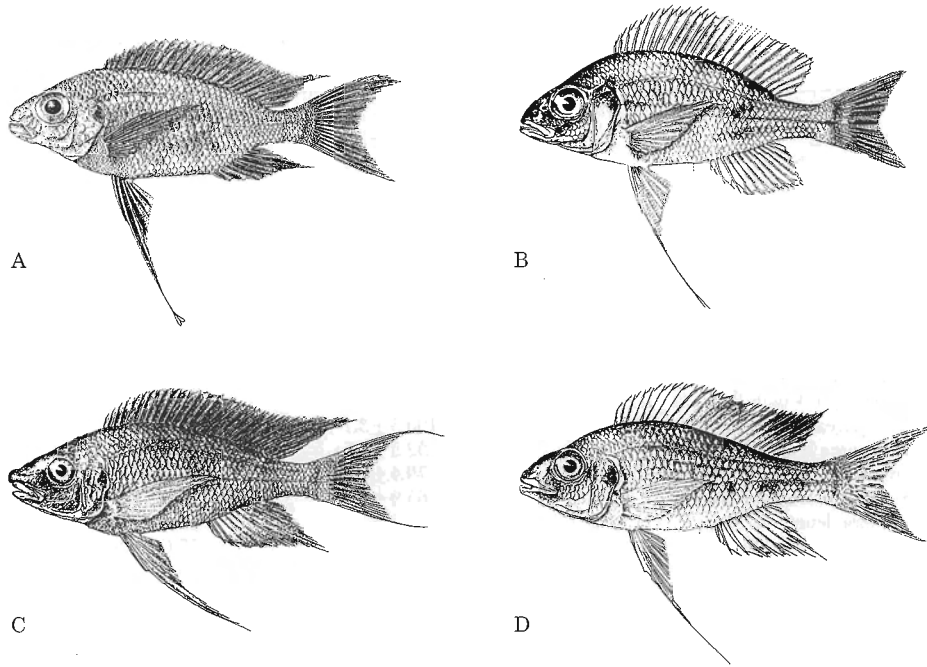


Figure 6. Lateral view of the four *Ophthalmotilapia* species: (A) *O. boops*, (B) *O. ventralis*, (C) *O. nasuta*, and (D) *O. heterodonta*. Figures after Poll & Matthes (1962), except *O. boops* after Poll (1986).

Distribution

O. boops is found on the southern part of the Tanzanian coast, from Cape Mpimbwe to Wampembe (Fig. 7). *O. nasuta* has a discontinuous circumlacustrine distribution. *O. ventralis* is found in the southern part of the lake, from the Kipili area in Tanzania, on the entire Zambian coast and up to Mwerasi on the Congolese coast, while *O. heterodonta* is confined to the northern part of the lake, currently found from Kalemie in Zaïre, to the north, in Burundi and on the Tanzanian coast north of Edith Bay. Specimens from the localities between Mtoto and Zongwe on the Congolese coast and from Mpimbwe on the Tanzanian coast belong to the unidentified races (see below).

DISCUSSION

The genus Ophthalmotilapia

Etymology

The genus name *Ophthalmotilapia* refers to the relatively large eye in this genus and is derived from the Greek *ὀφθαλμός*, which means 'eye' and *Tilapia*, the name of a widespread African cichlid genus.

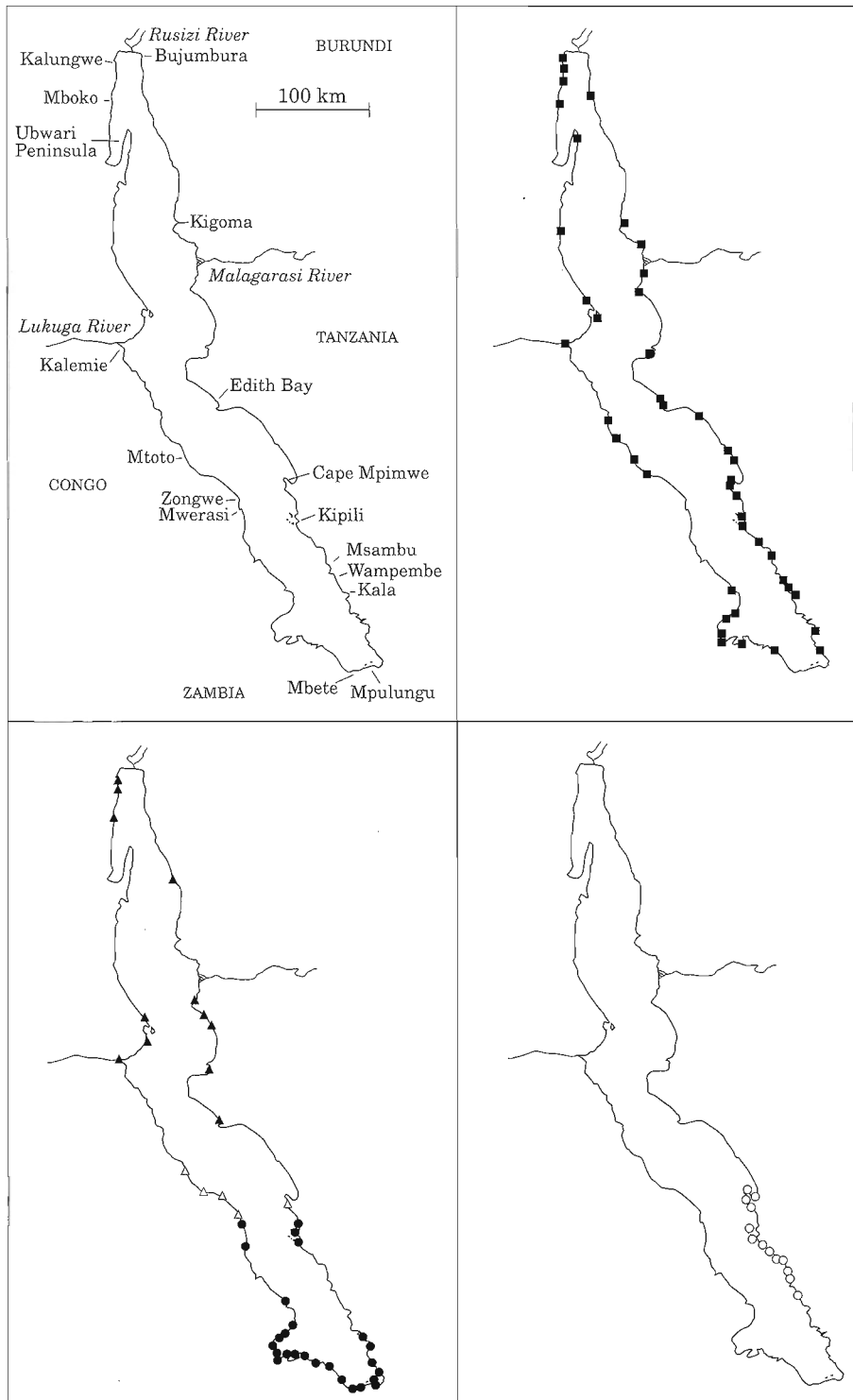


Figure 7. Distribution of the four *Ophthalmotilapia* species *O. nasuta* (■); *O. ventralis* (●); *O. heterodontia* (▲); unidentified Mtoto specimens (△); *O. boops* (○).

Description

All *Ophthalmotilapia* are relatively deep-bodied species, the body depth varying between 29.8 and 40.3% SL. The largest specimen examined had a standard length of 124.5 mm. The maximum size given by Poll (1986) is 125 mm SL, but several authors have reported larger specimens in *O. nasuta*, up to 200 mm total length (Brichard, 1978; Konings, 1988).

All species have a rounded head profile, which is more or less concave between the eyes. The top of the premaxillary pedicel is prominent. Oral teeth unicuspid or tricuspid, two to five teeth rows in upper and lower oral jaws, outer oral teeth larger than inner, tooth size decreasing towards the inner teeth rows. We counted maximally 115 outer oral teeth. Poll (1986) listed a maximum number of 100 outer oral teeth, while a maximum of 107 was given by Poll & Matthes (1962) in the description of *O. ventralis*. We counted 2–5 teeth rows in the oral jaws. Poll (1986) listed a maximum number of four, while previously for *O. boops* and *O. nasuta* a maximum of respectively five and six was given (Poll, 1956; Poll & Matthes, 1962).

The pharyngeal bone is triangular and densely covered with mainly bicuspid teeth, which are more or less rounded in cross-section.

The number of gill rakers on the ceratobranchial varies between 15 and 22, on the epibranchial between five and eight. We counted 12–16 dorsal fin spines, 13–15 soft dorsal fin rays. Poll (1986) listed a maximum of 14 dorsal fin spines and Poll & Matthes (1962) counted 15 dorsal fin spines in some *O. nasuta* specimens. All specimens possess three anal fin spines, 7–11 soft anal fin rays.

The unpaired fins are relatively high. The pectoral fin is long and reaches the anal fin base. The caudal fin is forked.

There is a clear sexual dimorphism in all *Ophthalmotilapia* species. Males attain a larger size than females and their relative body depth is generally larger than in females. Also, the morphology of the ventral and unpaired fins in both sexes is different. Unlike in female specimens, mature males have extremely prolonged ventral fins, almost reaching to the origin of the caudal fin and terminating in bifid spatulae. This character in mature males was given as one of the apomorphic characters by Liem (1981) to define the genus *Ophthalmotilapia*. Females have shorter ventral fins which generally attain the first part of the anal fin base. In males the soft fin rays of the unpaired fins are prolonged and may reach beyond the origin of the caudal fin; the outer rays of the caudal fin are long and filamentous.

Mature males show a specific colour pattern. Schupke (1994) reports that for certain Zambian populations of *O. ventralis*, this colour pattern is modified during courtship. Females are generally more pale and uniformly coloured.

The body is covered with ctenoid scales; small cycloid scales are present on the opercula and on the cheeks. The chest scales are very small in comparison to the scales on the body. The upper lateral line is almost complete.

Diagnosis (based on Poll, 1986)

A synopsis of the most important diagnostic characters to distinguish *Ophthalmotilapia* from the other Ectodini genera is given in Table 7. The genus *Ophthalmotilapia* can be distinguished from all other genera within the Ectodini by the presence of the bifid spatulae at the end of the extremely prolonged ventral fins.

The genera *Cyathopharynx*, *Cunningtonia* and *Aulonocranus* also possess prolonged ventral fins, that almost reach the origin of the caudal fin. However, they lack the

TABLE 7. Synopsis of the most important diagnostic characters to distinguish the genus *Ophthalmotilapia* from the other Ectodomi genera

	Body depth	Oral teeth rows	Gill rakers on ceratobranchial	Pharyngeal bone	Ventral fins (mature males)	Longitudinal line scales	Other diagnostic characters
<i>Ophthalmotilapia</i>	29.8–40.3% SL	3–5	15–21	triangular	prolonged with spatulae without spatulae	36–40	
<i>Cyathopharynx</i>		numerous		posterior border rounded	without spatulae	48–67	mobile oral teeth forming large band enlarged sensory pores on head and lower oral jaw
<i>Cunningtonia</i>							
<i>Auionocranus</i>							
<i>Cardiopharynx</i>		2		posterior border rounded	not prolonged		
<i>Callochromis</i>			10–12		not prolonged		
<i>Lestradea</i>	25–29% SL				not prolonged		
<i>Ectodus</i>	20–25% SL		12–14		not prolonged		
<i>Asprotilapia</i>	20% SL	2			not prolonged		conical nose, extends in front of inferior mouth
<i>Grammatotria</i>	22–25% SL		11–12		not prolonged	44–59	
<i>Xenotilapia</i>	20–29% SL				not prolonged, inverted		
<i>Enantiopus</i>	17–20% SL				symmetry		
					not prolonged, inverted		
<i>Microdonitochromis</i>	20–24% SL	1			symmetry		
					not prolonged, inverted		
					symmetry		

bifid spatulae that are present in *Ophthalmotilapia*. Brichard (1978, 1989) is the only author who reported the presence of spatulae in *Cyathopharynx furcifer* as well. We examined the ventral fins of 88 *Cyathopharynx* specimens and found the ventral fins to terminate in filamentous yellow tips, never in spatulae. Therefore, we assume that Brichard confounded *Cyathopharynx* with *Ophthalmotilapia*; in addition, two pictures of specimens identified as *Cyathopharynx furcifer* clearly belong to a Zambian race of *O. ventralis* (Brichard, 1978: 148–149).

Ophthalmotilapia differs in particular from *Cyathopharynx* and *Cardiopharynx* in the morphology of the lower pharyngeal jaw. In these two genera the posterior border of the lower pharyngeal bone is rounded, while it is triangular in *Ophthalmotilapia*. *Ophthalmotilapia* also differs from *Cunningtonia* in its oral dentition. In *Ophthalmotilapia* the inner teeth are in an erect position, straight or slightly recurved, while in *Cunningtonia* they point inwards. The oral dentition in *Cunningtonia* consists of a band formed by numerous rows of slender, densely packed and mobile tricuspid teeth, with a strongly recurved top (Poll, 1956). The genera *Cardiopharynx* and *Asprotilapia* possess only two rows of oral teeth, versus 3–5 in *Ophthalmotilapia*.

Cyathopharynx can furthermore be distinguished from *Ophthalmotilapia* in the number of lateral line scales, 48–67 (Hanssens, unpublished results) versus 36–40. The genus *Aulonocranus* differs from all other Ectodini by its extremely enlarged sensory pores in the head and lower oral jaw. The genera *Callochromis*, *Ectodus* and *Grammatotria* have a lower number of gill rakers on the ceratobranchial—less than 14. In *Ophthalmotilapia* (Poll, 1956) by contrast, there are 15–21.

Ophthalmotilapia differs from *Lestradea*, *Ectodus*, *Asprotilapia*, *Grammatotria*, *Xenotilapia*, *Enantiopus* and *Microdotochromis* in having a body depth of 29.0% SL; in the latter genera it varies between 29.8 and 40.3% SL (Poll, 1951b). In addition, the genus *Asprotilapia* is characterized by its long conical nose, which extends in front of the inferior mouth. The genus *Grammatotria* has 44–59 scales in longitudinal line. The genera *Xenotilapia*, *Enantiopus* and *Microdotochromis* are characterized by the inverted symmetry of their ventral fins; the internal finrays are longer than or of equal length to the external finrays. Finally, the genus *Microdotochromis* is characterized by its single row of small unicuspid oral teeth.

Taxonomy of the Ophthalmotilapia species

There are several errors in the designation and further references concerning the type specimens of *O. ventralis*. As mentioned above, the original description of this species (Boulenger, 1898) is based on nine specimens, eight from Kinyamkolo, one from Mbity Rocks.

Boulenger (1915) lists one type from Mbity Rocks and six types from Kinyamkolo; this corresponds to the origin and number of species from the original register, catalogue and specimen bottle labels from the British Museum of Natural History (Anne-Marie Woolger, pers. comm.) which are as follows: BMNH 1898.9.9:31 (types) *Paratilapia ventralis*, Mbity Rocks, 1 specimen; BMNH 1898.9.9:32–36 (types) *Paratilapia ventralis*, Kinyamkolo, six specimens (in this case the number of specimens does not correspond to the register number). Hence, the total number of registered specimens does not correspond to the number indicated in the original description.

Later, the specimen BMNH 1898.9.9:31 was registered as *Ophthalmotilapia ventralis* and then *Ophthalmochromis ventralis* (lectotype). The specimens BMNH 1898.9.9:32–36

were split as follows; BMNH 1898.9.9:32 was determined to be *Ophthalmotilapia ventralis* and then (by Poll, 1961, unpublished) as *Aulonocranus dewindti*. The remaining specimens BMNH 1898.9.9:33–36 were determined to be *Ophthalmotilapia ventralis* and then *Ophthalmochromis ventralis* (paralectotypes). One specimen from this series, BMNH 1898.9.9:36 from Kinyamkolo, was donated to the Africa Museum, Tervuren, and registered as MRAC 140, paralectotype of *Ophthalmochromis ventralis*.

However, Poll & Matthes (1962) designated one specimen from the series BMNH 1898.9.9:33–37 as lectotype. They did not mention the specimen registered as BMNH 1898.9.9:31 from Mbity Rocks. They reported six of the seven registered types, which corresponds to the total number from the series BMNH 1898.9.9:32–36 from Kinyamkolo. One specimen from this series was deposited in the MRAC (mentioned by Poll & Matthes, 1962) and another in the Muséum National d'Histoire Naturelle, Paris as MNHN 1898.698 [not indicated by Poll & Matthes (1962), this specimen was probably deposited after their study]. The list of type specimens given in CLOFFA IV by Maréchal & Poll (1991) corresponds to the data as provided by A.-M. Woolger. In CLOFFA IV the specimen BMNH 1898.9.9:31 from Mbity Rocks is listed as lectotype, the specimens from the series BMNH 1898.9.9:33–35 and both specimens deposited in the MRAC and MNHN as paralectotypes. This list does not correspond to that given by Poll & Matthes (1962). Furthermore, the register of the BMNH lists the specimens BMNH 1898.9.9:37–38 as *Paratilapia furcifer* (synonym of *Cyathopharynx furcifer*). Therefore, BMNH 1898.9.9:31 cannot be the lectotype of *O. ventralis*, but a specimen from the series BMNH 1898.9.9:32–36. The lectotype will be designated based on the data provided by Poll & Matthes (1962) in a future study on the 'ventralis-heterodonta' complex (Hanssens *et al.*, in prep.).

In their description of *Ophthalmochromis ventralis heterodontus*, Poll & Matthes listed a paratype originating from Mtoto, a locality far from the distribution area of the other *O. v. heterodontus* specimens, which were confined to the northern part of the lake. On the distribution map of the *Ophthalmochromis* species, Poll & Matthes (1962) reported three species from Mtoto (near Moba): *O. nasuta*, *O. v. heterodontus* and a specimen from the intermediate populations. The *O. v. heterodontus* specimen is listed without registration number, and we could find no trace of it in the collections of the MRAC, Tervuren, the RBINSc in Brussels and the BMNH in London (A.-M. Woolger, pers. comm.). The intermediate specimen is registered as RBINSc 11523. The data of Poll & Matthes (1962) furthermore show that the *O. v. heterodontus* specimen was caught at 'baic de Mtoto' on 7 March 1947, the same locality and date as for the specimen from the intermediate population. In his list of *Ophthalmochromis* specimens caught during the 'Exploration Hydrobiologique de lac Tanganika' expedition, Poll (1956) reports that only a single *Ophthalmochromis* specimen was caught at Mtoto that day. We therefore suspect that Poll & Matthes (1962) have listed this specimen twice, and that their claim that *O. v. heterodontus* occurs at this locality is probably incorrect. The specimen from the intermediate population, registered in the RBINSc, belongs to the unidentified Mtoto population (see below). The taxonomic status of this intermediate population will be subject of a future study (Hanssens *et al.*, in prep.). Next to the paratypes, Poll & Matthes (1962) listed 95 *O. v. heterodontus* specimens, without registration numbers. We were unable to trace these specimens; they were not deposited in the MRAC, the RBINSc, the BMNH or the MNHN.

Morphometry

Our results show that there are several errors in the currently available *Ophthalmotilapia* species diagnoses and identification keys (Poll, 1956; Poll & Matthes, 1962; Brichard, 1978; 1989).

Poll (1956) erroneously listed a total number of 62–74 scales in longitudinal line for *O. boops*. We counted 36–39. Brichard (1989) seems to have copied the data from Poll (1956) and Poll & Matthes (1962) in his key to the *Ophthalmotilapia* species; he also listed 62–74. In his key Brichard (1989) only recognized three *Ophthalmotilapia* species: *O. boops*, *O. nasuta* and *O. ventralis*. The diagnosis of the three species in the key was mainly based on the differences in longitudinal line scales. Apart from the incorrect number of longitudinal line scales listed for *O. boops*, this number also needs to be modified for *O. ventralis* and *O. nasuta*. We counted 37–40 longitudinal line scales in *O. nasuta* and 35–39 scales in *O. ventralis*, while Brichard (1989) listed 39 longitudinal scales in *O. ventralis* versus 33–37 in *O. nasuta*. Although we also found a difference in scale count between *O. nasuta* and *O. ventralis*, this is not a good diagnostic character due to the large overlap in numbers.

Identification of *O. ventralis* and *O. heterodonta* was difficult since the enlarged molariform teeth on the posterior part of the lower pharyngeal jaw, a diagnostic character used by Poll & Matthes (1962) to identify *O. heterodonta*, were not present on all *O. heterodonta* type specimens. It is also difficult to make a clear-cut distinction between the 'ventralis' and 'heterodonta' type. Our observations showed that this character changes gradually within and between these taxa. Also Brichard (1989) listed no morphological differences between *O. ventralis* and *O. heterodonta*. We identified these two species by a different number of scales between the upper and lower lateral line (three in *O. ventralis* versus two in *O. heterodonta*). The identification of *O. ventralis* and *O. heterodonta* on the basis of this difference in scale count was confirmed by further analyses based on metric characters (Hanssens *et al.*, in prep.). It is surprising that although they also counted the number of transverse line scales for both species, Poll & Matthes (1962) did not find differences in scale counts between *O. ventralis* and *O. heterodonta*.

We were unable to identify the specimens collected in Mtoto on the basis of the difference in scale count between the upper and lower lateral lines. For some of these specimens we counted two scales and for other specimens, three. It is important to point out that the Mtoto specimens clearly differ in coloration from the northern *O. heterodonta* or the southern *O. ventralis* populations. The taxonomic status of the Mtoto populations is presently uncertain (Hanssens *et al.*, in prep.).

Interestingly, we are to our knowledge the first to report the presence of the fleshy appendix in some female specimens of *O. nasuta*. As far as we know, the presence of this enlarged appendix on the nose was only reported in the males of this species.

In *O. ventralis* and *O. nasuta* we have found variation in some of the metric and meristic characters. These two species contain several populations which can be distinguished morphologically, and which are confined to particular areas of the lake. We can therefore refer to all *O. ventralis* and *O. heterodonta* populations, including the unidentified Mtoto specimens as the 'ventralis-heterodonta' complex; and to all *O. nasuta* populations as the 'nasuta' complex.

Distribution patterns of *Ophthalmotilapia*

In the genus *Ophthalmotilapia* we find three different distribution patterns. A discontinuous circumlacustrine distribution for *O. nasuta*, a complementary north -

south distribution for *O. ventralis* and *O. heterodonta* and a restricted distribution for *O. boops*.

In several areas of the lake more than one *Ophthalmotilapia* species are found sympatrically: In some localities on the Zambian and Tanzanian coast *O. nasuta* and *O. ventralis* are found syntopically, and on some localities along the Tanzanian coast *O. boops* was collected together with *O. ventralis* or *O. nasuta*. Finally, in the northern part of the lake, *O. heterodonta* lives sympatrically with *O. nasuta*. Hitherto, three *Ophthalmotilapia* species have never been collected in a single locality.

Ophthalmotilapia nasuta

Konings (1988) reports *O. nasuta* from the northern part of the lake, and states that in the southern part another species, *O. sp. aff. nasuta* is found. Our results, however, showed that the actual situation is probably more complex. For *O. nasuta*, more than two morphologically distinct populations are found. These populations are confined to particular areas of the lake. Different geographically restricted colour morphs have been reported in the aquarium literature (Schupke, 1993; Konings, 1988 and Konings & Dieckhoff, 1992). The status and distribution of these populations are the subjects of an ongoing study (Hanssens *et al.*, in prep.).

Schupke (1993) summarizes the distribution and colour patterns of the known races of *O. ventralis*. He also reported one population of *O. heterodonta* from the Tanzanian coast near Kigoma. The same picture was published before (Schupke, 1984) as *O. ventralis ventralis*. This specimen clearly shows a prolonged nose and therefore in our opinion most probably belongs to *O. nasuta*.

Ophthalmotilapia ventralis and *O. heterodonta*

The distribution of *O. heterodonta* and *O. ventralis* does not fully correspond to the distribution pattern given by Poll & Matthes (1962) and Konings (1988). Our data show that the distribution of *O. heterodonta* reaches further south than has been reported thus far. In Konings (1988: 63) the distribution of *O. heterodonta* is limited to the northern part of the lake, to the Ubwari peninsula on the western shoreline, and north of the Malagarasi river on the eastern shoreline. The southernmost locality where we identified *O. heterodonta* is Kalemie on the western and a locality north of Edith Bay on the eastern shoreline.

The occurrence of a complementary north–south distribution of two closely related species, as found for *O. ventralis*–*O. heterodonta*, has been reported by Poll (1956) for several other species. This distribution pattern between two closely related species or subspecies was related by Poll to the presence of two separated sub-basins during the lake's geological history. Poll & Matthes (1962) added *O. ventralis ventralis* and *O. ventralis heterodontus* to their list of so-called 'twin species couples' with a complementary north–south distribution. As for *O. nasuta*, different colour morphs have been reported in *O. ventralis*. The within-lake distributions of these different colour races have extensively been discussed by Schupke (1984, 1987, 1993, 1994), Konings (1988), Konings & Dieckhoff (1992) and Eysel (1993). Konings & Dieckhoff (1992) suggested that the distribution of the different *O. ventralis* colour races along the Congolese, Zambian and Tanzanian shorelines reflect that the yellow *O. ventralis* populations are ancestral to the southernmost bluish *O. ventralis*. Konings & Dieckhoff (1992) reported the occurrence of distinct colour races in the southernmost part of the lake for other species as well. This is probably due to the fact that these

populations colonized that part of the lake after the water level in Lake Tanganyika rose approximately 75 000 years ago (Coulter, 1991). Our analysis of the morphologically distinct populations and our records of the colour patterns of the specimens studied from these populations do not disagree with the evolutionary scenario as proposed by Konings & Dieckhoff (1992). However, to establish the 'true' status and the distributions of the taxa within the 'ventralis-heterodonta' complex, a more detailed study is required (Hanssens *et al.*, in prep.). Brichard (1978, 1989) erroneously listed *O. v. ventralis* as northern and *O. v. heterodontus* as southern subspecies.

Ophthalmotilapia boops

We collected *O. boops* only in the southern part of Lake Tanganyika between Mpimbwe and Wampembe. This is in disagreement with Konings (1988) who also reported an undescribed species—*O. sp. aff. boops* or 'white cap'—along the Tanzanian coast, from Kigoma to Kipili (distribution map page 63), overlapping in the south with the distribution of *O. boops*. It is important that Konings was not sure if *O. sp. aff. boops* belonged to the real *O. boops*, to the southern *O. ventralis* or to the so-called white cap, which consists of several populations. The coloration of these white-cap varieties corresponds to that of *O. boops*, but they lack the tricuspid teeth that are typical for *O. boops*. Based upon this evidence, it is remarkable that Konings refers to this taxon as *O. sp. aff. boops* instead of *O. sp. aff. ventralis*. Indeed, this taxon differs in morphology from the southern *O. ventralis* only by having a wider and larger mouth (Konings, 1988). Finally, the white-cap races resemble the unidentified Mtoto races in coloration pattern and therefore clearly belong to the 'ventralis-heterodonta' complex (see above).

History of Lake Tanganyika and distribution patterns in Ophthalmotilapia

The seemingly complex intralacustrine distribution patterns contrast with the earlier assumption that the majority of cichlids are present in all suitable biotopes of the lake. Poll (1956) has already drawn attention to some north-south distribution patterns of 'species couples' which were at that time reported as subspecies [viz. *Callochromis melanostigma* (Boulenger, 1906) and *C. macrops* (Boulenger, 1898), *Lestradia perspicax* and *L. stappersi*]. Poll related the distributions of these species to the presence of two separate sub-basins during the lake's geological history. To this list Poll & Matthes (1962) added *Ophthalmochromis v. heterodontus* and *O. v. ventralis*. In 1978, Poll mentioned some 'twin species couples' of *Lamprologus* Schilthuis, 1891 [*N. leloupi* (Poll, 1948) and *N. caudopunctatus* (Poll, 1978), *N. savoryi* (Poll, 1949) and *N. brichardi* (Poll, 1974), *A. compressiceps* (Boulenger, 1898) and *A. calvus* (Poll, 1978), *N. tretocephalus* (Boulenger, 1899) and *N. sexfasciatus* (Trewavas & Poll, 1952), *N. modestus* (Boulenger, 1898) and *N. petricola* (Poll, 1949), *N. hecqui* (Boulenger, 1899) and *N. meeli* (Poll, 1848)] considering these cichlid taxa to have resulted from geographical isolation during the previous existence of separate sub-basins (Poll, 1956). Since then new evidence has accumulated that periods of aridity have caused dramatic drops in water level that split Lake Tanganyika into three separate basins (e.g. Tiercelin and Mondegue, 1991; Scholz & Rosendahl, 1988). Recent studies have demonstrated that these separate sub-basins have played a major role in the distribution of the cichlids from rocky and intermediate shallow habitats (Sturmbauer & Meyer, 1992; Verheyen *et al.* 1996; Sturmbauer *et al.*, 1997).

Our results show that the originally proposed complementary north–south distribution of the ‘twin’ species pairs *O. ventralis*/*O. heterodonta* (Poll & Matthes, 1962) and *O. nasuta*/*O. sp. aff. nasuta* (Konings, 1988) are incorrect. Therefore, the origin of these *Ophthalmotilapia* taxa cannot be explained by the splitting of the Lake Tanganyika basin alone. The answers to such evolutionary problems cannot be based upon morphological data only. One of the major objectives of an ongoing mtDNA study (Hanssens *et al.*, in prep.) on these taxa is to evaluate their relative ages as compared to the ages of other cichlid taxa for which the effects of lake level fluctuations have been demonstrated (Sturmbauer & Meyer, 1992; Verheyen *et al.*, 1996; Sturmbauer *et al.*, 1997).

ACKNOWLEDGEMENTS

Fieldwork was carried out in collaboration with the Tanzanian Fisheries Research Institute (Prof. Dr P.O.J. Bwathondi), the University of Burundi (Dr G. Ntakimazi) and the Zambian Ministry of Agriculture Food and Fisheries (Dr H. G. Mudenda). We thank director Prof. Dr Ir. D.F.E. Thys van den Audenaerde (MRAC-Tervuren) for financial support to M.H. The fieldwork and the research were funded by the CASIMIR-SIAL project (Dr J. Klerkx, MRAC-Tervuren), the Belgian government (FJBR program 2.90004.90, FJBR.-MI grant 30–35 to E.V.), the Leopold III Foundation and a grant of the Belgian Science Foundation (to J.S. and E.V.). Mr O. Crimmen (BMNH) is acknowledged for the loan of the *O. boops* and *O. ventralis* types, Ms Anne-Marie Woolger (BMNH) is acknowledged for providing the information concerning the *O. ventralis* types. We are grateful to Mr Ad Konings for the loan of a slide collection on different colour races in *Ophthalmotilapia ventralis*, *O. nasuta* and *O. boops*.

REFERENCES

- Bookstein F, Chernoff B, Elder R, Humphries J, Smith G, Strauss R. 1985. *Morphometrics in Evolutionary Biology*. Special Publication 15. *Journal of the Academy of Natural Sciences of Philadelphia*.
- Boulenger GA. 1898. Report on the collection of fishes made by Mr. J.E.S. Moore in lake Tanganyika during his expedition 1895–1896, with an appendix by J.E.S. Moore. *Transactions of the Zoological Society, London* 15: 1–30.
- Boulenger GA. 1901a. Diagnoses of new fishes discovered by Mr. J.E.S. Moore in lakes Tanganyika and Kivu. *Ann Mag Nat Hist* (7)7:(37) 1–6.
- Boulenger GA. 1901b. *Les poissons du bassin du Congo*, vol. 12. Publ. Etat Indép. Congo, Bruxelles.
- Boulenger GA. 1915. *Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History)*, vol. 3. London.
- Brichard P. 1978. *Fishes of Lake Tanganyika*. Neptune, New Jersey: TFH.
- Brichard P. 1989. *Pierre Brichard's book of cichlids and all other fishes of Lake Tanganyika*. Neptune, New Jersey: TFH.
- Coulter GW. 1991. Zoogeography, affinities and evolution, with special regard to the fish. In: Coulter GW, ed. *Lake Tanganyika and its life*. Oxford: Oxford University Press, 275–305.
- Eysel W. 1993. Der Fadenmaulbüter *Ophthalmotilapia ventralis*. Teil II. Farbrassen und ihre Verbreitung. *Das Aquarium* 286: 9–16.
- Greenwood PH. 1983. The *Ophthalmotilapia* assemblage of cichlid fishes reconsidered. *Bulletin of the British Museum, Natural History (Zoology)* 44(4): 249–290.
- Humphries JM, Bookstein FL, Chernoff B, Smith GR, Elder RL, Poss SG. 1981. Multivariate discrimination by shape in relation to size. *Systematic Zoology* 30(3): 291–308.
- Kohda M, Yanagisawa Y, Sato T, Nakaya K, Niimura Y, Matsumoto K, Ochi H. 1996.

- Geographical colour variation in cichlid fishes at the southern end of Lake Tanganyika. *Env Biol Fish* **45**: 327–248.
- Konings A. 1988.** *Tanganyika Cichlids*. Verduijn Cichlids and Lake Fish Movies, Zevenhuizen, Holland, Herten West Germany.
- Konings A, Dieckhoff FW. 1992.** *Tanganyika secrets*. St Leon-Rot, Germany: Cichlid Press.
- Liem KF. 1981.** A phyletic study of the Lake Tanganyika cichlid genera *Asprotilapia*, *Ectodus*, *Lestradea*, *Cunningtonia*, *Ophthalmochromis* and *Ophthalmotilapia*. *Bulletin of the Museum of Comparative Zoology* **149**(3): 191–214.
- Maréchal C, Poll M. 1991.** *Ophthalmotilapia*. In: Daget J, Gosse J-P, Teugels GG, Thys van den Audenaered DFE, eds. *Check-list of the freshwater fishes of Africa*. ORSTOM, Michiels, Belgium: ISBN, MRAC.
- Meyer A. 1993.** Phylogenetic relationships and evolutionary processes in East African cichlid fishes. *Trends in Ecology and Evolution* **8**: 279–284.
- Meyer A, Knowles L, Verheyen E. 1996.** Widespread geographic distribution of mitochondrial haplotypes in Lake Tanganyika rock-dwelling cichlid fish. *Molecular Ecology* **5**: 341–350.
- Nakai K, Kawanabe H, Gashagaza MM. 1994.** Ecological studies on the littoral cichlid communities of Lake Tanganyika: the coexistence of many endemic species. In: Martens K, Goddeeris B, Coulter G, eds. *Speciation in Ancient Lakes*. *Arch Hydrobiol Beih Ergebn Limnol* **44**: 373–389.
- Pellegrin J. 1904.** Contribution à l'étude anatomique, biologique et taxonomique des poissons de la famille des Cichlides. *Mémoires de la Société Zoologie de France* **16**: 41–402.
- Poll M. 1946.** Révision de la faune ichthyologique du lac Tanganyika. *Annales du Musée royal du Congo Belge* (1) **4**(3): 141–364.
- Poll M. 1951a.** Histoire du peuplement et origine des espèces de la faune ichthyologique du lac Tanganyika. *Annals de la Société royal de Zoologie de Belgique* **81**: 111–140.
- Poll M. 1951b.** Troisième série de Cichlidae nouveaux recueillis par la Mission Hydrobiologique belge au lac Tanganika (1946–1947) (Suite 1). *Bull Inst r Sci nat Belg* **27**(30): 12 pp.
- Poll M. 1956.** *Poissons Cichlidae*. Résult. scient. Explor. hydrobiol. Lac Tanganika. *Inst r Sci nat Belg* **3** (5B).
- Poll M. 1978.** Contribution à la connaissance *Lamprologus* Schth. Description de quatre espèces nouvelles, réhabilitation de *Lamprologus mondabu* et synopsis remanié des espèces du lac Tanganyika. *Bull Cl Sci Acad r Belg* (5) **64**(11): 725–758.
- Poll M. 1986.** Classification des Cichlidae du lac Tanganika: tribus, genres et espèces. *Académie Royale de Belgique, Mémoires de la Classe de Sciences* (8) **45**(2).
- Poll M, Matthes H. 1962.** Trois poissons remarquables du lac Tanganika. *Annales du Musée royal de l'Afrique Centrale* **111**: 1–26.
- Regan CT. 1920.** The Classification of the Fishes of the Family Cichlidae. I. The Tanganyika genera. *Ann Mag nat Hist* (9) **5**(25) 33–53.
- Scholz C, Rosendahl B. 1988.** Low lake stands in Lake Malawi and Lake Tanganyika, east Africa delineated with multifold seismic data. *Science (Washington)* **240**: 1645–1648.
- Schupke P. 1984.** Die bekannten südlichen Rassen von *Ophthalmochromis ventralis ventralis*. *DATZ* **2/84**: 45–47.
- Schupke P. 1987.** Observations of *Ophthalmotilapia ventralis ventralis*. *Tropical Fish Hobbyist* **36**(4): 37–40, 43.
- Schupke P. 1993.** The spawning behaviour of *Ophthalmotilapia* in Lake Tanganyika. *Aqua Geographia* **5**: 76–82.
- Schupke P., 1994.** Die Pflege von *Ophthalmotilapia ventralis ventralis*. *DATZ* **6/94**: 350–354.
- Snoeks J. 1994.** The haplochromines (Teleostei, Cichlidae) of Lake Kivu (East Africa). *Annales du Musée royal de l'Afrique Centrale* **270**.
- Snoeks J, Rüber L, Verheyen E. 1994.** The Tanganyika problem: Taxonomy and distribution patterns of its ichthyofauna. In: Martens K, Goddeeris B, Coulter G, eds. *Speciation in Ancient Lakes*. *Arch Hydrobiol Beih Ergebn Limnol* **44**: 357–374.
- Sturmbauer C, Meyer A. 1992.** Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. *Nature (London)* **358**: 578–581.
- Sturmbauer C, Meyer A. 1993.** Mitochondrial Phylogeny of the Endemic Mouthbrooding Lineages of Cichlid Fishes from Lake Tanganyika in Eastern Africa. *Molecular Biology and Evolution* **10**: 751–768.
- Sturmbauer C, Verheyen E, Rüber L, Meyer A. 1997.** Phylogeographic patterns in populations of cichlid fishes from rock habitats in Lake Tanganyika. In: Kocher T, Stepien C, eds. *Molecular Systematics of Fishes*. London: Academic Press.

- Tiercelin J-J, Mondegue A. 1991.** The geology of the Tanganyika trough. In: Coulter GW, ed. *Lake Tanganyika and its life*. Oxford: Oxford University Press, 7-48.
- Verheyen E, Rüber L, Snoeks J, Meyer A. 1996.** Mitochondrial phylogeny of rock-dwelling cichlid fishes reflect historical lake level fluctuations in Lake Tanganyika. *Philosophical Transactions of the Royal Society of London* **B351**(1341): 797-805.

APPENDIX: SPECIMENS EXAMINED

All specimens of a given series have been examined, except when indicated.

O. ventralis

- BMNH 1898.9.9:31; Mbity Rocks, Lake Tanganyika; J.E.S. Moore, 9.ix.1898; paralectotype
- MRAC 107109-107114; Stat 184, Kapampa, plages Nord et Sud; M. Poll, Exp. hyd. biol. L. Tan., 22.iii.1947; 3 ex
- MRAC 107116; Stat 202, Mpulungu près du pier; M. Poll, Exp. hyd. biol. L. Tan., 27.iii.1947
- MRAC 107117; Stat 217, Moliro, pointe rocheuse Sud; M. Poll, Exp. hyd. biol. L. Tan., 01.iv.1947
- MRAC 107123-107128; Stat 319, Mwerazi, le long de la rive Sud; M. Poll, Exp. hyd. biol. L. Tan., 28.v.1947; 2 ex
- MRAC 140164; Kinyamkolo, Lac Tanganika; Moore, 1898; paralectotype
- MRAC 189693-189704; Mpulungu, Jetty, Lac Tanganika, Zambia; H. Matthes, 16.ii.1966; 2 ex
- MRAC 76 4-P-286-295; Cap Chipimbi, sud du Lac Tanganika, Zambia; P. Brichard, 15.i.1976; 3 ex
- MRAC 76-4-P-362-371; Cap Kabeyeye, à l'Est de Kasaba Bay, sud du Lac Tanganika, Zambia; P. Brichard, 17.i.1976; 5 ex
- MRAC 84-23-P-95-96; Crique de Mtoto, 10 km Nord de Moba, Lac Tanganika, Zaire; P. Brichard, 10.iv.1981; 2 ex
- MRAC 78-25-P-598-608; Cap Kachese, Sud du Lac Tanganika, Zambia; iii.1978; 3 ex
- MRAC 78-25-P-613-617; Cap Chaitika, Sud du Lac Tanganika, Zambia; P. Brichard; iii.1978; 2 ex
- MRAC 78-25-P-622-628; Cap Chaitika, Sud du Lac Tanganika, Zambia; P. Brichard; v.1978; 5 ex
- MRAC 92-81-P-543; locality 15, Mwsa Bay, northern point, Tanzania; coll. Tanganyika Expedition '92, 28.05.1992
- MRAC 95-81-P-30; locality 1, Tanganyika Lodge, Zambia; coll. Tanganyika Expedition '95, 03.04.1995
- MRAC 95-96-P-141; locality 10, Chisiki, Zambia; coll. Tanganyika Expedition '95, 10.04.1995
- MRAC 95-96-P-170; locality 15, Punda Point, Tanzania; coll. Tanganyika Expedition '95, 15.04.1995
- MRAC 95-96-P-271; locality 25, Kasanga, Tanzania; coll. Tanganyika Expedition '95, 21.04.1995

O. nasuta

- MRAC 107077; Stat 41, Baie de Mtoto, rochers de la côte Sud; M. Poll, Exp. hyd. biol. L. Tan., 30.vii.1946; paratype
- MRAC 107087-107096; Stat 95, Baie de Kabimba; M. Poll, Exp. hyd. biol. L. Tan., 29.i.1947; paratype; 4 ex
- MRAC 107118-107119; Stat 301, Kigoma, dans le bassin du slip; M. Poll, Exp. hyd. biol. L. Tan., 13.v.1947; paratypes
- MRAC 107122; Stat 316, Mtoto, rochers au Sud de la baie; M. Poll, Exp. hyd. biol. L. Tan., 27.v.1947
- MRAC 126356; Kalungwe, bassin Tanganika; H. Matthes, I.R.S.A.C., 1954; holotype
- MRAC 126357; Kalungwe, bassin Tanganika; H. Matthes, I.R.S.A.C., 1958; allotype
- MRAC 126372-126380; Ile de Mboko, Lac Tanganika, H. Matthes, I.R.S.A.C., 3.ix.1958; paratypes; 1 ex
- MRAC 126382-126401; Bemba, Lac Tanganika; H. Matthes, I.R.S.A.C., 22.vii-i.1958; paratypes; 3 ex
- MRAC 129074-129077; Rubana (Ubwari); H. Matthes, 4.xii.1959; paratypes; 4 ex
- MRAC 129697-129699; Luhanga, Lac Tanganika; G. Marlier, I.R.S.A.C., 30.x.1957 paratypes; 1 ex
- MRAC 78-25-P-582-584; Cap Kachese, Zambia; P. Brichard, i.1978; 1 ex
- MRAC 78-25-P-609-612; Cap Kachese, Zambia; P. Brichard, III.1978; 3 ex

- MRAC 84-9-P-349-351; 25 km S. de Yungu, côte ouest du Lac Tanganika, Zaire; P. Brichard, 13.iv.1984; 1 ex
 MRAC 84-9-P-384; 5me parallèle, côte ouest du Lac Tanganika, Zaire; P. Brichard, 14.iv.1984
 MRAC 78-25-P-618-619; Cap Chaitika, Zambia; P. Brichard; iii.1978; 1 ex
 MRAC 78-25-P-629-630; Cap Chaitika, Zambia; P. Brichard; iii.1978; 1 ex
 MRAC 92-81-P-84, 98, 100, 157, 159; locality 4b, Ulwile Island, northern shore, Tanzania; coll. Tanganyika Expedition '92, 27.05.1992
 MRAC 92-81-P-412-413, 415; Locality 9, Nokondwe Island, southern shore, Tanzania; coll. Tanganyika Expedition '92, 27.05.1992
 MRAC 92-81-P-431; Locality 10, Mpimbwe Hills, southern shore, southern shore of Katondo Point, Tanzania; coll. Tanganyika Expedition '92, 28.05.1992
 MRAC 92-81-P-685; Locality 21, north of Nkombe, Tanzania; coll. Tanganyika Expedition '92, 29.05.1992
 MRAC 92-81-P-1215; Locality 43, Kalela, Tanzania; coll. Tanganyika Expedition '92, 02.06.1992
 MRAC 92-81-P-1270-1271; Locality 45, Mkuyu Point, northern shore, Tanzania; coll. Tanganyika Expedition '92, 02.06.1992
 MRAC 92-81-P-1364-1365; Locality 49, Masaka Point, northern shore, military camp, Tanzania; coll. Tanganyika Expedition '92, 03.06.1992
 MRAC 92-81-P-1418, 1439-1440; Locality 47, Kiti point, southern shore, Tanzania; coll. Tanganyika Expedition '92, 03.06.1992
 MRAC 95-96-P-172; locality 15, Punda Point, Tanzania; coll. Tanganyika Expedition '95, 15.04.1995

O. boops

- BMNH 1906.9.6:152-153; Msamba, Lake Tanganyika; J.E.S. Moore, 6.ix.1906; type
 MRAC 92-81-P-101; Locality 4b, Ulwile Island, northern shore, Tanzania; coll. Tanganyika Expedition '92, 27.05.1992
 MRAC 92-81-P-314, 316; Locality 5, Ulwile Island, southern shore, south of Nkamba Hill, Tanzania; coll. Tanganyika Expedition '92, 27.05.1992
 MRAC 92-81-P-334-336; Locality 7, Nvuna Island, north-eastern shore, Tanzania; coll. Tanganyika Expedition '92, 27.05.1992
 MRAC 92-81-P-360; Locality 8, Nvuna Island, north-western shore, Tanzania; coll. Tanganyika Expedition '92, 27.05.1992
 MRAC 92-81-P-430; Locality 10, Mpimbwe Hills, southern shore, southern shore of Katondo Point, Tanzania; coll. Tanganyika Expedition '92, 28.05.1992
 MRAC 92-81-P-469, 474, 476; Locality 12, Kampemba, northern shore of Kampemba Point, Tanzania; coll. Tanganyika Expedition '92, 28.05.1992
 MRAC 92-81-P-614; Locality 19, Mpimbwe Hills, Shashete Bay, northern part, Tanzania; coll. Tanganyika Expedition '92, 29.05.1992
 MRAC 95-96-P-225; Locality 20, Msamba Bay, Tanzania; coll. Tanganyika Expedition '95, 18.04.1995

O. heterodonta

- MRAC 130671; Ile de Mboko, Lac Tanganika; H. Matthes, 2-4.IX.1958; holotype
 MRAC 130672; Ile de Mboko, Lac Tanganika; H. Matthes, 2-4.ix.1958; allotype
 MRAC 130673-684; Ile de Mboko, Lac Tanganika; H. Matthes, 2-4.ix.1958; paratypes; 9 ex
 MRAC 130687-689; Luhanga, Lac Tanganika; G. Marlier, 30.xi.1957; paratypes; 3 ex
 MRAC 130690; Luhanga, Lac Tanganika; N. Leleup, 1957; paratype
 MRAC 130691-693; Kigongo (Luhanga), Lac Tanganika; H. Matthes, 3.xii.1958; paratypes; 3 ex
 MRAC 130694; Bamba, Lac Tanganika; H. Matthes, 14.v.1958; paratype
 MRAC 81-29-P-152-153; Kalemie, Lac Tanganika; P. Brichard, 10.iv.1981
 MRAC 92-81-P-951; Locality 32, North of Edith Bay, Tanzania; coll. Tanganyika Expedition '92, 31.05.1992
 MRAC 92-81-P-1091-1092, 1128; Locality 40, South of Mkuyu Point, Tanzania; coll. Tanganyika Expedition '92, 01.06.1992
 MRAC 92-81-P-1171, 1173; Locality 41, Segunga, south of Segunga Bay, Tanzania; coll. Tanganyika Expedition '92, 01.06.1992
 MRAC 92-81-P-1209; Locality 43, Kalela, Tanzania; coll. Tanganyika Expedition '92, 02.06.1992
 MRAC 92-81-P-1309; Locality 49, Masaka Point, northern shore, military camp, Tanzania; coll. Tanganyika Expedition '92, 03.06.1992