ABSTRACT

SYSTEMATICS OF AFRICAN CICHLID FISHES: DETERMINATION OF THE MOST PRIMITIVE TAXON, AND STUDIES ON THE HAPLOCHROMINES OF LAKE MALAWI (TELEOSTEI: CICHLIDAE)

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The cichlids of Africa present many challenges to the taxonomist. Diverse systematic problems at three levels in cichlid phylogeny form the subject matter of this dissertation. At the most general level, I summarize current morphological evidence that supports cichlid monophyly and the most-inclusive groups of cichlids. With this review as a framework, I argue that the most phylogenetically primitive African cichlid is _Heterochromis multidens_, a little-known large cichlid from the Zaire River basin. I redescribe this monotypic genus and species and illustrate much of its osteology. It possesses a distinctive suite of derived characters, but is uniquely primitive among African cichlids in infraorbital morphology and other features.

At a less inclusive phylogenetic level, I examine the controversy over the monophyletic status of the "species flock" of haplochromine cichlids in Lake Malawi. A derived type of anal-fin markings present in a subset of the Malawian fauna is shared with many non-Malawian haplochromines, indicating that the species flock of Lake Malawi is not monophyletic. The two (or more) faunal components of Lake Malawi are ecologically distinct.

The remaining major parts of the study are concerned with particular assemblages of haplochromine cichlids in Lake Malawi. I present a detailed phylogenetic analysis of the *Cyrtocara livingstonii* species-group of ambush predators, and characterize a new species in the group. I also describe three new species of haplochromines with three lateral spots and present a key to the three-spot assemblage. Intralacustrine dispersion of Malawi cichlids is briefly addressed in appended material.

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by
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Ex Africa chaos.

P. H. Greenwood (pers. comm., 1971)

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I want to thank Frederick Cichocki for sharing with me, a decade ago, his unpublished information that cichlid infraorbitals are phylogenetically informative. This advice led me to survey them independently, and to discover that *Heterochromis* is among the most plesiomorphic of all cichlids. Cichocki's remarkable dissertation, filled with valuable data as well as provocative discussion, will surely remain indispensable to students of cichlid interrelationships.

My final dissertation committee at Yale consisted of J. David Archibald, James E. Rodman, Bruce H. Tiffney, and Keith S. Thomson (chairman). Each contributed precious support, friendship, advice, and/or philosophy.

My dear, patient wife, Joan, and parents, Kenneth and Madaline, have supported me all along in every way. I couldn't have done it without them and wouldn't have wanted to try. Zikomo wambiri!

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CHAPTER 1

GENERAL INTRODUCTION

> . . . Cichlid fishes . . . display such evolutionary exuberance, and have evolved so rapidly, in East African lakes that they are with justification held to represent some of the world's most dramatic examples of . . . explosive speciation. . . . Such richness poses immense taxonomic problems, whose solution is essential before meaningful ecological studies can be made and before schemes for the rational exploitation of fish stocks . . . can be embarked upon with reasonable hopes of success.
>
> Geoffrey Fryer (1982: 887)

In this dissertation, I address some phylogenetic problems in the study of African cichlids at three separate and nested levels of their hierarchy.

First, Chapter 2 concerns the most inclusive phylogenetic level, that of all African Cichlidae. I first survey the infraorbital bones of cichlids, emphasizing African taxa. The results of this survey complement those of Cichocki (1976), who concentrated on non-African cichlids. I found that one Zairean form, the poorly known monotypic genus *Heterochromis*, is unique among African taxa in retaining the primitive cichlid configuration of infraorbitals, elsewhere found only in the Malagasy-Indian genera and in the neotropical genus *Cichla*. Moreover, I found that *Heterochromis* retains the primitive number of two predorsal bones, previously known among African taxa only in *Tylochromis*. These characters suggest the novel hypothesis that *Heterochromis*, and not the commonly mentioned *Tylochromis* or *Hemichromis*, is the most phylogenetically primitive African cichlid, and indeed one of the most primitive of all cichlids. I present a taxonomic redescription of Heterochromis multidens, as well as osteological and certain other morphological data. This information enables testing Cichocki's hypothesis that all African cichlids comprise a monophyletic group, sharing a common ancestor that is not shared with any non-African cichlids. Furthermore, the relationships of Heterochromis and the distribution of character states in primitive cichlids lead me to reassess the status of several characters currently believed to be derived within subgroups of African cichlids. These new character interpretations provide critical evidence that I use in later chapters at lower taxonomic levels.

In Chapter 3, my emphasis shifts from African cichlids as a whole to those of Lake Malawi in particular. I examine the long-standing question of whether the very large, endemic "species flock" of haplochromine cichlids in Lake Malawi is monophyletic. Previous evidence in support of mono- or oligophyly, i.e., a fully scaled caudal fin, is rejected as being a plesiomorphy. However, I show that the anal-fin spots of Malawian haplochromines belong to two types, ocellate and nonocellate, as defined by Greenwood (1979) for riverine and Victoria-Edward-Kivu haplochromines. Among Lake Malawi endemics, the ocellate anal fin is confined to the 10 genera of the "mbuna" assemblage, whereas the nonocellate type is apparently found in all other endemic haplochromines of all major body color-pattern types. Neither component of the Malawian fauna can be hypothesized to be monophyletic on available evidence. However, the anal-fin evidence does indicate that all mbuna genera share a more recent common ancestor with some or all non-Malawian ocellate genera than with other Malawian genera. In other words, there are at least two separate haplochromine species flocks in Lake Malawi. This discovery is critically important for biological studies on the Malawian fauna. I point out several striking ecological differences between the two faunal components. Moreover, current models of sympatric speciation can apply only in cases of color polymorphism, which are restricted to the smaller (mbuna) assemblage.

Chapter 4 has a still narrower phylogenetic focus, highlighting a group of closely related Malawian species with nonocellate anal fins. I examine the monophyly of the *Cyrtocara livingstonii* species-group, which previously was treated less formally as a series of species within the same synopsis division (Trewavas, 1935). I interpret the apparent successive disruption of the barred color pattern into disconnected blotches during this group's phylogenesis as a transformation series supporting the monophyly of the group, and also providing evidence for the exclusion of one previously included species. Trewavas (1949) hypothesized that this group is most closely related to a nonendemic, widely distributed species, *Haplochromis callipterus* (=*Astatotilapia calliptera*). I reexamine her evidence, and reject the proposed relationship as being based on primitive or problematic character-states. I adduce new evidence suggesting that the *C. livingstonii* species-group is most closely related to two endemic Malawian species. One of these is herein described as new, and has remarkable trophic specializations. I characterize a new species-group for the nine species I recognize in this group. Further, I present a cladistic analysis of the species of this group, based principally on new data about their coloration and osteology.

In Chapter 5, I consider another assemblage that is currently defined by its distinctive color pattern, the Malawian haplochromines with three lateral spots. I suggest that this assemblage is not monophyletic. I introduce a descriptive system of terminology for the markings of these species. Three species collected during my three visits to Lake Malawi are described as new. I discuss the advantages of presenting linear-regression equations of morphometric proportions in addition to traditional ratios. A new key to the thirty-odd species in the three-spot assemblage concludes the chapter; this key includes many new data from my examination of virtually all pertinent type material and of specimens I collected and photographed during this study.

Little is known of the detailed geographic distribution of species within Lake Malawi, or of the factors that bring about their dispersal (dispersion) within the lake. These are issues of theoretical importance to future studies of their biogeography and evolution. In Appendix 1, therefore, I include a recently published study (co-authored by K. R. McKaye) reporting one fascinating means of intralacustrine dispersal, rafting by floating islands of swamp vegetation. In Appendix 2, I present the results of a preliminary study using tags of small, colored glass beads to monitor individual movements and behavior of rocky-shore cichlids over a 5-month period.

CHAPTER 2

RECOGNITION OF *HETEROCHROMIS MULTIDENS* (PELLEGRIN) FROM THE CENTRAL ZAIRE RIVER SYSTEM AS THE MOST PRIMITIVE AFRICAN CICHLID

INTRODUCTION

Heterochromis multidens (Fig. 1) is a little-known large cichlid found in forested backwater habitats throughout the *cuvette centrale* of the Zaire River system from SE Cameroon to NE Zaire. It was first described, as a species of *Paratilapia*, by Pellegrin in 1900. In 1922, Regan recognized the distinctiveness of this species by transferring it to *Heterochromis*, a new monotypic genus. When its relationships have been considered at all, *Heterochromis multidens* has been treated as a relative of *Tilapia* (Van Couvering, 1972: 10, 79, 83; Hoedeman, 1974: 1006), possibly because it has a black "tilapia-mark" in the dorsal fin, and bears no obvious resemblance to any other particular cichlid.

The genera commonly cited as the most primitive African cichlids are *Tylochromis* (Greenwood, pers. comm.) and, especially, *Hemichromis* (Pellegrin, 1903: 149; Cichocki, 1976: 184). *Heterochromis* has never previously been considered a phylogenetically primitive cichlid (except by Oliver, 1979, in an abstract of preliminary work). However, only *Heterochromis* and *Tylochromis* among African cichlids retain the primitive number of two predorsal bones, which is reduced to one or none in other African cichlids. Moreover, a distinctive, primitive configuration of the infraorbital bones is retained in *Heterochromis* but is modified in all other African cichlids surveyed, including

Tylochromis and Hemichromis. This primitive infraorbital state is otherwise found only in the endemic Malagasy and Indian genera and in the neotropical genus Cichla. These preliminary observations induced me to study Heterochromis multidens and to reevaluate the problem of identifying the most primitive of the African cichlids.

I would have liked to conduct a detailed comparative-morphological survey and perform a new cladistic analysis of the major groups of African cichlids, for such a study is urgently needed if the systematics of these fishes is to progress. Unfortunately, I have had to defer that project to the future. In the first part of this chapter, however, I summarize much of the current evidence for cichlid monophyly and for the higher-level phylogeny of cichlids. This phylogenetic framework enables me to show that Heterochromis lacks the synapomorphies that, according to Cichocki's assertion, characterize all African cichlids as a monophyletic group. These and other data indicate that Heterochromis is the most plesiomorphic African cichlid. Evidence from a survey of cichlid infraorbital bones suggests that Heterochromis is the sister group, not of other African cichlids alone, but of all other African cichlids and all neotropical cichlids except Cichla. In a second section, I give a full synonymy and illustrated taxonomic redescription of Heterochromis multidens as a basis for future studies of its biology, taxonomy, and biogeography.

CURRENT EVIDENCE ON THE INTERRELATIONSHIPS OF CICHLIDS

Comments on Cichocki's Study

The most significant modern attempt at elucidating the higher-level phylogeny of cichlids is the doctoral dissertation of Frederick Cichocki (1976). The importance of that study has not been widely recognized, since it has remained unpublished. For example, Van Couvering (1982) discussed cichlid phylogeny and derived a cladogram that is inconsistent with data presented by Cichocki (1976), which she did not cite. Cichocki studied 62 morphological character complexes in 47 cichlid species. He concentrated on the Malagasy and neotropical genera and the single Indian-Sri Lankan genus, but he also included four genera and five species of African cichlids in his formal analysis: *Tilapia mossambica* (= *Oreochromis mossambicus*, see Trewavas, 1981), *Hemichromis fasciatus*, "*Haplochromis strigigena*" (= *Pseudocrenilabrus multicolor*), *Pseudocrenilabrus philander*, and *Lamprologus elongatus*. Cichocki noted that his "synapomorphies which indicate that the African cichlids form a distinct holophyletic group are generally consistent for a variety of EUs [evolutionary units, i.e., species] cursorily surveyed [he lists 60 such African species, *Heterochromis multidens* not among them] . . . as well as for those formerly [*sic*; i.e., formally] analyzed" (Cichocki, 1976: 184).

Unfortunately for those who want to understand the sister-group relationships of cichlids, Cichocki did not analyze his extensive data with a truly phylogenetic method, i.e., one based on philosophical parsimony. Instead, he used a character-compatibility or clique method. Such methods "appear to be seriously defective on both theoretical and empirical grounds" (Mitter, 1980: 188). Among the most serious flaws of clique methods are the following: (1) They use only a subset of the character evidence (those characters exhibiting no homoplasy) to group taxa, instead of seeking the most parsimonious explanation of the distribution of all characters (Mickevich, 1980). (2) These methods assume that character evolution is irreversible (Farris and Kluge, 1979). (3) They do not permit reinterpretation of initial estimates of character polarity that are subsequently discovered to have been wrong (Mickevich and Parenti, 1980: 110). (4) Clique methods have not been shown theoretically to yield cladistic inferences, but are employed as if they did (Mickevich and Parenti, 1980: 109). Therefore, in using Cichocki's study, it is especially important to evaluate the data in his character-state table (table 1.2, which contains several typographical errors in data coding), and not merely to rely on his consensus tree (Cichocki, 1976, fig. 1.43). Furthermore, I have reservations about many of the transformation series or character-state trees Cichocki hypothesized, particularly those divided into multiple states (as many as 14).

However, these remarks are not intended to minimize the importance of Cichocki's work. Its morphological section contains a large compilation of cichlid characters, many of them newly discovered by Cichocki, and this alone suffices to insure it a place of lasting importance in the literature of cichlid systematics.

Summary of Published Evidence on Cichlid Phylogeny, and New Evidence on the Relationships of Heterochromis

In the following summary of the higher-level interrelationships of the cichlids, character numbers correspond with those shown on the cladogram (Fig. 2). This evidence is taken from recent literature (cited with each character), with the addition of original data on *Heterochromis* and, for infraorbitals and other features as noted, on other taxa as well.

A number of characters are currently hypothesized to be unique synapomorphies that corroborate the monophyly of the Cichlidae:

1. The transversus dorsalis anterior muscle is more complexly subdivided than in other perciforms (Anker, 1978: 256-258; Stiassny, 1981b: 309; Liem and Greenwood, 1981: 99-100; Kaufman and Liem, 1982). According to Anker (1978) the divisions of this dorsal gill-arch muscle are the transversus epibranchialis 4, the transversus epibranchialis 2 (subdivided into a pars dorsalis and a pars ventralis), and the transversus pharyngobranchialis 2. However, apparently only the latter part is unique to cichlids (Stiassny, 1982: 437, 450).
2. "The loss of a major structural association between parts A_2 and A_w of the adductor mandibulae muscle and the musculous insertion of a large ventral section of A_2 onto the posterior border of the ascending process of the anguloarticular" (Stiassny, 1981b: 309; 1982).

3. The functional decoupling of the premaxilla and maxilla from each other and from the lower jaw and suspensorium during protrusion of the upper jaw (Liem, 1979: 118-119; Kaufman and Liem, 1982; see also Lauder and Liem, 1983 fig. 52).
4. The second epibranchials have a large, anterior cartilaginous extension or cap (Fig. 3; Stiassny, 1981b, 1982).
5. The fourth epibranchials have an anteroventrally expanded articular head (Stiassny, 1981b, 1982). A similar condition is present in atherinomorphs (Rosen and Parenti, 1981: 6, figs. 6-19). In Heterochromis the articular head of the fourth epibranchial is not expanded (Fig. 3a); this appears to be a secondary reduction in this genus.
6. The microbranchiospines are of a characteristic type (Stiassny, 1981b).
7. The anterior parts of the gut are uniquely specialized, with (a) the stomach an extendible, blind median sac, (b) a left-hand exit to the anterior intestine, and (c) the first loop of the intestine situated to the left of the stomach (Zihler, 1982).

Cichlids are also unusual, but not unique, in lacking pyloric caeca (Zihler, 1982), lacking a subocular shelf (Smith and Bailey, 1962), and having only a single nostril on each side (Liem and Greenwood, 1981). At present it is not clear whether these are additional synapomorphies of the Cichlidae derived convergently in other groups, or are synapomorphies of a group including the Cichlidae and other taxa (i.e., plesiomorphies at the level of the Cichlidae). The phylogenetic assessment of these characters will, in my opinion, have to await a better-substantiated hypothesis of the sister group of the Cichlidae than Liem and Greenwood's (1981) proposal that it is the Embiotocidae.[1]

According to the data and analysis of Cichocki (1976), the Malagasy cichlid _Ptychochromis_ _oligacanthus_ (together, possibly, with the similar Malagasy form _Ptychochromoides_ _betsileanus_, of which he had no material for complete study) is the sister group of all other cichlids, because all others share the following synapomorphies that are absent in _Ptychochromis_:

8. The openings of the paired coronal lateralis canals (=NLF_0 of Barel et al., 1976) on the frontals are partially coalesced medially (character 3 state B of Cichocki).
9. The anterior and posterior processes of the first epibranchial are subequal in length (Fig. 3b; character 31 state B of Cichocki). Primitively, the anterior arm is

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[1] Liem and Greenwood (1981: fig. 10) advanced a single character in support of a sister-group relationship between embiotocids and cichlids: "lower pharyngeal jaw is suspended in a muscular sling of which the fourth levator externus is dominant both morphologically and functionally." The detailed morphology of the gill arches and associated muscles has not been widely surveyed in percomorphs, so cladistic hypotheses based on examination of a few families may be misleading. Further, the most plesiomorphic cichlids are the appropriate taxa for comparison with other groups, but Liem and Greenwood apparently based their descriptions of cichlid pharyngeal morphology and their functional analyses primarily on quite specialized, apomorphic cichlid taxa. Finally, it is difficult to account for the disjunct ranges of the cichlids (a continental group inhabiting Gondwanan land masses as far east as India) and embiotocids (a coastal marine group of the north Pacific, with one fresh-water representative in California) if the two families are sister-groups. However, the Liem-Greenwood hypothesis is explicit and testable.

longer than the posterior, or uncinate, process (see figures in Rosen, 1973, and Rosen and Parenti, 1981).

10. The second-epibranchial toothplate is lost (character 38 state B of Cichocki).
11. "Fourth ceratobranchials bearing median toothplates separate from outer gill rakers or plates absent" (character 39 state B of Cichocki, 1976: 148).

All cichlids except _Ptychochromis_ and _Paratilapia polleni_ of Malagasy are corroborated as a monophyletic group by the following synapomorphy:

12. The coronal lateralis canals (=NLF_0) are "coalesced medially producing a single median canal shared by both frontals" (character 3 state C of Cichocki, 1976: 148).

All cichlids except _Ptychochromis_, _Paratilapia_, and the sister taxa _Paretroplus_ (Malagasy) and _Etroplus_ (India-Sri Lanka) are corroborated as monophyletic by several characters:

13. "Epaxial cranial roof musculature extending medially and laterally to or anterior to the level of the coronal aperture [=NLF_0]" (Fig. 4; character 1 state B of Cichocki, 1976: 149).
14. There are diverging frontal ridges anterior to the single median coronal canal and pore (NLF_0) (Fig. 4; character 3 state D of Cichocki).
15. The pseudobranch (which is free and more or less gill-like in the more plesiomorphic taxa) is rudimentary, glandular, and covered by the buccal mucous membrane (character 35 state B of Cichocki).

16. "Swimbladder extending at most only slightly anterior to the epipleural ribs or with secondarily developed, narrow, short and thickened diverticula" (character 56 state C of Cichocki, 1976: 149). (Cichocki also defined a state D of this character [pp. 117, 118], but through a typographical error state D was not tabulated for any taxon [table 1.2]. However, he described [p. 237] and figured [fig. 1.27] state D in *Geophagus surinamensis*.)

Infraorbital bones.--The primitive infraorbital series of most living teleostean groups probably consists of a canal-less antorbital and six canal-bearing bones from lacrimal to dermosphenotic (Smith and Bailey, 1962; Nelson, 1969; see also Gosline, 1965). No cichlid is known to retain an antorbital. In the great majority of cichlids there are six infraorbitals from lacrimal to dermosphenotic, and the lacrimal has four neuromasts (Fig. 5).

Among all cichlids examined, the Malagasy genera *Ptychochromis*, *Paratilapia*, *Paretroplus* (modified in the Indian-Sri Lankan *Etroplus*), the neotropical genus *Cichla* (Cichocki, 1976), and the monotypic African genus *Heterochromis* (pers. obs.) are unique in sharing a distinctive condition of the infraorbital bones (Fig. 5a-e). In this condition, the anterior bone (the lacrimal) bears only three neuromasts. This bone is followed either by six other bones (infraorbitals 2-7, the most dorsal or seventh being the dermosphenotic), each with a single neuromast, or, as a common individual or species-typical variant, by five bones, one of which bears two neuromasts and represents a fusion of two infraorbitals, most frequently 3 + 4. Infraorbital 2 has the appearance of a piece of the lacrimal that has become detached, particularly since in several species these two bones share a ventrally directed lateralis pore and canal between the third and fourth neuromasts (Oliver, 1979).[2] Initially, I thought that this strange-looking condition was a synapomorphy. However, I now suspect that Cichocki (1976) is correct in interpreting this as the primitive state for cichlids. The bases for this interpretation are (1) the presence of the condition in the Malagasy cichlids, judged the most plesiomorphic on other evidence also, and (2) some out-group evidence (e.g., the broadly contiguous lacrimal and deep second infraorbital in some perciforms such as the sparoids [Akazaki, 1958; Smith and Bailey, 1962: pl. 2K; Johnson, 1980: 48 and tables 1 and 6] and the carangids [Smith and Bailey, 1962: pl. 3Q]). I am not aware, however, of any non-cichlids having both seven infraorbitals and a deep second bone.

In light of the above argument, I tentatively interpret the basic alternative to the seven-bone infraorbital series with a three-neuromast lacrimal and a deep second infraorbital as a synapomorphy of all neotropical cichlids except _Cichla_ and all African cichlids except _Heterochromis_ (Fig. 2):

17. Infraorbitals consisting of six bones (unless secondarily fused) from lacrimal to dermosphenotic, of which the anterior two bones are a lacrimal with three neuromasts

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[2] To try to clarify the homologies of these bones in cichlids, I have looked for ontogenetic change in the basic condition, such as subdivision of a four-neuromast lacrimal to form two bones with three and one neuromast, respectively. However, in the smallest available specimens of species having this condition as adults, namely postlarvae of _Cichla temensis_, the adult condition is already present, so the question is not resolved.

(possibly representing the primitive three-neuromast lacrimal co-ossified with the primitive deep second infraorbital; cf. discussion in Cichocki, 1976) and a shallow, simple, tubelike second infraorbital (which may correspond with the primitive third bone).

Cichocki (1976: 150) gave several characters as synapomorphies of all African cichlids:

18. "Branchial adductor fibers arising from the distal one-fourth of the anterior face of the first epibranchial bone along a developed axial ridge; interbranchial abductor fibers arising from the distal one-half to two-thirds of the epibranchial from along the same ridge" (character 33 state D of Cichocki). Although this state is unique to African cichlids, it is one of nine (A through I) that Cichocki defined for the character. He remarked, "Relationships among the states of this character are obscure except for states G, H, and I . . ." (1976: 88). I have not been able to determine the state of this character in Heterochromis.

19. The adductor arcus palatini muscle inserts partly on the palatine (character 22 state B of Cichocki). I find that the alternative state A (insertion of this muscle confined to a more posterior position on the suspensorium) characterizes Heterochromis, contrary to Cichocki's prediction (1976: 150) that state B is a synapomorphy of all African cichlids. Cichocki notes that state B occurs

also (and he presumably implies that it is independently derived) in the neotropical cichlids *Nannacara anomala* and two of three examined species of *Apistogramma* (Cichocki, 1976: table 1.2).

20. The axial lateral ridge of the palatine is lost (character 21 state C of Cichocki). I find that the inferred primitive state (a distinct axial lateral ridge retained) is found in *Heterochromis* (Figs. 6, 7a), contrary to Cichocki's prediction that the loss of the ridge characterizes all African cichlids. Cichocki records the loss of the ridge in *Paretroplus* and several neotropical genera.

21. First epibranchial with posterior arm much longer than anterior (character 31 state C of Cichocki). A different, more primitive state (my character 9 above; see Fig. 3b) occurs in *Heterochromis*, contrary to Cichocki's prediction.

22. Pars A2c of adductor mandibulae "undifferentiated" (character 28 state C of Cichocki, 1976: 82, 150). Cichocki tabulates (table 1.2) the same state in *Ptychochromis*, *Paretroplus*, and numerous neotropical taxa, so it is difficult to understand his use of this feature as a synapomorphy of African cichlids. I have not determined the state in *Heterochromis*.

23. "Medial tooth plates absent from the fourth ceratobranchials" (character 39 state B of Cichocki, 1976:

150). However, this description conflicts with the state given in table 1.2 of Cichocki.

Inexplicably, Cichocki (1976: 150) also lists as synapomorphies of African cichlids "all the character states given in V above" (i.e., those he considers to characterize all African cichlids together with the neotropical genus _Cichla_ in one of his two alternative interpretations).

At this level on the cladogram (Fig. 2), I would tentatively add two potential synapomorphies:

24. Loss of a sutured joint between hyomandibular and metapterygoid. Such a joint is widespread among percomorph out-groups (e.g., Centropomidae [Greenwood, 1976]; sparoids, lutjanoids, and haemuloids [Johnson, 1980]). Cichlids are very inadequately surveyed for this character, and the condition is unknown for _Ptychochromis_ and _Hemichromis_. The sutured joint is retained in _Heterochromis_ (Fig. 7a), _Paratilapia_ (Van Couvering, 1982: 14), and _Cichla_ (Machado-Allison, 1973: 173, 174; Van Couvering, 1982: fig. 7a). The suture is absent (lost, I presume) in _Etroplus_ (Van Couvering, 1982: fig. 7c), _Tylochromis_ and haplochromines (pers. obs.), and, possibly, neotropical cichlids other than _Cichla_ (figs. in Newsome, 1971).

25. Loss of the interarcual cartilage. Primitively in percomorphs, this is a rodlike cartilage present between the uncinate (posterior) process of the first epibranchial

and the second pharyngobranchial (Travers, 1981; Rosen and Parenti, 1981). As far as I know, a rodlike interarcual cartilage is unknown in cichlids. However, Travers (1981: 860) was wrong in stating that the Cichlidae lack an interarcual cartilage. Stiassny (1981a: 91), whom Travers cited, reports a specimen of the Lake Malawi haplochromine *Rhamphochromis* sp. as having a small interarcual cartilage, whereas other congeneric specimens lacked the cartilage. A small, spherical interarcual cartilage is retained in *Heterochromis* (Fig. 3a), as well as in "many Neotropical, Malagasy and Asian species" (Stiassny, 1981b: 295), including *Cichla* sp., *Etroplus* sp., and *Geophagus* sp. (Stiassny, 1981b: fig. 7A-C). The cartilage is lost in *Tylochromis* (Stiassny, 1981b: fig. 7D; pers. obs.), and in most African cichlids (Stiassny, 1981b: 295; pers. obs.), including most haplochromines (pers. obs.); however, Travers (1981: 858) reports it present in a haplochromine species, *Astatotilapia burtoni*.

Finally, all African cichlids except *Heterochromis* and *Tylochromis* share at least one synapomorphy (Fig. 2):

26. Predorsal bones reduced from two to one.

Notes on Additional Characters

In addition to the characters discussed above, several character-states that are present in *Heterochromis* and are currently used in cichlid taxonomy are discussed below. Some have a wider taxonomic distribution within the family than is commonly appreciated. The primitive or derived status of others appears to be misinterpreted in the taxonomic literature. These findings suggest that the monophyly or limits of some major subgroups of African cichlids, when based on any of these characters, should be reevaluated. Five such characters are discussed in this section: scale ctenoidy vs. cycloidy; the nuchal or frontal hump; the "tilapia-mark"; scaly dorsal and anal fins; and a fully scaled caudal fin. These characters may be conveniently discussed with reference to the cichlid cladogram (Fig. 2) derived above.

Ctenoid vs. cycloid scales

Greenwood (1979: 271) remarks that, "on the principle of commonality . . ., strongly ctenoid body scales should be looked upon as the primitive condition, and an increase in the area of the body covered by cycloid or reduced ctenoid scales should be considered the derived one."[3] However, he then proceeds to question this judgment on the ground that weakly ctenoid scales are present anteriorly on the body in Hemichromis, and are correlated with features he considers derived. He concludes: "In the face of such contradictory observations it would seem advisable not to use this type of scale ornamentation in phyletic analysis" (Greenwood, 1979: 271).

I suggest that out-group evidence justifies the hypothesis that ctenoid scales are primitive for cichlids, because ctenoid scales characterize most percomorphs as well as the several most phylogenetically primitive cichlids (as judged by other characters).

Van Couvering (1982: 17, 83) considers cycloid scales to be primitive for cichlids, and claims (p. 17): "The development of ctenoid scales has taken place only in the haplochromines." She uses the latter term in a very broad sense, including not only the haplochromines sensu Greenwood, but also Cichla and Hemichromis. Nevertheless, she is apparently unaware that ctenoid scales are found in cichlids outside these taxa. The scales of Heterochromis, which Van Couvering considered

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[3] Within-group commonality ("common equals primitive") is a logically indefensible criterion for inferring character polarity. This principle must lead to acceptance of the wrong inference every time a derived state is attained sufficiently early in a group's history to characterize a majority of included species (e.g., viviparity in mammals; reduction of the pseudobranch in cichlids). However, Greenwood's (1979: 279) use of commonality appears to approach the valid out-group method of judging character polarity.

to be a "tilapine," are unambiguously ctenoid over much of the body (see taxonomic redescription, below; Fig. 8). The scales are also reported to be, at least weakly, ctenoid in the Malagasy taxa *Oxylapia polli* (Kiener and Maugé, 1966: 74), *Paratilapia polleni* (Kiener, 1963: pl. 13; Kiener and Maugé, 1966: 70), *Ptychochromis oligacanthus* (Kiener, 1963: pl. 14; Kiener and Maugé, 1966: 80), *Ptychochromoides betsileanus* (Kiener and Maugé, 1966: 77), and *Paretroplus* spp. (Kiener, 1963: pl. 15; Kiener and Maugé, 1966: 58). Moreover, ctenoid scales are the rule in percomorphs generally. I suggest that ctenoid scales are primitive for cichlids and that cycloid scales arose two or more times in the family. A more detailed, better-corroborated cladogram of cichlids is necessary before this hypothesis can be evaluated more critically.

Frontal humps

In many cichlid species, a prominent hump is developed in the frontal or nuchal region of adult individuals, especially males (Table 1). This hump is, in some cichlids, a secondary sexual characteristic associated with spawning (Bleick, 1975). In at least a few species, though, such a hump is developed to some degree in all subadult and adult individuals irrespective of sex (e.g., *Cyrtocara moorii* of Lake Malawi; pers. obs.). In the neotropical species *Cichlasoma citrinellum* the nuchal hump tissue, located in the hypodermis, is a highly edematous adipose tissue whose swelling is due to water retention under endocrine control (Bleick, 1975). Humps of similar appearance are well developed in many of the cladistically most primitive cichlids, including *Cichla*, *Heterochromis*, *Ptychochromoides*, *Paratilapia*, and possibly *Ptychochromis* (for which conflicting statements exist; see Table 1), judged the sister-group of all other cichlids (Fig. 2; Cichocki, 1976). Therefore, I suggest that such humps may be primitive for cichlids and that independently their development has been suppressed several times. However, a more testable hypothesis again awaits the recognition of the closest sister-groups of the Cichlidae.

The "tilapia-mark"

Many species of African cichlids have a distinctive dark spot on the basal part of the dorsal fin, near the junction of the spinous and soft parts. In taxa having the spot, it is often lost or indistinct in adults, and has been interpreted as a juvenile shoaling mark (Fryer and Iles, 1972). This spot is commonly known as the "tilapia-mark," from its occurrence in most species of Tilapia sensu lato, and is considered an indication of phylogenetic relatedness (e.g., Trewavas, 1973). The available information on the taxonomic distribution of this feature is summarized in Table 2. The presence of the mark in two plesiomorphic, non-tilapiine cichlids, Paratilapia polleni of Malagasy and Heterochromis multidens (Fig. 9) of Africa, leads me to suggest that this character too may primitively characterize cichlids (or, at least, a larger subgroup of them than the tilapia group) and may have been repeatedly lost or suppressed within the family. It might be argued that similar marks arose repeatedly, perhaps because of convergences in the ecology of the various cichlids having them. One might, for example, attribute the strikingly similar marking in the neotropical genus Retroculus to such convergence. But, why should independently derived shoaling marks so precisely resemble each other in size, shape, color, and placement? Neotropical characids exhibit a wide range of shoaling marks, which vary widely in all of these attributes. Moreover, an a priori judgment that tilapia-marks are of multiple origin is unparsimonious. Perhaps they are multiply derived, but this will have to be deduced from a better-corroborated cladogram than is now available. I venture to suggest that the "pelmatochromis-mark" of several African cichlids, which is a dark spot on the dorsum below the dorsal-fin base and below the usual location of the tilapia-mark (Trewavas, 1973; Thys van den Audenaerde, 1968), is a homologue of the tilapia-mark.

Scaly dorsal and anal fins

Many but not all cichlids have scales embedded in the membranes of the dorsal and anal fins (Table 3). There is considerable variation in the size of the scales, the extent of their coverage of the fins, the degree to which they stiffen the fins, and in whether or not they form a basal sheath into which the fins can be depressed. The detailed distribution of these various related characters is unknown. However, the common development of dorsal- and anal-fin scales in percomorphs and in apparently primitive cichlids suggests that unpaired-fin squamation is primitive within the Cichlidae. Greenwood (1980b: 13) judged dorsal- and anal-fin scales to be derived within haplochromines, and underestimated their occurrence in that assemblage (see also Chapter 4).

Scaly caudal fin

As will be discussed in Chapter 3, the presence of a dense covering of small scales over most of the caudal fin in the Lake Malawi haplochromines has been held to define them as a natural group; i.e., to be a synapomorphy of them. However, the taxonomic distribution of this character refutes that hypothesis. A fully scaled caudal fin is widespread in cichlids (Table 4). The caudal fin is also scaly in many other percoid families. More information is necessary, as usual, for a rigorous formulation, but it appears that a scaly caudal fin is primitive for at least the haplochromines, if not for cichlids as a whole.

Caudal skeleton

The cichlid caudal skeleton shows little variation from one taxon to another, even when the most plesiomorphic cichlids are compared with haplochromines (Fig. 10). Moreover, considerable intraspecific variation occurs in the loss or fusion of various elements (Fig. 11), which complicates analysis. Two epurals appear to typify all living cichlids, contrary to some claims in the literature (Monod, 1968; Van Couvering, 1972). It is worth noting that all cichlids I have examined have a 1,7-7,1 caudal fin-ray formula (one unbranched and seven branched principal rays in each lobe). This condition represents a reduction from the primitive 1,8-7,1 formula, and may prove useful in resolving the relationships to other percomorphs.

Summary of Phylogenetic Section

The Cichlidae appears to be well corroborated as a monophyletic group by evidence from the gill arches and their muscles, the adductor mandibulae muscle, and the microbranchiospines (Stiassny, 1981b, 1982), and by gastrointestinal morphology (Zihler, 1982). However, the sister-group relationships of the cichlids to other percomorphs remain unclear. Resolution of this problem will permit significant progress in studies of cichlid interrelationships. The most plesiomorphic cichlids should be the taxa used in the search for the cichlid sister-group: the Malagasy genera *Ptychochromis*, *Ptychochromoides*, *Paratilapia*, and *Paretroplus*, the Indian genus *Etroplus*, the neotropical genus *Cichla*, and the African genus *Heterochromis*. The Malagasy cichlids (a paraphyletic assemblage) include the most plesiomorphic cichlids, since they lack derived characters common to all other cichlids (Cichocki, 1976). (The phylogenetic status of the monotypic Malagasy genus *Oxylapia* remains unknown; neither Cichocki nor I was able to examine material.)

Cichocki (1976) suggested that all African cichlids comprise a monophyletic group, based on several synapomorphies. However, that hypothesis is falsified by new evidence, presented here, that the monotypic African genus *Heterochromis* lacks most of these synapomorphies. *Heterochromis* is, thus, identified as the most plesiomorphic (phylogenetically primitive) African cichlid. Previously it was thought to be related to *Tilapia*. The interrelationships of African and neotropical cichlids remain obscure. However, infraorbital morphology suggests the working hypothesis that *Heterochromis* is the sister-group of other African and of most neotropical cichlids.

Evidence from the infraorbitals also implies trans-Atlantic sister-group relationships between certain neotropical and African cichlid genera. Moreover, particular conformations of the infraorbitals provide autapomorphies useful in defining several genera and suprageneric groups of African cichlids.

TAXONOMIC REDESCRIPTION OF *HETEROCHROMIS MULTIDENS*

Materials and Methods

Institutional abbreviations

AMNH, American Museum of Natural History, New York

BMNH, British Museum (Natural History), London

MKO, personal material of M. K. Oliver

MRAC, Musée Royal de l'Afrique Centrale, Tervuren

YPM, Peabody Museum of Natural History, Yale University, New Haven

Material examined

The specimens of *Heterochromis multidens* listed below were examined and subjected to various treatments, as indicated by the following abbreviations: [A], uncleared specimen stained with alizarin red S; [C], only counts taken because of distortion of specimen; [CS], specimen cleared and stained with alizarin red S; [D], dissected alcohol specimen; [M], taxonomic measurements and counts taken; [R], radiographed.

AMNH 5966 (3, approx. 120 [A], 135 [D], 223 [M] mm SL; Zaire: Poko [63°09'N, 26°53'E]; Lang and Chapin, August 1913 [material not mentioned by Nichols and Griscom, 1917: 660, 729-730, who reported material only from Rungu]).

MRAC 7779-7780 (1 [C], approx. 43 mm SL; Zaire: Poko; C. Christy, date?).

MRAC 21057 (1 [C], approx. 144 mm SL; Zaire: Djamba, R. Itimbiri; H. Schouteden, not later than 1932).

MRAC 21092 (1 [M], 238.5 mm SL; Zaire: Djamba, R. Itimbiri; H. Schouteden, not later than 1932).

MRAC 60890-60892 (3 [M], 44.7, 50.8, approx. 58 mm SL; Zaire: Buta [2°48'N, 24°44'E]; Rév. Frère Hutsebout, 1939).

MRAC 60893 (1 [CS], approx. 106 mm SL; Zaire: Buta; Hutsebout, 1939).

MRAC 61914-61915 (2 [M], 45.0-52.7 mm SL; Zaire: Buta; Hutsebout, 1939).

MRAC 61922 (1 [M], 143.5 mm SL; Zaire: Buta; Hutsebout, 1939).

MRAC 68969 (1 [M], 113.5 mm SL; Zaire: région de Bomili, R. Nepoko; A. Henrion, 1946).

MRAC 124604 (1 [M], 264.0 mm SL; Zaire: R. Mongala (Ubangi); A. Hulot, 24 July 1948).

MRAC 167924-167928 (4 [M], 50.0, 52.8, 57.5, 57.6 mm SL; Zaire: Zambi, R. Ubangi, terr. de Libenge; R. Cremer and M. Neumann, 1947).

MRAC 167929 (1 [M], 51.5 mm SL; Zaire: R. Ngupaya, afflt. R. Wasa, cours inférieur, terr. de Libenge, Ubangi; R. Cremer and M. Neumann, 10 April 1948).

Methods of taking taxonomic counts and measurements are detailed in Chapter 5.

Heterochromis Regan, 1922

Heterochromis Regan, 1922: 252 (type species: *Paratilapia multidens* Pellegrin, 1900, by original designation).

Diagnosis.--Unique among cichlids in having lost neurocranial lateral-line foramen 6 (Fig. 12).

Possibly, this condition in *Heterochromis* represents not the loss of NLF_6, but its coalescence with NLF_5, which would be equally unique. This possibility might be evaluated by examining very small specimens.

In other cichlids foramen NLF_6 is present and is situated at the posterodorsal corner of the pterotic (in, e.g., *Cyrtocara milomo*, [Fig. 32]; *Cichla temensis*, *Etroplus maculatus*, *Hemichromis fasciatus*, and *Tylochromis polylepis*, pers. obs.; *Astatotilapia elegans*, Barel et al., 1976: fig. 11 and pl. I; *Rhamphochromis longiceps* and *Bathybates ferox*, Stiassny, 1981a: fig. 12; *Tilapia guineensis*, Vandewalle, 1972: figs. 1-4, 11, 12, 17, 18; *T. tholloni*, Goedel, 1974: figs. 3-6, 8, 9, 13; *Sarotherodon melanotheron*, Goedel, 1974: figs. 13, 22; *S. galilaeus*, Peters, 1973: fig. 2). In cichlids with this normal condition, NLF_5 (just anterior to NLF_6) opens ventrolaterally near the most dorsal lateralis foramen of the preoperculum, and NLF_6 opens dorsolaterally near the middle foramen of the lateral extrascapular. However, in *Heterochromis*, the enlarged NLF_5 serves both the preoperculum and the lateral extrascapular.

In addition to this unique autapomorphy, *Heterochromis* also exhibits other unusual features that are either of unknown distribution, autapomorphic but convergent, or symplesiomorphic in *Heterochromis* and a few other cichlids: (1) The cephalic lateral-line canals and foramina are strongly hypertrophied (Figs. 1, 4, 7a, 12, 13, 15), probably an autapomorphy developed convergently in other cichlids. (2) There are broad bands of unicuspid teeth in the jaws (an autapomorphy or a plesiomorphy?). (3) The upper and lower lateral-line segments are separated over most of their length by three, rather than two, rows of scales (Fig. 1). However, the distribution of this character has not been surveyed, and its level of universality is, therefore, unknown. (4) There are two predorsals, which is clearly primitive from out-group evidence and from the presence of the same number in the Malagasy-Indian cichlid genera judged plesiomorphic to Heterochromis on other characters. Two predorsals are commonly found also in neotropical cichlids and in fossil African cichlids (Van Couvering, 1982). However, two predorsals are retained only in Heterochromis and Tylochromis among living African cichlids, the others having reduced the number of predorsals to 1 or 0 (pers. obs.; Cichocki, 1976: 182 and table 1.1; Vandewalle, 1971: 259, 275, 285, 289; Gosse, 1975: 17-18, 145).

Heterochromis multidens (Pellegrin, 1900)

Paratilapia multidens Pellegrin, 1900: 98 (original description, "Congo"); Blanc, 1962: 217 (museum register number of holotype).

Pelmatochromis taeniatus (non Boulenger, 1901) Boulenger, 1902a: 53, pl. 16 (original description, "Monsembé, Haut-Congo" [approx. 1°20'N, 19°E, see Poll and Gosse, 1963: 90, map, and Trewavas, 1973: 5]).

Pelmatochromis polyodon Boulenger, 1902b: 237 (nomen novum for *Pelmatochromis taeniatus* Boulenger, 1902a, non *Pelmatochromis taeniatus* Boulenger, 1901).

Pelmatochromis multidens: Pellegrin, 1903: 79, 285, fig. 16 (cephalic lateral-line system, synonymy, description); Boulenger, 1905: 55 (listed, "Congo"); Boulenger, 1915: 407, fig. 277 (synonymy, description, "Upper Congo"); Holly, 1930: 269 (keyed, "Kamerun"); Pellegrin, 1930: 210 (listed, R. Sangha).

Paratilapia habereri Steindachner, 1912: 448 (original description, South Cameroon: Molundu); Steindachner, 1914: 55, fig. 11, pl. 9 fig. 2 ("n. sp." [sic], fuller description).

Paratilapia xenodon Nichols and Griscom, 1917: 660, 729, fig. 30 (original description, Rungu [on R. Bomokandi, tributary of R. Uele]).

Heterochromis multidens: Regan, 1922: 250, 252 (new genus; *Paratilapia xenodon* a synonym); David and Poll, 1937: 241, fig. 25 (listed, Zaire: Djamba and Koteli); Poll, 1957: 16, 133, figs. 279-281 (keyed, Congo basin); Poll, 1963: 99 (absent from Upper Lualaba [genus listed without species]); Matthes, 1964: 12, 133, 167, 169, 191 (ecology, juvenile coloration, native name; R. Tshuapa at Ikela); Poll and

Gosse, 1963: 86 (listed, Central Congo); Van Couvering, 1972: 10, 79, 83, 219-220 (genus listed, doubtfully classified with "tilapines sensu stricto"; summary of biology and external morphology, compiled); Vandewalle, 1973: 278 (listed, caudal skeleton); Hoedeman, 1974: 1006 (genus listed, classified in subfamily Tilapiinae, tribe Tilapiini, subtribe Pelmatochromi); Oliver, 1979 (morphology, relationships).

Diagnosis.--Same as that of genus.

Taxonomic redescription.--Based on 18 specimens, 43.0-264.0 mm SL. (Numbers in parentheses are of examined specimens having a given count.) Dorsal-fin spines and segmented rays XIII,14 (1), XIV,14 (1), XIV,15 (8), XIV,16 (6), XV,14 (1), XVI,13 (1); anal-fin spines and segmented rays III,9 (13), III,10 (5). Lateral-line scales 28 (2), 29 (13); upper part with 17 (2), 18 (1), 19 (4), 20 (7), 21 (1); lower part with 11 (3), 12 (5), 13 (4), 14 (3); for lateral-line scales on caudal fin see paragraph on fins (below). Scales on flanks ctenoid (Fig. 8); transverse scales from dorsal-fin origin to lateral line 5 (12), 6 (2); full-size scales between dorsal-fin base and posterior end of upper lateral-line segment 1 (5), 1-1/2 (3), 2 (1); scales between upper and lower lateral-line segments 3 (but last 1-3 scales of upper segment are one row lower than the rest in many specimens, leaving only 2 scales between the segments posteriorly); predorsal scales approx. 13 (1), 14 (2), 15 (2), 16 (4), 17 (2); prepelvic scales approx. 20-30 (9), modal range 22-26 (in 7 of 9); scales between pectoral- and pelvic-fin bases 7 (2), 8 (3), 9 (8), 10 (1); belly scales between pelvic-fin spine and anal-fin origin 17 (3), 20 (1); scale rows on cheek 4-8, positively correlated with SL (in large specimens, scales are of reduced size ventrally); scales around caudal peduncle 16 (14). Gill rakers on outer arch 0 (2), 1 (2), 2 (9), 3 (5) + 1 + 4 (8), 5 (10); all rakers small, short, and unbranched. Vertebrae 14 + 13 (1). Hypurals unfused (1).

Morphometrics. (Expressed as thousandths of standard length or head length. For each ratio, the range, mean ± standard deviation, and number of specimens are given. Regression analyses of principal ratios, which document their isometry or allometry, are given in Table 5). Reaching 264 mm SL. In SL: Head length 330-389 ($\bar{x}$ = 370.6 ± 16.0, n = 14); body depth 433-496 ($\bar{x}$ = 453.7 ± 22.2, n = 14); predorsal length 425-450 ($\bar{x}$ = 439.6 ± 8.0, n = 14); prepelvic length 424-511 ($\bar{x}$ = 451.6 ± 23.4, n = 14); belly length 256-332 ($\bar{x}$ = 287.1 ± 19.9, n = 14); dorsal-fin base length 538-617 ($\bar{x}$ = 573.0 ± 25.0, n = 14); total dorsal-fin length 670-720 ($\bar{x}$ = 705.2 ± 17.5, n = 9); last dorsal-fin spine 120-180 ($\bar{x}$ = 154.5 ± 17.7, n = 12); anal-fin base length 156-199 ($\bar{x}$ = 178.8 ± 11.3, n = 14); total anal-fin length 307-424 ($\bar{x}$ = 352.7 ± 32.7, n = 11); last anal-fin spine 148-173 ($\bar{x}$ = 162.5 ± 8.5, n = 14); caudal-peduncle length 119-157 ($\bar{x}$ = 134.6 ± 11.5, n = 14); caudal-peduncle length/depth 0.72-0.99 ($\bar{x}$ = 0.86 ± 0.08, n = 14); pectoral-fin length 235-328 ($\bar{x}$ = 306.9 ± 25.4, n = 14); pelvic-fin length 230-338 ($\bar{x}$ = 299.9 ± 35.2, n = 14); caudal-fin length 229-316 ($\bar{x}$ = 287.5 ± 36.4, n = 8).

In HL: Head width 480-567 ($\bar{x}$ = 512.1 ± 25.0, n = 14); snout length 342-537 ($\bar{x}$ = 406.4 ± 64.8, n = 14); snout width 348-464 ($\bar{x}$ = 384.5 ± 36.8, n = 11); orbit length 226-401 ($\bar{x}$ = 331.9 ± 63.6, n = 14); preorbital depth 198-338 ($\bar{x}$ = 250.4 ± 52.2, n = 14); interorbital width 277-473 ($\bar{x}$ = 339.8 ± 75.3, n = 14); postorbital head length 344-389 ($\bar{x}$ =

355.6 $\pm$ 11.8, n = 14); cheek depth 220-390 ($\bar{x}$ = 277.7 $\pm$ 61.4, n = 14); upper-jaw length 283-383 ($\bar{x}$ = 318.7 $\pm$ 29.0, n = 14); premaxillary ascending processes 387-442 ($\bar{x}$ = 416.8 $\pm$ 19.4, n = 14); lower-jaw length 393-484 ($\bar{x}$ = 427.4 $\pm$ 25.3, n = 14); lower-jaw length/width 1.14-1.50 ($\bar{x}$ = 1.36 $\pm$ 0.11, n = 12); pharyngeal-bone length 154-207 ($\bar{x}$ = 172.7 $\pm$ 20.0, n = 7); pharyngeal-bone width 303-342 ($\bar{x}$ = 321.9 $\pm$ 18.3, n = 7).

Body moderately deep and compressed. Dorsal profile more pronounced than ventral. Ventral profile unevenly curved from chin to anus. Dorsal head profile smoothly rounded in small fishes, with a slight to prominent nuchal hump in specimens >140 mm SL. Profile not interrupted by premaxillary ascending processes. Orbit, in small fishes, close to frontal profile in lateral view, but separated from profile by 0.7-1.2 eye diameters in fishes >140 mm SL. Eye virtually round. Snout angle 40°-70° to horizontal (positively correlated with SL, $r = 0.780$, $p<0.001$, n = 14; snout angle = $[0.076 \pm 0.018]\mathrm{SL} + [41.049 \pm 2.281]$). Frontal angle (above orbit; if hump present, along anterior edge of hump) 30°-80° (positively correlated with SL, $r = 0.839$, $p<0.001$, n = 14; frontal angle = $[0.177 \pm 0.033]\mathrm{SL} + [31.722 \pm 4.279]$). Nuchal angle 10°-35° (not correlated with SL). Jaws rounded anteriorly in dorsal view. Dental arcade of lower jaw with distinctive shape, even in small fishes ($\geq$ 45 mm SL): in dorsal view, outline of arcade is basically a broad, convex arch, but with a slight concavity anterolaterally on each dentary and with an additional small concavity at symphysis. Gape horizontal or very slightly oblique; ventral profile of lower jaw inclined at 25°-45° to horizontal (not correlated with SL). Jaws equal, or lower projecting slightly. Chin rounded, receding, not protuberant. In lateral view, symphysis of lower jaw appears to be rotated outward and downward, so that anterior dentary teeth are visible when mouth of fish is closed. Premaxillae slightly beaklike. Posterior tip of maxilla not reaching vertical through anterior edge of orbit. Lips thickened, particularly in large fishes, but not lobate. Upper lip fold continuous across premaxillary symphysis; lower lip fold interrupted at dentary symphysis except in largest specimen, in which fold continues across symphysis. Cephalic lateral-line pores and canals strongly hypertrophied.

Caudal fin rounded, densely covered with small ctenoid scales (Fig. 8d) nearly to ends of rays. Lateral line tripartite on caudal; middle segment continues lateral line of body, upper and lower segments begin 1-2 scales posterior to hypural fold; upper, middle, and lower segments with 0-4 ($\bar{x} = 1.0$), 1-6 ($\bar{x} = 2.4$), and 2-14 ($\bar{x} = 6.2$) pored scales respectively ($n = 12$). Dorsal and anal fins densely covered with small ctenoid scales (Fig. 8c); scales extend for virtually entire length of each fin, and are arranged in 1-2 rows between and parallel to each two successive rays. On dorsal fin, vertical extent of scale coverage is greatest at or behind transition from spinous to soft portion of fin, and scales markedly stiffen fin, holding it semi-erect. In fishes approx. 45 mm SL, scales are restricted to basal portion of dorsal (Fig. 9) and anal, the interradial rows (counted parallel to fin rays) at most 4 or 5 scales long. In 264-mm SL fish, scales extend nearly to distal edge of dorsal and anal fins and comprise ≤ 36 scales per row on dorsal. In some specimens, scales along base of anal fin appear to form a sheath 1 scale high, into which fin spines can be partly depressed. Pectorals ovate to falciform. Pelvics with first segmented ray longest in small specimens, second ray longest in fishes >140 mm SL.

Teeth in outer row of each jaw slender to moderately robust, slightly movable; those of premaxilla (Fig. 7b) rather widely spaced, especially posteriorly. All teeth unicuspid, even in smallest fish (43 mm SL); crowns slightly incurved, acutely pointed (infrequently, crown is separated from shaft of tooth by a distinct neck). Number of teeth in outer row of upper jaw (total of both sides) 20-38 ($\bar{x} = 27.1 \pm 1.62$ SE, $n = 14$; positively correlated with SL, $r = 0.939$, $p<0.001$; number of teeth = $[0.070 \pm 0.007]$SL + $[19.405 \pm 0.998]$; intercept >0, $p<0.001$).

Inner teeth of each jaw smaller than those of outer row, unicuspid even in smallest fish (43 mm SL); arranged anteriorly in approx. 3-9 irregular, closely spaced rows in upper jaw (Fig. 7b), 4-10 in lower; number of rows in each jaw positively correlated with SL. No distinct gap separates inner rows from outer row of teeth.

Lower pharyngeal bone (Fig. 14) broadly V-shaped, posterior edge indented, horns rather long. Bone wide (1.66-2.05, $\bar{x} = 1.88 \pm 0.04$ times wider than long, $n = 7$), rather lightly built. Joint uniting halves of bone slightly to moderately sinuous in ventral view. Anterior blade short, slightly decurved relative to plane of dentigerous surface. Dentigerous area 1.67-2.05 ($\bar{x} = 1.92 \pm 0.05$, $n = 7$) times wider than long. Pharyngeal teeth uncrowded, rather robust, coarser medially and posteriorly, all cuspidate; undamaged teeth essentially unicuspid, cusp hemispherical to subconic, slightly compressed or not, erect or slightly hooked; 18-23 ($\bar{x} = 20.7 \pm 0.5$, $n = 9$) teeth in posterior row, 5-7 in median column, 4-5 in oblique posteromedian to midlateral row, 12-17 along lateral edge (all in fishes 44.7-238.5 mm SL).

Gut short, equal to and growing isometrically with standard length (gut 53 mm long in a fish of 52.8 mm SL, 225 mm in a 223-mm fish); arranged in coiling pattern C and lacking a flap-back-loop (Zihler, 1982).

Some of the cranial muscles and ligaments of *H. multidens* are illustrated in Fig. 13.

Additional notes on osteology.--As noted in the first section of this chapter, *H. multidens* is the only African cichlid known to have the primitive 7-bone infraorbital series (Fig. 5b). There is considerable ontogenetic change in the relative depth of the lacrimal (or its anterior part, as the case may be) and, consequently, in the degree to which the posterior edge of this bone overlaps the second and third ossicles (Fig. 15).

The basicranial apophysis for the upper pharyngeal bones (Fig. 16) is rather distinctive, and I find it difficult to reconcile with any of the apophysis types described by Greenwood (1978).

The hyoid bar and urohyal are unremarkable (Fig. 17).

The pelvic basipterygium is not distinctive (Fig. 18). The pectoral girdle (Fig. 19) has one unusual feature. The distal postcleithrum bears a short, but distinct, dorsally directed process or spine on its anterodorsal edge. Elsewhere among cichlids, a similar process is known only in the neotropical genera *Cichla* and *Crenicichla* (Cichocki, 1976; Stiassny, 1982). The process is longer in the neotropical taxa. The homology of this feature across these taxa is by no means clear, but is worth considering.

Coloration.--Unknown for live adults. Live juveniles colored as follows:

> Juveniles light brown with bronze highlights, silvery with blue-green highlights ventrally, 5 to 6 dark transverse bars on body and a longitudinal stripe from rear edge of eye to caudal base; a large black spot above pectorals where longitudinal stripe crosses second transverse bar. A dark band across occiput, crossing eye, extending obliquely in front of cheeks [against posterior edge of second infraorbital] and passing behind corner of mouth. Dark bars indistinct in life. Dorsal and anal fins reddish and yellow, base of soft dorsal with a large black spot (as in *Tilapia*), followed by several rows of black dots in oblique bands [see Fig. 9]; soft anal faintly speckled with black. Caudal and paired fins yellowish, pelvics more or less blackened in larger specimens (translated from Matthes, 1964: 133).

Preserved, juveniles often have 11-15 narrow, longitudinal dark stripes on flanks, each stripe extending along boundary of two adjacent scale rows; these stripes also evident on 223-mm specimen. "Tilapia-mark" obvious in juveniles, distinguishable even in preserved 238.5-mm SL fish.

Distribution.--Northern part of the *cuvette centrale* of the Zaire system, from extreme SE Cameroon eastward to NE Zaire (Fig. 20). The *cuvette centrale* is "the large shallow depression in the center of Africa" (Roberts, 1975: 271; see also Lambert, 1961). *Heterochromis* is endemic to the Zaire ichthyofaunal province of Roberts (1975), although he omitted it from his list of endemic riverine genera (Roberts, 1975: table 4).

Ecology.--Rather common, frequenting weedy shores; inhabits both large streams and backwaters. Juveniles omnivorous; stomach contents include sand and mud, plant debris, as well as chironomid, ceratopogonid, tipulid, trichopteran, and odonate larvae (Matthes, 1964: 12, 134, 166-167, 169, 191). Diet of adults unknown.

Etymology.--Generic name from Greek _heteros_, other or different, and _chromis_, a common stem for generic names of African cichlids. Specific name from Latin prefix _multi-_, many, and _dens_, tooth, referring to wide bands of jaw teeth. Matthes (1964: 12) gives native name near Ikela (Zaire) as _likoke_, which is also applied to some other cichlids.

Figure 1. *Heterochromis multidens*. (Holotype of *Pelmatochromis taeniatus*, from Boulenger, 1902a, pl. 16.)

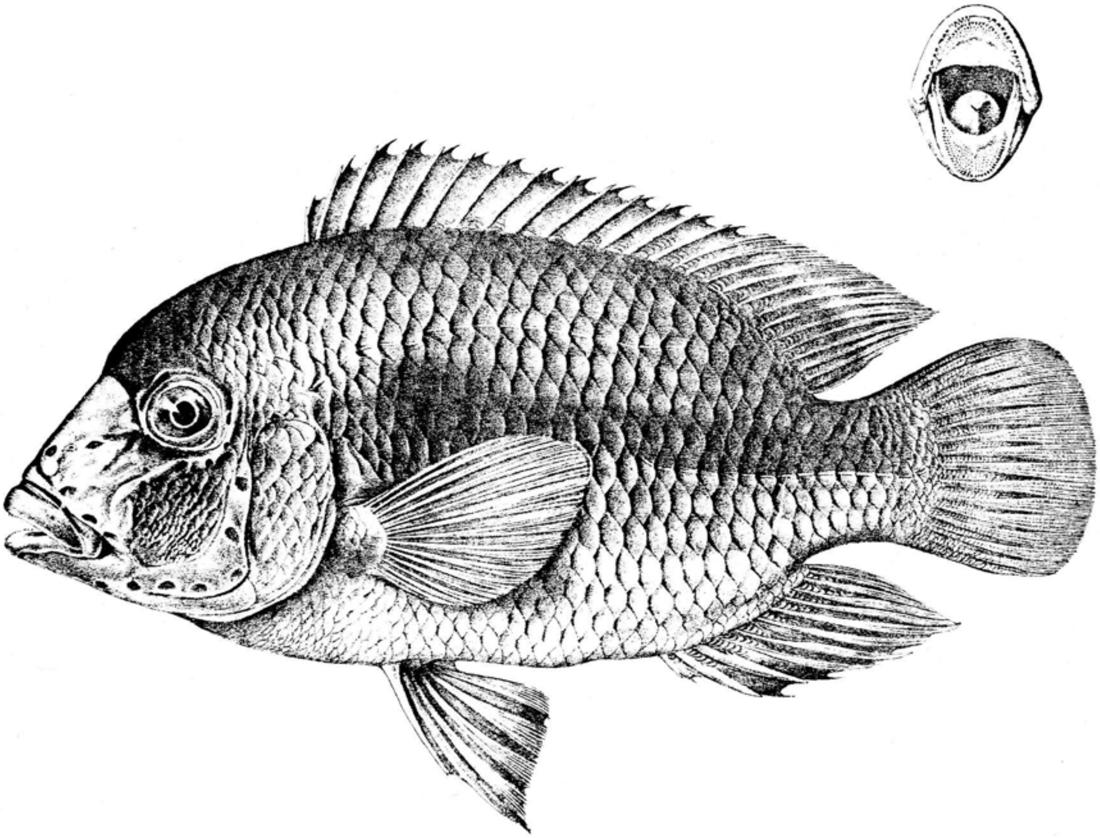


Figure 2. Cladogram summarizing information on character distribution among higher-level groups of cichlids. Numbered bars correspond to synapomorphies discussed in text. Abbreviations: (A), Africa; (I), India and Sri Lanka; (M), Malagasy; (N), Neotropical.

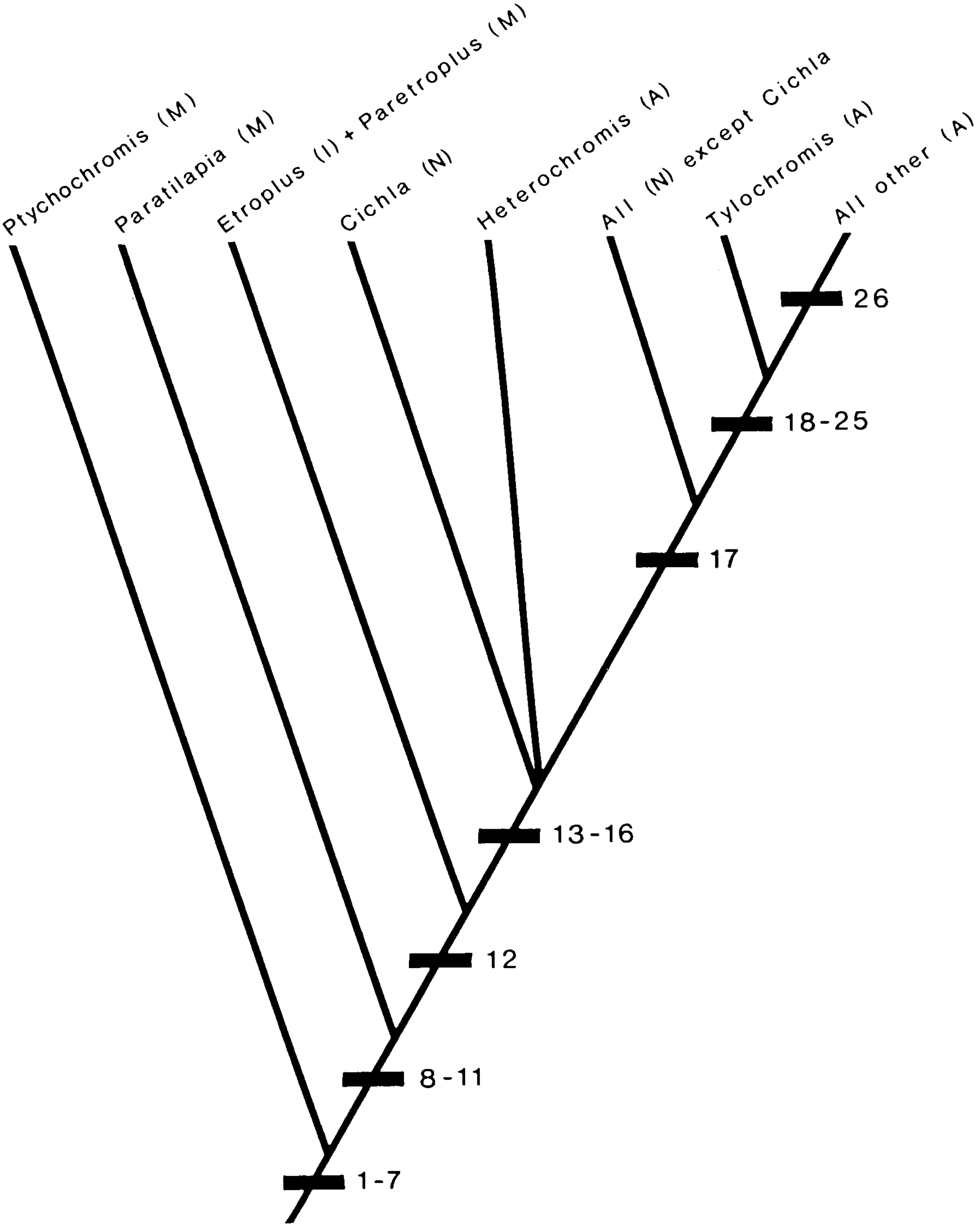
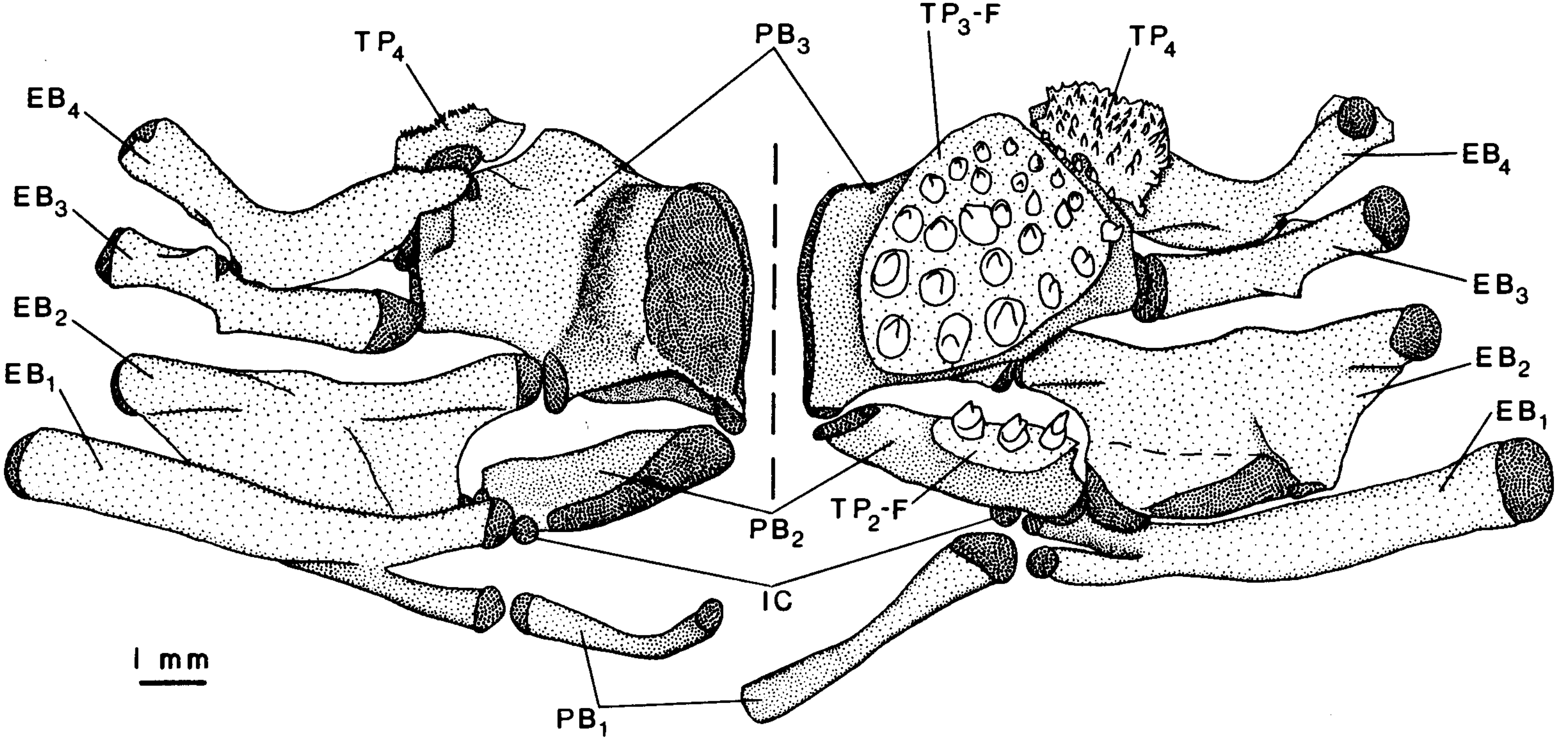

Ptychochromis (M)
Paratilapia (M)
Etroplus (I) + Paretroplus (M)
Cichla (N)
Heterochromis (A)
All (N) except Cichla
Tylochromis (A)
All other (A)
26
18-25
17
13-16
12
8-11
1-7

Figure 3a (opposite). a, dorsal gill-arch elements of right side in Heterochromis multidens (AMNH 5966). At left, dorsal view; at right, ventral view. b, right first epibranchial in dorsal view (parallel to plane of forked (medial) end. Abbreviations: EB_{1-4}, epibranchials; IC, interarcual cartilage; PB_{1-3}, pharyngobranchials; TP_{2-3}-F, tooth plates fused with the associated pharyngobranchials; TP_4, fourth tooth plate (unfused). Cartilage shown with heavy stipple pattern.

Figure 3b (overleaf). Right first epibranchial of Heterochromis multidens (AMNH 5966) in dorsal view (parallel to plane of forked end).


TP$_4$
PB$_3$
TP$_3$-F
TP$_4$
EB$_4$
EB$_4$
EB$_3$
EB$_3$
EB$_2$
EB$_2$
EB$_1$
EB$_1$
TP$_2$-F
PB$_2$
IC
1 mm
PB$_1$

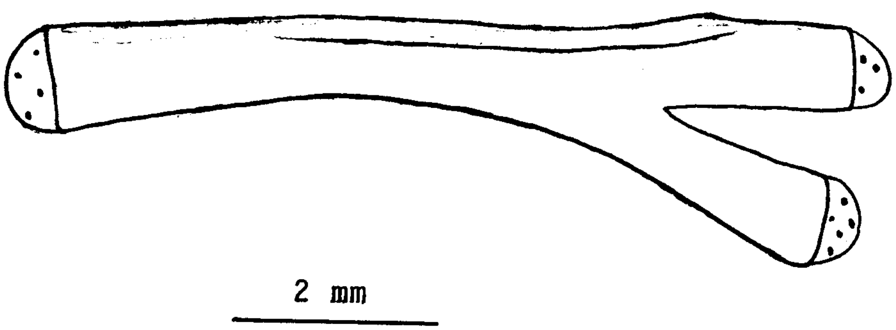

2 mm

Figure 4. Dorsal view of interorbital region of head of Heterochromis multidens (AMNH 5966) after removal of skin and nasals. Anterior is at top. Abbreviations: ASC, ascending process of premaxilla; B, blind cavity on both sides of head, not connected with lateral-line system; F, frontal; LE, lateral ethmoid; LPP, palatopalatine ligament; ME, epaxial muscles; NLF_{0-3}, lateral-line foramina.

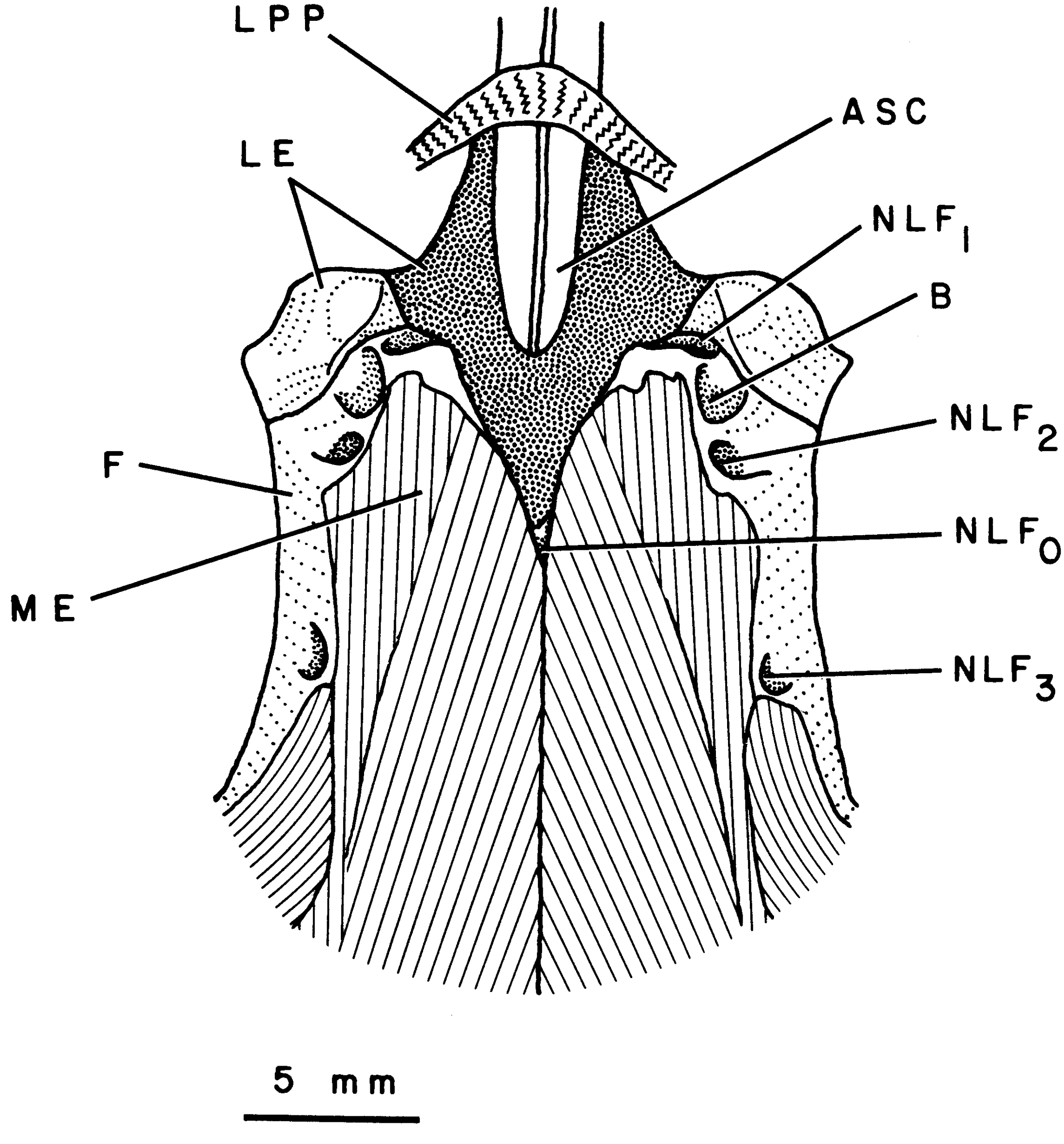
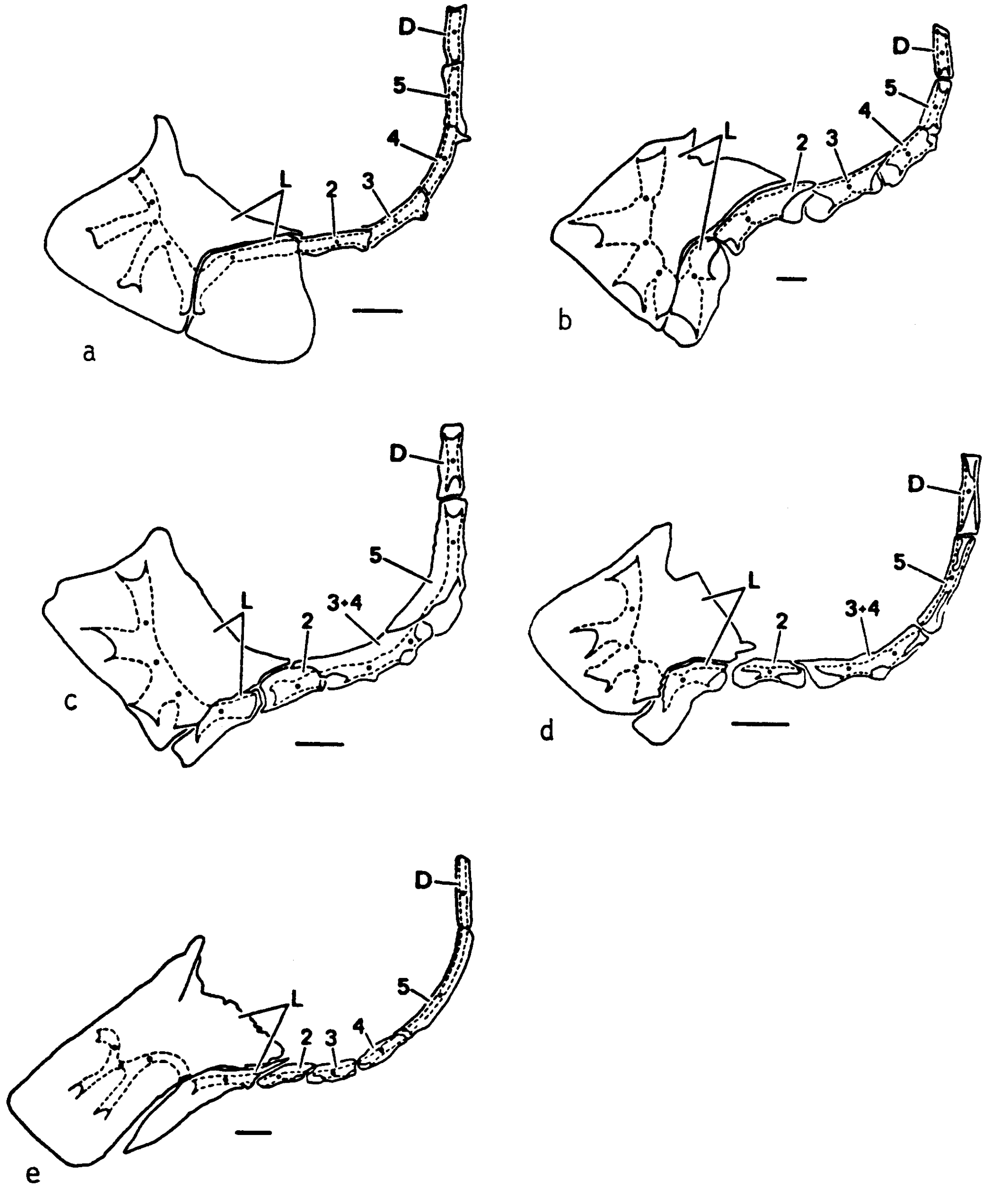

LPP
ASC
LE
NLF$_1$
B
NLF$_2$
F
NLF$_0$
ME
NLF$_3$
5 mm

Figure 5. Infraorbital bones of some cichlids in left lateral view. In most cases the right side was drawn and reversed. Semidiagrammatic; neuromasts shown by black circles. Scale bars = 2 mm. a-e, primitive cichlids: a, *Cichla ocellaris* (AMNH uncat., neotropical); b, *Heterochromis multidens* (AMNH 5966, Africa; redrawn from Fig. 15 for comparison with other taxa); c, *Paratilapia polleni* (AMNH 11709, Malagasy); d, *Ptychochromis oligacanthus* (AMNH 18841, Malagasy); e, *Paretroplus petiti* (AMNH 11707, Malagasy). In a-e, the anterior two bones are both identified with the lacrimal; see text for an alternative interpretation. f-k, neotropical cichlids: f, *Crenicichla lepidota* (AMNH 3756); g, *Geophagus surinamensis* (AMNH 13440); h, *Cichlasoma severum* (AMNH 18633); i, *Petenia splendida* (AMNH 25765); j, *Aequidens tetramerus* (AMNH 9632); k, *Chaetobranchus flavescens* (AMNH 12743). l-p, Lake Malawi cichlids: l, *Aristochromis christyi* (M. K. Oliver [MKO] uncat.); m, *Pseudotropheus zebra* (MKO uncat.); n, "*Trematocranus*" *jacobfreibergi* (AMNH 32436); o and p, *Diplotaxodon argenteus* (MKO uncat). q-z, lamprologine cichlids: q, *Lamprologus mocquardii* (AMNH 6106, Zaire region, riverine); r, *Teleogramma monogramma* (AMNH 12384, Zaire region, riverine); s, *Lamprologus modestus* (AMNH 11746, Lake Tanganyika); t, *L. callipterus* (AMNH 11745, Lake Tanganyika); u, *L. tretocephalus* (MKO uncat., Lake Tanganyika); v, *L. brichardi* (MKO uncat., Lake Tanganyika); w, *L. compressiceps* (MKO uncat., Lake Tanganyika); x, *L. elongatus* (MKO uncat., Lake Tanganyika); y, *Julidochromis marlieri* (MKO uncat., Lake Tanganyika); z, *Telmatochromis bifrenatus* (MKO uncat., Lake Tanganyika). aa-hh, Lake Tanganyika nonlamprologine cichlids: aa, *Cyphotilapia frontosa* (BMNH 1960.9.30: 1161-1162); bb, *Boulengerochromis microlepis* (AMNH 11727); cc, *Simochromis diagramma* (MKO uncat.; cf. hh); dd, *Tropheus moorei* (MKO uncat.); ee, *Spathodus marlieri* (MKO uncat.); ff, *Xenotilapia melanogenys* (AMNH 11726); gg, *Callochromis pleurospilus* (AMNH 11723); hh, *Simochromis dardennii* (AMNH 11724; identical in uncat. MKO specimen; cf. cc). ii-qq, African riverine cichlids: ii, *Oreochromis shiranus* (AMNH 31872); jj, *Tylochromis lateralis* (AMNH 19705; a second specimen is identical, a third has 4+5 fused and anterior canal on lacrimal directed downward); kk, *Serranochromis* (*Serranochromis*) *macrocephalus* (AMNH 14047, identical in 2 specimens); ll, *Orthochromis polyacanthus* (AMNH 5904; 4+5 fused in a second fish, separate in third fish); mm, *Hemichromis fasciatus* s. l. (AMNH 32769; 3+4 fused in a second fish); nn, *Pseudocrenilabrus multicolor* (AMNH 4352); oo, *Pelvicachromis humilis* (AMNH 12317; 2 other specimens identical); pp, *Thysia ansorgii* (MKO uncat.); qq, *Nanochromis* sp. (AMNH 6079). Abbreviations: D, dermosphenotic = last infraorbital; L, lacrimal = infraorbital 1.



D
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L
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3
a
D
L
2
3
4
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b
D
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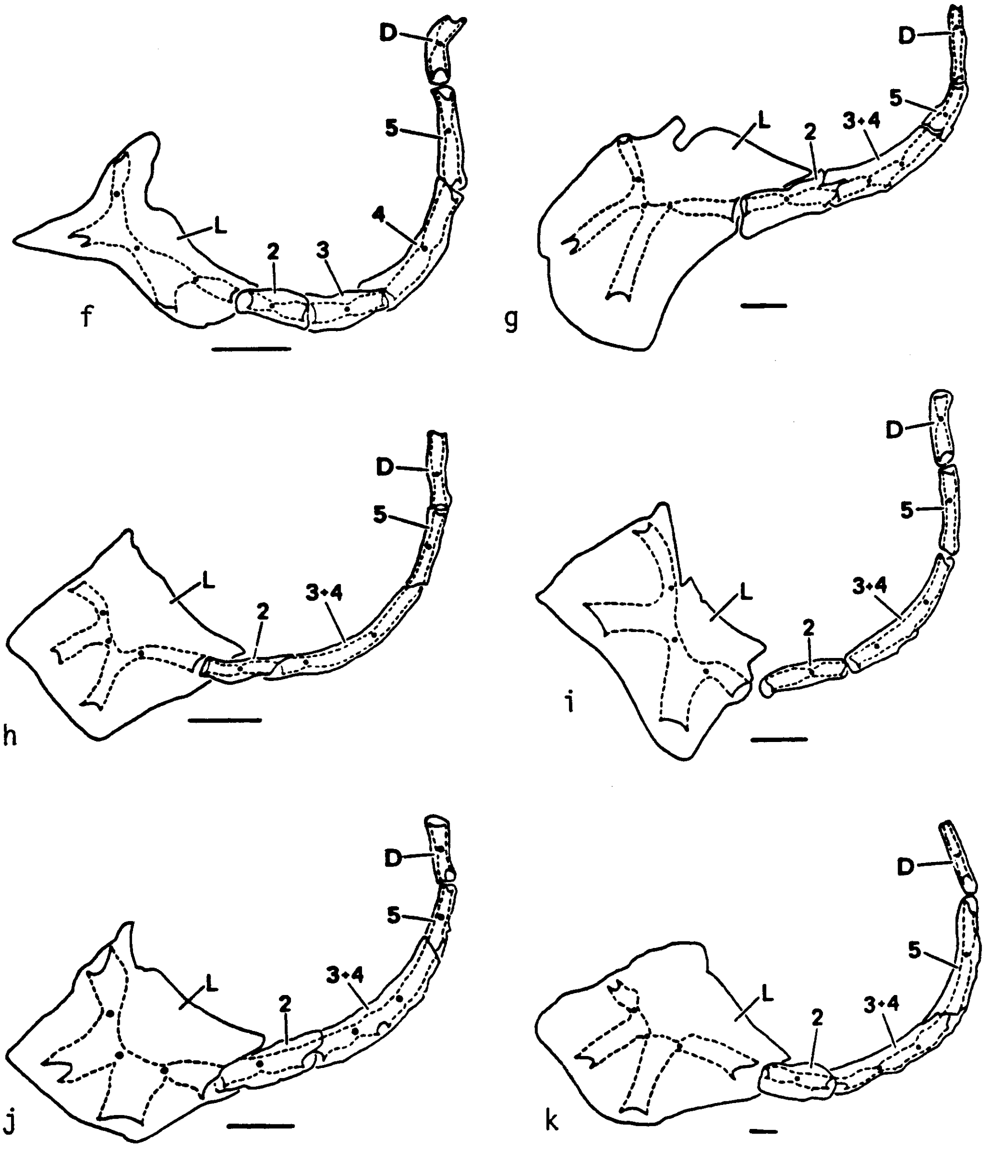
4
e



D
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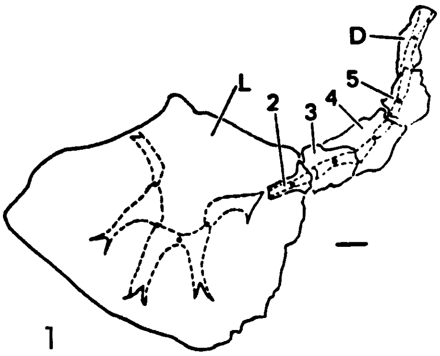

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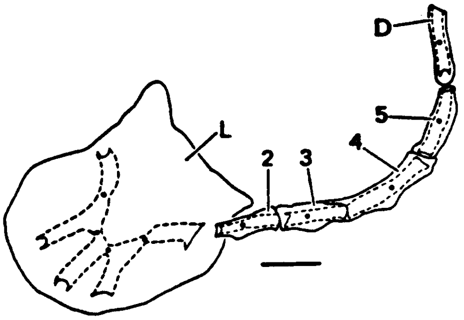

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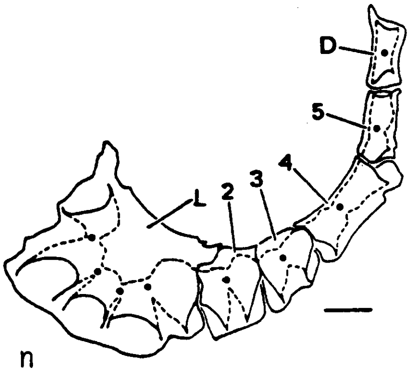

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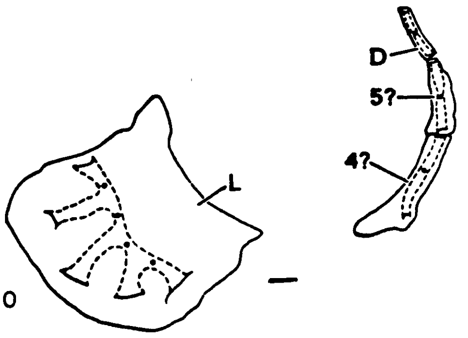

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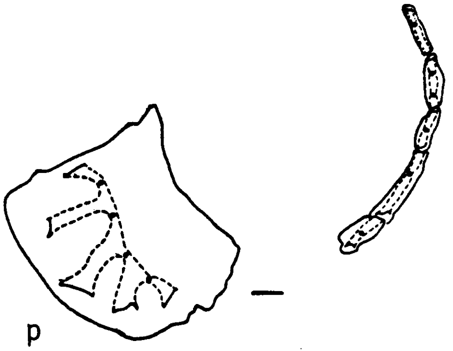

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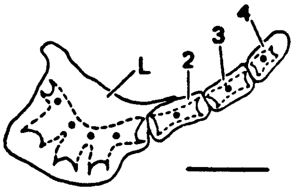

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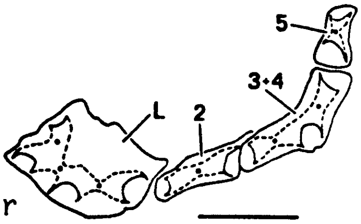

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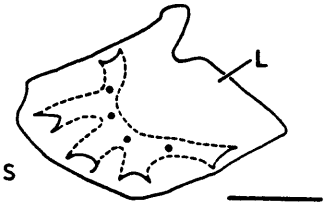

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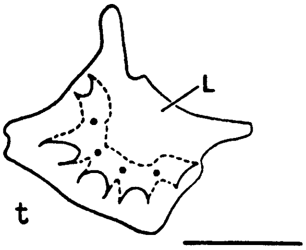

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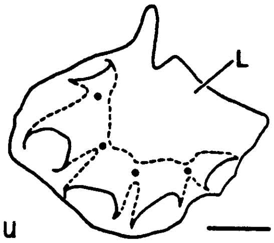

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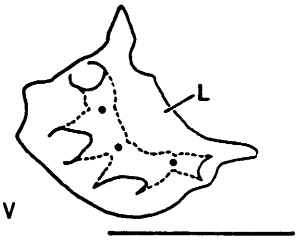

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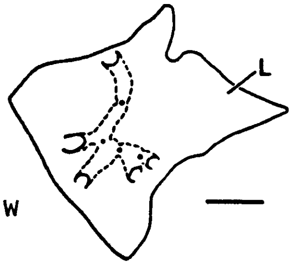

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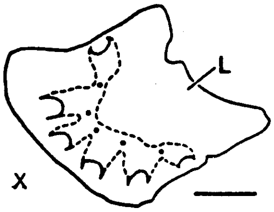

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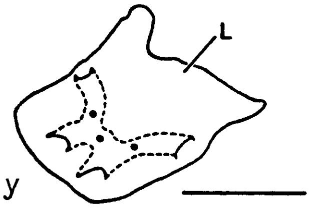

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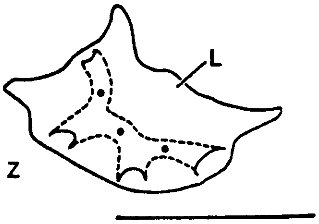

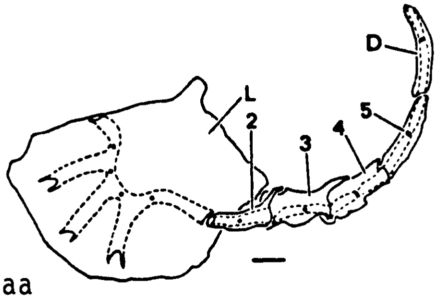

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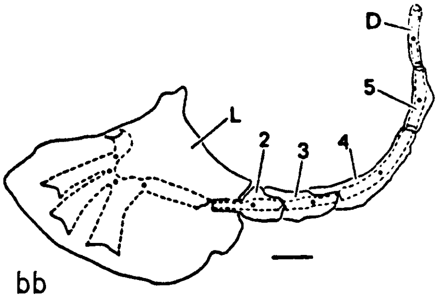

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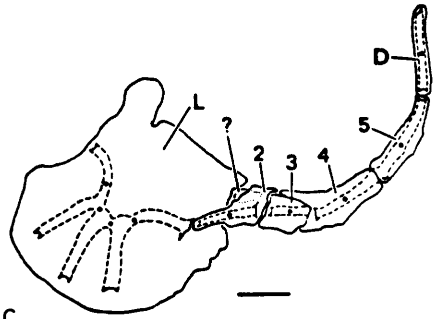

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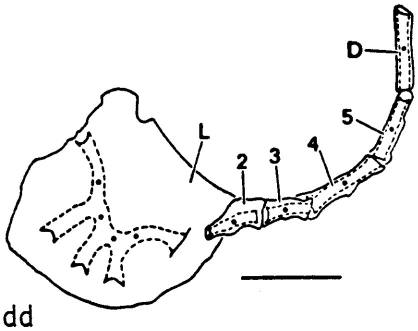

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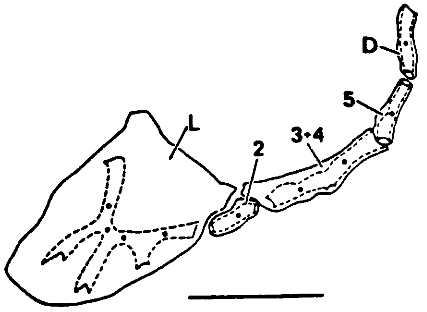

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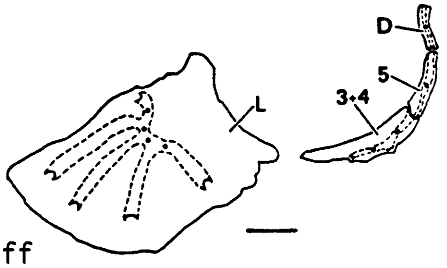

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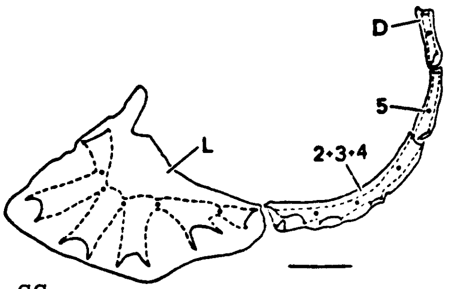

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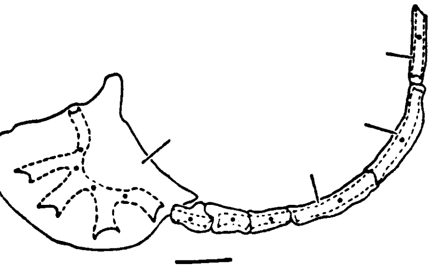

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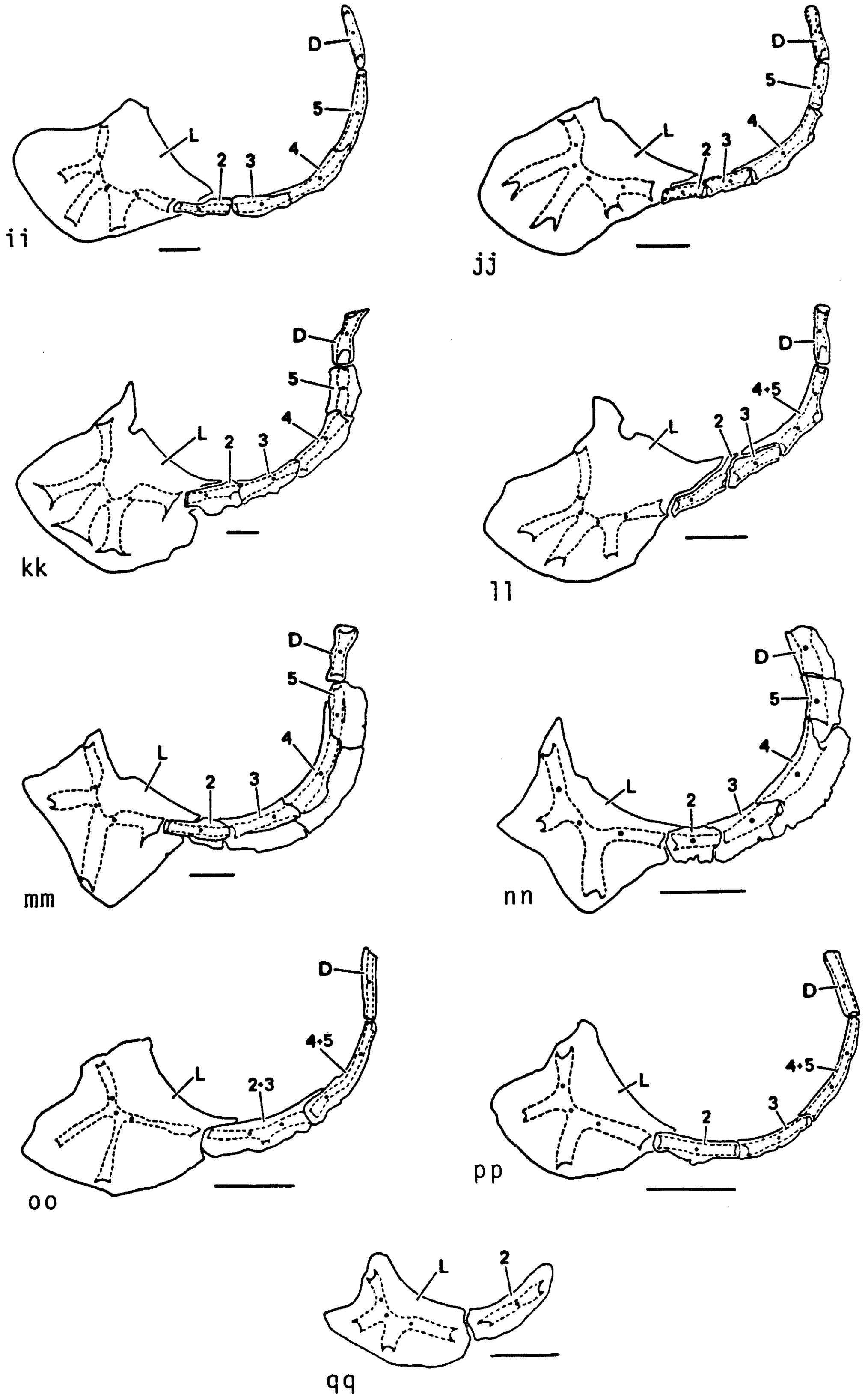
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pp
L
2
qq

Figure 6. Left palatine-ectopterygoid region of *Heterochromis multidens* (AMNH 5966) in lateral view. Abbreviations: ect, ectopterygoid; lapm, anterior palatomaxillary ligament; lat., lateral; lpp, palatopalatine ligament; max. proc., maxillary process of palatine.

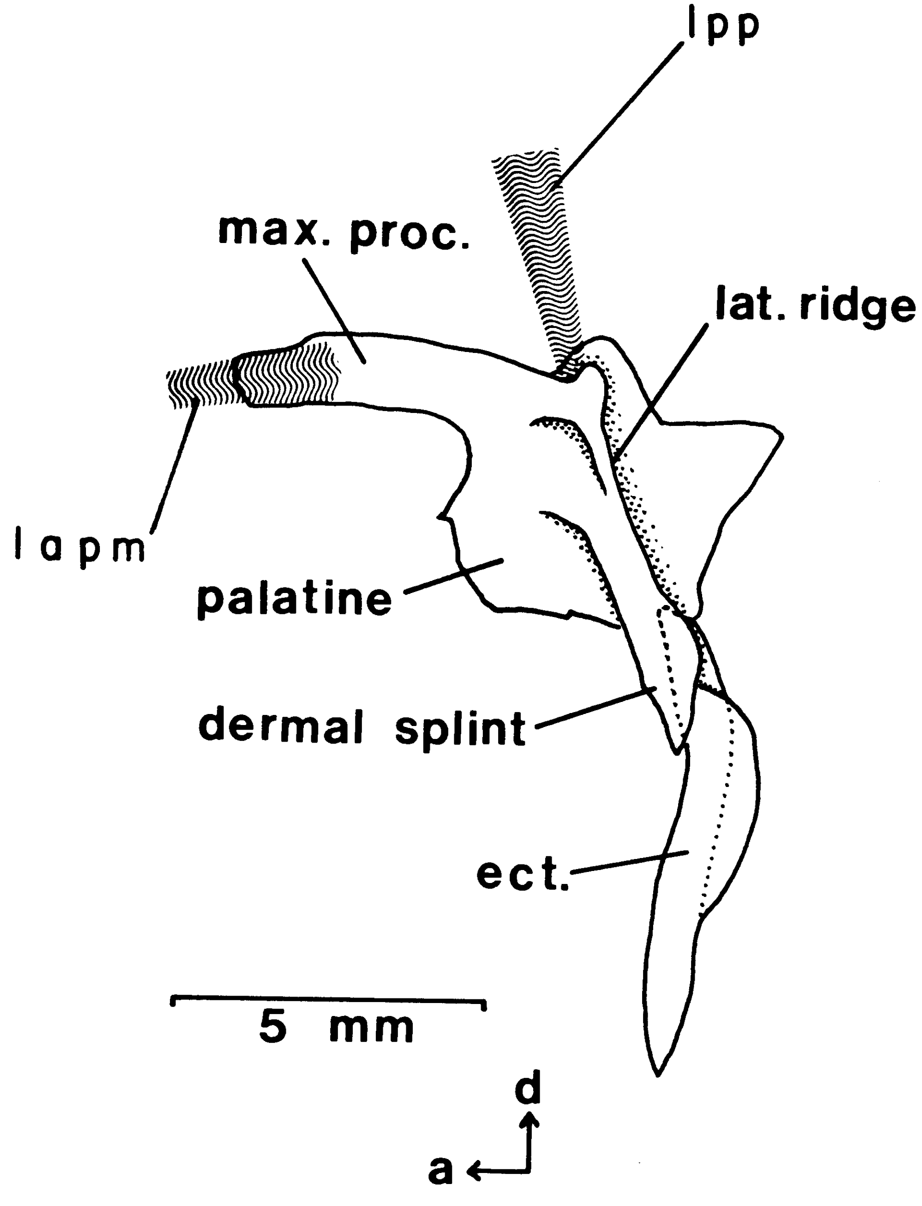
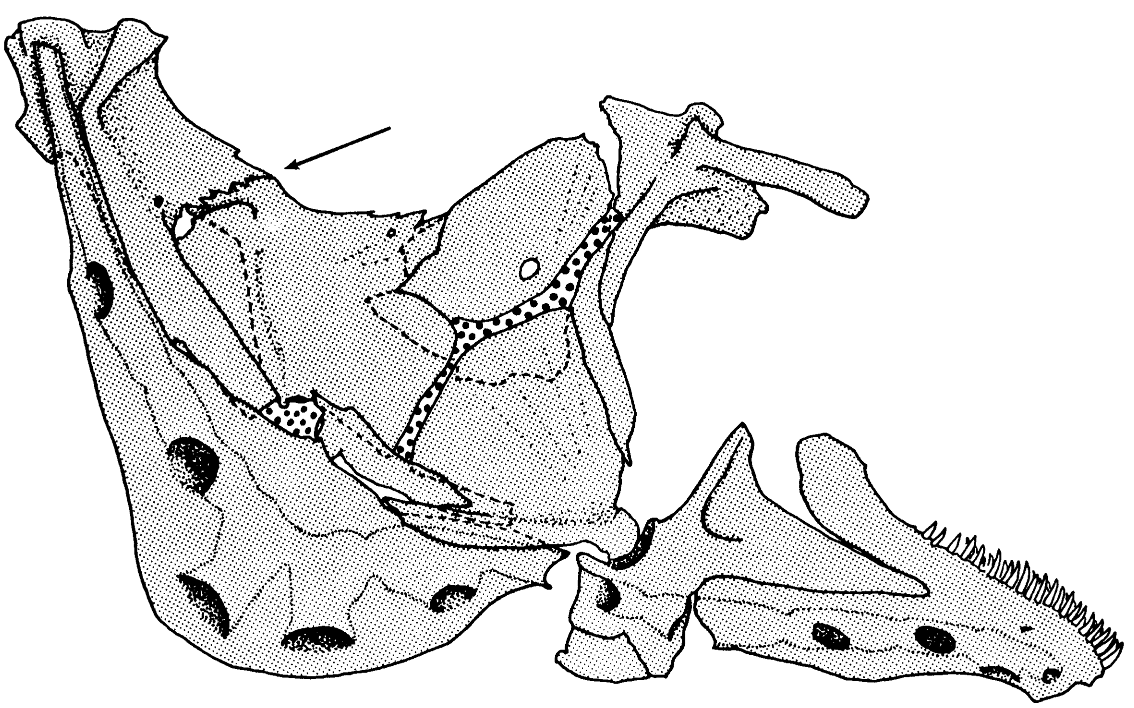
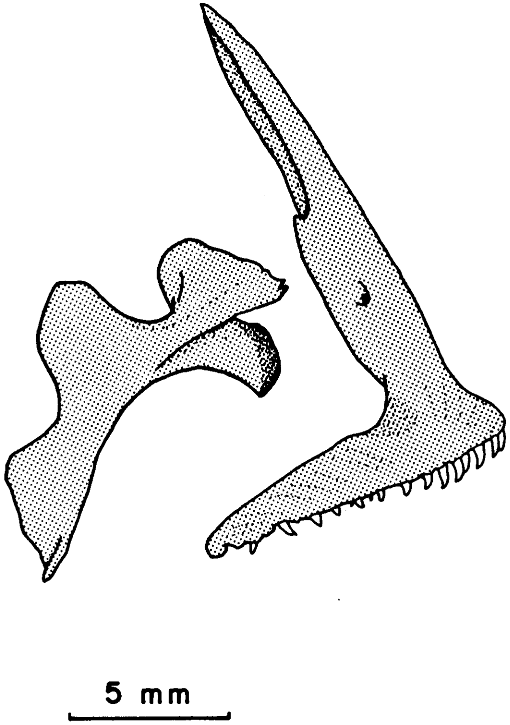

lpp
max. proc.
lat. ridge
lapm
palatine
dermal splint
ect.
5 mm
d
a

Figure 7a (opposite). Right suspensorium and jaws of *Heterochromis multidens* (MRAC 60893) in lateral view. Arrow points to sutured joint between hyomandibular and metapterygoid.

Figure 7b (overleaf). Part of right premaxilla of *Heterochromis multidens* (MRAC 60893) in lingual view, showing dentition.

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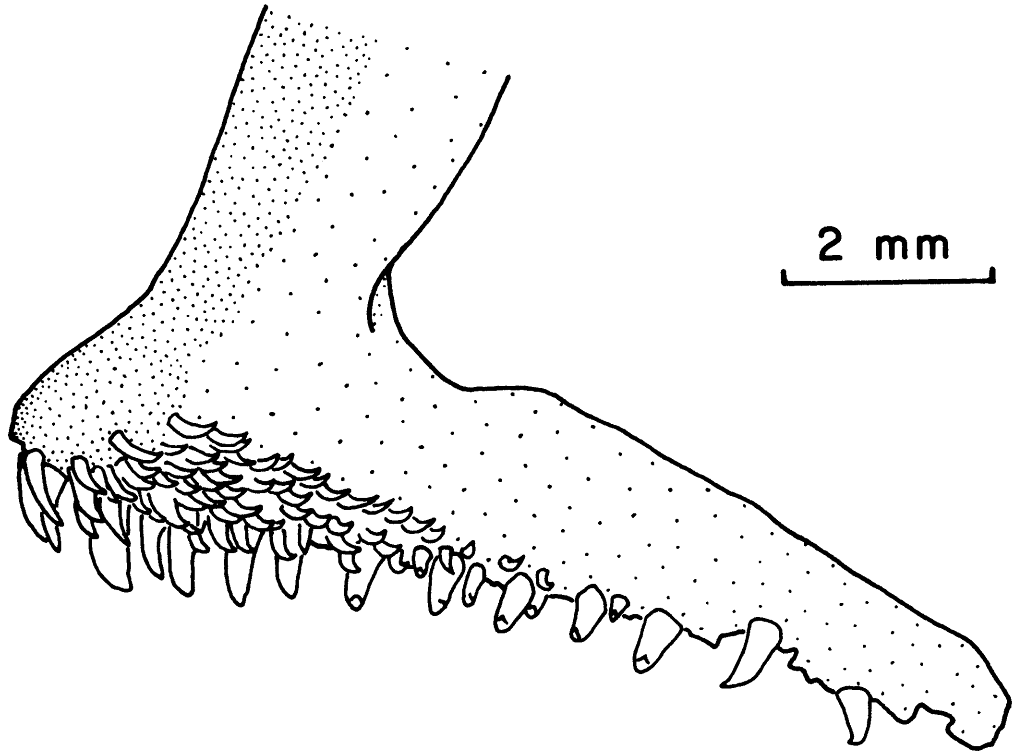

2 mm

Figure 8. Scales from left side of <u>Heterochromis</u> <u>multidens</u> (MRAC 21057, approx. 144 mm SL). a, typical ctenoid scale from between anal fin and lateral line. Dashed line indicates anterior limit of teeth, which cover posterior field of scale. At upper right, details of teeth and circuli are shown (drawn to same size as rest of scale). b, cycloid scale of "roman" type (Trewavas, 1973: 14, fig. 10) from below base of pectoral fin; all circuli are shown in posterior field but circuli ramify anteriorly and are much more numerous in anterior field than is shown. c, ctenoid scale from membrane of dorsal fin, distal to "tilapia-mark," showing all circuli and teeth. d, ctenoid scale from near distal edge of caudal fin, showing all circuli and teeth.

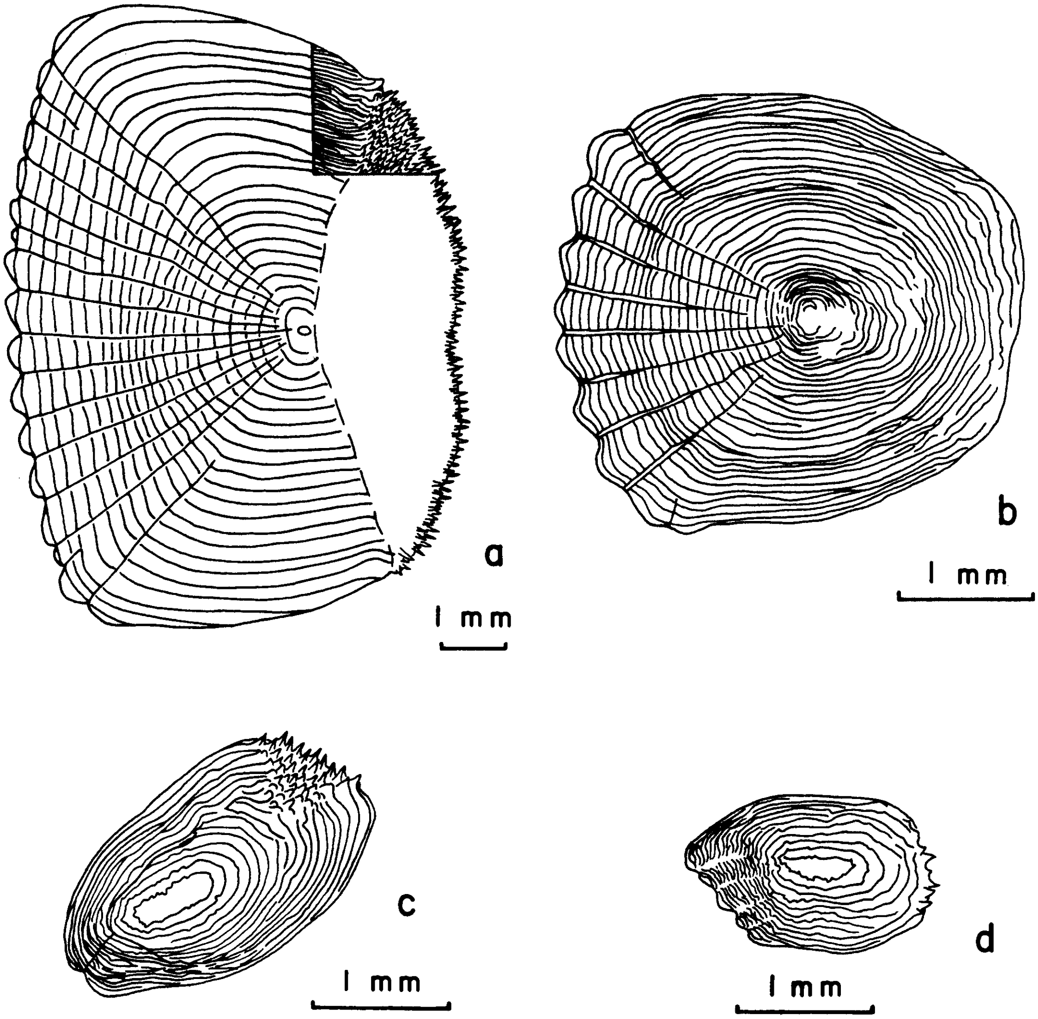

a
1 mm
b
1 mm
c
1 mm
d
1 mm

Figure 9. Posterior part of dorsal fin of young *Heterochromis multidens* (MRAC 60890-60893) in left lateral view, showing "tilapia mark," scaly basal sheath, and posterior end of upper lateral-line segment. Dashed line indicates level of fin-ray bases, as revealed by transmitted light.

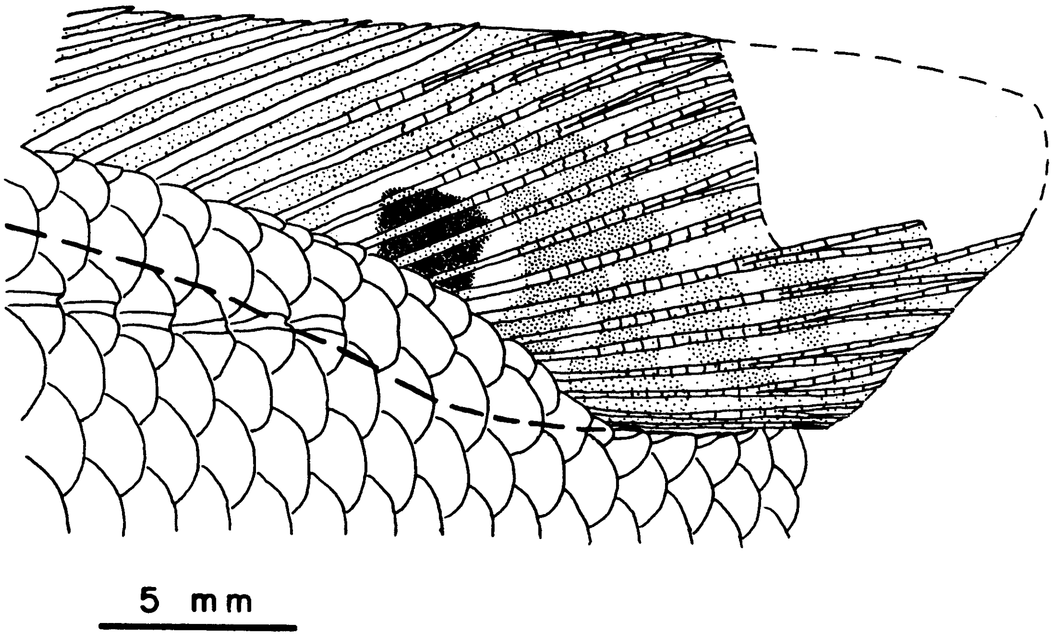

5 mm

Figure 10. Caudal skeletons of some cichlids. a, *Paratilapia polleni* (AMNH 11687, drawn from radiograph; note presence of only 2 epurals, as in all 11 individuals I have examined). b, *Etroplus maculatus* (YPM 6593; abnormal, interpretations of some elements uncertain. Note (1) apparent loss of PU_3, (2) autogenous NPU_3? with left side of this arch extending over next anterior centrum (right side of neural arch dotted), and (3) possible residual second preural neural arch represented by a separate, unfused element on each side of NPU_3?). c, *Heterochromis multidens* (AMNH 5966). d, *Cichla temensis* (USNM uncat., Peru: Rio Negro, coll. March 1963; similar to the 2 other specimens examined). e, *Tylochromis polylepis* (YPM 1946). f, *Cyrtocara moorii* (M. K. Oliver, uncatalogued aquarium material, 35 mm SL; similar to 2 other specimens examined). Abbreviations: EP, epurals; H_{1-5}, hypurals; HPU_{2-4}, hemal spines of preural centra; NPU_{2-3}, neural spines of preural centra; PH, parhypural; PU_{1-5}, preural centra; RNA, residual neural arch; U_1, ural centrum; UN, uroneural. Cartilage heavily stippled, shown only in e and f.

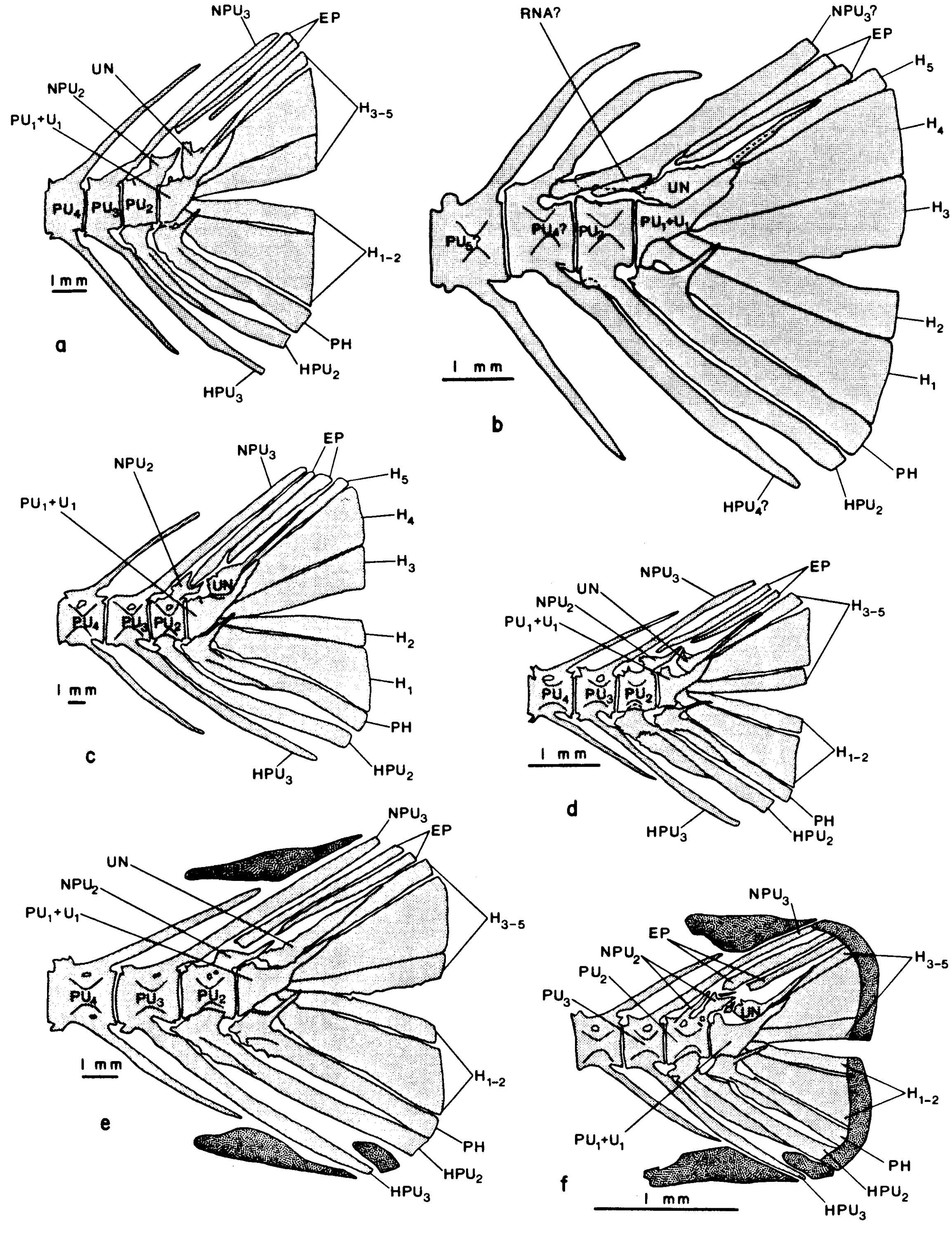
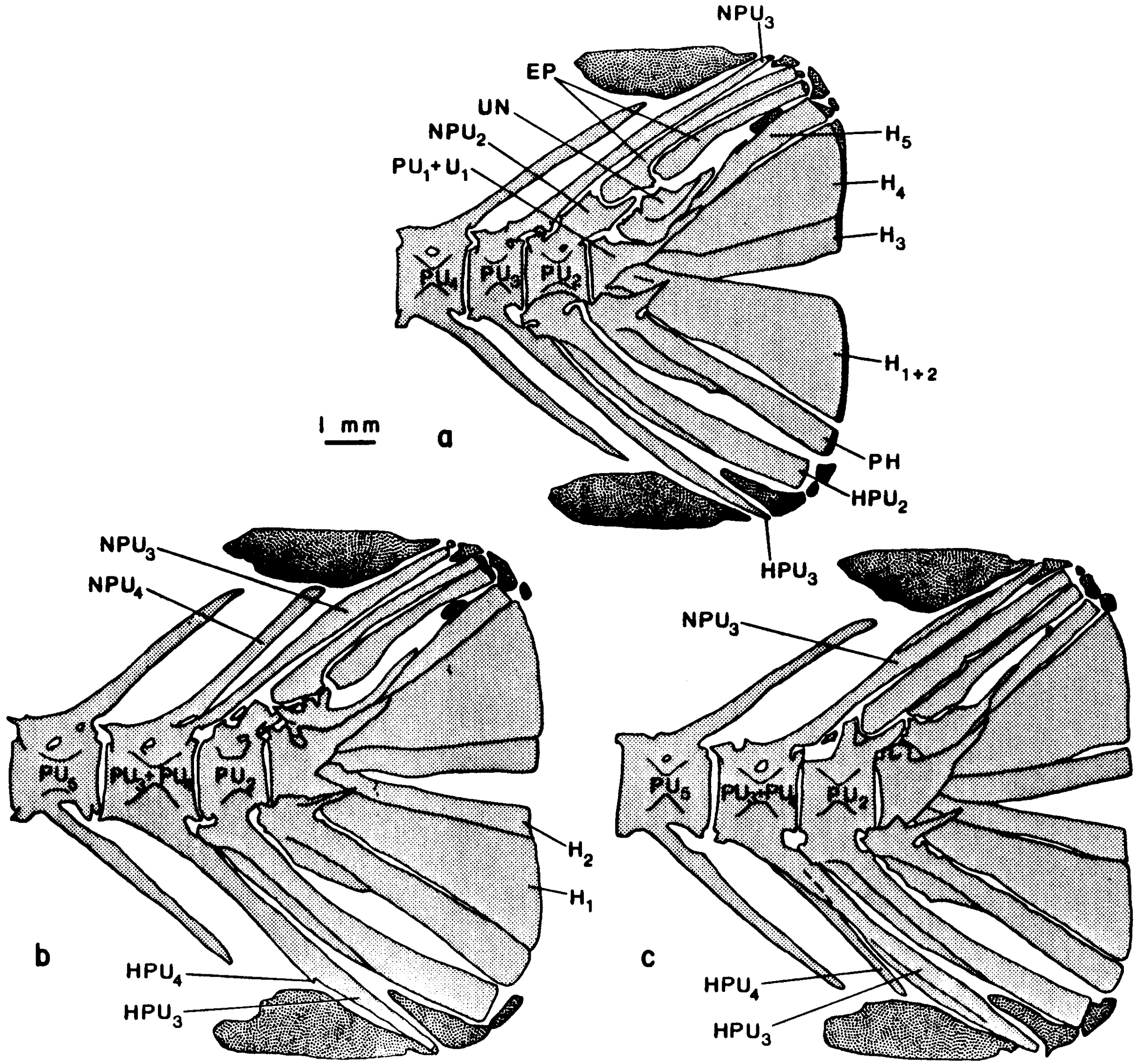

NPU3
EP
UN
NPU2
PU1+U1
H3-5
PU4
PU3
PU2
H1-2
1mm
a
PH
HPU2
HPU3
RNA?
NPU3?
EP
H5
H4
UN
H3
PU5?
PU4?
PU2
PU1+U1
H2
H1
1 mm
b
PH
HPU4?
HPU2
NPU3
EP
NPU2
H5
PU1+U1
H4
UN
H3
PU4
PU3
PU2
H2
H1
1 mm
PH
c
HPU3
HPU2
NPU3
EP
UN
NPU2
H3-5
PU1+U1
PU4
PU3
PU2
H1-2
1 mm
d
PH
HPU3
HPU2
NPU3
EP
UN
NPU2
H3-5
PU1+U1
PU4
PU3
PU2
1 mm
H1-2
e
PH
HPU2
HPU3
NPU3
EP
H3-5
NPU2
PU2
PU3
UN
H1-2
PU1+U1
PH
HPU2
f
1 mm
HPU3

Figure 11. Caudal skeletons of Astatotilapia calliptera (YPM 7815, fish farm at Chikwawa, Malawi), showing individual variation. Note fusions of hypurals in a, and of precaudal centra in b and c. Note variation in whether HPU_2 is autogenous (a) or fused with the centrum (b and c). Also note small cartilage between epural 2 and hypural 5 in all three specimens. All drawn to same scale. Abbreviations as in Fig. 10.



NPU$_3$
EP
UN
NPU$_2$
PU$_1$+U$_1$
H$_5$
H$_4$
H$_3$
PU$_4$
PU$_3$
PU$_2$
H$_{1+2}$
1 mm
a
PH
HPU$_2$
HPU$_3$
NPU$_3$
NPU$_4$
PU$_5$
PU$_3$+PU$_4$
PU$_2$
H$_2$
H$_1$
b
HPU$_4$
HPU$_3$
NPU$_3$
PU$_5$
PU$_3$+PU$_4$
PU$_2$
c
HPU$_4$
HPU$_3$

Figure 12. Neurocranium of Heterochromis multidens (AMNH 5966) in left lateral view. Abbreviations: B, blind cavity on both sides of head, not connected with lateral-line system; BOC, basioccipital; BS, basisphenoid; CC, external aperture of carotid canal; EO, epioccipital (epiotic); EOC, exoccipital; EOF, epioccipital facet for articulation with dorsal arm of posttemporal; F, frontal; IC, intercalar; IX, foramen of glossopharyngeal nerve; LE, lateral ethmoid; N, nasal; NLF_{1-5}, lateral-line foramina; PA, parietal; PRO, prootic; PS, parasphenoid; PTO, pterotic; PTS, pterosphenoid; PV, vomer; SOC, supraoccipital; SPH, sphenotic; X, foramen of vagus nerve.

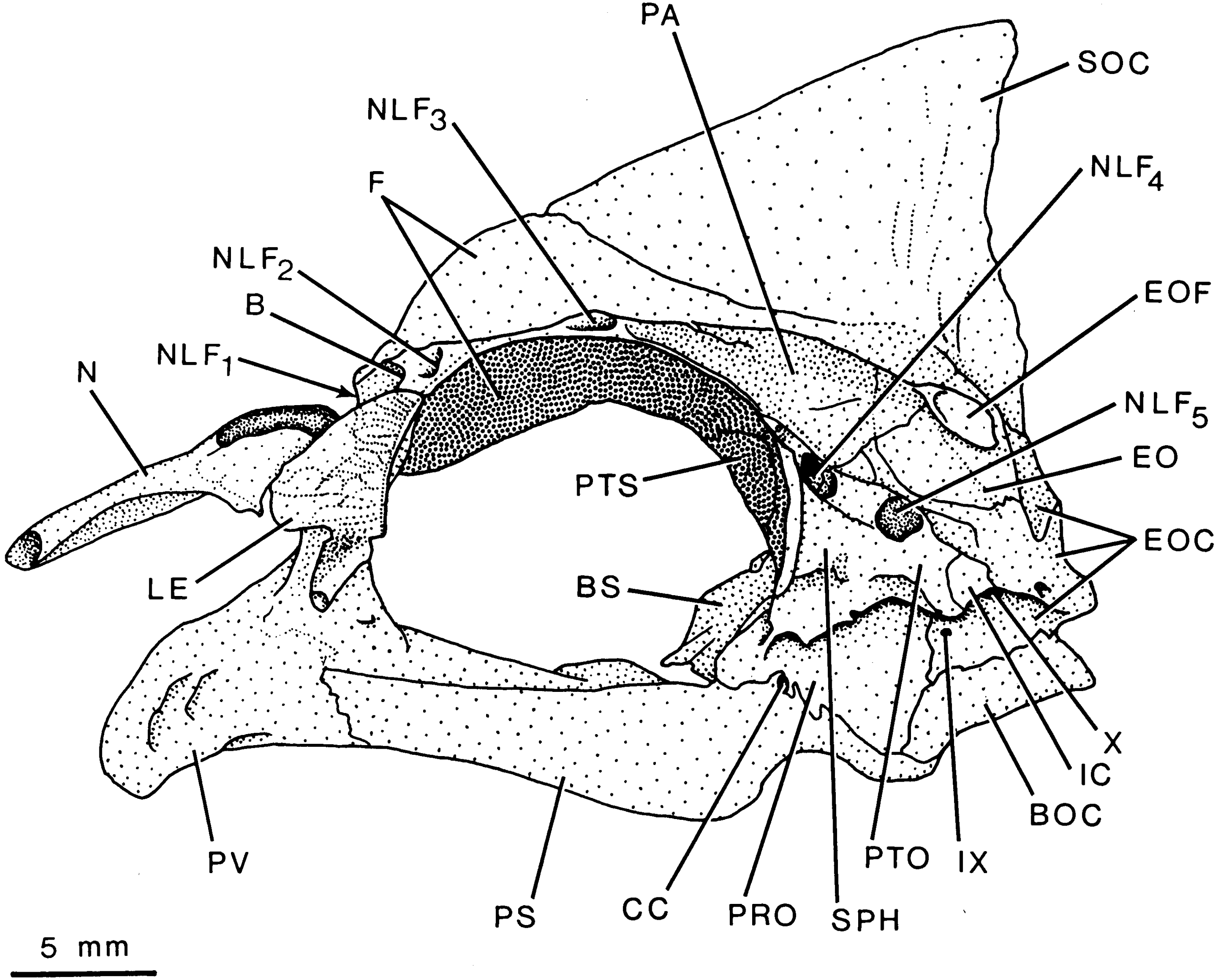
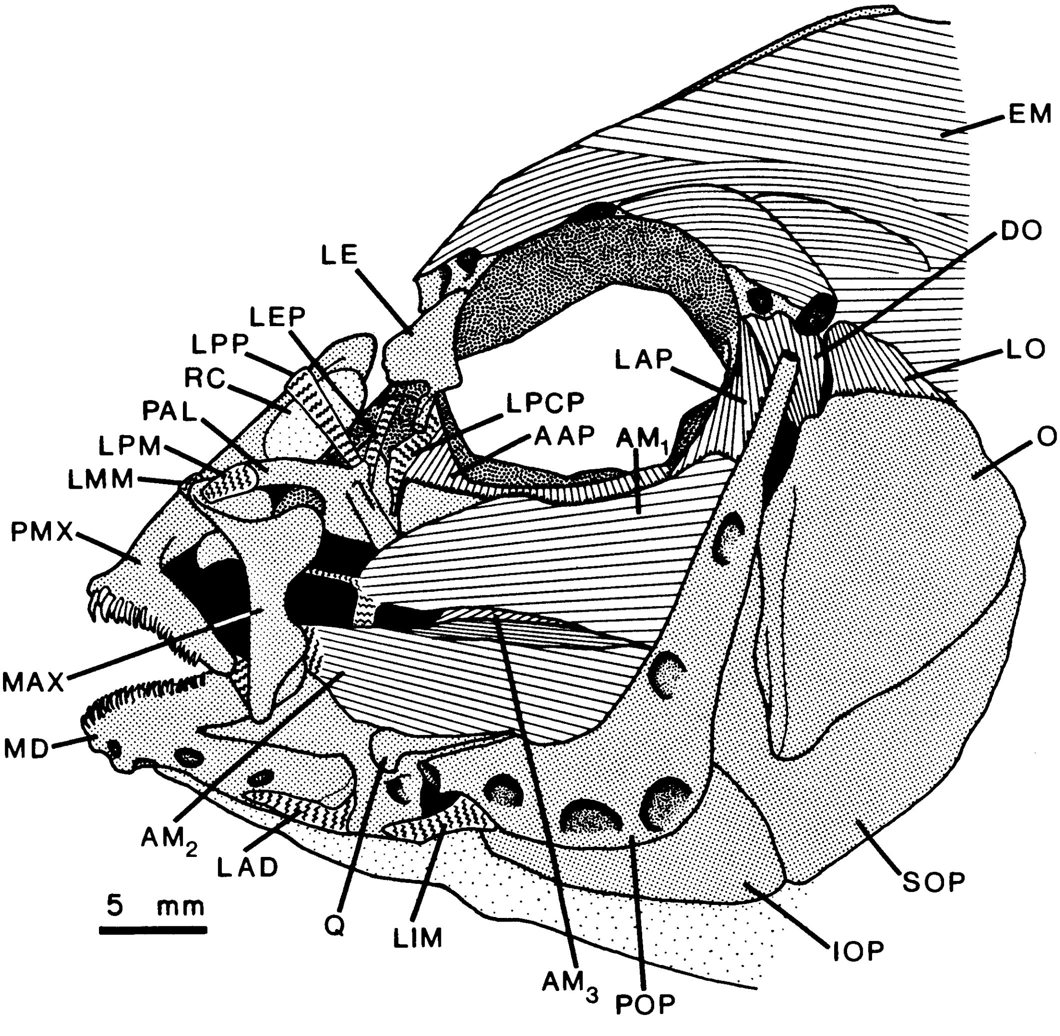

PA
SOC
NLF3
F
NLF4
NLF2
EOF
B
NLF1
N
NLF5
EO
PTS
EOC
LE
BS
X
IC
BOC
PV
PTO
IX
PS
CC
PRO
SPH
5 mm

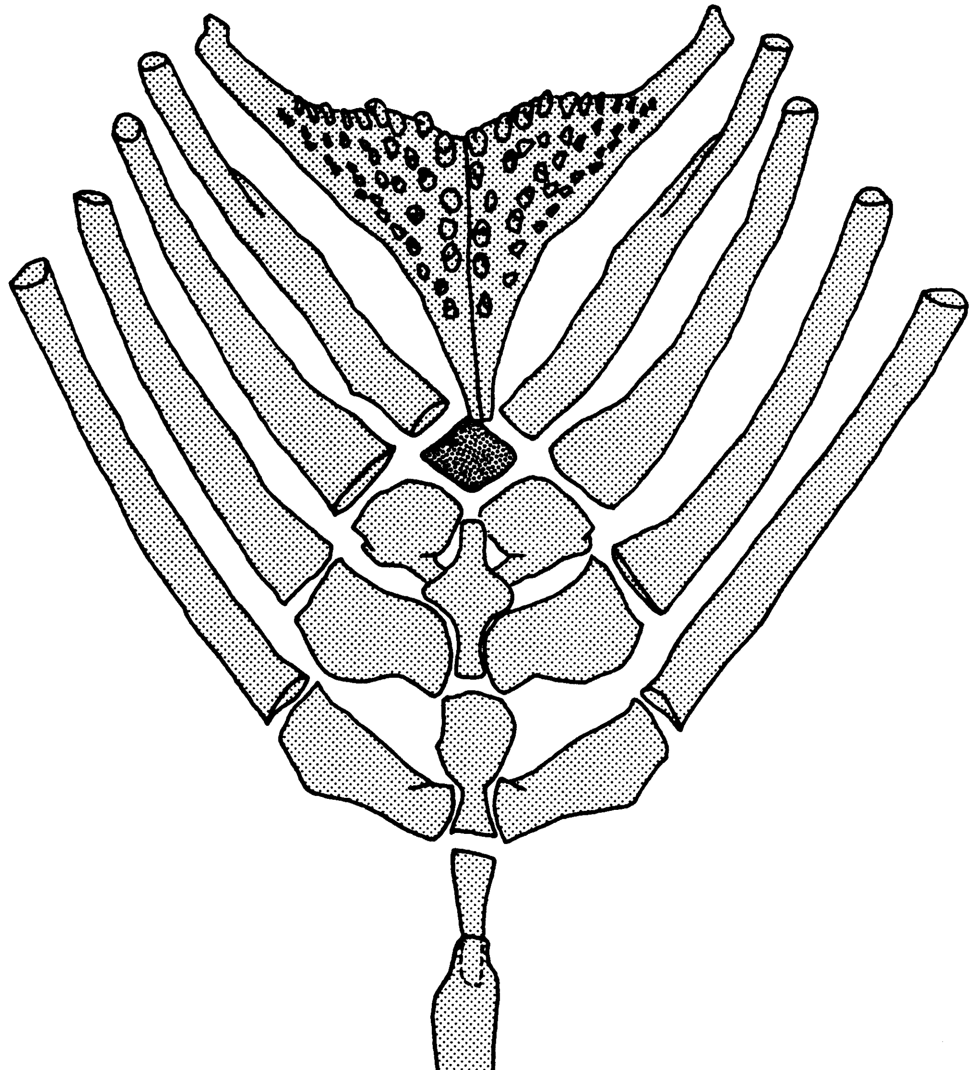
Figure 13. Head of Heterochromis multidens (AMNH 5966) after removal of skin, eyes, infraorbitals, and nasals. Abbreviations: AAP, adductor arcus palatini muscle; AM_{1-3}, divisions of adductor mandibulae muscle; DO, dilatator operculi muscle; EM, epaxial muscles; IOP, interoperculum; LAD, aguloarticulodentary ligament; LAP, levator arcus palatini muscle; LE, lateral ethmoid; LEP, ethmopalatine ligament; LIM, interoperculomandibular ligament; LMM, maxillomaxillary ligament; LO, levator operculi muscle; LPM, palatomaxillary ligament; LPCP, posterior craniopalatine ligament; LPP, palatopalatine ligament; MAX, maxilla; MD, dentary; OP, operculum; PAL, palatine; PMX, premaxilla; POP, preoperculum; Q, quadrate; RC, rostral cartilage; SOP, suboperculum.



EM
DO
LE
LEP
LPP
RC
LAP
LO
LPCP
PAL
AAP
AM_1
OP
LPM
LMM
PMX
MAX
MD
AM_2
LAD
5 mm
Q
LIM
AM_3
POP
IOP
SOP

Figure 14a (opposite). Ventral gill-arch elements of adult Heterochromis multidens (AMNH 5966). Cartilage shown with heavy stipple pattern.

Figure 14b (overleaf). Lower pharyngeal bone (fifth ceratobranchials) of juvenile Heterochromis multidens (MRAC 167924-167928), showing similarity to adult condition (cf. Fig. 14a). a, occlusal view; b, right lateral view.



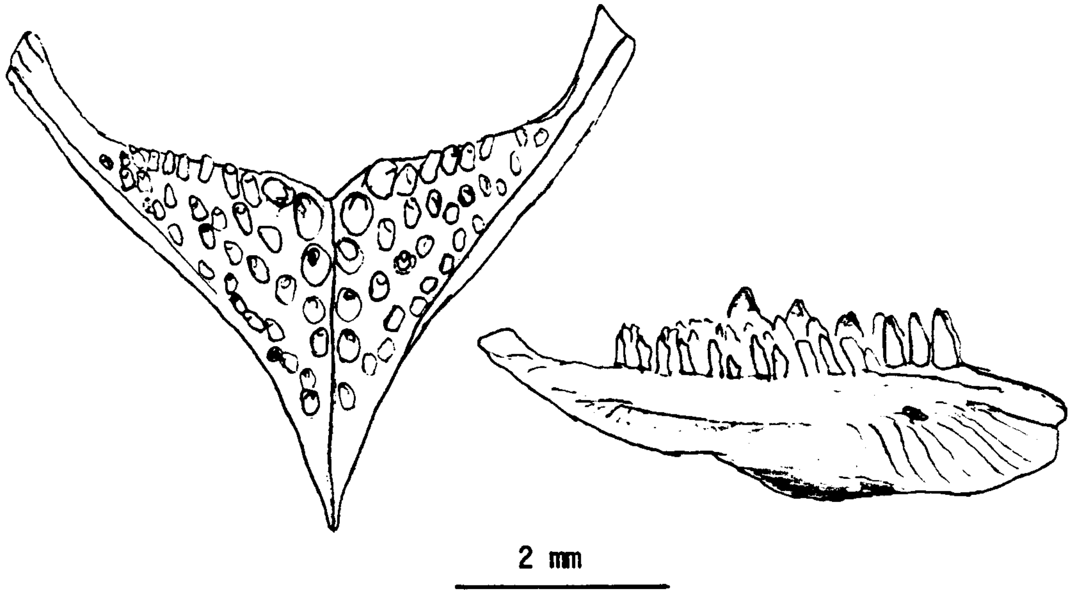
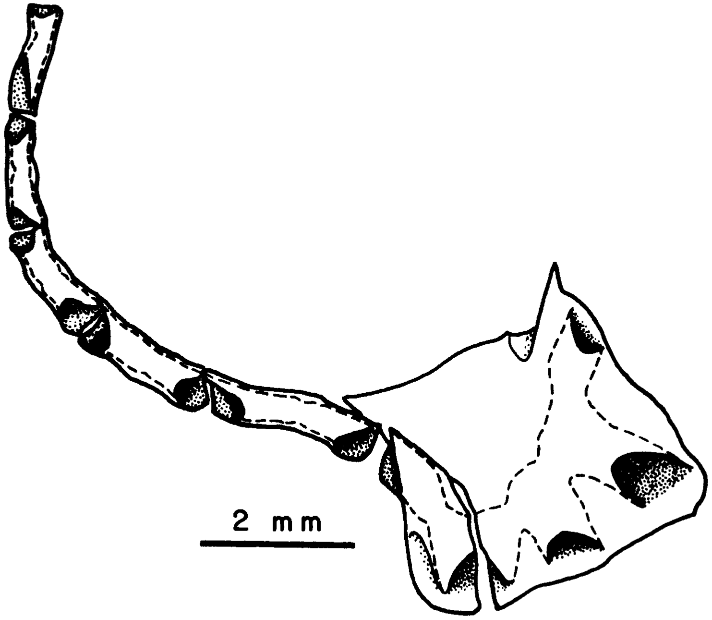
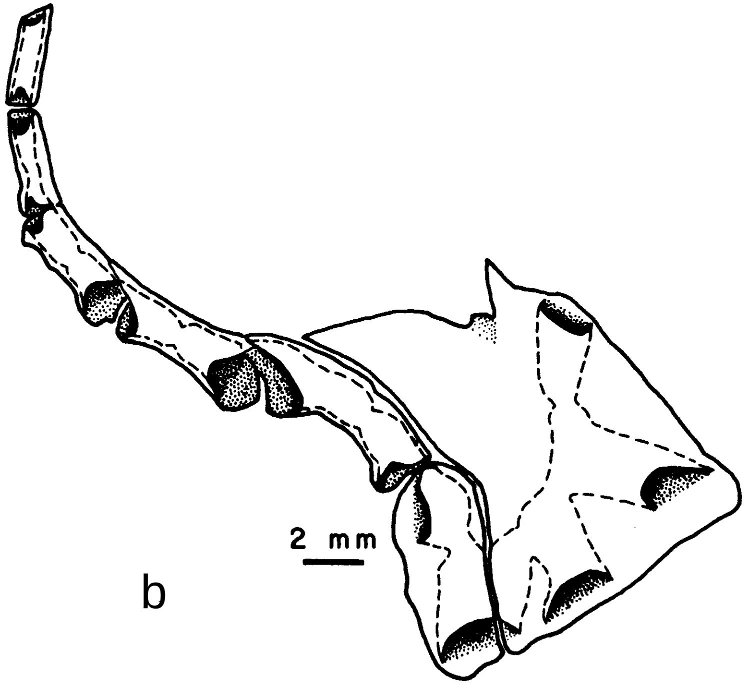

2 mm

Figure 15. Right infraorbitals of *Heterochromis multidens*. a, juvenile (MRAC 60890-60895); b, adult (AMNH 5966). Cf. *Ptychochromis* (Fig. 5d).



a



b

Figure 16. Heterochromis multidens (AMNH 5966). Neurocranial apophysis for upper pharyngeal bones in right lateral view. Abbreviations: apoph., apophysis; boc, basioccipital; lig. Baud., Baudelot's ligament; pro, prootic; ps, parasphenoid.

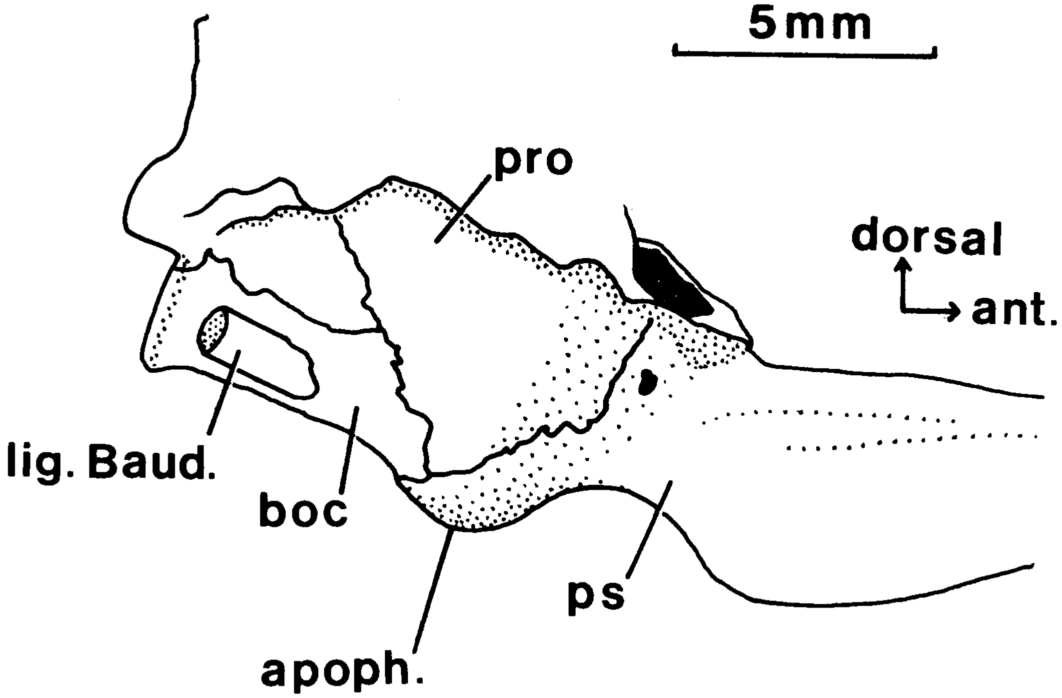

5mm
pro
dorsal
ant.
lig. Baud.
boc
ps
apoph.

Figure 17. Right hyoid bar and urohyal of Heterochromis multidens (AMNH 5966) in right lateral view. Abbreviations: ACH, anterior ceratohyal (=ceratohyal of authors); BR, branchiostegal rays; DHH, dorsal hypohyal; IH, interhyal; PCH, posterior ceratohyal (= epihyal of authors); UH, urohyal; VHH, ventral hypohyal. Dashed line on urohyal indicates extent of ventral fossa.

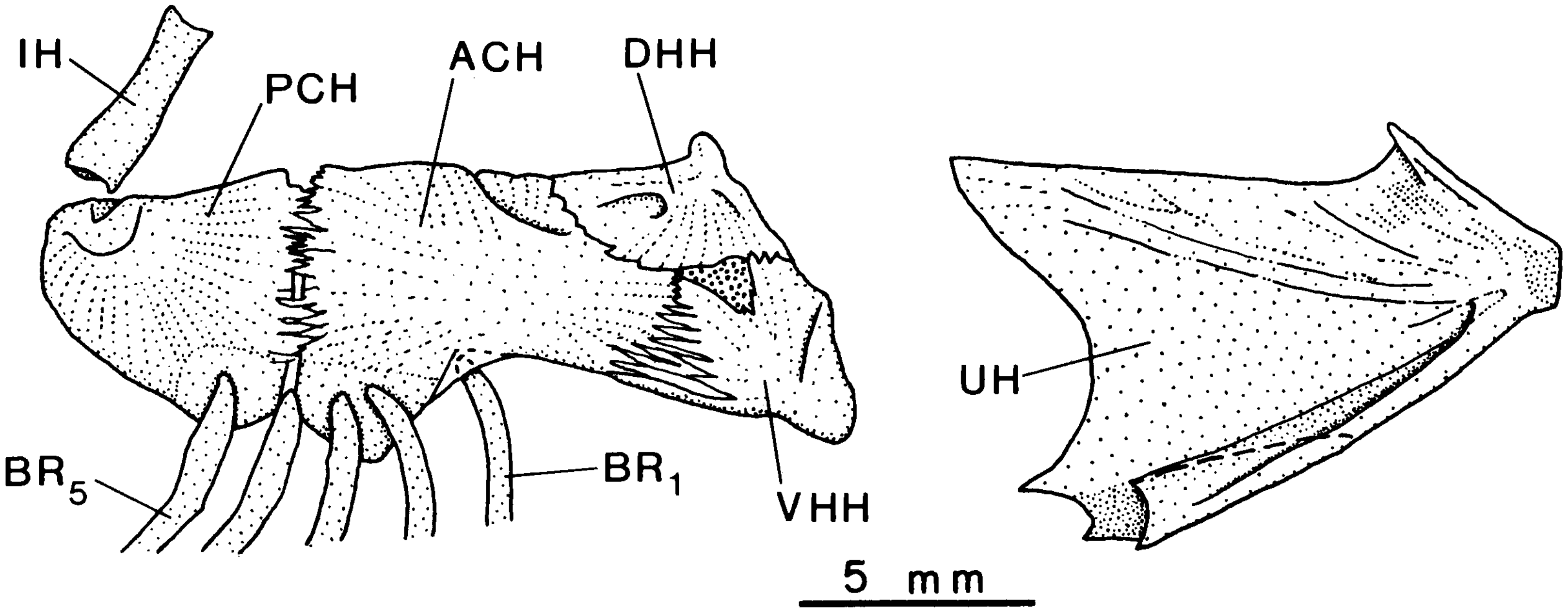
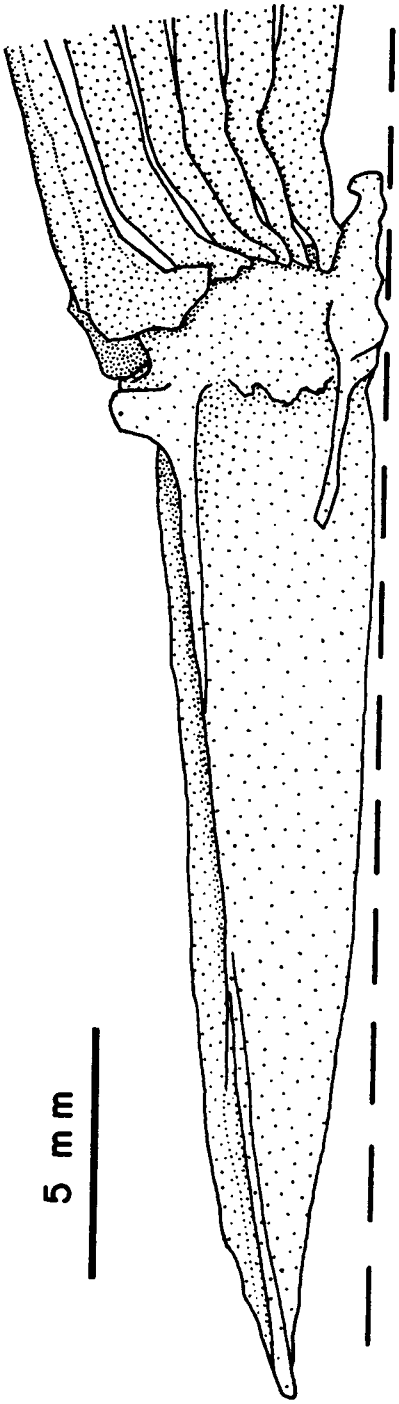

IH
PCH
ACH
DHH
BR5
BR1
VHH
UH
5 mm

Figure 18. Pelvic basipterygium of *Heterochromis multidens* (AMNH 5966), left side, ventral view. Dashed line indicates position of ventral midline of body.



5 mm

Figure 19. Part of left pectoral girdle of Heterochromis multidens (AMNH 5966) in medial view. Abbreviations: a, anterior; d, dorsal; dpc, distal postcleithrum; ppc, proximal postcleithrum.

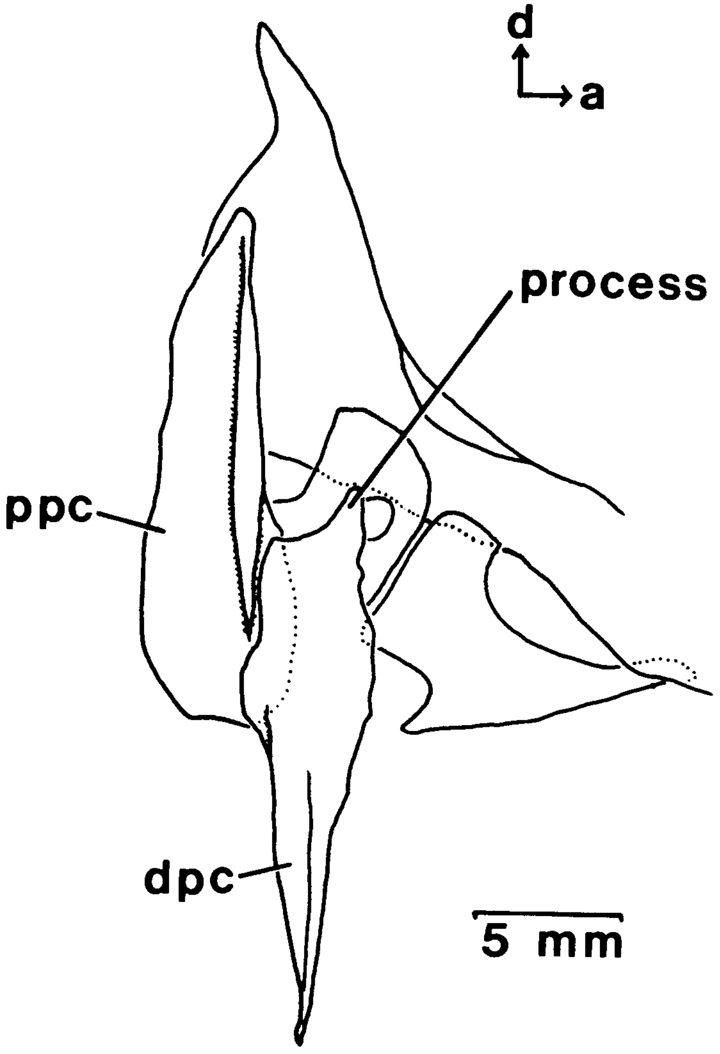

d
a
process
ppc
dpc
5 mm

Figure 20. Geographic distribution of _Heterochromis multidens_. (Redrawn from a map prepared by D. Thys van den Audenaerde [pers. comm.]).

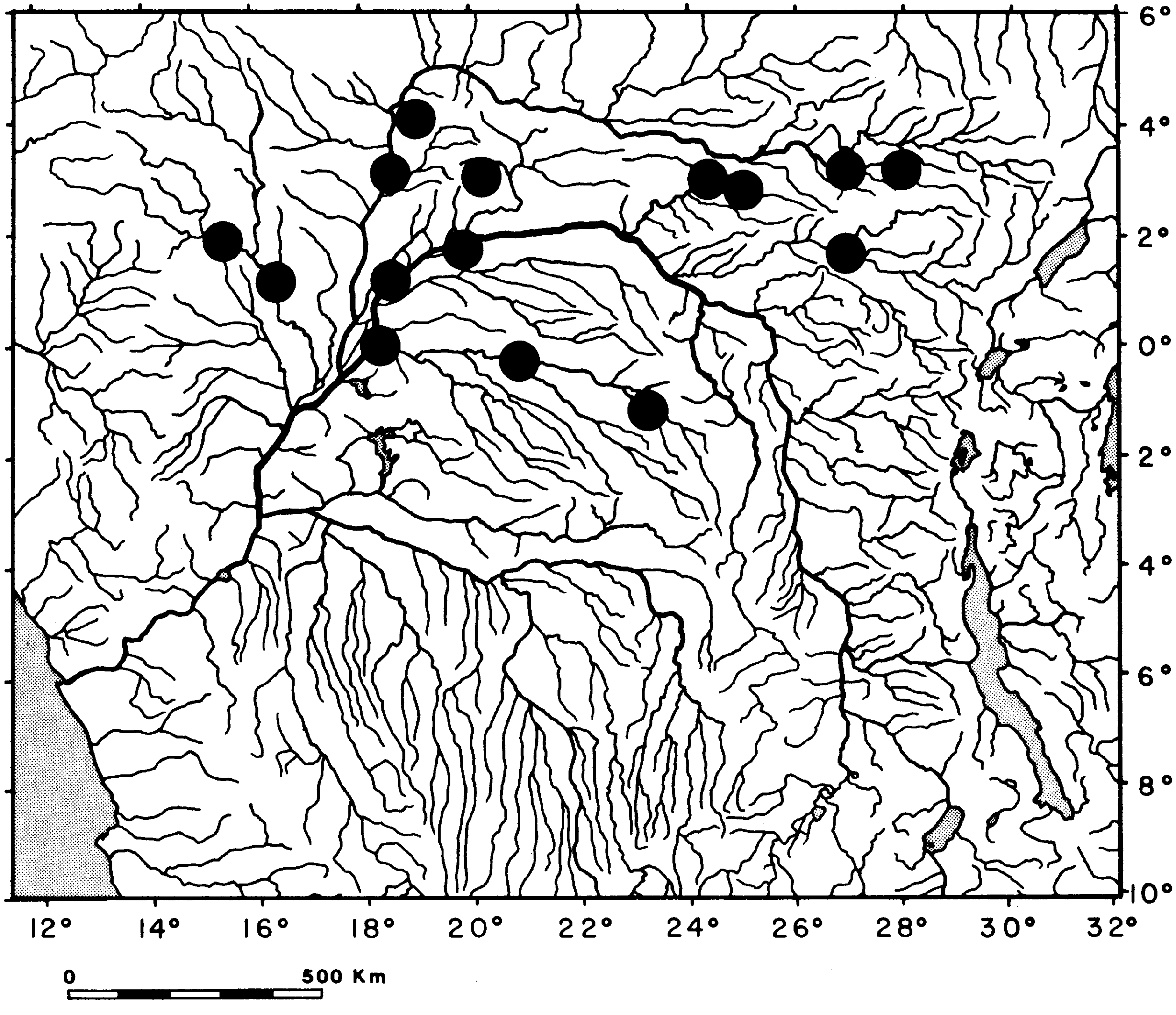

6°
4°
2°
0°
2°
4°
6°
8°
10°
12°
14°
16°
18°
20°
22°
24°
26°
28°
30°
32°
0
500 Km

Table 1. Summary of available information on taxonomic distribution of the frontal or nuchal gibbosity among cichlids.

Taxon	Gibbosity[1]	Reference
Malagasy and Indian cichlids		
<u>Etroplus</u> spp.	(-)	Goldstein, 1970: 33, figs.
<u>Oxylapia</u> <u>polli</u>	-	Kiener and Maugé, 1966: 57, 74
<u>Paratilapia</u> <u>polleni</u>	+	Legendre, 1918: 207
		Poisson, 1938: 94 footnote
		Kiener and Maugé, 1966: fig. 23
<u>Paretroplus</u> spp.	(-)	Kiener and Maugé, 1966
<u>Ptychochromis</u> <u>oligacanthus</u>	+	Pellegrin, 1907: 1169
		Kiener, 1963: 35
<u>Ptychochromis</u> <u>oligacanthus</u>	-	Kiener and Maugé, 1966: 54, 58, 80
<u>Ptychochromoides</u> <u>betsileanus</u>	++	Pellegrin, 1907
		Poisson, 1938: 84 footnote 3, 87 fig., 89 fig.
		Kiener, 1959: 501 fig., 502
		Kiener, 1963: 160, pl. 92, photo on p. 155 of fig. section
		Kiener and Maugé, 1966: 54, 57, 77, 80, fig. 23, pl. 3

Table 1 (continued)

Taxon	Gibbosity[1]	Reference
Neotropical cichlids		
Apistogramma spp.	(-)	Kullander, 1980: 42 and figs.
Biotodoma spp.	(-)	Gosse, 1975
Cichla ocellaris	++	Zaret, 1980: 147, fig. 2
Cichlasoma cyanoguttatum	++	Goldstein, 1970: photo p. 124
Cichlasoma citrinellum	+	Bleick, 1975
Cichlasoma irregulare, C. margaritiferum, C. melanurum	+	Pellegrin, 1903: 122
Cichlasoma panamense	-,+	Rogers, 1981: table 3
Cichlasoma, most other spp.?	(-)	
Geophagus crassilabrus	+	Gosse, 1975: 67, 70, fig. 13 Cichocki, 1976: 239
Geophagus pellegrini, G. steindachneri	+	Cichocki, 1976: 239
Geophagus, all other spp.	-	Gosse, 1975 Cichocki, 1976: 232, 237, 238, 240
Gymnogeophagus balzanii, G. brachyurus, (?) G. australe	+	Cichocki, 1976: 235-236
Gymnogeophagus gymnogenys	++	Gosse, 1975: 119, 123, 125-126, fig. 29 Cichocki, 1976: 235

Table 1 (continued)

Taxon	Gibbosity[1]	Reference
Gymnogeophagus, other spp.	(-)	Gosse, 1975 Cichocki, 1976
Neetroplus nematopus	-,+	Rogers, 1981: 291-292, table 3
Retroculus spp.	(-)	Gosse, 1971
Uaru amphiacanthoides	+	Sterba, 1983: 585
All other taxa?	(-)	Regan, 1905a,b, 1906a,b Lowe-McConnell, 1969: fig. 2
African cichlids		
Chalinochromis brichardi	+	Brichard, 1978: 145 lower photo
Cyphotilapia frontosa	++	Boulenger, 1915: 420-421 and fig. Poll, 1956: 76, fig. 12 Brichard, 1978: photos pp. 153, 195
Cyrtocara moorii	++	Boulenger, 1915: 445, fig. 304 Goldstein, 1970: photo p. 88
Cyrtocara (sensu Greenwood, 1979: 317), other spp.	-	Oliver, pers. obs.
Heterochromis multidens	++	Pellegrin, 1903: 79, fig. 16 Nichols and Griscom, 1917: fig. 30 David and Poll, 1939: fig. 25 Oliver, this thesis
Julidochromis regani	+	Brichard, 1978: photos p. 184
Lamprologus furcifer	+	Poll, 1956: fig. 105

Table 1 (continued)

Taxon	Gibbosity[1]	Reference
Lamprologus mocquardii	+	Poll, 1957: fig. 276
Petrotilapia sp.	+	Jackson and Ribbink, 1975: upper photo p. 65
Spathodus marlieri	++	Brichard, 1978: lower photo p. 285
Steatocranus spp. (including *Leptotilapia* and *Gobiochromis*)	+,++	Poll, 1957: 139, figs. 309, 312, 314 Roberts and Stewart, 1976: 292, pls. 11-12 Goldstein, 1970: photos p. 77
Telmatochromis caninus	+	Poll, 1957: fig. 419
Thoracochromis demeusii	++	Boulenger, 1915: 324-325, fig. 217 Pellegrin, 1903: 122 Regan, 1920a: 43-44 Thys van den Audenaerde, 1964: 157 Greenwood, 1979: 291
Tilapia tholloni congica	++	Poll and Thys van den Audenaerde, 1960
Tilapia, all other spp. and subspp.	-	Poll and Thys van den Audenaerde, 1960: 334
All other taxa?	(-)	Boulenger, 1915

Table 1 (continued)

Taxon	Gibbosity[1]	Reference
Middle Eastern and Southwest Asian cichlids		
Iranocichla hormuzensis	(-)	Coad, 1982
Tristramella spp.	(-)	Trewavas, 1942 Ben-Tuvia, 1959

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[1] ++, gibbosity reported or figured as highly developed; +, gibbosity reported or figured as definitely present but only slightly to moderately developed; (-), gibbosity not mentioned in description or not indicated in figure; -, gibbosity stated to be absent.

Table 2. Summary of available information on taxonomic distribution of the "tilapia-mark" among cichlids.

Taxon	Tilapia-mark[1]	Reference
Malagasy and Indian cichlids		
Etroplus spp.	(-)	Goldstein, 1970: 33, figs.
Oxylapia polli	(-)	Kiener and Maugé, 1966: 77
Paratilapia polleni	+	Legendre, 1918: 205
		Kiener, 1963: 33
Paretroplus spp.	(-)	Kiener and Maugé, 1966
		Kiener, 1963: pls. 15, 16
Ptychochromis oligacanthus	(-)	Kiener, 1963: pl. 14
Ptychochromoides betsileanus	(-)	Kiener, 1963: pl. 92
Neotropical cichlids		
Cichla ocellaris	(-)	Schroder and Zaret, 1979
Retroculus spp.	+?	Regan, 1906a: 50
		Gosse, 1971: 7, 10, 11, pls. 2-5
All other taxa?	(-)	Lowe-McConnell, 1969: fig. 2
		Regan, 1905a,b, 1906a,b
		Kullander, 1980: 42 and figs.
African cichlids		
Hemichromis spp.	-	Loiselle, 1979: 11

Table 2 (continued)

Taxon	Tilapia-mark[1]	Reference
Heterochromis multidens	+	David and Poll, 1937: 242 Matthes, 1964: 133 Oliver, this thesis
Konia spp.	-	Trewavas et al., 1972: 61
Myaka myaka	-	Trewavas et al., 1972: 60
Nanochromis splendens	+	Roberts and Stewart, 1976: 291 (variably present in females only)
Nanochromis, all other spp.	(-)	Roberts and Stewart, 1976: 284-292, pls. 9-11
Oreochromis spp.	+	(see Trewavas, 1981 for name change)
Pelmatochromis buettikoferi	-	Trewavas, 1973: 10, 12, 15
Pelmatochromis nigrofasciatus	+	Trewavas, 1973: 5, 7, 10, 12, 15
Pelmatochromis ocellifer	+	Trewavas, 1973: 5, 10, 12, 15, fig. 2
Pterochromis congicus	+	Trewavas, 1973: 15, fig. 6
Pungu maclareni	-	Trewavas et al., 1972: 66
Sarotherodon, most spp.	+	Trewavas, 1973: 15
Sarotherodon caroli	-	Trewavas et al., 1972: 54
Sarotherodon lohbergeri	-	Trewavas et al., 1972: 50

Table 2 (continued)

Taxon	Tilapia-mark[1]	Reference
Steatocranus spp. (including *Leptotilapia* and *Gobiochromis*)	+	Roberts and Stewart, 1976: 292 Roman, 1966: 176 Brichard, 1978: photo p. 92
Stomatepia mariae	+	Trewavas et al., 1972: 68, 69
Stomatepia mongo	-	Trewavas et al., 1972: 72
Stomatepia pindu	-,+	Trewavas et al., 1972: 68, 72
Thysia spp.	-	Loiselle and Welcomme, 1972: 53
Tilapia spp.	+	Trewavas, 1973: 15
Tylochromis spp.	(-)	Regan, 1920b Goldstein, 1970: upper photo p. 10 Brichard, 1978: photo p. 77
All other taxa?	(-)	Boulenger, 1915
Middle Eastern and Southwest Asian cichlids		
Iranocichla hormuzensis	+	Coad, 1982: 33, 34, fig. 1
Tristramella spp.	+	Ben-Tuvia, 1959: 182 footnote

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[1] +, "tilapia-mark" reported or figured as present, or a similarly shaped and placed mark figured as present; (-), mark not mentioned in color description or not shown on drawing of color pattern; -, mark stated to be absent.

Table 3. Summary of available information on taxonomic distribution of scaled dorsal and anal fins among cichlids.

Taxon	Fin scales[1]		Reference
	Dorsal	Anal	
Malagasy and Indian cichlids			
Etroplus spp.	+	+	Cichocki, 1976: 174 Oliver, pers. obs.
Oxylapia polli	+	+	Kiener and Maugé, 1966: 76
Paratilapia polleni	?	?	
Paretroplus spp.	+	+	Regan, 1920c: 423 Kiener, 1963: pls. 15, 16 Kiener and Maugé, 1966: 59
Ptychochromis oligacanthus	?	?	
Ptychochromoides betsileanus	?	?	
Neotropical cichlids			
Acaronia	-	-	Regan, 1905a: 346
Aequidens guianensis	+	+	Regan, 1905a: 332,341 Lowe-McConnell, 1969: 274
Aequidens maronii	+	+	Regan, 1905a: 344 Lowe-McConnell, 1969: 274
Aequidens portalegrensis	+	+	Regan, 1905a: 332, 341
Aequidens thayeri	+	+	Regan, 1905a: 332, 343
Aequidens, other spp.	(-)	(-)	

Table 3 (continued)

Taxon	Fin scales[1]		Reference
	Dorsal	Anal	
Apistogramma spp.	-	-	Regan, 1906a: 61
Astronotus ocellatus	+	+	Regan, 1905a: 329, 346-347 Regan, 1906b: 237
Chaetobranchopsis orbicularis	+	?	Regan, 1906b: 236
Chaetobranchus	?	?	
Cichla spp.	+	+	Machado-Allison, 1971: 463, 464, 471, 485
Cichla spp.	-	+	Regan, 1906b: 232, 233
Cichlasoma section 11 (*Thorichthys*): *C. affine*, *C. aureum*, *C. callolepis*	-	-	Regan, 1905b: 66, 320
Cichlasoma, all other spp.	+	?	Regan, 1905b: passim (see especially pp. 60, 320, 324, 339, 437)
Geophagus brasiliensis	+	?	Regan, 1906a: 58
Geophagus camopiensis	-	-	Gosse, 1975: 73
Geophagus surinamensis	+	?	Regan, 1906a: 56
Geophagus, other spp.	-	(-)	Regan, 1906a: passim
Gymnogeophagus	?	?	
Herotilapia multispinosa	+	?	Regan, 1905b: 439

Table 3 (continued)

Taxon	Fin scales[1] Dorsal	Fin scales[1] Anal	Reference
Nannacara anomala	?	?	Regan, 1905a: 344-345
Neetroplus nematopus	+	?	Regan, 1905b: 438
Petenia splendida	-	?	Regan, 1905b: 434
Pterophyllum spp.	+	?	Regan, 1905b: 442
Retroculus spp.	+	+	Gosse, 1971: pls. 2-5
Symphysodon discus	+	+	Regan, 1905b: 440
Uaru amphiacanthoides	+	?	Regan, 1905b: 440
All other taxa	?	?	
African cichlids			
Cyrtocara (sensu Greenwood, 1979: 317), some spp.	+	+	Oliver, this thesis (see Chapter 5)
Harpagochromis squamipinnis	+	+	Greenwood, 1973: 206, fig. 31 Greenwood, 1980b: 13
All other Victoria-Edward-Kivu haplochromines	-	-	Greenwood, 1980b: 13
Heterochromis multidens	+	+	Pellegrin, 1900: 99 Boulenger, 1902a: pl. 16 Steindachner, 1914: 56, fig. 11 Oliver, this thesis

Table 3 (continued)

Taxon	Fin scales[1]		Reference
	Dorsal	Anal	
Lamprologus christyi	+	+	Poll, 1956: fig. 128
Lamprologus leleupi	+	+	Poll, 1956: 592, fig. 130
Lamprologus moorei	+	+	Poll, 1956: fig. 102
Lamprologus niger	+	+	Poll, 1956: 595, fig. 131
Lamprologus pulcher	+	+	Poll, 1956: 580
Lamprologus savoryi	+	+	Poll, 1956: 577
Lamprologus tretocephalus	+	+	Oliver, pers. obs.
Lamprologus, other spp.	(-)	(-)	Poll, 1956, 1978
Cyrtocara, some spp.	+	+	Oliver, this thesis, Ch. 4
Tanganicodus irsacae	+	+	Poll, 1956: 451, fig. 93
Tylochromis polylepis	-	-	Oliver, pers. obs.
Middle Eastern and Southwest Asian cichlids			
Iranocichla hormuzensis	?	?	Coad, 1982
Tristramella spp.	?	?	

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[1] +, basal fin scales reported or figured as present; (-), fin scales not mentioned in description, apparently absent; -, fin scales stated to be absent; ?, condition of fin squamation unknown.

Table 4. Summary of available information on taxonomic distribution of fully scaled caudal fin among cichlids.

Taxon	Fully scaled caudal	Reference
Malagasy and Indian cichlids	?	
Neotropical cichlids		
Cichla spp.	+	Regan, 1906b: 232, 233
Geophagus camopiensis	+	Cichocki, 1976: 238
Geophagus surinamensis	+	Lowe-McConnell, 1969: 278, 281 Cichocki, 1976: 238
Geophagus, other spp.	-	Cichocki, 1976: 232, 237, 239, 240
Gymnogeophagus, some spp. of *Gy. gymnogenys* sp. group	+	Cichocki, 1976: 235
Retroculus spp.	+	Regan, 1906a: 50 Gosse, 1971: 6, pls. 2-5 Cichocki, 1976: 230
African cichlids		
Cyrtocara spp. sensu Greenwood, 1979: 317	+	Regan, 1921: 686 Trewavas, 1935: 66
Heterochromis multidens	+	Nichols and Griscom, 1917: 729, 730 Oliver, this thesis
Lamprologus moorei	+?	Poll, 1956: fig. 102
Serranochromis spp.	-	Trewavas, 1964: 6

Table 4 (continued)

Taxon	Fully scaled caudal	Reference
Thoracochromis fasciatus	+	Thys van den Audenaerde, 1964: 155, 168
Thoracochromis, other lower-Zaire species	-	Thys van den Audenaerde, 1964
Tylochromis spp.	+	Regan, 1920a: 163, 165 Poll, 1957: 137, fig. 303 Oliver, pers. obs.
All other taxa?	-	
Middle Eastern and Southwest Asian cichlids		
Iranocichla hormuzensis	-	Coad, 1982
Tristramella spp.	-?	

---

[1] +, caudal fin reported or figured as covered with small scales over nearly its entire length; (-), caudal not mentioned or not figured as fully scaled; -, caudal stated to be less than fully scaled.

Table 5. Linear regressions of morphometric variates (Y) on standard length or head length (X) in *Heterochromis multidens*.

Regression[1]	N	Range X (mm)	$\bar{X} \pm SE_X$	Range Y (mm)	$\bar{Y} \pm SE_Y$	$b \pm SE_b$	$a \pm SE_a$	r
HL on SL	14	44.7-264.0	103.221 ± 21.555	16.7- 94.0	37.271 ± 7.358	0.341*** ± 0.006	2.097* ± 0.737	0.998
BD on SL	14	44.7-264.0	103.221 ± 21.555	19.4-127.0	48.036 ± 10.458	0.484*** ± 0.007	-1.975 ± 0.952	0.999
PDL on SL	14	44.7-264.0	103.221 ± 21.555	19.5-118.1	45.236 ± 9.397	0.436*** ± 0.004	0.259 ± 0.529	0.999
PPL on SL	14	44.7-264.0	103.221 ± 21.555	20.2-113.0	45.543 ± 9.053	0.420*** ± 0.004	2.209*** ± 0.464	1.000
BEL on SL	14	44.7-264.0	103.221 ± 21.555	11.5- 79.2	30.693 ± 6.859	0.317*** ± 0.007	-2.050* ± 0.949	0.997
DBL on SL	14	44.7-264.0	103.221 ± 21.555	24.2-162.5	60.436 ± 13.159	0.609*** ± 0.012	-2.440 ± 1.498	0.998
CPL on SL	14	44.7-264.0	103.221 ± 21.555	5.7- 38.1	13.871 ± 2.962	0.137*** ± 0.004	-0.237 ± 0.523	0.995
PFL on SL	14	44.7-264.0	103.221 ± 21.555	14.4- 68.2	29.979 ± 5.443	0.250*** ± 0.011	4.209* ± 1.408	0.989
HW on HL	14	16.7- 94.0	37.271 ± 7.358	8.3- 49.2	19.557 ± 4.046	0.549*** ± 0.009	-0.907* ± 0.420	0.998
POD on HL	14	16.7- 94.0	37.271 ± 7.358	3.3- 27.8	10.493 ± 2.567	0.346*** ± 0.012	-2.421*** ± 0.540	0.993
IOW on HL	14	16.7- 94.0	37.271 ± 7.358	4.8- 44.2	14.543 ± 3.762	0.510*** ± 0.010	-4.466*** ± 0.472	0.998
SNL on HL	14	16.7- 94.0	37.271 ± 7.358	6.0- 46.1	16.700 ± 4.018	0.545*** ± 0.011	-3.600*** ± 0.521	0.997
OL on HL	14	16.7- 94.0	37.271 ± 7.358	6.3- 21.2	10.814 ± 1.431	0.194*** ± 0.005	3.597*** ± 0.235	0.996
CHD on HL	14	16.7- 94.0	37.271 ± 7.358	3.7- 36.7	11.836 ± 3.030	0.411*** ± 0.009	-3.470*** ± 0.418	0.997
UJL on HL	14	16.7- 94.0	37.271 ± 7.358	4.8- 36.0	12.514 ± 2.797	0.379*** ± 0.009	-1.606** ± 0.426	0.996
PMP on HL	14	16.7- 94.0	37.271 ± 7.358	6.7- 41.1	15.593 ± 3.108	0.420*** ± 0.014	-0.050 ± 0.631	0.994
LJL on HL	14	16.7- 94.0	37.271 ± 7.358	6.8- 42.8	15.957 ± 3.196	0.433*** ± 0.011	-0.170 ± 0.513	0.996
POH on HL	14	16.7- 94.0	37.271 ± 7.358	6.0- 36.6	13.400 ± 2.751	0.373*** ± 0.009	-0.491 ± 0.396	0.997

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[1] BD = body depth; BEL = belly length; CHD = cheek depth; CPL = caudal-peduncle length; DBL = dorsal-fin base length; HL = head length; HW = head width; IOW = interorbital width; LJL = lower-jaw length; OL = orbit length; PDL = predorsal length; PFL = pectoral-fin length; PMP = length of premaxillary ascending processes; POD = preorbital depth; POH = postorbital head length; PPL = prepelvic length; SL = standard length; SNL = snout length; UJL = upper-jaw length. Significance levels: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

CHAPTER 3

IS THE HAPLOCHROMINE "SPECIES FLOCK" OF LAKE MALAWI A MONOPHYLETIC GROUP?

HISTORY OF THE PROBLEM

The world's most speciose lacustrine ichthyofauna inhabits Lake Malawi, the southernmost of the Great Lakes of Africa. About 400 fish species are known from Lake Malawi. Of this total, about 35 species are members of some seven noncichlid families and the remainder all belong to the family Cichlidae. All but about four of the cichlid species are endemic to this lake. The endemic cichlids belong to two of the recognized groups of cichlids. The four endemic species of the first group, the Tribe Tilapiini, are all currently placed in the genus _Oreochromis_ subgenus _Nyasalapia_ (see Trewavas, 1981). All other cichlids endemic to Lake Malawi belong to the other group, the "haplochromines."[1] About 230 species of haplochromines have been

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[1] In the introduction to his collected papers on the East African cichlids, Greenwood (1981: i) defined "haplochromines": "Two papers [Greenwood, 1979, 1980b] are concerned with a reappraisal of the _Haplochromis_ generic concept. They represent a first attempt to split that polyphyletic 'genus' into a number of monophyletic lineages. . . . Each of those lineages is now accorded generic rank. As a result, the total number of _Haplochromis_ species in Africa is reduced from over 300 to a mere 5, but the number of _Haplochromis_-like genera has increased from 6 to 19 [here he cites the title page of Greenwood, 1980b, whose Contents there lists, by my count, 20 genera including _Haplochromis_, all of these being genera found in the Victoria-Edward-Kivu lakes]. These genera can be referred to, conveniently, as the 'haplochromines', it being understood that that name carries with it no phylogenetic implications." However, in the next paragraph Greenwood makes it clear that he does not mean to limit the term "haplochromine" to these 20 genera, or to Victoria-Edward-Kivu endemics, for he writes (loc. cit.): "The haplochromine species from Lake Turkana are members of a genus

described from Lake Malawi, and an additional 100+ species have been collected but are still undescribed. Undoubtedly, still more await discovery.

For more than 60 years biologists have pondered whether this haplochromine fauna of Lake Malawi was derived from a single ancestral species or from multiple ancestors. This question has important theoretical implications for studies of the systematics, ecology, behavior, character evolution, and speciation mechanisms of this fauna. Nevertheless, a definitive answer to it has remained elusive.

Regan (1921: 686), referring only to the species then assigned to *Haplochromis* and not to other endemic genera, wrote: ". . . The Nyassa [=Malawi] species are a natural group and may perhaps have evolved in the lake from a single ancestral form." He was led to this opinion by the truncate to emarginate caudal fin, which ". . . appears to be always

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widespread in the Nile and in the Zaire river system [here he cites the description of his new genus *Thoracochromis* in Greenwood, 1979]." Indeed, the title of the volume he is there introducing is "*The Haplochromine Fishes of the East African Lakes* . . .", so all of the genera that he therein treats in depth presumably qualify as "haplochromines."

In this thesis, I use "haplochromine" (both the noun and the adjective) in a broader sense, as I intended when I first used the term (Oliver and Loiselle, 1972: 309, 310). "Haplochromine" refers to cichlids thought to have a closer phylogenetic relationship with *Haplochromis* (sensu lato) than with any other informal suprageneric assemblage of cichlids such as lamprologines or tilapiines. Thus, I expect that haplochromines will eventually be characterizable as a monophyletic group, although its limits are still uncertain. I consider all of the Lake Malawi cichlids other than *Oreochromis* spp. to be haplochromines, irrespective of their pharyngeal-apophysis type (Greenwood, 1978). As will become evident later in this chapter, I also consider several Lake Tanganyika genera to be haplochromines. However, I am not entirely confident that *Pseudocrenilabrus* will prove to be related to the haplochromines, despite the anal-fin markings of this genus; it has a three-neuromast lacrimal (Fig. 5nn), which appears to be more primitive than the four-neuromast lacrimal of haplochromines (see Chapter 2).

nearly completely covered with small scales in the adult fish . . .", and by "the prevalence of a few distinctive types of coloration, and the absence of evident relationship to species found elsewhere. . . ." (loc. cit.). The following year, Regan repeated that the endemic Malawian Haplochromis ". . . appear to form a natural group and have evidently evolved in the lake from one or a few ancestral forms." Although adducing no additional evidence, he also briefly considered the relationships of the other endemic genera then recognized from Lake Malawi, including those that he believed were related to Tilapia. Regan concluded: "The indications are that the endemic Nyassa Cichlids have originated in the lake from about half-a-dozen ancestral forms" (Regan, 1922: 158). Thus, Regan supported a nonmonophyletic (albeit oligophyletic) status for what is today considered the endemic haplochromine fauna of Lake Malawi.

Trewavas (1949: 367-368) also addressed the question, but she extended Regan's evidence to include the "satellite" genera in addition to Haplochromis:

> The 100 species of Haplochromis and the endemic genera. Is there any evidence for or against a multiple origin of these? As Regan pointed out, they [Regan actually referred only to Haplochromis] are characterised by a covering of small scales on the caudal fin, which is usually emarginate. . . . There is little to recommend any of the species [of non-Great Lakes Haplochromis sensu Trewavas] more than the others as an alternative to H. callipterus [=Astatotilapia calliptera] for the ancestral rôle [in Lake Nyasa=Malawi]. The larger Zambezi species have more specialized teeth, and neither they nor their congeners of the Congo have the scaly, emarginate caudal fin of the Nyasa species.

Thus, Trewavas implied a monophyletic origin of the Malawian haplochromines, using the same evidence from which Regan had inferred a multiple but oligophyletic origin. Moreover, she proposed a living nonendemic species as a plausible ancestor of the group. (She also proposed that A. calliptera is most closely related specifically to the H. livingstonii group. This hypothesis is examined in Chapter 4.)

Fryer and Iles (1972: 491) followed Trewavas in considering that A. calliptera has "some claim to ancestral status" for the Malawian haplochromines, but they did not specifically advocate the monophyly of these fishes.

In contrast to Trewavas' and Fryer and Iles' more or less explicit hypotheses of single origin for the fauna, other writers have advocated a multiple origin. Mayr (1942) observed that ". . . no objections seem to exist against the assumption that species flocks originated by multiple colonizations . . ." (p. 214). Further, "That Lake Nyasa has more endemics than Lake Tanganyika is probably due to the fact that in its past history it was connected with a greater number of river systems" (p. 273). Mayr gave no evidence in support of this position. Barbour (1973: 553), again without morphological evidence, predicted from geological and hydrological considerations that: ". . . It will not be surprising if the phylogenies of the east African cichlid species flocks are found to cut across present lake boundaries in spite of their high numbers of endemic species." Fryer (1977: 153) dismissed this suggestion, at least in the case of Lake Victoria, on the basis of remarks made by Greenwood (1974: 99). However, according to the more recent work of Greenwood (1980b), Barbour was correct in that several interlake (Victoria-Edward-Kivu) lineages are now recognized. I will show below that Barbour may also be correct in the case of Lake Malawi.

The most explicit statement disputing the monophyly of the Malawian endemic haplochromines is that of Greenwood (1979: 314):

> It has been generally assumed . . . that the Malawi '<u>Haplochromis</u>'-group species were derived from an anatomically generalized fluviatile '<u>Haplochromis</u>' (i.e. <u>Astatotilapia</u>) species. I now suspect, however, that the story is far more complex, that the Malawi flock is probably of polyphyletic origin and that lineages related to <u>Thoracochromis</u> as well as to <u>Astatotilapia</u> and even to <u>Serranochromis</u> and <u>Chetia</u> may have contributed to the flock.

The testability of these suggestions is, unfortunately, diminished in that the particular Malawian taxa involved are not specified. Moreover, both <u>Thoracochromis</u> and <u>Astatotilapia</u> lack known synapomorphies that would define them as monophyletic (Greenwood, 1979: 284, 294). Although Greenwood presents no data to support his hypothesis of Malawian polyphyly, he adds: "Possibly some of the ideas put forward in this paper may contribute to the elucidation of that problem" (1979: 314). Indeed they do, as I show in the next section.

ANAL-FIN SPOTS AND HAPLOCHROMINE SYSTEMATICS

I have shown in Chapter 2 that a fully scaled caudal fin is widely distributed among cichlids, and that, on the basis of outgroup evidence and its presence in several plesiomorphic cichlid genera, this condition may be primitive for cichlids. Therefore, a scaly caudal fin cannot be used to support the Regan-Trewavas hypothesis of oligo- or monophyly of the Malawian haplochromines. However, this does not actually refute the hypothesis of monophyly, nor would the demonstration of diversity within the fauna do so. In order to show that the assemblage is nonmonophyletic, the minimum requirement is to demonstrate, by means of one or more shared derived characters (synapomorphies), that at least one endemic Malawian species shares a common ancestor with one or more non-Malawian species that is not shared with other Malawian species.

Recently, Greenwood (1979: 268, 274-275) has drawn attention to the potential phylogenetic significance of the presence and variety of the anal-fin markings of adult male haplochromines. In many if not most of these species, these brightly colored spots function as egg-dummies, mimicking the ova of the species. In spawning, the female extrudes several ova onto the substrate and then picks them up in her mouth. The male then spreads his anal fin near the substrate, displaying the spots. The female sees them and responds by mouthing them as if they were additional ova. The male ejaculates and the sperm are sucked into her mouth, fertilizing the ova there. This sequence is repeated until spawning is completed (work of W. Wickler, summarized by Fryer and Iles, 1972).[2]

Greenwood (1979: 275) distinguishes between true ocellae and nonocellar spots. The former are usually fewer, are generally arranged in longitudinal rows, and are invariably surrounded by a translucent, depigmented area, apparently enhancing their visibility. Nonocellar spots are usually more numerous and lack the clear surrounding ring. Greenwood considers nonocellar spots, as found in species of <u>Serranochromis</u> (Fig. 22a), to have a "near random arrangement" (1979: 283). I disagree; their dispersion pattern is uniform (regular) (see, e.g., Smith, 1980: 434, fig. 13-1). The two assemblages have different

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[2] Mayland (1982: 290-291) has recently questioned the role of the anal ocellae of males in promoting fertilization, partly because these markings may be present in female haplochromines as well. This is like arguing that the nipples of human mothers cannot function to nourish babies because men also have nipples. Mayland also mentioned experiments by Paulo (no publication or species cited) in which successful spawning occurs even if the male's ocellae are excised from the fin.

geographic centers of diversity. The genera that Greenwood recognized as having true ocellae (i.e., the Victoria-Edward-Kivu endemics and several riverine genera) may be considered "northern" taxa, whereas those with nonocellar spots (Serranochromis and Chetia sensu Greenwood, 1979) are "southern" taxa (Greenwood, 1979: 299).

I agree with Greenwood's hypothesis (1979: 275) that these classes of anal-fin markings were derived from the maculae common to the unpaired fins of most cichlids. Since such maculae are present in nonhaplochromines as well as haplochromines, they appear to be primitive with respect to both nonocellar and ocellar spots, which are confined to the haplochromines.[3] I also agree that true ocellae are derived and define a monophyletic group. Greenwood regarded the multiple, nonocellar type of spot as plesiomorphic within haplochromines (1979: 275, 309). I suggest tentatively that the evolution of anal-fin spots involved the phylogenetic conversion of numerous, dull-colored maculae (the nonhaplochromine condition) to fewer, more brightly colored spots (haplochromine nonocellar spots) to still fewer spots, each partly or completely surrounded by a clear ring (derived haplochromine true ocellae). Thus, nonocellar spots do not define a monophyletic group, since some taxa with this spot type may be more closely related to the ocellate taxa than to the other nonocellate taxa. But, all

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[3] With improved knowledge of the variation and taxonomic distribution of male anal-fin spots, this general character may prove to be a synapomorphy of the haplochromines, even if such spots were secondarily lost in a few taxa such as Orthochromis. Indeed, Van Couvering (1982: text-fig. 11), in effect, uses "egg dummies" as a synapomorphy of haplochromines other than Pseudocrenilabrus. However, it seems unlikely that all anal-fin spots of male haplochromines function as egg dummies, particularly since these markings take the form of elongate streaks in many species of Cyrtocara (e.g., C. lateristriga; Fig. 22e).

haplochromines with these multiple nonocellar spots, together with all those having true ocellae, would comprise a monophyletic group; all of the former would be more closely related to all those with true ocellae than to any species with unmodified, plesiomorphic anal-fin maculae.

Anal-fin spots in Lake Tanganyika cichlids

It is not widely realized that several endemic genera of Lake Tanganyika cichlids have anal-fin spots. These genera include, at least, the following:

(1) *Lobochilotes*, with one species, *L. labiatus*. Poll (1956: 68) described the ocellae in a live fish. Excellent color photographs in Brichard's book (1978: 244-245) clearly show the ocellae. Although the spots are rather small, each is surrounded by a depigmented area as in true ocellae. I conjecture that *L. labiatus* is the sister-species of an undisputed haplochromine, the endemic Lake Tanganyika species *Ctenochromis horii* (see Greenwood, 1979: 287-289 for new generic allocation of this species, formerly classified as a *Haplochromis*). These two species strikingly resemble each other in details of the coloration, color pattern (notably the pigmented spots on the head), general body shape, head profile, and in having thickened lips which are conspicuously lobed in large individuals of *L. labiatus*; representatives of the latter species attain a much larger size than those of *C. horii*. Compare photographs showing live individuals of the two species on pp. 168-169 and 319 of Brichard (1978). However, *Lobochilotes* has a fully-scaled chest (pers. obs.), unlike *Ctenochromis*.

(2) *Simochromis*, including *Limnotilapia* (see Greenwood, 1979: 317-319). The several species, and documentation of their anal-fin ocellae, are as follows:

S. babaulti. Poll, 1956: fig. 13 and p. 80; Brichard, 1978: photos on p. 276, clearly showing the small yellow spots and their depigmented surrounding areas, very much as in the mbuna of Lake Malawi (see below).

S. curvifrons (Nelissen recognizes a monotypic genus Pseudosimochromis for this species, but this action seems unwarranted since he postulates that it is most closely related to Simochromis). Poll, 1956: 94; Brichard, 1978: lower photograph on p. 277.

S. dardennii. Poll, 1956: 52.

S. diagramma. Poll, 1956: fig. 13 and p. 80; Nelissen, 1975: 204. It is of great interest that Nelissen (1975) describes the function of the small anal-fin spots of this species during spawning, and shows that they are true egg-dummies. This species "mostly shows one egg-spot at the end of the anal fin. However, sometimes more spots may evolve [i.e., develop during ontogeny]" (Nelissen, 1975: 204). He describes the beginning of true spawning thus (loc. cit.):

> Spawning starts as the quivering female, lying on its side, pushes out three eggs. The male takes the female's place--as with pseudo-spawning--swimming over the eggs and quivers, the frontal part of the body a little upward. As the female swims around to take the male's place, it picks up the eggs into the mouth and approaches the anal fin of the quivering male. The female snaps at the egg-spot on the male's anal fin, probably taking up some sperm.

This closely matches the behavior of Astatotilapia burtoni, a species studied by Wickler in formulating his egg-dummy theory of anal-fin spots. Moreover, and significantly in view of the small size of the anal ocellae in S. diagramma, Nelissen found the eggs of this species to be much smaller than Poll's (1956) report of 6 mm length. Nelissen (loc. cit.) measured a total of 140 eggs, from four different fish, and found a mean length and width of only 4.2 x 3.0 mm.

_S_. _loocki_. Poll, 1956: 64.

_S_. _marginatus_. Poll, 1956: 97.

(3) _Petrochromis_. The nominal species, and documentation of their anal-fin ocellae, are as follows:

_P_. _fasciolatus_. Brichard (1978: 256-257) gives photographs showing fishes with quite definite yellow ocellar spots. An unusual feature evident in these photos is that, in addition to ocellae with dark or depigmented rings along the middle part of the fin, the lappets between the anal spines are prominently colored with bright yellow set off distally and anteriorly by a black margin.

_P_. _polyodon_. Brichard (1978: 260-261) illustrates this and an unidentified _Petrochromis_ species, both with distinct yellow ocellae which appear to have darkly pigmented surrounding rings but not clear rings. These markings resemble in size and shape the ocellar egg-dummis of _Astatotilapia_ spp.

_P_. _trewavasae_. Poll (1956: 111) describes the anal ocellae.

(4) _Tropheus_. Some of the complex morphometric variation in this genus was recently studied by Nelissen (1979). Several species and many geographical color variants are now recognized. Although Poll (1956) neither mentioned nor figured distinct anal-fin markings in these fishes, the color photographs in Brichard (1978) clearly show such markings to be present in some individuals (sexually mature males?); see especially the following pages in Brichard's book: 305, 313, 316-317,

324-325, and 329.

THE ANAL-FIN SPOTS OF THE LAKE MALAWI HAPLOCHROMINES: NEW EVIDENCE AGAINST THE MONOPHYLY OF THIS "SPECIES FLOCK"

Little detailed information is published concerning the anal-fin markings of Malawian fishes. I have, therefore, surveyed them as extensively as is currently possible by examining my color transparencies of adult male haplochromines.

The result of this survey is the discovery that two anal-spot types are represented in the Malawian fauna. Although information is still limited to a few dozen species, a definite taxonomic pattern is already apparent. True ocellae, closely resembling those of Victoria-Edward-Kivu and ocellate riverine haplochromines, are found only among the mbuna genera and in the nonendemic species Astatotilapia calliptera (Fig. 21). Nonocellar spots, similar to those in Serranochromis and Chetia, occur only among non-mbuna genera, and are known in species representing every major body color-pattern type (Fig. 22). Although considerable interspecific variation in spot number, color, and arrangement exists within each type, I found no exceptions to this pattern of taxonomic distribution.[4]

Thus, the 10 nominal mbuna genera of Lake Malawi are corroborated as sharing a common ancestor with the extra-Malawian riverine and

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[4] After this chapter was substantially completed, I received a book by Hans Mayland in which he notes, in effect, the same two types of anal-fin markings among Malawian cichlids, and attributes a similar taxonomic distribution to them (Mayland, 1982: 290-291). However, Mayland's remarks are made in a functional context (see footnote 2, above) and he draws no phylogenetic conclusions from his observations.

lacustrine haplochromines with true ocellae, an ancestor that is not shared with the remainder of the Malawian endemics. Therefore, *Astatotilapia calliptera* cannot be considered ancestral to the entire assemblage, as Trewavas (1949) suggested. Neither the mbuna nor the non-mbuna can be hypothesized as monophyletic on the available evidence. However, future work on the biology of these fishes must be done with the recognition that at least two unrelated haplochromine assemblages, or species flocks, contribute to the diversity of the Lake Malawi superflock. Indeed, as the comparisons in Table 6 suggest, contrasts in life-history characteristics between the two faunal components contribute significantly to this diversity.

Remarks on the relationships of the mbuna

I have attempted to relate the mbuna to one or more of the riverine or Victoria-Edward-Kivu ocellate genera, without success. Greenwood (1979: 270-272) distinguished three types of thoracic-abdominal scale transitions in haplochromines. These are: (1) a presumed primitive type, in which the thoracic scales are not much smaller than the abdominal ones, or in which there is a gradual size reduction anteriorly, as in *Astatotilapia*; (2) a derived pattern characterized by an abrupt transition to smaller thoracic scales near a line connecting the pectoral- and pelvic-fin bases, as in *Thoracochromis*; and (3) another derived pattern, in which both thoracic and ventral abdominal scales are abruptly reduced in size, as in *Orthochromis* (Fig. 23). However, among the mbuna I found considerable diversity in the thoracic-abdominal squamation (Fig. 24). I have difficulty in identifying the observed pattern or patterns with Greenwood's types of transition.

The strong similarity in general appearance and in particular trophic specializations between the rock-dwelling mbuna genera of Lake Malawi and the genera *Simochromis*, *Petrotilapia*, and *Tropheus* of Lake Tanganyika has long been recognized. This similarity has, invariably, been attributed to convergence or parallelism. For example, Liem (1980: fig. 7 and its legend) gives scanning-electron micrographs of the unusual, tricuspid mandibular teeth of *Petrotilapia* (a Lake Malawi mbuna genus) and *Petrochromis polyodon* of Lake Tanganyika, remarking: "Note the striking convergence in shape of the dentition. . . ." Similarly, Fryer and Iles (1972: 514-516) discuss the similarity of *Tropheus* (L. Tanganyika) and *Pseudotropheus* (L. Malawi), and attribute the similarity to convergence. They also discuss (loc. cit.) *Petrochromis* and *Petrotilapia*, "which resemble each other in an almost uncanny manner not only in general appearance but in minute details of their anatomy. The form of the mouth and the dentition of these genera are extremely specialised and yet virtually identical." Fryer and Iles consider this to represent parallel evolution.

I venture to make the obvious suggestion that this and other "uncanny" resemblances between mbuna taxa and the mbuna-like Lake Tanganyika genera (*Tropheus*, *Petrochromis*, and *Simochromis*) may be due to immediate common ancestry between the taxa involved. This possibility no longer appears far-fetched, in view of two of the new ideas presented here. The first is that the densely scaled caudal fin of Malawian haplochromines cannot be used as evidence for the monophyly of that assemblage. The second is that the mbuna of Lake Malawi and the above-named Lake Tanganyika genera must be added to the haplochromine genera that possess the synapomorphy of anal-fin ocellae.

Figure 21. Anal fins of some adult male haplochromines with true ocellae. Transparent, lightly pigmented areas of fin membrane shown by crosshatching. Traced from projected color transparencies of live fishes in aquaria, usually photographed soon after capture. Each drawing represents a single individual. Not drawn to same scale. a, *Harpagochromis squamipinnis*, Lake George (fin pink, ocellar spots orange); b, *Astatotilapia aeneocolor*, Lake George (fin dark gray with pink flush, ocellar spots orange); c, *Astatotilapia calliptera*, Lake Malawi nonendemic (fin brownish, darker ventrally, ocellar spots yellow); d, e, two individuals of *Cyathochromis obliquidens*, Lake Malawi (fin iridescent light blue with black stripe, ocellar spots intense yellow); f, *Iodotropheus sprengerae*, Lake Malawi (fin iridescent purplish blue shading to orange-brown on ventral one-third, ocellar spots yellow).

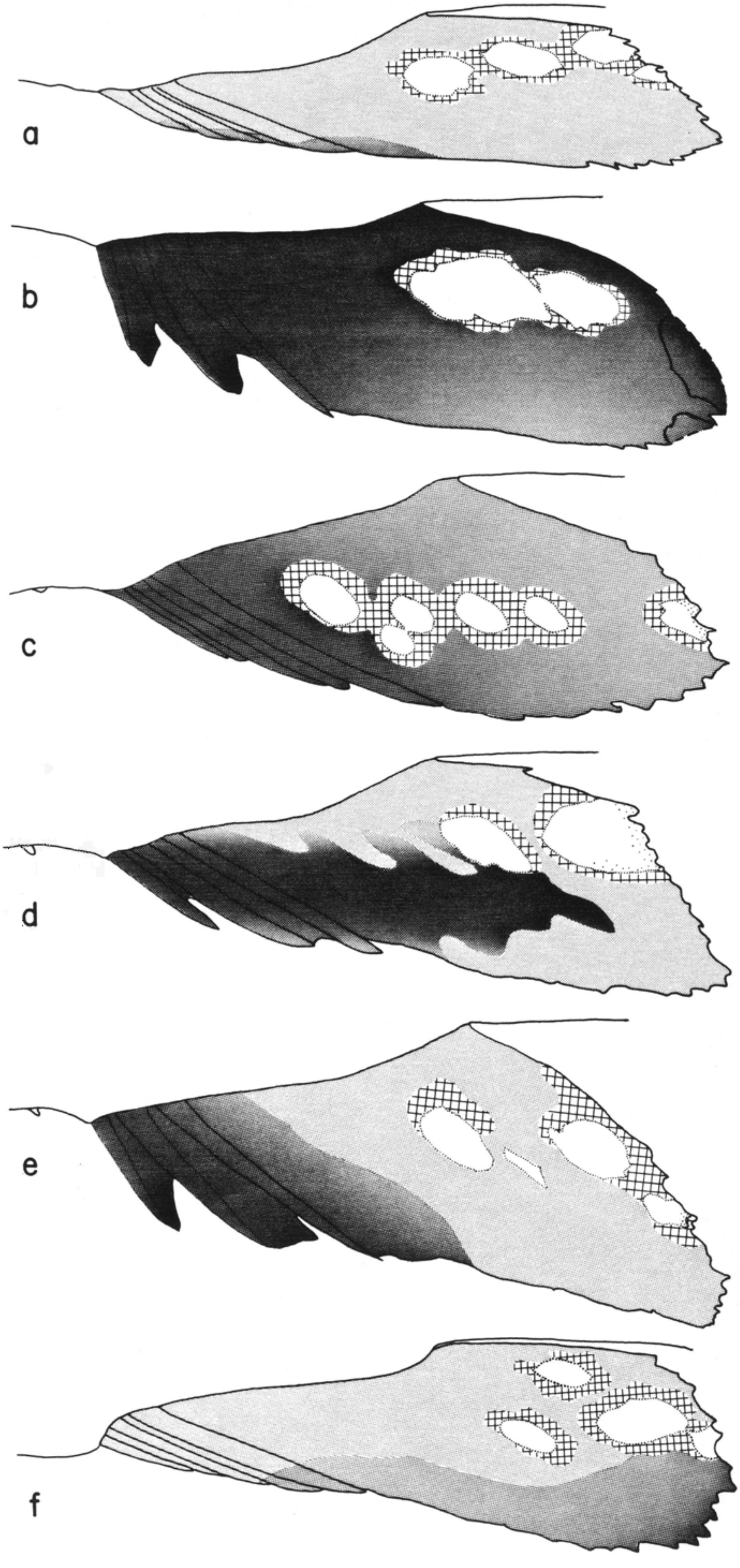
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Figure 22. Anal fins of some adult male haplochromines with nonocellate anal spots. Conventions as in Fig. 21. a, *Serranochromis* (*Serranochromis*) *longimanus*, Okavango and Upper Zambesi rivers (redrawn from fig. 19b of Trewavas, 1964); b, *Cyrtocara* cf. *polystigma*, Lake Malawi, sexually active aquarium specimen (fin dark orange-brown becoming tinged with yellow toward ventral margin, anal spots and streaks yellow with narrow dark margin [the large, brown oval spots characteristic of juveniles, females, and nonbreeding males are nearly obscured and not shown]); c, *Cyrtocara spilopterus*, Lake Malawi, body marked with horizontal stripes and vertical crossbars (fin gray with yellow-gray ventral margin, spots vivid yellow); d, *Cyrtocara tetrastigma*, Lake Malawi, body marked with 3 lateral spots (fin dark brown with orange flush, lappets of spinous part and ventral margin of soft part bright orange, spots pale orange); e, *Cyrtocara lateristriga*, Lake Malawi, body marked with oblique stripe (fin medium-gray on basal one-third, deep grayish orange on other two-thirds, ventral margin bright orange with white sections; spots and streaks with pale-gray centers shading gradually to medium-gray margins); f, *Lethrinops* cf. *argentea*, Lake Malawi, 7 vertical bars below dorsal-fin base, nape red (fin black with pale yellow basal stripe and narrow, pale yellow ventral margin; spots pale yellow).

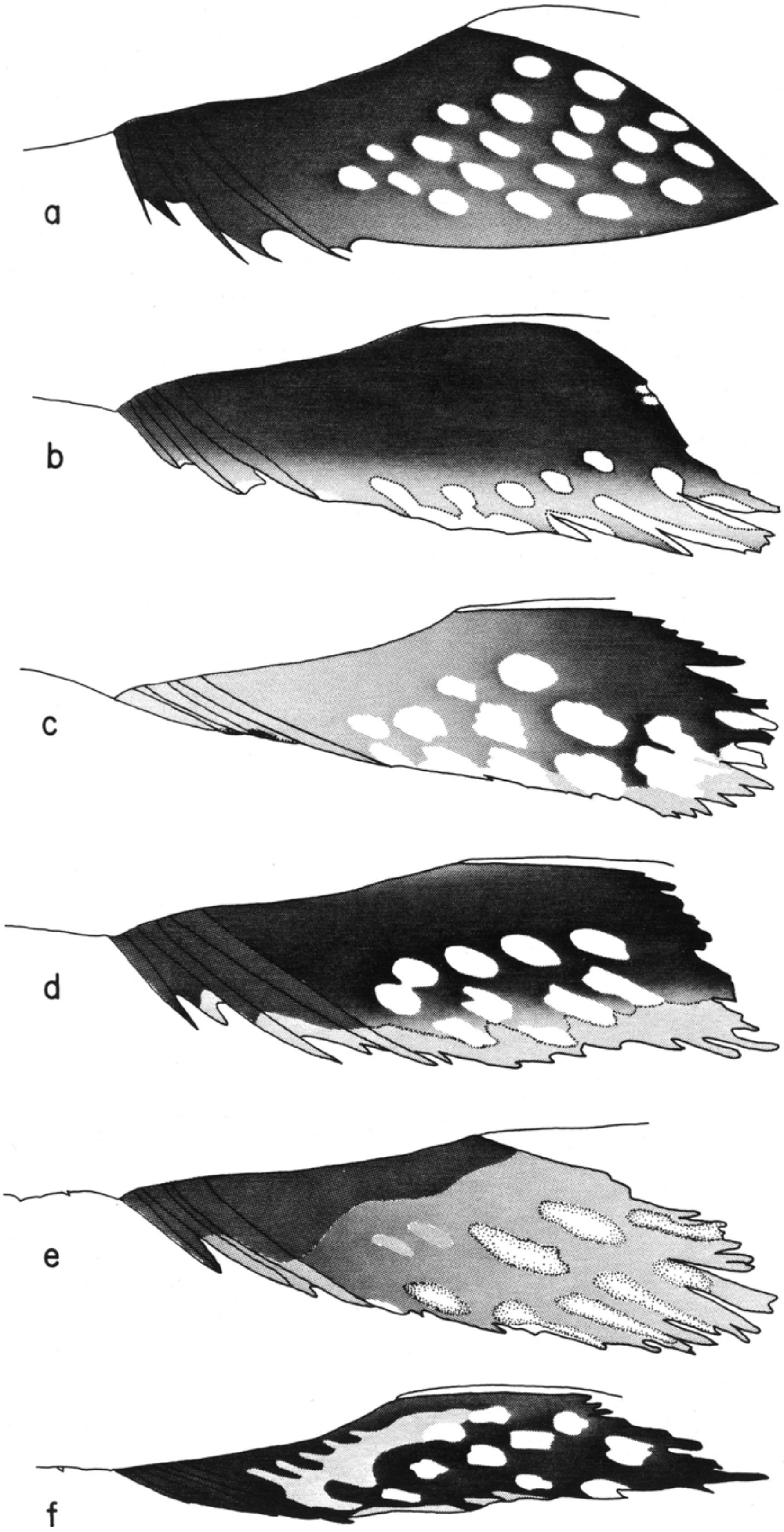
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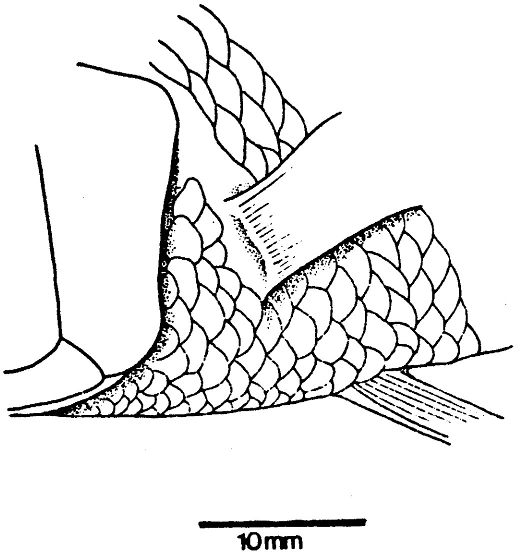
Figure 23. Thoracic-abdominal scale transition in some non-Malawian haplochromines, in left lateral view. a, *Astatotilapia nubila*; b, *Thoracochromis wingatii*; c, *Orthochromis oligacanthus*. (From Greenwood, 1979, figs. 1, 2, 3.)

a



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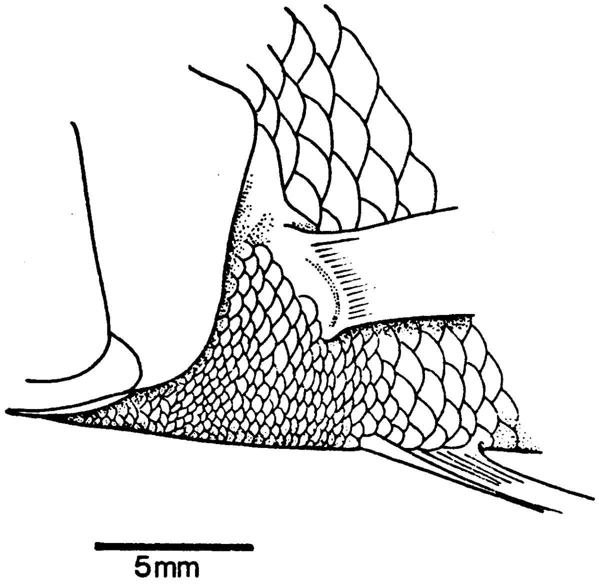


c

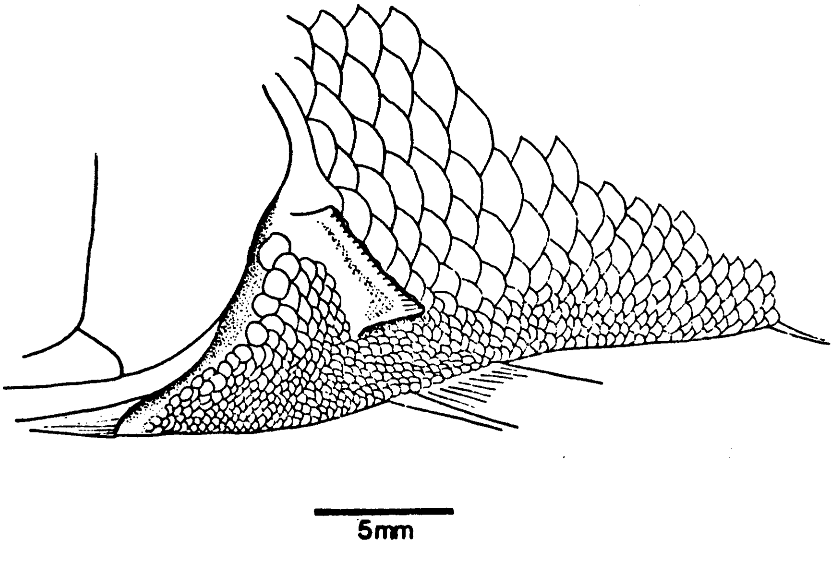
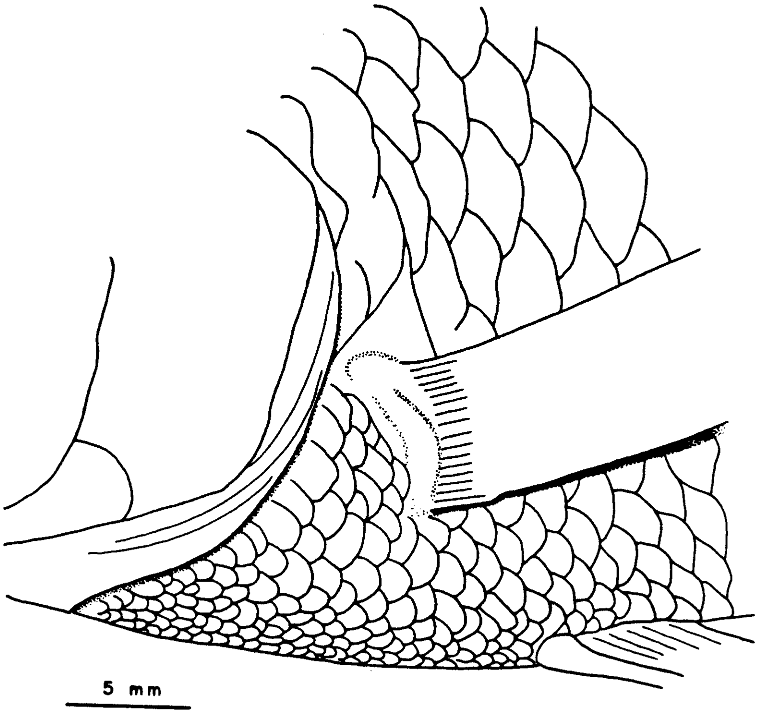


Figure 24. Thoracic-abdominal scale transition in Malawian haplochromines with ocellate anal fins, in left lateral view. Above, *Cyathochromis obliquidens*; below, *Pseudotropheus zebra* s. str. (BB morph).


5 mm

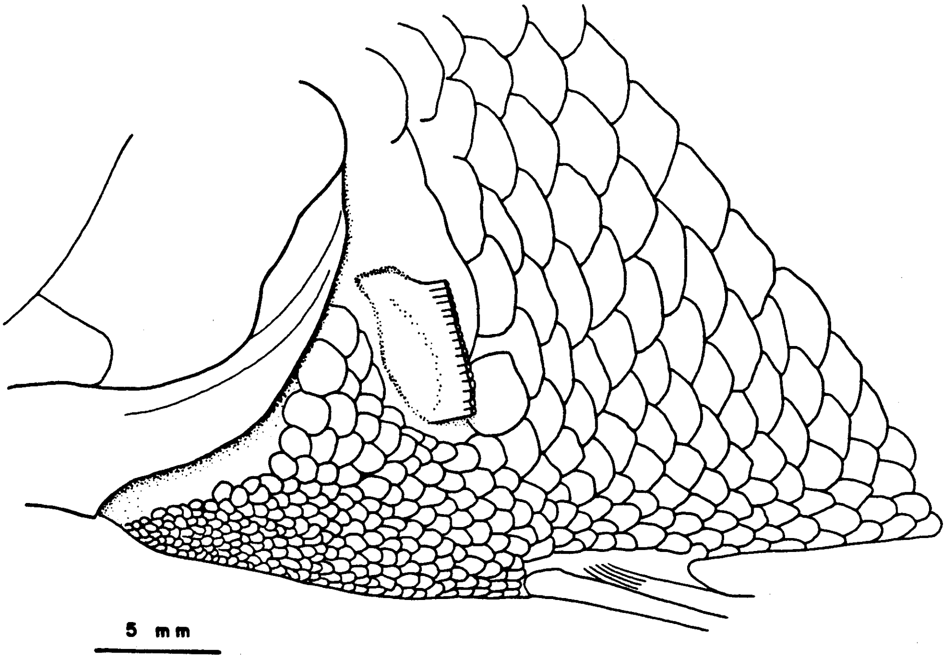

5 mm

Table 6.--Comparisons of the two Malawian haplochromine assemblages.

Attribute	Ocellate Malawian haplochromines	Nonocellate Malawian haplochromines
1. Included taxa	Nonendemic *Astatotilapia calliptera* Endemic The mbuna, i.e. *Cyathochromis*, *Cynotilapia*, *Genyochromis*, *Gephyrochromis*, *Iodotropheus*, *Labeotropheus*, *Labidochromis*, *Melanochromis*, *Petrotilapia*, *Pseudotropheus*	Nonendemic *Serranochromis r. robustus* Endemic *Aristochromis*, *Aulonocara*, *Chilotilapia*, *Corematodus*, *Cyrtocara* (=*Haplochromis* sensu Trewavas, 1935), *Diplotaxodon*, *Docimodus*, *Hemitilapia*, *Lethrinops*, *Lichnochromis*, *Rhamphochromis*, *Trematocranus*
2. Number of described endemic species	approx. 55	approx. 176
3. Conjectured proportion of total Malawian species in group described to date	40%	75%
4. Monophyly supported for all Malawian + extra-Malawian taxa of same anal-spot type?	Yes	No
5. Monophyly of Malawian component supported?	No	No
6. Nearest relatives of Malawian endemics	"Northern" haplochromines (ocellate riverine and Victoria-Edward-Kivu genera [Greenwood, 1979, 1980]) plus Lake Tanganyika genera *Simochromis*, *Pseudosimochromis*, *Tropheus*, and *Petrochromis*	Some or all "southern" haplochromines (*Serranochromis* and *Chetia* [Greenwood, 1979])
7. Largest reported total lengths of endemic species, in mm [mean ± SD (range, number of species)]	98.06 ± 26.33 (54-165, n = 39) (length data from Trewavas, 1935; Lewis, 1982)	190.22 ± 67.44 (53-430, n = 156) (length data from Trewavas, 1931, 1935; Iles, 1960)

Table 6 (continued)

	Attribute	Ocellate Malawian haplochromines	Nonocellate Malawian haplochromines
8.	Habitat	Rocky or intermediate rocky/sandy; only ca. 5 species on sand or mud	Sand, mud, soft bottom, or semipelagic; few species on rocks
9.	Trophic diversity (interspecific)	Moderate; primarily aufwuchs and small benthic invertebrates	Extremely high
10.	Morphological diversity (counts, proportions)	Moderate	High
11.	Population size (average)	Smaller?	Larger?
12.	Reproductive mode	Mouthbrooding	Mouthbrooding
13.	Clutch size	10-50 (Fryer, 1959: 255, 280) Fryer and Iles, 1972: 106; Kornfield, 1974: 30)	Larger (Fryer, 1959: 256; pers. obs.)
14.	Generation time (average)	Shorter?	Longer?
15.	Geographic variation in coloration	More common (Lewis, 1982: 261)	Less common
16.	Color polymorphism	Present in several genera, but ". . .The incidence of colour polymorphism in Lake Malawi has been exaggerated" (Lewis, 1982: 260)	Never reported
17.	Proposed speciation modes	Primarily intralacustrine allopatric (isolation in separate prior subbasins [Yairi, 1977], by stenotopy, and/or by distance); possibly sympatric in polymorphic species (differential depth or habitat preference by different color morphs)	Exclusively allopatric (isolation in separate prior subbasins, by stenotopy, and/or by distance)

CHAPTER 4

CHARACTERIZATION AND PHYLOGENY OF THE *CYRTOCARA LIVINGSTONII* SPECIES-GROUP FROM LAKE MALAWI, INCLUDING A NEW SPECIES WITH HYPERTROPHIED LIPS

INTRODUCTION

Specimens of the distinctive new cichlid species described below were first collected during the 1950's and 1960's by personnel of the Joint Fisheries Research Organization of Northern Rhodesia and Nyasaland (now the independent nations of Zambia and Malawi). During 1980 M. K. Oliver, K. R. McKaye, and T. D. Kocher made a large series of collections of Lake Malawi fishes for the Smithsonian Institution. These collections included a series of specimens of this new species from the Cape Maclear region of southern Lake Malawi, together with color photographs of live individuals, and limited ecological data on them. These materials form the basis of the present description of this endemic Lake Malawi cichlid.

If this new species had been described several years ago, it probably would have been assigned to the genus *Haplochromis*, an assemblage of several hundred nominal species of cichlids distributed throughout most of Africa but concentrated in lakes Victoria and Malawi. This "genus" consisted of species deemed insufficiently distinctive to be assigned to their own mono- or oligotypic genera under the principles of classic "evolutionary taxonomy" sensu Mayr (1969). However, dissatisfaction with the continued use of *Haplochromis* in this wide sense began to grow among some systematists during the 1970's. This dissatisfaction was prompted in part by increased acceptance of the principles of phylogenetic systematics ("cladism") as formulated by Hennig (1966) and modified by his followers. It became apparent that *Haplochromis* was not monophyletic, i.e., did not include all the descendants of a common ancestor. Greenwood (1979) restricted the genus *Haplochromis* to an apparently monophyletic group including the type species, *Chromis* (*Haplochromis*) *obliquidens* Hilgendorf, 1888, from Lake Victoria, and four other species from lakes Victoria, Nabugabo, Edward, George, and Kivu, East Africa. As a result, the more than 100 *Haplochromis* species already described from Lake Malawi became assignable to the next oldest available generic name with a type species from Lake Malawi, *Cyrtocara* Boulenger, 1902 (Greenwood, 1979). The type species of *Cyrtocara* is *C*. *moorii* Boulenger, 1902c. In specifying this replacement name, Greenwood (1979: 317) remarked: "Because it is obvious that the '*Haplochromis*' of Lake Malawi are a polyphyletic group, any generic placement at the present time must be considered merely a formal nomenclatural action unrelated to the phyletic affinities of the species." Further, Greenwood regarded *Cyrtocara* merely ". . .as a temporary formal name for the '*Haplochromis*' species of Lake Malawi. I thus propose that it be used in that capacity until the Malawi species are revised."

The present chapter is intended as a step toward a revision of the Lake Malawi haplochromines. The purposes of the chapter are: (1) to characterize a new species-group for the *Haplochromis livingstonii* group, which has been treated informally as a natural species group since the synopsis of Trewavas (1935) and is herein hypothesized to be monophyletic as now redefined. The taxonomic recognition of this unit as a new species-group is more precise and informative, and is therefore preferable, in my opinion, to the alternative of continuing to assign it simply to _Cyrtocara_, which is a large, nonmonophyletic genus; (2) to describe a new species in this group, distinguished in part by its strikingly enlarged lips; (3) to survey and illustrate certain external and osteologic features of members of this species-group; and (4) to present a cladistic analysis and classification of the species-group based on this information. Although I surveyed a wide variety of osteological, morphometric, meristic, and color characters, it became evident during my analysis that the species-group as a whole, and most of its subgroups, are defined primarily by characters of the color pattern. Remarkably, all of the previously described species in the group, with the exception of _C_. _maculimanus_ (Regan) and _C_. _pardalis_ (Trewavas), were illustrated in their original description or in a subsequent redescription. The original descriptions of the latter two species both mention that the pectoral fins are spotted. This unusual character is here hypothesized to be a synapomorphy of a subgroup of the _C_. _livingstonii_ species-group (see cladistic analysis, below). Its presence in _C_. _maculimanus_ and _C_. _pardalis_, therefore, is strong evidence that both nominal species are members of this monophyletic group. Since good published illustrations of the distinctive coloration or physiognomy of most of the species included in the group are available, taxonomic redescription of them is deferred to a later publication.

METHODS AND MATERIALS

Taxonomic counts and measurements, detailed in Chapter 5, are basically those defined by Greenwood (1973). Neurocranial measurements are also those of Greenwood (1979: 274; 1980b). Vertebral counts, made on cleared and counterstained as well as radiographed fishes, include the fused $PU_1 + U_1$ element which supports the parhypural and hypurals; my counts of total and of caudal vertebrae, therefore, are one greater than those of Greenwood (1973, 1979) who excludes this compound centrum.

Collections housing material examined are the American Museum of Natural History (AMNH), the Malawi Fisheries Research Unit at Monkey Bay (MFRU), and the U.S. National Museum of Natural History (USNM). Primary type material will be deposited in the USNM. Personnel of the former Joint Fisheries Research Organization of Northern Rhodesia and Nyasaland (JFRO) collected some of this material.

The specimens listed below were either cleared and counterstained (CC) for bone and cartilage by a slight modification of the procedure described by Dingerkus and Uhler (1977), or radiographed (R):

Cyrtocara fuscotaeniatus (Regan): USNM (4 specimens [CC], 77.5-88.0 mm standard length [SL]); AMNH 31805 (1 [R]); AMNH 31856 (1 [R]).

_C._ _johnstoni_ (Günther): USNM (2 [CC], 112.0-115.0 mm SL); AMNH 31775 (2 [R]); AMNH 31776 (1 [R]); material in collection of M. K. Oliver, field number MK068-VII-31 (1 [R]).

_C._ _linni_ (Burgess and Axelrod): USNM (1 [CC], 126.0 mm SL).

_C._ _livingstonii_ (Günther): USNM (3 [CC], 61.0-101.5 mm SL); AMNH 31777 (1 [R]); AMNH 31803 (5 [R]).

_C._ _milomo_, new species: USNM (2 paratypes [CC], 97.0-167.0 mm SL).

C. polystigma (Regan): USNM (3 [CC], 64.0-69.5 mm SL); USNM (1 [CC], 117.5 mm SL).

C. venustus (Boulenger): USNM (1 [CC], 119.0 mm SL); material in collection of M. K. Oliver, MK071-VII-14b (4 [R]).

In addition, I examined intact specimens of the above seven species during this study.

Cyrtocara maculimanus and *C. pardalis* are known to me only through their descriptions (Regan, 1921; Trewavas, 1935). *C.* sp. A is presently known only from color photographs, one of which is here reproduced as Fig. 27c.

The comparative osteologic material I consulted for outgroup comparison with the *C. livingstonii* species-group includes cleared and counterstained specimens of approximately 100 additional species of endemic Lake Malawi haplochromines, representing all 25 nominal genera, and similarly prepared material of some 20 species of non-Malawian haplochromine and nonhaplochromine cichlids. A detailed listing of this material will be given in future publications using that material. Intact preserved specimens of these and other Malawian and non-Malawian cichlids, as well as color transparencies of many haplochromines, were also consulted for data on external morphology and color patterns.

Standard cladistic methods were used to assess the ancestral or derived status of character states (Wiley, 1981). I attempted to employ both outgroup comparison and ontogenetic information in making such judgments of polarity. It may appear surprising that the data presented here exhibit no homoplasy. Undoubtedly, homoplasious features will be discovered, certainly among dental and meristic data, as the Malawian fauna is further studied. I derived the cladogram (Fig. 37) manually.

Subsequently, I used the WAGNER 78 program and found that it generates a Wagner tree with the same topology from these data.

The *Cyrtocara livingstonii* Species-Group, New Monophyletic Unit

Type species.--*Hemichromis livingstonii* Günther, 1893: 625 and Pl. 56B (=*Haplochromis livingstonii*).

Diagnosis.--The *C. livingstonii* species-group is distinguished from all other taxa of the haplochromine assemblage by a unique, derived suite of color patterns, here interpreted as a transformation series. Primitively within the group (but apomorphically with respect to other haplochromines), the color pattern of the body (Figs. 25c, 26a) consists of six prominent, dark, more or less vertical bars (five in exceptional specimens). (These markings may be masked by the overall dark ground color of sexually active males [Fig. 25a].) The first bar straddles the dorsal-fin origin and usually extends obliquely downward and backward to below the pectoral-fin base (exceptionally, this bar may extend ventrally only to above the operculum). Bars 2-6 are wider and more nearly vertical; bars 2-4 are placed below the dorsal-fin base and bars 5 and 6 are on the caudal peduncle. Thus, four bars are situated largely or entirely below the dorsal-fin base; in contrast, most other haplochromines have eight or more, narrower, fainter bars, six or more of them below the dorsal-fin base. The six basic (plesiomorphic) wide bars of the *C. livingstonii* group, as seen in *C. johnstoni* and *C. milomo*, are fragmented into disjunct spots in the more derived species (Figs. 26b, c, 27a, b; see cladistic analysis, below). These spots may be secondarily united to form interrupted or complete, wavy longitudinal stripes (Fig. 27c). (The relationships of *Cyrtocara fuscotaeniatus*, previously considered related to this group on the basis of its somewhat similar color pattern (Fig. 28), are considered below in a separate section.)

Individual and ontogenetic variation in the markings of species of the *C. livingstonii* species-group is shown in Figs. 29-31.

Description.--This section is provided to permit comparison of the *C. livingstonii* species-group with the generic descriptions in Greenwood's (1979, 1980b) reclassification of riverine and East African lacustrine haplochromines.

Size large; maximum adult size approx. 140 mm SL in *C. johnstoni*, 165-191 mm SL in the other eight nominal species. Eye nearly round. Reproductive mode is known for *C. johnstoni*, *C. livingstonii*, *C. polystigma*, and *C. linni*. These species are all female mouthbrooders.

Squamation. Scales ctenoid on flanks. Chest completely scaled. The anterior scales on the ventrolateral surfaces of the chest are small, but not minute or deeply embedded. The transition from these small anterior scales to the larger scales of the belly and flanks is gradual. In other words, the thoracic-abdominal scale transition in this species-group corresponds broadly with the type present in *Astatotilapia*, and particularly with the subtype present in the five species of *Astatotilapia* that have small chest scales (*A. flaviijosephi*, *A. desfontainesi*, *A. dolorosa*, *A. calliptera*, and *A. paludinosa*; see Greenwood, 1979: 270-271, 281; 1980a). Cheek fully scaled, with 2-5 horizontal scale rows. Lateral line with 31-33 (mode 32) scales in *C. johnstoni* and *C. milomo*, 32-35(-36) (modal range 33-34) in the other species of the species-group.

Neurocranium (Fig. 32). In most respects, the skull in members of this species-group resembles that of $Astatotilapia, which Greenwood (1979: 274, 282, fig. 6; 1980b: 8, fig. 4) considers the "generalized haplochromine type." However, the preotic length is greater (68%-71% of neurocranial length [NL], cf. 55%-60% in *Astatotilapia*). Greatest width across otic region (pterotics) 52%-59% of NL; preorbital skull depth approx. 23%-30% of NL; depth of orbit approx. 32%-39% of NL; depth of otic region approx. 45%-51% of NL except in *C. linni* (approx. 42%). Angle of preorbital profile approx. 40°-50°, except in *C. linni* (approx. 25°).

Ventral neurocranial apophysis for upper pharyngeal bones (Fig. 32b). Greenwood (1978: 317) examined specimens of *C. venustus*, *C. polystigma*, and *C. livingstonii* and found them to have apophyses of the *Haplochromis* type. I have confirmed this type in my cleared and counterstained material of these species, and also in that of *C. johnstoni*, *C. milomo*, and *C. linni* (and also in *C. fuscotaeniatus*).

Vertebrae: 30-32 (33 in single *C. linni* examined), comprising 13-15 precaudal and 16-18 caudal centra. The vertebral apophysis for the retractor dorsalis muscles is on the third vertebra.

Dentition: In *C. johnstoni* the outer teeth in both jaws apparently remain subequally bicuspid throughout life. In young fishes of all other members of this species-group some or all teeth are similarly bicuspid, but the definitive outer teeth in both jaws of adults are slender to robust unicuspids with incurved crowns. Such unicuspid teeth occur in most of these other species even in fishes smaller than the approx. 140 mm maximum SL of *C. johnstoni*, so the presence of unicuspids in these species is not caused simply by their larger maximum length.

(The definitive unicuspids predominate in individuals of *C. fuscotaeniatus* as small as 76.5 mm SL, the smallest available.) Inner teeth of all species unequally tricuspid in small fishes, unicuspid in adults.

Lower jaw (Fig. 33) not foreshortened, nor noticeably deepened posteriorly.

Upper jaw (Fig. 34) with premaxilla slightly beaked. Maxilla primitively with moderate curvature, apomorphically either more strongly curved or almost straight.

Lower pharyngeal bone and dentition: The dentigerous surface is triangular. In *C. johnstoni* and *C. milomo* (Fig. 35a, b) some posteromedian teeth are submolariform to molariform; in the former species the degree of enlargement of the crowns is, however, quite variable (Trewavas, 1935). In the remaining species of the *C. livingstonii* species-group, the bone is slightly narrower than in *C. johnstoni* and *C. milomo*, and all pharyngeal teeth are compressed and cuspidate (Fig. 35c). The bone is rather lightly built, even in the latter two species.

Gill arches (Fig. 36) similar in all species examined, and closely resembling those of other haplochromines.

Gill rakers 10-12(-13), except 13-15 in *C. milomo*.

Dorsal fin XV-XVIII, 9-11.

Anal fin III(-IV), 8-10. A single exceptional, four-spined individual of *C. milomo* is known.

Dorsal and anal fins with interradial rows of small basal scales (see also paragraph on fins under description of *C. milomo*, below.) I have confirmed the presence of such scales in all species of the species-group except *C. johnstoni*, *C. pardalis*, and *C. maculimanus*.

Caudal fin skeleton. The hypurals are unfused in 25 of 27 fishes examined, which represent all species except *C. pardalis* and *C. maculimanus*. The exceptional counts are from two of the six specimens of *C. johnstoni* examined, both of which have hypurals 3+4 fused. (The hypurals are also unfused in all six *C. fuscotaeniatus* examined.)

Caudal fin truncate to distinctly emarginate, never rounded; densely covered with small scales, nearly to end of fin in adults (pace Trewavas, 1949; see Relationships of the *C. livingstonii* Species-Group to Other Haplochromines, below).

Pelvic fin with the first branched ray longest.

Anal-fin markings in male fishes: Members of this group of species apparently lack true ocellar spots surrounded by translucent, depigmented rings, as defined by Greenwood (1979: 275). However, the nature of the anal spots in live, sexually active males of most species is unknown to me. *C. polystigma* and *C. linni* individuals of both sexes, whether juvenile or adult, have large, ovoid brown spots distributed throughout the anal fin (unless masked by overall dark pigment in mature males). Such spots, however, are quite distinct from the egg-dummies, which I have seen in a large, sexually active male of *C.* cf. *polystigma*. These markings (Fig. 22b) were smaller than the brown oval spots, and were yellow and ovoid, each with a narrow dark margin but lacking a clear surrounding ring.

Distribution.--The *C. livingstonii* species-group is endemic to the Lake Malawi basin. It would not be surprising if some of the species occur in the upper Shire River and in Lake Malombe, and perhaps even in the middle Shire.

Relationships of the *C. livingstonii* Species-Group to Other Haplochromines

The only previous hypothesis of which I am aware that specifies the phylogenetic relationships of the species here assigned to the *C. livingstonii* species-group sensu stricto is that of Trewavas (1949: 367). She stated: "Of the 100 species of *Haplochromis* [in Lake Malawi], the group related to *H. livingstonii* is perhaps nearest to *H. callipterus*, the caudal fin being but lightly and incompletely scaled, even in the adult, and either truncate or only slightly emarginate. Their dentition is more specialised and they feed on young fishes."[1] Trewavas (1949) did not specify the composition of this group, but it is presumably the same as that of group A in her synoptic key Trewavas, 1935: 81): *Haplochromis livingstonii*, *H. pardalis*, *H. polystigma*, *H. maculimanus*, *H. venustus*, and *H. fuscotaeniatus*. Although one recently described species (*Haplochromis linni*) has been added to this group, and although I suspect that the phylogenetic relationships of *C. fuscotaeniatus* lie outside the *C. livingstonii* species-group, this group A of Trewavas is otherwise coextensive with the latter species-group sensu stricto.

In her statements concerning the relationship of *H. callipterus* with the *H.* (= *C.*) *livingstonii* group, Trewavas implicitly recognized a morphocline (or two correlated morphoclines). Their stages would

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[1] Fryer and Iles (1972: 491) cited this hypothesis but diagrammed a modified, phylogenetically less specific version showing a "*Haplochromis callipterus*-like form" connected by a line with "*H. livingstonii* and allies," and the latter, in turn, connected with various specialized predatory species (Fryer and Iles, 1972: fig. 334). The caption of the figure describes it only as "An example of adaptive lines in L. Malawi. This may represent a phyletic diagram, but of the crudest kind."

progress phylogenetically from "caudal fin unscaled and slightly rounded" (the condition in _H_. _callipterus_), to "caudal lightly and incompletely scaled, and truncate or slightly emarginate" (in the _C_. _livingstonii_ group), and finally to "caudal completely scaled and emarginate" (in the remaining Malawian species of _Haplochromis_ sensu Trewavas). This hypothesis appeared quite reasonable, under the assumption that _H_. _callipterus_ was closely related to the endemic Malawian haplochromines ("_H_. _callipterus_ may well represent the ancestor of many [_Haplochromis_] species of Nyasa"; Trewavas, 1949: 367).

However, Greenwood (1979: 284) recently transferred _H_. _callipterus_ to the genus _Astatotilapia_ Pellegrin, which he concurrently removed from its long-standing synonymy with _Haplochromis_. As Greenwood redefined it, _Astatotilapia_ has no unique, derived characters, and so is not corroborated as monophyletic. It does, however, share one apparently derived character with the widespread haplochromine genera _Haplochromis_ sensu stricto, _Thoracochromis_, _Astatoreochromis_, the endemic Victoria-Edward-Kivu genera (Greenwood, 1980b), and the ten mbuna genera of Lake Malawi as well as several mbuna-like genera of Lake Tanganyika (see Chapter 3), but not with the _C_. _livingstonii_ species-group or the majority of other endemic Malawian haplochromines that I have seen alive. This synapomorphy is the presence of true, ocellar egg dummies in the anal fin of mature male fishes (Greenwood, 1979: 275). Thus, a close phylogenetic relationship between _Astatotilapia_ _calliptera_ and the endemic Malawian haplochromines that lack true anal ocellae, including the _C_. _livingstonii_ species-group, is refuted (see Chapter 3 for further discussion). The search for the sister group of this species-group sensu stricto must be directed elsewhere.

Even without this refutation of Trewavas' hypothesis, it is difficult to interpret confidently the two characters Trewavas advanced to support it. This difficulty stems partly from uncertainty about the taxonomic distribution of these characters, and partly from the inadequacy of higher-level hypotheses of the monophyly and interrelationships of haplochromines, and indeed of all African cichlids.

Concerning the fully scaled caudal fin supposed to characterize Malawian species of *Haplochromis*, Trewavas (1935: 66) quoted the original statement of Regan (1921: 686): "In the Nyassa species [of *Haplochromis* sensu Regan] the caudal fin is truncate or emarginate, and appears to be always nearly completely covered with small scales in the adult fish. . . ." She added (Trewavas, 1935: 66), "Even in young fish, although scales may be absent from the central part of the caudal fin, they extend along the upper and lower rays nearly to the end." Ontogenetic increase in the extent of caudal squamation, and the possibility of loss of caudal scales from preserved specimens, complicate assessment of the taxonomic distribution of this character. However, to judge from material I have examined, the caudal fin is scaled nearly to the ends of at least the uppermost and lowermost rays in adult fishes, not only of Malawian *Haplochromis* species sensu Trewavas, but also in all Malawian haplochromine genera (including the *C. livingstonii* species-group), and also in several cichlid genera of Lake Tanganyika. Moreover, the caudal fin is fully scaled in *Heterochromis multidens*, probably the most phylogenetically primitive African cichlid (see Chapter 2). Therefore, such a fully scaled caudal fin may prove to be primitive for African cichlids.

It is equally difficult to ascertain the phylogenetic significance of caudal-fin shape, the other character Trewavas advanced to support a close relationship between the taxa she referred to as *H. callipterus* and the *H. livingstonii* group. Even within the *C. livingstonii* species-group sensu stricto, the caudal fin varies in shape from truncate to distinctly emarginate. An equal (and, indeed, a greater) interspecific variation exists among the other Malawian species of *Haplochromis* sensu Trewavas. In some of these species the caudal fin is lunate or even nearly forked (but never rounded in any endemic Malawian haplochromine). Moreover, the primitive haplochromine caudal-fin shape is unknown. It is, then, premature to apply this character to problems of haplochromine interrelationships.

I propose, chiefly on the basis of the barlike blotches of *C. venustus*, that the blotches in members of the *C. livingstonii* species-group sensu stricto are derived from vertical bars. The available ontogenetic information on color pattern in members of this group is of little help in testing this hypothesis. The smallest specimens of the group that I have collected (*C. polystigma*, 28.5 mm SL, Fig. 31a; *C. livingstonii*, 37.8 mm SL, Fig. 30e) have blotches closely resembling those of conspecific adults. The same is true even for postlarval fishes within a few days of initial release from the mother's mouth (Jackson, 1961: 566, *C. livingstonii*; Bonnett, 1975: 55, photographs, and Mayland, 1982: 226-227, photograph, *C. polystigma*; *C. linni*, personal observations of several broods underwater in Lake Malawi). It would be valuable to know the color pattern of larval and young postlarval individuals of *C. venustus*, the *C. livingstonii*-group member with the most barlike blotches.

In contrast to Trewavas (1949), I suggest that her *Haplochromis livingstonii* group (approximately equal to the *C. livingstonii* species-group sensu stricto) is most closely related to other Malawian endemic species, i.e., *C. milomo* and *C. johnstoni* (see cladistic analysis, below). Because knowledge of the interrelationships of Malawian cichlids is still inadequate, I am unable to provide a corroborated hypothesis of the sister group of this species-group sensu lato. Judging by their color patterns, however, I suspect that the closest relatives of the species-group sensu lato may include *C. subocularis*, *C. ericotaenia*, *C. ornatus*, and possibly *C. rostratus* and *C. urotaenia*.

Included species

The *Cyrtocara livingstonii* species-group sensu stricto: *Hemichromis livingstonii* Günther, 1893: 625 (=*Haplochromis livingstonii*); *Haplochromis venustus* Boulenger, 1908: 241 (including *Haplochromis simulans* Regan, 1921: 689); *Haplochromis polystigma* Regan, 1921: 688; *Haplochromis maculimanus* Regan, 1921: 689; *Haplochromis pardalis* Trewavas, 1935: 89; *Haplochromis linni* Burgess and Axelrod, 1974: 36; and *Cyrtocara* sp. A (Figs. 27c, 30i). This species-group sensu lato includes the above 7 species and, in addition, the following two: *Chromis johnstoni* Günther, 1893: 622 (=*Haplochromis johnstoni*, including *Haplochromis sexfasciatus* Regan, 1921: 692); and *C. milomo*, new species.

Haplochromis fuscotaeniatus Regan, 1921: 696, formerly (Trewavas, 1935) classified with the *H. livingstonii* group, is not demonstrably related to this species-group on present evidence (see below). It is herein provisionally placed in the genus *Cyrtocara*, but its generic or infrageneric placement is likely to change when a revision of the

Malawian haplochromines yields data supporting a hypothesis of the actual relationships of this species.

Cyrtocara milomo, new species

Figs. 25, 29d-f, 32, 33c, 34c, 35b, 37, Table 7

Holotype.--USNM, a sexually active male 162.0 mm standard length (SL), field collection no. MKO-80-117, collected 13-14 August 1980 by M. K. Oliver, K. R. McKaye, and T. D. Kocher with trammel nets set overnight in 16-36 m depth, on a submerged rocky reef approx. 100 m S of the SE corner of Thumbi Island West, Lake Malawi, Malawi (14°01'25"S, 34°49'25" E).

Paratypes.--All from the Malawi shore of Lake Malawi. 1 specimen, USNM, 117.0 mm SL, MKO-80-37, 26-27 June 1980, same locality and collectors as holotype, trammel nets, depth 11-18 m; 1 specimen, USNM, 106.5 mm SL, MKO-80-64, 11-12 July 1980, same locality and collectors as holotype, trammel nets, depth 14-36 m; 1 specimen, USNM, 90.0 mm SL, MKO-80-66, 12-13 July 1980, same collectors as holotype, 200 m off E shore Thumbi Island West (approx. 14°01'S, 34°49'E), trammel nets, depth 30-50 m; 2 specimens, USNM, 97.0-167.0 mm SL (both fishes cleared and counterstained for bone and cartilage after examination), MKO-80-128, 18 August 1980, same collectors as holotype, 30 m off SE corner Thumbi Island West (14°01'22"S, 34°49'25"E), chased into block nets with SCUBA, depth 9 m; 1 specimen, USNM?, 187.0 mm SL, during or prior to 1968, JFRO, Nankumba Peninsula at Zambo Bay (approx. 14°03'S, 34°55'E), gill nets; 1 specimen, MFRU uncatalogued, 137.0 mm SL, 18 January 1969, JFRO personnel, same locality as USNM?, gill nets; 1 specimen, MFRU uncatalogued, 137.0 mm SL, 22-23 May 1963, JFRO personnel, Nkhata Bay at Chindozwa (approx. 11°36'S, 34°18'E), gill nets.

Diagnosis.--*C. milomo* can be distinguished from all other members of the *C. livingstonii* species-group by the hypertrophied, medially lobed lips. Of the other cichlid species in the Malawian fauna with enlarged lips, *Melanochromis labrosus* has 7 or 8 faint bars below dorsal-fin base, and minute scales on chest and nape (cf. 4 subdorsal bars, and thoracic and nuchal scales not minute in *C. milomo*); *Cyrtocara euchilus* and *Chilotilapia rhoadesii* have 2 or 3 broad, horizontal stripes but no bars (cf. 4 subdorsal bars but no stripes in *C. milomo*); *C. ornatus*, *C. lobochilus*, and *C. festivus* have lips less enlarged, and have 5 or more faint subdorsal bars that do not extend into dorsal fin and that alternate with spots on upper half of body (cf. lips greatly enlarged with conspicuous median lobes, and 4 subdorsal bars that are usually solid, at least 3 of them extending into dorsal fin in fishes <120 mm SL, in *C. milomo*; *Hemitilapia labifer* has the lips scarcely thickened and not lobate, and has 2 spots on the back and approx. 7 faint subdorsal bars.

In addition to the distinctive lips, *C. milomo* has the most strongly curved maxilla and the shortest and deepest dentary of any *C. livingstonii* species-group member. Also, the only member of the species-group sharing the 5-6 complete vertical bars of *C. milomo* is *C. johnstoni*; the two are distinguished in couplet 2 of the Key.

Description.--Based on 9 specimens, 90-187 mm SL. (Numbers in parentheses are of examined specimens having a given count. Asterisk denotes value for holotype.) Dorsal-fin spines and segmented rays XVI,10 (1), XVII,10* (6), XVIII,9 (1), XVIII,10 (1); anal-fin spines and segmented rays III,9 (6), III,10* (2), IV,9 (1). Lateral-line scales 31 (2), 32* (4), 33 (3); upper part with 22 (2), 23 (1), 25* (4), 26 (2); lower part[2] with 11 (1), 12 (1), 13 (2), 14 (1), 15 (2), 16* (1); lateral-line scales on caudal fin 0 (2), 1 (2), 2 (4), 3* (1). Transverse scales from dorsal-fin origin to lateral line 5* (5), 6 (4); predorsal scales 15* (5), 16 (1), 17 (1); prepelvic scales 18 (1), 19 (1), 20 (3), 21* (1), 22 (1); scales between pectoral- and pelvic-fin bases 5 (1), 6 (2), 8* (6); belly scales between pelvic-fin spine and anal-fin origin approx. 24 (2); scale rows on cheek 2 (1), 3* (4), 4 (3), 5 (1); scales around caudal peduncle 16* (8). Gill rakers on outer arch 4* (6), 5 (3) + 1* + 13 (4), 14* (4), 15 (1); rakers simple, tips acute in fishes <120 mm SL; posterior rakers frequently bifid, trifid, spatulate, or anvil-shaped in larger specimens. Vertebrae 14 + 16 (1) or 15 + 16 (1). Hypurals unfused (2).

Morphometrics. (Expressed as thousandths of standard length [SL] or head length [HL]. For each ratio, the range, mean ± standard deviation, and number of specimens are given. See also Table 6 for regression analyses of key morphometric ratios.) Reaching approx. 190

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[2] The 106.5-mm SL fish has irregular rows of scales on both sides of the caudal peduncle, perhaps caused by an injury. On left side, upper part of lateral line has 22 normal scales, lower part has scales of reduced size and irregular placement, but bearing normal canals. On right side, upper part has 21 scales but lower part is absent, none of the scales having lateral-line pores or canals. A similar abnormality of the lateral line, but involving no apparent injury, was reported for an individual of Labidochromis (Oliver, 1975).

mm SL. In SL: Head length 366-427 (396*) ($\bar{x}$ = 393.9 ± 18.9, n = 9); body depth 374-425 (422*) ($\bar{x}$ = 403.3 ± 19.0, n = 9); predorsal length 399-457 (430*) ($\bar{x}$ = 421.3 ± 17.9, n = 9); prepelvic length 437-492 (442*) ($\bar{x}$ = 459.1 ± 21.2, n = 7); belly length 273*-284 ($\bar{x}$ = 281.0 ± 3.7, n = 7); dorsal-fin base length 511-550* ($\bar{x}$ = 534.8 ± 12.5, n = 9); total dorsal-fin length 632-717 (686*) ($\bar{x}$ = 672.0 ± 31.1, n = 7); last dorsal-fin spine 120*-166 ($\bar{x}$ = 142.1 ± 14.5, n = 9); anal-fin base length 177-201* ($\bar{x}$ = 188.1 ± 8.0, n = 7); total anal-fin length 281-365 (356*) ($\bar{x}$ = 331.4 ± 32.2, n = 7); last anal-fin spine 110*-168 ($\bar{x}$ = 135.3 ± 20.6, n = 9); caudal-peduncle length 113-159 (128*) ($\bar{x}$ = 135.1 ± 14.4, n = 9); caudal-peduncle length/depth 0.84-1.22 (0.95*) ($\bar{x}$ = 1.01 ± 0.13, n = 9); pectoral-fin length 314-377 (331*) ($\bar{x}$ = 341.0 ± 23.0, n = 9); pelvic-fin length 237-349 (331*) ($\bar{x}$ = 296.8 ± 36.9, n = 9, relatively longest in large, sexually active males); caudal-fin length 212-246 ($\bar{x}$ = 229.5 ± 18.0, n = 4).

In HL: Head width 410-444 (428*) ($\bar{x}$ = 428.6 ± 10.7, n = 9); snout length 362-433* ($\bar{x}$ = 398.9 ± 21.6, n = 9); snout width 299-358 (324*) ($\bar{x}$ = 329.3 ± 21.6, n = 9); orbit length 213*-287 ($\bar{x}$ = 243.9 ± 25.5, n = 9); preorbital depth 186-233 (218*) ($\bar{x}$ = 207.4 ± 13.4, n = 9); interorbital width 225-283 (274*) ($\bar{x}$ = 248.9 ± 20.1, n = 9); postorbital head length 364-417 (377*) ($\bar{x}$ = 379.8 ± 17.4, n = 9); cheek depth 196-269 (257*) ($\bar{x}$ = 232.0 ± 25.0, n = 9); upper-jaw length 319-374 (336*) ($\bar{x}$ = 341.1 ± 20.8, n = 9); premaxillary ascending processes 359-393 (363*) ($\bar{x}$ = 368.2 ± 11.4, n = 9); lower-jaw length 420-467 (461*) ($\bar{x}$ = 450.4 ± 15.0, n = 9); lower-jaw length/width 1.43-1.85 (1.44*) ($\bar{x}$ = 1.57 ± 0.16, n = 9); pharyngeal-bone length 208-238 (235*) ($\bar{x}$ = 227.5 ± 11.6, n = 6); pharyngeal-bone width 252-284 (254*) ($\bar{x}$ = 267.0 ± 12.8, n = 7).

Body moderately deep and compressed. Dorsal profile more pronounced than ventral. Ventral profile irregularly curved from chin to anus. Dorsal head profile convexly curved over premaxillary ascending processes (producing bulge in profile), concave over orbit, convex along nape. Orbit approx. one-third eye depth below frontal profile in lateral view. Eye virtually round. Snout angle 30°-40° to horizontal; frontal angle (above orbit) 35°-50°; nuchal angle 15°-25° (these angles not correlated with SL). Jaws (i.e., lips) narrowly rounded anteriorly in dorsal view. Gape somewhat oblique; ventral profile of lower jaw inclined at 25°-45° to horizontal (not correlated with SL). Lower jaw projecting. Chin strong, with distinct ventral protuberance (Fig. 33c), hidden by lobe of lower lip. Premaxillae very slightly beaked (Fig. 34c), although projection hidden by lobe of upper lip. Posterior tip of maxilla reaching about midway between verticals through nostril and anterior edge of eye. Lips greatly thickened, papillose, each produced into a single conspicuous median lobe. Length of each lobe (measured from origin at jaw symphysis to tip of lobe) equals or exceeds orbit length and shows positive allometry with standard length. Upper and lower lip folds continuous across premaxillary and dentary symphyses respectively, not interrupted anteriorly. Cephalic lateral-line pores and canals not hypertrophied.

Caudal fin emarginate, lobes damaged in most specimens; densely scaled nearly to end of fin. Dorsal fin with rows of 2-8 small scales extending from body onto fin membrane parallel to rays; 1 or 2 such rows occur for each ray in region of posterior spines and anterior segmented rays. Anal fin with similar rows of 1-12 scales on fin membrane between first segmented ray and approximately penultimate ray.[3] Pectorals lanceolate. Pelvics with first ray slightly produced in mature males.

Teeth in outer row of each jaw (Figs. 33c, 34c) buried to crown in thickened oral mucosa; teeth robust, closely spaced (especially posteriorly), slightly movable; crowns not much compressed, somewhat incurved. Anterior teeth of upper jaw somewhat enlarged relative to lateral teeth; posterior teeth also slightly larger than lateral teeth. In fishes <120 mm SL, unequally or weakly bicuspids predominate in both jaws, at least anteriorly; posterior teeth tend to be unicuspids with conic crowns, or a mixture of such unicuspids and weakly bicuspids. In fishes approx. 135 mm SL unicuspids predominate over bicuspids. In fishes >160 mm SL all teeth are unicuspids. Number of teeth in outer row of upper jaw 44-73 ($\bar{x} = 59.9 \pm 11.6$, $n = 7$; positively correlated with SL, $r = 0.927$, $p<0.01$; number of teeth = $[0.317 \pm 0.057]SL + [17.267 \pm 7.922]$; intercept not significantly different from 0).

Inner teeth in 2-5 rows anteriorly in upper jaw, 1-4 rows in lower jaw; rows separated from outer teeth by a distinct gap laterally, gap narrower anteriorly. Crowns unequally tricuspid in smaller fishes; unicuspid, miniatures of outer teeth, in fishes >135 mm SL.

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[3] These basal scales on the dorsal and anal fins closely resemble those described by Greenwood (1973: 206, fig. 31; 1980b: 13) for a haplochromine cichlid from Lakes Edward and George, *Harpagochromis squamipinnis* (Regan). Although Greenwood (1980b: 13) considered *H. squamipinnis* to be unique among haplochromine species in having these dorsal and anal scales, such scales are present in several Malawian haplochromines, including both described and undescribed species (unpubl. observations). In *C. milomo* the scaled area of the dorsal fin begins more posteriorly (at approx. the fourteenth spine, cf. fourth to eleventh spine in *H. squamipinnis*) and ends more anteriorly (scales lacking between last few dorsal and anal segmented rays, cf. most frequently present along entire soft part of dorsal and anal fins in *H. squamipinnis*).

Lower pharyngeal bone (Fig. 35b) triangular, posterior edge straight or very slightly concave; bone moderately wide (1.08*-1.26, $\bar{x}$ = 1.17 ± 0.06 times wider than long, n = 6), rather robustly built. Joint uniting halves of bone straight or finely sinuous in ventral view. Anterior blade moderately deep, slightly decurved relative to plane of dentigerous surface. Dentigerous area 1.38*-1.55 ($\bar{x}$ = 1.46 ± 0.06, n = 7) times wider than long. Pharyngeal teeth mostly small, compressed, cuspidate; a group of approx. 8-22 enlarged teeth posteromedially, some of them submolariform, usually bearing a central cusp that is sometimes broken; 29*-44 ($\bar{x}$ = 33.4 ± 5.0, n = 7) teeth in posterior row, 8-13 (9*-10*) in median column, 6-8 (6*-7*) in oblique posteromedian to midlateral row, 24-28 along lateral edge.

Coloration.--The live holotype, a sexually active male 162 mm SL (Fig. 25a, b): Head blackish, overlaid with purple to blue except on lips and dorsal head surfaces. Lips dark gray, becoming lighter gray on oral surfaces. Branchiostegal membrane black. Iris of eye dusky with narrow, golden inner ring. An indistinct, wide dark bar on nape above operculum. Body with nape purplish, flank appearing predominantly orange, each scale being orange on anterior half of exposed part, iridescent blue-green to purple on posterior part. Chest colored like flank but with dusky overlay. Four wide, faint vertical bars below base of dorsal fin, not entering fin; a fifth on caudal peduncle. Fins: Dorsal iridescent purplish anteriorly with dark-edged orange maculae, more distinct in soft part of fin; fin becoming dusky submarginally; lappets of spinous part white proximally with orange tips; soft part of fin with narrow orange margin. Anal uniformly dusky with no distinct markings; fin narrowly edged with orange below. Caudal orange basally, remainder of fin grayish with orange maculae and vermiculations. Pelvics uniformly dusky, with narrow, white leading edges distally. Pectorals unspotted; rays black, membrane clear, colorless.

A live, quiescent female, 117 mm SL (Figs. 25c, 29e): Head and body pewter gray; lower lip paler than upper; iris of eye as described for male; a gray lacrimal stripe from eye to corner of mouth; a gray stripe across lower interorbital region; a black vertical bar (about as wide as pupil of eye) across top of head at level of posterior margin of orbit; another, wider black bar from midline of nape to above posterior edge of operculum, curving behind operculum and extending to behind pectoral-fin base. Four prominent black bars (wider than interspaces) below dorsal fin: the first from within anterior part of dorsal fin to pelvic-fin base, becoming much narrower ventrally and merging with continuation of nuchal bar behind pectoral-fin base; the second from basal third of dorsal fin to ventral midline of belly, curving backward slightly on its lower half; the third from basal third of dorsal fin at level of posterior spines and anterior segmented rays, obliquely downward and forward to upper lateral-line segment, then straight down to anal-fin origin; the fourth originating on basal half of posterior five dorsal rays, widening on body, and extending ventrally to posterior half of anal-fin base. Another black vertical bar at end of caudal peduncle, extending posteriorly as a blotch on base of caudal fin. Fins: Dorsal gray with tips of lappets narrowly edged with orange; soft part of fin with uniformly gray maculae. Anal gray. Caudal gray posterior to basal blotch, with darker maculae between rays. Pelvics dusky. Pectorals clear.

Preserved, the 117-mm quiescent female is unchanged except that the pewter ground color of head and body is light brown. The 162-mm sexually active male is uniformly blackish brown with slightly darker bars.

Individual variation in shape of body bars is considerable (Fig. 29d-f); some bars may be incomplete dorsally, much as in *C. venustus* (cf. Figs. 29d and 30a-d). The presence of four bars (or partial bars) below the dorsal-fin base is, however, invariable in the available *C. milomo* specimens.

Ontogenetic change in color pattern involves a withdrawal of the upper ends of the four subdorsal bars from the dorsal fin in large fishes (cf. Fig. 29e, f).

Distribution.--*Cyrtocara milomo* is known only from the Malawi shore of Lake Malawi. It has been collected at Nkhata Bay in the central part of the western shore, and in the south along the Nankumba Peninsula from Thumbi Island West to Zambo in the southeast arm.

Ecology.--*C. milomo*, a moderately common species from rocky shores, has been collected in depths ranging from 9 m to more than 30 m. I examined the guts of four fishes 90-167 mm SL. Three contained only fragmented insect larvae. The fourth contained several dozen whole ostracods as well as a few fragments of insect larvae and some diatoms. These meager data suggest that *C. milomo* feeds on small, benthic invertebrates. If so, it attains a larger size than most other insectivorous cichlids. Feeding has not been observed, so the function of the greatly enlarged, papillose lips remains speculative. They may be primarily sensory, being slowly pressed against the rocks to enable the tactile detection of small prey organisms, as Fryer (1959a: 185; Fryer and Iles, 1972: 81) described for the Malawian species *C.*

euchilus. Alternatively, perhaps the lips of *C. milomo* act as mechanical shock absorbers if the head is rapidly hit against rocks in feeding. Greenwood (1974: 31) postulated such a function for the thickened lips of *Paralabidochromis chilotes*, a haplochromine from Lake Victoria. A third, and quite plausible, hypothesis is that the soft, fleshy lips of *C. milomo* are molded to the irregularities of the rock when the narrow mouth is pressed into a crevice. Thus, the lips would form a seal against the crevice, permitting the fish to suck out small invertebrates (L. W. Buss, pers. comm.). These competing hypotheses are amenable to testing in the field and in the laboratory.

Etymology.--The specific name *milomo* (pronounced mĭ-lō'mō) is from the Chichewa word meaning lips and refers to the greatly hypertrophied, lobate lips in fishes of this species. *Milomo* is the nominative plural form (singular *mlomo*) of a second-class noun (Salaun, 1978). However, for nomenclatural purposes *milomo* is treated as a nominative singular standing in apposition to the generic name. This Chichewa word is not used as the fish's name by Malawians.

The Chichewa name *kawizuwizu* (pronounced ka-wē'zoo-wē"zoo) is employed for this species at Chembe, Malawi. This word also refers to the enlarged lips (J. B. Smart, pers. comm.).

Key to the Species of the *Cyrtocara livingstonii* Species-Group

1A. Color pattern of body consisting primarily of 5 or 6 vertical bars, usually 4 below base of dorsal fin and 2 on caudal peduncle; bars usually not broken into separate spots or, if partly broken, then lips hypertrophied and lobate; lower pharyngeal bone with some posteromedian teeth submolariform to molariform; diet omnivorous or insectivorous 2

1B. Color pattern not as above; lips normal; lower pharyngeal teeth all cuspidate, none with rounded, submolariform or moloriform crowns; diet piscivorous 3

2A. Lips normal, not thickened or medially lobate; gill rakers 10-12 on lower outer arch; premaxillary symphysis pointed; habitat sandy shores with weed beds .... *C. johnstoni*

2B. Lips hypertrophied, each with a conspicuous median lobe; gill rakers 13-15 on lower outer arch; premaxillary symphysis blunt; habitat rocky .... *C. milomo*

3A. Pectoral fin with small dark spots 4

3B. Pectoral fin unspotted 6

4A. Color pattern of body consisting of interconnecting dark blotches on pale ground, without additional small dark spots on head or on body scales; predatory behavior of adults >120 mm SL includes shamming death by lying motionless on side on substrate .... *C. livingstonii*

4B. Color pattern of head and body including small dark frecklelike spots, one on each scale of body, in addition to various larger dark markings; predatory behavior does not include shamming death, or is unknown 5

5A. Snout long, mouth subterminal; posterior ends of premaxillary ascending processes seen as a conspicuous bulge on snout when fish is viewed laterally; premaxillary ascending processes longer than alveolar processes; dentary dorsoventrally flattened; mesopterygoid elongate; palatine elongate, its length more than twice its height .... *C. linni*

5B. Snout moderate, mouth terminal; premaxillary ascending processes not bulging when fish is viewed laterally; premaxillary alveolar and ascending processes subequal; dentary not flattened; mesopterygoid of subequal height and length; length of palatine less than twice its height .... *C. polystigma*; ?also *C. pardalis* and *C. maculimanus*

6A. Dark markings on ventral half of body including discrete blotches or spots and lower ends of irregular vertical bars; ventral half of caudal fin plain yellow in living fishes except adult males; living, sexually active males with a blaze of sulphur yellow on midline of nape; dentary, viewed laterally, tapering to shallow depth at symphysis; anterior dentary teeth procumbent .... *C. venustus*

6B. Dark markings absent on ventral half of body, or consisting of a faint longitudinal stripe; ventral half of caudal fin not yellow in living fishes; nuchal coloration of sexually active males unknown; dentary symphysis blunt in lateral view; anterior dentary teeth erect, crowns incurved .... (*C. fuscotaeniatus*)

Cladistic Analysis of the *C. livingstonii* Species-Group (Fig. 37)

The *C. livingstonii* species-group sensu lato (Fig. 37, node A), is characterized as monophyletic by a single hypothesized synapomorphy (shared, derived character):

1. Color pattern of body consisting primarily of six broad, vertical bars, four of them situated partly or entirely below the dorsal-fin base (Figs. 25c, 26a, 29a-e).

This condition represents a reduction from the apparent primitive number of bars in haplochromines (approx. 7-10), as well as an increase in the relative width and intensity of each bar (see Diagnosis of the species-group, above). In exceptional individuals, the number of bars on the body is further reduced to five (Fig. 29f).

The basic derived character of the color pattern described above is, I hypothesize, phylogenetically further modified within subsets of the species-group as described below (characters 6-9).

Within the group, the following synapomorphies suggest that all species except *C. johnstoni* form a monophyletic subunit (Fig. 37, node B):

2. Lower pharyngeal bone widened (cf. Fig. 35b, c with Fig. 35a).
3. Definitive adult jaw teeth unicuspid (attained in fishes <120 mm SL in most species).
4. Maximum adult size increased from approx. 140 mm SL to at least 165 mm SL.

An additional character within node B merits comment here but is not counted as a synapomorphy since its presence in one species is subject to individual variation: Vertical bars on body somewhat broken or dorsally incomplete in some specimens of *C. milomo* (Fig. 29d) and invariably broken into spots in the remaining species (see character 6).

Within node B, all species except *C. milomo* comprise a monophyletic group (Fig. 37, node C: the *C. livingstonii* species-group sensu stricto) characterized by the following synapomorphies:

5. Pharyngeal teeth (Fig. 35c) all compressed, cuspidate, the posteromedian teeth never having rounded, submolariform to molariform crowns; associated with shift to a primarily piscivorous diet.
6. Some bars on flanks invariably broken into oblique series of 2 or 3 blotches (Figs. 26b, 30a-d).

Within node C, all species except *C. venustus* form a monophyletic subgroup (Fig. 37, node D) characterized by the following synapomorphy:

7. Pectoral-fin rays with small dark spots (Figs. 26c, 27a-c).

Although I have not examined the unique holotypes of the nominal species *C. pardalis* and *C. maculimanus*, their original descriptions mention that they have small spots on the pectoral fins. Indeed, the latter species is named for this feature. The presence of spotted pectorals is, I think, unique to node D among cichlids and very unusual among teleosts.

Within node D, at least *C. pardalis*, *C. polystigma*, and *C. linni* constitute a monophyletic subgroup (Fig. 37, node D: the *C. polystigma* species subgroup) characterized by a synapomorphy which is definitely absent in *C. livingstonii*. This synapomorphy is:

8. Body and head with small dark "freckles" superimposed on the pattern of blotches, the freckles distributed one to

each scale over most of the body (Figs. 27a, b). Freckles may be indistinct in sexually active males.

Trewavas (1935: 89) reported the presence of these freckles in *C. pardalis* ("This [holotype] shows the basic colour pattern of *H. livingstonii* with the spotting of *H. polystigma*. . . ."). It is uncertain if these freckles are present in *C. maculimanus* and *C.* species A (Fig. 27c).

Within node E, a further synapomorphy (Fig. 37, character 9) is shared by at least *C. polystigma* and *C. linni*. Its occurrence in *C. pardalis*, *C. maculimanus*, and *C.* sp. A is unknown at present, but it is known to be absent in *C. livingstonii*:

9. Pelvic fins with several distinct, brown oval spots (Fig. 27a; masked in breeding males).

Interestingly, most of the synapomorphies so far discovered in the *C. livingstonii* species-group, and described above, pertain to the color pattern. If the group were fossil, it might be impossible to infer its phylogeny. This contrasts strongly with the situation in most of the apparent lineages in Lake Malawi, in which a basic derived color pattern may define a group of some 20-30 species, but within which the synapomorphies are chiefly osteological (unpublished observations).

Autapomorphies in Species of the *C. livingstonii* Species-Group

The above characters are synapomorphies, or derived characters shared by two or more species and hypothesized to have arisen in their immediate common ancestor. In addition, this study uncovered or reexamined a number of derived characters that appear to be unique to particular members of the species-group, or that are most parsimoniously interpreted as independently derived within a particular member of the species-group and one or more species outside this group. These unique, derived characters (autapomorphies) of each species include the following (Fig. 37, characters 10-31):

C. johnstoni:

10. Premaxillary symphysis pointed (Fig. 34b).

Since the sister group of the species-group is still unknown, this character could prove to be more widely distributed.

C. milomo:

11. Lips greatly hypertrophied and medially lobate (Fig. 25).
12. Maxilla strongly curved (Fig. 34c).
13. Dentary short and deep (Fig. 33c).
14. Gill rakers on lower arm of outer arch increased to 13-15 (from a range of 10-12[-13]).

Hypertrophied lips are known in several other haplochromines. Within Lake Malawi, perhaps the most extreme hypertrophy outside that in *C. milomo* is found in "*Melanochromis*" *labrosus*, a member of the assemblage with ocellar anal-fin spots (the mbuna). Another Malawian species with enlarged lips is *Cyrtocara euchilus*, which is probably the sister species of the Malawian *Chilotilapia rhoadesii*, to judge from their shared specializations of the jaws and color pattern (Trewavas, 1935, and pers. obs.).

C. venustus:

15. Caudal fin (Fig. 26b) lacking the dark-edged, orange maculae that are primitively present in the species-group (see, e.g., Fig. 25c).
16. Ventral half of caudal fin yellow (this coloration masked

in adult males).

17. Breeding males with sulphur-yellow median blaze on nape.

18. Dentary, in lateral view, tapering anteriorly to shallow symphysis (Fig. 33d).

19. Anterior dentary teeth procumbent (Fig. 33d).

C. livingstonii:

20. Ground color chalky white in life (Fig. 26c, more apparent on original color transparency).

21. Distinctive feeding behavior, involving behavioral mimicry of a dead fish by dropping to substrate, lying motionless on side to lure small fishes as prey (Fryer and Iles, 1972; McKaye, 1981).

C. polystigma:

22. Maxilla nearly straight (Fig. 34f).

C. linni:

23. Snout elongate (Fig. 27b).

24. Mouth subterminal (Fig. 27b).

25. Dentary dorsoventrally flattened (Fig. 33g).

26. Ventral profile of retroarticular and anguloarticular forming an obtuse angle (instead of a straight line) with ventral profile of dentary (Fig. 33g).

27. Mesopterygoid much longer than deep (Fig. 33g).

28. Maxillary process of palatine elongate (Fig. 33g).

29. Premaxilla with ascending process longer than alveolar process, and angle between the two processes reduced (Fig. 34g).

30. Neurocranium elongate (reflected in reduced otic depth

and reduced angle of preorbital profile of skull).

31. Distinctive feeding behavior, involving ambush of small fishes from behind a rock with snout resting on top of rock.

Relationships of "Haplochromis" fuscotaeniatus

"Haplochromis" fuscotaeniatus Regan (Fig. 28) has been classified with the "H." (=Cyrtocara) livingstonii species-group since the synopsis of Trewavas (1935). There is certainly a resemblance in color pattern and physiognomy between that species and certain representatives of the C. livingstonii group, such as C. livingstonii itself. My reservations about including "H." fuscotaeniatus in this species-group stem from my difficulty in interpreting the color pattern of this species (Figs. 28, 29g-j) as part of the transformation series of color patterns that I hypothesize within the group. Specifically, the color pattern of "H." fuscotaeniatus appears to include elements derived from 7 or 8 vertical bars, apparently a plesiomorphic count (rather than the reduced number of 6, judged to be a synapomorphy of the C. livingstonii species-group). Also, "H." fuscotaeniatus has distinct elements of horizontal stripes. One, above the upper part of the lateral line, tends to be interrupted where it intersects vertical bars. Another, along the lateral body midline, intersects vertical elements but is quite straight between the intersections. A third stripe, which may be incomplete posteriorly, extends along the lower flank. This stripe may be more sinuous than the others but has straight segments. Stripes resembling, in position, at least the upper two of these are widespread among cichlids, and I therefore consider at least these two to be plesiomorphic within the

Malawian haplochromine assemblage. *C.* sp. A (Figs. 27c, 30i) also has horizontal stripes in these positions, but their wavy appearance suggests a secondary derivation from fused blotches. Moreover, *C.* sp. A shares a striking synapomorphy (spotted pectoral fins) with members of the *C. polystigma* species subgroup, and so is corroborated as a member of that subgroup. In contrast, I can find no derived character shared by "*H.*" *fuscotaeniatus* and any one or more species of the *C. livingstonii* species-group. The blotched, vaguely *C. livingstonii*-like color pattern of "*H.*" *fuscotaeniatus* seems best attributed to the intersection of plesiomorphic bars and stripes. Conversely, the blotched pattern in the *C. livingstonii* group sensu stricto is, I hypothesize, derived entirely from a reduced number of vertical bars. During the phylogenetic history of the group, these bars were first broken into distinct, vertically elongate spots. Within some species of node D the spots secondarily fused to become horizontally (and vertically) interconnected.

McKaye (1981) speculated that, like *C. livingstonii*, "*H.*" *fuscotaeniatus* may also feign death. However, he has not observed such behavior in the latter species. If he is correct, death-feigning behavior in "*H.*" *fuscotaeniatus* might be a synapomorphy with *C. livingstonii*. "*H.*" *fuscotaeniatus* should then be classified in the *C. livingstonii* species-group. However, if "*H.*" *fuscotaeniatus* were the actual sister species of *C. livingstonii*, this relationship would imply that it had secondarily lost the pectoral-fin spotting that characterizes node D (Fig. 37). Alternatively, if "*H.*" *fuscotaeniatus* were otherwise related within the species-group, the generality of death-feigning in this group would have to be reconsidered. Since "*H.*"

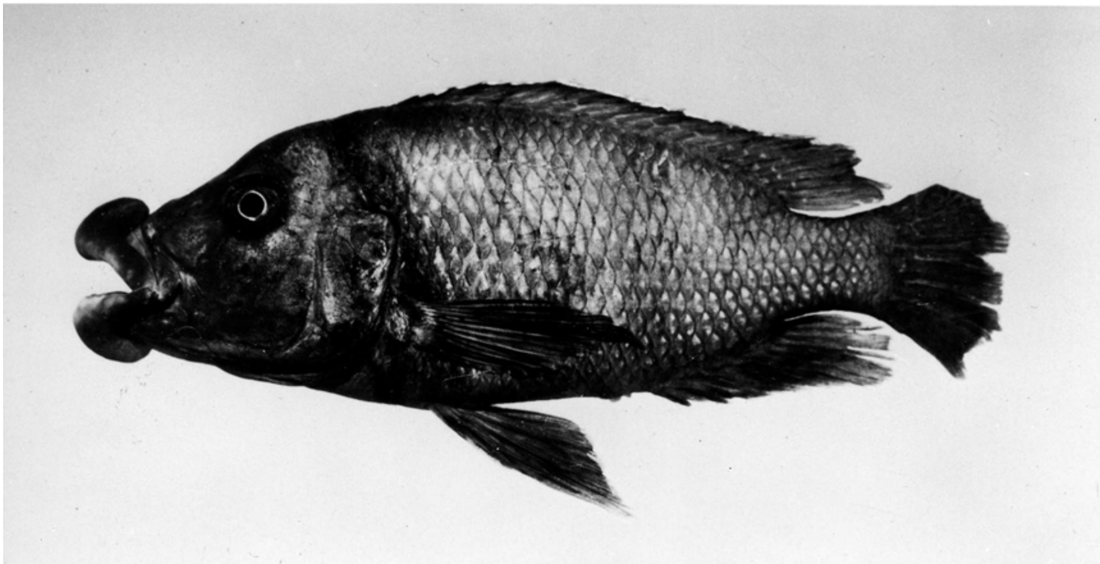
fuscotaeniatus has not been observed to feign death (not even during several 15-min behavioral watches in Lake Malawi devoted specifically to this species [P. Reinthal, pers. comm.]), and no other evidence suggests a relationship with the *C. livingstonii* unit, I classify this species provisionally in the gradal genus *Cyrtocara* Boulenger.

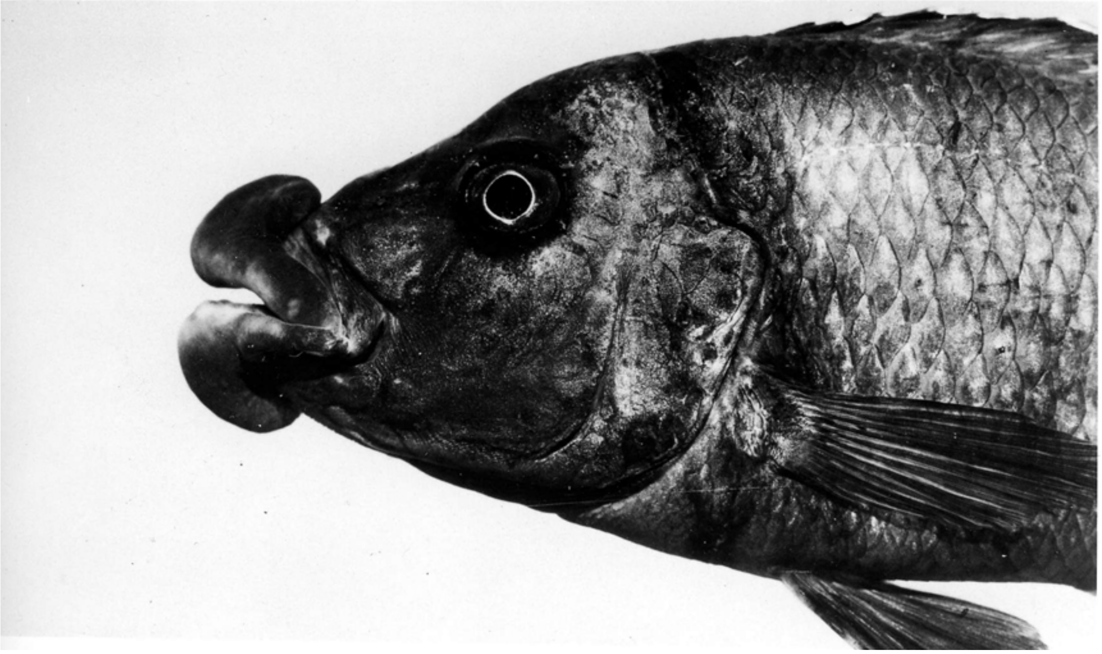
Classification of the *Cyrtocara livingstonii* Species-Group

The results of the above cladistic analysis are summarized in the following cladistic classification, which complements Fig. 37. This classification is annotated according to some of the conventions suggested by Wiley (1979, 1981). The members of a supraspecific taxon are subordinated beneath the name of that taxon. Taxa of the same rank that form successive dichotomies are sequenced. Thus, each species is to be understood as the sister group of all following taxa. The only exception to the sequencing convention in the following classification is that, within an inclusive taxon, all species annotated as "sedis mutabilis" form multiple furcations with each other on present evidence, and so are of interchangeable position.

- *Cyrtocara livingstonii* species-group, new, sensu lato
  - *C. johnstoni* (Günther, 1893)
  - *C. milomo*, new species
  - *C. livingstonii* species-group, sensu stricto
    - *C. venustus* (Boulenger, 1908)
    - *C. livingstonii* (Günther, 1893), sedis mutabilis
    - *C. maculimanus* (Regan, 1921), sedis mutabilis, species inquirenda
    - *C.* species A, sedis mutabilis
    - *C. polystigma* species subgroup (all species sedis mutabilis)
      - *C. pardalis* (Trewavas, 1935), species inquirenda
      - *C. polystigma* (Regan, 1921)
      - *C. linni* (Burgess and Axelrod, 1974)

Figure 25. *Cyrtocara milomo*, new species. a and b, live holotype (162 mm SL), a sexually active male. c, live paratype (117 mm SL, female); right side photographed and reversed. Cf. Fig. 29e.





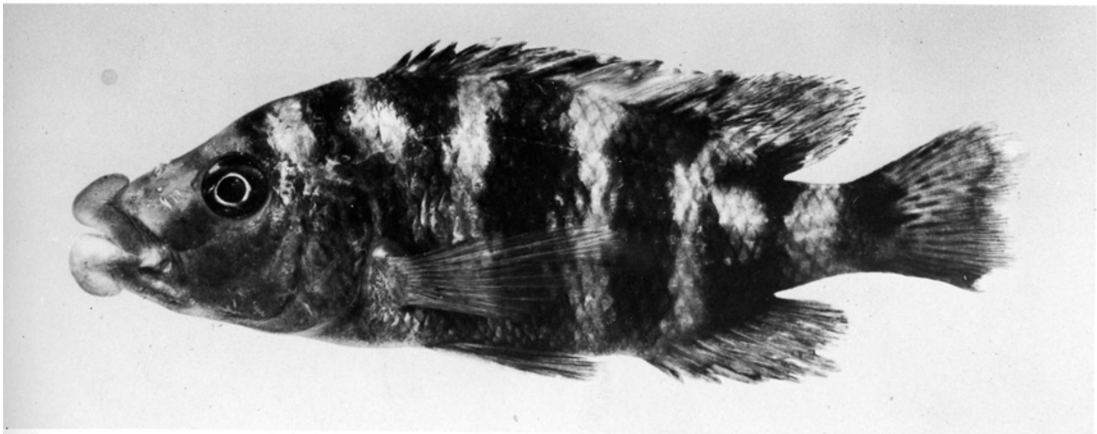
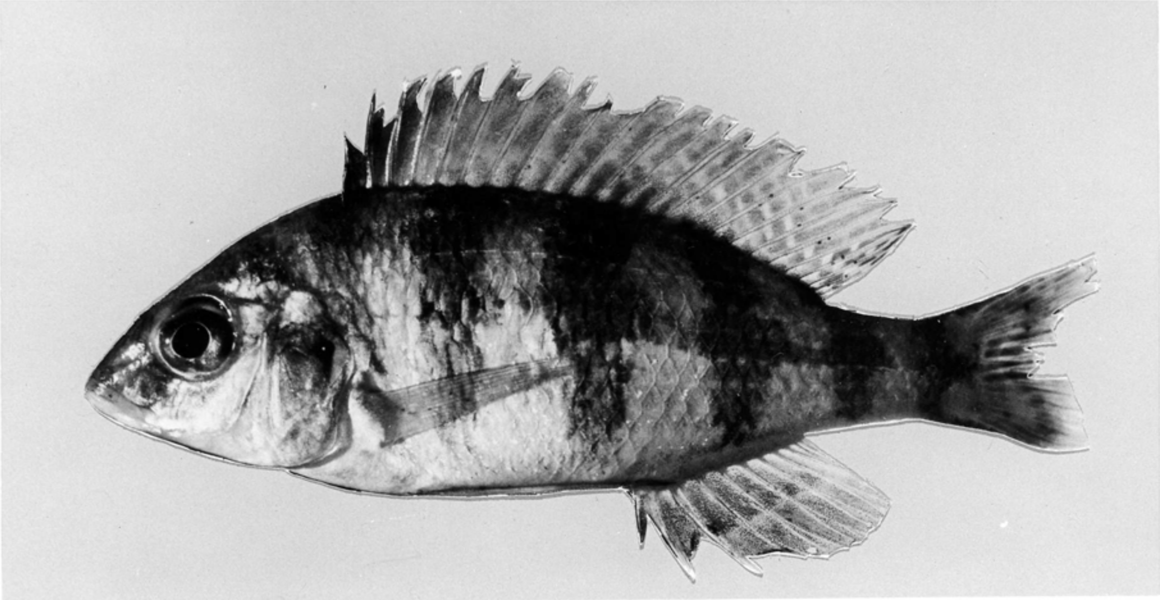
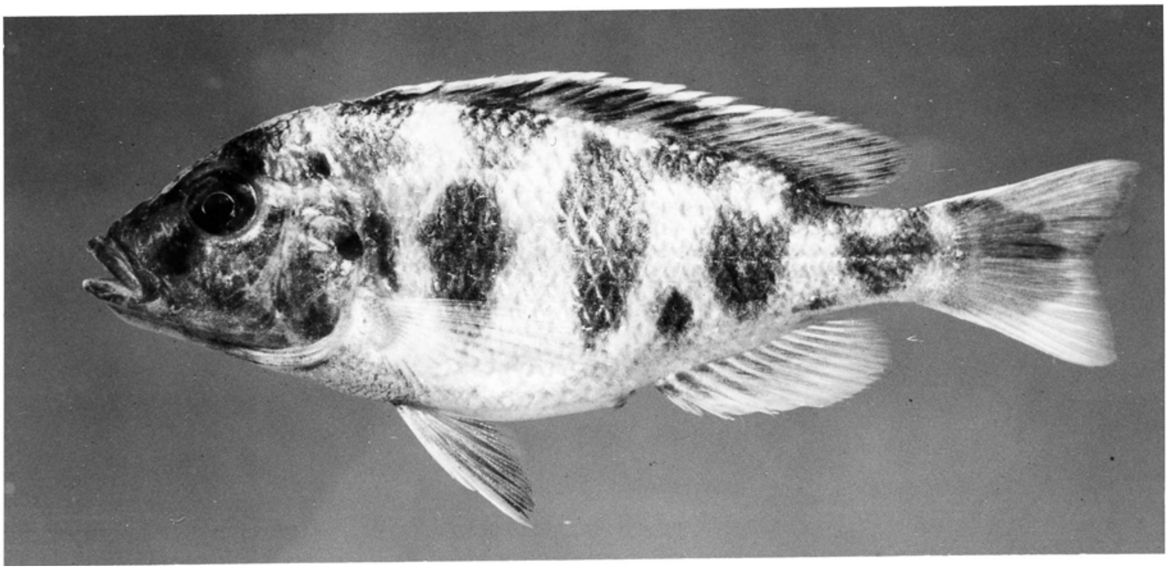


Figure 26. Live individuals of species of the *Cyrtocara livingstonii* species-group. a, *C. johnstoni*, approx. 90 mm SL; cf. Fig. 29a. b, *C. venustus*, adult female; cf. Fig. 30a. c, *C. livingstonii*, young adult; cf. Fig. 30f.





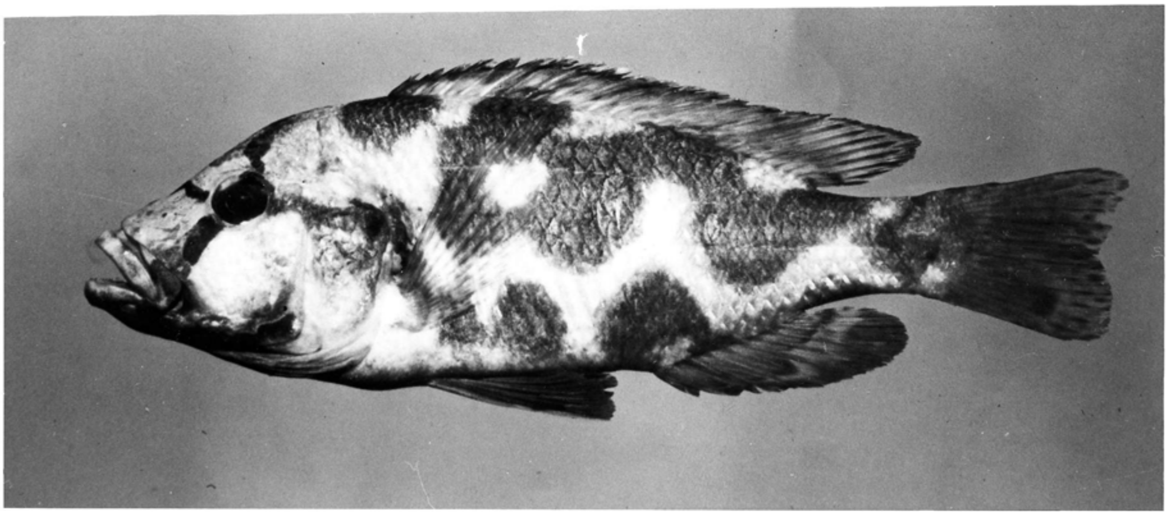
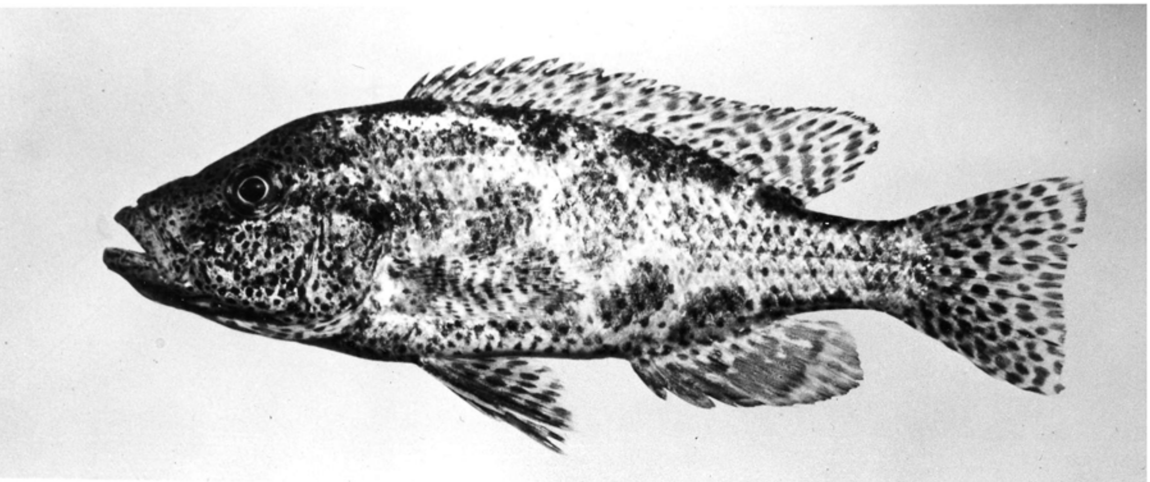
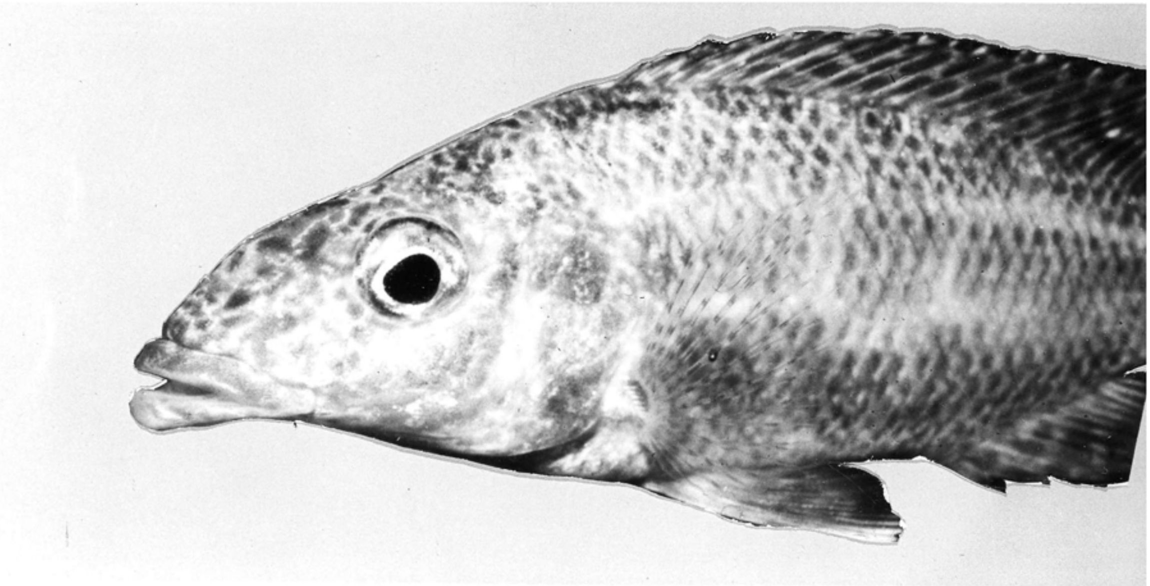


Figure 27. Live individuals of species of the *Cyrtocara livingstonii* species-group. a, *C. polystigma*, young adult; cf. Fig. 31j. b, *C. linni*, adult aquarium specimen owned by David Fenlon. c, *C.* sp. A, adult male aquarium specimen owned by Thomas Gray. Note spotted pectoral fin, and single spot (yellow) on middle of ventral margin of anal fin. Cf. Fig. 30i.





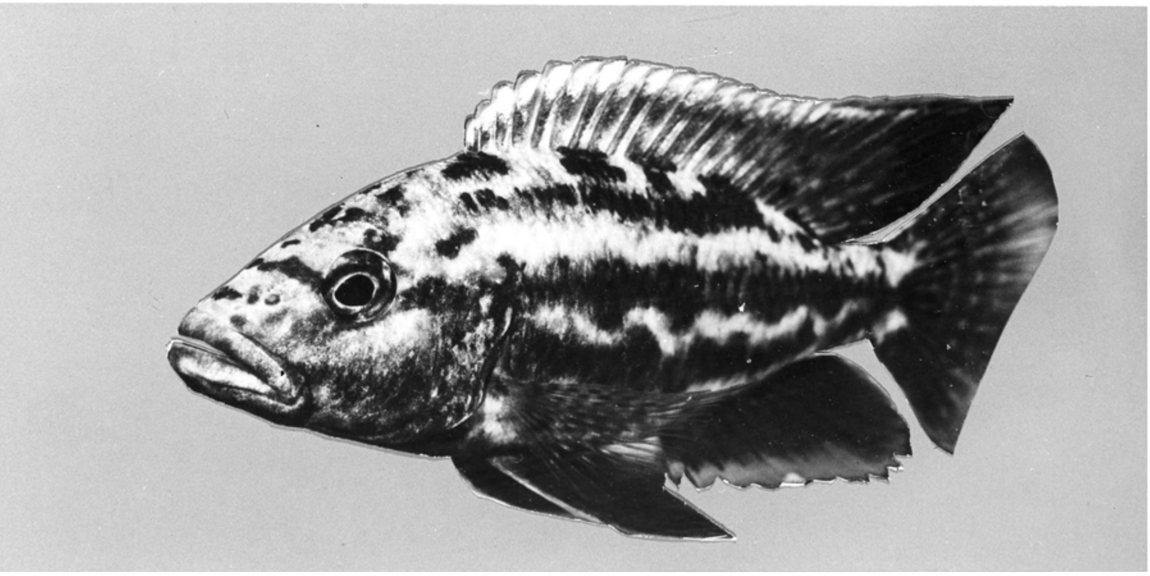


Figure 28. Cyrtocara fuscotaeniatus, holotype, after Regan (1921, fig. 12).

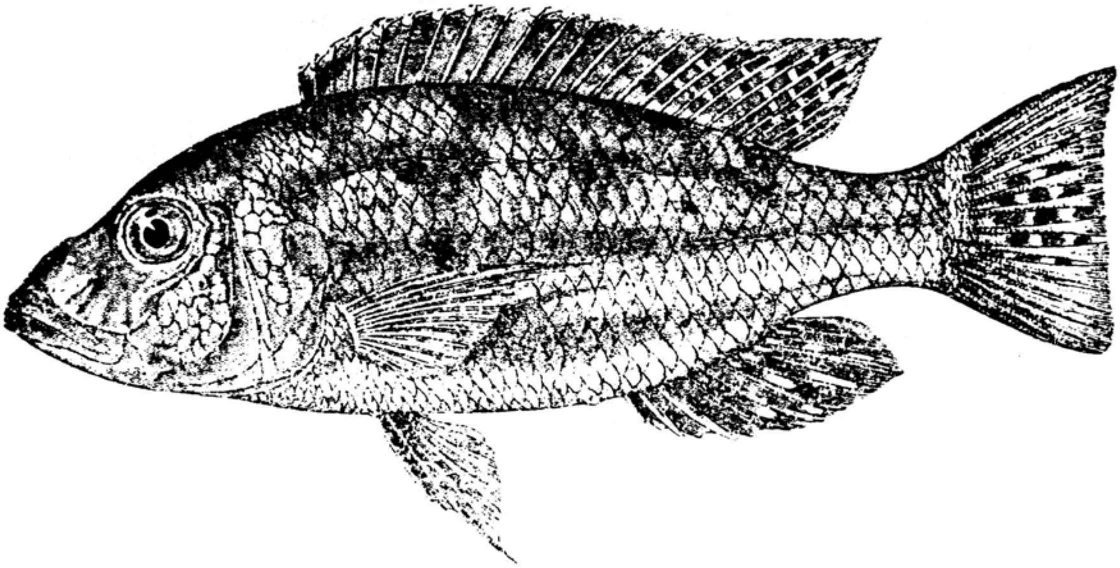


Figure 29. Variation in color pattern within and among species of the *Cyrtocara livingstonii* species-group sensu lato and in *Cyrtocara fuscotaeniatus*. Traced from photographs of actual individuals; not drawn to same scale. Head markings omitted if indistinct; some head markings were present in all specimens. a-c, *C. johnstoni*: a, subadult (approx. 90 mm SL; cf. Fig. 26a); b, adult (approx. 115 mm SL); c, adult. d-f, *C. milomo*: d, paratype (106.5 mm SL); e, paratype (117 mm SL; cf. Fig. 25c); f, BMNH unregistered, approx. 150 mm SL. g-j, *C. fuscotaeniatus*, subadults, 76.5-87.0 mm SL.

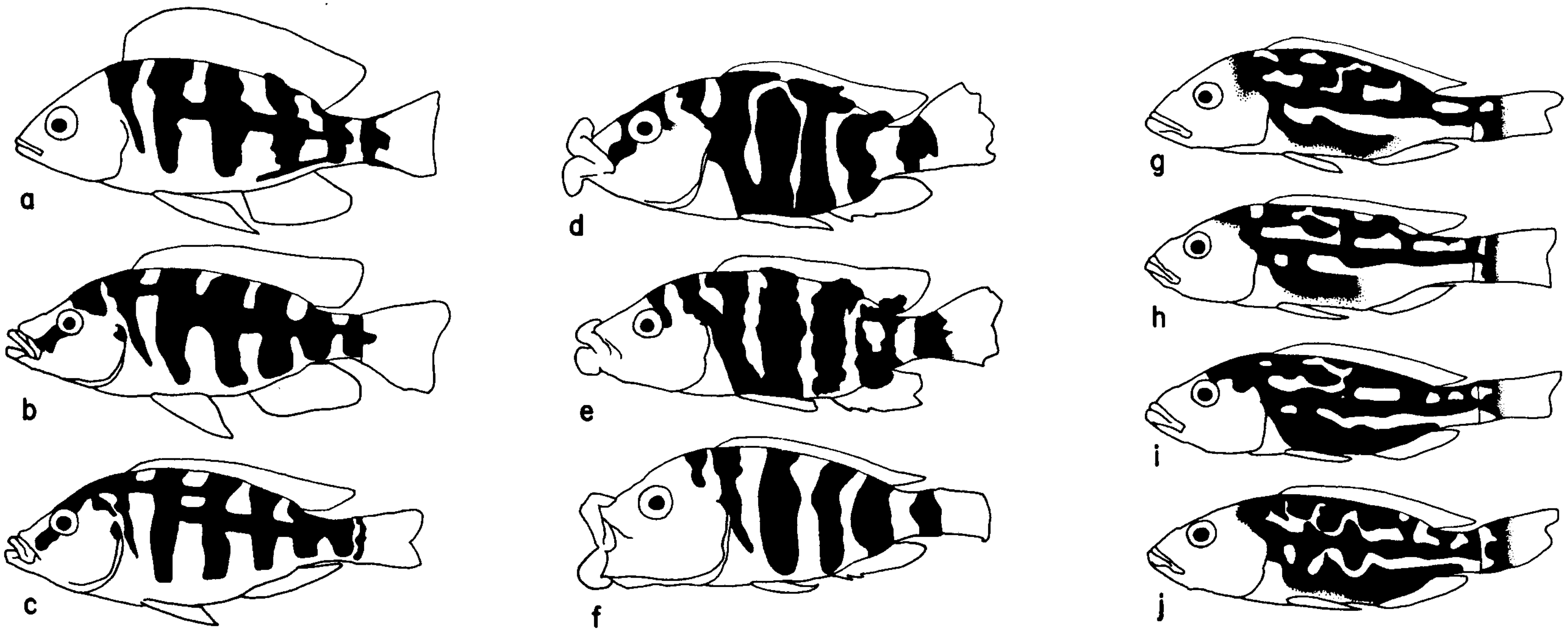

a
b
c
d
e
f
g
h
i
j

Figure 30. Variation in color pattern within and among species of the _Cyrtocara livingstonii_ species-group sensu stricto. Conventions as in Fig. 29. a-d, _C_. _venustus_: a, adult female (cf. Fig. 26b); b and c, adult males; d, juvenile, approx. 85 mm SL. e-g, _C_. _livingstonii_: e, juvenile (37.8 mm SL); f, young adult (cf. Fig. 26c); g, large adult, aquarium specimen, note that pectoral fin (dotted) hides part of blotch on belly. h, _C_. _linni_, adult (approx. 182 mm SL). "Freckles" (see Cladistic analysis) omitted. i, _C_. species A, adult male (cf. Fig. 27c).

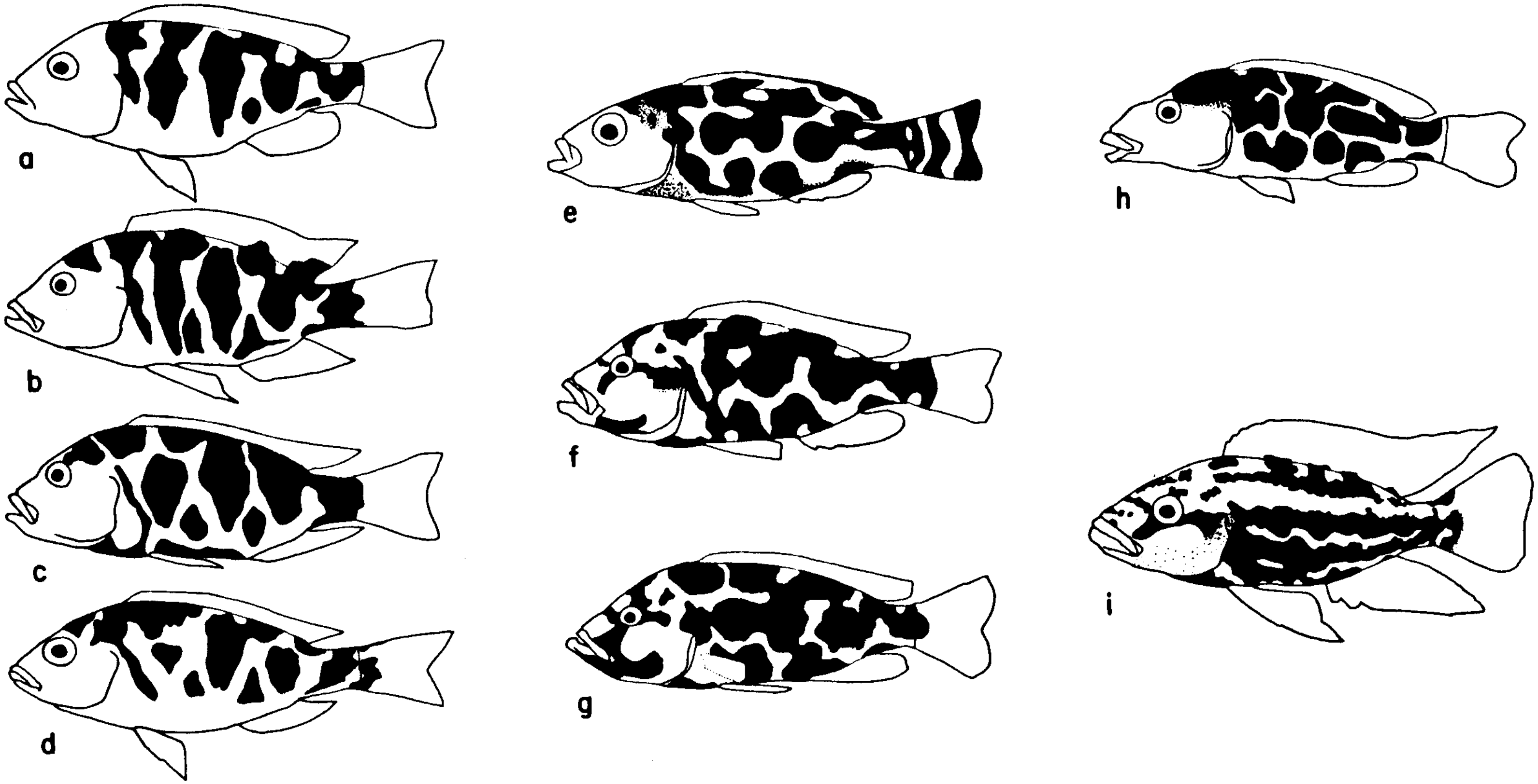
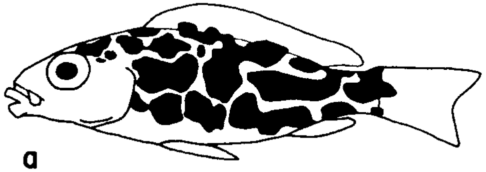
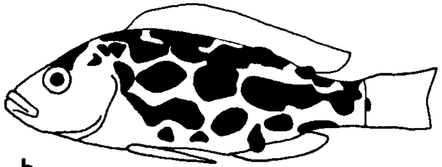

a
b
c
d
e
f
g
h
i

Figure 31. Variation in color pattern in _Cyrtocara polystigma_. "Freckles" omitted. Conventions as in Fig. 29. a-h, postlarva and juveniles, all caught swimming together in a small shoal: a, 28.5 mm SL; b-h, 70.0-89.0 mm SL, in order of increasing size. i, subadult. j, small adult (cf. Fig. 27a). k, _C_. cf. _polystigma_, large adult male.


a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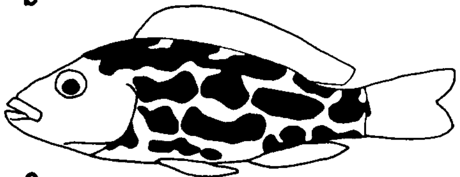
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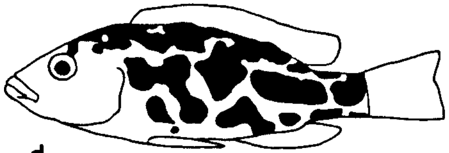
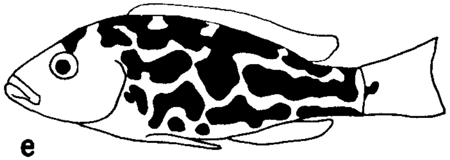
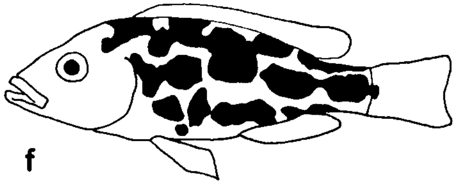

d


e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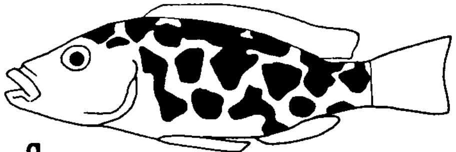
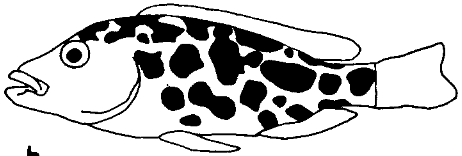
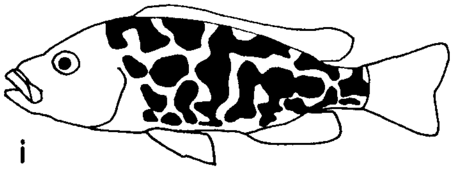
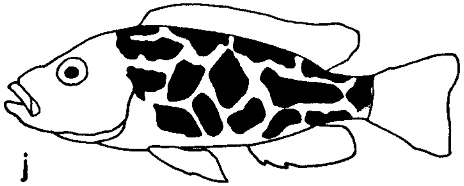

g


h


i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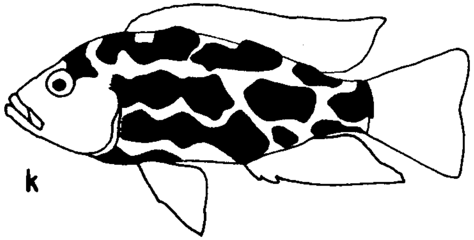
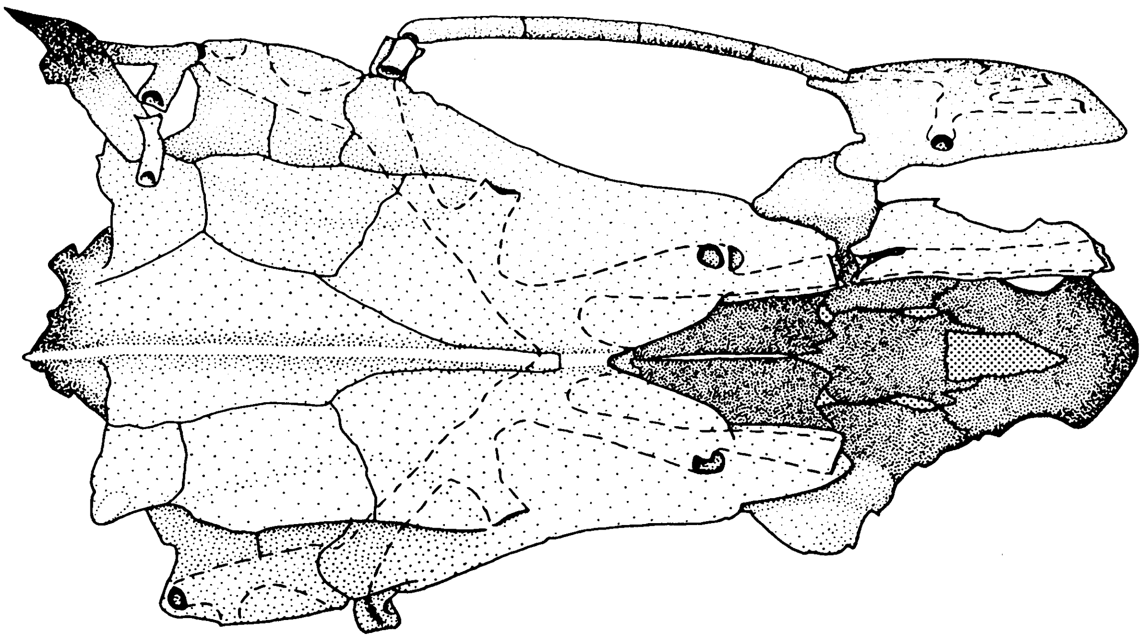

k

Figure 32. Neurocranium of Cyrtocara milomo, new species. Paratype (97 mm SL, neurocranial length 27.2 mm). above, dorsal view; below, lateral view.



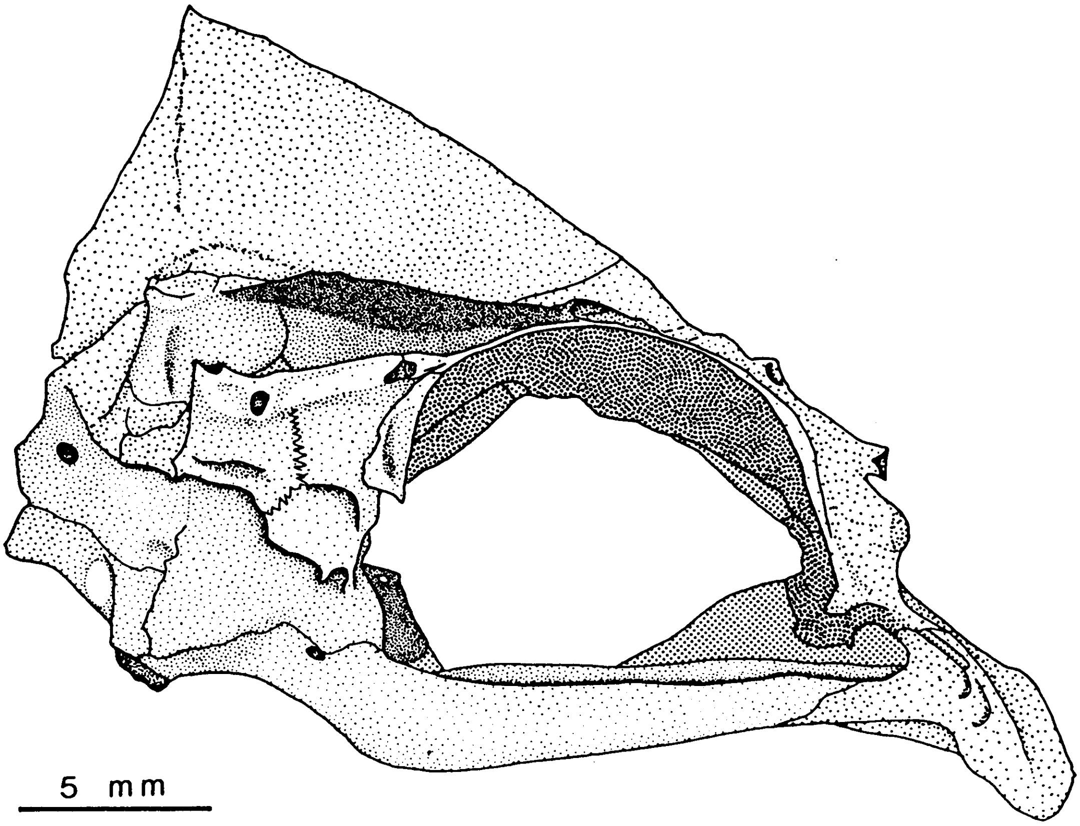

5 mm

Figure 33. Suspensorium in species of the *Cyrtocara livingstonii* species-group and in *C. fuscotaeniatus*. Lateral view. Cartilage heavily stippled. a, *C. fuscotaeniatus* (88 mm SL). b, *C. johnstoni* (112 mm SL); c, *C. milomo* (paratype, 97 mm SL); d, *C. venustus* (119 mm SL); e, *C. livingstonii* (101.5 mm SL); f, *C. polystigma* (64 mm SL); g, *C. linni* (126 mm SL). Abbreviations: AA, anguloarticular; DN, dentary; ECT, ectopterygoid; HM, hyomandibular; MES, mesopterygoid (entopterygoid); MET, metapterygoid; PAL, palatine; POP, preopercular; Q, quadrate; RAR, retroarticular; SYM, symplectic.

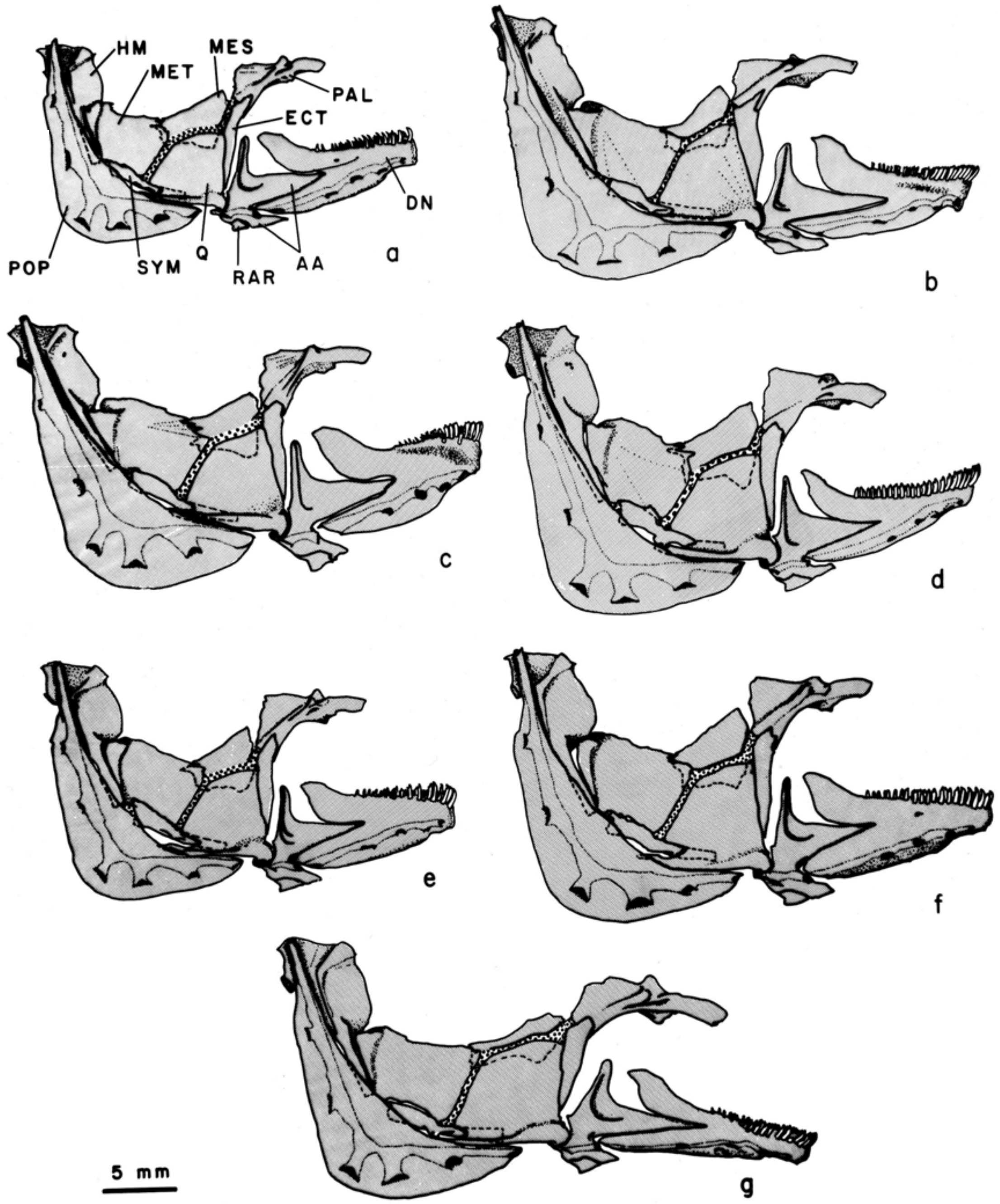

HM
MET
MES
PAL
ECT
DN
POP
SYM
Q
RAR
AA
a
b
c
d
e
f
g
5 mm

Figure 34. Upper jaw in species of the Cyrtocara livingstonii species-group and in C. fuscotaeniatus. Lateral view. Same specimens as in Fig. 33. a, C. fuscotaeniatus; b, C. johnstoni; c, C. milomo; d, C. venustus; e, C. livingstonii; f, C. polystigma; g, C. linni. Note replacement teeth in a, d, and e. Abbreviations: ALV, alveolar process of premaxilla; ASC, ascending process of premaxilla; MX, maxilla; S, premaxillary symphysis.

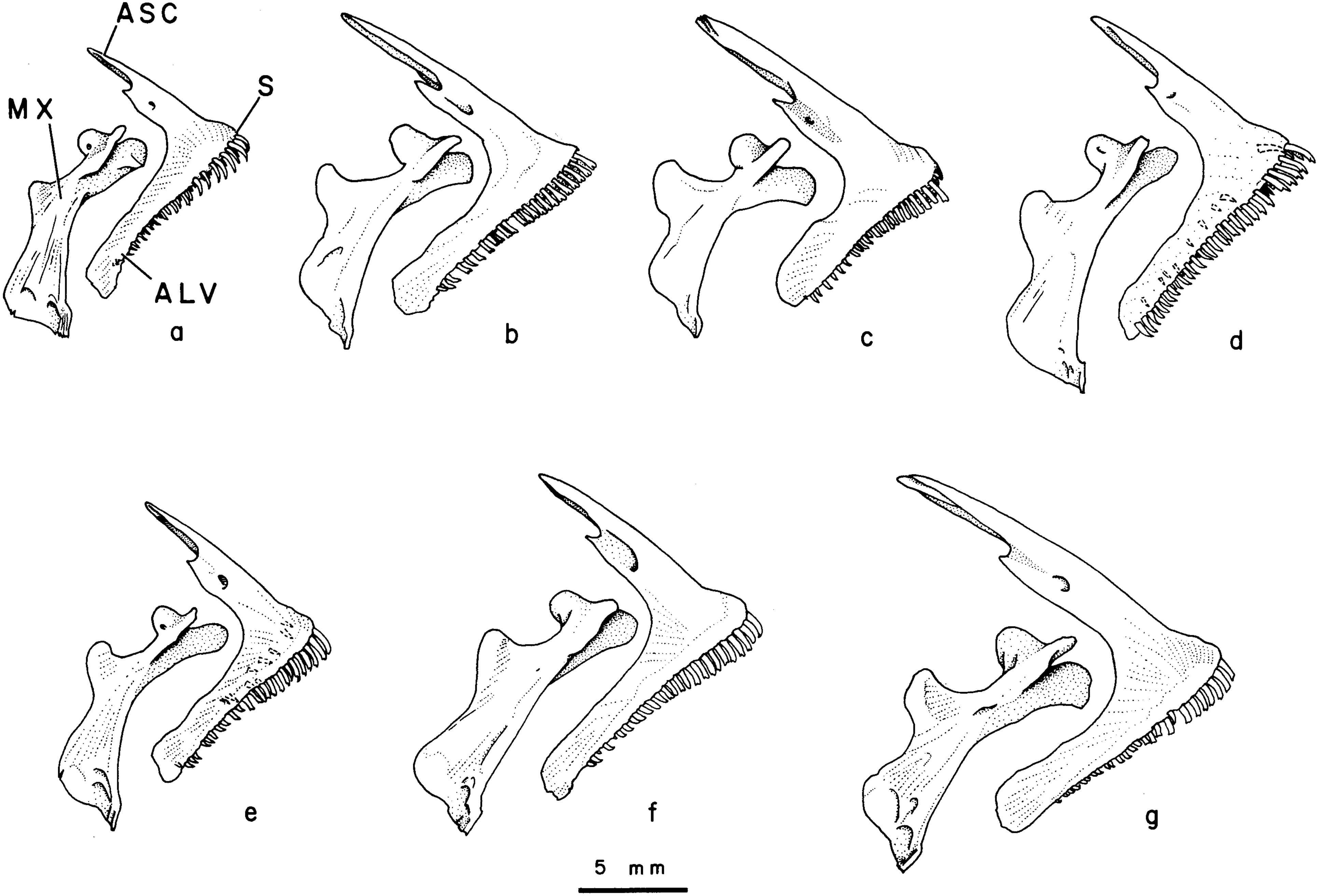

ASC
S
MX
ALV
a
b
c
d
e
f
g
5 mm

Figure 35. Lower pharyngeal bones of species of the *Cyrtocara livingstonii* species-group, in occlusal view. a, *C. johnstoni*, a specimen 112 mm SL with unusually weakly molarized median teeth; b, *C. milomo* (paratype, 97 mm SL); c, *C. venustus* (119 mm SL).

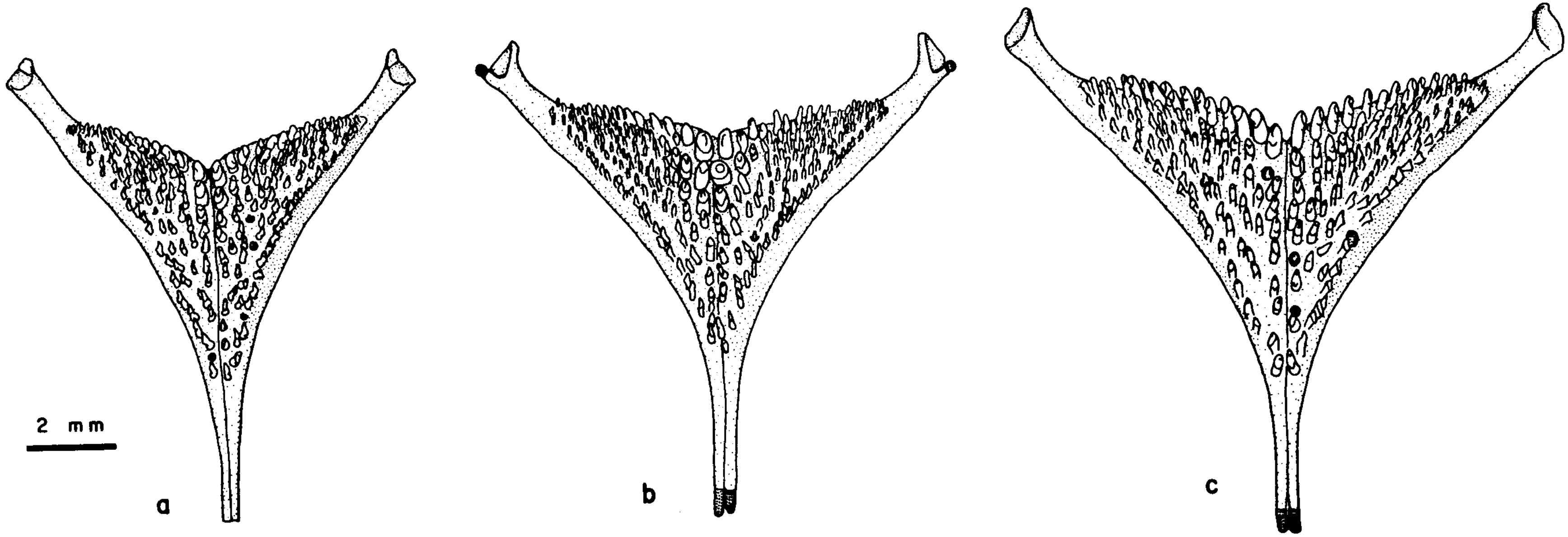
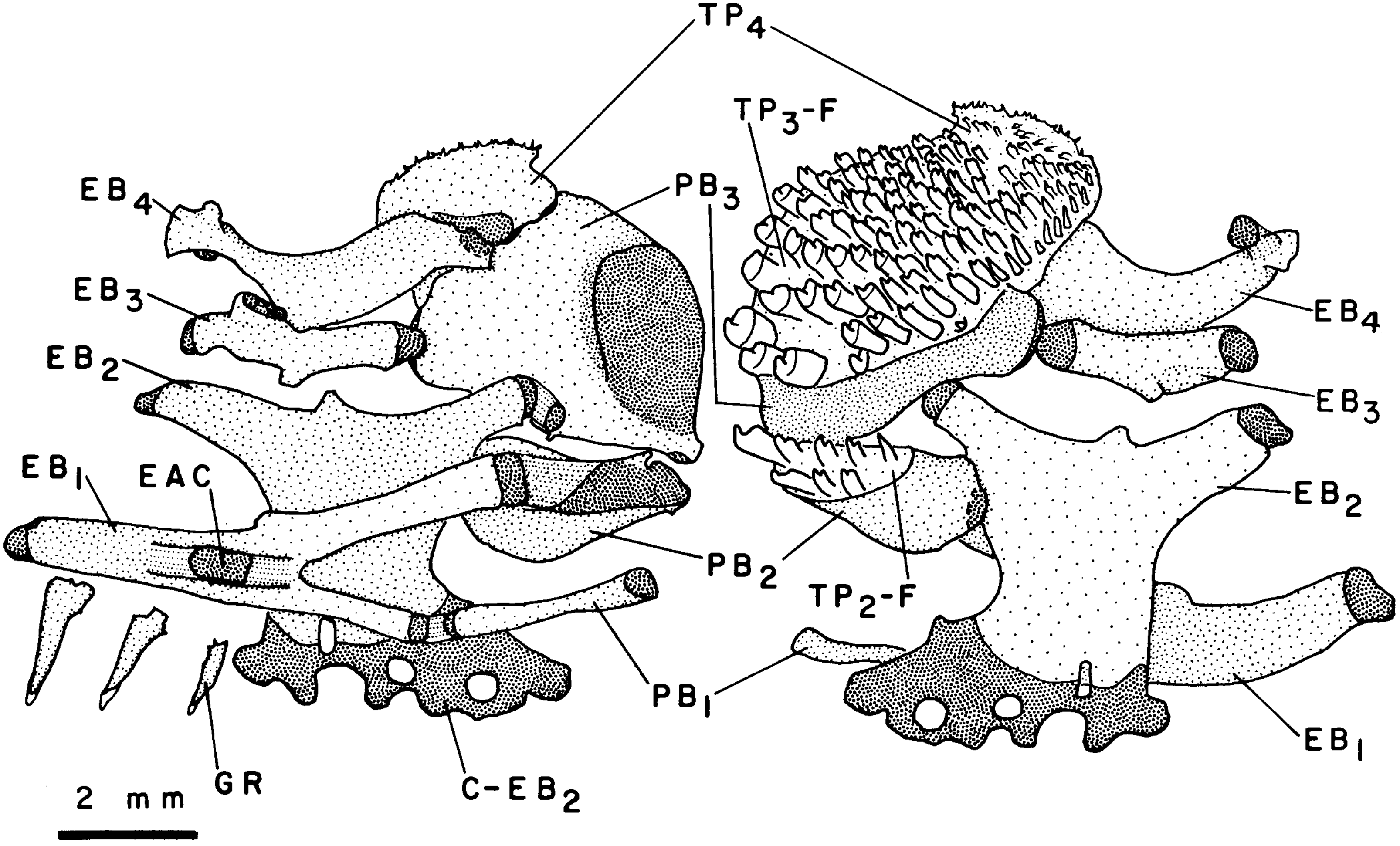

2 mm
a
b
c

Figure 36. Dorsal gill-arch elements of right side in _Cyrtocara venustus_ (119 mm SL). Left, dorsal view; right, ventral view. Abbreviations: C-EB_2, cartilaginous extension of second epibranchial; EAC, epibranchial accessory cartilage; EB_{1-4}, epibranchials; GR, uppermost gill raker of first arch; PB_{1-3}, pharyngobranchials; TP_{2-3}-F, tooth plates fused with the associated pharyngobranchials; TP_4, fourth tooth plate (unfused).



TP4
TP3-F
EB4
PB3
EB3
EB4
EB2
EB3
EB1
EAC
EB2
PB2
TP2-F
PB1
EB1
GR
C-EB2
2 mm

Figure 37. Cladogram showing the distribution of derived characters in the *Cyrtocara livingstonii* species-group, and the corresponding most parsimonious hypothesis of relationships of common ancestry in the group. Letters A-E correspond to nodes, and numbers to synapomorphies (1-9) and autapomorphies (10-31) discussed in the text. Certain species have not been examined for characters 8 and 9, as indicated by open boxes: *C. maculimanus* and *C. pardalis* are included solely on the basis of information given by Regan (1921) and Trewavas (1935); *C.* sp. A is known only from photographs. *C. fuscotaeniatus* is doubtfully related to the *C. livingstonii* species-group.

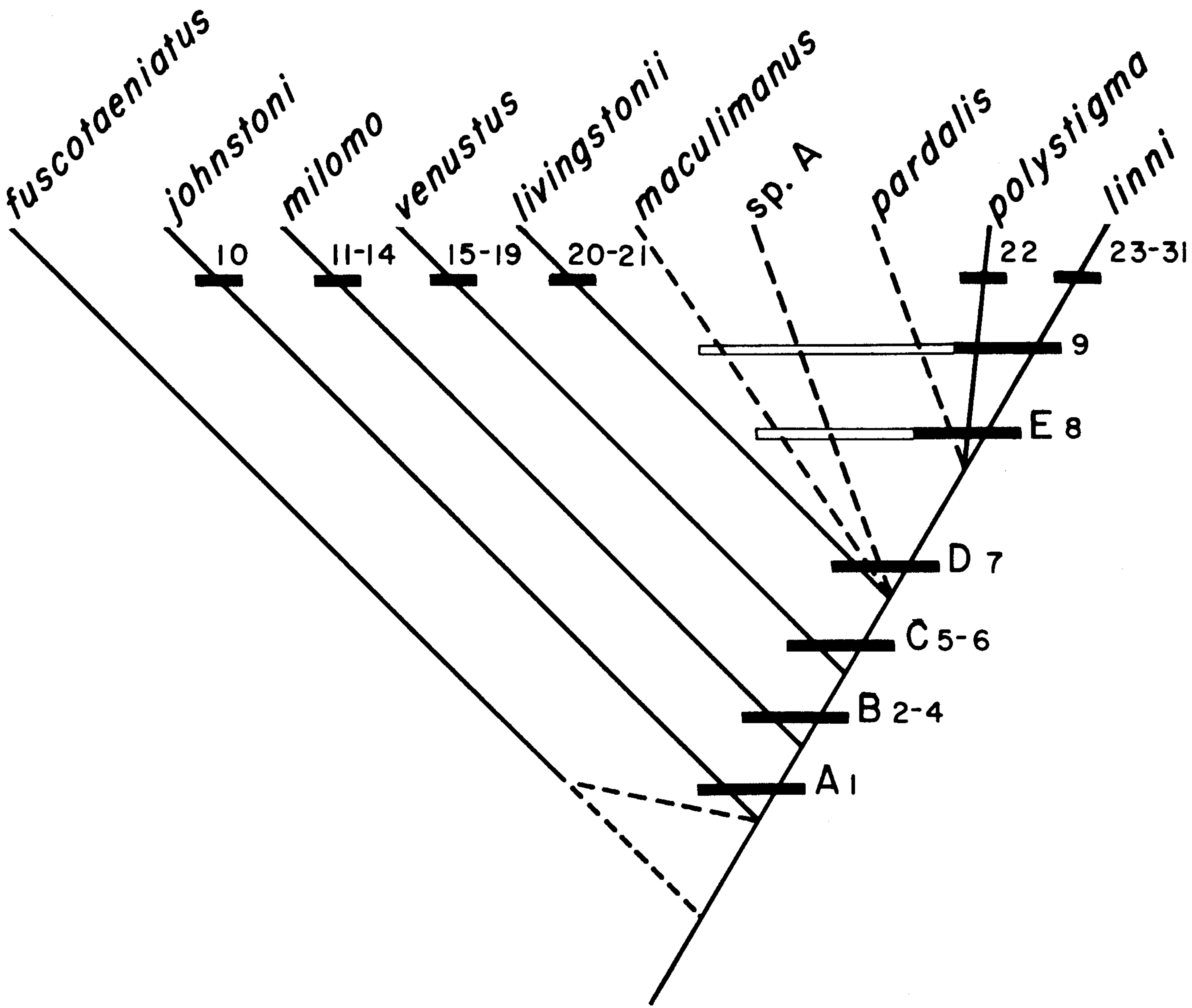

fuscotaeniatus
johnstoni
milomo
venustus
livingstonii
maculimanus
sp. A
pardalis
polystigma
linni
10
11-14
15-19
20-21
22
23-31
9
E 8
D 7
C 5-6
B 2-4
A 1

Table 7. Linear regressions of morphometric variates (Y) on standard length or head length (X) in *Pardochromis milomo*.

Regression[1]	N	Range X	$\bar{X} \pm SE_X$	Range Y	$\bar{Y} \pm SE_Y$	$b \pm SE_b$	$a \pm SE_a$	r
HL on SL	9	90.0-187.0	133.389 ± 11.209	34.2- 76.3	52.611 ± 4.591	0.402*** ± 0.030	-0.977 ± 4.121	0.981
BD on SL	9	90.0-187.0	133.389 ± 11.209	36.8- 79.5	53.889 ± 4.829	0.424*** ± 0.030	-2.615 ± 4.062	0.983
PDL on SL	9	90.0-187.0	133.389 ± 11.209	37.7- 81.0	56.222 ± 4.812	0.424*** ± 0.026	-0.321 ± 3.503	0.988
PPL on SL	7	90.0-187.0	132.357 ± 14.649	41.2- 92.0	60.957 ± 7.173	0.483*** ± 0.035	-3.007 ± 4.836	0.987
BEL on SL	7	90.0-187.0	132.357 ± 14.649	25.5- 52.8	37.186 ± 4.080	0.278*** ± 0.006	0.365 ± 0.858	0.999
DBL on SL	9	90.0-187.0	133.389 ± 11.209	48.7-101.0	71.422 ± 6.161	0.547*** ± 0.019	-1.593 ± 2.574	0.996
CPL on SL	9	90.0-187.0	133.389 ± 11.209	12.2- 24.9	17.856 ± 1.471	0.121*** ± 0.020	1.771 ± 2.680	0.919
PFL on SL	9	90.0-187.0	133.389 ± 11.209	30.1- 70.5	45.567 ± 4.177	0.358*** ± 0.039	-2.156 ± 5.401	0.960
HB on HL	9	34.2- 76.3	52.611 ± 4.591	15.1- 33.9	22.578 ± 2.048	0.444*** ± 0.016	-0.786 ± 0.865	0.996
POD on HL	9	34.2- 76.3	52.611 ± 4.591	6.9- 17.8	11.056 ± 1.187	0.257*** ± 0.012	-2.445** ± 0.665	0.992
IOW on HL	9	34.2- 76.3	52.611 ± 4.591	7.7- 21.6	13.289 ± 1.480	0.317*** ± 0.021	-3.410* ± 1.147	0.985
SNL on HL	9	34.2- 76.3	52.611 ± 4.591	13.0- 31.5	21.200 ± 2.146	0.465*** ± 0.017	-3.277** ± 0.923	0.995
OL on HL	9	34.2- 76.3	52.611 ± 4.591	9.8- 16.6	12.544 ± 0.717	0.154*** ± 0.010	4.436*** ± 0.525	0.986
CHD on HL	9	34.2- 76.3	52.611 ± 4.591	6.7- 20.5	12.478 ± 1.480	0.319*** ± 0.018	-4.303** ± 0.974	0.989
UJL on HL	9	34.2- 76.3	52.611 ± 4.591	11.2- 27.3	18.111 ± 1.818	0.391*** ± 0.023	-2.472 ± 1.247	0.988
PMP on HL	9	34.2- 76.3	52.611 ± 4.591	12.6- 29.1	19.422 ± 1.776	0.384*** ± 0.017	-0.793 ± 0.905	0.993
LJL on HL	9	34.2- 76.3	52.611 ± 4.591	15.0- 35.0	23.822 ± 2.241	0.487*** ± 0.014	-1.793* ± 0.741	0.997
POH on HL	9	34.2- 76.3	52.611 ± 4.591	12.5- 31.8	20.122 ± 2.017	0.435*** ± 0.024	-2.760 ± 1.283	0.990

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[1] BD = body depth; BEL = belly length; CHD = cheek depth; CPL = caudal-peduncle length; DBL = dorsal-fin base length; HL = head length; HW = head width; IOW = interorbital width; LJL = lower-jaw length; OL = orbit length; PDL = predorsal length; PFL = pectoral-fin length; PMP = length of premaxillary ascending processes; POD = preorbital depth; POH = postorbital head length; PPL = prepelvic length; SL = standard length; SNL = snout length; UJL = upper-jaw length. Significance levels: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

CHAPTER 5

THREE NEW HAPLOCHROMINE CICHLIDS WITH THREE LATERAL SPOTS FROM LAKE MALAWI, AND A KEY TO THE SPECIES OF THE THREE-SPOT ASSEMBLAGE

INTRODUCTION

The most recent taxonomically comprehensive treatment of the cichlid fishes of Lake Malawi is the synopsis of Trewavas (1931, 1935). She classified most of these species in *Haplochromis*, then a very large genus widely distributed in African lakes and rivers. Trewavas (1935) employed color patterns as the primary characters in most of the principal divisions of her synoptic key to the Malawian species of *Haplochromis*. The fishes of two of these main divisions (L and M) are characterized there by the presence of three spots on the side of the body, and the position of the most anterior spot. Some of the species in part N of that key share a similar pattern of three spots, as do a number of species that Trewavas assigned to several other genera. Finally, the single species of part O, *H. pleurostigma*, is also normally three-spotted although the unique specimen known to Trewavas was aberrant in having only the anteriormost spot. Groupings based on markings remain of paramount value today in identifying these fishes. Indeed, some monophyletic groups are definable on the basis of derived color patterns (pers. obs.)--although few if any of Trewavas's major polyspecific key divisions appear monophyletic as originally constituted.

This chapter is the first part of a revision of the three-spot assemblage. My first objective is to describe three new species in the group. Second, I make available a new, draft key to this assemblage, which is phenetically distinctive, and is, therefore, a convenient subject for a key. However, I conjecture that the assemblage is probably not monophyletic, some three-spotted species being more closely related to the oblique-striped taxa than to other three-spots.

Until recently, most authorities would certainly have referred the new species described here to _Haplochromis_. However, during the 1970's it became apparent that this genus was not definable by any unique shared-derived character states (synapomorphies), and that its continued recognition as a nonmonophyletic taxon was undesirable. Greenwood (1979) therefore restricted _Haplochromis_ to the type species, _H. obliquidens_ of Lake Victoria, and four other species (all from East African lakes) which do share a putative synapomorphy with it. The Malawian species, thus, are all assigned temporarily to the oldest available genus with a Lake Malawi type species, _Cyrtocara_ Boulenger, 1902c, type _C. moorii_ Boulenger, 1902c (Greenwood, 1979). Because the phylogenetic relationships of the new species described here are unclear, preventing their assignment to one or more monophyletic genera, I provisionally assign these new species to the gradal genus _Cyrtocara_.

METHODS

Institutional abbreviations

BMNH, British Museum (Natural History), London

LMTS, collected by Lake Malawi Trawling Survey

MFRU, collection of Malawi Fisheries Research Unit, Monkey Bay

USNM, U.S. National Museum of Natural History, Washington, D.C.

Counts

Numbers in parentheses are of examined specimens having a given count. An asterisk (*) denotes the value for the holotype.

Fin rays.--In the dorsal and anal fins, the last two segmented rays may be closely approximated, but they always articulate separately with the basal pterygiophore. Therefore, they are counted as two elements.

Lateral line.--The total count is taken by the method of Trewavas (1935): starting at the anterior end of the lateral line, the scales of the upper segment are counted; the oblique row containing the last pore-bearing scale is followed downward and forward until it intersects the longitudinal row containing the lower segment; the count is resumed with the next scale behind this oblique row and is terminated at the end of the hypural bones (located by bending the caudal fin laterally at a slight angle to the body). Lateral-line scales on the caudal fin are those posterior to this point. Separate counts of the upper and lower segments are also taken. The lower count begins with the most anterior pored scale (whether bearing a true canal or not) and is terminated at the end of the hypurals. Unpored scales interposed between pore-bearing scales are included in the counts.

Transverse scales from dorsal-fin origin to lateral line.--The minimum count from lateral edge of base of first spine, obliquely downward and backward to (but excluding) a lateral-line scale.

Predorsal scales.--Counted just to one side of nuchal midline, from first dorsal spine to over eye.

Prepelvic scales.--From either pelvic-fin spine to most anterior scale on isthmus.

Scales between pectoral- and pelvic-fin bases.--The minimum count.

Belly scales.--Counted along ventrolateral edge of belly from just above pelvic-fin spine to just above first spine of anal fin.

Scale rows on cheek.--The maximum vertical count below ventral margin of orbit.

Scales around caudal peduncle.--Counted in zigzag around middle of peduncle.

Gill rakers.--Counted on lateral edge of outer arch. Given as number on epibranchial + 1 raker in or nearest to angle + number on lower limb (including those on ceratobranchial and, often, one or more on hypobranchial). All rudiments are counted.

Vertebrae.--Given as abdominal + caudal. Unlike Greenwood (1973, 1979), I include the fused PU_1+U_1 centrum supporting the parhypural and hypurals. Therefore, my counts of caudal and total vertebrae exceed those of Greenwood by one.

Hypural fusion.--Adjacent hypurals are considered fused if they appear fused along all or part of their length.

Teeth in outer row of upper jaw.--Total of left and right sides, including newly erupted teeth and missing teeth indicated by gaps or empty alveoli.

Teeth on lower pharyngeal bone (Fig. 38).--Posterior row: all teeth implanted along posterodorsal edge of bone, most easily counted in posterodorsal view. Median column: all teeth implanted along one side of median joint of the bone. Oblique posteromedian to midlateral row: the minimum number of teeth from and including the posterior tooth of either median column, anterolaterally to approximately the midpoint of edge of toothed area on that side.

Bars below dorsal-fin base.--All bars with centers of upper ends between the levels of first and last dorsal-fin elements.

Measurements

Morphometrics are expressed as thousandths of the standard length (SL) or head length (HL). For each ratio, the range, mean ± standard deviation, and number of specimens are given. An asterisk (*) denotes the ratio in the holotype. Like Greenwood (1973) but unlike Trewavas (1935), I take all measurements directly, except as noted below. In a direct measurement, the tips of the dividers or calipers are placed on the two specified reference points. Some direct measurements (e.g., head length, snout length) are at an angle to the midsaggital plane. (Unlike Lewis [1982], I find direct measurements more precise than projected ones made with a measuring board.) "Horizontal" means parallel to the line along which standard length is measured; "vertical" means perpendicular to this.

Standard length.--Premaxillary symphysis (between anterior pair of teeth) to end of hypurals at lateral line.

Head length.--Premaxillary symphysis to most posterior point on opercular bone.

Body depth.--Ventral midline between bases of pelvic-fin spines vertically to base of dorsal fin (this measurement is less dependent on degree of fullness of gut and on whether belly has been slit than maximum depth would be).

Predorsal length.--Premaxillary symphysis to anterior base of first dorsal-fin spine.

Prepelvic length.--Dentary symphysis (between anterior pair of teeth) to anterior base of pelvic-fin spine.

Belly length.--Anterior base of pelvic-fin spine to anterior base of first anal-fin spine.

Dorsal- and anal-fin base length.--Anterior base of first spine to posterior base of last segmented ray.

Total dorsal- and anal-fin length.--Anterior base of first spine to posterior tip of distal fin margin.

Last dorsal- and anal-fin spines.--Anterior base to tip of spine.

Caudal-peduncle length.--Posterior base of last anal-fin segmented ray to level of end of hypurals; a projected measurement taken parallel to lower lateral-line segment. Contrasts with method of Iles (1960) and Jackson (1961), who measured from level of end of dorsal fin (usually giving a longer measurement).

Caudal-peduncle depth.--The least depth.

Pectoral-fin length.--Dorsal base of uppermost ray to tip of longest ray, with fin lying against body; longer fin measured.

Pelvic-fin length.--Anterior base of spine to tip of longest segmented ray (always the first ray in Malawian haplochromines), with fin lying against body; longer fin measured.

Caudal-fin length.--Base of longest ray to its tip.

Head width.--Width between upper ends of vertical arms of preopercular bones (this measurement is less dependent on degree of opercular adduction than greatest width would be).

Snout length.--Premaxillary symphysis to nearest point on anterior bony orbit.

Snout width.--Width across centers of lacrimal bones.

Orbit length.--Greatest diameter of bony orbital rim, from lateral ethmoid-lacrimal joint.

Preorbital depth.--Midpoint of orbital margin of lacrimal bone (preorbital bone of Trewavas) along a line continuing radius of eye at this point to ventral margin of this bone.

Interorbital width.--Minimum width between bony (frontal) margins of orbit.

Postorbital head length.--Posterior point on bony orbital rim to posterior point on opercular bone.

Cheek depth.--Most ventral point of orbit (along upper edge of an infraorbital bone) vertically to upper edge of lateral wing of quadrate (just above anterior end of preoperculum).

Upper-jaw length.--Premaxillary symphysis (between bases of anterior pair of teeth) to ventral tip of maxilla (with mouth closed).

Premaxillary ascending processes ("premaxillary pedicels" of Trewavas).--Premaxillary symphysis (between bases of anterior pair of teeth) to tip of processes (located, if necessary, by slitting skin overlying them).

Lower-jaw length.--Dentary symphysis (between anterior pair of teeth) to posterior tip of anguloarticular bone (found by abducting lower jaw and locating its articulation with quadrate).

Lower-jaw width.--Width across left and right anguloarticular-quadrate joints.

Pharyngeal bone (Fig. 38).--Length: median length of bone along median joint. Width: greatest width across posterior processes. Length of dentigerous area: anterior base of anteriormost tooth to posterior edge of crown of posteriormost tooth in either median column (even if this tooth and the anteriormost one are on opposite sides of the median joint). Width of dentigerous area: greatest width measured to lateral edge of most lateral tooth on each side.

Gut length.--From point where esophagus enters stomach, to posterior end of rectum (measured with gut dissected out of fish and gently stretched only until straight).

Angles.--Relative to the "horizontal" along which standard length is taken. Measured to nearest 5° using a transparent protractor held parallel to midsagittal plane of fish.

Regression statistics

When pairs of external measurements (e.g., body depth in mm vs. standard length in mm) from specimens of various sizes belonging to one cichlid species are plotted on a bivariate scatter diagram, a straight line almost invariably provides the best fit to the points. Even when the relationship between the two variates is allometric--as it frequently is--the linear equation still fits the data as well as or better than the allometric equation or a higher-order function.

A simple linear regression takes the form $Y=\underline{b}X+\underline{a}$, where Y and X are the dependent and independent variables respectively, $\underline{b}$ is the regression coefficient or slope of the line, and $\underline{a}$ is the intercept on the Y axis. By convention in systematic studies, the larger of two measurements composing a ratio is taken as the independent variable. Herein, the independent variable X is either standard length or head length, as indicated in the tables and text. Naturally, if the sample of specimens is adequate in number and length range to justify the regression analysis, the slope is always highly significant for morphometric proportions; the part grows along with the whole fish. This slope is preferable to the traditional ratios or percentages for comparing the proportions of different species. Unlike those measures, the slope allows prediction of the proportions in a fish of any size, and the regression equation corrects these estimates for allometry. An intercept value that differs significantly from zero signals the existence of allometry and provides a convenient means of quantifying it. I performed regression analyses on a pocket calculator using equations given by Sokal and Rohlf (1969), adapted for my purposes with the kind help of Dr. Leslie Marcus.

In the tables, statistical significance of slopes and intercepts is indicated by asterisks: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

The spot pattern and its terminology (Fig. 39)

The spotted cichlids treated here are often known collectively as the "three-spot assemblage" or by a similar expression. However, the three spots exhibit a wide range of variation--interspecific, intraspecific among adults, and ontogenetic. Moreover, additional taxonomically and phylogenetically important spots are present in some species. With the intent of minimizing confusion in discussing the various spots and their hypothesized homology in different species, I propose new descriptive names for them (Fig. 39). The three main spots of Trewavas's (1935) key are together known as the (main or primary) lateral spots. The anterior of these is the suprapectoral spot, the middle one the supraanal spot, and the posterior one the precaudal spot.

In some species, a row of rectangular markings is present along each side of the dorsum; these are the dorsal midline spots. Between the anteriormost dorsal midline spot and the suprapectoral spot, an accessory spot (or two such spots, which may be fused into a short longitudinal stripe) may be present; this can apparently fuse with the suprapectoral spot in some individuals and species.

Cyrtocara lithobates, new species

Figs. 40-44, Table 8

Trematocranus sp.: Axelrod and Burgess, 1976: 301 (2 color photographs).

Haplochromis of the *modestus*-complex: Axelrod and Burgess, 1976: 302 (two color photographs).

Cyrtocara species: Mayland, 1982: 283 (color photograph).

Holotype.--BMNH 1974.7.5:1, a sexually active male 86.5 mm SL (Figs. 40, 41), field collection number MKO-71-V-24, collected 24 May 1971 by Assan Mbaye, encircled with seine on rocky shore, middle of N shore Thumbi Island West (14°00'57"S, 34°48'52"E), Lake Malawi, Malawi.

Paratypes.--Specimens from which measurements were taken are indicated by the notation (M) after the catalogue number, specimens cleared and counterstained by (CC), and specimens radiographed by (R). 2 specimens, BMNH 1974.7.5:2-3 (M, R), 67.5-78.0 mm SL, collected 30 April 1971 by M. K. Oliver, A. Mbaye, Kingsize, and D. Davies, E end Thumbi Island West, seined on rocky shore; 2 specimens, USNM (M), 64.0-67.0 mm SL, 30 July 1968, M. K. Oliver and D. H. Eccles, Thumbi Island East, seined on rocky shore; 1 specimen, USNM (M, R), 72.5 mm SL, 5 June 1971, M. K. Oliver, NW corner Thumbi Island East below light, seined on rocky shore (14°03'31"S, 34°55'24"E); 3 specimens, USNM (M), 57.8-61.2 mm SL, 16 July 1971, M. K. Oliver and D. H. Eccles, same locality as immediately preceding; 16 specimens, USNM (M, one R), 52.0-73.5 mm SL, 10 August 1971, M. K. Oliver and D. H. Eccles, seined, same locality as immediately preceding; 3 specimens, USNM (CC), 62.0-67.0 mm SL, same collection data as immediately preceding; 2 specimens, USNM, 72.5-96.0 mm SL, MKO-80-90, 1 August 1980, M. K.

Oliver, I. Grace, A. Grace, T. D. Kocher, and K. R. McKaye, submerged rocky reef approx. 100 m S of SE corner Thumbi Island West (14°01'25"S, 34°49'25"E), chased into block net with SCUBA, depth 8-9 m; 9 specimens, USNM, 24.0-72.5 mm SL, MKO-80-93, 3 August 1980, M. K. Oliver, K. R. McKaye, T. D. Kocher, and A. Grace, W shore Domwe Island 40 m S of N end (13°58'07"S, 34°49'03"E), ichthyocide with SCUBA on steep rocky slope, depth 6-16 m; 3 specimens, USNM, 68.0-87.5 mm SL, field no. MKO-80-101, 8 August 1980, M. K. Oliver, K. R. McKaye, and T. D. Kocher, same locality as MKO-80-90, chased into block net with SCUBA, depth 8 m; 2 specimens, USNM (CC), 83.2-87.2 mm SL, same collection data as immediately preceding; 1 specimen, USNM, 67.3 mm SL, MKO-80-128, M. K. Oliver, K. R. McKaye, and T. D. Kocher, rocks on sand at SE corner Thumbi Island West, chased into block nets with SCUBA, depth 9 m; 6 specimens, USNM (M), 62.5-73.0 mm SL, collected week of 29 May 1972, aquarium fishes exported from Lake Malawi and received dead, precise locality unknown; 1 specimen, USNM (M), 106.8 mm SL, aquarium fish exported from Lake Malawi and maintained alive for unknown period, donated by B. Plotkin 1976.

Additional material examined.--1 specimen, USNM, 39.0 mm SL, MKO-80-85, 25 July 1980, M. K. Oliver, K. R. McKaye, and T. D. Kocher, Nkhata Bay (approx. 11°36'S, 34°18'E), middle of S bay near edge of dropoff, ichthyocide and chased into block nets with SCUBA, on sand and rock, depth 8-12 m. (This specimen is tentatively referred to _C. lithobates_.)

Diagnosis.--A small, elongate, three-spotted haplochromine (reaching approx. 100 mm SL in nature, larger in aquaria; body depth 29%-35% SL) with square to longitudinally elongate suprapectoral spot placed entirely below upper lateral-line segment (Figs. 40-42). Distinguishable from all other three-spotted cichlids in the Lake Malawi fauna by the above characteristics in combination with its moderately high gill-raker count (12-16, mode 14, on lower limb of outer arch), large eye (orbit length 32%-40% head length), and lower pharyngeal bone with several enlarged, submolariform posteromedian teeth (Fig. 43). Segmented rays of anal fin 7-9 with a strong mode of 8 (cf. 7-13, rarely 7 or 8, with mode of 9 or more in all other three-spotted haplochromines). See also key.

Description.--Based on holotype and 50 paratypes, 24.0-106.8 mm SL. Dorsal-fin spines and segmented rays XV,11 (1), XV,12 (2), XVI,10 (3), XVI,11* (24), XVII,10 (5), XVII,11 (1); anal-fin spines and segmented rays III,7 (1), III,8* (32), III,9 (3). Lateral-line scales 32 (3), 33* (21), 34 (3), 35 (1); upper part with 24 (2), 25 (3), 26 (7), 27 (8), 28 (2), 29 (3), 30* (3); lower part with 14 (4), 15 (3), 16 (7), 17* (9), 18 (5), 19 (1); lateral-line scales on caudal fin 1 (5), 2* (18), 3 (2). Scales ctenoid; transverse scales from dorsal-fin origin to lateral line 5 (3), 6* (7), 7 (1); predorsal scales approx. 13 (2), 14 (6), 15 (6), 16 (1), 18 (1); prepelvic scales approx. 18 (1), 20 (4); scales between pectoral- and pelvic-fin bases 5 (1), 6 (4), 7* (6), 8 (1); belly scales approx. 18 (1), 19 (3), 20* (4), 21 (2), 22 (2), 23 (1); scale rows on cheek 3* (13), 4 (2); scales around caudal peduncle 16* (27). Gill rakers on outer arch 5 (14), 6* (14), 7 (5) + 1* + 12 (4), 13 (7), 14 (14), 15* (8), 16 (1). Vertebrae 13 + 18 (1), 14 + 16 (2), 14 + 17* (4), 14 + 18 (2), 15 + 16 (1). Hypurals unfused* (10).

Morphometrics. (Regression analyses of principal ratios are given in Table 8.) Reaching approx. 100 mm SL (larger in aquaria). In SL:

Head length 323-366 (353*) ($\bar{x}$ = 344.3 ± 10.5, n = 30); body depth 295-344 (317*) ($\bar{x}$ = 321.0 ± 13.8, n = 29); predorsal length 351-384* ($\bar{x}$ = 372.5 ± 9.9, n = 18); prepelvic length 396-417 ($\bar{x}$ = 404.5 ± 6.5, n = 12); belly length 287-328 ($\bar{x}$ = 299.8 ± 12.4, n = 13); dorsal-fin base length 522-555 (543*) ($\bar{x}$ = 535.1 ± 9.7, n = 18); total dorsal-fin length 643-675 ($\bar{x}$ = 663.2 ± 10.3, n = 13); last dorsal-fin spine 153-181 (176*) ($\bar{x}$ = 165.6 ± 8.1, n = 17); anal-fin base length 160-190 ($\bar{x}$ = 175.1 ± 8.4, n = 15); total anal-fin length 281-316 ($\bar{x}$ = 296.5 ± 9.4, n = 11); last anal-fin spine 148-195 (171*) ($\bar{x}$ = 180.5 ± 10.6, n = 18); caudal-peduncle length 154-186 (161*) ($\bar{x}$ = 167.4 ± 8.4, n = 18); caudal-peduncle length/depth 1.27-1.66 (1.39*) ($\bar{x}$ = 1.45 ± 0.09, n = 18); pectoral-fin length 284-337 (287*) ($\bar{x}$ = 314.7 ± 16.9, n = 13); pelvic-fin length 244-325 (292*) ($\bar{x}$ = 275.0 ± 20.9, n = 16), longest in sexually active males; caudal-fin length 259-321 ($\bar{x}$ = 291.4 ± 21.8, n = 7).

In HL: Head width 420-486 (456*) ($\bar{x}$ = 465.9 ± 16.4, n = 18); snout length 278-326 (321*) ($\bar{x}$ = 301.1 ± 15.6, n = 18); snout width 284-361 (325*) ($\bar{x}$ = 327.2 ± 22.5, n = 18); orbit length 322-400 (370*) ($\bar{x}$ = 375.2 ± 14.9, n = 30); preorbital depth 148-194 (177*) ($\bar{x}$ = 171.6 ± 12.4, n = 18); interorbital width 147-204 (190*) ($\bar{x}$ = 183.7 ± 11.3, n = 30); postorbital head length 355-389 (361*) ($\bar{x}$ = 369.7 ± 10.2, n = 18); cheek depth 141-189 (157*) ($\bar{x}$ = 155.7 ± 13.0, n = 18); upper-jaw length 261-315* ($\bar{x}$ = 282.3 ± 16.6, n = 18); premaxillary ascending processes 277-309 (298*) ($\bar{x}$ = 288.3 ± 9.2, n = 18); lower-jaw length 369-420* ($\bar{x}$ = 393.3 ± 13.8, n = 17); lower-jaw length/width 1.19-1.75 (1.56*) ($\bar{x}$ = 1.48 ± 0.15, n = 17); pharyngeal-bone length 196-236 (216*) ($\bar{x}$ = 215.9 ± 12.5, n = 14); pharyngeal-bone width 257-300 (275*) ($\bar{x}$ = 277.3 ± 11.5, n

= 14).

Body rather elongate, moderately compressed. Dorsal profile more pronounced than ventral. Ventral profile virtually straight or smoothly rounded from chin to anus. Dorsal head profile at most slightly interrupted by premaxillary ascending processes; snout slightly convex, interorbital region straight to slightly concave, nape straight to slightly convex. Frontal profile usually tangent to orbit in lateral view, but orbit separated from profile by as much as 20% of eye depth in exceptional fishes. Eye large, slightly to markedly elliptical, its long axis longitudinal. Snout angle 40°-$50^{\circ *}$ to horizontal, frontal angle (above orbit) 20°-$35^{\circ *}$, nuchal angle 10°-$35^{\circ *}$ (these angles not correlated with SL). Jaws evenly rounded anteriorly in dorsal view. Gape slightly oblique. Ventral profile of lower jaw inclined at $25^{\circ *}$-45° to horizontal (negatively correlated with SL, $r = -0.530$, $p<0.05$, $n = 17$; lower-jaw angle = $[-0.234 \pm 0.096]\text{SL} + [50.587 \pm 6.778]$). Jaws equal or lower projecting slightly. Chin rounded, receding, without externally visible protuberance. Premaxillae slightly beaklike. Posterior tip of maxilla reaching or nearly reaching a vertical through anterior margin of orbit. Lips slightly thickened. Upper lip fold continuous across premaxillary symphysis, lower lip fold interrupted at dentary symphysis. Cephalic lateral-line pores and canals not enlarged.

Caudal fin distinctly emarginate, lower lobe a little shorter than upper; densely covered with small scales nearly to ends of outer rays, but only on proximal 1/3 on middle rays. Dorsal fin proximally with interradial rows of up to 5 small scales in posterior half of fin; soft part of anal with similar rows of up to 5 scales. Pectorals lanceolate.

Pelvics with first ray not noticeably produced in sexually active males.

Teeth in outer row of each jaw (Fig. 44) robust, rather closely spaced, slightly movable; crowns compressed, incurved. In upper jaw, anterior to lateral teeth all bicuspid, or a mixture of uni- and bicuspids or bi- and tricuspids; posterior and, frequently, posterolateral teeth unicuspid. Tricuspids never predominate in outer row. Bi- and tricuspid teeth with cusps of unequal size, usually acutely pointed, the axes slightly divergent. In lower jaw, anterior outer teeth usually bicuspid, posterior teeth unicuspid. Number of teeth in outer row of upper jaw 39-62* ($\bar{x}$ = 46.1 ± 6.3, n = 14; positively correlated with SL, r = 0.594, $p<0.05$; number of teeth = [0.270 ± 0.106]SL ± [27.326 ± 7.484]; intercept >0, $p<0.01$).

Inner teeth in 1-3 rows anteriorly in upper jaw, 1-2 rows in lower, modally 2 inner rows in each jaw; rows well-defined, separated by distinct gap from outer teeth. Crowns compressed, unequally tricuspid, posteriorly becoming unicuspid in large fishes; cusps acute. Dentary symphysis normal (inner teeth not elevated above level of outer teeth).

Lower pharyngeal bone (Fig. 43) subtriangular, its posterior edge slightly to distinctly indented; bone moderately wide (1.16-1.46 [1.27*], $\bar{x}$ = 1.29 ± 0.08 times wider than long, n = 14), moderately robust. Joint uniting halves of bone usually straight in ventral view, slightly sinuous in exceptional specimens. Anterior blade rather shallow, scarcely angled downward relative to plane of dentigerous surface. Dentigerous area 1.34-1.78 (1.57*) ($\bar{x}$ = 1.55 ± 0.15, n = 13) times wider than long. Anterior and lateral pharyngeal teeth rather small, with laterally compressed bicuspid crowns. In most specimens, about 4-8 posteromedian teeth (2-4 in each of middle two columns) are coarser, with rounded, submolariform but cuspidate crowns (with a distinct median and a small anterior cusp). (However, one of the exceptional fishes [72.5 mm SL] with a sinuous [i.e., a strengthened] median pharyngeal-bone joint has approx. 22 enlarged posteromedian teeth, about 8 of them unusually well molarized with flat-topped crowns having a small median cusp but no anterior cusp.) Pharyngeal teeth 30-43* ($\bar{x}$ = 35.7 ± 4.1, n = 14; not correlated with SL) in posterior row, 6-10 (9*, 10*) in median column, 5-9 (8*, 9*) in oblique posteromedian to midlateral row, approx. 20-22 along lateral edge.

Gut length approx. 150% of SL.

Coloration.--The live, 86.5-mm SL holotype, a sexually active male with coloration less than maximally intense (Fig. 40): Upper surfaces of nape and head dusky. Upper lip metallic blue-green, lacrimal and cheek washed with metallic deep blue. Branchiostegal membrane black. An indistinct blackish blotch posterior to eye. Opercular spot large, black. Iris of eye dusky with narrow golden inner ring. Body gray-brown dorsally; ventral half of flanks darker, scales in this region metallic blue-green. Blackish vertical bars: 1 on nape, 9 below dorsal-fin base, 2 on caudal peduncle. Seven quadrangular black dorsal midline spots, the first 5 along dorsal-fin base, the last 2 atop caudal peduncle. Three black primary lateral spots on body: suprapectoral spot 7 scales long by 2-1/2 scales high, in and above first longitudinal scale row above lateral body midline, below (downward and forward from) lateral-line scales 9-15 and separated from lateral line by 1/2-1 scale row; supraanal spot 5 scales long by 3 scales high, vertically centered in longitudinal scale row containing lower part of lateral line; precaudal spot vertically centered in same row as preceding, at end of caudal peduncle and extending onto caudal-fin base. Two small, longitudinally elongate accessory spots above upper part of lateral line: one centered below first dorsal-fin spine, other below fourth spine. Fins: Dorsal blackish, lappets orange distally, white proximally. Caudal blackish, outer rays darker. Anal blackish, without eggspots. Pelvics blackish, darkest anteriorly. Pectorals unspotted, rays brown, membrane colorless.

A live male in breeding condition from Domwe Island was almost uniformly blue-black on head and body, with bars faintly distinguishable but spot pattern entirely obscured; dorsal midline of nape with short (half length of eye) orange-white blaze immediately anterior to dorsal-fin origin; dorsal fin with proximal half deep blue, distal half vivid orange; anal fin uniformly blackish with no eggspots or other colored areas.

Live adult females (Fig. 42) and juveniles of both sexes are medium brown on head and body, somewhat lighter ventrally. Chest, belly, and ventral head surfaces whitish. Vertical bars indistinct; spots dark brown. Median fins brownish; dorsal anteriorly with broad dark brown margin, irregular brown maculae in posterior half of fin.

Preserved, the coloration is essentially unchanged except for loss of orange and metallic blue from sexually active males. Lateral spots, obscured or lost in highly colored males, reappear in death.

Individual variation in color pattern: There are invariably 3 primary lateral spots, but their shape is variable. The suprapectoral spot ranges from longitudinally elongate to virtually square. It may be separated from, or may touch, the upper lateral-line segment, but never extends distinctly above this part of the lateral line in this species.

(In the 39.0-mm SL fish from Nkhata Bay that is tentatively identified as C. lithobates, the suprapectoral spot is exceptionally elongate and medially faint, hence appearing double.) The vertical bars in C. lithobates vary considerably in number, with 5-9 (mode 7) below base of dorsal fin. Some fishes have 1 or more of the vertical bars Y-shaped. Dorsal midline spots 4-6 along base of dorsal fin and 0-2 along caudal peduncle. Accessory spots in nuchal region are quite variable, with from 1-1/2 to 3 on each side. Some fishes have a distinct lacrimal stripe from orbit to above posterior end of upper jaw.

Ontogenetic change in color pattern is minimal in this species. The accessory spot(s), present in larvae, are retained in adults (cf. lost in C. anagenys).

Distribution.--Widely distributed in southern Lake Malawi. A single juvenile tentatively referred to this species was collected at Nkhata Bay on the central western shore of the lake.

Ecology.--Cyrtocara lithobates is a common, diurnally active, small demersal species inhabiting rocky shores and feeding on zooplankton within about 1 m of the substrate. In some places it is the most abundant species of rocky-shore haplochromine, apart from members of the mbuna assemblage. I have frequently observed adults while skin- or SCUBA diving. The depth range of this species extends from near the surface to at least 20 m. Groups of up to 10 nonterritorial adults commonly feed in a group, picking individual plankters from the water column; the unusually large eyes of the species suggest that it has good vision.

Of 8 stomachs I examined, 7 (from fishes 53.5-78.0 mm SL representing two localities) contained ingested matter. This material consisted almost entirely of planktonic crustaceans, chiefly whole animals. Diaptomid copepods predominated, but the cladoceran <u>Diaphanosoma excisum</u> was present in 3 stomachs. In addition to zooplankton, one stomach contained some unidentified organic matter.

While collecting fishes with ichthyocide on 3 August 1980 near the northern tip of Domwe Island, I saw more than 100 individuals of <u>C. lithobates</u>. The substrate here was a steep rocky slope with large boulders and some sandy areas. This species was commoner here in 6-20 m than in <6 m. I saw at least 3 mouthbrooding females and 6 highly colored males in the former depth range. Also, on 19 August 1980 I saw a male in breeding color and 2 mouthbrooding females in 20 m off Thumbi Island West. However, reproductive activity is not restricted to August; the holotype, a sexually active male, was collected during May. Females as small as 67 mm SL have mature orange ovarian ova.

Etymology.--The specific name, derived from the Greek <u>lithos</u>, stone, and <u>bates</u>, one who haunts, refers to the rocky habitat of this species, which it shares with few Malawian haplochromines apart from members of the mbuna assemblage. The name is treated as a noun in apposition with the generic name.

The native name at Chembe, Malawi, is <u>kakhobwe</u> (pronounced ka-cob'weh). This Chichewa noun is the name of a spotted local variety of edible bean, an allusion to the spot pattern of the fish (E. S. Chamveka, pers. comm.).

Cyrtocara brooksi, new species

Figs. 45-48, Table 9

Holotype.--USNM, a sexually active male 114.5 mm SL (Fig. 45), field collection number MKO-80-130, collected 18-19 August 1980 by M. K. Oliver, K. R. McKaye, and T. D. Kocher using 182-m length of trammel net plus experimental gill net set in series obliquely to shore in N-S direction, overnight in 15-65 m depth, over large boulders with some sand at deep end, 75-200 m S of SW corner of Thumbi Island West (14°01'00"S, 34°48'17"E), Lake Malawi, Malawi.

Paratypes.--All from the Malawi side of Lake Malawi. 5 specimens, USNM, 113.5-123.2 mm SL, same data as holotype; 1 specimen, USNM, 115.7 mm SL, MKO-80-94, 3-4 August 1980, M. K. Oliver, K. R. McKaye, and T. D. Kocher, trammel net over sand with rocks, 20-200 m offshore from bay on S shore Thumbi Island West 200 m from its western tip (14°01'00"S, 34°48'23"E), depth 27-60 m; 1 specimen, USNM, 115.0 mm SL, MKO-80-95, 4-5 August 1980, same collectors and locality as immediately preceding, depth 41-67 m; 1 specimen, USNM, 118.0 mm SL, MKO-80-97, 5-6 August 1980, same collectors and locality as 2nd preceding, depth 41-67 m; 1 specimen, USNM, 117.0 mm SL, 16 July 1972, Lake Malawi Trawling Survey (LMTS), bottom trawled off Monkey Bay (approx. 14°04'S, 34°57'E), depth 73-91 m; 4 specimens, USNM, 101.0-115.5 mm SL, 22 July 1971, LMTS, bottom trawled, station Mid North (14°00'00"-14°01'12"S, 34°39'18"-34°39'43"E), depth 86 m; 6 specimens, USNM, 103.5-117.5 mm SL, 23 May 1968, LMTS, bottom trawled 5.6 km off Zambo (approx. 14°03'S, 34°58'E), depth 79-81 m; 2 specimens, USNM (cleared and counterstained), 109.0-113.0 mm SL, same data as immediately preceding.

Diagnosis.--A three-spotted haplochromine of moderate size (reaching approx. 125 mm SL) and body depth (32%-40% SL) with longitudinally elongate suprapectoral spot placed entirely below upper segment of lateral line (Figs. 45, 46). Distinguishable from all other three-spotted Malawian cichlids by the above characteristics together with the following: 11 or 12 gill rakers on lower limb of outer arch; crowns of pharyngeal teeth all laterally compressed and cuspidate (Fig. 47); head long (head length 36%-39% SL, predorsal length 37%-41% SL). See also key.

Description.--Based on holotype and 21 paratypes, 101.0-123.2 mm SL. Dorsal-fin spines and segmented rays XV,10 (1), XVI,9 (1), XVI,10^* (18), XVII,9 (2); anal-fin spines and segmented rays III,9^* (22). Lateral-line scales 31 (1), 32^* (14), 33 (5); upper part with 21 (1), 22 (2), 23 (4), 24^* (7), 25 (4), 26 (2); lower part with 5 (1), 8 (1), 10^* (2), 11 (1), 12 (3), 13 (3), 14 (1), 15 (5), 16 (1), 17 (1), 19 (1); lateral-line scales on caudal fin 0 (2), 1 (5), 2^* (10), 3 (1). Scales ctenoid; transverse scales from dorsal-fin origin to lateral line 4 (1), 5^* (12), 6 (5); predorsal scales approx. 16 (3), 17 (4), 18^* (8), 19 (1), 20 (2); prepelvic scales approx. 17 (1), 20 (3), 21 (3), 22^* (5), 24 (1), 26 (2), 27 (1); scales between pectoral- and pelvic-fin bases 6 (7), 7^* (11), 8 (1); belly scales approx. 20 (4), 21 (4), 22^* (3), 23 (1), 24 (3); scale rows on cheek 3 (1), 4^* (11), 5 (8); scales around caudal peduncle 16^* (20). Gill rakers on outer arch 4 (5), 5^* (15) + 1^* + 11 (6), 12^* (14); posterior rakers simple in a few fishes, but usually each with 2-4 lobes or points; anterior rakers simple, short. Vertebrae 14 + 16 (1), 14 + 17 (1). Hypurals unfused (1), or 3 + 4 fused (1).

Morphometrics. (Regression analyses of principal ratios are given in Table 9. Despite narrow length range of sample, regression coefficients and intercepts appear reasonable and correlation coefficients are high.) Reaching approx. 125 mm SL. In SL: Head length 361-388 (367*) ($\bar{x}$ = 372.7 ± 7.5, n = 20); body depth 327-376 (372*) ($\bar{x}$ = 352.7 ± 13.4, n = 20); predorsal length 374-411 (383*) ($\bar{x}$ = 390.0 ± 9.6, n = 20); prepelvic length 437-472 (461*) ($\bar{x}$ = 452.6 ± 10.2, n = 19); belly length 248-306 (289*) ($\bar{x}$ = 283.6 ± 15.0, n = 19); dorsal-fin base length 509-540 (515*) ($\bar{x}$ = 523.7 ± 8.8, n = 20); total dorsal-fin length 630-720 (712*) ($\bar{x}$ = 674.6 ± 27.0, n = 19); last dorsal-fin spine 122-150 (138*) ($\bar{x}$ = 135.9 ± 8.0, n = 18); anal-fin base length 168-188 (182*) ($\bar{x}$ = 177.0 ± 5.7, n = 20); total anal-fin length 286-383 (379*) ($\bar{x}$ = 321.2 ± 31.1, n = 20); last anal-fin spine 130-156 (146*) ($\bar{x}$ = 143.3 ± 7.5, n = 20); caudal-peduncle length 138*-165 ($\bar{x}$ = 149.0 ± 7.4, n = 20); caudal-peduncle length/depth 1.04*-1.36 ($\bar{x}$ = 1.17 ± 0.08, n = 20); pectoral-fin length 345-380 (369*) ($\bar{x}$ = 363.9 ± 10.8, n = 20); pelvic-fin length 258-322* ($\bar{x}$ = 282.3 ± 17.1, n = 20), longer in mature males than in females; caudal-fin length 241-293 (273*) ($\bar{x}$ = 268.9 ± 12.2, n = 18).

In HL: Head width 424-481 (469*) ($\bar{x}$ = 449.5 ± 14.1, n = 20); snout length 334-369* ($\bar{x}$ = 352.8 ± 10.2, n = 20); snout width 326-413 (405*) ($\bar{x}$ = 358.9 ± 24.8, n = 19); orbit length 265-296 (276*) ($\bar{x}$ = 275.8 ± 7.4, n = 20); preorbital depth 193-218 (207*) ($\bar{x}$ = 204.3 ± 6.1, n = 20); interorbital width 189-226* ($\bar{x}$ = 206.2 ± 9.8, n = 20); postorbital head length 379-418 (405*) ($\bar{x}$ = 401.4 ± 8.4, n = 20); cheek depth 245-279 (255*) ($\bar{x}$ = 258.6 ± 9.4, n = 20); upper-jaw length 352-378 (374*) ($\bar{x}$ = 364.0 ± 7.6, n = 20); premaxillary ascending processes 252-279 (267*) ($\bar{x}$ = 265.9 ± 7.2, n = 20); lower-jaw length 442-487 (476*) ($\bar{x}$ = 465.9 ±

13.3, n = 20); lower-jaw length/width 1.21-1.92 (1.35^{*}) ($\bar{x}$ = 1.61 ± 0.20, n = 18); pharyngeal-bone length 193-224 (207^{*}) ($\bar{x}$ = 212.9 ± 8.9, n = 12); pharyngeal-bone width 252^{*}-276 ($\bar{x}$ = 264.7 ± 7.3, n = 13).

Body moderately deep and compressed. Dorsal profile more pronounced than ventral. Ventral profile often sharply angled at posterior end of lower jaw, otherwise smoothly rounded from chin to anus. Dorsal head profile distinctly interrupted by prominent premaxillary ascending processes; snout straight or slightly convex, interorbital region straight to concave, nape convex. Orbit separated from profile by approx. 20%-40% of eye depth. Eye varying from virtually round to distinctly elliptical with long axis longitudinal. Snout angle 25°-40° ($30^{\circ *}$) to horizontal, frontal angle (above orbit) 30°-50° ($35^{\circ *}$), nuchal angle 10°-20° ($15^{\circ *}$). Jaws rather broadly rounded anteriorly in dorsal view, with prominent chin sometimes evident in middle of curve. Gape distinctly oblique. Ventral profile of lower jaw inclined at 35°-$40^{\circ *}$ to horizontal. Lower jaw moderately projecting in all specimens. Chin strong, varying from rounded to right-angled in profile, often with a ventrally directed protuberance. Premaxillae slightly beaklike in some specimens. Posterior tip of maxilla reaching a vertical through anterior orbital margin in a few fishes, but more commonly anterior to this level. Lips slightly thickened. Upper lip fold continuous across premaxillary symphysis, lower lip fold interrupted at dentary symphysis. Cephalic lateral-line pores and canals not enlarged.

Caudal fin distinctly emarginate, lower lobe a little shorter than upper; densely covered with small scales nearly to ends of outer rays and over at least proximal 75% on middle rays. Dorsal fin apparently lacking basal scales, or with only a few small, inconspicuous scales (at most in rows of 2) in region of posterior spines and anterior segmented rays. (However, more such basal scales are visible in the dorsal fin of the 113.0-mm SL cleared and counterstained fish. It has basal scales in the region between spine XIII and segmented ray 5, in 1 or 2 rows between each 2 consecutive rays, with 1-5 scales per row. This may approximate the typical condition for this species, which would only be evident when the basal scales are alizarin stained.) Anal fin with several rows of basal scales in each fish examined (n = 11), each row with 1-9 scales, longest row usually between spine III and segmented ray 1, or rays 1-2. Pectorals lanceolate. Pelvics elongate in sexually active males, but first ray not appreciably produced.

Teeth in outer row of each jaw (Fig. 48) small, closely spaced, slightly movable; crowns slightly compressed and incurved. In the upper jaw, the teeth are exclusively unicuspid in half the specimens (including the holotype). In most of the remaining fishes, the outer upper teeth are predominantly unicuspids, but bicuspids are also present, and these may even predominate anteriorly and anterolaterally). (In a single fish, most of the anterior and anterolateral teeth are tricuspids and all other teeth in this region are bicuspids; the midlateral teeth are intermixed bi- and unicuspids, and the posterolateral to posterior teeth are all unicuspids.) In the lower jaw, all outer teeth are unicuspid only in a minority of specimens (including the holotype). More commonly, the lower anterior to lateral teeth are a mixture of uni- and bicuspids, bi- and tricuspids, or all three types. Posteriorly, the lower-jaw teeth are likewise variable, being either bi- or unicuspids, but the latter definitely predominate.

In both jaws, the outer teeth have rather elongate crowns; unicuspids have a long, acutely pointed cusp, and bi- and tricuspids have the minor cusp(s) much smaller than the long, acute major cusp. Number of teeth in outer row of upper jaw 69-85 (84^*) ($\bar{x} = 77.0 \pm 5.0$, n = 22; positively correlated with SL, r = 0.492, $p<0.02$; number of teeth = $[0.396 \pm 0.157]SL \pm [32.363 \pm 17.666]$; intercept not significantly different from 0, $0.1>p>0.05$).

Inner teeth in 2-4 rows anteriorly in upper jaw, 2-3 rows in lower; rows well-defined, closely spaced, separated by a distinct gap from outer teeth. Crowns usually unicuspid, exceptionally bi- or tricuspid or a mixture of types; bi- and tricuspid teeth with small minor cusp(s) and acute major cusp. Dentary symphysis normal (inner teeth not elevated above level of outer teeth).

Lower pharyngeal bone (Fig. 47) Y-shaped, its posterior edge indented; bone moderately wide (1.17-1.36 [1.22^*], $\bar{x} = 1.25 \pm 0.05$ times wider than long, n = 12), rather lightly built. Joint uniting halves of bone usually straight in ventral view (with a short sinuous region posteriorly in 1 of 13 fishes). Anterior blade moderately deep, not angled downward relative to plane of dentigerous surface. Dentigerous area 1.23-1.45 (1.39^*) ($\bar{x} = 1.35 \pm 0.07$, n = 13) times wider than long. Pharyngeal teeth 22-30 (27^*) ($\bar{x} = 25.4 \pm 2.2$, n = 15; not correlated with SL) in posterior row, 8-13 (11^*) in median column, 5-7 (6^*) in oblique posteromedian to midlateral row, 15-23 along lateral edge (n = 15).

Gut length approx. 140% of SL.

Coloration.--The live, 114.5-mm SL holotype, a sexually active male (Fig. 45): Dorsal surfaces of nape and head blackish. Jaws and lateral head surfaces metallic blue-green. Branchiostegal membrane and ventral chest surface black. Opercular spot large, dark. Iris of eye dusky with golden inner ring. Body dusky greenish blue dorsally, light gray with blue overlay laterally, caudal peduncle dark gray with blue overlay. Belly gray. Blue-black vertical bars: 1 on nape, 7 below dorsal-fin base, 2 on caudal peduncle. Six indistinct quadrangular black dorsal midline spots, the first 4 below spinous dorsal fin, the last 2 atop caudal peduncle. Three blue-black lateral spots on body: suprapectoral spot approx. 7 scales long by 1 to 1-1/2 scales high, in first longitudinal scale row above lateral body midline, below lateral-line scales 8-14 and separated from lateral line by 1/2-1 scale row; supraanal spot approx. 7 scales long by 1 scale high, in longitudinal scale row containing lower part of lateral line; precaudal spot round, centered on base of caudal fin but extending slightly onto caudal peduncle. All 3 lateral spots faintly connected to form a longitudinal stripe. An indistinct longitudinal stripe above upper part of lateral line from lateral extrascapular bone to lateral-line scale 7. Fins: Dorsal gray with dark-edged, oval orange interradial maculae, more distinct on posterior half of fin; lappets and distal margin of soft dorsal orange distally, white proximally. Caudal dusky blue with faint maculae medially. Anal blackish tinged with orange; at least 3 opaque whitish, elliptical interradial spots, without distinct margins or colorless surrounding rings, along middle of fin and 3 similar but smaller spots along distal fin margin. Pelvics blackish with narrow pale leading edge. Pectorals clear, unspotted, colorless. (Described from color transparencies.)

In other sexually active males of this species, the anal spots were pale yellow or pinkish yellow.

Preserved, specimens retain the color pattern unchanged but the ground color becomes gray or brown, some specimens distinctly silvery on the lower flanks.

Individual variation in color pattern: Vertical bars 6-8 (usually 7 or 8) below base of dorsal fin. Dorsal midline spots 3 or 4 along dorsal-fin base (the last below origin of soft dorsal), 1 or 2 on caudal peduncle. Lateral spots: The suprapectoral spot is always longer than high, varying from 5 to 7 scales long. It is always completely below the upper lateral-line segment. The three lateral spots are discernible in all specimens, but often appear faintly connected as in the holotype, as if they are dark regions of a continuous longitudinal stripe. (However, this faint stripe never continues forward from the suprapectoral spot.) In several fishes no such faint stripe is discernible but the vertical bars between the suprapectoral and supraanal spots are darkened at the level where the stripe would be. The longitudinal stripe above the anterior portion of the upper lateral-line segment is also variable in length and continuity. At one extreme, it may consist entirely of 3 or 4 disconnected spots; at the other, it is a continuous stripe (often curved upward anteriorly, nearly reaching dorsal midline above eye) that extends posteriorly to above anterior third of suprapectoral spot, then continues backward along upper part of lateral line as darkened spots in the vertical bars, this row of dark spots extending to the posterior end of the dorsal-fin base.

Ontogenetic change in the color pattern is unknown, since the available specimens are all adult and represent a narrow range of standard lengths.

Distribution.--Known from southern Lake Malawi: southwest arm, Thumbi Island West, and southeast arm.

Ecology.--Cyrtocara brooksi is a demersal species (presumed to be a piscivore) from rather deep water; its known depth range is 60-86 m, but it probably occurs somewhat shallower and deeper. It occurs over both open sand or soft bottom, and boulders near sand.

Etymology.--The specific name is intended to honor John Langdon Brooks, distinguished student of lake faunas, whose classic review of speciation in ancient lakes (Brooks, 1950) helped to steer my interests toward Lake Malawi.

Cyrtocara anagenys, new species

Figs. 49-53

Undescribed three-spotted '*Haplochromis*' species: McKaye and Oliver, 1980: 1287 and pl. I (underwater photograph).

Holotype.--USNM, a mouthbrooding female 200.0 mm SL (Figs. 49, 50), field collection number MKO-80-94, collected 3-4 August 1980 by M. K. Oliver, K. R. McKaye, and T. D. Kocher using 182-m length of trammel net (10-inch square wall, 1-inch square mesh, 6 feet deep) set overnight in 27-60 m depth (specimen caught in midsection of net, therefore depth approx. 40-50 m), over sand with rocks, 20-200 m offshore from Thumbi Island West, Lake Malawi, Malawi, at a bay on the south shore of the island 200 m E of its western tip (14°01'00"S, 34°48'23"E).

Paratypes.--3 larval specimens, USNM, 15.4-16.1 mm SL, recovered from buccal cavity of holotype, same data as holotype; 1 specimen, USNM, 98.0 mm SL, collected during 1975 at unknown locality in Lake Malawi by S. Grant, found dead in shipment of aquarium fishes (jaw teeth and lips damaged); 1 specimen, MFRU, 147.0 mm SL, 12 November 1969, LMTS, otter trawl fished for approx. 5 km NNW from a point approx. 1 km W of northern tip of Boadzulu Island, SE arm of lake (approx. 14°13'S, 35°08'E), depth 37-40 m; 1 specimen, MFRU, approx. 180 mm SL (specimen badly distorted), 21 September 1976, LMTS, otter trawled during cruise out of Monkey Bay, exact locality and depth unknown.

Diagnosis.--A relatively large, elongate haplochromine (reaching at least 200 mm SL; body depth 26%-34% SL; 34-35 lateral-line scales) with longitudinally elongate suprapectoral spot placed entirely below upper lateral-line segment (Fig. 49). Distinguishable from all other "three-spotted" cichlids in the Lake Malawi fauna by its specialized jaws (Fig. 51). The premaxillae are laterally compressed and rather beaklike, their anterior symphysis projecting slightly but distinctly beyond the tip of the lower jaw. Furthermore, the anterior half of the alveolar process of each dentary appears rolled outward so that its dentigerous surface slopes outward and downward. As a consequence of this outward rotation, the lingual edge of the dentary symphysis is elevated to form a low median prominence that fits between the alveolar processes of the premaxillae when the mouth is closed. Consequently, the inner rows of dentary teeth are placed distinctly above the level of the outer dentary tooth row, which is implanted along the external surface of the bone. See also key.

Description.--Based primarily on 3 specimens, 98-200 mm SL. Data from three larvae (15.4-16.1 mm SL) are included as noted. Certain counts, and data on the pharyngeal bone of an additional, distorted paratype (approx. 180 mm SL) are also included. Dorsal-fin spines and segmented rays XVI,11 (1), XVI,12 (1), XVII,10 (1), XVII,11* (1); anal-fin spines and segmented rays III,8* (1), III,9 (3). Lateral-line scales 34 (1), 35* (3); upper part with 26* (2), 27 (1), 28 (1); lower part with 14 (1), 15 (1), 18* (1), 20 (1); lateral-line scales on caudal fin 1* (3), 2 (1). Scales ctenoid; transverse scales from dorsal-fin origin to lateral line 5 (1), 6* (1), 7 (1); predorsal scales approx. 15-19*; prepelvic scales approx. 20-26*; scales between pectoral- and pelvic-fin bases 7, 8*, 9*; belly scales approx. 24*-27; scale rows on cheek 3, 4*, 5*; scales around caudal peduncle 16*. Gill rakers on outer arch 3-4* + 1* + 10* (1), 11 (2), 12 (1). Vertebrae? Hypurals?

Morphometrics. Reaching 200 mm SL. In SL: Head length 354*-373

($\bar{x}$ = 360.8 ± 8.7, n = 4) (larvae: 329-342 [$\bar{x}$ = 334.0 ± 7.0, n = 3]); body depth 262-337 (285*) ($\bar{x}$ = 297.5 ± 31.9, n = 4) (larvae: 248-253 [$\bar{x}$ = 251.0 ± 2.6, n = 3]); predorsal length 367*-386 ($\bar{x}$ = 377.7 ± 9.7, n = 3); prepelvic length 406*-416 ($\bar{x}$ = 410.0 ± 5.3, n = 3); belly length 276*-285 ($\bar{x}$ = 279.3 ± 4.9, n = 3); dorsal-fin base length 507-532 (528*) ($\bar{x}$ = 522.3 ± 13.4, n = 3); total dorsal-fin length 623*-639 (n = 2); last dorsal-fin spine 114*-126 ($\bar{x}$ = 120.0 ± 6.0, n = 3); anal-fin base length 165*-168 ($\bar{x}$ = 166.7 ± 1.5, n = 3); total anal-fin length 244*-275 (n = 2); last anal-fin spine 104*-133 ($\bar{x}$ = 119.0 ± 14.5, n = 3); caudal-peduncle length 163-182* ($\bar{x}$ = 175.3 ± 10.7, n = 3); caudal-peduncle length/depth 1.33-1.78* ($\bar{x}$ = 1.57 ± 0.23, n = 3); pectoral-fin length 277*-313 (n = 2); pelvic-fin length 219*-237 (n = 2); caudal-fin length 220*-231 (n = 2).

In HL: Head width 371*-429 ($\bar{x}$ = 398.0 ± 29.2, n = 3); snout length 359-431* ($\bar{x}$ = 400.7 ± 37.3, n = 3) (larvae: 245 [n = 1]); snout width 282-307 (304*) ($\bar{x}$ = 297.7 ± 13.7, n = 3); orbit length 218*-287 ($\bar{x}$ = 247.3 ± 35.6, n = 3) (larvae: 377-396 [$\bar{x}$ = 388.3 ± 10.0, n = 3]); preorbital depth 178-219* ($\bar{x}$ = 202.3 ± 21.5, n = 3); interorbital width 167-187* ($\bar{x}$ = 180.0 ± 11.3, n = 3) (larvae: 208 [n = 1]); postorbital head length 382-400* ($\bar{x}$ = 388.3 ± 10.1, n = 3) (larvae: 415 [n = 1]); cheek depth 198-238* ($\bar{x}$ = 221.3 ± 20.8, n = 3); upper-jaw length 389-396* ($\bar{x}$ = 393.0 ± 3.6, n = 3); premaxillary ascending processes 336-347 (338*) ($\bar{x}$ = 340.3 ± 5.9, n = 3); lower-jaw length 442-463* ($\bar{x}$ = 450.0 ± 11.4, n = 3) (larvae: 377 [n = 1]); lower-jaw length/width 1.82*-2.04 ($\bar{x}$ = 1.93 ± 0.11, n = 3); pharyngeal-bone length 186-207 (201*) ($\bar{x}$ = 197.3 ± 9.0, n = 4); pharyngeal-bone width 253*-279 ($\bar{x}$ = 268.0 ± 11.6, n = 4).

Body elongate, moderately compressed. Dorsal and ventral profiles equally pronounced. Ventral profile slightly and smoothly rounded from chin to anus. Dorsal head profile interrupted by prominent premaxillary ascending processes, straight to concave above orbit, slightly convex along nape. Orbit close to frontal profile in lateral view (separated from profile by approx. 10%-20% of eye depth). Eye slightly elliptical, its long axis longitudinal. Snout angle $35^{\circ *}$ to horizontal, frontal angle (above orbit) $20^{\circ *}$-30°, nuchal angle $10^{\circ *}$-20°. Jaws evenly rounded anteriorly in dorsal view. Gape very slightly oblique; ventral profile of lower jaw inclined at 20°-30° ($25^{\circ *}$)to horizontal. Tip of lower jaw slightly behind level of upper-jaw tip. Chin rounded, receding, without externally visible protuberance. Premaxillae rather beaklike. Posterior tip of maxilla nearly reaching a vertical through anterior margin of orbit. Lips not thickened. Upper lip fold continuous across premaxillary symphysis, lower lip fold interrupted at dentary symphysis. Cephalic lateral-line pores and canals not enlarged.

Caudal fin emarginate, densely covered with small scales extending nearly to ends of outer rays. Dorsal and anal fins with a few small, sparsely distributed interradial scales on proximal 1/3 of each fin membrane. Pectorals lanceolate.

Teeth in outer row of each jaw small, slightly movable, buried nearly to crown in oral mucosa; crowns acutely conical, distinctly incurved. Number of teeth in outer row of upper jaw approx. 60 in 147-mm SL fish, 80 in 200-mm fish.

Inner teeth in 2-4 irregular rows anteriorly in each jaw. Inner rows separated by a small gap from outer teeth. Inner teeth conical, incurved, resembling miniatures of outer teeth. Because of apparent outward rotation of anterior portion of dentary during ontogeny, its dentigerous surface slopes outward and downward, and inner tooth rows are implanted distinctly above level of outer row (see Diagnosis [above] and Fig. 51).

Lower pharyngeal bone (Fig. 52) Y-shaped, its posterior edge concave; bone rather wide (1.26*-1.42, $\bar{x}$ = 1.36 ± 0.07 times wider than long, n = 4), rather lightly built. Posteriorly on ventral surface of bone there is a distinct, ventrally directed median bump. Pharyngeal bone distinctively shaped in posterior view (Fig. 52c); posterior processes appear bent downward so that dentigerous surface bulges upward along its midline. This unusual configuration is most pronounced in the holotype (the largest specimen); more information is required to determine whether it is an individual variation or a characteristic of large specimens. Joint uniting halves of bone straight or slightly sinuous in ventral view. Anterior blade rather deep, angled downward relative to midline of dentigerous surface. Dentigerous area 1.36*-1.49 ($\bar{x}$ = 1.43 ± 0.06, n = 4) times wider than long. Pharyngeal teeth robust, subcylindrical with prominent major cusp; 16-21 (18*) in posterior row, 7-10 (8*, 10*) in median column, 4-6 (4*, 5*) in oblique posteromedian to midlateral row, 14-17* along lateral edge (n = 4).

Gut short, 70% of SL (140 mm in the 200-mm SL holotype).

Coloration.--The freshly killed holotype, a mouthbrooding female 200 mm SL (Figs. 49, 50): Head brown, becoming darkish gray on snout and upper jaw. Underside of head white. Lower jaw white with gray longitudinal stripe on its anterior third. Iris of eye dusky with irregular golden inner ring. Opercular spot gray, indistinct. No distinct head bars. Body tan, darkest on dorsum, becoming white ventral to level of pectoral fin. No vertical bars. Five longitudinally elongate, black dorsal midline spots, the first 4 each about 4 scales long: first below dorsal-fin origin; second below middle of spinous dorsal; third below origin of soft dorsal; fourth below posterior end of dorsal fin and on anterior part of caudal peduncle; fifth shorter than other spots, at end of caudal peduncle. A small, round gray spot on dorsum between second and third dorsal midline spots. Three black lateral spots on body: suprapectoral spot 4 scales long by 1 scale high, in first longitudinal scale row above lateral body midline, below (downward and forward from) lateral-line scales 10-13 and separated from lateral line by 1 scale row; supraanal spot 3-4 scales long by 1-1/2 scales high, in longitudinal scale row containing lower lateral-line segment; precaudal spot in same scale row as preceding, at end of caudal peduncle and extending onto caudal-fin base, narrowly connected anteriorly with fifth dorsal midline spot above it. All lateral spots and dorsal midline spots nearly symmetrical on both sides of body. Fins: Dorsal blue-gray, anterior half broadly edged with black, lappets orange distally, white proximally; distinct round, dark-edged orange-brown interradial maculae, better defined in soft dorsal. Anal white proximally, becoming gray distally. Caudal orange-brown, with round interradial maculae posteriorly on middle of fin. Pelvics white. Pectorals unspotted, rays brown, membrane colorless.

Preserved, the coloration of the holotype is virtually unchanged except for loss of orange.

Individual variation in color pattern of juvenile and adult fishes is slight in the available material. There may be either 5 or 6 dorsal midline spots (4 or 5 of them along dorsal-fin base). The suprapectoral spot varies from 4 to 5 scales long and is quite consistent in placement, as are the other 2 lateral spots.

Ontogenetic change in color pattern. Larvae (Fig. 53) have 5 dorsal midline spots like those of juveniles and adults. The 3 lateral spots of the larvae are relatively larger than those of adults. Significantly, all 3 larvae have an additional small dark accessory spot on the upper lateral-line segment between the first dorsal midline spot and the suprapectoral spot. This accessory spot is lost in juvenile and adult _C_. _anagenys_ and related species, but is retained in adults of some other "three-spotted" Malawian haplochromines (e.g., _C_. _lithobates_, _C_. _heterodon_) either as 1-3 separate spots or as an anterodorsal extension of the suprapectoral spot. Larvae have 7 to 9 faint vertical bars on the body; in larvae with 7 bars the 3 main lateral spots appear as darkened widenings of the third, fifth, and seventh bars (Fig. 53).

Distribution.--Southern Lake Malawi (Thumbi Island West and southeast arm).

Ecology.--_Cyrtocara_ _anagenys_ is a demersal, piscivorous predator inhabiting moderately deep water. The species is known from both a sandy substrate and an area of sand-rock transition in depths of 25-50 m. One individual was seen to make unsuccessful predatory strikes at a mixed brood of young cichlids belonging to two species that were apparently being defended by a bagrid catfish (McKaye and Oliver, 1980).

The holotype, a mouthbrooding female 200 mm SL, was collected in early August. The ovaries of this fish are subequal in size (maximum diameter 4 mm), the left one slightly narrower, and do not appear to be fully enlarged. They contain oocytes and immature ova up to 1.0 mm in diameter, but no mature ova.

Etymology.--The specific name anagenys, from the Greek prefix ana-, backward or back, and genys, lower jaw, refers to the placement of the tip of the lower jaw behind the level of that of the upper jaw, a distinctly unusual condition in cichlids. The name is treated as a noun in apposition with the generic name.

The native name at Chembe, Malawi, is ngungu (pronounced n-goong'goo), a Chichewa word referring to the elongate body. The word is a proper noun used only in connection with this species (E. S. Chamveka, pers. comm.).

IDENTIFYING SPECIES IN THE THREE-SPOT ASSEMBLAGE

Anyone who has tried to use existing keys to identify Malawian haplochromines (e.g., those of Trewavas, 1931, 1935; Iles, 1960; Jackson, 1961) knows how frustrating the experience can be. The reasons include couplets in which alternatives overlap, qualitative judgments are vaguely distinguished, multiple typographical errors occur, or the variability of a species is underestimated. The entire cichlid fauna of Lake Malawi is in need of critical taxonomic revision to permit the detailed, illustrated description of all species and to provide the morphological data needed for improved keys.

Some recent authors have doubted that usable keys to closely related haplochromines can even be written, because most counts and measurements overlap (the ". . . lack of clear-cut morphological distinction [among Lewis's newly described species of Labidochromis, a haplochromine genus in Lake Malawi] makes an attempt to construct a morphological key rather pointless" [Lewis, 1982: 259]; one of "the practical difficulties frustrating taxonomic studies on haplochromine cichlids" [of Lake Victoria] is "the impossibility of constructing a simple identification-key" [Barel et al., 1977: 336, 337]). Yet, the publication of good keys is especially important in large, confusing groups like the cichlid species flocks. Writing a usable if imperfect key is admittedly a challenge, but is neither pointless nor impossible. If a species is real, it can be diagnosed; if diagnosable, it can be keyed.

A new key to the three-spot haplochromine assemblage of Lake Malawi is given below. It is based on my revisional studies of these fishes (work in progress), during which I have examined in detail the type material of nearly all described species with three spots. I have been able to collect, photograph alive, and examine additional specimens of most of these species. The sample sizes on which the key is based vary from a few to more than 60 fishes. The length range examined for most species extends from about 50-60 mm SL to the largest known adults. Therefore, it should be possible to key out even immature fishes of most species. For many metric characters, I assumed that actual parametric variation somewhat exceeds that in the sample available to me. Thus, two species distinginguished in a couplet are usually more different than the couplet implies.

The rationale of the key is that even a partly overlapping count or proportion has diagnostic value. Suppose that 10% of specimens belonging to each of two species overlap with the other species in character A, an easily examined feature. Suppose, further, that these species can be completely separated using character B, but that this feature is difficult to examine or interpret. There is no reason why character A cannot be used in one couplet to identify the 90% of specimens of one species that have values outside the range of overlap. The overlapping 10% of the first species can then be separated from the other species in the next couplet using difficult character B. Although the key is lengthened with such multiple entries, most specimens can thereby be identified using simple, unambiguous alternatives. Multiple entries do not imply that the species concerned are invalid, are polymodal for a character, or are even difficult to identify.

Several species are newly synonymized in the key, based on studies in progress. Full documentation will be published when the species are redescribed. In general, these species are synonymized because examination of new material, often extending the size range available to the original describer, led to the disappearance of the supposed gap (without the discovery of additional, valid distinctions).

In addition to the species here tentatively synonymized, several outstanding taxonomic problems in this assemblage are presently unresolved. (1) *Cyrtocara decorus* is doubtfully distinct from *C. argyrosoma* sensu Trewavas (and her material identified as the latter species may not be conspecific with the holotype of *C. argyrosoma*). Ambiguous specimens with conflicting scale and fin-ray counts (Trewavas, 1935: 87) are common. Until their status can be resolved, both species are retained here because two modal phenotypes are distinguishable. (2) The identity of *C. serranoides* is uncertain; the morphology reported in the key is based on my examination of the holotype, which retains no markings. This species is included in the key under the assumption that Trewavas (1935) was correct in assigning it to this assemblage. (3) Another problem concerns the identity of *C. quadrimaculatus*, whose type series may contain more than one species. *C. likomae* may be a valid species, but I cannot distinguish it from *C. quadrimaculatus* with the available evidence. (4) *C. jacksoni* and *C. borleyi* are not distinguishable by length of premaxillary ascending processes or pectoral fin (the criteria given by Iles, 1960: 280) according to my measurements of the type series of these species. These and other "utaka" species are in urgent need of revision, and the species concepts recognized here are sure to change.

The gender of the name *Cyrtocara* is unclear. In this dissertation I treat it as masculine so that the gender of species formerly classified in *Haplochromis* remains unchanged. This decision may prove to be incorrect.

Refer to Methods section for definitions of counts and measurements. Spot terminology is explained in Fig. 39. I would appreciate receiving suggestions on and corrections to this draft key.

KEY TO THE SPECIES OF MALAWIAN HAPLOCHROMINE CICHLIDS WITH THREE LATERAL SPOTS

1A. 7-14 gill rakers on lower limb of outer arch (excluding 1 in angle between upper and lower limb) 2

1B. More than 14 gill rakers on lower limb of outer arch 49

2A (1A). Suprapectoral spot entirely below upper part of lateral line, either separated from it or touching it from below (or this spot obscured by dark brown ground color of body) 3

2B. Suprapectoral spot extending, at least anteriorly, above upper part of lateral line 11

3A (2A). Lower pharyngeal bone with a posteromedian group of enlarged, submolariform teeth 4

3B. Lower pharyngeal bone with all teeth small to moderate, posteromedian teeth may be coarser than adjacent teeth but crowns all laterally compressed, none submolariform 5

4A (3A). Ground color of head and body brown or dark gray; body depth <35% SL; caudal-peduncle length <19% SL (habitat rocky shore) .... *Cyrtocara lithobates*, new species (part)

4B. Ground color of head and body silvery; body depth ≥ 35% SL; caudal-peduncle length >20% SL (habitat sandy or soft bottom) .... *Cyrtocara* new species P (part)

5A (3B). Ground color of head and body dark brown, even on ventral surfaces, usually obscuring lateral spots; suprapectoral spot, if visible, never longitudinally elongate; dorsal-fin lappets red in life .... *Cyrtocara modestus* (Günther, 1893)

5B. Ground color of head and body light to medium brown or gray, paler ventrally; lateral spots discernable, usually distinct;

suprapectoral spot longitudinally elongate or otherwise; dorsal-fin lappets not red in life, usually orange distally and white proximally 6

6A (5B). Upper jaw projecting slightly anterior to tip of lower jaw; toothed part of lower jaw appears rotated outward anteriorly so that its inner edge is elevated and inner teeth are implanted dorsal to outer teeth .... _Cyrtocara anagenys_, new species

6B. Lower jaw projecting anterior to upper jaw, or jaws equal; toothed part of lower jaw normal, not rotated outward anteriorly, its inner edge not elevated, inner teeth of lower jaw not implanted dorsal to outer teeth 7

7A (6B). Suprapectoral spot prominent and longitudinally elongate, its length at least twice its height, and separated by a gap from upper part of lateral line 8

7B. Suprapectoral spot prominent or indistinct, if prominent then not longitudinally elongate, its length less than twice its height, and touching upper part of lateral line 9

8A (7A). Head length <33% SL; predorsal length <37% SL; interorbital width >26% head length; premaxillary ascending processes >28% head length .... _Cyrtocara ovatus_ (Trewavas, 1935)

8B. Head length $\geq$36% SL; predorsal length >37% SL; interorbital width <23% head length; premaxillary ascending processes $\leq$28% head length .... _Cyrtocara brooksi_, new species

9A (7B). Lower jaw strong, chin prominent; premaxillary ascending processes prominent in frontal profile ..... _Cyrtocara serranoides_ (Ahl, 1927) (part) (=_Haplochromis ahli_ Trewavas, 1935, nom. nov.)

9B. Lower jaw rather weak, chin weak; premaxillary ascending processes not prominent 10

10A (9B). Dorsal fin with fewer than 17 spines; body depth <34% SL; maximum size <80 mm SL .... <u>Cyrtocara</u> <u>pleurospilus</u> (Trewavas, 1935) (part)

10B. Dorsal fin with 17 or more spines; body depth >35% SL; maximum size >200 mm SL .... <u>Cyrtocara</u> <u>auromarginatus</u> (Boulenger, 1908) (part)

11A (2B). In adult fishes: Suprapectoral spot, or supraanal spot, or both these spots extending dorsally to base of dorsal fin, forming saddle-like marking(s) .... (genus <u>Hemitilapia</u> Boulenger, 1902c, sensu Oliver, ms) 12

11B. In adult fishes: Neither suprapectoral nor supraanal spot extending dorsally to base of dorsal fin; or specimen not adult 16

12A (11A). Lower pharyngeal bone with a posteromedian group of enlarged teeth which have rounded, blunt crowns 13

12B. Lower pharyngeal bone with no distinctly enlarged teeth, crowns all laterally compressed and cuspidate 15

13A (12A, 21B, 22B). Lateral-line canals and pores of head distinctly enlarged; anterior teeth in outer row of upper and lower jaws slender and unicuspid in adults .... <u>Hemitilapia</u> <u>microstoma</u> (Trewavas, 1935) (part) (=<u>Trematocranus</u> <u>microstoma</u>, including <u>T.</u> <u>brevirostris</u> Trewavas, 1935)

13B. Lateral-line canals and pores of head not enlarged; anterior teeth in outer row of each jaw bicuspid throughout ontogeny 14

14A (13B). More than 65 teeth in outer row of upper jaw; lower pharyngeal bone somewhat enlarged, its median length ≤31% head length, its width <32% head length; joint uniting left and right halves of lower pharyngeal bone straight in ventral view; 11-15 teeth in median column of lower pharyngeal bone; head width ≤47.5% head length .... Hemitilapia intermedia (Trewavas, 1935) (part) (=Lethrinops intermedia)

14B. Fewer than 60 teeth in outer row of upper jaw; lower pharyngeal bone greatly enlarged, its median length ≥31% head length, its width ≥35% head length; joint uniting halves of lower pharyngeal bone sinuous in ventral view, forming a true suture; 5-8 teeth in median column of lower pharyngeal bone; head width 47.0%-53.3% head length .... Hemitilapia placodon (Regan, 1921) (part)

15A (12B). Outer jaw teeth movable, inclined toward symphysis, their crowns strongly compressed, spatulate, with rounded to obliquely truncate profile; teeth of lower pharyngeal bone small, fine, numerous, 9-16 in oblique posteromedian to midlateral row; precaudal spot present .... Hemitilapia oxyrhynchus Boulenger, 1902c (part)

15B. Outer jaw teeth scarcely movable, not inclined toward symphysis, their crowns weakly compressed, bi- or unicuspid, never spatulate with rounded to obliquely truncate profile; teeth of lower pharyngeal bone of moderate size, not numerous, 7-9 in oblique posteromedian to midlateral row; precaudal spot usually absent .... Hemitilapia labifer (Trewavas, 1935) (part)

16A (11B). Lower pharyngeal bone with at least a group of posteromedian teeth distinctly enlarged, their crowns varying from submolariform but weakly cuspidate to blunt or hemispherical 17

16B. Lower pharyngeal bone with no teeth distinctly enlarged, crowns all laterally compressed and cuspidate 25

17A (16A). Dorsal fin with 14-16 spines 18

17B. Dorsal fin with 17 or more spines 22

18A (17A). 7-12 gill rakers on lower limb of outer arch 19

18B. 13 or 14 gill rakers on lower limb of outer arch .... Cyrtocara new species P (part)

19A (18A). Head with a fatty hump; suprapectoral spot more or less rectangular, its long dimension longitudinal, its anteroventral corner often produced toward pelvic fin; live adults and subadults bright blue...................... Cyrtocara moorii Boulenger, 1902c

19B. Head without a fatty hump; suprapectoral spot more or less triangular, obliquely to transversely elongate, not produced anteroventrally; live adults and subadults not bright blue 20

20A (19B). Body depth ≤35% SL; dorsal-fin spines narrow and fragile; head length <32% SL .... Cyrtocara argyrosoma (Regan, 1921) (part)

20B. Body depth >35% SL; dorsal-fin spines normal, pungent; head length 31.5%-35.5% SL 21

21A (20B). Lower pharyngeal bone with <6 posteromedian teeth somewhat enlarged but distinctly cuspidate, not molariform, crowns laterally compressed; maximum size approx. 120 mm SL .... Cyrtocara tetrastigma (Günther, 1893) (part)

21B. Lower pharyngeal bone with >10 teeth enlarged and submolariform to molariform, crowns of largest teeth not laterally compressed; maximum size >140 mm SL .... 13 (above)

22A (17B). 32 or 33 scales in lateral line .... Cyrtocara heterodon (Trewavas, 1935) (part)

22B. 34-38 scales in lateral line 23

23A (22B). Dorsal fin with 10-13 segmented rays; 34-36 scales in lateral line 24

23B. Dorsal fin with 13 or 14 segmented rays; 36-38 scales in lateral line .... Cyrtocara decorus (Trewavas, 1935)

24A (23A). 0-2 indistinct dorsal midline spots; dorsal-fin spines narrow, fragile; head and body silvery in life (habitat sandy or soft bottom) .... Cyrtocara argyrosoma (Regan, 1921) (part)

24B. 4 or 5 well-defined dorsal midline spots; dorsal-fin spines normal, pungent; head and body not silvery in life (habitat rocky shore) .... Cyrtocara heterodon (Trewavas, 1935) (part)

25A (16B). Lower pharyngeal bone with 10 or more teeth in oblique posteromedian to midlateral row 26

25B. Lower pharyngeal bone with 9 or fewer teeth in oblique posteromedian to midlateral row 27

26A (25A). Outer jaw teeth movable, inclined toward symphysis, their crowns strongly compressed, spatulate, with rounded to obliquely truncate profile; lower-jaw length >38% head length .... Hemitilapia oxyrhynchus Boulenger, 1902c (part)

26B. Outer jaw teeth scarcely movable, not inclined toward symphysis, crowns moderately compressed, never spatulate, anterior to lateral teeth distinctly bicuspid or bi- and tricuspid, posterior teeth uni-, bi-, and/or tricuspid; lower-jaw length <36% head length .... Cyrtocara tetraspilus (Trewavas, 1935) (part)

27A (25B). Outer jaw teeth movable, inclined toward symphysis, their crowns strongly compressed, spatulate, with rounded to obliquely truncate profile .... Hemitilapia oxyrhynchus Boulenger, 1902c (part)

27B. Outer jaw teeth scarcely movable, not inclined toward symphysis, crowns moderately to strongly compressed, uni-, bi-, and/or tricuspid, never spatulate with rounded to obliquely truncate profile 28

28A (27B). Head length ≤32.5% SL 29

28B. Head length >32.5% SL 39

29A (28A). Dorsal fin with 14-16 spines 30

29B. Dorsal fin with 17 or more spines 35

30A (29A). 13 or 14 gill rakers on lower limb of outer arch 31

30B. 12 or fewer gill rakers on lower limb of outer arch 32

31A (30A). Lower-jaw length <36% head length; interorbital width >25% head length .... <u>Cyrtocara</u> <u>tetraspilus</u> (Trewavas, 1935) (part)

31B. Lower-jaw length >38% head length; interorbital width <24% head length .... <u>Cyrtocara</u> new species P (part)

32A (30B). Lower-jaw length <36% head length .... <u>Cyrtocara</u> <u>tetraspilus</u> (Trewavas, 1935) (part)

32B. Lower-jaw length >38% head head length 33

33A (32B). Suprapectoral spot smaller than eye; interorbital width <22% head length; upper-jaw length <30% head length; maximum size <80 mm SL .... <u>Cyrtocara</u> <u>pleurospilus</u> (Trewavas, 1935) (part)

33B. Suprapectoral spot larger than eye; interorbital width >22% head length; upper-jaw length >30% SL; maximum size >155 mm SL 34

34A (33B). Upper-jaw teeth <25, small, confined to anterior half of premaxilla, buried in thickened mucous membrane; head width >47% head length; snout wider than long (length ≤0.9 times width) .... <u>Cyrtocara</u> <u>chrysogaster</u> (Trewavas, 1935)

34B. Upper-jaw teeth >40, robust, extending nearly to posterior end of premaxilla, crowns emergent from mucous membrane; head width <46% head length; snout longer than wide (length ≥1.1 times width) .... *Hemitilapia labifer* (Trewavas, 1935) (part)

35A (29B). Lower-jaw length ≤35% head length 36

35B. Lower-jaw length >35% head length 37

36A (35A). Lower pharyngeal bone with posteromedian teeth very small, crowded, a minimum of 9 teeth in oblique posteromedian to midlateral row ...... *Cyrtocara tetraspilus* (Trewavas, 1935) (part)

36B. Lower pharyngeal bone with posteromedian teeth moderately small, uncrowded, 5-9 teeth in oblique posteromedian to midlateral row ... . *Cyrtocara auromarginatus* (Boulenger, 1908) (part)

37A (35B). Head width <46% head length; width of lower pharyngeal bone <26% head length and 1.00-1.14 times median length of bone .... *Hemitilapia labifer* (Trewavas, 1935) (part)

37B. Head width >47% head length; width of lower pharyngeal bone >27% head length and 1.17-1.45 times its median length of bone 38

38A (37B). Lateral spots and dorsal midline spots somewhat indistinct; no accessory spots on side of nape; head length 27.5%-31.5% SL; predorsal length 33%-37% SL; 11-17 (mode 15) gill rakers on lower limb of outer arch (habitat sandy shore) .... *Cyrtocara auromarginatus* (Boulenger, 1908) (part)

38B. Lateral spots and dorsal midline spots dark and prominent; one or two accessory spots (sometimes joined) on side of nape; head length 30.5%-35.5% SL; predorsal length 36%-41% SL; 9-15 (mode 10) gill rakers on lower limb of outer arch (habitat rocky shore) .... *Cyrtocara heterodon* (Trewavas, 1935) (part)

39A (28B). Premaxillary ascending processes ≤22% head length (18.9% in holotype) .... *Cyrtocara serranoides* (Ahl, 1927) (part) (=*Haplochromis ahli* Trewavas, 1935, nom. nov.)

39B. Premaxillary ascending processes 23%-33% head length 40

40A (39B). Interorbital width >26% head length 41

40B. Interorbital width ≤26% head length 42

41A (40A). Lower pharyngeal bone with 36-50 teeth in posterior row; head length <33% SL; caudal-peduncle length/depth 1.25-1.52; 32-33 scales in lateral line .... *Hemitilapia labifer* (Trewavas, 1935) (part)

41B. Lower pharyngeal bone with 20-34 teeth in posterior row; head length 32.7%-39.6% SL; caudal-peduncle length/depth 1.55-1.90; 33-36 (modal range 34-35) scales in lateral line .... *Cyrtocara speciosus* (Trewavas, 1935) (part)

42A (40B). Head width <41% head length .... *Cyrtocara woodi* (Regan, 1921) (including *Haplochromis pholidophorus* Trewavas, 1935)

42B. Head width >44% head length 43

43A (42B). 9-12 gill rakers on lower limb of outer arch 44

43B. 13 or 14 gill rakers on lower limb of outer arch 48

44A (43A). Body depth <34% SL 45

44B. Body depth ≥34% SL 46

45A (44A). <50 teeth in outer row of upper jaw; pectoral-fin length <32% SL; upper-jaw length <30% head length; caudal-peduncle length/depth <1.50 (maximum size <80 mm SL) .... *Cyrtocara pleurospilus* (Trewavas, 1935) (part)

45B. 59-101 teeth in outer row of upper jaw; pectoral-fin length 32%-43% SL; upper-jaw length >30% head length; caudal-peduncle length/depth 1.55-1.90 (maximum size 236 mm SL) ....

.... *Cyrtocara speciosus* (Trewavas, 1935) (part)

46A (44B). Suprapectoral spot distinctly larger than eye; 32-36 (rarely 32) lateral-line scales 47

46B. Suprapectoral spot not larger than eye; 31-33 (mode 32, rarely 33) lateral-line scales .... *Cyrtocara tetrastigma* (Günther, 1893) (part)

47A (46A, 48B). 32-51 teeth in outer row of upper jaw; caudal-peduncle length ≤16.5% SL; 7-10 (mode 9) vertical bars below base of dorsal fin (habitat rocky shore) .... *Cyrtocara heterodon* (Trewavas, 1935) (part)

47B. 59-101 teeth in outer row of upper jaw; caudal-peduncle length ≥16.7% SL; 4-7 (mode 6) vertical bars below base of dorsal fin (habitat sandy or soft substrate) .... *Cyrtocara speciosus* (Trewavas, 1935) (part)

48A (43B). No distinct accessory spots or dorsal midline spots; body markings confined to vertical bars and at most 3 lateral spots .... *Cyrtocara* new species P (part)

48B. 1-3 distinct accessory spots below origin of dorsal fin, and often several dorsal midline spots, in addition to vertical bars and lateral spots .... 47 (above)

49A (1B). 15-29 gill rakers on lower limb of outer arch 51

49B. 30 or more gill rakers on lower limb of outer arch 50

50A (49B). Lateral spots large, suprapectoral spot covering >18 scales and crossing 5-7 lateral-line scales; head length >36% SL; premaxillary ascending processes >35% head length; predorsal length >38% SL; cheek depth <21% head length; caudal-peduncle length <16.5% SL .... *Cyrtocara pictus* (Trewavas, 1935)

50B. Lateral spots moderate, suprapectoral spot covering <16 scales and crossing 3-4 lateral-line scales; head length <36% SL; premaxillary ascending processes <35% head length; predorsal length ≤37% SL; cheek depth >21% head length; caudal-peduncle length >16.5% SL .... Cyrtocara intermedius (Günther, 1864)

51A (49A). Suprapectoral spot entirely below upper part of lateral line, either separated from it or touching it from below 52

51B. Suprapectoral spot extending, at least anteriorly, above upper part of lateral line 63

52A (51A). Anal fin with 7 or 8 segmented rays .... Cyrtocara lithobates, new species (part)

52B. Anal fin with 9 or more segmented rays 53

53A (52B). Dorsal fin with 27 or fewer total spines and segmented rays 54

53B. Dorsal fin with 28 or more total spines and segmented rays 57

54A (53A). Body depth <35% SL 55

54B. Body depth >35% SL 56

55A (54A, 57A). 16 or fewer gill rakers on lower limb of outer arch; premaxillary ascending processes ≤31% head length; lower pharyngeal bone with a posteromedian group of enlarged, submolariform teeth .. .. Cyrtocara lithobates, new species (part)

55B. More than 18 gill rakers on lower limb of outer arch; premaxillary ascending processes >34% head length; lower pharyngeal bone with all teeth small, crowns all laterally compressed, none submolariform .... Cyrtocara nkatae (Iles, 1960) (part)

56A (54B). 17-21 (mode 19) gill rakers on lower limb of outer arch (17 in 2 of 24 fishes); premaxillary ascending processes ≥30.6% head

length in fishes >70 mm SL ....
.... *Cyrtocara chrysonotus* (Boulenger, 1908) (part)

56B. 17 or fewer (mode 15) gill rakers on lower limb of outer arch (17 in 1 of 23 fishes); premaxillary ascending processes ≤30.2% head length .... *Cyrtocara auromarginatus* (Boulenger, 1908) (part)

57A (53B). Body depth <35% SL .... 55 (above)

57B. Body depth >35% SL 58

58A (57B). 17 or fewer gill rakers on lower limb of outer arch ....
.... *Cyrtocara auromarginatus* (Boulenger, 1908) (part)

58B. 18 or more gill rakers on lower limb of outer arch 59

59A (58B). Suprapectoral spot small, covering about 2 scales; dorsal anal, and pelvic fins not yellow in life 60

59B. Suprapectoral spot moderate, covering about 8 scales; dorsal, anal, and pelvic fins yellow in life ....
.... *Cyrtocara pleurostigmoides* (Iles, 1960)

60A (59A). Anal fin with 12 or 13 segmented rays ....
.... *Cyrtocara jacksoni* (Iles, 1960) (part)

60B. Anal fin with fewer than 12 segmented rays 61

61A (60B). Dorsal fin with 30 total spines and segmented rays ....
.... *Cyrtocara jacksoni* (Iles, 1960) (part)

61B. Dorsal fin with fewer than 30 total spines and segmented rays ....
.... 62

62A (61B). Pectoral-fin length >32% SL; lower half of flanks not silvery in life .... *Cyrtocara borleyi* (Iles, 1960)

62B. Pectoral-fin length <30% SL; lower half of flanks silvery in life
.... *Cyrtocara jacksoni* (Iles, 1960) (part)

63A (51B). Dorsal fin with 29 or more total spines and segmented rays

.... 64

63B. Dorsal fin with 28 or fewer total spines and segmented rays ... 69

64A (63A). More than 20 gill rakers on lower limb of outer arch ....<u>Cyrtocara</u> <u>quadrimaculatus</u> (Regan, 1921) (part) (including <u>C</u>. <u>likomae</u> [Iles, 1960])

64B. Fewer than 20 gill rakers on lower limb of outer arch 65

65A (64B). Dorsal fin with 12 or more segmented rays .... <u>Cyrtocara</u> <u>nitidus</u> (Trewavas, 1935) (part)

65B. Dorsal fin with fewer than 12 segmented rays 66

66A (65B). Lower jaw dorsoventrally flattened; in ventral view, lower jaw bulges outward along middle of each side, appearing ()-shaped; usually 1 inner row of teeth anteriorly in lower jaw (2 rows in 4 of 41 fishes) .... <u>Cyrtocara</u> <u>nitidus</u> (Trewavas, 1935) (part)

66B. Lower jaw not dorsoventrally flattened; in ventral view, lateral edges of lower jaw appear nearly straight and approximately parallel; 2 or more inner rows of teeth anteriorly in lower jaw 67

67A (66B). 26 or fewer scales in upper part of lateral line .... <u>Cyrtocara</u> <u>auromarginatus</u> (Boulenger, 1908) (part)

67B. 27 or more scales in upper part of lateral line 68

68A (67B). Premaxillary ascending processes 25%-30% head length; lower pharyngeal bone with 30-42 teeth in posterior row .... <u>Cyrtocara</u> <u>auromarginatus</u> (Boulenger, 1908) (part)

68B. Premaxillary ascending processes 32%-36% head length; lower pharyngeal bone with 49-72 teeth in posterior row ...... <u>Cyrtocara</u> <u>pleurostigma</u> (Trewavas, 1935) (including <u>C</u>. <u>trimaculatus</u> [Iles, 1960])

69A (63B). 15-17 gill rakers on lower limb of outer arch 71

69B. 18 or more gill rakers on lower limb of outer arch 70

70A (69B). Lower jaw dorsoventrally flattened, bulging outward along middle of each side, lower jaw appearing ()-shaped in ventral view; suprapectoral and supraanal spots often anteroposteriorly elongate; suprapectoral spot produced toward nape .... Cyrtocara nitidus (Trewavas, 1935) (part)

70B. Lower jaw not dorsoventrally flattened, not bulging outward along middle of each side, sides of lower jaw appearing straight and approximately parallel in ventral view; suprapectoral and supraanal spots round to square (supraanal may be absent); suprapectoral spot not produced toward nape .... Cyrtocara chrysonotus (Boulenger, 1908) (part)

71A (69A). Premaxillary ascending processes >32% head length 72

71B. Premaxillary ascending processes ≤32% head length 74

72A (71A). Lower jaw bulging outward along middle of each side, appearing ()-shaped in ventral view .... Cyrtocara nitidus (Trewavas, 1935) (part)

72B. Lower jaw not bulging outward along middle of each side, sides of lower jaw appearing straight and approximately parallel in ventral view 73

73A (72B). Suprapectoral spot larger than eye, anteroposteriorly elongate, often produced toward nape; jaw teeth moderate, robustly built, crowns distinctly pigmented; posteromedian teeth of lower pharyngeal bone cuspidate but coarser than lateral and anterior teeth .... Cyrtocara heterodon (Trewavas, 1935) (part)

73B. Suprapectoral spot not larger than eye, not anteroposteriorly elongate, not produced toward nape; jaw teeth small, weak, crowns lightly pigmented; teeth of lower pharyngeal bone all small, laterally compressed, posteromedian teeth not coarse .... *Cyrtocara chrysonotus* (Boulenger, 1908) (part)

74A (71B). Lower pharyngeal teeth all small, laterally compressed .. 75

74B. Lower pharyngeal bone with a group of slightly enlarged teeth posteromedially 77

75A (74A). Lower pharyngeal teeth densely crowded, 9 or more in oblique posteromedian to midlateral row .... *Cyrtocara tetraspilus* (Trewavas, 1935) (part)

75B. Lower pharyngeal teeth not crowded, usually fewer than 9 in oblique posteromedian to midlateral row 76

76A (75B). Premaxillae strongly protractile; suprapectoral spot not produced toward nape .... *Cyrtocara chrysonotus* (Boulenger, 1908) (part)

76B. Premaxillae not strongly protractile; suprapectoral spot frequently produced toward nape .... *Cyrtocara auromarginatus* (Boulenger, 1908) (part)

77A (74B). Dorsal fin with 15 or 16 spines .... *Cyrtocara* new species P (part)

77B. Dorsal fin with 17 or 18 spines 78

78A (77B). Suprapectoral spot large, anteroposteriorly elongate, subrectangular, its ventral edge extending along lateral midline of body; head length 27%-31% SL (habitat rocky shore) .... *Cyrtocara heterodon* (Trewavas, 1935) (part)

78B. Suprapectoral spot moderate, not anteroposteriorly elongate, oval to triangular, its ventral edge not extending along lateral midline of body; head length 31%-35% SL (habitat sandy) ....

.... Cyrtocara auromarginatus (Boulenger, 1908)

Figure 38. Diagram of lower pharyngeal bone of a cichlid, showing counts and measurements. Tooth counts: posterior row, 27; median columns, 11 and 12; oblique rows, 7 and 8; lateral edges, 21 and 20. Measurements: a, median length of bone; b, width of bone; c, length of dentigerous surface; d, width of dentigerous surface.

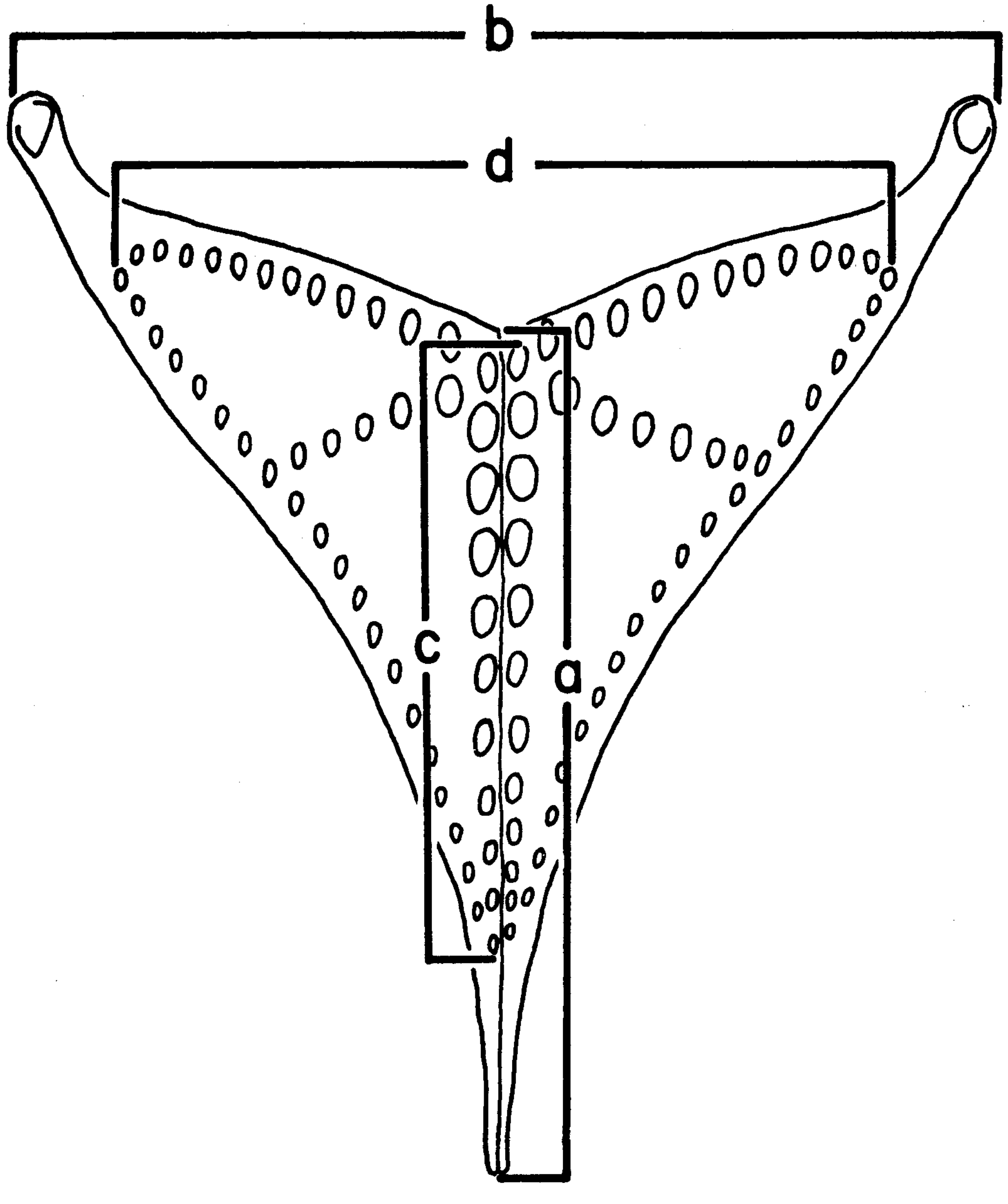

b
d
c
a

Figure 39. Terminology of spots in "three-spotted" haplochromines. Main lateral spots: SP, suprapectoral; SA, supraanal; PC, precaudal. Other spots: ac, accessory spot; dm, dorsal midline spot (6 dorsal midline spots are shown, 4 of them below dorsal-fin base and 2 on caudal peduncle).

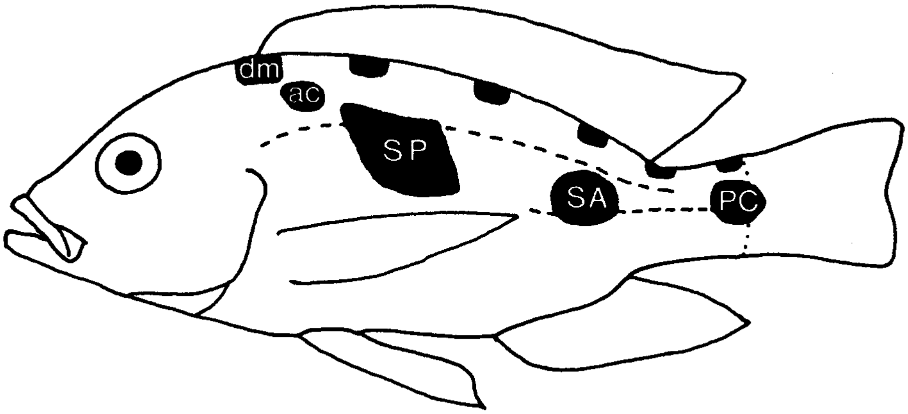

dm
ac
SP
SA
PC

Figure 40. <u>Cyrtocara lithobates</u>, new species. Live holotype (BMNH 1974.7.5:1), 86.5 mm SL, a sexually active male.

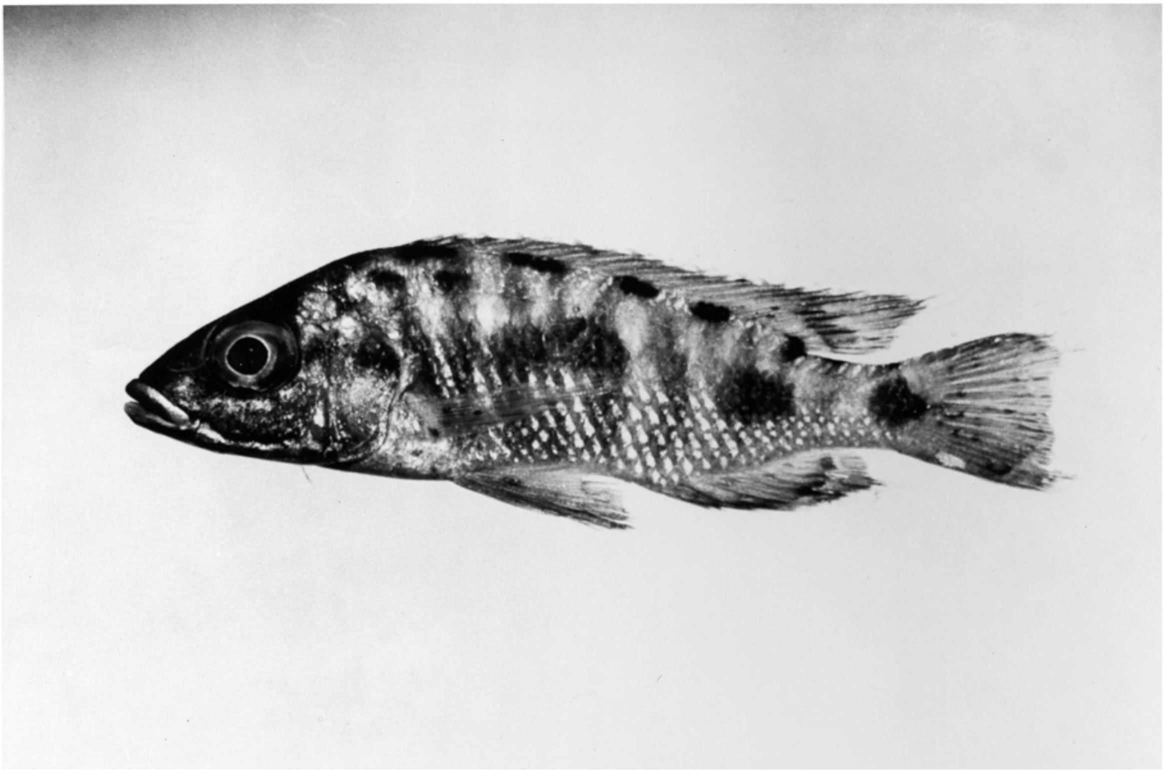


Figure 41. *Cyrtocara lithobates*. Holotype (BMNH 1974.7.5:1), 86.5 mm SL.

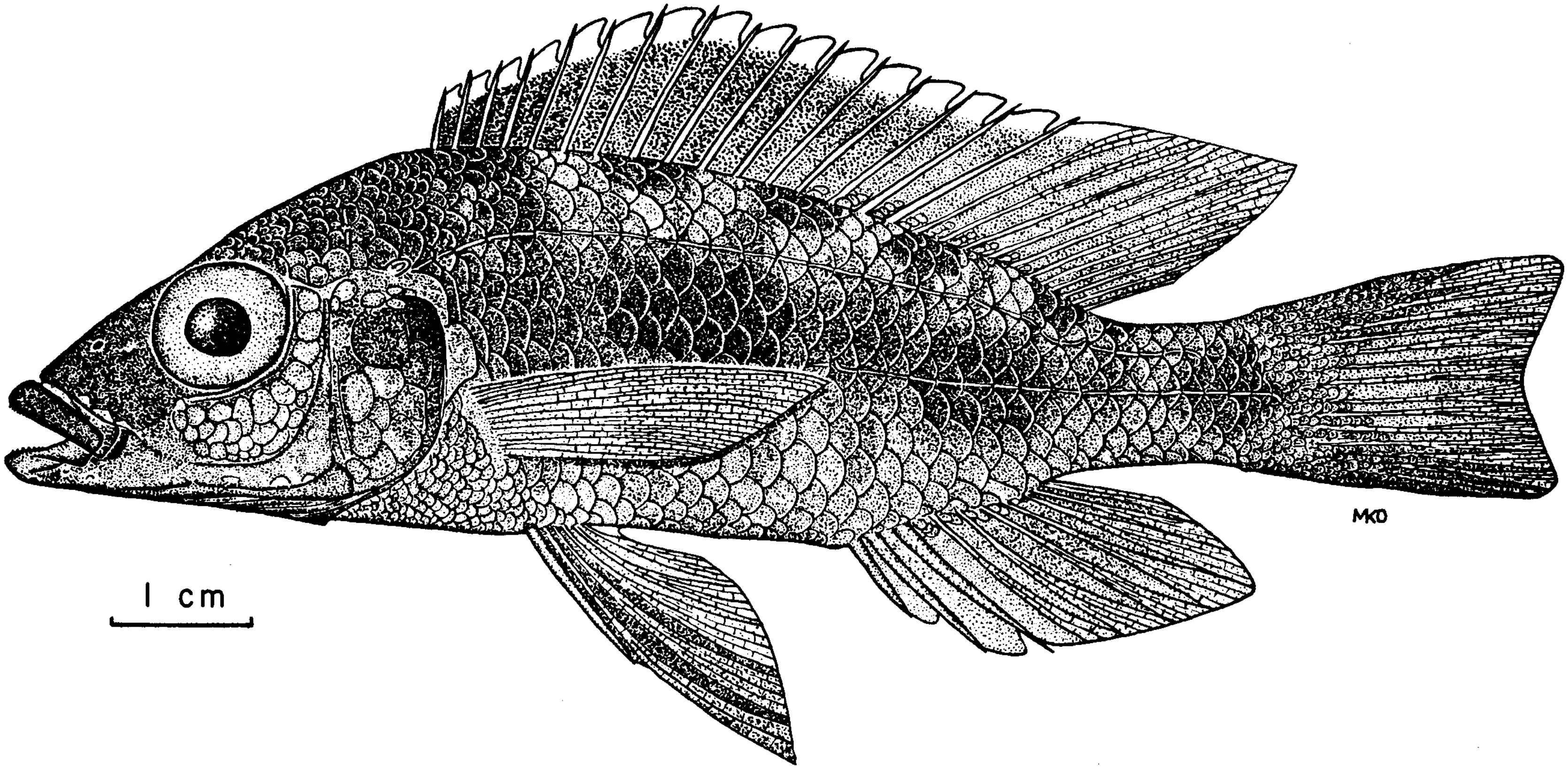

MKO
1 cm

Figure 42. Cyrtocara lithobates. Live paratype, 73.5 mm SL, a mature female. Posterior parts of unpaired fins are unnaturally pale because of necrosis.

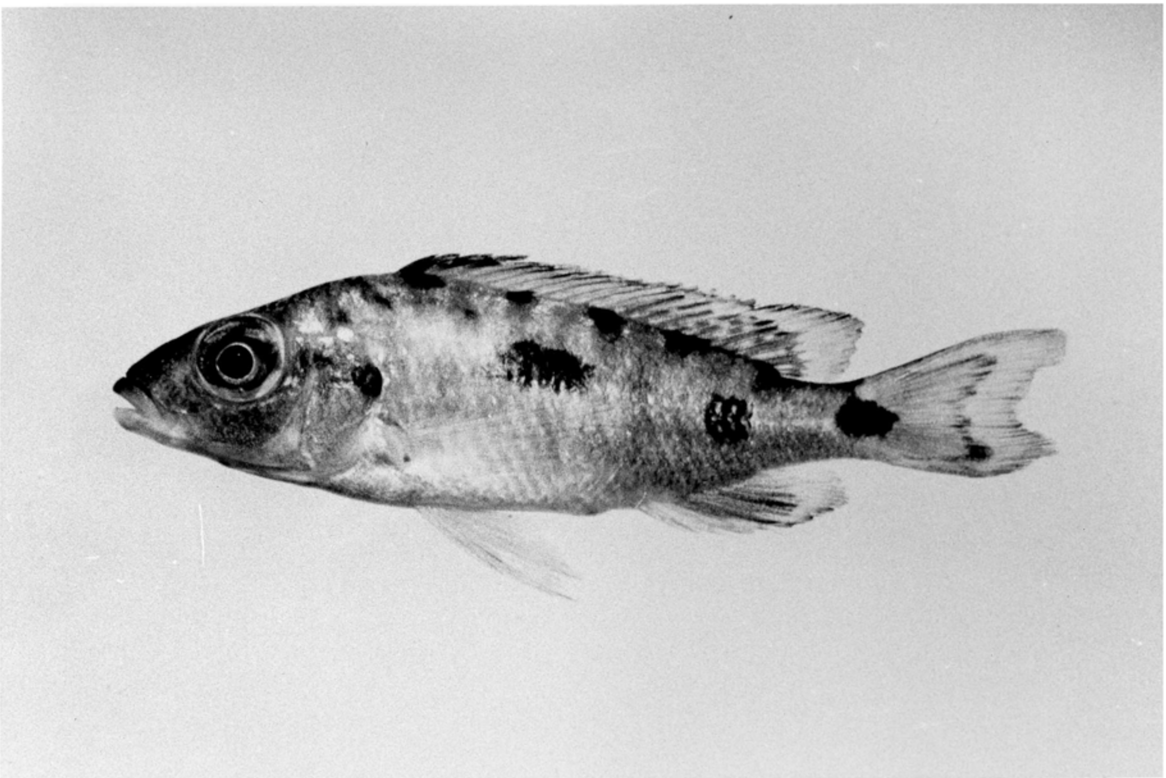
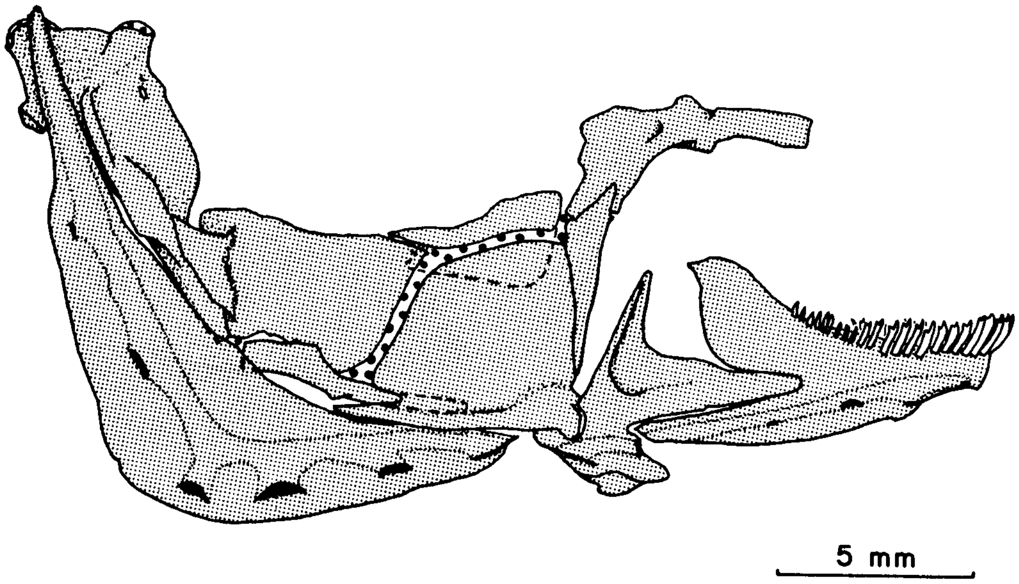


Figure 43. Lower pharyngeal bone of *Cyrtocara lithobates* in occlusal view. Drawn from a paratype 87.2 mm SL.

2 mm

Figure 44. Suspensorium and jaws of *Cyrtocara lithobates* in lateral view. Drawn from a paratype 87.2 mm SL.


5 mm

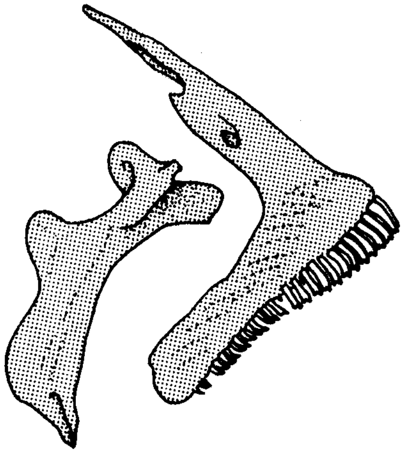


Figure 45. Cyrtocara brooksi, new species. Holotype, 114.5 mm SL, a sexually active male. Above, left side (lateral spots faded); below, right side photographically reversed (showing lateral spots; eye damaged by reduced pressure when fish brought to surface).

Figure 46. _Cyrtocara brooksi_. Live paratype, 115.0 mm SL, male. Damaged scales above suprapectoral spot appear as a light area.

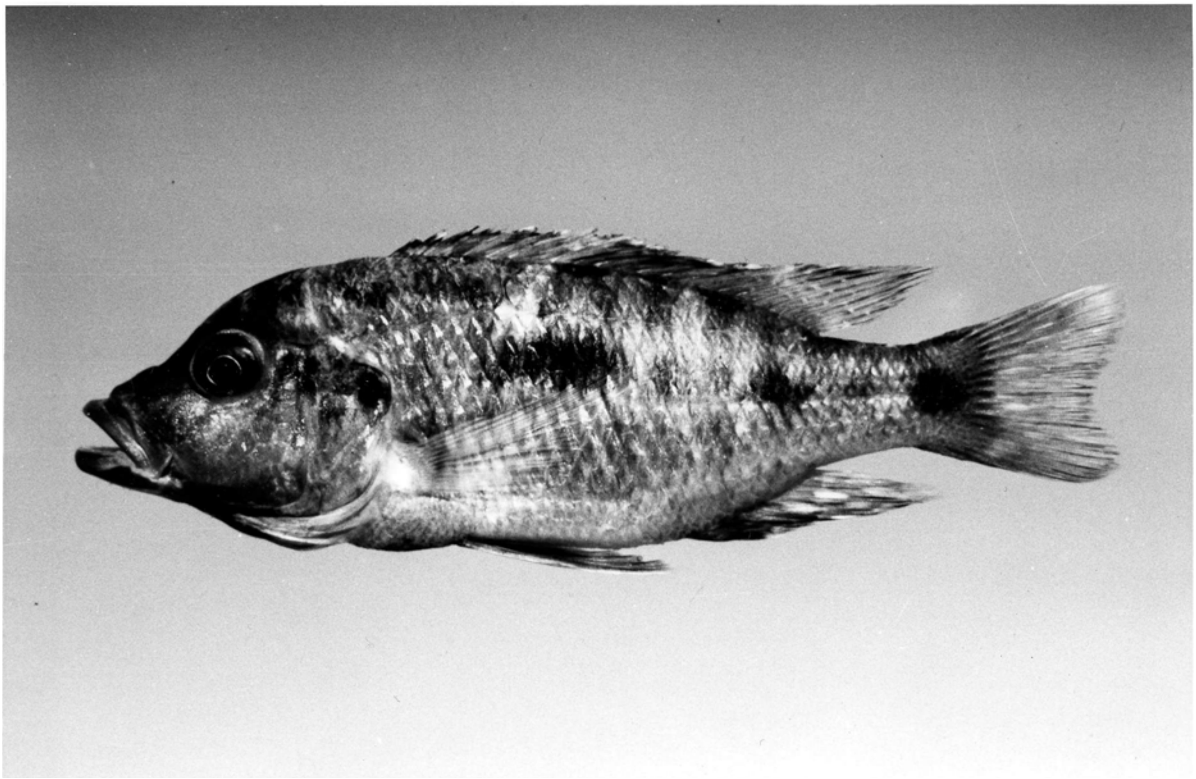


Figure 47. Lower pharyngeal bone of Cyrtocara brooksi in occlusal view. Drawn from holotype, 114.5 mm SL.

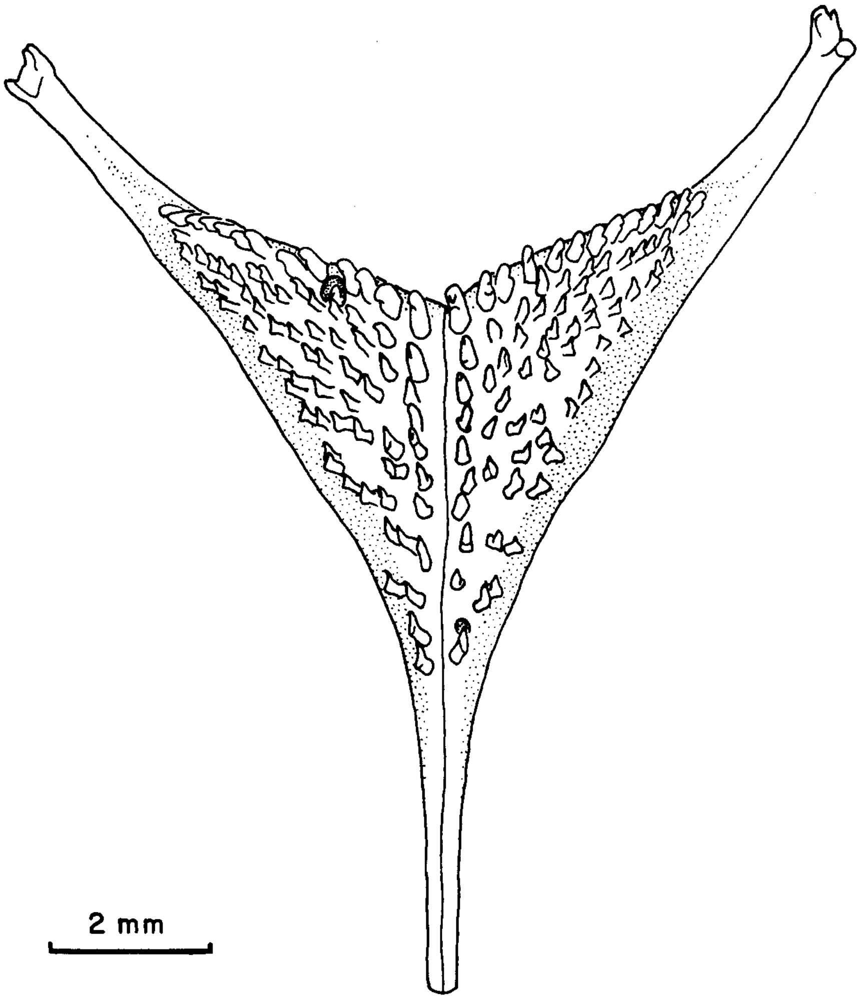

2 mm

Figure 48. Suspensorium and jaws of *Cyrtocara brooksi* in lateral view. Drawn from a paratype 109.0 mm SL.

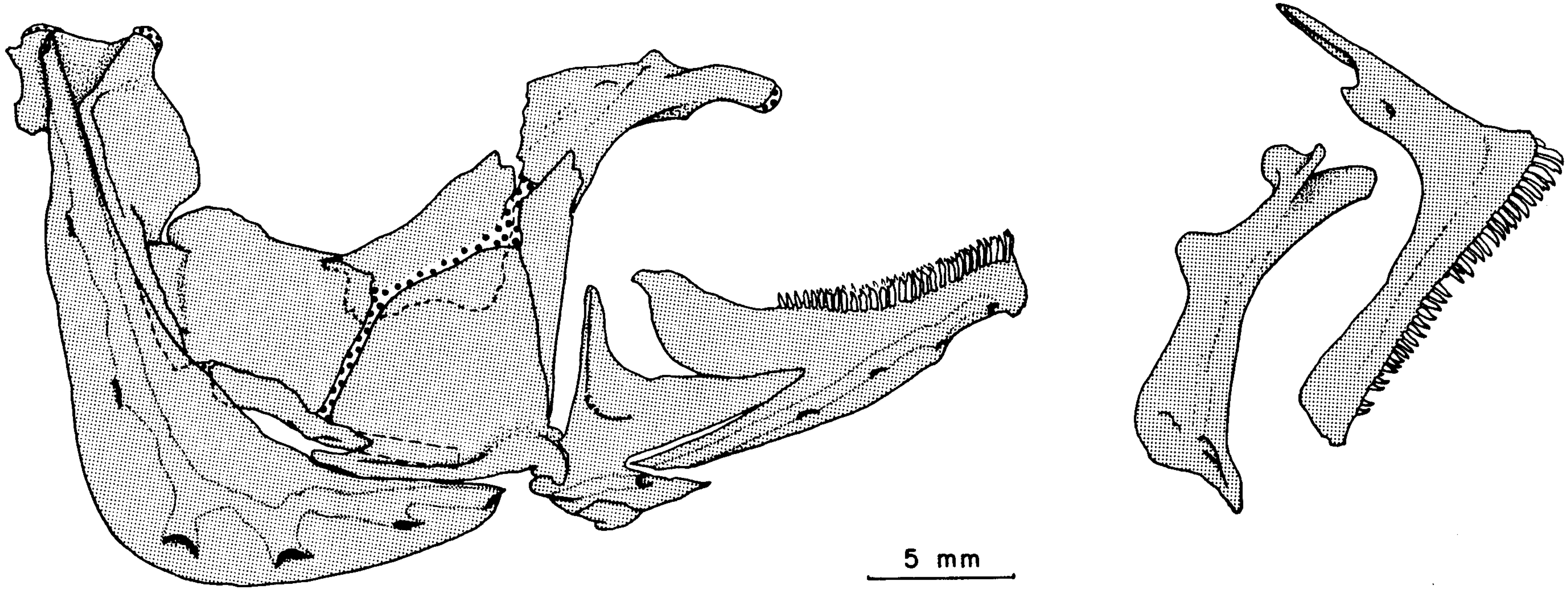

5 mm

Figure 49. _Cyrtocara anagenys_, new species. Freshly killed holotype, 200 mm SL, a mouthbrooding female. Right side photographed and reversed.

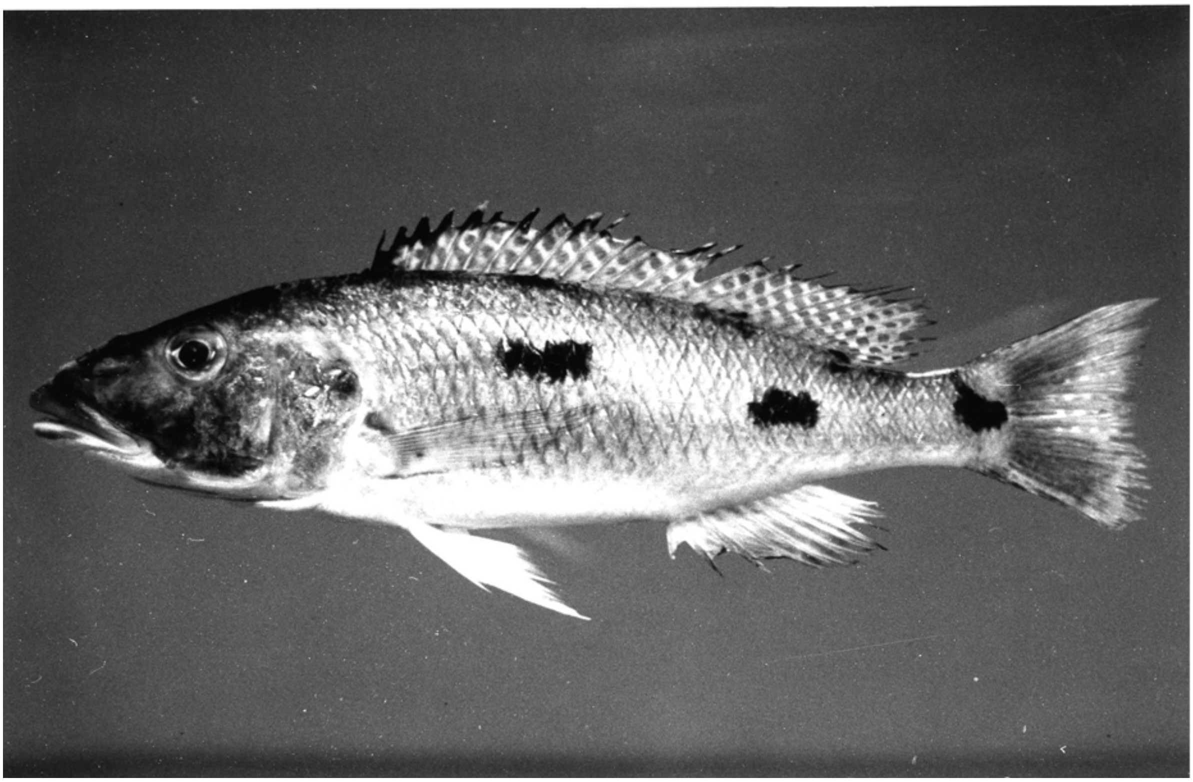


Figure 50. *Cyrtocara anagenys*. Head of freshly killed holotype. Right side photographed and reversed.

Figure 51. Jaws of Cyrtocara anagenys holotype in lateral view, showing dentition (exposed when oral mucosa allowed to dry slightly) and elevated lingual edge of dentary symphysis.

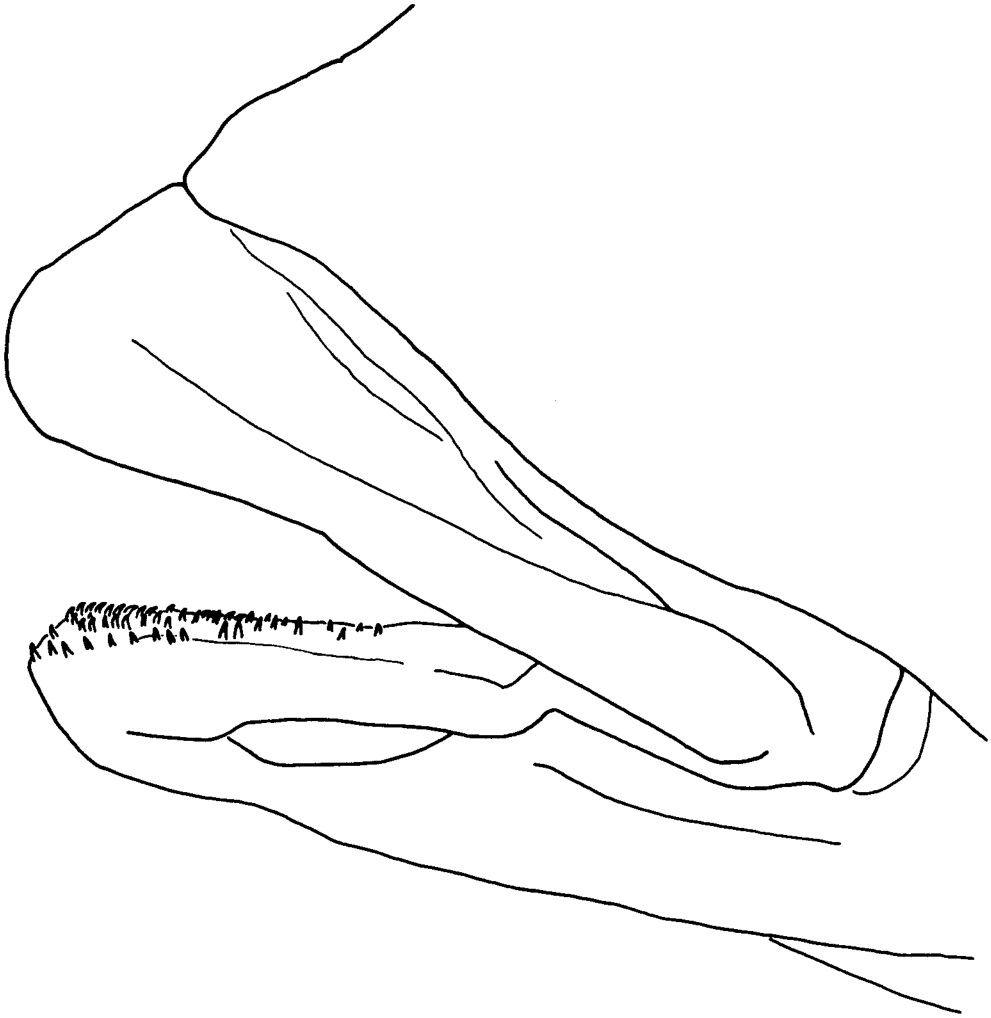


Figure 52. Lower pharyngeal bone of _Cyrtocara anagenys_. Drawn from holotype, 200 mm SL. a, occlusal view; b, left lateral view; c, posterior view.

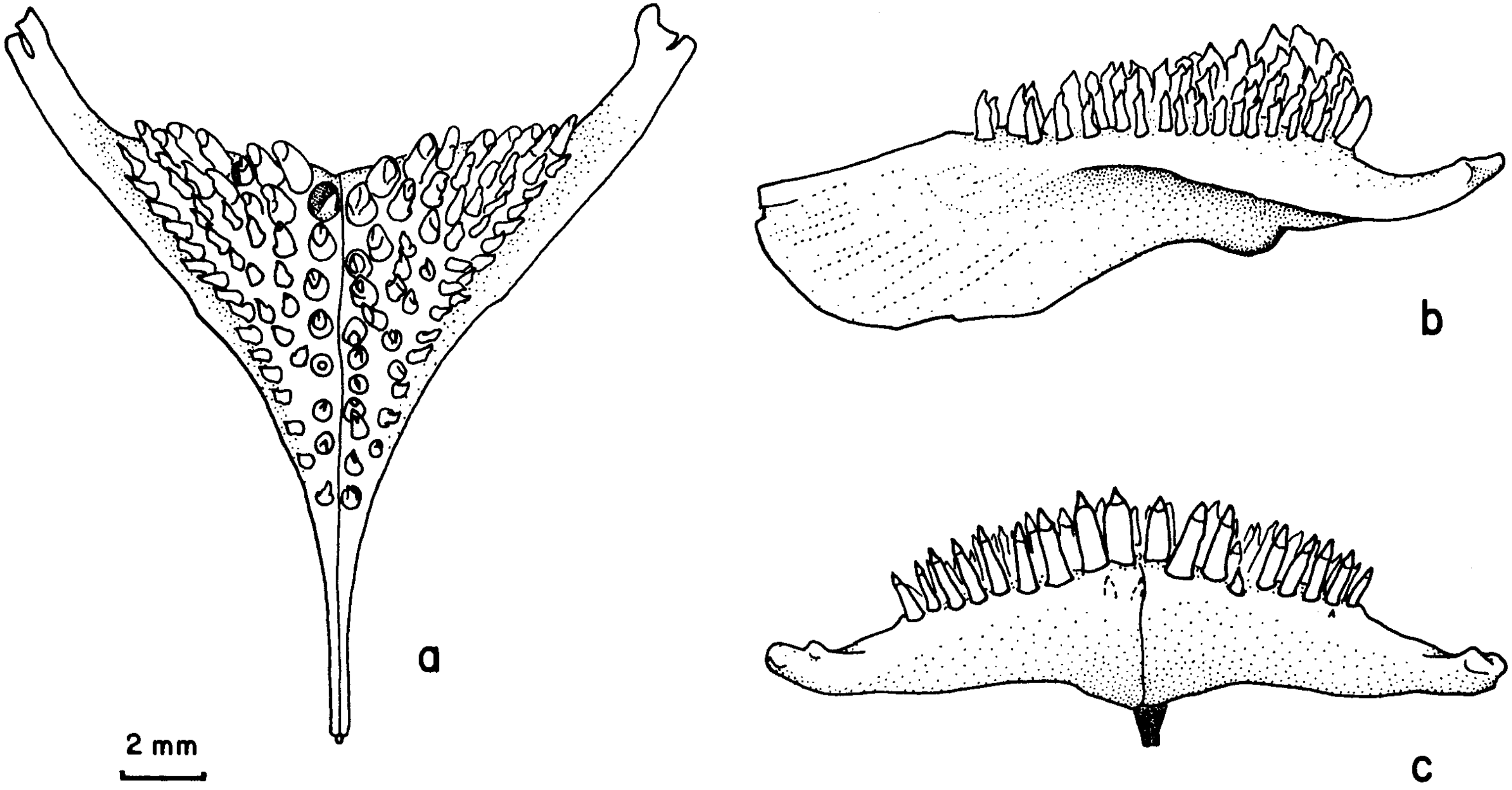

a
b
c
2 mm

Figure 53. Color pattern of *Cyrtocara anagenys* larva, shown somewhat diagrammatically (15.4-mm SL paratype).

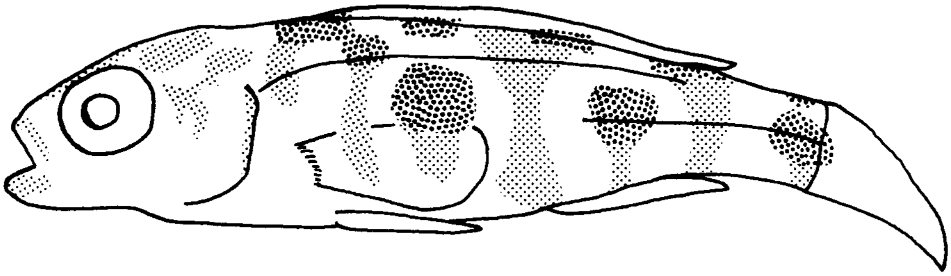


Table 8. Linear regressions of morphometric variates (Y) on standard length or head length (X) in *Cyrtocara lithobates*.

Regression[1]	N	Range X	$\bar{X} \pm SE_X$	Range Y	$\bar{Y} \pm SE_Y$	$b \pm SE_b$	$a \pm SE_a$	r
HL on SL	31	52.0-106.8	65.794 ± 1.919	17.6-36.0	22.694 ± 0.687	0.352*** ± 0.012	-0.497 ± 0.792	0.984
BD on SL	30	52.0-106.8	66.023 ± 1.953	17.0-34.5	21.180 ± 0.634	0.314*** ± 0.015	0.436 ± 1.027	0.968
PDL on SL	19	52.0-106.8	69.132 ± 2.749	19.3-37.5	25.758 ± 0.990	0.355*** ± 0.015	1.235 ± 1.068	0.985
PPL on SL	12	51.0- 72.2	60.467 ± 1.827	20.2-29.5	24.483 ± 0.822	0.448*** ± 0.014	-2.594* ± 0.847	0.995
BEL on SL	13	51.0- 72.2	60.800 ± 1.713	15.2-22.1	18.300 ± 0.630	0.350*** ± 0.034	-2.988 ± 2.071	0.952
DBL on SL	19	52.0-106.8	69.132 ± 2.749	28.1-57.7	37.053 ± 1.510	0.546*** ± 0.013	-0.713 ± 0.931	0.995
CPL on SL	19	52.0-106.8	69.132 ± 2.749	9.1-19.1	11.568 ± 0.491	0.172*** ± 0.012	-0.310 ± 0.831	0.962
PFL on SL	14	52.0-106.8	70.229 ± 3.667	15.9-32.4	22.164 ± 1.098	0.287*** ± 0.025	2.042 ± 1.797	0.957
HW on HL	19	17.6- 36.0	23.732 ± 0.984	8.5-16.0	11.021 ± 0.404	0.405*** ± 0.017	1.402** ± 0.399	0.986
POD on HL	19	17.6- 36.0	23.732 ± 0.984	2.6- 7.0	4.111 ± 0.228	0.228*** ± 0.011	-1.289*** ± 0.256	0.982
IOW on HL	31	17.6- 36.0	22.694 ± 0.687	3.0- 7.0	4.174 ± 0.138	0.189*** ± 0.013	-0.107 ± 0.292	0.940
SNL on HL	19	17.6- 36.0	23.732 ± 0.984	4.9-11.6	7.200 ± 0.368	0.370*** ± 0.013	-1.575*** ± 0.310	0.990
OL on HL	31	17.6- 36.0	22.694 ± 0.687	6.6-11.6	8.474 ± 0.213	0.299*** ± 0.015	1.688*** ± 0.340	0.966
CHD on HL	19	17.6- 36.0	23.732 ± 0.984	2.6- 6.8	3.732 ± 0.222	0.219*** ± 0.013	-1.468*** ± 0.319	0.970
UJL on HL	19	17.6- 36.0	23.732 ± 0.984	4.6-11.1	6.747 ± 0.362	0.363*** ± 0.015	-1.864*** ± 0.356	0.986
PMP on HL	19	17.6- 36.0	23.732 ± 0.984	4.9-10.0	6.853 ± 0.285	0.286*** ± 0.012	0.076 ± 0.296	0.985
LJL on HL	18	17.6- 36.0	23.828 ± 1.035	6.5-14.3	9.389 ± 0.452	0.432*** ± 0.016	-0.902* ± 0.395	0.989
POH on HL	19	17.6- 36.0	23.732 ± 0.984	6.7-14.0	8.763 ± 0.376	0.377*** ± 0.015	-0.188 ± 0.361	0.987

[1] BD = body depth; BEL = belly length; CHD = cheek depth; CPL = caudal-peduncle length; DBL = dorsal-fin base length; HL = head length; HW = head width; IOW = interorbital width; LJL = lower-jaw length; OL = orbit length; PDL = predorsal length; PFL = pectoral-fin length; PMP = length of premaxillary ascending processes; POD = preorbital depth; POH = postorbital head length; PPL = prepelvic length; SL = standard length; SNL = snout length; UJL = upper-jaw length. Significance levels: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

Table 9. Linear regressions of morphometric variates (Y) on standard length or head length (X) in *Cyrtocara brooksi*.

Regression[1]	N	Range X	$\bar{X} \pm SE_X$	Range Y	$\bar{Y} \pm SE_Y$	$b \pm SE_b$	$a \pm SE_a$	r
HL on SL	20	101.0-123.2	112.725 ± 1.448	38.0-45.2	42.000 ± 0.566	0.368*** ± 0.031	0.507 ± 3.529	0.941
BD on SL	20	101.0-123.2	112.725 ± 1.448	34.0-44.2	39.755 ± 0.618	0.359*** ± 0.054	-0.751 ± 6.146	0.841
PDL on SL	20	101.0-123.2	112.725 ± 1.448	38.9-46.8	43.940 ± 0.531	0.332*** ± 0.037	6.493 ± 4.148	0.905
PPL on SL	19	101.0-123.2	113.032 ± 1.492	44.9-56.4	51.174 ± 0.790	0.501*** ± 0.042	-5.411 ± 4.760	0.945
BEL on SL	19	101.0-123.2	113.032 ± 1.492	28.2-36.0	32.068 ± 0.614	0.316*** ± 0.064	-3.673 ± 7.238	0.768
DBL on SL	20	101.0-123.2	112.725 ± 1.448	52.8-64.3	59.030 ± 0.753	0.498*** ± 0.036	2.938 ± 4.031	0.957
CPL on SL	20	101.0-123.2	112.725 ± 1.448	14.0-18.3	16.780 ± 0.250	0.120*** ± 0.029	3.228 ± 3.290	0.697
PFL on SL	20	101.0-123.2	112.725 ± 1.448	34.8-46.5	41.000 ± 0.551	0.334*** ± 0.043	3.325 ± 4.850	0.878
HW on HL	20	38.0- 45.2	42.000 ± 0.566	16.9-21.4	18.890 ± 0.329	0.537*** ± 0.052	-3.677 ± 2.195	0.925
POD on HL	20	38.0- 45.2	42.000 ± 0.566	7.5- 9.5	8.585 ± 0.149	0.245*** ± 0.022	-1.724 ± 0.942	0.933
IOW on HL	20	38.0- 45.2	42.000 ± 0.566	7.2- 9.7	8.665 ± 0.152	0.214*** ± 0.038	-0.311 ± 1.615	0.795
SNL on HL	20	38.0- 45.2	42.000 ± 0.566	12.9-16.5	14.830 ± 0.266	0.448*** ± 0.033	-3.976** ± 1.378	0.955
OL on HL	20	38.0- 45.2	42.000 ± 0.566	10.5-12.5	11.580 ± 0.138	0.219*** ± 0.025	2.397* ± 1.056	0.899
CHD on HL	20	38.0- 45.2	42.000 ± 0.566	9.3-12.2	10.855 ± 0.165	0.243*** ± 0.038	0.660 ± 1.582	0.836
UJL on HL	20	38.0- 45.2	42.000 ± 0.566	13.6-16.6	15.285 ± 0.216	0.359*** ± 0.030	0.220 ± 1.275	0.941
PMP on HL	20	38.0- 45.2	42.000 ± 0.566	10.0-12.0	11.165 ± 0.136	0.214*** ± 0.025	2.189 ± 1.069	0.893
LJL on HL	20	38.0- 45.2	42.000 ± 0.566	17.0-21.8	19.575 ± 0.304	0.491*** ± 0.051	-1.032 ± 2.152	0.915
POH on HL	20	38.0- 45.2	42.000 ± 0.566	15.1-18.9	16.855 ± 0.227	0.376*** ± 0.033	1.128 ± 1.406	0.935

[1] BD = body depth; BEL = belly length; CHD = cheek depth; CPL = caudal-peduncle length; DBL = dorsal-fin base length; HL = head length; HW = head width; IOW = interorbital width; LJL = lower-jaw length; OL = orbit length; PDL = predorsal length; PFL = pectoral-fin length; PMP = length of premaxillary ascending processes; POD = preorbital depth; POH = postorbital head length; PPL = prepelvic length; SL = standard length; SNL = snout length; UJL = upper-jaw length. Significance levels: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

APPENDIX 1

FLOATING ISLANDS: A MEANS OF FISH DISPERSAL IN LAKE MALAWI, AFRICA[1]

Michael K. Oliver and Kenneth R. McKaye

ABSTRACT

Floating masses of vegetation are commonly seen in the southern region of Lake Malawi. These floating islands disperse littoral fishes across deep portions of the lake. Six islands were sampled and all yielded fishes. The 129 individuals collected belong to ten species, including one mormyrid, one cyprinid, two clariids, one cyprinodontid, four cichlids, and one mastacembelid. Most of the species are characteristic of lakeshore swamps and are not endemic to Lake Malawi. Dispersal by floating islands may increase gene flow between disjunct populations of widespread species, particularly those inhabiting swamps. Such dispersal, theoretically, could also serve to establish founder populations of geographically isolated species.

INTRODUCTION

Lake Malawi, the southernmost of the African Great Rift Lakes, contains the world's largest lacustrine fish fauna. At least 400 species of fishes are now known from the lake. More than 90% are

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[1] Published in Copeia 1982: 748-754.

cichlids, 99% of which are endemic to the Lake Malawi system, including Lake Malawi itself, the upper Shire River, and Lake Malombe.

The shoreline of Lake Malawi consists of three main types of habitat: sandy beach, rocky shore, and swamp. Alternating stretches of sandy beach and rocky shore predominate. River mouths and parts of the lakeshore are fringed with swamp vegetation, dominated by papyrus (Cyperus papyrus) and reeds (Phragmites communis and Typha sp.). Swamp is particularly extensive in the southwest arm, but reeds, at least, occur throughout Lake Malawi in suitable habitats (Ricardo Bertram et al., 1942). Each of the three shoreline habitats has a distinctive fish community, in part because many of the cichlid and other species are markedly stenotopic (Fryer and Iles, 1972). However, the fish community of the river mouths and lakeshore swamps owes its distinctive character to nonendemic forms, including several mormyrids, a number of cyprinids, a characid, three clariids, a cyprinodontid, several cichlids, and a mastacembelid (Jackson, 1961, and personal observations). Indeed, the lakeshore swamp is unique among the three types of shoreline in lacking any lacustrine endemics, either cichlid or noncichlid, that are characteristic of this habitat. Collections made in the swamp at Chembe, Cape Maclear, Lake Malawi contain several hundred fishes, but include only a few individuals of endemic lacustrine cichlids. All were probably incidental visitors from the adjacent sandy shore.

The shape of the boundary between swamps and the lake is constantly changing. The combined actions of wind and waves can loosen swamp vegetation and cause it to drift into the open waters of Lake Malawi as floating islands (Ricardo Bertram et al., 1942:14). The existence of these drifting masses of vegetation is well known to both African and

European boatmen. A chart of the southwest arm carries the warning that "towards the end of the rainy season large floating islands of reeds and sudd occur in this vicinity" (Southern Rhodesia Federal Government, 1958). Islands are seen at all times of the year, but they are most abundant during the rainy season (January-March). During February as many as twenty floating islands per day drift within sight of Cape Maclear Research Station.

Fishes are associated with these floating islands. This is not surprising, since it is reasonable to expect that small fishes should remain with, or be attracted to, floating vegetation that is dislodged from lakeshore swamps.

The association of fishes with floating islands is not unique to Lake Malawi. In the Amazon many fish species, from minute characids to the giant _Arapaima gigas_, regularly swim beneath or near the "floating meadows" of aquatic grasses that drift downriver (Junk, 1970). More than 1000 fishes were caught beneath a 25 m^2 piece of this vegetation (Junk, 1973).

The floating islands in Lake Malawi regularly shelter several species of swamp-dwelling fishes, and occasionally even endemic lacustrine cichlids, among their submerged parts. Littoral fishes have been collected from these islands as far as 8 km from the nearest land. Thus, the vegetation may serve to transport these fishes across several kilometers of deep water--a long distance to territorial, philopatric animals such as cichlids. This intralacustrine dispersal may be of importance to the evolution and speciation of fishes in Lake Malawi. We will summarize the collections from the six floating islands sampled, and then attempt a preliminary assessment of the significance of this dispersal mode.

METHODS

During the first exploration of a floating island (island 1) only SCUBA and a dipnet were available for fish collecting. Inspection beneath the island failed to reveal any fishes, but several were caught by scooping the dipnet along an arbitrarily chosen 2-m section of the island's perimeter from an inflatable Zodiac boat. These fishes undoubtedly represent only a small fraction of the total number in the vegetation. Each of the other islands (2-6) was sampled using 2-3 liters Noxfish emulsified rotenone, SCUBA, and hand nets. Even these ichthyocide collections seriously underestimate the numbers of fishes actually present. Most floating islands are too large for effective overall coverage by rotenone. Some fishes were seen to escape collection by swimming into unpoisoned areas of the vegetation.

The collections were made while the islands were 0.3-8.0 km from land and over water 10-100 m deep. All fishes are deposited in the U. S. National Museum of Natural History.

Our use of cichlid generic names requires some explanation. Greenwood (1979) restricted the genus Haplochromis to five East African species and suggested resurrecting Cyrtocara (not used since 1935) from synonymy with Haplochromis for all endemic Malawian species allocated to Haplochromis by Trewavas (1935). However, the generic nomenclature of many Malawian cichlids is currently undergoing revision (Oliver, in prep.). For the sake of continuity, therefore, we prefer to employ "Haplochromis" for species of Haplochromis sensu Trewavas (1935). We follow Greenwood (1979) in referring to the nonendemic species _H. callipterus_ as _Astatotilapia calliptera_.

RESULTS

Floating islands are composed primarily of either papyrus (Fig. 54) or reeds (Fig. 55). The submerged parts of this vegetation (Fig. 56) comprise a complex framework of closely spaced, densely tangled roots, providing many crevices in which small fishes can hide from larger, predatory fishes. The roots also provide substrata or shelter for edible organisms. Epiphytic algae were noted, and dragonfly and damselfly larvae, water scorpions (Hemiptera: Nepidae), atyid prawns (_Caridina nilotica_), and postlarval fishes were collected beneath floating islands.

The collection date, measurements, and dominant plant type of the six floating islands sampled are given in Table 9. The places of origin of these islands are unknown, but we suspect that they came from the extensive swamps of the southwest arm of the lake. The locations of the islands when sampled are shown in Fig. 57. Every island had fishes beneath it. A total of 129 fishes belonging to 6 families and 10 species was collected (Table 10). Except for young of two species of predatory cichlid, all the fishes belong to littoral, demersal, or paludal species not previously reported from epipelagic waters. Both the habitat preferences of these species and the observed absence of small fishes from the open water around the islands indicate that all the fishes collected were traveling among the submerged plant parts.

DISCUSSION

Several characteristics of the collections are immediately noteworthy.

(1) Most of the species are inhabitants of the lakeshore swamps and river mouths. This includes the only cichlid common on the floating islands, *Astatotilapia calliptera*[2], and both clariids[3] known from the islands.

(2) The species diversity of the collections is rather low, but 8 of the 10 species collected were represented on two or more of the six floating islands. Two species, *Clarias theodorae* and *Astatotilapia calliptera*, were collected on four of the six islands. Several species were abundant on at least one island.

(3) Few lake cichlids are present under floating islands. Only

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[2] Trewavas (1949) suggested that *Astatotilapia calliptera* "may very well represent the ancestor of many species" of haplochromine cichlids in Lake Malawi. It might, therefore, seem tempting to suspect that the dispersal of this species by floating islands, documented here, had special significance in the formation of the Malawian cichlid species fauna. But there is no evidence in the form of synapomorphic characters shared by *A. calliptera* and the Malawian endemic cichlids to substantiate a close cladistic relationship between them (Oliver, in prep.). The cladistic relationship of *A. calliptera* to other species outside Lake Malawi is equally unknown, and the genus *Astatotilapia* has no defining synapomorphies (Greenwood, 1979). Unless *A. calliptera* is indeed related to all or some of the Malawian endemic species, the significance of its dispersal to their speciation is probably limited to any role it may have in competition with them. It is thought to be trophically generalized (Trewavas, 1949), but too little is known of the biology of *A. calliptera*--and of most Malawian endemics--to permit assessment of even that possibility.

[3] The clariid catfishes have produced an endemic species flock in Lake Malawi (Jackson, 1959; Greenwood, 1961). However, the two clariid species known from floating islands (Table 10) are both nonendemic. Their cladistic relationships are unknown. Perhaps the dispersal of these clariids by floating islands played a role in promoting clariid speciation in Lake Malawi. This hypothesis could be refuted by showing

three species of endemic lacustrine cichlids occur in the collections, and each of these is represented by only a few juvenile individuals. One species, Sarotherodon cf. squamipinnis, mouthbroods its young in weedy or reedy areas (Lowe, 1953), which might explain the presence of some of these young on floating islands. However, the other two species, "Haplochromis" cf. kiwinge and Rhamphochromis sp., are not known to occur in swampy habitats. They are two of the commonest species of predatory cichlid found in more open water off rocky and sandy shores (Jackson, 1961; personal observations). The presence of young of these species on floating islands is discussed further in the next paragraph.

(4) Most fishes in the collections are small. Many are juvenile or subadult; the only adult fishes actually collected belong to species with a small adult size. This size distribution is probably not an artifact of sampling with ichthyocide. Inspection beneath the floating islands during collecting showed that the only large (>200 mm SL) fishes present were predatory cichlids (Rhamphochromis sp. and "Haplochromis" kiwinge) which sometimes appeared from open water after smaller fishes began emerging from the rotenone cloud. These adult predators were not collected. Perhaps some of them were females that were mouthbrooding their young and lost some in the vegetation while feeding on the emerging swamp fishes. Alternatively, these young may have been free-swimming fishes that joined the islands closer to shore; in this case, the presence of conspecific adults of these common species at the islands would be coincidental. Unfortunately, no data are available

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that neither of the species known to disperse is most closely related to the endemic Malawian clariids.

concerning the frequency and feeding behavior of these two species at undisturbed floating islands.

Hypothetical Dispersal Patterns

Four hypothetical patterns of dispersal by floating islands can be distinguished from the standpoint of the number of contacts an island makes with land subsequent to its formation, and the types of habitat occurring at the source and destination of the dispersing fishes. Although successful dispersal may never occur, this classification of possible patterns is helpful in organizing a discussion of the potential effects of such dispersal.

Single contact with land.--(1a) Swamp-swamp: The pattern perhaps most likely to favor survival of the dispersers and subsequent gene flow or colonization is dispersal from one patch of lakeshore swamp to another, similar patch. Dispersal of this type would have little or no importance for the speciation of lacustrine endemics, since they do not inhabit swamps, but would be important in maintaining gene flow among disjunct populations of swamp species.

(1b) Swamp-nonswamp: More interesting than (1), but perhaps less likely to occur, is successful dispersal from a patch of lakeshore swamp to a different habitat. On several occasions islands were observed to float against a sandy beach or a rocky permanent island. The floating islands remained lodged against the shore for days and eventually broke up there. It is uncertain whether a fish species usually occurring in swamps could survive and reproduce in an area of rock or bare sand. However, on 3 June 1980 we collected a single adult of *Astatotilapia calliptera* in a rocky bay with sandy bottom on the north shore of Mumbo

Island. This swamp-dwelling cichlid species has never previously been reported from any permanent island in Lake Malawi, but it occurs commonly on floating islands. Mumbo Island is within the area in which floating islands are frequently seen (Fig. 57). The individual caught on Mumbo may have arrived by floating island, but this speculation is, of course, untestable. Also, on 28 February 1981 we observed more than 100 individuals of _A_. _calliptera_, including males in breeding coloration and females mouthbrooding young, beneath a floating island that was lodged against the rocky south shore of Thumbi I. West. When this floating island broke up after 8 days, the fishes on it are presumed to have moved onto Thumbi I. West. Whether this species will become established there remains to be seen.

Multiple contacts with land.--(2a) Nonswamp-nonswamp: The third hypothetical pattern of dispersal by floating islands is from one patch of nonswamp habitat to another. For this to be possible, an island would have to make two encounters with land after leaving its swamp of origin. This would be the most interesting pattern because of its implications for the possibility of speciation by founder effect in the endemic cichlid fauna (see "Floating Islands and Speciation," below). But, for dispersal to occur, stenotopic cichlids would have to leave their preferred habitat for the very different habitat offered by floating vegetation. The limited collecting done under floating islands to date does not disclose enough dispersing cichlids of endemic lacustrine species to substantiate the occurrence of this dispersal pattern.

Rock-dwelling species of the genera _Petrotilapia_ and _Pseudotropheus_, and also "_Haplochromis_" _euchilus_, were seen feeding among the roots underneath an island that landed against Thumbi I. West. When approached by a diver these cichlids left the floating island for the protection of the rocks. Also, one nonendemic predatory cichlid, Serranochromis robustus (150 mm SL), was observed stalking prey among the roots. We observed the behavior of the fishes underneath this island on 4 of the 8 days that elapsed before it broke up. From these observations it appears that rock-dwelling adult cichlids will feed among the roots but probably leave the floating island if a shift in the wind or current causes it to move away from the rocks.

It is possible that mouthbrooding female cichlids occasionally lose some of their young among this floating vegetation while feeding under it. These young could then be transported to new localities. The collection of postlarvae of obligate rock-dwelling cichlids from floating islands away from shore would provide evidence to substantiate this speculation.

(2b) Nonswamp-swamp: A floating island could transport lacustrine species from a patch of nonswamp habitat to a lakeshore swamp. Such dispersal seems unlikely for the reasons discussed in (3) above, and in any case would probably be unimportant for speciation.

Floating Islands and Speciation

To explain the existence of cichlid species flocks, both intralacustrine allopatric (Fryer and Iles, 1972) and sympatric modes of speciation (Kosswig, 1947, 1963) have been discussed. For the intralacustrine allopatric mode, Fryer and Iles (1972) suggested two different models. First, since littoral cichlids are restricted to isolated patches of suitable habitat, the separated populations could diverge and become reproductively isolated (Type 1a of Bush, 1975:

allopatric speciation by subdivision). Alternatively, speciation could occur following colonization of a new isolated site (Type 1b of Bush, 1975: allopatric speciation by founder effect).

Testing these and other hypotheses concerning the geographic patterns of fish speciation requires detailed knowledge of the cladistic relationships and distribution of fishes within the lake. The methods of vicariance biogeography (Platnick and Nelson, 1978; Rosen, 1978) should permit the unique pattern (estimated by a unique area cladogram) formed when speciation occurs following an individual dispersal event to be distinguished from the repeated pattern (estimated by multiple, concordant area cladograms) formed when speciation takes place in several groups of organisms in a biota subjected to a common series of vicariance events.[4] Regrettably, the necessary cladistic and distributional data on Malawian fishes are still too scarce for effective tests of this kind to be made.

Two conflicting influences of dispersal on speciation processes are

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[4] The history of the present Lake Malawi basin (Banister and Clarke, 1980) appears to involve the consecutive north-south faulting and filling of three or four sub-basins now weakly delimited by submerged ridges (Yairi, 1977). The northernmost and oldest sub-basin is at most 2.5 my old; the southernmost may be less than 1 my old (R. Crossley, personal commun.). It is unknown whether these sub-basins have ever existed as a series of isolated lakes. If so, one might predict that, for a monophyletic group (X) of organisms with diagnosable representatives (X_1, X_2, X_3, X_4) in each sub-basin (B_1, B_2, B_3, B_4), each representative is the sister group of all those to the south: (X_1, (X_2, (X_3, X_4))). Indeed, if conspecific cichlid populations in Lake Malawi can be effectively isolated by distance, as Fryer and Iles (1972) suggest, this repeated cladistic pattern might occur even if the sub-basins were merely formed and filled sequentially but never isolated from one another. Thus, the postulated north-south extension of Lake Malawi provides a hypothetical series of vicariance events that can be compared with the cladograms of Malawian organisms. Deep coring on the ridges between the sub-basins could yield estimates of the absolute dates of formation and filling of the sub-basins.

possible. Dispersal by floating islands could either (1) promote allopatric speciation by establishing founder populations in new areas, or (2) inhibit allopatric speciation by increasing gene exchange between isolated populations. The result of any particular dispersal event would depend on the distribution and ecology of the fish species involved. A localized Malawian species, such as a cichlid endemic to a particular rocky island (Iles, 1960: 278; Oliver and Loiselle, 1972; Lewis, 1980), might undergo allopatric speciation following successful dispersal. Conversely, a widespread Malawian species would be more likely to encounter a conspecific population upon dispersing, and gene flow might occur.

At present, no persuasive evidence exists to suggest that dispersal by floating islands has led to the successful colonization of a new locality by any species, or even to suggest that such dispersal has enhanced gene flow between preexisting disjunct populations. We suspect, however, that the latter process may take place, since hundreds of floating islands and many thousands of associated fishes are drifting between dozens of disjunct habitat patches in southern Lake Malawi each year. Gene flow between disjunct populations of swamp fishes seems the most probable significant effect of such dispersal.

The occurrence of colonization or gene flow following dispersal by floating islands is potentially testable. The geographic distribution of rare electromorphs, direct observation of the behavior of dispersing fishes when floating islands form and when they contact land, and experimental manipulations of floating islands and their faunas would contribute to such tests.

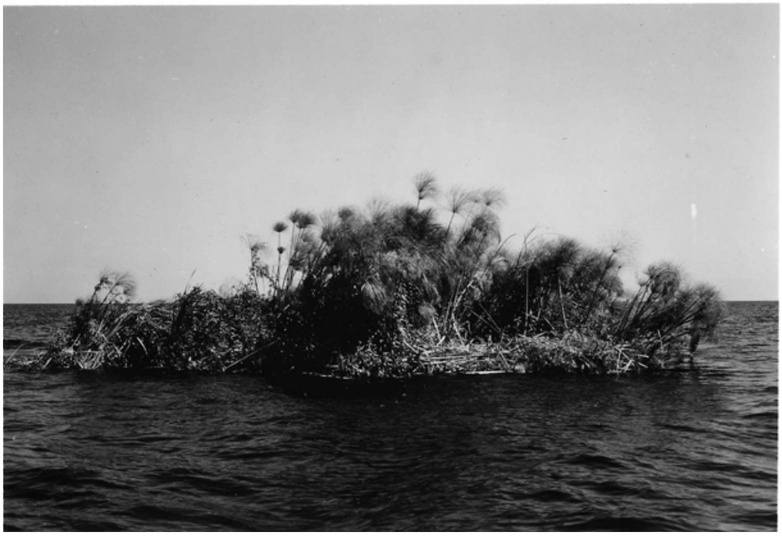
It is a pleasure to thank T. Kocher and the staff of the Cape

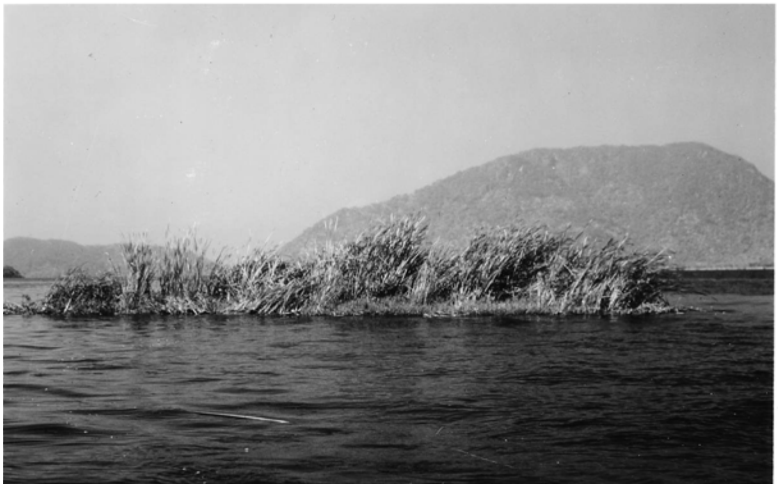
Maclear Research Station for their companionship and help with collecting in Malawi during 1980. We are grateful for the cooperation of the Malawi Government. G. Howes kindly spent much time and effort in a successful search for the collection of fishes from island 3, which we mislaid in the British Museum (Natural History). To G. Barlow, L. Buss, R. Grosberg, S. Louda, and B. Tiffney goes our appreciation for their help with one or more drafts of the manuscript. R. Harrison and an anonymous reviewer substantially improved the final draft. K. Banister identified *Barbus macrotaenia*, and L. Gall identified aquatic insects. Financial support was generously provided by the Smithsonian Oceanographic Sorting Center, the World Wildlife Fund, and NSF Grants DEB 79-12258 and DEB 80-05538.

Figure 54 (top). Floating island 1, length 14 m, composed mainly of *Cyperus papyrus*. 1 August 1980.

Figure 55 (middle). Floating island 2, length 21 m, composed mainly of reeds. 13 August 1980.

Figure 56 (bottom). Underwater view of floating island 2, looking obliquely upward, to show densely tangled submerged vegetation. 13 August 1980.





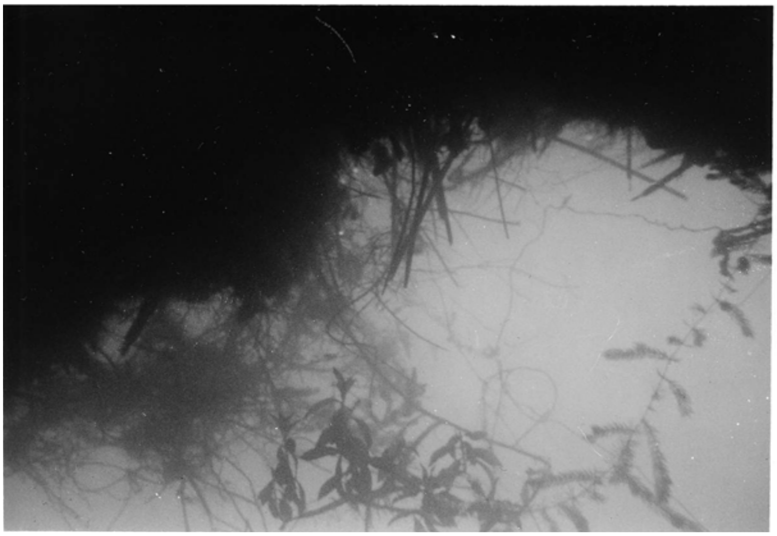


Figure 57. Approximate locations of floating islands (numbered circles) at time of fish collecting. Island numbers correspond to those in Tables 1 and 2. Estimated drift of island 3, as observed from vicinity of Cape Maclear Research Station, is indicated by arrows and dates in February-March 1981.

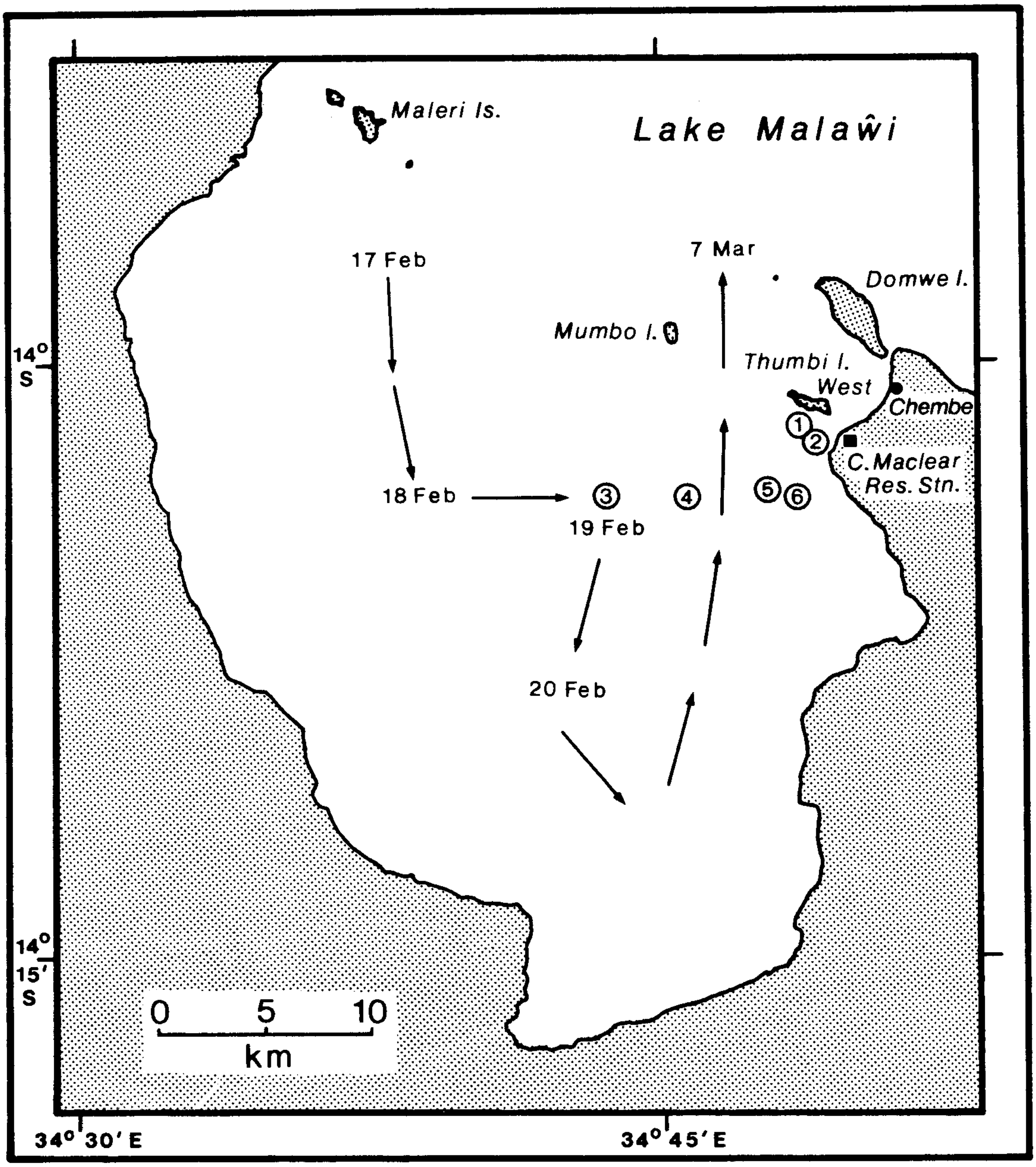

Maleri Is.
Lake Malaŵi
17 Feb
7 Mar
Domwe I.
Mumbo I.
Thumbi I.
West
Chembe
①
②
C. Maclear
Res. Stn.
18 Feb
③
④
⑤
⑥
19 Feb
20 Feb
14°
S
14°
15'
S
0
5
10
km
34° 30' E
34° 45' E

Table 10. Date of fish collection, dimensions, and dominant plant type for floating islands in Lake Malawi.

	Floating island					
	1	2	3	4	5	6
Collection date	1 Aug 80	13 Aug 80	19 Feb 81	19 Feb 81	20 Feb 81	20 Feb 81
Length X width (m)	14 X 7	21 X 6	50 X 25	10 X 5	20 X 8	10 X 5
Circumference at waterline (m)	35	46	170	30	65	33
Maximum height above water (m)	3.7	2.4	2.5	2	2	2
Maximum depth below water (m)	2.1	1.8	---	---	---	---
Dominant plant	Papyrus	Reeds	Reeds	Reeds	Reeds	Reeds

Table 11. Fishes collected beneath floating islands in Lake Malawi [number of specimens (SL in mm)].

Species	Floating island					
	1	2	3	4	5	6
Mormyridae						
Marcusenius nyasensis (Worthington)	---	---	---	1(140)	---	---
Cyprinidae						
Barbus macrotaenia Worthington	---	1(18)	1(30)	---	---	---
Clariidae						
Clarias theodorae Weber	---	2(70-157)	---	5(79-117)	2(78-111)	17(60-161)
C. mossambicus Peters	---	1(56)	---	---	---	3(54-90)
Cyprinodontidae						
Aplocheilichthys johnstoni (Günther)	5(10-12)	17(11-36)	---	---	---	---
Cichlidae						
Sarotherodon cf. *squamipinnis* (Günther)	---	1(34)	---	---	---	5(14-18)
Astatotilapia calliptera (Günther)	---	18(24-75)	2(40-78)	---	2(42-48)	36(15-54)
"*Haplochromis*" cf. *kiwinge* Ahl	1(25)	3(23-27)	---	---	---	---
Rhamphochromis sp.	---	---	---	---	---	3(15-19)
Mastacembelidae						
Mastacembelus shiranus Günther	---	---	---	---	1(138)	2(126-185)

APPENDIX 2

USE OF BEAD TAGS TO STUDY LONG-TERM TERRITORIALITY AMONG CICHLID FISHES OF ROCKY SHORES IN LAKE MALAWI[1]

INTRODUCTION

Among the 350 or more cichlid species endemic to Lake Malawi, Africa, the "mbuna" assemblage comprises an easily recognized phenetic group containing ten nominal genera and about 55 described species. The mbuna are small fishes, with maximum standard lengths (SL) of 60-200 mm. All but a few species inhabit rocky shores and islands. Many color morphs and species of mbuna are known to be geographically localized within the lake, apparently to a greater degree than the non-mbuna cichlids of Lake Malawi.

Since the classic work of Fryer (1959a), the mbuna have been the focus of continued evolutionary and ecological study. The mechanism of mbuna speciation has excited particular interest. Fryer (1959a,b, 1977; Fryer and Iles, 1972) has emphasized that rocky-shore mbuna are, ecologically and behaviorally, restricted quite rigorously to their habitat. Because rocky shoreline in Lake Malawi alternates with other types of substrate, principally sandy beach, Fryer has suggested that habitat restriction promoted intralacustrine allopatric speciation among the mbuna. Conversely, Holzberg (1978) proposed a sympatric model for the differentiation of two polychromatic sibling species of mbuna formerly classified as a single species, _Pseudotropheus zebra_. Notably, he remarked: "Such a manner of speciation could be facili[t]ated by the highly sedentary life of these fishes. The Mbuna are an outstanding

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[1] This unpublished manuscript, including figures, was prepared before I decided to adopt the name _Cyrtocara_ for Malawian "_Haplochromis_" species.

example of fishes living in a restricted area even over generations" (Holzberg, 1978: 184). Thus, presumed sedentariness has been invoked to support both sympatric and allopatric speciation in mbuna.

In addition to habitat restriction, territoriality is a second attribute that would limit the vagility of individual mbuna, not only between isolated sections of rocky shore but also within the same section. (Perhaps territoriality should be viewed as a component of habitat restriction rather than as a separate factor.) The existence of territoriality in male mbuna is well known (Fryer and Iles, 1972). Territories have been mapped and their depth distribution documented for a few species (Holzberg, 1978; Marsh et al., 1981). Little is known, however, about the mobility of individual mbuna, whether territorial or not. The chief reason such information is hard to obtain is that most mbuna are too small to mark using conventional tags. The difficulty of recognizing untagged individuals impedes the study of mbuna behavior and ecology.

In this note, I describe the use of colored glass beads in marking mbuna and other cichlids as small as 60 mm SL to permit recognition of individuals underwater. I also present preliminary evidence, obtained using bead tags, suggesting that adult, rocky-shore mbuna of several species are sedentary, occupying territories for as long as 4-5 months.

STUDY SITE AND METHODS

The study was conducted during April-December 1971 at Monkey Bay, Malawi (14°03'31"S, 34°55'24"E). I collected cichlids from depths of 0-4 m by seining over flat rocky slopes, and by angling among boulders with small, barbed hooks baited with pieces of earthworm.

I tagged a total of 80 cichlids at the following localities: (1) SW corner Thumbi Island East, 17 fishes, 29 April 1971; (2) NW corner Thumbi Island East, 51 fishes total, 13 and 15 May 1971; and (3) W shore Monkey Bay, 12 fishes, 14 May 1971 (Fig. 58). All fishes were released within 3 m of the capture site. At locality 2, tagged fishes were censused at irregular intervals between 15 May and 10 December 1971. Censuses were made by free diving in 0-4 m depth for 30-120 min. On each census dive, the shoreline was searched for a distance of 10-30 m in either direction from the capture site. Visibility underwater was 5-10 m. The species and tag colors of each tagged fish seen were recorded on an underwater slate and later transcribed. Localities 1 and 3 were rarely revisited and are ignored here except for observations of longshore movements by tagged fishes released at these sites.

The bead tag I used is a modification of the Petersen disc. It was briefly described by Stephens et al. (1970). Bead tags are prepared for use as follows. One end of a 5-cm length of nylon monofilament fishing line is heated near the flame of a butane cigarette lighter until the nylon melts and forms a small knob. (Alternatively, a battery-operated tagging gun with a heating element made of nichrome wire could be used to melt the line.) A colored glass handicraft bead (approx. 3.5 mm in diameter) is then threaded onto the untreated end of the line. A bundle of these prepared tags can be held together with a rubber band to prevent loss of the beads.

A fish is tagged by the following steps: (1) Remove a fish from holding container and grasp it so that nuchal region is exposed; (2) push a hypodermic needle (of a guage just large enough to admit the nylon line) transversely through fish, penetrating epaxial muscles at or slightly behind level of predorsal bone; (3) remove a tag from bundle and push its free end into tip of needle as far as it will go; (4) withdraw needle from fish, leaving tag in place, and pull end of line to draw bead gently against opposite side of fish; (5) thread a second bead onto free end of line, let it drop against fish, and cut off excess line to within 1 cm of bead; (6) melt this end near lighter flame until knob that is formed contacts bead and retains it; fish now has one bead attached to each side of body; (7) measure and sex fish (I inferred sex from coloration of body and fins), return it to holding container, and record bead colors and other data. The entire procedure can be completed in 1 min, but fishes can be dipped in the water periodically if necessary. Five percent of the fishes I tagged appeared moribund when returned to the holding container and were not released. Anesthesia might reduce trauma and delayed mortality related to tagging, but I did not anesthetize the fishes. Nevertheless, I observed that tagged fishes resumed normal feeding and territorial behavior within a few minutes of release.

I used eight colors of bead (black, white, red, orange, green, aqua, navy, and copper) and identified each tag with a two-letter code; thus, WB signifies left white, right black. All colors were readily distinguishable underwater at a distance of several meters in the well-lit, shallow waters of the study.

RESULTS AND DISCUSSION

Marked fishes were seen on every census dive at locality 2 from 15 May through 5 October 1971. None was found during several censuses made between 5 October and 10 December 1971, when the dives were discontinued.

Twenty-three (45%) of the 51 cichlids tagged at locality 2 were resighted at least once (Table 11). Census results and recaptures at this locality are summarized in Fig. 59.

A number of separate matters relating to this study are discussed below.

(1) Marked individuals of all mbuna species, considered as a group, were more likely to be resighted than marked "Haplochromis" taeniolatus, a non-mbuna cichlid ($X^2 = 4.79$, df = 1, $0.025<p<0.05$). This is a test of differential recapture probability. It is unclear what is responsible for this difference; recapture probability is itself a product of catchability (here meaning "sightability") and residence (i.e., population gains due to birth and immigration, plus population losses due to death and emigration; Begon, 1979). The data are insufficient to distinguish these factors. I suspect that differences in vagility between mbuna and "H." taeniolatus are involved. I observed several of the tagged male mbuna to hold territories. Conversely, all "H." taeniolatus I tagged were females and nonterritorial males, judging by their small size and dull coloration. Moreover, one observation shows that individuals of the latter species may swim a considerable distance. A 63-mm SL "H." taeniolatus of unknown sex, tagged on 29 April at locality 1, was seen on 15 May at locality 2 (Fig. 58), a distance of at least 0.5 km along nearly continuous rocky shore.

(2) Any short-term mortality caused by tagging was apparently independent of fish size over the SL range tagged. Sample sizes are small. However, the mean SL of all fishes tagged is identical with the mean SL of fishes resighted (Table 11). Moreover, there is no correlation between SL of fishes resighted and the time interval over which they were seen, i.e., the number of days between tagging and last sighting (for all cichlids, $r = -0.181$, $df = 21$, $0.5>p>0.2$; for mbuna only, $r = -0.223$, $df = 17$, $0.5>p>0.2$).

(3) McConnell (1975: 148) mentioned one of the fishes I tagged: "Some Mbuna are known to be territorial; one Pseudotropheus auratus [Melanochromis auratus WN; see Fig. 59] . . . marked with a coloured bead was observed within one metre of its home crevice on a rock slope over five months, from May to October (Oliver, personal communication)." One minor correction to McConnell's statement is necessary. On one occasion (29 May) I observed this fish up to 3 m from the crack that marked the center of its territory. This individual was sighted more times (12) and over a longer period (145 days) than any other tagged fish. Nevertheless, it was not seen on every census dive, sometimes despite intensive efforts to locate it.

(4) Although most of the tagged fishes that could be sexed were male, two female mbuna appeared to be as sedentary as males (Fig. 59).

(5) Loss of tags and invasion of tag wounds by disease:

(a) I saw a few tagged fishes chafe by rubbing the flanks against a rock, but these were not necessarily attempts at tag removal since similar chafing is normal in untagged fishes.

(b) One fish (Pseudotropheus zebra WO, a 90-mm SL territorial male) had both beads intact when seen on 15 May but had lost its orange bead when next sighted on 27 May. It could still be identified by its size and by the location of its territory (only two other conspecifics were marked). I saw a smaller, untagged P. zebra of unknown sex attempt to bite off the remaining bead, but the larger fish evaded it. P. zebra WO was seen twice more with its white bead intact. (Such attempts to bite the beads suggest cleaning behavior. A. Ribbink has observed cleaning by a species of Malawian cichlid [Witte and Witte-Maas, 1981: 226, footnote; Ribbink and Lewis, 1982].) Thus, bead tags can influence social interactions.

(c) On several marked fishes, a fluffy "fungus" appeared around the punctures caused by tagging. I do not know whether this organism was bacterial or truly fungal. The infection was not necessarily lethal. In one fish (Melanochromis melanopterus RO), fungus had formed bilaterally within 12 days after tagging, yet the fish appeared healthy when last seen 15 weeks later. Another fish, P. zebra WW (a 94-mm SL territorial male), was healthy, brightly colored (pale blue with black bars), and dominant when first sighted 22 August, 99 days after tagging. It displayed above a prominent rock. Thirteen days later it was seen near the bottom of the same rock. However, its coloration was now dull blue and black, it appeared emaciated and submissive, and there was fungus on its body (not near the tag). When last seen 18 days later, it was 4 m from its former territory and had fungus around one bead and on the dorsal fin.

(6) Holzberg (1978: 178) mapped territories of unmarked male Pseudotropheus zebra, remarking: "Males were individually recognisable by their particular number and arrangement of egg dummies on the anal fin, so tagging of individuals was not necessary." An observation of

mine casts doubt on the value of anal-fin spots as a natural mark, except for very short periods. When I tagged P. zebra WO on 13 May, I carefully spread the anal fin and counted two yellow egg dummies. Two days later, when I saw this fish underwater, three egg dummies were clearly visible. The newest and smallest spot had formed at the posterodorsal edge of the fin.

(7) Kornfield (1974) estimated the sizes of mbuna populations indirectly, pointing out that "territoriality . . . negates the use of mark-recapture techniques for population size estimation, since individuals may not randomly disperse once marked." The evidence I present here substantiates this warning; dispersion of tagged fishes was nonrandom.

(8) Perhaps, on rare occasions, chance dispersal agents such as the floating islands of vegetation with which swamp fishes can disperse (see Appendix 1) might provide transport for mbuna between isolated rocky habitats. However, no such agent has ever been documented for Malawian rocky-shore fishes.

(9) The disappearance of all tagged fishes by early October may simply mean that they died. However, an alternative possibility is that they migrated into deeper water as surface waters warmed during September-October with the onset of the hot, rainy season (D. H. Eccles, pers. comm.). Comparative information is lacking on the abundance of untagged mbuna during this period.

CONCLUSIONS

The bead tag described above shows promise as a means of individual recognition in field studies of small cichlids. These tags would facilitate such studies as mapping of territories, testing for homing behavior by displacing marked fishes from the place of capture, detection and measurement of home range, and estimation of life expectancy. The advantages of bead tags include low cost, relative ease of application, small size, and high visibility underwater. Disadvantages may include an increased susceptibility to infection by "fungus," and a possible influence of tags on social interactions.

Through the use of bead tags, I was able to locate individual mbuna over a 5-month period. The preliminary data presented here suggest that the mbuna are territorial and sedentary.

Figure 58. Map of Monkey Bay, Malawi, showing localities (numbered circles) at which cichlids were tagged and released. Arrow on W shore of bay indicates where a *Labeotropheus fuelleborni* (69 mm SL, ♂) released at locality 3 on 14 May 1971 was observed feeding 48 hrs later, 90 m to the north along continuous rocky shore.

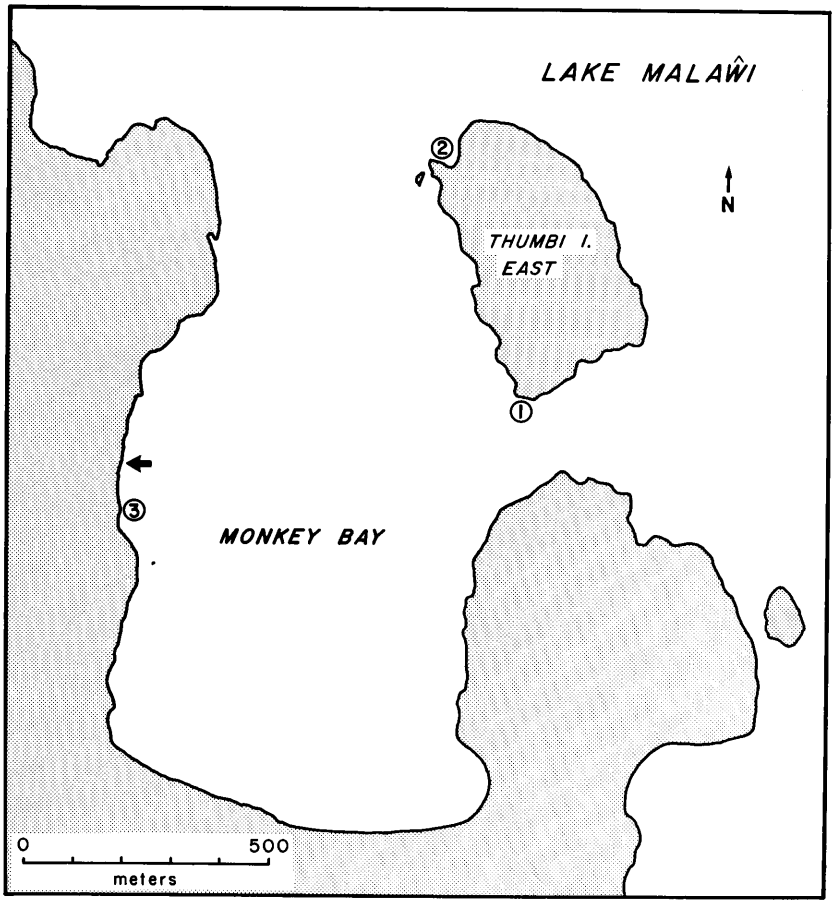
LAKE MALAŴI
THUMBI I. EAST
MONKEY BAY
①
②
③
N
0
500
meters

Figure 59. Summary of sightings of tagged fishes near locality 2 (NW corner Thumbi I. East) on 17 days during May-October 1971. All tagged fishes resighted at least once after day of release are represented; fishes never resighted (see Table 12) are not shown. For each individual, figure shows species, two-letter code for tag colors, sex, SL in mm when tagged, and date(s) of sighting. Left end of line indicates date of tagging (13 or 15 May). Each subsequent sighting is represented by a small triangle above line. Last triangle to right shows date of last sighting. Records for 13 June and 10 August represent fishes seined inadvertently and rereleased; records for 2 July were noted while swimming to set a seine net. Data for remaining 14 days are from dives made specifically to census tagged fishes. No tagged fishes were seen after 5 October 1971 although several census dives were made. The *Petrotilapia* sp. almost certainly belongs to the species provisionally labeled *Petrotilapia* OL by Marsh et al. (1981); the coloration of body and fins that I recorded while tagging it closely matches the diagnostic coloration reported for that species. Both individuals of *Pseudotropheus zebra* were of the BB morph, and thus belonged to *P. zebra* sensu stricto (see Holzberg, 1978).

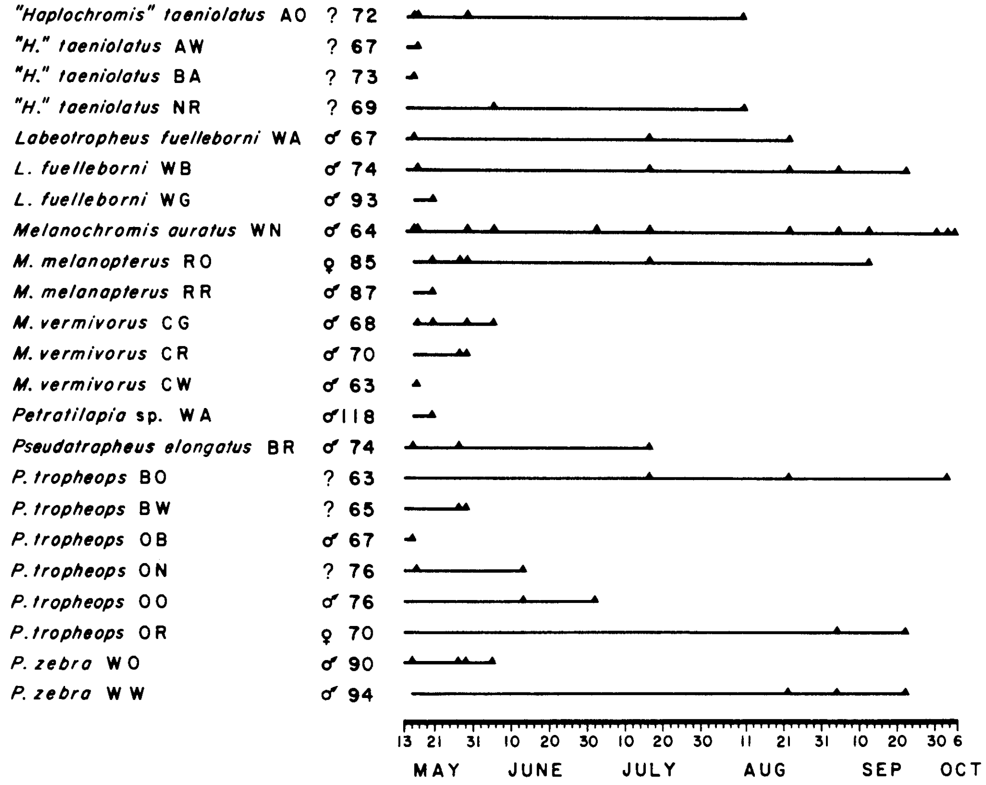
"Haplochromis" taeniolatus AO ? 72
"H." taeniolatus AW ? 67
"H." taeniolatus BA ? 73
"H." taeniolatus NR ? 69
Labeotropheus fuelleborni WA ♂ 67
L. fuelleborni WB ♂ 74
L. fuelleborni WG ♂ 93
Melanochromis auratus WN ♂ 64
M. melanopterus RO ♀ 85
M. melanapterus RR ♂ 87
M. vermivorus CG ♂ 68
M. vermivorus CR ♂ 70
M. vermivorus CW ♂ 63
Petratilapia sp. WA ♂118
Pseudatropheus elongatus BR ♂ 74
P. tropheops BO ? 63
P. tropheops BW ? 65
P. tropheops OB ♂ 67
P. tropheops ON ? 76
P. tropheops OO ♂ 76
P. tropheops OR ♀ 70
P. zebra WO ♂ 90
P. zebra WW ♂ 94
13 21 31 10 20 30 10 20 30 11 21 31 10 20 30 6
MAY
JUNE
JULY
AUG
SEP
OCT

Table 12

Numbers and sizes of all tagged cichlids released at locality 2 compared with those of cichlids resighted on one or more subsequent days

Species	Tagged		Resighted	
	N	SL range ($\bar{x}$) in mm	N	SL range ($\bar{x}$) in mm
Non-mbuna species				
"*Haplochromis*" *taeniolatus*	17	64- 93 (72.4)	4	67- 73 (70.3)
Mbuna species				
Labeotropheus fuelleborni	3	67- 93 (78.0)	3	67- 93 (78.0)
Melanochromis auratus	2	64- 74 (69.0)	1	64
M. melanopterus	7	70- 95 (84.4)	2	85- 87 (86.0)
M. vermivorus	4	63- 72 (68.3)	3	63- 70 (67.0)
Petrotilapia sp.	1	118	1	118
Pseudotropheus elongatus	1	74	1	74
P. tropheops	13	62- 79 (70.2)[1]	6	63- 76 (69.5)
P. zebra	3	90-110 (98.0)	2	90- 94 (92.0)
Total	51	Grand $\bar{x}$ (75.9)[2]	23	Grand $\bar{x}$ (75.9)[2]

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[1] N = 12.

[2] Calculated from individual standard lengths, not from means for each species.

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