INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

THE EOCENE CICHLIDS (PERCIFORMES: LABROIDEI) OF MAHENGE, TANZANIA

Alison M. Murray

Biology Department
McGill University, Montreal

December, 2000

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements of the degree of Doctor of Philosophy

© Alison M. Murray, 2000

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-70109-3

Canada

TABLE OF CONTENTS

List of Figures

General Introduction

Chapter 1.

Chapter 2.

Chapter 3

Abstract

A new genus and five new species of fossil cichlid fishes (Perciformes: Labroidei) are described from Mahenge, Tanzania. These cichlids represent the oldest confirmed fossils of the family, dating from the middle of the Eocene. The specimens share many lepidological characters, and, from comparison with other members of the family, are identified as being a monophyletic group. Therefore, they are described as belonging to a single genus, *Mahengechromis* gen.nov., named for the type locality. Detailed anatomical study of the well-preserved specimens allows five species to be identified, *M. plethos, M. rotundus, M. brachycranium, M. ellipticus,* and *M. curvifrons* spp. nov. These species are distinguished on the basis of osteological characters, including the shape of the frontal bones, hyomandibulae and opercular bones. The species are believed to be endemic to the type locality, which, along with monophyly of the species, indicates that these fishes formed a species flock. This suggests that the capacity for cichlids to form species flocks arose early in the family's history.

Previously published phylogenetic analyses of the family Cichlidae have included few characters that can be used to incorporate fossil material. Osteological features that may be useful for determining relationships are identified and used in a phylogenetic analysis of the family. The results of this analysis are compared with the results of previous analyses to determine the usefulness of the characters. This comparison indicates that most osteological characters are homoplastic among cichlids, although some of the characters may prove to be phylogenetically useful. Although phylogenetic analysis of osteologic characters does not result in a well-resolved phylogeny, the most parsimonious placement of the fossil cichlids from Mahenge is in a relatively basal position among the African lineages, as the sister group to the hemichromine cichlids from West Africa.

The biogeographic relationships of members of the Cichlidae are examined based on information from the fossil record and the interrelationships of the lineages within the family. Two suggestions have been made for the age of the family; either the cichlids originated in the Early Cretaceous or they evolved near the end of the Mesozoic. The later time of origin would have required a trans-Atlantic dispersal. Based on the distribution of Recent and fossil cichlids, the latter hypothesis is accepted. A reconstruction of the dispersal patterns and possible means of dispersal are evaluated.

Résumé

Un nouveau genre et cinq nouvelles espèces de cichlides fossile (Perciformes: Labroidei) sont décrits de Mahenge, Tanzanie. Ces cichlides représentent les fossiles les plus anciens de la famille, datant du milieu de l'Eocène. Les spécimens partagent beaucoup de caractères lépidologiques, et, par comparaison avec d'autres membres de la famille, sont identifiés comme étant un groupe monophylétique. Par conséquent, ils sont décrits comme appartenant à un seul genre, *Mahengechromis* gen. nov., nommé pour la localité-type. L'étude anatomique détaillée des spécimens bien-préservés permet d'identifier cinq espèces, *M .plethos, M. rotundus, M. brachycranium, M. ellipticus*, et *M. curvifrons* nov. spp. Ces espèces se distinguent à partir des caractères ostéologiques, incluant la forme des os frontaux, des os hyomandibulaires et des os operculaires. On pense que les espèces sont endémiques à la localité-type, qui, avec leur monophylie, indique que ces poissons ont formé un regroupement d'espèce. Ceci suggère que la capacité des cichlides à former des regroupements d'espèce ait surgi tôt dans les antécédents familiaux.

Les analyses phylogénétiques déjà publié de la famille des Cichlidés ont inclus peu de caractères qui peuvent être utilisés pour le matériel fossile incorporé. Des caractères ostéologiques pouvant être utiles à la détermination des relations sont identifiés et utilisés dans une analyse phylogénétique de la famille. Les résultats de cette analyse sont comparés aux résultats des analyses précédentes pour déterminer l'utilité des caractères. Cette comparaison indique que la plupart des caractères ostéologiques sont homoplastiques parmi les cichlides, bien que certains des caractères puissent s'avérer utiles pour les analyses phylogénétiques. Bien que l'analyse phylogénétique des

caractères ostéologiques résulte pas en une phylogénie bien-résolue, les cichlides fossiles de Mahenge se retrouvent dans une position relativement primitive parmi les lignées africaines, en tant que groupe-soeur des cichlides hemichromines d'Afrique occidentale.

Les rapports biogéographiques des membres des Cichlidés sont basés sur l'information de l'enregistrement de fossile et des corrélations entre les lignées chez la famille. Deux suggestions ont été faites pour l'âge de la famille; les cichlides sont issus du crétacé récent ou ils ont évolué vers la fin du mésozoïque. La période ultérieure d'origine aurait exigé une dispersion transatlantique. Basé sur la distribution des cichlides récents et fossiles, la dernière hypothèse est retenue. Une reconstruction les configurations de dispersion et des moyens possibles de dispersion sont évalués.

Original Contributions to Knowledge

1. This thesis includes the description of a new genus and five new species of fossil fishes collected by the author from the Eocene of Africa. These are the oldest confirmed members of the family Cichlidae. Based on comparison with modern cichlids, the five species are determined to be a monophyletic group. This, along with the apparent endemism of the fishes to the type locality, enable the five species to be recognized as the earliest species flock of cichlids, indicating that the capacity to form flocks arose early in the history of the family.
2. Osteological characters for both fossil and extant cichlids were found and examined for their usefulness in phylogenetic analyses. Most osteological characters are found to be homoplastic. Phylogenetic analysis based on osteological features alone leads to poorly resolved cladograms. However, several osteological characters are interpreted as having phylogenetic potential, including a hitherto undocumented character of the pectoral girdle, suturing of the coracoid and cleithrum.
3. Based on the phylogenetic analysis of osteological characters, and their integration with previously published analyses, the species from Mahenge are found to be the sister group to the West African hemichromine cichlids, a relatively basal lineage within the African Cichlidae.
4. The suggested East African origin and Gondwanan distribution of the Cichlidae were examined. Based on the fossil record, relationships of cichlids, and the biology of several lineages, an East African origin in the Early Cretaceous and a resulting Gondwanan distribution are rejected. Evidence is presented for a Madagascan origin

of cichlids in the Late Cretaceous at the earliest, followed by marine dispersal of one or more lineages.

Acknowledgements

As with any thesis, this project would not have been possible without a great deal of help from many people. I would like to thank Dr. Robert L. Carroll for supervising this work, and Drs. David Green and Graham Bell for being members of the supervisory committee.

Dr. Terry Harrison (New York University) gave me the opportunity to travel to Tanzania to work on the National Geographic Society sponsored field team. The Wembera Manonga Palaeontological Expedition Team provided good companionship in the field, and assisted in collecting the material for this project. The nine weeks spent with the field crew was a great learning experience (and very enjoyable). I am also grateful to the National Museum of Tanzania for lending me the fossil material.

I thank Susan Jewett, United States National Museum (USNM), and Darlene Balkwell, Canadian Museum of Nature (CMN), for lending the Recent comparative material and giving permission for them to be cleared and stained.

Rick Day (CMN) kindly instructed me in the ways of the microscope/camera equipment and spent considerable time helping me photograph scales of cichlids; Lisa Budney (CMN) scanned many radiographs of comparative material. I am grateful to them both, and apologize for not using the photographs or radiographs in the thesis. The descriptions of the species were greatly enhanced by three external reviewers of the publication that is reproduced here as Chapter 1, Drs. Gloria Arratia, Peter L. Forey and Mark V.H. Wilson.

Many of the staff of the Research and Collection divisions at the Canadian Museum of Nature provided intangible support and encouragement during the course of this work, for which I am grateful. Dr. Claude B. Renaud and Sylvie Laframboise

(CMN) kindly checked, then rewrote, the French translation of the abstract. The CMN also provided space and access to equipment which facilitated this work.

I am particularly grateful to Dr. Robert B. Holmes for providing helpful instructions in making latex peels and stipple drawings, and for continuing to help even after my patience had been exhausted. I also thank F. Murray, W. Overhoff and T. Murray who provided accomodations and financial assistance during the course of this work.

GENERAL INTRODUCTION

The family Cichlidae is a large group of predominantly tropical freshwater fishes in the order Perciformes. The number of Recent species in the family is estimated at about 1300 (Nelson, 1994), 1400 (Kullander and Nijssen, 1989) or more. These colourful fishes are well known in the aquarium trade, because they can be induced to breed quite readily and are of a suitable size for most aquaria. Cichlids, particularly the larger tilapiines, are also important in food fisheries and aquaculture, with populations now being farmed in many areas including Japan and Jamaica. Cichlids are also used in diverse scientific studies. Cichlids are important subjects in behavioural studies, for species vary from substrate breeders, with monogamous biparental care of eggs and young, to polygamous systems with maternal mouthbrooding (Barlow, 1991). Functional morphologists are also interested in cichlids, because some clades have undergone a functional diversification of the feeding apparatus that exceeds that of any other vertebrate family (Liem, 1991). Other aspects of the biology of these fishes, including physiological tolerances, are also being actively studied (e.g. Miyazaki et al., 1998).

Perhaps the greatest area of interest in cichlids is their evolutionary biology. The ability of these fishes to speciate readily, and the mechanisms underlying speciation events have been the subject of many studies and debates in the literature. While other species flocks are known (papers in Echelle and Kornfield, 1984), East African cichlid fishes are the classic examples of species flocks, with large numbers of closely related species endemic to restricted areas. The majority of cichlid species are found in the East African Great Lakes, with lakes Victoria, Malawi and Tanganyika, all having large numbers of endemic cichlids that have radiated rapidly (Casciotta and Arratia, 1993a; Dominey, 1984).

Although cichlids are some of the best-studied examples of species flocks, their interrelationships are still not well known. It is only recently that studies have shown the species flocks in lakes Victoria and Malawi to be monophyletic, based on molecular evidence (Meyer, 1993, Verheyen et al., 1996), although even with molecular techniques relationships of many lineages remain unclear (Kornfield and Parker, 1997).

The biogeography of cichlids is another area which is not well known. Stiassny (1987, 1991) considered the distribution of cichlids to be Gondwanan in origin. However, the modern distribution of the family Cichlidae is in Central and South America (with one species reaching into Texas), the West Indies, Africa, Madagascar, Israel, Syria, Sri Lanka, coastal India and Iran (Fig. 1), is not strictly Gondwanan. Many cichlids are not limited by salinity (e.g. Miyazaki et al., 1998), a factor of their biology that is often not considered when interpreting current distributions of members of the family.

Because the current distribution of cichlids has been attributed to a Gondwanan origin, and the early history of the family is poorly known, an Early Cretaceous origin has been suggested (Stiassny, 1987, 1991) and passed on in the literature. The most informative evidence of the history of a lineage is the fossil record, but there are no known cichlid fossils of Cretaceous age.

Fossil cichlids have the potential to provide much needed information on the history of this group. Fossils provide the only concrete evidence of the morphology or habitat of early members of a lineage, and can provide positive evidence of early distributions of species, as well as a sense of the timing of speciation events, by indicating the minimum ages at which different lineages arose.

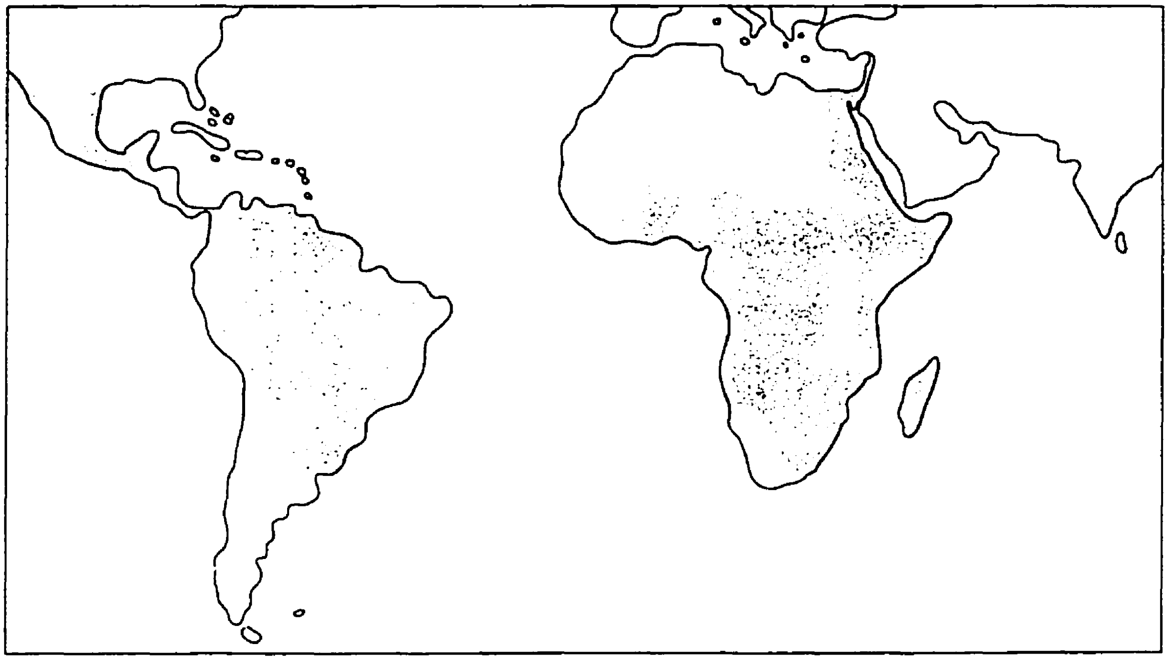

Figure 1. Distribution of the modern species of the Cichlidae. Light shaded area indicates discontinuous distribution in isolated water bodies throughout the area.

A new collection of fossils from East Africa includes many specimens of cichlid fishes. The age, abundance and quality of preservation permit them to contribute significant information to our knowledge of the anatomy, phylogenetic history, and palaeobiogeography of the family. They form the basis of this research project.

Background to the project

The fossil locality at Mahenge, Tanzania was discovered in the 1950's by George Mannard, a Ph.D. student at McGill University and employee of the Williamson Diamond Mines, Tanzania. Mannard sampled many kimberlite pipe formations for diamonds in the Singida Plateau, northern Tanzania. Although diamonds were not found, Mannard discovered fossil fish at Mahenge, which he sent to P.H. Greenwood at the Natural History Museum, London (formerly the British Museum (Natural History)).

In 1996, I joined the Wembere-Manonga Palaeontological Expedition (WMPE), led by Dr. Terry Harrison of New York University, for five weeks of field work at Mahenge, searching for more fossils. One of the original test-pits dug for Mannard was located and excavated. The pit was extended downwards and on two sides, with the removal of over 60 m^3 of rock, resulting in a sample of about 0.09% of the lake. The removed rock was split in the field to expose fossils, the best of which were borrowed for this project.

Ongoing studies indicate that Mahenge had a tropical climate (Bonnie Fine-Jacobs, pers. comm.), i.e. with a rainy season, at the time the lake existed. The Mahenge fauna may have colonized the lake through a temporary outlet stream that formed during the rainy season. Excavations at Mahenge have concentrated on sediments from the centre of the ancient crater lake, and therefore no inlet or outlet that may have existed has been discovered. The preservation of many of the fish with open mouths (jaw tetany) could indicate that the fish died when the lake waters turned over, depleting oxygen or bringing toxins to the surface. A lack of disarticulation of fossil fishes often indicates that the lake in which they are found had an anoxic bottom layer or the hypolimnion was cold and deep (Elder and Smith, 1988). The cycle between rainy and dry seasons at Mahenge might have resulted in stratification of the water, with a cooler, deeper, anoxic hypolimnion that allowed the preservation of the fishes with no post-mortem disruption.

Of the four non-cichlid taxa found at Mahenge, two species have been described, *Singida jacksonoides* (Greenwood and Patterson, 1967) assigned to the Osteoglossidae by Li and Wilson (1996), and *Palaeodenticeps tanganikae* (Greenwood, 1960), a clupeomorph fish in the family Denticipitidae. In the 1996 field season, we recovered specimens of two previously unidentified fish, a catfish (Siluriformes cf. Mochokidae) and a second osteoglossomorph (Fig. 2).

The most numerous fossils at Mahenge are cichlids. Greenwood (1960; 1974) and Greenwood and Patterson (1967) recorded the presence of a single species of cichlid at Mahenge (13 specimens), but felt the poorly-preserved remains did not warrant a formal description. In 1996 we recovered many more, much better preserved specimens (over 150), that allow detailed descriptions and analysis to be done.

Figure 2. Undescribed fish from Mahenge. A. Osteoglossomorpha, anterior to right, scale bar is in centimetres; B. catfish (Siluriformes, cf. Mochokidae), anterior to left. Arrow indicates pectoral spine. Scale bar is two centimetres.

The project

There are four goals of research for this thesis:

1. To describe and name the fossil cichlid fishes collected from Mahenge, East Africa.
2. To examine the osteology of representative Recent species and the new fossil species for use in a phylogenetic analysis, and to synthesize previously published schemes of relationships for cichlid fishes in order to test the usefulness of osteological characters for determining cichlid relationships.
3. To use the osteological data in order to determine the probable relationships of the fossil cichlids.
4. To explain the distribution of fossil and recent cichlids by reconstructing vicariant or dispersal events and patterns based on information from studies on the phylogeny and biology of these fishes.

1. Differentiating fossil species

The new collection of fossil fishes from Mahenge, Tanzania represents well preserved, fairly complete specimens, including over 150 that can be identified as belonging to the family Cichlidae. Some authors have pointed out that sexual dimorphism, polymorphisms, and ontogenetic changes in scales make it difficult to distinguish cichlid species. This variability may result in different sexes, morphs, or age groups of the same species being described as one or more different species.

Sexual dimorphisms have been noted by Snoeks et al. (1994). They found that females in one species tended to have longer heads, more posteriorly placed fins and shorter dorsal and anal fin bases, than males. Polymorphisms have been found in the anatomy of the pharyngeal jaw bones and musculature, and the pharyngeal jaw apophysis of some species (e.g. Meyer, 1992; Liem and Kaufman, 1984). For example, *Astatoreochromis alluaudi* has two morphs, a hypertrophied morph that crushes molluscs with its enlarged pharyngeal apparatus, and a non-hypertrophied morph that eats insect larvae (Greenwood, 1965; Huysseune, 1995; Smits et al., 1996). Meyer (1992) summarized polymorphisms associated with diet and habitat in several species of cichlids, and noted that the polymorphisms not only affect the pharyngeal jaws and teeth and muscles, but also the neurocranial apophysis on the base of the skull which articulates with the upper pharyngeal jaw.

Examples of ontogenetic changes related to characters of the scales and squamation include variation in the overlap pattern of the scales, or scaleless areas in young fish that may become scaled in adults. Scales themselves may change as radii "break up" the anterior edge of the scale causing differences in patterns, or more radii develop as the fish gets older, more circuli develop, or the focus of the scale may move as growth of the scale is not always equal in all fields (B. Coad, pers. comm.).

Clearly, these problems of sexual dimorphism, polymorphism and ontogenetic change all have the potential to cause recognition of more species than are actually present. To avoid these potential problems in establishing species among the Mahenge fossil cichlids, none of these characters will be used to differentiate species in this thesis.

If these factors are not considered, the actual number of species present at Mahenge is more likely be underestimated than overestimated. Many extant cichlid species are distinguished by biologists based on colour patterns and behaviour (e.g. Bowers and Stauffer, 1997) neither of which is preserved in the fossils. Dorit (1990) discussed the question of whether the true range of species present in the fossil record would be recognized. He concluded that the number or species in a fossil assemblage would be underestimated compared to a similar assemblage of Recent species. If these factors are taken into consideration it should be possible to establish at least the minimum number of species at Mahenge.

2. Testing the usefulness of osteological characters for determining cichlid relationships

Many of the studies of relationships of Recent cichlids have involved molecular techniques that cannot be applied to the study of fossils. Similarly, the few non-molecular characters that have been used for the family, such as details of jaw musculature and presence of microbranchiospines on the gill arches (Stiassny 1981), are associated with soft-tissue anatomy or structures that are not preserved in most fossils. Lepidological studies offer some characters that are useful for fossils in which the scales are preserved (as is the case with the Mahenge specimens), but not all fossils preserve scale covering. Osteological characters that have the potential for indicating phylogenetic relationships and are applicable to fossil material are needed to included fossil representatives in phylogenies. Because many of the Mahenge cichlids are complete and well-preserved, they, along with representatives of living lineages, can form the basis for a study on osteological characters that are potentially useful for indicating phylogenetic relationships.

Recent comparative material and the fossil material will be examined for osteological features that vary among species, and these will then be used in a phylogenetic analysis. The potential use of these osteological characters can then be analysed by comparing how well the phylogeny based on the osteological data agrees with currently accepted schemes of relationships for the Cichlidae based predominantly on DNA and soft anatomy. The various published phylogenies are not directly comparable, so a composite tree incorporating information from the different published trees will be created by combining the source trees (Baum, 1992; Purvis, 1995). This composite tree will then be compared to the tree based on osteological characters, with the degree of congruence indicating the usefulness of the osteological data.

3. Determining the relationships of the fossil cichlids

The relationships of the fossil cichlids from Mahenge can only be determined based on osteological characters. The osteological data, whether they produce a tree congruent with those previously published or not, can be used to determine the most parsimonious placement of the Mahenge cichlids within the family. Using the osteological data with manual manipulation of tree branches in a computer programme (MacClade) will allow each possible placement of the fossils to be assessed in relation to the others and the most probable (parsimonious) placement of the fossils to be determined.

4. Reconstruction of the palaeobiogeography of the Cichlidae

Previously it has been suggested that cichlid fishes arose in the Early Cretaceous (Stiassny, 1987, 1991). After this time, Africa and South America were no longer contiguous. Therefore, if the group originated after this date, members of the family must have undergone a trans-Atlantic dispersal. The palaeobiogeography of the family will be analysed in light of the fossil record, current distribution and the biology of the fishes, and the composite phylogenetic tree created for the test of osteological characters.

Literature Cited

Barlow, G.W. 1991. Mating systems among cichlid fishes. Pp. 173-190 in: Keenleyside, M.H.A. (ed.). *Cichlid Fishes, Behaviour, Ecology and Evolution.* Chapman and Hall, Fish and Fisheries Series 2, London.

Baum, B.R. 1992. Combining trees as a way or combining data sets for phylogenetic inference, and the desirability of combining gene trees. Taxon, 41:3-10.

Bowers, N. and J.R. Stauffer, Jr. 1997. Eight new species of rock-dwelling cichlids of the genus *Melanochromis* (Teleostei: Cichlidae) from Lake Malawi, Africa. Ichthyological Explorations of Freshwaters, 8(1):49-70.

Casciotta, J. and G. Arratia. 1993. Tertiary cichlid fishes from Argentina and reassessment of the phylogeny of New World cichlids (Perciformes: Labroidei). Kaupia - Darmstädter Beiträge zur Naturgeschichte, 2:195-240.

Dominey, W.J. 1984. Effects of sexual selection and life history on speciation: Species flocks in African cichlids and Hawaiian *Drosophila*. Pp. 231-249 *in*: Echelle, A.A. and Kornfield, I. Eds., Evolution of Fish Species Flocks, University of Maine at Orono Press.

Dorit, R.L. 1990. The correlates of high diversity in Lake Victoria haplochromine cichlids: a neontological perspective. Pages 322-353 in: Ross, R.M. and W.D. Allmon (eds.). Causes of Evolution: a paleontological perspective. University of Chicago Press, Chicago, Illinois.

Echelle, A.A. and I. Kornfield (Eds.). 1984. Evolution of Fish Species Flocks. University of Maine at Orono Press, 257 pp.

Elder, R.L. and Smith, G.R. 1988. Fish taphonomy and environmental inference in paleolimnology. Palaeogeography, Palaeoclimatology, Palaeoecology, 62:577-592.

Greenwood, P.H. 1960. Fossil denticipitid fishes from East Africa. Bulletin of the British Museum (Natural History) Geology, 5:1-11.

Greenwood, P.H. 1965. Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluaudi*, and their taxonomic implications. Proceedings of the Linnean Society of London, 176:1-10.

Greenwood, P.H. 1974. Review of Cenozoic freshwater fish faunas in Africa. Annals of the Geological Survey of Egypt, 4:211-232.

Greenwood, P.H. and C. Patterson. 1967. A fossil osteoglossoid fish from Tanzania (E. Africa). Journal of the Linnean Society (Zoology), 47(311):211-223.

Huysseune, A. 1995. Phenotypic plasticity in the lower pharyngeal jaw dentition of *Astatoreochromis alluaudi* (Teleostei: Cichlidae). Archives of Oral Biology, 40(11):1005-1014.

Kornfield, I. and A. Parker. 1997. Molecular systematics of a rapidly evolving species flock: The mbuna of Lake Malawi and the search for phylogenetic signal. Pages 25-37 *in*: Kocher, T.D. and C.A. Stepien (Eds.) Molecular Systematics of Fishes, Academic Press.

Kullander, S.O. and H. Nijssen. 1989. The cichlids of Surinam. Teleostei: Labroidei. E.J. Brill, Leiden, The Netherlands, xxx +256 pp.

Li G-q. and M.V.H. Wilson. 1996. Phylogeny of the Osteoglossomorpha. Pages 163-174, *in*: Stiassny, M.L.J., L. Parenti, and G.D. Johnson (Eds.). Interrelationships of Fishes Revisited. Academic Press, New York.

Liem, K.F. 1991. Functional morphology. Pp. 129-150 in: Keenleyside, M.H.A. (ed.). *Cichlid Fishes, Behaviour, Ecology and Evolution*. Chapman and Hall, Fish and Fisheries Series 2, London.

Liem, K.F. and L.S. Kaufman. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. Pp. 203-215 *in*: Echelle, A.A. and I. Kornfield (eds.). *Evolution of Fish Species Flocks*. University of Maine at Orono Press.

Meyer, A. 1992. Trophic polymorphisms in cichlid fish: Do they represent intermediate steps during sympatric speciation and explain their rapid adaptive radiation? GSF-Bericht, 7:257-266.

Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African cichlid fishes. Trends in Ecology and Evolution, 8(8):279-284.

Miyazaki, H., T. Kancko, S. Hasegawa and T. Hirano. 1998. Developmental changes in drinking rate and ion and water permeability during early life states of euryhaline tilapia, *Oreochromis mossambicus*, reared in fresh water and seawater. Fish Physiology and Biochemistry, 18:277-284

Nelson, J. S. 1994. *Fishes of the World*. John Wiley and Sons, Inc. Toronto, xvii + 600 pp.

Purvis, A. 1995. A modification to Baum and Ragan's method for combining phylogenetic trees. Systematic Biology, 44:251-255.

Smits, J.D., F. Witte and R.G. Van Veen. 1996. Functional changes in the anatomy of the pharyngeal jaw apparatus of *Astatoreochromis alluaudi* (Pisces, Cichlidae), and their effects on adjacent structures. Biological Journal of the Linnean Society, 59:389-409.

Snoeks, J., L. Rüber and E. Verheyen. 1994. The Tanganyika problem: comments on the taxonomy and distribution patterns of its cichlid fauna. Ergebnisse der Limnologie, 44:355-372.

Stiassny, M.L.J. 1981. The phyletic status of the family Cichlidae (Pisces: Perciformes): A comparative anatomical investigation. Netherlands Journal of Zoology, 31:275-314.

Stiassny, M.L.J. 1987. Cichlid familial intrarelationships and the placement of the Neotropical genus *Cichla* (Perciformes, Labroidei). Journal of Natural History, 21:1311-1331.

Stiassny, M.L.J. 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview. Pages 1-35 in: Keenleyside, M.H.A. (ed.). Cichlid Fishes. Behaviour, ecology and evolution. Chapman and Hall, London, New York.

Verheyen, E., L. Ruber, J. Snoeks and A. Meyer. 1996. Mitochondrial phylogeography of rock-dwelling cichlid fishes reveals evolutionary influence of historical lake level fluctuations of Lake Tanganyika, Africa. Philosophical Transactions of the Royal Society, London, series B, Biological Sciences, 351:797-805.

Connecting text

The fossil material collected from the Mahenge locality includes over 150 specimens belonging to the family Cichlidae. The first step in analysing this material is to describe these fishes in detail. The specimens have been sorted into five groups, based on differences in the opercular, frontal, hyomandibular and other bones. Each group of specimens is described as a unique species, and the five species are united in a single genus based on characters of the scales and squamation. Characters associated with sexual dimorphisms and polymorphisms, that have the potential to artificially increase the number of species, have been avoided. Lepidological characters, that might lead to recognition of different age groups as separate species, are only used to unite groups, not to differentiate them.

CHAPTER 1.

DESCRIPTION OF THE EOCENE CICHLID FISHES FROM MAHENGE, TANZANIA

The descriptions and some of the figures in this chapter form part of the paper:

Murray, A.M. 2000. Eocene cichlid fishes from Tanzania, East Africa. Journal of Vertebrate Paleontology, 20(4):651-664.

Introduction

The family Cichlidae is represented today in Central and South America, Africa, the West Indies, Madagascar, Israel, Syria, coastal India, Sri Lanka and Iran. It is extremely speciose, with estimates of over 1300 species (Nelson, 1994). The majority of these are the species that have radiated rapidly to form the species flocks of lakes Victoria, Malawi and Tanganyika in East Africa (Casciotta and Arratia, 1993; Dominey, 1984). While other fish species flocks are known (papers in Echelle and Kornfield, 1984), the East African Great Lakes cichlids are the classic examples of species flocks, with large numbers of closely related species endemic to restricted areas. Despite extensive research by many authors on phylogenetic relationships, behaviour, evolution, and all aspects of cichlid biology, we still do not have a good knowledge of the history of this family. One area in which knowledge is still critically lacking is the fossil record.

Most fossils that have been referred to the Cichlidae are isolated bones or at best incomplete specimens (e.g. Greenwood, 1957, 1972; Van Couvering, 1982) or referable to Recent genera or species (e.g. Murray and Stewart, 1999; White, 1937), with the exception of specimens described by Van Couvering (1982), but these are considered to have a "modern facies" (Stiassny, 1991). The two cichlid fossils previously credited with being the oldest and of Eocene age are *Macracara prisca*, from Maranhão, Brazil (Woodward, 1939), and an unnamed specimen from Italy (Frickhinger, 1995). Casciotta and Arratia (1993) accepted an Eocene date for the Brazilian cichlid, but added "... Van Couvering (1982) questioned the age of the Brazilian locality without offering arguments" (p. 196). In fact, although Van Couvering (1982: p. 9) did question the Eocene date, this can be interpreted better as the lack of certainty of the original describer

(Woodward, 1939). Woodward based his date (given as lower Tertiary) for the Brazilian site based on the inclusion of the Eocene *Priscacara* in the Cichlidae, and the occurrence at the Brazilian locality of a species of the clupeid, *Knightia*. The only information relating to the age of the Brazilian site given in Woodward's paper (1939: p. 453) is "*Priscacara*, from the Eocene Green River Shales of Wyoming, U.S.A., shows that the Cichlidae date back to the Lower Tertiary in America, and *Knightia* is Lower Tertiary both in America and in the Old World. The fish-bearing deposit at Nova York in Maranhão is therefore of Tertiary age; and as both the genera now described are extinct, they may belong to the earlier rather than to the later Tertiary."

These two reasons have since been discredited. *Priscacara* is probably not a cichlid. It has now been identified as "a percoid" (Grande and Buchheim, 1994: p. 45.) with family relationships still unknown (Grande, 1994: p. 28). The presence of the genus *Knightia* is also in error; this genus is not present at Maranhão (Grande, 1985). In fact, Frickhinger (1995: p. 861) later listed the Maranhão site as Miocene in age, although no reason or reference for this younger date was given. The date of Maranhão is further confused by Schaeffer (1947). Although he also mentioned Woodward's (1939) date as possibly Eocene, he then listed the locality (1947: tab. 1) as ?Pliocene. Furthermore, *Macracara prisca* is now being placed in the extant genus *Geophagus* (as *G. priscus*) (Casciotta and Arratia, 1993; Frickhinger, 1995), rendering an Eocene age for this fish, and therefore the locality, unlikely.

The second record of a possible fossil cichlid from the Eocene is given by Frickhinger (1995). This popular book is the only reference found for the Italian specimen, which is listed questionably as a member of the Cichlidae (p. 864). This fossil is an unnamed fish from the Eocene of Vicenza, Italy, owned privately by Leonhardt Interfoss, Ober-Kainsbach, Germany. Casciotta and Arratia (1993) also mentioned the specimen, but refer to the same book as the original source of information. The photograph in the book is of a whole-bodied specimen, that is superficially similar to cichlids. However, details of the skeleton are not visible, and there is no other evidence to include it in the Cichlidae.

The oldest confirmed members of the family Cichlidae previously known are from the Oligocene of East Africa and Saudi Arabia (Van Couvering, 1982; Casciotta and Arratia, 1993; Micklich and Roscher, 1990; Lippitsch and Micklich, 1998). The East African species are plausibly Oligocene, in that they occur in the Middle and Upper Daban Series of Somalia between beds dated as upper Eocene marine deposits and possible lower Miocene deposits (Van Couvering, 1982). The cichlids from this locality are the named *Macfadyena dabanensis* and four indeterminate forms. The other Oligocene cichlids are seven specimens recovered from Saudi Arabia (Micklich and Roscher, 1990; Lippitsch and Micklich, 1998). These represent at least three different lineages of cichlids, including one that has been identified as ?*Astatotilapia*.

Recently, remains identified as Cichlidae have been reported from Early Oligocene deposits in the Sultanate of Oman (Thomas et al., 1999). Unfortunately, none of the remains are illustrated or described, although the authors give the impression that the faunal remains from this area are predominantly isolated bones and teeth. In an unpublished review of the fauna from this area, Otero and Gayet do not mention any cichlid remains being present. Weiler (1970) reported cichlids of indeterminable genus and species from Jordan. These are from freshwater deposits dated as Late Oligocene or

Miocene. The above represents the totality of the meagre pre-Miocene history of the Cichlidae.

It is significant therefore, that a large collection of fossils containing more than 400 specimens of fishes, the majority of which are cichlids, has recently been recovered from a lacustrine locality at Mahenge, Tanzania. These specimens are extremely well preserved, allowing detailed descriptions of their osteology. At least five different species of cichlids are present.

Geology

The Mahenge site (Fig. 1) has been interpreted as a small, roughly circular lake, about 400 m wide, that formed in a kimberlite intrusion (Mannard, 1962). When the kimberlite erupted, the overlying granitic country rock was shattered, producing a crater surrounded by a tuffaceous cone of primarily fine-grained ashes. This steep-sided cone created a restricted shoreline for a lake, which was then filled with sediments from the surrounding pyroclastic kimberlites. The centre of the Mahenge palaeolake contains well-stratified, microlaminated shales and mudstones, in which the fossils are located (Harrison, 1997).

The age of the beds has recently been determined. Based on the ichthyofauna, Greenwood (1960) originally suggested the site was Miocene, but later (Greenwood and Patterson 1967) suggested an Oligocene age for Mahenge. An Eocene age for the site was suspected based on geological evidence. Kimberlites from elsewhere in the Singida field have been dated using U-Pb and fission track dating. These two methods correlate

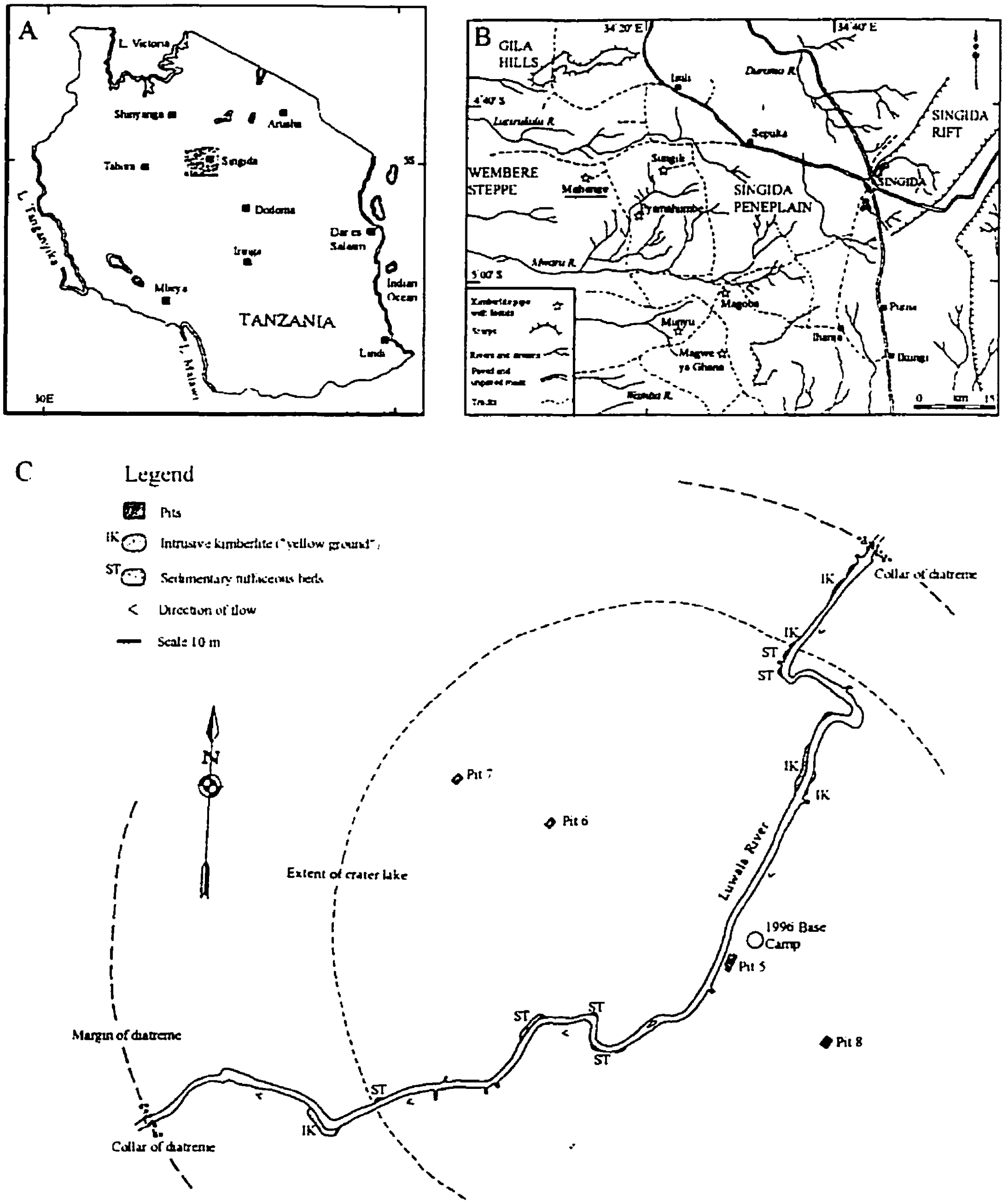

Figure 1. The Mahenge site. A. Tanzania; B. Detail of Singida Peneplain with Mahenge site marked; C. Diagram of the fossil locality with pit 5, from which fossils were collected. From Harrison, 1997.

well, and give an age of between 51 and 54 my for the other kimberlites. In 1996, the WMPE collected a zircon from the Mahenge pipe for radiometric dating. Geologists at Berkeley Geochron analysed the zircon and have established a $^{206}Pb/^{238}U$ date of 46.0 +/- 0.3 Ma, placing Mahenge in the mid-Eocene (Harrison et al., 1998).

Modern studies of crater lakes formed in a similar fashion indicate that the lake at Mahenge could have formed and been completely filled with sediments soon after the kimberlite intrusion (Hawthorne, 1975; Smith, 1986), and therefore the fossils would not be much younger than the kimberlite intrusion itself. Estimates of the sedimentation rate at Mahenge indicate that the fossiliferous deposits in the crater represent only 8000 to 22,700 years (Harrison et al., in press).

Material and Methods

Thirty-one of the most complete fossil specimens were prepared by dissolving any adhering bone with 5% acetic acid, then consolidating the resulting moulds with acryloid. Dyed latex was applied in thin coats, using an air brush, to make "positive" high-fidelity peels of the fossils. Drawings were made with a camera lucida attachment on a Wild M5 microscope.

Comparative Recent material (Appendix A) consists of alcohol preserved specimens, dried skeletons, material cleared and stained for both cartilage and bone, following the procedure of Taylor and Van Dyke (1985), and radiographs.

Institutional Abbreviations

NMC, Canadian Museum of Nature; USNM, United States National Museum, Smithsonian Institute, WM, Wembera-Manonga specimens belonging to the National Museum of Tanzania.

Abbreviations used in figures

art, articular; den, dentary; cl, cleithrum; fr, frontal; hyo, hyomandibula; io3, third infraorbital bone; iop, interopercle; lac, lacrimal; le, lateral ethmoid; l, left; mx, maxilla; na, nasal; op, opercle; pcl, postcleithrum; pd, predorsal bone (= supraneural bone); pl, palatine; pmx, premaxilla; pop, preopercle; psph, parasphenoid; ptt, posttemporal; qu, quadrate; r, right; sca, scapula; scl, supracleithrum; soc, supraoccipital crest; sop, subopercle; sym, symplectic.

Descriptions

Although cichlid monophyly has been supported with characters that are not preserved in fossils, such as details of jaw musculature and presence of microbranchiospines on the gill arches (Stiassny, 1987), the Mahenge specimens can be included in this family based on the structure of the lower pharyngeal jaw, the interrupted lateral line, the form of the scales and scale covering, and meristic characters, such as the number of vertebrae, fin spines and fin rays. The specimens can be grouped into five unique forms, which are described as different species. However, because all the specimens share many characters of the scales and squamation pattern, which have been found useful for characterizing genera (Lippitsch, 1993, 1995), they are described in a single genus.

Order PERCIFORMES Bleeker, 1859

Suborder LABROIDEA Bleeker, 1859

Family CICHLIDAE Gill, 1872

Genus *Mahengechromis* gen. nov.

Type species. *Mahengechromis plethos*, gen. et sp. nov.

Included species. *Mahengechromis rotundus, M. brachycranium, M. ellipticus, M. curvifrons* spp. nov.

Etymology. Named for the type locality, *Mahenge* (a kiswahili word, pronounced with a hard "g"), and *chromis*, (Greek) used to refer to cichlids; gender masculine.

Diagnosis. Distinguished from *Heterochromis* and *Tylochromis* by having a single predorsal bone (of the African cichlids only *Heterochromis* and *Tylochromis* have two, the rest have a single bone; Stiassny, 1991), and from the rest of the African Cichlidae by the combination of the following scale characters (from Lippitsch, 1995, 1998): ctenoid scales covering the body (cycloid scales are present on the body of hemichromines, chromidotilapiines, tilapiines and perissodines), cycloid scales on the opercular, preopercular, cheek, interopercular, subopercular, supraoccipital and frontal bones (cyprichromines have ctenoid scales on the cheek, lamprologines and eretmodines have no scales on the interopercular), and no arched granular area on the surface of the flank scales (a character present in the limnochromines and ectodines). Cycloid scales are present between the rays of the caudal fin and the jaws and pharyngeal bones bear unicuspid teeth. Although the states of the following characters are not known for all cichlids, potential synapomorphies for the five species of *Mahengechromis* are: 1. low number of vertebrae (22-25), considered an advanced state for cichlids (Cichocki, 1976; Kullander, 1998); 2. some of the upper lateral line scales bear only pores, not full canals, considered advanced for cichlids (Lippitsch, 1993), this state is also known in some other species (e.g. *Lamprologus moquardii*), but the other scale characters suggest this similarity to be homoplastic; and 3. at the posterior end of the lower lateral line in *Mahengechromis*, the last few scales have a canal with a pore dorsal and ventral to it.

Features common to the known species of *Mahengechromis*

All the specimens are preserved in lateral view indicating that these fish are fairly narrow in body width compared to depth. They range in size from 29 to 64 mm standard length (SL). The fishes have a body depth ranging from 0.35 to 0.47 SL. The head length ranges from 0.28 to 0.39 SL. The caudal peduncle is short and deep, and is almost square, with the depth being slightly greater than the length.

Skull. Figure 2 shows the reconstructed skulls of the five species. The supraoccipital crest is distinct and slants anteriorly to join the frontal over the posterior part of the orbit. The frontals vary in shape among the species. The mesethmoid is not visible in any specimen, suggesting that it may have been cartilaginous and not ossified. On three specimens (WM 271/96, WM 290/96, and WM 541/96) the pattern of the median frontal pores can be discerned. In these three, the left and right median pores (nfl 0, see Stiassny, 1991) are clearly separate, not meeting in the midline. This is similar to the

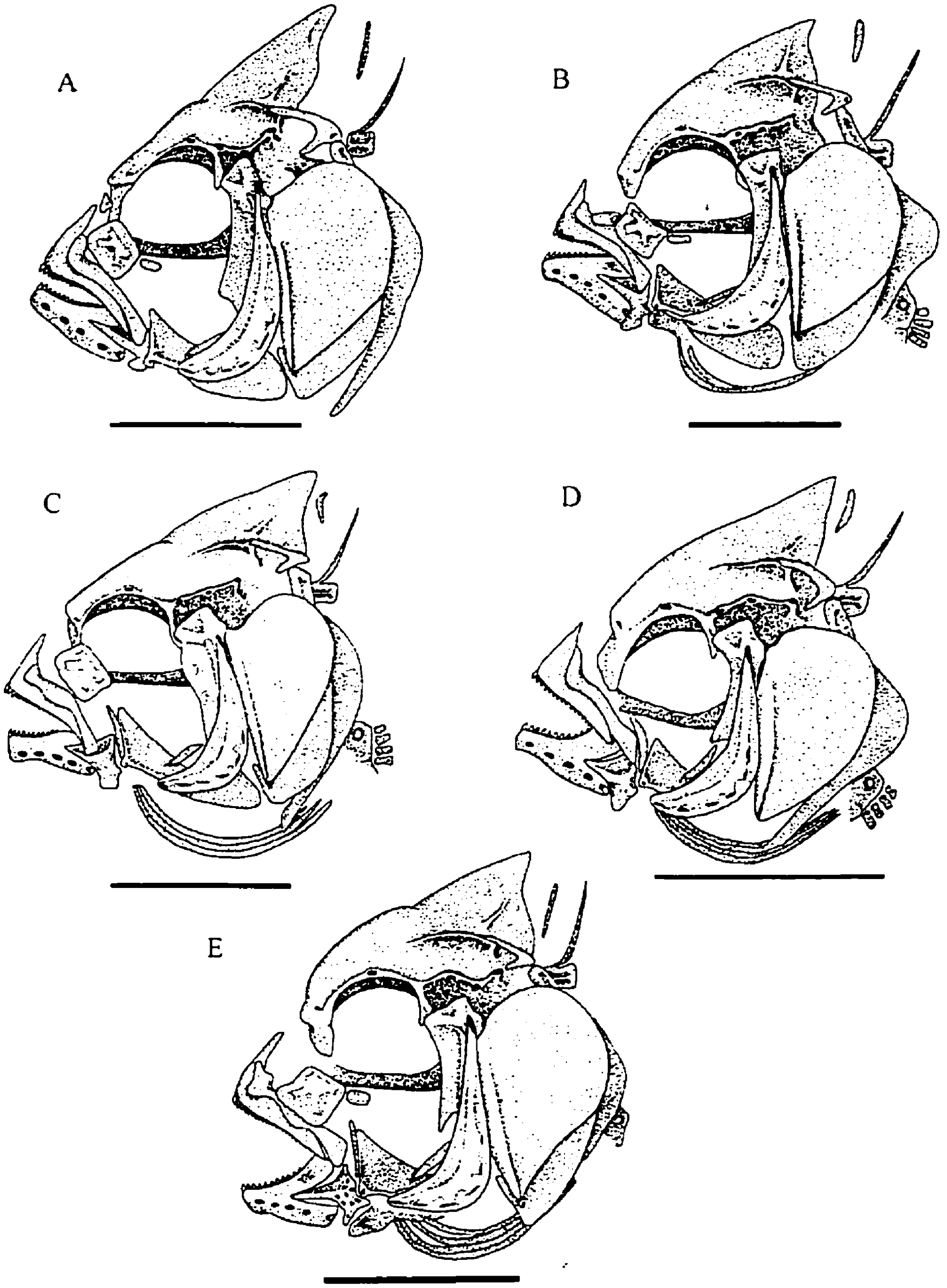

Figure 2. Reconstructions of the heads of the five species of *Mahengechromis* gen. nov. based on the holotypes. A. *M. plethos* sp. nov.; B. *M. rotundus* sp. nov.; C. *M. brachycranium* sp. nov.; D. *M. ellipticus* sp. nov.; E. *M. curvifrons* sp. nov. Scale bars = 1 cm.

primitive perciform condition, found also in ptychochromines and *Oxylapia* (Stiassny, 1991), which are considered primitive for cichlids.

Jaws and Suspensorium. The hyomandibula is long and narrow as in tilapiines, not short and broad as in *Hemichromis*. The hyomandibula head is single, and angles anteriorly in all the specimens, although other aspects of this bone vary among the species.

There are four large round pores in the dentary, with a fifth pore opening at the posterior edge of the ventral limb of the bone. The upper limb of the dentary is as deep as the lower. Striations ornament the posterior half of the upper limb and the posterior edge of the limb is flat, not pointed. Teeth are present on at least the anterior three-quarters of the dentary. Any teeth that have been preserved on the dentary and premaxilla are conical and unicuspid. Teeth on the dentary (Fig. 3) are about 2.5 times higher than wide, and have a cylindrical base topped by a small pointed hook. The hooked part of the tooth is about one third the height of the tooth. In specimens where dentary tooth rows are visible, there are four to five rows. The dentary, premaxilla and maxilla are all nearly equal in length. The premaxilla bears teeth to the posterior tip of the bone. The posterior end of the maxilla is blunt. The angulo-articular in general is only slightly longer than high, but the characteristics of this bone vary among the five species. Teeth on the pharyngeal bones, where preserved, are of two types, larger conical ones and smaller flat peg-like teeth, both of which are unicuspid (Fig. 4)

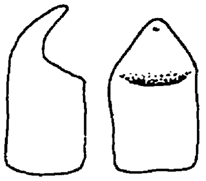

Figure 3. Drawing of a dentary tooth of *Mahengechromis* gen. nov. Tooth is approximately 0.5 mm in height.

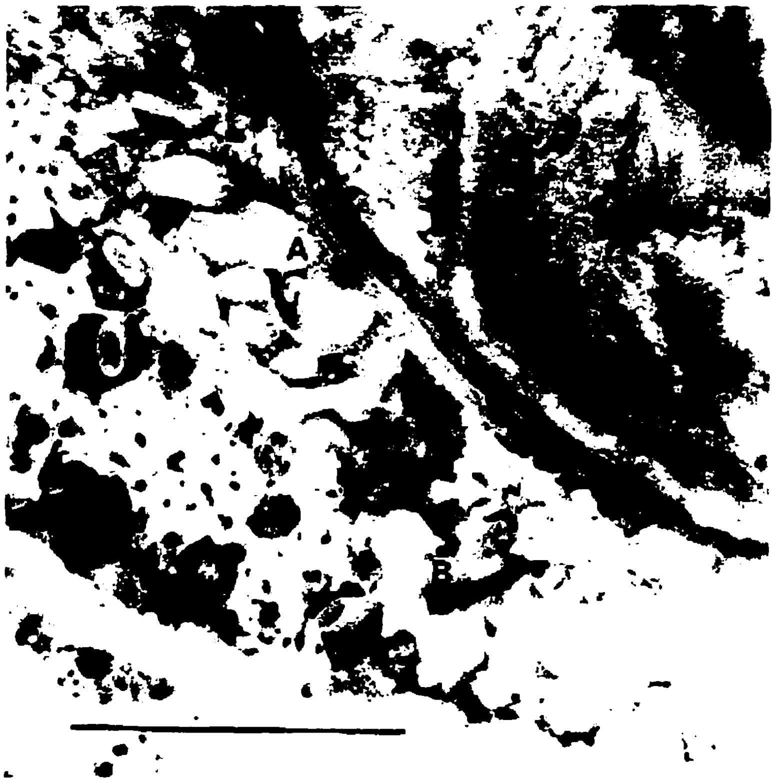

Figure 4. Photograph of the pharyngeal teeth of *Mahengechromis* n. gen., specimen WM 557/96. A. conical unicuspid teeth; B. flat, peg-like teeth. Scale bar is approximately 1 mm

Opercular region. The preopercular bone curves gently as in *Hemichromis*, and does not have a sharp angle at the posteroventral corner as in *Oreochromis*. The preopercle narrows dorsally and the sensory canal runs in an open groove for the dorsal quarter of the vertical limb. There are seven pores visible along the preopercle. The opercle is rounded dorsally, as in *Hemichromis* and *Pelviachromis*, not flat as in *Oreochromis*. The anterodorsal edge of the opercle is slightly truncated to angle straight to the facet for articulation with the hyomandibula. The subopercle and interopercle, when preserved, are similar among the species, and similar to other cichlids.

Pectoral girdle. In many specimens the scapula is preserved. It is similar to that of other members of the family, with a central foramen and thickened posterior and dorsal edges. The dorsal plate of the cleithrum is narrower than that of *Oreochromis* and in some specimens the posterior edge appears to be fluted, although this may be an artefact of preservation.

Post-cranial skeleton. There is only a single predorsal bone (or supraneural bone), visible in most specimens. The total number of vertebrae ranges from twenty-two to twenty-five, with eleven or twelve in front of the first anal pterygiophore and eleven to thirteen posterior to the first anal pterygiophore. In all the specimens, scales cover the vertebrae, so, although the number can be counted, details of the centra are not clearly visible, and the position of the first haemal spine cannot be determined. The caudal peduncle is also scale-covered, so details of the caudal skeleton cannot be determined.

The anal fin contains three spines and eight to ten rays. The first spine is long, about three-quarters the length of the second, and the third is the longest and most robust. The dorsal fin contains fifteen spines and eight or nine rays. The pectoral fins, with twelve to fourteen rays, are rounded, and do not reach as far posteriorly as the distal tips of the pelvic fins. The pelvic fins, with one spine and five rays each, do not reach the anal fin origin. The pelvic girdle is preserved in many specimens, with the ventral flange situated in the middle of the bone, not at the medial edge as in *Oreochromis*. On most specimens, the shape of the caudal fin cannot be determined.

Scales. Almost every specimen preserves the impression and details of the scales. Lippitsch (1993) lists many characters of scale morphology and squamation which she has shown to be useful for investigating relationships among cichlids. Of her characters, forty-six can be determined for the specimens from Mahenge (see Appendix B), and for each of these characters, the five species share the same state.

The body is covered by ctenoid scales, about thirty along the length of the body, and the chest scales are only slightly smaller than those on the flanks. The flank scales (Fig. 5) are ovoid, with a longer vertical axis than horizontal. The caudad field is ornamented with granulations that radiate out from the focus in roughly staggered rows. The anterior part of the scale has fine convex circuli between the radii, and the central focus is free of granulation. The chest scales are about 1.5 mm and those on the flanks about 2 mm across. Cycloid scales, up to 2.5 mm in diameter, are present on the frontal, interopercle, opercle, subopercle, supraoccipital crest, preopercle, cheek, and just in front of the dorsal fin. Small oval scales are present on the caudal fin between the rays. As in

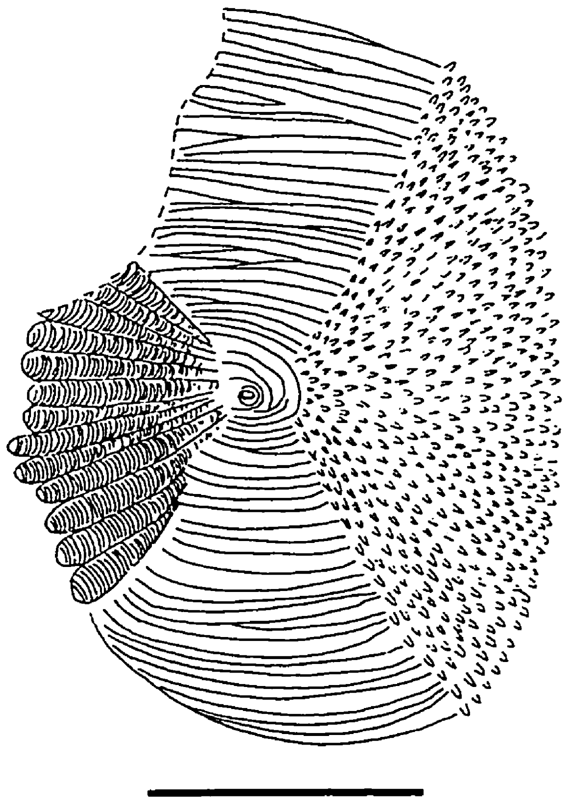

Figure 5. Drawing of a flank scale from specimen WM 397/96, scale bar = 1 mm.

most cichlids, the lateral line is in two parts, an anterior, upper part, and a posterior, lower part. The five species differ in the number of upper and lower lateral line scales.

Mahengechromis plethos sp. nov.

(Figs. 2A, 6 and 7)

Holotype. WM 339/96 a and b (part and counterpart).

Referred specimens. WM 261/96, 271/96, 290/96, 327/96, 374/96, 397/96, 409/96, 422/96, 455/96, 457/96, 525/96, 557/96, and 474/96.

Age. Eocene, about 45.83 +/- 0.17 Ma.

Locality. Mahenge, Singida Plateau, Tanzania, about 4° 47' 38" S, 34° 15' 28" E, about 53 km west of the town of Singida.

Etymology. From the Greek "*plethos*" meaning many, in reference to the fact that the majority of specimens belong to this species.

Diagnosis. Distinguished from other species of *Mahengechromis* by the supraoccipital crest being narrow in lateral view, with the dorsalmost tip being the most posterior point, rather than having the ventral half of the posterior edge protruding posteriorly as in the other four species, and the symplectic lying at a very shallow angle (about 20°) above the horizontal compared to the other species in which it lies at a 45° or greater angle.

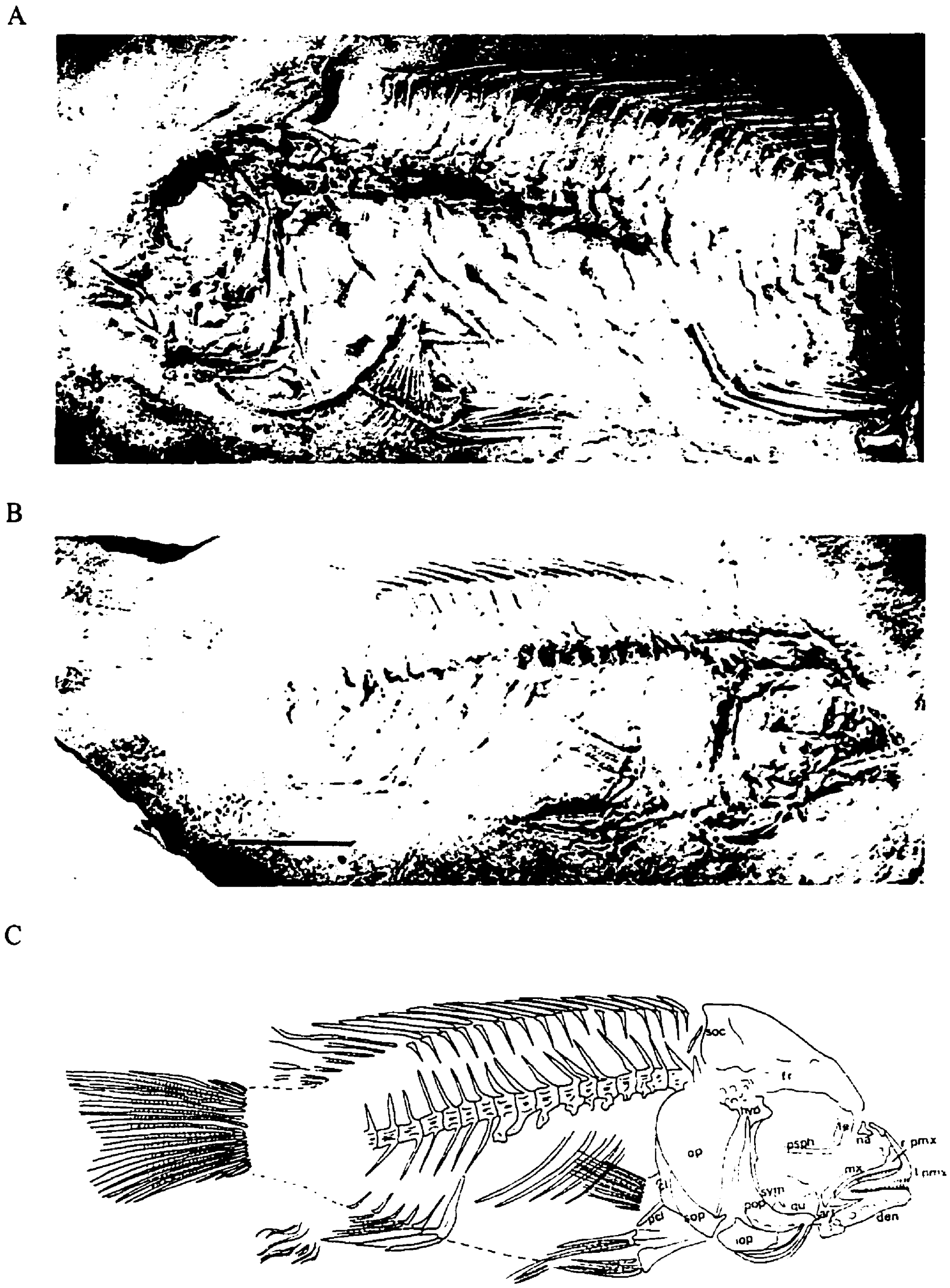

Figure 6. Photograph of part and counterpart and drawing of the holotype of *Mahengechromis plethos* n. sp., WM 339/96. Scale bar = 1 cm.

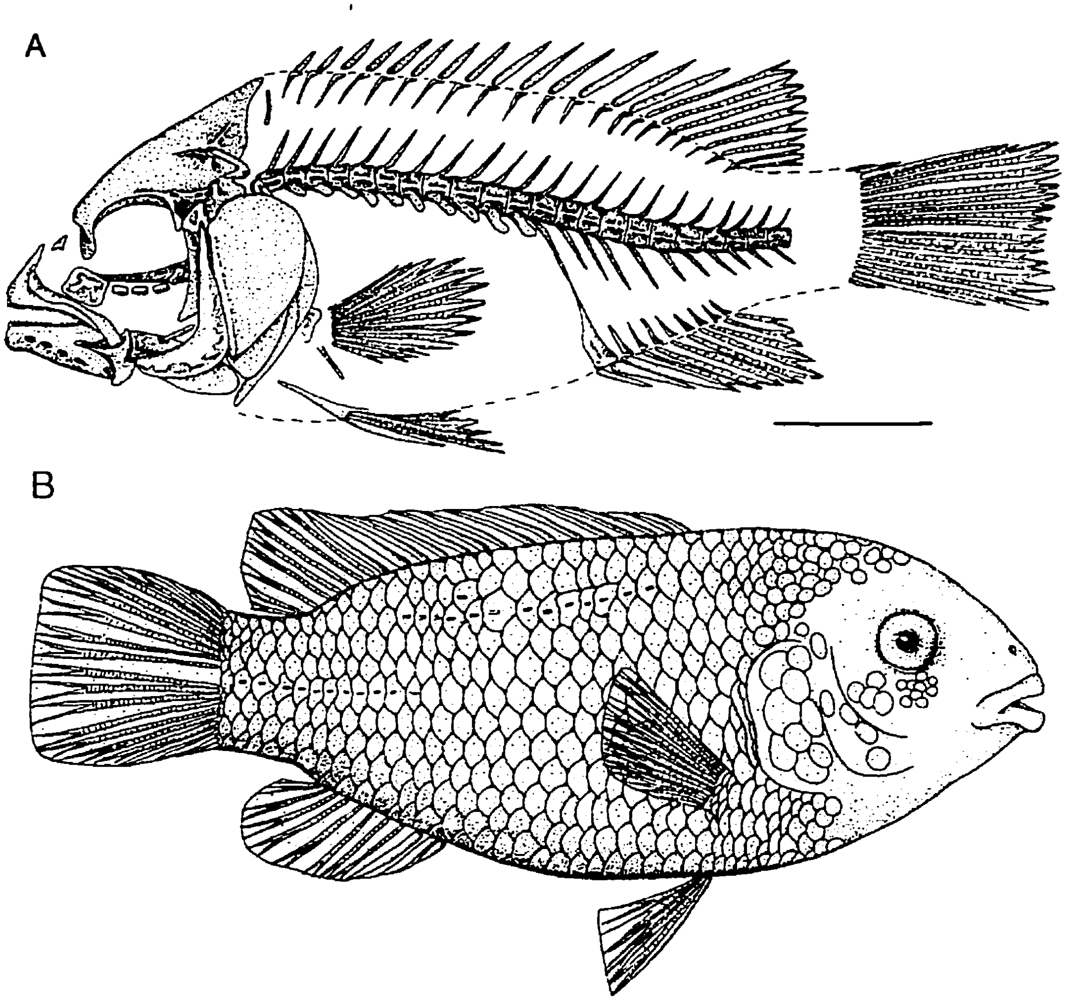

Figure 7. Reconstruction of *Mahengechromis plethos* sp. nov. A. skeleton based on the holotype; B. scales and body form based on WM 422/96. Scale bar = 1 cm.

Description

Neurocranium. This fish has a pronounced forehead that slopes sharply up to the dorsal fin. The supraoccipital crest, best preserved on WM 339/96 b, is steeper anteriorly and narrower in lateral view than the other species of *Mahengechromis*. The parietal crest is deep and continues anteriorly to the middle of the orbital rim. The basioccipital and right exoccipital are visible in lateral view on WM 339/96b. The basioccipital facet angles postero-dorsally, while the exoccipital facet angles posteroventrally. Both facets are similar in size, and extend farther posteriorly than does the posterior edge of the supraoccipital. The frontal is broad with the median frontal foramina visible in specimens WM 271/96 and WM 290/96. Both nasal bones, visible on WM 339/96a, are small, angled, and have pores for the sensory canal. The lateral ethmoid is large, filling the anterior third of the orbit above the parasphenoid, and the parasphenoid is narrow in lateral view, and may have a slight dorsal flange at the posterior edge of the orbit.

Suspensorium and hypobranchial region. The anterior flange on the hyomandibula is pointed anteroventrally and narrow, about the same width as the main shaft of the hyomandibula. The lateral flange seems to extend along the entire length of the bone. The symplectic is stout and large, lying at a shallow angle, about 20° to the horizontal. The endopterygoid and ectopterygoid are not preserved in most specimens, except as an area of crushed bone. Remains of only five branchiostegal rays can be seen in WM 339/96, but the anterior and posterior ceratohyals are not visible.

Jaws. The dorsal and ventral parts of the angulo-articular meet at an angle of less that 90°. The dorsal edge of the angulo-articular undulates as in *M. curvifrons* sp. nov., it is not straight as in the other three species. The posterior third of the maxilla angles sharply ventrally, and the posteroventral tip is narrower than in *M. ellipticus* sp. nov., but is round, not sharply pointed. There is a lateral flange on the middle third of the maxilla. The posterior third of the premaxilla also angles ventrally, ending in a point.

Infraorbitals. In the holotype, the left lacrimal preserves the remains of two pores. Traces of infraorbitals two and three, and possibly four, are also visible on the left side.

Opercular region. The ventral portion of the posterior edge of the opercle is straight, with the ventral tip slightly rounded, not pointed. The maximum width of the opercle is just ventral to the level of the hyomandibular facet.

Pectoral girdle. The posttemporal curves gently, and has a large posteroventral opening for the sensory canal. The supracleithrum has a smaller canal pore visible in the holotype, but the bone is not well-preserved. Only the postero-dorsal part of the cleithrum is preserved, but with no distinguishable details. The postcleithrum is robust and extends almost to the anterior point of the pelvic girdle. The thickened dorsal edge of the scapula is visible on WM 339/96a, along with three or four radials partially preserved, and 13 pectoral rays.

Postcranial skeleton. The greatest body depth is at the origin of the dorsal fin. The first vertebral centrum has a trapezoid shape, as in many extant cichlids. Ridges under the scale cover indicate the presence of at least eight ribs in the holotype.

Scales. In the holotype, the caudal fin rays are tightly aligned, which probably accounts for no scales being visible on the fin. In all of the referred specimens with caudal fins preserved, scales are visible between the fin rays. There are thirteen upper and at least eleven lower lateral line scales, and the two rows overlap by two scales.

Mahengechromis rotundus **sp. nov.**

(Figs. 2B, 8 and 9)

Holotype. WM 080/96.

Referred specimens. WM 019/96, WM 540/96

Age. Eocene, about 45.83 +/- 0.17 Ma.

Locality. Mahenge, Singida Plateau, Tanzania, about 4° 47' 38" S, 34° 15' 28" E, about 53 km west of the town of Singida.

Etymology. From the Latin "*rotundus*" meaning round, in reference to the greater body depth of this species in relation to the other four.

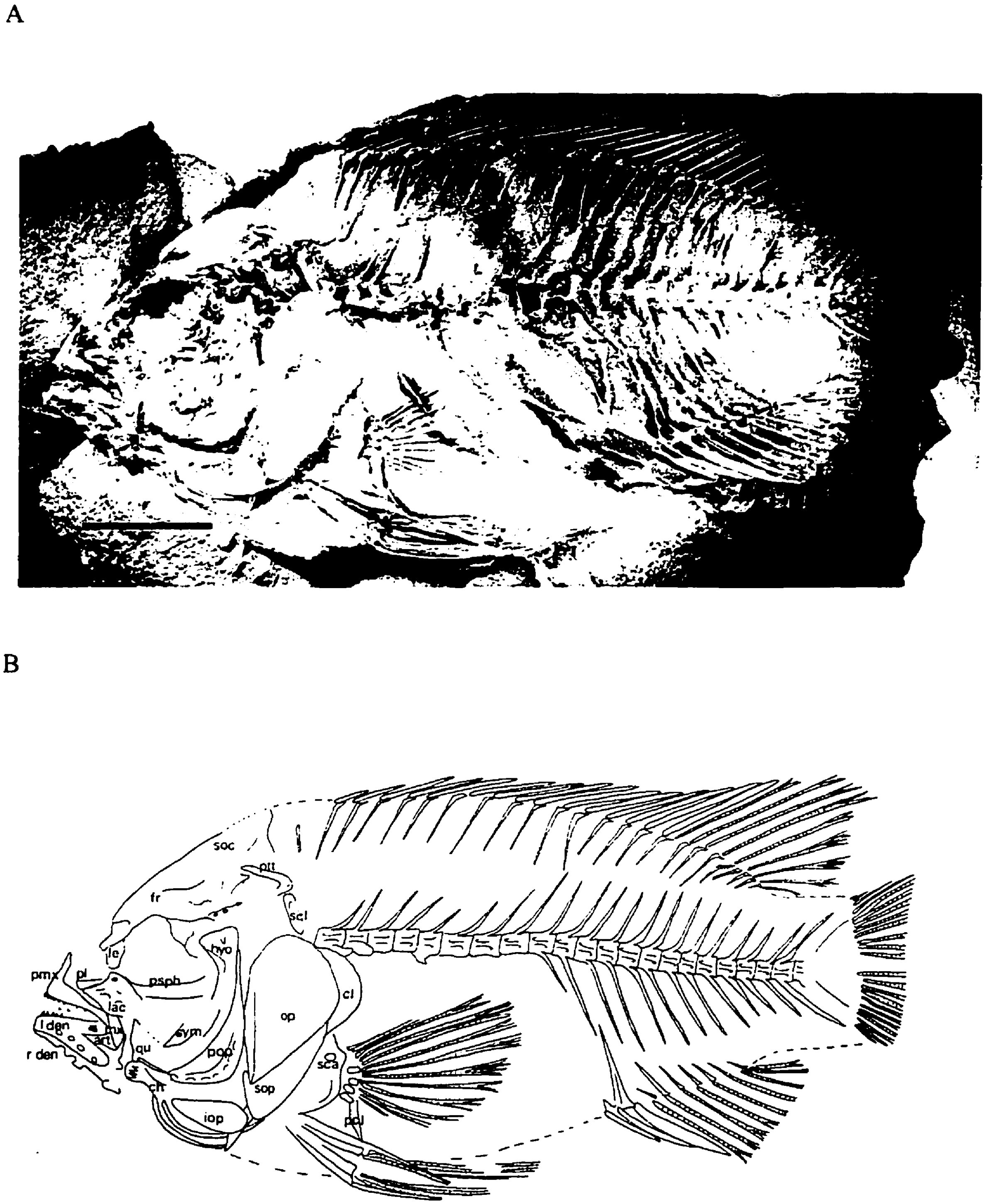

Figure 8. Photograph and drawing of the holotype of *Mahengechromis rotundus* n. sp., WM 080/96. Scale bar = 1 cm.

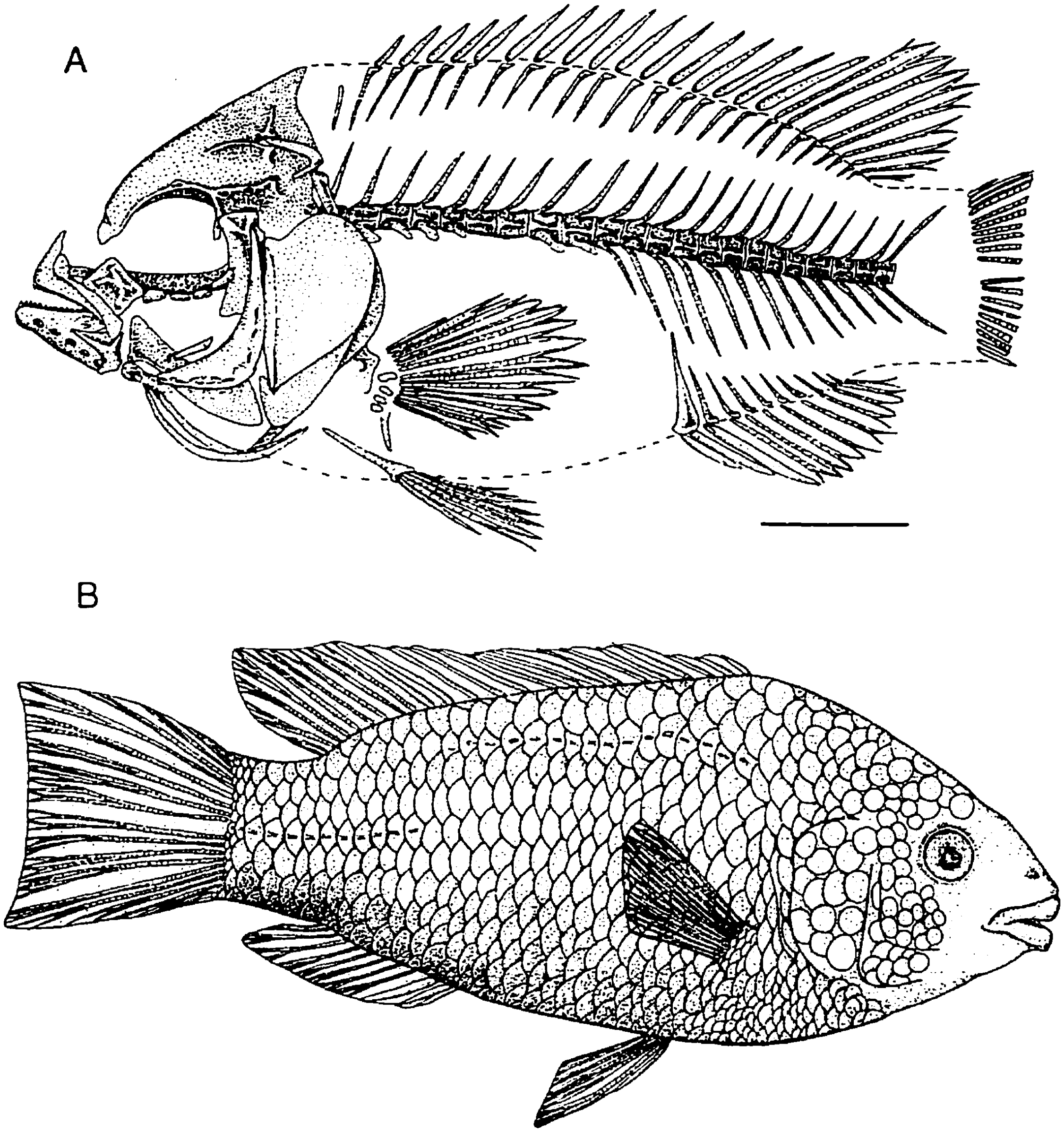

Figure 9. Reconstruction of *Mahengechromis rotundus* sp. nov. A. skeleton and B. scales and body form, both based on the holotype. Scale bar = 1 cm.

Diagnosis. Distinguished from other species of *Mahengechromis* by the frontal anteriorly having a greater curvature than that of *Mahengechromis plethos, M. ellipticus*, and *M. brachycranium* spp. nov., and a lesser curvature than that of *M. curvifrons* sp. nov. Further distinguished from *Mahengechromis plethos, M. ellipticus*, and *M. curvifrons* spp. nov. by the shape of the opercular bone ventrally being narrow antero-posteriorly, rather than broad as in *M. plethos* and *M. ellipticus* spp. nov., and having a straight posteroventral border rather than curved concavely as in *M. curvifrons* sp. nov. Distinguished from *M. brachycranium* sp. nov. by the anterior and ventral parts of the angulo-articular meeting at an angle of 90°, rather than forming an obtuse angle.

Description

Neurocranium. The supraoccipital meets the frontal over the mid point of the orbit and the two form a straight line in lateral view. The supraoccipital crest is not well preserved in any of the three specimens. The parietal crest also extends anteriorly to the junction of the supraoccipital and frontals. The frontal is broad and tapers anteriorly towards the midline. The nasal is not preserved in any of the specimens. The lateral ethmoid is relatively small, occupying only the anteriormost portion of the orbit above the parasphenoid.

Suspensorium and hypobranchial region. The anterior flange of the hyomandibula has a concave margin and ends ventrally in a point. The lateral flange is present but broken in WM 080/96. The symplectic is roughly rectangular but narrows posterodorsally and anteroventrally. It lies at about a 45° angle to the horizontal. The quadrate is deep, and the condyle is directed anteroventrally. Details of the metapterygoid are not clear in any specimen, but the bone appears triangular, and smaller than the quadrate.

The anterior ceratohyal is visible in WM 080/96, along with five branchiostegal rays. The posterior ceratohyal is covered by the interopercle. In WM 019/96 both the left and right anterior ceratohyals are partially visible, with four branchiostegal rays preserved on each. All branchiostegal rays articulate with the posterior portion of the anterior ceratohyal.

Jaws. There are four or five tooth rows visible on the dentary in the holotype. The anterior part of the angulo-articular is narrow, with a straight dorsal edge, not undulating as in *M. plethos* and *M. curvifrons* spp. nov. Its anterior extent is about three times its greatest height at the posterior edge. The facet for the quadratic condyle faces more posteriorly than dorsally. The ventral and anterior parts of the angulo-articular meet at almost 90°.

The premaxilla in WM 080/96 curves ventrally for the posterior quarter of the bone. The ascending process is fairly broad, compared to those in the other species of *Mahengechromis*. The posterior end of the maxilla is pointed at the ventral corner, not rounded as in *M. plethos*. There is a slight lateral flange on the maxilla at the midpoint of the bone, but the area where a dorsal projection might be expected is obscured by the only part of the palatine visible in the holotype, the large, rectangular articulation with the maxilla.

Infraorbitals. The lacrimal, almost square in shape, is partially preserved in WM 080/96. There are at least four pores present. Traces of infraorbitals two and three are also visible. Although they are crushed, it can be determined that these were small and rectangular in shape.

Opercular bones. The opercle (WM 080/96) is tall and narrow, rounded dorsally, and has a straight posteroventral edge. The ventral tip is rounded. The subopercle of WM 080/96 is attached tightly to the opercle. The interopercle is small and oval in shape.

Pectoral girdle. The cleithrum is not clearly visible in the holotype. The supracleithrum (WM 080/96) is broad and the canal is carried to the mid-lateral point, not to the posterior edge. The posttemporal is scale covered, but the anterior tip of the dorsal limb may have been blunt.

The postcleithrum is a short, stout bone, of roughly triangular shape. The coracoid is not well preserved in any specimen. There are four radials, three articulating with the scapula, and one straddling the scapula and coracoid. There are thirteen to fourteen rays in the pectoral fin.

Postcranial skeleton. Of all the species of *Mahengechromis*, this one has the greatest body depth, located at the level of the first and second dorsal fin spine. The back is flat along the anterior half. The caudal fin rays in WM 080/96 are missing posteriorly, but in WM 019/96 and WM 540/96 the tail is slightly rounded, and short, about 20% SL.

Scales. The upper lateral line on WM 080/96 covers sixteen scales, the lower twelve scales, and the two fail to overlap by one scale. Most of the lateral line scales have a canal only, but a few, including the ultimate and penultimate of the lower lateral line, have a canal with a pore on either side. A few of the scales at the posterior extent of the upper lateral line have a circular pore rather than an elongate canal.

***Mahengechromis brachycranium* sp. nov.**

(Figs. 2C, 10 and 11)

Holotype. WM 175/96.

Referred specimens. WM 240/96, WM 415/96, WM 421/96

Age. Eocene, about 45.83 +/- 0.17 Ma.

Locality. Mahenge, Singida Plateau, Tanzania, about 4° 47' 38" S, 34° 15' 28" E, about 53 km west of the town of Singida.

Etymology. From the Greek "*brachy*" meaning short, and "*cranium*" referring to the skull, in reference to the supraoccipital crest being lower than in the other species of *Mahengechromis*.

Diagnosis. Distinguished from all other species of *Mahengechromis* by the anterior flange of the hyomandibula being convex, curving anteriorly, rather than almost straight as in *M. curvifrons* sp. nov. or concave in the other species, and the symplectic being slightly curved, not straight as in the other species.

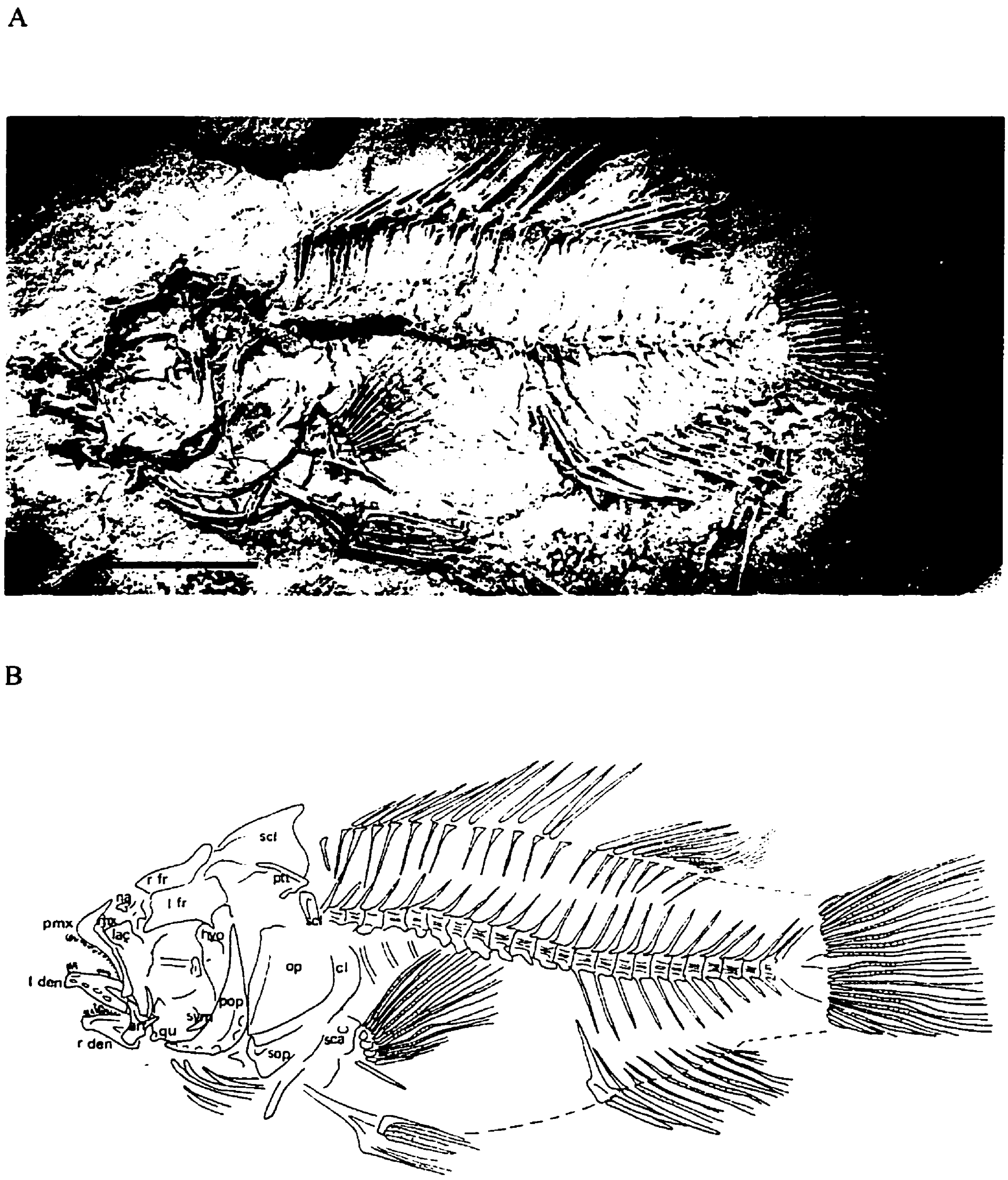

Figure 10. Photograph and drawing of the holotype of *Mahengechromis brachycranium* n. sp., WM 175/96. Scale bar = 1 cm.

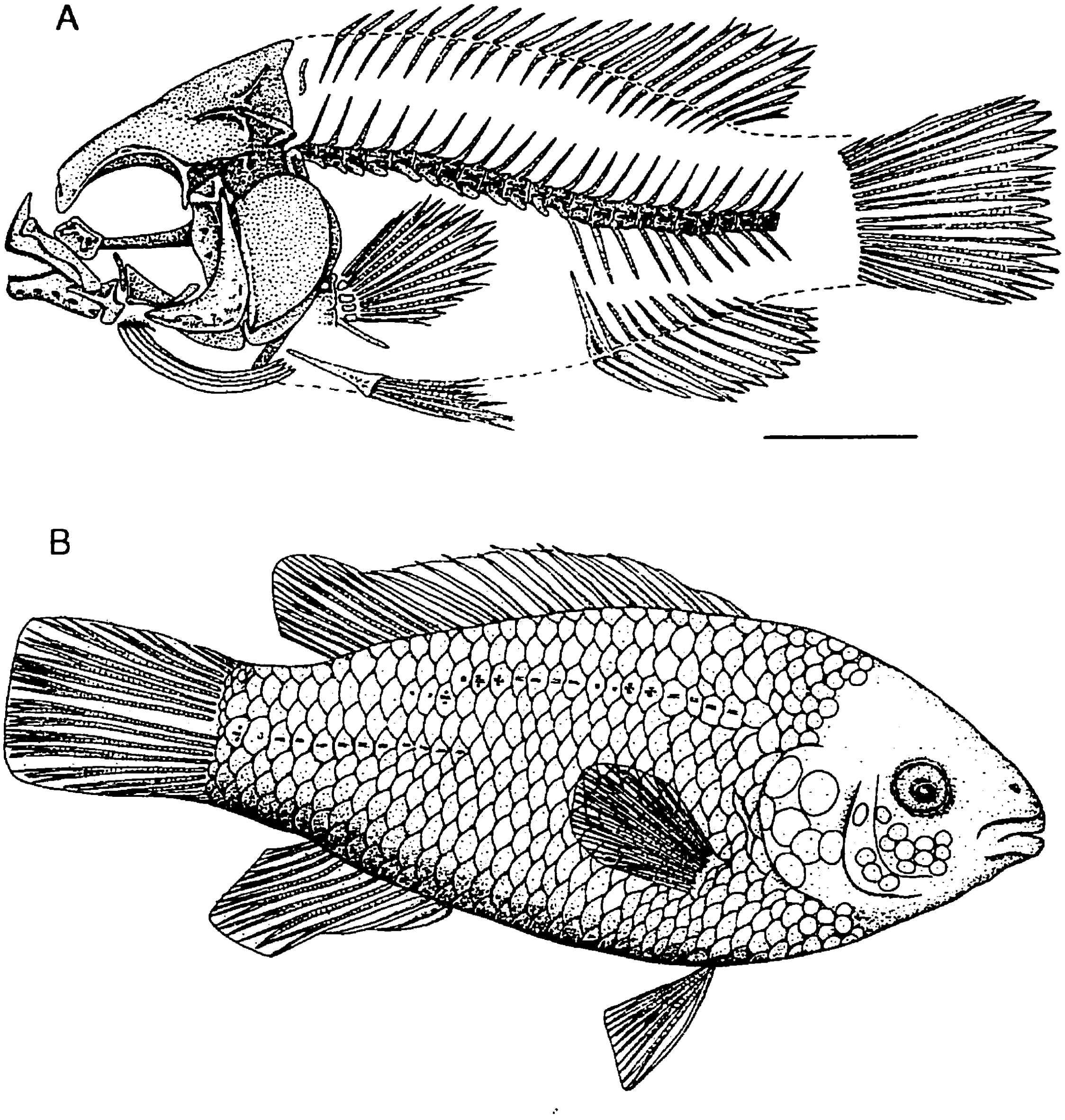

Figure 11. Reconstruction of *Mahengechromis brachycranium* n. sp., A. skeleton and B. scale pattern and body form, both based on WM 175/96. Scale bar = 1 cm.

Description

Neurocranium. The supraoccipital crest has a shallow angle, causing the crest to be lower than in the other species. The left and right frontals are preserved in nearly dorsal view on the holotype, although the median frontal pores cannot be seen. The frontals are pointed anteriorly, as in *M. rotundus*, unlike the blunt frontals of *M. curvifrons* sp. nov. A small cylindrical bone preserved in the holotype, presumably the right nasal, is a hollow tube with a small medial projection in its middle.

The lateral ethmoid is large, filling the anterior quarter of the orbit above the parasphenoid. The parasphenoid is also not preserved well, with only the thin lateral edge visible.

Suspensorium and hypobranchial region. The hyomandibula is clearly visible in WM 175/96. The dermosphenotic is displaced between the two articular condyles of the hyomandibular head, causing the head to appear divided, although this is probably not the case. The lateral flange of the hyomandibula is slightly broken, but extends at least half to two-thirds the length of the hyomandibula. The anterior flange is broad and convex. The ventral tip of the hyomandibula comes to a point and also curves anteriorly.

The symplectic is shorter than in the other species of *Mahengechromis*, and lies at about a forty-five degree angle. The quadrate is deep, similar to that of *M. curvifrons* sp. nov. The metapterygoid, ectopterygoid and endopterygoid are not well preserved.

The anterior ceratohyal and ventral hypohyal are visible in WM 421/96, showing the strong interdigitating sutures as in other cichlids. Remains of six left and five right branchiostegal rays are visible in the holotype.

Jaws. The dorsal edge of the angulo-articular is straight, not undulating. The anterior and ventral parts of the angulo-articular form an angle of about 120°. The angulo-articular facet for the quadrate faces dorsally.

The premaxillary dentigerous ramus curves ventrally for the posterior third or half of the bone. The maxilla may have a short, square, dorsal process in the middle of the bone, such as found in *M. ellipticus*; however this may instead be part of the lacrimal, which lies over the maxilla in the holotype. The anterior quarter of the maxilla does not form a flange separate from the maxillary head as in *M. plethos*. The maxilla curves ventrally for the posterior half of its length, with the tip pointed. The maxilla is more slender than the other species of *Mahengechromis*.

Infraorbital bones. The large, square, lacrimal bone is visible, but poorly preserved in WM 175/96 and WM 415/96. There appear to be four pores. No other infraorbitals can be distinguished.

Opercular region. The opercle has a curved postero-ventral edge. The thickened anterior edge is wide compared to the other species of *Mahengechromis*. The preopercle is fairly narrow in anterior-posterior width at the curve, compared to other species.

The subopercle is almost completely visible in the holotype because of the displacement of it and the opercle. It is similar in shape to that of other cichlids, with a dorsal depression for the insertion of the ventral tip of the opercle. The interopercle is not fully visible in any specimen.

Pectoral girdle. Four radials are visible in the holotype and WM 240/96, with three articulating on the scapula, and one at the junction of the scapula and coracoid. The coracoid is not well preserved. The supracleithum and posttemporal are not clearly visible in any specimen, but the posttemporal seems to be fairly long and slender with the dorsal limb arching downwards for the anterior quarter, where it rests on the epiotic. The postcleithrum is robust.

Postcranial skeleton. The back is arched so that the greatest body depth is at the level of the sixth dorsal fin spine. The predorsal bone is small and hooked; it does not quite reach the dorsal edge of the body.

Scales. There are eighteen lateral line scales in the upper row, and perhaps twelve in the lower row. The two lateral lines overlap by four scale rows. The posteriormost three pored scales in the upper lateral line have a single circular pore in the holotype; the scale anterior to these three has a longer canal with a pore dorsal and ventral to it.

***Mahengechromis ellipticus* sp. nov.**

(Figs. 2D, 12 and 13)

Holotype. WM 486/96 a and b (part and counterpart).

Referred specimens. WM 001/96, 045/96, and probably 468/96 based on overall head shape, although the specimen is too small for detailed study.

Age. Eocene, about 45.83 +/- 0.17 Ma.

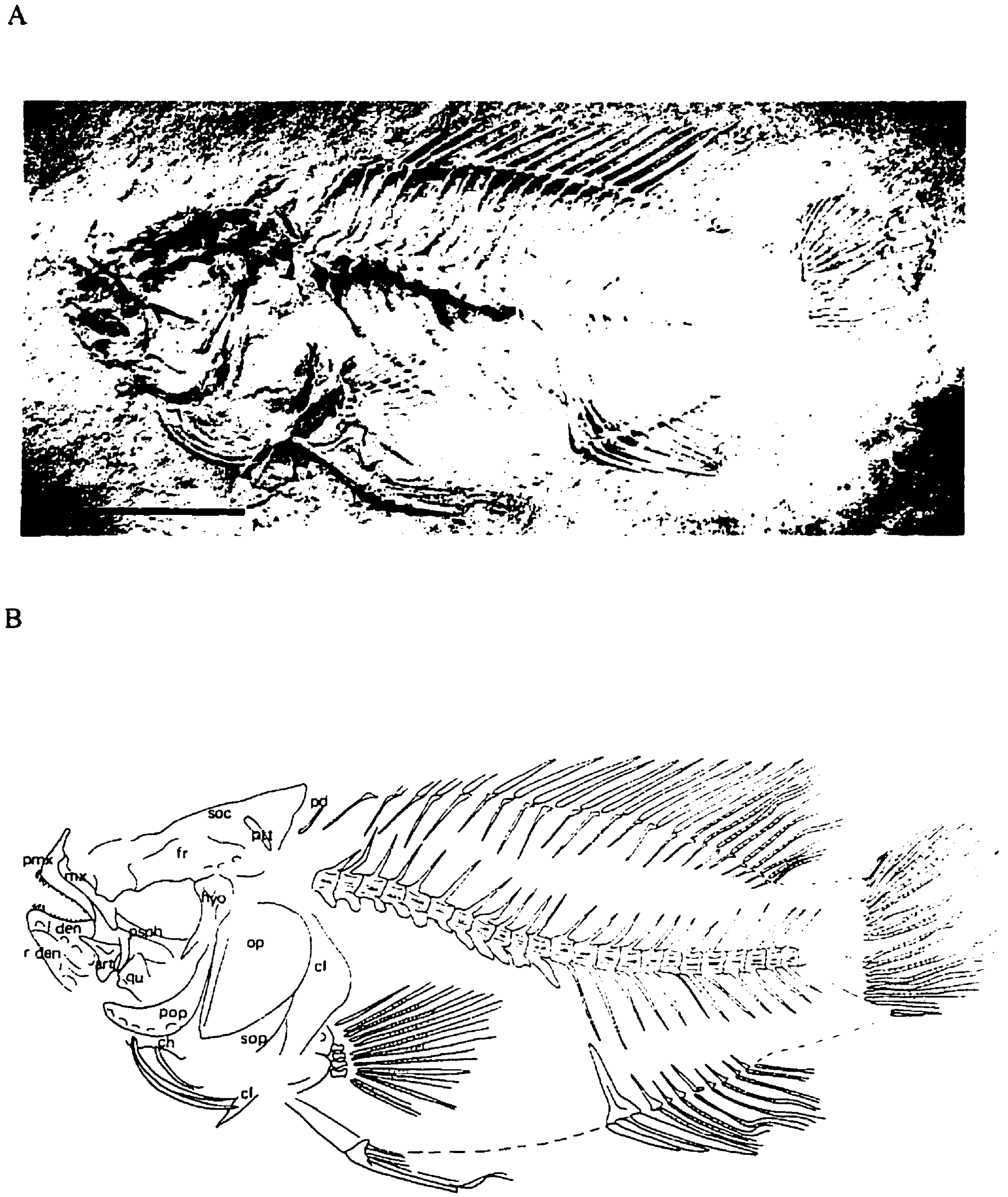

Figure 12. Photograph and drawing of the holotype of *Mahengechromis ellipticus* n. sp., WM 486/96 b. Scale bar = 1 cm.

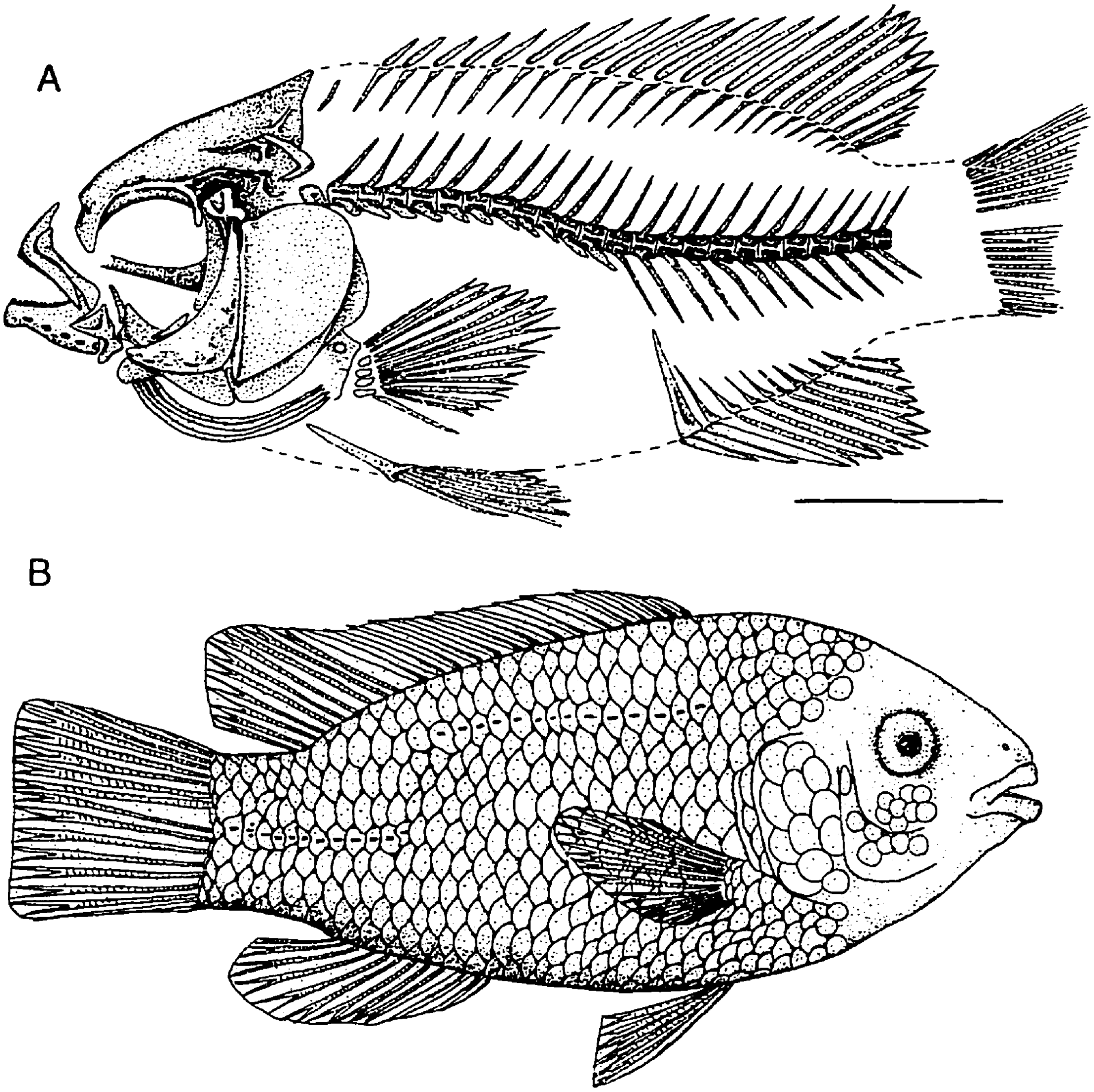

Figure 13. Reconstruction of *Mahengechromis ellipticus* sp. nov. A. skeleton and B. body form and scale pattern, both based on WM 486/96. Scale bar = 1 cm.

Locality. Mahenge, Singida Plateau, Tanzania, about 4° 47' 38" S, 34° 15' 28" E, about 53 km west of the town of Singida.

Etymology. From the Latin "*ellipsis*", originally meaning defective, as in a defective circle, but used to refer to an oval shape, in reference to the shape of the body which is more elliptical than in the other species of *Mahengechromis*.

Diagnosis. Distinguished from other species of *Mahengechromis* by the opercle having a convex postero-ventral edge rather than concave as in *M. curvifrons* sp. nov. or straight as in the other species, and the head and foot of the angulo-articular meeting at an angle of less than 90°, whereas all the other species have an angle of 90° or greater.

Description

Neurocranium. The forehead has a relatively gentle slope, as in *M. brachycranium*, with a shallower angle than the other species. The frontals are preserved in dorsolateral view on WM 486/96a, and in ventrolateral view on WM 486/96b and in ventral view in WM 045/96. Although the frontals are displaced, the supraoccipital does not seem to have been sharply angled compared to the frontal. The supraoccipital extends anteriorly almost to a position above the middle of the orbit and its posterior edge is almost vertical. The parietal crest is not well defined in the holotype, but extends to the middle of the orbital rim.

The parasphenoid is broad, and narrows anteriorly. There is a bulge on WM 486/96a under the anterior flange of the hyomandibula which is interpreted as a large ascending process on the parasphenoid.

Jaws. The maxilla may have a dorsal projection in the middle of its length, although the lacrimal obscures this area of the bone in all the specimens. The maxilla is pointed at the posteroventral tip. There is a slight shelf on the maxilla projecting over the premaxilla, similar to that of *M. brachycranium*, and less pronounced than the flange found in *M. plethos* and *M. curvifrons* sp. nov. The premaxilla horizontal ramus is distinctly downturned for the posterior quarter to third of the length of the ramus. The articular process is only slightly shorter than the ascending process.

The right dentary is preserved in medial view below the left dentary on WM 486/96b. The notch for the angulo-articular is broad and rounded. The angulo-articular is narrow anteriorly but robust. The angle of the ventral and anterior parts of the angulo-articular is more acute than the other species of *Mahengechromis*, being less than 90°.

Suspensorium and hypobranchial region. The anterior flange of the hyomandibula curves ventrally and has a pointed ventral corner. The lateral flange of the hyomandibula is crushed and details cannot be determined on any specimen. The symplectic is long and thin, and lies at about a 45° angle to the horizontal. The ectopterygoid is a curved cylindrical bone. The quadrate has a thickened anterior edge which narrows dorsally. The metapterygoid is not well preserved in any specimen.

There are five branchiostegal rays visible in the holotype of which at least four seem to articulate on the anterior ceratohyal. Details of the suture between the anterior and posterior ceratohyals is not visible. The urohyal is visible on WM 001/96a and WM 045/96. The anterior dorsal spike is straight, not angled.

Opercular region. The opercle is completely scale covered, but its shape can be determined. It is broader than that of the other species, and rounded postero-ventrally.

Infraorbital bones. The lacrimal is partially visible on WM 001/96a, but details are not clear. The second infraorbital is also visible but squashed and the third is a thin tubular bone, with the anterior pore visible. No others are visible in any specimen.

Pectoral girdle. The posttemporal is visible in lateral view on WM 486/96b. It has a fairly broad dorsal limb which is rounded at the tip where it articulates on the epioccipital. The ventral limb is much shorter and less robust. The supracleithrum is not preserved well on this specimen, but is about half as wide as it is high. The posterior flange of the supracleithrum is broad and rounded.

Scales. There are at least 11 lower and 14 upper lateral line scales visible in the holotype. The lateral lines do not overlap, having one scale between them.

***Mahengechromis curvifrons* sp. nov.**

(Figs. 2E, 14 and 15)

Holotype. WM 541/96.

Referred specimens. WM 365/96a and b, 376/96, 399/96, 564/96 and probably 472/96.

Age. Eocene, about 45.83 +/- 0.17 Ma.

Locality. Mahenge, Singida Plateau, Tanzania, about 4° 47' 38" S, 34° 15' 28" E, about 53 km west of the town of Singida.

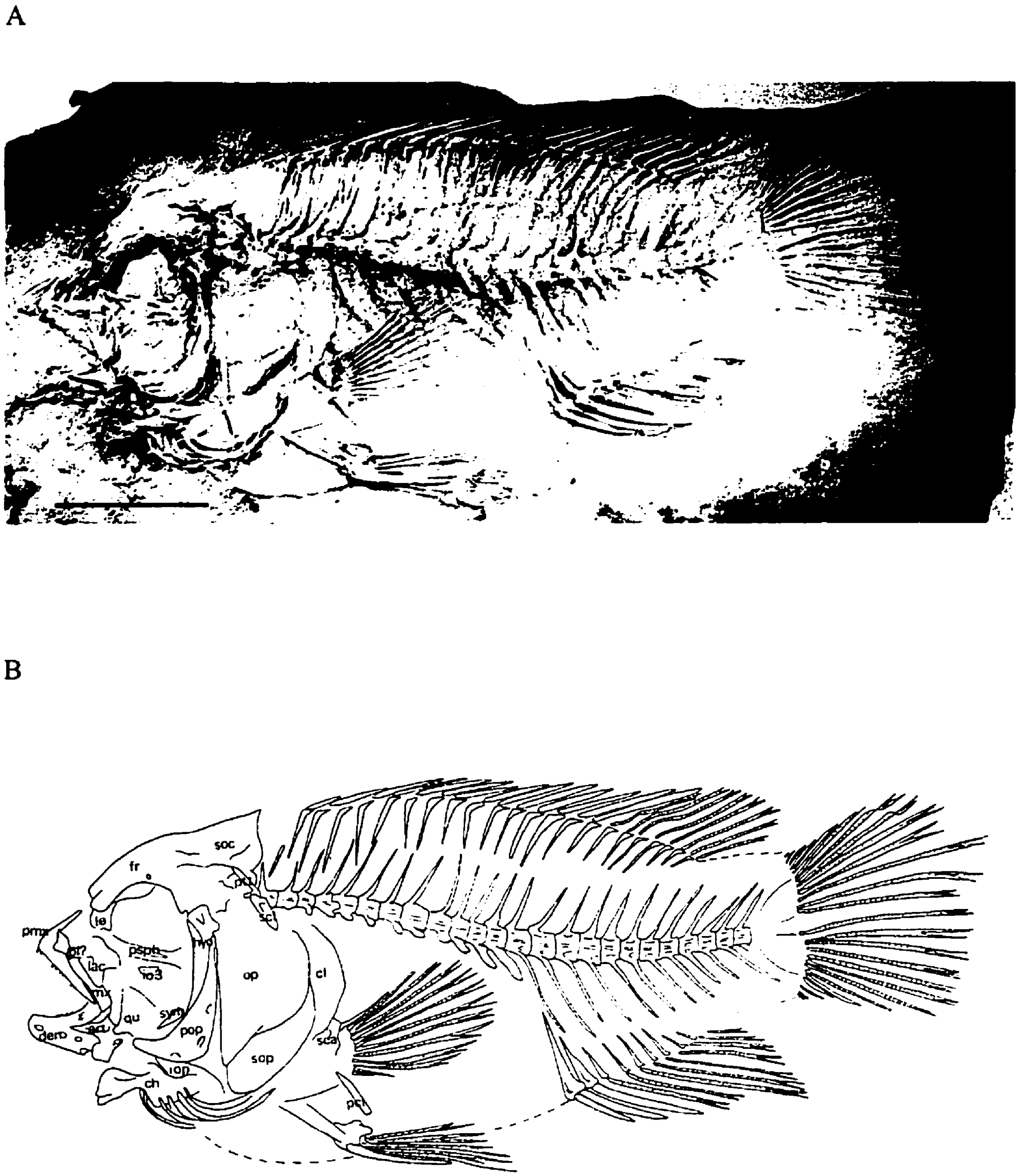

Figure 14. Photograph and drawing of the holotype of *Mahengechromis curvifrons* n. sp., WM 541/96 Scale bar = 1 cm.

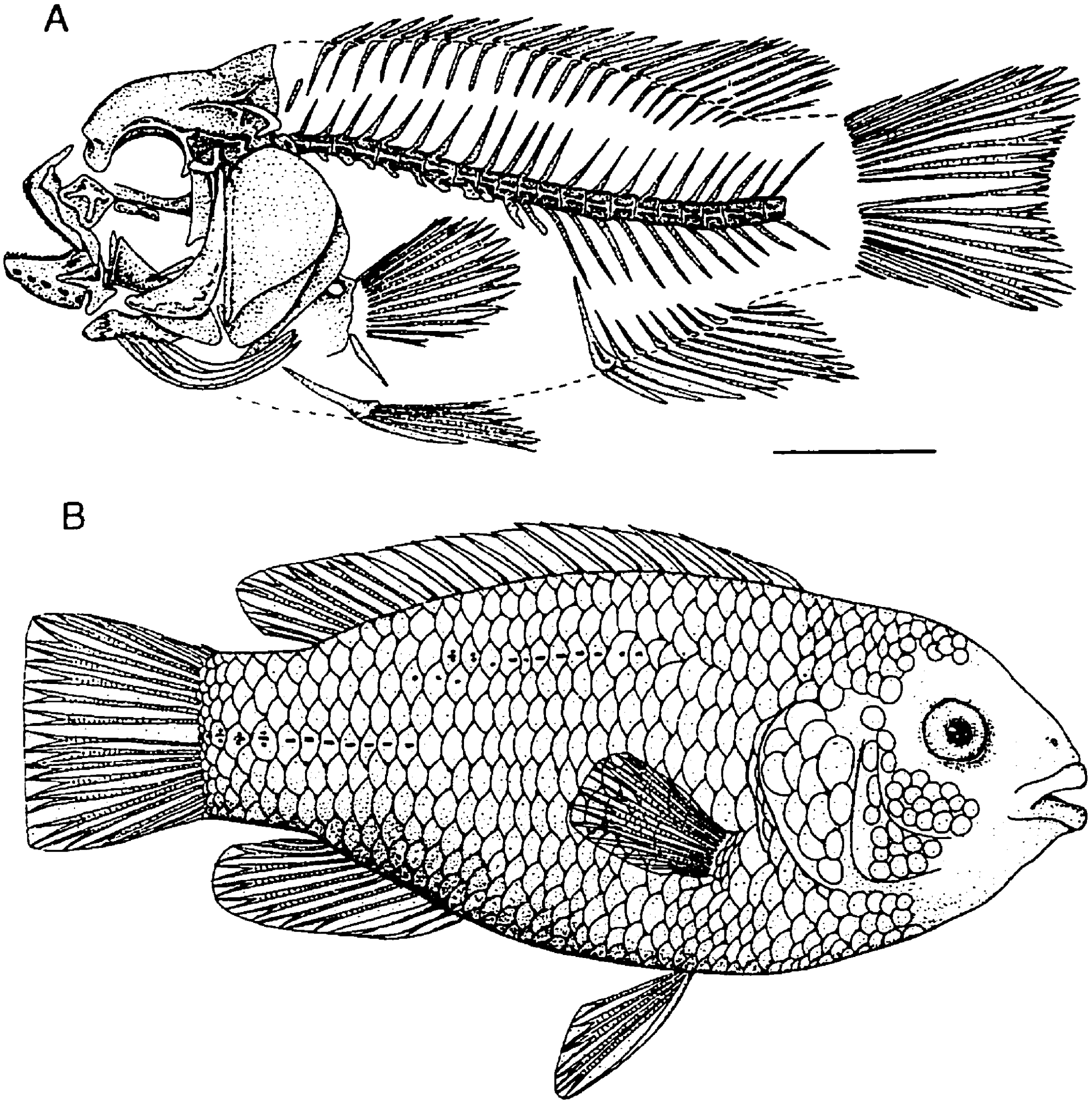

Figure 15. Reconstruction of *Mahengechromis curvifrons* sp. nov. A. skeleton and B. body form and scale pattern, both based on WM 541/96. Scale bar = 1 cm.

Etymology. From the Latin "*curvus*" meaning bent or curved, and "*frons*" meaning brow or forehead, in reference to the greater curvature of the frontals compared to other species of *Mahengechromis*.

Diagnosis. Distinguished from other species of *Mahengechromis* by the frontals in lateral view being greatly curved anteriorly, whereas the inclination of the frontals is closer to that of the supraoccipital crest in the other species. The symplectic lies at an angle of about 60° to the horizontal, rather than 45° or less in the other species, and the opercle has a posteroventral edge that is slightly concave, rather than convex as in *M. brachycranium*, or straight as in the other three species.

Description

Neurocranium. This cichlid has a pronounced forehead rising steeply above the anterior part of the orbit, then flattening posteriorly before the supraoccipital crest rises towards the dorsal fin. The parietal crest is short, not extending as far anteriorly as the middle of the orbital rim. The frontal is broad and significantly arched anteriorly. In the holotype the frontal canal pore pattern can be determined; the median pores are clearly separated. The anterior end of the frontal is blunt, not pointed as in *M. rotundus* and *M. brachycranium*.

The lateral ethmoid is fairly slender in lateral view, and does not fill a significant amount of the orbit. The sphenotic is present in the holotype but details are not clear. The parasphenoid is broad in lateral view, and angles slightly dorsally at both the anterior and posterior edges of the orbit. The dorsal edge appears to have been thicker or more robust than the ventral edge, although this may be an artefact of preservation.

Suspensorium and hypobranchial region. The hyomandibular head is narrower than in other species of *Mahengechromis*. The lateral flange, well preserved in WM 541/96, is narrow in lateral view, reaching at least three quarters of the length of the bone. The quadrate has a broadly thickened anterior edge. The metapterygoid and ectopterygoid are not well preserved in any specimen, although the ectopterygoid seems flatter and smaller than in *M. ellipticus*. The anterior ceratohyal, clearly visible in the holotype, is deep and ornamented with striations posteriorly; the deep interdigitating sutures with the hypohyals are clear. There are six branchiostegal rays preserved; the anterior two articulate with the ventral surface of the anterior ceratohyal, and the posterior four articulate on the lateral surface.

Jaws. The angulo-articular is well preserved in the holotype, including detail of the spongy bone pocked with pits comprising most of the ventral part. The dorsal edge of the angulo-articular is undulating, not straight. The ventral edge is robust and rounded. The posterodorsal edge, although slightly obscured by the maxilla, appears to be short.

The horizontal/dentigerous ramus of the premaxilla is straight. The ascending process is slightly damaged in the holotype but it appears that the articular process is short, only one third the height of the ascending process. There is a lateral flange on the maxilla which overhangs the middle of the premaxilla.

Infraorbitals. The lacrimal is present but poorly preserved in the holotype. The second infraorbital may be partially preserved, in which case it is either triangular, or this piece of bone is displaced from elsewhere. The rest of the infraorbitals have been lost except for ?io3 which is a small bone with a slight ventral flange below the enclosed tube for the sensory canal.

Opercular region. The opercle is well preserved in the holotype. Postero-ventrally it narrows abruptly, having a slightly concave edge, and it is broad and rounded posteriorly and dorsally. The preopercle is not well preserved, but the subopercular and interopercular are visible, and similar to other members of the genus.

Pectoral girdle and fin. There are thirteen pectoral fin rays supported by four hourglass-shaped radials, visible in the holotype. The supracleithrum is not well preserved. The posttemporal is visible in the holotype in position on the epiotic, but no distinctive features can be seen. The postcleithrum is robust and flattened.

Postcranial skeleton. The greatest body depth is at the level of the seventh dorsal fin spine. The single predorsal bone is positioned low, just above the vertebrae, not approaching the dorsal edge of the body.

Scales. There are fourteen upper lateral line scales visible in the holotype, with the posterior-most three being one scale line lower than the anterior scales. The lower lateral line contains at least twelve scales, and the two lateral lines overlap by one scale.

Discussion

To the best of our knowledge, the cichlids from Mahenge are a monophyletic group and endemic to their locality, and therefore, they comprise a species flock. A flock of five or more species in palaeolake Mahenge is reasonable, based on known Recent cichlid radiations in lakes Nabugabo (Uganda), Barombi Mbo and Bermin (both in Cameroon). Lake Nabugabo is larger than Mahenge but quite shallow, with a maximum depth of about 4.5 m, and, based on radiocarbon dating, is only 4000 years old (Greenwood, 1965). Within this time period, five endemic cichlid species have evolved (Greenwood, 1965). Lake Barombi Mbo supports a flock of eleven cichlids, and Lake Bermin, which is closer in size to the Mahenge crater (0.5 km diameter), supports a species flock of nine cichlids (Schliewen et al., 1994; Stiassny et al., 1992).

One of the requirements for species flock status is monophyly. Recent lepidological studies (Lippitsch 1993, 1995, 1998) have shown the potential of scale characters to be exploited for characterizing genera of cichlids. No other cichlid species are known that are more closely related to one or more of the Mahenge species than they are to one another. Therefore, these five species are considered to be monophyletic.

The second requirement for classification as a species flock is endemism. The Mahenge species are a group of closely related species adapted to lacustrine habitats in an isolated crater lake. It is probable that they, as in living cichlids in similar environments, would be endemic to this locality. The monophyly and endemism of these cichlids indicate that these fishes were an Eocene crater lake cichlid species flock.

Several fossil species flocks of non-cichlid fishes have been reported. McCune (1987) analysed semionotid fishes from the Early Jurassic Towaco Formation, Newark

Basin, and determined that a number of species were distinguishable based on morphometrics and dorsal scale pattern. Micklich (1996) described a probable flock of Percoid fishes from the Eocene Messel Formation and Smith (1987) described a radiation of sculpins in Pliocene Lake Idaho. Smith's analysis indicated that the sculpins had speciated by dispersing into progressively deeper waters, and therefore support intralacustrine (i.e. allopatric) speciation and Micklich accepted that the fossil percoids from Messel probably underwent intralacustrine speciation. The palaeolake of the Newark Basin was large, and presumably variable, suggesting intralacustrine speciation could also have occurred among the semionotid fishes.

The debate between supporters of sympatric versus supporters of allopatric speciation of cichlids is still very much on-going. The allopatric (or micro-allopatric) speciation model involves niche partitioning (or "ecological accommodation" of Dorit, 1990) whereby differential exploitation of resources by different morphs of a polytypic cichlid species eventually cause the morphs to develop into different species with isolating mechanisms that prevent gene flow. Lowe-McConnell (1994) concluded that there is strong evidence for micro-allopatric speciation of cichlids in the rocky shores of lakes Tanganyika and Malawi, because these species rarely leave their rocky area for other similar habitats since they will not cross the sandy areas in between. She further suggested that even in cases where there are no obvious physical barriers, such as in open waters, there may be physical or chemical barriers that are perceived by the fish. Microallopatric speciation is also considered to be the most important method for speciation in the flocks of lakes Victoria and Malawi by Meyer et al. (1994, 1996), who cited the extremely long and varied coast lines of these lakes as a major factor in cichlid speciation events.

A suggested method for sympatric speciation is preferential mating of females based on colour patterns of males, with the end result that different colour patterns eventually lead to isolating mechanisms among populations. Sexual selection by females for distinctly coloured males is considered to be the main force driving the generation and reproductive isolation of different morphs (Galis and Metz, 1998). Colouration seems to evolve quickly in at least some cichlids, such as *Tropheus*, in Lake Tanganyika, and the mbuna of Lake Malawi (Meyer et al., 1994). Several authors (e.g. Seehausen et al., 1997) have noted that the cichlids of Lake Victoria may be threatened by increased turbidity of the water caused by human activities. The increased turbidity seems to decrease the cichlids' ability to distinguish conspecifics based on colour pattern, leading to a break down of isolating mechanisms between species.

If niche partitioning based on trophic adaptation (i.e. microallopatric) is the method of speciation in cichlids, then the species should show diverse trophic morphologies (Albertson et al., 1999). Unique colour patterns in each species, such as those of the Lake Malawi genus *Melanochromis* (Bowers and Stauffer, 1997) with little trophic morphological variation, might indicate the higher importance of sexual selection (i.e. sympatric) for speciation. Clearly, the Mahenge species do not preserved details of colour patterns; on the other hand, the five species do not show distinctive jaw and tooth morphology, indicating that there were no structural specialisations among the species for different food types. Therefore, the Mahenge species do not support microallopatric speciation; there is, however, no specific evidence for sympatric speciation either.

The strongest support for sympatric speciation is found in the living flocks occurring in small crater lakes (Meyer et al., 1994). Schliewen et al. (1994) noted that in modern small crater lakes there are several reasons for believing that the cichlid species live in sympatry: the lakes are too small to restrict gene flow in mobile species, the shorelines are uniform and without physical barriers, crater lakes are uniform and conical so past water level fluctuations would not have created separate basins, and the crater rims isolate the lake from surrounding river systems. All of these factors apply to the palaeo-crater lake of Mahenge. The similar nature of the environment in all small crater lakes lends support to sympatric speciation being the method of speciation in the Mahenge species.

Not only are the Mahenge cichlids the oldest known species, but as a flock, they are the oldest record of any kind of species flock formation in the Cichlidae. Species flocks in lacustrine habitats have been described for tilapiine and haplochromine cichlids from Recent populations in Africa, and a "riverine flock" of cichlids has been described from South America (Lucena and Kullander 1992). The Mahenge cichlids provide the first fossil evidence to indicate that the ability of cichlids to form species flocks arose prior to forty million years ago.

Literature cited

Albertson, R.C., J.A. Markert, P.D. Danley, and T.D. Kocher. 1999. Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malawi, East Africa. Proceedings of the National Academy of Sciences of the U.S.A., 96(9):5107-5110.

Bowers, N. and J.R. Stauffer, Jr. 1997. Eight new species of rock-dwelling cichlids of the genus *Melanochromis* (Teleostei: Cichlidae) from Lake Malawi, Africa. Ichthyological Explorations of Freshwaters, 8(1):49-70.

Casciotta, J. and G. Arratia. 1993. Tertiary cichlid fishes from Argentina and reassessment of the phylogeny of New World cichlids (Perciformes: Labroidei). Kaupia - Darmstädter Beiträge zur Naturgeschichte 2:195-240.

Cichocki, F.P. 1976. Cladistic history of cichlid fishes and reproductive strategies of the American genera *Acarichthys, Biotodoma* and *Geophagus*. Ph.D. thesis, University of Michigan, vol. 1, 356 pp.

Dominey, W.J. 1984. Effects of sexual selection and life history on speciation: Species flocks in African cichlids and Hawaiian *Drosophila*. Pp. 231-249 *in*: Echelle, A.A. and Kornfield, I. Eds., Evolution of Fish Species Flocks, University of Maine at Orono Press.

Dorit, R.L. 1990. The correlates of high diversity in Lake Victoria haplochromine cichlids: a neontological perspective. Pages 322-353 in: Ross, R.M. and W.D. Allmon (eds.). Causes of Evolution: a paleontological perspective. University of Chicago Press, Chicago, Illinois.

Echelle, A.A. and I. Kornfield (eds.). 1984. Evolution of Fish Species Flocks. University of Maine at Orono Press, 257 pp.

Frickhinger, K.A. 1995. Fossil Atlas Fish. Translated by R.P.S. Jeffries. Tetra Press, Blacksburg VA. 1088 pp.

Galis, F. and Metz, J.A.J. 1998. Why are there so many cichlid species? Trends in Ecology and Evolution, 13(1):1-2.

Grande, L. 1985. Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. Bulletin of the American Museum of Natural History 181(2):231-372

Grande, L. 1994. Studies of paleoenvironments and historical biogeography in the Fossil Butte and Laney members of the Green River Formation. Contributions to Geology, University of Wyoming 30(1):15-32.

Grande, L. and H.P. Buchheim. 1994. Paleontological and sedimentological variation in early Eocene Fossil Lake. Contributions to Geology, University of Wyoming 30(1):33-56.

Greenwood, P.H. 1957. Fish remains from the Mumba Cave, Lake Eyasi. Mitteilungen aus dem Geologishen Staatsinstitut in Hamburg 26:125-130.

Greenwood, P.H. 1960. Fossil denticipitid fishes from East Africa. Bulletin of the British Museum (Natural History) Geology 5:1-11.

Greenwood, P.H. 1965. The cichlid fishes of Lake Nabugabo, Uganda. Bulletin of the British Museum (Natural History) Zoology 12:315-357.

Greenwood, P.H. 1972. Fish fossils from the late Miocene of Tunisia. Travaux de Géologie Tunisienne No. 6, Extrait des Notes du Service Géologique No. 37:41-72.

Greenwood, P.H. and C. Patterson. 1967. A fossil osteoglossoid fish from Tanzania (E. Africa). Journal of the Linnean Society (Zoology) 47(311):211-223.

Harrison, T. 1997. Wembere-Manonga Palaeontological Expedition: Field Report, 1996. Submitted to Dr. S.A.C. Waane, Director, Unit of Antiquities, P.O. Box 2280, Dar es Salaam, Tanzania.

Harrison, T., A. Murray, C.P. Msuya, B. Fine Jacobs, and A.M. Baez. 1998. Mahenge: An Early Eocene lagerstätte in Tanzania, East Africa. Journal of Vertebrate Paleontology 18(suppl. to 3):49A.

Harrison, T., C.P. Msuya, A.M. Murray, B. Fine Jacobs, A.M. Báez, R. Mundil and K.R. Ludwig. (in press). Paleontological investigations at the Eocene locality of Mahenge in north-central Tanzania, East Africa, *in* G.F. Gunnel (ed.). Eocene Vertebrates: Unusual Occurrences and Rarely Sampled Habitats. Topics in Geobiology, Plenum Press, New York.

Hawthorn, J.B. 1975. Model of a kimberlite pipe. Phys. Chem. Earth 9:1-15.

Kullander, S.O. 1998. A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes); pp. 461-498 *in* Malbarba, L.R., R.E. Reis, R.P. Vari, Z. M. S. Lucena, and C.A.S. Lucena (eds.), Phylogeny and Classification of Neotropical Fishes, Editora Universitária - EIPUCRS, Porto Alegre, Brasil.

Lippitsch, E. 1993. A phyletic study of lacustrine haplochromine fishes (Perciformes, Cichlidae) of East Africa, based on scale and squamation characters. Journal of Fish Biology 42:903-946.

Lippitsch, E. 1995. Scale and squamation character polarity and phyletic assessment in the family Cichlidae. Journal of Fish Biology 47:91-106.

Lippitsch, E. 1998. Phylogenetic study of cichlid fishes in Lake Tanganyika: a lepidological approach. Journal of Fish Biology 53:752-766.

Lippitsch, E. and N. Micklich. 1998. Cichlid fish biodiversity in an Oligocene lake. Italian Journal of Zoology, 65, supplement, Proceedings of the Ninth Congress of European Ichthyologists, 185-188.

Lowe-McConnell, R. 1994. The roles of ecological and behaviour studies of cichlids in understanding fish diversity and speciation in the African Great Lakes: a review. Ergebnisse der Limnologie, 44:335-345.

Lucena, C.A.S. de, and Kullander, S.O. 1992. The *Crenicichla* (Teleostei: Cichlidae) species of the Uruguai River drainage in Brazil. Ichthyological Explorations of Freshwaters 3(2), 97-160.

Mannard, G. 1962. The Geology of the Singida Kimberlite Pipes, Tanganyika. Ph.D. dissertation, McGill University, Montreal, Quebec, 348 pp.

McCune, A.R. 1987. Toward the phylogeny of a fossil species flock: Semionotid fishes from a lake deposit in the Early Jurassic Towaco Formation, Newark Basin. Peabody Museum of Natural History Yale University, Bulletin 43:1-108.

Meyer, A., C. Montero, and A. Spreinat. 1994. Evolutionary history of the cichlid fish species flocks of the East African great lakes inferred from molecular phylogenetic data. Arch. Hydrobiol. Beih. Ergebnisse der Limnologie, 44:407-425.

Meyer, A., C.M. Montero, and A. Spreinat. 1996. Molecular phylogenetic inferences about the evolutionary history of East African cichlid fish radiations. Pp. 303-323, in: Johnson, T.C. and E.O. Odada (eds.). The Limnology, Climatology and Paleoclimatology of the East African Lakes. Gordon and Breach Publishers.

Micklich, N. 1996. Percoids (Teleostei, Perciformes) from the oilshale of the Messel Formation (Middle Eocene, Lower Geiseltalian): An ancient speciation? Publ. Espec. Inst. Esp. Oceanogr. 21, 113-127.

Micklich, N. and B. Roscher. 1990. Neue Fischfunde aus der Baid-Formation (Oligozän; Tihamat Asir, SW Saudi-Arabien). Neues Jahrbuch fuer Geologie und Paläeontologie Abhandlungen, 180(2):139-175.

Murray, A.M. and K.M. Stewart. 1999. A new species of fossil tilapiine cichlid from the Pliocene Middle Awash, Ethiopia. Journal of Vertebrate Paleontology 19(2):293-301.

Nelson, J.S. 1994. *Fishes of the World.* John Wiley and Sons, Inc. Toronto, xvii + 600 pp.

Schaeffer, B. 1947. Cretaceous and Tertiary actinopterygian fishes from Brazil. Bulletin of the American Museum of Natural History 89(1):1-39.

Schliewen, U.K., D. Tautz, and S. Pääbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368:629-632.

Seehausen, O., J.J.M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science, 277:1808-1811.

Smith, G.R. 1987. Fish speciation in a western North American Pliocene rift lake. Palaios, 2: 436-445.

Smith, R.M.H.. 1986. Sedimentation and palaeoenvironments of Late Cretaceous crater-lake deposits in Bushmanland, South Africa. Sedimentology 33:369-386.

Stiassny, M.L.J. 1987. Cichlid familial intrarelationships and the placement of the Neotropical genus *Cichla* (Perciformes, Labroidei). Journal of Natural History 21:1311-1331.

Stiassny, M.L.J. 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview; pp. 1-35 *in* M.H.A. Keenleyside (ed.), Cichlid Fishes. Behaviour, Ecology and Evolution; Chapman and Hall, London, New York.

Stiassny, M.L.J., U.K. Schliewen, and W.J. Dominey. 1992. A new species flock of cichlid fishes from Lake Bermin, Cameroon, with a description of eight new species of *Tilapia* (Labroidei: Cichlidae). Ichthyological Explorations of Freshwaters 3(4):311-346.

Taylor, W.R. and G.C. VanDyke. 1985. Revised procedure for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107-119.

Thomas, H., J. Roger, S. Sen, M. Pickford, E. Gheerbrant, Z. Al-Sulaimani, and S. Al-Busaidi. 1999. Oligocene and Miocene terrestrial vertebrates in the southern Arabian Peninsula (Sultanate of Oman) and their geodynamic and palaeogeographic settings. Pp. 430-442 *in*: Whybrow, P.J. and A. Hill (Eds.). Fossil Vertebrates of Arabia. Yale University Press, New Haven and London.

Van Couvering, J.A.H. 1982. Fossil cichlid fish of Africa. Special Papers in Palaeontology no. 29:103 pp.

Weiler, W. 1970. Fischfunde aus dem Tertiär des Wadi Araba-Grabens in Jordanien. Geologische Jaarbuch, 89:193-208.

White, E.I. 1937. The fossil fishes of the terraces of Lake Bosumtwi, Ashanti. Bulletin of the Gold Coast Geographical Association 8:47-58.

Woodward, A.S. 1939. Tertiary fossil fishes from Maranhão, Brazil. Annals and Magazine of Natural History 11(3):450-453.

Appendix A. List of Comparative Material Examined

1. Cichlidae - specimens cleared and stained following the procedure of Taylor and VanDyke, 1985

Lamprologus mocquardi USNM 331358, 2 specimens

Tropheus moorei USNM 191512, 3 specimens

Copadichromis chrysonotus USNM 261836 3 specimens

Melanochromis vermivorus USNM 261830, 3 specimens

Rhamphochromis sp. USNM 280070, 1 specimen

Haplochromis flaviijosephi NMC 79-0694, 2 specimens

H. dashingi NMC 74-0522, 3 specimens

H. desfontainesi NMC 85-0499, 2 specimens

Astatotilapia bloyeti NMC 81-0188, 3 specimens

Astatotilapia bloyeti NMC 81-0195, 3 specimens

Psammochromis sp. NMC 81-0266, 3 specimens

Prognathochromis sp. NMC 81-0266, 2 specimens

Lipochromis sp. NMC 81-0266, 1 specimen

Yssichromis sp. NMC 81-0266, 1 specimen

Hemichromis guttatus uncatalogued, 2 specimens

Pseudotropheus sp. uncatalogued, 2 specimens

Pelviachromis kribensis uncatalogued, 1 specimen

2. Cichlidae specimens preserved in alcohol and x-rayed

Neotropical

Aequidens pulcher, NMC 76-0382, 2 specimens

Astronotus ocellatus, NMC 79-0918, 1 specimen, uncatalogued 1 specimen

Cichlasoma bimaculatum, NMC 77-0030, 3 specimens

Crenicichla wallacei, NMC 67-0138, 1 specimen; NMC 67-0144, 1 specimen

Geophagus brasiliensis, NMC 85-0125, 1; NMC 85-0130, 1 specimen

Geophagus surinamensis, NMC 67-0126, 3 specimens

Neetroplus nematops, NMC 89-0073, 2 specimens

Pterophyllum scalare, NMC 74-0084, 2 specimens

India/Madagascar/Middle East

Etroplus maculatus, NMC 81-0931, 1 specimen

Etroplus suratensis, NMC 81-0519, 1 specimen

Iranocichla hormuzensis, NMC 79-0138, 17 specimens

Tristramella simonis, NMC 80-0405, 2 specimen

Danakilia franchetti, NMC 82-0212, 1 specimen

Haplochromis flaviijosephi, NMC 79-0695, 6 specimens

African

Astatoreochromis alluaudi, NMC 81-0266, 1 specimen

Astatotilapia bloyeti, NMC 81-0195, 3 specimens; NMC 81-0188, 6 specimens

Haplochromis dashingi, NMC 74-0522, 7 specimens

Haplochromis desfontainesi, NMC 85-0499, 6 specimens

Haplochromis [*Prognathochromis*] sp., NMC 81-0266, 2 specimens

Haplochromis [*Lipochromis*] sp., NMC 81-0266, 2 specimens

Haplochromis [*Yssichromis*] *laparogramma*, NMC 81-0266, 2 specimens

Haplochromis [*Yssichromis*] sp., NMC 81-0266, 3 specimens

Haplochromis [*Psammochromis*] sp., NMC 81-0266, 7 specimens

Hemichromis sp., uncatalogued, 1 specimen

Pelviachromis sp., uncatalogued, 1 specimen

Lamprologus mocquardi, USNM 331358, 1 specimen

Rhamphochromis sp., USNM 280070, 2 specimens

Sarotherodon auratus, NMC 80-0831, 5 specimens

Serranochromis robustus, NMC 74-0521, 2 specimens

Tilapia rendahli, NMC 81-0228, 3; NMC 82-0228, 1 specimen

Tilapia zillii, uncatalogued, 1 specimen; NMC 80-0832, 5 specimens

3. Cichlidae specimens skeletonized

African

Hemichromis guttatus uncatalogued, 1 specimen

Oreochromis niloticus uncatalogued, 5 specimens

Pelviachromis kribensis uncatalogued, 1 specimen

Tilapia zillii uncatalogued, 1 specimen

Pseudotropheus sp. uncatalogued, 1 specimen

South American

Symphysodon sp. uncatalogued, 1 specimen

Appendix B. Scale Characters from Lippitsch (1993, 1995) applicable to the Mahenge Cichlids

Only the characters that can determined for *Mahengechromis* are listed. The state for *Mahengechromis* is given, and if it is the plesiomorphic state (as defined in Lippitsch, 1995) that is noted in brackets. For complete list of characters and states, refer to Lippitsch (1993). Characters that are not listed are either not applicable or not determinable in *Mahengechromis*, or the condition in *Mahengechromis* cannot clearly be allied with a single state based on the written descriptions.

1. Operculum - fully scaled (plesiomorphic)
2. Opercular scales - cycloid (plesiomorphic)
4. Suboperculum - fully scaled (plesiomorphic)
5. Subopercular scales - cycloid (plesiomorphic)
6. Interoperculum - fully scaled (plesiomorphic)
7. Interopercular scales - cycloid (plesiomorphic)
8. Preoperculum - fully scaled
9. Preopercular scales - cycloid
10. Cheek - fully scaled (plesiomorphic)
11. Cheek scales - cycloid (plesiomorphic)
13. Lacrimal - scaleless (plesiomorphic)
15. Occiput - fully scaled (plesiomorphic)
16. Scales on occiput - cycloid (plesiomorphic)

17. Size of occipital scales compared to dorsal scales - not significantly smaller (plesiomorphic)

18. Predorsal squamation pattern - uniserial (plesiomorphic)

19. Dorsum, rostrally - fully scaled (plesiomorphic)

20. Scales on dorsum, rostrally - cycloid (plesiomorphic)

21. Dorsum, caudally - fully scaled (plesiomorphic)

22. Scales on dorsum, caudally - moderately ctenoid (plesiomorphic)

23. Flank - fully scaled (plesiomorphic)

24. Flank scales - moderately ctenoid (plesiomorphic)

25. Flank scale overall form - ovoid, long axis vertical (plesiomorphic)

28. Form of granular area - sectorial (plesiomorphic)

29. Size of granular area - medium (90-150°)

30. Scale focus - free of granulation (plesiomorphic)

37. Region covered by pectoral fins - fully scaled (plesiomorphic)

38. Scales covered by pectoral fins - moderately ctenoid (plesiomorphic)

39. Caudal peduncle - fully scaled (plesiomorphic)

40. Scales on caudal peduncle (3) moderately ctenoid (plesiomorphic)

42. Chest laterally - fully scaled (plesiomorphic)

43. Scales on chest laterally - moderately ctenoid

44. Size of lateral chest scales compared to flank scales - not significantly smaller (plesiomorphic)

45. Transition from chest to flank scales - gradual (plesiomorphic)

46. Chest ventrally - fully scaled (plesiomorphic)

47. Scales on chest ventrally - moderately ctenoid

48. Size of ventral chest scales compared to flank scales - not significantly smaller (plesiomorphic)

49. Transition from ventral to lateral scales - gradual (plesiomorphic)

60. Dorsal fin - scaleless (plesiomorphic)

65. Caudal fin - partially scaled (plesiomorphic)

66. Scales on caudal fin - cycloid (plesiomorphic)

67. Caudal fin squamation pattern - oblong single row (plesiomorphic)

68. Anal fin - scaleless (plesiomorphic)

73. Pectoral fins - scaleless (plesiomorphic)

76. Pelvic fins - scaleless (plesiomorphic)

80. Lateral line - normal (plesiomorphic)

81. Lateral line - all scales perforated (plesiomorphic)

82. Lateral line scales - with channels or simple pores

83. lateral line of caudal fin - not present (plesiomorphic)

Connecting text

Most phylogenetic analyses of the family Cichlidae, or groups within the family, have been based on molecular data or features of soft anatomy that are not useful for characterizing fossil members of the family. In order to determine the relationships of the five species from Mahenge to other members of the family, osteological characters that are preserved in the fossils must be used. In the following chapter, an analysis of osteological characters is presented to test their usefulness in phylogenetic studies, and to determine the relationships of the Mahenge species within the Cichlidae.

CHAPTER 2

ANALYSIS OF OSTEOLOGICAL CHARACTERS AND RELATIONSHIPS OF *MAHENGECHROMIS* WITHIN THE CICHLIDAE

Introduction

Despite the many decades over which cichlid fishes have been studied, the relationships of these fishes are still not well resolved. The family Cichlidae has only recently been established as monophyletic (Gaemers, 1984; Kullander and Nijssen, 1989; Kaufman and Liem, 1982; Stiassny, 1991), with several characters proposed as synapomorphies for the family. Casciotta and Arratia (1993) summarized other authors and gave a list of ten cichlid synapomorphies:

1. The transversus dorsalis anterior muscle is subdivided into four sections.
2. There are separate A_2 and A_ω sections of the adductor mandibulae complex.
3. There is an extensive cartilaginous cap on the anterior border of the second epibranchial.
4. Microbranchiospines of a characteristic shape are present on the gill rakers.
5. The head of the fourth epibranchial is expanded.
6. There is an anterocaudal pseudocolliculum on the otolith sagitta having a long and thick ventral part which is separated from the crista inferior by a long, deep, and sharp furrow.
7. There is an extendible blind pouch of the stomach.
8. The anterior intestine exits on the left.
9. The first loop of the intestine is on the left side.
10. There is a "frayed zone," formed by one to seven shallow concavities, on the caudal margin of the fourth upper pharyngeal tooth plate.

Most of the phylogenetic analyses of part or all of the Cichlidae have used characters based on DNA or soft anatomy. Of the ten synapomorphies listed above, six relate to soft anatomy (numbers 1, 2, 4, 7, 8, and 9). Three of the rest (numbers 3, 5, and 10) relate to pharyngeal bones, including cartilaginous elements, which are located internal to the skull bones, and so, if present in fossil material, are not normally preserved in a position that allows examination of the character. Only one of the above synapomorphies, the otolith (number 6), is potentially useful for fossils, but none of the Mahenge cichlids have associated otoliths. Therefore, although the fossil material can be included in the family based on plesiomorphic characters or characters shared with other families (Chapter 1), not a single published synapomorphy can be used to identify the fossil material as belonging to the family Cichlidae.

Within the family, cichlids have been judged to be conservative in anatomy, with a diversity of external morphologies mainly associated with small changes in relative growth without major structural modification (Greenwood, 1974, 1984; Strauss, 1984; Stiassny, 1991). Moran et al. (1994) pointed out that the large amount of parallelism and the extensive radiation of species makes a cladistic analysis based on anatomical data difficult. However, they also noted that rapid species radiations has resulted in mtDNA analysis being as difficult as anatomical analysis. The level of genetic differences in mtDNA of some Lake Victoria cichlid species is as low as 3 base pairs among 803 examined (Meyer, et al., 1990). Moran et al. (1994) gave the differences among the haplochromine rock-dwelling mbuna species of Lake Malawi as 1% of the mtDNA, compared with 4% differences among populations of the centrarchid fish, *Lepomis punctatus*, in North America.

Previous phylogenetic analyses

The phylogenetic relationships of most genera within the Cichlidae are also unclear (Casciotta and Arratia, 1993). Several authors have published cladograms for the Cichlidae as a whole, or for lineages within the family. Five of these are shown in Figures 1 to 5. Lippitsch (1995: fig. 2) based her cladogram of the family predominantly on scale and squamation characters while Stiassny (1991: fig. 1.20) used a variety of anatomical characters, and Nishida (1991: fig. 3) used allozyme electrophoresis for the Tanganyikan lineages. Meyer, et al. (1994: fig. 4, 1996: fig. 6) used molecular data (predominantly mitochondrial DNA, but also nuclear DNA) for East African lineages. Unfortunately, the results from these studies are not directly comparable, as there is not complete overlap among the representative species or genera chosen for each study. Baum (1992) introduced a method for comparing trees that overlap by at least two taxa. Rather than creating a strict consensus tree, which leads to loss of resolution, the nodes from each tree are treated as a character. Clades within the node are coded as "1" and the other taxa are coded "0." Although Purvis (1995) later refined this method by restricting the "0" code only to the sister group and coding other taxa as missing data, the amount of missing data in this case caused the total number of possible trees generated to be greater than the computer programme could analyse. Therefore, Baum's method was used to create a composite of the five trees (Fig. 6), which represents our best approximation of the phylogeny of the Cichlidae based on the available data.

The composite tree shows the Madagascar and Indian genera as the basal groups in the family. Stiassny (1991) suggested that these cichlids may form a monophyletic group based on the unique excavation of the exoccipital bones; however, this character

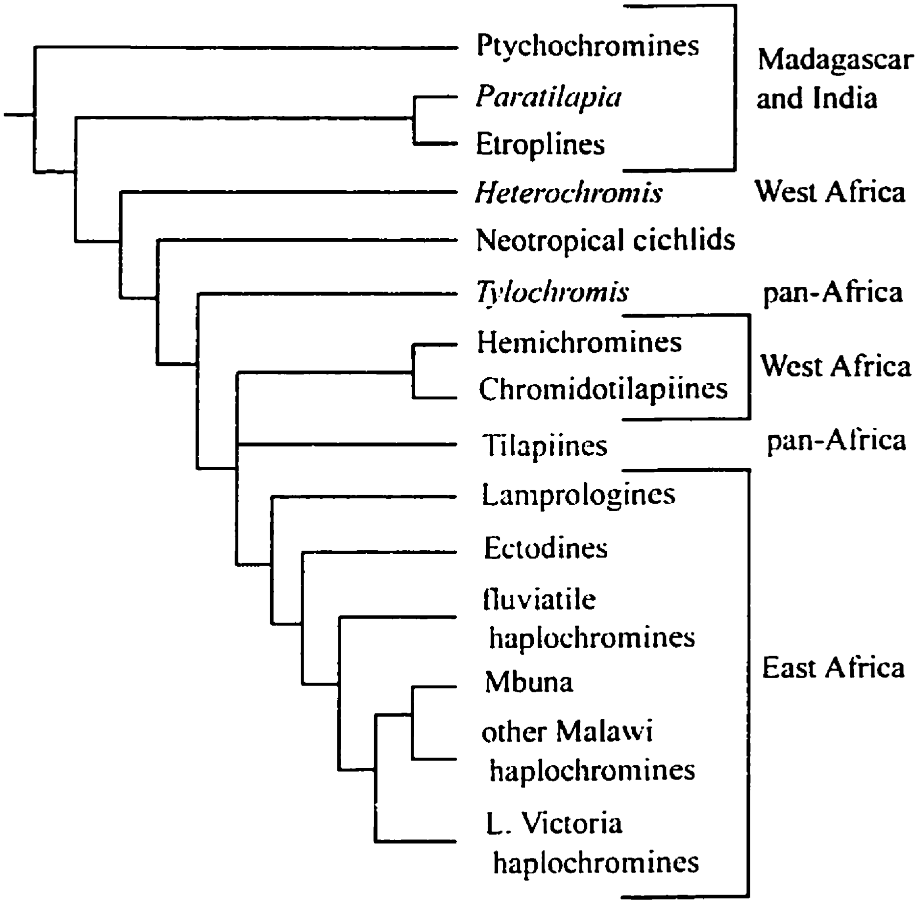

Figure 1. Cladogram of relationships for the Cichlidae. Redrawn from Lippitsch (1995: fig. 2).

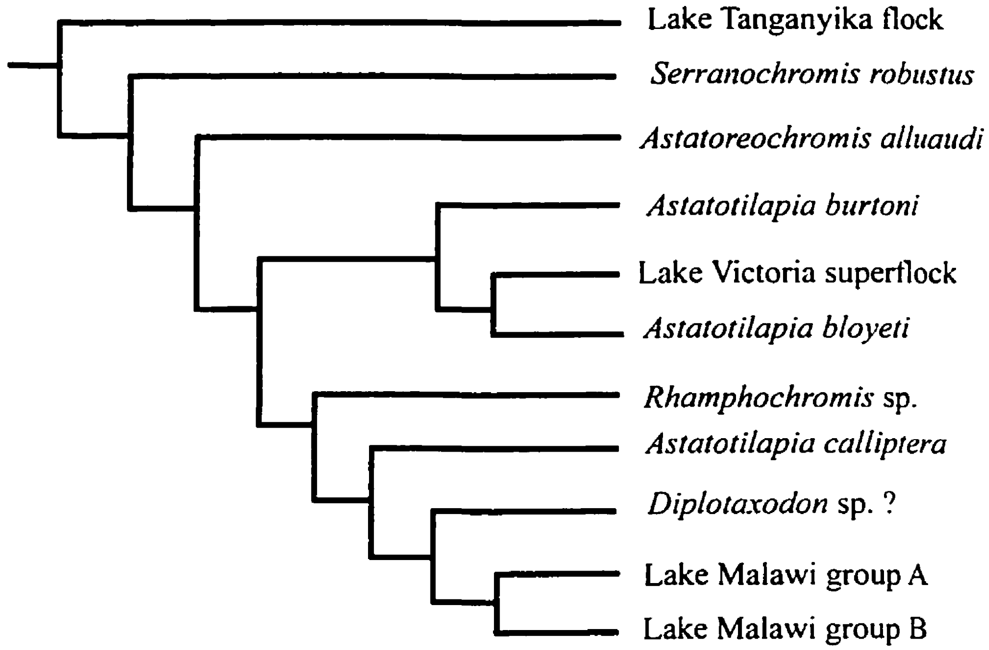

Figure 2. Cladogram of relationships for the East African Cichlidae. Redrawn from Meyer et al. (1996: fig. 6).

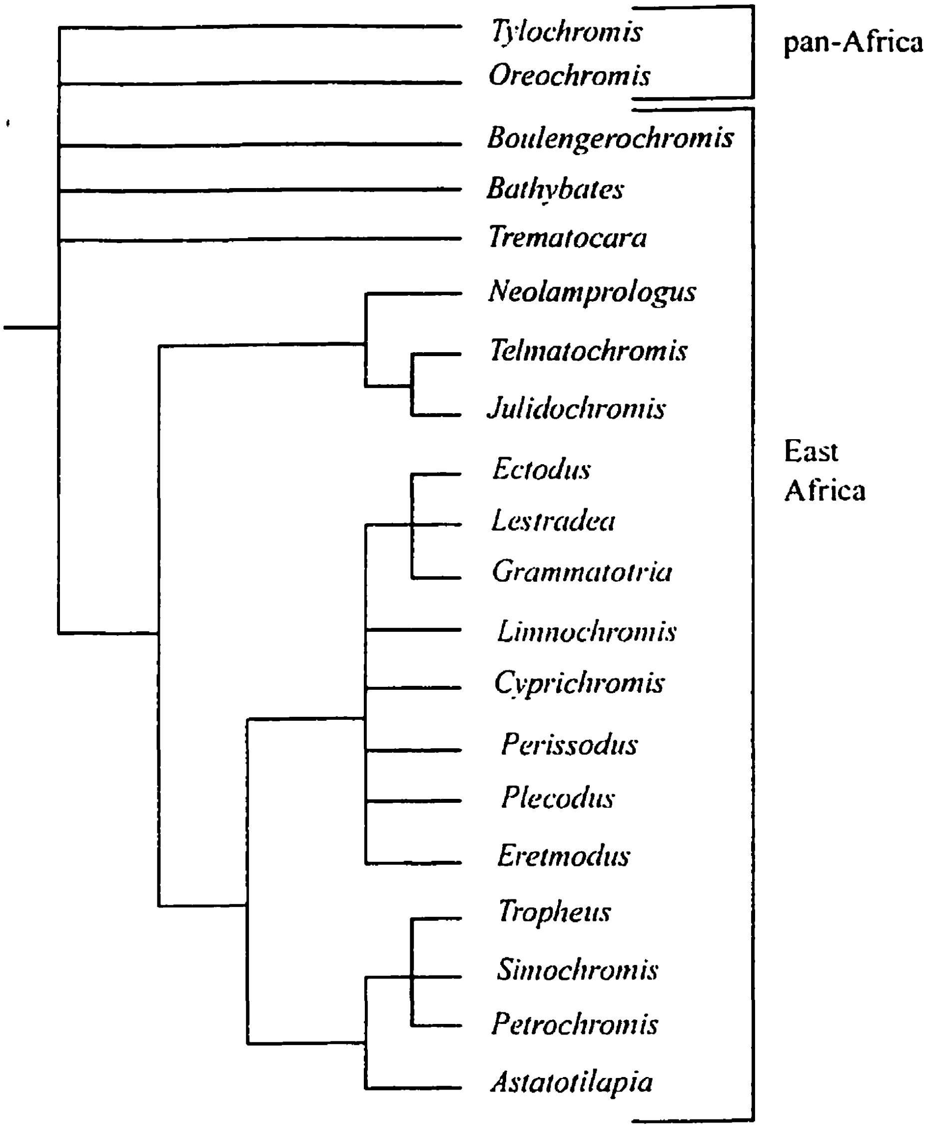

Figure 3. Cladogram of relationships for the Tanganyikan Cichlidae. Redrawn from Nishida (1991: fig. 3).

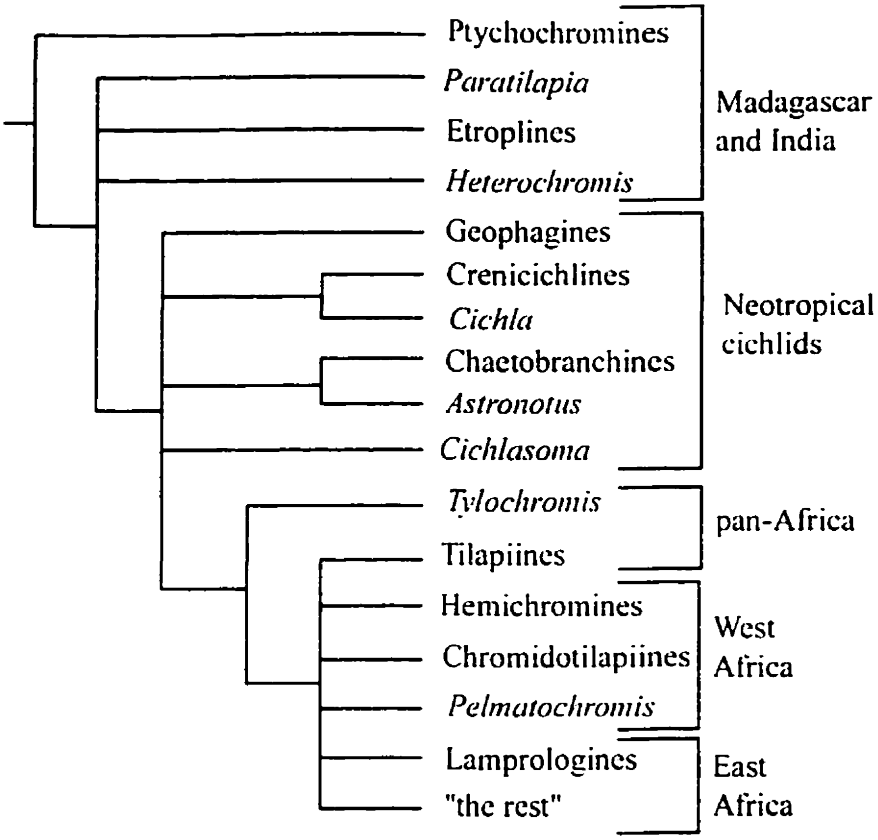

Figure 4. Cladogram of relationships for the Cichlidae. Redrawn from Stiassny (1991: fig. 1.20).

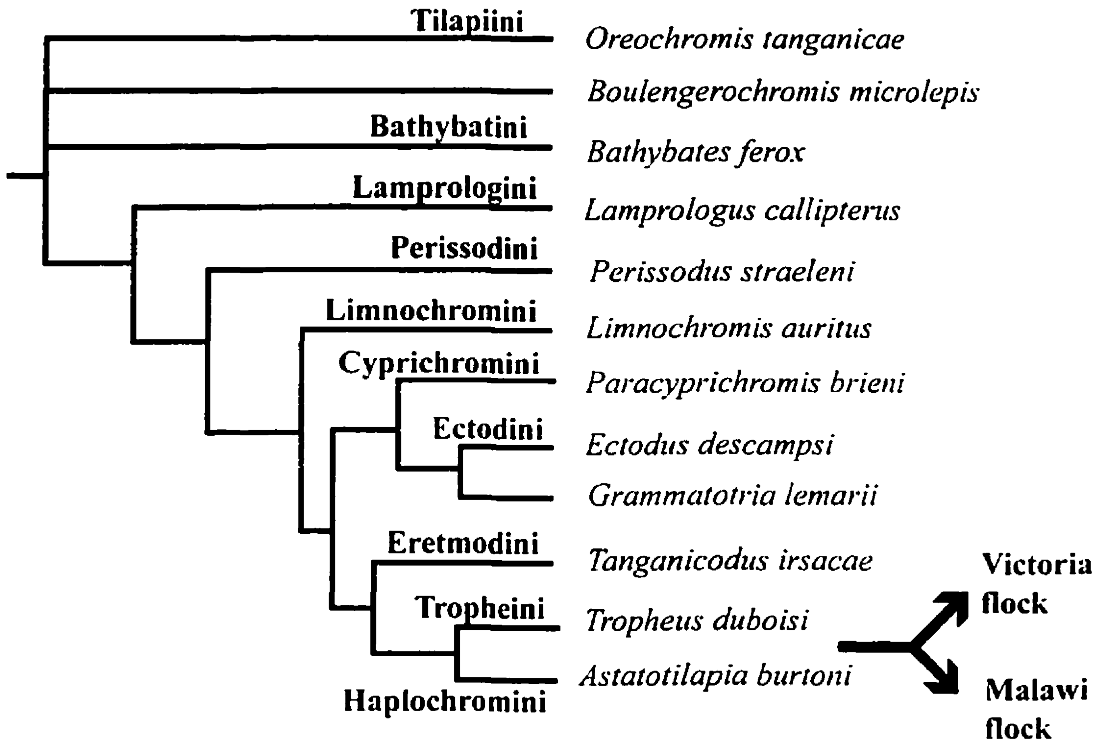

Figure 5. Cladogram of relationships for individual species of the East African Cichlidae, taken as representatives of major lineages. Redrawn from Meyer, et al. (1994: fig. 4).

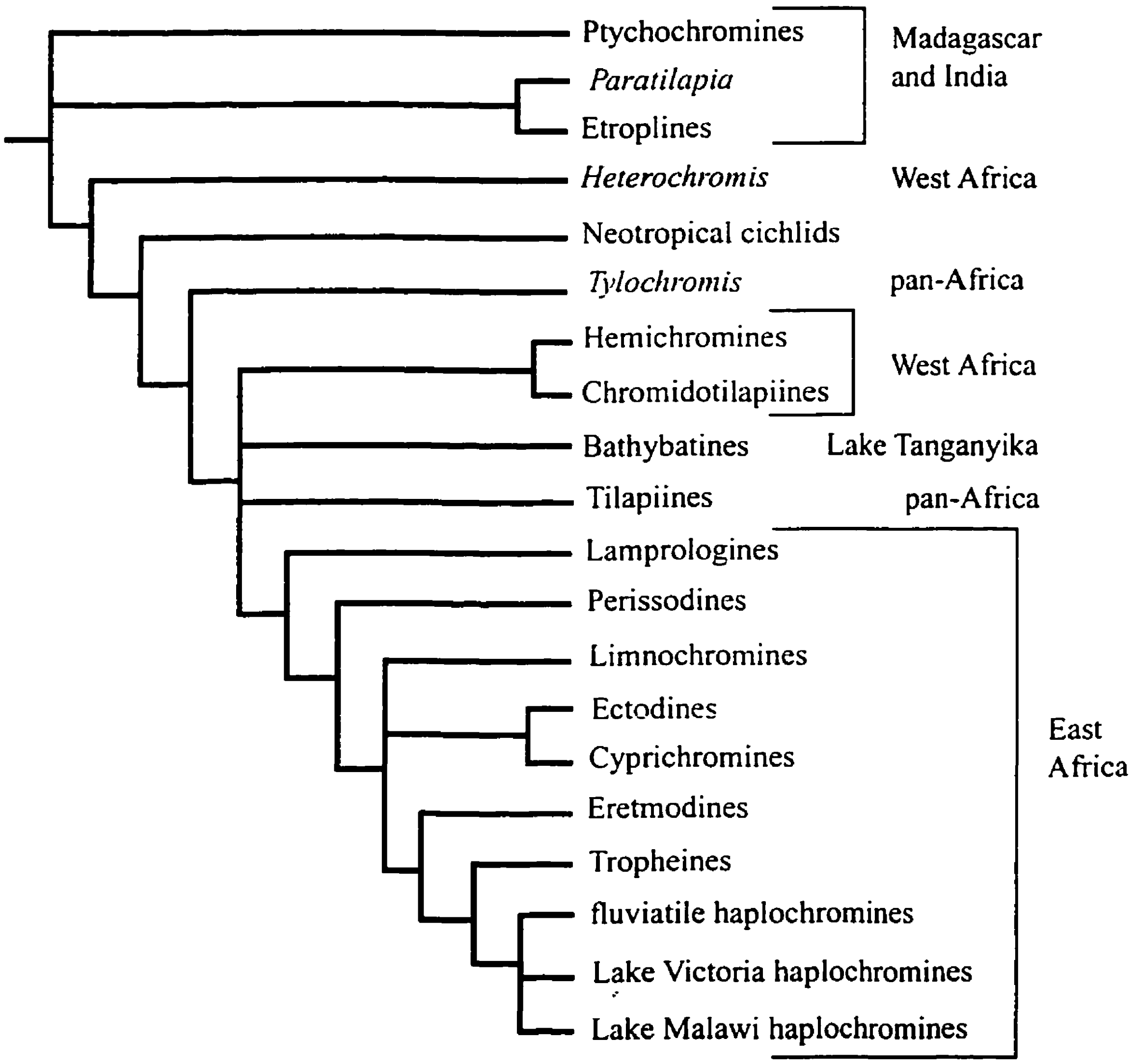

Figure 6. The composite tree of the family Cichlidae, based on Figures 1-5.

was interpreted as homoplastic in her cladistic analysis, and is still under investigation (Reinthal and Stiassny, 1997). Lippitsch's (1995) analysis grouped two of the lineages (the etroplines and paratilapiines) as a single monophyletic group. *Heterochromis*, from western Africa, is the sister group to the remainder of the family, comprising the Neotropical and African forms (Oliver, 1984; Stiassny, 1991). The monophyly of the Neotropical and African cichlids, excluding *Heterochromis*, is based on the presence of two derived character states, one of the pharyngobranchial apparatus, the second of the acoustico-lateralis system in the frontal bones. This second character, potentially visible in fossil material, relates to the positioning of the neurocranial lateral line foramen zero (nlf 0), and is discussed under the character descriptions below.

Stiassny (1991) suggested the Neotropical cichlids are monophyletic based upon a character of the vomer and parasphenoid. The Neotropical taxa examined by Stiassny have an interdigitating suture between these two bones; other cichlids and most other acanthomorph taxa have a straight suture. The exception is the African *Heterochromis*, which also has an interdigitating suture, but her analysis suggested that *Heterochromis* has independently evolved this character state. The remaining members of the family are placed in about 150 genera (with more than 980 species; Appendix A) - although this number changes regularly with new research. The majority of the African genera (well over 900 genera) are found in the Rift Lakes of East Africa. In the past decade, more than 130 new species of cichlids have been discovered in Lake Victoria alone, including previously unknown lineages, such as the mbibi, or rock cichlids (Seehausen et al, 1998). Many cichlid species are known that have yet to be formally described and named. The African cichlids (excluding *Heterochromis*) were considered by Stiassny (1991) to be monophyletic based on a suite of anatomical characters relating to the muscles and pharyngeal apparatus. Within this monophyletic group, the pan-African genus *Tylochromis* appears to be the sister group to the rest. The rest of the group has a single predorsal bone (instead of two) and possess a characteristic opercular spot.

Within the African cichlids, Meyer (1993), Meyer et al. (1996) and Moran et al. (1994) established relationships based on molecular work. Meyer et al. (1996) suggested that most of the Lake Malawi cichlids are monophyletic, and are represented by two species flocks which form the sister group to one another (group A and group B in Fig. 2). The rock dwelling cichlids of Lake Malawi (the mbuna) were found to be paraphyletic by Moran et al. (1994); however, a group including the mbuna (10 genera - see Appendix A) plus three other species (some from polyphyletic genera) form one monophyletic group within Lake Malawi. Most of the remaining non-mbuna can be grouped in the second clade of Moran et al (1994). Two species in Lake Malawi, *Rhamphochromis* sp. and *Serranochromis robustus*, are not part of this non-mbuna clade; *Rhamphochromis* sp. groups with the two flocks (predominantly-mbuna, and non-mbuna) and *Astatotilapia calliptera* (Meyer et al., 1994; Fig. 5) or is the sister to the two flocks plus *Copadichromis mloto, Diplotaxodon* sp. and *Astatotilapia calliptera* (Moran et al., 1994), while *Serranochromis robustus* is the sister group to all the species studied, from Lake Malawi and other lakes or rivers (Meyer et al., 1994), or forms a polytomy with the outgroups, *Tropheus moorei* and *Cyphotilapia frontosa*, from Lake Tanganyika (Moran et al., 1994). Meyer et al (1996) showed species of riverine cichlids forming the phylogenetic connections between the flocks of lakes Malawi and Victoria. The

Tropheini (of Lake Tanganyika) was considered by Meyer et al. (1994) to be closely related to the Lake Victoria and Malawi haplochromines (Fig. 5).

The Lake Victoria cichlids are also considered to be monophyletic and form a "super flock" with the addition of species in the Lake Victoria basin (including lakes George, Edward and Kivu) (Meyer, et al., 1996). *Astatotilapia* is a polyphyletic genus, with one species being closer to the Malawi cichlids, and two other species closer to the Victoria cichlids, and *Copadichromis* is also considered polyphyletic (Moran et al., 1994).

Use of Skeletal Characters in Classification

Clearly, the relationships of fossil members of the Cichlidae cannot be determined based on molecular and soft anatomy characters. In order to assess the relationships of *Mahengechromis* within the family, characters must be found that are specifically relevant to fossil material. Few such characters are known. Two previously identified characters, the pattern of the frontal canal pores on the skull roof and the number of predorsal bones, along with a suite of scale and squamation characters, conflict when included in the composite tree. Based on the pattern of the canal pores of the skull roof, the Mahenge cichlids are placed with the primitive cichlids (Fig. 7, position A). *Mahengechromis* has a single predorsal bone, which would place it within the African cichlids excluding *Heterochromis* and *Tylochromis* (Fig. 7, position B). Based on the possession and pattern of ctenoid scales (Lippitsch, 1995), *Mahengechromis* is placed in a polytomy with the lineages of the Great Lakes (Fig. 7, position C).

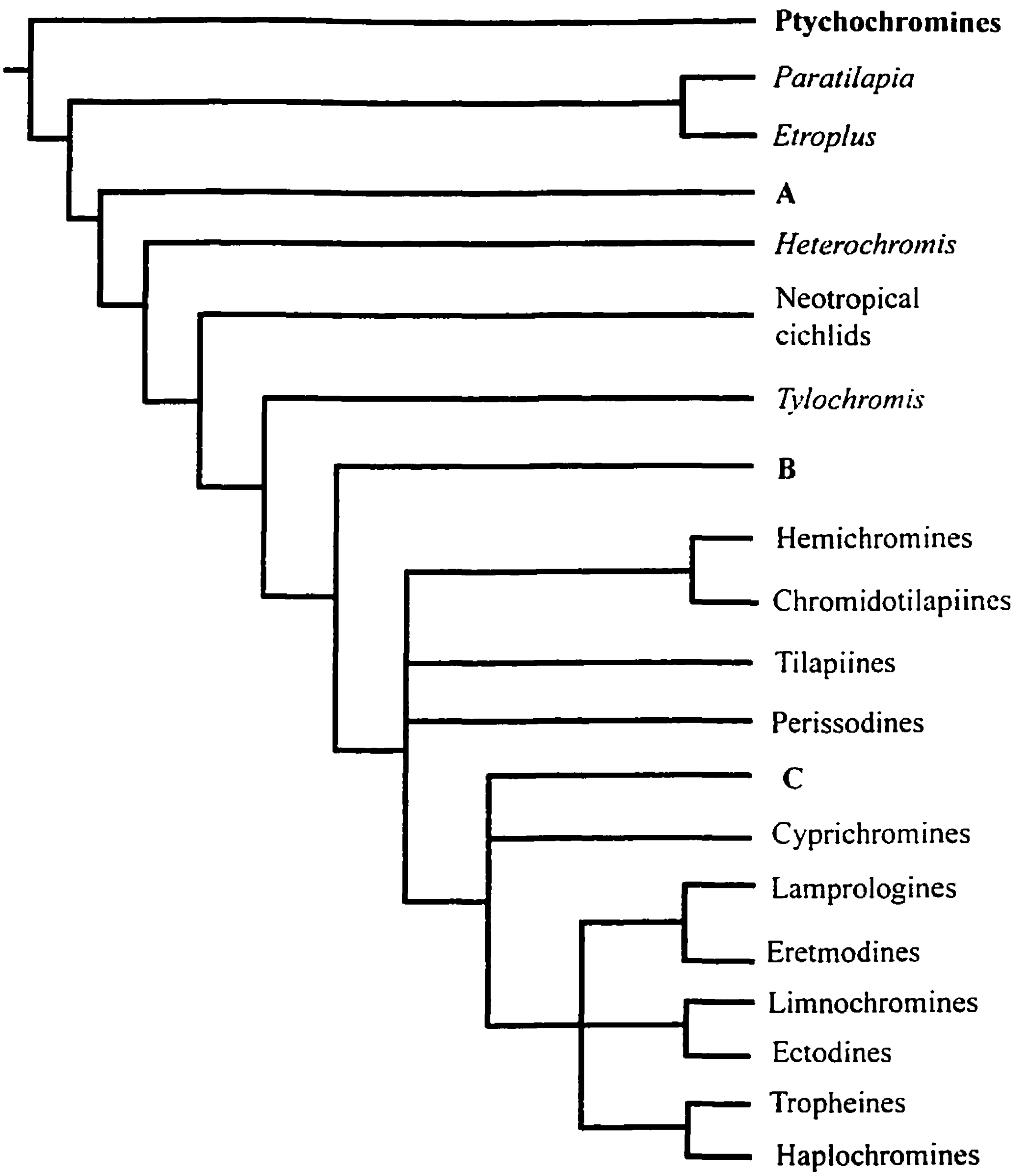

Figure 7. Different placements of *Mahengechromis* within the composite tree of the Cichlidae. Position A. based on the pattern of the frontal canal pores. Position B. based on the number of predorsal bones. Position C. based on scale and squamation characters.

Anatomical data have been frequently regarded as uninformative for phylogenetic studies of cichlids, but this may be because studies have concentrated on the feeding apparatus, particularly teeth, with little attention to other features (with notable exceptions being the theses of Cichocki, 1976, and Oliver, 1984). Reinthal (1990) analysed the mbuna (rock-dwelling cichlids) of Lake Malawi on the basis of a principal components analysis of measurements of the neurocranium, and suggested that the morphological variations were associated with heterochronic changes in relative growth rates and correlated with trophic habits. Nevertheless, some anatomical characters that were used for cichlid systematics (Trewavas, 1983) have been supported by molecular data (Seyoum, 1989).

In order to test the usefulness of osteological characters for a phylogenetic analysis of the Cichlidae, the result of an analysis of osteological characters should be compared with the composite tree (Fig. 6) based on non-osteological characters. The degree of congruence between the composite tree and the result of this study can be considered an indicator of the usefulness of osteological characters. In order to discover the relationships of *Mahengechromis*, the osteological data can be integrated with the topology of the composite tree, with manipulation of tree branches to find the most parsimonious placement for the fossil cichlids.

Material and Methods

Comparative osteological material was chosen from as many cichlid lineages as available. It was not possible to borrow specimens of many representative genera of African cichlids, or any of the forms from Madagascar, although loans were requested from museums with cichlid collections. Although the state of the characters is unknown for the majority of 1400 or more cichlid species, the representative cichlids included in this analysis are from a variety of lineages that complement information on other genera from the literature. These data can therefore provide a beginning step for future investigations with additional species.

Representative Recent species (Appendix B) were cleared and stained following the procedure of Taylor and Van Dyke (1985), or skeletonized by boiling. Pharyngeal characters were used by Greenwood (1980) to revise some of the Lake Victoria *Haplochromis* into several new genera (Appendix C); however, the species he studied have a range of morphologies (morphoclines) that overlap one another (Van Oijen, 1996). Greenwood's (1980) generic names, criticized by many authors and not in wide use, are not being used formally here. All of these genera are considered to be "*Haplochromis*" following Van Oijen (1996), but the generic name used by Greenwood is inserted in square brackets in the following text and list of comparative material in Appendix B (e.g. *Haplochromis* [*Yssichromis*] sp.) to indicate that these are not formal subgeneric names while allowing correlation with those authors who have used Greenwood's generic names (e.g. Lippitsch, 1997).

All specimens were examined for osteological differences that could be coded for use in a cladistic analysis, in which shared derived characters are used to infer relationships. The data set (Appendix D) was compiled in MacClade 3.05 and run using P.A.U.P. 3.1.1. Four characters (numbers 1, 8, 25, and 37) were set as ordered, as they are counts. For example, in order to change from three to one predorsal bones, it is assumed that the character evolved through a stage involving two predorsal bones.

Character 2 could be intuitively ordered, but when the data matrix was analysed with this character ordered, 909 shortest trees were generated, with little resolution. Therefore it has therefore been left as unordered. The other characters are either binary or could not be ordered definitively, and so were left unordered. The "all-zero" outgroup was compiled based on examined non-cichlid labroid material and from the literature. An heuristic search was run in P.A.U.P., with the outgroup defined and the ingroup set as monophyletic. A bootstrap analysis of the data set was run in order to test the stability of clades within the family. It was set at 100 iterations with minimum support for clades limited to 50%.

Character descriptions

Three theses have previously sought to determine the relationships of cichlids using at least some osteological characters. Newsome (1971) concentrated on South American genera. Her osteological characters were chosen from the bones of the neurocranium, branchiocranium, pectoral and pelvic girdles and caudal skeleton. She concluded (1971:257) that "the variations [in characters] are inconsistent and do not show distinct patterns" and (p. 279) that the fifteen taxa examined "are morphologically uniform" and "show few useful characters." Cichocki (1976) was the first to identify the Madagascan and Asian cichlids as the most primitive lineages. He concentrated particularly on the Neotropical genera, but included species from Madagascar, Asia and Africa. Of the sixty-two characters identified by Cichocki (1976) more than half are osteological. The third thesis is that of Oliver (1984), who, although noting the importance of the characters found by Cichocki (1976), discussed why the techniques used for reconstructing relationships in the latter do not represent a true phylogenetic analysis. Oliver (1984) identified *Heterochromis multidens* as the most primitive African genus. He examined African cichlids, particularly those of Lake Malawi, to investigate morphological evidence of cichlid monophyly and monophyly of the lineages within Lake Malawi.

The characters identified in these three theses have been examined by later authors. Newsome's work has been criticized because of her assumption that *Cichla* was a primitive genus, based on her interpretation of the specimen as having a double nostril when the nostril is actually single, and some relationships were made with inadequate justification (Cichocki, 1976: p. 176). Several of Cichocki's characters were examined by Stiassny (1991) and found to have merit, although some were modified by her. Kullander (1998) used characters in original or modified form from both Cichocki's and Oliver's theses for his phylogeny of South American cichlids. Unfortunately, few of Oliver's characters are related to osteology, and many of Cichocki's osteological characters are proportional angles or relative measurements. The latter are less useful for fossil material, which may not be preserved in a manner allowing such measurements, or may be distorted in preservation. Nevertheless, some characters from the theses are potentially useful in phylogenetic analysis of fossils, and are discussed below.

Another source of osteological characters used in a phylogenetic analysis of cichlids is Kullander's (1998) paper on South American members of the family. Of the ninety-one characters that Kullander lists, some are from other authors already mentioned (e.g. Cichocki, 1976; Stiassny, 1991), and some are features of soft anatomy or are not applicable to the fossil material from Mahenge. Other characters from Kullander (1998), and Casciotta and Arratia (1993) that are potentially useful for discerning the relationships of *Mahengechromis* have been included in the current analysis.

Each character is discussed below with its distribution among the specimens noted. Characters that are not explicitly identified as coming from another source, are those that were found by examination of the fossils and comparative material.

1. The number of predorsal (= supraneural) bones. Stiassny (1991) and Cichocki (1976) considered the primitive number of predorsal bones for the Cichlidae to be two (character state 0), which among the African cichlids occurs in *Heterochromis* and *Tylochromis*. The reduction to a single predorsal bone (state 1) is considered to be a synapomorphy uniting the African cichlids excluding these two genera. Stiassny (1991) noted that a similar reduction in number of predorsal bones occurs in the Neotropical cichlids. The Mahenge cichlids have a single predorsal bone.

2. The pattern of the median frontal pores. The sensory canal pores on the frontal bones (nfl 0, see Stiassny, 1991) occur in several different patterns. The primitive pattern (coded as state 0) is considered to be that of the Madagascan genus *Ptychochromis*, in which the left and right canals remain separated, and there is a pore for each side (Stiassny, 1991; Casciotta and Arratia, 1993). A second pattern (state 1) is that of the left and right canals each bearing a pore, but the pores are apposed at the midline. Stiassny (1991) considered this to be the condition in *Paratilapia, Heterochromis* and *Etroplus*; however, Casciotta and Arratia (1993) considered *Etroplus* and *Paretroplus* to have a different pattern, in which the left and right canals join at the midline, but the pores are absent. The pattern considered common for most cichlids (Casciotta and Arratia, 1993)

is the condition in which the left and right canals join in the midline and extend anteriorly as a short canal bearing the single median pore at its tip (state 3). Specimens of tilapiines examined (e.g. *Tilapia*) show this condition clearly (Fig. 8 A). In the haplochromines (e.g. *Haplochromis* [*Prognathochromis*], Fig. 8 B), there is a single pore facing anteriorly, but a median canal, if present, is short and not distinct (coded as state 2). Kullander (1998) listed *Ptychochromis* and *Biotoecus* as the only cichlids with separate median frontal lateralis canal openings, similar to the general percoid condition. He stated that all other cichlids had a single median opening. In the South American cichlid *Biotoecus*, the condition was considered to be derived and correlated with the small size of the species and a reduced lateralis system. *Iranocichla* also has separate pores that are apposed at the midline (Fig. 8 C). This is the same condition as found in *Copadichromis*, however, the examined specimens are juveniles, about 2 cm standard length. The pattern of the canal pores seems to change with growth. The Mahenge cichlids, of presumed adult size (Fig. 8 D), have the primitive state of left and right median pores separated.

3. Supraoccipital crest. Stiassny (1991) also noted that in some genera (*Etroplus, Paretroplus* and *Heterochromis*) the supraoccipital bone lies over the nfl 0 pores. This is considered to be the derived condition, coded as character state 1. In all other taxa she examined, including *Oxylapia*, the anterior margin of the supraoccipital lies posterior to the nfl 0 pores (state 0). In *Mahengechromis*, the supraoccipital does not cover the pore.

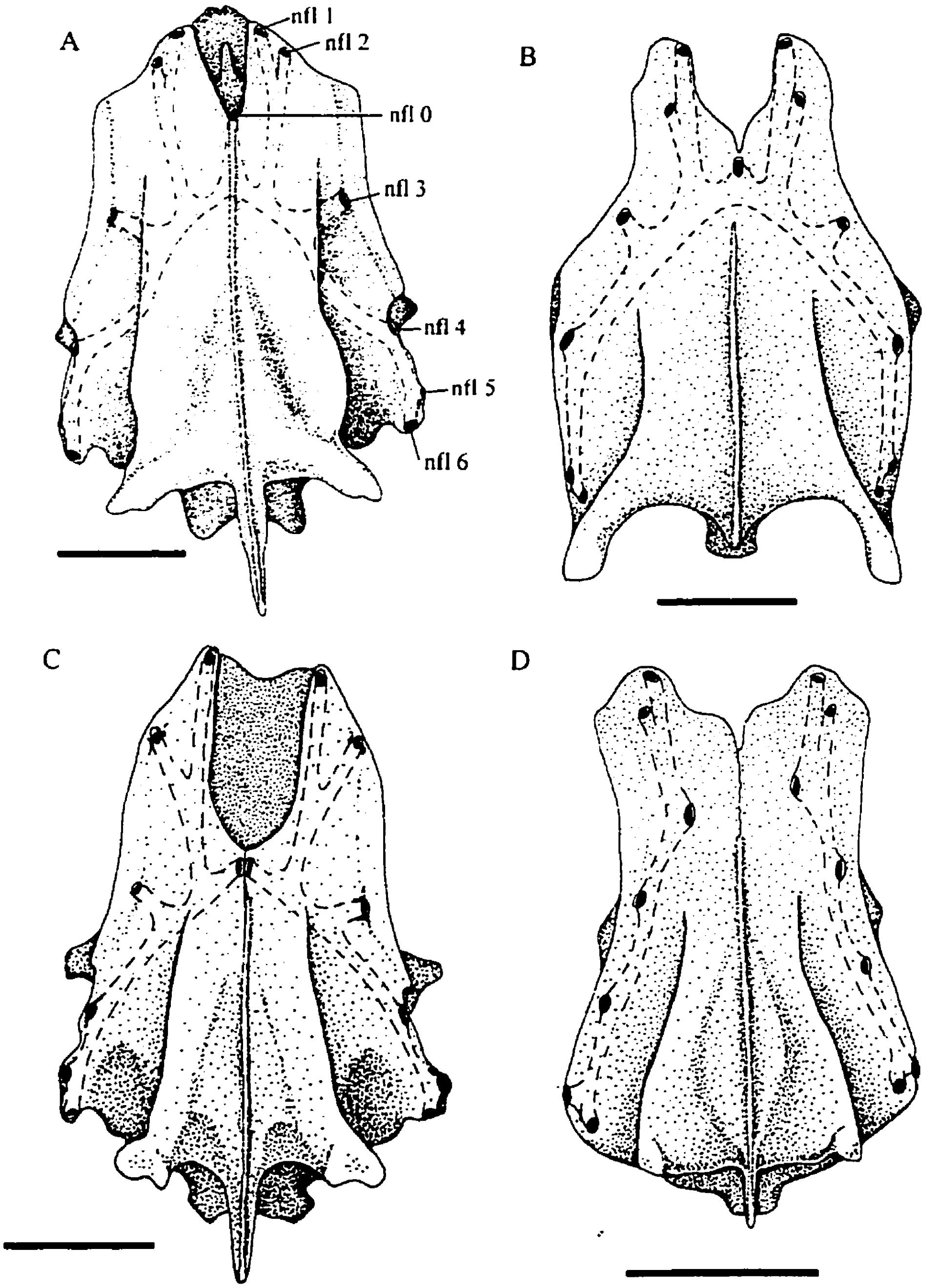

Figure 8. Dorsal skull of representative cichlids showing the pattern of the sensory canals and pores. A. *Tilapia zillii*, CMN uncatalogued; B. *Haplochromis* [*Prognathochromis*], NMC 81-0266; C. *Iranocichla hormuzensis*, NMC 79-0142; D. *Mahengechromis curvifrons*, WM 541/96. Scale bars = 5 mm.

Characters relating to the pectoral girdle (Fig. 9) have not been noted by other authors. These bones vary among species, and therefore may potentially provide useful characters.

4. The posteroventral corner of the dorsal plate of the cleithrum. The cleithrum has a small process at the posteroventral corner of the dorsal plate which in most species is developed as a rounded bump (Fig. 9 A, B). This is coded as the primitive condition (state 0). The process appears is absent in *Iranocichla* (an autapomorphy, state 2), whereas *Tropheus* (Fig. 9 C), *Lamprologus* and *Rhamphochromis* all have a distinctly square process (coded as state 1).

5. The position of the four pectoral fin radials on the scapula and coracoid. Most of the species (Fig. 9 A, B) have either three radials on the scapula and one on the coracoid, or the coracoid and cartilage (coded as state 0). *Tropheus* (Fig. 9 C) has all four radials supported on the scapula (derived state 1). Other cichlids have one or two radials on the scapula and the other two straddle the cartilage and bones (derived state 2, Fig. 9 B). *Mahengechromis* (Fig. 9 D, E) have state zero.

6. The connection between the coracoid and scapula. In most of the specimens examined, the coracoid and scapula are separated by cartilage, considered the primitive state (zero). In three species (*Haplochromis* [*Yssichromis*], *H.* [*Psammochromis*] and *H.* [*Lipochromis*]) the two bones have an interdigitating bony suture between them (Fig. 9 B). These have been coded as state 1. *Mahengechromis* specimens with the scapula and coracoid preserved have no suture between the two, and the position of the bones indicates that cartilage would have been present between them.

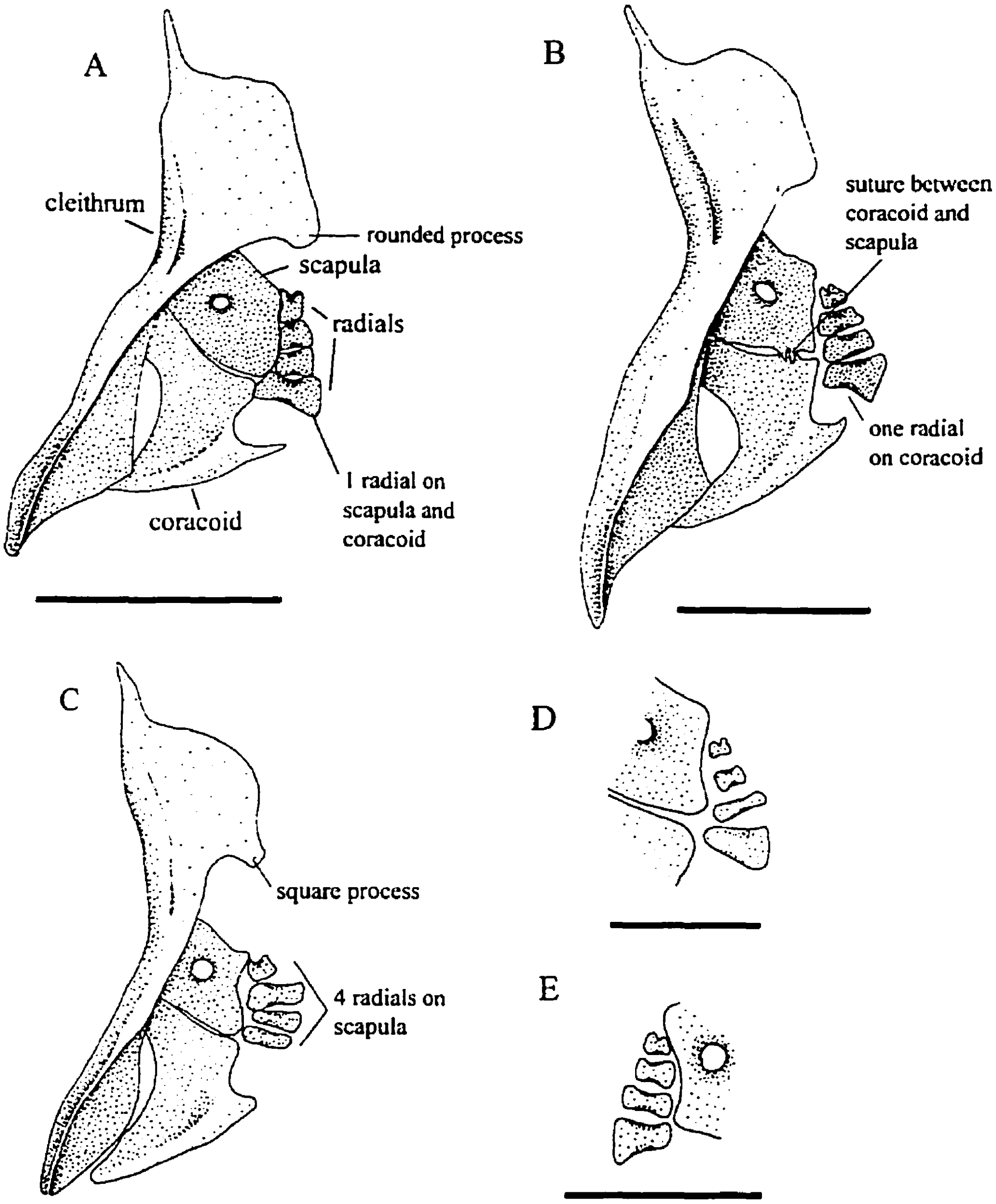

Figure 9. Left pectoral girdles in lateral view of representative cichlids. A. *Pelviachromis* sp., CMN uncatalogued; B. *Haplochromis* [*Yssichromis*], NMC 81-0266; C. *Tropheus moorei*, USNM 191512; D. left pectoral radials and part of scapula and coracoid, *Mahengechromis ellipticus*, WM 045/96; E. right pectoral radials and part of scapula, *Mahengechromis plethos*, WM 374/96. Scale bars = 5 mm.

The number of sensory canal pores on the preopercle have been noted by several authors, but other characters of bones of the opercular series (Fig. 10), such as the opercle and interopercle, have not been discussed.

7. The shape of the dorsal edge of opercle above the level of the hyomandibular facet. In *Hemichromis* (Fig. 10 A) about one quarter of the height of the opercle is dorsal to the facet for articulation with the hyomandibula (state 0). In *Tilapia* (Fig. 10 B) this is reduced (derived state 1) to about one eighth and in *Oreochromis* the dorsal edge is horizontal from the facet. In haplochromines (Fig. 10 C, D), only the posterodorsal portion of the opercle is developed dorsally above the level of the facet for articulation with the hyomandibula, and the whole dorsal edge is arched. This has been coded as derived state 2. *Mahengechromis* is similar to *Hemichromis*.

8. The number of preopercular canal pores. Kullander (1998) considered seven pores on the preopercular bone to be ancestral,and ubiquitous in Old World cichlids and found in a few Neotropical taxa, therefore it has been given the primitive state, zero. Stiassny (1991) noted the Madagascan, Asian and all African taxa have a seven-pore pattern (Fig. 10), whereas the Neotropical cichlids, with the exceptions of *Cichla*, *Astronotus*, *Retroculus* and chaetobranchines, have a six pore pattern, which is considered derived (state 1). *Mahengechromis* has seven pores on the preopercular bone. The derived state of six pores is found only in the Neotropical cichlids, and the second derived state (2) of five pores is found only in *Heterochromis* in this study.

9. The shape of the interopercle anterior edge. The interopercular bone in most of the examined material (Fig. 10) has a deep notch at the anterior end (state 0), into which a

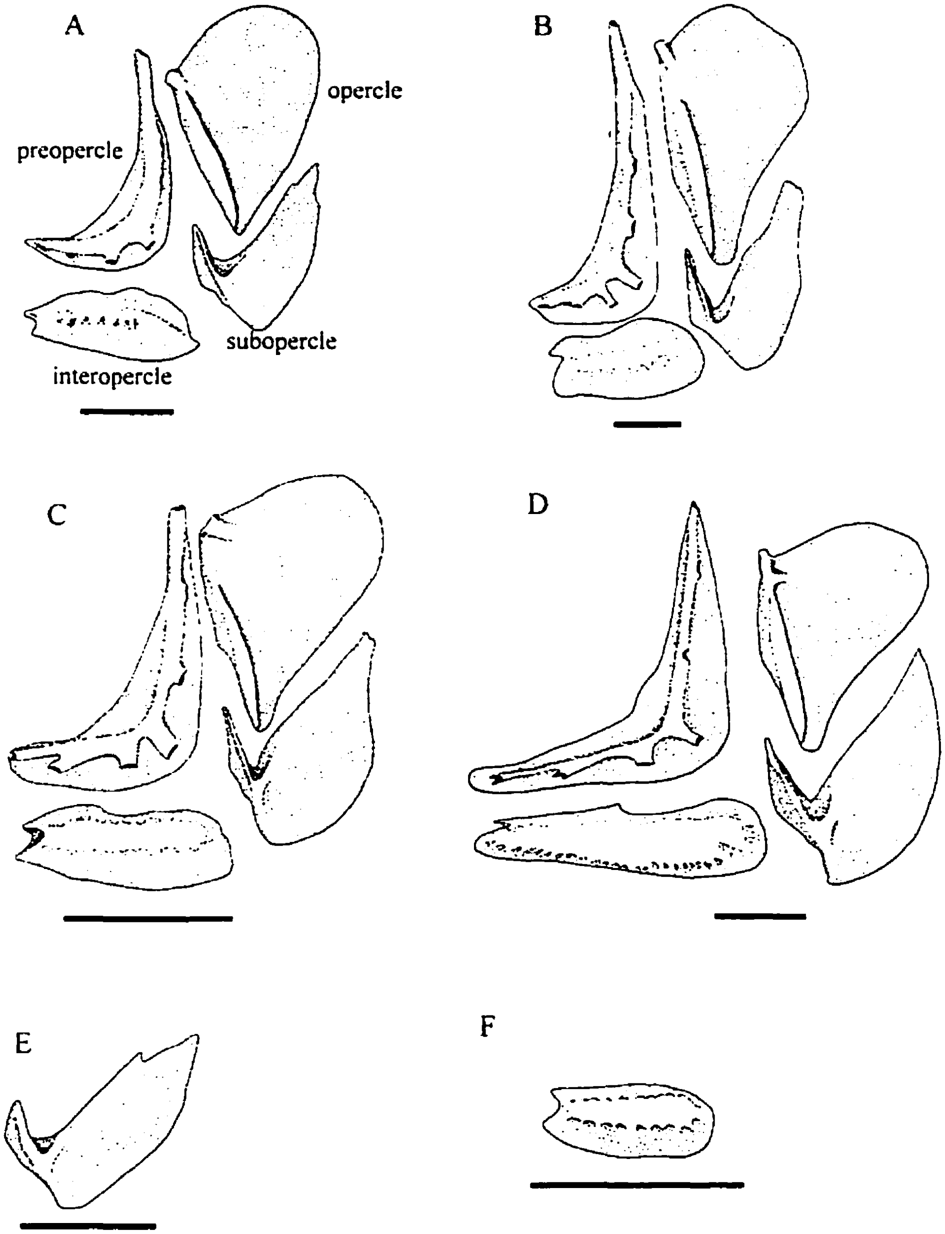

Figure 10. Left opercular bones in lateral view of representative cichlids. A. *Hemichromis* sp. CMN uncatalogued; B. *Tilapia zillii*, CMN uncatalogued; C. *Astatotilapia bloyeti*, NMC 81-0195; D. *Rhamphochromis* sp., USNM 280070; E. left subopercle of *Mahengechromis brachycranium*, WM 175/96; and F. right interopercle (reversed) of *Mahengechromis plethos*, WM 374/96a. Scale bars = 5 mm.

ligament inserts. The Neotropical *Symphysodon*, and African *Lamprologus* lack the notch (coded as state 1). *Mahengechromis* has a deep notch.

10. Shape of the interopercular bone. Most cichlids examine, including *Mahengechromis*, have a roughly oval shaped interopercle (state 0), however in *Rhamphochromis* (Fig. 10 D), *Tropheus*, and *Lamprologus*, the bone is long and narrow (state 1). The lengthening of the bone in *Rhamphochromis* is probably related to the piscivorous habitat, associated with a streamlining of the body.

11. The shape of the posteroventral edge of the opercular bone. In *Mahengechromis* the posteroventral edge of the opercle varies among the species, from convex through concave. In *Hemichromis*, the posteroventral edge of opercle is straight or slightly convex (Fig. 10 A) whereas in most of the other species examined (Figs. 10 B, C, D), it is concave. States were assigned randomly with state 0 = convex, state 1 = straight and state 2 = concave.

The posttemporal bone and supracleithrum (Fig. 11) also vary considerably among the cichlids examined, and so were included in the analysis.

12. The relative lengths of the dorsal and ventral limbs of the posttemporal bone. The ventral limb of the posttemporal bone in most specimens examined is similar in size to the dorsal limb (coded as state 0). In *Iranocichla*, *Tropheus* (Fig. 11 D) and *Mahengechromis* the ventral limb is distinctly shorter than the dorsal limb (state 1).

13. The shape of the posterior portion of the posttemporal bone. In the majority of species, including *Mahengechromis*, the posterior portion of the posttemporal bone has a tripartite form because of the distinct posterior projection which bears the sensory canal

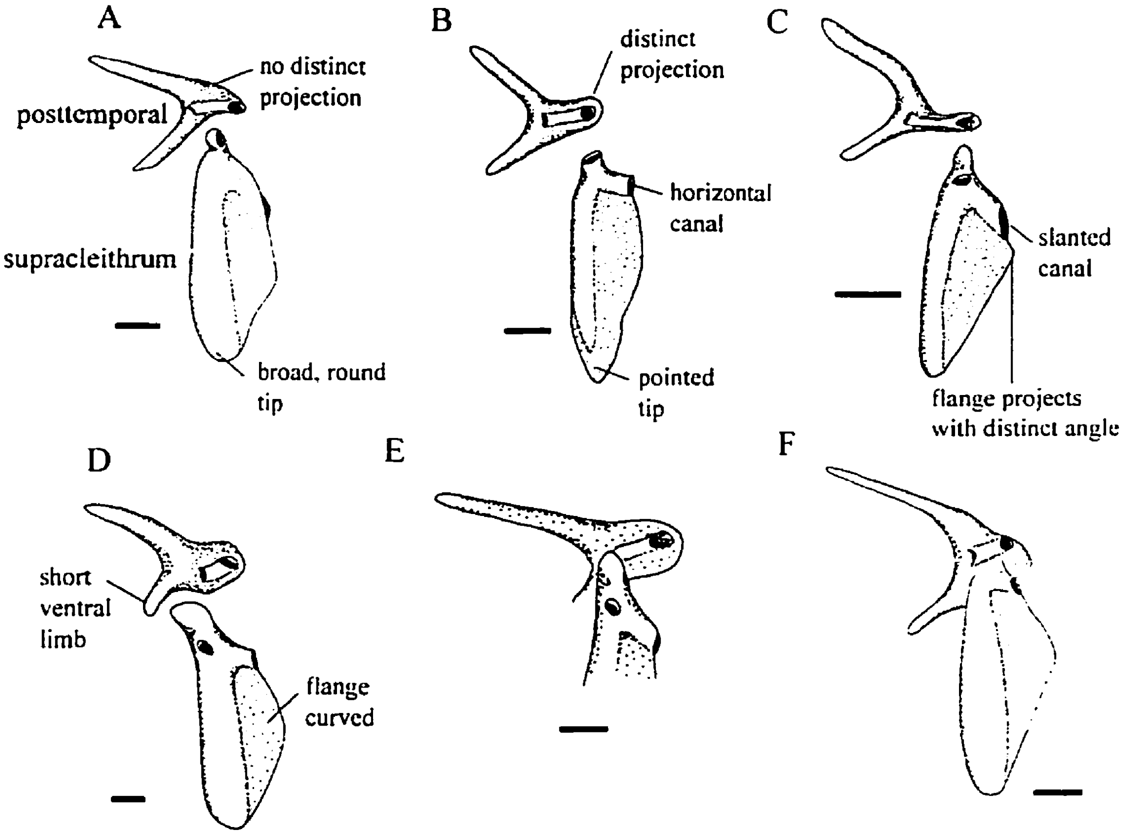

Figure 11. Left posttemporal bones and supracleithra in lateral view of representative cichlids. A. *Hemichromis* sp. CMN uncatalogued; B. *Pelviachromis* sp. CMN uncatalogued; C. *Astatotilapia bloyeti*, NMC 81-0195; D. *Tropheus moorei*, USNM 191512; E. *Mahengechromis rotundus*, WM 019/96; F. *Mahengechromis plethos*, WM 474/96. Scale bars = 1 mm.

(Fig. 11 B, C, D). This has been coded as primitive, state 0. In *Iranocichla, Hemichromis* (Fig. 11 A) and *Tilapia*, there is no distinct projection (state 1).

14. The position of the posterior canal and pore on the supracleithrum. The sensory canal on the supracleithrum in the majority of species (and therefore coded as state 0) is slanted (Fig. 11 C), as in *Mahengechromis*, with the posterior pore ventrally located. In several species the canal runs horizontally (state 1; Fig. 11 B).

15. The shape of the ventral tip of the supracleithrum. Ventrally, the supracleithrum in most examined specimens is broad and rounded (state 0; Fig. 11 A). *Symphysodon* has a pointed ventral tip, as does *Pelviachromis* (state 1; Fig. 11 B). The tip of the supracleithrum is not visible in *Mahengechromis* specimens.

16. The shape of the posterior edge of the supracleithrum. Posteriorly, the flange of the supracleithrum below the posterior sensory canal pore either has a distinct angle after projecting posteriorly past the pore (state 0; Fig. 11 C). (Fig. 11 D), or the flange is curved ventral to the pore (state 1). The latter is found in *Mahengechromis*.

The urohyal (Fig. 12) in cichlids usually bears a dorsal spine on which part of the pharyngohyoideus muscle inserts (Stiassny, 1982). The urohyal spine has been used as a character, particularly in analyses of the Neotropical cichlids, although other aspects of the bone have not been discussed.

17. Anterodorsal projection on the urohyal. Stiassny (1987) noted that the urohyal spine is rostrally directed in a Neotropical clade composed of *Cichla* + *Crenicichla* + *Teleocichla*, the latter of which has a vestigial spine interpreted as a secondary reduction. Kullander (1998) coded the spine being posteriorly or dorsally directed as the primitive

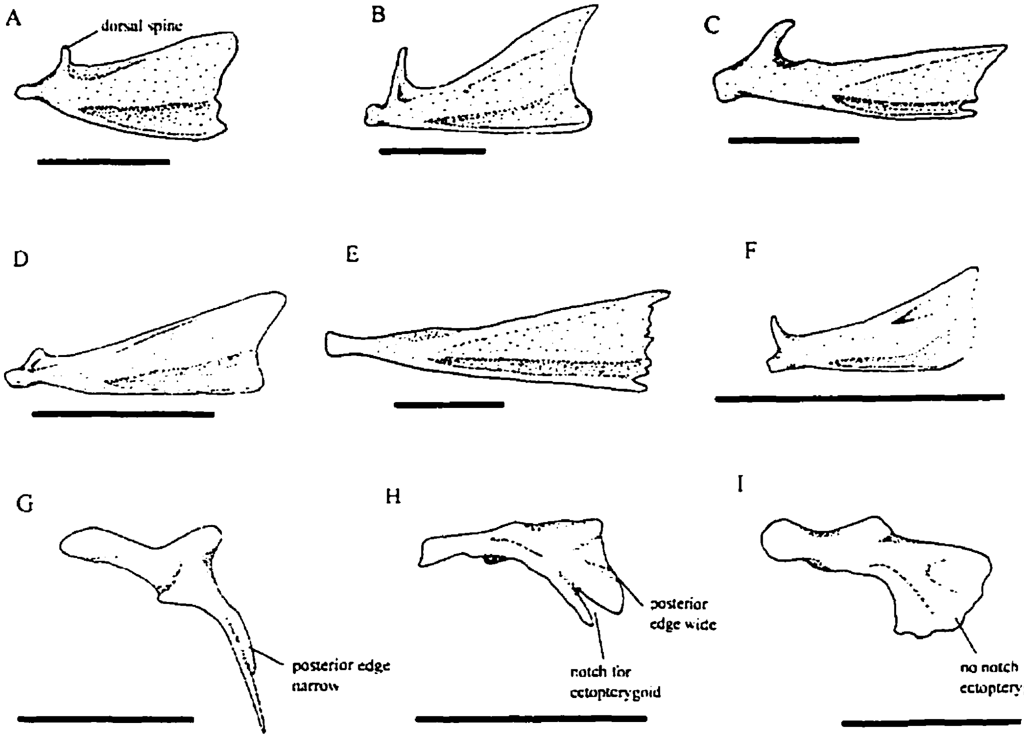

Figure 12. Urohyals (A to F) and left palatine bones (G to I) in left lateral view of representative cichlids. A. *Hemichromis* sp., CMN uncatalogued; B. *Tilapia zillii*, CMN uncatalogued; C. *Iranocichla hormuzensis*, NMC 79-0142; D. *Haplochromis* [*Yssichromis*], NMC 81-0266; E. *Rhamphochromis* sp., USNM 280070; F. *Mahengechromis ellipticus*, WM 045/96; G. *Hemichromis* sp., CMN uncatalogued; H. *Pseudotropheus* sp., CMN uncatalogued; I. *Iranocichla hormuzensis*, NMC 79-0142. Scale bars = 5 mm.

state (at least for Neotropical cichlids). In this analysis, the character was separated into five states: spine a low rounded projection (state 0; Fig. 12 D), spine oriented dorsally (state 1; Fig. 12 A, B), spine oriented anteriorly (state 2), spine directed posteriorly (state 3; Fig. 12 C), and absence a distinct spine (state 4; Fig. 12 E). In *Mahengechromis*, the spine is dorsally directed (Fig. 12 F). States were randomly assigned.

18. The depth of the urohyal just posterior to the anterodorsal projection. The dorso-ventral depth of the urohyal varies distinctly from deep (state 0) in *Hemichromis* (Fig. 12 A) and *Heterochromis* (Oliver, 1984: fig. 17), to very narrow (state 1) in *Copadichromis*. *Mahengechromis* is similar to the majority of other genera (narrow).

The palatine bone (Fig. 12) also varies among species and potentially has characters which may demonstrate cichlid relationships.

19. A notch in the palatine for the ectopterygoid. Most species have a notch in the postero-ventral edge of the palatine into which fits the ectopterygoid bone (Fig. 12 H), which has therefore been given the primitive state. *Iranocichla* (Fig. 12 I) and *Oreochromis* have a groove for the ectopterygoid, not a notch (state 1). The condition in *Mahengechromis* cannot be determined.

20. The depth of the palatine bone posteriorly. In the majority of the specimens examined the posterior edge of the palatine bone is wide (state 0), whereas in *Hemichromis* (Fig. 12 G) and *Symphysodon*, the palatine is narrow posteriorly (state 1).

The shape of the hyomandibular bone (Fig. 13) was considered to have the potential for phylogenetic use by Murray and Stewart (1999), at least in tilapiine cichlids. In

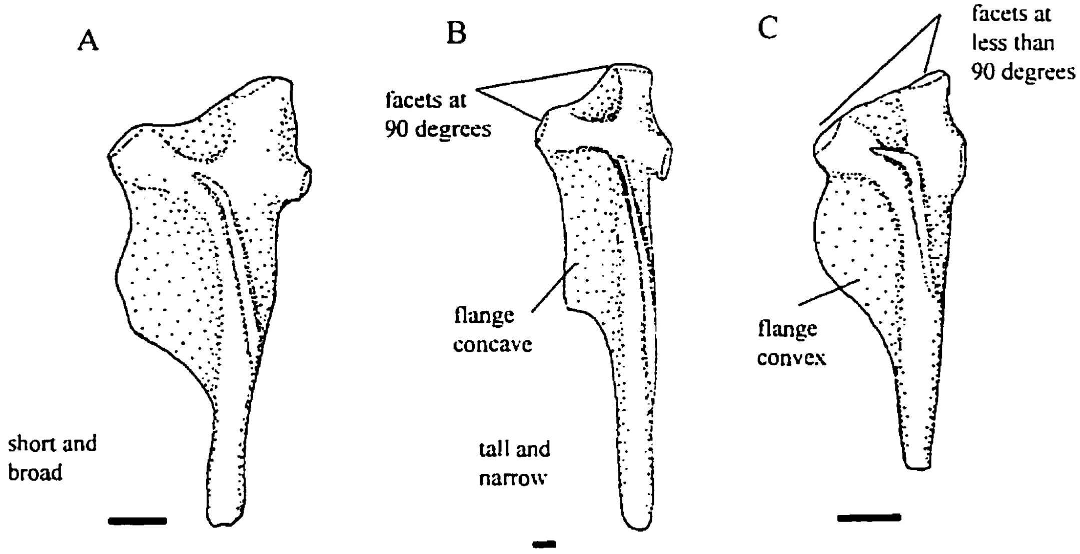

Figure 13. Left hyomandibular bones in lateral view of representative cichlids. A. *Hemichromis* sp., CMN uncatalogued; B. *Tilapia zillii*, CMN uncatalogued; C. *Astatotilapia bloyeti*, NMC 81-0195. Scale bars = 1 mm.

Mahengechromis, differences in the shape of the hyomandibula help to distinguish some of the species from one another. These characters were therefore included here to investigate if their usefulness may be confined to a particular hierarchical level, or if there is a mosaic of patterns among genera.

21. The shape of the hyomandibular head. The head of the hyomandibula has two points of articulation with the cranium. The angle between these two articulations is 90° (state 1) in *Tilapia* (Fig. 13 B), *Pelviachromis* and *Copadichromis*, but is distinctly less than 90° in the majority of species examined (state 0; Fig. 13 C). *Lamprologus* is one of the latter, but is unique in having a notched hyomandubular head (Stiassny, 1997). In *Mahengechromis*, the angle is less than 90°.

22. The shape of the hyomandibula. Van Couvering (1982) figured several hyomandibulae for fossil cichlids, in which the bone seemed quite short and wide. This is similar to the condition found in *Hemichromis* (state 0; Fig. 13 A). In most of the cichlids examined the bone is much taller and thinner (state 1; Fig. 13 B).

23. The shape of the anterior edge of the flange of the hyomandibula varies from convex (state 0; e.g. *Astatotilapia*., Fig. 13 C) through straight (state 1) to concave (state 2; e.g. *Tilapia*, Fig. 13 B). The states were randomly assigned.

Characters of the vertebral column have generally been counts, although other characters have been noted by some authors.

24. The number of vertebrae. Cichocki (1976) used total vertebral number as a character, with the states being 26-30; 31-34; 35-36; and less than 26. He noted that the outgroups among Sparidae and relatives nearly always have 24, while the Pomadasyidae

and Pomacentridae have 26-27 except one with 29, and the Labridae have 25-41 (with the numbers being higher in colder waters). Cichocki stated that most cichlids have 26-30, and so he considered this to be the primitive state for cichlids; the other states were interpreted as a trend towards increasing vertebral number. Kullander (1998) used different states for vertebral number in South American cichlids, and noted a difference between number of abdominal and caudal vertebrae. His states were: (0) number of abdominal vertebrae 14-15, caudal number equal or higher; (1) abdominal 13 or less, caudal equal or higher; (2) abdominal 15 or more, less than 30 total; (3) abdominal 15 or more, caudal fewer, more than 30 total. Casciotta and Arratia (1993), also examined Neotropical taxa, but had only two states for vertebral number, less than 34 or 34 to 41. Some of the species included in this analysis do not fit the states used by Kullander (1998), because of the differing number of abdominal vertebrae. The two states used by Casciotta and Arratia (1993) do not describe the range of variation. Cichocki's (1976) states have been used here, except that his states 0 and 1 have been combined (number of vertebrae 26 to 34), as some examined species overlapped both these states. The resulting states for vertebral number are: state 0 = 26-34; state 1 = 35-36; state 2 = less than 26.

25. The relative number of abdominal and caudal vertebrae. Kullander (1983) noted that the number of caudal vertebrae may be greater than, equal to, or less than the number of abdominal vertebrae. He could not assign any polarity to this character however. The polarity has been assigned here based on the outgroups, which have more caudal than abdominal vertebrae (state 0), which is the state for the Mahenge cichlids. It should be noted that for the fossils the caudal vertebrae are considered to be those that are posterior

to the insertion of the anal fin, based on the position of the first anal pterygiophore, since the haemal arches cannot be clearly seen. The derived conditions are state 1, equal numbers of abdominal and caudal vertebrae, and state 2, more abdominal than caudal.

The bones of the infraorbital (io) series (Fig. 14) have been examined by several authors. The number of pores on the lacrimal has been used by some, and a potential evolutionary pattern has been discussed by Cichocki (1976) and Stiassny (1991). As noted by Oliver (1984), cichlids have no antorbital bone (a bone that has no sensory canal), but have a lacrimal and six infraorbitals with a single neuromast or five infraorbitals (io), one with two neuromasts, most commonly caused by fusion of io3 and io4. Cichocki (1976) examined the overlap between the lacrimal bone and the dorsal margin of io2. The second infraorbital in *Heterochromis* and primitive cichlids has the appearance of a piece of lacrimal that has become detached, because the lacrimal and io2 share a ventrally directed lateralis pore and canal between the 3rd and 4th neuromasts (Oliver, 1984). Oliver agrees with Cichocki in interpreting this as the primitive state for cichlids, as it is present in the Madagascan cichlids and some perciforms. Lamprologines vary considerably in the pattern of infraorbital bones (Stiassny, 1997: fig. 8): the lacrimal pores vary from four to six, and there is varying reduction in the number of infraorbital bones, although one species has increased the number. These polymorphisms were noted in the data matrix.

26. The number of sensory pores on the lacrimal. Although the lacrimal is poorly preserved in most specimens of *Mahengechromis*, several specimens appear to have four pores (state 0), and in no specimen can more than this number be seen. Therefore this

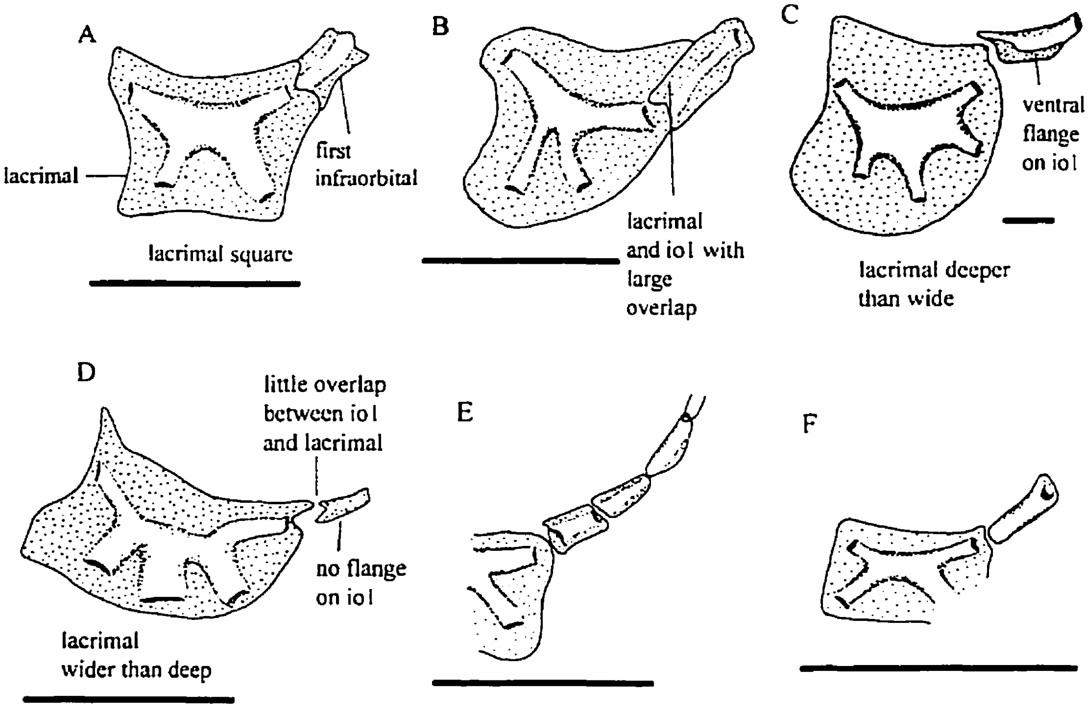

Figure 14. Lacrimal and one or more infraorbital bones of representative cichlids in left lateral view. A. *Hemichromis* sp., CMN uncatalogued; B. *Pelviachromis* sp., CMN uncatalogued; C. *Oreochromis niloticus*, CMN uncatalogued; D. *Haplochromis* [*Yssichromis*], NMC 81-0266; E. *Mahengechromis plethos*, WM 290/96; F. (right side reversed) *Mahengechromis plethos*, WM 374/96a. Scale bars = 5 mm.

genus has been coded with the primitive state. The examined specimen of *Pelviachromis* (Fig. 14 A, B) and *Hemichromis* also have four pores. Five pores is the only derived state, as no examined specimens had six pores.

27. The overlap between the edges of the lacrimal and the next infraorbital. *Pelviachromis* (Fig. 14 B) has significant overlap between the lacrimal and io1 (coded as the primitive state, following Cichocki, 1976). The majority of species examined, including *Mahengechromis*, have little overlap between the two bones (state 1; Fig. 14 C, D).

28. The shape of the lacrimal. Both Cichocki (1976) and Kullander (1998) used the overall shape of the lacrimal as a character in their analyses. The shape varies from almost square, as found in *Hemichromis* (state 0; Fig. 14 A), to deeper than wide (state 1), as in *Oreochromis* (Fig. 14 C), or wider than deep (state 2), as in haplochromines Fig. 14 D). In *Mahengechromis* the lacrimal is almost square. Lamprologines vary between wider than deep, and deeper than wide (Stiassny, 1991: fig. 8). States were randomly assigned.

29. The number of infraorbitals excluding the lacrimal. The number of infraorbital bones cannot be determined for *Mahengechromis*, for no specimen preserves all the bones around the orbit. However, based on several specimens, it does not appear that any infraorbital bones have been lost. Based on Cichocki (1976), the primitive state is five or more, and four or less is the derived state.

30. The coossification of infraorbitals. If fusion of the infraorbitals occurs, it is most commonly numbers three and four that fuse. This fusion may leave a middle canal pore at the point of fusion (derived state 1). This character state is found in *Iranocichla* and

Melanochromis. A middle pore may not remain after fusion, and this (derived state 2) is found only in *Tropheus* among the cichlids examined. *Mahengechromis* does not appear to have these infraorbital bones fused, the primitive state for the character.

31. The shape of the anterior two postlacrimal infraorbitals. Kullander (1998) noted a variation from thin tubular infraorbital bones (e.g. *Haplochromis* [*Yssichromis*], Fig. 14 D) coded as state 0, to those with a ventral flange (state 1; e.g. *Oreochromis*, Fig. 14 C). *Mahengechromis* seems to have a ventral flange on these infraorbital bones. States are randomly assigned.

For the most part, characters of the jaws and teeth have been exclude from this analysis because of the great variety of character states. Many other authors have examine cichlid jaws and teeth and either based relationships upon these characters or determined that there is a great deal of convergent evolution based on trophic adaptations (e.g. Greenwood, 1981). The presence of foramina in the premaxillae may, however, be useful for determining relationships and Kullander (1983) noted variation in the number of foramina on the dentary.

32. Foramen in the dorsal edge of the horizontal ramus of the premaxillae. The foramen is visible in several of the Mahenge specimens and is present in *Iranocichla* and *Tropheus*. States are randomly assigned, with state 0 = presence and state 1 = absence of the foramen

33. Dentary foramina. Kullander (1983) noted that most Neotropical and African cichlids examined by him have five foramina in the dentary, except for *Hemichromis*,

which has only four (state 1). Five foramina are considered the plesiomorphic character and is the number found in *Mahengechromis*.

34. Foramen in lateral face of ascending premaxilla (Cichocki, 1976). The foramen is present (state 0) in the included African specimens, with the exception of *Tylochromis*, and in *Heterochromis* and the Neotropical cichlids (state 1). The state in *Mahengechromis* is unknown.

Scale characters have been extensively used by Lippitsch (1993, 1995, 1998), who considered the possession of ctenoid scales to be a derived character state. Oliver (1984) used outgroup evidence to demonstrate that ctenoid scales are primitive for cichlids, because they are present in most percomorphs as well as several phylogenetically primitive cichlids. *Heterochromis* has ctenoid scales over much of the body and the Madagascan *Oxylapia polli, Paratilapia polleni, Ptychochromis oligacanthus, P. betsileanus* and *Paretroplus* spp. have at least weakly ctenoid scales. If ctenoid scales are primitive for cichlids, cycloid scales probably arose two or more times within the family. If Oliver is correct, then the placement of *Mahengechromis* based on Lippitsch's (1995) characters (Fig. 7, position C) is not supported. Because of this, most of Lippitsch's scale characters have not been included in this analysis. The characters relating to scale patterns that are included here are those that have also been used by other authors, including Kullander (1998), Oliver (1984), and Casciotta and Arratia (1993). Oliver (1984) noted that a fully scaled caudal fin is widespread in cichlids and many other percoid families, and therefore that a scaly caudal fin is primitive, at least for haplochromines. The species examined in this analysis all have scales on the caudal fin, and so this character was not included in the analysis.

35. Scales on the preopercular. Both Kullander (1998) and Casciotta and Arratia (1993) considered scales on the cheek and preopercular bones to be primitive, with regard to Neotropical cichlids. Lippitsch (1995) considered scales on the cheek to be primitive, and did not give the polarity of preopercular scales. Here, preopercular scales are considered primitively present (state 0), following the above authors and because they are present in *Etroplus*. *Mahengechromis* also has scales on the preopercular bone.

36. Pattern of scales in front of the dorsal fin. Most of the species have small irregularly placed scales on the nape (state 0), but a derived condition (state 1) is having the scales in a regular series (state 1) or loss of the scales (state 2). The condition in *Mahengechromis* is not clearly visible. States are from the above authors.

37. Number of spines in the anal fin. Most labroids have two anal fin spines and two or three is considered to be the primitive number (Cichocki, 1976); however, the Indian genus *Etroplus* has twelve spines in the anal fin (state 2). Most of the African cichlids have three, although some lamprologines have between four and ten (Stiassny, 1997; state 1). *Mahengechromis* has three spines in the anal fin.

Results

The phylogenetic analysis based on osteological characters produced forty-two minimum length trees of 143 steps. The strict consensus tree is shown in Figure 15, with

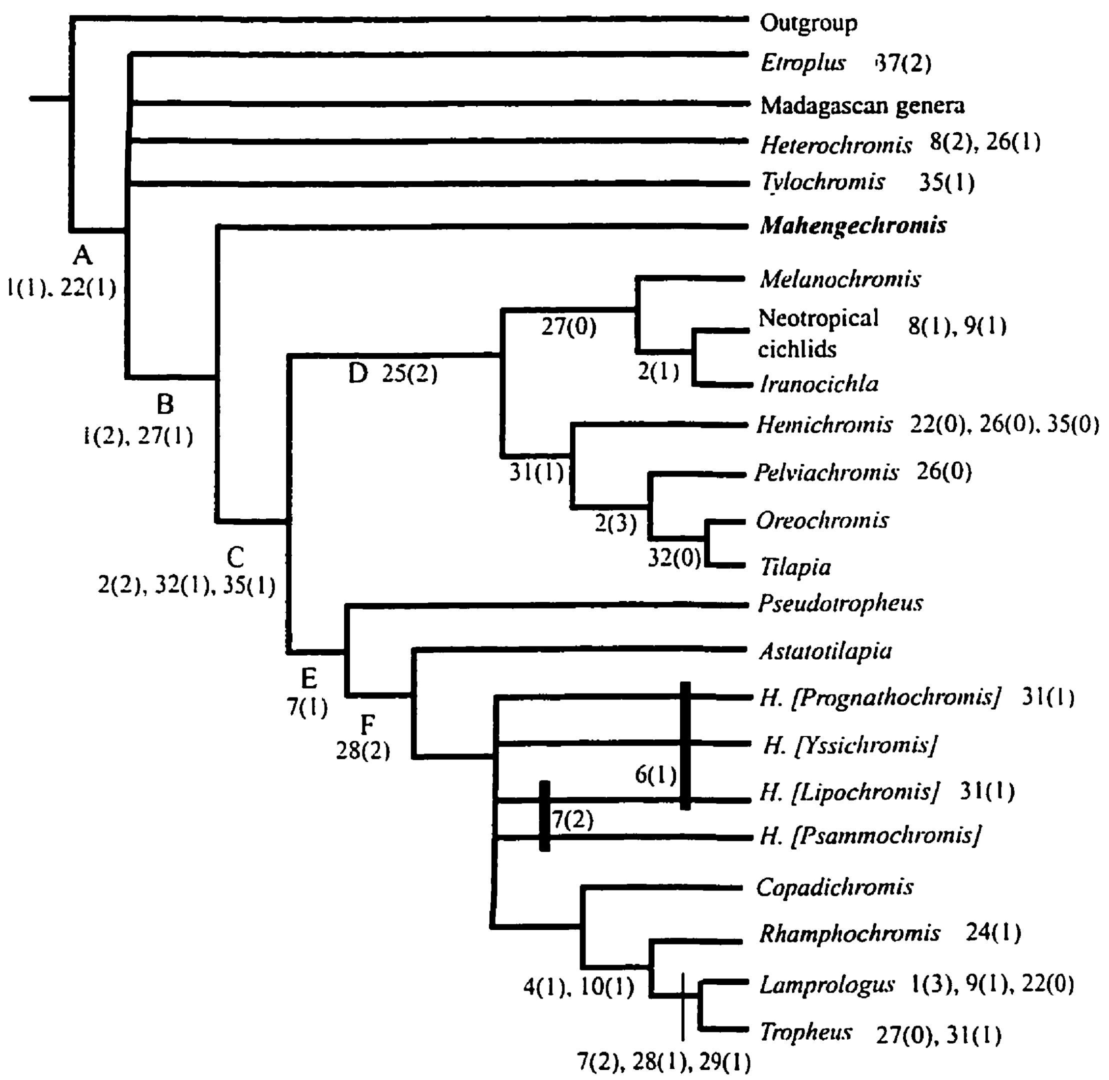

Figure 15. The strict consensus tree from the phylogenetic analysis based on osteological characters. Tree length = 143 steps, CI = 0.46, RI = 0.54. Numbers refer to characters and character states (in brackets) discussed in the text.

the less homoplastic characters plotted on the tree. The consistency index (CI), a measurement of the amount of homoplasy present in the data set, is 0.46. The retention index (RI), a measurement of how congruent the data are, is 0.54. These two measurements can range from 0 (indicating complete homoplasy in characters and no congruence) to 1 (indicating no homoplasy and full congruence). The CI and RI both indicate that the osteological characters are highly convergent (homoplastic) among the lineages within the family Cichlidae. A bootstrap analysis was run to test for the presence of any well supported clades within the data matrix. In a bootstrap analysis, the character data set is randomly sampled with replacement, allowing the variability of the phylogeny to be inferred (Felsenstein, 1985). Although the bootstrap analysis cannot produce absolute confidence intervals on clades, particularly with small data sets, it may give an approximate guide to the level of support for each clade (Kitching et al., 1998). The result of this analysis was that only a single clade, *Tropheus* + *Lamprologus*, was supported at above 50% (at 65%), further indicating the large amount of homoplasy in the data set among cichlid lineages suggested by the RI and CI.

Discussion of results

Distribution of osteological characters

Some of the osteological characters discussed above may be useful for inferring phylogenetic relationships. Most characters are interpreted as being homoplastic within two or more lineages. Individual consistency and retention indices (CI and RI) for each character are given in Appendix E. The rescaled consistency index (RC) for each character is noted below. This index is the product of the CI and RI, and can range from zero to one, with numbers closer to one indicating that a character is more phylogenetically useful.

The first three characters in the data set are those osteological characters from previous analyses. The reduction from three or more predorsal bones to two or less (character 1) is interpreted as a character of the family Cichlidae (Fig. 15, node A), with RC = one. Further reduction to one predorsal bone defines the African cichlids excluding *Heterochromis* and *Tylochromis* (Fig. 15, node B). Among African cichlids, only *Lamprologus* has lost all predorsal bones. The character states for character 2 (RC = 0.66), the pattern of the frontal canal pores, are interpreted as homoplastic throughout several lineages, with the exception of state three, in which the single median pore is born on a median canal. This state unites the two tilapiines (*Tilapia*, *Oreochromis*) and *Pelviachromis*. The advanced state of character 3, the supraoccipital crest overlying the median frontal canal pore (RC = 1), might unite *Heterochromis*, *Etroplus* and the Madagascan genera, as suggested by Stiassny (1991) with subsequent loss in some of the latter.

Characters of the pectoral girdle varied greatly in their usefulness. The advanced state of character 4, a distinctly square process on the postero-ventral corner of the cleithrum dorsal plate, uniting *Tropheus* (Fig. 11 C), *Lamprologus* and *Rhamphochromis* has an RC of one. Character five (position of the radials in the pectoral girdle) does not resolve any relationships in the phylogenetic analysis, and had an RC of only 0.14. The advanced state of character 6 (suturing of the coracoid and scapula) might unite a subset of *Haplochromis*, and may be important for resolving some of the relationships within this genus. Conflict with character 7 in the data set prevented this relationship from being supported, but character 6 has an RC of one, much larger than the RC of character 7, indicating that character 6 is a better indicator of relationship.

Characters of the opercular series also varied greatly in their phylogenetic usefulness. The reduction of the dorsal expanse of the opercle (character 7, RC = 0.21) is interpreted as uniting the haplochromines, *Lamprologus* and *Tropheus* (node E), with the latter two having a secondary modification. The condition in haplochromines is homoplastic with that of *Iranocichla*, and the secondary modification is also found in *Oreochromis*. One of the derived states of character 8, six pores on the preopercle, found only in Neotropical cichlids, and the other derived state, five pores, is an autapomorphy of *Heterochromis* in this study, and therefore the RC is zero. The Neotropical *Symphysodon*, and African *Lamprologus* lack the notch in the interopercle anterior edge (advanced state of character 9) - interpreted as autapomorphies of each and homoplastic in the two lineages, therefore the RC is zero.

The advanced state of character 10 (elongation of the interopercular bone) unites *Rhamphochromis*, *Tropheus*, and *Lamprologus* in the tree based on osteological characters, and has an RC of one. As suggested by its polymorphic state in *Mahengechromis*, the shape of the posteroventral edge of the opercular bone (character 11) is determined as not being phylogenetically useful because of the amount of homoplasy among lineages. The RC of this character is only 0.11.

None of the characters of the supracleithrum and posttemporal bones (12-16) were found to be phylogenetically useful, with an RC between zero and 0.1. All of the character states are interpreted as homoplastic among several genera.

The states of both characters of the urohyal (characters 17 and 18) do not seem to unite any lineages. Character 17 has an RC of 0.36 and 18 and RC of 0.24.

The advanced state of character 19 (a groove for the ectopterygoid in the palatine) may unite at least some of the tilapiine cichlids in a clade, but it is homoplastic with the condition in *Hemichromis*. The similarity between *Hemichromis* and *Symphysodon*, in which the posterior edge of the palatine is narrow (character 20; RC = 0.38), is interpreted as being homoplastic in these two genera.

The shape of the hyomandibular head (angle of articular facets, character 21) is interpreted as homoplastic in the three taxa in which it is found (*Tilapia, Pelviachromis*, and *Copadichromis*) and therefore has an RC of zero. The overall shape of the hyomandibula being tall and narrow (character 22) could be interpreted as a character uniting the Cichlidae, with reversals to the primitive state in *Hemichromis* and *Lamprologus*. The RC, however is zero. As suggested by the polymorphic condition in *Mahengechromis*, the shape of the anterior edge of the hyomandibular flange (character 23) is found to be homoplastic throughout the family (RC = 0.17), indicating that this is not a useful phylogenetic character. Although Murray and Stewart (1999) found the hyomandibula to be useful for determining intrageneric relationships among three genera of tilapiines, the results of this analysis suggests that characters of the hyomandibula may be useful only at lower taxonomic levels.

The total number of vertebrae does not seem to be an informative character, but relative numbers of abdominal to caudal vertebrae might be useful. *Rhamphochromis* is unique in having 35-36 vertebrae (character 24), but *Hemichromis* and *Mahengechromis* are convergent in having less than 26 vertebrae, and therefore the RC is 0. A larger number of abdominal than caudal vertebrae (advanced state of character 25) unites the tilapiines with the Neotropical cichlids and *Melanochromis*, and is homoplastic with *Hemichromis* (Fig. 15, node D; RC = 0.57).

Characters of the infraorbital bones for the most part were highly homoplastic among lineages. The presence of five pores on the lacrimal (advanced state of character 26) would unite the Neotropical cichlids and African cichlids excluding *Heterochromis, Tylochromis* and *Mahengechromis* (Fig. 15, node C) and be convergent in *Heterochromis*, but the RC is only 0.11. The advanced state of character 27, large overlap between the edges of the lacrimal and the next infraorbital, might define node B (Fig. 15, Neotropical cichlids and African cichlids excluding *Tylochromis* and *Heterochromis*), with secondary losses in the Neotropical cichlids, *Melanochromis*, *Iranocichla* and *Tropheus* (RC = 0.2)

The wider than deep state of the lacrimal (advanced state of character 28, RC = 0.29) unites the haplochromine cichlids excluding *Pseudotropheus*, with *Lamprologus* and *Tropheus* (node F), with a reversal (loss) of the state in some lamprologine species. The reduction in number of infraorbital bones (character 29) unites *Lamprologus* and *Tropheus* (RC = 1) in the tree based on osteological characters, but is interpreted as a homoplasy in the composite tree. One of the advanced states of character 30 (the coossification of infraorbital bones) is found in *Iranocichla* and *Melanochromis*, and the other advanced state is only found in *Tropheus*. These are all interpreted as being independently acquired, and therefore the RC is zero.

The states of character 31 (shape of the anterior two postlacrimal infraorbitals) are homoplastic (RC = 0.22) throughout the examined specimens of *Haplochromis, Tropheus, Pelviachromis*, *Oreochromis* and *Tilapia*.

Presence or absence of foramina in the jaw bones does not seem to be phylogenetically useful. The presence of a foramen in the dorsal edge of the horizontal ramus of the premaxillae (the advanced state of character 32) is interpreted as being a convergence between *Iranocichla* and *Tropheus*, with an RC of zero. The advanced state of character 33 (four dentary foramina) is interpreted as an autapomorphy of *Hemichromis*, and therefore the RC is zero. The advanced state of character 34 (foramen present in the lateral face of the ascending process of the premaxilla, RC = 0.33) may be a synapomorphy of node C (Fig. 15), with a reversal (loss) in *Oreochromis* and *Tilapia*.

The two scale characters included in this analysis indicate that scale characters should be reexamined to determine the polarity of these characters, as previously indicated by Oliver (1984). The presence or absence of preopercular scales (character 35) might seem to be a phylogenetically useful character with the derived state uniting node C - the Neotropical and African cichlids excluding *Heterochromis* (although the state is not known in this genus), *Tylochromis*, and *Mahengechromis*. However, in the tree based on osteological characters this causes the presence of scales on the preopercular bone in *Hemichromis* to be interpreted as a redevelopment of the trait, and the RC is 0.11. The scales in front of the dorsal fin being in a regular series (advanced state of character 36) may unite the family Cichlidae (Fig. 15, node A), with a reversal to irregular small scales in haplochromines, and complete loss of predorsal scales in *Iranocichla* and *Lamprologus*. The RC is 0.2.

The last character, 37, number of anal fin spines, did not indicate any relationships. One of the advanced states for this character is interpreted as an autapomorphy of *Etroplus* homoplastic with some lamprologines, and the other advanced state is found in some Neotropical cichlids, and some lamprologines. These are all interpreted as indicating convergence in these lineages, and cause the RC to be zero.

Few characters were not homoplastic in this analysis, supporting the assertion that there is a great deal of convergence in cichlid anatomy. In spite of the amount of autoapomorphous or homoplastic characters among lineages in this analysis, the results of this study, and several previously published analyses, indicate that there is potential for informative osteological characters to be found, and used to infer relationships, among lineages of cichlid fishes. The rescaled consistency indices (RC) of individual osteological characters indicate which characters are less homoplastic, and therefore better for using to infer relationships. Six of the characters, numbers 1, 3, 4, 6, 10, and 29, had RC values 1.00 (the best value possible). Two other characters, numbers 2 and 25, had values over 0.50 (0.66 and 0.57 respectively). These characters should be examined in a greater number of representative species to determine if their potential for indicating phylogenetic relationships is upheld in a larger sample.

Comparison between the tree based on osteological characters and the composite tree

In order to compare the results of this analysis with that of the previously published phylogenies, the representative genera or species from this analysis are shown in their relative placements based on non-osteological characters (the composite tree from Fig. 6) as shown in Figure 16 (*Mahengechromis* is excluded). At the highest level (the

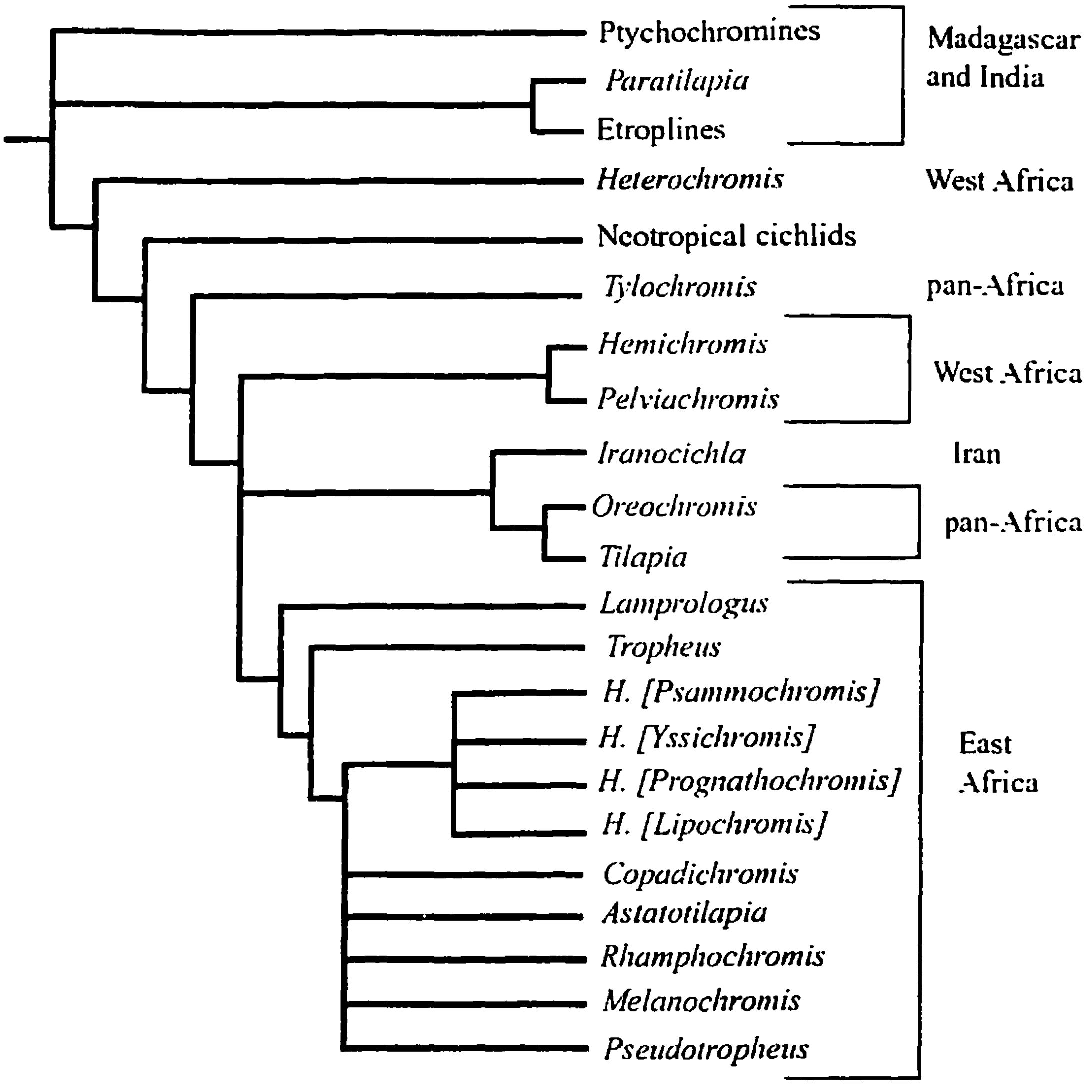

Figure 16. Taxa from this study arranged within the topology of the composite tree based on previous analyses shown in Figure 6.

family) both trees agree. Potential osteological characters that support the monophyly of the Cichlidae are characters 1, the reduction in the number of predorsal bones, 22, the shape of the hyomandibula (with a reversal in *Hemichromis*), and 32, the absence of a foramen in the horizontal ramus of the premaxilla (with reversals in *Tilapia*, *Oreochromis* and *Mahengechromis*).

The basal position of the Madagascan and Indian cichlids, and *Heterochromis* in the composite tree is not contradicted by any osteological characters. The main differences between the two trees is in the placement of *Hemichromis*, *Pelviachromis*, *Melanochromis*, the Neotropical cichlids, and the Lake Tanganyikan cichlids (*Lamprologus* and *Tropheus*).

The composite tree has the Neotropical cichlids placed as the sistergroup to the African cichlids excluding *Heterochromis*. In the result from this study, the Neotropical cichlids are placed as the sister group to *Iranocichla*, and the two together form the sister group to *Melanochromis*. It is unlikely that the Iranian endemic *Iranocichla* would be the sister to the monophyletic Neotropical clade, yet another indication that the osteological characters are homoplastic among groups. Similarly, *Melanochromis* of Lake Malawi, considered to be a derived haplochromine genus, is unlikely to be more closely related to the Neotropical cichlids and *Iranocichla* than to other haplochromines as found in this study. These inconsistencies are indicative of the convergence present among these lineages. The placement of *Hemichromis* and *Pelviachromis* in relatively derived positions in the tree based on osteological data is also unlikely. There are at least three reversals in character states in *Hemichromis* (characters 22, 26, and 35), and one in *Pelviachromis* (character 26) necessary to account for their placement.

In the tree based on osteological characters, the haplochromines are paraphyletic, with the Lake Tanganyika lineages (*Lamprologus* and *Tropheus*) nested among them in the most derived positions. The placement of the two Lake Tanganyika forms among the haplochromines is probably a reflection of the convergence of species in similar niches in the different lakes.

One character stands out as being potentially very useful for supporting the phylogenetic relationships of a subgroup of the genus *Haplochromis*. The suturing of the coracoid and scapula (character 6) is only present in the specimens representing *Haplochromis* [*Psammochromis*], *H.* [*Yssichromis*] and *H.* [*Lipochromis*]. It is not interpreted as a synapomorphy of this group in the tree because of the contradiction with character 7. Character 7 (the shape of the dorsal edge of the opercle) however, must be interpreted as homoplastic throughout the family. The genus *Haplochromis* has withstood many efforts to resolve intergeneric relationships (e.g. Greenwood, 1981). The potential use of this character should be examined further, as it indicates that osteological characters of the postcranial skeleton may enable some intergeneric relationships to be resolved.

The phylogenetic analysis based on osteological data produced some placements similar to those in the composite tree, including the position of the Indian and Madagascan genera as the most primitive cichlids, followed by *Tylochromis* and *Heterochromis*. The placement of the tilapiine cichlids is also similar in both trees. These similarities suggest that an analysis of additional osteological data with a larger number of representative cichlids may result in the establishment of a more reliable phylogeny. This will eventually lead to the ability to establish specific sister group relationships between fossil cichlids and well known living clades.

Placement of the Mahenge cichlids

In the tree based on osteological characters, *Mahengechromis* is in the position of sistergroup to the Neotropical cichlids and African cichlids excluding *Tylochromis* and *Heterochromis*. Although this placement of *Mahengechromis* cannot be accepted uncritically, the available data places the fossil genus as a relatively basal member of the family.

In order to determine the placement of *Mahengechromis* in the scheme of the composite tree, tree lengths for different placements of the genus were compared. The osteological data set was used, but the composite tree was manually generated in MacClade. The most parsimonious placement of *Mahengechromis* could then be found be comparing tree lengths for each possible position of the genus within the composite tree (Fig. 16). In this manner, the most parsimonious position (identified by having the shortest tree length) for *Mahengechromis* is as the sister group to *Hemichromis*, with a tree length of 133+ (the "+" in MacClade tree lengths indicates polytomies in the tree). The next shortest tree length is 135+ steps, when *Mahengechromis* is positioned as the sistergroup to the rest of the family. If *Mahengechromis* is positioned as the sistergroup to the family excluding *Etroplus* and the Madagascan cichlids, or to the family excluding these two and *Heterochromis*, the tree length rises to 136+ steps. If *Mahengechromis* is positioned anywhere else in the cladogram, the tree length rises to 137+ to 140+ steps.

Therefore *Mahengechromis* appears to be a basal member of the Cichlidae, and potentially more closely related to *Hemichromis* that any other lineage.

Hemichromis is found predominantly in West Africa. Greenwood (1960) pointed out the relationships between the Mahenge ichthyofauna and that of modern West Africa. The clupeomorph, *Palaeodenticeps tanganikae*, from Mahenge is a member of the Denticipitidae, which has its only extant member found in West Africa. Similarly, the osteoglossomorph from Mahenge, *Singida jacksonoides*, is more closely related to fishes from West Africa than modern or extinct East African faunas (Greenwood and Patterson, 1967). A sistergroup relationship between *Mahengechromis* and *Hemichromis* also supports the east-west relationships already known for the Mahenge fauna.

In summary, *Mahengechromis* can be considered a primitive cichlid in many ways. The five species are fully scaled, and the scales are ctenoid on the body, which is probably the primitive state (Oliver, 1984). In addition, they have simple conical, unicuspid teeth, and the pattern of the frontal canal pores is primitive. Further study of a greater number of cichlid species is still required, but a basal position of *Mahengechromis* within the family is most likely, and is not surprising, considering the Eocene age of the genus.

Literature cited

Baum, B.R. 1992. Combining trees as a way or combining data sets for phylogenetic inference, and the desirability of combining gene trees. Taxon, 41:3-10.

Casciotta, J. and G. Arratia. 1993. Tertiary cichlid fishes from Argentina and reassessment of the phylogeny of New World cichlids (Perciformes: Labroidei). Kaupia - Darmstädter Beiträge zur Naturgeschichte, 2:195-240.

Cichocki, F.P. 1976. Cladistic history of cichlid fishes and reproductive strategies of the American genera *Acarichthys, Biotodoma* and *Geophagus*. Ph.D. thesis, University of Michigan.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution, 39:783-791.

Gaemers, P.A.M. 1984. Taxonomic position of the Cichlidae (Pisces, Perciformes) as demonstrated by the morphology of their otoliths. Netherlands Journal of Zoology, 34(4):566-595.

Greenwood, P.H. 1960. Fossil denticipitid fishes from East Africa. Bulletin of the British Museum (Natural History) Geology, 5:1-11.

Greenwood, P.H. 1974. The cichlid fishes of Lake Victoria, East Africa: The biology and evolution of a species flock. Bulletin of the British Museum (Natural History) Zoology supplement 6:1-134.

Greenwood, P.H. 1980. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II; the species from Lakes Victoria, Nabugabo, Edward, George and Kivu. Bulletin of the British Museum (Natural History) Zoology series, 39(1):1-99.

Greenwood, P.H. 1981. The haplochromine fishes of the East African lakes. Collected papers on their taxonomy, biology and evolution. Cornell University Press, Ithaca, N.Y., 839 pp.

Greenwood, P.H. 1984. African cichlids and evolutionary theories. Pages 141-154 in: A.A. Echelle and I. Kornfield (eds.). Evolution of Fish Species Flocks. University of Maine at Orono Press.

Greenwood, P.H. and C. Patterson. 1967. A fossil osteoglossoid fish from Tanzania (E. Africa). Journal of the Linnean Society (Zoology), 47(311):211-223.

Kaufman, L.S. and K. F. Liem. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. Breviora, 472:1-19.

Kitching, I.J., P.L. Forey, C.J. Humphries and D.M. Williams. 1998. *Cladistics. The theory and practice of parsimony analysis*. Second edition. The Systematics Association Publication no. 11. Oxford University Press, Oxford, xii + 228 pp.

Kullander, S.O. 1983. Taxonomic studies on the percoid freshwater fish family Cichlidae in South America. Ph. D. thesis, University of Stockholm, 440 pp.

Kullander, S.O. 1998. A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes). Pp. 461-498 *in*: Malabarba, L.R., R.E. Reis, R.P. Vari, Z. M. S. Lucena, and C.A.S. Lucena (Eds.). Phylogeny and Classification of Neotropical Fishes, Editora Universitária - EIPUCRS, Porto Alegre, Brasil.

Kullander, S.O. and H. Nijssen. 1989. The cichlids of Surinam. Teleostei: Labroidei. E.J. Brill, Leiden, The Netherlands, xxx +256 pp.

Lippitsch, E. 1993. A phyletic study of lacustrine haplochromine fishes (Perciformes, Cichlidae) of East Africa, based on scale and squamation characters. Journal of Fish Biology, 42:903-946.

Lippitsch, E. 1995. Scale and squamation character polarity and phyletic assessment in the family Cichlidae. Journal of Fish Biology, 47:91-106.

Lippitsch, E. 1997. Phylogenetic investigations on the haplochromine Cichlidae of Lake Kivu (East Africa), based on lepidological characters. Journal of Fish Biology, 51:284-299.

Lippitsch, E. 1998. Phylogenetic study of cichlid fishes in Lake Tanganyika: a lepidological approach. Journal of Fish Biology, 53:752-766.

Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African cichlid fishes. Trends in Ecology and Evolution, 8(8):279-284.

Meyer, A., T.D. Kocher, P. Basasibwaki and A.C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature, 347(6293):550-553.

Meyer, A., C. Montero, and A. Spreinat. 1994. Evolutionary history of the cichlid fish species flocks of the East African great lakes inferred from molecular phylogenetic data. Arch. Hydrobiol. Beih. Ergebnisse der Limnologie, 44:407-425.

Meyer, A., C.M. Montero, and A. Spreinat. 1996. Molecular phylogenetic inferences about the evolutionary history of East African cichlid fish radiations. Pp. 303-323, in: Johnson, T.C. and E.O. Odada (eds.). The Limnology, Climatology and Paleoclimatology of the East African Lakes. Gordon and Breach Publishers.

Moran, P., I. Kornfield and P.N. Reinthal. 1994. Molecular systematics and radiation of the haplochromine cichlids (Teleostei: Perciformes) of Lake Malawi. Copeia, 1994(2):274-288.

Murray, A.M. and K.M. Stewart. 1999. A new species of fossil tilapiine cichlid from the Pliocene Middle Awash, Ethiopia. Journal of Vertebrate Paleontology, 19(2):293-301.

Newsome, Y.L. 1971. Comparative osteology and relationships of Neotropical cichlid fishes. Ph.D. Thesis, University of Illinois, Chicago, Illinois 303 pp.

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.

Oliver, M.K. 1984. Systematics of African cichlid fishes: Determination of the most primitive taxon, and studies on the haplochromines of Lake Malawi (Teleostei: Cichlidae). Ph.D. thesis, Yale University, 326 pp.

Purvis, A. 1995. A modification to Baum and Ragan's method for combining phylogenetic trees. Systematic Biology, 44:251-255.

Reinthal, P.N. 1990. Morphological analyses of the neurocranium of a group of rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa. Zoological Journal of the Linnean Society, 98:123-139.

Reinthal, P.N. and M.L.J. Stiassny. 1997. Revision of the Madagascan genus *Ptychochromoides* (Teleostei: Cichlidae), with description of a new species. Ichthyological Explorations of Freshwaters, 7(4):353-368.

Seehausen, O., E. Lippitsch, N. Bouton and H. Zwennes. 1998. Mbipi, the rock-dwelling cichlids of Lake Victoria: description of three new genera and fifteen new species (Teleostei). Ichthyological Explorations of Freshwaters, 9(2):129-228.

Seyoum, S. 1989. Stock identification and the evolutionary relationships of the tilapiine fishes of the genera *Oreochromis, Sarotherodon* and *Tilapia* (Pisces: Cichlidae) using allozyme analysis and restriction endonuclease analysis of mitochondrial DNA. Ph.D. thesis, Department of Biology, University of Waterloo, 336 pp.

Stiassny, M.L.J. 1982. The relationships of the Neotropical genus *Cichla* (Perciformes, Cichlidae): A phyletic analysis including some functional considerations. Journal of Zoology, London, 197:427-453.

Stiassny, M.L.J. 1987. Cichlid familial intrarelationships and the placement of the Neotropical genus *Cichla* (Perciformes, Labroidei). Journal of Natural History, 21:1311-1331.

Stiassny, M.L.J. 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview. Pages 1-35 in: Keenleyside, M.H.A. (ed.). Cichlid Fishes. Behaviour, ecology and evolution. Chapman and Hall, London, New York.

Stiassny, M.L.J. 1997. A phylogenetic overview of the lamprologine cichlids of Africa (Teleostei, Cichlidae): a morphological perspective. South African Journal of Science, 93:513-523.

Strauss, R.E. 1984. Allometry and functional feeding morphology in haplochromine cichlids. Pages 217-229 in: A.A. Echelle and I. Kornfield (eds.). Evolution of Fish Species Flocks. University of Maine at Orono Press.

Taylor, W.R. and G.C. VanDyke. 1985. Revised procedure for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium, 9:107-119.

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

Van Couvering, J.A.H. 1982. Fossil cichlid fish of Africa. Special Papers in Palaeontology no. 29:103 pp.

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

Appendix A. Classification of the Genera and Species of the Old World Cichlidae, with general distributions

Abbreviations: A, Lake Albert; Afr, Africa; E, Lake Edward; G, Lake George; M, Lake Malawi; T, Lake Tanganyika; V, Lake Victoria

Tribe Etroplini

1. *Etroplus* - India
  1. *Etroplus canarensis*
  2. *Etroplus coruchi*
  3. *Etroplus maculatus*
  4. *Etroplus meleagris*
  5. *Etroplus suratensis*

2. *Oxylapia* - Madagascar
  6. *Oxylapia polli*

3. *Paretroplus* - Madagascar
  7. *Paretroplus damii*
  8. *Paretroplus kieneri*
  9. *Paretroplus maculatus*
  10. *Paretroplus petiti*
  11. *Paretroplus polyactis*

Tribe Ptychochromini - Madagascar

4. *Ptychochromis*
  12. *Ptychochromis madagascariensis*
  13. *Ptychochromis oligacanthus*

5. *Ptychochromoides*
  14. *Ptychochromoides betsileanus*
  15. *Ptychochromoides katria*

Madagascan endemic

6. *Paratilapia*
  16. *Paratilapia polleni*
  17. *Paratilapia toddi*
  18. *Paratilapia voeltzkowi*

Tribe Heterochromini - W Africa

7. *Heterochromis*
  19. *Heterochromis multidens*

Tribe Tylochromini - pan-African

8. *Tylochromis*
  20. *Tylochromis aristoma* - E. Afr
  21. *Tylochromis bangwelensis*
  22. *Tylochromis elongatus*
  23. *Tylochromis intermedius* - W Afr
  24. *Tylochromis jentinki - Liberia*
  25. *Tylochromis labrodon*
  26. *Tylochromis lateralis* - W Afr
  27. *Tylochromis leonensis*
  28. *Tylochromis microdon* - W Afr
  29. *Tylochromis mylodon* - Zaire
  30. *Tylochromis polylepis* - T
  31. *Tylochromis praecox* - Zaire
  32. *Tylochromis pulcher* - Zaire
  33. *Tylochromis regani* - Zaire
  34. *Tylochromis robertsi* - Zaire
  35. *Tylochromis sudanensis* - W Afr
  36. *Tylochromis trewavasae* - W Afr
  37. *Tylochromis variabilis* - Zaire

Tribe Hemichromini

9. *Anomalochromis*- W Africa
  38. *Anomalochromis thomasi*

10. *Hemichromis* - Africa
  39. *Hemichromis angolensis*
  40. *Hemichromis bimaculatus*
  41. *Hemichromis cerasogaster*
  42. *Hemichromis elongatus*
  43. *Hemichromis fasciatus*
    H. fasciatus violacea
  44. *Hemichromis letourneuxi*
  45. *Hemichromis lifalili*

Tribe Chromidotilapini

11. *Chromidotilapia*- W Africa
  46. *Chromidotilapia batesii*
  47. *Chromidotilapia finleyi*

48. *Chromidotilapia guentheri*
49. *Chromidotilapia kingsleyae*
50. *Chromidotilapia linkei*
51. *Chromidotilapia schoutedeni*
12. *Limbochromis*- W Africa
52. *Limbochromis cavalliensis*
53. *Limbochromis robertsi*
13. *Nanochromis* - Africa
54. *Nanochromis consortus* - Zaire R
55. *Nanochromis dimidiatus* - W Afr
56. *Nanochromis minor* - Zaire R
57. *Nanochromis nudiceps* - Zaire
58. *Nanochromis parilus* - Zaire R.
59. *Nanochromis riomuniensis* - Afr
60. *Nanochromis splendens* - Zaire R
61. *Nanochromis squamiceps* - Zaire
62. *Nanochromis transvestitus*
14. *Parananochromis* - W Africa
63. *Parananochromis caudifasciatus*
64. *Parananochromis gabonicus*
65. *Parananochromis longirostris*
15. *Pelviachromis* - W Africa
66. *Pelviachromis humilis*
67. *Pelviachromis kribensis*
68. *Pelviachromis pulcher*
69. *Pelviachromis roloffi*
70. *Pelviachromis subocellatus*
71. *Pelviachromis taeniatus*
72. *Pelviachromis taeniatus*
16. *Thysochromis* - W Africa
73. *Thysochromis ansorgii*

Tribe Tilapiini
17. *Boulengerochromis*
74. *Boulengerochromis microlepis*
18. *Danakilia* Danakil Desert
75. *Danakilia franchettii*
19. *Iranocichla* - Iran
76. *Iranocichla hormuzensis*
20. *Konia*
77. *Konia dikume*
21. *Myaka*
78. *Myaka myaka*
22. *Oreochromis*
79. *Oreochromis alcalicus*
O. alcalicus grahami
80. *Oreochromis amphimelas*
81. *Oreochromis andersonii*
82. *Oreochromis angolensis*
83. *Oreochromis aureus*
84. *Oreochromis chungruruensis*
85. *Oreochromis esculenta*
86. *Oreochromis hunteri*
87. *Oreochromis ismailiaensis*
88. *Oreochromis jipe*
89. *Oreochromis karomo*
90. *Oreochromis karongae*
91. *Oreochromis korogwe*
92. *Oreochromis lepidurus*
93. *Oreochromis leucostictus*
94. *Oreochromis lidole*
95. *Oreochromis macrochir*
96. *Oreochromis malagarasi*
97. *Oreochromis mortimeri*
98. *Oreochromis mossambicus*
99. *Oreochromis mweruensis*
100. *Oreochromis niloticus*
O. niloticus baringoensis
O. niloticus filoa
O. niloticus sugutae
O. niloticus tana
O. niloticus vulcani
101. *Oreochromis pangani*
O. pangani girigan
102. *Oreochromis placidus*
O. placidus ruvumae
103. *Oreochromis rukwaensis*
104. *Oreochromis saka*
105. *Oreochromis salinicola*
106. *Oreochromis schwebischi*
107. *Oreochromis shiranus*
108. *Oreochromis shiranus chilwae*
109. *Oreochromis spilurus*
O. spilurus niger
110. *Oreochromis squamipinnis*
111. *Oreochromis tanganicae*
112. *Oreochromis upembae*
113. *Oreochromis urolepis*
O. urolepis hornorum
23. *Pungu* - W. Africa
114. *Pungu maclareni*
24. *Sarotherodon*

- 115. *Sarotherodon caroli*
- 116. *Sarotherodon caudomarginata*
- 117. *Sarotherodon galilaeus*
  - *S. galilaeus borkuana*
- 118. *Sarotherodon linnellii*
- 119. *Sarotherodon lohbergeri*
- 120. *Sarotherodon melanotheron*
  - *S. melanotheron heudelotii*
  - *S. melanotheron heudelotii*
  - *S. melanotheron nigripinnis*
  - *S. melanotheron paludinosus*
- 121. *Sarotherodon microcephalus*
- 122. *Sarotherodon mvogoi*
- 123. *Sarotherodon occidentalis*
- 124. *Sarotherodon steinbachi*
- 125. *Sarotherodon tournieri*
  - *S. tournieri leberiensis*

25. *Stomatepia* - W Africa

- 126. *Stomatepia mariae*
- 127. *Stomatepia mongo*
- 128. *Stomatepia pindu*

26. *Tilapia* - Africa

- 129. *Tilapia bakossiorum*
- 130. *Tilapia baloni*
- 131. *Tilapia bemini*
- 132. *Tilapia bilineata*
- 133. *Tilapia brevimanus*
- 134. *Tilapia busumanus*
- 135. *Tilapia buttikoferi*
- 136. *Tilapia bythobates*
- 137. *Tilapia cabrae*
- 138. *Tilapia camerunensis*
- 139. *Tilapia cessiana*
- 140. *Tilapia coffea*
- 141. *Tilapia congica*
- 142. *Tilapia crassa*
- 143. *Tilapia dageti*
- 144. *Tilapia deckerti*
- 145. *Tilapia discolor*
- 146. *Tilapia eisentrauti*
- 147. *Tilapia flava*
- 148. *Tilapia fuscomaculatus*
- 149. *Tilapia guinasana*
- 150. *Tilapia guineensis*
- 151. *Tilapia gutturosa*
- 152. *Tilapia imbriferna*
- 153. *Tilapia jallae*
- 154. *Tilapia joka*
- 155. *Tilapia kottae*
- 156. *Tilapia leonensis*
- 157. *Tilapia louka*
- 158. *Tilapia manyarae*
- 159. *Tilapia margaritacea*
- 160. *Tilapia mariae*
- 161. *Tilapia nyongana*
- 162. *Tilapia oligacanthus*
  - *T. oligacanthus nossibeensis*
- 163. *Tilapia rendalii*
- 164. *Tilapia rheophila*
- 165. *Tilapia ruweti*
- 166. *Tilapia snyderae*
- 167. *Tilapia sparrmanii*
- 168. *Tilapia spongotroktis*
- 169. *Tilapia stanleyi*
  - *T. stanleyi uniformis*
- 170. *Tilapia stigmatogenys*
- 171. *Tilapia tholloni*
- 172. *Tilapia thysi*
- 173. *Tilapia walteri*
- 174. *Tilapia zillii*

27. *Tristramella* - Israel

- 175. *Tristramella sacra*
- 176. *Tristramella simonis*
  - *T. simonis intermedia*
  - *T. simonus magdalenae*

Included in Trewavas' Tilapiini

28. *Gobiocichla* - W Africa, Sudan

- 177. *Gobiocichla ethelwynnae*
- 178. *Gobiocichla wonderi*

29. *Pelmatochromis*

- 179. *Pelmatochromis buettikoferi* - N Afr
- 180. *Pelmatochromis nigrofasciatus* - W Afr
- 181. *Pelmatochromis ocellifer* - W Afr
- 182. *Pelmatochromis pulcher*

30. *Petrochromis* - Lake Tanganyika

- 183. *Petrochromis famula*
- 184. *Petrochromis fasciolatus*
- 185. *Petrochromis macrognathus*

186. *Petrochromis polyodon*
187. *Petrochromis trewavasae*
31. *Steatocranus* - E Africa
188. *Steatocranus bleheri*
189. *Steatocranus casuarius*
190. *Steatocranus gibbiceps*
191. *Steatocranus glaber*
192. *Steatocranus irvinei*
193. *Steatocranus mpozoensis*
194. *Steatocranus rouxi*
195. *Steatocranus tinanti*
196. *Steatocranus ubanguiensis*

Tribe Bathybatini
32. *Bathybates-* Lake Tanganyika
197. *Bathybates fasciatus*
198. *Bathybates ferox*
199. *Bathybates graueri*
200. *Bathybates leo*
201. *Bathybates minor*
202. *Bathybates vittatus*
33. *Hemibates* - Lake Tanganyika
203. *Hemibates stenosoma*

Tribe Perissodini
34. *Perissodus* - Lake Tanganyika
204. *Perissodus eccentricus*
205. *Perissodus microlepis*

Tribe Limnochromini
35. *Limnochomis* - Lake Tanganyika
206. *Limnochromis auritus*
207. *Limnochromis abeelei*
208. *Limnochromis bellcrossi*
209. *Limnochromis staneri*

Tribe Lamprologini
36. *Altolamprologus* - Lake Tanganyika
210. *Altolamprologus calvus*
211. *Altolamprologus compressiceps*
37. *Chalinochromis* - Lake Tanganyika
212. *Chalinochromis brichardi*
213. *Chalinochromis popelini*
38. *Julidochromis* - Lake Tanganyika
214. *Julidochromis dickfeldi*
215. *Julidochromis marlieri*
216. *Julidochromis ornatus*
217. *Julidochromis regani*
218. *Julidochromis steindachneri*
219. *Julidochromis transcriptus*
39. *Lamprologus* - Africa
220. *Lamprologus callipterus* - M, T
221. *Lamprologus congoensis*
222. *Lamprologus finalimus* - T
223. *Lamprologus kungweensis* - T
224. *Lamprologus lemairii* - T
225. *Lamprologus lethops* - Zaire R
226. *Lamprologus meleagris* - T
227. *Lamprologus mocquardi* - WAf
228. *Lamprologus ocellatus* - T
229. *Lamprologus olivaceous*
230. *Lamprologus ornatipinnis* - T
231. *Lamprologus signatus* - T
232. *Lamprologus speciosus* - T
233. *Lamprologus stappersi* - E Afr
234. *Lamprologus symoensi* - Zaire
235. *Lamprologus tumbanus* - Zaire
236. *Lamprologus werneri* - Zaire
40. *Lepidolamprologus* - Lake Tanganyika
237. *Lepidolamprologus attenuatus*
238. *Lepidolamprologus cunningtoni*
239. *Lepidolamprologus elongatus* - L. Malawi?
240. *Lepidolamprologus kendalli*
241. *Lepidolamprologus nkambae*
242. *Lepidolamprologus profundicola*
41. *Neolamprologus* - Lake Tanganyika
243. *Neolamprologus bifasciatus*
244. *Neolamprologus boulengeri*
245. *Neolamprologus brevis*
246. *Neolamprologus brichardi*
247. *Neolamprologus bueschei*
248. *Neolamprologus cadopunctatus*
249. *Neolamprologus christyi*
250. *Neolamprologus crassus*
251. *Neolamprologus cylindricus*
252. *Neolamprologus falcicula*
253. *Neolamprologus fasciatus*
254. *Neolamprologus furcifer*
255. *Neolamprologus gracilis*

256. *Neolamprologus hecqui*
257. *Neolamprologus leleupi (*not *leloupi)*
258. *Neolamprologus leloupi (*not *leleupi)*
259. *Neolamprologus longicaudatus*
260. *Neolamprologus longior*
261. *Neolamprologus marunguensis*
262. *Neolamprologus meeli*
263. *Neolamprologus modestus*
264. *Neolamprologus mondabu*
265. *Neolamprologus moorii*
266. *Neolamprologus multifasciatus*
267. *Neolamprologus mustax*
268. *Neolamprologus niger*
269. *Neolamprologus nigriventris*
270. *Neolamprologus obscurus*
271. *Neolamprologus pectoralis*
272. *Neolamprologus petricola*
273. *Neolamprologus pleuromaculatus*
274. *Neolamprologus prochilus*
275. *Neolamprologus pulcher*
276. *Neolamprologus savoryi*
277. *Neolamprologus schreyeni*
278. *Neolamprologus sexfasciatus*
279. *Neolamprologus similis*
280. *Neolamprologus splendens*
281. *Neolamprologus tetracanthus* C Afr
282. *Neolamprologus toae*
283. *Neolamprologus tretocephalus* WAfr
284. *Neolamprologus variostigma*
285. *Neolamprologus ventralis*
286. *Neolamprologus wauthioni*

42. *Teleogramma*
287. *Teleogramma brichardi*
288. *Teleogramma depressum* - Zaire R.
289. *Teleogramma gracile* - C Afr
290. *Teleogramma monogramma* - Zaire

43. *Telmatochromis* - Lake Tanganyika
291. *Telmatochromis bifrenatus*
292. *Telmatochromis brichardi*
293. *Telmatochromis dhonti*
294. *Telmatochromis temporalis*
295. *Telmatochromis vittatus*

Tribe Ectodini

44. *Asprotilapia-* Tanzania
296. *Asprotilapia leptura*

45. *Aulonocranus* - Lake Tanganyika
297. *Aulonocranus dewindti*

46. *Baileychromis-* Lake Tanganyika
298. *Baileychromis centropomoides*

47. *Callochromis* - Lake Tanganyika
299. *Callochromis macrops*
300. *Callochromis melanostigma*
301. *Callochromis pleurospilus*
302. *Callochromis stappersii*

48. *Cardiopharynx* - Lake Tanganyika
303. *Cardiopharynx schoutedeni*

49. *Cunningtonia - Lake Tanganyika*
304. *Cunningtonia longiventralis*

50. *Cyathopharnx-* Lake Tanganyika
305. *Cyathopharnx furcifer*
306. *Cyathopharynx furcifus*

51. *Ectodus - Lake Tanganyika*
307. *Ectodus descampsi*
E. descampsii ornatipinnis

52. *Lestradea* - Lake Tanganyika
308. *Lestradea perspicax*
309. *Lestradea stappersii*

53. *Microdontochromis* - Lake Tanganyika
310. *Microdontochromis rotundiventralis*
311. *Microdontochromis tenuidentatus*

54. *Ophthalmotilapia* - Lake Tanganyika
312. *Ophthalmotilapia boops*
313. *Ophthalmotilapia heterodonta*
314. *Ophthalmotilapia nasuta*
315. *Ophthalmotilapia ventralis*

55. *Xenotilapia* - Lake Tanganyika
316. *Xenotilapia bathyphila*
317. *Xenotilapia boulengeri*
318. *Xenotilapia burtoni*
319. *Xenotilapia caudafasciata*
320. *Xenotilapia flavipinnis*

321. *Xenotilapia longispinis*
322. *Xenotilapia nasus - Burundi*
323. *Xenotilapia nigrolabiata*
324. *Xenotilapia ochrogenys*
325. *Xenotilapia ornatipinnis*
326. *Xenotilapia papilio*
327. *Xenotilapia sima*
328. *Xenotilapia spiloptera*

Tribe Cyprichromini

56. *Cyprichromis* - Lake Tanganyika
329. *Cyprichromis leptosoma*
330. *Cyprichromis microlepidotus*
331. *Cyprichromis pavo*

57. *Paracyprichromis* - Lake Tanganyika
332. *Paracyprichromis brieni*
333. *Paracyprichromis nigripinnis*

Tribe Eretmodini - Lake Tanganyika

58. *Eretmodus*
334. *Eretmodus cyanostictus*

59. *Spathodus*
335. *Spathodus erythrodon*
336. *Spathodus marlieri*

60. *Tanganicodus*
337. *Tanganicodus irsacae*

Tribe Tropheini

61. *Cyphotilapia* - Lake Tanganyika
338. *Cyphotilapia frontosa*

62. *Simochromis* - Lake Tanganyika
339. *Simochromis babaulti*
340. *Simochromis diagramma*
341. *Simochromis loocki*
342. *Simochromis margaretae*
343. *Simochromis marginatus*
344. *Simochromis pleurospilus*

63. *Tropheus* - Lake Tanganyika
345. *Tropheus annectens*
346. *Tropheus brichardi*
347. *Tropheus duboisi*
348. *Tropheus kasabae*
349. *Tropheus moorii*
350. *Tropheus polli*

"Serranochromines" ?monophyly

essentially fluviatile

64. *Chetia*
351. *Chetia brevis*
352. *Chetia flaviventris* - S Afr
353. *Chetia (was Serranochromis) gracilis* - Angola
354. *Chetia mola* - Zambia river
355. *Chetia welwitschi* - W Afr

65. *Pharyngochromis* - Zambesi R
356. *Pharyngochromis darlingi*
should really be *P. acuticeps*

66. *Sargochromis* (maybe a subgenus of *Serranochromis*)
357. *Serranochromis coulteri* - Angola
358. *Serranochromis carlottae*
359. *Serranochromis giardi* - C Afr
360. *Serranochromis greenwoodi* - C Afr.

67. *Serranochromis*
361. *Serranochromis altus* - E Afr
362. *Serranochromis angusticeps* - Zambia
363. *Serranochromis codringtoni* - S Afr
364. *Serranochromis janus* - Malagarazi swamp
365. *Serranochromis longimanus*
366. *Serranochromis macrocephalus* - M
367. *Serranochromis mellandi* - Zambia
368. *Serranochromis meridianus* - E Afr
369. *Serranochromis mortimeri* - Zambia
370. *Serranochromis robustus* - M, S. Afr, T
S. robustus jallae - S Afr
371. *Serranochromis spei*
372. *Serranochromis stappersi* - C Afr
373. *Serranochromis thumbergi*
374. *Serranochromis thysi* - W Afr

Tribe Haplochromini

- **68.** *Astatoreochromis* - E Africa
  - 375. *Astatoreochromis alluaudi* - V
    - *A. alluaudi occidentalis* - L Nakavali
  - 376. *Astatoreochromis straeleni* - Zaire
  - 377. *Astatoreochromis* vanderhorsti - T
- **69.** *Astatotilapia* - E Africa
  - 378. *Astatotilapia calliptera* - Mal
  - 379. *Astatotilapia desfontainii*
  - 380. *Astatotilapia flaviijosephi* - Syria
  - 381. *Astatotilapia roberti* - V
- **70.** *Grammatotria* - Lake Tanganyika
  - 382. *Grammatotria lemairii*
- **71.** *Haplochromis* - Africa
  - 383. *Haplochromis acidens* - V
  - 384. *Haplochromis acuticeps* - Angola
  - 385. *Haplochromis adolphifrederici* - Kivu
  - 386. *Haplochromis aelocephalus* - V
  - 387. *Haplochromis aeneocolor* - L.George
  - 388. *Haplochromis albertianus* - L. Albert
  - 389. *Haplochromis altigenis* - V
  - 390. *Haplochromis angustifrons* - L. Ed
  - 391. *Haplochromis annectidens* - L. Nabug.
  - 392. *Haplochromis apogonoides* - V
  - 393. *Haplochromis arcanus* - V
  - 394. *Haplochromis argenteus* - V
  - 395. *Haplochromis artaxerxes* - V
  - 396. *Haplochromis astatodon* - L. Kivu
  - 397. *Haplochromis avium* - A
  - 398. *Haplochromis bakongo* - Congo R.
  - 399. *Haplochromis barbarae* - E Afr
  - 400. *Haplochromis bareli* - V
  - 401. *Haplochromis bartoni* - V
  - 402. *Haplochromis bayoni* - V
  - 403. *Haplochromis beadlei* - L. Nabugabo
  - 404. *Haplochromis benthicola* - T
  - 405. *Haplochromis bloyeti* - T
  - 406. *Haplochromis boops* - V
  - 407. *Haplochromis brevis* - Mozambique
  - 408. *Haplochromis brownae* - V
  - 409. *Haplochromis bullatus* - L. Albert
  - 410. *Haplochromis burtoni* - T
  - 411. *Haplochromis buysi* - W Afr
  - 412. *Haplochromis callipterus* - M
  - 413. *Haplochromis cassius* - V
  - 414. *Haplochromis cavifrons* - V
  - 415. *Haplochromis centropristoides*
    - *H. centropristoides victorianus* - V
  - 416. *Haplochromis chilotes* - E Afr
  - 417. *Haplochromis chlorochrous* - V
  - 418. *Haplochromis chromogynos* - V
  - 419. *Haplochromis chrysogynaion* - V
  - 420. *Haplochromis cinctus* - V
  - 421. *Haplochromis cinerus* - V
  - 422. *Haplochromis cnester* - V
  - 423. *Haplochromis crassilabris* - V
  - 424. *Haplochromis crebidens* - L Kivu
  - 425. *Haplochromis crocopeplus* - V
  - 426. *Haplochromis cronus*
  - 427. *Haplochromis cryptodon* - V
  - 428. *Haplochromis cryptogramma* - V
  - 429. *Haplochromis decticostoma* - V
  - 430. *Haplochromis demeusii*
  - 431. *Haplochromis dentex* - V
  - 432. *Haplochromis desfontainii*
  - 433. *Haplochromis dichrourus* - V
  - 434. *Haplochromis diplotaenia* - V
  - 435. *Haplochromis dolichorhynchus* - V
  - 436. *Haplochromis dolorosus* - E Afr
  - 437. *Haplochromis eduardii* - E
  - 438. *Haplochromis elegans* - E/G

439. *Haplochromis empodisma*
440. *Haplochromis engystoma* - L Ed
441. *Haplochromis erythrocephalus* - V
442. *Haplochromis erythromaculatus* -C Afr
443. *Haplochromis estor* - V
444. *Haplochromis eutaenia* - V
445. *Haplochromis fasciatus* - T, W Afr
446. *Haplochromis flavipinnis* - V
447. *Haplochromis fuscus* - E
448. *Haplochromis fusiformis* - V
449. *Haplochromis gigliolii* - E Afr
450. *Haplochromis gilberti*
451. *Haplochromis gowersii* - V
452. *Haplochromis gracilior* - Kivu
453. *Haplochromis granti* - V
454. *Haplochromis graueri* - Kivu
455. *Haplochromis guiarti* - V
456. *Haplochromis harpakteridion* - V
457. *Haplochromis hiatus* - V
458. *Haplochromis horas* - T/V
459. *Haplochromis horei* - T
460. *Haplochromis howesi* - V
461. *Haplochromis humilior* - Nile
462. *Haplochromis humilis* - W Afr
463. *Haplochromis insidiae* - Kivu
464. *Haplochromis iris* - V
465. *Haplochromis ishmaeli* - V
466. *haplochromis kamiranzovu* - C Afr
467. *Haplochromis kujunjui* - V
468. *Haplochromis labiatus* - E
469. *Haplochromis labriformis* - V
470. *Haplochromis lacrimosus*
471. *Haplochromis lanceolatus* - A
472. *Haplochromis laparogramma* - V
473. *Haplochromis latifasciatus* - Kyoga
474. *Haplochromis limax* - E
475. *Haplochromis lividus* - V
476. *Haplochromis loati* - A
477. *Haplochromis longirostris* - V
478. *Haplochromis lucullae* - W Afr
479. *Haplochromis macconneli* - L Rudolf
480. *Haplochromis macrognathus* - V
481. *Haplochromis macrops* - V
482. *Haplochromis macropsoides* - L. Geo
483. *Haplochromis maculipinna*
484. *Haplochromis mahagiensis* - L Albert
485. *Haplochromis maisomei* - V
486. *Haplochromis malacophagus* - E Afr
487. *Haplochromis mandibularis* - V
488. *Haplochromis martini* - V
489. *Haplochromis maxillaris* - V
490. *Haplochromis megalops* - V
491. *Haplochromis melanopterus* - V
492. *Haplochromis melanopus* - V
493. *Haplochromis melichrous* - V
494. *Haplochromis mentatus* - E
495. *Haplochromis mento* - V
496. *Haplochromis michaeli* - V
497. *Haplochromis microchrysomelas* - Kivu
498. *Haplochromis microdon* - V
499. *Haplochromis moeruensis* - Zaire
500. *Haplochromis multiocellatus* - W Afr
501. *Haplochromis mylergates* - V
502. *Haplochromis mylodon* - George
503. *Haplochromis nanoserranus* - V
504. *Haplochromis nigrescens* - V
505. *Haplochromis nigricans* - Nile
506. *Haplochromis nigripinnis* - E
507. *Haplochromis nigroides* - Kivu
508. *Haplochromis niloticus*
509. *Haplochromis nubilus* - V
510. *Haplochromis nuchisquamulatus* - V
511. *Haplochromis nyanzae* - V

512. *Haplochromis nyererei* - V
513. *Haplochromis obesus* - V
514. *Haplochromis obliquidens* - V
515. *Haplochromis obtusidens* - V
516. *Haplochromis occultidens* - Kivu
517. *Haplochromis oligacanthus* - riverine
518. *Haplochromis olivaceus* - Kivu
519. *Haplochromis oregosoma* - G
520. *Haplochromis orthostoma* - E Afr
521. *Haplochromis pachycephalus* - V
522. *Haplochromis pallidus*
523. *Haplochromis paludinosus* - E Afr
524. *Haplochromis pappenheimi* - E
525. *Haplochromis paraguiarti* - E. Afr
526. *Haplochromis paraplagiostoma* - V
527. *Haplochromis paropius* - V
528. *Haplochromis parorthostoma* - E. Afr
529. *Haplochromis parvidens* - E. Afr
530. *Haplochromis paucidens* - Kivu
531. *Haplochromis pectoralis* - E. Afr
532. *Haplochromis pellegrini* - V
533. *Haplochromis percoides* - V
534. *Haplochromis perrieri* - V
535. *Haplochromis petronius* - G
536. *Haplochromis pharyngalis* - E
537. *Haplochromis pharyngomylus* - V
538. *Haplochromis phenochilus* - M
539. *Haplochromis phytophagus* - V
540. *Haplochromis piceatus* - V
541. *Haplochromis pitmani* - V
542. *Haplochromis placodus* - E Afr
543. *Haplochromis plagiodon* - V
544. *Haplochromis plagiostoma* - V
545. *Haplochromis plutonius* - V
546. *Haplochromis prodromus* - V
547. *Haplochromis prognathus* - V
548. *Haplochromis pseudopellegrini* - V
549. *Haplochromis ptistes* - V
550. *Haplochromis pyrrhocephalus* - V (thesis publication)
551. *Haplochromis pyrrhopteryx* - V
552. *Haplochromis riponianus* - E Afr
553. *Haplochromis rubescens* - Kivu
554. *Haplochromis rudolfianus* - Turkana
555. *Haplochromis sauvagei*
556. *Haplochromis saxicola* - E Afr
557. *Haplochromis scheffersi* - Kivu
558. *Haplochromis schubotzi* - L Ed
559. *Haplochromis schubotziellus* - G
560. *Haplochromis schwetzi* - W Afr
561. *Haplochromis serranus* - E Afr
562. *Haplochromis serridens* - E
563. *Haplochromis simpsoni* - E Afr
564. *Haplochromis spekii* - V
565. *Haplochromis squamipinnis* - E
566. *Haplochromis squamulatus* - E. Afr
567. *Haplochromis stanleyi* - V
568. *Haplochromis stappersii* - Zaire
569. *Haplochromis sulphureus* - E Afr
570. *Haplochromis swynnertoni*
571. *Haplochromis taurinus* - E
572. *Haplochromis teegelaari* - V
573. *Haplochromis teunisrasi* - V
574. *Haplochromis theliodon* - E Afr
575. *Haplochromis thereuterion* - V
576. *Haplochromis thuragnathus* - V
577. *Haplochromis torrenticola* - W Afr
578. *Haplochromis tridens* - V
579. *Haplochromis turkanae* - L Turkana
580. *Haplochromis tweddlei* - E Afr
581. *Haplochromis tyrianthinus* - V
582. *Haplochromis velifer* - E Afr
583. *Haplochromis venator* - E Afr

   584. *Haplochromis vicarius* - E Afr
   585. *Haplochromis victorianus*
   586. *Haplochromis vittatus* - Kivu
   587. *Haplochromis welcommei* - V
   588. *Haplochromis wingatii* - Sudan
   589. *Haplochromis worthingtoni*
   590. *Haplochromis xenognathus* - V
   591. *Haplochromis xenostoma* - V

72. *Hoplotilapia* - Lake Victoria
   592. *Hoplotilapia retrodens*

73. *Macropleurodus* - Lake Victoria
   593. *Macropleurodus bicolor*

74. *Orthochromis* - rheophilic haplochromines "goby cichlids" Malagarazi, T. drainage
   594. *Orthochromis kasuluensis*
   595. *Orthochromis luichensis*
   596. *Orthochromis malagaraziensis* (*was *Schwetzochromis)*
   597. *Orthochromis mazimeroensis*
   598. *Orthochromis mosoensis*
   599. *Orthochromis rubrolabialis*
   600. *Orthochromis rugufuensis*
   601. *Orthochromis uvinzae*

75. *Pallidochromis* - Lake Malawi
   602. *Pallidochromis tokolosh*

76. *Paralabidochromis* - Lake Victoria
   603. *Paralabidochromis victoriae*

77. *Platytaeniodus* - Lake Victoria
   604. *Platytaeniodus degeni*

78. *Pseudocrenilabrus*
   605. *Pseudocrenilabrus dispersus* - W Afr
   606. *Pseudocrenilabrus multicolor* - V
   607. *Pseudocrenilabrus nicholsi* - Zaire
   608. *Pseudocrenilabrus philander* - S&W Afr

79. *Schubotzia*
   609. *Schubotzia eduardiana* - L Edward

80. *Schwetzochromis*
   610. *Schwetsochromis kalungwishiensis - Zambia*
   611. *Schwetzochromis luongoensis* - Zaire R
   612. *Schwetzochromis machadoi* - W. Afr
   613. *Schwetzochromis malagaraziensis* - T *may now be in *Orthochromis*
   614. *Schwetzochromis neodon* - Zaire
   615. *Schwetzochromis neodon* - Zaire
   616. *Schwetzochromis polyacanthus* - Zaire
   617. *Schwetzochromis stormsi* - Zaire
   618. *Schwetzochromis torrenticola*

81. *Thoracochromis*
   619. *Thoracochromis brauschi*
   620. *Thoracochromis buysi* - Angola
   621. *Thoracochromis callichromus* - E Afr

82. *Triglachromis* - Lake Tanganyika
   622. *Triglachromis otostigma*

Mbuna group

83. *Alticorpus* - Lake Malawi
   623. *Alticorpus macrocleithrum*
   624. *Alticorpus mentale*
   625. *Alticorpus pectinatum*
   626. *Alticorpus peterdaviesi*
   627. *Alticorpus profundicola*

84. *Aulonocara*- Lake Malawi
   628. *Aulonocara aquilonium*
   629. *Aulonocara auditor*
   630. *Aulonocara baenschi*
   631. *Aulonocara brevinudus*
   632. *Aulonocara brevirostre*
   633. *Aulonocara ethelwynnae*
   634. *Aulonocara gertrudae*
   635. *Aulonocara guentheri*
   636. *Aulonocara hansbaenschi*
   637. *Aulonocara hueseri*
   638. *Aulonocara jacobfreibergi*
   639. *Aulonocara korneliae*
   640. *Aulonocara maylandi*

A. maylandi kandeensis
641. *Aulonocara nyassae*
642. *Aulonocara rostratum*
643. *Aulonocara saulosi*
644. *Aulonocara steveni*
645. *Aulonocara stuartgranti*
646. *Aulonocara trematocephala*
85. *Cyathochromis*- Lake Malawi
647. *Cyathochromis obliquidens*
86. *Iodotropheus* - Lake Malawi
648. *Iodotropheus declivitas*
649. *Iodotropheus sprengerae*
650. *Iodotropheus stuartgranti*
87. *Labeotropheus* - Lake Malawi
651. *Labeotropheus fuelleborni*
652. *Labeotropheus trewavasae*
88. *Labidochromis* - Lake Malawi
653. *Labidochromis caeruleus*
654. *Labidochromis chisumulae*
655. *Labidochromis flavigulis*
656. *Labidochromis freibergi*
657. *Labidochromis gigas*
658. *Labidochromis heterodon*
659. *Labidochromis ianthinus*
660. *Labidochromis lividus*
661. *Labidochromis maculicauda*
662. *Labidochromis mathotho*
663. *Labidochromis mbenjii*
664. *Labidochromis mylodon*
665. *Labidochromis pallidus*
666. *Labidochromis shiranus*
667. *Labidochromis strigatus*
668. *Labidochromis textilis*
669. *Labidochromis vellicans*
670. *Labidochromis zebroides*
89. *Lethrinops*- Lake Malawi
671. *Lethrinops albus*
672. *Lethrinops altus*
673. *Lethrinops argenta*
674. *Lethrinops auritus*
675. *Lethrinops christyi*
676. *Lethrinops gossei*
677. *Lethrinops leptodon*
678. *Lethrinops lethrinus*
679. *Lethrinops longimanus*
680. *Lethrinops longipinnis*
681. *Lethrinops lunaris*
682. *Lethrinops macracanthus*
683. *Lethrinops macrochir*
684. *Lethrinops macrophthalmus*
685. *Lethrinops marginatus*
686. *Lethrinops micrentodon*
687. *Lethrinops microdon*
688. *Lethrinops microstoma*
689. *Lethrinops mylodon*
690. *Lethrinops mylodon borealis*
691. *Lethrinops oculatus*
692. *Lethrinops parvidens*
693. *Lethrinops polli*
694. *Lethrinops stridei*
90. *Melanochromis* - Lake Malawi
695. *Melanochromis auratus*
696. *Melanochromis baliodigma*
697. *Melanochromis benetos*
698. *Melanochromis brevis*
699. *Melanochromis chipokae*
700. *Melanochromis cyaneorhabdos*
701. *Melanochromis dialeptos*
702. *Melanochromis elastodema*
703. *Melanochromis heterochromis*
704. *Melanochromis interruptus*
705. *Melanochromis joanjohnsonae*
706. *Melanochromis johannii*
707. *Melanochromis labrosus*
708. *Melanochromis lepidiadaptes*
709. *Melanochromis loriae*
710. *Melanochromis mellitus*
711. *Melanochromis melnaopterus*
712. *Melanochromis parallelus*
713. *Melanochromis perileucos*
714. *Melanochromis perspicax*
715. *Melanochromis robustus*
716. *Melanochromis simulans*
717. *Melanochromis vermivorus*
718. *Melanochromis xanthodigma*
91. *Petrotilapia* - Lake Malawi
719. *Petrotilapia chrysos*
720. *Petrotilapia genulutea*
721. *Petrotilapia nigra*
722. *Petrotilapia tridentiger*
92. *Pseudotropheus* - Lake Malawi
723. *Pseudotropheus ater*

724. *Pseudotropheus aurora*
725. *Pseudotropheus barlowi*
726. *Pseudotropheus crabro*
727. *Pseudotropheus cyaneus*
728. *Pseudotropheus demasoni*
729. *Pseudotropheus elegans*
730. *Pseudotropheus elongatus*
731. *Pseudotropheus estherae*
732. *Pseudotropheus fainzilberi*
733. *Pseudotropheus flavus*
734. *Pseudotropheus fuscoides*
735. *Pseudotropheus fuscus*
736. *Pseudotropheus hajomaylandi*
737. *Pseudotropheus heteropictus*
738. *Pseudotropheus lanisticola*
739. *Pseudotropheus livingstonii* - Zambesi
740. *Pseudotropheus lombardoi*
741. *Pseudotropheus longior*
742. *Pseudotropheus lucerna*
743. *Pseudotropheus macrophthalmus*
744. *Pseudotropheus microstoma*
745. *Pseudotropheus minutus*
746. *Pseudotropheus modestus*
747. *Pseudotropheus novemfasciatus*
748. *Pseudotropheus purpuratus*
749. *Pseudotropheus pursus*
750. *Pseudotropheus saulosi*
751. *Pseudotropheus tropheops*
    - *P. tropheops gracilior*
    - *P. tropheops romandi*
752. *Pseudotropheus tursiops*
753. *Pseudotropheus williamsi*
754. *Pseuodotropheus socolofi*

non-Mbuna, Lake Malawi group

93. *Aristochromis*- Lake Malawi
755. *Aristochromis christyi*

94. *Buccochromis* - Lake Malawi
756. *Buccochromis atritaeniatus*
757. *Buccochromis heterotaenia*
758. *Buccochromis lepturus*
759. *Buccochromis nototaenia*
760. *Buccochromis oculatus*
761. *Buccochromis rhoadesii*
762. *Buccochromis spectabilis*

95. *Caprichromis* - Lake Malawi
763. *Caprichromis leimi*

96. *Champsochromis*- Lake Malawi
764. *Champsochromis caeruleus*
765. *Champsochromis spilorhynchus*

97. *Chilotilapia*- Lake Malawi
766. *Chilotilapia rhoadesii*

98. *Copadichromis*- Lake Malawi
767. *Copadichromis azureus*
768. *Copadichromis boadzulu*
769. *Copadichromis borleyi*
770. *Copadichromis chrysogaster*
771. *Copadichromis chrysonotus*
772. *Copadichromis conophoros*
773. *Copadichromis cyaneus*
774. *Copadichromis cyclicos*
775. *Copadichromis eucinostomus*
776. *Copadichromis flavimanus*
777. *Copadichromis inornatus*
778. *Copadichromis jacksoni*
779. *Copadichromis likomae*
780. *Copadichromis mbenjii*
781. *Copadichromis mloto*
782. *Copadichromis nkatae*
783. *Copadichromis pleurostigma*
784. *Copadichromis pleurostigmoides*
785. *Copadichromis prostoma*
786. *Copadichromis quadrimaculatus*
787. *Copadichromis thinos*
788. *Copadichromis trimaculatus*
789. *Copadichromis verduyni*
790. *Copadichromis virginalis*

99. *Cyrtocara*
791. *Cyrtocara moorii*

100. *Dimidiochromis*- Lake Malawi
792. *Dimidiochromis compressiceps*
793. *Dimidiochromis dimidiatus*
794. *Dimidiochromis kiwingi*
795. *Dimidiochromis strigatus*

101. *Diplotaxodon*- Lake Malawi
796. *Diplotaxodon aeneus*
797. *Diplotaxodon apogon*
798. *Diplotaxodon argenteus*

   799. *Diplotaxodon ecclesi*
   800. *Diplotaxodon greenwoodi*
   801. *Diplotaxodon limnothrissa*
   802. *Diplotaxodon macrops*
102. *Docimodus*- Lake Malawi
   803. *Docimodus evelynae*
   804. *Docimodus johnstoni*
103. *Hemitilapia*- Lake Malawi
   805. *Hemitilapia oxyrhyncha*
104. *Maravichromis*- Lake Malawi
   806. *Maravichromis anaphyrmus*
   807. *Maravichromis balteatus*
   808. *Maravichromis epichorialis*
   809. *Maravichromis ericotaenia*
   810. *Maravichromis formosus*
   811. *Maravichromis guentheri*
   812. *Maravichromis incola*
   813. *Maravichromis labidodon*
   814. *Maravichromis lateristriga*
   815. *Maravichromis melanotaenia*
   816. *Maravichromis mola*
   817. *Maravichromis mollis*
   818. *Maravichromis obtusus*
   819. *Maravichromis plagiotaenia*
   820. *Maravichromis semipalatus*
   821. *Maravichromis sphaerodon*
105. *Nimbochromis* - Lake Malawi
   822. *Nimbochromis fuscotaeniatus*
   823. *Nimbochromis linni*
   824. *Nimbochromis livingstonii*
   825. *Nimbochromis maculimanus*
   826. *Nimbochromis pardalis*
   827. *Nimbochromis polystigma*
   828. *Nimbochromis venustus*
106. *Otopharynx* - Lake Malawi
   829. *Otopharynx argyrosoma*
   830. *Otopharynx auromarginatus*
   831. *Otopharynx brooksi*
   832. *Otopharynx decorus*
   833. *Otopharynx heterodon*
   834. *Otopharynx lithobates*
   835. *Otopharynx ovatus*
   836. *Otopharynx selenurus*
   837. *Otopharynx speciosus*
   838. *Otopharynx tetraspilus*
   839. *Otopharynx tetrastigma*
   840. *Otopharynx walteri*
107. *Placidochromis* - Lake Malawi
   841. *Placidochromis electra*
   842. *Placidochromis hennydaviesae*
   843. *Placidochromis johnstoni*
   844. *Placidochromis longimanus*
   845. *Placidochromis milomo*
   846. *Placidochromis stonemani*
   847. *Placidochromis subocularis*
108. *Protomelas* - Lake Malawi
   848. *Protomelas annectens*
   849. *Protomelas dejunctus*
   850. *Protomelas fenestratus*
   851. *Protomelas insignis*
   852. *Protomelas kirkii*
   853. *Protomelas labridens*
   854. *Protomelas macrodon*
   855. *Protomelas marginatus*
   856. *Protomelas marginatus vuae*
   857. *Protomelas pleurotaenia*
   858. *Protomelas similis*
   859. *Protomelas spilonotus*
   860. *Protomelas spilopterus*
   861. *Protomelas taeniolatus*
   862. *Protomelas triaenodon*
   863. *Protomelas virgatus*
109. *Rhamphochromis* - Lake Malawi
   864. *Rhamphochromis brevis*
   865. *Rhamphochromis esox*
   866. *Rhamphochromis ferox*
   867. *Rhamphochromis leptosoma*
   868. *Rhamphochromis longiceps*
   869. *Rhamphochromis lucius*
   870. *Rhamphochromis macrophthalmus*
   871. *Rhamphochromis woodi*
110. *Taeniochromis* - Lake Malawi
   872. *Taeniochromis holotaenia*
111. *Trematocranus* - Lake Malawi
   873. *Trematocranus labifer*
   874. *Trematocranus microstoma*
   875. *Trematocranus placodon*
112. *Tyrannochromis*
   876. *Tyrannochromis nigriventer*
   877. *Tyrranochromis macrostoma*
   878. *Tyrranochromis maculiceps*

879. *Tyrranochromis polyodon*

Other

113. *Benthochromis*- Lake Tanganyika
- 880. *Benthochromis melanoides*
- 881. *Benthochromis tricoti*

114. *Chaetodon*
- 882. *Chaetodon guttatissimus*

115. *Cheilochromis*- Lake Malawi
- 883. *Cheilochromis euchilus*
- 884. *Chilochromis duponti*

116. *Corematodus*- Lake Malawi
- 885. *Corematodus shiranus*
- 886. *Corematodus taeniatus*

117. *Ctenopharynx*- Lake Malawi
- 887. *Ctenopharynx nitidus*
- 888. *Ctenopharynx pictus*

118. *Cyclopharynx*
- 889. *Cyclopharynx fwae* - C Afr
- 890. *Cyclopharynx schwetzi* - Zaire

119. *Cynotilapia*- Lake Malawi
- 891. *Cynotilapia afer*
- 892. *Cynotilapia axelrodi*
- 893. *Cynotilapia zebroides*

120. *Eclectochromis*- Lake Malawi
- 894. *Eclectochromis festivus*
- 895. *Eclectochromis lobochilus*
- 896. *Eclectochromis ornatus*

121. *Enantiopus* - Lake Tanganyika
- 897. *Enantiopus albini*
- 898. *Enatniopus melanogenys*

122. *Exochochromis*- Lake Malawi
- 899. *Exochochromis anagenys*

123. *Fossorochromis*- Lake Malawi
- 900. *Fossorochromis rostratus*

124. *Genyochromis*- Lake Malawi
- 901. *Genyochromis mento*

125. *Gephyrochromis*- Lake Malawi
- 902. *Gephyrochromis lawsi*
- 903. *Gephyrochromis moorii*

126. *Gnathochromis* - Lake Tanganyika
- 904. *Gnathochromis permaxillaris*
- 905. *Gnathochromis pfefferi*

127. *Greenwoodochromis* - Lake Tanganyika
- 906. *Greenwoodochromis christyi*

128. *Haplotaxodon* - Lake Tanganyika
- 907. *Haplotaxodon microlepis*

129. *Hemitaeniochromis*- Lake Malawi
- 908. *Hemitaeniochromis urotaenia*

130. *Lichnochromis*- Lake Malawi
- 909. *Lichnochromis acuticeps*

131. *Limnotilapia* - Lake Tanganyika
- 910. *Limnotilapia dardennii*

132. *Lobochilotes* - Lake Tanganyika
- 911. *Lobochilotes labiatus*

133. *Metriaclima*- Lake Malawi
- 912. *Metriaclima benetos*
- 913. *Metriaclima callainos*
- 914. *Metriaclima chrysomallos*
- 915. *Metriaclima cyneusmarginatus*
- 916. *Metriaclima emmiltos*
- 917. *Metriaclima greshakei*
- 918. *Metriaclima mbenjii*
- 919. *Metriaclima melabranchion*
- 920. *Metriaclima phaeos*
- 921. *Metriaclima pyrsonotos*
- 922. *Metriaclima sandaracinos*
- 923. *Metriaclima thapsinogen*
- 924. *Metriaclima xanstomachus*
- 925. *Metriaclima zebra*

134. *Nyassachromis* - Lake Malawi
- 926. *Nyassachromis breviceps*
- 927. *Nyassachromis leuciscus*
- 928. *Nyassachromis nigritaeniatus*
- 929. *Nyassachromis purpurans*
- 930. *Nyassachromis serenus*
- 931. *Nyassochromis microcephalus*

135. *Platygnathochromis* - Lake Malawi
- 932. *Platygnathochromis melanonotus*

136. *Plecodus* - Lake Tanganyika
- 933. *Plecodus elaviae*
- 934. *Plecodus multidentatus*
- 935. *Plecodus paradoxus*
- 936. *Plecodus straeleni*

137. *Pseudosimochromis* - Lake Tanganyika
- 937. *Pseudosimochromis curvifrons*

138. *Pterochromis* - Lake Tanganyika
- 938. *Pterochromis congicus*
- 939. *Pterochromis polyodon*

139. *Reganochromis* - Lake Tanganyika
  940. *Reganochromis calliurus*
140. *Sciaenochromis* - Lake Malawi
  941. *Sciaenochromis ahli*
  942. *Sciaenochromis benthicola*
  943. *Sciaenochromis gracilis*
  944. *Sciaenochromis psammophilus*
  945. *Sciaenochromis spilostichus*
141. *Stigmatochromis* - Lake Malawi
  946. *Stigmatochromis modestus*
  947. *Stigmatochromis pholidophorus*
  948. *Stigmatochromis pleurospilus*
  949. *Stigmatochromis woodi*
142. *Taeniolethrinops* - Lake Malawi
  950. *Taeniolethrinops cyrtonotus*
  951. *Taeniolethrinops laticeps*
  952. *Taeniolethrinops praeorbitalis*
  953. *Taeniolethrinops surcicauda*
143. *Tangachromis* - Lake Tanganyika
  954. *Tangachromis dhanisi*
144. *Teleotrematocara* - Lake Tanganyika
  955. *Teleotrematocara macrostom*
145. *Tramitichromis* - Lake Malawi
  956. *Tramitichromis brevis*
  957. *Tramitichromis intermedius*
  958. *Tramitichromis lituris*
  959. *Tramitichromis trilineata*
  960. *Tramitichromis variabilis*
146. *Trematocara* - Lake Tanganyika
  961. *Trematocara caparti*
  962. *Trematocara kufferathi*
  963. *Trematocara marginatum*
  964. *Trematocara nigrifrons*
  965. *Trematocara stigmaticum*
  966. *Trematocara unimaculatum*
  967. *Trematocara variabile*
  968. *Trematocara zebra*
147. *Trematochromis* - Lake Tanganyika
  969. *Trematochromis schreyeni*

Mbibi - Lake Victoria
148. *Lithochormis* (+ 9 unnamed species)
  970. *Lithochromis rubripinnis*
  971. *Lithochromis rufus*
  972. *Lithochromis xanthopteryx*
149. *Mbipia* (+ 4 unnamed species)
  973. *Mbipia lutea*
  974. *Mbipia mbipia*
150. *Neochromis*
  975. *Neochromis gigas*
  976. *Neochromis greenwoodi*
  977. *Neochromis nigricans*
  978. *Neochromis omnicaeruleus*
  979. *Neochromis rufocaudalis*
  980. *Neochromis simotes*
151. *Pundamilia*
  981. *Pundamilia azurea*
  982. *Pundamilia igneopinnis*
  983. *Pundamilia macrocephala*
  984. *Pundamilia nyererei*
  985. *Pundamilia pundamilia*
152. *"rock picker" genus* (+ 9 unnamed species)
  986. *"Haplochromis" cyaneus*
"Haplochromis" flavu

Appendix B. List of Comparative Material Examined

1. Cichlidae - specimens cleared and stained following the procedure of Taylor and VanDyke, 1985

Lamprologus mocquardi USNM 331358, 2 specimens

Tropheus moorei USNM 191512, 3 specimens

Copadichromis chrysonotus USNM 261836 3 specimens

Melanochromis vermivorus USNM 261830, 3 specimens

Rhamphochromis sp. USNM 280070, 1 specimen

Haplochromis flaviijosephi NMC 79-0694, 2 specimens

H. dashingi NMC 74-0522, 3 specimens

H. desfontainesi NMC 85-0499, 2 specimens

Astatotilapia bloyeti NMC 81-0188, 3 specimens

Astatotilapia bloyeti NMC 81-0195, 3 specimens

Psammochromis sp. NMC 81-0266, 3 specimens

Prognathochromis sp. NMC 81-0266, 2 specimens

Lipochromis sp. NMC 81-0266, 1 specimen

Yssichromis sp. NMC 81-0266, 1 specimen

Hemichromis guttatus uncatalogued, 2 specimens

Pseudotropheus sp. uncatalogued, 2 specimens

Pelviachromis kribensis uncatalogued, 1 specimen

2. Cichlidae specimens preserved in alcohol and x-rayed

Neotropical

Aequidens pulcher, NMC 76-0382, 2 specimens

Astronotus ocellatus, NMC 79-0918, 1 specimen, uncatalogued 1 specimen

Cichlasoma bimaculatum, NMC 77-0030, 3 specimens

Crenicichla wallacei, NMC 67-0138, 1 specimen; NMC 67-0144, 1 specimen

Geophagus brasiliensis, NMC 85-0125, 1; NMC 85-0130, 1 specimen

Geophagus surinamensis, NMC 67-0126, 3 specimens

Neetroplus nematops, NMC 89-0073, 2 specimens

Pterophyllum scalare, NMC 74-0084, 2 specimens

India/Madagascar/Middle East

Etroplus maculatus, NMC 81-0931, 1 specimen

Etroplus suratensis, NMC 81-0519, 1 specimen

Iranocichla hormuzensis, NMC 79-0138, 17 specimens

Tristramella simonis, NMC 80-0405, 2 specimen

Danakilia franchetti, NMC 82-0212, 1 specimen

Haplochromis flaviijosephi, NMC 79-0695, 6 specimens

African

Astatoreochromis alluaudi, NMC 81-0266, 1 specimen

Astatotilapia bloyeti, NMC 81-0195, 3 specimens; NMC 81-0188, 6 specimens

Haplochromis dashingi, NMC 74-0522, 7 specimens

Haplochromis desfontainesi, NMC 85-0499, 6 specimens

Haplochromis [*Prognathochromis*] sp., NMC 81-0266, 2 specimens

Haplochromis [*Lipochromis*] sp., NMC 81-0266, 2 specimens

Haplochromis [*Yssichromis*] *laparogramma*, NMC 81-0266, 2 specimens

Haplochromis [*Yssichromis*] sp., NMC 81-0266, 3 specimens

Haplochromis [*Psammochromis*] sp., NMC 81-0266, 7 specimens

Hemichromis sp., uncatalogued, 1 specimen

Pelviachromis sp., uncatalogued, 1 specimen

Lamprologus mocquardi, USNM 331358, 1 specimen

Rhamphochromis sp., USNM 280070, 2 specimens

Sarotherodon auratus, NMC 80-0831, 5 specimens

Serranochromis robustus, NMC 74-0521, 2 specimens

Tilapia rendahli, NMC 81-0228, 3; NMC 82-0228, 1 specimen

Tilapia zillii, uncatalogued, 1 specimen; NMC 80-0832, 5 specimens

3. Cichlidae specimens skeletonized

African

Hemichromis guttatus uncatalogued, 1 specimen

Oreochromis niloticus uncatalogued, 5 specimens

Pelviachromis kribensis uncatalogued, 1 specimen

Tilapia zillii uncatalogued, 1 specimen

Pseudotropheus sp. uncatalogued, 1 specimen

South American

Symphysodon sp. uncatalogued, 1 specimen

Appendix C. Greenwood's (1980) generic names for species of the genus *Haplochromis* of Lake Victoria

***Astatotilapia* - (excluding non-Lake Victoria basin)**
Astatotilapia aeneocolor
A. barbarae
A. brownae
A. cinerea
A. eduardi
A. elegans
A. engyostoma
A. lacrimosa
A. latifasciata
A. macrops
A. macropsoides
A. martini
A. megalops
A. melanopus
A. oregosoma
A. pallida
A. piceata
A. schubotziella
A. velifer

Harpagochromis
H. serranus
H. victorianus
H. nyanzae
H. spekii
H. maculipinna
H. squamipinnis
H. boops
H. pachycephalus
H. thuragnathus
H. guiarti
H. artaxerxes
H. altigenis
H. pectoralis
H. plagiostoma
H. michaeli
H. diplotaenia
H. paraplagiostoma
H. worthingtoni

Prognathochromis (Prognathochromis)
P. arcanus
P. argenteus
P. bartoni
P. bayoni
P. decticostoma
P. dentex
P. dichrourus
P. estor
P. flavipinnis
P. gilberti
P. gowersi
P. longirostris
P. macrognathus
P. mandibularis
P. mento
P. nanoserranus
P. paraguiarti
P. pellegrini
P. percoides
P. prognathus
P. pseudopellegrini
P. venator
P. vittatus
P. xenostoms

Prognathochromis (Tridontochromis)
P. chlorochrous
P. crocopeplus
P. cryptogramma
P. dolichorhynchus
P. melichrous
P. plutonius
P. sulphureus
P. tridens
P. tyrianthinus
P. ?eutaenia

Yssichromis
Y. fusiformis
Y. laparogramma
Y. pappenheimi
Pyxichromis
P. orthostoma
P. parorthostoma

Lipochromis (Lipochromis)
L. taurinus
L. maxillaris
L. obesus
L. melanopterus

Lipochromis (Cleptochromis)
L. cryptodon
L. microdon
L. parvidens

Gaurochromis (Gaurochromis)
G. empodisma
G. simpsoni
G. angustifrons

Gaurochromis (Mylacochromis)
G. obtusidens

Labrochromis
L. humilior
L. ptistes
L. mylodon
L. ishmaeli
L. pharyngomylus

L. teegelaari
L. mylergates
L. adolphifrederici
L. placodus

Enterochromis
E. cinctus
E. paropius
E. nigripinnis
E. erythrocephalus

Xystichromis
X. bayoni
X. nuchisquamulatus
X. phytophagus

Neochromis
N. nigricans
N. serridens
N. fuscus

Haplochromis
H. limax
H. annectidens
H. lividus
H. astatodon
H. obliquidens

Psammochromis
P. graueri
P. schubotzi
P. riponianus
P. saxicola
P. aelocephalus
P. acidens
P. cassius

Allochromis
A. welcommei

Ptyochromis
P. sauvagei
P. annectens
P. granti
P. xenognathus

Paralabidochromis
P. beadlei
P. paucidens
P. crassilabris
P. labiatus
P. plagiodon
P. chromogynos
P. chilotes
P. victoriae

Hoplotilapia
H. retrodens

Platytaeniodus
P. degeni

Macropleurodus
M. bicolor

Schubotzia
S. eduardiana

Appendix D. Data matrix of osteological characters.

character species	1	2	3	4	5	6	7
Outgroup	0	0	0	0	0	0	0
Mahengechromis	2	0	1	-	2	0	0
Etroplus	1	1	0	0	3	0	0
Madagascan cichlids	1	0/1	0	-	-	-	-
Heterochromis	1	1	0	-	-	0	-
Neotropical cichlids	2/3	1	1	0	1	0	0
Tylochromis	1	1	1	-	-	-	0
Hemichromis	2	2	1	0	2	0	0
Pelviachromis	2	3	1	0	1	0	0
Oreochromis	2	3	1	0	-	0	2
Tilapia	2	3	1	0	2	0	0
Iranocichla	2	1	1	2	1	0	1
Lamprologus	3	2	1	1	3	0	2
Tropheus	2	2	1	1	1	0	2
Copadichromis	2	2	1	0	1	0	1
Astatotilapia	2	2	1	0	3	0	1
H. [*Psammochromis*]	2	2	1	0	1	1	2
H. [*Yssichromis*]	2	2	1	0	3	1	1
H. [*Prognathochromis*]	2	2	1	0	3	0	1
H. [*Lipochromis*]	2	2	1	0	3	1	2
Rhamphochromis	2	2	1	1	2	0	1
Melanochromis	2	2	1	0	3	0	1
Pseudotropheus	2	2	1	0	3	0	1

character species	8	9	10	11	12	13	14	15
Outgroup	0	0	0	0	0	0	0	0
Mahengechromis	0	0	0	0/1/2	1	0	2	-
Etroplus	0	0	0	1	-	-	1	0
Madagascan cichlids	0	-	-	-	-	-	-	-
Heterochromis	2	-	-	2	-	-	-	-
Neotropical cichlids	1	1	0	1	-	-	1	1
Tylochromis	0	-	-	2	-	-	-	-
Hemichromis	1	0	0	1	0	1	0	0
Pelviachromis	0	0	0	2	0	0	0	1
Oreochromis	0	0	0	1	0	0	1	0
Tilapia	0	0	0	2	0	1	0	0
Iranocichla	0	0	0	1	1	1	1	0
Lamprologus	0	1	1	1	0	0	1	0
Tropheus	0	0	2	1	1	0	1	0
Copadichromis	0	0	0	2	0	0	0	0
Astatotilapia	0	0	0	2	0	0	1	0
H. [*Psammochromis*]	0	0	0	0	0	0	1	0
H. [*Yssichromis*]	0	0	0	0	0	0	1	0
H. [*Prognathochromis*]	0	0	0	0	0	0	1	0
H. [*Lipochromis*]	0	0	0	2	0	0	1	0
Rhamphochromis	0	0	1	1	0	0	1	0
Melanochromis	0	0	0	2	0	0	1	0
Pseudotropheus	0	0	0	0	0	0	1	0

character	16	17	18	19	20	21	22
species							
Outgroup	0	0	0	0	0	0	0
Mahengechromis	0	1	1	-	-	0	1
Etroplus	0	-	0	-	0	0	1
Madagascan cichlids	-	-	-	-	-	-	-
Heterochromis	-	3	0	0	-	-	1
Neotropical cichlids	1	2	-	0	1	0	1
Tylochromis	-	-	-	-	-	-	-
Hemichromis	0	1	0	1	1	0	0
Pelviachromis	0	-	-	-	-	1	1
Oreochromis	1	1	0	1	0	0	1
Tilapia	1	1	0	1	0	1	1
Iranocichla	0	3	1	1	0	0	1
Lamprologus	1	0	0	0	0	0	0
Tropheus	1	0	0	0	0	0	1
Copadichromis	1	3	1	0	0	1	1
Astatotilapia	0	1	1	0	0	0	1
H. [*Psammochromis*]	0	0	1	0	0	0	1
H. [*Yssichromis*]	0	0	1	0	0	0	1
H. [*Prognathochromis*]	0	0	1	0	0	0	1
H. [*Lipochromis*]	0	1	1	0	0	0	1
Rhamphochromis	0	4	1	0	0	0	1
Melanochromis	0	3	1	1	1	0	1
Pseudotropheus	1	1	1	0	0	0	1

character species	23	24	25	26	27	28	29	30
Outgroup	0	0	0	0	0	0	0	0
Mahengechromis	0/1/2	2	0	0	1	0	-	0
Etroplus	1	0	0/1	0	0	1	0	0
Madagascan cichlids	-	-	0/1	-	-	-	-	-
Heterochromis	2	0	1	1	-	0	-	0
Neotropical cichlids	1	-	2	1	0	1	0	0
Tylochromis	0	0	0	-	-	-	-	-
Hemichromis	0	2	2	0	1	0	0	0
Pelviachromis	1	0	2	1	-	1	-	-
Oreochromis	1	0	2	1	1	1	0	0
Tilapia	1	0	2	1	1	1	0	0
Iranocichla	1	0	2	1	0	1	0	1
Lamprologus	1	0	0	1	1	1	1	0
Tropheus	0	0	0	1	0	1	1	2
Copadichromis	1	0	0	1	1	2	0	0
Astatotilapia	0	0	0	1	1	2	0	0
H. [*Psammochromis*]	0	0	0	1	1	2	0	0
H. [*Yssichromis*]	0	0	0	1	1	2	0	0
H. [*Prognathochromis*]	0	0	0	1	1	2	0	0
H. [*Lipochromis*]	0	0	0	1	1	2	0	0
Rhamphochromis	1	1	1	1	1	2	0	-
Melanochromis	0	0	2	1	0	0	0	1
Pseudotropheus	0	0	0	1	1	0	0	0

character species	31	32	33	34	35	36	37
Outgroup	0	0	0	0	0	0	0
Mahengechromis	-	0	0	1	0	-	0
Etroplus	0	-	0	-	0	1	2
Madagascan cichlids	-	-	-	-	-	-	-
Heterochromis	0	-	0	0	-	-	0
Neotropical cichlids	0	1	0	0	1	1	0/1
Tylochromis	-	-	0	-	1	-	0
Hemichromis	1	1	1	0	0	1	0
Pelviachromis	1	1	0	0	-	-	0
Oreochromis	1	0	0	0	-	-	0
Tilapia	1	0	0	0	1	1	0
Iranocichla	0	1	0	1	1	2	0
Lamprologus	0	1	0	-	1	2	1/2
Tropheus	1	1	0	1	1	0	0
Copadichromis	0	1	0	0	-	-	0
Astatotilapia	0	1	0	0	1	1	0
H. [*Psammochromis*]	0	1	0	0	1	0	0
H. [*Yssichromis*]	0	1	0	0	1	0	0
H. [*Prognathochromis*]	1	1	0	0	1	0	0
H. [*Lipochromis*]	1	1	0	1	1	0	0
Rhamphochromis	0	1	0	0	1	0	0
Melanochromis	0	1	0	0	1	0	0
Pseudotropheus	0	1	0	0	1	1	1

Appendix E. Indices for individual characters

character	Consistency Index	Retention Index	Rescaled Consistency Index
1	1.00	1.00	1.00
2	0.75	0.88	0.66
3	1.00	1.00	1.00
4	1.00	1.00	1.00
5	0.38	0.38	0.14
6	1.00	1.00	1.00
7	0.33	0.64	0.21
8	1.00	0.0	0.0
9	0.50	0.0	0.0
10	1.00	1.00	1.00
11	0.25	0.45	0.11
12	0.33	0.0	0.0
13	0.33	0.0	0.0
14	0.40	0.25	0.10
15	0.50	0.0	0.0
16	0.20	0.33	0.07
17	0.57	0.63	0.36
18	0.33	0.71	0.24
19	0.50	0.75	0.38
20	0.33	0.0	0.0
21	0.33	0.0	0.0
22	0.33	0.0	0.0
23	0.33	0.50	0.17
24	0.67	0.0	0.0
25	0.67	0.86	0.57
26	0.33	0.33	0.11
27	0.33	0.60	0.20
28	0.40	0.73	0.29
29	1.00	1.00	1.00
30	0.67	0.0	0.0
31	0.33	0.67	0.22
32	0.50	0.67	0.33
33	1.00	0.0	0.00
34	0.25	0.0	0.0
35	0.33	0.33	0.11
36	0.40	0.50	0.20
37	0.50	0.0	0.0

Connecting text

The palaeobiogeography of the family Cichlidae is reinterpreted in light of the fossil record. The oldest confirmed cichlids are those of Eocene age from Mahenge (Chapter 1). However, the age of origin for the family has been suggested as Early Cretaceous, because after this time, Africa and South America were separated by the marine waters of the Atlantic Ocean. An Early Cretaceous age of origin indicates a gap in the fossil record of about 75 million years from the origin of the family until the first known fossils. Although many lineages lack a good fossil record and this gap may not be unreasonable, an alternative explanation is that cichlids arose later and attained their modern distribution by crossing the Atlantic Ocean. The following chapter is an examination of fossil evidence for the origin of cichlids, and a reconstruction of the dispersal patterns and methods for the lineages based on the phylogeny, biology and distribution of modern and fossil species.

CHAPTER 3

BIOGEOGRAPHY AND THE ORIGIN OF CICHLIDS

Introduction

Stiassny (1987, 1991) proposed an Early Cretaceous origin for the family Cichlidae. This date was based upon the assertion that the distribution of cichlids conformed "...to an essentially Gondwanan pattern," and Eocene (in reference to a fossil now considered to be Miocene or Pliocene - see Chapter 1) and Oligocene fossils having "a modern facies," and thus "the origin of the group long predates its earliest fossil record" (1991:p. 3). Stiassny therefore stated that "the Cichlidae ... probably arose sometime early in the Cretaceous and taxonomic differentiation was well under way prior to the separation of the Gondwana fragments" (1991: p. 3). On the basis of Stiassny's conclusion, an Early Cretaceous origin for the Cichlidae seems to have been accepted and passed on in the literature (e.g. Greenwood, 1994; Lévêque, 1997, Farias et al., 1998). Implicit in this view is the assumption that cichlids are obligate freshwater fishes, since, as Lundberg (1993) has noted, South America and Africa were no longer in contact after the Early Cretaceous, and dispersal after this time would have required trans-Atlantic migration.

The above published statements not withstanding, the family Cichlidae is not confined to a strictly Gondwanan distribution. Furthermore, the distribution of cichlids is not limited by plate tectonics and continental drift, because cichlids are not strictly limited to fresh waters. Consequently, postulating an Early Cretaceous minimum age of origin is unnecessary. A more parsimonious interpretation of evidence indicates that the origin of cichlids probably occurred much later than the Early Cretaceous.

Gondwanan distribution

The distribution of modern organisms, particularly those that are terrestrial or confined to fresh waters, can often be related to the geographical position of continental land masses at certain points in their geological history. In the early part of the Mesozoic, most of the earth's land mass was coalesced in a single continent. By the Callovian (end of the Middle Jurassic, about 160 Ma), the single continental mass had split into a northern part, Laurasia, and a southern part, Gondwana separated by the Tethys Sea.

Faunas that have been described as showing a Gondwanan distribution pattern originated at two different periods of time. The first pattern originated in the Triassic, when the southern land mass was a single entity formed by the modern continents of South America, Africa, India, Antarctica and Australia, and the island of Madagascar. Triassic lungfish, with members in South America, Africa and Australia (Kemp, 1996) show a typical Gondwanan distribution pattern of this type. There are no cichlids in Australia, and a Triassic Gondwanan distribution has not been suggested for the Cichlidae.

The second Gondwanan distribution pattern is associated with the end of the Early Cretaceous (Albian), when Africa and South America were still united, but the connection with other land masses had been lost. It is this pattern, apparently, that Stiassny (1987, 1991) ascribes to the Cichlidae. However, by this time India and Madagascar were no longer in contact with South America and Africa, and the West Indies did not rise above sea level until the late Miocene (Smith et al., 1994). Yet

Cichlids occur in all these areas. Therefore, their distribution pattern is greater than just "Gondwanan," as that would be restricted by definition to Africa and South America.

Based on the palaeoreconstructions of the continents by Smith et al. (1994), Madagascar and India were last joined together in the Cenomanian (95 mya, Early Cretaceous) and the two were last joined with Africa, by a very narrow connection in the Tithonian (148 mya) via Antarctica and the southern tip of Africa. A more direct and larger connection between Madagascar/India and Africa (along with Australia, Antarctica and South America) was present in the Oxfordian (155 mya) and Kimmeridgian (153 mya) (Smith et al., 1994). If cichlids were restricted to fresh waters throughout their evolutionary history, the family must have been present in the Late Jurassic in order for them to be in freshwaters on both Madagascar and Africa. However, this still would not explain the presence of cichlids in the Caribbean islands, which have never been connected with larger land masses. Cichlids, however, are not restricted to freshwaters and therefore neither their dispersal nor age of origin is limited by continental connections.

Salinity tolerance

Myers (1949) was the first to separate freshwater fishes into several divisions, based on tolerance to salt waters. Freshwater fishes of the primary division are strictly intolerant to salt water, whereas fishes of the secondary division are less intolerant of salt water. Fishes of the peripheral division either undergo seasonal migrations between fresh and salt waters, live in fresh water only in the absence (or almost complete absence) of primary and secondary freshwater fishes, evolved from diadromous or complementary fishes, or can live and breed in both salt and fresh waters (Banarescu, 1990; Myers, 1949; Lowe-McConnell, 1975, 1987; Roberts, 1975; Lévêque, 1997). Cichlid fishes are secondary division freshwater fishes (Norman and Greenwood, 1975; Lowe-McConnell, 1975, 1987; Banarescu, 1990). This is not unexpected, as the families considered most closely related to the Cichlidae - the Embiotocidae, Labridae, and Pomacentridae (in the suborder Labroidei) - are all marine groups. In fact, 75% of the order Perciformes are marine shore fishes, with only about 14% inhabiting freshwater, mostly comprised of the families Percidae and Cichlidae (Nelson, 1994).

Some of the most primitive species of the Cichlidae are thought to be those genera found in Madagascar and India. Reinthal and Stiassny (1991) listed three of the nine endemic Madagascan cichlids as euryhaline. Several of these species are not only tolerant of brackish waters, but live in estuarine environments (Norman and Greenwood, 1975) and are occasionally found in marine waters (Banarescu, 1990). Two species of the Indian/Sri Lankan genus *Etroplus* are salt-tolerant, living preferentially in brackish waters (Kiener and Maugé, 1966; Loiselle, 1994).

Members of the tilapiine lineage not only tolerate but occasionally breed in salt waters and some *Tilapia* have been maintained in sea water for seven years (Myers, 1949). A species of *Oreochromis* has established a population in the sea (Greenwood, 1994). *Tilapia guineensis* and *Sarotherodon melanotheron* are euryhaline and capable of reproducing in brackish or salt coastal waters (Reid, 1996). Miyazaki et al. (1998) found that *Oreochromis mossambicus* can breed in either fresh or salt water, and there is no mortality of embryos and larvae transferred directly from one to the other. Other species are found in saline streams or lakes. *Iranocichla hormuzensis* inhabits salt rivers and streams, including waters that are highly saline (Coad, 1982). *Danakilia franchettii* is found in Lake Afrera which has high sodium and chlorine concentrations (Trewavas, 1983). *Oreochromis alcalicus grahami* inhabits highly saline peripheral lagoons in Kenya (Maina, 2000), and *Oreochromis alcalicus alcalicus* is in Lake Natron, which is rich in salts, particularly sodium (Trewavas; 1983). Two other species of *Oreochromis* are also found in saline waters, *O. salinicola*, in the saline springs of the Mwashia, Zaire, and *O. amphimelas* of lakes Manyara and Eyasi, which have high proportions of sodium chloride and sodium bicarbonate (Trewavas 1983). Even some American cichlids have been caught in brackish water (Kullander, 1983). Therefore, there is no reason to assume that salt water was a barrier to cichlid dispersal.

Secondary freshwater fishes, including the Cichlidae, have reached the West Indies and Madagascar, which has not been accomplished by primary division freshwater fishes. Of the thirty-eight endemic fishes in the fresh and brackish waters of Madagascar (Reinthal and Stiassny, 1991), not a single species is a primary division freshwater fish. Over fifty years ago, Myers (1949: p. 318) pointed out that the Cichlidae, which have been used by some zoogeographers as evidence for the previous connections between Africa and South America, and Madagascar and Africa, are not limited by salinity. Despite the evidence to the contrary, it is curious that the current consensus accepts a Gondwanan distribution circumscribed by the inability of cichlids to tolerate salt water.

Clearly, cichlid distribution is not strictly Gondwanan. Nor can cichlid distribution be explained solely in terms of a Gondwanan origin and continental drift because dispersals through marine waters are possible. Therefore, the circumstantial evidence of an Early Cretaceous origin (Stiassny, 1987, 1991) for cichlids collapses.

However, the distribution of fossils can contribute information on the age of origin by providing minimum ages at which a lineage inhabited a particular geographical place. This information, along with the distribution of modem cichlids can be used to indicate modes and patterns of dispersal for cichlid lineages.

Fossil evidence

As Banarescu (1990: p. 16) noted, "palaeontological data remain however the only data which surely prove that a certain lineage or species was present during a certain geological period in a certain area, while conclusions derived exclusively from recent distributions can only be pure speculation." Similarly, Lundberg (1998:52) noted "Fossils provide the only direct, physical evidence of ancient taxa, their morphology and prior geographic provenance." In addition, although a lack of fossils is not necessarily evidence that a particular animal was not present in a given place at a given time, complete absence of a particular animal from beds that would be expected to contain it is strong circumstantial evidence that the absence reflects a true absence of the animal, not just absence of fossilized remains. Although some deposits of a suitable nature are known in the Cretaceous, no remains attributable to a cichlid have been recovered.

Furthermore, an Early Cretaceous origin of cichlids has wider implications - it requires that the more inclusive clades containing cichlids (Labroidei, Perciformes, and Acanthomorpha) must necessarily have originated prior to this time. Yet, as noted below, there is no fossil evidence to support this.

Fossil record of the Acanthomorpha

The family Cichlidae is placed in the suborder Labroidei of the acanthomorph order Perciformes. Acanthomorph fishes first appear in the fossil record in the Cenomanian, at the beginning of the Late Cretaceous, with no members known from the Early Cretaceous (Patterson, 1993). However, acanthomorphs had also invaded freshwaters by the Cenomanian, as indicated by the recent discovery of an acanthomorph *incertae sedis*, from the Kem Kem beds of Morocco (Filleul and Dutheil, submitted), suggesting a slightly earlier origin of the group.

Fossil record of the Perciformes

Perciform fishes first appear in the Campanian, 20-25 million years after the first acanthomorphs (Patterson, 1993). A review of the Early Cretaceous Gondwanan fishes (Maisey, 2000) confirms there are no perciforms known prior to this. Cretaceous remains described as perciforms include *Cylindracanthus, Platacodon, Eoserranus* and *Nardoichthys*. *Cylindracanthus* (with three species) is based on spines that have been compared to the rostrum of *Blochius*, an Eocene xiphioid, from Italy (Patterson, 1993). *Platacodon nanus* was based on jaw and pharyngeal teeth and bones, but the dentaries have now been referred to the pike, *Estesesox foxi* (Esocidae), and the other *Placodon* material may prove to belong to the Ostariophysi (Wilson, et al., 1992). *Eoserranus hislopi*, from the Lameta Formation of India, described in the Serranidae, may be a percoid, but the deposits from which it comes may be Tertiary, not Cretaceous (Patterson, 1993). Other Indian remains were reported by Gayet et al. (1984) and identified as belonging to indeterminate Percoidei, and several perciform families (Labridae, Centropomidae, Sphyraenidae) but the age of these remains is also not definite, and they may be early Tertiary, not Cretaceous. *Nardoichthys*, from the Campanian of Italy, cannot be assigned to any lineage within the perciforms (Patterson, 1993) although it may indeed prove to belong in that order. The record of otoliths does provide more Cretaceous taxa, with seven acanthomorphs including five perciforms known from the Campanian of Mississippi (Nolf and Dockery, 1990), although none of these has been assigned to the more advanced perciform families.

Fossil record of the Cichlidae

Fossil cichlids are known from Africa, South and Central America, Arabia, and Europe, with the earliest in Eocene deposits ranging through to Holocene deposits. The oldest confirmed cichlids, those from Mahenge, are of Eocene age.

Oligocene members of the family Cichlidae are known from East Africa and Saudi Arabia (Van Couvering, 1982; Casciotta and Arratia, 1993; Micklich and Roscher, 1990; Lippitsch and Micklich, 1998). The East African species are questionably Oligocene, in that they occur in the Middle and Upper Daban Series of Somalia between beds dated as upper Eocene marine deposits and possible lower Miocene deposits (Van Couvering, 1982). The cichlids from this locality are the named *Macfadyena dabanensis*, and four indeterminate forms. The other Oligocene cichlids are specimens recovered from Saudi Arabia (Micklich and Roscher, 1990). These represent at least three different lineages of cichlids, possibly related to *Heterochromis*, tilapiines and haplochromines (Lippitsch and Micklich, 1998).

Recently, remains identified as Cichlidae have been reported from Early Oligocene deposits in the Sultanate of Oman (Thomas et al., 1999). Unfortunately, none of the remains are illustrated or described, however, the authors give the impression that the faunal remains from this area are predominantly isolated bones and teeth. In an unpublished manuscript, Otero and Gayet reviewed the fauna from this area. They did not mention any cichlid remains being present. Weiler (1970) reported cichlids of indeterminable genus and species from Jordan. These are from freshwater deposits dated as Late Oligocene or Miocene.

Remains of fossil cichlids are known from the mid to late Tertiary and Quaternary of Africa, and South and Central America, as described and summarized by Van Couvering (1978, 1982) and Casciotta and Arratia (1993). There are several fossil cichlids known from the Neotropics. *Geophagus prisca* (previously in the genus *Macracara;* Casciotta and Arratia, 1993) is considered to be Miocene or ?Pliocene (Schaeffer, 1947) or Miocene (Casciotta and Arratia, 1993). Cockerell (1923) reported several specimens from Haiti, which he placed in a Recent genus as *Cichlasoma (Parapetenia) woodringi*. Although the Haitian locality was considered Miocene by Cockerell, Casciotta and Arratia (1993) listed it as ?Pliocene. Miocene deposits in Argentina were reviewed and revised by Casciotta and Arratia (1993). According to these authors, the cichlids from these deposits are *Palaeocichla longirostrum* (previously in the genus *Acoronia*), *Aequidens saltensis* (which they consider should probably be in a geophagine genus) and material only tentatively referred to genera, cf. *Crenicichla* and cf. *Gymnogeophagus*. Schaeffer (1947) described *Aequidens pauloensis* from ?Pliocene deposits in Brazil.

Most of the African fossils discussed by Van Couvering are considered to be tilapiine cichlids (*sensu* Trewavas, 1983), including the possible Oligocene cichlid from Somalia, *Macfadyena* (Van Couvering, 1982). One of the more completely described tilapiine fossils, *Sarotherodon martyni*, (referred to *Oreochromis* by Murray and Stewart, 1999) is from the Late Miocene, between layers dated at 9.3 and 12 mya, from the Eastern Rift in Kenya, south of Lake Turkana (Van Couvering, 1982).

White (1937) also described quite complete remains dating from the Late Tertiary of Ghana as *Tilapia fossilis*. Another fossil genus, *Palaeochromis*, from the Upper Miocene of Algeria, may also be a tilapiine cichlid (Van Couvering, 1982). Murray and Stewart (1999) described fairly complete remains of several specimens from the Pliocene of Ethiopia as *Oreochromis harrisae*. Early Miocene remains with affinities to a tilapiine genus (Trewavas, 1983) are disarticulated bones representing two or more species referred to *Pelmatochromis* and *Palaeofulu kuluensis* (Van Couvering, 1982). These are the only fossil tilapiines described from the Late Tertiary other than isolated bones not identifiable to genus.

The record for non-tilapiine cichlids is even less well-known. The only determinable species Van Couvering (1982) listed is a single haplochromine, *Nderechromis cichloides*, from the Early Miocene (about 18 my old) Kulu Formation of Rusinga Island, Kenya. *Kalyptochromis hamulodentis* has unknown affinities (Van Couvering, 1982).

Pleistocene cichlid remains are mainly isolated bones, or fragments of bones, of indeterminate species (Greenwood, 1957, 1959, 1968; Greenwood and Todd, 1970), or are more complete remains referable to a Recent species (Trewavas, 1937; White, 1937).

This latter is the case of another Ethiopian cichlid, ?*Tilapia crassipina* Arambourg, 1943, from the Shungura Formation (Van Couvering, 1982), east of Lake Turkana, dated as Early Pleistocene (Cerling et al., 1979). Trewavas (1983) considered this fossil to be indistinguishable from the modern form, *Oreochromis niloticus vulcani*, in Lake Turkana. The affinities of Pliocene remains from Israel have not been determined.

Remains of cichlids from Europe have been recovered from Germany, Switzerland and Moravia (former Czechoslovakia). *Eurotilapia* sp. is known from otoliths and lower jaw fragments with teeth (Gaemers, 1989). Body fossils of tilapiine cichlids have also been recovered from the Miocene of Italy (Landini and Sorbini, 1989).

The Cichlidae is one of the few primarily freshwater families of the order Perciformes. At some point in the history of these fish, a marine perciform ancestor must have given rise to the Cichlidae. The fossil fishes of Africa, along with the environments in which they were found, have been reviewed recently (Murray, 2000). Particularly in north and west Africa, there are a number of Cretaceous sites that preserve shallow marine habitats, with coastal lagoons, such as the Jbel Tselfat locality (Cenomanian, beginning of the Late Cretaceous), that would presumably be the type of habitat that the marine cichlid ancestor would have inhabited, based on the biology of the related labroid families (Embiotocidae, Labridae, Pomacentridae, and Sparidae). Similarly, the Kem Kem beds of Morocco provide freshwater fishes of Cenomanian age. Both the Kem Kem beds and Jbel Tselfat have produced complete, articulated specimens that are well preserved. Although there are many fish (including acanthomorphs) from both these sites and other Cretaceous African localities, there are no cichlids, or even perciforms, at either site (Murray, 2000).

Remains of cichlids are regularly found in fossil deposits from the Miocene on (e.g. Murray and Stewart, submitted). Since there is no a priori reason to assume they should be rare in deposits of the early Tertiary and Cretaceous, it is reasonable to believe, as did Lundberg (1998), that in the case of cichlids, the absence of fossil cichlids in the Early Cretaceous can be taken as evidence of absence, and that cichlids had most likely not yet evolved by that time.

Proposed reconstruction of the early history of the Cichlidae

Age of origin for the family

Stiassny (1991:p. 3) considered that Eocene and Oligocene fossil cichlids were of a modern form and highly specialized, particularly in dental features, and thus "the origin of the group long predates its earliest fossil record." The Eocene fossil Stiassny referred to is the South American *Geophagus priscus*, now considered to be Miocene or Pliocene. The only verified Eocene members of the family known, the Mahenge cichlids, have simple conical teeth and do not exhibit any specialized features.

Although it is reasonable to assume that the origin of a lineage predates its first appearance in the fossil record, there is no set length of time for this gap, and cichlids are known to speciate extremely quickly. The flocks of lakes Victoria, Malawi, and Tanganyika had relatively short periods of time in which to evolve. Lake Victoria, the youngest of the three great lakes, started to form about 500,000 years ago (Fryer and Iles, 1972) and underwent an episode of drying, perhaps leaving small ponds and isolated lakes, as recently as 14,000 years ago, which may be when the current fauna arose. Rocky outcrops and islands in the southern end of Lake Malawi are known to have been surrounded by dry land only 200 years ago, and yet endemic species now inhabit the area and are believed to have originated since that time (Owen et al., 1990). Even if, as some have suggested (e.g. Meyer et al., 1994), the current fauna represents remnants of an older fauna that survived in small pools during periods of drought, the age of the lakes themselves, and therefore the ichthyofauna, cannot be older than the Miocene, when the rifting in East Africa began. Lake Tanganyika, the oldest of the Great Lakes at about nine to twelve million years old (Meyer et al., 1994), establishes the absolute maximum age of the diverse and speciose cichlid fauna.

Therefore, although the origin of the Cichlidae is expected to predate the earliest known fossils (45 my old) it is not necessary to postulate an extra 55 my (from the end of the Early Cretaceous [Albian]) for the origin of the family. The only reason to conclude an Albian minimum age for cichlids is if salt water is a barrier to their dispersal, which, as shown above, it is not. Based on the fossil record, an early Tertiary (Palaeocene), or end Cretaceous (Campanian or Maastrichtian), origin for cichlids is more plausible than the Early Cretaceous age proposed by Stiassny (1987, 1991).

Centre of origin and dispersal routes: The most parsimonious scenario

Reconstruction of palaeobiogeography benefits from a robust phylogeny of the group under study. Although the relationship of many cichlids are poorly known, the relationships of the higher lineages within the family are reasonably well supported. When considering directions in which dispersals occurred, it is more parsimonious to assume that a single lineage (i.e. a monophyletic group) dispersed, rather than multiple lineages, as noted by Lundberg (1993). This reasoning is used in the following reconstruction of dispersal events.

Based on five previously published phylogenies of the Cichlidae (Fig. 1, Chapter 2), the centre of origin of the family was probably in Madagascar, where the most primitive cichlids still occur. Although Kiener and Maugé (1966) noted that an ancestor to the cichlids of Madagascar could easily have reached Madagascar from Africa across the Mozambique channel (and then presumably became extinct, leaving no fossils or living descendants on the mainland), I suggest that the opposite happened: cichlids arose in Madagascar then crossed the channel to invade Africa. This is consistent with the phylogeny of the family, in which the Madagascan cichlids form a paraphyletic group, whereas the African and Neotropical cichlids together form a monophyletic group. From Madagascar, cichlids could have spread westwards to East Africa, and from there across Africa to the west coast and then on to South America.

The Indian/Sri Lankan cichlids (*Etroplus*) are most closely related to a subset of the Madagascan genera (Fig. 1). This suggests that a single lineage from Madagascar dispersed to the east, invading the waters of India, and from there to Sri Lanka. Madagascar and India had separated from one another by the Coniacian (88 Ma), and, although they remained fairly close to one another until the Campanian (80 Ma), the two were separated by about 800 km by the Maastrichtian (based on maps in Smith et al., 1994).

Two of the three Indian and Sri Lankan cichlids (*Etroplus suratensis* and *E. maculatus*) are for the most part salt-tolerant (Kiener and Maugé, 1966), and are found in coastal areas, preferentially in brackish waters (Loiselle, 1994), although they also enter

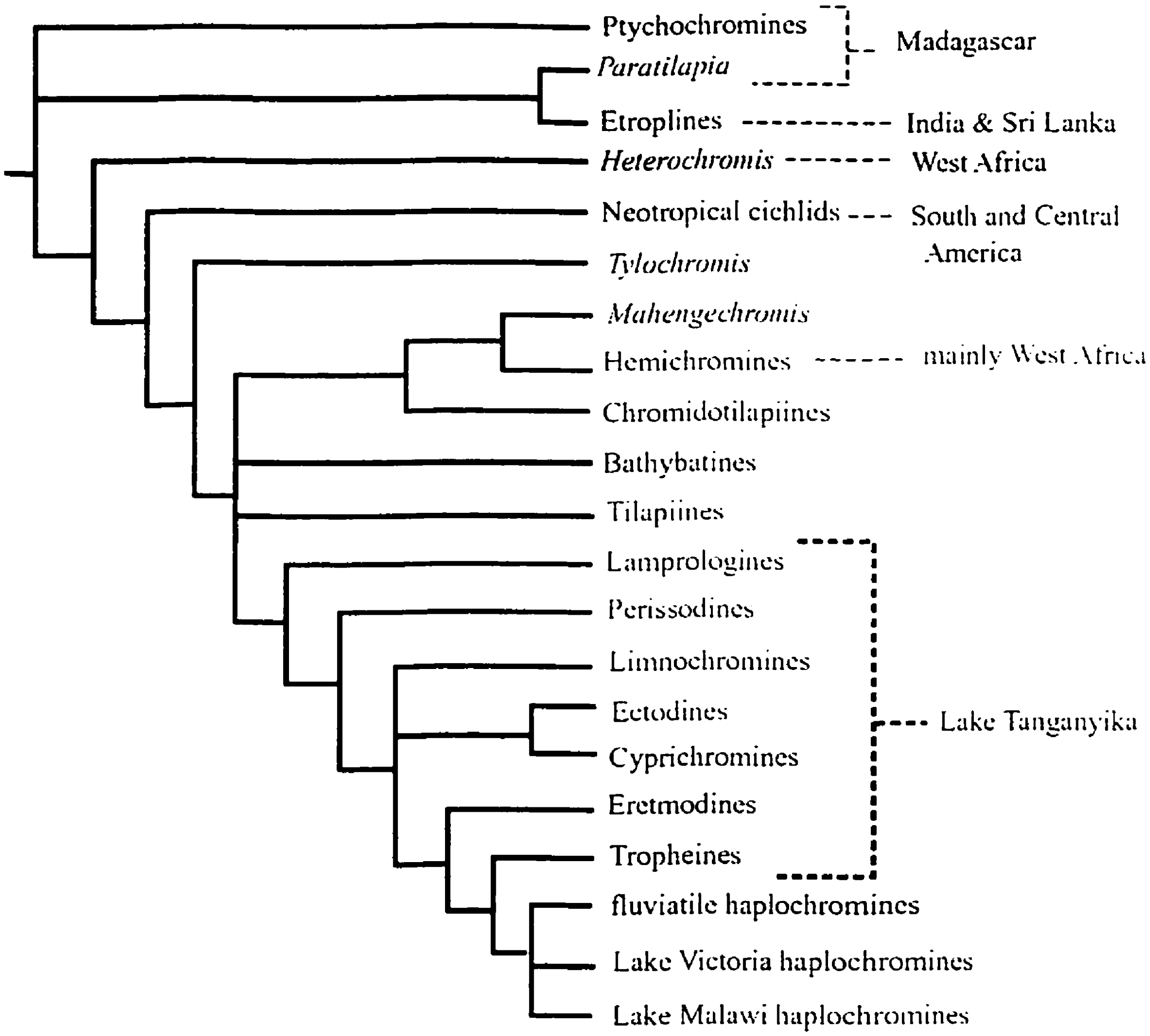

Figure 1. Relationships of the family Cichlidae (from Chapter 2).

fresh water and salt water (Banarescu, 1990). The third species (*Etroplus canarensis*) is found in coastal rivers, but its biology is not well known (Loiselle, 1994). It has been suggested that these species (or their ancestor) travelled to India and Sri Lanka along the coast from eastern Africa via Arabia sometime in the Tertiary (Goldstein, 1973) possibly by a progressive dispersal of populations through brackish waters of river mouths along the coastline of the Arabian plate. If so, there is no fossil record of such a migration. The only fossils known from Saudi Arabia are of Oligocene age; however, these fossils have been identified as belonging to three separate lineages, a basal *Heterochromis*-type, a possible tilapiine, and a possible haplochromine (Lippitsch and Micklich, 1998), none of which are closely related to the Indian cichlid. Furthermore, no cichlids currently inhabit this area, therefore, if these populations existed, they later became extinct and left no record. In addition, the suggestion that the Indian cichlids dispersed from Africa is not supported by the phylogeny of these fishes. Because of the close relationship between *Etroplus* and two of the Madagascan genera, it is more likely that the Indian lineage originated in Madagascar not East Africa.

A equally reasonable scenario is migration across marine waters from Madagascar to India, aided by ocean currents (Fig. 2). The present day currents in the Indian Ocean during August-September flow in a clockwise direction (Brown et al., 1989: fig. 5.10), which would aid fish moving from Madagascar, northwards up the African coast, then southwards down the west coast of India. These cichlids may only have reached India in the Early Miocene, when the subcontinent collided with Asia (map in Smith et al., 1994), as before this time, the currents were probably different from present day currents. Sri Lanka (which is also inhabited by *Etroplus*) was not above sea level until the Pliocene

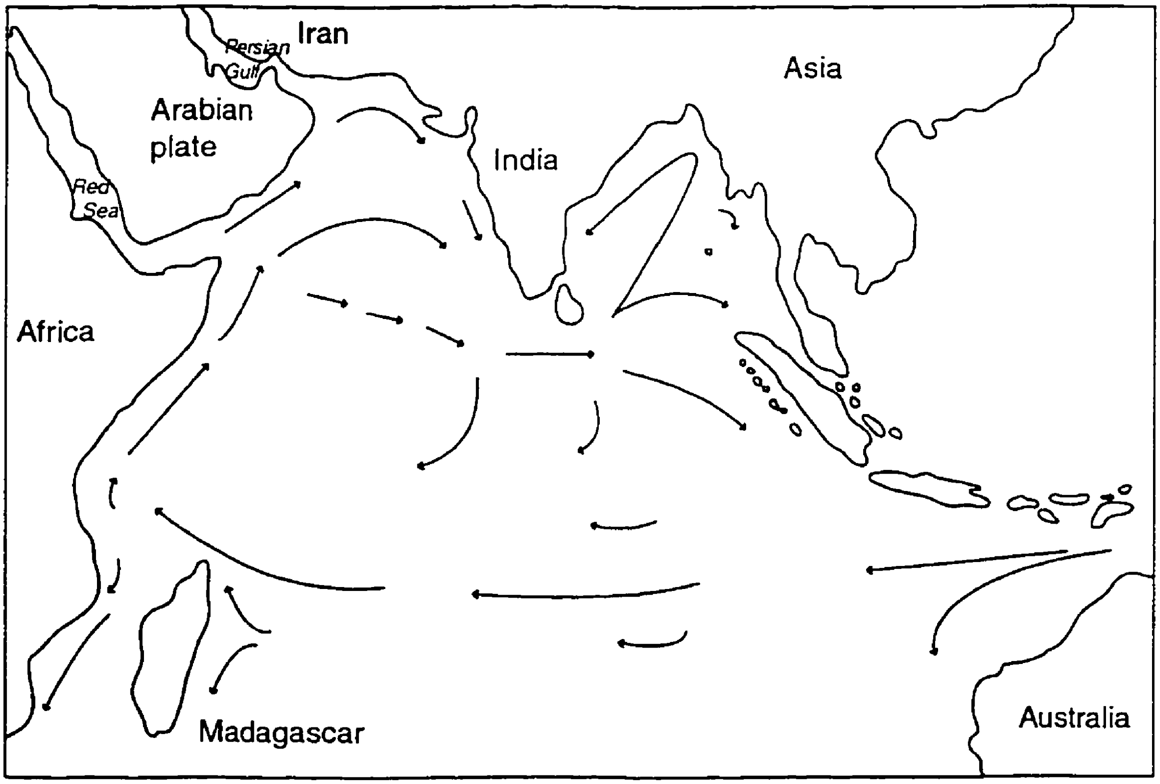

Figure 2. Modern day ocean currents of the Indian Ocean, showing current that could have aided cichlid dispersal from Madagascar to India and Sri Lanka. Based on Brown et al., 1989: fig. 5.10.

(map in Smith et al., 1994), at which point the cichlids would have been able to migrate across the channel from India.

Within the family, the Neotropical cichlids are considered to comprise a monophyletic group, whereas the African cichlids do not (Stiassny, 1991). Therefore, again it is more parsimonious to assume that a single lineage migrated to South America from Africa, rather than that multiple lineages migrated the other way (as previously noted by Lundberg, 1993). If cichlids from Africa dispersed to South America, then an absolute latest date for cichlid dispersal across the South Atlantic is determined by the late Oligocene or early Miocene fossil cichlids in the New World.

Admittedly, the sea barrier between South America and Africa that exists at present (about 3500 km) cannot be considered as narrow. Palaeoreconstructions of the continents, such as those by Smith et al. (1994) show the last connection between western Africa and Brazil at the end of the Early Cretaceous (Albian, 105 mya), but the continents were separated by marine waters by the earliest Late Cretaceous (Cenomanian). Between the Cenomanian (95 mya) and Santonian (85 mya) Africa and South America roughly maintained their distance. Not until the Campanian (80 mya) did they move progressively further from one another. In the Late Cretaceous and early Tertiary, there was a gap of between 500 and 1000 km between South America and Africa (based on maps 8-10 in Smith et al., 1994). This gap might be considered a long migration for a swimming cichlid, however, ocean currents may well have carried the fish across the Atlantic. Palaeoreconstructions of ocean currents in previous ages (Haq and Van Eysinga, 1987) show that the modern-day currents of the South Atlantic are essentially those that were present in the Late Cretaceous and Early Tertiary (Fig. 3). The South Equatorial Current

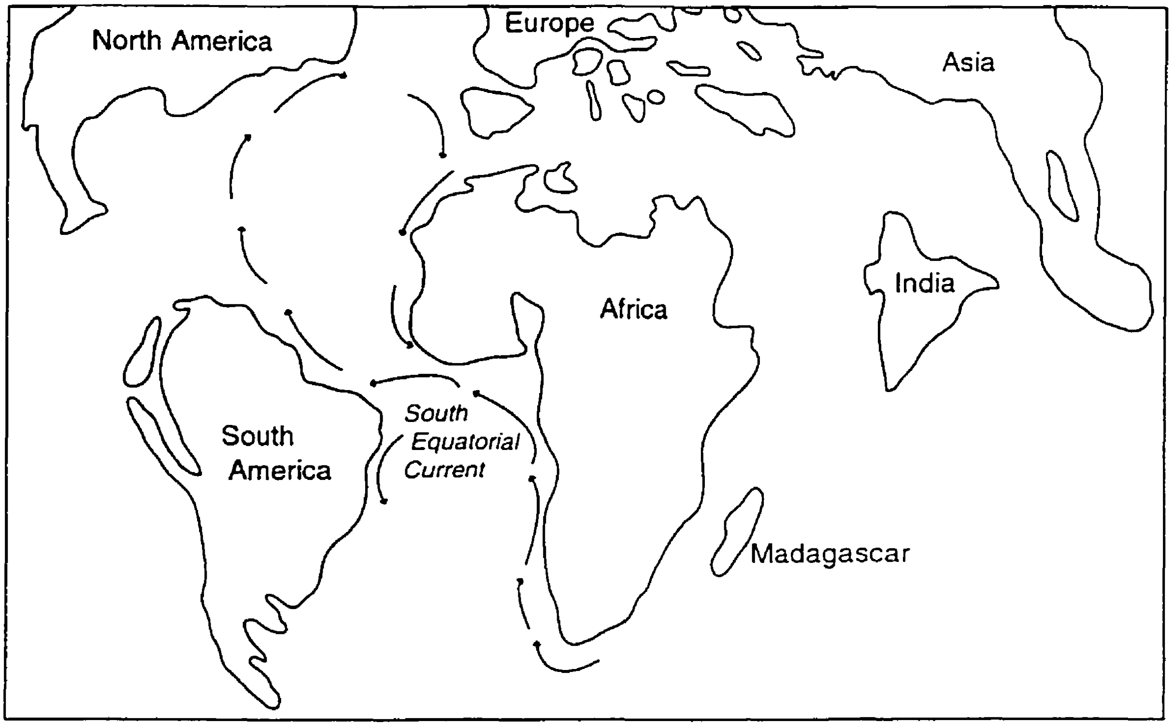

Figure 3. Late Cretaceous and Early Tertiary currents of the South Atlantic, which may have aided cichlid dispersal from West Africa to the east coast of South America. Based on Haq and Van Eysinga, 1987.

sweeps along the west coast of Africa, from the southern tip of the continent to the Gulf of Guinea, then straight across the Atlantic in the tropical zone (with a warm water temperature) to the northeastern coast of Brazil (Brown et al., 1989). The speed of an ocean current is variable, dependent upon factors including wind and temperature; however, based on maps in Couper (1983), a reasonable average speed for the South Equatorial current is 0.5 knots. At this speed, fishes could be carried 500 km in as little as 23 days. Even with a larger gap between continents, the current not travelling in a straight line, or with wind currents deflecting progress, it is probable that cichlids could have been swept across the Atlantic within their lifetimes. This current could have been responsible for dispersing cichlids from the west coast of Africa to the east coast of South America across the Atlantic Ocean.

Once cichlids had invaded the freshwaters of Brazil, they could easily have dispersed from there to Central America and as far north as Texas. Myers (1966) suggested that cichlids from South America invaded Central America sometime in the Late Tertiary (Neogene) by crossing open seas or following coast lines. No land bridges between the Caribbean islands and the mainland have been suggested. Cichlids must have invaded the West Indies by crossing narrow marine zones, sometime after those islands rose above sea level in the Miocene. The fossil cichlid from Haiti is probably Pliocene (maybe Miocene) in age, and therefore sets a minimum date for cichlids to have reached the West Indies. Cichlids presumably crossed a narrow sea barrier to reach Haiti after sea level dropped to expose this island, and the rest of the West Indies, in the Miocene (Smith et al., 1994).

An extant cichlid is also known from Iran, the endemic *Iranocichla hormuzensis*. If this fish were restricted to dispersal through fresh waters, it would have had to reach its current distribution from the north, and would not have been able to do so until the Late Miocene or Pliocene, when Africa, via Arabia, contacted the Iranian and Turkish areas of Asia (Fig. 4) allowing faunal exchange via land bridges (Lévêque, 1997) and presumably fresh water ponds. This fresh water scenario for dispersal is unlikely, as *Iranocichla* inhabits a small coastal plain blocked landwards by mountains which quickly rise to over 1000 m.

A simpler explanation is that *Iranocichla hormuzensis* reached Iran from the sea, either by travelling through brackish waters of river mouths along the coast of the Arabian plate, or through the waters of the Tethys Sea/Indian Ocean. Trewavas (1983) suggested that the sistergroup to *Iranocichla* is *Danakilia*, a genus endemic to Lake Afrera in the Danakil Depression of Ethiopia. A coastwise dispersal from Ethiopia, along Arabia and then around the Persian Gulf could have enabled *Iranocichla* to reach its current habitat. As mentioned above, there are no modern cichlid populations or fossils of related cichlids to support this gradual dispersal. Given that the waters in which *Iranocichla* is found are characterized by high salinity (Coad, 1982), so clearly these fish have a high salinity tolerance, it is simpler to hypothesize that *Iranocichla* migrated directly through marine waters to the Persian Gulf. The locality of *Iranocichla* was not above sea level until the Middle Miocene, setting this as the earliest date for the arrival of a cichlid in its present habitat.

It has been suggested that the cichlids in the Jordan Valley and Syria, *Tristramella* and *Sarotherodon galilaeus*, also dispersed to the Levant from Africa via a land bridge

(Lévêque, 1997). A dispersal only through fresh waters results in the time of arrival for cichlids in this area being restricted to prior to the Middle Miocene or after the end of the Miocene, as at other times, there was no direct land connection between Africa and the Arabian plate (Fig. 4). However, the Levant cichlids are members of the salinity-tolerant tilapiine lineage, and *Sarotherodon galilaeus* at least is known to be tolerant of salinity (Trewavas, 1983). These cichlids may well have travelled along the coastline of the Mediterranean Sea, or entered the Red Sea and travelled up it to attain their current range. An earliest date for the latter is set by the opening of the Red Sea in the Middle Miocene (Fig. 4).

Fossil cichlids are also known from Europe. Early, Middle and Late Miocene deposits have produced otoliths and jaw fragments with teeth that belong to cichlids (Gaemers, 1989). The deposits in Germany, Switzerland and Moravia (former Czechoslovakia) represent brackish or mixed brackish and freshwater environments. Gaemers (1989) postulated that these fish, *Eurotilapia*, invaded Central Europe after a regression in the Early Miocene created a land bridge through the Arabian Peninsula and southwestern Europe, and that later transgressions isolated the European cichlids which eventually became extinct because of the cooling of the European climate.

Other European cichlids are known from whole-body fossils. Landini and Sorbini (1989) reported cichlids from three Messinian (terminal Miocene) sites in Italy. All three sites represent coastal lagoons and had an environment that would have been close to the salinity of sea water. Landini and Sorbini (1989) suggested that an evaporitic event allowed the cichlids to cross a land bridge into Italy, although they postulated that the

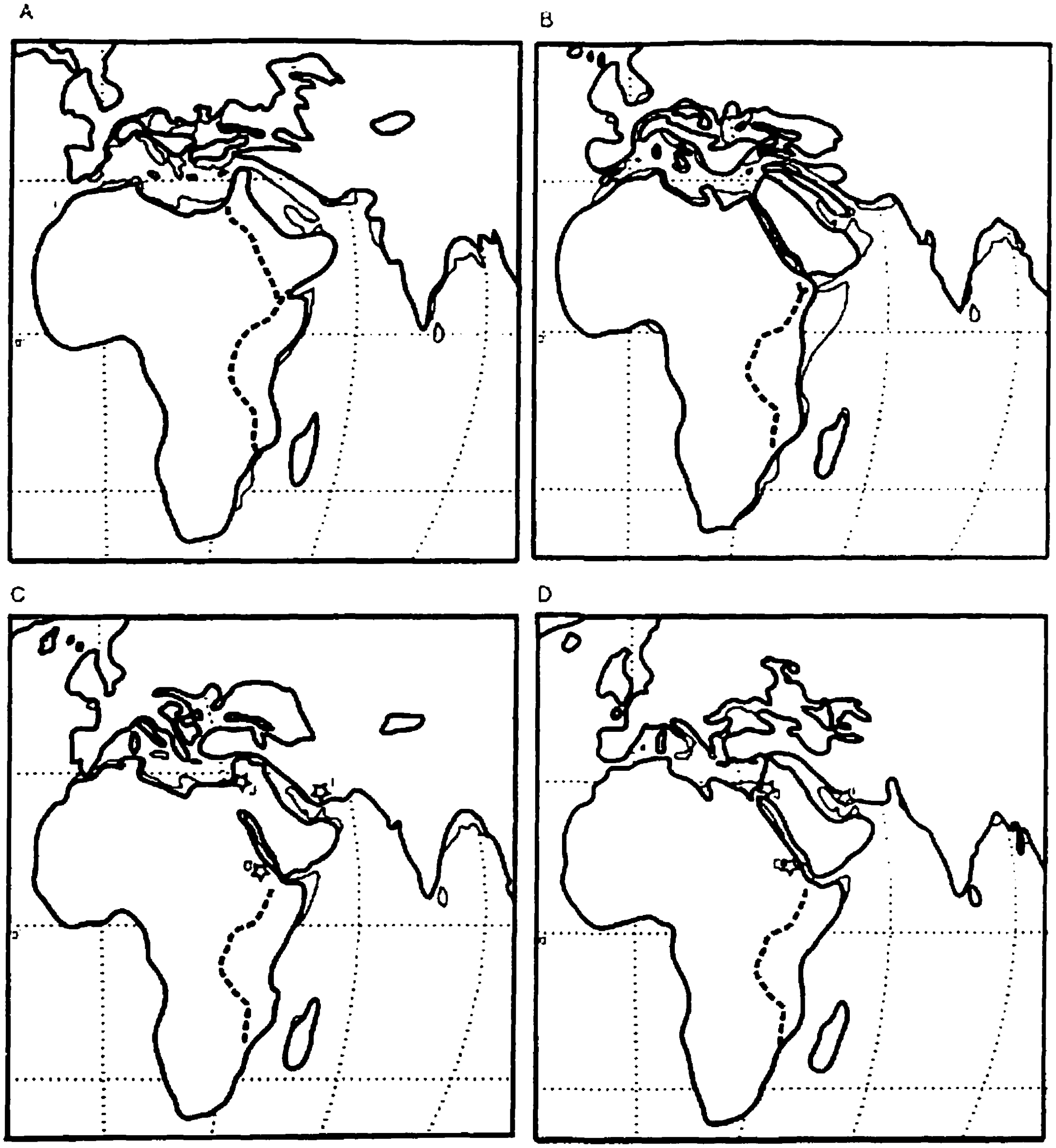

Figure 4. Previous configurations of Africa and nearby land masses. Thin unfilled lines indicate outline of modern land mass. A. Early Miocene, 20 mya; B. Middle Miocene, 12 mya; C. Late Miocene, 10 mya; D. Pliocene, 5 mya. Based on maps 1-4 in Smith et al. (1994). Lettered stars, marking modern locations of particular cichlids, are D, Danakil Depression (*Danakilia*); J, Jordan Valley (*Tristramella*) and I, Strait of Hormuz, Iran, (*Iranocichla*).

other fish from the same sites were relicts from the Tethys Sea. It seems unnecessary to postulate land bridges for cichlids that are were living in brackish or salt environments. I suggest it is more likely that all these Miocene cichlids crossed the Tethys Sea or circumnavigated the coastal waters, to reach Europe directly via marine waters.

The age of origin of lineages

The fossil record is the only evidence that a lineage existed at a given time. therefore, fossils from accurately dated localities give an absolute minimum time of origin for lineages. Based on phylogenetic relationships, the sistergroup of a lineage with an established minimum age must also have that minimum age. Although most of the lineages of cichlids do not have an associated fossil record, some ages of origin for individual lineages can be determined (Fig. 5). If *Mahengechromis*, the Eocene fossil cichlids, forms the sistergroup to the hemichromine cichlids (Chapter 2), then the latter lineage must have a minimum middle Eocene age. Reid (1996) previously noted the probability of a pre-Miocene continental hydrography shared by all regions of Africa which would explain some pan-African fish distributions. If this existed in the Eocene, it might explain the relationships between the Mahenge fauna and the West African hemichromines.

The minimum age for the tilapiine lineage is based on Oligocene fossil tilapiines. A third age can be assigned, that of the cichlids of lakes Malawi and Victoria. These lakes are considered to hold species flocks that arose in the lakes; however the lakes did not form until the rifting of the Miocene. The Miocene age for these lineages is therefore a maximum age. Fossils from Saudi Arabia were tentatively identified as belonging to

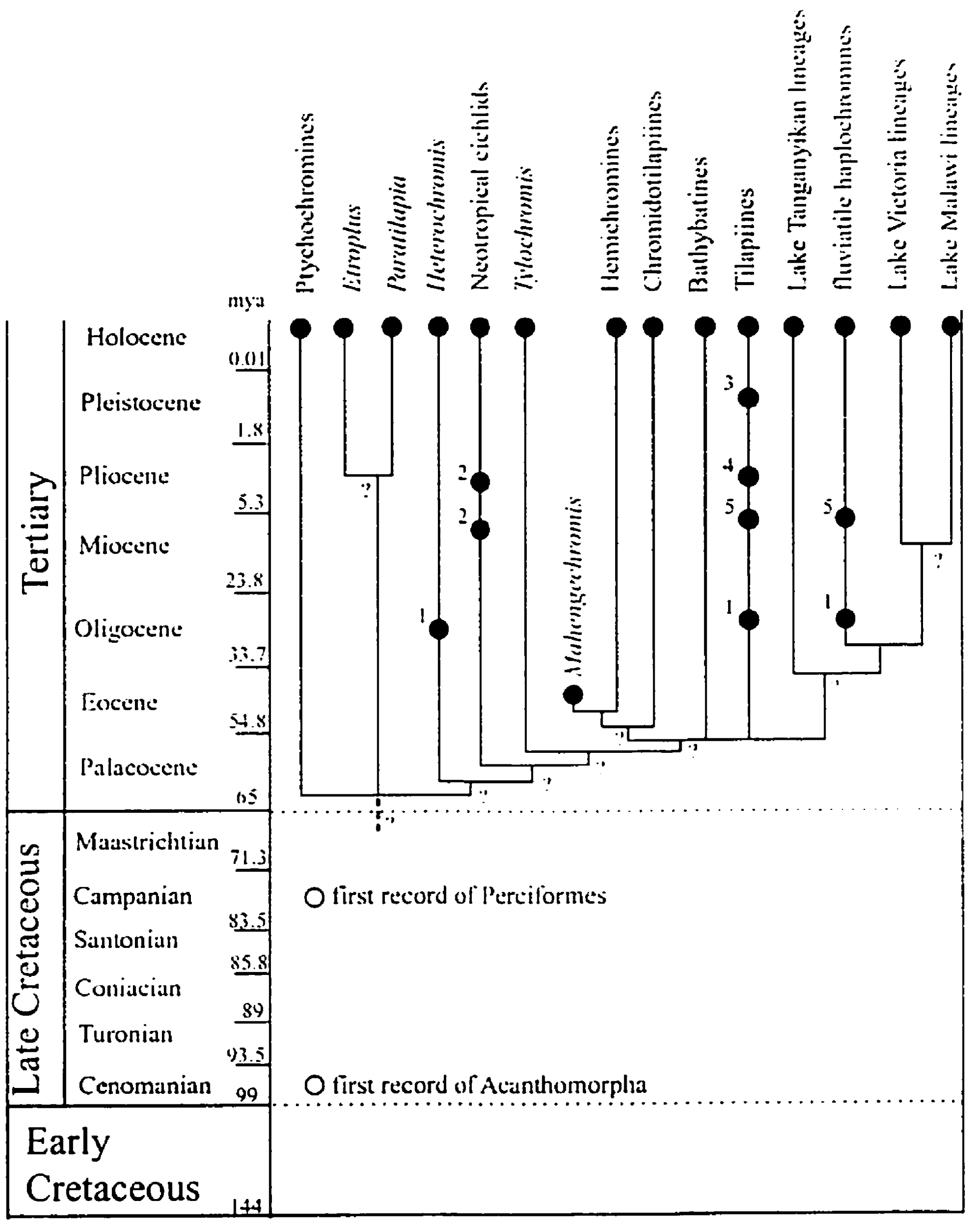

Figure 5. A composite tree of the family Cichlidae (from Chapter 2), superimposed on the geological time scale. Black circles indicate known cichlid occurrences. References for fossil occurrences are 1. Lippitsch and Micklich, 1998; 2. Casciotta and Arratia, 1993; 3. Greenwood, 1957, 1959, 1968; 4. Murray and Stewart, 1999; 5. Vancouvering, 1982.

three lineages, *Astatotilapia* (a riverine haplochromine), *Heterochromis*, and the tilapiine lineage (Lippitsch and Micklich, 1998). These fossils give an Oligocene date for these groups, and therefore the haplochromine lineage must have existed in the Oligocene before invading the Miocene African Rift Lakes.

The lineages of Lake Tanganyika do not form a monophyletic group, and therefore there is a possibility that the ancestors of the lineages invaded the lake separately. Although Lake Tanganyika also formed during Miocene rifting, giving a maximum age for the cichlids to have invaded the lake, these lineages cannot be given a minimum age of origin.

The Neotropical lineage can be given a minimum age of Miocene, based on fossil remains in South and Central America. But based on the phylogenetic relationships (Fig. 4), the Neotropical lineage, as well as *Tylochromis*, *Heterochromis* and the Madagascan and Indian cichlids must have arisen before the minimum Eocene origin of more derived lineages, provided by the fossil cichlids from Mahenge.

The distribution of organisms that are not strictly limited to fresh waters cannot be confirmed as being a result of vicariant events associated with the separation of continental land masses. For this reason, the age of origin of cichlids cannot be determined by the timing of the separation of the continents in which they are now found. The only firm evidence available for past distribution and age of origin for cichlid fishes is the fossil record.

Literature cited

Banarescu, P. 1990. Zoogeography of Fresh Waters. Vol. 1. General distribution and dispersal of freshwater animals. AULA-Verlag Wiesbaden, pp. 1-511.

Brown, J., A. Colling, D. Park, J. Phillips, D. Rothery and J. Wright. 1989. Ocean Circulation. Pergamon Press, Toronto and The Open University, Milton Keynes, England, 238 pp.

Casciotta, J. and G. Arratia. 1993. Tertiary cichlid fishes from Argentina and reassessment of the phylogeny of New World cichlids (Perciformes: Labroidei). Kaupia - Darmstädter Beiträge zur Naturgeschichte, 2:195-240.

Cerling, T.E., F.H. Brown, B.W. Cerling, G.H. Curtis and R.E. Drake. 1979. Preliminary correlations between the Koobi Fora and Shungura Formations, East Africa. Nature, 279(5709):118-121.

Cockerell, T.D.A. 1923 [1924]. A fossil cichlid fish from the Republic of Haiti. Proceedings of the U.S. National Museum, 63(7):1-3.

Coad, B.W. 1982. A new genus and species of cichlid endemic to Southern Iran. Copeia, 1982(1):28-37.

Couper, A. (ed). 1983. *The Times Atlas of the Oceans*. Times Books Ltd., London, 272 pp.

Farias, I.P., H. Schneider and I. Sampaio. 1998. Molecular phylogeny of Neotropical cichlids: The relationships of cichlasomines and heroines. Pp. 499-508, in: Malabarba, L.R., R.E. Reis, R.P. Vari, Z.M.S. Lucena and C.A.S. Lucena (eds.). Phylogeny and Classification of Neotropical Fishes, Editoria Universitária 0-EDIPUCRS, Porto Alegre, Brasil.

Filleul, A. and D.B. Dutheil. submitted. *Spinocaudichthys oumtkoutensis*, n. gen., n. sp., a freshwater acanthomorph from the Cenomanian of Morocco. Journal of Vertebrate Paleontology.

Fryer, G. and T.D. Iles. 1972. *The Cichlid fishes of the Great Lakes of Africa. Their Biology and Evolution*. T.F.H. Publications, Inc. Ltd., Neptune City, New Jersey, 641 pp.

Gaemers, P.A.M. 1989. The first cichlids (Perciformes, Pisces) from Europe: the new, fossil genus Eurotilapia, evidence from otoliths and teeth. Ann. Mus. Roy. Afr. Centr., Sc. Zool., 257:109-116.

Gayet, M., J.-C. Rage, and R.S. Rana. 1984. Nouvelles ichthyofaune et herpétofaune de Gitti Khadan, le plus ancien gisement connu du Deccan (Crétacé/Paléocène) à microvertébrés. Implications paléogéographiques. Memoires de la Societé geologique de France (Paris), 147:55-65.

Goldstein, R.J. 1973. Cichlids of the world. T.F.H. Publications Inc., Hong Kong, 382 pp.

Greenwood, P.H. 1957. Fish remains from the Mumba Cave, Lake Eyasi. Mitteilungen aus dem Geologishen Staatsinstitut in Hamburg, 26:125-130.

Greenwood, P.H. 1959. Quaternary fish-fossils. Exploration du Parc National Albert, Institut des Parcs nationaux du Congo belge, 4:3-80.

Greenwood, P.H. 1968. The osteology and relationships of the Denticipitidae, a family of clupeomorph fishes. Bulletin of the British Museum (Natural History) Zoology, 16(6):215-273.

Greenwood, P.H. 1994. Cichlids. Pp. 202-206, in: Paxton, J.R. and W.N. Eschmeyer, Encyclopedia of Fishes, Academic Press, San Diego.

Greenwood, P.H. and E.J. Todd. 1970. Fish remains from Olduvai. *In*: Leakey, L.S.B. and R.J.G Savage (eds.). Fossil Vertebrates of Africa, 2:225-241.

Haq, B.U. and F.W.B. Van Eysinga. 1987. Geological Time Table, 4th Ed. Elsevier Science Publishers, Amsterdam.

Kemp, A. 1996. Triassic lungfish from Gondwana. Pp. 409-416, *in*: Arratia, G. and G. Viohl (eds.). Mesozoic Fishes - Systematics and Paleoecology, Verlag Dr. Friedrich Pfeil, München, Germany.

Kiener, A. and M. Maugé. 1966. Contributions a l'étude systématique et écologique des poissons Cichlidae endémiques de Madagascar. Mémoires du Muséum National d'Histoire naturelle, Série A, Zoologie, 40(2):4-99.

Kullander, S.O. 1983. *A revision of the South American cichlid genus Cichlasoma (Teleostei: Cichlidae).* The Swedish Museum of Natural History, Stockholm, Sweden, 296 pp.

Landini, W. and L. Sorbini. 1989. Ichthyofauna of the evaporitic Messinian in the Romagna and Marche regions. Bollettino della Società Paleontologica Italiana, 28(2-3):287-293.

Lévêque, C. 1997. Biodiversity dynamics and conservation. The freshwater fish of tropical Africa. Cambridge University Press, Cambridge. 438 pp.

Lippitsch, E. and N. Micklich. 1998. Cichlid fish biodiversity in an Oligocene lake. Italian Journal of Zoology, 65 (suppl.):185-188.

Loiselle, P.V. 1994. The cichlid aquarium. Tetra Press, Germany, 447 pp.

Lowe-McConnell, R.H. 1975. Fish communities in tropical freshwaters. Their distribution, ecology and evolution. Longman, London and New York, 337 pp.

Lowe-McConnell, R.H. 1987. Ecological studies in tropical fish communities. Cambridge Tropical Biology Series, Cambridge University Press, Cambridge, 382 pp.

Lundberg, J.G. 1993. African-South American freshwater fish clades and continental drift: problems with a paradigm. *In*: Goldblatt, P. (ed.). *Biological relationships between Africa and South America*. Proceedings of the 37th Annual Systematics Symposium, Yale University Press, New haven and London. pp. 156-199.

Lundberg, J.G. 1998. The temporal context for the diversification of Neotropical fishes. Pp. 49-68, in: Malabarba, L.R., R.E. Reis, R.P. Vari, Z.M.S. Lucena and C.a.S. Lucena (eds.). Phylogeny and Classification of Neotropical Fishes, Editoria Universitária - EDIPUCRS, Porto Alegre, Brasil.

Maina, J.N. 2000. The highly specialized secretory epithelium in the buccal cavity of the alkalinity adapted Lake Magadi cichlid, *Oreochromis alcalicus grahami* (Teleostei: Cichlidae): a scanning and transmission electron microscope study. Journal of Zoology, London, 251:427-438.

Maisey, J.G. 2000. Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. Cretaceous Research, 21:281-314.

Meyer, A., C. Montero, and A. Spreinat. 1994. Evolutionary history of the cichlid fish species flocks of the East African great lakes inferred from molecular phylogenetic data. Arch. Hydrobiol. Beih. Ergebnisse der Limnologie, 44:407-425.

Micklich, N. and B. Roscher. 1990. Neue Fischfunde aus der Baid-Formation (Oligozän; Tihamat Asir, SW Saudi-Arabien). N. Jb. Geol., Paläont. Abh, 180(2):139-175.

Miyazaki, H., T. Kancko, S. Hasegawa and T. Hirano. 1998. Developmental changes in drinking rate and ion and water permeability during early life states of euryhaline tilapia, *Oreochromis mossambicus*, reared in fresh water and seawater. Fish Physiology and Biochemistry, 18:277-284

Murray, A.M. 2000. African fishes from the Palaeozoic, Mesozoic and Early Cenozoic of Africa. Fish and Fisheries, 1:111-145.

Murray, A.M. and K.M. Stewart. (submitted). Fish remains from the Late Pliocene Chiwondo Beds, Malawi. Kaupia Darmstädter Beiträge zur Naturgeschichte.

Murray, A.M. and K.M. Stewart. 1999. A new species of fossil tilapiine cichlid from the Pliocene Middle Awash, Ethiopia. Journal of Vertebrate Paleontology, 19(2):293-301.

Myers, G.S. 1949. Salt tolerance of freshwater fish groups in relation to zoogeographic problems. Bijdragen tot de Dierkunde, 28:315-322.

Myers, G.S. 1966. Derivation of the freshwater fish fauna of Central America. Copeia, 1966(4):766-773.

Nelson, J. S. 1994. *Fishes of the World.* John Wiley and Sons, Inc. Toronto, xvii + 600 pp.

Nolf, D. and D.T. Dockery III. 1990. Fish otoliths from the Coffee Sand (Campanian) of northeastern Mississippi. Mississippi Geology, 10(3):1-14.

Norman, J.R. and P.H. Greenwood. 1975. *A History of Fishes.* Ernest Benn Ltd. London, xxv + 467 pp.

Owen, R.B., R. Crossley, T.C. Johnson, D. Tweddle, I. Kornfield, S. Davison, D.H. Eccles and D.E. Engstrom. 1990. Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. Proceedings of the Royal Society, London, series B, 240:519-553.

Patterson, C. 1993. An overview of the early fossil record of acanthomorphs. Bulletin of Marine Science, 52(1):29-59.

Reid, G.M. 1996. Ichthyogeography of the Guinea-Congo rain forest, West Africa. Proceedings of the Royal Society of Edinburgh, 104B:285-312.

Reinthal, P.N. and M.L.J. Stiassny. 1991. The freshwater fishes of Madagascar: A study of an endangered fauna with recommendations for a conservation strategy. Conservation Biology, 5(2):231-243.

Roberts, T.R. 1975. Geographical distribution of African freshwater fishes. Zoological Journal of the Linnean Society, 57:249-319.

Schaeffer, B. 1947. Cretaceous and Tertiary actinopterygian fishes from Brazil. Bulletin of the American Museum of Natural History, 89(1):1-40.

Smith, A.G., D.G. Smith, and B.M. Funnell. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press, Cambridge, ix + 99 pp.

Stiassny, M.L.J. 1987. Cichlid familial intrarelationships and the placement of the Neotropical genus *Cichla* (Perciformes, Labroidei). Journal of Natural History, 21:1311-1331.

Stiassny, M.L.J. 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview. Pages 1-35 in: Keenleyside, M.H.A. (ed.). Cichlid Fishes. Behaviour, ecology and evolution. Chapman and Hall, London, New York.

Thomas, H., J. Roger, S. Sen, M. Pickford, E. Gheerbrant, Z. Al-Sulaimani, and S. Al-Busaidi. 1999. Oligocene and Miocene terrestrial vertebrates in the southern Arabian Peninsula (Sultanate of Oman) and their geodynamic and palaeogeographic settings. Pp. 430-442 *in*: Whybrow, P.J. and A. Hill (Eds.). Fossil Vertebrates of Arabia. Yale University Press, New Haven and London.

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

Van Couvering, J.A.H. 1977. Early records of freshwater fishes in Africa. Copeia, 1977:163-166.

Van Couvering, J.A.H. 1982. Fossil cichlid fish of Africa. Special Papers in Palaeontology no. 29:103 pp.

Weiler, W. 1970. Fischfunde aus dem Tertiär des Wadi Araba-Grabens in Jordanien. Geologische Jaarbuch, 89:193-208.

White, E.I. 1937. The fossil fishes of the terraces of Lake Bosumtwi, Ashanti. Bulletin of the Gold Coast Geographical Association, 8:47-58.

Wilson, M.V.H., D.B. Brinkman and A.G. Neuman. 1992. Cretaceous Esocoidei (Teleostei): early radiation of the pikes in North American fresh waters. Journal of Paleontology, 66:839-846.

SUMMARY

In 1996, the Wembere Manonga Palaeontological Expedition collected a large number of fossil fish from Mahenge, in the Singida Peneplain of northcentral Tanzania. These collections included over 100 extremely well-preserved specimens belonging to the family Cichlidae, which have formed the basis of this thesis.

The Mahenge site is a small crater lake, about 400 m wide. The crater has been given a radiometric date of about 45 Ma, a middle Eocene age. The sediments containing the fossils are considered to be only slightly younger than the crater itself. Therefore the cichlids from this site are the oldest known representatives of the family, and predate the next oldest cichlid fossils by at least fifteen million years.

Characters that have been used to support the monophyly of the Cichlidae are related to soft anatomy not preserved in fossils; however, the Mahenge specimens are included in this family based on the structure of the lower pharyngeal jaw, the interrupted lateral line, and the form of the scales and scale covering. The cichlid specimens represent five different species based on osteological characters, particularly of the skull bones. Scale characters, shown to be useful for characterizing genera of cichlids, are used to unite these five species in a single genus. Cichlids are popular organisms for the study of evolutionary patterns because these fish undergo adaptive radiations and speciate at very fast rates, and in great numbers. Based on the available evidence, the Mahenge cichlids form a monophyletic group, and are endemic to the type locality, therefore these fishes may be considered as an ancient species flock . This indicates that cichlids had the ability to form species flocks early in the history of this family.

Because there are few osteological characters previously used for phylogenetic analyses of cichlids, a study of the fossils and comparative material was undertaken in order to distinguish useful characters for including fossil and Recent material in an analysis. Although the results are not conclusive, and are not in complete agreement with previous phylogenetic analyses, predominantly based on molecular data or soft anatomy, several characters may prove to be useful in analyses including a larger number of species.

After reviewing the known fossils of the family and higher taxa, along with the salt tolerance of some species, I suggest that the Cichlidae arose in the Late Cretaceous (Maastrichtian) or Early Tertiary (Palaeocene), rather than in the Early Cretaceous, as has previously been suggested. This indicates that some cichlids attained their modern range predominantly by dispersal through marine waters, rather than because of vicariant events.