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Description of the Ethmovomerine Region in Tanganyikan Cichlid Fishes (Teleostei : Perciformes)

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Abstract

The ethmovomerine regions in all of the Tanganyikan cichlid genera are described for the purpose of proposing a basic morphological information, and classified into six types. Of these, the tylochromine, bathybatine, haplochromine and oreochromine types were found in the Limnochromini, Tilapiini and Tylochromini; Bathybatini and Trematocarini; Ectodini, Haplochromini, Limnochromini, Perissodini, Tilapiini and Tropheini; and Cypriochromini, Ectodini, Eretmodini, Lamprologini, Limnochromini and Tilapiini, respectively. The lepidiolamprologine and asprotilapiine types were interpreted as being synapomorphies of clades composed of the four Lamprologini and four Ectodini taxa examined, respectively.

Key words: Ethmovomerine Region, Osteology, Cichlidae, Tanganyika, Tribe

Introduction

Poll's (1986) classification of Tanganyikan cichlid fishes included the establishment of 12 tribes, supported by short descriptions of external morphology and references to Greenwood's (1978) observations of the pharyngeal apophysis. These tribes have been in approximate agreement with several molecular analyses, which have been undertaken in the last decade (Nishida, 1991, 1997; Kocher et al., 1995; Takahashi et al., 1998), although some contradictory points remained. Recently, emphasis on morphological studies of these fishes has decreased considerably, in contrast to the advance of molecular studies. This may be one of the main reasons why the taxonomy of Tanganyikan cichlids still includes many problematic areas. It is important that emphasis on morphological analyses is continued, if taxonomic problems are to be convincingly resolved.

The ethmovomerine region (anterior part of the neurocranium) includes a number of variations, which have been used in taxonomic and phylogenetic studies of the African cichlids. On the basis of such variations, Regan (1920) separated *Tropheus*-like genera from *Tilapia*-like genera, Stiassny (1981) united *Bathybates*, *Hemibates* and *Trematocara* as a monophyletic group, and Trewavas (1973, 1983) distinguished *Tilapia* from *Oreochromis* and *Sarotherodon*. However, a comprehensive study of the ethmovomerine region has not been made for Lake Tanganyikan cichlids and variations are not well understood.

Therefore, in the present study, the ethmovomerine regions in all Tanganyikan cichlid genera have been examined in order to establish a morphological database that lends itself to the resolution of taxonomic problems.

Materials and Methods

The ethmovomerine regions were examined in 86 Lake Tanganyikan cichlid fishes representing 57 genera and 12 tribes, plus four fluvial *Tylochromis* species and one Victorian *Haplochromis* species. Specimens were identified using the descriptions of Boulenger (1898, 1901), Trewavas (1953), Greenwood (1956), Poll (1956, 1974, 1978, 1979, 1981, 1985), Marlier (1959), Poll and Matthes (1962), Bailey and Stewart (1977), Stiassny (1989), De Vos et al. (1996) and Hatooka (2000). The ethmovomerine region of each was observed and drawn under a Nikon SMZ-1000 or Leica MZ12 binocular microscope. Osteological terminology follows Stiassny (1981).

Institutional codes are as follows: HUMZ, Laboratory of Marine Biodiversity, Graduate School of Fisheries Sciences, Hokkaido University, Japan; LBM, Lake Biwa Museum, Japan; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; and UMMZ, University of Michigan Museum of Zoology, U.S.A.

Description

The ethmovomerine region is that part of the neuro-

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cranium anterior to the frontals, composed of an unpaired vomer and mesethmoid, and paired lateral ethmoids (Fig. 1-6). The edentulous vomer occupies the anterior half of the ethmovomerine region, followed by the oval, plate-like mesethmoid, which is sandwiched between the lateral ethmoids and occasionally has a pair of anteriorly-directed arms usually reaching the vomer. The lateral ethmoid forms the lateral wall of the ethmovomerine region, usually with an anterior extension which also reaches the vomer (dorsal bony bridge). Three cartilaginous fenestrae are generally present; the rostral fenestra between the vomer and mesethmoid, the dorsolateral fenestra between the mesethmoid and lateral ethmoid, and the ovoid fenestra between the vomer and lateral ethmoid. Occasionally the fenestrae are fused.

The ethmovomerine regions in the Tanganyikan cichlids were classified into six types, based mainly on the degree of development of the anteriorly-directed mesethmoid arm: tylochromine, bathybatine, haplochromine, lepidiolamprologine, oreochromine and asprotilapiine types.

Tylochromine type (Fig. 1, Appendix)

Mesethmoid arm narrow, elongated, anteriorly reaching vomer; lateral ethmoid reaching vomer anteriorly. Dorsal bony bridge of similar or slightly greater width than mesethmoid arm; dorsolateral fenestra large.

Bathybatine type (Fig. 2, Appendix)

Mesethmoid arm broader than in tylochromine type, anteriorly reaching vomer and extending laterally to lateral ethmoid in *Telotrematocara macrostoma*, *Trematocara marginatum* and *T. unimaculatum* (Fig. 2D); anterior extension of lateral ethmoid reduced, sometimes not reaching vomer (*Bathybates fasciatus*, *Trematocara marginatum*, *T. stigmaticum* and *T. zebra*, Fig. 2B, C); dorsolateral fenestra usually large, fused with ovoid fenestra when lateral ethmoid separated from vomer.

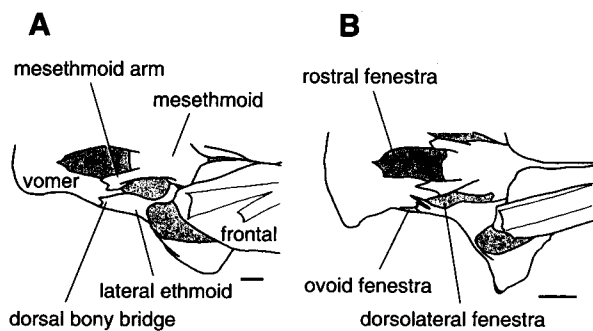


Fig. 1. Dorsal aspect of ethmovomerine region, representing tylochromine type. A, *Tylochromis polylepis*; B, *Reganochromis callurus*. Bar=1 mm.

Haplochromine type (Fig. 3, Appendix)

Mesethmoid arm shorter than in tylochromine type, anteriorly reaching vomer; lateral ethmoid reaching vomer anteriorly; dorsal bony bridge broader than arm of mesethmoid; dorsolateral fenestra narrow or absent.

Lepidiolamprologine type (Fig. 4, Appendix)

Mesethmoid arm short and broad, anteriorly reaching vomer; lateral ethmoid reaching vomer anteriorly; dorsal bony bridge much narrower than mesethmoid

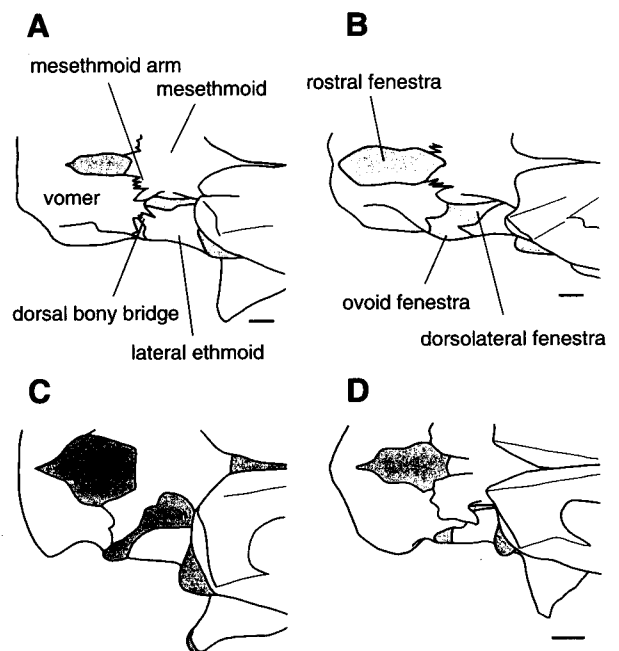


Fig. 2. Dorsal aspect of ethmovomerine region, representing bathybatine type. A, *Bathybates minor*; B, *B. fasciatus*; C, *Trematocara stigmaticum*; D, *Telotrematocara macrostoma*. Bar=1 mm.

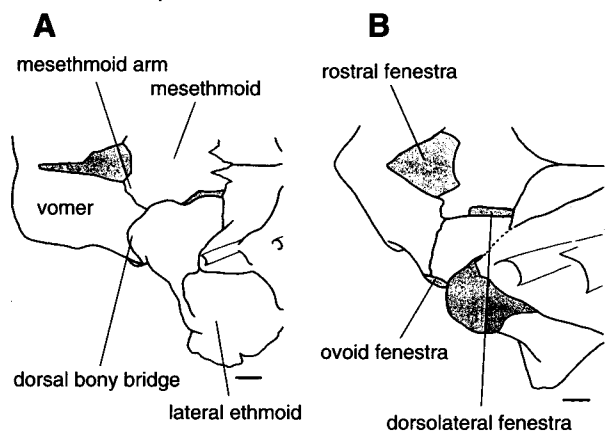


Fig. 3. Dorsal aspect of ethmovomerine region, representing haplochromine type. A, *Petrochromis fasciolatus*; B, *Cyathopharynx furcifer*. Bar=1 mm.

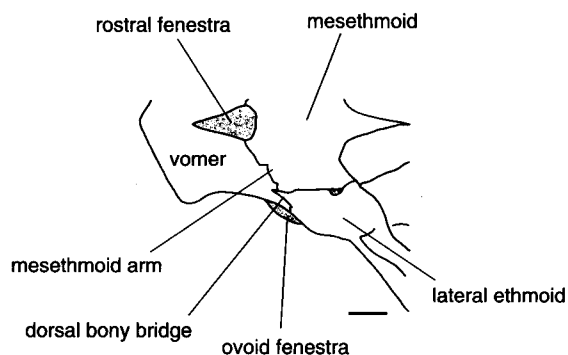


Fig. 4 Dorsal aspect of ethmovomerine region in *Lepidiolamprologus elongatus*, representing lepidiolamprologine type. Bar=1 mm.

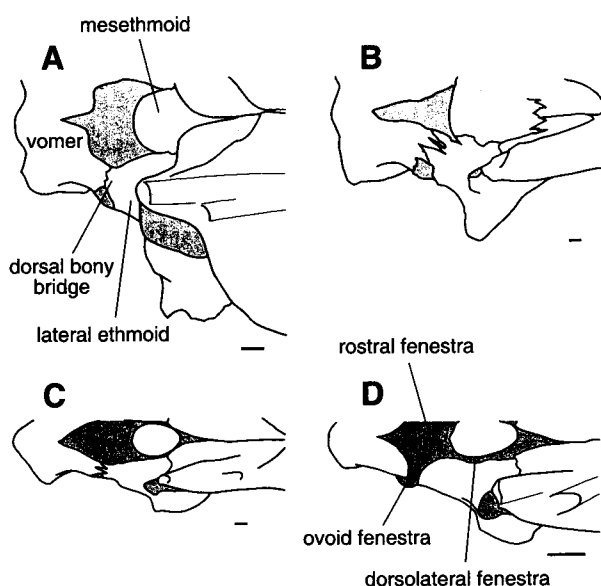


Fig. 5. Dorsal aspect of ethmovomerine region, representing oreochromine type. A, *Oreochromis (Oreochromis) niloticus*; B, *Lamprologus lemairii*; C, *Gnathochromis permaxillaris*; D, *Paracyprichromis brienii*. Bar=1 mm.

arm; dorsolateral fenestra absent.

Oreochromine type (Fig. 5, Appendix)

Mesethmoid arm absent and mesethmoid-vomer connection lost; lateral ethmoid usually reaching vomer anteriorly (not in *Cyprichromis microlepidotus*, *Paracyprichromis brienii* and *Oreochromis (Nyasalapia) karmo*, Fig. 5D); dorsolateral fenestra usually absent. In *Paracyprichromis brienii*, the narrow dorsolateral fenestra fused with the rostral and ovoid fenestrae.

Asprotilapiine type (Fig. 6, Appendix)

Mesethmoid arm short, not reaching vomer; lateral ethmoid reaching vomer anteriorly (not in *Microdontochromis tenuidentatus*, Fig. 6B); narrow dorsolateral

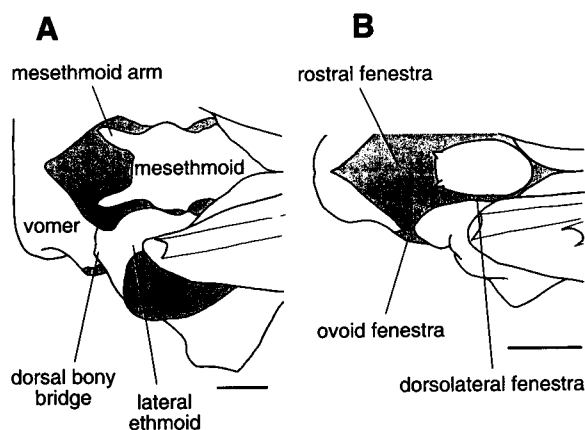


Fig. 6. Dorsal aspect of ethmovomerine region, representing asprotilapiine type. A, *Asprotilapia leptura*; B, *Microdontochromis tenuidentatus*. Bar=1 mm.

fenestra always fused with rostral fenestra (also with ovoid fenestra in *M. tenuidentatus*).

Key to the ethmovomerine types

- 1a. Mesethmoid arm absent..... oreochromine type
- 1b. Mesethmoid arm present 2
- 2a. Mesethmoid arm not reaching vomer
..... asprotilapiine type
- 2b. Mesethmoid arm reaching vomer..... 3
- 3a. Dorsal bony bridge similar width or broader than mesethmoid arm..... 4
- 3b. Dorsal bony bridge narrower than mesethmoid arm or absent..... 5
- 4a. Dorsolateral fenestra absent or narrow
..... haplochromine type
- 4b. Dorsolateral fenestra large..... tylochromine type
- 5a. Dorsolateral fenestra absent
..... lepidiolamprologine type
- 5b. Dorsolateral fenestra present, usually large
..... bathybatine type

Discussion

A comparison of Poll's (1986) tribes and the present ethmovomerine types showed that seven tribes were each represented by a monotypic ethmovomerine condition (Appendix), viz. Tylochromini (tylochromine type), Bathybatini and Trematocarini (bathybatine type), Haplochromini and Tropheini (haplochromine type), and Cyprichromini and Eretmodini (oreochromine type). The other five tribes, Tilapiini, Lamprologini, Ectodini, Limnochromini and Perissodini, each included two or three different types.

Tribe Tilapiini included three ethmovomerine types,

i.e. oreochromine (*Tilapia rendalli* and *Oreochromis* species), haplochromine (*Tilapia zillii*) and tylochromine (*Boulengerochromis microlepis*). Among the Tilapiini, *B. microlepis* is morphologically unique, having many, extremely small scales on the body, a forked caudal fin, and unicuspid outer teeth on jaws (Poll, 1986). According to two molecular phylogenies of Nishida (1997), this species alone formed a monophyletic branch separated from all other Tilapiini species. Therefore, it is considered that the differences in ethmovomerine type and some external morphological features of *B. microlepis* from other Tilapiini species reflect the difference in phylogenetic relationships.

Trewavas (1973, 1983) examined the ethmovomerine region of Tilapiini species belonging to *Tilapia*, *Oreochromis* and *Sarotherodon*, genera which closely resemble one another in external morphology. Although most species of *Tilapia* were found to have a mesethmoid arm (haplochromine type in the present study), *T. rendalli* and *T. tholloni* lacked that element (oreochromine type), as did *Oreochromis* and *Sarotherodon* species. These findings were confirmed by the present study, raising the possibility *T. rendalli* and *T. tholloni* may be better placed in *Oreochromis* or *Sarotherodon*. However, all *Tilapia* species are substrate brooders, whereas *Oreochromis* and *Sarotherodon* species are mouth brooders (Trewavas, 1983), and the monophyly of *Tilapia* (phylogenetically separated from an *Oreochromis* + *Sarotherodon* clade) has been supported by a molecular analysis (Franck et al., 1994). Thus, *T. rendalli* and *T. tholloni* are better left in the genus *Tilapia*, despite their ethmovomerine regions appearing more like those of *Oreochromis* and *Sarotherodon* species rather than other *Tilapia* species.

Although most species of the tribe Lamprologini have the oreochromine type ethmovomerine region, *Lepidiolamprologus attenuatus*, *L. elongatus*, *L. profundicola* and *Neolamprologus pleuromaculatus* have that of the lepidiolamprologine type, which could not be found in other Tanganyikan species examined. Sturmbauer et al.'s. (1994) molecular tree of Lamprologini species included only one species representing the latter type ethmovomerine region (*Lepidiolamprologus elongatus*). According to this molecular tree, *L. elongatus* was not basal to all Lamprologini species, indicating that the lepidiolamprologine type is probably a derived condition among the tribe, likely forming a monophyletic group. Stiassny (1997), in fact, proposed a monophyletic group including ten Lamprologini species, but gave no reasons. The present monophyletic group is in accordance with Stiassny's group, with the exception of *Lamprologus lemairii*, which is excluded from the former and may in fact be a sister group of it.

In the tribe Ectodini, the mesethmoid was generally large, reaching the vomer (haplochromine type), but was reduced (or absent) and not reaching the vomer in *Asprotilapia leptura*, *Enantiopus melanogenys*, *Microdontochromis tenuidentatus* (asprotilapiine type) and *Xenotilapia flavipinnis* (oreochromine type). The latter taxa also share a short outer soft ray on the pelvic fin (Poll, 1956, 1985), although this condition was also found in *Xenotilapia boulengeri* and *Grammatotria lemairii*. According to the molecular phylogenies of Sturmbauer and Meyer (1993) and Nishida (1997), these taxa formed a clade which was not basal to the Ectodini. Therefore, *Asprotilapia leptura*, *Enantiopus melanogenys*, *Microdontochromis tenuidentatus* and *Xenotilapia flavipinnis* probably represent a monophyletic group, which is supported by the reduced mesethmoid arm.

The asprotilapiine type ethmovomerine region (reduced mesethmoid arm) is also found in *Xenochromis hecqui*, a member of the tribe Perissodini and phylogenetically separated from Ectodini (Liem & Stewart, 1976; Nishida, 1997). Therefore, the asprotilapiine type ethmovomerine region is likely to represent a parallel development in a monophyletic group including four Ectodini taxa and *Xenochromis hecqui*.

The tribe Limnochromini includes the tylochromine (*Baileychromis centropomoides*, *Benthochromis tricoti*, *Greenwoodochromis christyi*, *Limnochromis auritus* and *Reganochromis calliurus*), haplochromine (*Gnathochromis pfefferi*), and oreochromine types (*Gnathochromis permaxillaris*, *Tangachromis dhanisi* and *Triglachromis otostigma*). According to the molecular phylogeny of Nishida (1997), this tribe comprises three monophyletic groups, the first including *Limnochromis auritus* and *Triglachromis otostigma*, the second including only *Benthochromis tricoti*, and the third group including only *Gnathochromis permaxillaris*. These three monophyletic groups are in complete disagreement with the present division of ethmovomerine types. Because of the present lack of data, this situation could not be resolved here, although some resolution is anticipated in a forthcoming study.

Materials examined

Bathybatini: *Bathybates fasciatus*, HUMZ 138010, 144.9 mm SL; *B. minor*; HUMZ 125382, 140.8 mm SL; *Hemibates stenosoma*, HUMZ 125365, 150.6 mm SL.

Cyprichromini: *Cyprichromis leptosoma*, HUMZ 157341, 80.0 mm SL; *C. microlepidotus*, HUMZ 137742, 91.4 mm SL; *Paracyprichromis brieni*, HUMZ 122560,

157399, 70.6–89.8 mm SL.

Ectodini : *Asprotilapia leptura*, LBM 25447, 25448, 80.1–84.0 mm SL ; *Aulonocranus dewindti*, HUMZ 127954, 76.0 mm SL ; *Callochromis macrops*, HUMZ 125813, 96.1 mm SL ; *Cardiopharynx schoutedeni*, HUMZ 125936, 85.6 mm SL ; *Cunningtonia longiventralis*, HUMZ 125773, 104.2 mm SL ; *Cyathopharynx furcifer*, HUMZ 118284, 127.6 mm SL ; *Ectodus descampsi*, HUMZ 116672, 70.4 mm SL ; *Enantiopus melanogenys*, HUMZ 125911, 112.9 mm SL ; *Grammatotria lemairii*, HUMZ 127521, 104.4 mm SL ; *Les-tradea perspicax*, HUMZ 116218, 86.0 mm SL ; *Microdontochromis tenuidentatus*, HUMZ 141873, 45.0 mm SL ; *Ophthalmotilapia nasuta*, HUMZ 138281, 120.3 mm SL ; *Xenotilapia boulengeri*, HUMZ 125887, 103.4 mm SL ; *X. flavipinnis*, LBM 25643, 66.9 mm SL.

Eretmodini : *Eretmodus cyanostictus*, HUMZ 125254, 67.0 mm SL ; *Spathodus marlieri*, HUMZ 128426, 57.8 mm SL ; *Tanganicodus irsacae*, HUMZ 137961, 47.0 mm SL.

Haplochromini : *Astatoreochromis straeleni*, MRAC 91-89-P-85, 99.1 mm SL ; *Astatotilapia burtoni*, HUMZ 125852, 61.4 mm SL ; *Ctenochromis benthicola*, HUMZ 127370, 80.3 mm SL ; *C. horei*, HUMZ 125557, 113.6 mm SL ; *Haplochromis obliquidens*, MRAC P.14864, 71.1 mm SL.

Lamprologini : *Altalamprologus calvus*, HUMZ 125416, 81.2 mm SL ; *A. compressiceps*, HUMZ 118292, 109.4 mm SL ; *Chalinochromis brichardi*, HUMZ 125327, 74.5 mm SL ; *Julidochromis marlieri*, HUMZ 116927, 87.8 mm SL ; *J. ornatus*, HUMZ 116930, 59.6 mm SL ; *Lamprologus callipterus*, HUMZ 132939, 107.7 mm SL ; *L. lemairii*, HUMZ 128372, 165.8 mm SL ; *L. ocellatus*, HUMZ 125032, 41.9 mm SL ; *L. ornatipinnis*, HUMZ 125022, 49.3 mm SL ; *Lepidiolamprologus attenuatus*, HUMZ 138293, 99.1 mm SL ; *L. cunningtoni*, HUMZ 125625, 99.0 mm SL ; *L. elongatus*, HUMZ 125634, 115.8 mm SL ; *L. profundicola*, HUMZ 118151, 95.9 mm SL ; *Neolamprologus brichardi*, HUMZ 125685, 60.5 mm SL ; *N. fasciatus*, HUMZ 127809, 100.5 mm SL ; *N. pleuromaculatus*, HUMZ 116784, 77.0 mm SL ; *N. tetracanthus*, HUMZ 125828, 85.0 mm SL ; *N. toae*, HUMZ 136250, 78.2 mm SL ; *Telmatochromis temporalis*, HUMZ 125133, 74.9 mm SL ; *Variabilichromis moorii*, HUMZ 125713, 70.6 mm SL.

Limnochromini : *Baileychromis centropomoides*, Dr. K. Nakai, private collection, 122.9 mm SL ; *Benthochromis tricoti*, HUMZ 128982, 111.2 mm SL ; *Gnathochromis permaxillaris*, HUMZ 123245, 123.8 mm SL ; *G. pfefferi*, HUMZ 118261, 99.5 mm SL ; *Greenwoodochromis christyi*, HUMZ 128465, 77.9 mm SL ; *Limnochromis auritus*, MRAC 95-098-P-209, 148.0 mm SL ;

Reganochromis calliurus, MRAC 115081, 80.8 mm SL ; *Tangachromis dhanisi*, MRAC 107302, 51.5 mm SL ; *Triglachromis otostigma*, MRAC 95-098-P-0268, 56.7 mm SL.

Perissodini : *Haplotaxodon microlepis*, HUMZ 128381, 192.4 mm SL ; *Perissodus microlepis*, HUMZ 125121, 91.0 mm SL ; *Plecodus paradoxus*, HUMZ 127963, 98.5 mm SL ; *Xenochromis hecqui*, HUMZ 116697, 110.7 mm SL.

Tilapiini : *Boulengerochromis microlepis*, HUMZ 123097, 159.5 mm SL ; *Oreochromis (Neotilapia) tangaicae*, HUMZ 116794, 122.2 mm SL ; *O. (Nyasalapia) karomo*, MRAC 93-152-P-103, 89.1 mm SL ; *O. (Oreochromis) niloticus*, HUMZ 116860, 131.1 mm SL ; *Tilapia rendalli*, MRAC P. 105567, 117.8 mm SL.

Trematocarini : *Telotreumatocara macrostoma*, UMMZ 196106, 88.0 mm SL ; *Trematocara caparti*, MRAC 111528, 48.4 mm SL ; *T. marginatum*, HUMZ 128729, 45.5 mm SL ; *T. nigrifrons*, HUMZ 125663, 66.0 mm SL ; *T. stigmaticum*, HUMZ 128683, 45.5 mm SL ; *T. unimaculatum*, HUMZ 125760, 90.9 mm SL ; *T. zebra*, MRAC 96-083-P-760, 59.5 mm SL.

Tropheini : *Cyphotilapia frontosa*, HUMZ 122999, 117.3 mm SL ; *Interochromis loocki*, HUMZ 163238, 107.8 mm SL ; *Limnotilapia dardennii*, HUMZ 122867, 136.8 mm SL ; *Lobochilotes labiatus*, HUMZ 127730, 109.5 mm SL ; *Petrochromis fasciolatus*, HUMZ 118088, 116.1 mm SL ; *Pseudosimochromis curvifrons*, HUMZ 123048, 90.6 mm SL ; *Simochromis babaulti*, HUMZ 117556, 71.3 mm SL ; *S. diagramma*, HUMZ 127930, 130.0 mm SL ; *Tropheus duboisi*, HUMZ 116846, 91.0 mm SL ; *T. moorii*, HUMZ 122563, 98.7 mm SL.

Tylochromini : *Tylochromis jentinki*, MRAC 74-014-P-7102, 101.2 mm SL ; *T. labrodon*, MRAC 90-002-P-24, 118.7 mm SL ; *T. lateralis*, MRAC 1063, 202.1 mm SL ; *T. polylepis*, HUMZ 125794, 95.3 mm SL ; *T. variabilis*, MRAC 34763, 163.2 mm SL.

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References

- Bailey, R.M. and Stewart, D.J. (1977). Cichlid fishes from Lake Tanganyika: additions to the Zambian fauna including two new species. *Occas. Pap. Mus. Zool. Univ. Michigan*, **679**, 1-30.
- Boulenger, G.A. (1898). Report on the collection of fishes made by Mr. J.E.S. Moore in Lake Tanganyika during his expedition, 1895-1896. *Trans. Zool. Soc. Lond.*, **15**, 1-30, 8 pls.
- Boulenger, G.A. (1901). Third contribution to the ichthyology of Lake Tanganyika. Report on the collection of fishes made by Mr. J.E.S. Moore in Lakes Tanganyika and Kivu during his second expedition, 1899-1900. *Trans. Zool. Soc. Lond.*, **16**, 137-178, pls. 12-20.
- De Vos, L., Nshombo, M. and Thys van den Audenaerde, D. (1996). *Trematocara zebra* (Perciformes; Cichlidae), nouvelle espèce du nord-ouest du lac Tanganyika (Zaire). *Belg. J. Zool.*, **126**, 3-20.
- Franck, J.P.C., Kornfield, I. and Wright, J.M. (1994). The utility of SATA satellite DNA sequences for inferring phylogenetic relationships among the three major genera of tilapiine cichlid fishes. *Mol. Phylogenet. Evol.*, **3**, 10-16.
- Greenwood, P.H. (1956). A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part I: *H. obliquidens* Hilgend., *H. nigricans* (Blgr.), *H. nuchisquamulatus* (Hilgend.) and *H. lividus*, sp.n. *Bull. Br. Mus. (Nat. Hist.) Zool.*, **4**, 225-244.
- Greenwood, P.H. (1978). A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. *Bull. Br. Mus. (Nat. Hist.) Zool.*, **33**, 297-323.
- Hatooka, K. (2000). Cichlidae. p. 916, Nakabo, T. (ed.), *Fishes of Japan with pictorial keys to the species. Second edition*. Tokai University Press, Tokyo.
- Kocher, T.D., Conroy, J.A., McKaye, K.R., Stauffer, J.R. and Lockwood, S.F. (1995). Evolution of NADH dehydrogenase subunit 2 in East African cichlid fish. *Mol. Phylogenet. Evol.*, **4**, 420-432.
- Liem, K.F. and Stewart, D.J. (1976). Evolution of the scale-eating cichlid fishes of Lake Tanganyika: a generic revision with a description of a new species. *Bull. Mus. Comparative Zool.*, **147**, 319-350.
- Marlier, G. (1959). Observations sur la biologie littorale du lac Tanganika. *Rev. Zool. Bot. Afr.*, **59**, 164-183, 2 pls.
- Nishida, M. (1991). Lake Tanganyika as an evolutionary reservoir of old lineages of East African cichlid fishes: Inferences from allozyme data. *Experientia*, **47**, 974-979.
- Nishida, M. (1997). Phylogenetic relationships and evolution of Tanganyikan cichlids: A molecular perspective. pp. 3-23, Kawanabe, H., Hori, M. and Nagoshi, M. (eds.), *Fish communities in Lake Tanganyika*. Kyoto University Press, Kyoto.
- Poll, M. (1956). Poissons Cichlidae. Résultats scientifiques. Exploration hydrobiologique du Lac Tanganyika (1946-1947). *Inst. R. Sci. Nat. Belg.*, **3**, 1-619.
- Poll, M. (1974). Contribution à la faune ichthyologique du lac Tanganika, d'après les récoltes de P. Brichard. *Rev. Zool. Afr.*, **88**, 99-110.
- Poll, M. (1978). Contribution à la connaissance du genre *Lamprologus* Schth. Description de quatre espèces nouvelles, réhabilitation de *Lamprologus mondabu* et synopsis remanié des espèces du lac Tanganika. *Bull. Cl. Sci. (Acad. R. Belg.) Ser. 5*, **64**, 725-758.
- Poll, M. (1979). Un *Haplochromis* rouge du lac Tanganika, femelle de *H. benthicola* Matthes 1962. *Rev. Zool. Afr.*, **93**, 467-475.
- Poll, M. (1981). Contribution à la faune ichthyologique du lac Tanganika. Révision du genre *Limnochromis* Regan, 1920. Description de trois genres nouveaux et d'une espèce nouvelle: *Cyprichromis brieni*. *Ann. Soc. R. Zool. Belg.*, **111**, 163-179.
- Poll, M. (1985). Description de *Xenotilapia flavipinnis* sp. n. du lac Tanganika (Pisces, Cichlidae). *Rev. Zool. Afr.*, **99**, 105-109.
- Poll, M. (1986). Classification des Cichlidae du lac Tanganika. Tribus, genres et espèces. *Mém. Cl. Sci.*, **45**: 1-163.
- Poll, M. and Matthes, H. (1962). Trois poissons remarquables du lac Tanganika. *Ann. Mus. R. Afr. Cent. Sci. Zool.*, **111**, 1-26.
- Regan, C.T. (1920). The classification of the fishes of the Family Cichlidae. I. The Tanganyika genera. *Ann. Mag. Nat. Hist. Zool. Bot. Geol. Ser. 9*, **5**, 33-53.
- Stiassny, M.L.J. (1981). Phylogenetic versus convergent relationship between piscivorous cichlid fishes from Lakes Malawi and Tanganyika. *Bull. Br. Mus. (Nat. Hist.)*, **40**, 67-101.
- Stiassny, M.L.J. (1989). A taxonomic revision of the African genus *Tylochromis* (Labroidei, Cichlidae); with notes on the anatomy and relationships of the group. *Ann. Mus. R. Afr. Cent.*, **258**, 1-161.
- Stiassny, M.L.J. (1997). A phylogenetic overview of the lamprologine cichlids of Africa (Teleostei: Cichlidae): A morphological perspective. *S. Afr. J. Sci.*, **93**, 513-523.
- Sturmbauer, C. and Meyer, A. (1993). Mitochondrial phylogeny of the endemic mouthbrooding lineages of cichlid fishes from Lake Tanganyika in Eastern Africa. *Mol. Biol. Evol.*, **10**, 751-768.
- Sturmbauer, C., Verheyen, E. and Meyer, A. (1994). Mitochondrial phylogeny of the Lamprologini, the major substrate spawning lineage of cichlid fishes from Lake Tanganyika in Eastern Africa. *Mol. Biol. Evol.*, **11**, 691-703.
- Takahashi, K., Terai, Y., Nishida, M. and Okada, N. (1998). A novel family of Short Interspersed Repetitive Elements (SINEs) from cichlids: The patterns of insertion of SINEs at orthologous loci support the proposed monophyly of four major groups of cichlid fishes in Lake Tanganyika. *Mol. Biol. Evol.*, **15**, 391-407.
- Trewavas, E. (1953). A new species of the cichlid genus *Limnochromis* of Lake Tanganyika. *Bull. Inst. R. Sci. Nat. Belg.*, **29**, 1-3.

Trewavas, E. (1973). On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. *Bull. Br. Mus. (Nat. Hist.) Zool.*, **25**, 3-

26.

Trewavas, E. (1983). *Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia*. Br. Mus. (Nat. Hist.), London.

Appendix. Type of ethmovomerine region.		Appendix. (Continued)	
	Tribe		Tribe
Tylochromine type		<i>Petrochromis fasciolatus</i>	Tropheini
<i>Baileychromis centropomoides</i>	Limnochromini	<i>Pseudosimochromis curvifrons</i>	Tropheini
<i>Benthochromis tricoti</i>	Limnochromini	<i>Simochromis babaulti</i>	Tropheini
<i>Greenwoodochromis christyi</i>	Limnochromini	<i>Simochromis diagramma</i>	Tropheini
<i>Limnochromis auritus</i>	Limnochromini	<i>Tropheus duboisi</i>	Tropheini
<i>Reganochromis calliurus</i>	Limnochromini	<i>Tropheus moorii</i>	Tropheini
<i>Boulengerochromis microlepis</i>	Tilapiini	Lepidiolamprologine type	
<i>Tylochromis jentinki</i>	Tylochromini	<i>Lepidiolamprologus attenuatus</i>	Lamprologini
<i>Tylochromis labrodon</i>	Tylochromini	<i>Lepidiolamprologus elongatus</i>	Lamprologini
<i>Tylochromis lateralis</i>	Tylochromini	<i>Lepidiolamprologus profundicola</i>	Lamprologini
<i>Tylochromis polylepis</i>	Tylochromini	<i>Neolamprologus pleuromaculatus</i>	Lamprologini
<i>Tylochromis variabilis</i>	Tylochromini	Oreochromine type	
Bathybatine type		<i>Cyprichromis leptosoma</i>	Cyprichromini
<i>Bathybates fasciatus</i>	Bathybatini	<i>Cyprichromis microlepidotus</i>	Cyprichromini
<i>Bathybates graueri</i>	Bathybatini	<i>Paracyprichromis brieni</i>	Cyprichromini
<i>Bathybates minor</i>	Bathybatini	<i>Xenotilapia flavipinnis</i>	Ectodini
<i>Hemibates stenosoma</i>	Bathybatini	<i>Eretmodus cyanostictus</i>	Eretmodini
<i>Telotrematocara macrostoma</i>	Trematocarini	<i>Spathodus marlieri</i>	Eretmodini
<i>Trematocara caparti</i>	Trematocarini	<i>Tanganicodus irsacae</i>	Eretmodini
<i>Trematocara marginatum</i>	Trematocarini	<i>Atolamprologus calvus</i>	Lamprologini
<i>Trematocara nigrifrons</i>	Trematocarini	<i>Atolamprologus compressiceps</i>	Lamprologini
<i>Trematocara stigmaticum</i>	Trematocarini	<i>Chalinochromis brichardi</i>	Lamprologini
<i>Trematocara unimaculatum</i>	Trematocarini	<i>Julidochromis marlieri</i>	Lamprologini
<i>Trematocara zebra</i>	Trematocarini	<i>Julidochromis ornatus</i>	Lamprologini
Haplochromine type		<i>Lamprologus callipterus</i>	Lamprologini
<i>Aulonocranus dewindti</i>	Ectodini	<i>Lamprologus lemairii</i>	Lamprologini
<i>Callochromis macrops</i>	Ectodini	<i>Lamprologus ocellatus</i>	Lamprologini
<i>Cardiopharynx schoutedeni</i>	Ectodini	<i>Lamprologus ornatipinnis</i>	Lamprologini
<i>Cunningtonia longiventralis</i>	Ectodini	<i>Lepidiolamprologus cunningtoni</i>	Lamprologini
<i>Cyathopharynx furcifer</i>	Ectodini	<i>Neolamprologus brichardi</i>	Lamprologini
<i>Ectodus descampsi</i>	Ectodini	<i>Neolamprologus fasciatus</i>	Lamprologini
<i>Grammatotria lemairii</i>	Ectodini	<i>Neolamprologus tetracanthus</i>	Lamprologini
<i>Lestradea perspicax</i>	Ectodini	<i>Neolamprologus toae</i>	Lamprologini
<i>Ophthalmotilapia nasuta</i>	Ectodini	<i>Telmatochromis temporalis</i>	Lamprologini
<i>Xenotilapia boulengeri</i>	Ectodini	<i>Variabilichromis moorii</i>	Lamprologini
<i>Astatoreochromis straeleni</i>	Haplochromini	<i>Gnathochromis permaxillaris</i>	Limnochromini
<i>Astatotilapia burtoni</i>	Haplochromini	<i>Tangachromis dhanisi</i>	Limnochromini
<i>Ctenochromis benthicola</i>	Haplochromini	<i>Triglachromis otostigma</i>	Limnochromini
<i>Ctenochromis horei</i>	Haplochromini	<i>Oreochromis (Neotilapia) tanganicae</i>	Tilapiini
<i>Haplochromis obliquidens</i>	Haplochromini	<i>Oreochromis (Nyasalapia) karomo</i>	Tilapiini
<i>Gnathochromis pfefferi</i>	Limnochromini	<i>Oreochromis (Oreochromis) niloticus</i>	Tilapiini
<i>Haplotaxodon microlepis</i>	Perissodini	<i>Tilapia rendalli</i>	Tilapiini
<i>Perissodus microlepis</i>	Perissodini	Asprotilapiine type	
<i>Plecodus paradoxus</i>	Perissodini	<i>Asprotilapia leptura</i>	Ectodini
<i>Tilapia zillii</i>	Tilapiini	<i>Enantiopus melanogenys</i>	Ectodini
<i>Cyphotilapia frontosa</i>	Tropheini	<i>Microdontochromis tenuidentatus</i>	Ectodini
<i>Interochromis loocki</i>	Tropheini	<i>Xenotilapia flavipinnis</i>	Ectodini
<i>Limnotilapia dardennii</i>	Tropheini	<i>Xenochromis hecqui</i>	Perissodini